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Mathematical Analysis on a Droop Model with Intraguild Predation

Sze-Bi Hsu, Yi-hui Ho and Feng-Bin Wang*

In memory of Professor Hwai-Chiuan Wang

Abstract. In this paper, we analyze a predator-prey chemostat system with internal storage, in which the predator not only competes for a single inorganic nutrient with the prey species but also consumes the prey for growth. The outcome for the corresponding model without intraguild predation is that the competitive exclusion holds, that is, the superior species will win the competition, and coexistence will not happen. When the mechanism of intraguild predation is added into the system, our analysis indicates that coexistence can be possible.

1. Introduction

In this paper we shall analyze a well-mixing chemostat model with intraguild predation and internal storage, which was proposed in [20]. For the system with intraguild predation, predators not only feed upon prey species but also compete against the prey for the same inorganic nutrients [1, 11, 14]. Therefore, intraguild predators represent a combination of predation and competition in an ecosystem, and may play a central role in the structure of ecological communities [5, 10, 19, 22].

Next, we describe the chemostat model proposed in [20], where two species, *Ochromonas* (a mixotrophic organism) and *Microcystis* (an autotrophic prey), compete for *ammonium* (a nitrogen resource), and *Ochromonas* also consumes *Microcystis* for growth. The nutrient (ammonium) is supplied at the rate D, and the input concentrations is $R^{(0)}$. There is a compensating outflow also at rate D of the well-stirred contents of the chemostat. Let $R(t)$ be the nutrient (ammonium) concentration at time t; $N_1(t)$ and $N_2(t)$ denote the population densities of the autotroph and mixotroph, respectively; $Q_i(t)$ represents the average amount of stored nutrient per cell of i-th population at time t, $i = 1, 2$. We also assume that the chemostat is well mixing, and the factors affecting growth are kept

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*Corresponding author.

constant. Then we consider the following ODE system [20]:

$$
\begin{aligned}
&\frac{dR}{dt} = (R^{(0)} - R)D - f_1(R,Q_1)N_1 - f_2(R,Q_2)N_2,\\
&\frac{dN_1}{dt} = [\mu_1(Q_1) - D]N_1 - g(N_1)N_2,\\
&\frac{dQ_1}{dt} = f_1(R,Q_1) - \mu_1(Q_1)Q_1,\\
&\frac{dN_2}{dt} = [\mu_2(Q_2) - D]N_2,\\
&\frac{dQ_2}{dt} = f_2(R,Q_2) - \mu_2(Q_2)Q_2 + g(N_1)Q_1,\\
&R(0) \geq 0, \quad N_i(0) \geq 0, \quad Q_i(0) \geq Q_{\min,i}, \quad i = 1,2.
\end{aligned}
\tag{1.1}
$$

Here $\mu_i(Q_i)$ is the growth rate of species i as a function of cell quota Q_i; $f_i(R,Q_i)$ is the per capita nutrient uptake rate, per cell of species i as a function of nutrient concentration R and cell quota Q_i; $Q_{\min,i}$ denotes the threshold cell quota below which no growth of species i occurs. The term $g(N_1)Q_1$ describes the assimilation of nutrients from ingested prey [20].

The authors in [20] assume that the predation rate, $g(N_1)$, of the mixotroph feeding on the autotroph is a Holling type III functional response. Thus, $g(N_1)$ takes the forms

$$
g(N_1) = \frac{g_{\max} N_1^b}{K_{\max}^b + N_1^b}, \tag{1.2}
$$

where $b > 1$. The growth rate $\mu_i(Q_i)$ takes the forms [2–4, 20]:

$$
\mu_i(Q_i) = \mu_{i\infty}\left(1 - \frac{Q_{\min,i}}{Q_i}\right)
$$

or

$$
\mu_i(Q_i) = \mu_{i\infty}\frac{(Q_i - Q_{\min,i})_+}{a_i + (Q_i - Q_{\min,i})_+},
$$

or

$$
\mu_i(Q_i) = \mu_{\max,i}\left(1 - \frac{Q_{\max,i} - Q_i}{Q_{\max,i} - Q_{\min,i}}\right), \tag{1.3}
$$

where $\mu_{i\infty}$ is the maximal growth rate at infinite quotas (i.e., as $Q_i \to \infty$) of the species i; $(Q_i - Q_{\min,i})_+$ is the positive part of $(Q_i - Q_{\min,i})$; $\mu_{\max,i}$ is the maximum specific growth rate of species i; $Q_{\min,i}$ is the minimum cellular quota content required for growth of the species i; $Q_{\max,i}$ is the maximum cellular quota content of the species i.

According to [7, 13], the uptake rate $f_i(R,Q_i)$ takes the form:

$$
\begin{aligned}
f_i(R,Q_i) &= \rho_{\max,i}(Q_i)\frac{R}{K_i + R},\\
\rho_{\max,i}(Q_i) &= \rho_{\max,i}^{\text{high}} - (\rho_{\max,i}^{\text{high}} - \rho_{\max,i}^{\text{low}})\frac{Q_i - Q_{\min,i}}{Q_{\max,i} - Q_{\min,i}},
\end{aligned}
$$

where $Q_{\min,i} \le Q_i \le Q_{\max,i}$. Cunningham and Nisbet [2, 3] took $\rho_{\max,i}(Q_i)$ to be a constant. The uptake rate in [20] takes the form

$$f_i(R, Q_i) = \frac{u_{\max,i} R}{K_i + R} \left(\frac{Q_{\max,i} - Q_i}{Q_{\max,i} - Q_{\min,i}} \right), \tag{1.4}$$

where $Q_{\min,i} \le Q_i \le Q_{\max,i}$.

Motivated by these examples, we assume that $\mu_i(Q_i)$ is defined and continuously differentiable for $Q_i \ge Q_{\min,i} > 0$ and satisfies

$$\mu_i(Q_i) \ge 0,\ \mu_i'(Q_i) > 0 \text{ and is continuous for } Q_i \ge Q_{\min,i},\ \mu_i(Q_{\min,i}) = 0. \tag{1.5}$$

We assume that $f_i(R, Q_i)$ and $\frac{\partial f_i(R,Q_i)}{\partial R}$ are Lipschitz continuous for $R \ge 0$ and $Q_i \ge Q_{\min,i}$; $\frac{\partial f_i(R,Q_i)}{\partial R} \ge 0$, $\frac{\partial f_i(R,Q_i)}{\partial Q_i} \le 0$ and $f_i(R, Q_i) \ge 0$ for a.e. $R \ge 0$ and $Q_i \ge Q_{\min,i}$; there exists $Q_{Bi} \in (Q_{\min,i}, +\infty]$ such that

$$\begin{gathered} f_i(R, Q_i) > 0,\ \frac{\partial f_i(R, Q_i)}{\partial R} > 0 \text{ in } (R, Q_i) \in \mathbb{R}_+ \times [Q_{\min,i}, Q_{Bi}), \\ f_i(R, Q_i) = 0 \ \text{ in } \{(R, Q_i) \in \mathbb{R}_+ \times [Q_{\min,i}, +\infty) : R = 0 \text{ or } Q_i \ge Q_{Bi}\}. \end{gathered} \tag{1.6}$$

(When $Q_{Bi} = +\infty$, it is understood that $f_i(R, Q_i) = 0$ if and only if $R = 0$.)

The organization of the rest of this paper is as follows. The mathematical analysis is presented in the next section. Basically, we show that if both semitrivial equilibria for the system are invasible then there is at least one coexistence equilibrium. In Section 3, we compare the system (1.1) with the model without predation. Brief discussions are presented in Section 4.

2. Mathematical analysis

The following set is the region of interest for the system (1.1):

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

It is easy to show that Ω is positively invariant for (1.1) and any solution of (1.1) with initial value in Ω exists globally on $[0, \infty)$.

Let

$$W(t) = R^{(0)} - R - Q_1 N_1 - Q_2 N_2.$$

Then we can rewrite (1.1) as follows:

$$
\begin{aligned}
&\frac{dN_1}{dt} = [\mu_1(Q_1) - D]N_1 - g(N_1)N_2,\\
&\frac{dQ_1}{dt} = f_1(R^{(0)} - Q_1N_1 - Q_2N_2 - W, Q_1) - \mu_1(Q_1)Q_1,\\
&\frac{dN_2}{dt} = [\mu_2(Q_2) - D]N_2,\\
&\frac{dQ_2}{dt} = f_2(R^{(0)} - Q_1N_1 - Q_2N_2 - W, Q_2) - \mu_2(Q_2)Q_2 + g(N_1)Q_1,\\
&\frac{dW}{dt} = -DW,\\
&N_i(0) \geq 0, \quad Q_i(0) \geq Q_{\min,i}, \quad i = 1, 2
\end{aligned}
\tag{2.1}
$$

with initial values in the domain

$$\widetilde{\Sigma} = \{(N_1, Q_1, N_2, Q_2, W) \in \mathbb{R}^5_+ : Q_i \geq Q_{\min,i}, Q_1N_1 + Q_2N_2 + W \leq R^{(0)}\}. \tag{2.2}$$

Biologically, $R(t) := R^{(0)} - Q_1N_1 - Q_2N_2 - W$ in (2.1) should be nonnegative. Indeed, if there exists a t_0 such that $R^{(0)} - Q_1(t_0)N_1(t_0) - Q_2(t_0)N_2(t_0) - W(t_0) = 0$ then

$$
\begin{aligned}
R'(t_0) &= (R^{(0)} - Q_1N_1 - Q_2N_2 - W)'(t_0)\\
&= -f_1(R^{(0)} - Q_1(t_0)N_1(t_0) - Q_2(t_0)N_2(t_0) - W(t_0), Q_1(t_0))N_1(t_0)\\
&\quad - f_2(R^{(0)} - Q_1(t_0)N_1(t_0) - Q_2(t_0)N_2(t_0) - W(t_0), Q_2(t_0))N_2(t_0)\\
&\quad + D[Q_1(t_0)N_1(t_0) + Q_2(t_0)N_2(t_0) + W(t_0)]\\
&= DR^{(0)} \geq 0,
\end{aligned}
$$

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

From the equations for N_i and Q_i, along with (1.5) and (1.6) imply that $N_i(t) \geq 0$ and $Q_i(t) \geq Q_{\min,i}$ for all $t \geq 0$, $i = 1, 2$. Since W satisfies $\frac{dW}{dt} = -DW$ and then $\lim_{t\to\infty} W(t) = 0$. Therefore $N_i(t) \leq \frac{R^{(0)}+\epsilon}{Q_i(t)} \leq \frac{R^{(0)}+\epsilon}{Q_{min,i}}$, $i = 1, 2$.

Therefore, solutions of (1.1) (or (2.2)) are ultimately bounded on Ω (on $\widetilde{\Sigma}$). Putting $W = 0$ in (2.1), we arrive at the following reduced system of (1.1):

$$
\begin{aligned}
&\frac{dN_1}{dt} = [\mu_1(Q_1) - D]N_1 - g(N_1)N_2,\\
&\frac{dQ_1}{dt} = f_1(R^{(0)} - Q_1N_1 - Q_2N_2, Q_1) - \mu_1(Q_1)Q_1,\\
&\frac{dN_2}{dt} = [\mu_2(Q_2) - D]N_2,\\
&\frac{dQ_2}{dt} = f_2(R^{(0)} - Q_1N_1 - Q_2N_2, Q_2) - \mu_2(Q_2)Q_2 + g(N_1)Q_1,\\
&N_i(0) \geq 0, \quad Q_i(0) \geq Q_{\min,i}, \quad i = 1, 2
\end{aligned}
\tag{2.3}
$$

with initial values in the domain

$$\Sigma = \{(N_1, Q_1, N_2, Q_2) \in \mathbb{R}^4_+ : Q_i \geq Q_{\min,i}, Q_1 N_1 + Q_2 N_2 \leq R^{(0)}\}. \tag{2.4}$$

The trivial steady-state solution of (2.3), labeled E_0, corresponds to the absence of both species. It is given by

$$E_0 = (0, Q_1^0, 0, Q_2^0)$$

and it always exists. Here, Q_i^0 is the unique solution of

$$f_i(R^{(0)}, Q_i) - \mu_i(Q_i)Q_i = 0, \quad i = 1, 2. \tag{2.5}$$

One of the semi-trivial steady-state solution of (2.3), labeled E_1, corresponds to the presence of species 1 and the absence of species 2. It is given by

$$E_1 = (N_1^*, Q_1^*, 0, Q_2^{**}),$$

where

$$\begin{gathered} \mu_1(Q_1^*) = D, \quad f_1(R^{(0)} - Q_1^* N_1^*, Q_1^*) = DQ_1^*, \\ f_2(R^{(0)} - Q_1^* N_1^*, Q_2^{**}) - \mu_2(Q_2^{**})Q_2^{**} + g(N_1^*)Q_1^* = 0. \end{gathered} \tag{2.6}$$

The other semi-trivial steady-state solution of (2.3), labeled E_2, corresponds to the presence of species 2 and the absence of species 1. It is given by

$$E_2 = (0, Q_1^{**}, N_2^*, Q_2^*),$$

where

$$\begin{gathered} \mu_2(Q_2^*) = D, \quad f_2(R^{(0)} - Q_2^* N_2^*, Q_2^*) = DQ_2^*, \\ f_1(R^{(0)} - Q_2^* N_2^*, Q_1^{**}) - \mu_1(Q_1^{**})Q_1^{**} = 0. \end{gathered} \tag{2.7}$$

The local stability of E_0 is determined by the Jacobian matrix of (2.3) at E_0, denoted by

$$J_0 = \begin{pmatrix} \mu_1(Q_1^0) - D & 0 & 0 & 0 \\ -Q_1^0 \frac{\partial f_1(R^{(0)}, Q_1^0)}{\partial R} & a_{22} & -Q_2^0 \frac{\partial f_1(R^{(0)}, Q_1^0)}{\partial R} & 0 \\ 0 & 0 & \mu_2(Q_2^0) - D & 0 \\ -Q_1^0 \frac{\partial f_2(R^{(0)}, Q_2^0)}{\partial R} + g'(0)Q_1^0 & 0 & -Q_2^0 \frac{\partial f_2(R^{(0)}, Q_2^0)}{\partial R} & a_{44} \end{pmatrix},$$

where

$$\begin{aligned} a_{22} &= \frac{\partial f_1(R^{(0)}, Q_1^0)}{\partial Q_1} - [\mu_1(Q_1^0) + \mu_1'(Q_1^0)Q_1^0] < 0, \\ a_{44} &= \frac{\partial f_2(R^{(0)}, Q_2^0)}{\partial Q_2} - [\mu_2(Q_2^0) + \mu_2'(Q_2^0)Q_2^0] < 0. \end{aligned}$$

It is easy to see the eigenvalues of J_0 are its diagonal entries and the two eigenvalues $\mu_1(Q_1^0) - D$ and $\mu_2(Q_2^0) - D$ determine the stability of E_0, since the other two eigenvalues are negative.

Lemma 2.1. *The following statements are true:*

(i) E_0 *is locally asymptotically stable if both* $\mu_i(Q_i^0) < D$, $i = 1, 2$;

(ii) E_0 *is unstable if* $\mu_i(Q_i^0) > D$, *for some* i;

(iii) E_i *exists if and only if* $\mu_i(Q_i^0) > D$, $i = 1, 2$.

Proof. From our previous discussions, Parts (i) and (ii) are obvious. Next, we show that Part (iii) is true. If $\mu_1(Q_1^0) > D$ then, by (1.5), there exists a $Q_1^* < Q_1^0$ such that $\mu_1(Q_1^*) = D$. Therefore,

$$f_1(R^{(0)}, Q_1^*) > f_1(R^{(0)}, Q_1^0) = \mu_1(Q_1^0)Q_1^0 > \mu_1(Q_1^*)Q_1^* = DQ_1^*.$$

Hence, there exists a $N_1^* > 0$ such that $f_1(R^{(0)} - Q_1^* N_1^*, Q_1^*) = DQ_1^*$. On the other hand, it is easy to see that

$$G(Q_2) := f_2(R^{(0)} - Q_1^* N_1^*, Q_2) - \mu_2(Q_2)Q_2 + g(N_1^*)Q_1^*$$

is strictly decreasing in Q_2, $G(Q_{\min,2}) = f_2(R^{(0)} - Q_1^* N_1^*, Q_{\min,2}) + g(N_1^*)Q_1^* > 0$, and $\lim_{Q_2 \to \infty} G(Q_2) = -\infty$. This implies that there is a unique $Q_2^{**} \geq Q_{\min,2}$ such that $G(Q_2^{**}) = 0$, and hence, E_1 exists. Conversely, if E_1 exists then

$$f_1(R^{(0)}, Q_1^*) > f_1(R^{(0)} - Q_1^* N_1^*, Q_1^*) = DQ_1^* = \mu_1(Q_1^*)Q_1^*.$$

This implies that

$$\mu_1(Q_1^0)Q_1^0 - f_1(R^{(0)}, Q_1^0) = 0 > \mu_1(Q_1^*)Q_1^* - f_1(R^{(0)}, Q_1^*).$$

By using the monotonicity of $\mu_1(Q)Q - f_1(R^{(0)}, Q)$, it follows that $Q_1^0 > Q_1^*$ and consequently,

$$\mu_1(Q_1^0) > \mu_1(Q_1^*) = D.$$

Similarly, we can show that $\mu_2(Q_2^0) > D$ if and only if E_2 exists. □

The local stability of E_1 is determined by the Jacobian matrix of (2.3) at E_1, denoted by

$$J_1 = \begin{pmatrix} c_{11} & \mu_1'(Q_1^*)N_1^* & -g(N_1^*) & 0 \\ c_{21} & c_{22} & c_{23} & 0 \\ 0 & 0 & c_{33} & 0 \\ c_{41} & c_{42} & c_{43} & c_{44} \end{pmatrix},$$

where

$$
\begin{aligned}
&c_{11} = \mu_1(Q_1^*) - D = 0, \quad c_{21} = -Q_1^* \frac{\partial f_1(R^{(0)} - Q_1^* N_1^*, Q_1^*)}{\partial R} < 0, \\
&c_{41} = -Q_1^* \frac{\partial f_2(R^{(0)} - Q_1^* N_1^*, Q_2^{**})}{\partial R} + g'(N_1^*) Q_1^*, \\
&c_{22} = -N_1^* \frac{\partial f_1(R^{(0)} - Q_1^* N_1^*, Q_1^*)}{\partial R} + \frac{\partial f_1(R^{(0)} - Q_1^* N_1^*, Q_1^*)}{\partial Q_1} - [\mu_1(Q_1^*) + \mu_1'(Q_1^*) Q_1^*] < 0, \\
&c_{42} = -N_1^* \frac{\partial f_2(R^{(0)} - Q_1^* N_1^*, Q_2^{**})}{\partial R} + g(N_1^*), \quad c_{23} = -Q_2^{**} \frac{\partial f_1(R^{(0)} - Q_1^* N_1^*, Q_1^*)}{\partial R}, \\
&c_{33} = \mu_2(Q_2^{**}) - D, \quad c_{43} = -Q_2^* \frac{\partial f_2(R^{(0)} - Q_1^* N_1^*, Q_2^{**})}{\partial R}, \\
&c_{44} = \frac{\partial f_2(R^{(0)} - Q_1^* N_1^*, Q_2^{**})}{\partial Q_2} - [\mu_2(Q_2^{**}) + \mu_2'(Q_2^{**}) Q_2^{**}] < 0.
\end{aligned}
$$

It is not hard to see that the eigenvalues of J_1 are c_{33}, c_{44} and the eigenvalues of

$$
\widetilde{J}_1 = \begin{pmatrix} c_{11} & \mu_1'(Q_1^*) N_1^* \\ c_{21} & c_{22} \end{pmatrix}.
$$

Since $c_{11} = 0$, $c_{21} < 0$ and $c_{22} < 0$, it follows from the Routh-Hurwitz criterion (see, e.g., [12, Chapter 3]) that the real part of the eigenvalues of $\widetilde{J}_1$ are negative. Thus, the sign of $c_{33} = \mu_2(Q_2^{**}) - D$ determines the stability of E_1. A parallel arguments shows that the stability of E_2, if it exists, is determined by the sign of $\mu_1(Q_1^{**}) - D$. We summarize our above discussions in next lemma.

Lemma 2.2. *Suppose that E_1 and E_2 exist.*

(i) *E_1 is locally asymptotically stable if $\mu_2(Q_2^{**}) - D < 0$, and unstable if $\mu_2(Q_2^{**}) - D > 0$.*

(ii) *E_2 is locally asymptotically stable if $\mu_1(Q_1^{**}) - D < 0$, and unstable if $\mu_1(Q_1^{**}) - D > 0$.*

Before we state our main results, we consider the following system which is necessary for subsequent discussions:

$$
\begin{gathered}
\frac{dN_i}{dt} = [\mu_i(Q_i) - D] N_i, \quad \frac{dQ_i}{dt} = f_i(R^{(0)} - Q_i N_i, Q_i) - \mu_i(Q_i) Q_i, \\
N_i(0) \geq 0, \quad Q_i(0) \geq Q_{\min,i}
\end{gathered}
\tag{2.8}
$$

with initial values in the domain

$$
\mathbb{Y}_i = \{(N_i, Q_i) \in \mathbb{R}_+^2 : Q_i \geq Q_{\min,i}, Q_i N_i \leq R^{(0)}\}.
$$

By [17, Theorem 8.2.1], we have the following result which describes the dynamics of (2.8).

Lemma 2.3. *Assume that Q_i^0 is given by* (2.5). *Then the following statements are true:*

(i) *If $\mu_i(Q_i^0) - D < 0$, then every solution of* (2.8) *satisfies*

$$\lim_{t\to\infty}(N_i(t), Q_i(t)) = (0, Q_i^0);$$

(ii) *If $\mu_i(Q_i^0) - D > 0$, then every solution of* (2.8) *with $N_i(0) > 0$ satisfies*

$$\lim_{t\to\infty}(N_i(t), Q_i(t)) = \mathcal{E}_i,$$

where $\mathcal{E}_1 = (N_1^*, Q_1^*)$ and $\mathcal{E}_2 = (N_2^*, Q_2^*)$ are given by the first two equations in (2.6) *and* (2.7), *respectively.*

In contrast to the model without predation in [17, Chapter 8] or [16], we are able to show that stable coexistence is possible for the system (2.3) (or (1.1)) under suitable conditions. We give the following assumptions:

(A0) Both E_1 and E_2 exist, that is, $\mu_i(Q_i^0) > D$, $i = 1, 2$.

(A1) E_1 is unstable, that is, $\mu_2(Q_2^{**}) - D > 0$.

(A2) E_2 is unstable, that is, $\mu_1(Q_1^{**}) - D > 0$.

Let

$$\Sigma_0 = \{(N_1, Q_1, N_2, Q_2) \in \Sigma : N_1 > 0, N_2 > 0\}, \quad \partial\Sigma_0 := \Sigma \setminus \Sigma_0.$$

Theorem 2.4. *Let* (A0), (A1) *and* (A2) *hold. Then system* (2.3) *is uniformly persistent with respect to* $(\Sigma_0, \partial\Sigma_0)$ *in the sense that there is an $\eta > 0$ such that for any* $(N_1(0), Q_1(0), N_2(0), Q_2(0) \in \Sigma_0$, *the solution* $(N_1(t), Q_1(t), N_2(t), Q_2(t))$ *of* (2.3) *satisfies*

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

Further, system (2.3) *admits at least one positive (coexistence) solution.*

Proof. Suppose $\Psi_t \colon \Sigma \to \Sigma$ are the solution flows associated with system (2.3), that is,

$$\Psi_t(N_1(0), Q_1(0), N_2(0), Q_2(0)) = (N_1(t), Q_1(t), N_2(t), Q_2(t)),$$

where $(N_1(0), Q_1(0), N_2(0), Q_2(0)) \in \Sigma$. Let $\omega(x)$ be the omega-limit set of the orbit of Ψ_t with initial values $x \in \Sigma$. It is easy to see that $\Psi_t(\Sigma_0) \subset \Sigma_0$. Since solutions of the system (2.3) are ultimately bounded, it follows that Ψ_t is point dissipative and compact.

Recall that E_0, E_1 and E_2 are fixed points of Ψ_t. Further, $\{E_0\}$, $\{E_1\}$ and $\{E_2\}$ are pairwise disjoint, compact and isolated invariant sets for Ψ_t in $\partial\Sigma_0$. We are going to show the following property

$$\bigcup_{x\in\partial\Sigma_0} \omega(x) \subset \{E_0, E_1, E_2\}. \tag{2.9}$$

In the case where $N_1(0) > 0$ and $N_2(0) = 0$, we have $N_1(t) > 0$ and $N_2(t) = 0$, $\forall\, t \geq 0$. Then $(N_1(t), Q_1(t))$ satisfies system (2.8) with $i = 1$, and initial values are in the domain $\mathbb{Y}_1$. By (A0) and Lemma 2.3, it follows that

$$\lim_{t\to\infty} (N_1(t), Q_1(t)) = (N_1^*, Q_1^*).$$

Then, the equation for $Q_2(t)$ in (2.3) is asymptotic to

$$\frac{dQ_2}{dt} = f_2(R^{(0)} - Q_1^* N_1^*, Q_2) - \mu_2(Q_2)Q_2 + g(N_1^*)Q_1^*.$$

From the theory for asymptotically autonomous semiflows (see, e.g., [18, Corollary 4.3]), it follows that

$$\lim_{t\to\infty} Q_2(t) = Q_2^{**},$$

where Q_2^{**} is given in (2.6). It then follows that

$$\lim_{t\to\infty} \Psi_t(N_1(0), Q_1(0), N_2(0), Q_2(0)) = E_1.$$

In the case where $N_1(0) = 0$ and $N_2(0) > 0$, we can use the similar arguments to show that

$$\lim_{t\to\infty} \Psi_t(N_1(0), Q_1(0), N_2(0), Q_2(0)) = E_2.$$

In the case where $N_1(0) = 0$ and $N_2(0) = 0$, we can also show that

$$\lim_{t\to\infty} \Psi_t(N_1(0), Q_1(0), N_2(0), Q_2(0)) = E_0.$$

Consequently, $\Psi_t\colon \Sigma \to \Sigma$ satisfies the property (2.9). It is obvious that no subset of $\{E_0, E_1, E_2\}$ forms a cycle in $\partial\Sigma_0$.

Claim: For $j = 0, 1, 2$, E_j is a uniform weak repeller for Σ_0 in the sense that there exists a $\delta_j > 0$ such that

$$\limsup_{t\to\infty} \|\Psi_t(x) - E_j\| \geq \delta_j, \tag{2.10}$$

for any $x \in \Sigma_0$.

In the case where $j = 2$, from (1.2), we rewrite the first equation of (2.3) as follows

$$\frac{dN_1}{dt} = [\mu_1(Q_1) - D - c(N_1, N_2)]N_1, \tag{2.11}$$

where

$$c(N_1, N_2) = \frac{g_{\max} N_1^{b-1}}{K_{\max}^b + N_1^b} N_2, \quad b > 1. \tag{2.12}$$

Let $\epsilon_2 := \frac{1}{2}(\mu_1(Q_1^{**}) - D) > 0$. Then it follows from the continuity of $\mu_1(Q_1)$ and $c(N_1, N_2)$ that there exists $\delta_2 > 0$ such that

$$|\mu_1(Q_1) - \mu_1(Q_1^{**})| < \frac{1}{2}\epsilon_2, \quad \forall\, |Q_1 - Q_1^{**}| < \delta_2 \tag{2.13}$$

and

$$|c(N_1, N_2) - c(0, N_2^*)| < \frac{1}{2}\epsilon_2, \quad \forall\, \|(N_1, N_2) - (0, N_2^*)\| < \delta_2. \tag{2.14}$$

We next show that

$$\limsup_{t\to\infty} \|\Psi_t(x) - E_2\| \geq \delta_2, \quad \forall\, x \in \Sigma_0.$$

Suppose not. Then there exists an $x_0 \in \Sigma_0$ such that $\limsup_{t\to\infty} \|\Psi_t(x_0) - E_2\| < \delta_2$. Thus, there exists $t_2 > 0$ such that

$$|Q_1(t, x_0) - Q_1^{**}| < \delta_2 \quad \text{and} \quad \|(N_1(t, x_0), N_2(t, x_0)) - (0, N_2^*)\| < \delta_2, \quad \forall\, t \geq t_2.$$

Using $c(0, N_2^*) = 0$, together with (2.13) and (2.14), it follows that

$$\begin{aligned} &\big|[\mu_1(Q_1(t, x_0)) - D - c(N_1(t, x_0), N_2(t, x_0))] - [\mu_1(Q_1^{**}) - D]\big| \\ &< \frac{1}{2}\epsilon_2 + \frac{1}{2}\epsilon_2 = \epsilon_2, \quad \forall\, t \geq t_2. \end{aligned}$$

Then

$$\mu_1(Q_1(t, x_0)) - D - c(N_1(t, x_0), N_2(t, x_0)) > [\mu_1(Q_1^{**}) - D] - \epsilon_2 = \epsilon_2, \quad \forall\, t \geq t_2.$$

This inequality and (2.11) imply that

$$\frac{dN_1(t, x_0)}{dt} > \epsilon_2 N_1(t, x_0), \quad \forall\, t \geq t_2,$$

which shows that $\lim_{t\to\infty} N_1(t, x_0) = \infty$, a contradiction. Similarly, we can show that (2.10) is true for $j = 0, 1$.

Therefore, each E_j is isolated in Σ and $\mathcal{W}^s(E_j) \cap \Sigma_0 = \emptyset$, where $\mathcal{W}^s(E_j)$ is the stable set of E_j (see [21]). Since $\Psi_t \colon \Sigma \to \Sigma$ is point dissipative and compact, we conclude from [21, Theorem 1.1.3] that there exists a global attractor $\mathcal{A}$ for Ψ_t in Σ. By [21, Theorem 1.3.1] on strong repellers, $\Psi_t \colon \Sigma \to \Sigma$ is uniformly persistent with respect to $(\Sigma_0, \partial\Sigma_0)$. It follows from [21, Theorem 1.3.6] that there exists a global attractor $\mathcal{A}_0$ for Ψ_t in Σ_0 and Ψ_t has at least one fixed point

$$(\widetilde{N}_1, \widetilde{Q}_1, \widetilde{N}_2, \widetilde{Q}_2) \in \Sigma_0.$$

It then follows that $(\widetilde{N}_1, \widetilde{Q}_1, \widetilde{N}_2, \widetilde{Q}_2)$ is a positive steady-state solution for (2.3). This completes the proof. $\square$

We are going to lift the dynamics of the reduced system (2.3) to the full system (1.1).

Theorem 2.5. *Let* (A0)*,* (A1) *and* (A2) *hold. Then system* (1.1) *admits at least one positive (coexistence) solution, and there is an* $\eta > 0$ *such that for any initial value* $(R(0), N_1(0), Q_1(0), N_2(0), Q_2(0)) \in \Omega$ *with* $N_1(0) > 0$ *and* $N_2(0) > 0$*, the corresponding solution of* (1.1) *satisfies*

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

Proof. Since systems (1.1) and (2.1) are equivalent, it suffices to study system (2.1). Assume that

$$\widetilde{\Sigma}_0 = \{(N_1, Q_1, N_2, Q_2, W) \in \widetilde{\Sigma} : N_1 > 0, N_2 > 0\}, \quad \partial\widetilde{\Sigma}_0 := \widetilde{\Sigma} \setminus \widetilde{\Sigma}_0,$$

where $\widetilde{\Sigma}$ is given by (2.2). Let $\widetilde{\Psi}_t \colon \widetilde{\Sigma} \to \widetilde{\Sigma}$ be the solution flows associated with system (2.1), that is,

$$\widetilde{\Psi}_t(N_1(0), Q_1(0), N_2(0), Q_2(0), W(0)) = (N_1(t), Q_1(t), N_2(t), Q_2(t), W(t)),$$

where $(N_1(0), Q_1(0), N_2(0), Q_2(0), W(0)) \in \widetilde{\Sigma}$. Recall that $\Psi_t \colon \Sigma \to \Sigma$ are the solution flows associated with system (2.3). Let $\widetilde{\omega} := \widetilde{\omega}(x)$ be the omega-limit set of the orbit of $\widetilde{\Psi}_t$ with initial values $x \in \widetilde{\Sigma}$. From the fifth equation of the system (2.1), it follows that

$$\lim_{t\to\infty} W(t) = 0.$$

Thus, there exists a set $\mathcal{I} \subset \mathbb{R}^4_+$ such that $\widetilde{\omega} = \mathcal{I} \times \{0\}$.

Since $\widetilde{\Sigma}$ is closed, it follows that $\widetilde{\omega} \subset \widetilde{\Sigma}$. For any given $(N_1, Q_1, N_2, Q_2) \in \mathcal{I}$, we have $(N_1, Q_1, N_2, Q_2, 0) \in \widetilde{\omega} \subset \widetilde{\Sigma}$. By the definition of $\widetilde{\Sigma}$, it follows that $(N_1, Q_1, N_2, Q_2) \in \Sigma$. Thus, $\mathcal{I} \subset \Sigma$. By [21, Lemma 1.2.1′], $\widetilde{\omega}$ is a compact, invariant and internal chain transitive set for $\widetilde{\Psi}_t$. Moreover, if $x^0 := (N_1^0, Q_1^0, N_2^0, Q_2^0) \in \mathbb{R}^4_+$ with $(x^0, 0) \in \widetilde{\omega}$, there holds

$$\widetilde{\Psi}_t\Big|_{\widetilde{\omega}}(x^0, 0) = (\Psi_t(x^0), 0),$$

where $\Psi_t(x^0)$ are the solution maps associated with (2.3) on Σ. It then follows from the definition of internally chain transitive sets that $\mathcal{I}$ is a compact, invariant and internal chain transitive set for $\Psi_t \colon \Sigma \to \Sigma$.

In order to use [21, Theorem 1.3.1] with $L = \mathcal{I}$, we must first verify that $\mathcal{I} \notin \{\{E_0\}, \{E_1\}, \{E_2\}\}$. We only prove the claim that $\mathcal{I} \neq \{E_2\}$ since other two claims can be proved in a similar way. Suppose, by contradiction, that $\mathcal{I} = \{E_2\}$, then

$$\widetilde{\omega} = (E_2, 0) := \widetilde{E}.$$

Thus, we have

$$\lim_{t\to\infty} \widetilde{\Psi}_t(N_1^0, Q_1^0, N_2^0, Q_2^0, W^0) = (E_2, 0).$$

From this, we have that

$$\lim_{t\to\infty} N_1(t) = 0, \quad \lim_{t\to\infty} Q_1(t) = Q_1^{**} \quad \text{and} \quad \lim_{t\to\infty} N_2(t) = N_2^*.$$

Let $\epsilon_2 := \frac{1}{2}(\mu_1(Q_1^{**}) - D) > 0$. Then it follows from the continuity that there is a $T > 0$ such that for all $t \geq T$, we have

$$\big|[\mu_1(Q_1) - D - c(N_1, N_2)] - [\mu_1(Q_1^{**}) - D - c(0, N_2^*)]\big| < \epsilon_2, \quad \forall\, t \geq T,$$

where $c(N_1, N_2)$ is defined in (2.12). This implies that

$$\mu_1(Q_1) - D - c(N_1, N_2) > \epsilon_2, \quad \forall\, t \geq T,$$

and hence

$$\frac{dN_1(t, x_0)}{dt} > \epsilon_2 N_1(t, x^0), \quad \forall\, t \geq T,$$

which shows that $\lim_{t\to\infty} N_1(t, x^0) = \infty$, a contradiction. Similarly, we can prove $\mathcal{I} \neq \{E_0\}$ and $\mathcal{I} \neq \{E_1\}$. Thus, $\mathcal{I} \notin \{\{E_0\}, \{E_1\}, \{E_2\}\}$.

By using [21, Theorem 1.3.1] with $L = \mathcal{I}$, it follows that there exists a $\delta > 0$ such that

$$\inf_{x\in\mathcal{I}} d(x, \partial\Sigma_0) \geq \delta.$$

Since

$$(N_1(t), Q_(t), N_2(t), Q_2(t), W(t)) \to \widetilde{\omega} = \mathcal{I} \times \{0\} \quad \text{as } t \to \infty,$$

it follows that there exists an η, such that

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

This implies that the solution flows $\widetilde{\Psi}_t \colon \widetilde{\Sigma} \to \widetilde{\Sigma}$ are uniformly persistent with respect to $(\widetilde{\Sigma}_0, \partial\widetilde{\Sigma}_0)$. By [21, Theorem 1.3.6], it follows that system (2.1) admits at least one positive (coexistence) solution. Since systems (1.1) and (2.1) are equivalent, we complete our proof. □

3. Globally asymptotic behavior

Putting $g(N_1) \equiv 0$ into (2.3) (i.e., the reduced system of (1.1)), we have the following system without predation:

$$\begin{aligned}
&\frac{dN_1}{dt} = [\mu_1(Q_1) - D]N_1,\\
&\frac{dQ_1}{dt} = f_1(R^{(0)} - Q_1N_1 - Q_2N_2, Q_1) - \mu_1(Q_1)Q_1,\\
&\frac{dN_2}{dt} = [\mu_2(Q_2) - D]N_2,\\
&\frac{dQ_2}{dt} = f_2(R^{(0)} - Q_1N_1 - Q_2N_2, Q_2) - \mu_2(Q_2)Q_2,\\
&N_i(0) \geq 0, \quad Q_i(0) \geq Q_{\min,i}, \quad i = 1, 2
\end{aligned} \tag{3.1}$$

with initial values in the domain (2.4). The main purpose in this section is to compare our system (1.1) with the model (3.1). The trivial steady-state solution of (3.1), labeled $\widetilde{E}_0$, corresponds to the absence of both species. It is given by

$$\widetilde{E}_0 = (0, Q_1^0, 0, Q_2^0),$$

where Q_i^0 is the unique solution of (2.5). One of the semi-trivial steady-state solution of (3.1), labeled $\widetilde{E}_2$, corresponds to the presence of species 2 and the absence of species 1. It is given by

$$\widetilde{E}_2 = (0, Q_1^{**}, N_2^*, Q_2^*),$$

whose components are defined in (2.7). The other semi-trivial steady-state solution of (3.1), labeled $\widetilde{E}_1$, corresponds to the presence of species 1 and the absence of species 2. It is given by

$$\widetilde{E}_1 = (N_1^*, Q_1^*, 0, \widetilde{Q}_2^{**}),$$

where N_1^* and Q_1^* are defined in the first two equalities of (2.6), and $\widetilde{Q}_2^{**}$ satisfies

$$f_2(R^{(0)} - Q_1^*N_1^*, \widetilde{Q}_2^{**}) - \mu_2(\widetilde{Q}_2^{**})\widetilde{Q}_2^{**} = 0. \tag{3.2}$$

From (2.6) and (3.2), we see that

$$\widetilde{Q}_2^{**} < Q_2^{**}. \tag{3.3}$$

We first discuss the case where species 2 is a better competitor for system (3.1), that is, the system without predation.

(H1) Assume species N_2 is a better competitor in system (3.1), i.e., $0 < \lambda_2 < \lambda_1 < R^{(0)}$, where $\lambda_2 = R^{(0)} - Q_2^*N_2^*$, $\lambda_1 = R^{(0)} - Q_1^*N_1^*$.

By (H1), it follows from [16] or [17, Chapter 8] that $\widetilde{E}_1$ is unstable and $\widetilde{E}_2$ is locally asymptotically stable for system (3.1), or equivalently

$$\mu_2(\widetilde{Q}_2^{**}) - D > 0 \quad \text{and} \quad \mu_1(Q_1^{**}) - D < 0. \tag{3.4}$$

From (3.3) and (3.4), we have

$$\mu_2(Q_2^{**}) - D > 0 \quad \text{and} \quad \mu_1(Q_1^{**}) - D < 0,$$

which implies that E_1 is unstable and E_2 is locally asymptotically stable for system (2.3) (see Lemma 2.2). In fact, we can further show that E_2 is globally asymptotically stable for system (2.3). To this end, we put $U_1 = Q_1 N_1$ and $U_2 = Q_2 N_2$ into system (2.3) and we arrive at the following system

$$\begin{aligned}
\frac{dN_1}{dt} &= \left[\mu_1\left(\frac{U_1}{N_1}\right) - D\right] N_1 - g(N_1)N_2,\\
\frac{dU_1}{dt} &= f_1\left(R^{(0)} - U_1 - U_2, \frac{U_1}{N_1}\right) N_1 - DU_1 - g(N_1)\frac{U_1}{N_1}N_2,\\
\frac{dN_2}{dt} &= \left[\mu_2\left(\frac{U_2}{N_2}\right) - D\right] N_2,\\
\frac{dU_2}{dt} &= f_2\left(R^{(0)} - U_1 - U_2, \frac{U_2}{N_2}\right) N_2 - DU_2 + g(N_1)\frac{U_1}{N_1}N_2,\\
N_i(0) &\geq 0, \quad U_i(0) \geq 0, \quad i = 1, 2.
\end{aligned} \tag{3.5}$$

Suppose Φ_t is the solution flow associated with system (3.5) in an appropriately feasible domain, and Π_t is the solution flow associated with the following system

$$\begin{aligned}
\frac{dN_1}{dt} &= \left[\mu_1\left(\frac{U_1}{N_1}\right) - D\right] N_1,\\
\frac{dU_1}{dt} &= f_1\left(R^{(0)} - U_1 - U_2, \frac{U_1}{N_1}\right) N_1 - DU_1,\\
\frac{dN_2}{dt} &= \left[\mu_2\left(\frac{U_2}{N_2}\right) - D\right] N_2,\\
\frac{dU_2}{dt} &= f_2\left(R^{(0)} - U_1 - U_2, \frac{U_2}{N_2}\right) N_2 - DU_2,\\
N_i(0) &\geq 0, \quad U_i(0) \geq 0, \quad i = 1, 2.
\end{aligned} \tag{3.6}$$

From system (3.5), it is not hard to see that

$$\begin{aligned}
\frac{dN_1}{dt} &= \left[\mu_1\left(\frac{U_1}{N_1}\right) - D\right] N_1 - g(N_1)N_2 \leq \left[\mu_1\left(\frac{U_1}{N_1}\right) - D\right] N_1,\\
\frac{dU_1}{dt} &= f_1\left(R^{(0)} - U_1 - U_2, \frac{U_1}{N_1}\right) N_1 - DU_1 - g(N_1)\frac{U_1}{N_1}N_2
\end{aligned}$$

$$
\begin{aligned}
&\le f_1\left(R^{(0)} - U_1 - U_2, \frac{U_1}{N_1}\right) N_1 - DU_1,\\
\frac{dN_2}{dt} &= \left[\mu_2\left(\frac{U_2}{N_2}\right) - D\right] N_2,\\
\frac{dU_2}{dt} &= f_2\left(R^{(0)} - U_1 - U_2, \frac{U_2}{N_2}\right) N_2 - DU_2 + g(N_1)\frac{U_1}{N_1} N_2\\
&\ge f_2\left(R^{(0)} - U_1 - U_2, \frac{U_2}{N_2}\right) N_2 - DU_2.
\end{aligned}
$$

Then the comparison principle implies that

$$\Phi_t(N_1(0), U_1(0), N_2(0), U_2(0)) \le_K \Pi_t(N_1(0), U_1(0), N_2(0), U_2(0)), \tag{3.7}$$

where the partial order $\le_K$ (see, e.g., [15]) is induced by the positive cone $K := \mathbb{R}^2_+ \times (-\mathbb{R}^2_+)$ in $\mathbb{R}^4$. Note that systems (3.1) and (3.6) are equivalent under the transformation $U_1 = Q_1 N_1$ and $U_2 = Q_2 N_2$. Under assumption (H1), species 2 is a better competitor in the model without predation (i.e., system (3.1), or equivalently, (3.6)), it follows from [16] or [17, Chapter 8] that

$$\lim_{t\to\infty} \Pi_t(N_1(0), U_1(0), N_2(0), U_2(0)) = (0, 0, N_2^*, U_2^*), \tag{3.8}$$

where $U_2^* = N_2^* Q_2^*$. By (3.7) and (3.8), we obtain $\lim_{t\to\infty}(N_1(t), U_1(t)) = (0, 0)$. Thus, the equations for (N_2, U_2) in (3.5) are asymptotic to the following system

$$\frac{dN_2}{dt} = \left[\mu_2\left(\frac{U_2}{N_2}\right) - D\right] N_2 \quad \text{and} \quad \frac{dU_2}{dt} = f_2\left(R^{(0)} - U_2, \frac{U_2}{N_2}\right) N_2 - DU_2.$$

Then the theory for asymptotically autonomous semiflows (see, e.g., [18, Corollary 4.3]) implies that

$$\lim_{t\to\infty} (N_2(t), U_2(t)) = (N_2^*, U_2^*).$$

The we conclude that

$$\lim_{t\to\infty} \Phi_t(N_1(0), U_1(0), N_2(0), U_2(0)) = (0, 0, N_2^*, U_2^*),$$

which proves that E_2 is globally asymptotically stable for system (2.3). Thus we have

Proposition 3.1. *Let* $0 < \lambda_2 < \lambda_1 < R^{(0)}$*, then the solution of* (1.1) *satisfies* $\lim_{t\to\infty} R(t) = \lambda_2$, $\lim_{t\to\infty} N_1(t) = 0$, $\lim_{t\to\infty} Q_1(t) = Q_1^{**}$, $\lim_{t\to\infty} N_2(t) = N_2^*$, *and* $\lim_{t\to\infty} Q_2(t) = Q_2^*$.

Next, we consider the case where species 1 is a better competitor for system without predation (3.1).

(H2) From now on, we assume species N_1 is superior in system without predation (3.1), i.e., $0 < \lambda_1 < \lambda_2 < R^{(0)}$, where $\lambda_1 = R^{(0)} - Q_1^* N_1^*$, $\lambda_2 = R^{(0)} - Q_2^* N_2^*$.

By (H2), it follows from [16] or [17, Chapter 8] that $\widetilde{E}_1$ is locally asymptotically stable and $\widetilde{E}_2$ is unstable for system (3.1), or equivalently

$$\mu_2(\widetilde{Q}_2^{**}) - D < 0 \quad \text{and} \quad \mu_1(Q_1^{**}) - D > 0. \tag{3.9}$$

Proposition 3.2. *Under assumption* (H2)*, the following results are true:*

- (i) E_2 *is always unstable;*
- (ii) *there exists a unique* $\widehat{g}_{\max} > 0$ *such that* E_1 *is locally asymptotically stable if* $0 \le g_{\max} < \widehat{g}_{\max}$*, and* E_1 *is unstable if* $g_{\max} > \widehat{g}_{\max}$.

Proof. Suppose that $0 < \lambda_1 < \lambda_2 < R^{(0)}$. Then from (3.6) and (3.7), we have

$$\begin{aligned}\mu_1(Q_1^*)Q_1^* - f_1(\lambda_1, Q_1^*) &= 0\\ &= \mu_1(Q_1^{**})Q_1^{**} - f_1(\lambda_2, Q_1^{**})\\ &< \mu_1(Q_1^{**})Q_1^{**} - f_1(\lambda_1, Q_1^{**})\end{aligned}$$

implying that

$$Q_1^* < Q_1^{**}.$$

From $Q_1^* < Q_1^{**}$, we have

$$\mu_1(Q_1^{**}) - D > 0,$$

and we see that E_2 is unstable for system (2.3) (see Lemma 2.2).

From Lemma 2.2(i), E_1 is locally asymptotically stable if $\mu_2(Q_2^{**}) < D$ and E_1 is unstable if $\mu_2(Q_2^{**}) > D$. In fact, we can use the parameter $g_{\max}$, which is defined in (1.2), to determine the local stability of E_1. From (1.2) and the third equality of (2.6), we have

$$f_2(R^{(0)} - Q_1^*N_1^*, Q_2^{**}) - \mu_2(Q_2^{**})Q_2^{**} + g_{\max} \cdot \frac{(N_1^*)^b Q_1^*}{K_{\max}^b + (N_1^*)^b} = 0. \tag{3.10}$$

For convenience, we treat Q_2^{**} as a function of $g_{\max}$, that is $Q_2^{**} = Q_2^{**}(g_{\max})$. From (3.10), it follows that

$$Q_2^{**}(g_{\max}) \text{ is strictly increasing in } g_{\max},\ Q_2^{**}(0) = \widetilde{Q}_2^{**}, \text{ and } \lim_{g_{\max}\to\infty} Q_2^{**}(g_{\max}) = \infty.$$

This implies that $\mu_2(Q_2^{**}) - D := \mu_2(Q_2^{**}(g_{\max})) - D$ is strictly increasing in $g_{\max}$, and

$$\lim_{g_{\max}\to 0^+}[\mu_2(Q_2^{**}(g_{\max})) - D] = \mu_2(\widetilde{Q}_2^{**}) - D < 0, \quad \lim_{g_{\max}\to\infty}[\mu_2(Q_2^{**}(g_{\max})) - D] > 0,$$

where we have used the first inequality in (3.9). Then there exists a unique $\widehat{g}_{\max} > 0$ such that

$$\mu_2(Q_2^{**}(g_{\max})) - D \begin{cases} < 0 & \text{for all } 0 \le g_{\max} < \widehat{g}_{\max},\\ > 0 & \text{foe all } g_{\max} > \widehat{g}_{\max}.\end{cases} \tag{3.11}$$

From (3.11), we see that E_1 is locally asymptotically stable for system (2.3) if $0 \le g_{\max} < \widehat{g}_{\max}$, and E_1 is unstable for system (2.3) if $g_{\max} > \widehat{g}_{\max}$. □

4. Discussion

This study analyzed the chemostat model (1.1) proposed in [20], where two species ($N_1(t)$ and $N_2(t)$) compete for a nitrogen resource ($R(t)$), and the species 2 ($N_2(t)$) also consumes species 1 ($N_1(t)$) for growth. In the assumption (H1), we assume species 2 is a better competitor for the system without predation, (3.1), then we can prove that species 2 will win the competition in the system with predation, (1.1) (see Proposition 3.1). In the assumption (H2), we assume species 1 is a better competitor for the system without predation, (3.1), then we can prove that E_2 is always unstable, and E_1 becomes unstable if the maximal predation rate $g_{\max}$ exceeds a critical value (see Proposition 3.2). When E_1 and E_2 are both unstable, we can show that system (1.1) is permanent, and system (1.1) admits at least one positive (coexistence) solution by using the abstract theory of uniform persistence (see Theorems 2.4 and 2.5).

Next, we shall adopt a different approach to discuss the existence and uniqueness of the positive equilibrium of system (1.1) under the assumption (H2). From (2.6) and (2.7), we also note that

$$f_i(\lambda_i, Q_i^*) = DQ_i^*, \quad i = 1, 2. \tag{4.1}$$

In order to find the positive equilibrium of system (1.1), we assume that $\frac{dR}{dt} = \frac{dN_i}{dt} = \frac{dQ_i}{dt} = 0$, $i = 1, 2$, $N_1 > 0$ and $N_2 > 0$ in (1.1). In view of the fourth equation of (1.1), it follows that $Q_2 = Q_2^*$, where Q_2^* is given in (2.7). From the third equation of (1.1), we see that $R = R(Q_1)$ satisfies

$$f_1(R(Q_1), Q_1) - \mu_1(Q_1)Q_1 = 0. \tag{4.2}$$

Differentiating both sides of the equation (4.2) with respect to Q_1, we get

$$R'(Q_1) = \frac{\mu_1(Q_1) + \mu_1'(Q_1)Q_1 - \frac{\partial f_1}{\partial Q_1}(R(Q_1), Q_1)}{\frac{\partial f_1}{\partial R}(R(Q_1), Q_1)} > 0. \tag{4.3}$$

From (4.2), it is easy to see that

$$R(Q_{\min,1}) = 0, \quad R(Q_1^*) = \lambda_1 \quad \text{and} \quad R(Q_1^0) = R^{(0)}, \tag{4.4}$$

where Q_1^0 and Q_1^* are given in (2.5) and (2.6), respectively. By (H2), it follows that

$$0 < \lambda_1 < \lambda_2 < R^{(0)}. \tag{4.5}$$

In view of (4.3), (4.4) and (4.5), we see that there exists a unique $\widehat{Q}_1 \in (Q_1^*, Q_1^0)$ such that

$$R(\widehat{Q}_1) = \lambda_2. \tag{4.6}$$

In view of the fifth equation of (1.1), it follows that

$$f_2(R(Q_1), Q_2^*) - \mu_2(Q_2^*)Q_2^* + g(N_1(Q_1))Q_1 = 0.$$

Then

$$g(N_1(Q_1)) = \frac{\mu_2(Q_2^*)Q_2^* - f_2(R(Q_1), Q_2^*)}{Q_1} = \frac{f_2(\lambda_2, Q_2^*) - f_2(R(Q_1), Q_2^*)}{Q_1}, \tag{4.7}$$

where we have used (4.1) with $i = 2$. Thus

$$g(N_1(Q_1)) > 0 \quad \Longleftrightarrow \quad R(Q_1) < \lambda_2 = R(\widehat{Q}_1) \quad \Longleftrightarrow \quad Q_1 < \widehat{Q}_1.$$

From (4.7), it is easy to verify that

$$N_1'(Q_1) = \frac{-g(N_1(Q_1)) - \frac{\partial f_2}{\partial R}(R(Q_1), Q_2^*)R'(Q_1)}{Q_1 g'(N_1(Q_1))} < 0.$$

Furthermore,

$$N_1(Q_1) = g^{-1}\left(\frac{f_2(\lambda_2, Q_2^*) - f_2(R(Q_1), Q_2^*)}{Q_1}\right), \quad Q_1 < \widehat{Q}_1.$$

In view of the second equation of (1.1), we see that

$$N_2 = N_2(Q_1) = \frac{(\mu_1(Q_1) - D)N_1(Q_1)}{g(N_1(Q_1))},$$

and hence

$$N_2(Q_1) > 0 \quad \Longleftrightarrow \quad Q_1 > Q_1^*.$$

Let

$$F(Q_1) = (R^{(0)} - R(Q_1))D - f_1(R(Q_1), Q_1)N_1(Q_1) - f_2(R(Q_1), Q_2^*)N_2(Q_1). \tag{4.8}$$

If we can find a $Q_{1c} > 0$ satisfying $F(Q_1) = 0$, $Q_1^* < Q_1 < \widehat{Q}_1$, then the positive equilibrium of system (1.1) takes the form

$$\mathcal{E}_c = (R_c, N_{1c}, Q_{1c}, N_{2c}, Q_{2c}),$$

where $R_c = R(Q_{1c})$, $N_1 = N_1(Q_{1c})$, and $N_2 = N_2(Q_{1c})$. In view of (4.6) and (4.7), we see that

$$g(N_1(\widehat{Q}_1)) = 0, \quad \text{or} \quad N_1(\widehat{Q}_1) = 0.$$

Then

$$\begin{aligned} N_2(\widehat{Q}_1^-) &= \lim_{Q_1 \uparrow \widehat{Q}_1} N_2(Q_1) = \lim_{Q_1 \uparrow \widehat{Q}_1} \frac{\mu_1(Q_1) - D}{g(N_1(Q_1))/N_1(Q_1)} \\ &= \lim_{Q_1 \uparrow \widehat{Q}_1} \frac{\mu_1(Q_1) - D}{g_{\max}(N_1(Q_1))^{b-1}/[K_{\max}^b + (N_1(Q_1))^b]}, \end{aligned} \tag{4.9}$$

where $b > 1$ and we have used (1.2). Since $\widehat{Q}_1 \in (Q_1^*, Q_1^0)$, we see that

$$\mu_1(\widehat{Q}_1) - D > \mu_1(Q_1^*) - D = 0, \tag{4.10}$$

where we have used the first equality in (2.6). In view of (4.9) and (4.10), it follows that

$$N_2(\widehat{Q}_1^-) = \lim_{Q_1 \uparrow \widehat{Q}_1} N_2(Q_1) = +\infty.$$

Thus,

$$\begin{aligned} F(\widehat{Q}_1^-) &= \lim_{Q_1 \uparrow \widehat{Q}_1} F(Q_1) \\ &= (R^{(0)} - R(\widehat{Q}_1^-))D - f_1(R(\widehat{Q}_1^-), \widehat{Q}_1^-)N_1(\widehat{Q}_1^-) - f_2(R(\widehat{Q}_1^-), Q_2^*)N_2(\widehat{Q}_1^-) \\ &= -\infty. \end{aligned} \tag{4.11}$$

Since $N_2(Q_1^*) = 0$, it follows from (4.8) that

$$F(Q_1^*) = (R^{(0)} - \lambda_1)D - f_1(\lambda_1, Q_1^*)N_1(Q_1^*). \tag{4.12}$$

Using (4.12) and the fact $(R^{(0)} - \lambda_1)D = f_1(\lambda_1, Q_1^*)N_1^*$, we see that

$$F(Q_1^*) = f_1(\lambda_1, Q_1^*)[N_1^* - N_1(Q_1^*)]. \tag{4.13}$$

In view of the third equation in (2.6), it follows that

$$f_2(\lambda_1, Q_2^{**}) + g(N_1^*)Q_1^* = \mu_2(Q_2^{**})Q_2^{**}.$$

If $Q_2^{**} < Q_2^*$, it is not hard to see that

$$\begin{aligned} f_2(\lambda_1, Q_2^*) + g(N_1^*)Q_1^* < f_2(\lambda_1, Q_2^{**}) + g(N_1^*)Q_1^* &= \mu_2(Q_2^{**})Q_2^{**} \\ &< \mu_2(Q_2^*)Q_2^* = DQ_2^* = f_2(\lambda_2, Q_2^*), \end{aligned}$$

and hence,

$$g(N_1^*)Q_1^* < f_2(\lambda_2, Q_2^*) - f_2(\lambda_1, Q_2^*),$$

which implies

$$g(N_1^*) < g(N_1(Q_1^*)), \tag{4.14}$$

where we have used the second identity in (4.4), and (4.7). From (4.14), it follows that $N_1^* < N_1(Q_1^*)$, and hence,

$$F(Q_1^*) < 0, \tag{4.15}$$

where we have used (4.13). Similarly, if $Q_2^{**} > Q_2^*$, we can show that

$$F(Q_1^*) > 0. \tag{4.16}$$

From Lemma 2.2, we see that E_1 is locally asymptotically stable (resp. unstable) if $Q_2^{**} < Q_2^*$ (resp. $Q_2^{**} > Q_2^*$), which is equivalent to that (4.15) (resp. (4.16)) holds. If E_1 is unstable, it follows from (4.11) and (4.16) that there exists a $Q_{1c} > 0$ satisfying $Q_1^* < Q_{1c} < \widehat{Q}_1$ and $F(Q_{1c}) = 0$, that is, the positive equilibrium of system (1.1), $\mathcal{E}_c$, exists. This result is consistent with Theorem 2.5. From our extensive numerical simulations, we conjecture that

$$F'(Q_1) < 0, \quad \forall\, Q_1^* < Q_1 < \widehat{Q}_1.$$

Under the assumption (H2), it follows that E_2 is always unstable (see Proposition 3.2), and we have the following conjecture:

- If E_1 is locally asymptotically stable (i.e., (4.15) holds), we conjecture that there is no positive equilibrium for system (1.1);
- If E_1 is unstable (i.e., (4.16) holds), we conjecture that there exists a unique positive equilibrium for system (1.1).

Here, we further conjecture that if E_1 is locally asymptotically stable then E_1 is globally asymptotically stable; if E_1 is unstable then the positive equilibrium $\mathcal{E}_c$ is unique and it is globally asymptotically stable.

Quantity	Value	Quantity	Value
D	0.12 day^{-1}	$R^{(0)}$	2.0×10^{-5} mol l^{-1}
$u_{max,1}$	12.0×10^{-14} mol cell^{-1} day^{-1}	$u_{max,2}$	24.0×10^{-14} mol cell^{-1} day^{-1}
K_1	9.0×10^{-7} mol l^{-1}	K_2	6.5×10^{-7} mol l^{-1}
$\mu_{max,1}$	0.70 day^{-1}	$\mu_{max,2}$	2.2 day^{-1}
$Q_{min,1}$	2.6×10^{-14} mol cell^{-1}	$Q_{min,2}$	1.0×10^{-13} mol cell^{-1}
$Q_{max,1}$	9.5×10^{-14} mol cell^{-1}	$Q_{max,2}$	32×10^{-13} mol cell^{-1}
g_{max}	53.0 cells cell^{-1} day^{-1}	K_{max}	4.0×10^{8} cells l^{-1}
b	2.37		

Table 4.1: Default Parameters [20].

Finally, we perform a numerical simulation to show that under the assumption (H2), the conditions (A0), (A1) and (A2) can be met, and coexistence is possible. Numerical simulations of system (1.1) or (2.3) were implemented using (1.3) for growth rate $\mu_i(Q_i)$, and (1.4) for uptake rate $f_i(R, Q_i)$. The function $g(N_1)$ represents the predation rate of the mixotroph feeding on the autotroph is taken as the form in (1.2). Parameter values we used are given by [20]. Using the parameter values in Table 4.1, our numerical results are as follows:

$$\begin{aligned}
&E_0 = (0, Q_1^0, 0, Q_2^0) = (0, 6.9162 \times 10^{-14}, 0, 5.7864 \times 10^{-13}),\\
&E_1 = (N_1^*, Q_1^*, 0, Q_2^{**}) = (5.2756 \times 10^8, 3.7829 \times 10^{-14}, 0, 1.4191 \times 10^{-12}),\\
&E_2 = (0, Q_1^{**}, N_2^*, Q_2^*) = (0, 4.5749 \times 10^{-14}, 7.3926 \times 10^7, 2.6909 \times 10^{-13}),\\
&E_c = (N_{1c}, Q_{1c}, N_{2c}, Q_{2c}) = (1.2019 \times 10^7, 4.5541 \times 10^{-14}, 7.1898 \times 10^7, 2.6909 \times 10^{-13}),
\end{aligned}$$

and

$$\begin{aligned}
\mu_1(Q_1^0) - D = 0.3179, &\qquad \mu_2(Q_2^0) - D = 0.2197,\\
\mu_2(Q_2^{**}) - D = 0.8162, &\qquad \mu_1(Q_1^{**}) - D = 0.0803.
\end{aligned}$$

Thus, we numerically show that conditions (A0), (A1) and (A2) can be met, and coexistence occurs. Those observations are consistent with our theoretical results in Theorems 2.4 and 2.5. From our simulations, it is likely that if two species can coexist, then the coexistence steady-state solution is unique, and it is globally asymptotically stable.

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Sze-Bi Hsu and Yi-hui Ho
Department of Mathematics, National Tsing Hua University, Hsinchu 300, Taiwan
E-mail address: `sbhsu@math.nthu.edu.tw`, `oopsxoxolalala@gmail.com`

Feng-Bin Wang
Department of Natural Science in the Center for General Education, Chang Gung University, Guishan Taoyuan 333, Taiwan
and
Community Medicine Research Center, Chang Gung Memorial Hospital, Keelung, Keelung 204, Taiwan
E-mail address: `fbwang@mail.cgu.edu.tw`