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Existence, uniqueness and stability analysis of allelopathic stimulatory phytoplankton model [☆]

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ABSTRACT

In this paper we consider the two species competitive delay plankton allelopathy stimulatory model system. We show the existence and uniqueness of the solution of the deterministic model. Moreover, we study the persistence of the model and the stability properties of its equilibrium points. We illustrate the theoretical results by some numerical simulations.

1. Introduction

The term plankton refers to the freely floating and weakly swimming organisms within aquatic environment. The plant species commonly known as phytoplankton are unicellular and microscopic in size. Phytoplankton have a significant utility in marine life and they play a vital role at the base of the marine food chain. They also control the global carbon cycle which has a significant impact on the climate regulation. The regular change and abrupt fluctuation of phytoplankton density within aquatic environment are controlled by several factors, e.g., variation of available nutrients, environmental forcing due to seasonal change in environment and many others (for details, see [1]). A remarkable feature associated with many phytoplankton populations is the occurrence of bloom formation. A drastic increase in phytoplankton population, up by several orders of magnitude which is shortly followed by a sudden collapse whereby phytoplankton population returns to its original low-level. This kind of rapid growth followed by sudden decay in phytoplankton population is known as '*phytoplankton bloom*'. There has been a global increase in harmful plankton blooms in the last two decades and considerable scientific attention has been paid towards harmful algal blooms in recent years [2–5].

An important observation made by several researchers is that the change in population density of one phytoplankton species has the ability to affect the growth of several other species by producing toxic substances, and this is a responsible factor for bloom formation of various phytoplankton species. The term "allelopathy" was first introduced by Molisch (1937), and then defined extensively for plankton communities by Rice [6]. According to Rice [6], allelopathy is the effect of one plant species on the growth of another by releasing a chemical compound into the surrounding environment. These types of chemical compounds released by various plants are known as "allelochemicals" [7]. Allelochemicals released by one species of phytoplankton may have both positive and negative effects on the growth of another species. For example, the green alga,

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Enteromorpha linza, produces allelochemicals which are auto-stimulatory and stimulatory to the growth of another phytoplankton species named as *Enteromorpha species* [8]. On the other hand, unicellular green alga, *Chlorella vulgaris* produces autotoxin which has the ability to regulate the growth of its own population and inhibits the growth of *Asterionella formosa* and *Nitzschia frustulum* [9,10].

The first mathematical model for allelopathic interaction between two competing species is introduced by Maynard-Smith [11]. The model is based upon a two-species Lotka–Volterra competition model with an additional term to take into account the effect of toxic substances released by one species to another. Detailed mathematical analysis is carried out by Chattopadhyay [12] to study the interaction between two competing allelopathic–phytoplankton species where each species is capable to produce toxic substances. The allelopathic term is proportional to the product of the square of the concentration of the non-toxic species with the concentration of the toxic species. In terms of mathematical notations, if $N_1(t)$ denotes the density of the affected species and $N_2(t)$ that of the toxic one at any instant of time t, then the allelopathic interaction term takes the form $\gamma N_1^2(t)N_2(t)$ where γ is the allelopathic interaction parameter. Mukhopadhyay et al. [13] studied the interaction between two competing phytoplankton species for the situations, where either species inhibits the growth of other species or for the case where either species stimulates the growth of the second phytoplankton species. They have incorporated discrete time delay to take account of the fact that the production of allelopathic substance is not instantaneous but rather delayed by some time required for maturation of the species. The dynamics of competitive models of phytoplankton in presence of toxic substances have received significant attention now a days. Various dynamical aspects, like, persistence, extinction of either species for ordinary differential equation models as well as delay differential equation models explore the effect of toxic substances on the evolution of phytoplankton populations. For detailed discussion in this direction, interested readers may concern the recent works [14–18].

The purpose of the present paper is to consider the dynamic behavior of two competing phytoplankton species where one species releases auxin and has a positive feedback on the growth of the other phytoplankton species. A discrete time delay parameter is introduced to model the time required for the maturation of one phytoplankton species such that it is capable to produce allelopathic substance.

The organization of this paper is as follows: In Section 2 we describe the basic model system for two competitive phytoplankton species and study the related dynamical behavior. In Section 3 we discuss the existence, uniqueness and persistence and stability of the delay model system. We also perform some numerical simulation to validate the analytical results.

2. Basic mathematical model

The classical Lotka–Volterra model for two competing phytoplankton species is governed by the following system of coupled nonlinear ordinary differential equations

$$\begin{aligned}\frac{du(t)}{dt}&=u(t)\big(k_1-\alpha_1u(t)-\beta_{12}v(t)\big),\\ \frac{dv(t)}{dt}&=v(t)\big(k_2-\alpha_2v(t)-\beta_{21}u(t)\big),\end{aligned}\tag{2.1}$$

where $u(t)$ and $v(t)$ denote the densities of two phytoplankton species at any instant of time 't'. $k_1, k_2 > 0$ are the cell proliferation rates per time unit, $\alpha_1, \alpha_2 > 0$ are the rates of intra-specific competition for the first and the second species respectively, and $\beta_{12}, \beta_{21} > 0$ stand for the rates of interspecific competition between the first and the second and between the second and the first species respectively. The quantities $\frac{k_1}{\alpha_1}$ and $\frac{k_2}{\alpha_2}$ are the environmental carrying capacities for the two species, e.g., $(u, v) = (0, \frac{k_2}{\alpha_2})$ and $(u, v) = (\frac{k_1}{\alpha_1}, 0)$ are stationary solutions of (2.1). Next we assume that the first species is capable to release allelopathic substances which stimulate the growth of the second species. As we have discussed in the Introduction, we incorporate an additional term into the growth equation of the second species to model the allelopathic interaction as follows

$$\begin{aligned}\frac{du(t)}{dt}&=u(t)\big(k_1-\alpha_1u(t)-\beta_{12}v(t)\big),\\ \frac{dv(t)}{dt}&=v(t)\big(k_2-\alpha_2v(t)-\beta_{21}u(t)+\gamma u(t)v(t)\big),\end{aligned}\tag{2.2}$$

where γ denotes the rate of allelopathic substance released by the first phytoplankton species. System (2.2) can be written as $\frac{d}{dt}U(t) = f(U(t))$ for $U(t) := (u(t), v(t))$ and the locally Lipschitz continuous function

$$f:\mathbb{R}^2\to\mathbb{R}^2,\quad (u,v)\mapsto\big(u(k_1-\alpha_1u-\beta_{12}v),\,v(k_2-\alpha_2v-\beta_{21}u+\gamma uv)\big).$$

Hence, by the Picard–Lindelöf theorem, the solution of (2.2) with initial condition $(u(0), v(0)) = (u_0, v_0)$ exists locally and is unique.

From now on, we restrict our attention to the biologically relevant initial conditions $u_0 \geqslant 0$, $v_0 \geqslant 0$. In Section 3, we will prove for a delay system which contains (2.2) as a special case, that for sufficiently small $u(0)$ the solution exists globally

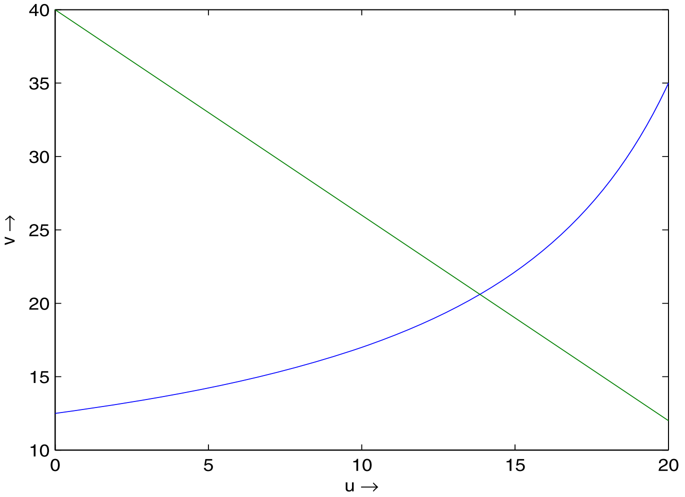

Fig. 1. u-isocline and v-isocline intersect at E_*.

and remains bounded, provided

$$\alpha_1\alpha_2 > k_1\gamma \tag{2.3}$$

(see Theorem 3.6). We will also see that the solutions are persistent (see Theorem 3.9).

We are also interested in the equilibrium points of the model system (2.2) in $\mathbb{R}^2_{\geqslant 0} := \{(u, v) \in \mathbb{R}^2\colon\ u \geqslant 0,\ v \geqslant 0\}$. These equilibria are the corresponding zeros of the function f, namely

$$\begin{aligned}
&E_1 = (0, 0) \quad \text{trivial equilibrium point},\\
&E_2 = \left(\frac{k_1}{\alpha_1}, 0\right) \quad \text{first axial equilibrium point},\\
&E_3 = \left(0, \frac{k_2}{\alpha_2}\right) \quad \text{second axial equilibrium point},\\
&E_* = (u_*, v_*) \quad \text{co-existing equilibrium points}.
\end{aligned}$$

The components of the co-existing equilibrium points E_* are given by

$$v_* = \frac{k_1 - \alpha_1 u_*}{\beta_{12}}, \tag{2.4}$$

where u_* is a positive real root of the quadratic equation

$$\alpha_1\gamma x^2 + (\beta_{12}\beta_{21} - k_1\gamma - \alpha_1\alpha_2)x + k_1\alpha_2 - \beta_{12}k_2 = 0.$$

Depending upon the parameters there are, even under condition (2.3), two, one or no co-existing equilibrium points $E_* \in \mathbb{R}^2_{\geqslant 0}$.

Observe, that equilibrium points are the intersections of the zero growth isoclines for the two phytoplankton species. In particular, the co-existing equilibrium points E_* are the intersections of the curves

$$k_1 - \alpha_1 u - \beta_{12} v = 0, \tag{2.5}$$

$$k_2 - \alpha_2 v - \beta_{21} u + \gamma u v = 0 \tag{2.6}$$

in the first quadrant. The second equation represents a rectangular hyperbola. One branch of it meets the v-axis at the boundary equilibrium $(0, \frac{k_2}{\alpha_2})$ and has the vertical asymptote $u = \frac{\alpha_2}{\gamma}$. First equation represents a straight line passing through the points $(\frac{k_1}{\alpha_1}, 0)$ and $(0, \frac{k_1}{\beta_{12}})$. A sufficient condition for the existence of an interior equilibrium point is $\frac{k_2}{\alpha_2} < \frac{k_1}{\beta_{12}}$. A suitable choice of parameters is $k_1 = 2$, $k_2 = 1$, $\alpha_1 = 0.07$, $\alpha_2 = 0.08$, $\beta_{12} = 0.05$, $\beta_{21} = 0.015$, $\gamma = 0.003$. For dimensions and ecological justification of the chosen values readers can consult the papers by Bandyopadhyay [5] and Mukhopadhyay et al. [13]. For this chosen set of parameter values the model system has unique interior equilibrium point $E_* = (13.85, 20.61)$. The isoclines are plotted in Fig. 1.

3. Existence, stability and persistence results for the delay system

It has been observed that some algae produce auxins which stimulate the growth of the other algae, for more details we refer to [8,13]. The production of the allelopathic substance will not be instantaneous, but delayed by some discrete time lag required for maturity of the species. Hence we consider the following model with delay of the allelopathic stimulatory system in which the first species produces a substance stimulatory to the growth of the second species,

$$\begin{aligned} \frac{du(t)}{dt} &= u(t)\big(k_1 - \alpha_1 u(t) - \beta_{12} v(t)\big), \\ \frac{dv(t)}{dt} &= v(t)\big(k_2 - \alpha_2 v(t) - \beta_{21} u(t) + \gamma u(t-\tau) v(t)\big) \end{aligned} \tag{3.1}$$

for $t > 0$. This system is well posed if we prescribe the following initial conditions:

$$\begin{aligned} &u(t) = \phi(t) > 0 \quad \text{for } t \in [-\tau, 0], \\ &v(0) = v_0 > 0. \end{aligned} \tag{3.2}$$

Here, $\tau \geqslant 0$ is the time required for the maturity of the first species and $\phi \in C^0([-\tau, 0]; \mathbb{R}_{>0})$ a given function.

In this section we first show the existence and uniqueness of the solutions of the allelopathic stimulatory phytoplankton model (3.1)–(3.2) and then analyze the persistence and boundedness of the solutions. We use the following definition:

Definition 3.1. System (3.1)–(3.2) is said to be persistent if every solution (u, v) satisfies the two conditions

(1) $u(t) > 0$ and $v(t) > 0$ for all $t > 0$,
(2) $\liminf_{t\to\infty} u(t) > 0$ and $\liminf_{t\to\infty} v(t) > 0$.

Remark 3.2. The two conditions in Definition 3.1 can be expressed equivalently by the single condition

(3) $\inf_{t>0} u(t) > 0$ and $\inf_{t>0} v(t) > 0$.

The following elementary lemma will be useful later (see [19]):

Lemma 3.3. *If $a, b > 0$ and $u'(t) \leqslant (\geqslant)\, u(t)(b - au(t))$, $u(t_0) > 0$, then we have*

$$\limsup_{t\to\infty} u(t) \leqslant \frac{b}{a} \quad \left(\liminf_{t\to\infty} u(t) \geqslant \frac{b}{a}\right).$$

In fact, we have the following quantitative statement:

Lemma 3.4. *If $a, b > 0$ and $u'(t) \leqslant u(t)(b - au(t))$, $u(0) > 0$, then, for all $t \geqslant 0$,*

$$u(t) \leqslant \frac{b}{a - ce^{-bt}}$$

with $c = a - \frac{b}{u(0)}$. In particular, $u(t) \leqslant \max\{u(0), \frac{b}{a}\}$ for all $t \geqslant 0$.

Proof. Let $\mu(t) := \frac{\bar{b}}{a - ce^{-\bar{b}t}}$ with $c := a - \frac{\bar{b}}{u(0)}$ and $\bar{b} > b$. Then, $u(0) = \mu(0)$ and $\mu' = \mu(\bar{b} - a\mu)$. Suppose, $u(\delta) > \mu(\delta)$ for some $\delta > 0$. Then, there is a maximal interval $[0, t]$ on which $u \leqslant \mu$. In t, we have $u'(t) \leqslant u(t)(b - au(t)) = \mu(t)(b - a\mu(t)) < \mu(t)(\bar{b} - a\mu(t)) = \mu'(t)$. Hence $u \leqslant \mu$ on some interval $[0, t + \epsilon]$ for a positive ϵ, contradicting the maximality of t. Hence, we have $u \leqslant \mu$ for all $t \geqslant 0$. As $\bar{b} > b$ was arbitrary, the claim follows. □

Now we want to prove global existence and uniqueness of solutions of (3.1)–(3.2) by continuous induction. We consider

$$I := \big\{t \geqslant 0\colon\ \forall s < t\ \exists \text{ a unique solution of (3.1)–(3.2) on } [0, s)\big\}$$

and we will show that

(1) I is non-empty,
(2) I is open,
(3) I is closed.

Indeed, this implies $I = \mathbb{R}_{\geqslant 0}$, and hence a global unique solution of (3.1)–(3.2) exists. As the system is not globally Lipschitz, and therefore a suitable a priori estimate will be necessary to show that solutions stay bounded.

First step. I is non-empty: On the interval $[0,\tau]$, we have

$$\begin{aligned}\frac{du(t)}{dt} &= u(t)\big(k_1 - \alpha_1 u(t) - \beta_{12} v(t)\big),\\ \frac{dv(t)}{dt} &= v(t)\big(k_2 - \alpha_2 v(t) - \beta_{21} u(t) + \gamma\phi(t-\tau)v(t)\big),\end{aligned} \tag{3.3}$$

with initial condition $(u(0), v(0)) = (\phi(0), v_0)$. Notice that this system is non-autonomous and equivalent to $\frac{d}{dt}U(t) = f(t, U(t))$ for $U(t) := (u(t), v(t))$ and the function

$$\begin{aligned}&f : [0,t] \times \mathbb{R}^2 \to \mathbb{R}^2,\\ &(t,u,v) \mapsto \big(u(k_1 - \alpha_1 u - \beta_{12} v), v\big(k_2 - \alpha_2 v - \beta_{21} u + \gamma\phi(t-\tau)v\big)\big).\end{aligned}$$

The function f is continuous and locally uniformly Lipschitz continuous in (u,v). Hence, by the Picard–Lindelöf theorem, there exists a unique solution of (3.1)–(3.2) on an open interval $[0,\epsilon)$ for some $\epsilon > 0$, hence I is non-empty.

Before we start with the second step, we prove the following lemma:

Lemma 3.5. *Let* $(\bar{u}, \bar{v})$ *be a solution of* (3.1)–(3.2) *on an interval* $[0,s)$. *Then* $\bar{u} > 0$ *and* $\bar{v} > 0$ *on* $[0,s)$.

Proof. Suppose that $\bar{v}(\bar{t}) = 0$ for some $\bar{t} \in [0,s)$ and $\bar{v} > 0$ on $(0,\bar{t})$. Then we would have two different local solutions of the (non-delayed) system

$$\begin{aligned}\frac{du(t)}{dt} &= u(t)\big(k_1 - \alpha_1 u(t) - \beta_{12} v(t)\big),\\ \frac{dv(t)}{dt} &= v(t)\big(k_2 - \alpha_2 v(t) - \beta_{21} u(t) + \gamma\bar{u}(t-\tau)v(t)\big),\end{aligned}$$

on an interval $(\bar{t}-\epsilon, \bar{t}]$ with the same initial values in $\bar{t}$, contradicting the uniqueness in the Picard–Lindelöf theorem. Indeed, these two solutions are $(\bar{u}, \bar{v})$ and $(\tilde{u}, 0)$, where $\tilde{u}$ solves $\tilde{u}' = \tilde{u}(k_1 - \alpha_1\tilde{u})$.

A similar argument applies if we assume $\bar{u}(\bar{t}) = 0$ for some $\bar{t} \in [0,s)$. □

Second step. I is open: Let $t_0 \in I$. We need to show that there exists an $\epsilon > 0$ such that $t_0 + \epsilon \in I$. Because $t_0 \in I$ we have that for all $s < t_0$ there exists a unique solution of (3.1)–(3.2) on $[0,s)$. Consider a strictly increasing sequence $s_i \nearrow t_0$. Then, in particular, there exists a unique solution (u_i, v_i) of (3.1)–(3.2) on $[0,s_i)$. By uniqueness, the restriction of (u_{i+1}, v_{i+1}) to $[0,s_i)$ is (u_i, v_i). In particular, we can extend (u_i, v_i) to $[0,s_i]$ by setting $(u_i(s_i), v_i(s_i)) = (u_{i+1}(s_i), v_{i+1}(s_i))$. Then, we have

$$\begin{aligned}\big|u_{i+1}(s_{i+1}) - u_i(s_i)\big| &= \big|u_{i+1}(s_{i+1}) - u_{i+1}(s_i)\big|\\ &= \big|u'_{i+1}(\xi)\big||s_{i+1} - s_i|,\end{aligned} \tag{3.4}$$

for some $\xi \in (s_i, s_{i+1})$. From the first equation of (3.1) and Lemma 3.5 we have

$$u'_i(t) \leqslant u_i(t)\big(k_1 - \alpha_1 u_i(t)\big)$$

and together with Lemma 3.4, we conclude

$$0 \leqslant u_i(t) \leqslant \max\left\{u(0), \frac{k_1}{\alpha_1}\right\} =: M \tag{3.5}$$

for all i and all $t \in [0,s_i]$. In the same way, we have

$$\begin{aligned}\big|v_{i+1}(s_{i+1}) - v_i(s_i)\big| &= \big|v_{i+1}(s_{i+1}) - v_{i+1}(s_i)\big|\\ &= \big|v'_{i+1}(\xi)\big||s_{i+1} - s_i|,\end{aligned} \tag{3.6}$$

for some $\xi \in (s_i, s_{i+1})$. From the second equation of (3.1) we have

$$v'_i(t) \leqslant v_i(t)\big(k_2 - \alpha_2 v_i(t) + \gamma u_i(t-\tau)v_i(t)\big).$$

If we denote $\overline{M} := \max\{M, \|\phi\|_\infty\}$, we can further estimate

$$v'_i(t) \leqslant v_i(t)\big(k_2 - \alpha_2 v_i(t) + \gamma\overline{M}v_i(t)\big)$$

by using (3.2) and (3.5).

In order to continue, we need to assume that $\alpha_2 - \gamma\overline{M} > 0$. In that case, by using Lemma 3.4 once more, we obtain

$$0 \leqslant v_i(t) \leqslant \max\left\{v(0), \frac{k_2}{\alpha_2 - \gamma\overline{M}}\right\}. \tag{3.7}$$

From the bounds (3.5) and (3.7) which are valid for $t > 0$, and the fact that $0 < u_i(t-\tau) \leqslant \|\phi\|_\infty$ for $t \in [-\tau, 0]$, we get by (3.1) that there exists a uniform bound K such that

$$|u_i'| \leqslant K \quad \text{and} \quad |v_i'| \leqslant K$$

for all i and all $t \in [0, s_i]$. Hence, it follows from (3.4) and (3.6) that $(u_i(s_i), v_i(s_i))$ is a Cauchy sequences in $\mathbb{R}^2_{\geqslant 0}$ since s_i is a Cauchy sequence. Therefore $(u_i(s_i), v_i(s_i))$ converges to a point $(\bar{u}, \bar{v})$ as $i \to \infty$. But then, analogous to the first step, there exists a local unique solution of (3.1) with prescribed $u(t) \in C^0$ on the interval $[t_0 - \tau, t_0]$ and prescribed $v(t_0) = \bar{v}$. It is easy to see that this solution extends the solution on $[0, t_0)$ and therefore, there exists $\epsilon > 0$ such that $t_0 + \epsilon \in I$.

Third step. Finally, we show that I is closed. Let $t_i \nearrow t^*$, where $t_i \in I$. By the definition of I, (3.1)–(3.2) has a unique solution on $[0, s)$ for all $s < t_i$. Then, for an arbitrary $s < t^*$, there exists an index i with $s < t_i$, and a unique solution of (3.1)–(3.2) exists on $[0, s)$. Thus, $t^* \in I$.

Summarizing, we have proven the following theorem:

Theorem 3.6. *Suppose $\tau \geqslant 0$, $k_i > 0$, $\alpha_i > 0$, $\beta_{ij} \geqslant 0$ $(i, j \in \{1, 2\}, i \neq j)$, $\gamma \geqslant 0$ and*

$$\alpha_2 - \gamma \max\left\{u(0), \frac{k_1}{\alpha_1}, \|\phi\|_\infty\right\} > 0.$$

Then, the initial value problem (3.1)–(3.2) *has a unique global solution* (u, v) *with*

$$0 < u(t) \leqslant \max\left\{u(0), \frac{k_1}{\alpha_1}\right\} \quad \textit{and}$$

$$0 < v(t) \leqslant \max\left\{v(0), \frac{k_2}{\alpha_2 - \gamma \max\{u(0), \frac{k_1}{\alpha_1}, \|\phi\|_\infty\}}\right\}.$$

Remark 3.7. This theorem includes in particular the case of the non-delayed system with $\tau = 0$.

To conclude, we finally consider the asymptotic bounds of the solutions of (3.1). Let us suppose, that (u, v) is a global solution of (3.1) with $u > 0$, $v > 0$.

From the first equation in (3.1) and the positivity of u we have

$$\frac{du(t)}{dt} \leqslant u(t)\bigl(k_1 - \alpha_1 u(t)\bigr).$$

Using Lemma 3.3 one gets

$$\limsup_{t\to\infty} u(t) \leqslant \frac{k_1}{\alpha_1} =: M_1. \tag{3.8}$$

So, for any arbitrary $\epsilon > 0$ there exists a number $t_0(\epsilon) > \tau$ such that

$$u(t) \leqslant M_1 + \epsilon$$

as $t \geqslant t_0(\epsilon)$.

Using this we get from the second equation in (3.1) and the positivity of v

$$\frac{dv(t)}{dt} \leqslant v(t)\bigl(k_2 - \alpha_2 v(t) + \gamma(M_1 + \epsilon)v(t)\bigr)$$

for all $t \geqslant t_0(\epsilon) + \tau$. Assume that $\alpha_2 - \gamma M_1 > 0$. (Note that this assumption is automatically satisfied under the hypotheses of Theorem 3.6.) Then, by choosing $\epsilon > 0$ sufficiently small, we have $\alpha_2 - \gamma(M_1 + \epsilon) > 0$. Therefore, by Lemma 3.3 again, we get

$$\limsup_{t\to\infty} v(t) \leqslant \frac{k_2}{\alpha_2 - \gamma(M_1 + \epsilon)}.$$

Since $\epsilon > 0$ is arbitrary, we actually have

$$\limsup_{t\to\infty} v(t) \leqslant \frac{k_2}{\alpha_2 - \gamma M_1} = \frac{\alpha_1 k_2}{\alpha_1\alpha_2 - \gamma k_1} =: M_2. \tag{3.9}$$

Hence, we have proven the following theorem:

Theorem 3.8. *Suppose* $\tau \geqslant 0$, $k_i > 0$, $\alpha_i > 0$, $\beta_{ij} \geqslant 0$ $(i, j \in \{1,2\}, i \neq j)$, $\gamma \geqslant 0$ *and*

$$\alpha_1\alpha_2 - \gamma k_1 > 0.$$

Then any positive global solution (u, v) *of system* (3.1) *satisfies*

$$\limsup_{t\to\infty} u(t) \leqslant \frac{k_1}{\alpha_1}, \qquad \limsup_{t\to\infty} v(t) \leqslant \frac{k_2}{\alpha_2 - \gamma\frac{k_1}{\alpha_1}}.$$

On the other hand, from the first equation in (3.1) and by (3.9), we get for an arbitrary $\epsilon > 0$

$$\frac{du(t)}{dt} \geqslant u(t)\big(k_1 - \alpha_1 u(t) - \beta_{12}(M_2 + \epsilon)\big)$$

for t sufficiently large. If we assume that $k_1 - \beta_{12}M_2 > 0$, then for $\epsilon > 0$ sufficiently small, we have $k_1 - \beta_{12}(M_2 + \epsilon) > 0$. Therefore by Lemma 3.3, we have

$$\liminf_{t\to\infty} u(t) \geqslant \frac{k_1 - \beta_{12}(M_2 + \epsilon)}{\alpha_1}.$$

Since $\epsilon > 0$ was arbitrary, we even have

$$\liminf_{t\to\infty} u(t) \geqslant \frac{k_1 - \beta_{12}M_2}{\alpha_1}. \tag{3.10}$$

The second equation of the system (3.1) together with (3.8) gives

$$\frac{dv(t)}{dt} \geqslant v(t)\big(k_2 - \alpha_2 v(t) - \beta_{21}(M_1 + \epsilon)\big)$$

for t sufficiently large. By the same reasoning as above, we get

$$\liminf_{t\to\infty} v(t) \geqslant \frac{k_2 - \beta_{21}M_1}{\alpha_2}$$

if $k_2 - \beta_{21}M_1 > 0$. We have actually proven the following theorem:

Theorem 3.9. *Suppose* $\tau \geqslant 0$, $k_i > 0$, $\alpha_i > 0$, $\beta_{ij} \geqslant 0$ $(i, j \in \{1,2\}, i \neq j)$, $\gamma \geqslant 0$ *and*

$$\alpha_1\alpha_2 - \gamma k_1 > 0, \qquad k_1 - \beta_{12}M_2 > 0 \quad \textit{and} \quad k_2\alpha_1 - k_1\beta_{21} > 0,$$

where M_2 *is given in* (3.9). *Then any positive global solution* (u, v) *of system* (3.1) *satisfies*

$$\liminf_{t\to\infty} u(t) \geqslant \frac{k_1 - \beta_{12}M_2}{\alpha_1}, \qquad \liminf_{t\to\infty} v(t) \geqslant \frac{k_2\alpha_1 - k_1\beta_{21}}{\alpha_1\alpha_2}.$$

In particular, the system (3.1) *is persistent in this case.*

The last question we want to address concerns the stability of equilibrium points of (3.1). The delayed system has the same equilibrium points as the non-delayed system (see the end of Section 2). In a first step, we center the system (3.1) around one of the equilibrium points (u^*, v^*) in $\mathbb{R}^2_{\geqslant 0}$. We get the system

$$\begin{aligned}
\frac{dx(t)}{dt} &= \big(x(t) + u^*\big)\big(k_1 - \alpha_1\big(x(t) + u^*\big) - \beta_{12}\big(y(t) + v^*\big)\big),\\
\frac{dy(t)}{dt} &= \big(y(t) + v^*\big)\big(k_2 - \alpha_2\big(y(t) + v^*\big) - \beta_{21}\big(x(t) + u^*\big) + \gamma\big(x(t-\tau) + u^*\big)\big(y(t) + v^*\big)\big),
\end{aligned} \tag{3.11}$$

where $x(t) = u(t) - u^*$, $y(t) = v(t) - v^*$. Denote

$$\begin{aligned}
&A = k_1 - 2\alpha_1 u^* - \beta_{12}v^*, \qquad B = -u^*\beta_{12}, \qquad C = -v^*\beta_{21},\\
&D = k_2 + 2\gamma u^* v^* - 2\alpha_2 v^* - \beta_{21}u^*, \qquad E = \gamma {v^*}^2, \qquad a_{11} = -\beta_{12},\\
&a_{20} = -\alpha_1, \qquad b_{11} = -\beta_{21}, \qquad b_{02} = -\big(\alpha_2 - \gamma u^*\big), \qquad b'_{11} = 2\gamma v^*, \qquad b'_{12} = \gamma.
\end{aligned}$$

Simplifying and using these notations the system (3.11) can be written as

$$\begin{aligned}
\frac{dx(t)}{dt} &= Ax(t) + By(t) + a_{11}x(t)y(t) + a_{20}x^2(t),\\
\frac{dy(t)}{dt} &= Cx(t) + Dy(t) + Ex(t-\tau) + b_{11}x(t)y(t) + b_{02}y^2(t) + b'_{11}x(t-\tau)y(t) + b'_{12}x(t-\tau)y^2(t).
\end{aligned} \tag{3.12}$$

The stability discussion will be based upon the linear part of the system (3.12) which is given by

$$\begin{aligned}\frac{dx(t)}{dt} &= Ax(t) + By(t),\\ \frac{dy(t)}{dt} &= Cx(t) + Dy(t) + Ex(t-\tau).\end{aligned}\tag{3.13}$$

The characteristic equation associated to (3.13) is given by

$$\Delta(\lambda,\tau) := \lambda^2 - (A+D)\lambda + (AD - BC) - BEe^{-\lambda\tau} = 0.\tag{3.14}$$

For more details on the characteristic equation, the reader may consult [20]. In order to study the stability properties of the equilibrium (u^*, v^*) of (3.1) we have to study the nature of the roots of the characteristic equation (3.14).

We start by the discussion for $\tau = 0$. In a second step below, we consider $\tau > 0$.

Stability for $\boldsymbol{\tau = 0}$. The matrix of the linearized system (3.13) is

$$M := \begin{pmatrix} A & B \\ C+E & D \end{pmatrix}.$$

Recall that if the real part of all eigenvalues of the matrix M of the linearized system (3.13) in the equilibrium E^* is strictly negative, then E^* is asymptotically stable. On the other hand, if an eigenvalue has a strictly positive real part, then E^* is unstable. The eigenvalues are the roots of $\Delta(\lambda, 0)$.

Equilibrium $\boldsymbol{E_1 = (0,0)}$. In this case, Eq. (3.14) takes the form

$$\lambda^2 - (k_1 + k_2)\lambda + k_1k_2 = 0.$$

The roots k_1, k_2 are strictly positive, therefore the zero equilibrium E_1 is always unstable.

Equilibrium $\boldsymbol{E_2 = (\frac{k_1}{\alpha_1}, 0)}$. In this case, Eq. (3.14) takes the form

$$(\lambda + k_1)\left(\lambda - k_2 + \frac{\beta_{21}k_1}{\alpha_1}\right) = 0.$$

Thus E_2 is asymptotically stable if $\frac{k_2}{k_1} < \frac{\beta_{21}}{\alpha_1}$ and unstable if $\frac{k_2}{k_1} > \frac{\beta_{21}}{\alpha_1}$. In the latter case, the eigenvalue $-k_1$ belongs to the eigenvector $(1, 0)$, hence the equilibrium is contracting in the direction of the u-axis and expanding in the direction of the second eigenvector.

Equilibrium $\boldsymbol{E_3 = (0, \frac{k_2}{\alpha_2})}$. In this case, Eq. (3.14) takes the form

$$(\lambda + k_2)\left(\lambda - k_1 + \frac{\beta_{12}k_2}{\alpha_2}\right).$$

Thus E_3 is asymptotically stable if $\frac{k_1}{k_2} < \frac{\beta_{12}}{\alpha_2}$ and it is unstable if $\frac{k_1}{k_2} > \frac{\beta_{12}}{\alpha_2}$. In the latter case, the eigenvalue $-k_2$ belongs to the eigenvector $(0, 1)$, hence the equilibrium is contracting in the direction of the v-axis and expanding in the direction of the second eigenvector.

It is clear, that asymptotic stability of E_2 or E_3 is incompatible with the persistency of the system (3.1). In fact, we have:

Remark 3.10. The hypotheses in Theorem 3.9 imply that

$$\frac{k_j}{k_i} > \frac{\beta_{ji}}{\alpha_i} \quad \text{for } i, j \in \{1,2\},\ i \neq j.\tag{3.15}$$

This is equivalent to the condition that both E_2 and E_3 are unstable. In fact, for $\gamma = 0$, the hypotheses in Theorem 3.9 are actually equivalent to (3.15).

Equilibrium $\boldsymbol{E_* = (u_*, v_*)}$. By direct calculation of the eigenvalues or by applying the Routh–Hurwitz criterion, we find that the inequalities

$$A + D < 0 \quad \text{and} \quad AD - B(C+E) > 0\tag{3.16}$$

imply asymptotic stability of E_*. Using (2.5) and (2.6) to eliminate k_1 and k_2, it is easy to see that these two conditions can be expressed in the original parameters of the problems, namely as

$$\gamma < \frac{\alpha_1}{v_*} + \frac{\alpha_2}{u_*} \quad \text{and} \quad \alpha_1\alpha_2 - \beta_{12}\beta_{21} > (u_*\alpha_1 - v_*\beta_{12})\gamma.\tag{3.17}$$

We illustrate the result numerically. For the parameter values chosen at the end of Section 2, both inequalities are satisfied and hence E_* is locally asymptotically stable (see Fig. 2).

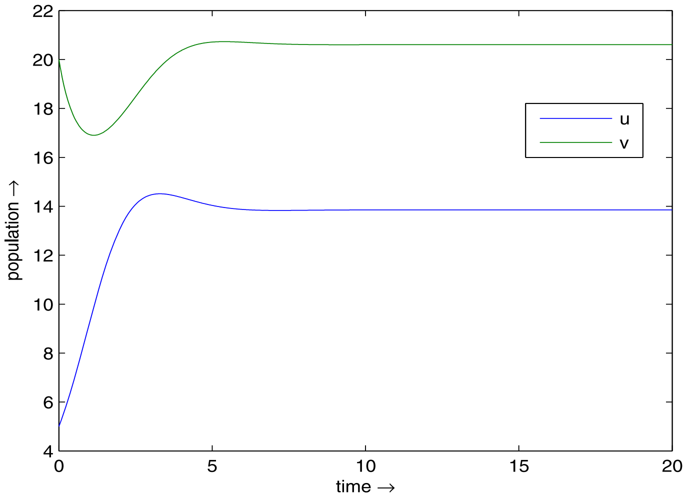

Fig. 2. Stable population distribution for u and v.

Stability for $\tau > 0$. Every point $E \in \{E_1, E_2, E_3, E_*\}$ is also an equilibrium for $\tau > 0$ in the sense that $[-\tau, \infty) \to \mathbb{R}^2$, $t \mapsto E$, is a solution of (3.1) for $t \geqslant 0$. E is called stable, if for every $\epsilon > 0$ there exists a $\delta > 0$ such that for every solution (u, v) of (3.1) on $(0, \infty)$ satisfying $\|E - (u, v)\|_{C^0(-\tau,0)} < \delta$ we have $\|E - (u, v)\|_{C^0(0,\infty)} < \epsilon$. Moreover, E is asymptotically stable, if it is stable and if in addition (u, v) converges to E as $t \to \infty$.

We recall the following result for the stability of equilibria of a nonlinear delay equation from [20, Theorem 3.7.1]:

Theorem 3.11. *The necessary and sufficient conditions for an equilibrium to be asymptotically stable for all $\tau \geqslant 0$ are the following*:

(1) *The real part of the roots of $\Delta(\lambda, 0) = 0$ is negative.*
(2) *For all real μ and all $\tau \geqslant 0$, $\Delta(i\mu, \tau) \neq 0$.*

Observe, that for E_1, E_2 and E_3, the product $BE = 0$. Therefore, in these three cases, $\Delta(\lambda, \tau) \equiv \Delta(\lambda, 0)$ for all λ and τ.

Equilibrium $E_2 = (\frac{k_1}{\alpha_1}, 0)$. We have seen that under the condition $\frac{k_2}{k_1} < \frac{\beta_{21}}{\alpha_1}$, E_2 is asymptotically stable for $\tau = 0$. In fact, this is precisely the condition for the roots of $\Delta(\lambda, 0)$ to have strictly negative real parts, and hence, condition (1) of Theorem 3.11 is satisfied. But since $\Delta(i\mu, \tau) = \Delta(i\mu, 0)$, also condition (2) of Theorem 3.11 is satisfied. Hence, if $\frac{k_2}{k_1} < \frac{\beta_{21}}{\alpha_1}$, then E_2 is asymptotically stable for all $\tau \geqslant 0$.

Equilibrium $E_3 = (0, \frac{k_2}{\alpha_2})$. By a similar reasoning as above, we obtain: If $\frac{k_1}{k_2} < \frac{\beta_{12}}{\alpha_2}$ then E_3 is asymptotically stable for all $\tau \geqslant 0$.

Equilibrium $E_* = (u_*, v_*)$. Using (2.5) and (2.6) to eliminate k_1 and k_2 in A and D, we obtain the following convenient expressions for the coefficients:

$$A = -u^*\alpha_1, \qquad B = -u^*\beta_{12}, \qquad C = -v^*\beta_{21},$$
$$D = v^*(\gamma u^* - \alpha_2), \qquad E = \gamma v^{*2}.$$

As seen in the stability discussion of E_* in the case $\tau = 0$, a necessary and sufficient condition for condition (1) of Theorem 3.11 to hold is (3.16). In order to discuss condition (2) we rewrite $\Delta(i\mu, \tau) = 0$ as:

$$-\mu^2 + (AD - BC) - BE\cos(\mu\tau) = 0, \tag{3.18}$$
$$-(A + D)\mu + BE\sin(\mu\tau) = 0. \tag{3.19}$$

By squaring and adding both equations above we get

$$\mu^4 + (A^2 + D^2 + 2BC)\mu^2 + (AD - BC + BE)(AD - BC - BE) = 0. \tag{3.20}$$

A corresponding possible positive root of Eq. (3.20) is given by

$$\mu^2 = \frac{1}{2}\left(-(A^2 + D^2 + 2BC) + \sqrt{(A^2 + D^2 + 2BC)^2 - 4\left((AD - BC)^2 - (BE)^2\right)}\right) \geqslant 0. \tag{3.21}$$

Now, it is easy to check that the following statements are equivalent:

- Condition (2) of Theorem 3.11 is not satisfied.
- $\exists\mu \in \mathbb{R}$, $\exists\tau \geqslant 0$ such that (3.18) and (3.19) hold.

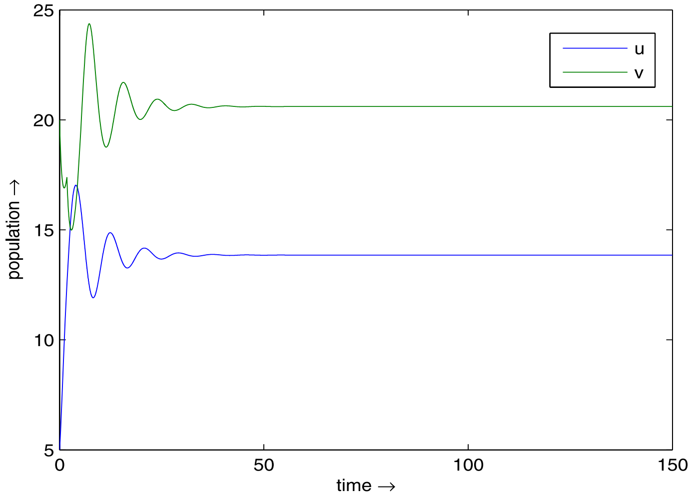

Fig. 3. Numerical simulation results for delayed model system for $\tau = 1.8$.

- $\exists \mu \in \mathbb{R}$, $\exists \tau \geqslant 0$ such that (3.20) and (3.19) hold.
- $\exists \mu \in \mathbb{R}$, $\exists \tau \geqslant 0$ such that (3.21) and (3.19) hold.

From this, it follows that

- $\exists \mu \in \mathbb{R}$ such that (3.21) holds,

which in turn implies, that

- $(AD - BC)^2 \leqslant (BE)^2$ holds.

Hence, $(AD - BC)^2 > (BE)^2$ implies condition (2) of Theorem 3.11. We conclude that, by Theorem 3.11, if

$$A + D < 0 \quad \text{and} \quad AD - BC > BE \quad \text{and} \quad |AD - BC| > |BE|$$

it follows that E_* is asymptotically stable for all $\tau \geqslant 0$.

The stability properties of E_* in the parametric region $(AD - BC)^2 < (BE)^2$ have been discussed in [13]. We mention the corresponding results:

Theorem 3.12. *(See Theorem 3.3 in [13].) If $A + D < 0$, then in the parametric region $BE < AD - BC < -BE$ the interior equilibrium E_* of the allelopathic stimulatory system* (3.1) *is asymptotically stable for* $0 < \tau < \frac{A+D}{BE}$.

It is also shown in [13] that there exists a threshold τ_0 such that the following is true:

Lemma 3.13. *(See Lemma 4.2 in [13].) For $\tau < \tau_0$, E_* is asymptotically stable. For $\tau > \tau_0$, E_* is unstable. Further as τ increases through τ_0, E_* bifurcates into small amplitude periodic solutions.*

Now we consider the numerical simulation results of the delayed model system for the same set of parametric values as we have mentioned at the end of Section 2. For the chosen parametric values we have $\frac{A+D}{BE} = 1.997$ and hence E_* is asymptotically stable for $0 < \tau < 1.997$. Fig. 3 shows the stable population distribution of both phytoplankton species for $\tau = 1.8$. If we increase the magnitude of τ without changing any other parameter then the system undergoes a Hopf-bifurcation and the interior equilibrium point becomes unstable. A small amplitude periodic solution bifurcates from the interior equilibrium point and we observe numerically a periodic solution around E_* (see Fig. 4).

4. Discussion

In this paper we have considered mainly the global existence and uniqueness of solutions to a delayed model of two interacting phytoplankton species where one species has the ability to stimulate the growth of the other species. We have obtained the parametric restrictions under which both species persist for all future time. The analysis of the linearized problem provides information about the local behavior of trajectories in the vicinity of various equilibria. Considering the

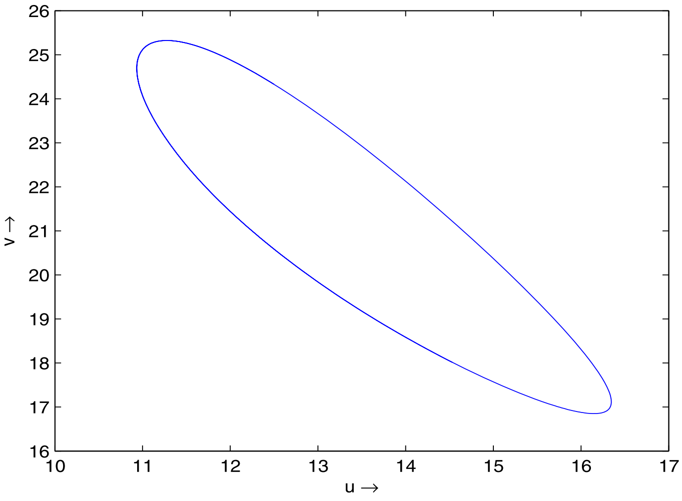

Fig. 4. Hopf-bifurcating limit cycle around E_* for $\tau = 4.26 > \tau_0$.

discrete time delay as a bifurcation parameter we got a threshold value for the existence of small amplitude periodic solutions. This result gives us the opportunity to conclude that oscillatory co-existence of the species is also possible when the time delay parameter crosses its threshold magnitude. The analytical findings are substantiated with numerical simulations. Finally we like to remark that the incorporation of discrete time delay has ability to induce oscillations in plankton population but they do not affect the positivity of solution, boundedness and persistence of solution trajectories. These findings agree well with some other findings [21–23].

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