A Survey of Mathematical Models with Variable Quotas

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In memory of Professor Hwai-Chiuan Wang

Abstract. In this paper, we shall survey recent developments in variable-internal-stores models with multiple resources or spatial/temporal inhomogeneity, which may enhance coexistence of species and diversity in competitor communities. On the other hand, it was known that basic limiting resources for growth usually include nutrients (e.g., nitrogen and phosphorus), light, and inorganic carbon. Thus, the proposed models will involve the competition between the species for nutrients (e.g., nitrogen and phosphorus), or light, or both of nutrients and light, or inorganic carbon.

1. Introduction

The understanding of competition between species for resources is a fundamental ecological issue [13, 18, 53]. Classical phytoplankton competition studies often assume a simple, well-mixed laboratory system, such as the chemostat culture system, in which a nutrient medium is pumped, balanced by an outflow that removes nutrients and organisms [51]. The chemostat is a basic piece of ideal apparatus and it has been regarded as a lake or pond in a laboratory. Any mathematical model that explicitly addresses both resource and population dynamics must specify how much resource is consumed in the production of one new individual [14, 15, 18]. Previous 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. The simplest model is under the assumption that the consumption of resource and production of i-th species are directly proportional through a quota constant q_i, leading to the following system [1, 26]:

$$
\begin{aligned}
\frac{dS}{dt} &= (S^{(0)} - S)D - \sum_{i=1}^{n} q_i f_i(S) u_i, \\
\frac{du_i}{dt} &= (f_i(S) - D) u_i, \\
S(0) &\geq 0, \quad u_i(0) > 0, \quad i = 1, 2, \ldots, n.
\end{aligned}
$$

(1.1)

In the chemostat model (1.1), the nutrient is supplied with a constant concentration $S^{(0)}$ at dilution rate D. There is a compensating outflow also at rate D of the well-stirred contents of the chemostat. $S(t)$ denotes the nutrient concentration at time t; $u_i(t)$ represents the concentrations of species i in the culture vessel, $i = 1, 2, \ldots, n$. $f_i(S)$ is the per capita nutrient uptake rate, per cell of species i as a increasing and continuously differentiable function of nutrient concentration S, and $f_i(0) = 0$. A usual example for $f_i(S)$ is the form:

$$f_i(S) = \frac{m_i S}{a_i + S},$$

where m_i and a_i are the maximal growth rate and the Michaelis-Menten (or half saturation) constant of i-th species, respectively.

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, leading to variable-internal-stores models [11, 25, 50, 51]:

(1.2)
$$\frac{dS}{dt} = (S^{(0)} - S)D - \sum_{j=1}^{n} f_j(S, Q_j)u_j,$$
$$\frac{du_i}{dt} = (\mu_i(Q_i) - D)u_i, \qquad\qquad i = 1, 2, \ldots, n,$$
$$\frac{dQ_i}{dt} = f_i(S, Q_i) - \mu_i(Q_i)Q_i, \qquad\qquad i = 1, 2, \ldots, n,$$
$$S(0) \geq 0, \quad u_i(0) \geq 0, \quad Q_i(0) \geq Q_{\min,i}, \qquad i = 1, 2, \ldots, n.$$

For $i = 1, 2, \ldots, n$, $Q_i(t)$ 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, $f_i(S, Q_i)$ is the per capita nutrient uptake rate, per cell of species i as a function of nutrient concentration S and cell quota Q_i, $Q_{\min,i}$ denotes the threshold cell quota below which no growth of species i occurs. From the third equation of (1.2), we note that the quota decreases at a rate $-\mu_i(Q_i)Q_i$, which is the dilution by growth [13].

The growth rate $\mu_i(Q_i)$ takes the forms [4, 5, 7]:

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

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 [12], the uptake rate $f_i(S, Q_i)$ takes the form:

$$f_i(S, Q_i) = \rho_{\max,i}(Q_i)\frac{S}{a_i + S},$$
$$\rho_{\max,i}(Q_i) = \rho_{\max,i}^{\text{high}} - (\rho_{\max,i}^{\text{high}} - \rho_{\max,i}^{\text{low}})\frac{Q_i - Q_{\min,i}}{Q_{\max,i} - Q_{\min,i}},$$

where $Q_{\min,i} \leq Q_i \leq Q_{\max,i}$. Cunningham and Nisbet [4, 5] 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

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

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

$$f_i(0, Q_i) = 0, \quad \frac{\partial f_i}{\partial S} > 0, \quad \frac{\partial f_i}{\partial Q_i} \leq 0.$$

In particular, $f_i(S, Q_i) > 0$ when $S > 0$.

For a competition model with a single limiting resource in a well mixed habitat, we usually expect *the Competitive Exclusion Principle* to be valid, that is, two or more species cannot coexist [13]. Mathematically, this conclusion has been established for the system (1.1) with constant quota (see, e.g., [1, 23, 26]) as well as the system (1.2) for variable-internal-stores models (see, e.g., [25, 50, 51]). However, in a real ecosystem, outcomes such as coexistence of two or more species, or bistability where outcomes depend on initial conditions could be observed. Those observations motivate us to do some modifications of the aforementioned systems.

In Section 2, we survey some spatially homogeneous systems (ODE models). The competitive exclusion principle of system (1.2) is shown in Section 2.1. In Section 2.2, we consider a Droop model with two competing species for a single nutrient with periodic input. Section 2.3 is devoted to the study of a Droop model with two competing species for two complementary/essential nutrients with periodic input. In Section 2.4, we consider a Droop model with two competing species for a single nutrient and light in which the input concentration of nutrient is a constant. In Section 3, we survey Droop models in the form of reaction-diffusion(-advection) systems. The results of a Droop model with two competing species for a single nutrient (resp. two complementary/essential nutrients) in an unstirred chemostat are presented in Section 3.1 (resp. Section 3.2). In Section 3.3, we consider a Droop model with a single species consuming a single nutrient in a water column. In Section 3.4, we investigate the effect/role of inorganic carbon on global warming. More precisely, we survey a Droop model with a single species consuming inorganic carbon that is stored internally in a water column. Assuming the cell quota is proportional to cell size, we survey size-structured models in Section 4. In Section 4.1, we first review a size-structured model in which the resource is assumed to be unlimited, and hence, the governing equation of nutrient is ignored. In Section 4.2 (resp. Section 4.3), we consider a size-structured model in a well-mixed chemostat (resp. an unstirred chemostat) where the

governing equation of a single nutrient is added. In Section 4.4, we survey a size-structured model with light limitation.

2. ODE models

Classical models of competition usually consider a simple, well-mixed habitat, such as the chemostat culture system, in which a nutrient resource is supplied via an inflow, and a balancing outflow removes nutrient and organisms [51]. Since the spatial gradients of resource and species are neglected, the governing systems are ODE equations. In this section, we shall survey several ODE systems modeling the interactions of species and resources that are stored within individuals.

2.1. Analysis of a Droop model in a simple chemostat

Substituting $U_i = u_i Q_i$, $i = 1, 2, \ldots, n$ into (1.2), leading to the following system

$$
\begin{aligned}
\frac{dS}{dt} &= (S^{(0)} - S)D - \sum_{j=1}^{n} f_j(S, \tfrac{U_j}{u_j})u_j, & \\
\frac{du_i}{dt} &= (\mu_i(\tfrac{U_i}{u_i}) - D)u_i, & i = 1, 2, \ldots, n, \\
\frac{dU_i}{dt} &= f_i(S, \tfrac{U_i}{u_i})u_i - DU_i, & i = 1, 2, \ldots, n, \\
S(0) \geq 0, \quad u_i(0) \geq 0, \quad U_i(0) \geq 0, & & i = 1, 2, \ldots, n.
\end{aligned}
$$

(2.1)

Let $\Sigma(t) = S(t) + \sum_{i=1}^{n} U_i(t)$. Then we have the following mass conservation

$$
\frac{d\Sigma(t)}{dt} = (S^{(0)} - \Sigma(t))D,
$$

(2.2)

and hence,

$$
\Sigma(t) \to S^{(0)} \quad \text{as } t \to \infty.
$$

Thus, we conclude that the limiting system of (2.1) takes the form

$$
\begin{aligned}
\frac{du_i}{dt} &= (\mu_i(\tfrac{U_i}{u_i}) - D)u_i, & i = 1, 2, \ldots, n, \\
\frac{dU_i}{dt} &= f_i\left(S^{(0)} - \sum_{j=1}^{n} U_j(t), \tfrac{U_i}{u_i}\right)u_i - DU_i, & i = 1, 2, \ldots, n, \\
u_i(0) \geq 0, \quad U_i(0) \geq 0, & & i = 1, 2, \ldots, n.
\end{aligned}
$$

(2.3)

We note that the solutions of the limiting system (2.3) have the same asymptotic behavior as the solutions of the full system (2.1) (see, e.g., [52] or [51, Appendix F]). Alternatively, one can also use the theory of chain transitive sets (see [21] or [57, Section 1.2]) to lift the

dynamics of the limiting system (2.3) to the full system (2.1). Thus, it suffices to study the global dynamics of system (2.3).

Putting $n = 2$ into (2.3), leading to the following system

(2.4)
$$\frac{du_1}{dt} = (\mu_1(\tfrac{U_1}{u_1}) - D)u_1,$$
$$\frac{dU_1}{dt} = f_1(S^{(0)} - U_1 - U_2, \tfrac{U_1}{u_1})u_1 - DU_1,$$
$$\frac{du_2}{dt} = (\mu_2(\tfrac{U_2}{u_2}) - D)u_2,$$
$$\frac{dU_2}{dt} = f_2(S^{(0)} - U_1 - U_2, \tfrac{U_2}{u_2})u_2 - DU_2,$$
$$u_i(0) \geq 0, \quad U_i(0) \geq 0, \quad i = 1, 2.$$

In [50], Smith and Waltman show that the semiflow associated with system (2.4) preserves the partial ordering defined by

$$(u_1, U_1, u_2, U_2) \leq_K (\widetilde{u}_1, \widetilde{U}_1, \widetilde{u}_2, \widetilde{U}_2)$$

if and only if

$$u_1 \leq \widetilde{u}_1, \quad U_1 \leq \widetilde{U}_1, \quad u_2 \geq \widetilde{u}_2, \quad U_2 \geq \widetilde{U}_2.$$

Then one can prove that the competitive exclusion principle holds for system (2.4) by applying the theory of monotone dynamical system (see [50]) or directly using the abstract results in [34, Theorem B].

The authors in [25] proved that the competitive exclusion principle also holds for n species competing for a single nutrient in the system (2.3) with $n \geq 3$. Basically, their idea is to apply fluctuating lemma (see, e.g., [22]) to the following system

$$\frac{dU_i(t)}{dt} = f_i\left(S^{(0)} - \sum_{j=1}^{n} U_j(t), Q_i(t)\right)\frac{U_i(t)}{Q_i(t)} - DU_i(t), \qquad i = 1, 2, \ldots, n,$$

$$\frac{dQ_i(t)}{dt} = f_i\left(S^{(0)} - \sum_{j=1}^{n} U_j(t), Q_i(t)\right) - \mu_i(Q_i(t))Q_i(t), \qquad i = 1, 2, \ldots, n,$$

$$U_i(0) \geq 0, \quad Q_i(0) \geq Q_{\min,i}, \qquad\qquad\qquad\qquad i = 1, 2, \ldots, n,$$

where $\sum_{j=1}^{n} U_j(t) \leq S^{(0)}$. We note that the arguments in [25] is based on the conservation (2.2), that is, the assumption of the same dilution rate for each species and nutrient are necessary. Here, we propose an open problem with different removable rates.

Open problem. Show the competitive exclusion principle holds for the following system:

$$\frac{dS}{dt} = (S^{(0)} - S)D - \sum_{j=1}^{n} f_j(S, Q_j)u_j,$$

$$\frac{du_i}{dt} = (\mu_i(Q_i) - d_i)u_i, \qquad\qquad i = 1, 2, \ldots, n,$$

$$\frac{dQ_i}{dt} = f_i(S, Q_i) - \mu_i(Q_i)Q_i, \qquad\qquad i = 1, 2, \ldots, n,$$

$$S(0) \geq 0, \quad u_i(0) \geq 0, \quad Q_i(0) \geq Q_{\min,i}, \qquad i = 1, 2, \ldots, n,$$

where $D, d_1, d_2, \ldots, d_n$ are mutually different.

2.2. A periodic Droop model with a single nutrient

An explanation for the coexistence of many species of phytoplankton in a seemingly temporally constant environment is the non-steady state dynamics [38]. In fact, temporal variations can promote coexistence of species and diversity in competitor communities (see, e.g., [10, 24, 38, 43]). The authors in [49, 55] investigated a system modeling two species competition for one nutrient with internal storage and a periodic input:

$$\frac{dS}{dt} = (S^{(0)}(t) - S)D - \sum_{j=1}^{2} f_j(S, Q_j)u_j,$$

(2.5)

$$\frac{du_i}{dt} = (\mu_i(Q_i) - D)u_i, \qquad\qquad i = 1, 2,$$

$$\frac{dQ_i}{dt} = f_i(S, Q_i) - \mu_i(Q_i)Q_i, \qquad\qquad i = 1, 2,$$

$$S(0) \geq 0, \quad u_i(0) \geq 0, \quad Q_i(0) \geq Q_{\min,i}, \qquad i = 1, 2,$$

where $S^{(0)}(t)$ satisfies $S^{(0)}(t + \tau) = S^{(0)}(t) \geq 0$, for some period $\tau > 0$. For system (2.5), it was shown in [49, 55] that coexistence occurs in the competition for one nutrient with internal storage and a periodic input.

2.3. Competition models for two essential nutrients

In [36], we consider a model for two phytoplankton species competing for two complementary/essential nutrients with internal storage in the well mixed chemostat. Let $S(t)$ and $R(t)$ denote the concentrations of the limiting nutrients in the chemostat at time t. Assume that $u_i(t)$ stands for the concentrations of species i in the culture vessel, and $Q_i(t)$ represents the average amount of stored nutrient per cell of i-th population at time t, $i = 1, 2$. Then the model is governed by the following ordinary differential system

(see [36, 40–42]):

$$\frac{dS}{dt} = (S^{(0)}(t) - S)D - f_{S1}(S, Q_{S1})u_1 - f_{S2}(S, Q_{S2})u_2,$$

$$\frac{dR}{dt} = (R^{(0)}(t) - R)D - f_{R1}(R, Q_{R1})u_1 - f_{R2}(R, Q_{R2})u_2,$$

$$\frac{dQ_{Si}}{dt} = f_{Si}(S, Q_{Si}) - \min\{\mu_{Si}(Q_{Si}), \mu_{Ri}(Q_{Ri})\}Q_{Si}, \qquad i = 1, 2,$$

(2.6)

$$\frac{dQ_{Ri}}{dt} = f_{Ri}(R, Q_{Ri}) - \min\{\mu_{Si}(Q_{Si}), \mu_{Ri}(Q_{Ri})\}Q_{Ri}, \qquad i = 1, 2,$$

$$\frac{du_i}{dt} = [\min\{\mu_{Si}(Q_{Si}), \mu_{Ri}(Q_{Ri})\} - D]u_i, \qquad i = 1, 2,$$

$$S(0) \geq 0, \quad R(0) \geq 0, \quad u_i(0) \geq 0, \qquad i = 1, 2,$$

$$Q_{Si}(0) \geq Q_{\min,Si}, \quad Q_{Ri}(0) \geq Q_{\min,Ri}, \qquad i = 1, 2.$$

Here $f_{Si}(S, Q_{Si})$ (resp. $f_{Ri}(R, Q_{Ri})$) is the per capita uptake rate of species i as a function of resource concentration S (resp. R) and cell quota Q_{Si} (resp. Q_{Ri}). In (2.6), the two nutrients are essential, sometimes also referred to as complementary, meaning that a minimum amount of each nutrient is required for population growth. "Liebig's Law of the Minimum" is used to describe the dependence of species growth on cell quotas, that is, growth rate of species i is determined by the minimum of two Droop functions, $\mu_{Si}(Q_{Si})$ and $\mu_{Ri}(Q_{Ri})$. $Q_{\min,Ni}$ denotes threshold cell quota below which no growth of species i occurs, where $N = S, R$. Here, we assume that there exists a period $\tau > 0$ such that $S^{(0)}(t)$ and $R^{(0)}(t)$ satisfy

$$S^{(0)}(t + \tau) = S^{(0)}(t) \geq 0, \quad R^{(0)}(t + \tau) = R^{(0)}(t) \geq 0.$$

We note that the authors in [41, 42] studied system (2.6) in the case of constant input, that is,

$$S^{(0)}(t) = S^{(0)} > 0, \quad R^{(0)}(t) = R^{(0)} > 0.$$

It is shown that system (2.6) with constant input exhibits the results of competitive exclusion, coexistence, and bi-stability (see [42]).

In order to investigate the global dynamics of (2.6), the authors in [36] first consider the case of single species growth. By applying the theory of monotone dynamical system as well as the property of sub-homogeneous systems (see [57]), it was established that the associated single population system is washed out if a sub-threshold criterion holds, while there is a globally stable positive periodic solution if a super-threshold criterion holds. Then both uniform persistence and the existence of periodic coexistence state of the two-species model (2.6) are established provided that there is mutual invasibility of both semitrivial periodic solution (see [36]). In the Discussion section of [36], it was numerically shown that the outcomes of competition may be reversed if we increase the amplitude of periodic input.

2.4. A Droop model under light limitation

It has been known that growth of population is critically affected by the supply of two fundamental types of resources: light and mineral nutrients. In phytoplankton communities, species typically compete for two essential resources, nutrient and light. The authors in [48] proposed the following system:

(2.7)
$$\frac{dS}{dt} = (S^{(0)} - S)D - \sum_{j=1}^{2} f_j(S, Q_j)u_j,$$

$$\frac{dQ_i}{dt} = f_i(S, Q_i) - \min\{\mu_i(Q_i), g_i(I)\}Q_i, \qquad i = 1, 2,$$

$$\frac{du_i}{dt} = [\min\{\mu_i(Q_i), g_i(I)\} - D]u_i, \qquad i = 1, 2,$$

$$S(0) \geq 0, \quad Q_i(0) \geq Q_{\min,i}, \quad u_i(0) \geq 0, \qquad i = 1, 2.$$

Here, we assume that the specific growth rate $g_i(I)$ satisfy

$$g_i(0) = 0, \quad g_i'(I) > 0 \quad \text{for } I > 0, i = 1, 2.$$

The light intensity $I(t)$ takes the form

$$I(t) = I_{\text{in}} \exp\left(-k_0 z_m - \sum_{j=1}^{2} k_j z_m u_j\right).$$

An usual example is the Monod functions (Michaelis-Menten forms):

$$g_i(I) = \frac{m_i I}{a_i + I}, \quad i = 1, 2.$$

In [30], the authors apply the theory of monotone dynamical system to determining the outcomes of competition of system (2.7): extinction of two species, competitive exclusion, stable coexistence and bistability (outcomes dependent on initial conditions). They also propose a graphical presentation to classify the results of competition.

3. PDE models

In the past decades, there have been several developments in the study of interactions of populations and dissolved nutrients that are distributed in spatially variable habitats [2,3,14–17,19,27,28,33,35,45]. Investigating ecological model systems with variable quotas in a spatially variable habitat are important and significant since those individuals could obtain resources in a rich zone of a habitat and for their later use to grow when they travel to a poor zone [14,15]. Due to the complexities and difficulties in modeling as well as mathematical analysis, there are quite few papers that involve in this direction.

One approach of modeling is the reaction-diffusion system [27] or the reaction-diffusion-advection system [15], which describes the dynamics of dissolved nutrient concentration, the total concentration of stored nutrient by a species at a given point, and the corresponding population density. Although this approach may risk errors, the author in [15] recently pointed out that errors caused by the approach were relatively modest, and mathematical modeling in [15, 27] can be a good approximation.

3.1. A Droop model with a single nutrient in an unstirred chemostat

In [27], we consider two species competing for a single nutrient with internal storage in an unstirred chemostat. The governing equations take the following form:

$$S_t = dS_{xx} - f_1(S, \tfrac{U_1}{u_1})u_1 - f_2(S, \tfrac{U_2}{u_2})u_2,$$

(3.1)
$$(U_i)_t = d(U_i)_{xx} + f_i(S, \tfrac{U_i}{u_i})u_i,$$

$$(u_i)_t = d(u_i)_{xx} + \mu_i(\tfrac{U_i}{u_i})u_i, \qquad\qquad i = 1, 2,$$

in $(x, t) \in (0, 1) \times (0, \infty)$ with boundary conditions

(3.2)
$$S_x(0, t) = -S^{(0)}, \quad S_x(1, t) + \gamma S(1, t) = 0, \qquad t > 0,$$

$$\vartheta_x(0, t) = \vartheta_x(1, t) + \gamma\vartheta(1, t) = 0, \qquad\qquad \vartheta = U_i, u_i, \ i = 1, 2, \ t > 0,$$

in $t \in (0, \infty)$ and initial conditions

(3.3)
$$S(x, 0) = S^0(x) \geq 0, \qquad x \in (0, 1),$$

$$\vartheta(x, 0) = \vartheta^0(x) \geq 0, \qquad \vartheta = U_i, u_i, \ i = 1, 2, \ x \in (0, 1).$$

First, we establish a conservation principle to reduce the dimension of the above system (3.1)–(3.3) by eliminating the equation of nutrient S. The reduced/limiting system generates a monotone semiflow in its feasible domain under a partial order $\leq_K$. For the case of single species growth, it was shown that extinction (resp. persistence) occurs if the diffusion rate is relatively large (resp. small). Further, if the single species can persist, then there exists a unique positive steady-state solution which is globally asymptotically stable. However, the question of extinction/persistence is left open for intermediate diffusion rates. The authors in [33] pushed further the results in [27] and obtained a threshold result by defining, in an abstract way, the threshold diffusion rate to be "the supremum of diffusion rates where a lower solution can be constructed". Finally, suitable upper/lower solutions are constructed to study the uniform persistence of limiting system of (3.1)–(3.3), and the existence of coexistence steady-state solution is also established. It is worth noting that a threshold type result on the extinction/persistence of (3.1)–(3.3) can be also established in terms of the sign of the principal eigenvalue of a nonlinear eigenvalue problem similar to the one developed in [29].

3.2. A Droop model with two essential nutrients in an unstirred chemostat

The authors in [28] consider the competition of two species for two complementary/essential nutrients. The governing system is the following system of partial differential equations:

$$S_t = dS_{xx} - f_{S1}(S, \tfrac{U_{S1}}{u_1})u_1 - f_{S2}(S, \tfrac{U_{S2}}{u_2})u_2,$$
$$R_t = dR_{xx} - f_{R1}(R, \tfrac{U_{R1}}{u_1})u_1 - f_{R2}(R, \tfrac{U_{R2}}{u_2})u_2,$$
$$(3.4) \qquad (U_{Si})_t = d(U_{Si})_{xx} + f_{Si}(S, \tfrac{U_{Si}}{u_i})u_i,$$
$$(U_{Ri})_t = d(U_{Ri})_{xx} + f_{Ri}(R, \tfrac{U_{Ri}}{u_i})u_i,$$
$$(u_i)_t = d(u_i)_{xx} + \min\big\{\mu_{Si}(\tfrac{U_{Si}}{u_i}), \mu_{Ri}(\tfrac{U_{Ri}}{u_i})\big\}u_i, \qquad i = 1,2,$$

in $(x,t) \in (0,1) \times (0,\infty)$ with boundary conditions

$$S_x(0,t) = -S^{(0)}, \quad S_x(1,t) + \gamma S(1,t) = 0, \qquad t > 0,$$
$$(3.5) \quad R_x(0,t) = -R^{(0)}, \quad R_x(1,t) + \gamma R(1,t) = 0, \qquad t > 0,$$
$$\vartheta_x(0,t) = \vartheta_x(1,t) + \gamma\vartheta(1,t) = 0, \qquad\qquad \vartheta = U_{Si}, U_{Ri}, u_i,\ i = 1,2,\ t > 0,$$

and initial conditions

$$(3.6) \quad \begin{aligned} S(x,0) &= S^0(x) \geq 0, \ \ R(x,0) = R^0(x) \geq 0, \quad x \in (0,1),\\ \vartheta(x,0) &= \vartheta^0(x) \geq 0, \qquad\qquad\qquad\qquad \vartheta = U_{Si}, U_{Ri}, u_i,\ i = 1,2,\ x \in (0,1). \end{aligned}$$

Two conservation principles are established, and system (3.4)–(3.6) can be reduced to a monotone dynamical system. Thus, one can first study the extinction and persistence of the single species growth, then the possibility of coexistence of system (3.4)–(3.6) can be investigated. The arguments in [28] are inspired by those in [27].

3.3. Growth with internal storage in a water column

In [15], the author proposes a competition model with variable quota and nutrient storage in a water column, where a periodically varying nutrient concentration was imposed at the bottom. Assuming that the supply of the nutrient is constant, the authors in [45] investigated the single population model associated with the system proposed in [15]. The equations take the form:

$$(3.7) \quad \begin{aligned} S_t &= dS_{xx} - f(S, \tfrac{U}{u})u, & x \in (0,L),\ t > 0,\\ U_t &= dU_{xx} - \nu U_x + f(S, \tfrac{U}{u})u, & x \in (0,L),\ t > 0,\\ u_t &= du_{xx} - \nu u_x + \mu(\tfrac{U}{u})u, & x \in (0,L),\ t > 0, \end{aligned}$$

with boundary conditions

$$(3.8) \quad \begin{aligned} S_x(0,t) &= 0, \quad S(L,t) = S^{(0)}, & t > 0,\\ \nu\vartheta(0,t) - d\vartheta_x(0,t) &= 0, & \vartheta = U, u,\\ U(L,t) &= u(L,t) = 0, & t > 0, \end{aligned}$$

and initial conditions

$$(3.9) \quad S(x,0) = S^0(x) \geq 0, \quad U(x,0) = U^0(x) \geq 0, \quad u(x,0) = u^0(x) \geq 0, \quad 0 < x < L.$$

Here, the spatial coordinate x represents depth of a water column, with $x = 0$ being the surface and $x = L$ the bottom. Dissolved nutrient $S(x,t)$ diffuses with diffusivity d. The boundary conditions of $S(x,t)$ are zero-flux condition at the surface ($x = 0$), and a constant supply of the nutrient, $S^{(0)}$, at the bottom of the habitat ($x = L$). Population density transports at the same diffusivity d and moves by advection toward the bottom of the habitat at the sinking speed ν. The nutrient taken up by individuals is carried within these individuals, so we assume that $U(x,t)$ follows the same transport processes as $u(x,t)$. The boundary conditions of $U(x,t)$ and $u(x,t)$ are zero-flux conditions at the surface of the habitat, and absorbing conditions at the bottom; $Q(x,t) := U(x,t)/u(x,t)$ is the average quota at a location.

We note that system (3.7)–(3.9) cannot be reduced into a monotone dynamical system, due to the lack of a conservation principle. In order to study the extinction/persistence, the authors in [45] compare system (3.7)–(3.9) with two auxiliary systems, which are both cooperative. Thus, the standard comparison principle can be used to investigate the threshold dynamics of the single population model (3.7)–(3.9).

3.4. Competition for inorganic carbon

The basic limiting resources for growth of population are nutrients (e.g., nitrogen and phosphorus), light, and inorganic carbon. Several previous works have considered the competition between the species for nutrients (e.g., nitrogen and phosphorus), or light, or both of them. However, the competition for inorganic carbon have received very little attention, perhaps due to the difficulty in the biochemistry of inorganic carbon. The authors in [54] proposed a system of ODEs modeling the competition of the species for inorganic carbon that is stored internally in a well-mixed chemostat, in which dissolved CO2 and carbonic acid are regarded as one resource (denoted as "CO2"), and bicarbonate and carbonate ions are regarded as another (denoted as "CARB"). The resources "CO2" and "CARB" are substitutable in their effects on algal growth. To make the mathematics more tractable, we adopt the ideas in [47] to do some simplifications in the complex processes of "CO2" and "CARB" involved, and modified the ODE system proposed in [54] to the following variable-internal-storage model:

$$\frac{dR}{dt} = (R^{(0)} - R)D - f_R(R, Q)u - \omega_r R + \omega_s S,$$
$$\frac{dS}{dt} = (S^{(0)} - S)D - f_S(S, Q)u + \omega_r R - \omega_s S,$$

$$\frac{dQ}{dt} = f_R(R,Q) + f_S(S,Q) - \mu(Q)Q,$$

$$\frac{du}{dt} = [\mu(Q) - D]u,$$

$$R(0) \geq 0, \quad S(0) \geq 0, \quad Q(0) \geq Q_{\min}, \quad u(0) \geq 0.$$

Here, $R(t)$ represents the total concentration of "CO2" (i.e., dissolved CO2 and carbonic acid); $S(t)$ represents the total concentration of "CARB" (i.e., bicarbonate and carbonate ions); $u(t)$ denotes the population density of the species; $Q(t)$ stands for the cellular carbon content. The effect of respiration in system (3.4) is ignored. Then the first equation represents the changes in the concentration of dissolved "CO2" through the influx $R^{(0)}$ and efflux of water containing dissolved "CO2", through gas exchange with atmospheric CO2, and through the chemical reaction from dissolved "CO2" to "CARB" and vice versa, and through uptake of "CO2" ($f_R(R,Q)u$) by the species; the second equation describes changes in the total concentration of "CARB" through the influx $S^{(0)}$ and efflux of water containing these inorganic carbon species, through the chemical reaction from "CARB" to dissolved "CO2" and vice versa, and through uptake of "CARB" ($f_S(S,Q)u$) by the species [54]. The third equation in (3.4) describes the cellular carbon content of the species, which increases through uptake of "CO2" ($f_R(R,Q)$) and "CARB" ($f_S(S,Q)$), and decrease through consumption of cellular carbon for growth ($\mu(Q)Q$). We further assume that carbonic acid loses a proton to become bicarbonate at the rate ω_r, and the rate of the reverse reaction is denoted by ω_s [47].

The following "unstirred chemostat model" associated with system (3.4) was discussed in [29]:

$$
\begin{aligned}
&R_t = dR_{xx} - f_R(R, \tfrac{U}{u})u - \omega_r R + \omega_s S, & & x \in (0,1), \ t > 0, \\
&S_t = dS_{xx} - f_S(S, \tfrac{U}{u})u + \omega_r R - \omega_s S, & & x \in (0,1), \ t > 0, \\
&U_t = dU_{xx} + f_R(R, \tfrac{U}{u})u + f_S(S, \tfrac{U}{u})u, & & x \in (0,1), \ t > 0, \\
\text{(3.10)} \quad &u_t = du_{xx} + \mu(\tfrac{U}{u})u, & & x \in (0,1), \ t > 0, \\
&N_x(0,t) = -N^{(0)}, \quad N_x(1,t) + \gamma N(1,t) = 0, & & N = R, S, \ t > 0, \\
&w_x(0,t) = 0, \quad w_x(1,t) + \gamma w(1,t) = 0, & & w = U, u, \ t > 0, \\
&w(x,0) = w^0(x) \geq (\not\equiv)0, & & w = R, S, U, u, \ x \in (0,1),
\end{aligned}
$$

where the chemostat is tubular, and hence, the spatial dimension in (3.10) is one; the constants d and γ represent the diffusion coefficient and the washout constant, respectively.

The authors in [29] also considered a reaction-advection-diffusion system associated with system (3.4) that models the dynamics in another natural habitat, the water column of lakes and oceans (see also [14, 15, 47, 56]). In a water column, the phytoplankton, which is relatively homogeneously distributed horizontally, may be moved up or down by

turbulence diffusion. In addition, it also has a tendency to sink or float. The spatial coordinate $x \in [0, L]$ represents the depth of a water column, with $x = 0$ being the surface and $x = L$ the bottom. Assuming that CO2 enters via water-atmospheric interface ($x = 0$), whereas CARB enters via the sedimentary interface ($x = L$), we propose the following model for a phytoplankton species with internal storage in the water column [29]:

(3.11)
$$
\begin{aligned}
& R_t = (D_R(x)R_x)_x - f_R(R, \tfrac{U}{u})u - \omega_r R + \omega_s S, && x \in (0, L),\ t > 0, \\
& S_t = (D_S(x)S_x)_x - f_S(S, \tfrac{U}{u})u + \omega_r R - \omega_s S, && x \in (0, L),\ t > 0, \\
& U_t = (d(x)U_x - \nu(x)U)_x + f_R(R, \tfrac{U}{u})u + f_S(S, \tfrac{U}{u})u - mU, && x \in (0, L),\ t > 0, \\
& u_t = (d(x)u_x - \nu(x)u)_x + \mu(\tfrac{U}{u})u - mu, && x \in (0, L),\ t > 0, \\
& \gamma_R R(0, t) - R_x(0, t) = \gamma_R R^{(0)}, \quad R_x(L, t) = 0, && t > 0, \\
& S_x(0, t) = 0, \quad S_x(L, t) + \gamma_S S(L, t) = \gamma_S S^{(0)}, && t > 0, \\
& d(x)w_x(x, t) - \nu(x)w(x, t) = 0, && w = U, u,\ x = 0\ \text{or}\ L,\ t > 0, \\
& w(x, 0) = w^0(x) \geq (\not\equiv)0, && w = R, S, U, u,\ x \in (0, L),
\end{aligned}
$$

where $D_R(x)$, $D_S(x)$, and $d(x)$ are the vertical turbulent diffusion coefficient of resources R, S, and species u, respectively; $\nu(x)$ is the sinking velocity ($\nu(\cdot) > 0$) or the buoyant velocity ($\nu(\cdot) < 0$) of species. We assume no boundary flux for species u and total stored resources U, that is, species do not leave or enter the water column at $x = 0$ and $x = L$. In (3.11), we further assume that resource R (resp. S) enter the water column only from the surface (resp. the bottom sediment), and $R^{(0)}$ (resp. $S^{(0)}$) is the source concentration of R (resp. S) at the surface (resp. the bottom) of the water column. γ_R is the transfer velocity of nutrients relative to $D_R(0)$ at the surface; γ_S is the transfer velocity of nutrients relative to $D_S(L)$ at the sediment interface [56]. There is another type of boundary conditions for CO2 and CARB in the models of [47]. Using the boundary conditions for resources in [47], we have the following alternative model in the water column [29]:

(3.12)
$$
\begin{aligned}
& R_t = (D_R(x)R_x)_x - f_R(R, \tfrac{U}{u})u - \omega_r R + \omega_s S, && x \in (0, L),\ t > 0, \\
& S_t = (D_S(x)S_x)_x - f_S(S, \tfrac{U}{u})u + \omega_r R - \omega_s S, && x \in (0, L),\ t > 0, \\
& U_t = (d(x)U_x - \nu(x)U)_x + f_R(R, \tfrac{U}{u})u + f_S(S, \tfrac{U}{u})u - mU, && x \in (0, L),\ t > 0, \\
& u_t = (d(x)u_x - \nu(x)u)_x + \mu(\tfrac{U}{u})u - mu, && x \in (0, L),\ t > 0, \\
& \gamma_R R(0, t) - R_x(0, t) = \gamma_R \widehat{R}, \quad R(L, t) = R^{(0)}, && t > 0, \\
& S_x(0, t) = 0, \quad S(L, t) = S^{(0)}, && t > 0, \\
& d(x)w_x(x, t) - \nu(x)w(x, t) = 0, && w = U, u,\ x = 0\ \text{or}\ L,\ t > 0, \\
& w(x, 0) = w^0(x) \geq (\not\equiv)0, && w = R, S, U, u,\ x \in (0, L).
\end{aligned}
$$

Here, the constant $\widehat{R} > 0$ is the thermodynamic equilibrium concentration of CO2 in

water, whose biological explanations can be found in the introduction of [47]; $R^{(0)}$ and $S^{(0)}$ are the source concentration of CO2 and CARB at the bottom of the water column, respectively [47].

In [29], the authors directly investigated the following general model for the growth of single species that includes the habitats in the unstirred chemostat (see (3.10)) and in the water column (see (3.11) and (3.12)):

(3.13)
$$R_t = (D_R(x)R_x)_x - f_R(R, \tfrac{U}{u})u - \omega_r R + \omega_s S, \qquad x \in (0, L), \ t > 0,$$
$$S_t = (D_S(x)S_x)_x - f_S(S, \tfrac{U}{u})u + \omega_r R - \omega_s S, \qquad x \in (0, L), \ t > 0,$$
$$U_t = (d(x)U_x - \nu(x)U)_x + f_R(R, \tfrac{U}{u})u + f_S(S, \tfrac{U}{u})u - mU, \quad x \in (0, L), \ t > 0,$$
$$u_t = (d(x)u_x - \nu(x)u)_x + \mu(\tfrac{U}{u})u - mu, \qquad x \in (0, L), \ t > 0,$$
$$\mathcal{B}_{N,x}[N] = c_{N,x} \geq 0, \qquad N = R, S, \ x = 0 \text{ or } L, \ t > 0,$$
$$\mathbb{B}^x[w] = 0, \qquad w = U, u, \ x = 0 \text{ or } L, \ t > 0,$$
$$w(x, 0) = w^0(x) \geq (\not\equiv)0, \qquad w = R, S, U, u, \ x \in (0, L),$$

where $m \geq 0$. For the definitions of $\mathcal{B}_{N,x}[N]$, $c_{N,x}$ and $\mathbb{B}^x[w]$, we refer the readers to [29, Section 1].

The main difficulties in mathematical analysis for the system (3.13) and models in [27, 28, 33] are caused by the singularity in the ratio U/u at the extinction steady state with $(U, u) = (0, 0)$. Thus, standard techniques such as linearization and bifurcation are not applicable. In previous works [27, 28, 33], it was essential that the limiting system is monotone, as they are based on upper/lower solution arguments. We point out that the arguments developed in [27, 28, 33] can not be applied to (3.13) since the general system (3.13) can not be reduced to a monotone system. Recently, J. Mallet-Paret and R. D. Nussbaum [44] proposed a Krein-Rutman type theorem involving two separate cones, and hence, the existence of the principal eigenvalue of a nonlinear eigenvalue problem can be proved. Then the authors in [29] establish a threshold type result on the extinction/persistence of the general system (3.13) in terms of the death rate and the principal eigenvalue associated with a nonlinear eigenvalue problem.

4. PDE models with cell quota structure

Assuming that quota is proportional to cell size, the authors in [18] build on previous work addressing size-structured populations (see, e.g., [6, 46]), extending it to a size-structured competition model in the chemostat. More precisely, the ideas in [18] are as follows: the quota of resource for an individual is proportional to its size, and individuals reproduce by simple division into two equally-sized daughters.

4.1. A size-structured model

In this subsection, we briefly introduce a size-structured model developed in [6, 20, 46], and the equation takes the following form:

$$(4.1) \qquad \frac{\partial n(t,q)}{\partial t} + \frac{\partial (g(q)n(t,q))}{\partial q} = -\mu(q)n(t,q) - b(q)n(t,q) + 4b(2q)n(t,2q).$$

Here t denotes time, q represents the size of an individual cell. n is the population density function, that is, $\int_{q_1}^{q_2} n(t,q)\,dq$ represents the number of cells with size between q_1 and q_2 at time t. The functions $\mu(q)$, $b(q)$ and $g(q)$ are the rates at which cells of size q die, divide and grow, respectively. The second term at the left hand side (The first term at the right hand side) denotes changes due to the growth (death or dilution) of cells. The last two terms describe the reproduction process. The factor 4 in the birth term may be strange to the readers. We refer the Appendix in [6] for a derivation of equation (4.1).

We assume that an individual cannot divide before reaching a minimal size $q_{\min} > 0$. Consequently, cells with size less than $\frac{1}{2}q_{\min}$ can not exist, which is expressed by the boundary condition

$$n(t, \tfrac{1}{2}q_{\min}) = 0.$$

Furthermore, we assume that cells have to divide before reaching a maximal size which is denoted by $q_{\max}$. Thus we have to impose the following condition on b:

$$\int_{q_{\min}}^{q_{\max}} b(q)\,dq = \infty.$$

4.2. A size-structured model in a well-mixed chemostat

We next consider the following system describing competition between n competitors with quota structure in a well-mixed chemostat [18]:

$$
\begin{aligned}
(4.2) \qquad \frac{\partial n_i(t,q_i)}{\partial t} &= \beta_i(S)\left\{ -\frac{\partial(g_i(q_i)n_i(t,q_i))}{\partial q_i} - b_i(q_i)n_i(t,q_i) + 4b_i(2q_i)n_i(t,2q_i) \right\} \\
&\quad - D_i n_i(t,q_i), \\
\frac{dS(t)}{dt} &= D(S^{(0)} - S(t)) - \sum_{i=1}^{n} \alpha_i \beta_i(S) \int_{q_{\min,i}/2}^{q_{\max,i}} g_i(q_i)n_i(t,q_i)\,dq_i, \\
n_i(t, \tfrac{q_{\min,i}}{2}) &= 0, \quad 1 \le i \le n, \\
n_i(0,q_i) &= n_i^0(q_i), \quad 1 \le i \le n, \\
S(0) &= S_0.
\end{aligned}
$$

Here $n_i(t,q_i)$ denotes the concentration at time t with quota q_i for the i-th competitor, $1 \le i \le n$; $S(t)$ denotes the concentration of nutrient at time t; D is the dilution rate;

q_i and D_i are respectively the cell quota and the death rate for i-th microorganism. $\beta_i(S) := \mu_{\max,i} S/(a_i + S)$ is the Monod function.

In [18], the authors showed that the competitive exclusion principle holds for system (4.2), that is to say, when size-structured species compete for a single resource in a spatially uniform habitat–one species wins which has the lowest break-even concentration for the nutrient. With size structure, the break-even concentration also depends on the principal eigenvalue that summarizes the relationships among cell growth, cell division, and cell size. Thus, the model with quota structure may reverse the outcome of competition for the classical model without quota structure (see [18, Remark 2.2]).

4.3. A size-structured model in an unstirred chemostat

In this subsection, we study a two-species competition with quota structure in an unstirred chemostat, that is, we shall incorporate diffusion terms into our system. The governing equations take the form [18]:

$$\frac{\partial S(t,x)}{\partial t} = d\frac{\partial^2 S}{\partial x^2} - \sum_{i=1}^{2} \alpha_i \beta_i(S) \int_{q_{\min,i}/2}^{q_{\max,i}} g_i(q_i) n_i(t,q_i,x)\, dq_i,$$

(4.3)
$$\frac{\partial n_i(t,q_i,x)}{\partial t} = d\frac{\partial^2 n_i}{\partial x^2} + \beta_i(S)\Bigg\{ -\frac{\partial[g_i(q_i)n_i(t,q_i,x)]}{\partial q_i} - b_i(q_i)n_i(t,q_i,x)$$
$$+ 4b_i(2q_i)n_i(t,2q_i,x) \Bigg\}, \quad i = 1,2,$$

with boundary conditions

(4.4)
$$\frac{\partial S(t,0)}{\partial x} = -S^{(0)}, \quad \frac{\partial S(t,1)}{\partial x} + \gamma S(t,1) = 0,$$
$$\frac{\partial n_i(t,q_i,0)}{\partial x} = 0, \quad \frac{\partial n_i(t,q_i,1)}{\partial x} + \gamma n_i(t,q_i,1) = 0, \quad \frac{q_{\min,i}}{2} < q_i < q_{\max,i}, \quad t > 0,$$
$$n_i(t, \tfrac{q_{\min,i}}{2}, x) = 0, \quad 1 \le i \le 2,$$

and initial conditions

(4.5)
$$S(0,x) = S^0(x), \quad n_i(0,q_i,x) = n_i^0(q_i,x), \quad 1 \le i \le 2.$$

Here $S(t,x)$ denotes the density of the nutrient at time t and position $x \in (0,1)$. $S^{(0)}$ is the input concentration of the nutrient; $n_i(t,q_i,x)$ represents the density of i-th individuals having quota q_i at time t and spatial location x in $(0,1)$, $i = 1,2$. The parameter d is the diffusion coefficient and the constant γ in (4.4) represents the washout rate. The rest of the parameters are same as those we defined in (4.2).

In [18], the authors have demonstrated that outcomes of system (4.3)–(4.5) are similar to competition models for spatially structured habitats that lack population size-structure [34, 35]. Coexistence of two competitors is possible, depending on parameter

values, and both persistence of one population and coexistence of two are related to principal eigenvalue problems similar to those arising in other spatial models [3, 17, 34, 35]. We emphasize that the calculation of competitive outcomes depends on the principal eigenvalue that also summarizes relationships among cell growth, cell division, and cell size [18].

4.4. A size-structured model with light limitation

In [32], the authors consider the dynamics of a single species in a water column, where the species depends only on light for its growth. They further assume that the amount of light absorbed by individuals is proportional to cell size, which varies for populations that reproduce by simple division into two equally-sized daughters, and species move by vertical turbulent diffusion and advection. Let x denote the depth within the water column, where x runs from 0 (top) to L (bottom); $n(t, q, x)$ represent the density of species having quota q at time t and depth x. We assume that phytoplankton transport is governed by turbulent diffusion D and sinking term ν ($\nu > 0$), due to mathematical restrictions. The specific growth rate can be determined by a production term $\beta(I(x, t))$ and cell size, which varies for populations that reproduce by division; $dn(t, q, x)$ represents a loss term of species. We assume that the specific production rate of a species, $\beta(I(x, t))$, is an increasing and possibly saturating function of light intensity $I(x, t)$. There is no production without light, that is, $\beta(0) = 0$. Typically, the Monod function is $\beta(I) := \mu_{\max} I / (a + I)$.

The light intensity at each depth can be described by Lambert-Beer law [37, 39], that is, the amount of light absorbed at depth x is proportional to the light intensity at depth x:

$$(4.6) \qquad \frac{\partial I(x, t)}{\partial x} = -K(x, t) I(x, t).$$

We assume that the constant of proportionality, $K(x, t)$, consists of all components that absorb light, including the water itself and the number of cells with size between $q_{\min}/2$ and $q_{\max}$ at time t and depth x:

$$(4.7) \qquad K(x, t) = k_0 + k_1 \int_{q_{\min}/2}^{q_{\max}} n(t, q, x) \, dq,$$

where k_0 is the background turbidity that summarizes light absorption by all nonphytoplankton components, and k_1 is the specific light attenuation coefficient of phytoplankton species. From (4.6) and (4.7), it follows that the light intensity $I(x, t)$ is given by

$$I = I(x, t) = I_0 \exp\left(-k_0 x - k_1 \int_0^x \int_{q_{\min}/2}^{q_{\max}} n(t, q, s) \, dq \, ds\right),$$

where I_0 is the incident light intensity. Then the model takes the form [32]:

$$
\begin{aligned}
\frac{\partial n(t,q,x)}{\partial t} &= D\frac{\partial^2 n}{\partial x^2} - \nu\frac{\partial n}{\partial x} \\
&\quad + \beta(I(x,t))\left\{ -\frac{\partial[g(q)n(t,q,x)]}{\partial q} - b(q)n(t,q,x) + 4b(2q)n(t,2q,x) \right\} \\
&\quad - dn(t,q,x), \quad t > 0, \ \frac{q_{\min}}{2} < q < q_{\max}, \ 0 < x < L,
\end{aligned}
$$

(4.8)

$$
\nu n(t,q,0) - D\frac{\partial n}{\partial x}(t,q,0) = n(t,q,L) = 0, \quad t > 0, \ \frac{q_{\min}}{2} < q < q_{\max},
$$

$$
n(t,\tfrac{q_{\min}}{2},x) = 0, \quad t > 0, \ 0 < x < L,
$$

$$
n(0,q,x) = n^0(q,x), \quad \frac{q_{\min}}{2} < q < q_{\max}, \ 0 < x < L.
$$

Motivated by [15], the boundary conditions of $n(t,q,x)$ at the top (resp. bottom) of the habitat are the zero-flux conditions (resp. absorbing conditions).

The authors in [32] first study the structure of the semigroup for a population operator with turbulent diffusion and sinking term. Then the property of the asymptotic behavior of this semigroup can reduce the model (4.8) into a nonlocal reaction-diffusion-advection equation similar to those in [8, 9, 31], but their boundary condition at the bottom of the water column are different. Thus, we may not directly apply the previous results in [8, 9, 31] to our system, and hence, the detailed analyses of the reduced system are also given in [32, Section 5]. Basically, the authors in [32] define a critical death rate then they show that the phytoplankton survives if and only if its death rate is less than a critical death rate that depends on the reproductive rate, the characteristics of the water column (e.g., turbulent diffusion rate, sinking, depth), cell growth, cell division, and cell size.

Acknowledgments

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