

## GROWTH OF SINGLE PHYTOPLANKTON SPECIES WITH INTERNAL STORAGE IN A WATER COLUMN

LINFENG MEI

Department of Mathematics  
Henan Normal University, Xinxiang, 453007, China

SZE-BI HSU

Department of Mathematics  
National Tsing Hua University, Hsinchu 300, Taiwan

FENG-BIN WANG

Department of Natural Science, Center for General Education  
Chang Gung University  
Kwei-Shan, Taoyuan 333, Taiwan

**ABSTRACT.** In this paper, we analyze a system modeling the growth of single phytoplankton populations in a water column, where population growth increases monotonically with the nutrient quota stored within individuals. We establish a threshold result on the global extinction and persistence of phytoplankton. Condition for persistence is shown to depend on the principal eigenvalue of a boundary value problem, which is related to the physical transport properties of the water column (i.e. the diffusivity and the sinking speed), nutrient uptake rate, and growth rate.

**1. Introduction.** In ecology, the understanding of competition between species for resources is a fundamental ecological issue. Much classical competition theory was developed for populations in well-mixed habitats, such as chemostats, in which a nutrient resource is supplied via an inflow, and a balancing outflow removes nutrient and organisms [26]. Classical competition models assume a direct relationship between the external concentration of nutrients and the population growth of organisms, without any intermediate steps of nutrient storage within cells. More precisely, those models ignore differences between individuals, using one ordinary differential equation to govern the growth of each species. These population growth are coupled to dynamics of one or more resources by assuming a constant quota of nutrient per individual, or equivalently, a constant yield of individuals from consumption of a unit of resource [6].

---

2010 *Mathematics Subject Classification.* Primary: 35B40, 35K57; Secondary: 92D25.

*Key words and phrases.* Steady states, threshold dynamics, internal storage, spatial variations, a water column.

Correspondence should be directed to F.-B. Wang: fbwang@mail.cgu.edu.tw. Research of L. Mei is supported in part by Startup funding for Doctors of Henan Normal University under grant No. qd14154, and the National Natural Science Foundation of China under grant No. 11371117. Research of S.B. Hsu and F.B. Wang are supported in part by Ministry of Science and Technology, Taiwan.

In phytoplankton ecology, it has long been known that the quota is not a fixed constant. It can vary depending on the growth rate of population. This led to the following internal storage model [4, 25, 26]:

$$\begin{cases} \frac{dR}{dt} = (R^{(0)} - R)d - \sum_{j=1}^2 \rho_j(R, Q_j)N_j, \\ \frac{dN_i}{dt} = (\mu_i(Q_i) - d)N_i, & i = 1, 2, \\ \frac{dQ_i}{dt} = \rho_i(R, Q_i) - \mu_i(Q_i)Q_i, & i = 1, 2 \\ R(0) \geq 0, N_i(0) \geq 0, Q_i(0) \geq Q_{\min,i}, & i = 1, 2. \end{cases} \quad (1.1)$$

For  $i=1,2$ ,  $Q_i(t)$  represents the average amount of stored nutrient per cell of  $i$ -th population at time  $t$ ,  $\mu_i(Q_i)$  is the growth rate of species  $i$  as a function of cell quota  $Q_i$ ,  $\rho_i(R, Q_i)$  is the per capita nutrient uptake rate, per cell of species  $N_i$  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 growth rate  $\mu_i(Q_i)$  takes the forms [2, 3, 4]:

$$\begin{aligned} \mu_i(Q_i) &= \mu_{i\infty} \left( 1 - \frac{Q_{\min,i}}{Q_i} \right), \\ \text{or} \\ \mu_i(Q_i) &= \mu_{i\infty} \frac{(Q_i - Q_{\min,i})_+}{K_i + (Q_i - Q_{\min,i})_+}, \end{aligned} \quad (1.2)$$

where  $(Q_i - Q_{\min,i})_+$  is the positive part of  $(Q_i - Q_{\min,i})$  and  $\mu_{i\infty}$  is the maximal growth rate of the species. According to Grover [5], the uptake rate  $\rho_i(R, Q_i)$  takes the form:

$$\begin{aligned} \rho_i(R, Q_i) &= \rho_{\max,i}(Q_i) \frac{R}{k_i + R}, \\ \rho_{\max,i}(Q_i) &= \rho_{\max,i}^{\text{high}} - (\rho_{\max,i}^{\text{high}} - \rho_{\max,i}^{\text{low}}) \frac{Q_i - Q_{\min,i}}{Q_{\max,i} - Q_{\min,i}}, \end{aligned} \quad (1.3)$$

where  $Q_{\min,i} \leq Q_i \leq Q_{\max,i}$ . Cunningham and Nisbet [2, 3] took  $\rho_{\max,i}(Q_i)$  to be a constant.

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

$$\mu_i(Q_i) \geq 0, \mu_i'(Q_i) > 0 \text{ and is continuous for } Q_i \geq Q_{\min,i}, \mu_i(Q_{\min,i}) = 0. \quad (1.4)$$

We assume that  $\rho_i(R, Q_i)$  is continuously differentiable for  $R > 0$  and  $Q_i \geq Q_{\min,i}$  and satisfies

$$\rho_i(0, Q_i) = 0, \frac{\partial \rho_i}{\partial R} > 0, \frac{\partial \rho_i}{\partial Q_i} \leq 0. \quad (1.5)$$

In particular,  $\rho_i(R, Q_i) > 0$  when  $R > 0$ .

Next, we assume that  $U_i = N_i Q_i$ ,  $i = 1, 2$ , is the total amount of stored nutrient at time  $t$  for the species  $i$ . Dividing the quantity  $U_i$  by  $N_i$ , then yields the average quota per individual, which is identical to the quantity  $Q_i$  under the assumption of a well mixed system. Then system (1.1) can be rewritten as follows:

$$\begin{aligned} \frac{dR}{dt} &= (R^{(0)} - R)d - \sum_{j=1}^2 \rho_j(R, \frac{U_j}{N_j})N_j, \\ \frac{dN_i}{dt} &= [\mu_i(\frac{U_i}{N_i}) - d]N_i, \quad i = 1, 2, \end{aligned} \quad (1.6)$$

$$\begin{aligned}\frac{dU_i}{dt} &= \rho_i\left(R, \frac{U_i}{N_i}\right)N_i - dU_i, \quad i = 1, 2, \\ R(0) &\geq 0, \quad U_i(0) \geq 0, \quad N_i(0) \geq 0, \quad i = 1, 2.\end{aligned}$$

It is not hard to see that the following conservation properties hold (see, e.g., [25, 26]):

$$R + U_1 + U_2 = R^{(0)} + O(e^{-dt}) \text{ as } t \rightarrow \infty.$$

Thus, system (1.6) can be reduced into a limiting system which is a type- $K$  monotone system (see, e.g., [25, 26]). Smith and Waltman [25, 26] used the theory of monotone dynamical system to prove only one species can survive for this internal storage model (1.1). Therefore, for models with constant quota [13] as well as for variable-internal-stores models [17, 25], we have conclusions that two or more species cannot coexist in a well mixed habitat with only a single limiting resource, a result known as the Competitive Exclusion Principle [6].

For competition models with constant quota, several works have now considered populations and resources that are distributed in spatially variable habitats. A typical model is the unstirred chemostat model [13, 20, 21] that was introduced as a poorly mixed analog of the chemostat with transport of nutrient and organisms by diffusion. Similar systems were also constructed for competition in the flow reactor habitat, with transport of nutrient and organisms by both advection and diffusion [1, 10]. The flow reactor and its modifications are very relevant because they can provide a simple model for riverine reservoirs [9, 10]. In contrast to models in a well-mixed habitat, it is possible for two species with constant quota to coexist on a single limiting resource in a spatially variable habitat. As mentioned in the previous paragraphs, it was known that for many microorganisms the quota of nutrient per individual varies dynamically, so that nutrient is stored internally within individuals. Intuitively, quota variation in spatially variable habitats could allow individuals to obtain nutrient in a rich zone of a habitat, for later use to survive passage through a poor zone [12]. A full description of quota variation in a spatially variable habitat should represent the distribution of quotas over individuals, as well as that of individuals and nutrient over space. The existing models are mathematically difficult [11] and computationally challenging [7].

Hsu et al. [18] suggested another approach that arises from averaging over differences among individuals at a given location, in their amounts of stored nutrient. The authors in [12] extend the results obtained concerning competition with variable quota and nutrient storage in the unstirred chemostat [18] to the flow reactor habitat, using a similar approach. In [8], the author further proposes the following competition model with variable quota and nutrient storage in a water column:

$$\begin{cases} \frac{\partial R}{\partial t} = \delta \frac{\partial^2 R}{\partial x^2} - \rho_1\left(R, \frac{U_1}{N_1}\right)N_1 - \rho_2\left(R, \frac{U_2}{N_2}\right)N_2, & x \in (0, L), \quad t > 0, \\ \frac{\partial N_i}{\partial t} = \delta \frac{\partial^2 N_i}{\partial x^2} - \nu_i \frac{\partial N_i}{\partial x} + \mu_i\left(\frac{U_i}{N_i}\right)N_i, & x \in (0, L), \quad t > 0, \quad i = 1, 2, \\ \frac{\partial U_i}{\partial t} = \delta \frac{\partial^2 U_i}{\partial x^2} - \nu_i \frac{\partial U_i}{\partial x} + \rho_i\left(R, \frac{U_i}{N_i}\right)N_i, & x \in (0, L), \quad t > 0, \quad i = 1, 2, \end{cases} \quad (1.7)$$

with boundary conditions

$$\begin{cases} \frac{\partial R}{\partial x}(0, t) = 0, \quad R(L, t) = R^{(0)}(t), \\ \nu_i N_i(0, t) - \delta \frac{\partial N_i}{\partial x}(0, t) = \nu_i U_i(0, t) - \delta \frac{\partial U_i}{\partial x}(0, t) = 0, \quad i = 1, 2, \\ N_i(L, t) = U_i(L, t), \quad i = 1, 2, \quad t > 0, \end{cases} \quad (1.8)$$

and initial conditions

$$\begin{cases} R(x, 0) = R^0(x) \geq 0, & N_i(x, 0) = N_i^0(x) \geq 0, \\ U_i(x, 0) = U_i^0(x) \geq 0, & 0 < x < L, \quad i = 1, 2, \end{cases} \quad (1.9)$$

where the initial-value functions  $N_i^0(x)$ ,  $U_i^0(x)$  satisfy  $\frac{U_i^0(x)}{N_i^0(x)} \geq Q_{\min, i}$ ,  $i = 1, 2$ . The spatial coordinate  $x$  represents depth of a water column, with  $x = 0$  being the surface and  $x = L$  the bottom. Dissolved nutrient  $R(x, t)$  diffuses with diffusivity  $\delta$ . The boundary conditions of  $R(x, t)$  are zero-flux condition at the surface ( $x = 0$ ), and a periodically varying supply of the nutrient,  $R^{(0)}(t)$ , at the bottom of the habitat ( $x = L$ ). Population density transports at the same diffusivity  $\delta$  and moves by advection toward the bottom of the habitat at the sinking speed  $\nu_i$ . The nutrient taken up by individuals is carried within these individuals, so we assume that  $U_i(x, t)$  follows the same transport processes as  $N_i(x, t)$ . The boundary conditions of  $U_i(x, t)$  and  $N_i(x, t)$  are zero-flux conditions at the surface of the habitat, and absorbing conditions at the bottom. The functions  $\mu_i(Q_i)$  and  $\rho_i(R, Q_i)$  satisfy (1.4) and (1.5) respectively,  $i = 1, 2$ . Note that we can calculate the average quota at a location as  $Q_i(x, t) = \frac{U_i(x, t)}{N_i(x, t)}$ , and apply the functions  $\mu_i$  and  $\rho_i$  to this average.

In this paper, we shall focus on the analysis of the single population model corresponding to system (1.7)-(1.9) with a constant supply of the nutrient,  $R^{(0)}(t) \equiv R^{(0)}$ . Mathematically, it simply means that we set  $R^{(0)}(t) \equiv R^{(0)}$ , and  $(N_1, U_1) = (0, 0)$  or  $(N_2, U_2) = (0, 0)$ . In order to simplify notation, all subscripts are dropped in the remaining equations and we consider

$$\begin{cases} \frac{\partial R}{\partial t} = \delta \frac{\partial^2 R}{\partial x^2} - \rho(R, \frac{U}{N})N, & x \in (0, L), \quad t > 0, \\ \frac{\partial N}{\partial t} = \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \mu(\frac{U}{N})N, & x \in (0, L), \quad t > 0, \\ \frac{\partial U}{\partial t} = \delta \frac{\partial^2 U}{\partial x^2} - \nu \frac{\partial U}{\partial x} + \rho(R, \frac{U}{N})N, & x \in (0, L), \quad t > 0, \end{cases} \quad (1.10)$$

with boundary conditions

$$\begin{cases} \frac{\partial R}{\partial x}(0, t) = 0, & R(L, t) = R^{(0)}, \\ \nu N(0, t) - \delta \frac{\partial N}{\partial x}(0, t) = \nu U(0, t) - \delta \frac{\partial U}{\partial x}(0, t) = 0, \\ N(L, t) = U(L, t) = 0, & t > 0, \end{cases} \quad (1.11)$$

and initial conditions

$$\begin{cases} R(x, 0) = R^0(x) \geq 0, & N(x, 0) = N^0(x) \geq 0, \\ U(x, 0) = U^0(x) \geq 0, & 0 < x < L. \end{cases} \quad (1.12)$$

The organization of this paper is as follows. In section 2, we study the well-posedness and establish a threshold result on the global extinction and persistence for system (1.10)-(1.12) in terms of the principal eigenvalue of an eigenvalue problem by appealing to the theory of uniformly persistence. The loss of a conservative law in our system makes our analysis quite different from those in [18]. A brief discussion section completes the paper.

**2. Mathematical analysis of system (1.10)-(1.12).** This section is devoted to the analysis of system (1.10)-(1.12). Note that the boundary condition (1.11) at  $x = L$  is Dirichlet-type. Let the following transformation:

$$W(x, t) = R^{(0)} - R(x, t).$$

Then system (1.10)-(1.12) becomes

$$\begin{cases} \frac{\partial W}{\partial t} = \delta \frac{\partial^2 W}{\partial x^2} + \rho(R^{(0)} - W, \frac{U}{N})N, & x \in (0, L), t > 0, \\ \frac{\partial N}{\partial t} = \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \mu(\frac{U}{N})N, & x \in (0, L), t > 0, \\ \frac{\partial U}{\partial t} = \delta \frac{\partial^2 U}{\partial x^2} - \nu \frac{\partial U}{\partial x} + \rho(R^{(0)} - W, \frac{U}{N})N, & x \in (0, L), t > 0, \end{cases} \quad (2.1)$$

with boundary conditions

$$\begin{cases} \frac{\partial W}{\partial x}(0, t) = 0, W(L, t) = 0, \\ \nu N(0, t) - \delta \frac{\partial N}{\partial x}(0, t) = \nu U(0, t) - \delta \frac{\partial U}{\partial x}(0, t) = 0, \\ N(L, t) = U(L, t) = 0, t > 0, \end{cases} \quad (2.2)$$

and initial conditions

$$\begin{cases} W(x, 0) = W^0(x) \geq 0, N(x, 0) = N^0(x) \geq 0, \\ U(x, 0) = U^0(x) \geq 0, 0 < x < L. \end{cases} \quad (2.3)$$

Let  $\Omega = (0, L) \subseteq \mathbb{R}$ , and  $p \in (1, \infty)$  be fixed. For each  $\beta \in (\frac{1}{2} + \frac{1}{2p}, 1)$ , let  $\mathbb{X}_\beta$  be the fractional power space of  $L^p(\Omega)$  with respect to the operator  $-\frac{\partial^2}{\partial x^2}$  and the boundary condition  $\frac{\partial W}{\partial x}(0, t) = 0, W(L, t) = 0$  (see, e.g., [14]). Then  $\mathbb{X}_\beta$  is an ordered Banach space with the order cone  $\mathbb{X}_\beta^+$  consisting of all non-negative functions in  $\mathbb{X}_\beta$ , and  $\mathbb{X}_\beta^+$  has non-empty interior  $\text{Int}(\mathbb{X}_\beta^+)$ . Moreover,  $\mathbb{X}_\beta \subseteq C^{1+\lambda}(\bar{\Omega})$  with continuous inclusion for  $\lambda \in [0, 2\beta - 1 - \frac{1}{p}]$  (see, e.g., [16]). Similarly, we assume that  $\mathbb{Y}_\beta$  is the fractional power space of  $L^p(\Omega)$  with respect to the operator  $-\frac{\partial^2}{\partial x^2} + \nu \frac{\partial}{\partial x}$  and the boundary condition  $\nu N(0, t) - \delta \frac{\partial N}{\partial x}(0, t) = 0, N(L, t) = 0$ . Let  $E = \mathbb{X}_\beta \times \mathbb{Y}_\beta \times \mathbb{Y}_\beta$  and  $\mathbb{P} = \mathbb{X}_\beta^+ \times \mathbb{Y}_\beta^+ \times \mathbb{Y}_\beta^+$ . Then  $E$  is an ordered Banach space with the order cone  $\mathbb{P}$  consisting of all non-negative functions in  $E$ , and  $\mathbb{P}$  has non-empty interior  $\text{Int}(\mathbb{P})$ . Denote the norm on  $E$  by  $\|\cdot\|_\beta$ . Then, there exists a constant  $k_\beta > 0$  such that

$$\|\phi\|_\infty := \max_{x \in \Omega} |(\phi_1(x), \phi_2(x), \phi_3(x))| \leq k_\beta \|\phi\|_\beta, \forall \phi \in E. \quad (2.4)$$

The biologically relevant domain for the system (2.1)-(2.3) is given by

$$\mathbf{X} = \left\{ (W^0, N^0, U^0) \in \mathbb{P} : 0 \leq W^0(\cdot) \leq R^{(0)}, \frac{U^0(\cdot)}{N^0(\cdot)} \geq Q_{\min} \right\}. \quad (2.5)$$

**Lemma 2.1.** *For any  $(W^0, N^0, U^0) \in \mathbf{X}$ , system (2.1)-(2.3) has a unique mild solution  $(W(\cdot, t), N(\cdot, t), U(\cdot, t))$  with  $(W(\cdot, 0), N(\cdot, 0), U(\cdot, 0)) = (W^0(\cdot), N^0(\cdot), U^0(\cdot))$  and  $(W(\cdot, t), N(\cdot, t), U(\cdot, t)) \in \mathbf{X}$ , for  $t \in [0, \tau)$ , where  $\tau \leq \infty$ .*

*Proof.* By [24, Corollary 7.3.2], it is easy to see that if  $(W^0, N^0, U^0) \in \mathbb{P}$  then  $(W(\cdot, t), N(\cdot, t), U(\cdot, t)) \in \mathbb{P}$ , for  $t \in [0, \tau)$ , where  $\tau \leq \infty$ . From the first equation of system (1.10)-(1.12), it is obvious that

$$\text{if } 0 \leq R(\cdot, 0) \leq R^{(0)}, \text{ then } 0 \leq R(x, t) \leq R^{(0)}, \forall x \in [0, L], t \in [0, \tau).$$

Thus, if  $0 \leq W(\cdot, 0) = R^{(0)} - R(\cdot, 0) \leq R^{(0)}$ , then  $0 \leq W(\cdot, t) = R^{(0)} - R(\cdot, t) \leq R^{(0)}$ , for  $t \in [0, \tau)$ .

Next, we shall that if  $\frac{U^0(\cdot)}{N^0(\cdot)} \geq Q_{\min}$ , then  $\frac{U(\cdot, t)}{N(\cdot, t)} \geq Q_{\min}$ , for  $t \in [0, \tau)$ . It is easy to see that

$$\mu(Q) = G(Q)(Q - Q_{\min}) \quad \text{where } G(Q) = \int_0^1 \mu'(sQ + (1-s)Q_{\min})ds > 0.$$

Introducing

$$H = U - Q_{\min}u,$$

we get that

$$\mu\left(\frac{U}{u}\right) = G\left(\frac{U}{u}\right)\frac{H}{u}.$$

By calculation,

$$dH_{xx} - H_t - Q_{\min}G\left(\frac{U}{u}\right)H \leq 0, \quad x \in (0, L), \quad t > 0,$$

with the boundary conditions

$$\nu H(0, t) - \delta \frac{\partial H}{\partial x}(0, t) = H(L, t) = 0, \quad t > 0.$$

Thus,

$$H(\cdot, t) \geq 0, \quad \forall t \in [0, \tau].$$

□

Let

$$\tilde{N}(x, t) = e^{-\frac{\nu}{2\delta}x}N(x, t), \quad \tilde{U}(x, t) = e^{-\frac{\nu}{2\delta}x}U(x, t). \quad (2.6)$$

Then the system (2.1)-(2.3) becomes

$$\begin{cases} \frac{\partial W}{\partial t} = \delta \frac{\partial^2 W}{\partial x^2} + \rho(R^{(0)} - W, \frac{\tilde{U}}{\tilde{N}})e^{\frac{\nu}{2\delta}x}\tilde{N}, & x \in (0, L), \quad t > 0, \\ \frac{\partial \tilde{N}}{\partial t} = \delta \frac{\partial^2 \tilde{N}}{\partial x^2} - \frac{\nu^2}{4\delta}\tilde{N} + \mu\left(\frac{\tilde{U}}{\tilde{N}}\right)\tilde{N}, & x \in (0, L), \quad t > 0, \\ \frac{\partial \tilde{U}}{\partial t} = \delta \frac{\partial^2 \tilde{U}}{\partial x^2} - \frac{\nu^2}{4\delta}\tilde{U} + \rho(R^{(0)} - W, \frac{\tilde{U}}{\tilde{N}})\tilde{N}, & x \in (0, L), \quad t > 0, \end{cases} \quad (2.7)$$

with boundary conditions

$$\begin{cases} \frac{\partial W}{\partial x}(0, t) = 0, \quad W(L, t) = 0, \\ -\frac{\partial \tilde{N}}{\partial x}(0, t) = -\frac{\nu}{2\delta}\tilde{N}(0, t), \quad \tilde{N}(L, t) = 0, \\ -\frac{\partial \tilde{U}}{\partial x}(0, t) = -\frac{\nu}{2\delta}\tilde{U}(0, t), \quad \tilde{U}(L, t) = 0, \quad t > 0, \end{cases} \quad (2.8)$$

and initial conditions

$$\begin{cases} W(x, 0) = W^0(x) \geq 0, \quad \tilde{N}(x, 0) = N^0(x)e^{-\frac{\nu}{2\delta}x} \geq 0, \\ \tilde{U}(x, 0) = U^0(x)e^{-\frac{\nu}{2\delta}x} \geq 0, \quad 0 < x < L. \end{cases} \quad (2.9)$$

**Lemma 2.2.** *For any  $(W^0, N^0, U^0) \in \mathbf{X}$ , the system (2.1)-(2.3) has a unique solution  $(W(\cdot, t), N(\cdot, t), U(\cdot, t)) \in \mathbf{X}$  defined on  $[0, \infty)$  with  $(W(\cdot, 0), N(\cdot, 0), U(\cdot, 0)) = (W^0(\cdot), N^0(\cdot), U^0(\cdot))$  and it generates a semiflow  $\Psi(t) : \mathbf{X} \rightarrow \mathbf{X}$  defined by*

$$\Psi(t)\phi = (W(\cdot, t), N(\cdot, t), U(\cdot, t)), \quad t \geq 0. \quad (2.10)$$

Furthermore,  $\Psi(t) : \mathbf{X} \rightarrow \mathbf{X}$  has a global compact attractor in  $\mathbf{X}$ ,  $\forall t \geq 0$ .

*Proof.* We first show that

$$\limsup_{t \rightarrow \infty} [e^{-\frac{\nu}{2\delta}x}U(x, t)] \leq R^{(0)}, \quad \text{uniformly for } x \in [0, L]. \quad (2.11)$$

Let

$$V(x, t) = \tilde{U}(x, t) - W(x, t).$$

Then it follows from the first and third equations of (2.7) that  $V(x, t)$  satisfies

$$\begin{cases} \frac{\partial V}{\partial t} \leq \delta \frac{\partial^2 V}{\partial x^2}, & x \in (0, L), \quad t > 0, \\ -\frac{\partial V}{\partial x}(0, t) = -\frac{\nu}{2\delta}U(0, t) \leq 0, \quad V(L, t) = 0, & t > 0. \end{cases} \quad (2.12)$$

By [24, Theorem 7.3.4], it then follows that

$$V(x, t) \leq \hat{V}(x, t), \quad \forall (x, t) \in (0, L) \times (0, \tau), \tag{2.13}$$

where  $\tau$  is defined in Lemma 2.1, and  $\hat{V}(x, t)$  satisfies

$$\begin{cases} \frac{\partial \hat{V}}{\partial t} = \delta \frac{\partial^2 \hat{V}}{\partial x^2}, & x \in (0, L), t > 0, \\ -\frac{\partial \hat{V}}{\partial x}(0, t) = 0, \quad \hat{V}(L, t) = 0, & t > 0, \\ \hat{V}(x, 0) = V(x, 0), & x \in (0, L). \end{cases} \tag{2.14}$$

It is easy to see that  $\lim_{t \rightarrow \infty} \hat{V}(x, t) = 0$  uniformly for  $x \in [0, L]$ . Therefore,

$$\lim_{t \rightarrow \infty} V(x, t) \leq 0, \quad \text{uniformly for } x \in [0, L].$$

Thus,

$$\limsup_{t \rightarrow \infty} \tilde{U}(x, t) = \limsup_{t \rightarrow \infty} [V(x, t) + W(x, t)] \leq R^{(0)}, \quad \text{uniformly for } x \in [0, L].$$

From Lemma 2.1, it follows that  $\frac{\tilde{U}(x, t)}{\tilde{N}(x, t)} = \frac{U(x, t)}{N(x, t)} \geq Q_{\min}$ , for  $x \in [0, L]$ ,  $t \in [0, \tau)$ , which implies that

$$\limsup_{t \rightarrow \infty} \tilde{N}(x, t) \leq \frac{R^{(0)}}{Q_{\min}}, \quad \text{uniformly for } x \in [0, L].$$

Thus, there exists  $r > 0$  such that  $\limsup_{t \rightarrow \infty} \|(W(\cdot, t), N(\cdot, t), U(\cdot, t))\|_{\infty} \leq r$ . By the same arguments as in the proof of [28, Theorem 3.1], we conclude that there exists  $\hat{r} > 0$  such that

$$\limsup_{t \rightarrow \infty} \|(W(\cdot, t), N(\cdot, t), U(\cdot, t))\|_{\beta} \leq \hat{r},$$

which completes the proof of (2.11). This implies that  $\Psi(t) : \mathbf{X} \rightarrow \mathbf{X}$  is point dissipative. Obviously,  $\Psi(t) : \mathbf{X} \rightarrow \mathbf{X}$  is compact,  $\forall t > 0$ . By [15, Theorem 3.4.8], it follows that  $\Psi(t) : \mathbf{X} \rightarrow \mathbf{X}$ ,  $t \geq 0$ , has a global compact attractor.  $\square$

Next, we consider a special case where the growth and uptake functions are chosen specifically [8]. In this case, we can further obtain an improved relevant domain for the system (2.1)-(2.3).

**Proposition 2.1.** *Let*

$$\mathbf{Y} = \left\{ (W^0, N^0, U^0) \in \mathbb{P} : 0 \leq W^0(\cdot) \leq R^{(0)}, Q_{\min} \leq \frac{U^0(\cdot)}{N^0(\cdot)} \leq Q_{\max} \right\}.$$

*Assume that  $\mu(Q)$  takes the form in the first equation of (1.2),  $\rho(R, Q)$  takes the form in (1.3), and*

$$\mu_{\infty} \geq \frac{\rho_{\max}^{\text{low}}}{Q_{\max} - Q_{\min}}. \tag{2.15}$$

*Then for any  $(W^0, N^0, U^0) \in \mathbf{Y}$ , system (2.1)-(2.3) has a unique mild solution  $(W(\cdot, t), N(\cdot, t), U(\cdot, t))$  with  $(W(\cdot, 0), N(\cdot, 0), U(\cdot, 0)) = (W^0(\cdot), N^0(\cdot), U^0(\cdot))$  and  $(W(\cdot, t), N(\cdot, t), U(\cdot, t)) \in \mathbf{Y}$ , for  $t \in [0, \tau)$ , where  $\tau \leq \infty$ .*

*Proof.* From Lemma 2.1, it suffices to show that if  $\frac{U^0(\cdot)}{N^0(\cdot)} \leq Q_{\max}$ , then  $\frac{U(\cdot, t)}{N(\cdot, t)} \leq Q_{\max}$ , for  $t \in [0, \tau)$ . Set  $E = \tilde{U} - Q_{\max}\tilde{N}$  and  $Q = \frac{\tilde{U}}{\tilde{N}}$ . Indeed, from (2.7)-(2.9), we have

$$\begin{aligned} & \rho(R^{(0)} - W, Q)\tilde{N} - Q_{\max}\mu(Q)\tilde{N} \\ & \leq \tilde{N} \left[ \rho_{\max}^{\text{high}} - (\rho_{\max}^{\text{high}} - \rho_{\max}^{\text{low}}) \left( \frac{Q - Q_{\min}}{Q_{\max} - Q_{\min}} \right) - \frac{Q_{\max}\rho_{\max}^{\text{low}}}{Q_{\max} - Q_{\min}} \left( 1 - \frac{Q_{\min}}{Q} \right) \right] \\ & = \tilde{N} \left[ -\rho_{\max}^{\text{high}} \left( \frac{Q - Q_{\max}}{Q_{\max} - Q_{\min}} \right) + \rho_{\max}^{\text{low}} \left( \frac{Q - Q_{\min}}{Q_{\max} - Q_{\min}} \right) \left( \frac{Q - Q_{\max}}{Q} \right) \right] \\ & = [(Q - Q_{\max})\tilde{N}] \left[ -\rho_{\max}^{\text{high}} \left( \frac{1}{Q_{\max} - Q_{\min}} \right) + \rho_{\max}^{\text{low}} \left( \frac{Q - Q_{\min}}{Q_{\max} - Q_{\min}} \right) \left( \frac{1}{Q} \right) \right] \\ & = c(x, t)E, \end{aligned} \tag{2.16}$$

where

$$c(x, t) = -\rho_{\max}^{\text{high}} \left( \frac{1}{Q_{\max} - Q_{\min}} \right) + \rho_{\max}^{\text{low}} \left( \frac{Q - Q_{\min}}{Q_{\max} - Q_{\min}} \right) \left( \frac{1}{Q} \right)$$

is clearly bounded. From the equations for  $\tilde{U}$  and  $\tilde{N}$  we then deduce

$$E_t \leq \delta E_{xx} + [c(x, t) - \nu^2/(4\delta)]E.$$

Since  $E(\cdot, 0) \leq 0$ , it follows from the comparison principle to conclude that

$$E(\cdot, t) \leq 0, \quad \forall t \in [0, \tau).$$

□

**Remark 2.1.** The condition (2.15) is essential when we establish the inequality (2.16). In fact, the author in [8] takes  $\mu_{\infty}$  as follows:

$$\mu_{\infty} = \frac{\rho_{\max}^{\text{low}}}{Q_{\max} - Q_{\min}}.$$

Consider the following system

$$\begin{cases} \frac{dQ}{dt} = \rho(R^{(0)}, Q) - \mu(Q)Q, \\ Q(0) \geq Q_{\min}. \end{cases} \tag{2.17}$$

It is easy to see that there exists  $Q_c$  such that  $Q_c$  is the unique equilibria of system (2.17), and hence,

$$\rho(R^{(0)}, Q_c) - \mu(Q_c)Q_c = 0. \tag{2.18}$$

Then we consider the following eigenvalue problem:

$$\begin{cases} \delta\phi''(x) - \nu\phi'(x) + \mu(Q_c)\phi(x) = \lambda\phi(x), \quad x \in (0, L), \\ \nu\phi(0) - \delta\phi'(0) = \phi(L) = 0. \end{cases} \tag{2.19}$$

Suppose  $\lambda^0$  is the principal eigenvalue corresponding to the positive eigenfunction  $\phi_0(x)$  which is uniquely determined by the normalization  $\max_{[0, L]}\phi_0(x) = 1$ .

Recall that  $\mathbf{X}$  is the biologically relevant domain for system (2.1)-(2.3), which is defined in (2.5). For convenience, we set

$$\mathbf{X}_0 := \{(W^0(\cdot), N^0(\cdot), U^0(\cdot)) \in \mathbf{X} : W^0(\cdot) \not\equiv 0, N^0(\cdot) \not\equiv 0, U^0(\cdot) \not\equiv 0\},$$

and  $\partial\mathbf{X}_0 := \mathbf{X} \setminus \mathbf{X}_0$ .

**Theorem 2.1.** *Assume that  $\lambda^0$  is principal eigenvalue of (2.19). For any  $(W^0, N^0, U^0) \in \mathbf{X}$ , let  $(W(\cdot, t), N(\cdot, t), U(\cdot, t))$  be the solution of the system (2.1)-(2.3) with*

$$(W(\cdot, 0), N(\cdot, 0), U(\cdot, 0)) = (W^0(\cdot), N^0(\cdot), U^0(\cdot)).$$

*Then the following statements are valid:*

- (i) *If  $\lambda^0 < 0$ , then  $\lim_{t \rightarrow \infty} \|(W(\cdot, t), N(\cdot, t), U(\cdot, t))\|_\beta = 0$ ;*
- (ii) *If  $\lambda^0 > 0$ , then system (2.1)-(2.3) is uniformly persistent with respect to  $(\mathbf{X}_0, \partial\mathbf{X}_0)$  in the sense that there is an  $\eta > 0$  such that for any  $(W^0, N^0, U^0) \in \mathbf{X}_0$ , we have*

$$\liminf_{t \rightarrow \infty} \|(W(\cdot, t), N(\cdot, t), U(\cdot, t))\|_\beta \geq \eta.$$

*Furthermore, the system (2.1)-(2.3) admits at least one (componentwise) positive steady state  $(\hat{W}(x), \hat{N}(x), \hat{U}(x))$ .*

*Proof.* We first prove Part (i). From the last two equations of (2.1), it follows that

$$\begin{cases} \frac{\partial N}{\partial t} = \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \mu \left(\frac{U}{N}\right)N, & x \in (0, L), t > 0, \\ \frac{\partial U}{\partial t} \leq \delta \frac{\partial^2 U}{\partial x^2} - \nu \frac{\partial U}{\partial x} + \rho(R^{(0)}, \frac{U}{N})N, & x \in (0, L), t > 0. \end{cases} \quad (2.20)$$

Consider the following auxiliary system

$$\begin{cases} \frac{\partial N}{\partial t} = \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \mu \left(\frac{U}{N}\right)N, & x \in (0, L), t > 0, \\ \frac{\partial U}{\partial t} = \delta \frac{\partial^2 U}{\partial x^2} - \nu \frac{\partial U}{\partial x} + \rho(R^{(0)}, \frac{U}{N})N, & x \in (0, L), t > 0, \\ \nu N(0, t) - \delta \frac{\partial N}{\partial x}(0, t) = \nu U(0, t) - \delta \frac{\partial U}{\partial x}(0, t) = 0, \\ N(L, t) = U(L, t) = 0, t > 0. \end{cases} \quad (2.21)$$

Note that (2.21) is a cooperative system. Given  $C > 0$ , we set

$$\bar{N}(x, t) = Ce^{\lambda^0 t} \phi_0(x), \quad \bar{U}(x, t) = CQ_c e^{\lambda^0 t} \phi_0(x),$$

where  $\phi_0(x)$  is the eigenfunction corresponding to  $\lambda^0$ . With (2.18), it is easy to see that  $(\bar{N}(x, t), \bar{U}(x, t))$  satisfies system (2.21) and  $\bar{N}(x, 0) = C\phi_0(x)$ ,  $\bar{U}(x, 0) = CQ_c\phi_0(x)$ . Choosing  $C > 0$  such that  $(N^0, U^0) \leq (\bar{N}(x, 0), \bar{U}(x, 0))$ . Then the Comparison Principle implies that

$$(N(x, t), U(x, t)) \leq (\bar{N}(x, t), \bar{U}(x, t)), t > 0.$$

Since  $\lambda^0 < 0$ , it follows that  $\lim_{t \rightarrow \infty} (\bar{N}(x, t), \bar{U}(x, t)) = (0, 0)$  uniformly for  $x \in [0, L]$ . This implies that  $\lim_{t \rightarrow \infty} (N(x, t), U(x, t)) = (0, 0)$  uniformly for  $x \in [0, L]$ . Thus, the equation for  $W$  is asymptotic to the reaction-diffusion equation

$$\begin{cases} \frac{\partial W}{\partial t} = \delta \frac{\partial^2 W}{\partial x^2}, & x \in (0, L), t > 0, \\ \frac{\partial W}{\partial x}(0, t) = 0, W(L, t) = 0, & t > 0, \end{cases} \quad (2.22)$$

with initial condition. Then the theory for asymptotically autonomous semiflows (see, e.g., [27, Corollary 4.3]) implies that  $\lim_{t \rightarrow \infty} W(x, t) = 0$  uniformly for  $x \in [0, L]$ . Thus,  $\lim_{t \rightarrow \infty} \|(W(\cdot, t), N(\cdot, t), U(\cdot, t))\|_\infty = 0$ . By the same arguments as in the proof of [28, Theorem 3.2 (1)], we conclude that  $\lim_{t \rightarrow \infty} \|(W(\cdot, t), N(\cdot, t), U(\cdot, t))\|_\beta = 0$ . The proof of part (i) is finished.

Next, we are in a position to prove part (ii). By the strong maximum principle and the Hopf boundary lemma (see [23]), it follows that for any  $\mathbf{u}^0(\cdot) := (R^0(\cdot), N^0(\cdot), U^0(\cdot)) \in \mathbf{X}_0$ , we have

$$W(x, t, \mathbf{u}^0) > 0, \quad N(x, t, \mathbf{u}^0) > 0, \quad U(x, t, \mathbf{u}^0) > 0, \quad \forall x \in [0, L], \quad t > 0,$$

that is,  $\Psi(t)\mathbf{X}_0 \subseteq \mathbf{X}_0$  for all  $t \geq 0$ .

Let

$$M_\partial := \{\mathbf{u}^0 \in \partial\mathbf{X}_0 : \Psi(t)\mathbf{u}^0 \in \partial\mathbf{X}_0, \forall t \geq 0\},$$

and  $\omega(\mathbf{u}^0)$  be the omega limit set of the orbit  $O^+(\mathbf{u}^0) := \{\Psi(t)\mathbf{u}^0 : t \geq 0\}$ . We have following claim.

**Claim 1.**  $\omega(\psi) = \{(0, 0, 0)\}$ ,  $\forall \psi \in M_\partial$ .

For any given  $\psi \in M_\partial$ , we have  $\Psi(t)\psi \in M_\partial$ ,  $\forall t \geq 0$ , that is,  $N(\cdot, t, \psi) \equiv 0$  or  $W(\cdot, t, \psi) \equiv 0$  or  $U(\cdot, t, \psi) \equiv 0$ , for any given  $t \geq 0$ . In case where  $N(\cdot, t, \psi) \equiv 0$ , for any given  $t \geq 0$ . From Lemma 2.1, it follows that  $\frac{U(\cdot, t, \psi)}{N(\cdot, t, \psi)} \geq Q_{\min}$ ,  $t \geq 0$ . This implies that  $W$  satisfies system (2.22), and hence,  $\lim_{t \rightarrow \infty} W(x, t) = 0$  uniformly for  $x \in [0, L]$ . Similarly,  $U$  satisfies

$$\begin{cases} \frac{\partial U}{\partial t} = \delta \frac{\partial^2 U}{\partial x^2} - \nu \frac{\partial U}{\partial x}, & x \in (0, L), \quad t > 0, \\ \nu U(0, t) - \delta \frac{\partial U}{\partial x}(0, t) = U(L, t) = 0, & t > 0, \end{cases}$$

and hence,  $\lim_{t \rightarrow \infty} U(x, t) = 0$  uniformly for  $x \in [0, L]$ . This shows that  $\omega(\psi) = \{(0, 0, 0)\}$ . In case where  $N(x_0, t_0, \psi) \neq 0$ , for some  $x_0 \in [0, L]$  and  $t_0 > 0$ . By the strong maximum principle and the Hopf boundary lemma (see [23]), it follows that  $N(x, t, \psi) > 0$ , for any  $x \in [0, L]$  and  $t \geq t_0$ . This implies that  $W(\cdot, t, \psi) \equiv 0$  or  $U(\cdot, t, \psi) \equiv 0$ , for any given  $t \geq t_0$ . In case where  $W(\cdot, t, \psi) \equiv 0$ , for any given  $t \geq t_0$ , we substitute  $W(\cdot, t, \psi) \equiv 0$  into the first equation of (2.1) and we obtain

$$\rho(R^{(0)}, \frac{U(\cdot, t, \psi)}{N(\cdot, t, \psi)})N(\cdot, t, \psi) \equiv 0,$$

which implies that  $N(\cdot, t, \psi) \equiv 0$ , for any given  $t \geq t_0$ , which is a contradiction. In case where  $W(\hat{x}_0, \hat{t}_0, \psi) \neq 0$ , for some  $\hat{x}_0 \in [0, L]$  and  $\hat{t}_0 \geq t_0 > 0$ . By the strong maximum principle and the Hopf boundary lemma (see [23]), it follows that  $W(x, t, \psi) > 0$ , for any  $x \in [0, L]$  and  $t \geq \hat{t}_0$ . This implies that  $U(\cdot, t, \psi) \equiv 0$ , for any given  $t \geq \hat{t}_0$ . From Lemma 2.1, it follows that  $N(\cdot, t, \psi) \equiv 0$ , for any given  $t \geq \hat{t}_0$ . This contradiction finishes the proof of claim 1.

Since  $\lambda^0 > 0$ , there exists  $\epsilon_0 > 0$  such that  $\lambda_{\epsilon_0}^0 > 0$  is the principal eigenvalue of the following eigenvalue problem:

$$\begin{cases} \delta \phi''(x) - \nu \phi'(x) + [\mu(Q_c) - \frac{\epsilon_0}{Q_c}] \phi(x) = \lambda \phi(x), & x \in (0, L), \\ \nu \phi(0) - \delta \phi'(0) = \phi(L) = 0. \end{cases} \quad (2.23)$$

Suppose  $\phi_{\epsilon_0}^0(x)$  is the positive eigenfunction corresponding to  $\lambda_{\epsilon_0}^0$ , and  $\phi_{\epsilon_0}^0(x)$  is uniquely determined by the normalization  $\max_{[0, L]} \phi_{\epsilon_0}^0(x) = 1$ . It follows from

$$\lim_{W \rightarrow 0} \rho(R^{(0)} - W, \frac{U}{N}) = \rho(R^{(0)}, \frac{U}{N})$$

that we can choose  $\sigma_0 > 0$  such that

$$\rho(R^{(0)} - W, \frac{U}{N}) > \rho(R^{(0)}, \frac{U}{N}) - \epsilon_0, \quad \text{for any } |W| < \sigma_0.$$

Let  $\hat{\sigma}_0 := \frac{\sigma_0}{k_\beta}$ , where  $k_\beta$  is defined in (2.4). Then we further prove the following claim.

**Claim 2.**  $(0, 0, 0)$  is a uniform weak repeller for the system (2.1)-(2.3) in the sense that

$$\limsup_{t \rightarrow \infty} \|\Psi(t)(W^0, N^0, U^0) - (0, 0, 0)\|_\beta \geq \hat{\sigma}_0, \quad \forall (W^0, N^0, U^0) \in \mathbf{X}_0.$$

Suppose, by contradiction, there exists  $(W^0, N^0, U^0) \in \mathbf{X}_0$  such that

$$\limsup_{t \rightarrow \infty} \|\Psi(t)(W^0, N^0, U^0) - (0, 0, 0)\|_\beta < \hat{\sigma}_0.$$

Then, there exists  $t_1 > 0$  such that

$$\begin{aligned} \|\Psi(t)(W^0, N^0, U^0)\|_\infty &\leq k_\beta \|\Psi(t)(W^0, N^0, U^0)\|_\beta \\ &< k_\beta \hat{\sigma}_0 = \sigma_0, \quad \forall t \geq t_1, \quad x \in [0, L]. \end{aligned}$$

Thus, there exists  $t_1 > 0$  such that

$$|W(x, t)| < \sigma_0, \quad \forall t \geq t_1, \quad x \in [0, L].$$

This implies that

$$\rho(R^{(0)} - W(x, t), \frac{U}{N}) > \rho(R^{(0)}, \frac{U}{N}) - \epsilon_0, \quad \forall t \geq t_1, \quad x \in [0, L]. \quad (2.24)$$

From the last two equations of (2.1) and (2.24), it follows that

$$\begin{cases} \frac{\partial N}{\partial t} \geq \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \mu \left(\frac{U}{N}\right) N - \frac{\epsilon_0}{Q_c} N, & x \in (0, L), \quad t \geq t_1, \\ \frac{\partial U}{\partial t} \geq \delta \frac{\partial^2 U}{\partial x^2} - \nu \frac{\partial U}{\partial x} + [\rho(R^{(0)}, \frac{U}{N}) - \epsilon_0] N, & x \in (0, L), \quad t \geq t_1. \end{cases} \quad (2.25)$$

Consider the following auxiliary system

$$\begin{cases} \frac{\partial N}{\partial t} = \delta \frac{\partial^2 N}{\partial x^2} - \nu \frac{\partial N}{\partial x} + \mu \left(\frac{U}{N}\right) N - \frac{\epsilon_0}{Q_c} N, & x \in (0, L), \quad t \geq t_1, \\ \frac{\partial U}{\partial t} = \delta \frac{\partial^2 U}{\partial x^2} - \nu \frac{\partial U}{\partial x} + [\rho(R^{(0)}, \frac{U}{N}) - \epsilon_0] N, & x \in (0, L), \quad t \geq t_1, \\ \nu N(0, t) - \delta \frac{\partial N}{\partial x}(0, t) = \nu U(0, t) - \delta \frac{\partial U}{\partial x}(0, t) = 0, \\ N(L, t) = U(L, t) = 0, \quad t \geq t_1. \end{cases} \quad (2.26)$$

Note that (2.26) is a cooperative system. Given  $m > 0$ , we set

$$\hat{N}(x, t) = m e^{\lambda_{\epsilon_0} t} \phi_{\epsilon_0}^0(x), \quad \hat{U}(x, t) = m Q_c e^{\lambda_{\epsilon_0} t} \phi_{\epsilon_0}^0(x).$$

With (2.18), it is easy to see that  $(\hat{N}(x, t), \hat{U}(x, t))$  satisfies system (2.26) and  $\hat{N}(x, t_1) = m e^{\lambda_{\epsilon_0} t_1} \phi_{\epsilon_0}^0(x)$ ,  $\hat{U}(x, t_1) = m Q_c e^{\lambda_{\epsilon_0} t_1} \phi_{\epsilon_0}^0(x)$ . Since  $\mathbf{v}^0 := (R^0, N^0, U^0) \in \mathbf{X}_0$ , it follows that

$$N(x, t, \mathbf{v}^0) > 0, \quad \forall x \in [0, L], \quad t > 0.$$

From Lemma 2.1, it follows that  $\frac{U(\cdot, t, \mathbf{v}^0)}{N(\cdot, t, \mathbf{v}^0)} \geq Q_{\min}$ ,  $t \geq 0$ . This implies that

$$U(x, t, \mathbf{v}^0) > 0, \quad \forall x \in [0, L], \quad t > 0.$$

Thus, we may choose  $m > 0$  such that

$$(N(x, t_1, \mathbf{v}^0), U(x, t_1, \mathbf{v}^0)) \geq (\hat{N}(x, t_1), \hat{U}(x, t_1)).$$

Then the Comparison Principle implies that

$$(N(x, t, \mathbf{v}^0), U(x, t, \mathbf{v}^0)) \geq (\hat{N}(x, t), \hat{U}(x, t)), \quad t \geq t_1.$$

Since  $\lambda_{\epsilon_0}^0 > 0$ , it follows that  $\lim_{t \rightarrow \infty} \hat{N}(x, t) = \infty$ , and hence,  $\lim_{t \rightarrow \infty} N(x, t, \mathbf{v}^0) = \infty$ . This contradiction proves claim 2.

By Claims 1, Claims 2 and the continuous-time version of [29, theorem 1.3.3], it follows that  $\Psi(t) : \mathbf{X} \rightarrow \mathbf{X}$  is uniformly persistent with respect to  $(\mathbf{X}_0, \partial\mathbf{X}_0)$  in the sense that there is an  $\eta > 0$  such that for any  $(W^0, N^0, U^0) \in \mathbf{X}_0$ , we have

$$\lim_{t \rightarrow \infty} \|\Psi(t)(W^0(\cdot), N^0(\cdot), U^0(\cdot))\|_{\beta} \geq \eta.$$

Then, the uniform persistence stated in statement (ii) are true. By [22, Theorem 3.7 and Remark 3.10], it follows that  $\Psi(t) : \mathbf{X}_0 \rightarrow \mathbf{X}_0$  has a global attractor  $A_0$ . It then follows from [22, Theorem 4.7] that  $\Psi(t)$  has a steady-state solution  $(\hat{R}, \hat{N}, \hat{U}) \in \mathbf{X}_0$ , which satisfies  $\hat{W}(x) > 0$ ,  $\hat{N}(x) > 0$  and  $\hat{U}(x) > 0$ , for any  $x \in [0, L]$ . We complete the proof of Part (ii).  $\square$

**3. Discussion.** In this paper, we analyze a PDE system (1.10)-(1.12), or equivalently (2.1)-(2.3) that models the growth of single phytoplankton species consuming nutrients in a water column, which are capable of storing the nutrient within their cells. Due to the loss of a conservative law, our system can not be reduced to a monotone system, and the arguments used in [18] can not be applied to our model. We first show that the biologically relevant domain for system (2.1)-(2.3) is positively invariant (see Lemma 2.1), and solutions of our system are eventually bounded (see Lemma 2.2). We can also obtain another biologically relevant domain for system (2.1)-(2.3) if the growth and uptake functions are specifically chosen as in [8] (see Proposition 2.1 and Remark 2.1). Next, we use theory of uniform persistence to prove that the extinction/persistence of phytoplankton species is determined by the principal eigenvalue of (2.19) (see Theorem 2.1). The principal eigenvalue involves the diffusivity, the sinking speed, nutrient uptake rate, and growth rate (see (2.18) and (2.19)). It is worth noting that the crucial observations in the proof of Theorem 2.1 are two auxiliary systems, (2.21) and (2.26). Since systems (2.21) and (2.26) are both cooperative, the standard comparison principle can be used in our analysis.

From Theorem 2.1, we know that  $\lambda^0$ , the principal eigenvalue of (2.19), plays a central role in the extinction/persistence of phytoplankton species. Next, we shall adopt the results in [19, Section 5.3] to summarize how  $\lambda^0$  changes as  $\delta$  or  $\nu$  varies, and give some biological interpretations. For a continuous function  $\Phi(x)$ , consider the eigenvalue problem

$$\begin{cases} -\delta\phi_{xx} + \nu\phi_x + \Phi(x)\phi = \Lambda\phi, & 0 < x < L, \\ \delta\phi_x(0) - \nu\phi(0) = \phi(L) = 0. \end{cases} \quad (3.1)$$

We assume that the principal eigenvalue of (3.1) is denoted by  $\Lambda_1(\Phi(x))$ . Then  $\lambda^0 = -\Lambda_1(-\mu(Q_c))$ , and it follows from [19, Theorem 5.3] and [19, Theorem 5.4] that we have the following observations and interpretations:

- If we consider  $\lambda^0$  as a function of  $\nu$  ( $\nu > 0$ ), that is,  $\lambda^0 = \lambda^0(\nu)$ , then  $\lambda^0(\nu)$  is a decreasing function of  $\nu > 0$ , and

$$\lim_{\nu \rightarrow \infty} \lambda^0(\nu) = -\infty.$$

For sufficiently large sinking rate  $\nu$ , we have shown that  $\lambda^0(\nu)$  must be negative, and hence, the phytoplankton species goes to extinction. The larger  $\nu$  is, the greater the tendency is for the species to sink, that is, the phytoplankton species will tend towards the bottom of water columns. Due to the absorbing boundary conditions

at the bottom (i.e.,  $N(L) = 0$ ), this makes it easier for the phytoplankton species to die out.

- If we consider  $\lambda^0$  as a function of  $\delta$ , that is,  $\lambda^0 = \lambda^0(\delta)$ , then for any  $\nu \geq 0$  and  $L > 0$ , we have

$$\lim_{\delta \rightarrow \infty} \lambda^0(\delta) = -\infty; \quad \lim_{\delta \rightarrow 0^+} \lambda^0(\delta) = \begin{cases} \mu(Q_c) & \text{if } \nu = 0, \\ -\infty & \text{if } \nu > 0. \end{cases}$$

Although we are unable to investigate the monotonicity of the principal eigenvalue  $\lambda^0(\delta)$  on the turbulent diffusion rate  $\delta$ , we determine the asymptotic behaviors of  $\lambda^0(\delta)$  for small turbulent diffusion rate  $\delta$ , and large turbulent diffusion rate  $\delta$  under the case where the advection  $\nu \geq 0$ . For sufficiently large turbulent diffusion rate  $\delta$ , we have shown that  $\lambda^0(\delta)$  must be negative, and hence, the phytoplankton species cannot bloom. In such situation, the habitat is a well-mixing water column and the density of the phytoplankton species is the same at any position of the habitat. Then the absorbing boundary conditions at the bottom (i.e.,  $N(L) = 0$ ) ensures that the phytoplankton species cannot bloom. For sufficiently small turbulent diffusion rate  $\delta$  (poorly mixing water columns), we showed that the phytoplankton species will always persist if advection  $\nu = 0$ , while the phytoplankton species will always go to extinction if advection  $\nu > 0$ . We point out that the asymptotic behaviors of  $\lambda^0(\nu)$  or  $\lambda^0(\delta)$  remains open when advection  $\nu$  is negative. Although it will be of interest to understand the asymptotic behaviors of  $\lambda^0(L)$  for large/small water column depth  $L$ , it remains unclear to us.

We have discussed the extinction/persistence of phytoplankton species, and established the existence of steady-state solutions of the single population model (2.1)-(2.3) under suitable conditions (see Theorem 2.1). However, the uniqueness of steady-state solutions of system (2.1)-(2.3) remains open. To make the analysis more tractable, we also assumed that the supply of the nutrient from the bottom of the habitat is a constant, and we only investigated the single population model in this study. In the near future, we shall study the two-species model (1.7)-(1.9) with variable quota and nutrient storage in a water column, where the supply of the nutrient is a time-periodic function.

**Acknowledgments.** We would like to thank the anonymous referee for careful reading and helpful suggestions which led to improvements of our original manuscript.

## REFERENCES

- [1] J. V. Baxley and S. B. Robinson, [Coexistence in the unstirred chemostat](#), *Appl. Math. Computation*, **89** (1998), 41–65.
- [2] A. Cunningham and R. M. Nisbet, [Time lag and co-operativity in the transient growth dynamics of microalgae](#), *J. Theoret. Biol.*, **84** (1980), 189–203.
- [3] A. Cunningham and R. M. Nisbet, [Transient and oscillation in continuous culture](#), *Mathematics in microbiology*, 77–103, Academic Press, London, 1983.
- [4] M. Droop, [Some thoughts on nutrient limitation in algae](#), *J. Phycol.*, **9** (1973), 264–272.
- [5] J. P. Grover, [Constant- and variable-yield models of population growth: Responses to environmental variability and implications for competition](#), *J. Theoret. Biol.*, **158** (1992), 409–428.
- [6] J. P. Grover, [Resource Competition](#), Chapman and Hall, London, 1997.
- [7] J. P. Grover, [Is storage an adaptation to spatial variation in resource availability?](#), *The American Naturalist*, **173** (2009), E44–E61.
- [8] J. P. Grover, [Resource storage and competition with spatial and temporal variation in resource availability](#), *The American Naturalist*, **178** (2011), E124–E148.

- [9] J. P. Grover, K. W. Crane, J. W. Baker, B. W. Brooks and D. L. Roelke, [Spatial variation of harmful algae and their toxins in flowing-water habitats: a theoretical exploration](#), *Journal of Plankton Research*, **33** (2011), 211–227.
- [10] J. P. Grover, S. B. Hsu and F. B. Wang, [Competition and coexistence in flowing habitats with a hydraulic storage zone](#), *Mathematical Biosciences*, **222** (2009), 42–52.
- [11] J. P. Grover, S. B. Hsu and F. B. Wang, [Competition between microorganisms for a single limiting resource with cell quota structure and spatial variation](#), *Journal of Mathematical Biology*, **64** (2012), 713–743.
- [12] J. P. Grover and F.-B. Wang, [Dynamics of a model of microbial competition with internal nutrient storage in a flowing habitat](#), *Applied Mathematics and Computation*, **225** (2013), 747–764.
- [13] S. B. Hsu, S. Hubbell and P. Waltman, [Mathematical theory for single nutrient competition in continuous cultures of microorganisms](#), *SIAM J. Appl. Math.*, **32** (1977), 366–383.
- [14] D. Henry, *Geometric Theory of Semilinear Parabolic Equations*, Lecture Notes in Mathematics, vol. 840, Berlin, New York, Springer, 1981.
- [15] J. Hale, *Asymptotic Behavior of Dissipative Systems*, American Mathematical Society Providence, RI, 1988.
- [16] P. Hess, *Periodic-parabolic Boundary Value Problem and Positivity*, Pitman Res. Notes Math., 247, Longman Scientific and Technical, 1991.
- [17] S. B. Hsu and T. H. Hsu, [Competitive exclusion of microbial species for a single-limited resource with internal storage](#), *SIAM J. Appl. Math.*, **68** (2008), 1600–1617.
- [18] S. B. Hsu, J. Jiang and F. B. Wang, [On a system of reaction-diffusion equations arising from competition with internal storage in an unstirred chemostat](#), *J. Diff. Eqns.*, **248** (2010), 2470–2496.
- [19] S. B. Hsu, L. Mei and F. B. Wang, [On a nonlocal reaction-diffusion-advection system modelling the growth of phytoplankton with cell quota structure](#), *J. Diff. Eqns.*, **259** (2015), 5353–5378.
- [20] S. B. Hsu, H. L. Smith and P. Waltman, Dynamics of competition in the unstirred chemostat, *Canad. Appl. Math. Quart.*, **2** (1994), 461–483.
- [21] S. B. Hsu and P. Waltman, [On a system of reaction-diffusion equations arising from competition in an unstirred chemostat](#), *SIAM J. Appl. Math.*, **53** (1993), 1026–1044.
- [22] P. Maga and X.-Q. Zhao, [Global attractors and steady states for uniformly persistent dynamical systems](#), *SIAM J. Math. Anal.*, **37** (2005), 251–275.
- [23] M. H. Protter and H. F. Weinberger, *Maximum Principles in Differential Equations*, Springer-Verlag, 1984.
- [24] H. L. Smith, *Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems*, Mathematical Surveys and Monographs 41, American Mathematical Society, Providence, RI, 1995.
- [25] H. L. Smith and P. E. Waltman, [Competition for a single limiting resource in continuous culture: The variable-yield model](#), *SIAM J. Appl. Math.*, **54** (1994), 1113–1131.
- [26] H. L. Smith and P. E. Waltman, *The Theory of the Chemostat*, Cambridge Univ. Press, 1995.
- [27] H. R. Thieme, [Convergence results and a Poincaré-Bendixson trichotomy for asymptotically autonomous differential equations](#), *J. Math. Biol.*, **30** (1992), 755–763.
- [28] K. F. Zhang and X.-Q. Zhao, [Asymptotic behaviour of a reaction-diffusion model with a quiescent stage](#), *Proc. R. Soc. A.*, **463** (2007), 1029–1043.
- [29] X.-Q. Zhao, *Dynamical Systems in Population Biology*, Springer, New York, 2003.

Received December 2014; 1st revision July 2015; 2nd revision August 2015.

*E-mail address:* [lfmei@outlook.com](mailto:lfmei@outlook.com)

*E-mail address:* [sbhsu@math.nthu.edu.tw](mailto:sbhsu@math.nthu.edu.tw)

*E-mail address:* [fbwang@mail.cgu.edu.tw](mailto:fbwang@mail.cgu.edu.tw)