GLOBAL DYNAMICS IN A CHEMOSTAT AND AN EPIDEMIC MODEL

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by

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A Thesis Submitted to the

School of Graduate Studies

in partial fulfillment of the

requirements for the degree of

Master of Science

Department of Mathematics and Statistics

Memorial University of Newfoundland

March 2008

St. John's, Newfoundland, Canada

ABSTRACT

Two models are studied in this work; a periodically forced Droop model for phytoplankton growth with two competing species in a chemostat and a time-delayed SIR epidemic model with dispersal.

For the competition model, both uniform persistence and the existence of periodic coexistence state are established for a periodically forced Droop model on two phytoplankton species competition in a chemostat under some appropriate conditions. Numerical simulations using biological data are presented as well to illustrate the main result.

The global dynamics of a time-delayed model with population dispersal between two patches is also investigated. For a general class of birth functions, persistence theory is applied to prove that a disease is persistent when the basic reproduction number is greater than one. It is also shown that the disease will die out if the basic reproduction number is less than one, provided that the invasion intensity is not strong. Numerical simulations are presented using some typical birth functions

from biological literature to illustrate the main ideas and the relevance of dispersal.

ACKNOWLEDGEMENTS

I would like to thank my supervisor Dr. Xiaoqiang Zhao for his guidance and instruction throughout my masters program. His insights and suggestions were essential in the development of my thesis. I'm especially grateful for the time he spent reading my work and helping me to improve upon it.

I would also like to thank the many professors in the Department of Mathematics and Statistics who have instructed me over the years and guided my education in mathematics.

Finally, I would like to thank my family and friends for their encouragement throughout my studies. In particular, my sincere thanks goes to Shannon Sullivan who assisted me in formatting this thesis.

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1. INTRODUCTION

This thesis is a study of two models using dynamical systems theory. One is the periodic Droop model for phytoplankton growth in a lake environment; two species competing for nutrients is the main consideration here. The other is an epidemic model where the population can travel between patches (e.g. cities, countries, etc) and a time delay is incorporated to better describe the length of time that an infected person is infectious. The application of persistence theory to each of these is the common thread in this work.

The main concepts in this thesis are uniform persistence and basic reproduction numbers. In biological terms, uniform persistence means that the size of a population or another important biological quantity will not decrease to zero over time. This is a very useful result because the possibility of extinction is an important characteristic of a biological model. This is true in the case of population models where extinction is typically not the desired outcome and in the case of epidemic models where extinction of the disease is the best case. The basic reproduction of an epidemic model is a very

important threshold-type value; it is the expected number of new infections caused by one typical infected person. This means that when this quantity is less than one, the disease will die out in the long term and when it is greater than one, the infection will be persistent.

A typical goal in the application of dynamical systems theory to a real-life problem is to determine conditions under which biologically relevant states are globally asymptotically stable. This is often difficult to prove for nonlinear systems as the dimension becomes higher or the equations become more complicated, which is a consequence of analyzing more realistic mathematical models. Uniform persistence is not as strong but its application still provides us with important information: the conditions under which biologically important quantities will remain positive for all time. From a mathematical viewpoint, this is another type of global analysis since, like global asymptotic stability, it applies to all solutions in our defined interior. From the theory of persistence we also have that uniform persistence implies the existence of a coexistence state inside an interior global attractor, which is a very nice result in applications.

This thesis is organized in the following way. In chapter two, important definitions and theorems are provided for each of the following chapters. Next, the periodic Droop model is described with reference to earlier works. Conditions under which

uniform persistence is guaranteed are established and simulations are presented to illustrate the coexistence phenomena. Finally, chapter 4 is devoted to the time-delayed epidemic model with dispersal. The prior work where this was first studied is reviewed, including the derivation of the time-delay model. The generalization of the earlier results, including the case when the infected population is persistent, are proven and simulations are given to explore the effect of dispersal on the spread of infections.

2. PRELIMINARIES

In this thesis, there are many definitions and theory that are needed in the following chapters. Some of these are not very well known so the purpose of this section is to set the framework for the results that are derived and proved in the remainder of this work. Many of these are found in a more abstract setting and, as such, are usually only found in some published papers. In that way, this section also serves as an overview of the work that precedes and motivates the topics in this thesis.

First we need to define what is meant by a periodic semiflow (see [26]).

Definition 2.1 *Let X be a complete metric space with metric d, and let $p > 0$. A family of mappings $T(t) : X \to X$, $t \geq 0$, is called a p-periodic semiflow on X if it has the following properties:*

(1) $T(0) = I$, where I is the identity on X;

(2) $T(t+p) = T(t) \circ T(p)$, $\forall t \geq 0$;

(3) $T(t)x$ is continuous in $(t, x) \in [0, \infty) \times X$.

This a natural step from the definition of an autonomous semiflow. If property

(2) holds for *any* $p > 0$ rather than a fixed period, then $T(t)$ is called an autonomous semiflow.

Next we recall the definition of a Poincaré map.

Definition 2.2 *Let $T(t)$ be a p-periodic semiflow on a complete metric space X. Then $P := T(p)$ is called the Poincaré (or period) map associated with $T(t)$.*

Note that the existence, uniqueness and stability of the fixed points of a period map are equivalent to those of the $p-$periodic solutions of its associated periodic semiflow.

We will now give a precise mathematical definition of uniform persistence (see [26]). For the following definitions, we assume that X is a complete metric space. Let $f : X \to X$ be a continuous map and $X_0 \subset X$ be an open set. Define $\partial X_0 := X \setminus X_0$ and $M_\partial = \{x \in \partial X_0 : f^n(x) \in \partial X_0,\ n \geq 0\}$.

Definition 2.3 *A map $f : X \to X$ is said to be uniformly persistent with respect to X_0 if there exists an $\eta > 0$ such that*

$$\liminf_{n\to\infty} d(f^n(x), \partial X_0) \geq \eta \ \text{ for all } x \in X_0.$$

Here, the ∂X_0 is not to be confused with the boundary of X. In applications, ∂X_0 will often be only a part of the boundary because usually we are concerned with

quantities such as population remaining positive for all time. For continuous-time dynamical systems, there is an analogous definition.

Definition 2.4 *A periodic semiflow $T(t) : X \to X$ is said to be uniformly persistent with respect to X_0 if there exists an $\eta > 0$ such that*

$$\liminf_{t\to\infty} d(T(t)x, \partial X_0) \geq \eta \text{ for all } x \in X_0.$$

Persistence theory is a well-developed area of dynamical systems research and, as such, there are many theorems for establishing that property in a variety of settings and for many types of equations. We will make use of one in particular that shows that the set ∂X_0 is repelling. First, however, we need a few more concepts.

Definition 2.5 *A continuous mapping $f : X \to X$ is said to be point dissipative if there is a bounded set B_0 in X such that B_0 attracts each point in X.*

We remark that point dissipative and ultimately bounded are equivalent. The following are discrete-time and continuous-time results for the existence of a global attractor.

Lemma 2.6 *If $f : X \to X$ is completely continuous and point dissipative, then there is a connected global attractor A that attracts each bounded set in X.*

Lemma 2.7 *If there is a $t_1 \geq 0$ such that the semiflow $T(t) : X \to X$ is completely continuous for $t > t_1$ and point dissipative, then there is a global attractor A that attracts each bounded set in X.*

Definition 2.8 *Let $f : X \to X$ and $B \subset X$ be a nonempty invariant set. B is called internally chain transitive if the following condition holds: for $a, b \in B$ and any $\epsilon > 0$, there is a finite sequence $x_1, \cdots, x_m$ $(m > 1)$ in B with $x_1 = a, x_m = b$ such that $d(f(x_i), x_{i+1}) < \epsilon,\ 1 \leq i \leq m-1$.*

A natural example of an internally chain transitive is the omega limit set of any precompact (i.e., its closure is compact) positive orbit. The proof of this is given in [26]. The notation $\omega(x)$ will be used throughout this work to denote the omega limit set of a point x. With that, we now state the theorem on strong repellers, which is important in this thesis.

Theorem 2.9 *Assume that*

(C1) $f(X_0) \subset X_0$ and f has global attractor A;

(C2) There exists a finite sequence $\mathbb{M} = \{M_1, \cdots, M_k\}$ of disjoint, compact and isolated invariant sets in ∂X_0 such that

(1) $\cup_{x \in M_\partial} \omega(x) \subset \cup_{i=1}^{k} M_i$;

(2) no subset of $\mathbb{M}$ forms a cycle in ∂X_0;

(3) M_i is isolated in X;

(4) $W^s(M_i) \cap X_0 = \emptyset$ for each $1 \leq i \leq k$. Then there exists a $\delta > 0$ 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 $\inf_{x \in L} d(x, \partial X_0) > \delta$.

In our application of this theorem, we take $L = \omega(x)$ for any $x \in X_0$. As a direct consequence, the map f is uniformly persistent with respect to X_0. It is natural to expect that under uniform persistence there will also be a fixed point in X_0. The following theorem from [26] gives the conditions under which this is true.

Theorem 2.10 *Assume that X is a closed subset of a Banach space E, and that X_0 is a convex and relatively open subset in X. Let $f : X \to X$ be a continuous map with $f(X_0) \subset X_0$. Assume that*

(1) $f : X \to X$ is point dissipative;

(2) f is completely continuous;

(3) f is uniformly persistent with respect to X_0.

Then there exists a global attractor A_0 for f in X_0 that attracts strongly bounded sets in X_0, and f has a fixed point $x_0 \in A_0$.

These theorems have continuous-time analogues for the most part but, since the chemostat model has a periodic forcing term for its nutrient inflow, we will use the

period or Poincaré map extensively in the analysis of the model. The following theorem (from [26]) gives the conditions under which uniform persistence of a given periodic semiflow is equivalent to that of its associated Poincaré map.

Theorem 2.11 *Let $T(t)$ be an $p-$periodic semiflow on X with $T(t)X_0 \subset X_0$, $\forall t \geq 0$. Assume that $P = T(p)$ satisfies the following conditions:*

(1) P is point dissipative in X;

(2) P is compact.

Then uniform persistence of P with respect to X_0 implies that of $T(t) : X \to X$.

The following Lemma comes from [17, Proposition 1.1], which is used for a single-species model in a chemostat.

Lemma 2.12 *Assume $S^*(t)$ is a non-negative $p-$periodic function and suppose that $Q(t) \geq Q_{min} > 0$, $\forall t \geq 0$. We further assume that the functions $\mu(Q)$ and $\rho(S, Q)$ have the following properties*

(1) $\mu(Q_{min}) = 0, \quad \mu'(Q) > 0, \quad \forall Q \geq Q_{min}$;

(2) $\rho(0, Q) = 0, \quad \frac{\partial \rho}{\partial S} > 0, \quad \frac{\partial \rho}{\partial Q} \leq 0.$

Then the equation $Q' = \rho(S^*(t), Q) - \mu(Q)Q$ has a unique $p-$periodic solution $Q^*(t)$ to which all solutions are attracted.

In addition, with more than one species in the chemostat, the following theorem

from [26] is useful.

Theorem 2.13 *Let P be the Poincaré map associated with the $p-$periodic system $u_i' = f_i(t,u) = f_i(t+p,u)$, $1 \leq i \leq n$, where $u = (u_1, \cdots, u_n) \in \mathbb{R}^n_+$ and $f = (f_1, \cdots, f_n)$ is continuous. Assume that there exists some $1 \leq i \leq n$ and a continuous $p-$periodic function $F_i(t,u)$ such that $f_i(t,u) \geq u_i F_i(t,u)$, $\forall t \geq 0$, $u \in \mathbb{R}^n_+$. Further assume that*

$$u^*(t) = (u_1^*(t), \cdots, u_{i-1}^*(t), 0, u_{i+1}^*(t), \cdots, u_n^*(t))$$

is a $p-$periodic solution with $u_j^*(0) \geq 0$, $\forall 1 \leq j \leq n$, $j \neq i$, and $u^*(t)$ satisfies $\int_0^p F_i(t, u^*(t))dt > 0$. Then there exists a $\delta > 0$ such that

$$\limsup_{n\to\infty} d(P^n(u), u^*(0)) \geq \delta, \ \forall u \in int(\mathbb{R}^n_+).$$

We now turn our attention to results needed for the time-delayed epidemic model with dispersal. It is natural from an epidemiological viewpoint that a model has a unique disease-free equilibrium. The theory of cooperative systems is very useful here and, for an autonomous system of ODEs, the following theorem (adapted from [24, Corollary 3.2]) is used to establish this.

Definition 2.14 *Let $f : \mathbb{R}^n_+ \to \mathbb{R}^n$ be a continuously differentiable map. If every off-diagonal element of $Df(x)$ is nonnegative, then f is called a cooperative map.*

Theorem 2.15 *Let $f : \mathbb{R}^n_+ \to \mathbb{R}^n$ be a continuously differentiable map. Assume that*

(1) f is cooperative on $\mathbb{R}^n_+$ and $Df(x)$ is irreducible for every $x \in \mathbb{R}^n_+$;

(2) $f(0) = 0$ and $f_i(x) \geq 0$ for all $x \in \mathbb{R}^n_+$ with $x_i = 0$, $i = 1, 2, \cdots, n$;

(3) f is strictly subhomogeneous on $\mathbb{R}^n_+$, i.e., for any $\alpha \in (0, 1)$ and any $x >> 0$, $f(\alpha x) > \alpha f(x)$.

If the stability modulus satisfies $s(Df(0)) > 0$ and solutions of $x' = f(x)$, $x \in \mathbb{R}^n$ are ultimately bounded, then this system admits a unique componentwise-positive equilibrium x^* that is globally asymptotically stable in $\mathbb{R}^n_+ \setminus \{0\}$.

The continuous-time analogue of the earlier abstract theorem on strong repellers is not suited for the practical persistence of a time-delay system due to the use of the distance in the space of functions. Another theorem ([19, Theorem 3]) is needed for that. First, however, we need to define what is meant by a generalized distance function.

Definition 2.16 *A continuous function $p : X \to \mathbb{R}_+$ is called a generalized distance function for the autonomous semiflow $T(t) : X \to X$ if $p(T(t)x) > 0$, $\forall t > 0$ and either $p(x) = 0$ with $x \in X_0$ or $p(x) > 0$.*

Theorem 2.17 *Let $p(x)$ be a generalized distance function for the autonomous semiflow $T(t) : X \to X$. Assume that*

(C1) $T(t)X_0 \subset X_0$, $\forall t \geq 0$, *and* $T(t)$ *has global attractor* A *on* X;

(C2) There exists a finite sequence $\mathbb{M} = \{M_1, \cdots, M_k\}$ *of disjoint, compact and isolated invariant sets in* ∂X_0 *such that*

(1) $\cup_{x \in M_\partial} \omega(x) \subset \cup_{i=1}^{k} M_i$;

(2) no subset of $\mathbb{M}$ *forms a cycle in* ∂X_0;

(3) M_i *is isolated in* X;

(4) $W^s(M_i) \cap p^{-1}(0, \infty) = \emptyset$ *for each* $1 \leq i \leq k$.

Then there exists a $\delta > 0$ *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* $\min_{x \in L} p(x) > \delta$.

As before, we take $L = \omega(x)$ for any $x \in X_0$ and then have uniform persistence with respect to X_0. One final result is needed before we move on to the analysis of the forced Droop model with competition. The following is a perturbation theorem ([20, Theorem 2.2]) for a continuous-time case.

Theorem 2.18 *Let* $T_\lambda(t) : X \to X$ *be an autonomous semiflow parameterized by* $\lambda \in \Lambda$ *and* $U \subset X$. *Let* $(x_0, \lambda_0) \in U \times \Lambda$, $B_X(x_0, \delta) \subset U$ *for some* $\delta > 0$ *and assume that* $D_x T(x, t, \lambda)$ *exists for* $(x, t, \lambda) \in B_X(x_0, \delta) \times [0, \infty) \times \Lambda$ *and for each fixed* $t \geq 0$, $D_x T(x, t, \lambda)$ *is continuous on* $B_X(x_0, \delta) \times \Lambda$. *Suppose that* $T_{\lambda_0}(t)x_0 = x_0$ *for all* $t \geq 0$, $U(t) := D_x T_{\lambda_0}(t)x_0$ *defines a strongly continuous semiflow with* $\rho(U(t)) = \exp(-\omega t)$ *with* $\omega > 0$, *and* $\lim_{t \to \infty} T_\lambda(t)x = x_0$ *for each* $x \in U$. *In addition, suppose that*

(1) For each $\lambda \in \Lambda$, there is a subset B_λ of U such that for each $x \in U$, $T_\lambda(t)x \in B_\lambda$ for all large t.

(2) $\overline{\cup_{\lambda\in\Lambda} T_\lambda(s)B_\lambda}$ is compact in U for some $s > 0$.

Then there exists an $\epsilon_0 > 0$ and a continuous map $\hat{x} : B_\Lambda(\lambda_0, \epsilon_0) \to U$ such that $\hat{x}(\lambda_0) = x_0$, $T_\lambda(t)\hat{x}(\lambda) = \hat{x}(\lambda)$ for $t \geq 0$, and

$$\lim_{t\to\infty} T_\lambda(t)x = \hat{x}(\lambda), \quad \forall x \in U, \ \ \lambda \in B_\Lambda(\lambda_0, \epsilon_0).$$

3. A TWO-SPECIES PERIODIC DROOP MODEL

3.1 Overview

A chemostat model characterizes the growth of organisms in a lake environment (see, e.g., [18]). The Droop model [6,7] of phytoplankton growth is essential in theoretical phytoplankton ecology. This is evidenced in the book by Nisbet and Gurney [14] and papers such as those by Morel [13], Grover [8,9] and the references therein. The Droop model takes into consideration that phytoplankton cells store nutrient and that the growth rate depends on the stored nutrient. Algae can uptake nutrient in excess of current needs and continue to grow during nutrient poor conditions. These nutrients are supplied from an external reservoir; in several earlier works, this concentration is assumed to be constant. Following the work of Pascual [15] and Smith [16, 17], we consider a general model with two competing species of phytoplankton with nutrient concentration inflow varying periodically with time.

The system consists of five ordinary differential equations, one for each of the

population biomasses, one for the amount of stored nutrient per unit biomass and one more for ambient nutrient concentration. It is nonautonomous because the concentration inflow is time dependent. This inflow function is periodic and, while a more realistic approach would be a randomly varying nutrient inflow, the assumption of periodicity is not unreasonable particularly if the period is allowed to be large. The period is denoted as p and throughout this paper, all periodic functions have common period p. There is a growth rate function, μ_i, for each species and a nutrient uptake function, ρ_i. These adhere to the Droop model and the characteristics of these functions, as well as the formulation of the model, can be found in the next section.

This work was motivated by Smith [17], where the Droop model was presented with general functions for growth and uptake. It has been proved that under certain threshold conditions, there is a unique, positive periodic solution that is globally asymptotically stable. The threshold condition was related to phytoplankton growth rate and the dilution rate parameter. In this work, two species of phytoplankton are competing for a limiting resource in order to survive. The growth and uptake of each species will be different for each as these are the most important characteristics of each species. The system is nonlinear; for this reason, we use a dynamical systems approach to analyze the model. Since the inflow (forcing) function is periodic, the analysis of the period map is essential. It allows us to establish the existence and

stability of periodic solutions. In addition, a 4−dimensional limiting system is used to produce results for the original system. This is achieved by using the theory of chain transitive sets which allow us to prove that properties of the limiting system are valid for the 5−dimensional system. The existence of a positive periodic solution and uniform persistence of the phytoplankton populations are proved by appealing to the theory of uniform persistence. Thus, the main result is coexistence of two species in spite of competition for a limited resource.

In the following section, the model and its limiting system are presented. In the third section, the main results are stated and proved. Section 4 provides an illustrative example through numerical simulations. The numerical solutions exhibit the behavior as suggested by the theory using functions and parameters from biological literature in the general model. The last section gives a brief discussion of the main results and their biological implications.

3.2 The model

Let N_1, N_2 be population biomass concentrations of two species of phytoplankton, Q_1, Q_2 be the cell quota for each species and S be the ambient nutrient concentration in the chemostat. The following is an extension of the general Droop model to two

competing species of phytoplankton:

$$\begin{aligned} N_i' &= N_i(\mu_i(Q_i) - D) \\ Q_i' &= \rho_i(S, Q_i) - \mu_i(Q_i)Q_i, \quad i = 1, 2 \\ S' &= D(S^0(t) - S) - \sum_{i=1}^{2} N_i \rho_i(S, Q_i), \end{aligned} \tag{3.1}$$

where $S \geq 0, N_i \geq 0, Q_i \geq Q_{min}^i$, $i = 1, 2$ and $S^0(t) = S^0(t + p) \geq 0$ for some period $p > 0$. We assume that for $i = 1, 2$, $\mu_i(\cdot)$ and $\rho_i(\cdot, \cdot)$ satisfy the following the conditions.

(H1) $\mu_i(Q_{min}^i) = 0$, $\mu_i'(Q_i) > 0$, $\forall Q_i \geq Q_{min}^i$.

(H2) $\rho_i(0, Q_i) = 0$, $\frac{\partial \rho_i}{\partial S} > 0$, $\frac{\partial \rho_i}{\partial Q_i} \leq 0$, $\forall Q_i \geq Q_{min}^i$.

Let

$$X := \{(N_1, Q_1, N_2, Q_2, S) \in \mathbb{R}_+^5 \ : \ Q_i \geq Q_{min}^i, \ i = 1, 2\}.$$

It is easy to show that X is positively invariant for (3.1). For $N_i = 0$ in the last equation of (3.1) we have

$$S' = D(S^0(t) - S). \tag{3.2}$$

This linear equation has a unique globally attractive positive periodic solution $S = S^*(t) = S^*(t + p) > 0$ which describes the amount of nutrient in the phytoplankton-

free chemostat. Putting $S = S^*(t)$ in the second equation of (3.1) results in

$$Q_i' = \rho_i(S^*(t), Q_i) - \mu_i(Q_i)Q_i. \tag{3.3}$$

By Lemma 2.12, this scalar equation has a unique globally attractive periodic solution $Q_i = Q_i^*(t) = Q_i^*(t+p) > Q_{min}^i$. Further, any solution of (3.1) with initial value in X exists globally on $[0, \infty)$.

For convenience, we write the time-average of a $p-$periodic function as

$$\langle f(t) \rangle = p^{-1} \int_0^p f(t)dt.$$

Let $Z = S^*(t) - S - Q_1N_1 - Q_2N_2$. Then (3.1) becomes the following system:

$$\begin{aligned} N_i' &= N_i(\mu_i(Q_i) - D) \\ Q_i' &= \rho_i(S^*(t) - Q_1N_1 - Q_2N_2 - Z, Q_i) - \mu_i(Q_i)Q_i, \ i = 1, 2 \\ Z' &= -DZ \end{aligned} \tag{3.4}$$

with initial values in the domain

$$Y := \{(N_1, Q_1, N_2, Q_2, Z) \in \mathbb{R}^5_+ \ : \ Q_i \geq Q_{min}^i, \ i = 1, 2, \ \sum_{i=1}^{2} Q_iN_i + Z \leq S^*(0)\}.$$

Note that $S(t) = S^*(t) - Q_1(t)N_1(t) - Q_2(t)N_2(t) - Z(t)$ should be nonnegative in order to remain biologically relevant. Indeed, if there exists a t_0 such that $S^*(t_0) -$

$Q_1(t_0)N_1(t_0) - Q_2(t_0)N_2(t_0) - Z(t_0) = 0$, then

$$\begin{aligned} S'(t_0) &= (S^* - Q_1N_1 - Q_2N_2 - Z)'(t_0) \\ &= D(S^0 - S^* + Q_1N_1 + Q_2N_2 + Z)(t_0) = DS^0(t_0) \geq 0, \end{aligned}$$

which implies that $S(t) \geq 0$ for all $t \geq 0$.

Clearly, $Z(t) \to 0$ as $t \to \infty$. By integrating the equation for N_i, it is clear that $N_1 \geq 0$ for all $t \geq 0$. The equation for Q_i, along with (H1) and (H2) imply that $Q_i \geq Q^i_{min}$ for all $t \geq 0$. Therefore, solutions of (3.1) are ultimately bounded on X. By putting $Z = 0$ in (3.4) we arrive at the following periodic limiting system

$$\begin{aligned} N_i' &= N_i(\mu_i(Q_i) - D) \\ Q_i' &= \rho_i(S^*(t) - Q_1N_1 - Q_2N_2, Q_i) - \mu_i(Q_i)Q_i, \ i = 1, 2, \end{aligned} \tag{3.5}$$

with initial values in the domain

$$\Omega := \{(N_1, Q_1, N_2, Q_2) \in \mathbb{R}^4_+ \ : \ Q_i \geq Q^i_{min}, \ i = 1, 2, \ \sum_{i=1}^{2} Q_iN_i \leq S^*(0)\}.$$

3.3 *Uniform persistence*

In this section, we first prove uniform persistence for the limiting system (3.5), and then lift this result to the model system (3.1).

We start by considering the following 2-dimensional system

$$\begin{aligned} N' &= N(\mu(Q) - D) \\ Q' &= \rho(S^*(t) - QN, Q) - \mu(Q)Q. \end{aligned} \tag{3.6}$$

By [17, Proposition 1.3] and the theory of asymptotically periodic semiflows (see [25]), we have the following result.

Lemma 3.1 *Let $Q^*(t)$ be the unique positive p-periodic solution of $Q' = \rho(S^*(t), Q) - \mu(Q)Q$. If $\langle \mu(Q^*(t)) \rangle < D$, then all solutions $(N(t), Q(t))$ of (3.6) satisfy $\lim_{t\to\infty} |(N(t), Q(t)) - (0, Q^*(t))| = 0$. If, instead, $\langle \mu(Q^*(t)) \rangle > D$ holds, then there exists a unique positive $p-$periodic solution $(\bar{N}(t), \bar{Q}(t))$ and $\lim_{t\to\infty} |(N(t), Q(t)) - (\bar{N}(t), \bar{Q}(t))| = 0$ for all solutions $(N(t), Q(t))$ of (3.6) with $N(0) > 0$.*

Assume that

(A0) $\langle \mu_i(Q_i^*(t)) \rangle > D$, $i = 1, 2$.

Then Lemma 3.1 implies that there exists a globally attractive positive p-periodic solution $(\bar{N}_i(t), \bar{Q}_i(t))$ of (3.6) with $\mu = \mu_i$ and $\rho = \rho_i$, $i = 1, 2$, respectively,

Let $\bar{Q}_1^*(t)$ be the unique $p-$periodic solution of

$$Q_1' = \rho_1(S^*(t) - \bar{N}_2(t)\bar{Q}_2(t), Q_1) - \mu_1(Q_1)Q_1,$$

and $\bar{Q}_2^*(t)$ be the unique $p-$periodic solution of

$$Q_2' = \rho_2(S^*(t) - \bar{N}_1(t)\bar{Q}_1(t), Q_2) - \mu_2(Q_2)Q_2.$$

We further make the following assumptions:

(A1) $\langle \mu_1(\bar{Q}_1^*(t)) \rangle > D$.

(A2) $\langle \mu_2(\bar{Q}_2^*(t)) \rangle > D$.

The growth rate of each species, μ_i, depends on the internal nutrient pool Q. Since the system is periodic, the growth rates are periodic as well. The above conditions assert that the average of the growth rate is greater than the (constant) dilution rate in the chemostat. This average growth rate, however, is evaluated at a solution for Q where there is no phytoplankton. This asserts that (A0) is required for a small amount of either phytoplankton species to grow since its growth rate exceeds the dilution. The inequality (A1) says that a small amount of the first species would grow in a chemostat that is devoid of the first species but has a thriving population of the other species already present. Condition (A2) is analogous to (A1).

Define

$$\Omega_0 := \{(N_1, Q_1, N_2, Q_2) \in \Omega \ : \ N_1 > 0, N_2 > 0\}, \quad \partial\Omega_0 := \Omega \setminus \Omega_0.$$

We then have the following result on the dynamics of the 4-dimensional limiting system.

Theorem 3.2 *Assume that (A0), (A1) and (A2) hold. Then system* (3.5) *admits a positive periodic solution, and* $N_1(t)$ *and* $N_2(t)$ *are uniformly persistent with respect to* $\partial\Omega_0$ *in the sense that there is an* $\eta > 0$ *such that for any* $(N_1(0), Q_1(0), N_2(0), Q_2(0)) \in \Omega_0$, *the solution* $(N_1(t), Q_1(t), N_2(t), Q_2(t))$ *of* (3.5) *satisfies*

$$\liminf_{t\to\infty} N_i(t) \geq \eta, \quad \forall i = 1, 2.$$

Proof. We apply the uniform persistence theorem for discrete-time dynamical systems. Define the Poincaré map $P : \Omega \to \Omega$ for (3.5) by

$$P(N_1(0), Q_1(0), N_2(0), Q_2(0)) = (N_1(p), Q_1(p), N_2(p), Q_2(p)).$$

Clearly, $P(\Omega_0) \subset \Omega_0$. Since solutions of (3.5) are ultimately bounded, P is point dissipative and compact. Let $M_0 = \{(0, Q_1^*(0), 0, Q_2^*(0))\}$, $M_1 = \{(\bar{N}_1(0), \bar{Q}_1(0), 0, \bar{Q}_2^*(0))\}$ and $M_2 = \{(0, \bar{Q}_1^*(0), \bar{N}_2(0), \bar{Q}_2(0))\}$. Note that all M_j, $j = 0, 1, 2$, are fixed points of P, and are pairwise disjoint, compact and isolated invariant sets for P in $\partial\Omega_0$.

In the case where $N_1(0) = 0$ and $N_2(0) > 0$, we have $N_1(t) = 0$ and $N_2(t) > 0, \forall t \geq 0$. Further, $(Q_1(t), N_2(t), Q_2(t))$ satisfies

$$\begin{aligned} Q_1' &= \rho_1(S^*(t) - Q_2N_2, Q_1) - \mu_1(Q_1)Q_1 \\ N_2' &= N_2(\mu_2(Q_2) - D) \\ Q_2' &= \rho_2(S^*(t) - Q_2N_2, Q_2) - \mu_2(Q_2)Q_2. \end{aligned}$$

Since $\langle \mu_2(Q_2^*(t)) \rangle > D$, by Lemma 3.1 we have that

$$\lim_{t\to\infty} |(N_2(t), Q_2(t)) - (\bar{N}_2(t), \bar{Q}_2(t))| = 0.$$

By Lemma 2.12 and the theory of asymptotically periodic semiflows (see [25]), we further obtain $\lim_{t\to\infty}(Q_1(t) - \bar{Q}_1^*(t)) = 0$. Note that

$$P^n(0, Q_1(0), N_2(0), Q_2(0)) = (0, Q_1(np), N_2(np), Q_2(np)).$$

It then follows that

$$\lim_{n\to\infty} P^n(0, Q_1(0), N_2(0), Q_2(0)) = (0, \bar{Q}_1^*(0), \bar{N}_2(0), \bar{Q}_2(0)).$$

In the case where $N_1(0) = 0$ and $N_2(0) = 0$, we have $N_1(t) = 0$ and $N_2(t) = 0, \forall t \geq 0$. Thus,

$$\lim_{n\to\infty} P^n(0, Q_1(0), 0, Q_2(0)) = (0, Q_1^*(0), 0, Q_2^*(0)).$$

For the case where where $N_2(0) = 0$, we have similar observations. Consequently, $P : \Omega \to \Omega$ has the property that

$$\cup_{x\in\partial\Omega_0}\omega(x) \subset M_0 \cup M_1 \cup M_2.$$

It is easy to see that no cycles among M_0, M_1 and M_2 exist in $\partial\Omega_0$. Next, we essentially apply Theorem 2.13 which comes from [26, Lemma 5.1.1]. Each M_j gives rise to a periodic solution with at least one component that is identically zero. By (A0), (A1)

and (A2), using the same arguments as in [26, Lemma 5.1.1], there exists a $\delta > 0$ such that

$$\limsup_{n\to\infty} d(P^n(u), M_j) \geq \delta, \ \forall u \in \Omega_0, \ j = 0, 1, 2.$$

Therefore, each M_j is isolated in Ω and $W^s(M_j) \cap \Omega_0 = \emptyset$.

By Theorem 2.9 on strong repellers, $P : \Omega \to \Omega$ is uniformly persistent with respect to $(\Omega_0, \partial\Omega_0)$. Since P is point dissipative and compact on Ω, we conclude from Theorem 2.10 that there exists a global attractor A_0 for P in Ω_0 and P has a fixed point $x_0 \in \Omega_0$. Thus, there exists a positive periodic solution for (3.5) corresponding to the fixed point of the period map. By Theorem 2.11, it follows that the periodic semiflow $T(t) : \Omega \to \Omega$ associated with (3.5) is uniformly persistent with respect to $(\Omega_0, \partial\Omega_0)$. □

In the rest of this section, we extend the conclusion in Theorem 3.2 to our original system (3.1) by appealing to the theory of chain transitive sets. Recall that

$$X := \{(N_1, Q_1, N_2, Q_2, S) \in \mathbb{R}^5_+ \ : \ Q_i \geq Q^i_{min}, \ i = 1, 2\}$$

and

$$Y := \{(N_1, Q_1, N_2, Q_2, Z) \in \mathbb{R}^5_+ \ : \ Q_i \geq Q^i_{min}, \ i = 1, 2, \ \sum_{i=1}^{2} Q_i N_i + Z \geq S^*(0)\},$$

corresponding to systems (3.1) and (3.4), respectively. We define

$$X_0 := \{(N_1, Q_1, N_2, Q_2, S) \in X \ : \ N_1 > 0, N_2 > 0\}$$

and

$$Y_0 := \{(N_1, Q_1, N_2, Q_2, Z) \in Y \ : \ N_1 > 0, N_2 > 0\}$$

with $\partial X_0 := X \setminus X_0$ and $\partial Y_0 := Y \setminus Y_0$.

In the proof of the following theorem, we use (3.4), which is equivalent to (3.1), for convenience.

Theorem 3.3 *Assume that (A0), (A1) and (A2) hold. Then system* (3.1) *admits a positive periodic solution, and there is an* $\eta > 0$ *such that for any initial value* $(N_1(0), Q_1(0), N_2(0), Q_2(0), S(0)) \in X_0$, *the corresponding solution of* (3.1) *satisfies*

$$\liminf_{t\to\infty} N_i(t) \geq \eta, \ i = 1, 2.$$

Proof. Let $\omega := \tilde{\omega} \times \{0\}$ be the omega limit set for any point corresponding to the Poincaré map of (3.4). Then ω is an internally chain transitive set as a consequence. It follows from the definition of internally chain transitive sets that $\tilde{\omega} \subset \mathbb{R}^4$ is an internally chain transitive set for the Poincaré map P of (3.5) on Ω. In order to use Theorem 2.9 with $L = \tilde{\omega}$, we must first verify that $\tilde{\omega} \not\subset M_j$ for $j = 0, 1, 2$.

First, assume by way of contradiction that $\tilde{\omega} \subset M_0$. Then $\tilde{\omega} = M_0$ and $\omega = M_0 \cup \{0\}$. Let $P_1 : Y \to Y$ for (3.4) be defined by

$$P_1(N_1(0), Q_1(0), N_2(0), Q_2(0), Z(0)) = (N_1(p), Q_1(p), N_2(p), Q_2(p), Z(p)).$$

Then $P_1^n(N_1(0), Q_1(0), N_2(0), Q_2(0), Z(0)) \to \omega$ as $n \to \infty$. Equivalently,

$$\lim_{t\to\infty} |(N_1(t), Q_1(t), N_2(t), Q_2(t), Z(t)) - (0, Q_1^*(t), 0, Q_2^*(t), 0)| = 0.$$

From this we have that $\lim_{t\to\infty}(Q_1(t) - Q_1^*(t)) = 0$. Since $\mu_1(\cdot)$ is increasing, for any $\epsilon > 0$, there is a $T > 0$ such that for all $t \geq T$

$$\mu_1(Q_1(t)) - D \geq \mu_1(Q_1^*(t)) - D - \epsilon.$$

Set $\epsilon = \frac{1}{2}(\langle\mu_1(Q_1^*(t))\rangle - D)$. This gives the following differential inequality:

$$N_1'(t) \geq N_1(t)(\mu_1(Q_1^*(t)) - D - \epsilon),\ \forall t \geq T.$$

Without loss of generality, let $T = mp$ for some natural number m. By setting $t = np$ with $n \geq m$ we arrive at

$$N_1(np) \geq N_1(mp) \exp\left(\int_{mp}^{np} (\mu_1(Q_1^*(t)) - D - \epsilon)dt\right),\ \forall n \geq m.$$

Since Q_1^* is a periodic function, using (A0), we obtain

$$N_1(np) \geq N_1(mp) \exp\left(p(n-m)(\langle\mu_1(Q_1^*(t))\rangle - D - \epsilon)\right) \to \infty \text{ as } n \to \infty,$$

a contradiction. Thus, $\tilde{\omega} \not\subset M_0$. Using similar arguments, it can be shown using (A1) that $\tilde{\omega} \not\subset M_1$ and, using (A2), that $\tilde{\omega} \not\subset M_2$.

By Theorem 2.9 as applied to $P : \Omega \to \Omega$, there exists a $\delta > 0$ such that

$$\inf_{x\in\tilde{\omega}} d(x, \partial Y_0) \geq \delta.$$

Since

$$(N_1(np), Q_1(np), N_2(np), Q_2(np), Z(np)) \to \omega = \tilde{\omega} \times \{0\} \text{ as } n \to \infty,$$

it follows that there exists an $\eta > 0$ such that

$$\liminf_{n\to\infty} N_1(np) \geq \eta, \quad \liminf_{n\to\infty} N_2(np) \geq \eta.$$

This implies that the map $P_1 : Y \to Y$ is uniformly persistent with respect to $(Y_0, \partial Y_0)$. By Theorem 2.11, it then follows that the periodic system (3.4) is uniformly persistent with respect to $(Y_0, \partial Y_0)$. As in Theorem 3.2, Theorem 2.10 implies that (3.4) admits a positive periodic solution. Since system (3.1) and (3.4) are equivalent, this completes the proof. □

3.4 Simulations

As stated earlier, the conditions (A0),(A1) and (A2) are required for the coexistence of two phytoplankton species. The condition (A0) is required for the survival of any phytoplankton in the system since these inequalities are used in the single species case. Assume that (A0) is satisfied. In the competition case, (A1) and (A2) are both required for coexistence. If only one of the conditions (A1) and (A2) is satisfied, then numerical simulations suggest that one species will win the competition and the other will die out in the long term. The inequality (A1) corresponds to the first species

while (A2) corresponds to the second. In the following simulations, the adjustment of the dilution rate will change which of these inequalities are valid.

In order to perform numerical simulations, we will need to choose a specific case for the general model. The usual choice for μ in the literature, satisfying (H1), is

$$\mu(Q) = \mu_m(1 - \frac{Q_{min}}{Q}).$$

Examples of the function ρ are often independent of Q and a common choice (which satisfies (H2)) is

$$\begin{aligned} \rho(S,Q) &= \rho_{max}(Q)\frac{S}{S+K}, \\ \rho_{max}(Q) &= \rho^{hi} - (\rho^{hi} - \rho^{lo})\frac{Q - Q_{min}}{Q_{max} - Q_{min}}. \end{aligned}$$

This equation is most often simplified by assuming that $\rho^{hi} = \rho^{lo} = \rho_m$. It is then independent of Q. Under this assumption we can write equation (3.1) as

$$\begin{aligned} N_1' &= N_1(\mu_m^1(1 - \frac{Q_{min}^1}{Q_1}) - D) \\ N_2' &= N_2(\mu_m^2(1 - \frac{Q_{min}^2}{Q_2}) - D) \\ Q_1' &= \rho_m^1\left(\frac{S}{S+K_1}\right) - \mu_m^1(Q_1 - Q_{min}^1) \\ Q_2' &= \rho_m^2\left(\frac{S}{S+K_2}\right) - \mu_m^2(Q_2 - Q_{min}^2) \\ S' &= D(S^0(t) - S) - \rho_m^1 N_1\left(\frac{S}{S+K_1}\right) - \rho_m^2 N_2\left(\frac{S}{S+K_2}\right). \end{aligned} \tag{3.7}$$

By non-dimensionalizing this system with $\bar{N}_1 = N_1 \frac{Q^1_{min}}{K_1}$, $\bar{N}_2 = N_2 \frac{Q^2_{min}}{K_2}$, $\bar{Q}_1 = \frac{Q_1}{Q^1_{min}}$, $\bar{Q}_2 = \frac{Q_2}{Q^2_{min}}$, $\bar{S} = \frac{S}{K_1}$ and $\bar{t} = \mu^1_m t$, we arrive at the following system:

$$\begin{aligned} N_1' &= N_1\left(1 - \frac{1}{Q_1} - u\right) \\ N_2' &= \mu N_2\left(1 - \frac{1}{Q_2}\right) - uN_2 \\ Q_1' &= L_1\left(\frac{S}{S+1}\right) - Q_1 + 1 \\ Q_2' &= \mu\left(L_2\left(\frac{S}{S+K}\right) - Q_2 + 1\right) \\ S' &= u(S^0(t) - S) - L_1\left(\frac{S}{S+1}\right)N_1 - L_2 K\mu\left(\frac{S}{S+K}\right)N_2. \end{aligned} \tag{3.8}$$

Note that the bars have been left out and the variables re-labeled for convenience. The phase space which is biologically relevant is

$$\{(N_1, Q_1, N_2, Q_2, S) \in \mathbb{R}^5 \ : \ S > 0, \ N_i > 0, \ Q_i > 1, \ i = 1, 2\},$$

which is positively invariant. The forcing function $S^0(t)$ has been scaled by a factor of K_1 and the dimensionless equations have the following parameters

$$u = \frac{D}{\mu^1_m}, \quad \mu = \frac{\mu^2_m}{\mu^1_m}, \quad K = \frac{K_2}{K_1}, \quad L_1 = \frac{\rho^1_m}{\mu^1_m Q^1_{min}}, \quad L_2 = \frac{\rho^2_m}{\mu^2_m Q^2_{min}}.$$

As in [15], for given species of phytoplankton, the parameters L_1, L_2, K and μ can be determined from the biological literature (see, for example, [5]), with appropriate ranges dictated by experimental uncertainty. The dilution rate u is under experimental control and $u < 1$ should be chosen so that the maximum growth rate exceeds

the dilution for at least one phytoplankton species. The nutrient input, given by the p-periodic forcing function $S^0(t)$, is also under experimental control.

The function $S^0(t)$ is a proportion of the half saturation constant K_1. Thus, a typical function $S^0(t)$ must lie between 0 and 2; we choose $S^0(t) = 1 + 0.9\sin(\frac{\pi}{25}t)$ for this purpose (that is, a period of 50 time units). The dilution rate parameter u will be varied. Parameter sets from [5] for the species *Thalassiosira pseudonana* and *Skeletonema costatum* when the limiting nutrient is Silica are used. The maximum growth rate for *Thalassiosira pseudonana* is $\mu_m^1 = 2.75$ and for *Skeletonema costatum* is $\mu_m^2 = 2.88$. The half-saturation constants are $K_1 = 5.2$ and $K_2 = 1.3$. The growth rate is given per day and half-saturation constants are in micro moles per litre. These units are not very important since we only need the dimensionless parameters, $\mu = 1.05$ and $K = 0.25$. The species are characterized by $L_1 = 3.4$ and $L_2 = 1.1$.

In the following figures, the transient time in these figures is 10000 units to allow for the solutions to converge to a solution. The initial conditions used are $N_1(0) = 0.8$, $N_2(0) = 0.6$, $Q_1(0) = 1.1$, $Q_2(0) = 1.2$ and $S(0) = 0.7$. Since the theory ensures that the properties of the solution are independent of initial conditions, it is only important to choose initial data from the positively invariant set described earlier.

Using symbolic software such as Maple, we can check whether the inequalities (A0),(A1) and (A2) are satisfied for a given u. This is achieved by finding a numerical

solution and approximating the integral in the inequalities. We find that the pair of inequalities in (A0) are both satisfied $u < 0.453$. Condition (A1) is satisfied for $u > 0.238$ and (A2) for $0 \leq u < 0.257$. The numerical simulations show that *Thalassiosira pseudonana* dies out while *Skeletonema costatum* survives for $u < 0.238$. The coexistence of the competing species of phytoplankton occurs for $0.238 < u < 0.257$. On the other hand, *Thalassiosira pseudonana* wins the competition for $u > 0.257$. These ranges are determined by increasing the parameter by small increments until there is a change in the inequalities and, thus, a change in the behavior of the simulation.

In figures 3.1 and 3.2, we find that for $u = 0.25$ there is coexistence of the two species. The solution curves for N_1, N_2, Q_1, Q_2 and S are periodic with a period of 50 as expected. Figure 3.6 is the solution for the coexisting populations in the N_1N_2 plane.

An example of a case where *Thalassiosira pseudonana* dies off and *Skeletonema costatum* persists is $u = 0.21$ (see figures 3.7 and 3.8). This suggests that for low dilution rates, the superior competitor will cause the competition to die off. On the other hand, there is a range of values beyond the coexistence values where *Skeletonema costatum* dies off and *Thalassiosira pseudonana* persists. See figures 3.9 and 3.10 for an example. This suggests that *Thalassiosira pseudonana* is better at surviving in a

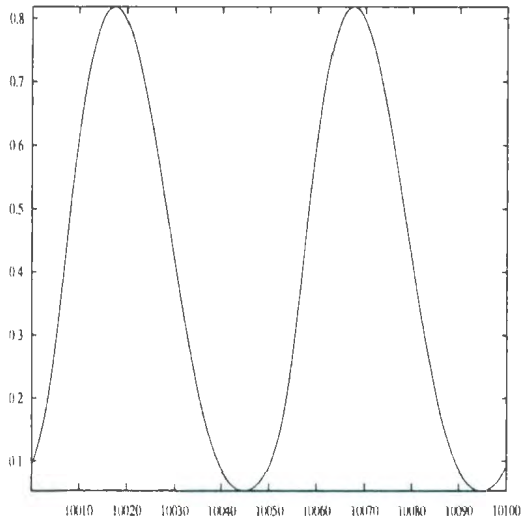

Fig. 3.1: u=0.25, N1 vs t

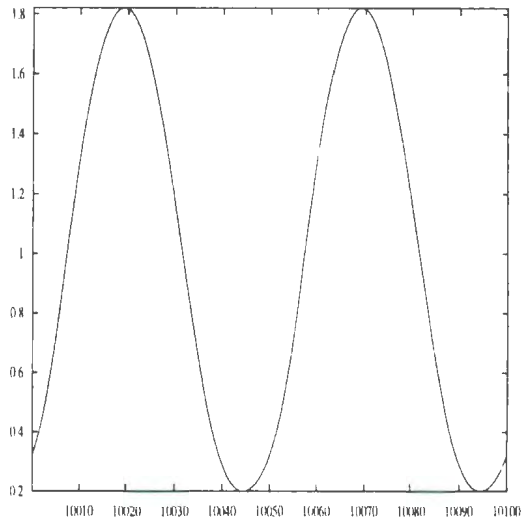

Fig. 3.2: u=0.25, N2 vs t

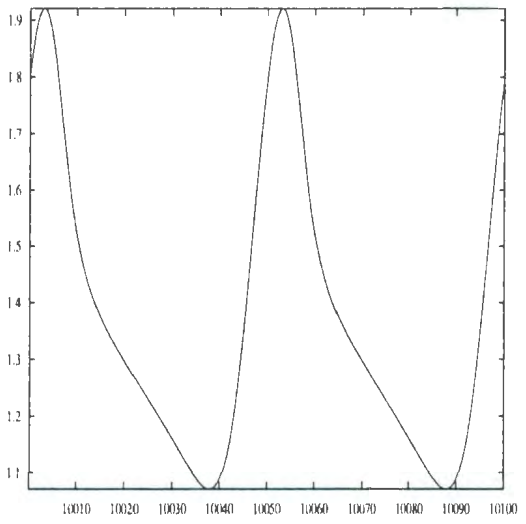

Fig. 3.3: u=0.25, Q1 vs t

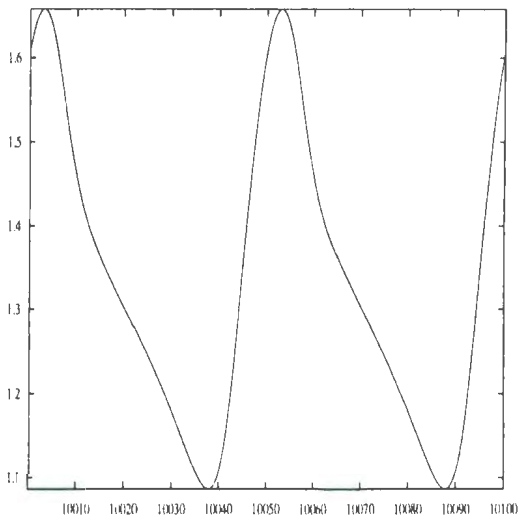

Fig. 3.4: u=0.25, Q2 vs t

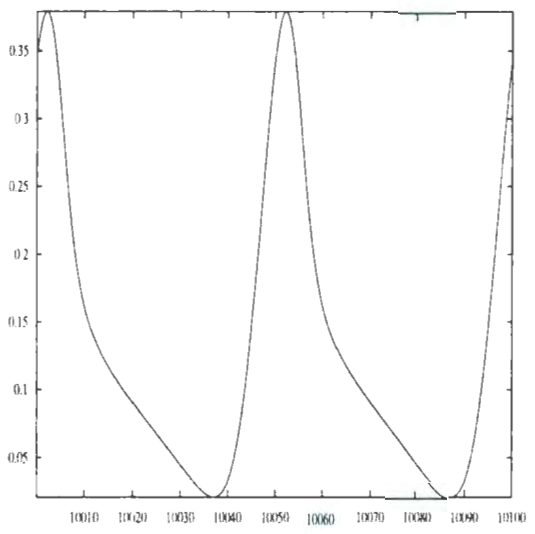

Fig. 3.5: u=0.25, S vs t

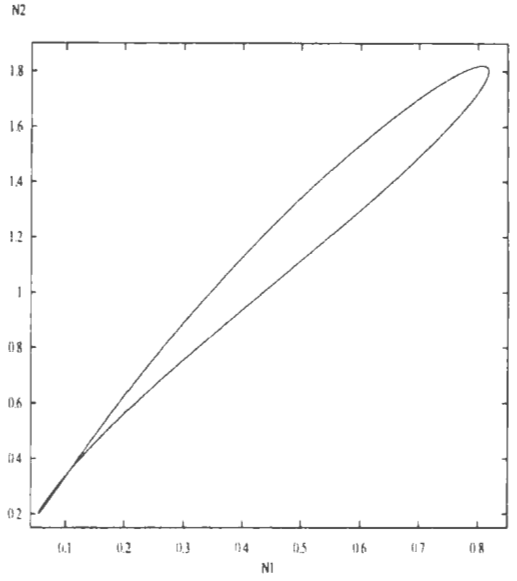

Fig. 3.6: u=0.25, N1 vs N2

more dilute environment than *Skeletonema costatum* even though it is not the stronger competitor for low dilution rates.

3.5 Discussion

In this project, a periodic Droop model for two phytoplankton species competition in a chemostat was analyzed in detail. The species compete for a single, limiting resource in an environment where nutrient is added to chemostat by way of a periodic forcing function. The model was analyzed in general, without specifying functions for the growth and uptake rates. There were, however, monotonicity conditions imposed on

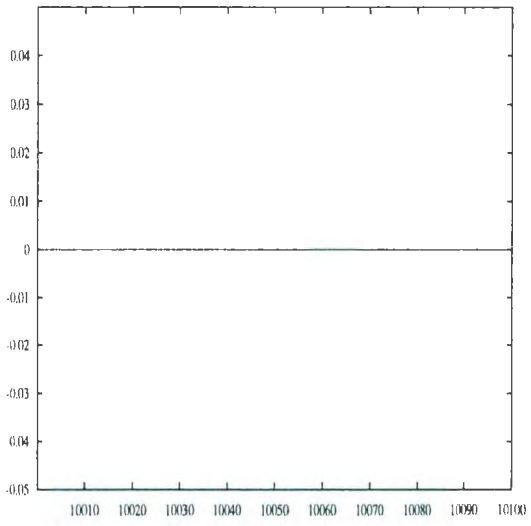

Fig. 3.7: u=0.21, N1 vs t

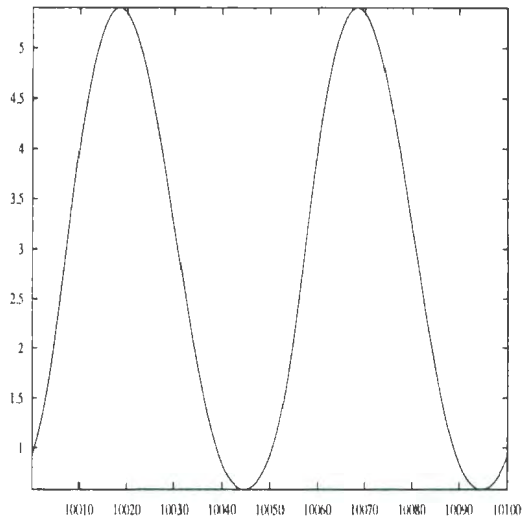

Fig. 3.8: u=0.21, N2 vs t

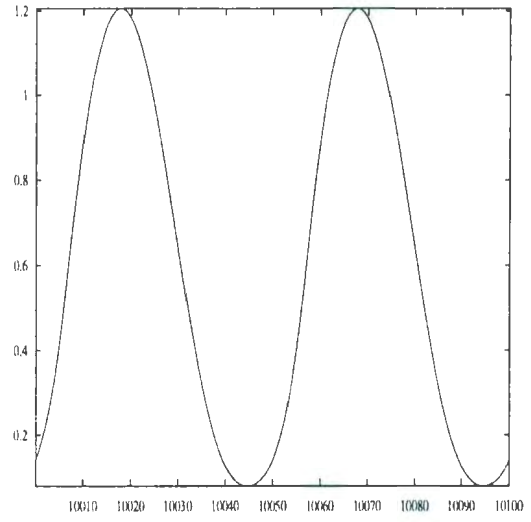

Fig. 3.9: u=0.28, N1 vs t

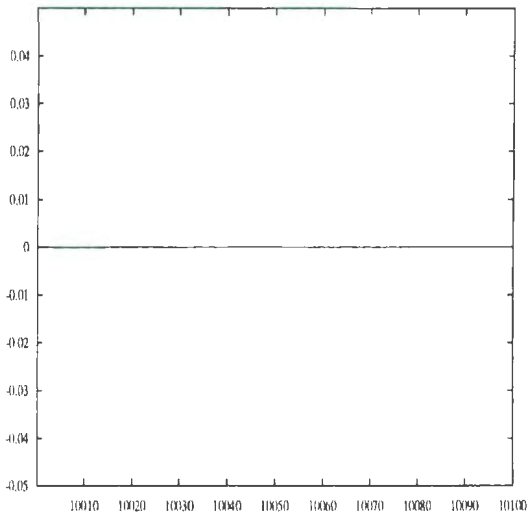

Fig. 3.10: u=0.28, N2 vs t

these functions to make the model appropriate in the biological sense. It is known that in the single species case a threshold condition, $\mu(Q^*(t)) > D$, is required for the global stability of the unique periodic orbit. The model with two species requires that this condition holds for each species ($\mu_i(Q_i^*(t)) > D, i = 1, 2$) as a necessary condition for survival of either species. Analysis of the competitive model reveals that there are two other threshold conditions, one associated with each species, and that each of these is required for the uniform persistence of both species. In addition, our numerical simulations suggest that each inequality by itself allows for a case where one species survives and the other dies out *due to the competition.* A proof of this assertion would be a natural step in followup work.

The numerical simulations in this work were achieved by using biological data for the phytoplankton species *Thalassiosira pseudonana* and *Skeletonema costatum* to make the model concrete. As expected from the theory, we found parameter ranges where each species dominated the competition and a range when there was coexistence. It was particularly interesting that for low dilution rates *Skeletonema costatum* dominated the competition while only *Thalassiosira pseudonana* persisted for higher dilution rates and coexistence occured for moderate dilution rates. The conclusion drawn here is that while a species may be a superior competitor it may not be better at surviving at higher rates of dilution. This shows how the ability to

compete against another species of phytoplankton is a separate characteristic from its survival capability in increasingly dilute environments.

This work suggests that, for additional species, an analogous result may be obtained. The details of this could be investigated in the future. Also there are a number of parameters in the model which could be varied in time instead of, or in addition to, the nutrient inflow $S^0(t)$. For example, the dilution rate or the volume of the chemostat itself is suggested in [17]. These ideas are left for future investigation.

4. A TIME-DELAYED EPIDEMIC MODEL WITH DISPERSAL

4.1 Overview

The dynamics of infectious diseases is an important research area in mathematical epidemiology. Some commonly studied types are SIR models where a disease spreads through contact and a population is divided among three classes: susceptible, infective and recovered. In many studies, the goal is to understand the key factors in disease transmission (see, for example, [2, 3, 10]) and this often includes (but is not limited to) determining a threshold condition for the persistence and extinction of the disease. The basic reproduction number, R_0, is the expected number of new infected individuals from one typical infected individual. Hence, R_0 is a threshold: the disease goes extinct when $R_0 < 1$; while it persists in the population when $R_0 > 1$.

Many diseases such as influenza, measles and sexually transmitted diseases are easily spread between countries, regions or cities due to travel. This population

dispersal is an important aspect to consider when studying the spread of a disease. We consider a disease transmission model with population dispersal among n patches, as in papers such as [1,22]. As in [4], the population demographic is described by

$$N' = B(N)N - \mu N,$$

where N is the size of a population, $B(N)$ is the birth rate of the population and μ is its death rate.

Often the duration of an infectious period is described by an exponential distribution. It is more realistic to assume that individuals have a constant length of infection τ. This new feature of the standard patch model is studied in [23] using a typical example of the function $B(N)$ found in biological literature. In that work, $B(N)N$ is a linear function which simplifies the analysis. Our purpose in the current paper is to extend the results in [23] to the general function $B(N)$ and numerically investigate the impact of the other typical functions (where $B(N)N$ is nonlinear) on the basic reproduction number.

In the following section, the model is established and preliminary results are given. Section 3 is devoted to establishing the basic reproduction number for the model with the general birth rate function and the proofs of the associated threshold-type results. In the fourth section, we use numerical simulations for some typical functions $B(N)$ to illustrate the effect of dispersal. The last section gives a discussion of the main

results and the examples.

4.2 The model

In this section, we present an epidemic model with population dispersal and infection period, which is based on [23].

Let S_i, I_i and R_i denote the density of susceptible, infective and recovered individuals in patch i. The population size, N_i, is therefore given by $N_i = S_i + I_i + R_i$ and we assume that the demographic structure is described by

$$\frac{dN_i(t)}{dt} = B_i(N_i(t))N_i(t) - \mu_i N_i(t),$$

where B_i is the per capita birth rate and μ_i the per capita death rate. Birth rate functions satisfy the following conditions:

(B1) $B_i(N_i) > 0,\ i = 1, 2.$

(B2) $B_i(N_i)$ is continuously differentiable with $B_i'(N_i) < 0,\ i = 1, 2.$

(B3) $\mu_i > B_i(\infty),\ i = 1, 2.$

When the patches are connected, the dynamics of disease transmission is described

by

$$\begin{aligned}
\frac{dS_1}{dt} &= B_1(N_1(t))N_1(t) - (\mu_1 + d_1)S_1(t) - k_1 S_1(t)I_1(t) + d_2 S_2(t), \\
\frac{dS_2}{dt} &= B_2(N_2(t))N_2(t) - (\mu_2 + d_2)S_2(t) - k_2 S_2(t)I_2(t) + d_1 S_1(t), \\
\frac{dI_1}{dt} &= k_1 S_1(t)I_1(t) - (\mu_1 + \gamma_1 + b_1)I_1(t) + b_2 I_2(t), \\
\frac{dI_2}{dt} &= k_2 S_2(t)I_2(t) - (\mu_2 + \gamma_2 + b_2)I_2(t) + b_1 I_1(t), \\
\frac{dR_1}{dt} &= \gamma_1 I_1(t) - (\mu_1 + c_1)R_1(t) + c_2 R_2(t), \\
\frac{dR_2}{dt} &= \gamma_2 I_2(t) - (\mu_2 + c_2)R_2(t) + c_1 R_1(t),
\end{aligned} \tag{4.1}$$

where k_i is the disease transmission coefficient and γ_i is the recovery rate of infected individuals, with $i = 1, 2$. Migration of susceptible individuals from the first patch to the second is given by d_1 while migration from the second patch to the first is given by d_2. Similarly, b_1, b_2 and c_1, c_2 describe the migration of infective individuals and recovered individuals respectively.

Since we assume that the length of infection for all infectious individuals is the constant τ, let a be the infection age and let $I_i(a,t)$ be the density of infected individuals at time t with respect to infection age a in the ith patch. Assuming that the number of individuals recovered due to treatment per unit is proportional to the number of infectious individuals, then the force of infection in patch i at time t is

$$k_i \int_0^\tau I_i(a,t)da$$

and (4.1) can be written as

$$\begin{aligned}
\frac{dS_1}{dt} &= B_1(N_1(t))N_1(t) - (\mu_1 + d_1)S_1(t) - \lambda_1(t)S_1(t) + d_2S_2(t),\\
\frac{dS_2}{dt} &= B_2(N_2(t))N_2(t) - (\mu_2 + d_2)S_2(t) - \lambda_2(t)S_2(t) + d_1S_1(t),\\
\frac{\partial I_1}{dt} &+ \frac{\partial I_1}{da} = -(\mu_1 + r_1 + b_1)I_1(a,t) + b_2I_2(a,t), \quad 0 < a \le \tau\\
\frac{\partial I_2}{dt} &+ \frac{\partial I_2}{da} = -(\mu_2 + r_2 + b_2)I_2(a,t) + b_1I_1(a,t), \quad 0 < a \le \tau \qquad (4.2)\\
\frac{dR_1}{dt} &= r_1\int_0^\tau I_1(a,t)da + I_1(\tau,t) - (\mu_1 + c_1)R_1(t) + c_2R_2(t),\\
\frac{dR_2}{dt} &= r_2\int_0^\tau I_2(a,t)da + I_2(\tau,t) - (\mu_2 + c_2)R_2(t) + c_1R_1(t),\\
\lambda_i(t) &= k_i\int_0^\tau I_i(a,t)da,\\
N_i(t) &= S_i(t) + R_i(t) + \int_0^\tau I_i(a,t)da,\\
I_i(0,t) &= \lambda_i(t)S_i(t), \quad i = 1,2,
\end{aligned}$$

with initial conditions given by

$$S_i(0) = S_i^0 > 0, \quad R_i(0) = R_i^0 \ge 0, \quad i = 1,2,$$

$$I_i(a,0) = f_i(a) \ge 0, \quad 0 \le a \le \tau, \quad i = 1,2.$$

Let $P_i(t) = \int_0^\tau I_i(a,t)da$ be the total density of infected members at time t in the ith patch. Set $V_i(a,t) = I_i(t-a,t)$ for $0 \le t-a \le \tau$ and $\mathbf{V}(a,t) = (V_1(a,t), V_2(a,t))^T$, where T represents the transpose of a vector. Then $\mathbf{V}$ satisfies

$$\frac{\partial \mathbf{V}(a,t)}{\partial t} = \mathbf{B}\mathbf{V}(a,t), \quad a \le t \le a + \tau, \qquad (4.3)$$

where

$$\mathbf{B} = \begin{bmatrix} -\mu_1 - r_1 - b_1 & b_2 \\ b_1 & -\mu_2 - r_2 - b_2 \end{bmatrix}.$$

Integrating (4.3) from a to t, we have

$$\mathbf{V}(a,t) = \exp(\mathbf{B}(t-a))(I_1(0,a), I_2(0,a))^T, \quad a \le t \le a+\tau,$$

and therefore

$$\mathbf{I}(a,t) = \mathbf{V}(t-a,t) = \exp(\mathbf{B}a)(I_1(0,t-a), I_2(0,t-a))^T, \quad a \le \tau.$$

We define $(b_{ij}(a)) := \exp(\mathbf{B}a)$ and $Q_i(t) := k_i S_i(t) P_i(t)$. Then it follows from (4.2) that

$$\begin{aligned} I_1(a,t) &= b_{11}(a)Q_1(t-a) + b_{12}(a)Q_2(t-a), \\ I_2(a,t) &= b_{21}(a)Q_1(t-a) + b_{22}(a)Q_2(t-a) \end{aligned} \tag{4.4}$$

for $t \ge \tau \ge a$.

Integrating (4.4) from 0 to τ, we get

$$\begin{aligned} P_1(t) &= \int_0^\tau b_{11}Q_1(t-a)da + \int_0^\tau b_{12}(a)Q_2(t-a)da, \quad t \ge \tau, \\ P_2(t) &= \int_0^\tau b_{21}Q_1(t-a)da + \int_0^\tau b_{22}(a)Q_2(t-a)da, \quad t \ge \tau, \end{aligned}$$

which is equivalent to

$$\mathbf{P}(t) = \int_0^\tau \exp(\mathbf{B}a)\mathbf{Q}(t-a)da = \int_{t-\tau}^t \exp(\mathbf{B}(t-s))\mathbf{Q}(s)ds, \quad t \ge \tau, \tag{4.5}$$

where $\mathbf{P}(t) = (P_1(t), P_2(t))^T$ and $\mathbf{Q}(t) = (Q_1(t), Q_2(t))^T$.

It then follows that

$$\frac{d\mathbf{P}}{dt} = \mathbf{Q}(t) - \exp(\mathbf{B}\tau)\mathbf{Q}(t-\tau) + \mathbf{B}\mathbf{P}(t), \quad t \geq \tau.$$

Define

$$\gamma_i(t) := r_i P_i(t) + b_{i1}(\tau)Q_1(t-\tau) + b_{i2}(\tau)Q_2(t-\tau), \quad i = 1, 2.$$

Then we arrive at the following time-delayed model:

$$\begin{aligned}
\frac{dS_1}{dt} &= B_1(N_1(t))N_1(t) - (\mu_1 + d_1)S_1(t) - Q_1(t) + d_2 S_2(t), \\
\frac{dS_2}{dt} &= B_2(N_2(t))N_2(t) - (\mu_2 + d_2)S_2(t) - Q_2(t) + d_1 S_1(t), \\
\frac{d\mathbf{P}}{dt} &= \mathbf{Q}(t) - \exp(\mathbf{B}\tau)\mathbf{Q}(t-\tau) + \mathbf{B}\mathbf{P}(t), \\
\frac{dR_1}{dt} &= \gamma_1(t) - (\mu_1 + c_1)R_1(t) + c_2 R_2(t), \\
\frac{dR_2}{dt} &= \gamma_2(t) - (\mu_2 + c_2)R_2(t) + c_1 R_1(t), \\
N_i(t) &= S_i(t) + R_i(t) + P_i(t), \quad i = 1, 2
\end{aligned} \tag{4.6}$$

for $t \geq \tau$. By (4.5), we require that initial functions satisfy the following condition

$$\mathbf{P}(\tau) = \int_0^\tau \exp(\mathbf{B}(\tau - s))\mathbf{Q}(s)ds.$$

Equation (4.6) is an autonomous functional differential equation system defined on $C([0, \tau], \mathbb{R}^6_+)$. After a time translation, we will consider, without loss of generality,

(4.6) on $C([-\tau,0],\mathbb{R}^6_+)$ under the condition

$$\mathbf{P}(0)=\int_{-\tau}^{0}\exp(-\mathbf{B}(s))\mathbf{Q}(s)ds.$$

The well-posedness of system (4.6) and the positivity of its solutions were considered in [23]. Assume that each $B_i(N_i)N_i$ extends to a C^1 function $G_i(N_i)$ on $[0,\infty)$ with $G_i(0)\geq 0$. Let $\mathbf{u}(t)=(\mathbf{S}(t),\mathbf{P}(t),\mathbf{R}(t))$ be a continuous function from $[-\tau,\sigma)$ to $\mathbb{R}^6_+$ for some $\sigma>0$. For each $t\in[0,\sigma)$, we define $\mathbf{u}_t\in C([-\tau,0],\mathbb{R}^6_+)$ by $\mathbf{u}_t(s)=\mathbf{u}(t+s)$ for all $s\in[-\tau,0]$. Set

$$X:=\left\{(\mathbf{S},\mathbf{P},\mathbf{R})\in C([-\tau,0],\mathbb{R}^6_+)\ :\mathbf{P}(0)=\int_{-\tau}^{0}\exp(-\mathbf{B}s)\mathbf{Q}(s)ds\right\}.$$

By the standard theory of functional differential equations (see [11]), for any $\phi\in C([-\tau,0],\mathbb{R}^6_+)$ there exists a unique solution $\mathbf{u}(t,\phi)$ of system (4.6) satisfying $\mathbf{u}_0=\phi$, which is defined on its maximal interval of existence $[0,\sigma_\phi)$.

We first observe that X is positively invariant. Define

$$\mathbf{W}(t):=\int_{t-\tau}^{t}\exp(\mathbf{B}(t-s))\mathbf{Q}(s)ds,\quad \forall t\in[0,\sigma_\phi).$$

It follows that

$$\frac{\mathbf{dW}(t)}{dt}=\mathbf{Q}(t)-\exp(\mathbf{B}\tau)\mathbf{Q}(t-\tau)+\mathbf{BW}(t),\quad \forall t\in[0,\sigma_\phi),$$

and

$$\frac{d(\mathbf{P}(t)-\mathbf{W}(t))}{dt}=\mathbf{B}(\mathbf{P}(t)-\mathbf{W}(t)),\quad \forall t\in[0,\sigma_\phi).$$

Since $\phi \in X$, we have $\mathbf{P}(0) = \mathbf{W}(0)$ and hence,

$$\mathbf{P}(t) - \mathbf{W}(t) = \exp(\mathbf{B}(t)(\mathbf{P}(0) - \mathbf{W}(0)) = \mathbf{0} \quad \forall t \in [0, \sigma_\phi).$$

This means that

$$\mathbf{P}(t) = \int_{t-\tau}^{t} \exp(\mathbf{B}(t-s))\mathbf{Q}(s)ds = \int_{-\tau}^{0} \exp(-\mathbf{B}(s))\mathbf{Q}(t+s)ds \quad \forall t \in [0, \sigma_\phi). \quad (4.7)$$

By (4.7) and the differential equations for $S_1(t), S_2(t), R_1(t), R_2(t)$, it follows that for any $\phi \in X$, $\mathbf{u}(t, \phi)$ is (componentwise) nonnegative on $[0, \sigma_\phi)$, and $\mathbf{u}_t(\phi) \in X$ for all $t \in [0, \sigma_\phi)$.

4.3 Threshold dynamics

In addition to (B1)-(B3), we further make the following assumptions on $B_i(N_i)$.

(H) $\mu_i, k_i, b_i,\ i = 1, 2$ are positive constants; d_i and c_i are nonnegative constants for $i = 1, 2$.

Define

$$X_L := \left\{ \phi = (\phi_1, \cdots, \phi_6) \in X \ : \ \sum_{i=1}^{6} \phi_i(0) \leq L \right\}, \ \ \forall L \geq 0.$$

Lemma 4.1 *Let (H) hold. Then there exists an L^* such that for any $L > L^*$ the set X_L is positively invariant for solution maps of (4.6), and every solution $\mathbf{u}(t,\phi)$ of (4.6) with $\phi \in X$ eventually enters into $[0,L]^6$.*

Proof. By (4.6), we have

$$\frac{dN_1}{dt} = (B_1(N_1) - \mu_1)N_1 - d_1S_1 + d_2S_2 - b_1P_1 + b_2P_2 - c_1R_1 + c_2R_2,$$
$$\frac{dN_2}{dt} = (B_2(N_2) - \mu_2)N_2 - d_2S_2 + d_1S_1 - b_2P_2 + b_1P_1 - c_2R_2 + c_1R_1.$$

Let $N = N_1 + N_2$. Since $B_1(N_1)$ is continuous and $\mu_1 > B_1(\infty)$, there exists an L_1 such that $\mu_1 > B_1(N_1)$ for all $N_1 > L_1$. Similarly, there exists an L_2 such that $\mu_2 > B_2(N_2)$ for all $N_2 > L_2$. Set $L^* = L_1 + L_2$ and $m := \min\{B_1(L^*) - \mu_1, B_2(L^*) - \mu_2\} < 0$. Therefore,

$$\frac{d}{dt}(N_1 + N_2) = (B_1(N_1) - \mu_1)N_1 + (B_2(N_2) - \mu_2)N_2 \leq mN, \quad \forall N > L^*$$

Thus, the standard comparison theorem completes the proof. □

Let $\mathbf{\Phi}(t) : X \to X$ be the solution semiflow associated with (4.6). This means that $\mathbf{\Phi}(t)\phi = \mathbf{u}_t(\phi)$, $\phi \in X$, $t \geq 0$. By Lemma 4.1, solutions of (4.6) are ultimately bounded and uniformly bounded. It then follows that the semiflow $\mathbf{\Phi}(t)$ is point dissipative on X and $\mathbf{\Phi}(t) : X \to X$ is compact for each $t > \tau$. By Lemma 2.7, $\mathbf{\Phi}(t)$ admits a global attractor that attracts every bounded set in X.

In order to find the disease-free equilibrium, which is needed for the basic reproduction number, we consider

$$\begin{aligned}\frac{dS_1}{dt} &= B_1(S_1)S_1 - (\mu_1 + d_1)S_1 + d_2S_2,\\ \frac{dS_2}{dt} &= B_2(S_2)S_2 - (\mu_2 + d_2)S_2 + d_1S_1.\end{aligned} \tag{4.8}$$

Let $F : \mathbb{R}^2_+ \to \mathbb{R}^2$ be defined by the right-hand side of (4.8) and $S = (S_1, S_2)$. Clearly, F is continuously differentiable and $F(0) = 0$. Recall that $G_i(N_i) = B_i(N_i)N_i, \forall N_i > 0$, $i = 1, 2$. Then the Jacobian $DF(S)$ is given by

$$DF(S) = \begin{bmatrix} G_1'(S_1) - (\mu_1 + d_1) & d_2 \\ d_1 & G_2'(S_2) - (\mu_2 + d_2) \end{bmatrix}.$$

Since the off-diagonal elements of $DF(S)$ are positive, F is cooperative for every $S \in \mathbb{R}^2_+$. Note also that $DF(S)$ is irreducible. Let $\alpha \in (0, 1)$ and $S \in \text{int}(\mathbb{R}^2_+)$. Then the following holds

$$\alpha B_1(\alpha S_1)S_1 - \alpha(\mu_1 + d_1)S_1 + d_2\alpha S_2 > \alpha[B_1(S_1)S_1 - (\mu_1 + d_1)S_1 + d_2S_2],$$

$$\alpha B_2(\alpha S_2)S_2 - \alpha(\mu_2 + d_2)S_2 + d_1\alpha S_1 > \alpha[B_2(S_2)S_2 - (\mu_2 + d_2)S_2 + d_1S_1].$$

Thus, F is strongly subhomogeneous on $\mathbb{R}^2_+$.

Recall that the stability modulus of a square matrix M, denoted by $s(M)$, is defined by

$$s(M) := \max\{\text{Re}\lambda : \lambda \text{ is an eigenvalue of } M\}.$$

In order for (4.8) to admit a positive equilibrium, we need to assume that

(B4) $s(DF(0)) > 0$.

By Lemma 4.1, as applied to the constant initial data $\phi(\theta) = (\mathbf{S}(0), \mathbf{0}, \mathbf{0})$, $\forall \theta \in [-\tau, 0]$, solutions of (4.8) are ultimately bounded. It then follows from Theorem 2.15 that (4.8) admits a unique positive equilibrium $S^* = (S_1^*, S_2^*)$ and that S^* is globally asymptotically stable for $S \in \mathbb{R}^2_+ \setminus \{0\}$. Thus, $E_0 = (S_1^*, S_2^*, 0, 0, 0, 0)$ is a disease-free equilibrium of (4.6).

As in [23], we first determine the basic reproduction number, which is the average number of secondary cases an infected individual will cause in a population. Assume that the population is near the disease-free equilibrium E_0. Then it follows from (4.7) that

$$\begin{aligned} P_1(t) &= k_1 S_1^* \int_0^\tau b_{11}(a) P_1(t-a)da + k_2 S_2^* \int_0^\tau b_{12}(a) P_2(t-a)da, \\ P_2(t) &= k_1 S_1^* \int_0^\tau b_{21}(a) P_1(t-a)da + k_2 S_2^* \int_0^\tau b_{22}(a) P_2(t-a)da. \end{aligned} \tag{4.9}$$

Set

$$\mathbf{U} = \begin{bmatrix} k_1 S_1^* \int_0^\tau b_{11}(a)da & k_2 S_2^* \int_0^\tau b_{12}(a)da \\ k_1 S_1^* \int_0^\tau b_{21}(a)da & k_2 S_2^* \int_0^\tau b_{22}(a)da \end{bmatrix}.$$

Since $\mathbf{U}$ is a positive matrix, its spectral radius $\rho(\mathbf{U})$ is a simple eigenvalue with a positive eigenvector (see, e.g., [18]). Let $\psi(a) = (\psi_1, \psi_2)^T$ be an initial distribution

of infected members in the patches during the infection period, where ψ_1 and ψ_2 are constants. Set

$$\mathcal{F} = \begin{bmatrix} k_1 S_1^* & 0 \\ 0 & k_2 S_2^* \end{bmatrix}.$$

Thus, $\mathcal{F}\psi$ is the rate of infectious individuals in the two patches. In [23], it was concluded that $b_{ij}(a)$ is the probability that an infective person initially in patch j at infection age zero is in patch i at infection age a. Then $\mathbf{U}\psi = \int_0^\tau \exp(\mathbf{B}a)\mathcal{F}\psi da$ gives the number of infected individuals in the patches at the end of an infection period. As in [21, 23], $\mathbf{U}$ is called the next infection matrix and $\rho(\mathbf{U})$ is defined as the basic reproduction number R_0 of (4.8).

Our first result shows the uniform persistence of the disease if $R_0 > 1$. The proof of this theorem from [23] is modified here and a form for the function $B_i(N_i)$ is not assumed. Instead, the function $G_i(N_i) = B_i(N_i)N_i$ is used.

Theorem 4.2 *Let (H) hold. If $R_0 > 1$, then the disease is uniformly persistent in the sense that there is a positive number ϵ such that for any $\phi \in X$ with $\phi_3(0) > 0$ and $\phi_4(0) > 0$, the solution $(\mathbf{S}(t,\phi), \mathbf{P}(t,\phi), \mathbf{R}(t,\phi))$ of (4.6) satisfies $\liminf_{t\to\infty} P_i(t,\phi) \geq \epsilon$, $i = 1, 2$.*

Proof. As in [23], we use persistence theory. We established earlier that the solution

semiflow $\mathbf{\Phi}(t)$ of (4.6) has a global attractor on X. Define

$$X_0 := \{\phi \in X \ : \phi_3(0) > 0, \phi_4(0) > 0\}, \quad \partial X_0 := X \setminus X_0.$$

Let $(\mathbf{S}(t,\phi), \mathbf{P}(t,\phi), \mathbf{R}(t,\phi))$ be a solution of (4.6) with $\phi \in X$. We claim that if $P_i(0,\phi) > 0$ for some i, then $S_i(t,\phi) > 0, \forall t > 0$. Indeed, we see from (4.6) that

$$\frac{dS_i(t)}{dt} \geq -(\mu_i + d_i + k_i P_i(t))S_i(t), \ \forall t \geq 0.$$

It then follows that if $S_i(t_0) > 0$ for some $t_0 \geq 0$, then $S_i(t) > 0, \forall t \geq t_0$. In the case where $S_i(0,\phi) > 0$, we have $S_i(t,\phi) > 0, \forall t \geq 0$. In the case where $S_i(0,\phi) = 0$, we see from (4.6) that $\frac{dS_i(0,\phi)}{dt} > 0$ since $N_i(0,\phi) \geq P_i(0,\phi) > 0$. Thus, $S_i(t_0,\phi) > 0$ for all sufficiently small $t_0 > 0$, which implies that $S_i(t,\phi) > 0$, $\forall t > 0$. In view of the above claim and (4.7), we see that X_0 is positively invariant for $\mathbf{\Phi}(t)$. Note that

$$\partial X_0 = \{\phi \in X \ : \phi_3(0) = 0 \text{ or } \phi_4(0) = 0\},$$

which is relatively closed in X. Let $L \in (L^*, \infty)$ be fixed. Then Lemma 4.1 implies that every solution of (4.6) enters $[0, L]^6$ ultimately. Define

$$M_\partial := \{\phi \in X \ : \ \mathbf{\Phi}(t)\phi \in \partial X_0, \ \forall t \geq 0\}.$$

Since $b_1, b_2 > 0$ imply that $\exp(\mathbf{B}a) > 0$, assume that $(\mathbf{S}_0(\phi), \mathbf{P}_0(\phi), \mathbf{R}_0(\phi)) = \phi$. Then

$$M_\partial = \{\phi \in X_0 \ : \ \mathbf{P}(t,\phi) = 0, \ \forall t \geq 0\}.$$

Set

$$\mathbf{U}_\epsilon = \begin{bmatrix} k_1(S_1^* - \epsilon)\int_0^\tau b_{11}(a)da & k_2(S_2^* - \epsilon)\int_0^\tau b_{12}(a)da \\ k_1(S_1^* - \epsilon)\int_0^\tau b_{21}(a)da & k_2(S_2^* - \epsilon)\int_0^\tau b_{22}(a)da \end{bmatrix}.$$

Since $\rho(\mathbf{U}_\epsilon)$ is continuous in ϵ, we can restrict $\epsilon > 0$ small enough such that $\mathbf{U}_\epsilon$ is positive and $\rho(\mathbf{U}_\epsilon) > 1$. Now consider the following system:

$$\begin{aligned} \frac{du_1}{dt} &= B_1(u_1 + \eta)u_1 - (\mu_1 + d_1 + k_1\eta)u_1(t) + d_2u_2(t), \\ \frac{du_2}{dt} &= B_2(u_2 + \eta)u_2 - (\mu_2 + d_2 + k_2\eta)u_2(t) + d_1u_1(t), \end{aligned} \tag{4.10}$$

where $\eta > 0$ is a small number. Arguing as before, (4.10) satisfies the conditions of Theorem 2.15 and, as such, it admits an equilibrium $(u_1^*(\eta), u_2^*(\eta))$ which is globally asymptotically stable. Moreover, since this system is a perturbation of (4.8), we have that $(u_1^*(\eta), u_2^*(\eta)) \to (S_1^*, S_2^*)$ as $\eta \to 0$. By the implicit function theorem, we choose $\eta = \eta(\epsilon) > 0$ small enough so that $u_i^*(\eta) > S_i^* - \epsilon,\ i = 1, 2$. It follows that every positive solution $(u_1(t), u_2(t))$ of (4.10) satisfies $u_i(t) > S_i^* - \epsilon,\ i = 1, 2$ for all large t. We define

$$M_i := r_i + L(b_{i1}(\tau)k_1 + b_{i2}(\tau)k_2),\ i = 1, 2,$$

and consider

$$\begin{aligned} \frac{dw_1(t)}{dt} &= \delta M_1 - (\mu_1 + c_1)w_1 + c_2w_2, \\ \frac{dw_2(t)}{dt} &= \delta M_2 - (\mu_2 + c_2)w_2 + c_1w_1. \end{aligned} \tag{4.11}$$

This is a linear, nonhomogeneous system. The origin is globally asymptotically stable for the corresponding homogeneous system and it is easy to show that the particular solution of (4.11) is a constant which tends to zero as $\delta \to 0$. Therefore, (4.11) has a globally asymptotically stable equilibrium $(w_1^*(\delta), w_2^*(\delta))$ which satisfies $(w_1^*(\delta), w_2^*(\delta)) \to (0,0)$ as $\delta \to 0$. Thus we can fix δ with $0 < \delta < \frac{\eta}{2}$ such that $w_i^*(\delta) < \frac{\eta}{2}, i = 1,2$. It then follows that every positive solution of (4.11) satisfies $w_i(t) < \frac{\eta}{2},\ i = 1,2$ for large t. We now have the following claim.

Claim. $\limsup_{t\to\infty} \max\{P_1(t,\phi), P_2(t,\phi)\} \geq \delta$ for any $\phi \in X_0$.

Assume, by way of contradiction, that the claim does not hold for some $\phi \in X_0$. Then $P_i(t) := P_i(t,\phi) < \delta < \frac{\eta}{2},\ i = 1,2$ for all large t. Since solutions of (4.6) are ultimately bounded, we have that $Q_i(t) \leq k_i S_i(t)\delta \leq k_i L\delta < k_i L\eta,\ i = 1,2$ for large t. It then follows that $\gamma_i(t) \leq \delta M_i,\ i = 1,2$, for large t, and hence

$$\begin{aligned} \frac{dR_1(t)}{dt} &\leq \delta M_1 - (\mu_1 + c_1)R_1 + c_2 R_2, \\ \frac{dR_2(t)}{dt} &\leq \delta M_2 - (\mu_2 + c_2)R_2 + c_1 R_1. \end{aligned}$$

By the comparison theorem for cooperative systems (see, e.g., [18]), we have $R_i(t) \leq w_i(t) < \frac{\eta}{2},\ i = 1,2$ for large t. It follows that for all large t,

$$N_i(t) \leq S_i(t) + \eta, \quad i = 1,2,$$

and

$$B_i(N_i(t))N_i(t) \geq B_i(S_i(t)+\eta)S_i(t), \quad i=1,2.$$

Therefore, we see that for large t,

$$\begin{aligned}
\frac{dS_1}{dt} &> B_1(S_1+\eta)S_1 - (\mu_1+d_1+k_1\eta)S_1(t) + d_2S_2(t), \\
\frac{dS_2}{dt} &> B_2(S_2+\eta)S_2 - (\mu_2+d_2+k_2\eta)S_2(t) + d_1S_1(t). \qquad (4.12)
\end{aligned}$$

By the comparison theorem, it follows that $S_i(t) > u_i(t) > S_i^* - \epsilon$, $i=1,2$, for all large t. Thus, (4.5) implies that there is a $t_0 > 0$ such that for all $t \geq t_0$,

$$\begin{aligned}
P_1(t) &> k_1(S_1^*-\epsilon)\int_0^\tau b_{11}(a)P_1(t-a)da + \\
&\quad k_2(S_2^*-\epsilon)\int_0^\tau b_{12}(a)P_2(t-a)da, \\
P_2(t) &> k_1(S_1^*-\epsilon)\int_0^\tau b_{21}(a)P_1(t-a)da + \\
&\quad k_2(S_2^*-\epsilon)\int_0^\tau b_{22}(a)P_2(t-a)da. \qquad (4.13)
\end{aligned}$$

Let $\mathbf{v} = (v_1, v_2)^T$ be a positive right eigenvector of $\mathbf{U}_\epsilon$ with respect to $\rho(\mathbf{U}_\epsilon)$. Choose $l > 0$ small enough such that $lv_i < \min\{P_i(t) : t_0 \leq t \leq t_0+\tau\}$ for $i=1,2$. Then the following inequality is true:

$$lv_i < P_i(t), \quad i=1,2, \quad \forall t \geq t_0. \qquad (4.14)$$

To see this, we set

$$t_1 = \inf\{t \in [t_0,\infty) : lv_1 = P_1(t) \text{ or } lv_2 = P_2(t)\}.$$

Clearly, $t_1 > t_0 + \tau$. Then $lv_i < P_i(t)$, $i = 1, 2$, for $t_0 \leq t < t_1$ and $lv_1 = P_1(t_1)$ or $lv_2 = P_2(t_1)$. But, we see from (4.13) that

$$\begin{aligned} P_1(t) &> k_1(S_1^* - \epsilon)lv_1 \int_0^\tau b_{11}(a)da + k_2(S_2^* - \epsilon)lv_2 \int_0^\tau b_{12}(a)da = \rho(\mathbf{U}_\epsilon)lv_1, \\ P_2(t) &> k_1(S_1^* - \epsilon)lv_1 \int_0^\tau b_{21}(a)da + k_2(S_2^* - \epsilon)lv_2 \int_0^\tau b_{22}(a)da = \rho(\mathbf{U}_\epsilon)lv_2, \end{aligned}$$

which contradicts $lv_1 = P_1(t_1)$ or $lv_2 = P_2(t_1)$. Thus, (4.14) holds.

Now suppose that for some $n \geq 1$,

$$\rho^{n-1}(\mathbf{U}_\epsilon)lv_i < P_i(t), \quad i = 1, 2, \quad \forall t \geq t_0 + (n-1)\tau. \tag{4.15}$$

We want to prove that

$$\rho^n(\mathbf{U}_\epsilon)lv_i < P_i(t), \quad i = 1, 2, \quad \forall t \geq t_0 + n\tau. \tag{4.16}$$

By (4.13) and (4.15) we have that

$$\rho^n(\mathbf{U}_\epsilon)lv_i < P_i(t_0 + n\tau), \ i = 1, 2.$$

If (4.16) does not hold, then there is a $t_2 > t_0 + n\tau$ such that $\rho^n(\mathbf{U}_\epsilon)lv_i < P_i(t)$, $i = 1, 2$, for $t_0 + n\tau \geq t < t_2$, and $\rho^n(\mathbf{U}_\epsilon)lv_1 = P_1(t_2)$ or $\rho^n(\mathbf{U}_\epsilon)lv_2 = P_2(t_2)$. By (4.13)

and (4.15) it follows that for $t \in (t_0 + n\tau, t_2]$,

$$\begin{aligned} P_1(t) > \quad & k_1(S_1^* - \epsilon)\rho^{n-1}(\mathbf{U}_\epsilon) l v_1 \int_0^\tau b_{11}(a)da \\ & + k_2(S_2^* - \epsilon)\rho^{n-1}(\mathbf{U}_\epsilon) l v_2 \int_0^\tau b_{12}(a)da = \rho^n(\mathbf{U}_\epsilon) l v_1, \\ P_2(t) > \quad & k_1(S_1^* - \epsilon)\rho^{n-1}(\mathbf{U}_\epsilon) l v_1 \int_0^\tau b_{21}(a)da \\ & + k_2(S_2^* - \epsilon)\rho^{n-1}(\mathbf{U}_\epsilon) l v_2 \int_0^\tau b_{22}(a)da = \rho^n(\mathbf{U}_\epsilon) l v_2, \end{aligned}$$

which contradicts $\rho^n(\mathbf{U}_\epsilon) l v_1 = P_1(t_2)$ or $\rho^n(\mathbf{U}_\epsilon) l v_2 = P_2(t_2)$. By induction, we conclude that (4.16) holds for all $n \geq 0$. Since $\rho(\mathbf{U}_\epsilon) > 1$, we obtain

$$\lim_{t\to\infty} P_i(t) \geq \lim_{n\to\infty} \rho^n(\mathbf{U}_\epsilon) l v_i = \infty,$$

a contradiction. This proves our claim.

Define $p : X \to \mathbb{R}_+$ by

$$p(\phi) = \min\{\phi_3(0), \phi_4(0)\} \quad \forall \phi \in X.$$

It is easy to see that $X_0 = p^{-1}(0, \infty)$ and $\partial X_0 = p^{-1}(0)$. Note that p is a generalized distance function for the semiflow $\mathbf{\Phi}(t) : X \to X$. Clearly, any forward orbit of $\mathbf{\Phi}(t)$ in M_∂ converges to E_0. By our claim, we see that E_0 is an isolated invariant set in X, and that $W^s(E_0) \cap X_0 = \emptyset$. By Theorem 2.17 (see also [26, Theorem 1.3.2]), we conclude that there exists a $\delta > 0$ such that $\min\{p(\psi) : \psi \in \omega(\phi)\} > \delta$ for any $\phi \in X_0$. This implies the uniform persistence of solutions of system (4.6), as required. □

Next we show that the disease dies out if $R_0 < 1$, provided that there is only a small invasion.

Theorem 4.3 *Let (H) hold. If $R_0 < 1$, then for every $L \geq L^*$, there exists a $\zeta = \zeta(L) > 0$ such that for any $\phi \in X_L$ with $(\phi_3(0), \phi_4(0)) \in [0, \zeta]^2$, the solution $(\mathbf{S}(t, \phi), \mathbf{P}(t, \phi), \mathbf{R}(t, \phi))$ of (4.6) converges to E_0 as $t \to \infty$.*

Proof. Let $L \geq L^*$ be given. By Lemma 4.1 and its proof, X_L is positively invariant for the solution semiflow of (4.6). We then have

$$(\mathbf{S}(t, \phi), \mathbf{P}(t, \phi), \mathbf{R}(t, \phi)) \in [0, L]^6, \forall t \geq 0, \phi \in X_L. \tag{4.17}$$

Set

$$V_\epsilon = \begin{bmatrix} k_1(S_1^* + \epsilon) \int_0^\tau b_{11}(a)da & k_2(S_2^* + \epsilon) \int_0^\tau b_{12}(a)da \\ k_1(S_1^* + \epsilon) \int_0^\tau b_{21}(a)da & k_2(S_2^* + \epsilon) \int_0^\tau b_{22}(a)da \end{bmatrix}.$$

By the continuity of the spectral radius of V_ϵ with respect to ϵ, we can restrict $\epsilon > 0$ small enough such that $\rho(V_\epsilon) < 1$. Now consider the following system:

$$\begin{aligned} \frac{du_1(t)}{dt} &= B_1(u_1(t))(u_1(t) + \xi_1) - (\mu_1 + d_1)u_1(t) + d_2 u_2(t), \\ \frac{du_2(t)}{dt} &= B_2(u_2(t))(u_2(t) + \xi_1) - (\mu_2 + d_2)u_2(t) + d_1 u_1(t). \end{aligned} \tag{4.18}$$

This cooperative system is a perturbation of (4.10). According to Theorem 2.18, for a small number $\xi_1 > 0$, this system has a globally asymptotically stable equilibrium

$(u_1(\xi_1), u_2(\xi_1))$ with the property $(u_1(\xi_1), u_2(\xi_2)) \to (S_1^*, S_2^*)$ as $\xi_1 \to 0$ for all positive solutions. Thus, we can choose a large number $T_1 = T_1(L) > 0$ such that, for any solution $(u_1(t), u_2(t))$ of (4.18) with $(u_1(0), u_2(0)) \in [0, L]^2$, we have $u_i(t) < S_i^* + \epsilon$, $i = 1, 2$, for all $t \geq T_1$. Similarly, we can select a small number $\xi_2 > 0$ and a large number $T_2 = T_2(L) > 0$ such that for any solution $(w_1(t), w_2(t))$ of the system

$$\begin{aligned} \frac{dw_1(t)}{dt} &= \xi_2 - (\mu_1 + c_1)w_1(t) + c_2 w_2(t), \\ \frac{dw_2(t)}{dt} &= \xi_2 - (\mu_2 + c_2)w_2(t) + c_1 w_1(t) \end{aligned} \tag{4.19}$$

with $(w_1(0), w_2(0)) \in [0, L]^2$, we have $w_i(t) < \xi_1/2$, $i = 1, 2$, for all $t \geq T_2$.

Let $v = (v_1, v_2)^T$ be a positive right eigenvector of V_ϵ associated with $\rho(V_\epsilon)$. Choose $\xi_3 > 0$ small enough such that

$$\xi_3(r_i v_i + b_{i1}(\tau)k_1 L v_1 + b_{i2}(\tau)k_2 L v_2) < \xi_2, \quad \xi_3 v_i < \xi_1/2, \quad i = 1, 2. \tag{4.20}$$

Let $T_3 = T_3(L) := \max\{T_1, T_2\} + \tau$ and $W := \mathrm{diag}(k_1 L, k_2 L)$. Then there exists $\zeta = \zeta(L) > 0$ such that for every solution $(P_1(t), P_2(t))$ of the linear system

$$\frac{dP(t)}{dt} = (W + B)P(t), \quad t \geq 0,$$

with $(P_1(0), P_2(0)) \in [0, \zeta]^2$, we have $P_i(t) < \xi_3 v_i$, $i = 1, 2$, for all $t \in [0, 2T_3]$. For a given $\phi \in X_L$ with $(\phi_3(0), \phi_4(0)) \in [0, \zeta]^2$, we let

$$(\mathbf{S}(t), \mathbf{P}(t), \mathbf{R}(t)) = (\mathbf{S}(t, \phi), \mathbf{P}(t, \phi), \mathbf{R}(t, \phi)).$$

By (4.6) and (4.17), we then have

$$\frac{d\mathbf{P}(t)}{dt} \leq (W + B)\mathbf{P}(t), \forall t \geq 0.$$

Since $\mathbf{P}(0) \in [0, \zeta]^2$, the comparison principle implies that

$$P_i(t) < \xi_3 v_i, \quad \forall t \in [0, 2T_3], \quad i = 1, 2. \tag{4.21}$$

We further claim that (4.21) holds for all $t \geq 0$. If the claim is not true, then there exists a $T_4 = T_4(\phi) > 2T_3$ such that $P_i(t) < \xi_3 v_i$ for $0 \leq t < T_4, i = 1, 2$, and $P_j(T_4) = \xi_3 v_j$ for $j = 1$ or $j = 2$. It follows from (4.6) and (4.20) that

$$\begin{aligned} \frac{dR_1(t)}{dt} &\leq \xi_2 - (\mu_1 + c_1)R_1(t) + c_2 R_2(t), \\ \frac{dR_2(t)}{dt} &\leq \xi_2 - (\mu_2 + c_2)R_2(t) + c_1 R_1(t), \end{aligned} \tag{4.22}$$

for $\tau \leq t \leq T_4$. By the comparison principle and the properties of system (4.19), we have $R_i(t) < \xi_1/2$, $i = 1, 2$, for all $t \in [T_3, T_4]$. It follows from (4.6) that

$$\begin{aligned} \frac{dS_1(t)}{dt} &< B_1(S_1(t))(S_1(t) + \xi_1) - (\mu_1 + d_1)S_1(t) + d_2 S_2(t), \\ \frac{dS_2(t)}{dt} &< B_2(S_2(t))(S_2(t) + \xi_1) - (\mu_2 + d_2)S_2(t) + d_1 S_1(t), \end{aligned} \tag{4.23}$$

for all $t \in [T_3, T_4]$. By the comparison principle and the properties of system (4.18), we obtain $S_i(t) < S_i^* + \epsilon$, $\forall t \in [T_3 + T_1, T_4], i = 1, 2$. Hence, (4.7) implies that for any

$t \in [2T_3, T_4]$, there hold

$$\begin{aligned} P_1(t) &< k_1(S_1^* + \epsilon) \int_0^\tau b_{11}(a) P_1(t-a) da + \\ &\quad k_2(S_2^* + \epsilon) \int_0^\tau b_{12}(a) P_2(t-a) da, \\ P_2(t) &< k_1(S_1^* + \epsilon) \int_0^\tau b_{21}(a) P_1(t-a) da + \\ &\quad k_2(S_2^* + \epsilon) \int_0^\tau b_{22}(a) P_2(t-a) da. \end{aligned} \tag{4.24}$$

It then follows that

$$P_1(t) < k_1(S_1^* + \epsilon)\xi_3 v_1 \int_0^\tau b_{11}(a)da + k_2(S_2^* + \epsilon)\xi_3 v_2 \int_0^\tau b_{12}(a)da = \rho(V_\epsilon)\xi_3 v_1,$$

$$P_2(t) < k_1(S_1^* + \epsilon)\xi_3 v_1 \int_0^\tau b_{21}(a)da + k_2(S_2^* + \epsilon)\xi_3 v_2 \int_0^\tau b_{22}(a)da = \rho(V_\epsilon)\xi_3 v_2,$$

for all $t \in [2T_3, T_4]$. Since $\rho(V_\epsilon) < 1$, we obtain $P_j(T_4) < \xi_3 v_j$ for $j = 1, 2$, which contradicts $P_j(T_4) = \xi_3 v_j$ for $j = 1$ or $j = 2$. This shows that $P_i(t) < \xi_3 v_i$, $i = 1, 2$, for all $t \geq 0$, and hence (4.24) holds for all $t \geq 2T_3$. By an induction argument similar to that in the proof of Theorem 4.2, it follows that $P_i(t) < \rho^n(V_\epsilon)\xi_3 v_i, \forall t \geq 2T_3 + n\tau$, $n \geq 0$, $i = 1, 2$, which implies that $\lim_{t\to\infty} P_i(t) = 0$, $i = 1, 2$. By the theory of chain transitive sets (see, e.g., [26, Theorem 1.2.1]), as argued in [22, Theorem 2.2], we further obtain that $(S_1(t), S_2(t), R_1(t), R_2(t)) \to (S_1^*, S_2^*, 0, 0)$ as $t \to \infty$. □

4.4 Examples

In this section, we analyze the effect of population dispersal on the spread of the disease. In doing this we must consider the behavior of the disease when the patches are isolated and compare this to when they are connected. In epidemiology the basic reproduction number R_0 characterizes this disease spread; if $R_0 > 1$ then the disease will persist and if $R_0 < 1$ the infection will die out in the long term. Therefore, for a given model, we can calculate a basic reproduction number as if the patches were disconnected and we can calculate the actual reproduction number when the dispersal parameters (b_i, c_i, d_i) are nonzero.

First we consider the disconnected system:

$$\begin{aligned}
\frac{dS_1}{dt} &= B_1(N_1)N_1 - \mu_1 S_1(t) - Q_1(t), \\
\frac{dP_1(t)}{dt} &= Q_1(t) - e^{-(\mu_1+r_1)\tau}Q_1(t-\tau) - (\mu_1 + r_1)P_1(t), \\
\frac{dR_1}{dt} &= r_1 P_1(t) + e^{-(\mu_1+r_1)\tau}Q_1(t-\tau) - \mu_1 R_1(t), \qquad (4.25) \\
N_1(t) &= S_1(t) + R_1(t) + P_1(t), t \geq 0, \\
P_1(0) &= \int_{-\tau}^{0} e^{(\mu_1+r_1)s}Q_1(s)ds,
\end{aligned}$$

and

$$\begin{aligned}
\frac{dS_2}{dt} &= B_2(N_2)N_2 - \mu_2 S_2(t) - Q_2(t), \\
\frac{dP_2(t)}{dt} &= Q_2(t) - e^{-(\mu_2+r_2)\tau}Q_2(t-\tau) - (\mu_2+r_2)P_2(t), \\
\frac{dR_2}{dt} &= r_2 P_2(t) + e^{-(\mu_2+r_2)\tau}Q_2(t-\tau) - \mu_2 R_2(t), \\
N_2(t) &= S_2(t) + R_2(t) + P_2(t), t \geq 0, \\
P_2(0) &= \int_{-\tau}^{0} e^{(\mu_2+r_2)s}Q_2(s)ds.
\end{aligned} \tag{4.26}$$

As in the proof of Lemma 4.1, by the properties of $B_i(N_i)$, there exists a unique $L_i > 0$ such that $B_i(L_i) = \mu_i$. Therefore, $E_{0i} = (L_i, 0, 0)$, $i = 1, 2$, is the disease-free equilibrium for patch i. Let R_{0i} be the basic reproduction number for patch i. By similar arguments as those for model (4.6), it then follows that

$$R_{0i} = k_i S_{0i}^* \int_0^\tau e^{-(\mu_i+r_i)a}da = k_i L_i \frac{(1-\exp(-(\mu_i+r_i)\tau))}{(\mu_i+r_i)},$$

and that $R_{0i} > 1$ implies that the disease is uniformly persistent in the isolated patch i. The next result shows that, for an isolated patch, the disease dies out if $R_{0i} < 1$.

Theorem 4.4 *Let the two patches be isolated. Then the disease-free equilibrium E_{0i} is globally attractive if $R_{0i} < 1$.*

Proof. We consider patch 1 since the proof for patch 2 is similar. It follows from

(4.25) that

$$\frac{dN_1}{dt} = (B_1(N_1) - \mu_1)N_1(t),$$

for an isolated patch. Therefore, as in the proof of Lemma 4.1 and as noted earlier,

$$N_1(t) \to L_1 \text{ as } t \to \infty. \tag{4.27}$$

Since $R_{01} < 1$, we can choose $\epsilon > 0$ small enough such that

$$R_{01}^{\epsilon} := \frac{k_1(L_1 + \epsilon)(1 - \exp(-(\mu_1 + r_1)\tau))}{\mu_1 + r_1} < 1. \tag{4.28}$$

We can choose $\bar{t} > 0$ large enough such that

$$S_1(t) < L_1 + \epsilon \text{ for } t \geq \bar{t}.$$

Since

$$P_1(t) = \int_{t-\tau}^{t} e^{-(\mu_1+r_1)(t-s)}Q_1(s)ds = \int_{-\tau}^{0} e^{(\mu_1+r_1)s}Q_1(t+s)ds, \qquad \forall t \geq 0,$$

it follows that

$$P_1(t) < k_1(S_{01}^{*} + \epsilon)\int_0^{\tau} e^{-(\mu_1+r_1)a}P_1(t-a)da, \quad \forall t \geq \bar{t} + \tau.$$

Fix a $\bar{v} > 0$ such that $P_1(t) < \bar{v}$ for $\bar{t} + \tau \leq t \leq \bar{t} + 2\tau$. By an induction argument similar to that in the proof of Theorem 4.3, it follows that

$$P_1(t) < (R_{01}^{\epsilon})^n \bar{v}, \forall t \geq \bar{t} + (n+1)\tau, n \geq 0.$$

Since $R_{01}^{\epsilon} < 1$, we have $P_1(t) \to 0$ as $t \to \infty$. By using the theory of chain transitive sets, we further obtain that $(S_1(t), R_1(t)) \to (L_1, 0)$ as $t \to \infty$. □

In order to perform numerical simulations, we must choose a specific birth function. The following birth rate functions are found frequently in biological literature:

(C1) $B_i(N_i) = H_i e^{-A_i N_i}$ with $A_i > 0, H_i > 0$.

(C2) $B_i(N_i) = \frac{p_i}{q_i + N_i^{m_i}}$ with $p_i > 0, q_i > 0, m_i > 0$.

(C3) $B_i(N_i) = \frac{A_i}{N_i} + H_i$ with $A_i > 0, H_i > 0$.

In [23] the birth rate function (C3) is used both in the proofs of the theorems in the previous section and in the numerical examples. Those simulations suggest that dispersal is often very important. There are cases where different levels of dispersal cause "switches" in R_0 being less than or larger than one. There are even cases where low and high dispersal have $R_0 > 1$ while a moderate dispersal has $R_0 < 1$. This may be due to the birth rate function; since $B_i(N_i)N_i = A_i + H_i N_i$ is a linear function, the number of births is proportional to the number of individuals with no saturation.

The function $G_i(N_i) = B_i(N_i)N_i$ behaves differently for large N_i in cases (C1),(C2) and (C3). For (C3), $G_i(N_i)$ is unbounded. For (C1), $G_i(N_i)$ tends to zero as $N_i \to \infty$. And for (C2), $G_i(N_i)$ tends to the constant p_i when we take $m_i = 1$. Depending on

the type of function used, it can lead to significant changes in the numerical modeling of a population.

In this project, we use the birth rate functions (C1) and (C2) for simulations. The objective is to find some interesting and representative dynamical behavior over several examples. It is also important to pay careful attention to the dispersal parameters since they characterize the patch environment. First, however, consider the following systems:

$$\begin{aligned}
\frac{dS_1}{dt} &= H_1 N_1(t) e^{-A_1 N_1} - \mu_1 S_1(t) - Q_1(t), \\
\frac{dP_1(t)}{dt} &= Q_1(t) - e^{-(\mu_1+r_1)\tau} Q_1(t-\tau) - (\mu_1 + r_1) P_1(t), \\
\frac{dR_1}{dt} &= r_1 P_1(t) + e^{-(\mu_1+r_1)\tau} Q_1(t-\tau) - \mu_1 R_1(t), \\
N_1(t) &= S_1(t) + R_1(t) + P_1(t), t \geq 0, \\
P_1(0) &= \int_{-\tau}^{0} e^{(\mu_1+r_1)s} Q_1(s) ds,
\end{aligned} \tag{4.29}$$

and

$$\begin{aligned}
\frac{dS_2}{dt} &= H_2 N_2(t) e^{-A_2 N_2} - \mu_2 S_2(t) - Q_2(t), \\
\frac{dP_2(t)}{dt} &= Q_2(t) - e^{-(\mu_2+r_2)\tau} Q_2(t-\tau) - (\mu_2 + r_2) P_2(t), \\
\frac{dR_2}{dt} &= r_2 P_2(t) + e^{-(\mu_2+r_2)\tau} Q_2(t-\tau) - \mu_2 R_2(t), \\
N_2(t) &= S_2(t) + R_2(t) + P_2(t), t \geq 0, \\
P_2(0) &= \int_{-\tau}^{0} e^{(\mu_2+r_2)s} Q_2(s) ds.
\end{aligned} \tag{4.30}$$

Systems (4.29) and (4.30) are isolated patches; that is, there is no dispersal between the patches. With the birth function (C1), the disease-free equilibrium for each is given by $E_{01} = (S_{01}^*, 0, 0)$ and $E_{02} = (S_{02}^*, 0, 0)$, where $S_{01}^* = \frac{1}{A_1}\ln(H_1/\mu_1)$, $S_{02}^* = \frac{1}{A_2}\ln(H_2/\mu_2)$. Thus, the basic reproduction number is given by:

$$R_{0i} = \ln\left(\frac{H_i}{\mu_i}\right) \frac{k_i(1 - \exp(-(\mu_i + r_i)\tau))}{A_i(\mu_i + r_i)}. \tag{4.31}$$

In the following examples, comparisons are made between the disease behavior in

the isolated patches and in the connected system:

$$\begin{aligned}
\frac{dS_1}{dt} &= H_1 N_1(t) e^{-A_1 N_1} - (\mu_1 + d_1) S_1(t) - Q_1(t) + d_2 S_2(t), \\
\frac{dS_2}{dt} &= H_2 N_2(t) e^{-A_2 N_2} - (\mu_2 + d_2) S_2(t) - Q_2(t) + d_1 S_1(t), \\
\frac{d\mathbf{P}}{dt} &= \mathbf{Q}(t) - \exp(\mathbf{B}\tau)\mathbf{Q}(t-\tau) + \mathbf{B}\mathbf{P}(t), \\
\frac{dR_1}{dt} &= \gamma_1(t) - (\mu_1 + c_1) R_1(t) + c_2 R_2(t), \\
\frac{dR_2}{dt} &= \gamma_2(t) - (\mu_2 + c_2) R_2(t) + c_1 R_1(t), \\
N_i(t) &= S_i(t) + R_i(t) + P_i(t), \quad i = 1, 2.
\end{aligned} \tag{4.32}$$

In these examples, we fix $A_1 = 0.2, A_2 = 0.3, H_1 = 2.6, H_2 = 2.0$. As in [23], we take the delay $\tau = 1$, the constant death rate to be $\mu_1 = \mu_2 = 0.2$ and the treatment rates to be $r_1 = r_2 = 0$. The parameter c_i, which is the dispersal rate of recovered individuals between the patches, is negligible since we assume that recovered individuals do not travel very much (in comparison to the rest of the population) after their recovery. Thus, we set $c_1 = c_2 = 0$. However, for the susceptible and infective patches, set $d_1 = d_2 = d$ and $b_1 = b_2 = 0.01d$. This means that individuals travel between the patches but that 99 percent of infected individuals cannot travel to screening and regulations while the other one percent represents the failure of control strategies. The parameter k_i is the force of infection in patch i and we adjust both k_i and d in these simulations. The initial data used here is: $S_1(0) = 1.5, S_2(0) =$

$1.2, R_1(0) = 0.5, R_2(0) = 0.3, P_1(\theta) = 0.8, P_2(\theta) = 0.6$ for $\theta \in [-\tau, 0]$. We note that the long-term behavior of these solutions does not change when many other (positive) initial data is used.

Example 1: $k_1 = 0.05, k_2 = 0.05$

The reproduction numbers for the isolated patches can be easily calculated by formula (4.31). We have that $R_{01} = 0.581$ and $R_{02} = 0.348$. Each is below 1 so the disease will die out over time and the disease-free equilibriums E_{01} and E_{02} are globally asymptotically stable. From an epidemiological standpoint, $1 > R_{01} > R_{02}$ means that the disease will last longer in patch 1 than in patch 2. This is explained by the parameters of the birth rate functions; in patch 1 the per capita birth rate is higher than in patch 2. When these patches are connected, the disease-free equilibrium (S_1^*, S_2^*) and R_0 can be calculated numerically. For $d = 0.5$, we find that $(S_1^*, S_2^*) = (11.25, 9.58)$ and that $R_0 = 0.509$. This means that the disease will die out, which is reasonable given that the disease does not persist in either patch by itself and the force of infection is low.

For $d = 5$, a much higher dispersion, $R_0 = 0.478$ which is a little lower but not much different. There is a change in value of the disease-free equilibrium; now, $(S_1^*, S_2^*) = (10.64, 10.41)$ and this is reasonable due to the large increase in dispersal between the patches. This change, however, is not very significant since we are much

more concerned with the basic reproduction number. In this case, the disease does not persist in isolated patches and does not persist when the patches are connected. This is a fairly typical result, observed here for both low and high levels of dispersal. See Figures 4.1-4.4 for plots of P_i versus t for both levels of dispersal.

Example 2: $k_1 = 0.05, k_2 = 0.13$

Here the disease transmission coefficient k_2 is larger than in our first example. This means that the disease spreads more easily in patch 2 than in patch 1. This is reflected by the reproduction numbers; $R_{01} = 0.581$ and $R_{02} = 0.904$. Thus, the disease will not persist in either patch. For the connected system, however, $R_0 = 1.13$ when $d = 0.5$. Here, dispersal facilitates persistence and from Figures 4.5 and 4.6, the relative levels of infected individuals is quite small. Note that the size of the infected population converges to a constant fairly quickly.

For $d = 5$, $R_0 = 1.20$ which is not much of a change. But the size of the infected populations in each patch has grown considerably (see Figures 4.7 and 4.8). This result shows that dispersal can allow a disease to persist when it would not in each isolated patch. However it appears that, for this choice of birth rate function, the value of d is not very important.

Example 3: $k_1 = 0.13, k_2 = 0.05$

In this example, $R_{01} = 1.51$ and $R_{02} = 0.348$. The introduction of low dispersal,

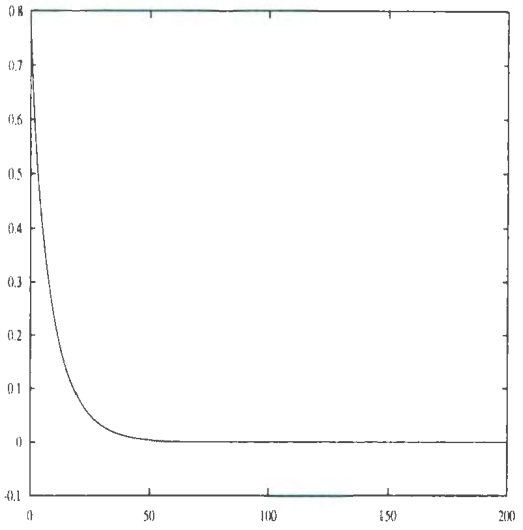

Fig. 4.1: d=0.5, P1 vs t

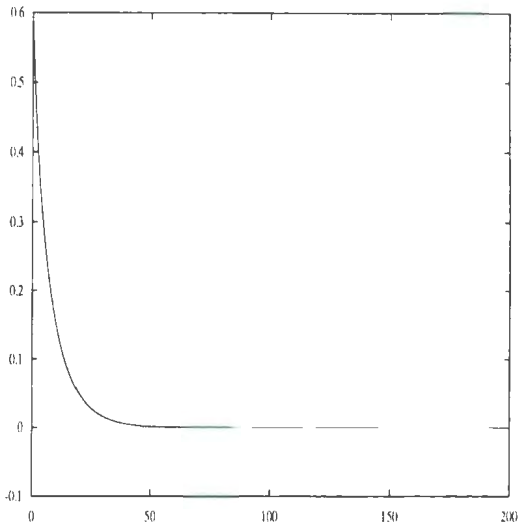

Fig. 4.2: d=0.5, P2 vs t

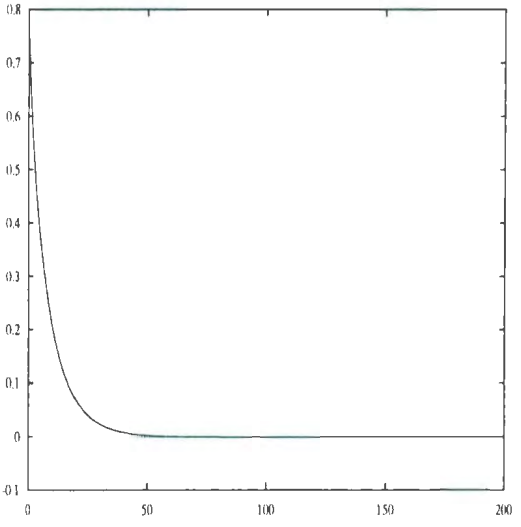

Fig. 4.3: d=5, P1 vs t

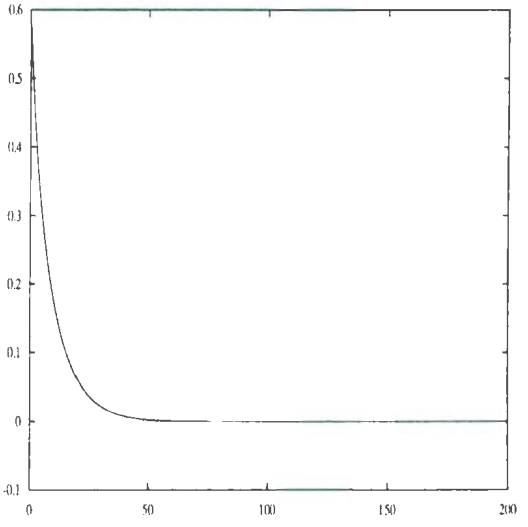

Fig. 4.4: d=5, P2 vs t

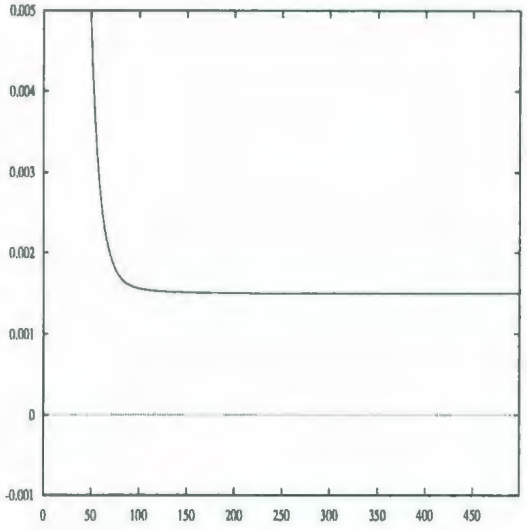

Fig. 4.5: d=0.5, P1 vs t

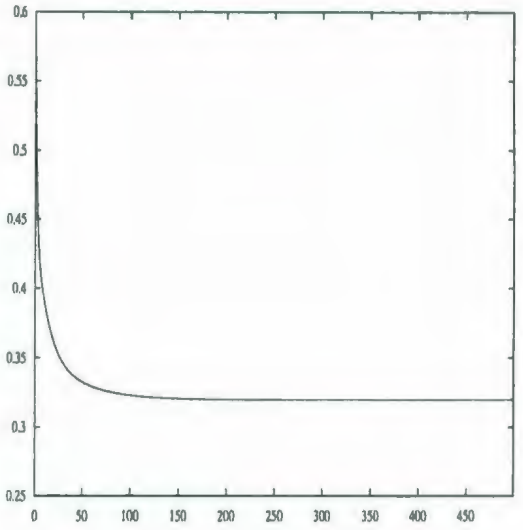

Fig. 4.6: d=0.5, P2 vs t

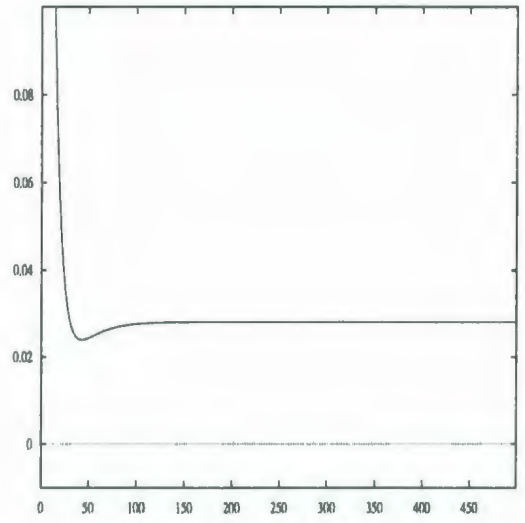

Fig. 4.7: d=5, P1 vs t

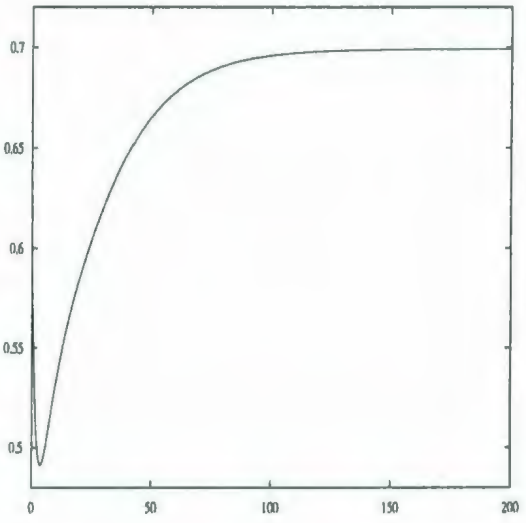

Fig. 4.8: d=5, P2 vs t

$d = 0.5$, yields $R_0 = 1.32$. In this case, dispersal promotes persistence of the disease. For $d = 5$, the reproduction number $R_0 = 1.22$ and although it has decreased, it is still larger than one. As in the previous example the size of the epidemic populations in each patch has grown significantly with the larger value of d (see Figures 4.9-4.12).

It appears that dispersal does not affect R_0 very much but does affect epidemic population sizes for the birth rate function (C1). We now consider (C2).

$$\begin{aligned}
\frac{dS_1}{dt} &= \frac{p_1}{q_1 + N_1} - (\mu_1 + d_1)S_1(t) - Q_1(t) + d_2 S_2(t), \\
\frac{dS_2}{dt} &= \frac{p_1}{q_1 + N_1} - (\mu_2 + d_2)S_2(t) - Q_2(t) + d_1 S_1(t), \\
\frac{d\mathbf{P}}{dt} &= \mathbf{Q}(t) - \exp(\mathbf{B}\tau)\mathbf{Q}(t-\tau) + \mathbf{B}\mathbf{P}(t), \\
\frac{dR_i}{dt} &= \gamma_1(t) - (\mu_1 + c_1)R_1(t) + c_2 R_2(t), \\
\frac{dR_2}{dt} &= \gamma_2(t) - (\mu_2 + c_2)R_2(t) + c_1 R_1(t), \\
N_i(t) &= S_i(t) + R_i(t) + P_i(t), \quad i = 1, 2
\end{aligned} \tag{4.33}$$

Then $S_{01}^* = \frac{p_1}{\mu_1} - q_1$, $S_{02}^* = \frac{p_2}{\mu_2} - q_2$ and the basic reproduction number is given by:

$$R_{0i} = k_i(p_i - q_i\mu_i)\frac{(1 - \exp(-(\mu_i + r_i)\tau))}{\mu_i(\mu_i + r_i)}. \tag{4.34}$$

We now look at two examples. Set $p_1 = 1.6, p_2 = q_1 = q_2 = 1.0$.

Example 4: $k_1 = 0.10, k_2 = 0.10$

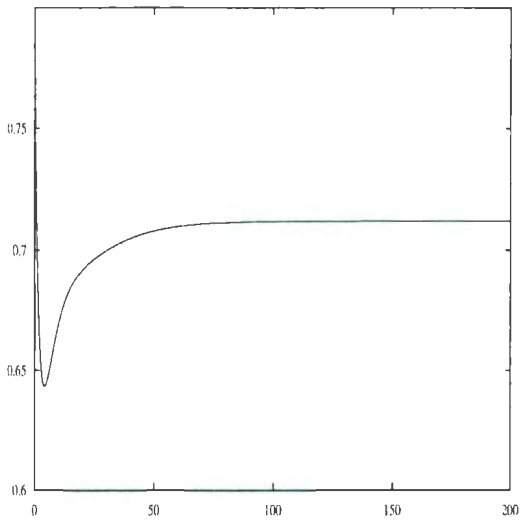

Fig. 4.9: d=0.5, P1 vs t

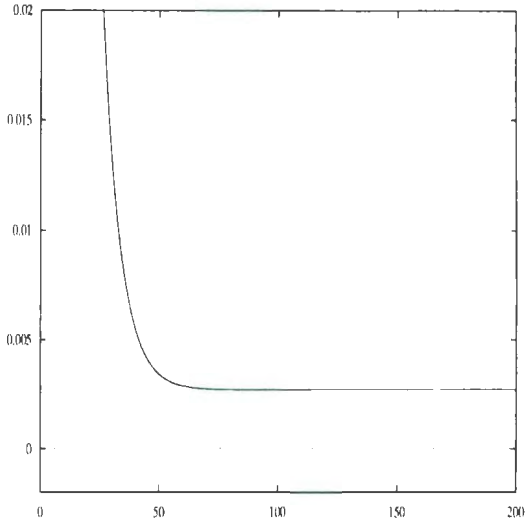

Fig. 4.10: d=0.5, P2 vs t

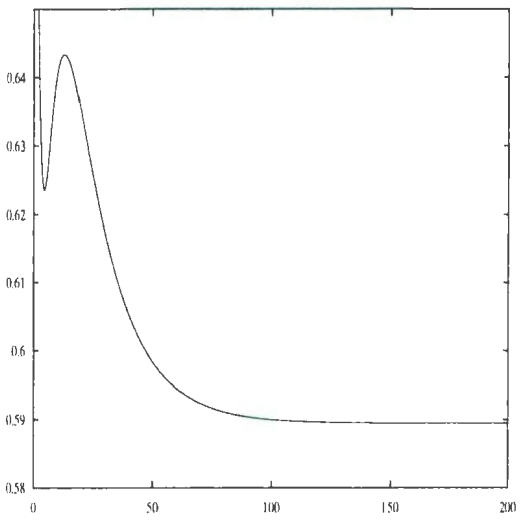

Fig. 4.11: d=5, P1 vs t

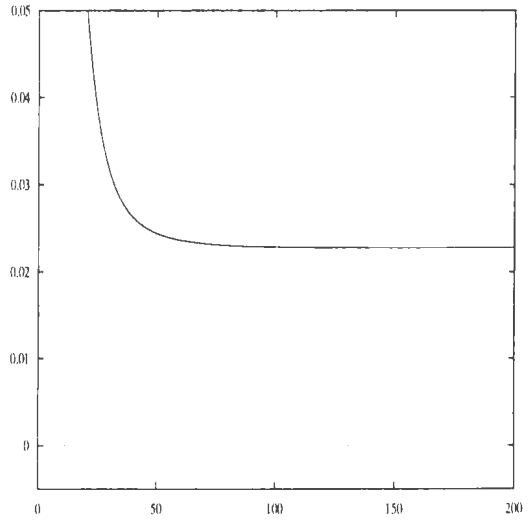

Fig. 4.12: d=5, P2 vs t

Here we have the same force of infection in each patch. The reproduction numbers for the isolated patches are $R_{01} = 0.634$ and $R_{02} = 0.363$. Therefore, patch 1 is not as good as patch 2 from an epidemiological standpoint. The disease does not persist in either patch, though, since each reproduction number is less than one. When $d = 0.5$, the reproduction number for the connected system is $R_0 = 0.518$. If the dispersal is increased significantly, for example $d = 5$, then we have $R_0 = 0.499$. As in example 1, there is not much of a change. In fact, for $d = 0.5$, $(S_1^*, S_2^*) = (5.72, 5.29)$ and, for $d = 5$, $(S_1^*, S_2^*) = (5.53, 5.48)$. This is similar to the first example because a higher dispersion seems to lead to the equilibriums of each patch becoming closer to equal as dispersion increases. This is illustrated in Figures 4.13-4.16.

Example 5: $k_1 = 0.20, k_2 = 0.10$

Now the force of infection in patch 1 is twice that of patch 2. Without dispersal, $R_{01} = 1.27$ and $R_{02} = 0.363$ so the disease is persistent in one patch and not in the other. Introducing a low level of dispersion, $d = 0.5$, the overall reproduction number is $R_0 = 1.04$. This means that the disease is persistent but the size of the endemic populations may be quite small. See, for example, Figures 4.17 and 4.18.

To contrast this, we find that a high dispersal, $d = 5$, causes a major change. Now $R_0 = 0.980$ and through numerical simulations, we confirm that the disease will die out over time. The convergence is slower since the value of R_0 is so close to one.

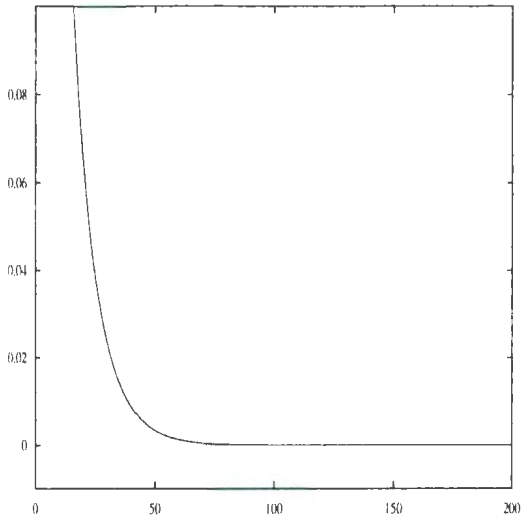

Fig. 4.13: d=0.5, P1 vs t

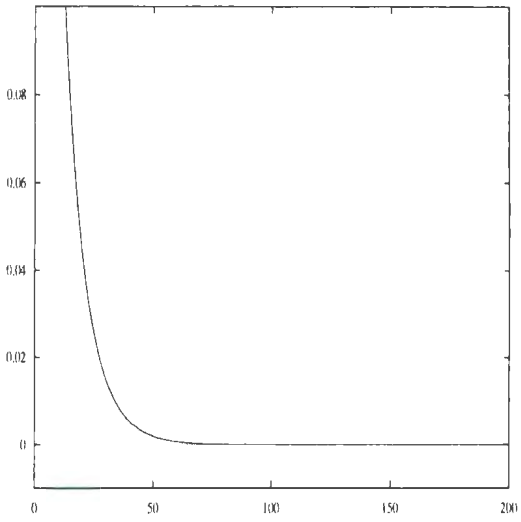

Fig. 4.14: d=0.5, P2 vs t

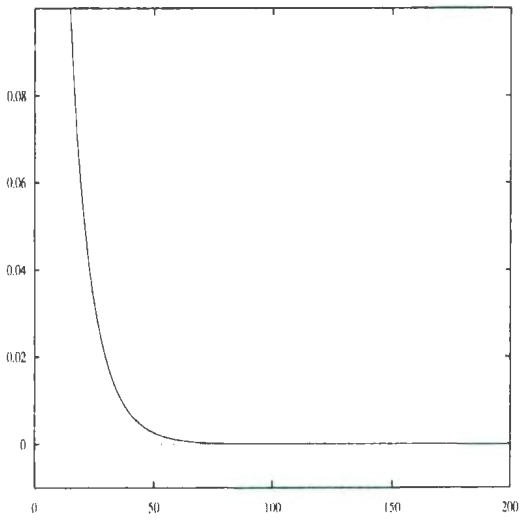

Fig. 4.15: d=5, P1 vs t

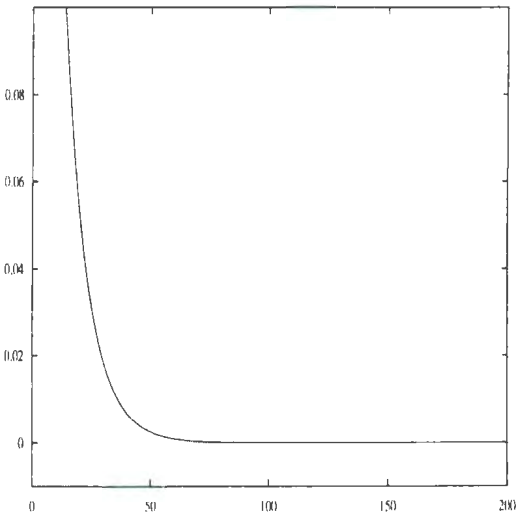

Fig. 4.16: d=5, P2 vs t

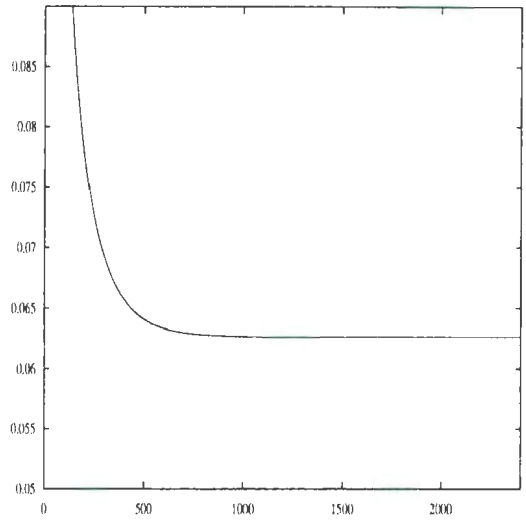

Fig. 4.17: d=0.5, P1 vs t

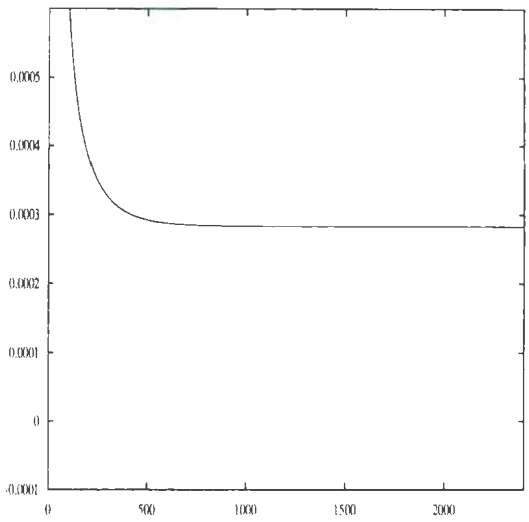

Fig. 4.18: d=0.5, P2 vs t

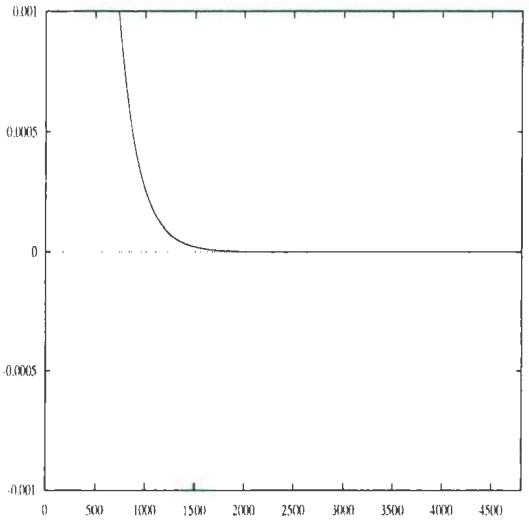

Fig. 4.19: d=5, P1 vs t

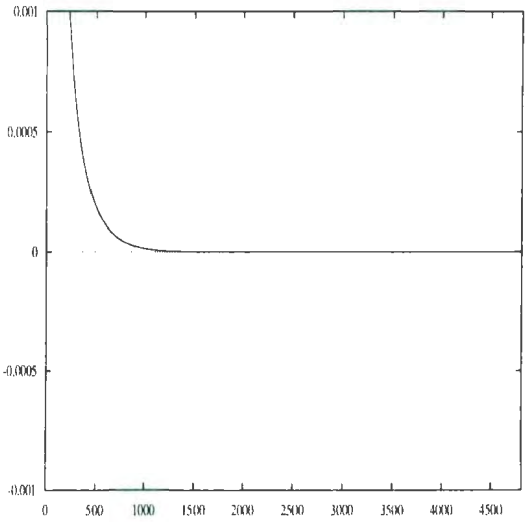

Fig. 4.20: d=5, P2 vs t

Figures 4.19 and 4.20 illustrate this phenomenon.

4.5 Discussion

In this project, we analysed an epidemic model proposed in [23] to simulate the dynamics of disease transmission when the population is dispersed among patches. This model, which incorporates a constant infection period, uses dispersal to represent the movements of people by travel or migration from different cities, regions or countries. Using the assumptions that the death rates, disease transmission coefficients, the treatment rates and the migration rates are constant for infected individuals, this model becomes a time-delayed differential system. As in [23], we define the basic reproduction number.

This model uses the standard nonlinear birth function $B(N)$ discussed in [4]. We have proven that for two patches the disease is uniformly persistent if $R_0 > 1$ and the disease cannot invade if $R_0 < 1$, provided that the invasion intensity is not strong. The choice of the function $B(N)N$ for numerical simulations is very important; here, we use two common nonlinear birth functions different from the simulations in [23] where $B(N)N = A + HN$, a linear function. Examples 1 through 3 suggest that dispersal is not very significant when the birth function $B(N) = H\exp(-AN)$ is used since only small changes in the reproduction number is shown with low and high

dispersal rates. Examples 4 and 5 suggest that dispersal is somewhat significant for models where $B(N) = \frac{pN}{q+N}$. Indeed, the last example shows a case where larger levels of dispersal cause the disease to go extinct. In [23] examples are used to illustrate that dispersal can both help eliminate or promote disease transmission, so this agrees with those conclusions.

In [23], the linearity of $B(N)N$ allowed for an explicit calculation of the disease-free equilibrium. This simplified the numerical simulations and made it easier to plot R_0 versus d. For more complicated birth rate functions, these more illustrative techniques are more difficult (and sometimes impossible) to employ. In future work, it would be interesting to expand on the simulations here with the other birth functions. From a theoretical standpoint, future work could include an age-structure in this model through death rates, infection force or migration rates.

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