

Competition for two essential resources with internal storage and periodic input

Sze-Bi Hsu* Feng-Bin Wang[†] Xiao-Qiang Zhao[‡]

Abstract

We study a mathematical model of two species competing in a chemostat for two internally stored essential nutrients, where the nutrients are added to the culture vessel by way of periodic forcing functions. Persistence of a single species happens if the nutrient supply is sufficient to allow it to acquire a threshold of average stored nutrient quota required for growth to balance dilution. More precisely, the population is washed out if a sub-threshold criterion holds, while there is a globally stable positive periodic solution if a super-threshold criterion holds. When there is mutual invasibility of both semitrivial periodic solution of the two-species model, both uniform persistence and the existence of periodic coexistence state are established.

Keywords. The Droop model, internal storage, variable yield, global stability, positive periodic solution, uniform persistence, coexistence

Mathematics Subject Classification (2010) 34C12, 34D20, 34D23

1 Introduction

Competition for resources is a fundamental interaction between species and there has been a lot of experimental and theoretical works of nutrient-limited phyto-

*Department of Mathematics, National Tsing Hua University, Hsinchu 300, Taiwan. Research supported in part by Ministry of Science and Technology, Taiwan.

[†]Department of Natural Science in the Center for General Education, Chang Gung University, Kwei-Shan, Taoyuan 333, Taiwan. Research supported in part by Ministry of Science and Technology, Taiwan.

[‡]Department of Mathematics and Statistics, Memorial University of Newfoundland, St. John's, NL A1C 5S7, Canada. Research supported in part by the NSERC of Canada.

plankton growth and competition. Monod [21] proposed a now classical model of microbial growth on a single limiting resource. In Monod's model, the basic assumption is that the nutrient uptake rate is proportional to the reproductive rate, that is, growth is directly coupled to nutrient uptake. For this classical model with a single growth-limiting resource, there is a simple outcome about competitive dynamics: the species with the lowest break-even concentration for the nutrient resource will win the competition [9, 13]. That is, the species with the lowest break even nutrient concentration will exclude all other competitors, independent of initial conditions.

There are some modifications of the above-mentioned Monod model. The first accounts for the fact that phytoplankton can store nutrients within their cells, and population growth increases monotonically with the nutrient quota stored within individuals, that is, nutrient uptake and growth are decoupled. This led to the formulation of the "variable-yield model" [4]. There is only one outcome when species compete for one nutrient with internal storage: the superior nutrient competitor will win the competition [12, 24, 25]. Outcomes such as coexistence of species, or bistability where outcomes depend on initial conditions do not occur when species compete for one nutrient with or without internal storage. The second modification of the Monod model is to include multiple potentially limiting nutrients such as nitrogen and phosphorus. In phytoplankton ecology, it has been generally accepted that growth stops when either resource falls below a certain level, known as Liebig's law of the minimum [5]. This law reflects that two resources are essential but non-substitutable.

The competition among these microbial species are usually studied in the well-mixed chemostat [24], a simple model habitat. In this environment, the growth-limiting nutrient is supplied at a constant concentration flowing in at a constant dilution rate, with a balancing outflow that removes all constituents. The chemostat (see, e.g., [25]) is a piece of laboratory apparatus, yet it plays an important role in theoretical ecology. It serves as a simple system of natural habitats such as lakes, and is also the basis for many models involving spatial or temporal inhomogeneity. In reality, nutrient levels in natural environments usually vary temporally as a result of diurnal or seasonal variations. Thus, it is more reasonable to incorporate such complication and assume the environment varies periodically. Motivated by the works in [19, 20, 23, 24, 27, 28], we will consider a variable-yield model with two species of phytoplankton competing for two essential nutrients with nutrient concentration inflow varying periodically in time.

A chemostat with fluid volume V is supplied with two essential nutrients at concentration $S^{(0)}(t)$ and $R^{(0)}(t)$, from an external reservoir at the volumetric rate F . A matching out at rate F from the chemostat contains both medium and phytoplankton cells. The dilution rate is the ratio $D = F/V$ whose reciprocal gives the residence time of a cell in the chemostat. We consider a model for two species of phytoplankton with variable internal stores of two essential resources in the chemostat. Competition occurs in the sense that each population consumes nutrients, thereby making it unavailable for its competitor. Let $S(t)$ and $R(t)$ denote the concentrations of the limiting resources 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:

$$\begin{cases} \frac{dS}{dt} = (S^{(0)}(t) - S)D - f_{S1}(S, Q_{S1})u_1 - f_{S2}(S, Q_{S2})u_2, \\ \frac{dR}{dt} = (R^{(0)}(t) - R)D - f_{R1}(R, Q_{R1})u_1 - f_{R2}(R, Q_{R2})u_2, \\ \frac{dQ_{S_i}}{dt} = f_{S_i}(S, Q_{S_i}) - \min\{\mu_{S_i}(Q_{S_i}), \mu_{R_i}(Q_{R_i})\}Q_{S_i}, \quad i = 1, 2, \\ \frac{dQ_{R_i}}{dt} = f_{R_i}(R, Q_{R_i}) - \min\{\mu_{S_i}(Q_{S_i}), \mu_{R_i}(Q_{R_i})\}Q_{R_i}, \quad i = 1, 2, \\ \frac{du_i}{dt} = [\min\{\mu_{S_i}(Q_{S_i}), \mu_{R_i}(Q_{R_i})\} - D]u_i, \quad i = 1, 2, \\ S(0) \geq 0, \quad R(0) \geq 0, \quad u_i(0) \geq 0, \quad i = 1, 2, \\ Q_{S_i}(0) \geq Q_{\min, S_i}, \quad Q_{R_i}(0) \geq Q_{\min, R_i}, \quad i = 1, 2. \end{cases} \quad (1.1)$$

Here $f_{S_i}(S, Q_{S_i})$ ($f_{R_i}(R, Q_{R_i})$) is the per capita uptake rate of species i as a function of resource concentration S (R) and cell quota Q_{S_i} (Q_{R_i}). ‘‘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, $\mu_{S_i}(Q_{S_i})$ and $\mu_{R_i}(Q_{R_i})$. This law reflects that the two resources are complementary, not substitutable. Q_{\min, N_i} denotes threshold cell quota below which no growth of species i occurs, where $N = S, R$. We assume that there exists a period $\tau > 0$ such that $S^{(0)}(t)$ and $R^{(0)}(t)$ satisfy $S^{(0)}(t + \tau) = S^{(0)}(t) \geq 0$, $R^{(0)}(t + \tau) = R^{(0)}(t) \geq 0$.

According to [3, 4, 5], for $N = S, R$ and $i = 1, 2$, the growth rate $\mu_{N_i}(Q_{N_i})$ takes the forms :

$$\begin{aligned} \mu_{N_i}(Q_{N_i}) &= \mu_{\infty, N_i} \left(1 - \frac{Q_{\min, N_i}}{Q_{N_i}} \right), \quad \text{or} \\ \mu_{N_i}(Q_{N_i}) &= \mu_{\infty, N_i} \frac{(Q_{N_i} - Q_{\min, N_i})_+}{A_{N_i} + (Q_{N_i} - Q_{\min, N_i})_+}, \end{aligned}$$

where $Q_{\min, Ni}$ is the minimum cell quota necessary to allow cell division and $(Q_{Ni} - Q_{\min, Ni})_+$ is the positive part of $(Q_{Ni} - Q_{\min, Ni})$ and $\mu_{\infty, Ni}$ is the maximal growth rate at infinite quotas (i.e., as $Q_{Ni} \rightarrow \infty$) of the species i . From these two examples, we see that the specific growth rate of the species is an increasing and saturating function of nutrient quota.

According to [1, 2, 8], for $N = S, R$, and $i = 1, 2$, the uptake rate $f_{Ni}(N, Q_{Ni})$ takes the form:

$$f_{Ni}(N, Q_{Ni}) = \rho_{Ni}(Q_{Ni}) \frac{N}{K_{Ni} + N},$$

where $\rho_{Ni}(Q_{Ni})$, $Q_{\min, Ni} \leq Q_{Ni} \leq Q_{\max, Ni}$, is defined as follows:

$$\begin{aligned} \rho_{Ni}(Q_{Ni}) &= \rho_{\max, Ni}^{\text{high}} - (\rho_{\max, Ni}^{\text{high}} - \rho_{\max, Ni}^{\text{low}}) \frac{Q_{Ni} - Q_{\min, Ni}}{Q_{\max, Ni} - Q_{\min, Ni}}, \text{ or} \\ \rho_{Ni}(Q_{Ni}) &= \rho_{\max, Ni}. \end{aligned}$$

Thus, the nutrient uptake of the species is assumed to be a non-increasing function of internal nutrient stores and an increasing function of the external nutrient concentration.

In view of the above classical examples, we assume that for each $i = 1, 2$ and $N = S, R$, the functions $\mu_{Ni}(Q_{Ni})$ and $f_{Ni}(N, Q_{Ni})$ satisfy the following assumptions:

- (H1) $\mu_{Ni}(Q_{Ni})$ is continuously differentiable for $Q_{Ni} \geq Q_{\min, Ni}$, $\mu_{Ni}(Q_{\min, Ni}) = 0$, $\mu_{Ni}(Q_{Ni}) \geq 0$ and $\mu'_{Ni}(Q_{Ni}) > 0$ for $Q_{Ni} \geq Q_{\min, Ni}$.
- (H2) $f_{Ni}(N, Q_{Ni})$ is continuously differentiable for $N > 0$ and $Q_{Ni} \geq Q_{\min, Ni}$, $f_{Ni}(0, Q_{Ni}) = 0$, $\frac{\partial f_{Ni}(N, Q_{Ni})}{\partial N} > 0$ and $\frac{\partial f_{Ni}(N, Q_{Ni})}{\partial Q_{Ni}} \leq 0$.

In [20] (see also [19]), the authors considered the temporally homogeneous system of (1.1), that is, they assumed $S^{(0)}(t) \equiv S^{(0)}$ and $R^{(0)}(t) \equiv R^{(0)}$ in (1.1). In order to ensure that the temporally constant system of (1.1) is differentiable at the equilibrium, it was assumed that

$$\mu_{Si}(Q_{Si}) \neq \mu_{Ri}(Q_{Ri}) \text{ at equilibrium, } \forall i = 1, 2. \quad (1.2)$$

With the condition (1.2), a simple linearization argument become possible. For the single population model of the temporally homogeneous system of (1.1), it

is proved that if a nontrivial equilibrium exists, then it is unique and globally stable [19, 20]. For the temporally homogeneous system of (1.1), it exhibits outcomes of competitive exclusion, bistability, and globally stable coexistence [20], depending on tradeoffs between abilities to compete for the nutrient and growth requirements under the additional assumption (1.2). However, the techniques used for the autonomous system [19, 20] may not apply to our non-autonomous model (1.1). This is because it does not make sense to impose a similar condition to assumption (1.2) for our periodic system (1.1). Thus, we cannot do local stability analysis for our periodic system by the method of linearization. To overcome this difficulty, we use the following strategy. We first determine the extinction periodic solution $(S^*(t), R^*(t), Q_S^*(t), Q_R^*(t), 0)$ of the single species growth model (2.1), where $(S^*(t), R^*(t))$ represents the available nutrient in a species-free chemostat and $(Q_S^*(t), Q_R^*(t))$ describes cell quota without the presence of species. The proofs of the existence and uniqueness of $(Q_S^*(t), Q_R^*(t))$ are given in Lemma 2.1, whose mathematical arguments are nontrivial and quite different from those in [20, Lemma 9]. By using a mass conservation constraint, we can reduce system (2.1) to the limiting system (2.11), which is essentially equivalent to the monotone system (2.12). To study the stability of $(Q_S^*(t), Q_R^*(t), 0)$ for system (2.11), we construct a suitable upper solution $(\bar{U}_S(t), \bar{U}_R(t), \bar{u}(t))$ for system (2.12), and employ the comparison principle to show $(Q_S^*(t), Q_R^*(t), 0)$ is actually globally asymptotically stable for system (2.11) when a the sub-threshold criterion holds (see Lemma 2.3). In Lemma 2.4, when the super-threshold criterion holds, we first prove that system (2.11) is uniformly persistent, and hence, system (2.11) admits at least one positive periodic solution by appealing to the theory of uniform persistence for periodic semiflows (see, e.g., [30]). Then the uniqueness and global attractivity of positive periodic solution can be obtained since we can further prove that the solution semiflow generated by system (2.12) is monotone and strongly subhomogeneous (see Lemma 2.2). Finally, we use the theory of chain transitive sets (see [14] or [30, Section 1.2]) to establish the global dynamics for system (2.1) (see Theorem 2.1). Note that returning to the autonomous system studied in [19, 20], our methods and results are still true for the single population model without technical assumption (1.2).

The remaining part of the paper is organized as follows. Section 2 is devoted to the establishment of a threshold type result on the global dynamics of the single species growth model by appealing to the theories of monotone dynamical systems and chain transitive sets. Under appropriate conditions, it is shown in section 3

that two competing species are uniformly persistent and the model system (1.1) admits at least one positive periodic solution. A brief discussion section completes the paper.

2 Single species growth

In this section, we first consider the single species growth model. Mathematically, it simply means that we set $u_1 = 0$ or $u_2 = 0$ in model (1.1). In order to simplify notation, we dropped all subscripts in the remaining equations and consider

$$\begin{cases} \frac{dS}{dt} = (S^{(0)}(t) - S)D - f_S(S, Q_S)u, \\ \frac{dR}{dt} = (R^{(0)}(t) - R)D - f_R(R, Q_R)u, \\ \frac{dQ_S}{dt} = f_S(S, Q_S) - \min\{\mu_S(Q_S), \mu_R(Q_R)\}Q_S, \\ \frac{dQ_R}{dt} = f_R(R, Q_R) - \min\{\mu_S(Q_S), \mu_R(Q_R)\}Q_R, \\ \frac{du}{dt} = [\min\{\mu_S(Q_S), \mu_R(Q_R)\} - D]u, \end{cases} \quad (2.1)$$

with initial values in the domain $\mathbf{X} := \{(S, R, Q_S, Q_R, u) \in \mathbb{R}_+^5 : Q_S \geq Q_{\min, S}, Q_R \geq Q_{\min, R}\}$.

It is easy to see that \mathbf{X} is positively invariant for system (2.1). Putting $u = 0$ in the first two equations of (2.1) results in

$$\frac{dS}{dt} = (S^{(0)}(t) - S)D, \quad (2.2)$$

and

$$\frac{dR}{dt} = (R^{(0)}(t) - R)D. \quad (2.3)$$

The linear equations (2.2) and (2.3) have globally attractive positive τ -periodic solutions $S = S^*(t) = S^*(t + \tau)$ and $R = R^*(t) = R^*(t + \tau)$, respectively, which describe the available nutrient in a phytoplankton-free chemostat.

Now putting $S = S^*(t)$ and $R = R^*(t)$ in system (2.1), we obtain

$$\begin{cases} \frac{dQ_S}{dt} = f_S(S^*(t), Q_S) - \min\{\mu_S(Q_S), \mu_R(Q_R)\}Q_S, \\ \frac{dQ_R}{dt} = f_R(R^*(t), Q_R) - \min\{\mu_S(Q_S), \mu_R(Q_R)\}Q_R, \end{cases} \quad (2.4)$$

with initial values in the domain $\Gamma := \{(Q_S, Q_R) \in \mathbb{R}_+^2 : Q_N \geq Q_{\min, N}, N = S, R\}$. It is easy to see that Γ is positively invariant for system (2.4).

Lemma 2.1. *System (2.4) has a unique τ -periodic solution $(Q_S^*(t), Q_R^*(t))$ to which all solutions are attracted.*

Proof. We first show that every solution of system (2.4) exists for all $t \geq 0$. Let $[0, \sigma)$ be the maximal interval of existence. We need to prove that $\sigma = +\infty$. By the continuation theorem, it suffices to prove that the solution is bounded on $[0, \sigma)$. Motivated by the proofs in [19, Proposition 3], we consider the dynamics of the variable $V(t) = \frac{1}{2}[(Q_S(t))^2 + (Q_R(t))^2]$. By the monotonicity of f_N , the inequality $x \leq \frac{1}{2}(1 + x^2)$ and the fact that $Q_N \geq Q_{\min, N}$, for $N = S, R$, it follows that $V(t)$ satisfies

$$\begin{aligned} \frac{dV(t)}{dt} &= \frac{dQ_S(t)}{dt}Q_S + \frac{dQ_R(t)}{dt}Q_R \\ &\leq f_S(S^*(t), Q_S)Q_S + f_R(R^*(t), Q_R)Q_R \\ &\leq \frac{1}{2}f_S(S_{\max}^*, Q_{\min, S})[1 + Q_S^2] + \frac{1}{2}f_R(R_{\max}^*, Q_{\min, R})[1 + Q_R^2] \quad (2.5) \\ &\leq \frac{1}{2}f_S(S_{\max}^*, Q_{\min, S}) + \frac{1}{2}f_R(R_{\max}^*, Q_{\min, R}) \\ &\quad + \max\{f_S(S_{\max}^*, Q_{\min, S}), f_R(R_{\max}^*, Q_{\min, R})\}V(t), \end{aligned}$$

where $S_{\max}^* := \max_{t \in [0, \tau]} S^*(t)$ and $R_{\max}^* := \max_{t \in [0, \tau]} R^*(t)$. The resulting inequality implies that $V(t)$ are bounded in finite time intervals, and so are $Q_S(t)$ and $Q_R(t)$.

Next, we show that solutions of system (2.4) are ultimately bounded. By the first equation of (2.4), it follows that $\frac{dQ_S}{dt} \geq f_S(S_{\min}^*, Q_S) - \mu_S(Q_S)Q_S$, where $S_{\min}^* := \min_{t \in [0, \tau]} S^*(t)$. The resulting inequality and the global existence of solutions of (2.4) imply that $\liminf_{t \rightarrow \infty} Q_S(t) \geq Q_S^0$, where Q_S^0 is the unique root of $f_S(S_{\min}^*, Q_S) - \mu_S(Q_S)Q_S = 0$, and hence, $Q_S^0 > Q_{\min, S}$. Similarly, it follows from the second equation of (2.4) that there exists a unique constant $Q_R^0 > Q_{\min, R}$ such that $\liminf_{t \rightarrow \infty} Q_R(t) \geq Q_R^0 > Q_{\min, R}$. By the above discussions and (H1), it follows that there exists $\delta_0 > 0$ and $T > 0$ such that $\min\{\mu_S(Q_S(t)), \mu_R(Q_R(t))\} \geq \delta_0$, $\forall t \geq T$. In view of (2.4), we have

$$\begin{cases} \frac{dQ_S}{dt} \leq f_S(S_{\max}^*, Q_S) - \delta_0 Q_S, \quad \forall t \geq T, \\ \frac{dQ_R}{dt} \leq f_R(R_{\max}^*, Q_R) - \delta_0 Q_R, \quad \forall t \geq T, \end{cases}$$

where S_{\max}^* and R_{\max}^* were defined in the previous discussion. This implies that solutions of system (2.4) are ultimately bounded.

Note that system (2.4) is a planar, competitive, periodic system of differential equations. A well-known result for such a system is that every bounded solution is asymptotic to a periodic solution (see, e.g., [25, Section 7.4]). Let $(Q_S^*(t), Q_R^*(t))$ be a periodic solution of system (2.4). Then (H1) and (H2) imply that $Q_S^*(t) \geq Q_{\min,S}$ and $Q_R^* \geq Q_{\min,R}$ for all $t \geq 0$, and hence, $(Q_S^*(t), Q_R^*(t))$ is a positive periodic solution of system (2.4). If we can prove that the positive periodic solution $(Q_S^*(t), Q_R^*(t))$ of system (2.4) is unique, then the proof is done. Suppose, by contradiction, that $(Q_S^{1*}(t), Q_R^{1*}(t))$ and $(Q_S^{2*}(t), Q_R^{2*}(t))$ are two different positive τ -periodic solutions of system (2.4). Then we have $(Q_S^{1*}(0), Q_R^{1*}(0)) \neq (Q_S^{2*}(0), Q_R^{2*}(0))$. Note that any two points in \mathbb{R}^2 are order related either in \leq or \leq_K . Without loss of generality, we can assume that either $(Q_S^{2*}(0), Q_R^{2*}(0)) < (Q_S^{1*}(0), Q_R^{1*}(0))$, or $(Q_S^{2*}(0), Q_R^{2*}(0)) <_K (Q_S^{1*}(0), Q_R^{1*}(0))$.

In the case where $(Q_S^{2*}(0), Q_R^{2*}(0)) < (Q_S^{1*}(0), Q_R^{1*}(0))$, we have

$$(Q_S^{2*}(\tau), Q_R^{2*}(\tau)) = (Q_S^{2*}(0), Q_R^{2*}(0)) < (Q_S^{1*}(0), Q_R^{1*}(0)) = (Q_S^{1*}(\tau), Q_R^{1*}(\tau)).$$

By the backward comparison theorem (see, e.g., [15, Lemma 2.2] and [25, Lemma 7.4.1]), it follows that $(Q_S^{2*}(t), Q_R^{2*}(t)) \leq (Q_S^{1*}(t), Q_R^{1*}(t))$ for all $t \in [0, \tau]$. Without loss of generality, we assume that $Q_S^{2*}(0) < Q_S^{1*}(0)$ and define $g(t) := Q_S^{1*}(t) - Q_S^{2*}(t)$. Otherwise, we have $Q_R^{2*}(0) < Q_R^{1*}(0)$ and then choose $g(t) := Q_R^{1*}(t) - Q_R^{2*}(t)$. Then it follows from the first equation of (2.4) that

$$\begin{aligned} g'(t) &= [f_S(S^*(t), Q_S^{1*}(t)) - \min\{\mu_S(Q_S^{1*}(t)), \mu_R(Q_R^{1*}(t))\}Q_S^{1*}(t)] \\ &\quad - [f_S(S^*(t), Q_S^{2*}(t)) - \min\{\mu_S(Q_S^{2*}(t)), \mu_R(Q_R^{2*}(t))\}Q_S^{2*}(t)]. \end{aligned}$$

Using (H1) and (H2), we see that $g(t)$ satisfies $g'(t) \leq 0$, for all $t \in [0, \tau]$, and $g'(t) < 0$ when $t \in [0, \tau]$ is sufficiently close to 0 or τ . This implies that $g(\tau) < g(0)$, which contradicts the fact that $g(t)$ is a τ -periodic function.

In the case where $(Q_S^{2*}(0), Q_R^{2*}(0)) <_K (Q_S^{1*}(0), Q_R^{1*}(0))$, by the forward comparison theorem (see, e.g., [25, Theorem B.4]), we have

$$(Q_S^{2*}(t), Q_R^{2*}(t)) \leq_K (Q_S^{1*}(t), Q_R^{1*}(t)), \quad \forall t \in [0, \tau].$$

Dividing the first (second) equation of (2.4) by $Q_S(t)$ ($Q_R(t)$) and integrating the resulting equation in $t \in [0, \tau]$, we have

$$0 = \int_0^\tau \frac{1}{Q_S^{1*}(t)} d(Q_S^{1*}(t)) = \int_0^\tau \frac{f_S(S^*(t), Q_S^{1*}(t))}{Q_S^{1*}(t)} dt - \int_0^\tau \min\{\mu_S(Q_S^{1*}(t)), \mu_R(Q_R^{1*}(t))\} dt,$$

and

$$0 = \int_0^\tau \frac{1}{Q_R^{1*}(t)} d(Q_R^{1*}(t)) = \int_0^\tau \frac{f_R(R^*(t), Q_R^{1*}(t))}{Q_R^{1*}(t)} dt - \int_0^\tau \min\{\mu_S(Q_S^{1*}(t)), \mu_R(Q_R^{1*}(t))\} dt.$$

Therefore,

$$\int_0^\tau \frac{f_S(S^*(t), Q_S^{1*}(t))}{Q_S^{1*}(t)} dt = \int_0^\tau \frac{f_R(R^*(t), Q_R^{1*}(t))}{Q_R^{1*}(t)} dt. \quad (2.6)$$

Similarly, we can prove that

$$\int_0^\tau \frac{f_S(S^*(t), Q_S^{2*}(t))}{Q_S^{2*}(t)} dt = \int_0^\tau \frac{f_R(R^*(t), Q_R^{2*}(t))}{Q_R^{2*}(t)} dt. \quad (2.7)$$

By virtue of (H2), we have $\frac{\partial f_N(N, Q_N)}{\partial Q_N} \leq 0$, for each $N = S, R$. This and the fact $(Q_S^{2*}(0), Q_R^{2*}(0)) <_K (Q_S^{1*}(0), Q_R^{1*}(0))$ imply that

$$\int_0^\tau \frac{f_S(S^*(t), Q_S^{1*}(t))}{Q_S^{1*}(t)} dt \leq \int_0^\tau \frac{f_S(S^*(t), Q_S^{2*}(t))}{Q_S^{2*}(t)} dt, \quad (2.8)$$

and

$$\int_0^\tau \frac{f_R(R^*(t), Q_R^{1*}(t))}{Q_R^{1*}(t)} dt \geq \int_0^\tau \frac{f_R(R^*(t), Q_R^{2*}(t))}{Q_R^{2*}(t)} dt. \quad (2.9)$$

Note that when $t \in [0, \tau]$ is sufficiently close to zero or τ , we have $(Q_S^{2*}(t), Q_R^{2*}(t)) <_K (Q_S^{1*}(t), Q_R^{1*}(t))$, and hence, at least one of two inequalities in (2.8) and (2.9) is strict. This, together with (2.6) and (2.7), leads to a contradiction. \square

Now we show that every solution $(S(t), R(t), Q_S(t), Q_R(t), u(t))$ of system (2.1) exists for all $t \geq 0$. By the continuation theorem, it suffices to prove that the solution of system (2.1) is bounded on finite time intervals. To this end, we let $T_S(t) = S(t) + Q_S(t)u(t)$ and $T_R(t) = R(t) + Q_R(t)u(t)$. Then $T_S(t)$ and $T_R(t)$ satisfy the linear systems (2.2) and (2.3), respectively. Hence, $T_S(t)$ and $T_R(t)$ are bounded on finite time intervals, and so are $S(t)$, $R(t)$, $Q_S(t)u(t)$ and $Q_R(t)u(t)$. Since $Q_S(t) \geq Q_{\min, S}$ and $Q_R(t) \geq Q_{\min, R}$, it follows that $u(t)$ is bounded on finite time intervals. It remains to show that $Q_S(t)$ and $Q_R(t)$ are bounded on finite time intervals. Let $\tilde{V}(t) = \frac{1}{2}[(Q_S(t))^2 + (Q_R(t))^2]$. Since $S(t)$ and $R(t)$ in system (2.1) are bounded on finite time intervals, we can use the same arguments as in (2.5) to prove that $\tilde{V}(t)$ is bounded in finite time intervals, and so are $Q_S(t)$ and $Q_R(t)$. Thus, every solution of system (2.1) exists globally.

Let $Z_S = S^*(t) - S - Q_S u$ and $Z_R = R^*(t) - R - Q_R u$. Then (2.1) becomes

$$\begin{cases} \frac{dQ_S}{dt} = f_S(S^*(t) - Q_S u - Z_S, Q_S) - \min\{\mu_S(Q_S), \mu_R(Q_R)\}Q_S, \\ \frac{dQ_R}{dt} = f_R(R^*(t) - Q_R u - Z_R, Q_R) - \min\{\mu_S(Q_S), \mu_R(Q_R)\}Q_R, \\ \frac{du}{dt} = [\min\{\mu_S(Q_S), \mu_R(Q_R)\} - D]u, \\ \frac{dZ_S}{dt} = -DZ_S, \\ \frac{dZ_R}{dt} = -DZ_R, \end{cases} \quad (2.10)$$

with initial values in the domain

$$\mathbb{X} := \{(Q_S, Q_R, u, Z_S, Z_R) \in \mathbb{R}_+^5 : Q_N \geq Q_{\min, N}, Q_N u + Z_N \leq N^*(0), N = S, R\}.$$

Biologically, $S(t) = S^*(t) - Q_S u - Z_S$ and $R(t) = R^*(t) - Q_R u - Z_R$ should be nonnegative. Indeed, if there exists a t_0 such that $S^*(t_0) - Q_S(t_0)u(t_0) - Z_S(t_0) = 0$ then

$$\begin{aligned} S'(t_0) &= (S^*(t) - Q_S u - Z_S)'(t_0) \\ &= D(S^{(0)} - S^*(t) + Q_S u + Z_S)(t_0) = DS^{(0)}(t_0) \geq 0, \end{aligned}$$

which implies that $S(t) \geq 0$ for all $t \geq 0$. Similarly, we can show that $R(t) \geq 0$ for all $t \geq 0$.

From the equations for u , Q_S and Q_R , together with (H1) and (H2), we see that $u(t) \geq 0$, $Q_S(t) \geq Q_{\min, S}$ and $Q_R(t) \geq Q_{\min, R}$ for all $t \geq 0$. Obviously, $Z_S(t), Z_R(t) \rightarrow 0$ as $t \rightarrow \infty$. Therefore, solutions of (2.1) are ultimately bounded on \mathbb{X} . By putting $Z_S = 0$ and $Z_R = 0$ in (2.10), we obtain the following periodic limiting system:

$$\begin{cases} \frac{dQ_S}{dt} = f_S(S^*(t) - Q_S u, Q_S) - \min\{\mu_S(Q_S), \mu_R(Q_R)\}Q_S, \\ \frac{dQ_R}{dt} = f_R(R^*(t) - Q_R u, Q_R) - \min\{\mu_S(Q_S), \mu_R(Q_R)\}Q_R, \\ \frac{du}{dt} = [\min\{\mu_S(Q_S), \mu_R(Q_R)\} - D]u, \end{cases} \quad (2.11)$$

with initial values in the domain

$$\mathbb{Y} := \{(Q_S, Q_R, u) \in \mathbb{R}_+^3 : Q_N \geq Q_{\min, N}, Q_N u \leq N^*(0), N = S, R\}.$$

Let $P : \mathbb{Y} \rightarrow \mathbb{Y}$ be the Poincaré map associated with system (2.11), that is,

$$P(Q_S(0), Q_R(0), u(0)) = (Q_S(\tau), Q_R(\tau), u(\tau)), \quad \forall (Q_S(0), Q_R(0), u(0)) \in \mathbb{Y},$$

where $(Q_S(t), Q_R(t), u(t))$ is the unique solution of system (2.11). It is easy to see that

$$P^n(Q_S(0), Q_R(0), u(0)) = (Q_S(n\tau), Q_R(n\tau), u(n\tau)), \quad \forall n \geq 0.$$

By Lemma 2.1, $(Q_S^*(t), Q_R^*(t), 0)$ is the trivial τ -periodic solution of (2.11). We may not study the local stability of $(Q_S^*(t), Q_R^*(t), 0)$ via the linearization method since the reaction functions in (2.11) are not differentiable. However, we are able to obtain the global stability of $(Q_S^*(t), Q_R^*(t), 0)$ by appealing to theories of monotone dynamics and chain transitive sets (see, e.g., [22, 30]). In the following, we first convert (2.11) to a cooperative system. Let $U_S = Q_S u$ and $U_R = Q_R u$. Then (2.11) becomes

$$\begin{cases} \frac{dU_S}{dt} = -DU_S + f_S(S^*(t) - U_S, \frac{U_S}{u})u, \\ \frac{dU_R}{dt} = -DU_R + f_R(R^*(t) - U_R, \frac{U_R}{u})u, \\ \frac{du}{dt} = [\min\{\mu_S(\frac{U_S}{u}), \mu_R(\frac{U_R}{u})\} - D]u, \end{cases} \quad (2.12)$$

with initial values in the domain

$$\mathbf{Y} := \{(U_S, U_R, u) \in \mathbb{R}_+^3 : u > 0, Q_{\min, N} u \leq U_N \leq N^*(0) \quad \forall N = S, R\}.$$

Lemma 2.2. *Let $\Phi_t(u_0)$ be the solution of system (2.12) with initial data $u_0 \in \mathbf{Y}$. Then the following statements are valid:*

- (i) *For each $t \geq 0$, the map Φ_t is monotone in the sense that $\Phi_t(u) \geq \Phi_t(v)$ whenever $u \geq v$ in \mathbf{Y} .*
- (ii) *For each $t > 0$, the map Φ_t is strongly subhomogeneous in the sense that $\Phi_t(\theta u_0) \gg \theta \Phi_t(u_0)$ for all $u_0 \gg 0$ in \mathbf{Y} and $\theta \in (0, 1)$.*

Proof. For convenience, we let $(u_1, u_2, u_3) := (U_S, U_R, u)$ and rewrite (2.12) as follows:

$$\begin{cases} \frac{du_1}{dt} = -Du_1 + f_S(S^*(t) - u_1, \frac{u_1}{u_3})u_3 := H_1(t, u_1, u_2, u_3), \\ \frac{du_2}{dt} = -Du_2 + f_R(R^*(t) - u_2, \frac{u_2}{u_3})u_3 := H_2(t, u_1, u_2, u_3), \\ \frac{du_3}{dt} = [\min\{\mu_S(\frac{u_1}{u_3}), \mu_R(\frac{u_2}{u_3})\} - D]u_3 := H_3(t, u_1, u_2, u_3). \end{cases} \quad (2.13)$$

For any $(u_1, u_2, u_3) \geq (v_1, v_2, v_3)$ with $u_i = v_i$, it is easy to see that $H_i(t, u_1, u_2, u_3) \geq H_i(t, v_1, v_2, v_3)$, that is, system (2.13) satisfies the Kamke condition. By [22, Proposition 3.1.1] or [26, Theorem 2], it follows that the map Φ_t is monotone. This proves statement (i).

Given $u_0 \gg 0$ in \mathbf{Y} and $\theta \in (0, 1)$, we set $V(t) := (V_1(t), V_2(t), V_3(t)) = \Phi_t(\theta u_0)$, and $Y(t) := (Y_1(t), Y_2(t), Y_3(t)) = \theta \Phi_t(u_0)$. Clearly, we have

$$\begin{cases} \frac{dV_1}{dt} = -DV_1 + f_S(S^*(t) - V_1, \frac{V_1}{V_3})V_3, \\ \frac{dV_2}{dt} = -DV_2 + f_R(R^*(t) - V_2, \frac{V_2}{V_3})V_3, \\ \frac{dV_3}{dt} = [\min\{\mu_S(\frac{V_1}{V_3}), \mu_R(\frac{V_2}{V_3})\} - D]V_3, \\ V(0) = \theta u_0. \end{cases} \quad (2.14)$$

By assumption (H2), we further obtain

$$\begin{cases} \frac{dY_1}{dt} < -DY_1 + f_S(S^*(t) - Y_1, \frac{Y_1}{Y_3})Y_3, \\ \frac{dY_2}{dt} < -DY_2 + f_R(R^*(t) - Y_2, \frac{Y_2}{Y_3})Y_3, \\ \frac{dY_3}{dt} = [\min\{\mu_S(\frac{Y_1}{Y_3}), \mu_R(\frac{Y_2}{Y_3})\} - D]Y_3, \\ Y(0) = \theta u_0. \end{cases} \quad (2.15)$$

It follows from (2.14), (2.15), and the comparison theorem that

$$V_i(t) \geq Y_i(t), \quad \forall t \geq 0, i = 1, 2, 3. \quad (2.16)$$

Let $s > 0$ be given. We first show that $V_1(s) > Y_1(s)$ and $V_2(s) > Y_2(s)$. Assume, by contradiction, that $V_1(s) = Y_1(s)$. It follows from (2.16) that $V_1'(s) = Y_1'(s)$, and hence,

$$\begin{aligned} & -DV_1(s) + f_S\left(S^*(s) - V_1(s), \frac{V_1(s)}{V_3(s)}\right) V_3(s) \\ & < -DY_1(s) + f_S\left(S^*(s) - Y_1(s), \frac{Y_1(s)}{Y_3(s)}\right) Y_3(s). \end{aligned}$$

This, together with $V_1(s) = Y_1(s)$, gives rise to

$$f_S\left(S^*(s) - V_1(s), \frac{V_1(s)}{V_3(s)}\right) V_3(s) < f_S\left(S^*(s) - V_1(s), \frac{V_1(s)}{Y_3(s)}\right) Y_3(s). \quad (2.17)$$

In view of (H2), we have

$$f_S\left(S^*(t) - u_1, \frac{u_1}{u_3}\right) > 0, \quad \frac{\partial}{\partial u_3} \left[f_S\left(S^*(t) - u_1, \frac{u_1}{u_3}\right) u_3 \right] > 0$$

for all $u_3 > 0$, $Q_{\min, S} u_3 \leq u_1 < S^*(t)$. It then follows from (2.17) that $V_3(s) < Y_3(s)$, which contradicts (2.16). Thus, we have $V_1(s) > Y_1(s)$. Similarly, we can prove that $V_2(s) > Y_2(s)$.

Next we show that $V_3(s) > Y_3(s)$. Assume that $V_3(s) = Y_3(s)$. It follows from (2.16) that $V_3'(s) = Y_3'(s)$, which implies that

$$\min \left\{ \mu_S \left(\frac{V_1(s)}{V_3(s)} \right), \mu_R \left(\frac{V_2(s)}{V_3(s)} \right) \right\} = \min \left\{ \mu_S \left(\frac{Y_1(s)}{Y_3(s)} \right), \mu_R \left(\frac{Y_2(s)}{Y_3(s)} \right) \right\}. \quad (2.18)$$

In the case where $\mu_S \left(\frac{V_1(s)}{V_3(s)} \right) \leq \mu_R \left(\frac{V_2(s)}{V_3(s)} \right)$, we see from (2.18) that

$$\mu_S \left(\frac{V_1(s)}{V_3(s)} \right) \leq \mu_S \left(\frac{Y_1(s)}{Y_3(s)} \right) = \mu_S \left(\frac{Y_1(s)}{V_3(s)} \right).$$

It then follows from (H1) that $V_1(s) \leq Y_1(s)$, which contradicts the fact that $V_1(s) > Y_1(s)$. In the case where $\mu_S \left(\frac{V_1(s)}{V_3(s)} \right) > \mu_R \left(\frac{V_2(s)}{V_3(s)} \right)$, we see from (2.18) that

$$\mu_R \left(\frac{V_2(s)}{V_3(s)} \right) \leq \mu_R \left(\frac{Y_2(s)}{Y_3(s)} \right) = \mu_R \left(\frac{Y_2(s)}{V_3(s)} \right)$$

Using (H1) again, we obtain $V_2(s) \leq Y_2(s)$, which contradicts the fact that $V_2(s) > Y_2(s)$. Consequently, we have $\Phi_s(\theta u_0) \gg \theta \Phi_s(u_0)$. This proves statement (ii). \square

Let $\mathbf{P} : \mathbf{Y} \rightarrow \mathbf{Y}$ be the Poincaré map associated with system (2.12), that is,

$$\mathbf{P}(U_S(0), U_R(0), u(0)) = (U_S(\tau), U_R(\tau), u(\tau)), \quad \forall \tilde{x} := (U_S(0), U_R(0), u(0)) \in \mathbf{Y},$$

where $(U_S(t), U_R(t), u(t))$ is the unique solution of system (2.12).

For convenience, we define the time-average of a τ -periodic function $f(t)$ as $\langle f(t) \rangle := \frac{1}{\tau} \int_0^\tau f(t) dt$. The following result is concerned with the extinction of species for system (2.11).

Lemma 2.3. *Let $(Q_S(t), Q_R(t), u(t))$ be the unique solution of system (2.11) with the initial data in \mathbb{Y} . If $\langle \min\{\mu_S(Q_S^*(t)), \mu_R(Q_R^*(t))\} - D \rangle < 0$, then*

$$\lim_{t \rightarrow \infty} |(Q_S(t), Q_R(t), u(t)) - (Q_S^*(t), Q_R^*(t), 0)| = 0,$$

where $(Q_S^*(t), Q_R^*(t))$ is the unique periodic solution of system (2.4).

Proof. We first show that every solution of system (2.11) in \mathbb{Y} satisfies $\lim_{t \rightarrow \infty} u(t) = 0$. Note that if $u(0) = 0$, then $u(t) \equiv 0$. Thus, we assume that $u(0) > 0$. Since systems (2.11) and (2.12) are essentially equivalent, it suffices to show that every solution of system (2.12) in \mathbf{Y} satisfies $\lim_{t \rightarrow \infty} u(t) = 0$. Let us extend $f_N(N, Q_N)$, $N = S, R$, to the domain $\mathbb{R} \times [Q_{\min, N}, \infty)$ by defining

$$F_N(N, Q_N) = \begin{cases} f_N(N, Q_N) & \text{for } N \geq 0, Q_N \geq Q_{\min, N}, \\ 0 & \text{for } N < 0, Q_N \geq Q_{\min, N}. \end{cases}$$

Then we consider the extended system corresponding to system (2.12):

$$\begin{cases} \frac{dU_S}{dt} = -DU_S + F_S(S^*(t) - U_S, \frac{U_S}{u})u, \\ \frac{dU_R}{dt} = -DU_R + F_R(R^*(t) - U_R, \frac{U_R}{u})u, \\ \frac{du}{dt} = [\min\{\mu_S(\frac{U_S}{u}), \mu_R(\frac{U_R}{u})\} - D]u. \end{cases} \quad (2.19)$$

Note that if $(U_S(0), U_R(0), u(0)) \in \mathbf{Y}$ and $(U_S(t), U_R(t), u(t))$ is a solution of system (2.12), then $(U_S(t), U_R(t), u(t))$ satisfies

$$u(t) > 0, \quad Q_{\min, N}u(t) \leq U_N(t) \leq N^*(t), \quad \forall N = S, R, \quad t \geq 0. \quad (2.20)$$

This implies that $(U_S(t), U_R(t), u(t))$ is also a solution of system (2.19).

For any given $\delta > 0$, let $\bar{u}(t) = \bar{u}(t, \delta)$ be the unique solution of

$$\begin{cases} \frac{d\bar{u}}{dt} = [\min\{\mu_S(Q_S^*(t)), \mu_R(Q_S^*(t))\} - D]\bar{u}, \\ \bar{u}(0) = \delta, \end{cases} \quad (2.21)$$

and set

$$\bar{U}_S(t) = Q_S^*(t)\bar{u}(t) \quad \text{and} \quad \bar{U}_R(t) = Q_R^*(t)\bar{u}(t). \quad (2.22)$$

It is easy to see that

$$\frac{\bar{U}_N(t)}{\bar{u}(t)} = Q_N^*(t) \geq Q_{\min, N}, \quad \text{for all } N = S, R \text{ and } t \geq 0.$$

However, we cannot guarantee that $S^*(t) - \bar{U}_S(t) \geq 0$ and $R^*(t) - \bar{U}_R(t) \geq 0$ for all $t \geq 0$. This is the reason why we consider the extended system (2.19) instead of (2.12).

Based on (2.4), (2.21) and (2.22), we are ready to show the following inequalities:

$$\begin{cases} \frac{d\bar{U}_S}{dt} \geq -D\bar{U}_S + F_S(S^*(t) - \bar{U}_S, \frac{\bar{U}_S}{\bar{u}})\bar{u}, \\ \frac{d\bar{U}_R}{dt} \geq -D\bar{U}_R + F_R(R^*(t) - \bar{U}_R, \frac{\bar{U}_R}{\bar{u}})\bar{u}, \\ \frac{d\bar{u}}{dt} = [\min\{\mu_S(\frac{\bar{U}_S}{\bar{u}}), \mu_R(\frac{\bar{U}_R}{\bar{u}})\} - D]\bar{u}. \end{cases} \quad (2.23)$$

The third equation in (2.23) is obvious. Since the establishments of the first two inequalities in (2.23) are similar, we only verify the first one. By direct computations, it follows that

$$\begin{aligned} \frac{d\bar{U}_S}{dt} &= \frac{dQ_S^*(t)}{dt}\bar{u}(t) + \frac{d\bar{u}(t)}{dt}Q_S^*(t) \\ &= [f_S(S^*(t), Q_S^*(t)) - \min\{\mu_S(Q_S^*(t)), \mu_R(Q_R^*(t))\}Q_S^*(t)]\bar{u}(t) \\ &\quad + [\min\{\mu_S(Q_S^*(t)), \mu_R(Q_S^*(t))\} - D]\bar{u}(t)Q_S^*(t) \\ &= -DQ_S^*(t)\bar{u}(t) + f_S(S^*(t), Q_S^*(t))\bar{u}(t) = -D\bar{U}_S + f_S(S^*(t), \frac{\bar{U}_S}{\bar{u}})\bar{u} \\ &\geq -D\bar{U}_S + F_S(S^*(t) - \bar{U}_S, \frac{\bar{U}_S}{\bar{u}})\bar{u}. \end{aligned}$$

Note that $\bar{U}_S(0) = Q_S^*(0)\bar{u}(0) = Q_S^*(0) \cdot \delta$, $\bar{U}_R(0) = Q_R^*(0)\bar{u}(0) = Q_R^*(0) \cdot \delta$, where δ is defined as in (2.21). Since $(U_S(0), U_R(0), u(0)) \in \mathbf{Y}$, it follows that $(U_S(t), U_R(t), u(t))$ satisfies (2.20), and hence, we can fix a suitable $\delta > 0$ such that

$$(\bar{U}_S(0), \bar{U}_R(0), \bar{u}(0)) \geq (U_S(0), U_R(0), u(0)). \quad (2.24)$$

Since (2.19) is a monotone system (see Lemma 2.2(i)), it follows from the comparison theorem, together with (2.23) and (2.24), that

$$(\bar{U}_S(t), \bar{U}_R(t), \bar{u}(t)) \geq (U_S(t), U_R(t), u(t)), \forall t \geq 0,$$

and hence, $\bar{u}(t) \geq u(t)$, $\forall t \geq 0$. By the assumption $\langle \min\{\mu_S(Q_S^*(t)), \mu_R(Q_R^*(t))\} - D \rangle < 0$, we have $\lim_{t \rightarrow \infty} \bar{u}(t) = 0$. This implies that $\lim_{t \rightarrow \infty} u(t) = 0$.

Recall that $P : \mathbb{Y} \rightarrow \mathbb{Y}$ is the Poincaré map associated with system (2.11). Given $x^0 = (Q_S(0), Q_R(0), u(0)) \in \mathbb{Y}_0$, let $\omega(x^0)$ be the omega limit set of x^0 for the period map P associated with (2.11), that is,

$$\omega = \omega(x^0) := \{x^* : \exists \{m_k\} \rightarrow \infty \text{ such that } \lim_{k \rightarrow \infty} P^{m_k}(x^0) = x^*\}.$$

Since $\lim_{t \rightarrow \infty} u(t) = 0$, it follows that there exists a set $\mathcal{C} \subset \mathbb{R}_+^2$ such that $\omega = \mathcal{C} \times \{0\}$. For any given $(Q_S^0, Q_R^0) \in \mathcal{C}$, we have $(Q_S^0, Q_R^0, 0) \in \omega \subset \mathbb{Y}$. By the definition of \mathbb{Y} , it follows that $(Q_S^0, Q_R^0) \in \Gamma$, and hence, $\mathcal{C} \subset \Gamma$. In view of the property of the set Γ , we see that $\mathcal{C} \neq \{(0, 0)\}$.

Assume that $\hat{P} : \Gamma \rightarrow \Gamma$ is the Poincaré map associated with system (2.4) and we define

$$W^s(Q_S^*(0), Q_R^*(0)) := \{(Q_S^0, Q_R^0) : \hat{P}^m(Q_S^0, Q_R^0) \rightarrow (Q_S^*(0), Q_R^*(0)) \text{ as } m \rightarrow \infty\}.$$

By [30, Lemma 1.2.1], ω is a compact, invariant and internal chain transitive set for P . Moreover, if $(Q_S^0, Q_R^0) \in \mathbb{R}_+^2$ with $(Q_S^0, Q_R^0, 0) \in \omega$, there holds $P|_\omega(Q_S^0, Q_R^0, 0) = (\hat{P}(Q_S^0, Q_R^0), 0)$. It then follows that \mathcal{C} is a compact, invariant and internal chain transitive set for $\hat{P} : \Gamma \rightarrow \Gamma$. Since $\mathcal{C} \neq \{(0, 0)\}$ and $\{(Q_S^*(0), Q_R^*(0))\}$ is globally attractive for \hat{P} in Γ , we have $\mathcal{C} \cap W^s(Q_S^*(0), Q_R^*(0)) \neq \emptyset$. By [30, Theorem 1.2.1], it follows that $\mathcal{C} = \{(Q_S^*(0), Q_R^*(0))\}$, and hence, $\omega = \{(Q_S^*(0), Q_R^*(0), 0)\}$. This complete the proof. \square

Now we turn to the existence and the global stability of positive periodic solutions for the limiting system (2.11). Let $\mathbb{Y}_0 := \{(Q_S, Q_R, u) \in \mathbb{Y} : u > 0\}$, $\partial\mathbb{Y}_0 := \mathbb{Y} \setminus \mathbb{Y}_0$.

Lemma 2.4. *If $\langle \min\{\mu_S(Q_S^*(t)), \mu_R(Q_R^*(t))\} - D \rangle > 0$, then system (2.11) admits a globally attractive positive τ -periodic solution $(\tilde{Q}_S(t), \tilde{Q}_R(t), \tilde{u}(t))$ in \mathbb{Y}_0 , that is, $\lim_{t \rightarrow \infty} |(Q_S(t), Q_R(t), u(t)) - (\tilde{Q}_S(t), \tilde{Q}_R(t), \tilde{u}(t))| = 0$ for any $(Q_S(0), Q_R(0), u(0)) \in \mathbb{Y}_0$.*

Proof. We proceed with two steps. First, we show that system (2.11) is uniformly persistent, and hence, system (2.11) admits at least one positive periodic solution. Secondly, we prove the uniqueness and global attractivity of positive periodic solution by applying the theory of monotone and subhomogeneous systems (see, e.g., [30]) to (2.12). Note that systems (2.11) and (2.12) are essentially equivalent.

Claim 1. System (2.11) is uniformly persistent with respect to $(\mathbb{Y}_0, \partial\mathbb{Y}_0)$ in the sense that there is an $\eta > 0$ such that for any $(Q_S(0), Q_R(0), u(0)) \in \mathbb{Y}_0$, the solution $(Q_S(t), Q_R(t), u(t))$ of (2.11) satisfies $\liminf_{t \rightarrow \infty} u(t) \geq \eta$, and system (2.11) admits at least one positive periodic solution.

To prove this claim, we appeal to the theory of uniform persistence for discrete-time dynamical systems. Recall that $P : \mathbb{Y} \rightarrow \mathbb{Y}$ is the Poincaré map associated

with system (2.11). It is easy to see that $P(\mathbb{Y}_0) \subset \mathbb{Y}_0$. Further, P is point dissipative and compact since solutions of system (2.11) are ultimately bounded. Let $E_0 := \{(Q_S^*(0), Q_R^*(0), 0)\}$. Then E_0 is a fixed point of P and is a compact and isolated invariant set for P in $\partial\mathbb{Y}_0$.

In the case where $u(0) = 0$, we have $u(t) = 0$ for any $t \geq 0$. Thus, (Q_S, Q_R) satisfies system (2.4) and it follows from Lemma 2.1 that $\lim_{t \rightarrow \infty} |(Q_S(t), Q_R(t)) - (Q_S^*(t), Q_R^*(t))| = 0$. Consequently, $P : \mathbb{Y} \rightarrow \mathbb{Y}$ has the property that

$$\omega(Q_S(0), Q_R(0), u(0)) = \{(Q_S^*(0), Q_R^*(0), 0)\}, \quad \forall (Q_S(0), Q_R(0), u(0)) \in \partial\mathbb{Y}_0,$$

where $\omega(x^0)$ is the omega-limit set of the orbit of P with initial values x^0 . It is obvious that there is no cycle in $\partial\mathbb{Y}_0$ from E_0 to E_0 .

Note that $\langle \min\{\mu_S(Q_S^*(t)), \mu_R(Q_R^*(t))\} - D \rangle > 0$ and the third component of E_0 is identically zero. By the same arguments as in [30, Lemma 5.1.1], it follows that there exists a $\delta_0 > 0$ such that E_0 is a uniform weak repeller for \mathbb{Y}_0 in the sense that $\limsup_{n \rightarrow \infty} \|P^n(Q_S(0), Q_R(0), u(0)) - E_0\| \geq \delta_0$, for any $(Q_S(0), Q_R(0), u(0)) \in \mathbb{Y}_0$. Therefore, E_0 is isolated in \mathbb{Y} and $W^s(E_0) \cap \mathbb{Y}_0 = \emptyset$, where $W^s(E_0)$ is the stable set of E_0 (see [30]).

Since $P : \mathbb{Y} \rightarrow \mathbb{Y}$ is point dissipative and compact, we conclude from [30, Theorem 1.1.3] that there exists a global attractor A for P in \mathbb{Y} . By [30, Theorem 1.3.1] on strong repellers, $P : \mathbb{Y} \rightarrow \mathbb{Y}$ is uniformly persistent with respect to $(\mathbb{Y}_0, \partial\mathbb{Y}_0)$. It follows from [30, Theorem 1.3.6] that there exists a global attractor A_0 for P in \mathbb{Y}_0 and P has a fixed point $(\tilde{Q}_S, \tilde{Q}_R, \tilde{u}) \in \mathbb{Y}_0$. Thus, there exists a positive periodic solution for (2.11) corresponding to the fixed point of the period map. By [30, Theorem 3.1.1], it follows that the periodic semiflow $T(t) : \mathbb{Y} \rightarrow \mathbb{Y}$, $t \geq 0$, associated with (2.11) is uniformly persistent with respect to $(\mathbb{Y}_0, \partial\mathbb{Y}_0)$.

Next we will show that the positive periodic solution is unique and globally asymptotically stable. Recall that $\mathbf{P} : \mathbf{Y} \rightarrow \mathbf{Y}$ is the Poincaré map associated with system (2.12). By Lemma 2.2, it follows that $\mathbf{P} : \mathbf{Y} \rightarrow \mathbf{Y}$ is monotone, and strongly subhomogeneous in the sense that $\mathbf{P}(\theta\tilde{x}) \gg \theta\mathbf{P}(\tilde{x})$, $\forall \tilde{x} \in \mathbf{Y}$, $\theta \in (0, 1)$ (see [30, section 2.3]). Thus, [30, Theorem 2.3.2] implies that the following observation.

Claim 2. If $\mathbf{P} : \mathbf{Y} \rightarrow \mathbf{Y}$ admits a nonempty compact invariant set $K \subset \text{Int}(\mathbb{R}_+^3)$, then \mathbf{P} has a fixed point $e \gg 0$ such that every nonempty compact invariant set of \mathbf{P} in $\text{Int}(\mathbb{R}_+^3)$ consists of e .

For any given $\tilde{x} := (U_S(0), U_R(0), u(0)) \in \mathbf{Y}$, let $(U_S(t), U_R(t), u(t))$ be the unique solution of (2.12). It follows that $(\frac{U_S(0)}{u(0)}, \frac{U_R(0)}{u(0)}, u(0)) \in \mathbb{Y}_0$, and $(\frac{U_S(t)}{u(t)}, \frac{U_R(t)}{u(t)}, u(t))$ is a solution of system (2.11). By Claim 1, there is an $\eta > 0$ such that $\liminf_{t \rightarrow \infty} u(t) \geq$

η . It then follows that $\tilde{\omega}(\tilde{x}) \subset \text{Int}(\mathbb{R}_+^3)$, where $\tilde{\omega}(\tilde{x})$ is the omega-limit set of the orbit through $\tilde{x} \in \mathbf{Y}$ for \mathbf{P} . By Claim 2, there is an $e \gg 0$ such that $\tilde{\omega}(\tilde{x}) = \{e\}$ for all $\tilde{x} \in \mathbf{Y}$. This implies that e is globally attractive for \mathbf{P} in \mathbf{Y} . Corresponding to the fixed point of the period map \mathbf{P} , system (2.12) has a globally attractive positive τ -periodic solution $(\tilde{U}_S(t), \tilde{U}_R(t), \tilde{u}(t))$ in \mathbf{Y} . Let $\tilde{Q}_S(t) = \frac{\tilde{U}_S(t)}{\tilde{u}(t)}$ and $\tilde{Q}_R(t) = \frac{\tilde{U}_R(t)}{\tilde{u}(t)}$. Then (2.11) has a globally attractive positive τ -periodic solution $(\tilde{Q}_S, \tilde{Q}_R, \tilde{u})$ in \mathbb{Y}_0 . \square

Let $\mathbf{X}_0 := \{(S, R, Q_S, Q_R, u) \in \mathbf{X} : u > 0\}$ and $\partial\mathbf{X}_0 := \mathbf{X} \setminus \mathbf{X}_0$. Then we have the following result on the global dynamics of the model system (2.1).

Theorem 2.1. *Let $(Q_S^*(t), Q_R^*(t))$ be the unique periodic solution of system (2.4), and $S^*(t)$ and $R^*(t)$ be the globally attractive positive τ -periodic solutions of the linear equations (2.2) and (2.3), respectively. Let $(S(t), R(t), Q_S(t), Q_R(t), u(t))$ be the solution of system (2.1). Then the following statements are valid:*

(i) *If $\langle \min\{\mu_S(Q_S^*(t)), \mu_R(Q_R^*(t))\} - D \rangle < 0$, then*

$$\lim_{t \rightarrow \infty} |(S(t), R(t), Q_S(t), Q_R(t), u(t)) - (S^*(t), R^*(t), Q_S^*(t), Q_R^*(t), 0)| = 0$$

for any $(S(0), R(0), Q_S(0), Q_R(0), u(0)) \in \mathbf{X}$.

(ii) *If $\langle \min\{\mu_S(Q_S^*(t)), \mu_R(Q_R^*(t))\} - D \rangle > 0$, then system (2.1) admits a globally attractive positive τ -periodic solution $(\tilde{S}(t), \tilde{R}(t), \tilde{Q}_S(t), \tilde{Q}_R(t), \tilde{u}(t))$ in \mathbf{X}_0 , that is, for any*

$$(S(0), R(0), Q_S(0), Q_R(0), u(0)) \in \mathbf{X}_0,$$

we have

$$\lim_{t \rightarrow \infty} |(S(t), R(t), Q_S(t), Q_R(t), u(t)) - (\tilde{S}(t), \tilde{R}(t), \tilde{Q}_S(t), \tilde{Q}_R(t), \tilde{u}(t))| = 0,$$

where $\tilde{S}(t) = S^(t) - \tilde{Q}_S(t)\tilde{u}(t)$ and $\tilde{R}(t) = R^*(t) - \tilde{Q}_R(t)\tilde{u}(t)$.*

Proof. Since system (2.1) and (2.10) are equivalent, it suffices to analyze system (2.10). Set

$$\mathbb{X}_0 := \{(Q_S, Q_R, u, Z_S, Z_R) \in \mathbb{X} : u > 0\}, \quad \partial\mathbb{X}_0 := \mathbb{X} \setminus \mathbb{X}_0.$$

Let $P_1 : \mathbb{X} \rightarrow \mathbb{X}$ be the Poincaré map associated with system (2.10) and $\omega_1(x^1)$ be the omega-limit set of the orbit of P_1 with initial values $x^1 \in \mathbb{X}$.

From the last two equations of (2.10), it follows that $\lim_{t \rightarrow \infty} Z_S(t) = 0$ and $\lim_{t \rightarrow \infty} Z_R(t) = 0$. Thus, there exists a set $\mathcal{I} \subset \mathbb{R}_+^3$ such that $\omega_1(x^1) = \mathcal{I} \times \{(0, 0)\}$. For any given $(Q_S^0, Q_R^0, u^0) \in \mathcal{I}$, we have $(Q_S^0, Q_R^0, u^0, 0, 0) \in \omega_1(x^1) \subset \mathbb{X}$. By the definition of \mathbb{X} , we have $(Q_S^0, Q_R^0, u^0) \in \mathbb{Y}$, and hence, $\mathcal{I} \subset \mathbb{Y}$.

By [30, Lemma 1.2.1], $\omega_1(x^1)$ is a compact, invariant and internal chain transitive set for P_1 . Moreover, if $x^0 \in \mathbb{R}_+^3$ with $(x^0, 0, 0) \in \omega_1(x^1)$, there holds $P_1|_{\omega_1(x^1)}(x^0, 0, 0) = (P(x^0), 0, 0)$, where $P : \mathbb{Y} \rightarrow \mathbb{Y}$ is the Poincaré map associated with system (2.11). It then follows that \mathcal{I} is a compact, invariant and internal chain transitive set for $P : \mathbb{Y} \rightarrow \mathbb{Y}$.

In the case where $\langle \min\{\mu_S(Q_S^*(t)), \mu_R(Q_R^*(t))\} - D \rangle < 0$, by Lemma 2.3, (2.11) has a globally attractive positive τ -periodic solution $(Q_S^*(t), Q_R^*(t), 0)$ in \mathbb{Y} . Since \mathcal{I} is a compact, invariant and internal chain transitive set for $P : \mathbb{Y} \rightarrow \mathbb{Y}$, it follows from [30, Theorem 1.2.1] that \mathcal{I} is a fixed point of P . That is, $\mathcal{I} = \{(Q_S^*(0), Q_R^*(0), 0)\}$, and hence, $\omega_1(x^1) = \mathcal{I} \times \{(0, 0)\} = \{(Q_S^*(0), Q_R^*(0), 0, 0, 0)\}$. This implies that $(Q_S^*(0), Q_R^*(0), 0, 0, 0)$ is globally attractive for P_1 in \mathbb{X} . Corresponding to the fixed point of the period map P_1 , system (2.10) has a globally attractive positive τ -periodic solution $(Q_S^*(t), Q_R^*(t), 0, 0, 0)$ in \mathbb{X} . This implies that statement (i) holds true.

In the case where $\langle \min\{\mu_S(Q_S^*(t)), \mu_R(Q_R^*(t))\} - D \rangle > 0$, it follows from Lemma 2.4 that system (2.11) has a globally attractive positive τ -periodic solution $(\tilde{Q}_S(t), \tilde{Q}_R(t), \tilde{u}(t))$ in \mathbb{Y}_0 . Note that $(Q_S^*(t), Q_R^*(t), 0)$ is also a τ -periodic solution of (2.11). This implies that the possible fixed points $(Q_S^*(0), Q_R^*(0), 0)$ and $(\tilde{Q}_S(0), \tilde{Q}_R(0), \tilde{u}(0))$ are isolated invariant sets in \mathbb{Y} and no subset of $(Q_S^*(0), Q_R^*(0), 0)$ and $(\tilde{Q}_S(0), \tilde{Q}_R(0), \tilde{u}(0))$ forms a cycle in \mathbb{Y} . Since \mathcal{I} is a compact, invariant and internal chain transitive set for $P : \mathbb{Y} \rightarrow \mathbb{Y}$, it follows from [30, Theorem 1.2.2] that either $\mathcal{I} = \{(Q_S^*(0), Q_R^*(0), 0)\}$ or $\mathcal{I} = \{(\tilde{Q}_S(0), \tilde{Q}_R(0), \tilde{u}(0))\}$.

Suppose, by contradiction, that $\mathcal{I} = \{(Q_S^*(0), Q_R^*(0), 0)\}$. This implies that

$$P_1^n(Q_S(0), Q_R(0), u(0), Z_S(0), Z_R(0)) = (Q_S(n\tau), Q_R(n\tau), u(n\tau), Z_S(n\tau), Z_R(n\tau))$$

converges to $(Q_S^*(0), Q_R^*(0), 0, 0, 0)$ as $n \rightarrow \infty$. Equivalently,

$$\lim_{t \rightarrow \infty} |(Q_S(t), Q_R(t), u(t), Z_S(t), Z_R(t)) - (Q_S^*(t), Q_R^*(t), 0, 0, 0)| = 0,$$

and hence, $\lim_{t \rightarrow \infty} |(Q_S(t), Q_R(t)) - (Q_S^*(t), Q_R^*(t))| = 0$. Let

$$\epsilon_0 := \frac{1}{2} \langle \min\{\mu_S(Q_S^*(t)), \mu_R(Q_R^*(t))\} - D \rangle > 0.$$

Then there is a $T > 0$ such that

$$\min\{\mu_S(Q_S(t)), \mu_R(Q_R(t))\} - D \geq \min\{\mu_S(Q_S^*(t)), \mu_R(Q_R^*(t))\} - D - \epsilon_0$$

for all $t \geq T$. By the third equation of (2.10), we have

$$\frac{du(t)}{dt} \geq [\min\{\mu_S(Q_S^*(t)), \mu_R(Q_R^*(t))\} - D - \epsilon_0]u, \quad \forall t \geq T.$$

Without loss of generality, letting $T = n_1\tau$ and $t = n_2\tau$ for some natural number n_1 and n_2 with $n_2 > n_1$, we then obtain

$$u(n_2\tau) \geq u(n_1\tau) \exp \left[\int_{n_1\tau}^{n_2\tau} [\min\{\mu_S(Q_S^*(t)), \mu_R(Q_R^*(t))\} - D - \epsilon_0] dt \right].$$

Since $Q_S^*(t)$ and $Q_R^*(t)$ are τ -periodic functions, it follows that

$$u(n_2\tau) \geq u(n_1\tau) \exp [(n_2 - n_1)\tau (\langle \min\{\mu_S(Q_S^*(t)), \mu_R(Q_R^*(t))\} - D \rangle - \epsilon_0)],$$

that is,

$$u(n_2\tau) \geq u(n_1\tau) \exp \left[\frac{(n_2 - n_1)\tau}{2} \langle \min\{\mu_S(Q_S^*(t)), \mu_R(Q_R^*(t))\} - D \rangle \right].$$

Since $\langle \min\{\mu_S(Q_S^*(t)), \mu_R(Q_R^*(t))\} - D \rangle > 0$, we see that $u(n_2\tau) \rightarrow \infty$ as $n_2 \rightarrow \infty$, which is a contradiction. Thus, we have $\mathcal{I} = \{(\tilde{Q}_S(0), \tilde{Q}_R(0), \tilde{u}(0))\}$, and hence, $\omega_1(x^1) = \mathcal{I} \times \{(0, 0)\} = \{(\tilde{Q}_S(0), \tilde{Q}_R(0), \tilde{u}(0), 0, 0)\}$. This implies that $(\tilde{Q}_S(0), \tilde{Q}_R(0), \tilde{u}(0), 0, 0)$ is globally attractive for P_1 in \mathbb{X} . Corresponding to the fixed point of the period map P_1 , system (2.10) has a globally attractive positive τ -periodic solution $(\tilde{Q}_S(t), \tilde{Q}_R(t), \tilde{u}(t), 0, 0)$ in \mathbb{X} . It then follows that statement (ii) is valid. \square

3 Two species competition

In this section, we study the coexistence periodic solutions and uniform persistence for two species phytoplankton model (1.1). Note that the region of interest for system (1.1) is

$$\Omega = \{(S, R, Q_{S1}, Q_{R1}, u_1, Q_{S2}, Q_{R2}, u_2) \in \mathbb{R}_+^8 : Q_{Si} \geq Q_{\min, Si}, Q_{Ri} \geq Q_{\min, Ri}, i = 1, 2\}.$$

It is easy to show that Ω is positively invariant for (1.1). We further claim that any solution $(S(t), R(t), Q_{S1}(t), Q_{R1}(t), u_1(t), Q_{S2}(t), Q_{R2}(t), u_2(t))$ of (1.1) with initial value in Ω exists globally on $[0, \infty)$. Indeed, by the continuation theorem, it suffices to prove that the solution of system (1.1) is bounded on finite time intervals. To this end, we let $\mathcal{T}_S(t) = S(t) + Q_{S1}(t)u_1(t) + Q_{S2}(t)u_2(t)$ and $\mathcal{T}_R(t) = R(t) + Q_{R1}(t)u_1(t) + Q_{R2}(t)u_2(t)$. Then $\mathcal{T}_S(t)$ and $\mathcal{T}_R(t)$ satisfy the linear systems (2.2) and (2.3), respectively. Thus, $\mathcal{T}_S(t)$ and $\mathcal{T}_R(t)$ are bounded on finite time intervals, and hence, so are $S(t)$, $R(t)$, $Q_{S_i}(t)u_i(t)$ and $Q_{R_i}(t)u_i(t)$, $i = 1, 2$. Since $Q_{S_i} \geq Q_{\min, S_i}$ and $Q_{R_i} \geq Q_{\min, R_i}$, it follows that $u_i(t)$ is bounded on finite time intervals, $i = 1, 2$. We are ready to prove $Q_{S_i}(t)$ and $Q_{R_i}(t)$ are bounded on finite time intervals, $i = 1, 2$. Let $\mathcal{V}_i(t) = \frac{1}{2}[(Q_{S_i}(t))^2 + (Q_{R_i}(t))^2]$, $i = 1, 2$. We can use the same arguments as in (2.5) to show that for each $i = 1, 2$,

$$\begin{aligned} \frac{d\mathcal{V}_i(t)}{dt} &\leq \frac{1}{2}f_{S_i}(S(t), Q_{\min, S_i}) + \frac{1}{2}f_{R_i}(R(t), Q_{\min, R_i}) \\ &\quad + \max\{f_{S_i}(S(t), Q_{\min, S_i}), f_{R_i}(R(t), Q_{\min, R_i})\}\mathcal{V}_i(t). \end{aligned} \quad (3.1)$$

Since $S(t)$ and $R(t)$ in (3.1) are bounded on finite time intervals, we see that $\mathcal{V}_i(t)$ is bounded in finite time intervals, and hence, so are $Q_{S_i}(t)$ and $Q_{R_i}(t)$, $i = 1, 2$. Thus, every solution of system (1.1) exists globally.

Let

$$W_S(t) = S^*(t) - S - Q_{S1}u_1 - Q_{S2}u_2 \text{ and } W_R(t) = R^*(t) - R - Q_{R1}u_1 - Q_{R2}u_2, \quad (3.2)$$

where $S^*(t)$ and $R^*(t)$ are the globally attractive positive τ -periodic solutions of (2.2) and (2.3), respectively. Then W_S and W_R satisfy $\frac{dW_S}{dt} = -DW_S$ and $\frac{dW_R}{dt} = -DW_R$, respectively. Obviously,

$$\lim_{t \rightarrow \infty} W_S(t) = 0 \text{ and } \lim_{t \rightarrow \infty} W_R(t) = 0. \quad (3.3)$$

Therefore, solutions of (1.1) are ultimately bounded on Ω .

From Lemma 2.1, we see that $(Q_{S_i}^*(t), Q_{R_i}^*(t))$ is the globally attractive positive τ -periodic solution for the system (2.4) with $f_S = f_{S_i}$, $f_R = f_{R_i}$, $\mu_S = \mu_{S_i}$ and $\mu_R = \mu_{R_i}$, $i = 1, 2$, respectively. This implies that

$$(S^*(t), R^*(t), Q_{S1}^*(t), Q_{R1}^*(t), 0, Q_{S2}^*(t), Q_{R2}^*(t), 0)$$

is the trivial τ -periodic solution for (1.1).

Assume that

$$\langle \min\{\mu_{S_i}(Q_{S_i}^*(t)), \mu_{R_i}(Q_{R_i}^*(t))\} - D \rangle > 0, \quad i = 1, 2. \quad (3.4)$$

It then follows from Theorem 2.1 that $(\bar{S}(t), \bar{R}(t), \bar{Q}_{S1}(t), \bar{Q}_{R1}(t), \bar{u}_1(t))$ is the globally attractive positive τ -periodic solution of the system (2.1) in its feasible domain with $f_S = f_{S1}$, $f_R = f_{R1}$, $\mu_S = \mu_{S1}$ and $\mu_R = \mu_{R1}$, that is,

$$\begin{cases} \frac{dS}{dt} = (S^{(0)}(t) - S)D - f_{S1}(S, Q_{S1})u_1, \\ \frac{dR}{dt} = (R^{(0)}(t) - R)D - f_{R1}(R, Q_{R1})u_1, \\ \frac{dQ_{S1}}{dt} = f_{S1}(S, Q_{S1}) - \min\{\mu_{S1}(Q_{S1}), \mu_{R1}(Q_{R1})\}Q_{S1}, \\ \frac{dQ_{R1}}{dt} = f_{R1}(R, Q_{R1}) - \min\{\mu_{S1}(Q_{S1}), \mu_{R1}(Q_{R1})\}Q_{R1}, \\ \frac{du_1}{dt} = [\min\{\mu_{S1}(Q_{S1}), \mu_{R1}(Q_{R1})\} - D]u_1. \end{cases} \quad (3.5)$$

By the arguments similar to those in Lemma 2.1, we see that $(\bar{Q}_{S2}(t), \bar{Q}_{R2}(t))$ is the globally attractive positive τ -periodic solution for the following system:

$$\begin{cases} \frac{dQ_{S2}}{dt} = f_{S2}(\bar{S}(t), Q_{S2}) - \min\{\mu_{S2}(Q_{S2}), \mu_{R2}(Q_{R2})\}Q_{S2}, \\ \frac{dQ_{R2}}{dt} = f_{R2}(\bar{R}(t), Q_{R2}) - \min\{\mu_{S2}(Q_{S2}), \mu_{R2}(Q_{R2})\}Q_{R2}. \end{cases} \quad (3.6)$$

This implies that $(\bar{S}(t), \bar{R}(t), \bar{Q}_{S1}(t), \bar{Q}_{R1}(t), \bar{u}_1(t), \bar{Q}_{S2}(t), \bar{Q}_{R2}(t), 0)$ is the semi-trivial τ -periodic solution for (1.1). Similarly,

$$(\hat{S}(t), \hat{R}(t), \hat{Q}_{S1}(t), \hat{Q}_{R1}(t), 0, \hat{Q}_{S2}(t), \hat{Q}_{R2}(t), \hat{u}_2(t))$$

is the semi-trivial τ -periodic solution for (1.1), where $(\hat{S}(t), \hat{R}(t), \hat{Q}_{S2}(t), \hat{Q}_{R2}(t), \hat{u}_2(t))$ is the globally attractive positive τ -periodic solution of the system (2.1) in its feasible domain with $f_S = f_{S2}$, $f_R = f_{R2}$, $\mu_S = \mu_{S2}$ and $\mu_R = \mu_{R2}$, and $(\hat{Q}_{S1}(t), \hat{Q}_{R1}(t))$ is the globally attractive positive τ -periodic solution for the following system:

$$\begin{cases} \frac{dQ_{S1}}{dt} = f_{S1}(\hat{S}(t), Q_{S1}) - \min\{\mu_{S1}(Q_{S1}), \mu_{R1}(Q_{R1})\}Q_{S1}, \\ \frac{dQ_{R1}}{dt} = f_{R1}(\hat{R}(t), Q_{R1}) - \min\{\mu_{S1}(Q_{S1}), \mu_{R1}(Q_{R1})\}Q_{R1}. \end{cases}$$

We further assume that

$$\langle \min\{\mu_{S1}(\hat{Q}_{S1}(t), \mu_{R1}(\hat{Q}_{R1}(t)))\} - D \rangle > 0, \quad (3.7)$$

and

$$\langle \min\{\mu_{S2}(\bar{Q}_{S2}(t), \mu_{R2}(\bar{Q}_{R2}(t)))\} - D \rangle > 0. \quad (3.8)$$

Let $\Omega_0 := \{(S, R, Q_{S1}, Q_{R1}, u_1, Q_{S2}, Q_{R2}, u_2) \in \Omega : u_1 > 0, u_2 > 0\}$, $\partial\Omega_0 := \Omega \setminus \Omega_0$. Then we have the following result on the global dynamics of the model system (1.1).

Theorem 3.1. *Let (3.4), (3.7) and (3.8) hold. Then system (1.1) is uniformly persistent with respect to $(\Omega_0, \partial\Omega_0)$ in the sense that there is an $\eta > 0$ such that for any*

$$(S(0), R(0), Q_{S1}(0), Q_{R1}(0), u_1(0), Q_{S2}(0), Q_{R2}(0), u_2(0)) \in \Omega_0,$$

the solution $(S(t), R(t), Q_{S1}(t), Q_{R1}(t), u_1(t), Q_{S2}(t), Q_{R2}(t), u_2(t))$ of (1.1) satisfies

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

Further, system (1.1) admits at least one positive periodic solution.

Proof. Let $P_2 : \Omega \rightarrow \Omega$ be the Poincaré map associated with system (1.1), that is,

$$\begin{aligned} P_2(S(0), R(0), Q_{S1}(0), Q_{R1}(0), u_1(0), Q_{S2}(0), Q_{R2}(0), u_2(0)) \\ = ((S(\tau), R(\tau), Q_{S1}(\tau), Q_{R1}(\tau), u_1(\tau), Q_{S2}(\tau), Q_{R2}(\tau), u_2(\tau))), \end{aligned}$$

where $(S(0), R(0), Q_{S1}(0), Q_{R1}(0), u_1(0), Q_{S2}(0), Q_{R2}(0), u_2(0)) \in \Omega$. Let $\omega_2(x)$ be the omega-limit set of the orbit of P_2 through $x \in \Omega$. It is easy to see that $P_2(\Omega_0) \subset \Omega_0$. Since solutions of system (1.1) are ultimately bounded, it follows that P_2 is point dissipative and compact.

Let

$$\begin{aligned} M_0 &= (S^*(0), R^*(0), Q_{S1}^*(0), Q_{R1}^*(0), 0, Q_{S2}^*(0), Q_{R2}^*(0), 0), \\ M_1 &= (\bar{S}(0), \bar{R}(0), \bar{Q}_{S1}(0), \bar{Q}_{R1}(0), \bar{u}_1(0), \bar{Q}_{S2}(0), \bar{Q}_{R2}(0), 0), \end{aligned}$$

and

$$M_2 = (\hat{S}(0), \hat{R}(0), \hat{Q}_{S1}(0), \hat{Q}_{R1}(0), 0, \hat{Q}_{S2}(0), \hat{Q}_{R2}(0), \hat{u}_2(0)).$$

Then M_0 , M_1 and M_2 are fixed points of P_2 and are pairwise disjoint, compact and isolated invariant sets for P_2 in $\partial\Omega_0$. We are going to show that

$$\bigcup_{x \in \partial\Omega_0} \omega_2(x) \subset M_0 \cup M_1 \cup M_2. \quad (3.9)$$

In the case where $u_1(0) > 0$ and $u_2(0) = 0$, we have $u_1(t) > 0$ and $u_2(t) = 0$, $\forall t \geq 0$. Then $(S(t), R(t), Q_{S1}(t), Q_{R1}(t), u_1(t))$ satisfies the system (3.5). Since $\langle \mu_{S1}(Q_{S1}^*(t)) \mu_{R1}(Q_{R1}^*(t)) - D \rangle > 0$, it follows from Theorem 2.1 that

$$\lim_{t \rightarrow \infty} |(S(t), R(t), Q_{S1}(t), Q_{R1}(t), u_1(t)) - (\bar{S}(t), \bar{R}(t), \bar{Q}_{S1}(t), \bar{Q}_{R1}(t), \bar{u}_1(t))| = 0.$$

Thus, the equations for $Q_{S_2}(t)$ and $Q_{R_2}(t)$ in (1.1) are asymptotic to the system (3.6). By the theory of asymptotically periodic semiflows (see, e.g., [29] or [30, Section 3.2]) and the arguments similar to those in Lemma 2.1, it follows that $\lim_{t \rightarrow \infty} |(Q_{S_2}(t), Q_{R_2}(t)) - (\bar{Q}_{S_2}(t), \bar{Q}_{R_2}(t))| = 0$. Since

$$\begin{aligned} & P_2^n(S(0), R(0), Q_{S_1}(0), Q_{R_1}(0), u_1(0), Q_{S_2}(0), Q_{R_2}(0), 0) \\ &= ((S(n\tau), R(n\tau), Q_{S_1}(n\tau), Q_{R_1}(n\tau), u_1(n\tau), Q_{S_2}(n\tau), Q_{R_2}(n\tau), 0), \end{aligned}$$

it follows that $\lim_{n \rightarrow \infty} P_2^n(S(0), R(0), Q_{S_1}(0), Q_{R_1}(0), u_1(0), Q_{S_2}(0), Q_{R_2}(0), 0) = M_1$. In the case where $u_1(0) = 0$ and $u_2(0) > 0$, we can use the similar arguments to show that

$$\lim_{n \rightarrow \infty} P_2^n(S(0), R(0), Q_{S_1}(0), Q_{R_1}(0), 0, Q_{S_2}(0), Q_{R_2}(0), u_2(0)) = M_2.$$

In the case where $u_1(0) = 0$ and $u_2(0) = 0$, we can show that

$$\lim_{n \rightarrow \infty} P_2^n(S(0), R(0), Q_{S_1}(0), Q_{R_1}(0), 0, Q_{S_2}(0), Q_{R_2}(0), 0) = M_0.$$

Consequently, $P_2 : \Omega \rightarrow \Omega$ satisfies the property (3.9). It is easy to see that no subset of $\{M_0, M_1, M_2\}$ forms a cycle in $\partial\Omega_0$.

Each M_j corresponds to a periodic solution with at least one component that is identically zero. By (3.4), (3.7), (3.8) and the same arguments as in [30, Lemma 5.1.1], there exists a $\delta > 0$ such that each M_j is a uniform weak repeller for Ω_0 in the sense that $\limsup_{n \rightarrow \infty} \|P_2^n(x) - M_j\| \geq \delta$ for any $x \in \Omega_0$. Therefore, each M_j is isolated in Ω and $\mathcal{W}^s(M_j) \cap \Omega_0 = \emptyset$, where $\mathcal{W}^s(M_j)$ is the stable set of M_j (see [30]).

Since $P_2 : \Omega \rightarrow \Omega$ is point dissipative and compact, we conclude from [30, Theorem 1.1.3] that there exists a global attractor \mathcal{A} for P_2 in Ω . By [30, Theorem 1.3.1] on strong repellers, $P_2 : \Omega \rightarrow \Omega$ is uniformly persistent with respect to $(\Omega_0, \partial\Omega_0)$. It follows from [30, Theorem 1.3.6] that there exists a global attractor \mathcal{A}_0 for P_2 in Ω_0 and P_2 has at least one fixed point $x \in \Omega_0$. Thus, there exists a positive periodic solution for (1.1) corresponding to the fixed point x of the period map. By [30, Theorem 3.1.1], it follows that the periodic semiflow $\mathcal{T}(t) : \Omega \rightarrow \Omega$, $t \geq 0$, associated with (1.1) is uniformly persistent with respect to $(\Omega_0, \partial\Omega_0)$. \square

To finish this section, we remark that by a change of variables

$$U_{S_i} = Q_{S_i}u_i \text{ and } U_{R_i} = Q_{R_i}u_i, \quad i = 1, 2,$$

together with (3.2), we can rewrite (1.1) as the following system:

$$\begin{cases} \frac{dU_{Si}}{dt} = -DU_{Si} + f_{Si}(S^*(t) - U_{S1} - U_{S2} - W_S, \frac{U_{Si}}{u_i})u_i, \\ \frac{dU_{Ri}}{dt} = -DU_{Ri} + f_{Ri}(R^*(t) - U_{R1} - U_{R2} - W_R, \frac{U_{Ri}}{u_i})u_i, \\ \frac{du_i}{dt} = [\min\{\mu_{Si}(\frac{U_{Si}}{u_i}), \mu_{Ri}(\frac{U_{Ri}}{u_i})\} - D]u_i, \quad i = 1, 2, \\ \frac{dW_S}{dt} = -DW_S, \\ \frac{dW_R}{dt} = -DW_R, \end{cases} \quad (3.10)$$

with initial values in its feasible domain. In view of (3.3), we see that (3.10) has a limiting system:

$$\begin{cases} \frac{dU_{Si}}{dt} = -DU_{Si} + f_{Si}(S^*(t) - U_{S1} - U_{S2}, \frac{U_{Si}}{u_i})u_i, \\ \frac{dU_{Ri}}{dt} = -DU_{Ri} + f_{Ri}(R^*(t) - U_{R1} - U_{R2}, \frac{U_{Ri}}{u_i})u_i, \\ \frac{du_i}{dt} = [\min\{\mu_{Si}(\frac{U_{Si}}{u_i}), \mu_{Ri}(\frac{U_{Ri}}{u_i})\} - D]u_i, \quad i = 1, 2. \end{cases} \quad (3.11)$$

It is easy to see that the Poincaré map associated with system (3.11) is monotone with respect to the partial order \leq_K (see, e.g., [22]), which is induced by the positive cone $K := \mathbb{R}_+^3 \times \mathbb{R}_-^3$ in \mathbb{R}^6 . Consequently, if system (1.1) admits at most one positive periodic solution, then we can conclude that the positive periodic solution obtained in Theorem 3.1 is globally attractive in Ω_0 by appealing to the theory of monotone systems. Note that the uniqueness of positive periodic solution of the high dimensional periodic system (1.1) remains a challenging problem, and we leave it for future investigation.

4 Discussion

In this paper, we have studied a chemostat model of competition for two complementary (essential) nutrients that can be stored within individuals in a temporally varying environment. These resources are supplied from an external reservoir at concentrations that could vary periodically with time. In contrast to the classical Monod models, nutrient uptake and species growth are assumed to be decoupled. Our model system assumes that species growth is related to not only the external concentrations of limiting nutrients but also the internal nutrients concentrations. To reflect the reality in nature, it is more reasonable to include multiple potentially limiting resources in the system. When both resources are essential for growth, the

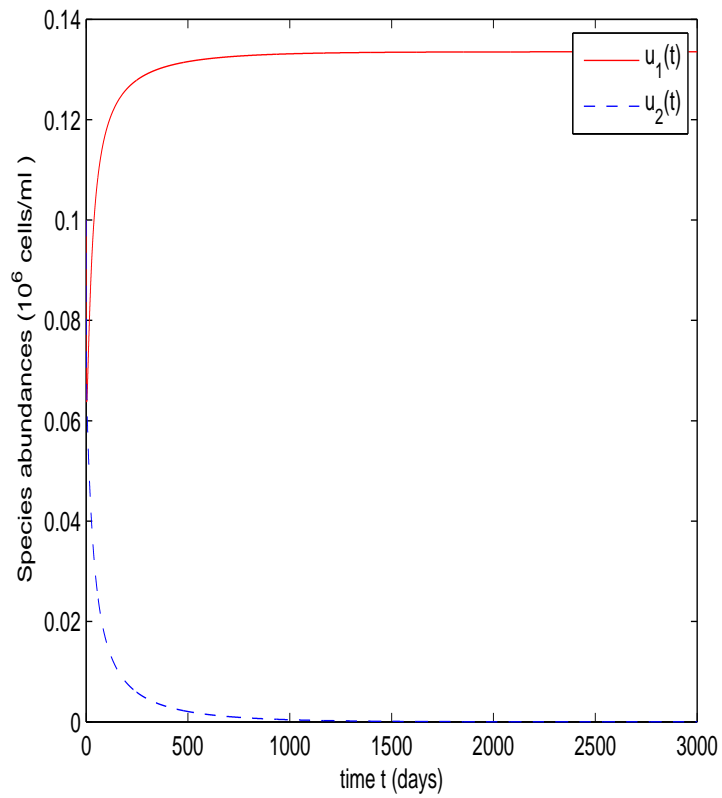


Figure 4.1: Species 1 is a superior competitor when $S^{(0)}(t) \equiv 20$ ($\mu\text{mol liter}^{-1}$) and $R^{(0)}(t) \equiv 3$ ($\mu\text{mol liter}^{-1}$).

resource in least supply usually limits growth, known as Liebig's law of the minimum [5].

For the population growth model (2.1), persistence of a single species depends on a threshold criterion that is related to the dilution rate and the characteristics of nutrient uptake and growth kinetics required for survival. More precisely, the population is washed out if the sub-threshold criterion holds. It is also proved that there is a globally stable positive periodic solution if the super-threshold criterion holds (see Theorem 2.1). The full system (1.1) represents competition between two species. It was shown in [20] that the temporally homogeneous system of (1.1) exhibits outcomes of competitive exclusion independent of initial conditions, competitive exclusion that depends on initial conditions (bistability), and globally stable coexistence, depending on tradeoffs between abilities to compete for the nutrient and growth requirements under the additional assumption (1.2). For the full system (1.1), Theorem 2.1 implies that at least three unique τ -periodic solutions occur, a trivial τ -periodic solution with neither competitor present, and two semitrivial τ -periodic solutions with just one of the competitors persistent. Biologically, the condition (3.4) indicates that both species have sufficient resources to meet their breakeven requirements (super-threshold criteria), which guarantee that either species can invade an empty habitat and establish a persistent population that approaches a single species, and hence, each semitrivial τ -periodic solution exists. Invasibility depends on whether the missing competitor obtains sufficient quotas to exceed its average threshold under the nutrient conditions established by the resident species, permitting a growth rate exceeding the loss rate to outflow. The conditions (3.7) and (3.8) ensure that there is mutual invasibility of both semitrivial τ -periodic solutions, and the full system (1.1) admits at least one positive τ -periodic solution representing coexistence of the competitors (see Theorem 3.1). It doesn't make sense to impose a similar condition to (1.2) for our periodic system (1.1), so we are unable to linearize system (1.1) at the trivial, semi-trivial τ -periodic solutions. However, we still give predictions on the other possibilities when the condition (3.4) is met: competitive exclusion occurs if one of the inequalities in (3.7) and (3.8) is reversed; bistability, in which both semitrivial τ -periodic solutions are stable and the outcome depends on initial conditions, occurs if both of the inequalities in (3.7) and (3.8) are reversed.

It was understood that temporal variations can alter competitive outcomes, perhaps promoting coexistence of species and diversity in competitor communities (see, e.g., [6, 10, 17]). As mentioned in [10], non-steady state dynamics may ex-

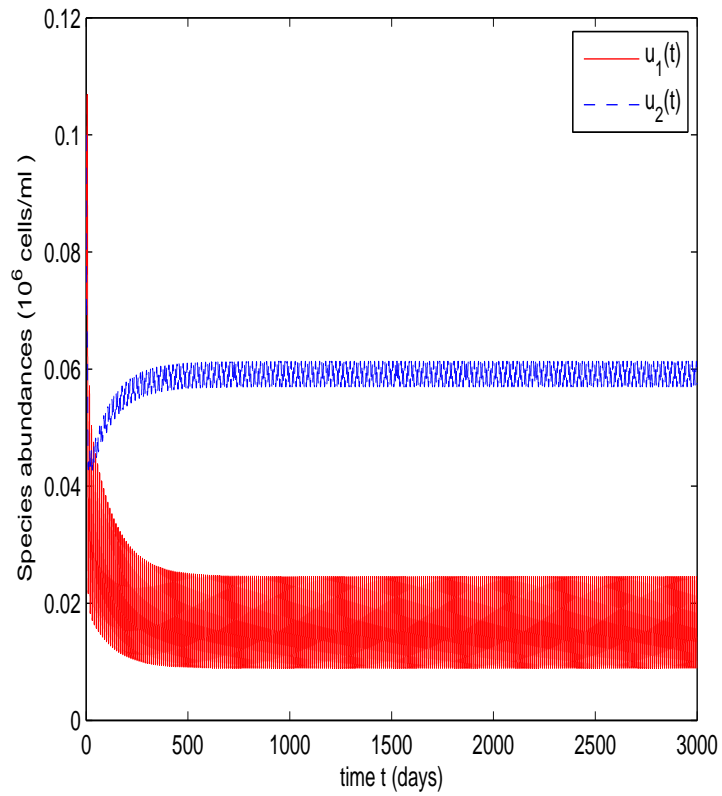


Figure 4.2: Coexistence occurs when $S^{(0)}(t) = 20 + 19.9\sin(\frac{\pi}{5}t)$ ($\mu\text{mol liter}^{-1}$) and $R^{(0)}(t) = 3 + 0.7\sin(\frac{\pi}{5}t)$ ($\mu\text{mol liter}^{-1}$).

plain the coexistence of many species of phytoplankton in a seemingly temporally constant environment. This was confirmed in [11], where the Monod kinetics is used as the growth rate of two species to show that seasonally varying nutrient can allow coexistence. In nature, phytoplankton can store nutrients from pulses within their cells, which affects competitive dynamics in variable environments. Ecologists have understood that competitive exclusion proceeds more slowly in the presence of resource pulses [7]. It was shown in [27] that coexistence occurs in the competition for one nutrient with internal storage and a periodic input. In order to investigate the effects of temporal heterogeneity in the two-nutrients system (1.1), we perform numerical computations. For simplicity, we make the following choices for the growth rate and uptake rate in the model system (1.1). For $N = S, R$ and $i = 1, 2$,

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

and

$$f_{Ni}(N, Q_{Ni}) = \rho_{\max, Ni} \frac{N}{K_{Ni} + N},$$

so that the uptake function of species i for resource N is independent of quota and has a constant maximal uptake rate [1]. We fix $\rho_{\max, S1} = 341$ ($10^{-9} \mu\text{mol cell}^{-1} \text{day}^{-1}$), $\rho_{\max, R1} = 12.3$ ($10^{-9} \mu\text{mol cell}^{-1} \text{day}^{-1}$), $K_{S1} = 5.6$ ($\mu\text{mol liter}^{-1}$), $K_{R1} = 0.2$ ($\mu\text{mol liter}^{-1}$), $\mu_{\infty, S1} = 1.35$ (day^{-1}), $\mu_{\infty, R1} = 1.35$ (day^{-1}), $Q_{\min, S1} = 45.4$ ($10^{-9} \mu\text{mol cell}^{-1}$), $Q_{\min, R1} = 1.64$ ($10^{-9} \mu\text{mol cell}^{-1}$); $\rho_{\max, S2} = 380$ ($10^{-9} \mu\text{mol cell}^{-1} \text{day}^{-1}$), $\rho_{\max, R2} = 24$ ($10^{-9} \mu\text{mol cell}^{-1} \text{day}^{-1}$), $K_{S2} = 7.2$ ($\mu\text{mol liter}^{-1}$), $K_{R2} = 0.4$ ($\mu\text{mol liter}^{-1}$), $\mu_{\infty, S2} = 1.3$ (day^{-1}), $\mu_{\infty, R2} = 1.3$ (day^{-1}), $Q_{\min, S2} = 15$ ($10^{-9} \mu\text{mol cell}^{-1}$), $Q_{\min, R2} = 7$ ($10^{-9} \mu\text{mol cell}^{-1}$). These parameter values were used in [20] to do the numerical simulations of the constant case of (1.1). Next, we let $D = 0.875$ (day^{-1}), $S^{(0)}(t) = 20 + b_s \sin(\frac{\pi}{5}t)$ ($\mu\text{mol liter}^{-1}$) and $R^{(0)}(t) = 3 + b_r \sin(\frac{\pi}{5}t)$ ($\mu\text{mol liter}^{-1}$), where b_s and b_r vary. When we choose $b_s = b_r = 0$, we find that species 1 is a superior competitor for nutrient, excluding species 2 in the temporally homogeneous environment (see Fig. 4.1). When we choose $b_s = 19.9$ and $b_r = 0.7$, we find that there exists a positive (coexistence) periodic solution (see Fig. 4.2). It has been predicted that the fluctuation of nutrients may reverse the outcomes of the competition [16, 17, 18], and our numerical simulations on system (1.1) confirm this prediction. In Fig. 4.1, there is no fluctuation of the nutrients, and species 1 win the competition. However, in Fig. 4.2, with the fluctuation of the nutrients the species may coexist, even reverse the outcome of the competition

(i.e. species 2 win the competition).

Acknowledgments. This research project was initiated when Feng-Bin Wang made an academic visit to Memorial University of Newfoundland (MUN), and his sincere thanks goes to the NSERC of Canada for the financial support and the Department of Mathematics and Statistics in MUN for the kind hospitality. We would like to thank the anonymous referee for careful reading and helpful suggestions which led to improvements of our original manuscript.

References

- [1] A. CUNNINGHAM AND R. M. NISBET, *Time lag and co-operativity in the transient growth dynamics of microalgae*, J. Theoret. Biol., 84 (1980), pp. 189–203.
- [2] A. CUNNINGHAM AND R. M. NISBET, *Transient and oscillation in continuous culture*, in Mathematics in Microbiology, M. J. Bazin, ed., Academic press, New York, 1983.
- [3] M. DROOP, *Vitamin B12 and marine ecology. IV. The kinetics of uptake, growth and inhibition in Monochrysis Lutheri*, J. Mar. Biol. Assoc. UK, 48 (1968), pp. 689-733
- [4] M. DROOP, *Some thoughts on nutrient limitation in algae*, J. Phycol., 9 (1973), pp. 264–272.
- [5] M. DROOP, *The nutrient status of algal cells in continuous culture*, J. Mar. Biol. Assoc. UK, 54 (1974), pp. 825-855.
- [6] J. P. GROVER, *Non-steady state dynamics of algal population growth: experiments with two chlorophytes*, Journal of Phycology, 27 (1991), pp. 70–79.
- [7] J. P. GROVER, *Resource competition in a variable environment: phytoplankton growing according to the variable-internal-stores model*, American Naturalist, 138 (1991), 811–835.
- [8] J. P. GROVER, *Constant- and variable-yield models of population growth: Responses to environmental variability and implications for competition*, J. Theoret. Biol., 158 (1992), pp. 409–428.

- [9] J. P. GROVER, *Resource Competition*, Chapman and Hall, London, 1997.
- [10] G. E. HUTCHINSON, *The paradox of the plankton*, *American Naturalist*, 95 (1961), 137–145.
- [11] S.-B. HSU, *A competition model for a seasonally fluctuating nutrient*, *J. Math. Biol.*, 9 (1980), pp. 115–132.
- [12] 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), pp. 1600–1617.
- [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), pp. 366–383.
- [14] W. M. HIRSCH, H. L. SMITH AND X. -Q. ZHAO, *Chain transitivity, attractivity, and strong repellers for semidynamical systems*, *J. Dynam. Differential Equations*, 13 (2001), pp. 107–131.
- [15] S.-B. HSU AND X.-Q. ZHAO, *A Lotka-Volterra competition model with seasonal succession.*, *J. Math. Biol.*, 64 (2012), pp. 109–130.
- [16] E. LITCHMAN, *Competition and coexistence of phytoplankton under fluctuating light: experiments with two cyanobacteria*, *Aquatic Microbial Ecology*, 31 (2003), 241–248.
- [17] E. LITCHMAN AND C.A. KLAUSMEIER, *Competition of phytoplankton under fluctuating light*, *American Naturalist*, 157 (2001), 170–187.
- [18] E. LITCHMAN, C.A. KLAUSMEIER AND P. BOSSARD, *Phytoplankton nutrient competition under dynamic light regimes*, *Limnology and Oceanography*, 49 (2004), 1457–1462.
- [19] P. D. LEENHEER, S. A. LEVIN, E. D. SONTAG AND C. A. KLAUSMEIER, *Global stability in a chemostat with multiple nutrients.*, *J. Math. Biol.*, 52 (2006), pp. 419–438.
- [20] B. LI AND H. L. SMITH, *Global dynamics of microbial competition for two resources with internal storage*, *J. Math. Biol.*, 55 (2007), no. 4, pp. 481–515.

- [21] J. MONOD, *La technique de culture continue; theorie et applications*, Ann. Inst. Pasteur, 79 (1950), pp. 390-410.
- [22] H. L. SMITH, *Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems*, Math. Surveys Monogr 41, American Mathematical Society Providence, RI, 1995.
- [23] H. L. SMITH, *The periodically forced Droop model for phytoplankton growth in a chemostat*, J. Math. Biol., 35 (1997), no. 5, pp. 545–556.
- [24] H. L. SMITH AND P. E. WALTMAN, *Competition for a single limiting resource in continuous culture: the variable-yield model*, SIAM J. Appl. Math., 34 (1994), pp. 1113–1131.
- [25] H. L. SMITH AND P. E. WALTMAN, *The Theory of the Chemostat*, Cambridge Univ. Press, 1995.
- [26] W. WALTER, *On strongly monotone flows*, Annales Polonici Mathematici, LXVI (1997), pp. 269–274.
- [27] M. WHITE AND X.-Q. ZHAO, *A periodic Droop model for two species competition in a chemostat*, Bull. Math. Biology, 71(2009), pp. 145–161.
- [28] G. S. K. WOLKOWICZ AND X.-Q. ZHAO, *N-species competition in a periodic chemostat*, Differential and Integral Equations, 11(1998), 465-491.
- [29] X.-Q. ZHAO, *Asymptotic behavior for asymptotically periodic semiflows with applications*, Commun. Appl. Nonlinear Anal., 3 (1996), pp. 43–66.
- [30] X.-Q. ZHAO, *Dynamical Systems in Population Biology*, Springer, New York, 2003.