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Dynamical Systems in Population Biology

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Second Edition

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To Hong and Bob

Preface

Population dynamics is an important subject in mathematical biology. A central problem is to study the long-term behavior of modeling systems. Most of these systems are governed by various evolutionary equations such as difference, ordinary, functional, and partial differential equations (see, e.g., [253, 206, 334, 167, 77]). As we know, interactive populations often live in a fluctuating environment. For example, physical environmental conditions such as temperature and humidity and the availability of food, water, and other resources usually vary in time with seasonal or daily variations. Therefore, more realistic models should be nonautonomous systems. In particular, if the data in a model are periodic functions of time with commensurate period, a periodic system arises; if these periodic functions have different (minimal) periods, we get an almost periodic system. The existing reference books, from the dynamical systems point of view, mainly focus on autonomous biological systems. The book of Hess [152] is an excellent reference for periodic parabolic boundary value problems with applications to population dynamics. Since the publication of this book, there have been extensive investigations on periodic, asymptotically periodic, almost periodic, and even general nonautonomous biological systems, which in turn have motivated further development of the theory of dynamical systems.

In order to explain the dynamical systems approach to periodic population problems, let us consider, as an illustration, two species periodic competitive systems

$$\begin{aligned} \frac{du_1}{dt} &= f_1(t, u_1, u_2), \\ \frac{du_2}{dt} &= f_2(t, u_1, u_2), \end{aligned} \tag{0.1}$$

where f_1 and f_2 are continuously differentiable and ω-periodic in t, and $\partial f_i / \partial u_j \leq 0$, $i \neq j$. We assume that, for each $v \in \mathbb{R}^2$, the unique solution $u(t, v)$ of system (0.1) satisfying $u(0) = v$ exists globally on $[0, \infty)$.

Let $X = \mathbb{R}^2$, and define a family of mappings $T(t) : X \to X, t \geq 0$, by $T(t)x = u(t, x)$, $\forall x \in X$. It is easy to see that $T(t)$ satisfies the following properties:

(1) $T(0) = I$, where I is the identity map on X.
(2) $T(t + \omega) = T(t) \circ T(\omega)$, $\forall t \geq 0$.
(3) $T(t)x$ is continuous in $(t, x) \in [0, \infty) \times X$.

$T(t)$ is called the periodic semiflow generated by periodic system (0.1), and $P := T(\omega)$ is called its associated Poincaré map (or period map). Clearly, $P^n v = u(n\omega, v)$, $\forall n \geq 1$, $v \in \mathbb{R}^2$. It then follows that the study of the dynamics of (0.1) reduces to that of the discrete dynamical system $\{P^n\}$ on $\mathbb{R}^2$.

If $u = (u_1, u_2), v = (v_1, v_2) \in \mathbb{R}^2$, then we write $u \leq v$ whenever $u_i \leq v_i$ holds for $i = 1, 2$. We write $u \leq_K v$ whenever $u_1 \leq v_1$ and $u_2 \geq v_2$. By the well-known Kamke comparison theorem, it follows that the following key properties hold for competitive system (0.1) (see, e.g., [334, Lemma 7.4.1]):

(P1) If $u \leq_K v$, then $Pu \leq_K Pv$.
(P2) If $Pu \leq Pv$, then $u \leq v$.

Then the Poincaré map P, and hence the discrete dynamical system $\{P^n\}$, is monotone with respect to the order $\leq_K$ on $\mathbb{R}^2$. Consequently, system (0.1) admits convergent dynamics (see [334, Theorem 7.4.2]).

Theorem *Every bounded solution of a competitive planar periodic system asymptotically approaches a periodic solution.*

We use the proof provided in [334, Theorem 7.4.2]. Indeed, it suffices to prove that every bounded orbit of $\{P^n\}$ converges to a fixed point of P. Given two points $u, v \in \mathbb{R}^2$, one or more of the four relations $u \leq v$, $v \leq u$, $u \leq_K v$, $v \leq_K u$ must hold. Now, if $P^{n_0}u_0 \leq_K P^{n_0+1}u_0$ (or the reverse inequality) holds for some $n_0 \geq 0$, then (P1) implies that $P^n u_0 \leq_K P^{n+1}u_0$ (or the reverse inequality) holds for all $n \geq n_0$. Therefore, $\{P^n u_0\}$ converges to some fixed point $\bar{u}$, since the sequence is bounded and eventually monotone. The proof is complete in this case, so we assume that there does not exist such an n_0 as just described. In particular, it follows that u_0 is not a fixed point of P. Then it follows that for each n we must have either $P^{n+1}u_0 \leq P^n u_0$ or the reverse inequality. Suppose for definiteness that $u_0 \leq Pu_0$, the other case being similar. We claim that $P^n u_0 \leq P^{n+1}u_0$ for all n. If not, there exists n_0 such that

$$u_0 \leq Pu_0 \leq P^2 u_0 \leq \cdots \leq P^{n_0-1}u_0 \leq P^{n_0}u_0$$

but $P^{n_0}u_0 \geq P^{n_0+1}u_0$. Clearly, $n_0 \geq 1$ since $u_0 \leq Pu_0$. Applying (P2) to the displayed inequality yields $P^{n_0-1}u_0 \geq P^{n_0}u_0$ and therefore $P^{n_0-1}u_0 = P^{n_0}u_0$. Since P is one to one, u_0 must be a fixed point, in contradiction to our assumption. This proves the claim and implies that the sequence $\{P^n u_0\}$ converges to some fixed point $\bar{u}$.

It is hoped that the reader will appreciate the elegance and simplicity of the arguments supporting the above theorem, which are motivated by a now classical paper of deMottoni and Schiaffino [92] for the special case of periodic Lotka–Volterra systems. This example also illustrates the roles that Poincaré maps and monotone discrete dynamical systems may play in the study of periodic systems. For certain nonautonomous perturbations of a periodic system (e.g., an asymptotically periodic system), one may expect that the Poincaré map associated with the unperturbed periodic system (e.g., the limiting periodic system) should be very helpful in understanding the dynamics of the original system. For a nonperiodic nonautonomous system (e.g., almost periodic system), we are not able to define a continuous or discrete-time dynamical system on its state space. The skew-product semiflow approach has proved to be very powerful in obtaining dynamics for certain types of nonautonomous systems (see, e.g., [303, 300, 311]).

The main purpose of this book is to provide an introduction to the theory of periodic semiflows on metric spaces and its applications to population dynamics. Naturally, the selection of the material is highly subjective and largely influenced by my personal interests. In fact, the contents of this book are predominantly from my own and my collaborators' recent works. Also, the list of references is by no means exhaustive, and I apologize for the exclusion of many other related works.

Chapter 1 is devoted to abstract discrete dynamical systems on metric spaces. We study global attractors, chain transitivity, strong repellers, and perturbations. In particular, we will show that a dissipative, uniformly persistent, and asymptotically compact system must admit a coexistence state. This result is very useful in proving the existence of (all or partial componentwise) positive periodic solutions of periodic evolutionary systems.

The focus of Chapter 2 is on global dynamics in certain types of monotone discrete dynamical systems on ordered Banach spaces. Here we are interested in the abstract results on attracting order intervals, global attractivity, and global convergence, which may be easily applied to various population models.

In Chapter 3, we introduce the concept of periodic semiflows and prove a theorem on the reduction of uniform persistence to that of the associated Poincaré map. The asymptotically periodic semiflows, nonautonomous semiflows, skew-product semiflows, and continuous processes are also discussed.

In Chapter 4, as a first application of the previous abstract results, we analyze in detail a discrete-time, size-structured chemostat model that is described by a system of difference equations, although in this book our main concern is with global dynamics in periodic and almost periodic systems. The reason for this choice is that we want to show how the theory of discrete dynamical systems can be applied to discrete-time models governed by difference equations (or maps).

In the rest of the book, we apply the results in Chapters 1–3 to continuous-time periodic population models: in Chapter 5 to the N-species competition in a periodic chemostat, in Chapter 6 to almost periodic competitive systems, in Chapter 7 to competitor–competitor–mutualist parabolic systems, and in Chapter 8 to a periodically pulsed bioreactor model. Of course, for each chapter, we need to use different qualitative methods and even to develop certain ad hoc techniques.

Chapter 9 is devoted to the global dynamics in an autonomous, nonlocal, and delayed predator–prey model. Clearly, the continuous-time analogues of the results in Chapters 1 and 2 can find applications in autonomous models. Note that an autonomous semiflow can be viewed as a periodic one with the period being any fixed positive real number, and hence it is possible to get some global results by using the theory of periodic semiflows. However, we should point out that there do exist some special theory and methods that are applicable only to autonomous systems. The fluctuation method in this chapter provides such an example.

The existence, attractivity, uniqueness, and exponential stability of periodic traveling waves in periodic reaction–diffusion equations with bistable nonlinearities are discussed in Chapter 10, which is essentially independent of the previous chapters. We appeal only to a convergence theorem from Chapter 2 to prove the attractivity and uniqueness of periodic waves. Here the Poincaré-type map associated with the system plays an important role once again.

Over the years, I have benefited greatly from the communications, discussions, and collaborations with many colleagues and friends in the fields of differential equations, dynamical systems, and mathematical biology, and I would like to take this opportunity to express my gratitude to all of them. I am particularly indebted to Herb Freedman, Morris Hirsch, Hal Smith, Horst Thieme, Gail Wolkowicz, and Jianhong Wu, with whom I wrote research articles that are incorporated in the present book.

Finally, I gratefully appreciate, financial support for my research from the National Science Foundation of China, the Royal Society of London, and the Natural Sciences and Engineering Research Council of Canada.

Preface to the Second Edition

For this edition, I have corrected some typos, revised Sections 1.1 and 1.3.4 by using the concepts of global attractors and strong global attractors, deleted the original subsection on order persistence from Section 1.3, and added three new sections about persistence and attractors (Section 1.3.3), saddle point behavior for monotone semiflows (Section 2.5), and solution maps of abstract nonautonomous functional differential equations (Section 3.5), respectively. I have also mentioned more related references in the notes sections of Chapters 1–10.

In addition, I have added four new chapters. Chapter 11 is devoted to the general theory of basic reproduction ratios R_0 for compartmental models of periodic functional differential equations and autonomous reaction–diffusion systems. Chapter 12 deals with the threshold dynamics in terms of R_0 for a new class of population models with time periodic delays. In Chapter 13, we study a periodic reaction–diffusion SIS system and investigate the effect of spatial and temporal heterogeneities on the extinction and persistence of the infectious disease. The final chapter, Chapter 14, provides a complete analysis of the disease-free dynamics and global dynamics for a nonlocal spatial model of Lyme disease. It is expected that Chapters 12–14 may serve as templates for future investigations on other population models with spatial and temporal heterogeneities.

My sincere thanks goes to Jifa Jiang, Xing Liang, Yijun Lou, Pierre Magal, Rui Peng, Wendi Wang, and Xiao Yu, whose joint research articles with me have been incorporated in the second edition. I am also very grateful to all collaborators and friends for their encouragements, suggestions, and assistance with this revision.

St. John's, NL, Canada Xiao-Qiang Zhao

Contents

1

Dissipative Dynamical Systems

There are many discrete-time population models governed by difference equations (or maps), and as we mentioned in the Preface, the dynamics of a periodic differential system can be investigated via its associated Poincaré map. The aim of this chapter is to introduce basic definitions and develop main tools in the theory of discrete dynamical systems. In Section 1.1 we present concepts of limit sets and attractors and some fundamental theorems such as the LaSalle invariance principle, the asymptotic fixed point theorem, and the global attractor theorems.

Chain transitivity has remarkable connections to the structure of attractors. In Section 1.2 we first give typical examples and characteristics of chain transitive sets. Then we show that the Butler–McGehee properties of omega limit sets are shared by chain transitive sets for a dynamical system, which enable us to obtain further important properties of chain transitive sets such as strong attractivity and convergence, and to prove the equivalence between acyclic coverings and Morse decompositions.

Uniform persistence is an important concept in population dynamics, since it characterizes the long-term survival of some or all interacting species in an ecosystem. Looked at abstractly, it is the notion that a closed subset of the state space is repelling for the dynamics on the complementary set, and then it gives a uniform estimate for omega limit sets, which sometimes is essential to obtain a more detailed global dynamics. In Section 1.3 we prove a strong repeller theorem in terms of chain transitive sets, which unifies earlier results on uniform persistence, and implies robustness of uniform persistence. Then we show that a dissipative, uniformly persistent, and asymptotically compact system must have at least one coexistence steady state, which provides a dynamic approach to some static problems (e.g., existence of positive steady states and periodic solutions). We also introduce the concept of generalized distance functions in abstract persistence theory so that the practical persistence can be easily obtained for certain infinite-dimensional biological systems.

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In Section 1.4 we discuss persistence under perturbations. We prove a general result on the perturbation of a globally stable steady state. Then we prove uniform persistence uniform in parameters, which is very useful in establishing the robustness of global asymptotic stability of an equilibrium solution. A dissipative and uniformly persistent system is often said to be permanent. For a class of autonomous Kolmogorov systems of ordinary differential equations we also obtain a robust permanence theorem.

1.1 Limit Sets and Global Attractors

Let $\mathbb{N}$ be the set of integers and $\mathbb{N}_+$ the set of nonnegative integers. Let X be a complete metric space with metric d and $f : X \to X$ a continuous map. For a nonempty invariant set M (i.e., $f(M) = M$), the set $W^s(M) := \{x \in X : \lim_{n\to\infty} d(f^n(x), M) = 0\}$ is called the stable set of M. The omega limit set of x is defined in the usual way as $\omega(x) = \{y \in X : f^{n_k}(x) \to y, \text{ for some } n_k \to \infty\}$. A negative orbit through $x = x_0$ is a sequence $\gamma^-(x) = \{x_k\}_{k=-\infty}^0$ such that $f(x_{k-1}) = x_k$ for integers $k \leq 0$. There may be no negative orbit through x, and even if there is one, it may not be unique. Of course, a point of an invariant set always has at least one negative orbit contained in the invariant set. For a given negative orbit $\gamma^-(x)$ we define its alpha limit set as $\alpha(\gamma^-) = \{y \in X : x_{n_k} \to y \text{ for some } n_k \to -\infty\}$. If $\gamma^+(x) = \{f^n(x) : n \geq 0\}$ $(\gamma^-(x))$ is precompact (i.e., it is contained in a compact set), then $\omega(x)$ $(\alpha(\gamma^-))$ is nonempty, compact, and invariant(see, e.g., [141, Lemma 2.1.2]).

Let $e \in X$ be a fixed point of f (i.e., $f(e) = e$). Recall that e is said to be stable for $f : X \to X$ if for each $\epsilon > 0$ there exists $\delta > 0$ such that for any $x \in X$ with $d(x, e) < \delta$, we have $d(f^n(x), e) < \epsilon$, $\forall n \geq 0$. The following simple observation is useful in proving the convergence of a precompact positive orbit to a fixed point.

Lemma 1.1.1. (Convergence) *Let e be a stable fixed point and $\gamma^+(x)$ a precompact positive orbit for $f : X \to X$. If $e \in \omega(x)$, then $\omega(x) = \{e\}$.*

Proof. Let $\epsilon > 0$ be given. By stability of e for $f : X \to X$, there exists $\delta > 0$ such that for any $y \in X$ with $d(y, e) < \delta$, we have $d(f^m(y), e) < \epsilon, \forall m \geq 0$. Since $e \in \omega(x)$, there is a subsequence $n_k \to \infty$ with $f^{n_k}(x) \to e$, and hence an index k_0 such that $d(f^{n_{k_0}}(x), e) < \delta$. Thus $d(f^{n_{k_0}+m}(x), e) < \epsilon$, $\forall m \geq 0$, which implies that $\omega(x) \subset \{z \in X : d(z, e) \leq \epsilon\}, \forall \epsilon > 0$. Letting $\epsilon \to 0$, we get $\omega(x) = \{e\}$. ∎

Definition 1.1.1. *Let G be a closed subset of X. A continuous function $V : G \to \mathbb{R}$ is said to be a Liapunov function on G of the map $f : G \to G$ (or the discrete system $x_{n+1} = f(x_n)$, $n \geq 0$) if $\dot{V}(x) := V(f(x)) - V(x) \leq 0$ for all $x \in G$.*

Theorem 1.1.1. (LaSalle invariance principle) *Assume that V is a Liapunov function on G of f, and that $\gamma^+(x)$ is a precompact orbit of f and*

$\gamma^+(x) \subset G$. Then $\omega(x) \subset M \cap V^{-1}(c)$ for some $c = c(x)$, where M is the largest invariant set in $E := \{x \in G : \dot{V}(x) = 0\}$, and $V^{-1}(c) := \{x \in G : V(x) = c\}$.

Proof. Clearly, the continuous function V is bounded on the compact set $\overline{\gamma^+(x)} \subset G$. Let $x_n = f^n(x)$, $n \geq 0$. Then

$$V(x_{n+1}) - V(x_n) = V(f(x_n)) - V(x_n) = \dot{V}(x_n) \leq 0,$$

and hence $V(x_n)$ is nonincreasing with respect to n and is bounded from below. Therefore, there is a real number $c = c(x)$ such that $\lim_{n\to\infty} V(x_n) = c$. For any $y \in \omega(x) \subset G$, there is a sequence $n_k \to \infty$ such that $\lim_{k\to\infty} x_{n_k} = y$. Since V is continuous, $\lim_{k\to\infty} V(x_{n_k}) = V(y) = c$, and $\omega(x) \subset V^{-1}(c)$. Since $\omega(x)$ is invariant, $V(f(y)) = c$ and $\dot{V}(y) = 0$. Therefore, $\omega(x) \subset E$, and hence $\omega(x) \subset M$. ∎

Recall that a set U in X is said to be a neighborhood of another set V provided that V is contained in the interior $\text{int}(U)$ of U. For any subsets A, $B \subset X$ and any $\epsilon > 0$, we define

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

$$N(A, \epsilon) := \{x \in X : d(x, A) < \epsilon\} \text{ and } \overline{N}(A, \epsilon) := \{x \in X : d(x, A) \leq \epsilon\}.$$

The Kuratowski measure of noncompactness, α, is defined by

$$\alpha(B) = \inf\{r : B \text{ has a finite open cover of diameter } \leq r\},$$

for any bounded set B of X. We set $\alpha(B) = +\infty$, whenever B is unbounded.

For various properties of Kuratowski's measure of noncompactness, we refer to [242, 91] and [304, Lemma 22.2]. The proof of the following lemma is straightforward.

Lemma 1.1.2. *The following statements are valid:*

(a) Let $I \subset [0, +\infty)$ be unbounded, and $\{A_t\}_{t\in I}$ be a nonincreasing family of nonempty closed subsets (i.e., $t \leq s$ implies $A_s \subset A_t$). Assume that $\alpha(A_t) \to 0$, as $t \to +\infty$. Then $A_\infty = \bigcap_{t\geq 0} A_t$ is nonempty and compact, and $\delta(A_t, A_\infty) \to 0$, as $t \to +\infty$.

(b) For each $A \subset X$ and $B \subset X$, we have $\alpha(B) \leq \alpha(A) + \delta(B, A)$.

For a subset $B \subset X$, let $\gamma^+(B) := \bigcup_{m\geq 0} f^m(B)$ be the positive orbit of B for f, and

$$\omega(B) := \bigcap_{n\geq 0} \overline{\bigcup_{m\geq n} f^m(B)}$$

the omega limit set of B. A subset $A \subset X$ is positively invariant for f if $f(A) \subset A$. We say that a subset $A \subset X$ attracts a subset $B \subset X$ for f if $\lim_{n\to\infty} \delta(f^n(B), A) = 0$.

It is easy to see that B is precompact (i.e., $\overline{B}$ is compact) if and only if $\alpha(B) = 0$. A continuous mapping $f : X \to X$ is said to be compact (completely continuous) if f maps any bounded set to a precompact set in X.

The theory of attractors is based on the following fundamental result, which is related to [141, Lemmas 2.1.1 and 2.1.2].

Lemma 1.1.3. *Let B be a subset of X and assume that there exists a compact subset C of X which attracts B for f. Then $\omega(B)$ is nonempty, compact, invariant for f and attracts B.*

Proof. Let $I = \mathbb{N}_+$, the set of all nonnegative integers, and

$$A_n = \overline{\bigcup_{m\geq n} f^m(B)}, \forall n \geq 0.$$

Since C attracts B, from Lemma 1.1.2 (b) we deduce that

$$\alpha(A_n) \leq \alpha(C) + \delta(A_n, C) = \delta(A_n, C) \to 0, \text{ as } n \to +\infty.$$

So the family $\{A_n\}_{n\geq 0}$ satisfies the conditions of assertion (a) in Lemma 1.1.2, and we deduce that $\omega(B)$ is nonempty, compact, and $\delta(A_n, \omega(B)) \to 0$, as $n \to +\infty$. So $\omega(B)$ attracts B for f. Moreover, we have

$$f\left(\bigcup_{m\geq n} f^m(B)\right) = \bigcup_{m\geq n+1} f^m(B), \forall n \geq 0,$$

and since f is continuous, we obtain

$$f(A_n) \subset A_{n+1}, \text{ and } A_{n+1} \subset \overline{f(A_n)}, \forall n \geq 0.$$

Finally, since $\delta(A_n, \omega(B)) \to 0$, as $n \to +\infty$, we have $f(\omega(B)) = \omega(B)$. ∎

Definition 1.1.2. *A continuous mapping $f : X \to X$ is said to be point (compact, bounded) dissipative if there is a bounded set B_0 in X such that B_0 attracts each point (compact set, bounded set) in X; α-condensing (α-contraction of order k, $0 \leq k < 1$) if f takes bounded sets to bounded sets and $\alpha(f(B)) < \alpha(B)$ ($\alpha(f(B)) \leq k\alpha(B)$) for any nonempty closed bounded set $B \subset X$ with $\alpha(B) > 0$; α-contracting if $\lim_{n\to\infty}\alpha(f^n(B)) = 0$ for any bounded subset $B \subset X$; asymptotically smooth if for any nonempty closed bounded set $B \subset X$ for which $f(B) \subset B$, there is a compact set $J \subset B$ such that J attracts B.*

Clearly, a compact map is an α-contraction of order 0, and an α-contraction of order k is α-condensing. It is well known that α-condensing maps are asymptotically smooth (see, e.g., [141, Lemma 2.3.5]). By Lemma 1.1.2, it follows that $f : X \to X$ is asymptotically smooth if and only if $\lim_{n\to\infty} \alpha(f^n(B)) = 0$

for any nonempty closed bounded subset $B \subset X$ for which $f(B) \subset B$. This implies that any α-contracting map is asymptotically smooth.

A positively invariant subset $B \subset X$ for f is said to be stable if for any neighborhood V of B, there exists a neighborhood $U \subset V$ of B such that $f^n(U) \subset V, \forall n \geq 0$. We say that A is globally asymptotically stable for f if, in addition, A attracts points of X for f.

By the proof that (i) implies (ii) in [141, Theorem 2.2.5], we have the following result.

Lemma 1.1.4. *Let $B \subset X$ be compact, and positively invariant for f. If B attracts compact subsets of some neighborhood of itself, then B is stable.*

Definition 1.1.3. *A nonempty, compact, and invariant set $A \subset X$ is said to be an attractor for f if A attracts some open neighborhood of itself; a global attractor for f if A is an attractor that attracts every point in X; and a strong global attractor for f if A attracts every bounded subset of X.*

Remark 1.1.1. The notion of attractor and global attractor was used in [164, 304]. The strong global attractor was defined as global attractor in [141, 358, 286]. In the case where the dimension of X is finite, it is easy to see that both global attractor and strong global attractor are equivalent. In the infinite-dimensional case of X, however, there exist discrete- and continuous-time dynamical systems that admit global attractors, but no strong global attractors, see Example 1.3.3 and [241, Sections 5.1–5.3].

The following result is essentially the same as [142, Theorem 3.2]. Note that the proof of this result was not provided in [142]. For completeness, we state it in terms of global attractors and give an elementary proof below.

Theorem 1.1.2. (Global Attractors) *Let $f : X \to X$ be a continuous map. Assume that*

(a) f is point dissipative and asymptotically smooth;
(b) Positive orbits of compact subsets of X for f are bounded.

Then f has a global attractor $A \subset X$. Moreover, if a subset B of X admits the property that $\gamma^+(f^k(B))$ is bounded for some $k \geq 0$, then A attracts B for f.

Proof. Assume that (a) is satisfied. Since f is point dissipative, we can find a closed and bounded subset B_0 in X such that for each $x \in X$, there exists $k = k(x) \geq 0$, $f^n(x) \in B_0, \forall n \geq k$. Define

$$J(B_0) := \{y \in B_0 : f^n(y) \in B_0, \forall n \geq 0\}.$$

Thus, $f(J(B_0)) \subset J(B_0)$, and for every $x \in X$, there exists $k = k(x) \geq 0$ such that $f^k(x) \in J(B_0)$. Since $J(B_0)$ is closed and bounded, and f is asymptotically smooth, Lemma 1.1.3 implies that $\omega(J(B_0))$ is compact invariant, and attracts points of X.

Assume, in addition, that (b) is satisfied. We claim that there exists an $\varepsilon > 0$ such that $\gamma^+(N(\omega(J(B_0)), \varepsilon))$ is bounded. Assume, by contradiction, that $\gamma^+\left(N\left(\omega(J(B_0)), \frac{1}{n+1}\right)\right)$ is unbounded for each $n > 0$. Let $z \in X$ be fixed. Then we can find a sequence $x_n \in N\left(\omega(J(B_0)), \frac{1}{n+1}\right)$, and a sequence of integers $m_n \geq 0$ such that $d(z, f^{m_n}(x_n)) \geq n$. Since $\omega(J(B_0))$ is compact, we can always assume that $x_n \to x \in \omega(J(B))$, as $n \to +\infty$. Since $H := \{x_n : n \geq 0\} \cup \{x\}$ is compact, assumption (b) implies that $\gamma^+(H)$ is bounded, a contradiction. Let $D = \overline{\gamma^+(N(\omega(J(B_0)), \varepsilon))}$. Then D is closed, bounded, and positively invariant for f. Since $\omega(J(B_0))$ attracts points of X for f, and $\omega(J(B_0)) \subset N(\omega(J(B_0)), \varepsilon) \subset int(D)$, we deduce that for each $x \in X$, there exists $k = k(x) \geq 0$ such that $f^k(x) \in int(D)$. It then follows that for each compact subset C of X, there exists an integer $k \geq 0$ such that $f^k(C) \subset D$. Thus, the set $A := \omega(D)$ attracts every compact subset of X. Fix a bounded neighborhood V of A. By Lemma 1.1.4, it follows that A is stable, and hence, there is a neighborhood W of A such that $f^n(W) \subset V$, $\forall n \geq 0$. Clearly, the set $U := \cup_{n \geq 0} f^n(W)$ is a bounded neighborhood of A, and $f(\overline{U}) \subset \overline{U}$. Since f is asymptotically smooth, there is a compact set $J \subset \overline{U}$ such that J attracts $\overline{U}$. By Lemma 1.1.3, $\omega(\overline{U})$ is nonempty, compact, invariant for f, and attracts $\overline{U}$. Since A attracts $\omega(\overline{U})$, we have $\omega(\overline{U}) \subset A$. Thus, A is a global attractor for f.

To prove the last part of the theorem, without loss of generality we assume that B is a bounded subset of X and $\gamma^+(B)$ is bounded. We set $K = \overline{\gamma^+(B)}$. Then $f(K) \subset K$. Since K is bounded and f is asymptotically smooth, there exists a compact C which attracts K for f. Note that $f^k(B) \subset f^k(\gamma^+(B)) \subset f^k(K)$, $\forall k \geq 0$. Thus, C attracts B for f. By Lemma 1.1.3, we deduce that $\omega(B)$ is nonempty, compact, invariant for f and attracts B. Since A is a global attractor for f, it follows that A attracts compact subsets of X. By the invariance of $\omega(B)$ for f, we deduce that $\omega(B) \subset A$, and hence, A attracts B for f. ∎

Remark 1.1.2. From the first part of the proof of Theorem 1.1.2, it is easy to see that if f is point dissipative and asymptotically smooth, then there exists a nonempty, compact, and invariant subset C of X for f such that C attracts every point in X for f.

The following lemma provides sufficient conditions for the positive orbit of a compact set to be bounded.

Lemma 1.1.5. *Assume that f is point dissipative. If C is a compact subset of X with the property that for every bounded sequence $\{x_n\}_{n\geq 0}$ in $\gamma^+(C)$, $\{x_n\}_{n\geq 0}$ or $\{f(x_n)\}_{n\geq 0}$ has a convergent subsequence, then $\gamma^+(C)$ is bounded in X.*

Proof. Since f is point dissipative, we can choose a bounded and open subset V of X such that for each $x \in X$ there exists $n_0 = n_0(x) \geq 0$ such that

$f^n(x) \in V$, $\forall n \geq n_0$. By the continuity of f and the compactness of C, it follows that there exists a positive integer $r = r(C)$ such that for any $x \in C$, there exists an integer $k = k(x) \leq r$ such that $f^k(x) \in V$. Let $z \in X$ be fixed. Assume, by contradiction, that $\gamma^+(C)$ is unbounded. Then there exists a sequence $\{x_p\}$ in $\gamma^+(C)$ such that

$$x_p = f^{m_p}(z_p),\ z_p \in C,\ \text{and}\ \lim_{p\to\infty} d(z, x_p) = \infty.$$

Since f is continuous and C is compact, without loss of generality we can assume that

$$\lim_{p\to\infty} m_p = \infty,\ \text{ and }\ m_p > r,\ x_p \notin V,\ \forall p \geq 1.$$

For each $z_p \in C$, there exists an integer $k_p \leq r$ such that $f^{k_p}(z_p) \in V$. Since $x_p = f^{m_p}(z_p) \notin V$, there exists an integer $n_p \in [k_p, m_p)$ such that

$$y_p = f^{n_p}(z_p) \in V,\ \text{ and }\ f^l(y_p) \notin V,\ \forall 1 \leq l \leq l_p = m_p - n_p.$$

Clearly, $x_p = f^{l_p}(y_p)$, $\forall p \geq 1$, and $\{y_p\}$ is a bounded sequence in $\gamma^+(C)$.

We only consider the case where $\{y_p\}$ has a convergent subsequence since the proof for the case where $\{f\,(y_p)\}$ has a convergent subsequence is similar. Thus, without loss of generality we can assume that $\lim_{p\to\infty} y_p = y \in \overline{V}$. In the case where the sequence $\{l_p\}$ is bounded, there exist an integer $\hat{l}$ and sequence $p_k \to \infty$ such that $l_{p_k} = \hat{l}$, $\forall k \geq 1$, and hence,

$$d(z, f^{\hat{l}}(y)) = \lim_{k\to\infty} d(z, f^{\hat{l}}(y_{p_k})) = \lim_{k\to\infty} d(z, x_{p_k}) = \infty,$$

which is impossible. In the case where the sequence $\{l_p\}$ is unbounded, there exists a subsequence $l_{p_k} \to \infty$ as $k \to \infty$. Then for each fixed $m \geq 1$, there exists an integer k_m such that $m \leq l_{p_k}$, $\forall k \geq k_m$, and hence,

$$f^m(y_{p_k}) \in X \setminus V,\ \forall k \geq k_m.$$

Letting $k \to \infty$, we obtain

$$f^m\,(y) \in X \setminus V,\ \forall m \geq 1,$$

which contradicts the definition of V. ∎

The following result on the existence of strong global attractors is implied by [142, Theorems 3.1 and 3.4]. Since the proof of this result was not provided in [142], we include a simple proof of it.

Theorem 1.1.3. (Strong Global Attractors) *Let $f : X \to X$ be a continuous map. Assume that f is point dissipative on X, and one of the following conditions holds:*

(a) f^{n_0} *is compact for some integer* $n_0 \geq 1$, *or*
(b) f *is asymptotically smooth, and for each bounded set* $B \subset X$, *there exists* $k = k(B) \geq 0$ *such that* $\gamma^+(f^k(B))$ *is bounded.*

Then there is a strong global attractor A *for* f.

Proof. The conclusion in case (b) is an immediate consequence of Theorem 1.1.2. In the case of (a), since f^{n_0} is compact for some integer $n_0 \geq 1$, it suffices to show that for each compact subset $C \subset X$, $\bigcup_{n \geq 0} f^n(C)$ is bounded. By applying Lemma 1.1.5 to $\widetilde{f} = f^{n_0}$, we deduce that for each compact subset $C \subset X$, $\bigcup_{n \geq 0} \widetilde{f}^n(C)$ is bounded. So Theorem 1.1.2 implies that $\widetilde{f}$ has a global attractor $\widetilde{A} \subset X$. We set $\widetilde{B} = \bigcup_{0 \leq k \leq n_0 - 1} f^k\left(\widetilde{A}\right)$. By the continuity of f, it then follows that $\widetilde{B}$ is compact and attracts every compact subset of X for f, and hence, the result follows from Theorem 1.1.2. ∎

Remark 1.1.3. It is easy to see that a metric space (X, d) is complete if and only if for any subset B of X, $\alpha(B) = 0$ implies that $\overline{B}$ is compact. However, we can prove that Lemmas 1.1.3 and 1.1.4 also hold for non-complete metric spaces by employing the equivalence between the compactness and the sequential compactness for metric spaces. It then follows that Theorems 1.1.2 and 1.1.3 are still valid for any metric space. We refer to [64, 286] for the existence of strong global attractors of continuous-time semiflows on a metric space.

Clearly, if the global attractor is a singleton $\{e\}$, then e is a globally attractive fixed point. Let A be the global attractor claimed in Theorem 1.1.2 with X being a Banach space and with "asymptotically smooth" replaced by "α-condensing." The following asymptotic fixed point theorem implies that there is at least one fixed point in A. For a proof of it, we refer to [257, 143] or [141, Section 2.6].

Theorem 1.1.4. (Asymptotic fixed point theorem) *Suppose* E *is a Banach space. If* $f : E \to E$ *is* α*-condensing and compact dissipative, then* f *has a fixed point.*

Let Λ be a metric space. The family of continuous mappings $f_\lambda : X \to X, \lambda \in \Lambda$, is said to be collectively asymptotically smooth if for any nonempty closed bounded set $B \subset X$ for which $f_\lambda(B) \subset B, \lambda \in \Lambda$, there is a compact set $J_\lambda = J(\lambda, B) \subset B$ such that J_λ attracts B under f_λ and $\cup_{\lambda \in \Lambda} J_\lambda$ is precompact in X. We then have the following result on the upper semicontinuity of global attractors. For a proof, we refer to [141, Theorem 2.5.3].

Theorem 1.1.5. *Let* $f : \Lambda \times X \to X$ *be continuous,* $f_\lambda =: f(\lambda, \cdot)$, *and suppose there is a bounded set* B *that attracts points of* X *under* f_λ *for each* $\lambda \in \Lambda$, *and for any bounded set* U, *the set* $V = \cup_{\lambda \in \Lambda} \cup_{n \geq 0} f_\lambda^n(U)$ *is bounded. If the family*

$\{f_\lambda : \lambda \in \Lambda\}$ is collectively asymptotically smooth, then the global attractor A_λ of f_λ is upper semicontinuous in the sense that $\lim_{\lambda\to\lambda_0} \sup_{x\in A_\lambda} d(x, A_{\lambda_0}) = 0$ *for each $\lambda_0 \in \Lambda$.*

1.2 Chain Transitivity and Attractivity

In this section we continue to assume that X is a metric space with metric d, and that $f : X \to X$ is a continuous map.

1.2.1 Chain Transitive Sets

Definition 1.2.1. *A point $x \in X$ is said to be chain recurrent if for any $\epsilon > 0$, there is a finite sequence of points $x_1, \dots, x_m$ in X ($m > 1$) with $x_1 = x = x_m$ such that $d(f(x_i), x_{i+1}) < \epsilon$ for all $1 \le i \le m-1$. The set of all chain recurrent points for $f : X \to X$ is denoted by $R(X, f)$. Let $A \subset X$ be a nonempty invariant set. We call A internally chain recurrent if $R(A, f) = A$, and internally chain transitive if the following stronger condition holds: For any $a, b \in A$ and any $\epsilon > 0$, there is a finite sequence $x_1, \dots, x_m$ in A with $x_1 = a, x_m = b$ such that $d(f(x_i), x_{i+1}) < \epsilon$, $1 \le i \le m-1$. The sequence $\{x_1, \dots, x_m\}$ is called an ϵ-chain in A connecting a and b.*

Following LaSalle [212], we call a compact invariant set A invariantly connected if it cannot be decomposed into two disjoint closed nonempty invariant sets. An internally chain recurrent set need not have this property, e.g., a pair of fixed points. However, it is easy to see that every internally chain transitive set is invariantly connected.

We give some examples of internally chain transitive sets.

Lemma 1.2.1. *Let $f : X \to X$ be a continuous map. Then the omega (alpha) limit set of any precompact positive (negative) orbit is internally chain transitive.*

Proof. Let $x \in X$ and set $x_n = f^n(x)$. Assume that x has a precompact orbit $\gamma = \{x_n\}$, and denote its omega limit set by ω. Then ω is nonempty, compact, and invariant, and $\lim_{n\to\infty} d(x_n, \omega) = 0$. Let $\epsilon > 0$ be given. By the continuity of f and compactness of ω, there exists $\delta \in (0, \frac{\epsilon}{3})$ with the following property: If u, v are points in the open δ-neighborhood U of ω with $d(u, v) < \delta$, then $d(f(u), f(v)) < \frac{\epsilon}{3}$. Since x_n approaches ω as $n \to \infty$, there exists $N > 0$ such that $x_n \in U$ for all $n \ge N$.

Let $a, b \in \omega$ be arbitrary. There exist $k > m \ge N$ such that $d(x_m, f(a)) < \frac{\epsilon}{3}$ and $d(x_k, b) < \frac{\epsilon}{3}$. The sequence

$$\{y_0 = a,\ y_1 = x_m, \dots, y_{k-m} = x_{k-1},\ y_{k-m+1} = b\}$$

is an $\frac{\epsilon}{3}$-chain in X connecting a and b. Since for each $y_i \in U$, $1 \le i \le k-m$, we can choose $z_i \in \omega$ such that $d(z_i, y_i) < \delta$. Let $z_0 = a$ and $z_{k-m+1} = b$. Then for $i = 0, 1, \ldots, k-m$ we have

$$\begin{aligned} d(f(z_i), z_{i+1}) &\le d(f(z_i), f(y_i)) + d(f(y_i), y_{i+1}) + d(y_{i+1}, z_{i+1}) \\ &< \epsilon/3 + \epsilon/3 + \epsilon/3. \end{aligned}$$

Thus the sequence $z_0, z_1, \ldots, z_{k-m}, z_{k-m+1}$ is an ϵ-chain in ω connecting a and b. Therefore, ω is internally chain transitive. By a similar argument, we can prove the internal chain transitivity of alpha limit sets of precompact negative orbits. ∎

Let $\{S_n : X \to X\}_{n\ge 0}$ be a sequence of continuous maps. The discrete dynamical process (or process for short) generated by $\{S_n\}$ is the sequence $\{T_n : X \to X\}_{n\ge 0}$ defined by $T_0 = I =$ the identity map of X and

$$T_n = S_{n-1} \circ S_{n-2} \circ \cdots \circ S_1 \circ S_0, \quad n \ge 1.$$

The orbit of $x \in X$ under this process is the set $\gamma^+(x) = \{T_n(x) : n \ge 0\}$, and its omega limit set is

$$\omega(x) = \left\{ y \in X : \exists n_k \to \infty \quad \text{such that} \quad \lim_{k\to\infty} T_{n_k}(x) = y \right\}.$$

If there is a continuous map S on X such that $S_n = S$, $\forall n \ge 0$, so that T_n is the nth iterate S^n, then $\{T_n\}$ is a special kind of process called the discrete semiflow generated by S. By an abuse of language we may refer to the map S as a discrete semiflow.

Definition 1.2.2. *The process $\{T_n : X \to X\}$ is asymptotically autonomous if there exists a continuous map $S : X \to X$ such that*

$$n_j \to \infty, \quad x_j \to x \Rightarrow \lim_{j\to\infty} S_{n_j}(x_j) = S(x).$$

We also say that $\{T_n\}$ is asymptotic to S.

It is easy to see from the triangle inequality that if $\lim_{n\to\infty} S_n = S$ uniformly on compact sets, then the process generated by $\{S_n\}$ is asymptotic to S.

Lemma 1.2.2. *Let $T_n : X \to X$, $n \ge 0$, be an asymptotically autonomous discrete process with limit $S : X \to X$. Then the omega limit set of any precompact orbit of $\{T_n\}$ is internally chain transitive for S.*

Proof. Let $\overline{\mathbb{N}}_+ = \mathbb{N}_+ \cup \{\infty\}$. For any given strictly increasing continuous function $\phi : [0, \infty) \to [0, 1)$ with $\phi(0) = 0$ and $\phi(\infty) = 1$ (e.g., $\phi(s) = \frac{s}{1+s}$), we can define a metric ρ on $\overline{\mathbb{N}}_+$ as $\rho(m_1, m_2) = |\phi(m_1) - \phi(m_2)|$, for any $m_1, m_2 \in \overline{\mathbb{N}}_+$, and then $\overline{\mathbb{N}}_+$ is compactified. Let $\widetilde{X} := \overline{\mathbb{N}}_+ \times X$. Define a mapping $\widetilde{S} : \widetilde{X} \to \widetilde{X}$ by

$$\widetilde{S}(m,x) = (1+m, S_m(x)), \quad \widetilde{S}(\infty,x) = (\infty, S(x)), \ \forall m \in \mathbb{N}_+, \ x \in X.$$

By Definition 1.2.2, $\widetilde{S} : \widetilde{X} \to \widetilde{X}$ is continuous. Let $\gamma^+(x)$ be a precompact orbit of T_n. Since

$$\widetilde{S}^n((0,x)) = (n, S_{n-1} \circ S_{n-2} \circ \cdots \circ S_1 \circ S_0(x)) = (n, T_n(x)), \ \forall n \geq 0,$$

and $\overline{\mathbb{N}}_+$ is compact, it follows that the orbit $\gamma^+((0,x))$ of $\widetilde{S}^n$ is precompact and $\{\infty\} \times \omega(x) = \omega(0,x)$, where $\omega(0,x)$ is the omega limit set of $(0,x)$ for $\widetilde{S}^n$. By Lemma 1.2.1, $\omega(0,x)$ is invariant and internally chain transitive for $\widetilde{S}$, which, together with the definition of $\widetilde{S}$, implies that $\omega(x)$ is invariant and internally chain transitive for S. ∎

Definition 1.2.3. *Let $S : X \to X$ be a continuous map. A sequence $\{x_n\}$ in X is an asymptotic pseudo-orbit of S if*

$$\lim_{n\to\infty} d(S(x_n), x_{n+1}) = 0.$$

The omega limit set of $\{x_n\}$ is the set of limits of subsequences.

Let $\{T_n\}$ be a discrete process in X generated by a sequence of continuous maps S_n that converges to a continuous map $S : X \to X$ uniformly on compact subsets of X. It is easy to see that every precompact orbit of $T_n : X \to X$, $n \geq 0$, is an asymptotic pseudo-orbit of S.

Example 1.2.1. Consider the nonautonomous difference equation

$$x_{n+1} = f(n, x_n), \ n \geq 0,$$

on the metric space X. If we define $S_n = f(n,\cdot) : X \to X$, $n \geq 0$, and let

$$T_0 = I, \ T_n = S_{n-1} \circ \cdots \circ S_1 \circ S_0 : X \to X, \ n \geq 1,$$

then $x_n = T_n(x_0)$, and $\{x_n : n \geq 0\}$ is an orbit of the discrete process T_n. If $f(n,\cdot) \to \bar{f} : X \to X$ uniformly on compact subsets of X, then T_n is asymptotically autonomous with limit $\bar{f}$. Furthermore, in this case any precompact orbit of the difference equation is an asymptotic pseudo-orbit of $\bar{f}$, since $d(\bar{f}(x_n), x_{n+1}) = d(\bar{f}(x_n), f(n, x_n)) \to 0$.

Lemma 1.2.3. *The omega limit set of any precompact asymptotic pseudo-orbit of a continuous map $S : X \to X$ is nonempty, compact, invariant, and internally chain transitive.*

Proof. Let $(\overline{\mathbb{N}}_+, \rho)$ be the compact metric space defined in the proof of Lemma 1.2.2. Let $\{x_n : n \geq 0\}$ be a precompact asymptotic pseudo-orbit of $S : X \to X$, and denote its compact omega limit set by ω. Define a metric space

$$Y = (\{\infty\} \times X) \cup \{(n, x_n) : n \geq 0\}$$

and

$$g : Y \to Y, \quad g(n, x_n) = (n+1, x_{n+1}), \quad g(\infty, x) = (\infty, S(x)).$$

By Definition 1.2.3 and the fact that $d(x_{n+1}, S(x)) \le d(x_{n+1}, S(x_n)) + d(S(x_n), S(x))$ for $x \in X, n \ge 0$, it easily follows that $g : Y \to Y$ is continuous. Let $\gamma^+(0, x_0) = \{(n, x_n) : n \ge 0\}$ be the positive orbit of $(0, x_0)$ for the discrete semiflow $g^n : Y \to Y, n \ge 0$. Then $\gamma^+(0, x_0)$ is precompact in Y, and its omega limit $\omega(0, x_0)$ is $\{\infty\} \times \omega$, which by Lemma 1.2.1 is invariant and internally chain transitive for g. Applying the definition of g, we see that ω is invariant and internally chain transitive for S. ∎

Let A and B be two nonempty compact subsets of X. Recall that the Hausdorff distance between A and B is defined by

$$d_H(A, B) := \max\left(\sup\{d(x, B) : x \in A\}, \quad \sup\{d(x, A) : x \in B\}\right).$$

We then have the following result.

Lemma 1.2.4. *Let $S, S_n : X \to X$, $\forall n \ge 1$, be continuous. Let $\{D_n\}$ be a sequence of nonempty compact subsets of X with $\lim_{n\to\infty} d_H(D_n, D) = 0$ for some compact subset D of X. Assume that for each $n \ge 1$, D_n is invariant and internally chain transitive for S_n. If $S_n \to S$ uniformly on $D \cup (\cup_{n\ge1} D_n)$, then D is invariant and internally chain transitive for S.*

Proof. Observe that the set $K = D \bigcup (\cup_{n\ge1} D_n)$ is compact. Indeed, since an open cover of K also covers D, a finite subcover provides a neighborhood of D that must also contain D_n for all large n. If $x \in D$, then there exist $x_n \in D_n$ such that $x_n \to x$. Since $S_n(x_n) \in D_n$ and $S_n(x_n) \to S(x)$, we see that $S(x) \in D$. Thus $S(D) \subset D$. On the other hand, there exist $y_n \in D_n$ such that $S_n(y_n) = x_n$. Since $d_H(D_{n_i}, D) \to 0$, we can assume that $y_{n_i} \to y \in D$ for some subsequence y_{n_i}. Then $x_{n_i} = S_{n_i}(y_{n_i}) \to S(y) = x$, showing that $S(D) = D$.

By uniform continuity and uniform convergence, for any $\epsilon > 0$ there exist $\delta \in (0, \epsilon/3)$ and a natural number N such that for $n \ge N$ and $u, v \in K$ with $d(u, v) < \delta$, we have

$$d(S_n(u), S(v)) \le d(S_n(u), S(u)) + d(S(u), S(v)) < \epsilon/3.$$

Fix $n > N$ such that $d_H(D_n, D) < \delta$. For any $a, b \in D$, there are points $x, y \in D_n$ such that $d(x, a) < \delta$ and $d(y, b) < \delta$. Since D_n is internally chain transitive for S_n, there is a δ-chain $\{z_1 = x, z_2, \dots, z_{m+1} = y\}$ in D_n for S_n connecting x to y. For each $i = 2, \dots, m$ we can find $w_i \in D$ with $d(w_i, z_i) < \delta$, since D_n is contained in the δ-neighborhood of D. Let $w_1 = a, w_{m+1} = b$. We then have

$$\begin{aligned} d(S(w_i), w_{i+1}) &\le d(S(w_i), S_n(z_i)) + d(S_n(z_i), z_{i+1}) + d(z_{i+1}, w_{i+1}) \\ &< \epsilon/3 + \delta + \delta < \epsilon \end{aligned}$$

for $i = 1, \dots, m$. Thus $\{w_1 = a, w_2, \dots, w_{m+1} = b\}$ is an ϵ-chain for S in D connecting a to b. ∎

Let $\Phi(t) : X \to X$, $t \geq 0$, be a continuous-time semiflow. That is, $(x,t) \to \Phi(t)x$ is continuous, $\Phi(0) = \mathrm{I}$ and $\Phi(t) \circ \Phi(s) = \Phi(t+s)$ for $t, s \geq 0$. A nonempty invariant set $A \subset X$ for $\Phi(t)$ (i.e., $\Phi(t)A = A$, $\forall t \geq 0$) is said to be internally chain transitive if for any $a, b \in A$ and any $\epsilon > 0, t_0 > 0$, there is a finite sequence $\{x_1 = a, x_2, \dots, x_{m-1}, x_m = b; t_1, \dots, t_{m-1}\}$ with $x_i \in A$ and $t_i \geq t_0, 1 \leq i \leq m-1$, such that $d(\Phi(t_i, x_i), x_{i+1}) < \epsilon$ for all $1 \leq i \leq m-1$. The sequence $\{x_1, \dots, x_m; t_1, \dots, t_{m-1}\}$ is called an (ϵ, t_0)-chain in A connecting a and b. We then have the following result.

Lemma 1.2.1′ *Let $\Phi(t) : X \to X$, $t \geq 0$, be a continuous-time semiflow. Then the omega (alpha) limit set of any precompact positive (negative) orbit is internally chain transitive.*

Proof. Let $\omega = \omega(x)$ be the omega limit set of a precompact orbit $\gamma(x) = \{\Phi(t)x : t \geq 0\}$ in X. Then ω is nonempty, compact, invariant and $\lim_{t\to\infty} d(\Phi(t)x, \omega) = 0$. Let $\epsilon > 0$ and $t_0 > 0$ be given. By the uniform continuity of $\Phi(t)x$ for (t,x) in the compact set $[t_0, 2t_0] \times \omega$, there is a $\delta = \delta(\epsilon, t_0) \in (0, \frac{\epsilon}{3})$ such that for any $t \in [t_0, 2t_0]$ and u and v in the open δ-neighborhood U of ω with $d(u,v) < \delta$, we have $d(\Phi(t)u, \Phi(t)v) < \frac{\epsilon}{3}$. It then follows that there exists a sufficiently large $T_0 = T_0(\delta) > 0$ such that $\Phi(t)x \in U$, for all $t \geq T_0$. For any $a, b \in \omega$, there exist $T_1 > T_0$ and $T_2 > T_0$ with $T_2 > T_1 + t_0$ such that $d(\Phi(T_1)x, \Phi(t_0)a) < \frac{\epsilon}{3}$ and $d(\Phi(T_2)x, b) < \frac{\epsilon}{3}$. Let m be the greatest integer that is not greater than $\frac{T_2 - T_1}{t_0}$. Then $m \geq 1$. Set

$$y_1 = a, y_i = \Phi(T_1 + (i-2)t_0)x, \quad i = 2, \dots, m+1, \quad y_{m+2} = b,$$

and

$$t_i = t_0 \text{ for } i = 1, \dots, m; \; t_{m+1} = T_2 - T_1 - (m-1)t_0.$$

Then $t_{m+1} \in [t_0, 2t_0)$. It follows that $d(\Phi(t_i)y_i, y_{i+1}) < \frac{\epsilon}{3}$ for all $i = 1, \dots, m+1$. Thus the sequence

$$\{y_1 = a, y_2, \dots, y_{m+1}, y_{m+2} = b; t_1, t_2, \dots, t_{m+1}\}$$

is an $(\frac{\epsilon}{3},\, t_0)$-chain in X connecting a and b. Since $y_i \in U$ for $i = 2, \dots, m+1$, we can choose $z_i \in \omega$ such that $d(z_i, y_i) < \delta$. Let $z_1 = a$ and $z_{m+2} = b$. It then follows that

$$\begin{aligned} d(\Phi(t_i)z_i, z_{i+1}) &\leq d(\Phi(t_i)z_i, \Phi(t_i)y_i) + d(\Phi(t_i)y_i, y_{i+1}) + d(y_{i+1}, z_{i+1}) \\ &< \epsilon/3 + \epsilon/3 + \epsilon/3, \quad i = 1, \dots, m+1. \end{aligned}$$

This proves that the sequence $\{z_1 = a, z_2, \dots, z_{m+1}, z_{m+2} = b; t_1, t_2, \dots, t_{m+1}\}$ is an (ϵ, t_0)-chain in ω connecting a and b. Therefore, ω is internally chain transitive. By a similar argument we can prove the internal chain transitivity of alpha limit sets of precompact negative orbits. ∎

With Lemma 1.2.1′ it is easy to see that there are analogues of Lemmas 1.2.2 and 1.2.3 for continuous-time semiflows. The following result is an analogue of Lemma 1.2.4 for continuous-time semiflows.

Lemma 1.2.4′ *Let Φ and Φ^n be continuous-time semiflows on X for $n \geq 1$. Let $\{D_n\}$ be a sequence of nonempty compact subsets of X with $\lim_{n\to\infty} d_H(D_n, D) = 0$ for some compact subset D of X. Assume that for each $n \geq 1$, D_n is invariant and internally chain transitive for Φ^n. If for each $T > 0$, $\Phi^n \to \Phi$ uniformly for $(x,t) \in (D \cup (\cup_{n\geq 1} D_n)) \times [0,T]$, then D is invariant and internally chain transitive for Φ.*

Proof. It is easy to see that $K = D \bigcup (\cup_{n\geq 1} D_n)$ is compact and D is invariant for Φ. By uniform continuity and uniform convergence, for any $\epsilon > 0$ and $t_0 > 0$ there exists $\delta \in (0, \epsilon/3)$ and a natural number N such that for $n \geq N$, $t \in [0, 2t_0]$, and $u, v \in K$ with $d(u,v) < \delta$, we have $d(\Phi_t^n(u), \Phi_t(v)) \leq d(\Phi_t^n(u), \Phi_t(u)) + d(\Phi_t(u), \Phi_t(v)) < \epsilon/3$. Fix $n > N$ such that $d_H(D_n, D) < \delta$. For any $a, b \in D$, there are points $x, y \in D_n$ such that $d(x,a) < \delta$ and $d(y,b) < \delta$. Since D_n is chain transitive for Φ^n, there is a (δ, t_0)-chain $\{z_1 = x, z_2, \ldots, z_{m+1} = y; t_1, \ldots, t_m\}$ in D_n for Φ^n, with $t_0 \leq t_i < 2t_0$ connecting x to y. For each $i = 2, \ldots, m$ we can find $w_i \in D$ with $d(w_i, z_i) < \delta$, since D_n is contained in the δ-neighborhood of D. Let $w_1 = a, w_{m+1} = b$. We then have

$$\begin{aligned} d(\Phi_{t_i}(w_i), w_{i+1}) &\leq d(\Phi_{t_i}(w_i), \Phi_{t_i}^n(z_i)) + d(\Phi_{t_i}^n(z_i), z_{i+1}) + d(z_{i+1}, w_{i+1}) \\ &< \epsilon/3 + \delta + \delta < \epsilon \end{aligned}$$

for $i = 1, \ldots, m$. Thus $\{w_1 = a, w_2, \ldots, w_{m+1} = b; t_1, \ldots, t_m\}$ is an (ϵ, t_0)-chain for Φ in D connecting a to b. ∎

Example 1.2.2. Note that if in Lemma 1.2.4′ D_n is an omega limit set for Φ_n (and therefore internally chain transitive by Lemma 1.2.1′), the set D need not be an omega limit set for the limit semiflow Φ, although it must be chain transitive. Easy examples are constructed with $\Phi^n = \Phi$, $\forall n \geq 1$. For example, consider the flow generated by the planar vector field given in polar coordinates by

$$r' = 0, \quad \theta' = 1 - r.$$

The unit circle $D = \{r = 1\}$, consisting of equilibria, is chain transitive but is not an omega limit set of any point, yet D is the Hausdorff limit of the omega limit sets $D_n = \{r = 1 + \frac{1}{n}\}$.

Lemma 1.2.5. *A nonempty compact invariant set M is internally chain transitive if and only if M is the omega limit set of some asymptotic pseudo-orbit of f in M.*

Proof. The sufficiency follows from Lemma 1.2.3. To prove the necessity, we can choose a point $x \in M$ since M is nonempty. For any $\epsilon > 0$, the compactness of M implies that there is a finite sequence of points

$\{x_1 = x, x_2, \ldots, x_m, x_{m+1} = x\}$ in M such that its ϵ-net in X covers M; i.e., $M \subset \cup_{i=1}^m B(x_i, \epsilon)$, where $B(x_i, \epsilon) := \{y \in X : d(y, x_i) < \epsilon\}$. For each $1 \le i \le m$, since M is internally chain transitive, there is a finite ϵ-chain $\{y_1^i = x_i, y_2^i, \ldots, y_{n_i}^i, y_{n_i+1}^i = x_{i+1}\}$ in M connecting x_i and x_{i+1}. Then the sequence $\{y_1^1, \ldots, y_{n_1}^1, y_1^2, \ldots, y_{n_2}^2, \ldots, y_1^m, \ldots, y_{n_m}^m, y_{n_m+1}^m\}$ is a finite ϵ-chain in M connecting x and x, and its ϵ-net in X covers M.

For each integer k, letting $\epsilon = \frac{1}{k}$ in the above claim, we have a finite $\frac{1}{k}$-chain $\{z_1^k = x, z_2^k, \ldots, z_{l_k}^k, z_{l_k+1}^k = x\}$ in M whose $\frac{1}{k}$-net in X covers M. It then easily follows that the infinite sequence of points

$$\{z_1^1, \ldots, z_{l_1}^1, z_1^2, \ldots, z_{l_2}^2, \ldots, z_1^k, \ldots, z_{l_k}^k, \ldots\}$$

is an asymptotic pseudo-orbit of f in M and its omega limit set is M. ∎

Block–Franke Lemma ([33], Theorem A) *Let K be a compact metric space and $f : K \to K$ a continuous map. Then $x \notin R(K, f)$ if and only if there exists an attractor $A \subset K$ such that $x \in W^s(A) \setminus A$.*

Lemma 1.2.6. *A nonempty compact invariant set M is internally chain transitive if and only if $f|_M : M \to M$ has no proper attractor.*

Proof. *Necessity.* Assume that there is a proper attractor A for $f|_M : M \to M$. Then $A \neq \emptyset$ and $M \setminus A \neq \emptyset$. Since A is an attractor, there is an $\epsilon_0 > 0$ such that A attracts the open ϵ_0-neighborhood U of A in M. Choose $a \in M \setminus A$ and $b \in A$ and let $\{x_1 = a, x_2, \ldots, x_m = b\}$ be an ϵ_0-chain in M connecting a and b. Let $k = \min\{i : 1 \le i \le m,\ x_i \in A\}$. Since $b \in A$ and $a \notin A$, we have $2 \le k \le m$. Since $d(f(x_{k-1}), x_k) < \epsilon_0$, we have $f(x_{k-1}) \in U$ and hence $x_{k-1} \in W^s(A) \setminus A$. By the Block–Franke lemma, $x_{k-1} \notin R(M, f)$, which proves that M is not internally chain recurrent, and a fortiori not internally chain transitive.

Sufficiency. For any subset $B \subset X$ we define $\omega(B)$ to be the set of limits of sequences of the form $\{f^{n_k}(x_k)\}$, where $n_k \to \infty$ and $x_k \in B$. Since $f|_M : M \to M$ has no proper attractor, the Block–Franke lemma implies that M is internally chain recurrent. Given $a, b \in M$ and $\epsilon > 0$, let V be the set of all points x in M for which there is an ϵ-chain in M connecting a to x; this set contains a. For any $z \in V$, let $\{z_1 = a, z_2, \ldots, z_{m-1}, z_m = z\}$ be an ϵ-chain in M connecting a to z. Since

$$\lim_{x \to z} d(f(z_{m-1}), x) = d(f(z_{m-1}), z) < \epsilon,$$

there is an open neighborhood U of z in M such that for any $x \in U$, $d(f(z_{m-1}), x) < \epsilon$. Then $\{z_1 = a, z_2, \ldots, z_{m-1}, x\}$ is an ϵ-chain in M connecting a and x, and hence $U \subset V$. Thus V is an open set in M. We further claim that $f(\overline{V}) \subset V$. Indeed, for any $z \in \overline{V}$, by the continuity of f at z, we can choose $y \in V$ such that $d(f(y), f(z)) < \epsilon$. Let $\{y_1 = a, y_2, \ldots, y_{m-1}, y_m = y\}$ be an ϵ-chain in M connecting a and y. It then follows that $\{y_1 = a, y_2, \dots, y_{m-1}, y_m = y, y_{m+1} = f(z)\}$ is an ϵ-chain in M connecting a and $f(z)$, and hence $f(z) \in V$. By the compactness of M and [141, Lemma 2.1.2] applied to $f : M \to M$, it then follows that $\omega(\overline{V})$ is nonempty, compact, invariant, and $\omega(\overline{V})$ attracts $\overline{V}$. Since $f(\overline{V}) \subset V$, we have $\omega(\overline{V}) \subset \overline{V}$ and hence $\omega(\overline{V}) = f(\omega(\overline{V})) \subset V$. Then $\omega(\overline{V})$ is an attractor in M. Now the nonexistence of a proper attractor for $f : M \to M$ implies that $\omega(\overline{V}) = M$ and hence $V = M$. Clearly, $b \in M = V$, and hence, by the definition of V, there is an ϵ-chain in M connecting a and b. Therefore, M is internally chain transitive. ∎

1.2.2 Attractivity and Morse Decompositions

Recall that a nonempty invariant subset M of X is said to be isolated for $f : X \to X$ if it is the maximal invariant set in some neighborhood of itself.

Lemma 1.2.7. (Butler–McGehee-type lemma) *Let M be an isolated invariant set and L a compact internally chain transitive set for $f : X \to X$. Assume that $L \cap M \neq \emptyset$ and $L \not\subset M$. Then*

(a) there exists $u \in L \setminus M$ such that $\omega(u) \subset M$;
(b) there exist $w \in L \setminus M$ and a negative orbit $\gamma^-(w) \subset L$ such that its α-limit set satisfies $\alpha(w) \subset M$.

Proof. Since M is an isolated invariant set, there exists an $\epsilon > 0$ such that M is the maximal invariant set in the closed ϵ-neighborhood of M. By the assumption, we can choose $a \in L \cap M$ and $b \in L$ with $d(b, M) > \epsilon$. For any integer $k \geq 1$, by the internal chain transitivity of L, there exists a $\frac{1}{k}$-chain $\{y_1^k = a, \dots, y_{l_k+1}^k = b\}$ in L connecting a and b, and a $\frac{1}{k}$-chain $\{z_1^k = b, \dots, z_{m_k+1}^k = a\}$ in L connecting b and a. Define a sequence of points by

$$\{x_n : n \geq 0\} := \{y_1^1, \dots, y_{l_1}^1, z_1^1, \dots, z_{m_1}^1, \dots, y_1^k, \dots, y_{l_k}^k, z_1^k, \dots, z_{m_k}^k, \dots\}.$$

Then for any $k > 0$ and for all $n \geq N(k) := \sum_{j=1}^k (l_j + m_j)$, we have $d(f(x_n), x_{n+1}) < \frac{1}{k+1}$, and hence $\lim_{n\to\infty} d(f(x_n), x_{n+1}) = 0$. Thus $\{x_n\}_{n\geq 0} \subset L$ is a precompact asymptotic pseudo-orbit of $f : X \to X$. Then there are two subsequences x_{m_j} and x_{r_j} such that $x_{m_j} = a$ and $x_{r_j} = b$ for all $j \geq 1$. Note that $d(x_{s_j+1}, f(x)) \leq d(x_{s_j+1}, f(x_{s_j})) + d(f(x_{s_j}), f(x))$. By induction, it then follows that for any convergent subsequence $x_{s_j} \to x \in X, j \to \infty$, we have $\lim_{j\to\infty} x_{s_j+n} = f^n(x)$ for any integer $n \geq 0$. We can further choose two sequences l_j and n_j with $l_j < m_j < n_j$ and $\lim_{j\to\infty} l_j = \infty$ such that $d(x_{l_j}, M) > \epsilon$, $d(x_{n_j}, M) > \epsilon$, and $d(x_k, M) \leq \epsilon$ for any integer $k \in (l_j, n_j), j \geq 1$. Since $\{x_n : n \geq 0\}$ is a subset of the compact set L, we can assume that upon taking a convergent subsequence, $x_{l_j} \to u \in L$ as $j \to \infty$. Clearly, $d(u, M) \geq \epsilon$ and hence $u \in L \setminus M$. Since $u \in L$ and L is a compact invariant set, we have $\omega(u) \subset L$. We further claim that $\omega(u) \subset M$, which proves (a). Indeed, if the sequence $n_j - l_j$ is bounded, then $m_j - l_j$ is also bounded, and hence we can assume that, after choosing a subsequence, $m_j - l_j = m$, where m is an integer. Thus we have $a = \lim_{j\to\infty} x_{m_j} = \lim_{j\to\infty} x_{l_j+m} = f^m(u)$, and hence $\omega(u) = \omega(a) \subset M$. If the sequence $n_j - l_j$ is unbounded, we can assume that, by taking a subsequence, $n_j - l_j \to \infty$ as $j \to \infty$. Then for any integer $n \geq 1$, there is an integer $J = J(n) \geq 1$ such that $n_j - l_j > n$ for all $j \geq J$. Then we have $l_j < l_j + n < n_j$ and hence $d(x_{l_j+n}, M) \leq \epsilon, \forall j \geq J(n)$. Thus $f^n(u) = \lim_{j\to\infty} x_{l_j+n}$ satisfies $d(f^n(u), M) \leq \epsilon, \forall n \geq 1$, and hence the choice of ϵ implies that $\omega(u) \subset M$. In a similar way we can also prove (b). ∎

Theorem 1.2.1. (Strong attractivity) *Let A be an attractor and C a compact internally chain transitive set for $f : X \to X$. If $C \cap W^s(A) \neq \emptyset$, then $C \subset A$.*

Proof. Clearly, A is isolated for $f : X \to X$. Let $x \in C \cap W^s(A)$. By the compactness and invariance of C, $\omega(x) \subset C$ and hence $\omega(x) \subset C \cap A$. Then $C \cap A \neq \emptyset$. Assume, by contradiction, that $C \not\subset A$. Then by Lemma 1.2.7, there exists $w \in C \setminus A$ with a full orbit $\gamma(w) = \{w_n : n \in Z\} \subseteq C$ and $\alpha(w) \subset A$. Since $w \notin A$, there exists an open neighborhood V of A such that $w \notin V$. Then, by the attractivity of A, there exist an open neighborhood U of A and an integer $n_0 > 0$ such that $S^n(U) \subset V$ for all $n \geq n_0$. Since $\alpha(w) \subset A$, there exists an integer $n_1 > n_0$ such that $w_{-n_1} \in U$, and hence $w = w_0 = S^{n_1}(w_{-n_1}) \in V$, which contradicts $w \notin V$. ∎

Let A and B be two isolated invariant sets . The set A is said to be chained to B, written $A \to B$, if there exists a full orbit through some $x \notin A \cup B$ such that $\omega(x) \subset B$ and $\alpha(x) \subset A$. A finite sequence $\{M_1, \dots, M_k\}$ of invariant sets is called a chain if $M_1 \to M_2 \to \cdots \to M_k$. The chain is called a cycle if $M_k = M_1$.

Theorem 1.2.2. (Convergence) *Assume that each fixed point of f is an isolated invariant set, that there is no cyclic chain of fixed points, and that every precompact orbit converges to some fixed point of f. Then any compact internally chain transitive set is a fixed point of f.*

Proof. Let C be a compact internally chain transitive set for $f : X \to X$. Then for any $x \in C$, we have $\gamma^+(x) \subset C$ and $\omega(x) \subset C$. Thus the convergence of $\gamma^+(x)$ implies that C contains some fixed point of f. Let $E = \{e \in C : f(e) = e\}$. Then $E \neq \emptyset$, and by the compactness of C and the isolatedness of each fixed point of f, $E = \{e_1, e_2, \dots, e_m\}$ for some integer $m > 0$. Assume by way of contradiction that C is not a singleton. Since $E \neq \emptyset$, there exists some i_1 $(1 \leq i_1 \leq m)$ such that $e_{i_1} \in C$; i.e., $C \cap \{e_{i_1}\} \neq \emptyset$. Since $C \not\subset \{e_{i_1}\}$, by Lemma 1.2.7 there exist $w_1 \in C \setminus \{e_{i_1}\}$ and a full orbit $\gamma(w_1) \subset C$ such that $\alpha(w_1) = e_{i_1}$. Since $\gamma^+(w_1) \subset C$, there exists some i_2 $(1 \leq i_2 \leq m)$ such that $\omega(w_1) = e_{i_2}$. Therefore, e_{i_1} is chained to e_{i_2}; i.e., $e_{i_1} \to e_{e_2}$. Since $C \cap \{e_{i_2}\} \neq \emptyset$ and $C \not\subset \{e_{i_2}\}$, again by Lemma 1.2.7 there exist $w_2 \in C \setminus \{e_{i_2}\}$ and a full orbit $\gamma(w_2) \subset C$ such that $\alpha(w_2) = e_{i_2}$. We can repeat the above argument to get an i_3 ($1 \le i_3 \le m$) such that $e_{i_2} \to e_{i_3}$. Since there is only a finite number of e_i's, we will eventually arrive at a cyclic chain of some fixed points of f, which contradicts our assumption. ∎

Definition 1.2.4. *Let S be a compact metric space and $f : S \to S$ a continuous map with $f(S) = S$. An ordered collection $\{M_1, \dots, M_k\}$ of disjoint, compact, and invariant subsets of S is called a Morse decomposition of S if for each $x \in S \setminus \cup_{i=1}^k M_i$ there is an i with $\omega(x) \subset M_i$ and for any negative orbit γ^- through x there is a $j > i$ with $\alpha(\gamma^-) \subset M_j$; A collection $\{M_1, \dots, M_k\}$ of disjoint, compact, and invariant subsets of S is called an acyclic covering of $\Omega(S) := \cup_{x \in S} \omega(x)$ if each M_i is isolated in S, $\Omega(S) \subset \cup_{i=1}^k M_i$, and no subset of M_i's forms a cycle in S.*

By replacing each e_j in the proof of Theorem 1.2.2 with M_j, we can easily get the following result.

Lemma 1.2.8. *Let $\{M_1, \dots, M_k\}$ be an acyclic covering of $\Omega(S)$. Then any compact internally chain transitive set of $f : S \to S$ is contained in some M_i.*

By [299, Theorems 3.1.7 and 3.1.8] and their discrete-time versions, the current definition for Morse decomposition is equivalent to that in terms of Conley's repeller–attractor pairs (see, e.g., [299, Definition 3.1.5] for semiflows and [336, Definition 4.2] for maps). The concept of acyclic coverings is very important in persistence theory (see, e.g., [45, 146]). The equivalence between acyclic coverings and Morse decompositions was first observed by Garay for (two-sided) continuous flow on the boundary (see [128, Lemma]). In the following lemma, we formulate it in a general setting and give a complete proof, which also provides an algorithm on how to reorder an acyclic covering into an ordered Morse decomposition.

Lemma 1.2.9. *A finite sequence $\{M_1, \dots, M_k\}$ of disjoint, compact, and invariant sets of f in S is an acyclic covering of $\Omega(S)$ if and only if (after reordering) it is a Morse decomposition of S.*

Proof. *Necessity.* We first claim that for any subcollection $\mathcal{M}$ of M_i's, there exists an element $D \in \mathcal{M}$ such that D cannot be chained to any element in $\mathcal{M}$. Indeed, by contradiction, the nonexistence of such D would imply that some subset of M_i's from this finite collection $\mathcal{M}$ forms a cycle, which contradicts the acyclic condition. By this claim, we can reorder the total collection $\mathcal{M}_0 := \{M_1, \dots, M_k\}$ by induction. First we choose an element, denoted by D_1, from the collection $\mathcal{M}_0$ such that D_1 cannot be chained to any element in $\mathcal{M}_0$. Suppose that we have chosen $D_1, \dots, D_m$. We further choose an element, denoted by D_{m+1}, from the collection $\mathcal{M}_m := \mathcal{M}_0 \setminus \{D_1, \dots, D_m\}$ such that D_{m+1} cannot be chained to any element in $\mathcal{M}_m$. After k steps, we then get a reordered collection $\mathcal{D} := \{D_1, \dots, D_k\}$. Moreover, for any $1 \le i < j \le k$, clearly we have $D_i, D_j \in \mathcal{M}_{i-1}$. Therefore, by the choice of D_i, D_i cannot be chained to any element in $\mathcal{M}_{i-1}$, and hence D_i cannot be chained to D_j.

For any $x \in S \setminus \cup_{i=1}^k D_i$, by the assumption, we have $\omega(x) \subset \cup_{i=1}^k D_i$, and hence the invariant connectedness of $\omega(x)$ implies that $\omega(x) \subset D_i$ for some i. Let γ^- be any given negative orbit of f through x and let $\alpha = \alpha(\gamma^-)$. By Lemma 1.2.1, α is internally chain transitive for f. We further claim that $\alpha \subset D_j$ for some j. Indeed, assume, by contradiction, that $\alpha \not\subset D_m$ for all $1 \leq m \leq k$. Since $\alpha \subset S$ is compact and invariant, $\alpha \cap (\cup_{i=1}^k D_i) \neq \emptyset$, and hence there exists some D_{i_1} $(1 \leq i_1 \leq k)$ such that $\alpha \cap D_{i_1} \neq \emptyset$. By Lemma 1.2.7, there exist $w_1 \in \alpha \setminus D_{i_1}$ and a full orbit $\gamma(w_1) \subset \alpha$ such that $\alpha(w_1) \subset D_{i_1}$. Since $w_1 \in \alpha \subset S$, we have $\omega(w_1) \subset \cup_{i=1}^k D_i$, and hence by the invariant connectedness of $\omega(w_1)$, there exists some D_{i_2} $(1 \leq i_2 \leq k)$ such that $\omega(w_1) \subset D_{i_2}$. Therefore, D_{i_1} is chained to D_{i_2}; i.e., $D_{i_1} \to D_{i_2}$. Clearly, $\omega(w_1) \subset \alpha$. Then $\alpha \cap D_{i_2} \neq \emptyset$. Again by Lemma 1.2.7, there exist $w_2 \in \alpha \setminus D_{i_2}$ and a full orbit $\gamma(w_2) \subset \alpha$ such that $\alpha(w_2) \subset D_{i_2}$. We can repeat the above argument to get an i_3 $(1 \leq i_3 \leq k)$ such that $D_{i_2} \to D_{i_3}$. Since there is only a finite number of D_m's, we will eventually arrive at a cyclic chain of some D_m for f in S, which contradicts the no-cycle condition. It then follows that $D_j \to D_i$, and hence by the property of $\{D_1, \ldots, D_k\}$, we have $j > i$. Therefore, $\{D_1, \ldots, D_k\}$ is a Morse decomposition of S.

Sufficiency. Since the M_i, $1 \leq i \leq k$, are pairwise disjoint and compact, there exist k pairwise disjoint and closed subsets N_i of S such that M_i is contained in the interior of N_i, $1 \leq i \leq k$. In order to see that M_m is isolated in S, suppose that there exists an invariant set $M \subset \mathrm{Int} N_m$ but $M \not\subset M_m$. It follows that there is an $x \in M \cap (S \setminus \cup_{i=1}^k M_i)$. Let $\gamma \subset M$ be a full orbit through x. Clearly, $\omega(x) \subset \overline{M}$ and $\alpha(x) \subset \overline{M}$. Since $\{M_1, \ldots, M_k\}$ is a Morse decomposition of S, there exists $j > i$ such that $\omega(x) \subset M_i$ and $\alpha(x) \subset M_j$. Then $M_i \cap N_m \neq \emptyset$ and $M_j \cap N_m \neq \emptyset$, and hence $i = m = j$, which contradicts $j > i$. Thus each M_i is isolated in S. Clearly, the definition of Morse decompositions implies that $\Omega(S) \subset \cup_{i=1}^k M_i$. We further claim that if $M_{i_1} \to M_{i_2}$, then $i_1 > i_2$. Indeed, let $\gamma(x)$ be a full orbit through some $x \notin M_{i_1} \cup M_{i_2}$ such that $\omega(x) \subset M_{i_2}$ and $\alpha(x) \subset M_{i_1}$. If $x \in M_l$ for some l, we have $\omega(x) \subset M_l \cap M_{i_2}$ and $\alpha(x) \subset M_l \cap M_{i_1}$, and hence $i_1 = l = i_2$, contradicting that $x \notin M_{i_1} \cup M_{i_2}$. It follows that $x \in S \setminus \cup_{i=1}^k M_i$. Since $\{M_1, \ldots, M_k\}$ is a Morse decomposition of S, there exists $j > i$ such that $\omega(x) \in M_i$ and $\alpha(x) \in M_j$. Then we have $i_1 = j > i = i_2$. By this claim, it is easy to see that no subset of M_i's forms a cycle in S. Therefore, $\{M_1, \ldots, M_k\}$ is an acyclic covering of $\Omega(S)$. ∎

1.3 Strong Repellers and Uniform Persistence

Let $f : X \to X$ be a continuous map and $X_0 \subset X$ an open set. Define $\partial X_0 := X \setminus X_0$, and $M_\partial := \{x \in \partial X_0 : f^n(x) \in \partial X_0, n \geq 0\}$, which may be empty. Note that ∂X_0 need not be the boundary of X_0 as the notation suggests. This peculiar notation has become standard in persistence theory (see, e.g., [365]). We assume that every positive orbit of f is precompact.

1.3.1 Strong Repellers

There are two traditional approaches in persistence theory, one using Morse decompositions and the other using acyclic coverings. The next lemma, together with Lemma 1.2.9, shows that the two approaches are equivalent.

Lemma 1.3.1. *Suppose that there exists a maximal compact invariant set A_∂ of f in ∂X_0; that is, A_∂ is compact, invariant, possibly empty, and contains every compact invariant subset of ∂X_0. Then a finite sequence $\{M_1, \ldots, M_k\}$ of disjoint, compact, and invariant subsets of ∂X_0, each of which is isolated in ∂X_0, is an acyclic covering of $\Omega(M_\partial)$ in ∂X_0 if and only if (after reordering) it is a Morse decomposition of A_∂.*

Proof. Let $S = A_\partial$. Then we have $S \subset M_\partial$ and hence $\Omega(S) \subset \Omega(M_\partial)$. It follows that $\{M_1, \ldots, M_k\}$ is also an acyclic covering of $\Omega(S)$. So the necessity follows from Lemma 1.2.9. To prove the sufficiency, assume that $\{M_1, \ldots, M_k\}$ is a Morse decomposition of S. By Lemma 1.2.9, $\{M_1, \ldots, M_k\}$ is an acyclic covering of $\Omega(S)$ in S. Since S is the maximal compact invariant set in ∂X_0, any compact invariant set in ∂X_0 is a subset of S. Consequently, no subset of M_i's forms a cycle in ∂X_0 because such a cycle is compact and invariant so necessarily belongs to S, violating that $\{M_1, \ldots, M_k\}$ is a Morse decomposition of S. We further claim that $\Omega(M_\partial) \subset \cup_{i=1}^{k} M_i$. Indeed, for any $x \in M_\partial$, $\omega(x)$ is a compact, invariant, internally chain transitive set in ∂X_0 (by Lemma 1.2.1). Then $\omega(x) \subset S$, and hence Lemma 1.2.8 implies that $\omega(x) \subset M_i$ for some $1 \leq i \leq k$. Therefore, $\{M_1, \ldots, M_k\}$ is an acyclic covering of $\Omega(M_\partial)$ in ∂X_0. ∎

Theorem 1.3.1. (Strong repellers) *Assume that*

(C1) $f(X_0) \subset X_0$ and f has a global attractor A;
(C2) The maximal compact invariant set $A_\partial = A \cap M_\partial$ of f in ∂X_0, possibly empty, admits a Morse decomposition $\{M_1, \ldots, M_k\}$ with the following properties:
  (a) M_i is isolated in X;
  (b) $W^s(M_i) \cap X_0 = \emptyset$ for each $1 \leq i \leq k$.

Then there exists $\delta > 0$ such that for any compact internally chain transitive set L with $L \not\subset M_i$ for all $1 \leq i \leq k$, we have $\inf_{x \in L} d(x, \partial X_0) > \delta$.

Proof. We first prove the following weaker conclusion:

Claim. There is an $\epsilon > 0$ such that if L is a compact internally chain transitive set not contained in any M_i, then $\sup_{x \in L} d(x, \partial X_0) > \epsilon$.

Indeed, assume that, by contradiction, there exists a sequence of compact internally chain transitive sets $\{D_n : n \geq 1\}$ with $D_n \not\subset M_i, 1 \leq i \leq k$, such that

$$\lim_{n \to \infty} \sup_{x \in D_n} d(x, \partial X_0) = 0.$$

Since $W^s(A) = X$, by Theorem 1.2.1 we have $D_n \subset A$ for all $n \geq 1$. In the compact metric space of compact nonempty subsets of A with Hausdorff distance d_H, the sequence $\{D_n : n \geq 1\}$ has a convergent subsequence. Without loss of generality, we assume that for some nonempty compact set $D \subset A$, $\lim_{n\to\infty} d_H(D_n, D) = 0$. Then for any $x \in D$, there exists $x_n \in D_n$ such that $\lim_{n\to\infty} x_n = x$. Clearly, $\lim_{n\to\infty} d(x_n, \partial X_0) = 0$, and hence there exists $y_n \in \partial X_0$ such that $\lim_{n\to\infty} d(x_n, y_n) = 0$. It then follows that $\lim_{n\to\infty} y_n = x$, and hence $x \in \overline{\partial X_0} = \partial X_0$. Thus $D \subset \partial X_0$. By Lemma 1.2.4 with $S_n = f$, D is internally chain transitive for f. It then follows that $D \subset A_\partial$, and Lemmas 1.2.8 and 1.2.9 imply that $D \subset M_i$ for some i. Since $D_n \to M_i$ as $n \to \infty$, the isolatedness of M_i in X implies that $D_n \subset M_i$ for all large n, contradicting our assumption. This proves the claim.

We now prove the theorem by contradiction. Assume that there exists a sequence of compact internally chain transitive sets $\{L_n : n \geq 1\}$ with $L_n \not\subset M_i$, $1 \leq i \leq k, n \geq 1$, such that $\lim_{n\to\infty} \inf_{x\in L_n} d(x, \partial X_0) = 0$. As in the proof of the above claim, we can assume that $\lim_{n\to\infty} d_H(L_n, L) = 0$, where L is a compact internally chain transitive set for $f : X \to X$ and $L \not\subset M_i$ for each $1 \leq i \leq k$. Clearly, there exist $x_n \in L_n, n \geq 1$, such that $\lim_{n\to\infty} d(x_n, \partial X_0) = 0$, and hence $L \cap \partial X_0 \neq \emptyset$. By the above claim, we can choose $a \in L \cap \partial X_0$ and $b \in L$ with $d(b, \partial X_0) > \epsilon$. As in the proof of Lemma 1.2.7, let $\{x_n : n \geq 0\}$ be the asymptotic pseudo-orbit determined by a and b in L. Then there are two subsequences x_{m_j} and x_{r_j} such that $x_{m_j} = a$ and $x_{r_j} = b$ for all $j \geq 1$, and for any convergent subsequence $x_{s_j} \to x \in X$, $j \to \infty$, we have $\lim_{j\to\infty} x_{s_j+n} = f^n(x)$, $\forall n \geq 0$. We can further choose two sequences l_j and n_j with $l_j < m_j < n_j$ and $\lim_{j\to\infty} l_j = \infty$ such that $d(x_{l_j}, \partial X_0) > \epsilon$, $d(x_{n_j}, \partial X_0) > \epsilon$, and $d(x_k, \partial X_0) \leq \epsilon$ for any integer $k \in (l_j, n_j)$, $j \geq 1$. Since $\{x_n : n \geq 0\}$ is a subset of the compact set L, we can assume, after taking a convergent subsequence, that $x_{l_j} \to x \in L$ as $j \to \infty$. Clearly, $d(x, \partial X_0) \geq \epsilon$ and hence $x \in X_0$. We further claim that the sequence $n_j - l_j$ is unbounded. Assume that, by contradiction, $n_j - l_j$ is bounded. Then $m_j - l_j$ is also bounded, and hence we can assume, after choosing a subsequence, that $m_j - l_j = m$, where m is an integer. Since $f(X_0) \subset X_0$, we have $a = \lim_{j\to\infty} x_{m_j} = \lim_{j\to\infty} x_{l_j+m} = f^m(x) \in X_0$, which contradicts $a \in \partial X_0$. Thus we can assume, by taking a subsequence, that $n_j - l_j \to \infty$ as $j \to \infty$. Then for any integer $n \geq 1$, there is an integer $J = J(n) \geq 1$ such that $n_j - l_j > n$ for all $j \geq J$. Then we have $l_j < l_j + n < n_j$ and hence $d(x_{l_j+n}, \partial X_0) \leq \epsilon, \forall j \geq J(n)$. Thus $f^n(x) = \lim_{j\to\infty} x_{l_j+n}$ satisfies $d(f^n(x), \partial X_0) \leq \epsilon, \forall n \geq 1$. Since $x \in L$, we have $f^n(x) \in L, n \geq 0$. Thus, by Lemma 1.2.1, $\omega(x)$ is a compact internally chain transitive set for $f : X \to X$. Moreover, $\sup_{y\in\omega(x)} d(y, \partial X_0) \leq \epsilon$. Appealing again to the claim, we conclude that $\omega(x) \subset M_i$ for some $1 \leq i \leq k$, and hence $x \in W^s(M_i) \cap X_0$. But this contradicts assumption (C2). ∎

Remark 1.3.1. It easily follows from Lemma 1.3.1 that the conclusion of Theorem 1.3.1 is still valid if condition (C2) is replaced by the following one:

(C2′) There exists a finite sequence $\mathcal{M} = \{M_1, \ldots, M_k\}$ of disjoint, compact, and isolated invariant sets in ∂X_0 such that
- (a) $\Omega(M_\partial) := \cup_{x \in M_\partial} \omega(x) \subset \cup_{i=1}^k M_i$;
- (b) no subset of $\mathcal{M}$ forms a cycle in ∂X_0;
- (c) M_i is isolated in X;
- (d) $W^s(M_i) \cap X_0 = \emptyset$ for each $1 \leq i \leq k$.

We observe that Theorem 1.3.1 requires that the open set X_0 be positively invariant for f, which may limit its applications. Moreover, in the infinite-dimensional case of X(e.g., space of continuous functions on a compact set), the distance function $d(x, \partial X_0)$ only gives rise to an abstract repelling property of ∂X_0 (e.g., the maximum norm induced distance). In the rest of this subsection we extend strong repellers to a more general case.

Definition 1.3.1. *A lower semicontinuous function $p : X \to \mathbb{R}_+$ is called a generalized distance function for $f : X \to X$ if for every $x \in (X_0 \cap p^{-1}(0)) \cup p^{-1}(0, \infty)$, we have $p(f^n(x)) > 0$, $\forall n \geq 1$.*

Theorem 1.3.2. *Let p be a generalized distance function for continuous map $f : X \to X$. Assume that*

(P1) f has a global attractor A;

(P2) There exists a finite sequence $M = \{M_1, \ldots, M_k\}$ of disjoint, compact, and isolated invariant sets in ∂X_0 with the following properties:
- *(a) $\cup_{x \in M_\partial} \omega(x) \subset \cup_{i=1}^k M_i$;*
- *(b) no subset of M forms a cycle in ∂X_0;*
- *(c) M_i is isolated in X;*
- *(d) $W^s(M_i) \cap p^{-1}(0, \infty) = \emptyset$ for each $1 \leq i \leq k$.*

Then there exists $\delta > 0$ such that for any compact chain transitive set L with $L \not\subset M_i$ for all $1 \leq i \leq k$, we have $\min_{x \in L} p(x) > \delta$.

Proof. Since the proof is similar to that of Theorem 1.3.1, we only sketch modifications. The first claim is that there exists $\epsilon > 0$ such that $\sup\{p(x) : x \in L\} > \epsilon$ holds for all chain transitive sets L not contained in any M_i. Arguing by contradiction as in the original proof we arrive at a chain transitive set D (limit of sets D_n) satisfying $p(x) = 0$, $\forall x \in D$. If $x \in D \cap X_0$, then $p(f(x)) > 0$, a contradiction to $f(x) \in D$, so we conclude that $D \subset \partial X_0$. The remainder of the proof of the claim is unchanged.

The second part of the proof begins by contradicting the conclusion of the result, obtaining a chain transitive set L, with L not contained in any M_i, as a limit of chain transitive sets L_n, each not contained in any M_i, and with $\lim_{n \to \infty} \inf\{p(x) : x \in L_n\} = 0$. So we find $x_n \in L_n$ with $p(x_n) \to 0$. Without loss of generality, we assume $x_n \to a \in L$ as $n \to \infty$. By the lower semicontinuity of p at a and the fact that $p(a) \geq 0$, it easily follows that $p(a) = 0$. By the claim, we can find point $b \in L$ such that $p(b) > \epsilon$. At this point the proof continues as in Theorem 1.3.1 with the construction of an asymptotic pseudo-orbit, except that $d(y, \partial X_0)$ is replaced in each occurrence by $p(y)$. We conclude that the subsequential limit $x \in L$ of the pseudo-orbit satisfies $p(x) \geq \epsilon$, but this doesn't imply $x \in X_0$. Furthermore, since we do not assume that X_0 is positively invariant, the argument that $m_j - l_j$ is unbounded can be modified as follows: $a = f^m(x)$ contradicts that $p(a) = 0 = p(f^m(x))$, $p(x) \geq \epsilon$, and Definition 1.3.1, which requires $p(f^m(x)) > 0$. Continuing as in the original argument, we arrive at $p(f^n(x)) \leq \epsilon$, $\forall n \geq 1$. Thus, the lower semicontinuity of p implies that $p(y) \leq \epsilon$ on the chain transitive set $\omega(x) \subset L$. But this contradicts (P2) as in the original proof. ∎

1.3.2 Uniform Persistence

In this subsection we discuss uniform persistence and its robustness in terms of sequences of discrete semiflows.

Definition 1.3.2. *A function $f : X \to X$ is said to be uniformly persistent with respect to $(X_0, \partial X_0)$ if there exists $\eta > 0$ such that $\liminf_{n\to\infty} d(f^n(x), \partial X_0) \geq \eta$ for all $x \in X_0$. If "inf" in this inequality is replaced with "sup", then f is said to be weakly uniformly persistent with respect to $(X_0, \partial X_0)$.*

Clearly, $W^s(M_i) \cap X_0 = \emptyset$ implies that $\omega(x) \not\subset M_i$, $\forall x \in X_0$. By Lemma 1.2.1 and Theorem 1.3.1, it then follows that $f : X \to X$ is uniformly persistent under assumptions (C1) and (C2). In particular, we have the following interesting result.

Theorem 1.3.3. *Let $f : X \to X$ be a continuous map with $f(X_0) \subset X_0$. Assume that f has a global attractor A. Then weak uniform persistence implies uniform persistence.*

Proof. Let A_∂ be the maximal compact invariant set of f in ∂X_0. Clearly, A_∂ is a Morse decomposition of $f : A_\partial \to A_\partial$. It is easy to see that weak uniform persistence of f implies that $W^s(A_\partial) \cap X_0 = \emptyset$ and that A_∂ is isolated in X_0, and hence isolated in X. By Theorem 1.3.1 with $L = \omega(x)$, $\forall x \in X_0$, f is uniformly persistent with respect to $(X_0, \partial X_0)$. ∎

Definition 1.3.3. *Let p be a generalized distance function for a continuous map $f : X \to X$. Then f is said to be uniformly persistent with respect to $(X_0, \partial X_0, p)$ if there exists $\eta > 0$ such that $\liminf_{n\to\infty} p(f^n(x)) \geq \eta$ for all $x \in X_0$.*

By Definition 1.3.1, it is easy to see that for every $x \in X_0$, either $p(x) > 0$ or $p(f(x)) > 0$. Note that $\omega(x) = \omega(f(x))$. Thus, $W^s(M_i) \cap p^{-1}(0, \infty) = \emptyset$ implies $\omega(x) \not\subset M_i$, $\forall x \in X_0$. By Lemma 1.2.1 and Theorem 1.3.2, it then follows that f is uniformly persistent with respect to $(X_0, \partial X_0, p)$ under assumptions (P1) and (P2).

Let $S_m : X \to X$, $m \geq 0$, be a sequence of continuous maps such that every positive orbit for S_m has compact closure. Let $\omega_m(x)$ denote the omega limit of x for discrete semiflow S_m, and set $W = \overline{\cup_{m\geq 0, x\in X}\omega_m(x)}$. The following two results show that uniform persistence is robust under appropriate conditions.

Theorem 1.3.4. (Robustness of uniform persistence) *Assume that $S_m(X_0) \subset X_0$, $\forall m \geq 0$, W is compact, and $S_m \to S_0$ uniformly on W. In addition, suppose that*

(A1) S_0 satisfies (C1) and either of (C2) and (C2′);
(A2) There exist $\eta_0 > 0$ and a positive integer N_0 such that for $m \geq N_0$ and $x \in X_0$, $\limsup_{n\to\infty} d(S_m^n(x), M_i) \geq \eta_0$, $1 \leq i \leq k$.

Then there exist $\eta > 0$ and a positive integer N such that $\liminf_{n\to\infty} d(S_m^n(x), \partial X_0) \geq \eta$ for $m \geq N$ and $x \in X_0$.

Proof. Assume, by contradiction, that there exists a sequence $\{x_k\}$ in X_0 and positive integers $m_k \to \infty$ satisfying $\liminf_{n\to\infty} d(S_{m_k}^n(x_k), \partial X_0) \to 0$ as $k \to \infty$. By Lemma 1.2.1, $\omega_{m_k}(x_k)$ is a compact internally chain transitive set for S_{m_k}. In the compact metric space of all compact subsets of W with Hausdorff distance d_H, the sequence $\{\omega_{m_k}(x_k)\}$ has a convergent subsequence. Without loss of generality, we assume that for some nonempty compact $L \subset W$, $\lim_{k\to\infty} d_H(\omega_{m_k}(x_k), L) = 0$. Clearly, there exist $y_k \in \omega_{m_k}(x_k)$ such that $\lim_{k\to\infty} d(y_k, \partial X_0) = 0$, and hence $L \cap \partial X_0 \neq \emptyset$. By Lemma 1.2.4, L is internally chain transitive for S_0. Since $L \cap \partial X_0 \neq \emptyset$, Theorem 1.3.1, applied to S_0, implies that $L \subset M_i$ for some i. Therefore, $\lim_{k\to\infty} \sup\{d(x, M_i) : x \in \omega_{m_k}(x_k)\} = 0$, and hence there exists a $k_0 > 0$ such that $m_{k_0} > N_0$ and $\omega_{m_{k_0}}(x_{k_0}) \subset \{x : d(x, M_i) < \frac{\eta_0}{2}\}$. Since $S_{m_{k_0}}^n(x_{k_0}) \to \omega_{m_{k_0}}(x_{k_0})$ as $n \to \infty$, we have $\limsup_{n\to\infty} d(S_{m_{k_0}}^n(x_{k_0}), M_i) \leq \frac{\eta_0}{2}$, which is a contradiction to assumption (A2). ∎

Theorem 1.3.5. (Robustness of uniform persistence) *Assume that W is compact and $S_m \to S_0$ uniformly on W. In addition, suppose that*

(1) S_0 satisfies (P1) and (P2) of Theorem 1.3.2 with a generalized distance function p for S_0;
(2) There exist $\eta_0 > 0$ and a positive integer N_0 such that for $m \geq N_0$ and $x \in X_0$, $\limsup_{n\to\infty} d(S_m^n(x), M_i) \geq \eta_0$, $1 \leq i \leq k$.

Then there exist $\eta > 0$ and a positive integer N such that $\liminf_{n\to\infty} p(S_m^n(x)) \geq \eta$ for $m \geq N$ and $x \in X_0$.

Proof. Assume, by contradiction, that there exists a sequence $\{x_k\}$ in X_0 and positive integers $m_k \to \infty$ satisfying $\liminf_{n\to\infty} p(S_{m_k}^n(x_k)) \to 0$ as $k \to \infty$. As in the proof of Theorem 1.3.4, we can assume that for some nonempty compact $L \subset W$, $\lim_{k\to\infty} d_H(\omega_{m_k}(x_k), L) = 0$. Then there exist $y_k \in \omega_{m_k}(x_k)$ such that $\lim_{k\to\infty} p(y_k) = 0$. Let $y \in L$ be the limit of some convergent subsequence of $\{y_k\}$. Since p is lower semicontinuous at y and $p(y) \geq 0$, it follows that $p(y) = 0$. By Lemma 1.2.4, L is internally chain transitive for S_0. Since $L \cap p^{-1}(0) \neq \emptyset$, Theorem 1.3.2, as applied to S_0, implies $L \subset M_i$ for some i. But $\omega_{m_k}(x_k) \to L$ gives a contradiction to assumption (2). ∎

In the applications of results in Subsections 1.3.1 and 1.3.2 to infinite-dimensional discrete- and continuous-time semiflows associated with evolutionary equations, we may get practical persistence by choosing suitable generalized distance functions instead of the distance function $d(x, \partial X_0)$. Below we give two examples for delay differential equations and reaction–diffusion systems, respectively.

Example 1.3.1. Let $r \geq 0$ and $C := C([-r, 0], \mathbb{R}^m)$. For a continuous map $u : [-r, \sigma) \to \mathbb{R}^m$ with $\sigma > 0$, and each $t \in [0, \sigma)$, we define $u_t \in C$ by $u_t(s) = u(t + s)$, $\forall s \in [-r, 0]$. Consider evolutionary systems of delayed differential equations

$$\begin{aligned} \frac{du(t)}{dt} &= f(u_t), \quad t \geq 0, \\ u_0 &= \phi \in C. \end{aligned} \tag{1.1}$$

Under appropriate assumptions on $f : C \to \mathbb{R}^m$, system (1.1) has a unique solution $u(t, \phi)$ on $[0, \infty)$ for each $\phi \in X := C([-r, 0], \mathbb{R}^m_+)$, and defines a continuous-time semiflow $\Phi(t)$ on X by $\Phi(t)\phi = u_t(\phi)$. Define

$$p(\phi) := \min_{1 \leq i \leq m} \{\phi_i(0)\}, \quad \forall \phi = (\phi_1, \ldots, \phi_m) \in X.$$

Thus, $p : X \to \mathbb{R}_+$ is continuous, and we may obtain the practical persistence by appealing to Theorem 1.3.2.

Example 1.3.2. Consider reaction–diffusion systems

$$\begin{aligned} &\frac{\partial u_i}{\partial t} = d_i \Delta u_i + f_i(x, u_1, \ldots, u_m) \quad \text{in } \Omega \times (0, \infty), \\ &B u_i = 0 \quad \text{on } \partial\Omega \times (0, \infty), \end{aligned} \tag{1.2}$$

where $d_i > 0$, Δ is the Laplacian operator, Ω is a bounded domain in $\mathbb{R}^n$ with smooth boundary, and $Bu = 0$ denotes either Robin type (case (R)) or Dirichlet boundary condition (case (D)). Let $X = C(\overline{\Omega}, \mathbb{R}^m_+)$ in case (R), and $X = C_0(\overline{\Omega}, \mathbb{R}^m_+)$ in case (D). Under appropriate assumptions on $f = (f_1, \ldots, f_m)$, system (1.2) has a unique solution $u(t, x, \phi)$ on $[0, \infty)$ satisfying $u(0, \cdot, \phi) = \phi$ for each $\phi \in X$, and defines a continuous-time semiflow $\Phi(t)$ on X by $\Phi(t)\phi = u(t, \cdot, \phi)$. Let $Z := C_0^1(\overline{\Omega}, \mathbb{R}^m)$, $Z^+ := C_0^1(\overline{\Omega}, \mathbb{R}^m_+)$, and fix an $e \in \operatorname{int}(Z^+)$. Define

$$p(\phi) := \min_{1 \leq i \leq m} \left\{ \min_{x \in \overline{\Omega}} \phi_i(x) \right\}, \quad \forall \phi = (\phi_1, \ldots, \phi_m) \in X$$

in case (R), and

$$p(\phi) := \sup\{\beta \in \mathbb{R}_+ : \phi_i(x) \geq \beta e_i(x),\ \forall x \in \overline{\Omega}, 1 \leq i \leq m\},$$
$$\forall \phi = (\phi_1, \ldots, \phi_m) \in X$$

in case (D), respectively. It is easy to see that the first p-function is continuous, and the second one is lower semicontinuous. Therefore, Theorem 1.3.2 may be used to obtain the practical persistence.

Remark 1.3.2. By using similar arguments, we can prove analogues of Theorems 1.2.1, 1.2.2, and 1.3.1–1.3.5 for continuous-time semiflows.

1.3.3 Persistence and Attractors

Let X_0 and ∂X_0 be given as in the beginning of Section 1.3. We assume that $f : X \to X$ is a continuous map with $f(X_0) \subset X_0$. The purpose of this subsection is to establish appropriate conditions under which a uniformly persistent system admits a global attractor in X_0.

A subset $B \subset X_0$ is said to be strongly bounded if B is bounded in (X, d) and $\inf_{x \in B} d(x, \partial X_0) > 0$. For convenience, we set $\rho(x) := d(x, \partial X_0)$, $\forall x \in X$. In order to make X_0 become a complete metric space, we define a new metric function d_0 on X_0 by

$$d_0(x, y) = \left| \frac{1}{\rho(x)} - \frac{1}{\rho(y)} \right| + d(x, y),\ \forall x, y \in X_0. \tag{1.3}$$

Lemma 1.3.2. (X_0, d_0) *is a complete metric space.*

Proof. It is easy to see that d_0 is a metric function. Let $\{x_n\}_{n \geq 0}$ be a Cauchy sequence in (X_0, d_0). Since $d(x, y) \leq d_0(x, y)$, $\forall x, y \in X_0$, we deduce that $\{x_n\}_{n \geq 0}$ is a Cauchy sequence in (X, d), and there exists $x \in M$, such that $d(x_n, x) \to 0$ as $n \to +\infty$. To prove that $d_0(x_n, x) \to 0$ as $n \to +\infty$, it is sufficient to show that $x \in X_0$. Given $\varepsilon > 0$, since $\{x_n\}_{n \geq 0}$ is a Cauchy sequence in (X_0, d_0), there exists $n_0 \geq 0$ such that $d_0(x_n, x_p) \leq \varepsilon$, $\forall n, p \geq n_0$. In particular, we have $d_0(x_n, x_{n_0}) \leq \varepsilon, \forall n \geq n_0$. Then

$$\left| \frac{1}{\rho(x_n)} - \frac{1}{\rho(x_{n_0})} \right| \leq \varepsilon, \forall n \geq n_0,$$

So there exists $r > 0$ such that $\inf_{n \geq 0} \rho(x_n) \geq r$. Since ρ is continuous and $d(x_n, x) \to 0$ as $n \to +\infty$, we deduce that $\rho(x) \geq r$, and hence $x \in X_0$. Thus, (X_0, d_0) is complete. ∎

We denote for each couple of subsets $A, B \subset X$,

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

and if $A, B \subset X_0$, we denote

$$\delta_0(B, A) = \sup_{x \in B} \inf_{y \in A} d_0(x, y).$$

Lemma 1.3.3. *The following two statements are valid:*

(1) Let $\{B_t\}_{t \in I}$ be a family of subsets of X_0, where I is a unbounded subset of $[0, +\infty)$. If $A \subset X_0$ is compact in (X, d) and $\lim_{t \to \infty} \delta(B_t, A) = 0$, then $\lim_{t \to \infty} \delta_0(B_t, A) = 0$.

(2) If f is asymptotically smooth, then f is asymptotically smooth in (X_0, d_0).

Proof. (1) We denote $k := \frac{1}{2} \inf_{x \in A} \rho(x) > 0$. Assume, by contradiction, that $\lim_{t \to +\infty} \sup \delta_0(B_t, A) > \varepsilon > 0$. Then we can find a sequence $\{t_p\}_{p \geq 0} \subset I$ such that $t_p \to +\infty$, $p \to +\infty$, and a sequence $\{x_{t_p}\}_{p \geq 0} \subset X_0$ such that $x_{t_p} \in B_{t_p}, d_0(x_{t_p}, A) \geq \varepsilon, \forall p \geq 0$. Since $d(x_{t_p}, A) \to 0,$ as $p \to +\infty$, without loss of generality we can assume that there exists $x \in A$ such that $d(x_{t_p}, x) \to 0,$ as $p \to +\infty$. Since ρ is continuous and $\rho(x) > k$, there exists $p_0 \geq 0$ such that $\rho(x_{t_p}) \geq k, \forall p \geq p_0$. Thus, we have

$$0 < \varepsilon \leq d_0(x_{t_p}, x) \leq k^{-2} \left| \rho(x_{t_p}) - \rho(x) \right| + d(x_{t_p}, x) \to 0 \text{ as } p \to +\infty,$$

a contradiction.

(2) It is easy to see that $f : (X_0, d_0) \to (X_0, d_0)$ is continuous. Let B be a bounded subset in (X_0, d_0) such that $f(B) \subset B$. Since f is asymptotically smooth, there exists a compact subset $C \subset X$ which attracts B for f. So $C_0 = C \cap \overline{B} \subset X_0$ is compact and attracts B for f. It easily follows that C_0 is also compact in (X_0, d_0). Since C_0 attracts B for f, the statement (1) implies that C_0 attracts B for $f : (X_0, d_0) \to (X_0, d_0)$. ∎

Theorem 1.3.6. *Assume that f is asymptotically smooth and uniformly persistent with respect to $(X_0, \partial X_0)$, and that f has a global attractor A. Then $f : (X_0, d) \to (X_0, d)$ has a global attractor A_0. Moreover, if a subset B of X_0 has the property that $\gamma^+(f^k(B))$ is strongly bounded for some $k \geq 0$, then A_0 attracts B for f.*

Proof. We consider the continuous map $f : (X_0, d_0) \to (X_0, d_0)$. Since f is point dissipative and uniformly persistent, f is point dissipative in (X_0, d_0). Moreover, Lemma 1.3.3 implies that f is asymptotically smooth in (X_0, d_0). Let C be a compact subset in (X_0, d_0), and $\{x_p\}$ a bounded sequence in $\gamma^+(C)$ in (X_0, d_0). Then $x_p = T^{m_p}(z_p)$, $z_p \in C$, $\forall p \geq 1$, and the sequence $\{x_p\}$ is strongly bounded in (X, d). Since C is also compact in (X, d), we have $\lim_{m \to \infty} \delta(f^m(C), A) = 0$. Thus, $\{x_p\}$ has a convergent subsequence $x_{p_k} \to x$ in (X, d) as $k \to \infty$. By the continuity of ρ and the strong boundedness of $\{x_p\}$, it follows that $\rho(x) > 0$, i.e., $x \in X_0$, and hence, $x_{p_k} \to x$ in (X_0, d_0) as $k \to \infty$. Thus, Lemma 1.1.5 implies that positive orbits of compact sets are bounded for $f : (X_0, d_0) \to (X_0, d_0)$. Then the conclusion for $f : (X_0, d) \to (X_0, d)$ follows from Theorem 1.1.2, as applied to $f : (X_0, d_0) \to (X_0, d_0)$. ∎

Theorem 1.3.7. *Assume that f is point dissipative on X and uniformly persistent with respect to $(X_0, \partial X_0)$, and that one of the following conditions holds:*

(a) There exists some integer $n_0 \geq 1$ such that f^{n_0} is compact on X, and f^{n_0} maps strongly bounded subset of X_0 onto strongly bounded sets in X_0, or
(b) f is asymptotically smooth on X, and for every strongly bounded subset $B \subset X_0$, there exists $k = k(B) \geq 0$ such that $\gamma^+\left(f^k(B)\right)$ is strongly bounded in X_0.

Then $f : (X_0, d) \to (X_0, d)$ has a global attractor A_0, and A_0 attracts every strongly bounded subset in X_0 for f.

Proof. Clearly, $f : (X_0, d_0) \to (X_0, d_0)$ is point dissipative. It is easy to see that condition (a) implies that $f^{n_0} : (X_0, d_0) \to (X_0, d_0)$ is compact, and that condition (b) implies that the condition (b) of Theorem 1.1.3 holds for $f : (X_0, d_0) \to (X_0, d_0)$. By Theorem 1.1.3, there is a strong global attractor A_0 for $f : (X_0, d_0) \to (X_0, d_0)$. Consequently, A_0 is a global attractor for $f : (X_0, d) \to (X_0, d)$, and A_0 attracts every strongly bounded subset in X_0 for f. ∎

Remark 1.3.3. A result similar to Theorem 1.3.7 was already presented for discrete- and continuous-time dynamical systems in [430] and [146], respectively. The only difference, compared with the earlier results, is that we add a strong boundedness assumption for case (a). In general, this assumption is necessary for the existence of a strong global attractor in X_0 for f, which can be seen from the counter example below.

Example 1.3.3. Let $C([0,1], \mathbb{R})$ be the Banach space with the norm $\|\phi\| = \sup_{a \in [0,1]} |\phi(a)|$, and $X := C([0,1], \mathbb{R}_+)$ be endowed with the metric $d(\phi, \psi) = \|\phi - \psi\|$. Consider the map $f : X \to X$ defined by

$$f(\phi) = \delta \frac{\mathcal{F}_\beta(\phi)}{1 + \mathcal{F}_\beta(\phi)} 1_{[0,1]}, \ \forall \phi \in X,$$

where $1_{[0,1]}(a) = 1, \forall a \in [0,1]$, and $\mathcal{F}_\beta(\phi) = \int_0^1 \beta(a)\phi(a)da, \forall \phi \in X$. We assume that

$$\delta > 1, \beta \in C\left([0,1], \mathbb{R}\right), \int_0^1 \beta(a)da = 1, \beta(a) > 0, \forall a \in [0,1), \textit{and } \beta(1) = 0.$$

It is easy to see that the map f is continuous, and maps bounded sets into compact sets of X. Note that $f(X) \subset [0,\delta]\, 1_{[0,1]} = \left\{\alpha 1_{[0,1]} : \alpha \in [0,\delta]\right\}$ is bounded. Thus, f is compact and point dissipative, and has a strong global attractor in X. Set $\partial X_0 = \{0\}$ and $X_0 = X \setminus \{0\}$. Clearly, $\rho(\phi) = \|\phi\|$, $f(X_0) \subset X_0$, $f(\partial X_0) \subset \partial X_0$, and the fixed points of f are 0 and $\overline{u} = (\delta - 1)\, 1_{[0,1]}$. It then easily follows that for each $\phi \in X_0$, $f^m(\phi) \to \overline{u}$, as $m \to +\infty$. So f is uniformly persistent with respect to $(X_0, \partial X_0)$. Let $\overline{\alpha} = (\delta - 1)$ and $B := \{\phi \in X : \|\phi\| = \overline{\alpha}\}$. Since $\beta(1) = 0$, we have $\mathcal{F}_\beta(B) = (0, \overline{\alpha}]$. Moreover, $f(B) = \left\{\alpha 1_{[0,1]} : \alpha \in (0, \overline{\alpha}]\right\}$, and $f^n(B) = f(B)$, $\forall n \geq 1$. Thus, there exists no compact subset in X_0 that attracts B for f. In particular, there is no strong global attractor for $f : (X_0, d_0) \to (X_0, d_0)$, where d_0 is defined as in (1.3).

Remark 1.3.4. By similar arguments we can prove the analogs of Theorems 1.3.6 and 1.3.7 for a continuous-time semiflow $\Phi(t)$ on X with $\Phi(t)(X_0) \subset X_0$ for all $t \geq 0$.

1.3.4 Coexistence States

In this subsection we always assume that X is a closed subset of a Banach space E, and that X_0 is a convex and relatively open subset of X. Then $\partial X_0 := X \setminus X_0$ is relatively closed in X. Let d be the distance induced by the norm $\|\cdot\|$ in E, and set $\underline{d}(A, B) := \inf_{x \in A} d(x, B)$ for $A, B \subset E$. Recall that a subset B of X_0 is said to be strongly bounded in X_0 if B is bounded and $\underline{d}(B, \partial X_0) > 0$.

Given a set $A \subset E$, let $co(A)$ be the convex hull of A and $\overline{co}(A)$ the closed convex hull of A, respectively. To prove the existence of coexistence states for uniformly persistent maps, we need the following two lemmas.

Lemma 1.3.4. *If A is a compact subset of X_0, then $\overline{co}(A) \subset X_0$ and $\underline{d}(\overline{co}(A), \partial X_0) > 0$.*

Proof. Since $A \subset X_0$ is compact and ∂X_0 is closed, we have $\underline{d}(A, \partial X_0) > 0$. For any $x \in X$ and $\delta > 0$, set $B(x, \delta) = \{y \in X : \|y - x\| < \delta\}$ and $\overline{B}(x, \delta) = \{y \in X : \|y - x\| \leq \delta\}$. Let $\delta_0 = \frac{1}{2}\underline{d}(A, \partial X_0) > 0$. Then for every $x \in A$, $\overline{B}(x, \delta_0) \subset X_0$ and $A \subset \cup_{x \in A} B(x, \delta_0)$. Again by the compactness of A, there exist finitely many $x_1, x_2, \ldots, x_k \in A$ such that $A \subset \cup_{i=1}^k B(x_i, \delta_0)$. Let $A_i = A \cap \overline{B}(x_i, \delta_0), (i = 1, 2, \ldots, k)$. Then $A = \cup_{i=1}^k A_i$. Clearly, A_i is compact and $A_i \subset \overline{B}(x_i, \delta_0) \subset X_0$, and hence $\overline{co}(A_i) \subset \overline{B}(x_i, \delta_0) \subset X_0$ $(i = 1, 2, \ldots, k)$. Therefore, since X_0 is convex, $co(\cup_{i=1}^k \overline{co}(A_i)) \subset X_0$. By [199, Theorem 2.1 (v)] and finite induction, it follows that for any finitely many nonempty subsets C_i of Banach space E, $1 \leq i \leq n$,

$$co(\cup_{i=1}^n C_i) = \left\{ \sum_{i=1}^n \alpha_i x_i : \alpha_i \geq 0, \sum_{i=1}^n \alpha_i = 1, x_i \in co(C_i), \forall 1 \leq i \leq n \right\}.$$

Since $co(\overline{co}(A_i)) = \overline{co}(A_i)$, $1 \leq i \leq k$, we get

$$\begin{aligned} co(\cup_{i=1}^k \overline{co}(A_i)) &= \left\{ \sum_{i=1}^k \alpha_i x_i : \alpha_i \geq 0, \sum_{i=1}^k \alpha_i = 1, x_i \in \overline{co}(A_i), \forall 1 \leq i \leq k \right\} \\ &= F(\Lambda_n \times \overline{co}(A_1) \times \cdots \times \overline{co}(A_k)), \end{aligned}$$

where

$$F(\alpha, x) = \sum_{i=1}^k \alpha_i x_i, \quad \forall \alpha = (\alpha_1, \ldots, \alpha_k) \in \mathbb{R}^k, \ x = (x_1, \ldots, x_k) \in E^k,$$

and

$$\Lambda_k = \left\{ (\alpha_1, \ldots, \alpha_k) \in \mathbb{R}^k : \alpha_i \geq 0, \, 1 \leq i \leq k \, \text{and} \, \sum_{i=1}^{k} \alpha_i = 1 \right\}.$$

Since the closed hull of any precompact subset of given Banach space is compact (see, e.g., [425, Proposition 11.3 (10)]), $\overline{co}(A)$ and $\overline{co}(A_i)$, $1 \leq i \leq k$, are all compact. By the continuity of $F : \mathbb{R}^k \times E^k \to E$ and the compactness of $\Lambda_k \times \overline{co}(A_1) \times \cdots \times \overline{co}(A_k)$ in $R^k \times E^k$, it follows that $co(\cup_{i=1}^k \overline{co}(A_i))$ is compact and hence closed. Consequently, we have

$$\overline{co}(A) = \overline{co}(\cup_{i=1}^k A_i) \subset \overline{co}(\cup_{i=1}^k \overline{co}(A_i)) = co(\cup_{i=1}^k \overline{co}(A_i)) \subset X_0.$$

By the compactness of $\overline{co}(A)$ and closedness of ∂X_0, it then follows that $\underline{d}(\overline{co}(A), \partial X_0) > 0$. ∎

Lemma 1.3.5. *If A is a convex and compact subset of X_0, then for any $\epsilon > 0$, there exists an open and convex set $N_\epsilon \subset X_0$ such that $A \subset N_\epsilon \subset N(A, \epsilon)$, where $N(A, \epsilon) = \{x \in E : d(x, A) < \epsilon\}$ is the ϵ-neighborhood of A.*

Proof. Since $A \subset X_0$ is compact, $\underline{d}(A, \partial X_0) > 0$. For any $\epsilon > 0$, let $\delta = \min\left(\epsilon, \frac{1}{2}\underline{d}(A, \partial X_0)\right)$. As in the proof of Lemma 1.3.4, there exist $x_1, x_2, \ldots, x_k \in A$ such that $A \subset \cup_{i=1}^k B(x_i, \delta) \subset X_0$. Therefore, since X_0 is convex, $A \subset co(\cup_{i=1}^k B(x_i, \delta)) \subset X_0$. Since the convex hull of any open subset of given linear topological space is open, $N_\epsilon = co(\cup_{i=1}^k B(x_i, \delta))$ is open in X. Since each $B(x_i, \delta)$ is convex, as in the proof of Lemma 1.3.4,

$$N_\epsilon = \left\{ \sum_{i=1}^{k} \alpha_i y_i : \alpha_i \geq 0, \, \sum_{i=1}^{k} \alpha_i = 1 \, \text{and} \, y_i \in B(x_i, \delta), \, 1 \leq i \leq k \right\}.$$

Thus, for any $x \in N_\epsilon$, we have $x = \sum_{i=1}^k \alpha_i y_i$ for some $y_i \in B(x_i, \delta)$ and $\alpha_i \geq 0 \, (i = 1, 2, \ldots, k)$ with $\sum_{i=1}^k \alpha_i = 1$. Then

$$\left\| x - \sum_{i=1}^{k} \alpha_i x_i \right\| = \left\| \sum_{i=1}^{k} \alpha_i (y_i - x_i) \right\| \leq \sum_{i=1}^{k} \alpha_i \|y_i - x_i\| < \sum_{i=1}^{k} \alpha_i \delta = \delta \leq \epsilon.$$

Since A is convex, we have $\sum_{i=1}^k \alpha_i x_i \in A$, and hence $d(x, A) < \epsilon$. Thus, $N_\epsilon \subset N(A, \epsilon)$. ∎

We also need the following Hale and Lopes fixed point theorem in a Banach space, which is a consequence of [141, Lemmas 2.6.5 and 2.6.6] or [143, Theorems 5 and 6].

Lemma 1.3.6. (Hale–Lopes fixed point theorem) *Suppose $K \subset B \subset S$ are convex subsets of a Banach space E with K compact, S closed and bounded, and B open in S. If $f : S \to E$ is α-condensing, $\gamma^+(B) \subset S$, and K attracts compact sets of B, then f has a fixed point in B.*

Now we turn to the discrete semidynamical system $\{f^n\}_{n=1}^{\infty}$ defined by a continuous map $f : X \to X$ with $f(X_0) \subset X_0$. A point $x_0 \in X$ is called a coexistence state of $\{f^n\}_{n=1}^{\infty}$ if x_0 is a fixed point of f in X_0, i.e., $x_0 \in X_0$ and $f(x_0) = x_0$. We have the following result on the existence of coexistence states.

Theorem 1.3.8. *Assume that f is α-condensing. If $f : X_0 \to X_0$ has a global attractor A_0, then f has a fixed point $x_0 \in A_0$.*

Proof. Let $K = \overline{co}(A_0)$. Since $A_0 \subset X_0$ is compact, K is compact. By Lemma 1.3.4, $K \subset X_0$ and $\underline{d}(K, \partial X_0) > 0$. Since $f : X_0 \to X_0$ has a global attractor A_0, there exists an $\epsilon_0 > 0$ such that $N(K, \epsilon_0) \subset X_0$ is attracted by A_0. By Lemma 1.3.5, there is an open and convex neighborhood B of K such that $B \subset N(K, \epsilon_0)$. Then K attracts B and $\gamma^+(B)$ is bounded in X_0. Since X_0 is convex and X is closed in the Banach space E, $S = \overline{co}(\gamma^+(B)) \subset \overline{X_0} \subset X$, and S is bounded in X. Therefore, $K \subset B \subset S$ satisfy all conditions of Lemma 1.3.6. It then follows that f has a fixed point x_0 in $B \subset X_0$, and clearly, $x_0 \in A_0$. ∎

Remark 1.3.5. In the case that $f : X \to X$ is compact, there is an alternative proof for the existence of the coexistence state. Indeed, by Lemma 1.3.4, there is an open and convex neighborhood U of K such that $U \subset N(K, \epsilon_0/2) \cap X_0$. Then $\overline{U} \subset N(K, \epsilon_0) \cap X \subset X_0$. Since A_0 attracts $N(K, \epsilon_0)$, there is an $n_0 = n_0(\overline{U}) > 0$ such that for any $n \geq n_0$, $f^n(\overline{U}) \subset U$. By an asymptotic generalized Schauder fixed point theorem ([425, Theorem 17.B.]), f has a fixed point x_0 in U.

To generalize Theorem 1.3.8 to another class of maps, we need the following fixed point theorem, which is a combination of Theorems 3 and 5 in [143] (see also [141, Lemma 2.6.5]).

Lemma 1.3.7. *Assume that $K \subset B \subset S$ are convex subsets of a Banach space E with K compact, S closed and bounded, and B open in S. If $f : S \to E$ is continuous, $f^n(B) \subset S, \forall n \geq 0$, and K attracts compact subsets of B, then there exists a closed bounded and convex subset $C \subset S$ such that $C = \overline{co}\left(\cup_{j \geq 1} f^j\left(B \cap C\right)\right)$. Moreover, if C is compact, then f has a fixed point in B.*

We should point out that in the above fixed point theorem the claim that f has a fixed point in B follows from the proof of [141, Lemma 2.6.5], where the Horn's fixed point theorem [169] was used.

Definition 1.3.4. *Let X be a closed and convex subset of a Banach space E, and $f : X \to X$ a continuous map. Define $\widehat{f}(B) = \overline{co}\,(f(B))$ for each $B \subset X$. f is said to be convex α-contracting if $\lim_{n\to\infty} \alpha(\widehat{f}^n(B)) = 0$ for any bounded subset $B \subset X$.*

Theorem 1.3.9. *Assume that f is convex α-contracting. If $f : X_0 \to X_0$ has a global attractor A_0, then f has a fixed point $x_0 \in A_0$.*

Proof. Since A_0 is a global attractor for $f : X_0 \to X_0$, the proof of Theorem 1.3.8 implies that there are three convex subsets, $K \subset B \subset S \subset X$, such that $K \subset X_0$, $B \subset X_0$, and the assumptions of Lemma 1.3.7 hold for f. Let C be defined in Lemma 1.3.7. Define $\widehat{C} := \cup_{j\geq 1} f^j (B \cap C)$. Then we have

$$\widehat{C} = f(B \cap C) \cup f\left(\widehat{C}\right) \text{ and } C = \overline{co}\left(\widehat{C}\right),$$

and hence, $\widehat{C} \subset f(C)$. Thus, we further obtain

$$C \subset \widehat{f}(C) \subset \widehat{f}^2(C) \subset \ldots \subset \widehat{f}^n(C), \ \forall n \geq 0.$$

Since f is convex α-contracting, it follows that $\alpha(C) \leq \alpha(\widehat{f}^n(C)) \to 0$, as $n \to \infty$. Then $\alpha(C) = 0$, and hence, C is compact. Now Lemma 1.3.7 implies the existence of a fixed point of f in A_0. ∎

Combining Theorems 1.1.2, 1.1.3, 1.3.6, 1.3.8, and 1.3.9 together, we have the following result on the existence of coexistence steady states for uniformly persistent systems, which is a generalization of [430, Theorem 2.3].

Theorem 1.3.10. *Assume that*

(1) f is point dissipative and uniformly persistent with respect to $(X_0, \partial X_0)$;
(2) One of the following two conditions holds:
   (2a) f^{n_0} is compact for some integer $n_0 \geq 1$, or
   (2b) Positive orbits of compact subsets of X are bounded.
(3) Either f is α-condensing or f is convex α-contracting.

Then $f : X_0 \to X_0$ admits a global attractor A_0, and f has a fixed point in A_0.

For an autonomous semiflow $\Phi(t) : X \to X$, $t \geq 0$, we have the following result.

Theorem 1.3.11. *Let $\Phi(t)$ be a continuous-time semiflow on X with $\Phi(t)(X_0) \subset X_0$ for all $t \geq 0$. Assume that either $\Phi(t)$ is α-condensing for each $t > 0$, or $\Phi(t)$ is convex α-contracting for each $t > 0$, and that $\Phi(t) : X_0 \to X_0$ has a global attractor A_0. Then $\Phi(t)$ has an equilibrium $x_0 \in A_0$, i.e., $\Phi(t)x_0 = x_0$, $\forall t \geq 0$.*

Proof. Let $\{\omega_m\}_{m=1}^{\infty}$ be any given sequence with $\omega_m > 0$ and $\lim_{m\to\infty} \omega_m = 0$. By Theorems 1.3.8 and 1.3.9, $\Phi(\omega_m)$ has a fixed point $x_m \in X_0$, $\forall m \geq 1$. By the global attractivity of A_0 in X_0, for each fixed x_m, $\lim_{t\to\infty} d(\Phi(t)x_m, A_0) = 0$, and hence, $0 = \lim_{n\to\infty} d(\Phi(n\omega_m)x_m, A_0) = d(x_m, A_0)$. Then the compactness of A_0 implies that $x_m \in A_0$, $\forall m \geq 1$. Again by the compactness of A_0, $\{x_m\}_{m=1}^{\infty}$ has a convergent subsequence to $x_0 \in A_0$. We further show that x_0 is an equilibrium point of $\Phi(t)$. Changing the notation if necessary, we may assume that $\lim_{m\to\infty} x_m = x_0$. Let $k_m(t)$ be the integer defined by

$k_m(t)\omega_m \le t < (k_m(t)+1)\omega_m$. Clearly, $\lim_{m\to\infty} k_m(t)\omega_m = t$, $\forall t \ge 0$, and $\Phi(k_m(t)\omega_m)x_m = x_m$, $\forall m \ge 1$. Letting $m \to \infty$ in the inequality

$$\begin{aligned}|\Phi(t)x_0 - x_0| \le &|\Phi(t)x_0 - \Phi(k_m(t)\omega_m)x_0| + \\ &|\Phi(k_m(t)\omega_m)x_0 - \Phi(k_m(t)\omega_m)x_m| + |x_m - x_0|,\end{aligned}$$

we then get $\Phi(t)x_0 = x_0$, $\forall t \ge 0$. ∎

1.4 Persistence Under Perturbations

Given a uniformly persistent biological system, naturally one may ask whether its nearby systems are also uniformly persistent. In this section we will discuss this problem, from the perturbation point of view, for three special cases: discrete-time semiflows with a globally stable steady state, discrete-time semiflows with parameters, and Kolmogorov-type ordinary differential systems.

1.4.1 Perturbation of a Globally Stable Steady State

Let $f : U \times \Lambda \to U$ be continuous, where $U \subset X$, X is a Banach space, and Λ is a metric space with metric ρ. We sometimes write $f_\lambda = f(\cdot, \lambda)$ and use the notation $B_X(x,s)$ $(B_\Lambda(\lambda,s))$ for the open ball of radius s about the point $x \in X$ $(\lambda \in \Lambda)$. For a linear operator A on X, we write $r(A)$ for its spectral radius.

Theorem 1.4.1. *Let $(x_0,\lambda_0) \in U \times \Lambda$, $B_X(x_0,\delta) \subset U$ for some $\delta > 0$ and assume that $D_x f(x,\lambda)$ exists and is continuous in $B_X(x_0,\delta) \times \Lambda$. Suppose that $f(x_0,\lambda_0) = x_0$, $r(D_x f(x_0,\lambda_0)) < 1$, and $f_{\lambda_0}^n(x) \to x_0$ for every $x \in U$. In addition, suppose that*

(1) For each $\lambda \in \Lambda$, there is a set $B_\lambda \subset U$ such that for each $x \in U$, there exists an integer $N = N(x,\lambda)$ such that $f_\lambda^N(x) \in B_\lambda$;
(2) $C := \overline{\cup_{\lambda\in\Lambda} f_\lambda(B_\lambda)}$ is compact in U.

Then there exist $\epsilon_0 > 0$ and a continuous map $\hat{x} : B_\Lambda(\lambda_0,\epsilon_0) \to U$ such that $\hat{x}(\lambda_0) = x_0$, $f(\hat{x}(\lambda),\lambda) = \hat{x}(\lambda)$, and $f_\lambda^n x \to \hat{x}(\lambda)$, $\forall x \in U$, $\lambda \in B_\Lambda(\lambda_0,\epsilon_0)$.

Proof. We may suppose that the norm on X is such that $\|D_x f(x_0,\lambda_0)\| < \rho < 1$ (see [425, page 795]). Since $D_x f(x,\lambda)$ is continuous, there exist $\epsilon_1, \eta > 0$ such that $\|D_x f(x,\lambda)\| < \rho$ for $x \in \overline{B_X(x_0,\eta)}$ and $\lambda \in B_\Lambda(\lambda_0,\epsilon_1)$. Choose $\epsilon_0 < \epsilon_1$ such that $\|f(x_0,\lambda_0) - f(x_0,\lambda)\| < (1-\rho)\eta$ for $\lambda \in B_\Lambda(\lambda_0,\epsilon_0)$. Then, for $x, x' \in \overline{B_X(x_0,\eta)}$ and $\lambda \in B_\Lambda(\lambda_0,\epsilon_0)$, we have

$$\|f(x,\lambda) - f(x',\lambda)\| \le \int_0^1 \|D_x f(sx + (1-s)x',\lambda)\| ds \cdot \|x - x'\| \le \rho\|x - x'\|$$

and

$$\begin{aligned}\|f(x,\lambda)-x_0\| &\le \|f(x,\lambda)-f(x_0,\lambda)\|+\|f(x_0,\lambda)-f(x_0,\lambda_0)\| \\ &< \rho\|x-x_0\|+(1-\rho)\eta \le \eta.\end{aligned}$$

Thus, f_λ is a uniform contraction self-mapping of $\overline{B_X(x_0,\eta)}$ for $\lambda \in B_\Lambda(\lambda_0,\epsilon_0)$. Then the uniform contraction mapping theorem implies the existence of the continuous map $\hat{x} : B_\Lambda(\lambda_0,\epsilon_0) \to \overline{B_X(x_0,\eta)}$ such that $\hat{x}(\lambda_0) = x_0$ and $f(\hat{x}(\lambda),\lambda) = \hat{x}(\lambda)$. Furthermore, $f_\lambda^m x \to \hat{x}(\lambda)$ for every $x \in \overline{B_X(x_0,\eta)}$ and $\lambda \in B_\Lambda(\lambda_0,\epsilon_0)$.

By choosing ϵ_0 smaller, if necessary, we claim that for $\lambda \in B_\Lambda(\lambda_0,\epsilon_0)$ and $x \in C$, $f_\lambda^m x \in B(x_0,\eta)$ for some m. If not, there exist $\lambda_n \in \Lambda, \lambda_n \to \lambda_0$, and $x_n \in C$ such that $\|f_{\lambda_n}^m x_n - x_0\| \ge \eta$ for all $m \ge 0, n \ge 1$. Since C is compact, we may assume that $x_n \to x \in C$. But x_0 is globally attracting for f_{λ_0}, so there is a p such that $\|f_{\lambda_0}^p x - x_0\| < \frac{\eta}{2}$. Hence, by continuity of the function $F(x,\lambda) := f_\lambda^p x$, $F(x_n,\lambda_n) \to F(x,\lambda_0) = f_{\lambda_0}^p x$, and therefore $\|f_{\lambda_n}^p x_n - x_0\| < \eta$ for all large n, a contradiction. The claim is established.

Now, given $x \in U$ and $\lambda \in B_\Lambda(\lambda_0,\epsilon_0)$, there exists N such that $f_\lambda^N x \in B_\lambda$, so $f_\lambda^{N+1} x \in C$. By the previous paragraph, $f_\lambda^m x \in B_X(x_0,\eta)$ for some, and hence all large, m. Obviously, $f_\lambda^m x \to \hat{x}(\lambda)$. ∎

Remark 1.4.1. The assumption that x_0 is an interior point of U is unnecessarily restrictive. An examination of the proof indicates that it is sufficient to assume that f can be extended to $B_X(x_0,\delta) \times \Lambda$ for some $\delta > 0$ and has a continuous derivative in that set and $B_X(x_0,\delta) \cap U$ is convex. Alternatively, one-sided derivatives with respect to some cone or wedge in X may also be used (see, e.g., [12]).

1.4.2 Persistence Uniform in Parameters

Let Λ be a metric space with metric ρ. For each $\lambda \in \Lambda$, let $S_\lambda : X \to X$ be a continuous map such that $S_\lambda(x)$ is continuous in (λ, x). Assume that every positive orbit for S_λ has compact closure in X, and that the set $\bigcup_{\lambda\in\Lambda, x\in X} \omega_\lambda(x)$ has compact closure, where $\omega_\lambda(x)$ denotes the omega limit of x for discrete semiflow $\{S_\lambda^n\}$.

Theorem 1.4.2. (Uniform persistence uniform in parameters) *Assume that $S_\lambda(X_0) \subset X_0$, $\forall \lambda \in \Lambda$. Let $\lambda_0 \in \Lambda$ be fixed, and assume further that*

(B1) $S_{\lambda_0} : X \to X$ has a global attractor, and either the maximal compact invariant set A_∂ of f in ∂X_0 admits a Morse decomposition $\{M_1, \ldots, M_k\}$, or there exists an acyclic covering $\{M_1, \ldots, M_k\}$ of $\Omega(M_\partial)$ for f in ∂X_0;

(B2) There exists $\delta_0 > 0$ such that for any $\lambda \in \Lambda$ with $\rho(\lambda,\lambda_0) < \delta_0$ and any $x \in X_0$, $\limsup_{n\to\infty} d(S_\lambda^n(x), M_i) \ge \delta_0$, $1 \le i \le k$.

Then there exists $\delta > 0$ such that $\liminf_{n\to\infty} d(S_\lambda^n x, \partial X_0) \ge \delta$ for any $\lambda \in \Lambda$ with $\rho(\lambda,\lambda_0) < \delta$ and any $x \in X_0$.

Proof. Clearly, (B1) and (B2) imply that (A1) holds for $S_0 := S_{\lambda_0} : X \to X$. If the conclusion were false, we could find sequences $x_k \in X_0$ and λ_k with $\lambda_k \to \lambda_0$ such that $\liminf_{n\to\infty} d(S_k^n(x_k), \partial X_0) \to 0$ as $k \to \infty$, where $S_k := S_{\lambda_k} \to S_0$ uniformly on W. But this contradicts Theorem 1.3.4. ∎

Theorem 1.4.3. (Uniform persistence uniform in parameters) *Let $\lambda_0 \in \Lambda$ be fixed, and assume that*

(1) S_{λ_0} satisfies (P1) and (P2) of Theorem 1.3.2 with generalized distance function p for S_{λ_0};
(2) There exists $\delta_0 > 0$ such that for any $\lambda \in \Lambda$ with $\rho(\lambda, \lambda_0) < \delta_0$ and any $x \in X_0$, $\limsup_{n\to\infty} d(S_\lambda^n(x), M_i) \geq \delta_0$, $1 \leq i \leq k$.

Then there exists $\delta > 0$ such that $\liminf_{n\to\infty} p(S_\lambda^n(x)) \geq \delta$ for any $\lambda \in \Lambda$ with $\rho(\lambda, \lambda_0) < \delta$ and any $x \in X_0$.

Proof. Clearly, assumption (1) of Theorem 1.3.5 holds for $S_0 := S_{\lambda_0}$. If the conclusion were false, we could find sequences $x_k \in X_0$ and λ_k with $\lambda_k \to \lambda_0$ such that $\liminf_{n\to\infty} p(S_k^n(x_k)) \to 0$ as $k \to \infty$, where $S_k := S_{\lambda_k} \to S_0$ uniformly on W. But this contradicts Theorem 1.3.5. ∎

Remark 1.4.2. By similar arguments, the analogues of Theorems 1.4.2 and 1.4.3 hold for continuous-time semiflows.

1.4.3 Robust Permanence

As an application of Theorem 1.4.2, consider the Kolmogorov-type ordinary differential equation

$$x_i' = x_i f_i(x) \equiv F_i(x) \tag{1.4}$$

on $P \equiv \mathbb{R}_+^n$ where f is a C^1 vector field on P. For $M > 0$ let $P_M = \{x \in P : x_i \leq M, 1 \leq i \leq n\}$ and $P_M^0 = \{x \in P_M : x_i > 0, 1 \leq i \leq n\}$. Denote by ϕ_t^f the semiflow generated by (1.4). Let $C_L = C_{Lip}(P_M, \mathbb{R}^n)$ be the space of Lipschitz vector fields on P_M. Below, $\|x\|$ denotes a norm of the vector $x \in \mathbb{R}^n$.

A compact invariant K of ϕ_t^f is said to be unsaturated if

$$\min_{\mu \in \mathcal{M}(f,K)} \max_{1\leq i\leq n} \int f_i \, d\mu > 0,$$

where $\mathcal{M}(f, K)$ is the set of ϕ_t^f-invariant Borel probability measures with support contained in K. It is known that an equilibrium e of ϕ_t^f is unsaturated if and only if $f_i(e) > 0$ for some $1 \leq i \leq n$, and a periodic orbit $\gamma = \{u(t) : t \in [0, T]\}$ of ϕ_t^f, with minimal period $T > 0$, is unsaturated if and only if $\int_0^T f_i(u(s))ds > 0$ for some $1 \leq i \leq n$ (see [302]).

Theorem 1.4.4. (Robust permanence) *Assume that*

(D1) There exists $M > 0$ such that $x \in P_M$ and $x_i = M$ implies $f_i(x) \le 0$;
(D2) The maximal compact invariant set of ϕ_t^f on $P_M \setminus P_M^0$ admits a Morse decomposition $\{M_1, \dots, M_k\}$ such that each M_i is unsaturated for ϕ_t^f.

Then there exist $\epsilon, \eta > 0$ such that for $g \in C_L$ satisfying (D1) and

$$\sup_{x \in P_M} \|f(x) - g(x)\| < \epsilon \tag{1.5}$$

and for $x \in P_M^0$, it follows that

$$\eta \le y_i \le M,\ 1 \le i \le n,\ \ \forall y \in \omega_g(x). \tag{1.6}$$

Here $\omega_g(x)$ denotes the omega limit set of x for the system $x_i' = x_i g_i(x)$.

Proof. Let $\Lambda = \{g \in C_L : (D1)\,\text{holds for}\ g\}$ (endowed with the uniform metric), and consider the family of semiflows ϕ_t^g on $X = P_M$ with $X_0 = P_M^0$. Here ϕ_t^g denotes the semiflow generated by $x_i' = x_i g_i(x) \equiv G_i(x)$. The continuity of the map $(g, x, t) \to \phi_t^g(x)$ is well known. The closure of $\bigcup_{g \in \Lambda, x \in P_M} \omega_g(x)$ is compact in P_M. Clearly, $\phi_t^f : X \to X$ has a global attractor. By (the continuous-time version of) Theorem 1.4.2, it suffices to prove that condition (B2) holds, which is implied by the following lemma. ∎

Lemma 1.4.1. *Let $\lambda_0 = f \in \Lambda$. If $K \subset P_M$ is an unsaturated compact invariant set for ϕ_t^f, then condition (B2) holds for K.*

Proof. Assume, by contradiction, that (B2) is not true for K. We will use a similar idea as in [302] to construct a ϕ_t^f-invariant Borel measure $\mu \in \mathcal{M}(f, K)$ such that μ is saturated for ϕ_t^f. It then follows that there exist two sequences $g^m \in \Lambda$ and $y^m \in X_0$ such that $\rho(g^m, f) := \sup_{x \in P_M} \|g^m(x) - f(x)\| < \frac{1}{m}$ and

$$\limsup_{t \to \infty} d(\phi_t^{g^m}(y^m), K) < \frac{1}{m},\ \forall m \ge 1, \tag{1.7}$$

and hence there is a sequence of s_m such that

$$d(\phi_t^{g^m}(y^m), K) < \frac{1}{m},\ \forall t \ge s_m, m \ge 1.$$

Let $x^m = \phi^{g^m}(s_m, y^m)$. Then $x^m \in X_0$, and the flow property of $\phi_t^{g^m}$ implies that

$$d(\phi_t^{g^m}(x^m), K) < \frac{1}{m},\ \forall t \ge 0,\ m \ge 1. \tag{1.8}$$

Let $f = (f_1, \dots, f_n)$. Note that

$$\ln\left(\frac{[\phi_t^{g^m}(x^m)]_i}{x_i^m}\right) = \int_0^t g_i^m(\phi_s^{g^m}(x^m))ds,\ \forall t \in \mathbb{R},\ 1 \le i \le n,\ m \ge 1. \tag{1.9}$$

By inequality (1.8), it then easily follows that

$$\limsup_{t\to\infty} \frac{1}{t} \int_0^t g_i^m(\phi_s^{g^m}(x^m))ds \le 0,\ 1 \le i \le n,\ m \ge 1. \tag{1.10}$$

Then we can choose a sequence t_m such that $t_m \ge m$ and

$$\frac{1}{t_m} \int_0^{t_m} g_i^m(\phi_s^{g^m}(x^m))ds < \frac{1}{m},\ 1 \le i \le n,\ m \ge 1. \tag{1.11}$$

Define a sequence of Borel probability measures μ_m on $\mathbb{R}_+^n$ by

$$\int h\, d\mu_m = \frac{1}{t_m} \int_0^{t_m} h(\phi_s^{g^m}(x^m))ds,\ m \ge 1, \tag{1.12}$$

for any continuous function $h \in C(\mathbb{R}_+^n, \mathbb{R})$. By inequality (1.8), it then follows that μ_m lies in the space $\mathcal{M}(V)$ of Borel probability measures with support in the compact set $V = \{x \in \mathbb{R}_+^n : d(x, K) \le 1\}$. By the weak* compactness of $\mathcal{M}(V)$, we can assume that μ_m converges in the weak* topology to some $\mu \in \mathcal{M}(V)$ as $m \to \infty$. We claim that μ is invariant under ϕ_t^f; i.e., $\mu(\phi_t^f(B)) = \mu(B)$ for any $t \in \mathbb{R}$ and any Borel set $B \subseteq \mathbb{R}_+^n$. It suffices to verify that $\int h \circ \phi_t^f\, d\mu = \int h\, d\mu$ for any $h \in C(\mathbb{R}_+^n, \mathbb{R})$ and $t \in \mathbb{R}$. For any fixed $t > 0$, since

$$\begin{aligned}
&\textstyle\int_0^{t_m} \left(h \circ \phi_t^{g^m}(\phi_s^{g^m}(x^m)) - h(\phi_s^{g^m}(x^m))\right) ds \\
&= \int_0^{t_m} h \circ \phi_{t+s}^{g^m}(x^m)ds - \int_0^{t_m} h(\phi_s^{g^m}(x^m))ds \\
&= \left(\int_0^{t_m - t} h \circ \phi_{t+s}^{g^m}(x^m)ds + \int_{t_m - t}^{t_m} h \circ \phi_{t+s}^{g^m}(x^m)ds\right) \\
&\quad - \left(\int_0^t h(\phi_s^{g^m}(x^m))ds + \int_t^{t_m} h(\phi_s^{g^m}(x^m))ds\right) \\
&= \left(\int_0^{t_m - t} h \circ \phi_{t+s}^{g^m}(x^m)ds + \int_0^t h \circ \phi_{t_m+u}^{g^m}(x^m)du\right) \\
&\quad - \left(\int_0^t h(\phi_s^{g^m}(x^m))ds + \int_0^{t_m - t} h(\phi_{t+v}^{g^m}(x^m))dv\right) \\
&= \int_0^t \left(h\left(\phi_{t_m+s}^{g^m}(x^m)\right) - h(\phi_s^{g^m}(x^m))\right) ds,
\end{aligned}$$

we obtain

$$\begin{aligned}
\left|\int (h \circ \phi_t^f - h)d\mu\right| &= \lim_{m\to\infty} \left|\int (h \circ \phi_t^f - h)d\mu_m\right| \\
&= \lim_{m\to\infty} \left|\frac{1}{t_m}\int_0^{t_m} \left(h \circ \phi_t^f(\phi_s^{g^m}(x^m)) - h(\phi_s^{g^m}(x^m))\right) ds\right| \\
&\le \limsup_{m\to\infty} \frac{1}{t_m}\left(\left|\int_0^{t_m} \left(h \circ \phi_t^{g^m}(\phi_s^{g^m}(x^m)) - h(\phi_s^{g^m}(x^m))\right) ds\right|\right. \\
&\quad \left. + \left|\int_0^{t_m} \left(h \circ \phi_t^f(\phi_s^{g^m}(x^m)) - h \circ \phi_t^{g^m}(\phi_s^{g^m}(x^m))\right) ds\right|\right) \\
&= \limsup_{m\to\infty} \frac{1}{t_m}\left(\left|\int_0^{t} \left(h(\phi_{t_m+s}^{g^m}(x^m)) - h(\phi_s^{g^m}(x^m))\right) ds\right|\right. \\
&\quad \left. + \left|\int_0^{t_m} \left(h \circ \phi_t^f(\phi_s^{g^m}(x^m)) - h \circ \phi_t^{g^m}(\phi_s^{g^m}(x^m))\right) ds\right|\right).
\end{aligned}$$

Therefore, using inequality (1.8), the boundedness of $h(\cdot)$ on V, and uniform convergence of $g^m \to f$ (and hence of $\phi_t^{g^m} \to \phi_t^f$) on P_M, we have $\int (h \circ \phi_t^f - h)d\mu = 0$ for any $h \in C(\mathbb{R}_+^n, \mathbb{R})$ and $t > 0$. For any $t > 0$ and $p \in C(\mathbb{R}_+^n, \mathbb{R})$, letting $h = p \circ \phi_{-t}^f$, we then get $\int (p - p \circ \phi_{-t}^f)d\mu = \int (p \circ \phi_{-t}^f \circ \phi_t^f - p \circ \phi_{-t}^f)d\mu = 0$. Then μ is invariant for ϕ_s^f, $s \in \mathbb{R}$. By inequality (1.8) and weak* convergence, it follows that $\mu \in \mathcal{M}(f, K)$. For any $1 \le i \le n$, using the uniform convergence of g^m to f on V and inequality (1.11), we further have

$$\begin{aligned}
\int f_i du &= \lim_{m\to\infty} \int f_i d\mu_m \\
&\le \lim_{m\to\infty} \frac{1}{t_m}\int_0^{t_m} (f_i - g_i^m)(\phi_s^{g^m}(x^m))ds \\
&\quad + \limsup_{m\to\infty} \frac{1}{t_m}\int_0^{t_m} g_i^m(\phi_s^{g^m}(x^m))ds \le 0.
\end{aligned}$$

But this contradicts the unsaturatedness of K for ϕ_t^f. ∎

For many practical biological systems one can verify that every bounded orbit on the boundary converges to an equilibrium or a nontrivial periodic orbit. By a critical element of (1.4) we mean an equilibrium point or a nontrivial periodic orbit. Our usual notation for a critical element is $\gamma = \{u(t) : 0 \le t \le T\}$, where $u(t)$ is a T-periodic solution of (1.4) and T is the minimal period, which may be zero for an equilibrium.

Theorem 1.4.5. (Robust permanence) *Let (D1) hold, and assume that*

(D3) There exist hyperbolic critical elements $\gamma^i \in \partial P \cap P_{M'}$ for some $M' < M$, $1 \le i \le m$, satisfying
  (a) $\partial P \subset \cup_{i=1}^m W^s(\gamma^i)$;

(b) for each γ^i, there exists k such that $x_k = 0$ on γ^i and $\int_0^{T_i} f_k(u^i(s))ds > 0$;
(c) no subset of $\{\gamma^1, \gamma^2, \ldots, \gamma^m\}$ forms a cycle in ∂P.

Then the conclusion of Theorem 1.4.4 holds.

Proof. By assumptions (D1) and (D3) and Lemma 1.3.1, $\{\gamma^1, \gamma^2, \ldots, \gamma^m\}$ is a Morse decomposition of the maximal compact invariant set for ϕ_t^f on $P_M \setminus P_M^0$. Since (D3)(b) implies that each γ^i is unsaturated for ϕ_t^f (see [302, Section 3]), the conclusion follows from Theorem 1.4.4. Here we give an alternative and more elementary proof without using the concept of invariant measures. As in the proof of Theorem 1.4.4, clearly (B1) holds, and then it suffices to prove that condition (B2) holds, which is implied by the following claim:

Claim. For each γ^i, there is $\epsilon > 0$ such that for $g \in C_L$ satisfying (1.5) and $x \in P_M^0$ with $d(x, \gamma^i) < \epsilon$ there exists $t > 0$ such that $d(\phi_t^g(x), \gamma^i) \geq \epsilon$.

Indeed, without loss of generality suppose that

$$u(t) = u(t+T) = u^i(t) = (0, \ldots, 0, u_l(t), \ldots, u_n(t))$$

with $u_j(t) > 0$ for all t. We will argue the case where γ is a nontrivial periodic orbit ($T > 0$), since the case for an equilibrium is simpler. Set $\lambda = T^{-1} \int_0^T f_k(u(s))ds > 0$, where $k < l$ is an index as in (D3)(b) above. Let K be a common Lipschitz constant for f and F on P_M. Choose $\epsilon > 0$ such that

$$\epsilon[1 + K(1 + MT)\exp(KT)] < \lambda/2.$$

A standard Gronwall argument shows that if $d(x, \gamma) < \epsilon$, so $\|x - u(s)\| < \epsilon$ for some $s \in [0, T)$, and (1.5) holds, then

$$\|x(t) - u(t+s)\| \leq \epsilon(1 + MT)\exp(KT),\ 0 \leq t \leq T.$$

Here we have simplified notation by setting $x(t) = \phi_t^g(x)$, and we use that $\sup_{x \in P_M} \|F(x) - G(x)\| < \epsilon M$. Now suppose by way of contradiction that $d(x(t), \gamma) < \epsilon$ for all $t \geq 0$. The inequality

$$\begin{aligned} g_k(x(t)) &\geq f_k(u(s+t)) - |g_k(x(t)) - f_k(x(t))| - |f_k(x(t)) - f_k(u(t+s))| \\ &\geq f_k(u(t+s)) - \epsilon - \epsilon K(1 + MT)\exp(KT) \\ &\geq f_k(u(t+s)) - \lambda/2, \end{aligned}$$

which holds for $0 \leq t \leq T$, implies that $x_k(t)$ satisfies

$$x_k'(t) \geq x_k(t)[f_k(u(t+s)) - \lambda/2].$$

Integrating, we have

$$x_k(T) \geq x_k(0)\exp(\lambda T/2).$$

By assumption, $d(x(T), \gamma) < \epsilon$, so we may apply the previous argument again to get $x_k(2T) \geq x_k(0)\exp(2\lambda T/2)$, and by induction, we have that $x_k(nT) \geq x_k(0)\exp(n\lambda T/2)$. Since the right-hand side increases without bound as n increases, we contradict that $d(x(t), \gamma) < \epsilon$ for $t \geq 0$. This proves the claim. Because (B2) holds, our result follows from (the continuous-time version of) Theorem 1.4.2. ∎

1.5 Notes

Theorem 1.1.1 is due to LaSalle [212]. Theorem 1.1.3 (a) with $n_0 = 1$ is due to Billotti and LaSalle [36]. Theorem 1.1.4 is due to Nussbaum [257] and Hale and Lopes [143]. Theorems 1.1.2 and 1.1.3, Lemma 1.1.5, and their proofs are adapted from Magal and Zhao [241].

Section 1.2 is adapted from Hirsch, Smith and Zhao [164]. Lemma 1.2.4′ and Example 1.2.2 are taken from Smith and Zhao [340]. The notion of chain recurrence was introduced by Conley [65]. Bowen [37] proved that omega limit sets of precompact orbits of continuous invertible maps are internally chain transitive. Robinson [294] proved that omega limit sets of precompact orbits of continuous maps are internally chain recurrent. Thieme [364, 366, 367] studied the long-term behavior in asymptotically autonomous differential equations, and Mischaikow, Smith, and Thieme [249] discussed chain recurrence and Liapunov functions in asymptotically autonomous semiflows. Asymptotic pseudo-orbits were introduced by Benaïm and Hirsch [35] for continuous-time semiflows. The embedding approach in the proof of Lemma 1.2.2 was used earlier by Zhao [433, 435] to prove that the omega limit set of a precompact orbit of an asymptotically autonomous process is nonempty, compact, invariant, and internally chain recurrent for the limiting map (see [433, Theorem 2.1] and [435, Theorem 1.2]). Freedman and So ([122, Theorem 3.1]) proved the Butler–McGehee lemma of limit sets for continuous maps. By an embedding approach and [122, Theorem 3.1], Hirsch, Smith and Zhao ([164, Lemma 3.3]) proved Lemma 1.2.7. Theorem 1.2.1 was proved earlier by Smith and Zhao ([336, Lemma 4.1]).

Uniform persistence (permanence) has received extensive investigation for both continuous- and discrete-time dynamical systems. We refer to Waltman [381], Hutson and Schmitt [186], and Hofbauer and Sigmund [167] for surveys and reviews, and to Thieme [369], Zhao [436], Smith and Thieme [333], and references therein for further developments.

Subsections 1.3.1 and 1.3.2 are adapted from Hirsch, Smith and Zhao [164] and Smith and Zhao [340]. Theorem 1.3.3 was generalized to nonautonomous semiflows by Thieme [368, 369]. The concept of a generalized distance function was motivated by ideas in Thieme [369], where uniform ρ-persistence was developed for nonautonomous semiflows. General theorems on uniform persistence were established earlier by Hale and Waltman [146], Thieme [365] for autonomous semiflows, and Freedman and So [122], Hofbauer and So [168] for continuous maps.

Various concepts of practical persistence were utilized by Hutson and Schmitt [186], Cantrell, Cosner and Hutson [54], Hutson and Zhao [443], Cosner [67], Cantrell and Cosner [52], Hutson and Mischaikow [184], Smith and Zhao [336, 337], and Ruan and Zhao [298]. The p-function in Example 1.3.1 was employed by Thieme [369] for a scalar functional differential equation. Two p-functions in Example 1.3.2 were used by Smith and Zhao [340] and Zhao [439], respectively, for an autonomous microbial population growth model and almost periodic predator–prey reaction–diffusion systems.

Subsection 1.3.3 is taken from Magal and Zhao [241], and Subsection 1.3.4 is adapted from Zhao [430] and Magal and Zhao [241]. For a class of continuous Kolmogorov-type maps on $\mathbb{R}^m_+$, Hutson and Moran [185] proved that the existence of a compact attracting set in $\text{int}(\mathbb{R}^m_+)$ implies that of a (componentwise) positive fixed point. By applying Theorem 1.3.8 to the Poincaré map associated with a periodic semiflow, one can obtain the existence of a periodic orbit in X_0, and hence that of periodic coexistence solutions for periodic systems of differential equations. Freedman and Yang [419, Theorem 4.11] proved the existence of interior periodic solutions for periodic, dissipative, and uniformly persistent systems of ODEs. For periodic and uniformly persistent Kolmogorov systems of ODEs, Zanolin [424, Lemma 1] also proved the existence of positive periodic solutions. For autonomous Kolmogorov systems of ODEs and a class of autonomous differential equations with finite delay, Hutson [183] proved the existence of positive equilibria. Hofbauer [166] generalized an index theorem for dissipative ordinary differential systems, which implies the existence of a positive equilibrium (see also [167]). For autonomous 2-species Kolmogorov reaction–diffusion systems, Cantrell, Cosner and Hutson [54, Theorem 6.2] also proved a result on the existence of stationary coexistence states under appropriate assumptions.

Subsection 1.4.1 is taken from Smith and Waltman [335]. Subsection 1.4.2 is adapted from Hirsch, Smith and Zhao [164] and Smith and Zhao [340]. Subsection 1.4.3 is taken from Hirsch, Smith and Zhao [164]. Smith and Zhao [336, Theorem 4.3] proved a similar result on uniform persistence uniform in parameter. Earlier, Hutson [182] discussed robustness of permanence for autonomous ordinary differential systems defined on $\mathbb{R}^n_+$ by using Liapunov function techniques. Schreiber [302] established criteria for C^r–robust permanence, $r \geq 1$, of autonomous Kolmogorov ordinary differential systems.

2

Monotone Dynamics

As we illustrated in the Preface, some population models can generate continuous- or discrete-time dynamical systems with monotonicity: Ordered initial states lead to ordered subsequent states. This chapter is aimed at monotone dynamics. We are primarily interested in some global results that may be effectively applied to both discrete-time and periodic biological systems. In Section 2.1 we prove the existence and global attractivity of an order interval defined by two fixed points, and a theorem on fixed points and connecting orbits for continuous and monotone maps on an ordered Banach space E.

In Section 2.2 we first prove global attractivity of a unique fixed point and zero fixed point for monotone maps. Then we establish a global convergence theorem for strongly monotone maps under the assumption that E does not contain three ordered fixed points. A convergence result is also obtained for monotone maps on a closed and order convex subset of E in the case that there is a totally ordered and closed arc of stable fixed points. For the latter use, at the end of this section we state three general results on convergence and attractivity in monotone autonomous semiflows.

In Section 2.3 we develop the theory of subhomogeneous (or sublinear) dynamical systems. We show existence and global attractivity of a strongly positive fixed point, and establish threshold dynamics for two classes of maps: either monotone and strongly subhomogeneous, or strongly monotone and strictly subhomogeneous. A convergence result is proved for subhomogeneous and strongly monotone maps. In order to get global dynamics in monotone and subhomogeneous almost periodic systems, we also prove a global attractivity theorem for a class of skew-product semiflows.

Section 2.4 is devoted to discussing competitive systems on ordered Banach spaces. We establish a limit set trichotomy and a compression theorem by appealing to a generalized Dancer–Hess connecting orbit theorem and a convergence theorem for chain transitive sets in the previous chapter.

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In Section 2.5 we establish generalized saddle point behavior for monotone semiflows with two ordered and locally stable equilibria. This result is also extended to the case where there are more than two totally ordered and locally stable equilibria. Then we obtain the analogs of these results for two-species competitive systems on ordered Banach spaces.

In Section 2.6 we introduce an exponential ordering for a Banach space of continuous functions, give an analytic characterization of such an ordering for points in the phase space with sufficient regularity, and establish monotonicity and a strong order-preserving property for mild solutions of general abstract functional differential equations with a quasi-monotone nonlinearity.

2.1 Attracting Order Intervals and Connecting Orbits

Let E be an ordered Banach space with positive cone P such that $\mathrm{int}(P) \neq \emptyset$. For $x, y \in E$ we write $x \geq y$ if $x - y \in P$, $x > y$ if $x - y \in P \setminus \{0\}$, and $x \gg y$ if $x - y \in \mathrm{int}(P)$. If $a < b$, we define $[a, b] := \{x \in E : a \leq x \leq b\}$. If $a \ll b$, then $[[a, b]] := \{x \in E : a \ll x \ll b\}$. Since P is a closed subset of E, it is easy to see that the topology and ordering on E are compatible in the sense that if $u_n \geq v_n$, $u_n \to u$, $v_n \to v$, then $u \geq v$.

Definition 2.1.1. *Let U be a subset of E, and $f : U \to U$ a continuous map. The map f is said to be monotone if $x \geq y$ implies that $f(x) \geq f(y)$; strictly monotone if $x > y$ implies that $f(x) > f(y)$; strongly monotone if $x > y$ implies that $f(x) \gg f(y)$.*

Theorem 2.1.1. (Attracting order interval) *Let $f : E \to E$ be completely continuous and monotone. Assume that f maps order intervals to precompact sets, that the set of fixed points of f in E is bounded, and that each positive orbit of f is bounded. Then there exist maximal and minimal fixed points x_M and x_m in E such that for each $x \in E$, $\omega(x) \subset [x_m, x_M]$. Moreover, $\lim_{n\to\infty} f^n(x) = x_m$ for each $x \leq x_m$, and $\lim_{n\to\infty} f^n(x) = x_M$ for each $x \geq x_M$.*

Proof. For any $x \in E$, $\gamma^+(x)$ is precompact by our assumption, and hence its omega limit set $\omega(x)$ is nonempty, compact, and invariant for f. Thus $\omega(x)$ is contained in some order interval since $\mathrm{int}(P) \neq \emptyset$. We first prove the following claim.

Claim. For each $x \in E$, there exist two fixed points w_1 and w_1 of f such that $\omega(z) \subset [w_1, w_2]$.

Indeed, since $\omega(z)$ is order bounded, there exists $u \in E$ such that $\omega(z) \leq u$. Then the invariance of $\omega(z)$ implies that $\omega(z) \leq f^n u$ for all $n \geq 0$, and hence $\omega(z) \leq \omega(u)$, since P is closed. Now $\omega(u)$ is order bounded, and hence there exists $s \in E$ such that $\omega(u) \leq s$. As before, it follows that $\omega(u) \leq \omega(s)$.

Let $S := \{x \in E : \omega(z) \leq x \leq \omega(s)\}$. Then S is the interaction of closed order intervals, and hence it is closed and convex. Since $\omega(z) \leq \omega(u) \leq \omega(s)$, S is nonempty. By our assumption, $f(S)$ is precompact. Since $f(\omega(z)) = \omega(z)$, $f(\omega(s)) = \omega(s)$, and f is monotone, we have $f(S) \subset S$. Thus, by the Schauder fixed point theorem, there exists a fixed point w_2 of f in S, and hence $\omega(z) \leq w_2$. The existence of the required w_1 can be obtained in a similar way.

Let F be the set of fixed points of f in E. Since F is bounded, the compactness of f ensures that F is compact. By a simple Zorn's lemma argument, there exists $x_M \in F$ weakly maximal, that is, $u > x_M$ implies $u \notin F$. We deduce that x_M is maximal in the stronger sense that $u \leq x_M$ if $u \in F$. Suppose by way of contradiction that v is another fixed point of f such that $v \notin (-\infty, x_M]$. Note that a cone K with nonempty interior is reproducing in the sense that $E = K - K$. Then there exists $u \in E$ such that $u \geq x_M$ and $u \geq v$. By the monotonicity of f, we get $f^n(u) \geq f^n(x_M) = x_M$ for all $n \geq 0$, and hence $\omega(u) \geq x_M$. Similarly, $\omega(u) \geq v$. However, by the claim above, there exists a fixed point w such that $\omega(u) \leq w$. Hence $w \geq x_M$ and $w \geq v$. This is impossible, since x_M is weakly maximal and $v \notin (-\infty, x_M]$. Thus x_M is maximal in the strong sense. Similarly, we can prove the existence of a minimal fixed point x_m.

Now suppose $x \in E$. By the claim above and the maximality of x_M, $\omega(x) \leq x_M$. Similarly, $\omega(x) \geq x_m$. Hence $\omega(x) \subset [x_m, x_M]$. If $x \leq x_m$, then $f^n x \leq f^n x_m = x_m$ for all $n \geq 0$ by the monotonicity of f, and hence $\omega(x) \leq x_m$. Thus, by the first part of the statement, $\omega(x) = \{x_m\}$. The other part is proved similarly. ∎

Remark 2.1.1. If we assume that $f : E \to E$ is α-condensing, compact dissipative, and monotone, then the conclusion of Theorem 2.1.1 is also valid. Indeed, by the proof of Theorem 2.1.1, it is necessary to prove only that the map f has a fixed point in S and the set F is compact. Since S is a closed and convex subset of E, one can apply Theorem 1.1.4 to the map $f : S \to S$ instead of the Schauder fixed point theorem. It is easy to see that F is bounded and closed, and $f(F) = F$. Since f is α-condensing, we get $\alpha(F) = 0$, which implies that $\overline{F} = F$ is compact in E.

Remark 2.1.2. The conclusion in Theorem 2.1.1 and Remark 2.1.1 also holds when f is restricted to a closed and convex subset K of E with $f(K) \subset K$. In applications one may choose a positively invariant order interval (including the positive cone P) in E as K.

Let $f : U \subset E \to U$ be continuous. A sequence $\{z_n\}_{n=-\infty}^{\infty}$ in U with $z_{n+1} = f(z_n), \forall n \in \mathbb{N}$, is called an entire orbit of f. The following connecting orbit theorem is very important in monotone dynamics. For a proof of it, we refer to [86, Proposition 1] or [152, Proposition 2.1].

Dancer–Hess Lemma (Connecting orbit) *Let $u_1 < u_2$ be fixed points of the strictly monotone continuous mapping $f : U \to U$, let $I := [u_1, u_2] \subset U$,* *and assume that $f(I)$ is precompact and f has no fixed point distinct from u_1 and u_2 in I. Then either*

(a) there exists an entire orbit $\{x_n\}_{n=-\infty}^{\infty}$ of f in I such that $x_{n+1} > x_n, \forall n \in \mathbb{N}$, and $\lim_{n\to-\infty} x_n = u_1$ and $\lim_{n\to\infty} x_n = u_2$, or
(b) there exists an entire orbit $\{y_n\}_{n=-\infty}^{\infty}$ of f in I such that $y_{n+1} < y_n, \forall n \in \mathbb{N}$, and $\lim_{n\to-\infty} y_n = u_2$ and $\lim_{n\to\infty} x_n = u_1$.

Let C be a convex subset of X and $e \in C$. Then e is said to be an extreme point of C if there do not exist points $x, y \in C \setminus \{e\}$ such that $e = \frac{1}{2}(x + y)$. A fixed point u of $f : U \to U$ is said to be an ejective fixed point if there is an open subset V of U containing u such that for every $x \in V \setminus \{u\}$ there is an integer m such that $f^m(x) \notin V$.

Remark 2.1.3. If f has an ejective fixed point $e \in I \setminus \{u_1, u_2\}$ that is an extreme point of I, and f has no fixed point distinct from u_1, u_2, e in I, then the conclusion of the Dancer–Hess lemma is still valid. Indeed, the fixed point index of an ejective fixed point that is an extreme point of I vanishes, and therefore the fixed point arguments in [86] can be adapted to this case (see [174, Proposition 2.1]).

Remark 2.1.4. By [88, Section 5], the conclusion of the Dancer–Hess lemma also holds if we replace the condition that $f(I)$ be precompact in I with the following weaker one:

(A) $f : I \to I$ is α-condensing and $f(I)$ is bounded in E.

Recall that a linear operator L on E is said to be positive if $L(P) \subset P$, strongly positive if $L(P \setminus \{0\}) \subset \mathrm{int}(P)$. The cone P is said to be normal if there exists a constant M such that $0 \le x \le y$ implies that $\|x\| \le M\|y\|$. In what follows, by $Df(a)$ we denote the Fréchet derivative of f at $u = a$ if it exists, and let $r(Df(a))$ be the spectral radius of the linear operator $Df(a) : E \to E$. The following result is helpful in proving uniform persistence and existence of a connecting orbit for monotone systems when we know the existence of only a single unstable steady state.

Theorem 2.1.2. *Let the positive cone P be normal. Assume that*

(1) $S : V = a + P \to V$ is asymptotically smooth and monotone;
(2) $S(a) = a$, $DS(a)$ is compact and strongly positive, and $r(DS(a)) > 1$.

Then either

(a) for any $u > a$, $\lim_{n\to\infty} \|S^n(u)\| = +\infty$, or
(b) there exists $u^* = S(u^*) \gg a$ such that for any $a < u \le u^*$, $\lim_{n\to\infty} S^n(u) = u^*$, and there exists a monotone entire orbit connecting a and u^*.

Proof. By the Krein–Rutman theorem (see, e.g., [152, Section I.7]), $r = r(DS(a))$ is the principal eigenvalue of $DS(a)$. Let $e \gg 0$ be the principal eigenvector of $DS(a)$ with $\|e\|_E = 1$; i.e., $DS(a)e = re$. For $\epsilon > 0$, we then have

$$S(a + \epsilon e) = S(a) + DS(a)(\epsilon e) + o(\epsilon) = a + \epsilon \left[re + \frac{o(\epsilon)}{\epsilon} \right].$$

Since $r > 1$ and $(r-1)e \in \mathrm{int}(P)$, there exists $\epsilon_0 > 0$ such that for any $\epsilon \in (0, \epsilon_0]$, $(r-1)e + \frac{o(\epsilon)}{\epsilon} \in \mathrm{int}(P)$, and hence

$$S(a + \epsilon e) - (a + \epsilon e) = \epsilon \left[(r-1)e + \frac{o(\epsilon)}{\epsilon} \right] \gg 0.$$

Thus for any $\epsilon \in (0, \epsilon_0]$, $S(a + \epsilon e) \gg a + \epsilon e$. We further have the following two claims.

Claim 1. For any $u > a$, $S(u) \gg a$.

Indeed, for any given $u > a$, let $u = a + v$. Then $v > 0$. For $t > 0$, we have

$$S(a + tv) = S(a) + DS(a)(tv) + o(t) = a + t \left(DS(a)v + \frac{o(t)}{t} \right).$$

Since $v > 0$ and $DS(a)$ is strongly positive, $DS(a)v \in \mathrm{int}(P)$, and hence there exists $t_0 \in (0, 1]$ such that for any $t \in (0, t_0]$, $DS(a)v + \dfrac{o(t)}{t} \in \mathrm{int}(P)$. Then for any $t \in (0, t_0]$, $S(a + tv) \gg a$. Therefore, by the monotonicity of S, we get $S(u) = S(a + v) \geq S(a + tv) \gg a$, $\forall t \in (0, t_0]$.

Claim 2. For any $u > a$ with $S(u) = u$, $u \gg a + \epsilon_0 e$.

In fact, let $\epsilon_1 = \sup\{\epsilon \geq 0 : \ u \geq a + \epsilon e\}$. By Claim 1, $u \gg a$, and hence $\epsilon_1 > 0$. Assume, by contradiction, that $\epsilon_1 \leq \epsilon_0$. Since $u \geq a + \epsilon_1 e$, $u = S(u) \geq S(a + \epsilon_1 e) \gg a + \epsilon_1 e$. It follows that there exists $\epsilon_2 > \epsilon_1$ such that $u \gg a + \epsilon_2 e$, which contradicts the definition of ϵ_1. Therefore, $\epsilon_1 > \epsilon_0$, and hence $u \geq a + \epsilon_1 e \gg a + \epsilon_0 e$.

As shown above, for any $\epsilon \in (0, \epsilon_0]$, $S(a + \epsilon e) \gg a + \epsilon e$, and then the monotonicity of S implies that

$$a + \epsilon e \ll S(a + \epsilon e) \leq S^2(a + \epsilon e) \leq \cdots \leq S^n(a + \epsilon e) \leq S^{n+1}(a + \epsilon e) \leq \cdots.$$

By the normality of P, we may assume that $\|\cdot\|_E$ is nondecreasing, and hence, $\|S^n(a + \epsilon e)\| \leq \|S^{n+1}(a + \epsilon e)\|$, $\forall n \geq 1$. We distinguish two cases:

(a) for any $\epsilon \in (0, \epsilon_0]$, $\{S^n(a + \epsilon e)\}_{n=1}^{\infty}$ is unbounded. Then $\lim_{n\to\infty} \|S^n(a + \epsilon e)\| = +\infty$. For any $u > a$, by Claim 1, $S(u) \gg a$. Then there exists $\epsilon \in (0, \epsilon_0]$ such that $S(u) \geq a + \epsilon e$, and hence $S^{n+1}(u) \geq S^n(a + \epsilon e)$, $\|S^{n+1}(u)\| \geq \|S^n(a + \epsilon e)\|, \forall n \geq 1$. Therefore, $\lim_{n\to\infty} \|S^n(u)\| = +\infty$.

(b) there exists $\epsilon_1 \in (0, \epsilon_0]$ such that $\{S^n(a+\epsilon_1 e)\}_{n=1}^\infty$ is bounded. Then there exists a sufficiently large $\epsilon^* > 0$ such that $S^n(a+\epsilon_1 e) \in [a, a+\epsilon^* e]$, $\forall n \geq 1$. Therefore, by the monotonicity of S, for any $\epsilon \in (0, \epsilon_1]$ and all $n \geq 1$, $a + \epsilon e \ll S(a+\epsilon e) \leq S^n(a+\epsilon e) \leq S^n(a+\epsilon_1 e) \leq a + \epsilon^* e$, and hence $\|S^n(a+\epsilon e)\| \leq \|a + \epsilon^* e\|$. Since $S : V \to V$ is asymptotically smooth, every bounded positive orbit is precompact (see [141, Corollary 2.2.4]). By the precompactness of $\gamma^+(a+\epsilon e)$ and monotonicity of $\{S^n(a+\epsilon e)\}_{n=1}^\infty$, we then have

$$\lim_{n\to\infty} S^n(a+\epsilon e) = u(\epsilon),\ S(u(\epsilon)) = u(\epsilon) \gg a,\ \forall \epsilon \in (0, \epsilon_1].$$

Clearly, $u(\epsilon) \leq u(\epsilon_1)$. For any $\epsilon \in (0, \epsilon_1]$, by Claim 2, $u(\epsilon) \gg a + \epsilon_0 e \geq a + \epsilon_1 e$, and hence $u(\epsilon) \geq S^n(a+\epsilon_1 e), \forall n \geq 1$. Therefore, $u(\epsilon_1) = \lim_{n\to\infty} S^n(a + \epsilon_1 e) \leq u(\epsilon)$. Then for any $\epsilon \in (0, \epsilon_1], u(\epsilon) = u(\epsilon_1)$. Let $u^* = u(\epsilon_1)$, then $u^* \gg a$ and $\lim_{n\to\infty} S^n(a+\epsilon e) = u^*$. For any $a < u \leq u^*$, by Claim 1, $a \ll S(u) \leq u^*$, and hence there exists $\epsilon \in (0, \epsilon_1]$ such that $a+\epsilon e \leq S(u) \leq u^*$ and $S^n(a+\epsilon e) \leq S^{n+1}(u) \leq u^*$, $\forall n \geq 1$. Then, by the normality of P, $\lim_{n\to\infty} S^n(u) = u^*$. Note that there exists a strict subequilibrium $a + \epsilon e, \forall \epsilon \in (0, \epsilon_0]$, as close to a as we wish. By the asymptotic smoothness of S, it easily follows that for any $v_k \in B = [a, u^*]$, $k \geq 1$, and $n_k \to \infty$, $\{S^{n_k}(v_k)\}_{k=1}^\infty$ is precompact. Therefore, a careful diagonalization argument given in the Dancer–Hess connecting orbit theorem (see [86, Proposition 1] or [152, Proposition 2.1]) proves the existence of the monotone entire orbit connecting a and u^*. ∎

Remark 2.1.5. If we replace the normality of P with the boundedness of positive orbits of S in V, then the alternative (b) in Theorem 2.1.2 holds.

Remark 2.1.6. In the case where $V = a - P$, it is easy to see that there exists $\epsilon_0 > 0$ such that for any $\epsilon \in (0, \epsilon_0], S(a - \epsilon e) \ll a - \epsilon e$, and hence $a - \epsilon e$ is a strict superequilibrium. Then an analogous conclusion holds.

2.2 Global Attractivity and Convergence

Throughout this and the next section we assume that (E, P) is an ordered Banach space with $\text{int}(P) \neq \emptyset$.

Theorem 2.2.1. (Global attractivity) *Assume that*

(1) $f : E \to E$ is α-condensing and point dissipative, and orbits of compact sets are bounded;
(2) $f : E \to E$ is monotone;
(3) f has exactly one fixed point e in E.

Then e is globally attractive for f in E.

Proof. By Theorem 1.1.2, $f : E \to E$ admits a global attractor A in E, and hence $f : E \to E$ is compact dissipative. Thus Theorem 2.1.1 and Remark 2.1.1 imply that $\omega(x) = e$ for all $x \in E$. ∎

It is natural to expect that the unique fixed point in Theorem 2.2.1 is globally asymptotically stable. The following result shows that this is true under some additional assumptions.

Lemma 2.2.1. *Let P be normal, and $S : E \to E$ a continuous and monotone map. Assume that S has a fixed point $x^* \in E$ such that*

(1) $S(x) \ll x^* \ll S(y)$ whenever $x \ll x^* \ll y$;
(2) x^* attracts every point in some open neighborhood W of x^*.

Then x^* is Liapunov stable for S.

Proof. Since P is normal, without loss of generality, we can assume that the norm $\|\cdot\|$ is monotone on P. Fix an $e \in \text{int}(P)$. Let $\epsilon > 0$ be given such that $B(x^*, \epsilon) := \{x \in E : \|x - x^*\| < \epsilon\} \subset W$. Set

$$\lambda = \frac{\epsilon}{6\|e\|}, \quad u = x^* - \lambda e, \quad v = x^* + \lambda e.$$

Clearly, $u \ll v$. We claim that $[u, v] \subset B(x^*, \epsilon)$. Indeed, for every $x \in [u, v]$, since

$$0 \le x^* + \lambda e - x \le x^* + \lambda e - (x^* - \lambda e) = 2\lambda e,$$

we have $\|x^* + \lambda e - x\| \le 2\lambda\|e\|$, and hence

$$\|x - x^*\| \le \|x^* + \lambda e - x\| + \| - \lambda e\| \le 3\lambda\|e\| = \frac{\epsilon}{2}.$$

Since $u \ll x^* \ll v$ and $\lim_{n\to\infty} S^n(u) = x^* = \lim_{n\to\infty} S^n(v)$, there exists a positive integer n_0 such that

$$u \ll S^n(u) \ll x^* \ll S^n(v) \ll v, \quad \forall n \ge n_0.$$

Let $V := [[S^{n_0}(u), S^{n_0}(v)]]$. It then follows that

$$u \ll S^{n+n_0}(u) \le S^n(x) \le S^{n+n_0}(v) \ll v, \quad \forall n \ge 0,\ x \in V.$$

Thus, $S^n(V) \subset [u, v] \subset B(x^*, \epsilon)$, $\forall n \ge 0$. Since V is an open subset of E and $x^* \in V$, there exists $\delta = \delta(\epsilon) > 0$ such that $B(x^*, \delta) \subset V$, and hence

$$S^n(B(x^*, \delta)) \subset S^n(V) \subset B(x^*, \epsilon), \forall n \ge 0.$$

This proves the Liapunov stability of x^* for S. ∎

Theorem 2.2.2. (Global attractivity) *Let either $V = [0, b]_E$ with $b \gg 0$ or $V = P$, and assume that*

(1) $f : V \to V$ is monotone and every positive orbit of f in V is precompact;
(2) $f(0) = 0$, $Df(0)$ is compact and strongly positive, and $r(Df(0)) \le 1$;
(3) $f(u) < Df(0)u$ for any $u \in V$ with $u \gg 0$.

Then $u = 0$ is globally attractive for f in V.

Proof. By Claim 1 in the proof of Theorem 2.1.2, for any $u > 0$, $f(u) \gg 0$. We first show that there exists no positive fixed point of f in V. Assume, by contradiction, that there exists $u \in V, u > 0$ such that $u = f(u)$. Then $u \gg 0$, and hence by assumption (3),

$$(-u) - Df(0)(-u) = Df(0)u - f(u) > 0.$$

By the Krein–Rutman theorem (see, e.g., [152, Theorem 7.3]), $r(Df(0)) > 1$, which contradicts our assumption $r(Df(0)) \leq 1$.

Now we let $V = P$. For $V = [0, b]_E$, the proof is much easier. Let $e \gg 0$ be the principal eigenvector of $Df(0)$. Then $Df(0)e = r(Df(0))e$, and hence for any $t > 0$, by assumptions (2) and (3),

$$f(te) < Df(0)(te) = t \cdot r(Df(0))e \leq te.$$

That is, te is a strict superequilibrium of f. For any $u \in P$, there exists $t > 0$ such that $u \in [0, te]_E$. Thus, by assumption (1), $\gamma^+(te)$ is precompact. By a standard monotone iteration scheme (see, e.g., [152, Lemma 1.1]) and the nonexistence of a positive fixed point of f, we get $0 \leq f^n(u) \leq f^n(te) \to 0$, as $n \to \infty$. Thus $\lim_{n\to\infty} f^n(u) = 0$. ∎

Theorem 2.2.3. (Global convergence) *Assume that*

(1) $f : E \to E$ is α-condensing and point dissipative, and orbits of bounded sets are bounded;
(2) $f : E \to E$ is strongly monotone;
(3) E does not contain fixed points u, v, w such that $u < v < w$.

Then there are at most two fixed points of f in E, and every positive orbit of f converges to one of them.

Proof. By Theorem 2.1.1, there exist maximal and minimal fixed points x_M and x_m in E such that for each $x \in E$, $\omega(x) \subset [x_m, x_M]$. If $x_m = x_M$, we are done. So we assume that $x_m < x_M$. By assumption (3) and the Dancer–Hess connecting orbit lemma, without loss of generality we assume that there exists an entire orbit $\{x_n\}_{n=-\infty}^{\infty}$ of f in $[x_m, x_M]$ such that $x_{n+1} > x_n, \forall n \in \mathbb{N}$, and $\lim_{n\to-\infty} x_n = x_m$ and $\lim_{n\to\infty} x_n = x_M$. For any $y \in [x_m, x_M] \setminus \{x_m, x_M\}$, we have $x_m < y < x_M$, and hence assumption (2) implies that $x_m \ll f(y) \ll x_M$. Thus we can choose a sufficiently large integer n_0 such that $x_{-n_0} \ll f(y)$. Thus $f^n(x_{-n_0}) = f^{n-n_0}(x_0) = x_{n-n_0} \leq f^{n+1}(y) \leq x_M, \forall n \geq 0$. Letting $n \to \infty$, we get $\omega(y) = x_M$. Clearly, x_m and x_M are isolated invariant sets of $f : [x_m, x_M] \to [x_m, x_M]$, and there is no cyclic chain of these two fixed points. By Theorem 1.2.2, every internally chain transitive set of f in $[x_m, x_M]$ is a fixed point, which implies that $\omega(x)$ is a fixed point for any $x \in E$, since $\omega(x)$ is internally chain transitive for $f : E \to E$ and $\omega(x) \subset [x_m, x_M]$. ∎

Remark 2.2.1. By the proof above, it is easy to see that Theorem 2.2.3 holds if condition (2) is replaced by the assumption that $f : E \to E$ is strictly monotone, and for any fixed point e of f in E, and $x, y \in E$ with $x > e$ and $y < e$, we have $f(x) \gg e$ and $f(y) \ll e$.

For two subsets A and B of E, we write $A \geq B$ if $x - y \in P$ for any $x \in A$ and $y \in B$; $A > B$ if $x - y \in P \setminus \{0\}$ for any $x \in A$ and $y \in B$; and $A \gg B$ if $x - y \in \mathrm{int}(P)$ for any $x \in A$ and $y \in B$.

Theorem 2.2.4. (Convergence) *Let U be a closed and order convex subset of E, and $f : U \to U$ continuous and monotone. Assume that there exists a monotone homeomorphism h from $[0,1]$ onto a subset of U such that*

(1) For each $s \in [0,1]$, $h(s)$ is a stable fixed point for $f : U \to U$;
(2) Each orbit of f in $[h(0), h(1)]_E$ is precompact;
(3) One of the following two properties holds:

- *(3a) If $\omega(x) > h(s_0)$ for some $s_0 \in [0,1)$ and $x \in [h(0), h(1)]_E$, then there exists $s_1 \in (s_0, 1)$ such that $\omega(x) \geq h(s_1)$;*
- *(3b) If $\omega(x) < h(r_1)$ for some $r_1 \in (0,1]$ and $x \in [h(0), h(1)]_E$, then there exists $r_0 \in (0, r_1)$ such that $\omega(x) \leq h(r_0)$.*

Then for any precompact orbit $\gamma^+(y)$ of f in U with $\omega(y) \cap [h(0), h(1)]_E \neq \emptyset$, there exists $s^* \in [0,1]$ such that $\omega(y) = h(s^*)$.

Proof. We consider only the case where (3a) holds, since a similar argument applies to the case where (3b) holds. Let $e_i = h(i)$, $i = 0, 1$, and $I := [e_0, e_1]_E$. Clearly, $I \subset U$, and $f(I) \subset I$ by the monotonicity of f. We first show that for each $x \in I$, $\omega(x) = h(s^*)$ for some $s^* \in [0,1]$. Clearly, $\omega(x) \subset I$. Define $\sigma = \sup\{s \in [0,1] : h(s) \leq \omega(x)\}$. Thus $\sigma \in [0,1]$ and $h(\sigma) \leq \omega(x) \leq e_1$. Assume, by contradiction, that $h(\sigma) \notin \omega(x)$. Then $\sigma \in [0,1)$ and $h(\sigma) < \omega(x)$. By assumption (3a) and the monotonicity of h, it follows that there is $\sigma_1 \in (\sigma, 1)$ such that $h(s) \leq \omega(x)$, $\forall s \in [\sigma, \sigma_1]$, which contradicts the maximality of σ. Thus $h(\sigma) \in \omega(x)$. By assumption (1), $h(\sigma)$ is stable for $f : I \to I$, and hence by Lemma 1.1.1 we get $\omega(x) = h(\sigma)$. Let $z \in \omega(y) \cap I \neq \emptyset$. Then the invariance of $\omega(y)$ (i.e., $f(\omega(y)) = \omega(y)$) implies that $\omega(z) \subset \omega(y)$. By what we have proved, $\omega(z) = h(s^*)$ for some $s^* \in [0,1]$, and hence $h(s^*) \in \omega(y)$. Thus assumption (1) and Lemma 1.1.1 imply that $\omega(y) = h(s^*)$. ∎

Recall that $f : U \to U$ is said to be strongly order-preserving if for any $x, y \in U$ with $x < y$, $f(V_x) \leq f(V_y)$ for some open neighborhoods V_x and V_y of x and y, respectively. Clearly, strongly monotone maps are strongly order-preserving. By the compactness and invariance of omega limit sets, it is easy to see that both (3a) and (3b) hold in the case where $f : U \to U$ is strongly monotone.

A continuous semiflow $\Phi(t)$ on E is said to be monotone if for each $t \geq 0$, $\Phi(t) : E \to E$ is a monotone map. In the rest of this section we state three general results on convergence and attractivity in monotone semiflows, which will be used in Chapters 7 and 9.

Theorem 2.2.5. (Hirsch convergence criterion) *([160, Theorem 6.4]) Assume that the monotone semiflow $\Phi(t)$ on E admits a precompact positive orbit $\gamma^+(x)$ such that $\Phi(t_0)x \gg x$ or $\Phi(t_0)x \ll x$ for some $t_0 \in (0, \infty)$. Then $\Phi(t)x$ converges as $t \to \infty$ to an equilibrium.*

Theorem 2.2.6. (Hirsch attractivity theorem) *([157, Theorem 3.3]) Assume that the monotone semiflow $\Phi(t)$ on E admits an attractor K such that K contains only one equilibrium p. Then every trajectory attracted to K converges to p.*

Let X be an ordered metric space with metric d and partial order relation $\leq$. We say that a point $x \in X$ can be approximated from below (above) in X if there exists a sequence $\{x_n\}$ in X satisfying $x_n < x_{n+1} < x$ $(x < x_{n+1} < x_n)$ for $n \geq 1$ and $x_n \to x$ as $n \to \infty$. The following generic convergence theorem is a special case of [330, Theorem 2.4] (see also [326, Theorem 2.4.7 and Remark 2.4.1]).

Theorem 2.2.7. (Generic convergence theorem) *Let X be an ordered metric space with metric d and partial order relation $\leq$ such that each point of X can be approximated either from above or from below in X, and let $\Phi(t)$ be a monotone semiflow on X. Assume that every positive orbit in X is precompact and that if $\{x_n\}_{n\geq 1}$ approximates x_0 from below or from above, then $\cup_{n\geq 0}\omega(x_n)$ has compact closure contained in X. Suppose that there exists an ordered Banach space (Y, Y_+) with $\mathrm{int}(Y_+) \neq \emptyset$ such that*

(1) $Z := X \cap Y$ is a nonempty order convex subset of Y, $\Phi(t)Z \subset Z$, $\forall t \geq 0$, the restriction of the order relation $\leq_Y$ on Y to Z agrees with the restriction of the order relation $\leq$ on X to Z, and the identity map from (Z, d) to (Z, d_Y) is continuous, where d_Y is the metric induced by the norm on Y;
(2) There exists $t_0 > 0$ such that $\Phi(t_0)X \subset Z$, $\Phi(t_0) : X \to Z$ is continuous, and $\Phi(t_0)x_2 - \Phi(t_0)x_1 \in \mathrm{int}(Y_+)$ whenever $x_1, x_2 \in X$ and $x_1 < x_2$;
(3) For each equilibrium e, $\Phi_{t_0} := \Phi(t_0)$ is continuously differentiable on a neighborhood of e in Z, the Fréchet derivative $\Phi'_{t_0}(e)$ is compact, and $\Phi'_{t_0}(e)(Y_+ \setminus \{0\}) \subset \mathrm{int}(Y_+)$.

Then there is an open and dense subset W of X such that for every $x \in W$, $\Phi(t)x$ converges as $t \to \infty$ to an equilibrium.

2.3 Subhomogeneous Maps and Skew-Product Semiflows

Recall that a subset K of E is said to be order convex if $[u, v]_E \subset K$ whenever $u, v \in E$ satisfy $u < v$. In this section we assume that $U \subset P$ is a nonempty, closed, and order convex set.

Definition 2.3.1. *A continuous map $f : U \to U$ is said to be subhomogeneous if $f(\lambda x) \geq \lambda f(x)$ for any $x \in U$ and $\lambda \in [0, 1]$; strictly subhomogeneous if $f(\lambda x) > \lambda f(x)$ for any $x \in U$ with $x \gg 0$ and $\lambda \in (0, 1)$; strongly subhomogeneous if $f(\lambda x) \gg \lambda f(x)$ for any $x \in U$ with $x \gg 0$ and $\lambda \in (0, 1)$.*

Lemma 2.3.1. *Assume that one of the following two condition holds:*

(C1) $f : U \to U$ *is monotone and strongly subhomogeneous;*
(C2) $f : U \to U$ *is strongly monotone and subhomogeneous.*

Then for any two fixed points $u, v \in U \cap \operatorname{int}(P)$*, there is* $\sigma > 0$ *such that* $v = \sigma u$*.*

Proof. By assumption, $u \gg 0$ and $v \gg 0$. Without loss of generality we may assume that $u \neq v$ and $u \notin [0, v]$. Set $\sigma_0 := \sup\{\sigma \geq 0 : \sigma u \leq v\}$. Clearly, $\sigma_0 u \leq v$ and $\sigma_0 \in (0, 1)$. We claim that $\sigma_0 u = v$. Assume, by contradiction, that $\sigma_0 u < v$. Then

$$\sigma_0 u = \sigma_0 f(u) \ll f(\sigma_0 u) \leq f(v) = v \quad \text{if (C1) holds,}$$

and

$$\sigma_0 u = \sigma_0 f(u) \leq f(\sigma_0 u) \ll f(v) = v \quad \text{if (C2) holds.}$$

Thus in either case we get $v - \sigma_0 u \gg 0$, which contradicts the maximality of σ_0. ∎

Theorem 2.3.1. *Assume that either (C1) or (C2) holds. If* $K \subset U \cap \operatorname{int}(P)$ *is a nonempty compact invariant of* f*, then there are fixed points* $p, q \in K$ *such that* $p \leq K \leq q$*.*

Proof. For each $x \in K$, define $\beta(x) := \sup\{\sigma \geq 0 : \sigma x \leq K\}$. Since $K \subset \operatorname{int}(P)$ and $\beta(x)x \leq K$, we get $0 < \beta(x) \leq 1, \forall x \in K$. It also easily follows that $\beta : K \to \mathbb{R}$ is continuous. Let μ be the maximal value of β on K. Then $\mu \in (0, 1]$. Fix $a \in K$ with $\beta(a) = \mu$. Then $\mu a \leq K$. We further claim that $\mu a \in K$. Assume, by contradiction, that $\mu a \notin K$. Then $\mu \in (0, 1)$ and $\mu a < K$. Since K is invariant, we get $f(a) \in K$, and hence $\beta(f(a)) \leq \mu$. It then follows that

$$\beta(f(a))f(a) \leq \mu f(a) \ll f(\mu a) \leq K \quad \text{if (C1) holds,}$$

and

$$\beta(f(a))f(a) \leq \mu f(a) \leq f(\mu a) \ll K \quad \text{if (C2) holds.}$$

Thus in either case we get $\beta(f(a))f(a) \ll K$, which contradicts the maximality of $\beta(f(a))$. Let $p = \mu a$. Then $p \in K$ and $p \leq K$. By the invariance of K and the monotonicity of f, we get $f(p) \in K$ and $f(p) \leq f(K) = K$. Thus $p \leq f(p)$ and $f(p) \leq p$, which implies that p is a fixed point of f. Similarly, we can prove the existence of the required fixed point q. ∎

Theorem 2.3.2. *Assume that either (C1) or the following (C3) holds:*

(C3) $f : U \to U$ *is strongly monotone and strictly subhomogeneous.*

If $f : U \to U$ *admits a nonempty compact invariant set* $K \subset \operatorname{int}(P)$*, then* f *has a fixed point* $e \gg 0$ *such that every nonempty compact invariant set of* f *in* $\operatorname{int}(P)$ *consists of* e*.*

Proof. By Lemma 2.3.1, it is easy to see that f admits at most one fixed point in $\mathrm{int}(P)$ in either case of (C1) and (C3). Then Theorem 2.3.1 implies that there is a fixed point $e \gg 0$ such that $K = \{e\}$. Thus Theorem 2.3.1, together with the uniqueness of the fixed point of f in $\mathrm{int}(P)$, completes the proof. ∎

Theorem 2.3.3. *Assume that (C2) holds. If x has a compact orbit closure in* $\mathrm{int}(P)$*, then $f^n(x)$ converges to a fixed point.*

Proof. By Theorem 2.3.1 and Lemma 2.3.1, $\omega(x)$ contains fixed points e and ρe for some $\rho \geq 1$ and $e \leq \omega(x) \leq \rho e$. Then it suffices to prove $\rho = 1$. Assume, by contradiction, that $\rho > 1$. We first claim that for any $t \in [1, \rho]$, te is a fixed point of f. Indeed, by the subhomogeneity of f, we have $f(te) \leq tf(e) = te$, and $f(te) = f((t/\rho)\rho e) \geq (t/\rho)f(\rho e) = (t/\rho)(\rho e) = te$. So $f(te) = te$. Since $e, \rho e \in \omega(x)$ and $e \ll \rho e$, there exists an integer n_0 such that $f^{n_0}(x) \gg e$. Let $y = f^{n_0}(x)$. Then $\omega(y) = \omega(x)$ and $f^n(y) \geq e, \forall n \geq 0$. It follows that for any $t \in (1, \rho]$, since $e \in \omega(y)$, there exists an integer n_1 such that $e \leq f^{n_1}(y) \leq te$. Thus $e = f^n(e) \leq f^{n_1+n}(y) \leq f^n(te) = te, \forall n \geq 0$, and hence $e \leq \omega(y) \leq te$. Letting $t \to 1$, we get $\omega(y) = e$, contradicting $\rho e \in \omega(y)$. ∎

Lemma 2.3.2. *Let either $V = [0, b]$ with $b \gg 0$ or $V = P$. Assume that $S : V \to V$ is continuous, $S(0) = 0$, and $DS(0)$ exists. If S is subhomogeneous, then $S(u) \leq DS(0)u, \forall u \in V$; If S is strictly subhomogeneous, then $S(u) < DS(0)u, \forall u \in V \cap \mathrm{int}(P)$.*

Proof. For any $u \in V$ with $u > 0$, we have $\|u\| > 0$. In the case where S is subhomogeneous, since $S(0) = 0$ and for any $0 < \alpha < 1$,

$$S(u) \leq \frac{S(\alpha u)}{\alpha} = \frac{S(0) + DS(0)(\alpha u) + o(\|\alpha u\|)}{\alpha} = DS(0)u + \frac{o(\|\alpha u\|)}{\|\alpha u\|} \cdot \|u\|,$$

letting $\alpha \to 0$, we get $S(u) \leq DS(0)u$. If S is strictly subhomogeneous, we further show that $S(u) < DS(0)u$ for all $u \in V$ with $u \gg 0$. Indeed, assume that there exists $u_0 \in V$ with $u_0 \gg 0$ such that $S(u_0) = DS(0)(u_0)$. Then for any $0 < \alpha < 1$, we have $\alpha u_0 \gg 0$ and

$$\alpha S(u_0) < S(\alpha u_0) \leq DS(0)(\alpha u_0) = \alpha DS(0)(u_0) = \alpha S(u_0),$$

which is a contradiction. ∎

Theorem 2.3.4. (Threshold dynamics) *Let either $V = [0, b]_E$ with $b \gg 0$ or $V = P$. Assume that*

(1) $f : V \to V$ satisfies either (C1) or (C3);
(2) $f : V \to V$ is asymptotically smooth, and every positive orbit of f in V is bounded;
(3) $f(0) = 0$, and $Df(0)$ is compact and strongly positive.

Then there exist threshold dynamics:

(a) If $r(Df(0)) \leq 1$, then every positive orbit in V converges to 0;
(b) If $r(Df(0)) > 1$, then there exists a unique fixed point $u^* \gg 0$ in V such that every positive orbit in $V \setminus \{0\}$ converges to u^*.

Proof. Note that the assumption (2) implies that every positive orbit of f in V is precompact, and hence its omega limit set is nonempty, compact, and invariant for f. Then Lemma 2.3.2 and Theorem 2.2.2 prove the conclusion (a). In the case that $r(Df(0)) > 1$, Theorem 2.1.2 and Remark 2.1.5 with $a = 0$ imply that there exists $u^* = f(u^*) \gg 0$ such that for any $0 < u \leq u^*$, $\lim_{n\to\infty} f^n(u) = u^*$. For each $v \in V \setminus \{0\}$, by Claim 1 in the proof of Theorem 2.1.2, we have $f(v) \gg 0$. Then there exists a sufficiently small number $\epsilon \in (0, 1]$ such that $\epsilon u^* \leq f(v)$, and hence the monotonicity of f implies that $f^n(\epsilon u^*) \leq f^{n+1}(v), \forall n \geq 0$. Since $\lim_{n\to\infty} f^n(\epsilon u^*) = u^*$, we get $0 \ll u^* \leq \omega(v)$. Thus $\omega(v) \subset \text{int}(P)$. Then Theorem 2.3.2 implies that $\omega(v) = u^*$. ∎

Remark 2.3.1. The conclusion (a) also holds in the case where $V = P$, (C2) holds, and $r(Df(0)) < 1$. Indeed, for each $u \in P$, by Lemma 2.3.2, $f(u) \leq Df(0)u$, and hence the monotonicity of f implies that $0 \leq f^n(u) \leq (Df(0))^n u, \forall n \geq 0$. Since $r(Df(0)) < 1$, we get $(Df(0))^n u \to 0$, and hence $f^n(u) \to 0$ as $n \to \infty$.

Recall that $f : P \to P$ is said to be strongly concave if for every $u \gg 0$ and $\alpha \in (0, 1)$, there exists $\eta = \eta(u, \alpha) > 0$ such that $f(\alpha u) \geq (1 + \eta)\alpha f(u)$ (see [204]). Clearly, strong concavity implies strict subhomogeneity. In [317], $f : P \to P$ is said to be concave if f is (Fréchet) differentiable on P and $Df(v) - Df(u) > 0$ for all $u \gg v \gg 0$. It is easy to see that concavity also implies strict subhomogeneity. Indeed, for any $0 < \alpha < 1$, $u \gg 0$,

$$\begin{aligned} f(\alpha u) &= f(0) + \alpha \int_0^1 Df(s\alpha \cdot u)u \cdot ds \\ &> f(0) + \alpha \int_0^1 Df(su)u \cdot ds \\ &= (1 - \alpha)f(0) + \alpha f(u) \geq \alpha f(u). \end{aligned}$$

Let $\mathbb{R}_+ = [0, \infty)$, and let Y be a compact metric space with metric d. Recall that a flow $\sigma : Y \times \mathbb{R} \to Y$ is said to be minimal if Y contains no nonempty, proper, closed invariant subset; distal if for any two distinct points y_1 and y_2 in Y, $\inf_{t\in\mathbb{R}} d(\sigma(y_1, t), \sigma(y_2, t)) > 0$. Clearly, a flow $\sigma : Y \times \mathbb{R} \to Y$ is minimal if and only if every full orbit is dense in Y.

In the rest of this section we assume that $\sigma : Y \times \mathbb{R} \to Y$ is a minimal and distal flow, and consider a continuous semiflow $\Pi : P \times Y \times \mathbb{R}^+ \to P \times Y$ of the form

$$\Pi(x, y, t) = (u(x, y, t), \sigma(y, t)), \ \forall (x, y, t) \in P \times Y \times \mathbb{R}^+;$$

that is, Π is a skew-product semiflow on $P \times Y$. We set $p : X \times Y \to Y$ as the natural projection, and also use the notation $\sigma(t)(y) = \sigma(y,t)$ and $\Pi_t(x,y) = \Pi(x,y,t)$. It is well known that for any precompact forward orbit $\gamma^+(x,y) := \{\Pi_t(x,y) : t \geq 0\}$ in P, its omega limit set $\omega(x,y)$ is a compact and (positively) invariant set for Π. Then we have the following result.

Theorem 2.3.5. (Global attractivity) *Let Π_t be a skew-product semiflow on $P \times Y$. Assume that*

(A1) For any $\lambda \in (0,1), x_1, x_2 \in \mathrm{int}(P)$, $\lambda x_1 \leq x_2 \leq \lambda^{-1} x_1$ implies that $\lambda u(x_1,y,t) \leq u(x_2,y,t) \leq \lambda^{-1} u(x_1,y,t)$, $\forall (y,t) \in Y \times \mathbb{R}^+$;
(A2) There exist $y_0 \in Y$ and $t_0 > 0$ such that for any $\lambda \in (0,1), x_1, x_2 \in \mathrm{int}(P)$, $\lambda x_1 \leq x_2 \leq \lambda^{-1} x_1$ implies that $\lambda u(x_1,y_0,t_0) \ll u(x_2,y_0,t_0) \ll \lambda^{-1} u(x_1,y_0,t_0)$.

If Π_t has a precompact forward orbit with its omega limit set $K_0 \subset \mathrm{int}(P) \times Y$, then the semiflow $\Pi_t : K_0 \to K_0$ admits a flow extension such that $p : (\Pi, K_0) \to (\sigma, Y)$ is a flow isomorphism, and for every compact omega limit set $\omega(x,y) \subset \mathrm{int}(P) \times Y$, we have $\omega(x,y) = K_0$ and $\lim_{t\to\infty} \|u(x,y,t) - u(x^*,y,t)\| = 0$, where $(x^*,y) = K_0 \cap p^{-1}(y)$. Moreover, the map $h : Y \to P$, defined by $h(y) = x^*$, $\forall y \in Y$, is continuous.

Proof. We define the part metric ρ on $\mathrm{int}(P)$ by

$$\rho(x_1,x_2) := \inf\{\ln \alpha : \alpha \geq 1 \,\mathrm{and}\, \alpha^{-1} x_1 \leq x_2 \leq \alpha x_1\},\ \forall x_1, x_2 \in \mathrm{int}(P).$$

Then $(\mathrm{int}(P), \rho)$ is a metric space (see, e.g., [373, 259]). By the triangle inequality for metric functions, it is easy to see that $\rho(\cdot,\cdot) : \mathrm{int}(P) \times \mathrm{int}(P) \to \mathbb{R}$ is continuous with respect to the product topology induced by the metric ρ. Given $x_0 \in \mathrm{int}(P)$, we can choose a real number $r > 0$ such that the closed norm ball $\overline{B}(x_0, 2r) := \{x \in X : \|x - x_0\| \leq 2r\}$ is contained in $\mathrm{int}(P)$. Then for any $x \in \overline{B}(x_0, r)$, $\overline{B}(x, r) \subset \mathrm{int}(P)$. By [205, Lemma 2.3 (i)], we have

$$\rho(x, x_0) \leq \ln\left(1 + \frac{\|x - x_0\|}{r}\right),\ \forall x \in \overline{B}(x_0, r).$$

Thus $\lim_{n\to\infty} \|x_n - x_0\|$ implies $\lim_{n\to\infty} \rho(x_n, x_0) = 0$ for any sequence $\{x_n\}$ and point x_0 in $\mathrm{int}(P)$. It then follows that $\rho(\cdot,\cdot) : \mathrm{int}(P) \times \mathrm{int}(P) \to \mathbb{R}$ is also continuous with respect to the product topology induced by the norm $\|\cdot\|$. With (A1) and (A2), we further have the following two claims, respectively.

Claim 1. $\rho(u(x_1,y,t), u(x_2,y,t)) \leq \rho(x_1,x_2)$, $\forall x_1, x_2 \in \mathrm{int}(P)$ and $(y,t) \in Y \times \mathbb{R}^+$ with $u(x_i,y,t) \in \mathrm{int}(P), i = 1, 2$.

Indeed, let $\rho(x_1,x_2) = \ln \alpha_0 > 0$. Then $\alpha_0 > 1$, and hence $0 < \alpha_0^{-1} < 1$. Since $\alpha_0^{-1} x_1 \leq x_2 \leq \alpha_0 x_1$, by assumption (A1),

$$\alpha_0^{-1} u(x_1,y,t) \leq u(x_2,y,t) \leq \alpha_0 u(x_1,y,t), \forall (y,t) \in Y \times \mathbb{R}^+.$$

It then follows that $\rho(u(x_1,y,t), u(x_2,y,t)) \leq \ln \alpha_0 = \rho(x_1,x_2), \forall (y,t) \in Y \times \mathbb{R}^+$.

Claim 2. $\rho(u(x_1, y_0, t_0), u(x_2, y_0, t_0)) < \rho(x_1, x_2), \forall x_1, x_2 \in \text{int}(P)$ with $x_1 \neq x_2$ and $u(x_i, y_0, t_0) \in \text{int}(P), i = 1, 2$.

In fact, let α_0 be as in the proof of Claim 1. By assumption (A2), we get

$$\alpha_0^{-1} u(x_1, y_0, t_0) \ll u(x_2, y_0, t_0) \ll \alpha_0 u(x_1, y_0, t_0).$$

Since $\text{int}(P)$ is an open subset of X, we can choose an $\alpha_1 \in (1, \alpha_0)$ sufficiently close to α_0 such that

$$\alpha_1^{-1} u(x_1, y_0, t_0) \ll u(x_2, y_0, t_0) \ll \alpha_1 u(x_1, y_0, t_0).$$

It then follows that $\rho(u(x_1, y_0, t_0), u(x_2, y_0, t_0)) \leq \ln \alpha_1 < \ln \alpha_0 = \rho(x_1, x_2)$.

Let $Z := \{((x_1, y), (x_2, y)) : x_1, x_2 \in \text{int}(P),\ y \in Y\}$, and define a continuous function $\tilde{\rho} : Z \to \mathbb{R}^+$ by $\tilde{\rho}((x_1, y), (x_2, y)) = \rho(x_1, x_2)$, $\forall (x_1, y), (x_2, y) \in Z$. Since $K_0 \subset \text{int}(P) \times Y$, Claim 1 implies that the skew-product semiflow $\Pi_t : K_0 \to K_0$ is contracting with respect to $\tilde{\rho}$ in the sense that

$$\tilde{\rho}(\Pi(x_1, y, t), \Pi(x_2, y, t)) \leq \tilde{\rho}((x_1, y), (x_2, y)), \quad \forall (x_1, y), (x_1, y) \in K_0,\ t \geq 0.$$

Clearly, $\tilde{\rho}((x_1, y), (x_2, y)) = 0$ if and only if $(x_1, y) = (x_2, y)$. Since K_0 is the omega limit set of a precompact forward orbit, every point in K_0 admits a backward orbit in K_0. By [311, Lemma II.2.10 1) and 2)], it then follows that $\Pi_t : K_0 \to K_0$ admits a flow extension (i.e., every point in K_0 has a unique backward orbit), and this flow is distal. We further claim that $\text{card}(K_0 \cap p^{-1}(y_0)) = 1$. Suppose for contradiction that there are two distinct points (x_1, y_0) and (x_2, y_0) in $K_0 \cap p^{-1}(y_0)$. Then (x_1, y_0) and (x_2, y_0) are distal for the flow $\Pi_t : K_0 \to K_0$. By an Ellis semigroup argument (see, e.g., the proof of [311, Lemma II.2.10 3)]), there exists a sequence $t_n \to \infty$ such that $\lim_{n\to\infty} \Pi_{t_n}(x_i, y_0) = (x_i, y_0)$, and hence $\lim_{n\to\infty} u(x_i, y_0, t_n) = x_i$, $i = 1, 2$. Let $(\bar{x}_i, \bar{y}) = \Pi_{t_0}(x_i, y_0) \in K_0 \subset \text{int}(P) \times Y$, $i = 1, 2$. Then $\Pi_{t_n}(x_i, y_0) = \Pi_{t_n - t_0}(\bar{x}_i, \bar{y}), \forall n \geq 1$. By Claims 1 and 2, we get

$$\begin{aligned}
\rho(x_1, x_2) &= \lim_{n\to\infty} \rho(u(x_1, y_0, t_n), u(x_2, y_0, t_n)) \\
&= \lim_{n\to\infty} \rho(u(\bar{x}_1, \bar{y}, t_n - t_0), u(\bar{x}_2, \bar{y}, t_n - t_0)) \\
&\leq \rho(\bar{x}_1, \bar{x}_2) = \rho(u(x_1, y_0, t_0), u(x_2, y_0, t_0)) \\
&< \rho(x_1, x_2),
\end{aligned}$$

a contradiction. By the structure theorem of skew-product flows ([300, Theorem 1]), as applied to the flow $\Pi_t : K_0 \to K_0$, it then follows that card $(K_0 \cap p^{-1}(z)) = 1$, $\forall z \in Y$, and hence $p : (\Pi, K_0) \to (\sigma, Y)$ is a flow isomorphism. In particular, $\Pi_t : K_0 \to K_0$ is minimal.

Let $K = \omega(x, y) \subset \mathrm{int}(P) \times Y$. By what we have proved, the flow extension of the semiflow $\Pi_t : K \to K$ is distal and minimal, and card $(K \cap p^{-1}(z)) = 1$, $\forall z \in Y$. In order to prove $K = K_0$, by the minimality of both $\Pi_t : K_0 \to K_0$ and $\Pi_t : K \to K$, it suffices to prove that $K_0 \cap K \neq \emptyset$. Assume for contradiction that $K_0 \cap K = \emptyset$, then $d(K_0, K) > 0$, where d is the metric on the product space $X \times Y$. Let $(x_1, y_0) = K_0 \cap p^{-1}(y_0)$ and $(x_2, y_0) = K \cap p^{-1}(y_0)$. Then (x_1, y_0) and (x_2, y_0) are distal for the flow $\Pi_t : K_0 \cup K \to K_0 \cup K$. Using the same arguments as in the last paragraph, we get a contradiction. Therefore, $K = K_0$. To prove $\lim_{t\to\infty} \|u(x, y, t) - u(x^*, y, t)\| = 0$, suppose, by contradiction, that there exist an $\epsilon_0 > 0$ and a sequence $t_n \to \infty$ such that $\|u(x, y, t_n) - u(x^*, y, t_n)\| \geq \epsilon_0$, $\forall n \geq 1$. Since $\gamma^+(x, y)$ and $\gamma^+(x^*, y)$ are precompact, without loss of generality we assume that $\lim_{n\to\infty} \Pi(x, y, t_n) = (x_1^*, y^*) \in K$ and $\lim_{n\to\infty} \Pi(x^*, y, t_n) = (x_2^*, y^*) \in K$. Since $K = K_0$ and $\mathrm{card}(K_0 \cap p^{-1}(y^*)) = 1$, we get $x_1^* = x_2^*$. Thus $0 = \|x_1^* - x_2^*\| = \lim_{n\to\infty} \|u(x, y, t_n) - u(x^*, y, t_n)\| \geq \epsilon_0$, a contradiction. It then follows that $\lim_{t\to\infty} \|u(x, y, t) - u(x^*, y, t)\| = 0$. Since $\sigma : Y \times \mathbb{R} \to Y$ is a minimal and distal flow and $p : (\Pi, K_0) \to (\sigma, Y)$ is a flow isomorphism, [311, Theorem I.2.6] implies that $p : K_0 \to Y$ is an open map. Thus, $p^{-1} : Y \to K_0$ is continuous. In view of $p^{-1}(y) = (h(y), y)$, $\forall y \in Y$, we then get the continuity of h on Y. ∎

Remark 2.3.2. It is easy to see that the following two conditions are sufficient for (A1) and (A2):

(A1)′ For each $(y, t) \in Y \times \mathbb{R}^+$, $u(\cdot, y, t)$ is monotone and subhomogeneous on P;

(A2)′ There exist $y_0 \in Y$ and $t_0 > 0$ such that $u(\cdot, y_0, t_0)$ is strongly subhomogeneous on P.

Remark 2.3.3. If we assume that (A1)′ holds, then the following condition implies (H2)′:

(A2)″ There exist $y_0 \in Y$, $t_1 > 0$, and $t_2 > 0$ such that $u(\cdot, y_0, t_1)$ is strictly subhomogeneous on P and $u(\cdot, \sigma(t_1)y_0, t_2)$ is strongly monotone on P.

Indeed, given $\lambda \in (0, 1)$ and $x \in \mathrm{int}(P)$, the strict subhomogeneity of $u(\cdot, y_0, t_1)$ implies that $u(\lambda x, y_0, t_1) > \lambda u(x, y_0, t_1)$. By the strong monotonicity of $u(\cdot, \sigma(t_1)y_0, t_2)$ and assumption (A1)′, it follows that

$$\begin{aligned} u(u(\lambda x, y_0, t_1), \sigma(t_1)y_0, t_2) \gg & u(\lambda u(x, y_0, t_1), \sigma(t_1)y_0, t_2) \\ \geq & \lambda u(u(x, y_0, t_1), \sigma(t_1)y_0, t_2). \end{aligned}$$

Since $\Pi_{t_2} \circ \Pi_{t_1} = \Pi_{t_1+t_2}$, we get $u(\lambda x, y_0, t_1 + t_2) \gg \lambda u(x, y_0, t_1 + t_2)$. Thus (A2)′ holds with $t_0 = t_1 + t_2 > 0$.

2.4 Competitive Systems on Ordered Banach Spaces

For $i = 1, 2$, let X_i be ordered Banach spaces with positive cones X_i^+ such that $\mathrm{int}(X_i^+) \neq \emptyset$. Let $X = X_1 \times X_2$, $X^+ = X_1^+ \times X_2^+$, and $K = X_1^+ \times (-X_2^+)$. Then $\mathrm{int}(X^+) = \mathrm{int}(X_1^+) \times \mathrm{int}(X_2^+) \neq \emptyset$ and $\mathrm{int}(K) = \mathrm{int}(X_1^+) \times (-\mathrm{int}(X_2^+)) \neq \emptyset$. We will make the following hypotheses, which capture the essence of competition between two adequate competitors:

(D1) $f : X^+ \to X^+$ is order compact and strictly monotone with respect to $<_K$;
(D2) 0 is a repelling fixed point of f in the sense that there exists a neighborhood U_0 of 0 in X^+ such that for each $x \in U_0$ with $x \neq 0$, there is an integer $n = n(x)$ such that $f^n(x) \notin U_0$;
(D3) $f(X_1^+ \times \{0\}) \subset X_1^+ \times \{0\}$, and there exists $\hat{x}_1 \in \mathrm{int}(X_1^+)$ such that $f((\hat{x}_1, 0)) = (\hat{x}_1, 0)$ and $\omega((x_1, 0)) = (\hat{x}_1, 0)$ for every $x_1 \in X_1^+ \setminus \{0\}$. The symmetric conditions hold for f on $\{0\} \times X_2$, and the fixed point is denoted by $(0, \tilde{x}_2)$;
(D4) If $x, y \in X^+$ satisfy $x <_K y$ and either x or y belongs to $\mathrm{int}(X^+)$, then $f(x) \ll_K f(y)$. If $x = (x_1, x_2) \in X^+$ with $x_i \neq 0, i = 1, 2$, then $f(x) \gg 0$.

Let $E_0 = (0, 0)$, $E_1 = (\hat{x}_1, 0)$, $E_2 = (0, \tilde{x}_2)$. We say that a fixed point E_* of f is positive if $E_* \in \mathrm{int}(X^+)$. Let $I = [E_2, E_1]_K$. It is easy to see that $I = [0, \hat{x}_1] \times [0, \tilde{x}_2]$. The following result says that for a competitive system, either there is a positive fixed point of f, representing coexistence of the two populations, or one population drives the other to extinction.

Theorem 2.4.1. (TRICHOTOMY) *Let (D1)–(D4) hold. Then the omega limit set of every orbit in X^+ is contained in I, and exactly one of the following holds:*

(a) There exists a positive fixed point E_* of f in I;
(b) $\omega(x) = E_1$ for every $x = (x_1, x_2) \in I$ with $x_i \neq 0, i = 1, 2$;
(c) $\omega(x) = E_2$ for every $x = (x_1, x_2) \in I$ with $x_i \neq 0, i = 1, 2$.

Finally, if (b) or (c) holds and $x = (x_1, x_2) \in X^+ \setminus I$ with $x_i \neq 0, i = 1, 2$, then either $\omega(x) = E_1$ or $\omega(x) = E_2$.

Proof. We begin by showing that I attracts all orbits. By (D3)–(D4), we may assume that $f^n(x) \gg 0, \forall n \geq 0$. If $x = (x_1, x_2)$, let $u = (x_1, 0)$ and $v = (0, x_2)$ and observe that $v <_K x <_K u$. Consequently,

$$f^n(v) <_K f^n(x) <_K f^n(u), \forall n \geq 1.$$

$(D2)$ implies that $f^n(v) \to E_2$ and $f^n(u) \to E_1$. In particular, if $s > 1$, then $f^n(x) \in [0, s\hat{x}_1] \times [0, s\tilde{x}_2]$ for all large n. Since f is order compact, we conclude that $\gamma^+(x)$ is precompact in X, and hence $\omega(x)$ exists and is compact and invariant for f. Thus the inequality above implies that $\omega(x) \subset I$.

We then consider $f : I := [E_2, E_1]_K \to I$. Clearly, E_0 is an extreme point of I, and by (D2), it is an ejective fixed point of f. By the Dancer–Hess connecting orbit lemma and Remark 2.1.3, at least one of the following holds:

(a) f has a fixed point distinct from E_0, E_1, E_2 in I;
(b) there exists an entire orbit $\{x_n\}_{n=-\infty}^{\infty}$ of f in I such that $x_{n+1} >_K x_n, \forall n \in \mathbb{N}$, and $\lim_{n\to-\infty} x_n = E_2$ and $\lim_{n\to\infty} x_n = E_1$;
(c) there exists an entire orbit $\{y_n\}_{n=-\infty}^{\infty}$ of f in I such that $y_{n+1} <_K y_n, \forall n \in \mathbb{N}$, and $\lim_{n\to-\infty} y_n = E_1$ and $\lim_{n\to\infty} y_n = E_2$.

Clearly, $E_2 \ll_K E_1$. We claim that (b) and (c) cannot both hold. For in that case, since $\lim_{n\to-\infty} y_n = E_1 \gg_K E_2 = \lim_{n\to-\infty} x_n$, there exist $m_0, n_0 \in \mathbb{N}$ such that $x_{m_0} \ll_K y_{n_0}$. By the strict monotonicity of f with respect to $<_K$, we then get $x_{m_0+l} = f^l(x_{m_0}) <_K f^l(y_{n_0}) = y_{n_0+l}, \forall l \geq 0$. Letting $l \to \infty$ leads to the contradiction $E_1 \leq_K E_2$. If $E_* = (x_1, x_2)$ is a fixed point of f distinct from E_0, E_1, E_2 in I, then $x_i \neq 0$ for $i = 1, 2$ by (D3). By (D4), $E_* = f(E_*) \gg 0$. Again by (D4), we get $E_2 \ll_K E_* \ll_K E_1$. We further show that (a) and (b) and (a) and (c) are incompatible. Suppose (a) and (b) hold for f and let $\{x_n\}_{n\in\mathbb{N}}$ be the entire orbit described in (b). Then f has a fixed point $u \in [[E_2, E_1]]_K$, and $x_{n_0} \ll u$ for some $n_0 \in \mathbb{N}$. Then the strict monotonicity of f implies that $x_{n_0+l} <_K u, \forall l \geq 0$. Letting $l \to \infty$ leads to the contradiction $E_1 \leq u$. A similar contradiction follows in case (a) and (c) hold. It then follows that precisely one of the alternatives (a), (b), (c) above holds. In the case where (b) holds, for any $x = (x_1, x_2) \in I$ with $x_i \neq 0, i = 1, 2$, by (D4), $f(x) \gg 0$. Since $E_2 <_K f(x) <_K E_1$, (D4) implies that $E_2 \ll_K f^2(x) \ll_K E_1$. Thus we can choose $n \in \mathbb{N}$ such that $x_n \ll_K f^2(x)$. By monotonicity, it follows that $x_{n+l} \ll_K f^{l+2}(x) \ll_K E_1$, $\forall l \geq 0$. Letting $l \to \infty$ and noting that $\gamma^+(x)$ is precompact, we get $\omega(x) = E_1$. Similarly, we can prove the convergence in the case where (c) holds.

In the case where either (b) or (c) holds, every orbit in I converges to one of three fixed points E_0, E_1, E_2. Clearly, each E_i is an isolated invariant set for $f : I \to I$, and there is no cyclic chain among the E_i's. By Theorem 1.2.2, every internally chain transitive set for $f : I \to I$ is a fixed point. For any $x \in X^+$, we have shown that $\omega(x) \subset I$, and hence $\omega(x)$ is internally chain transitive for $f : I \to I$. Thus, $\omega(x)$ consists of one of E_0, E_1, E_2. If $x \neq 0$, (D2) implies that *either* $\omega(x) = E_1$ *or* $\omega(x) = E_2$. ∎

Remark 2.4.1. By Theorem 2.4.1, it is easy to see that if E_1 and E_2 are simultaneously either stable or unstable for $f : I \to I$; or if there exists a point $x \in X^+$ such that $\omega(x) \cap \mathrm{int}(X^+) \neq \emptyset$, then there is a positive fixed point of f.

Proposition 2.4.1. *Let (D1)–(D4) hold and assume that f has a positive fixed point. If E_1 is an isolated fixed point of f, then there exists a positive fixed point E_* in I such that exactly one of the following holds:*

(i) $\omega(x) = E_*$ *for every* $x = (x_1, x_2)$ *satisfying* $E_* \leq_K x <_K E_1$ *and* $x_2 \neq 0$*;*

(ii) $\omega(x) = E_1$ *for every* $x = (x_1, x_2)$ *satisfying* $E_* <_K x \leq_K E_1$.

A symmetric conclusion holds if E_2 *is an isolated fixed point of* f.

Proof. Let x_* denote a positive fixed point of f, which by (D4) must satisfy $E_2 \ll_K x_* \ll_K E_1$. The set $W := \{\bar{x} : f(\bar{x}) = \bar{x}, x_* \leq_K \bar{x} \ll_K E_1\}$ is partially ordered by $\leq_K$. Using the compactness of the set of fixed points, the fact that E_1 is an isolated fixed point, and a simple Zorn's lemma argument, one can show that W contains a weakly maximal element E_* in the sense that $u \in W$ and $u \geq_K E_*$ implies that $u = E_*$. Obviously, the order interval $[E_*, E_1]_K$ contains no fixed points of f other than E_* and E_1. By the Dancer–Hess connecting orbit lemma, there exists a monotone entire orbit $\{x_n\}$ that either connects E_* to E_1 or connects E_1 to E_*. Suppose the former holds. Then, arguing as in the proof of Theorem 2.4.1(b), we have $\omega(x) = E_1$ for any $x = (x_1, x_2)$ satisfying $E_* <_K x \leq_K E_1$ and $x_2 \neq 0$. The same conclusion holds if $x_2 = 0$ by (D3). A similar argument shows that (i) holds if $\{x_n\}$ connects E_1 to E_*. ∎

Theorem 2.4.2. (Compression) *Let (D1)–(D4) hold and assume that* E_1 *and* E_2 *are isolated fixed points of* f. *Let* $W^s(E_i)$ *be the stable set of* E_i *for* $f : X^+ \to X^+$. *If* $W^s(E_i) \cap \mathrm{int}(X^+) = \emptyset$, $i = 1, 2$, *then there exist positive fixed points* $E_{**} \leq_K E_*$ *of* f *such that* $\omega(x) = E_*$ *for every* $x = (x_1, x_2)$ *satisfying* $E_* \leq_K x <_K E_1$ *and* $x_2 \neq 0$, $\omega(x) = E_{**}$ *for every* $x = (x_1, x_2)$ *satisfying* $E_2 <_K x \leq_K E_{**}$ *and* $x_1 \neq 0$, *and the order interval* $[E_{**}, E_*]_K$ *attracts any point in* $(X_1^+ \setminus \{0\}) \times (X_2^+ \setminus \{0\})$.

Proof. Since $W^s(E_i) \cap \mathrm{int}(X^+) = \emptyset, i = 1, 2$, either (b) or (c) in Theorem 2.4.1 does not hold. By Theorem 2.4.1, there exists a positive fixed point of f in I. Thus, by Proposition 2.4.1, there exist positive fixed points E_{**} and E_* of f in I such that $\omega(x) = E_*$ for every $x = (x_1, x_2)$ satisfying $E_* \leq_K x <_K E_1$ and $x_2 \neq 0$, and $\omega(x) = E_{**}$ for every $x = (x_1, x_2)$ satisfying $E_2 <_K x \leq_K E_{**}$ and $x_1 \neq 0$. By (D4), we have $E_2 \ll_K E_{**}, E_* \ll_K E_1$. Let $x \in (X_1^+ \setminus \{0\}) \times (X_2^+ \setminus \{0\})$ be given. Then $f(x) \in \mathrm{int}(X^+)$ by (D4). By Theorem 2.4.1, $\omega(x) \subset I$. We further claim that $\omega(x) \cap \mathrm{int}(X^+) \neq \emptyset$. Indeed, suppose that $\omega(x) \cap \mathrm{int}(X^+) = \emptyset$. Then (D4) and the invariance of $\omega(x)$ imply that $\omega(x) \subset Y := \{(x_1, x_2) \in X^+ : x_1 = 0 \,\mathrm{or}\, x_2 = 0\}$. Thus, $\omega(x)$ is an internally chain transitive set for $f : Y \to Y$. By applying Theorem 1.2.2 to $f : Y \to Y$, we get $\omega(x) = E_i$, and hence $f(x) \in W^s(E_i) \cap \mathrm{int}(X^+)$ for some $0 \leq i \leq 2$, which contradicts our assumption. Let $y \in \omega(x) \cap \mathrm{int}(X^+)$. Then $E_2 <_K y <_K E_1$, and $E_2 \ll_K f(y) \ll_K E_1$ by (D4). Since $f(y) \in \omega(x)$ and $[[E_2, E_1]]$ is an open set, there is a positive integer m such that $E_2 \ll_K f^m(x) \ll_K E_1$. Thus we can further choose two points u and v such that $E_2 \ll_K u \ll_K E_{**}$, $E_* \ll_K v \ll_K E_1$ and $u \ll_K f^m(x) \ll_K v$. By the monotonicity of f, $f^n(u) \leq_K f^{m+n}(x) \leq_K f^n(v)$, $\forall n \geq 0$. Letting $n \to \infty$, we then get $E_{**} = \lim_{n\to\infty} f^n(u) \leq_K \omega(x) \leq_K \lim_{n\to\infty} f^n(v) = E_*$. ∎

2.5 Saddle Point Behavior

Let (X, X^+) be an ordered Banach space with positive cone X^+ having nonempty interior $\text{int}(X^+)$. A subset M of X^+ is said to be unordered if there are no two points $x, y \in M$ with $x < y$. We write $[a, \infty]] = \{x \in X^+ : x \geq a\}$, and similarly for $[[-\infty, b]$. A subset Y of X is said to be lower closed if $[[-\infty, b] \subset Y$ whenever $b \in Y$, and upper closed if $[a, \infty]] \subset Y$ whenever $a \in Y$.

Let $\Phi := \{\Phi_t\}_{t\geq 0}$ be a continuous semiflow on X^+. For any $x \in X^+$, we use $\omega(x)$ to denote the omega limit set of the positive orbit $\gamma^+(x) := \{\Phi_t(x) : t \geq 0\}$. An equilibrium e is a point for which $\Phi_t(e) = e, \forall t \geq 0$. An equilibrium e is said to be locally stable if for any neighborhood U of e, there is another neighborhood V of e such that $\Phi_t(V) \subset U, \forall t \geq 0$; asymptotically stable if it is stable and there is a neighborhood U of e such that $\omega(y) = \{e\}, \forall y \in U$. We say that x is convergent if $\omega(x)$ is a singleton, and quasiconvergent if $\omega(x)$ consists of equilibria. Recall that Φ is monotone if $\Phi_t(x) \leq \Phi_t(y)$ whenever $x, y \in X^+$ with $x \leq y$ and $t > 0$; strongly order-preserving, SOP for short, provided Φ is monotone and for any $x < y$, there are some $t_0 > 0$ and open subsets U, V of X^+ with $x \in U,\ y \in V$ such that $\Phi_{t_0}(U) < \Phi_{t_0}(V)$; strongly monotone if $\Phi_t(x) \ll \Phi_t(y)$ whenever $x, y \in X^+$ with $x < y$ and $t > 0$.

For a fixed $v \in \text{int}(X^+)$, the order norm is defined by

$$|x|_v = \inf\{\lambda \in \mathbb{R}^+ : -\lambda v \leq x \leq \lambda v\},$$

which induces the order topology in X. If the cone is normal, then the order norm is equivalent to the original one. Throughout this section, we use $\alpha(B)$ to denote the Kuratowski measure of noncompactness for a bounded set B.

Let $M \subset X^+$ be a subset. A point z is in the lower boundary of M, $\partial_- M$, provided there is a sequence $\{s_i\}$ in M converging to z with $s_i \gg z$, but no sequence $\{x_i\}$ in M converging to z with $x_i \ll z$. The upper boundary, $\partial_+ M$, is defined analogously.

Definition 2.5.1. *A pair (A, B) is called an order decomposition of X^+ if it has the following three properties:*

(1) A and B are nonempty and closed subsets of X^+;
(2) A is lower closed and B is upper closed;
(3) $A \cup B = X^+$ and $\text{int}(A \cap B) = \emptyset$.

An order decomposition (A, B) of X^+ is called invariant if A and B are positively invariant, that is, $\Phi_t(A) \subset A$ and $\Phi_t(B) \subset B, \forall t \geq 0$. The set $H = A \cap B$ is called the boundary of the order decomposition (A, B) of X^+. A d-hypersurface is any subset H of X^+ such that $H = A \cap B$ for some order decomposition (A, B) of X^+.

Note that the boundary H of an order decomposition (A, B) of X^+ satisfies

$$H = \partial A = \partial B,$$

where ∂ is the boundary symbol in X^+, and H is unordered and positively invariant whenever (A, B) is invariant.

Lemma 2.5.1. (Takáč [351, Proposition 1.3]) *Let Φ be a SOP semiflow with all positive orbits being precompact, and Φ_τ be strongly monotone for some positive number τ. Then the boundary of every order decomposition is an unordered and positively invariant one-codimensional Lipschitz manifold in the ordered norm $|\cdot|_v$.*

Lemma 2.5.2. (Generalized Krein-Rutman theorem, Nussbaum [258]) *Let $L : X \to X$ be a strongly positive and bounded linear operator. Assume that the essential spectral radius $r_e(L)$ of L is less than the spectral radius $r(L)$ of L. Then $r(L)$ is an algebraically simple eigenvalue of L with an eigenvector $v \in \mathrm{int}(K)$, and all other eigenvalues of L have their absolute values less than $r(L)$.*

Lemma 2.5.3. (Smith and Thieme [332, Proof of Theorem 3.4]) *Let U be an open subset of X and $S : U \to X$ be a continuous and monotone map. Assume that S has a fixed point $x^* \in U$ such that*

(a) The Frechét derivative $DS(x^*) : X \to X$ exists, $DS(x^*)$ is strongly positive and bounded, and $r(DS(x^*)) = 1$;
(b) x^* does not attract any point $x \in U$ with either $x > x^*$ or $x < x^*$.

Then there is a $\delta > 0$ such that the set $W^s_\delta := \{x \in U : \|x - x^*\| < \delta, \lim\limits_{n\to\infty} S^n(x) = x^*\}$ is a local strongly stable manifold of S at x^*.

We will impose the following assumptions on Φ:

(H1) There is a positive number τ such that the mapping Φ_τ is a strict α-contraction, that is, there is a positive number $k < 1$ such that $\alpha(\Phi_\tau(B)) \le k\alpha(B)$ for any bounded subset $B \subset X^+$;
(H2) The semiflow Φ is uniformly bounded in the sense that $\gamma^+(B) := \bigcup\limits_{t\ge 0} \Phi_t(B)$ is bounded whenever B is a bounded subset of X^+.

Theorem 2.5.1. *Suppose that the SOP semiflow Φ satisfies* (H1)–(H2)*, that Φ has exactly three equilibria a, c, b such that $a \ll c \ll b$, and a, b are locally stable in X^+, and that the mapping Φ_τ is continuously differentiable in a neighborhood of c and $D_x\Phi_\tau(c)$ is strongly positive. Then $M = X^+ \backslash \{B_a \cup B_b\}$ is an unordered and positively invariant set, where B_a, B_b are the basins of attraction of a, b, respectively.*

Proof. First, we prove that every positive orbit has compact closure and $\omega(B) := \cap_{s>0}\overline{\Phi_s(\gamma^+(B))}$ is compact for any bounded subset $B \subset X^+$. It is easy to see that the orbit arc on $[0, \tau]$ is compact, where τ is given in the assumption (H1). By assumption (H2), it follows that

$$\alpha(\gamma^+(x)) = \alpha(\gamma^+(\Phi_\tau(x))) = \alpha(\Phi_\tau(\gamma^+(x))) \le k\alpha(\gamma^+(x)).$$

Since $0 < k < 1$, we have $\alpha(\gamma^+(x)) = 0$. Thus, $\gamma^+(x)$ is precompact, that is, $\gamma^+(x)$ has compact closure for every $x \in X^+$. By induction, it is not difficult to show that $\alpha(\Phi_{n\tau}(B)) \le k^n\alpha(B), \forall n \ge 1$. By the definition of $\omega(B)$, it follows that

$$\alpha(\omega(B)) \le \alpha(\overline{\Phi_{n\tau}(\gamma^+(B))}) = \alpha(\Phi_{n\tau}(\gamma^+(B))) \le k^n\alpha(B), \forall n \ge 1.$$

Letting $n \to \infty$, we obtain that $\alpha(\omega(B)) = 0$, and hence, $\omega(B)$ is compact. Consequently, for any fixed $x \in X^+$ and any sequence $\{x_n\}$ satisfying $x_n < x_{n+1} < x(x < x_{n+1} < x_n), \forall n \ge 1$, and $x_n \to x$ as $n \to \infty$, $\bigcup_{n\ge 0}\omega(x_n)$ has compact closure in X^+, that is, the condition (C) in [326, Chapter 1] is satisfied. Applying [326, Theorem 1.4.3], we conclude that the quasiconvergence is generic. Since Φ possesses exactly three equilibria, we have generic convergence for Φ in X^+, that is, X^+ contains an open and dense subset such that any orbit from this subset converges to one of the equilibria $a,\ c,\ b$. Furthermore, utilizing Dancer–Hess Lemma of connecting orbits and the monotonicity for Φ, we get that $[a, c]\backslash\{c\} \subset B_a$ and $[c, b]\backslash\{c\} \subset B_b$, where B_a, B_b are the basins of attraction of $a,\ b$, respectively.

Suppose, by contradiction, that the theorem does not hold. Then there are two points $x, y \in M$ with $x < y$. Since M is positively invariant and Φ is SOP, there is a neighborhood U' of x such that $\Phi_{t_0}(U') < \Phi_{t_0}(y)$, where t_0 is given in the definition of SOP. On the other hand, we can find an open subset U'' of U' such that $x < U''$ since X^+ has a nonempty interior. Since U'' is generically convergent, c attracts an open subset U of U''. We claim that we can choose U as close to c as we wish. In fact, we can find two points $z, z' \in U$ with $z < z'$ and then $\Phi_t(z) < \Phi_t(z'), \forall t > 0$. For sufficiently large t, $\Phi_t(z), \Phi_t(z')$ are close to c enough. Using $\Phi_t(z), \Phi_t(z')$ to replace x, y and repeating above step, we prove our claim.

Now we consider the mapping Φ_τ. As aforementioned, $[a, c]\backslash\{c\} \subset B_a$ and $[c, b]\backslash\{c\} \subset B_b$. This means that $r = r(D_x\Phi_\tau(c)) \ge 1$. By [91, Proposition 2.9.1(b)], it follows that $D_x\Phi_\tau(c)$ is a strict α-contraction with the same k as in (H1), and hence, $r_e(D_x\Phi_\tau(c)) \le k < 1$ (see [91, Theorem 2.9.9]).

In the case where $r > 1$, there exists a local center-stable manifold, $W^{cs}(c)$, of c which is a graph of a Lipschitz function over the center-stable subspace of $D_x\Phi_\tau(c)$(see [313, Theorem III.8 and Exercise III.2]). Thus, choosing U sufficiently close to c, we then get $U \subset W^{cs}(c)$, which is a contradiction since any graph cannot contain an open set. In the case where $r = 1$, by Lemma 2.5.3, the domain of attraction of c is locally contained in the local strongly stable manifold, $W^{ss}(c)$, of the map Φ_τ at c. But this is impossible since $W^{ss}(c)$ is a Lipschitz graph(see [313, Theorem III.8 and Exercise III.2]) and hence it cannot contain an open set. ∎

Theorem 2.5.1 shows that the dynamics for Φ behaves like a saddle together with other two stable equilibria, which often appears in ordinary differential systems. In what follows, we introduce this concept in an abstract way.

A dynamical system is said to admit a saddle point behavior if it possesses three equilibria a, b, and c such that a and b are stable attractors, and the state space is divided into three disjoint and invariant parts: the basin of attraction B_1 of a, the basin of attraction B_2 of b, and one-codimensional (at least Lipschtiz) manifold M containing c. Such an M is usually called the separatrix of the domains of attraction B_1 and B_2. If the equilibrium c is replaced by a set of some equilibria and the same statements as above hold, then such a system is said to admit a generalized saddle point behavior. In this case, we still call M a separatrix.

The following theorem is about generalized saddle point behavior for monotone semiflows.

Theorem 2.5.2. *Let the SOP semiflow Φ be C^1 on X^+ and satisfy* (H1)–(H2) *with Φ_τ being strongly monotone. Suppose that Φ has exactly two locally stable equilibria $a < b$, and for any other possible equilibrium c, $D_x\Phi_\tau(c)$ is strongly positive and $r(D_x\Phi_\tau(c)) > 1$. Then $M = X^+\backslash\{B_a \cup B_b\}$ is an unordered and positively invariant Lipschiz submanifold with codimension one in the order norm $|\cdot|_v$. Furthermore, such an M is a C^1-submanifold if Φ_τ is compact.*

Proof. We first prove that $b + X^+$ cannot contain any other equilibrium except b. Otherwise, there is an equilibrium c in $(b+X^+)\backslash\{b\}$. Since $D_x\Phi_\tau(c)$ is strongly positive and $r(D_x\Phi_\tau(c)) > 1$, there is an orbit originating from c and tangent to the principal eigenvector at c such that it monotone increasingly tends to another equilibrium $d > c$. Therefore, d is lower stable, contradicting to the assumption that $r(D_x\Phi_\tau(d)) > 1$. Similarly, $[0, a]$ cannot contain any other equilibrium except a. Since the mapping Φ_τ is a strict α-contraction, we can define the index for fixed points. Applying Cac and Gatica's fixed point theorem [49], we obtain that there is at least one equilibrium between a and b but distinct from a, b.

We further claim that all equilibria in $[a, b]$ except a, b are unordered. Suppose not, then there is a pair of equilibria c, d in $[a, b]$ with $c, d \notin \{a, b\}$ and $c < d$. As argued in the previous paragraph, there exists a lower stable equilibrium $e \in [c, d]$, which contradicts the assumption that $r(D_x\Phi_\tau(e)) > 1$ since $a < e < b$. Thus, the claim follows.

Next we show that the semiflow Φ is generically convergent. Given an equilibrium $e \neq a, b$, we then have $\rho(e) := r(D_x\Phi_\tau(e)) > 1$. By [91, Proposition 2.9.1 (b)], $D_x\Phi_\tau(e)$ is a strict α-contraction with the same k as in (H1) and hence, $r_e(D_x\Phi_\tau(e)) \leq k < 1$ (see [91, Theorem 2.9.9]). By Lemma 2.5.2, it then follows that $\rho(e)$ is a simple eigenvalue of $D_x\Phi_\tau(e)$ and $N(\rho(e)I - D_x\Phi_\tau(e))$ is a one-dimensional space spanned by the principal eigenvector $v \gg 0$ associated with $\rho(e)$. Thus, the generic convergence follows from the general result established in [330].

Now we conclude that $M = X^+\backslash\{B_a \cup B_b\}$ is unordered. Suppose not, then there are two points $x, y \in M$ with $x < y$. Since Φ is SOP, we can choose two neighborhoods U and V of x and y, respectively, such that $\Phi_{t_0}(U) < \Phi_{t_0}(V)$. Thus, the generic convergence implies that there are two points $u \in U$

and $v \in V$ with $x < u$ and $v < y$ such that $\Phi_t(u)$ and $\Phi_t(v)$ converge to two equilibria e and d, respectively. Obviously, $\omega(x) \le e \le d \le \omega(y)$. Since $\omega(x), \omega(y) \subset M$ and M is invariant, we have $e, d \in M$, and hence, $\{e, d\} \cap \{a, b\} = \emptyset$. By the nonordering property of those equilibria distinct from a, b, we further get $e = d$. It then follows that the equilibrium $e = d$ attracts an open subset. By using the assumption $\rho(e) > 1$ and the theory of center-stable manifolds, we can get a contradiction as in the proof of Theorem 2.5.1.

In the case where the mapping Φ_τ is strongly monotone, $(M \cup B_a, M \cup B_b)$ is an order decomposition with the boundary M(see Definition 2.5.1). By Lemma 2.5.1, it follows that M is a Lipschiz submanifold in the order norm $|\cdot|_v$ with codimension one. Moreover, M is a C^1-submanifold if the mapping Φ_τ is compact (see Tereščák [360]). ∎

In order to generalize Theorem 2.5.2 to the case where the number of stable equilibria is greater than two, we need the following result.

Proposition 2.5.1. *Let Φ be a SOP semiflow satisfying* (H1) *and* (H2) *with Φ_τ being strongly monotone. If a is a stable attractor and its basin of attraction $B_a \neq X^+$, then $\partial_- B_a$ and $\partial_+ B_a$ are positively invariant and unordered one-codimensional Lipschitz manifolds in the order norm $|\cdot|_v$.*

Proof. We only consider the upper boundary, the lower boundary being similar. Define

$$A^0 := \bigcup_{x \in B_a} [[-\infty, x]], \quad A := \overline{A^0}, \quad \text{and} \quad B := X^+ \setminus A^0.$$

Since B_a is open, it is easy to see A^0 is open, and hence, A is closed and lower closed. Since $B_a \neq X^+$, A^0, and hence A is not the whole state space X^+. Thus, B is a nonempty closed subset of X^+. By [351, Lemma 1.4], B is also upper closed. Obviously, $A \cup B = X^+$ and $A \cap B = \partial_+ B_a$. By Lemma 2.5.1, $\partial_+ B_a$ is an unordered and positively invariant one-codimensional Lipschitz manifold in the order norm $|\cdot|_v$. ∎

Theorem 2.5.3. *Let the SOP semiflow Φ be C^1 on X^+ and satisfy* (H1)–(H2) *with Φ_τ being strongly monotone. Suppose that Φ has exactly m locally stable equilibria $a_1 \ll a_2 \ll \cdots \ll a_m$, and for any other possible equilibrium c, $D_x\Phi_\tau(c)$ is strongly positive and $r(D_x\Phi_\tau(c)) > 1$. Let B_i be the basin of attraction of a_i. Then the following statements are valid:*

(i) For each $1 \le i \le m-1$, $\partial_+ B_i = \partial_- B_{i+1}$ is an unordered and positively invariant one-codimensional Lipschitz manifold in the order norm $|\cdot|_v$, and furthermore, C^1-manifold if Φ_τ is compact;

(ii) $X^+ = \cup_{i=1}^m B_i \bigcup \cup_{i=1}^{m-1} \partial_+ B_i$.

Proof. Suppose, by contradiction, that $\partial_+ B_i \neq \partial_- B_{i+1}$ for some $1 \leq i \leq m-1$. Since $a_i < a_{i+1}$, $\partial_- B_{i+1}$ is above $\partial_+ B_i$ in the sense that if there is a point $x \in \partial_+ B_i$ but $x \notin \partial_- B_{i+1}$, then there exists a point $y \in \partial_- B_{i+1}$ with $y > x$. By the strong monotonicity of Φ and the positive invariance of $\partial_+ B_i$ and $\partial_- B_{i+1}$, it follows that for any $\tau > 0$, $\Phi_\tau(x) \ll \Phi_\tau(y)$, $\Phi_\tau(x) \in \partial_+ B_i$ and $\Phi_\tau(y) \in \partial_- B_{i+1}$. Without loss of generality, we may assume that $x \in \partial_+ B_i$ and $y \in \partial_- B_{i+1}$ with $x \ll y$. Note that the generic convergence theorem [330] still holds under our assumptions on Φ. By the definition of upper and lower boundary points, it is easy to see that $a_i \ll \omega(x)$, $\omega(y) \ll a_{i+1}$. By generic convergence, we choose $w \gg x$ and $z \ll y$ with w and z sufficiently close to x and y, respectively, so that $\omega(w) = \{a\}$ and $\omega(z) = \{b\}$ with $a \leq b$. Clearly, $a_i \ll a \leq b \ll a_{i+1}$. We claim that a must be equal to b. Otherwise, since $\rho(a) := r(D_x \Phi_\tau(a)) > 1$, there is an orbit originating from a such that it strictly increasingly converges to another equilibrium $e \leq b$. Then $\rho(e) := r(D_x \Phi_\tau(e)) \leq 1$. But $a_i \ll a \ll e \leq b \ll a_{i+1}$, contradicting the assumption that $\rho(e) > 1$. Thus, $a = b$ attracts the open order interval $[[w, z]]$, which is impossible by the theory of center-stable manifolds(see the proof of Theorem 2.5.1). Consequently, we have $\partial_+ B_i = \partial_- B_{i+1}, \forall 1 \leq i \leq m-1$. By Proposition 2.5.1, each $\partial_+ B_i$ is a one-dimensional Lipschitz manifold in the order norm $|\cdot|_v$. If Φ_τ is compact, the C^1-smoothness of $\partial_+ B_i$ follows from Tereščák [360]. This proves statement (i). Since $\partial_+ B_i = \partial_- B_{i+1}$ separates the adjacent basins of attraction B_i and B_{i+1}, it is easy to see that statement (ii) holds. ∎

In the rest of this section, we consider the generalized saddle point behavior for two-species competitive systems on ordered Banach spaces.

Let X_1 and X_2 be ordered Banach spaces with positive cones X_1^+ and X_2^+ having nonempty interiors. Let the order in both spaces be denoted by "$\leq$". Let $X^+ := X_1^+ \times X_2^+$. Clearly, $\mathrm{int}(X^+) = \mathrm{int}(X_1^+) \times \mathrm{int}(X_2^+)$. Define $K := X_1^+ \times (-X_2^+)$. Then $X = X_1 \times X_2$ is an ordered Banach space with positive cone K. We use $\leq_K$ $(<_K, \ll_K)$ to denote the (strict, strong) order induced by K. Let $u \gg_K 0$ be fixed. Set $C_0 = X_1^+ \backslash \{0\} \times X_2^+ \backslash \{0\}$, $C_1 = \{(x_1, 0) : x_1 \in X_1^+\}$, and $C_2 = \{(0, x_2) : x_2 \in X_2^+\}$. Suppose that $\Phi := \{\Phi_t\}_{t \geq 0}$ is a continuously differentiable semiflow on X^+ satisfying (H1)–(H2) and the following additional assumptions:

(H3) $\Phi_t(C_i) \subset C_i, \forall t \geq 0, 0 \leq i \leq 2$; Φ is strictly K-monotone on X^+, strongly K-order-preserving on C_0, and SOP on C_i with respect to the order induced by $X_i^+, \forall i = 1, 2$;

(H4) The set $\mathcal{E}$ of all equilibria of Φ in X^+ is the union of $E_0 = (0, 0)$, $E_1 = (\bar{x}_1, 0)$ with $\bar{x}_1 \in \mathrm{int}(X_1)$, $E_2 = (0, \bar{x}_2)$ with $\bar{x}_2 \in \mathrm{int}(X_2)$, and a nonempty set $\mathcal{E}^0$ of coexistence equilibria in $\mathrm{int}(X^+)$; E_0 does not attract any point in $X^+ \backslash \{E_0\}$, and E_i is locally stable in $X^+, \forall i = 1, 2$; For each $e \in \mathcal{E}^0$, $D_x \Phi_\tau(e)$ is strongly K-positive, and $\rho(e) := r(D_x \Phi_\tau(e)) > 1$ if $\mathcal{E}^0$ is not a singleton.

By an argument similar to that of Theorem 2.5.2, we have the following result.

Theorem 2.5.4. *Assume that the C^1-semiflow Φ satisfies* (H1)–(H4)*, and Φ_τ is strongly K-monotone in* $\mathrm{int}(X^+)$*. Then $M = X^+ \backslash (B_1 \cup B_2) \subset C_0 \cup \{E_0\}$ is an unordered with respect to type-K order and positively invariant Lipschiz manifold with codimension one in the type-K order norm $|\cdot|_u$. Furthermore, M is C^1 if Φ_τ is compact.*

In order to generalize Theorem 2.5.3 to abstract competitive systems, we need to replace (H4) with the following assumption:

(H4)′ $\mathcal{E} = \{E_0, E_1, E_2\} \cup \mathcal{E}_s \cup \mathcal{E}_u$, where E_0, E_1, and E_2 are the same as in (H4), $\mathcal{E}_u$ is the set of all strongly K-positive equilibria e with $D_x\Phi_\tau(e)$ being strongly K-positive and $r(D_x\Phi_\tau(e)) > 1$, and $\mathcal{E}_s = \{c_1 \ll_K c_2 \ll_K \cdots \ll_K c_m\}$ consists of m locally stable equilibria with $E_1 \ll_K c_i \ll_K E_2, \forall 1 \leq i \leq m$.

Set $c_0 = E_1$ and $c_{m+1} = E_2$. Then we have

$$c_0 \ll_K c_1 \ll_K c_2 \ll_K \cdots \ll_K c_m \ll_K c_{m+1}.$$

For each $0 \leq i \leq m+1$, let B_i be the basin of attraction of c_i, and let $\partial_+ B_i$ and $\partial_- B_i$ be the upper and lower boundaries of B_i in type-K order, respectively. By an argument similar to that of Theorem 2.5.3, we have the following result.

Theorem 2.5.5. *Assume that the semiflow Φ on X^+ satisfies* (H1)–(H3) *and* (H4)′*, and Φ is strongly K-monotone on C_0. Then the following statements hold true:*

(i) For each $1 \leq i \leq m-1$, $\partial_+ B_i = \partial_- B_{i+1}$ is an unordered with respect to type-K order and positively invariant one-codimensional Lipschitz manifold in the order norm $|.|_u$, and furthermore, C^1-manifold if Φ_τ is compact;
(ii) $X^+ = \cup_{i=0}^{m+1} B_i \bigcup \cup_{i=0}^{m} \partial_+ B_i$.

Remark 2.5.1. Smith [319, page 870] conjectured that the set of steady states in $[a_1, a_m]$ or $[c_0, c_{m+1}]_K$ is composed of a lattice of alternating bands each of which consists of unordered steady states of the same stability type. He also proved that this conjecture is true for some two-dimensional cooperative and competitive systems (see [321, Theorem 4.8] and [320, Theorem 4.7]). Theorems 2.5.3 and 2.5.5 above give an affirmative answer to this conjecture under the condition that all stable steady states are totally ordered. In general, this additional condition is necessary for Smith's conjecture to be valid, see [195, Example 2.1].

2.6 Exponential Ordering Induced Monotonicity

Reaction–diffusion equations with delayed reaction terms and, more generally, abstract functional differential equations have been widely used to model the evolution of a physical system distributed over a spatial domain [408]. In the celebrated work of Martin and Smith [243, 244], the monotonicity of the semiflow generated by an abstract functional differential equation was established, and the powerful theory of monotone dynamical systems was applied to obtain some detailed descriptions of the generic dynamics of the semiflow. In order for the semiflow to be order-preserving with respect to the pointwise ordering of the phase space, the aforementioned work requires that the nonlinear reaction term satisfy a certain quasi-monotonicity condition, which, in the special case of a reaction–diffusion equation with delay, requires that the reaction term be monotone and thus limits the applications in some cases. It is therefore natural to ask whether the quasi-monotonicity condition in the work of Martin and Smith can be relaxed. This question was addressed in Smith and Thieme [329, 331] for the case of ordinary functional differential equations (that is, the spatial diffusion is absent), where they established the monotonicity of the semiflow in a restricted but sufficiently large subspace with a nonstandard exponential ordering. In this section we extend the exponential ordering and its induced monotonicity to abstract functional differential equations and delayed reaction–diffusion equations. These results will be used to obtain threshold dynamics for a nonlocal and delayed reaction–diffusion population model in Chapter 9.

Let $A : \mathrm{Dom}(A) \to X$ be the infinitesimal generator of an analytic semigroup $T(t)$ satisfying $T(t)P \subset P, \forall t \geq 0$. For convenience, we denote $T(t)$ by e^{At}. Let $r \geq 0$ be fixed and let $C := C([-r, 0], X)$. For $\mu \geq 0$, we define

$$K_\mu = \{\phi \in C : \phi(s) \geq_X 0, \forall s \in [-r, 0], \text{ and } \phi(t) \geq_X e^{(A-\mu I)(t-s)}\phi(s), \\ \forall 0 \geq t \geq s \geq -r\}.$$

Then K_μ is a closed cone in C. Let $\geq_\mu$ be the partial ordering on C induced by K_μ. The meaning of $\leq_\mu$ and $\leq_X$ should be clear.

Lemma 2.6.1. *Assume that $\phi \in C$ is differentiable on $(-r, 0)$ and $\phi(t) \in \mathrm{Dom}(A), \forall t \in (-r, 0)$. Then $\phi \geq_\mu 0$ if and only if*

$$\phi(-r) \geq_X 0, \text{ and } \frac{d\phi(t)}{dt} - (A - \mu I)\phi(t) \geq_X 0, \forall t \in (-r, 0).$$

Proof. Assume that $\phi \geq_\mu 0$; that is, $\phi \in K_\mu$. It then follows that $\phi(-r) \geq_X 0$, and for any $t \in (-r, 0)$ and $h > 0$ with $t + h \in [-r, 0]$,

$$\frac{\phi(t+h) - \phi(t)}{h} \geq_X \frac{e^{(A-\mu I)h}\phi(t) - \phi(t)}{h}.$$

Since ϕ is differentiable at t and $\phi(t) \in \mathrm{Dom}(A)$, letting $h \to 0^+$ and using the definition of infinitesimal generators (see, e.g., [272]), we get

$$\frac{d\phi(t)}{dt} = \lim_{h\to 0^+} \frac{\phi(t+h)-\phi(t)}{h} \geq_X (A-\mu I)\phi(t), \ \forall t \in (-r,0).$$

Conversely, assume that $\phi(-r) \geq_X 0$ and $\frac{d\phi(t)}{dt} - (A-\mu I)\phi(t) \geq_X 0$, $\forall t \in (-r,0)$. Let $t \in (-r,0]$ be fixed. Clearly, the function $u(s) := e^{(A-\mu I)(t-s)}\phi(s)$ is differentiable for $s \in (-r,t)$. By the property of analytic semigroups (see, e.g., [150, 272]) and the positivity of $e^{(A-\mu I)(t-s)} = e^{-\mu(t-s)}e^{A(t-s)}$, we have

$$\begin{aligned}
\frac{du(s)}{ds} &= -(A-\mu I)e^{(A-\mu I)(t-s)}\phi(s) + e^{(A-\mu I)(t-s)}\frac{d\phi(s)}{ds} \\
&= -e^{(A-\mu I)(t-s)}(A-\mu I)\phi(s) + e^{(A-\mu I)(t-s)}\frac{d\phi(s)}{ds} \\
&= e^{(A-\mu I)(t-s)}\left(\frac{d\phi(s)}{ds} - (A-\mu I)\phi(s)\right) \geq_X 0.
\end{aligned}$$

Thus we get $\phi(t) - e^{(A-\mu I)(t-s)}\phi(s) = u(t) - u(s) = \int_s^t \frac{du(\tau)}{d\tau}d\tau \geq_X 0$, $\forall s \in [-r,t]$. This, together with $\phi(-r) \geq_X 0$, implies $\phi \in K_\mu$. ∎

Let $\sigma > 0$ and let $u : [-r,\sigma) \to X$ be a continuous map. For each $t \in [0,\sigma)$, we define $u_t \in C$ by $u_t(s) = u(t+s), \forall s \in [-r,0]$. Let D be an open subset of C. Assume that $F : D \to X$ is continuous and satisfies a Lipschitz condition on each compact subset of D. We consider the abstract functional differential equation

$$\begin{aligned}
\frac{du(t)}{dt} =& Au(t) + F(u_t), \ t > 0, \\
u_0 =& \phi \in D.
\end{aligned} \tag{2.1}$$

By the standard theory (see, e.g., [243, 408]), for each $\phi \in D$, equation (2.1) admits a unique mild solution $u(t,\phi)$ on its maximal interval $[0,\sigma_\phi)$. Moreover, if $\sigma_\phi > r$, then $u(t,\phi)$ is a classical solution to (2.1) for $t \in (r,\sigma_\phi)$. In order to get a monotone solution semiflow of (2.1) with respect to $\geq_\mu$, we will impose the following monotonicity condition on F:

(M_μ) $\quad \mu(\psi(0)-\phi(0)) + F(\psi) - F(\phi) \geq_X 0 \quad$ for $\phi,\psi \in D$ with $\phi \leq_\mu \psi$.

Theorem 2.6.1. *Let (M_μ) hold. If $\phi \leq_\mu \psi$, then $u_t(\phi) \leq_\mu u_t(\psi)$ for all $t \geq 0$ such that both solutions are defined.*

Proof. Let $v^* \in \text{int}(P)$ be fixed. For any $\epsilon > 0$, define $F_\epsilon(\phi) := F(\phi) + \epsilon v^*$ for $\phi \in D$, and let $u^\epsilon(t,\psi)$ be the unique mild solution of the following equation

$$\begin{aligned}
\frac{du(t)}{dt} =& Au(t) + F_\epsilon(u_t), \ t > 0, \\
u_0 =& \psi \in D.
\end{aligned} \tag{2.2}$$

Without loss of generality, we assume that $u(t,\phi)$ and $u^\epsilon(t,\psi)$ are both defined on $[0,\infty)$ (if not, we replace $[0,\infty)$ by the intersection of their maximal intervals of existence). Let $y^\epsilon(t) := u^\epsilon(t,\psi) - u(t,\phi)$ and define

$$P = \{t \in [0, \infty) : \quad y_t^\epsilon \geq_\mu 0\}.$$

Clearly, P is closed and $0 \in P$. We claim that if $t_0 \in P$, then there exists $\delta_0 > 0$ such that $[t_0, t_0 + \delta_0] \subset P$. Indeed, by the abstract integral forms of equations (2.1) and (2.2), we have

$$y^\epsilon(t) = e^{(A-\mu I)(t-s)} y^\epsilon(s) + \int_s^t e^{(A-\mu I)(t-\tau)} \\ (F(u_\tau^\epsilon(\psi)) - F(u_\tau(\phi)) + \mu (u^\epsilon(\tau, \psi) - u(\tau, \phi)) + \epsilon v^*)\, d\tau \tag{2.3}$$

for all $t \geq s \geq 0$. By the condition $u_{t_0}^\epsilon(\psi) \geq_\mu u_{t_0}(\phi)$ and assumption (M_μ), it then follows that

$$(F(u_t^\epsilon(\psi)) - F(u_t(\phi)) + \mu (u^\epsilon(t, \psi) - u(t, \phi)) + \epsilon v^*)|_{t=t_0} \geq_X \epsilon v^* \gg_X 0.$$

Thus there exists $\delta_0 > 0$ such that

$$F(u_t^\epsilon(\psi)) - F(u_t(\phi)) + \mu (u^\epsilon(t, \psi) - u(t, \phi)) + \epsilon v^* \geq_X 0, \forall t \in [t_0, t_0 + \delta_0].$$

By the integral equation (2.3) and the positivity of the semigroup $e^{(A-\mu I)t}$, we then get

$$y^\epsilon(t) \geq_X e^{(A-\mu I)(t-s)} y^\epsilon(s), \quad \forall t_0 \leq s \leq t \leq t_0 + \delta_0,$$

which, together with the definition of (K_μ), implies that $u_t^\epsilon(\psi) \geq_\mu u_t(\phi)$, $\forall t \in [t_0, t_0 + \delta_0]$.

Let $P_1 := \{t : [0, t] \subset P\}$. We claim that $\sup P_1 = \infty$. Assume, by way of contradiction, that $t^* = \sup P_1 < \infty$. Then there is a sequence $\{t_n\} \subset P_1 \subset P$ such that $t_n \to t^*$. Thus the closedness of P implies that $t^* \in P$. By the claim in the previous paragraph, $[t^*, t^* + \delta^*] \subset P$ for some $\delta^* > 0$, and hence $t^* + \delta^* \in P_1$, which contradicts the definition of t^*. It then follows that $[0, \infty) \subset P$, and hence $P = [0, \infty)$.

By a standard argument, we have $\lim_{\epsilon \to 0^+} u_t^\epsilon(\psi) = u_t(\psi), \forall t \geq 0$. Letting $\epsilon \to 0^+$ in $y_t^\epsilon = u_t^\epsilon(\psi) - u_t(\phi) \geq_\mu 0$, we get $u_t(\psi) - u_t(\phi) \geq_\mu 0$, and hence $u_t(\psi) \geq_\mu u_t(\phi), \forall t \geq 0$. ∎

For simplicity, in the rest of this section we assume that for each $\phi \in C$, equation (2.1) admits a unique mild solution $u(t, \phi)$ defined on $[0, \infty)$. Then (2.1) generates a semiflow on C by $\Phi(t)(\phi) = u_t(\phi)$, $\phi \in C$. Clearly, condition (M_μ) is sufficient for $\Phi(t) : C \to C$ to be monotone with respect to $\leq_\mu$ in the sense that $\Phi(t)(\phi) \leq_\mu \Phi(t)(\psi)$ whenever $\phi \leq_\mu \psi$ and $t \geq 0$. In some applications of monotone dynamical systems, however, we need a strong order-preserving property (see, e.g., [326]). The semiflow $\Phi(t) : C \to C$ is said to be strongly order-preserving with respect to $\leq_\mu$ if it is monotone and if whenever $\phi <_\mu \psi$, there exist open subsets U, V of C with $\phi \in U$ and $\psi \in V$ and $t_0 > 0$ such that $\Phi(t_0)(U) \leq_\mu \Phi(t_0)(V)$. Next we show that the following slightly stronger condition than (M_μ) is sufficient for $\Phi(t)$ to be strongly order-preserving:

(SM_μ) $\mu(\psi(0)-\phi(0))+F(\psi)-F(\phi)\gg_X 0$ for $\phi,\psi\in C$ with $\phi\leq_\mu\psi$ and $\phi(s)\ll_X\psi(s)$, $\forall s\in[-r,0]$.

Theorem 2.6.2. *Assume that $T(t)(P\setminus\{0\})\subset \mathrm{int}(P)$, $\forall t>0$, and (SM_μ) holds. Then the solution semiflow $\Phi(t)$ is strongly order-preserving on C with respect to $\leq_\mu$.*

Proof. Let $v^*\in\mathrm{int}(P)$ be fixed, and define $\phi^*\in C$ by

$$\phi^*(t)=e^{(A-\mu I)(t+r)}v^*,\ \forall t\in[-r,0].$$

Then $\phi^*(s)\gg_X 0$, $\forall s\in[-r,0]$, and Lemma 2.6.1 implies that $\phi^*\geq_\mu 0$. For any $\psi\in C$, the sequence of points $\psi_n=\psi+\frac{1}{n}\phi^*$ in C satisfies $\psi<_\mu\psi_{n+1}<_\mu\psi_n,\forall n\geq 1$, and $\psi_n\to\psi$ as $n\to\infty$. By this property and the continuity of F, it is easy to see that (SM_μ) implies (M_μ). Then we conclude from Theorem 2.6.1 that $\Phi(t)$ is monotone on C. Moreover, for each $\phi\in C$, $u(t,\phi)\in\mathrm{Dom}(A)$, $\forall t>r$. For every $\phi<_\mu\psi$, the strong positivity of $T(t)=e^{At}$ implies that $\phi(0)<_X\psi(0)$, and hence, in view of $u_t(\phi)\leq_\mu u_t(\phi)$, $\forall t\geq 0$, we have $u(t,\phi)\ll_X u(t,\psi)$ for all $t>0$. Fix a real number $t_0>2r$ and let $\phi^0<_\mu\psi^0$ be given. By condition (SM_μ), the continuity of F, and the compactness of $[t_0-r,t_0]$, it then follows that there is a sufficiently small $\epsilon_0>0$ such that

$$F(u_t(\psi^0))-F(u_t(\phi^0))+\mu\left(u(t,\psi^0)-u(t,\phi^0)\right)\geq_X\epsilon_0 v^*,\ \forall t\in[t_0-r,t_0].$$

Since

$$\lim_{(\phi,\psi)\to(\phi^0,\psi^0)}(u(t_0-r,\psi)-u(t_0-r,\phi))=u(t_0-r,\psi^0)-u(t_0-r,\phi^0)\gg_X 0$$

and

$$\begin{aligned}\lim_{(\phi,\psi)\to(\phi^0,\psi^0)} F\ (u_t(\psi))-F(u_t(\phi))+\mu\left(u(t,\psi)-u(t,\phi)\right)\\ =F(u_t(\psi^0))-F(u_t(\phi^0)+\mu\left(u(t,\psi^0)-u(t,\phi^0)\right)\end{aligned}$$

uniformly for $t\in[t_0-r,t_0]$, there exist open subsets U, V of C with $\phi^0\in U$ and $\psi^0\in V$ such that for every $\phi\in U$ and $\psi\in V$, we have $u(t_0-r,\psi)-u(t_0-r,\phi)\gg_X 0$ and

$$\begin{aligned}&\frac{d(u(t,\psi)-u(t,\phi))}{dt}-(A-\mu I)(u(t,\psi)-u(t,\phi))\\&\quad=F(u_t(\psi))-F(u_t(\phi))+\mu\left(u(t,\psi)-u(t,\phi)\right)\gg_X 0,\ \forall t\in[t_0-r,t_0].\end{aligned}$$

Note that $u(t,\phi)$ and $u(t,\psi)$ are both classical solutions for $t>r$. By Lemma 2.6.1, we then get $u_{t_0}(\psi)-u_{t_0}(\phi)\geq_\mu 0$, $\forall\psi\in V$, $\phi\in U$, and hence $u_{t_0}(U)\leq_\mu u_{t_0}(V)$. ∎

Note that in the case where $X = \mathbb{R}$ and A is the zero operator, $\leq_\mu$ reduces to the exponential ordering introduced by Smith and Thieme [329] for scalar non-quasi-monotone ordinary delay differential equations.

Let (X_i, P_i), $1 \leq i \leq n$, be ordered Banach spaces with $\mathrm{int}(P_i) \neq \emptyset$, and let $A_i : \mathrm{Dom}(A_i) \to X_i$ be the infinitesimal generator of an analytic semigroup $T_i(t)$ satisfying $T_i(t)P_i \subset P_i, \forall t \geq 0$. Let $X = \prod_{i=1}^n X_i$, $P = \prod_{i=1}^n P_i$, $T(t) = \prod_{i=1}^n T_i(t)$, $A = \prod_{i=1}^n A_i$, $\mathrm{Dom}(A) = \prod_{i=1}^n \mathrm{Dom}(A_i)$. Then $A : \mathrm{Dom}(A) \to X$ is the infinitesimal generator of the analytic semigroup $T(t)$ defined on the ordered Banach space (X, P). Let $B = (b_{ij})$ be an $n \times n$ matrix with $b_{ij} \geq 0$, $\forall 1 \leq i \neq j \leq n$. Define

$$\begin{aligned} K_B = \{\phi \in C : \ & \phi(s) \geq_X 0, \forall s \in [-r, 0], \text{ and } \phi(t) \geq_X e^{A(t-s)} e^{B(t-s)} \phi(s), \\ & \forall\, 0 \geq t \geq s \geq -r\}. \end{aligned}$$

Then K_B is a closed cone in C and induces a partial order $\geq_B$ on C.

Remark 2.6.1. By an argument similar to that in Theorem 2.6.1, we can prove that the solution semiflow of (2.1) is monotone with respect to $\leq_B$ under the following monotonicity condition:

$$(M_B) \qquad F(\psi) - F(\phi) \geq_X B(\psi(0) - \phi(0)) \quad \text{for } \phi, \psi \in D \text{ with } \phi \leq_B \psi.$$

Clearly, in the case where $n = 1$ and $B = -\mu$, $\geq_B$ reduces to $\geq_\mu$. Replacing $-\mu$ with B in (SM_μ), we get a stronger condition (SM_B). By a similar argument as in Theorem 2.6.2, we should be able to prove that the solution semiflow of (2.1) is strongly order-preserving with respect to $\leq_B$ under (SM_B) and an additional irreducibility assumption. For the details in the special case where $X = \mathbb{R}^n$ and $A = 0$, we refer to [331].

2.7 Notes

There have been extensive investigations on monotone dynamical systems (see, e.g., Hess [152], Smith [326] and the references therein). For strongly monotone continuous-time dynamical systems one has generic convergence: There is an open and dense subset of the phase space such that any orbit emanating from it converges to an equilibrium (see Hirsch [160], Poláčik [279] and Smith and Thieme [330]). However, for strongly monotone discrete-time dynamical systems there is no generic convergence to fixed points; see, e.g., Takáč [353] and Dancer and Hess [87] for counterexamples in periodic differential equations, the Poincaré (period) maps of which define strongly monotone discrete-time dynamical systems. It is well known that for smooth strongly monotone discrete-time dynamical systems one has generic convergence to cycles (see Poláčik and Tereščák [280, 281]).

Theorem 2.1.1 is due to Dancer [84]. Remark 2.1.1 seems to be new. Remark 2.1.3 is due to Hsu, Smith and Waltman [174]. Theorem 2.1.2 is due to Zhao and Jing [444], which is a generalization of Smith [318, Theorem 2.1].

Theorem 2.2.1 extends Smith [326, Theorem 2.3.1] on strongly order-preserving continuous-time semiflows to monotone semiflows. A related result is Jiang and Yu [193, Theorem 3] on global asymptotic order stability for monotone maps on a strongly ordered space X with the property that every nonempty and compact subset has both a greatest lower bound and a least upper bound in X. Theorem 2.2.2 is due to Zhao [432]. Theorem 2.2.3 seems to be new and is a variant of Smith [326, Theorem 2.3.2]. In the proof of Theorem 2.2.3, we have used Theorem 1.2.2 for global convergence. Theorem 2.2.4 seems to be new and extends Ogiwara and Matano [265, Theorem 2.4] on local convergence to global convergence. Takáč [355] also investigated convergence to a fixed point for a class of strongly monotone discrete-time dynamical systems in a strongly ordered Banach space.

Theorems 2.3.1, 2.3.2, and 2.3.3 are due to Hirsch [162]. Condition (C3) was introduced by Zhao [432, Lemma 1] for uniqueness of positive fixed points. Lemma 2.3.2 is due to Zhao [432], and Theorem 2.3.4 is a generalization of [432, Theorem 2.3]. Takáč [349] established global convergence for subhomogeneous (sublinear) and strongly monotone maps, which is an extension of a result in Smith [317] concerning monotone and concave maps. Jiang [191] proved convergence for finite-dimensional monotone and subhomogeneous (sublinear) discrete-time dynamical systems. This result was generalized by Wang [383] to the Poincaré maps associated with periodic subhomogeneous and quasi-monotone reaction–diffusion systems subject to Neumann boundary conditions, and by Wang and Zhao [387] to monotone and subhomogeneous discrete dynamical systems on product Banach spaces. Monotone and strictly subhomogeneous (sublinear) semiflows generated by cooperative systems of functional differential equations and quasi-monotone reaction–diffusion systems with delays were studied by Zhao and Jing [444] and Freedman and Zhao [124], respectively. Theorems 2.2.2 and 2.3.2 were applied to a nonlocal reaction–diffusion model by Freedman and Zhao [125]. The part metric was introduced by Thompson [373]. Krause and Nussbaum [205] proved a limit set trichotomy for part metric contractive maps on solid and normal cones in Banach spaces, and made a very interesting observation that a monotone map with strong subhomogeneity is contractive for the part metric on the interior of the cone. Takáč [354] also utilized the concept of part metric for convergence in discrete dynamical systems. Theorem 2.3.5 and Remarks 2.3.2 and 2.3.3 are due to Zhao [438]. For global convergence in monotone and uniformly stable skew-product semiflows, we refer to Jiang and Zhao [194].

Theorem 2.4.1 and Proposition 2.4.1 are due to Hsu, Smith and Waltman [174]. In the proof of Theorem 2.4.1, we have used Theorem 1.2.2 for global convergence. The notion of compression was introduced by Hess and Lazer [154]. Theorem 2.4.2 is a generalization of a result in [154]. In the proof of Theorem 2.4.2, again we have used Theorem 1.2.2. Smith and Thieme [332] studied stable coexistence and bistability for competitive continuous-time semiflows on ordered Banach spaces, and showed that a "thin" separatrix separates the basins of attraction of the two locally stable single-population steady states under the assumption that the coexistence steady state is unique. Wang and Jiang [384, 385] also obtained some general properties for strongly competitive discrete-time dynamical systems on strongly ordered topological vector spaces.

Section 2.5 is adapted from Jiang, Liang and Zhao [195], where these results were also applied to three reaction–diffusion systems modelling man-environment-man epidemics, single-loop positive feedback, and two-species competition, respectively. The concepts of upper and lower boundaries, order decomposition, and d-hypersurface were introduced by Hirsch [159] and well developed by Takáč [350, 351], Wang and Jiang [385], and Liang and Jiang [224]. Takáč [355] also employed the d-hypersurface to study the convergence for monotone discrete-time dynamical systems and two-species periodic competitive reaction–diffusion systems.

Section 2.6 is taken from Wu and Zhao [411] and was motivated by Smith and Thieme [329, 331], where a nonstandard positive cone was introduced and applied to non-quasi-monotone ordinary differential equations and systems with delays. The exponential ordering was also used earlier by Hadeler and Tomiuk [140] to show the existence of nontrivial periodic solutions of a class of scalar difference–differential equations.

The theory of abstract competitive systems has found nontrivial applications to two-species Lotka–Volterra competition reaction–diffusion systems, see, e.g., He and Ni [147], Lou, Xiao and Zhou [235], Zhao and Zhou [447] and the references therein. Hsu and Zhao [172] also gave a complete classification for the global dynamics of a two-species Lotka–Volterra competition model with seasonal succession. For abstract competitive systems, Lam and Munther [210] obtained two sufficient conditions that guarantee, in the absence of coexistence steady states, the global asymptotic stability of one of two semitrivial steady states.

The monotone dynamical systems approach to traveling waves and spreading speeds has been well developed for discrete- and continuous-time evolution systems admitting the comparison principle, we refer to Weinberger [401], Lui [239], Weinberger [402], Li, Weinberger and Lewis [220], Liang and Zhao [225, 226], Liang, Yi and Zhao [227], Fang and Zhao [110], Ding and Liang [97] for the theory of monostable waves and spreading speeds; Fang and Zhao [111] for the general theory of bistable waves.

3

Nonautonomous Semiflows

There are many nonautonomous models that describe the population dynamics in a fluctuating environment. Solutions of these systems can generate nonautonomous semiflows on phase spaces. The purpose of this chapter is to develop the theory of nonautonomous semiflows. It is well known that the existence and stability of periodic solutions of a periodic differential system are equivalent to those of fixed points of its associated Poincaré map (see, e.g., [152]). In Section 3.1 we introduce the concept of periodic semiflows and prove that uniform persistence of a periodic semiflow also reduces to that of its associated Poincaré map under a general abstract setting. To illustrate the applications of the theory of monotone discrete dynamical systems to periodic problems, we then discuss periodic cooperative ordinary differential systems and scalar parabolic equations. In particular, we establish threshold dynamics in terms of principal multipliers and eigenvalues, and show how to obtain corresponding results for autonomous cases of these systems. Two practical examples are also provided.

In Section 3.2 we introduce the concept of asymptotically periodic semiflows, and show that the long-time behavior of an asymptotically periodic semiflow reduces to that of a nonautonomous discrete process that is asymptotic to the autonomous semiflow defined by the Poincaré map of the limiting periodic semiflow. Then we prove that an asymptotically periodic differential system can give rise to an asymptotically periodic semiflow under appropriate conditions, and discuss global dynamics in asymptotically periodic Kolmogorov parabolic equations and a periodic mutualism parabolic system as an illustrative example.

In Section 3.3 we apply the global attractivity theorem for monotone and subhomogeneous skew-product semiflows in the previous chapter to almost periodic cooperative ordinary differential systems, scalar delay differential equations, and reaction–diffusion equations. The existence and global attractivity

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of positive almost periodic solutions are proved. A threshold dynamics result is also established in terms of principal spectrum points for almost periodic parabolic problems.

Section 3.4 is devoted to a discussion of continuous processes on a metric space. We introduce some basic concepts such as limits sets and chain transitive quasi-invariant sets. Then we generalize the no-cycle theorem on uniform persistence for autonomous semiflows to processes by a skew-product semiflow approach. We also prove an equivalence theorem on two types of skew-product semiflows, which enables one to work directly on a concrete nonautonomous system rather than its generated continuous process in practice.

In Section 3.5 we study solution maps of a large class of abstract functional differential equations (FDEs). Under appropriate assumptions, we show that the solution maps of such an equation are α-contractions in the phase space equipped with an equivalent norm. This result can be applied to the Poincaré maps of periodic evolution systems with time delay, e.g., time-delayed reaction–diffusion equations, to obtain the existence of periodic solutions without assuming that the time period is greater than or equals the time delay.

3.1 Periodic Semiflows

Let X be a complete metric space with metric d, and let $\omega > 0$. A family of mappings $T(t) : X \to X$, $t \geq 0$, is called an ω-periodic semiflow on X if it satisfies the following properties:

(1) $T(0) = I$, where I is the identity map on X;
(2) $T(t+\omega) = T(t) \circ T(\omega)$, $\forall t \geq 0$;
(3) $T(t)x$ is continuous in $(t, x) \in [0, \infty) \times X$.

A point x_0 corresponds to an ω-periodic orbit if $T(t+\omega)x_0 = T(t)x_0$, $\forall t \geq 0$. For an ω-periodic semiflow, these x_0 coincide with the fixed points of its associated Poincaré map $T(\omega)$. The notion of periodic semiflows was motivated by the investigation of periodic problems, since solutions $u(t, x)$ of an ω-periodic differential system on a suitable phase space X satisfying $u(0, x) = x$ define an ω-periodic semiflow under appropriate assumptions on existence and uniqueness of solutions.

3.1.1 Reduction to Poincaré Maps

Let X_0 and ∂X_0 be open and closed subsets of X, respectively, such that $X_0 \cap \partial X_0 = \emptyset$ and $X = X_0 \cup \partial X_0$, and let $T(t) : X \to X$, $t \geq 0$, be an ω-periodic semiflow with $T(t)X_0 \subset X_0, \forall t \geq 0$; that is, X_0 is positively invariant for $T(t)$. Note that we do not require ∂X_0 to be positively invariant for $T(t)$.

Definition 3.1.1. *A periodic semiflow $T(t)$ is said to be uniformly persistent with respect to $(X_0, \partial X_0)$ if there exists $\eta > 0$ such that for any $x \in X_0$,* $\liminf_{t\to\infty} d(T(t)x, \partial X_0) \geq \eta$.

The following result shows that uniform persistence of a periodic semiflow $T(t)$ is equivalent to that of its associated discrete semidynamical system $\{S^n\}$ defined by $S = T(\omega)$.

Theorem 3.1.1. *Let $T(t)$ be an ω-periodic semiflow on X with $T(t)X_0 \subset X_0$, $\forall t \geq 0$, and $S = T(\omega)$. Assume that $S : X \to X$ is asymptotically smooth and has a global attractor. Then uniform persistence of S with respect to $(X_0, \partial X_0)$ implies that of $T(t) : X \to X$. More precisely, $S : X_0 \to X_0$ admits a global attractor $A_0 \subset X_0$, and the compact set $A_0^* = \cup_{0\leq t\leq\omega} T(t)A_0 \subset X_0$ attracts every point in X_0 for $T(t)$ in the sense that* $\lim_{t\to\infty} d(T(t)x, A_0^*) = 0$ *for any $x \in X_0$.*

Proof. Assume that $S : X \to X$ is uniformly persistent with respect to $(X_0, \partial X_0)$. Then Theorem 1.3.6 implies that $S : X_0 \to X_0$ admits a global attractor $A_0 \subset X_0$. By the compactness of A_0 and the continuity of $T(t)x$ for $x \in X$ uniformly on the compact set $[0, \omega]$, it easily follows that for any $\epsilon > 0$, there is $\delta > 0$ such that for any $x \in N(A_0, \delta)$, the δ-neighborhood of A_0, and any $t \in [0, \omega]$, $T(t)x \in N(T(t)A_0, \epsilon)$, and hence

$$\lim_{x\to A_0} d(T(t)x, T(t)A_0) = 0 \quad \text{uniformly for } t \in [0, \omega]. \tag{3.1}$$

Since A_0 is invariant for S (i.e., $S(A_0) = A_0$) and $T(t)$ is an ω-periodic semiflow, $A_0 = S^n(A_0) = T(n\omega)A_0$ for all $n \geq 1$.

Let $x_0 \in X_0$ be given. By the global attractivity of A_0 in X_0, it follows that

$$\lim_{n\to\infty} d(T(n\omega)x_0, A_0) = \lim_{n\to\infty} d(S^n x_0, A_0) = 0. \tag{3.2}$$

For any $t \geq 0$, let $t = n\omega + t'$, where $n = [t/\omega]$ is the greatest integer less than or equal to t/ω and $t' \in [0, \omega)$. Then

$$\begin{aligned} d\left(T(t)x_0, T(t)A_0\right) &= d\left(T(t')T(n\omega)x_0, T(t')T(n\omega)A_0\right) \\ &= d\left(T(t')T(n\omega)x_0, T(t')A_0\right), \end{aligned}$$

and hence (3.1) and (3.2) imply that

$$\lim_{t\to\infty} d\left(T(t)x_0, T(t)A_0\right) = 0. \tag{3.3}$$

By the continuity of $T(t)x$ for $(t, x) \in [0, \infty) \times X$ and the compactness of $[0, \omega] \times A_0$, it follows that $A_0^* = \cup_{0\leq t\leq\omega} T(t)A_0$ is compact. Since $T(t)X_0 \subset X_0$, $\forall t \geq 0$, we have $A_0^* \subset X_0$. In view of the invariance of A_0 for $S = T(\omega)$, we further obtain $\cup_{t\geq 0} T(t)A_0 = \cup_{0\leq t\leq\omega} T(t)A_0 = A_0^*$. Consequently, (3.3) implies $\lim_{t\to\infty} d(T(t)x_0, A_0^*) = 0$. ∎

By Theorem 3.1.1 above, we can reduce uniform persistence of a given periodic (autonomous) system of differential equations to that of its associated Poincaré map (the time ω-map for any fixed $\omega > 0$).

3.1.2 Monotone Periodic Systems

Let $\omega > 0$ be fixed. We first consider periodic systems of ordinary differential equations

$$\begin{aligned}\frac{dx}{dt} &= F(t,x),\\ x(0) &= x_0 \in \mathbb{R}^n_+,\end{aligned} \tag{3.4}$$

where $x = (x_1, \ldots, x_n) \in \mathbb{R}^n$ and $\mathbb{R}^n_+ = \{x \in \mathbb{R}^n : x_i \geq 0, 1 \leq i \leq n\}$. We assume that $F : \mathbb{R}^1_+ \times \mathbb{R}^n_+ \to \mathbb{R}^n$ is continuous and ω-periodic in t, and that all partial derivatives $\partial F_i/\partial x_j$, $1 \leq i,j \leq n$, exist and are continuous on $\mathbb{R}^1_+ \times \mathbb{R}^n_+$.

In what follows, we take $\mathbb{R}^n$ as an ordered Banach space with its natural cone $\mathbb{R}^n_+$ and denote the interior of $\mathbb{R}^n_+$ by $\mathrm{int}(\mathbb{R}^n_+)$. An $n \times n$ matrix A is said to be quasi-positive if its off-diagonal entries are nonnegative. It is irreducible if viewed as a linear mapping from $\mathbb{R}^n$ to $\mathbb{R}^n$, it does not leave invariant any proper linear subspace spanned by a subset of the standard basis vectors of $\mathbb{R}^n$. For other equivalent definitions of irreducibility, we refer to [19, 158]. Assume that

(A1) $F_i(t,x) \geq 0$ for every $x \geq 0$ with $x_i = 0$, $t \in \mathbb{R}^1_+$, $1 \leq i \leq n$;
(A2) $\frac{\partial F_i}{\partial x_j} \geq 0$, $i \neq j$, $\forall (t,x) \in \mathbb{R}^1_+ \times \mathbb{R}^n_+$, and $D_xF(t,x) = (\partial F_i/\partial x_j)_{1\leq i,j\leq n}$ is irreducible for each $t \in \mathbb{R}^1_+$, $x \in \mathbb{R}^n_+$.

Then for every $x \in \mathbb{R}^n_+$, there exists a unique solution $\varphi(t,x)$ of (3.4) with the maximal interval of existence $I^+(x) \subset [0,+\infty)$ and $\varphi(t,x) \geq 0$, $\forall t \in I^+(x)$. If there exists a relatively open and convex subset U of $\mathbb{R}^n_+$ such that for every $x \in U$, $\varphi(t,x)$ is bounded on $I^+(x)$, then $I^+(x) = +\infty$. We can define the Poincaré map $S : U \to \mathbb{R}^n_+$ by

$$S(u) = \varphi(\omega, u), \ \forall u \in U.$$

By a Kamke's theorem argument, it follows that $S : U \to \mathbb{R}^n_+$ is strongly monotone (e.g., see [158, Theorem 1.5]). Now let $x(t)$ be a nonnegative ω-periodic solution of (3.4) and consider the corresponding linear periodic systems

$$\frac{dz}{dt} = D_xF(t,x(t))z. \tag{3.5}$$

By (A2), $A(t) := D_xF(t,x(t))$ is a continuous, ω-periodic, quasi-positive, and irreducible matrix function. Let I be the $n \times n$ identity matrix and let $\phi(t)$ be the fundamental matrix solution of (3.5) with $\phi(0) = I$. By [19, Lemma 2] or [158, Theorem 1.1], for each $t > 0$, $\phi(t)$ is a matrix with all entries positive, and hence for each $t > 0$, $\phi(t) : \mathbb{R}^n \to \mathbb{R}^n$ is a compact and strongly positive linear operator. By the continuity and differentiability of solutions for initial values, it easily follows that the Poincaré map S associated with (3.4) is defined in a neighborhood of $x_0 = x(0)$ and differentiable at x_0, with $DS(x_0) = \phi(\omega)$. The eigenvalues of $\phi(\omega)$ are often called the Floquet multipliers of (3.5). Based on the Krein–Rutman theorem (or on the Perron-Frobenius theorem in our present finite-dimensional case), we call $\rho = r(\phi(\omega))$ the principal Floquet multiplier of (3.5).

In what follows, we further impose the following conditions on F:

(A3) For each $t \geq 0$, $F(t, \cdot)$ is strictly subhomogeneous on $\mathbb{R}^n_+$ in the sense that $F(t, \alpha x) > \alpha F(t, x)$, $\forall x \gg 0$, $\alpha \in (0, 1)$;
(A4) $F(t, 0) \equiv 0$, and $F(t, x) < D_x F(t, 0)x$, $\forall t \geq 0$, $x \gg 0$.

Let $A(t), t \geq 0$, be a continuous, quasi-positive, and irreducible matrix function, and let $\phi(t, \tau)$, $t \geq \tau \geq 0$, be the fundamental matrix solution of $dx/dt = A(t)x$ with $\phi(\tau, \tau) = I$. By the proof of [19, Lemma 2] or [158, Theorem 1.1], it follows that for each $t > \tau$, $\phi(t, \tau) : \mathbb{R}^n \to \mathbb{R}^n$ is a strongly positive linear operator. By using the variation of constants formula for inhomogeneous linear ordinary differential equations, one can easily prove that (A3) implies the strict subhomogeneity of the Poincaré map on $\mathbb{R}^n_+$, and that (A4) implies $S(x) < DS(0)x$, $\forall x \gg 0$. Thus, we can apply the theory of monotone and subhomogeneous systems in Chapter 2 to the Poincaré map associated with (3.4). As an illustration of Theorem 2.3.4, we have the following result.

Theorem 3.1.2. *Let (A1),(A2), and (A3) hold. Assume that* $F(t, 0) \equiv 0$ *and that there exists a bounded subset* B *of* $\mathbb{R}^n_+$ *such that every solution* $x(t)$ *of (3.4) ultimately lies in* B*. Let* ρ *be the principal Floquet multiplier of (3.5) with* $x(t) \equiv 0$*.*

(a) If $\rho \leq 1$*, then* $x(t) \equiv 0$ *is a globally asymptotically stable periodic solution of (3.4) with respect to the initial values in* $\mathbb{R}^n_+$*;*
(b) If $\rho > 1$*, then (3.4) has a unique positive* ω*-periodic solution* $x(t)$*, and* $x(t)$ *is globally asymptotically stable with respect to initial values in* $\mathbb{R}^n_+ \setminus \{0\}$*.*

Example 3.1.1. Consider single-loop positive feedback systems in $\mathbb{R}^n_+$ (see [317, 349]):

$$\begin{aligned} \frac{dx_1}{dt} &= f(x_n, t) - \alpha_1(t)x_1, \\ \frac{dx_i}{dt} &= x_{i-1} - \alpha_i(t)x_i, \quad 2 \leq i \leq n. \end{aligned} \tag{3.6}$$

Assume that $\alpha_i(\cdot)$ and $f(x_n, \cdot)$ are continuous and ω-periodic in $t \in [0, \infty)$, that $f(0, t) \equiv 0$, $f(u, t) \geq 0$, $\frac{\partial f}{\partial u}(u, t) > 0$ is continuous in $\mathbb{R}^2_+$, and that for each $t \geq 0$, $f(\cdot, t)$ is strictly subhomogeneous on $\mathbb{R}^1_+$; that is, for any $t \geq 0$, $u > 0$, and $0 < \alpha < 1$, $f(\alpha u, t) > \alpha f(u, t)$. It is easy to verify that (A1), (A2), and (A3) are satisfied for (3.6). Set $\alpha_i := \min_{0 \leq t \leq \omega} \alpha_i(t)$, $\forall 1 \leq i \leq n$. If we further assume that there exist two positive numbers a and b such that

$$f(u, t) \leq au + b, \, \forall (u, t) \in \mathbb{R}^2_+, \;\; \alpha_i > 0, \, \forall 1 \leq i \leq n, \;\; \text{and } a < \prod_{i=1}^{n} \alpha_i,$$

then the ultimate boundedness of (3.6) follows from that of a nonhomogeneous linear system that majorizes (3.6) (for some details, see [317]). Thus, Theorem 3.1.2 applies to (3.6). A similar result was proved in [317] under the assumption that $f(\cdot, t)$ is strongly concave.

Let $\Omega \subset \mathbb{R}^N$ $(N \geq 1)$ be a bounded domain with boundary $\partial\Omega$ of class $C^{2+\theta}$ $(0 < \theta \leq 1)$. We then consider periodic scalar parabolic equations

$$\begin{aligned} \frac{\partial u}{\partial t} + A(t)u = f(x,t,u) \quad \text{in } \Omega \times (0,\infty), \\ Bu = 0 \quad \text{on } \partial\Omega \times (0,\infty), \\ u(\cdot, 0) = u_0 \quad \text{in } \Omega, \end{aligned} \tag{3.7}$$

where

$$A(t) = -\sum_{i,j=1}^{N} a_{ij}(x,t)\frac{\partial^2}{\partial x_i \partial x_j} + \sum_{i=1}^{N} a_i(x,t)\frac{\partial}{\partial x_i} + a_0(x,t)$$

is uniformly elliptic for each $t \in [0, \omega]$; $a_{ij}(x,t)$, $a_i(x,t)$, $1 \leq i,j \leq N$, and $f(x,t,u)$ are ω-periodic in t; $Bu = u$ or $Bu = \frac{\partial u}{\partial v} + b_0(x)u$, where $\frac{\partial}{\partial v}$ denotes the differentiation in the direction of the outward normal; and $b_0(x) \geq 0$. Let $Q_\omega = \Omega \times [0, \omega]$. We suppose that

(B1) $a_{jk} = a_{kj}$ and $a_i \in C^{\theta,\theta/2}(\overline{Q}_\omega), \forall 1 \leq j,k \leq N, 0 \leq i \leq N$, and $b_0 \in C^{1+\theta}(\partial\Omega, \mathbb{R})$;
(B2) $f \in C(\overline{Q}_\omega \times \mathbb{R}, \mathbb{R})$, $\frac{\partial f}{\partial u}$ exists, and $\frac{\partial f}{\partial u} \in C(\overline{Q}_\omega \times \mathbb{R}, \mathbb{R})$ with $f(\cdot,\cdot,u)$ and $\frac{\partial f}{\partial u}(\cdot,\cdot,u) \in C^{\theta,\theta/2}(\overline{Q}_\omega, \mathbb{R})$ uniformly for u in bounded subsets of $\mathbb{R}$.

Let $X = L^p(\Omega)$, $N < p < \infty$, and for $\beta \in (1/2 + N/(2p), 1]$, let X_β be the fractional power space of X with respect to $(A(0), B)$ (see [150]). Then X_β is an ordered Banach space with the order cone X_β^+ consisting of nonnegative functions. Moreover,

$$X_1 = W_B^{2,p}(\Omega) := \Big\{u \in W^{2,p}(\Omega);\ Bu = 0\Big\}, \quad X_\beta \subset C^{1+\lambda}(\overline{\Omega}),$$

with continuous inclusion for $\lambda \in [0, 2\beta - 1 - N/p)$, and X_β^+ has nonempty interior. By [152, Section III.20], it follows that for every $u_0 \in X_\beta$, there exists a unique regular solution $\varphi(t, u_0)$ of (3.7) with the maximal interval of existence $I^+(u_0) \subset [0, \infty)$, and $\varphi(t, u_0)$ is globally defined, provided that there is an L^∞-bound on $\varphi(t, u_0)$.

Let $E = X_\beta$ with $\beta \in (1/2 + N/(2p), 1]$ and assume that there exists an open subset U of E such that for every $u \in U$, $\varphi(t, u)$ is L^∞-bounded on $I^+(u)$. Then $I^+(u) = +\infty$. We define the Poincaré map $S : U \to E$ by $S(u) = \varphi(\omega, u)$. By an argument similar to that of [152, Proposition 21.2], it follows that $S : U \to E$ is continuous and strongly monotone. Moreover, S maps any order interval in U to a precompact set in E. Clearly, a fixed point u_0 of S corresponds to an ω-periodic solution $\varphi(t, u_0)$ of (3.7).

Let $u(t,x)$ be an ω-periodic solution of (3.7). Consider the corresponding linear periodic parabolic equation

$$\begin{aligned}\frac{\partial v}{\partial t} + A(t)v &= \frac{\partial f}{\partial u}(x,t,u(t,x))v,\\ Bv &= 0;\end{aligned}$$

that is,

$$\begin{aligned}\frac{\partial v}{\partial t} + \overline{A}(t)v &= 0,\\ Bv &= 0,\end{aligned} \tag{3.8}$$

where $\overline{A}(x,t)v = A(x,t)v - \frac{\partial f}{\partial u}(x,t,u(t,x))v$. According to [152, Chapter II], (3.8) admits an evolution operator $\overline{U}(t,\tau)$, $0 \le \tau \le t \le \omega$, and for any $0 \le \tau < t \le \omega$, $\overline{U}(t,\tau)$ is a compact and strongly positive operator on $E = X_\beta$. By [152, Proposition 23.1], the Poincaré map S associated with (3.7) is defined in a neighborhood of $u_0 = u(0,\cdot)$ and Fréchet differentiable at u_0, with $DS(u_0) = \overline{U}(\omega,0)$. Let $r = r(DS(u_0))$. Then by [152, Proposition 14.4], $\mu = -\frac{1}{T}\log(r)$ is the unique principal eigenvalue of the periodic–parabolic eigenvalue problem

$$\begin{aligned}&\frac{\partial v}{\partial t} + \overline{A}(t)v = \mu v,\\ &Bv = 0,\\ &v\ \omega\text{-periodic}.\end{aligned} \tag{3.9}$$

For various properties and estimates of principal eigenvalues of linear periodic–parabolic problems, we refer to [152, Sections II.15 and 17] and [188, 187].

In what follows, we further assume that

(B3) $f(x,t,0) \ge 0$, and for every $(x,t) \in \overline{\Omega} \times \mathbb{R}$, $f(x,t,\cdot)$ is subhomogeneous on $I \subset [0,\infty)$; that is, $f(x,t,\alpha u) \ge \alpha f(x,t,u)$ for every $\alpha \in (0,1)$ and $u \in I$ with $u > 0$; and for at least one $(x_0,t_0) \in \Omega \times \mathbb{R}$, $f(x_0,t_0,\cdot)$ is strictly subhomogeneous; that is, $f(x_0,t_0,\alpha u) > \alpha f(x_0,t_0,u)$ for every $\alpha \in (0,1)$ and $u \in I$ with $u > 0$.

(B4) $f(\cdot,\cdot,0) \equiv 0$, $f(x,t,u) \le \frac{\partial f(x,t,0)}{\partial u} \cdot u, \forall (x,t) \in \overline{\Omega} \times \mathbb{R}, u > 0$, and there exists $(x_0,t_0) \in \Omega \times \mathbb{R}$ such that $f(x_0,t_0,u) < \frac{\partial f(x_0,t_0,0)}{\partial u} \cdot u, \forall u > 0$.

Let $V = \{u \in U : u(x) \ge 0 \text{ and } u(x) \in I, \forall x \in \overline{\Omega}\}$. By the strong positivity of the evolution operator $U(t,\tau)$ on E for $0 \le \tau < t \le \omega$ and the variation of constants formula for inhomogeneous linear evolution equations, it easily follows that (B3) implies the strict subhomogeneity of the Poincaré map S on V, and (B4) implies $S(u) < DS(0)u$, $\forall u \in V$ with $u \gg 0$. In the case where $f(x,t,0) \equiv 0$, we have $DS(0)u = \varphi_0(\omega,u)$, $\forall u \in E$, where $\varphi_0(t,u) = \overline{U}(t,0)u$ is the regular solution of (3.8) with $u(t,x) \equiv 0$.

In the case where $f(x,t,u) = uF(x,t,u)$, let $\mu = \mu(A(t), F(x,t,0))$ be the principal eigenvalue of the periodic parabolic problem

$$\begin{aligned}
&\frac{\partial v}{\partial t} + A(t)v = F(x,t,0)v + \mu v,\\
&Bv = 0, \\
&v \ \omega\text{-periodic},
\end{aligned} \tag{3.10}$$

and let $v^*(x,t)$ be a principal (positive) eigenfunction associated with $\mu(A(t), F(x,t,0))$. Then we have the following results.

Theorem 3.1.3. *Let $f(x,t,u) = uF(x,t,u)$ and let (B1) and (B2) hold. Assume that*

(1) There exists $K_0 > 0$ such that $F(x,t,u) < 0$, $\forall (x,t) \in \overline{\Omega} \times [0,\omega]$, $u \geq K_0$;
(2) $\mu(A(t), F(x,t,0)) < 0$.

Then there exist two positive ω-periodic solutions $u_1(t) \leq u_2(t)$ of (3.7) such that for any solution $u(t)$ of (3.7) with $u(0) \in X_\beta^+ \setminus \{0\}$,

$$\lim_{t\to\infty} \operatorname{dist}_{X_\beta}(u(t), [u_1(t), u_2(t)]) = 0.$$

Proof. By assumption (1), every constant $K \geq K_0$ is a supersolution of (3.7), and hence for every $u_0 \in X_\beta^+ \setminus \{0\}$, the solution $\varphi(t, u_0)$ of (3.7) exists globally on $I^+(u_0) = [0, \infty)$. Let $S : u_0 \to \varphi(\omega, u_0)$ be the associated Poincaré map. It is easy to see that every possible nonnegative ω-periodic solution $u(t,x)$ satisfies $0 \leq u(t,x) < K_0$. By a standard iteration argument for S, it follows that for every $u_0 \in E$ with $u_0 \geq 0$, there exists $N = N(u_0) > 0$ such that $0 \leq S^n(u_0)(x) \leq K_0$, $\forall x \in \overline{\Omega}, n \geq N$. According to [85, Section 2] or [152, Section III.21], we may assume, without loss of generality, $K_0 \in E$. Consequently, the conclusion of the theorem follows from Theorem 2.1.1 with Remark 2.1.2, and Theorem 2.1.2 with Remark 2.1.5, as applied to $S : [0, K_0]_E \to [0, K_0]_E$. ∎

Theorem 3.1.4. *Let $f(x,t,u) = uF(x,t,u)$ and let (B1) and (B2) hold. Assume that*

(1) For any $(x,t) \in \overline{\Omega} \times [0,\omega]$ and any $u > 0$, $F(x,t,u) \leq F(x,t,0)$, and for at least one $(x_0,t_0) \in \Omega \times [0,\omega]$ and any $u > 0$, $F(x_0,t_0,u) < F(x_0,t_0,0)$;
(2) $\mu(A(t), F(x,t,0)) \geq 0$.

Then $u = 0$ is globally asymptotically stable with respect to initial values in X_β^+.

Proof. For each $u_0 \in X_\beta^+$, there is positive number k such that $u_0 \leq kv^*(\cdot, 0)$. By assumption (1) and the comparison theorem of scalar parabolic equations, it follows that the solution $\varphi(t, u_0)$ of (3.7) exists on $[0, +\infty)$, and

$$\varphi(t,u_0)(x) \leq ke^{-\mu t}v^*(x,t) \leq kv^*(x,t), \ \forall t \geq 0, x \in \Omega.$$

In particular, $S^n(u_0) = \varphi(n\omega, u_0) \subset [0, kv^*(\cdot,0)]_E$, $\forall n \geq 0$. Thus, the precompactness of $S([0, kv^*(\cdot, 0)]_E)$ implies that the positive orbit $\gamma^+(u_0) := \{S^n(u_0) : n \geq 0\}$ is also precompact in E. Clearly, assumption (1) implies (B4). Now the conclusion follows from Theorem 2.2.2 with $V = X_\beta^+$. ∎

Theorem 3.1.5. *Let $f(x,t,u) = uF(x,t,u)$ and let (B1) and (B2) hold. Assume that*

(1) For each $(x,t) \in \overline{\Omega} \times [0,\omega]$, $F(x,t,\cdot)$ is decreasing on $[0,\infty)$, and for at least one $(x_0,t_0) \in \Omega \times [0,\omega]$, $F(x_0,t_0,\cdot)$ is strictly decreasing on $(0,\infty)$;
(2) There exists a positive supersolution $\overline{V}$ for the periodic boundary value problem (3.7).

Then the following threshold dynamics hold:

(a) If $\mu(A(t),F(x,t,0) \geq 0$, then $u = 0$ is globally asymptotically stable with respect to initial values in X_β^+;
(b) If $\mu(A(t),F(x,t,0) < 0$, then there exists a positive ω-periodic solution $u_0(t)$ of (3.7), and $u_0(t)$ is globally asymptotically stable with respect to initial values in $X_\beta^+ \setminus \{0\}$.

Proof. For any $\rho \geq 1$, assumption (2) implies that $\rho\overline{V}$ is also a supersolution of (3.7). Thus, every solution of (3.7) with nonnegative initial values exists globally on $[0,\infty)$. Obviously, assumption (1) implies (B3) with $I = [0,\infty)$ and hence the strict subhomogeneity of the associated Poincaré map $S : X_\beta^+ \to X_\beta^+$. Without loss of generality, we may assume that $\overline{V}(0) \in E = X_\beta$ (see [85, Section 2] or [152, Chapter III.21]). Then Theorem 2.3.4 with $V = [0, \rho\overline{V}(0)]_E$, $\forall \rho \geq 1$, completes the proof. ∎

Now we discuss the case that (3.7) is autonomous, that is, $A(x,t) = A(x)$ and $F(x,t,u) = F(x,u)$. We distinguish two cases:

(I) $a_0(x) \geq 0$, with $a_0(x) \not\equiv 0$ if $b_0(x) \equiv 0$;
(N) $a_0(x) \equiv 0$, $b_0(x) \equiv 0$.

In case (I), we assume $m \in C^\theta(\overline{\Omega})$ and $m(x) > 0$ at some $x \in \overline{\Omega}$. By [152, Theorem 16.1 and Remark 16.5], it follows that the elliptic eigenvalue problem

$$\begin{aligned} A(x)u &= \lambda m(x)u \quad \text{in } \Omega, \\ Bu &= 0 \quad \text{on } \partial\Omega, \end{aligned} \tag{3.11}$$

has a unique positive principal eigenvalue $\lambda_1(m)$. For any $\omega > 0$, let $\mu(A, m(x), \omega)$ be the principal eigenvalue of periodic parabolic problem (3.10) with $F(x,t,0)$ replaced by $m(x)$. By [152, Section II.15 and Remark 16.5], it follows that if $\lambda_1(m) < 1$, then $\mu(A,m(x),\omega) < 0$, and if $\lambda_1(m) \geq 1$, then $\mu(A,m(x),\omega) \geq 0$. As a corollary of Theorem 3.1.5, we have the following result.

Theorem 3.1.6. *Let $A(x,t) = A(x)$, $f(x,t,u) = uF(x,u)$ and let (B1), (B2), and (I) hold. Assume that*

(1) $F(x,0) > 0$ for some $x \in \Omega$;
(2) For any $x \in \overline{\Omega}$, $F(x,\cdot)$ is decreasing on $[0,\infty)$, and for at least one $x_0 \in \Omega$, $F(x_0,\cdot)$ is strictly decreasing on $(0,\infty)$;

(3) There exists a positive supersolution $\overline{V}$ for the corresponding steady state problem

$$\begin{aligned} A(x)u &= uF(x,u) \quad \text{in } \Omega, \\ Bu &= 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{3.12}$$

Then the following threshold dynamics hold:

(a) If $\lambda_1(F(x,0)) \geq 1$, then (3.12) has no positive solution in X_β, and $u = 0$ is a globally asymptotically stable solution of (3.7) with respect to initial values in X_β^+;
(b) If $\lambda_1(F(x,0)) < 1$, then (3.12) has a unique positive solution u_0 in X_β, and $u = u_0$ is a globally asymptotically stable solution of (3.7) with respect to initial values in $X_\beta \setminus \{0\}$.

Proof. Let $\omega > 0$ be fixed, and we view autonomous parabolic equation (3.7) as an ω-periodic one. Then the conclusion (a) follows from Theorem 3.1.5(a). In the second case, by Theorem 3.1.5(b), (3.7) has a unique positive ω-periodic solution $u_0(t,x)$, and $u_0(t,x)$ is globally asymptotically stable in $X_\beta \setminus \{0\}$. For any $s > 0$, since (3.7) is autonomous, $u_0(t+s,x)$ is also an ω-periodic solution of (3.7). By the uniqueness of the positive ω-periodic solution, we then get $u_0(t+s,x) = u_0(t,x)$, $\forall t \in [0,\omega]$, $x \in \Omega$. This implies that $u_0(t,x) = u_0(0,x)$, $\forall t \in [0,\omega], x \in \Omega$, and hence u_0 is a steady-state-solution of (3.7). ∎

For the case (N), according to [152, Theorem 16.3 and Remark 16.5], we can also discuss the global asymptotic stability of steady-state-solutions of the corresponding autonomous equation (3.7) in a similar way.

Example 3.1.2. We consider a reaction–diffusion equation of single population growth, which is deduced from a competition model in an unstirred chemostat (see [344, 171]):

$$\begin{aligned} &\frac{\partial u}{\partial t} = d\frac{\partial^2 u}{\partial x^2} + F(\phi(x) - u)u, \; t > 0, \, 0 < x < 1, \\ &\frac{\partial u}{\partial x}(t,0) = 0, \; \frac{\partial u}{\partial x}(t,1) + \gamma u(t,1) = 0, \\ &u(0,x) = u_0(x) \text{ with } 0 \leq u_0(x) \leq \phi(x), \, \forall x \in (0,1), \end{aligned} \tag{3.13}$$

where $d > 0$, $\phi(x) = S^{(0)}\left(\frac{1+\gamma}{\gamma} - x\right)$, $0 < x < 1$, $S^{(0)} > 0$, $\gamma > 0$, and F is the typical Michaelis–Menten–Monod response function

$$F(s) = \frac{ms}{a+s}, \; \forall s \geq 0, \quad \text{with } m > 0, \, a > 0.$$

In what follows, we consider a more general function $F(s)$ satisfying

$$F(0) = 0 \text{ and } F'(s) > 0, \forall s \geq 0. \tag{3.14}$$

Let $\lambda_0 = \lambda_0(F(\phi(x))) > 0$ be the first eigenvalue of

$$\begin{aligned} &d\frac{d^2v}{dx^2} + \lambda F(\phi(x))v = 0, \\ &v'(0) = 0,\ v'(1) + \gamma v(1) = 0. \end{aligned} \tag{3.15}$$

Then we have the following result.

Proposition 3.1.1. *Assume that (3.14) holds. Then we have the following threshold dynamics:*

(a) If $\lambda_0(F(\phi(x))) \geq 1$, then $u = 0$ is a globally asymptotically stable steady-state-solution of (3.13) with respect to nonnegative initial values.
(b) If $\lambda_0(F(\phi(x))) < 1$, then (3.13) has a globally asymptotically stable positive steady-state-solution $u_0(x)$ with $u_0(x) < \phi(x)$, $\forall x \in (0,1)$, with respect to positive initial values.

Proof. For the use of Theorem 3.1.6, let $\hat{F}(s), s \in \mathbb{R}$, be a continuously differentiable extension of $F(s)$ on $[0,\infty)$ to $\mathbb{R}$ satisfying $\hat{F}'(s) > 0, \forall s \in \mathbb{R}$. Consider the autonomous parabolic equation

$$\begin{aligned} &\frac{\partial u}{\partial t} = d\frac{\partial^2 u}{\partial x^2} + \hat{F}(\phi(x) - u)u,\ t > 0,\ 0 < x < 1, \\ &\frac{\partial u}{\partial x}(t,0) = 0,\ \frac{\partial u}{\partial x}(t,1) + \gamma u(t,1) = 0, \\ &u(0,x) = u_0(x) \geq 0. \end{aligned} \tag{3.16}$$

Let $K_0 = S^{(0)} \cdot \frac{1+\gamma}{\gamma}$. Then $\phi(x) \leq K_0$, $\forall x \in (0,1)$, and hence $\hat{F}(\phi(x) - K_0) \leq 0$. Then Theorem 3.1.6 implies the corresponding conclusion for (3.16). By a comparison argument, it easily follows that for any $0 \leq u_0(x) \leq \phi(x)$, the solution $u(t,x)$ of (3.16) satisfies $0 \leq u(t,x) \leq \phi(x)$, $\forall t \geq 0, x \in \Omega$, and hence the conclusion for (3.13) follows. ∎

3.2 Asymptotically Periodic Semiflows

Let (X,d) be a metric space. A continuous mapping $\Phi : \Delta_0 \times X \to X$, $\Delta_0 = \{(t,s) : 0 \leq s \leq t < \infty\}$, is called a nonautonomous semiflow if Φ satisfies the following properties:

(i) $\Phi(s,s,x) = x, \quad \forall s \geq 0,\ x \in X$;
(ii) $\Phi(t,s,\Phi(s,r,x)) = \Phi(t,r,x), \quad \forall t \geq s \geq r \geq 0$.

Definition 3.2.1. *A nonautonomous semiflow $\Phi : \Delta_0 \times X \to X$ is called asymptotically periodic with limit ω-periodic semiflow $T(t) : X \to X, t \geq 0$, if*

$$\Phi(t_j + n_j\omega, n_j\omega, x_j) \to T(t)x,\ as\, j \to \infty,$$

for any three sequences $t_j \to t, n_j \to \infty, x_j \to x$, with $x, x_j \in X$.

3.2.1 Reduction to Asymptotically Autonomous Processes

Let $\Phi : \Delta_0 \times X \to X$ be an asymptotically periodic semiflow with limit ω-periodic semiflow $T(t) : X \to X$, $t \geq 0$. Define

$$S(x) = T(\omega)(x), \ \forall x \in X; \quad T_n(x) = \Phi(n\omega, 0, x), \ \forall n \in \mathbb{N}, \ x \in X;$$

and

$$S_n(x) = \Phi((n+1)\omega, n\omega, x), \ \forall n \in \mathbb{N}, \ x \in X.$$

By the properties of nonautonomous semiflows, it then follows that

$$T_n(x) = S_{n-1} \circ S_{n-2} \circ \cdots \circ S_1 \circ S_0(x), \quad \forall n \geq 1, \ x \in X.$$

By Definition 3.2.1, it is easy to see that $\lim_{(n,x)\to(\infty,x_0)} S_n(x) = S(x_0)$. Consequently, $T_n : X \to X$, $n \geq 0$, is an asymptotically autonomous discrete process with limit autonomous discrete semiflow $S^n : X \to X$, $n \geq 0$, in the sense of Definition 1.2.2.

We are now in a position to prove the main result of this subsection.

Theorem 3.2.1. *Let $\Phi : \Delta_0 \times X \to X$ be an asymptotically periodic semiflow with limit ω-periodic semiflow $T(t) : X \to X, t \geq 0$, and $T_n(x) = \Phi(n\omega, 0, x)$, $n \geq 0$, $x \in X$, and $S(x) = T(\omega)x$, $x \in X$. Assume that A_0 is a compact S-invariant subset of X. If for some $y \in X$, $\lim_{n\to\infty} d(T_n(y), A_0) = 0$, then $\lim_{t\to\infty} d(\Phi(t, 0, y), T(t)A_0) = 0$.*

Proof. We first prove the following claim.

Claim. $\lim_{(n,x)\to(\infty,A_0)} d(\Phi(t+n\omega, n\omega, x), T(t)A_0) = 0$ uniformly for $t \in [0, \omega]$. More precisely, for any $\epsilon > 0$, there exist $\delta = \delta(\epsilon) > 0$ and $N = N(\epsilon) > 0$ such that for any $x \in B(A_0, \delta)$, $n \geq N$, and $t \in [0, \omega]$, we have $\Phi(t + n\omega, n\omega, x) \in B(T(t)A_0, \epsilon)$, where $B(A_0, \delta) = \{x : d(x, A_0) < \delta\}$ is the δ-neighborhood of A_0.

Indeed, let $x_0 \in X$ be given. For any $\epsilon > 0$, since $T(t)x_0$ is uniformly continuous for t in the compact set $[0, \omega]$, there exists $\delta_0 = \delta_0(\epsilon) > 0$ such that for any $t_1, t_2 \in [0, \omega]$ with $|t_1 - t_2| < \delta_0$,

$$\|T(t_1)x_0 - T(t_2)x_0\| < \epsilon/2.$$

For any $t_0 \in [0, \omega]$, by Definition 3.2.1, $\lim_{(t,n,x)\to(t_0,\infty,x_0)} \Phi(t + n\omega, n\omega, x) = T(t_0)x_0$, and hence there exist $\delta = \delta(t_0, \epsilon) \leq \delta_0$ and $N = N(t_0, \epsilon) > 0$ such that for any $|t - t_0| < \delta, \ n \geq N$, and $x \in B(x_0, \delta)$, we have

$$\|\Phi(t + n\omega, n\omega, x) - T(t_0)x_0\| < \epsilon/2.$$

Let $I(t_0, \delta) = (t_0 - \delta, t_0 + \delta)$. Since $\cup_{t_0\in[0,\omega]} I(t_0, \delta) \supseteq [0, \omega]$, the compactness of $[0, \omega]$ implies that there exist $t_1, t_2, \ldots, t_m \in [0, \omega]$ such that $\cup_{i=1}^m I(x_i, \delta_i) \supseteq [0, \omega]$. Let $N^* = \max_{1\leq i\leq m}\{N(t_i, \epsilon)\}$, $\delta^* = \min_{1\leq i\leq m}\{\delta_i = \delta(t_i, \epsilon)\}$. Then for any $x \in B(x_0, \delta^*)$, $n \geq N^*$, and $t \in [0, \omega]$, there exists some $1 \leq i \leq m$ such that $t \in I(t_i, \delta_i)$. Since $n \geq N^* \geq N_i$, $\|x - x_0\| < \delta^* \leq \delta_i$, and $|t - t_i| < \delta_i \leq \delta_0$, we get

$$\begin{aligned} \|\Phi(t + n\omega, n\omega, x) - T(t)x_0\| &\leq \|\Phi(t + n\omega, n\omega, x) - T(t_i)x_0\| \\ &\quad + \|T(t_i)x_0 - T(t)x_0\| \\ &< \epsilon/2 + \epsilon/2 = \epsilon. \end{aligned}$$

Then

$$\lim_{(n,x)\to(\infty,x_0)} (\Phi(t + n\omega, n\omega, x) - T(t)x_0) = 0, \text{ uniformly for } t \in [0, \omega].$$

For any $\epsilon > 0$ and $x_0 \in A_0$, there exist $\delta = \delta(\epsilon, x_0) > 0$ and $N = N(\epsilon, x_0) > 0$ such that for any $x \in N(x_0, \delta)$, $n \geq N$, and $t \in [0, \omega]$,

$$\Phi(t + n\omega, n\omega, x) \in B(T(t)x_0, \epsilon).$$

Since $A_0 \subseteq \cup_{x_0 \in A_0} B(x_0, \delta/2)$, by the compactness of A_0,there exist $x_1, x_2, \ldots, x_k \in A_0$ such that $A_0 \subseteq \cup_{i=1}^k B(x_i, \delta_i/2)$. Let $\delta^* = \min_{1\leq i\leq k}\{\delta_i/2\}$. For any $z \in B(A_0, \delta^*)$, there exists $x \in A_0$ such that $d(x, z) < \delta^*$. Then there exists x_i, $1 \leq i \leq k$, such that $x \in B(x_i, \delta_i/2)$. Thus

$$d(z, x_i) \leq d(x, z) + d(x, x_i) < \delta^* + \delta_i/2 \leq \delta_i/2 + \delta_i/2 = \delta_i;$$

that is, $z \in N(x_i, \delta_i)$. Then $N(A_0, \delta^*) \subseteq \cup_{i=1}^k B(x_i, \delta_i)$. Therefore, for any $x \in B(A_0, \delta^*)$, $n \geq N^* = \max_{1\leq i\leq k}\{N(\epsilon, x_i)\}$, and $t \in [0, \omega]$, there exists some x_i, $1 \leq i \leq k$, such that $x \in B(x_i, \delta_i)$, and hence $n \geq N^* \geq N_i(\epsilon, x_i)$. Then we have

$$\Phi(t + n\omega, n\omega, x) \in B(T(t)x_i, \epsilon),$$

which implies $d(\Phi(t + n\omega, n\omega, x), T(t)A_0) < \epsilon$, and hence

$$\lim_{(n,x)\to(\infty,A_0)} d(\Phi(t + n\omega, n\omega, x), T(t)A_0) = 0, \text{ uniformly for } t \in [0, \omega].$$

For any $t \geq 0$, let $t = n\omega + t'$, where $n = [t/\omega]$ is the greatest integer less than or equal to t/ω and $t' \in [0, \omega)$. Then $\Phi(t, 0, y) = \Phi(t, n\omega, \Phi(n\omega, 0, y))$, and by the S-invariance of A_0, $T(t)A_0 = T(t')T(n\omega)A_0 = T(t')A_0$. Since $\lim_{n\to\infty} d(\Phi(n\omega, 0, y), A_0) = \lim_{n\to\infty} d(T_n(y), A_0) = 0$, the claim above implies that

$$\lim_{t\to\infty} d(\Phi(t, 0, y), T(t)A_0) = \lim_{t\to\infty} d(\Phi(t' + n\omega, n\omega, \Phi(n\omega, 0, y)), T(t')A_0) = 0.$$

This completes the proof. ∎

By Theorem 3.2.1, we can reduce the study of asymptotic behavior of an asymptotically periodic semiflow $\Phi : \Delta_0 \times X \to X$ with limit ω-periodic semiflow $T(t) : X \to X$, $t \geq 0$, to that of its associated asymptotically autonomous discrete process $T_n : X \to X, n \geq 0$, with limit autonomous discrete semiflow $S^n : X \to X, n \geq 0$, where $S = T(\omega) : X \to X$ is the usual Poincaré map associated with the ω-periodic semiflow $T(t) : X \to X, t \geq 0$.

3.2.2 Asymptotically Periodic Systems

In this subsection we show that an asymptotically periodic differential system can give rise to an asymptotically periodic semiflow under appropriate conditions, and give some illustrative examples.

Consider the nonautonomous parabolic systems

$$\begin{aligned} \frac{\partial u_i}{\partial t} + A_i(t)u_i = f_i(x, t, u_1, \dots, u_m) \quad \text{in } \Omega \times (0, \infty), \\ B_i u_i = 0 \quad \text{on } \partial\Omega \times (0, \infty), \end{aligned} \tag{3.17}$$

where $1 \le i \le m$, $\Omega \subset \mathbb{R}^N$ $(N \ge 1)$ is a bounded domain with boundary $\partial\Omega$ of class $C^{2+\theta}$ $(0 < \theta \le 1)$,

$$A_i(t)v = -\sum_{j,k=1}^{N} a_{jk}^{(i)}(x, t)\frac{\partial^2 v}{\partial x_j \partial x_k} + \sum_{j=1}^{N} a_j^{(i)}(x, t)\frac{\partial v}{\partial x_j} + a_0^{(i)}(x, t)v, \ 1 \le i \le m,$$

are linear uniformly elliptic differential expressions of second order for each $t \in [0, \omega]$, $\omega > 0$, and $A_i(t)$ are ω-periodic in t, and $B_i v = v$ or $B_i v = \frac{\partial v}{\partial n} + b_0^{(i)}(x)v$, where $\frac{\partial}{\partial n}$ denotes differentiation in the direction of the outward normal n to $\partial\Omega$. We assume that $a_{jk}^{(i)} = a_{kj}^{(i)}$, $a_j^{(i)}$ and $a_0^{(i)} \in C^{\theta,\theta/2}(\overline{Q}_\omega)$, $a_0^{(i)} \ge 0$, $1 \le j, k \le N, 1 \le i \le m$, $Q_\omega = \Omega \times [0, \omega]$, and $b_0^{(i)} \in C^{1+\theta}(\partial\Omega, \mathbb{R})$, $b_0^{(i)} \ge 0$, $1 \le i \le m$.

We further impose the following smoothness condition on $f = (f_1, \dots, f_m)$:

(H) $f_i \in C(\overline{\Omega} \times \mathbb{R}_+ \times \mathbb{R}^m, \mathbb{R})$, $\frac{\partial f_i}{\partial u_j}$ exists and $\frac{\partial f_i}{\partial u_j} \in C(\overline{\Omega} \times \mathbb{R}_+ \times \mathbb{R}^m, \mathbb{R})$, and for each $T > 0$, we have $f_i(\cdot, \cdot, u)$ and $\frac{\partial f_i}{\partial u_j}(\cdot, \cdot, u) \in C^{\theta,\theta/2}(\overline{Q}_T, \mathbb{R})$ uniformly for $u = (u_1, \dots, u_m)$ in bounded subsets of $\mathbb{R}^m$, $1 \le i, j \le m$.

Let $X = L^p(\Omega)$, $N < p < \infty$, and for $\beta \in (1/2 + N/(2p), 1)$, let $E_i = X_\beta^{(i)}, 1 \le i \le m$, be the fractional power space of X with respect to $(A_i(0), B_i)$ (e.g., see Henry [150]). Then E_i is an ordered Banach space with the order cone P_i consisting of all nonnegative functions in E_i, and P_i has nonempty interior $\text{int}(P_i)$. Let $P = \prod_{i=1}^m P_i$ and $E = \prod_{i=1}^m E_i$. Then (E, P) is an order Banach space. By an easy extension of some results in [152, Section III.20] to systems, it follows that for every $u = (u_1, \dots, u_m) \in E$ and every $s \ge 0$, there exists a unique regular solution $\phi(t, s, u)$ of (3.17) satisfying $\phi(s, s, u) = u$ with its maximal interval of existence $I^+(s, u) \subset [s, \infty)$, and $\phi(t, s, u)$ is globally defined, provided that there is an L^∞-bound on $\phi(t, s, u)$.

We assume that each f_i^0 is ω-periodic in t and satisfies (H). For any $u \in E$, let $\phi_0(t, s, u)$ be the unique solution of the following ω-periodic system of parabolic equations:

$$\begin{aligned} \frac{\partial u_i}{\partial t} + A_i(t)u_i = f_i^0(x, t, u_1, \dots, u_m) \quad \text{in } \Omega \times (0, \infty), \\ B_i u_i = 0 \quad \text{on } \partial\Omega \times (0, \infty), \end{aligned} \tag{3.18}$$

with $\phi_0(s,s,u) = u$, and let $T(t)u = \phi_0(t,0,u)$. Then we have the following result.

Proposition 3.2.1. *Let* $f = (f_1,\ldots,f_m)$, $f_0 = (f_1^0,\ldots,f_m^0)$, $\|u\|_E = \sum_{i=1}^m \|u_i\|_{E_i}$, $\forall u \in E$, *and* $|u| = \sum_{i=1}^m |u_i|$, $\forall u \in \mathbb{R}^m$. *Assume that*

(1) $\lim_{t\to\infty} |f(x,t,u) - f_0(x,t,u)| = 0$ *uniformly for* $x \in \overline{\Omega}$ *and* u *in any bounded set of* $\mathbb{R}^m$*;*
(2) Solutions of (3.17) and (3.18) are uniformly bounded in E; that is, for any $r > 0$, *there exists* $B = B(r) > 0$ *such that for any* $u \in E$ *with* $\|u\| \le r$, *we have* $\|\phi(t,s,u)\| \le B(r)$ *and* $\|\phi_0(t,s,u)\| \le B(r)$, $\forall t \ge s \ge 0$.

Then for any given positive integer k *and real number* $r > 0$, *we have*

$$\lim_{n\to\infty} \|\phi(t+n\omega, n\omega, u) - T(t,u)\|_E = 0$$

uniformly for $t \in [0,k\omega]$ *and* $\|u\| \le r$. *In particular, for any* $u \in E$, $\gamma^+(u) = \{\phi(n\omega,0,u); n \ge 0\}$ *is precompact in* E, *and* $\phi : \Delta_0 \times E \to E$ *is an asymptotically periodic semiflow with limit periodic semiflow* $T(t) : E \to E$, $t \ge 0$.

Proof. For any $u \in E$, the uniform boundedness implies that for any $s \ge 0$, $\phi(t,s,u)$ and $\phi_0(t,s,u)$ exist globally on $[s,\infty)$. Given $r > 0$, let $B = B(r)$ be as in assumption (2). Then there exists $B_1 = B_1(B) > 0$ such that $\|\phi((t,s,u)\|_{C(\overline{\Omega})} \le B_1$ and $\|\phi_0((t,s,u)\|_{C(\overline{\Omega})} \le B_1$ for all $t \ge s \ge 0$ and $u \in E$ with $\|u\| \le r$. Let

$$\phi(t,n\omega,u) = \tilde{u}(t) = (\tilde{u}_1(t),\ldots,\tilde{u}_m(t)),\ \forall t \ge n\omega,\ n \ge 0,$$

and

$$\phi_0(t,n\omega,u) = u(t) = (u_1(t),\ldots,u_m(t)),\ \forall t \ge n\omega,\ n \ge 0.$$

Let $U_i(t,\tau)$ be the evolution operator generated by $A_i(t)$, $1 \le i \le n$ (see [152, II.11]). Then, by the variation of constants formula (see, e.g., [152, III.19]), we get

$$\tilde{u_i}(t) = U_i(t,n\omega)u_i + \int_{n\omega}^t U_i(t,s)f_i(\cdot,s,\tilde{u}(s))ds$$

and

$$u_i(t) = U_i(t,n\omega)u_i + \int_{n\omega}^t U_i(t,s)f_i^0(\cdot,s,u(s))ds,\ \forall t \in [n\omega,(n+k)\omega].$$

Let $D_m = \overline{\Omega} \times [n\omega,(n+k)\omega] \times [0,B_1]^m \subset \mathbb{R}^N \times \mathbb{R}_+ \times \mathbb{R}^m$. Then

$$\begin{aligned}\|\tilde{u}_i(t) - u_i(t)\|_\beta \le & \int_{n\omega}^{t} \|U_i(t,s)\|_{0,\beta} \cdot \left\|f_i^0(\cdot,s,\tilde{u}(s)) - f_i^0(\cdot,s,u(s))\right\|_0 ds \\ & + \int_{n\omega}^{t} \|U_i(t,s)\|_{0,\beta} \cdot \left\|f_i(\cdot,s,\tilde{u}(s)) - f_i^0(\cdot,s,\tilde{u}(s))\right\|_0 ds \\ \le & \, c_0 \int_{n\omega}^{t} \|U_i(t,s)\|_{0,\beta} \cdot \|\tilde{u}(s)) - u(s))\|_\beta \, ds \\ & + \int_{n\omega}^{t} \|U_i(t,s)\|_{0,\beta} \cdot \left\|f_i - f_i^0\right\|_{C(D_m,\mathbb{R})} ds.\end{aligned}$$

For a fixed $\alpha \in (\beta, 1)$, using the estimates (see [152, II.11])

$$\|U_i(t,s)\|_{0,\beta} \le c_i(t-s)^{-\alpha}, \ \forall t > s,$$

and

$$\int_{n\omega}^{t} (t-s)^{-\alpha} ds \le \frac{(k\omega)^{1-\alpha}}{1-\alpha}, \quad \forall n\omega \le s < t \le (n+k)\omega,$$

we have

$$\begin{aligned}\|\tilde{u}(t) - u(t)\|_E = & \sum_{i=1}^{m} \|\tilde{u}_i(t) - u_i(t)\|_\beta \\ \le & \, c \int_{n\omega}^{t} (t-s)^{-\alpha} \|\tilde{u}(s) - u(s)\|_\beta \, ds \\ & + c \int_{n\omega}^{t} (t-s)^{-\alpha} \|f - f_0\|_{C(D_m,\mathbb{R}^m)} ds,\end{aligned}$$

where $c = c(k, r) > 0$, and hence, by a version of Gronwall's inequality (see, e.g., [152, Lemma 19.4]), we get

$$\|\phi(t, n\omega, u) - \phi_0(t, n\omega, u)\|_E = \|\tilde{u}(t) - u(t)\|_E \le \bar{c} \|f - f_0\|_{C(D_m,\mathbb{R}^m)}$$

for all $t \in [n\omega, (n+k)\omega]$ and $\|u\|_E \le r$. Since (3.18) is an ω-periodic system, we have $\phi_0(n\omega + t, n\omega, u) = \phi_0(t, 0, u) = T(t)u$. Thus, for any $t \in [0, k\omega]$ and $\|u\| \le r$,

$$\begin{aligned}\|\phi(n\omega + t, n\omega, u) - T(t)u\|_\beta = & \|\phi(n\omega + t, n\omega, u) - \phi_0(n\omega + t, n\omega, u)\|_\beta \\ \le & \, \bar{c} \|f - f_0\|_{C(D_m,\mathbb{R}^m)} .\end{aligned}$$

It then follows that

$$\lim_{n\to\infty} (\phi(n\omega + t, n\omega, u) - T(t)u) = 0 \tag{3.19}$$

uniformly for $t \in [0, k\omega]$ and $\|u\| \le r$. For any $u \in E$, let $T_n(u) = \phi(n\omega, 0, u)$, $S_n(u) = \phi((n+1)\omega, n\omega, u)$, and $S(u) = T(\omega, u)$. Then (3.19) implies that

$$\lim_{n\to\infty} \|S_n(u) - S(u)\|_E = 0, \text{ uniformly for } \|u\| \le r.$$

For any $u \in E$, by the uniform boundedness of solutions of (3.17), there exists $r > 0$ such that $\|\phi(t,s,u)\|_E \le r$, $\forall t \ge s \ge 0$. Then $\|T_n(u)\|_E = \|\phi(n\omega, 0, u)\| \le r, n \ge 0$, and hence

$$\lim_{n\to\infty} \|T_{n+1}(u) - S(T_n(u))\|_E = \lim_{n\to\infty} \|S_n(T_n(u)) - S(T_n(u))\|_E = 0. \quad (3.20)$$

Since S is the Poincaré map of the periodic parabolic system (3.18), $S : E \to E$ is continuous and compact (see, e.g., [152, III.21]). Then $S(\gamma^+(u))$ is precompact in E, and hence (3.20) implies that $\gamma^+(u) = \{T_n(u) : n \ge 0\}$ is precompact in E.

For any $(t_0, u_0) \in \mathbb{R}_+ \times E$, let $k \in \mathbb{N}$, $k > 0$, and $r > 0$ be such that $t_0 \in [0, k\omega]$ and $\|u_0\| < r$. For any $t \in [0, k\omega]$ and $\|u\| \le r$,

$$\begin{aligned}
&\|\phi(t+n\omega, n\omega, u) - T(t_0)u_0\|_E \\
&\qquad \le \|\phi(t+n\omega, n\omega, u) - T(t)u\|_E + \|T(t)u - T(t_0)u_0)\|_E .
\end{aligned}$$

By (3.19) and the continuity of $T(t)u$ for $(t,u) \in \mathbb{R}_+ \times E$, it then follows that

$$\lim_{(t,u,n)\to(t_0,u_0,\infty)} \|\phi(t+n\omega, n\omega, u) - T(t_0)u_0\|_E = 0.$$

Thus, $\phi(t,s,u) : \Delta_0 \times E \to E$ is asymptotic to the ω-periodic semiflow $T(t) : E \to E$. ∎

We then consider systems of ordinary differential equations

$$\frac{du}{dt} = f(u,t), \quad u \in \mathbb{R}^m \quad (3.21)$$

and

$$\frac{du}{dt} = f_0(u,t), \quad u \in \mathbb{R}^m. \quad (3.22)$$

Assume that $f(u,t) : \mathbb{R}^m \times \mathbb{R}_+ \to \mathbb{R}^m$ is continuous and locally Lipschitz in u, and that $f_0(u,t) : \mathbb{R}^m \times \mathbb{R}_+ \to \mathbb{R}^m$ is continuous, ω-periodic in t, and locally Lipschitz in u uniformly for $t \in [0,\omega]$. Let $\phi(t,s,u)$ and $\phi_0(t,s,u)$ be the unique solutions of (3.21) and (3.22) with $\phi(s,s,u) = u$ and $\phi_0(s,s,u) = u\,(s \ge 0)$, respectively, and let $T(t)u = \phi_0(t,0,u)$, $t \ge 0$.

By a similar Gronwall's inequality argument as in Proposition 3.2.1, we can prove the following result.

Proposition 3.2.2. *Assume that*

(1) $\lim_{t\to\infty} |f(u,t) - f_0(u,t)| = 0$ *uniformly for u in any bounded subset of* $\mathbb{R}^m$*;*

(2) Solutions of (3.21) and (3.22) are uniformly bounded in $\mathbb{R}^m$*.*

Then for any $k \in \mathbb{N}, k > 0$, *and* $r > 0$,

$$\lim_{n\to\infty} |\phi(t+n\omega, n\omega, u) - T(t)u| = 0$$

uniformly for $t \in [0, k\omega]$ *and* $|u| \le r$, *and in particular,* $\phi : \Delta_0 \times \mathbb{R}^m \to \mathbb{R}^m$ *is asymptotic to the* ω*-periodic semiflow* $T(t) : \mathbb{R}^m \to \mathbb{R}^m$, $t \ge 0$.

For any $m \in C^{\theta,\frac{\theta}{2}}(\overline{Q}_\omega)$, let $\mu(A_i(t), m(x,t))$ be the principal eigenvalue of the periodic parabolic eigenvalue problem (see [152])

$$\begin{aligned} &\frac{\partial v}{\partial t} + A_i(t)v = m(x,t)v + \mu v \quad \text{in } \Omega \times \mathbb{R}, \\ &B_i v = 0 \quad \text{on } \partial\Omega \times \mathbb{R}, \\ &v \ \ \omega\text{-periodic in } t. \end{aligned} \tag{3.23}$$

The following result is useful in the applications of the theory of asymptotically periodic semiflows to asymptotically periodic parabolic systems.

Proposition 3.2.3. *Assume that conditions (1) and (2) of Proposition 3.2.1 with* $f_i = u_i G_i(x,t,u)$ *and* $f_i^0 = u_i G_i^0(x,t,u)$, $\forall 1 \le i \le m$, *hold. Let* $u^*(t) = (u_1^*(t), \dots, u_m^*(t))$ *be a nonnegative* ω*-periodic solution of (3.17) with* $u_k^*(t) \equiv 0$ *for some* $1 \le k \le m$. *If* $\mu(A_k(t), G_k^0(x,t,u^*(t))) < 0$, *then*

$$\widetilde{W}^s(u^*(0)) \cap X_0 = \emptyset,$$

where $X_0 = \{u \in P : u_i(\cdot) \not\equiv 0, \forall 1 \le i \le m\}$, *and* $\widetilde{W}^s(u^*(0))$ *is the stable set of* $u^*(0)$ *with respect to* $T_n = \phi(n\omega, 0, \cdot) : P \to P$, $n \ge 0$.

Proof. Assume, by contradiction, that there exists a $u_0 \in X_0 \cap \widetilde{W}^s(u^*(0))$, i.e., $u_0 \in X_0$, and $T_n(u_0) \to u^*(0)$ as $n \to \infty$. Then $u(t) := \phi(t, 0, u_0)$ satisfies $u(t) \gg 0$ for all $t > 0$, and by Theorem 3.2.1, $\lim_{t\to\infty} \|u(t) - u^*(t)\|_E = 0$. Thus, $\lim_{t\to\infty} \|u(t) - u^*(t)\|_{C(\overline{\Omega})} = 0$. Then there exists $M > 0$ such that $\|u(t)\|_{C(\overline{\Omega})} \le M$ and $\|u^*(t)\|_{C(\overline{\Omega})} \le M$, $\forall t \ge 0$. Since for all $x \in \Omega$ and $t \ge 0$,

$$\begin{aligned} |G_k(x,t,u(t)) - G_k^0(x,t,u^*(t))| \le\, &|G_k(x,t,u(t)) - G_k^0(x,t,u(t))| \\ &+ |G_k^0(x,t,u(t)) - G_k^0(x,t,u^*(t))|, \end{aligned}$$

it follows that $\lim_{t\to\infty} |G_k(x,t,u(t)) - G_k^0(x,t,u^*(t))|_{C(\overline{\Omega})} = 0$. By [152, Lemma 15.7], we can choose a sufficiently small positive number ϵ such that $\mu_\epsilon^{(k)} = \mu(A_k(t), G_k^0(x,t,u^*(t)) - \epsilon) < 0$. Then there exists $N = N(\epsilon) > 0$ such that $G_k(x,t,u(t)) \ge G_k^0(x,t,u^*(t)) - \epsilon$, $\forall x \in \Omega$, $t \ge N\omega$. Therefore, $u_k(t,x)$ satisfies

$$\frac{\partial u_k}{\partial t} + A_k(t)u_k \ge u_k\left(G_k^0(x,t,u^*(t)) - \epsilon\right) > u_k\left(G_k^0(x,t,u^*(t)) - \epsilon\right) + \mu_\epsilon^{(k)} u_k,$$

for all $x \in \Omega$ and $t \ge N\omega$. Let $\varphi_k \gg 0$ be the principal eigenfunction corresponding to $\mu_\epsilon^{(k)}$; that is, φ_k satisfies

$$\frac{\partial \varphi_k}{\partial t} + A_k(t)\varphi_k = \varphi_k(G_k^0(x,t,u^*(t)) - \epsilon) + \mu_\epsilon^{(k)}\varphi_k \quad \text{in } \Omega \times (0,\infty),$$
$$B_k\varphi_k = 0 \quad \text{on } \partial\Omega \times (0,\infty),$$
$$\varphi_k \quad \omega\text{-periodic in } t.$$

Since $u_k(N\omega) \gg 0$ in E_k, there exists $\delta = \delta(\epsilon, u_0) > 0$ such that $u_k(N\omega) \geq \delta\varphi_k(N\omega, \cdot) = \delta\varphi(0, \cdot)$. By the standard comparison theorem, we then get

$$u_k(t) \geq \delta\varphi_k(t, \cdot), \quad \forall t \geq N\omega.$$

In particular, $u_k(n\omega) \geq \delta\varphi(0, \cdot)$, $\forall n \geq N$, which contradicts the assumption that $\lim_{n\to\infty} u_k(n\omega) = 0$ in E_k. ∎

As an illustration we discuss the global dynamics of a scalar nonautonomous parabolic Kolmogorov equation

$$\begin{aligned} \frac{\partial u}{\partial t} + A(t)u = uF(x,t,u) \quad &\text{in } \Omega \times (0,\infty), \\ Bu = 0 \quad &\text{on } \partial\Omega \times (0,\infty), \end{aligned} \tag{3.24}$$

which is asymptotic to the periodic parabolic equation

$$\begin{aligned} \frac{\partial u}{\partial t} + A(t)u = uF_0(x,t,u) \quad &\text{in } \Omega \times (0,\infty), \\ Bu = 0 \quad &\text{on } \partial\Omega \times (0,\infty), \end{aligned} \tag{3.25}$$

where $A(t)$, B and Ω satisfy the same conditions as A_i, B_i, and Ω in (3.17); F_0 is ω-periodic for some $\omega > 0$; and F and F_0 satisfy the smoothness condition (H). We assume that

(H1) $\lim_{t\to\infty} |F(x,t,u) - F_0(x,t,u)| = 0$ uniformly for $x \in \overline{\Omega}$ and u in any bounded subset of $\mathbb{R}^+$, and there exists $K > 0$ such that $F(x,t,u) \leq 0$ for all $(x,t) \in \overline{\Omega} \times \mathbb{R}_+$ and $u \geq K$;
(H2) For each $(x,t) \in \overline{Q}_\omega$, $F_0(x,t,u)$ is nonincreasing for u, and for at least one $(x_0,t_0) \in Q_\omega$, $F_0(x_0,t_0,u)$ is strictly nonincreasing for u, and there exists $K_0 > 0$ such that $F_0(x,t,K_0) \leq 0$ for all $(x,t) \in \overline{Q}_\omega$.

Let $(X_\beta, \|\cdot\|_\beta)$ be the Banach space defined in Section 3.1. For any $u \in X_\beta^+$ and $s \geq 0$, let $\phi(t,s,u)$ and $\phi_0(t,s,u)$ be the unique solutions of (3.24) and (3.25) with $\phi(s,s,u) = u$ and $\phi_0(s,s,u) = u$, respectively. Then we have the following threshold-type result.

Theorem 3.2.2. *Assume that (H1) and (H2) hold. Then the following statements are valid:*

(a) If $\mu(A(t), F_0(x,t,0)) \geq 0$, *then* $\lim_{t\to\infty} \|\phi(t,0,u_0)\|_\beta = 0$, $\forall u_0 \in X_\beta^+$;
(b) If $\mu(A(t), F_0(x,t,0)) < 0$, *then* $\lim_{t\to\infty} \|\phi(t,0,u_0) - u^*(t)\|_\beta = 0$, $\forall u_0 \in X_\beta^+ \setminus \{0\}$, *where* $u^*(t)$ *is the unique positive* ω*-periodic solution of (3.25).*

Proof. By conditions (H1) and (H2), it is easy to see that for any $s \geq 0$, $\phi(t,s,u)$ and $\phi_0(t,s,u)$ exist globally on $[s,\infty)$ and are uniformly bounded in X_β^+. Let $T_n(u) := \phi(n\omega,0,u)$, $\forall u \in X_\beta^+$, $n \geq 0$. By Proposition 3.2.1, it follows that $\phi(t,s,u)$ is asymptotic to an ω-periodic semiflow $T(t)u = \phi_0(t,0,u)$, $t \geq 0$, in X_β^+, and for any $u \in X_\beta^+$, $\gamma^+(u) = \{T_n(u) : n \geq 0\}$ is precompact in X_β^+, and hence its omega limit set $\omega(u)$ exists. By Theorem 3.2.1, it suffices to prove that $\lim_{n\to\infty} T_n(u) = 0$ for any $u \in X_\beta^+$ in case (a), and $\lim_{n\to\infty} T_n(u) = u^*(0)$ for any $u \in X_\beta^+ \setminus \{0\}$ in case (b), respectively. Note that $T_n : X_\beta^+ \to X_\beta^+, n \geq 0$, is an asymptotically autonomous discrete process with limit discrete semiflow $S^n : X_\beta^+ \to X_\beta^+, n \geq 0$, where $S = T(\omega)$ is the Poincaré map associated with the periodic equation (3.25).

In the case where $\mu(A(t), F_0(x,t,0)) \geq 0$, Theorem 3.1.5 implies that $u = 0$ is a globally asymptotically stable fixed point of S, and then $W^s(0) = X_\beta^+$, where $W^s(0)$ is the stable set of 0 for S in X_β^+. For any $u \in X_\beta^+$, $\omega(u)$ is a chain transitive set for $S : X_\beta^+ \to X_\beta^+$ (see Lemma 1.2.2). Clearly, $\omega(u) \cap X_\beta^+ \neq \emptyset$. Then Theorem 1.2.1 implies that $\omega(u) = 0$, and hence $\lim_{n\to\infty} T_n(u) = 0$.

In the case where $\mu(A(t), F_0(x,t,0)) < 0$, Theorem 3.1.5 implies that $u = u^*(0)$ is a globally asymptotically stable fixed point of S in $X_\beta^+ \setminus \{0\}$, and hence $W^s(u^*(0)) = X_\beta^+ \setminus \{0\}$, where $W^s(u^*(0))$ is the stable set of $u^*(0)$ for S. By Proposition 3.2.3, we get $\widetilde{W^s}(0) \cap (X_\beta^+ \setminus \{0\}) = \emptyset$. Thus, for any $u \in X_\beta^+ \setminus \{0\}$, we have $\omega(u) \cap (X_\beta^+ \setminus \{0\}) \neq \emptyset$; that is, $\omega(u) \cap W^s(u^*(0)) \neq \emptyset$. By Theorem 1.2.1, it follows that for any $u \in X_\beta^+ \setminus \{0\}$, $\omega(u) = u^*(0)$, and hence $\lim_{n\to\infty} \|T_n(u) - u^*(0)\|_\beta = 0$. ∎

Finally, we apply Theorem 3.2.2 to a periodic mutualism parabolic system.

Example 3.2.1. Consider 2-species periodic mutualism parabolic systems

$$\begin{aligned} &\frac{\partial u_1}{\partial t} + A_1(t)u_1 = u_1 G_1(x,t,u_1) \quad \text{in } \Omega \times (0,+\infty), \\ &\frac{\partial u_2}{\partial t} + A_2(t)u_2 = u_2 G_2(x,t,u_1,u_2) \quad \text{in } \Omega \times (0,+\infty), \\ &B_1 u_1 = B_2 u_2 = 0 \quad \text{on } \partial\Omega \times (0,+\infty), \end{aligned} \tag{3.26}$$

where $A_i(t)$, B_i, and Ω are as in (3.17), and $G = (G_1, G_2)$ is ω-periodic in t and satisfies (H) with $m = 2$ and the following conditions:

(H3) $\frac{\partial G_1}{\partial u_1} < 0$, $\forall (x,t,u_1) \in \overline{Q}_\omega \times \mathbb{R}_+$, and there exists $K_1 > 0$ such that $G_1(x,t,K_1) \leq 0$, $\forall (x,t) \in \overline{Q}_\omega$;
(H4) $\frac{\partial G_2}{\partial u_1} \geq 0$ and $\frac{\partial G_2}{\partial u_2} < 0$, $\forall (x,t,u_1,u_2) \in \overline{Q}_\omega \times \mathbb{R}_+^2$, and for each $u_1 > 0$, there exists $K_2 = K_2(u_1) > 0$ such that $G_2(x,t,u_1,K_2) \leq 0$, $\forall (x,t) \in \overline{Q}_\omega$.

Let $E_i = X_\beta^{(i)}$, $\dot{P}_i = P_i \setminus \{0\}$, $1 \leq i \leq 2$, and let $\varphi(t,u)$ be the unique solution of (3.26) satisfying $\varphi(0,u) = u \in P_1 \times P_2$. Then we have the following result.

Proposition 3.2.4. *Let (H3) and (H4) hold. Assume that*

(H5) $\mu(A_1(t), G_1(x,t,0,0)) < 0$ *and* $\mu(A_2(t), G_2(x,t,u_1^*(x,t),0)) < 0$*, where* $u_1^*(x,t)$ *is the unique positive* ω*-periodic solution of the scalar periodic equation* $\frac{\partial u_1}{\partial t} + A_1(t)u_1 = u_1 G_1(x,t,u_1)$ *with* $B_1 u_1 = 0$.

Then for any $u \in \dot{P}_1 \times \dot{P}_2$, $\lim_{t\to\infty} ||\varphi(t,u) - (u_1^*(t), \overline{u}_2(t))||_E = 0$*, where* $u_1^*(t)(x) = u_1^*(x,t)$ *and* $\overline{u}_2(t)(x) = \overline{u}_2(x,t)$ *is the unique positive* ω*-periodic solution of the scalar periodic equation* $\frac{\partial u_2}{\partial t} + A_2(t)u_2 = u_2 G_2(x,t,u_1^*(x,t),u_2)$ *with* $B_2 u_2 = 0$.

Proof. Clearly, the existence and uniqueness of $u_1^*(t)$ and $\overline{u}_2(t)$ are guaranteed by Theorem 3.1.5. Let $X = P_1 \times P_2$, $X_0 = \{u = (u_1, u_2) \in X : u_i(\cdot) \not\equiv 0, \forall 1 \le i \le 2\}$, and $\partial X_0 = X \setminus X_0$. By assumptions (H3) and (H4) and a standard comparison argument, it easily follows that for any $u \in X$, the unique solution $\varphi(t,u)$ of (3.26) exists globally on $[0, +\infty)$.

By the continuous dependence of $\mu(A(t), m(x,t))$ on $m(x,t)$ ([152, Lemma 15.7]), we can choose a sufficiently small $\epsilon_0 > 0$ such that

$$\mu(A_2(t),\ G_2(x,t,u_1^*(x,t)+\epsilon_0, 0) < 0.$$

For any $u \in X$, let $\varphi(t,u)(x) = (u_1(x,t), u_2(x,t))$. By Theorem 3.1.5, together with $E_1 \hookrightarrow C(\Omega)$, it follows that there exists $T_1 > 0$ such that $u_1(x,t) \le u_1^*(x,t) + \epsilon_0$ for $t \ge T_1$. Then $u_2(x,t)$ satisfies

$$\frac{\partial u_2}{\partial t} + A_2(t)u_2 \le u_2 G_2(x,t,u_1^*(x,t)+\epsilon_0, u_2), \quad \forall t \ge T_1.$$

Let $U_2(t)$ be the solution of

$$\begin{aligned} &\frac{\partial U_2}{\partial t} + A_2(t)U_2 = U_2 G_2(x,t,u_1^*(x,t)+\epsilon_0, U_2) \quad \text{in } \Omega \times (T_1, +\infty), \\ &B_2 U_2 = 0 \quad \text{on } \partial\Omega \times (T_1, +\infty), \end{aligned} \tag{3.27}$$

with $U_2(T_1) = u_2(T_1)$. By the comparison theorem, we get

$$u_2(t) \le U_2(t), \quad \forall t \ge T_1.$$

By Theorem 3.1.5, $U_2(t)$ converges to the unique positive ω-periodic solution $U_2^*(t)$ of (3.27). Then there exists $M > 0$ such that for any $u \in X$, there is $t_0 = t_0(u) > 0$ such that $\varphi(t,u)(x) = (u_1(x,t), u_2(x,t))$ satisfies

$$0 \le u_i(x,t) \le M, \quad \forall t \ge t_0,\ x \in \overline{\Omega},\ 1 \le i \le 2.$$

By a standard argument, it follows that there exists $B > 0$ such that for any $u \in X$, there is $t_0 = t_0(u) > 0$ such that

$$||\varphi(t,u)||_E = ||u_1(t)||_{E_1} + ||u_2(t)||_{E_2} \le B, \quad \forall t \ge t_0.$$

Consequently, $\varphi(t,\cdot) : X \to X$ is point dissipative.

For any given $u \in \dot{P}_1 \times \dot{P}_2$, let $(u_1(x,t), u_2(x,t)) = \varphi(t,u)(x)$. Then $u_2(x,t)$ satisfies the nonautonomous parabolic equation

$$\begin{aligned} &\frac{\partial u_2}{\partial t} + A_2(t)u_2 = u_2 G_2(x,t,u_1(x,t),u_2) \quad \text{in } \Omega \times (0,+\infty), \\ &B_2 u_2 = 0 \quad \text{on } \partial\Omega \times (0,+\infty). \end{aligned} \tag{3.28}$$

Since $\lim_{t\to\infty} \|u_1(\cdot,t) - u_1^*(\cdot,t)\|_{E_1} = 0$, equation (3.28) is asymptotic to the following periodic equation:

$$\begin{aligned} &\frac{\partial u_2}{\partial t} + A_2(t)u_2 = u_2 G_2(x,t,u_1^*(x,t),u_2) \quad \text{in } \Omega \times (0,+\infty), \\ &B_2 u_2 = 0 \quad \text{on } \partial\Omega \times (0,+\infty). \end{aligned} \tag{3.29}$$

Thus, Theorem 3.2.2 (b) implies that $\lim_{t\to\infty} \|u_2(\cdot,t) - \bar{u}_2^*(t)\|_{E_2} = 0$. ∎

3.3 Monotone and Subhomogeneous Almost Periodic Systems

In this section we discuss global dynamics in monotone and subhomogeneous almost periodic ordinary differential systems, delay differential equations, and reaction–diffusion equations. We start with some basic definitions.

Let (X,d) be a metric space. A function $f \in C(\mathbb{R}, X)$ is said to be almost periodic if for any $\epsilon > 0$, there exists $l = l(\epsilon) > 0$ such that every interval of $\mathbb{R}$ of length l contains at least one point of the set $T(\epsilon) := \{\tau \in \mathbb{R} : d(f(t+\tau), f(t)) < \epsilon, \forall t \in \mathbb{R}\}$. Let $D \subset \mathbb{R}^m$. A function $f \in C(\mathbb{R} \times D, X)$ is said to be uniformly almost periodic in t if $f(\cdot,x)$ is almost periodic for each $x \in D$, and for any compact set $E \subset D$, f is uniformly continuous on $\mathbb{R} \times E$.

A point $x \in X$ is said to be an almost periodic point of an autonomous flow $\Phi : X \times \mathbb{R} \to X$ if $\Phi(x,\cdot) : \mathbb{R} \to X$ is almost periodic. In this case, the full orbit $\gamma(x) := \{\Phi(x,t) : t \in \mathbb{R}\}$ is called an almost periodic orbit of Φ. A compact minimal flow $\sigma : Y \times \mathbb{R} \to Y$ is said to be almost periodic if it admits an almost periodic orbit that is dense in Y. Note that if $\sigma : Y \times \mathbb{R} \to Y$ is a compact, almost periodic minimal flow, then every point in Y is an almost periodic point of σ (see [303, Lemma VI.9]).

First we consider almost periodic ordinary differential systems

$$\begin{aligned} \frac{du}{dt} &= f(t,u), \quad t > 0, \\ u(0) &= v \in \mathbb{R}^n_+, \end{aligned} \tag{3.30}$$

where $u = (u_1, \ldots, u_n) \in \mathbb{R}^n$. We assume that

(C1) $f(t,u) \in C^1(\mathbb{R} \times \mathbb{R}^n_+, \mathbb{R}^n)$ is uniformly almost periodic in t, and $\partial f_i / \partial u_j \geq 0$, $\forall (t,u) \in \mathbb{R}^{n+1}_+$, $i \neq j$;

(C2) $f(\cdot, 0) \equiv 0$, and for each $1 \le i \le n$, $f_i(t,u) \ge 0, \forall (t,u) \in \mathbb{R}_+^{n+1}$ with $u_i = 0$;

(C3) The Jacobian matrix $D_u f(t,u)$ is irreducible, $\forall (t,u) \in \mathbb{R}_+^{n+1}$, and $f(t,\cdot)$ is strictly subhomogeneous on $\mathbb{R}_+^n$, $\forall t \in \mathbb{R}_+$.

A simple example for such $f(t,u)$ with $n = 2$ is the function

$$(f_1(t,u_1,u_2), f_2(t,u_1,u_2)) := \left(-a_{11}(t)u_1 + a_{12}(t)u_2,\ \frac{m(t)u_1}{a_{21}(t) + u_1} - a_{22}u_2 \right),$$

where $a_{ij}(t)$, $1 \le i,j \le 2$, and $m(t)$ are positive almost periodic functions. The resulting system is a special case of the almost periodic version of an epidemic model with positive feedback in [55].

Theorem 3.3.1. (Global attractor) *Let (C1), (C2), and (C3) hold. Then each solution $u(t,v)$ of (3.30) exists globally on $[0,\infty)$. If (3.30) admits a bounded solution $u(t,v^0) = (u_1(t,v^0),\dots,u_n(t,v^0))$ such that $\liminf_{t\to\infty} u_i(t,v^0) > 0$, $\forall 1 \le i \le n$, then there exists a unique positive almost periodic solution $u^*(t)$ of (3.30), and $\lim_{t\to\infty} |u(t,v) - u^*(t)| = 0, \forall v \in \mathbb{R}_+^n \setminus \{0\}$.*

Proof. Let $H(f)$ be the closure of all time translates of f under the compact open topology on $C(\mathbb{R} \times \mathbb{R}_+, \mathbb{R})$. Define $\sigma(t)g = g_t$, $g \in H(f)$, $t \in \mathbb{R}$. Then $\sigma(t) : H(f) \to H(f)$ is a compact, almost periodic minimal and distal flow (see [303, Section VI.C]). For each $(v,g) \in \mathbb{R}_+^n \times H(f)$, let $u(t,v,g)$ be the unique solution of (3.30) with f replaced by g. Let $A(t) = D_u f(t,0)$. Thus assumption (C3) implies that $f(t,u) \le A(t)u, \forall (t,u) \in \mathbb{R}_+^{n+1}$. By (C1), (C2), and the comparison theorem for cooperative systems (see, e.g., [326, Proposition 3.1.1 and Remark 3.1.2]), each $u(t,v,g)$ exists globally on $[0,\infty)$ and $u(t,v,g) \ge 0, \forall t \ge 0$. We define the skew-product semiflow $\Pi_t : \mathbb{R}_+^n \times H(f) \to \mathbb{R}_+^n \times H(f)$ by $\Pi_t(v,g) = (u(t,v,g), g_t)$. By the comparison theorem for irreducible cooperative systems (see, e.g., [326, Theorem 4.1.1]) and the variation of constants formula for inhomogeneous linear systems, it then follows that $u(t,\cdot,g)$ is monotone and subhomogeneous on $\mathbb{R}_+^n$, $\forall (t,g) \in \mathbb{R}_+ \times H(f)$, and $u(t,\cdot,f_s)$ is strongly monotone and strictly subhomogeneous on $\mathbb{R}_+^n$, $\forall t > 0$ and $s \ge 0$ (see, e.g., [432, 444]). Thus $(A1)'$ and $(A2)''$ in Remarks 2.3.2 and 2.3.3 hold for the skew-product semiflow Π_t on $\mathbb{R}_+^n \times H(f)$. By our assumption, the omega limit set $\omega(v^0, f)$ is compact and $\omega(v^0,f) \subset \operatorname{int}(\mathbb{R}_+^n) \times H(f)$. By Theorem 2.3.5, $\Pi_t : \omega(v^0,f) \to \omega(v^0,f)$ extends to a compact, almost periodic minimal and distal flow, and hence $u(t,v^*,f)$ is almost periodic in t (see [303, Lemma VI.9]), where $(v^*,f) \in \omega(v^0,f)$. Clearly, $u(t,v^*,f) \gg 0, \forall t \in \mathbb{R}$. By assumption (C3), it is easy to verify that for each $\epsilon \in (0,1)$, $\epsilon u(t,v^*,f)$ and $\epsilon^{-1}u(t,v^*,f)$ are sub- and super-solutions of (3.30), respectively. Fix $t_0 > 0$. For any $v \in \mathbb{R}_+^n \setminus \{0\}$, since $u(t_0,v,f) \gg 0$, we can choose a sufficiently small $\epsilon_0 \in (0,1)$ such that $\epsilon_0 u(t_0,v^*,f) \le u(t_0,v,f) \le \epsilon_0^{-1} u(t_0,v^*,f)$. By the comparison theorem, it then follows that

$$\epsilon_0 u(t, v^*, f) \leq u(t, v, f) \leq \epsilon_0^{-1} u(t, v^*, f), \quad \forall t \geq t_0.$$

Thus, $u(t, v, f)$ is bounded and $\omega(v, f) \subset \mathrm{int}(\mathbb{R}^n_+) \times H(f)$. Again by Theorem 2.3.5, we then get $\lim_{t\to\infty} |u(t, v, f) - u(t, v^*, f))| = 0$. ∎

Remark 3.3.1. The conclusion of Theorem 3.3.1 is valid for all $v \in \mathrm{int}(\mathbb{R}^n_+)$ if we replace assumption (C3) by the following one:

(C3)′ $f(t, \cdot)$ is strongly subhomogeneous on $\mathbb{R}^n_+$, $\forall t \in \mathbb{R}_+$.

Indeed, for any $v \gg 0$, [326, Proposition 3.1.1 and Remark 3.1.2] imply that $u(t, v, f) \gg 0$, $\forall t \geq 0$. By the variation of constants formula and the fact that

$$f(t, \lambda u(t, v, f)) - \lambda f(t, u(t, v, f)) \gg 0,\ \forall t \geq 0,\ \lambda \in (0, 1),$$

it follows that $u(t, \cdot, f)$ is strongly subhomogeneous on $\mathbb{R}^n_+$ for each $t > 0$. Thus, $(A1)'$ and $(A2)'$ in Remark 2.3.2 hold for the skew-product semiflow Π_t. Letting $t_0 = 0$ in the proof of Theorem 3.3.1, we then get the same conclusion for all $v \in \mathrm{int}(\mathbb{R}^n_+)$.

One can easily apply Theorem 3.3.1 and Remark 3.3.1 to the almost periodic versions of general epidemic models with positive feedback in [55], single species discrete diffusion systems in [237], and periodic single species models of dispersal in a patchy environment in [119] to get some reasonable conditions for the existence and global attractivity of positive almost periodic solutions.

Next we consider the almost periodic delay differential equations

$$\begin{aligned} \frac{du(t)}{dt} &= f(t, u(t), u(t-\tau)), \quad t > 0, \\ u(s) &= \phi(s),\ \forall s \in [-\tau, 0], \end{aligned} \tag{3.31}$$

where $\tau > 0$, $u \in \mathbb{R}$, and $\phi \in C^+ := C([-\tau, 0], \mathbb{R}_+)$. We assume that

(D1) $f(t, u, v) \in C^1(\mathbb{R} \times \mathbb{R}^2_+, \mathbb{R})$ is uniformly almost periodic in t, and $f'_v(t, u, v) \geq 0$, $\forall (t, u, v) \in \mathbb{R}^3_+$;
(D2) $f(\cdot, 0, 0) \equiv 0$, and $f(t, 0, v) \geq 0$, $\forall (t, v) \in \mathbb{R}^2_+$;
(D3) For each $t \in \mathbb{R}_+$, $f(t, \cdot) : \mathbb{R}^2_+ \to \mathbb{R}$ is strictly subhomogeneous.

A simple example for such $f(t, u, v)$ is the function $\alpha(t)v - \beta(t)u^2$, where $\alpha(t)$ and $\beta(t)$ are two positive almost periodic functions. The resulting equation is an almost periodic version of the autonomous equation for a single species at the mature stage in a time-delay model of single species growth with stage structure introduced by Aiello and Freedman [4].

Theorem 3.3.2. (Global attractor) *Let (D1), (D2), and (D3) hold. Then each solution $u(t, \phi)$ of (3.31) exists globally on $[0, \infty)$. If (3.31) admits a bounded solution $u(t, \phi^0)$ such that $\liminf_{t\to\infty} u(t, \phi^0) > 0$, then there exists a unique positive almost periodic solution $u^*(t)$ of (3.31), and $\lim_{t\to\infty} |u(t, \phi) - u^*(t)| = 0, \forall \phi \in C^+$ with $\phi(0) > 0$.*

Proof. Let $H(f)$ be the closure of all time translates of f under the compact open topology on $C(\mathbb{R} \times \mathbb{R}^2_+, \mathbb{R})$. Define $\sigma(t)g = g_t$, $g \in H(f)$, $t \in \mathbb{R}$. Then $\sigma(t) : H(f) \to H(f)$ is a compact, almost periodic minimal and distal flow (see [303, Section VI.C]). For each $(\phi, g) \in C^+ \times H(f)$, let $u(t, \phi, g)$ be the unique solution of (3.31) with f replaced by g. Let $a(t) = f'_u(t, 0, 0)$ and $b(t) = f'_v(t, 0, 0)$. Thus assumption (D3) implies that $f(t, u, v) \leq a(t)u + b(t)v$, $\forall (t, u, v) \in \mathbb{R}^3_+$. By (D1), (D2), the comparison theorem for cooperative delay differential equations ([326, Theorem 5.1.1]), and the positivity theorem ([326, Theorem 5.2.1]), each $u(t, \phi, g)$ exists globally on $[0, \infty)$, and $u(t, \phi, g) \geq 0$, $\forall t \geq 0$. We define the skew-product semiflow $\Pi_t : C^+ \times H(f) \to C^+ \times H(f)$ by $\Pi_t(\phi, g) = (u_t(\phi, g), g_t)$, where $u_t(\phi, g)(s) = u(t+s, \phi, g)$, $\forall s \in [-\tau, 0]$. By the comparison theorem and the variation of constants formula for inhomogeneous linear systems, it then follows that $u_t(\cdot, g)$ is monotone and subhomogeneous on $C^+, \forall (t, g) \in \mathbb{R}_+ \times H(f)$ (see, e.g., [444]). For each $\phi \in C^+$ with $\phi(0) > 0$, $u(t, \phi, f)$ satisfies the following differential inequality:

$$\begin{aligned} \frac{du(t)}{dt} &= f(t, u(t), u(t-\tau)) \geq f(t, u(t), 0), \quad t > 0, \\ u(0) &= \phi(0) > 0. \end{aligned}$$

Then the standard comparison theorem implies that $u(t, \phi, f) > 0$, $\forall t \geq 0$, and hence $u_t(\phi, f) \gg 0$, $\forall t \geq \tau$. We further claim that $u_t(\cdot, f)$ is strongly subhomogeneous on C^+, $\forall t > \tau$. Indeed, let $\phi \gg 0$ and $\lambda \in (0, 1)$ be fixed, and let $w(t) = u(t, \lambda\phi, f) - \lambda u(t, \phi, f)$. Then $u(t, \phi, f) > 0$, $u(t, \lambda\phi, f) > 0$, and $w(t) \geq 0$, $\forall t \geq -\tau$. Let

$$\begin{aligned} c(t, s) &= s u(t, \lambda\phi, f) + (1-s)\lambda u(t, \phi, f), \\ \tilde{a}(t) &= \int_0^1 f'_u(t, c(t, s), c(t-\tau, s)) ds, \\ \tilde{b}(t) &= \int_0^1 f'_v(t, c(t, s), c(t-\tau, s)) ds, \end{aligned}$$

and

$$h(t) = f(t, \lambda u(t, \phi, f), \lambda u(t-\tau, \phi, f)) - \lambda f(t, u(t, \phi, f), u(t-\tau, \phi, f)).$$

Then $\tilde{b}(t) \geq 0$ and $h(t) > 0$, $\forall t \geq 0$. It easily follows that $w(t)$ satisfies the following differential inequality:

$$\begin{aligned} \frac{dw(t)}{dt} &= \tilde{a}(t)w(t) + \tilde{b}(t)w(t-\tau) + h(t) \geq \tilde{a}(t)w(t) + h(t), \quad t > 0, \\ w(0) &= 0. \end{aligned}$$

Thus $w(t) \geq \int_0^t e^{\int_s^t \tilde{a}(\theta)d\theta} h(s) ds > 0$, $\forall t > 0$, and hence

$$w_t = u_t(\lambda\phi, f) - \lambda u_t(\phi, f) \gg 0, \ \forall t > \tau.$$

Therefore, $(A1)'$ and $(A2)'$ in Remark 2.3.2 hold for the skew-product semiflow Π_t on $C^+ \times H(f)$. By our assumption, the omega limit set $\omega(\phi^0, f)$ is compact and $\omega(\phi^0, f) \subset \mathrm{int}(C^+) \times H(f)$. By Theorem 2.3.5, $\Pi_t : \omega(\phi^0, f) \to \omega(\phi^0, f)$ extends to a compact, almost periodic minimal and distal flow, and hence $u_t(\phi^*, f)$ is almost periodic in t (see [303, Lemma VI.9]), where $(\phi^*, f) \in \omega(\phi^0, f)$. Clearly, $u(t, \phi^*, f) > 0, \forall t \in \mathbb{R}$. By assumption (D3), it is easy to verify that for each $\epsilon \in (0,1)$, $\epsilon u(t, \phi^*, f)$ and $\epsilon^{-1} u(t, \phi^*, f)$ are sub- and super-solutions of (3.31), respectively. Fix a $t_0 \geq \tau$. For any $\phi \in C^+$ with $\phi(0) > 0$, since $u_{t_0}(\phi, f) \gg 0$, we can choose a sufficiently small $\epsilon_0 \in (0,1)$ such that

$$\epsilon_0 u(s, \phi^*, f) \leq u(s, \phi, f) \leq \epsilon_0^{-1} u(s, \phi^*, f),\ \forall s \in [t_0 - \tau, t_0].$$

By the comparison theorem ([326, Theorem 5.1.1]), it then follows that

$$\epsilon_0 u(t, \phi^*, f) \leq u(t, \phi, f) \leq \epsilon_0^{-1} u(t, \phi^*, f), \quad \forall t \geq t_0.$$

Thus $u(t, \phi, f)$ is bounded, and $\omega(\phi, f) \subset \mathrm{int}(C^+) \times H(f)$. Again by Theorem 2.3.5, we then get $\lim_{t\to\infty} \|u_t(\phi, f) - u_t(\phi^*, f))\| = 0$. ∎

Let the integer $N > 0$ and the real number $\theta > 0$ be fixed. Let Ω be a bounded and open subset of $\mathbb{R}^N$ with $\partial\Omega \in C^{2+\theta}$. We use $\frac{\partial}{\partial n}$ to denote differentiation in the direction of the outward normal n to $\partial\Omega$, and Δ to denote the Laplacian operator on $\mathbb{R}^N$. Let $d(\cdot) \in C(\mathbb{R}, \mathbb{R})$ be an almost periodic function bounded below by a positive real number, let $m(\cdot) \in C^{\theta,\theta/2}(\overline{\Omega} \times \mathbb{R}, \mathbb{R})$ be such that $m(x,t)$ is uniformly almost periodic in t, and let $H(d,m)$ be the closure of $\{(d_s, m_s) : s \in \mathbb{R}\}$ under the compact open topology, where $(d_s, m_s) \in C(\mathbb{R}, \mathbb{R}) \times C(\overline{\Omega} \times \mathbb{R}, \mathbb{R})$ is defined by

$$d_s(t) = d(s+t),\ m_s(x,t) = m(x, t+s),\ \forall x \in \overline{\Omega},\ t \in \mathbb{R}.$$

According to [188], there exists a unique principal spectrum point $\lambda(d(\cdot), m(\cdot))$ associated with the linear almost periodic parabolic problem

$$\begin{aligned} &\frac{\partial v}{\partial t} = d(t)\Delta v + m(x,t)v, \quad x \in \overline{\Omega},\ t \in \mathbb{R}, \\ &Bv = 0, \quad x \in \partial\Omega,\ t \in \mathbb{R}, \end{aligned} \tag{3.32}$$

where either $Bv = v$ or $Bv = \frac{\partial v}{\partial n} + \alpha v$ for some nonnegative function $\alpha \in C^{1+\theta}(\partial\Omega, \mathbb{R})$. Moreover, for each $(\mu, k) \in H(d,m)$, there exists an almost periodic function $a(t; \mu, k)$ such that

$$\lambda(d,m) = \lim_{t\to\infty} \frac{1}{t} \int_0^t a(s; \mu, k) ds$$

and the linear almost periodic parabolic problem

$$\begin{aligned} &\frac{\partial \varphi}{\partial t} = \mu(t)\Delta\varphi + k(x,t)\varphi - a(t;\mu,k)\varphi, \quad x \in \overline{\Omega},\, t \in \mathbb{R}, \\ &B\varphi = 0, \quad x \in \partial\Omega,\, t \in \mathbb{R}, \end{aligned} \tag{3.33}$$

admits a positive solution $\varphi(x,t;\mu,k)$ that is uniformly almost periodic in t. It is easy to verify that $v = e^{\int_0^t a(s;\mu,k)ds}\varphi(x,t;\mu,k)$ is a solution of (3.32) with $d(t)$ and $m(x,t)$ replaced by $\mu(t)$ and $k(x,t)$, respectively.

Finally, we consider the scalar almost periodic Kolmogorov-type parabolic equations

$$\begin{aligned} &\frac{\partial u}{\partial t} = d(t)\Delta u + uf(x,t,u) \quad \text{ in } \Omega \times (0,\infty) \\ &Bu = 0 \quad \text{ on } \partial\Omega \times (0,\infty). \end{aligned} \tag{3.34}$$

We assume that

(E1) $d(\cdot) \in C(\mathbb{R},\mathbb{R})$ is almost periodic, and for some $d_0 > 0$, $d(t) \geq d_0$, $\forall t \in \mathbb{R}$;
(E2) $f(x,t,u) \in C^2(\overline{\Omega} \times \mathbb{R} \times \mathbb{R}_+, \mathbb{R})$ is uniformly almost periodic in t, and $f'_u(x,t,u) < 0$, $\forall (x,t,u) \in \overline{\Omega} \times \mathbb{R} \times \mathbb{R}_+$;
(E3) There exists $M_0 > 0$ such that $f(x,t,M_0) < 0$, $\forall (x,t) \in \overline{\Omega} \times \mathbb{R}$.

A simple example for such $f(x,t,u)$ is the function $b(x,t) - a(x,t)u$, where $a(x,t)$ and $b(x,t)$ are uniformly almost periodic in t, and $a(x,t) > 0$. Then the resulting equation is the almost periodic logistic reaction–diffusion model.

Let $p \in (N,\infty)$ be fixed. For each $\beta \in (1/2 + N/(2p), 1)$, let X_β be the fractional power space of $X = L^p(\Omega)$ with respect to $(-\Delta, B)$ (see, e.g., [150]). Then X_β is an ordered Banach space with the cone X_β^+ consisting of all nonnegative functions in X_β, and X_β^+ has nonempty interior $\operatorname{int}(X_\beta^+)$. Moreover, $X_\beta \subset C^{1+\nu}(\overline{\Omega})$ with continuous inclusion for $\nu \in [0, 2\beta - 1 - N/p)$. We denote the norm in X_β by $\|\cdot\|_\beta$.

Let $H(d,f)$ be the closure of $\{(d_s,f_s) : s \in \mathbb{R}\}$ under the compact open topology, where $(d_s,f_s) \in C(\mathbb{R},\mathbb{R}) \times C(\overline{\Omega} \times \mathbb{R} \times \mathbb{R}_+, \mathbb{R})$ is defined by

$$d_s(t) = d(s+t),\ f_s(x,t,u) = f(x,t+s,u),\ \forall (x,t,u) \in \overline{\Omega} \times \mathbb{R} \times \mathbb{R}_+.$$

Define $\sigma(t)(\mu,g) = (\mu_t, g_t)$, $(\mu,g) \in H(d,f), t \in \mathbb{R}$. Then $\sigma(t) : H(d,f) \to H(d,f)$ is a compact, almost periodic minimal and distal flow (see [303, Section VI.C]).

By the theory of semilinear parabolic differential equations (see, e.g., [152, Section III.20]), it follows that for every $\phi \in X_\beta^+$ and $(\mu,g) \in H(d,f)$, the parabolic problem

$$\begin{aligned} &\frac{\partial u}{\partial t} = \mu(t)\Delta u + ug(x,t,u) \quad \text{ in } \Omega \times (0,\infty), \\ &Bu = 0 \quad \text{ on } \partial\Omega \times (0,\infty), \\ &u(\cdot,0) = \phi, \end{aligned} \tag{3.35}$$

has a unique regular solution $u(x,t,\phi,\mu,g)$ with the maximal interval of existence $I(\phi,\mu,g) \subset [0,\infty)$, and $I(\phi,\mu,g) = [0,\infty)$, provided that $u(\cdot,t,\phi,\mu,g)$ has an L^∞-bound on $I(\phi,\mu,g)$.

We are now in a position to prove the following result on the global dynamics of (3.34).

Theorem 3.3.3. (Threshold dynamics) *Let (E1), (E2), and (E3) hold. Then the following statements are valid:*

(1) If $\lambda(d(\cdot), f(\cdot,\cdot,0)) < 0$, then $\lim_{t\to\infty} \|u(\cdot,t,\phi,d,f)\|_\beta = 0$ for every $\phi \in X_\beta^+$;
(2) If $\lambda(d(\cdot), f(\cdot,\cdot,0)) > 0$, then (3.34) admits a unique positive almost periodic solution $u^*(x,t)$, and $\lim_{t\to\infty} \|u(\cdot,t,\phi,d,f) - u^*(\cdot,t)\|_\beta = 0$ for every $\phi \in X_\beta^+ \setminus \{0\}$.

Proof. For any $(\mu,g) \in H(d,f)$, both (E2) and (E3) imply that $u = M$, $M \geq M_0$, is an upper solution of (3.35), and hence by the comparison theorem and a priori estimates of parabolic equations (see, e.g., [152]), each solution $u(x,t,\phi,\mu,g)$ exists globally on $[0,\infty)$, and for any $t_0 > 0$, the set $\{u(\cdot,t,\phi,\mu,g) : t \geq t_0\}$ is precompact in X_β^+. We define the skew-product semiflow $\Pi_t : X_\beta^+ \times H(d,f) \to X_\beta^+ \times H(d,f)$ by $\Pi_t(\phi,\mu,g) = (u(\cdot,t,\phi,\mu,g),\mu_t,g_t)$. Then for each $(\phi,\mu,g) \in X_\beta^+ \times H(d,f)$, the omega limit set $\omega(\phi,\mu,g)$ of the forward orbit $\gamma^+(\phi,\mu,g) := \{\Pi_t(\phi,\mu,g) : t \geq 0\}$ is well defined, compact, and invariant under Π_t, $t \geq 0$. Moreover, the maximum principle for parabolic equations implies that

$$\Pi_t((X_\beta^+ \setminus \{0\}) \times H(d,f)) \subset \mathrm{int}(X_\beta^+) \times H(d,f),\ \forall t > 0.$$

In the case that $\lambda(d(\cdot), f(\cdot,\cdot,0)) < 0$, let $\varphi(x,t)$ and $a(t)$ be the functions associated with $\lambda(d(\cdot), f(\cdot,\cdot,0))$ as in (3.33) with $\mu(\cdot) = d(\cdot)$ and $k = f(\cdot,\cdot,0)$. Then $\varphi(\cdot,t) \gg 0$ in X_β, $\forall t \in \mathbb{R}$, and

$$\lim_{t\to\infty} \frac{1}{t}\int_0^t a(s)ds = \lambda(d(\cdot), f(\cdot,\cdot,0)) < 0.$$

Clearly, $u(x,t,\phi,d,f)$ satisfies the following differential inequality:

$$\begin{aligned} &\frac{\partial u}{\partial t} \leq d(t)\Delta u + uf(x,t,0) \quad \text{in } \Omega \times (0,\infty), \\ &Bu = 0 \quad \text{on } \partial\Omega \times (0,\infty). \end{aligned} \tag{3.36}$$

For any $\phi(\cdot) \in X_\beta^+$, there exists a sufficiently large $\eta > 0$ such that $\phi \leq \eta\varphi(\cdot,0)$. By the comparison theorem, it then follows that

$$0 \leq u(x,t,\phi,d,f) \leq \eta e^{\int_0^t a(s)ds}\varphi(x,t),\ \forall x \in \Omega,\ t \geq 0.$$

Since $\varphi(x,t)$ is uniformly almost periodic in t and

$$\lim_{t\to\infty} e^{\int_0^t a(s)ds} = \lim_{t\to\infty} \left(e^{\frac{1}{t}\int_0^t a(s)ds}\right)^t = 0,$$

we get $\lim_{t\to\infty} u(x,t,\phi,d,f) = 0$ uniformly for $x \in \overline{\Omega}$. For any $(\psi,\mu,g) \in \omega(\phi,d,f)$, there exists a sequence $t_n \to \infty$ such that $\lim_{n\to\infty} \Pi_{t_n}(\phi,d,f) = (\psi,\mu,g)$. Thus $\lim_{n\to\infty} \|u(\cdot,t_n,\phi,d,f) - \psi\|_\beta = 0$. Since $X_\beta \subset C^1(\overline{\Omega})$ with continuous inclusion, we have $\lim_{n\to\infty} u(x,t_n,\phi,d,f) = \psi(x)$ uniformly for $x \in \overline{\Omega}$. Then $\psi(\cdot) \equiv 0$, and hence $\omega(\phi,d,f) = \{0\} \times H(d,f)$, which implies that $\lim_{t\to\infty} \|u(\cdot,t,\phi,d,f)\|_\beta = 0$.

In the case that $\lambda(d(\cdot), f(\cdot,\cdot,0)) > 0$, we first prove the following two claims.

Claim 1. There exists a $\delta > 0$ such that $\limsup_{t\to\infty} \|u(\cdot,t,\phi,\mu,g)\|_\beta \geq \delta$, $\forall (\phi,\mu,g) \in (X_\beta^+ \setminus \{0\}) \times H(d,f)$.

Indeed, we can choose a sufficiently small $\epsilon_0 > 0$ such that $\lambda(d(\cdot), f(\cdot,\cdot,0) - \epsilon_0) > 0$. Since f is uniformly almost periodic in t and $H(f)$ is compact, there exists a $\delta_0 > 0$ such that

$$|g(x,t,u) - g(x,t,0)| < \epsilon_0, \quad \forall x \in \overline{\Omega},\, t \in \mathbb{R},\, u \in [0,\delta_0],\, g \in H(f).$$

Since $X_\beta \subset C^1(\overline{\Omega})$ with continuous inclusion, there is a $\delta > 0$ such that for any $\phi \in X_\beta$, $\|\phi\|_\beta \leq \delta$ implies that $\|\phi\|_\infty \leq \delta_0$. Suppose for contradiction that for some $(\phi,\mu,g) \in (X_\beta^+ \setminus \{0\}) \times H(d,f)$, $\limsup_{t\to\infty} \|u(\cdot,t,\phi,\mu,g)\|_\beta < \delta$. Then there is a $t_0 > 0$ such that $\|u(\cdot,t,\phi,\mu,g)\|_\beta < \delta$, $\forall t \geq t_0$, and hence $\|u(\cdot,t,\psi,\gamma,h)\|_\beta < \delta$, $\forall t \geq 0$, where $(\psi,\gamma,h) = (u(\cdot,t_0,\phi,\mu,g), \mu_{t_0}, g_{t_0}) \in \mathrm{int}(X_\beta^+) \times H(d,f)$. By the choice of δ_0 and δ, it then follows that $u(\cdot,t,\psi,\gamma,h)$ satisfies the following differential inequality:

$$\begin{aligned} &\frac{\partial u}{\partial t} \geq \gamma(t)\Delta u + u\left(h(x,t,0) - \epsilon_0\right) \quad \text{ in } \Omega \times (0,\infty), \\ &Bu = 0 \quad \text{ on } \partial\Omega \times (0,\infty). \end{aligned} \tag{3.37}$$

Clearly, $(\gamma, h(\cdot,\cdot,0) - \epsilon_0) \in H(d, f(\cdot,\cdot,0) - \epsilon_0)$. Let $\tilde{\varphi}(x,t)$ and $\tilde{a}(t)$ be the functions associated with $\lambda(d(\cdot), f(\cdot,\cdot,0) - \epsilon_0)$ as in (3.33) with $\mu(\cdot) = \gamma(\cdot)$ and $k = h(\cdot,\cdot,0) - \epsilon_0$. Then $\tilde{\varphi}(\cdot,t) \gg 0$ in X_β, $\forall t \in \mathbb{R}$, and

$$\lim_{t\to\infty} \frac{1}{t}\int_0^t \tilde{a}(s)ds = \lambda(d(\cdot), f(\cdot,\cdot,0) - \epsilon_0) > 0.$$

Choose a sufficiently small $\epsilon > 0$ such that $\psi \geq \epsilon\tilde{\varphi}(\cdot,0)$. By the standard comparison theorem, we then get

$$u(x,t,\psi,\gamma,h) \geq \epsilon e^{\int_0^t \tilde{a}(s)ds}\tilde{\varphi}(x,t),\ \forall x \in \Omega,\ t \geq 0.$$

Since $\tilde{\varphi}(x,t)$ is uniformly almost periodic in t, and

$$\lim_{t\to\infty} e^{\int_0^t \tilde{a}(s)ds} = \lim_{t\to\infty} \left(e^{\frac{1}{t}\int_0^t \tilde{a}(s)ds}\right)^t = \infty,$$

we get $\lim_{t\to\infty} u(x,t,\psi,\gamma,h) = \infty$, $\forall x \in \Omega$, a contradiction.

Claim 2. $\omega(\phi,\mu,g) \subset \text{int}(X_\beta^+) \times H(d,f)$, $\forall (\phi,\mu,g) \in (X_\beta^+ \setminus \{0\}) \times H(d,f)$.

In fact, let $A = \{0\} \times H(d,f)$. It is easy to see that Claim 1 above implies that A is an isolated invariant set of Π_t and $\omega(\phi,\mu,g) \not\subset A$, and hence the Butler–McGehee lemma (see, e.g., [45, 105] or Lemma 1.2.7) implies that

$$\omega(\phi,\mu,g) \cap A = \emptyset,\ \forall (\phi,\mu,g) \in (X_\beta^+ \setminus \{0\}) \times H(d,f).$$

Then Claim 2 follows from the invariance of $\omega(\phi,\mu,g)$ and the fact that $\Pi_t((X_\beta^+ \setminus \{0\}) \times H(d,f)) \subset \text{int}(X_\beta^+) \times H(d,f), \forall t > 0$.

Let $u(\phi,\mu,g,t) := u(\cdot,t,\phi,\mu,g)$, $t \geq 0$. By the standard comparison theorem, it then follows that $u(\cdot,\mu,g,t)$ is strongly monotone on X_β^+ for each $(\mu,g,t) \in H(d,f)\times(0,\infty)$. It is easy to see that (E2) implies that the function $uf(x,t,u)$ is strictly subhomogeneous in u, and hence each function $ug(x,t,u)$, $g \in H(f)$, is subhomogeneous in u for any fixed $(x,t) \in \overline{\Omega} \times \mathbb{R}_+$. By the integral version of parabolic equation (3.35) (see, e.g., [152, 162, 432]), it then follows that $u(\cdot,\mu,g,t)$ is subhomogeneous on X_β^+ for each $(\mu,g,t) \in H(d,f) \times \mathbb{R}_+$, and $u(\cdot,d,f,t)$ is strictly subhomogeneous on X_β^+ for each $t > 0$. Thus $(A1)'$ and $(A2)''$ in Remarks 2.3.2 and 2.3.3 hold for the skew-product semiflow Π_t on $X_\beta^+ \times H(d,f)$. Let $\phi_0 \in X_\beta^+ \setminus \{0\}$ be fixed and let $K_0 = \omega(\phi_0,d,f)$. By Theorem 2.3.5 and Remarks 2.3.2–2.3.3, together with Claim 2 above, it follows that for every $\phi \in X_\beta^+\setminus\{0\}$, $\lim_{t\to\infty} \|u(\cdot,t,\phi,d,f)-u(\cdot,t,\phi^*,d,f)\|_\beta = 0$, where $(\phi^*,d,f) \in K_0$. Since $\Pi_t : K_0 \to K_0$ is an almost periodic minimal flow, $\Pi_t(\phi^*,d,f) = (u(\cdot,t,\phi^*,f),d_t,f_t)$ is an almost periodic motion (see [303, Lemma VI.9]). Therefore, $u(\cdot,t,\phi^*,d,f)$ is a unique positive almost periodic solution of (3.34). ∎

The global attractivity of a unique positive almost periodic solution of (3.34) with $d(t) \equiv 1$ and $Bu = \frac{\partial u}{\partial n}$ is proved in [312, Theorem 4.1] under the assumption that there is a positive solution $u_0(x,t)$ of (3.34) such that $\inf_{t\in\mathbb{R}_+} \|u_0(\cdot,t)\|_\beta > 0$. In this case, $\epsilon u_0(x,t)$ is a subsolution of (3.34) for each $\epsilon \in (0,1)$. By the standard parabolic comparison theorem and the invariance of omega limit sets, it then easily follows that $\omega(\phi,d,f) \subset \text{int}(X_\beta^+) \times H(d,f)$ for each $\phi \in X_\beta^+ \setminus \{0\}$, and hence the global attractivity of a unique positive almost periodic solution of (3.34) follows from Theorem 2.3.5.

In the case that $f(x,t,u) \equiv f(t,u)$ and $Bu = \frac{\partial u}{\partial n}$, it is easy to see that $\lambda(d(\cdot),f(\cdot,0)) = \lim_{t\to\infty} \frac{1}{t}\int_0^t f(s,0)ds$. Clearly, each solution of $\frac{du}{dt} = uf(t,u)$ is also a solution of (3.34). By the global attractivity of $u^*(x,t)$, it follows that $u^*(x,t)$ is independent of the spatial variable $x \in \Omega$. Then Theorem 3.3.3 implies a threshold result for the almost periodic ordinary differential equation $\frac{du}{dt} = uf(t,u)$.

In the case that $d(t)$ and $f(x,t,u)$ are ω-periodic in t, the conclusion in Theorem 3.3.3(2) implies that the periodic system (3.34) is uniformly persistent. By Theorem 1.3.8, as applied to the Poincaré map associated with the

ω-periodic system (3.34), it then follows that there exists a positive ω-periodic solution of (3.34), and hence by the uniqueness of positive almost periodic solutions, $u^*(x,t)$ is ω-periodic in t. Therefore, Theorem 3.3.3 is a generalization of Theorem 3.1.5 (see also [432, Theorems 3.2 and 3.3]).

3.4 Continuous Processes

Let X be a metric space with metric d. A process on X is a continuous map $u : \mathbb{R}^+ \times \mathbb{R} \times X \to X$ such that

$$u(0,s,x) = x,\ u(t,r+s,u(r,s,x)) = u(t+r,s,x),\ \ \forall t \geq 0, r \geq 0, s \in \mathbb{R}, x \in X.$$

A process u is said to be autonomous if $u(t,s,x)$ is independent of s; that is, $u(t,0,x) = u(t,s,x), \forall t \geq 0, s \in \mathbb{R}, x \in X$. Then $u(t,0,\cdot)$ is an autonomous semiflow on X.

Let $\Delta := \{(t,s) \in \mathbb{R}^2 : -\infty < s \leq t < \infty\}$. A nonautonomous semiflow is a continuous map $\Phi : \Delta \times X \to X$ such that

$$\Phi(s,s,x) = x,\ \Phi(t,r,\Phi(r,s,x)) = \Phi(t,s,x),\ \ \forall t \geq r \geq s, s \in \mathbb{R}, x \in X.$$

For a nonautonomous semiflow Φ on X, define ϕ by

$$\phi(t,s,x) = \Phi(t+s,s,x),\ \forall t \geq 0, s \in \mathbb{R}, x \in X.$$

It is easy to verify that ϕ is a process on X. We call it the process associated with the nonautonomous semiflow Φ.

Let W be the set of all processes on X. For $u \in W$, define the translation $\sigma(\tau), \tau \in \mathbb{R}$, of the process as

$$(\sigma(\tau)u)(t,s,x) = u(t,\tau+s,x).$$

Throughout this section we let ϕ be a given process on X and assume that

(A) There is a subset V of W and a metric ρ on V such that the set $\gamma_\sigma^+(\phi) := \{\sigma(t)\phi : t \geq 0\} \subset V$ has compact closure $H(\phi) \subset V$, and the map $\pi : \mathbb{R}^+ \times X \times H(\phi) \to X \times H(\phi)$, defined by

$$\pi(t,x,u) = (u(t,0,x), \sigma(t)u),$$

is continuous.

Clearly, the continuity of π implies that if $u_n \to u$ in $H(\phi)$ as $n \to \infty$, then $u_n(t,0,x) \to u(t,0,x)$ in X for any $(t,x) \in \mathbb{R}^+ \times X$. Under assumption (A), it is also easy to verify that $\pi(t) : X \times H(\phi) \to X \times H(\phi)$ and $\sigma(t) : H(\phi) \to H(\phi)$ are C^0-semiflows (see, e.g., [141, Section 3.7]). The semiflow $\pi(t)$ is called the skew-product semiflow of the process ϕ, and $H(\phi)$ is called the hull of ϕ. Let $\omega_\sigma(\phi)$ be the omega limit set of ϕ for the autonomous semiflow $\sigma(t) : H(\phi) \to$

$H(\phi)$. Clearly, $\omega_\sigma(\phi)$ is a nonempty, compact, and invariant set for $\sigma(t)$. If $\omega_\sigma(\phi) = \{u\}$ for some autonomous process u, we call ϕ an asymptotically autonomous process. In what follows we will use P_X to denote the projection map of $X \times H(\phi)$ onto X, defined by $P_X(x,u) = x, \forall (x,u) \in X \times H(\phi)$.

For any $x \in X$, the positive orbit $\gamma_u^+(x)$ for a process u is defined as $\gamma_u^+(x) := \{u(t,0,x) : t \geq 0\}$. The omega limit set of x is defined in the usual way as $\omega_u(x) := \{y \in X : u(t_n, 0, x) \to y \,\text{for some}\, t_n \to \infty\}$. A negative orbit through x for u is a function $g : \mathbb{R}^- \to X$ such that $g(0) = x$ and for any $s \leq 0$, $u(t,s,g(s)) = g(t+s)$ for $t \in [0,-s]$. For a given negative orbit $\gamma_u^-(x) := \{g(t) : t \leq 0\}$ we define its alpha limit set as $\alpha_u(x) := \{y \in X : g(t_n) \to y \,\text{for some}\, t_n \to -\infty\}$. We further define $u(t,0,x) := g(t), \forall t \leq 0$, and call the set $\{u(t,0,x) : t \in \mathbb{R}\}$ a full orbit through x.

Definition 3.4.1. *A subset $M \subset X$ is said to be quasi-invariant for ϕ if for every $x \in M$ there exist $u \in \omega_\sigma(\phi)$ and a full orbit through x for u such that $u(t,0,x) \in M$ for all $t \in \mathbb{R}$. A nonempty quasi-invariant set $A \subset X$ for ϕ is said to be internally chain transitive if for every a, $b \in A$ and every $\epsilon > 0, t_0 > 0$, there is a finite sequence $\{x_1 = a, x_2, \ldots, x_{m-1}, x_m = b; u_1, \ldots, u_m; t_1, \ldots, t_{m-1}\}$ with $x_i \in A, u_i \in \omega_\sigma(\phi)$, and $t_i \geq t_0$ such that $u_i(t,0,x_i) \in A, \forall t \in \mathbb{R}, 1 \leq i \leq m$, $d(u_i(t_i,0,x_i), x_{i+1}) < \epsilon$, and $d(\sigma(t_i)u_i, u_{i+1}) < \epsilon$, $\forall 1 \leq i \leq m-1$.*

Lemma 3.4.1. *The omega (alpha) limit set of any precompact positive (negative) orbit of a process ϕ on X is nonempty, compact, quasi-invariant, and internally chain transitive for ϕ.*

Proof. Let $\gamma^+(x) := \{\phi(t,0,x) : t \in \mathbb{R}^+\}$ be a precompact positive orbit through $x \in X$, and let $\omega_\phi(x)$ be its omega limit for ϕ. Clearly, $\gamma^+(x,\phi) := \{(\phi(t,0,x), \sigma(t)\phi) : t \in \mathbb{R}^+\}$ is a precompact positive orbit of the autonomous semiflow $\pi(t) : X \times H(\phi) \to X \times H(\phi)$. Then, by Lemma 1.2.1′, its omega limit set $\omega_\pi(x,\phi)$ is nonempty, compact, invariant, and internally chain transitive for π. It is easy to verify that $\omega_\pi(x,\phi) \subset \omega_\phi(x) \times \omega_\sigma(\phi)$ and $P_X(\omega_\pi(x,\phi)) = \omega_\phi(x)$. It then follows that $\omega_\phi(x)$ is nonempty, compact, and quasi-invariant for ϕ. For any two points $a, b \in \omega_\phi(x)$, there exist $v, w \in \omega_\sigma(\phi)$ such that $(a,v), (b,w) \in \omega_\pi(x,\phi)$. Thus the internal chain transitivity of $\omega_\pi(x,\phi)$ for π implies that $\omega_\phi(x)$ is internally chain transitive for ϕ. A similar argument applies to alpha limit sets. ∎

A nonempty quasi-invariant set M for ϕ is said to be isolated if it is the maximal invariant set in some neighborhood of itself. For a quasi-invariant set M of ϕ, we define

$$\tilde{M} := \{(x,u) : x \in M, u \in \omega_\sigma(\phi), u(t,0,x) \in M, \forall t \in \mathbb{R}\}.$$

Clearly, $P_X(\tilde{M}) = M$.

Lemma 3.4.2. *If M is a quasi-invariant (and isolated) set in X for ϕ, then $\tilde{M}$ is an invariant (and isolated) set in $X \times H(\phi)$ for $\pi(t)$.*

Proof. For any $(x,u) \in \tilde{M}$, the invariance of $\omega_\sigma(\phi)$ for $\sigma(t)$ implies that there is a full orbit $\sigma(t)u, t \in \mathbb{R}$, in $\omega_\sigma(\phi)$. Then $\pi(t)(x,u) = (u(t,0,x), \sigma(t)u)$, $t \in \mathbb{R}$, is a full orbit of $\pi(t)$. We further claim that this full orbit is contained in $\tilde{M}$. For any $\tau \in \mathbb{R}$, $u(\tau,0,x) \in M$, and $(\sigma(\tau)u)(t,0,u(\tau,0,x)) = u(t,\tau,u(\tau,0,x)) = u(t+\tau,0,x) \in M, \forall t \in \mathbb{R}$, and hence, $\pi(\tau)(x,u) = (u(\tau,0,x), \sigma(\tau)u) \in \tilde{M}, \forall \tau \in \mathbb{R}$. Then $\tilde{M}$ is invariant for π. If M is isolated, then there is an open neighborhood U of M such that if there are $x \in U$ and $u \in \sigma_\omega(\phi)$ such that u admits a full orbit through x in U, then this full orbit is contained in M. Clearly, $U \times H(\phi)$ is an open neighborhood of $\tilde{M}$. Assume that there is $(y,v) \in U \times H(\phi)$ such that a full orbit $\pi(t)(y,v) = (v(t,0,y), \sigma(t)v) \in U \times H(\phi), \forall t \in \mathbb{R}$. Since $\omega_\sigma(\phi)$ is the maximal invariant set for the autonomous semiflow $\sigma(t)$ in $H(\phi)$, we have $\sigma(t)v \in \omega_\sigma(\phi), \forall t \in \mathbb{R}$. Thus the choice of U implies that $v(t,0,y) \in M, \forall t \in \mathbb{R}$. Then for any given $\tau \in \mathbb{R}$, we have $v(\tau,0,y) \in M, \sigma(\tau)v \in \omega_\sigma(\phi)$, and $(\sigma(\tau)v)(t,0,v(\tau,0,y)) = v(t,\tau,v(\tau,0,y)) = v(t+\tau,0,y) \in M, \forall t \in \mathbb{R}$. Thus $\pi(\tau)(y,v) \in \tilde{M}, \forall \tau \in \mathbb{R}$; that is, the full orbit $\pi(t)(y,v), t \in \mathbb{R}$, is contained in $\tilde{M}$. It follows that $\tilde{M}$ is isolated. ∎

Let A and B be two quasi-invariant sets for ϕ. The set A is said to be chained to B, written $A \to B$, if there exist $u \in \omega_\sigma(\phi)$ and a full orbit $\gamma_u(x)$ for u with $\gamma_u(x) \not\subset A \cup B$ such that $\omega_u(x) \subset B$ and $\alpha_u(x) \subset A$. A finite sequence $\{M_1, \ldots, M_k\}$ of quasi-invariant sets is called a chain if $M_1 \to M_2 \to \ldots \to M_k$. The chain is called a cycle if $M_k = M_1$.

Definition 3.4.2. *Let X_0 be an open subset of X and define $\partial X_0 := X \setminus X_0$. A process ϕ on X, with $\phi(t,0,X_0) \subset X_0, \forall t \geq 0$, is said to be uniformly persistent with respect to $(X_0, \partial X_0)$ if there exists $\eta > 0$ such that $\liminf_{t\to\infty} d(\phi(t,0,x), \partial X_0) \geq \eta$ for all $x \in X_0$. If "inf" in this inequality is replaced with "sup", ϕ is said to be weakly uniformly persistent with respect to $(X_0, \partial X_0)$.*

Theorem 3.4.1. (Uniform persistence) *Let ϕ be a process on X such that (A) holds and $u(t,0,X_0) \subset X_0, \forall u \in H(\phi), t \geq 0$. Assume that*

(1) There is a compact set $A \subset X$ such that $\lim_{t\to\infty} d(u(t,0,x), A) = 0, \forall x \in X, u \in \omega_\sigma(\phi)$;
(2) There exists a finite sequence $\mathcal{M} = \{M_1, \ldots, M_k\}$ of disjoint, compact, and quasi-invariant sets for ϕ in ∂X_0 such that each $\tilde{M}_i$ is isolated in $X \times \omega_\sigma(\phi)$ for $\pi(t)$, that no subset of $\mathcal{M}$ forms a cycle in ∂X_0, and that for any $x \in \partial X_0$ and $u \in \omega_\sigma(\phi)$ with $u(t,0,x) \in \partial X_0, \forall t \geq 0$, we have $\omega_u(x) \subset M_i$ for some $1 \leq i \leq k$;
(3) Every positive orbit for ϕ is precompact in X, and $\omega_\pi(x,\phi) \not\subset \tilde{M}_i$, $\forall x \in X_0$, $1 \leq i \leq k$.

Then ϕ is uniformly persistent with respect to $(X_0, \partial X_0)$.

Proof. Let $Y = X \times \omega_\sigma(\phi), Y_0 = X_0 \times \omega_\sigma(\phi)$, and $\partial Y_0 = Y \setminus Y_0 = \partial X_0 \times \omega_\sigma(\phi)$. Clearly, $\pi(t)Y \subset Y$, $\pi(t)Y_0 \subset Y_0, t \geq 0$, the compact set $A \times \omega_\sigma(\phi)$ attracts every orbit of $\pi(t)$ on Y, and $\tilde{M}_i \subset M_i \times \omega_\sigma(\phi)$. It is easy to verify that each $\tilde{M}_i$ is a compact subset of Y. By condition (2), each $\tilde{M}_i$ is an isolated invariant set of $\pi(t)$ in ∂Y_0, and $\tilde{M}_i$ is also isolated in Y. We claim that $\tilde{M}_i \to \tilde{M}_j$ for $\pi(t)$ implies $M_i \to M_j$ for ϕ. Indeed, let $\pi(t)(x,u)$, $t \in \mathbb{R}$, be a full orbit of π through some $(x,u) \notin \tilde{M}_i \cup \tilde{M}_j$ such that $\omega_\pi(x,u) \subset \tilde{M}_j$ and $\alpha_\pi(x,u) \subset \tilde{M}_i$. Since $\pi(t)(x,u) = (u(t,0,x), \sigma(t)u) \in Y, \forall t \in \mathbb{R}$, we have $\omega_u(x) \subset M_j$ and $\alpha_u(x) \subset M_i$. In particular, $u = \sigma(0)u \in \omega_\sigma(\phi)$. Thus $\gamma_u(x) \not\subset M_i \cup M_j$, and hence $M_i \to M_j$ for ϕ. By condition (2), it then follows that no subset of $\tilde{M}_i$'s forms a cycle for π in ∂Y_0. Let $M_\partial := \{(x,u) \in \partial Y_0 : \pi(t)(x,u) \in \partial Y_0, \forall t \geq 0\}$. We then claim that $\cup_{(x,u)\in M_\partial} \omega_\pi(x,u) \subset \cup_{i=1}^k \tilde{M}_i$. Indeed, for any $(x,u) \in M_\partial$, condition (2) implies that $\omega_\pi(x,u) \subset \omega_u(x) \times \omega_\sigma(\phi) \subset M_i \times \omega_\sigma(\phi)$ for some $1 \leq i \leq k$. For any $(y,v) \in \omega_\pi(x,u)$, the invariance of omega limit sets for the autonomous semiflow $\pi(t)$ implies that $\omega_\pi(x,u)$ contains a full orbit $\pi(t)(y,v)$, $t \in \mathbb{R}$. Then $v(t,0,y) \in M_i$, $\forall t \in \mathbb{R}$, and hence $(y,v) \in \tilde{M}_i$. Thus $\omega_\pi(x,u) \subset \tilde{M}_i$. By the continuous-time versions of Theorem 1.3.1 and Remark 1.3.1, it then follows that there exists $\eta > 0$ such that for any compact internally chain transitive set L for $\pi(t) : Y \to Y$ with $L \not\subset \tilde{M}_i$, $\forall 1 \leq i \leq k$, we have $\inf_{(x,u)\in L} \tilde{d}((x,u), \partial Y_0) > \eta$, where $\tilde{d}$ is the metric on $X \times V$ defined by $\tilde{d}((y,v),(z,w)) := d(y,z) + \rho(v,w)$. For every $x \in X_0$, the positive orbit $\gamma_\pi(x,\phi)$ for the autonomous semiflow $\pi(t) : X \times H(\phi) \to X \times H(\phi)$ is precompact, and hence its omega limit set $\omega_\pi(x,\phi)$ is compact and internally chain transitive for $\pi(t)$. Since $\omega_\pi(x,\phi) \subset \omega_\phi(x) \times \omega_\sigma(\phi)$, we have $\omega_\pi(x,\phi) \subset Y$. By condition (3), $\omega_\pi(x,\phi) \not\subset \tilde{M}_i$ for every $1 \leq i \leq k$. Letting $L = \omega_\pi(x,\phi)$, we get $\inf_{(y,u)\in\omega_\pi(x,\phi)} \tilde{d}((y,u), \partial Y_0) > \eta$. Then the uniform persistence of ϕ follows from the fact that $P_X(\omega_\pi(x,\phi)) = \omega_\phi(x)$. ∎

In the case that ϕ is an autonomous process on X, letting $V = \{\phi\}$, we then have $H(\phi) = \omega_\sigma(\phi) = \{\phi\}$. Thus Theorem 3.4.1 is just a restatement of a well-known no-cycle theorem on uniform persistence for the autonomous semiflow $\phi(t,0,\cdot)$(see [45, 146, 365]). In the case that ϕ is asymptotic to an autonomous process u, we have $\omega_\sigma(\phi) = \{u\}$. Then $\tilde{M}_i = M_i \times \{u\}$ and $\pi(t) : X \times \{u\} \to X \times \{u\}$ is equivalent to the autonomous semiflow $u(t,0,\cdot) : X \to X$. Thus Theorem 3.4.1 gives a no-cycle theorem on uniform persistence for asymptotically autonomous processes (and then for asymptotically autonomous semiflows), which is an analogue of [433, Theorem 2.5] on asymptotically autonomous discrete processes. For related materials, we refer to [249, 364].

Remark 3.4.1. By the proof of Theorem 3.4.1, the positive number η in the uniform persistence depends only on the autonomous semiflow $\pi(t) : X \times \omega_\sigma(\phi) \to X \times \omega_\sigma(\phi)$. Consequently, η is also uniform for all processes in V that satisfy the conditions of Theorem 3.4.1 and have the same omega limit for $\sigma(t)$.

Remark 3.4.2. Note that if $\omega_\pi(x,\phi) \subset \tilde{M}_i$, then $\pi(t)(x,\phi) = (\phi(t,0,x), \sigma(t)\phi) \to \tilde{M}_i$ as $t \to \infty$, and hence $\phi(t,0,x) \to P_X(\tilde{M}_i) = M_i$ as $t \to \infty$.

In particular, let M be the compact and maximal quasi-invariant set for ϕ in ∂X_0. By Lemma 3.4.2 and Theorem 3.4.1, it then follows that weak uniform persistence implies uniform persistence for processes (and then for nonautonomous semiflows).

In the application of Theorem 3.4.1 to a concrete nonautonomous evolutionary system, it is often more convenient to work directly on the system itself rather than the continuous process associated with the nonautonomous semiflow generated by the system. The subsequent theorem shows that this can be done by choosing an equivalent skew-product semiflow associated with a given nonautonomous system.

Let Z_1 and Z_2 be two metric spaces and let $\mathcal{F}$ be the set of some maps from $\mathbb{R}\times Z_1$ to Z_2 with the property that $g \in \mathcal{F}$ implies that $\tilde{\sigma}(t)g := g(t+\cdot,\cdot) \in \mathcal{F}$ for any $t \in \mathbb{R}$. Let $f \in \mathcal{F}$ be given, and assume that

(B) There is a metric m on $\mathcal{F}$ such that the set $\{\tilde{\sigma}(t)f : t \geq 0\}$ has a compact closure $H(f) \subset \mathcal{F}$, and there is a one-to-one map $h : H(f) \to W$ such that $\sigma(t) \circ h = h \circ \tilde{\sigma}(t)$, $\forall t \geq 0$, and such that the map $\tilde{\pi} : \mathbb{R}^+ \times X \times H(f) \to X \times H(f)$, defined by

$$\tilde{\pi}(t,x,g) = (h(g)(t,0,x), \tilde{\sigma}(t)g),$$

is continuous.

By assumption (B) and the property of processes $h(g)$, $g \in H(f)$, it is easy to verify that $\tilde{\pi}(t) : X \times H(f) \to X \times H(f)$ is an autonomous semiflow. Let I_X be the identity map on X. Let $V_0 = h(H(f))$, and for any $u, v \in V_0$ define $\rho_0(u,v) := m(h^{-1}(u), h^{-1}(v))$. Then $V_0 \subset W$, (V_0, ρ_0) is a metric space, and $h : (H(f), m) \to (V_0, \rho_0)$ is a homeomorphism. We further have the following result.

Theorem 3.4.2. (Equivalence) *Let (B) hold and let $\phi = h(f)$. Then assumption (A) holds for (V_0, ρ_0), and the skew-product semiflow $\pi(t)$ on $H(\phi)$ is equivalent to the skew-product semiflow $\tilde{\pi}(t)$ on $H(f)$. More precisely, the map $I_X \times h : X \times H(f) \to X \times H(\phi)$ is a homeomorphism and $\pi(t) \circ (I_X \times h) = (I_X \times h) \circ \tilde{\pi}(t)$ on $X \times H(f)$ for all $t \geq 0$.*

Proof. By assumption (B), we have $\sigma(t)\phi = \sigma(t)(h(f)) = h(\tilde{\sigma}(t)f), \forall t \geq 0$. Then $H(\phi)$ exists and is a compact subset of V_0. We further claim that $V_0 := h(H(f)) = H(\phi)$. Indeed, for any $g \in H(f)$, there is a sequence $t_n \to \infty$ such that $\tilde{\sigma}(t_n)f \to g$ as $n \to \infty$. Since $h : H(f) \to V_0$ is continuous, we have $\sigma(t_n)\phi = h(\tilde{\sigma}(t_n)f) \to h(g)$ as $n \to \infty$, and hence $h(g) \in H(\phi)$. Thus $h(H(f)) \subset H(\phi)$. For any $u \in H(\phi)$, there is a sequence $t_n \to \infty$ such that $\sigma(t_n)\phi = h(\tilde{\sigma}(t_n)f) \to u$ as $n \to \infty$. By the compactness of $H(f)$, we can assume that there exists $g \in H(f)$ such that $\tilde{\sigma}(t_n)f \to g$ as $n \to \infty$. Then $h(\tilde{\sigma}(t_n)f) \to h(g)$ as $n \to \infty$, and hence $u = h(g) \in h(H(f))$. Thus $H(\phi) \subset h(H(f)$. By assumption (B), we have $\sigma(t) = h\circ\tilde{\sigma}(t)\circ h^{-1} : H(\phi) \to H(\phi), \forall t \geq$

0. It then follows that $\pi(t)(t,x,u) = (u(t,0,x), \sigma(t)u) = (h(h^{-1}u)(t,0,x), h \circ \tilde{\sigma}(t)(h^{-1}(u)))$ is continuous in (t,x,u). Thus assumption (A) holds. Clearly, the map $I_X \times h : X \times H(f) \to X \times H(\phi)$ is a homeomorphism. For any $(x,g) \in X \times H(f)$ and $t \geq 0$, we have

$$\begin{aligned}
\pi(t) \circ (I_X \times h)(x,g) &= \pi(t)(x,h(g)) \\
&= (h(g)(t,0,x), \sigma(t)(h(g))) \\
&= (h(g)(t,0,x), h(\tilde{\sigma}(t)g)) \\
&= (I_X \times h)(h(g)(t,0,x), \tilde{\sigma}(t)g) \\
&= (I_X \times h) \circ \tilde{\pi}(t)(x,g).
\end{aligned}$$

Then $\pi(t) \circ (I_X \times h) = (I_X \times h) \circ \tilde{\pi}(t)$ for all $t \geq 0$. ∎

3.5 Abstract Nonautonomous FDEs

In this section, we study the weak compactness of solution maps associated with a class of abstract nonautonomous functional differential equations (FDEs). We start with a generalized Arzela–Ascoli theorem.

Generalized Arzela–Ascoli Theorem *Let $a < b$ be two real numbers and $\mathcal{X}$ be a complete metric space. Assume that a sequence of functions $\{f_n\}$ in $C([a,b], \mathcal{X})$ satisfies the following conditions:*

(1) The family $\{f_n(s)\}_{n \geq 1}$ is uniformly bounded on $[a,b]$;
(2) For each $s \in [a,b]$, the set $\{f_n(s) : n \geq 1\}$ is precompact in $\mathcal{X}$;
(3) The family $\{f_n(s)\}_{n \geq 1}$ is equi-continuous on $[a,b]$.

Then $\{f_n\}$ has a convergent subsequence in $C([a,b], \mathcal{X})$, that is, there exists a subsequence of functions $\{f_{n_k}(s)\}$ which converges in $\mathcal{X}$ uniformly for $s \in [a,b]$.

Let τ be a positive real number, X be a Banach space, and $C := C([-\tau, 0], X)$. For any $\phi \in C$, define $\|\phi\| = \sup_{-\tau \leq \theta \leq 0} \|\phi(\theta)\|_X$. Then $(C, \|\cdot\|)$ is a Banach space. Let A be the infinitesimal generator of a C_0-semigroup $\{T(t)\}_{t \geq 0}$ on X. Assume that $T(t)$ is compact for each $t > 0$, and there exists $M > 0$ such that $\|T(t)\| \leq M$ for all $t \geq 0$.

We consider the abstract nonautonomous functional differential equation

$$\begin{aligned}
&\frac{du(t)}{dt} = Au(t) + F(t, u_t), \qquad t > 0, \\
&u_0 = \phi \in C.
\end{aligned} \tag{3.38}$$

Here $F : [0, \infty) \times C \to X$ is continuous and maps bounded sets into bounded sets, and $u_t \in C$ is defined by $u_t(\theta) = u(t + \theta)$, $\forall \theta \in [-\tau, 0]$.

Theorem 3.5.1. *Assume that for each $\phi \in C$, equation (3.38) has a unique solution $u(t,\phi)$ on $[0,\infty)$, and solutions of (3.38) are uniformly bounded in the sense that for any bounded subset B_0 of C, there exists a bounded subset $B_1 = B_1(B_0)$ of C such that $u_t(\phi) \in B_1$ for all $\phi \in B_0$ and $t \geq 0$. Then for any given $r > 0$, there exists an equivalent norm $\|\cdot\|_r^*$ on C such that the solution maps $Q(t) := u_t$ of equation (3.38) satisfy $\alpha(Q(t)B) \leq e^{-rt}\alpha(B)$ for any bounded subset B of C and $t \geq 0$, where α is the Kuratowski measure of noncompactness in $(C, \|\cdot\|_r^*)$.*

Proof. Define $\|x\|^* = \sup_{t\geq 0}\|T(t)x\|$, $\forall x \in X$. Then $\|x\| \leq \|x\|^* \leq M\|x\|$, and hence, $\|x\|^*$ is an equivalent norm on X. It is easy to see that

$$\|T(t)x\|^* = \sup_{s\geq 0}\|T(s)T(t)x\| = \sup_{s\geq 0}\|T(s+t)x\| \leq \|x\|^*,\ \ \forall x \in X,\ t \geq 0,$$

which implies that $\|T(t)\|^* \leq 1$ for all $t \geq 0$. Thus, without loss of generality, we assume that $M = 1$.

Let $r > 0$ be given. Note that for each $\phi \in C$, the solution $u(t,\phi)$ of (3.38) satisfies the following integral equation

$$\begin{aligned} u(t) &= \hat{T}(t)\phi(0) + \int_0^t \hat{T}(t-s)\hat{F}(s,u_s)ds, \qquad t \geq 0,\\ u_0 &= \phi \in C, \end{aligned} \tag{3.39}$$

where $\hat{T}(t) = e^{-rt}T(t)$ and $\hat{F}(t,\varphi) = r\varphi(0) + F(t,\varphi)$, $\forall t \geq 0$, $\varphi \in C$. Then $\hat{T}(t)$ is also a C_0-semigroup on X and $\|\hat{T}(t)\| \leq e^{-rt}$, $\forall t \geq 0$. Let $h(\theta) = e^{-r\theta}, \forall\ \theta \in [-\tau, 0]$, and define

$$\|\phi\|_r^* = \sup_{-\tau\leq\theta\leq 0}\frac{\|\phi(\theta)\|_X}{h(\theta)},\ \ \forall\ \phi \in C.$$

Then $\frac{1}{h(-\tau)}\|\phi\|_C \leq \|\phi\|_r^* \leq \|\phi\|_C$, and hence $\|\cdot\|_r^*$ is equivalent to $\|\cdot\|_C$. Clearly, $\|\phi(0)\|_X \leq \|\phi\|_r^*$, $\forall \phi \in C$. Define

$$(L(t)\phi)(\theta) = \begin{cases} \hat{T}(t+\theta)\phi(0), & t+\theta > 0,\\ \phi(t+\theta), & t+\theta \leq 0, \end{cases}$$

and

$$(\bar{Q}(t)\phi)(\theta) = \begin{cases} \int_0^{t+\theta}\hat{T}(t+\theta-s)\hat{F}(s,u_s(\phi))ds, & t+\theta > 0,\\ 0, & t+\theta \leq 0. \end{cases}$$

Thus, $Q(t)\phi = L(t)\phi + \bar{Q}(t)\phi, \forall\ t \geq 0, \phi \in C$, that is, $Q(t) = L(t) + \bar{Q}(t)$, $\forall\ t \geq 0$.

We first show that $L(t)$ is an α-contraction on $(C, \|\cdot\|_r^*)$ for each $t > 0$. It is easy to see that $L(t)$ is compact for each $t > \tau$. Without loss of generality, we may assume that $t \in (0,\tau]$ is fixed. For any $\phi \in C$, we have

$$
\begin{aligned}
\|L(t)\phi\|_r^* &= \sup_{-\tau\le\theta\le 0} \frac{\|(L(t)\phi)\|_X}{h(\theta)} \\
&\le \max\left\{ \sup_{-\tau\le\theta\le -t} \frac{\|\phi(t+\theta)\|_X}{h(t+\theta)} \frac{h(t+\theta)}{h(\theta)}, \quad \sup_{-t\le\theta\le 0} \frac{\|\hat{T}(t+\theta)\phi(0)\|_X}{h(\theta)} \right\} \\
&\le \max\left\{ e^{-rt}\|\phi\|_r^*, \quad \sup_{-t\le\theta\le 0} \frac{e^{-r(t+\theta)}\|\phi(0)\|_X}{h(\theta)} \right\} \\
&= \max\left\{ e^{-rt}\|\phi\|_r^*,\ e^{-rt}\|\phi(0)\|_X \right\} \le e^{-rt}\|\phi\|_r^*,
\end{aligned}
$$

which implies that $\alpha(L(t)B) \le e^{-rt}\alpha(B)$ for any bounded subset B of C. Thus, this contraction property holds true for all $t > 0$.

Next we prove that $\bar{Q}(t) : C \to C$ is compact for each $t > 0$. Let $t > 0$ and the bounded subset B of C be given. By the uniform boundedness of solutions, there exists a real number $K > 0$ such that $\|\hat{F}(s, u_s(\phi))\|_X \le K$, $\forall s \in [0,t]$, $\phi \in B$. It then follows that $\bar{Q}(t)B$ is bounded in C. We only need to show that $\bar{Q}(t)B$ is precompact in C. In view of the generalized Arzela–Ascoli theorem for the space $C := C([-\tau,0],X)$, it suffices to prove that (i) for each $\theta \in [-\tau,0]$, the set $\{(\bar{Q}(t)\phi)(\theta) : \phi \in B\}$ is precompact in X; and (ii) the set $\bar{Q}(t)B$ is equi-continuous in $\theta \in [-\tau,0]$. Clearly, statement (i) holds true if $t+\theta \le 0$. In the case where $t+\theta > 0$, for any given $\epsilon \in (0, t+\theta)$, we have

$$
\begin{aligned}
(\bar{Q}(t)\phi)(\theta) &= \int_0^{t+\theta-\epsilon} \hat{T}(t+\theta-s)\hat{F}(s,u_s(\phi))ds \\
&\quad + \int_{t+\theta-\epsilon}^{t+\theta} \hat{T}(t+\theta-s)\hat{F}(s,u_s(\phi))ds \\
&= \hat{T}(\epsilon) \int_0^{t+\theta-\epsilon} \hat{T}(t+\theta-\epsilon-s)\hat{F}(s,u_s(\phi))ds \\
&\quad + \int_{t+\theta-\epsilon}^{t+\theta} \hat{T}(t+\theta-s)\hat{F}(s,u_s(\phi))ds.
\end{aligned}
$$

Define

$$
S_1 := \left\{ \hat{T}(\epsilon) \int_0^{t+\theta-\epsilon} \hat{T}(t+\theta-\epsilon-s)\hat{F}(s,u_s(\phi))ds : \phi \in B \right\}
$$

and

$$
S_2 := \left\{ \int_{t+\theta-\epsilon}^{t+\theta} \hat{T}(t+\theta-s)\hat{F}(s,u_s(\phi))ds : \phi \in B \right\}.
$$

Let $\hat{\alpha}$ be the Kuratowski measure of noncompactness in X. Since $\hat{T}(\epsilon)$ is compact, it follows that

$$
\hat{\alpha}\left(\{(\bar{Q}(t)\phi)(\theta) : \phi \in B\} \right) \le \hat{\alpha}(S_1) + \hat{\alpha}(S_2) \le 0 + 2K\epsilon = 2K\epsilon.
$$

Letting $\epsilon \to 0^+$, we obtain $\hat{\alpha}\left(\{(\bar{Q}(t)\phi)(\theta) : \phi \in B\}\right) = 0$, which implies that the set $\{(\bar{Q}(t)\phi)(\theta) : \phi \in B\}$ is precompact in X. It remains to verify statement (ii). Since $\hat{T}(s)$ is compact for each $s > 0$, $\hat{T}(s)$ is continuous in the uniform operator topology for $s > 0$ (see [272, Theorem 2.3.2]). It then follows that for any $\epsilon \in (0, t)$, there exists a $\delta = \delta(\epsilon) < \epsilon$ such that

$$\|\hat{T}(s_1) - \hat{T}(s_2)\| < \epsilon, \quad \forall s_1, s_2 \in [\epsilon, t] \text{ with } |s_1 - s_2| < \delta. \tag{3.40}$$

We first consider the case where $t \in (0, \tau]$. It is easy to see that

$$\|(\bar{Q}(t)\phi)(\theta)\|_X \le K(t+\theta) \le K\epsilon,\ \forall \theta \in [-t, -t+\epsilon],\ \phi \in B. \tag{3.41}$$

For any $\phi \in B$ and $\theta_1, \theta_2 \in [-t+\epsilon, 0]$ with $0 < \theta_2 - \theta_1 < \delta$, it follows from (3.40) that

$$\begin{aligned}
&\left\|(\bar{Q}(t)\phi)(\theta_2) - (\bar{Q}(t)\phi)(\theta_1)\right\|_X \\
&= \left\|\int_0^{t-\epsilon+\theta_1} (\hat{T}(t+\theta_2-s) - \hat{T}(t+\theta_1-s))\hat{F}(s, u_s(\phi))ds\right\|_X \\
&\quad + \left\|\int_{t-\epsilon+\theta_1}^{t+\theta_2} \hat{T}(t+\theta_2-s)\hat{F}(s, u_s(\phi))ds\right\|_X \\
&\quad + \left\|-\int_{t-\epsilon+\theta_1}^{t+\theta_1} \hat{T}(t+\theta_1-s)\hat{F}(s, u_s(\phi))ds\right\|_X \\
&\le \epsilon K t + K(\theta_2 - \theta_1 + \epsilon) + K\epsilon \\
&< (t+3)K\epsilon.
\end{aligned} \tag{3.42}$$

Combining (3.41) and (3.42), we then obtain

$$\|(\bar{Q}(t)\phi)(\theta_2) - (\bar{Q}(t)\phi)(\theta_1)\|_X < 2K\epsilon + (t+3)K\epsilon = (t+5)K\epsilon,$$

for all $\theta_1, \theta_2 \in [-t, 0]$ with $0 \le \theta_2 - \theta_1 < \delta$. Since $(\bar{Q}(t)\phi)(\theta) = 0, \forall \theta \in [-\tau, -t]$, it follows that $\bar{Q}(t)B$ is equi-continuous in $\theta \in [-\tau, 0]$. In the case where $t > \tau$, for any $\epsilon \in (0, t-\tau)$, the estimate in (3.42) implies that

$$\|(\bar{Q}(t)\phi)(\theta_2) - (\bar{Q}(t)\phi)(\theta_1)\|_X < (t+3)K\epsilon,$$

for all $\theta_1, \theta_2 \in [-\tau, 0]$ with $0 \le \theta_2 - \theta_1 < \delta$, and $\phi \in B$. Thus, $\bar{Q}(t)B$ is equi-continuous in $\theta \in [-\tau, 0]$. It then follows that $\bar{Q}(t) : C \to C$ is compact for each $t > 0$.

Consequently, for any $t > 0$ and any bounded subset B of C, we have

$$\alpha(Q(t)B) \le \alpha(L(t)B) + \alpha(\bar{Q}(t)B) \le e^{-rt}\alpha(B).$$

This completes the proof. ∎

As an application example, we consider the following ω-periodic reaction–diffusion system with time delay

$$\begin{cases} \frac{\partial u}{\partial t} = D\triangle u + f(t, u_t), & x \in \Omega,\ t > 0, \\ \frac{\partial u}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \end{cases} \tag{3.43}$$

where $D = diag\,(d_1, \dots, d_m)$ with each $d_i > 0$, $\Omega \subset \mathbb{R}^n$ is a bounded domain with the smooth boundary $\partial\Omega$, and $f(t, \phi)$ is ω-periodic in $t \in [0, \infty)$ for some $\omega > 0$. Let $Y := C(\bar{\Omega}, \mathbb{R}^m)$ and assume that f is continuous and maps bounded subsets of $[0, \infty) \times C([-\tau, 0], Y)$ into bounded subsets of Y. Let $T(t)$ be the semigroup on Y generated by $\frac{\partial u(t,x)}{\partial t} = D\triangle u(t, x)$ subject to the boundary condition $\frac{\partial u}{\partial \nu} = 0$. It is easy to see that $\|T(t)\| \le 1, \forall t \ge 0$. By Theorem 3.5.1, we then have the following result.

Theorem 3.5.2. *Assume that solutions of system (3.43) exist uniquely on $[0, \infty)$ for any initial data in $C := C([-\tau, 0], Y)$ and are uniformly bounded. Then for each $r > 0$, there exists an equivalent norm $\|\cdot\|_r^*$ on C such that for each $t > 0$, the solution map $Q(t) = u_t$ of system (3.43) is an α-contraction on $(C, \|\cdot\|_r^*)$ with the contraction constant being e^{-rt}.*

Remark 3.5.1. By using the theory of evolution operators (see, e.g., [152, Section II.11] and [272, Section 5.6]), we may extend Theorem 3.5.1 to the abstract functional differential equation $\frac{du(t)}{dt} = A(t)u(t) + F(t, u_t)$ with $u_0 = \phi \in C$ under appropriate assumptions.

3.6 Notes

Theorem 3.1.1 is due to Zhao [430]. Subsection 3.1.2 is taken from Zhao [432]. The notion of periodic semiflows was introduced by Hale and Lopes [143]. Hess [152, Theorem 28.1] established threshold dynamics for a periodic parabolic logistic equation, that is, equation (3.7) with $f(x, t, u) = u[m(x, t) - b(x, t)u]$. Results similar to the second conclusion of Theorem 3.1.6 were proved by Cantrell and Cosner [50, Theorems 2.1 and 2.3] and [51, Theorem 2.4 with Corollary 3.3] for a diffusive logistic equation subject to the Dirichlet boundary condition under the assumption that there exists $K_0 > 0$ such that $F(x, K_0) \le 0$, $\forall x \in \overline{\Omega}$. In the noncritical case (i.e., $\lambda_0(F(\phi(x))) \ne 1$), Hsu and Waltman [171, Theorems 3.1 and 3.2] obtained Proposition 3.1.1 for system (3.13) with F being Michaelis–Menten–Monod response functions.

Section 3.2 is adapted from Zhao [433], except that Proposition 3.2.4 is modified from Zhao [434, Section 2]. Asymptotically autonomous semiflows were studied extensively by Thieme [364, 366, 367], Mischaikow, Smith and Thieme [249], Benaïm and Hirsch [35]. The global dynamics in asymptotically periodic parabolic Fisher equations was established by Hess [153]. A set of sufficient conditions for uniform persistence in asymptotically periodic parabolic predator–prey systems was obtained by Zhao [433].

Sections 3.3 and 3.4 are taken from Zhao [438] and [436], respectively. Under appropriate assumptions, Shen and Yi [312, Theorem 4.1] obtained global attractivity of a unique positive almost periodic solution for equation (3.34) subject to the Neumann boundary condition. Thieme [368, 369] proved that weak uniform persistence implies uniform persistence for nonautonomous semiflows. The skew-product semiflow approach to nonautonomous evolutionary systems has become standard; see, e.g., Sell [303], Dafermos [79], LaSalle [212], Hale [141], Shen and Yi [311], and the references therein. Nussbaum [260] and Thieme [363] studied weak ergodicity and asymptotic proportionality in monotone and sublinear nonautonomous semiflows.

Hale [141, Theorem 4.1.1] first proved that the solution maps of FDEs on $\mathbb{R}^n$ are α-contractions in an equivalent norm on $C([-\tau, 0], \mathbb{R}^n)$. However, the decomposition technique for solution maps in [141, Theorem 4.1.1] cannot be used to prove the α-contraction property for the solution maps of FDEs on an infinite-dimensional Banach space X. This is because bounded sets in such X are not precompact in general. Liang and Zhao [226, pages 879–880] employed this decomposition to show that the solution maps of time-delayed reaction–diffusion systems are conditional α-contractions (see (A3)$'$ in [226, Remark 4.1]). Theorem 3.5.1 is a nontrivial generalization of [141, Theorem 4.1.1] to abstract FDEs since a quite different decomposition for solution maps was utilized in our proof.

4

A Discrete-Time Chemostat Model

The chemostat is an important laboratory apparatus used for the continuous culture of microorganisms. In ecology it is often viewed as a model of a simple lake system, of the wastewater treatment process, or of biological waste decomposition. Mathematical models of microbial growth and competition for a limiting substrate in a chemostat have played a central role in population biology. See [334] for a treatment of chemostat models. However, the classical model ignores the size structure of the population and the observation that many microbes roughly double in size before dividing. Size-structured chemostat models formulated by Metz and Diekmann [248] and by Cushing [76] lead to hyperbolic partial differential equations with nonlocal boundary conditions. A conceptually simpler approach to modeling size structure was taken by Gage, Williams and Horton [127], who formulated what is now referred to as a nonlinear matrix model for the evolution, in discrete-time steps, of a finite set of biomass classes. Smith [327] modified this model and showed that competitive exclusion holds for two competing microbial populations. The purpose of the present chapter is to give a thorough mathematical analysis of this model of any number of competing populations.

In Section 4.1 we introduce the model under some appropriate assumptions, and derive a conservation principle for the total nutrient. In Section 4.2 we show that the model leads to a lower-dimensional system of difference equations for the total biomass of each population and that conservation of total nutrient allows a further reduction to a limiting system where the nutrient is effectively eliminated. The global dynamics and chain transitive sets of the resulting limiting system are analyzed. In Section 4.3 we prove that competitive exclusion holds for the full size-structured system. The winner is the population able to grow at the lowest nutrient concentration.

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4.1 The Model

In order to formulate a discrete, size-structured model of m-species competition for a limiting nutrient in a chemostat, a simple open system with a constant input of fresh nutrient at concentration $S^0 \in (0, \infty)$ at rate $E \in (0, 1)$ and a constant removal of nutrient and organisms at rate E, we make the following biological assumptions (see Gage et al. [127]):

(1) An organism approximately doubles in size as it moves from its smallest to its largest size class;
(2) Cells divide into two daughter cells of approximately equal size;
(3) Cell growth is exponential if the concentration of the limiting nutrient remains constant;
(4) The average nutrient uptake rate per unit biomass is constant across all size classes;
(5) Respiration and mortality are negligible;
(6) Washout is constant across all size classes per unit biomass;
(7) The only organism-to-organism interaction is mediated through the nutrient concentration.

For the ith species we choose r_i size classes such that the average biomass in class j, $1 \le j \le r_i$, is $M_i^{j-1} b_i$, where $M_i = 2^{1/r_i}$ and b_i is the average biomass of a newly divided cell. Let $x^i = (y_i^1, y_i^2, \dots, y_i^{r_i}) \in \mathbb{R}^{r_i}$, where y_i^j denotes the biomass in size class j, $1 \le j \le r_i$. Then the number of cells in size class j is $n_i(j) = y_i^j/(M_i^{j-1} b_i)$. Let S be the nutrient concentration, and $f_i(S)$ the nutrient uptake rate computed per unit biomass per iteration period. It is assumed that population biomass is measured in nutrient-equivalent units so that $f_i(S)$ is also the rate of increase in biomass per iteration period per unit biomass. Thus $y_i^j f_i(S)/(M_i^j b_i - M_i^{j-1} b_i) = n_i(j) f_i(S)(M_i - 1)^{-1}$ is the number of individuals in size class j that can gain enough biomass during an iteration period to move up to size class $j+1$, and hence $P_i = f_i(S)(M_i - 1)^{-1}$ is the proportion of individuals that would move from size class j to size class $j+1$ per iteration period in the absence of washout. Accounting for the ratio M_i of cell size in class $j+1$ to cell size in class j and the washout rate E, the proportion of biomass in class j projected into class $j+1$ over an iteration period is $(1-E)M_i P_i$. The proportion $(1-E)(1-P_i)$ of individuals remains in class j.

The discrete-time, size-structured model of m-species competition in the chemostat is then given by

$$\begin{aligned} x_{n+1}^i &= A_i(S_n) x_n^i, \qquad 1 \le i \le m, \\ S_{n+1} &= (1-E)\left(S_n - \sum_{j=1}^m f_j(S_n) U_n^j\right) + ES^0, \end{aligned} \tag{4.1}$$

where the vector $x_n^i \in \mathbb{R}_+^{r_i}$, $r_i > 0$, gives the distribution of biomass (in nutrient-equivalent units) of the ith microbial population among r_i size classes at the nth time step, and S_n is the nutrient concentration at the nth time step. The total biomass of the ith population at the nth time step is given by $U_n^i = x_n^i \cdot \mathbf{1}$, the scalar product of x_n^i and $\mathbf{1} = (1, \dots, 1) \in \mathbb{R}^{r_i}$. The nutrient uptake rate for the ith population is $f_i(S)$, and the $r_i \times r_i$ projection matrix for that population is given by

$$A_i(S) = (1-E)\begin{bmatrix} 1-P_i & 0 & \cdots & & & M_iP_i \\ M_iP_i & 1-P_i & 0 & & \cdots & 0 \\ 0 & M_iP_i & 1-P_i & 0 & \cdots & 0 \\ & & \ddots & & & \\ 0 & \cdots & & 0 & M_iP_i & 1-P_i \end{bmatrix}, \tag{4.2}$$

where

$$M_i = 2^{1/r_i}, \quad P_i = f_i(S)(M_i-1)^{-1}, \quad 1 \le i \le m.$$

Throughout this chapter, we assume that

(H1) For each $1 \le i \le m$, $f_i \in C^1(\mathbb{R}_+, \mathbb{R}), f_i(0) = 0, f_i'(S) > 0, f_i'(S) \le f_i'(0)$, $S \in \mathbb{R}_+$;

(H2) $f_i(+\infty)(M_i-1)^{-1} < 1, 1 \le i \le m$, and there exist $W > S^0$ and $\eta \in (0,1)$ such that $W\sum_{i=1}^m f_i'(0) < \eta$.

Clearly, (H1) and the mean value theorem imply that $f_i(S) \le f_i'(0)S$, for $S \ge 0$. The prototypical nutrient uptake rate, which satisfies (H1), is the Michaelis–Menten function

$$f(S) = \frac{mS}{a+S}, \qquad S \in \mathbb{R}_+,$$

where m is the maximum uptake rate and $a > 0$ is the Michaelis-Menten (or half saturation) constant. In (H2), W is an appropriate upper bound on the total biomass of all species and the nutrient, and η an acceptable tolerance. We refer to [327] for a discussion of subtle issues involving the time step and growth rates in order that the model make biological sense.

Using the fact that $\mathbf{1} = (1, \dots, 1) \in \mathbb{R}^{r_i}$ is the Perron–Frobenius (principal) eigenvector of the nonnegative, irreducible, and primitive matrix $A_i(S)$ associated with its Perron–Frobenius (principal) eigenvalue $(1-E)(1+f_i(S))$ (see, e.g., [77, Theorem 1.1.1]), it follows that the total biomass $U_n^i = x_n^i \cdot \mathbf{1}$ satisfies the difference equations

$$U_{n+1}^i = (1-E)(1+f_i(S_n))U_n^i, \quad 1 \le i \le m. \tag{4.3}$$

Let $\Sigma_n = S_n + \sum_{i=1}^m U_n^i$, $n \ge 0$. Equation (4.3) and the second equation of (4.1) imply that the evolution of Σ_n can be decoupled from the rest of the system

$$\Sigma_{n+1} = (1-E)\Sigma_n + ES^0, \quad n \ge 0, \tag{4.4}$$

resulting in

$$\Sigma_n = S^0 - (1-E)^n(S^0 - \Sigma_0), \quad n \ge 0. \tag{4.5}$$

Clearly, (4.5) implies $\lim_{n\to\infty} \Sigma_n = S^0$, which is a conservation principle for the total nutrient.

4.2 The Limiting System

For the dynamics of system (4.1), we may consider its population level dynamics, which is described by equation (4.3) and the second equation in (4.1). In view of $S_n = \Sigma_n - \sum_{i=1}^m U_n^i$ and $\lim_{n\to\infty} \Sigma_n = S^0$, we may pass to the limiting system

$$U_{n+1}^i = (1-E)\left(1 + f_i(S^0 - \sum_{j=1}^m U_n^j)\right) U_n^i, \quad 1 \le i \le m, \tag{4.6}$$

with the initial value $(U_0^1, \dots, U_0^m)$ in the domain

$$D := \left\{(U^1, \dots, U^m) \in \mathbb{R}_+^m : \quad \sum_{i=1}^m U^i \le S^0\right\}.$$

Denote by F the mapping determined by the right side of (4.6), so we have

$$(U_{n+1}^1, \dots, U_{n+1}^m) = F(U_n^1, \dots, U_n^m).$$

Then the following result implies that D is positively invariant for system (4.6), and hence (4.6) defines a discrete dynamical system on D.

Lemma 4.2.1. *$F(D) \subset \left\{(U^1, \dots, U^m) \in \mathbb{R}_+^m : \sum_{i=1}^m U^i \le (1-E)S^0\right\} \subset D$.*

Proof. For any $(U^1, \dots, U^m) \in D$, let $(V^1, \dots, V^m) = F(U^1, \dots, U^m)$ and $t = \sum_{i=1}^m U^i$. Then $V^i \ge 0$, $1 \le i \le m$, and $t \in [0, S^0]$. If $t > 0$, then

$$\begin{aligned}
\sum_{i=1}^m V^i &= (1-E)t\left(1 + \sum_{i=1}^m f_i(S^0 - t)\frac{U^i}{t}\right) \\
&\le (1-E)t\left(1 + \max_{1\le i\le m}\{f_i(S^0 - t)\}\right) \\
&\le (1-E)\max_{1\le i\le m}\{(1 + f_i(S^0 - t))t\}.
\end{aligned} \tag{4.7}$$

By (H1) and (H2), we have

$$\begin{aligned}
\frac{d}{dt}\big((1 + f_i(S^0 - t))t\big) &= 1 + f_i(S^0 - t) - f_i'(S^0 - t)t \\
&\ge 1 - f_i'(0)W + f_i(S^0 - t) > 1 - \eta > 0.
\end{aligned} \tag{4.8}$$

Consequently, the function $(1 + f_i(S^0 - t))t$ is strictly increasing with respect to $t \in [0, S^0]$, attaining its maximum value S^0 at $t = S^0$. Thus (4.7) yields $\sum_{i=1}^m V^i \le (1-E)S^0$. ∎

We define the break-even nutrient concentration for ith population as the solution λ_i of

$$(1-E)(1+f_i(S)) = 1,$$

where $\lambda_i = +\infty$ if no such solution exists. If the supplied nutrient does not exceed the nutrient requirements of a population, then it is eliminated.

Lemma 4.2.2. *If $\lambda_i \geq S^0$, then $\lim_{n\to\infty} U_n^i = 0$ for every solution $(U_n^1, \ldots, U_n^m)$ of (4.6).*

Proof. $U_{n+1}^i \leq (1-E)(1+f_i(S^0 - U_n^i))U_n^i \equiv g(U_n^i)$, so, since g is increasing by (4.8), $U_n^i \leq V_n^i$, where $V_{n+1}^i = g(V_n^i)$ and $V_0^i = U_0^i$. We show that $V_n^i \to 0$. Our hypothesis ensures that $(1-E)(1+f_i(S^0 - U)) < 1$ if $U \in (0, S^0]$, so $g(U) < U$ for $U \in (0, S^0]$. Consequently, $V_{n+1}^i < V_n^i$ if $V_0^i > 0$, so V_n^i converges to the only fixed point of g, namely, zero. ∎

In view of (4.3), the biomass of a population can grow at a lower nutrient concentration than the biomass of the other populations, and consequently, we expect that the population with the lowest nutrient concentration is the superior competitor. The following result on the global dynamics of system (4.6) is, therefore, plausible.

Theorem 4.2.1. *Assume that $\lambda_1 < S^0$, and $\lambda_1 < \lambda_i$ for all $i \geq 2$. Then for any $(U_0^1, \ldots, U_0^m) \in D$ with $U_0^1 > 0$, the solution of (4.6) satisfies*

$$\lim_{n\to\infty} (U_n^1, U_n^2, \ldots, U_n^m) = (S^0 - \lambda_1, 0, \ldots, 0).$$

Proof. For any $(U^1, \ldots, U^m) \in D$, let $(V^1, \ldots, V^m) = F(U^1, \ldots, U^m)$. Define

$$D_1 := \left\{ (U^1, \ldots, U^m) \in D : \quad \sum_{i=1}^m U^i \geq S^0 - \lambda_1 \right\}$$

and $W_1(U^1, \ldots, U^m) = \sum_{i=1}^m U^i$. If $(U^1, \ldots, U^m) \in D_1$, then for system (4.6),

$$\begin{aligned}
\dot{W}_1(U^1, \ldots, U^m) &:= W_1(F(U^1, \ldots, U^m)) - W_1(U^1, \ldots, U^m) \\
&= \sum_{i=1}^m V^i - \sum_{i=1}^m U^i \\
&= \sum_{i=1}^m \left[(1-E) \left(1 + f_i(S^0 - \sum_{j=1}^m U^j) \right) - 1 \right] U^i \\
&\leq \sum_{i=1}^m \left[(1-E)(1+f_i(\lambda_1)) - 1 \right] U^i \\
&= \sum_{i=2}^m \left[(1-E)(1+f_i(\lambda_1)) - 1 \right] U^i \leq 0. \qquad (4.9)
\end{aligned}$$

Thus W_1 is a Liapunov function of (4.6) on D_1 (see Definition 1.1.1). By the fact that each term in large brackets in the third line of (4.9) is nonpositive in D_1, it follows that

$$\begin{aligned} E_1 &:= \{(U^1, \ldots, U^m) \in D_1 : \quad \dot{W}_1(U^1, \ldots, U^m) = 0\} \\ &= \{(S^0 - \lambda_1, 0, \ldots, 0)\}. \end{aligned} \tag{4.10}$$

Let $u_n = (U_n^1, \ldots, U_n^m)$ be the solution of (4.6) with $u_0 \in D$, and let $\omega(u_0)$ be the omega limit of the positive orbit $\gamma^+(u_0) := \{u_n; n \geq 0\}$. If $\gamma^+(u_0) \subset D_1$, then the LaSalle invariance principle (see Theorem 1.1.1) implies that $\omega(u_0) = (S^0 - \lambda_1, 0, \ldots, 0)$.

Define

$$D_2 := \left\{ (U^1, \ldots, U^m) \in \mathbb{R}_+^m : \quad \sum_{i=1}^m U^i \leq S^0 - \lambda_1 \right\}.$$

Clearly, $D_2 \subset D$. By (4.8), when $t = S^0 - \lambda_1$ the strictly increasing function $(1+f_i(S^0-t))t$ on $[0, S^0-\lambda_1]$ attains its maximum value $(1+f_i(\lambda_1))(S^0-\lambda_1)$. Note that $(1 + f_i(\lambda_1)) \leq (1 + f_i(\lambda_i)) = 1/(1 - E)$, $1 \leq i \leq m$. Then (4.7) implies that $\sum_{i=1}^m V^i \leq S^0 - \lambda_1$. Thus $(V^1, \ldots, V^m) \in D_2$, and hence D_2 is positively invariant for system (4.6). Define $W_2(U^1, \ldots, U^m) = -U^1$. If $(U^1, \ldots, U^m) \in D_2$, then for system (4.6),

$$\begin{aligned} \dot{W}_2(U^1, \ldots, U^m) &:= W_2(F(U^1, \ldots, U^m)) - W_2(U^1, \ldots, U^m) \\ &= -V^1 - (-U^1) = U^1 - V^1 \\ &= U^1 - (1 - E) \left(1 + f_1 \left(S^0 - \sum_{j=1}^m U^j \right) \right) U^1 \\ &\leq U^1 \left[1 - (1 - E)(1 + f_1(\lambda_1) \right] = 0. \end{aligned} \tag{4.11}$$

Thus W_2 is a Liapunov function of (4.6) on D_2. Let

$$L := \left\{ (U^1, \ldots, U^m) \in \mathbb{R}_+^m : \quad U^1 = 0, \sum_{i=1}^m U^i < S^0 - \lambda_1 \right\},$$

and

$$\Delta := \left\{ (U^1, \ldots, U^m) \in \mathbb{R}_+^m : \quad \sum_{i=1}^m U^i = S^0 - \lambda_1 \right\}.$$

By (4.11), we then have

$$E_2 := \{(U^1, \ldots, U^m) \in D_2 : \quad \dot{W}_2(U^1, \ldots, U^m) = 0\} = L \cup \Delta. \tag{4.12}$$

If $u_0 = (U_0^1, \ldots, U_0^m) \in D_2$ with $U_0^1 > 0$, then $\gamma^+(u_0) \subset D_2$. By the LaSalle invariance principle (see Theorem 1.1.1), $\omega(u_0) \subset L \cup \Delta$. Note that $0 \geq$

$\dot{W}_2(u_n) = W_2(u_{n+1}) - W_2(u_n) = U_n^1 - U_{n+1}^1, \forall n \geq 0$. Then we get $U_{n+1}^1 \geq U_n^1$, $\forall n \geq 0$, and hence $U_n^1 \geq U_0^1 > 0$, $\forall n \geq 0$. Thus $\omega(u_0) \subset \Delta$. Clearly, (4.10) implies that for any $u \in \Delta \setminus \{(S^0 - \lambda_1, 0, \ldots, 0)\}$, we have $\dot{W}_1(u) < 0$, and hence

$$F(u) \subset \left\{ (U^1, \ldots, U^m) \in D : \quad \sum_{i=1}^{m} U^i < S^0 - \lambda_1 \right\}.$$

So $(S^0 - \lambda_1, 0, \ldots, 0)$ is the only invariant set in Δ. Thus $\omega(u_0) = (S^0 - \lambda_1, 0, \ldots, 0)$.

For any $u_0 = (U_0^1, \ldots, U_0^m) \in D$ with $U_0^1 > 0$, let $u_n = (U_n^1, \ldots, U_n^1)$, $n \geq 0$, be the solution of (4.6). Clearly, $U_n^1 > 0$, $\forall n \geq 0$, and *either* $\gamma^+(u_0) \subset D_1$, *or* there is an $n_0 \geq 0$ such that $u_{n_0} \in D_2$. Note that $\omega(u_0) = \omega(u_{n_0})$. Then in either case, by what we have proved above, $\omega(u_0) = (S^0 - \lambda_1, 0, \ldots, 0)$, and hence $\lim_{n\to\infty} u_n = (S^0 - \lambda_1, 0, \ldots, 0)$. This completes the proof. ∎

Theorem 4.2.2. *Assume that $\lambda_1 < \lambda_2 < \ldots < \lambda_m$. Then every compact internally chain transitive set for F is a fixed point of F itself.*

Proof. Let $e_0 = \mathbf{0} \in \mathbb{R}^m$, and in the case that $\lambda_i < S^0$, let $e_i = (0, \ldots, 0, S^0 - \lambda_i, 0, \ldots, 0) \in \mathbb{R}^m$ with its ith component being $(S^0 - \lambda_i)$ and the others being 0. Clearly, all these e_i are fixed points of $F : D \to D$. For any $v_0 \in D$ with $v_0 \neq e_0$, there exists $1 \leq k \leq m$ such that $v_0 = (0, \ldots, 0, V_0^k, \ldots, V_0^m)$ with $V_0^k > 0$. Let $v_n = (V_n^1, \ldots, V_n^m)$ be the solution of (4.6). Clearly, $V_n^i = 0$, $\forall n \geq 0, 1 \leq i < k$. If $\lambda_k < S^0$, then Theorem 4.2.1 implies that $\lim_{n\to\infty} v_n = e_k$. If $\lambda_k \geq S^0$, then $\lambda_i \geq S^0$, $\forall i \geq k$, and hence Lemma 4.2.2 implies that $\lim_{n\to\infty} v_n = e_0$. This convergence result also implies that each e_i is an isolated invariant set in $D \subset \mathbb{R}^m$ for F, and that no subset of e_i's forms a cyclic chain in D. By a convergence theorem (see Theorem 1.2.2), any compact internally chain transitive set for F is a fixed point of F. ∎

4.3 Global Dynamics

In this section we first lift the result for the limiting system (4.6) to the reduced system at the total population level (see (4.13) below), and then consider the global dynamics of the full size-structured system (4.1).

The population level dynamics are described by

$$\begin{aligned} U_{n+1}^i &= (1-E)\left(1 + f_i(S_n)\right) U_n^i, \quad 1 \leq i \leq m, \\ S_{n+1} &= (1-E)\left(S_n - \sum_{j=1}^{m} f_j(S_n) U_n^j\right) + ES^0, \end{aligned} \tag{4.13}$$

with the initial value $(U_0^1, \ldots, U_0^m, S_0)$ in the domain

$$\Omega := \left\{ (U^1, \ldots, U^m, S) \in \mathbb{R}_+^{m+1} : \quad \sum_{i=1}^{m} U^i + S \leq W \right\}.$$

Denote by G the mapping determined by the right side of (4.13), so we have

$$(U^1_{n+1}, \ldots, U^m_{n+1}, S_{n+1}) = G(U^1_n, \ldots, U^m_n, S_n).$$

If $(U^1, \ldots, U^m, S) \in \Omega$, then

$$S - \sum_{i=1}^{m} f_i(S)U^i \geq S\left(1 - \sum_{i=1}^{m} W f_i'(0)\right) > (1-\eta)S \geq 0.$$

By the conservation principle (4.4) and the fact that $S^0 < W$, it then follows that $G(U^1, \ldots, U^m, S) \in \Omega$, and hence $G(\Omega) \subset \Omega$. Thus system (4.13) defines a discrete dynamical system on Ω. The following result describes the competitive exclusion dynamics of (4.13).

Theorem 4.3.1. *Assume that $\lambda_1 < S^0$ and $\lambda_1 < \lambda_2 < \ldots < \lambda_m$. Then for any $(U^1_0, \ldots, U^m_0, S_0) \in \Omega$ with $U^1_0 > 0$, the solution of (4.13) satisfies*

$$\lim_{n\to\infty} (U^1_n, U^2_n, \ldots, U^m_n, S_n) = (S^0 - \lambda_1, 0, \ldots, 0, \lambda_1).$$

Proof. Fix $(U^1_0, \ldots, U^m_0, S_0) \in \Omega$ with $U^1_0 > 0$, and let $(U^1_n, \ldots, U^m_n, S_n)$ be the solution of system (4.13). Clearly, $U^1_n > 0, \forall n \geq 0$. Let $\Sigma_n = S_n + \sum_{i=1}^m U^i_n$, $n \geq 0$. By (4.4), $u_n = (U^1_n, \ldots, U^m_n, \Sigma_n)$ satisfies the following system

$$\begin{aligned} U^i_{n+1} =& (1-E)\left(1 + f_i(\Sigma_n - \sum_{j=1}^{m} U^j_n)\right) U^i_n, \quad 1 \leq i \leq m, \\ \Sigma_{n+1} =& (1-E)\Sigma_n + ES^0. \end{aligned} \tag{4.14}$$

Let $\omega = \omega(u_0)$ be the omega limit set of the positive orbit $\gamma^+(u_0)$ of (4.14). Then

$$\omega \subset \left\{(U^1, \ldots, U^m, \Sigma) \in \mathbb{R}^{m+1}_+ : \quad \Sigma \leq W\right\}.$$

Note that $\Sigma_n - \sum_{i=1}^m U^i_n = S_n \geq 0$, $n \geq 0$, and $\lim_{n\to\infty} \Sigma_n = S^0$. It then follows that for any $(U^1, \ldots, U^m, \Sigma) \in \omega$, we have $\sum_{i=1}^m U^i \leq \Sigma$ and $\Sigma = S^0$. Thus, there exists a set $\tilde{\omega} \subset D$ such that $\omega = \tilde{\omega} \times \{S^0\}$. Denote by H the mapping determined by the right side of (4.14), so $(U^1_{n+1}, \ldots, U^m_{n+1}, \Sigma_{n+1}) = H(U^1_n, \ldots, U^m_n, \Sigma_n)$. By Lemma 1.2.1, ω is a compact, invariant, and internally chain transitive set for H. Moreover,

$$H|_\omega(U^1, \ldots, U^m, S^0) = \left(F(U^1, \ldots, U^m), S^0\right).$$

It then follows that $\tilde{\omega}$ is a compact, invariant, and internally chain transitive set for $F : D \to D$. By Theorem 4.2.2, we get $\tilde{\omega} = e_l$ for some $0 \leq l \leq p$, where p is the maximal index such that $\lambda_p < S^0$, and hence, $\omega = \tilde{\omega} \times \{S^0\} = (e_l, S^0)$. Thus

$$\lim_{n\to\infty} u_n = \lim_{n\to\infty} (U^1_n, \ldots, U^m_n, \Sigma_n) = (e_l, S^0). \tag{4.15}$$

It remains to prove that $l = 1$. Suppose, by contradiction, that $l \neq 1$. Define

$$\delta_l = \begin{cases} \frac{1}{2}\left(1 + (1-E)(1 + f_1(S^0))\right) & \text{if } l = 0, \\ \frac{1}{2}\left(1 + (1-E)(1 + f_1(\lambda_l))\right) & \text{if } l \geq 2. \end{cases}$$

Since $\lambda_1 < S^0$ and $\lambda_l > \lambda_1$ if $l \geq 2$, we have

$$1 < \delta_0 < (1-E)(1 + f_1(S^0)), \text{ and } 1 < \delta_l < (1-E)(1 + f_1(\lambda_l)) \text{ if } l \geq 2.$$

By (4.15), it follows that

$$\lim_{n \to \infty} (1-E)\left(1 + f_1\left(\Sigma_n - \sum_{j=1}^{m} U_n^j\right)\right) = (1-E)(1 + f_1(\lambda_l)) \text{ if } l \geq 2,$$

and

$$\lim_{n \to \infty} (1-E)\left(1 + f_1\left(\Sigma_n - \sum_{j=1}^{m} U_n^j\right)\right) = (1-E)(1 + f_1(S^0)) \text{ if } l = 0.$$

Then there is an $n_0 > 0$ such that

$$(1-E)\left(1 + f_1\left(\Sigma_n - \sum_{j=1}^{m} U_n^j\right)\right) > \delta_l, \quad \forall n \geq n_0,$$

and hence $U_{n+1}^1 \geq \delta_l U_n^1, \quad \forall n \geq n_0$. In view of the fact that $\delta_l > 1$ and $U_n^1 > 0$, $\forall n \geq 0$, we get $\lim_{n \to \infty} U_n^1 = +\infty$, which contradicts the boundedness of $\{U_n^1 : n \geq 0\}$. By (4.15), it then follows that $\lim_{n \to \infty}(U_n^1, \ldots, U_n^m, \Sigma_n) = (e_1, S^0)$, and hence

$$\lim_{n \to \infty} (U_n^1, \ldots, U^n, S_n) = (e_1, \lambda_1) = (S^0 - \lambda_1, 0, \ldots, 0, \lambda_1).$$

This completes the proof. ∎

To get the global dynamics of the full system (4.1), we need the following weak ergodic theorem of Golubitsky, Keeler and Rothschild (see [132, Corollary 3.2]).

Weak Ergodic Theorem *Suppose that T_k is a sequence of nonnegative, irreducible, and primitive $m \times m$ matrices and that $T_k \to T$ as $k \to \infty$, where T is also irreducible and primitive. If e is the Perron–Frobenius eigenvector of T satisfying $e \cdot \mathbf{1} = 1$, and $x_{k+1} = T_k x_k$ is a sequence starting with $x_0 \geq 0$ and $x_0 \neq 0$, then $\frac{x_k}{x_k \cdot \mathbf{1}} \to e$ as $k \to \infty$.*

Let $r = \sum_{i=1}^m r_i$ and set $\Gamma :=$

$$\left\{(x^1, \ldots, x^m, S) \in \mathbb{R}_+^{r+1} : x^i \in \mathbb{R}^{r_i}, 1 \le i \le m, \text{ and } \sum_{i=1}^m x^i \cdot \mathbf{1} + S \le W\right\}.$$

Clearly, the positive invariance of Ω for (4.13) implies that of Γ for (4.1). So (4.1) defines a discrete dynamical system on Γ. The next result shows that the surviving population asymptotically approaches a stable, uniform size distribution.

Theorem 4.3.2. *Assume that $\lambda_1 < S^0$ and $\lambda_1 < \lambda_2 < \ldots < \lambda_m$. Then for any $(x_0^1, \ldots, x_0^m, S_0) \in \Gamma$ with $x_0^1 \neq \mathbf{0}$, the solution of (4.1) satisfies*

$$\lim_{n\to\infty} (x_n^1, x_n^2, \ldots, x_n^m, S_n) = \left(\frac{S^0 - \lambda_1}{r_1}\mathbf{1}, \mathbf{0}, \ldots, \mathbf{0}, \lambda_1\right).$$

Proof. Given $(x_0^1, \ldots, x_0^m, S_0) \in \Gamma$ with $x_0^1 \neq \mathbf{0}$, let $U_n^i = x_n^i \cdot \mathbf{1}, \forall 1 \le i \le m$, $n \ge 0$. Then $(U_0^1, \ldots, U_0^m, S_0) \in \Omega$ with $U_0^1 > 0$. By Theorem 4.3.1, $\lim_{n\to\infty}(U_n^1, U_n^2, \ldots, U_n^m, S_n) = (S^0 - \lambda_1, 0, \ldots, 0, \lambda_1)$. Then $\lim_{n\to\infty} A_i(S_n) = A_i(\lambda_1)$, $1 \le i \le m$. As mentioned in Section 4.1, $A_i(S_n)$ and $A_i(\lambda_1)$ are nonnegative, irreducible, and primitive, and they have $e = \frac{1}{r_i}\mathbf{1}$ as their Perron–Frobenius eigenvectors with $e \cdot \mathbf{1} = 1$. By the aforementioned weak ergodic theorem, we then have

$$\lim_{n\to\infty} \frac{x_n^i}{x_n^i \cdot \mathbf{1}} = \lim_{n\to\infty} \frac{x_n^i}{U_n^i} = e = \frac{1}{r_i}\mathbf{1}, \quad \forall 1 \le i \le m.$$

Since $\lim_{n\to\infty} U_n^1 = S^0 - \lambda_1$ and $\lim_{n\to\infty} U_n^i = 0$, $\forall\, 2 \le i \le m$, we conclude that

$$\lim_{n\to\infty} (x_n^1, x_n^2, \ldots, x_n^m, S_n) = \left(\frac{S^0 - \lambda_1}{r_1}\mathbf{1}, \mathbf{0}, \ldots, \mathbf{0}, \lambda_1\right).$$

This completes the proof. ∎

4.4 Notes

The model (4.1) was formulated by Gage, Williams and Horton [127] and was further developed by Smith [327]. This chapter is adapted from Smith and Zhao [339]. The proof of Theorem 4.2.1 was motivated by a similar LaSalle invariance principle argument in Armstrong and McGehee [18] for the classical chemostat system of ordinary differential equations. Theorems 4.2.1, 4.3.1, and 4.3.2 were proved for the case of two-species competition in [327], where monotonicity and Butler–McGehee lemma arguments were applied. Recently, Arino, Gouzé and Sciandra [17] extended the model (4.1) with $m = 1$ to the case where cell division (and consequently, cell birth) can happen for cells in several biomass classes, the effective size at division being distributed following some probability density, and showed that the model system admits one nonzero globally stable equilibrium. There have been extensive investigations on both discrete and continuous structured population models; see, e.g., Cushing [77] and the references therein.

5

N-Species Competition in a Periodic Chemostat

As we see from the previous chapter, the models of exploitative competition in a well-stirred chemostat operated under constant input and dilution, with competition for a nonreproducing substrate, predict that at most one competitor population avoids extinction. However, the coexistence of competing populations is obvious in nature, and so in order to explain this, it seems necessary to relax at least one of the assumptions in these models. One natural approach is to introduce periodic coefficients to represent, for example, daily or seasonal variations in the environment. The aim of this chapter is to present a general framework to study models of n-species competition in a periodically operated chemostat. Nutrient input, dilution, and species-specific removal rates are all permitted to be periodic (but of commensurate period). Furthermore, each species-specific nutrient uptake function is assumed to be a monotone increasing function of the substrate concentration, but can be periodic as a function of time (but again of commensurate period). Differential species-specific removal rates are also permitted.

In Section 5.1 we discuss periodic weak repellers in periodic and asymptotically periodic Kolmogorov systems of ordinary differential equations. In Section 5.2 a threshold-type result on the global dynamics of scalar asymptotically periodic Kolmogorov equations is first proved, and then single species growth in the periodically operated chemostat is considered. In the case that the species-specific removal rate is permitted to be different from the dilution rate, we obtain sufficient conditions that guarantee the existence of at least one positive periodic solution and ensure that the species is uniformly persistent. On the other hand, when the species-specific removal rate is assumed to be equal to the dilution rate, a threshold-type result for uniform persistence versus global extinction of the species is obtained. In Section 5.3 the n-species competition model in a general periodic chemostat is studied. Sufficient conditions are obtained that guarantee the uniform persistence of all n-species and the existence of at least one positive periodic solution of

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the full system. The special case where the species-specific removal rates of all of the species equal the nutrient dilution rate is also discussed, and an improved result is given when there are only two competing species. Finally, in Section 5.4 the 3-species competition model is studied under the additional assumptions that the species-specific removal rates of all of the species equal the nutrient dilution rate and that the positive periodic solutions to each of the three 2-species subsystems of the limiting 3-species competition system is unique. We determine sufficient conditions, which are more easily satisfied than those given in Section 5.3, that guarantee the uniform persistence of the three interacting species and prove existence of at least one positive periodic solution for the full model system.

5.1 Weak Periodic Repellers

In the applications of the theory of discrete-time semidynamical systems to n-dimensional Kolmogorov periodic and asymptotically periodic biological systems, the dynamics on the boundary prove to be very useful. In this section we discuss a weakly repelling property of semitrivial periodic solutions for these systems.

Consider first n-dimensional Kolmogorov periodic systems

$$\frac{du_i}{dt} = u_i F_{0i}(t, u), \qquad 1 \le i \le n, \tag{5.1}$$

where $u = (u_1, \ldots, u_n) \in \mathbb{R}^n_+$. We assume that $F_0 = (F_{01}, \ldots, F_{0n}) : \mathbb{R}^{n+1}_+ \to \mathbb{R}^n_+$ is continuous and ω-periodic with respect to $t\,(\omega > 0)$, and that the solution $\phi_0(t, u)$ of (5.1) with $\phi_0(0, u) = u$ exists uniquely on $[0, \infty)$. Let $S = \phi_0(\omega, \cdot) : \mathbb{R}^n_+ \to \mathbb{R}^n_+$. Then $S^n(u) = \phi_0(n\omega, u)$, $\forall u \in \mathbb{R}^n_+$.

Lemma 5.1.1. *If for some* $1 \le i \le n$,

$$u^*(t) = (u_1^*(t), \ldots, u_{i-1}^*(t), 0, u_{i+1}^*(t), \ldots, u_n^*(t))$$

is an ω-periodic solution of (5.1) with $u_j^*(0) \ge 0$, $\forall 1 \le j \le n$, $j \ne i$, *and* $u^*(t)$ *satisfies* $\int_0^\omega F_{0i}(t, u^*(t))dt > 0$, *then there exists* $\delta > 0$ *such that*

$$\limsup_{n\to\infty} d(S^n(u), u^*(0)) \ge \delta, \ \forall u \in \mathrm{int}(\mathbb{R}^n_+).$$

Proof. It suffices to prove that there exists $\delta > 0$ such that for any $u \in B(u^*(0), \delta) \cap \mathrm{int}(R^n_+)$, where $B(u^*(0), \delta) = \{u \in \mathbb{R}^n : |u - u^*(0)| < \delta\}$, there exists $N = N(u) \ge 1$ such that $S^N(u) \notin B(u^*(0), \delta)$. Let ϵ be a fixed real number such that $0 < \epsilon < \frac{1}{\omega}\int_0^\omega F_{0i}(t, u^*(t))dt$. By the uniform continuity of $F_{0i}(t, u)$ on the compact subset $[0, \omega] \times [0, b]^n \subset \mathbb{R}^{n+1}$, where $b = \max_{0\le t\le\omega} |u^*(t)| + 1$, there exists $\delta_0 \in (0, 1)$ such that for any u and $v \in [0, b]^n$ with $|u - v| < \delta_0$, and all $t \in [0, \omega]$,

$$|F_{0i}(t,u) - F_{0i}(t,v)| < \epsilon.$$

By the continuous dependence of solutions on initial values, it then follows that there exists $\delta > 0$ such that for any $u \in B(u^*(0), \delta) \cap \mathbb{R}^n_+$,

$$|\phi_0(t,u) - u^*(t)| = |\phi_0(t,u) - \phi_0(t, u^*(0))| < \delta_0, \quad \forall t \in [0, \omega].$$

Proceeding by contradiction, assume that there exists $u_0 \in B(u^*(0), \delta) \cap \text{int}(\mathbb{R}^n_+)$ such that $S^n(u_0) = \phi_0(n\omega, u_0) \in B(u^*(0), \delta)$, $\forall n \geq 1$. For any $t \geq 0$, let $t = n\omega + t'$, where $t' \in [0, \omega)$ and $n = [t/\omega]$ is the greatest integer less than or equal to t/ω. Then we get

$$|\phi_0(t, u_0) - u^*(t)| = |\phi_0(t', \phi_0(n\omega, u_0)) - u^*(t')| < \delta_0.$$

Therefore,

$$|F_{0i}(t, \phi_0(t, u_0)) - F_{0i}(t, u^*(t))| < \epsilon, \quad \forall t \geq 0.$$

Let $\phi_0(t, u_0) = (\phi_1(t, u_0), \ldots, \phi_n(t, u_0))$. Then $\phi_0(t, u_0) \in \text{int}(\mathbb{R}^n_+)$, $\forall t \geq 0$, and hence $\phi_i(t, u_0)$ satisfies

$$\frac{d\phi_i}{dt} = \phi_i F_{0i}(t, \phi_0(t)) \geq \phi_i(F_{0i}(t, u^*(t)) - \epsilon), \qquad \forall t \geq 0.$$

Thus, by the standard comparison theorem, we have

$$\phi_i(t, u_0) \geq \phi_i(0, u_0) \cdot e^{\int_0^t (F_{0i}(t, u^*(t)) - \epsilon) ds}, \quad \forall t \geq 0.$$

In particular,

$$\phi_i(n\omega, u_0) \geq \phi_i(0, u_0) \cdot e^{n \int_0^\omega (F_{0i}(t, u^*(t)) - \epsilon) ds}, \quad \forall n \geq 0.$$

By the choice of ϵ, $\lim_{n \to \infty} \phi_i(n\omega, u_0) = +\infty$, which contradicts our assumption that $S^n(u_0) = \phi_0(n\omega, u_0) \in B(u^*(0), \delta)$, $\forall n \geq 1$. Consequently, $\limsup_{n \to \infty} d(S^n(u), u^*(0)) \geq \delta$, $\forall u \in \text{int}(\mathbb{R}^n_+)$. ∎

Remark 5.1.1. It is easy to see that Lemma 5.1.1 also holds true for ω-periodic system $\frac{du}{dt} = f_i(t, u)$, $1 \leq i \leq n$, if we assume that $\mathbb{R}^n_+$ is positively invariant for solution maps of it and $f_i(t, u) \geq u_i F_{0i}(t, u)$ on $\mathbb{R}^{n+1}_+$ for some $1 \leq i \leq n$.

We then consider n-dimensional nonautonomous Kolmogorov systems

$$\frac{du_i}{dt} = u_i F_i(t, u), \qquad 1 \leq i \leq n, \tag{5.2}$$

where $u = (u_1, \ldots, u_n) \in \mathbb{R}^n_+$. We assume that $F = (F_1, \ldots, F_n) : \mathbb{R}^{n+1}_+ \to \mathbb{R}^n_+$ is continuous and locally Lipschitz in u. For each $s \geq 0$, let $\phi_0(t, s, u)$ and $\phi(t, s, u)$ be the unique solutions of (5.1) and (5.2) with $\phi_0(s, s, u) = u$ and $\phi(s, s, u) = u$, respectively. Define $T_n(u) := \phi(n\omega, 0, u)$, $T(t)u := \phi_0(t, 0, u)$ and $S(u) := T(\omega)u$, $\forall n \geq 0, t \geq 0, u \in \mathbb{R}^n_+$.

Lemma 5.1.2. *Assume that* $\lim_{t\to\infty}|F(u,t)-F_0(t,u)|=0$ *uniformly for* u *in any bounded subset of* $\mathbb{R}^n_+$, *and that solutions of (5.1) and (5.2) are uniformly bounded in* $\mathbb{R}^n_+$. *If for some* $1\le i\le n$,

$$u^*(t)=(u_1^*(t),\ldots,u_{i-1}^*(t),0,u_{i+1}^*(t),\ldots,u_n^*(t))$$

is an ω*-periodic solution of (5.1) with* $u_j^*(0)\ge 0$, $\forall 1\le j\le n, j\ne i$, *and* $u^*(t)$ *satisfies* $\int_0^\omega F_{0i}(t,u^*(t))dt>0$, *then*

$$\widetilde{W}^s(u^*(0))\cap \mathrm{int}(\mathbb{R}^n_+)=\emptyset,$$

where $\widetilde{W}^s(u^*(0))=\left\{u\in\mathbb{R}^n_+ : \lim_{n\to\infty}T_n(u)=u^*(0)\right\}$.

Proof. By Proposition 3.2.2, $\phi(t,s,u)$, $t\ge s\ge 0, u\in\mathbb{R}^n_+$, is asymptotic to the ω-periodic semiflow $T(t):\mathbb{R}^n\to\mathbb{R}^n$, and hence, $T_n(u):\mathbb{R}^n_+\to\mathbb{R}^n_+$, $n\ge 0$, is an asymptotically autonomous discrete dynamical process with the limiting autonomous discrete semiflow $S^n:\mathbb{R}^n_+\to\mathbb{R}^n_+$, $n\ge 0$. Assume, by contradiction, that there exists $u_0\in\widetilde{W}^s(u^*(0))\cap\mathrm{int}(\mathbb{R}^n_+)$. Then, $\lim_{n\to\infty}T_n(u_0)=u^*(0)$, and hence Theorem 3.2.1 implies that

$$\lim_{t\to\infty}(\phi(t,0,u_0)-u^*(t))=\lim_{t\to\infty}(\phi(t,0,u_0)-T(t)u^*(0))=0.$$

Since $\lim_{t\to\infty}|F(t,u)-F_0(t,u)|=0$ uniformly for u in any bounded subset of $\mathbb{R}^n_+$, it easily follows that

$$\lim_{t\to\infty}(F(t,\phi(t,0,u_0))-F_0(t,u^*(t)))=0.$$

In particular,

$$\lim_{t\to\infty}(F_i(t,\phi(t,0,u_0))-F_{0i}(t,u^*(t)))=0.$$

Let ϵ be a fixed positive number such that $0<\epsilon<\frac{1}{\omega}\int_0^\omega F_{0i}(t,u^*(t))dt$. Then there exists $N=N(\epsilon)>0$ such that

$$F_i(t,\phi(t,0,u_0))\ge F_{0i}(t,u^*(t))-\epsilon,\ \forall t\ge N\omega.$$

Let $\phi(t,0,u_0)=(\phi_1(t),\ldots,\phi_n(t))=\phi(t)$. Then $\phi(t)\in\mathrm{int}(\mathbb{R}^n_+)$, $\forall t\ge 0$. Therefore, $\phi_i(t)$ satisfies

$$\frac{d\phi_i(t)}{dt}=\phi_i(t)F_i(t,\phi(t))\ge\phi_i(t)(F_{0i}(t,u^*(t))-\epsilon),\ \forall t\ge N\omega.$$

By the comparison theorem, it follows that

$$\phi_i(t)\ge\phi_i(N\omega)e^{\int_{N\omega}^t(F_{0i}(s,u^*(s))-\epsilon)ds},\ \forall t\ge N\omega.$$

In particular, we get

$$\phi_i(n\omega)\ge\phi_i(N\omega)e^{(n-N)\int_0^\omega(F_{0i}(s,u^*(s))-\epsilon)ds},\ \forall n\ge N.$$

Then the choice of ϵ implies that $\lim_{n\to\infty}\phi_i(n\omega)=+\infty$, which contradicts $\lim_{t\to\infty}(\phi(t,0,u_0)-u^*(t))=0$. ∎

5.2 Single Population Growth

We first consider the nonautonomous Kolmogorov equation on single species population growth

$$\frac{du}{dt} = uF(t,u), \qquad u \in \mathbb{R}_+ = [0,\infty), \tag{5.3}$$

where $F(t,u) : \mathbb{R}^2_+ \to \mathbb{R}$ is continuous and locally Lipschitz in u. Let $F_0(t,u) : \mathbb{R}^2_+ \to \mathbb{R}$ be continuous, ω-periodic in t $(\omega > 0)$, and locally Lipschitz in u uniformly for $t \in [0,\omega]$. Let $\phi(t,s,u)$, $t \geq s \geq 0$, be the unique solution of (5.3) with $\phi(s,s,u) = u$. Assume that

(A1) $\lim_{t\to\infty} |F(t,u) - F_0(t,u)| = 0$ uniformly for u in any bounded subset of $\mathbb{R}_+$, and there exists $K > 0$ such that $F(t,u) \leq 0$, $\forall t \geq 0, u \geq K$;
(A2) For any $t \geq 0$, $F_0(t,u)$ is strictly decreasing for u, and there exists $K_0 > 0$ such that $F_0(t,K_0) \leq 0$, $\forall t \geq 0$.

We then have the following threshold dynamics for the asymptotically periodic equation (5.3).

Theorem 5.2.1. *Assume that (A1) and (A2) hold.*

(a) If $\int_0^\omega F_0(t,0)dt \leq 0$, *then* $\lim_{t\to\infty} \phi(t,0,u) = 0$, $\forall u \in \mathbb{R}_+$;
(b) If $\int_0^\omega F_0(t,0)dt > 0$, *then* $\lim_{t\to\infty}(\phi(t,0,u) - u^*(t)) = 0$, $\forall u \in \mathbb{R}_+ \setminus \{0\}$, *where* $u^*(t)$ *is the unique positive* ω*-periodic solution of the periodic Kolmogorov equation* $\frac{du}{dt} = uF_0(t,u)$.

Proof. Let $\phi_0(t,s,u)$, $t \geq s \geq 0$, be the unique solution of the ω-periodic Kolmogorov equation

$$\frac{du}{dt} = uF_0(t,u), \qquad u \in \mathbb{R}_+, \tag{5.4}$$

with $\phi_0(s,s,u) = u \in \mathbb{R}_+$. We first claim that the following threshold result on the global asymptotics of (5.4) holds:

(i) If $\int_0^\omega F_0(t,0)dt \leq 0$, then $\lim_{t\to\infty} \phi_0(t,0,u) = 0, \forall u \in \mathbb{R}_+$;
(ii) If $\int_0^\omega F_0(t,0)dt > 0$, then (5.4) admits a unique positive periodic solution $u^*(t)$, and $\lim_{t\to\infty}(\phi_0(t,0,u) - u^*(t)) = 0$, $\forall u \in \mathbb{R}_+ \setminus \{0\}$.

Note that if $F_0(t,u)$ is continuously differentiable with respect to u, the above claim is a simple corollary of Theorem 3.1.2 with $n = 1$. But we need to prove it under the assumption that $F_0(t,u)$ is continuous and locally Lipschitz in u uniformly for $t \in [0,\omega]$. Let $Q : \mathbb{R}_+ \to \mathbb{R}_+$ be the Poincaré map associated with the periodic system (5.4). For any $u > 0$, we have $u(t) := \phi_0(t,0,u) > 0$, $\forall t > 0$, and hence the strict monotonicity of $F_0(t,u)$ for $u > 0$ implies that

$$\frac{du}{dt} = u(t)F_0(t,u(t)) < u(t)F_0(t,0), \qquad \forall t > 0.$$

By the comparison theorem, it then follows that

$$u(t) < u(0)e^{\int_0^t F_0(s,0)ds}, \qquad \forall t > 0.$$

In the case where $\int_0^\omega F_0(t,0)dt \le 0$, the Poincaré map $Q : \mathbb{R}_+ \to \mathbb{R}_+$ satisfies

$$Q(u) = u(\omega) < u(0)e^{\int_0^\omega F(s,0)ds} \le u(0) = u, \, \forall u > 0,$$

which implies that $Q : \mathbb{R}_+ \to \mathbb{R}_+$ admits no positive fixed point, and that for any $u > 0$,

$$0 < Q^{n+1}(u) < Q^n(u), \qquad \forall n \ge 0.$$

Thus, there exists $\bar{u} \ge 0$ such that $\lim_{n\to\infty} Q^n(u) = \bar{u}$. Since $\bar{u} = Q(\bar{u})$, the nonexistence of positive fixed points of Q implies $\bar{u} = 0$. Then $\lim_{n\to\infty} Q^n(u) = 0$, $\forall u > 0$, and hence $\lim_{t\to\infty} u(t) = 0$. In the case where $\int_0^\omega F_0(t,0)dt > 0$, Lemma 5.1.1 with $n = 1$ implies that $\{0\}$ is an isolated invariant set for Q, and $W^s(0) \cap \mathrm{int}(\mathbb{R}_+) = \emptyset$. By Theorem 1.3.1 and Remark 1.3.1, as applied to $Q : X := \mathbb{R}_+ \to X$ with $X_0 = \mathrm{int}(\mathbb{R}_+)$ and $\partial X_0 = \{0\}$, $\{0\}$ is a strong repeller in the sense that there exists $\delta > 0$ such that $\omega(u) \ge \delta$, $\forall u > 0$. It is easy to see that $Q : \mathbb{R}_+ \to \mathbb{R}_+$ is strongly monotone and strictly subhomogeneous. By Theorem 2.3.2, it then follows that Q admits a unique positive fixed point u^*, and $\lim_{n\to\infty} Q^n(u) = u^*$, $\forall u > 0$. Thus, the conclusion in (ii) holds with $u^*(t) = \phi_0(t, 0, u^*)$.

By conditions (A1) and (A2), it easily follows that for any $u \in \mathbb{R}_+$ and $s \ge 0$, $\phi(t, s, u)$ and $\phi_0(t, s, u)$ exist globally on $[s, \infty)$, and solutions of (5.3) and (5.4) are uniformly bounded. By Proposition 3.2.2, $\phi(t, s, u)$ is asymptotic to the ω-periodic semiflow $T(t) := \phi_0(t, 0, \cdot) : \mathbb{R}_+ \to \mathbb{R}_+$, and hence $T_n(u) := \phi(n\omega, 0, u)$, $n \ge 0$, is an asymptotically autonomous discrete process with limit discrete semiflow $Q^n : \mathbb{R}_+ \to \mathbb{R}_+, n \ge 0$. By Theorem 3.2.1, it suffices to prove in case (a) that $\lim_{n\to\infty} T_n(u) = 0$, $\forall u \in \mathbb{R}_+$, and in case (b) that $\lim_{n\to\infty} T_n(u) = u^*(0)$, $\forall u \in \mathbb{R}_+ \setminus \{0\}$.

In case (a), by conclusion (i) above, $u = 0$ is a global attractor for $Q : \mathbb{R}_+ \to \mathbb{R}_+$. Thus, Theorem 1.2.1 implies that for any $u \in \mathbb{R}_+, \omega(u) = 0$, and hence $\lim_{n\to\infty} T_n(u) = 0$.

In case (b), by conclusion (ii) above, $u = u^*(0)$ is a globally attractive fixed point of Q in $\mathbb{R}_+ \setminus \{0\}$. Thus, the only fixed points of Q in $\mathbb{R}_+$ are 0 and $u^*(0)$; both are isolated invariant sets, and there is no Q-cyclic chain among them. Then Theorem 1.2.2 implies that for any $u \in \mathbb{R}_+$, either $\omega(u) = 0$ or $\omega(u) = u^*(0)$. By Lemma 5.1.2 with $n = 1$, we have $\widetilde{W^s}(0) \cap (\mathbb{R}^+ \setminus \{0\}) = \emptyset$; that is, $\omega(u) \ne 0$, $\forall u > 0$. Consequently, for any $u > 0$, $\omega(u) = u^*(0)$, and hence $\lim_{n\to\infty} T_n(u) = u^*(0)$. ∎

Now we consider a single population growth model in a periodic chemostat

$$\begin{aligned} \frac{dS(t)}{dt} &= (S^0(t) - S(t))D_0(t) - x(t)P(t, S(t)), \\ \frac{dx(t)}{dt} &= x(t)(P(t, S(t)) - D_1(t)). \end{aligned} \tag{5.5}$$

Here $S(t)$ denotes the concentration of the nutrient, $x(t)$ denotes the biomass of the species at time t, $P(t,s)$ represents the specific per capita nutrient uptake function, $S^0(t)$ and $D_0(t)$ are the input nutrient concentration and the dilution rate, respectively, and $D_1(t)$ represents the specific removal rate of the species. We assume that $S^0(t),\ \ D_0(t)$, and $D_1(t)$ are all continuous, ω-periodic, positive functions, and that $P(t,s):\mathbb{R}^2_+\to\mathbb{R}_+$ is continuous, ω-periodic in t, and satisfies

(B1) $P(t,s)$ is locally Lipschitz in s;
(B2) $P(t,0)=0,\ \forall t\geq 0$, and for each $t\geq 0,\ \ P(t,s)$ is strictly increasing for $s\in\mathbb{R}_+$.

Let $D(t):\mathbb{R}_+\to\mathbb{R}_+$ be a continuous, ω-periodic, and positive function. For the linear periodic equation

$$\frac{dV(t)}{dt}=S^0(t)D_0(t)-D(t)V(t), \tag{5.6}$$

it easily follows that (5.6) admits a unique positive ω-periodic solution $V^*(t)$ such that every solution $V(t)$ of (5.6) with $V(0)\geq 0$ satisfies $\lim_{t\to\infty}(V(t)-V^*(t))=0$. Moreover, $V^*(t)$ can be expressed explicitly as

$$V^*(t)=e^{-\int_0^t D(s)ds}\left[\frac{\int_0^\omega e^{\int_0^s D(u)du}S^0(s)D_0(s)ds}{e^{\int_0^\omega D(s)ds}-1}\right.$$
$$\left.+\int_0^t e^{\int_0^s D(u)du}S^0(s)D_0(s)ds\right].$$

Let $\overline{D}(t)=\max(D_0(t),D_1(t))$ and $\underline{D}(t)=\min(D_0(t),D_1(t))$. Then, $\overline{D}(t)$ and $\underline{D}(t):R_+\to R_+$ are continuous, ω-periodic, and positive functions. Let $V_1^*(t)$ and $V_2^*(t)$ be the unique positive ω-periodic solutions of (5.6) with $D(t)$ replaced by $\underline{D}(t)$ and $\overline{D}(t)$, respectively. By the comparison theorem and the global attractivity of each $V_i^*(t)$, it easily follows that $V_2^*(t)\leq V_1^*(t),\ \forall t\geq 0$.

Theorem 5.2.2. *Let (B1) and (B2) hold. Then the following threshold dynamics hold:*

(a) If $\int_0^\omega(P(t,V_2^*(t))-D_1(t))dt>0$, then system (5.5) admits a positive (componentwise) ω-periodic solution, and there exist $\alpha>0$ and $\beta>0$ such that every solution $(S(t),x(t))$ of (5.5) with $S(0)\geq 0$ and $x(0)>0$ satisfies

$$\alpha\leq\liminf_{t\to\infty}x(t)\leq\limsup_{t\to\infty}x(t)\leq\beta.$$

(b) If $\int_0^\omega(P(t,V_1^*(t))-D_1(t))dt\leq 0$, then every solution $(S(t),x(t))$ of (5.5) with $S(0)\geq 0$ and $x(0)\geq 0$ satisfies $\lim_{t\to\infty}x(t)=0$.

Interpreting the predictions of the model biologically, Theorem 5.2.2 implies that in case (a) the model system admits a periodic coexistence state and the species is uniformly persistent, but in case (b) the species ultimately goes to extinction.

Proof. Let $\hat{P}(t,s) : \mathbb{R}_+ \times \mathbb{R} \to \mathbb{R}$ be a continuous extension of $P(t,s)$ on $\mathbb{R}_+ \times \mathbb{R}_+$ to $\mathbb{R}_+ \times \mathbb{R}$ such that $\hat{P}(t,s)$ is ω-periodic in t and locally Lipschitz in s, and for any $t \geq 0$, $\hat{P}(t,s)$ is strictly increasing for $s \in \mathbb{R}$.

In case (a), since $V_1^*(t) \geq V_2^*(t), \forall t \in [0,\omega]$, and $\hat{P}(t, V_i^*(t)) = P(t, V_i^*(t))$, $\forall t \in [0,\omega]$, $1 \leq i \leq 2$, Theorem 5.2.1 (in the periodic case) implies that the periodic equation

$$\frac{dx(t)}{dt} = x(t)(\hat{P}(t, V_i^*(t) - x(t)) - D_1(t))$$

admits a unique positive ω-periodic solution $x_i^*(t)$, and $x_i^*(t)$ is globally attractive in $\mathbb{R}_+ \setminus \{0\}$, $1 \leq i \leq 2$. By the comparison theorem, it easily follows that $x_1^*(t) \geq x_2^*(t), \forall t \in [0,\omega]$. We further claim that $V_1^*(t) > x_1^*(t), \forall t \in [0,\omega]$. Indeed, let $x_1^*(t_1) = \max_{0 \leq t \leq \omega} x_1^*(t)$, $t_1 \in [0,\omega]$. Then $\frac{dx_1^*(t_1)}{dt} = 0$, and hence

$$\hat{P}(t_1, V_1^*(t_1) - x_1^*(t_1)) = D_1(t_1) > 0.$$

Since $\hat{P}(t_1, s)$ is strictly increasing for $s \in R$, $V_1^*(t_1) > x_1^*(t_1)$. Let $y(t) = V_1^*(t) - x_1^*(t)$. Then $y(t)$ satisfies the periodic differential equation

$$\frac{dy}{dt} = S^0(t)D_0(t) - \underline{D}(t)V_1^*(t) - (V_1^*(t) - y)(\hat{P}(t,y) - D_1(t)). \tag{5.7}$$

Since $y(t_1) > 0$ and

$$\left.\frac{dy}{dt}\right|_{y=0} = S^0(t)D_0(t) + (D_1(t) - \underline{D}(t))V_1^*(t) \geq S^0(t)D_0(t) > 0,$$

it follows that $y(t) > 0$, $\forall t \geq t_1$. Thus, the ω-periodicity of $y(t)$ implies that $y(t) > 0$, $\forall t \geq 0$, that is, $V_1^*(t) > x_1^*(t)$, $\forall t \geq 0$.

For any $(S_0, x_0) \in \mathbb{R}_+^2$ with $S_0 \geq 0$ and $x_0 > 0$, let $(S(t), x(t))$ be the unique solution of (5.5) satisfying $S(0) = S_0$ and $x(0) = x_0$ with $[0,\beta)$ as its maximal existence interval. It then easily follows that $S(t) > 0$ and $x(t) > 0$, $\forall t \in (0,\beta)$. Let $V(t) = S(t) + x(t)$. Then

$$S^0(t)D_0(t) - \overline{D}(t)V(t) \leq \frac{dV(t)}{dt} \leq S^0(t)D_0(t) - \underline{D}(t)V(t), \quad \forall t \in [0,\beta).$$

Let $\overline{V}(t)$ be the unique solution of the linear ω-periodic equation

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

satisfying $\overline{V}(0) = V(0)$, and let $\underline{V}(t)$ be the unique solution of the linear ω-periodic equation

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

satisfying $\underline{V}(0) = V(0)$. Then the standard comparison theorem implies that

$$\underline{V}(t) \leq V(t) \leq \overline{V}(t), \qquad \forall t \in [0, \beta). \tag{5.8}$$

Since $\overline{V}(t)$ and $\underline{V}(t)$ exist globally on $[0, \infty)$, $\beta = \infty$. Therefore, $x(t)$ satisfies

$$x(t)\left(\hat{P}(t, \underline{V}(t) - x(t)) - D_1(t)\right) \leq \frac{dx(t)}{dt} \leq x(t)\left(\hat{P}(t, \overline{V}(t) - x(t)) - D_1(t)\right)$$

for all $t \geq 0$. Then, by the comparison theorem,

$$\underline{x}(t) \leq x(t) \leq \overline{x}(t), \qquad \forall t \geq 0, \tag{5.9}$$

where $\bar{x}(t)$ is the unique solution of the nonautonomous equation

$$\frac{dx(t)}{dt} = x(t)\left(\hat{P}(t, \overline{V}(t) - x(t)) - D_1(t)\right), \tag{5.10}$$

with $\bar{x}(0) = x_0$, and $\underline{x}(t)$ is the unique solution of the nonautonomous equation

$$\frac{dx(t)}{dt} = x(t)\left(\hat{P}(t, \underline{V}(t) - x(t)) - D_1(t)\right), \tag{5.11}$$

with $\underline{x}(0) = x_0$. Since $\lim_{t\to\infty}(\overline{V}(t) - V_1^*(t)) = 0$ and $\lim_{t\to\infty}(\underline{V}(t) - V_2^*(t)) = 0$, we have

$$\lim_{t\to\infty}(\hat{P}(t, \overline{V}(t) - x) - \hat{P}(t, V_1^*(t) - x)) = 0$$

and

$$\lim_{t\to\infty}(\hat{P}(t, \underline{V}(t) - x) - \hat{P}(t, V_2^*(t) - x)) = 0$$

uniformly for x in any bounded subset of $\mathbb{R}_+$. In case (a), since

$$\begin{aligned}\int_0^\omega (\hat{P}(t, V_1^*(t)) - D_1(t))dt &\geq \int_0^\omega (\hat{P}(t, V_2^*(t)) - D_1(t))dt,\\ &= \int_0^\omega (P(t, V_2^*(t)) - D_1(t))dt > 0,\end{aligned}$$

Theorem 5.2.1(b) implies that

$$\lim_{t\to\infty}(\bar{x}(t) - x_1^*(t)) = 0 \quad \text{and} \quad \lim_{t\to\infty}(\underline{x}(t) - x_2^*(t)) = 0.$$

By (5.9), it then follows that

$$\liminf_{t\to\infty}(x(t) - x_2^*(t)) \geq \lim_{t\to\infty}(\underline{x}(t) - x_2^*(t)) = 0 \tag{5.12}$$

and

$$\limsup_{t\to\infty}(x(t) - x_1^*(t)) \leq \lim_{t\to\infty}(\overline{x}(t) - x_1^*(t)) = 0, \tag{5.13}$$

and hence there exist $\alpha > 0$ and $\beta > 0$ such that $x(t)$ satisfies

$$\alpha \leq \liminf_{t\to\infty} x(t) \leq \limsup_{t\to\infty} x(t) \leq \beta.$$

In case (b), since

$$\begin{aligned}\int_0^\omega (\hat{P}(t, V_2^*(t)) - D_1(t))dt &\leq \int_0^\omega (\hat{P}(t, V_1^*(t)) - D_1(t))dt, \\ &= \int_0^\omega P(t, V_1^*(t)) - D_1(t))dt \leq 0,\end{aligned}$$

Theorem 5.2.1(a) implies that $\lim_{t\to\infty} \bar{x}(t) = 0$ and $\lim_{t\to\infty} \underline{x}(t) = 0$. By (5.9), we get $\lim_{t\to\infty} x(t) = 0$.

In case (a), it remains to prove the existence of a positive periodic solution of (5.5). Under the abstract setting of periodic semiflows, this can be done by using Theorem 1.3.8 as in the latter part of the proof of Theorem 5.3.1. Instead, we give an alternative, more elementary proof. Let $V = S + x$. Then the system (5.5) is transformed into the following ω-periodic system

$$\begin{aligned}\frac{dV}{dt} &= S^0(t)D_0(t) - D_0(t)(V - x) - D_1(t)x, \\ \frac{dx}{dt} &= x\left(\hat{P}(t, V - x) - D_1(t)\right).\end{aligned} \tag{5.14}$$

Then the positive invariance of $\mathbb{R}^2_+$ with respect to (5.5) implies that the closed and convex set $W := \{(V, x) : V \geq x \geq 0\} \subset \mathbb{R}^2_+$ is positively invariant with respect to (5.14). Moreover, for any $S_0 \geq 0$ and $x_0 > 0$, since the first equation of (5.5) implies that $S'(t)|_{S=0} = S^0(t)D_0(t) > 0$, the unique solution $(S(t), x(t))$ of (5.5) with $S(0) = S_0$ and $x(0) = x_0$ satisfies $S(t) > 0$ and $x(t) > 0, \forall t > 0$. That is, for any $V_0 \geq x_0 > 0$, the unique solution $(V(t), x(t))$ of (5.14) with $V(0) = V_0$ and $x(0) = x_0$ satisfies $V(t) > x(t) > 0, \forall t > 0$. Let $G : W \to W$ be the Poincaré map associated with (5.14); that is, for every $(V_0, x_0) \in W, G(V_0, x_0) = (V(\omega), x(\omega))$. Clearly, the continuous dependence of solutions on initial data implies that $G : W \to W$ is continuous. Let

$$W_0 := \{(V, x) \in W : V_2^*(0) \leq V \leq V_1^*(0), x_2^*(0) \leq x \leq x_1^*(0)\}.$$

Since $0 < x_1^*(t) < V_1^*(t)$, $\forall t \in [0, \omega]$, $(V_1^*(0), x_1^*(0))$ is in the interior of W, and hence W_0 is a nonempty, closed, bounded, and convex subset of $\mathbb{R}^2_+$. For each $(V_0, x_0) \in W_0$, the corresponding solution $(V(t), x(t))$ of (5.14) with $V(0) = V_0$ and $x(0) = x_0$ satisfies

$$(V(t), x(t)) \in W, \qquad \forall t \geq 0; \tag{5.15}$$

that is, $V(t) \geq x(t) \geq 0,\ \forall t \geq 0$. Then $V(t)$ satisfies

$$S^0(t)D_0(t) - \overline{D}(t)V(t) \leq \frac{dV(t)}{dt} \leq S^0(t)D_0(t) - \underline{D}(t)V(t), \quad \forall t \geq 0.$$

Since $V_2^*(0) \le V_0 \le V_1^*(0)$, the comparison theorem implies that

$$V_2^*(t) \le V(t) \le V_1^*(t), \qquad \forall t \ge 0. \tag{5.16}$$

Therefore, $x(t)$ satisfies

$$x(t)\left(\hat{P}(t, V_2^*(t) - x(t)) - D_1(t)\right) \le \frac{dx(t)}{dt}, \qquad \forall t \ge 0,$$

and

$$\frac{dx(t)}{dt} \le x(t)\left(\hat{P}(t, V_1^*(t) - x(t)) - D_1(t)\right), \qquad \forall t \ge 0.$$

Since $x_2^*(0) \le x_0 \le x_1^*(0)$, again by the comparison theorem we get

$$x_2^*(t) \le x(t) \le x_1^*(t), \qquad \forall t \ge 0. \tag{5.17}$$

Then (5.16) and (5.17) imply that

$$\begin{aligned} V_2^*(0) &= V_2^*(\omega) \le V(\omega) \le V_1^*(\omega) = V_1^*(0), \\ x_2^*(0) &= x_2^*(\omega) \le x(\omega) \le x_1^*(\omega) = x_1^*(0). \end{aligned} \tag{5.18}$$

By (5.15) and (5.18), it follows that $G(V_0, x_0) = (V(\omega), x(\omega)) \in W_0$, and hence $G(W_0) \subset W_0$. By the Brouwer fixed point theorem, there exists $(V^*, x^*) \in W_0$ such that $G(V^*, x^*) = (V^*, x^*)$. Clearly, the unique solution $(V^*(t), x^*(t))$ of (5.14) with $(V^*(0), x^*(0)) = (V^*, x^*)$ is an ω-periodic solution of (5.14). Since $V^* \ge x^* > 0$, by the previous claim, we have $V^*(t) > x^*(t) > 0$, $\forall t > 0$. By the ω-periodicity of $V^*(t)$ and $x^*(t)$, it then follows that $V^*(t) > x^*(t) > 0$, $\forall t \ge 0$. Consequently, $(S^*(t), x^*(t)) = (V^*(t) - x^*(t), x^*(t))$ is a positive (componentwise) ω-periodic solution of system (5.5). ∎

In the case that $D_0(t) = D_1(t)$, $\forall t \in [0, \omega]$, it is easy to see that $V_1^*(t) = V_2^*(t)$, $x_1^*(t) = x_2^*(t)$, $\forall t \in [0, \omega]$. Thus, (5.12) and (5.13) imply the following threshold dynamics for the model system.

Corollary 5.2.1. *Let (B1) and (B2) hold and assume that $D_0(t) = D_1(t)$, $\forall t \in [0, \omega]$. Then the following statements are valid:*

(a) If $\int_0^\omega (P(t, V_1^*(t)) - D_1(t)) > 0$, then system (5.5) admits a unique positive, periodic solution $(S^*(t), x_1^*(t)) = (V_1^*(t) - x_1^*(t), x_1^*(t))$, and every solution $(S(t), x(t))$ of (5.5) with $S(0) \ge 0$ and $x(0) > 0$ satisfies $\lim_{t\to\infty}(S(t) - S^*(t)) = 0$ and $\lim_{t\to\infty}(x(t) - x^*(t)) = 0$.

(b) If $\int_0^\omega (P(t, V_1^*(t)) - D_1(t)) \le 0$, then every solution $(S(t), x(t))$ of (5.5) with $S(0) \ge 0$ and $x(0) \ge 0$ satisfies $\lim_{t\to\infty}(S(t) - V_1^*(t)) = 0$ and $\lim_{t\to\infty} x(t) = 0$.

5.3 N-Species Competition

In this section we consider the n-species competition model in the periodic chemostat

$$\begin{aligned}\frac{dS(t)}{dt} &= (S^0(t) - S(t))D_0(t) - \sum_{i=1}^{n} P_i(t, S(t))x_i(t),\\ \frac{dx_i(t)}{dt} &= x_i(t)(P_i(t, S(t)) - D_i(t)), \qquad 1 \le i \le n.\end{aligned} \tag{5.19}$$

Here $S(t)$ denotes the concentration of the nutrient, $x_i(t)$ denotes the biomass of the ith species at time t, $P_i(t, s)$ represents the specific per capita nutrient uptake function of the ith species, $S^0(t)$ and $D_0(t)$ are the input nutrient concentration and the dilution rate, respectively, and $D_i(t)$ represents the specific removal rate, or washout rate, of species x_i. We assume that $S^0(t)$ and $D_i(t)$, $1 \le i \le n$, are all continuous, ω-periodic, and positive functions, and that each $P_i(t, s)$ satisfies conditions (B1) and (B2).

Let

$$\overline{P}_i(t, s) = \begin{cases} P_i(t, s) & \text{if } t \ge 0,\ s \ge 0,\\ 0 & \text{if } t \ge 0,\ s \le 0.\end{cases}$$

Then each $\overline{P}_i : \mathbb{R}_+ \times \mathbb{R} \to \mathbb{R}$ is a continuous extension of $P_i(t, s)$ on $\mathbb{R}_+ \times \mathbb{R}_+$ to $\mathbb{R}_+ \times \mathbb{R}$. Let

$$\overline{D}(t) = \max(D_0(t), D_1(t), \ldots, D_n(t))$$

and

$$\underline{D}(t) = \min(D_0(t), D_1(t), \ldots, D_n(t)).$$

Then $\overline{D}(t)$ and $\underline{D}(t) : \mathbb{R}_+ \to \mathbb{R}_+$ are continuous, ω-periodic, and positive functions. Let $V_1^*(t)$ and $V_2^*(t)$ be the unique positive ω-periodic solutions of (5.6) with $D(t)$ replaced by $\underline{D}(t)$ and $\overline{D}(t)$, respectively. As shown in the previous section, $V_2^*(t) \le V_1^*(t)$, $\forall t \ge 0$.

We are now in a position to prove the main result of this section.

Theorem 5.3.1. *Assume that*

(1) $\int_0^\omega (P_i(t, V_1^*(t)) - D_i(t))\, dt > 0, \quad \forall 1 \le i \le n;$
(2) $\int_0^\omega \left(\overline{P}_i(t, V_2^*(t) - \sum_{j=1, j\ne i}^{n} x_j^*(t)) - D_i(t)\right) dt > 0, \forall 1 \le i \le n,$ *where each* $x_j^*(t)$ *is the unique positive* ω*-periodic solution of the scalar periodic equation* $\frac{dx_j}{dt} = x_j(P_j(t, V_1^*(t) - x_j) - D_j(t)).$

Then system (5.19) admits a positive ω*-periodic solution, and there exist* $\alpha > 0$ *and* $\beta > 0$ *such that any solution* $(S(t), x_1(t), \ldots, x_n(t))$ *of (5.19) with* $S(0) \ge 0$ *and* $x_i(0) > 0, \forall 1 \le i \le n$*, satisfies*

$$0 < \alpha \le \liminf_{t\to\infty} x_i(t) \le \limsup_{t\to\infty} x_i(t) \le \beta, \quad \forall 1 \le i \le n.$$

Proof. Let $\hat{P}_i(t,s) : \mathbb{R}_+ \times \mathbb{R} \to \mathbb{R}$ be any continuous extension of $P_i(t,s)$ on $\mathbb{R}_+ \times \mathbb{R}_+$ to $\mathbb{R}_+ \times \mathbb{R}$ such that $\hat{P}_i(t,s)$ is ω-periodic in t and locally Lipschitz in s, and for each $t \geq 0$, $\hat{P}_i(t,s)$ is strictly increasing with respect to $s \in \mathbb{R}$, $\forall 1 \leq i \leq n$. By Theorem 5.2.1 (in the periodic case), condition (1) implies that for each $1 \leq i \leq n$, the periodic equation

$$\frac{dx_i}{dt} = x_i(\hat{P}_i(t, V_1^*(t) - x_i) - D_i(t))$$

admits a unique ω-periodic solution $x_i^*(t)$, and $x_i^*(t)$ is globally attractive in $\mathbb{R}_+ \setminus \{0\}$. As in the proof of Theorem 5.2.2, $V_1^*(t) > x_i^*(t)$, $\forall t \in [0,\omega]$. Then $x_i^*(t)$ is a unique positive ω-periodic solution of the periodic equation

$$\frac{dx_i}{dt} = x_i(P_i(t, V_1^*(t) - x_i) - D_i(t));$$

that is, $x_i^*(t)$ is independent of the choice of the extension $\hat{P}_i(t,s)$ of $P_i(t,s)$. Let

$$\hat{P}_{i\epsilon}(t,s) = \begin{cases} P_i(t,s) & \text{if } t \geq 0,\ s \geq 0, \\ \epsilon s & \text{if } t \geq 0,\ s \leq 0. \end{cases}$$

By the boundedness of $V_2^*(t) - \sum_{j=1,j\neq i}^{n} x_j^*(t)$ on $[0,\infty)$, it easily follows that for each $1 \leq i \leq n$,

$$\lim_{\epsilon \to 0^+} \int_0^\omega \hat{P}_{i\epsilon}\left(t, V_2^*(t) - \sum_{j=1,j\neq i}^{n} x_j^*(t)\right) dt$$
$$= \int_0^\omega \left(\overline{P}_i(t, V_2^*(t) - \sum_{j=1,j\neq i}^{n} x_j^*(t))\right) dt.$$

Then condition (2) implies that there exists $\epsilon > 0$ such that

$$\int_0^\omega \left(\hat{P}_{i\epsilon}(t, V_2^*(t) - \sum_{j=1,j\neq i}^{n} x_j^*(t)) - D_i(t)\right) dt > 0, \quad \forall 1 \leq i \leq n. \tag{5.20}$$

In what follows, for simplicity, we denote $\hat{P}_{i\epsilon}(t,s)$ by $\hat{P}_i(t,s)$, $\forall 1 \leq i \leq n$.

For any $(S_0, x_0) = (S_0, x_1^0, \ldots, x_n^0) \in \mathbb{R}_+^{n+1}$ with $x_i^0 > 0$, $\forall 1 \leq i \leq n$, let $(S(t), x(t)) = (S(t), x_1(t), \ldots, x_n(t))$ be the unique solution of (5.19) satisfying $S(0) = S_0,\ x(0) = x_0$ on the maximal interval of existence $[0,\beta)$. Since $S'(t)|_{S=0} = S^0(t)D_0(t) > 0$, it follows that $S(t) > 0$, and $x(t) > 0$, $\forall t \in [0,\beta)$. Let $V(t) := S(t) + \sum_{i=1}^{n} x_i(t)$. Then

$$S^0(t)D_0(t) - \overline{D}(t)V(t) \leq \frac{dV(t)}{dt} \leq S^0(t)D_0(t) - \underline{D}(t)V(t).$$

Therefore, by the comparison theorem, we get

$$\underline{V}(t) \le V(t) \le \overline{V}(t), \qquad \forall t \in [0, \beta), \tag{5.21}$$

where $\overline{V}(t)$ is the unique solution of the linear ω-periodic equation

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

with $\overline{V}(0) = V(0)$, and $\underline{V}(t)$ is the unique solution of linear ω-periodic equation

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

with $\underline{V}(0) = V(0)$. The global existence of $\overline{V}(t)$ on $[0, \infty)$ implies that $\beta = \infty$. Since $\lim_{t\to\infty}(\overline{V}(t) - V_1^*(t)) = 0$, $V(t)$ and hence $S(t)$ and $x(t) = (x_1(t), \ldots, x_n(t))$ are ultimately bounded. That is, system (5.19) is point dissipative on $\mathbb{R}_+^{n+1}$. Therefore, for all $t \ge 0$, $1 \le i \le n$,

$$\begin{aligned}\frac{x_i(t)}{dt} &= x_i(t)\left(\hat{P}_i\left(t, V(t) - \sum_{j=1}^n x_j(t)\right) - D_i(t)\right)\\ &\le x_i(t)(\hat{P}_i(t, V(t) - x_i(t)) - D_i(t)).\end{aligned}$$

By the comparison theorem, it then follows that

$$x_i(t) \le \bar{x}_i(t), \qquad \forall t \ge 0,\ 1 \le i \le n, \tag{5.22}$$

where $\bar{x}_i(t)$ is the unique solution of the nonautonomous equation

$$\frac{dx_i(t)}{dt} = x_i(t)(\hat{P}_i(t, \overline{V}(t) - x_i) - D_i(t)), \tag{5.23}$$

with $\bar{x}_i(0) = x_i(0) > 0$, $\forall 1 \le i \le n$. Since $\lim_{t\to\infty}(\overline{V}(t) - V_1^*(t)) = 0$, we get

$$\lim_{t\to\infty}(\hat{P}_i(t, \overline{V}(t) - x_i) - \hat{P}(t, V_1^*(t) - x_i) = 0$$

uniformly for x_i in any bounded subset of $\mathbb{R}_+$. Since

$$\int_0^\omega (\hat{P}_i(t, V_1^*(t)) - D_i(t))dt = \int_0^\omega (P_i(t, V_1^*(t)) - D_i(t))dt > 0,$$

Theorem 5.2.1(b) implies that

$$\lim_{t\to\infty}(\bar{x}_i(t) - x_i^*(t)) = 0, \qquad \forall 1 \le i \le n. \tag{5.24}$$

By (5.21) and (5.22), it then follows that for any $1 \le i \le n$ and $t \ge 0$,

$$\begin{aligned}\frac{dx_i(t)}{dt} &= x_i(t)\left(\hat{P}_i\left(t, V(t) - \sum_{j=1}^n x_j(t)\right) - D_i(t)\right)\\ &\ge x_i(t)\left(\hat{P}_i\left(t, \underline{V}(t) - \sum_{j=1, j\ne i}^n \bar{x}_j(t) - x_i(t)\right) - D_i(t)\right)\end{aligned} \tag{5.25}$$

and hence by the comparison theorem,

$$x_i(t) \geq \underline{x}_i(t), \qquad \forall t \geq 0,\, 1 \leq i \leq n, \tag{5.26}$$

where $\underline{x}_i(t)$ is the unique solution of the nonautonomous equation

$$\frac{dx_i}{dt} = x_i(t)\left(\hat{P}_i\left(t, \underline{V}(t) - \sum_{j=1, j\neq i}^{n} \bar{x}_j(t) - x_i\right) - D_i(t)\right) \tag{5.27}$$

with $\underline{x}_i(0) = x_i(0)$, $\forall 1 \leq i \leq n$. Since $\lim_{t\to\infty}(\underline{V}(t) - V_2^*(t)) = 0$, we have

$$\lim_{t\to\infty}\left(\hat{P}_i\left(t, \underline{V}(t) - \sum_{j=1, j\neq i}^{n} x_j^*(t) - x_i\right)\right.$$
$$\left. - \hat{P}_i\left(t, V_2^*(t) - \sum_{j=1, j\neq i}^{n} x_j^*(t) - x_i\right)\right) = 0$$

uniformly for x_i in any bounded subset of $\mathbb{R}_+$, $\forall 1 \leq i \leq n$. Then (5.20) and Theorem 5.2.1(b) imply that

$$\lim_{t\to\infty}(\underline{x}_i(t) - \underline{x}_i^*(t)) = 0, \tag{5.28}$$

where $\underline{x}_i^*(t)$, $\forall 1 \leq i \leq n$, is the unique positive ω-periodic solution of the periodic equation

$$\frac{dx_i}{dt} = x_i(t)\left(\hat{P}_i\left(t, V_2^*(t) - \sum_{j=1, j\neq i}^{n} x_j^*(t) - x_i\right) - D_i(t)\right). \tag{5.29}$$

By (5.22), (5.24), (5.26), and (5.28), it then follows that

$$\liminf_{t\to\infty}(x_i(t) - \underline{x}_i^*(t) \geq 0 \geq \limsup_{t\to\infty}(x_i(t) - x_i^*(t)),\ \forall 1 \leq i \leq n. \tag{5.30}$$

Clearly, (5.30) implies that there exist $\alpha > 0$ and $\beta > 0$ such that any solution $(S(t), x_1(t), \ldots, x_n(t))$ of (5.19) with $S(0) \geq 0$ and $x_i(0) > 0$, $\forall 1 \leq i \leq n$, satisfies

$$0 < \alpha \leq \liminf_{t\to\infty} x_i(t) \leq \limsup_{t\to\infty} x_i(t) \leq \beta, \qquad \forall 1 \leq i \leq n.$$

To prove the existence of a positive ω-periodic solution of (5.19), let $X := \mathbb{R}_+^{n+1}$,

$$X_0 := \{(S, x_1, \ldots, x_n) \in \mathbb{R}_+^{n+1} :\, x_i > 0,\ \forall 1 \leq i \leq n\}, \text{ and } \partial X_0 := X \setminus X_0.$$

For any $y = (S, x_1, \ldots, x_n) \in X$, let $\phi(t, y)$ be the unique solution of (5.19) with $\phi(0, y) = y$. Clearly, $T(t) = \phi(t, \cdot) : X \to X$ is a periodic semiflow, and $T(t)X_0 \subset X_0$, $\forall t \geq 0$. As we have shown, $T(t)$ is point dissipative (i.e., ultimately bounded) in X and uniformly persistent with respect to $(X_0, \partial X_0)$ in the sense that there exists $\eta > 0$ such that $\liminf_{t\to\infty} d(T(t)y, \partial X_0) \geq \eta$, $\forall y \in X_0$. Let $Q = T(\omega) : X \to X$ be the Poincaré map associated with (5.19). Note that the ultimate boundedness implies the uniform boundedness of solutions for periodic systems of ordinary differential equations (see, e.g., [421, Theorem 8.5]). Thus, $Q : X \to X$ is compact. By Theorem 1.3.8, it follows that Q admits a fixed point $y_0 \in X_0$, and hence, $\phi(t, y_0)$ is a periodic solution of (5.19). Let $y_0 = (S_0, x_1^0, \ldots, x_n^0) \in X_0$. Then $S_0 \geq 0, x_i^0 > 0$, $\forall 1 \leq i \leq n$. It then follows that $\phi(t, y_0) = (S(t), x_1(t), \ldots, x_n(t))$ satisfies $S(t) > 0$ and $x_i(t) > 0$, $\forall t > 0, 1 \leq i \leq n$. Clearly, the ω-periodicity of $\phi(t, y_0)$ implies that $S(t) > 0$ and $x_i(t) > 0$, $\forall t \geq 0, 1 \leq i \leq n$. Consequently, $\phi(t, y_0)$ is a positive ω-periodic solution of (5.19). ∎

In the case where $D_i(t) = D_0(t)$, $\forall t \in [0, \omega]$, $1 \leq i \leq n$, it is easy to see that $\underline{D}(t) = \overline{D}(t) = D_0(t)$, $V_1^*(t) = V_2^*(t)$, $\forall t \in [0, \omega]$. Then we have the following corollary of Theorem 5.3.1.

Corollary 5.3.1. *Let $D_i(t) = D_0(t)$, $\forall t \in [0, \omega]$, $1 \leq i \leq n$. Assume that*

(1) $\int_0^\omega (P_i(t, V_1^*(t)) - D_0(t))\, dt > 0, \quad \forall 1 \leq i \leq n$;
(2) $\int_0^\omega \left(\overline{P}_i(t, V_1^*(t) - \sum_{j=1, j\neq i}^n x_j^*(t)) - D_0(t)\right) dt > 0, \quad \forall 1 \leq i \leq n$, where each $x_j^*(t)$ is the unique positive ω-periodic solution of the scalar periodic equation $dx_j/dt = x_j(P_j(t, V_1^*(t) - x_j) - D_0(t))$.

Then system (5.19) admits a positive ω-periodic solution, and all n-species are uniformly persistent.

As shown in the proof of Theorem 5.2.2, in the case where $D_i(t) = D_0(t)$, $\forall t \in [0, \omega]$, $1 \leq i \leq n$, it easily follows that $V_1^*(t) > x_i^*(t)$, $\forall t \in [0, \omega]$, $1 \leq i \leq n$. Thus, we have the following result for 2-species competition.

Corollary 5.3.2. *Let $D_i(t) = D_0(t)$, $\forall t \in [0, \omega]$, $1 \leq i \leq 2$. Assume that*

(1) $\int_0^\omega (P_i(t, V_1^*(t)) - D_0(t))\, dt > 0, \quad 1 \leq i \leq 2$;
(2) $\int_0^\omega \left(P_i(t, V_1^*(t) - x_j^*(t)) - D_0(t)\right) dt > 0$, $1 \leq i, j \leq 2$, $i \neq j$, where each $x_j^*(t)$ is the unique positive ω-periodic solution of the scalar periodic equation $dx_j/dt = x_j(P_j(t, V_1^*(t) - x_j) - D_0(t))$.

Then system (5.19) admits a positive, ω-periodic solution, and both species are uniformly persistent.

5.4 3-Species Competition

For 2-species competition in a periodic chemostat with $D_1(t) = D_2(t) = D_0(t), \forall t \in [0, \omega]$, it follows easily that $(x_1^*(t), 0)$ and $(0, x_2^*(t))$ are the semitrivial periodic solutions of the limiting 2-species competition system. Then, condition (2) in Corollary 5.3.2 is a natural invasibility condition. However, for n-species competition in the periodic chemostat, even with $D_j(\cdot) = D_0(\cdot), \forall 1 \leq j \leq n$, we see that each $(x_1^*(t), \dots, x_{i-1}^*(t), 0, x_{i+1}^*(t), \dots, x_n^*(t))$ is not the solution of the limiting n-species competition system determined using the conservation principle, and hence, due to our overestimation of the effect of competition, condition (2) in Corollary 5.3.1 is a stronger invasibility condition than necessary. In this section we show that whenever the positive, periodic solutions to each of the three, 2-species subsystems of the limiting 3-species competition system are unique, the expected natural invasibility conditions are sufficient to guarantee the uniform persistence of the three interacting species and enough to ensure the existence of at least one positive periodic solution for the full model system. We also give conditions for competition-mediated coexistence. Here, in at least one of the two species subsystems, one of the species is driven to extinction, regardless of the initial conditions. However, when the third species is introduced all three species coexist, again independent of the initial conditions, provided that they are all positive.

Consider the 3-species competition model in the periodic chemostat

$$\begin{aligned} \frac{dS(t)}{dt} &= (S^0(t) - S(t))D_0(t) - \sum_{i=1}^{3} P_i(t, S(t))x_i(t), \\ \frac{dx_i(t)}{dt} &= x_i(t)(P_i(t, S(t)) - D_0(t)), \qquad 1 \leq i \leq 3. \end{aligned} \tag{5.31}$$

Here $S^0(t)$, $D_0(t)$, and each $P_i(t,s)$, $1 \leq i \leq 3$, satisfy the same conditions as in (5.19), with $D_i(t) = D_0(t)$, $\forall t \in [0, \omega], 1 \leq i \leq 3$. Let $V_0^*(t)$ be the unique globally attractive positive ω-periodic solution of

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

For each $1 \leq i \leq 3$, let (E_i) be the 2-species periodic competition system

$$\frac{dx_j}{dt} = x_j \left(P_j \left(t, V_0^* - \sum_{k=1, k \neq i}^{3} x_k \right) - D_0(t) \right), \ 1 \leq j \leq 3, \ j \neq i. \tag{5.32}$$

We will distinguish three cases:

(C1) Each (E_i), $1 \leq i \leq 3$, admits at most one positive ω-periodic solution;
(C2) Each (E_i), $2 \leq i \leq 3$, admits at most one positive ω-periodic solution, and (E_1) admits no positive ω-periodic solution;

(C3) (E_2) admits at most one positive ω-periodic solution, and each (E_i), $i = 1, 3$, admits no positive ω-periodic solution.

Theorem 5.4.1. *Let (C1) hold. Assume that*

(1) $\mu_i := \int_0^\omega (P_i(t, V_0^*(t)) - D_0(t))dt > 0, \quad \forall 1 \le i \le 3$;
(2) $\mu_{ji} := \int_0^\omega (P_i(t, V_0^*(t) - x_j^*(t)) - D_0(t))dt > 0, \quad \forall 1 \le i, j \le 3,\ i \ne j$;
(3) $\bar{\mu}^i := \int_0^\omega (P_i(t, V_0^*(t) - \sum_{j=1, j\ne i}^3 \bar{x}_j^i(t)) - D_0(t))dt > 0, \quad \forall 1 \le i \le 3$;

where each $x_i^*(t)$ *is the unique positive* ω*-periodic solution of the scalar periodic equation*

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

and $(\bar{x}_2^1(t), \bar{x}_3^1(t)), (\bar{x}_1^2(t), \bar{x}_3^2(t))$ *and* $(\bar{x}_1^3(t), \bar{x}_2^3(t))$ *are the unique positive* ω*-periodic solutions of* $(E_1), (E_2)$*, and* (E_3)*, respectively. Then system (5.31) admits a positive* ω*-periodic solution, and there exist* $\alpha > 0$ *and* $\beta > 0$ *such that any solution* $(S(t), x_1(t), x_2(t), x_3(t))$ *of (5.31) with* $S(0) \ge 0$ *and* $x_i(0) > 0$, $\forall 1 \le i \le 3$, *satisfies*

$$0 < \alpha \le \liminf_{t\to\infty} x_i(t) \le \limsup_{t\to\infty} x_i(t) \le \beta, \quad \forall 1 \le i \le 3.$$

Proof. Let $\hat{P}_i(t, s) : \mathbb{R}_+ \times \mathbb{R} \to \mathbb{R}$ be any continuous extension of $P_i(t, s)$ on $\mathbb{R}_+ \times \mathbb{R}_+$ to $\mathbb{R}_+ \times \mathbb{R}$ such that $\hat{P}_i(t, s)$ is ω-periodic in t and locally Lipschitz in s, and for any $t \ge 0$, $\hat{P}_i(t, s)$ is strictly increasing with respect to $s \in \mathbb{R}$, $1 \le i \le 3$. As in the proof of Theorem 5.3.1, condition (1) implies that for each $1 \le i \le 3$, the periodic equation

$$\frac{dx_i}{dt} = x_i(P_i(t, V_0^*(t) - x_i) - D_i(t)) \tag{5.33}$$

admits a unique positive ω-periodic solution $x_i^*(t)$ with $V_0^*(t) > x_i^*(t)$, $\forall t \in [0, \omega]$, and $x_i^*(t)$ is globally attractive for the periodic equation

$$\frac{dx_i}{dt} = x_i(\hat{P}_i(t, V_0^*(t) - x_i) - D_i(t)) \tag{5.34}$$

in $\mathbb{R}_+ \setminus \{0\}$. For each $1 \le i \le 3$, let $(\hat{E}_i)$ be the system (5.32) with P_j replaced by $\hat{P}_j$, $j \ne i$. For the 2-species periodic competition system $(\hat{E}_3)$

$$\begin{aligned} \frac{dx_1}{dt} &= x_1(\hat{P}_1(t, V_0^*(t) - x_1 - x_2) - D_0(t)), \\ \frac{dx_2}{dt} &= x_2(\hat{P}_2(t, V_0^*(t) - x_1 - x_2) - D_0(t)), \end{aligned} \tag{5.35}$$

we claim that if $(\tilde{x}_1(t), \tilde{x}_2(t))$ is a positive ω-periodic solution to $(\hat{E}_3)$, then $(\tilde{x}_1(t), \tilde{x}_2(t))$ satisfies $V_0^*(t) > \tilde{x}_1(t) + \tilde{x}_2(t)$, $\forall t \in [0, \omega]$. Indeed, let $\tilde{x}_1(t_1) = \max_{0\le t\le\omega} \tilde{x}_1(t)$, $t_1 \in [0, \omega]$. Then $\frac{d\tilde{x}_1(t_1)}{dt} = 0$, and hence

$$\hat{P}_1(t_1, V_0^*(t_1) - \tilde{x}_1(t_1) - \tilde{x}_2(t_1)) = D_0(t_1) > 0.$$

Thus, since $\hat{P}_1(t_1, s)$ is strictly increasing for $s \in R$, we have $V_0^*(t_1) > \tilde{x}_1(t_1) + \tilde{x}_2(t_1)$. Let $y(t) = V_0^*(t) - \tilde{x}_1(t) - \tilde{x}_2(t)$. It then easily follows that $y(t)$ satisfies the following periodic differential equation

$$\frac{dy}{dt} = S^0(t)D_0(t) - D_0(t)y - \tilde{x}_1(t)\hat{P}_1(t, y) - \tilde{x}_2(t)\hat{P}_2(t, y).$$

Since $y(t_1) > 0$ and

$$\left.\frac{dy}{dt}\right|_{y=0} = S^0(t)D_0(t) > 0,$$

we have $y(t) > 0$, $\forall t \geq t_1$. Then the ω-periodicity of $y(t)$ implies that $y(t) > 0$, $\forall t \geq 0$; that is, $V_0^*(t) > \tilde{x}_1(t) + \tilde{x}_2(t)$, $\forall t \geq 0$. By conditions (1) and (2) with $1 \leq i, j \leq 2$, $i \neq j$, and Theorem 2.4.2, as applied to the Poincaré map associated with $(\hat{E}_3)$, or an argument similar to that in [152, IV.33], [325, Chapter 7], and [334], it easily follows that there are two positive ω-periodic solutions $(\underline{x}_1(t), \underline{x}_2(t))$ and $(\overline{x}_1(t), \overline{x}_2(t))$ to $(\hat{E}_3)$ with $0 < \underline{x}_1(t) \leq \overline{x}_1(t)$ and $0 < \overline{x}_2(t) \leq \underline{x}_2(t)$, $\forall t \in [0, \omega]$, such that each solution $(x_1(t), x_2(t))$ of $(\hat{E}_3)$ with $x_1(0) > 0$ and $x_2(t) > 0$ satisfies

$$\lim_{t \to \infty} d\left(x_1(t), [\underline{x}_1(t), \overline{x}_1(t)]\right) = 0$$

and

$$\lim_{t \to \infty} d\left(x_2(t), [\overline{x}_2(t), \underline{x}_2(t)]\right) = 0.$$

By the previous claim, we get $V_0^*(t) > \underline{x}_1(t) + \underline{x}_2(t)$ and $V_0^*(t) > \overline{x}_1(t) + \overline{x}_2(t)$, and hence both $(\underline{x}_1(t), \underline{x}_2(t))$ and $(\overline{x}_1(t), \overline{x}_2(t))$ are also positive periodic solutions of (E_3). Therefore, by the uniqueness assumption (C1), $(\underline{x}_1(t), \underline{x}_2(t)) = (\overline{x}_1(t), \overline{x}_2(t))$, $\forall t \in [0, \omega]$, and hence (E_3) admits a unique positive ω-periodic solution $(\bar{x}_1^3(t), \bar{x}_2^3(t))$ with $V_0^*(t) > \bar{x}_1^3(t) + \bar{x}_2^3(t)$, $\forall t \in [0, \omega]$. Furthermore, $(\bar{x}_1^3(t), \bar{x}_2^3(t))$ is globally attractive for $(\hat{E}_3)$ in $\mathrm{int}(\mathbb{R}_+^2)$. By a similar argument, it follows that (E_1) and (E_2) admit unique positive, ω-periodic solutions $(\bar{x}_2^1(t), \bar{x}_3^1(t))$ and $(\bar{x}_1^2(t), \bar{x}_3^2(t))$ with $V_0^*(t) > \bar{x}_2^1(t) + \bar{x}_3^1(t)$ and $V_0^*(t) > \bar{x}_1^2(t) + \bar{x}_3^2(t)$, $\forall t \in [0, \omega]$, respectively.

For the 3-species periodic competition system

$$\frac{dx_i}{dt} = x_i \left(\hat{P}_i \left(t, V_0^*(t) - \sum_{j=1}^{3} x_j \right) - D_0(t) \right), \ 1 \leq i \leq 3, \tag{5.36}$$

let $\phi_0(t, x)$ be the unique solution of (5.36) with $\phi_0(0, x) = x \in \mathbb{R}_+^3$. By a standard comparison theorem argument, it then easily follows that $\phi_0(t, x)$ exists globally on $[0, \infty)$, and solutions of (5.36) are uniformly and ultimately bounded. Let $X = \mathbb{R}_+^3$, and let $Q = \phi_0(\omega, \cdot)$ be the Poincaré map associated with (5.36). Then, $Q : X \to X$ is compact and point dissipative. Let

$$X_0 := \{(x_1, x_2, x_3) \in \mathbb{R}^3_+ : x_i > 0, \quad \forall 1 \leq i \leq 3\}, \quad \text{and} \quad \partial X_0 = X \setminus X_0.$$

Let $M_1 = (0,0,0)$, $M_2 = (x_1^*(0), 0, 0)$, $M_3 = (0, x_2^*(0), 0)$, $M_4 = (0, 0, x_3^*(0))$, $M_5 = (0, \bar{x}_2^1(0), \bar{x}_3^1(0))$, $M_6 = (\bar{x}_1^2(0), 0, \bar{x}_3^2)$, and $M_7 = (\bar{x}_1^3(0), \bar{x}_2^3, 0)$. Then each M_i is a fixed point of Q. For each $x \in X$, let $\omega(x)$ be the ω-limit set of x with respect to the discrete semiflow $\{Q^n\}_{n=0}^{\infty}$. Then, by our previous analysis, $\cup_{x \in \partial X_0} \omega(x) = \{M_1, M_2, \ldots, M_7\}$, and no subset of the M_i's forms a cycle for $Q|_{\partial X_0} : \partial X_0 \to \partial X_0$. By conditions (1), (2), and (3) and Lemma 5.1.1, it follows that each M_i is an isolated invariant set for Q in X_0, and hence isolated in X, since M_i is isolated for $Q|_{\partial X_0}$ in ∂X_0, and $Q : X_0 \to X_0$. Therefore, $\cup_{i=1}^7 M_i$ is an isolated and acyclic covering of $\cup_{x \in \partial X_0} \omega(x)$ in ∂X_0. Again by Lemma 5.1.1, we have $W^s(M_i) \cap X_0 = \emptyset$, $\forall 1 \leq i \leq 7$. By Theorem 1.3.1 and Remark 1.3.1, it follows that $Q : X \to X$ is uniformly persistent with respect to $(X_0, \partial X_0)$. Therefore, Theorem 1.3.6 implies that $Q : X_0 \to X_0$ has a global attractor A_0, and hence A_0 is globally asymptotically stable for Q in X_0.

Let $(S(t), x(t)) = (S(t), x_1(t), x_2(t), x_3(t))$ be a given solution of (5.31) with $S(0) \geq 0$ and $x_i(0) > 0, \forall 1 \leq i \leq 3$, and let $V(t) := S(t) + \sum_{i=1}^3 x_i(t)$, $\forall t \geq 0$. Then $S(t) > 0, x_i(t) > 0$, $\forall t > 0, 1 \leq i \leq 3$, and $V(t)$ satisfies

$$\frac{dV(t)}{dt} = (S^0(t) - V(t))D_0(t). \tag{5.37}$$

Thus, $(S(t), x(t))$ exists globally on $[0, \infty)$. It follows that $\lim_{t \to \infty} |V(t) - V_0^*(t)| = 0$, and $x(t)$ satisfies the 3-dimensional nonautonomous system

$$\frac{dx_i}{dt} = x_i \left(\hat{P}_i \left(t, V(t) - \sum_{j=1}^{3} x_j \right) - D_0(t) \right), \quad 1 \leq i \leq 3, \tag{5.38}$$

with

$$\lim_{t \to \infty} \left(\hat{P}_i \left(t, V(t) - \sum_{i=1}^{3} x_j \right) - \hat{P} \left(t, V_0^*(t) - \sum_{i=1}^{3} x_j \right) \right) = 0 \tag{5.39}$$

uniformly for $x = (x_1, x_2, x_3)$ in any bounded subset of $\mathbb{R}^3_+$, $1 \leq i \leq 3$. By the boundedness of $V(t)$, it is easy to see that solutions of (5.38) are uniformly bounded in $\mathbb{R}^3_+$. Let $\phi(t, s, x)$, $t \geq s$, be the unique solution of (5.38) with $\phi(s, s, x) = x \in X := \mathbb{R}^3_+$. By Proposition 3.2.2, $\phi(t, s, x)$ is asymptotic to the ω-periodic semiflow $T(t) = \phi_0(t, \cdot) : X \to X$, and hence $T_n(x) = \phi(n\omega, 0, x) : X \to X$, $n \geq 0$, is an asymptotically autonomous discrete process with limiting autonomous discrete semiflow $Q^n : X \to X, n \geq 0$, where $Q = T(\omega)$ is the Poincaré map associated with (5.36). By conditions (1), (2), and (3) and Lemma 5.1.2, it follows that $\widetilde{W}^s(M_i) \cap X_0 = \emptyset, \forall 1 \leq i \leq 7$. By Lemma 1.2.2, every ω-limit set $\omega(x)$ of $\gamma^+(x) = \{T_n(x) : n \geq 0\}$ is internally chain transitive for $Q : X \to X$. By Theorem 1.2.1, we get $\omega(x) \subset A_0$. Then Theorem 3.2.1 implies that

$$\lim_{t\to\infty} d(\phi(t,0,x), T(t)A_0) = 0, \quad \forall x \in X_0.$$

Since $T(\omega)A_0 = A_0$ and $T(t)$ is an ω-periodic semiflow, it follows that

$$\lim_{t\to\infty} d(\phi(t,0,x), A_0^*) = 0,$$

where $A_0^* = \cup_{t\in[0,\omega]} T(t)A_0$ is a compact subset of X_0. In particular, since $x(0) \in X_0$, we have

$$\lim_{t\to\infty} d(x(t), A_0^*) = \lim_{t\to\infty} d(\phi(t,0,x(0)), A_0^*) = 0.$$

Therefore, there exist $\alpha > 0$ and $\beta > 0$, which depend only on A_0^*, such that the solution $(S(t), x(t))$ of (5.31) with $S(0) \geq 0$ and $x_i(0) > 0$, $\forall 1 \leq i \leq 3$, satisfies

$$0 < \alpha \leq \liminf_{t\to\infty} x_i(t) \leq \limsup_{t\to\infty} x_i(t) \leq \beta, \quad \forall 1 \leq i \leq 3.$$

By the last part of the proof of Theorem 5.3.1, it follows that system (5.31) admits a positive periodic solution. ∎

Theorem 5.4.2. *Let (C2) hold. Assume that*

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

where $x_i^*(t)$*,* $(\bar{x}_1^2(t), \bar{x}_3^2(t))$ *and* $(\bar{x}_1^3(t), \bar{x}_2^3(t))$ *are as in Theorem 5.4.1. Then the conclusion of Theorem 5.4.1 holds.*

Proof. We use the same notation as in the proof of Theorem 5.4.1. By the a priori estimate on the positive periodic solution of $(\hat{E}_1)$ claimed in the proof of Theorem 5.4.1, (C2) implies that $(\hat{E}_1)$ admits no positive periodic solution. Since $\int_0^\omega (P_2(t, V_0^*(t) - x_3^*(t)) - D_0(t))dt > 0$, by Theorem 2.4.1, as applied to the Poincaré map associated with $(\hat{E}_1)$, or an argument similar to that in the proof of [152, Theorem 34.1], it easily follows that $(u_2^*(t), 0)$ is globally attractive for $(\hat{E}_1)$ in $\mathrm{int}(\mathbb{R}_+^2)$. Clearly, $\cup_{x\in\partial X_0}\omega(x) = \{M_1, M_2, M_3, M_4, M_6, M_7\}$. Then, as in the proof of Theorem 5.4.1, $\cup_{i=1, i\neq 5}^7 M_i$ is an isolated and acyclic covering of $\cup_{x\in\partial X_0}\omega(x)$ in ∂X_0. Now an argument similar to that given in Theorem 5.4.1 completes the proof. ∎

It is worth pointing out that Theorem 5.4.2 shows competition-mediated coexistence in the following sense. If species one is absent, and species two and three compete, then species two drives species three to extinction. However, this extinction of species three is avoided simply by introducing competitor one. Once competitor one is introduced, all three species persist in sustained oscillation.

Theorem 5.4.3. *Let (C3) hold. Assume that*

(1) $\mu_i := \int_0^\omega (P_i(t, V_0^*(t)) - D_0(t))dt > 0, \quad \forall 1 \le i \le 3$*;*
(2) $\mu_{3i} := \int_0^\omega (P_i(t, V_0^*(t) - x_3^*(t)) - D_0(t))dt > 0, \quad \forall 1 \le i \le 2$, $\mu_{21} := \int_0^\omega (P_1(t, V_0^*(t) - x_2^*(t)) - D_0(t))dt > 0$, *and* $\mu_{13} := \int_0^\omega (P_3(t, V_0^*(t) - x_1^*(t)) - D_0(t))dt > 0$*;*
(3) $\bar{\mu}^2 := \int_0^\omega (P_2(t, V_0^*(t) - \sum_{j=1, j\neq 2}^3 \bar{x}_j^2(t)) - D_0(t))dt > 0$*;*

where $x_i^*(t)$ *and* $(\bar{x}_1^2(t), \bar{x}_3^2(t))$ *are as in Theorem 5.4.1. Then the conclusion of Theorem 5.4.1 holds.*

Proof. Again we use the same notation as in the proof of Theorem 5.4.1. As in the proof of Theorem 5.4.2, (C3) implies that $(u_2^*(t), 0)$ and $(u_1^*(t), 0)$ are globally attractive for $(\hat{E}_1)$ and $(\hat{E}_3)$ in $\mathrm{int}(\mathbb{R}_+^2)$, respectively. Clearly, $\cup_{x \in \partial X_0} \omega(x) = \{M_1, M_2, M_3, M_4, M_6\}$. Then, as in the proof of Theorem 5.4.1, $\cup_{i=1, i\neq 5}^6 M_i$ is an isolated and acyclic covering of $\cup_{x\in\partial X_0}\omega(x)$ in ∂X_0. Now again, an argument similar to that given in Theorem 5.4.1 completes the proof. ∎

Remark 5.4.1. If instead of assumption (C1), we let M_5, M_6, and M_7, in the proof of Theorem 5.4.1, be three positive global attractors of the Poincaré maps associated with the three 2-dimensional competition systems $(\hat{E}_1)$, $(\hat{E}_2)$, and $(\hat{E}_3)$, respectively, then by a similar argument, the conclusion of Theorem 5.4.1 holds with condition (3) replaced by a revised invasibility condition. For example, let $(\underline{x}_1(t), \underline{x}_2(t))$ and $(\overline{x}_1(t), \overline{x}_2(t))$ be as in the proof of Theorem 5.4.1. Then, under condition (3) with $i = 3$ and $(\bar{x}_1^3(t), \bar{x}_2^3(t))$ replaced by $(\overline{x}_1(t), \underline{x}_2(t))$, one can prove that M_7 is an isolated invariant set of Q in X and $\widetilde{W}^s(M_7) \cap X_0 = \emptyset$, by using the compressivity of $(\hat{E}_3)$ and arguments similar to those given in Lemmas 5.1.1 and 5.1.2.

5.5 Notes

This chapter is adapted from Wolkowicz and Zhao [407]. Smith and Waltman [334, Chapter 7] discussed in detail 2-species competition in the chemostat with periodic dilution rate by appealing to the theory of monotone dynamical systems. There are some other researches on models of the chemostat involving either periodic nutrient input or periodic dilution rates (see, e.g., [347, 170, 316, 92, 144, 47, 419, 217, 218, 274]). A model of two species competition in the unstirred chemostat with periodic input and washout was studied by Pilyugin and Waltman [278]. Furthermore, the periodic gradostat was considered by Smith [322, 325]. The elementary comparison and fixed point arguments for the existence of positive periodic solutions in Theorem 5.2.2 were motivated by ideas in Zhao [429].

Smith [328] studied a periodically forced Droop model for phytoplankton growth in a chemostat, and White and Zhao [404] considered a periodic Droop model for two species competition in a chemostat. Recently, Hsu, Wang and Zhao [177] investigated the global dynamics of a variable-yield model of two species competing for two essential nutrients with nutrient concentration inflow varying periodically in time.

6

Almost Periodic Competitive Systems

In the periodic chemostat model discussed in the previous chapter, we assumed that the nutrient input, dilution, and species-specific removal rates were all periodic with commensurate period. It is possible for these parameters to have different periods. Ecologically, a population may be of some inherent periodic variation that may be different from the seasonal variation. This way we naturally obtain special almost periodic systems. Moreover, the almost periodicity can also be viewed as a deterministic version of a random variation in the environment. This chapter is devoted to the study of the long-term behavior of solutions and almost periodic coexistence states in almost periodic Kolmogrov competitive systems of ordinary differential equations and an almost periodic chemostat. We also discuss competitive coexistence in nonautonomous two-species competitive Lotka–Volterra systems.

In Section 6.1 we establish a threshold-type result for scalar asymptotically almost periodic Kolmogrov equations: Either the trivial solution or the unique positive almost periodic solution of the limiting almost periodic equation attracts all positive solutions, depending on the linear stability of the trivial solution. In Section 6.2, by the threshold-type result and the comparison technique, we obtain a set of sufficient conditions for n competing species to be uniformly persistent. Under further conditions of main diagonally dominant nature, we prove the existence and global attractivity of a unique positive periodic solution by constructing a Liapunov function. Section 6.3 is devoted to the study of a single population growth model in an almost periodic chemostat. In the case where the nutrient input and washout rate and the specific removal rate of the species are identical, we prove that the convergence of the species to zero (extinction) or to a positive almost periodic function (survival) is completely characterized by the mean value of the uptake function along a certain almost periodic function. The permanence and extinction are also considered when the nutrient input and washout rate is different from the specific removal rate of the species. In Section 6.4, as an application of the

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no-cycle theorem on uniform persistence in processes (nonautonomous semiflows), we obtain a natural invasion condition for the competitive coexistence in nonautonomous two-species competitive Lotka–Volterra systems.

6.1 Almost Periodic Attractors in Scalar Equations

In this section we first establish threshold dynamics for scalar almost periodic Kolmogrov equations, and then extend them to the asymptotically almost periodic case.

Let $g : \mathbb{R} \to \mathbb{R}$ be a continuous almost periodic function. Then the mean value $m(g) := \lim_{T\to+\infty} \frac{1}{T}\int_0^T g(t)dt$ exists and $\lim_{v\to\infty} \frac{1}{v}\int_{t-v}^t g(s)ds = m(g)$ uniformly for $t \in \mathbb{R}$ (see [117, Theorem 3.1 and Corollary 3.2]). Moreover, we have the following result.

Lemma 6.1.1. *Let $p(\cdot)$ be a continuous almost periodic function on $\mathbb{R}$ with $m(p) < 0$, and let $q : \mathbb{R}_+ \to \mathbb{R}$ be a continuous function. If $q(\cdot)$ is bounded, then solutions of the linear nonautonomous equation*

$$\frac{dx}{dt} = p(t)x + q(t), \qquad t \geq 0, \tag{6.1}$$

are ultimately bounded; If $\lim_{t\to\infty} q(t) = 0$, then every solution $x(t)$ of (6.1) satisfies $\lim_{t\to\infty} x(t) = 0$.

Proof. For $x_0 \in \mathbb{R}$, let $x(t)$ be the unique solution of (6.1) with $x(0) = x_0$. Then

$$x(t) = x_0 e^{\int_0^t p(s)ds} + \int_0^t e^{\int_u^t p(s)ds} q(u)du, \quad \forall t \geq 0,$$

and hence

$$|x(t)| \leq |x_0| e^{\int_0^t p(s)ds} + \sup_{t\in\mathbb{R}_+} \{|q(t)|\} \int_0^t e^{\int_u^t p(s)ds} du, \ \forall t \geq 0.$$

Let $p_0 := m(p) < 0$. Then there exists $t_0 > 0$ such that

$$\frac{1}{t}\int_0^t p(s)ds < \frac{p_0}{2}, \qquad \forall t \geq t_0,$$

and hence $\lim_{t\to\infty} e^{\int_0^t p(s)ds} = 0$. Since $p(t)$ is almost periodic,

$$\lim_{v\to\infty} \frac{1}{v}\int_{t-v}^t p(s)ds = p_0 < 0, \qquad \text{uniformly for} \quad t \in \mathbb{R}.$$

Then there exists $T_0 > 0$ such that for all $v \geq T_0$,

$$\frac{1}{v}\int_{t-v}^t p(s)ds < \frac{p_0}{2} < 0, \qquad \forall t \in \mathbb{R}.$$

Let $\bar{p} := \sup_{t\in\mathbb{R}_+}\{|p(t)|\}$. Then for $t \geq T_0$,

$$\begin{aligned}\int_0^t e^{\int_u^t p(s)ds}du &= \int_0^{T_0} e^{\int_{t-v}^t p(s)ds}dv + \int_{T_0}^t e^{\int_{t-v}^t p(s)ds}dv \\ &\leq \int_0^{T_0} e^{\bar{p}v}dv + \int_{T_0}^t e^{\frac{p_0}{2}v}dv \\ &= \frac{1}{\bar{p}}\left(e^{\bar{p}T_0}-1\right) + \frac{2}{p_0}\left(e^{\frac{p_0}{2}t} - e^{\frac{p_0}{2}T_0}\right).\end{aligned}$$

Clearly, $\lim_{t\to+\infty} e^{\frac{p_0}{2}t} = 0$. It then follows that for sufficiently large t, $|x(t)|$ is bounded by

$$B = \sup_{t\in\mathbb{R}_+}\{|q(t)|\}\left[\frac{1}{\bar{p}}\left(e^{\bar{p}T_0}-1\right) - \frac{2}{p_0}e^{\frac{p_0}{2}T_0}\right] + 1 > 0.$$

Note that B is independent of the choice of $x_0 \in \mathbb{R}$. So solutions of (6.1) are ultimately bounded for B.

In the case where $\lim_{t\to\infty} q(t) = 0$, let $M = \sup_{t\in\mathbb{R}_+}\{|q(t)|\} \geq 0$. For $\epsilon > 0$, since $\lim_{t\to\infty} e^{\frac{p_0}{2}t} = 0$, there exists $T_1 = T_1(\epsilon) \geq T_0$ such that $\frac{4M}{|p_0|}e^{\frac{p_0}{2}T_1} < \frac{\epsilon}{2}$. Since $\lim_{t\to\infty} q(t) = 0$, there exists $T_2 = T_2(\epsilon) \geq T_1$ such that

$$\int_0^{T_1(\epsilon)} e^{\bar{p}v}|q(t-v)|dv < \frac{\epsilon}{2}, \qquad \forall t \geq T_2.$$

It follows that for all $t \geq T_2$,

$$\begin{aligned}\left|\int_0^t e^{\int_u^t p(s)ds}q(u)du\right| &= \left|\int_0^t e^{\int_{t-v}^t p(s)ds}q(t-v)dv\right| \\ &\leq \int_0^{T_1} e^{\int_{t-v}^t p(s)ds}|q(t-v)|dv + \int_{T_1}^t e^{\frac{p_0}{2}v}|q(t-v)|dv \\ &\leq \int_0^{T_1} e^{\bar{p}v}|q(t-v)|dv + \frac{4M}{|p_0|}e^{\frac{p_0}{2}T_1} \\ &< \frac{\epsilon}{2} + \frac{\epsilon}{2} = \epsilon.\end{aligned}$$

Then $\lim_{t\to\infty}\int_0^t e^{\int_u^t p(s)ds}q(u)du = 0$, and hence $\lim_{t\to\infty} x(t) = 0$. ∎

Consider first a scalar almost periodic Kolmogorov equation

$$\frac{du}{dt} = uf(t,u) \tag{6.2}$$

where $f : \mathbb{R}\times\mathbb{R}_+ \to \mathbb{R}$ is continuous and almost periodic with respect to t uniformly for u in any bounded subset of $\mathbb{R}_+$. Moreover, we assume that $f(t,u)$ is continuously differentiable with respect to $u \in \mathbb{R}_+$ and $f_u(t,u) := \frac{\partial f(t,u)}{\partial u}$ is bounded for all $t \in \mathbb{R}$ and for all u in any bounded subset of $\mathbb{R}_+$. We will impose the following conditions on (6.2):

(C1) Solutions of equation (6.2) in $\mathbb{R}_+$ are ultimately bounded for a bound $K > 0$; that is, for any $u_0 \in \mathbb{R}_+$, there exists $T = T(u_0) > 0$ such that the unique solution $u(t)$ of (6.2) with $u(0) = u_0$ satisfies $|u(t)| \leq K$, $\forall t \geq T$;

(C2) $f(t, u) \leq f(t, 0)$, $\forall u \geq 0$, and there exist a continuously differentiable $\beta : (0, \infty) \to (0, \infty)$, an almost periodic function $b : \mathbb{R} \to \mathbb{R}$ with $m(b) < 0$, and a real number $K_1 > K$ such that $\frac{\partial(f(t,u)\beta(u))}{\partial u} \leq 0$, $\forall t \in \mathbb{R}_+$, $u \in (0, K_1]$; and $\frac{\partial(f(t,u)\beta(u))}{\partial u} \leq b(t)$, $\forall t \in R, u \in (0, K]$.

Then we have the following threshold-type result on the global dynamics of (6.2).

Theorem 6.1.1. *Let* $(C1)$ *and* $(C2)$ *hold.*

(a) If $m(f(\cdot, 0)) < 0$*, then* $u = 0$ *is a globally asymptotically stable solution of (6.2) in* $\mathbb{R}_+$*;*

(b) If $m(f(\cdot, 0)) > 0$*, then (6.2) admits a unique positive almost periodic solution, which is globally asymptotically stable in* $\mathbb{R}_+ \setminus \{0\}$*.*

Proof. For $u_0 \in \mathbb{R}_+$, let $\phi(t, u_0)$ be the unique solution of (6.2) with $\phi(0, u_0) = u_0$. Then condition (C1) implies that $\phi(t, u_0)$ exists globally on $[0, \infty)$. Clearly, for any $u_0 \in \mathbb{R}_+$, $\phi(t, u_0) \geq 0$, $\forall t \geq 0$.

In the case where $m(f(\cdot, 0)) < 0$, by condition (C2), for any $u_0 \in \mathbb{R}_+$, $u(t) := \phi(t, u_0)$ satisfies

$$\frac{du}{dt} = uf(t, u) \leq uf(t, 0), \qquad \forall t \geq 0.$$

By the comparison theorem, it follows that

$$\phi(t, u_0) \leq u_0 e^{\int_0^t f(s,0)ds}, \quad \forall t \geq 0, \qquad u \in \mathbb{R}_+.$$

Since $m(f(\cdot, 0)) < 0$, $\lim_{t\to\infty} e^{\int_0^t f(s,0)ds} = 0$. This implies that $u = 0$ is globally asymptotically stable with respect to nonnegative initial values.

In the case where $m(f(\cdot, 0)) > 0$, let $h(t) = \min_{0 \leq u \leq K} f_u(t, u)$, $\forall t \in \mathbb{R}$. Then $h : \mathbb{R} \to \mathbb{R}$ is a bounded and continuous function. For any $u_0 > 0$, by the ultimate boundedness of $\phi(t, u_0)$, there exists $t_0 = t_0(u_0) > 0$ such that $u(t) = \phi(t, u_0) \in (0, K]$, $\forall t \geq t_0$. Let $u_1(t) = u(t + t_0)$. Then $u_1(t) \in (0, K]$, $\forall t \geq 0$, and $u_1(t)$ satisfies

$$\begin{aligned}
\frac{du_1(t)}{dt} &= u_1(t) f(t + t_0, u_1(t)) \\
&= u_1(t) \left[f(t + t_0, 0) + \int_0^1 \frac{d}{ds} f(t + t_0, su_1(t)) ds \right] \\
&= u_1(t) \left[f(t + t_0, 0) + \left(\int_0^1 f_u(t + t_0, su_1(t)) ds \right) u_1(t) \right] \\
&\geq u_1(t) \left[f(t + t_0, 0) + h(t + t_0) u_1(t) \right], \quad \forall t \geq 0.
\end{aligned}$$

By the comparison theorem, it follows that

$$u_1(t) \geq \phi_0(t, u_0), \quad \forall t \geq 0,$$

where $\phi_0(t, u_0)$ is the unique solution of the nonautonomous equation

$$\frac{du}{dt} = u\left[f(t + t_0, 0) + h(t + t_0)u\right] \tag{6.3}$$

with $\phi_0(0, u_0) = u_0 > 0$. Clearly, $\phi_0(t, u_0) > 0, \forall t \geq 0$. Let $v = \frac{1}{u}$, $u > 0$. Then (6.3) is transformed into the following linear equation

$$\frac{dv}{dt} = -f(t + t_0, 0)v - h(t + t_0). \tag{6.4}$$

Since $m(-f(\cdot + t_0, 0)) = -m(f(\cdot, 0)) < 0$, by the almost periodicity of $f(\cdot, 0)$, the boundedness of $m(\cdot)$, the choice of T_0, and the explicit expression of the bound B in Lemma 6.1.1, it follows that there exists $B_0 > 0$, independent of $t_0 > 0$, such that solutions of (6.4) are ultimately bounded by B_0. Then $u_1(t)$, and hence $u(t)$, is ultimately bounded below by $\alpha = 1/B_0$. Therefore, equation (6.2) is permanent in $\mathbb{R}_+$; that is, for any $u_0 > 0$, there exists $T = T(u_0) > 0$ such that $0 < \alpha \leq \phi(t, u_0) \leq K, \quad \forall t \geq T$.

Let $u(t)$ be the solution of (6.2) with $u(0) > 0$. Then there exists $T_0 > 0$ such that $0 < \alpha \leq u(t) \leq K, \quad \forall t \geq T_0$. We further claim that $u(t)$, $t \geq 0$, has the property that for any sequence $\{t'_k\}$ with $t'_k > 0$ and $t'_k \to \infty$ as $k \to \infty$, there exists a subsequence $\{t_m\}$ of $\{t'_k\}$ such that $u(t + t_m)$ converges uniformly on $\mathbb{R}_+$. Indeed, since $\{u(t'_k)\}_{k=1}^{\infty}$ is bounded and $f(t, u)$ is almost periodic in t uniformly for u in any bounded subset of $\mathbb{R}_+$, we can choose a subsequence $\{t_m\}$ of $\{t'_k\}$ with $t_m \geq T_0$, $m \geq 1$, such that $u(t_m)$ converges and $f(t + t_m, u)$ converges uniformly on $\mathbb{R} \times [0, K]$ as $m \to \infty$ (see [421, Theorem 2.2]). Let $u_m(t) = u(t + t_m)$, $\forall t \geq 0, m \geq 1$. Then

$$\alpha \leq u_m(t) \leq K, \quad \forall t \geq 0, m \geq 1. \tag{6.5}$$

Define

$$\gamma(s) := \beta(s)/s, \ \forall s > 0, \quad \text{and} \quad V(u, v) := \left(\int_u^v \gamma(s)ds\right)^2, \ \forall u, v > 0.$$

Since $\gamma(s) > 0, \ \forall s \in [\alpha, K]$, there exist D_1 and $D_2 \in (0, \infty)$ such that

$$D_1^2(u - v)^2 \leq V(u, v) \leq D_2^2(u - v)^2, \qquad \forall u, v \in [\alpha, K]. \tag{6.6}$$

Let $V'(t) = \frac{d}{dt}V(u_m(t), u_n(t))$ and

$$g(t, t_m, t_n) = 2\int_{u_n(t)}^{u_m(t)} \gamma(s)ds \cdot \beta(u_n(t))\left[f(t + t_m, u_n(t)) - f(t + t_n, u_n(t))\right].$$

Then by the mean value theorem and condition (C2), we have

$$\begin{aligned} V'(t) &= 2\int_{u_n}^{u_m} \gamma(s)ds\,[\beta(u_m)f(t+t_m,u_m)-\beta(u_n)f(t+t_n,u_n)] \\ &= 2\int_{u_n}^{u_m} \gamma(s)ds\,[\beta(u_m)f(t+t_m,u_m)-\beta(u_n)f(t+t_m,u_n)] \\ &\quad + g(t,t_m,t_n) \\ &= 2(u_m-u_n)\int_{u_n}^{u_m} \gamma(s)ds\,\left.\frac{\partial(\beta(u)f(t+t_m,u))}{\partial u}\right|_{u=\xi} \\ &\quad + g(t,t_m,t_n) \\ &\le \frac{2}{D_2}V(u_n(t),u_m(t))b(t+t_m)+g(t,t_m,t_n), \end{aligned}$$

where $\xi=\xi(t)$ is between $u_m(t)$ and $u_n(t)$. By the comparison theorem, we get

$$\begin{aligned} V(u_n(t),u_m(t)) \le{} & V(u_n(0),u_m(0))e^{\int_0^t \frac{2}{D_2}b(s+t_m)ds} \\ & + \int_0^t e^{\int_u^t \frac{2}{D_2}b(s+t_m)ds}g(u,t_m,t_n)du. \end{aligned} \tag{6.7}$$

Using the almost periodicity of $b(\cdot)$ on $\mathbb{R}$, as in the proof of Lemma 6.1.1, we can obtain $B_1>0$ and $B_2>0$, which are independent of t_m, $m\ge 1$, such that

$$e^{\int_0^t \frac{2}{D_2}b(s+t_m)ds} \le B_1 \quad \text{and} \quad \int_0^t e^{\int_u^t \frac{2}{D_2}b(s+t_m)ds}du \le B_2, \quad \forall t\ge 0.$$

By (6.5) and the choice of $\{t_m\}_{m=1}^{\infty}$, we have $\lim_{m,n\to\infty}(u(t_n)-u(t_m))=0$, and hence

$$\lim_{m,n\to\infty} V(u_n(0),u_m(0)) = \lim_{m,n\to\infty} V(u(t_n),u(t_m))=0$$

and

$$\lim_{m,n\to\infty} g(t,t_m,t_n)=0, \text{ uniformly for } t\in\mathbb{R}_+.$$

By (6.7), it follows that

$$\lim_{m,n\to\infty} V(u_n(t),u_m(t))=0, \text{ uniformly for } t\in\mathbb{R}_+.$$

Then (6.6) implies that

$$\lim_{m,n\to\infty}(u(t+t_m)-u(t+t_n))=0, \text{ uniformly for } t\in\mathbb{R}_+.$$

That is, $\{u(t+t_m)\}$ converges uniformly on $\mathbb{R}_+$. By [421, Theorems 3.10 and 3.9], it then follows that $u(t)$ is asymptotic to an almost periodic function $p(t)$; that is, $\lim_{t\to\infty}(u(t)-p(t))=0$. By [421, Theorem 16.1], $p(t)$ is an almost periodic solution of (6.2). Since $p(t)$ is almost periodic, there exists a sequence $\tau_k\to\infty$ such that $p(t+\tau_k)\to p(t)$ uniformly for $t\in\mathbb{R}$ as $k\to\infty$. Let

$q(t) = u(t) - p(t)$. Then $\lim_{t\to\infty} q(t) = 0$. For any $t \in \mathbb{R}$, when k is sufficiently large, $t + \tau_k \geq T_0$, and hence $\alpha \leq u(t + \tau_k) = p(t + \tau_k) + q(t + \tau_k) \leq K$. Taking $k \to \infty$, we get $\alpha \leq p(t) \leq K$, $\forall t \in \mathbb{R}$. Let $p_1(t)$ and $p_2(t)$ be two almost periodic solutions of (6.2) with $p_i(t) \in [\alpha, K]$, $\forall t \in \mathbb{R}, i = 1, 2$. Then, as in the previous argument, we have

$$\frac{d}{dt}V(p_1(t), p_2(t)) \leq \frac{2}{D_2}b(t)V(p_1(t), p_2(t)), \quad \forall t \in \mathbb{R}.$$

Hence, by the comparison theorem, we get

$$V(p_1(t), p_2(t)) \leq V(p_1(0), p_2(0))e^{\int_0^t \frac{2}{D_2}b(s)ds}, \quad \forall t \geq 0.$$

Since $p_1(t) - p_2(t)$ are almost periodic, there exists a sequence $t_k \to \infty$ such that

$$\lim_{k\to\infty}[p_1(t + t_k) - p_2(t + t_k)] = p_1(t) - p_2(t), \text{ uniformly for } t \in \mathbb{R}.$$

For any $t \in \mathbb{R}$, when k is sufficiently large, $t + t_k \geq 0$, and hence

$$\begin{aligned} D_1^2[p_1(t + t_k) - p_2(t + t_k]^2 &\leq V(p_1(t + t_k), p_2(t + t_k)) \\ &\leq V(p_1(0), p_2(0))e^{\frac{2}{D_2}\int_0^{t+t_k} b(s)ds}. \end{aligned}$$

Taking $k \to \infty$ and using the fact $\lim_{t\to\infty} e^{\frac{2}{D_2}\int_0^t b(s)ds} = 0$, we have $D_1^2[p_1(t) - p_2(t)]^2 = 0$. Then $p_1(t) = p_2(t)$, $\forall t \in \mathbb{R}$. Therefore, there exists a unique almost periodic solution $p(t)$ with $p(t) \in [\alpha, K]$, $\forall t \in \mathbb{R}$, such that every solution $u(t)$ of (6.2) with $u(0) > 0$ satisfies $\lim_{t\to\infty}(u(t) - p(t)) = 0$.

It remains to prove the stability of $p(t)$ with respect to (6.2). Let $\alpha_1 \in (0, \alpha)$ be fixed. Since $p(t) \in [\alpha, K]$, $\forall t \in \mathbb{R}$, there exists $\delta > 0$ such that

$$\alpha_1 < p(t) + y < K_1, \qquad \forall t \in \mathbb{R}, \quad y \in (-\delta, \delta).$$

Let $W(t, y) = V(y + p(t), p(t))$, $\forall t \geq 0, |y| < \delta$. Then for some $\bar{D}_1$ and $\bar{D}_2 \in (0, \infty)$, dependent on α_1 and K_1, we have

$$\bar{D}_1^2 y^2 \leq W(t, y) \leq \bar{D}_2^2 y^2, \ \forall t \geq 0, \ |y| < \delta.$$

By condition (C2), it follows, under the transformation $y = x - p(t)$, that the derivative function of $W(t, y)$ for the resulting equation satisfies

$$\frac{dW}{dt}(t, y) = 2\int_{p(t)}^{y+p(t)} \gamma(s)ds\,[\beta(y + p(t))f(t, y + p(t)) - \beta(p(t))f(t, p(t))] \leq 0$$

for all $t \geq 0, |y| < \delta$. Thus, by the standard Liapunov stability theorem, $y = 0$ is a stable solution of the resulting equation, and hence $p(t)$ is a stable solution of (6.2). ∎

Remark 6.1.1. By the proof of Theorem 6.1.1, if we assume, instead of (C2), that $\frac{\partial(f(t,u)\beta(u))}{\partial u} \leq 0$, $\forall t \in \mathbb{R}, u \in (0, K]$, and that there exists an almost periodic function $b : \mathbb{R} \to \mathbb{R}$ such that $m(b(\cdot)) < 0$ and $\frac{\partial(f(t,u)\beta(u))}{\partial u} \leq b(t)$, $\forall t \in \mathbb{R}, u \in (0, K]$, then we have the global attractivity of a unique positive almost periodic solution of (6.2) in case (b).

We now extend the above result to an asymptotically almost periodic Kolmogorov equation

$$\frac{du}{dt} = uf(t,u) \tag{6.8}$$

where $f : \mathbb{R} \times \mathbb{R}_+ \to \mathbb{R}$ is continuous and locally Lipschitz for $u \in \mathbb{R}$, and there exists a continuous function $f_0 : \mathbb{R} \times \mathbb{R}_+ \to \mathbb{R}$, continuously differentiable with respect to $u \in \mathbb{R}_+$ and almost periodic with respect to t uniformly for u in any bounded subset of $\mathbb{R}_+$, such that

(B1) $\lim_{t\to+\infty} |f(t,u) - f_0(t,u)| = 0$ uniformly for u in any bounded subset of $\mathbb{R}_+$.

We further assume that

(B2) Solutions of the equation $\frac{du}{dt} = uf_0(t,u)$ in $\mathbb{R}_+$ are ultimately bounded;
(B3) $f_0(t,u) \leq f_0(t,0)$, $\forall t \geq 0, u \geq 0$; and there is a continuously differentiable $\beta : (0,\infty) \to (0,\infty)$ such that
  (i) $\frac{\partial(f_0(t,u)\beta(u))}{\partial u} \leq 0$, $\forall t \geq 0$, $u \geq 0$;
  (ii) for any given $a > 0$, there exists an almost periodic function $b : \mathbb{R} \to \mathbb{R}$ with $m(b) < 0$ such that $\frac{\partial(f_0(t,u)\beta(u))}{\partial u} \leq b(t)$, $\forall t \in \mathbb{R}$, $u \in (0, a]$.

Then we have the following result.

Theorem 6.1.2. *Let (B1)–(B3) hold.*

(1) If $m(f_0(\cdot,0)) < 0$, then for any bounded solution $u(t)$ of (6.8) with $u(0) \geq 0$, $\lim_{t\to+\infty} u(t) = 0$;
(2) If $m(f_0(\cdot,0)) > 0$, then there exists a unique positive almost periodic solution $u^*(t)$ of $\frac{du}{dt} = uf_0(t,u)$ such that for any bounded solution $u(t)$ of (6.8) with $u(0) > 0$, $\lim_{t\to+\infty}(u(t) - u^*(t)) = 0$.

Proof. Let $u(t)$ be a given bounded solution of (6.8) with $u(0) > 0$. Clearly, $u(t) > 0$, $\forall t \geq 0$.

In the case where $m(f_0(\cdot,0)) < 0$, since $u(t)$ satisfies

$$\frac{du}{dt} = uf(t,u) = uf_0(t,u) + u[f(t,u) - f_0(t,u)], \ \forall t \geq 0, \tag{6.9}$$

we have

$$\frac{du}{dt} \leq f_0(t,0)u + g_1(t), \qquad \forall t \geq 0,$$

where $g_1(t) := u(t)\,[f(t,u(t)) - f_0(t,u(t))]$. Then the boundedness of $u(t)$ and assumption (B1) imply that $\lim_{t\to+\infty} g_1(t) = 0$. By the comparison theorem, it follows that

$$0 \le u(t) \le \bar{u}(t), \qquad \forall t \ge 0, \tag{6.10}$$

where $\bar{u}(t)$ is the unique solution of the linear nonautonomous equation

$$\frac{du}{dt} = f_0(t,0)u + g_1(t) \tag{6.11}$$

with $\bar{u}(0) = u(0) > 0$. Since $m(f_0(\cdot,0)) < 0$, by Lemma 6.1.1 we have $\lim_{t\to\infty} \bar{u}(t) = 0$. Therefore, (6.10) implies $\lim_{t\to\infty} u(t) = 0$.

In the case where $m(f_0(\cdot,0)) > 0$, let $u^*(t)$ be the unique positive almost periodic solution of the almost periodic equation $\frac{du}{dt} = uf_0(t,u)$ claimed in Theorem 6.1.1 with $\beta \equiv 1$. As in case (b) of the proof of Theorem 6.1.1, we have

$$u(t) \ge u_0(t), \quad \forall t \ge 0,$$

where $u_0(t)$ is the unique solution with $u_0(0) = u(0) > 0$ of the nonautonomous equation

$$\frac{du}{dt} = u\,[f_0(t,0) + h(t)u + g_2(t)]\,, \tag{6.12}$$

where $h(t) := \min_{0\le u\le H} \frac{\partial f_0(t,u)}{\partial u}$, $\forall t \in \mathbb{R}$, $H := \sup_{t\in\mathbb{R}_+} |u(t)| \ge 0$, and $g_2(t) := f(t,u(t)) - f_0(t,u(t))$. Note that $h : \mathbb{R} \to \mathbb{R}$ is a bounded continuous function, $\lim_{t\to+\infty} g_2(t) = 0$, and $u_0(t) > 0$, $\forall t \ge 0$. Let $v = 1/u$, $u > 0$. Then (6.12) can be transformed into the linear nonautonomous equation

$$\frac{dv}{dt} = -f_0(t,0)v - g_2(t)v - h(t). \tag{6.13}$$

Let $0 < \epsilon_0 < m(f_0(\cdot,0))$ be fixed. Since $\lim_{t\to\infty} g_2(t) = 0$, there exists $t_0 > 0$ such that $g_2(t) + \epsilon_0 > 0$, $\forall t \ge t_0$. For solution $v(t)$ of (6.13), let

$$w(t) = v(t+t_0)e^{\int_0^t [g_2(s+t_0)+\epsilon_0]ds}, \quad \forall t \ge 0.$$

Then $w(t)$ satisfies the following linear equation

$$\frac{dw}{dt} = [-f_0(t+t_0,0) + \epsilon_0]w - h(t+t_0)e^{\int_0^t [g_2(s+t_0)+\epsilon_0]ds}. \tag{6.14}$$

Let $\bar{h}(t) = -h(t+t_0)$, $p(t) = -f_0(t+t_0,0) + \epsilon_0$, $M = \lim_{t\in\mathbb{R}} |h(t)|$ and $g(t) = g_2(t+t_0) + \epsilon_0$. Then, by the choice of ϵ_0, $m(p) = \epsilon_0 - m(f_0(\cdot + t_0, 0)) = \epsilon_0 - m(f_0(\cdot,0)) < 0$, and $g(t) > 0$, $\forall t \ge 0$. Therefore, the solution $w(t)$ of (6.14) with $w(0) = w_0$ satisfies

$$w(t) = w_0 e^{\int_0^t p(s)ds} + \int_0^t e^{\int_u^t p(s)ds}\bar{h}(u)e^{\int_0^u g(s)ds}du, \quad \forall t \ge 0.$$

It then follows that

$$|w(t)| \le |w_0| e^{\int_0^t p(s)ds} + M e^{\int_0^t g(s)ds} \cdot \int_0^t e^{\int_u^t p(s)ds} du.$$

As in the proof of Lemma 6.1.1, there exist $B_1 > 0$ and $T_1 > 0$ such that

$$\int_0^t e^{\int_u^t p(s)ds} du < B_1, \qquad \forall t \ge T_1,$$

and hence

$$|w(t| \le |w_0| e^{\int_0^t p(s)ds} + M B_1 e^{\int_0^t g(s)ds}, \qquad \forall t \ge T_1.$$

This, together with the fact that $g(t) > 0$ for $t \ge 0$, implies that the solution $v(t)$ of (6.13) satisfies

$$\begin{aligned} |v(t+t_0)| &\le |v(t_0)| e^{\int_0^t p(s)ds} e^{-\int_0^t g(s)ds} + MB_1 \\ &\le |v(t_0)| e^{\int_0^t p(s)ds} + MB_1, \quad \forall t \ge T_1. \end{aligned}$$

Since $\lim_{t\to\infty} e^{\int_0^t p(s)ds} = 0$, the solutions of (6.13) are ultimately bounded for the bound $B_2 = MB_1 + 1 > 0$. In particular, there exists $T_0 = T_0(u(0)) > 0$ such that for all $t \ge T_0$, $0 < \frac{1}{u_0(t)} \le B_2$; that is, $u_0(t) \ge 1/B_2 > 0, \forall t \ge T_0$. Therefore, there exist $\delta > 0$ and $\overline{H} > 0$ such that $\delta \le u(t), u^*(t) \le \overline{H}, \quad \forall t \ge 0$.

Let $V(t) := \left(\int_{u^*(t)}^{u(t)} \frac{\beta(s)}{s} ds \right)^2, \forall t \ge 0$. Then we have

$$\begin{aligned} \frac{dV(t)}{dt} &= 2 \int_{u^*(t)}^{u(t)} \frac{\beta(s)}{s} ds \left[f(t,u)\beta(u) - f_0(t,u^*)\beta(u^*) \right] \\ &= 2 \int_{u^*(t)}^{u(t)} \frac{\beta(s)}{s} ds \left[f_0(t,u)\beta(u) - f_0(t,u^*)\beta(u^*) \right] \\ &\quad + 2 \int_{u^*(t)}^{u(t)} \frac{\beta(s)}{s} ds \left[f(t,u) - f_0(t,u) \right] \beta(u) \\ &\le \gamma b(t) V(t) + g_3(t), \end{aligned}$$

where $\gamma = \gamma(\delta, \overline{H}) > 0$, $b(t)$ is defined as in the assumption (B3) with $a = \overline{H}$, and

$$g_3(t) = 2 \int_{u^*(t)}^{u(t)} \frac{\beta(s)}{s} ds [f(t,u(t)) - f_0(t,u(t))) \beta(u(t)].$$

Since $\delta \le u(t), u^*(t) \le \overline{H}, \forall t \ge 0$, the assumption (B1) implies that $\lim_{t\to+\infty} g_3(t) = 0$. Since $m(\gamma b(\cdot)) = \gamma m(b) < 0$, by the comparison theorem and Lemma 6.1.1 it follows that $\lim_{t\to+\infty} V(t) = 0$, which implies that $\lim_{t\to+\infty}(u(t) - u^*(t)) = 0$. ∎

6.2 Competitive Coexistence

In this section we derive conditions for permanence and existence of positive almost periodic solutions in multi-species competitive systems.

Consider almost periodic n-species competitive Kolmogorov systems

$$\frac{du_i}{dt} = u_i F_i(t, u_1, \ldots, u_n), \qquad 1 \le i \le n, \tag{6.15}$$

where $F_i : \mathbb{R} \times \mathbb{R}^n_+ \to \mathbb{R}$ is continuous and almost periodic with respect to t uniformly for u in any bounded subset of $\mathbb{R}^n_+$, and is continuously differentiable with respect to $u \in \mathbb{R}^n_+$, $1 \le i \le n$. We further assume that

(A1) For each $1 \le i \le n$, $F_i(t, u)$ is decreasing with respect to u_j when all other arguments are fixed, $\forall 1 \le j \le n$, $j \ne i$;
(A2) For each $1 \le i \le n$, there exist $a_i > 0$ and $K_i > 0$ such that $F_i(t, 0, \ldots, 0, K_i, 0, \ldots, 0) \le -a_i, \quad \forall t \ge 0$;
(A3) For each $1 \le i \le n$, there exist $\overline{K}_i > K_i$ and a nonpositive almost periodic function $b_i : \mathbb{R} \to \mathbb{R}$ with $m(b_i) < 0$ such that $\frac{\partial(\beta_i(u_i)F_i(t,u))}{\partial u_i} \le b_i(t)$, $\forall t \in \mathbb{R}$, $u \in \prod_{i=1}^n [0, \overline{K}_i]$.

For $u_0 \in \mathbb{R}^n_+$, let $\phi(t, u_0) = (\phi_1(t, u_0), \ldots, \phi_n(t, u_0))$ be the unique solution of (6.15) with $\phi(0, u_0) = u_0$. Then we have the following result.

Theorem 6.2.1. *Let (A1), (A2), and (A3) hold. Assume that*

(A4) For each $1 \le i \le n$, $m(F_i(\cdot, 0, \ldots, 0)) > 0$ and

$$m(F_i(\cdot, u_1^*(\cdot), \ldots, u_{i-1}^*(\cdot), 0, u_{i+1}^*(\cdot), \ldots, u_n^*(\cdot))) > 0,$$

where $u_i^*(t)$ is the unique positive almost periodic solution of the almost periodic scalar Kolmogorov equation $\frac{du_i}{dt} = u_i F_i(t, 0, \ldots, 0, u_i, 0, \ldots, 0)$.

Then system (6.15) is permanent; that is, there exist $M > \eta > 0$ such that for any $u_0 \in \operatorname{int}(\mathbb{R}^n_+)$, there is $T = T(u_0) > 0$ such that $\phi(t, u_0)$ satisfies

$$\eta \le \phi_i(t, u_0) \le M, \qquad \forall t \ge T, \ 1 \le i \le n.$$

Proof. For $u_0 = (u_{01}, \ldots, u_{0n}) \in \mathbb{R}^n_+$, let $I^+(u_0) = [0, \beta(u_0))$ be the maximal interval of existence of $\phi(t, u_0)$. Then $\phi_i(t, u_0) \ge 0$, $\forall t \in I^+(u_0)$, $1 \le i \le n$. By assumption (A1), $u_i(t) = \phi_i(t, u_0)$ satisfies

$$\frac{du_i}{dt} \le u_i F_i(t, 0, \ldots, 0, u_i, 0, \ldots, 0).$$

By the comparison theorem, it follows that

$$0 \le u_i(t) \le \bar{u}_i(t), \qquad \forall t \in I(u_0), \tag{6.16}$$

where $\bar{u}_i(t)$ is the unique solution of the scalar almost periodic equation

$$\frac{du_i}{dt} = u_i F_i(t, 0, \ldots, 0, u_i, 0, \ldots, 0) \tag{6.17}$$

with $\bar{u}_i(0) = u_i(0)$. Since $\bar{u}_i(t)$ exists globally on $[0, \infty)$, we get $I^+(u_0) = [0, \infty)$. Therefore, for any given $u_0 \in \mathrm{int}(\mathbb{R}^n_+)$, we get

$$0 < u_i(t) = \phi_i(t, u_0) \leq \bar{u}_i(t), \qquad \forall t \geq 0.$$

For each $1 \leq i \leq n$ and $\epsilon \in \mathbb{R}_+$, define

$$\bar{F}_i(t, \epsilon) = F_i(t, u_1^*(t) + \epsilon, \ldots, u_{i-1}^*(t) + \epsilon, 0, u_{i+1}^*(t) + \epsilon, \ldots, u_n^*(t) + \epsilon),\ t \in \mathbb{R}.$$

Then $\bar{F}_i(t, \epsilon)$ is almost periodic in t uniformly for ϵ in any bounded subset of $\mathbb{R}_+$. Hence, by [117, Theorem 3.1], we have

$$\lim_{\epsilon \to 0} m(\bar{F}_i(\cdot, \epsilon)) = m(\bar{F}_i(\cdot, 0)) = m(F_i(\cdot, u_1^*(\cdot), \ldots, u_{i-1}^*(\cdot), 0, u_{i+1}^*(\cdot), \ldots, u_n^*(\cdot)).$$

Applying Theorem 6.1.1 with $\beta \equiv 1$, we conclude that $\lim_{t \to \infty}(\bar{u}_i(t) - u_i^*(t)) = 0$ and $0 < u_i^*(t) \leq K_i$, $\forall t \in \mathbb{R}$, $1 \leq i \leq n$. Therefore, by (A4), we can choose $\epsilon_0 > 0$ such that

$$u_i^*(t) + \epsilon_0 \leq \overline{K}_i,\ \ \forall t \in \mathbb{R}, \quad \text{and} \quad m(\bar{F}_i(\cdot, \epsilon_0)) > 0,\ \ \forall 1 \leq i \leq n. \tag{6.18}$$

Then there exists $t_0 = t_0(u, \epsilon_0) > 0$ such that

$$0 < u_i(t) \leq \bar{u}_i(t) \leq u_i^*(t) + \epsilon_0, \qquad \forall t \geq t_0,\ 1 \leq i \leq n. \tag{6.19}$$

Let $v_i(t) = u_i(t + t_0)$, $1 \leq i \leq n$. Then each $v_i(t)$ satisfies the following differential inequality

$$\begin{aligned} \frac{dv_i}{dt} \geq v_i F_i \big(& t + t_0, u_1^*(t + t_0) + \epsilon_0, \ldots, u_{i-1}^*(t + t_0) + \epsilon_0, v_i, \\ & u_{i+1}^*(t + t_0) + \epsilon_0, \ldots, u_n^*(t + t_0) + \epsilon_0\big). \end{aligned} \tag{6.20}$$

By the comparison theorem, it follows that

$$v_i(t) \geq \underline{v}_i(t), \qquad \forall t \geq 0,\ 1 \leq i \leq n,$$

where $\underline{v}_i(t)$ is the unique solution of the scalar almost periodic equation

$$\begin{aligned} \frac{dv_i}{dt} = v_i F_i \big(& t + t_0, u_1^*(t + t_0) + \epsilon_0, \ldots, \\ & u_{i-1}^*(t + t_0) + \epsilon_0, v_i, u_{i+1}^*(t + t_0) + \epsilon_0, \ldots, u_n^*(t + t_0) + \epsilon_0\big) \end{aligned} \tag{6.21}$$

with $\underline{v}_i(0) = v_i(0) = u_i(t_0)$. Since $m(\bar{F}_i(\cdot + t_0, \epsilon_0)) = m(\bar{F}_i(\cdot, \epsilon_0)) > 0$, $\forall 1 \leq i \leq n$, applying (A2), (A3) and Theorem 6.1.1 with $\beta \equiv 1$, we get

$$\lim_{t \to \infty} (\underline{v}_i(t) - v_{i*}(t)) = 0, \tag{6.22}$$

where $v_{i*}(t)$ is the unique positive almost periodic solution of (6.21). By (6.18) and Theorem 6.1.1 with $\beta \equiv 1$, it follows that for each $1 \le i \le n$, the scalar almost periodic equation

$$\frac{du_i}{dt} = u_i F_i(t, u_1^*(t)+\epsilon_0, \ldots, u_{i-1}^*(t)+\epsilon_0, u_i, u_{i+1}^*(t)+\epsilon_0, \ldots, u_n^*(t)+\epsilon_0) \quad (6.23)$$

admits a unique almost periodic solution $u_{i*}(t)$, which is globally asymptotically stable for (6.23) in $\mathbb{R}_+ \setminus \{0\}$. Clearly, $u_{i*}(t+t_0)$ is an almost periodic solution of (6.21). Hence, by the uniqueness, $v_{i*}(t) = u_{i*}(t+t_0)\, \forall\, t \in \mathbb{R}$. Let $0 < \epsilon_1 < \inf_{t\in\mathbb{R}_+} u_{i*}(t)$, $1 \le i \le n$. Then (6.22) implies that there exists $T = T(u_1(t_0), \ldots, u_n(t_0)) = T(u) > 0$ such that

$$u_i(t+t_0) = v_i(t) \ge \underline{v}_i(t) \ge v_{i*}(t) - \epsilon_1 = u_{i*}(t+t_0) - \epsilon_1, \qquad \forall t \ge T,\ 1 \le i \le n.$$

Thus, we have

$$u_i(t) \ge u_{i*}(t) - \epsilon_1, \quad \forall t \ge T + t_0 > 0, \quad 1 \le i \le n. \quad (6.24)$$

By (6.19) and (6.24), it follows that for each $1 \le i \le n$,

$$0 < \inf_{t\in\mathbb{R}_+} u_{i*}(t) - \epsilon_1 \le u_i(t) \le \sup_{t\in\mathbb{R}_+} u_i^*(t) + \epsilon_0, \qquad \forall t \ge T + t_0.$$

This completes the proof. ∎

Suppose we strengthen condition (A3) into the following one:

(A5) There exist continuously differentiable functions $\beta_i : (0,\infty) \to (0,\infty)$, $1 \le i \le n$, and a nonpositive almost periodic function $b : \mathbb{R} \to \mathbb{R}$ with $m(b) < 0$ such that

$$\frac{\partial(\beta_i(u_i)F_i(t,u))}{\partial u_i} + \sum_{j=1, j\ne i}^{n} \beta_j(u_j) \left| \frac{\partial F_j(t,u)}{\partial u_j} \right| < b(t)$$

for all $t \in \mathbb{R}$, $u \in \prod_{i=1}^n [0, \overline{K}_i]$, $1 \le i \le n$.

Then we have the following result on the existence and global attractivity of a unique almost periodic solution of (6.15).

Theorem 6.2.2. *Let (A1), (A2), (A4), and (A5) hold. Then (6.15) admits a globally attractive positive almost periodic solution $u^*(t)$ in int$(\mathbb{R}_+^n)$; that is, for any $u_0 \in \mathrm{int}(\mathbb{R}_+^n)$, the solution $u(t)$ of (6.15) with $u(0) = u_0$ satisfies $\lim_{t\to\infty}(u(t) - u^*(t)) = 0$.*

Proof. Clearly, condition (A5) implies (A3). Then, by Theorem 6.2.1, system (6.15) is permanent, and hence there exists $\alpha > 0$ such that any solution $u(t)$ of (6.15) with $u(0) \in \mathrm{int}(\mathbb{R}_+^n)$ ultimately lies in $\prod_{i=1}^n [\alpha, \overline{K}_i]$. Define

$$V(u,v) := \sum_{i=1}^{n} \left| \int_{u_i}^{v_i} \frac{\beta_i(s)}{s} ds \right|, \quad \forall u = (u_1, \ldots, u_n),\ v = (v_1, \ldots, v_n) \in \operatorname{int}(\mathbb{R}_+^n).$$

Since $\beta_i(s)/s > 0,\ \forall s \in [\alpha, \bar{K}_i]$, there exist D_1 and $D_2 \in (0, \infty)$ such that

$$D_1 \sum_{i=1}^{n} |u_i - v_i| \leq V(u,v) \leq D_2 \sum_{i=1}^{n} |u_i - v_i|, \qquad \forall u, v \in \prod_{i=1}^{n} [\alpha, \overline{K}_i]. \tag{6.25}$$

For $t_1, t_2 \in [0, \infty)$, let $u(t) = (u_1(t), \ldots, u_n(t))$ and $v(t) = (v_1(t), \ldots, v_n(t))$ be the solutions of two systems $du_i/dt = u_i F_i(t + t_1, u)$ and $dv_i/dt = v_i F_i(t + t_2, v)$, respectively, such that $u(t), v(t) \in \prod_{i=1}^{n} [\alpha, \overline{K}_i]$, $\forall t \geq 0$. Then we get

$$\begin{aligned}
\frac{d}{dt} \int_{u_i(t)}^{v_i(t)} \frac{\beta_i(s)}{s} ds &= \beta_i(v_i(t)) F_i(t + t_2, v(t)) - \beta_i(u_i(t)) F_i(t + t_1, u(t)) \\
&= \int_0^1 \frac{d}{ds} \left(\beta_i(s v_i + (1-s) u_i) F_i(t + t_2, sv + (1-s)u \right) ds \\
&\quad + \beta_i(u_i(t)) \left[F_i(t + t_2, u(t)) - F_i(t + t_1, u(t)) \right] \\
&= \int_0^1 \left[\left. \frac{\partial (\beta_i(p_i) F_i(t + t_2, p))}{\partial p_i} \right|_{p = sv + (1-s)u} \cdot (v_i - u_i) \right. \\
&\quad + \beta_i(s v_i + (1-s) u_i) \cdot \\
&\quad \left. \sum_{j=1, j \neq i}^{n} \left. \frac{\partial F_i(t + t_2, p)}{\partial p_j} \right|_{p = sv + (1-s)u} (v_j - u_j) \right] ds \\
&\quad + \beta_i(u_i(t)) \left[F_i(t + t_2, u(t)) - F_i(t + t_1, u(t)) \right].
\end{aligned}$$

Let $D^+ V(u(t), v(t))$ be the upper right derivative of $V(u(t), v(t))$ with respect to t. By condition (A5) and (6.25), it follows that for all $t \geq 0$,

$$\begin{aligned}
&D^+ V(u(t), v(t)) \\
&\leq \sum_{i=1}^{n} \int_0^1 \left[\left. \frac{\partial (\beta_i(p_i) F_i(t + t_2, p))}{\partial p_i} \right|_{p = sv + (1-s)u} \cdot |v_i - u_i| \right. \\
&\quad \left. + \beta_i(s v_i + (1-s) u_i) \cdot \sum_{j=1, j \neq i}^{n} \left| \frac{\partial F_i(t + t_2, sv + (1-s)u)}{\partial p_j} \right| \cdot |v_j - u_j| \right] ds \\
&\quad + \sum_{i=1}^{n} \beta_i(u_i(t)) \left[F_i(t + t_2, u(t)) - F_i(t + t_1, u(t)) \right]
\end{aligned}$$

$$
\begin{aligned}
&= \int_0^1 \left[\sum_{i=1}^n \left(\frac{\partial(\beta_i(p_i)F_i(t+t_2,p))}{\partial p_i}\bigg|_{p=sv+(1-s)u} \right.\right. \\
&\quad \left.\left. + \sum_{j=1,j\neq i} \beta_j(sv_j+(1-s)u_j) \left| \frac{\partial F_j(t+t_2, sv+(1-s)u)}{\partial p_i} \right| \right) |v_i-u_i| \right] ds \\
&\quad + \sum_{i=1}^n \beta_i(u_i(t)) \left[F_i(t+t_2,u(t)) - F_i(t+t_1,u(t)) \right] \\
&\le b(t+t_2) \sum_{i=1}^n |v_i-u_i| + \sum_{i=1}^n \beta_i(u_i(t)) \left[F_i(t+t_2,u(t)) - F_i(t+t_1,u(t)) \right] \\
&\le \frac{b(t+t_2)}{D_2} V(u(t),v(t)) + \sum_{i=1}^n \beta_i(u_i(t)) \left[F_i(t+t_2,u(t)) - F_i(t+t_1,u(t)) \right].
\end{aligned}
\tag{6.26}
$$

Consequently, the existence, uniqueness, and global attractivity of a positive almost periodic solution of (6.15) follow from the permanence of (6.15), estimate (6.26), and an argument similar to the proof of Theorem 6.1.1. ∎

Consider almost periodic n-species competitive Lotka–Volterra systems

$$
\frac{du_i}{dt} = u_i \left(a_i(t) - \sum_{j=1}^n b_{ij}(t) u_j \right), \quad 1 \le i \le n, \tag{6.27}
$$

where a_i and b_{ij} are continuous almost periodic functions. If there exists a constant $b_0 > 0$ such that $b_{ij}(t) \ge 0, \forall i \neq j,$ and $b_{ii}(t) \ge b_0$, $\forall t \in \mathbb{R}$, $1 \le i, j \le n$, then conditions (A1), (A2), and (A3) are satisfied, and hence Theorems 6.2.1 and 6.2.2 enable us to obtain sufficient conditions for system (6.27) to be permanent and to admit a globally attractive positive almost periodic solution.

6.3 An Almost Periodic Chemostat Model

Consider a single population growth model in an almost periodic chemostat

$$
\begin{aligned}
\frac{dS(t)}{dt} &= (S^0(t) - S(t))D_0(t) - x(t)P(t,S(t)), \\
\frac{dx(t)}{dt} &= x(t)(P(t,S(t)) - D_1(t)),
\end{aligned}
\tag{6.28}
$$

where $S(t)$ denotes the concentration of the nutrient, $x(t)$ denotes the biomass of the species at time t, $P(t,S)$ represents the specific per capita nutrient uptake function, $S^0(t)$ and $D_0(t)$ are the input nutrient concentration and washout rate, respectively, and $D_1(t)$ represents the specific removal rate of the species. Here we assume that $S^0(t)$, $D_0(t)$, and $D_1(t)$ are continuous, positive, and almost periodic functions with $m(S^0(\cdot)D_0(\cdot)) > 0$ and $m(\underline{D}) > 0$, $\underline{D}(t) := \min\{D_0(t), D_1(t)\}$, and that $P(t,S) : \mathbb{R} \times \mathbb{R}_+ \to \mathbb{R}_+$ is continuous, almost periodic in t uniformly for S in any bounded subset of $\mathbb{R}_+$, and continuously differentiable with respect to $S \in \mathbb{R}_+$. We further suppose that

(H) $P(t,0) = 0$, $\forall t \geq 0$; and for any $a > 0$ there exists $b = b(a) > 0$ such that $\frac{\partial P(t,S)}{\partial S} \geq b$, $\forall t \in \mathbb{R}$, $S \in [0,a]$.

In the case where $D_1(\cdot) \equiv D_0(\cdot)$, we have the following threshold result on the global dynamics of (6.28).

Theorem 6.3.1. *Let (H) hold and $D_1(t) \equiv D_0(t)$, $\forall t \in \mathbb{R}$, and let $V^*(t)$ be the unique positive almost periodic solution of $\frac{dV}{dt} = S^0(t)D_0(t) - D_0(t)V$.*

(a) If $m(P(\cdot, V^*(\cdot)) - D_0(\cdot)) < 0$, then every solution $(S(t), x(t))$ of (6.28) with $S(0) \geq 0$ and $x(0) \geq 0$ satisfies $\lim_{t\to\infty}(S(t) - V^*(t)) = 0$ and $\lim_{t\to\infty} x(t) = 0$;

(b) If $m(P(\cdot, V^*(\cdot)) - D_0(\cdot)) > 0$, then system (6.28) admits a positive almost periodic solution $(S^*(t), x^*(t)) = (V^*(t) - x^*(t), x^*(t))$ such that every solution $(S(t), x(t))$ of (6.28) with $S(0) \geq 0$ and $x(0) > 0$ satisfies $\lim_{t\to\infty}(S(t) - S^*(t)) = 0$ and $\lim_{t\to\infty}(x(t) - x^*(t)) = 0$.

Proof. Let $\hat{P} : \mathbb{R} \times \mathbb{R} \to \mathbb{R}$ be a continuous extension of P from $\mathbb{R} \times \mathbb{R}_+$ to $\mathbb{R} \times \mathbb{R}$ such that $\hat{P}$ is almost periodic in t uniformly for S in any bounded subset of $\mathbb{R}$, and satisfies (H) for $t \in \mathbb{R}$ and $S \in [-a,a]$.

For $(S_0, x_0) \in \mathbb{R}^2_+$ with $x_0 > 0$, let $(S(t), x(t))$ be the unique solution of (6.28) satisfying $S(0) = S_0$ and $x(0) = x_0$, and let $[0,\beta)$ be its maximal interval of existence. Since $\frac{dS}{dt}\big|_{S=0} = S^0(t)D_0(t) > 0$, we have $S(t) > 0$ and $x(t) > 0$, $\forall t \in (0,\beta)$. Let $V(t) = S(t) + x(t)$. Then $(V(t), x(t))$ satisfies the following equation

$$\begin{aligned} \frac{dV(t)}{dt} &= S^0(t)D_0(t) - D_0(t)V(t), \\ \frac{dx(t)}{dt} &= x(t)(P(t, V(t) - x(t)) - D_0(t)). \end{aligned} \tag{6.29}$$

Let $u = 1/V$, $V > 0$. Then the scalar almost periodic linear equation

$$\frac{dV(t)}{dt} = S^0(t)D_0(t) - D_0(t)V(t) \tag{6.30}$$

can be transformed into the almost periodic logistic equation $du/dt = u[D_0(t) - S^0(t)D_0(t)u]$. Hence, applying Theorem 6.1.1 with $\beta \equiv 1$, we conclude that equation (6.30) admits a unique positive almost periodic solution $V^*(t)$, and every solution $V(t)$ of (6.30) with $V(0) > 0$ satisfies $\lim_{t\to\infty}(V(t) - V^*(t)) = 0$. Consequently, $(S(t), x(t))$ exists globally on $[0, +\infty)$.

Let $V(t)$ be the unique solution of (6.30) with $V(0) = S_0 + x_0 > 0$. Thus, $\lim_{t\to\infty}(V(t) - V^*(t)) = 0$, and $x(t)$ satisfies the following nonautonomous equation

$$\frac{dx}{dt} = x\left[\hat{P}(t, V(t) - x) - D_0(t)\right]. \tag{6.31}$$

Note that for any compact subset K of $\mathbb{R}$, $\hat{P}(t, s)$ is continuous in $s \in K$ uniformly for $t \in \mathbb{R}$ (see, e.g., [117, Theorem 2.10]). It then follows that

$$\lim_{t\to\infty}\left[\hat{P}(t, V(t) - x) - \hat{P}(t, V^*(t) - x)\right] = 0$$

uniformly for x in any bounded subset of $\mathbb{R}_+$. This shows that (6.31) is asymptotic to the almost periodic equation

$$\frac{dx}{dt} = x\left[\hat{P}(t, V^*(t) - x) - D_0(t)\right]. \tag{6.32}$$

Since $x(t)$ is a bounded solution of (6.31) with $x(0) = x_0 > 0$, by Theorem 6.1.2 with $\beta \equiv 1$, we have two cases:

(a) If $m(\hat{P}(\cdot, V^*(\cdot)) - D_0(\cdot)) = m(P(\cdot, V^*(\cdot)) - D_0(\cdot)) < 0$, then $\lim_{t\to\infty} x(t) = 0$;
(b) If $m(\hat{P}(\cdot, V^*(\cdot)) - D_0(\cdot)) = m(P(\cdot, V^*(\cdot)) - D_0(\cdot)) > 0$, then $\lim_{t\to\infty}(x(t) - x^*(t)) = 0$, where $x^*(t)$ is the unique positive almost periodic solution of (6.32).

Let $\underline{x}(t)$ be a given solution of (6.32) with $0 < \underline{x}(0) < V^*(0)$. Note that $V^*(t)$ satisfies

$$\frac{dV^*(t)}{dt} = S^0(t)D_0(t) - D_0(t)V^*(t) > V^*(t)[\hat{P}(t, V^*(t) - V^*(t)) - D_0(t)], \ \forall t \geq 0,$$

that is, $V^*(t)$ is a supersolution of (6.32). By the comparison theorem, we then have

$$0 < \underline{x}(t) < V^*(t), \qquad \forall t \geq 0.$$

Let $q(t) = \underline{x}(t) - x^*(t)$. Thus, Theorem 6.1.1 with $\beta \equiv 1$ implies $\lim_{t\to\infty} q(t) = 0$. Let $p(t) = V^*(t) - x^*(t)$, $t \in \mathbb{R}$. Then $p(t) > q(t)$, $\forall t \geq 0$. Since $p(t)$ is an almost periodic function, there exists a sequence $\tau_k \to +\infty$ such that $p(t + \tau_k) \to p(t)$ uniformly for $t \in \mathbb{R}$ as $k \to \infty$. For $t \in \mathbb{R}$, when k is sufficiently large, we have $t + \tau_k \geq 0$ and hence $p(t + \tau_k) > q(t + \tau_k)$. Then, letting $k \to \infty$, we get $p(t) \geq 0$, $\forall t \in \mathbb{R}$; that is, $V^*(t) \geq x^*(t)$, $\forall t \in \mathbb{R}$. By (6.30) and (6.32), it follows that $(V^*(t), x^*(t))$ is a solution to system (6.29). Let $S^*(t) = V^*(t) - x^*(t)$. Then $(S^*(t), x^*(t))$ is an almost periodic solution of (6.28) with $S^*(t) \geq 0$ and $x^*(t) > 0$, $\forall t \in \mathbb{R}$. We further claim that $S^*(t) > 0$, $\forall t \in \mathbb{R}$. Indeed, for $\tau \in \mathbb{R}$, let $\bar{S}(t) = S^*(t+\tau)$, and $\bar{x}(t) = x^*(t+\tau)$, $\forall t \in \mathbb{R}$. Then $(\bar{S}(t), \bar{x}(t))$ satisfies the almost periodic equations

$$\begin{aligned}\frac{d\bar{S}}{dt} &= (S^0(t+\tau)-\bar{S})D_0(t+\tau)-\bar{x}P(t+\tau,\bar{S}),\\ \frac{d\bar{x}}{dt} &= \bar{x}(P(t+\tau,\bar{S})-D_0(t+\tau)),\end{aligned} \tag{6.33}$$

with $\bar{S}(0)=S^*(\tau)\geq 0$ and $\bar{x}(0)=x^*(\tau)>0$. Since

$$\bar{S}'(t)\big|_{\bar{S}=0}=S^0(t+\tau)D_0(t+\tau)>0,\ \forall t\geq 0,$$

we get $\bar{S}(t)>0$, $\forall t>0$. In particular, $S^*(\tau+1)=\bar{S}(1)>0$. By the arbitrary choice of $\tau\in\mathbb{R}$, it follows that $S^*(t)>0$, $\forall t\in\mathbb{R}$. Consequently, $(S^*(t),x^*(t))$ is a positive almost periodic solution of (6.28). ∎

In the case where $D_1(\cdot)\not\equiv D_0(\cdot)$, let

$$\overline{D}(t):=\max\{D_0(t),D_1(t)\},\ \text{and}\ \underline{D}(t):=\min\{D_0(t),D_1(t)\}.$$

Then, by our previous assumptions, $\overline{D}$ and $\underline{D}:\mathbb{R}\to\mathbb{R}$ are continuous and positive almost periodic functions with $m(\overline{D})\geq m(\underline{D})>0$. By the argument for (6.30) in the proof of Theorem 6.3.1, it is easy to see that the scalar almost periodic linear equations

$$\frac{dV(t)}{dt}=S^0(t)D_0(t)-\underline{D}(t)V(t) \tag{6.34}$$

and

$$\frac{dV(t)}{dt}=S^0(t)D_0(t)-\overline{D}(t)V(t) \tag{6.35}$$

admit globally attractive positive almost periodic solutions $V_1^*(t)$ and $V_2^*(t)$, respectively. By the comparison theorem and almost periodicity and global attractivity of $V_i^*(t)$, $1\leq i\leq 2$, it easily follows that $V_1^*(t)\geq V_2^*(t)$, $\forall t\in\mathbb{R}$. We then have the following result on the permanence and extinction of the species growing in the chemostat.

Theorem 6.3.2. *Let (H) hold.*

(a) If $m(P(\cdot,V_2^*(\cdot))-D_1(\cdot))>0$, then there exist $\alpha>0$ and $\beta>0$ such that every solution $(S(t),x(t))$ of (6.28) with $S(0)\geq 0$ and $x(0)>0$ satisfies

$$\alpha\leq\liminf_{t\to\infty}x(t)\leq\limsup_{t\to\infty}x(t)\leq\beta;$$

(b) If $m(P(\cdot,V_1^*(\cdot))-D_1(\cdot))<0$, then every solution $(S(t),x(t))$ of (6.28) with $S(0)\geq 0$ and $x(0)\geq 0$ satisfies $\lim_{t\to\infty}x(t)=0$.

Proof. Let $\hat{P}:\mathbb{R}\times\mathbb{R}\to\mathbb{R}$ be as in the proof of Theorem 6.3.1. For $(S_0,x_0)\in\mathbb{R}_+^2$ with $S_0\geq 0$ and $x_0>0$, let $(S(t),x(t))$ be the unique solution of (6.28) satisfying $S(0)=S_0$ and $x(0)=x_0$ with $[0,\beta)$ as its maximal interval of existence. Then it easily follows that $S(t)>0$ and $x(t)>0$, $\forall t\in(0,\beta)$. Let $V(t)=S(t)+x(t)$. Then

$$S^0(t)D_0(t) - \overline{D}(t)V(t) \le \frac{dV(t)}{dt} \le S^0(t)D_0(t) - \underline{D}(t)V(t), \quad \forall t \in [0, \beta).$$

Let $\overline{V}(t)$ be the unique solution of (6.34) with $\overline{V}(0) = V(0)$, and let $\underline{V}(t)$ be the unique solution of (6.35) with $\underline{V}(0) = V(0)$. Then the comparison theorem implies that

$$\underline{V}(t) \le V(t) \le \overline{V}(t), \qquad \forall t \in [0, \beta). \tag{6.36}$$

Since $\overline{V}(t)$ and $\underline{V}(t)$ exist globally on $[0, \infty)$, we get $\beta = \infty$. Therefore, $x(t)$ satisfies

$$x(t)\left(\hat{P}(t, \underline{V}(t) - x(t)) - D_1(t)\right) \le \frac{dx(t)}{dt} \le x(t)\left(\hat{P}(t, \overline{V}(t) - x(t)) - D_1(t)\right)$$

for all $t \ge 0$. Then by the comparison theorem,

$$\underline{x}(t) \le x(t) \le \overline{x}(t), \qquad \forall t \ge 0, \tag{6.37}$$

where $\bar{x}(t)$ is the unique solution of the nonautonomous equation

$$\frac{dx(t)}{dt} = x(t)\left(\hat{P}(t, \overline{V}(t) - x(t)) - D_1(t)\right) \tag{6.38}$$

with $\bar{x}(0) = x_0$, and $\underline{x}(t)$ is the unique solution of the nonautonomous equation

$$\frac{dx(t)}{dt} = x(t)\left(\hat{P}(t, \underline{V}(t) - x(t)) - D_1(t)\right) \tag{6.39}$$

with $\underline{x}(0) = x_0$. Since $\lim_{t\to\infty}(\overline{V}(t) - V_1^*(t)) = 0$ and $\lim_{t\to\infty}(\underline{V}(t) - V_2^*(t)) = 0$, it follows that

$$\lim_{t\to\infty}(\hat{P}(t, \overline{V}(t) - x) - \hat{P}(t, V_1^*(t) - x)) = 0$$

and

$$\lim_{t\to\infty}(\hat{P}(t, \underline{V}(t) - x) - \hat{P}(t, V_2^*(t) - x)) = 0$$

uniformly for x in any bounded subset of $\mathbb{R}_+$.

In the case where $m(P(\cdot, V_2^*(\cdot)) - D_1(\cdot)) > 0$, since $V_1^*(t) \ge V_2^*(t)$, $\forall t \in \mathbb{R}$, and $\hat{P}(t, V_i^*(t)) = P(t, V_i^*(t))$, $\forall t \in \mathbb{R}$, $1 \le i \le 2$, Theorem 6.1.1 with $\beta \equiv 1$ implies that the almost periodic equation

$$\frac{dx(t)}{dt} = x(t)(\hat{P}(t, V_i^*(t) - x(t)) - D_1(t)) \tag{6.40}$$

admits a unique positive almost periodic solution $x_i^*(t)$, and $x_i^*(t)$ is globally attractive in $\mathbb{R}_+ \setminus \{0\}$. By the comparison theorem and the almost periodicity of $x_i^*(t)$, it easily follows that $x_1^*(t) \ge x_2^*(t)$, $\forall t \in \mathbb{R}$. Since

$$m(\hat{P}(\cdot, V_1^*(\cdot)) - D_1(\cdot)) \ge m(\hat{P}(\cdot, V_2^*(\cdot)) - D_1(\cdot)) = m(P(\cdot, V_2^*(\cdot)) - D_1(\cdot)) > 0,$$

Theorem 6.1.2(b) with $\beta \equiv 1$ implies that

$$\lim_{t\to\infty}(\bar{x}(t) - x_1^*(t)) = 0 \quad \text{and} \quad \lim_{t\to\infty}(\underline{x}(t) - x_2^*(t)) = 0.$$

By (6.37), it then follows that

$$\liminf_{t\to\infty}(x(t) - x_2^*(t)) \geq \lim_{t\to\infty}(\underline{x}(t) - x_2^*(t)) = 0 \tag{6.41}$$

and

$$\limsup_{t\to\infty}(x(t) - x_1^*(t)) \leq \lim_{t\to\infty}(\overline{x}(t) - x_1^*(t)) = 0. \tag{6.42}$$

Thus, there exist $\alpha > 0$ and $\beta > 0$ such that $x(t)$ satisfies

$$\alpha \leq \liminf_{t\to\infty} x(t) \leq \limsup_{t\to\infty} x(t) \leq \beta.$$

In the case where $m(P(\cdot, V_2^*(\cdot)) - D_1(\cdot)) < 0$, we have

$$m(\hat{P}(\cdot, V_2^*(\cdot)) - D_1(\cdot)) \leq m(\hat{P}(\cdot, V_1^*(\cdot)) - D_1(\cdot)) = m(P(\cdot, V_1^*(\cdot)) - D_1(\cdot)) < 0.$$

By Theorem 6.1.2(a) with $\beta \equiv 1$, it follows that $\lim_{t\to\infty} \bar{x}(t) = 0$ and $\lim_{t\to\infty} \underline{x}(t) = 0$, and hence (6.37) implies that $\lim_{t\to\infty} x(t) = 0$. ∎

6.4 Nonautonomous 2-Species Competitive Systems

Consider the nonautonomous two-species competitive Lotka–Volterra model

$$\frac{dx_i(t)}{dt} = x_i(t)\left(b_i(t) - \sum_{j=1}^{2} a_{ij}(t)x_j(t)\right), \quad i = 1, 2, \tag{6.43}$$

where $b_i(t)$ and $a_{ij}(t)$ are uniformly continuous on $\mathbb{R}$ and are bounded above and below by positive reals. To get the global dynamics of system (6.43) on the boundary, we need the following result on the scalar nonautonomous Kolmogorov equations.

Lemma 6.4.1. *Let $a, b,$ and K be three positive constants, and let $\delta : (0, \infty) \to (0, \infty)$ be a given function. Assume that*

(H1) $g \in C(\mathbb{R} \times \mathbb{R}_+, \mathbb{R})$ and $g(t, x)$ is locally Lipschitz in x uniformly for $t \in \mathbb{R}$;
(H2) $g(t, x) \geq a$, $\forall t \in \mathbb{R}, x \in [0, b]$, and $g(t, K) \leq 0$, $\forall t \in \mathbb{R}$;
(H3) For each $t \in \mathbb{R}$, we have $g(t, \cdot) \in C^1((0, \infty), \mathbb{R})$; and $\frac{\partial g(t,x)}{\partial x} \leq -\delta(k)$, $\forall k \in (0, \infty)$, $t \in \mathbb{R}, x \in (0, k]$.

Then the equation $\frac{dx(t)}{dt} = x(t)g(t,x)$ *admits a unique global solution* $x^*(t,g)$ *on* $\mathbb{R}$ *that is bounded above and below by positive real numbers, and every solution* $x(t,g)$ *with* $x(0,g) > 0$ *satisfies* $\lim_{t\to\infty}(x(t,g) - x^*(t,g)) = 0$. *Moreover, for any sequence of functions* $\{g_k : k \geq 1\}$ *such that each* g_k *satisfies conditions (H1)–(H3) and* $\lim_{k\to\infty} g_k(t,x) = g(t,x)$ *uniformly for* (t,x) *in every compact subset of* $\mathbb{R} \times \mathbb{R}_+$, *we have* $\lim_{k\to\infty} x^*(0,g_k) = x^*(0,g)$.

Proof. The existence, uniqueness, and global attractivity of $x^*(t,g)$ follows from [41, Lemma 2.2] with $\beta(x) = 1/x$, $x > 0$. Let

$$\mathcal{G} := \{g \in C(\mathbb{R} \times \mathbb{R}_+, \mathbb{R}) : g \text{ satisfies } (H1) - (H3)\}.$$

By the proof of [41, Lemma 2.2], there exist two positive real numbers $c = c(a,b,\delta(\cdot))$ and $d = d(a,b,\delta(\cdot))$ such that $c < x^*(t,g) < d$, $\forall t \in \mathbb{R}$, $g \in \mathcal{G}$. By conditions (H2) and (H3), we can further choose c and d such that for any $g \in \mathcal{G}$, $s \in R$, $y \in (c,d)$, the unique solution $x(t,s,y,g)$ of the equation $\frac{dx(t)}{dt} = x(t)g(t,x)$ with $x(s) = y$ exists globally on $[s,\infty)$, and $c \leq x(t,s,y,g) \leq d$, $\forall t \in [s,\infty)$. Let

$$u_n(t,g) = x\left(t, -n, \frac{1}{2}(c+d), g\right), \; t \geq -n, \; n \geq 1,$$

and define

$$V(x,y) := (\ln y - \ln x)^2, \quad x,y \in [c,d].$$

Then there exist two positive numbers $m_1 = m_1(c,d)$ and $m_2 = m_2(c,d)$ such that

$$m_1(x-y)^2 \leq V(x,y) \leq m_2(x-y)^2, \; \forall x,y \in [c,d].$$

By the mean value theorem and condition (H3), it then easily follows that there exists $m = m(c,d,\delta(d)) > 0$ such that

$$\frac{d}{dt}V(u_n(t,g), x^*(t,g)) \leq -mV(u_n(t,g), x^*(t,g)), \; \forall t \geq -n,$$

and hence we have

$$\begin{aligned} V(u_n(t,g), x^*(t,g)) &\leq V\left(\frac{1}{2}(c+d), x^*(-n,g)\right) e^{-m(t+n)} \\ &\leq Le^{-m(t+n)}, \; \forall t \geq -n, \end{aligned}$$

where $L = L(c,d) > 0$. In particular, we get

$$V(u_n(0,g), x^*(0,g)) \leq Le^{-mn}, \quad \forall n \geq 1.$$

It then follows that $\lim_{n\to\infty} u_n(0,g) = x^*(0,g)$ uniformly for $g \in \mathcal{G}$. Clearly, for fixed $n \geq 1$, we have $\lim_{k\to\infty} u_n(0,g_k) = u_n(0,g)$. Now the inequality

$$\begin{aligned} |x^*(0,g_k) - x^*(0,g)| \leq& |x^*(0,g_k) - u_n(0,g_k)| + |u_n(0,g_k) - u_n(0,g)| \\ &+ |u_n(0,g) - x^*(0,g)| \end{aligned}$$

completes the proof. ∎

It is easy to verify that the scalar logistic equation

$$\frac{dx_i(t)}{dt} = x_i(t)\left(b_i(t) - a_{ii}(t)x_i(t)\right) \tag{6.44}$$

satisfies conditions (H1)–(H3). Let $x_i^*(t)$ be the unique global solution on $\mathbb{R}$ of equation (6.44) that is bounded above and below by positive reals. Clearly, each $x_i^*(t)$ is uniformly continuous on $\mathbb{R}$. For the two-species competitive system (6.43), we have the following result.

Theorem 6.4.1. *Assume that*

(D1) There exist $\mu_1 > 0$, $s_1 > 0$, and a sequence $\sigma_k \to \infty$ such that $\frac{1}{\sigma_k}\int_0^{\sigma_k}(b_1(r+s) - a_{12}(r+s)x_2^*(r+s))dr > \mu_1, \forall k \geq 1, s \geq s_1$;
(D2) There exist $\mu_2 > 0$, $s_2 > 0$, and a sequence $\tau_k \to \infty$ such that $\frac{1}{\tau_k}\int_0^{\tau_k}(b_2(r+s) - a_{21}(r+s)x_1^*(r+s))dr > \mu_2, \forall k \geq 1, s \geq s_2$.

Then there is an $\eta > 0$ such that for any solution $x(t) = (x_1(t), x_2(t))$ of equation (6.43) with $x_i(0) > 0$, $\forall i = 1, 2$, $\liminf_{t\to\infty} x_i(t) \geq \eta$, $\forall i = 1, 2$.

Proof. Let $Z_1 = \mathbb{R}^2_+$ and $Z_2 = \mathbb{R}^2$ and equip $C(\mathbb{R}\times Z_1, Z_2)$ with the compact open topology, which is metrizable with metric m, say. Define

$$f(t,x) := \left(b_1(t) - a_{11}(t)x_1 - a_{12}x_2, b_2(t) - a_{21}(t)x_1 - a_{22}(t)x_2\right),$$

where $x = (x_1, x_2) \in Z_1$ and $t \in \mathbb{R}$. For $t \in \mathbb{R}$, we define $\tilde{\sigma}(t) : C(\mathbb{R} \times Z_1, Z_2) \to C(\mathbb{R} \times Z_1, Z_2)$ by $\tilde{\sigma}(t)g = g(t + \cdot, \cdot)$, $\forall g \in C(\mathbb{R} \times Z_1, Z_2)$. By [303, Theorem III.7], the set $\gamma^+_{\tilde{\sigma}}(f) := \{\tilde{\sigma}(t)f : t \geq 0\}$ has compact closure $H(f)$ in $C(\mathbb{R} \times Z_1, Z_2)$. Let $\mathcal{F} = H(f)$ and $X = \mathbb{R}^2_+$. It then follows that for any $g = (g_1, g_2) \in H(f), s \in \mathbb{R}, x \in X$, the system of ordinary differential equations

$$\frac{dx_i(t)}{dt} = x_i(t)g_i(t, x(t)), \quad t \geq s, \quad i = 1, 2, \tag{6.45}$$

has a unique global solution $\Phi(t, s, x, g)$ on $[s, \infty)$ satisfying $\Phi(s, s, x, g) = x$. Given $g \in H(f)$, define $h(g)(t, s, x) = \Phi(t + s, s, x, g), t, s \in \mathbb{R}, x \in X$. Then $h(g)$ is a process on X. By the continuity of g, equation (6.45) and the uniqueness of solution $\Phi(t, s, x, g)$, it easily follows that $h : H(f) \to W$ is one-to-one, and $\sigma(t) \circ h = h \circ \tilde{\sigma}(t)$ on $H(f)$, $\forall t \geq 0$. Clearly, we have

$$\tilde{\pi}(t, x, g) := (h(g)(t, 0, x), \tilde{\sigma}(t)g) = (\Phi(t, 0, x, g), \tilde{\sigma}(t)g),\ \forall t \geq 0,\ x \in X.$$

By [303, Theorem 4], $\tilde{\pi} : \mathbb{R}^+ \times X \times H(f) \to X \times H(f)$ is continuous. Then condition (B) in Section 3.4 holds for f.

Let $\phi = h(f)$, $X_0 = \{(x_1, x_2) : x_1 > 0, x_2 > 0\}$ and $\partial X_0 = X \setminus X_0$. Then $\phi(t, 0, x) = \Phi(t, 0, x, f), t \geq 0, x \in X$. To prove the theorem, it suffices to prove that ϕ is uniformly persistent with respect to $(X_0, \partial X_0)$. Clearly, $h(g)(t, 0, X_0) = \Phi(t, 0, , X_0, g) \subset X_0, \forall g \in H(f), t \geq 0$. In what follows, we verify conditions (1)–(3) in Theorem 3.4.1 for the skew-product semiflow $\tilde{\pi}(t)$. For any $g = (g_1, g_2) \in \omega_{\tilde{\sigma}}(f)$, there is a sequence $t_n \to \infty$ such that $\tilde{\sigma}(t_n)f \to g$, and hence, $\lim_{n\to\infty} f(t+t_n, x) = g(t, x)$ uniformly for (t, x) in any compact subset of $\mathbb{R}\times X$. Let δ_0 and K_0 be the positive numbers such that $\delta_0 \leq b_i(t), a_{ij}(t), x_i^*(t) \leq K_0, \forall 1 \leq i, j \leq 2$. By the uniform continuity of $b_i(t), a_{ij}(t)$ on $\mathbb{R}$ and the Arzela–Ascoli theorem, we can assume that $\lim_{n\to\infty} b_i(t+t_n) = \bar{b}_i(t)$, $\lim_{n\to\infty} a_{ij}(t+t_n) = \bar{a}_{ij}(t)$ uniformly for t in any compact subset of $\mathbb{R}$. It then follows that

$$g(t,x) = \left(\bar{b}_1(t) - \bar{a}_{11}(t)x_1 - \bar{a}_{12}(t)x_2, \bar{b}_2(t) - \bar{a}_{21}(t)x_1 - \bar{a}_{22}(t)x_2\right)$$

for all $x = (x_1, x_2) \in \mathbb{R}^2_+, t \in \mathbb{R}$, and

$$\delta_0 \leq \bar{b}_i(t), \quad \bar{a}_{ij}(t) \leq K_0,\ \forall t \in \mathbb{R},\ 1 \leq i,\ j \leq 2.$$

Thus $\Phi(t, s, x, g)$ satisfies the nonautonomous Lotka–Volterra system

$$\frac{dx_i(t)}{dt} = x_i(t)\left(\bar{b}_i(t) - \sum_{j=1}^{2} \bar{a}_{ij}(t)x_i(t)\right), \quad t \geq s, \quad i = 1, 2. \tag{6.46}$$

By a standard comparison argument, it follows that the condition (1) in Theorem 3.4.1 holds for $h(g)(t, 0, x) = \Phi(t, 0, x, g)$, $g \in \omega_{\tilde{\sigma}}(f)$.

For each $g \in \omega_{\tilde{\sigma}}(f)$, by Lemma 6.4.1 the scalar logistic equation

$$\frac{dx_i(t)}{dt} = x_i(t)\left(\bar{b}_i(t) - \bar{a}_{ii}(t)x_i(t)\right) \tag{6.47}$$

admits a unique global solution $x_i^*(t, g)$ on $\mathbb{R}$ that is bounded above and below by positive reals, and every solution $x_i(t)$ of equation (6.47) with $x_i(0) > 0$ satisfies $\lim_{t\to\infty}(x_i(t) - x_i^*(t, g)) = 0$. Clearly, each $x_i^*(t, g)$ is uniformly continuous on $\mathbb{R}$. By the integral form of equation (6.44), uniform continuity of $x_i^*(t)$ on $\mathbb{R}$, and the uniqueness of $x_i^*(t, g)$, after choosing a subsequence of $\{t_n : n \geq 1\}$, we can further assume that $\lim_{n\to\infty} x_i^*(t+t_n) = x_i^*(t, g)$ uniformly for t in any compact subset of $\mathbb{R}$, $i = 1, 2$. Then $\delta_0 \leq x_i^*(t, g) \leq K_0, \forall g \in \omega_{\tilde{\sigma}}(f)$, $t \in \mathbb{R}$, $i = 1, 2$. By Lemma 6.4.1, it then follows that $x_i^*(0, \cdot) : H(f) \to \mathbb{R}$ is a continuous map. Let $M_0 = \{(0, 0)\}$, $M_1 = \{(x_1^*(0, g), 0) : g \in \omega_{\tilde{\sigma}}(f)\}$, and $M_2 = \{(0, x_2^*(0, g)) : g \in \omega_{\tilde{\sigma}}(f)\}$. Then each M_i is a compact and quasi-invariant set for $\phi = h(f)$ in ∂X_0. For each $g \in \omega_{\tilde{\sigma}}(f)$, $h(g)(t, 0, x) = \Phi(t, 0, x, g)$ has only three full orbits $(0, 0)$, $(x_1^*(t, g), 0)$, and $(0, x_2^*(t, g))$ on ∂X_0, which are contained entirely in one of M_0, M_1, and M_2. Thus no subset of $\{M_0, M_1, M_2\}$ forms a cycle on ∂X_0. Note that every positive solution of equation (6.47) is asymptotic to $x_i^*(t, g)$. By the compactness of $\omega_{\tilde{\sigma}}(\phi)$ and the continuity of $x_i^*(0, \cdot)$, it then follows that for any $x \in \partial X_0$ and $g \in \omega_{\tilde{\sigma}}(\phi)$ with $h(g)(t, 0, x) = \Phi(t, 0, x, g) \in \partial X_0, \forall t \geq 0$, we have $\omega_{h(g)}(x) \subset M_i$ for some $0 \leq i \leq 2$. The following claim implies the isolatedness of $\tilde{M}_i$ in $X \times \omega_{\tilde{\sigma}}(f)$ for $\tilde{\pi}(t)$. Thus, condition (2) in Theorem 3.4.1 holds.

Claim. For each $i = 0, 1, 2$, there exist a positive number r_i and an open neighborhood U_i of $\tilde{M}_i$ such that U_i contains no positive orbit of $\tilde{\pi}(t)$ in $X_0 \times (\{\tilde{\sigma}(\tau)f : \tau \geq r_i\} \cup \omega_{\tilde{\sigma}}(f))$.

Indeed, we can choose a positive number ϵ such that $\epsilon < \min\{\delta_0, \frac{\mu_1}{2}, \frac{\mu_2}{2}\}$. It then follows that there is positive number $c = c(\delta_0, K_0, \epsilon) < 1$ such that for each $1 \leq i \leq 2$,

$$|g_i(t,x) - g_i(t,y)| < \epsilon,\ \forall x, y \in [0, K_0 + 1]^2 \text{ with } \|x - y\| < c,\ g \in H(f),\ t \in \mathbb{R}.$$

By the continuity of $x_1^*(0, \cdot)$ on the compact set $H(f)$, there is a positive number $c_1 = c_1(c) < \frac{c}{2}$ such that $|x_1^*(0, g_1) - x_1^*(0, g_2)| < \frac{c}{2}$ for all $g_1, g_2 \in H(f)$ with $m(g_1, g_2) < c_1$. Let $r_1 = s_2$ and let U_1 be the c_1-neighborhood of $\tilde{M}_1$. Assume, by contradiction, that there is $(x, g) \in X_0 \times (\{\tilde{\sigma}(\tau)f : \tau \geq r_1\} \cup \omega_{\tilde{\sigma}}(f))$ such that $\tilde{d}(\tilde{\pi}(t)(x, g), \tilde{M}_1) = \tilde{d}((\Phi(t, 0, x, g), \tilde{\sigma}(t)g), \tilde{M}_1) < c_1, \forall t \geq 0$. Clearly, $\tilde{M}_1 = \{((x_1^*(0, g), 0), g) : g \in \omega_{\tilde{\sigma}}(f)\}$. Then for each $t \geq 0$ there is $g^t \in \omega_{\tilde{\sigma}}(f)$ such that $\|\Phi(t, 0, x, g) - (x_1^*(0, g^t), 0)\| < c_1$ and $m(\tilde{\sigma}(t)g, g^t) < c_1$. Thus, we have

$$\begin{aligned}
\|\Phi(t,0,x,g) - (x_1^*(t,g),0)\| &= \|\Phi(t,0,x,g) - (x_1^*(0,\tilde{\sigma}(t)g),0)\| \\
&\leq \|\Phi(t,0,x,g) - (x_1^*(0,g^t),0)\| \\
&\quad + \|(x_1^*(0,g^t),0) - (x_1^*(0,\tilde{\sigma}(t)g),0)\| \\
&< c_1 + \frac{c}{2} < c, \quad \forall t \geq 0.
\end{aligned}$$

By the choice of c, it follows that

$$g_2(t, \Phi(t,0,x,g)) \geq g_2(t, x_1^*(t,g), 0) - \epsilon, \quad \forall t \geq 0.$$

Let $(x_1(t), x_2(t)) = \Phi(t, 0, x, g)$ and $\alpha(t) := g_2(t, x_1^*(t, g), 0) - \epsilon$, $t \geq 0$. Then $x_2(0) > 0$, and $x_2(t)$ satisfies

$$\frac{dx_2(t)}{dt} \geq \alpha(t) x_2(t),\ t \geq 0.$$

Then the comparison theorem implies that

$$x_2(t) \geq x_2(0) e^{\int_0^t \alpha(r) dr} = x_2(0) \left(e^{\frac{1}{t} \int_0^t \alpha(r) dr} \right)^t,\ \forall t > 0.$$

In the case that $g = \tilde{\sigma}(\tau) f$ for some $\tau \geq r_1$, we have $x_1^*(t, g) = x_1^*(\tau + t)$, and hence by condition (D2),

$$\begin{aligned}
\frac{1}{\tau_k} \int_0^{\tau_k} \alpha(r) dr &= \frac{1}{\tau_k} \int_0^{\tau_k} g_2(r, x_1^*(r,g), 0) dr - \epsilon \\
&= \frac{1}{\tau_k} \int_0^{\tau_k} \left(b_2(\tau + r) - a_{21}(\tau + r) x_1^*(\tau + r) \right) dr - \epsilon \\
&> \mu_2 - \epsilon > 0,\ \forall k \geq 1.
\end{aligned}$$

In the case that $g \in \omega_{\tilde{\sigma}}(f)$, let $t_n \to \infty$ be chosen as before. Then

$$\begin{aligned}\lim_{n\to\infty} (b_2(t_n+r) - a_{21}(t_n+r)x_1^*(t_n+r)) &= \bar{b}_2(r) - \bar{a}_{21}(r)x_1^*(r,g)\\ &= g_2(r, x_1^*(r,g), 0)\end{aligned}$$

uniformly for r in any compact subset of $\mathbb{R}$. Thus, for any τ_k, we can choose an integer $N = N(\tau_k, \epsilon)$ such that $t_N \geq s_2$ and

$$|\,(b_2(t_N+r) - a_{21}(t_N+r)x_1^*(t_N+r)) - g_2(r, x_1^*(r,g), 0)| < \epsilon,\ \forall r \in [0, \tau_k].$$

Again by condition (D2), we have

$$\begin{aligned}\frac{1}{\tau_k}\int_0^{\tau_k} \alpha(r)dr &= \frac{1}{\tau_k}\int_0^{\tau_k} g_2(r, x_1^*(r,g), 0)dr - \epsilon\\ &\geq \frac{1}{\tau_k}\int_0^{\tau_k} (b_2(t_N+r) - a_{21}(t_N+r)x_1^*(t_N+r) - \epsilon)\,dr - \epsilon\\ &> \mu_2 - 2\epsilon > 0, \quad \forall k \geq 1.\end{aligned}$$

It then follows that $\lim_{k\to\infty} x_2(\tau_k) = \infty$, which contradicts the boundedness of $x_2(t)$. A similar argument applies to $\tilde{M}_0$ and $\tilde{M}_2$.

By a standard comparison argument, it follows that every positive orbit $\phi(t,0,x) = \Phi(t,0,x,f), t \geq 0$, is precompact. Note that if $\omega_{\tilde{\pi}}(x,f) \subset \tilde{M}_i$ for some $0 \leq i \leq 2$, then there is a $t_0 \geq r_i$ such that $\tilde{\pi}(t+t_0)(x,f) = (\Phi(t+t_0,0,x,f), \tilde{\sigma}(t+t_0)f) \in U_i, \forall t \geq 0$. Let $y = \Phi(t_0,0,x,f)$ and $g = \tilde{\sigma}(t_0)f$. Thus $\tilde{\pi}(t)(y,g) = (\Phi(t,0,y,g), \tilde{\sigma}(t)g) = (\Phi(t+t_0,0,x,f), \tilde{\sigma}(t+t_0)f)$, $t \geq 0$, is a positive orbit contained in U_i. Then the above claim implies that condition (3) in Theorem 3.4.1 holds for $\tilde{\pi}(t)$. Now Theorems 3.4.1 and 3.4.2 complete the proof. ∎

Remark 6.4.1. It is easy to see that sufficient conditions for (D1) and (D2), respectively, are

(D1)′ $\liminf_{t,s\to\infty} \frac{1}{t}\int_0^t (b_1(r+s) - a_{12}(r+s)x_2^*(r+s))dr > 0$;
(D2)′ $\liminf_{t,s\to\infty} \frac{1}{t}\int_0^t (b_2(r+s) - a_{21}(r+s)x_1^*(r+s))dr > 0$.

Note that if $\beta(\cdot) : \mathbb{R} \to \mathbb{R}$ is an almost periodic function, then its mean value

$$M[\beta] = \lim_{t\to\infty} \frac{1}{t}\int_s^{t+s} \beta(r)dr = \lim_{t\to\infty} \frac{1}{t}\int_0^t \beta(s+r)dr$$

exists and is independent of s, and the convergence is uniform in $s \in \mathbb{R}$. It then easily follows that $\lim_{t,s\to\infty} \frac{1}{t}\int_0^t \beta(s+r)dr = M[\beta]$. If $b_i(t), a_{ii}(t), i = 1,2$, are almost periodic, then each $x_i^*(t)$ is also almost periodic (see Theorem 6.1.1(b) with $\beta(\cdot) \equiv 1$). Thus, in the case that all coefficient functions in system (1.7) are almost periodic, conditions (D1)′ and (D2)′ are equivalent to $M[b_1(\cdot) - a_{12}(\cdot)x_2^*(\cdot)] > 0$ and $M[b_2(\cdot) - a_{21}(\cdot)x_1^*(\cdot)] > 0$, respectively.

A similar approach and techniques as in the proof of Theorem 6.4.1 can be used to study nonautonomous competitive Kolmogorov systems

$$\frac{dx_i(t)}{dt} = x_i(t) f_i(t, x_1, x_2), \quad i = 1, 2, \tag{6.48}$$

under some appropriate conditions on $f = (f_1, f_2)$.

6.5 Notes

Sections 6.1–6.3 are taken from Wu, Zhao and He [410], and Section 6.4 is taken from Zhao [436]. Gatica and So [130, Theorem 2.1] proved the existence and global stability of positive almost periodic solutions for the almost periodic equation $dx/dt = xg(x, K(t))$. Burton and Hutson [41, Lemma 2.2] established the existence and global stability of positive and bounded solutions on $\mathbb{R}$ for scalar nonautonomous Kolmogorov equations. The comparison argument in Theorem 6.2.1 was used earlier by Zhao [429] for periodic n-species competitive Lotka–Volterra systems.

Gopalsamy [134] and Ahmad [1] discussed the global asymptotic stability in almost periodic Lotka–Volterra competitive systems of ODEs, and Gopalsamy and He [135] considered oscillations and convergence in a delayed and almost periodic 2-species Lotka–Volterra competitive system of ODEs.

Redheffer [289, 290] studied asymptotic behavior and coexistence states in general nonautonomous multi-species Lotka–Volterra systems of ODEs. Ellermeyer, Pilyugin and Redheffer [107] established persistence criteria for a nonautonomous single-species chemostat model. Sufficient conditions for competitive exclusion were obtained by Ahmad [2] and Montes de Oca and Zeeman [251] for nonautonomous Lotka–Volterra competitive systems of ODEs.

Vuillermot [378, 379, 380] investigated almost periodic attractors for a class of nonautonomous reaction–diffusion equations on $\mathbb{R}^n$. Shen and Yi [312] studied convergence in almost periodic Fisher and Kolmogorov reaction–diffusion equations, and Hetzer and Shen [156] also discussed convergence in almost periodic two-species competitive reaction–diffusion systems.

7

Competitor–Competitor–Mutualist Systems

In order to model mutualism phenomena in population biology, Rai et al. [285] proposed and analyzed a competitor–competitor–mutualist system of ordinary differential equations. Zheng [449] then considered a competitor–competitor–mutualist reaction–diffusion system of Lotka–Volterra type with constant coefficients, and Tineo [374] studied a similar model with spatial-varying and time-periodic coefficients and subject to the zero Neumann boundary condition. In this chapter we consider a more general periodic parabolic competitor–competitor–mutualist model with spatial heterogeneity and subject to a general boundary condition. Let $\omega > 0$ be fixed, and let $\Omega \subset \mathbb{R}^N$, $N \geq 1$, be a bounded domain with the boundary $\partial\Omega$ of class of $C^{2+\theta}$ for some $\theta \in (0,1]$. Assume that u_1 and u_2 are the population densities of two competitors, and u_3 is the population density of the mutualist that decreases the effect of u_2 on u_1. Then the model takes the following form

$$\begin{aligned}
&\frac{\partial u_1}{\partial t} + A_1(t)u_1 = u_1[g_1(x,t,u_1) - q_1(x,t,u_1,u_2,u_3)] \text{ in } \Omega \times (0,+\infty),\\
&\frac{\partial u_2}{\partial t} + A_2(t)u_2 = u_2[g_2(x,t,u_2) - q_2(x,t,u_1,u_2)] \text{ in } \Omega \times (0,+\infty),\\
&\frac{\partial u_3}{\partial t} + A_3(t)u_3 = u_3 h(x,t,u_1,u_3)] \text{ in } \Omega \times (0,+\infty),\\
&\quad B_1u_1 = B_2u_2 = B_3u_3 = 0 \text{ on } \partial\Omega \times (0,+\infty),
\end{aligned} \tag{7.1}$$

where

$$A_i(t)u_i = -\sum_{j,k=1} a_{jk}^{(i)}(x,t)\frac{\partial^2 u_i}{\partial x_j \partial x_k} + \sum_{j=1}^{N} a_j^{(i)}(x,t)\frac{\partial u_i}{\partial x_j} + a_0^{(i)}(x,t)u_i, \ 1 \leq i \leq n,$$

are linear uniformly elliptic differential expressions of second order for each $t \in [0,\omega]$; $A_i(t)$, $g_i(x,t,\cdot), q_i(x,t,\cdot)$, and $h(x,t,\cdot)$ are ω-periodic in t; and

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$B_i u_i = u_i$ or $B_i u_i = \frac{\partial u_i}{\partial \nu} + b_0^{(i)}(x)u_i$, where $\frac{\partial}{\partial \nu}$ denotes differentiation in the direction of the outward normal ν to $\partial \Omega$. We assume that $a_{jk}^{(i)} = a_{kj}^{(i)}$, $a_j^{(i)}$ and $a_0^{(i)} \in C^{\theta,\theta/2}(\overline{Q}_\omega)$, $a_0^{(i)} \geq 0$, $\forall 1 \leq j,k \leq N$, $1 \leq i \leq n$, $Q_\omega = \Omega \times [0,\omega]$, and $b_0^{(i)} \in C^{1+\theta}(\partial\Omega, \mathbb{R})$, $b_0^{(i)} \geq 0$, $\forall 1 \leq i \leq n$, and that the functions g_i, q_i, and h and their first order partial derivatives with respect to each u_j are continuous and in the class of $C^{\theta,\theta/2}(\overline{Q}_\omega, \mathbb{R})$ uniformly for $u = (u_1, u_2, u_3)$ in bounded subsets of $\mathbb{R}^3$.

Taking into account biological implications of the model, we assume that

(H1) $g_1(x,t,0) > 0$ and $\frac{\partial g_1}{\partial u_1} < 0$, $\forall (x,t) \in \overline{Q}_\omega$, $u_1 \in \mathbb{R}_+$, and there exists $K_1 > 0$ such that $g_1(x,t,K_1) \leq 0$, $\forall (x,t) \in \overline{Q}_\omega$;
(H2) $g_2(x,t,0) > 0$ and $\frac{\partial g_2}{\partial u_2} < 0$, $\forall (x,t) \in \overline{Q}_\omega$, $u_2 \in \mathbb{R}_+$, and there exists $K_2 > 0$ such that $g_2(x,t,K_2) \leq 0$, $\forall (x,t) \in \overline{Q}_\omega$;
(H3) $q_1(x,t,u_1,0,u_3) \equiv 0$, $\frac{\partial q_1}{\partial u_1} \geq 0$, $\frac{\partial q_1}{\partial u_2} > 0$, $\forall (x,t) \in \overline{Q}_\omega$, $(u_1,u_2,u_3) \in \mathbb{R}_+^3$, and $\frac{\partial q_1}{\partial u_3} < 0$, $\forall (x,t) \in \overline{Q}_\omega$, $(u_1,u_2,u_3) \in \mathbb{R}_+^3$ with $u_2 > 0$;
(H4) $q_2(x,t,0,u_2) \equiv 0$, $\frac{\partial q_2}{\partial u_1} > 0$, and $\frac{\partial q_2}{\partial u_2} \geq 0$, $\forall (x,t) \in \overline{Q}_\omega$, $(u_1,u_2) \in \mathbb{R}_+^2$;
(H5) $h(x,t,u_1,0) > 0$, $\forall (x,t) \in \overline{Q}_\omega$, $u_1 \in \mathbb{R}_+$, $\frac{\partial h}{\partial u_1} > 0$, $\forall (x,t) \in \overline{Q}_\omega$, $(u_1,u_3) \in \mathbb{R}_+^2$ with $u_3 > 0$, $\frac{\partial h}{\partial u_3} < 0$, $\forall (x,t,u_1,u_3) \in \overline{Q}_\omega \times \mathbb{R}_+^2$, and for any $u_1 > 0$, there exists $K_3 = K_3(u_1) > 0$ such that $h(x,t,u_1,K_3) \leq 0$, $\forall (x,t) \in \overline{Q}_\omega$.

We are interested in the case where each species stabilizes eventually at a positive periodic equilibrium state in the absence of the other two-species. In view of Theorem 3.1.5, we impose a set of analytical conditions on the model system (7.1) accordingly:

(H6) $\mu(A_1(t), g_1(x,t,0)) < 0$, $\mu(A_2(t), g_2(x,t,0)) < 0$, and $\mu(A_3(t), h(x,t,0,0)) < 0$, where $\mu(A_i(t), m(x,t))$, $m \in C^{\theta,\frac{\theta}{2}}(\overline{Q}_\omega)$, denotes the unique principal eigenvalue of the periodic–parabolic eigenvalue problem (see [152])

$$\begin{aligned} &\frac{\partial v}{\partial t} + A_i(t)v = m(x,t)v + \mu v \quad \text{in } \Omega \times \mathbb{R}, \\ &B_i v = 0 \quad \text{on } \partial\Omega \times \mathbb{R}, \\ &v \ \omega\text{-periodic in } t. \end{aligned} \tag{7.2}$$

The aim of this chapter is to study the global dynamics of system (7.1) and bifurcations of periodic solutions. In Section 7.1 we prove a result on weak periodic repellers for periodic parabolic systems in order to apply persistence theory to the model system. In Sections 7.2 and 7.3 we establish the global coexistence of all interacting species and the extinction of one of the competing species, respectively. We also use a special case of (7.1) to illustrate the main results. Section 7.4 is devoted to a discussion of the existence and multiplicity of positive periodic solutions via bifurcation methods.

7.1 Weak Periodic Repellers

In this section we prove the weakly repelling property of a semitrivial periodic solution to a periodic parabolic system under appropriate conditions.

Consider the periodic parabolic system

$$\begin{aligned} \frac{\partial u_i}{\partial t} + A_i(t)u_i &= f_i(x,t,u_1,\ldots,u_m) \quad \text{in } \Omega \times (0,+\infty), \\ B_i u_i &= 0 \quad \text{on } \partial\Omega \times (0,+\infty), \end{aligned} \tag{7.3}$$

where $A_i(t), B_i$, and Ω are as in (3.17), and $f = (f_1,\ldots,f_m)$ is ω-periodic in t and satisfies the smoothness condition (H) in Section 3.2. Let (E_i, P_i), $1 \le i \le m$, be the ordered Banach spaces defined in Section 3.2, and let $\varphi(t,u)$ be the unique solution of (7.3) satisfying $\varphi(0,u) = u \in P := \prod_{i=1}^m P_i$. We assume that for each $u \in P$, the solution $\varphi(t,u)$ exists globally on $[0,+\infty)$ and remains in P for all $t \ge 0$. Then we have the following result.

Proposition 7.1.1. (Weak periodic repellers) *Assume that there exist some $1 \le k \le m$ and a smooth function $F_k(x,t,u)$, ω-periodic in t, such that*

(1) $f_k(x,t,u) \ge u_k F_k(x,t,u)$, $\forall (x,t,u) \in \overline{\Omega} \times \mathbb{R}^{m+1}$;
(2) The system (7.3) admits a nonnegative ω-periodic solution

$$u^*(t) = (u_1^*(t),\ldots,u_{k-1}^*(t),0,u_{k+1}^*(t),\ldots,u_m^*(t))$$

with $\mu(A_k(t), F_k(x,t,u^*(t)(x))) < 0$.

Then there exists $\delta > 0$ such that $\limsup_{n\to\infty} \|\varphi(n\omega,u) - u^*(0)\| \ge \delta$ for all $u \in P$ with $u_k(\cdot) \not\equiv 0$.

Proof. Let $M = u^*(0)$ and let $S : P \to P$ be defined by $S(u) = \varphi(\omega,u)$. It then suffices to prove that there exists $\delta > 0$ such that for any $u \in N(M,\delta)$ with $u_k(\cdot) \not\equiv 0$, where $N(M,\delta)$ is the δ-neighborhood of M in P, there exists $n = n(u) \ge 1$ such that $S^n(u) \notin N(M,\delta)$. Let $\mu = \mu(A_k(t), F_k^0(x,t,u^*(t)(x)))$, and fix $\epsilon_0 \in (0,-\mu)$. By the uniform continuity of $F_k(x,t,u)$ on the compact set $\overline{Q}_\omega \times \prod_{i=1}^m [0,b_i]$, where $b_i = \max_{(x,t)\in\overline{Q}_\omega} u_i^*(t,x)+1$, there exists $\delta_0 \in (0,1)$ such that for any u and $v \in \prod_{i=1}^m [0,b_i]$ with $|u_i - v_i| < \delta_0$, $\forall 1 \le i \le m$, and all $(x,t) \in \overline{Q}_\omega$,

$$|F_k(x,t,u) - F_k(x,t,v)| < \epsilon_0.$$

Since $\lim_{u\to M} \varphi(t,u) = \varphi(t,M) = u^*(t)$ in $E := \prod_{i=1}^m E_i$ uniformly for $t \in [0,\omega]$ and $E \hookrightarrow \prod_{i=1}^m C(\overline{\Omega})$, there exists $\delta > 0$ such that for any $u \in N(M,\delta) \cap P$,

$$\|\varphi_i(t,u) - u_i^*(t)\|_{C(\overline{\Omega})} < \delta_0,\ \forall i \ne k, \qquad \|\varphi_k(t,u)\|_{C(\overline{\Omega})} < \delta_0,\ \ \forall t \in [0,\omega].$$

Assume, by contradiction, that there exists $w \in N(M,\delta) \cap P$ with $w_k(\cdot) \not\equiv 0$ such that $S^n(w) = \varphi(n\omega,w) \in N(M,\delta)$, $\forall n \ge 1$. For any $t \ge 0$, let $t = n\omega + t'$, where $t' \in [0, \omega)$ and $n = [t/\omega]$ is the greatest integer less than or equal to t/ω. Then we have

$$\|\varphi_i(t, w) - u_i^*(t)\|_{C(\overline{\Omega})} = \|\varphi_i(t', \varphi(n\omega, w)) - u_i^*(t')\|_{C(\overline{\Omega})} < \delta_0, \ \forall i \neq k,$$

and

$$\|\varphi_k(t, w)\|_{C(\overline{\Omega})} = \|\varphi_k(t', \varphi(n\omega, w))\|_{C(\overline{\Omega})} < \delta_0.$$

Let $u^*(t, x) = u^*(t)(x)$ and $u(t, x) = \varphi(t, w)(x)$. By the ω-periodicity of $F_k(x, t, u)$ with respect to t, we then get

$$F_k(x, t, u(t, x)) > F_k(x, t, u^*(t, x)) - \epsilon_0, \qquad \forall x \in \overline{\Omega}, \ t \geq 0.$$

Let $\varphi_k(t, x)$ be a positive eigenfunction corresponding to the principal eigenvalue μ. Then $\varphi_k(t, x)$ satisfies

$$\begin{aligned} &\frac{\partial \varphi_k}{\partial t} + A_k(t)\varphi_k = F_k(x, t, u^*(t, x))\varphi_k + \mu\varphi_k \quad \text{in } \Omega \times (0, \infty), \\ &B_k\varphi_k = 0 \quad \text{on } \partial\Omega \times (0, \infty), \\ &\varphi_k \ \ \omega\text{-periodic in}\, t. \end{aligned} \tag{7.4}$$

Then $\varphi_k(0, \cdot) \gg 0$ in $E_k = X_\beta^{(k)}$ (i.e., $\varphi_k(0, \cdot) \in \operatorname{int}(P_k)$). Since $u_k(0, \cdot) = w_k \not\equiv 0$, the parabolic maximum principle, as applied to the u_k equation in system (7.3), implies that $u_k(t, \cdot) \gg 0$ in E_k, $\forall t > 0$. Without loss of generality, we can assume $u_k(0, \cdot) \in \operatorname{int}(P_k)$. Then there exists $\eta > 0$ such that $u_k(0, x) \geq \eta\varphi_k(0, x)$, $\forall x \in \overline{\Omega}$. Consequently, $u_k(t, x)$ satisfies

$$\begin{aligned} \frac{\partial u_k}{\partial t} + A_k(t)u_k &\geq u_k\left(F_k(x, t, u^*(t, x)) - \epsilon_0\right) \quad \text{in } \Omega \times (0, \infty), \\ u_k(0, x) &\geq \eta\varphi_k(0, x) \quad \text{on } \overline{\Omega}. \end{aligned} \tag{7.5}$$

By (7.4), it easily follows that $v(t, x) = \eta e^{(-\mu - \epsilon_0)t}\varphi_k(t, x)$ satisfies

$$\begin{aligned} \frac{\partial v}{\partial t} + A_k(t)v &= v\left(F_k(x, t, u^*(t, x)) - \epsilon_0\right) \quad \text{in } \Omega \times (0, \infty), \\ v(0, x) &= \eta\varphi_k(0, x) \quad \text{on } \overline{\Omega}. \end{aligned} \tag{7.6}$$

By (7.5), (7.6), and the standard comparison principle, it follows that

$$u_k(t, x) \geq \eta e^{(-\mu - \epsilon_0)t}\varphi_k(t, x), \qquad \forall t \geq 0, \ x \in \Omega.$$

For each $x \in \Omega$, since $\varphi_k(t, x)$ is a positive ω-periodic function in t, we have $\lim_{t \to \infty} u_k(t, x) = +\infty$. In view of the fact that $E_k = X_\beta^{(k)} \hookrightarrow C(\overline{\Omega})$, we then get $\lim_{t \to \infty} \|u_k(t, \cdot)\|_{E_k} = +\infty$, which contradicts the assumption that $S^n(w) = u(n\omega, \cdot) \in N(M, \delta)$, $\forall n \geq 1$. ∎

7.2 Competitive Coexistence

In this section we establish a set of conditions for the existence of at least one positive periodic solution and the competitive coexistence in the model system (7.1).

Let $N < p < +\infty$, and for $\beta \in (1/2 + N/(2p), 1]$, let $E_i = X_\beta^{(i)}$ be the fractional power space of $L^p(\Omega)$ with respect to $(A_i(0), B_i)$ (see, e.g., [150]). Then each E_i is an ordered Banach space with the order cone P_i consisting of all nonnegative functions in E_i, and P_i has nonempty interior $\text{int}(P_i)$. Let $\dot{P}_i = P_i \setminus \{0\}$, and let $E = E_1 \times E_2 \times E_3$. By an easy extension of some results in [152, Section III.20] to systems, it follows that for every $u_0 = (u_1^0, u_2^0, u_3^0) \in E$, there exists a unique regular solution $\varphi(t, u_0)$ of (7.1) satisfying $\varphi(0, u_0) = u_0$ with its maximal interval of existence $I^+(u_0) \subset [0, +\infty)$, and $\varphi(t, u_0)$ is globally defined, provided that there is an L^∞-bound on $\varphi(t, u_0)$. Moreover, a standard invariant principle argument (see, e.g., [6, 343]) implies that any solution $\varphi(t, u_0)$ of (7.1) with nonnegative initial values remains nonnegative.

According to Theorem 3.1.5, let $u_1^*(x,t)$, $u_2^*(x,t)$, $u_3^*(x,t)$ be the unique positive ω-periodic solutions of scalar parabolic equations

$$\begin{aligned} &\frac{\partial u_1}{\partial t} + A_1(t)u_1 = u_1 g_1(x,t,u_1) \quad \text{in } \Omega \times (0,+\infty), \\ &\qquad B_1 u_1 = 0 \quad \text{on } \partial\Omega \times (0,+\infty); \end{aligned} \tag{7.7}$$

$$\begin{aligned} &\frac{\partial u_2}{\partial t} + A_2(t)u_2 = u_2 g_2(x,t,u_2) \quad \text{in } \Omega \times (0,+\infty), \\ &\qquad B_2 u_2 = 0 \quad \text{on } \partial\Omega \times (0,+\infty); \end{aligned} \tag{7.8}$$

$$\begin{aligned} &\frac{\partial u_3}{\partial t} + A_3(t)u_3 = u_3 h(x,t,0,u_3) \quad \text{in } \Omega \times (0,+\infty), \\ &\qquad B_3 u_3 = 0 \quad \text{on } \partial\Omega \times (0,+\infty); \end{aligned} \tag{7.9}$$

respectively. Since $h(x,t,u_1^*(x,t),0) > h(x,t,0,0)$, $\forall (x,t) \in \overline{Q}_\omega$, by [152, Lemma 15.5] we have

$$\mu(A_3(t), h(x,t,u_1^*(x,t),0) < \mu(A_3(t), h(x,t,0,0)) < 0,$$

and hence Theorem 3.1.5 implies that there is a unique positive ω-periodic solution $\overline{u}_3(x,t)$ to the scalar equation

$$\begin{aligned} &\frac{\partial u_3}{\partial t} + A_3(t)u_3 = u_3 h(x,t,u_1^*(x,t),u_3) \quad \text{in } \Omega \times (0,+\infty), \\ &\qquad B_3 u_3 = 0 \quad \text{on } \partial\Omega \times (0,+\infty). \end{aligned} \tag{7.10}$$

We claim that $u_3^*(t) \ll \overline{u}_3(t)$ in E_3, $\forall t \geq 0$. Indeed, (H5) implies that $\overline{u}_3(t)$ satisfies

$$\frac{\partial \overline{u}_3}{\partial t} + A_3(t)\overline{u}_3 - \overline{u}_3 h(x,t,0,\overline{u}_3) > \frac{\partial \overline{u}_3}{\partial t} + A_3(t)\overline{u}_3 - \overline{u}_3 h(x,t,u_1^*(x,t),\overline{u}_3) = 0,$$

and hence $\overline{u}_3(x,t)$ is a strict supersolution of (7.9). Then it easily follows that $u_3^*(0) < \overline{u}_3(0)$ in E_3, and hence the comparison theorem of scalar parabolic equations implies that $u_3^*(t) \ll \overline{u}_3(t)$ in E_3, $\forall t > 0$. By the ω-periodicity of $u_3^*(t)$ and $\overline{u}_3(t)$, we get $u_3^*(t) \ll \overline{u}_3(t)$ in E_3, $\forall t \geq 0$.

Let $X = P_1 \times P_2 \times P_3$, $X_0 = \{(u_1, u_2, u_3) \in X : u_i(\cdot) \not\equiv 0, \forall 1 \leq i \leq n\}$ and $\partial X_0 = X \setminus X_0$. Clearly, X_0 and ∂X_0 are relatively open and closed in X, respectively, and X_0 is convex. By assumptions (H1)–(H5) and a comparison argument, it follows that for any $u \in X$, the unique solution $\varphi(t,u)$ of (7.1) exists globally on $[0, +\infty)$. It is easy to see that system (7.1) is majorized by the following system

$$
\begin{aligned}
&\frac{\partial u_1}{\partial t} + A_1(t)u_1 = u_1 g_1(x,t,u_1) \quad \text{in } \Omega \times (0,+\infty),\\
&\frac{\partial u_2}{\partial t} + A_2(t)u_2 = u_2 g_2(x,t,u_2) \quad \text{in } \Omega \times (0,+\infty),\\
&\frac{\partial u_3}{\partial t} + A_3(t)u_3 = u_3 h(x,t,u_1,u_3) \quad \text{in } \Omega \times (0,+\infty),\\
&\quad B_1u_1 = B_2u_2 = B_3u_3 = 0 \quad \text{on } \partial\Omega \times (0,+\infty).
\end{aligned}
\tag{7.11}
$$

Then Theorem 3.1.5 and Proposition 3.2.4 imply that system (7.11), and hence (7.1), is point dissipative.

Let $S : X \to X$ be the Poincaré map associated with (7.1); that is, $S(u) = \varphi(\omega, u)$, $\forall u \in X$. It then follows that $S : X \to X$ is a continuous, point dissipative, and compact map with $S(X_0) \subset X_0$ and $S(\partial X_0) \subset \partial X_0$. Moreover, by Theorem 1.1.3, $S : X \to X$ admits a strong global attractor $A \subset X$.

Proposition 7.2.1. *Let (H1)–(H6) hold. Assume that*

(C1) $\mu_1 := \mu(A_1(t), g_1(x,t,0) - q_1(x,t,0,u_2^*(x,t),u_3^*(x,t))) < 0$;
(C2) $\mu_2 := \mu(A_2(t), g_2(x,t,0) - q_2(x,t,u_1^*(x,t),0)) < 0$.

Then $S : X \to X$ *is uniformly persistent with respect to* $(X_0, \partial X_0)$.

Proof. Let A_∂ be the maximal compact invariant set of S in ∂X_0, and let M_1 be the global attractor of $S : P_1 \times P_2 \times \{0\} \to P_1 \times P_2 \times \{0\}$, $M_2 = (0, u_2^*(0), u_3^*(0))$, $M_3 = (0, 0, u_3^*(0))$, and $M_4 = (u_1^*(0), 0, \overline{u}_3(0))$. For $u \in X = P_1 \times P_2 \times P_3$, let $\omega(u)$ be the omega limit set of u for $S : X \to X$ and let $\varphi(t,u) = (u_1(t), u_2(t), u_3(t))$. By Theorem 3.1.5, it follows that

$$u_1(t) \equiv 0, \quad \lim_{t\to\infty} \|u_i(t) - u_i^*(t)\|_{E_i} = 0, \forall u \in \{0\} \times \dot{P}_2 \times \dot{P}_3,\ i = 2, 3,$$

and

$$u_1(t) = u_2(t) \equiv 0, \quad \lim_{t\to\infty} \|u_3(t) - u_3^*(t)\|_{E_3} = 0, \forall u \in \{0\} \times \{0\} \times \dot{P}_3.$$

By Proposition 3.2.4, we have

$$u_2(t) \equiv 0, \ \lim_{t\to\infty} \|u_1(t) - u_1^*(t)\|_{E_1} = 0, \ \lim_{t\to\infty} \|u_3(t) - \overline{u}_3(t)\|_{E_3} = 0,$$

for all $u \in \dot{P}_1 \times \{0\} \times \dot{P}_3$. Thus, $\tilde{A}_\partial = \cup_{u\in A_\partial}\, \omega(u) \subset \cup_{i=1}^4 M_i$, and M_1, M_2, M_3, and M_4 are disjoint, compact, and isolated invariant sets of $S_\partial = S|_{A_\partial}$ in A_∂. Clearly, Proposition 7.1.1 implies that M_2, M_3, and M_4 are isolated in X_0 and hence isolated in X, and $W^s(M_i) \cap X_0 = \emptyset$, $\forall 2 \le i \le 4$. For $u \in X_0$, since $\varphi(t,u) = (u_1(t), u_2(t), u_3(t))$ satisfies $u_i(t) \gg 0$ in E_i, $\forall t > 0$, $1 \le i \le 3$, we have

$$\frac{\partial u_3}{\partial t} + A_3(t)u_3 = u_3 h(x,t,u_1,u_3) \ge u_3 h(x,t,0,u_3), \ \forall t \ge 0.$$

Let $v_3(t)$ be the solution of (7.9) with $v_3(0) = u_3(0) > 0$. Then the comparison theorem implies that $u_3(t) \ge v_3(t)$, $\forall t \ge 0$. By Theorem 3.1.5, $\lim_{t\to\infty} \|v_3(t) - u_3^*(t)\|_{E_3} = 0$. Then $S^n(u) = (u_1(n\omega), u_2(n\omega), u_3(n\omega))$ satisfies $u_3(n\omega) \ge v_3(n\omega)$, $\forall n \ge 0$, and $\lim_{n\to\infty} v_3(n\omega) = u_3^*(0) \gg 0$ in E_3. It follows that M_1 is isolated in X_0 and hence in X, and $W^s(M_1) \cap X_0 = \emptyset$. It is easy to see that $\cup_{i=1}^4 M_i$ is acyclic for S_∂ in A_∂. Consequently, Theorem 1.3.1 and Remark 1.3.1 imply that $S : X \to X$ is uniformly persistent with respect to $(X_0, \partial X_0)$. ∎

Note that if $S : X \to X$ is uniformly persistent, then Theorem 1.3.10 implies that $S : X_0 \to X_0$ admits a global attractor A_0, and S has a fixed point $x_0 \in A_0 \subset X_0$. Thus, system (7.1) admits a positive ω-periodic solution. Moreover, Theorem 3.1.1 implies that $\varphi(t,\cdot) : X \to X$, $t \ge 0$, is uniformly persistent with respect to $(X_0, \partial X_0)$. Since $A_0 = S(A_0) \subset \mathrm{int}(P_1 \times P_2 \times P_3)$, we have $A_0^* := \cup_{0\le t\le\omega}\varphi(t, A_0) \subset \mathrm{int}(P_1 \times P_2 \times P_3)$. By the compactness and global attractivity of A_0^* (see Theorem 3.1.1), it then follows that there exists a $\beta > 0$ such that for any $u = (u_1,u_2,u_3) \in \dot{P}_1 \times \dot{P}_2 \times \dot{P}_3$, there exists $t_0 = t_0(u) > 0$ such that $\varphi(t,u) = (u_1(t), u_2(t), u_3(t))$ satisfies

$$u_i(t)(x) \ge \beta e_i(x), \qquad \forall t \ge t_0, \ x \in \overline{\Omega}, \ 1 \le i \le 3,$$

where

$$e_i(x) = \begin{cases} e(x) & \text{if } B_i v = v, \\ 1 & \text{if } B_i v = \frac{\partial v}{\partial \nu} + b_0^{(i)} v, \end{cases}$$

and $e \in C^2(\overline{\Omega})$ is given such that $e(x) > 0, \forall x \in \Omega$; and $e(x) = 0$ and $\frac{\partial e}{\partial \nu} < -\gamma < 0$, $\forall x \in \partial\Omega$.

For $a \ll b$ in E_i, let $[[a,\, b]] := \{u :\, a \ll u \ll b \,\text{in}\, E_i\}$. Then we have the following result.

Proposition 7.2.2. *Let (H1)–(H6) and (C1)–(C2) hold. Then* $\omega(u) \subset [[0, u_1^*(0)]] \times [[0, u_1^*(0)]] \times [[u_3^*(0), \overline{u}_3(0)]]$, $\forall u = (u_1,u_2,u_3) \in \dot{P}_1 \times \dot{P}_2 \times \dot{P}_3$.

Proof. Given $u = (u_1, u_2, u_3) \in X_0 = \dot{P}_1 \times \dot{P}_2 \times \dot{P}_3$, let $\varphi(t, u) = (u_1(t), u_2(t), u_3(t))$. Then $u_i(t) \gg 0$ in E_i, $\forall t > 0$, $1 \le i \le 3$. By Proposition 7.2.1, $S : X \to X$ is uniformly persistent, and hence $\omega(u) \subset X_0$. For $v = (v_1, v_2, v_3) \in \omega(u)$, the invariance of $\omega(u)$ for S (i.e., $\omega(u) = S(\omega(u))$) implies that there exists $w = (w_1, w_2, w_3) \in \omega(u)$ such that $(v_1, v_2, v_3) = S((w_1, w_2, w_3))$ with $w_i > 0$ in E_i, $\forall 1 \le i \le 3$. By the parabolic maximum principle, it follows that $v_i \gg 0$ in E_i, $\forall 1 \le i \le 3$.

Let $\overline{u}_1(t)$ and $\overline{u}_2(t)$ be the solutions of (7.7) and (7.8) with $\overline{u}_1(0) = u_1(0)$ and $\overline{u}_2(0) = u_2(0)$, respectively. Then the comparison theorem of scalar parabolic equations implies that $u_i(t) \le \overline{u}_i(t)$, $\forall t \ge 0$, $1 \le i \le 2$. Since $\lim_{t\to\infty} \|\overline{u}_i(t) - u_i^*(t)\|_{E_i} = 0$, it easily follows that for any $v = (v_1, v_2, v_3) \in \omega(u)$, we have $0 \ll v_i \le u_i^*(0)$, $\forall 1 \le i \le 2$, and hence $\varphi(t, v) = (v_1(t), v_2(t), v_3(t))$ satisfies

$$0 \ll v_i(t) \le u_i^*(t) \text{ in } E_i, \ \forall t \ge 0, 1 \le i \le 2.$$

Therefore, $v_3(t)$ satisfies

$$v_3 h(x, t, 0, v_3) \le \frac{\partial v_3}{\partial t} + A_3(t) v_3 \le v_3 h(x, t, u_1^*(t), v_3).$$

Let $\overline{v}_3(t)$ and $\overline{\overline{v}}_3(t)$ be the solutions of (7.9) and (7.10) with $\overline{v}_3(0) = \overline{\overline{v}}_3(0) = v_3$, respectively. By the comparison theorem, we get

$$\overline{v}_3(t) \le v_3(t) \le \overline{\overline{v}}_3(t), \forall t \ge 0.$$

Let $\bar{S} : P_3 \to P_3$ and $\overline{\overline{S}} : P_3 \to P_3$ be the Poincaré maps associated with (7.9) and (7.10), respectively. It then follows that for all $n \ge 1$,

$$P^n(v) = (v_1(n\omega), v_2(n\omega), v_3(n\omega)) \subset [0, u_1^*(0)] \times [0, u_2^*(0)] \times \left[\overline{S}^n(v_3), \overline{\overline{S}}^n(v_3)\right].$$

Since $\omega(u)$ is compact and $\omega(u) \subset \mathrm{int}(P_1) \times \mathrm{int}(P_2) \times \mathrm{int}(P_3)$, there exist $\overline{w}_3 \gg 0$, $\overline{\overline{w}}_3 \gg 0$ in E_3 such that $\overline{w}_3 \le v_3 \le \overline{\overline{w}}_3$, $\forall (v_1, v_2, v_3) \in \omega(u)$. Thus,

$$P^n(v) \subset [0, u_1^*(0)] \times [0, u_2^*(0)] \times \left[\overline{S}^n(\overline{w}_3), \overline{\overline{S}}^n(\overline{\overline{w}}_3)\right], \forall v \in \omega(u), n \ge 1,$$

which implies that

$$\omega(u) = P^n(\omega(u)) \subset [0, u_1^*(0)] \times [0, u_2^*(0)] \times \left[\overline{S}^n(\overline{w}_3), \overline{\overline{S}}^n(\overline{\overline{w}}_3)\right], \quad \forall n \ge 1.$$

Letting $n \to \infty$, we then have $\omega(u) \subset [0, u_1^*(0)] \times [0, u_2^*(0)] \times [u_3^*(0), \overline{u}_3(0)]$.

For $v = (v_1, v_2, v_3) \in \omega(u)$, let $\varphi(t, v) = (v_1(t), v_2(t), v_3(t))$. Then the comparison theorem of scalar equations implies that

$$0 \ll v_i(t) \le u_i^*(t) \text{ and } u_3^*(t) \le v_3(t) \le \overline{u}_3(t), \forall t \ge 0, 1 \le i \le 2.$$

By our assumptions, we then get

$$q_1(x,t,v_1(t)(x),v_2(t)(x),v_3(t)(x)) \not\equiv 0, \quad q_2(x,t,v_1(t)(x),v_2(t)(x)) \not\equiv 0,$$

and $h(x,t,v_1(t)(x),v_3(t)(x)) \not\equiv h(x,t,0,v_3(t)(x))$, $\forall (x,t) \in \overline{Q}_\omega$, and hence there exist t_1, t_2, and $t_3 \in [0,\omega]$ such that $v_1(t_1) < u_1^*(t_1)$ in E_1, $v_2(t_2) < u_2^*(t_2)$ in E_2 and $v_3(t_3) > u_3^*(t_3)$ in E_3, respectively. By the parabolic maximum principle, it follows that $v_i(t) \ll u_i^*(t)$ in E_i, $\forall t > t_i$, $1 \le i \le 2$, and $v_3(t) \gg u_3^*(t)$ in E_3, $\forall t > t_3$. In particular, $v_i(2\omega) \ll u_i^*(0)$, $\forall 1 \le i \le 2$, and $v_3(2\omega) \gg u_3^*(0)$. It then follows that for any $w = (w_1,w_2,w_3) \in \omega(u) = S^2(\omega(u))$, there exists $v = (v_1,v_2,v_3) \in \omega(u)$ such that $w = (w_1,w_2,w_3) = P^2(v) = (v_1(2\omega),v_2(2\omega),v_3(2\omega))$, and hence, $w_i \ll u_i^*(0)$, $\forall 1 \le i \le 2$, and $w_3 \gg u_3^*(0)$. Thus, we have $\omega(u) \subset [[0,u_1^*(0)]] \times [[0,u_2^*(0)]] \times [[u_3^*(0),\overline{u}_3(0)]$.

It remains to prove that $w_3 \ll \overline{u}_3(0)$ in E_3, $\forall w = (w_1,w_2,w_3) \in \omega(u)$. For $v = (v_1,v_2,v_3) \in \omega(u)$, let $\varphi(t,v) = (v_1(t),v_2(t),v_3(t))$. Then the comparison theorem implies that $0 \ll v_i(t) \ll u_i^*(t)$ in E_i, and $u_3^*(t) \ll v_3(t) \le \overline{u}_3(t)$ in E_3, $\forall t \ge 0, 1 \le i \le 2$, and hence, $v_3(t)$ satisfies

$$\frac{\partial v_3}{\partial t} + A_3(t)v_3 < v_3 h(x,t,u_1^*(t)(x),v_3),\ \forall (x,t) \in \Omega \times (0,\infty),$$

which implies that there exists $t_4 \in [0,\omega]$ such that $v_3(t_4) \not\equiv \overline{u}_3(t_4)$, and hence, $v_3(t_4) < \overline{u}_3(t_4)$. Therefore, by the parabolic maximum principle, we get $v_3(t) \ll \overline{u}_3(t)$, $\forall t > t_4$, and in particular, $v_3(2\omega) \ll \overline{u}_3(2\omega) = \overline{u}_3(0)$. It then follows that for any $w = (w_1,w_2,w_3) \in \omega(u) = S^2(\omega(u))$, there exists $v = (v_1,v_2,v_3) \in \omega(u)$ such that $w = (w_1,w_2,w_3) = S^2(v) = (v_1(2\omega),v_2(2\omega),v_3(2\omega))$, and hence $w_3 \ll \overline{u}_3(0)$. ∎

Let $P = P_1 \times (-P_2) \times P_3$. Then (E,P) is an ordered Banach space with the cone P having the nonempty interior $\mathrm{int}(P) = \mathrm{int}(P_1) \times (-\mathrm{int}(P_2)) \times \mathrm{int}(P_3)$. Let $S : X \to X$ be the Poincaré map associated with (7.1). Then $U_1^* = (0,u_2^*(0),u_3^*(0))$ and $U_2^* = (u_1^*(0),0,\overline{u}_3(0))$ are two fixed points of S with $U_1^* \ll U_2^*$ in E (i.e., $U_2^* - U_1^* \in \mathrm{int}(P)$). To prove our main result in this section, we also need two lemmas.

Lemma 7.2.1. *Let (H1)–(H6) hold and assume that*

$$\mu_1 := \mu(A_1(t), g_1(x,t,0) - q_1(x,t,0,u_2^*(x,t),u_3^*(x,t)) < 0.$$

Then $DS(U_1^*)$ exists and $r_2 = e^{-\mu_1\omega}$ is an eigenvalue of $DS(U_1^*)$ with an eigenvector $e_1 \gg 0$ in E.

Proof. We consider the linearized periodic parabolic system of (7.1) at its ω-periodic solution $(0,u_2^*(x,t),u_3^*(x,t))$,

$$\begin{aligned} \frac{\partial w}{\partial t} + A(t)w &= H(x,t)w \quad \text{in}\, \Omega \times (0,\infty), \\ Bw &= 0 \quad \text{on}\, \partial\Omega \times (0,\infty), \end{aligned} \tag{7.12}$$

where $w = (w_1,w_2,w_3)^T$, $A(t) = \mathrm{diag}(A_1(t),A_2(t),A_3(t))$, $B = \mathrm{diag}(B_1,B_2,B_3)$, and

$$H(x,t) = \begin{bmatrix} H_{11}(x,t) & 0 & 0 \\ -u_2^* \frac{\partial q_2(x,t,0,u_2^*)}{\partial u_1} & H_{22}(x,t) & 0 \\ u_3^* \frac{\partial h(x,t,0,u_3^*)}{\partial u_1} & 0 & H_{33}(x,t) \end{bmatrix}$$

with

$$\begin{aligned} H_{11}(x,t) &:= g_1(x,t,0) - q_1(x,t,0,u_2^*,u_3^*), \\ H_{22}(x,t) &:= \frac{\partial}{\partial u_2}(u_2 g_2(x,t,u_2))|_{u_2=u_2^*}, \\ H_{33}(x,t) &:= \frac{\partial}{\partial u_3}(u_3 h(x,t,0,u_3))|_{u_3=u_3^*}. \end{aligned}$$

Let $U_1(t,s)$, $0 \le s \le t \le \omega$, be the evolution operator of the equation

$$\begin{aligned} \frac{\partial w_1}{\partial t} + A_1(t) w_1 &= (g_1(x,t,0) - q_1(x,t,0,u_2^*(x,t),u_3^*(x,t)))w_1, \\ B_1 w_1 &= 0, \end{aligned} \tag{7.13}$$

and let $U_2(t,s)$ and $U_3(t,s)$, $0 \le s \le t \le \omega$, be the evolution operators of the linearized equations of (7.8) at $u_2^*(x,t)$ and (7.9) at $u_3^*(x,t)$, respectively. By the variation of constants formula for scalar parabolic equations (see, e.g., [152]), it then easily follows that $U(t,s): E \to E$, $0 \le s \le t \le \omega$, defined by

$$U(t,s) \begin{pmatrix} \phi_1 \\ \phi_2 \\ \phi_3 \end{pmatrix} = \begin{pmatrix} U_1(t,s)\phi_1 \\ U_2(t,s)\phi_2 + \int_s^t U_2(t,\tau)h_{21}(\tau)U_1(\tau,s)\phi_1 d\tau \\ U_3(t,s)\phi_3 + \int_s^t U_3(t,\tau)h_{31}(\tau)U_1(\tau,s)\phi_1 d\tau \end{pmatrix}$$

for $\phi = (\phi_1,\phi_2,\phi_3)^T \in E$, where

$$h_{21}(t) = -u_2^*(t)\frac{\partial q_2(\cdot,t,0,u_2^*(t))}{\partial u_1}, \quad h_{31}(t) = u_3^*(t)\frac{\partial h(\cdot,t,0,u_3^*(t))}{\partial u_1}, \forall t \ge 0,$$

is the evolution operator of (7.12). It is easy to prove that $DS(U_1^*)$ exists and $DS(U_1^*) = U(\omega,0)$ (see, e.g., the proof of [152, Proposition 23.1]). Let r_1, r_2, and r_3 be spectral radii (and hence principal eigenvalues) of the compact and strongly positive linear operators $U_1(\omega,0)$, $U_2(\omega,0)$, and $U_3(\omega,0)$, respectively. By the definition of periodic principal eigenvalue ([152]) and Theorem 3.1.5, we have $r_1 = e^{-\mu_1 T} > 1$, and $r_i \le 1$, $\forall 2 \le i \le 3$. Let $h_1 \in \mathrm{int}(P_1)$ be a principal eigenvector of $U_1(\omega,0)$ (i.e., $U_1(\omega,0)h_1 = r_1 h_1$). By the Krein–Rutman theorem (see, e.g., [152, Theorem 7.3]), it follows that

$$(r_1 - U_2(\omega,0))h_2 = -\int_0^\omega U_2(\omega,\tau)h_{21}(\tau)U_1(\omega,0)h_1 d\tau \gg 0$$

and

$$(r_1 - U_3(\omega,0))h_3 = \int_0^\omega U_3(\omega,\tau)h_{31}(\tau)U_1(\omega,0)h_1 d\tau \gg 0$$

have unique positive solutions h_2 and h_3 with $h_i \gg 0$ in E_i, $\forall 2 \le i \le 3$, respectively. Thus, $e_1 = (h_1,-h_2,h_3)^T \gg 0$ in E, and $U(\omega,0)e_1 = r_1 e_1$. Then r_1 is an eigenvalue of $DS(U_1^*)$ with an eigenvector $e_1 \gg 0$ in E. ∎

For $U_2^* = (u_1^*(0), 0, \overline{u}_3(0))$, we consider the linearized periodic system of (7.1) at its ω-periodic solution $(u_1^*(t), 0, \overline{u}_3(t))$:

$$\begin{aligned} \frac{\partial w}{\partial t} + A(t)w = G(x,t)w \quad &\text{in } \Omega \times (0,\infty), \\ Bw = 0 \quad &\text{on } \partial\Omega \times (0,\infty), \end{aligned} \tag{7.14}$$

where $w = (w_1, w_2, w_3)^T$, $A(t)$ and B are as in (7.12), and

$$G(x,t) = \begin{bmatrix} G_{11}(x,t) & -u_1^* \frac{\partial q_1(x,t,u_1^*,0,\overline{u}_3)}{\partial u_2} & 0 \\ 0 & G_{22}(x,t) & 0 \\ \overline{u}_3 \frac{\partial h(x,t,u_1^*,\overline{u}_3)}{\partial u_1} & 0 & G_{33}(x,t) \end{bmatrix}$$

with

$$\begin{aligned} G_{11}(x,t) &:= \frac{\partial}{\partial u_1}(u_1 g_1(x,t,u_1))|_{u_1 = u_1^*}, \\ G_{22}(x,t) &:= g_2(x,t,0) - q_2(x,t,u_1^*,0), \\ G_{33}(x,t) &:= \frac{\partial}{\partial u_3}(u_3 h(x,t,u_1^*,u_3)|_{u_3 = \overline{u}_3}. \end{aligned}$$

By an argument similar to that in Lemma 7.2.1, we have the following result.

Lemma 7.2.2. *Let (H1)–(H6) hold and assume that*

$$\mu_2 := \mu(A_2(t), g_2(x,t,0) - q_2(x,t,u_1^*(x,t),0)) < 0.$$

Then $DS(U_2^*)$ exists and $r_2 = e^{-\mu_2 \omega}$ is an eigenvalue of $DS(U_2^*)$ with an eigenvector $e_2 \gg 0$ in E.

Now we are in a position to prove our main result of this section.

Theorem 7.2.1. *Assume that (H1)–(H6) and (C1)–(C2) hold. Then (7.1) admits two positive ω-periodic solutions $U_*(t) = (w_{1*}(t), w_2^*(t), w_{3*}(t))$ and $U^*(t) = (w_1^*(t), w_{2*}(t), w_3^*(t))$ with $0 \ll w_{i*}(t) \le w_i^*(t)$, $\forall t \ge 0$, $1 \le i \le 3$, such that for any $u \in \dot{P}_1 \times \dot{P}_2 \times \dot{P}_3$, $\varphi(t,u) = (u_1(t), u_2(t), u_3(t))$ satisfies* $\lim_{t\to\infty} d(u_i(t), [w_{i*}(t), w_i^*(t)]) = 0,\ \forall 1 \le i \le 3$.

Proof. It suffices to prove that the Poincaré map $S : X \to X$ admits two positive fixed points U_* and U^* in $\operatorname{int}(P_1) \times \operatorname{int}(P_2) \times \operatorname{int}(P_3)$ with $U_* \le U^*$ in (E, P) such that $\omega(u) \subset [U_*, U^*]_E$, $\forall u \in \dot{P}_1 \times \dot{P}_2 \times \dot{P}_3$.

Let $v_1 = u_1, v_2 = -u_2, v_3 = u_3$. Then (7.1) is transformed into the system

$$\begin{aligned} \frac{\partial v_i}{\partial t} + A_i(t)v_i = F_i(x,t,v) \quad &\text{in } \Omega \times (0,\infty), \quad 1 \le i \le 3, \\ B_i v_i = 0 \quad &\text{on } \partial\Omega \times (0,\infty), \quad 1 \le i \le 3, \end{aligned} \tag{7.15}$$

where $v = (v_1, v_2, v_3) \in \Sigma := \mathbb{R}_+ \times (-\mathbb{R}_+) \times \mathbb{R}_+$, and

$$\begin{aligned}
F_1(x,t,v) &= v_1[g_1(x,t,v_1) - q_1(x,t,v_1,-v_2,v_3)],\\
F_2(x,t,v) &= v_2[g_2(x,t,-v_2) - q_2(x,t,v_1,-v_2)],\\
F_3(x,t,v) &= v_3 h(x,t,v_1,v_3).
\end{aligned}$$

It is easy to see that $\frac{\partial F_i}{\partial v_j} \geq 0$, $i \neq j$, $\forall (x,t) \in \overline{Q}_\omega,\ v \in \Sigma$. By the parabolic maximum principle of weakly coupled parabolic systems (see, e.g., [283, Theorem 13 of Section 3.8]) and hence the corresponding comparison theorem (see, e.g., [236, Theorem 4.1]), it then follows that $\varphi(t,\cdot) : X = P_1 \times P_2 \times P_3 \to X$ is order-preserving in the sense that for any $u, w \in X$ with $u \leq w$ in (E,P), we have $\varphi(t,u) \leq \varphi(t,w)$ in (E,P), $\forall t \geq 0$, where $\varphi(t,u)$ is the unique solution of (7.1) with $\varphi(0,u) = u \in X$. Therefore, $S : X \to X$, defined by $S(u) = \varphi(T,u)$, $u \in X$, is a monotone (nondecreasing) map.

Let $F = \{u \in \dot{P}_1 \times \dot{P}_2 \times \dot{P}_3 : S(u) = u\}$. By Proposition 7.2.1, it follows that there exists $\delta > 0$ such that $\|u_i\|_{E_i} \geq \delta$, $\forall u = (u_1,u_2,u_3) \in F$, $1 \leq i \leq 3$, and hence F is closed in E. Let A be the global attractor of $S : X \to X$. Clearly, $F \subset A$. Thus, the compactness of A implies that F is compact in E. For any $u \in F$, by Proposition 7.2.2, we have $u = \omega(u) \in [[U_1^*, U_2^*]]_E$, and hence $F \subset [[U_1^*, U_2^*]]_E$. Let $e_i \gg 0$ be given as in Lemmas 7.2.1 and 7.2.2, respectively. Then the compactness of F implies that there exists $\beta_0 > 0$ such that

$$F \subset [[U_1^* + \beta_0 e_1, U_2^* - \beta_0 e_2]]_E.$$

By Lemmas 7.2.1 and 7.2.2, $DS(U_i^*)e_i = r_i e_i$ with $r_i > 1,\ 1 \leq i \leq 2$. Then there exists $0 < \epsilon_0 \leq \beta_0$ such that for any $\epsilon \in (0,\epsilon_0]$, $U_1^* + \epsilon e_1 \ll U_2^* - \epsilon e_2$ and

$$S(U_1^* + \epsilon e_1) \gg U_1^* + \epsilon e_1,\ S(U_2^* - \epsilon e_2) \ll U_2^* - \epsilon e_2.$$

By the compactness and monotonicity of $S : X \to X$, it follows that $S^n(U_1^* + \epsilon e_1)$ converges increasingly to the minimal fixed point $U_1(\epsilon)$ of S and $S^n(U_2^* - \epsilon e_2)$ converges decreasingly to the maximal fixed point $U_2(\epsilon)$ of S in the interval $[U_1^* + \epsilon e_1, U_2^* - \epsilon e_2]_E$. Clearly, $U_1^* \ll U_1^* + \epsilon e_1 \ll U_1(\epsilon) \leq U_2(\epsilon) \ll U_2^* - \epsilon e_2 \ll U_2^*$. We further claim that $U_1(\epsilon)$ and $U_2(\epsilon)$ are independent of $\epsilon \in (0,\epsilon_0]$. Indeed, for any $\epsilon_1, \epsilon_2 \in (0,\epsilon_0]$, since $U_i(\epsilon_j) \in F$, $\forall 1 \leq i,j \leq 2$, and $\epsilon_0 \leq \beta_0$, we have

$$U_1^* + \epsilon_j e_1 \leq U_1^* + \beta_0 e_1 \ll U_1(\epsilon_i) \leq U_2(\epsilon_i) \ll U_2^* - \beta_0 e_2 \leq U_2^* - \epsilon_j e_2$$

for all $1 \leq i,j \leq 2$. It then follows that

$$U_1(\epsilon_j) \leq U_1(\epsilon_i) \leq U_2(\epsilon_i) \leq U_2(\epsilon_j),\ \ \forall 1 \leq i,j \leq 2,$$

which implies that

$$U_1(\epsilon_1) = U_1(\epsilon_2),\ U_2(\epsilon_1) = U_2(\epsilon_2).$$

Let $U_1(\epsilon) = U_*, U_2(\epsilon) = U^*$. Thus, $U_1^* \ll U_* \leq U^* \ll U_2^*$, and for any $\epsilon \in (0,\epsilon_0]$,

$$\lim_{n\to\infty} S^n(U_1^* + \epsilon e_1) = U_* \le U^* = \lim_{n\to\infty} S^n(U_2^* - \epsilon e_2).$$

For $u \in \dot{P}_1 \times \dot{P}_2 \times \dot{P}_3$, by Proposition 7.2.2, $\omega(u) \subset [[U_1^*, U_2^*]]_E$. Then the compactness of $\omega(u)$ implies that there exists $\epsilon = \epsilon(u) \in (0, \epsilon_0]$ such that $\omega(u) \subset [[U_1^* + \epsilon e_1, U_2^* - \epsilon e_2]]_E$, and hence

$$S^n(U_1^* + \epsilon e_1) \le S^n(\omega(u)) = \omega(u) \le S^n(U_2^* - \epsilon e_2), \ \forall n \ge 1.$$

Letting $n \to \infty$, we get $\omega(u) \subset [U_*, U^*]_E$. ∎

In the case that (7.1) is autonomous, that is, $A_i(x,t) = A_i(x)$, $\forall 1 \le i \le 3$, $g_i(x,t,\cdot) = g_i(x,\cdot)$, $q_i(x,t,\cdot) = q_i(x,\cdot)$, $\forall 1 \le i \le 2$, and $h(x,t,\cdot) = h(x,\cdot)$, there is an analogous result of Theorem 7.2.1. As an illustration, let A_i and B_i be such that $a_0^{(i)} \ge 0$, with $a_0^{(i)}(x) \not\equiv 0$ if $b_0^{(i)} \equiv 0$, $\forall 1 \le i \le 3$. For any $m \in C^\theta(\overline{\Omega})$ with $m(x) > 0$ for some $x \in \overline{\Omega}$, according to [152, Theorem 16.1 and Remark 16.5], let $\lambda_1(A_i(\cdot), m(\cdot))$ be the unique positive principal eigenvalue of the elliptic eigenvalue problem

$$\begin{aligned} A_i(x)u &= \lambda m(x) u \quad \text{in } \Omega, \\ B_i u &= 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{7.16}$$

We then have the following result.

Theorem 7.2.2. *Let (H1)–(H5) hold for the autonomous case of (7.1). Assume that*

(1) $\lambda_1(A_i(x), g_i(x,0)) < 1$, $\forall i = 1,2$, *and* $\lambda_1(A_3(x), h(x,0,0)) < 1$*;*
(2) $\lambda_1(A_1(x), g_1(x,0) - q_1(x,0,u_2^*(x),u_3^*(x))) < 1$*;*
(3) $\lambda_1(A_2(x), g_2(x,0) - q_2(x,u_1^*(x),0) < 1$*;*

where $u_1^*(x)$, $u_2^*(x)$, *and* $u_3^*(x)$ *are the unique positive steady-state-solutions of autonomous equations (7.7), (7.8), and (7.9), respectively. Then autonomous system (7.1) admits two positive steady-state-solutions* $U_* = (w_{1*}, w_2^*, w_{3*})$ *and* $U^* = (w_1^*, w_{2*}, w_3^*)$ *with* $0 \ll w_{i*} \le w_i^*$, $\forall 1 \le i \le 3$, *such that for any* $u \in \dot{P}_1 \times \dot{P}_2 \times \dot{P}_3$, $\varphi(t,u) = (u_1(t), u_2(t), u_3(t))$ *satisfies* $\lim_{t\to\infty} d(u_i(t), [w_{i*}, w_i^*]) = 0$, $\forall 1 \le i \le 3$.

Proof. As shown in Theorem 7.2.1, now $\varphi(t,\cdot) : X = P_1 \times P_2 \times P_3 \to X$, $t \ge 0$, is a monotone semiflow. For $\omega > 0$, we view the autonomous parabolic system (7.1) as an ω-periodic one. Let $\mu(A, m(\cdot), \omega)$ be the principal eigenvalue of ω-periodic parabolic problem (7.2). By [152, Chapter II.15 and Remark 16.5], it follows that conditions (1), (2), and (3) imply (H6), (C1), and (C2), respectively. As in the proof of Theorem 7.2.1, for any $\epsilon \in (0, \epsilon_0]$, we have $\lim_{n\to\infty} S^n(U_1^* + \epsilon e_1) = U_* \gg U_1^* + \epsilon e_1$. Then there exists $N > 0$ such that $\varphi(n\omega, U_1^* + \epsilon e_1) = S^n(U_1^* + \epsilon e_1) \gg U_1^* + \epsilon e_1$, $\forall n \ge N$. By the Hirsch convergence criterion for monotone semiflows (see Theorem 2.2.5), $\varphi(t, U_1^* + \epsilon e_1)$ converges to an equilibrium as $t \to \infty$, which implies that U_* is an equilibrium; that is, $\varphi(t, U_*) = U_*(t) = U_*$, $\forall t \ge 0$. Similarly, we can prove $U^*(t) = U^*$, $\forall t \ge 0$. Now Theorem 7.2.1 completes the proof. ∎

7.3 Competitive Exclusion

In this section we establish conditions under which at least one species goes to extinction via the Poincaré map $S : X \to X$ associated with (7.1).

Proposition 7.3.1. *Let (H1)–(H6) and (C2) hold. Then for every* $u \in \dot{P}_1 \times \dot{P}_2 \times \dot{P}_3$*, we have* $\omega(u) \subset [U_1^*, U_2^*]]_E$*; that is,* $0 \le v_1 \ll u_1^*(0)$*,* $0 \ll v_2 \le u_2^*(0)$*, and* $u_3^*(0) \le v_3 \ll \overline{u}_3(0)$*,* $\forall v = (v_1, v_2, v_3) \in \omega(u)$*.*

Proof. Let $Y_0 := \{(u_1, u_2, u_3) \in X : \ u_2(\cdot) \not\equiv 0 \,\text{and}\, u_3(\cdot) \not\equiv 0\} = P_1 \times \dot{P}_2 \times \dot{P}_3$ and $\partial Y_0 := X \setminus X_0$. Then Y_0 and ∂Y_0 are relatively open and closed in X, respectively. Clearly, $S(Y_0) \subset Y_0$ and $S(\partial Y_0) \subset \partial Y_0$. Let A_∂ be the maximal compact invariant set of S in ∂Y_0, and let M_1 be the global attractor of $S : P_1 \times P_2 \times \{0\} \to P_1 \times P_2 \times \{0\}$, $M_2 = (0, 0, u_3^*(0))$, and $M_3 = (u_1^*(0), 0, \overline{u}_3(0))$. By an argument similar to that in Proposition 7.2.1, it easily follows that $\cup_{i=1}^3 M_3$ is an isolated and acyclic covering of $\cup_{u \in A_\partial} \omega(u)$ and $W^s(M_i) \cap Y_0 = \emptyset$. Then Theorem 1.3.1 and Remark 1.3.1 imply that $S : X \to X$ is uniformly persistent with respect to $(Y_0, \partial Y_0)$.

As in the proof of Proposition 7.2.2, for $u \in \dot{P}_1 \times \dot{P}_2 \times \dot{P}_3$, we have $\omega(u) \subset [0, u_1^*(0)] \times [0, u_2^*(0)] \times [u_3^*(0), \overline{u}_3(0)]$. It remains to prove that for any $v = (v_1, v_2, v_3) \in \omega(u)$, $v_1 \ll u_1^*(0)$, $v_2 \gg 0$, and $v_3 \ll \overline{u}_3(0)$. By the uniform persistence of S with respect to $(Y_0, \partial Y_0)$ and the invariance of $\omega(u)$ (see the proof of Proposition 7.2.2), it follows that for any $v = (v_1, v_2, v_3) \in \omega(u)$, we have $v_2 \gg 0$, $v_3 \gg 0$. Then $\varphi(t, v) = (v_1(t), v_2(t), v_3(t))$ satisfies $v_1(t) \ge 0$, $v_2(t) \gg 0$, and $v_3(t) \gg 0$, $\forall t \ge 0$. If $v_1 = 0$, then $v_1(t) = 0$, $\forall t \ge 0$, and hence $v_1(2\omega) \ll u_1^*(0)$ in E_1. If $v_1 > 0$, then $v_1(t) \gg 0$, $\forall t > 0$. Since $q_1(x, t, v_1(t), v_2(t), v_3(t)) \not\equiv 0$ for $(x, t) \in Q_\omega$, by a maximum principle argument (see the proof of Proposition 7.2.2), we get $v_1(2\omega) \ll u_1^*(0)$. It then follows that for any $v = (v_1, v_2, v_3) \in \omega(u) = S^2(\omega(u))$, we have $v_1 \ll u_1^*(0)$. Consequently, $v_1(t) \ll u_1^*(t)$ and $v_3(t) \gg 0$, $\forall t \ge 0$, and hence $v_3(t)$ satisfies

$$\frac{\partial v_3}{\partial t} + A_3(t) v_3 < v_3 h(x, t, u_1^*(t), v_3), \ \forall (x, t) \in \Omega \times (0, \infty).$$

As in the proof of Proposition 7.2.2, it follows that $v_3(2\omega) \ll \overline{u}_3(0)$. Thus, for any $v = (v_1, v_2, v_3) \in \omega(u) = S^2(\omega(u))$, we have $v_3 \ll \overline{u}_3(0)$. ∎

By a similar argument, we can prove the following result.

Proposition 7.3.2. *Let (H1)–(H6) and (C1) hold. Then for every* $u \in \dot{P}_1 \times \dot{P}_2 \times \dot{P}_3$*, we have* $\omega(u) \in [[U_1^*, U_2^*]_E$*; that is,* $0 \ll v_1 \le u_1^*(0)$*,* $0 \le v_2 \ll u_2^*(0)$*, and* $u_3^*(0) \ll v_3 \le \overline{u}_3(0)$*,* $\forall v = (v_1, v_2, v_3) \in \omega(u)$*.*

Now we are in a position to prove the main result of this section.

Theorem 7.3.1. *Let (H1)–(H6) and (C2) hold. Assume that (7.1) admits no positive* ω*-periodic solution (in* $\mathrm{int}(P_1) \times \mathrm{int}(P_2) \times \mathrm{int}(P_3)$*). Then for every* $u \in \dot{P}_1 \times \dot{P}_2 \times \dot{P}_3$*, the solution* $\varphi(t, u)$ *of (7.1) satisfies* $\lim_{t \to \infty}(\varphi(t, u) - U_1^*(t)) = 0$ *in* E*, where* $U_1^*(t) = (0, u_2^*(t), u_3^*(t))$*.*

Proof. It suffices to prove that for every $u \in \dot{P}_1 \times \dot{P}_2 \times \dot{P}_3$, we have $\omega(u) = U_1^* = U_1^*(0)$. For $u \in \dot{P}_1 \times \dot{P}_2 \times \dot{P}_3$, by Proposition 7.3.1, we have $\omega(u) \subset [U_1^*, U_2^*]]$. Then the compactness of $\omega(u)$ and Lemma 7.2.2 imply that there exists an $\epsilon > 0$ such that $\omega(u) \subset [U_1^*, U_2^* - \epsilon e_2]]$ and $S(U_2^* - \epsilon e_2) \ll U_2^* - \epsilon e_2$, where $e_2 \gg 0$ in (E, P) is as given in Lemma 7.2.2. Thus,

$$U_1^* \leq S^n(\omega(u)) = \omega(u) \leq S^n(U_2^* - \epsilon e_2),\ \forall n \geq 1.$$

By the monotonicity and compactness of S, it follows that $S^n(U_2^* - \epsilon e_2)$ converges decreasingly to a fixed point U^* with $U_1^* \leq U^* \ll U_2^*$ in E. Let $U^* = (U_1, U_2, U_3)$. Then $0 \leq U_1 \ll u_1^*(0)$, $0 \ll U_2 \leq u_2^*(0)$, and $0 \ll u_3^*(0) \leq U_3 \ll \overline{u}_3(0)$. By the nonexistence of a positive ω-periodic solution of (7.1) and hence that of the positive fixed point of S in $\mathrm{int}(P_1) \times \mathrm{int}(P_2) \times \mathrm{int}(P_3)$, it follows that $U_1 = 0$. Let $\varphi(t, U) = (U_1(t), U_2(t), U_3(t))$. Then $U_1(t) \equiv 0$, and hence in view of $U_2 \gg 0$ and $U_3 \gg 0$, we get $U_2(t) \equiv U_2^*(t),\ U_3(t) \equiv U_3^*(t),\ \forall t \geq 0$. Consequently, $\lim_{n\to\infty} S^n(U_2^* - \epsilon e_2) = U^* = (U_1(0), U_2(0), U_3(0)) = U_1^*$, and hence $\omega(u) = U_1^*$. ∎

By a similar argument, together with Proposition 7.3.2, we can prove the following result on the global extinction of u_2.

Theorem 7.3.2. *Let (H1)–(H6) and (C1) hold. Assume that (7.1) admits no positive ω-periodic solution (in $\mathrm{int}(P_1)\times\mathrm{int}(P_2)\times\mathrm{int}(P_3)$). Then for every $u \in \dot{P}_1 \times \dot{P}_2 \times \dot{P}_3$, the solution $\varphi(t, u)$ of (7.1) satisfies $\lim_{t\to\infty}(\varphi(t, u) - U_2^*(t)) = 0$ in E, where $U_2^*(t) = (u_1^*(t), 0, \overline{u}_3(t))$.*

Remark 7.3.1. As illustrated in previous section (see, e.g., the proof of Theorem 7.2.2), for the autonomous case of (7.1), there are also analogous results of Theorems 7.3.1 and 7.3.2. In particular, we need to assume that the autonomous system (7.1) admits no positive stead state solution in $\mathrm{int}(P_1) \times \mathrm{int}(P_2) \times \mathrm{int}(P_3)$.

As an example, we consider a special case of system (7.1) (see [285] for ordinary differential systems and [374] for reaction–diffusion systems)

$$\begin{aligned}
&\frac{\partial u_1}{\partial t} + A_1(t)u_1 = \beta_1(x,t)u_1\left[1 - \frac{u_1}{a_1(x,t)} - \frac{a_2(x,t)u_2}{1 + a_3(x,t)u_3}\right] \text{ in } \Omega \times (0,\infty),\\
&\frac{\partial u_2}{\partial t} + A_2(t)u_2 = \beta_2(x,t)u_2\left[1 - b_1(x,t)u_1 - \frac{u_2}{b_2(x,t)}\right] \text{ in } \Omega \times (0,\infty),\\
&\frac{\partial u_3}{\partial t} + A_3(t)u_3 = \beta_3(x,t)u_3\left[1 - \frac{u_3}{c_0(x,t) + c_1(x,t)u_1}\right] \text{ in } \Omega \times (0,\infty),\\
&\quad B_1u_1 = B_2u_2 = B_3u_3 = 0 \text{ on } \partial\Omega \times (0,\infty),
\end{aligned} \tag{7.17}$$

where $\Omega, A_i(t), B_i(t)$, $1 \leq i \leq 3$, are as in system (7.1), and $\beta_i, a_i, b_i, c_i : \overline{\Omega} \times \mathbb{R}_+ \to \mathbb{R}$ are positive continuous functions and ω-periodic in t. Assume that

(A1) $\mu(A_i(t), \beta_i(x,t)) < 0$, $\forall 1 \le i \le 3$.

According to Theorem 3.1.5, let u_1^*, u_2^*, u_3^*, and $\overline{u}_3$ be the unique positive ω-periodic solutions of the scalar parabolic equation

$$\begin{aligned} \frac{\partial u}{\partial t} + A(t)u &= uF(x,t,u) \quad \text{in } \Omega \times (0,\infty), \\ Bu &= 0 \quad \text{on } \partial\Omega \times (0,\infty), \end{aligned} \tag{7.18}$$

with $(A,B,F) = (A_1, B_1, \beta_1(1-\frac{u_1}{a_1}))$, $(A_2, B_2, \beta_2(1-\frac{u_2}{b_2})$, $(A_3, B_3, \beta_3(1-\frac{u_3}{c_0}))$, and $(A_3, B_3, \beta_3(1-\frac{u_3}{c_0+c_1u_1^*}))$, respectively. In the case where $A_i = -k_i(t)\Delta$ and $B_i u = \frac{\partial u}{\partial \nu}$, $\forall 1 \le i \le 3$, it is easy to see that $a_{1L} \le u_1^*(x,t) \le a_{1M}$, $b_{2L} \le u_2^*(x,t) \le b_{2M}$, and $c_{0L} \le \overline{u}_3(x,t) \le c_{0M}$, $\forall (x,t) \in \overline{Q}_\omega$, where f_M and f_L denote the supremum and infimum of a bounded function f, respectively.

By Theorems 7.2.1, 7.3.1, and 7.3.2, we then have the following three results on the global asymptotic behavior of (7.17).

Proposition 7.3.3. *Let (A1) hold. Assume that*

(A2) $\mu(A_1(t), \beta_1(1-\frac{a_2u_2^*}{1+a_3u_3^*})) < 0$;
(A3) $\mu(A_2(t), \beta_2(1-b_1u_1^*)) < 0$.

Then the conclusion of Theorem 7.2.1 holds for (7.17).

Proposition 7.3.4. *Let (A1) and (A3) hold. Assume that (7.17) admits no positive ω-periodic solution. Then the conclusion of Theorem 7.3.1 holds for (7.17).*

Proposition 7.3.5. *Let (A1) and (A2) hold. Assume that (7.17) admits no positive ω-periodic solution. Then the conclusion of Theorem 7.3.2 holds for (7.17).*

For various estimates of principal eigenvalues of periodic–parabolic eigenvalue problems, we refer to [152, Lemma 15.6 and Section II.17], [188], and [187]. In particular, let $Bu = \frac{\partial u}{\partial \nu}$, and $A = -k(t)\Delta$, where $k \in C^{\theta/2}(\mathbb{R},\mathbb{R})$ is ω-periodic and positive. Then [152, Example 17.2] implies that for any given $m \in C^{\theta,\theta/2}(\overline{Q}_\omega)$, we have

(I) $\mu(A(t), m(x,t)) < 0$ if either $\int\int_{Q_\omega} m(x,t)dx\,dt > 0$ or $\int\int_{Q_\omega} m(x,t)dx\,dt \ge 0$ with $m(x,t)$ depending nontrivially on x;
(II) $\mu(m(x,t)) > 0$ if $\int\int_{Q_\omega} m(x,t)dx\,dt < 0$ and $\int_0^\omega \max_{x\in\overline{\Omega}} m(x,t)dt \le 0$.

By an approach similar to that in Sections 7.2 and 7.3, we can discuss the global asymptotic behavior in a more general periodic competitor–competitor–mutualist model

$$\begin{aligned}
&\frac{\partial u_1}{\partial t} + A_1(t)u_1 = u_1 G_1(x,t,u_1,u_2,u_3) \quad \text{in } \Omega \times (0,\infty),\\
&\frac{\partial u_2}{\partial t} + A_2(t)u_2 = u_2 G_2(x,t,u_1,u_2) \quad \text{in } \Omega \times (0,\infty),\\
&\frac{\partial u_3}{\partial t} + A_3(t)u_3 = u_3 G_3(x,t,u_1,u_3) \quad \text{in } \Omega \times (0,\infty),\\
&\quad B_1u_1 = B_2u_2 = B_3u_3 = 0 \quad \text{on } \partial\Omega \times (0,\infty),
\end{aligned}$$

where the continuously differentiable functions G_i are such that for all $u_i \geq 0$, $1 \leq i \leq 3$,

$$\frac{\partial G_1}{\partial u_2} \leq 0, \qquad \frac{\partial G_1}{\partial u_3} \geq 0, \qquad \frac{\partial G_2}{\partial u_1} \leq 0, \qquad \text{and} \qquad \frac{\partial G_3}{\partial u_1} \geq 0.$$

7.4 Bifurcations of Periodic Solutions: A Case Study

In this section we use bifurcation methods to study the existence and multiplicity of positive ω-periodic solutions of a special case of (7.1). We first state two general bifurcation theorems in Banach spaces.

Simple Eigenvalues Theorem ([68, Theorem 1.7]) *Let X, Y be Banach spaces, V a neighborhood of 0 in X, and $F : (-1,1) \times V \to Y$ a continuous function. Assume that*

(a) $F(\lambda, 0) = 0$, $\forall \lambda \in (-1,1)$;
(b) The partial derivatives F_λ, F_x, and $F_{\lambda x}$ exist and are continuous;
(c) $N(F_x(0,0))$ and $Y \setminus R(F_x(0,0))$ are one-dimensional, where $N(F_x(0,0))$ and $R(F_x(0,0))$ denote the null space and range of the linear operator $F_x(0,0)$, respectively;
(d) $F_{\lambda x}(0,0)x_0 \notin R(F_x(0,0))$, where $N(F_x(0,0)) = \mathrm{span}\{x_0\}$.

If Z is a complement of $N(F_x(0,0))$ in X, then there are a neighborhood U of $(0,0)$ in $\mathbb{R} \times X$, an interval $(-\delta, \delta)$, and continuous functions $\phi : (-\delta,\delta) \to \mathbb{R}$, $\psi : (-\delta,\delta) \to Z$ such that $\phi(0) = 0$, $\psi(0) = 0$, and

$$F^{-1}(0) \cap U = \{(\phi(s), sx_0 + s\psi(s)) : s \in (-\delta,\delta)\} \cup \{(\lambda, 0) : (\lambda, 0) \in U\}.$$

If F_{xx} is also continuous, the functions ϕ and ψ are once continuously differentiable.

Let L be a linear and compact operator on a Banach space E, and let $\sigma(L)$ be its spectrum set. For $\mu \in \{\mu \in \mathbb{R} : \mu^{-1} \in \sigma(L)\}$, the multiplicity of μ is defined to be the dimension of $\cup_{i\geq 0} N((I - \mu L)^i)$.

Global Bifurcation Theorem ([284, Theorem 1.3]) *Suppose $G(\lambda, u) = \lambda L u + H(\lambda, u)$, where L is linear and compact, H is compact, and $o(\|u\|)$ as $u \to 0$ on bounded λ intervals. Let S be the closure of the set $\{(\lambda, u) :$*

$u = G(\lambda, u), u \neq 0\}$ in $\mathbb{R} \times E$. If $\mu \in \{\mu \in \mathbb{R} : \mu^{-1} \in \sigma(L)\}$ is of odd multiplicity, then S has a maximal closed and connected subset C that contains $(\mu, 0)$ and is either unbounded in $\mathbb{R} \times E$ or contains $(\hat{\mu}, 0)$, where $\mu \neq \hat{\mu} \in \{\mu \in \mathbb{R} : \mu^{-1} \in \sigma(L)\}$.

We then consider a periodic competitor–competitor–mutualist model with parameter $\lambda \in \mathbb{R}$:

$$\begin{aligned}
&\frac{\partial u_1}{\partial t} = \alpha_1 \Delta u_1 + u_1(\lambda\beta_1 - a_1 u_1 - a_2 u_2/(1 + a_3 u_3)) \quad \text{in } \Omega \times (0, \infty),\\
&\frac{\partial u_2}{\partial t} = \alpha_2 \Delta u_2 + u_2(\beta_2 - b_1 u_1 - b_2 u_2) \quad \text{in } \Omega \times (0, \infty),\\
&\frac{\partial u_3}{\partial t} = \alpha_3 \Delta u_3 + u_3(\beta_3 - c_3 u_3/(1 + c_1 u_1)) \quad \text{in } \Omega \times (0, \infty),\\
&Bu_1 = Bu_2 = Bu_3 = 0 \quad \text{on } \partial\Omega \times (0, \infty),
\end{aligned} \tag{7.19}$$

where Ω and B are as in system (7.1), and $\alpha_i, \beta_i, a_i, b_i$, and c_i are all positive functions of $(x, t) \in \overline{\Omega} \times \mathbb{R}_+$ and are ω-periodic in t for some $\omega > 0$.

We are to find the ranges of λ for which system (7.19) has positive periodic solutions. Let $\theta \in (0, 1)$ be fixed, and define

$$X = \{w \in C^{\theta,\theta/2}(\overline{\Omega} \times \mathbb{R}) : w \text{ is } \omega\text{-periodic in } t\}$$

and

$$Y = \{w \in C^{2+\theta,1+\theta/2}(\overline{\Omega} \times \mathbb{R}) : w \,\text{is}\, \omega\text{-periodic in}\, t \,\text{and}\, Bw = 0 \,\text{on}\, \partial\Omega \times \mathbb{R}\}.$$

For $d, q \in X$, let $\lambda_1(d, q) := \mu(-d\Delta, -q)$. Throughout this section we assume that $\alpha_i, \beta_i, a_i, b_i, c_i \in X$, $\lambda_1(\alpha_2, -\beta_2) < 0$, and $\lambda_1(\alpha_3, -\beta_3) < 0$.

For a fixed $u \in X$, consider the scalar periodic equation

$$v_t - \alpha_2 \Delta v = (\beta_2 - b_1 u)v - b_2 v^2, \qquad v \in Y. \tag{7.20}$$

By Theorem 3.1.5, (7.20) has a unique positive solution v_u if and only if $\lambda_1(\alpha_2, -\beta_2 + b_1 u) < 0$. Let

$$v(u) = \begin{cases} 0 & \text{if}\, \lambda_1(\alpha_2, -\beta_2 + b_1 u) \geq 0,\\ v_u & \text{if}\, \lambda_1(\alpha_2, -\beta_2 + b_1 u) < 0. \end{cases}$$

Then the following lemma follows from a simple variant of [38, Lemma 4.2].

Lemma 7.4.1. *The function $v : X \to X$ has the following properties:*

(i) $u \to v(u)$ *is continuous from X to X;*
(ii) *If $u_1 \leq u_2$, then $v(u_1) \geq v(u_2)$;*
(iii) $v(u) \leq v(0) =: U_2$ *for any $u \geq 0$.*

For a fixed $u \in X$, we consider the equation

$$w_t - \alpha_3 \Delta w = \beta_3 w - \frac{c_3}{1 + c_1 \max\{u, 0\}} w^2, \qquad w \in Y. \tag{7.21}$$

Again by Theorem 3.1.5, (7.21) has a unique positive solution $w(u)$. As in [38], we can easily prove the following result.

Lemma 7.4.2. *The function $w : X \to X$ has the following properties:*

(i) $u \to w(u)$ *is continuous from X to X;*
(ii) *If $u_1 \leq u_2$, then $w(u_1) \leq w(u_2)$;*
(iii) $w(u) \geq w(0) =: U_3$ *for any $u \geq 0$.*

Let

$$n(u) = \frac{a_2 v(u)}{1 + a_3 w(u)},$$

and consider now the problem

$$u_t - \alpha_1 \Delta u = \lambda \beta_1 u - n(u) u - a_1 u^2, \qquad u \in Y. \tag{7.22}$$

Clearly, if u is a positive solution of (7.22), then $(u_1, u_2, u_3) = (u, v(u), w(u))$ is a nonnegative solution of (7.19), and it is a positive solution of (7.19) if $v(u) > 0$. Conversely, if (u_1, u_2, u_3) is any positive solution of (7.19), then $u_2 = v(u_1)$, $u_3 = w(u_1)$ and u_1 is a positive solution of (7.22). Therefore, finding positive solutions of (7.19) is equivalent to finding positive solutions of (7.22) for which $v(u) > 0$.

By Lemmas 7.4.1 and 7.4.2, it follows that

(N1) $u \to n(u)$ is continuous from X to X;
(N2) $u_1 \leq u_2$ implies that $n(u_1) \geq n(u_2)$;
(N3) $0 \leq n(u) \leq \frac{a_2 U_2}{1 + a_3 U_3}$ for any $u \geq 0$.

These three facts guarantee that the upper and lower solution method can be used to solve (7.22).

Lemma 7.4.3. *Suppose that $v \in Y$ is a lower solution of (7.22) and $V \in Y$ is an upper solution of (7.22) and that $0 \leq v \leq V$. Then (7.22) has a minimal solution u_* and a maximal solution u^* in the order interval $[v, V]$ in Y.*

Proof. Choose a constant $k > 0$ so large that

$$k + \lambda \beta_1 - \frac{a_2 U_2}{1 + a_3 U_3} - 2 a_1 V > 0, \, \forall (x, t) \in \overline{\Omega} \times [0, \omega].$$

Then it is easy to see that for $u \in [v, V]$,

$$u \to F(u) \equiv \lambda \beta_1 u - n(u) u - a_1 u^2 + k u$$

is an increasing mapping from $[v, V] \subset Y$ to X. Define $Lu = u_t - \alpha_1 \Delta u + k u$. Then $u \in [v, V]$ solves (7.22) if and only if $u = L^{-1} F(u) =: S u$.

Now we have $v \leq Sv$, $SV \leq V$, and that $u \to Su$ is an increasing mapping. By regularity results in [152], the L^∞ boundedness of $[v, V]$ implies that $S^2([v, V])$ is compact in Y. It then follows by a compactness argument that the monotone increasing sequence $\{S^n v\}$ and the monotone decreasing sequence $\{S^n V\}$ are both convergent in Y. Let $S^n v \to u_*$ and $S^n V \to u^*$. Then it follows from a standard argument that u_* and u^* are the minimal and maximal fixed points of S in $[v, V]$. ∎

Since

$$0 \leq n(u) \leq \frac{a_2 U_2}{1 + a_3 U_3}, \; \forall u \geq 0,$$

any positive solution u_0 of (7.22) satisfies

$$(u_0)_t - \alpha_1 \Delta u_0 \geq \left(\lambda \beta_1 - \frac{a_2 U_2}{1 + a_3 U_3} \right) u_0 - a_1 u_0^2$$

and

$$(u_0)_t - \alpha_1 \Delta u_0 \leq \lambda \beta_1 u_0 - a_1 u_0^2.$$

Hence u_0 is an upper solution of the problem

$$u_t - \alpha_1 \Delta u = \left(\lambda \beta_1 - \frac{a_2 U_2}{1 + a_3 U_3} \right) u - a_1 u^2, \qquad u \in Y, \tag{7.23}$$

and is a lower solution of the problem

$$u_t - \alpha_1 \Delta u = \lambda \beta_1 u - a_1 u^2, \qquad u \in Y. \tag{7.24}$$

By Theorem 3.1.5, it follows that (7.23) has a unique positive solution if and only if $\lambda_1(\alpha_1, -\lambda\beta_1 + \frac{a_2 U_2}{1+a_3 U_3}) < 0$, or equivalently, if and only if $\lambda > \lambda_0$, where $\lambda = \lambda_0$ is the unique solution of $\lambda_1(\alpha_1, -\lambda\beta_1 + \frac{a_2 U_2}{1+a_3 U_3}) = 0$. We denote this unique positive solution by θ_λ. Again by Theorem 3.1.5, (7.24) has a positive solution if and only if $\lambda_1(\alpha_1, -\lambda\beta_1) < 0$, or equivalently, if and only if $\lambda > \Lambda^0$, where $\lambda = \Lambda^0$ is the unique solution of $\lambda_1(\alpha_1, -\lambda\beta_1) = 0$. We use θ^λ to denote this solution. It follows easily that

$$\theta_\lambda \leq u_0 \leq \theta^\lambda \tag{7.25}$$

whenever θ_λ and θ^λ are defined and u_0 is a positive solution of (7.22).

Next we derive some estimates on θ_λ. Choose a constant $M > 0$ so large that $\beta_1 - a_1 M < 0$. Then one easily sees that λM is an upper solution of (7.23). If $\lambda_1(\alpha_1, -\lambda\beta_1 + \frac{a_2 U_2}{1+a_3 U_3}) < 0$, then one can always construct a lower solution of (7.23) by using the corresponding principal eigenfunction. Hence, we always have $\theta_\lambda < \lambda M$. Now suppose that θ_λ is defined. Then for $v = \lambda \theta_\lambda$, we have

$$\begin{aligned}
v_t - \alpha_1 \Delta v &= \lambda\beta_1 v - \frac{a_2 U_2}{1 + a_3 U_3} v - a_1 v^2/\lambda \\
&\le \lambda\beta_1 v + a_1 v^2 - \frac{a_2 U_2}{1 + a_3 U_3} v - a_1 v^2 \\
&\le (\lambda\beta_1 + a_1 \lambda^2 M) v - \frac{a_2 U_2}{1 + a_3 U_3} v - a_1 v^2 \\
&\le \lambda(1 + \sigma\lambda)\beta_1 v - \frac{a_2 U_2}{1 + a_3 U_3} v - a_1 v^2,
\end{aligned}$$

where $\sigma = \frac{\max a_1}{\min \beta_1} M$. Thus, v is a lower solution of (7.23) with λ replaced by $\lambda(1 + \sigma\lambda)$. This implies that

$$\theta_{\lambda(1+\sigma\lambda)} \ge v = \lambda\theta_\lambda.$$

If we define $\mu(\lambda) = (\sqrt{1 + 4\sigma\lambda} - 1)/(2\sigma)$, we can express the above inequality by

$$\theta_\lambda \ge \mu(\lambda)\theta_{\mu(\lambda)}.$$

By an upper and lower solution argument, it is easy to show that $\theta_{\lambda_1} < \theta_{\lambda_2}$ if $\lambda_1 < \lambda_2$. Thus if we fix a λ_0 such that $\theta_{\mu(\lambda_0)}$ is defined, then for $\lambda \ge \lambda_0$,

$$\theta_\lambda \ge \mu(\lambda)\theta_{\mu(\lambda_0)}. \tag{7.26}$$

We show now that

$$\lambda_1(\alpha_2, -\beta_2 + b_1\theta_\lambda) \to \infty \text{ as } \lambda \to \infty. \tag{7.27}$$

We suppose first that $Bu = 0$ is not of Dirichlet type. Then $\min(\theta_\lambda) > 0$. Therefore, (7.26) implies that for $\lambda \ge \lambda_0$,

$$\begin{aligned}
\lambda_1(\alpha_2, -\beta_2 + b_1\theta_\lambda) &\ge \lambda_1(\alpha_2, -\max(\beta_2) + \min(b_1)\mu(\lambda)\min(\theta_{\mu(\lambda_0)})) \\
&= -\max(\beta_2) + \min(b_1)\mu(\lambda)\min(\theta_{\mu(\lambda_0)}),
\end{aligned}$$

and hence $\lambda_1(\alpha_2, -\beta_2 + b_1\theta_\lambda) \to \infty$ as $\lambda \to \infty$. Since the principal eigenvalue under Dirichlet boundary conditions is greater than that under Neumann boundary conditions (see [152]), the above argument shows that (7.27) is true in the case of general boundary condition $Bu = 0$.

Since $\theta^\lambda > \theta_\lambda$, we obtain from (7.27) that

$$\lambda_1(\alpha_2, -\beta_2 + b_1\theta^\lambda) \to \infty \text{ as } \lambda \to \infty.$$

A simple upper and lower solution argument shows that $\lambda \to \theta^\lambda$ is strictly increasing. Now consider the continuous function $\lambda \to h(\lambda) := \lambda_1(\alpha_2, -\beta_2 + b_1\theta^\lambda)$. It satisfies $h(\Lambda^0) = \lambda_1(\alpha_1, -\beta_2) < 0$, $h(\lambda) \to \infty$ as $\lambda \to \infty$, and it is strictly increasing. Therefore, there exists a unique $\lambda^0 > \Lambda^0$ such that $h(\lambda^0) = 0$. Similarly, there is a unique $\Lambda_0 > \lambda_0$ such that $\lambda(\alpha_2, -\beta_2 + b_1\theta_{\Lambda_0}) = 0$.

Now let us go back to equation (7.22). We use a bifurcation argument as in the proof of [38, Lemma 3.4]. Since λ_0 is a simple eigenvalue of the linearization of (7.22) at $u = 0$, a local bifurcation result shows that there is a positive solution branch $\Gamma = \{(\lambda, u)\}$ of (7.22) bifurcating from $(\lambda_0, 0)$. Then global bifurcation theorem and the strong maximum principle can be used to show that this branch is contained in a connected component Σ that joins $(\lambda_0, 0)$ to ∞ in $\mathbb{R} \times Y$ and $u > 0, \ \ \forall(\lambda, u) \in \Sigma \setminus \{(\lambda_0, 0)\}$.

Suppose that $(\lambda, u) \in \Sigma \setminus \{(\lambda_0, 0)\}$. In view of

$$u_t - \alpha_1 \Delta u - [\lambda\beta_1 - n(u) - a_1 u]u = 0, \ u > 0,$$

we obtain that

$$0 = \lambda_1(\alpha_1, -\lambda\beta_1 + n(u) + a_1 u) > \lambda_1(\alpha_1, -\lambda\beta_1).$$

This implies that $\lambda > 0$. Note that (7.25) implies L^∞ boundedness of u. By standard regularity results, we can prove as in [38] that for $(\lambda, u) \in \Sigma$, $\|u\|_Y$ is bounded in any bounded range of λ. Thus, the only way that Σ can approach ∞ is as $\lambda \to \infty$.

By (7.25) and the definition of $v(u)$, it follows that if $(\lambda, u) \in \Sigma$ and $\lambda \geq \Lambda_0$, then $v(u) \equiv 0$. Then (7.22) reduces to (7.24), and $u \equiv \theta^\lambda$. This implies that

$$\Sigma \cap ([\Lambda_0, \infty) \times Y) = \{(\lambda, \theta^\lambda) : \lambda \geq \Lambda_0\},$$

and hence

$$U := \{(\lambda, \theta^\lambda) : \lambda > \lambda^0\} \subset \Sigma.$$

We are now in a position to prove the main result of this section.

Theorem 7.4.1. *There exist λ_* and λ^* with $\lambda_* \leq \min\{\lambda_0, \lambda^0\}$, $\lambda^* \geq \max\{\lambda_0, \lambda^0\}$ such that (7.19) has no positive solution for $\lambda \notin [\lambda_*, \lambda^*]$, and has at least one positive solution for $\lambda \in (\lambda_*, \lambda^*)$. Moreover,*

(i) If $\lambda_* < \min\{\lambda_0, \lambda^0\}$, then (7.19) has at least two positive solutions for $\lambda_* < \lambda < \min\{\lambda_0, \lambda^0\}$, and at least one positive solution for $\lambda = \lambda_*$;
(ii) If $\lambda^* > \max\{\lambda_0, \lambda^0\}$, then for $\max\{\lambda_0, \lambda^0\} < \lambda < \lambda^*$, (7.19) has at least two positive solutions, and for $\lambda = \lambda^*$, there is at least one positive solution;
(iii) If $\lambda_* = \lambda^*$, then (7.19) has a continuum of positive solutions for $\lambda = \lambda_*$.

Proof. Our arguments are essentially the same as in [104]. Here we give only a sketch of the proof. Define

$$\Lambda = \{\lambda : \text{(7.19) has a positive solution for } \lambda\}.$$

Let $\lambda_* = \inf \Lambda$ and $\lambda^* = \sup \Lambda$. By the discussions before Theorem 7.4.1, we then have $\lambda_* \geq 0$ and $\lambda^* \leq \Lambda_0$.

Step 1. $\Sigma_0 := \Sigma \setminus U$ is a connected set that joins $(\lambda_0, 0)$ to $\left(\lambda^0, \theta^{\lambda^0}\right)$. Moreover, if $(\lambda, u) \in \Sigma_0$ is different from these two points, then $u > 0$, $v(u) > 0$, and hence such a (λ, u) corresponds to a positive solution of (3.1). Note that $v(\theta^{\lambda^0}) = 0$. Hence $u = \theta^{\lambda^0}$ corresponds to a semitrivial solution of (7.19). Let $U_1 := \theta^{\lambda^0}$. Then Σ_0 corresponds to a positive solution branch of (7.19) that joins the semitrivial solutions $(\lambda_0, 0, U_2, U_3)$ and $(\lambda^0, U_1, 0, W_3)$. We refer to the proof of [104, Theorem 3.1] for a detailed proof of these facts.

This proves that (7.19) has a positive solution for λ between λ_0 and λ^0. This also proves statement (iii) in Theorem 7.4.1.

Step 2. If $\lambda_* < \min\{\lambda_0, \lambda^0\}$, then (7.22) has a positive solution u_* satisfying $v(u_*) > 0$ for $\lambda = \lambda_*$. For any $\lambda \in (\lambda_*, \lambda^0)$, u_* is a lower solution of (7.22) and θ^λ is an upper solution of (7.22). By (7.25), we have $u_* \leq \theta^{\lambda_*} < \theta^\lambda$. This gives, by Lemma 7.4.3, a maximal solution u^λ of (7.22). Moreover, $u_* < u^\lambda < \theta^\lambda$ and $v(u^\lambda) > 0$, because

$$\lambda_1(\alpha_2, -\beta_2 + b_1 u^\lambda) < \lambda_1(\alpha_2, -\beta_2 + b_1 \theta^{\lambda^0}) = 0.$$

We refer to the proof of [104, Lemmas 2.5 and 2.6] for a detailed proof of these facts.

This step shows that (7.22) has a positive solution for $\lambda \in [\lambda_*, \lambda^0)$.

Step 3. If $\lambda_* < \lambda < \min\{\lambda_0, \lambda^0\}$, then (7.22) has a positive solution $u \neq u^\lambda$ with $v(u) > 0$. One essential fact in the proof of this statement is that $\{(\lambda, u^\lambda) : \lambda_* < \lambda < \lambda^0\} \subset \Sigma_0$. We refer to the proof of [104, Theorems 3.2 and 3.3] for more details.

This step and Step 2 prove statement (i) in Theorem 7.4.1.

Step 4. If $\lambda^* > \max\{\lambda_0, \lambda^0\}$, then (7.22) has a positive solution u^* satisfying $v(u^*) > 0$ for $\lambda = \lambda^*$. For $\lambda \in (\lambda_0, \lambda^*)$, $\theta_\lambda < u^*$ is a pair of lower and upper solutions of (7.22). Therefore, there is a minimal solution u_λ of (7.22) satisfying $\theta_\lambda < u_\lambda < u^*$. We have $v(u_\lambda) > 0$ because

$$\lambda_1(\alpha_2, -\beta_2 + b_1 u_\lambda) < \lambda_1(\alpha_2, -\beta_2 + b_1 u^*) < 0.$$

Details of the proof of these facts can be found in the proofs of [104, Lemmas 2.5 and 2.6].

This step proves that (7.22) has a positive solution for $\lambda \in (\lambda_0, \lambda^*]$.

Step 5. If $\lambda^* > \lambda > \max\{\lambda_0, \lambda^0\}$, then (7.22) has a positive solution $u \neq u_\lambda$ with $v(u) > 0$. A key fact in proving this is that $\{(\lambda, u_\lambda) : \lambda_0 < \lambda < \lambda^*\} \subset \Sigma_0$. See the proofs of [104, Theorems 3.2 and 3.3] for more details.

This and Step 4 prove (ii) in Theorem 7.4.1.

Step 6. If $\lambda_* < \lambda^0 < \lambda^*$, then (7.22) has at least one positive solution u with $v(u) > 0$ for $\lambda = \lambda^0$. If $\lambda_* < \lambda_0 < \lambda^*$, then for $\lambda = \lambda^0$, (7.22) has at least one positive solution u satisfying $v(u) > 0$. We refer to the proof of [104, Theorem 3.4] for a proof of this fact.

This last step together with Steps 1, 2, and 4 shows that there is always a positive solution of (7.22) for $\lambda \in (\lambda_*, \lambda^*)$. Now every case has been covered, and the proof of Theorem 7.4.1 is complete. ∎

Remark 7.4.1. It is easy to check that when the condition

(D1) $\lambda_1\left(\alpha_1, -\beta_1 + \dfrac{a_2U_2}{1+a_3U_3}\right) > 0, \quad \lambda_1(\alpha_2, -\beta_2 + b_1U_1) > 0,$

holds, then $\lambda_0 > 1 > \lambda^0$. Therefore, by Theorem 7.4.1, (7.19) has a positive solution for $\lambda = 1$. Similarly, when the condition

(D2) $\lambda_1\left(\alpha_1, -\beta_1 + \dfrac{a_2U_2}{1+a_3U_3}\right) < 0, \quad \lambda_1(\alpha_2, -\beta_2 + b_1U_1) < 0,$

holds, then $\lambda_0 < 1 < \lambda^0$, and again it follows from Theorem 7.4.1 that (7.19) has a positive solution for $\lambda = 1$.

Remark 7.4.2. In general, it is difficult to find good estimates for λ_* and λ^*. Clearly, any such estimates give sufficient conditions for existence and nonexistence of positive solutions of (7.19). For example, the estimate

$$0 < \lambda_* \le \min\{\lambda_0, \lambda^0\}, \ \max\{\lambda_0, \lambda^0\} \le \lambda^* \le \Lambda_0,$$

implies that (7.19) has at least one positive solution if $\min\{\lambda_0, \lambda^0\} < \lambda < \max\{\lambda_0, \lambda^0\}$, and that (7.19) has no positive solution if $\lambda > \Lambda_0$.

It can be easily checked that if (a) $\lambda_* < \min\{\lambda_0, \lambda^0\}$ and $\lambda \in (\lambda_*, \min\{\lambda_0, \lambda^0\})$, or (b) $\max\{\lambda_0, \lambda^0\} < \lambda^*$ and $\lambda \in (\max\{\lambda_0, \lambda^0\}, \lambda^*)$, then neither of conditions (D1) and (D2) in Remark 7.4.1 is satisfied. But Theorem 7.4.1 implies that if (a) or (b) occurs, then (7.19) has at least two positive solutions. In the rest of this section we will show that both cases (a) and (b) can occur.

This is done by using techniques of bifurcation from simple eigenvalues. An essential step is to decide the direction of the bifurcation branch of positive solutions of (7.19) from $(\lambda_0, 0, U_2, U_3)$.

Define $F : \mathbb{R} \times Y^3 \to X^3$ by

$$F(\lambda, u_1, u_2, u_3) := \begin{pmatrix} (u_1)_t - \alpha_1 \Delta u_1 - u_1(\lambda\beta_1 - a_1u_1 - \frac{a_2u_2}{1+a_3u_3}) \\ (u_2)_t - \alpha_2 \Delta u_2 - u_2(\beta_2 - b_1u_1 - b_2u_2) \\ (u_3)_t - \alpha_3 \Delta u_3 - u_3(\beta_3 - \frac{c_3u_3}{1+c_1u_1}) \end{pmatrix}^T.$$

By a simple calculation, it follows that for every $h = (h_1, h_2, h_3) \in Y^3$,

$$F_u(\lambda_0, 0, U_2, U_3)h = \begin{pmatrix} (h_1)_t - \alpha_1 \Delta h_1 - \lambda_0\beta_1 h_1 + \frac{a_2U_2}{1+a_3U_3}h_1 \\ (h_2)_t - \alpha_2 \Delta h_2 - \beta_2 h_2 + 2b_2U_2h_2 + b_1U_2h_1 \\ (h_3)_t - \alpha_3 \Delta h_3 - \beta_3 h_3 + 2c_3U_3h_3 - c_3U_3^2c_1h_1 \end{pmatrix}^T.$$

It is easy to check that

$$N(F_u(\lambda_0, 0, U_2, U_3)) = \text{span}\{(\phi_1, \phi_2, \phi_3)\},$$

where $\phi_1 > 0$ satisfies

$$(\phi_1)_t - \alpha_1 \Delta\phi_1 = \left(\lambda_0\beta_1 - \frac{a_2U_2}{1+a_3U_3}\right)\phi_1, \qquad \phi_1 \in Y,$$

ϕ_2 is the unique solution of

$$K_2\phi := \phi_t - \alpha_2\Delta\phi - \beta_2\phi + 2b_2U_2\phi = -b_1U_2\phi_1, \qquad \phi \in Y,$$

and ϕ_3 is the unique solution of

$$K_3\phi := \phi_t - \alpha_3\Delta\phi - \beta_3\phi + 2c_3U_3\phi = c_3U_3^2c_1\phi_1, \qquad \phi \in Y.$$

Here the fact that K_2 and K_3 are invertible comes from

$$\lambda_1(\alpha_2, -\beta_2 + 2b_2U_2) > \lambda_1(\alpha_2, -\beta_2 + b_2U_2) = 0,$$
$$\lambda_1(\alpha_3, -\beta_3 + 2c_3U_3) > \lambda_1(\alpha_3, -\beta_3 + c_3U_3) = 0.$$

These also imply that K_2^{-1} and K_3^{-1} are strongly positive operators from X to Y. Thus, $\phi_2 < 0$ and $\phi_3 > 0$.

It is easy to see that

$$F_{\lambda u}(\lambda_0, 0, U_2, U_3)(h_1, h_2, h_3) = (\beta_1 h_1, 0, 0).$$

Now we prove a technical result.

Lemma 7.4.4. *Suppose that ϕ_1, ϕ_2, and ϕ_3 are defined as above. Then*

$$F_{\lambda u}(\lambda_0, 0, U_2, U_3)(\phi_1, \phi_2, \phi_3) \notin R(F_u(\lambda_0, 0, U_2, U_3)).$$

Proof. Suppose for contradiction that

$$F_{\lambda u}(\lambda_0, 0, U_2, U_3)(\phi_1, \phi_2, \phi_3) \in R(F_u(\lambda_0, 0, U_2, U_3)).$$

Then there exists $(h_1, h_2, h_3) \in Y^3$ such that

$$F_{\lambda u}(\lambda_0, 0, U_2, U_3)(\phi_1, \phi_2, \phi_3) = F_u(\lambda_0, 0, U_2, U_3)(h_1, h_2, h_3).$$

This gives in particular that

$$(h_1)_t - \alpha_1\Delta h_1 - \lambda_0\beta_1 h_1 + \frac{a_2U_2}{1+a_3U_3}h_1 = \beta_1\phi_1. \tag{7.28}$$

Let $Lu := u_t - \alpha_1\Delta u + \frac{a_2U_2}{1+a_3U_3}u$. Then $L^{-1} : Y \to Y$ is compact and strongly positive. Define $Ku := L^{-1}(\beta_1 u)$. Then $K : Y \to Y$ is compact and strongly positive. It follows from (7.28) that

$$K(\phi_1 + \lambda_0 h_1) = h_1. \tag{7.29}$$

By the definition of ϕ_1, we have $K\phi_1 = \lambda_0^{-1}\phi_1$. This implies that $r(K) = \lambda_0^{-1}$. By the Krain-Rutman theorem, there exists $l_1 \in Y^*$ such that $l_1(x) > 0$ for

$x \in P_Y \setminus \{0\}$, where P_Y is the natural positive cone of Y, and such that $K^* l_1 = \lambda_0^{-1} l_1$. Therefore, (7.29) implies that

$$l_1[K(\phi_1 + \lambda_0 h_1)] = l_1(h_1),$$

and hence

$$l_1(h_1) = (K^* l_1)(\phi_1 + \lambda_0 h_1) = \lambda_0^{-1} l_1(\phi_1 + \lambda_0 h_1) = \lambda_0^{-1} l_1(\phi_1) + l_1(h_1).$$

This gives $\lambda_0^{-1} l_1(\phi_1) = 0$, which contradicts the fact that $\phi_1 > 0$. ∎

It is easy to see that the use of the theory of bifurcation from simple eigenvalues is justified. We obtain that for any complement Z of span$\{(\phi_1, \phi_2, \phi_3)\}$ in Y^3, there exist $\delta > 0$ and continuously differentiable functions $\tau : (-\delta, \delta) \to R$, $\psi = (\psi_1, \psi_2, \psi_3) : (-\delta, \delta) \to Z$ such that $\tau(0) = 0$, $(\psi_1(0), \psi_2(0), \psi_3(0)) = 0$ and such that the solutions of (7.19) near $(\lambda_0, 0, U_2, U_3)$ and different from the trivial branch $(\lambda, 0, U_2, U_3)$ form a curve:

$$\begin{aligned}&(\lambda(s), u_1(s), u_2(s), u_3(s))\\&\quad = (\lambda_0 + \tau(s), s\phi_1 + s\psi_1(s), U_2 + s\phi_2 + s\psi_2(s), U_3 + s\phi_3 + s\psi_3(s)),\end{aligned} \tag{7.30}$$

for $s \in (-\delta, \delta)$. Clearly, the sign of $\lambda'(0)$ determines the direction of the positive solution branch

$$\{(\lambda(s), u_1(s), u_2(s), u_3(s)) : 0 < s < \delta\}.$$

It follows that that if $\lambda'(0) > 0$, then $\lambda^* > \lambda_0$; if $\lambda'(0) < 0$, then $\lambda_* < \lambda_0$.

Next we are to find some expressions of $\lambda'(0)$. We start from the identity

$$(u_1(s))_t = \alpha_1 \Delta u_1(s) + u_1(s)\left(\lambda(s)\beta_1 - a_1 u_1(s) - \frac{a_2 u_2(s)}{1 + a_3 u_3(s)}\right).$$

Dividing this identity by s, using (7.30) we obtain

$$\begin{aligned}(\phi_1 + \psi_1(s))_t = &\alpha_1 \Delta(\phi_1 + \psi_1(s))\\&+ (\phi_1 + \psi_1(s))\left(\lambda(s)\beta_1 - a_1 u_1(s) - \frac{a_2 u_2(s)}{1 + a_3 u_3(s)}\right).\end{aligned} \tag{7.31}$$

Differentiating (7.31) with respect to s at $s = 0$, we obtain

$$\begin{aligned}(\psi_1'(0))_t = &\alpha_1 \Delta(\psi_1'(0)) + \psi_1'(0)(\lambda_0\beta_1 - \frac{a_2 U_2}{1 + a_3 U_3})\\&+ \phi_1\left(\lambda'(0)\beta_1 - a_1\phi_1 - \frac{a_2\phi_2}{1 + a_3 U_3} + \frac{a_2 U_2}{(1 + a_3 U_3)^2} a_3\phi_3\right).\end{aligned} \tag{7.32}$$

Define

$$\Phi := \phi_1\left(-a_1\phi_1 - \frac{a_2\phi_2}{1 + a_3 U_3} + \frac{a_2 U_2}{(1 + a_3 U_3)^2} a_3\phi_3\right).$$

By the definition of K, we can rewrite (7.32) as

$$\psi_1'(0) = \lambda_0 K(\psi_1'(0)) + \lambda'(0)K(\phi_1) + K(\Phi/\beta_1).$$

Applying l_1 to this identity, together with $K^*(l_1) = \lambda_0^{-1}l_1$, we get

$$l_1(\psi_1'(0)) = l_1(\psi_1'(0)) + \lambda'(0)\lambda_0^{-1}l_1(\phi_1) + \lambda_0^{-1}l_1(\Phi/\beta_1),$$

which implies that

$$\lambda'(0) = -\frac{l_1(\Phi/\beta_1)}{l_1(\phi_1)}. \tag{7.33}$$

Recall that $\lambda'(0) > 0$ implies $\lambda^* > \lambda_0$ and that $\lambda'(0) < 0$ implies $\lambda_* < \lambda_0$. To determine whether we have $\lambda_* < \min\{\lambda_0, \lambda^0\}$ or $\lambda^* > \max\{\lambda_0, \lambda^0\}$, we need to estimate λ^0. For this purpose, we vary a_1 and b_1. Suppose from now on that

$$a_1 = \xi a_1^0, \;\; b_1 = \eta b_1^0,$$

where $a_1^0 > 0$ and $b_1^0 > 0$ are fixed and ξ, η are considered parameters.

One easily sees that U_2 and U_3 are independent of (ξ, η). Therefore, λ_0 and ϕ_1 are independent of (ξ, η). By the definitions of ϕ_2 and ϕ_3, it follows that ϕ_3 is independent of (ξ, η) but ϕ_2 depends linearly on η:

$$\phi_2 = \phi_2(\eta) = \eta\phi_2(1).$$

It is also easy to see that the dependence of θ^λ on ξ is given by

$$\theta^\lambda(\xi) = \theta^\lambda(1)/\xi.$$

Suppose that $\sigma = \sigma_0$ is the unique solution of

$$\lambda_1(\alpha_2, -\beta_2 + \sigma b_1^0 \theta^{\lambda^0}(1)) = 0.$$

Thus, for $\eta = \sigma_0 \xi$, we have

$$\lambda_1(\alpha_2, -\beta_2 + \eta b_1^0 \theta^{\lambda^0}(\xi)) = \lambda_1(\alpha_2, -\beta_2 + \sigma_0 b_1^0 \theta^{\lambda^0}(1)) = 0,$$

which implies that $\lambda^0 = \lambda_0$.

Define

$$\Delta(\sigma) := \frac{l_1}{\beta_1\, l_1(\phi_1)} \left(a_1^0 \phi_1^2 + \sigma \frac{a_2 \phi_2(1)}{1 + a_3 U_3} \phi_1 \right)$$

and

$$\Delta_0 := \frac{l_1}{\beta_1\, l_1(\phi_1)} \left(\frac{a_2 U_2}{(1 + a_3 U_3)^2} a_3 \phi_3 \phi_1 \right).$$

Clearly, $\Delta_0 > 0$. By (7.33) and the definition of Φ, it follows that

$$\lambda'(0) = -\xi \Delta(\eta/\xi) + \Delta_0.$$

Choose $\sigma \geq \sigma_0$ and let $\eta = \sigma\xi$. Thus, for $a_1 = \xi a_1^0$, $b_1 = \eta b_1^0 = \sigma\xi b_1^0$, we have

$$\lambda_1(\alpha_2, -\beta_2 + b_1\theta^{\lambda_0}) = \lambda_1(\alpha_2, -\beta_2 + \sigma b_1^0\theta^{\lambda_0}(1)) \geq 0.$$

Then $\lambda^0 \leq \lambda_0,\ \forall \xi > 0$. But

$$\lambda'(0) = -\xi\Delta(\sigma) + \Delta_0 > 0$$

at least for all small positive ξ. Then $\lambda^0 \leq \lambda_0 < \lambda^*$ in this case. This gives cases where (7.19) has more than one positive solutions.

Now suppose that $\Delta(\sigma_0) > 0$ (we will show a little later that this case does occur if we choose the parameters properly). Then we can arrange the parameters so that $\lambda_* < \lambda_0 \leq \lambda^0$. In fact, if we choose $\sigma \leq \sigma_0$ but still keep $\Delta(\sigma) > 0$, then for $a_1 = \xi a_1^0$, $b_1 = \sigma\xi b_1^0$, we have $\lambda_0 \leq \lambda^0$ and

$$\lambda'(0) = -\xi\Delta(\sigma) + \Delta_0 < 0$$

for all large positive ξ. Therefore, $\lambda_* < \lambda_0 \leq \lambda^0$ in this case.

It remains to show that $\Delta(\sigma_0) > 0$ is possible. Suppose that α_i, $i = 1, 2, 3$, and β_i, a_i, c_i, $i = 1, 3$, are all fixed, and that $\alpha_1 = \alpha_2$. Since we do not use the variables ξ and η, we assume $\xi = 1$ and $\eta = 1$ in the following discussions. Hence $a_1 = a_1^0$, $b_1 = b_1^0$. We will vary b_1, b_2, β_2, and a_2.

Let $b_2 = \zeta b_2^0$, $a_2 = \sqrt{\zeta} a_2^0$, with b_2^0, a_2^0 fixed and ζ being a parameter. We will define β_2 and b_1 also as functions of ζ. First, let $\beta_2 = s\beta_1 + \epsilon_0 U_3$, where s is a parameter and $\epsilon_0 > 0$ small is to be specified later. Then $U_2 = U_2(s, \zeta) = U_2(s, 1)/\zeta$ and $s \to U_2(s, 1)$ is increasing. Since

$$0 = \lambda_1\left(\alpha_1, -\lambda_0\beta_1 + \frac{a_2U_2}{1 + a_3U_3}\right) = \lambda_1\left(\alpha_1, -\lambda_0\beta_1 + \frac{a_2^0U_2(s,1)/\sqrt{\zeta}}{1 + a_3U_3}\right),$$

$\lambda_0 = \lambda_0(s, \zeta)$ is a continuous function of s and ζ. Moreover, $s \to \lambda_0(s, \zeta)$ is increasing, and $\zeta \to \lambda_0(s, \zeta)$ is decreasing. Furthermore, $\lambda_0(s, \zeta) \to \lambda_0(s, \infty)$ exists as $\zeta \to \infty$, and

$$\lambda_1(\alpha_1, -\lambda_0(s, \infty)\beta_1) = 0.$$

Thus, $\lambda_0(s, \infty) = \lambda_0(\infty)$ is independent of s, and $0 \leq \lambda_0(\infty) < 1$.

Let $s_1 = \lambda_0(\infty)$, $s_2 = \lambda_0(\infty) + 1$. Then $\lambda_0(s_1, \zeta) > s_1$ for all ζ, and $\lambda_0(s_2, \zeta) < s_2$ for all large ζ. This implies that for all large ζ, we can find some $s = s(\zeta) \in (\lambda_0(\infty), \lambda_0(\infty) + 1)$ such that

$$\lambda_0(s(\zeta), \zeta) = s(\zeta).$$

We first define

$$\beta_2 = \beta_2(\zeta) := s(\zeta)\beta_1 + \epsilon_0 U_3.$$

It follows that

$$\lambda_1(\alpha_2, -\beta_2) < \lambda_1(\alpha_1, -s(\zeta)\beta_1) < \lambda_1(\alpha_1, -\lambda_0(\infty)\beta_1) = 0.$$

Since

$$\lambda_0(\infty)\beta_1 + \epsilon_0 U_3 \le \beta_2(\zeta) \le (\lambda_0(\infty)+1)\beta_1 + \epsilon_0 U_3$$

for all large ζ, it is easy to see that there is some $M_0 > 0$ such that $U_3/U_2(s(\zeta),1) < M_0$ for all large ζ and all $\epsilon_0 < 1$. Here we need to use the strong maximum principle when the Dirichlet boundary condition is used. Thus, we can choose $\epsilon_0 > 0$ small enough such that for all large ζ,

$$2b_2^0 - \frac{\epsilon_0 U_3}{U_2(s(\zeta),1)} \ge 2\delta_0 > 0$$

for some fixed constant δ_0.

Next we choose b_1. We suppose from now on that ζ is sufficiently large and that a_2, b_2, β_2 are functions of ζ as defined above. Define

$$b_1 = b_1^0 = 2b_2 - \frac{a_2}{1+a_3U_3} + \frac{\lambda_0\beta_1 - \beta_2}{U_2}.$$

It easily follows that

$$b_1 = b_1(\zeta) = \zeta\left[2b_2^0 - \frac{a_2^0/\sqrt{\zeta}}{1+a_3U_3} - \frac{\epsilon_0 U_3}{U_2(s(\zeta),1)}\right] \ge \zeta\delta_0 > 0.$$

Using the choice of b_1 and $\alpha_1 = \alpha_2$, one can verify that $\phi_2 = -\phi_1$.

It is easy to see that θ^λ is independent of ζ. Since

$$0 = \lambda_1\left(\alpha_2, -\beta_2 + \sigma_0 b_1^0 \theta^{\lambda^0}(1)\right) = \lambda_1\left(\alpha_2, -\beta_2(\zeta) + \sigma_0 b_1(\zeta)\theta^{\lambda^0}(1)\right),$$

$\beta_2(\zeta)$ is L^∞ bounded, and $b_1(\zeta) \ge \zeta\delta_0$, we necessarily have

$$\sigma_0 = \sigma_0(\zeta) \le M/\zeta$$

for some constant $M > 0$ independent of ζ. Thus, for large ζ,

$$a_1^0 - \sigma_0(\zeta)\frac{a_2}{1+a_3U_3} \ge a_1^0 - \frac{M}{\sqrt{\zeta}}\frac{a_2^0}{1+a_3U_3} > 0.$$

Using $\phi_2 = -\phi_1$, we then get

$$\Delta(\sigma_0) = \Delta(\sigma_0(\zeta)) = \frac{l_1}{\beta_1\, l_1(\phi_1(\zeta))}\left(a_1^0 - \sigma_0(\zeta)\frac{a_2}{1+a_3U_3}\right)\phi_1^2(\zeta) > 0.$$

Finally, we find explicit expressions for $\lambda'(0)$ in the following cases of α_1:

(a) $\alpha_1(x,t) \equiv \alpha_1(t)$; that is, α_1 is independent of x;
(b) $\alpha_1(x,t) \equiv \alpha_1(x)$; that is, α_1 is independent of t;
(c) $\int_0^\omega \int_\Omega \phi_1\tilde{\phi_1}(\alpha_1^{-1})_t dx\, dt \ne 0$, where $\tilde{\phi}_1(t,x) = \phi_1(-t,x)$.

In case (a), multiplying (7.32) by $\tilde{\phi}_1$ and integrating over $\overline{\Omega} \times [0,\omega]$, we obtain

$$\begin{aligned}
&\int_0^\omega \int_\Omega \tilde{\phi}_1(\lambda'(0)\beta_1\phi_1 + \Phi)dx\,dt \\
&\quad = \int_0^\omega \int_\Omega \tilde{\phi}_1 \left[(\psi_1'(0))_t - \alpha_1 \Delta(\psi_1'(0)) - \psi_1'(0)\left(\lambda_0\beta_1 - \frac{a_2U_2}{1+a_3U_3}\right)\right] dx\,dt \\
&\quad = \int_0^\omega \int_\Omega \psi_1'(0) \left[-(\tilde{\phi}_1)_t - \alpha_1 \Delta\tilde{\phi}_1 - \tilde{\phi}_1\left(\lambda_0\beta_1 - \frac{a_2U_2}{1+a_3U_3}\right)\right] dx\,dt = 0,
\end{aligned}$$

which implies that

$$\lambda'(0) = -\frac{\int_0^\omega \int_\Omega \Phi\tilde{\phi}_1 dx\,dt}{\int_0^\omega \int_\Omega \phi_1\tilde{\phi}_1\beta_1 dx\,dt}. \tag{7.34}$$

In case (b), multiplying (7.32) by $\tilde{\phi}_1/\alpha_1$ and integrating over $\Omega \times [0,\omega]$, we then get

$$\int_0^\omega \int_\Omega (\tilde{\phi}_1/\alpha_1)(\lambda'(0)\beta_1\phi_1 + \Phi)dx\,dt = 0,$$

which implies that

$$\lambda'(0) = -\frac{\int_0^\omega \int_\Omega (\Phi\tilde{\phi}_1/\alpha_1) dx\,dt}{\int_0^\omega \int_\Omega (\beta_1\phi_1\tilde{\phi}_1/\alpha_1) dx\,dt}. \tag{7.35}$$

In case (c), it follows that

$$Z := \left\{(u_1,u_2,u_3) \in Y^3 : \int_0^\omega \int_\Omega \tilde{\phi}_1 u_1 (\alpha_1^{-1})_t\, dx\,dt = 0\right\}$$

is a complement of span$\{(\phi_1,\phi_2,\phi_3)\}$ in Y^3. Using this Z in (7.30), we have

$$\int_0^\omega \int_\Omega \psi_1'(0)\tilde{\phi}_1(\alpha_1^{-1})_t\, dx\,dt = 0.$$

As in case (b), it then follows that $\lambda'(0)$ satisfies (7.35).

7.5 Notes

Proposition 7.1.1 is modified from a claim in the proof of [430, Theorem 3.1]. Sections 7.2 and 7.3 are adapted from Zhao [434], and Section 7.4 is taken from Du [102]. The existence of positive periodic solutions of an ω-periodic system similar to (7.17) was also discussed in Du [102] via a degree argument. The decoupling technique and bifurcation argument in Section 7.4 goes back to Blat and Brown [32]. The competitor–competitor–mutualist model is due to Rai, Freedman and Addicott [285]. A special autonomous reaction–diffusion version of it was studied in Zheng [449]. A similar model with spatial-varying and time-periodic coefficients and subject to the zero Neumann boundary condition was investigated in Tineo [374]. The existence of positive periodic solutions of a periodic competitor–competitor–mutualist reaction–diffusion model of Lotka–Volterra type with nonlinear boundary conditions was discussed by Pao [269]. The periodic competitor–competitor–mutualist parabolic system with discrete delays was analyzed by Zhou and Fu [450] and Pao [270] via the method of upper and lower solutions. Liang and Jiang [223] investigated uniform persistence, global asymptotic stability, and convergence everywhere in infinite-dimensional type-K monotone discrete-time dynamical systems and time-periodic reaction–diffusion systems.

8

A Periodically Pulsed Bioreactor Model

In recent work of Ballyk et al. [27], it is argued that the plug-flow reactor, aside from its importance in chemical and bioengineering, is a good candidate as a surrogate model of the mammalian large intestine. In that work, a model of competition between different strains of microorganisms for a scarce nutrient in a plug-flow reactor, formulated by Kung and Baltzis [207], was studied with special attention given to the effects of random motility of the organisms on their ability to persist in the reactor and be good competitors in a mixed culture. The growth-limiting nutrient is assumed to enter the reactor tube at constant concentration at the upstream end of the reactor, so that the model equations take the form of a time-independent system of reaction–advection–diffusion equations. However, if the plug-flow reactor is to stand as a surrogate model of the intestine, then it is much more realistic to consider input nutrient concentration as being time-dependent. In the present chapter we consider this competition model with periodically varying input nutrient concentration, including pulsed input where the concentration may fall to zero over part of the cycle.

In Section 8.1 we briefly introduce the model and then discuss the well-posedness of the initial–boundary value problem and the positivity of its solutions. Section 8.2 is devoted to the special case of the model system with identical diffusivities and vanishing cell death rates. After consideration of the washout solution, we establish a conservation principle. We then consider single-population growth in the reactor, showing that when the washout solution is linearly stable, then it is globally stable, and when it is unstable, there is a unique, single-population periodic solution that attracts all solutions with nonzero initial data and is asymptotically stable in the linear approximation. Finally, we show that for two competing populations, where each single population periodic solution is unstable to invasion by the other population, we have persistence of both populations and the existence of a positive periodic solution representing coexistence. Section 8.3 is devoted to the perturbed system with different diffusivities and inclusion of cell death rates. We carry over

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the bulk of the results of Section 8.2 to the case where the random motility coefficients do not differ much from the diffusion constant of the nutrient and the cell death rates are small.

8.1 The Model

The plug-flow reactor may be thought of as a tube, of length L, through which a liquid medium flows with constant (small) velocity v. At the upstream end of the tube, $x = 0$, the nutrient concentration in the medium is maintained at the periodically varying concentration $S^0(t) = S^0(t + \omega)$. Downstream, bacteria consume nutrient, grow, divide, and die or leave the reactor at $x = L$. Bacteria are assumed to be motile, but their motility is random in the sense that it is modeled by an effective diffusion coefficient and is independent of nutrient concentration (chemotaxis is not considered here). The concentrations of nutrient S and microbial strains u_i, $i = 1, 2$, are governed by the equations (we have scaled variables so that $L = 1$)

$$\begin{aligned} \frac{\partial S}{\partial t} &= d_0 \frac{\partial^2 S}{\partial x^2} - v \frac{\partial S}{\partial x} - u_1 f_1(S) - u_2 f_2(S), \\ \frac{\partial u_i}{\partial t} &= d_i \frac{\partial^2 u_i}{\partial x^2} - v \frac{\partial u_i}{\partial x} + u_i(f_i(S) - k_i),\ i = 1, 2, \end{aligned} \tag{8.1}$$

where the d_i are the random motility coefficients of strain u_i, k_i is its death rate, and $f_i(S)$ is its uptake and growth rate. The quantity d_0 is the diffusion constant for nutrient S. Since the rate of change of the total nutrient concentration equals the difference between the inflow and outflow rates of the nutrient minus the consumption of the nutrient, we have

$$\frac{d}{dt} \int_0^1 S(x,t)dx = v\left(S^0(t) - S(1,t)\right) - \sum_{i=1}^{2} \int_0^1 u_i(x,t) f_i(S(x,t))dx.$$

On the other hand,

$$\begin{aligned} \frac{d}{dt} \int_0^1 S(x,t)dx &= \int_0^1 \frac{\partial S(x,t)}{\partial t} dx \\ &= \int_0^1 \left(d_0 \frac{\partial^2 S}{\partial x^2} - v \frac{\partial S}{\partial x} - u_1 f_1(S) - u_2 f_2(S) \right) dx \\ &= \left(d_0 \frac{\partial S(1,t)}{\partial x} - vS(1,t) \right) - \left(d_0 \frac{\partial S(0,t)}{\partial x} - vS(0,t) \right) \\ &\quad - \sum_{i=1}^{2} \int_0^1 u_i(x,t) f_i(S(x,t))dx. \end{aligned}$$

It then follows that

$$d_0 \frac{\partial S}{\partial x}(0,t) - vS(0,t) = -vS^0(t) \quad \text{and} \quad \frac{\partial S}{\partial x}(1,t) = 0.$$

Since the rate of change of the total concentration of species u_i is the difference between the natural growth and death rates of the species minus the washout rate of the species, we have

$$\frac{d}{dt}\int_0^1 u_i(x,t)dx = \int_0^1 u_i(x,t)(f_i(S(x,t)) - k_i)dx - vu_i(1,t).$$

On the other hand,

$$\begin{aligned}
\frac{d}{dt}\int_0^1 u_i(x,t)dx &= \int_0^1 \frac{\partial u_i(x,t)}{\partial t}dx \\
&= \int_0^1 \left(d_i \frac{\partial^2 u_i}{\partial x^2} - v\frac{\partial u_i}{\partial x} + u_i(f_i(S) - k_i) \right) dx \\
&= \left(d_i \frac{\partial u_i(1,t)}{\partial x} - vu_i(1,t) \right) - \left(d_i \frac{\partial u_i(0,t)}{\partial x} - vu_i(0,t) \right) \\
&\qquad + \int_0^1 u_i(x,t)(f_i(S(x,t)) - k_i)dx.
\end{aligned}$$

Thus we get

$$d_i \frac{\partial u_i}{\partial x}(0,t) - vu_i(0,t) = 0 \quad \text{and} \quad \frac{\partial u_i}{\partial x}(1,t) = 0.$$

Consequently, we impose on the model system the boundary conditions

$$\begin{aligned}
&d_0 \frac{\partial S}{\partial x}(0,t) - vS(0,t) = -vS^0(t), \\
&d_i \frac{\partial u_i}{\partial x}(0,t) - vu_i(0,t) = 0,\ i = 1,2, \\
&\frac{\partial S}{\partial x}(1,t) = \frac{\partial u_i}{\partial x}(1,t) = 0,\ i = 1,2,
\end{aligned} \tag{8.2}$$

and nonnegative initial conditions

$$S(x,0) = S_0(x), \quad u_i(x,0) = u_{0i}(x), \quad 0 \le x \le 1. \tag{8.3}$$

Next we discuss the well-posedness of the initial–boundary value problem (8.1)–(8.3) and the positivity of its solutions. Assume that the initial data in (8.3) satisfy $(S_0, u_{01}, u_{02}) \in X^+ = C([0,1], \mathbb{R}^3_+)$, the positive cone in the Banach space $X = C([0,1], \mathbb{R}^3)$ with uniform norm. For local existence and positivity of solutions in the space X^+, we follow [243], where existence and uniqueness and positivity are treated simultaneously, ignoring issues related to time delays treated there. The idea is to consider mild solutions of the system of abstract integral equations (we set $u_0 = S$ and $u_{00} = S_0$ to simplify notation)

$$
\begin{aligned}
u_0(t) &= V(t,0)u_{00} + \int_0^t T_0(t-r)B_0(u(r))dr, \\
u_i(t) &= T_i(t)u_{0i} + \int_0^t T_i(t-r)B_i(u(r))dr,\ i=1,2,
\end{aligned}
\tag{8.4}
$$

where $u(t) = (u_0(t), u_1(t), u_2(t)) \equiv (S(\cdot,t), u_1(\cdot,t), u_2(\cdot,t)) \in X_+$. $T_i(t)$ is the positive, nonexpansive, analytic semigroup on $C([0,1],\mathbb{R})$ (see [326, Chapter 8]) such that $u = T_i(t)u_{0i}$ satisfies the linear initial value problem

$$
\begin{aligned}
&\frac{\partial u}{\partial t} = d_i \frac{\partial^2 u}{\partial x^2} - v\frac{\partial u}{\partial x}, \\
&-d_i \frac{\partial u}{\partial x}(0,t) + vu(0,t) = 0 = \frac{\partial u}{\partial x}(1,t), \\
&u(x,0) = u_{0i}(x),
\end{aligned}
\tag{8.5}
$$

$V(t,s)$, $t > s$, is the family of affine operators on $C([0,1],\mathbb{R})$ such that $u = V(t,s)u_{00}$ satisfies the linear system with inhomogeneous, periodic boundary conditions, with start time s, given by

$$
\begin{aligned}
&\frac{\partial u}{\partial t} = d_0 \frac{\partial^2 u}{\partial x^2} - v\frac{\partial u}{\partial x},\ t > s, \\
&-d_0 \frac{\partial u}{\partial x}(0,t) + vu(0,t) = vS^0(t),\ t > s, \\
&\frac{\partial u}{\partial x}(1,t) = 0,\ t > s, \\
&u(x,s) = u_{00}(x).
\end{aligned}
\tag{8.6}
$$

Due to the periodicity of the inhomogeneity in the boundary conditions, $S^0(t+\omega) = S^0(t)$, we have that $V(t,s) = V(t+\omega, s+\omega)$ for $t > s$. The nonlinear operator $B_i : C([0,1],\mathbb{R}_+) \to C([0,1],\mathbb{R})$ is defined by

$$
\begin{aligned}
B_0(u) &= -u_1 f_1(u_0) - f_2(u_0)u_2, \\
B_i(u) &= [f_i(u_0) - k_i]u_i,\ i = 1,2.
\end{aligned}
$$

The result [243, Theorem 1] can be used to give local existence and positivity of noncontinuable solutions of (8.1)–(8.3), although the elliptic operator in that setting is slightly different. The reason is that the semigroups T_i and evolution operator V defined above have the same properties as those in [243] (so [243, Corollary 4] may be applied). Indeed, $V(t,s)$ satisfies $V(t,s)C([0,1],\mathbb{R}_+) \subset C([0,1],\mathbb{R}_+)$ for $t > s$, by standard maximum principle arguments, and similarly (see [326, Chapter 8]), $T_i(t)C([0,1],\mathbb{R}_+) \subset C([0,1],\mathbb{R}_+)$ for $t > 0$. The operator V and semigroup T_0 are related as below (1.9) in [243] on setting $\gamma(x,t) = S^0(t)$. Since we assume that $f_i(0) = 0$, it follows that $B_i(u)(x) = 0$ whenever $u_i(x) = 0$ for some x; hence, $B = (B_0, B_1, B_2)$ is quasi-positive. Thus, [243, Theorem 1 and Remark 1.1] imply that (8.1)–(8.3) has a unique nonnegative noncontinuable solution that satisfies (8.1)–(8.2) in the classical sense for $t > 0$.

8.2 Unperturbed Model

Consider the system of equations with identical diffusivities and vanishing cell death rates

$$\begin{aligned}
\frac{\partial S}{\partial t} &= d_0 \frac{\partial^2 S}{\partial x^2} - v \frac{\partial S}{\partial x} - u_1 f_1(S) - u_2 f_2(S), \quad 0 < x < 1,\, t > 0, \\
\frac{\partial u_i}{\partial t} &= d_0 \frac{\partial^2 u_i}{\partial x^2} - v \frac{\partial u_i}{\partial x} + u_i f_i(S), \quad i = 1, 2,\; 0 < x < 1,\, t > 0,
\end{aligned} \tag{8.7}$$

with boundary conditions

$$\begin{aligned}
& d_0 \frac{\partial S(0,t)}{\partial x} - vS(0,t) = -vS^0(t), \quad t > 0, \\
& d_0 \frac{\partial u_i(0,t)}{\partial x} - vu_i(0,t) = 0, \quad i = 1, 2,\, t > 0, \\
& \frac{\partial S(1,t)}{\partial x} = \frac{\partial u_i(1,t)}{\partial x} = 0, \quad i = 1, 2,\, t > 0,
\end{aligned} \tag{8.8}$$

and initial value conditions

$$S(x, 0) = S_0(x) \geq 0,\; u_i(x, 0) = u_{0i}(x) \geq 0,\, i = 1, 2,\, 0 \leq x \leq 1, \tag{8.9}$$

where $d_0 > 0$, $v > 0$, and $S^0(\cdot) \in C^2(\mathbb{R}_+, \mathbb{R})$, with $S^0(t) \geq 0, S^0(\cdot) \not\equiv 0$, $S^0(t + \omega) = S^0(t)$ for some real number $\omega > 0$, and $f_i(\cdot) \in C^2(\mathbb{R}_+, \mathbb{R}_+)$ satisfies

(H) $\quad f_i(0) = 0, \quad f_i'(S) > 0, \forall S \in \mathbb{R}_+,\, i = 1, 2.$

Let n be the outward normal to the boundary of $(0, 1)$. Clearly, for any $\phi(\cdot) \in C^1([0, 1], \mathbb{R})$,

$$\frac{\partial \phi(0)}{\partial n} = -\frac{\partial \phi(0)}{\partial x} \quad \text{and} \quad \frac{\partial \phi(1)}{\partial n} = \frac{\partial \phi(1)}{\partial x}.$$

Therefore, the boundary condition (8.8) is equivalent to the following one:

$$\begin{aligned}
& d_0 \frac{\partial S(0,t)}{\partial n} + vS(0,t) = vS^0(t), \qquad t > 0, \\
& d_0 \frac{\partial u_i(0,t)}{\partial n} + vu_i(0,t) = 0, \qquad i = 1, 2,\; t > 0, \\
& \frac{\partial S(1,t)}{\partial n} = \frac{\partial u_i(1,t)}{\partial n} = 0, \qquad i = 1, 2,\; t > 0.
\end{aligned} \tag{8.10}$$

Let $X^+ = C([0, 1], \mathbb{R}^3_+)$. As mentioned in Section 8.1, [243, Theorem 1 and Remark 1.1] imply that for any $\phi = (S_0(\cdot), u_{01}(\cdot), u_{02}(\cdot)) \in X^+$, there exists a unique (mild) solution $(S(x, t, \phi), u_1(x, t, \phi), u_2(x, t, \phi))$ of (8.7)-(8.8), defined on its maximal interval of existence $[0, \sigma_\phi)$, satisfying

$$S(x, t, \phi) \geq 0,\; u_i(x, t, \phi) \geq 0,\, \forall x \in [0, 1],\, t \in [0, \sigma_\phi),\, i = 1, 2.$$

Moreover, $(S(x, t, \phi), u_1(x, t, \phi), \; u_2(x, t, \phi))$ is a classical solution of (8.7)–(8.8) for $t \in (0, \sigma_\phi)$.

8.2.1 Conservation Principle

Since we have scaled the u_i in nutrient-equivalent units, the total nutrient $W(x,t) = S(x,t)+u_1(x,t)+u_2(x,t)$ should eventually come into balance with the input $S^0(t)$. Then $W(x,t)$ satisfies the following scalar linear equation

$$\begin{aligned}
&\frac{\partial W}{\partial t} = d_0 \frac{\partial^2 W}{\partial x^2} - v\frac{\partial W}{\partial x}, \quad 0 < x < 1,\, t > 0,\\
&d_0 \frac{\partial W(0,t)}{\partial n} + vW(0,t) = vS^0(t), \quad t > 0,\\
&\frac{\partial W(1,t)}{\partial n} = 0, \quad t > 0.
\end{aligned} \tag{8.11}$$

Note that equations (8.7)–(8.8) reduce to (8.11) for $W = S$ when $u_i = 0,\, i = 1, 2$. In what follows, we use $B\phi = 0$ to denote the homogeneous boundary conditions $d_0 \frac{\partial \phi(0)}{\partial n} + v\phi(0) = 0$ and $\frac{\partial \phi(1)}{\partial n} = 0$.

Proposition 8.2.1. *System (8.11) admits a unique positive ω-periodic solution $W^*(x,t) > 0$, and for any $W_0(\cdot) \in C([0,1],\mathbb{R})$, the unique (mild) solution $W(x,t)$ of (8.11) with $W(\cdot,0) = W_0(\cdot)$ satisfies $\lim_{t\to\infty}(W(x,t)-W^*(x,t)) = 0$ uniformly for $x \in [0,1]$.*

Proof. Let $u(x,t) = W(x,t) - S^0(t)$ and $S_1(t) = -\frac{dS^0(t)}{dt}$, $t \geq 0$. Then $u(x,t)$ satisfies

$$\begin{aligned}
&\frac{\partial u}{\partial t} = d_0 \frac{\partial^2 u}{\partial x^2} - v\frac{\partial u}{\partial x} + S_1(t), \quad 0 < x < 1,\, t > 0,\\
&d_0 \frac{\partial u(0,t)}{\partial n} + vu(0,t) = 0, \quad t > 0,\\
&\frac{\partial u(1,t)}{\partial n} = 0, \quad t > 0.
\end{aligned} \tag{8.12}$$

Since the boundary conditions in (8.12) are homogeneous, (8.12) can then be written as an abstract ordinary differential equation in $C([0,1],\mathbb{R})$ given by

$$\begin{aligned}
&\frac{du}{dt} = Au(t) + S_1(t), \quad t > 0,\\
&u(0) = \phi \in C([0,1]),\mathbb{R}),
\end{aligned} \tag{8.13}$$

where A is the closure in $C([0,1],\mathbb{R})$ of $A^0 = d_0\partial/\partial x^2 - v\partial/\partial x$ with

$$D(A^0) = \left\{\phi \in C^2((0,1)) \cap C^1([0,1]) :\ A^0\phi \in C([0,1]), B\phi = 0\right\}.$$

For any $\phi \in C([0,1],\mathbb{R})$, the mild solution of (8.12) can be expressed as

$$u(t) = T(t)\phi + \int_0^t T(t-s)S_1(s)ds, \tag{8.14}$$

where $T(t)$ is the analytic semigroup generated by A in $C([0,1],\mathbb{R})$ (see, e.g., [272] and [326, Chapter 7.1]). It easily follows that $u(t)$ is an ω-periodic solution of (8.13) if and only if $u_0 = u(0)$ satisfies

$$(I - T(\omega))u_0 = \int_0^\omega T(t-s)S_1(s)ds. \tag{8.15}$$

By an argument similar to that in [326, Section 8.1], it follows that $\sigma = \sup\{\mathrm{Re}\lambda : \lambda \in \sigma(A)\} < 0$. Then the radius of the spectrum of the compact operator $T(\omega)$ satisfies $r(T(\omega)) < 1$, and hence (8.13) admits a unique ω-periodic solution $u^*(t)$. Let $v(t) = u(t) - u^*(t)$. Then $v(t)$ satisfies

$$\frac{dv(t)}{dt} = Av(t), \quad t > 0. \tag{8.16}$$

By [272, Theorem 4.4.3], there exist $M > 0$ and $\mu > 0$ such that $\|T(t)\| \le Me^{-\mu t}, t \ge 0$, and hence $\lim_{t\to\infty} v(t) = 0$ in $C([0,1],\mathbb{R})$. Then $\lim_{t\to\infty}(u(x,t) - u^*(x,t)) = 0$ uniformly for $x \in [0,1]$.

Let $W^*(x,t) = u^*(x,t) + S^0(t)$, $x \in [0,1], t \ge 0$. It then follows that $W^*(x,t)$ is an ω-periodic solution of (8.11), and for any $W_0(\cdot) \in C([0,1],\mathbb{R})$, the unique (mild) solution $W(x,t)$ of (8.11) with $W(\cdot,0) = W_0(\cdot)$ satisfies

$$\lim_{t\to\infty}(W(x,t) - W^*(x,t)) = 0, \text{ uniformly for } x \in [0,1]. \tag{8.17}$$

For any $W_0(\cdot) \in C([0,1],\mathbb{R}_+)$, by [243, Theorem 1 and Remark 1.1], the unique solution $W(x,t)$ of (8.11) with $W(\cdot,0) = W_0(\cdot)$ satisfies

$$W(x,t) \ge 0, \ \forall x \in [0,1], \ t \ge 0. \tag{8.18}$$

It remains to prove that $W^*(x,t) > 0$, for all $x \in [0,1]$ and $t \ge 0$. For any $t \ge 0$, by (8.17) we have $\lim_{n\to\infty}(W(x,t+n\omega) - W^*(x,t+n\omega)) = \lim_{n\to\infty}(W(x,t+n\omega) - W^*(x,t)) = 0$, uniformly for $x \in [0,1]$. Then $W^*(x,t) = \lim_{n\to\infty} W(x,t+n\omega) \ge 0, \forall x \in [0,1], t \ge 0$. Since $S^0(t) \ge 0, S^0(\cdot) \not\equiv 0$, there exists $t_0 > 0$ such that $S^0(t_0) > 0$. It is easy to see that $d_0\frac{\partial u^*(0,t_0)}{\partial n} + vu^*(0,t_0) = 0$ implies $u^*(\cdot,t_0) \not\equiv -S^0(t_0)$. Then $W^*(\cdot,t_0) = u^*(\cdot,t_0) + S^0(t_0) \not\equiv 0$. By the standard parabolic maximum principle, it follows that

$$W^*(x,t) > 0, \ \forall x \in [0,1], \ t > t_0. \tag{8.19}$$

Then, by the ω-periodicity of $W^*(x,\cdot)$, we have $W^*(x,t) > 0$, $\forall x \in [0,1]$, $t \ge 0$. ∎

8.2.2 Single Species Growth

If only one microbial species is present in the reactor, we have the single species model

$$\begin{aligned} \frac{\partial S}{\partial t} &= d_0\frac{\partial^2 S}{\partial x^2} - v\frac{\partial S}{\partial x} - uf(S), \quad 0 < x < 1, \ t > 0, \\ \frac{\partial u}{\partial t} &= d_0\frac{\partial^2 u}{\partial x^2} - v\frac{\partial u}{\partial x} + uf(S), \quad 0 < x < 1, \ t > 0, \end{aligned} \tag{8.20}$$

with boundary conditions

$$
\begin{aligned}
&d_0 \frac{\partial S(0,t)}{\partial x} - vS(0,t) = -vS^0(t), \quad t > 0,\\
&d_0 \frac{\partial u(0,t)}{\partial x} - vu(0,t) = 0, \quad t > 0,\\
&\frac{\partial S(1,t)}{\partial x} = \frac{\partial u(1,t)}{\partial x} = 0, \quad t > 0,
\end{aligned}
\tag{8.21}
$$

and initial conditions

$$
S(x,0) = S_0(x) \geq 0,\ u(x,0) = u_0(x) \geq 0,\ \forall x \in [0,1], \tag{8.22}
$$

where $d_0 > 0, v > 0,\ f(\cdot) \in C^2(\mathbb{R}_+, \mathbb{R}_+)$ satisfies (H) and $S^0(\cdot)$ is as in (8.8). Let $Y^+ = C([0,1], \mathbb{R}^2_+)$. It then follows that for any $\phi = (S_0(\cdot), u_0(\cdot)) \in Y^+$, (8.20)–(8.22) admits a unique (mild) solution $(S(x,t,\phi), u(x,t,\phi))$, defined on its maximal interval of existence $[0, \sigma_\phi)$, satisfying $S(x,t,\phi) \geq 0, u(x,t,\phi) \geq 0$, $\forall x \in [0,1], t \in [0, \sigma_\phi)$. By the conservation principle in Subsection 8.2.1, for each $\phi \in Y^+, \sigma_\phi = \infty$.

We determine stability of periodic solutions in the following way. For any $m \in C^1([0,1] \times \mathbb{R}, \mathbb{R})$ with $m(x, t+\omega) = m(x,t), \forall x \in [0,1], t \in \mathbb{R}$, let $\mu(m(\cdot,\cdot))$ be the unique principal eigenvalue of the periodic–parabolic eigenvalue problem (see [152, Section II.14])

$$
\begin{aligned}
&\frac{\partial \varphi}{\partial t} = d_0 \frac{\partial \varphi}{\partial x^2} - v\frac{\partial \varphi}{\partial x} + m(x,t)\varphi + \mu\varphi, \qquad x \in (0,1),\ t \in \mathbb{R},\\
&d_0 \frac{\partial \varphi(0,t)}{\partial x} - v\varphi(0,t) = \frac{\partial \varphi(1,t)}{\partial x} = 0, \quad t \in \mathbb{R},\\
&\varphi\ \omega\text{-periodic in } t.
\end{aligned}
\tag{8.23}
$$

The main result of this subsection says that if the washout periodic solution $(S,u) = (W^*, 0)$ is stable or neutrally stable in the linear approximation then it is globally stable, while if it is unstable then there exists a unique positive periodic solution representing survival of the population to which all other solutions with $u_0 \neq 0$ approach asymptotically.

Theorem 8.2.1. *Let $W^*(x,t)$ be as in Proposition 8.2.1.*

(a) If $\mu(f(W^*(x,t))) \geq 0$, then for any $\phi = (S_0(\cdot), u_0(\cdot)) \in Y^+$, $\lim_{t\to\infty}(S(x,t,\phi) - W^*(x,t)) = 0$ and $\lim_{t\to\infty} u(x,t,\phi) = 0$ uniformly for $x \in [0,1]$;

(b) If $\mu(f(W^*(x,t))) < 0$, then (8.20)–(8.21) admits a unique positive ω-periodic solution $(S^*(x,t), u^*(x,t))$ and for any $\phi = (S_0(\cdot), u_0(\cdot)) \in Y^+$ with $u_0(\cdot) \not\equiv 0$, $\lim_{t\to\infty}(S(x,t,\phi) - S^*(x,t)) = 0$ and $\lim_{t\to\infty}(u(x,t,\phi) - u^*(x,t)) = 0$ uniformly for $x \in [0,1]$. Moreover, $(S^*(x,t), u^*(x,t))$ is linearly asymptotically stable for (8.20)–(8.21).

Proof. Let $\hat{f}(\cdot) : \mathbb{R} \to \mathbb{R}$ be a smooth extension of $f(\cdot) : \mathbb{R}_+ \to \mathbb{R}_+$ such that $\hat{f}(0) = 0, \hat{f}'(s) > 0, \quad \forall s \in \mathbb{R}$, and $\hat{f}(s) = f(s), \forall s \in \mathbb{R}_+$. Let $W = S + u$. Then system (8.20) with (8.21) is equivalent to the system

$$\begin{aligned}
\frac{\partial W}{\partial t} &= d_0 \frac{\partial^2 W}{\partial x^2} - v\frac{\partial W}{\partial x}, \quad 0 < x < 1,\, t > 0, \\
\frac{\partial u}{\partial t} &= d_0 \frac{\partial^2 u}{\partial x^2} - v\frac{\partial u}{\partial x} + uf(W-u), \quad 0 < x < 1,\, t > 0,
\end{aligned} \tag{8.24}$$

with boundary conditions

$$\begin{aligned}
& d_0 \frac{\partial W(0,t)}{\partial x} - vW(0,t) = -vS^0(t), \quad t > 0, \\
& d_0 \frac{\partial u(0,t)}{\partial x} - vu(0,t) = 0, \quad t > 0, \\
& \frac{\partial W(1,t)}{\partial x} = \frac{\partial u(1,t)}{\partial x} = 0, \quad t > 0.
\end{aligned} \tag{8.25}$$

Given $\phi = (S_0(\cdot), u_0(\cdot)) \in Y^+$, let $(W(x,t), u(x,t))$ be the unique solution of (8.24)–(8.25) satisfying $(W(x,0), u(x,0)) = (S_0(x) + u_0(x), u_0(x)), x \in [0,1]$. Then $U(x,t) = u(x, t+\omega)$, $x \in [0,1]$, $t \geq 0$, satisfies the nonautonomous scalar parabolic equation

$$\begin{aligned}
& \frac{\partial u}{\partial t} = d_0 \frac{\partial^2 u}{\partial x^2} - v\frac{\partial u}{\partial x} + u\hat{f}(W(x,t+\omega) - u), \quad 0 < x < 1,\, t > 0, \\
& d_0 \frac{\partial u(0,t)}{\partial x} - vu(0,t) = \frac{\partial u(1,t)}{\partial x} = 0, \quad t > 0.
\end{aligned} \tag{8.26}$$

By the conservation principle, $\lim_{t\to\infty}(W(x,t) - W^*(x,t)) = 0$ uniformly for $x \in [0,1]$, and hence (8.26) is asymptotic to the following periodic scalar parabolic equation

$$\begin{aligned}
& \frac{\partial u}{\partial t} = d_0 \frac{\partial^2 u}{\partial x^2} - v\frac{\partial u}{\partial x} + u\hat{f}(W^*(x,t) - u), \quad 0 < x < 1,\, t > 0, \\
& d_0 \frac{\partial u(0,t)}{\partial x} - vu(0,t) = \frac{\partial u(1,t)}{\partial x} = 0, \quad t > 0.
\end{aligned} \tag{8.27}$$

Let $1 < p < \infty$, and let $X^0 = L^p(0,1)$ and $X^1 = W^2_{p,B}(0,1)$. For $\beta \in (1/2 + 1/(2p), 1)$, let X^β be the fractional power space of X^0 with respect to (A^0, B) (see, e.g., [150]). Then $X^1 \subset X^\beta \subset X^0$ and $X^\beta \hookrightarrow C^{1+\lambda}[0,1]$ for some $\lambda > 0$. Clearly, $U(\cdot, 0) = u(\cdot, \omega) \in X^1 \subset X^\beta$. By Theorem 3.2.2, it follows that

(a) If $\mu(f(W^*(x,t))) \geq 0$, $\lim_{t\to\infty} U(x,t) = 0$, and hence $\lim_{t\to\infty} u(x,t) = 0$, uniformly for $x \in [0,1]$;
(b) If $\mu(f(W^*(x,t))) < 0$, (8.27) admits a unique positive ω-periodic solution $u^*(x,t)$ and $\lim_{t\to\infty}(U(x,t) - u^*(x,t)) = 0$, and hence $\lim_{t\to\infty}(u(x,t) - u^*(x,t)) = \lim_{t\to\infty}(U(x,t-\omega) - u^*(x,t-\omega)) = 0$, uniformly for $x \in [0,1]$.

In case (a), $\lim_{t\to\infty}(S(x,t) - W^*(x,t)) = \lim_{t\to\infty}[(W(x,t) - W^*(x,t)) - u(x,t)] = 0$ uniformly for $x \in [0,1]$; In case (b), let $S^*(x,t) = W^*(x,t) - u^*(x,t)$. Then $\lim_{t\to\infty}(S(x,t) - S^*(x,t)) = \lim_{t\to\infty}[(W(x,t) - W^*(x,t)) - (u(x,t) - u^*(x,t))] = 0$ uniformly for $x \in [0,1]$. We further claim that $(S^*(x,t), u^*(x,t))$ is a positive ω-periodic solution of (8.20)–(8.21). It then suffices to prove that $W^*(x,t) > u^*(x,t)$, $\forall x \in [0,1], t \geq 0$. Since $d_0 \frac{\partial W^*(0,t)}{\partial n} + vW^*(x,t) = vS^0(t) \geq 0$ and $\frac{\partial W^*(1,t)}{\partial n} = 0, t > 0$, $W^*(x,t)$ is an upper solution of (8.27). Let $u_0(x,t)$ be the unique solution of (8.27) with $u_0(\cdot,0) = W^*(\cdot,0)$. Then $u_0(x,t) \leq W^*(x,t)$, $\forall x \in [0,1]$, $t \geq 0$. It then follows that

$$u_0(x,t+n\omega) \leq W^*(x,t+n\omega) = W^*(x,t),\ \forall t \geq 0,\ n \geq 0. \tag{8.28}$$

Since $\lim_{t\to\infty}(u_0(x,t) - u^*(x,t)) = 0$ uniformly for $x \in [0,1]$, letting $n \to \infty$ in (8.28), we have

$$u^*(x,t) \leq W^*(x,t), \quad \forall x \in [0,1],\ t \geq 0.$$

Let $t_0 > 0$ be such that $S^0(t_0) > 0$. Clearly, the boundary conditions for $W^*(x,t)$ and $u^*(x,t)$ in (8.11) and (8.27) imply that $u^*(\cdot,t_0) \not\equiv W^*(\cdot,t_0)$. Then, by the parabolic maximum principle, we get

$$u^*(x,t) < W^*(x,t), \quad \forall x \in [0,1],\ t > t_0,$$

and hence by the ω-periodicity of $u^*(x,t)$ and $W^*(x,t)$,

$$u^*(x,t) < W^*(x,t), \quad \forall x \in [0,1],\ t \geq 0.$$

Let $P : Y^+ \to Y^+$ be the Poincaré map associated with (8.20)–(8.21); that is, $P(\phi) = (S(\cdot,\omega,\phi), u(\cdot,\omega,\phi))$, $\forall \phi = (S_0(\cdot), u_0(\cdot)) \in Y^+$. Let $\phi_0 = (S^*(\cdot,0), u^*(\cdot,0))$. Clearly, $P(\phi_0) = \phi_0$. It remains to prove the linear asymptotic stability of the positive periodic solution $(S^*(x,t), u^*(x,t))$ in the sense that $r(D_\phi P(\phi_0)) < 1$. Let $\bar{S} = S - S^*, \bar{u} = u - u^*$. We then get the linearization of (8.20)–(8.21) at $(S^*(x,t), u^*(x,t))$ given by

$$\begin{aligned} \frac{\partial \bar{S}}{\partial t} &= d_0 \frac{\partial^2 \bar{S}}{\partial x^2} - v\frac{\partial \bar{S}}{\partial x} - u^*(x,t)f'(S^*(x,t))\bar{S} - f(S^*(x,t))\bar{u}, \\ \frac{\partial \bar{u}}{\partial t} &= d_0 \frac{\partial^2 \bar{u}}{\partial x^2} - v\frac{\partial \bar{u}}{\partial x} + u^*(x,t)f'(S^*(x,t))\bar{S} + f(S^*(x,t))\bar{u}, \end{aligned} \tag{8.29}$$

with homogeneous boundary conditions

$$\begin{aligned} &d_0 \frac{\partial \bar{S}(0,t)}{\partial x} - v\bar{S}(0,t) = 0, \quad t > 0, \\ &d_0 \frac{\partial \bar{u}(0,t)}{\partial x} - v\bar{u}(0,t) = 0, \quad t > 0, \\ &\frac{\partial \bar{S}(1,t)}{\partial x} = \frac{\partial \bar{u}(1,t)}{\partial x} = 0, \quad t > 0. \end{aligned} \tag{8.30}$$

Let $\overline{U}(t,s)$, $t \geq s \geq 0$, be the evolution operator of linear system (8.29)–(8.30). It easily follows that $D_\phi P(\phi_0) = \overline{U}(\omega, 0)$. Under the change of variables $w = \bar{S} + \bar{u}$, $z = \bar{u}$, that is,

$$\begin{pmatrix} w \\ z \end{pmatrix} = \begin{pmatrix} 1 & 1 \\ 0 & 1 \end{pmatrix} \begin{pmatrix} \bar{S} \\ \bar{u} \end{pmatrix},$$

(8.29)–(8.30) is then transformed into the system

$$\begin{aligned} \frac{\partial w}{\partial t} &= d_0 \frac{\partial^2 w}{\partial x^2} - v\frac{\partial w}{\partial x}, \quad 0 < x < 1,\ t > 0, \\ \frac{\partial z}{\partial t} &= d_0 \frac{\partial^2 z}{\partial x^2} - v\frac{\partial z}{\partial x} + u^*(x,t) f'(S^*(x,t)) w \\ &\quad + \left(f(S^*(x,t)) - u^*(x,t) f'(S^*(x,t))\right) z, \quad 0 < x < 1,\ t > 0, \end{aligned} \tag{8.31}$$

with boundary conditions

$$\begin{aligned} & d_0 \frac{\partial w(0,t)}{\partial x} - v w(0,t) = 0, \quad t > 0, \\ & d_0 \frac{\partial z(0,t)}{\partial x} - v z(0,t) = 0, \quad t > 0, \\ & \frac{\partial w(1,t)}{\partial x} = \frac{\partial z(1,t)}{\partial x} = 0, \quad t > 0. \end{aligned} \tag{8.32}$$

Let $U_1(t,s)$, $t \geq s \geq 0$, be the evolution operator of the linear equation

$$\begin{aligned} & \frac{\partial w}{\partial t} = d_0 \frac{\partial^2 w}{\partial x^2} - v\frac{\partial w}{\partial x}, \quad 0 < x < 1,\ t > 0, \\ & d_0 \frac{\partial w(0,t)}{\partial x} - v w(0,t) = \frac{\partial w(1,t)}{\partial x} = 0, \quad t > 0, \end{aligned} \tag{8.33}$$

and let $U_2(t,s)$, $t \geq s \geq 0$, be the evolution operator of the periodic linear equation

$$\begin{aligned} & \frac{\partial z}{\partial t} = d_0 \frac{\partial^2 z}{\partial x^2} - v\frac{\partial z}{\partial x} + \left(f(S^*(x,t)) - u^*(x,t) f'(S^*(x,t))\right) z, \\ & d_0 \frac{\partial z(0,t)}{\partial x} - v z(0,t) = \frac{\partial z(1,t)}{\partial x} = 0. \end{aligned} \tag{8.34}$$

Then

$$U(t,s) = \begin{pmatrix} U_1(t,s) & 0 \\ \int_s^t U_2(t,\tau) u^*(\cdot,\tau) f'(S^*(\cdot,\tau)) U_1(\tau,s) d\tau & U_2(t,s) \end{pmatrix} \tag{8.35}$$

is the evolution operator of periodic linear system (8.31)–(8.32). In particular,

$$U(\omega,0) = \begin{pmatrix} U_1(\omega,0) & 0 \\ \int_0^\omega U_2(\omega,\tau) u^*(\cdot,\tau) f'(S^*(\cdot,\tau)) U_1(\tau,0) d\tau & U_2(\omega,0) \end{pmatrix}. \tag{8.36}$$

As claimed in Subsection 8.2.1, $r(U_1(\omega,0))<1$. By the definition of principal eigenvalue (see [152, Proposition 14.4]), we have

$$\mu(f(S^*(x,t)-u^*(x,t)f'(S^*(x,t)))=-\frac{1}{\omega}\ln(r(U_2(\omega,0))).$$

Since $(S^*(x,t),u^*(x,t))$ is an ω-periodic solution of (8.20)–(8.21), $u^*(x,t)$ satisfies the periodic linear equation

$$\begin{aligned}&\frac{\partial u}{\partial t}=d_0\frac{\partial^2 u}{\partial x^2}-v\frac{\partial u}{\partial x}+f(S^*(x,t))u,\ 0<x<1,\, t>0,\\&d_0\frac{\partial u(0,t)}{\partial x}-vu(0,t)=\frac{\partial u(1,t)}{\partial x}=0,\ t>0.\end{aligned}\tag{8.37}$$

Then, by the uniqueness of the principal eigenvalue, we have $\mu(f(S^*(x,t)))=0$. Since $f(S^*(x,t))-u^*(x,t)f'(S^*(x,t))<f(S^*(x,t))$, by the monotonicity of the principal eigenvalue ([152, Lemma 15.5]),

$$\mu\left(f^*(S^*(x,t)-u^*(x,t)f'(S^*(x,t))\right)>\mu\left(f(S^*(x,t))\right)=0.$$

Therefore, $r(U_2(\omega,0))<1$. Clearly, $U(\omega,0):Y=C([0,1],R)\times C([0,1],\mathbb{R}^2)\to Y$ is a compact and positive operator. We further claim that $r(U(\omega,0))<1$. Indeed, let $\alpha=r(U(\omega,0))$. If $\alpha=0$, obviously we have $r(U(\omega,0))<1$. In the case where $\alpha>0$, by the Krein–Rutman theorem (see, e.g., [152, Theorem 7.1]), there exists $\phi=\begin{pmatrix}\phi_1\\\phi_2\end{pmatrix}>0$ in Y such that

$$U(\omega,0)\begin{pmatrix}\phi_1\\\phi_2\end{pmatrix}=\alpha\begin{pmatrix}\phi_1\\\phi_2\end{pmatrix}.$$

Then $U_1(\omega,0)\phi_1=\alpha\phi_1$. If $\phi_1>0$, then $\alpha=r(U_1(\omega,0))<1$. If $\phi_1=0$, then $\phi_2>0$ and $U_2(\omega,0)\phi_2=\alpha\phi_2$, and hence, $\alpha=r(U_2(\omega,0))<1$. Clearly,

$$\overline{U}(\omega,0)=\begin{pmatrix}1&-1\\0&1\end{pmatrix}U(\omega,0)\begin{pmatrix}1&-1\\0&1\end{pmatrix}^{-1}.$$

It then follows that $r(D_\phi P(\phi_0))=r(\overline{U}(\omega,0))=r(U(\omega,0))<1$. ∎

8.2.3 Two-Species Competition

For any $\phi=(S_0(\cdot),u_{01}(\cdot),u_{02}(\cdot))\in X^+$, let

$$\Phi(x,t,\phi)=(S(x,t),u_1(x,t),u_2(x,t))$$

be the unique (mild) solution of (8.7)–(8.8) with $\Phi(\cdot,0,\phi)=\phi$. Then $S(x,t)\geq 0, u_i(x,t)\geq 0$, $\forall x\in[0,1]$, $t\in[0,\sigma_\phi)$, $i=1,2$. By the conservation principle, for each $\phi\in Y^+$, $\sigma_\phi=\infty$.

In the case where $\mu(f_i(W^*(x,t))) < 0$, $i = 1, 2$, according to Theorem 8.2.1, let $(S_i^*(x,t), u_i^*(x,t))$ be the unique positive ω-periodic solution of (8.20)–(8.21) with $f(\cdot) = f_i(\cdot)$, $i = 1, 2$, respectively. As shown in the proof of Theorem 8.2.1, for each $1 \le i \le 2$,

$$W^*(x,t) > u_i^*(x,t), \quad S_i^*(x,t) = W^*(x,t) - u_i^*(x,t),\ \forall x \in [0,1],\ t \ge 0,$$

and $u_i^*(x,t)$ is the unique positive ω-periodic solution of the periodic-parabolic equation

$$\begin{aligned}
&\frac{\partial u_i}{\partial t} = d_0 \frac{\partial^2 u_i}{\partial x^2} - v \frac{\partial u_i}{\partial x} + u_i f_i(W^*(x,t) - u_i), \quad 0 < x < 1,\ t > 0,\\
&d_0 \frac{\partial u_i(0,t)}{\partial x} - v u_i(0,t) = \frac{\partial u_i(1,t)}{\partial x} = 0, \quad t \ge 0.
\end{aligned}$$

We now show that if each population can survive in the bioreactor in the absence of competition and if each population can invade the other's single-population periodic solution, then there exist two, not necessarily distinct, positive periodic solutions, each representing coexistence of the two populations, and system (8.7)–(8.8) is uniformly persistent.

Theorem 8.2.2. *Assume that*

(1) $\mu(f_i(W^*(x,t))) < 0$, $\forall i = 1, 2$;
(2) $\mu(f_1(S_2^*(x,t))) < 0$ *and* $\mu(f_2(S_1^*(x,t))) < 0$.

Then system (8.7)–(8.8) admits two positive ω-periodic solutions $(\bar{S}_1^*(x,t), \bar{u}_{1*}(x,t),\ \bar{u}_2^*(x,t))$ *and* $(\bar{S}_2^*(x,t), \bar{u}_1^*(x,t), \bar{u}_{2*}(x,t))$ *with*

$$\bar{u}_i^*(x,t) \ge \bar{u}_{i*}(x,t),\ \forall x \in [0,1], t \in \mathbb{R}_+, i = 1, 2,$$

and for any $\phi = (S_0(\cdot), u_{01}(\cdot), u_{02}(\cdot)) \in X^+$ *with* $u_{0i}(\cdot) \not\equiv 0$, $\forall i = 1, 2$, $\Phi(x,t,\phi) = (S(x,t), u_1(x,t), u_2(x,t))$ *satisfies*

$$\lim_{t \to \infty} d(u_i(x,t), [\bar{u}_{i*}(x,t), \bar{u}_i^*(x,t)]) = 0,\ i = 1, 2,\ \text{uniformly for } x \in [0,1].$$

Proof. For each $1 \le i \le 2$, let $\hat{f}_i(\cdot) : \mathbb{R} \to \mathbb{R}$ be a smooth extension of $f_i(\cdot) : \mathbb{R}_+ \to \mathbb{R}$ such that $\hat{f}_i(0) = 0$, $\hat{f}_i'(s) > 0$, $\forall s \in \mathbb{R}$, and $\hat{f}_i(s) = f_i(s)$, $\forall s \in \mathbb{R}_+$. Let $W = S + u_1 + u_2$. Then system (8.7) with (8.8) is equivalent to the system

$$\begin{aligned}
&\frac{\partial W}{\partial t} = d_0 \frac{\partial^2 W}{\partial x^2} - v \frac{\partial W}{\partial x}, \quad 0 < x < 1,\ t > 0,\\
&\frac{\partial u_i}{\partial t} = d_0 \frac{\partial^2 u_i}{\partial x^2} - v \frac{\partial u_i}{\partial x}\\
&\qquad + u_i f_i(W - u_1 - u_2), \quad i = 1, 2,\ 0 < x < 1,\ t > 0,
\end{aligned} \tag{8.38}$$

with boundary conditions

$$
\begin{aligned}
& d_0 \frac{\partial W(0,t)}{\partial x} - vW(0,t) = -vS^0(t), \quad t > 0, \\
& d_0 \frac{\partial u_i(0,t)}{\partial x} - vu_i(0,t) = 0, \quad i = 1, 2,\ t > 0, \\
& \frac{\partial W(1,t)}{\partial x} = \frac{\partial u_i(1,t)}{\partial x} = 0, \quad i = 1, 2,\ t > 0.
\end{aligned} \tag{8.39}
$$

Given $\phi = (S_0(\cdot), u_{01}(\cdot), u_{02}(\cdot)) \in X^+$, let

$$\Phi(x, t, \phi) = (S(x,t), u_1(x,t), u_2(x,t)),\ \forall x \in [0,1],\ t \geq 0,$$

and let

$$(U_1(x,t), U_2(x,t)) = (u_1(x, t+\omega), u_2(x, t+\omega)),\ \forall x \in [0,1],\ t \geq 0.$$

Then $(U_1(x,t), U_2(x,t))$ satisfies the following nonautonomous parabolic system

$$
\begin{aligned}
& \frac{\partial u_i}{\partial t} = d_0 \frac{\partial^2 u_i}{\partial x^2} - v \frac{\partial u_i}{\partial x} + u_i \hat{f}_i(W(x, t+\omega) - u_1 - u_2), \quad i = 1, 2, \\
& Bu_i = 0, \quad i = 1, 2.
\end{aligned} \tag{8.40}
$$

By the conservation principle, $\lim_{t\to\infty}(W(x,t) - W^*(x,t)) = 0$ uniformly for $x \in [0,1]$, and hence (8.40) is asymptotic to the following periodic-parabolic system

$$
\begin{aligned}
& \frac{\partial u_i}{\partial t} = d_0 \frac{\partial^2 u_i}{\partial x^2} - v \frac{\partial u_i}{\partial x} + u_i \hat{f}_i(W^*(x,t) - u_1 - u_2), \quad i = 1, 2, \\
& Bu_i = 0, \quad i = 1, 2.
\end{aligned} \tag{8.41}
$$

Let X^β be as in the proof of Theorem 8.2.1, let $Z = X^\beta \times X^\beta$, and let Z^+ be the usual positive cone of Z. Since $(U_1(\cdot, 0), U_2(\cdot, 0)) = (u_1(\cdot, \omega), u_2(\cdot, \omega)) \in Z$, we consider systems (8.40) and (8.41) with initial values in Z^+. Let $\Delta = \{(t,s) : 0 \leq s \leq t < \infty\}$. Define $\tilde{\Phi} : \Delta \times Z^+ \to Z^+$ by $\tilde{\Phi}(t,s,\psi) = \tilde{u}(\cdot, t, s, \psi), t \geq s \geq 0, \psi \in Z^+$, where $\tilde{u}(x,t,s,\psi) = (\tilde{u}_1(x,t,s,\psi), \tilde{u}_2(x,t,s,\psi))$ is the unique solution of (8.40) with $\tilde{u}(\cdot, s, s, \psi) = \psi$. Define $T_n : Z^+ \to Z^+, n \geq 0$, by $T_n(\psi) = \tilde{\Phi}(n\omega, 0, \psi), \psi \in Z^+$. Let $T(t) : Z^+ \to Z^+$, $t \geq 0$, be the periodic semiflow generated by periodic system (8.41), i.e., $T(t)\psi = u(\cdot, t, \psi)$, where $u(x, t, \psi)$ is the unique solution of (8.41) with $u(\cdot, 0, \psi) = \psi$. Clearly, $Q = T(\omega) : Z^+ \to Z^+$ is the Poincaré map associated with the periodic system (8.41). Then, by Proposition 3.2.1, $\tilde{\Phi} : \Delta \times Z^+ \to Z^+$ is an asymptotically periodic semiflow with limit ω-periodic semiflow $T(t) : Z^+ \to Z^+, t \geq 0$, and hence $T_n : Z^+ \to Z^+, n \geq 0$, is an asymptotically autonomous discrete process with limit $Q : Z^+ \to Z^+$. Moreover, for any $\psi \in Z^+$, $\gamma^+(\psi) = \{T_n(\psi) : n \geq 0\}$ is precompact in Z^+. Let (Z, P) be the ordered Banach space with the positive cone $P = X^\beta_+ \times (-X^\beta_+)$, where X^β_+ is the usual positive cone of X^β, and denote its order by $\leq_P$. It then follows that $T(t) : Z^+ \to Z^+$, $t \geq 0$, is monotone with respect to $\leq_P$ in the sense that if $\phi, \psi \in Z^+$ with $\phi \leq_P \psi$, then $T(t)\phi \leq_P T(t)\psi$, $\forall t \geq 0$.

Clearly, condition (2) implies $\mu(f_1(W^*(x,t) - u_2^*(x,t))) = \mu(f_1(S_2^*(x,t))) < 0$ and $\mu(f_2(W^*(x,t) - u_1^*(x,t))) = \mu(f_2(S_1^*(x,t))) < 0$. By Theorem 2.4.2, as applied to the Poincaré map associated with (8.41), or an argument similar to that in [152, Theorem 33.3], it then follows that (8.41) admits two positive ω-periodic solutions $(\bar{u}_{1*}(x,t), \bar{u}_2^*(x,t))$ and $(\bar{u}_1^*(x,t), \bar{u}_{2*}(x,t))$ with

$$\bar{u}_{i*}(x,t) \leq \bar{u}_i^*(x,t),\ \forall x \in [0,1],\ t \geq 0,$$

such that the compressive dynamics stated in Theorem 8.2.2 holds for (8.41) on Z^+. Let $E_1^* = (\bar{u}_{1*}(\cdot,0), \bar{u}_2^*(\cdot,0))$ and $E_2^* = (\bar{u}_1^*(\cdot,0), \bar{u}_{2*}(\cdot,0))$. Clearly, $Q(E_i^*) = E_i^*$, $i = 1,2$. Let $Z_0 := \{(\phi_1, \phi_2) \in Z^+ : \phi_i(\cdot) \not\equiv 0, i = 1,2\}$ and $\partial Z_0 := Z^+ \setminus Z_0$. Clearly, $Q : Z_0 \to Z_0$, and $Q : \partial Z_0 \to \partial Z_0$. It then follows that $Q : Z_0 \to Z_0$ admits a global attractor $A_0 \subset [E_1^*, E_2^*]_P$. Let $M_0 = (0,0)$, $M_1 = (u_1^*(\cdot,0), 0)$, and $M_2 = (0, u_2^*(\cdot,0))$. It is easy to see that $\cup_{i=0}^2 M_i$ is an isolated and acyclic covering of $\cup_{\phi \in \partial Z_0} \omega(\phi)$ for $Q : \partial Z_0 \to \partial Z_0$. By our assumptions and Proposition 3.2.3, we have $\tilde{W}^s(M_i) \cap Z_0 = \emptyset$, $\forall i = 0,1,2$, where $\tilde{W}^s(M_i)$ is the stable set of M_i with respect to $T_n : Z^+ \to Z^+, n \geq 0$. By Lemma 1.2.2, every ω-limit set $\omega(\phi)$ of $\gamma^+(\phi) = \{T_n(\phi) : n \geq 0\}$ is internally chain transitive for $Q : Z^+ \to Z^+$. By Theorem 1.2.1, it then follows that $\omega(\psi) \subset A_0$, $\forall \psi \in Z_0$. By Theorem 3.2.1, $\lim_{t\to\infty} d(\tilde{u}(\cdot,t,0,\psi), T(t)A_0) = 0$. Since $E_1^* \leq_P A_0 \leq_P E_2^*$, by the monotonicity of $T(t) : Z^+ \to Z^+$, $t \geq 0$, we have

$$T(t)E_1^* \leq_P T(t)A_0 \leq_P T(t)E_2^*, \quad \forall t \geq 0. \tag{8.42}$$

Note that

$$T(t)E_1^* = (\bar{u}_{1*}(\cdot,t), \bar{u}_2^*(\cdot,t)), \quad \text{and} \quad T(t)E_2^* = (\bar{u}_1^*(\cdot,t), \bar{u}_{2*}(\cdot,t)),\ \forall t \geq 0.$$

For any $\phi = (S_0(\cdot), u_{01}(\cdot), u_{02}(\cdot)) \in X^+$ with $u_{0i}(\cdot) \not\equiv 0$, $\forall i = 1,2$, since $(U_1(\cdot,0), U_2(\cdot,0)) \in Z_0$, we have

$$\begin{aligned}
&\lim_{t\to\infty} d(u_i(x,t), [\bar{u}_{i*}(x,t), \bar{u}_i^*(x,t)]) \\
&\quad = \lim_{t\to\infty} d(U_i(x,t-\omega), [\bar{u}_{i*}(x,t-\omega), \bar{u}_i^*(x,t-\omega)]) = 0,\ \forall i = 1,2,
\end{aligned}$$

uniformly for $x \in [0,1]$.

Let $\bar{S}_1^*(x,t) = W^*(x,t) - \bar{u}_{1*}(x,t) - \bar{u}_2^*(x,t)$ and $\bar{S}_2^*(x,t) = W^*(x,t) - \bar{u}_1^*(x,t) - \bar{u}_{2*}(x,t)$. We need to confirm that

$$(\bar{S}_1^*(x,t), \bar{u}_{1*}(x,t), \bar{u}_2^*(x,t)) \quad \text{and} \quad (\bar{S}_2^*(x,t), \bar{u}_1^*(x,t), \bar{u}_{2*}(x,t))$$

are two positive ω-periodic solutions of (8.7)–(8.8). It suffices to prove that

$$W^*(x,t) > \bar{u}_1^*(x,t) + \bar{u}_{2*}(x,t),\ W^*(x,t) > \bar{u}_{1*}(x,t) + \bar{u}_2^*(x,t),$$

for all $x \in [0,1]$ and $t \geq 0$. Since $u_1^*(\cdot,0) \ll_P W^*(\cdot,0)$, we can choose $\psi^0 = (\psi_1^0, \psi_2^0) \in Z_0$ such that

$$E_2^* \leq_P \psi^0 \ll_P M_1 = (u_1^*(\cdot,0),0) \text{ and } \psi_1^0(x) + \psi_2^0(x) \leq W^*(x,0),\ \forall x \in [0,1].$$

Let $(u_1^0(x,t), u_2^0(x,t))$ be the unique solution of (8.41) with $(u_1^0(\cdot,0), u_2^0(\cdot,0)) = \psi^0$, and let $\bar{f}(s) = \max\{\hat{f}_1(s), \hat{f}_2(s)\}$, $\forall s \in \mathbb{R}$. Then

$$V(x,t) = u_1^0(x,t) + u_2^0(x,t),\ x \in [0,1],\ t \geq 0,$$

satisfies $V(x,0) \leq W^*(x,0)$, $\forall x \in [0,1]$, and

$$\begin{aligned} &\frac{\partial V}{\partial t} \leq d_0 \frac{\partial^2 V}{\partial x^2} - v\frac{\partial V}{\partial x} + V\bar{f}(W^*(x,t) - V),\ 0 < x < 1,\ t > 0, \\ &BV = 0,\ t > 0. \end{aligned} \tag{8.43}$$

Note that $W^*(x,t)$ satisfies

$$\begin{aligned} &\frac{\partial W^*}{\partial t} = d_0 \frac{\partial^2 W^*}{\partial x^2} - v\frac{\partial W^*}{\partial x} + W^*\bar{f}(W^*(x,t) - W^*(x,t)), \\ &BW^* \geq 0 \end{aligned} \tag{8.44}$$

for $0 < x < 1$ and $t > 0$. By the standard comparison theorem, it follows that

$$u_1^0(x,t) + u_2^0(x,t) = V(x,t) \leq W^*(x,t),\ \forall x \in [0,1],\ t \geq 0. \tag{8.45}$$

By Theorem 2.4.2, $Q^n(\psi^0) = (u_1^0(\cdot, n\omega), u_2^0(\cdot, n\omega)) \to E_2^*$ as $n \to \infty$, and hence

$$\lim_{t\to\infty}(u_1^0(x,t) - \bar{u}_1^*(x,t)) = 0 \ \text{ and } \ \lim_{t\to\infty}(u_2^0(x,t) - \bar{u}_{2*}(x,t)) = 0$$

uniformly for $x \in [0,1]$. By (8.45), we have

$$u_1^0(x, t+n\omega) + u_2^0(x, t+n\omega) \leq W^*(x, t+n\omega) = W^*(x,t) \tag{8.46}$$

for all $x \in [0,1]$ and $t \geq 0$. Letting $n \to \infty$ in (8.46), we get

$$\bar{u}_1^*(x,t) + \bar{u}_{2*}(x,t) \leq W^*(x,t),\ \forall x \in [0,1],\ t \geq 0. \tag{8.47}$$

Since $V^* = \bar{u}_1^*(x,t) + \bar{u}_{2*}(x,t)$ satisfies (8.43) and $W^*(x,t)$ satisfies (8.11), as argued in the proof that $W^*(x,t) > u^*(x,t)$ in Subsection 8.2.2, we further have $\bar{u}_1^*(x,t) + \bar{u}_{2*}(x,t) < W^*(x,t)$, $\forall x \in [0,1]$, $t \geq 0$. Similarly, we can prove that $\bar{u}_{1*}(x,t) + \bar{u}_2^*(x,t) < W^*(x,t)$, $\forall x \in [0,1]$, $t \geq 0$. ∎

8.3 Perturbed Model

In order to apply abstract perturbation-type results to periodic systems with parameters, we first consider the weak repellers uniform in parameters and the continuity of solutions on parameters uniformly for initial values.

8.3.1 Periodic Systems with Parameters

Let Λ be a subset of $\mathbb{R}^l$. We consider the periodic-parabolic system with parameter (E_λ):

$$\begin{aligned} &\frac{\partial u_i}{\partial t} = A_i(\lambda)u_i + F_i(x,t,u,\lambda) \quad \text{in } \Omega \times (0,\infty),\ 1 \le i \le m, \\ &B_i u_i = 0 \quad \text{on } \partial\Omega \times (0,\infty),\ 1 \le i \le m, \end{aligned} \tag{8.48}$$

where $u = (u_1, \ldots, u_m) \in \mathbb{R}^m, \lambda \in \Lambda$, $B_i u_i = \frac{\partial u_i}{\partial n} + \alpha_i u_i$, $\alpha_i \ge 0$, $A_i(\lambda)$ are uniform elliptic operators with coefficients continuous in (x,λ), F_i are smooth functions, and for some real number $\omega > 0$, $F_i(x,t+\omega,u,\lambda) = F_i(x,t,u,\lambda)$, $\forall 1 \le i \le m$. We assume that for any $\phi = (\phi_1, \ldots, \phi_m) \in C^+ = C(\overline{\Omega}, R^m_+)$, the unique (mild) solution $u(x,t,\phi,\lambda)$ of (E_λ) with $u(\cdot,0,\phi,\lambda) = \phi$ exists globally on $[0,\infty)$ and $u_i(x,t,\phi,\lambda) \ge 0$, $\forall x \in \overline{\Omega}$, $t \ge 0$, $1 \le i \le m$.

For each $1 \le i \le m$ and any $m \in C^1([0,1] \times \mathbb{R}, \mathbb{R})$ with $m(x,t+\omega) = m(x,t)$, $\forall x \in [0,1]$, $t \in \mathbb{R}$, let $\mu(A_i(\lambda), m(\cdot,\cdot))$ be the unique principal eigenvalue of the periodic–parabolic eigenvalue problem (see [152, Chapter II])

$$\begin{aligned} &\frac{\partial \varphi}{\partial t} = A_i(\lambda)\varphi + m(x,t)\varphi + \mu\varphi, \quad x \in \overline{\Omega},\ t \in \mathbb{R}, \\ &B_i\varphi = 0, \quad x \in \partial\Omega,\ t \in \mathbb{R}, \\ &\varphi\ \omega\text{-periodic in}\, t. \end{aligned}$$

Then we have the following result on the uniform weak repeller .

Proposition 8.3.1. *Let $\lambda_0 \in \Lambda$ be fixed. Assume that there exists some $1 \le i \le m$ such that $F_i(x,t,u,\lambda) = u_i G_i(x,t,u,\lambda)$, and (E_λ) admits a nonnegative periodic solution*

$$u_0^*(x,t) = (u_{01}^*(x,t), \ldots, u_{0i-1}^*(x,t), 0, u_{0i+1}^*(x,t), \ldots, u_{0n}^*(x,t))$$

with $\mu(A_i(\lambda_0), G_i(x,t,u_0^*(x,t),\lambda_0)) < 0$. Then there exist $\eta > 0$ and $\delta > 0$ such that for any $|\lambda - \lambda_0| < \delta$ and any $\phi \in C^+$ with $\phi_i(\cdot) \not\equiv 0$, we have

$$\limsup_{n\to\infty} \|(u(\cdot,n\omega,\phi,\lambda) - u_0^*(\cdot,0)\| \ge \eta.$$

Proof. Let $M = u_0^*(\cdot,0)$ and let $B(M,r)$ denote the open ball in $C = C(\overline{\Omega}, R^m)$ centered at the point M and with radius r. By the definition of the principal eigenvalue in [152, Proposition 14.4] and the continuous dependence of evolution operators on parameters (see, e.g., [13] and [89, Section III.11]), we have

$$\lim_{\lambda\to\lambda_0} \mu(A_i(\lambda), G_i(x,t,u_0^*(x,t),\lambda_0)) = \mu(A_i(\lambda_0), G_i(x,t,u_0^*(x,t),\lambda_0)) < 0.$$

Then there exists $\delta_0 > 0$ such that for any $|\lambda - \lambda_0| < \delta_0$,

$$\mu(A_i(\lambda), G_i(x,t,u_0^*(x,t),\lambda_0)) < \frac{1}{2}\mu(A_i(\lambda_0), G_i(x,t,u_0^*(x,t),\lambda_0)).$$

Let $\epsilon_0 = -\frac{1}{2}\mu\left(A_i(\lambda_0), G_i(x,t,u_0^*(x,t),\lambda_0)\right)$. Then for any $|\lambda - \lambda_0| < \delta_0$,

$$-\mu(A_i(\lambda), G_i(x,t,u_0^*(x,t),\lambda_0)) > \epsilon_0 > 0.$$

Let $r = \max_{x\in\overline{\Omega},\, t\in[0,\omega]} |u_0^*(x,t)| + 1$. Therefore, the uniform continuity of $G_i(x,t,u,\lambda)$ on the compact set $\overline{\Omega} \times [0,\omega] \times \overline{B(0,r)} \times \overline{B(\lambda_0,\delta_0)}$ implies that there exist $\delta_1 \in (0,\delta_0)$ and $\eta_1 \in (0,1)$ such that for any $u, v \in \overline{B(0,r)}$ with $|u - v| < \eta_1$ and $|\lambda - \lambda_0| < \delta_1$,

$$|G_i(x,t,u,\lambda) - G_i(x,t,v,\lambda_0)| < \epsilon_0, \ \ \forall x \in \overline{\Omega},\ t \in [0,\omega]. \tag{8.49}$$

Since $\lim_{(\phi,\lambda)\to(M,\lambda_0)} u(\cdot,t,\phi,\lambda) = u(\cdot,t,M,\lambda_0) = u_0^*(\cdot,t)$ in C uniformly for $t \in [0,\omega]$, there exist $\delta_2 \in (0,\delta_1)$ and $\eta_2 > 0$ such that for any $\phi \in B(M,\eta_2) \subset C$, $|\lambda - \lambda_0| < \delta_2$,

$$|u(x,t,\phi,\lambda) - u_0^*(x,t)| < \eta_1, \ \ \forall x \in \overline{\Omega},\ t \in [0,\omega].$$

We claim that for any $|\lambda - \lambda_0| < \delta_2$ and $\phi \in B(M,\eta_2) \cap C^+$ with $\phi_i(\cdot) \not\equiv 0$, there exists $n_0 = n_0(\lambda,\phi) \geq 1$ such that

$$u(\cdot, n_0\omega, \phi, \lambda) \notin B(M,\eta_2). \tag{8.50}$$

Assume, by contradiction, that there exist $\phi_0 \in B(M,\eta_2)\cap C^+$ with $\phi_{0i}(\cdot) \not\equiv 0$ and $|\lambda_1 - \lambda_0| < \delta_2$ such that for all $n \geq 1$,

$$u(\cdot, n\omega, \phi_0, \lambda_1) \in B(M,\eta_2). \tag{8.51}$$

For any $t \geq 0$, let $t = n\omega + t'$, where $t' \in [0,\omega)$ and $n = [t/\omega]$ is the greatest integer less than or equal to t/ω. Then we have

$$|u(x,t,\phi_0,\lambda_1) - u_0^*(x,t)| = |u(x,t',u(\cdot,n\omega,\phi_0,\lambda_1),\lambda_1) - u_0^*(x,t')| < \eta_1 \tag{8.52}$$

for all $x \in \overline{\Omega}$, and hence

$$|u(x,t,\phi_0,\lambda_1)| < |u^*(x,t)| + \eta_1 \leq \max_{x\in\overline{\Omega},t\in[0,\omega]} |u_0^*(x,t)| + 1 = r$$

for all $t \geq 0$ and $x \in \overline{\Omega}$. Therefore, by (8.49) and the ω-periodicity of $G_i(x,t,u,\lambda_1)$ with respect to t,

$$G_i(x,t,u(x,t,\phi_0,\lambda_1),\lambda_1) > G_i(x,t,u_0^*(x,t),\lambda_0) - \epsilon_0, \ \ \forall x \in \overline{\Omega},\ t \geq 0. \tag{8.53}$$

Let $\psi_i(x,t)$ be a positive eigenfunction corresponding to the principal eigenvalue $\mu = \mu(A_i(\lambda_1), G_i(x,t,u_0^*(x,t),\lambda_0))$; that is, $\psi_i(x,t)$ satisfies

$$\begin{aligned}
&\frac{\partial \psi_i}{\partial t} = A_i(\lambda_1)\psi_i + G_i(x,t,u_0^*(x,t),\lambda_0)\psi_i + \mu\psi_i \quad \text{in } \Omega \times \mathbb{R}, \\
&B_i\psi_i = 0 \quad \text{on } \partial\Omega \times \mathbb{R}, \\
&\psi_i \ \ \omega\text{-periodic in}\, t.
\end{aligned} \tag{8.54}$$

Then $\psi(\cdot,0) \gg 0$ in $C(\overline{\Omega},\mathbb{R})$. Let

$$u(x,t,\phi_0,\lambda_1) = (u_1(x,t,\phi_0,\lambda_1),\ldots,u_m(x,t,\phi_0,\lambda_1)).$$

Since $\phi_{0i}(\cdot) > 0$ in $C(\overline{\Omega},\mathbb{R})$, by applying the parabolic maximum principle to the ith component of (E_{λ_1}), we have $u_i(\cdot,t,\phi_0,\lambda_1) \gg 0$ in $C(\overline{\Omega},\mathbb{R})$ for all $t>0$. Let $u_i(x,t) = u_i(x,t+\omega,\phi_0,\lambda_1)$. Then $u_i(\cdot,0) = u_i(\cdot,\omega,\phi_0,\lambda_1) \gg 0$ in $C(\overline{\Omega},\mathbb{R})$, and hence there exists $k>0$ such that $u_i(\cdot,0) \geq k\psi_i(\cdot,0)$. Therefore, by (8.53), $u_i(x,t)$ satisfies

$$\begin{aligned}
&\frac{\partial u_i}{\partial t} \geq A_i(\lambda_1)u_i + u_i\left(G_i(x,t,u_0^*(x,t),\lambda_0) - \epsilon_0\right) \quad \text{in } \Omega\times(0,\infty),\\
&B_i u_i = 0 \quad \text{on } \partial\Omega\times(0,\infty),\\
&u_i(x,0) \geq k\psi_i(x,0) \quad \text{on } \overline{\Omega}.
\end{aligned} \tag{8.55}$$

By (8.54), it easily follows that $v(x,t) = ke^{(-\mu-\epsilon_0)t}\psi_i(x,t)$ satisfies

$$\begin{aligned}
&\frac{\partial v}{\partial t} = A_i(\lambda_1)v + v\left(G_i(x,t,u_0^*(x,t),\lambda_0) - \epsilon_0\right) \quad \text{in } \Omega\times(0,\infty),\\
&B_i v = 0 \quad \text{on } \partial\Omega\times(0,\infty),\\
&v(x,0) = k\psi_i(x,0) \quad \text{on } \overline{\Omega}.
\end{aligned} \tag{8.56}$$

By (8.55), (8.56), and the standard comparison theorem, we get

$$u_i(x,t) \geq ke^{(-\mu-\epsilon_0)t}\psi_i(x,t), \quad \forall t\geq 0,\ x\in\Omega.$$

Then $\lim_{t\to\infty} u_i(x,t) = \infty$ for any $x\in\Omega$, which contradicts (8.51). It follows that for any $|\lambda-\lambda_0| < \delta_2$ and any $\phi\in C^+$ with $\phi_i(\cdot)\not\equiv 0$, $\limsup_{n\to\infty} d(u(\cdot,n\omega,\phi,\lambda),M) \geq \eta_2$. ∎

By the continuous dependence of the evolution operator on parameters (see, e.g., [13] and [89, Section III.11]), the variation of constants formula, and a generalized Gronwall's inequality argument (see, e.g., [152, Lemma 19.4] and the proof of Proposition 3.2.1), we can prove the following result on the continuity of solutions on parameters uniformly for initial values.

Proposition 8.3.2. *Assume that solutions of (E_λ) are uniformly bounded uniformly for $\lambda\in\Lambda$; that is, for any $r>0$, there exists $B=B(r)>0$ such that for any $\phi\in C^+$ with $\|\phi\|\leq r$, $\|u(\cdot,t,\phi,\lambda)\| \leq B(r), \forall t\geq 0$, $\lambda\in\Lambda$. Then for any $\lambda_0\in\Lambda$ and any integer $k>0$,*

$$\lim_{\lambda\to\lambda_0} \|u(\cdot,t,\phi,\lambda) - u(\cdot,t,\phi,\lambda_0)\| = 0$$

uniformly for $t\in[\omega,k\omega]$ and ϕ in any bounded subset of C^+.

8.3.2 Single Species Growth

Consider the single species growth model with not necessarily identical diffusivities and nonvanishing cell death rate

$$\begin{aligned}\frac{\partial S}{\partial t} &= d_0\frac{\partial^2 S}{\partial x^2} - v\frac{\partial S}{\partial x} - uf(S), \quad 0<x<1,\, t>0,\\ \frac{\partial u}{\partial t} &= d\frac{\partial^2 u}{\partial x^2} - v\frac{\partial u}{\partial x} + u(f(S)-k), \quad 0<x<1,\, t>0,\end{aligned} \tag{8.57}$$

with boundary conditions

$$\begin{aligned}&d_0\frac{\partial S(0,t)}{\partial x} - vS(0,t) = -vS^0(t), \quad t>0,\\ &d\frac{\partial u(0,t)}{\partial x} - vu(0,t) = 0, \quad t>0,\\ &\frac{\partial S(1,t)}{\partial x} = \frac{\partial u(1,t)}{\partial x} = 0, \quad t>0,\end{aligned} \tag{8.58}$$

where $d_0>0, d>0, v>0$, and $k \ge 0$, and $S^0(\cdot)$ and $f(\cdot)$ are as in (8.20)–(8.21). Let $Y^+ = C([0,1],\mathbb{R}^2_+)$. Let $d_0>0$ and $v>0$ be fixed and let $\lambda = (d,k), d>0, k\ge 0$. As argued in Section 8.1, [243, Theorem 1 and Remark 1.1] imply that for any $\phi = (S_0(\cdot),u_0(\cdot)) \in Y^+$, (8.57)–(8.58) has a unique solution $(S(x,t,\phi,\lambda),u(x,t,\phi,\lambda))$, defined on its maximal interval of existence $[0,\sigma_\phi)$, satisfying $(S(\cdot,0,\phi,\lambda),u(\cdot,0,\phi,\lambda)) = \phi$. Moreover,

$$S(x,t,\phi,\lambda)\ge 0, \qquad u(x,t,\phi,\lambda)\ge 0,\ \forall x\in[0,1],\, t\in[0,\sigma_\phi).$$

We further have the following result.

Lemma 8.3.1. *Let $\Lambda = \{(d,k) : \frac{d_0}{2} \le d \le 2d_0,\ k\ge 0\}$. Then for each $\lambda \in \Lambda$, $\phi\in Y^+$, $(S(x,t,\phi,\lambda),u(x,t,\phi,\lambda))$ exists globally on $[0,\infty)$, and solutions of (8.57)–(8.58) are uniformly bounded and ultimately bounded uniformly for $\lambda\in\Lambda$.*

Proof. Given $\phi = (S_0(\cdot),u_0(\cdot))\in Y^+$, for convenience, let

$$(S(x,t),u(x,t)) = (S(x,t,\phi,\lambda),u(x,t,\phi,\lambda)), \quad \forall x\in[0,1],\, t\in[0,\sigma_\phi).$$

Then $S(x,t)$ satisfies

$$\begin{aligned}&\frac{\partial S}{\partial t} \le d_0\frac{\partial^2 S}{\partial x^2} - v\frac{\partial S}{\partial x}, \quad 0<x<1,\, t>0,\\ &d_0\frac{\partial S(0,t)}{\partial x} - vS(0,t) = -vS^0(t), \quad t>0,\\ &\frac{\partial S(1,t)}{\partial x} = 0, \quad t>0.\end{aligned} \tag{8.59}$$

By the parabolic comparison theorem, we have

$$S(x,t) \le \bar{S}(x,t), \quad \forall x \in [0,1],\, t \in [0,\sigma_\phi), \tag{8.60}$$

where $\bar{S}(x,t)$ is the unique solution of (8.11) with $\bar{S}(x,0) = S(x,0)$. By Proposition 8.2.1, $\bar{S}(x,t)$ exists globally on $[0,\infty)$ and $\lim_{t\to\infty}(\bar{S}(x,t) - W^*(x,t)) = 0$ uniformly for $x \in [0,1]$.

Let μ be the unique positive solution to equation $\tan\mu = \frac{v}{2\mu d_0}$ on the interval $[0, \frac{\pi}{2})$. Clearly, $\sin(\mu x) \ge 0, \cos(\mu x) > 0, x \in [0,1]$. Then for any $\lambda \in \Lambda$, by using (8.57) and (8.58) and integration by parts, we have

$$\begin{aligned}
\frac{d}{dt}\int_0^1 S(x,t)\cos(\mu x)dx &= \int_0^1 \frac{\partial S}{\partial t}\cos(\mu x)dx \\
&= vS^0(t) - S(1,t)(v\cos\mu - \mu d_0 \sin\mu) - \mu v\int_0^1 S(x,t)\sin(\mu x)dx \\
&\quad - d_0\mu^2\int_0^1 S(x,t)\cos(\mu x)dx - \int_0^1 u(x,t)f(S(x,t))\cos(\mu x)dx \\
&\le vS^0(t) - d_0\mu^2\int_0^1 S(x,t)\cos(\mu x)dx \\
&\quad - \int_0^1 u(x,t)f(S(x,t))\cos(\mu x)dx
\end{aligned} \tag{8.61}$$

and

$$\begin{aligned}
\frac{d}{dt}\int_0^1 u(x,t)\cos(\mu x)dx &= \int_0^1 \frac{\partial u}{\partial t}\cos(\mu x)dx \\
&= -u(x,t)[v\cos\mu - \mu d\sin\mu] - v\int_0^1 u(x,t)\sin(\mu x)dx \\
&\quad - d\mu^2\int_0^1 u(x,t)\cos(\mu x)dx + \int_0^1 u(x,t)(f(S(x,t) - k)\cos(\mu x)dx \\
&\le -d\mu^2\int_0^1 u(x,t)\cos(\mu x)dx + \int_0^1 u(x,t)f(S(x,t))\cos(\mu x)dx.
\end{aligned} \tag{8.62}$$

Let $y(t) = \int_0^1 (S(x,t) + u(x,t))\cos(\mu x)dx$, $\forall t \in [0,\sigma_\phi)$. Then we get

$$\frac{dy(t)}{dt} \le vS^0(t) - \frac{d_0\mu^2}{2}y(t), \quad t \in [0,\sigma_\phi).$$

By the standard comparison theorem for ordinary differential equations, it then follows that for all $t \in [0,\sigma_\phi)$,

$$y(t) \le y^*(t) - \exp\left(-\frac{d_0\mu^2 t}{2}\right)y^*(0) + \exp\left(-\frac{d_0\mu^2 t}{2}\right)y(0), \tag{8.63}$$

where $y^*(t)$ is the unique positive ω-periodic solution of linear ordinary differential equations

$$\frac{dy}{dt} = vS^0(t) - \frac{d_0\mu^2}{2}y(t).$$

Since $S(x,t) \geq 0, u(x,t) \geq 0$, and $\cos(\mu x) \geq \min_{x\in[0,1]} \cos(\mu x) = m > 0$, $\forall x \in [0,1]$, (8.63) implies that for all $t \in [0, \sigma_\phi)$,

$$\int_0^1 u(x,t)dx \leq \frac{1}{m}\left[y^*(t) - exp\left(-\frac{d_0\mu^2 t}{2}\right)y^*(0) + \exp\left(-\frac{d_0\mu^2 t}{2}\right)\int_0^1 (S_0(x) + u_0(x))\cos(\mu x)dx\right]. \tag{8.64}$$

Then $u(\cdot,t)$ is L_1-bounded on $[0,\sigma_\phi)$. By (8.60), (8.64), and an argument similar to that in [6, Theorem 3.1], [186, Lemma 3.13], and [215, Proposition 2.4 and Theorem 2.5], it follows that for each $\phi \in Y^+$, $(S(x,t,\phi,\lambda), u(x,t,\phi,\lambda))$ is L^∞-bounded, and hence $\sigma_\phi = \infty$, and solutions of (8.57)–(8.58) are uniformly L^∞-bounded and ultimately L^∞-bounded uniformly for $\lambda \in \Lambda$. ∎

Now we show that the hypothesis of Theorem 8.2.1(b) for the unperturbed system implies the existence of a globally attracting single-population periodic solution for the perturbed system at least when the perturbation is small.

Theorem 8.3.1. *Let $\lambda = (d,k)$, $\lambda_0 = (d_0, 0)$, and $W^*(x,t)$ and $\mu(m(\cdot,\cdot))$ be as in Section 8.2. Assume that $\mu(f(W^*(x,t))) < 0$ and let $(S^*(x,t), u^*(x,t))$ be as in Theorem 8.2.1. Then there exists $\delta_0 > 0$ such that for any $|\lambda - \lambda_0| < \delta_0$, (8.57)–(8.58) admits a unique positive ω-periodic solution $(S^*(x,t,\lambda), u^*(x,t,\lambda))$ with*

$$(S^*(x,t,\lambda_0), u^*(x,t,\lambda_0)) = (S^*(x,t), u^*(x,t)),\ \forall x \in [0,1],\ t \geq 0,$$

and such that the map $\lambda \to (S^*(\cdot,\cdot,\lambda), u^*(\cdot,\cdot,\lambda))$ is continuous. Moreover, for any $(S_0(\cdot), u_0(\cdot)) \in Y^+$ with $u_0(\cdot) \not\equiv 0$,

$$\lim_{t\to\infty}(S(x,t,\phi,\lambda) - S^*(x,t,\lambda)) = 0 \text{ and } \lim_{t\to\infty}(u(x,t,\phi,\lambda) - u^*(x,t,\lambda)) = 0,$$

uniformly for $x \in [0,1]$.

Proof. Let $k_0 > 0$ be given and let $\Lambda_0 = \{(d,k) : \frac{d_0}{2} \leq d \leq 2d_0, 0 \leq k \leq k_0\}$. For any $\lambda \in \Lambda_0$, let $S_\lambda = S(\lambda,\cdot) : Y^+ \to Y^+$ be the Poincaré map associated with (8.57)–(8.58); that is, $S(\lambda,\phi) = (S(\cdot,\omega,\phi,\lambda), u(\cdot,\omega,\phi,\lambda))$, $\phi \in Y^+$. Then $S(\cdot,\cdot) : \Lambda_0 \times Y^+ \to Y^+$ is continuous. By Lemma 8.3.1, it follows that for each $\lambda \in \Lambda_0$, $S_\lambda : Y^+ \to Y^+$ is compact and point dissipative uniformly for $\lambda \in \Lambda_0$; that is, there exists a bounded and closed subset B_0 of Y^+, independent of $\lambda \in \Lambda_0$, such that for any $\phi \in Y^+$, $\lambda \in \Lambda_0$, there exists $N = N(\phi,\lambda)$ such that $S_\lambda^n(\phi) \in B_0$ for all $n \geq N$. Then, by Theorem 1.1.3, for each $\lambda \in \Lambda_0$, there exists a global attractor A_λ for $S_\lambda : Y^+ \to Y^+$. Clearly, $A_\lambda \subset B_0$. By a change of variables

$$\bar{S}(x,t) = S(x,t) - W^*(x,t),\ \ \bar{u}(x,t) = \exp\left(\frac{v(x-1)^2}{2d}\right)u(x,t),$$

the boundary conditions (8.58) then become the homogeneous ones

$$d_0 \frac{\partial \bar{S}(0,t)}{\partial x} - v\bar{S}(0,t) = \frac{\partial \bar{S}(1,t)}{\partial x} = 0, \quad t > 0,$$
$$\frac{\partial \bar{u}(0,t)}{\partial x} = \frac{\partial \bar{u}(1,t)}{\partial x} = 0, \quad t > 0,$$

which is independent of parameter λ. By Lemma 8.3.1 and Proposition 8.3.2, when applied to the resulting system with parameter λ under the above change of variables and the above boundary conditions, it then follows that $S(\cdot,\phi) : \Lambda_0 \to Y^+$ is continuous uniformly for ϕ in any bounded subset of Y^+. We further have the following claim:

Claim. For any bounded subset $B \subset Y^+$, $\overline{\cup_{\lambda\in\Lambda_0} S_\lambda(B)}$ is compact in Y^+.

Indeed, for any sequence $\{\psi_n\}$ in $\cup_{\lambda\in\Lambda_0} S_\lambda(B)$, we have $\psi_n = S_{\lambda_n}(\phi_n)$, $\lambda_n \in \Lambda_0, \phi_n \in B, n \geq 0$. By the compactness of Λ_0, without loss of generality we can assume that for some $\lambda_1 \in \Lambda_0$, $\lambda_n \to \lambda_1$ as $n \to \infty$. Since $S_{\lambda_1}(B)$ is precompact, there exist $\psi_0 \in Y^+$ and a subsequence $n_k \to \infty$ such that $S_{\lambda_1}(\phi_{n_k}) \to \psi_0$ as $k \to \infty$. Combining the continuity of $S(\cdot,\phi) : \Lambda_0 \to Y^+$ uniformly for $\phi \in B$ and the inequality

$$\begin{aligned} \|\psi_{n_k} - \psi_0\| &= \left\| S_{\lambda_{n_k}}(\phi_{n_k}) - \psi_0 \right\| \\ &\leq \left\| S_{\lambda_{n_k}}(\phi_{n_k}) - S_{\lambda_1}(\phi_{n_k}) \right\| + \|S_{\lambda_1}(\phi_{n_k}) - \psi_0\|, \end{aligned}$$

we get $\psi_{n_k} \to \psi_0$, $k \to \infty$. Therefore, $\cup_{\lambda\in\Lambda_0} S_\lambda(B)$ is precompact.

Let

$$Y_0 := \left\{ (S(\cdot), u(\cdot)) \in Y^+ : \quad u(\cdot) \not\equiv 0 \right\} \text{ and } \partial Y_0 := Y^+ \setminus Y_0.$$

Then $S_\lambda : Y_0 \to Y_0$ and $S_\lambda : \partial Y_0 \to \partial Y_0$. Let $\phi_0 = (S^*(\cdot,0), u^*(\cdot,0))$. Then $S_{\lambda_0}(\phi_0) = \phi_0$. By Theorem 8.2.1, $r(D_\phi S(\lambda_0,\phi_0)) < 1$, and $\lim_{n\to\infty} S^n_{\lambda_0}\phi = \phi_0$ for every $\phi \in Y_0$. For each $\lambda \in \Lambda_0$, by Proposition 8.2.1,

$$\lim_{n\to\infty} S^n_\lambda(\phi) = (W^*(\cdot,0),0), \ \forall \phi \in \partial Y_0.$$

Clearly, $M = (W^*(\cdot,0),0)$ is a global attractor for $S_\lambda : \partial Y_0 \to \partial Y_0$. Note that $(W^*(x,t),0)$ is a nonnegative ω-periodic solution of (8.57)–(8.58) and $\mu(f(W^*(x,t))) < 0$. By a change of variables

$$\bar{S}(x,t) = S(x,t) - W^*(x,t), \quad \bar{u}(x,t) = \exp\left(\frac{v(x-1)^2}{2d}\right) u(x,t),$$

and Proposition 8.3.1, as applied to the resulting system, it then follows that there exist $\delta_1 > 0$ and $\eta_1 > 0$ such that for any $|\lambda - \lambda_0| < \delta_1$ and any $\phi \in Y_0$, we have

$$\limsup_{n\to\infty} d\left(S_\lambda^n(\phi), M\right) = \limsup_{n\to\infty} d\left((S(\cdot, n\omega, \phi, \lambda), u(\cdot, n\omega, \phi, \lambda)), M\right) \geq \eta_1,$$

which implies that M is isolated for $S_\lambda : Y^+ \to Y^+$, and $W_\lambda^s(M) \cap Y_0 = \emptyset$, $|\lambda - \lambda_0| < \delta_1$, where $W_\lambda^s(M)$ is the stable set of M with respect to S_λ. By Theorem 1.3.1, S_λ is uniformly persistent with respect to $(Y_0, \partial Y_0)$ for each $|\lambda - \lambda_0| < \delta_1$. Therefore, there exists a global attractor $A_\lambda^0 \subset Y_0$ for $S_\lambda : Y_0 \to Y_0$ (see, e.g., Theorem 1.3.6). Clearly, $A_\lambda^0 \subset B_0$, and $\overline{\cup_{\lambda\in\Lambda_0,\phi\in Y^+}\omega_\lambda(\phi)} \subset \overline{\cup_{\lambda\in\Lambda_0} S_\lambda(B_0)}$. Then by the previous claim, $\overline{\cup_{\lambda\in\Lambda_0,\phi\in Y^+}\omega_\lambda(\phi)}$ is compact. By Theorem 1.4.2, it follows that there exist $\delta_2 > 0$ and $\eta_2 > 0$ such that for any $|\lambda - \lambda_0| \leq \delta_2$, $\phi \in Y_0$, $\liminf_{n\to\infty} d(S_\lambda^n \phi, \partial Y_0) \geq \eta_2$. Then there exists a bounded and closed subset B_0^* of Y_0 such that $A_\lambda^0 \subset B_0^*$ for all $|\lambda - \lambda_0| \leq \delta_2$. Let $\Lambda_1 = \Lambda_0 \cap \overline{B(\lambda_0, \delta_2)}$, where $B(\lambda_0, \delta_2) = \{\lambda : |\lambda - \lambda_0| < \delta_2\}$. Since $\overline{\cup_{\lambda\in\Lambda_1} S_\lambda(A_\lambda^0)} \subset \overline{\cup_{\lambda\in\Lambda_1} S_\lambda(B_0^*)}$, by the previous claim $\overline{\cup_{\lambda\in\Lambda_1} S_\lambda(A_\lambda^0)}$ is compact. Moreover, $\overline{\cup_{\lambda\in\Lambda_1} S_\lambda(A_\lambda^0)} = \overline{\cup_{\lambda\in\Lambda_1} A_\lambda^0} \subset \overline{B_0^*} = B_0^* \subset Y_0$. By applying Theorem 1.4.1 on the perturbation of a globally stable fixed point to $S_\lambda(\cdot) : Y^+ \to Y^+$ with $U = Y_0$ and $B_\lambda = A_\lambda^0, \lambda \in \Lambda_1$, we complete the proof. ∎

8.3.3 Two-Species Competition

Consider two-species competition with unequal diffusivities and nonvanishing cell death rates

$$\begin{aligned}
\frac{\partial S}{\partial t} &= d_0 \frac{\partial^2 S}{\partial x^2} - v\frac{\partial S}{\partial x} - u_1 f_1(S) - u_2 f_2(S), \quad 0 < x < 1,\, t > 0, \\
\frac{\partial u_i}{\partial t} &= d_i \frac{\partial^2 u_i}{\partial x^2} - v\frac{\partial u_i}{\partial x} + u_i(f_i(S) - k_i), \quad i = 1, 2,\, 0 < x < 1,\, t > 0,
\end{aligned} \tag{8.65}$$

with boundary conditions

$$\begin{aligned}
& d_0 \frac{\partial S(0,t)}{\partial x} - vS(0,t) = -vS^0(t), \quad t > 0, \\
& d_i \frac{\partial u_i(0,t)}{\partial x} - vu_i(0,t) = 0, \quad i = 1, 2,\, t > 0, \\
& \frac{\partial S(1,t)}{\partial x} = \frac{\partial u_i(1,t)}{\partial x} = 0, \quad i = 1, 2,\, t > 0,
\end{aligned} \tag{8.66}$$

where $d_0 > 0, v > 0, d_i > 0$, and $k_i \geq 0$, and $S^0(\cdot)$ and $f_i(\cdot)$, $i = 1, 2$, are as in (8.7)–(8.8). Let $X^+ = C([0,1], \mathbb{R}_+^3)$. Let $d_0 > 0$ and $v > 0$ be fixed and let $\lambda = (d_1, d_2, k_1, k_2), d_i > 0, k_i \geq 0, i = 1, 2$. As mentioned in Section 8.1, for any $\phi = (S_0(\cdot), u_{01}(\cdot), u_{02}(\cdot)) \in X^+$, (8.65)–(8.66) has a unique solution $(S(x,t,\phi,\lambda), u_1(x,t,\phi,\lambda), u_2(x,t,\phi,\lambda))$, defined on its maximal interval of existence $[0, \sigma_\phi)$, satisfying $(S(\cdot,0,\phi,\lambda), u_1(\cdot,0,\phi,\lambda), u_2(\cdot,0,\phi,\lambda)) = \phi$. Moreover,

$$S(x,t,\phi,\lambda) \geq 0, \quad u_i(x,t,\phi,\lambda) \geq 0,\ \forall x \in [0,1],\ t \in [0,\sigma_\phi),\ i = 1, 2.$$

By a similar argument as in Lemma 8.3.1, we have the following result on the boundedness of solutions uniformly for λ.

Lemma 8.3.2. *Let $\Lambda = \{(d_1, d_2, k_1, k_2) : \frac{d_0}{2} \leq d_i \leq 2d_0,\ k_i \geq 0,\ i = 1, 2\}$. Then for each $\lambda \in \Lambda$, $\phi \in X^+$, $(S(x, t, \phi, \lambda), u_1(x, t, \phi, \lambda), u_2(x, t, \phi, \lambda))$ exists globally on $[0, \infty)$, and solutions of (8.65)–(8.66) are uniformly bounded and ultimately bounded uniformly for $\lambda \in \Lambda$.*

Now we can state one of the main results of this chapter. It says that both species persist for the perturbed system and there exists a positive periodic solution when the hypotheses of Theorem 8.2.2 hold for the unperturbed system and the perturbation is sufficiently small.

Theorem 8.3.2. *Let $\lambda = (d_1, d_2, k_1, k_2)$ and $\lambda_0 = (d_0, d_0, 0, 0)$. Assume that all conditions in Theorem 8.2.2 hold. Then there exist $\delta > 0$ and $\beta > 0$ such that for any $|\lambda - \lambda_0| < \delta$, (8.65)–(8.66) admits at least one positive ω-periodic solution, and for any $\phi = (S_0(\cdot), u_{01}(\cdot), u_{02}(\cdot)) \in X^+$ with $u_{0i}(\cdot) \not\equiv 0$, $\forall i = 1, 2$, there exists $t_0 = t_0(\phi, \lambda)$ such that*

$$u_i(x, t, \phi, \lambda) \geq \beta, \quad \forall x \in [0, 1],\ t \geq t_0,\ i = 1, 2.$$

Proof. Let $k_0 > 0$ be given and let

$$\Lambda_0 = \{(d_1, d_2, k_1, k_2) : \frac{d_0}{2} \leq d_i \leq 2d_0,\ 0 \leq k_i \leq k_0,\ i = 1, 2\}.$$

For each $\lambda \in \Lambda_0$, let $S_\lambda(\cdot) = S(\lambda, \cdot) : X^+ \to X^+$ be the Poincaré map associated with (8.65)–(8.66); that is,

$$S(\lambda, \phi) = (S(\cdot, \omega, \phi, \lambda), u_1(\cdot, \omega, \phi, \lambda), u_2(\cdot, \omega, \phi, \lambda)),\ \forall \phi \in X^+.$$

Then $S(\cdot, \cdot) : \Lambda_0 \times X^+ \to X^+$ is continuous. By Lemma 8.3.2, for each $\lambda \in \Lambda_0$, $S_\lambda : X^+ \to X^+$ is compact and point dissipative uniformly for $\lambda \in \Lambda_0$, and hence, by Theorem 1.1.3, there exists a global attractor A_λ for $S_\lambda : X^+ \to X^+$. Let

$$X_0 := \left\{(S(\cdot), u_{01}(\cdot), u_{02}(\cdot)) \in X^+ :\ u_{0i}(\cdot) \not\equiv 0,\ \forall i = 1, 2\right\}$$

and $\partial X_0 := X^+ \setminus X_0$. Then $S_\lambda : X_0 \to X_0$ and $S_\lambda : \partial X_0 \to \partial X_0$. By Theorem 8.2.1, $(S_i^*(x, t), u_i^*(x, t))$ is the unique positive ω-periodic solution of (8.20)–(8.21) with $f(\cdot) = f_i(\cdot)$, $i = 1, 2$, respectively. Clearly, $(W^*(x, t), 0, 0)$, $(S_1^*(x, t), u_1^*(x, t), 0)$ and $(S_2^*(x, t), 0, u_2^*(x, t))$ are nonnegative periodic solutions of (8.65)–(8.66) with $\lambda = \lambda_0$. Let

$$M_0 = (W^*(\cdot, 0), 0, 0),\ M_1^0 = (S_1^*(\cdot, 0), u_1^*(\cdot, 0), 0),\ M_2^0 = (S_2^*(\cdot, 0), 0, u_2^*(\cdot, 0)).$$

Then $S_{\lambda_0}(M_0) = M_0$, $S_{\lambda_0}(M_i^0) = M_i^0$, $\forall i = 1, 2$. By a change of variables

$$\bar{S}(x, t) = S(x, t) - W^*(x, t),\ \bar{u}_i(x, t) = \exp\left(\frac{v(x-1)^2}{2d_i}\right) u_i(x, t),\ i = 1, 2,$$

and Proposition 8.3.1, as applied to the resulting system, it follows that there exist $\delta_0 > 0$ and $\eta_0 > 0$ such that for any $\lambda \in \Lambda_0$ with $|\lambda - \lambda_0| < \delta_0$, and for any $\phi \in X_0$,

$$\limsup_{n\to\infty} d(S_\lambda^n(\phi), M_0) \geq \eta_0, \ \limsup_{n\to\infty} d(S_\lambda^n(\phi), M_i^0) \geq \eta_0, \ i = 1, 2. \tag{8.67}$$

By Proposition 8.2.1 and Theorem 8.2.1, it follows that M_0, M_1^0, and M_2^0 are acyclic for S_{λ_0} in ∂X_0, and $\cup_{\phi\in\partial X_0}\omega_{\lambda_0}(\phi) = M_0 \cup M_1^0 \cup M_2^0$, where $\omega_{\lambda_0}(\phi)$ is the omega limit set of ϕ for S_{λ_0}. Moreover, (8.67) implies that $M_0 \cup M_1^0 \cup M_2^0$ is an isolated covering of $\overline{\cup_{\phi\in\partial X_0}\omega_{\lambda_0}(\phi)}$ for S_{λ_0} in ∂X_0 and that $W^s_{\lambda_0}(M_0) \cap X_0 = \emptyset$ and $W^s_{\lambda_0}(M_i^0) \cap X_0 = \emptyset$, $\forall i = 1, 2$, where $W^s_{\lambda_0}(M)$ denotes the stable set of M with respect to S_{λ_0}. By Theorem 1.3.1 and Remark 1.3.1, it follows that $S_{\lambda_0} : X^+ \to X^+$ is uniformly persistent with respect to $(X_0, \partial X_0)$, and hence there exists a global attractor $A^0_{\lambda_0} \subset X_0$ for $S_{\lambda_0} : X_0 \to X_0$ (see, e.g., Theorem 1.3.6).

Let $\Lambda_1 = \Lambda_0 \cap \overline{B(\lambda_0, \delta_0)}$. Again by a change of variables

$$\bar{S}(x,t) = S(x,t) - W^*(x,t), \ \bar{u}_i(x,t) = \exp\left(\frac{v(x-1)^2}{2d_i}\right) u_i(x,t), \ i = 1, 2,$$

Lemma 8.3.2, and Proposition 8.3.2, as applied to the resulting system, it follows that $S_\lambda : X^+ \to X^+$ is point dissipative uniformly for $\lambda \in \Lambda_1$ and $S(\cdot, \phi) : \Lambda_1 \to X^+$ is continuous uniformly for ϕ in any bounded subset of X^+. Therefore, by the same argument as in the claim in the proof of Theorem 8.3.1, for any bounded subset B of X^+, $\overline{\cup_{\lambda\in\Lambda_1} S_\lambda(B)}$ is compact. It then follows that, as argued in Theorem 8.3.1, $\overline{\cup_{\lambda\in\Lambda_1,\phi\in X^+}\omega_\lambda(\phi)}$ is compact. Therefore, by (8.67) and Theorem 1.4.2, there exist $\delta_1 \in (0, \delta_0)$ and $\eta > 0$ such that for any $\lambda \in \Lambda_0$ with $|\lambda - \lambda_0| \leq \delta_1$, and any $\phi \in X_0$, $\liminf_{n\to\infty} d(S_\lambda^n \phi, \partial X_0) \geq \eta$. Moreover, by Theorem 1.3.10, S_λ admits a fixed point $S_\lambda(\phi_\lambda) = \phi_\lambda \in X_0$, and hence (8.65)–(8.66) with $|\lambda - \lambda_0| \leq \delta_1$ admits a nonnegative ω-periodic solution $(S(x,t,\phi_\lambda,\lambda), u_1(x,t,\phi_\lambda,\lambda), u_2(x,t,\phi_\lambda,\lambda))$ with $u_i(\cdot,t,\phi_\lambda,\lambda) \gg 0$ in $C([0,1],\mathbb{R})$, $\forall t \geq 0, i = 1, 2$. By parabolic maximum principle and the fact that $S^0(\cdot) \geq 0$ with $S^0(\cdot) \not\equiv 0$, it then easily follows that $S(\cdot,t,\phi_\lambda,\lambda) \gg 0$ in $C([0,1],\mathbb{R})$, $\forall t \geq 0$. Thus, $(S(x,t,\phi_\lambda,\lambda), u_1(x,t,\phi_\lambda,\lambda), u_2(x,t,\phi_\lambda,\lambda))$ is a positive ω-periodic solution of (8.65)–(8.66).

It remains to prove the practical persistence claimed in the theorem. Let $\Lambda_2 = \Lambda_0 \cap \overline{B(\lambda_0, \delta_1)}$. By both the point dissipativity and the uniform persistence of S_λ with respect to $(X_0, \partial X_0)$ uniformly for $\lambda \in \Lambda_2$, it follows that there exists a closed and bounded set $B_0 \subset X_0$, independent of λ, such that $\underline{d}(B_0, \partial X_0) = \inf_{\phi\in B_0} d(\phi, \partial X_0) > 0$ and B_0 attracts points in X_0. As argued in Theorem 8.3.1, for each $\lambda \in \Lambda_2$, $S_\lambda : X_0 \to X_0$ admits a global attractor $A_\lambda^0 \subset X_0$, and hence A_λ^0 attracts any compact subset of X_0. Clearly, for each $\lambda \in \Lambda_2$, $A_\lambda^0 \subset B_0$, and hence B_0 attracts compact subsets of X_0 under S_λ. Since for each $\lambda \in \Lambda_2$, $S_\lambda : X^+ \to X^+$ is compact, and for any bounded subset B of X^+, as claimed in the previous paragraph, $\cup_{\lambda\in\Lambda_2} S_\lambda(B)$ is precompact, it follows that $\{S_\lambda : \lambda \in \Lambda_2\}$ is collectively compact. By Theorem 1.1.5, it then follows that A_λ^0 is upper semicontinuous in $\lambda \in \Lambda_2$. In particular,

$$\lim_{\lambda \to \lambda_0} \sup_{\phi \in A_\lambda^0} d(\phi, A_{\lambda_0}^0) = 0. \tag{8.68}$$

Let $\Phi_\lambda(t, \cdot) : X^+ \to X^+$ be defined by

$$\Phi_\lambda(t, \phi) = \left(S(\cdot, t, \phi, \lambda), u_1(\cdot, t, \phi, \lambda), u_2(\cdot, t, \phi, \lambda)\right), \ \phi \in X^+.$$

Clearly, $S_\lambda = \Phi_\lambda(\omega, \cdot)$ and $S_\lambda^n = \Phi_\lambda(n\omega, \cdot)$. It then follows that $\Phi_\lambda : \mathbb{R}_+ \times X^+ \to X^+$ is a periodic semiflow. Moreover, by Theorem 3.1.1, $\lim_{t\to\infty} d(\Phi_\lambda(t, \phi),\ \tilde{A}_\lambda^0) = 0,\ \ \forall \phi \in X_0$, where $\tilde{A}_\lambda^0 = \cup_{t\in[0,\omega]} \Phi_\lambda(t, A_\lambda^0) \subset X_0$. Since $A_\lambda^0 = S_\lambda(A_\lambda^0)$, $\tilde{A}_\lambda^0 = \cup_{t\in(0,\omega]} \Phi_\lambda(t, A_\lambda^0)$. By the compactness of $\tilde{A}_{\lambda_0}^0$ and the parabolic maximum principle, it then follows that there exists $\beta_0 > 0$ such that for any $\phi = (\phi_0, \phi_1, \phi_2) \in \tilde{A}_{\lambda_0}^0$, $\phi_i(x) \geq \beta_0$, $\forall x \in [0, 1]$, $i = 1, 2$. By (8.68), we have $\lim_{\lambda\to\lambda_0} \sup_{\phi\in\tilde{A}_\lambda^0} d(\phi, \tilde{A}_{\lambda_0}^0) = 0$. Consequently, there exist $\delta_2 \in (0, \delta_1)$ and $\beta_1 > 0$ such that for any $|\lambda - \lambda_0| < \delta_2$, and any $\phi = (\phi_0, \phi_1, \phi_2) \in \tilde{A}_\lambda^0$, we have $\phi_i(x) \geq \beta_1$, $\forall x \in [0, 1]$, $i = 1, 2$. Now the global attractivity of $\tilde{A}_\lambda^0$ in X_0 for Φ_λ completes the proof. ∎

Remark 8.3.1. In the case where the velocity of the flow of medium in the bioreactor varies periodically as well, that is, $v = v(t) = v(t + \omega)$, a change of variables

$$\bar{S}(x, t) = \exp\left(\frac{v(t)(x-1)^2}{2d_0}\right)\left(S(x, t) - W^*(x, t)\right),$$
$$\bar{u}_i(x, t) = \exp\left(\frac{v(t)(x-1)^2}{2d_i}\right) u_i(x, t),\ i = 1, 2,$$

results in the boundary conditions becoming homogeneous Neumann boundary conditions, and using similar ideas as in Sections 8.2 and 8.3, we can also discuss the global dynamics of the modified model systems.

Remark 8.3.2. In the case of constant nutrient input, that is, $S^0(\cdot) \equiv S^0$, it follows that the ω-periodic solutions in Sections 8.2 and 8.3 reduce to steady states of the corresponding autonomous reaction–diffusion systems, and hence we have the analogous results of Theorems 8.2.1, 8.2.2, 8.3.1, and 8.3.2.

8.4 Notes

This chapter is adapted from Smith and Zhao [336]. The model with constant nutrient input was formulated by Kung and Baltzis [207], and was studied in Ballyk, Le, Jones and Smith [27]. Smith and Zhao [341] established the existence of traveling waves for this model in the case of single species growth. The transformations in Section 8.3 converting Robin-type boundary conditions to Neumann boundary conditions were motivated by Pilyugin and Waltman [278]. Similar perturbation ideas as in Section 8.3 were used for two-species periodic competitive parabolic systems under perturbations in Zhao [437].

Hsu, Wang and Zhao [175] studied a periodically pulsed bioreactor model in a flowing water habitat with a hydraulic storage zone in which no flow occurs, and obtained sufficient conditions in terms of principal eigenvalues for the persistence of single population and the coexistence of two competing populations. Yu and Zhao [422] investigated the spatial dynamics of a periodic reaction–advection–diffusion model for a stream population, and established a threshold-type result on the global stability of either zero or the positive periodic solution in the case of a bounded domain.

9

A Nonlocal and Delayed Predator–Prey Model

The celebrated Lotka–Volterra model proposed by Lotka [230] in the context of chemical reactions and by Volterra [377] for prey–predator dynamics has been generalized in several directions: to include many species with complicated interactions, to include spatial effects in either a discrete way or a continuous way, and to include delays or internal population structure. Sometimes these generalizations combine diffusion and delays (see, e.g., [408]). While most of the delayed diffusion equations in the literature are local, nonlocal effects very naturally appear in diffusive prey–predator models with delays if one carefully models the delay as condensation of the underlying retarding process and takes into account that individuals move during this process (see [136]). In the predator equation, the delay is often caused by the conversion of consumed prey biomass into predator biomass, whether in the form of body size growth or of reproduction.

The purpose of this chapter is to present a nonlocal and delayed predator–prey model and analyze its global dynamics. In Section 9.1 we derive a nonlocal and delayed predator equation and supplement it by a standard prey equation with diffusion and without delays to get the model. We then show that under appropriate conditions solutions exist and are unique and bounded for all forward times, and that the associated solution semiflow has a compact global attractor. In Section 9.2, given persistence of the prey, we derive conditions for uniform persistence of the predator and existence of a steady state in which both prey and predator coexist. These conditions are sharp, for we show in Section 9.3 that the predator becomes extinct if they are violated. In this case the prey converges to a unique positive steady state. We also present conditions for both predator and prey to become extinct. In Section 9.4 we discuss the global attractivity of steady states for a special model system. In particular, we demonstrate how to use a fluctuation method to prove the global attractivity of a positive constant steady state. In Section 9.5 we consider a nonlocal and delayed single species model, which is derived by replacing the biomass gain rate function $f(x, u, v)$ in the predator equation of the model

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system with the birth rate function $g(x, v)$ of the matured population, and establish threshold dynamics (extinction or persistence/convergence to positive equilibria) by using the exponential ordering and the theory of monotone dynamical systems.

9.1 The Model

Let $v(t, x)$ denote the predator biomass density, $u(t, x)$ the prey biomass density. Often, an equation of the form

$$\frac{\partial v(t,x)}{\partial t} = d\Delta_x v(t,x) - \mu(x)v(t,x) + f\big(x, u(t-\tau,x), v(t-\tau,x)\big) \qquad (9.1)$$

is considered for the predator biomass density, where $\mu(x)$ is the per capita predator mortality rate at point x and $f\big(x, u(t-\tau, x), v(t-\tau, x)\big)$ is the biomass gain rate of the predator at point x and at time t.

If τ is interpreted as the average time it takes to convert prey biomass into predator biomass, the problem arises that the diffusing predator that is at x at time t was, with probability one, not at x at time $t - \tau$.

In order to incorporate the movements of a predator during the assimilation process, let us consider an age-structured model and let $w(t, a, x)$ denote the generalized predator biomass (predator biomass plus prey biomass ingested by the predator that has not yet been assimilated) of class age a, with a being the time since ingestion. If $P(a)$ denotes the probability that generalized biomass of age a has been assimilated into predator biomass, the predator biomass at location x and at time t is given by

$$v(t,x) = \int_0^\infty w(t,a,x)P(a)da.$$

If conversion occurs after a fixed delay τ, then P takes the form of a step function, $P = 0$ on $[0, \tau)$ and $P = 1$ on (τ, ∞). The generalized biomass density w satisfies the following partial differential equation with nonlocal boundary condition

$$\begin{aligned} \frac{\partial w(t,a,x)}{\partial t} + \frac{\partial w(t,a,x)}{\partial a} &= d\Delta_x w(t,a,x) - \mu(x)w(t,a,x), \\ w(t,0,x) &= f(x, u(t,x), v(t,x)). \end{aligned} \qquad (9.2)$$

The parameters in this system have the same meaning as in equation (9.1): $\mu(x)$ is the per capita mortality rate of the predator, and $f(x, u, v)$ is the rate at which the predators ingest prey biomass at point x, if the prey biomass at x is u and the predator biomass is v, times a factor that anticipates the conversion of prey into predator biomass. We integrate the equation along characteristics setting $\phi(r, a, x) = w(a + r, a, x)$. For simplicity we do not consider an initial value problem, but assume that from some moment on, the whole past is given. Then

$$\frac{\partial \phi(r,a,x)}{\partial a} = d\Delta_x \phi(r,a,x) - \mu(x)\phi(r,a,x),$$
$$\phi(r,0,x) = f(x,u(r,x),v(r,x)).$$

Integrating this equation, we get

$$\phi(r,a,x) = \int_\Omega \Gamma(x,y,a) f(y,u(r,y),v(r,y))dy,$$

where Γ is the appropriate Green's function or fundamental solution associated with $d\Delta_x - \mu(x)$ and possibly boundary conditions. Returning to w,

$$w(t,a,x) = \int_\Omega \Gamma(x,y,a) f\big(y,u(t-a,y),v(t-a,y)\big)dy.$$

This yields the following integral equation for the predator biomass v:

$$v(t,x) = \int_0^\infty \left(\int_\Omega \Gamma(x,y,a) f\big(y,u(t-a,y),v(t-a,y)\big)dy \right) P(a)da.$$

With a fixed delay τ one obtains

$$v(t,x) = \int_\tau^\infty \int_\Omega \Gamma(x,y,a) f(y,u(t-a,y),v(t-a,y))dy\, da.$$

In semigroup language, with $v(t) = v(t,\cdot), u(t) = u(t,\cdot)$, and T the operator semigroup generated by $d\Delta_x - \mu(x)$,

$$v(t) = \int_\tau^\infty T(a) f(\cdot,u(t-a),v(t-a))da. \tag{9.3}$$

In order to compare the derived equation with (9.1), let us rewrite v as

$$v(t,x) = \int_{-\infty}^{t-\tau} \left(\int_\Omega \Gamma(x,y,t-s) f(y,u(s,y),v(s,y))dy \right) ds.$$

Differentiating this equation, we have

$$\begin{aligned} \frac{\partial v(t,x)}{\partial t} &= (d\Delta_x - \mu(x))\, v(t,x) \\ &\quad + \int_\Omega \Gamma(x,y,\tau) f(y,u(t-\tau,y),v(t-\tau,y))dy, \end{aligned} \tag{9.4}$$

or, as an abstract Cauchy problem,

$$v'(t) = Av(t) + T(\tau) f(\cdot,u(t-\tau),v(t-\tau)),$$

where $A = d\Delta_x - \mu(\cdot)I$ is the infinitesimal generator of T.

Comparison of (9.1) with (9.4) shows the nonlocal effect that is caused by predators moving during biomass assimilation.

In contrast to Gourley and Britton [136], we incorporate nonlocal terms in the predator rather than in the prey equation, because we believe the case to be stronger there. If the prey is herbivorous, delayed logistic terms due to deleted plant resources may actually be local, because while the prey moves, the plants do not. In any case, some modeling of the nature of the retardation seems appropriate in order to determine whether or not it leads to nonlocal effects.

Let Ω be a bounded domain in $\mathbb{R}^n$ and let $X = C(\overline{\Omega}, \mathbb{R}^2)$ be the Banach space of continuous functions with values in the real plane with the norm $\|u\|_X$ being the supremum norm. Let $\tau \geq 0$ and $C_\tau = C([-\tau, 0], X)$. For any $\phi \in C_\tau$, define $\|\phi\| = \max_{\theta \in [-\tau,0]} \|\phi(\theta)\|_X$. Then C_τ is a Banach space. Let $\hat{}$ denote the inclusion $X \to C_\tau$ by $u \to \hat{u}$, $\hat{u}(\theta) = u$, $\theta \in [-\tau, 0]$. Given a function $u(t) : [-\tau, \sigma) \to X$ $(\sigma > 0)$, define $u_t \in C_\tau$ by $u_t(\theta) = u(t + \theta)$, $\theta \in [-\tau, 0]$.

Assume that Ω has a smooth boundary $\partial\Omega$ and let $Y = C(\overline{\Omega}, \mathbb{R})$ and let Δ be the Laplace operator in $\mathbb{R}^n$. For each $1 \leq i \leq 2$, let $d_i > 0$, $B_i w = \frac{\partial w}{\partial \nu} + \alpha_i(x) w$, where $\alpha_i \in C(\overline{\Omega}, \mathbb{R}^+)$ is Hölder continuous and $\frac{\partial}{\partial \nu}$ denotes the derivative along the outward normal direction ν to $\partial\Omega$.

By adding to (9.4) a standard prey equation with diffusion and without delays, we then get a nonlocal and delayed predator–prey reaction–diffusion system

$$
\begin{aligned}
\frac{\partial u_1(t,x)}{\partial t} =& d_1 \Delta u_1(t,x) + u_1(t,x) g(x, u_1(t,x)) \\
& - f_1(x, u_1(t,x), u_2(t,x)), \quad x \in \Omega,\ t > 0, \\
\frac{\partial u_2(t,x)}{\partial t} =& d_2 \Delta u_2(t,x) - \mu(x) u_2(t,x) \\
& + \int_\Omega \Gamma_2(x,y,\tau) f_2(y, u_1(t-\tau,y), u_2(t-\tau,y)) dy, \\
& x \in \Omega,\ t > 0, \\
B_i u_i =& 0, \quad x \in \partial\Omega, t > 0,\ i = 1,2, \\
u_i(t,x) =& \phi_i(t,x), \quad x \in \Omega, -\tau \leq t \leq 0.
\end{aligned}
\tag{9.5}
$$

Here $\mu(x)$ is a positive Hölder continuous function on $\overline{\Omega}$, $\Gamma_2(x,y,t)$ is the Green's function associated with $d_2\Delta - \mu(\cdot)I$ and $B_2 u_2 = 0$ [129, VIII, Theorem 2.1], $f_i \in C^1(\overline{\Omega} \times \mathbb{R}^+ \times \mathbb{R}^+, \mathbb{R}^+)$, $\forall i = 1,2$, $g \in C^1(\overline{\Omega} \times \mathbb{R}^+, \mathbb{R})$, and $\phi = (\phi_1, \phi_2) \in C_\tau$ are the initial data of problem (9.5). We will assume that

(H1) $f_1(\cdot, 0, \cdot) \equiv 0$ and $f_1(\cdot, \cdot, 0) \equiv 0$;
(H2) $\partial_1 f_2(x, u_1, u_2) := \frac{\partial f_2(x,u_1,u_2)}{\partial u_1} > 0$, $\forall x \in \overline{\Omega}, u_1 \geq 0, u_2 > 0$, and $\partial_2 f_2(x, u_1, u_2) := \frac{\partial f_2(x,u_1,u_2)}{\partial u_2} > 0$, $\forall x \in \overline{\Omega}, u_1 > 0, u_2 \geq 0$;
(H3) $f_2(x, u_1, u_2) \leq \partial_2 f_2(x, u_1, 0) u_2$, and there exists a $k > 0$ such that $f_2(x, u_1, u_2) \leq k f_1(x, u_1, u_2)$, $\forall x \in \overline{\Omega}, u_1 \geq 0, u_2 \geq 0$;
(H4) For each $x \in \overline{\Omega}$, $g(x, \cdot)$ is decreasing on $\mathbb{R}^+$, and for some $x_0 \in \Omega$, $g(x_0, \cdot)$ is strictly decreasing on $\mathbb{R}^+$;

(H5) There exists a $K_0 > 0$ such that $g(x, K_0) \leq 0$, $\forall x \in \overline{\Omega}$.

It is easy to see that assumption (H3) implies that (H1) also holds for f_2. Let $T_1(t)$ and $T_2(t) : Y \to Y$, $t \geq 0$, be the semigroups associated with $d_1\Delta$ and $B_1u_1 = 0$, and $d_2\Delta - \mu(\cdot)I$ and $B_2u_2 = 0$, respectively, and let $A_i : D(A_i) \to Y$ be the generator of $T_i(t)$, $i = 1, 2$. Clearly,

$$T_2(t)\phi = \int_\Omega \Gamma_2(\cdot, y, t)\phi(y)dy, \ \forall \phi \in Y, \, t \geq 0.$$

Moreover, $T(t) = (T_1(t), T_2(t)) : X \to X$, $t \geq 0$, is a semigroup generated by the operator $A = (A_1, A_2)$ defined on $D(A) = D(A_1) \times D(A_2)$. Then for each $t > 0$, $T(t) : X \to X$ is compact and positive (see, e.g., [326, Section 7.1 and Corollary 7.2.3]).

Define $F = (F_1, F_2) : C_\tau^+ \to C_\tau^+$ by

$$\begin{aligned} F_1(\phi_1, \phi_2)(x) &= \phi_1(0, x)g(x, \phi_1(0, x)) - f_1(x, \phi_1(0, x), \phi_2(0, x)), \\ F_2(\phi_1, \phi_2)(x) &= \int_\Omega \Gamma_2(x, y, \tau)f_2(y, \phi_1(-\tau, y), \phi_2(-\tau, y))dy, \end{aligned} \tag{9.6}$$

for all $\phi = (\phi_1, \phi_2) \in C_\tau^+$, $x \in \overline{\Omega}$. Then equation (9.5) can be written as an abstract functional differential equation

$$\begin{aligned} \frac{du}{dt} &= Au + F(u_t), \quad t > 0, \\ u_0 &= \phi \in C_\tau^+. \end{aligned} \tag{9.7}$$

Since $T_2(t) : Y \to Y$ is positive, it is easy to verify that

$$\lim_{h \to 0^+} \frac{1}{h} \operatorname{dist}(\phi(0) + hF(\phi), X^+) = 0, \quad \forall \phi \in C_\tau^+.$$

By [243, Proposition 3 and Remark 2.4], it then follows that for every $\phi \in C_\tau^+$, (9.5) admits a unique noncontinuable mild solution $u(t, \phi)$ satisfying $u_0 = \phi$ and $u(t, \phi) \in X^+$ for any t in its maximal interval of existence $[0, \sigma_\phi)$. We further have the following result.

Theorem 9.1.1. *Let (H1)–(H5) hold. Then for each $\phi \in C_\tau^+$, a unique solution $u(t, \phi)$ of (9.5) globally exists on $[0, \infty)$, and the solution semiflow $\Phi(t) = u_t(\cdot) : C_\tau^+ \to C_\tau^+$, $t \geq 0$, has a strong global attractor.*

Proof. For the scalar parabolic equation

$$\begin{aligned} \frac{\partial u_1(t, x)}{\partial t} &= d_1\Delta u_1(t, x) + u_1(x, t)g(x, u_1(x, t)), \ x \in \Omega, \, t > 0, \\ B_1u_1 &= 0, \, x \in \partial\Omega, \, t > 0, \end{aligned} \tag{9.8}$$

by conditions (H4) and (H5) and Theorem 3.1.5 (see also [124, Corollary 2.2]), either the trivial solution or the unique positive steady state in Y^+ is a global attractor for solutions that are not identically zero. The prey equation in (9.5) is dominated by equation (9.8), and so the standard parabolic comparison theorem implies that $u_1(t,\phi)$ is bounded on $[0,\sigma_\phi)$. Thus (H2) and (H3) imply that the predator equation is dominated by a scalar linear reaction–diffusion equation with delay. By the global existence of solutions of this linear equation (see, e.g., [408, Theorem 2.1.1]), it follows that $\sigma_\phi = \infty$ for each $\phi \in C_\tau^+$. Then there is a $B_1 > 0$ such that for any $\phi \in C_\tau^+$, there exists a $t_1(\phi) > 0$ with $u_1(t,\phi)(x) \le B_1$, $\forall x \in \overline{\Omega}, t \ge t_1$. Given $\phi \in C_\tau^+$, let

$$(u_1(t,x),u_2(t,x)) = (u_1(t,\phi)(x),u_2(t,\phi)(x)),\ \bar{u}_i(t) = \int_\Omega u_i(t,x)dx,\ \forall i = 1,2.$$

Note that $\mu_0 := \min_{x\in\overline{\Omega}} \mu(x) > 0$. By (9.5) and Green's formula, it then follows that

$$\frac{d\bar{u}_1(t)}{dt} \le \int_\Omega u_1(t,x)g(x,u_1(t,x))dx - \int_\Omega f_1(x,u_1(t,x),u_2(t,x))dx,\ \forall t > 0;$$

that is,

$$\int_\Omega f_1(x,u_1(t,x),u_2(t,x))dx \le -\frac{d\bar{u}_1(t)}{dt} + \int_\Omega u_1(t,x)g(x,u_1(t,x))dx,\ \forall t > 0.$$

By (9.5) and (H3), there exist two positive numbers k_1 and k_2, both independent of ϕ, such that

$$\frac{d\bar{u}_2(t)}{dt} \le -\mu_0\bar{u}_2(t) - k_1\frac{d\bar{u}_1(t-\tau)}{dt} + k_2, \quad \forall t \ge t_1 + \tau;$$

that is,

$$\frac{d\left(e^{\mu_0 t}\bar{u}_2(t)\right)}{dt} \le -k_1\frac{d\bar{u}_1(t-\tau)}{dt}e^{\mu_0 t} + k_2 e^{\mu_0 t}, \quad \forall t \ge t_1 + \tau.$$

Integrating by parts the above inequality over $[t_1+\tau,t]$, we can find a positive number k_3, independent of ϕ, and a positive number $k_4 = k_4(\phi)$, dependent on ϕ, such that

$$\bar{u}_2(t) \le k_4(\phi)e^{-\mu_0 t} + k_3, \quad \forall t \ge t_1 + \tau.$$

Since $\Gamma_2(\cdot,\tau)$ and u_1 are bounded, the predator equation in (9.5) and the second part of the hypothesis (H3) provide the inequality

$$\frac{\partial u_2(t,x)}{\partial t} \le d_2\Delta u_2(t,x) - \mu(x)u_2(t,x) + c\bar{u}_2(t),$$

with some constant $c > 0$. By a standard parabolic comparison theorem, there exist a positive number B_2, independent of ϕ, and $t_2 = t_2(\phi) > t_1(\phi) + \tau$ such that $u_2(t,\phi)(x) \le B_2$, $\forall x \in \overline{\Omega}, t \ge t_2$. Therefore, the solution semiflow $\Phi(t) = u_t(\cdot) : C_\tau^+ \to C_\tau^+$ is point dissipative. By [408, Theorem 2.2.6], $\Phi(t) : C_\tau^+ \to C_\tau^+$ is compact for each $t > \tau$. Thus, the continuous-time version of Theorem 1.1.3 (see [141, Theorem 3.4.8]) implies that $\Phi(t)$ has a strong global attractor on C_τ^+. ∎

9.2 Global Coexistence

In this section we establish the uniform persistence of both predator and prey and the existence of a positive steady state in terms of principal eigenvalues.

For $m(\cdot) \in Y$ with $m(x) > 0, x \in \overline{\Omega}$, we let $\lambda_0(d_1, m)$ denote the principal eigenvalue of the elliptic eigenvalue problem (see, e.g., [326, Theorem 7.6.1])

$$\begin{aligned} \lambda w &= d_1 \Delta w + m(x) w, \quad x \in \Omega, \\ B_1 w &= 0, \quad x \in \partial\Omega, \end{aligned} \tag{9.9}$$

and by a similar argument as in [326, Theorem 7.6.1], it follows that the nonlocal elliptic eigenvalue problem

$$\begin{aligned} &\lambda w(x) = d_2 \Delta w - \mu(x) w(x) + \int_\Omega \Gamma_2(x, y, \tau) m(y) w(y) dy, \quad x \in \Omega, \\ &B_2 w = 0, \quad x \in \partial\Omega, \end{aligned} \tag{9.10}$$

also has a principal eigenvalue, which is denoted by $\lambda_0(d_2, \tau, m)$. Moreover, for the nonlocal eigenvalue problem

$$\begin{aligned} &\lambda w(x) = d_2 \Delta w - \mu(x) w(x) + \int_\Omega \Gamma_2(x, y, \tau) m(y) w(y) dy \cdot e^{-\lambda\tau}, \quad x \in \Omega, \\ &B_2 w = 0, \quad x \in \partial\Omega, \end{aligned} \tag{9.11}$$

we have the following result.

Theorem 9.2.1. *There exists a principal eigenvalue $\bar{\lambda}_0(d_2, \tau, m)$ of (9.11) associated with a strictly positive eigenvector, and for any $\tau \geq 0$, $\bar{\lambda}_0(d_2, \tau, m)$ has the same sign as $\lambda_0(d_2, \tau, m)$.*

Proof. Let $E = C([-\tau, 0], Y)$ and let $B = A_2$. Define $L : E \to Y$ by

$$L\phi(x) = \int_\Omega \Gamma_2(x, y, \tau) m(y) \phi(-\tau, y) dy, \quad x \in \Omega, \ \phi \in E.$$

Clearly, Y is a Banach lattice and L is positive; i.e., $L(E^+) \subset Y^+$. For each $\lambda \in \mathbb{R}$, we define $L_\lambda : Y \to Y$ by

$$L_\lambda(\varphi) = L(e^{\lambda \cdot} \varphi), \quad \varphi \in Y,$$

where $e^{\lambda \cdot} \varphi \in E$ is defined by

$$(e^{\lambda \cdot} \varphi)(\theta, x) = e^{\lambda\theta} \varphi(x), \quad \theta \in [-\tau, 0], \ x \in \overline{\Omega}.$$

Let $U(t) : E \to E$, $t \geq 0$, be the solution semiflow associated with the abstract delay equation

$$\begin{aligned} \frac{dv(t)}{dt} &= Bv(t) + Lv_t, \quad t \geq 0, \\ v_0 &= \phi \in E, \end{aligned} \tag{9.12}$$

and let $A_U : D(A_U) \to E$ be its generator (see, e.g., [408]). Then $U(t) : E \to E$ is positive (see, e.g., [200, Section 4]). Let

$$s(A_U) := \sup\{\mathrm{Re}(\lambda) : \lambda \in \sigma(A_U)\}$$

be the spectral bound of A_U. Then $s(A_U)$ is a spectral value of A_U and has the same sign as the spectral bound $s(B + L_0)$ (see [200, Section 4]). By the definition of L_0, it follows that $s(B + L_0) = \lambda_0(d_2, \tau, m)$. It suffices to prove that $s(A_U)$ is a point spectral value of A_U and that $s(A_U)$ has a strongly positive eigenvector $\psi \in \mathrm{int}(E^+)$. To this end, we will show that the operators $U(t)$ are eventually strongly positive, and then apply the Krein–Rutman theorem.

For any $\phi \in E^+ \setminus \{\hat{0}\}$, let $v(t, x) = v(t, \phi)(x),\ x \in \Omega,\ t \geq 0$, be the solution of (9.12); i.e., $v_t(\phi) = U(t)\phi$. We claim that $v(t, x) > 0$ for all $x \in \overline{\Omega}$ and $t > \tau$. Indeed, if $\phi(0, \cdot) \not\equiv 0$, the positivity of L and the parabolic maximum principle imply that $v(t, x) > 0$ for all $x \in \overline{\Omega}$ and $t > 0$. So we can assume that $\tau > 0$ and that there is a $\theta_0 \in (0, \tau)$ such that $\phi(-\theta_0, \cdot) \not\equiv 0$. We first show that $v(\tau - \theta_0, \cdot) \not\equiv 0$, by contradiction. Let us assume that $v(\tau - \theta_0, \cdot) \equiv 0$. Then (9.12) with $t = \tau - \theta_0 > 0$ implies that

$$\frac{\partial v(\tau - \theta_0, x)}{\partial t} = T_2(\tau)(m(\cdot)\phi(-\theta_0, \cdot))(x) > 0,\ x \in \Omega.$$

Here we have used the strong positivity of $T_2(t)$ for $t > 0$ (i.e., the parabolic maximum principle). On the other hand, since $v(t, x) \geq 0, t \geq 0, x \in \Omega$, and $v(\tau - \theta_0, x) = 0, x \in \Omega$, we have $\frac{\partial v(\tau-\theta_0,x)}{\partial t} \leq 0$, which is a contradiction. Once we know that $v(\tau - \theta_0) \not\equiv 0$, again by the positivity of L and the parabolic maximum principle, we have $v(t, x) > 0$ for all $x \in \overline{\Omega}$ and $t > \tau - \theta_0$.

Therefore, $U(t) : E \to E$ is strongly positive for each $t > 2\tau$. Moreover, as in the nonlinear case, $U(t) : E \to E$ is compact for each $t > \tau$. Now fix some $t > 2\tau$. By the Krein–Rutman theorem (see, e.g., [326, Theorem 2.4.1]), the spectral radius $r = r(U(t))$ is a positive eigenvalue of $U(t)$, and hence by the point spectral mapping theorem ([272, Theorem 2.2.4]) there is a point spectral value $\bar{\lambda}$ of A_U such that $r = e^{t\bar{\lambda}}$. Clearly, $\bar{\lambda} \in \mathbb{R}$ and $\bar{\lambda} \leq s(A_U)$. Moreover, by the fact that $s(A_U) \in \sigma(A_U)$ and the spectral mapping theorem ([272, Theorem 2.2.3]), $e^{ts(A_U)} \in \sigma(U(t))$. Then $e^{ts(A_U)} \leq r = e^{t\bar{\lambda}}$, and hence $s(A_U) \leq \bar{\lambda}$. Thus, $s(A_U) = \bar{\lambda}$ is a point spectral value of A_U. Let $\psi \in E \setminus \{\hat{0}\}$ be an eigenvector associated with $s(A_U)$. Then $U(t)\psi = e^{ts(A_U)}\psi = r\psi$, and hence again by the Krein–Rutman theorem, $\psi \in \mathrm{int}(E^+)$. Consequently, $s(A_U)$ is the principal eigenvalue of A_U. ∎

Now we are in a position to prove the main result of this section.

Theorem 9.2.2. *Let (H1)–(H5) hold. Assume that*

(A1) $\lambda_0(d_1, g(\cdot, 0)) > 0$ *and* $\lambda_0\big(d_2, \tau, \partial_2 f_2\big(\cdot, u_1^*(\cdot), 0\big)\big) > 0$, *where* $u_1^*(\cdot)$ *is the unique positive steady state of the scalar equation* $\frac{\partial u_1}{\partial t} = d_1 \Delta u_1 + u_1 g(x, u_1)$ *with* $B_1 u_1 = 0$.

Then system (9.5) admits at least one positive steady state and is uniformly persistent. More precisely, there exists $\beta_0 > 0$ such that for any $\phi = (\phi_1, \phi_2) \in C_\tau^+$ with $\phi_1(0, \cdot) \not\equiv 0$ and $\phi_2(0, \cdot) \not\equiv 0$, there exists $t_0 = t_0(\phi) > 0$ such that the solution $u(t, \phi)(x) = (u_1(t, x), u_2(t, x))$ of (9.5) satisfies

$$u_i(t, x) \geq \beta_0, \quad \forall t \geq t_0,\, x \in \overline{\Omega},\, i = 1, 2.$$

Proof. Note that the existence and uniqueness of $u_1^*(\cdot)$ follow from Theorem 3.1.5 (see also [124, Corollary 2.2]) and the first part of assumption (A1). Let

$$Z_0 := \{(\phi_1, \phi_2) \in C_\tau^+ : \phi_i(0, \cdot) \not\equiv 0, \forall i = 1, 2\}, \qquad \partial Z_0 := C_\tau^+ \setminus Z_0.$$

By the standard comparison theorem, as applied to two scalar equations in (9.5), it suffices to prove that the uniform persistence holds for any $\phi \in Z_0$. Clearly, $\Phi(t)Z_0 \subset Z_0$, $\forall t \geq 0$. Let $Z_1 := \{\phi \in \partial Z_0 : \Phi(t)\phi \in \partial Z_0, t \geq 0\}$. Let $M_1 = (\hat{0}, \hat{0})$ and $M_2 = (\hat{u}_1^*, \hat{0})$. It then easily follows that $\cup_{\phi \in Z_1} \omega(\phi) = \{M_1, M_2\}$. Moreover, for any $\phi \in Z_0$, $\Phi(t)\phi \in \mathrm{int}(C_\tau^+)$, $\forall t > 2\tau$ (see, e.g., the proof of Theorem 9.2.1). By Theorem 9.2.1 and the second part of assumption (A1), $\bar{\lambda}_0(d_2, \tau, \partial_2 f_2(\cdot, u_1^*(\cdot), 0)) > 0$. By the existence of strongly positive eigenvectors associated with the principal eigenvalues $\lambda_0(d_1, g(\cdot, 0)) > 0$ and $\bar{\lambda}_0(d_2, \tau, \partial_2 f_2(\cdot, u_1^*(\cdot), 0)) > 0$, and a similar argument by contradiction as in the proof of [298, Lemma 3.1] (see also Proposition 7.1.1), we can further prove that there exists $\delta > 0$ such that

$$\limsup_{t \to \infty} \|\Phi(t)\phi - M_i\| \geq \delta, \qquad \forall \phi \in Z_0,\, i = 1, 2.$$

Thus, $M_1 \cup M_2$ is an acyclic isolated covering of $\cup_{\phi \in Z_1} \omega(\phi)$, and each M_i is a weak repeller for Z_0. By Theorem 9.1.1 and Theorem 1.3.1 with Remarks 1.3.1 and 1.3.2 (see also [365, Theorem 4.6]), $\Phi(t)$ is uniformly persistent with respect to $(Z_0, \partial Z_0)$ in the sense that there exists $\eta > 0$ such that

$$\liminf_{t \to \infty} \ \mathrm{dist}\ (\Phi(t)\phi, \partial Z_0) \geq \eta, \qquad \forall \phi \in Z_0.$$

As mentioned above, $\Phi(t) : C_\tau^+ \to C_\tau^+$ is compact for $t > \tau$. By the continuous-time version of Theorem 1.3.6, $\Phi(t) : Z_0 \to Z_0$ has a global attractor A_0. Then $A_0 = \Phi(t)A_0 \subset \mathrm{int}(C_\tau^+)$, $\forall t > 2\tau$. In view of the compactness of A_0, there exists $\beta_0 > 0$ such that $A_0 \gg \beta_0 e$ with $e = \hat{1} \in \mathrm{int}(C_\tau^+)$. Thus, the global attractivity of A_0 in Z_0 implies the desired order persistence. To prove the existence of a positive steady state of (9.5), we let $\Phi_0(t) : C^+(\overline{\Omega}, \mathbb{R}^2) \to C^+(\overline{\Omega}, \mathbb{R}^2)$, $t \geq 0$, be the solution semiflow of the nonlocal reaction–diffusion system

$$
\begin{aligned}
\frac{\partial u_1(t,x)}{\partial t} &= d_1 \Delta u_1(t,x) + u_1(t,x) g(x, u_1(t,x)) \\
&\quad - f_1(x, u_1(t,x), u_2(t,x)), \quad x \in \Omega,\ t > 0, \\
\frac{\partial u_2(t,x)}{\partial t} &= d_2 \Delta u_2(t,x) - \mu(x) u_2(t,x) \\
&\quad + \int_\Omega \Gamma_2(x,y,\tau) f_2(y, u_1(t,y), u_2(t,y)) dy, \quad x \in \Omega,\ t > 0, \\
B_i u_i &= 0, \quad x \in \partial\Omega,\ t > 0,\ i = 1, 2.
\end{aligned}
\tag{9.13}
$$

As proven for $\Phi(t) : C_\tau^+ \to C_\tau^+$, it follows that $\Phi_0(t) : C^+(\overline{\Omega}, \mathbb{R}^2) \to C^+(\overline{\Omega}, \mathbb{R}^2)$ is point dissipative, compact for each $t > 0$, and uniformly persistent with respect to $(W_0, \partial W_0)$, where $W_0 := \{(\phi_1, \phi_2) \in C^+(\overline{\Omega}, \mathbb{R}^2) : \phi_i(\cdot) \not\equiv 0, \forall i = 1, 2\}$ and $\partial W_0 := C^+(\overline{\Omega}, \mathbb{R}^2) \setminus W_0$. Then, by Theorem 1.3.11, $\Phi_0(t)$ has an equilibrium $\phi^* \in W_0$; i.e., $\Phi_0(t)\phi^* = \phi^*$, $\forall t \geq 0$. Clearly, $\phi^*(x)$ is a positive steady state of system (9.5). ∎

9.3 Global Extinction

In this section we discuss the global extinction of the predator species and the global extinction of both prey and predator species.

Theorem 9.3.1. *Let (H1)–(H5) hold. Assume that the principal eigenvalues of (9.9) and (9.10) satisfy*

(A2) $\lambda_0(d_1, g(\cdot, 0)) > 0$ *and* $\lambda_0(d_2, \tau, \partial_2 f_2(\cdot, u_1^*(\cdot), 0)) < 0$, *where* $u_1^*(\cdot)$ *is the unique positive steady state of the scalar equation* $\frac{\partial u_1}{\partial t} = d_1 \Delta u_1 + u_1 g(x, u_1)$ *with* $B_1 u_1 = 0$.

Then for any $\phi = (\phi_1, \phi_2) \in C_\tau^+$ *with* $\phi_1(0, \cdot) \not\equiv 0$, *the solution* $u(t, \phi)$ *of system (9.5) satisfies*

$$
\lim_{t \to \infty} u(t, \phi)(x) = (u_1^*(x), 0)
$$

uniformly for $x \in \overline{\Omega}$.

Proof. For any $\phi \in C_\tau^+$, $u(t, \phi)(x) = (u_1(t,x), u_2(t,x))$ satisfies $u_i(x,t) \geq 0$, $\forall t \geq 0$, $x \in \overline{\Omega}$, $i = 1, 2$. Since

$$
\lim_{\varepsilon \to 0} \lambda_0(d_2, \tau, \partial_2 f_2(\cdot, u_1^*(\cdot) + \varepsilon), 0)) = \lambda_0(d_2, \tau, \partial_2 f_2(\cdot, u_1^*(\cdot), 0)) < 0,
$$

we can choose some $\varepsilon_0 > 0$ such that $\lambda_0(d_2, \tau, \partial_2 f_2(\cdot, u_1^*(\cdot) + \varepsilon, 0)) < 0$. Moreover, $u_1(x,t)$ satisfies

$$
\frac{\partial u_1}{\partial t} \leq d_1 \Delta u_1 + u_1 g(x, u),\ \forall x \in \Omega,\ t > 0.
$$

The assumption $\lambda_0(d_1, g(\cdot, 0)) > 0$ and Theorem 3.1.5 (see also [124, Corollary 2.2]) guarantee the existence of a unique positive steady state $u_1^*(\cdot)$ of the prey equation without predators, which attracts all solutions that are not identically equal to zero. A standard comparison theorem provides $t_0 = t_0(\phi) > 0$ such that

$$u_1(x,t) \le u_1^*(x) + \varepsilon_0, \quad \forall x \in \overline{\Omega} \text{ and } t \ge t_0.$$

By (H2) and (H3), it follows that $v(x,t) = u_2(x, t + t_0 + \tau),\ t \ge 0$, satisfies

$$\begin{aligned} \frac{\partial v(t,x)}{\partial t} &\le d_2 \Delta v(t,x) - \mu(x) v(t,x) \\ &\quad + \int_\Omega \Gamma_2(x,y,\tau) \partial_2 f_2(y, u_1^*(y) + \varepsilon_0, 0) v(t-\tau, y) dy,\ x \in \Omega,\ t > 0, \\ B_2 v &= 0,\ x \in \partial\Omega,\ t > 0. \end{aligned} \tag{9.14}$$

By the second part of assumption (A2) and by Theorem 9.2.1,

$$\bar{\lambda}_0(d_2, \tau, \partial_2 f_2(\cdot, u_1^*(\cdot) + \varepsilon_0, 0)) < 0.$$

The standard comparison theorem and [408, Theorem 3.1.7] imply that $\lim_{t\to\infty} v(t,\cdot) = 0$, and hence $\lim_{t\to\infty} u_2(x,t) = 0$ uniformly for $x \in \overline{\Omega}$.

For any $\phi^0 = (\phi_1^0, \phi_2^0) \in C_\tau^+$ with $\phi_1^0(0,\cdot) \not\equiv 0$, let

$$u(t, \phi^0)(x) = (u_1(t,x), u_2(t,x)),\ \forall x \in \Omega,\ t \ge 0.$$

Then we can regard $u_2(t,x)$ as a fixed function on $\mathbb{R}^+ \times \overline{\Omega}$. Therefore, $u_1(x,t)$ satisfies the nonautonomous reaction–diffusion equation

$$\begin{aligned} \frac{\partial u_1}{\partial t} &= d_1 \Delta u_1 + u_1 g(x, u_1) \\ &\qquad - f_1(x, u_1(t,s), u_2(t,x)), \quad x \in \Omega, \quad t > 0, \\ B_1 u_1 &= 0, \quad x \in \partial\Omega, \quad t > 0. \end{aligned} \tag{9.15}$$

Since $\lim_{t\to\infty} u_2(x,t) = 0$ uniformly for $x \in \overline{\Omega}$, it follows that (9.15) is asymptotic to an autonomous reaction–diffusion equation

$$\begin{aligned} \frac{\partial u_1}{\partial t} &= d_1 \Delta u_1 + u_1 g(x, u_1), \quad x \in \Omega, \quad t > 0, \\ B_1 u_1 &= 0, \quad x \in \partial\Omega, \quad t > 0. \end{aligned} \tag{9.16}$$

Since $\lambda_0(d_1, g(\cdot, 0)) > 0$, Theorem 3.1.5 (see also [124, Corollary 2.2]) implies that $u_1 = u_1^*(\cdot)$ is globally asymptotically stable in $C^+(\overline{\Omega}, \mathbb{R}) \setminus \{0\}$. Moreover, Proposition 3.2.3 (see also [298, Lemma 3.1] with $m = 1$) implies that $u_1(t,\cdot)$ cannot converge to 0 as $t \to \infty$. By Theorem 1.2.1 with Remark 1.3.2 (see also [364, Theorem 4.1]), we have $\lim_{t\to\infty} u_1(t,\cdot) = u_1^*(\cdot)$, and hence $\lim_{t\to\infty} u_1(t,x) = u_1^*(x)$ uniformly for $x \in \overline{\Omega}$. ∎

Theorem 9.3.2. *Let (H1)–(H5) hold. Assume that* $\lambda_0(d_1, g(\cdot,0)) \le 0$. *Then for any* $\phi = (\phi_1, \phi_2) \in C_\tau^+$, *the solution* $u(t,\phi)$ *of system (9.5) satisfies* $\lim_{t\to\infty} u(t,\phi)(x) = (0,0)$ *uniformly for* $x \in \overline{\Omega}$.

Proof. For any $\phi \in C_\tau^+$, let $u(t,\phi)(x) = (u_1(x,t), u_2(x,t))$, $\forall x \in \Omega$, $t \ge 0$. Then $u_1(x,t)$ satisfies

$$\frac{\partial u_1}{\partial t} \le d_1 \Delta u_1 + u_1 g(x,u_1), \qquad x \in \Omega,\ t > 0.$$

Since $\lambda_0(d_1, g(\cdot,0)) \le 0$, by the standard comparison theorem and Theorem 3.1.5 (see also [124, Corollary 2.2]), we have $\lim\limits_{t\to\infty} u_1(x,t) = 0$ uniformly for $x \in \overline{\Omega}$. We regard $u_2(x,t)$ as a solution of the nonautonomous reaction–diffusion equation

$$\begin{aligned} \frac{\partial u_2}{\partial t} &= d_2 \Delta u_2 - \mu(x) u_2 + \\ &\qquad \int_\Omega \Gamma_2(x,y,\tau) f_2(y, u_1(t-\tau,y), u_2(t-\tau,y))dy,\ x \in \Omega,\ t > 0, \\ B_2 u_2 &= 0,\ x \in \partial\Omega, t > 0. \end{aligned} \tag{9.17}$$

Since $u_2(t,x)$ is bounded and $\lim\limits_{t\to\infty} u_1(x,t) = 0$ uniformly for $x \in \overline{\Omega}$, it follows that (9.17) is asymptotic to a linear autonomous reaction–diffusion equation

$$\begin{aligned} &\frac{\partial u_2}{\partial t} = d_2 \Delta u_2 - \mu(x) u_2,\ x \in \Omega,\ t > 0, \\ &B_i u_i = 0,\ x \in \partial\Omega,\ t > 0. \end{aligned} \tag{9.18}$$

Clearly, $u_2^* = 0$ is globally asymptotically stable for (9.18) in $C^+(\overline{\Omega}, \mathbb{R})$. By Theorem 1.2.1 with Remark 1.3.2 (see also [364, Theorem 4.1]), we have $\lim\limits_{t\to\infty} u_2(x,t) = 0$ uniformly for $x \in \overline{\Omega}$. ∎

9.4 Global Attractivity: A Fluctuation Method

In this section, as illustrations of the results in Sections 9.2 and 9.3 and a fluctuation method, we discuss the global attractivity of steady states for spatially homogeneous delayed predator–prey reaction–diffusion systems.

Consider the predator–prey reaction–diffusion system with delay

$$\begin{aligned} \frac{\partial u_1(t,x)}{\partial t} &= d_1 \Delta u_1(t,x) + u_1(t,x)(c_0 - c_1 u_1(t,x)) \\ &\qquad - a_0 u_1(t,x) u_2(t,x), \quad x \in \Omega,\ t > 0, \\ \frac{\partial u_2(t,x)}{\partial t} &= d_2 \Delta u_2(t,x) - \mu u_2(t,x) + \\ &\qquad \int_\Omega \Gamma_2(x,y,\tau) \frac{u_1(t-\tau,y) u_2(t-\tau,y)}{b_0 + b_2 u_2(t-\tau,y)} dy, \quad x \in \Omega,\ t > 0, \\ &\frac{\partial u_i}{\partial \nu} = 0, \quad x \in \partial\Omega,\ t > 0,\ i = 1,2, \end{aligned} \tag{9.19}$$

where a_0, μ, b_0, b_2, and c_1 are positive numbers, $c_0 \in \mathbb{R}$, $\Gamma_2(x,y,t)$ is the Green's function associated with $d_2\Delta - \mu I$ and $\frac{\partial u_2}{\partial \nu} = 0$. The prey grows logistically in absence of the predator, and the encounters between prey and predators obey the law of mass action, while the term $b_2 u(t-\tau, y)$ reflects competition of predators for eating the prey once it has been killed.

Theorem 9.4.1. *For any $\phi = (\phi_1, \phi_2) \in C_\tau^+$, let $u(t,\phi) = (u_1(t,\phi), u_2(t,\phi))$ be the unique solution of system (9.19) with $u_0 = \phi$.*

(i) If $c_0 > 0$ and $\frac{c_0}{c_1 b_0} > \mu e^{\mu\tau} > \frac{a_0}{c_1 b_2}$, then system (9.19) has a unique positive constant steady state $(\bar{u}_1, \bar{u}_2)$, and for any $\phi = (\phi_1, \phi_2) \in C_\tau^+$ with $\phi_1(0,\cdot) \not\equiv 0$ and $\phi_2(0,\cdot) \not\equiv 0$, $\lim_{t\to\infty} u(t,\phi)(x) = (\bar{u}_1, \bar{u}_2)$ uniformly for $x \in \overline{\Omega}$.

(ii) If $c_0 > 0$ and $\frac{c_0}{c_1 b_0} < \mu e^{\mu\tau}$, then for any $\phi = (\phi_1, \phi_2) \in C_\tau^+$ with $\phi_1(0,\cdot) \not\equiv 0$, $\lim_{t\to\infty} u(t,\phi)(x) = (\frac{c_0}{c_1}, 0)$ uniformly for $x \in \overline{\Omega}$.

(iii) If $c_0 \le 0$, then for any $\phi = (\phi_1, \phi_2) \in C_\tau^+$, $\lim_{t\to\infty} u(t,\phi)(x) = (0,0)$ uniformly for $x \in \overline{\Omega}$.

Proof. Let $f_1(u_1, u_2) := a_0 u_1 u_2$, $f_2(u_1,u_2) := \frac{u_1 u_2}{b_0 + b_2 u_2}$, and $g := c_0 - c_1 u$. Clearly, (H1)–(H5) are satisfied, and if $c_0 > 0$, then $u_1^*(\cdot) \equiv \frac{c_0}{c_1}$. Note that $\int_\Omega \Gamma_2(s,x,y)dy = e^{-\mu s}$, $\forall s > 0, x \in \Omega$. By choosing the eigenvector as 1, we have that $\lambda_0(d_1, g(0)) = c_0$ and $\lambda_0(d_2, \tau, \partial_2 f_2(u_1^*, 0)) = -\mu + \frac{e^{-\mu\tau} c_0}{b_0 c_1}$ in the case where $c_0 > 0$. Thus, conclusions (ii) and (iii) follow from Theorems 9.3.1 and 9.3.2, respectively. In the case where $c_0 > 0$ and $\frac{c_0}{c_1 b_0} > \mu e^{\mu\tau}$, Theorem 9.2.2 implies that system (9.19) is uniformly persistent. We further claim that system (9.19) admits at most one positive constant steady state. Indeed, assume that (u_1, u_2) with $u_i > 0$, $i = 1, 2$, is a constant solution of (9.19). It then easily follows that (u_1, u_2) satisfies the algebraic equations

$$\begin{aligned} a_0 u_2 &= g(u_1), \\ u_1 &= e^{\mu\tau}\mu(b_0 + b_2 g(u_1)/a_0). \end{aligned} \tag{9.20}$$

Clearly, the monotonicity of $g(\cdot)$ implies that the second equation of (9.20) has at most one positive solution for u_1, and hence (9.20) has at most one positive solution for (u_1, u_2). In order to prove (i), it then suffices to prove that for every $\phi = (\phi_1, \phi_2) \in C_\tau^+$ with $\phi_1(0,\cdot) \not\equiv 0$ and $\phi_2(0,\cdot) \not\equiv 0$, $u(t,\phi)(x)$ converges to a positive constant steady state in $C(\overline{\Omega}, \mathbb{R}^2)$ as $t \to \infty$. Since $(u_1(t,\cdot), u_2(t,\cdot)) := u(t,\phi), t \ge 0$, is bounded (see Theorem 9.1.1), we can choose a constant $c > 0$ such that the function $cu_1 + u_1 g(u_1) - f_1(u_1, u_2)$ is monotone increasing in u_1 for all values taken by the solution. Using the Green's function Γ_1 associated with $d_1\Delta$ and the Neumann boundary condition, we have

$$\begin{aligned} u_1(t,x) = e^{-ct}\int_\Omega &\Gamma_1(t,x,y)u_1(0,y)dy + \\ &\int_0^t e^{-cs}\int_\Omega \Gamma_1(s,x,y)\Big[cu_1(t-s,y) + u_1(t-s,y)g(u_1(t-s,y)) \\ &\qquad - f_1(u_1(t-s,y), u_2(t-s,y))\Big]dy\,ds. \end{aligned}$$

Let

$$u_i^\infty(x) := \limsup_{t\to\infty} u_i(t,x), \quad u_{i\infty}(x) := \liminf_{t\to\infty} u_i(t,x), \ \forall i=1,2.$$

By the uniform persistence of (9.19), there exists $\delta > 0$ such that

$$u_i^\infty(x) \geq u_{i\infty}(x) \geq \delta, \ \forall x \in \overline{\Omega}, \ i=1,2.$$

By Fatou's lemma, we then get

$$u_1^\infty(x) \leq \int_0^\infty e^{-cs} \int_\Omega \Gamma_1(s,x,y) \Big[c u_1^\infty(y) + u_1^\infty(y) g(u_1^\infty(y)) \\ - f_1(u_1^\infty(y), u_{2\infty}(y)) \Big] dy\, ds.$$

Let

$$\alpha_i^\infty := \sup_{x\in\overline{\Omega}} u_i^\infty(x), \quad \alpha_{i\infty} := \inf_{x\in\overline{\Omega}} u_{i\infty}(x), \quad \forall i=1,2.$$

Clearly, $\alpha_i^\infty \geq \alpha_{i\infty} \geq \delta$, $\forall i=1,2$. Since

$$\int_\Omega \Gamma_1(s,x,y)dy = 1, \quad \forall s>0, x\in\Omega,$$

we have

$$\alpha_1^\infty \leq \frac{1}{c}\left[c\alpha_1^\infty + \alpha_1^\infty g(\alpha_1^\infty) - f_1(\alpha_1^\infty, \alpha_{2\infty})\right].$$

Simplifying this inequality, we obtain

$$0 \leq g(\alpha_1^\infty) - a_0 \alpha_{2\infty}. \tag{9.21}$$

Similarly, we can get

$$0 \geq g(\alpha_{1\infty}) - a_0 \alpha_2^\infty. \tag{9.22}$$

Using the Green's function Γ_2 associated with $d_2\Delta - \mu$, we have

$$u_2(t,x) = \int_\Omega \Gamma_2(t,x,y) u_2(0,y) dy + \\ \int_0^t \int_\Omega \Gamma_2(s+\tau,x,y) f_2(u_1(t-s-\tau,y), u_2(t-s-\tau,y)) dy\, ds.$$

Arguing as before and using that

$$\int_\Omega \Gamma_2(s,x,y)dy = e^{-\mu s}, \quad \forall s>0, x\in\Omega,$$

we have

$$1 \leq \frac{e^{-\mu\tau}}{\mu} \frac{\alpha_1^\infty}{b_0 + b_2\alpha_2^\infty}.$$

After reorganization of the terms, we have

$$b_2\alpha_2^\infty \leq \frac{e^{-\mu\tau}}{\mu}\alpha_1^\infty - b_0. \tag{9.23}$$

Similarly, we can obtain

$$b_2\alpha_{2\infty} \geq \frac{e^{-\mu\tau}}{\mu}\alpha_{1\infty} - b_0. \tag{9.24}$$

Combining (9.21)–(9.24), we get

$$\begin{aligned} 0 &\leq g(\alpha_1^\infty) - \frac{a_0}{b_2}\left(\frac{e^{-\mu\tau}}{\mu}\alpha_{1\infty} - b_0\right), \\ 0 &\geq g(\alpha_{1\infty}) - \frac{a_0}{b_2}\left(\frac{e^{-\mu\tau}}{\mu}\alpha_1^\infty - b_0\right). \end{aligned} \tag{9.25}$$

Subtracting the first inequality from the second yields

$$g(\alpha_{1\infty}) - g(\alpha_1^\infty) \leq \frac{a_0}{b_2}\frac{e^{-\mu\tau}}{\mu}(\alpha_1^\infty - \alpha_{1\infty}).$$

Since $g(u) = c_0 - c_1 u$ and $c_1 > \frac{a_0}{b_2}\frac{e^{-\mu\tau}}{\mu}$, we have $\alpha_1^\infty = \alpha_{1\infty}$ and, by (9.23)–(9.24), also $\alpha_2^\infty = \alpha_{2\infty}$. It follows that

$$\lim_{t\to\infty} u(t,\phi)(x) = (\alpha_1^\infty, \alpha_2^\infty), \qquad \forall x \in \overline{\Omega}. \tag{9.26}$$

Let $\omega(\phi)$ be the omega limit set of ϕ for the solution semiflow $\Phi(t)$ associated with (9.19). For every $\psi \in \omega(\phi)$, there exists a sequence $t_n \to \infty$ such that $\Phi(t_n)\phi \to \psi$ in C_τ as $n \to \infty$. Then

$$\lim_{n\to\infty} u(t_n,\phi)(x) = \psi(x)$$

uniformly for $x \in \overline{\Omega}$, and by (9.26), $\psi(\cdot) = (\alpha_1^\infty, \alpha_2^\infty)$. Then $\omega(\phi) = \{(\alpha_1^\infty, \alpha_2^\infty)\}$, which implies that $u(t,\phi)(x)$ converges to $(\alpha_1^\infty, \alpha_2^\infty)$ in $C(\overline{\Omega}, \mathbb{R}^2)$ as $t \to \infty$. Since $\Phi(t)(\omega(\phi)) = \omega(\phi)$, $\forall t \geq 0$, $(\alpha_1^\infty, \alpha_2^\infty)$ is a positive constant steady state of (9.19). ∎

9.5 Threshold Dynamics: A Single Species Model

In this section we illustrate how the exponential ordering and the theory of monotone dynamical systems can be applied to nonlocal and delayed reaction–diffusion models in population dynamics.

Consider the growth of a single species with immature and mature stage structure. For simplicity, we assume that $r \geq 0$ is the average maturation time for the species, and that both mature and immature populations have the same random diffusive rate $d > 0$ and the per capita mortality rate $k(x) > 0$ at location x. By replacing the biomass gain rate function $f(x, u, v)$ in the predator equation (9.4) with the birth rate function $g(x, v)$ of the mature population, we then get a nonlocal and diffusive model of the mature population growth in a habitat Ω:

$$\begin{aligned}\frac{\partial v(t,x)}{\partial t} =& d\Delta v(t,x) - k(x)v(t,x) + \\ & \int_\Omega \Gamma(x,y,r)g(y, v(t-r,y))dy,\ x \in \Omega,\ t > 0, \\ Bv(t,x) =& 0, \qquad x \in \partial\Omega,\ t > 0, \\ v(t,x) =& \phi(t,x) \geq 0,\ x \in \Omega,\ t \in [-r, 0],\end{aligned} \tag{9.27}$$

where Ω is a bounded and open subset of $\mathbb{R}^N$ with $\partial\Omega \in C^{2+\theta}$ for a real number $\theta > 0$, Δ denotes the Laplacian operator on $\mathbb{R}^N$, *either* $Bv = v$ *or* $Bv = \frac{\partial v}{\partial n} + \alpha v$ for some nonnegative function $\alpha \in C^{1+\theta}(\partial\Omega, \mathbb{R})$, $\frac{\partial}{\partial n}$ denotes the differentiation in the direction of the outward normal n to $\partial\Omega$, Γ is the Green's function associated with $A := d\Delta - k(\cdot)I$ and boundary condition $Bv = 0$, and ϕ is a given function to be specified later.

Let $p \in (N, \infty)$ be fixed. For each $\beta \in (1/2 + N/(2p), 1)$, let X_β be the fractional power space of $L^p(\Omega)$ with respect to $(-A, B)$ (see, e.g., [150]). Then X_β is an ordered Banach space with the cone X_β^+ consisting of all nonnegative functions in X_β, and X_β^+ has nonempty interior $\mathrm{int}(X_\beta^+)$. Moreover, $X_\beta \subset C^{1+\nu}(\overline{\Omega})$ with continuous inclusion for $\nu \in [0, 2\beta - 1 - N/p)$. We denote the norm in X_β by $\|\cdot\|_\beta$. It is well known that A generates an analytic semigroup $T(t)$ on $L^p(\Omega)$. Moreover, the standard parabolic maximum principle implies that the semigroup $T(t) : X_\beta \to X_\beta$ is strongly positive; that is, $T(t)(X_\beta^+) \setminus \{0\}) \subset \mathrm{int}(X_\beta^+)$, $\forall t > 0$. Let $C := C([-r, 0], X_\beta)$ and $C^+ := C([-r, 0], X_\beta^+)$. Then model (9.27) can be written as the following abstract functional differential equation

$$\begin{aligned}\frac{dv(t)}{dt} &= Av(t) + T(r)g(\cdot, v(t-r)),\ t > 0, \\ v_0 &= \phi \in C^+.\end{aligned} \tag{9.28}$$

We further assume that $k(\cdot)$ is a positive Hölder continuous function on $\overline{\Omega}$ and $g \in C^1(\overline{\Omega} \times \mathbb{R}^+, \mathbb{R}^+)$ satisfies the following condition:

(G) $g(\cdot, 0) \equiv 0$, $\partial_v g(x, 0) > 0, \forall x \in \Omega$, g is bounded on $\overline{\Omega} \times \mathbb{R}^+$, and for each $x \in \Omega$, $g(x, \cdot) : \mathbb{R}^+ \to \mathbb{R}^+$ is strictly subhomogeneous in the sense that $g(x, \alpha v) > \alpha g(x, v)$, $\forall \alpha \in (0, 1)$, $v > 0$.

Using a similar argument as in [326, Theorem 7.6.1], we can show that the nonlocal elliptic eigenvalue problem

$$\begin{aligned}&\lambda w(x) = d\Delta w - k(x)w(x) + \int_\Omega \Gamma(x,y,r)\partial_v g(y,0)w(y)dy,\ x \in \Omega,\\&Bw = 0,\ x \in \partial\Omega,\end{aligned} \tag{9.29}$$

has a principal eigenvalue, which is denoted by $\lambda_0(d, r, \partial_v g(\cdot, 0))$.

For $\phi \in C^+$, let $v(t,\phi)$ denote the solution of (9.27). Define

$$\begin{aligned}k_0 &:= \min\{k(x) : x \in \overline{\Omega}\},\\ b(r) &:= \sup\left\{\int_\Omega \Gamma(x,y,r)g(y,\varphi(y))dy : x \in \overline{\Omega},\ \varphi \in X_\beta^+\right\},\\ M(r) &:= \frac{b(r)}{k_0},\\ L(r) &:= \min\{\partial_v g(x,v) : x \in \overline{\Omega}, v \in [0, M(r)]\}.\end{aligned}$$

Then we have the following threshold dynamics for model system (9.27): If the zero solution of (9.27) is linearly stable, then the species goes to extinction; if it is linearly unstable, then the species is uniformly persistent.

Theorem 9.5.1. *Let $v^* \in \operatorname{int}(X_\beta)$ be fixed and let (G) hold.*

(1) If $\lambda_0(d, r, \partial_v g(\cdot, 0)) < 0$, then $\lim_{t\to\infty} \|v(t,\phi)\|_\beta = 0$ for every $\phi \in C^+$;
(2) If $\lambda_0(d, r, \partial_v g(\cdot, 0)) > 0$, then (9.27) admits at least one steady-state solution φ^* with $\varphi^*(x) > 0, \forall x \in \Omega$, and there exists $\delta > 0$ such that for every $\phi \in C^+$ with $\phi(0,\cdot) \not\equiv 0$, there is $t_0 = t_0(\phi) > 0$ such that $v(t,\phi) \geq \delta v^*(x)$, $\forall x \in \overline{\Omega}$, $t \geq t_0$.

Proof. Define $F : C^+ \to X_\beta$ by $F(\phi) = T(r)g(\cdot, \phi(-r)), \forall \phi \in C^+$. Then equation (9.27) can be written as the following abstract functional differential equation

$$\begin{aligned}\frac{dv(t)}{dt} &= Av(t) + F(v_t),\ t > 0,\\ v_0 &= \phi \in C^+.\end{aligned} \tag{9.30}$$

Since $T(t) : X_\beta \to X_\beta$ is strongly positive, we have

$$\lim_{h\to 0^+} \frac{1}{h} \operatorname{dist}(\phi(0) + hF(\phi), X_\beta^+) = 0, \quad \forall \phi \in C^+.$$

By [243, Proposition 3 and Remark 2.4] and using a similar argument in the case of a Dirichlet boundary condition (see also [243, Remark 1.10]), we conclude that for every $\phi \in C^+$, (9.27) admits a unique noncontinuable mild solution $v(t,\phi)$ satisfying $v_0 = \phi$ and $v(t,\phi) \in X_\beta^+$ for any t in its maximal interval of existence $[0, \sigma_\phi)$. Thus $v(t,\phi)(x)$ satisfies the following parabolic inequality

$$\begin{aligned}&\frac{\partial v(t,x)}{\partial t} \leq d\Delta v(t,x) - k_0 v(t,x) + b(r),\ x \in \Omega,\ t \in (0, \sigma_\phi),\\ &Bv(t,x) = 0,\ x \in \partial\Omega,\ t \in (0, \sigma_\phi).\end{aligned} \tag{9.31}$$

Let $u(t)$ be the unique solution of the ordinary differential equation

$$\frac{du(t)}{dt} = -k_0 u(t) + b(r)$$

satisfying $u(0) = \max_{x\in\overline{\Omega}} \phi(0)(x)$. Using the standard parabolic comparison theorem, we then get

$$v(t,\phi)(x) \le u(t) = \left(\max_{x\in\overline{\Omega}} \phi(0)(x) - M(r)\right) e^{-k_0 t} + M(r) \tag{9.32}$$

for all $x \in \Omega$ and $t \in (0, \sigma_\phi)$. Thus $\sigma_\phi = \infty$, $\forall \phi \in C^+$, and (9.27) defines a semiflow $\Phi(t) : C^+ \to C^+$ by $\Phi(t)\phi = v_t(\phi)$. By inequality (9.32) and the properties of the fractional power space X_β, it follows that $\Phi(t) : C^+ \to C^+$ is point dissipative. Moreover, $\Phi(t) : C^+ \to C^+$ is compact for each $t > r$ (see [408, Theorem 2.2.6]). By the continuous-time version of Theorem 1.1.3 (see [141, Theorem 3.4.8]), $\Phi(t)$ admits a strong global attractor on C^+.

It is easy to see that $g(x,v) \le \partial_v g(x,0)v$, $\forall x \in \overline{\Omega}, v \ge 0$. Then the comparison theorem for quasi-monotone abstract functional differential equations (see [243, 244]) implies that

$$v(t,\phi)(x) \le u(t,\phi)(x),\ \forall x \in \Omega,\ t \ge 0,$$

where $u(t,\phi)$ is the unique solution of the following linear, nonlocal, and delayed parabolic equation

$$\begin{aligned} \frac{\partial v(t,x)}{\partial t} &= d\Delta v(t,x) - k(x)v(t,x) + \int_\Omega \Gamma(x,y,r)\partial_v g(y,0)v(t-r,y)dy, \\ Bv(t,x) &= 0,\ x \in \partial\Omega,\ t > 0, \\ v(t,x) &= \phi(t,x),\ x \in \Omega,\ t \in [-r,0]. \end{aligned} \tag{9.33}$$

By Theorem 9.2.1 and a similar argument in the case of a Dirichlet boundary condition, it follows that the nonlocal elliptic eigenvalue problem

$$\begin{aligned} \lambda w(x) &= d\Delta w - k(x)w(x) + e^{-\lambda r}\int_\Omega \Gamma(x,y,r)\partial_v g(y,0)w(y)dy, \\ Bw &= 0,\ x \in \partial\Omega, \end{aligned} \tag{9.34}$$

has a principal eigenvalue $\bar\lambda_0(d,r,\partial_v g(\cdot,0))$, and $\bar\lambda_0(d,r,\partial_v g(\cdot,0))$ has the same sign as $\lambda_0(d,r,\partial_v g(\cdot,0))$. Then in the case where $\lambda_0(d,r,\partial_v g(\cdot,0)) < 0$, the properties of principal eigenvalues and linear semigroups imply that $\lim_{t\to\infty} \|u(t,\phi)\|_\beta = 0$, $\forall \phi \in C$, and hence $\lim_{t\to\infty} \|v(t,\phi)\|_\beta = 0$, $\forall \phi \in C^+$.

In the case where $\lambda_0(d,r,\partial_v g(\cdot,0)) > 0$, let

$$Z_0 = \{\phi \in C^+ :\ \phi(0,\cdot) \not\equiv 0\}, \quad \partial Z_0 := C^+ \setminus Z_0.$$

Since $g(x,v) \ge 0$, equation (9.27) implies that

$$\frac{\partial v(t,x)}{\partial t} \geq d\Delta v(t,x) - k(x)v(t,x), \qquad \forall x \in \Omega,\, t > 0.$$

By the standard parabolic maximum principle, it then follows that $\Phi(t)Z_0 \subset \mathrm{int}(C^+)$, $\forall t > 0$. Let

$$Z_1 = \{\phi \in \partial Z_0 : \Phi(t)\phi \in \partial Z_0, \forall t \geq 0\}.$$

Then $\cup_{\phi \in Z_1} \omega(\phi) = \{0\}$, where $\omega(\phi)$ denotes the omega limit set of the orbit $\gamma^+(\phi) := \{\Phi(t)\phi : \forall t \geq 0\}$. Clearly, $g(x,v)$ can be written as $g(x,v) = vh(x,v)$ with $h(x,0) = \partial_v g(x,0)$. By the condition $\bar{\lambda}_0(d,r,\partial_v g(\cdot,0)) > 0$ and an argument of contradiction similar to that in the proof of [298, Lemma 3.1] (see also Proposition 7.1.1), we can prove that $\{0\}$ is a uniform weak repeller for Z_0; that is, there exists $\delta_0 > 0$ such that $\limsup_{t\to\infty} \|\Phi(t)\phi\|_\beta \geq \delta_0$, $\forall \phi \in Z_0$. By Theorem 1.3.1 with Remarks 1.3.1 and 1.3.2 (see also [365, Theorem 4.6]), $\Phi(t)$ is uniformly persistent with respect to Z_0 in the sense that there exists an $\eta > 0$ such that $\liminf_{t\to\infty} \mathrm{dist}(\Phi(t)\phi, \partial Z_0) \geq \eta$, $\forall \phi \in Z_0$. As $\Phi(t) : C^+ \to C^+$ is compact for $t > r$, it follows from the continuous-time version of Theorem 1.3.6 that $\Phi(t) : Z_0 \to Z_0$ has a global attractor A_0. Then $A_0 = \Phi(t)A_0 \subset \mathrm{int}(C^+)$, $\forall t > 0$. By the compactness of A_0, there exists $\delta > 0$ such that $A_0 \gg \delta e$ with $e = v^* \in \mathrm{int}(C^+)$. Thus, the global attractivity of A_0 in Z_0 implies the desired order persistence. It remains to prove the existence of a positive steady state of (9.27). Let $\Phi_0(t) : X_\beta^+ \to X_\beta^+,\ t \geq 0$, be the solution semiflow of the following nonlocal reaction–diffusion equation

$$\begin{aligned}
\frac{\partial u(t,x)}{\partial t} =& \, d\Delta u(t,x) - k(x)u(t,x) + \\
& \int_\Omega \Gamma(x,y,r)g(y,u(t,y))dy,\ x \in \Omega,\ t > 0, \\
Bu(t,x) =& \, 0,\ \ x \in \partial\Omega,\ \ t > 0, \\
u(0,x) =& \, \varphi(x),\ \ x \in \Omega.
\end{aligned} \tag{9.35}$$

Since $\frac{\partial u(t,x)}{\partial t} \geq d\Delta u(t,x) - k(x)u(t,x)$, the standard parabolic maximum principle implies that $\Phi_0(t)(X_\beta^+ \setminus \{0\}) \subset \mathrm{int}(X_\beta^+)$, $\forall t > 0$. As proven for $\Phi(t) : C^+ \to C^+$, it follows that $\Phi_0(t)$ is point dissipative on X_β^+, compact for each $t > 0$, and uniformly persistent with respect to $X_\beta^+ \setminus \{0\}$. Then, by Theorem 1.3.11, $\Phi_0(t)$ has an equilibrium $\varphi^* \in X_\beta^+ \setminus \{0\}$; that is, $\Phi_0(t)\varphi^* = \varphi^*$ for all $t \geq 0$. Fix $t > 0$. We then get $\varphi^* = \Phi_0(t)\varphi^* \in \mathrm{int}(X_\beta^+)$. ∎

As an application of the theory of monotone dynamical systems, we are able to obtain sufficient conditions under which the species stabilizes eventually at positive steady states in the case (2) of Theorem 9.5.1.

Theorem 9.5.2. *Assume that* (G) *holds and* $\lambda_0(d,r,\partial_v g(\cdot,0)) > 0$.

(1) If $L(r) \geq 0$*, then (9.27) admits a unique positive steady state* φ^**, and* $\lim_{t\to\infty} \|v(t,\phi) - \varphi^*\|_\beta = 0$ *for every* $\phi \in C^+$ *with* $\phi(0,\cdot) \not\equiv 0$.

(2) If $L(r) < 0$ and $r|L(r)| < 1/e$, then there exists an open and dense subset S of C^+ with the property that for every $\phi \in S$ with $\phi(0, \cdot) \not\equiv 0$, there is a positive steady state φ of (9.27) such that $\lim_{t\to\infty} \|v(t, \phi) - \varphi\|_\beta = 0$.

Proof. Let $\Phi(t) : C^+ \to C^+$ be the solution semiflow of (9.27) and let $\Phi_0(t)$: $X_\beta^+ \to X_\beta^+$ be the solution semiflow of (9.35). Define

$$Y := \{\phi \in C^+ : \phi(s, x) \le M(r),\, \forall s \in [-r, 0],\, x \in \Omega\}$$

and

$$Y_0 := \{\phi \in X_\beta^+ : \phi(x) \le M(r),\, \forall x \in \Omega\}.$$

Then inequality (9.32) implies that every omega limit set $\omega(\phi)$ of $\Phi(t)$ is contained in Y, and Y is positively invariant for $\Phi(t)$. In particular, every nonnegative steady state φ of (9.27) is contained in Y_0.

In the case where $L(r) \ge 0$, [243, Corollary 5] implies that $\Phi(t) : Y \to Y$ is a monotone semiflow with respect to the pointwise ordering of C induced by C^+. We further claim that (9.27) admits at most one positive steady state. Indeed, it suffices to prove that the semiflow $\Phi_0(t)$ has at most one positive equilibrium in Y_0. By [243, Corollary 5] with $\tau = 0$, it then follows that $\Phi_0(t) : Y_0 \to Y_0$ is a monotone semiflow with respect to the pointwise ordering of X_β induced by X_β^+. Moreover, for any $\varphi_1, \varphi_2 \in Y_0$ with $\varphi_1 - \varphi_2 \in X_\beta^+ \setminus \{0\}$, $w(t) := \Phi_0(t)\varphi_1 - \Phi_0(t)\varphi_2$ satisfies

$$\frac{\partial w(t, x)}{\partial t} \ge d\Delta w(t, x) - k(x)w(t, x), \quad \forall x \in \Omega,\, t > 0.$$

Then the standard parabolic maximum principle implies that $w(t) \in \operatorname{int}(X_\beta^+)$ $\forall t > 0$; that is, $\Phi_0(t) : Y_0 \to Y_0$ is strongly monotone. By the strict subhomogeneity of g, it easily follows that for each $t > 0$, $\Phi_0(t) : Y_0 \to Y_0$ is strictly subhomogeneous. Now fix a real number $t_0 > 0$. Then Lemma 2.3.1 (see also [432, Lemma 1]) implies that the map $\Phi_0(t_0)$ has at most one positive fixed point in Y_0, and hence the semiflow $\Phi_0(t)$ has at most one positive equilibrium in Y_0. As shown in Theorem 9.5.1, $\Phi(t) : C^+ \to C^+$ is compact for each $t > r$, admits a global compact attractor in C^+, and is uniformly persistent with respect to Z_0. By the continuous-time version of Theorem 1.3.6, $\Phi(t) : Y \cap Z_0 \to Y \cap Z_0$ has a global attractor A_0. Clearly, Theorem 9.5.1(2), together with the uniqueness of the positive steady state, implies that A_0 contains only one equilibrium φ^*. By the Hirsch attractivity theorem (see Theorem 2.2.6), it then follows that φ^* attracts every point in $Y \cap Z_0$. Consequently, every orbit in Y converges to either the trivial equilibrium or the positive equilibrium φ^*, and hence together with Theorem 9.5.1(2), equilibria 0 and φ^* are also two isolated invariant sets in Y, and there is no cyclic chain of equilibria. By Theorem 1.2.2 and Remark 1.3.2, every compact internally chain transitive set of $\Phi(t) : Y \to Y$ is an equilibrium. Let $\phi \in C^+$ be given. As mentioned above, $\omega(\phi) \subset Y$. Since every compact omega limit set is an internally chain transitive set (see Lemma 1.2.1′), $\omega(\phi)$ is an equilibrium. If $\phi \in C^+$ with $\phi(0,\cdot) \not\equiv 0$, we then get $\omega(\phi) = \varphi^*$ in view of Theorem 9.5.1 (2).

In the case where $L(r) < 0$ and $r|L(r)| < 1/e$, we define $f(\alpha) := \alpha + L(r)e^{\alpha r}$, $\forall \alpha \in [0,\infty)$. It then follows that $f(0) < 0$ and $f''(\alpha) \leq 0, \forall \alpha \in [0,\infty)$. If $r = 0$, then $f(\alpha) > 0$ for all $\alpha > |L(0)|$. If $0 < r|L(r)| < \frac{1}{e}$, then $f(\alpha)$ reaches its maximum value at $\alpha_0 = -\frac{1}{r}\ln(r|L(r)|) > 0$ and $f(\alpha_0) > 0$. Consequently, we can fix a real number $\mu > 0$ such that $f(\mu) = \mu + L(r)e^{\mu r} > 0$. Let $F : C^+ \to X_\beta$ be defined as in the proof of Theorem 9.5.1, and let K_μ be defined as in Section 2.6 with $X = X_\beta$, $P = X_\beta^+$, and $A = d\Delta - k(\cdot)I$. By the definition of $L(r)$, we have

$$g(x, v_2) - g(x, v_1) \geq L(r)(v_2 - v_1),\ \forall x \in \overline{\Omega},\ 0 \leq v_1 \leq v_2 \leq M(r).$$

Assume that $\phi, \psi \in Y$ satisfy

$$\phi \leq_\mu \psi \text{ and } \phi(s) \ll_{X_\beta} \psi(s),\ \forall s \in [-r, 0].$$

Clearly, $\psi - \phi \in K_\mu$ implies that

$$\begin{aligned} \psi(0) - \phi(0) &\geq_{X_\beta} e^{(A-\mu I)r}(\psi(-r) - \phi(-r)) \\ &= T(r)e^{-\mu r}(\psi(-r) - \phi(-r)). \end{aligned} \tag{9.36}$$

It then follows that

$$\begin{aligned} &\mu(\psi(0) - \phi(0)) + F(\psi) - F(\phi) \\ &\quad \geq_{X_\beta} \mu(\psi(0) - \phi(0)) + L(r)T(r)(\psi(-r) - \phi(-r)) \\ &\quad \geq_{X_\beta} (\mu + L(r)e^{\mu r})\, e^{-\mu r}T(r)(\psi(-r) - \phi(-r)) \\ &\quad \gg_{X_\beta} 0. \end{aligned} \tag{9.37}$$

Thus condition (SM_μ) holds for $F : Y \to X_\beta$, and hence by Theorem 2.6.2, $\Phi(t) : Y \to Y$ is strongly order-preserving with respect to $\leq_\mu$. Let $\phi^* \geq_\mu 0$ be defined as in the proof of Theorem 2.6.2. Recall that $\phi^*(s) \gg_{X_\beta} 0$, $\forall s \in [-r, 0]$. Then for every $\psi \in Y$, either the sequence of points $\psi + \frac{1}{n}\phi^*$ or the sequence of points $\psi - \frac{1}{n}\phi^*$ is eventually contained in Y and approaches ψ as $n \to \infty$, and hence each point of Y can be approximated either from above or from below in Y. Clearly, $\Phi(t) : Y \to Y$ has a global compact attractor in Y. Note that the cone K_μ has empty interior in C. Fix a $\psi(\cdot) \in \text{int}(X_\beta^+)$ such that $d\Delta\psi - k(x)\psi \leq 0$, $\forall x \in \Omega$, and $B\psi = 0$, $\forall x \in \partial\Omega$ (e.g., taking $\psi(x)$ as a positive steady state of (9.27)). Then Lemma 2.6.1 implies that $\psi \in K_\mu$. Define

$$C_\psi = \{\phi \in C :\ \text{there exists}\, \beta \geq 0\ \text{ such that } -\beta\psi \leq_\mu \phi \leq_\mu \beta\psi\}$$

and

$$\|\phi\|_\psi = \inf\{\beta \geq 0 :\ -\beta\psi \leq_\mu \phi \leq_\mu \beta\psi\},\ \forall \phi \in C_\psi.$$

Then $(C_\psi, \|\cdot\|_\psi)$ is a Banach space and $C_\psi^+ := C_\psi \cap K_\mu$ is a closed cone in C_ψ with nonempty interior (see [12]). Using the smoothing property of the semiflow $\Phi(t)$ on C^+ and the fundamental theory of abstract functional differential equations, we can show that for each $t > r$, $\Phi(t)Y \subset Y \cap C_\psi$, $\Phi(t) : Y \to Y \cap C_\psi$ is continuous, $\Phi(t)\phi_2 - \Phi(t)\phi_1 \in \mathrm{int}(C_\psi^+)$ for any $\phi_1, \phi_2 \in Y$ with $\phi_2 >_\mu \phi_1$, and for each nonnegative equilibrium φ of $\Phi(t)$, the Fréchet derivative at φ of $\Phi(t) : Y \cap C_\psi \to Y \cap C_\psi$ exists and is compact and strongly positive on C_ψ^+ (see, e.g., [331]). By the generic convergence theorem (see Theorem 2.2.7), it then follows that there is an open and dense subset U of Y such that every orbit of $\Phi(t)$ starting from U converges to an equilibrium in Y. Clearly, the condition that $L(r) < 0$ and $r|L(r)| < 1/e$ still holds under small perturbations of $b(r)$. It then follows that there is a small $\epsilon > 0$ such that the generic convergence also holds in

$$Y_\epsilon := \{\phi \in C^+ : \phi(s,x) \le M_\epsilon(r),\ \forall s \in [-r,0],\ x \in \Omega\},$$

where $M_\epsilon(r) := b_\epsilon(r)/k_0 = M(r) + \epsilon/k_0$ and $b_\epsilon(r) := b(r) + \epsilon$. By inequality (9.32), every orbit of $\Phi(t)$ in C^+ eventually enters into Y_ϵ. Now the conclusion (2) follows from the generic convergence in Y_ϵ and Theorem 9.5.1(2). ∎

Example 9.5.1. Consider the model (9.27) with $k(x) = k$, $g(x,v) = g(v) := pve^{-qv}$, where k, p, and q are all positive constants. Let $T_0(t)$ be the analytic semigroup generated by $d\Delta$ with boundary condition $Bv = 0$. Clearly, $T(t) = e^{-kt}T_0(t)$, and condition (G) is satisfied. A direct computation shows that $g'(v) = pe^{-qv}(1-qv)$, $g''(v) = -pqe^{-qv}(2-qv)$, and $g(v)$ reaches its maximum value $g(1/q) = \frac{p}{q}e^{-1}$.

In the case of the Neumann boundary condition $Bv = \frac{\partial v}{\partial n} = 0$, it easily follows that

$$\lambda_0(d,r,g'(0)) = pe^{-kr} - k, \quad b(r) = \frac{p}{q}e^{-(1+kr)}, \quad M(r) = \frac{p}{kq}e^{-(1+kr)},$$

and

$$L(r) = \begin{cases} g'(M(r)) = p\left(1 - \frac{p}{k}e^{-(1+kr)}\right)\exp\left(-\frac{p}{k}e^{-(1+kr)}\right) & \text{if}\, M(r) \le 2/q, \\ g'(2/q) = -pe^{-2} & \text{if}\, M(r) > 2/q. \end{cases}$$

Clearly, if $\lambda_0(d,r,g'(0)) > 0$, then the model has a positive constant steady state $\frac{1}{q}\ln\left(\frac{p}{ke^{kr}}\right)$.

In the case of Dirichlet boundary condition $Bv = v = 0$, $\lambda_0(d,r,g'(0))$, $b(r)$, and $L(r)$ depend nontrivially on the diffusion rate d and the domain Ω, and any positive steady state is spatially inhomogeneous. It is possible to get the explicit expressions or estimates for these quantities in some special cases of the dimensions and shapes of Ω. For example, let $\Omega = \prod_{i=1}^N (0,\pi)$, and define $w_0(x) := \prod_{i=1}^N \sin x_i$, $\forall x = (x_1,\ldots,x_N) \in \Omega$. It is easy to verify that $T_0(t)w_0 = e^{-Ndt}w_0$, $\forall t \ge 0$, and that $w_0(x)$ is a positive solution of the nonlocal elliptic eigenvalue problem (9.29) with $k(x) = k$, $g(x, v) = g(v)$, and $\lambda = g'(0)e^{-(Nd+k)r} - (Nd + k)$. It then follows that $\lambda_0(d, r, g'(0)) = g'(0)e^{-(Nd+k)r} - (Nd + k)$.

9.6 Notes

Sections 9.1–9.4 are taken from Thieme and Zhao [371], and Section 9.5 is taken from Wu and Zhao [411]. The function $g(v)$ in Example 9.5.1 was introduced by Gurney, Blythe and Nisbet [139] in a delayed ordinary differential model of an adult fly population. A predator–prey reaction–diffusion system with nonlocal effects was introduced by Gourley and Britton [136]. Freedman and Zhao [125] investigated a nonlocal reaction–diffusion system modeling the dispersal of a population among islands. So, Wu and Zou [345] derived a nonlocal and delayed reaction–diffusion model for a single species with age structure, and proved the existence of monotone traveling waves in the case of Gurney, Blythe, and Nisbet's birth rate function. Gourley and Kuang [137] studied traveling waves and global stability in another nonlocal and time-delayed population model with stage structure. For a large class of nonlocal and time-delayed reaction–diffusion models including those in [345, 137], Thieme and Zhao [372] established the existence of minimal wave speeds for monotone traveling waves and showed that they coincide with the asymptotic speeds of spread for solutions with initial functions having compact support. Fang and Zhao [109] further developed the theory in [372] to nonmonotone integral equations including some nonlocal reaction–diffusion models with time delays.

Jin and Zhao [197] investigated the spatial dynamics of a nonlocal periodic reaction–diffusion population model with stage structure. In the case of a bounded domain, they obtained a threshold result on the global attractivity of either zero or a positive periodic solution. In the case of an unbounded domain, they established the existence of spreading spread and its coincidence with the minimal wave speed for monotone periodic traveling waves.

The method of fluctuations developed in [371] was further used in Zhao [440] for the global attractivity in a class of nonmonotone reaction–diffusion equations with time delay; in Lou, Xu and Zhao [233, 418] for the global dynamics of reaction–diffusion malaria models with incubation period in the vector population; and in Wang and Zhao [392] for the disease-free dynamics of a spatial model for Lyme disease.

10

Traveling Waves in Bistable Nonlinearities

We consider the asymptotic behavior, as $t \to \infty$, of the solutions of the problem

$$\begin{aligned} &u_t - u_{zz} - f(u,t) = 0, \quad z \in \mathbb{R},\ t > 0, \\ &u(z,0) = g(z), \quad z \in \mathbb{R}, \end{aligned} \tag{10.1}$$

where $f(u,\cdot)$ is ω-periodic for some $\omega > 0$, i.e., $f(u,\omega+t) = f(u,t)$, $\forall (u,t) \in \mathbb{R}^2$, and g is an arbitrary bounded function having certain asymptotic behavior as $z \to \pm\infty$. A typical example of f is the cubic potential

$$f = (1-u^2)(2u - \gamma(t)),$$

where $\gamma(\cdot) \in C(\mathbb{R}, (-2,2))$ is ω-periodic. Throughout this chapter we assume that f satisfies the following structure hypothesis:

(H) $f(\cdot,\cdot) \in C^{2,1}(\mathbb{R}\times\mathbb{R},\mathbb{R})$, the Poincaré (period) map $P(\alpha) := w(\alpha,\omega)$, where $w(\alpha,t)$ is the solution to

$$w_t = f(w,t), \quad \forall t \in \mathbb{R}, \quad w(\alpha,0) = \alpha \in \mathbb{R}, \tag{10.2}$$

has exactly three fixed points $\alpha^-, \alpha^0, \alpha^+$ satisfying $\alpha^- < \alpha^0 < \alpha^+$, and they are nondegenerate and $\alpha^\pm$ are stable; i.e.,

$$\frac{d}{d\alpha}P(\alpha^\pm) < 1 < \frac{d}{d\alpha}P(\alpha^0). \tag{10.3}$$

Clearly, $P : [\alpha^-,\alpha^+] \to [\alpha^-,\alpha^+]$ is strongly monotone. By the Dancer–Hess connecting orbit lemma, it is easy to see that $\lim_{t\to\infty}(w(\alpha,t) -w(\alpha^-,t)) = 0$ for each $\alpha \in [\alpha^-,\alpha^0)$, and $\lim_{t\to\infty}(w(\alpha,t) - w(\alpha^+,t)) = 0$ for each $\alpha \in (\alpha^0,\alpha^+]$.

A periodic traveling wave solution of (10.1a) connecting two stable periodic solutions of (10.2) is the solution that has the form

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$$u(z,t) = U(z-ct,t), \quad U(\cdot,t+\omega) = U(\cdot,t),$$

with

$$U(\pm\infty,t) := \lim_{\xi\to\pm\infty} U(\xi,t) = w(\alpha^{\pm},t),\ \forall t \in \mathbb{R},$$

where c is some real number, in other words, a wave with speed c, which, when viewed from the standpoint of the moving coordinate frame (i.e., in $\xi := z-ct$), has a profile that oscillates periodically in time. If $U(z-ct,t)$ is a periodic traveling wave solution of (10.1a) connecting $w(\alpha^-,t)$ and $w(\alpha^+,t)$, so is its translation $u(z+s,t) = U(z-ct+s,t)$ for each $s \in \mathbb{R}$. By a change of variable $\xi = z-ct$, it follows that $U(\xi,t)$ is an ω-periodic solution of the following periodic-parabolic equation

$$\begin{aligned} &U_t - cU_\xi - U_{\xi\xi} - f(U,t) = 0, \quad \forall(\xi,t) \in \mathbb{R}^2, \\ &U(\pm\infty,t) = w(\alpha^{\pm},t), \quad \forall t \in \mathbb{R}. \end{aligned} \tag{10.4}$$

If, in addition, $U(\xi,t)$ is bounded on $\mathbb{R}\times[0,\omega]$, by the local regularity and a priori estimates for parabolic equations, U_ξ and $U_{\xi\xi}$ are also bounded on $\mathbb{R}\times[0,\omega]$. It then follows that $U(\pm\infty,t) = w(\alpha^{\pm},t)$ and $U_\xi(\pm\infty,t) = 0$ uniformly for $t \in [0,\omega]$.

In this chapter we will study the existence, global attractivity, stability with phase shift, and uniqueness up to translation of periodic traveling waves of (10.1a) connecting $w(\alpha^-,t)$ and $w(\alpha^+,t)$. As an application of these results, a spruce budworm population model in a temporally homogeneous environment will be also discussed.

10.1 Existence of Periodic Traveling Waves

Let $M \geq 1$ be any fixed constant. Set $\Omega_M = (-M,M)$ and $Q_M = \Omega_M \times (0,\omega]$. For every constant $c \in \mathbb{R}$, consider the initial–boundary value problem

$$\begin{aligned} &\mathcal{L}^c(V) := V_t - cV_\xi - V_{\xi\xi} - f(V,t) = 0, \quad (\xi,t) \in Q_M, \\ &V(\pm M,t) = W^{\pm}(t), \quad t \in [0,\omega], \\ &V(\xi,0) = g(\xi), \quad \xi \in \Omega_M, \end{aligned} \tag{10.5}$$

where $W^{\pm}(t) := w(\alpha^{\pm},t)$, and g is any element in the function class $\mathcal{X}_M$ defined by

$$\mathcal{X}_M := \{g \in C^0([-M,M]) \,:\, g(\pm M) = \alpha^{\pm}, g(0) = \alpha^0, g_\xi(\cdot) \geq 0 \text{ in } \Omega_M\}.$$

Lemma 10.1.1. *Let $M \geq 1$ be any fixed constant. The following hold:*

(1) For every $c \in \mathbb{R}$ and $g \in \mathcal{X}_M$, problem (10.5) admits a unique solution $V = V(g,c;\xi,t)$, and the solution satisfies

$$W^-(t) < V(g,c;\xi,t) < W^+(t), \quad V_\xi(g,c;\xi,t) > 0, \quad V_c(g,c;\xi,t) > 0$$

for all $(\xi,t) \in Q_M$.

(2) There exist constants $C^+(M)$ and $C^-(M)$ such that $C^-(M) < C^+(M)$ and

$$\inf_{g\in\mathcal{X}_M} V(g, C^+(M); 0, \omega) \geq \alpha^0, \quad \sup_{g\in\mathcal{X}_M} V(g, C^-(M); 0, \omega) \leq \alpha^0.$$

Consequently, for every $g \in \mathcal{X}_M$, there exists a unique $c = C(M, g) \in \mathbb{R}$ such that $V(g, c; \cdot, \omega) \in \mathcal{X}_M$.

(3) There exists $g^M \in \mathcal{X}_M$ such that $V(g^M, C(M, g^M); \cdot, \omega) = g^M$; namely, there exists a solution (C^M, V^M) to the following problem:

$$\begin{aligned}
&\mathcal{L}^{C^M}(V^M) := V^M_t - V^M_{\xi\xi} - C^M V^M_\xi - f(V^M, t) = 0 \quad \text{in } Q_M,\\
&V^M(\pm M, t) = W^\pm(t) \quad \text{in } [0, \omega],\\
&V^M(\cdot, 0) = V^M(\cdot, \omega).
\end{aligned} \tag{10.6}$$

Proof. (1) Though f is nonlinear so that the solution of (10.5) may blow up, the property of g in $\mathcal{X}_M$ and a comparison principle yield the a priori estimate $W^-(t) < V(\xi, t) < W^+(t)$ for any $(\xi, t) \in Q_M$. Hence, (10.5) admits a unique solution $V = V(g, c; \xi, t)$. Since the a priori estimate implies that $V_\xi \geq 0$ at $\xi = \pm M$, the assumption $g_\xi \geq 0$ and the maximum principle for the equation satisfied by V_ξ then immediately yield $V_\xi > 0$ in Q_M. Notice that $V_c := \frac{\partial}{\partial c} V$ satisfies

$$(V_c)_t - (V_c)_{\xi\xi} - c(V_c)_\xi - f_u(V, t)V_c = V_\xi > 0 \qquad \text{in } Q_M$$

and $V_c = 0$ on the parabolic boundary of Q_M; it then follows that $V_c > 0$ in Q_M. This establishes the first assertion.

(2) Let $W(\xi, t)$ (depending on M) be any fixed function having the following properties:

$$\begin{aligned}
&W(0, T) = \alpha^0, \quad W(\xi, 0) < \alpha^-, \ \forall \xi \in [-M, M],\\
&W(\pm M, t) \leq W^\pm(t), \ \forall t \in [0, \omega],\\
&W_\xi(\xi, t) > 0, \ \forall (\xi, t) \in [-M, M] \times [0, \omega].
\end{aligned}$$

Since $\alpha^- < \alpha^0 < \alpha^+$, such a function can be easily constructed. For example, pick any monotonic function $\zeta(\xi)$ satisfying $\zeta_\xi > 0$ in $[-M, M]$, $\zeta(\pm M) = \alpha^\pm$, $\zeta(0) = \alpha^0$. Then the function $W(\xi, t) := \zeta(\xi) - K(\omega - t)$ with sufficiently large K will satisfy all the properties needed. Define

$$C^+(M) := \sup_{(\xi,t)\in[-M,M]\times[0,\omega]} \frac{W_t - W_{\xi\xi} - f(W, t)}{W_\xi}.$$

Then one can verify that when $c = C^+(M)$, W is a subsolution of (10.5a), (10.5b), and $W(\cdot, 0) < g$ for any $g \in \mathcal{X}_M$. Hence, by comparison, $W(\xi, t) \leq V(g, C^+(M); \xi, t)$ in Q_M for any $g \in \mathcal{X}_M$. Consequently, $\alpha^0 = W(0, \omega) \leq$

$V(g, C^+(M); 0, \omega)$. This proves the existence of $C^+(M)$. The existence of $C^-(M)$ can be proved by a similar construction.

Recall that for any fixed $g \in \mathcal{X}_M$, $V(g, c; 0, \omega)$ is strictly monotonic in $c \in \mathbb{R}$. By the properties of $C^{\pm}(M)$, there exists a unique $C = C(M, g)$ such that $V(g, C; 0, \omega) = \alpha^0$. Moreover, recalling that $V_\xi(g, c; \cdot, \omega) > 0$ in Ω_M and $V(g, c; \pm M, \omega) = W^{\pm}(\omega) = \alpha^{\pm}$, we have that $V(g, C(M, g); \cdot, \omega) \in \mathcal{X}_M$. The second assertion of the lemma thus follows.

(3) For every $g \in \mathcal{X}_M$ define a mapping $\mathcal{T} : \mathcal{X}_M \to \mathcal{X}_M$ by

$$\mathcal{T}(g) = V(g, C(M, g); \cdot, \omega).$$

Then we know the following: (a) $\mathcal{X}_M$ is a closed convex subset of $C^0([-M, M])$ and $\mathcal{T}$ maps $\mathcal{X}_M$ into itself; (b) Since $V_c > 0$ and the solution $V(\cdot, c; \xi, t)$ depends on g continuously, $C(M, g)$ is continuous in g, and consequently, $\mathcal{T}$ is continuous from $\mathcal{X}_M$ to $\mathcal{X}_M$; (c) By a parabolic estimate, $\mathcal{T}(\mathcal{X}_M)$ is a bounded set in $C^2([-M, M])$, so that $\mathcal{T}$ is compact. Therefore, by Schauder fixed point theorem, there exists $g \in \mathcal{X}_M$ such that $\mathcal{T}(g) = g$. ∎

We will find estimates for the solution to (10.6) that are independent of M, so that we can take the limit as $M \to \infty$ to obtain an ω-periodic solution of (10.4). The basic idea is to use the following comparison principle.

Lemma 10.1.2. *Let $M \geq 1$ be any fixed constant and (C^M, V^M) be any solution to (10.6).*

(1) If $(\bar{c}, \bar{V})$ satisfies

$$\begin{aligned}
&\bar{V}_t - \bar{V}_{\xi\xi} - \bar{c}\bar{V}_\xi - f(\bar{V}, t) \leq 0, \quad (\xi, t) \in Q_M, \\
&\bar{V}(\pm M, t) \leq W^{\pm}(t), \quad \forall t \in [0, \omega], \quad \bar{V}(0, 0) \geq \alpha^0, \\
&\bar{V}(\xi, 0) \leq \bar{V}(\xi, \omega), \quad \xi \in [-M, M],
\end{aligned} \tag{10.7}$$

then $C^M \leq \bar{c}$.

(2) If $\hat{V}$ satisfies

$$\begin{aligned}
&\hat{V}_t - \hat{V}_{\xi\xi} - C^M \bar{V}_\xi - f(\hat{V}, t) \leq 0, \quad (\xi, t) \in [0, M] \times [0, \omega], \\
&\hat{V}(M, t) \leq W^+(t), \quad \hat{V}(0, t) \leq V^M(0, t), \ \forall t \in [0, \omega], \\
&\hat{V}(\xi, 0) \leq \max\{\alpha^0, \hat{V}(\xi, \omega)\}, \quad \xi \in [0, M],
\end{aligned} \tag{10.8}$$

then $\hat{V} \leq V^M$ in $[0, M] \times [0, \omega]$.

Proof. (1) Assume for contradiction that $C^M > \bar{c}$. Then, since $V^M_\xi > 0$ in Q_M,

$$\mathcal{L}^{\bar{c}}(V^M) := (V^M)_t - V^M_{\xi\xi} - \bar{c}V^M_\xi - f(V^M, t) = (C^M - \bar{c})V^M_\xi > 0 \text{ in } Q_M.$$

Define

$$m_0 = \inf\left\{m \in (-2M, 2M) \,:\, V^M(\xi, 0) > \bar{V}(\xi - m, 0),\ \forall \xi \in I_m\right\},$$

where $I_m := (-M, M) \cap (m - M, m + M)$. Since $V^M(M, 0) = \alpha^+ > \bar{V}(-M, 0)$ and $V^M(0, 0) = \alpha^0 \le \bar{V}(0, 0)$, we have $m_0 \in [0, 2M)$. In addition, there exists $\xi_0 \in \Omega^M_{m_0} := (m_0 - M, M)$ such that $V^M(\xi_0, 0) = \bar{V}(\xi_0 - m_0, 0)$. Notice that the boundary conditions of V^M and $\bar{V}$ imply that on the parabolic boundary of $\Omega^M_{m_0} \times (0, \omega]$, $V^M(\xi, t) \ge \bar{V}(\xi - m_0, t)$. Thus, applying a comparison principle to the functions $V^M(\xi, t)$ and $\bar{V}(\xi - m_0, t)$ in the domain $\Omega^M_{m_0} \times [0, \omega]$, we have that $V^M(\xi, \omega) > \bar{V}(\xi - m_0, \omega)$ for all $\xi \in \Omega^M_{m_0}$. But this is impossible, since $V^M(\xi_0, \omega) = V^M(\xi_0, 0) = \bar{V}(\xi_0 - m_0, 0) \le \bar{V}(\xi_0 - m_0, \omega)$. Hence we must have $C^M \le \bar{c}$.

(2) Define $m_0 = \inf\Big\{m \ge 0 \,:\, V^M(\xi, 0) \ge \hat{V}(\xi - m, 0) \text{ in } [m, M]\Big\}$. Using a comparison principle in $(m_0, M) \times (0, \omega]$, one can follow the idea in (1) to deduce that $m_0 = 0$. ∎

Now we apply the first comparison principle in Lemma 10.1.2 to estimate C^M.

Lemma 10.1.3. *There exists $M_0 > 1$ such that for each $M \ge M_0$, any solution (V^M, C^M) of (10.6) satisfies the estimate*

$$|C^M| \le 1 + \tfrac{1}{2} \sup\left\{(W^+(t) - W^-(t) + 2)|f_{uu}(u, t)| \,:\, u \in I_t,\ t \in [0, \omega]\right\},$$

where $I_t := [W^-(t) - 1, W^+(t) + 1]$.

Proof. Let $\zeta(s) = \frac{1}{2}[1 + \tanh(\frac{s}{2})]$, so that $\zeta' = \zeta(1 - \zeta)$ and $\zeta'' = \zeta'(1 - 2\zeta)$. Set $w_1(t) = W^+(t)$ and $w_2(t) = w(\alpha^- - \varepsilon_0, t)$, where ε_0 is a small constant such that $w_2(t) \ge W^-(t) - 1$ in $[0, \omega]$. Consider the function

$$\bar{V}(\xi, t) = w_1(t)\zeta(\xi + \xi_0) + w_2(t)[1 - \zeta(\xi + \xi_0)],$$

where ξ_0 is a constant such that $\zeta(\xi_0) = \frac{\alpha^0 - \alpha^- + \varepsilon_0}{\alpha^+ - \alpha^- + \varepsilon_0}$. Since $w_1(\omega) = w_1(0)$ and $w_2(\omega) > w_2(0)$, $\bar{V}(\cdot, \omega) > \bar{V}(\cdot, 0)$. Also, $\bar{V}(0, 0) = \alpha^0$, $\bar{V}_\xi > 0$, $\bar{V}(\infty, 0) = \alpha^+$, and $\bar{V}(-\infty, 0) = \alpha^- - \varepsilon_0$.

Observe, by Taylor's expansion, that

$$\zeta f(w_1, t) + (1 - \zeta) f(w_2, t) - f(\zeta w_1 + (1 - \zeta) w_2, t) = \frac{1}{2}\zeta(1 - \zeta)(w_1 - w_2)^2 f_{uu}(\theta, t)$$

for some $\theta \in (w_2, w_1)$. Taking

$$\bar{c} = 1 + \tfrac{1}{2} \sup\left\{(W^+(t) - W^-(t) + 2)|f_{uu}(u, t)| \,:\, u \in I_t,\ t \in [0, \omega]\right\},$$

we have that for all $(\xi, t) \in \mathbb{R} \times [0, \omega]$,

$$\begin{aligned}
\mathcal{L}^{\bar{c}}(\bar{V}) &= [-\bar{c}\zeta' - \zeta''](w_1 - w_2) \\
&\qquad + [\zeta f(w_1, t) + (1 - \zeta) f(w_2, t) - f(\zeta w_1 + (1 - \zeta) w_2, t)] \\
&= -\zeta(1 - \zeta)(w_1 - w_2)[\bar{c} + 1 - 2\zeta - \tfrac{1}{2}(w_1 - w_2) f_{uu}(\theta, t)] < 0.
\end{aligned}$$

Thus, by Lemma 10.1.2 (1), for all M satisfying $\zeta(-M) \leq \frac{\varepsilon_0}{\alpha^+ - \alpha^- - \varepsilon_0}$ (so that $\bar{V}(-M, 0) \leq \alpha^-$), we have $C^M \leq \bar{c}$. Similarly, one can establish the lower bound of C^M, thereby completing the proof of the lemma. ∎

The following result says that equation (10.1a) has a monotone periodic traveling wave solution connecting two stable periodic solutions of (10.2).

Theorem 10.1.1. *There exists a solution* (c, U) *to the problem*

$$\begin{aligned} &U_t - cU_\xi - U_{\xi\xi} - f(U, t) = 0, \quad \forall (\xi, t) \in \mathbb{R}^2, \\ &U(\pm\infty, t) = w(\alpha^\pm, t), \quad \forall t \in \mathbb{R}, \\ &U(\cdot, \omega) = U(\cdot, 0), \quad U(0, 0) = \alpha^0, \end{aligned} \tag{10.9}$$

with $U_\xi(\cdot, \cdot) > 0$ *in* $\mathbb{R}^2$.

Proof. For each integer $M \geq 1$, by Lemma 10.1.1, problem (10.6) admits a solution (C^M, V^M). From Lemma 10.1.3, we know that $\{C^M\}_{M \geq M_0}$ is uniformly bounded. Hence, by parabolic estimates [209], $\sup_{M \geq M_0} \|V^M\|_{C^{2,1}(Q_M)}$ is uniformly bounded also. Therefore, we can select a subsequence $\{M_j\}_{j=1}^\infty$ such that as $j \to \infty$, $M_j \to \infty$, $C^{M_j} \to c^*$, and $V^{M_j} \to U^*$ (uniformly in any compact subset of $\mathbb{R} \times [0, \omega]$), where (c^*, U^*) satisfies the following equations

$$\begin{aligned} &U_t^* - U_{\xi\xi}^* - c^* U_\xi^* - f(U^*, t) = 0 \quad \text{in } \mathbb{R} \times [0, \omega], \\ &U^*(0, 0) = \alpha^0, \quad U^*(\cdot, 0) = U^*(\cdot, \omega) \quad \text{in } \mathbb{R}, \\ &U_\xi^* \geq 0 \quad \text{in } \mathbb{R} \times [0, \omega]. \end{aligned}$$

Thus, to show that (c^*, U^*) solves (10.9), we need only show that $U^*(\pm\infty, t) = W^\pm(t)$.

Assume for the moment that U^* is nontrivial; i.e., $U^*(\cdot, t) \not\equiv w(\alpha^0, t)$. Then $U_\xi^* \not\equiv 0$, so that by the condition $U_\xi^* \geq 0$ in $\mathbb{R} \times [0, \omega]$ and the strong maximum principle, we have $U_\xi^* > 0$ in $\mathbb{R} \times [0, \omega]$. Consequently, $U^*(\pm\infty, t) := \lim_{\xi \to \pm\infty} U^*(\xi, t)$ exist and $U^*(-\infty, 0) < \alpha^0 < U^*(\infty, 0)$. Since $U^*(\cdot, t)$ is monotonic, U_ξ^* and $U_{\xi\xi}^*$ approach zero weakly as $|\xi| \to \infty$. It then follows that $U^*(\infty, t)$ and $U^*(-\infty, t)$ are periodic solutions of $w_t = f(w, t)$. Hence, by the assumption on f, we must have $U^*(\pm\infty, t) = W^\pm(t)$.

Thus, to finish the proof, we need only show that U^* is nontrivial. Without loss of generality, we assume that $c^* \geq 0$. Also, we can assume that $U^*(0, t) \geq w(\alpha^0, t)$, $\forall t \in [0, \omega]$, since otherwise, $U^*(\cdot, t) \not\equiv w(\alpha^0, t)$, so that U^* is not trivial. Under these assumptions, we have that

$$\lim_{j \to \infty} C^{M_j} \geq 0, \qquad \lim_{j \to \infty} \min_{t \in [0, \omega]} \{V^{M_j}(0, t) - w(\alpha^0, t)\} \geq 0.$$

We shall use Lemma 10.1.2(2) to show that U^* is nontrivial.

Since $w_\alpha = \exp\left(\int_0^t f_u(w(\alpha, s), s) ds\right) > 0$, it follows that

$$K = \max\left\{\frac{|w_{\alpha\alpha}(\alpha,t)|}{w_\alpha(\alpha,t)} + 1 : \alpha \in [\alpha^-, \alpha^+],\, t \in [0,\omega]\right\}$$

is finite. Take $\delta = \min\left\{\frac{1}{16K}, \frac{\alpha^+ - \alpha^0}{8}\right\}$. Let $\zeta(\cdot) \in C^\infty([0,\infty), \mathbb{R})$ be a function such that

$$\begin{aligned}
&\zeta(s) = \alpha^0 + (s + \sqrt{\delta})^2 - 2\delta \text{ if } s \in [0, \sqrt{\delta}],\\
&0 \le \zeta'(s) < 5\sqrt{\delta},\ \alpha^0 + 2\delta \le \zeta(s) < \alpha^0 + 7\delta,\ |\zeta''(s)| \le 2 \text{ if } s \in [\sqrt{\delta}, \infty).
\end{aligned}$$

For any $\delta_1 > 0$, let $\hat{w}(\alpha,t)$ be the solution to

$$\hat{w}_t = f(\hat{w},t) - \delta_1\Big(\max\{0, \hat{w} - w(\alpha^0 + \delta, t)\}\Big)^3, \qquad \hat{w}(\alpha,0) = \alpha.$$

Clearly, $\hat{w}(\alpha,t) = w(\alpha,t)$, $\forall \alpha \le \alpha^0 + \delta$. Since $P(\alpha) > \alpha$, $\forall \alpha \in (\alpha^0, \alpha^+)$, for every positive δ_1 sufficiently small, $\hat{w}(\alpha,T) > \alpha$, $\forall \alpha \in (\alpha^0, \alpha^0 + 7\delta]$. In addition, by taking smaller δ_1 if necessary, we have that

$$\max_{\alpha \in [\alpha^0 - \delta, \alpha^0 + 7\delta], t \in [0,\omega]} \frac{|\hat{w}_{\alpha\alpha}(\alpha,t)|}{\hat{w}_\alpha(\alpha,t)} \le K.$$

We henceforth fix such $\delta_1 > 0$. Also, we set

$$\delta_2 := \min_{t \in [0,\omega]} \{\hat{w}(\alpha^0 + 2\delta, t) - \hat{w}(\alpha^0 + \delta, t)\}.$$

Let ε be a small positive constant to be determined. Consider the function $\hat{V}(\xi,t) = \hat{w}(\zeta(\varepsilon\xi),t)$. One can calculate

$$\begin{aligned}
\mathcal{L}^{C^{M_j}}(\hat{V}) = &-\delta_1\Big(\max\{0, \hat{w}(\zeta,t) - \hat{w}(\alpha^0 + \delta, t)\}\Big)^3\\
&- \hat{w}_\alpha\Big(\varepsilon^2\zeta'' + \varepsilon C^{M_j}\zeta' + \varepsilon^2\frac{\hat{w}_{\alpha\alpha}}{\hat{w}_\alpha}(\zeta')^2\Big),
\end{aligned}$$

where $\hat{w}$ is evaluated at $(\zeta(\varepsilon\xi),t)$. We want to show that $\mathcal{L}^{C^{M_j}}(\hat{V}) < 0$ in $[0,\infty) \times [0,\omega]$ by considering two cases: (i) $\zeta \ge \alpha^0 + 2\delta$; (ii) $\zeta < \alpha^0 + 2\delta$.

In the first case,

$$\begin{aligned}
\mathcal{L}^{C^{M_j}}(\hat{V}) &\le -\delta_1\delta_2^3 + \varepsilon\hat{w}_\alpha\Big(2\varepsilon - 5\sqrt{\delta}\min\{C^{M_j}, 0\} + 25\varepsilon K\delta\Big)\\
&\le -\delta_1\delta_2^3 - C\varepsilon < 0
\end{aligned}$$

if we take ε small enough.

In the second case, with ε fixed as above, let $s := \varepsilon\xi \in [0, \sqrt{\delta})$, so that $\zeta'' = 2$ and $\zeta' = 2(s + \sqrt{\delta}) < 4\sqrt{\delta}$. It then follows that

$$\mathcal{L}^{C^{M_j}}(\hat{V}) \le -\hat{w}_\alpha\varepsilon\Big(2\varepsilon + 4\min\{C^{M_j}, 0\}\sqrt{\delta} - 16\varepsilon K\delta\Big) < 0$$

if we take j large enough such that $C^{M_j} \geq -\frac{\varepsilon}{8\sqrt{\delta}}$.

In summary, there exist $\varepsilon > 0$ and $J > 0$ such that $\mathcal{L}^{C^{M_j}}(\hat{V}) < 0$ in $[0, \infty) \times [0, \omega]$ for all $j \geq J$.

Finally, observe that for all $t \in [0, \omega]$,

$$\hat{V}(0,t) = \hat{w}(\zeta(0),t) = \hat{w}(\alpha^0 - \delta, t) = w(\alpha^0 - \delta, t) < V^{M_j}(0,t)$$

if we take j large enough. Also, for any $M \in [1, \infty)$,

$$\hat{V}(M,t) \leq \hat{w}(\alpha^0 + 7\delta, t) < w(\alpha^0 + 7\delta, t) < W^+(t).$$

Furthermore, if $\hat{V}(\xi, 0) > \alpha^0$, then $\zeta = \zeta(\varepsilon\xi) > \alpha^0$, so that

$$\hat{V}(\xi,0) = \hat{w}(\zeta(\varepsilon\xi),0) = \zeta(\varepsilon\xi) < \hat{w}(\zeta(\varepsilon\xi),\omega) = \hat{V}(\xi,\omega).$$

Thus, by Lemma 10.1.2 (2), for all j large enough, $V^{M_j} \geq \hat{V}$ in $[0, M_j] \times [0, \omega]$. Consequently, $U^* \geq \hat{V}$ in $[0, \infty) \times [0, \omega]$, and therefore U^* cannot be trivial. This completes the proof of Theorem 10.1.1. ∎

10.2 Attractivity and Uniqueness of Traveling Waves

In this section we study the asymptotic behavior, as $t \to \infty$, for the initial value problem (10.1) for a large class of initial conditions g. The analysis can be naturally divided into two parts. In the first part one shows that a solution develops, after some time, a wave-like profile. In the second part, one shows that the solution converges to a translate of the monotone traveling wave solution claimed in Theorem 10.1.1.

Let $\mathcal{X} := BUC(\mathbb{R}, \mathbb{R})$ be the Banach space of all bounded and uniformly continuous functions from $\mathbb{R}$ to $\mathbb{R}$ with L^∞-norm, and let $\mathcal{X}_+ := \{g \in \mathcal{X} : g(z) \geq 0, z \in \mathbb{R}\}$ be its positive cone. In the sequel we shall denote by $U^g(\xi, t)$ the solution of

$$\begin{aligned} &\mathcal{L}^c(U^g) := U^g_t - cU^g_\xi - U^g_{\xi\xi} - f(U^g, t) = 0 \quad \text{in } \mathbb{R} \times (0, \infty), \\ &U^g(\cdot, 0) = g(\cdot) \quad \text{on } \mathbb{R}, \end{aligned} \tag{10.10}$$

where c is the speed of the traveling wave solution of (10.9). Clearly, the solution u in (10.1) is given by $u(z,t) = U^g(z - ct, t)$. We set $\|\cdot\| = \|\cdot\|_{L^\infty(\mathbb{R})}$.

Lemma 10.2.1. *Let (c, U) be a solution of (10.9) and let $U^g(\xi, t)$ be the solution of (10.10) for $g \in \mathcal{X}$.*

(1) If there exist constants $\alpha_1 \in (\alpha^+, \infty)$ and $\alpha_2 \in (\alpha^-, \alpha^0)$ such that

$$g(\xi) \leq \alpha_1 \ \textit{ in } \ \mathbb{R}, \qquad g(\xi) \leq \alpha_2 \ \textit{ in } \ (-\infty, 0), \tag{10.11}$$

then for any $\varepsilon > 0$, there exist a positive number $\hat{z}$ and a positive integer $\hat{k}$ such that

$$U^g(\xi, \hat{k}\omega) \leq U(\xi + \hat{z}, 0) + \varepsilon, \qquad \forall \xi \in \mathbb{R}.$$

(2) If $g \in \mathcal{X}$ satisfies

$$\limsup_{z\to-\infty} g(z) < \alpha^0, \qquad \liminf_{z\to\infty} g(z) > \alpha^0, \tag{10.12}$$

then for every $\varepsilon > 0$, there exist a positive number $\hat{z} = \hat{z}(\varepsilon, g)$ and a positive integer $\hat{k} = \hat{k}(\varepsilon, g)$ such that

$$U(\xi - \hat{z}, 0) - \varepsilon \le U^g(\xi, \hat{k}\omega) \le U(\xi + \hat{z}, 0) + \varepsilon, \qquad \forall\, \xi \in \mathbb{R}. \tag{10.13}$$

Proof. (1) Set $\zeta(s) = \frac{1}{2}[1 + \tanh \frac{s}{2}]$, $w_1(t) = w(2\alpha_1 - \alpha_2, t)$, and $w_2(t) = w(\alpha_2, t)$, where $w(\alpha, t)$ is the solution of (10.2). Define

$$\hat{c} = c + 1 + \tfrac{1}{2} \sup\{(w_1(t) - w_2(t))|f_{uu}(\theta, t)| \ : \theta \in [w_2(t), w_1(t)], t \in [0, \infty)\}$$

and

$$V(\xi, t) = w_1(t)\zeta(\xi + \hat{c}t) + w_2(t)[1 - \zeta(\xi + \hat{c}t)].$$

Then, by (10.11), $V(\cdot, 0) \ge g(\cdot)$. The same computation as in the proof of Lemma 10.1.3 shows that $\mathcal{L}^c(V) > 0$ in $\mathbb{R}\times[0,\infty)$. A comparison principle then yields $U^g(\xi, t) \le V(\xi, t)$ in $\mathbb{R} \times [0, \infty)$. The first assertion of the lemma thus follows from the fact that $\lim_{k\to\infty} w_2(k\omega + t) = W^-(t)$, $\lim_{k\to\infty} w_1(k\omega + t) = W^+(t)$.

(2) The second assertion follows from (1) and a similar estimate on the lower bound of the solution. ∎

Lemma 10.2.2. *Let (c, U) be a solution of (10.9) and $g \in \mathcal{X}$.*

(1) There exist positive constants $\varepsilon_0, K_0, \rho_0$ such that if for some $\varepsilon \in (0, \varepsilon_0]$ and $\hat{z} \in \mathbb{R}$,

$$g(\cdot) \le U(\cdot + \hat{z}, 0) + \varepsilon \quad \Big(or\ \ g(\cdot) \ge U(\cdot - \hat{z}, 0) - \varepsilon\Big),$$

then for all $t \ge 0$,

$$U^g(\cdot, t) \le U(\cdot + \hat{z} + K_0\varepsilon, t) + K_0\varepsilon e^{-\rho_0 t}$$

$$\Big(or\ \ U^g(\cdot, t) \ge U(\cdot - \hat{z} - K_0\varepsilon, t) - K_0\varepsilon e^{-\rho_0 t}\Big).$$

(2) There exists a positive constant K_1 such that if $\|g(\cdot) - U(\cdot, 0)\| \le \varepsilon$ for some $\varepsilon \in (0, \varepsilon_0]$, then

$$\|U^g(\cdot, t) - U(\cdot, t)\| \le K_1\varepsilon, \qquad \forall\, t \ge 0.$$

Proof. We need only prove (1), since (2) is a direct consequence of (1). Without loss of generality, we assume that $\hat{z} = 0$.

Let $W^{\pm}(t) := w(\alpha^{\pm}, t)$ and define

$$\begin{aligned}\nu^{\pm} &= -\frac{1}{\omega}\int_0^{\omega} f_u(W^{\pm}(t),t)\,dt,\\ a^{\pm}(t) &= \exp\left(\frac{\nu^{\pm}t}{2} + \int_0^t f_u(W^{\pm}(\tau),\tau)\,d\tau\right).\end{aligned} \tag{10.14}$$

Since $P'(\alpha^{\pm}) = \exp\left(\int_0^{\omega} f_u(W^{\pm}(t),t)\,dt\right) < 1$, we have $\nu^{\pm} > 0$ and $a^{\pm}(\omega) = \exp\left(-\frac{\nu^{\pm}\omega}{2}\right) < 1$. Let $I^{\pm}_{t,\eta} := [W^{\pm}(t) - \eta, W^{\pm}(t) + \eta]$ and define

$$\begin{aligned}\delta_0 &:= \frac{\sup\left\{\eta > 0 :\, |f_u(u,t) - f_u(W^{\pm}(t),t)| \le \nu^{\pm}/2, \forall t \in [0,\omega], u \in I^{\pm}_{t,\eta}\right\}}{2\|a^{+}(\cdot)\|_{C^0([0,\omega])} + 2\|a^{-}(\cdot)\|_{C^0([0,\omega])}},\\ \xi_0 &= \inf\left\{\hat{\xi} \ge 1 :\, |U(\pm\xi,t) - W^{\pm}(t)| \le \frac{\delta_0}{2}, \forall\,\xi \in [\hat{\xi},\infty),\, t \in [0,\omega]\right\}.\end{aligned} \tag{10.15}$$

Since $U(\pm\infty,t) = W^{\pm}(t)$ uniformly for $t \in [0,\omega]$, both δ_0 and ξ_0 are well defined.

Let $\zeta(\cdot) \in C^2(\mathbb{R},\mathbb{R})$ be a function satisfying

$$\begin{aligned}&\zeta(s) = 1 \text{ in } [3,\infty), \quad \zeta(s) = 0 \text{ in } (-\infty,0],\\ &0 \le \zeta'(s) \le 1 \text{ and } |\zeta''(s)| \le 1 \text{ in } \mathbb{R}.\end{aligned}$$

Define

$$A(\xi,t) = \zeta(\xi)a^{+}(t) + (1 - \zeta(\xi))a^{-}(t), \tag{10.16}$$

$$B(t) = \textstyle\int_0^t \max\{a^{+}(\tau), a^{-}(\tau)\}\,d\tau, \tag{10.17}$$

$$K = \left(\nu^{+} + \nu^{-} + 1 + |c| + 2\|f_u\|\right)\Big/\left(\min_{t\in[0,\omega],\xi\in[-\xi_0,\xi_0]} U_{\xi}(\xi,t)\right), \tag{10.18}$$

$$V(\xi,t) = U(\xi + K\varepsilon B(t),t) + \varepsilon A(\xi,t),$$

where $\|f_u\| = \max\{|f_u(u,t)| \,:\, t \in [0,\omega], u \in [W^{-}(t) - 1, W^{+}(t) + 1]\}$. Note that

$$a^{\pm}(t) \le C\exp\left(-\frac{\nu^{\pm}t}{2}\right), \quad \forall t \in [0,\infty),$$

where $C = \sup_{t\in[0,\omega]}\exp(\nu^{\pm}t + \int_0^t f_u(W^{\pm},\tau)\,d\tau)$. It follows that as $t \to \infty$, $a^{\pm}(t)$ and $\|A(\cdot,t)\|_{C^0(\mathbb{R})}$ approach zero exponentially fast, and $B(t)$ is uniformly bounded. We take $\varepsilon_0 = \delta_0/(2KB(\infty))$. We want to show that $U^g(\cdot,\cdot) \le V(\cdot,\cdot)$ in $\mathbb{R} \times [0,\infty)$.

When $t = 0$, $V(\cdot,0) = U(\cdot,0) + \varepsilon \ge g(\cdot) = U^g(\cdot,0)$. Also, we can calculate

$$\mathcal{L}^c(V) = K\varepsilon B_t U_{\xi} + \varepsilon[A_t - cA_{\xi} - A_{\xi\xi} - Af_u(U + \varepsilon\theta A,t)]$$

for some $\theta(\xi,t) \in (0,1)$.

Now we claim that $\mathcal{L}^c V \geq 0$, $\forall \varepsilon \in (0, \varepsilon_0]$. We consider three cases: (i) $\xi \in [\xi_0, \infty)$, (ii) $\xi \in (-\infty, -\xi_0]$, and (iii) $\xi \in [-\xi_0, \xi_0]$.

In the first case, $\zeta = 1$, $A_\xi = A_{\xi\xi} = 0$, $B_t U_\xi > 0$, $|f_u(U + \varepsilon\theta A, t) - f_u(W^+(t), t)| \leq \frac{\nu^+}{2}$, and $A_t = A[\frac{\nu^+}{2} + f_u(W^+(t), t)]$. It then follows that $\mathcal{L}^c V \geq 0$ in $[\xi_0, \infty) \times [0, \infty)$. Similarly, $\mathcal{L}^c V \geq 0$ in the second case.

In the third case, i.e., $\xi \in [-\xi_0, \xi_0]$, we have that

$$|A_t - cA_\xi - A_{\xi\xi} - Af_u(U + \varepsilon\theta A, t)| \leq \bar{a}(t)(\nu^+ + \nu^- + 2\|f_u\| + |c| + 1),$$

where $\bar{a}(t) := \max\{a^+(t), a^-(t)\}$. On the other hand, we have that

$$B_t U_\xi \geq \max\{a^+(t), a^-(t)\} \min\{U_\xi : t \in [0, \omega], \xi \in [-\xi_0, \xi_0]\}.$$

Hence, by the definition of K, $\mathcal{L}^c V \geq 0$ in $[-\xi_0, \xi_0] \times [0, \infty)$.

In conclusion, $\mathcal{L}^c V \geq 0$ in $\mathbb{R} \times [0, \infty)$. Therefore, by the comparison principle, $U^g \leq V$ in $\mathbb{R} \times [0, \infty)$. The assertion of the lemma thus follows. ∎

Theorem 10.2.1. *Let (c, U) be a solution of (10.9) and let $u(z, t, g)$ denote the solution of (10.1). Then for any $g \in \mathcal{X}$ satisfying (10.12), there exists $s_g \in \mathbb{R}$ such that $\lim_{t\to\infty} |u(z, t, g) - U(z - ct + s_g, t)| = 0$ uniformly for $z \in \mathbb{R}$. Moreover, any periodic traveling wave solution of (10.1a) connecting $w(\alpha^\pm, t)$ is a translation of U.*

Proof. Let $V = [\alpha^-, \alpha^+]_{\mathcal{X}}$, and define $\Phi_t(g) := U^g(\cdot, t)$, $g \in V, t \geq 0$. Then $\Phi_t(\cdot)$ is the periodic semiflow generated by periodic equation (10.10). Let $S : V \to V$ be the Poincaré map associated with $\Phi_t(\cdot)$; that is, $S(g) := \Phi_\omega(g) = U^g(\cdot, \omega)$, $g \in V$. Clearly, $S^n(g) = U^g(\cdot, n\omega)$, $\forall n \geq 0$. Then $S : V \to V$ is monotone. By Lemmas 10.2.1 and 10.2.2(1), there exist a positive integer $\hat{k}$ and a large number $\hat{z}$ such that for all $(\xi, t) \in \mathbb{R} \times [\hat{k}\omega, \infty)$,

$$U(\xi - \hat{z} - K_0\varepsilon_0, t) - K_0\varepsilon_0 e^{-\rho_0 t} \leq \Phi_t(g)(\xi) \leq U(\xi + \hat{z} + K_0\varepsilon_0, t) + K_0\varepsilon_0 e^{-\rho_0 t}. \tag{10.19}$$

Notice that $\{S^n(g)\}_{n=1}^\infty$ is a bounded sequence in $C^1(\mathbb{R}, \mathbb{R})$, and that $U(\xi, t)$ approaches $W^\pm(t)$ as $\xi \to \pm\infty$, uniformly in $t \in [0, \omega]$. Consequently, the positive orbit $\gamma^+(g) := \{S^n(g) : n \geq 0\}$ is precompact in $\mathcal{X}$, and hence its omega limit set $\omega(g)$ is nonempty, compact, and invariant (i.e., $S(\omega(g)) = \omega(g)$). Letting $a = \hat{z} + K_0\varepsilon_0$ and $t = n\omega \to \infty$ in (10.19), we then get $\omega(g) \subset I := [U(\cdot - a, 0), U(\cdot + a, 0)]_{\mathcal{X}}$. Define $h(s) = U(\cdot + s, 0), \forall s \in [-a, a]$. Then h is a monotone homeomorphism from $[-a, a]$ onto a subset of I. By Lemma 10.2.2(2), each $h(s)$ is a stable fixed point for $S : V \to V$. Clearly, each $\phi \in I$ satisfies (10.12), and hence Lemmas 10.2.1 and 10.2.2(1), as applied to ϕ, imply that $\gamma^+(\phi)$ is precompact. To get the convergence of $\gamma^+(g)$, it then suffices to verify condition (3a) in Theorem 2.2.4. Assume that $U(\cdot + s_0, 0) < \omega(\phi_0)$ for some $s_0 \in [-a, a)$ and $\phi_0 \in I$. Then for each $\phi \in \omega(\phi_0)$, $U(\cdot + s_0, 0) \leq \phi(\cdot)$ and $U(\cdot + s_0, 0) \not\equiv \phi(\cdot)$. By the strong maximum principle, $U(\xi + s_0, t) < \Phi_t(\phi)(\xi)$, $\forall \xi \in \mathbb{R}$, $t > 0$, and hence, letting $t = \omega$, we get

$U(\xi + s_0, 0) < S(\phi)(\xi)$, $\forall \xi \in \mathbb{R}$. By the invariance of $\omega(\phi_0)$ for S, it then follows that

$$U(\xi + s_0, 0) < \phi(\xi),\ \forall \xi \in \mathbb{R},\ \forall \phi \in \omega(\phi_0).$$

Since $\lim_{\xi \to \pm\infty} U_\xi(\xi, 0) = 0$, we can choose a large positive constant $b \in (a, \infty)$ such that $\hat{\delta} := \sup_{|\xi| \geq b-a} U_\xi(\xi, 0) \leq \frac{1}{4K_0}$. By the compactness of $\omega(\phi_0)$, there exists a number $\sigma_0 \in (s_0, a)$ such that

$$U(\xi + \sigma_0, 0) < \phi(\xi),\ \forall \xi \in [-b, b],\ \forall \phi \in \omega(\phi_0).$$

For each $\phi \in \omega(\phi_0)$, there is a sequence $n_j \to \infty$ such that $S^{n_j}(\phi_0) \to \phi$, as $j \to \infty$. Fix an integer n_k such that $\|S^{n_k}(\phi_0) - \phi\| < \hat{\delta}(\sigma_0 - s_0)$. Since

$$\phi(\xi) - U(\xi + \sigma_0, 0) > 0,\ \forall \xi \in [-b, b],$$

and

$$\phi(\xi) - U(\xi + \sigma_0, 0) \geq U(\xi + s_0, 0) - U(\xi + \sigma_0, 0),\ \forall \xi \in \mathbb{R},$$

we have

$$\begin{aligned} S^{n_k}(\phi_0)(\xi) - U(\xi + \sigma_0, 0) &\geq -\|S^{n_k}(\phi_0) - \phi\| + \phi(\xi) - U(\xi + \sigma_0, 0) \\ &\geq -\hat{\delta}(\sigma_0 - s_0) - \sup_{|z| \geq b} |U(z + s_0, 0) - U(z + \sigma_0, 0)| \\ &\geq -2\hat{\delta}(\sigma_0 - s_0), \qquad \forall \xi \in \mathbb{R}. \end{aligned}$$

Thus, by Lemma 10.2.2 (1),

$$\Phi_t(S^{n_k}(\phi_0)) \geq U(\cdot + \sigma_0 - 2K_0\hat{\delta}(\sigma_0 - s_0), t) - 2K_0\hat{\delta}(\sigma_0 - s_0)e^{-\rho_0 t},\ \forall t > 0.$$

Letting $t = (n_j - n_k)\omega$ and $j \to \infty$, we then get

$$\phi(\cdot) \geq U(\cdot + \sigma_0 - 2K_0\hat{\delta}(\sigma_0 - s_0), 0) \geq U(\cdot + (\sigma_0 + s_0)/2, 0).$$

Let $s_1 = \frac{1}{2}(\sigma_0 + s_0) \in (s_0, \sigma_0)$. Thus $\omega(\phi_0) \geq U(\cdot + s_1, 0)$. By Theorem 2.2.4, there exists $s_g \in (-a, a)$ such that $\omega(g) = h(s_g) = U(\cdot + s_g, 0)$. Then $\lim_{n \to \infty} S^n(g) = U(\cdot + s_g, 0)$, and hence $\lim_{t \to \infty} \|\Phi_t(g) - U(\cdot + s_g, t)\| = 0$. Since $u(z, t, g) = \Phi_t(g)(z - ct)$, we have

$$\lim_{t \to \infty} (u(z, t, g) - U(z - ct + s_g, t)) = 0$$

uniformly for $z \in \mathbb{R}$.

Let $\tilde{U}(z - \tilde{c}t, t)$ be a periodic traveling wave solution of (10.1a) with $\tilde{U}(\pm\infty, t) = w(\alpha^\pm, t)$. Clearly, $\tilde{U}(\cdot, 0)$ satisfies (10.12). By what we have proved above, there exists $\tilde{s} \in \mathbb{R}$ such that

$$\lim_{t \to \infty} \|\tilde{U}(\cdot - \tilde{c}t, t) - U(\cdot - ct + \tilde{s}, t)\| = 0.$$

By a change of variable $\xi = z - ct$, it then follows that

$$\lim_{t\to\infty} \|\tilde{U}(\cdot + (c-\tilde{c})t, t) - U(\cdot + \tilde{s}, t)\| = 0,$$

and hence, letting $t = n\omega$, we get

$$\lim_{n\to\infty} \tilde{U}(\cdot + (c-\tilde{c})n\omega, 0) = U(\cdot + \tilde{s}, 0).$$

Since $\tilde{U}(\pm\infty, 0) = \alpha^{\pm}$ and $U(\cdot, 0)$ is strictly increasing on $\mathbb{R}$, we deduce that $c = \tilde{c}$, and hence $\tilde{U}(\cdot, 0) = U(\cdot + \tilde{s}, 0)$. Thus, $\tilde{U}(\cdot, t) = \Phi_t(\tilde{U}(\cdot, 0)) = \Phi_t(U(\cdot + \tilde{s}, 0)) = U(\cdot + \tilde{s}, t)$, $\forall t \geq 0$. ∎

10.3 Exponential Stability of Traveling Waves

In Section 10.1 we established the existence of a traveling wave solution $(c, U(\xi, t))$ for (10.1a). Since (10.1a) is translation invariant in z, this traveling wave solution provides a one-dimensional manifold of special solutions to (10.1a):

$$\tilde{\mathcal{M}} = \{u(z, t) = U(z - ct - z_0, t) \ : \ z_0 \in \mathbb{R}\}.$$

By Theorem 10.2.1, $\tilde{\mathcal{M}}$ attracts a large class of solutions of (10.1). In this section we will show that the convergence is also uniformly exponential with respect to this class of solutions via spectral analysis.

As in the proof of Theorem 10.2.1, we use the traveling coordinates (ξ, t), where $\xi = z - ct$, and consider the resulting periodic-parabolic equation:

$$v_t - cv_\xi - v_{\xi\xi} - f(v, t) = 0, \quad \xi \in \mathbb{R}, \ t > 0. \tag{10.20}$$

Thus, the original problem now can be recast as the stability of the manifold of stationary states:

$$\mathcal{M} := \{v(\xi, t) = U(\xi + s, 0) \ : \ s \in \mathbb{R}\}$$

in the class of solutions of (10.20). Notice that any element in $\mathcal{M}$ is a fixed point of the Poincaré map $S : V = [\alpha^-, \alpha^+]_{\mathcal{X}} \to V$ associated with (10.20). Hence $\mathcal{M}$ is an invariant manifold of S. We are interested in the linearization of S about points in $\mathcal{M}$. Without loss of generality, we need only consider the point $U_0 = U(\cdot, 0)$. One can easily show that the derivative $S'(U_0)$ is given by $S'(U_0)v = H(\cdot, \omega)$, where $H(\xi, t)$ is the solution to

$$\begin{aligned} &H_t - cH_\xi - H_{\xi\xi} - f_u(U_0(\xi, t), t)H = 0, \quad \xi \in \mathbb{R}, t > 0, \\ &H(\cdot, 0) = v(\cdot). \end{aligned} \tag{10.21}$$

Lemma 10.3.1. *Let*

$$\nu^{\pm} = -\frac{1}{\omega}\int_0^{\omega} f_u(W^{\pm}(t), t)dt, \quad \nu_0 = \min\{\nu^+, \nu^-\}.$$

Then the essential spectrum of $S'(U_0)$ is contained in the disk $\{\lambda \in C : |\lambda| \leq e^{-\nu_0\omega}\}$. Thus, if λ is in the spectrum of $S'(U_0)$ and $|\lambda| > e^{-\nu_0\omega}$, then λ is an eigenvalue, and for any $r > e^{-\nu_0\omega}$, there are only a finite number of eigenvalues of $S'(U_0)$ in $\{\lambda \in C : |\lambda| \geq r\}$.

Proof. Let $\zeta(\cdot) \in C^\infty(\mathbb{R}, \mathbb{R})$ be a function satisfying $\zeta(\xi) = 0$ for $\xi \leq -1$, $\zeta(\xi) = 1$ for $\xi \geq 1$, and $\zeta' \geq 0$ in $\mathbb{R}$. Consider an operator $\mathcal{K}$ defined, for every bounded v, by $\mathcal{K}v = \hat{H}(\cdot, \omega)$, where $\hat{H}(\xi, t)$ is the solution to

$$\begin{aligned}
&\hat{H}_t - c\hat{H}_\xi - \hat{H}_{\xi\xi} + [\nu^+\zeta + \nu^-(1-\zeta)]\hat{H} = 0, \quad \xi \in \mathbb{R}, t > 0, \\
&\hat{H}(\cdot, 0) = v(\cdot).
\end{aligned}$$

Since $\nu^+\zeta + (1-\zeta)\nu^- \geq \nu_0$, the maximum principle shows that

$$\|\hat{H}(\cdot, t)\|_{L^\infty(\mathbb{R})} \leq e^{-\nu_0 t}\|v\|_{L^\infty(\mathbb{R})}, \ \forall t > 0.$$

In particular, $\|\mathcal{K}v\|_{L^\infty(\mathbb{R})} \leq e^{-\nu_0\omega}\|v\|_{L^\infty(\mathbb{R})}$. Therefore, the spectral radius of $\mathcal{K}$ is at most $e^{-\nu_0\omega}$.

To connect the essential spectrum of $S'(U_0)$ with that of $\mathcal{K}$, we make the following transformation for the solution of (10.21):

$$H(\xi, t) = \bar{H}(\xi, t)P(\xi, t),$$

where

$$\begin{aligned}
P(\xi, t) &= p^+(t)\zeta(\xi) + p^-(t)(1 - \zeta(\xi)), \\
p^\pm(t) &= \exp\Big(\int_0^t f_u(W^\pm(\tau), \tau)d\tau + \nu^\pm t\Big).
\end{aligned}$$

Note that $p^+(t), p^-(t), P(\cdot, t)$ are positive and periodic in t, and $p^\pm(\omega) = 1$, $P(\cdot, \omega) \equiv 1$. It then follows that $S'(U_0)v = H(\cdot, \omega) = \bar{H}(\cdot, \omega)$. Direct calculation shows that $\bar{H}$ satisfies

$$\bar{H}_t - \bar{c}(\xi, t)\bar{H}_\xi - \bar{H}_{\xi\xi} - \bar{q}\bar{H} = 0,$$

where

$$\begin{aligned}
\bar{c}(\xi, t) &= c + \tilde{c}(\xi, t), \qquad \tilde{c}(\xi, t) = 2(p^+ - p^-)\zeta'/P, \\
\bar{q} &= f_u(U_0, t) + [c(p^+ - p^-)\zeta' + (p^+ - p^-)\zeta'' - p_t^+\zeta - p_t^-(1-\zeta)]/P \\
&= -\nu^+\zeta - \nu^-(1-\zeta) + \tilde{q}(\xi, t), \\
\tilde{q}(\xi, t) &= (\tilde{q}_1(\xi, t) + \tilde{q}_2(\xi, t) + \tilde{q}_3(\xi, t))/P, \\
\tilde{q}_1(\xi, t) &= [f_u(U_0, t) - f_u(W^+(t), t)]p^+\zeta, \\
\tilde{q}_2(\xi, t) &= [f_u(U_0, t) - f_u(W^-(t), t)]p^-(1-\zeta), \\
\tilde{q}_3(\xi, t) &= \zeta(1-\zeta)(\nu^+ - \nu^-)(p^- - p^+) + (p^+ - p^-)(c\zeta' + \zeta'').
\end{aligned}$$

Notice that $\tilde{c} \equiv 0$ if $|\xi| \geq 1$ and $\tilde{q}$ approaches zero exponentially fast as $|\xi| \to \infty$. One can show that $\mathcal{K} - S'(U_0)$ is compact from $\mathcal{X}$ into $\mathcal{X}$ by using the fact that parabolic equations are smoothing.

Now by Weyl's well-known result, the essential spectrum of $S'(U_0)$ is the same as that of $\mathcal{K}$. Hence, $\tilde{\rho}(S'(U_0))$, the radius of the essential spectrum of $S'(U_0)$, is not bigger than $e^{-\nu_0\omega}$. ∎

Lemma 10.3.2. *Assume that λ is an eigenvalue of $S'(U_0)$ with eigenfunction v. If $v \notin span\{U_\xi(\cdot,0)\}$, then $|\lambda| < 1$.*

Proof. Assume that λ is an eigenvalue with eigenfunction $v \in \mathcal{X}$ and $v \notin \text{span}\{U_\xi(\cdot,0)\}$. Denote by $H(\xi,t)$ the solution of (10.21) with initial value v. Let

$$h(\xi,t) = e^{\mu t}H(\xi,t), \quad \text{where} \quad \mu = -\frac{1}{\omega}\text{Log}\lambda.$$

Then an easy calculation shows that (μ, h) satisfies

$$\begin{aligned} &h_t - ch_\xi - h_{\xi\xi} - f_u(U_0(\xi,t),t)h = \mu h, \quad \xi \in \mathbb{R},\, t > 0, \\ &h(\cdot,0) = h(\cdot,\omega). \end{aligned} \tag{10.22}$$

Hence (10.22) can be viewed as the spectral problem associated with the operator

$$L := \partial_t - c\partial_\xi - \partial_{\xi\xi} - f_u\left(U_0(\xi,t),t\right) \tag{10.23}$$

in an appropriate space of periodic functions.

The eigenvalue λ of the linearized period map $S'(U_0)$ is called a characteristic multiplier, while the associated μ is called a characteristic exponent. Since Log is multi-valued, it is easy to see that if (μ, h) is a characteristic exponent/eigenfunction pair, so is $(\mu + \frac{2\pi \mathrm{i} n}{\omega}, he^{\frac{2\pi \mathrm{i} n t}{\omega}})$, where $\mathrm{i} = \sqrt{-1}$. Notice that all these exponents produce the same multiplier.

Clearly, to show that $|\lambda| < 1$, we need only show that $\text{Re}(\mu)$, the real part of μ, is positive. Our proof is by contradiction. Assume that $\mu_1 := \text{Re}(\mu) \le 0$. Consider the polar representation of h: $h = re^{\mathrm{i}\theta}$, where both r and θ are real and $r \ge 0$. In the set where r does not vanish, θ is well defined and is smooth. Substituting this polar representation into (10.22) and taking the real part, we obtain

$$Lr = (\mu_1 - \theta_\xi^2)r \le 0$$

on the set where $r > 0$.

We first claim that $r \le MU_\xi$ for some M large enough. For this purpose, consider the periodic functions

$$Q^\pm(\xi,t) := e^{\gamma^\pm \xi}\exp\left(\int_0^t f_u(W^\pm(\tau),\tau)d\tau + \nu^\pm t\right),$$

where $\gamma^\pm = (-c \pm \sqrt{c^2 + 2\nu^\pm})/2$. An easy calculation shows that for some ξ_0 large enough,

$$\begin{aligned} LQ^\pm &= Q^\pm[f_u(W^\pm(t),t) - f_u(U_0,t) + \nu^\pm - c\gamma^\pm - (\gamma^\pm)^2] \\ &= Q^\pm[f_u(W^\pm(t),t) - f_u(U_0,t) + \nu^\pm/2] > 0 \end{aligned}$$

for all $|\xi| \geq \xi_0$ and $t \in \mathbb{R}$. Now let M_1 be a large constant such that $M_1 U_\xi(\pm\xi_0, t) > r(\pm\xi_0, t)$, $\forall t \in [0, \omega]$. We claim that $r < M_1 U_\xi$ in $[\xi_0, \infty) \times [0, \omega]$. In fact, if this is not true, then since $\nu^+ > 0$, we have $Q^+ \to \infty$ as $\xi \to \infty$, and so there exists $\delta \geq 0$ and $(\xi_1, t_1) \in (\xi_0, \infty) \times [0, \omega)$ such that $r \leq M_1 U_\xi + \delta Q^+$ in $[\xi_0, \infty) \times [0, \omega]$ and the equal sign holds at (ξ_1, t_1). Set $w = M_1 U_\xi + \delta Q^+ - r$. Then $Lw > 0$ in $[\xi_0, \infty) \times [0, 2\omega] \cap \{r \neq 0\}$. In addition, $w \geq 0$ in $[\xi_0, \infty) \times [0, 2\omega]$ and $w > 0$ on $\{r = 0\}$. Hence, applying locally the Harnack inequality to each of the components where r does not vanish, we have that $w > 0$ in $[\xi_0, \infty) \times (t_1, t_1 + \omega]$. This contradicts, by the periodicity of w, the assumption that $0 = w(\xi_1, t_1) = w(\xi_1, t_1 + \omega)$. Hence, $r < M_1 U_\xi$ in $[\xi_0, \infty) \times [0, \omega]$. Similarly, this inequality holds also on $(-\infty, -\xi_0] \times [0, \omega]$. Thus, there exists a positive M such that $r \leq M U_\xi$ in $\mathbb{R} \times [0, \omega]$.

Now let M_0 be the minimum real number such that $r \leq M_0 U_\xi$ in $\mathbb{R} \times [0, \omega]$. Consider the case that $r \not\equiv M_0 U_\xi$. Then, applying locally Harnack's inequality in the set where r does not vanish, we obtain $r < M_0 U_\xi$ in $\mathbb{R} \times [0, \omega]$. Consequently, there exists $\epsilon \in (0, M_0)$ such that $r < (M_0 - \epsilon) U_\xi$ in $[-\xi_0, \xi_0] \times [0, \omega]$. Then as before, utilizing the function $Q^\pm$, we can conclude that $r < (M_0 - \epsilon) U_\xi$ in $\mathbb{R} \times [0, \omega]$, which contradicts the definition of M_0. Hence $r \equiv M_0 U_\xi > 0$ in $\mathbb{R} \times [0, \omega]$. Consequently, $(\mu_1 - \theta_\xi^2) r \equiv 0$. Thus, $\mu_1 = 0$ and $\theta_\xi \equiv 0$. Using the θ equation, we then conclude that $\theta_t \equiv 0$, and hence θ is a constant function. That is, $h = re^{i\theta}$ is a multiple of U_ξ, which contradicts the assumption that $h \notin \operatorname{span}\{U_\xi\}$. This contradiction shows that $\operatorname{Re}(\mu) > 0$, i.e., $|\lambda| < 1$. ∎

Theorem 10.3.1. *There exists a positive constant $\mu > 0$ such that for every $g \in \mathcal{X}$ satisfying (10.12), the solution $u(z, t, g)$ of (10.1) satisfies*

$$|u(z, t, g) - U(z - ct + s_g, t)| \leq C_g e^{-\mu t}, \quad \forall\, z \in \mathbb{R},\, t \geq 0,$$

for some constants $s_g \in \mathbb{R}$ and $C_g > 0$.

Proof. Notice that $v = U_\xi(\cdot, 0)$ is an eigenfunction of $S'(U_0)$ with eigenvalue 1. This is a simple geometric fact, since $U_\xi(\cdot, 0)$ is the tangent to the one-dimensional invariant manifold $\mathcal{M}$ at $U(\cdot, 0)$. By Lemmas 10.3.1 and 10.3.2, it follows that 1 is a simple eigenvalue of $S'(U_0)$, and the rest of the spectrum of $S'(U_0)$ is contained in a disk of radius $\tilde{\rho}(S'(U_0))$ strictly less than 1. Thus, by a well-known result (see [150, Section 9.2]), the manifold $\mathcal{M}$ is locally exponentially stable with asymptotic phase for $S : V \to V$. By the fact that $\Phi_t(\cdot) : V \to V$ is an ω-periodic semiflow, together with Theorem 10.2.1, it then follows that there exists a positive constant $\mu > 0$ such that for every $g \in \mathcal{X}$ satisfying (10.12), $\Phi_t(g)$ satisfies

$$\|\Phi_t(g) - U(\cdot + s_g, t)\| \leq C_g e^{-\mu t}, \quad \forall\, t \geq 0,$$

for some constants s_g and C_g. In addition, the exponent μ can be taken arbitrarily close to $-\ln(\tilde{\rho}(S'(U_0)))$. ∎

10.4 Autonomous Case: A Spruce Budworm Model

In this section we consider the autonomous case of problem (10.1), i.e., $f(u,t) = f(u)$, $\forall (u,t) \in \mathbb{R}^2$. Biologically, this models a temporally homogeneous environment. Then we have the following problem:

$$\begin{aligned} &u_t - u_{zz} - f(u) = 0, \quad z \in \mathbb{R},\, t > 0, \\ &u(z,0) = g(z), \quad z \in \mathbb{R}, \end{aligned} \tag{10.24}$$

and the structure hypothesis on f reduces to

(H′) $f(\cdot,\cdot) \in C^{2,1}(\mathbb{R} \times \mathbb{R}, \mathbb{R})$, and f admits three zeros $\alpha^- < \alpha^0 < \alpha^+$ such that α^0 is the unique zero of f in (α^-, α^+) and $f'(\alpha^\pm) < 0$ and $f'(\alpha^0) > 0$.

Let $u(t, u_0)$ be the solution to the scalar autonomous equation

$$\begin{aligned} &\frac{du}{dt} = f(u), \quad t > 0, \\ &u(0) = u_0 \in \mathbb{R}. \end{aligned} \tag{10.25}$$

Then (10.25) generates a strongly monotone autonomous semiflow

$$\Phi_t^0(\cdot) := u(t,\cdot) : [\alpha^-, \alpha^+] \to [\alpha^-, \alpha^+].$$

Clearly, $\alpha^\pm$ are two linearly stable equilibria of $\Phi_t^0(\cdot)$, and α^0 is a linearly unstable equilibrium of $\Phi_t^0(\cdot)$. By the continuous-time version of the Dancer–Hess connecting orbit lemma, it easily follows that $\lim_{t\to\infty} u(t,u_0) = \alpha^-$ for each $u_0 \in [\alpha^-, \alpha^0)$, and $\lim_{t\to\infty} u(t,u_0) = \alpha^+$ for each $u_0 \in (\alpha^0, \alpha^+]$.

Theorem 10.4.1. *Let (H′) hold. Then (10.24a) admits a monotone traveling wave solution $U(z-ct)$ connecting α^- and α^+ such that any traveling wave solution of (10.24a) connecting α^- and α^+ is a translation of U. Moreover, the sign of the wave speed c is opposite to that of $\int_{\alpha^-}^{\alpha^+} f(u)du$, and there exists a positive constant $\mu > 0$ such that for every $g \in \mathcal{X}$ satisfying (10.12), the solution $u(z,t,g)$ of (10.24) satisfies*

$$|u(z,t,g) - U(z - ct + s_g)| \le C_g e^{-\mu t}, \quad \forall z \in \mathbb{R},\, t \ge 0,$$

for some constants $s_g \in \mathbb{R}$ and $C_g > 0$.

Proof. Let $f(u,t) := f(u)$, $\forall (u,t) \in \mathbb{R}^2$. Clearly, $f(u,\cdot)$ is ω-periodic for any $\omega > 0$. By Theorem 10.1.1, (10.24) has a monotone 1-periodic traveling wave solution $U(z-ct,t)$ connecting α^- and α^+, and for any integers $m,n > 0$, (10.24) also has a monotone $\frac{n}{m}$-periodic traveling wave solution $\bar{U}(z - \bar{c}t, t)$ connecting α^- and α^+. Since both $U(z-ct,t)$ and $\bar{U}(z-\bar{c}t,t)$ are monotone n-periodic traveling wave solutions, Theorem 10.2.1 with $\omega = n$ implies that $c = \bar{c}$ and for some $s \in \mathbb{R}$, $U(\xi,t) = \bar{U}(\xi + s, t)$, $\forall \xi \in \mathbb{R}$, $t \in \mathbb{R}$. Thus, for each

$\xi \in \mathbb{R}$, $U(\xi, \cdot)$ is also $\frac{n}{m}$-periodic, which implies $U(\xi, t) = U(\xi)$, $\forall \xi \in \mathbb{R}$, $t \in \mathbb{R}$. The exponential stability with phase shift then follows from Theorem 10.3.1. Note that $U(\xi)$ satisfies

$$cU_\xi + U_{\xi\xi} + f(U(\xi)) = 0, \quad \forall \xi \in \mathbb{R}. \tag{10.26}$$

Multiplying equation (10.26) by $U_\xi > 0$ and integrating from $-\infty$ to ∞, we get

$$\int_{-\infty}^{\infty} [U'U'' + c(U')^2 + f(U)U']d\xi = 0.$$

Since $U'(\pm\infty) = 0, U(\pm\infty) = \alpha^\pm$, this can be integrated to give

$$c\int_{-\infty}^{\infty} (U')^2 d\xi = -\int_{-\infty}^{\infty} f(U)U' d\xi = -\int_{\alpha^-}^{\alpha^+} f(U)dU,$$

and hence the sign of c is opposite to that of $\int_{\alpha^-}^{\alpha^+} f(u)du$. ∎

A practical model that exhibits two positive linearly stable steady state populations is that for the spruce budworm, which can, with ferocious efficiency, defoliate the balsam fir. Ludwig et al. [238] presented a budworm population model

$$\frac{dN}{dt} = r_B N\left(1 - \frac{N}{K_B}\right) - \frac{BN^2}{A^2 + N^2}. \tag{10.27}$$

Here r_B is the linear birth rate of the budworm, and K_B is the carrying capacity, which is related to the density of foliage available on the trees. The term $\frac{BN^2}{A^2+N^2}$ with $A, B > 0$ represents predation, generally by birds. If we introduce nondimensional quantities by

$$u = \frac{N}{A}, \quad r = \frac{Ar_B}{B}, \quad q = \frac{K_B}{A}, \quad \tau = \frac{Bt}{A}, \tag{10.28}$$

then equation (10.27) becomes

$$\frac{du}{d\tau} = f(u; r, q) := ru\left(1 - \frac{u}{q}\right) - \frac{u^2}{1 + u^2}. \tag{10.29}$$

Clearly, the positive steady states are solutions of

$$r\left(1 - \frac{u}{q}\right) = \frac{u}{1 + u^2}.$$

That is, the positive equilibria are given by the intersections on the (u, v)-plane of the straight line $v = r(1 - u/q)$ and $v = \frac{u}{1+u^2}$. It easily follows that there is a domain in the r, q parameter space where there are exactly three positive equilibria $\alpha^- < \alpha^0 < \alpha^+$ and $f'(\alpha^\pm) < 0$ and $f'(\alpha^0) > 0$.

Field observation shows that there are three possible positive steady states for the population. The smallest steady state α^- is the refuge equilibrium, while α^+ is the outbreak equilibrium. From a pest control point of view, we should try to keep the population at a refuge state rather than allow it to reach an outbreak situation. In order to take into account the spatial dispersal of the budworm, we consider the reaction–diffusion model

$$u_t - u_{zz} - f(u; r, q) = 0, \quad z \in \mathbb{R},\, t > 0. \tag{10.30}$$

By Theorem 10.4.1, (10.30) has a monotone traveling wave $U(z - ct)$ connecting α^- and α^+, and it is globally asymptotically stable with phase shift. If $c < 0$, then $u \to \alpha^+$ as $t \to \infty$, and hence the outbreak spreads into the refuge area. On the other hand, if $c > 0$, then $u \to \alpha^-$ as $t \to \infty$, and hence the outbreak is eliminated. Now there is a practical question:

If a budworm outbreak occurs and is spreading, how can we alter the local conditions so that the infestation or outbreak wave is either contained or reversed?

From the above, we must thus locally change the budworm growth dynamics so that the wave speed c becomes positive. By Theorem 10.4.1, we need to require

$$\int_{\alpha^-}^{\alpha^+} f(u)du = \int_{\alpha^-}^{\alpha^0} f(u)du + \int_{\alpha^0}^{\alpha^+} f(u)du < 0.$$

Clearly, $\int_{\alpha^-}^{\alpha^0} f(u)du < 0$ and $\int_{\alpha^0}^{\alpha^+} f(u)du > 0$. Thus $c > 0$ if α^0 and α^+ are very close together. Note that the curve $v = \frac{u}{1+u^2}$ is fixed on the (u, v)-plane, but we can change the straight line $v = r(1 - u/q)$. Thus we can make α^0 and α^+ closer by reducing the dimensionless parameter q. Recall that $q = \frac{K_B}{A}$. So a practical reduction in q could be made by, for example, spraying a strip to reduce the carrying capacity of the tree foliage. In this way an infestation "break" would be created, and hence the wave speed c in the above analysis is no longer negative. A more practical question, of course, is how wide such a "break" must be to stop the outbreak getting through, which needs careful modeling consideration.

10.5 Notes

All results in Sections 10.1–10.3 are due to Alikakos, Bates and Chen [8], and the proofs of them are modified from [8]. In the proof of Theorem 10.1.1, we did not use the uniqueness of solutions to equation (10.6). In the proof of Theorem 10.2.1, we first applied Theorem 2.2.4 to prove the global attractivity with phase shift of the given monotone periodic traveling wave, and then obtain easily the uniqueness of periodic traveling waves. The biological interpretations for traveling waves in a spruce budworm model in Section 10.4 is adapted from Murray [253, Section 11.5].

There are many investigations on traveling waves in bistable nonlinearities. The global exponential stability in Theorem 10.4.1 is due to Fife and McLeod [116]. Theorem 10.4.1 is a special case of Chen [59] concerning the existence, uniqueness, and asymptotic stability of traveling waves in nonlocal evolution equations. The results on periodic traveling waves in [8] were also extended to a more general periodic nonlocal integro–differential model by Bates and Chen [30]. Schaaf [301] studied the existence of traveling waves in delayed reaction–diffusion equations, and the global exponential stability and uniqueness were proved by Smith and Zhao [338]. Shen [306, 307] investigated these problems for almost periodic traveling wave solutions. Ogiwara and Matano [265] discussed the monotonicity and stability with phase shift of pseudo-traveling waves for certain class of quasilinear diffusion equations and systems in the setting of order-preserving dynamical systems under a group action.

A general theory of bistable waves for monotone semiflows was developed by Fang and Zhao [111], where the existence of bistable waves was also obtained for time-periodic and cooperative reaction–diffusion systems. This theory and Theorem 2.2.4 were used to study the existence and global stability of bistable waves in Zhang and Zhao [426] for a reaction–diffusion competition model with seasonal succession and in Bao and Wang [28] for a periodic Lotka–Volterra competition system. The dynamical systems approach via Theorem 2.2.4 to the global stability of traveling waves was employed in Xu and Zhao [416] for a reaction–diffusion system modeling man–environment–man epidemics; in Jin and Zhao [196] for a class of degenerate reaction–diffusion systems; and in Ding, Hamel and Zhao [99] for scalar reaction–diffusion equations in a periodic habitat. Recently, the existence and qualitative properties of transition fronts were also investigated in Ding, Hamel and Zhao [98] for spatially periodic reaction–diffusion equations with bistable nonlinearities.

11

The Theory of Basic Reproduction Ratios

The basic reproduction number (ratio) R_0 is one of the most important concepts in population biology, see, e.g., [16, 94, 148, 149, 78] and the references therein. In epidemiology, R_0 is the expected number of secondary cases produced, in a completely susceptible population, by a typical infective individual during the infectious period, and R_0 is also a commonly used measure of the effort needed to control an infectious disease. Diekmann, Heesterbeek and Metz [95] introduced the next generation matrices (NGM) approach to R_0 for models of infectious diseases in heterogeneous populations; van den Driessche and Watmough [376] developed the theory of R_0 for autonomous ordinary differential equations (ODE) models with compartmental structure; and Diekmann, Heesterbeek and Roberts [96] provided a recipe for the construction of the NGM for compartmental epidemic models. These works have found numerous applications in the study of various models of infectious diseases. For population models in a periodic environment, Bacaër and Guernaoui [24] proposed a general definition of R_0, that is, R_0 is the spectral radius of an integral operator on the space of continuous periodic functions. Wang and Zhao [388] characterized R_0 for periodic compartmental ODE models and proved that it is a threshold parameter for the local stability of the disease-free periodic solution. Further, Thieme [370] presented the theory of spectral bound and reproduction number for infinite-dimensional population structure and time heterogeneity. Bacaër and Ait Dads [22, 23] also found a more biological interpretation of R_0 for periodic models and showed that it is the asymptotic ratio of total infections in two successive generations of the infection tree. Recently, Inaba [189] introduced the concept of a generation evolution operator to give a new definition of R_0 for structured populations in heterogeneous environments, which unifies two definitions in [95, 24] and has intuitively clear biological meaning.

The purpose of this chapter is to present the theory of basic reproduction ratios R_0 for two important classes of population models with compartmental structure. In Section 11.1, we first introduce R_0 for periodic and time-delayed

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models, then prove the stability equivalence theorem and give a characterization of R_0. We also obtain an explicit formula for R_0 in the autonomous case. In Section 11.2, we apply the developed theory of R_0, together with the persistence theory for periodic semiflows, to a periodic SEIR model of a disease transmission, and establish a threshold-type result on its global dynamics in terms of R_0.

In Section 11.3, we develop the theory of R_0 for reaction–diffusion epidemic models. We formulate R_0 as the spectral radius of the next generation operator induced by a new infection rate matrix and an evolution operator of an infective distribution, and characterize R_0 in terms of the principal eigenvalue of an elliptic eigenvalue problem. In Section 11.4, we apply the obtained results to a spatial model of rabies, and show that the disease-free steady state is asymptotically stable if $R_0 < 1$, and unstable if $R_0 > 1$. At the end of this section, we also provide a numerical scheme to compute R_0.

11.1 Periodic Systems with Time Delay

Let $\tau \geq 0$ be a given number, $C = C([-\tau, 0], \mathbb{R}^m)$, and $C^+ = C([-\tau, 0], \mathbb{R}^m_+)$. Then (C, C^+) is an ordered Banach space equipped with the maximum norm and the positive cone C^+. Let $F : \mathbb{R} \to \mathcal{L}(C, \mathbb{R}^m)$ be a map and $V(t)$ be a continuous $m \times m$ matrix function on $\mathbb{R}$. Assume that $F(t)$ and $V(t)$ are ω-periodic in t for some real number $\omega > 0$. For a continuous function $u : [-\tau, \sigma) \to \mathbb{R}^m$ with $\sigma > 0$, define $u_t \in C$ by

$$u_t(\theta) = u(t + \theta), \quad \forall \theta \in [-\tau, 0]$$

for any $t \in [0, \sigma)$.

We consider a linear and periodic functional differential system:

$$\frac{du(t)}{dt} = F(t)u_t - V(t)u(t), \quad t \geq 0. \tag{11.1}$$

System (11.1) may come from the equations of infectious variables in the linearization of a given ω-periodic and time-delayed compartmental epidemic model at a disease-free ω-periodic solution. As such, m is the total number of the infectious compartments, and the newly infected individuals at time t depend linearly on the infectious individuals over the time interval $[t - \tau, t]$, which is described by $F(t)u_t$. Further, the internal evolution of individuals in the infectious compartments (e.g., natural and disease-induced deaths, and movements among compartments) is governed by the linear ordinary differential system:

$$\frac{du(t)}{dt} = -V(t)u(t). \tag{11.2}$$

Of course, we may also obtain system (11.1) by linearizing a population growth model with m patches (or types) at its zero solution, where the word "birth" should be used to replace "infection."

Throughout this section, we assume that $F(t) : C \to \mathbb{R}^m$ is given by

$$F(t)\phi = \int_{-\tau}^{0} d[\eta(t,\theta)]\phi(\theta), \quad \forall t \in \mathbb{R},\ \phi \in C,$$

where $\eta(t,\theta)$ is an $m \times m$ matrix function which is measurable in $(t,\theta) \in \mathbb{R}\times\mathbb{R}$ and normalized so that $\eta(t,\theta) = 0$ for all $\theta \geq 0$ and $\eta(t,\theta) = \eta(t,-\tau)$ for all $\theta \leq -\tau$. Further, $\eta(t,\theta)$ is continuous from the left in θ on $(-\tau, 0)$ for each t, and the variation of $\eta(t,\cdot)$ on $[-\tau, 0]$ satisfies $Var_{[-\tau,0]}\eta(t,\cdot) \leq g(t)$ for some $g \in \mathcal{L}_1^{\mathrm{loc}}((-\infty,\infty),\mathbb{R})$, the space of functions from $(-\infty,\infty)$ into $\mathbb{R}$ that are Lebesgue integrable on each compact set of $(-\infty,\infty)$. Since $F(t)$ is ω-periodic in t, we have

$$\sup_{t\in\mathbb{R}} \|F(t)\| = \sup_{0\leq t\leq\omega} \|F(t)\| \leq \sup_{0\leq t\leq\omega} g(t).$$

By the general theory of linear functional differential equations in [145, section 6.1], it follows that for any $s \in \mathbb{R}$ and $\phi \in C$, system (11.1) has a unique solution $u(t,s,\phi)$ on $[s,\infty)$ with $u_s = \phi$. We define the evolution operators $U(t,s)$ on C associated with (11.1) as

$$U(t,s)\phi = u_t(s,\phi),\ \forall \phi \in C,\ t \geq s,\ s \in \mathbb{R},$$

where $u_t(s,\phi)(\theta) = u(t+\theta,s,\phi)$, $\forall \theta \in [-\tau,0]$. Then each operator $U(t,s)$ is continuous and

$$U(s,s) = I,\ U(t,s)U(s,r) = U(t,r),\ U(t+\omega,s+\omega) = U(t,s),\ \forall t \geq s \geq r. \tag{11.3}$$

Let $\Phi(t,s)$, $t \geq s$, be the evolution matrices associated with system (11.2), that is, $\Phi(t,s)$ satisfies

$$\frac{\partial}{\partial t}\Phi(t,s) = -V(t)\Phi(t,s),\ \forall t \geq s, \quad \text{and} \quad \Phi(s,s) = I,\ \forall s \in \mathbb{R},$$

and $\hat{\omega}(\Phi)$ be the exponential growth bound of $\Phi(t,s)$, that is,

$$\hat{\omega}(\Phi) = \inf\{\tilde{\omega} :\ \exists M \geq 1 \text{ such that } \|\Phi(t+s,s)\| \leq Me^{\tilde{\omega}t},\ \forall s \in \mathbb{R},\ t \geq 0\}.$$

In order to introduce the basic reproduction ratio for system (11.1), throughout this section we always assume that

(A1) Each operator $F(t) : C \to \mathbb{R}^m$ is positive in the sense that $F(t)C^+ \subseteq \mathbb{R}^m_+$;
(A2) Each matrix $-V(t)$ is cooperative, and $\hat{\omega}(\Phi) < 0$.

In view of the periodic environment, we suppose that $v(t)$, ω-periodic in t, is the distribution of the initial infectious individuals among compartments at time t. For any given $s \geq 0$, $F(t-s)v_{t-s}$ is the distribution of newly infected individuals at time $t-s$, which is produced by the infectious individuals who were introduced over the time interval $[t-s-\tau, t-s]$. Then $\Phi(t,t-s)F(t-s)$

v_{t-s} is the distribution of those infected individuals who were newly infected at time $t-s$ and remain in the infected compartments at time t. It follows that

$$\int_0^\infty \Phi(t,t-s)F(t-s)v_{t-s}ds = \int_0^\infty \Phi(t,t-s)F(t-s)v(t-s+\cdot)ds$$

is the distribution of accumulative new infections at time t produced by all those infectious individuals introduced at all previous times to t.

Note that for any given $s \geq 0$, $\Phi(t,t-s)v(t-s)$ gives the distribution of those infectious individuals who were introduced at time $t-s$ and remain in the infected compartments at time t, and hence, $w(t) := \int_0^\infty \Phi(t,t-s)v(t-s)ds$ is the distribution of accumulative infectious individuals who were introduced at all previous times to t and remain in the infected compartments at time t. Thus, the distribution of newly infected individuals at time t is

$$F(t)w_t = F(t)\left(\int_0^\infty \Phi(t+\cdot,t-s+\cdot)v(t-s+\cdot)ds\right).$$

Let C_ω be the ordered Banach space of all continuous and ω-periodic functions from $\mathbb{R}$ to $\mathbb{R}^m$, which is equipped with the maximum norm and the positive cone $C_\omega^+ := \{v \in C_\omega : \ v(t) \geq 0, \forall t \in \mathbb{R}\}$. Then we can define two linear operators on C_ω by

$$[Lv](t) = \int_0^\infty \Phi(t,t-s)F(t-s)v(t-s+\cdot)ds, \ \forall t \in \mathbb{R}, \, v \in C_\omega,$$

and

$$[\hat{L}v](t) = F(t)\left(\int_0^\infty \Phi(t+\cdot,t-s+\cdot)v(t-s+\cdot)ds\right), \ \forall t \in \mathbb{R}, \, v \in C_\omega.$$

Let A and B be two bounded linear operators on C_ω defined by

$$[Av](t) = \int_0^\infty \Phi(t,t-s)v(t-s)ds, \ [Bv](t) = F(t)v_t, \forall t \in \mathbb{R}, \, v \in C_\omega.$$

It then follows that $L = A \circ B$ and $\hat{L} = B \circ A$, and hence, L and $\hat{L}$ have the same spectral radius.

Motivated by the concept of next generation operators in [95, 376, 24, 388, 370], we define the spectral radius of L and $\hat{L}$ as the basic reproduction ratio

$$R_0 := r(L) = r(\hat{L}).$$

for periodic system (11.1).

For any given $\lambda \in \mathbb{R}$, let E_λ be a linear operator on C defined by

$$[E_\lambda \phi](\theta) = e^{\lambda\theta}\phi(\theta), \ \forall \theta \in [-\tau, 0], \, \phi \in C.$$

It then easily follows that $\|E_\lambda\| \le \max\{1, e^{-\lambda\tau}\}$, $\forall \lambda \in \mathbb{R}$. Now we introduce a family of linear operators L_λ on C_ω:

$$[L_\lambda v](t) = \int_0^\infty e^{-\lambda s} \Phi(t, t-s) F(t-s) E_\lambda v(t-s+\cdot) ds, \ \forall t \in \mathbb{R}, \ v \in C_\omega. \quad (11.4)$$

Clearly, $L_0 = L$, and L_λ is well defined for all $\lambda > \hat{\omega}(\Phi)$. Further, we have the following observation.

Lemma 11.1.1. *For each $\lambda > \hat{\omega}(\Phi)$, the operator L_λ is positive, continuous, and compact on C_ω.*

Proof. Let $\lambda > \hat{\omega}(\Phi)$ be given. Clearly, E_λ is a positive linear operator on C. By virtue of (A1) and (A2), $F(t)$ and $\Phi(t,s)$ $(t \ge s)$ are positive linear operators. This implies that L_λ is positive on C_ω. Since $\hat{\omega}(\Phi) < 0$ and

$$\|\Phi(t, t-s) F(t-s) E_\lambda\| \le M_0 e^{\hat{\omega}(\Phi)s} \cdot \sup_{0 \le r \le \omega} g(r) \cdot \|E_\lambda\|, \ \forall t \in \mathbb{R}, \ s \in [0, \infty),$$

for some $M_0 > 0$, we see that L_λ is bounded, and hence, continuous on C_ω. In view of

$$[L_\lambda v](t) = \int_{-\infty}^t e^{-\lambda(t-s)} \Phi(t,s) F(s) E_\lambda v_s ds, \quad \forall t \in \mathbb{R}, \ v \in C_\omega,$$

we easily obtain

$$\frac{d}{dt}[L_\lambda v](t) = F(t) E_\lambda v_t - (V(t) + \lambda I)[L_\lambda v](t), \quad \forall t \in \mathbb{R}, \ v \in C_\omega. \qquad (11.5)$$

It then follows that for any $a > 0$, there exists $K = K(a) > 0$ such that $|\frac{d}{dt}[L_\lambda v](t)| \le K$ for all $t \in [0, \omega]$ and $v \in C_\omega$ with $\|v\| \le a$. Thus, the Ascoli-Arzela theorem implies that L_λ is compact on C_ω. ∎

Let $M_0 > 0$ be fixed such that $\|\Phi(t,s)\| \le M_0 e^{\hat{\omega}(\Phi)(t-s)}$, $\forall t \ge s$. For any given $\epsilon > 0$, we set $V_\epsilon(t) = V(t) - \epsilon E$, where E is the $m \times m$ matrix with each element being 1. Let $\Phi_\epsilon(t,s)$ be the evolution operators associated with the linear periodic system $\frac{du(t)}{dt} = -V_\epsilon(t) u(t)$. Then we have the following estimate.

Lemma 11.1.2. *Let $c = \epsilon M_0 \|E\|$. Then for any $\epsilon > 0$, there holds*

$$\|\Phi_\epsilon(t, t-s) - \Phi(t, t-s)\| \le c M_0 s e^{(\hat{\omega}(\Phi) + c)s}, \ \forall t \in \mathbb{R}, \ s \ge 0.$$

Proof. By the constant-variation formula, we obtain

$$\Phi_\epsilon(t,s)x = \Phi(t,s)x + \int_s^t \Phi(t,r) \epsilon E \Phi_\epsilon(r,s) x dr, \ \forall t \ge s, \ s \in \mathbb{R}, \ x \in \mathbb{R}^m.$$

This implies that $\Phi_\epsilon(t,s)$ satisfies the abstract Volterra integral equation:

$$\Phi_\epsilon(t,s) = \Phi(t,s) + \int_s^t \Phi(t,r)\epsilon E \Phi_\epsilon(r,s)dr, \ \forall t \geq s, \ s \in \mathbb{R}. \tag{11.6}$$

Let $h_1(t,s) := \Phi(t,s)\epsilon E$, and define

$$h_n(t,s) = \int_s^t h_1(t,r)h_{n-1}(r,s)dr, \ \forall n \geq 2.$$

Since $\|h_1(t,s)\| \leq ce^{\hat{\omega}(\Phi)(t-s)}$, $\forall t \geq s, \ s \in \mathbb{R}$, it follows from an induction argument that

$$\|h_n(t,s)\| \leq \frac{c^n}{(n-1)!} e^{\hat{\omega}(\Phi)(t-s)}(t-s)^{n-1}, \ \forall n \geq 1, \ t \geq s, \ s \in \mathbb{R},$$

and hence, $\sum_{n=1}^\infty \|h_n(t,s)\| \leq ce^{(\hat{\omega}(\Phi)+c)(t-s)}$. Thus, the linear operator $h(t,s) := \sum_{n=1}^\infty h_n(t,s)$ is well defined for any $t \geq s, s \in \mathbb{R}$, and $\|h(t,s)\| \leq ce^{(\hat{\omega}(\Phi)+c)(t-s)}$. By the proof of [89, Theorem 9.1], $\Phi_\epsilon(t,s)$ can be represented as

$$\Phi_\epsilon(t,s) = \Phi(t,s) + \int_s^t h(t,r)\Phi(r,s)dr, \ \forall t \geq s, \ s \in \mathbb{R}. \tag{11.7}$$

It then follows that

$$\begin{aligned}
\|\Phi_\epsilon(t,t-s) - \Phi(t,t-s)\| &\leq \int_{t-s}^t \|h(t,r)\| \cdot \|\Phi(r,t-s)\|dr \\
&\leq \int_{t-s}^t ce^{(\hat{\omega}(\Phi)+c)(t-r)} M_0 e^{\hat{\omega}(\Phi)(r-(t-s))}dr \\
&= M_0 e^{\hat{\omega}(\Phi)s}(e^{cs}-1) \\
&\leq cM_0 s e^{(\hat{\omega}(\Phi)+c)s}, \ \ \forall t \in \mathbb{R}, \ s \geq 0.
\end{aligned}$$

Here we have used the inequality that $e^{cs} - 1 \leq cse^{cs}$, $\forall s \geq 0$. ∎

For any $\lambda > \hat{\omega}(\Phi)$, let $\mu(\lambda)$ be the spectral radius of L_λ, that is, $\mu(\lambda) := r(L_\lambda)$. Then we have the following two results on properties of the function $\mu(\lambda)$.

Proposition 11.1.1. *The following statements are valid:*

(i) $\mu(\lambda)$ *is continuous and nonincreasing on* $(\hat{\omega}(\Phi), \infty)$, *and* $\mu(\infty) = 0$.
(ii) $\mu(\lambda) = 1$ *has at most one solution in* $(\hat{\omega}(\Phi), \infty)$.

Proof. (i) Let $\lambda_0 \in (\hat{\omega}(\Phi), \infty)$ be given and choose a small number $\delta > 0$ such that $[\lambda_0 - \delta, \lambda_0 + \delta] \subset (\hat{\omega}(\Phi), \infty)$. It is easy to see that

$$\|E_\lambda - E_{\lambda_0}\| \leq \tau \max\{1, e^{-(\lambda_0-\delta)\tau}\}|\lambda - \lambda_0|, \ \forall \lambda \in [\lambda_0 - \delta, \lambda_0 + \delta].$$

As a result, there exist two positive numbers K_1 and K_2 such that for any $\lambda \in [\lambda_0 - \delta, \lambda_0 + \delta]$, we have

$$\begin{aligned}\|L_\lambda - L_{\lambda_0}\| &\le K_1 \int_0^\infty \left|e^{-\lambda s} - e^{-\lambda_0 s}\right| e^{\hat{\omega}(\Phi)s} ds + \\ &\quad K_2|\lambda - \lambda_0| \int_0^\infty e^{-\lambda_0 s} e^{\hat{\omega}(\Phi)s} ds \\ &\le K_1|\lambda - \lambda_0| \int_0^\infty s e^{-(\lambda_0-\delta)s} e^{\hat{\omega}(\Phi)s} ds + \\ &\quad K_2|\lambda - \lambda_0| \int_0^\infty e^{-\lambda_0 s} e^{\hat{\omega}(\Phi)s} ds \\ &= \frac{K_1|\lambda-\lambda_0|}{(\lambda_0 - \delta - \hat{\omega}(\Phi))^2} + \frac{K_2|\lambda - \lambda_0|}{\lambda_0 - \hat{\omega}(\Phi)}.\end{aligned}$$

This implies that $\lim_{\lambda\to\lambda_0} \|L_\lambda - L_{\lambda_0}\| = 0$. By the continuity of spectral radius for compact linear operators (see, e.g., [90, Theorem 2.1 (a)]), we then obtain that $\lim_{\lambda\to\lambda_0} \mu(\lambda) = \mu(\lambda_0)$. Thus, $\mu(\lambda)$ is continuous on $(\hat{\omega}(\Phi), \infty)$. It is easy to verify that

$$[L_{\lambda_1} v](t) \ge [L_{\lambda_2} v](t),\ \forall \hat{\omega}(\Phi) < \lambda_1 \le \lambda_2,\ t \in \mathbb{R},\ v \in C_\omega^+.$$

Since each L_λ is a positive and bounded linear operator on C_ω, [40, Theorem 1.1] implies that $\mu(\lambda) = r(L_\lambda)$ is a nonincreasing function of λ on $(\hat{\omega}(\Phi), \infty)$. Note that $\|\Phi(t,s)\| \le M_0 e^{\hat{\omega}(\Phi)(t-s)}$, $\forall t \ge s$, and $\|E_\lambda\| \le 1$, $\forall \lambda \ge 0$. It then follows that

$$\|L_\lambda\| \le M_0 \sup_{0\le t\le\omega} \|F(t)\| \int_0^\infty e^{-\lambda s} e^{\hat{\omega}(\Phi)s} ds = \frac{M_0 \sup_{0\le t\le\omega} \|F(t)\|}{\lambda - \hat{\omega}(\Phi)},\ \forall \lambda \ge 0.$$

In view of $0 \le \mu(\lambda) = r(L_\lambda) \le \|L_\lambda\|$, we obtain $\mu(\infty) = \lim_{\lambda\to\infty} \mu(\lambda) = 0$.

(ii) Assume, by contradiction, that $\mu(\lambda) = 1$ has two solutions $\lambda_1 < \lambda_2$ in $(\hat{\omega}(\Phi), \infty)$. Since $\mu(\lambda)$ is nonincreasing on $(\hat{\omega}(\Phi), \infty)$, we must have $\mu(\lambda) = 1$, $\forall \lambda \in [\lambda_1, \lambda_2]$. Let $\lambda \in [\lambda_1, \lambda_2]$ be given. Since L_λ is a positive and compact linear operator on C_ω and $r(L_\lambda) = \mu(\lambda) = 1 > 0$, the Krein-Rutman theorem implies that $L_\lambda v = v$ for some $v \in C_\omega^+ \setminus \{0\}$. By virtue of (11.5), we obtain

$$\frac{d}{dt} v(t) = F(t) E_\lambda v_t - (V(t) + \lambda I) v(t), \quad \forall t \in \mathbb{R}.$$

Let $u(t) := e^{\lambda t} v(t)$. Since $u_t = e^{\lambda t} E_\lambda v_t$, $\forall t \in \mathbb{R}$, it follows from a straightforward computation that

$$\frac{d}{dt} u(t) = F(t) u_t - V(t) u(t), \quad \forall t \in \mathbb{R}.$$

Set $\phi := u_0 = E_\lambda v_0$. Then $U(t,0)\phi = u_t$, $\forall t \ge 0$, which implies that $\phi \in C^+ \setminus \{0\}$ since $u(\cdot) \not\equiv 0$ on $[0, \infty)$. Clearly, the ω-periodicity of $v(t)$ yields $v_{t+\omega} = v_t$, $\forall t \in \mathbb{R}$. In particular, we have

$$U(\omega, 0)\phi = u_\omega = e^{\lambda\omega} E_\lambda v_\omega = e^{\lambda\omega} E_\lambda v_0 = e^{\lambda\omega}\phi.$$

It follows that $e^{\lambda\omega}$ is an eigenvalue of $U(\omega,0)$, and hence $e^{\lambda n\omega}$ is an eigenvalue of $U(n\omega,0)=(U(\omega,0))^n$ for any integer $n\geq 1$. Now we fix an integer $n_0>0$ such that $n_0\omega\geq\tau$. By [145, Theorem 3.6.1], the operator $U(n_0\omega,0)$ is compact on C. Thus, $e^{\lambda n_0\omega}$ is an eigenvalue of $U(n_0\omega,0)$ for all $\lambda\in[\lambda_1,\lambda_2]$. But this is impossible since the compact linear operator $U(n_0\omega,0)$ has only countably many eigenvalues. ∎

Proposition 11.1.2. *If $r(U(\omega,0))>r(\Phi(\omega,0))$, then $\lambda^*:=\frac{\ln r(U(\omega,0))}{\omega}$ satisfies $\mu(\lambda^*)=1$.*

Proof. For any given $\epsilon>0$, let $V_\epsilon(t)$ and $\Phi_\epsilon(t,s)$ be defined as in Lemma 11.1.2, and define $F_\epsilon(t)\phi=F(t)\phi+\epsilon\phi(-\tau)$, $\forall\phi\in C$. We consider small perturbations of system (11.1):

$$\frac{du(t)}{dt}=F_\epsilon(t)u_t-V_\epsilon(t)u(t),\quad t\geq 0. \tag{11.8}$$

Let $U_\epsilon(t,s)$ be the evolution operators associated with the linear functional differential system (11.8). By [370, Proposition A.2], it follows that $\hat{\omega}(\Phi_\epsilon)=\frac{\ln r(\Phi_\epsilon(\omega,0))}{\omega}$. Since $\hat{\omega}(\Phi)<0$, we have $\hat{\omega}(\Phi_\epsilon)<0$ for sufficiently small $\epsilon>0$. Let L_λ^ϵ be defined as in (11.4) with $F(t)$ and $\Phi(t,s)$ replaced by $F_\epsilon(t)$ and $\Phi_\epsilon(t,s)$, respectively. By [326, Lemma 5.3.2], $U_\epsilon(t,0)$ is strongly positive on C for any $t\geq(m+1)\tau$. Choose an integer $n_0>0$ such that $n_0\omega\geq(m+1)\tau$. Since $(U_\epsilon(\omega,0))^{n_0}=U_\epsilon(n_0\omega,0)$ is compact and strongly positive, [225, Lemma 3.1] implies that $r(U_\epsilon(\omega,0))$ is a simple eigenvalue of $U_\epsilon(\omega,0)$ having a strongly positive eigenvector, and the modulus of any other eigenvalue is less than $r(U_\epsilon(\omega,0))$. Let $\lambda_\epsilon^*:=\frac{\ln r(U_\epsilon(\omega,0))}{\omega}$. By the proof of [417, Proposition 2.1], it then follows that there is a positive ω-periodic function $v^\epsilon(t)$ such that $u^\epsilon(t)=e^{\lambda_\epsilon^* t}v^\epsilon(t)$ is a positive solution of (11.8) for all $t\in\mathbb{R}$. Thus, the constant-variation formula yields

$$u^\epsilon(t)=\Phi_\epsilon(t,r)u^\epsilon(r)+\int_r^t\Phi_\epsilon(t,s)F_\epsilon(s)u_s^\epsilon ds,\ \forall t\geq r,\ r\in\mathbb{R}. \tag{11.9}$$

On substituting $u^\epsilon(t)=e^{\lambda_\epsilon^* t}v^\epsilon(t)$ into (11.9), we obtain

$$v^\epsilon(t)=e^{-\lambda_\epsilon^*(t-r)}\Phi_\epsilon(t,r)v^\epsilon(r)+\int_r^t e^{-\lambda_\epsilon^*(t-s)}\Phi_\epsilon(t,s)F_\epsilon(s)E_{\lambda_\epsilon^*}v_s^\epsilon ds \tag{11.10}$$

for all $t\geq r$, $r\in\mathbb{R}$. Since $\lim_{\epsilon\to 0^+}(r(U_\epsilon(\omega,0))-r(\Phi_\epsilon(\omega,0))=r(U(\omega,0))-r(\Phi(\omega,0))>0$, it follows that $r(U_\epsilon(\omega,0))-r(\Phi_\epsilon(\omega,0))>0$, and hence, $\lambda_\epsilon^*>\hat{\omega}(\Phi_\epsilon)$, for sufficiently small $\epsilon>0$. Note that the positive ω-periodic function $v^\epsilon(t)$ is bounded on $\mathbb{R}$, and

$$\|e^{-\lambda_\epsilon^*(t-r)}\Phi_\epsilon(t,r)\|\leq M_\epsilon e^{(\hat{\omega}(\Phi_\epsilon)-\lambda_\epsilon^*)(t-r)},\ \forall t\geq r,\ r\in\mathbb{R},$$

for some number $M_\epsilon>0$. Letting $r\to-\infty$ in (11.10), we then have

$$v^\epsilon(t) = \int_{-\infty}^{t} e^{-\lambda_\epsilon^*(t-s)} \Phi_\epsilon(t,s) F_\epsilon(s) E_{\lambda_\epsilon^*} v_s^\epsilon ds = [L_{\lambda_\epsilon^*}^\epsilon v^\epsilon](t), \ \ \forall t \in \mathbb{R},$$

that is, $L_{\lambda_\epsilon^*}^\epsilon v^\epsilon = v^\epsilon$. Since $L_{\lambda_\epsilon^*}^\epsilon$ is compact and strongly positive, the Krein-Rutman theorem implies that $r(L_{\lambda_\epsilon^*}^\epsilon) = 1$ for sufficiently small $\epsilon > 0$.

In view of $\lambda^* > \hat{\omega}(\Phi)$, we can fix a small number $\delta > 0$ such that $\lambda^* - \delta > \hat{\omega}(\Phi)$. Since $\lim_{\epsilon \to 0^+} \lambda_\epsilon^* = \lambda^*$ and $\lim_{\epsilon \to 0^+} \hat{\omega}(\Phi_\epsilon) = \hat{\omega}(\Phi)$, there is a small number $\epsilon_0 > 0$ such that $\hat{\omega}(\Phi) - \lambda^* + \delta + \epsilon_0 M_0 \|E\| < 0$ and

$$\lambda_\epsilon^* \in [\lambda^* - \delta, \lambda^* + \delta], \quad \lambda^* - \delta > \hat{\omega}(\Phi_\epsilon), \quad \forall \epsilon \in [0, \epsilon_0].$$

Recall that $c = \epsilon M_0 \|E\|$. Let

$$A_\epsilon := \sup_{0 \le t \le \omega} \|F_\epsilon(t)\|, \qquad B_\epsilon := \sup_{0 \le t \le \omega} \|F_\epsilon(t) - F(t)\|.$$

By virtue of Lemma 11.1.2 and the fact that $\|\Phi(t, t-s)\| \le M_0 e^{\hat{\omega}(\Phi)s}$, it easily follows that for all $\epsilon \in [0, \epsilon_0]$ and $\lambda \in [\lambda^* - \delta, \lambda^* + \delta]$, there holds

$$\begin{aligned}
\|L_\lambda^\epsilon - L_\lambda\| &\le \int_0^\infty e^{-\lambda s} \left(c M_0 s e^{(\hat{\omega}(\Phi)+c)s} A_\epsilon + M_0 e^{\hat{\omega}(\Phi)s} B_\epsilon \right) \|E_\lambda\| ds \\
&= \|E_\lambda\| \int_0^\infty \left(c M_0 s e^{(\hat{\omega}(\Phi)-\lambda+c)s} A_\epsilon + B_\epsilon M_0 e^{(\hat{\omega}(\Phi)-\lambda)s} \right) ds \\
&= \frac{c M_0 \|E_\lambda\| A_\epsilon}{(\hat{\omega}(\Phi) - \lambda + c)^2} + \frac{M_0 \|E_\lambda\| B_\epsilon}{\hat{\omega}(\Phi) - \lambda} \\
&\le \frac{\epsilon M_0^2 \|E\| \cdot \|E_\lambda\| (\sup_{0 \le t \le \omega} \|F(t)\| + \epsilon)}{(\hat{\omega}(\Phi) - \lambda + \epsilon M_0 \|E\|)^2} + \frac{\epsilon M_0 \|E_\lambda\|}{\hat{\omega}(\Phi) - \lambda}.
\end{aligned}$$

This implies that $\lim_{\epsilon \to 0^+} \|L_\lambda^\epsilon - L_\lambda\| = 0$ for each $\lambda \in [\lambda^* - \delta, \lambda^* + \delta]$, and hence,

$$\lim_{\epsilon \to 0^+} r(L_\lambda^\epsilon) = r(L_\lambda) = \mu(\lambda), \quad \forall \lambda \in [\lambda^* - \delta, \lambda^* + \delta].$$

Let $\epsilon_n = \frac{1}{n}$ and $\mu_n(\lambda) = r(L_\lambda^{\epsilon_n})$. By Proposition 11.1.1, $\mu(\lambda)$ and $\mu_n(\lambda)$ are continuous on $[\lambda^* - \delta, \lambda^* + \delta]$. Since $L_\lambda^{\epsilon_{n+1}} v \le L_\lambda^{\epsilon_n} v$ for all $v \in C_\omega^+$, it follows that $\mu_n(\lambda)$ is a nonincreasing sequence of functions. Thus, Dini's theorem implies that $\lim_{n \to \infty} \mu_n(\lambda) = \mu(\lambda)$ uniformly for $\lambda \in [\lambda^* - \delta, \lambda^* + \delta]$. Since

$$|\mu_n(\lambda_{\epsilon_n}^*) - \mu(\lambda^*)| \le |\mu_n(\lambda_{\epsilon_n}^*) - \mu(\lambda_{\epsilon_n}^*)| + |\mu(\lambda_{\epsilon_n}^*) - \mu(\lambda^*)|,$$

we obtain $\lim_{n \to \infty} \mu_n(\lambda_{\epsilon_n}^*) = \mu(\lambda^*)$. On the other hand, the conclusion in the last paragraph implies that $\mu_n(\lambda_{\epsilon_n}^*) = r(L_{\lambda_{\epsilon_n}^*}^{\epsilon_n}) = 1$ for sufficiently large n. Letting $n \to \infty$ in this equality, we then have $\mu(\lambda^*) = 1$. ∎

Now we are ready to prove that R_0 is a threshold value for the stability of the zero solution of periodic system (11.1). Recall that $U(\omega, 0)$ is the Poincaré (period) map of system (11.1) on C.

Theorem 11.1.1. *The following statements are valid:*

(i) $R_0 = 1$ *if and only if* $r(U(\omega, 0)) = 1$.
(ii) $R_0 > 1$ *if and only if* $r(U(\omega, 0)) > 1$.
(iii) $R_0 < 1$ *if and only if* $r(U(\omega, 0)) < 1$.

Thus, $R_0 - 1$ *has the same sign as* $r(U(\omega, 0)) - 1$.

Proof. In view of $\hat{\omega}(\Phi) = \frac{\ln r(\Phi(\omega,0))}{\omega} < 0$, we have $r(\Phi(\omega, 0)) < 1$.

(i) (a) If $R_0 = 1$, then $\mu(0) = 1$. By the proof of Proposition 11.1.1 (ii), it follows that $e^{0\omega} = 1$ is an eigenvalue of $U(\omega, 0)$, and hence, $r(U(\omega, 0)) \geq 1 > r(\Phi(\omega, 0))$. Thus, Proposition 11.1.2 implies that $\mu(\lambda^*) = 1$. By Proposition 11.1.1 (ii), we further obtain $\lambda^* = 0$, that is, $r(U(\omega, 0)) = 1$. (b) If $r(U(\omega, 0)) = 1$, then $\lambda^* = 0$. Since $r(\Phi(\omega, 0)) < 1$, Proposition 11.1.2 implies that $\mu(0) = 1$, that is, $R_0 = 1$.

(ii) (a) If $R_0 > 1$, then $\mu(0) > 1$. Since $\mu(\lambda)$ is continuous on $(\hat{\omega}(\Phi), \infty)$ and $\mu(\infty) = 0$ (see Proposition 11.1.1 (i)), there exists $\lambda_0 > 0$ such that $\mu(\lambda_0) = 1$. By the proof of Proposition 11.1.1 (ii), we see that $e^{\lambda_0 \omega}$ is an eigenvalue of $U(\omega, 0)$, and hence, $r(U(\omega, 0)) \geq e^{\lambda_0 \omega} > 1$. (b) If $r(U(\omega, 0)) > 1$, then $\lambda^* > 0$. Since $r(\Phi(\omega, 0)) < 1$, it follows from Proposition 11.1.2 that $\mu(\lambda^*) = 1$, and hence, $R_0 = \mu(0) \geq \mu(\lambda^*) = 1$. But Proposition 11.1.1 (ii) implies that $R_0 = \mu(0) \neq 1$. Thus, we must have $R_0 > 1$.

Clearly, statement (iii) is a straightforward consequence of the conclusions (i) and (ii) above. ∎

For any given $\lambda \in (0, \infty)$, we consider the following linear and periodic system:

$$\frac{du(t)}{dt} = \frac{1}{\lambda} F(t) u_t - V(t) u(t), \quad t \geq 0. \tag{11.11}$$

Let $U(t, s, \lambda)$ $(t \geq s)$ be the evolution operators on C associated with system (11.11). Then we have the following result.

Theorem 11.1.2. *If* $R_0 > 0$, *then* $\lambda = R_0$ *is the unique solution of the equation* $r(U(\omega, 0, \lambda)) = 1$.

Proof. By replacing $F(t)$ with $\frac{1}{\lambda} F(t)$, we can define the basic reproduction ratio, $R(\lambda)$, for system (11.11). It then follows that $R(\lambda) = r\left(\frac{1}{\lambda} L\right) = \frac{1}{\lambda} R_0$. By Theorem 11.1.1, we have

$$sign(R(\lambda) - 1) = sign(r(U(\omega, 0, \lambda) - 1), \quad \forall \lambda \in (0, \infty).$$

Letting $\lambda = R_0 > 0$ in the above equation, we then obtain $r(U(\omega, 0, R_0)) = 1$.

It remains to prove that $r(U(\omega, 0, \lambda)) = 1$ has at most one positive solution for λ. Since $F(t)$ is a positive operator and $-V(t)$ is cooperative, the comparison theorem (see [326, Theorem 5.1.1]) implies that

$$U(\omega, 0, \lambda_1)\phi \geq U(\omega, 0, \lambda_2)\phi, \quad \forall 0 < \lambda_1 \leq \lambda_2, \ \phi \in C^+.$$

Note that each $U(\omega, 0, \lambda)$ is a positive and bounded linear operator on C. It then follows from [40, Theorem 1.1] that $r(U(\omega, 0, \lambda))$ is a nonincreasing function of λ on $(0, \infty)$. Assume, by contradiction, that $r(U(\omega, 0, \lambda) = 1$ has two positive solutions $\lambda_1 < \lambda_2$. Then $r(U(\omega, 0, \lambda)) = 1, \forall \lambda \in [\lambda_1, \lambda_2]$. We choose an integer $n_0 > 0$ such that $n_0\omega \geq \tau$. In view of [145, Theorem 3.6.1], each operator $U(n_0\omega, 0, \lambda)$ is compact on C. Let $\lambda \in [\lambda_1, \lambda_2]$ be given. Since

$$r(U(n_0\omega, 0, \lambda)) = r((U(\omega, 0, \lambda))^{n_0}) = (r(U(\omega, 0, \lambda))^{n_0} = 1 > 0,$$

the Krein-Rutman theorem implies that 1 is an eigenvalue of $U(n_0\omega, 0, \lambda)$ with an eigenvector $\phi^* \in C^+ \setminus \{0\}$. Since $U(n_0\omega, 0, \lambda)\phi^* = \phi^*$, it follows that $u(t) := [U(t, 0, \lambda)\phi^*](0)$ is an $n_0\omega$-periodic solution of system (11.11). By the constant-variation formula, we have

$$u(t) = \Phi(t, r)u(r) + \int_r^t \Phi(t, s)\frac{1}{\lambda}F(s)u_s ds, \quad \forall t \geq r, \, r \in \mathbb{R}. \tag{11.12}$$

Note that $\|\Phi(t, s)\| \leq M_0 e^{\hat{\omega}(\Phi)(t-s)}$, $\forall t \geq s$, $s \in \mathbb{R}$, for some $M_0 > 0$. Since $\hat{\omega}(\Phi) < 0$ and $u(t)$ is bounded on $\mathbb{R}$, letting $r \to -\infty$ in (11.12), we further obtain

$$u(t) = \int_{-\infty}^t \Phi(t, s)\frac{1}{\lambda}F(s)u_s ds, \quad \forall t \in \mathbb{R},$$

and hence, $Lu = \lambda u$. Since L also defines a compact linear operator on $C_{n_0\omega}$ (see Lemma 11.1.1), it follows that λ is an eigenvalue of L on $C_{n_0\omega}$. Thus, any $\lambda \in [\lambda_1, \lambda_2]$ is an eigenvalue of L on $C_{n_0\omega}$, which is impossible since the compact linear operator L on $C_{n_0\omega}$ has only countably many eigenvalues. ∎

For any given $F \in \mathcal{L}(C, \mathbb{R}^m)$, we define $\hat{F} \in \mathcal{L}(\mathbb{R}^m, \mathbb{R}^m)$ by

$$\hat{F}u = F(\hat{u}), \; \forall u \in \mathbb{R}^m,$$

where $\hat{u}(\theta) = u$, $\forall \theta \in [-\tau, 0]$. Clearly, $\hat{F}$ can be regarded as an $m \times m$ matrix. Then we have the following result.

Corollary 11.1.1. *Let $F(t) \equiv F \in \mathcal{L}(C, \mathbb{R}^m)$ and $V(t) \equiv V$. Then $R_0 = r(V^{-1}\hat{F}) = r(\hat{F}V^{-1})$.*

Proof. Clearly, $r(V^{-1}\hat{F}) = r(\hat{F}V^{-1})$. Without loss of generality, we may assume that $r(V^{-1}\hat{F}) > 0$ and for all $\lambda > 0$, $U(t, 0, \lambda)$ is eventually strongly positive on C (see [326, Section 5.3]). Otherwise, we can choose appropriate small perturbations F_ϵ and V_ϵ instead of F and V, respectively, and then use a limiting argument as $\epsilon \to 0$. In view of $V^{-1} = \int_0^\infty e^{-Vs}ds$ and $\Phi(t, s) = e^{-V(t-s)}$, it easily follows that

$$Lv = V^{-1}\hat{F}v, \quad \forall v \in \mathbb{R}^m.$$

Note that $r(V^{-1}\hat{F})$ is an eigenvalue of $V^{-1}\hat{F}$ with an eigenvector $v^* \in \mathbb{R}^m_+ \setminus \{0\}$. Then $r_0 := r(V^{-1}\hat{F})$ is also an eigenvalue of L, and hence, $R_0 > 0$. Since

$V^{-1}\hat{F}v^* = r_0 v^*$, we have $\frac{1}{r_0}\hat{F}v^* - Vv^* = 0$, which implies that $u(t) = v^*$ is a constant solution to

$$\frac{du(t)}{dt} = \frac{1}{r_0}Fu_t - Vu(t).$$

Thus, $U(t,0,r_0)v^* = v^*$, $\forall t \geq 0$. We fix a large integer $n_0 > 0$ such that $U(n_0\omega, 0, r_0)$ is compact and strongly positive. By the Krein-Rutman theorem, we then obtain $r(U(n_0\omega, 0, r_0)) = 1$. Since

$$r(U(n_0\omega, 0, r_0)) = r((U(\omega, 0, r_0))^{n_0}) = (r(U(\omega, 0, r_0)))^{n_0},$$

it follows that $r(U(\omega, 0, r_0)) = 1$. Now Theorem 11.1.2 implies that $R_0 = r_0$. ∎

In the case where $\tau = 0$, Theorems 11.1.1 and 11.1.2 reduce to Theorems 2.2 and (2.1)(ii) of [388], respectively, and Corollary 11.1.1 is consistent with the formula of R_0 given in [376]. More recently, the basic reproduction number was addressed in [415] for linear autonomous systems with discrete delays:

$$\frac{dI(t)}{dt} = F_1 I(t-\tau_1) + F_2 I(t-\tau_2) - VI(t),$$

where F_1 and F_2 are nonnegative matrices and $-V$ is a cooperative matrix. Taking $F(\phi) = F_1\phi(-\tau_1) + F_2\phi(-\tau_2)$ and $\tau = \max\{\tau_1, \tau_2\}$, we have $\hat{F} = F_1 + F_2$. Thus, Corollary 11.1.1 implies that $R_0 = r((F_1 + F_2)V^{-1})$, which is the same as the formula obtained in [415]. Clearly, Corollary 11.1.1 also applies to more general linear autonomous systems with distributed delays.

Remark 11.1.1. Theorem 11.1.2 can be used to compute R_0 numerically. Indeed, it is easy to verify that $r(U(\omega, 0, \lambda)) = \lim_{n\to\infty} \|U(n\omega, 0, \lambda)e\|^{\frac{1}{n}}$ for any given $e \in \operatorname{int}\big(C([-\tau, 0], \mathbb{R}^m_+)\big)$. Combining this observation with the bisection method, one can find a numerical solution to $r(U(\omega, 0, \lambda)) = 1$, which is an approximation of R_0.

Remark 11.1.2. The theory of basic reproduction ratio in this section can be extended to abstract periodic linear systems with time delay if we replace $\mathbb{R}^m$ with an ordered Banach space E and assume that each $-V(t)$ is a linear operator such that the linear equation $\frac{du}{dt} = -V(t)u$ generates a positive evolution operator $\Phi(t,s)$ on E. Thus, one can apply the generalized theory to periodic and time-delayed reaction-diffusion population models. For example, letting Ω be a bounded domain with smooth boundary, $E = C(\bar{\Omega}, \mathbb{R}^m)$ and $-V(t)u = D(t)\Delta u - W(t)u$, we can consider the following periodic linear system:

$$\frac{\partial u}{\partial t} = D(t)\Delta u + F(t)u_t - W(t)u,$$

subject to the Neumann boundary condition. Here $\Delta u = (\Delta u_1, \ldots, \Delta u_m)^T$, $[D(t)](x) = diag(d_1(t,x), \ldots, d_m(t,x))$ with $d_i(t,x) > 0$, $1 \leq i \leq m$, and for each $t \in \mathbb{R}$, $F(t) \in \mathcal{L}(C([-\tau, 0], E), E)$ and $-[W(t)](x)$ is an $m\times m$ cooperative matrix function of $x \in \bar{\Omega}$.

11.2 A Periodic SEIR Model

We consider a continuous-time SEIR model of a disease transmission. Let $S(t)$, $E(t)$, $I(t)$, and $R(t)$ be the total numbers at time t of the susceptible, exposed, infective, and recovered (or removed) populations, respectively. For simplicity, we assume that the latent period of the disease is τ, and the incidence rate function $f(t, S, I)$ depends on time t and variables S and I. Let $\mu(t)$ be the natural death rate of the population. It then follows that the rate of entry into the infective class from the exposed one at time t is

$$e^{-\int_{t-\tau}^{t} \mu(r)dr} f(t-\tau, S(t-\tau), I(t-\tau)).$$

As discussed in [361], $E(t)$ can be represented as

$$E(t) = \int_{t-\tau}^{t} e^{-\int_{s}^{t} \mu(r)dr} f(s, S(s), I(s))ds.$$

Thus, we obtain the following nonautonomous SEIR model:

$$\begin{aligned}
\frac{dS(t)}{dt} &= \Lambda(t) - f(t, S(t), I(t)) - \mu(t)S(t) + \alpha(t)R(t), \\
E(t) &= \int_{t-\tau}^{t} e^{-\int_{s}^{t} \mu(r)dr} f(s, S(s), I(s))ds, \\
\frac{dI(t)}{dt} &= e^{-\int_{t-\tau}^{t} \mu(r)dr} f(t-\tau, S(t-\tau), I(t-\tau)) - (\mu(t) + d(t) + \gamma(t))I(t), \\
\frac{dR(t)}{dt} &= \gamma(t)I(t) - \mu(t)R(t) - \alpha(t)R(t).
\end{aligned} \tag{11.13}$$

Here $\Lambda(t)$ is the recruitment rate, $d(t)$ is the disease-induced death rate, $\gamma(t)$ is the recovery rate, and $\alpha(t)$ is the loss of immunity rate.

According to [42], we need to impose the following compatibility condition:

$$E(0) = \int_{-\tau}^{0} e^{-\int_{s}^{0} \mu(r)dr} f(s, S(s), I(s))ds. \tag{11.14}$$

It is easy to verify that

$$\frac{dE(t)}{dt} = f(t, S(t), I(t)) - e^{-\int_{t-\tau}^{t} \mu(r)dr} f(t-\tau, S(t-\tau), I(t-\tau)) - \mu(t)E(t).$$

Thus, model (11.13) reduces to the following nonautonomous functional differential system:

$$\begin{aligned}
\frac{dS(t)}{dt} &= \Lambda(t) - f(t, S(t), I(t)) - \mu(t)S(t) + \alpha(t)R(t), \\
\frac{dE(t)}{dt} &= f(t, S(t), I(t)) - e^{-\int_{t-\tau}^{t} \mu(r)dr} f(t-\tau, S(t-\tau), I(t-\tau)) - \mu(t)E(t), \\
\frac{dI(t)}{dt} &= e^{-\int_{t-\tau}^{t} \mu(r)dr} f(t-\tau, S(t-\tau), I(t-\tau)) - (\mu(t) + d(t) + \gamma(t))I(t), \\
\frac{dR(t)}{dt} &= \gamma(t)I(t) - \mu(t)R(t) - \alpha(t)R(t),
\end{aligned} \tag{11.15}$$

subject to condition (11.14).

We assume that $f(t, S, I)$ and all these time-dependent coefficients are ω-periodic in t for some real number $\omega > 0$. It is then easy to see that the function

$$p(t) := e^{-\int_{t-\tau}^{t} \mu(r)dr}$$

is also ω-periodic, and hence, model (11.15) is an ω-periodic and time-delayed system. To study the evolution dynamics of system (11.15), we make the following assumptions:

(B1) $\Lambda(t)$, $\mu(t)$, $\alpha(t)$, $d(t)$, and $\gamma(t)$ are all nonnegative and continuous functions with $\Lambda(t) > 0$, $\int_0^\omega \mu(t)dt > 0$, and $\int_0^\omega \gamma(t)dt > 0$;

(B2) $f(t, S, I)$ is a C^1-function with the following properties:

(i) $f(t, S, 0) \equiv 0$, $f(t, 0, I) \equiv 0$, and $\frac{\partial f(t,S,0)}{\partial I}$ are positive and nondecreasing for all $S > 0$.

(ii) $\frac{\partial f(t,S,I)}{\partial S} \geq 0$ and $f(t, S, I) \leq \frac{\partial f(t,S,0)}{\partial I} I$ for all $(t, S, I) \in \mathbb{R} \times \mathbb{R}_+^2$.

A prototypical example for incidence function is $f(t, S, I) = \frac{\beta(t)SI}{1+c(t)I}$ with $c(t) \geq 0$. For more general time-independent incidence functions, we refer to [203] and references therein.

By virtue of (B1), we see that the scalar linear periodic equation

$$\frac{dS(t)}{dt} = \Lambda(t) - \mu(t)S(t) \tag{11.16}$$

has a unique positive ω-periodic solution $S^*(t)$, which is globally stable in $\mathbb{R}$. Linearizing system (11.15) at its disease-free periodic solution $(S^*(t), 0, 0, 0)$, we then obtain the following periodic linear equation for the infective variable I:

$$\frac{dI(t)}{dt} = a(t)I(t-\tau) - b(t)I(t), \tag{11.17}$$

where

$$a(t) = p(t)\frac{\partial f(t-\tau, S^*(t-\tau), 0)}{\partial I}, \qquad b(t) = \mu(t) + d(t) + \gamma(t).$$

Following the procedure in Section 11.1, we take $m = 1$, $F(t)\phi = a(t)\phi(-\tau)$, and $V(t) = b(t)$. It then easily follows that

$$\Phi(t, s) = e^{-\int_s^t b(r)dr}, \quad \forall t \geq s,\ s \in \mathbb{R},$$

and

$$\begin{aligned}
[Lv](t) &= \int_0^\infty \Phi(t, t-s)F(t-s)v(t-s+\cdot)ds \\
&= \int_0^\infty \Phi(t, t-s)a(t-s)v(t-s-\tau)ds \\
&= \int_\tau^\infty \Phi(t, t-s+\tau)a(t-s+\tau)v(t-s)ds \\
&= \int_0^\infty K(t, s)v(t-s)ds, \quad \forall t \in \mathbb{R},\ v \in C_\omega,
\end{aligned}$$

where

$$K(t,s) = \begin{cases} \Phi(t, t-s+\tau)a(t-s+\tau), & \text{if } s \geq \tau \\ 0, \quad \text{if } s < \tau. \end{cases}$$

According to the definition in Section 11.1, we have $R_0 = r(L)$.

Since the S, I, and R equations in model (11.15) do not depend on variable E, it suffices to study the following ω-periodic system with time delay:

$$\begin{aligned} \frac{dS(t)}{dt} &= \Lambda(t) - f(t, S(t), I(t)) - \mu(t)S(t) + \alpha(t)R(t), \\ \frac{dI(t)}{dt} &= p(t)f(t-\tau, S(t-\tau), I(t-\tau)) - (\mu(t) + d(t) + \gamma(t))I(t), \\ \frac{dR(t)}{dt} &= \gamma(t)I(t) - \mu(t)R(t) - \alpha(t)R(t). \end{aligned} \tag{11.18}$$

Let $X = C([-\tau, 0], \mathbb{R}^3_+)$. By the standard theory of functional differential equations (see, e.g., [145]), system (11.18) admits a unique nonnegative solution $v(t, \phi) = (S(t), I(t), R(t))$ satisfying $v_0(\phi) = \phi \in X$. Define

$$D := \left\{ \psi \in C([-\tau, 0], \mathbb{R}^4_+) : \psi_2(0) = \int_{-\tau}^0 e^{-\int_s^0 \mu(r)dr} f(s, \psi_1(s), \psi_3(s))ds \right\}.$$

It then easily follows that for any $\psi \in D$, system (11.15) has a unique nonnegative solution $u(t, \psi) = (S(t), E(t), I(t), R(t))$ satisfying $u_0(\psi) = \psi$. Let $N(t) = S(t) + E(t) + I(t) + R(t)$. Then we have

$$\frac{dN(t)}{dt} = \Lambda(t) - \mu(t)N(t) - d(t)I(t) \leq \Lambda(t) - \mu(t)N(t), \quad t \geq 0. \tag{11.19}$$

Thus, the global stability of $S^*(t)$ for (11.16), together with the comparison argument, implies that solutions of system (11.15) with initial data in D, and hence (11.18) in X, exist globally on $[0, \infty)$ and are ultimately bounded.

Let $X_0 = \{\phi = (\phi_1, \phi_2, \phi_3) \in X : \phi_2(0) > 0\}$. The subsequent result shows that R_0 serves as a threshold value for the global extinction and uniform persistence of the disease.

Theorem 11.2.1. *Let (B1) and (B2) hold. Then the following statements are valid:*

(i) If $R_0 < 1$, then the disease-free periodic solution $(S^*(t), 0, 0)$ is globally attractive for system (11.18) in X.
(ii) If $R_0 > 1$, then system (11.18) admits a positive ω-periodic solution $(\bar{S}(t), \bar{I}(t), \bar{R}(t))$, and there exists a real number $\eta > 0$ such that the solution $v(t, \phi) = (S(t), I(t), R(t))$ satisfies $\liminf_{t\to\infty} I(t) \geq \eta$ for any $\phi \in X_0$.

Proof. Let $P(t)$ be the solution maps of the scalar linear equation (11.17) on $Y := C([-\tau, 0], \mathbb{R})$, that is, $P(t)\psi = w_t(\psi)$, $t \geq 0$, where $w(t, \psi)$ is the unique solution of (11.17) satisfying $w_0 = \psi \in Y$. Then $P := P(\omega)$ is the Poincaré (period) map associated with system (11.17). In view of Theorem 11.1.1, we have $sign(R_0 - 1) = sign(r(P) - 1)$. Since $p(t)\frac{\partial f(t-\tau, S^*(t-\tau), 0)}{\partial I} > 0$, it follows from [145, Theorem 3.6.1] and [326, Lemma 5.3.2] that for each $t \geq 2\tau$, the linear operator $P(t)$ is compact and strongly positive on Y. Choose an integer $n_0 > 0$ such that $n_0\omega \geq 2\tau$. Since $P^{n_0} = P(n_0\omega)$, [225, Lemma 3.1] implies that $r(P)$ is a simple eigenvalue of P having a strongly positive eigenvector, and the modulus of any other eigenvalue is less than $r(P)$. Let $\mu = \frac{\ln r(P)}{\omega}$. By the proof of [417, Proposition 2.1], it then follows that there is a positive ω-periodic function $v(t)$ such that $u(t) = e^{\mu t}v(t)$ is a positive solution of (11.17).

In the case where $R_0 < 1$, we have $r(P) < 1$. Let P_ϵ be the Poincaré map of the following perturbed linear periodic equation

$$\frac{dI(t)}{dt} = p(t)\frac{\partial f(t-\tau, S^*(t-\tau)+\epsilon, 0)}{\partial I}I(t-\tau) - (\mu(t) + d(t) + \gamma(t))I(t). \tag{11.20}$$

Since $\lim_{\epsilon \to 0} r(P_\epsilon) = r(P) < 1$, we can fix a sufficiently small number $\epsilon > 0$ such that $r(P_\epsilon) < 1$. As discussed in the last paragraph, there is a positive ω-periodic function $v_\epsilon(t)$ such that $u_\epsilon(t) = e^{\mu_\epsilon t}v_\epsilon(t)$ is a positive solution of (11.20), where $\mu_\epsilon = \frac{\ln r(P_\epsilon)}{\omega} < 0$. For any given $\phi \in X$, let $v(t, \phi) = (S(t), I(t), R(t))$. In view of (11.19) and the global stability of $S^*(t)$ for (11.16), it follows that there exists a sufficiently large integer $n_1 > 0$ such that $n_1\omega \geq \tau$ and $S(t) \leq S^*(t) + \epsilon$, $\forall t \geq n_1\omega - \tau$. By assumption (A2), we then have

$$\frac{dI(t)}{dt} \leq p(t)\frac{\partial f(t-\tau, S^*(t-\tau)+\epsilon, 0)}{\partial I}I(t-\tau) - (\mu(t) + d(t) + \gamma(t))I(t)$$

for all $t \geq n_1\omega$. Choose a sufficiently large number $K > 0$ such that $I(t) \leq Ku_\epsilon(t)$, $\forall t \in [n_1\omega - \tau, n_1\omega]$. Thus, the comparison theorem for delay differential equations ([326, Theorem 5.1.1]) implies that

$$I(t) \leq Ku_\epsilon(t) = Ke^{\mu_\epsilon t}v_\epsilon(t), \quad \forall t \geq n_1\omega,$$

and hence, $\lim_{t\to\infty} I(t) = 0$. By using the chain transitive sets arguments (see, e.g., [232, Theorem 4.1 (a)]), it easily follows that $\lim_{t\to\infty} R(t) = 0$ and $\lim_{t\to\infty}(S(t) - S^*(t)) = 0$.

In the case where $R_0 > 1$, we have $r(P) > 1$. Let $Q(t)\phi = v_t(\phi)$, $\forall \phi \in X$, and $Q = Q(\omega)$. Note that for each $t \geq \tau$, $Q(t)$ is compact (see [145, Theorem 3.6.1]). It then follows from Theorem 1.1.3 that $Q : X \to X$ has a strong global attractor A. Clearly, $\{Q(t)\}_{t\geq 0}$ is an ω-periodic semiflow on X, and $Q^n = Q(n\omega)$, $\forall n \geq 0$. Let M_δ be the Poincaré map of the following perturbed linear periodic equation

$$\frac{dI(t)}{dt} = p(t)\left(\frac{\partial f(t-\tau, S^*(t-\tau), 0)}{\partial I} - \delta\right) I(t-\tau) - (\mu(t) + d(t) + \gamma(t))I(t). \tag{11.21}$$

Since $\lim_{\delta \to 0} r(M_\delta) = r(P) > 1$, we can fix a small number $\delta > 0$ such that $r(M_\delta) > 1$. It then follows that there is a small number $\eta_0 > 0$ such that

$$f(t-\tau, S^*(t-\tau) - \eta_0, I) \geq \left(\frac{\partial f(t-\tau, S^*(t-\tau), 0)}{\partial I} - \delta\right) I, \ \forall I \in [0, \eta_0].$$

Let $M_1 = (S_0^*, 0, 0)$. Then $Q(t)M_1 = (S_t^*, 0, 0)$, $\forall t \geq 0$, and $Q(M_1) = M_1$. Since $\lim_{\phi \to M_1} Q(t)\phi = Q(t)M_1$ uniformly for $t \in [0, \omega]$, there exists $\eta_1 = \eta_1(\eta_0) > 0$ such that

$$\|Q(t)\phi - Q(t)M_1\| < \eta_0, \ \forall t \in [0, \omega], \ \|\phi - M_1\| < \eta_1.$$

We further prove the following claim.

Claim. $\limsup_{n \to \infty} \|Q^n(\phi) - M_1\| \geq \eta_1, \ \forall \phi \in X_0.$

Assume, by contradiction, that the claim is not true. Since $Q(t)(X_0) \subset X_0, \forall t \geq 0$, it follows that there exists $\psi = (\psi_1, \psi_2, \psi_3) \in X_0$ with $\psi_2(\theta) > 0, \forall \theta \in [-\tau, 0]$, such that $\|Q^n(\psi) - M_1\| < \eta_1, \ \forall n \geq 0$. For any $t \geq 0$, letting $t = n\omega + t'$ with $t' \in [0, \omega)$ and $n = [t/\omega]$, we have

$$\|Q(t)\psi - Q(t)M_1\| = \|Q(t')(Q^n(\psi)) - Q(t')M_1\| < \eta_0.$$

In view of (B2), we see that $f(t, S, I)$ is nondecreasing in S. Thus, $v(t, \psi) = (S(t), T(t), R(t))$ satisfies

$$\frac{dI(t)}{dt} \geq p(t)\left(\frac{\partial f(t-\tau, S^*(t-\tau), 0)}{\partial I} - \delta\right) I(t-\tau) - (\mu(t) + d(t) + \gamma(t))I(t)$$

for all $t \geq 0$. Note that $\psi_2 \gg 0$ in $C([-\tau, 0], \mathbb{R})$ and $r(M_\delta) > 1$. By the comparison argument similar to that in case (i), we then obtain $\lim_{t \to \infty} I(t) = \infty$, a contradiction.

The above claim implies that M_1 is an isolated invariant set for Q in X and $W^s(M_1) \cap X_0 = \emptyset$, where $W^s(M_1)$ is the stable set of M_1 for Q. Set $\partial X_0 = X \setminus X_0$ and

$$M_\partial = \{\phi \in \partial X_0 : \ Q^n(\phi) \in \partial X_0, \forall n \geq 0\}.$$

Since

$$\frac{dI(t)}{dt} \geq -(\mu(t) + d(t) + \gamma(t))I(t), \ \forall t \geq 0,$$

it is easy to see that if $I(t_0) > 0$ for some $t_0 \geq 0$, then $I(t) > 0$ for all $t \geq t_0$. This property implies that $I(t) = 0$, $\forall t \geq 0$, whenever $\phi \in M_\partial$. It then follows that $\omega(\phi) = M_1$ for any $\phi \in M_\partial$, and M_1 cannot form a cycle for Q in ∂X_0. By the acyclicity theorem on uniform persistence for maps (see Theorem 1.3.1 and

Remark 1.3.1), $Q : X \to X$ is uniformly persistent with respect to $(X_0, \partial X_0)$. Note that for any integer n with $n\omega \geq \tau$, $Q^n = Q(n\omega) : X \to X$ is compact. Further, in view of Theorem 3.5.1 (see also [141, Theorem 4.1.1] and [226, pages 879–880]), $Q(t)$ is an α-contraction with respect to an equivalent norm in $C([-\tau, 0], \mathbb{R}^3)$ for any $t > 0$. It then follows from Theorem 1.3.10 that there exists a global attractor A_0 for Q: $X_0 \to X_0$ and Q has a fixed point $\phi^* \in A_0$. Clearly, $v(t, \phi^*) = (\bar{S}(t), \bar{I}(t), \bar{R}(t))$ is an ω-periodic solution of system (11.18) with $\bar{I}(t) > 0$, $\forall t \geq 0$. Since $\gamma(t) \not\equiv 0$ and $f(t, 0, I) \equiv 0$, it is easy to see that $\bar{S}(t) > 0$ and $\bar{R}(t) > 0$ for all $t \geq 0$. Since $A_0 = Q(A_0) = Q(\omega)A_0$, we have $\phi_2(0) > 0$, $\forall \phi \in A_0$. Let $B_0 := \bigcup_{t \in [0,\omega]} Q(t)A_0$. Then $B_0 \subset X_0$, and Theorem 3.1.1 implies that $\lim_{t\to\infty} d(Q(t)\phi, B_0) = 0, \forall \phi \in X_0$. Define a continuous function $p : X \to \mathbb{R}_+$ by $p(\phi) = \phi_2(0)$, $\forall \phi = (\phi_1, \phi_2, \phi_3) \in X$. Since B_0 is a compact subset of X_0, it follows that $\inf_{\phi \in B_0} p(\phi) = \min_{\phi \in B_0} p(\phi) > 0$. Consequently, there exists $\eta > 0$ such that $\liminf_{t\to\infty} I(t, \phi) = \liminf_{t\to\infty} p(Q(t)\phi) \geq \eta$ for any $\phi \in X_0$. ∎

11.3 Reaction–Diffusion Systems

In this section, we develop the theory of basic reproduction ratios for compartmental epidemic models of parabolic type. We start with the presentation of two results on the principal eigenvalue for the associated elliptic eigenvalue problem.

Let (E, E_+) be an ordered Banach space, and A be a closed linear operator on E. We use $\sigma(A)$ to denote the spectrum of A, and define the spectral bound of A as

$$s(A) = \sup\{Re\, \lambda : \ \lambda \in \sigma(A)\}.$$

A is said to be resolvent-positive if the resolvent set of A, $\rho(A)$, contains a ray (α, ∞), and $(\lambda I - A)^{-1}$ is a positive operator for all real number $\lambda > \alpha$.

Let Ω be a domain in $\mathbb{R}^l$ with the smooth boundary $\partial\Omega$, and ν be the unit normal vector on $\partial\Omega$. For a given integer $k > 0$, let $X = C(\overline{\Omega}, \mathbb{R}^k)$ and $X_+ = C(\overline{\Omega}, \mathbb{R}^k_+)$. Set $u_K = (u_1, \ldots, u_k)^T$ and

$$\nabla \cdot (d_K(x) \nabla u_K) = \mathrm{diag}\left(\nabla \cdot (d_1(x)\nabla u_1), \ldots, \nabla \cdot (d_k(x)\nabla u_k)\right).$$

Let $M(x)$ be a continuous $k \times k$ matrix-valued function of $x \in \overline{\Omega}$. We consider the following elliptic eigenvalue problem

$$\begin{aligned} &\nabla \cdot (d_K(x)\nabla u_K) + M(x)u_K = \lambda u_K, \qquad x \in \Omega, \\ &\frac{\partial u_i}{\partial \nu} = 0, \quad \forall\, 1 \leq i \leq k \text{ with } d_i > 0, \quad x \in \partial\Omega. \end{aligned} \tag{11.22}$$

For convenience, we set $L(\phi)(x) = \nabla \cdot (d_K(x)\nabla\phi(x))$, and let M denote the multiplication operator defined by $M(\phi)(x) = M(x)\phi(x)$. Recall that a square matrix is said to be cooperative if its off-diagonal elements are nonnegative. Assume that

(D1) There exists a $d_0 > 0$ such that $d_i(x) \geq d_0$, $\forall x \in \overline{\Omega}$, $1 \leq i \leq k$.

Theorem 11.3.1. ([390, Theorem 2.2]) *Let (D1) hold. If $M(x)$ is cooperative for all $x \in \overline{\Omega}$ and there is an $x_0 \in \Omega$ such that $M(x_0)$ is irreducible, then $\lambda^* := s(L+M)$ is an algebraically simple eigenvalue of* (11.22) *with a strongly positive eigenvector, and $Re(\lambda) < \lambda^*$ for all $\lambda \in \sigma(L+M) \setminus \{\lambda^*\}$.*

To consider the case where some diffusion coefficients in (11.22) are zero, without loss of generality, we assume that

(D2) There exist a number $d_0 > 0$ and an integer $1 \leq i_1 < k$ such that $d_i(x) \geq d_0$, $\forall x \in \overline{\Omega}$, $1 \leq i \leq i_1$, and $d_{i_1+i}(x) = 0$, $\forall x \in \overline{\Omega}$, $1 \leq i \leq i_2 := k - i_1$.

Let $Y_1 = C(\overline{\Omega}, \mathbb{R}^{i_1})$ and $Y_2 = C(\overline{\Omega}, \mathbb{R}^{i_2})$. We split the cooperative matrix $M(x)$ into

$$M(x) = \begin{pmatrix} M_{11}(x) & M_{12}(x) \\ M_{21}(x) & M_{22}(x) \end{pmatrix},$$

where M_{11} is an $i_1 \times i_1$ matrix and M_{22} is an $i_2 \times i_2$ matrix. Let

$$L_1(\mathbf{u}_{i_1}) = \nabla \cdot (\mathbf{d}_{i_1}(x) \nabla \mathbf{u}_{i_1}) := diag\left(\nabla \cdot (d_1(x)\nabla u_1), \ldots, \nabla \cdot (d_{i_1}(x)\nabla u_{i_1})\right),$$

and define $T_2(t)\phi_2(x) = e^{M_{22}(x)t}\phi_2(x)$. Then $T_2(t)$ is a positive C_0-semigroup on Y_2 with its generator M_{22} being resolvent-positive. It follows from [370, Theorem 3.12] that

$$(\lambda I - M_{22})^{-1}\phi_2 = \int_0^\infty e^{-\lambda t} T_2(t)\phi_2 dt, \quad \forall \lambda > s(M_{22}),\ \phi_2 \in Y_2. \tag{11.23}$$

Thus, we can define a one-parameter family of linear operators:

$$\mathcal{L}_\lambda = L_1 + M_{11} + M_{12}(\lambda I - M_{22})^{-1} M_{21}, \quad \forall \lambda > s(M_{22}).$$

Theorem 11.3.2. ([390, Theorem 2.3]) *Let (D2) hold, and assume that $M(x)$ is cooperative for all $x \in \overline{\Omega}$ and for any $\lambda > s(M_{22})$, there exists some $x_\lambda \in \Omega$ such that $M_{11}(x_\lambda) + M_{12}(\lambda I - M_{22})^{-1} M_{21}(x_\lambda)$ is irreducible. If there exist $\lambda_0 > s(M_{22})$ and $\phi_0 > 0$ in Y_1 such that $\mathcal{L}_{\lambda_0}\phi_0 \geq \lambda_0\phi_0$, then the following statements are valid:*

(1) $s(B)$ is a geometrically simple eigenvalue of (11.22) *with a positive eigenvector;*

(2) $s(B)$ is the unique $\lambda \in (s(M_{22}), \infty)$ with $s(\mathcal{L}_\lambda) = \lambda$;

(3) $s(B)$ has the same sign as $s(\mathcal{L}_0)$ provided that $s(M_{22}) < 0$.

Remark 11.3.1. Theorem 11.3.2 is still valid if the condition $\mathcal{L}_{\lambda_0}\phi_0 \geq \lambda_0\phi_0$ is replaced with a weaker assumption that $u(t,x) := e^{\lambda_0 t}\phi_0(x)$ is a subsolution of the integral form of the linear system $u_t = \mathcal{L}_{\lambda_0} u$.

Remark 11.3.2. If we replace $-L$ or $-L_1$ with uniformly x-dependent elliptic operators and use Dirichlet or Robin-type boundary conditions in (11.22), then Theorems 11.3.1 and 11.3.2 and Remark 11.3.1 are still valid.

Now we consider the following linear reaction–diffusion system

$$\begin{aligned} &\frac{\partial u}{\partial t} = \nabla \cdot (d(x)\nabla u) + F(x)u - V(x)u, \quad t > 0, \;\; x \in \Omega, \\ &\frac{\partial u_i}{\partial \nu} = 0, \quad \forall\, 1 \le i \le m \text{ with } d_i > 0, \quad t > 0, \;\; x \in \partial\Omega. \end{aligned} \tag{11.24}$$

System (11.24) may come from the equations of infectious variables in the linearization of a given reaction-diffusion epidemic model at a disease-free steady state. As such, m is the total number of the infectious compartments, and $F(x)$ is the infection rate matrix at location x. Moreover, the internal evolution of individuals in the infectious compartments (e.g., random diffusion, natural and disease-induced deaths, and movements among compartments) is governed by the linear reaction–diffusion system:

$$\begin{aligned} &\frac{\partial u}{\partial t} = \nabla \cdot (d(x)\nabla u) - V(x)u, \quad t > 0, \;\; x \in \Omega, \\ &\frac{\partial u_i}{\partial \nu} = 0, \quad \forall\, 1 \le i \le m \text{ with } d_i > 0, \quad t > 0, \;\; x \in \partial\Omega. \end{aligned} \tag{11.25}$$

For a reaction–diffusion model of population growth with m patches (or types), we may also obtain system (11.24) by linearizing it at the zero solution, where the word "birth" should be used to replace "infection." Throughout this section, we assume that

(H1) $F(x)$ is a continuous and nonnegative $m \times m$ matrix function on $\overline{\Omega}$;
(H2) $-V(x)$ is a continuous and cooperative $m \times m$ matrix function on $\overline{\Omega}$, and $s(\nabla \cdot (d(x)\nabla) - V) < 0$.

Note that (H2) reflects the observation that the internal evolution of individuals in the infectious compartments due to random diffusion, deaths, and movements among the compartments is dissipative, and exponentially decays in many cases because of the loss of infective members from natural and disease-induced mortalities.

Set $X_1 := C(\overline{\Omega}, \mathbb{R}^m)$ and $X_1^+ := C(\overline{\Omega}, \mathbb{R}^m_+)$. Let $T(t)$ be the solution semigroup on X_1 associated with the linear system (11.25). In order to define the basic reproduction ratio, we let $\phi(x)$ be the density distribution of initial infectious individuals among compartments. Under the synthetical influences of mobility, mortality, and transfer of individuals in infected compartments, the distribution of those infective members becomes $[T(t)\phi](x)$ as time evolves. Thus, the distribution of new infective members at time t is $F(x)[T(t)\phi](x)$. Consequently, the distribution of total new infective members is

$$\int_0^\infty F(x)[T(t)\phi](x)dt. \tag{11.26}$$

Define

$$L(\phi)(x) := \int_0^\infty F(x)[T(t)\phi](x)dt = F(x)\int_0^\infty [T(t)\phi](x)dt. \tag{11.27}$$

Then L is a continuous and positive operator which maps the initial infection distribution ϕ to the distribution of the total infective members produced during the infection period. Following the idea of next generation operators (see, e.g., [95, 376, 389]), we define the spectral radius of L as the basic reproduction ratio

$$R_0 := r(L) \tag{11.28}$$

for model (11.24).

Let $\mathcal{B}$ be a resolvent-positive operator with $s(\mathcal{B}) < 0$, $\mathcal{F}$ be a bounded and positive operator, and $\mathcal{T}(t)$ be the positive semigroup generated by $\mathcal{A} := \mathcal{B} + \mathcal{F}$. It was shown in [370, Theorem 3.5] that $s(\mathcal{A})$ has the same sign as $r(-\mathcal{F}\mathcal{B}^{-1}) - 1$. If $s(\mathcal{A}) < 0$, then $\lim_{t\to\infty} \mathcal{T}(t)\phi = 0$ for all $\phi \in D(\mathcal{A})$ (see, e.g., [370, Theorem 3.13]). For nonlinear PDE models, however, the spectral bound of the variational operator may not decide about the local stability of the disease-free steady state. For this purpose, we need to use the exponential growth bound of the semigroup generated by this variational operator. Once the equality of these two bounds is known, the aforementioned result implies that R_0 is a threshold value for the local stability of the disease-free equilibrium (see [370, Section 3.3]).

For convenience, let $B := \nabla \cdot (d(x)\nabla) - V$. Then we have the following result.

Theorem 11.3.3. *Let (H1) and (H2) hold. Then $R_0 - 1$ has the same sign as $\lambda^* := s(B + F)$.*

Proof. Clearly, B is the generator of the semigroup $T(t)$ on X_1. Note that $T(t)$ is a positive semigroup in the sense that $T(t)X_1^+ \subseteq X_1^+$ for all $t \geq 0$. It then follows from [370, Theorem 3.12] that B is resolvent-positive, and

$$(\lambda I - B)^{-1}\phi = \int_0^\infty e^{-\lambda t}T(t)\phi\, dt, \quad \forall \lambda > s(B),\ \phi \in X_1. \tag{11.29}$$

From assumption (H2), we have $s(B) < 0$. Letting $\lambda = 0$ in (11.29), we obtain

$$-B^{-1}\phi = \int_0^\infty T(t)\phi\, dt,\ \forall \phi \in X_1.$$

It follows that $L = -FB^{-1}$. Define the linear operator $A := B + F$. In view of (11.24), the operator A generates a positive C_0-semigroup. Then [370, Theorem 3.12] implies that A is resolvent-positive. Thus, it follows from [370, Theorem 3.5] that $s(A)$ has the same sign as $r(-FB^{-1}) - 1 = R_0 - 1$. ∎

Next we characterize the basic reproduction ratio in terms of the principal eigenvalue of an elliptic eigenvalue problem.

Theorem 11.3.4. *Let (H1) and (H2) hold, and assume that there exists $d_0 > 0$ such that $d_i(x) \geq d_0$ for all $1 \leq i \leq m$. If the elliptic eigenvalue problem*

$$\begin{aligned} &-\nabla \cdot (d(x)\nabla\phi) + V(x)\phi = \mu F(x)\phi, \qquad x \in \Omega, \\ &\frac{\partial \phi}{\partial \nu} = 0, \quad x \in \partial\Omega. \end{aligned} \tag{11.30}$$

admits a unique positive eigenvalue μ_0 with a positive eigenfunction, then $R_0 = r(-FB^{-1}) = r(-B^{-1}F) = 1/\mu_0$.

Proof. Set

$$F_\epsilon(x) = F(x) + \epsilon E, \quad V_\epsilon(x) = V(x) - \epsilon E$$

where $\epsilon > 0$ is a constant and E is an $m \times m$ matrix whose elements are all 1. Consider

$$\begin{aligned} &\frac{\partial u}{\partial t} = \nabla \cdot (d(x)\nabla u) - V_\epsilon(x)u, \qquad x \in \Omega, \\ &\frac{\partial u}{\partial \nu} = 0, \quad t > 0, \ x \in \partial\Omega. \end{aligned} \tag{11.31}$$

Let $T_\epsilon(t)$ be the solution semigroup on X_1 associated with linear system (11.31). Then we define

$$L_\epsilon(\phi)(x) := F_\epsilon(x) \int_0^\infty [T_\epsilon(t)\phi](x)dt. \tag{11.32}$$

Clearly, L_ϵ is a strongly positive and compact operator. Thus, its spectral radius denoted by $R_0(\epsilon)$ is positive and is an eigenvalue with algebraic multiplicity one and a positive eigenvector ϕ_ϵ. Then we have

$$F_\epsilon \int_0^\infty T_\epsilon(t)\phi_\epsilon dt = R_0(\epsilon)\phi_\epsilon. \tag{11.33}$$

Let B_ϵ be the generator of the continuous semigroup $T_\epsilon(t)$. Then

$$B_\epsilon\phi = \nabla \cdot [d(x)\nabla(\phi)] - V_\epsilon(x)\phi. \tag{11.34}$$

Since $T_\epsilon(t)$ is a positive semigroup, [370, Theorem 3.12] implies that B_ϵ is resolvent-positive, and

$$(\lambda I - B_\epsilon)^{-1}\phi = \int_0^\infty e^{-\lambda t} T_\epsilon(t)\phi \, dt, \quad \forall \lambda > s(B_\epsilon), \, \phi \in X_1. \tag{11.35}$$

By assumption (H2), it follows from the continuity of the spectral bound on parameters that one can restrict ϵ small enough such that $s(B_\epsilon) < 0$.

Letting $\lambda = 0$ in (11.35), we obtain $-B_\epsilon^{-1}\phi = \int_0^\infty T_\epsilon(t)\phi \, dt, \forall \phi \in X_1$. Thus, we have

$$-F_\epsilon B_\epsilon^{-1}\phi_\epsilon = R_0(\epsilon)\phi_\epsilon. \tag{11.36}$$

Set

$$\psi_\epsilon := -B_\epsilon^{-1}\phi_\epsilon.$$

It is easy to see that ψ_ϵ is positive and (11.36) implies

$$F_\epsilon\psi_\epsilon = -R_0(\epsilon)B_\epsilon\psi_\epsilon. \tag{11.37}$$

Therefore, we have

$$\begin{aligned} &-\nabla\cdot(d(x)\nabla\psi_\epsilon(x)) + V_\epsilon(x)\psi_\epsilon(x) = \frac{1}{R_0(\epsilon)}F_\epsilon(x)\psi_\epsilon(x), && x\in\Omega,\\ &\frac{\partial\psi_\epsilon}{\partial\nu} = 0, && x\in\partial\Omega. \end{aligned} \tag{11.38}$$

By similar arguments to those in [151], it follows that the following eigenvalue problem

$$\begin{aligned} &-\nabla\cdot(d(x)\phi) + V_\epsilon(x)\phi = \mu F_\epsilon(x)\phi, && x\in\Omega,\\ &\frac{\partial\phi}{\partial\nu} = 0, && x\in\partial\Omega \end{aligned} \tag{11.39}$$

has a unique positive eigenvalue μ_ϵ with a positive eigenfunction. Since ψ_ϵ is positive, it follows that $\mu_\epsilon = 1/R_0(\epsilon)$, and hence, $R_0(\epsilon) = 1/\mu_\epsilon$. Letting $\epsilon\to 0$ and using the perturbation theory of linear operators (see [198]), we then obtain $R_0 = 1/\mu_0$. ∎

In the case where some $d_i(x)$ are identically zero, we can reduce the computation of R_0 to that of the principal eigenvalue of a lower-dimensional elliptic eigenvalue problem under additional conditions. Without loss of generality, we assume that $d(x) = (d_1(x),\ldots,d_m(x))$ satisfies (D2) with $k = m$. For convenience, let $\mathbf{u}_{i_1} = (u_1,\ldots,u_{i_1})^T$, $\mathbf{u}_{i_2} = (u_{i_1+1},\ldots,u_m)^T$, and

$$\nabla\cdot(\mathbf{d}_{i_1}(x)\nabla\mathbf{u}_{i_1}) = diag\left(\nabla\cdot(d_1(x)\nabla u_1),\ldots,\nabla\cdot(d_{i_1}(x)\nabla u_{i_1})\right).$$

We split two $m\times m$ matrices $F(x)$ and $V(x)$ into

$$F(x) = \begin{pmatrix} F_{11}(x) & F_{12}(x)\\ F_{21}(x) & F_{22}(x)\end{pmatrix},\quad V(x) = \begin{pmatrix} V_{11}(x) & V_{12}(x)\\ V_{21}(x) & V_{22}(x)\end{pmatrix},$$

where F_{11} and V_{11} are $i_1\times i_1$ matrices, F_{22} and V_{22} are $i_2\times i_2$ matrices, and $i_1+i_2 = m$. Then we have the following results.

Theorem 11.3.5. *Let (H1) and (H2) hold and assume that $s(-V_{22})<0$. Let $B_1 := \nabla\cdot(\mathbf{d}_{i_1}\nabla) - V_1$, where $V_1 := V_{11} - V_{12}V_{22}^{-1}V_{21}$. Then the following statements are valid:*

(i) If $F_{12} = 0$ and $F_{22} = 0$, then $R_0 = r(-B^{-1}F) = r(-B_1^{-1}F_1)$, where $F_1 = F_{11} - V_{12}V_{22}^{-1}F_{21}$.
(ii) If $F_{21} = 0$ and $F_{22} = 0$, then $R_0 = r(-B^{-1}F) = r(-B_1^{-1}F_2)$, where $F_2 := F_{11} - F_{12}V_{22}^{-1}V_{21}$.

Proof. Since $-V_{22}$ is cooperative and $s(-V_{22}) < 0$, it follows that V_{22}^{-1} exists and $V_{22}^{-1}(x) = \int_0^\infty e^{-V_{22}(x)t} dt$ is a nonnegative matrix for any $x \in \overline{\Omega}$. Let $\hat{L} := -B^{-1}F$. Clearly, we have $R_0 = r(\hat{L})$. For any given $\phi \in X_1$, let $\psi = \hat{L}\phi$. Since $-B\psi = F\phi$, we have

$$\begin{aligned} -\nabla \cdot (\mathbf{d}_{i_1} \nabla \psi_1) + V_{11}\psi_1 + V_{12}\psi_2 &= F_{11}\phi_1 + F_{12}\phi_2, \\ V_{21}\psi_1 + V_{22}\psi_2 &= F_{21}\phi_1 + F_{22}\phi_2. \end{aligned}$$

A straightforward computation shows that

$$\begin{aligned} -B_1\psi_1 &= (F_{11} - V_{12}V_{22}^{-1}F_{21})\phi_1 + (F_{12} - V_{12}V_{22}^{-1}F_{22})\phi_2, \\ \psi_2 &= V_{22}^{-1}(F_{21}\phi_1 + F_{22}\phi_2) - V_{22}^{-1}V_{21}\psi_1. \end{aligned} \tag{11.40}$$

In the case where $F_{12} = 0$ and $F_{22} = 0$, it follows from (11.40) that

$$\psi_1 = -B_1^{-1}F_1\phi_1 := A\phi_1, \quad \psi_2 = \left(V_{22}^{-1}F_{21} + V_{22}^{-1}V_{21}B_1^{-1}F_1\right)\phi_1 := B\phi_1.$$

Thus, $\hat{L}\phi = (A\phi_1, B\phi_1)$, $\forall \phi = (\phi_1, \phi_2) \in X_1$. By induction, we further have

$$\hat{L}^n(\phi_1, \phi_2) = \left(A^n\phi_1, BA^{n-1}\phi_1\right), \ \forall n \geq 2, \ \phi = (\phi_1, \phi_2) \in X_1.$$

Note that both $A : Y_1 \to Y_1$ and $B : Y_1 \to Y_2$ are linear operators. It then easily follows that

$$\|A^n\| \leq \|\hat{L}^n\| \leq \left(\|A^n\|^2 + \|B\|^2 \cdot \|A^{n-1}\|^2\right)^{\frac{1}{2}}, \ \forall n \geq 2.$$

By the formula of spectral radius, we then obtain $r(\hat{L}) = r(A) = r(-B_1^{-1}F_1)$.

In the case where $F_{21} = 0$ and $F_{22} = 0$, we have $\psi_2 = -V_{22}^{-1}V_{21}\psi_1$. Set

$$Z := \{\phi = (\phi_1, \phi_2) \in X_1 : \ \phi_2 = -V_{22}^{-1}V_{21}\phi_1\}.$$

Thus, Z is a subspace of the Banach space X_1 and $\hat{L}(X_1) \subset Z$. Let $\hat{L}_Z$ be the restriction of $\hat{L}$ to Z. Then $\hat{L}_Z$ is a linear operator on Z. In view of (11.40), it follows that

$$\hat{L}_Z(\phi) = \left(-B_1^{-1}F_2\phi_1, -V_{22}^{-1}V_{21}(-B_1^{-1}F_2\phi_1)\right), \ \forall \phi = (\phi_1, \phi_2) \in Z.$$

By the same argument as in the proof of $r(\hat{L}) = r(A)$ in the last paragraph, we then have $r(\hat{L}_Z) = r(-B_1^{-1}F_2)$. Further, it is easy to verify that

$$\|\hat{L}_Z^n\| \leq \|\hat{L}^n\| \leq \|\hat{L}_Z^{n-1}\| \cdot \|\hat{L}\|, \quad \forall n \geq 2.$$

This, together with the formula of spectral radius, implies that $r(\hat{L}) = r(\hat{L}_Z) = r(-B_1^{-1}F_2)$. ∎

Remark 11.3.3. If we replace the nonzero diffusion terms $-\nabla \cdot (d_i(x)\nabla)$ in system (11.24) with uniformly x-dependent elliptic operators and use Dirichlet or Robin-type boundary conditions in (11.24), then Theorems 11.3.3, 11.3.4, and 11.3.5 are still valid.

The following result shows that the reaction–diffusion epidemic model in a spatially homogenous habitat with the Neumann boundary condition admits the same basic reproduction ratio as that of its ordinary differential equations counterpart (see [376]).

Theorem 11.3.6. *If each d_i is a positive constant for $1 \le i \le m$, and $F(x) = F$ and $V(x) = V$ are independent of $x \in \overline{\Omega}$, then $R_0 = r(FV^{-1})$.*

Proof. Let $F_\epsilon = F + \epsilon E, \quad V_\epsilon = V - \epsilon E$, where $\epsilon > 0$. As shown in the proof of Theorem 11.3.4, $R_0(\epsilon)$ is the principal eigenvalue of L_ϵ with a positive eigenfunction. On the other hand, the Perron-Frobenius theorem implies that $r(F_\epsilon V_\epsilon^{-1})$ is an eigenvalue of $F_\epsilon V_\epsilon^{-1}$ with a positive eigenvector w^*. It then follows that

$$L_\epsilon w^* = F_\epsilon \int_0^\infty T_\epsilon(t) w^* dt = F_\epsilon \int_0^\infty e^{-V_\epsilon t} w^* dt = F_\epsilon V_\epsilon^{-1} w^* = r(F_\epsilon V_\epsilon^{-1}) w^*.$$

By the uniqueness of the principal eigenvalue, it follows that $R_0(\epsilon) = r(F_\epsilon V_\epsilon^{-1})$. Letting $\epsilon \to 0$, we then obtain $R_0 = r(FV^{-1})$. ∎

11.4 A Spatial Model of Rabies

In this section, we apply the theory developed in Section 11.3 to a reaction-diffusion model of rabies, and show that R_0 is a spatial invasion threshold of the disease.

Consider the spatial model of rabies (see [252]):

$$\begin{aligned}
\frac{\partial E}{\partial t} &= \beta IS - \sigma E - \left[b + (a-b)\frac{N}{K} \right] E, \\
\frac{\partial I}{\partial t} &= \frac{\partial}{\partial x}\left(D \frac{\partial I}{\partial x} \right) + \sigma E - \alpha I - \left[b + (a-b)\frac{N}{K} \right] I, \\
\frac{\partial S}{\partial t} &= (a-b) S \left(1 - \frac{N}{K} \right) - \beta IS,
\end{aligned} \tag{11.41}$$

where S is the density of susceptible foxes, E is the density of infected but non-infectious foxes, I is the density of rabid foxes, $N = S + E + I$ is the total fox population, D is the diffusion coefficient, a is the birth rate, b is the intrinsic death rate, and K is the environmental carrying capacity, β is the disease transmission coefficient, σ is the per capita rate of infected foxes becoming infectious, α is the disease-induced death rate of rabid fox, and x is the one-dimensional space variable. The term $(a - b)N/K$ represents the death rate due to depletion of the food supply by all foxes. Moreover, $a > b$ is assumed to ensure sustainable population size.

For simplicity, we confine ourselves to one-dimensional habitat $\Omega = (0,1)$ and impose the Neumann boundary conditions for model (11.41):

$$\frac{\partial I}{\partial x}\Big|_{x=0} = \frac{\partial I}{\partial x}\Big|_{x=1} = 0. \tag{11.42}$$

We assume that a, b, σ, and K are positive constants. Rabies, as a zoonotic disease, is crucially influenced by landscape heterogeneity and spatial distribution of reservoirs [287, 342], which could result in spatially dependent transmission coefficient, disease-free steady state and diffusion coefficient. Furthermore, the spatial control of rabies such as culling and vaccinations [296, 314] induces spatially dependent death rates of populations and disease-free steady state. Hence, we allow the diffusion coefficient D, the disease transmission coefficient β and the death rate α of infected foxes to be spatially dependent. We further assume that $D(x) \geq D_0$, $\forall x \in [0,1]$, for some constant $D_0 > 0$, $\beta(x)$ and $\alpha(x)$ are nonnegative continuous functions on $[0,1]$ with $\beta(x) \not\equiv 0$.

Under the above assumptions, system (11.41) admits a disease-free steady sate $(0,0,K)$. From the first two equations of the linearized system at $(0,0,K)$, it then follows that

$$F(x) = \begin{pmatrix} 0 & \beta(x)K \\ 0 & 0 \end{pmatrix}, \qquad V(x) = \begin{pmatrix} \sigma + a & 0 \\ -\sigma & \alpha(x) + a \end{pmatrix}.$$

We first consider the elliptic eigenvalue problem associated with linear parabolic system (11.24):

$$\begin{aligned} &-(\sigma + a)E + \beta(x)KI = \lambda E,\ x \in (0,1), \\ &\frac{d}{dx}\left(D(x)\frac{dI}{dx}\right) + \sigma E - (\alpha(x) + a)I = \lambda I,\ x \in (0,1), \\ &\frac{dI}{dx}\Big|_{x=0} = \frac{dI}{dx}\Big|_{x=1} = 0. \end{aligned} \tag{11.43}$$

Lemma 11.4.1. *Problem (11.43) has a principal eigenvalue λ^* with a positive eigenfunction.*

Proof. In order to use Theorem 11.3.2, we write the eigenvalue problem into the following equivalent one:

$$\begin{aligned} &\frac{d}{dx}\left(D(x)\frac{d\phi_1}{dx}\right) - (\alpha(x) + a)\phi_1 + \sigma\phi_2 = \lambda\phi_1,\ x \in (0,1), \\ &\beta(x)K\phi_1 - (\sigma + a)\phi_2 = \lambda\phi_2,\ x \in (0,1), \\ &\frac{d\phi_1}{dx}\Big|_{x=0} = \frac{d\phi_1}{dx}\Big|_{x=1} = 0. \end{aligned} \tag{11.44}$$

Thus, the linear operators $\mathcal{L}_\lambda$ defined in Section 11.3 become

$$\mathcal{L}_\lambda \phi = \frac{d}{dx}\left(D(x)\frac{d\phi}{dx}\right) - (\alpha(x) + a)\phi + \frac{\sigma\beta(x)K}{\lambda + (\sigma + a)}\phi,\ \forall \lambda > -(\sigma + a).$$

Since $\beta(x) \geq 0$ and $\beta(x) \not\equiv 0$, there exists an interval $[c, d] \subset (0, 1)$ such that $\beta(x) > 0$, $\forall x \in [c, d]$. Let $A := \sigma \cdot \min_{x\in[c,d]} \beta(x) \cdot K$, and let λ_1 be the principal eigenvalue of the following elliptic eigenvalue problem

$$\begin{aligned}
&\frac{d}{dx}\left(D(x)\frac{d\phi}{dx}\right) - (\alpha(x) + a)\phi = \lambda\phi, \quad x \in (c, d),\\
&\phi(c) = \phi(d) = 0,
\end{aligned}$$

with a positive eigenfunction $\phi^*(x)$. Set

$$\lambda_0 := \frac{\lambda_1 - (\sigma + a) + \sqrt{(\lambda_1 + \sigma + a)^2 + 4A}}{2}.$$

Since $A > 0$, we have $\lambda_0 > -(\sigma + a)$. It then follows that

$$\begin{aligned}
\mathcal{L}_{\lambda_0}\phi^*(x) &\geq \frac{d}{dx}\left(D(x)\frac{d\phi^*(x)}{dx}\right) - (\alpha(x) + a)\phi^*(x) + \frac{A}{\lambda_0 + (\sigma + a)}\phi^*(x)\\
&= \left(\lambda_1 + \frac{A}{\lambda_0 + (\sigma + a)}\right)\phi^*(x)\\
&= \lambda_0\phi^*(x), \quad \forall x \in (c, d).
\end{aligned}$$

Now we define a continuous function $\phi_0(x)$ on $[0, 1]$ by

$$\phi_0(x) = \begin{cases} \phi^*(x), & \text{if} \quad x \in [c, d],\\ 0, & \text{if} \quad x \in [0, 1] \setminus [c, d]. \end{cases}$$

Then we have $\mathcal{L}_{\lambda_0}\phi_0(x) \geq \lambda_0\phi_0(x)$, $\forall x \in (0, 1) \setminus \{c, d\}$. Consequently, $e^{\lambda_0 t}\phi_0(x)$ is a subsolution of the integral form of the linear system $u_t = \mathcal{L}_{\lambda_0}u$. By Theorem 11.3.2 and Remark 11.3.1, problem (11.44) has an eigenvalue with geometric multiplicity one and a nonnegative eigenfunction. Using (11.44) and its associated parabolic system, we see that this eigenfunction is positive. ∎

Let R_0 be the basic reproduction ratio of system (11.41), as defined in Section 11.3. Then we have the following observation.

Lemma 11.4.2. *Let μ_1 be the unique positive eigenvalue of the following eigenvalue problem:*

$$\begin{aligned}
&-\frac{d}{dx}\left(D(x)\frac{d\phi}{dx}\right) + (\alpha(x) + a)\phi = \mu\frac{\sigma K\beta(x)}{\sigma + a}\phi, \quad x \in (0, 1),\\
&\left.\frac{d\phi}{dx}\right|_{x=0} = \left.\frac{d\phi}{dx}\right|_{x=1} = 0,
\end{aligned} \tag{11.45}$$

with a positive eigenfunction. Then $R_0 = 1/\mu_1$.

Proof. In order to use Theorem 11.3.5, we define

$$\hat{F}(x) := \begin{pmatrix} 0 & 0 \\ \beta(x)K & 0 \end{pmatrix}, \qquad \hat{V}(x) := \begin{pmatrix} \alpha(x)+a & -\sigma \\ 0 & \sigma+a \end{pmatrix},$$

and $\hat{B} := \text{diag}\left(\frac{d}{dx}\left(D(x)\frac{d}{dx}\right), 0\right) - \hat{V}$. It then follows that $R_0 = r(-B^{-1}F) = r(-\hat{B}^{-1}\hat{F})$. Since $\hat{F}_{12} = 0$ and $\hat{F}_{22} = 0$, Theorem 11.3.5 (i) implies that

$$R_0 = r(-\hat{B}^{-1}\hat{F}) = r(-\hat{B}_1^{-1}\hat{F}_1),$$

where $\hat{B}_1\phi_1 := \frac{d}{dx}\left(D(x)\frac{d\phi_1}{dx}\right) - \hat{V}_1\phi_1$, $\hat{V}_1\phi_1 = (\alpha(x)+a)\phi_1$, and $\hat{F}_1\phi_1 = \frac{\sigma K\beta(x)}{\sigma+a}\phi_1$. By Theorem 11.3.4, as applied to the triple $(\hat{B}_1, \hat{F}_1, \hat{V}_1)$, it follows that $r(-\hat{B}_1^{-1}\hat{F}_1) = 1/\mu_1$, where μ_1 is the unique positive eigenvalue of $-\hat{B}_1\phi_1 = \mu\hat{F}_1\phi_1$ with a positive eigenfunction. Thus, we have $R_0 = 1/\mu_1$. ∎

The subsequent result implies that R_0 is a threshold value for the local stability of the disease-free equilibrium $(0,0,K)$ of the model system (11.41).

Theorem 11.4.1. *The following statements are valid:*

(i) If $R_0 < 1$, then the disease-free steady state $(0,0,K)$ is asymptotically stable for system (11.41).
(ii) If $R_0 > 1$, then there exists $\epsilon_0 > 0$ such that any positive solution of system (11.41) satisfies $\limsup_{t\to\infty} \|(E(t,\cdot), I(t,\cdot), S(t,\cdot)) - (0,0,K)\| \geq \epsilon_0$.

Proof. By linearizing system (11.41) at $(0,0,K)$, we obtain

$$\begin{aligned} &\frac{\partial u}{\partial t} = \nabla\cdot(d(x)\nabla u) + (F(x) - V(x))\,u, \;\; t>0, \;\; x\in\Omega, \\ &\frac{\partial u_3}{\partial t} = -(a-b)u_1 - (a-b+\beta(x)K)u_2 - (a-b)u_3, \, t>0, \;\; x\in\Omega, \\ &\frac{\partial u_2}{\partial \nu} = 0, \;\; t>0, \;\; x\in\partial\Omega, \end{aligned} \tag{11.46}$$

where $u = (u_1, u_2)^T$, $d(x) = (0, D(x))^T$. Let $Bu = \nabla\cdot(d(x)\nabla u) - V(x)u$, $Q(t)$ be the solution semigroup of the u equation of (11.46) subject to the boundary condition $\frac{\partial u_2}{\partial\nu} = 0$, and $\hat{\omega}(Q)$ be the exponential growth bound of $Q(t)$. Then $B+F$ is the generator of $Q(t)$. In the case where $R_0 < 1$, Theorem 11.3.3 implies that $s(B+F) < 0$. By [370, Theorem 3.14], we obtain $\hat{\omega}(Q) = s(B+F) < 0$. Let $\Phi(t)$ be the solution semigroup of system (11.46), and $\hat{\omega}(\Phi)$ be its exponential growth bound. Since the first equation of system (11.46) is decoupled from the second one, we easily see that $\hat{\omega}(\Phi) < 0$. Thus, the local asymptotic stability of $(0,0,K)$ for the nonlinear system (11.41) follows from [93, Theorem 2.1].

In the case where $R_0 > 1$, Theorem 11.3.3 implies that $\lambda^* > 0$, where λ^* is the principal eigenvalue of (11.43) with a positive eigenfunction due to

Lemma 11.4.1. For any given $\epsilon \in (0, K)$, we consider the following eigenvalue problem:

$$\begin{aligned}
&\beta(x)I(K-\epsilon) - \sigma E - \left[b + (a-b)\frac{K+3\epsilon}{K}\right] E = \lambda E,\ x \in (0,1),\\
&\frac{d}{dx}\left(D(x)\frac{dI}{dx}\right) + \sigma E - \alpha(x)I - \left[b + (a-b)\frac{K+3\epsilon}{K}\right] I = \lambda I,\ x \in (0,1),\\
&\frac{d}{dx}\Big|_{x=0} = \frac{dI}{dx}\Big|_{x=1} = 0.
\end{aligned} \tag{11.47}$$

By the same argument as in Lemma 11.4.1, problem (11.47) has a principal eigenvalue λ_ϵ^* with a positive eigenfunction $\phi_\epsilon^*(x)$. Since $\lim_{\epsilon\to 0}\lambda_\epsilon^* = \lambda^* > 0$, we can fix a small $\epsilon_0 \in (0, K)$ such that $\lambda_{\epsilon_0}^* > 0$. Assume, for the sake of contradiction, that there exists a positive solution $(E(t,x), I(t,x), S(t,x))$ of (11.41) such that

$$\limsup_{t\to\infty} \|(E(t,\cdot), I(t,\cdot), S(t,\cdot)) - (0,0,K)\| < \epsilon_0. \tag{11.48}$$

Then there exists a large $t_0 > 0$ such that

$$\begin{aligned}
&\frac{\partial E}{\partial t} \geq \beta(x)I(K-\epsilon_0) - \sigma E - \left[b + (a-b)\frac{K+3\epsilon_0}{K}\right] E,\\
&\frac{\partial I}{\partial t} \geq \frac{\partial}{\partial x}\left(D(x)\frac{\partial I}{\partial x}\right) + \sigma E - \alpha(x)I - \left[b + (a-b)\frac{K+3\epsilon_0}{K}\right] I,
\end{aligned} \tag{11.49}$$

for all $t \geq t_0$. Since $(E(t_0,\cdot), I(t_0,\cdot)) \gg 0$ in $C([0,1],\mathbb{R}^2)$, we can choose a sufficiently small number $\eta > 0$ such that $(E(t_0,\cdot), I(t_0,\cdot)) \geq \eta\phi_{\epsilon_0}^*(\cdot)$. Note that $\eta e^{\lambda_{\epsilon_0}^*(t-t_0)}\phi_{\epsilon_0}^*(x)$ is a solution of the following linear system:

$$\begin{aligned}
&\frac{\partial E}{\partial t} = \beta(x)I(K-\epsilon_0) - \sigma E - \left[b + (a-b)\frac{K+3\epsilon_0}{K}\right] E,\\
&\frac{\partial I}{\partial t} = \frac{\partial}{\partial x}\left(D(x)\frac{\partial I}{\partial x}\right) + \sigma E - \alpha(x)I - \left[b + (a-b)\frac{K+3\epsilon_0}{K}\right] I,\\
&\frac{\partial I}{\partial x}\Big|_{x=0} = \frac{\partial I}{\partial x}\Big|_{x=1} = 0,
\end{aligned} \tag{11.50}$$

for all $t \geq t_0$. It then follows from (11.49) and the comparison principle that

$$(E(t,x), I(t,x)) \geq \eta e^{\lambda_{\epsilon_0}^*(t-t_0)}\phi_{\epsilon_0}^*(x), \quad \forall x \in [0,1],\ t \geq t_0,$$

and hence, $E(t,x)$ and $I(t,x)$ approach ∞ as $t \to \infty$, which contradicts (11.48). This proves statement (ii). ∎

At the end of this section, we present our numerical scheme on the computation of R_0 for model (11.41) via the principal eigenvalue of the eigenvalue problem (11.45).

Let $h = 1/(n+1)$ and $x_i = ih$ for $1 \le i \le n$ with $x_0 = 0$ and $x_{n+1} = 1$. Then we approximate the derivative by

$$\frac{d}{dx}\Big(D(x)\frac{d\phi}{dx}\Big)\big|_{x_i} \approx \frac{1}{h^2}[D(x_{i+1})\phi(x_{i+1}) - (D(x_{i+1}) + D(x_i))\phi(x_i) + D(x_i)\phi(x_{i-1})]$$

for all $1 \le i \le n$. Under the Neumann boundary condition, (11.45) can be approximated by

$$Au + Qu = \mu F u, \tag{11.51}$$

where $u = (u_1, u_2, \ldots, u_n)^T$,

$$A = \frac{1}{h^2}\begin{pmatrix} D(x_2) & -D(x_2) & 0 & \cdots & 0 \\ -D(x_2) & D(x_2)+D(x_3) & -D(x_3) & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \cdots & D(x_{n-1})+D(x_n) & -D(x_n) \\ 0 & 0 & \cdots & -D(x_n) & D(x_n) \end{pmatrix},$$

$$F = \begin{pmatrix} \frac{K\sigma\beta(x_1)}{\alpha(x_1)+a} & 0 & 0 & \cdots & 0 \\ 0 & \frac{K\sigma\beta(x_2)}{\alpha(x_2)+a} & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \cdots & \frac{K\sigma\beta(x_{n-1})}{\alpha(x_{n-1})+a} & 0 \\ 0 & 0 & \cdots & 0 & \frac{K\sigma\beta(x_n)}{\alpha(x_n)+a} \end{pmatrix},$$

and $Q = diag\,(\alpha(x_1) + a, \ldots, \alpha(x_n) + a)$. If $C = A + Q$, then (11.51) becomes

$$Cu = \mu F u. \tag{11.52}$$

Let $u_0 = (1, 1, \ldots, 1)^T$ and define an iteration sequence

$$\begin{aligned} v_k &= C^{-1}Fu_{k-1}, & k \ge 1, \\ u_k &= \frac{v_k}{\|v_k\|_\infty}, & k \ge 1, \end{aligned}$$

where v_k is obtained by solving the linear system

$$Cv_k = Fu_{k-1}.$$

If the eigenvalues of $C^{-1}F$ are given by

$$\mu_1 > |\mu_2| \ge |\mu_3| \ge \cdots \ge |\mu_n|$$

and w_1 is an eigenvector corresponding to μ_1, then the classical method in numerical analysis indicates

$$\begin{aligned} \lim \|v_k\|_\infty &= \mu_1, \\ \lim u_k &= \frac{w_1}{\|w_1\|_\infty}, \end{aligned}$$

which gives the approximations of μ_1 and its eigenfunction, respectively. By Lemma 11.4.2, we then have $R_0 = \mu_1$.

11.5 Notes

Sections 11.1 and 11.2 are taken from Zhao [442]. It seems difficult to directly use the general theory developed in Thieme [370] to prove that R_0 is a threshold value for the linear stability associated with periodic and time-delayed population models with or without spatial diffusion. For some specific periodic models, one may derive linear periodic Volterra integral equations for infectious variables and then utilize the renewal theory (see, e.g., [362, 22] and the references therein) after a careful verification of certain technical conditions (see, e.g., [288] and the references therein). Our introduction of a one-parameter family of positive linear operators on the space of continuous periodic functions was motivated by an eigenvalue problem associated with the renewal theory.

Recently, there have been a few applications of the theory and methods developed in [442], see, e.g., Bai [25] for a time-delayed SEIRS model with pulse vaccination; Zhang, Wang and Zhao [428] for a periodic reaction–diffusion epidemic model with latent period; Wang and Zhao [393] for a periodic vector-bias malaria model with incubation period; Lou and Zhao [234] for a population model with time-periodic delay; Wang and Zhao [394] for a time-delayed Lyme disease model with seasonality. For the theory of basic reproduction ratios in almost periodic compartmental ODE models, we refer to Wang and Zhao [391].

Sections 11.3 and 11.4 are adapted from Wang and Zhao [390]. Earlier, Wang and Zhao [389] introduced a next generation operator to define the basic reproduction ratio R_0 for a nonlocal and time-delayed reaction–diffusion model of dengue fever, and proved that R_0 is a threshold value for the local extinction and uniform persistence of the disease by appealing to the abstract results in Thieme [370] and persistence theory. Other studies in this vein are given in Lou and Zhao [233] for a nonlocal reaction–diffusion malaria model; in Guo, Wang and Zou [138] for an infective disease model with a fixed latent period and nonlocal infections; in Mckenzie, Jin, Jacobsen and Lewis [247] for an advection–diffusion–reaction population model; and in Peng and Zhao [277] for a periodic reaction–diffusion SIS epidemic model. Recently, the theory and methods developed in [390] have been applied to two advection-dispersion-reaction models of harmful algae and zooplankton in Hsu, Wang and Zhao [176], a reaction-diffusion-advection model of harmful algae growth with toxin degradation in Wang, Hsu and Zhao [398], and a benthic-drift model for a stream population in Huang, Jin and Lewis [179].

It is worthy to point out that Allen, Bolker, Lou and Nevai [9] used a variational expression to define R_0 for a reaction-diffusion model with one infectious compartment. The biological meaning of such R_0 can be easily confirmed via Theorem 11.3.4 combined with the variational characterization of the principal eigenvalue, see, e.g., [277, Lemmas 2.1 and 2.4].

12

A Population Model with Periodic Delay

The rhythm of life on earth, occurring on daily or annual scales, is driven by seasonal changes in the environment [348] which regulate various physiological and behavioral processes, as well as the population dynamics of species. Many plant and animal species have demonstrated seasonal population dynamics in response to seasonal environmental changes, in particular, the weather conditions. Mosquito species *Culex pipiens* and *Culex restuans*, main vectors of West Nile virus transmission, are very sensitive to long-term variations in climate and short-term variations in weather [397], in particular, temperature condition affects the rates of immature mosquito development and activity of adults, and precipitation determines the amount and quality of larval habitats. Temperature also affects the host-seeking activity of ticks and their rates from one life stage to the next one, as a result, it is proposed as a statistically significant determinant and possible driver of emergence of the tick in Canada [262]. Seasonal forcing in host and parasite biology also determines the risk of infectious diseases through the following aspects [10]: (a) host social behavior and aggregation; (b) vector population and activity; (c) parasite stages in the environment; (d) timing of reproduction and pulses of susceptible hosts; and (e) host susceptibility and immune defences.

Given the significant roles that seasonal environment factors play in population growth, disease transmission, and other life systems, theoretical models have been formulated to incorporate the seasonality of parameters in phenomenological ways such as those reported in [10]. Many model parameters in ecosystems are influenced by the environmental conditions in a nonlinear way [250], and in previous models, it is well accepted to assume the parameters subject to seasonal factors change periodically. A growing body of literature reported that the developmental duration can be driven by seasonal forcing, and thus be periodic. For example, the developmental duration of mosquito species *Culex pipiens* and *Culex restuans* is affected by temperature conditions. In the transmission cycle of malaria, the extrinsic incubation period (EIP) of the parasite within the mosquito is one of the most critical parameters to

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evaluate the disease risk. During EIP, malaria parasites go through various developmental stages and distinct replication cycles before migrating to the salivary glands where they can be transmitted to humans. The speed of this development depends on host, parasite, and environmental factors with estimate order of 10–14 days in areas of high malaria transmission. However, 90% of the female mosquitoes die within 12 days and are therefore unlikely to contribute to malaria transmission. On the other side, the extrinsic incubation period is extremely temperature sensitive [267], and hence, it is pivotal to incorporate this seasonally forced incubation period in the description of malaria transmission. For these two aforementioned scenarios, the developmental durations for immature mosquitoes and incubation period for parasites are periodic functions of time, which brings new challenges into model formulation where careful mathematical derivation and biological justification are needed. The purpose of this chapter is to propose a synthesized mathematical approach to the study of biological systems with seasonal forcing, in particular, with seasonal variations on developmental duration.

In Section 12.1, we use the host-macroparasite interaction as a motivating example to present our approach. The host-parasite interaction has attracted great attention since the pioneering work of Anderson and May [15], with most models aiming to figure out the basic reproduction number R_0 of parasite (measuring "the expected lifetime reproductive output of a new born larva" for macroparasite [250]). Here we develop a theoretical framework to investigate the population dynamics with time-dependent developmental duration for the parasitic nematodes with a direct life cycle and endotherm hosts [250]. This framework can be extended to the population growth, pathogen transmission, and in-host viral dynamics. In Section 12.2, we introduce the basic reproduction ratio R_0 for the model system and establish a threshold-type result on its global dynamics in terms of R_0. In Section 12.3, we show how to write the next generation operator into the integral form in Posny and Wang [282] so that their numerical method remains applicable to the computation of R_0 for our model system. For reader's convenience, we also include the algorithm of [282] at the end of this section.

12.1 Model Formulation

Before introducing the whole model system for host-parasite interaction, we investigate a two-stage single population growth scenario as a toy example, in the hope of presenting the modelling idea through a simpler case.

We start with a two-stage model, with population containing first stage $I(t)$ and second stage $M(t)$ defined, respectively, as those of age less than, and greater than, some threshold age $\tau(t)$ (the maturation time for the cohort that matures at time t), which is assumed to be seasonal due to the seasonal variations of weather conditions. That is, at time t, the individuals with age greater (less) than $\tau(t)$ are in the second stage (remaining in the first stage).

Within each age group, all individuals have the same age-independent birth and death rates. Let $\rho(t,a)$ be the population density of age a at time t, then the numbers $I(t)$ and $M(t)$ of individuals in the first and second stages, respectively, are given by

$$I(t) = \int_0^{\tau(t)} \rho(t,a)\,da \quad \text{and} \quad M(t) = \int_{\tau(t)}^{\infty} \rho(t,a)\,da.$$

The age density $\rho(t,a)$ satisfies the following McKendrick von-Foerster type equation [77, 400]

$$\frac{\partial\rho(t,a)}{\partial t} + \frac{\partial\rho(t,a)}{\partial a} = -\mu(a,t)\rho(t,a), \tag{12.1}$$

with the age-dependent death rates

$$\mu(a,t) = \mu_1(t) \text{ if } a \le \tau(t) \quad \text{and} \quad \mu(a,t) = \mu_2(t) \text{ if } a > \tau(t).$$

Taking the derivatives of $I(t)$ and $M(t)$, and using (12.1), we obtain

$$\begin{aligned} \tfrac{dI(t)}{dt} &= \rho(t,0) - (1-\tau'(t))\rho(t,\tau(t)) - \mu_1(t)I(t), \\ \tfrac{dM(t)}{dt} &= (1-\tau'(t))\rho(t,\tau(t)) - \mu_2(t)M(t) - \rho(t,\infty). \end{aligned}$$

Since no individual can live forever, $\rho(t,\infty)$ is taken as zero. The term $\rho(t,0)$ represents the flow in rate to the first stage at time t, supposed to be $\rho(t,0) = b(t) = B(t,M(t))$, a function of time t and population density $M(t)$. Mathematically, we also assume the delay $\tau(t)$ involved is continuously differentiable in $[0,\infty)$ and bounded away from zero and infinity. To close the system, we calculate $\rho(t,\tau(t))$ in terms of $\rho(t-\tau(t),0) = b(t-\tau(t)) = B(t-\tau(t),M(t-\tau(t)))$, which is achieved by the technique of integration along characteristics with the aid of the variable $V^s(t) = \rho(t,t-s)$. By direct calculations, we arrive at

$$\frac{d}{dt}V^s(t) = -\mu_1(t)V^s(t)$$

for $t - s \le \tau(t)$, with $V^s(s) = \rho(s,0) = b(s)$. It follows that

$$V^s(t) = V^s(s)e^{-\int_s^t \mu_1(\xi)\,d\xi} = B(s,M(s))e^{-\int_s^t \mu_1(\xi)\,d\xi}.$$

Setting $s = t - \tau(t)$, we have, for $t \ge \hat\tau$ with $\hat\tau = \max\{\tau(t)\}$,

$$\rho(t,\tau(t)) = V^{t-\tau(t)}(t) = B(t-\tau(t),M(t-\tau(t)))e^{-\int_{t-\tau(t)}^t \mu_1(\xi)\,d\xi}.$$

Hence, we obtain a closed system to describe two age groups subject to seasonal effects for $t \ge \hat\tau$:

$$\begin{aligned} \tfrac{dI(t)}{dt} &= B(t,M(t)) - (1-\tau'(t))B(t-\tau(t),M(t-\tau(t)))e^{-\int_{t-\tau(t)}^t \mu_1(\xi)\,d\xi} \\ &\quad -\mu_1(t)I(t), \\ \tfrac{dM(t)}{dt} &= (1-\tau'(t))B(t-\tau(t),M(t-\tau(t)))e^{-\int_{t-\tau(t)}^t \mu_1(\xi)\,d\xi} - \mu_2(t)M(t). \end{aligned} \tag{12.2}$$

This model turns out to be a differential system with periodic time delay, which is different from the traditional delay differential models without seasonal effects in the sense that the term $1-\tau'(t)$ is included in the development rate from the first stage to the next one:

$$(1-\tau'(t))B(t-\tau(t), M(t-\tau(t)))e^{-\int_{t-\tau(t)}^{t}\mu_1(\xi)\,d\xi}. \tag{12.3}$$

An alternative approach, more biologically oriented, to describe the population growth of two stages (especially the maturation term (12.3)) is also feasible. The first stage population size $I(t)$ at time t counts all accumulation of individuals born at moment ξ with rate $b(\xi)$ between $t-\tau(t)$ to t but remain alive with the survival probability $e^{-\int_{\xi}^{t}\mu_1(s)\,ds}$. Intuitively, the size $I(t)$ depends on the duration of $\tau(t)$ for individuals staying in the first stage. Motivated by these biological inductions, we can represent $I(t)$ by an integral form

$$I(t) = \int_{t-\tau(t)}^{t} b(\xi)e^{-\int_{\xi}^{t}\mu_1(s)\,ds}d\xi.$$

Taking the derivative of $I(t)$, we get the differential equation version of this variable in the first equation of (12.2). The maturation rate should be the birth rate at time $t-\tau(t)$, $b(t-\tau(t))$, multiplied with survival probability to time t, $e^{-\int_{t-\tau(t)}^{t}\mu_1(s)\,ds}$, and corrected with the rate of change for $t-\tau(t)$.

In parameterizing the delay $\tau(t)$, the developmental proportion $r(\xi)$ at time ξ is taken into consideration such that the accumulative proportion from $t-\tau(t)$ to t reaches unity when the individual moves to the next stage. Theoretically, we use the following relation to determine $\tau(t)$

$$1 = \int_{t-\tau(t)}^{t} r(\xi)d\xi, \tag{12.4}$$

where $r(\xi)$ is the time-periodic development proportion at moment ξ. The periodicity of $r(\xi)$ in ξ implies the periodicity of the delay $\tau(t)$ in time variable t. Taking the derivative with respect to t, we have

$$0 = r(t) - (1-\tau'(t))r(t-\tau(t))$$

from which we obtain

$$1-\tau'(t) = \frac{r(t)}{r(t-\tau(t))},$$

and hence, the conversion rate in (12.3) can be expressed as

$$\frac{r(t)}{r(t-\tau(t))}b(t-\tau(t))e^{-\int_{t-\tau(t)}^{t}\mu_1(\xi)\,d\xi}.$$

Thanks to this relation, we can always assume that $1-\tau'(t) > 0$ for any biologically reasonable developmental delay.

Next, we extend the two-stage model (12.2) to describe host-parasite interaction, where the parasite developmental duration is dependent on time. Motivated by the fundamental modelling frameworks in Anderson and May [15] and Dobson and Hudson [100], we consider four stages: Free living larvae not infective $X(t)$, free living larvae infective $L(t)$, arrested larvae in the host $Y(t)$, and adult parasites $P(t)$. We are concerned with two delays in the parasite life cycle, one in the free-living stage and the other within the host population: (i) the developmental delay $\tau_L(t)$ between the moment when newly shed parasites enter the environment and the moment they reach the infective larval stage and (ii) the time period $\tau_P(t)$ needed for the arrested larvae infecting the host to develop to pathogenic adults [100]. Since the development time to the infectivity stage depends on metabolic rate and hence the temperature condition, we assume the developmental duration is a time-periodic parameter with the period being one year (365 days) as temperature changes seasonally [250]. Much attention should be paid to estimate these time-dependent delays. Other life cycle components may also be temperature-dependent, and therefore, be periodic in time t.

Host population dynamics may be regulated by parasites, which is a crucial assumption for some host-parasite models [291]. However, here we are more concerned with the reproduction ratio analysis, and therefore, we ignore the host survival or fecundity affected by the arrested parasites since the metabolic activity in arrested larvae is very low [100]. This assumption becomes much more reasonable for farmed animal hosts, whose density is largely controlled by the farm owner [291]. Therefore, the host population $H(t)$ is considered to be seasonal, analogous to those constant host population assumptions in [292, 293, 346].

Based on the conversion rate with periodic delays (12.3), we can write the model system as follows:

$$\begin{aligned}
\frac{dX(t)}{dt} &= \lambda P(t) - \mu_X(t)X(t) \\
&\quad -\lambda(1-\tau_L'(t))P(t-\tau_L(t))e^{-\int_{t-\tau_L(t)}^{t}\mu_X(\xi)\,d\xi}, && (12.5a)\\
\frac{dL(t)}{dt} &= \lambda(1-\tau_L'(t))P(t-\tau_L(t))e^{-\int_{t-\tau_L(t)}^{t}\mu_X(\xi)\,d\xi} - \mu_L(t)L(t) \\
&\quad -\beta(t)H(t)L(t), && (12.5b)\\
\frac{dY(t)}{dt} &= \beta(t)H(t)L(t) - (\mu_Y(t)+\mu_H(t))Y(t) \\
&\quad -(1-\tau_P'(t))\beta(t-\tau_P(t))H(t-\tau_P(t)) \times \\
&\quad e^{-\int_{t-\tau_P(t)}^{t}(\mu_Y(\xi)+\mu_H(\xi))\,d\xi}L(t-\tau_P(t)), && (12.5c)\\
\frac{dP(t)}{dt} &= (1-\tau_P'(t))\beta(t-\tau_P(t))H(t-\tau_P(t)) \times \\
&\quad e^{-\int_{t-\tau_P(t)}^{t}(\mu_Y(\xi)+\mu_H(\xi))\,d\xi}L(t-\tau_P(t)) \\
&\quad -(\mu_P(t)+\mu_H(t))P(t) - \alpha_H\left(1+\frac{P(t)}{H(t)}\frac{k+1}{k}\right)P(t). && (12.5d)
\end{aligned}$$

System (12.5) describes the change of densities for the four compartments: (1) The free living larvae $X(t)$ are regained through the birth of adult parasite at rate λ, lost by either mortality (at rate $\mu_X(t)$) or development to free living infected larvae (the last term of equation (12.5a)); (2) The density of free living infected larvae $L(t)$ increases from the development of uninfected larvae (the first term of equation (12.5b)) and decreases with the death rate $\mu_L(t)$ and host uptake at rate $\beta(t)H(t)$, which is dependent on the host population $H(t)$; (3) Ingested larvae $Y(t)$ enter the host population with rate $\beta(t)H(t)$. They stay in the host for $\tau_P(t)$ unit time, which is the developmental duration from infective larvae to adult parasite. The development rate to adult parasite is described by the last term of equation (12.5c). Their density decreases due to the natural death rate $\mu_Y(t)$ and host death rate $\mu_H(t)$ as the larvae will also die when hosts die; (4) The density of adult parasites $P(t)$ increases with the development from larvae (first term of (12.5d)), decreases with the mortality, both the natural death at rate $\mu_P(t)$ and host death at rate $\mu_H(t)$. The burden of adult parasite also decreases due to the aggregated distribution of parasites in the host population, by assuming the distribution of parasites within the host population to be negative binomial with exponent k (also known as aggregation parameter) [15]. As argued previously, we can replace $(1-\tau_L'(t))$ and $(1-\tau_P'(t))$, respectively, with the developmental proportions

$$1-\tau_L'(t)=\frac{r_L(t)}{r_L(t-\tau_L(t))} \text{ and } 1-\tau_P'(t)=\frac{r_P(t)}{r_P(t-\tau_P(t))},$$

where $r_L(t)$ and $r_P(t)$ are the corresponding developmental proportions.

12.2 Threshold Dynamics

In this section, we first introduce the basic reproduction ratio R_0 for model (12.5), and then establish a threshold-type result on its global dynamics.

In system (12.5), the equations (12.5a) and (12.5c) can be decoupled since variables X and Y do not appear in the other two equations. Therefore, we start with the decoupled system:

$$\begin{aligned}
\frac{dL}{dt} &= \lambda(1-\tau_L'(t))e^{-\int_{t-\tau_L(t)}^t \mu_X(\xi)\,d\xi}P(t-\tau_L(t))-\mu_L(t)L(t)-\beta(t)H(t)L(t),\\
\frac{dP}{dt} &= (1-\tau_P'(t))\beta(t-\tau_P(t))H(t-\tau_P(t))e^{-\int_{t-\tau_P(t)}^t(\mu_Y(\xi)+\mu_H(\xi))\,d\xi}L(t-\tau_P(t))\\
&\quad -(\mu_P(t)+\mu_H(t))P(t)-\alpha_H\left(1+\frac{P(t)}{H(t)}\frac{k+1}{k}\right)P(t).
\end{aligned}\tag{12.6}$$

Further, we can rewrite the other two variables into integral forms:

$$\begin{aligned}
X(t) &= \int_{t-\tau_L(t)}^t \lambda P(\xi)e^{-\int_\xi^t \mu_X(s)\,ds}d\xi,\\
Y(t) &= \int_{t-\tau_P(t)}^t \beta(\xi)H(\xi)L(\xi)e^{-\int_\xi^t(\mu_Y(s)+\mu_H(s))\,ds}d\xi.
\end{aligned}\tag{12.7}$$

Once the dynamics of two variables $L(t)$ and $P(t)$ are obtained, that of $X(t)$ and $Y(t)$ can be deduced naturally.

To address the well-posedness of system (12.6), we introduce some notations. Let $\hat{\tau} = \max\{\max_{t\in[0,\omega]} \tau_L(t), \max_{t\in[0,\omega]} \tau_P(t)\}$ and $\mathcal{X} := C([-\hat{\tau}, 0], \mathbb{R}^2)$ equipped with the maximum norm. For a function $x(\cdot) \in C([-\hat{\tau}, \infty), \mathbb{R}^2)$, we can define $x_t \in \mathcal{X}$ as $x_t(\theta) = x(t+\theta), \forall \theta \in [-\hat{\tau}, 0]$. For any $\phi \in \mathcal{X}$, we define $f(t, \phi) = (f_1(t, \phi), f_2(t, \phi))$ with

$$f_1(t,\phi) = \lambda(1-\tau_L'(t))e^{-\int_{t-\tau_L(t)}^t \mu_X(\xi)\,d\xi}\phi_2(-\tau_L(t)) - \mu_L(t)\phi_1(0) - \beta(t)H(t)\phi_1(0),$$

$$\begin{aligned} f_2(t,\phi) = (1-\tau_P'(t))\beta(t-\tau_P(t))H(t-\tau_P(t))e^{-\int_{t-\tau_P(t)}^t (\mu_Y(\xi)+\mu_H(\xi))\,d\xi}\phi_1(-\tau_P(t)) \\ -(\mu_P(t)+\mu_H(t)+\alpha_H)\phi_2(0) - \tfrac{k+1}{k}\tfrac{\alpha_H}{H(t)}\phi_2^2(0). \end{aligned}$$

Due to the ω-periodicity of $\tau_L(t)$, $\mu_L(t)$, $\beta(t)$, $H(t)$, $\tau_P(t)$, $\mu_P(t)$, and $\mu_H(t)$, it is easy to see that $f(t+\omega, \phi) = f(t, \phi)$. Thus, (12.6) is an ω-periodic functional differential system. For notational simplicity, we rewrite system (12.6) into

$$\begin{aligned} \frac{dL}{dt} &= b_L(t)P(t-\tau_L(t)) - d_L(t)L(t), \\ \frac{dP}{dt} &= b_P(t)L(t-\tau_P(t)) - d_P(t)P(t) - \alpha(t)P^2(t), \end{aligned} \tag{12.8}$$

where

$$\begin{aligned} b_L(t) &= \lambda(1-\tau_L'(t))e^{-\int_{t-\tau_L(t)}^t \mu_X(\xi)\,d\xi}, \quad d_L(t) = \mu_L(t) + \beta(t)H(t), \\ b_P(t) &= (1-\tau_P'(t))\beta(t-\tau_P(t))H(t-\tau_P(t))e^{-\int_{t-\tau_P(t)}^t (\mu_Y(\xi)+\mu_H(\xi))\,d\xi}, \\ d_P(t) &= \mu_P(t) + \mu_H(t) + \alpha_H, \quad \text{and} \quad \alpha(t) = \frac{\alpha_H(k+1)}{kH(t)}. \end{aligned}$$

Clearly, all these coefficients are positive ω-periodic functions.

For a given continuous ω-periodic function $g(t)$, let

$$\hat{g} = \max_{t\in[0,\omega]} g(t), \qquad \overline{g} = \min_{t\in[0,\omega]} g(t).$$

The following result shows that system (12.6) is well-posed on

$$\mathcal{X}_+ := C([-\hat{\tau}, 0], \mathbb{R}_+^2),$$

and hence, the derived model system is also biologically reasonable.

Lemma 12.2.1. *For any $\phi = (\phi_1, \phi_2) \in \mathcal{X}_+$, system (12.6) has a unique nonnegative and bounded solution $v(t, \phi)$ with $v_0 = \phi$ on $[0, \infty)$.*

Proof. Note that $f(t, \phi)$ is continuous and Lipschitzian in ϕ in each compact subset of $\mathcal{X}_+$. It follows that for any $\phi \in \mathcal{X}_+$, system (12.6) admits a unique solution $u(t,\phi)$ with $u_0=\phi$ on its maximal interval of existence. Let $x^*=(x_1^*,x_2^*):=\left(\frac{\hat{b}_L}{d_L}\frac{\hat{b}_p\hat{b}_L}{\overline{\alpha}\overline{d}_L},\frac{\hat{b}_p\hat{b}_L}{\overline{\alpha}\overline{d}_L}\right)$. For any given $\rho\geq 1$, let $[0,\rho x^*]_{\mathcal{X}}$ be the order interval in $\mathcal{X}$, that is,

$$[0,\rho x^*]_{\mathcal{X}}:=\{\phi\in\mathcal{X}:\,0\leq\phi(\theta)\leq\rho x^*,\forall\theta\in[-\hat{\tau},0]\}.$$

It is easy to verify that whenever $\psi\in[0,\rho x^*]_{\mathcal{X}}$, $t\in\mathbb{R}$, and $\psi_i(0)=0$ ($\psi_i(0)=\rho x_i^*$) for some i, then $f_i(t,\psi)\geq 0$ ($f_i(t,\psi)\leq 0$). By [326, Theorem 5.2.1 and Remark 5.2.1], it follows that $[0,\rho x^*]_{\mathcal{X}}$ is positively invariant for system (12.6). Since ρ can be chosen as large as we wish, this proves the positivity and boundedness of solutions in $\mathcal{X}_+$. ∎

Next we use the theory in Section 11.1 to introduce the basic reproduction ratio for our model system with periodic time delays. Linearizing system (12.8) at its parasite-free steady state $(0,0)$, we obtain the following linear periodic system:

$$\begin{aligned}\frac{dL}{dt}&=b_L(t)P(t-\tau_L(t))-d_L(t)L(t),\\ \frac{dP}{dt}&=b_P(t)L(t-\tau_P(t))-d_P(t)P(t).\end{aligned}\tag{12.9}$$

Let

$$F(t)\begin{pmatrix}\phi_1\\ \phi_2\end{pmatrix}=\begin{pmatrix}b_L(t)\phi_2(-\tau_L(t))\\ b_P(t)\phi_1(-\tau_P(t))\end{pmatrix}\text{ and }V(t)=\begin{pmatrix}d_L(t)&0\\ 0&d_P(t)\end{pmatrix}.$$

Then the linear system (12.9) can be written as

$$\frac{du(t)}{dt}=F(t)u_t-V(t)u(t),\quad\forall t\geq 0.$$

Note that $F(t)$ and $V(t)$ are ω-periodic in t and the newly "birth" parasites is described by $F(t)$ while the growth of the parasites except birth is described by the following evolution system

$$\frac{du(t)}{dt}=-V(t)u(t).$$

Let $Z(t,s)$, $t\geq s$, be the evolution matrix of the above linear system. That is, for each $s\in\mathbb{R}$, the 2×2 matrix $Z(t,s)$ satisfies

$$\frac{d}{dt}Z(t,s)=-V(t)Z(t,s),\quad\forall t\geq s,\quad Z(s,s)=I,$$

where I is the 2×2 identity matrix. Clearly, we have

$$Z(t,s)=\begin{pmatrix}e^{-\int_s^t d_L(\xi)d\xi}&0\\ 0&e^{-\int_s^t d_P(\xi)d\xi}\end{pmatrix}.$$

Recall that the exponential growth bound of $Z(t,s)$ is defined as

$$\hat{\omega}(Z) := \inf\left\{\widetilde{\omega} : \exists M \geq 1 \text{ such that } \|Z(t+s,s)\| \leq Me^{\widetilde{\omega}t},\ \forall s \in \mathbb{R},\ t \geq 0\right\}.$$

It is easy to see that $\hat{\omega}(Z) \leq -\min\{\overline{d}_L, \overline{d}_P\}$. Therefore, $F(t)$ and $V(t)$ satisfy the following assumptions:

(A1) $F(t) : \mathcal{X} \to \mathbb{R}^2$ is positive in the sense that $F(t)\mathcal{X}_+ \subseteq \mathbb{R}^2_+$;
(A2) The periodic matrix $-V(t)$ is cooperative, and $\hat{\omega}(Z) < 0$.

Let C_ω be the Banach space of all ω-periodic functions from $\mathbb{R}$ to $\mathbb{R}^2$, equipped with the maximum norm and the positive cone $C_\omega^+ := \{u \in C_\omega : u(t) \geq 0,\ \forall t \in \mathbb{R}\}$. Suppose $v \in C_\omega$ is the initial distribution of larval and adult parasites in this periodic environment, then $F(t-s)v_{t-s}$ is the distribution of newly born parasites at time $t-s$ with $t \geq s \geq 0$, and $Z(t,t-s)F(t-s)v_{t-s}$ represents the distribution of those parasites who were newly reproduced at time $t-s$ and still survive in the environment at time t for $t \geq s$. Hence,

$$\int_0^\infty Z(t,t-s)F(t-s)v_{t-s}ds = \int_0^\infty Z(t,t-s)F(t-s)v(t-s+\cdot)ds$$

gives the distribution of accumulative parasite burden at time t produced by those parasites introduced at all previous time.

We define the next generation operator $L : C_\omega \to C_\omega$ by

$$[Lv](t) = \int_0^\infty Z(t,t-s)F(t-s)v(t-s+\cdot)ds, \quad \forall t \in \mathbb{R}, \quad v \in C_\omega.$$

According to Section 11.1, the basic reproduction ratio is $R_0 := r(L)$, the spectral radius of L.

For any given $t \geq 0$, let $W(t)$ be the time-t map of the linear periodic system (12.9) on $\mathcal{X}$, that is, $W(t)\phi = w_t(\phi)$, where $w(t,\phi)$ is the unique solution of (12.9) with $w_0 = \phi \in \mathcal{X}$. By Theorem 11.1.1, we have the following result, which indicates that $R_0 - 1$ is a threshold value for the stability of the zero solution of system (12.9).

Lemma 12.2.2. $R_0 - 1$ *has the same sign as* $r(W(\omega)) - 1$.

To study the global dynamics of the model system in terms of R_0, our strategy is to use the theory of monotone and subhomogeneous semiflows in Section 2.3. We start with a new phase space on which system (12.6) generates an eventually strongly monotone periodic semiflow.

Let

$$\mathcal{Y} := C([-\tau_P(0), 0], \mathbb{R}) \times C([-\tau_L(0), 0], \mathbb{R}),$$

and

$$\mathcal{Y}_+ := C([-\tau_P(0), 0], \mathbb{R}_+) \times C([-\tau_L(0), 0], \mathbb{R}_+).$$

Then $(\mathcal{Y}, \mathcal{Y}_+)$ is an ordered Banach space. For a continuous function $u : [-\tau_P(0), +\infty) \times [-\tau_L(0), +\infty) \to \mathbb{R}^2$ and $t \geq 0$, we define $u_t \in \mathcal{Y}$ by

$$(u_t)_1(\theta) = u_1(t+\theta),\ \forall \theta \in [-\tau_P(0), 0], \quad (u_t)_2(\eta) = u_2(t+\eta),\ \forall \eta \in [-\tau_L(0), 0].$$

Lemma 12.2.3. *For any $\phi \in \mathcal{Y}_+$, system* (12.8) *admits a unique nonnegative solution $u(t, \phi)$ on $[0, \infty)$ with $u_0 = \phi$.*

Proof. Let $\bar{\tau} = \min\{\overline{\tau}_L, \overline{\tau}_P\}$. For any $t \in [0, \bar{\tau}]$, since $t - \tau_L(t)$ is strictly increasing, we have

$$-\tau_L(0) = 0 - \tau_L(0) \leq t - \tau_L(t) \leq \bar{\tau} - \tau_L(\bar{\tau}) \leq \bar{\tau} - \bar{\tau} = 0,$$

and hence

$$P(t - \tau_L(t)) = \phi_2(t - \tau_L(t)).$$

Similarly,

$$L(t - \tau_P(t)) = \phi_1(t - \tau_P(t)).$$

Therefore, we have the following equations for $t \in [0, \bar{\tau}]$:

$$\begin{aligned}
\frac{dL}{dt} &= b_L(t)\phi_2(t - \tau_L(t)) - d_L(t)L(t), \\
\frac{dP}{dt} &= b_P(t)\phi_1(t - \tau_P(t)) - d_P(t)P(t) - \alpha(t)P^2(t).
\end{aligned}$$

Given $\phi \in \mathcal{Y}_+$, the solution $(L(t), P(t))$ of the above system exists for $t \in [0, \bar{\tau}]$. In other words, we obtain the values of $u_1(\theta) = L(\theta)$ for $\theta \in [-\tau_P(0), \bar{\tau}]$ and $u_2(\eta) = P(\eta)$ for $\eta \in [-\tau_L(0), \bar{\tau}]$.

For any $t \in [\bar{\tau}, 2\bar{\tau}]$, we have

$$-\tau_L(0) = 0 - \tau_L(0) \leq \bar{\tau} - \tau_L(\bar{\tau}) \leq t - \tau_L(t) \leq 2\bar{\tau} - \tau_L(2\bar{\tau}) \leq 2\bar{\tau} - \bar{\tau} = \bar{\tau},$$

and hence, $P(t - \tau_L(t)) = u_2(t - \tau_L(t))$ is known. Similarly, $L(t - \tau_P(t)) = u_1(t - \tau_P(t))$ is also given from the previous step. Solving the following ordinary differential system for $t \in [\bar{\tau}, 2\bar{\tau}]$ with $L(\bar{\tau}) = u_1(\bar{\tau})$ and $P(\bar{\tau}) = u_2(\bar{\tau})$:

$$\begin{aligned}
\frac{dL}{dt} &= b_L(t)u_2(t - \tau_L(t)) - d_L(t)L(t), \\
\frac{dP}{dt} &= b_P(t)u_1(t - \tau_P(t)) - d_P(t)P(t) - \alpha(t)P^2(t),
\end{aligned}$$

we then get the solution $(L(t), P(t))$ on the interval $[\bar{\tau}, 2\bar{\tau}]$.

We can extend this procedure to $[n\bar{\tau}, (n+1)\bar{\tau}]$ for all $n \in \mathbb{N}$. It then follows that for any initial data $\phi \in \mathcal{Y}_+$, the solution $(L(t), P(t))$ exists uniquely for all $t \geq 0$. ∎

Remark 12.2.1. By the uniqueness of solutions in Lemmas 12.2.1 and 12.2.3, it follows that for any $\psi \in \mathcal{X}_+$ and $\phi \in \mathcal{Y}_+$ with $\psi_1(\theta) = \phi_1(\theta), \forall \theta \in [-\tau_P(0), 0]$ and $\psi_2(\eta) = \phi_2(\eta),\ \forall \eta \in [-\tau_L(0), 0]$, then $u(t, \phi) = v(t, \psi)$, $\forall t \geq 0$, where $u(t, \phi)$ and $v(t, \psi)$ are solutions of system (12.8) satisfying $u_0 = \phi$ and $v_0 = \psi$, respectively.

Lemma 12.2.4. *Let $Q_t(\phi) = u_t(\phi)$, $t \geq 0$. Then Q_t is an ω-periodic semiflow on $\mathcal{Y}_+$ in the sense that (i) $Q_0 = I$; (ii) $Q_{t+\omega} = Q_t \circ Q_\omega, \forall t \geq 0$; and (iii) $Q_t(\phi)$ is continuous in $(t, \phi) \in [0, \infty) \times \mathcal{Y}_+$.*

Proof. Clearly, property (i) holds true, and property (iii) follows from a standard argument. It suffices to prove (ii). Denote $v(t) = u(t + \omega, \phi)$, we need to show that $v(t) = u(t, u_\omega(\phi)), \forall t \geq 0$. To do this, we first check

$$\begin{aligned}\frac{dv_1(t)}{dt} &= \frac{du_1(t+\omega,\phi)}{dt} \\ &= b_L(t+\omega)u_2(t+\omega-\tau_L(t+\omega),\phi) - d_L(t+\omega)u_1(t+\omega,\phi) \\ &= b_L(t)u_2(t+\omega-\tau_L(t+\omega),\phi) - d_L(t)u_1(t+\omega,\phi) \\ &= b_L(t)v_2(t-\tau_L(t)) - d_L(t)v_1(t).\end{aligned}$$

Similarly, we have

$$\frac{dv_2(t)}{dt} = b_P(t)v_1(t-\tau_P(t)) - d_P(t)v_2(t) - \alpha(t)(v_2(t))^2.$$

This shows that $v(t)$ is also a solution of system (12.8). Moreover, we have $v_1(\theta) = u_1(\theta + \omega, \phi)$ for $\theta \in [-\tau_P(0), 0]$ and $v_2(\eta) = u_2(\eta + \omega, \phi)$ for $\eta \in [-\tau_L(0), 0]$. On the other side, let $w(t) = u(t, u_\omega(\phi))$, then $w(t)$ is also a solution of system (12.8), and $w_1(\theta) = u_1(\theta, u_\omega(\phi)) = u_\omega(\phi)_1(\theta) = u_1(\theta+\omega, \phi)$ for $\theta \in [-\tau_P(0), 0]$ and $w_2(\eta) = u_2(\eta, u_\omega(\phi)) = u_\omega(\phi)_2(\eta) = u_2(\eta+\omega, \phi)$ for $\eta \in [-\tau_L(0), 0]$. Thus, $v(t)$ and $w(t)$ are solutions of system (12.8) with the same initial data. By the uniqueness of solutions, we see that $v(t) = w(t), \forall t \geq 0$, that is,

$$u(t+\omega,\phi) = u(t, u_\omega(\phi)), \quad \forall t \geq 0.$$

For any $t \geq 0$ and $\theta \in [-\tau_P(0), 0]$, if $t + \theta \geq 0$, we have $u_1(t + \theta + \omega, \phi) = u_1(t+\theta, u_\omega(\phi))$, that is, $u_{t+\omega}(\phi)_1(\theta) = u_t \circ u_\omega(\phi)_1(\theta)$; if $t+\theta < 0$, then $u_1(t+\theta, u_\omega(\phi)) = u_\omega(\phi)_1(t+\theta) = u_1(t+\theta+\omega, \phi)$, which also implies $u_t \circ u_\omega(\phi)_1(\theta) = u_{t+\omega}(\phi)_1(\theta)$. Similarly, we can show that $u_t \circ u_\omega(\phi)_2(\eta) = u_{t+\omega}(\phi)_2(\eta)$ for all $\eta \in [-\tau_L(0), 0]$ and $t \geq 0$. It then follows that $u_t \circ u_\omega(\phi) = u_{t+\omega}(\phi)$, and hence, $Q_{t+\omega}(\phi) = Q_t \circ Q_\omega(\phi)$ for all $\phi \in \mathcal{Y}_+$ and $t \geq 0$. ∎

The following two lemmas indicate that the periodic semiflow Q_t is eventually strongly monotone and strictly subhomogeneous.

Lemma 12.2.5. *For any ϕ and ψ in $\mathcal{Y}_+$ with $\phi > \psi$ (that is, $\phi \geq \psi$ but $\phi \neq \psi$), the solutions $u(t)$ and $v(t)$ of system (12.8) with $u_0 = \phi$ and $v_0 = \psi$, respectively, satisfy $u_i(t) > v_i(t)$ for all $t > 2\hat{\tau}$, $i = 1, 2$, and hence, $Q_t(\phi) \gg Q_t(\psi)$ in $\mathcal{Y}$ for all $t > 3\hat{\tau}$.*

Proof. As in the proof of Lemma 12.2.3, a simple comparison argument on each interval $[n\bar{\tau}, (n+1)\bar{\tau}]$, $n \in \mathbb{N}$, implies that $u_i(t) \geq v_i(t)$ for all $t \geq 0$. By Lemma 12.2.1 and Remark 12.2.1, both $u(t)$ and $v(t)$ are bounded on $[0, \infty)$, and hence, there exists a real number $b > 0$ such that u_t and v_t are in the order interval $[(0,0),(b,b)]_{\mathcal{Y}}$ for all $t \geq 0$. Thus, we can choose a large number $M > 0$ such that for each $t \in \mathbb{R}$, $g_1(t,L) := -d_L(t)L + ML$ is increasing in $L \in [0,b]$ and $g_2(t,P) := -d_P(t)P - \alpha(t)P^2 + MP$ is increasing in $P \in [0,b]$. It then follows that both $u(t)$ and $v(t)$ satisfy the following system of integral equations:

$$\begin{aligned} L(t) &= e^{-Mt}L(0) + \int_0^t e^{-M(t-s)}g_1(s,L(s))ds + \int_0^t e^{-M(t-s)}b_L(s)P(s-\tau_L(s))ds, \\ P(t) &= e^{-Mt}P(0) + \int_0^t e^{-M(t-s)}g_2(s,P(s))ds + \int_0^t e^{-M(t-s)}b_P(s)L(s-\tau_P(s))ds, \end{aligned} \tag{12.10}$$

for all $t \geq 0$. Since both $m_L(t) := t-\tau_L(t)$ and $m_P(t) := t-\tau_P(t)$ are increasing in $t \in \mathbb{R}$, it easily follows that $[-\tau_L(0),0] \subseteq m_L([0,\hat{\tau}])$ and $[-\tau_P(0),0] \subseteq m_P([0,\hat{\tau}])$. Without loss of generality, we assume that $\phi_2 > \psi_2$. Then there exists an $\eta \in [-\tau_L(0),0]$ such that $u_2(\eta) > v_2(\eta)$. In view of the first equation of (12.10), we have $u_1(t) > v_1(t)$ for all $t > \hat{\tau}$. Note that if $s > 2\hat{\tau}$, then $s - \tau_P(s) > 2\hat{\tau} - \hat{\tau} = \hat{\tau}$. By the second equation of (12.10), it follows that $u_2(t) > v_2(t)$ for all $t > 2\hat{\tau}$. This shows that $u_i(t) > v_i(t)$ for all $t > 2\hat{\tau}$, $i = 1,2$, and hence, the solution map Q_t is strongly monotone whenever $t > 3\hat{\tau}$. ∎

Lemma 12.2.6. *For any $\phi \gg 0$ in $\mathcal{Y}$ and any $\gamma \in (0,1)$, we have $u_i(t,\gamma\phi) > \gamma u_i(t,\phi)$ for all $t > \hat{\tau}$, $i = 1,2$, and hence, $Q_\omega^n(\gamma\phi) \gg \gamma Q_\omega^n(\phi)$ in $\mathcal{Y}$ for all integers n with $n\omega > 2\hat{\tau}$.*

Proof. Let $w(t) = u(t,\gamma\phi)$ and $v(t) = \gamma u(t,\phi)$, where $u(t,\phi)$ is the unique solution of system (12.8) with $u_0 = \phi \gg 0$ in $\mathcal{Y}$. As in the proof of Lemma 12.2.3, we see that $w(t) > 0$ and $v(t) > 0$ for all $t \geq 0$. Moreover, for all $\theta \in [-\tau_P(0),0]$ and $\eta \in [-\tau_L(0),0]$, we have

$$w_1(\theta) = \gamma\phi_1(\theta) = v_1(\theta) \text{ and } w_2(\eta) = \gamma\phi_2(\eta) = v_2(\eta).$$

It is easy to see that $v(t)$ satisfies the following system:

$$\begin{aligned} \frac{dv_1(t)}{dt} &= b_L(t)v_2(t-\tau_L(t)) - d_L(t)v_1(t), \\ \frac{dv_2(t)}{dt} &= b_P(t)v_1(t-\tau_P(t)) - d_P(t)v_2(t) - \frac{\alpha(t)}{\gamma}v_2^2(t), \end{aligned}$$

and hence,

$$v_1(t) = \left[v_1(0) + \int_0^t b_L(\xi)v_2(\xi-\tau_L(\xi))\exp(\int_0^\xi d_L(\eta)d\eta)d\xi\right]\exp\left(-\int_0^t d_L(\eta)d\eta\right)$$

for all $t \geq 0$. For any $0 \leq t \leq \bar{\tau}$, we have

$$-\tau_L(0) \leq t - \tau_L(t) \leq \bar{\tau} - \tau_L(\bar{\tau}) \leq 0$$

and

$$\begin{aligned}
w_1(t) &= \left[w_1(0) + \int_0^t b_L(\xi) w_2(\xi - \tau_L(\xi)) \exp(\int_0^\xi d_L(\eta) d\eta) d\xi\right] \exp\left(-\int_0^t d_L(\eta) d\eta\right) \\
&= \left[v_1(0) + \int_0^t b_L(\xi) v_2(\xi - \tau_L(\xi)) \exp(\int_0^\xi d_L(\eta) d\eta) d\xi\right] \exp\left(-\int_0^t d_L(\eta) d\eta\right) \\
&= v_1(t).
\end{aligned}$$

On the other side, the derivative of $v_2(t)$ at $t = 0$:

$$\begin{aligned}
\left.\frac{dv_2(t)}{dt}\right|_{t=0} &= b_P(0) v_1(0 - \tau_P(0)) - d_P(0) v_2(0) - \frac{\alpha(0)}{\gamma} v_2^2(0) \\
&< b_P(0) v_1(0 - \tau_P(0)) - d_P(0) v_2(0) - \alpha(0) v_2^2(0) \\
&= b_P(0) w_1(-\tau_P(0)) - d_P(0) w_2(0) - \alpha(0) w_2^2(0) \\
&= \left.\frac{dw_2(t)}{dt}\right|_{t=0}.
\end{aligned}$$

Since $v_2(0) = w_2(0) > 0$, it follows that there exists an $\epsilon \in (0, \bar{\tau})$ such that $0 < v_2(t) < w_2(t)$ for all $0 < t < \epsilon$. We claim that $v_2(t) < w_2(t)$ for all $0 < t \leq \bar{\tau}$. Assume not, then there exists $t_0 \in (0, \bar{\tau}]$ such that $v_2(t) < w_2(t)$ for all $0 < t < t_0$ while $v_2(t_0) = w_2(t_0)$, which implies $v_2'(t_0) \geq w_2'(t_0)$. However, we have

$$\begin{aligned}
\left.\frac{dv_2(t)}{dt}\right|_{t=t_0} &= b_P(t_0) v_1(t_0 - \tau_P(t_0)) - d_P(t_0) v_2(t_0) - \frac{\alpha(t_0)}{\gamma} v_2^2(t_0) \\
&< b_P(t_0) v_1(t_0 - \tau_P(t_0)) - d_P(t_0) v_2(t_0) - \alpha(t_0) v_2^2(t_0) \\
&= b_P(t_0) w_1(t_0 - \tau_P(t_0)) - d_P(t_0) w_2(t_0) - \alpha(t_0) w_2^2(t_0) \\
&= \left.\frac{dw_2(t)}{dt}\right|_{t=t_0},
\end{aligned}$$

a contradiction. This shows that $v_2(t) < w_2(t)$ for all $0 < t \leq \bar{\tau}$.

Similar arguments for any interval $(n\bar{\tau}, (n+1)\bar{\tau}]$ imply that $v_1(t) \leq w_1(t)$ and $v_2(t) < w_2(t)$ for all $t \in (n\bar{\tau}, (n+1)\bar{\tau}]$ with $n \in \mathbb{N}$. In particular, $\xi - \tau_L(\xi) > \hat{\tau} - \hat{\tau} = 0$ and $w_2(\xi - \tau_L(\xi)) > v_2(\xi - \tau_L(\xi))$ for all $\xi > \hat{\tau}$. Therefore, for any $t > \hat{\tau}$, we have

$$\begin{aligned}
w_1(t) &= \left[w_1(0) + \int_0^t b_L(\xi) w_2(\xi - \tau_L(\xi)) \exp(\int_0^\xi d_L(\eta) d\eta) d\xi\right] \exp\left(-\int_0^t d_L(\eta) d\eta\right) \\
&> \left[v_1(0) + \int_0^t b_L(\xi) v_2(\xi - \tau_L(\xi)) \exp(\int_0^\xi d_L(\eta) d\eta) d\xi\right] \exp\left(-\int_0^t d_L(\eta) d\eta\right) \\
&= v_1(t).
\end{aligned}$$

It follows that $v_1(t) < w_1(t)$ and $v_2(t) < w_2(t)$ for all $t > \hat{\tau}$, that is, $u_i(t, \gamma\phi) > \gamma u_i(t, \phi)$ for all $t > \hat{\tau}$, $i = 1, 2$. Thus, $Q_\omega^n(\gamma\phi) = Q_{n\omega}(\gamma\phi) \gg \gamma Q_{n\omega}(\phi) = \gamma Q_\omega^n(\phi)$ for all integer n with $n\omega > 2\hat{\tau}$. ∎

For any given $t \geq 0$, let $G(t)$ be the time-t map of the linear periodic system (12.9) on $\mathcal{Y}$, that is, $G(t)\phi = z_t(\phi)$, where $z(t,\phi)$ is the unique solution of (12.9) with $z_0 = \phi \in \mathcal{Y}$. The subsequent result shows that the stability of the zero solution for system (12.9) on $\mathcal{X}$ is equivalent to that on $\mathcal{Y}$.

Lemma 12.2.7. *Two Poincaré maps $W(\omega) : \mathcal{X} \to \mathcal{X}$ and $G(\omega) : \mathcal{Y} \to \mathcal{Y}$ have the same spectral radius, that is, $r(W(\omega)) = r(G(\omega))$.*

Proof. We fix an integer n_0 such that $n_0\omega > 3\hat{\tau}$. By the proof of Lemma 12.2.5, we see that $G(\omega)^{n_0} = G(n_0\omega)$ is strongly positive on $\mathcal{Y}$. Further, [145, Theorem 3.6.1] implies that $G(\omega)^{n_0}$ is compact. Then $r(G(\omega)) > 0$ according to the Krein-Rutmann theorem, as applied to the linear operator $(G(\omega))^{n_0}$, together with the fact that $r(G(\omega)^{n_0}) = (r(G(\omega)))^{n_0}$. For any given $\phi = (\phi_1, \phi_2) \in \mathcal{Y}$, we define $\tilde{\phi} = (\tilde{\phi}_1, \tilde{\phi}_2) \in \mathcal{X}$ by

$$\tilde{\phi}_1(\theta) = \begin{cases} \phi_1(-\tau_P(0)) & \text{if } \theta \in [-\hat{\tau}, -\tau_P(0)], \\ \phi_1(\theta) & \text{if } \theta \in [-\tau_P(0), 0]; \end{cases}$$

and

$$\tilde{\phi}_2(\theta) = \begin{cases} \phi_2(-\tau_L(0)) & \text{if } \theta \in [-\hat{\tau}, -\tau_L(0)], \\ \phi_2(\theta) & \text{if } \theta \in [-\tau_L(0), 0]. \end{cases}$$

Clearly, $\|\phi\|_{\mathcal{Y}} = \|\tilde{\phi}\|_{\mathcal{X}}$. By Remark 12.2.1, it follows that for all integer n with $n\omega > \hat{\tau}$,

$$\|G(n\omega)\phi\|_{\mathcal{Y}} \leq \|W(n\omega)\tilde{\phi}\|_{\mathcal{X}} \leq \|W(n\omega)\|_{\mathcal{X}} \cdot \|\tilde{\phi}\|_{\mathcal{X}} = \|W(n\omega)\|_{\mathcal{X}} \cdot \|\phi\|_{\mathcal{Y}}, \ \forall \phi \in \mathcal{Y},$$

and hence, $\|G(n\omega)\|_{\mathcal{Y}} \leq \|W(n\omega)\|_{\mathcal{X}}$. Since

$$r(G(\omega)) = \lim_{n\to\infty} \|G(\omega)^n\|_{\mathcal{Y}}^{\frac{1}{n}} = \lim_{n\to\infty} \|G(n\omega)\|_{\mathcal{Y}}^{\frac{1}{n}}$$

and

$$r(W(\omega)) = \lim_{n\to\infty} \|W(\omega)^n\|_{\mathcal{X}}^{\frac{1}{n}} = \lim_{n\to\infty} \|W(n\omega)\|_{\mathcal{X}}^{\frac{1}{n}},$$

we then have $r(W(\omega)) \geq r(G(\omega)) > 0$.

It remains to prove that $r(W(\omega)) \leq r(G(\omega))$. In view of [326, Theorem 5.1.1] and [145, Theorem 3.6.1], we see that the linear operator $W(\omega)^{n_0} = W(n_0\omega)$ is positive and compact on $\mathcal{X}$. By the Krein-Rutmann theorem (see, e.g., [152, Theorem 7.1]), $r(W(\omega)^{n_0})$ is an eigenvalue of $W(\omega)^{n_0}$ with an eigenvector $\phi^* > 0$ in $\mathcal{X}$. For any $\phi \in \mathcal{X}$, we define $\underline{\phi} \in \mathcal{Y}$ as

$$\underline{\phi}_1(\theta) = \phi_1(\theta), \ \forall \theta \in [-\tau_P(0), 0], \text{ and } \underline{\phi}_2(\eta) = \phi_2(\eta), \ \forall \eta \in [-\tau_L(0), 0].$$

By Remark 12.2.1, we have $u(t,\phi) = v(t,\underline{\phi})$, $\forall t \geq 0$, where $u(t,\phi)$ and $v(t,\underline{\phi})$ are the unique solutions of system (12.9) with $u_0 = \phi \in \mathcal{X}$ and $v_0 = \underline{\phi} \in \mathcal{Y}$, respectively. We further claim that $\underline{\phi^*} > 0$ in $\mathcal{Y}$. Otherwise, $\underline{\phi^*} = 0$, and hence, $u(t, \phi^*) = v(t, \underline{\phi^*}) = 0$, $\forall t \geq 0$. This implies that

$$(r(W(\omega)))^{n_0}\phi^* = r(W(\omega)^{n_0})\phi^* = W(\omega)^{n_0}\phi^* = W(n_0\omega)\phi^* = 0,$$

and hence, $\phi^* = 0$ in $\mathcal{X}$, which is a contradiction. Since

$$G(\omega)^{n_0}\underline{\phi^*} = \underline{W(\omega)^{n_0}\phi^*} = \underline{r(W(\omega))^{n_0})\phi^*} = (r(W(\omega)))^{n_0}\underline{\phi^*},$$

$(r(W(\omega)))^{n_0}$ is a positive eigenvalue of $G(\omega)^{n_0}$ with $\underline{\phi^*}$ being a positive eigenvector in $\mathcal{Y}$. It then follows that $(r(W(\omega)))^{n_0} \leq r(\overline{G}(\omega)^{n_0}) = (r(G(\omega)))^{n_0}$, and hence $r(W(\omega)) \leq r(G(\omega))$. Consequently, we have $r(W(\omega)) = r(G(\omega))$. ∎

Now we are in a position to prove the main result of this section.

Theorem 12.2.1. *The following statements are valid:*

(1) If $R_0 \leq 1$, then $(0, 0)$ is globally asymptotically stable for system (12.8) in $\mathcal{Y}_+$.
(2) If $R_0 > 1$, then system (12.8) admits a unique positive ω-periodic solution $(L^*(t), P^*(t))$, and it is globally asymptotically stable for system (12.8) in $\mathcal{Y}_+ \setminus \{(0, 0)\}$.

Proof. We fix an integer n_0 such that $n_0\omega > 3\hat{\tau}$. In view of Lemma 12.2.4, Q_t can be regarded as an $n_0\omega$-periodic semiflow on $\mathcal{Y}_+$. By Lemmas 12.2.5 and 12.2.6, $Q_{n_0\omega}$ is a strongly monotone and strictly subhomogeneous map on $\mathcal{Y}_+$. Applying Theorem 2.3.4 and Lemma 2.2.1 to the map $Q_{n_0\omega}$, we have the following threshold-type result:

(a) If $r(DQ_{n_0\omega}(0)) \leq 1$, then $(0, 0)$ is globally asymptotically stable for system (12.8) in $\mathcal{Y}_+$.
(b) If $r(DQ_{n_0\omega}(0)) > 1$, then system (12.8) admits a unique positive $n_0\omega$-periodic solution $(L^*(t), P^*(t))$, and it is globally asymptotically stable for system (12.8) in $\mathcal{Y}_+ \setminus \{(0, 0)\}$.

Note that $r(DQ_{n_0\omega}(0)) = r(G(n_0\omega)) = (r(G(\omega)))^{n_0}$. By Lemmas 12.2.2 and 12.2.7, we then see that

$$sign(R_0 - 1) = sign(r(DQ_{n_0\omega}(0)) - 1).$$

Thus, it suffices to show that in case (b), $(L^*(t), P^*(t))$ is also ω-periodic. Let $\psi^* = v_0^* \in \mathcal{Y}$ with $v^*(t) = (L^*(t), P^*(t))$. Then $Q_{n_0\omega}\psi^* = \psi^*$. Note that

$$Q_\omega^{n_0}(Q_\omega\psi^*) = Q_\omega(Q_\omega^{n_0}\psi^*) = Q_\omega(Q_{n_0\omega}\psi^*) = Q_\omega(\psi^*).$$

By the uniqueness of the positive fixed point of $Q_\omega^{n_0} = Q_{n_0\omega}$, it follows that $Q_\omega\psi^* = \psi^*$, which implies that $(L^*(t), P^*(t)) = u(t, \psi^*)$ is an ω-periodic solution of system (12.8). ∎

In the rest of this section, we deduce the dynamics for the other two variables $X(t)$ and $Y(t)$ in system (12.5), which do not appear in system (12.6). In the case where $R_0 > 1$, we have

$$\lim_{t\to\infty}[(L(t), P(t)) - (L^*(t), P^*(t))] = 0$$

for any solution of system (12.6) through nonzero initial data. By using the integral form for the free living uninfected larvae $X(t)$ and arrested larvae $Y(t)$ in (12.7), we obtain

$$\lim_{t\to\infty}\left[X(t) - \int_{t-\tau_L(t)}^{t} \lambda P^*(\xi) e^{-\int_\xi^t \mu_X(s)\,ds} d\xi\right] = 0, \text{ and}$$
$$\lim_{t\to\infty}\left[Y(t) - \int_{t-\tau_P(t)}^{t} \beta(\xi)H(\xi)L^*(\xi) e^{-\int_\xi^t (\mu_Y(s)+\mu_H(s))\,ds} d\xi\right] = 0.$$

Moreover, it is easy to verify that both

$$X^*(t) := \int_{t-\tau_L(t)}^{t} \lambda P^*(\xi) e^{-\int_\xi^t \mu_X(s)\,ds} d\xi$$

and

$$Y^*(t) := \int_{t-\tau_P(t)}^{t} \beta(\xi)H(\xi)L^*(\xi) e^{-\int_\xi^t (\mu_Y(s)+\mu_H(s))\,ds} d\xi$$

are positive ω-periodic functions. In the case where $R_0 \leq 1$, we have

$$\lim_{t\to\infty}(L(t), P(t)) = (0, 0).$$

By using the integral form in (12.7) again, we obtain

$$\lim_{t\to\infty}(X(t), Y(t)) = (0, 0).$$

In summary, we have the following result on the global dynamics of the full model system.

Theorem 12.2.2. *The following statements hold for system* (12.5)*:*

(1) If $R_0 \leq 1$, then $(0, 0, 0, 0)$ is globally attractive.
(2) If $R_0 > 1$, then there exists a positive ω-periodic solution

$$(X^*(t), L^*(t), Y^*(t), P^*(t)),$$

and it is globally attractive for all nontrivial solutions.

12.3 Numerical Computation of R_0

To numerically compute the basic reproduction ratio, we are going to rewrite the linear operator L into the form of equation (3) in [282], where an algorithm is proposed for the R_0 computation of periodic ordinary differential systems.

Note that

$$F(t-s)\begin{pmatrix}\phi_1\\ \phi_2\end{pmatrix} = \begin{pmatrix} b_L(t-s)\phi_2(-\tau_L(t-s))\\ b_P(t-s)\phi_1(-\tau_P(t-s))\end{pmatrix}.$$

It then follows that

$$\begin{aligned}
[Lv](t) &= \int_0^\infty Z(t,t-s)F(t-s)v(t-s+\cdot)ds\\
&= \int_0^\infty \begin{pmatrix} e^{-\int_{t-s}^t d_L(\xi)d\xi} & 0\\ 0 & e^{-\int_{t-s}^t d_P(\xi)d\xi}\end{pmatrix}\begin{pmatrix} b_L(t-s)v_2(t-s-\tau_L(t-s))\\ b_P(t-s)v_1(t-s-\tau_P(t-s))\end{pmatrix}ds\\
&= \begin{pmatrix} \int_0^\infty e^{-\int_{t-s}^t d_L(\xi)d\xi} b_L(t-s)v_2(t-s-\tau_L(t-s))ds\\ \int_0^\infty e^{-\int_{t-s}^t d_P(\xi)d\xi} b_P(t-s)v_1(t-s-\tau_P(t-s))ds\end{pmatrix}.
\end{aligned}$$

Let $t-s-\tau_L(t-s) = t-s_1$. Since the function $y = x-\tau_L(x)$ is strictly increasing, the inverse function exists and we can solve $x = h_L(y)$. Hence, we obtain $t-s = h_L(t-s_1)$, that is,

$$s = t-h_L(t-s_1), \quad ds_1 = d(s+\tau_L(t-s)) = (1-\tau_L'(t-s))ds,$$

and $ds = \frac{1}{1-\tau_L'(h_L(t-s_1))}ds_1$. Therefore,

$$\begin{aligned}
&\int_0^\infty e^{-\int_{t-s}^t d_L(\xi)d\xi} b_L(t-s)v_2(t-s-\tau_L(t-s))ds\\
&= \int_{\tau_L(t)}^\infty \frac{e^{-\int_{h_L(t-s_1)}^t d_L(\xi)d\xi} b_L(h_L(t-s_1))}{1-\tau_L'(h_L(t-s_1))} v_2(t-s_1)ds_1\\
&= \int_{\tau_L(t)}^\infty \frac{e^{-\int_{h_L(t-s)}^t d_L(\xi)d\xi} b_L(h_L(t-s))}{1-\tau_L'(h_L(t-s))} v_2(t-s)ds.
\end{aligned}$$

Similarly, let $t-s-\tau_P(t-s) = t-s_2$. Assume that the inverse function of $y = x-\tau_P(x)$ is $y = h_P(x)$. Solving $t-s = h_P(t-s_2)$, we get

$$s = t-h_P(t-s_2), ds_2 = (1-\tau_P'(t-s))ds, \text{ and } ds = \frac{1}{1-\tau_P'(h_P(t-s_2))}ds_2.$$

Therefore,

$$\begin{aligned}
&\int_0^\infty e^{-\int_{t-s}^t d_P(\xi)d\xi} b_P(t-s)v_1(t-s-\tau_P(t-s))ds\\
&= \int_{\tau_P(t)}^\infty \frac{e^{-\int_{h_P(t-s_2)}^t d_P(\xi)d\xi} b_P(h_P(t-s_2))}{1-\tau_P'(h_P(t-s_2))} v_1(t-s_2)ds_2\\
&= \int_{\tau_P(t)}^\infty \frac{e^{-\int_{h_P(t-s)}^t d_P(\xi)d\xi} b_P(h_P(t-s))}{1-\tau_P'(h_P(t-s))} v_1(t-s)ds.
\end{aligned}$$

Define

$$K_{12}(t,s) = \begin{cases} 0, & s < \tau_L(t) \\ \frac{e^{-\int_{h_L(t-s)}^t d_L(\xi)d\xi} b_L(h_L(t-s))}{1-\tau_L'(h_L(t-s))}, & s \geq \tau_L(t) \end{cases}$$

and

$$K_{21}(t,s) = \begin{cases} 0, & s < \tau_P(t) \\ \frac{e^{-\int_{h_P(t-s)}^t d_P(\xi)d\xi} b_P(h_P(t-s))}{1-\tau_P'(h_P(t-s))}, & s \geq \tau_P(t) \end{cases}$$

while $K_{11}(t,s) = K_{22}(t,s) = 0$. Then we have

$$\begin{aligned}[Lv](t) &= \int_0^\infty K(t,s)v(t-s)ds \\ &= \sum_{j=0}^\infty \int_{j\omega}^{(j+1)\omega} K(t,s)v(t-s)ds \\ &= \sum_{j=0}^\infty \int_0^\omega K(t,j\omega+s)v(t-s-j\omega)ds \\ &= \int_0^\omega G(t,s)v(t-s)ds\end{aligned}$$

with

$$G(t,s) = \sum_{j=0}^\infty K(t,j\omega+s),$$

which is of the integral form

$$[L\phi](t) = \int_0^\omega G(t,s)\phi(t-s)ds. \tag{12.11}$$

Below we present a numerical algorithm, which is due to Posny and Wang [282], for the computation of the spectral radius of the integral operator given by (12.11).

Let us partition the interval $[0,\omega]$ uniformly into n nodes labeled as $t_i = i \cdot \frac{\omega}{n}$ for $i = 0, \ldots, n-1$. Using the trapezoidal rule, one of the most common numerical integration techniques, we can approximate the integral in (12.11) with second-order accuracy:

$$[L\phi](t) \approx \frac{\omega}{n}\left(\sum_{i=1}^{n-1} G(t,t_i)\phi(t-t_i) + \frac{1}{2}G(t,t_0)\phi(t-t_0) + \frac{1}{2}G(t,t_n)\phi(t-t_n)\right).$$

Since $\phi(t)$ is ω-periodic, it is clear that $\phi(t-t_0) = \phi(t-t_n)$. For convenience, we let

$$\tilde{G}(t,t_0) = \frac{1}{2}[G(t,t_0) + G(t,t_n)].$$

Then

$$[L\phi](t) \approx \frac{\omega}{n}\left[\tilde{G}(t,t_0)\phi(t-t_0) + \sum_{i=1}^{n-1} G(t,t_i)\phi(t-t_i)\right].$$

Now $[L\phi](t) = \lambda\phi(t)$ can be written as a matrix equation:

$$\frac{\omega}{n}[\tilde{G}(t,t_0) \ \ G(t,t_1) \ \ G(t,t_2) \ \ \cdots \ \ G(t,t_{n-1})]\begin{bmatrix} \phi(t-t_0) \\ \phi(t-t_1) \\ \phi(t-t_2) \\ \vdots \\ \phi(t-t_{n-1}) \end{bmatrix} = \lambda\phi(t).$$

Setting $t = t_j (0 \le j \le n-1)$ in the above equation yields

$$\frac{\omega}{n}[\tilde{G}(t_j,t_0) \ \ G(t_j,t_1) \ \ G(t_j,t_2) \ \ \cdots \ \ G(t_j,t_{n-1})]\begin{bmatrix} \phi(t_j-t_0) \\ \phi(t_j-t_1) \\ \phi(t_j-t_2) \\ \vdots \\ \phi(t_j-t_{n-1}) \end{bmatrix} = \lambda\phi(t_j). \quad (12.12)$$

Again, by the periodicity of $\phi(t)$, it follows that

$$\begin{array}{lll} \phi(t_j-t_0)=\phi(t_j), & \phi(t_j-t_1)=\phi(t_{j-1}), & \ldots, \\ \phi(t_j-t_{j-1})=\phi(t_1), & \phi(t_j-t_j)=\phi(t_0), & \phi(t_j-t_{j+1})=\phi(t_{n-1}), \\ \ldots, & \phi(t_j-t_{n-2})=\phi(t_{j+2}), & \phi(t_j-t_{n-1})=\phi(t_{j+1}), \end{array}$$

and we can rearrange the terms in (12.12) to obtain

$$\frac{\omega}{n}\Big[G(t_j,t_j) \ \ \ldots \ \ \tilde{G}(t_j,t_0) \ \ G(t_j,t_{n-1}) \ \ \ldots \ \ G(t_j,t_{j+1})\Big]\begin{bmatrix} \phi(t_0) \\ \phi(t_1) \\ \vdots \\ \phi(t_j) \\ \vdots \\ \phi(t_{n-2}) \\ \phi(t_{n-1}) \end{bmatrix} = \lambda\phi(t_j). \quad (12.13)$$

Note that this equation holds for all $j = 0, \ldots, n-1$, and hence, it generates a matrix system. The coefficient matrix, denoted by A, is given by

$$A = \begin{bmatrix} \tilde{G}(t_0,t_0) & G(t_0,t_{n-1}) & \cdots & \cdots & \cdots & G(t_0,t_2) & G(t_0,t_1) \\ G(t_1,t_1) & \tilde{G}(t_1,t_0) & \cdots & \cdots & \cdots & G(t_1,t_3) & G(t_1,t_2) \\ \vdots & \vdots & \ddots & \ddots & \ddots & \vdots & \vdots \\ G(t_j,t_j) & G(t_j,t_{j-1}) & \cdot & \tilde{G}(t_j,t_0) & \cdot & G(t_j,t_{j+2}) & G(t_j,t_{j+1}) \\ \vdots & \vdots & \ddots & \ddots & \ddots & \vdots & \vdots \\ G(t_{n-2},t_{n-2}) & G(t_{n-2},t_{n-3}) & \ldots & \cdots & \cdots & \tilde{G}(t_{n-2},t_0) & G(t_{n-2},t_{n-1}) \\ G(t_{n-1},t_{n-1}) & G(t_{n-1},t_{n-2}) & \cdots & \cdots & \cdots & G(t_{n-1},t_1) & \tilde{G}(t_{n-1},t_0) \end{bmatrix}. \quad (12.14)$$

It then follows that (12.13) can be put into a compact form:

$$\frac{\omega}{n}A\tilde{\phi} = \lambda\tilde{\phi}, \quad (12.15)$$

where A, defined in (12.14), is a matrix of dimension $(nm) \times (nm)$, and $\tilde{\phi} = [\phi(t_0), \phi(t_1), \ldots, \phi(t_{n-1})]^T$ is a vector of dimension $(nm) \times 1$.

Consequently, to compute the basic reproduction ratio $R_0 := \rho(L)$, it suffices to find the maximum λ such that (12.15) is valid, that is, $R_0 \approx \frac{\omega}{n}\rho(A)$.

12.4 Notes

Sections 12.1, 12.2, and 12.3 are taken from Lou and Zhao [234] with the exception that the numerical algorithm in Section 12.3 comes from Posny and Wang [282].

The introduction of the term $1 - \tau'(t)$ is due to the incorporation of state-dependent delay in Barbarossa, Hadeler and Kuttler [26] and Kloosterman, Campbell and Poulin [202]. A similar term was formulated in models proposed by Wu et al. [414] and some others, see, e.g., McCauley et al. [246] and the references therein, to describe the population growth with threshold age τ depending on time t.

Model (12.6) was proposed earlier by Molnár et al. [250], where L in equations (8b) and (1b) should be $L(t - \tau_P)$. There are also some other algorithms to compute R_0 for periodic population models with constant time delay, see, e.g., Bacaër [21].

13

A Periodic Reaction–Diffusion SIS Model

It has been commonly accepted that spatial diffusion and environmental heterogeneity are important factors that should be considered in the spread of infectious diseases. In order to understand the impact of spatial heterogeneity of the environment and movement of individuals on the persistence and extinction of a disease, Allen et al. [9] proposed a frequency-dependent SIS (susceptible-infected-susceptible) reaction–diffusion model for a population in a continuous spatial habitat. They assumed that both rates of the transmission and recovery of the disease depend on spatial variables. Another feature of this SIS model is that the total population number is constant. The habitat is characterized as low-risk (or high-risk) if the spatial average of the transmission rate of the disease is less than (or greater than) the spatial average of its recovery rate. The individual site is also characterized as low-risk (or high-risk) if the local transmission rate of the disease is less than (or greater than) its local recovery rate, which corresponds to the case where the local reproduction number is less than (or greater than) one.

Assume that the habitat $\Omega \subset \mathbb{R}^m \, (m \geq 1)$ is a bounded domain with smooth boundary $\partial\Omega$ (when $m > 1$), and ν is the outward unit normal vector on $\partial\Omega$ and $\frac{\partial}{\partial\nu}$ means the normal derivative along ν on $\partial\Omega$. The global stability of the unique disease-free equilibrium and asymptotic profiles of the unique endemic equilibrium were established in [9] for the following SIS reaction-diffusion system:

$$\begin{array}{ll} \frac{\partial\overline{S}}{\partial t} - d_S\Delta\overline{S} = -\frac{\beta(x)\overline{S}\,\overline{I}}{\overline{S}+\overline{I}} + \gamma(x)\overline{I}, & x \in \Omega,\ t > 0, \\ \frac{\partial\overline{I}}{\partial t} - d_I\Delta\overline{I} = \frac{\beta(x)\overline{S}\,\overline{I}}{\overline{S}+\overline{I}} - \gamma(x)\overline{I}, & x \in \Omega,\ t > 0, \\ \frac{\partial\overline{S}}{\partial\nu} = \frac{\partial\overline{I}}{\partial\nu} = 0, & x \in \partial\Omega,\ t > 0, \end{array} \tag{13.1}$$

where $\overline{S}(x,t)$ and $\overline{I}(x,t)$, respectively, represent the density of susceptible and infected individuals at location x and time t; the positive constants d_S and d_I denote the diffusion rates of susceptible and infected populations; and $\beta(x)$

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and $\gamma(x)$ are positive Hölder continuous functions on Ω which account for the rates of disease transmission and disease recovery at x, respectively. The homogeneous Neumann boundary conditions mean that there is no population flux across the boundary $\partial\Omega$ and both the susceptible and infected individuals live in a self-contained environment.

In model (13.1), it was assumed that the rates of disease transmission and recovery depend only on the spatial variable. However, the rates of disease transmission and disease recovery may be spatially and temporally heterogeneous. Typically, they vary periodically in time, for instance, due to the seasonal fluctuation and periodic availability of vaccination strategies. A natural consideration of a spatially heterogeneous and temporally periodic environment leads us to the study of the following system:

$$\begin{array}{ll} \frac{\partial \overline{S}}{\partial t} - d_S \Delta \overline{S} = -\frac{\beta(x,t)\overline{S}\,\overline{I}}{\overline{S}+\overline{I}} + \gamma(x,t)\overline{I}, & x \in \Omega,\ t > 0, \\ \frac{\partial \overline{I}}{\partial t} - d_I \Delta \overline{I} = \frac{\beta(x,t)\overline{S}\,\overline{I}}{\overline{S}+\overline{I}} - \gamma(x,t)\overline{I}, & x \in \Omega,\ t > 0, \\ \frac{\partial \overline{S}}{\partial \nu} = \frac{\partial \overline{I}}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ \overline{S}(x,0) = S_0(x),\ \overline{I}(x,0) = I_0(x), & x \in \Omega. \end{array} \tag{13.2}$$

In the current situation, the functions $\beta(x,t)$ and $\gamma(x,t)$ represent the rates of disease transmission and recovery at location x and time t, respectively.

It is easy to see that the function $\overline{S}\,\overline{I}/(\overline{S}+\overline{I})$ is a Lipschitz continuous function of $\overline{S}$ and $\overline{I}$ in the first open quadrant. Thus, we can extend its definition to the entire first quadrant by defining it to be zero when either $\overline{S} = 0$ or $\overline{I} = 0$. Throughout this chapter, we make the following assumption:

(A) The functions $\beta(x,t)$ and $\gamma(x,t)$ are Hölder continuous and nonnegative but not zero identically on $\overline{\Omega} \times \mathbb{R}$, and ω-periodic in t for some number $\omega > 0$.

From the classical theory for parabolic equations (see, e.g., [228]), we know that for any $(S_0, I_0) \in C(\overline{\Omega}, \mathbb{R}^2_+)$, system (13.2) has a unique classical solution $(\overline{S}, \overline{I}) \in C^{2,1}(\overline{\Omega} \times (0,\infty))$. By the strong maximum principle and the Hopf boundary lemma for parabolic equations (see, e.g., [283]), it follows that if $I_0(x) \not\equiv 0$, then both $\overline{S}(x,t)$ and $\overline{I}(x,t)$ are positive for $x \in \overline{\Omega}$ and $t \in (0,\infty)$. Following [9], we define

$$N := \int_\Omega [S_0(x) + I_0(x)]\, dx > 0 \tag{13.3}$$

to be the total number of individuals in Ω at $t = 0$. We add two equations in (13.2) and then integrate over Ω by parts to obtain

$$\frac{\partial}{\partial t}\int_\Omega (\overline{S} + \overline{I})\, dx = \int_\Omega \Delta(d_S \overline{S} + d_I \overline{I})\, dx = 0, \quad \forall t > 0.$$

This implies that the total population size is a constant, i.e.,

$$\int_\Omega [\overline{S}(x,t) + \overline{I}(x,t)]\, dx = N, \quad \forall t \geq 0, \tag{13.4}$$

which also shows that both $\|\overline{S}(\cdot,t)\|_{L^1(\Omega)}$ and $\|\overline{I}(\cdot,t)\|_{L^1(\Omega)}$ are bounded on $[0,\infty)$. From now on, we let N be a given positive constant.

A nonnegative ω-periodic solution $(\tilde{S},\tilde{I})$ of system (13.2)–(13.3) is said to be disease-free if $\tilde{I}\equiv 0$ on $\overline{\Omega}\times\mathbb{R}$; and endemic if $\tilde{I}\geq 0,\not\equiv 0$ on $\overline{\Omega}\times\mathbb{R}$. It is easy to observe from (13.2)–(13.3) that the unique disease-free ω-periodic solution is $(\tilde{S},0)=(N/|\Omega|,0)$ (see [9, Lemma 2.1]), and henceforth we call this solution the disease-free constant solution. Hereafter, $|\Omega|$ always represents the volume of the domain Ω. Moreover, the maximum principle and the Hopf boundary lemma for parabolic equations imply that an endemic ω-periodic solution $(\tilde{S},\tilde{I})$ is positive on $\overline{\Omega}\times[0,\infty)$, that is, $\tilde{S}(x,t)>0$, $\tilde{I}(x,t)>0$, $\forall(x,t)\in\overline{\Omega}\times[0,\infty)$.

The purpose of this chapter is to investigate the effect of spatial and temporal heterogeneities on the extinction and persistence of the infectious disease for system (13.2)–(13.3). In Section 13.1, we first introduce the basic reproduction ratio R_0 and then provide its analytical characterizations. In particular, we obtain the asymptotic behavior of R_0 as d_I tends to zero or infinity. It turns out that when β and γ depend only on the temporal variable (namely, $\beta(x,t)=\beta(t)$ and $\gamma(x,t)=\gamma(t)$), R_0 is a constant independent of d_I, and when β and γ depend on the spatial variable alone (namely, $\beta(x,t)=\beta(x)$ and $\gamma(x,t)=\gamma(x)$), R_0 is a nonincreasing function of d_I. In sharp contrast, our result shows that in general, R_0 is not a monotone function of d_I. In the case where $\beta(x,t)$ is a constant, we also address an optimization problem concerning R_0 when the average of the function $\gamma(x,t)$ is given.

In Section 13.2, we derive a threshold-type dynamics for system (13.2)–(13.3) in terms of R_0. More specifically, we prove that the disease-free constant solution is globally stable if $R_0<1$; while if $R_0>1$, system (13.2)–(13.3) admits at least one endemic ω-periodic solution and the disease is uniformly persistent. In order to establish a uniform upper bound for positive solutions to system (13.2)–(13.3), we re-formulate the general theory developed in [214] in such a way that it applies to system (13.2)–(13.3) (see Lemma 13.2.1).

In Section 13.3, we establish the global attractivity of the positive ω-periodic solution (and hence its uniqueness) of system (13.2)–(13.3) for some special cases. However, it remains a challenging problem to study the uniqueness of the endemic ω-periodic solution for the general case. The biological interpretations of our analytical results are presented in Section 13.4.

13.1 Basic Reproduction Ratio

In this section, we introduce the basic reproduction ratio for the periodic reaction–diffusion system (13.2), and analyze its properties. As a first step, we need to define the next infection operator for system (13.2), which is a combination of the idea in [388] for periodic ordinary differential models with that in [389] for autonomous reaction–diffusion systems.

Let C_ω be the ordered Banach space consisting of all ω-periodic and continuous functions from $\mathbb{R}$ to $C(\overline{\Omega}, \mathbb{R})$, which is equipped with the maximum norm $\|\cdot\|$ and the positive cone $C_\omega^+ := \{\phi \in C_\omega : \ \phi(t)(x) \geq 0, \forall t \in \mathbb{R}, x \in \overline{\Omega}\}$. For any given $\phi \in C_\omega$, we also use the notation $\phi(x,t) := \phi(t)(x)$. Let $V(t,s)$ be the evolution operator of the reaction-diffusion equation

$$\begin{aligned} &I_t - d_I \Delta I = -\gamma(x,t)I, && x \in \Omega, \ t > 0, \\ &\frac{\partial I}{\partial \nu} = 0, && x \in \partial\Omega, \ t > 0. \end{aligned} \tag{13.5}$$

By the standard theory of evolution operators, it follows that there exist positive constants K and c_0 such that

$$\|V(t,s)\| \leq K e^{-c_0(t-s)}, \quad \forall t \geq s, \ t, \, s \in \mathbb{R}. \tag{13.6}$$

Suppose that $\phi \in C_\omega$ is the density distribution of initial infectious individuals at the spatial location $x \in \Omega$ and the time s. Then the term $\beta(x,s)\phi(x,s)$ means the density distribution of the new infections produced by the infected individuals who were introduced at time s. Thus, for given $t \geq s$, $V(t,s)\beta(x,s)\phi(x,s)$ is the density distribution at location x of those infected individuals who were newly infected at time s and remains infected at time t. Therefore, the integral

$$\int_{-\infty}^{t} V(t,s)\beta(\cdot,s)\phi(\cdot,s)ds = \int_0^\infty V(t,t-a)\beta(\cdot,t-a)\phi(\cdot,t-a)da$$

represents the density distribution of the accumulative new infections at location x and time t produced by all those infected individuals $\phi(x,s)$ introduced at all the previous time to t.

As in [388], we introduce the linear operator $L : \ C_\omega \longmapsto C_\omega$:

$$L(\phi)(t) := \int_0^\infty V(t,t-a)\beta(\cdot,t-a)\phi(\cdot,t-a)da, \tag{13.7}$$

which we may call as the next generation operator. Under our assumption on β and γ, it is easy to see that L is continuous, compact on C_ω and positive (i.e., $L(C_\omega^+) \subset C_\omega^+$). We define the spectral radius of L as the basic reproduction ratio

$$R_0 = \rho(L) \tag{13.8}$$

for system (13.2).

In what follows, we first obtain a characterization of the basic reproduction ratio R_0. This leads us to consider the following linear periodic-parabolic eigenvalue problem

$$\begin{aligned} &\psi_t - d_I \Delta \psi = -\gamma(x,t)\psi + \frac{\beta(x,t)}{\mu}\psi, && x \in \Omega, \ t > 0, \\ &\frac{\partial \psi}{\partial \nu} = 0, && x \in \partial\Omega, \ t > 0, \\ &\psi(x,0) = \psi(x,\omega), && x \in \Omega. \end{aligned} \tag{13.9}$$

By [152, Theorem 16.3], problem (13.9) has a unique principal eigenvalue μ_0, which is positive and corresponds to an eigenvector $\psi_0 \in C_\omega$ and $\psi_0 > 0$ on $\mathbb{R}$.

Lemma 13.1.1. $R_0 = \mu_0 > 0$.

Proof. Since (μ_0, ψ_0) satisfies (13.9), it follows from the constant-variation formula that

$$\psi_0(x,t) = V(t,\tau)\psi_0(x,\tau) + \int_\tau^t V(t,s)\frac{\beta(x,s)}{\mu_0}\psi_0(x,s)ds. \qquad (13.10)$$

Using (13.6) and the boundedness of ψ_0 on $\mathbb{R}$, by letting $\tau \to -\infty$, we obtain

$$\psi_0(x,t) = \int_{-\infty}^t V(t,s)\frac{\beta(x,s)}{\mu_0}\psi_0(x,s)ds, \quad \forall t \in \mathbb{R},$$

which implies $L\psi_0 = \mu_0\psi_0$ due to (13.7).

Note that under our assumption (A), the operator L may not be strongly positive. To show $R_0 = \mu_0$, we use a perturbation argument. For any given $\epsilon > 0$, we define

$$L_\epsilon(\phi)(t) := \int_0^\infty V(t,t-a)(\beta(\cdot,t-a)+\epsilon)\phi(\cdot,t-a)da, \qquad (13.11)$$

and its spectral radius $\mathcal{R}_{\epsilon,0} = \rho(L_\epsilon)$. As $\beta(x,t)+\epsilon > 0$ on $\overline{\Omega}\times\mathbb{R}$, $L_\epsilon : C_\omega \longmapsto C_\omega$ is continuous, compact, and strongly positive. By the upper semicontinuity of the spectrum ([198, Sect. IV.3.1]) and the continuity of a finite system of eigenvalues ([198, Sect. IV.3.5]), we then derive

$$\mathcal{R}_{\epsilon,0} \to R_0 \quad \text{as } \epsilon \to 0. \qquad (13.12)$$

On the other hand, we denote by $\mu_{\epsilon,0}$ the unique positive principal eigenvalue of (13.9) with $\beta(x,t)$ replaced by $\beta(x,t)+\epsilon$, which corresponds to a positive eigenvector $\psi_{\epsilon,0} \in C_\omega$. Arguing as above, we see that $L_\epsilon\psi_{\epsilon,0} = \mu_{\epsilon,0}\psi_{\epsilon,0}$. By virtue of the strong positivity of L_ϵ and the Krein-Rutman theorem (see, e.g., [152, Theorem 7.2]), we have $\mathcal{R}_{\epsilon,0} = \mu_{\epsilon,0}$. Furthermore, from the continuity of the principal eigenvalue on the weight function ([152]), it follows that $\mathcal{R}_{\epsilon,0} = \mu_{\epsilon,0} \to \mu_0$ as $\epsilon \to 0$. This fact, together with (13.12), implies $R_0 = \mu_0$. ∎

For our later purpose, we consider the periodic-parabolic eigenvalue problem

$$\begin{cases} \varphi_t - d_I\Delta\varphi = \beta(x,t)\varphi - \gamma(x,t)\varphi + \lambda\varphi, & x \in \Omega,\ t > 0, \\ \dfrac{\partial\varphi}{\partial\nu} = 0, & x \in \partial\Omega,\ t > 0, \\ \varphi(x,0) = \varphi(x,\omega), & x \in \Omega. \end{cases} \qquad (13.13)$$

Let λ_0 be the unique principal eigenvalue of (13.13) (see, e.g., [152]). Then we have the following observation.

Lemma 13.1.2. $1 - R_0$ *has the same sign as* λ_0.

Proof. This lemma is a straightforward consequence of [370, Theorem 5.7]. Here we provide an elementary proof. In view of Lemma 13.1.1, it suffices to prove that $1 - \mu_0$ has the same sign as λ_0. Due to [152, Theorem 7.2], we can assert that λ_0 is also the principal eigenvalue of the adjoint problem of (13.13):

$$\begin{aligned} &-\varphi_t^* - d_I \Delta\varphi^* = \beta(x,t)\varphi^* - \gamma(x,t)\varphi^* + \lambda\varphi^*, && x \in \Omega,\ t > 0, \\ &\frac{\partial\varphi^*}{\partial\nu} = 0, && x \in \partial\Omega,\ t > 0, \\ &\varphi^*(x,0) = \varphi^*(x,\omega), && x \in \Omega, \end{aligned} \tag{13.14}$$

where $\varphi^* \in C_\omega$ and $\varphi^* > 0$ on $\mathbb{R}$. We multiply the equation (13.9) that (μ_0, ψ_0) satisfies by φ^* and then integrate over $\Omega \times (0,\omega)$ by parts to obtain

$$\Big(1 - \frac{1}{\mu_0}\Big) \int_0^\omega \int_\Omega \beta\psi_0\varphi^* dxdt + \lambda_0 \int_0^\omega \int_\Omega \psi_0\varphi^* dxdt = 0.$$

Since $\int_0^\omega \int_\Omega \beta\psi_0\varphi^* dxdt$ and $\int_0^\omega \int_\Omega \psi_0\varphi^* dxdt$ are both positive, it follows that $1 - \frac{1}{\mu_0}$ and λ_0 have the opposite signs, which thereby deduces our result. ∎

From now on, we present some quantitative properties for the basic reproduction ratio R_0. First of all, when $\beta(x,t) - \gamma(x,t)$ or both $\beta(x,t)$ and $\gamma(x,t)$ are spatially homogeneous, we have the following result.

Lemma 13.1.3. *The following statements hold true:*

(a) *If* $\beta(x,t) \equiv \beta(t)$ *and* $\gamma(x,t) \equiv \gamma(t)$, *then* $R_0 = \int_0^\omega \beta(t)dt / \int_0^\omega \gamma(t)dt$.
(b) *If* $\beta(x,t) - \gamma(x,t) \equiv h(t)$, *then* $R_0 - 1$ *has the same sign as* $\int_0^\omega h(t)dt$.

Proof. We first prove (a). For simplicity, let

$$\mu^* = \frac{\int_0^\omega \beta(t)dt}{\int_0^\omega \gamma(t)dt}.$$

Consider the ordinary differential equation:

$$u_t = \Big(-\gamma(t) + \frac{1}{\mu^*}\beta(t) \Big) u, \quad u(0) = 1. \tag{13.15}$$

It is easy to see that (13.15) admits a unique positive solution

$$u(t) = e^{\int_0^t (-\gamma(s) + \frac{1}{\mu^*}\beta(s))ds},$$

which also satisfies $u(\omega) = u(0) = 1$. So $u(t)$ is a positive ω-periodic solution to (13.15). Thanks to the uniqueness of the principal eigenvalue of (13.9), we have $\mu_0 = \mu^*$, and hence (a) holds since $R_0 = \mu_0$.

We then verify (b). In this case, we consider the following ordinary differential problem:

$$u_t - h(t)u = \lambda u, \;\; u(0) = u(\omega) = 1. \tag{13.16}$$

Clearly, (13.16) has a unique positive solution if and only if

$$\lambda = -\frac{1}{\omega}\int_0^\omega h(t)dt.$$

Furthermore, such a unique positive ω-periodic solution can be expressed as $u(t) = e^{\int_0^t (h(s)+\lambda)ds}$. Observe that

$$\lambda = -\frac{1}{\omega}\int_0^\omega h(t)dt \quad \text{and} \quad \psi(t) = e^{\int_0^t (h(s)+\lambda)ds}$$

satisfy (13.13). By the uniqueness of the principal eigenvalue, we immediately have

$$\lambda_0 = -\frac{1}{\omega}\int_0^\omega h(t)dt.$$

Therefore, applying Lemma 13.1.2, we see that (b) holds true. ∎

Secondly, if $\beta(x,t)-\gamma(x,t)$ or both $\beta(x,t)$ and $\gamma(x,t)$ depend on the spatial factor alone, we have the following result.

Lemma 13.1.4. *Assume that $\beta(x,t) - \gamma(x,t) \equiv h(x)$. Then the following assertions hold true:*

(a) *If $\int_\Omega h(x)dx \geq 0$ and $h \not\equiv 0$ in Ω, then $R_0 > 1$ for all d_I;*
(b) *If $\int_\Omega h(x)dx < 0$ and $h(x) \leq 0$ on $\overline{\Omega}$, then $R_0 < 1$ for all d_I;*
(c) *If $\int_\Omega h(x)dx < 0$ and $\max_{\overline{\Omega}} h(x) > 0$, then there exists a threshold value $d_I^* \in (0,\infty)$ such that $R_0 > 1$ for $d_I < d_I^*$, $R_0 = 1$ for $d_I = d_I^*$, and $R_0 < 1$ for $d_I > d_I^*$.*

In particular, if $\beta(x,t) \equiv \beta(x)$ and $\gamma(x,t) \equiv \gamma(x)$, we have

$$R_0 = \sup_{\varphi\in H^1(\Omega),\, \varphi\neq 0}\left\{\frac{\int_\Omega \beta\varphi^2 dx}{\int_\Omega \left(d_I|\nabla\varphi|^2 + \gamma\varphi^2\right)dx}\right\} \tag{13.17}$$

and R_0 is a nonincreasing function of d_I with $R_0 \to \max_{\overline{\Omega}}\{\frac{\beta(x)}{\gamma(x)}\}$ as $d_I \to 0$, and $R_0 \to \int_\Omega \beta(x)dx/\int_\Omega \gamma(x)dx$ as $d_I \to \infty$. Here and in what follows, when $\max_{\overline{\Omega}}\{\frac{\beta(x)}{\gamma(x)}\} = \infty$, we understand $R_0 \to \infty$ as $d_I \to 0$.

Proof. To prove our assertions, we resort to problem (13.13). First, when $\beta(x,t) - \gamma(x,t) \equiv h(x)$, we consider the elliptic eigenvalue problem

$$-d_I \Delta u - h(x)u = \lambda u, \quad x \in \Omega; \quad \frac{\partial u}{\partial \nu} = 0, \quad x \in \partial\Omega. \tag{13.18}$$

It is well known that (13.18) possesses a unique principal eigenvalue, denoted by λ_*. From the uniqueness of the principal eigenvalue for (13.13) and (13.18), it is necessary that $\lambda_0 = \lambda_*$ in the present situation. By [9, Lemma 2.2] and its proof, we further see that λ_0 is nondecreasing with respect to $d_I > 0$, and if additionally $h(x)$ is not a constant in Ω, then λ_0 is strictly increasing in $d_I > 0$. Moreover, $\lambda_0 \to -\max_{\overline{\Omega}} h(x)$ as $d_I \to 0$ and $\lambda_0 \to -\frac{1}{|\Omega|}\int_\Omega h(x)dx$ as $d_I \to \infty$. Hence, the assertions (a)–(c) follow from these properties and Lemma 13.1.2.

In the case of $\beta(x,t) \equiv \beta(x)$ and $\gamma(x,t) \equiv \gamma(x)$, we recall that $R_0 = \mu_0$. As above, it is easy to see from (13.9) that R_0 is the principal eigenvalue of the elliptic problem:

$$-d_I \Delta\psi = -\gamma(x)\psi + \frac{\beta(x)}{\mu}\psi, \quad x \in \Omega; \quad \frac{\partial\psi}{\partial\nu} = 0, \quad x \in \partial\Omega. \tag{13.19}$$

Then the formula (13.17) follows from the well-known variational characterization of the principal eigenvalue for problem (13.19) (see, e.g., [108, Sect. II. 6.5]). Thus, the properties of R_0 are straightforward consequences of [9, Lemma 2.3]. ∎

Remark 13.1.1. In [9, Lemma 2.3], the right-hand side expression of (13.17) is directly defined as the basic reproduction number for the autonomous system (13.1). Lemma 13.1.4 above shows that this definition is indeed meaningful biologically. Moreover, if $\beta(x) \not\equiv \gamma(x)$ on $\overline{\Omega} \times [0,\omega]$, according to the proof of [9, Lemma 2.3], R_0 is a strictly decreasing function of d_I.

The subsequent result presents some analytical properties of R_0 for the general case of β and γ.

Theorem 13.1.1. *The following statements are valid:*

(a) $R_0 \geq \frac{\int_0^\omega \int_\Omega \beta(x,t)dxdt}{\int_0^\omega \int_\Omega \gamma(x,t)dxdt}$ *for all* d_I*, and the equality holds if and only if the function* $\frac{\beta(x,t)}{\int_0^\omega \int_\Omega \beta(x,t)dxdt} - \frac{\gamma(x,t)}{\int_0^\omega \int_\Omega \gamma(x,t)dxdt}$ *is spatially homogeneous (that is,* x*-independent);*
(b) $R_0 < 1$ *for all* $d_I > 0$ *if* $\int_0^\omega \max_{x\in\overline{\Omega}}(\beta(x,t) - \gamma(x,t))dt \leq 0$ *and* $\beta(x,t) - \gamma(x,t)$ *nontrivially depends on* x*;*
(c) $R_0 \to \frac{\int_0^\omega \int_\Omega \beta(x,t)dxdt}{\int_0^\omega \int_\Omega \gamma(x,t)dxdt}$ *as* $d_I \to \infty$*;*
(d) $R_0 \to \max_{x\in\overline{\Omega}} \left\{ \frac{\int_0^\omega \beta(x,t)dt}{\int_0^\omega \gamma(x,t)dt} \right\}$ *as* $d_I \to 0$*;*
(e) In general, $R_0(d_I) := R_0$ *is not a nonincreasing function of* d_I*; particularly, if* $\beta(x,t) = p(x)q_1(t)$ *and* $\gamma(x,t) = p(x)q_2(t)$ *with* $p > 0$ *on* $\overline{\Omega}$*,* $p \not\equiv$ *constant,* q_1*,* $q_2 \in C_\omega$*,* q_1*,* $q_2 > 0$ *on* $[0,\omega]$ *and* $q_1 - q_2 \not\equiv$ *constant, then there exist* $0 < d_I^1 < d_I^2$ *such that* $R_0(d_I^1) = R_0(d_I^2)$*.*

Proof. To obtain our assertions, we use similar arguments to those in [187, Lemma 2.4]. Since some necessary modifications are required, here we provide a detailed proof.

We first prove (a). Let ψ_0 be defined as before. Since $\psi_0 > 0$ on $\overline{\Omega} \times \mathbb{R}$, we divide the equation (13.9) that ψ_0 satisfies by ψ_0 and integrate the resulting equation over $\Omega \times (0, \omega)$ by parts to get

$$-d_I \int_0^\omega \int_\Omega \frac{|\nabla \psi_0|^2}{\psi_0^2} dxdt = -\int_0^\omega \int_\Omega \gamma dxdt + \frac{1}{R_0} \int_0^\omega \int_\Omega \beta dxdt.$$

This implies $R_0 \geq \int_0^\omega \int_\Omega \beta(x,t)dxdt / \int_0^\omega \int_\Omega \gamma(x,t)dxdt$, $\forall d_I > 0$. Moreover, the equality holds if and only if

$$\int_0^\omega \int_\Omega \frac{|\nabla \psi_0|^2}{\psi_0^2} dxdt = 0,$$

which is equivalent to the condition that the function $\frac{\beta(x,t)}{\int_0^\omega \int_\Omega \beta(x,t)dxdt} - \frac{\gamma(x,t)}{\int_0^\omega \int_\Omega \gamma(x,t)dxdt}$ is spatially homogeneous.

The assertion (b) follows from [152, Lemma 15.6]. Indeed, by taking $m(x,t) = \beta(x,t) - \gamma(x,t)$ and $\lambda = 1$ in [152, Lemma 15.6], we have $\mu(0) = 0$ and

$$\mu(1) > -\frac{1}{\omega} \int_0^\omega \max_{x \in \overline{\Omega}} (\beta(x,t) - \gamma(x,t))dt \geq 0$$

under our hypothesis. Using the notation here, we obtain $\lambda_0 = \mu(1)$, and hence, Lemma 13.1.2 deduces (b).

To verify (c), we first assume that $\gamma > 0$ on $\overline{\Omega} \times \mathbb{R}$. In this case, by directly integrating the equation (13.9) that ψ_0 satisfies over $\Omega \times (0, \omega)$, we easily find

$$R_0 = \frac{\int_0^\omega \int_\Omega \beta \psi_0 dxdt}{\int_0^\omega \int_\Omega \gamma \psi_0 dxdt} \leq \frac{\max_{\overline{\Omega} \times [0,\omega]} \beta}{\min_{\overline{\Omega} \times [0,\omega]} \gamma}. \tag{13.20}$$

Hence, this and the assertion (a) show that R_0 has boundedness independent of $d_I > 0$.

By normalizing ψ_0, we may further assume that

$$\int_0^\omega \int_\Omega \psi_0^2 dxdt = 1. \tag{13.21}$$

We now multiply (13.9) with $\psi = \psi_0$ by ψ_0 and integrate to yield

$$d_I \int_0^\omega \int_\Omega |\nabla \psi_0|^2 dxdt = -\int_0^\omega \int_\Omega \gamma \psi_0^2 dxdt + \frac{1}{R_0} \int_0^\omega \int_\Omega \beta \psi_0^2 dxdt,$$

and so we can find a positive constant c such that

$$\int_0^\omega \int_\Omega |\nabla \psi_0|^2 dxdt \leq \frac{c}{d_I}. \tag{13.22}$$

Here and in the sequel, the constant c does not depend on $d_I > 0$ and may vary from place to place.

On the other hand, we set

$$\overline{\psi}_0(t) = \frac{1}{|\Omega|}\int_\Omega \psi_0(x,t)dx \quad \text{and} \quad \Psi(x,t) = \psi_0(x,t) - \overline{\psi}_0(t).$$

Note that $\int_\Omega \Psi dx = 0$ for all $t \in \mathbb{R}$. Then, from the well-known Poincaré inequality it follows that

$$\int_\Omega \Psi^2 dx \le c\int_\Omega |\nabla\Psi|^2 dx, \text{ for all } t.$$

Therefore, as $\nabla\Psi = \nabla\psi_0$, making use of (13.22), we have

$$\int_0^\omega \int_\Omega \Psi^2 dxdt \le \frac{c}{d_I}, \quad \text{and hence,} \quad \int_0^\omega \int_\Omega |\Psi| dxdt \le \frac{c}{\sqrt{d_I}}. \tag{13.23}$$

Furthermore, by integrating (13.9) with $\psi = \psi_0$ over Ω, it is easy to see that

$$\frac{d}{dt}\Big(\overline{\psi}_0\Big) = \int_\Omega \Big[-\gamma + \frac{1}{R_0}\beta\Big]dx \cdot \overline{\psi}_0 + \int_\Omega \Big(-\gamma + \frac{1}{R_0}\beta\Big)\Psi dx. \tag{13.24}$$

Using (a), (13.20), and (13.23), one has

$$\int_0^\omega \Big|\int_\Omega \Big(-\gamma + \frac{1}{R_0}\beta\Big)\Psi dx\Big| dt = O(\frac{1}{\sqrt{d_I}}).$$

Henceforth, solving the ordinary equation (13.24), we obtain

$$\overline{\psi}_0(t) = e^{\int_0^t \int_\Omega (-\gamma + \frac{1}{R_0}\beta)dxds} \cdot \overline{\psi}_0(0) + O\left(\frac{1}{\sqrt{d_I}}\right). \tag{13.25}$$

Because of $\overline{\psi}_0(\omega) = \overline{\psi}_0(0)$, as $d_I \to \infty$, it is clear that either $\overline{\psi}_0(0) \to 0$, or

$$\int_0^\omega \int_\Omega \Big(-\gamma + \frac{1}{R_0}\beta\Big)dxdt \to 0.$$

The latter will lead to our assertion (c). So it suffices to exclude the possibility of $\overline{\psi}_0(0) \to 0$ as $d_I \to \infty$. Supposing $\overline{\psi}_0(0) \to 0$ as $d_I \to \infty$, by (13.25) we would have $\overline{\psi}_0(t) \to 0$ uniformly on $[0,\omega]$, which, together with (13.23), implies that $\int_0^\omega \int_\Omega \psi_0^2 dxdt \to 0$, contradicting (13.21).

In the general case of $\gamma \ge, \not\equiv 0$ on $\overline{\Omega} \times \mathbb{R}$, we proceed as above except that γ is replaced by $\gamma + \epsilon$ for any given $\epsilon > 0$ to get

$$R_0 \to \frac{\int_0^\omega \int_\Omega \beta(x,t)dxdt}{\int_0^\omega \int_\Omega [\gamma(x,t) + \epsilon]dxdt}, \quad \text{as } d_I \to \infty,$$

and we then obtain the desired result by letting $\epsilon \to 0$.

We are in a position to prove (d). Without loss of generality, we can assume that β, $\gamma > 0$ on $\overline{\Omega} \times \mathbb{R}$. For the general case, as above, we can replace β and

γ with $\beta+\epsilon$ and $\gamma+\epsilon$, respectively, and then get the result by letting $\epsilon \to 0$. For sake of simplicity, we denote

$$\delta = \frac{\int_0^\omega \beta(x_0,t)dt}{\int_0^\omega \gamma(x_0,t)dt} = \max_{\overline{\Omega}} \left\{ \frac{\int_0^\omega \beta(x,t)dt}{\int_0^\omega \gamma(x,t)dt} \right\} \quad \text{for some } x_0 \in \overline{\Omega}.$$

For a positive constant μ to be determined later, we rewrite the equation that (μ_0, ψ_0) satisfies as

$$(\psi_0)_t - d_I \Delta\psi_0 - \Big(\frac{1}{\mu}\beta - \gamma\Big)\psi_0 = \Big(\frac{1}{\mu_0} - \frac{1}{\mu}\Big)\beta\psi_0. \tag{13.26}$$

Before going further, we need some preliminaries on the following eigenvalue problem with the positive weight function $\beta(x,t)$:

$$\begin{cases} \psi_t - d_I\Delta\psi - m(x,t)\psi = \lambda\beta(x,t)\psi, & x \in \Omega,\ t > 0, \\ \dfrac{\partial\psi}{\partial\nu} = 0, & x \in \partial\Omega,\ t > 0, \\ \psi(x,0) = \psi(x,\omega), & x \in \Omega, \end{cases} \tag{13.27}$$

where $m(x,t) \in C_\omega$. Arguing as in [152], problem (13.27) admits the principal eigenvalue λ_* with a positive eigenvector $\psi_* \in C_\omega$. Moreover, the same analysis as in the proof of [152, Propositions 17.1 and 17.3] implies that the following statements hold:

(i) If there exists $x_* \in \overline{\Omega}$ such that $\int_0^\omega m(x_*,t)dt > 0$, then $\lambda_* < 0$ for all small d_I.
(ii) If $\int_0^\omega m(x,t)dt < 0$ for all $x \in \overline{\Omega}$, then $\lambda_* > 0$ for all small d_I.

Here we should point out that $\int_0^\omega \max_{\overline{\Omega}} m(x,t)dt > 0$ does not imply $\int_0^\omega m(x^*,t)dt > 0$ for some $x^* \in \overline{\Omega}$, and it is even possible that $\int_0^\omega m(x,t)dt < 0$ for all $x \in \overline{\Omega}$.

Now we choose μ such that $0 < \mu < \delta$. For any such μ, by the definition of δ, it follows that

$$\int_0^\omega \Big(\frac{1}{\mu}\beta(x_0,t) - \gamma(x_0,t)\Big)dt > 0.$$

Applying the above claim (i) to problem (13.26) with $m(x,t) = \frac{1}{\mu}\beta - \gamma$, we have

$$\frac{1}{R_0} - \frac{1}{\mu} = \frac{1}{\mu_0} - \frac{1}{\mu} < 0 \quad \text{for all small } d_I,$$

that is, $R_0 > \mu$. Thanks to the arbitrariness of μ, we obtain

$$\liminf_{d_I \to 0} R_0 \geq \delta = \max_{\overline{\Omega}} \left\{ \frac{\int_0^\omega \beta(x,t)dt}{\int_0^\omega \gamma(x,t)dt} \right\}. \tag{13.28}$$

On the other hand, by taking $\mu > \delta$ and noticing

$$\int_0^\omega \Big(\frac{1}{\mu}\beta(x,t) - \gamma(x,t)\Big)dt < 0 \quad \text{for all } x \in \overline{\Omega},$$

we see from the previous claim (ii) that

$$\frac{1}{R_0} - \frac{1}{\mu} = \frac{1}{\mu_0} - \frac{1}{\mu} > 0 \quad \text{for all small } d_I,$$

which implies

$$\limsup_{d_I \to 0} R_0 \le \delta = \max_{\overline{\Omega}} \left\{ \frac{\int_0^\omega \beta(x,t)dt}{\int_0^\omega \gamma(x,t)dt} \right\}. \tag{13.29}$$

Combining (13.28) and (13.29), we derive the assertion (d).

Finally, we verify (e). By the choice of β and γ, we easily see from (a), (c), and (d) that

$$R_0(d_I) > \frac{\int_0^\omega \int_\Omega \beta(x,t)dxdt}{\int_0^\omega \int_\Omega \gamma(x,t)dxdt} \quad \text{for all } d_I,$$

and

$$\lim_{d_I \to 0} R_0(d_I) = \lim_{d_I \to \infty} R_0(d_I) = \frac{\int_0^\omega \int_\Omega \beta(x,t)dxdt}{\int_0^\omega \int_\Omega \gamma(x,t)dxdt}.$$

As a consequence, one can find $0 < d_I^1 < d_I^2$ such that $R_0(d_I^1) = R_0(d_I^2)$. ∎

In the rest of this section, we present a bang-bang type configuration optimization result for the basic reproduction ratio R_0 in the case where the maximum, the minimum, and the average of the function $\gamma(x,t)$ are fixed while $\beta(x,t) \equiv \beta$ is a fixed positive constant.

Theorem 13.1.2. *Assume that $\beta(x,t) \equiv \beta$ is a fixed positive constant. Let*

$$\Upsilon = \Big\{ \gamma \in L^\infty(\Omega \times (0,\omega)) : \ \gamma_* \le \gamma(x,t) \le \gamma^* \quad a.e.\ x,t,$$
$$\gamma(x,t) \text{ is } \omega\text{-periodic in } t,\ \frac{1}{\omega|\Omega|}\int_0^\omega \int_\Omega \gamma(x,t)dxdt = \mathcal{N} \Big\},$$

where $\gamma_* \ge 0, \gamma^* > 0$ and $\mathcal{N} > 0$ are given constants such that the set Υ is nonempty. Then the following statements are valid:

(a) The function $R_0 = R_0(\gamma)$ reaches its maximum over Υ when γ is of the form $\gamma(x,t) = \gamma_*\chi_A + \gamma^*\chi_{((\Omega\times(0,\omega))\setminus A)}$, where A is a measurable subset of $\Omega \times (0,\omega)$ such that $\gamma_*|A| + \gamma^*|(\Omega \times (0,\omega))\setminus A| = \omega|\Omega|\mathcal{N}$, and χ_A is the characteristic function over A.

(b) The function $R_0 = R_0(\gamma)$ reaches its minimum $\frac{\beta}{\mathcal{N}}$ over Υ only when $\gamma \in \Upsilon$ is an x-independent function.

Proof. By the standard compactness analysis and the eigenvalue theory, it is easily seen that $R_0 = R_0(\gamma)$ is a continuous function of γ in the sense that if γ_n is a bounded sequence in $L^\infty(\Omega \times (0,\omega))$, then there exists a subsequence $\gamma_{n'}$ of γ_n such that $R_0(\gamma_{n'}) \to R_0(\gamma)$ for some $\gamma \in L^\infty(\Omega \times (0,\omega))$. It is also well known that $\frac{\beta}{R_0(\gamma)}$ is concave with respect to γ. Thus, the arguments in the proof of [254, Lemma 7.2 and Theorem 3.11], as applied to (13.9) with $\mu = R_0$, imply that assertion (a) holds.

We now verify (b). By virtue of (13.9) and Lemma 13.1.1, it follows that if $\gamma(x,t) \equiv \mathcal{N} \in \Upsilon$, then $R_0(\gamma) = \frac{\beta}{\mathcal{N}}$ and 1 is an associated positive eigenfunction. For any given $\gamma \in \Upsilon$, let ψ_0 be the positive eigenfunction associated with $R_0(\gamma)$. Since $\psi_0 > 0$ on $\overline{\Omega} \times [0,\omega]$, we may assume that $\psi_0 > 1$ on $\overline{\Omega} \times [0,\omega]$. Thus, $(R_0(\gamma), \psi_0)$ satisfies (13.9) with $\mu = R_0(\gamma)$.

Let $\gamma^0 = \gamma - \mathcal{N}$ and $\psi^0 = \psi_0 - 1$. Clearly, $\psi^0 > 0$ on $\overline{\Omega} \times [0,\omega]$, and (γ^0, ψ^0) satisfies

$$
\begin{aligned}
&(\psi^0)_t - d_I \Delta\psi^0 + \gamma^0(x,t)\psi^0 = \left(\frac{\beta}{R_0(\gamma)} - \mathcal{N}\right)\psi^0, && x \in \Omega,\ t > 0,\\
&\frac{\partial \psi^0}{\partial \nu} = 0, && x \in \partial\Omega,\ t > 0,\\
&\psi^0(x,0) = \psi^0(x,\omega), && x \in \Omega.
\end{aligned} \tag{13.30}
$$

Dividing (13.30) by ψ^0 and integrating the resulting equation over $\Omega \times (0,\omega)$, we obtain

$$
- d_I \int_0^\omega \int_\Omega \frac{|\nabla \psi^0|^2}{(\psi^0)^2} dxdt + \int_0^\omega \int_\Omega \gamma^0 dxdt = \frac{\beta}{R_0(\gamma)} - \mathcal{N}.
$$

Since $\int_0^\omega \int_\Omega \gamma^0 dxdt = 0$, it easily follows from the above identity that $R_0(\gamma) \geq \frac{\beta}{\mathcal{N}}$, and $R_0(\gamma) = \frac{\beta}{\mathcal{N}}$ if and only if $\gamma(x,t) \equiv \gamma(t)$. ∎

13.2 Threshold Dynamics

In this section, we establish the threshold dynamical behavior of system (13.2)–(13.3) in terms of R_0. We start with the uniform bound of its nonnegative solutions.

Under the condition (13.3) (and so (13.4) holds), we can easily apply [150, Exercise 4 of Section 3.5] (or [6, Theorem 3.1]) to the second equation in (13.2) to derive the uniform bound of $\|\overline{I}(\cdot,t)\|_{L^\infty(\Omega)}$ for all $t \geq 0$. In order to obtain a similar estimate for $\|\overline{S}(\cdot,t)\|_{L^\infty(\Omega)}$, we appeal to the theory developed in [214], which is a generalization of [6, Theorem 3.1]. The following result is a straightforward consequence of [214, Theorem 1 and Corollary 1].

Lemma 13.2.1. *Consider the parabolic system*

$$\begin{array}{ll} \dfrac{\partial u_i}{\partial t} - d_i \Delta u_i = f_i(x,t,u), & x \in \Omega,\ t > 0,\ i = 1, \cdots, \ell \\ \dfrac{\partial u_i}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ u_i(x,0) = u_i^0(x), & x \in \Omega, \end{array}$$

where $u = (u_1, \cdots, u_\ell)$, $u_i^0 \in C(\overline{\Omega}, \mathbb{R})$, d_i is a positive constant, $i = 1, \cdots, \ell$, and assume that, for each $k = 1, \cdots, \ell$, the functions f_k satisfy the polynomial growth condition:

$$|f_k(x,t,u)| \le c_1 \sum_{i=1}^{\ell} |u_i|^\sigma + c_2$$

for some nonnegative constants c_1 and c_2, and positive constant σ. Let p_0 be a positive constant such that $p_0 > \frac{m}{2}\max\{0, (\sigma-1)\}$ and $\tau(u^0)$ be the maximal time of existence of the solution u corresponding to the initial data u^0. Suppose that there exists a positive number $C_1 = C_1(u^0)$ such that $\|u(\cdot,t)\|_{L^{p_0}(\Omega)} \le C_1$, $\forall t \in [0, \tau(u^0))$. Then the solution u exists for all time and there is a positive number $C_2 = C_2(u^0)$ such that $\|u(\cdot,t)\|_{L^\infty(\Omega)} \le C_2$, $\forall t \in [0,\infty)$. Moreover, if there exist two nonnegative numbers ϱ and $K_1 = K_1(\varrho)$, independent of initial data, such that $\|u(\cdot,t)\|_{L^{p_0}(\Omega)} \le K_1$, $\forall t \in [\varrho, \infty)$, then there is a positive number $K_2 = K_2(\varrho)$, independent of initial data, such that $\|u(\cdot,t)\|_{L^\infty(\Omega)} \le K_2$, $\forall t \in [\varrho,\infty)$.

By applying Lemma 13.2.1 with $\sigma = p_0 = 1$ and $\varrho = 0$ to system (13.2), we obtain the following result.

Lemma 13.2.2. *There exists a positive constant B, independent of the initial data $(S_0, I_0) \in C(\overline{\Omega}, \mathbb{R}_+^2)$ satisfying condition (13.3), such that for the corresponding unique solution $(\overline{S}, \overline{I})$ of system (13.2), we have*

$$\|\overline{S}(\cdot,t)\|_{L^\infty(\Omega)} + \|\overline{I}(\cdot,t)\|_{L^\infty(\Omega)} \le B, \quad \forall t \in [0,\infty).$$

Let

$$Y := \left\{ (u,v) \in C(\overline{\Omega}, \mathbb{R}_+^2) : \quad \int_\Omega (u(x) + v(x))dx = N \right\}$$

and $Y_0 = \{(u,v) \in Y : v(x) \not\equiv 0\}$. We equip Y with the metric induced by the maximum norm. Then Y is a complete metric space and Y_0 is open in Y. Now we are ready to present the main result of this section, which gives the threshold dynamics of system (13.2)–(13.3).

Theorem 13.2.1. *The following statements are valid:*

(i) If $R_0 < 1$, then for any $(S_0, I_0) \in Y$, the solution $(\overline{S}, \overline{I})$ of system (13.2)–(13.3) satisfies $\lim_{t\to\infty}(\overline{S}(x,t), \overline{I}(x,t)) = (N/|\Omega|, 0)$ uniformly for $x \in \overline{\Omega}$.

(ii) If $R_0 > 1$, then system (13.2)–(13.3) *has at least one endemic ω-periodic solution, and there exists a constant $\eta > 0$ such that for any $(S_0, I_0) \in Y_0$, the solution $(\overline{S}, \overline{I})$ of system* (13.2)–(13.3) *satisfies*

$$\liminf_{t\to\infty} \overline{S}(x,t) \geq \eta \quad \textit{and} \quad \liminf_{t\to\infty} \overline{I}(x,t) \geq \eta$$

uniformly for $x \in \overline{\Omega}$.

Proof. We define an ω-periodic semiflow $\Phi(t) : Y \to Y$ by

$$\Phi(t)((S_0, I_0)) = (\overline{S}(\cdot, t, ,(S_0, I_0)), \overline{I}(\cdot, t, (S_0, I_0)), \quad \forall (S_0, I_0) \in Y,\ t \geq 0,$$

where $(\overline{S}(x, t, (S_0, I_0)), \overline{I}(x, t, (S_0, I_0))$ is the unique solution of system (13.2). Let $P := \Phi(\omega)$ be the Poincaré map associated with system (13.2) on Y. Note that $\Phi(t) : Y \to Y$ is compact for each $t > 0$. It then follows from Lemma 13.2.2 and Theorem 1.1.3 that $P : Y \to Y$ has a strong global attractor.

Given $(S_0, I_0) \in Y$, let $\omega(S_0, I_0)$ be the omega limit set of the forward orbit through (S_0, I_0) for $P : Y \to Y$. Since $\frac{\overline{S}}{\overline{S}+\overline{I}} \leq 1$, $\overline{I}(x,t)$ satisfies

$$\frac{\partial \overline{I}}{\partial t} - d_I \Delta \overline{I} \leq (\beta(x,t) - \gamma(x,t))\overline{I}, \quad x \in \Omega,\, t > 0.$$

In the case where $R_0 < 1$, we see from Lemma 13.1.2 that $\lambda_0 > 0$. This, together with the comparison principle, implies that $\overline{I}(x,t) \to 0$ uniformly on $\overline{\Omega}$ as $t \to \infty$. It then easily follows that $\omega(S_0, I_0) = \tilde{\omega} \times \{0\}$, where $\tilde{\omega}$ is a compact and internally chain transitive set for the Poincaré map P_1 associated with the following ω-periodic system

$$\begin{aligned} &\tilde{S}_t - d_S \Delta \tilde{S} = 0, && x \in \Omega,\ t > 0, \\ &\frac{\partial \tilde{S}}{\partial \nu} = 0, && x \in \partial\Omega,\ t > 0, \end{aligned} \tag{13.31}$$

on the space $Y_1 := \left\{u \in C(\overline{\Omega}, \mathbb{R}_+) :\ \int_\Omega u(x)dx = N\right\}$ equipped with the uniform convergence topology. By a well-known result on the heat equation in a bounded domain (see, e.g., [255, Section 1.1.2]), we conclude that the constant $\frac{N}{|\Omega|}$ is a globally asymptotically stable steady state for system (13.31) on Y_1. In view of Theorem 1.2.1, we obtain $\tilde{\omega} = \{\frac{N}{|\Omega|}\}$, and hence $\omega(S_0, I_0) = \{(\frac{N}{|\Omega|}, 0)\}$. This implies that assertion (i) holds true.

To prove assertion (ii), we use similar arguments to those in the proof of [430, Theorem 3.1] on a periodic predator–prey reaction–diffusion system. Let $\partial Y_0 := Y \setminus Y_0 = \{(S_0, I_0) \in Y\ :\ I_0 \equiv 0\}$. Clearly, Y_0 is convex, $\Phi(t)Y_0 \subset Y_0$, and $\Phi(t)\partial Y_0 \subset \partial Y_0$ for all $t \geq 0$. For any $(S_0, I_0) \in \partial Y_0$, $\overline{I}(x,t) \equiv 0$, and hence $\overline{S}(x,t)$ is a solution of system (13.31). It then follows that $\overline{S}(x,t) \to \frac{N}{|\Omega|}$ uniformly on $\overline{\Omega}$ as $t \to \infty$. This implies that $\cup_{(S_0,I_0)\in\partial Y_0} \omega(S_0, I_0) = \{(\frac{N}{|\Omega|}, 0)\}$, where $\omega(S_0, I_0)$ is the omega limit set of the forward orbit through (S_0, I_0) for $P : Y \to Y$. For simplicity, we denote $M = (\frac{N}{|\Omega|}, 0)$. Then $\{M\}$ is a compact and isolated invariant set for $P : \partial Y_0 \to \partial Y_0$. Let $X := C(\overline{\Omega}, \mathbb{R})$ and $X_+ := C(\overline{\Omega}, \mathbb{R}_+)$. Then (X, X_+) is an ordered Banach space with the maximum norm $\|\cdot\|_X$. We further have the following claim.

Claim. There exists a real number $\delta > 0$ such that $\limsup_{n\to\infty} \|P^n(S_0, I_0) - M\|_{X\times X} \geq \delta$ for all $(S_0, I_0) \in Y_0$.

Indeed, let λ_0 be defined as in the preceding section. Under the assumption $R_0 > 1$, Lemma 13.1.2 implies that $\lambda_0 < 0$. It then follows that we can choose a small positive number ϵ_0 such that $\lambda_0(\epsilon_0) < 0$, where $\lambda_0(\epsilon_0)$ is the unique principal eigenvalue of the periodic-parabolic problem

$$\begin{aligned} &\varphi_t - d_I \Delta\varphi = \frac{\beta(x,t)(N/|\Omega| - \epsilon_0)}{N/|\Omega| + 2\epsilon_0}\varphi - \gamma(x,t)\varphi + \lambda\varphi, && x \in \Omega,\ t > 0, \\ &\frac{\partial\varphi}{\partial\nu} = 0, && x \in \partial\Omega,\ t > 0, \\ &\varphi(x,0) = \varphi(x,\omega), && x \in \Omega. \end{aligned} \tag{13.32}$$

According to the continuous dependence of solutions on the initial data, we observe that

$$\lim_{(S_0,I_0)\to M} \Phi(t)(S_0, I_0) = \lim_{(S_0,I_0)\to M} (\overline{S}(\cdot,t), \overline{I}(\cdot,t)) = M$$

in $X \times X$ uniformly for $t \in [0, \omega]$. Thus, there exists a real number $\delta_0 = \delta_0(\epsilon_0) > 0$ such that for any $(S_0, I_0) \in B(M, \delta_0)$, an open ball in $X \times X$ centered at M and with the radius δ_0, we have

$$\|\overline{S}(\cdot,t) - N/|\Omega|\|_X + \|\overline{I}(\cdot,t)\|_X < \epsilon_0,\ \forall t \in [0, \omega].$$

Assume, for the sake of contradiction, that the claim above does not hold for $\delta = \delta_0$. Since $P^n Y_0 \subset Y_0$, $\forall n \geq 0$, it then follows that there exists $(S_0^*, I_0^*) \in B(M, \delta_0) \cap Y_0$ such that $P^n(S_0^*, I_0^*) = \Phi(n\omega)(S_0^*, I_0^*)) \in B(M, \delta_0)$, $\forall n \geq 1$. For any $t \geq 0$, let $t = n\omega + t'$ with $t' \in [0, \omega)$ and $n = [t/\omega]$ being the integer part of t/ω. Note that $(\overline{S}^*(\cdot,t), \overline{I}^*(\cdot,t)) := \Phi(t)((S_0^*, I_0^*)) = \Phi(t')(\Phi(n\omega)(S_0^*, I_0^*))$. Thus, we have

$$\|\overline{S}^*(\cdot,t) - N/|\Omega|\|_X + \|\overline{I}^*(\cdot,t)\|_X < \epsilon_0, \quad \forall t \in [0, \infty). \tag{13.33}$$

Let φ_0 be a positive eigenvector corresponding to $\lambda_0(\epsilon_0)$ in (13.32). Clearly, $\varphi_0 > 0$ on $\overline{\Omega} \times \mathbb{R}$. In particular, $\varphi_0(\cdot, 0) \in \text{int}(X_+)$. On the other hand, as $(S_0^*, I_0^*) \in Y_0$, the strong maximum principle for parabolic equations shows that $\overline{S}^*(\cdot,t)$, $\overline{I}^*(\cdot,t) \in \text{int}(X_+) \times \text{int}(X_+)$ for any $t > 0$. Therefore, without loss of generality, we may assume that $(S_0^*, I_0^*) \in \text{int}(X_+) \times \text{int}(X_+)$. So one can find a small positive number c^* such that $I_0^* \geq c^*\varphi_0(\cdot, 0)$ in X. By means of (13.33) and the choice of δ_0, it follows that $\overline{I}^*(x,t)$ is a super-solution to the problem

$$
\begin{aligned}
&w_t - d_I \Delta w = \frac{\beta(x,t)(N/|\Omega| - \epsilon_0)}{N/|\Omega| + 2\epsilon_0} w - \gamma(x,t)w, && x \in \Omega,\ t > 0,\\
&\frac{\partial w}{\partial \nu} = 0, && x \in \partial\Omega,\ t > 0,\\
&w(x,0) = c^* \varphi_0(x,0), && x \in \Omega.
\end{aligned} \tag{13.34}
$$

Furthermore, it is easy to see that $c^* e^{-\lambda_0(\epsilon_0)t}\varphi_0(x,t)$ is the unique solution to problem (13.34). By the parabolic comparison principle, we deduce

$$\overline{I}^*(x,t) \geq c^* e^{-\lambda_0(\epsilon_0)t}\varphi_0(x,t) \to \infty \ \text{ uniformly for } x \in \overline{\Omega}, \quad \text{as } t \to \infty,$$

which contradicts (13.33). Thus, the claim holds true for $\delta = \delta_0$.

The above claim implies that M is an isolated invariant set for $P : Y \to Y$, and $W^s(M) \cap Y_0 = \emptyset$, where $W^s(M)$ is the stable set of M for $P : Y \to Y$. As a result, Theorem 1.3.1 and Remark 1.3.1 assert that P is uniformly persistent with respect to $(Y, \partial Y_0)$. Further, Theorem 1.3.10 implies that P has a fixed point ϕ^* in Y_0, and hence, system (13.2) has an ω-periodic solution $\Phi(t)\phi^*$ in Y_0. In view of Theorem 1.3.10, we further see that $P : Y_0 \to Y_0$ has a global attractor A_0. Clearly, $\phi^* \in A_0$. Let $B_0 := \bigcup_{t\in[0,\omega]} \Phi(t)A_0$. Then $B_0 \subset Y_0$, and Theorem 3.1.1 implies that $\lim\limits_{t\to\infty} d(\Phi(t)\phi, B_0) = 0$ for all $\phi \in Y_0$, where d is the norm-induced distance in $X \times X$. Since $A_0 \subset Y_0$ and $A_0 = S(A_0) = \Phi(\omega)A_0$, we have $A_0 \subset \text{int}(X_+) \times \text{int}(X_+)$, and hence $B_0 \subset \text{int}(X_+) \times \text{int}(X_+)$. Obviously, $\Phi(t)\phi^* \in B_0$, and so $\Phi(t)\phi^*$ is a positive ω-periodic solution of system (13.2). By virtue of the compactness and global attractiveness of B_0 for $\Phi(t)$ in Y_0, we conclude that there exists $\eta > 0$ such that $\liminf\limits_{t\to\infty} \Phi(t)\phi \geq (\eta, \eta)$ for all $\phi \in Y_0$, which implies the desired uniform persistence. ∎

As a consequence of Lemmas 13.1.3 and 13.1.4, and Theorems 13.1.1 and 13.2.1, we have the following result.

Theorem 13.2.2. *The following statements are valid:*

(i) *The disease-free constant solution $(N/|\Omega|, 0)$ is globally attractive for system (13.2)–(13.3) if one of the following conditions holds:*
  (i-a) $\beta(x,t) - \gamma(x,t) = h(t)$ *and* $\int_0^\omega h(t)dt < 0$;
  (i-b) $\beta(x,t) - \gamma(x,t) = h(x)$ *and either* $h \leq 0, \not\equiv 0$ *on* $\overline{\Omega}$ *or* $\max_{\overline{\Omega}} h(x) > 0$ *and* $\int_\Omega h(x)dx < 0$ *but* $d_I > d_I^*$, *where* d_I^* *is given in Lemma 13.1.4;*
  (i-c) $\int_0^\omega \int_\Omega (\beta(x,t) - \gamma(x,t))dxdt < 0$ *and* d_I *is sufficiently large;*
  (i-d) $\int_0^\omega \max_{x\in\overline{\Omega}}(\beta(x,t) - \gamma(x,t))dt \leq 0$ *and* $\beta(x,t) - \gamma(x,t)$ *nontrivially depends on the spatial variable.*

(ii) *The uniform persistence holds for system (13.2)–(13.3) if one of the following conditions holds:*
  (ii-a) $\beta(x,t) - \gamma(x,t) = h(t)$ *and* $\int_0^\omega h(t)dt > 0$;
  (ii-b) $\beta(x,t) - \gamma(x,t) = h(x)$, *either* $h \not\equiv 0$ *and* $\int_\Omega h(x)dx \geq 0$ *or* $\max_{\overline{\Omega}} h(x) > 0$ *and* $\int_\Omega h(x)dx < 0$ *but* $0 < d_I < d_I^*$;
  (ii-c) $\int_0^\omega \int_\Omega (\beta(x,t) - \gamma(x,t))dxdt > 0$;
  (ii-d) $\max_{x\in\overline{\Omega}} \left\{ \frac{\int_0^\omega \beta(x,t)dt}{\int_0^\omega \gamma(x,t)dt} \right\} > 1$ *and* d_I *is sufficiently small.*

13.3 Global Attractivity

The uniqueness and global attractivity of the endemic ω-periodic solution to reaction-diffusion system (13.2) is a challenging problem. In [9], it was conjectured that the unique endemic equilibrium of the autonomous system (13.1) is globally stable. A partial answer to this problem was given in [275], but it remains unsolved in the general case. In this section, we address this issue for periodic system (13.2) in two special cases.

When no diffusion is taken into account, by assuming the total population number is unchanged and $\beta(x,t) \equiv \beta(t)$, $\gamma(x,t) \equiv \gamma(t)$ are ω-periodic continuous functions, we obtain the following ordinary differential system:

$$\begin{aligned}
&\overline{S}_t = -\frac{\beta(t)\overline{S}\,\overline{I}}{\overline{S}+\overline{I}} + \gamma(t)\overline{I}, && t>0,\\
&\overline{I}_t = \frac{\beta(t)\overline{S}\,\overline{I}}{\overline{S}+\overline{I}} - \gamma(t)\overline{I}, && t>0,\\
&\overline{S}+\overline{I} = N, && t \ge 0,\\
&\overline{S}(0) = S_0 \ge 0, \quad \overline{I}(0) = I_0 > 0.
\end{aligned} \tag{13.35}$$

An analysis as in Section 13.2 shows that the basic reproduction ratio is

$$R_0 = \frac{\int_0^\omega \beta(t)dt}{\int_0^\omega \gamma(t)dt}.$$

For system (13.35), we have a threshold-type result on its global dynamics. Indeed, it is easy to see that $\overline{I}(t)$ satisfies the scalar ordinary differential equation:

$$\frac{d\overline{I}}{dt} = \left(\frac{\beta(t)(N-I)}{N} - \gamma(t)\right) I, \ \ t \ge 0; \quad \overline{I}(0) = I_0 \in [0, N]. \tag{13.36}$$

By Theorem 3.1.2, it follows that the zero solution is globally asymptotically stable for system (13.36) in $[0, N]$ in the case where $R_0 \le 1$; and system (13.36) has a globally asymptotically stable positive ω-periodic solution $I^*(t)$ in $(0, N]$ in the case where $R_0 > 1$. Biologically, this implies that the infectious disease dies out if $R_0 \le 1$ and it persists if $R_0 > 1$.

Returning to the reaction–diffusion system (13.2)–(13.3), we are able to obtain the global attractivity of the endemic ω-periodic solution in two special cases. The first one we shall cope with is that the diffusion rate of the susceptible individuals is equal to that of the infected individuals (i.e., $d_S = d_I$). In this situation, we can give a complete description of the global attractivity of the disease-free constant solution and the endemic ω-periodic solution.

Theorem 13.3.1. *Assume that $d_S = d_I$. If $R_0 \le 1$, then $(N/|\Omega|, 0)$ is globally attractive for system (13.2)–(13.3); If $R_0 > 1$, then system (13.2)–(13.3) admits a globally attractive endemic ω-periodic solution.*

Proof. In the case where $d_S = d_I$, $\overline{N}(x,t) := \overline{S}(x,t) + \overline{I}(x,t)$ is a solution of system (13.31) on Y_1, and hence $\lim_{t\to\infty} \overline{N}(x,t) = \frac{N}{|\Omega|}$ uniformly for $x \in \overline{\Omega}$. It follows that $\overline{I}(x,t)$ satisfies the following nonautonomous equation

$$\frac{\partial \overline{I}}{\partial t} - d_I \Delta \overline{I} = \left[\beta(x,t)\left(1 - \frac{\overline{I}}{\overline{N}(x,t)}\right) - \gamma(x,t)\right]\overline{I},\ x \in \Omega,\ t > 0, \tag{13.37}$$

which is asymptotic to a periodic equation

$$\frac{\partial \overline{I}}{\partial t} - d_I \Delta \overline{I} = \left[\beta(x,t)\left(1 - \frac{|\Omega|}{N}\overline{I}\right) - \gamma(x,t)\right]\overline{I},\ x \in \Omega,\ t > 0. \tag{13.38}$$

By Lemma 13.1.2 and Theorem 3.2.2, as applied to the asymptotically periodic system (13.37), it follows that the desired threshold dynamics holds for system (13.2)–(13.3) in terms of R_0. ∎

Next, we consider the case where $\beta(x,t) = r\gamma(x,t)$ for some real number $r \in (0,\infty)$. It is easy to see that when $r > 1$,

$$(\tilde{S}, \tilde{I}) = \left(\frac{1}{r}\frac{N}{|\Omega|},\ \frac{r-1}{r}\frac{N}{|\Omega|}\right)$$

is an endemic ω-periodic solution of system (13.2)–(13.3). Since system (13.2) is periodic, we may not be able to use the LaSalle invariance principle type argument to prove the global attractivity of $(\tilde{S}, \tilde{I})$. Instead, we will employ the following result, which comes from [268, Lemma 1].

Lemma 13.3.1. *Let a and b be positive constants. Assume that $\phi, \psi \in C^1([a,\infty))$, $\psi \geq 0$, and ϕ is bounded from below on $[a,\infty)$. If $\phi'(t) \leq -b\psi(t)$ and $\psi'(t) \leq K$ on $[a,\infty)$ for some positive constant K, then $\lim_{t\to\infty} \psi(t) = 0$.*

We are now in a position to prove the following threshold-type result on the global dynamics of system (13.2)–(13.3).

Theorem 13.3.2. *Assume that $\beta(x,t) = r\gamma(x,t)$ on $\overline{\Omega}\times\mathbb{R}$ for some constant $r \in (0,\infty)$. If $r < 1$, then $(N/|\Omega|, 0)$ is globally attractive for system (13.2)–(13.3); If $r > 1$, then $(\tilde{S}, \tilde{I})$ is globally attractive for system (13.2)–(13.3).*

Proof. From (13.9) and Lemma 13.1.1, it is easy to see that $\mathcal{R}_0 = r$. In the case where $r < 1$, Theorem 13.2.1 (i) implies that $(N/|\Omega|, 0)$ is globally attractive. It remains to handle the case where $r > 1$. For any given positive solution $(\overline{S}(x,t), \overline{I}(x,t))$ of (13.2)–(13.3), we follow [275] to define the function

$$H(t) := \int_\Omega \left(\overline{S}(x,t) + \frac{\tilde{S}^2}{\overline{S}(x,t)} + \overline{I}(x,t) + \frac{\tilde{I}^2}{\overline{I}(x,t)}\right) dx. \tag{13.39}$$

It then follows that

$$
\begin{aligned}
\frac{dH(t)}{dt} &= \int_\Omega (\overline{S}_t + \overline{I}_t)\,dx - \int_\Omega \left(\frac{\widetilde{S}^2 \cdot \overline{S}_t}{\overline{S}^2} + \frac{\widetilde{I}^2 \cdot \overline{I}_t}{\overline{I}^2} \right) dx \\
&= -\int_\Omega \frac{\widetilde{S}^2}{\overline{S}^2} \left(d_S \triangle \overline{S} - \frac{\beta \overline{S} \cdot \overline{I}}{\overline{S} + \overline{I}} + \gamma \overline{I} \right) dx - \int_\Omega \frac{\widetilde{I}^2}{\overline{I}^2} \left(d_I \triangle \overline{I} + \frac{\beta \overline{S} \cdot \overline{I}}{\overline{S} + \overline{I}} - \gamma \overline{I} \right) dx \\
&= H_1(t) + H_2(t),
\end{aligned}
$$

where

$$
\begin{aligned}
H_1(t) &= -\int_\Omega \left(d_S \frac{\widetilde{S}^2}{\overline{S}^2} \cdot \triangle \overline{S} + d_I \frac{\widetilde{I}^2}{\overline{I}^2} \cdot \triangle \overline{I} \right) dx \\
&= -\int_\Omega \left(\frac{2 d_S \widetilde{S}^2}{\overline{S}^3} \cdot |\nabla \overline{S}|^2 + \frac{2 d_I \widetilde{I}^2}{\overline{I}^3} \cdot |\nabla \overline{I}|^2 \right) dx
\end{aligned}
$$

and

$$
\begin{aligned}
H_2(t) &= -\int_\Omega \left\{ \left(\frac{\widetilde{I}^2}{\overline{I}^2} - \frac{\widetilde{S}^2}{\overline{S}^2} \right) \cdot \left(\frac{\beta \overline{S} \cdot \overline{I}}{\overline{S} + \overline{I}} - \gamma \overline{I} \right) \right\} dx \\
&= -\int_\Omega \left\{ \beta \overline{I} \cdot \left(\frac{\widetilde{I}^2}{\overline{I}^2} - \frac{\widetilde{S}^2}{\overline{S}^2} \right) \cdot \left(\frac{\overline{S}}{\overline{S} + \overline{I}} - \frac{1}{r} \right) \right\} dx \\
&= -\int_\Omega \left\{ \beta \overline{I} \cdot \left(\frac{\widetilde{I}^2}{\overline{I}^2} - \frac{\widetilde{S}^2}{\overline{S}^2} \right) \cdot \left(\frac{\overline{S}}{\overline{S} + \overline{I}} - \frac{\widetilde{S}}{\widetilde{S} + \widetilde{I}} \right) \right\} dx \\
&= -\int_\Omega \left\{ \beta \overline{S} \cdot \overline{I}^2 \cdot \left(\frac{\widetilde{I}^2}{\overline{I}^2} - \frac{\widetilde{S}^2}{\overline{S}^2} \right) \cdot \left(\frac{\frac{\widetilde{I}}{\overline{I}} - \frac{\widetilde{S}}{\overline{S}}}{(\overline{S} + \overline{I}) \cdot (\widetilde{S} + \widetilde{I})} \right) \right\} dx \\
&= -\int_\Omega \left\{ \frac{\beta \overline{S} \cdot \overline{I}^2}{(\overline{S} + \overline{I}) \cdot (\widetilde{S} + \widetilde{I})} \cdot \left(\frac{\widetilde{I}}{\overline{I}} + \frac{\widetilde{S}}{\overline{S}} \right) \cdot \left(\frac{\widetilde{I}}{\overline{I}} - \frac{\widetilde{S}}{\overline{S}} \right)^2 \right\} dx.
\end{aligned}
$$

Thus, we obtain

$$
\begin{aligned}
\frac{dH(t)}{dt} = -\int_\Omega \Big\{ & d_S \frac{2\tilde{S}^2}{\overline{S}^3} |\nabla \overline{S}|^2 + d_I \frac{2\tilde{I}^2}{\overline{I}^3} |\nabla \overline{I}|^2 \\
& + \frac{\beta(x,t) \overline{S}\,\overline{I}^2}{(\tilde{S} + \tilde{I})(\overline{S} + \overline{I})} \Big(\frac{\tilde{S}}{\overline{S}} + \frac{\tilde{I}}{\overline{I}} \Big) \Big(\frac{\tilde{S}}{\overline{S}} - \frac{\tilde{I}}{\overline{I}} \Big)^2 \Big\}\, dx.
\end{aligned}
$$

In view of Lemma 13.2.2 and Theorem 13.2.1 (ii), there exist positive constants C_0 and T_0 such that

$$
\frac{dH(t)}{dt} \leq -C_0 \int_\Omega \Big\{ |\nabla \overline{S}|^2 + |\nabla \overline{I}|^2 \} + \Big(\frac{\tilde{S}}{\overline{S}} - \frac{\tilde{I}}{\overline{I}} \Big)^2 \Big\}\, dx =: -\psi(t), \quad \forall t \geq T_0.
$$

By the standard Hölder regularity theory for parabolic equations (see, e.g., [126, Theorem 9]) and the embedding theorems (see, e.g., [209, Lemma II. 3.3]) (see also the proof of Theorems A1 and A2 of [39]), together with Lemma 13.2.2 and Theorem 13.2.1 (ii), it is easy to see that $\psi'(t)$ is bounded on $[T_0, \infty)$. Thus, Lemma 13.3.1 implies that $\psi(t) \to 0$ as $t \to \infty$, and hence we have

$$\lim_{t\to\infty} \int_\Omega \left(|\nabla \overline{S}|^2 + |\nabla \overline{I}|^2\right) dx = 0 \tag{13.40}$$

and

$$\lim_{t\to\infty} \int_\Omega \left|(r-1)\overline{S}(x,t) - \overline{I}(x,t)\right| dx = 0. \tag{13.41}$$

From (13.41) and (13.4), it follows that

$$\lim_{t\to\infty} \frac{1}{|\Omega|} \int_\Omega \overline{S}(x,t)dx = \tilde{S}, \quad \lim_{t\to\infty} \frac{1}{|\Omega|} \int_\Omega \overline{I}(x,t)dx = \tilde{I}. \tag{13.42}$$

Let us recall the well-known Poincaré inequality:

$$\mu_1 \int_\Omega (g-\hat{g})^2\, dx \le \int_\Omega |\nabla g|^2\, dx, \quad \forall g \in H^1(\Omega),$$

where $\hat{g} = \frac{1}{|\Omega|}\int_\Omega g(x)dx$ and μ_1 is the first positive eigenvalue of the Laplacian operator $-\Delta$ with zero Neumann boundary condition on $\partial\Omega$. As a consequence, by Hölder inequality, there holds

$$\int_\Omega |g-\hat{g}|\, dx \le \Big(\frac{|\Omega|}{\mu_1}\Big)^{1/2} \Big(\int_\Omega |\nabla g|^2\, dx\Big)^{1/2}, \quad \forall g \in H^1(\Omega).$$

This, in conjunction with (13.40) and (13.42), gives rise to

$$\lim_{t\to\infty} \int_\Omega (|\overline{S}(x,t) - \tilde{S}| + |\overline{I}(x,t) - \tilde{I}|)dx = 0. \tag{13.43}$$

Let X, $\Phi(t)$, P and Y_0 be defined as in the proof of Theorem 13.2.1. For any given $\phi \in Y_0$, let $\omega(\phi)$ be the omega-limit set of the forward orbit through ϕ for the discrete-time semiflow $\{P^n\}_{n\ge 0}$. It then follows that for any $\psi = (\psi_1, \psi_2) \in \omega(\phi)$, there exists a sequence $n_k \to \infty$ such that $\lim_{k\to\infty} P^{n_k}(\phi) = \lim_{k\to\infty} \Phi(n_k\omega)\phi = \psi$ in $X \times X$. Letting $(\overline{S}(x,t), \overline{I}(x,t)) = [\Phi(t)\phi](x)$ and $t = n_k\omega$ in (13.43), we obtain

$$\int_\Omega (|\psi_1(x) - \tilde{S}| + |\psi_2(x) - \tilde{I}|)dx = 0,$$

and so $\psi(x) \equiv (\tilde{S}, \tilde{I})$. Thus, we have $\omega(\phi) = \{(\tilde{S}, \tilde{I})\}$. This implies that $\lim_{t\to\infty} \Phi(t)\phi = (\tilde{S}, \tilde{I})$ in $X \times X$, yielding the global attractivity of $(\tilde{S}, \tilde{I})$. ∎

13.4 Discussion

In this section, we give some biological interpretations of the analytical results obtained for model (13.2)–(13.3).

Following the terminology in [9], we say that x is a low-risk site if the local disease transmission rate $\int_0^\omega \beta(x,t)dt$ is lower than the local disease recovery rate $\int_0^\omega \gamma(x,t)dt$. A high-risk site is defined in a reversed manner. We also say that Ω is a low-risk habitat if $\int_0^\omega \int_\Omega \beta(x,t)dxdt < \int_0^\omega \int_\Omega \gamma(x,t)dxdt$ and a high-risk habitat if $\int_0^\omega \int_\Omega \beta(x,t)dxdt > \int_0^\omega \int_\Omega \gamma(x,t)dxdt$. We may call the habitat a moderate-risk one if $\int_0^\omega \int_\Omega \beta(x,t)dxdt = \int_0^\omega \int_\Omega \gamma(x,t)dxdt$.

Firstly, in the ideal case where the rates of disease transmission and recovery depend on the temporal factor alone, Theorem 13.2.2 (i-a) and (ii-a) show that a low-risk habitat always leads to the extinction of the disease while a high-risk habitat leads to the persistence. In the ideal case where the rates of disease transmission and recovery depend solely on the spatial factor, it follows from Theorem 13.2.2 (ii-b) that the disease will be persistent once a high-risk habitat exists. In such a situation, however, a low-risk habitat does not always contribute to the disease eradication. Actually, this is true only when each location of the domain is low-risk. Once the habitat contains at least one high-risk site, according to Theorem 13.2.2 (i-b) and (ii-b), there exists a threshold value $d_I^* \in (0,\infty)$ such that the disease extinction happens only if the movement rate d_I of the infected population is greater than d_I^*; otherwise, if $d_I < d_I^*$, the disease will persist.

In the general situation where the rates of disease transmission and recovery depend on the spatial and temporal variables, our results assert that if either the habitat is a high-risk type or there exists at least one high-risk site and the movement of the infected population is extremely slow, then the disease will persist; see Theorem 13.2.2 (ii-c) and (ii-d). On the contrary, if the habitat is a low-risk one and the movement of the infected population is sufficiently quick, the disease will die out; see Theorem 13.2.2 (i-c).

We next discuss how the heterogeneous and time-periodic environment affects the extinction and persistence of the disease. We assume that

$$\beta(x,t) = p(x)q_1(t) \quad \text{and} \quad \gamma(x,t) = p(x)q_2(t),$$

where p is a positive Hölder continuous function on $\overline{\Omega}$ and q_1, q_2 are ω-periodic positive Hölder continuous functions on $\mathbb{R}$. If $q_1 \equiv q_2$, we get a moderate-risk habitat and Theorem 13.3.2 tells us that the disease will eventually die out regardless of the movement rates. We now assume that p is not a constant, $q_1 \not\equiv q_2$, and $\int_0^\omega q_1(t)dt = \int_0^\omega q_2(t)dt$ so that the habitat is still a moderate-risk one. By Theorem 13.1.1, we see that the basic reproduction ratio $R_0(d_I) = R_0 > 1$ for any $d_I > 0$ and $R_0(d_I) \to 1$ as either $d_I \to 0$ or $d_I \to \infty$. Therefore, Theorem 13.2.1 implies that for this moderate-risk habitat, the disease will persist.

As a consequence, our results suggest that the combination of spatial heterogeneity and temporal periodicity tends to enhance the persistence of the infectious disease for the SIS model (13.2)–(13.3). In other words, the infection risk of the model (13.2)–(13.3) would be underestimated if only temporal periodicity or spatial heterogeneity is taken into account.

Furthermore, the above discussion also shows that in the case where p is not a constant, $q_1 \not\equiv q_2$, and $\int_0^\omega q_1(t)dt = \int_0^\omega q_2(t)dt$, when the infected population migrates at the speed $d_I = \hat{d}_I$, where $\hat{d}_I > 0$ satisfies $R_0(\hat{d}_I) = \max_{d_I \in (0,\infty)} R_0(d_I) > 1$, the persistence property of the disease will be maximized; on the other hand, the small or large migration rate of the infected population will reduce the value of the basic reproduction ratio close to unity so that the persistence of the disease will be weakened.

Finally, we try to give a biological interpretation of Theorem 13.1.2. Assume that the disease has the same transmission rate at any location in the entire habitat and at any time (namely, β is a positive constant), and that the available treatment for the disease is fixed which hence indicates that $\int_0^\omega \int_\Omega \gamma(x,t)dxdt$ is a positive constant. If the treatment is made mainly in a specific part of the habitat, Theorem 13.1.2 shows that R_0 can reach its maximum. Thus, such an allocation of the treatment results in the largest risk for the control of the disease. On the other hand, R_0 will attain its minimum if the treatment is equally distributed over the entire habitat at any time. Therefore, Theorem 13.1.2 suggests that the latter treatment strategy would be more effective for the eradication of the disease.

13.5 Notes

Sections 13.1–13.4 are adapted from Peng and Zhao [277]. Here we give a new proof for Theorem 13.2.1 (i) and Theorem 13.3.1, respectively. The asymptotic profiles of steady states and global dynamics for autonomous reaction–diffusion SIS epidemic models were investigated by Allen, Bolker, Lou and Nevai [9], Peng [273], Peng and Liu [275], Huang, Han and Liu [178], Peng and Yi [276], Cui and Lou [69], Wu and Zou [413], Li, Peng and Wang [221]. Recently, Wang, Zhang and Zhao [399] also studied time-periodic traveling waves for a periodic reaction–diffusion SIR model.

14

A Nonlocal Spatial Model for Lyme Disease

Lyme disease is a worldwide vector-borne infection caused by the spirochete bacterium *Borrelia burgdorferi*, whose primary vector in North America is the black-legged tick (also known as Ixodes scapularis). The black-legged tick normally has a two-year life cycle including three feeding stages: larva, nymph, and adult. In those stages, ticks could acquire blood meals from a variety of hosts like rodents and mammals. In particular, Larvae and nymphs mainly feed on white-footed mouse *Peromyscus leucopus*, and adult ticks obtain blood meals almost exclusively from the white-tailed deer *Odocoileus virginianus* [56]. Since nymphs are too tiny (less than 2mm) to detect, humans may carry Lyme disease through the bites of infectious nymphs. For more biological discussions about the infection of Lyme disease, we refer to [29, 261, 240, 208, 382, 201] and the references therein.

To understand the invasion of Lyme disease, many mathematical modeling efforts are made through investigating the tick and host populations dynamics [180, 256, 131, 295, 231]. More specifically, Caraco et al. [57] proposed a reaction–diffusion model to study the effects of the tick's stage structure on the spatial expansion of Lyme disease in the northeast United States. The global dynamics and the spreading speed were obtained in Zhao [441] for the spatial model of [57]. To take the climate changes into account, Ogden et al. [263, 262] presented simulation models, Wu et al. [414] established a temperature-driven map of the basic reproduction number of Lyme disease in Canada, and Zhang and Zhao [427] modified the model in [57] to a reaction–diffusion system with seasonality and studied its global dynamics and propagation phenomena. Note that the spatially homogeneous environment is basically assumed in these works, but the spatial heterogeneity is also vital. Geographic variations of food resources and climates could limit the activity and the population size of ticks and hosts. Biological studies [43, 211] show that spatial patterns of the disease is highly linked to the spatial configurations coupled with dispersal by vertebrates like mice. Furthermore, there are few mathematical models incorporating the spatial variation to estimate the

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Lyme disease risk. The patch models were presented in [43, 165] to consider the tick population dynamics with the dispersal of ticks on vertebrate hosts among multiple habitats, or between woodland and pasture, both of which are based on the assumption that the interactions are homogeneous in every habitat. To formulate a continuous-time model of Lyme disease including spatially dependent parameters, Wang and Zhao [392] adapted the model of Carco et.al. [57] in the following aspects:

(a) allow a spatially dependent carrying capacity of hosts (mice), spatial-dependent diffusion rates of hosts and disease transmission coefficients;
(b) consider the influence of deers on disease transmissions;
(c) replace the random mobility of ticks in [57] with nonlocal terms to reveal the spatial movements of larvae, nymphs, and adult ticks determined by their hosts (mice or deers).

The purpose of this chapter is to modify the nonlocal spatial model in [392] by incorporating the self-regulation mechanism for the tick population, as discussed in [56], and to establish the global dynamics of the model system in terms of the basic reproduction ratio. In Section 14.1, we present the spatial model of Lyme disease and give biological interpretations of the related parameters.

In Section 14.2, we study the global dynamics of the disease-free system. We first show that the forward orbits of an associated limiting system are asymptotically compact, and the linearized system at its zero solution admits a geometrically simple eigenvalue with a positive eigenfunction. Then we use the comparison arguments and the theory of monotone and subhomogeneous system to obtain a threshold-type result on the disease-free dynamics.

In Section 14.3, we investigate the global dynamics of the full model system. We first introduce a next generation operator $\hat{F}$ and define its spectral radius as the basic reproduction ratio R_0. Then we give a computation formula of R_0 in terms of the principal eigenvalue of a nonlocal eigenvalue problem. Finally, we prove that R_0 serves as a threshold value for the global attractivity of the disease-free or endemic steady state by appealing to the theory of chain transitive sets.

14.1 The Model

We consider the Lyme disease transmission in a bounded habitat $\Omega \subset \mathbb{R}^2$ with a smooth boundary $\partial\Omega$. Let $\Gamma(t, x, y, D)$ be the Green function associated with the linear parabolic equation:

$$\begin{aligned}
\frac{\partial u}{\partial t} &= \nabla \cdot (D(x)\nabla u),\ t > 0, x \in \Omega,\\
\frac{\partial u}{\partial \nu} &= 0,\ t > 0, x \in \partial\Omega,
\end{aligned}$$

Table 14.1. Biological interpretations of parameters

r_M	Maximal individual birth rate of mice.
r	Individual birth rate of ticks.
r_h	Birth rate of deers.
μ_M	Mortality rate per mouse.
μ_L	Mortality rate per tick larva.
μ_N	Mortality rate per tick nymph.
μ_A	Mortality rate per adult tick.
μ_h	Mortality rate per deer.
α	Attack rate, juvenile ticks on mice.
γ	Attack rate, tick nymphs on humans.
ξ	Coefficient of an adult tick to attach to deers.
δ_A	Self-regulation coefficient for adult ticks.
τ_l	Feeding duration of tick larvae on mice.
τ_n	Feeding duration of tick nymphs on mice.
τ_a	Feeding duration of adult ticks on deers.
$D_M(x)$	Diffusion coefficient for mice at location x.
$D_H(x)$	Diffusion coefficient for deers at location x.
$K_M(x)$	Carrying capacity for mice at location x.
$\beta(x)$	Susceptibility to infection in mice at location x.
$\beta_T(x)$	Susceptibility to infection in ticks at location x.

where ν is the outward normal vector to $\partial\Omega$. It then follows that if a diffusive species has spatial density $\varphi(x)$ at time s, then the integral $\int_\Omega \Gamma(t-s,x,y,D)\varphi(y)dy$ gives the spatial density at time $t \geq s$ due to the diffusion.

Let $M(t,x)$ and $m(t,x)$ be the densities of susceptible and pathogen-infected mice, $L(t,x)$ be the density of questing larvae, $N(t,x)$ and $n(t,x)$ be the densities of susceptible and infectious questing nymphs, $A(t,x)$ and $a(t,x)$ be the densities of uninfected and pathogen-infected adult ticks, and $H(t,x)$ be the density of deers, at time t and location x. The parameters are shown as in Table 14.1.

In view of the attaching rates of larvae to mice and the disease transmission mechanisms in the model of [57], it follows that the drop-off rate of susceptible larvae from a mouse is

$$N_b = P_l \int_\Omega \Gamma(\tau_l,x,y,D_M)[M(t-\tau_l,y)+(1-\beta_T(y))m(t-\tau_l,y)]L(t-\tau_l,y)dy,$$

where $P_l = \alpha e^{-(\mu_L+\mu_M)\tau_l}$. The drop-off rates of infected larvae, susceptible nymphs and infected nymphs from mice can be described in a similar way. Moreover, the density of egg-laying adult ticks, that is, the drop-off rate of adult ticks from deers after blood meals is given by

$$T_b = \xi e^{-(\mu_A+\mu_h)\tau_a} \int_\Omega \Gamma(\tau_a,x,y,D_H)(A(t-\tau_a,y)+a(t-\tau_a,y))H(t-\tau_a,y)dy.$$

The per capita birth rate $B(x,u)$ of mice is taken in [392] as the negative exponential function:

$$B(x,u) = r_M \exp\left(-\frac{u}{K_M(x)}\right),$$

where $K_M(x)$ is a continuous and positive function on $\overline{\Omega}$. Unlike the model in [392], we use the linear birth rate rT_b for the tick population. Assume that the self-regulation process for adult ticks is mainly due to some density-dependent death terms and intra-competition. Then terms $\delta_A(A+a)A$ and $\delta_A(A+a)a$ represent the self-regulation for uninfected and infected adult ticks, respectively. Let $P_n = \alpha e^{-(\mu_L+\mu_M)\tau_n}$. Accordingly, the earlier model in [392] can be modified as

$$\begin{aligned}
\frac{\partial M}{\partial t} &= \nabla\cdot(D_M(x)\nabla M) + (M+m)B(x,M+m) - \mu_M M - \alpha\beta(x)Mn,\\
\frac{\partial m}{\partial t} &= \nabla\cdot(D_M(x)\nabla m) + \alpha\beta(x)Mn - \mu_M m,\\
\frac{\partial L}{\partial t} &= rT_b - \mu_L L - \alpha L(M+m),\\
\frac{\partial N}{\partial t} &= N_b - [\gamma + \alpha(M+m) + \mu_N]N,\\
\frac{\partial n}{\partial t} &= n_b - [\gamma + \alpha(M+m) + \mu_N]n,\\
\frac{\partial A}{\partial t} &= A_b - (\mu_A + \xi H)A - \delta_A(A+a)A,\\
\frac{\partial a}{\partial t} &= a_b - (\mu_A + \xi H)a - \delta_A(A+a)a,\\
\frac{\partial H}{\partial t} &= \nabla\cdot(D_H(x)\nabla H) + r_h - \mu_h H,
\end{aligned}\tag{14.1}$$

where three terms

$$\begin{aligned}
n_b &= P_l \int_\Omega \Gamma(\tau_l,x,y,D_M)\beta_T(y)m(t-\tau_l,y)L(t-\tau_l,y)dy,\\
A_b &= P_n \int_\Omega \Gamma(\tau_n,x,y,D_M)[M(t-\tau_n,y) + (1-\beta_T(y))m(t-\tau_n,y)]N(t-\tau_n,y)dy,\\
a_b &= P_n \int_\Omega \Gamma(\tau_n,x,y,D_M)[(M(t-\tau_n,y) + m(t-\tau_n,y))n(t-\tau_n,y)\\
&\qquad + \beta_T(y)m(t-\tau_n,y)N(t-\tau_n,y)]dy
\end{aligned}$$

describe the drop-off rates of infected larvae, susceptible and infected nymphs from mice, respectively.

We suppose that all constant parameters in (14.1) are positive, $D_M(x)$, $D_H(x)$ are positive and continuously differentiable on $\overline{\Omega}$, and $\beta(x)$ is a continuous function on $\overline{\Omega}$ with $0 \le \beta(x) \le 1$ but $\beta(x) \not\equiv 0$, so is $\beta_T(x)$. Further, we impose the Neumann boundary condition for M, m and H:

$$\frac{\partial M}{\partial \nu} = \frac{\partial m}{\partial \nu} = \frac{\partial H}{\partial \nu} = 0, \quad \forall t>0, x\in\partial\Omega.$$

14.2 Disease-Free Dynamics

In this section, we study the disease-free steady state and its global attractivity. Note that in the absence of infection of Lyme disease, system (14.1) reduces to

$$\begin{aligned}
\frac{\partial M}{\partial t} &= \nabla \cdot (D_M(x)\nabla M) + MB(x,M) - \mu_M M,\\
\frac{\partial L}{\partial t} &= P_a \int_\Omega \Gamma(\tau_a,x,y,D_H)A(t-\tau_a,y)H(t-\tau_a,y)dy - (\mu_L+\alpha M)L,\\
\frac{\partial N}{\partial t} &= P_l \int_\Omega \Gamma(\tau_l,x,y,D_M)M(t-\tau_l,y)L(t-\tau_l,y)dy - (\gamma+\alpha M+\mu_N)N, \quad (14.2)\\
\frac{\partial A}{\partial t} &= P_n \int_\Omega \Gamma(\tau_n,x,y,D_M)M(t-\tau_n,y)N(t-\tau_n,y)dy - (\mu_A+\xi H)A - \delta_A A^2,\\
\frac{\partial H}{\partial t} &= \nabla \cdot (D_H(x)\nabla H) + r_h - \mu_h H,
\end{aligned}$$

where $P_a = r\xi e^{-(\mu_A+\mu_h)\tau_a}$, and M and H are subject to the Neumann boundary condition:

$$\frac{\partial M}{\partial \nu} = \frac{\partial H}{\partial \nu} = 0, \quad \forall t>0, x\in\partial\Omega.$$

It is easy to see that

$$\begin{aligned}
\frac{\partial H}{\partial t} &= \nabla \cdot (D_H(x)\nabla H) + r_h - \mu_h H, \quad t>0,\ x\in\Omega,\\
\frac{\partial H}{\partial \nu} &= 0, \quad \forall t>0,\ x\in\partial\Omega
\end{aligned}$$

has a positive steady state $H^* = \frac{r_h}{\mu_h}$, which is globally asymptotically stable in $C(\overline{\Omega},\mathbb{R}_+)$. Moreover, we assume that

(H1) $r_M > \mu_M$.

By a standard convergence result on the logistic type reaction-diffusion equations (see, e.g., Theorems 2.3.4 and 3.1.6), it then follows that the following reaction-diffusion system

$$\begin{aligned}
\frac{\partial M}{\partial t} &= \nabla \cdot (D_M(x)\nabla M) + MB(x,M) - \mu_M M, \quad t>0,\ x\in\Omega,\\
\frac{\partial M}{\partial \nu} &= 0, \quad \forall t>0,\ x\in\partial\Omega
\end{aligned}$$

admits a globally asymptotically positive steady state $M^*(x)$ in $C(\overline{\Omega},\mathbb{R}_+)\backslash\{0\}$. Thus, we first study the global dynamics of the following limiting system:

$$\begin{aligned}
\frac{\partial L}{\partial t} &= P_a H^* \int_\Omega \Gamma(\tau_a,x,y,D_H)A(t-\tau_a,y)dy - [\mu_L+\alpha M^*(x)]L,\\
\frac{\partial N}{\partial t} &= P_l \int_\Omega \Gamma(\tau_l,x,y,D_M)M^*(y)L(t-\tau_l,y)dy - [\gamma+\alpha M^*(x)+\mu_N]N, \quad (14.3)\\
\frac{\partial A}{\partial t} &= P_n \int_\Omega \Gamma(\tau_n,x,y,D_M)M^*(y)N(t-\tau_n,y)dy - (\mu_A+\xi H^*)A - \delta_A A^2.
\end{aligned}$$

Let $\tau_0 = \max\{\tau_a, \tau_l, \tau_n\}$ and

$$X = C(\overline{\Omega}, \mathbb{R}^3), X_+ = C(\overline{\Omega}, \mathbb{R}^3_+),\ Y = C([-\tau_0, 0], X), Y_+ = C([-\tau_0, 0], X_+).$$

Then (X, X_+) and (Y, Y_+) are ordered Banach spaces. As usual, we identify an element $\varphi \in Y$ with a function from $[-\tau_0, 0] \times \mathbb{R}$ into $\mathbb{R}^3$ defined by $\varphi(\theta, x) = \varphi(\theta)(x)$. For any function $u \in C([-\tau_0, a), X)$ with some $a > 0$ and any $t \in [0, a)$, we define $u_t \in Y$ by $u_t(\theta) = u(t+\theta), \forall \theta \in [-\tau_0, 0]$.

Define linear semigroups $T_i(t)$, $1 \le i \le 3$, on $C(\overline{\Omega}, \mathbb{R})$ by

$$T_1(t)\phi_1 = e^{-[\mu_L + \alpha M^*(x)]t}\phi_1,\ T_2(t)\phi_2 = e^{-[\gamma + \alpha M^*(x) + \mu_N]t}\phi_2,$$

and

$$T_3(t)\phi_3 = e^{-(\mu_A + \xi H^*)t}\phi_3,$$

respectively. Let A_i^0 be the generator of $T_i(t)$. Then $T(t) = (T_1(t), T_2(t), T_3(t)) : X \to X$ is a semigroup generated by the operator $A^0 = (A_1^0, A_2^0, A_3^0)$. Define $F = (F_1, F_2, F_3) : Y \to X$ by

$$\begin{aligned}
F_1(\phi)(x) &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H)\phi_3(-\tau_a, y)dy, \\
F_2(\phi)(x) &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) M^*(y)\phi_1(-\tau_l, y)dy, \\
F_3(\phi)(x) &= P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M^*(y)\phi_2(-\tau_n, y)dy - \delta_A \phi_3^2(0, x),
\end{aligned}$$

for $x \in \overline{\Omega}$ and $\phi = (\phi_1, \phi_2, \phi_3)^T \in Y$. Then system (14.3) can be written as the following abstract functional differential equation:

$$\begin{aligned}
&\frac{du}{dt} = A^0 u + F(u_t), \quad t > 0, \\
&u_0 = \phi \in Y_+.
\end{aligned} \tag{14.4}$$

From the expression of F, we see that $F(\phi)$ is locally Lipschitz continuous on Y_+, and $F(\phi)$ is quasi-monotone on Y_+ in the sense that whenever $\phi \le \psi$ and $\phi_i(0) = \psi_i(0)$ for some $i \in \{1, 2, 3\}$, then $F_i(\phi) \le F_i(\psi)$.

In view of [243, Corollary 5], it follows that for any $\phi \in Y_+$, system (14.4) admits a unique nonnegative continuous solution

$$u(t, x, \phi) = (L(t, x, \phi), N(t, x, \phi), A(t, x, \phi))$$

on $[0, t_\phi)$ with $u(\theta, x, \phi) = \phi(\theta, x)$ for all $(\theta, x) \in [-\tau_0, 0] \times \overline{\Omega}$ and $u_t \in Y_+$ for $t \ge 0$, and the comparison principle holds for upper and lower solutions of system (14.4). Note that there exists a positive vector $\zeta = (\zeta_1, \zeta_2, \zeta_3) \in \mathbb{R}^3$ such that

$$P_a H^* \zeta_3 - \mu_L \zeta_1 = 0,\ P_l M^*_{\max}\zeta_1 - (\gamma + \mu_N)\zeta_2 = 0,\ P_n M^*_{\max}\zeta_2 - \delta_A \zeta_3^2 \le 0,$$

where $M^*_{\max} = \max_{\overline{\Omega}} M^*(x)$. Then it is easy to see that for any $k \geq 1$, $k\zeta$ is an upper solution of system (14.4). This implies that $t_\phi = \infty$ and solutions of system (14.4) are uniformly bounded. Next, we prove the asymptotic compactness of forward orbits for the solution semiflow of system (14.3).

Lemma 14.2.1. *For any $\phi \in Y_+$, the forward orbit $\gamma^+(\phi) := \{u_t(\phi) : t \geq 0\}$ for system (14.3) is asymptotically compact in the sense that for any sequence $t_n \to \infty$, there exists a subsequence $t_{n_k} \to \infty$ such that $u_{t_{n_k}}(\phi)$ converges in Y as $k \to \infty$.*

Proof. In view of the boundedness of solutions and the generalized Arzela–Ascoli theorem in Section 3.5, it is suffices to prove that the solution $u(t, x, \phi)$ is asymptotically compact in the sense that for any sequence $t_n \to \infty$, there exists a subsequence $t_{n_k} \to \infty$ such that $u(t_{n_k}, \cdot, \phi)$ converges in X as $k \to \infty$. Our arguments are motivated by [175, Lemma 4.1]. Note that for any given $\phi = (\phi_1, \phi_2, \phi_3) \in Y_+$, there exists $\eta > 0$ such that

$$|L(t, x, \phi)| \leq \eta,\ |N(t, x, \phi)| \leq \eta,\ |A(t, x, \phi)| \leq \eta, \quad \forall t \geq 0,\ x \in \overline{\Omega}.$$

In view of the Arezla-Ascoli theorem, it suffices to prove that $\{u(t_n, x, \phi)\}_{n\geq 1}$ is equicontinuous in $x \in \overline{\Omega}$ for all $n \geq 1$. We first show that $\{A(t_n, x, \phi)\}_{n\geq 1}$ is equicontinuous in $x \in \overline{\Omega}$ for all $n \geq 1$. By the uniform boundedness of $N(t, x, \phi)$, it is easy to see that

$$f(x, t) := P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M^*(y) N(t - \tau_n, y, \phi) dy$$

is uniformly continuous in $x \in \overline{\Omega}$ uniformly for $t \geq 0$, that is, $\forall \varepsilon > 0$, there exists $\delta > 0$ such that

$$|f(x_1, t) - f(x_2, t)| < \varepsilon^2, \quad \forall t \geq 0,\ x_1, x_2 \in \overline{\Omega},$$

provided that $|x_1 - x_2| < \delta$. As in the proof of [175, Lemma 4.1], we define $v_n(t, x) = A(t + t_n, x, \phi), \forall t \geq -t_n, x \in \overline{\Omega}$. Set $r := \mu_A + \xi H^* > 0$. It is easy to see that

$$\begin{aligned}
&\frac{\partial}{\partial t}[v_n(t, x_1) - v_n(t, x_2)]^2 \\
&= 2(v_n(t, x_1) - v_n(t, x_2))[f(x_1, t + t_n) - f(x_2, t + t_n) \\
&\quad -r(v_n(t, x_1) - v_n(t, x_2)) - \delta_A(v_n^2(t, x_1) - v_n^2(t, x_2))] \\
&\leq 4\eta |f(x_1, t + t_n) - f(x_2, t + t_n)| - 2r(v_n(t, x_1) - v_n(t, x_2))^2 \\
&\leq 4\eta\varepsilon^2 - 2r(v_n(t, x_1) - v_n(t, x_2))^2
\end{aligned}$$

for all $t \geq -t_n$, $|x_1 - x_2| < \delta, x_1, x_2 \in \overline{\Omega}$. By the variation of constants formula and the comparison argument, we have

$$|v_n(t, x_1) - v_n(t, x_2)|^2 \leq e^{-2r(t-s)} |v_n(s, x_1) - v_n(s, x_2)|^2 + 4\eta\varepsilon^2 \int_s^t e^{-2r(t-\theta)} d\theta,$$

for all $t \geq s \geq -t_n$. Letting $t = 0$ and $s = -t_n$ in the above inequality, we further obtain

$$|v_n(0, x_1) - v_n(0, x_2)|^2 \leq e^{-2rt_n}|v_n(-t_n, x_1) - v_n(-t_n, x_2)|^2 + \frac{2\eta\varepsilon^2}{r},$$

that is,

$$|A(t_n, x_1, \phi) - A(t_n, x_2, \phi)|^2 \leq |\phi_3(0, x_1) - \phi_3(0, x_2)|^2 + \frac{2\eta\varepsilon^2}{r},$$

for all $n \geq 1$, $|x_1 - x_2| < \delta$, $x_1, x_2 \in \overline{\Omega}$. Since $\phi_3(0, x)$ is uniformly continuous for $x \in \overline{\Omega}$, there exists $\delta_1 > 0$ such that $|\phi_3(0, x_1) - \phi_3(0, x_2))| < \varepsilon$ whenever $|x_1 - x_2| < \delta_1$. Thus, for any $|x_1 - x_2| < \delta_0 := \min\{\delta_1, \delta\}$, $x_1, x_2 \in \overline{\Omega}$, we have

$$|A(t_n, x_1, \phi) - A(t_n, x_2, \phi)|^2 \leq \varepsilon^2 + \frac{2\eta\varepsilon^2}{r} \leq (1 + \frac{2\eta}{r})\varepsilon^2.$$

Similarly, we can verify that $\{L(t_n, x, \phi)\}_{n\geq 1}$ and $\{N(t_n, x, \phi)\}_{n\geq 1}$ are also equicontinuous in $x \in \overline{\Omega}$ for all $n \geq 1$. ∎

Linearizing (14.3) at its zero solution, we obtain

$$\begin{aligned}
\frac{\partial L}{\partial t} &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H) A(t - \tau_a, y) dy - [\mu_L + \alpha M^*(x)]L, \\
\frac{\partial N}{\partial t} &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) M^*(y) L(t - \tau_l, y) dy - [\gamma + \alpha M^*(x) + \mu_N]N, \\
\frac{\partial A}{\partial t} &= P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M^*(y) N(t - \tau_n, y) dy - (\mu_A + \xi H^*)A.
\end{aligned} \tag{14.5}$$

Define an operator $A = (A_1, A_2, A_3)$ on X by

$$\begin{aligned}
A_1(\phi) &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H)\phi_3(y) dy - [\mu_L + \alpha M^*(x)]\phi_1, \\
A_2(\phi) &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) M^*(y)\phi_1(y) dy - [\gamma + \alpha M^*(x) + \mu_N]\phi_2, \\
A_3(\phi) &= P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M^*(y)\phi_2(y) dy - (\mu_A + \xi H^*)\phi_3.
\end{aligned} \tag{14.6}$$

Clearly, A is a closed and resolvent-positive operator (see, e.g., [370, Theorem 3.12]). Let $s(\tilde{A})$ be the spectral bound of an operator $\tilde{A}$, that is, $s(\tilde{A}) = \sup\{\mathrm{Re}\lambda : \lambda \in \sigma(\tilde{A})\}$, where $\sigma(\tilde{A})$ is the spectral set of $\tilde{A}$, and $\mathcal{N}(\lambda I - \tilde{A})$ and $\mathcal{R}(\lambda I - \tilde{A})$ be the null space and range space of $\lambda I - \tilde{A}$, respectively, where I is the identity operator. Then we have the following observation.

Lemma 14.2.2. *Assume that (H1) holds. Then $s(A)$ is a geometrically simple eigenvalue of A with a positive eigenfunction.*

Proof. Let $M_m^* = \min_{x\in\overline{\Omega}} M^*(x)$ and

$$c_0 := \min\{\mu_L + \alpha M_m^*, \gamma + \alpha M_m^* + \mu_N, \mu_A + \xi H^*\}.$$

For any $\phi = (\phi_1, \phi_2, \phi_3) \in \mathcal{N}(\lambda I - A)$, we have

$$\begin{aligned}
\lambda\phi_1 &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H)\phi_3(y)dy - (\mu_L + \alpha M^*(x))\phi_1, \\
\lambda\phi_2 &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) M^*(y)\phi_1(y)dy - (\gamma + \alpha M^*(x) + \mu_N)\phi_2, \quad (14.7) \\
\lambda\phi_3 &= P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M^*(y)\phi_2(y)dy - (\mu_A + \xi H^*)\phi_3.
\end{aligned}$$

For $\lambda > -c_0$, we obtain from the first and second equations of (14.7) that

$$\begin{aligned}
\phi_1(x) &= \frac{P_a H^*}{\lambda + \mu_L + \alpha M^*(x)} \int_\Omega \Gamma(\tau_a, x, y, D_H)\phi_3(y)dy, \\
\phi_2(x) &= \frac{P_l}{\lambda + \gamma + \alpha M^*(x) + \mu_N} \int_\Omega \Gamma(\tau_l, x, y, D_M) M^*(y)\phi_1(y)dy. \quad (14.8)
\end{aligned}$$

It then follows that

$$\begin{aligned}
\phi_2(x) = &\int_\Omega \Gamma(\tau_l, x, y, D_M) \frac{M^*(y)}{\lambda + \mu_L + \alpha M^*(y)} \int_\Omega \Gamma(\tau_a, y, s, D_H)\phi_3(s)dsdy \\
&\cdot \frac{P_a P_l H^*}{\lambda + \gamma + \alpha M^*(x) + \mu_N} := F(\lambda, \phi_3)(x) \quad (14.9)
\end{aligned}$$

Substituting this into the third equation of (14.7), we obtain

$$L_\lambda(\phi_3) := P_n \int_\Omega \Gamma(\tau_n, \cdot, y, D_M) M^*(y) F(\lambda, \phi_3)(y)dy - (\mu_A + \xi H^*)\phi_3 = \lambda\phi_3. \quad (14.10)$$

Let

$$G(\lambda) := (\lambda + \gamma + \alpha M_m^* + \mu_N)(\lambda + \mu_A + \xi H^*)(\lambda + \mu_L + \alpha M_m^*) - P_a P_n P_l H^* M_m^{*2}.$$

Since $G(-c_0) = -P_a P_n P_l H^* M_m^{*2} < 0$, $G(+\infty) = +\infty$, and $G(\lambda)$ is strictly increasing on $[-c_0, +\infty)$, it follows that there exists a unique $\lambda_0 \in (-c_0, \infty)$ such that $G(\lambda_0) = 0$. Note that for any $x \in \overline{\Omega}$,

$$\frac{M^*(x)}{\lambda_0 + \mu_L + \alpha M^*(x)} \geq \frac{M_m^*}{\lambda_0 + \mu_L + \alpha M_m^*},$$

and

$$\frac{M^*(x)}{\lambda_0 + \gamma + \alpha M^*(x) + \mu_N} \geq \frac{M_m^*}{\lambda_0 + \gamma + \alpha M_m^* + \mu_N}.$$

Thus, if we choose $\phi_3 \equiv 1$, then we have

$$L_{\lambda_0}(\phi_3) \geq \frac{P_a P_n P_l H^* M_m^{*2}}{(\lambda_0 + \gamma + \alpha M_m^* + \mu_N)(\lambda_0 + \mu_L + \alpha M_m^*)} - (\mu_A + \xi H^*) = \lambda_0 \phi_3.$$

Since L_λ admits a principle eigenvalue $\mu(\lambda)$, by the essentially same arguments as in [390, Theorem 2.3], it follows that $s(A)$ is a geometrically simple eigenvalue with a positive eigenfunction. ∎

Now we are in position to prove a threshold-type result on the global dynamics of system (14.2) in terms of $s(A)$.

Theorem 14.2.1. *Let (H1) hold. Then the following statements are valid:*

(i) If $s(A) < 0$, then $(M^*(x), 0, 0, 0, H^*)$ is globally attractive for positive solutions of system (14.2).
(ii) If $s(A) > 0$, then system (14.2) admits a unique positive steady state $E_0 := (M^*(x), L^*(x), N^*(x), A^*(x), H^*)$, and E_0 is globally attractive for positive solutions of system (14.2).

Proof. Note that $M^*(x)$ and H^* are globally attractive for positive solutions of the first equation and the last equation of system (14.2), respectively. By the theory of asymptotically autonomous semiflows (see, e.g., [364]), it suffices to prove the threshold-type result on the global dynamics of system (14.3). To do so, we first consider the following nonlocal evolution system without time delay:

$$\begin{aligned}
\frac{\partial L}{\partial t} &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H) A(t, y) dy - [\mu_L + \alpha M^*(x)] L, \\
\frac{\partial N}{\partial t} &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) M^*(y) L(t, y) dy - [\gamma + \alpha M^*(x) + \mu_N] N, \\
\frac{\partial A}{\partial t} &= P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M^*(y) N(t, y) dy - (\mu_A + \xi H^*) A - \delta_A A^2.
\end{aligned} \tag{14.11}$$

It then easily follows that for each $t > 0$, the time-t map of (14.11) is strongly monotone and strictly subhomogeneous on X_+. Since the linearized system of (14.11) at $(0, 0, 0)$ is

$$\begin{aligned}
\frac{\partial L}{\partial t} &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H) A(t, y) dy - [\mu_L + \alpha M^*(x)] L, \\
\frac{\partial N}{\partial t} &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) M^*(y) L(t, y) dy - [\gamma + \alpha M^*(x) + \mu_N] N, \\
\frac{\partial A}{\partial t} &= P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M^*(y) N(t, y) dy - (\mu_A + \xi H^*) A,
\end{aligned} \tag{14.12}$$

we see that A is the generator of the solution semigroup of (14.12). By Lemma 14.2.2, there exists a positive function ϕ^* such that $A\phi^* = s(A)\phi^*$, that is,

$$\begin{aligned}
s(A)\phi_1^* &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H) \phi_3^*(y) dy - (\mu_L + \alpha M^*(x)) \phi_1^*, \\
s(A)\phi_2^* &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) M^*(y) \phi_1^*(y) dy - (\gamma + \alpha M^*(x) + \mu_N) \phi_2^*, \\
s(A)\phi_3^* &= P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M^*(y) \phi_2^*(y) dy - (\mu_A + \xi H^*) \phi_3^*.
\end{aligned}$$

We first consider the case where $s(A) < 0$. For any given $\varphi \in Y$, we can choose a sufficiently large number $K > 0$ such that $-K\phi^*(x) \leq \varphi(\theta, x) \leq K\phi^*(x)$, $\forall(\theta, x) \in [-\tau_0, 0] \times \overline{\Omega}$. Let $v(t, x, \varphi)$ be the unique solution of linear system (14.5) with time delay. By the comparison principle, we obtain

$$-Kv(t, x, \phi^*) \leq v(t, x, \varphi) \leq Kv(t, x, \phi^*), \quad \forall t \geq 0,\, x \in \Omega. \tag{14.13}$$

Let $v^+(t, x) := \phi^*(x)$, $\forall t \in [-\tau_0, \infty)$, $x \in \overline{\Omega}$. It is easy to see that $v^+(t, x)$ is an upper solution of system (14.5) on $[0, \infty)$. Then the comparison principle implies that

$$0 \leq v(t, x, \phi^*) \leq v^+(t, x) = \phi^*(x), \quad \forall t \geq -\tau_0,\, x \in \Omega. \tag{14.14}$$

Let v_t be the solution semiflow of system (14.5) on Y, that is, $v_t(\varphi)(\theta) = v(t + \theta, \cdot, \varphi)$, $\forall t \geq 0$, $\theta \in [-\tau_0, 0]$. In view of (14.14) and the comparison principle again, we obtain that

$$v_{t+s}(\phi^*) = v_s(v_t(\phi^*)) \leq v_s(\phi^*) \leq \phi^*,\ \forall t, s \geq 0.$$

This implies $v_t(\phi^*)$ is nonincreasing in $t \in [0, \infty)$, and hence $v(t, x, \phi^*)$ converges, as $t \to \infty$, pointwise to some function $e(x)$ for $x \in \Omega$. Further, it follows from similar arguments to those in Lemma 14.2.1 that the bounded forward orbit $\gamma^+(\phi^*) = \{v_t(\phi^*) : t \geq 0\}$ is asymptotically compact in Y, and hence, its omega limit set $\omega(\phi^*)$ is nonempty, compact, and invariant for the solution semiflow v_t on Y. Thus, $\omega(\phi^*)=\{e\}$ with $e(x)$ being a nonnegative steady state of system (14.5). In view of (14.5) and (14.12), we know that $e(x)$ is also a steady state of system (14.12). Since $s(A) < 0$ and for any $M \in \mathbb{R}$, $Me^{s(A)t}\phi^*(x)$ is a solution of the linear system (14.12), it follows from the comparison arguments that every solution of (14.12) converges to zero, which implies that $e(x) \equiv 0$ and $\lim_{t\to\infty} v_t(\phi^*) = 0$. With (14.13), we conclude that $\lim_{t\to\infty} v_t(\varphi) = 0$. Moreover, it is easy to see that every nonnegative solution of system (14.3) satisfies

$$\begin{aligned}
\frac{\partial L}{\partial t} &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H) A(t - \tau_a, y)dy - [\mu_L + \alpha M^*(x)]L,\\
\frac{\partial N}{\partial t} &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) M^*(y) L(t - \tau_l, y)dy - [\gamma + \alpha M^*(x) + \mu_N]N,\\
\frac{\partial A}{\partial t} &\leq P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M^*(y) N(t - \tau_n, y)dy - (\mu_A + \xi H^*)A,
\end{aligned} \tag{14.15}$$

that is, every nonnegative solution of system (14.3) is a lower solution of system (14.5). Thus, the comparison principle proves statement (i).

Next we consider the case where $s(A) > 0$. Note that the solution semiflow of system (14.3) is monotone and subhomogeneous. We first show that that system (14.11) admits a globally attractive steady state $(L^*(x), N^*(x), A^*(x))$. For small $\epsilon > 0$, we consider the following linear system without time delay:

$$\begin{aligned}
\frac{\partial L}{\partial t} &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H) A(t, y) dy - [\mu_L + \alpha M^*(x)]L, \\
\frac{\partial N}{\partial t} &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) M^*(y) L(t, y) dy - [\gamma + \alpha M^*(x) + \mu_N]N, \\
\frac{\partial A}{\partial t} &= P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M^*(y) N(t, y) dy - (\mu_A + \xi H^* + \epsilon \delta_A)A.
\end{aligned} \tag{14.16}$$

Let A_ϵ be the generator of the solution semigroup of (14.16). By virtue of Lemma 14.2.2, we obtain that $s(A_\epsilon)$ is also a geometrically simple eigenvalue with a positive eigenfunction ϕ_ϵ. Note that when $\epsilon > 0$ is small enough, the spectral bound depends continuously on ϵ. It then follows that there exists a sufficiently small $\epsilon_0 > 0$ such that $s(A_{\epsilon_0}) > 0$. Let $\hat{u}(t, \cdot, \phi)$ be the solution of system (14.11) with initial data ϕ. We further prove the following two claims.

Claim 1. $\limsup_{t\to\infty} \|\hat{u}(t, \cdot, \phi)\| \geq \epsilon_0$, $\forall \phi \in X_+ \backslash \{0\}$.

For the sake of contradiction, we assume that $\limsup_{t\to\infty} \|\hat{u}(t, \cdot, \phi)\| < \epsilon_0$ for some $\phi_0 \in X_+ \backslash \{0\}$. Then there exists $t_0 > 0$ such that $\hat{u}(t, \cdot, \phi_0) < \boldsymbol{\epsilon_0} := (\epsilon_0, \epsilon_0, \epsilon_0)$, $\forall t \geq t_0$. It follows that for all $t \geq t_0$, $\hat{u}(t, \cdot, \phi_0)$ satisfies

$$\begin{aligned}
\frac{\partial L}{\partial t} &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H) A(t, y) dy - [\mu_L + \alpha M^*(x)]L, \\
\frac{\partial N}{\partial t} &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) M^*(y) L(t, y) dy - [\gamma + \alpha M^*(x) + \mu_N]N, \\
\frac{\partial A}{\partial t} &\geq P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M^*(y) N(t, y) dy - (\mu_A + \xi H^* + \epsilon_0 \delta_A)A.
\end{aligned} \tag{14.17}$$

Since $\hat{u}(t_0, \cdot, \phi_0) \gg 0$, we can choose a small real number $\rho > 0$ such that $\hat{u}(t_0, x, \phi_0) \geq \rho e^{s(A_{\epsilon_0})t_0} \phi_{\epsilon_0}(x)$, $\forall x \in \overline{\Omega}$. Note that $\rho e^{s(A_{\epsilon_0})t} \phi_{\epsilon_0}(x)$ is the solution of linear system (14.16) with $\epsilon = \epsilon_0$ and $s(A_{\epsilon_0}) > 0$. It follows from (14.17) and the comparison principle that $\hat{u}(t, x, \phi_0) \geq \rho e^{s(A_{\epsilon_0})t} \phi_{\epsilon_0}(x)$, $\forall t \geq t_0$, $x \in \overline{\Omega}$. Letting $t \to \infty$, we see that $\hat{u}(t, x, \phi_0)$ is unbounded, a contradiction to the boundedness of $\hat{u}(t, x, \phi_0)$.

Claim 2. Let $\omega(\phi)$ be the omega limit set of the forward orbit $\gamma^+(\phi) := \{\hat{u}(t, \cdot, \phi) : t \geq 0\}$. Then $\omega(\phi) \subset \text{int}(X_+)$, $\forall \phi \in X_+ \backslash \{0\}$.

By adapting the proof in Lemma 14.2.1, we see that $\gamma^+(\phi)$ is asymptotically compact, and hence, $\omega(\phi)$ is nonempty, compact, and invariant. Let $\phi \in X_+ \backslash \{0\}$ be given and $Q(t)\phi := \hat{u}(t, \cdot, \phi)$. It then follows from Claim 1 that set $A := \{0\}$ is an isolated invariant set for the semiflow $Q(t)$ and $\omega(\phi) \not\subseteq A$. Thus, the generalized Butler-McGehee lemma (see Lemma 1.2.7) implies that $\omega(\phi) \cap A = \emptyset$, and hence, $\omega(\phi) \subset X_+ \backslash \{0\}$. By the strong monotonicity of $Q(t)$ and the invariant of $\omega(\phi)$ for $Q(t)$, it follows that $\omega(\phi) \subset \text{int}(X_+)$.

Let $t_1 > 0$ be fixed. Then $Q(t_1)$ is strongly monotone and strictly subhomogeneous on $X_+\backslash\{0\}$. Note that $\omega(\phi)$ is also a compact and invariant set for Q_{t_1}. It then follows from Claim 2 and Theorem 2.3.2 with $K = \omega(\phi)$ that Q_{t_1} has a unique fixed point $u_e = (L^*(\cdot), N^*(\cdot), A^*(\cdot)) \gg 0$ such that $\omega(\phi) = \{u_e\}$, $\forall \phi \in X_+\backslash\{0\}$. Since $Q(t)\omega(\phi) = \omega(\phi)$ for all $t \geq 0$, we see that u_e is a positive steady state of system (14.11). This shows that system (14.11) admits a unique positive steady state $(L^*(x), N^*(x), A^*(x))$, which is globally attractive in $X_+\backslash\{0\}$. Clearly, $\varphi^*(x) = (L^*(x), N^*(x), A^*(x))$ is also the unique positive steady state of system (14.3). Let $\Phi(t)$ be the solution semiflow of system (14.3) on $Y_+ := C([-\tau_0, 0], X_+)$. For any given componentwise positive initial function φ, there exist two real numbers $s \in (0, 1)$ and $\rho > 1$ such that

$$s\varphi^*(x) \leq \varphi(\theta, x) \leq \rho\varphi^*(x),\ \forall \theta \in [-\tau_l, 0],\ x \in \overline{\Omega}.$$

By the comparison principle, we then have

$$s\varphi^* = s\Phi(t)\varphi^* \leq \Phi(t)(s\varphi^*) \leq \Phi(t)\varphi \leq \Phi(t)(\rho\varphi^*) \leq \rho\Phi(t)\varphi^* = \rho\varphi^* \quad (14.18)$$

for all $t \geq 0$. Thus, $\Phi(t)(s\varphi^*)$ is nondecreasing in $t \geq 0$ and $\Phi(t)(\rho\varphi^*)$ is nonincreasing in $t \geq 0$. Note that the forward orbits $\gamma^+(s\varphi^*)$ and $\gamma^+(\rho\varphi^*)$ for $\Phi(t)$ are asymptotically compact (see Lemma 14.2.1). It then follows from the uniqueness of the positive steady state that

$$\lim_{t\to\infty} \Phi(t)(s\varphi^*) = \varphi^* = \lim_{t\to\infty} \Phi(t)(\rho\varphi^*).$$

By virtue of (14.18), we obtain $\lim_{t\to\infty} \Phi(t)\varphi = \varphi^*$. This shows that statement (ii) holds true. ∎

14.3 Global Dynamics

In this section, we introduce the basic reproduction ratio for model (14.1) and study the global dynamics of Lyme disease invasion. Throughout this section, we assume that (H1) holds and $s(A) > 0$, where A is defined as in (14.6).

By Theorem 14.2.1, it follows that system (14.2) admits a globally attractive positive steady state $(M^*(x), L^*(x), N^*(x), A^*(x), H^*)$, and hence, system (14.1) has a unique disease-free steady state

$$E_1 = (M^*(x), 0, L^*(x), N^*(x), 0, A^*(x), 0, H^*).$$

Linearizing (14.1) at E_1 and then considering only the equations of infective compartments, we get

$$\begin{aligned}
\frac{\partial m}{\partial t} =&\nabla \cdot (D_M(x)\nabla m) + \alpha\beta(x)M^*(x)n - \mu_M m,\\
\frac{\partial n}{\partial t} =&P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)m(t-\tau_l, y)dy - [\gamma + \alpha M^*(x) + \mu_N]n,\\
\frac{\partial a}{\partial t} =&P_n \int_\Omega \Gamma(\tau_n, x, y, D_M)K_a^*(t-\tau_n, y)dy - [\mu_A + \xi H^* + \delta_A A^*(x)]a, \quad (14.19)
\end{aligned}$$

where m is subject to the Neumann boundary condition and

$$K_a^*(t-\tau_n,y)=M^*(y)n(t-\tau_n,y)+\beta_T(y)N^*(y)m(t-\tau_n,y).$$

Note that the third equation of system (14.19) is decoupled from the first two equations. Thus, we can simply use the first two equations to define the basic reproduction ratio for model (14.1). Let $\tilde{X}=C(\overline{\Omega},\mathbb{R}^2)$ and $\tilde{X}_+=C(\overline{\Omega},\mathbb{R}^2_+)$. We assume that the state variables are near the disease-free steady state E_1. Then we introduce infected individuals with the density distribution $\phi=(\phi_1,\phi_2)\in\tilde{X}_+$ into the population at $t=0$. As time evolves, the density distribution of the infective individuals m and n under the synthetical influences of mortality, mobility and transfer of individuals among the infected compartments is described by

$$\begin{aligned}\frac{\partial m}{\partial t}=&\nabla\cdot(D_M(x)\nabla m)-\mu_M m,\\ \frac{\partial n}{\partial t}=&-[\gamma+\alpha M^*(x)+\mu_N]n,\end{aligned}$$

where m satisfies the Neumann boundary condition. Let $(m(t,\phi),n(t,\phi))$ denote the density distribution of the infective individuals at time $t>0$. Then we have

$$\begin{aligned}m(t,\phi)(x)&=e^{-\mu_M t}\int_\Omega\Gamma(t,x,y,D_M)\phi_1(y)dy,\\ n(t,\phi)(x)&=e^{-(\gamma+\alpha M^*(x)+\mu_N)t}\phi_2(x).\end{aligned}$$

It follows that the distribution of new infections of mice produced by the infective agents at time t is

$$F_1(t,\phi)(x)=\alpha\beta(x)M^*(x)n(t,\phi)(x),$$

and the distribution of new infections of nymphs produced by the infective agents at time t is

$$F_2(t,\phi)(x)=\begin{cases}0, & \text{if } t\in(0,\tau_l),\\ P_l\int_\Omega\Gamma(\tau_l,x,y,D_M)\beta_T(y)L^*(y)m(t-\tau_l,\phi)(y)dy, & \text{if } t\geq\tau_l.\end{cases}$$

Consequently, the distribution of total new infections of mice is

$$\int_0^\infty F_1(t,\phi)dt:=\hat{F}_1(\phi),$$

and the distribution of total new infections of nymphs is

$$\int_0^\infty F_2(t,\phi)dt=P_l\int_0^\infty\int_\Omega\Gamma(\tau_l,\cdot,y,D_M)\beta_T(y)L^*(y)m(t,\phi)(y)dydt:=\hat{F}_2(\phi). \tag{14.20}$$

Clearly, $\hat{F} = (\hat{F}_1, \hat{F}_2)$ is a continuous and positive operator, which maps the initial infection distribution ϕ to the distribution of the total infective members produced during the infection period. Following the idea of next generation operators (see, e.g., [95, 389, 392]), we define $R_0 := r(\hat{F})$, the spectral radius of $\hat{F}$, for model (14.1). Direct calculations lead to

$$\hat{F}_1(\phi)(x) = \frac{\alpha\beta(x)M^*(x)}{\gamma + \alpha M^*(x) + \mu_N}\phi_2(x).$$

Define the operator B_1 by

$$B_1(\phi_1) = \nabla \cdot (D_M(x)\nabla\phi_1) - \mu_M\phi_1$$

By [370, Theorem 3.12], we have

$$\int_0^\infty m(t,\phi)dt = \int_0^\infty m(t,\phi_1)dt = -B_1^{-1}\phi_1.$$

It then follows from (14.20) that

$$\hat{F}_2(\phi)(x) = -P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)[B_1^{-1}\phi_1](y)dy.$$

To show that R_0 is a threshold value for the disease invasion, we first suppress time delays in (14.19) and then consider the following subsystem without time delay:

$$\begin{aligned}\frac{\partial m}{\partial t} =& \nabla \cdot (D_M(x)\nabla m) + \alpha\beta(x)M^*(x)n - \mu_M m,\\ \frac{\partial n}{\partial t} =& P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)m(t,y)dy - [\gamma + \alpha M^*(x) + \mu_N]n,\end{aligned} \tag{14.21}$$

where m is subject to the Neumann boundary condition. For $\phi = (\phi_1, \phi_2) \in \tilde{X}_+$, we define two operators $C = (C_1, C_2)$ by

$$\begin{aligned}C_1(\phi)(x) &= \alpha\beta(x)M^*(x)\phi_2(x),\\ C_2(\phi)(x) &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)\phi_1(y)dy,\end{aligned}$$

and $B = (B_1, B_2)$ by

$$\begin{aligned}B_1(\phi)(x) &= \nabla \cdot (D_M(x)\nabla\phi_1) - \mu_M\phi_1(x),\\ B_2(\phi)(x) &= -[\gamma + \alpha M^*(x) + \mu_N]\phi_2(x),\end{aligned}$$

and set $\mathcal{A} = C + B$. It is easy to see that the spectral bound $s(B)$ is negative.

Our next goal is to show that $R_0 - 1$ has the same sign as $s(\mathcal{A})$, and $s(\mathcal{A})$ is the principal eigenvalue of $\mathcal{A}$. To do so, we need the following assumption:

(H2) There exists some $x_0 \in \overline{\Omega}$ such that $\beta(x_0)$ and $\beta_T(x_0)$ are positive.

Biologically, this means that there exists some small region where infectious nymphs can infect mice and pathogen-infected mice can also infect ticks in return.

Lemma 14.3.1. *Let (H1) and (H2) hold. Then $R_0 - 1$ has the same sign as the spectral bound $s(\mathcal{A})$ of $\mathcal{A}$, and $s(\mathcal{A})$ is a geometrically simple eigenvalue of $\mathcal{A}$ with a positive eigenfunction.*

Proof. By [370, Theorem 3.5], we see that $s(\mathcal{A})$ has the same sign as $r(-CB^{-1}) - 1$. It suffices to show that $R_0 = r(-CB^{-1})$. Letting $T(t)$ be the solution semigroup generated by B, we then have

$$(\lambda - B)^{-1}\phi = \int_0^\infty e^{-\lambda t} T(t)\phi dt, \quad \lambda > s(B), \ \ \phi \in \tilde{X}.$$

Since $s(B) < 0$, it follows that

$$-B^{-1}\phi = \int_0^\infty T(t)\phi dt, \quad \forall \phi \in \tilde{X}. \tag{14.22}$$

As a consequence, we have

$$-B_2^{-1}\phi = \frac{1}{\gamma + \alpha M^*(x) + \mu_N}\phi_2.$$

Now, by direct calculations, we obtain

$$\begin{aligned}
C_1(-B^{-1}\phi) &= \alpha\beta(x)M^*(x)(-B_2^{-1}\phi) = \hat{F}_1(\phi),\\
C_2(-B^{-1}\phi) &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)[-B_1^{-1}\phi_1](y)dy = \hat{F}_2(\phi).
\end{aligned}$$

This implies that $-CB^{-1} = \hat{F}$, and hence $r(-CB^{-1}) = r(\hat{F}) = R_0$.

To verify $s(\mathcal{A})$ is an eigenvalue, letting $\phi = (\phi_1, \phi_2) \in \mathcal{N}(\lambda I - \mathcal{A})$, we have

$$\begin{aligned}
&\nabla \cdot (D_M(x)\nabla\phi_1) + \alpha\beta(x)M^*(x)\phi_2 - \mu_M\phi_1 = \lambda\phi_1,\\
&P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)\phi_1(y)dy - [\gamma + \alpha M^*(x) + \mu_N]\phi_2 = \lambda\phi_2.
\end{aligned} \tag{14.23}$$

For $\lambda > -(\gamma + \alpha M_m^* + \mu_N)$ with $M_m^* = \min_{x\in\overline{\Omega}} M^*(x)$, we obtain from the second equation of (14.23) that

$$\phi_2(x) = \frac{P_l}{\lambda + \gamma + \alpha M^*(x) + \mu_N}\int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)\phi_1(y)dy := \zeta(\lambda, \phi_1)(x).$$

Substituting it into the first equation of (14.23), we get

$$L_\lambda(\phi_1)(x) := \nabla \cdot (D_M(x)\nabla\phi_1) + \alpha\beta(x)M^*(x)\zeta(\lambda, \phi_1)(x) - \mu_M\phi_1(x) = \lambda\phi_1(x). \tag{14.24}$$

It easily follows from (H2) that there exists an open neighborhood $U \subset \Omega$ such that $\beta(x) > 0, \beta_T(x) > 0, \forall x \in \overline{U} \subset \Omega$. Let λ_1 be the principal eigenvalue of the elliptic eigenvalue problem

$$\begin{aligned}&\nabla \cdot (D_M(x)\nabla\phi) - \mu_M\phi = \lambda\phi, \quad x \in U,\\ &\phi = 0, \quad x \in \partial U,\end{aligned}$$

with the positive eigenfunction $\phi^*(x)$. Now define a continuous function ϕ^0 as follows:

$$\phi^0(x) = \begin{cases} \phi^*(x) & \text{if} \quad x \in \overline{U} \\ 0 & \text{if} \quad x \in \overline{\Omega} \setminus \overline{U}. \end{cases}$$

Since $\beta_T(x)L^*(x)\phi^0(x) \geq 0 (\not\equiv 0), \forall x \in \overline{\Omega}$, the standard maximum principle implies that $\int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)\phi^0(y)dy > 0$, $\forall x \in \overline{\Omega}$. Set

$$A = \min_{x\in\overline{\Omega}} P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)\phi^0(y)dy,\ \underline{\beta} = \min_{x\in\overline{U}} \beta(x),\ \phi^*_{\max} = \max_{x\in\overline{U}} \phi^*(x),$$

and

$$\begin{aligned}\lambda_0 &= \frac{\lambda_1 - (\gamma + \alpha M^*_m + \mu_N) + \sqrt{(\lambda_1 + \gamma + \alpha M^*_m + \mu_N)^2 + 4\frac{\alpha\underline{\beta}M^*_m A}{\phi^*_{\max}}}}{2}\\ &> \frac{\lambda_1 - (\gamma + \alpha M^*_m + \mu_N) + |\lambda_1 + \gamma + \alpha M^*_m + \mu_N|}{2}\\ &= \max\{\lambda_1, -(\gamma + \alpha M^*_m + \mu_N)\}.\end{aligned}$$

Clearly, $L_{\lambda_0}(\phi^0)(x) \geq \lambda_0\phi^0(x)$, $\forall x \in \Omega \setminus \overline{U}$. Moreover, for any $x \in U$, we have

$$\begin{aligned}L_{\lambda_0}(\phi^0)(x) &= \nabla \cdot (D_M(x)\nabla\phi^0) + \alpha\beta(x)M^*(x)\zeta(\lambda, \phi^0)(x) - \mu_M\phi^0(x)\\ &\geq \lambda_1\phi^*(x) + \frac{\alpha\underline{\beta}M^*_m A}{\lambda_0 + \gamma + \alpha M^*_m + \mu_N}\\ &= \lambda_1\phi^*(x) + \phi^*_{\max}(\lambda_0 - \lambda_1)\\ &\geq \lambda_1\phi^*(x) + \phi^*(x)(\lambda_0 - \lambda_1)\\ &= \lambda_0\phi^*(x) = \lambda_0\phi^0(x).\end{aligned}$$

Thus, $e^{\lambda_0 t}\phi^0(x)$ is a subsolution of the integral form of the linear system $v_t = L_{\lambda_0}u$. By the arguments similar to those in [390, Theorem 2.3 and Remark 2.1], we conclude that $s(\mathcal{A})$ is a geometrically simple eigenvalue with a positive eigenfunction. ∎

Remark 14.3.1. Let λ_1^Ω be the principal eigenvalue of the elliptic eigenvalue problem

$$\nabla \cdot (D_M(x)\nabla\phi_1) - \mu_M\phi_1(x) = \lambda\phi_1(x), \quad x \in \Omega$$

subject to the Neumann boundary condition, and $\phi_1^*(x)$ be the associated positive eigenfunction. Instead of (H2), we assume that $\lambda_1^\Omega > -(\gamma + \alpha M^*_m + \mu_N)$. It then follows that $L_{\lambda_1^\Omega}(\phi_1^*)(x) \geq \lambda_1^\Omega\phi_1^*(x)$, and hence, $s(\mathcal{A})$ is a geometrically simple eigenvalue with a positive eigenfunction (see also [390, Corollary 2.4]).

Next we characterize the basic reproduction ratio in terms of the principal eigenvalue of the following eigenvalue problem

$$\begin{aligned} & -\nabla \cdot (D_M(x)\nabla\varphi(x)) + \mu_M\varphi(x) = \mu g(\varphi)(x), \qquad x \in \Omega, \\ & \frac{\partial\varphi}{\partial\nu} = 0, \quad x \in \partial\Omega, \end{aligned} \tag{14.25}$$

where

$$g(\varphi)(x) := \frac{P_l\alpha\beta(x)M^*(x)}{\gamma + \alpha M^*(x) + \mu_N}\int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)\varphi(y)dy.$$

Theorem 14.3.1. *Let (H1) and (H2) hold. If the eigenvalue problem (14.25) admits a unique positive eigenvalue μ with a positive eigenfunction, then $R_0 = 1/\sqrt{\mu}$.*

Proof. Let $\varphi(x)$ be a positive eigenfunction associated with the positive eigenvalue μ of problem (14.25). Define

$$\phi_1 = -B_1\varphi, \quad \phi_2 = \sqrt{\mu}P_l\int_\Omega \Gamma(\tau_l, \cdot, y, D_M)\beta_T(y)L^*(y)\varphi(y)dy.$$

Clearly, $\varphi = -B_1^{-1}\phi_1$, and $\phi_1 \not\equiv 0$. In view of (14.25), we have $\frac{1}{\mu}\phi_1 = g(-B_1^{-1}\phi_1)$. It then easily follows that

$$\begin{aligned} & \frac{\alpha\beta(x)M^*(x)}{\gamma + \alpha M^*(x) + \mu_N}\phi_2 = \frac{1}{\sqrt{\mu}}\phi_1, \\ & -P_l\int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)[B_1^{-1}\phi_1](y)dy = \frac{1}{\sqrt{\mu}}\phi_2, \end{aligned} \tag{14.26}$$

that is, $\hat{F}(\phi_1, \phi_2) = \frac{1}{\sqrt{\mu}}(\phi_1, \phi_2)$. This implies that $\frac{1}{\sqrt{\mu}}$ is an eigenvalue of $\hat{F}$, and hence $R_0 = r(\hat{F}) \geq \frac{1}{\sqrt{\mu}} > 0$.

For any given $\lambda \in (0, \infty)$, we define

$$\mathcal{A}_\lambda := \frac{1}{\lambda}C + B \quad \text{and} \quad R(\lambda) := r\left(-(\frac{1}{\lambda}C)B^{-1}\right).$$

By the proof of Lemma 14.3.1, it follows that

$$R(\lambda) = \frac{1}{\lambda}R_0, \quad sign(R(\lambda) - 1) = sign\left(s(\mathcal{A}_\lambda)\right), \tag{14.27}$$

and $s(\mathcal{A}_\lambda)$ is a geometrically simple eigenvalue of $\mathcal{A}_\lambda$ with a (componentwise) positive eigenfunction ϕ_λ. Letting $\lambda = R_0 > 0$ in (14.27), we obtain $s(\mathcal{A}_{R_0}) = 0$, and hence $\psi := \phi_{R_0} = (\psi_1, \psi_2)$ satisfies $\mathcal{A}_{R_0}\psi = \frac{1}{R_0}C\psi + B\psi = 0$. It then follows that

$$\frac{P_l \alpha \beta(x) M^*(x)}{R_0^2(\gamma + \alpha M^*(x) + \mu_N)} \int_\Omega \Gamma(\tau_l, x, y, D_M) \beta_T(y) L^*(y) \psi_1(y) dy = [-B_1\psi_1](x), \tag{14.28}$$

and hence,

$$\begin{aligned} &-\nabla \cdot (D_M(x)\nabla\psi_1(x)) + \mu_M \psi_1(x) = \frac{1}{R_0^2} g(\psi_1)(x), \qquad x \in \Omega, \\ &\frac{\partial \psi_1}{\partial \nu} = 0, \quad x \in \partial\Omega. \end{aligned} \tag{14.29}$$

Since μ is the unique eigenvalue of problem (14.25) with a positive eigenfunction, it follows from (14.29) that $\mu = \frac{1}{R_0^2}$, and hence $R_0 = 1/\sqrt{\mu}$. ∎

In order to show that the sign of $R_0 - 1$ determines the global dynamics of system (14.1), we let $\mathcal{M} = M + m$, $\mathcal{N} = N + n$, $\mathcal{A} = A + a$. Then system (14.1) is equivalent to the following system:

$$\begin{aligned} \frac{\partial \mathcal{M}}{\partial t} =& \nabla \cdot (D_M(x)\nabla \mathcal{M}) + \mathcal{M} B(x, \mathcal{M}) - \mu_M \mathcal{M}, \\ \frac{\partial L}{\partial t} =& P_a \int_\Omega \Gamma(\tau_a, x, y, D_H) \mathcal{A}(t-\tau_a, y) H(t-\tau_a, y) dy - (\mu_L + \alpha\mathcal{M})L, \\ \frac{\partial \mathcal{N}}{\partial t} =& P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) \mathcal{M}(t-\tau_l, y) L(t-\tau_l, y) dy - (\gamma + \alpha\mathcal{M} + \mu_N)\mathcal{N}, \\ \frac{\partial \mathcal{A}}{\partial t} =& P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) \mathcal{M}(t-\tau_l, y) \mathcal{N}(t-\tau_l, y) dy - (\mu_A + \xi H)\mathcal{A} - \delta_A \mathcal{A}^2, \\ \frac{\partial H}{\partial t} =& \nabla \cdot (D_H(x)\nabla H) + r_h - \mu_h H, \\ \frac{\partial m}{\partial t} =& \nabla \cdot (D_M(x)\nabla m) + \alpha\beta(x)(\mathcal{M} - m)n - \mu_M m, \\ \frac{\partial n}{\partial t} =& P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) \beta_T(y) m(t-\tau_l, y) L(t-\tau_l, y) dy - (\gamma + \alpha\mathcal{M} + \mu_N)n, \\ \frac{\partial a}{\partial t} =& P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) K_a(t-\tau_n, y) dy - (\mu_A + \xi H)a - \delta_A \mathcal{A} a, \end{aligned} \tag{14.30}$$

where $\mathcal{M}$, H, and m are subject to the Neumann boundary condition, and

$$K_a(t, y) = \mathcal{M}(t, y) n(t, y) + \beta_T(y) m(t, y)(\mathcal{N}(t, y) - n(t, y)).$$

By virtue of Theorem 14.2.1, $(M^*(x), L^*(x), N^*(x), A^*(x), H^*)$ is a globally attractive steady state of system (14.2), which is exactly the same as the first five equations of system (14.30). By similar discussions to those in the last section, we may confine ourselves into

$$\begin{aligned} \frac{\partial m}{\partial t} =& \nabla \cdot (D_M(x)\nabla m) + \alpha\beta(x)(M^*(x) - m)n - \mu_M m, \\ \frac{\partial n}{\partial t} =& P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) \beta_T(y) m(t-\tau_l, y) L^*(y) dy - [\gamma + \alpha M^*(x) + \mu_N]n, \\ \frac{\partial a}{\partial t} =& P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) K_a^*(t-\tau_n, y) dy - (\mu_A + \xi H^* + \delta_A A^*(x))a, \end{aligned} \tag{14.31}$$

where m is subject to the Neumann boundary condition, and

$$K_a^*(t,y) = M^*(y)n(t,y) + \beta_T(y)m(t,y)(N^*(y) - n(t,y)).$$

Since the first two equations in (14.31) do not depend on the variable a, we first consider the following subsystem:

$$\begin{aligned}\frac{\partial m}{\partial t} =& \nabla \cdot (D_M(x)\nabla m) + \alpha\beta(x)(M^*(x) - m)n - \mu_M m,\\ \frac{\partial n}{\partial t} =& P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)m(t-\tau_l, y)L^*(y)dy - [\gamma + \alpha M^*(x) + \mu_N]n.\end{aligned} \tag{14.32}$$

Let $\mathbb{C}_{M^*} = \{\varphi \in C(\overline{\Omega}, \mathbb{R}_+) : \varphi(x) \leq M^*(x),\ \forall x \in \overline{\Omega}\}$, and

$$\mathcal{X} := C([-\tau_l, 0], \mathbb{C}_{M^*}) \times C(\overline{\Omega}, \mathbb{R}_+).$$

Note that

$$\nabla \cdot (D_M(x)\nabla M^*) - \mu_M M^*(x) = -r_M M^*(x) \exp\left(-\frac{M^*(x)}{K_M(x)}\right) \leq 0.$$

By [243, Corollary 4], it then follows that for any $\phi \in \mathcal{X}$, system (14.32) admits a unique mild solution $\hat{v}(t,\cdot,\phi) = (\hat{v}_1(t,\cdot,\phi), \hat{v}_2(t,\cdot,\phi))$ on $[0,\infty)$ with $\hat{v}_1(\theta,\cdot,\phi) = \phi_1(\theta)$, $\hat{v}_2(0,\cdot,\phi) = \phi_2$, $\forall \theta \in [-\tau_l, 0]$, and $(\hat{v}_{1t}(\phi), \hat{v}_2(t,\cdot,\phi)) \in \mathcal{X}$ for all $t \geq 0$. Note that system (14.32) is eventually strongly monotone and strictly subhomogeneous on $\mathcal{X}$. It is also easy to see that there exists a real number $B_0 > 0$ such that $(M^*(x), B)$ is an upper solution of system (14.32) for any constant $B \geq B_0$. By Lemma 14.3.1 and similar arguments to those for system (14.3) in Theorem 14.2.1, with $\rho\varphi^*$ replaced by $(M^*(x), B)$, we have the following result for system (14.32).

Lemma 14.3.2. *Assume that (H1) and (H2) hold and $s(A) > 0$. Then the following statements are valid:*

(i) If $R_0 < 1$, then $(0,0)$ is globally attractive for system (14.32) in $\mathcal{X}$.
(ii) If $R_0 > 1$, then system (14.32) admits a positive steady state $(\bar{m}(x), \bar{n}(x))$ which is globally attractive in $\mathcal{X}\backslash\{0\}$.

Now we are ready to prove the main result of this section on the global dynamics of system (14.1) on $W := C([-\tau_0, 0], C(\overline{\Omega}, \mathbb{R}_+^8))$.

Theorem 14.3.2. *Assume that (H1) and (H2) hold and $s(A) > 0$. Then the following statements are valid:*

(i) If $R_0 < 1$, then every positive solution $U(t,x)$ of system (14.1) satisfies $lim_{t\to\infty} U(t,x) = (M^*(x), 0, L^*(x), N^*(x), 0, A^*(x), 0, H^*)$ uniformly for $x \in \overline{\Omega}$.
(ii) If $R_0 > 1$, then system (14.1) admits a positive steady state $U^*(x) = (M^*(x) - \bar{m}(x), \bar{m}(x), L^*(x), N^*(x) - \bar{n}(x), \bar{n}(x), A^*(x) - \bar{a}(x), \bar{a}(x), H^*)$, and every positive solution $U(t,x)$ satisfies $lim_{t\to\infty} U(t,x) = U^*(x)$ uniformly for $x \in \overline{\Omega}$.

Proof. Let

$$E := \left\{(\phi_1, \ldots, \phi_7) \in C([-\tau_0, 0], C(\overline{\Omega}, \mathbb{R}^7_+)) : \ \phi_1(\theta) \geq \phi_6(\theta), \forall \theta \in [-\tau_0, 0]\right\}.$$

Since the first seven equations in (14.30) do not depend on variable a, it follows that for each $\phi \in E$, this subsystem admits a unique mild solution $w(t, x, \phi)$ satisfying $w(\theta, x, \phi) = \phi(\theta, x)$ for all $(\theta, x) \in [-\tau_0, 0] \times \overline{\Omega}$. For each $t \geq 0$, define

$$[\Psi(t)\phi](\theta) = w(t + \theta, \cdot, \phi), \ \forall \theta \in [-\tau_0, 0], \, \phi \in E.$$

Then $\Psi(t)$ is an autonomous semiflow on E. Let

$$w(t, x, \phi) = (\mathcal{M}(t, x), L(t, x), \mathcal{N}(t, x), \mathcal{A}(t, x), H(t, x), m(t, x), n(t, x))$$

be a given positive solution. In view of Theorem 14.2.1, we have

$$\lim_{t\to\infty} (\mathcal{M}(t, x), L(t, x), \mathcal{N}(t, x), \mathcal{A}(t, x), H(t, x)) = (M^*(x), L^*(x), N^*(x), A^*(x), H^*)$$

uniformly for $x \in \overline{\Omega}$. By the generalized Arzela–Ascoli theorem and similar arguments to those in [175, Lemma 5.2]), it follows that the forward orbit $\gamma^+(\phi) := \{\Psi(t)\phi \, : \, t \geq 0\}$ is asymptotically compact in E. Thus, its omega limit set $\omega(\phi)$ is a compact, invariant, and internally chain transitive set for the semiflow $\Psi(t)$ (see Lemma 1.2.1′). It easily follows that

$$\omega(\phi) = \{(M^*(\cdot), L^*(\cdot), N^*(\cdot), A^*(\cdot), H^*)\} \times \tilde{\omega},$$

where $\tilde{\omega}$ is a subset of $S := C([-\tau_0, 0], \mathbb{C}_{M^*} \times C(\overline{\Omega}, \mathbb{R}_+))$. Further, $\tilde{\omega}$ is a compact, invariant, and internally chain transitive set for the solution semiflow generated by system (14.32) on S. In the case where $R_0 < 1$, Lemma 14.3.2, Theorem 1.2.1, and Remark 1.3.2 imply that $\tilde{\omega} = (0, 0)$, and hence, $\omega(\phi) = (M^*(\cdot), L^*(\cdot), N^*(\cdot), A^*(\cdot), H^*, 0, 0)$.

In the case where $R_0 > 1$, it follows from Lemma 14.3.2 and Theorem 1.2.2 and Remark 1.3.2 that either $\tilde{\omega} = (0, 0)$ or $\tilde{\omega} = (\bar{m}(\cdot), \bar{n}(\cdot))$, and hence, either $\omega(\phi) = (M^*(\cdot), L^*(\cdot), N^*(\cdot), A^*(\cdot), H^*, 0, 0)$ or $\omega(\phi) = (M^*(\cdot), L^*(\cdot), N^*(\cdot), A^*(\cdot), H^*, \bar{m}(\cdot), \bar{n}(\cdot))$.

For small $\epsilon > 0$, we consider the following linear system without time delay:

$$\begin{aligned}
\frac{\partial m}{\partial t} =& \nabla \cdot (D_M(x) \nabla m) + \alpha\beta(x)(M^*(x) - 2\epsilon)n - \mu_M m, \\
\frac{\partial n}{\partial t} =& P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)(L^*(y) - \epsilon)m(t, y)dy - [\gamma + \alpha(M^*(x) + \epsilon) + \mu_N]n.
\end{aligned} \tag{14.33}$$

Let A_ϵ denote the generator of the solution semigroup of (14.33). By repeating the arguments of Lemma 14.3.1, we see that $s(A_\epsilon)$ is a geometrically simple eigenvalue A_ϵ with a positive eigenfunction. Since the spectral bound depends continuously on ϵ, we can fix an $\epsilon_0 > 0$ small enough so that $s(A_{\epsilon_0}) > 0$. Let ϕ_{ϵ_0} be a positive eigenfunction ϕ_{ϵ_0} associated with $s(A_{\epsilon_0})$.

Suppose, by contradiction, that $\omega(\phi) = (M^*(\cdot), L^*(\cdot), N^*(\cdot), A^*(\cdot), H^*, 0, 0)$, then $\lim_{t\to\infty}(m(t,x), n(t,x)) = (0,0)$ uniformly for $x \in \bar{\Omega}$. Without loss of generality, we can assume that for the above fixed ϵ_0, $|(m(t,x), n(t,x))| < \epsilon_0$ and

$$|(\mathcal{M}(t,x), L(t,x), \mathcal{N}(t,x), \mathcal{A}(t,x), H(t,x)) - (M^*(x), L^*(x), N^*(x), A^*(x), H^*)| < \epsilon_0$$

for all $t \geq 0$ and $x \in \bar{\Omega}$. Hence, for any $t \geq 0$, we have

$$\begin{aligned} \frac{\partial m}{\partial t} \geq & \nabla \cdot (D_M(x)\nabla m) + \alpha\beta(x)(M^*(x) - 2\epsilon_0)n - \mu_M m, \\ \frac{\partial n}{\partial t} \geq & P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)(L^*(y) - \epsilon_0)m(t-\tau_l, y)dy \\ & - [\gamma + \alpha(M^*(x) + \epsilon_0) + \mu_N]n. \end{aligned} \tag{14.34}$$

Consider the linear time-delayed evolution system:

$$\begin{aligned} \frac{\partial m}{\partial t} = & \nabla \cdot (D_M(x)\nabla m) + \alpha\beta(x)(M^*(x) - 2\epsilon_0)n - \mu_M m, \\ \frac{\partial n}{\partial t} = & P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)(L^*(y) - \epsilon_0)m(t-\tau_l, y)dy \\ & - [\gamma + \alpha M^* + \epsilon_0\alpha + \mu_N]n. \end{aligned} \tag{14.35}$$

For any $\varphi \in C([-\tau_0, 0], C(\overline{\Omega}, \mathbb{R}^2))$, let $\hat{w}(t, x, \varphi)$ be the unique mild solution of system (14.35) on $[0, \infty)$ with $\hat{w}(\theta, x, \varphi) = \phi(\theta, x)$ for all $(\theta, x) \in [-\tau_0, 0] \times \overline{\Omega}$. Let

$$v^-(t,x) := \phi_{\epsilon_0}(x), \quad \forall t \in [-\tau_0, \infty),\ x \in \overline{\Omega}.$$

Since $s(A_{\epsilon_0}) > 0$, it is easy to see that $v^-(t,x)$ is a lower solution of system (14.35) on $[0, \infty)$. Then the comparison principle implies that

$$0 \leq \phi_{\epsilon_0}(x) = v^-(t,x) \leq \hat{w}(t, x, \phi_{\epsilon_0}), \quad \forall t \geq -\tau_0,\ x \in \Omega. \tag{14.36}$$

Let $\hat{w}_t$ be the solution semiflow associated with system (14.35). It then follows from (14.36) that $\phi_{\epsilon_0} \leq \hat{w}_t(\phi_{\epsilon_0})$, $\forall t \geq 0$. By the comparison principle again, we obtain

$$\hat{w}_s(\phi_{\epsilon_0}) \leq \hat{w}_s(\hat{w}_t(\phi_{\epsilon_0})) = \hat{w}_{t+s}(\phi_{\epsilon_0}),\ \forall t, s \geq 0.$$

This implies that $\hat{w}_t(\phi_{\epsilon_0})$ is nondecreasing in $t \in [0, \infty)$. We further claim that the solution $\hat{w}(t, x, \phi_{\epsilon_0})$ is unbounded. Otherwise, the forward orbit $\gamma^+(\phi_{\epsilon_0})$ for the semiflow $\hat{w}_t$ is asymptotically compact. It then follows that its omega limit set $\omega(\phi_{\epsilon_0}) = e^*$, where $e^*(x)$ is a positive equilibrium of system (14.35). Clearly, $e^*(x)$ is also a positive equilibrium of linear system (14.33) with $\epsilon = \epsilon_0$. On the other hand, since $s(A_{\epsilon_0}) > 0$ and $e^{s(A_{\epsilon_0})t}\phi_{\epsilon_0}(x)$ is a solution of the linear system (14.33) with $\epsilon = \epsilon_0$, it follows from the comparison arguments that every positive solution of system (14.33) with $\epsilon = \epsilon_0$ is unbounded, and hence, system (14.33) with $\epsilon = \epsilon_0$ admits no positive equilibrium. This contradiction shows that the solution $\hat{w}(t, x, \phi_{\epsilon_0})$ is unbounded. Now we choose a sufficiently small number $\delta > 0$ such that

$$(m(\theta, x), n(\theta, x)) \geq \delta\phi_{\epsilon_0}(x), \quad \forall\theta \in [-\tau_0, 0] \times \overline{\Omega}.$$

In view of (14.34) and the comparison principle, we then have

$$(m(t, x), n(t, x)) \geq \delta\hat{w}(t, x, \phi_{\epsilon_0}), \quad \forall t \geq 0,\, x \in \overline{\Omega}.$$

This implies that $(m(t, x), n(t, x))$ is unbounded, which contradicts the uniform convergence of $(m(t, x), n(t, x))$ to $(0, 0)$ on $\bar{\Omega}$, as $t \to \infty$. Thus, $\omega(\phi) = (M^*, L^*, N^*, A^*, H^*, \bar{m}(\cdot), \bar{n}(\cdot))$.

By the theory of asymptotically autonomous semiflows (see [364]), as applied to the last equation in (14.30), it easily follows that that $\lim_{t\to\infty} a(t, \cdot) = 0$ in the case where $R_0 < 1$, and $\lim_{t\to\infty} a(t, \cdot) = \bar{a}(\cdot)$ in the case where $R_0 > 1$.

It remains to prove the positivity of the steady state of model (14.1) in the case where $R_0 > 1$. It suffices to prove that $\overline{M}(x) := M^*(x) - \bar{m}(x) > 0, \forall x \in \overline{\Omega}$. Clearly, we have $M^*(x) \geq \bar{m}(x), \forall x \in \overline{\Omega}$. In view of the integral form of the following equation

$$\begin{aligned}
\frac{\partial M}{\partial t} &= \nabla \cdot (D_M(x)\nabla M) + M^*B(x, M^*) - (\mu_M + \alpha\beta(x)\bar{n}(x))\, M,\ x \in \Omega,\ t > 0,\\
\frac{\partial M}{\partial \nu} &= 0, \quad x \in \partial\Omega,\ t > 0,
\end{aligned}$$

we have

$$\begin{aligned}
\overline{M}(x) = {}& e^{-(\mu_M+\alpha\beta(x)\bar{n}(x))t} \int_\Omega \Gamma(t, x, y, D_M)\overline{M}(y)dy +\\
& \int_0^t e^{-(\mu_M+\alpha\beta(x)\overline{n}(x))(t-s)} \int_\Omega \Gamma(t-s, x, y, D_M)M^*(y)B(y, M^*(y))dyds,
\end{aligned}$$

for all $t \geq 0$. By the standard maximum principle (see, e.g., [326, Theorem 7.2.2 and Corollary 7.2.3]), it easily follows that $\overline{M}(x) > 0, \forall x \in \overline{\Omega}$. Thus, a straightforward computation shows that

$$\begin{aligned}
N^*(x) - \bar{n}(x) &= \frac{P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\tilde{K}_N(y)dy}{\gamma + \alpha M^*(x) + \mu_N}, \quad x \in \overline{\Omega}\\
A^*(x) - \bar{a}(x) &= \frac{P_n \int_\Omega \Gamma(\tau_n, x, y, D_M)\tilde{K}_A(y)dy}{\mu_A + \xi H^* + \delta_A A^*(x)}, \quad x \in \overline{\Omega}
\end{aligned}$$

with

$$\begin{aligned}
\tilde{K}_N(y) &= [M^*(y) - \beta_T(y)\bar{m}(y)]L^*(y),\\
\tilde{K}_A(y) &= [M^*(y) - \beta_T(y)\bar{m}(y)](N^*(y) - \bar{n}(y)).
\end{aligned}$$

Since $0 \leq \beta_T(y) \leq 1$, it follows that $\tilde{K}_N(y) > 0, \forall y \in \overline{\Omega}$, and hence, $N^*(x) - \bar{n}(x) > 0$, and $\tilde{K}_A(x) > 0$, $\forall x \in \overline{\Omega}$. Thus, we obtain $A^*(x) - \bar{a}(x) > 0$ for all $x \in \overline{\Omega}$. ∎

Remark 14.3.2. The results in Sections 14.2 and 14.3 are still valid if we take a general per capita birth rate function $B(x,u)$ satisfying the following conditions:

(D1) $B(x,u) \geq 0(\not\equiv 0)$, $\quad \forall (x,u) \in \overline{\Omega} \times [0,+\infty)$.
(D2) $B(x,u)$ is continuous on $\overline{\Omega} \times [0,+\infty)$ and strictly decreasing in $u \in [0,\infty)$, and $B(x,u_0) \leq 0$ on $\overline{\Omega}$ for some $u_0 > 0$.
(D3) There exists $M > 0$ such that $\frac{1}{|\Omega|}\int_\Omega B(x,0)dx > \mu_M > B(x,u)$ for all $u > M$ and $x \in \overline{\Omega}$.

It is easy to see that the birth rate function $B(x,u) = r_M \exp\left(-\frac{u}{K_M(x)}\right)$ satisfies (D1)–(D3). Another prototypical birth rate function (see, e.g., [57, 389]) is

$$B(x,u) = \begin{cases} r_M\left(1 - \dfrac{u}{k_M(x)}\right), & 0 \leq u \leq K_M(x),\ x \in \overline{\Omega}, \\ 0, & u > K_M(x),\ x \in \overline{\Omega}. \end{cases}$$

14.4 Notes

This chapter is modified from Yu and Zhao [423], where the spreading speed and traveling waves were also studied for the limiting system (14.32) in an unbounded habitat. The nonlocal terms in system (14.1) were first introduced by Wang and Zhao [392] for another spatial model of Lyme disease. The comparison arguments via linear systems without time delay in the proof of Theorem 14.2.1 were developed in [392, Proposition 3.7], and the lifting method using the theory of chain transitive sets in the proof of Theorem 14.3.2 was illustrated in [392, Theorem 3.8]. Here we give a new proof for Theorem 14.3.1, which is different from that of [392, Corollary 3.2].

The numerical results in [423] show that the spatial averaged system would underestimate the disease risk, that both self-regulation mechanism of ticks and random movements of mice would alleviate the infection, but random movements of deers would take no evident effect, and that the carrying capacity of mice with strong spatial heterogeneity would increase the infection risk. Moreover, the intensive self-regulation of ticks would force the disease to spread more slowly and even to go extinct, and cooling down the random movements of mice could deteriorate the infection locally, but this might slow down the invasion of the disease in a large area.

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