

Global asymptotic behaviour of aquatic vegetation in a periodical mediated system

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Abstract: In this paper, we consider a competition model between two species in an aquatic system. The operating parameters and the species specific response functions are periodic functions of time. Species-specific removal rates are also permitted to be periodic. A threshold result on the global dynamics of the scalar asymptotically periodic Kolmogorov equation is applied to a growth model of two species. Sufficient conditions ensure uniform persistence of all the species and guarantee that the full system admits at least one positive, periodic solution. The qualitative behaviour of this model is determined analytically and numerically.

Key words: Periodic Kolmogorov equations, asymptotically periodic semiflows.

AMS (MOS) subject classifications: 94A15, 92A17, 34C15, 34C35.

I. Introduction

Mathematical models of a chemostat-like model of two species of vegetation competing exploitatively for an essential, non-reproducing, growth-limiting nutrient whose concentration varies periodically with time predict competitive exclusion. That is, they predict that at most one competitor population avoids extinction (see, e.g., [1], [1], [20], [2]). However, the coexistence of competing populations is common in nature, and so in order to explain this, it seems necessary and natural to introduce periodic coefficients to represent, for example, seasonal variations in the environment.

We consider the chemostat-like model where nutrient supply, specific death rates and species-specific nutrient uptake function are assumed to be periodic with commensurate periods. The model incorporating periodic coefficients takes the following form:

$$\begin{aligned} \dot{S}(t) &= (S^0(t) - S(t))D_0(t) - \sum_{i=1}^2 c_i P_i(t, S(t))x_i(t), \\ \dot{x}_i(t) &= (P_i(t, S(t)) - D_i(t))x_i(t), \\ S(0) &= S_0 > 0, \quad x_i(0) = x_{i0}, \quad i = 1, 2. \end{aligned} \tag{1}$$

where $x_i(t)$ denotes the density of the i^{th} species or biomass at time t , $S(t)$ denotes the nutrient concentration in the water external to the plant cells at time t , $S^0(t)$ is the periodic inflow concentrations at time t , c_i is the content (or concentration) of the nutrient in the plant tissue of species i . Here, $D_0(t)$ is the rate at which the nutrient enters and leaves the aquatic system, and $D_i(t)$ is the specific removal and death rate of the i^{th} species at time t . The function

$$P_i(t, S(t)) := \frac{\mu_i(t)S(t)}{K_i + S(t)},$$

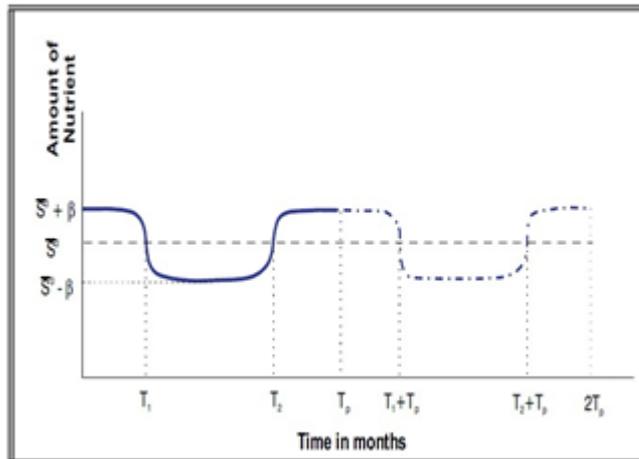
is similar to the Holling type II function [Error! Reference source not found.] and describes the per capita nutrient uptake rate of the i^{th} species, where $\mu_i(t)$ is the maximal specific growth rate of the i^{th} species at time t , K_i is the half saturation

constant for nutrient-limited growth for the i^{th} species. The model structure of Equation 1 that originates from the chemostat theory is suitable for modeling aquatic systems, since all the parameters involved in it can be measured in the field (see [2], [Error! Reference source not found.], [Error! Reference source not found.], [1]).

The periodic coefficients in the model are reasonable. Consider a situation of a fresh water lake that receives its nutrients mainly from streams draining the watershed. As seasons change, stream drainage patterns change causing variations in the supply of nutrients. This is particularly true in many fresh water lakes of East Africa. Moreover, the inflow rate $D_0(t)$ is not

constant but periodic and the period is the same as that of $S^0(t)$. In some cases, the vegetation is fed on by beetles that are their natural biological control. The beetles' rate of reproduction and rate of feeding on the vegetation is positively correlated to the temperature of the season (see [Error! Reference source not found.], [Error! Reference source not found.]). Thus $D_i(t)$, and $\mu_i(t)$, $i = 1, 2$ need to have periods that are commensurate to that of $S^0(t)$. During warmer seasons, the nutrient supply is low while in the colder seasons, the opposite is true. We assume a seasonal input nutrient concentration of the form illustrated in Figure 1.

Figure 1: Variation of Nutrient Concentration with Time



Let $S^0(t)$ represent the periodic input concentration, which fluctuates about a mean value \tilde{S} thus,

$$S^0(t) = \begin{cases} \tilde{S}^0 + \beta, & 0 \leq t \leq T_1; \\ \tilde{S}^0 - \beta, & T_1 \leq t \leq T_2; \\ \tilde{S}^0 + \beta, & T \leq t \leq T_p. \end{cases}$$

The period is T_p , which could be measured in weeks or months and $\beta > 0$ indicates the deviation from the mean value \tilde{S}^0 .

Since $S^0(t)$ sketched in Figure 1 is even, it can be represented by a Fourier series of the form,

$$S^0(t) = \tilde{S}^0 + \beta + 2\beta \frac{(T_1 - T_2)}{T_p} + \alpha(t), \quad (2)$$

where

$$\alpha(t) = \sum_{n=1}^{\infty} \frac{4\beta}{n\pi} \cos\left(\frac{n\pi}{T_p}(T_1 + T_2)\right) \sin\left(\frac{n\pi}{T_p}(T_1 + T_2)\right) \cos\frac{2\pi nt}{T_p}. \quad (3)$$

From Equation (3) we observe that $|\alpha(t)| \leq \frac{4\beta}{\pi}$. The nutrient supplied at any instant satisfies the inequality

$$S^0 - |\alpha(t)| \leq S^0(t) \leq S^0 + |\alpha(t)|$$

We know for practical purposes that $S^0 \leq \frac{4\beta}{\pi}$. This condition means that the amplitude of nutrient fluctuation about \tilde{S}^0 must be small in comparison to S^0 . Also,

$$D_0(t) = \tilde{D}_0 + \beta_0 + 2\beta_0 \frac{(T_1 - T_2)}{T_p} + \alpha_0(t),$$

where \tilde{D}_0 is the mean inflow rate, β_0 indicates the deviation from the mean value \tilde{D}_0 , and $\alpha_0(t)$ is similar to $\alpha(t)$ in (3) with β replaced by β_0 . From the biological and seasonal response thus far discussed, we have that if D_{i0} is the mean value of $D_i(t)$, then

$$D_i(t) = \begin{cases} \tilde{D}_{i0} - \beta_i, & 0 \leq t \leq T_1; \\ \tilde{D}_{i0} + \beta_i, & T_1 \leq t \leq T_2; \\ \tilde{D}_{i0} - \beta_i, & T \leq t \leq T_p, \end{cases}$$

$i = 1, 2$ where $\beta_i > 0$, are non-negative constants and $\alpha_i(t)$ is similar to $\alpha(t)$ in (3) with β replaced by $-\beta_i$. Thus,

$$D_i(t) = \tilde{D}_{i0} + \beta_i + 2\beta_i \frac{(T_1 - T_2)}{T_p} + \alpha_i(t),$$

where, without loss of generality, we have assumed that the period of $D_0(t)$ and $D_i(t)$ are the same. The shape of the $\mu_i(t)$ curve is similar to that of $D_i(t)$.

There has been some research on models similar to that in (1) involving either periodic nutrient input or periodic dilution rates (see [1], [Error! Reference source not found.], [Error! Reference source not found.], [1], [1], [1], [1], [1]). Some discussion on the periodic gradostat has also been considered (see [1], [1]). In most of the previous analytical studies of the periodic chemostat, the powerful theory of monotone dynamical systems was applied to limiting systems obtained using certain conservation principles. However, the theory of monotone dynamical systems can only be applied in this context to study the competition between at most two species. Also, in order to apply a conservation law to obtain the limiting systems, it is necessary to assume that all the removal rates are equal, thus ignoring all the species-specific death rates and only considering the dilution rate.

In this paper, we apply the theory of asymptotically periodic semiflows [Error! Reference source not found.] and the comparison method [Error! Reference source not found.] to determine criteria that guarantees the existence of at least one positive periodic solution for the full system and the uniform persistence of all the interacting species.

This paper is organized as follows. In section 2, we give some preliminaries while in section 3, the two-species model is studied and a statement of the main results is presented. In section 4, we give numerical results that seem to confirm the analytical findings. We conclude with a discussion in section 5.

II. Preliminaries

Consider the n -dimensional Kolmogorov periodic system

$$\dot{u} = uF_0(t, u), \tag{4}$$

Where $u = (u_1, u_2, \dots, u_n) \in \square_+^n$. We assume that $F_0 = (F_{01}, F_{02}, \dots, F_{0n}) : \square_+^{n+1} \rightarrow \square_+^n$ is continuous and ω -periodic with respect to t ($\omega > 0$), and that the solution $\phi_0(t, u)$ of (4) with $\phi_0(0, u) = u$ exists uniquely on $[0, \infty)$. Let

$S = \phi_0(\omega, \cdot) : \square_+^n \rightarrow \square_+^n$. Then $S^m(u) = \phi_0(m\omega, u), \forall u \in \square_+^n$.

Lemma 2.1. *If for some $1 \leq i \leq n$,*

$u^*(t) = (u_1^*(t), \dots, u_{i-1}^*(t), 0, u_{i+1}^*(t), \dots, u_n^*(t))$, *is an ω -periodic solution of (4) with $u_j^*(0) \geq 0, \forall 1 \leq j \leq n, j \neq i$, and*

$u^*(t)$ *satisfies $\int_0^\omega F_{0i}(t, u^*(t)) dt > 0$ then there exists a $\delta > 0$ such that $\limsup_{m \rightarrow \infty} d(S^m(u), u^*(0)) \geq \delta, \forall u \in \text{int}(\square_+^n)$.*

Also consider the n -dimensional non autonomous Kolmogorov system

$$\dot{u} = uF(t, u) \quad 1 \leq i \leq n, \tag{5}$$

Where $u = (u_1, u_2, \dots, u_n) \in \square_+^n$. We assume that $F = (F_1, F_2, \dots, F_n) : \square_+^{n+1} \rightarrow \square_+^n$ is continuous and locally Lipschitz in u . For $s \geq 0$, let $\phi_0(t, s, u)$ and $\phi(s, s, u) = u$ respectively.

Define $T_m := \phi(m\omega, 0, u)$, $T(t)u := \phi_0(t, 0, u)$ and $S(u) := T(\omega)u, \forall m \geq 0, t \geq 0, u \in \square_+^n$.

Lemma 2.2. *Assume that $\lim_{t \rightarrow \infty} |F(t, u) - F_0(t, u)| = 0$ uniformly for u in any bounded subset of \square_+^n , and that solutions of*

(4) and (5) are uniformly bounded in \square_+^n . If for some $1 \leq i \leq n$,

$$u^*(t) = (u_1^*(t), \dots, u_{i-1}^*(t), 0, u_{i+1}^*(t), \dots, u_n^*(t))$$

is an ω -periodic solution of (4) with $u_j^(0) \geq 0, \forall 1 \leq j \leq n, j \neq i$, and $u^*(t)$ satisfies $\int_0^\omega F_{0i}(t, u^*(t)) dt > 0$ then,*

$$\tilde{W}^s(u^*(0)) \cap \text{int}(\square_+^n) = \emptyset,$$

where

$$\tilde{W}^s(u^*(0)) = \left\{ u \in \square_+^n : \lim_{m \rightarrow \infty} T_m(u) = u^*(0) \right\}.$$

Consider equations (4) and (5) with $n = 1$. This will represent a single population growth model. Assume that

(A1) $\lim_{t \rightarrow \infty} |F(t, u) - F_0(t, u)| = 0$ uniformly for u in any bounded subset of \square_+^n , and

there exists $K > 0$ such that $F(t, u) \leq 0, t \geq 0, u \geq K$;

(A2) For any $t \geq 0, F_0(t, u)$ is strictly decreasing for u , and there exists $K_0 > 0$

such that $F_0(t, K_0), t \geq 0$.

We have the following threshold dynamics for the asymptotically periodic equation (5) with $n = 1$.

Lemma 2.3. Assume that A1 and A2 hold

(a) If $\int_0^\omega F_0(t, 0)dt \leq 0$, then $\lim_{t \rightarrow \infty} \phi(t, 0, u) = 0, \forall u \in \mathbb{R}_+$;

(b) $\int_0^\omega F_0(t, 0)dt > 0$ then $\lim_{t \rightarrow \infty} (\phi(t, 0, u) - u^*(t)) = 0, \forall u \in \mathbb{R}_+ \setminus \{0\}$, where $u^*(t)$ is the unique positive ω -periodic solution of the periodic Kolmogorov equation (4) with $n = 1$.

The reader is referred to [1] for proof of these lemmas.

III. Analysis of the Model

If we let $\bar{x}_i(t) = c_i x_i(t)$ and ignore the bars for notational brevity, system (1) becomes

$$\begin{aligned} \dot{S}(t) &= (S^0(t) - S(t))D_0(t) - \sum_{i=1}^2 P_i(t, S(t))x_i(t), \\ \dot{x}_i(t) &= (P_i(t, S(t)) - D_i(t))x_i(t), \\ S(0) &= S_0 > 0, x_i(0) = x_{i0}, i = 1, 2. \end{aligned} \tag{6}$$

Throughout this paper, we identify the unique solution of Equation (6) by the set

$$(S(t), x_1(t), x_2(t)) \in \mathbb{R}_+^3, S \geq 0, x_i \geq 0, 1 \leq i \leq 2,$$

Where \mathbb{R}_+^3 is a real 3-dimensional non-negative vector space. By asserting that $(S(t), x_1(t), x_2(t))$ is positive, we mean that each component of the solution is positive for all $t > 0$.

The following results found, for example, in [1] will be useful in our analysis.

Let $D(t) : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ be a continuous, ω -periodic, and positive function. The linear periodic equation

$$\dot{V}(t) = S^0(t)D_0(t) - D(t)V(t), V(0) \geq 0, \tag{7}$$

has a unique positive ω -periodic solution $V^*(t)$ such that every solution $V(t)$ of (7) with $V(0) \geq 0$ satisfies

$$\lim_{t \rightarrow \infty} (V(t) - V^*(t)) = 0.$$

Indeed, $V^*(t)$ is given by

$$V^*(t) = e^{-\int_0^t D(s)ds} \left[\frac{\int_0^\omega e^{\int_0^s D(u)du} S^0(s)D_0(s)ds}{\int_0^\omega D(s)ds - 1} + \int_0^t e^{\int_0^s D(u)du} S^0(s)D_0(s)ds \right].$$

Let $\bar{D}(t) = \max\{D_0(t), D_1(t), D_2(t)\}$ and $\underline{D}(t) = \min\{D_0(t), D_1(t), D_2(t)\}$. Clearly $\bar{D}(t)$ and $\underline{D}(t) : \mathbb{R}_+ \rightarrow \mathbb{R}_+$

are continuous, ω -periodic and positive functions. Let $V_1^*(t)$ and $V_2^*(t)$ be the unique positive ω -periodic solutions of (7)

with $D(t)$ replaced by $\underline{D}(t)$ and $\bar{D}(t)$ respectively. By the comparison theorem and the global attractivity of

$V_i^*(t), i = 1, 2$, it easily follows that $V_2^*(t) \leq V_1^*(t), \forall t \geq 0$.

The following result concerns the periodic solution of the model in Equation (6).

Theorem 3.1. Assume that

1) $\int_0^\omega (P_i(t, V_1^*(t)) - D_i(t))dt > 0, i = 1, 2;$

2) $\int_0^\omega (P_i(t, V_2^*(t)) - x_j(t)) - D_i(t)dt > 0, i, j = 1, 2, i \neq j$ where $x_j^*(t)$ is the unique positive, ω -periodic

solution of the scalar periodic equation $\dot{x}_j = x_j(P_j(t, V_1^*(t)) - x_j) - D_j(t), 1 \leq j \leq n$. Then system (6) admits a

positive ω -periodic solution, and there exists $\alpha > 0$ and $\beta > 0$ such that any solution $(S(t), x_1(t), x_2(t))$ of (6) satisfies

$$0 < \alpha \leq \liminf_{t \rightarrow \infty} x_i(t) \leq \limsup_{t \rightarrow \infty} x_i(t) \leq \beta, i = 1, 2.$$

Proof. We first show that the solution to (6) is positive.

By Lemma 2.3, condition (1) implies that the periodic equation

$$\dot{x}_i(P_i(t, V_1^*(t)) - x_i) - D_i(t), i = 1, 2,$$

admits a unique ω -periodic solution $x_i(t)$ that is globally attractive in $\mathbb{R}_+ \setminus \{0\}$. We further claim that

$V_1^*(t) > x_i^*(t), \forall t \in [0, \omega]$. Indeed, let $x_i^*(t_1) = \max_{0 \leq t \leq \omega} x_i^*(t), t_1 \in [0, \omega], i = 1, 2$. Then $\dot{x}_i^*(t_1) = 0$, and hence

$$P(t_1, V_1^*(t_1) - x_i^*(t_1)) = D_1(t_1) > 0.$$

Since $P(t, s)$ is strictly increasing for $s \in \mathbb{R}_+, V_1^*(t_1) > x_i^*(t_1)$. Let $y(t) = V_1^*(t) - x_i^*(t)$. Then $y(t)$ satisfies the periodic differential equation

$$\dot{y} = S^0(t)D_0(t) - \underline{D}(t)V_1^*(t) - (V_1^*(t) - y)(P(t, y) - D_1(t)). \tag{8}$$

Since $y(t_1) > 0$ and

$$\dot{y}|_{y=0} = S^0(t)D_0(t) + (D_1(t) - \underline{D}(t))V_1^*(t) \geq S^0(t)D_0(t) > 0$$

it follows that $y(t) > 0, \forall t \geq t_1$. Thus the ω -periodicity of $y(t)$ implies that $y(t) > 0, \forall t \geq 0$; that is,

$$V_1^*(t) > x_i^*(t), \forall t \geq 0.$$

For any $(S_0, x_0) = (S(0), x_1(0), x_2(0)) \in \mathbb{R}_+^3$ with $x_i(0) > 0, i = 1, 2$, let $(S(t), x(t)) = (S(t), x_1(t), x_2(t))$ be the unique solution of (6) on the maximal interval of existence $[0, t_+)$. Since $\dot{S}(t)|_{s=0} = S^0(t)D_0(t) > 0$, it follows that $S(t) > 0$, and $x(t) > 0, \forall t \in [0, t_+)$.

We now show that the solution is bounded.

Let $V(t) := S(t) + x_1(t) + x_2(t)$. Then

$$S^0(t)D_0(t) - \bar{D}(t)V(t) \leq \dot{V}(t) \leq S^0(t)D_0(t) - \underline{D}(t)V(t)$$

Therefore, by the comparison theorem, we get

$$\underline{V}(t) \leq V(t) \leq \bar{V}(t), \forall t \in [0, t_+), \tag{9}$$

where $\bar{V}(t)$ is the unique solution of the linear ω -periodic equation

$$\dot{\bar{V}}(t) = S^0(t)D_0(t) - \underline{D}(t)\bar{V}(t)$$

with $\bar{V}(0) = V(0)$, and $\underline{V}(t)$ is the unique solution of the linear ω -periodic equation

$$\dot{\underline{V}}(t) = S^0(t)D_0(t) - \bar{D}(t)\underline{V}(t)$$

with $\underline{V}(0) = V(0)$. The global existence of $\bar{V}(t)$ on $[0, \infty)$ implies that $t_+ = \infty$. Since $\lim_{t \rightarrow \infty} (\bar{V}(t) - V_1^*(t)) = 0$, $V(t)$ and

hence $S(t)$ and $x(t)$ are ultimately bounded; that is, system (6) is point dissipative on \mathbb{R}_+^3 . Therefore, for all $t \geq 0, i = 1, 2$,

$$\dot{x}_i(t) = x_i(t) \left(P_i(t, V(t) - \sum_{j=1}^2 x_j(t)) - x_i(t) - D_i(t) \right) \leq x_i(t) (P_i(t, V(t)) - D_i(t)).$$

By the comparison theorem, it follows that

$$x_i(t) \leq \bar{x}_i(t), \forall t \geq 0, i = 1, 2, \tag{10}$$

where $\bar{x}_i(t)$ is the unique solution of the non autonomous equation

$$\dot{\bar{x}}_i(t) = \bar{x}_i(t) (P_i(t, \bar{V}(t) - \bar{x}_i(t)) - D_i(t)), \bar{x}_i(0) = x_i(0) > 0, i = 1, 2. \tag{11}$$

Since $\lim_{t \rightarrow \infty} (\bar{V}(t) - V_1^*(t)) = 0$, we get

$$\lim_{t \rightarrow \infty} (P_i(t, \bar{V}(t) - \bar{x}_i(t)) - (P_i(t, V_1^*(t)) - x_i(t))) = 0$$

uniformly for x_i in any bounded subset of \mathbb{R}_+ . Since

$$\int_0^\omega (P_i(t, V_1^*(t)) - D_i(t)) dt > 0,$$

by lemma 2.3b we have that

$$\lim_{t \rightarrow \infty} (\bar{x}_i(t) - x_i^*(t)) = 0, i = 1, 2 \tag{12}$$

By (9) and (10), it then follows that for any $i = 1, 2$, and $t \geq 0$,

$$\dot{x}_i(t) = x_i(t) \left(P_i(t, V(t) - \sum_{j=1}^2 x_j(t)) - D_i(t) \right) \geq x_i(t) (P_i(t, \underline{V}(t)) - \bar{x}_j(t) - x_i(t) - D_i(t)), \quad (13)$$

$i, j = 1, 2, \quad i \neq j$

and hence, by the comparison theorem,

$$x_i(t) \geq \underline{x}_i(t), \quad t \geq 0, \quad i = 1, 2, \quad (14)$$

where $\underline{x}_i(t)$ is the unique solution of the non autonomous equation

$$\dot{x}_i(t) = x_i(t) (P_i(t, \underline{V}(t) - x_j(t) - x_i(t)) - D_i(t)), \quad i, j = 1, 2 \quad i \neq j \quad (15)$$

with $\underline{x}_i(0) = x_i(0) > 0, \quad i = 1, 2$. Since $\lim_{t \rightarrow \infty} (\underline{V}(t) - V_2^*(t)) = 0$, we have

$$\lim_{t \rightarrow \infty} (P_i(t, \underline{V}(t) - x_j^*(t) - x_i(t)) - P_i(t, V_2^*(t) - x_j^*(t) - x_i(t))) = 0, \quad i, j = 1, 2 \quad i \neq j \quad (16)$$

uniformly for x_i in any bounded subset of \square_+ . Since

$$\int_0^\omega (P_i(t, V_2^*(t) - x_j(t)) - D_i(t)) dt > 0, \quad i, j = 1, 2, \quad i \neq j$$

by lemma 2.3b we have that

$$\lim_{t \rightarrow \infty} (\underline{x}_i(t) - \underline{x}_i^*(t)) = 0, \quad i = 1, 2 \quad (17)$$

where $\underline{x}_i^*(t), \quad i = 1, 2$, is the unique positive ω -periodic solution of the periodic equation

$$\dot{x}_i(t) = x_i(t) (P_i(t, V_2^*(t) - x_j^*(t) - x_i(t)) - D_i(t)), \quad i, j = 1, 2, \quad i \neq j \quad (18)$$

By (10), (12), (14), and (17), it then follows that

$$\liminf_{t \rightarrow \infty} (x_i(t) - \underline{x}_i^*(t)) \geq 0 \geq \limsup_{t \rightarrow \infty} (x_i(t) - \underline{x}_i^*(t)), \quad i = 1, 2. \quad (19)$$

Clearly, (19) implies that there exists $\alpha > 0$ and $\beta > 0$ such that any solution $(S(t), x(t))$ of (6) with $S(0) \geq 0$ and $x_i(0) > 0, \quad i = 1, 2$ satisfies

$$0 < \alpha \leq \liminf_{t \rightarrow \infty} x_i(t) \leq \limsup_{t \rightarrow \infty} x_i(t) \leq \beta, \quad i = 1, 2.$$

We now prove the existence of a positive ω -periodic solution to equation (6).

Let $X := \square_+^3$,

$$X_0 := \{(S(t), x_1(t), x_2(t)) \in \square_+^3 : x_i > 0, \quad \forall 1 \leq i \leq 2\},$$

and

$$\partial X_0 := \{(S(t), x_1(t), x_2(t)) \in \square_+^3 : x_i > 0, \quad \text{for some } 1 \leq i \leq 2\}.$$

Then, $X = X_0 \cup \partial X_0$. For any $y = (S_0, x_0) \in X$, equation (6) has a unique solution, $\phi(t, y)$, with $\phi(0, y) = y$.

The map $T(t) = \phi(t, \cdot) : X \rightarrow X$ is a periodic semiflow [2] and $T(t)X_0 \subset X_0, \quad \forall t \geq 0$. We also know that $T(t)$ is point dissipative; that is ultimately bounded in X and uniformly persistent with respect to $(X_0, \partial X_0)$, in the sense that there exists $\eta > 0$ such that for any $y \in X_0, \quad \liminf_{t \rightarrow \infty} d(T(t)y, \partial X_0) \geq \eta$. Let $Q = T(\omega) : X \rightarrow X$ be the Poincare map associated with equation (6). Then by [22] theorem 8.5, the ultimate boundedness of solutions of a periodic system of ordinary differential equations implies the uniform boundedness of solutions, and hence $Q : X \rightarrow X$ is compact.

Therefore, by [2] theorem 2.3, Q admits a fixed point $y_0 \in X_0$ and hence $\phi(t, y_0)$ is a periodic solution of equation (6). Let

$y_0 = (S(0), x_1(0), x_2(0)) \in X_0$. Then $S_0 > 0; \quad x_1(0) > 0$ and $x_2(0) > 0$. It then follows that

$\phi(t, y_0) = (S(t), x_1(t), x_2(t))$ satisfies $S(t) > 0$ and $x_1(t) > 0, \quad x_2(t) > 0$. Consequently, $\phi(t, y_0)$ is a positive ω -periodic solution of (6).

4 Numerical Results

In our model, the nutrient supply and specific death rates are assumed to be periodic with commensurate periods. The nutrient input concentration is described by (2) and (3). We use the following explicit Fourier series to describe the nutrient input function:-

$$S^0(t) = \tilde{S}^0 + \beta \sum_{j=1}^n \cos(j\omega t) \quad (20)$$

As an example, if we set $\tilde{S}^0 = 11$, $n = 9$ we obtain Figure 2 that describes the input nutrient concentrations:-

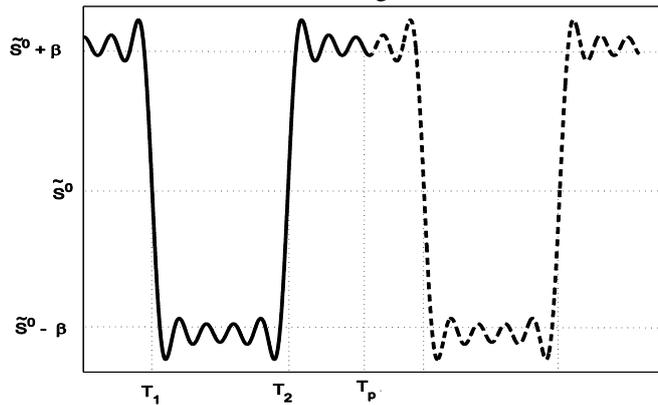


Figure 2: Nutrient Input as described by (20)

Clearly, this figure approximates that envisaged by Figure 1. The level of accuracy of the function may be increased by adding more harmonics to the function, that is making n to be as large as we desire.

It is reasonable to take input nutrient supply of the form

$$D^0(t) = \tilde{D}_0 - \alpha \sum_{j=1}^n \cos(j\omega t), \tag{21}$$

so that the nutrient supply and death rates have commensurate periods. For practical purposes, the fluctuations of the nutrient supply must not be very large, and specifically, we choose our values such that (20) is non-negative, that is

$$\tilde{S}^0 \geq \left| \beta \sum_{j=1}^n \cos(j\omega t) \right|. \text{ For simplicity, we let } D_0(t) = D_1(t) = D_2(t) = \tilde{D}_0 - \alpha \sum_{j=1}^n \cos(j\omega t).$$

We have assumed a Holling type II function for species specific nutrient uptake function $P_i(t, S(t))$ defined by

$$P_i(t, S(t)) = \frac{\mu_i(t)S(t)}{K_i + S(t)}. \text{ With these, (6) is explicitly given by}$$

$$\dot{S}(t) = \left(\tilde{S}^0 + \beta \sum_{j=1}^n \cos(j\omega t) - S(t) \right) \left(\tilde{D}_0 - \alpha \sum_{j=1}^n \cos(j\omega t) \right) - \frac{x_1 \mu_1(t) S(t)}{K_1 + S(t)} - \frac{x_2 \mu_2(t) S(t)}{K_2 + S(t)}$$

$$\dot{x}_1(t) = \left(\frac{\mu_1(t)S(t)}{K_1 + S(t)} - (\tilde{D}_0 - \alpha \sum_{j=1}^n \cos(j\omega t)) \right) x_1(t) \tag{22}$$

$$\dot{x}_2(t) = \left(\frac{\mu_2(t)S(t)}{K_2 + S(t)} - (\tilde{D}_0 - \alpha \sum_{j=1}^n \cos(j\omega t)) \right) x_2(t).$$

We then select the following parameter values that satisfy Lemma 2.3b that give the time plot of numerical solutions of (22) given by Figure 3.

Table 1. Parameter values used in (22) for Figure 3

Parameter	D_0	β	S^0	ω	μ_1	K_1	μ_2	K_2	$x_1(0)$	$x_2(0)$	n	α
Value	0.4675	$\frac{4}{\pi}$	11	1.5	1	1	0.7	0.4	10	10	9	0.3

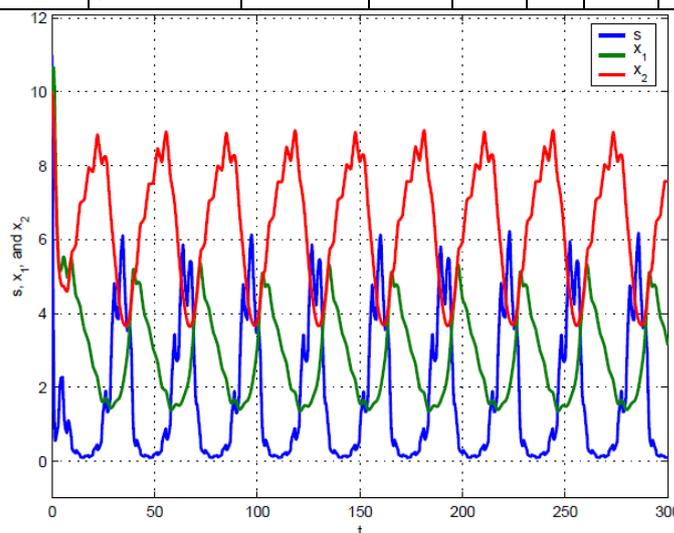


Figure 3: Time Plot for (22)

Figure 3 shows a more realistic existence of each of the competing species as well as the nutrient. As is observed in nature, there are some perturbations in the species at all times. This is reasonable given that deaths occur at all times even when the population is increasing. It is also naturally observed that there will be small increases in population when the general trend is a decline in species biomass.

The numerical results above are confirmed by the following 3-D plot of $S(t)$, $x_1(t)$, and $x_2(t)$.

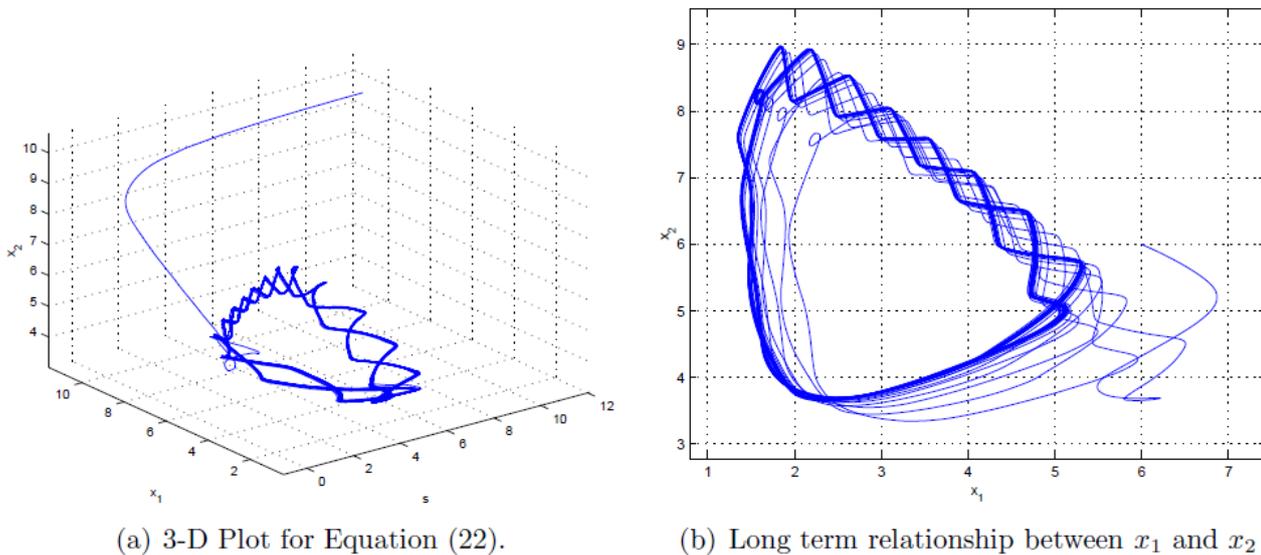


Figure 4: Biomass of x_1 and x_2

We can clearly see from Figures 3 and 4(a) that the solution of (22) remains in the positive interior of (S, x_1, x_2) , meaning that $(S(t), x_1(t), x_2(t)) \in \text{int } \mathbb{R}_+^3$, $0 \leq t \leq \infty$. This behaviour is consistent with what we have determined analytically. The fact that both competing species do not explode (grow without bound) and do not become extinct is clearly demonstrated by the 2-D time plot in Figure 4(b) of x_1 against x_2 . These results are important because models with non-periodic coefficients consistently predict competitive exclusion while we observe that in nature, species competing for a nutrient often exist.

IV. Conclusion

In this paper, we have shown, both analytically and numerically, that (6) admits at least one positive, periodic solution that ensures uniform persistence of all the competing species as predicted by Theorem 3.1. The choice of Fourier series for input and dilution rates is reasonable. In nature, during the warm season, there are temperature variations during the day and at night. The same applies during the cold season. For the case of fresh water lake, assuming nutrients are delivered by run off from rain water, we expect more nutrients during the wet season. However, during this season, it does not rain everyday. Hence we expect some variations in input concentrations within this time as well. The same case would apply during the dry season. During this time, there are usually some light drizzles that would keep the input nutrient concentration fluctuating. In addition, we can modify various parameters in the Fourier series to model specific cases by increasing the amplitude or the period of the function.

Models of the chemostat that assume constant parameters always predicts competitive exclusion, [2]. Our model predicts co-existence and agrees more with what is observed in nature.

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