Mathematical Biosciences 222 (2009) 42–52

Contents lists available at ScienceDirect

Mathematical Biosciences

journal homepage: www.elsevier.com/locate/mbs

Competition and coexistence in flowing habitats with a hydraulic storage zone

James P. Grover [a,*], Sze-Bi Hsu [b], Feng-Bin Wang [b]

[a] Department of Biology and Program in Environmental and Earth Sciences, University of Texas at Arlington, Box 19498, Arlington, TX 76019, United States
[b] Department of Mathematics, National Tsing-Hua University, Hsinchu 300, Taiwan

ARTICLE INFO

Article history:
Received 12 March 2009
Received in revised form 13 August 2009
Accepted 19 August 2009
Available online 23 August 2009

Keywords:
Competition
Coexistence
Chemostat
Monotone dynamical system
Theoretical ecology
Hydraulic storage zone
Flow reactor
Flowing habitats
Maximum principle
Upper solutions
Lower solutions
Global stability

ABSTRACT

This paper examines a model of a flowing water habitat with a hydraulic storage zone in which no flow occurs. In this habitat, one or two microbial populations grow while consuming a single nutrient resource. Conditions for persistence of one population and coexistence of two competing populations are derived from eigenvalue problems, the theory of bifurcation and the theory of monotone dynamical systems. A single population persists if it can invade the trivial steady state of an empty habitat. Under some conditions, persistence occurs in the presence of a hydraulic storage zone when it would not in an otherwise equivalent flowing habitat without such a zone. Coexistence of two competing species occurs if each can invade the semi-trivial steady state established by the other species. Numerical work shows that both coexistence and enhanced persistence due to a storage zone occur for biologically reasonable parameters.
© 2009 Elsevier Inc. All rights reserved.

1. Introduction

In ecology, the understanding of competition between species for resources has been greatly facilitated by the theory of the chemostat. The chemostat is a continuous culture device of constant volume for microorganisms into which a nutrient medium is pumped, balanced by an outflow that removes nutrients and organisms. Resident species compete for the nutrient resource(s) needed for growth, and the culture vessel is well mixed. Under this mixing assumption, an extensive body of theory addresses competition and coexistence [12,29].

The chemostat provides a simple model for many microbial habitats, but the assumption of idealized mixing is often questionable, and several models have been introduced where the habitat is not well mixed. For the unstirred chemostat, flow enters at one boundary supplying nutrient resource(s), and exits at another, removing nutrients and organisms, while diffusion transports organisms and nutrient across the habitat domain [13]. The flow reactor model has similar boundary flows, but with advective transport in addition to diffusion [2,18,27]. Assuming that a single nutrient governs population growth, conditions for persistence of a single species and for coexistence of two competing species in these habitats have been derived by similar approaches. One species persists and reaches steady state if it invades under the nutrient conditions pertaining to the trivial equilibrium, expressed as a principal eigenvalue problem. If two species can each persist alone, then the two can also coexist if each can invade the semi-trivial equilibrium defined by the steady state of the other species. These invasion conditions again involve principal eigenvalue problems. For flow reactor models, these persistence conditions involve the advective flow term, among others.

Motivated by considering habitats such as broad high-order rivers or riverine reservoirs constructed by damming a river, we introduce a modification of the flow reactor model. Rapid advective flow in such habitats can prevent persistence even of one species for realistic parameters. The presence of hydraulic storage zones in flowing water habitats might resolve this persistence paradox [25]. Storage zones were originally introduced in hydraulic models to accurately describe transport of non-reactive tracers [3]. Here we introduce a storage zone model for phytoplankton growing in both the flowing zone and the storage zone and derive conditions for persistence of a single species and coexistence of two competing species.

2. The model

The model represents the dynamics of one nutrient and one or two phytoplankton populations in a channel of length L. The cross-

* Corresponding author. Tel.: +1 817 272 2405; fax: +1 817 272 2855.
E-mail address: grover@uta.edu (J.P. Grover).

0025-5564/$ - see front matter © 2009 Elsevier Inc. All rights reserved.
doi:10.1016/j.mbs.2009.08.006

section of the channel is partitioned into a flowing zone of area A, and a static storage zone of area A_S (assumed to be constants here). Exchange of nutrient and populations between the flowing and storage zones occurs by Fickian diffusion with rate α (time^{-1}). Flow enters at the upstream end of the channel ($x = 0$), and an equal flow exits at the downstream end ($x = L$). Flow is parameterized as a constant dilution rate D (time^{-1}), and assuming constant water volume in the channel implies that advection occurs at a speed v ($v = DL$). The habitat for organisms occupies the portion of the channel from $x = 0$ to $x = L$ in which the populations $N_i(x,t),\ i = 1, 2$ compete for nutrient $R(x,t)$. The competition is purely exploitative in the sense that organisms simply consume the nutrient, thereby making it unavailable for competitors. The flow of water in the channel in the direction of increasing x brings fresh nutrient at a constant concentration $R^{(0)}$ into the reactor at $x = 0$ and carries medium, unused nutrient and organisms out of the reactor at $x = L$. Nutrient and organisms are assumed to diffuse throughout the vessel with the same diffusivity δ. Both advective and diffusive transport occur at the upstream boundary ($x = 0$). The downstream boundary is assumed to be a dam, over which there is advective flow but through which no diffusion can take place. Let $R_S(x,t),\ N_{S,i}(x,t)$ denote nutrient concentration and population densities in the storage zone respectively. Given these assumptions, the governing equations are

$$\begin{aligned}
\frac{\partial R}{\partial t} &= \delta\frac{\partial^2 R}{\partial x^2} - v\frac{\partial R}{\partial x} - q_1 f_1(R)N_1 - q_2 f_2(R)N_2 + \alpha(R_S - R),\\
\frac{\partial N_1}{\partial t} &= \delta\frac{\partial^2 N_1}{\partial x^2} - v\frac{\partial N_1}{\partial x} + \alpha(N_{S,1} - N_1) + f_1(R)N_1,\\
\frac{\partial N_2}{\partial t} &= \delta\frac{\partial^2 N_2}{\partial x^2} - v\frac{\partial N_2}{\partial x} + \alpha(N_{S,2} - N_2) + f_2(R)N_2,\\
\frac{\partial R_S}{\partial t} &= -\alpha\frac{A}{A_S}(R_S - R) - q_1 f_1(R_S)N_{S,1} - q_2 f_2(R_S)N_{S,2},\\
\frac{\partial N_{S,1}}{\partial t} &= -\alpha\frac{A}{A_S}(N_{S,1} - N_1) + f_1(R_S)N_{S,1},\\
\frac{\partial N_{S,2}}{\partial t} &= -\alpha\frac{A}{A_S}(N_{S,2} - N_2) + f_2(R_S)N_{S,2}, \quad 0 < x < L,\ \ t > 0
\end{aligned} \tag{2.1}$$

with boundary conditions

$$\begin{aligned}
&vR(0,t) - \delta\frac{\partial R}{\partial x}(0,t) = vR^{(0)},\\
&vN_i(0,t) - \delta\frac{\partial N_i}{\partial x}(0,t) = 0,\\
&\frac{\partial R}{\partial x}(L,t) = \frac{\partial N_i}{\partial x}(L,t) = 0, \quad i = 1,2,
\end{aligned} \tag{2.2}$$

and initial conditions

$$\begin{aligned}
&R(x,0) = R^0(x) \geqslant 0, \quad N_i(x,0) = N_i^0(x) \geqslant 0, \quad 0 < x < L,\\
&R_S(x,0) = R_S^0(x) \geqslant 0, \quad N_{S,i}(x,0) = N_{S,i}^0(x) \geqslant 0, \quad i = 1,2,
\end{aligned} \tag{2.3}$$

where q_i is the constant nutrient quota for species i.

The non-linear functions $f_i(R)$ describe the nutrient uptake and growth rates of species i at nutrient concentration R. We assume that these functions satisfy

$$f_i(0) = 0, \quad f_i'(R) > 0, \quad f_i \in C^2, \quad i = 1,2.$$

A usual example is the Monod function

$$f_i(R) = \frac{\mu_{\max,i}R}{K_{\mu,i} + R}.$$

In the following, we will demonstrate that mass conservation is satisfied in the flow and storage zones for the equations given by (2.1)–(2.3). Let

$$T(x,t) = R(x,t) + q_1N_1(x,t) + q_2N_2(x,t),$$

and

$$U(x,t) = R_S(x,t) + q_1N_{S,1}(x,t) + q_2N_{S,2}(x,t).$$

Then $T(x,t)$ and $U(x,t)$ satisfy the following coupled differential equations

$$\begin{aligned}
\frac{\partial T}{\partial t} &= \delta\frac{\partial^2 T}{\partial x^2} - v\frac{\partial T}{\partial x} + \alpha U - \alpha T,\\
\frac{\partial U}{\partial t} &= -\alpha\frac{A}{A_S}U + \alpha\frac{A}{A_S}T, \quad 0 < x < L,\ \ t > 0
\end{aligned} \tag{2.4}$$

with boundary conditions

$$vT(0,t) - \delta\frac{\partial T}{\partial x}(0,t) = vR^{(0)}, \frac{\partial T}{\partial x}(L,t) = 0, \tag{2.5}$$

and initial conditions

$$T(x,0) = T^0(x) \geqslant 0, \quad U(x,0) = U^0(x) \geqslant 0. \tag{2.6}$$

Let

$$\Sigma = \{(T^0, U^0) \in (C([0,L]))^2 | T^0(x) \geqslant 0, U^0(x) \geqslant 0 \text{ on } [0,L]\}.$$

Obviously, (2.4), (2.5) and (2.6) is a cooperative system and its solutions generate a strongly monotone semiflow in the interior of Σ ([27]). From ([27, p. 130]), we note that $(M,M)((m,m))$ is a strictly upper (lower) solution for the system (2.4), (2.5) and (2.6) provided that $M > R^{(0)}(m < R^{(0)})$. It is easy to see that (2.4), (2.5) and (2.6) has a unique steady-state solution $(R^{(0)}, R^{(0)})$. For a monotone dynamical system, the unique steady state is globally asymptotically stable if and only if every forward orbit has compact closure (see [14, Theorem D]). Thus, $(R^{(0)}, R^{(0)})$ is globally asymptotically stable, that is,

$$\lim_{t\to\infty}(T(x,t), U(x,t)) = (R^{(0)}, R^{(0)}) \text{ uniformly for } x \in [0,L].$$

Thus, we conclude that the limiting systems of (2.1), (2.2) and (2.3) take the forms

$$\begin{aligned}
\frac{\partial N_1}{\partial t} &= \delta\frac{\partial^2 N_1}{\partial x^2} - v\frac{\partial N_1}{\partial x} + \alpha(N_{S,1} - N_1) + f_1(R^{(0)} - q_1N_1 - q_2N_2)N_1,\\
\frac{\partial N_{S,1}}{\partial t} &= -\alpha\frac{A}{A_S}(N_{S,1} - N_1) + f_1(R^{(0)} - q_1N_{S,1} - q_2N_{S,2})N_{S,1}, 0 < x < L,\ t > 0\\
\frac{\partial N_2}{\partial t} &= \delta\frac{\partial^2 N_2}{\partial x^2} - v\frac{\partial N_2}{\partial x} + \alpha(N_{S,2} - N_2) + f_2(R^{(0)} - q_1N_1 - q_2N_2)N_2,\\
\frac{\partial N_{S,2}}{\partial t} &= -\alpha\frac{A}{A_S}(N_{S,2} - N_2) + f_2(R^{(0)} - q_1N_{S,1} - q_2N_{S,2})N_{S,2},
\end{aligned} \tag{2.7}$$

with boundary conditions

$$\begin{aligned}
&vN_i(0,t) - \delta\frac{\partial N_i}{\partial x}(0,t) = 0,\\
&\frac{\partial N_i}{\partial x}(L,t) = 0, \quad i = 1,2,
\end{aligned} \tag{2.8}$$

and initial conditions

$$\begin{aligned}
&N_i(x,0) = N_i^0(x) \geqslant 0,\\
&N_{S,i}(x,0) = N_{S,i}^0(x) \geqslant 0, \quad 0 < x < L, \quad i = 1,2.
\end{aligned} \tag{2.9}$$

From the biological viewpoint, the initial value functions for the limiting system (2.7), (2.8) and (2.9) are given by

$$\begin{aligned}
\Omega = \Big\{ &\left(N_1^0, N_{S,1}^0, N_2^0, N_{S,2}^0\right) \in (C([0,L]))^4 | N_i^0(x) \geqslant 0, N_{S,i}^0(x) \geqslant 0, q_1N_1^0(x)\\
&+ q_2N_2^0(x) \leqslant R^{(0)},\ q_1N_{S,1}^0(x) + q_2N_{S,2}^0(x) \leqslant R^{(0)} \text{ on } [0,L],\ i = 1,2. \Big\}.
\end{aligned} \tag{2.10}$$

A similar model of competition between two species for a nutrient in a habitat with flow was formulated by Kung and Baltzis in [18] and analyzed by Smith [27]. Their governing equations are

$$\frac{\partial R}{\partial t} = \delta\frac{\partial^2 R}{\partial x^2} - v\frac{\partial R}{\partial x} - q_1 f_1(R)N_1 - q_2 f_2(R)N_2,$$
$$\frac{\partial N_1}{\partial t} = \delta\frac{\partial^2 N_1}{\partial x^2} - v\frac{\partial N_1}{\partial x} + f_1(R)N_1, \tag{2.11}$$
$$\frac{\partial N_2}{\partial t} = \delta\frac{\partial^2 N_2}{\partial x^2} - v\frac{\partial N_2}{\partial x} + f_2(R)N_2, \quad 0 < x < L, \ t > 0$$

with the usual boundary conditions (2.2) and initial conditions.

This earlier model lacks a hydraulic storage zone but is otherwise similar to system (2.1), (2.2) and (2.3), and in particular it has the following limiting system:

$$\frac{\partial N_1}{\partial t} = \delta\frac{\partial^2 N_1}{\partial x^2} - v\frac{\partial N_1}{\partial x} + f_1(R^{(0)} - q_1N_1 - q_2N_2)N_1,$$
$$\frac{\partial N_2}{\partial t} = \delta\frac{\partial^2 N_2}{\partial x^2} - v\frac{\partial N_2}{\partial x} + f_2(R^{(0)} - q_1N_1 - q_2N_2)N_2, \tag{2.12}$$
$$0 < x < L, \ t > 0$$

with boundary conditions (2.8) and initial conditions that resemble (2.7), (2.8) and (2.9) with terms relating to the storage zone omitted. System (2.1), (2.2) and (2.3) generalizes these earlier models by adding a hydraulic storage zone, and has some similar properties as elaborated below. In another related work [1], the model in [18,27] is generalized by considering cell death and dropping the assumption that diffusivities of nutrient and organisms are identical.

3. Single population model

In this section, we first consider the single population model. Mathematically, it simply means that we set $(N_1, N_{S,1}) = (0, 0)$ or $(N_2, N_{S,2}) = (0, 0)$ in equations (2.7), (2.8) and (2.9). In order to simplify notation, all subscripts are dropped in the remaining equations and we consider

$$\frac{\partial N}{\partial t} = \delta\frac{\partial^2 N}{\partial x^2} - v\frac{\partial N}{\partial x} + \alpha(N_S - N) + f(R^{(0)} - qN)N,$$
$$\frac{\partial N_S}{\partial t} = -\alpha\frac{A}{A_S}(N_S - N) + f(R^{(0)} - qN_S)N_S, \quad 0 < x < L, \ t > 0, \tag{3.1}$$

with boundary conditions

$$vN(0,t) - \delta\frac{\partial N}{\partial x}(0,t) = 0,$$
$$\frac{\partial N}{\partial x}(L,t) = 0, \tag{3.2}$$

and initial conditions

$$N(x,0) = N^0(x) \geqslant 0,$$
$$N_S(x,0) = N_S^0(x) \geqslant 0, \quad 0 < x < L. \tag{3.3}$$

The biologically relevant domain for the system (3.1), (3.2) and (3.3) is given by

$$\Delta = \Big\{\Big(N^0, N_S^0\Big) \in (C([0,L]))^2 | N^0(x) \geqslant 0, \ N_S^0(x) \geqslant 0,$$
$$qN^0(x) \leqslant R^{(0)}, \ qN_S^0(x) \leqslant R^{(0)} \text{ on } [0,L]\Big\}.$$

By the theory of C_0 semigroups of bounded linear operators in a Banach space (see [23]) and in [19, Theorem 1, Remark 1.1, 1.10] (taking delay as zero), it follows that for every initial value function (N^0, N_S^0) in a suitable space, system (3.1), (3.2) and (3.3) has a unique non-continuable solution

$$\Big(N(x,t,(N^0,N_S^0)), N_S\Big(x,t,\Big(N^0,N_S^0\Big)\Big)\Big),$$

with the maximal interval of existence $[0, \tau\Big(N^0, N_S^0\Big))$ and $\tau\Big(N^0, N_S^0\Big) = \infty$ provided $(N\Big(x,t,\Big(N^0,N_S^0\Big)\Big), N_S\Big(x,t,\Big(N^0,N_S^0\Big)\Big)$ has an L^∞-bound on $[0, \tau\Big(N^0, N_S^0\Big))$. The solution semiflow is defined by

$$\Phi_t(N^0, N_S^0) = \Big(N\Big(.,t,\Big(N^0,N_S^0\Big)\Big), N_S\Big(.,t,\Big(N^0,N_S^0\Big)\Big)\Big).$$

In order to prove the positive invariance of the set Δ under the semi-flow Φ_t generated by (3.1), (3.2) and (3.3), we need to extend the function $f(R)$ in a natural way as follows:

$$\hat{f}(R) = \begin{cases} f(R) & \text{for } R \geqslant 0, \\ -f(|R|) & \text{for } R < 0. \end{cases} \tag{3.4}$$

Introduce

$$Y = R^{(0)} - qN, \ Y_S = R^{(0)} - qN_S.$$

Now, we consider the extended system corresponding to (3.1), (3.2) and (3.3)

$$\frac{\partial N}{\partial t} = \delta\frac{\partial^2 N}{\partial x^2} - v\frac{\partial N}{\partial x} + \alpha(N_S - N) + \hat{f}(Y)N,$$
$$\frac{\partial N_S}{\partial t} = -\alpha\frac{A}{A_S}(N_S - N) + \hat{f}(Y_S)N_S, \quad 0 < x < L, \ t > 0, \tag{3.5}$$

with boundary conditions (3.2) and initial conditions (3.3).

Proposition 3.1. *The interior of Δ is positively invariant under the semiflow Φ_t generated by* (3.1), (3.2) and (3.3).

Proof. It suffices to show that the set Δ is positively invariant under the semiflow Φ_t generated by (3.5). Fix any pair of initial value functions (N^0, N_S^0) in Δ. By the continuity of the solutions with respect to initial value functions, we may assume that $0 < N^0(x) < \frac{R^{(0)}}{q}$ and $0 < N_S^0(x) < \frac{R^{(0)}}{q}$ on $[0, L]$. Thus $\Phi_t(N^0, N_S^0) \in \Delta$ for all sufficiently small t.

Suppose that the Proposition is false. Let

$$t^* = \sup\{\tau \Phi_t\Big(N^0, N_S^0\Big) \in \Delta \text{ on } [0,\tau]\}.$$

Then $0 < t^* < \tau(N^0, N_S^0)$. This implies that one of the following four cases (see Fig. 1) must occur.

(I) $N(x,t) > 0$ for all $0 \leqslant x \leqslant L$, $0 \leqslant t < t^*$, and $N(x^*, t^*) = 0$ for some x^* in $[0, L]$, and $N_S(x,t) \geqslant 0$, $Y(x,t) \geqslant 0$, $Y_S(x,t) \geqslant 0$ on $[0,L] \times [0,t^*]$;

(II) $N_S(x,t) > 0$ for all $0 \leqslant x \leqslant L$, $0 \leqslant t < t^*$, $N_S(x^*, t^*) = 0$ for some x^* in $[0, L]$, and $Y(x,t) \geqslant 0$, $Y_S(x,t) \geqslant 0$, $N(x,t) > 0$ on $[0,L] \times [0,t^*]$;

(III) $Y(x,t) > 0$ for all $0 \leqslant x \leqslant L$, $0 \leqslant t < t^*$, for any $t > t^*$ sufficiently close to t^* there is a point $(\bar{x}, \bar{t}) \in [0,L] \times (t^*, t)$ such that $Y(\bar{x}, \bar{t}) < 0$, and $Y_S(x,t) \geqslant 0$, $N(x,t) > 0$, $N_S(x,t) > 0$ on $[0,L] \times [0,t^*]$;

(IV) $Y_S(x,t) > 0$ for all $0 \leqslant x \leqslant L$, $0 \leqslant t < t^*$, for any $t > t^*$ sufficiently close to t^* there is a point $(\bar{x}, \bar{t}) \in [0,L] \times (t^*, t)$ such that $Y_S(\bar{x}, \bar{t}) < 0$, and $Y(x,t) > 0$, $N(x,t) > 0$, $N_S(x,t) > 0$ on $[0,L] \times [0,t^*]$.

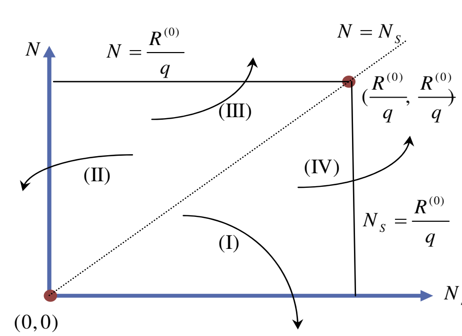

Fig. 1. One of four cases must occur if Δ is not positively invariant under Φ_t.

Let $\Omega_t = (0,L)\times(0,t]$. In each case, we shall deduce a contradiction as follows.

Suppose that the case I occurs. Then

$$Y(x,t) = R^{(0)} - qN(x,t) \geqslant 0 \text{ in } \bar{\Omega}_{t^*}.$$

By the assumptions of the case I, it follows that:

$$\delta N_{xx} - \nu N_x - N_t - \alpha N = -\alpha N_S(x,t) - f(Y)N \leqslant 0 \text{ on } \Omega_{t^*}.$$

We note that $N(x,t) \geqslant 0$ on $\bar{\Omega}_{t^*}$ and $N(x^*,t^*) = 0$. Applying the strong maximum principle ([24, p. 174, Theorem 7]), we obtain that $N(x,t) \equiv 0$ on $\bar{\Omega}_{t^*}$ if $0 < x^* < L$, which is impossible because $N(x,0) = N^0(x) > 0$ on $[0,L]$. Thus $x^* = 0$ or L. Assume that $x^* = 0$, that is, $N(0,t^*) = 0$. Then by [24, p. 170, Theorem 3], $N_x(0,t^*) > 0$, that is, $\nu N(0,t^*) - \delta N_x(0,t^*) < 0$, contradicting (3.2). Assume $x^* = L$. By the same theorem in [24], it follows that $N_x(L,t^*) < 0$, contradicting (3.2) again.

Suppose case II occurs. Then

$$\left.\frac{\partial N_S}{\partial t}\right|_{t=t^*,x=x^*} = -\alpha\frac{A}{A_S}(N_S(x^*,t^*) - N(x^*,t^*)) + \hat{f}(Y_S(x^*,t^*))N_S(x^*,t^*)$$
$$= \alpha\frac{A}{A_S}N(x^*,t^*) > 0,$$

which contradicts the direction of the semi-flow Φ_t near the boundary: $N_S(x,t) \equiv 0, 0 < N(x,t) \leqslant \frac{R^{(0)}}{q}$.

Suppose case III occurs. Then

$$\delta Y_{xx} - \nu Y_x - Y_t = q\alpha(N_S - N) + q\hat{f}(Y)N \text{ on } \Omega_{\tilde{t}}.$$

Let $Y(x,t)$ attain its minimum at the point $\widetilde{P} = (\tilde{x},\tilde{t})$ on $\overline{\Omega}_{\tilde{t}}$. By assumption, $Y(\widetilde{P}) \leqslant Y(\bar{x},\bar{t}) < 0$, which implies that $Y_x(\widetilde{P}) = 0$ and $Y_t(\widetilde{P}) = 0$ in the case $0 < \tilde{x} < L$. From the definition of $\widetilde{P}$ and the picture in Fig. 1, it follows that $N_S(\widetilde{P}) \leqslant N(\widetilde{P})$. Thus, $Y_{xx}(\widetilde{P}) = \frac{q\alpha}{\delta}(N_S(\widetilde{P}) - N(\widetilde{P})) + \frac{q}{\delta}\hat{f}(Y(\widetilde{P}))N(\widetilde{P}) < 0$, contradicting the necessary condition for a function to have a minimum at a point. If $\tilde{x} = 0$, then $Y_x(0,\tilde{t}) = -qN_x(0,\tilde{t}) = -\frac{q\nu}{\delta}N(0,\tilde{t}) < 0$ by the boundary condition (3.2). Therefore, $Y(x,\tilde{t})$ is strictly decreasing as $0 < x \ll L$, contradicting that Y attains a minimum at $(0,\tilde{t})$. Assume that $\tilde{x} = L$. Then $Y_x(L,\tilde{t}) < 0$ by [24, p. 170, Theorem 3]. On the other hand, $Y_x(L,\tilde{t}) = -qN_x(L,\tilde{t}) = 0$ by the boundary condition (3.2). This yields a contradiction.

Suppose case IV occurs. By the assumptions of case IV and the picture in Fig. 1, it follows that $N_S(\bar{x},\bar{t}) > N(\bar{x},\bar{t})$. However,

$$\left.\frac{\partial N_S}{\partial t}\right|_{t=\bar{t},x=\bar{x}} = -\alpha\frac{A}{A_S}(N_S(\bar{x},\bar{t}) - N(\bar{x},\bar{t})) + \hat{f}(Y_S(\bar{x},\bar{t}))N_S(\bar{x},\bar{t}) < 0.$$

This contradicts the direction of the semi-flow Φ_t near the boundary: $0 < N_S(x,t) \leqslant \frac{R^{(0)}}{q}, N(x,t) \equiv \frac{R^{(0)}}{q}$. $\square$

3.1. Steady state solution of (3.1), (3.2) and (3.3)

The steady-state solutions corresponding to (3.1), (3.2) and (3.3) take the form

$$\delta N'' - \nu N' + \alpha(N_S - N) + f(R^{(0)} - qN)N$$
$$= 0, -\alpha\frac{A}{A_S}(N_S - N) + f(R^{(0)} - qN_S)N_S = 0, \quad 0 < x < L, \tag{3.6}$$

with boundary conditions

$$\nu N(0) - \delta N'(0) = 0, \quad N'(L) = 0. \tag{3.7}$$

Let

$$\widetilde{N} = e^{-\frac{\nu}{2\delta}x}N, \quad \widetilde{N}_S = e^{-\frac{\nu}{2\delta}x}N_S. \tag{3.8}$$

Then (3.6) and (3.7) is equivalent to

$$\delta\widetilde{N}'' + \alpha(\widetilde{N}_S - \widetilde{N}) - \frac{\nu^2}{4\delta}\widetilde{N} + f\left(R^{(0)} - qe^{\frac{\nu}{2\delta}x}\widetilde{N}\right)\widetilde{N} = 0,$$
$$-\alpha\frac{A}{A_S}(\widetilde{N}_S - \widetilde{N}) + f\left(R^{(0)} - qe^{\frac{\nu}{2\delta}x}\widetilde{N}_S\right)\widetilde{N}_S = 0, \quad 0 < x < L, \tag{3.9}$$

with boundary conditions

$$\frac{\nu}{2}\widetilde{N}(0) - \delta\widetilde{N}'(0) = 0, \quad \frac{\nu}{2}\widetilde{N}(L) + \delta\widetilde{N}'(L) = 0. \tag{3.10}$$

We use the bifurcation result of Crandall–Rabinowitz [5] or [28, Theorem1.2] to establish the existence of positive solutions to (3.9) and (3.10).

Let $X = \{\widetilde{N} \in C^2([0,L]) : \frac{\nu}{2}\widetilde{N}(0) - \delta\widetilde{N}'(0) = 0, \frac{\nu}{2}\widetilde{N}(L) + \delta\widetilde{N}'(L) = 0\}$, and $Y = C([0,L])$. Define $F : \mathbf{R}\times X \to Y$ by

$$F(R^{(0)},\widetilde{N}) = \delta\widetilde{N}'' + \alpha(\widetilde{N}_S - \widetilde{N}) - \frac{\nu^2}{4\delta}\widetilde{N} + f\left(R^{(0)} - qe^{\frac{\nu}{2\delta}x}\widetilde{N}\right)\widetilde{N}, \tag{3.11}$$

where $\widetilde{N}_S \equiv \widetilde{N}_S(R^{(0)},\widetilde{N})$ can be determined by the second equation of (3.9).

Suppose η_0 is the principal eigenvalue of the eigenvalue problem

$$\delta\psi_1'' + \eta\psi_1 = 0, \quad \frac{\nu}{2}\psi_1(0) - \delta\psi_1'(0) = 0, \quad \frac{\nu}{2}\psi_1(L) + \delta\psi_1'(L) = 0. \tag{3.12}$$

From [27, (p. 147–p. 148)], the principal eigenvalue η_0 is positive and the corresponding positive eigenfunction $\psi_1(x)$ is uniquely determined by the normalization $\max_{[0,L]}\psi_1(x) = 1$. Let R^* satisfy

$$f(R^*) + \frac{\alpha f(R^*)}{\alpha\frac{A}{A_S} - f(R^*)} - \frac{\nu^2}{4\delta} = \eta_0 \quad\text{and}\quad f(R^*) \neq \alpha\frac{A}{A_S}. \tag{3.13}$$

From the second equation of (3.9) we have the following results:

$$\left.\frac{\partial\widetilde{N}_S}{\partial\widetilde{N}}\right|_{\widetilde{N}_S=\widetilde{N}=0,R^{(0)}=R^*} = \frac{\alpha\frac{A}{A_S}}{\alpha\frac{A}{A_S} - f(R^*)},$$
$$\left.\frac{\partial\widetilde{N}_S}{\partial R^{(0)}}\right|_{\widetilde{N}_S=\widetilde{N}=0,R^{(0)}=R^*} = 0,$$
$$\frac{\partial}{\partial R^{(0)}}\left.\left(\frac{\partial\widetilde{N}_S}{\partial\widetilde{N}}\right)\right|_{\widetilde{N}_S=\widetilde{N}=0,R^{(0)}=R^*} = \frac{f'(R^*)\alpha\frac{A}{A_S}}{(\alpha\frac{A}{A_S} - f(R^*))^2},$$

and

$$\frac{\partial}{\partial\widetilde{N}}\left(\frac{\partial\widetilde{N}_S}{\partial\widetilde{N}}\right)\Big|_{\widetilde{N}_S=\widetilde{N}=0,R^{(0)}=R^*} = -2qe^{\frac{\nu}{2\delta}x}f'(R^*)\frac{(\alpha\frac{A}{A_S})^2}{(\alpha\frac{A}{A_S} - f(R^*))^3}.$$

From (3.11) we have the following results:

$$F_{\widetilde{N}}(R^*,0)[\psi] = \delta\psi'' + \left[\alpha\left(\left.\frac{\partial\widetilde{N}_S}{\partial\widetilde{N}}\right|_{\widetilde{N}_S=\widetilde{N}=0,R^{(0)}=R^*} - 1\right) - \frac{\nu^2}{4\delta} + f(R^*)\right]\psi$$
$$= \delta\psi'' + \left[\alpha\left(\frac{\alpha\frac{A}{A_S}}{\alpha\frac{A}{A_S} - f(R^*)} - 1\right) - \frac{\nu^2}{4\delta} + f(R^*)\right]\psi$$
$$= \delta\psi'' + \left[\frac{\alpha f(R^*)}{\alpha\frac{A}{A_S} - f(R^*)} - \frac{\nu^2}{4\delta} + f(R^*)\right]\psi = \delta\psi'' + \eta_0\psi,$$
$$F_{R^{(0)},\widetilde{N}}(R^*,0)[\psi] = \left[\alpha\left(\frac{\partial}{\partial R^{(0)}}\left.\left(\frac{\partial\widetilde{N}_S}{\partial\widetilde{N}}\right)\right|_{\widetilde{N}_S=\widetilde{N}=0,R^{(0)}=R^*}\right) + f'(R^*)\right]\psi$$
$$= \left[\frac{\alpha^2 f'(R^*)\frac{A}{A_S}}{(\alpha\frac{A}{A_S} - f(R^*))^2} + f'(R^*)\right]\psi, \tag{3.14}$$

and

$$F_{\widetilde{N},\widetilde{N}}(R^*,0)[\psi]^2 = \left[\alpha\left(\frac{\partial}{\partial\widetilde{N}}\left(\frac{\partial\widetilde{N}_S}{\partial\widetilde{N}}\right)\bigg|_{\widetilde{N}_S=\widetilde{N}=0,R^{(0)}=R^*}\right) - 2qe^{\frac{v}{2\delta}x}f'(R^*)\right]\psi^2$$
$$= -2qe^{\frac{v}{2\delta}x}f'(R^*)\left[\frac{\alpha^3\frac{A^2}{A_S^2}}{\left(\alpha\frac{A}{A_S}-f(R^*)\right)^3}+1\right]\psi^2. \quad (3.15)$$

Thus,

$$F_{\widetilde{N}}(R^*,0)[\psi_1] = \delta\psi_1'' + \eta_0\psi_1 = 0,$$

that is the kernel

$$N(F_{\widetilde{N}}(R^*,0)) = \mathrm{span}\{\psi_1\},$$

where ψ_1 is the eigenfunction of (3.12). Next, we will show that the range

$$R(F_{\widetilde{N}}(R^*,0)) = \left\{g\in Y : \int_0^L g(x)\psi_1(x)\,dx = 0\right\}.$$

In fact, $g \in R(F_{\widetilde{N}}(R^*,0))$ if and only if $g = \delta\psi'' + \eta_0\psi$, for some $\psi \in X$. Thus $\int_0^L g(x)\psi_1(x)\,dx = \int_0^L[\delta\psi''(x)\psi_1(x)]\,dx + \int_0^L[\eta_0\psi(x)\psi_1(x)]\,dx$. By integration by parts and the boundary conditions of ψ and ψ_1, it follows that $\int_0^L[\delta\psi''(x)\psi_1(x)]\,dx = \delta\left[\psi_1(x)\psi'(x) - \psi_1'(x)\psi(x)\right]\Big|_0^L + \int_0^L\left[\delta\psi(x)\psi_1''(x)\right]dx = \int_0^L\left[\delta\psi(x)\psi_1''(x)\right]dx$. Therefore,

$$\int_0^L g(x)\psi_1(x)\,dx = \int_0^L\left[\delta\psi(x)\psi_1''(x) + \eta_0\psi(x)\psi_1(x)\right]dx$$
$$= \int_0^L\left[\delta\psi_1''(x) + \eta_0\psi_1(x)\right]\psi(x)\,dx = 0.$$

From (3.14), it follows that:

$$\int_0^L\{F_{R^{(0)},\widetilde{N}}(R^*,0)[\psi_1]\}\psi_1\,dx = \int_0^L\left[\frac{\alpha^2 f'(R^*)\frac{A}{A_S}}{(\alpha\frac{A}{A_S}-f(R^*))^2}+f'(R^*)\right]\psi_1^2\,dx > 0.$$

Thus we have proved that $F_{R^{(0)},\widetilde{N}}(R^*,0)[\psi_1] \in /R(F_{\widetilde{N}}(R^*,0))$.

Thus we can apply in [28, Theorem 1.2] to conclude that the set of positive solutions to (3.9) and (3.10) near $(R^{(0)},\widetilde{N}) = (R^*,0)$ is a smooth curve

$$\Gamma = \{(R^{(0)}(s),\widetilde{N}(s)) : s\in(-\delta,\delta),\ \text{for some } \delta>0\} \quad (3.16)$$

with $R^{(0)}(0) = R^*, \widetilde{N}(0) = 0,\ \widetilde{N}'(0) = \psi_1$. Moreover, $\frac{d}{ds}R^{(0)}(s)\Big|_{s=0}$ can be calculated by Formula (4.5) in [28, (p. 507)] (see also Refs. [7–9]):

$$\frac{d}{ds}R^{(0)}(s)\Big|_{s=0} = -\frac{\langle F_{\widetilde{N},\widetilde{N}}(R^*,0)[\psi_1]^2, l\rangle}{2\langle F_{R^{(0)},\widetilde{N}}(R^*,0)[\psi_1], l\rangle}, \quad (3.17)$$

where l is a linear functional on Y defined as $\langle g,l\rangle = \int_0^L g(x)\psi_1(x)\,dx$. By (3.14) and (3.15), it follows that:

$$F_{R^{(0)},\widetilde{N}}(R^*,0)[\psi_1] = \left[\frac{\alpha^2 f'(R^*)\frac{A}{A_S}}{(\alpha\frac{A}{A_S}-f(R^*))^2}+f'(R^*)\right]\psi_1,$$

and

$$F_{\widetilde{N},\widetilde{N}}(R^*,0)[\psi_1]^2 = -2qe^{\frac{v}{2\delta}x}f'(R^*)\left[\frac{\alpha^3\frac{A^2}{A_S^2}}{(\alpha\frac{A}{A_S}-f(R^*))^3}+1\right]\psi_1^2.$$

Thus,

$$\frac{d}{ds}R^{(0)}(s)\Big|_{s=0} = \frac{\int_0^L qe^{\frac{v}{2\delta}x}f'(R^*)\left[\frac{\alpha^3\frac{A^2}{A_S^2}}{(\alpha\frac{A}{A_S}-f(R^*))^3}+1\right]\psi_1^3(x)\,dx}{\int_0^L\left[\frac{\alpha^2 f'(R^*)\frac{A}{A_S}}{(\alpha\frac{A}{A_S}-f(R^*))^2}+f'(R^*)\right]\psi_1^2(x)\,dx}. \quad (3.18)$$

The uniqueness of non-negative solutions to (3.9) and (3.10) (or (3.6) and (3.7)) will be established in Theorem 3.1. Due to the uniqueness and the bound obtained for positive solutions of (3.9) and (3.10), a standard global bifurcation consideration as in ([10, p.1135]) will ensure the following results:

Lemma 3.1. *Suppose the value of (3.18) is positive. Then*

(1) If $R^{(0)} \leqslant R^*$, then the trivial solution of (3.9) and (3.10) is the unique non-negative solution;
(2) If $R^{(0)} > R^*$, then there exists exactly one solution $\widetilde{N}$ of (3.9) and (3.10) with $\widetilde{N}(x) > 0$ for $0 \leqslant x \leqslant L$.

Remark 3.1. It is worth noting that the value of (3.18) must be positive provided that $\alpha\frac{A}{A_S} - f(R^*) > 0$.

From Lemma 3.1 and the relation (3.8), the following results hold.

Lemma 3.2. *Suppose the value of (3.18) is positive.*

(1) If $R^{(0)} \leqslant R^*$, then the trivial solution $(0,0)$ of (3.6) and (3.7) is the unique non-negative solution;
(2) If $R^{(0)} > R^*$, then there exists exactly one solution (N,N_S) of (3.6) and (3.7) with $N(x) > 0$ and $N_S(x) > 0$ for $0 \leqslant x \leqslant L$.

3.2. Dynamics of (3.1), (3.2) and (3.3)

Since one equation in (3.1), (3.2) and (3.3) has no diffusion term, its solution semiflow Φ_t is not compact. Due to the lack of compactness, we need to impose the following condition:

$$\alpha\frac{A}{A_S} > f(R^{(0)}). \quad (3.19)$$

We note that the condition (3.19) holds if the function f satisfies (3.38). Under the condition (3.19), we can further prove that Φ_t is asymptotically compact in the sense that $\lim_{t\to\infty}\alpha(\Phi_t(B)) = 0$ for any bounded set $B\subset\Delta$, where α is the Kuratowski-measure of non-compactness (see [6,16]). By the continuous-time version in [22, Theorem 2.6], Φ_t has a global attractor that attracts each bounded set in Δ.

In order to prove the global behavior of the solutions of the single population model (3.1), (3.2) and (3.3), we need some notation and preliminary results. Let $X = (C([0,L]))^2$ and (X,X^+) be an ordered Banach space with positive cone X^+ having non-empty interior $\mathrm{Int}X^+$. We use $\leqslant$($<$ and $\ll$) to denote the (strict and strong) order relation defined by the cone X^+. Let $a,b \in X$, we define two order intervals as follows: $[[a,b] = \{x \in X|a \ll x \leqslant b\}$ (provided that $a \ll b$) and $[a,\infty]] = \{x\in X^+|a \leqslant x\}$.

Theorem 3.1. *Suppose the value of (3.18) is positive. Then the following statements hold:*

(1) If $R^{(0)} > R^*$, then system (3.1), (3.2) and (3.3) has a unique positive steady state which is globally asymptotically stable in the feasible set Δ.
(2) If $R^{(0)} \leqslant R^*$, then there is no positive steady state in Δ and every solution of the system (3.1), (3.2) and (3.3) with initial condition in Δ satisfies $(N(\cdot,t),N_S(\cdot,t)) \to (0,0)$ as $t\to\infty$.

Proof. The existence of steady-state solutions of (3.1), (3.2) and (3.3) has been proved in Lemma 3.2. Now we assert that the steady state in Δ is unique and globally asymptotically stable.

The uniqueness of positive solution for the system (3.1), (3.2) and (3.3) is due to the sublinear property. Rewrite the system (3.1), (3.2) and (3.3) in vector form. Let $V = (N,N_S)$ and

$$G(V) = (\alpha(N_S-N)+f(R^{(0)}-qN)N, -\alpha\frac{A}{A_S}(N_S-N)+f(R^{(0)}-qN_S)N_S),$$

$$\mathscr{D} = \begin{pmatrix}\delta & 0\\ 0 & 0\end{pmatrix},\quad E = \begin{pmatrix}v & 0\\ 0 & 0\end{pmatrix}.$$

Then (3.1), (3.2) and (3.3) takes the form

$$V_t = \mathscr{D}V_{xx} - EV_x + G(V), \quad 0 < x < 1, \; t > 0,$$
$$\nu V(0,t) - \delta\frac{\partial V}{\partial x}(0,t) = 0, \quad \frac{\partial V}{\partial x}(L,t) = 0.$$

It is easy to verify the following sublinear property of G: for any $0 < \tau < 1$,

$$G(\tau V) > \tau G(V).$$

If $V(x,0) = \tau P \in \Delta$ then $V(x,t) = \Phi_t(\tau P)$. Let $Y(x,t) = \tau\Phi_t(P)$. Then

$$\begin{aligned} Y_t &= \tau[\mathscr{D}(\Phi_t(P))_{xx} - E(\Phi_t(P))_x + G(\Phi_t(P))] \\ &= \mathscr{D}(\tau\Phi_t(P))_{xx} - E(\tau\Phi_t(P))_x + \tau G(\Phi_t(P)) \\ &< \mathscr{D}(\tau\Phi_t(P))_{xx} - E(\tau\Phi_t(P))_x + G(\tau\Phi_t(P)) = \mathscr{D}Y_{xx} - EY_x + G(Y). \end{aligned}$$

Since Φ_t is strongly monotone in the interior of Δ, from the comparison principle, it follows that:

$$\tau\Phi_t(P) = Y(x,t) < V(x,t) = \Phi_t(\tau P).$$

Hence the system (3.1), (3.2) and (3.3) is sublinear. Such kinds of systems have been studied extensively (see [11,15,17,26,30,31]). Therefore, the solution semiflow has the property:

$$\Phi_t(\tau(N^0, N_S^0)) > \tau\Phi_t(N^0, N_S^0) \quad \text{for } 0 < \tau < 1 \quad \text{and} \quad (N^0, N_S^0) \in \Delta. \tag{3.20}$$

Suppose that P^* is a positive steady state in Δ for the system (3.1), (3.2) and (3.3), that is, $P^* \gg 0$. Thus $\tau P^* \in \Delta$ for each $0 < \tau < 1$. We claim that P^* is globally asymptotically stable. In fact, by (3.20),

$$\Phi_t(\tau P^*) > \tau P^* \quad \text{for } 0 < \tau < 1 \quad \text{and} \quad t > 0.$$

Since the solution semiflow is strongly monotone in the interior of Δ,

$$\Phi_t(\tau P^*) \gg \tau P^* \quad \text{for } 0 < \tau < 1 \quad \text{and} \quad t > 0. \tag{3.21}$$

Thus by the Convergence Criterion for monotone semiflows (see [27, p. 3, Theorem 2.1]), $\Phi_t(\tau P^*)$ converges to a steady state of (3.1), (3.2) and (3.3) for each $0 < \tau < 1$.

Similarly, we can prove that

$$\Phi_t(\tau P^*) \ll \tau P^* \quad \text{for } \tau > 1 \text{ such that } \tau P^* \in \Delta \quad \text{and} \quad t > 0. \tag{3.22}$$

Now we assert that the steady state in Δ is unique. If not, then there exists another positive steady state $Q^* \in \Delta$. It is easy to see that $[[0, P^*] \cap \Delta$ and $[P^*, \infty]] \cap \Delta$ are positively invariant. We may assume that there is a unique number $0 < \beta < 1$ such that βQ^* lies on the boundary of $[[0, P^*] \cap \Delta$. The above (3.21) shows that

$$\Phi_t(\beta Q^*) \gg \beta Q^* \text{ for any } t > 0.$$

This contradicts the invariance for $[[0, P^*] \cap \Delta$. Similarly, we may assume that there is a unique number $\beta > 1$ such that βQ^* lies on the boundary of $[P^*, \infty]] \cap \Delta$. The above (3.22) shows that

$$\Phi_t(\beta Q^*) \ll \beta Q^* \text{ for any } t > 0.$$

This contradicts the invariance for $[P^*, \infty]] \cap \Delta$. Hence, the steady state P^* is unique. For a monotone dynamical system, the unique steady state is globally asymptotically stable if and only if every forward orbit has compact closure (see [14, Theorem D]). Thus, P^* is globally asymptotically stable in Δ.

In the rest of this subsection, we discuss the stability of the trivial solution of (3.1), (3.2) and (3.3). The stability properties of the trivial solution are governed by the eigenvalue problem

$$\begin{aligned} &\lambda\phi_1(x) = \delta\phi_1''(x) - \nu\phi_1'(x) + \alpha(\phi_2(x) - \phi_1(x)) + f(R^{(0)})\phi_1(x), \\ &\quad x \in (0,L), \lambda\phi_2(x) = -\alpha\frac{A}{A_s}(\phi_2(x) - \phi_1(x)) + f(R^{(0)})\phi_2(x), \\ &\nu\phi_1(0) - \delta\phi_1'(0) = \phi_1'(L) = 0. \end{aligned} \tag{3.23}$$

□

Remark 3.2 (*The existence of the principal eigenvalue for (3.23)*). Consider the following differential equations:

$$\begin{aligned} \frac{\partial u}{\partial t} &= \delta\frac{\partial^2 u}{\partial x^2} - \nu\frac{\partial u}{\partial x} + \alpha(v - u) + f(R^{(0)})u, \\ \frac{\partial v}{\partial t} &= -\alpha\frac{A}{A_S}(v - u) + f(R^{(0)})v, \quad 0 < x < L, \; t > 0, \end{aligned} \tag{3.24}$$

with boundary conditions

$$\nu u(0,t) - \delta\frac{\partial u}{\partial x}(0,t) = 0, \quad \frac{\partial u}{\partial x}(L,t) = 0, \tag{3.25}$$

and initial conditions

$$u(x,0) = u^0(x) \geqslant 0, \quad v(x,0) = v^0(x) \geqslant 0, \quad 0 < x < L. \tag{3.26}$$

It is easy to see that $(u, v) = (0, 0)$ is a steady-state solution to (3.24), (3.25) and (3.26) and the stability of (0,0) is determined by (3.23). Although the solution semiflow generated by (3.24), (3.25) and (3.26) is not compact, we can prove that it is an α-contraction on X^+ ([16, p. 316]), where $X = (C([0,L]))^2$. Note that system (3.24), (3.25) and (3.26) is cooperative and irreducible. By the proof of [27, Theorem 7.6.1] and a generalized Krein–Rutman Theorem (e.g. [16], Lemma 2.2), it follows that the principal eigenvalue and the corresponding positive eigenfunctions of (3.23) exist.

We denote λ^0 to be the principal eigenvalue of the eigenvalue problem (3.23) with the corresponding positive eigenfunctions $\phi_1(x)$ and $\phi_2(x)$ uniquely determined by normalization. From ([27, p. 138, Theorem 6.2] and [20, p. 21–24]), it follows that the trivial solution of (3.1), (3.2) and (3.3) is unstable (asymptotically stable) if $\lambda^0 > 0 (\lambda^0 < 0)$. The next results show that a single population persists if the trivial steady-state solution is unstable, and washes out if it is stable.

Theorem 3.2. *The following statements hold*

1. If $\lambda^0 > 0$, then system (3.1), (3.2) and (3.3) has a unique steady state which is globally asymptotically stable in the feasible set Δ.
2. If $\lambda^0 \leqslant 0$, then there is no steady state in Δ and every solution of the system (3.1), (3.2) and (3.3) with initial condition in Δ satisfies $(N(\cdot,t), N_S(\cdot,t)) \to (0,0)$ as $t \to \infty$.

Proof.

(1) Suppose that $\lambda^0 > 0$.

Claim 1.

$(\overline{N}, \overline{N}_S) = \left(\frac{R^{(0)}}{q}, \frac{R^{(0)}}{q}\right)$ *is a strictly upper solution* ([27], p. 130) *for the system* (3.1), (3.2) and (3.3), *since*

$$\nu\overline{N}(0,t) - \delta\frac{\partial\overline{N}}{\partial x}(0,t) = \frac{\nu R^{(0)}}{q} > 0, \quad \frac{\partial\overline{N}}{\partial x}(L,t) = 0 \geqslant 0,$$

and

$$\begin{aligned} &-\frac{\partial\overline{N}}{\partial t} + \delta\frac{\partial^2\overline{N}}{\partial x^2} - \nu\frac{\partial\overline{N}}{\partial x} + \alpha(\overline{N}_S - \overline{N}) + f(R^{(0)} - q\overline{N})\overline{N} = 0 \leqslant 0, \\ &-\frac{\partial\overline{N}_S}{\partial t} - \alpha\frac{A}{A_S}(\overline{N}_S - \overline{N}) + f(R^{(0)} - q\overline{N}_S)\overline{N}_S = 0 \leqslant 0. \end{aligned}$$

Thus Claim 1 is proved.

Claim 2. $(\underline{N}(\epsilon), \underline{N}_S(\epsilon)) = (\epsilon\phi_1, \epsilon\phi_2)$ *is a strictly lower solution* ([27], p. 130) *for the system* (3.1), (3.2) and (3.3), *where* (ϕ_1, ϕ_2) *is the eigenfunction of* (3.23) *and* ϵ *is small enough, since*

$$
\begin{aligned}
&-\frac{\partial \underline{N}(\epsilon)}{\partial t}+\delta\frac{\partial^2\underline{N}(\epsilon)}{\partial x^2}-v\frac{\partial \underline{N}(\epsilon)}{\partial x}+\alpha(\underline{N}_S(\epsilon)-\underline{N}(\epsilon))+f(R^{(0)}\\
&\quad-q\underline{N}(\epsilon))\underline{N}(\epsilon)\\
&\quad=\epsilon\delta\phi_1''-\epsilon v\phi_1'+\epsilon\alpha(\phi_2-\phi_1)+f(R^{(0)}-\epsilon q\phi_1)\epsilon\phi_1\\
&\quad=\epsilon[\lambda^0\phi_1-f(R^{(0)})\phi_1]+f(R^{(0)}-\epsilon q\phi_1)\epsilon\phi_1\\
&\quad=\epsilon[\lambda^0-f(R^{(0)})+f(R^{(0)}-\epsilon q\phi_1)]\phi_1\geqslant 0,
\end{aligned}
$$

and

$$
\begin{aligned}
&-\frac{\partial \underline{N}_S(\epsilon)}{\partial t}-\alpha\frac{A}{A_S}(\underline{N}_S(\epsilon)-\underline{N}(\epsilon))+f(R^{(0)}-q\underline{N}_S(\epsilon))\underline{N}_S(\epsilon)\\
&\quad=-\epsilon\alpha\frac{A}{A_S}(\phi_2-\phi_1)+f(R^{(0)}-q\epsilon\phi_2)\epsilon\phi_2\\
&\quad=\epsilon[\lambda^0-f(R^{(0)})+f(R^{(0)}-\epsilon q\phi_2)]\phi_2\geqslant 0,
\end{aligned}
$$

provided that $\lambda^0>0$ and ϵ is small enough. Thus Claim 2 holds.

By applying Proposition 3.1, it follows that $\Phi_t(\underline{N},\underline{N}_S)(\Phi_t(\overline{N},\overline{N}_S))$ is in Δ for all $t>0$. Thus, one obtains that $\Phi_t(\underline{N},\underline{N}_S)(\Phi_t(\overline{N},\overline{N}_S))$ is increasing (decreasing) in Δ as t is increasing (see, for example, p. 132, Corollary 3.6 of [27]). Therefore, as t goes to infinity, $\Phi_t(\underline{N},\underline{N}_S)(\Phi_t(\overline{N},\overline{N}_S))$ converges to a minimal (maximal) solution $(N_{**},N_{S**})((N^{**},N_S^{**}))$ to the system (3.1), (3.2) and (3.3) satisfying the inequality:

$$(\underline{N},\underline{N}_S)\leqslant(N_{**},N_{S**})\leqslant(N^{**},N_S^{**})\leqslant(\overline{N},\overline{N}_S).$$

By the same argument in the proof of Theorem 3.1, it follows that the steady state of (3.1), (3.2) and (3.3) is unique and globally asymptotically stable in Δ.

(2) Suppose that $\lambda^0\leqslant 0$.

Claim 3.

$(\widehat{N}(\epsilon),\widehat{N}_S(\epsilon))=(\epsilon\phi_1,\epsilon\phi_2)$ *is a strictly upper solution* ([27], p. 130) *for the system* (3.1), (3.2) and (3.3), *where* (ϕ_1,ϕ_2) *is the eigenfunction of* (3.23) *and ϵ is a positive number, since*

$$
\begin{aligned}
&-\frac{\partial \widehat{N}(\epsilon)}{\partial t}+\delta\frac{\partial^2\widehat{N}(\epsilon)}{\partial x^2}-v\frac{\partial \widehat{N}(\epsilon)}{\partial x}+\alpha(\widehat{N}_S(\epsilon)-\widehat{N}(\epsilon))+f(R^{(0)}-q\widehat{N}(\epsilon))\widehat{N}(\epsilon)\\
&\quad=\epsilon\delta\phi_1''-\epsilon v\phi_1'+\epsilon\alpha(\phi_2-\phi_1)+f(R^{(0)}-\epsilon q\phi_1)\epsilon\phi_1\\
&\quad<\epsilon\delta\phi_1''-\epsilon v\phi_1'+\epsilon\alpha(\phi_2-\phi_1)+f(R^{(0)})\epsilon\phi_1\\
&\quad=\epsilon\lambda^0\phi_1\leqslant 0,
\end{aligned}
$$

and

$$
\begin{aligned}
&-\frac{\partial \widehat{N}_S(\epsilon)}{\partial t}-\alpha\frac{A}{A_S}(\widehat{N}_S(\epsilon)-\widehat{N}(\epsilon))+f(R^{(0)}-q\widehat{N}_S(\epsilon))\widehat{N}_S(\epsilon)\\
&\quad=-\epsilon\alpha\frac{A}{A_S}(\phi_2-\phi_1)+f(R^{(0)}-q\epsilon\phi_2)\epsilon\phi_2\\
&\quad<-\epsilon\alpha\frac{A}{A_S}(\phi_2-\phi_1)+f(R^{(0)})\epsilon\phi_2\\
&\quad=\epsilon\lambda^0\phi_2\leqslant 0.
\end{aligned}
$$

Thus Claim 3 holds.

Since $P(\epsilon):=(\widehat{N}(\epsilon),\widehat{N}_S(\epsilon))$ is an upper solution of system (3.1), (3.2) and (3.3) for ϵ sufficiently small. Thus $\Phi_t(P(\epsilon))$ is decreasing as t increases. It is not difficult to see that $N(.,t,P(\epsilon))$ tends to zero as $t\to\infty$. From the second equation of (3.1), (3.2) and (3.3), $N_S(.,t,P(\epsilon))$ also converges to zero. Let $P\in\Delta$ and $\omega(P)$ be its ω-limit set. Suppose that $\omega(P)\neq\{0\}$. Then since Δ is convex, $\omega(P)$ has the least upper bound $Q\in\Delta$. Then $\Phi_t(\omega(P))\leqslant\Phi_t(Q)$ for all t and $\omega(P)\leqslant\Phi_t(Q)$ by the invariance of ω-limit set. Thus $Q\leqslant\Phi_t(Q)$. Therefore, by the Convergence Criterion (see [27, p. 3, Theorem 2.1]), $\Phi_t(Q)$ converges to a steady state $P^*\gg 0$. The proof of part (1) (or the proof of Theorem 3.1) shows that P^* is globally asymptotically stable in Δ, contradicting that $\Phi_t(P(\epsilon))$ converges to zero. This completes the proof. □

3.3. Does a system with storage zones facilitate persistence of planktonic algae in flowing habitats?

In order to compare a system with a storage zone with a system without such a zone, we reconsider the single population model corresponding to (2.12), that is,

$$\frac{\partial N}{\partial t}=\delta\frac{\partial^2 N}{\partial x^2}-v\frac{\partial N}{\partial x}+f(R^{(0)}-qN)N,\quad 0<x<L,\ t>0 \tag{3.27}$$

with boundary conditions (3.2) and initial conditions (3.3). The steady-state solutions corresponding to (3.27) take the form

$$\delta N''-vN'+f(R^{(0)}-qN)N=0,\quad 0<x<L \tag{3.28}$$

with boundary conditions

$$vN(0)-\delta N'(0)=0,\quad N'(L)=0. \tag{3.29}$$

The above single population model had been discussed in [27, (p. 151)], but we will use the theory of bifurcation to analyze it again.

Let

$$\widetilde{N}=e^{-\frac{v}{2\delta}x}N \tag{3.30}$$

Then (3.28) and (3.29) is equivalent to

$$\delta\widetilde{N}''+f(R^{(0)}-qe^{\frac{v}{2\delta}x})\widetilde{N}-\frac{v^2}{4\delta}\widetilde{N}=0,\quad 0<x<L, \tag{3.31}$$

with boundary conditions

$$\frac{v}{2}\widetilde{N}(0)-\delta\widetilde{N}'(0)=0,\quad \frac{v}{2}\widetilde{N}(L)+\delta\widetilde{N}'(L)=0. \tag{3.32}$$

Let R^{**} satisfy

$$f(R^{**})-\frac{v^2}{4\delta}=\eta_0, \tag{3.33}$$

where η_0 is defined in (3.12). We use the similar arguments in Section 3.1 to ensure the following results:

Lemma 3.3. *(Existence for single population model in simple channels)*

1. If $R^{(0)}\leqslant R^{**}$, then the trivial solution $\widetilde{N}\equiv 0$ of (3.31) and (3.32) (or $N\equiv 0$ of (3.28) and (3.29)) is the unique non-negative solution;
2. If $R^{(0)}>R^{**}$, then there exists exactly one positive solution of (3.31) and (3.32) (or (3.28) and (3.29)) in its feasible domain for $0\leqslant x\leqslant L$.

From (3.13) and (3.33), it follows that:

$$f(R^*)+\frac{\alpha f(R^*)}{\alpha\frac{A}{A_S}-f(R^*)}=f(R^{**}). \tag{3.34}$$

It is not hard to see that R^* and R^{**} are uniquely determined by (3.13) and (3.33), respectively. We discuss two cases.

Case 1. Suppose $\alpha\frac{A}{A_S}-f(R^*)>0$. From (3.34), it follows that:

$$f(R^*)<f(R^*)+\frac{\alpha f(R^*)}{\alpha\frac{A}{A_S}-f(R^*)}=f(R^{**}),$$

that is,

$$R^*<R^{**}. \tag{3.35}$$

Moreover, the value of (3.18) is always positive in this case. From Lemmas 3.2 and 3.3 and (3.35), we conclude that the positive solution of (3.6) and (3.7) is easier to exist when it is compared with (3.28) and (3.29).

Case 2. Suppose $\alpha\frac{A}{A_S} - f(R^*) < 0$. From (3.34), it follows that:

$$f(R^*) > f(R^*) + \frac{\alpha f(R^*)}{\alpha\frac{A}{A_S} - f(R^*)} = f(R^{**}),$$

that is,

$$R^* > R^{**}. \tag{3.36}$$

Moreover, the value of (3.18) will be positive if the following inequality holds:

$$\frac{\alpha^3\frac{A^2}{A_S^2}}{(\alpha\frac{A}{A_S} - f(R^*))^3} + 1 > 0. \tag{3.37}$$

From Lemmas 3.2 and 3.3, (3.36) and (3.37) we conclude that the positive solution of (3.6) and (3.7) is harder to obtain when it is compared with (3.28) and (3.29).

Remark 3.3. If the Monod function $f(R)$ satisfies

$$f(R) = \frac{\mu_{\max}R}{K_\mu + R} \text{ with } \mu_{\max} < \alpha\frac{A}{A_S}, \tag{3.38}$$

then it follows that

$$f(R^*) = \mu_{\max}\frac{R^*}{K_\mu + R^*} < \mu_{\max} < \alpha\frac{A}{A_S}.$$

This is exactly case 1 and our numerical simulations confirm that a system with a storage zone facilitates persistence of planktonic algae in flowing habitats when the Monod function satisfies (3.38) (see the first paragraph in Section 5). We note that conditions (3.38) means that the cross-section of the storage zone is small or the exchange rate is large.

3.4. How does advection v affect the existence of positive steady state for (3.6) and (3.7)?

In this subsection, we want to know how (3.6) and (3.7) depends on the parameter v. Consider (3.12):

$$\begin{aligned} &\delta\psi_1'' + \eta_0(v)\psi_1 = 0,\\ &\frac{v}{2}\psi_1(0) - \delta\psi_1'(0) = 0, \quad \frac{v}{2}\psi_1(L) + \delta\psi_1'(L) = 0, \end{aligned} \tag{3.39}$$

where $\eta_0(v)$ is the principal eigenvalue of above eigenvalue problem. It is not hard to prove that $\eta_0(v)$ is increasing in v and bounded above, thus

$$\lim_{v\to\infty}\eta_0(v) := \eta_{0,\infty} > 0 \text{ exists.}$$

From (3.13),

$$f(R^*) + \frac{\alpha f(R^*)}{\alpha\frac{A}{A_S} - f(R^*)} = \frac{v^2}{4\delta} + \eta_0(v) \;\to\; \infty \text{ as } v \to \infty. \tag{3.40}$$

If we choose $f(R)$ to be the Monod function and satisfies (3.38), it follows that $\alpha\frac{A}{A_S} - f(R^*)$ is always positive and the function in the L.H.S. of (3.40) is bounded above. Thus, R^* does not exist, that is, bifurcation never occurs as v becomes sufficiently large. This means that the species is washed out as $v \to \infty$ for the system (3.6) and (3.7).

Let $v = 0$ in (3.39). Then (3.39) becomes

$$\delta\psi_1'' + \eta_0(0)\psi_1 = 0, \quad \psi_1'(0) = 0, \quad \psi_1'(L) = 0. \tag{3.41}$$

It is easy to see that $\eta_0(0) = 0$. From (3.13),

$$f(R^*) + \frac{\alpha f(R^*)}{\alpha\frac{A}{A_S} - f(R^*)} = \frac{v^2}{4\delta} + \eta_0(v) \;\to\; 0 \text{ as } v \to 0. \tag{3.42}$$

This implies that $R^* \to 0$ as $v \to 0$ and it means that species will always persist as $v \to 0$ for the system (3.6) and (3.7). In fact, if we choose $v = 0$ in (3.6) and (3.7), it follows that

$$\begin{aligned} &\delta N'' + \alpha(N_S - N) + f(R^{(0)} - qN)N = 0,\\ &-\alpha\frac{A}{A_S}(N_S - N) + f(R^{(0)} - qN_S)N_S = 0, \quad 0 < x < L, \end{aligned} \tag{3.43}$$

with boundary conditions

$$N'(0) = 0,\; N'(L) = 0. \tag{3.44}$$

It is easy to see that $\left(\frac{R^{(0)}}{q}, \frac{R^{(0)}}{q}\right)$ is always a positive constant solution of the above system.

We would like to ask for the exact range of v for which R^* exists since the range of v appears to be important for the existence of a positive steady state. But it is still an open problem for us.

4. Coexistence

Since two equations in (2.7), (2.8) and (2.9) have no diffusion terms, its solution semiflow Π_t is not compact and we require the following conditions in this section:

$$\alpha\frac{A}{A_S} > f_i(R^{(0)}), \quad i = 1, 2. \tag{4.1}$$

By similar arguments as in Section 3.2, it follows that Π_t has a global attractor that attracts each bounded set in Ω, where Ω is defined in (2.10).

Theorem 3.1 can be applied to either of the two systems obtained from (2.7), (2.8) and (2.9) by setting one of the two ordered pairs $(N_1, N_{S,1})$ or $(N_2, N_{S,2})$ to be $(0, 0)$. Therefore, we conclude that the system (2.7), (2.8) and (2.9) has the following equilibria:

(i) Trivial solution $E_0 = (0, 0, 0, 0)$ always exists;
(ii) Semi-trivial solution $E_1 = (N_1^*, N_{S,1}^*, 0, 0)$ exists provided that the conditions for $f = f_1$ and $q = q_1$ in Theorem 3.1 are satisfied;
(iii) Semi-trivial solution $E_2 = (0, 0, N_2^*, N_{S,2}^*)$ exists provided that the conditions for $f = f_2$ and $q = q_2$ in Theorem 3.1 are satisfied.

Here, $(N_i^*, N_{S,i}^*)$ denotes the unique positive solution of (3.1), (3.2) and (3.3) resulting from putting $f = f_i$ and $q = q_i$. Of course, there may be additional equilibria as well and these must be positive. The two organisms can coexist if a positive equilibrium exists.

In order to discuss the persistence of (2.7), (2.8) and (2.9), we denote Λ_1 to be the principal eigenvalue of the eigenvalue problem,

$$\begin{aligned} &\Lambda_1\hat\phi_1(x) = \delta\hat\phi_1''(x) - v\hat\phi_1'(x) + \alpha(\hat\phi_2(x) - \hat\phi_1(x))\\ &\quad + f_2(R^{(0)} - q_1N_1^*)\hat\phi_1(x), \quad x \in (0, L),\\ &\Lambda_1\hat\phi_2(x) = -\alpha\frac{A}{A_s}(\hat\phi_2(x) - \hat\phi_1(x)) + f_2(R^{(0)} - q_1N_{S,1}^*)\hat\phi_2(x),\\ &v\hat\phi_1(0) - \delta\hat\phi_1'(0) = \hat\phi_1'(L) = 0, \end{aligned} \tag{4.2}$$

with the corresponding positive eigenfunctions $\hat\phi_1(x)$ and $\hat\phi_2(x)$ uniquely determined by normalization.

Remark 4.1 (*The existence of* $\Lambda_1, \hat\phi_1(x)$ *and* $\hat\phi_2(x)$). Consider the following differential equations:

$$\begin{aligned} &\frac{\partial u}{\partial t} = \delta\frac{\partial^2 u}{\partial x^2} - v\frac{\partial u}{\partial x} + \alpha(v - u) + f_2(R^{(0)} - q_1N_1^*)u,\\ &\frac{\partial v}{\partial t} = -\alpha\frac{A}{A_S}(v - u) + f_2(R^{(0)} - q_1N_{S,1}^*)v, \quad 0 < x < L, \; t > 0, \end{aligned} \tag{4.3}$$

with boundary conditions (3.25) and initial conditions (3.26). It is easy to see that $(u, v) = (0, 0)$ is a steady-state solution to (4.3) and the stability of (0,0) is determined by (4.2). We can use similar arguments as in Remark 3.2 to show that the principal eigenvalue and the corresponding positive eigenfunctions of (4.2) exist.

Similarly, we denote Λ_2 to be the principal eigenvalue of the eigenvalue problem,

$$\begin{aligned}\Lambda_2\hat{\psi}_1(x) &= \delta\hat{\psi}_1''(x) - v\hat{\psi}_1'(x) + \alpha(\hat{\psi}_2(x) - \hat{\psi}_1(x))\\ &\quad + f_1(R^{(0)} - q_2N_2^*)\hat{\psi}_1(x), \quad x \in (0, L),\\ \Lambda_2\hat{\psi}_2(x) &= -\alpha\frac{A}{A_s}(\hat{\psi}_2(x) - \hat{\psi}_1(x)) + f_1(R^{(0)} - q_2N_{S,2}^*)\hat{\psi}_2(x),\\ v\hat{\psi}_1(0) &- \delta\hat{\psi}_1'(0) = \hat{\psi}_1'(L) = 0,\end{aligned} \tag{4.4}$$

with the corresponding positive eigenfunctions $\hat{\psi}_1(x)$ and $\hat{\psi}_2(x)$ uniquely determined by normalization.

Proposition 4.1. *The interior of Ω is positively invariant under the semiflow Π_t generated by (2.7), (2.8) and (2.9), where the region Ω is defined in (2.10).*

Proof. The proof is similar to the proof in Proposition 3.1 and we omit it.

From now on, we restrict our attention to the system (2.7), (2.8) and (2.9) with initial condition in the feasible set Ω. The Jacobian of the reaction terms in (2.7), (2.8) and (2.9) with respect to $(N_1, N_{S,1}, N_2, N_{S,2})$ at points $(N_1, N_{S,1}, N_2, N_{S,2}) \in \Omega$ has the form

$$J = \begin{pmatrix} * & + & - & 0\\ + & * & 0 & -\\ - & 0 & * & +\\ 0 & - & + & * \end{pmatrix}.$$

Obviously, J has the block structure characteristic of a type K monotone system [27], consisting of diagonal 2×2 blocks with non-negative off-diagonal entries and off-diagonal 2×2 non-positive blocks, where $K = \left\{\left(N_1^0, N_{S,1}^0, N_2^0, N_{S,2}^0\right) \in (C([0, L]))^4 | N_1^0 \geqslant 0, N_{S,1}^0 \geqslant 0; N_2^0 \leqslant 0, N_{S,2}^0 \leqslant 0\right\}$. Thus, the semiflow Π_t generated by the system (2.7), (2.8) and (2.9) is monotone [27] under the partial order $\leqslant_K$. Furthermore, J is irreducible (See Appendix in [29]), which implies that such a semiflow Π_t is strongly monotone in the interior of Ω.

In order to present our final result on coexistence or persistence, we need some notation and preliminary results. Set $C := (C([0, L]))^4$. For $P, Q \in C$ with $P \ll_K Q$, define type$-K$ order intervals

$$[P, Q]_K = \{R \in C | P \leqslant_K R \leqslant_K Q\},$$

and

$$[[P, Q]]_K = \{R \in C | P \ll_K R \ll_K Q\}.$$

For $i = 1, 2$, recall the following single population model:

$$\begin{aligned}\frac{\partial N_i}{\partial t} &= \delta\frac{\partial^2 N_i}{\partial x^2} - v\frac{\partial N_i}{\partial x} + \alpha(N_{S,i} - N_i) + f_i(R^{(0)} - q_iN_i)N_i,\\ \frac{\partial N_{S,i}}{\partial t} &= -\alpha\frac{A}{A_S}(N_{S,i} - N_i) + f_i(R^{(0)} - q_iN_{S,i})N_{S,i},\\ 0 &< x < L, \quad t > 0,\end{aligned} \tag{4.5}$$

with the boundary conditions (2.8) and initial conditions (2.9). If the conditions for f_i and q_i in Theorem 3.1 are satisfied, it follows that (4.5) has a unique positive steady state $(N_i^*, N_{S,i}^*)$ which is globally asymptotically stable in its feasible region by Theorem 3.1. $\square$

Lemma 4.1. *Suppose that semi-trivial solution $E_1 = \left(N_1^*, N_{S,1}^*, 0, 0\right)$ and $E_2 = \left(0, 0, N_2^*, N_{S,2}^*\right)$ both exist. Then $\omega(P) \subset [E_2, E_1]_K$ for any $P \in \Omega$.*

Proof. Fix a point $P = \left(N_1^0, N_{S,1}^0, N_2^0, N_{S,2}^0\right) \in \Omega$. Let $\Pi_t(P) = (N_1(., t, P), N_{S,1}(., t, P), N_2(., t, P), N_{S,2}(., t, P))$ be the solution of (2.7), (2.8) and (2.9) with initial data P. Then $(N_i(., t, P), N_{S,i}(., t, P))$ satisfies

$$\begin{aligned}\frac{\partial N_i}{\partial t} &\leqslant \delta\frac{\partial^2 N_i}{\partial x^2} - v\frac{\partial N_i}{\partial x} + \alpha(N_{S,i} - N_i) + f_i(R^{(0)} - q_iN_i)N_i,\\ \frac{\partial N_{S,i}}{\partial t} &\leqslant -\alpha\frac{A}{A_S}(N_{S,i} - N_i) + f_i(R^{(0)} - q_iN_{S,i})N_{S,i}, \quad 0 < x < L, \ t > 0,\end{aligned} \tag{4.6}$$

with boundary conditions (2.8) and initial conditions (2.9).

From [27, p. 130, Theorem 3.4] it follows that for any $t > 0$, for $i = 1, 2$:

$$(N_i(., t, P), N_{S,i}(., t, P)) \leqslant \Pi_t^{(i)}\left(N_i^0, N_{S,i}^0\right),$$

where $\Pi_t^{(i)}(N_i^0, N_{S,i}^0)$ is the solution for (4.5). Thus, applying Theorem 3.1, we obtain that

$$Q^{(i)}\omega(P) \leqslant \left(N_i^*, N_{S,i}^*\right),$$

where

$$Q^{(i)}\left(N_1^0, N_{S,1}^0, N_2^0, N_{S,2}^0\right) = \left(N_i^0, N_{S,i}^0\right), \quad i = 1, 2,$$

is a projection mapping, that is,

$$\omega(P) \subset [E_2, E_1]_K.$$

Let $E_1(\epsilon_1) = \left(N_1^*, N_{S,1}^*, \epsilon_1\hat{\phi}_1, \epsilon_1\hat{\phi}_2\right)$ and $E_2(\epsilon_2) = \left(\epsilon_2\hat{\psi}_1, \epsilon_2\hat{\psi}_2, N_2^*, N_{S,2}^*\right)$, where $(\hat{\phi}_1, \hat{\phi}_2)$ and $(\hat{\psi}_1, \hat{\psi}_2)$ are defined in (4.2) and (4.4), respectively. $\square$

Lemma 4.2. *Suppose that semi-trivial solution $E_1 = (N_1^*, N_{S,1}^*, 0, 0)$ and $E_2 = (0, 0, N_2^*, N_{S,2}^*)$ both exist.*

(i) Let $\Lambda_1 > 0$. Then for $\varepsilon_1 > 0$ sufficiently small, $E_1(\epsilon_1)$ is a strict upper solution for the system (2.7), (2.8) and (2.9).
(ii) Let $\Lambda_2 > 0$. Then for $\varepsilon_2 > 0$ sufficiently small, $E_2(\epsilon_2)$ is a strict lower solution for the system (2.7), (2.8) and (2.9).

Proof. Let

$$(\overline{N}_1, \overline{N}_{S,1}, \underline{N}_2, \underline{N}_{S,2}) := E_1(\epsilon_1) = \left(N_1^*, N_{S,1}^*, \epsilon_1\hat{\phi}_1, \epsilon_1\hat{\phi}_2\right).$$

It is straight forward to show the following inequalities:

$$\begin{aligned}&-\frac{\partial\overline{N}_1}{\partial t} + \delta\frac{\partial^2\overline{N}_1}{\partial x^2} - v\frac{\partial\overline{N}_1}{\partial x} + \alpha(\overline{N}_{S,1} - \overline{N}_1) + f_1(R^{(0)} - q_1\overline{N}_1 - q_2\underline{N}_2)\overline{N}_1\\ &= \delta\frac{\partial^2 N_1^*}{\partial x^2} - v\frac{\partial N_1^*}{\partial x} + \alpha(N_{S,1}^* - N_1^*) + f_1(R^{(0)} - q_1N_1^* - q_2\epsilon_1\hat{\phi}_1)N_1^*\\ &< \delta\frac{\partial^2 N_1^*}{\partial x^2} - v\frac{\partial N_1^*}{\partial x} + \alpha(N_{S,1}^* - N_1^*) + f_1(R^{(0)} - q_1N_1^*)N_1^* = 0,\\ &-\frac{\partial\overline{N}_{S,1}}{\partial t} - \alpha\frac{A}{A_S}(\overline{N}_{S,1} - \overline{N}_1) + f_1(R^{(0)} - q_1\overline{N}_{S,1} - q_2\underline{N}_{S,2})\overline{N}_{S,1}\\ &= -\alpha\frac{A}{A_S}(N_{S,1}^* - N_1^*) + f_1(R^{(0)} - q_1N_{S,1}^* - q_2\epsilon_1\hat{\phi}_2)N_{S,1}^*\\ &< -\alpha\frac{A}{A_S}(N_{S,1}^* - N_1^*) + f_1(R^{(0)} - q_1N_{S,1}^*)N_{S,1}^* = 0,\\ &-\frac{\partial\underline{N}_2}{\partial t} + \delta\frac{\partial^2\underline{N}_2}{\partial x^2} - v\frac{\partial\underline{N}_2}{\partial x} + \alpha(\underline{N}_{S,2} - \underline{N}_2) + f_2(R^{(0)} - q_1\overline{N}_1 - q_2\underline{N}_2)\underline{N}_2\\ &= \epsilon_1\left[\delta\hat{\phi}_1''(x) - v\hat{\phi}_1'(x) + \alpha(\hat{\phi}_2(x) - \hat{\phi}_1(x)) + f_2\left(R^{(0)} - q_1N_1^* - \epsilon_1q_2\hat{\phi}_1\right)\hat{\phi}_1\right]\\ &= \epsilon_1\left[\Lambda_1 - f_2\left(R^{(0)} - q_1N_1^*\right) + f_2(R^{(0)} - q_1N_1^* - \epsilon_1q_2\hat{\phi}_1)\right]\hat{\phi}_1\\ &\geqslant 0, \text{ provided that } \Lambda_1 > 0 \text{ and } \epsilon_1 \text{ is small enough,}\end{aligned}$$

and

$$
\begin{aligned}
&-\frac{\partial \underline{N}_{S,2}}{\partial t}-\alpha\frac{A}{A_S}(\underline{N}_{S,2}-\underline{N}_2)+f_2(R^{(0)}-q_1\overline{N}_{S,1}-q_2\underline{N}_{S,2})\underline{N}_{S,2}\\
&=-\epsilon_1\alpha\frac{A}{A_s}(\hat{\phi}_2(x)-\hat{\phi}_1(x))+\epsilon_1 f_2(R^{(0)}-q_1N^*_{S,1}-\epsilon_1 q_2\hat{\phi}_2)\hat{\phi}_2\\
&=\epsilon_1[\Lambda_1-f_2(R^{(0)}-q_1N^*_{S,1})+f_2(R^{(0)}-q_1N^*_{S,1}-\epsilon_1 q_2\hat{\phi}_2)]\hat{\phi}_2\\
&\geqslant 0,\ \text{provided that } \Lambda_1>0 \text{ and } \epsilon_1 \text{ is small enough.}
\end{aligned}
$$

From the discussions above, it follows that part(i) is true. Part(ii) can be proved in a similar way and we omit it. □

Theorem 4.1. *Suppose that semi-trivial solution $E_1=\left(N^*_1,N^*_{S,1},0,0\right)$ and $E_2=\left(0,0,N^*_2,N^*_{S,2}\right)$ both exist and $\Lambda_i>0,\ i=1,2$. Then there is a minimal steady state $E^-\in\Omega$ which is lower asymptotically stable and a maximal steady state $E^+\in\Omega$ which is upper asymptotically stable such that*

$\omega(P)\subset[E^-,E^+]_K\cap\Omega$ for any $P\in\Omega$.

The system (2.7), (2.8) and (2.9) is uniformly persistent and $\Pi_t(P)$ tends to a steady state for P in an open and dense subset in Ω.

Proof. Combining Theorem 3.4 in [27, p.130], Lemma 4.2 and strong monotonicity for Π_t, we get that for any $t>0$

$E_2(\epsilon_2)\ll_K\Pi_t(E_2(\epsilon_2))\ll_K\Pi_t(E_1(\epsilon_1))\ll_K E_1(\epsilon_1)$.

The Convergence Criterion in [27, p. 3, Theorem 2.1] implies that $\Pi_t(E_2(\epsilon_2))$ converges to a lower asymptotically stable steady state $E^-(\epsilon_2)\gg_K E_2(\epsilon_2)$, and $\Pi_t(E_1(\epsilon_1))$ tends to an upper asymptotically stable steady state $E^+(\epsilon_1)\ll_K E_1(\epsilon_1)$. Since $E^+(\epsilon_1)$ attracts $E_1(\epsilon_1)$ for an open neighborhood of $\epsilon_1, E^+(\epsilon_1)$ is independent of ϵ_1 for $\epsilon_1>0$ sufficiently small, similarly for $E^-(\epsilon_2)$.

By Lemma 4.1,

$\omega(P)\subset[E_2,E_1]_K$ for any $P\in\Omega$.

Then

$E_2\leqslant_K\Pi_t(P)\leqslant_K E_1$ for any $P\in\Omega,\ t>0$.

The strong monotonicity for Π_t implies that

$E_2\leqslant_K\Pi_s(E_2)\ll_K\Pi_{t+s}(P)\ll_K\Pi_s(E_1)\leqslant_K E_1$ for any $P\in\Omega,\quad t>0,\ s>0$.

Thus for t sufficiently large, say $t\geqslant t_0$,

$E_2\ll_K\Pi_t(P)\ll_K E_1$.

This implies that for $\epsilon_1>0,\epsilon_2>0$ sufficiently small,

$E_2(\epsilon_2)\ll_K\Pi_t(P)\ll_K E_1(\epsilon_1)$.

From the discussions above, it follows that

$E^-\leqslant_K\omega(P)\leqslant_K E^+$.

The remaining results follow from the theory of strongly monotone dynamical systems (see [27]). □

5. Numerical work

Numerical simulations of dynamics were conducted using an implementation of the MacCormack algorithm, a generalization of the improved Euler method [4]. We first illustrate conditions for persistence, fixing all parameters for a single species and varying the dilution rate (D) and nutrient supply ($R^{(0)}$), using parameters assigned to represent phosphorus-limited algae. For fixed $R^{(0)}$, washout occurs when D exceeds a critical value, and persistence occurs below this value (Fig. 2), as judged from simulated invasions of the trivial steady state. For a channel of a given length, the critical dilution rate corresponds to a critical advective flow above which washout occurs. Through the biologically relevant range of $R^{(0)}$, the critical value of D depends only weakly on $R^{(0)}$. Moreover, the critical value of D is higher for a system with a storage zone, than for an otherwise equivalent simple channel without such a zone. Thus persistence is possible at higher advective flows in the system with a storage zone. These results illustrate cases covered by Remark 3.3 (above).

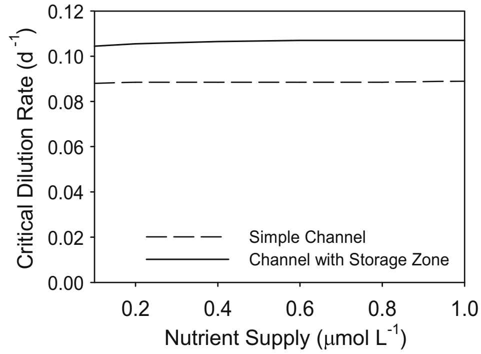

Fig. 2. Critical dilution rate below which persistence of a single species occurs. Parameter values were $L=10$ km; $A:A_S=4$; $\delta=3\times10^5$ m$^2/d$; $\alpha=0.5$; $\mu_{max}=0.7\ d^{-1}$; $K_\mu=0.002$ μmol/l; $q=4\times10^{-9}$ μmol/cell.

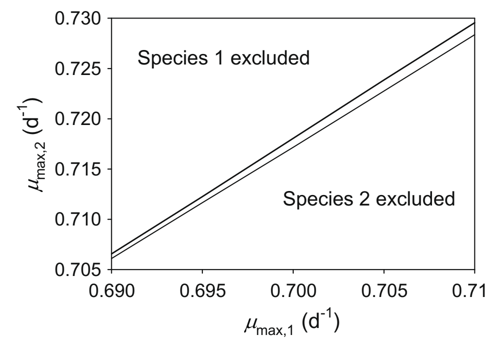

Fig. 3. Coexistence of two competitors in a system with a hydraulic storage zone occurs for a narrow range of maximal growth rates when other parameters are fixed (band in the middle of the graph). Parameter values were $L=10$ km; $A:A_S=4$; $\delta=3\times10^5$ m$^2/d$; $\alpha=0.5$; $K_{\mu,1}=0.002$ μmol /l; $K_{\mu,2}=0.005$ μmol/l; $q_1=q_2=4\times10^{-9}$ μmol/cell.

Next, we illustrate conditions for coexistence, as judged from simulated invasions of the semi-trivial steady states. We fix all parameters except the maximal growth rates of the two species ($\mu_{max,1},\mu_{max,2}$). For appropriate choices of these parameters, coexistence (mutual invasibility) occurs for a narrow range of values (Fig. 3). Outside of this range, competitive exclusion occurs.

6. Discussion

Conditions for persistence and coexistence in a flowing habitat with a hydraulic storage zone are similar to those for the flow reactor model without such a zone, and are derived by a similar analysis. Quantitatively, however, species can persist at higher flow rates when a storage zone is present than when it is not (Fig. 2) provided the conditions of Remark 3.3 are satisfied. Thus such zones might be important to the persistence of planktonic algae in rivers and riverine habitats, as previously suggested [25].

The magnitude of this effect on persistence depends on the physical parameters characterizing flow and transport. These parameters vary widely from small rapidly flowing streams that likely have very strong advective transport and small storage zones

[3], to slow-flowing wetland channels with extensive fringing vegetation that likely have large storage zones [21]. Intuitively, the latter habitat should be more conducive to persistence of planktonic algae than the former, but quantitative evaluations are now needed.

Like the unstirred chemostat and the flow reactor without a storage zone, coexistence in flowing systems with a storage zone appears to require a narrow balance of relevant biological parameters. This might be interpreted as indicating that competitive exclusion is nearly inevitable, but at least two considerations moderate this conclusion. First, the number of species available in the vicinity of any realistic habitat and likely to colonize it (the "species pool") is large. Thus parameters might be sufficiently densely distributed so that the necessary combination for coexistence exists among species reaching a habitat. Second, competitive exclusion of species whose parameters are close to the coexistence zone is a slow process (as it is in the flow reactor model, e.g. [2]). Thus there may be transient persistence of weakly competitive species over time intervals of practical interest.

Acknowledgement

We thank the National Center for Theoretical Sciences, Tsing-Hua University, and the National Science Council of Taiwan for supporting this research. This research was also partially supported by US National Science Foundation under Grant no. DEB-0444844.

References

[1] Mary Ballyk, L.E. Dung, D.A. Jones, Hal L. Smith, Effects of random motility on microbial growth and competition in a flow reactor, SIAM J. Appl. Math. 59 (1998) 573–596.
[2] J.V. Baxley, S.B. Robinson, Coexistence in the unstirred chemostat, Appl. Math. Comput. 89 (1998) 41–65.
[3] K.E. Bencala, R.A. Walters, Simulation of solute transport in a mountain pool-and-riffle stream: a transient storage model, Water Resour. Res. 19 (1983) 718–724.
[4] S.C. Chapra, Surface Water-Quality Modeling, McGraw-Hill, NY, 1997.
[5] M.G. Crandall, P.H. Rabinowitz, Bifurcation from simple eigenvalues, J. Funct. Anal. 8 (1971) 321–340.
[6] K. Deimling, Nonlinear Functional Analysis, Springer-Verlag, Berlin, 1988.
[7] Y. Du, J. Shi, Some recent results on diffusive predator–prey models in spatially heterogeneous environment, Nonlinear Dynamics and Evolution Equations, Fields Institute Communications, vol. 48, American Mathematical Society, 2006. pp. 321–340..
[8] Y. Du, J. Shi, Spatially heterogeneous predator–prey model with protect zone for prey, J. Differen. Eqns. 229 (2006) 63–91.
[9] Y. Du, J. Shi, Allee effect and bistability in a spatially heterogeneous predator–prey model, Trans. Amer. Math. Soc. 359 (2007) 4557–4593.
[10] S.B. Hsu, Steady state of a system of P.D.E. modeling microbial ecology, SIAM J. Math. Anal. 14 (1983) 1130–1138.
[11] M.W. Hirsch, The dynamical systems approach to differential equations, Bull. Amer. Math. Soc. 11 (1984) 1–64.
[12] S.B. Hsu, S. Hubbell, P. Waltman, Mathematical theory for single nutrient competition in continuous cultures of microorganisms, SIAM J. Appl. Math. 32 (1977) 366–383.
[13] S.B. Hsu, P. Waltman, On a system of reaction–diffusion equations arising from competition in an unstirred chemostat, SIAM J. Appl. Math. 53 (1993) 1026–1044.
[14] J. Jiang, On the global stability of cooperative systems, Bull. Lond. Math. Soc. 26 (1994) 455–458.
[15] J. Jiang, Sublinear discrete-time order-preserving dynamical systems, Math. Proc. Canb. Phil. Soc. 119 (1996) 561–574.
[16] J. Jiang, X. Liang, X.Q. Zhao, Saddle point behavior for monotone semiflows and reaction–diffusion models, J. Differen. Eqns. (2004) 313–330.
[17] J. Jiang, X. Zhao, Convergence in monotone and uniformly stable skew-product semiflows with application, J. Reine Angew. Math. 589 (2005) 21–55.
[18] C.M. Kung, B. Baltzis, The growth of pure and simple microbial competitors in a moving distributed medium, Math. Biosci. 111 (1992) 295–313.
[19] R. Martin, H.L. Smith, Abstract functional differential equations and reaction–diffusion systems, Trans. A.M.S. 321 (1990) 1–44.
[20] R. Martin, H.L. Smith, Reaction–diffusion systems with time delays: monotonicity invariance comparison and convergence, J. Reine Angew. Math. 413 (1991) 1–35.
[21] C.J. Martinez, W.R. Wise, Analysis of constructed treatment wetland hydraulics with the transient storage model OTIS, Ecol. Eng. 20 (2003) 211–222.
[22] P. Magal, X.Q. Zhao, Global attractors and steady states for uniformly persistent dynamical systems, SIAM. J. Math. Anal 37 (2005) 251–275.
[23] A. Pazy, Semigroups of Linear Operators and Application to Partial Differential Equations, Springer-Verlag, 1983.
[24] M.H. Protter, H.F. Weinberger, Maximum Principles in Differential Equations, Springer-Verlag, 1984.
[25] C.S. Reynolds, Potamoplankton: paradigms, paradoxes and prognoses, in: F.E. Round (Ed.), Algae and the Aquatic Environment, Biopress, Bristol, UK, 1990.
[26] H.L. Smith, Cooperative systems of differential equations with concave nonlinearities, Nonlinear Anal. TMA 10 (1986) 1037–1052.
[27] H.L. Smith, Monotone dynamical systems:an introduction to the theory of competitive and cooperative systems, Math. Surveys Monogr., vol. 41, American Mathematical Society, Providence, RI, 1995.
[28] Junping Shi, Persistence and bifurcation of degenerate solutions, J. Funct. Anal. 169 (2) (1999) 494–531.
[29] H.L. Smith, P.E. Waltman, The Theory of the Chemostat, Cambridge Univ. Press, 1995.
[30] P. Takac, Convergence to equilibrium on invariant *d*-hypersurfaces for strongly increasing discrete-time semigroups, J. Math. Anal. Appl. 148 (1990) 223–244.
[31] X. Zhao, Global attractivity and stability in some monotone discrete dynamical systems, Bull. Aust. Math. Soc. 53 (1996) 305–324.