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Threshold dynamics of a diffusive nonlocal phytoplankton model with age structure☆

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In this paper, a reaction–diffusion equation with age structure and nonlocal effect for the maturation, growth and spatial distribution of phytoplankton in a water column is derived, and the threshold dynamics for the model is completely classified. It is shown that the death rate and maturation time of the phytoplankton both affect the dynamics of the model. The phytoplankton species could die out if the death rate is greater than a critical death rate. However, when the death rate is less than the critical value, there exists another threshold for the maturation period such that the unique positive steady state (respectively, the trivial steady state) is globally attractive if the maturation period is less (respectively, greater) than the threshold value.

1. Introduction

Phytoplankton are drifting organisms that live in the water column of oceans, seas, lakes and rivers, and they play a fundamental role in the global carbon cycle and marine food webs. The growth of phytoplankton needs two essential resources: light and nutrients, but in eutrophic ecosystems with ample nutrient supply, phytoplankton tend to compete only for light. Reaction–diffusion models have been proposed to study the effect of incomplete mixing on the growth of the phytoplankton species in an eutrophic environment [1–4].

It is known that the propagation of the phytoplankton could be accomplished through cell division or production of spores, see [5] for modeling the phytoplankton species which reproduce by simple division. Therefore, it takes time for the phytoplankton population from birth to maturity. Also for some algae, such as some kinds of *Cyanophyta* and *Rhodophyta*, the nonmotile aplanospores are the dominant contribution for propagation. Hence in these cases, the effect of maturation time should be incorporated into the mathematical modeling of phytoplankton growth and spatial distribution in a water column.

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Here considering the maturation time of phytoplankton, we derive a reaction–diffusion model of phytoplankton population concentration with age structure by using the baseline model in [1,4] and the diffusive age structured population models in [6–8]. Let $z(x,t,a)$ be the density of the phytoplankton of age a at depth x and time t, and let τ be the period of maturation. Then the density of the mature phytoplankton is

$$u(x,t) = \int_{\tau}^{\infty} z(x,t,a)da. \tag{1.1}$$

We start from the standard age-structured equation (see [7]):

$$\frac{\partial z(x,t,a)}{\partial t} + \frac{\partial z(x,t,a)}{\partial a} = D(a)\frac{\partial^2 z(x,t,a)}{\partial x^2} - d(a)z(x,t,a), \tag{1.2}$$

where $D(a)$ and $d(a)$ are the diffusion coefficient and death rate of the phytoplankton, respectively, and x is the depth of the water column where $x = 0$ is the water surface and $x = L$ is the bottom of the water column. The birth rate of the phytoplankton is given by (see [1,4])

$$z(x,t,0) = g(I(x,t))u(x,t) = g\left(I_0 e^{-k_0 x - k\int_0^x u(s,t)ds}\right)u(x,t), \tag{1.3}$$

where $g(I)$ is the growth rate per capita of the phytoplankton species as a function of light intensity $I(x,t)$, and it satisfies

$$g(0) = 0,\ g'(I) > 0 \ \text{ for } \ I \geq 0; \tag{1.4}$$

and the light intensity $I(x,t)$ takes the form

$$I(x,t) = I_0 e^{-k_0 x}\exp\left(-k\int_0^x u(s,t)ds\right). \tag{1.5}$$

For the simplicity of modeling, we impose the following two assumptions:

(i) The diffusion and death rates of the immature and mature phytoplankton are constants, respectively.
(ii) The diffusion rate of the immature phytoplankton is very small, and we assume it is equal to zero. That is, the immature phytoplankton (spore etc.) are nonmotile.

From these assumptions, we have

$$D(a) = \begin{cases} 0, & a \leq \tau, \\ D, & a > \tau. \end{cases},\quad d(a) = \begin{cases} \gamma, & a \leq \tau, \\ d, & a > \tau. \end{cases}$$

Combining these assumptions, we have

$$\begin{aligned} \frac{\partial u}{\partial t} &= \int_{\tau}^{\infty} \frac{\partial z}{\partial t}da = D\frac{\partial^2 u}{\partial x^2} - du - \int_{\tau}^{\infty}\frac{\partial z}{\partial a}da \\ &= D\frac{\partial^2 u}{\partial x^2} - du + z(x,t,\tau), \end{aligned} \tag{1.6}$$

where $z(x,t,\tau)$ is the adult recruitment term. Since

$$\frac{\partial z(x,t,a)}{\partial t} + \frac{\partial z(x,t,a)}{\partial a} = -\gamma z(x,t,a) \ \text{ for } \ a \leq \tau, \tag{1.7}$$

invoking Eq. (1.3), we have

$$z(x,t,\tau) = e^{-\gamma\tau}g(I(x,t-\tau))u(x,t-\tau).$$

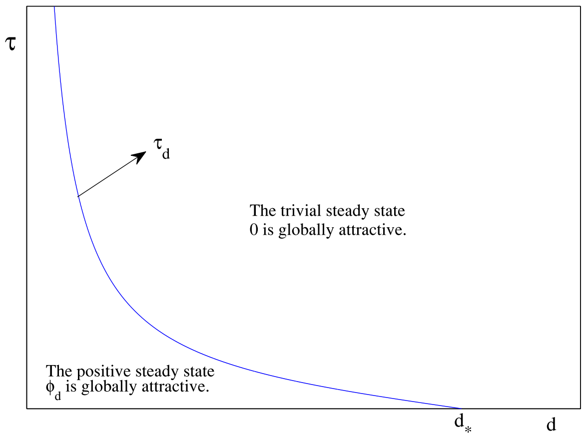

Fig. 1. Threshold dynamics of model (1.8) with respect to parameters d and τ.

Therefore the density of the mature phytoplankton $u(x,t)$ satisfies

$$\begin{cases} \dfrac{\partial u}{\partial t} = D\dfrac{\partial^2 u}{\partial x^2} + e^{-\gamma\tau} g(I(x,t-\tau))u(x,t-\tau) - du, & x \in (0,L),\ t > 0, \\ \dfrac{\partial u(0,t)}{\partial x} = \dfrac{\partial u(L,t)}{\partial x} = 0, & t > 0, \\ u(x,t) = \phi(x,t) \geq 0, & x \in (0,L),\ t \in [-\tau, 0], \end{cases} \tag{1.8}$$

where $D, d, \gamma > 0$ and $\tau \geq 0$, g and I satisfy Eqs. (1.4) and (1.5) respectively. Without loss of generality, we assume that $L = 1$ and $I_0 = 1$ throughout the paper. Notice that when $\tau = 0$, (1.8) becomes the previous model studied in [1,4]. In that case, detailed mathematical analysis for the single and two species cases is derived in [1], and further investigation on the nonlocal phytoplankton models could also be found in [2,9–11] and references therein. Mathematical models of phytoplankton growth and nutrient abundance have also been constructed and analyzed [12–18].

Denote

$$\Psi_0(x) := -g(e^{-k_0 x}),\ d_* = -\lambda_1(\Psi_0), \tag{1.9}$$

where $\lambda_1(\Psi)$ is defined as the smallest eigenvalue of the following equation

$$\begin{cases} -D\psi'' + \Psi(x)\psi = \lambda\psi,\ x \in (0,1), \\ \psi'(0) = 0,\ \psi'(1) = 0. \end{cases} \tag{1.10}$$

For the case of $\tau = 0$, Du and Hsu [1] obtained that if $d \geq d_*$, model (1.8) has no positive steady state, and the trivial steady state 0 attracts all the solutions $u(x,t)$ with the initial condition $u(x,0) \geq 0$, and if $d \in (0, d_*)$, Eq. (1.8) has a unique positive steady state ϕ_d which attracts all the solutions $u(x,t)$ with the initial condition $u(x,0) \geq (\not\equiv) 0$. In this paper, we mainly deal with the dynamics of model (1.8) for the case of $\tau > 0$, and our main results are as follows:

(i) If $d \geq d_*$, then $u(x,t)$ converges uniformly to the trivial steady state as $t \to \infty$.
(ii) If $d < d_*$, then there exists $\tau_d > 0$ such that when $0 < \tau < \tau_d$, $u(x,t)$ converges uniformly to the positive steady state ϕ_d as $t \to \infty$, and when $\tau \geq \tau_d$, $u(x,t)$ converges uniformly to the trivial steady state as $t \to \infty$. Moreover τ_d is strictly decreasing in d and $\tau_d \to 0$ as $d \to d_*^-$ (see Fig. 1).

Delayed reaction–diffusion equations have been investigated extensively, regarding the stability of the equilibrium, and the associated steady state and Hopf bifurcations, see [19–24] and references therein. Here the time delay could account for the maturation time for population species or the incubation period for diseases, and a large time delay may lead to temporal oscillation [25–30] or be harmless [31–35]. For instance, the following diffusive Nicholson's blowflies model

$$\begin{cases} u_t = d\Delta u + pu(x,t-\tau)e^{-au(x,t-\tau)} - \delta u, & x \in \Omega,\ t > 0, \\ \partial_n u = 0, & x \in \partial\Omega,\ t > 0, \end{cases} \tag{1.11}$$

was studied in [36], and it was shown that if $1 \le p/\delta \le e$, the delay is harmless, which means that the positive equilibrium is globally asymptotically stable regardless of the magnitude of delay τ, and if $p/\delta > e^2$, delay may be harmful and make the positive equilibrium unstable through Hopf bifurcation. For the gap range $e < p/\delta \le e^2$, it was proved in [37] that the delay is harmless. Dirichlet boundary value problem of (1.11) is also considered in [38,39]. Moreover, we refer to [40–46] and references therein for the effect of delay on the diffusive logistic population model.

The rest of this paper is organized as follows. In Section 2, we prove the global existence of solutions of (1.8). In Section 3, motivated by the method of [1], we obtain the global attractivity of the nonnegative steady states for model (1.8). Some numerical simulations are included to support our theoretical results at the end.

2. Global existence

In this section, we show that the solution of model (1.8) exists on $[-r,\infty)$. Firstly, denote $X = C([0,1],\mathbb{R})$, $\mathcal{C} = C([-\tau,0],X)$, and $A : Dom(A) \subset X \to X$ by

$$A\psi = \frac{d^2\psi}{dx^2} - d\psi.$$

where

$$Dom(A) = \{\phi(x) \in C^2([0,1],\mathbb{R}) : \phi_x(0) = \phi_x(1) = 0\}.$$

Moreover, denote $\mathcal{C}_+ := \{\psi(x,t) \in \mathcal{C} : \psi(x,t) \ge 0 \text{ for } 0 \le x \le 1, -\tau \le t \le 0\}$ and $X_+ = \{\psi(x) \in X : \psi(x) \ge 0 \text{ for } 0 \le x \le 1\}$. It is known that A generates an analytic, compact and strongly positive semigroup $T(t)$ on X. Define $F : \mathcal{C} \to X$ by

$$F(\Phi) = e^{-\gamma\tau} g\left(e^{-k_0 x - k\int_0^x \Phi(s,-\tau)ds}\right)\Phi(x,-\tau), \tag{2.1}$$

where $\Phi \in \mathcal{C}$. Then we consider the following integral equation

$$\begin{cases} u(t) = T(t)\phi(0) + \displaystyle\int_0^t T(t-s)F(u_s)ds, & t > 0, \\ u(t) = \phi \in \mathcal{C}, & -\tau \le t \le 0. \end{cases} \tag{2.2}$$

for which the solution is called the mild solution of (1.8). Here $u_s = u(x, s+\theta)(\theta \in [-\tau,0]) \in \mathcal{C}$.

Proposition 2.1. *For any $\phi \in \mathcal{C}^+$, Eq. (2.2) has a unique solution $u(t,\phi)$ existing on $[0,\infty)$, and $u(t,\phi)$ is a classical solution of Eq. (1.8) when $t > \tau$.*

Proof. We first prove that for any $\phi \in \mathcal{C}^+$, there exists a unique solution $u(t,\phi)$ defined on its maximal interval of existence $[-r,t_\phi)$. For any $R > 0$, if $\|\Phi\|_{\mathcal{C}},\ \|\Psi\|_{\mathcal{C}} \le R$, we have

$$\begin{aligned} &\|F(\Phi)(x) - F(\Psi)(x)\|_X \\ \le&\|g\left(e^{-k_0 x - k\int_0^x \Phi(s,-\tau)ds}\right)\Phi(x,-\tau) - g\left(e^{-k_0 x - k\int_0^x \Psi(s,-\tau)ds}\right)\Psi(x,-\tau)\|_X \\ =&(g(1) + R\max_{x\in[0,1]}|g'(x)|)\|\Phi - \Psi\|_{\mathcal{C}}, \end{aligned} \tag{2.3}$$

which implies that $F : \mathcal{C} \to X$ is locally Lipschitz continuous. It follows from [24, Chapter 2, Theorem 2.6] that, for any $\phi \in \mathcal{C}$, there exists a unique solution $u(t,\phi)$ of (2.2) on its maximal interval $[-r, t_\phi)$, and $u(t,\phi)$ is a classical solution of Eq. (1.8) when $t > \tau$. Moreover, a direct calculation implies that $\|F(\Phi)(x)\|_X \leq g(1)\|\Phi\|_{\mathcal{C}}$ for any $\Phi \in \mathcal{C}$, which yields $t_\phi = \infty$ from [24, Chapter 2, Theorem 2.3]. □

Then we can arrive at the following global existence result.

Theorem 2.2. *For any initial value $\phi \in \mathcal{C}_+$, the corresponding solution $u(t,\phi)$ of (2.2) satisfies $u(t,\phi) \in X_+$ for any $t \in (0,\infty)$. Especially, if $\phi(x,0) \in X_+$ and $\phi(x,0) \not\equiv 0$, then $u(t,\phi) \subset Int(X_+)$ for any $t \in (0,\infty)$, where*

$$Int(X_+) = \{\phi \in X_+ : \phi(x) > 0 \text{ for } x \in [0,1]\}.$$

Proof. For any initial value $\phi \in \mathcal{C}_+$, the corresponding solution $u(t,\phi)$ satisfies

$$\begin{cases} u(t) = T(t)\phi(0) + \displaystyle\int_0^t T(t-s)F(u_s)ds, & t > 0, \\ u(0) = \phi(x,0). \end{cases}$$

Since $g(I) \geq 0$ for any $I \geq 0$, it follows that $F(u_s) \in X_+$ for any $0 < s \leq \tau$. Noticing that $T(t)$ is a strongly positive semigroup on X, we have $u(t,\phi)(x) \geq T(t)\phi(0)(x) \geq 0$ for $t \in [0,\tau]$. Therefore, by the method of step, we obtain that the corresponding solution $u(t,\phi)$ of (2.2) satisfies $u(t,\phi) \in X_+$ for any $t \in [0,\infty)$. Then, by virtue of the maximum principle, we see that $u(t,\phi) \subset \mathrm{Int}(X_+)$, if $\phi(x,0) \in X_+$ and $\phi(x,0) \not\equiv 0$. □

3. Globally attractivity

In this section, we aim to prove the threshold dynamics for model (1.8). Firstly, we modify the arguments in the proof of [1, Lemma 3.1] to derive the following comparison lemma for the delayed case.

Lemma 3.1. *Assume that $u, \tilde{u} \in C^{2,1}([0,1] \times (0,\infty)) \cap C([0,1] \times [-\tau,\infty))$ satisfy*

$$\begin{cases} \dfrac{\partial u(x,t)}{\partial t} \leq D\dfrac{\partial^2 u(x,t)}{\partial x^2} - du(x,t) \\ \qquad + e^{-\gamma\tau} g\left(e^{-k_0 x - k\int_0^x u(s,t-\tau)ds}\right) u(x,t-\tau), & x \in (0,1),\ t > 0, \\ \dfrac{\partial u(0,t)}{\partial x} = \dfrac{\partial u(1,t)}{\partial x} = 0, & t > 0, \end{cases}$$

and

$$\begin{cases} \dfrac{\partial \tilde{u}(x,t)}{\partial t} \geq D\dfrac{\partial^2 \tilde{u}(x,t)}{\partial x^2} - d\tilde{u}(x,t), \\ \qquad + e^{-\gamma\tau} g\left(e^{-k_0 x - k\int_0^x \tilde{u}(s,t-\tau)ds}\right) \tilde{u}(x,t-\tau) & x \in (0,1),\ t > 0, \\ \dfrac{\partial \tilde{u}(0,t)}{\partial x} = \dfrac{\partial \tilde{u}(1,t)}{\partial x} = 0, & t > 0. \end{cases}$$

If $u(x,t) < \tilde{u}(x,t)$ for $x \in [0,1]$, $t \in [-\tau,0]$, then

$$v(x,t) = \int_0^x u(s,t)ds < \tilde{v}(x,t) = \int_0^x \tilde{u}(s,t)ds \tag{3.1}$$

for any $x \in (0,1]$, $t > 0$.

Proof. We only prove that $v(x,t) < \tilde{v}(x,t)$ for $x \in (0,1],\ t \in [0,\tau]$, and then Eq. (3.1) can be obtained by the method of step.

Noticing that $v(x,t) = \int_0^x u(s,t)ds$, we have

$$\begin{aligned}\frac{\partial v}{\partial t} \le & D\frac{\partial^2 v}{\partial x^2} - dv + e^{-\gamma\tau}\int_0^x g\left(e^{-k_0 x - kv(s,t-\tau)}\right)u(s,t-\tau)ds \\ = & D\frac{\partial^2 v}{\partial x^2} - dv - k_0 k^{-1} e^{-\gamma\tau}\int_0^x g\left(e^{-k_0 s - kv(s,t-\tau)}\right)ds \\ & + k^{-1}e^{-\gamma\tau}\int_0^x g\left(e^{-k_0 x - kv(s,t-\tau)}\right)d(k_0 s + kv(s,t-\tau)) \\ = & D\frac{\partial^2 v}{\partial x^2} - dv - k_0 k^{-1} e^{-\gamma\tau}\int_0^x g\left(e^{-k_0 s - kv(s,t-\tau)}\right)ds + G(k_0 x + kv(x,t-\tau)),\end{aligned}$$

where $G(x) = k^{-1}e^{-\gamma\tau}\int_0^x g(e^{-y})dy$. Denote $w(t) := v(1,t) = \int_0^1 u(s,t)ds$, which satisfies

$$w'(t) \le -dw + G(k_0 + kv(1,t-\tau)) - k_0 k^{-1} e^{-\gamma\tau}\int_0^1 g\left(e^{-k_0 s - kv(s,t-\tau)}\right)ds.$$

Similarly, we have

$$\frac{\partial \tilde{v}}{\partial t} \ge D\frac{\partial^2 \tilde{v}}{\partial x^2} - d\tilde{v} + G(k_0 x + k\tilde{v}(x,t-\tau)) - k_0 k^{-1} e^{-\gamma\tau}\int_0^x g\left(e^{-k_0 s - k\tilde{v}(s,t-\tau)}\right)ds.$$

Letting $\tilde{w}(t) := \tilde{v}(1,t) = \int_0^1 \tilde{u}(s,t)ds$, we also obtain that

$$\tilde{w}'(t) \ge -dw + G(k_0 + k\tilde{v}(1,t-\tau)) - k_0 k^{-1} e^{-\gamma\tau}\int_0^1 g\left(e^{-k_0 s - k\tilde{v}(s,t-\tau)}\right)ds.$$

Since $u(x,t) < \tilde{u}(x,t)$ for $x \in [0,1],\ t \in [-\tau,0]$, it follows that $v(x,t-\tau) < \tilde{v}(x,t-\tau)$ for $x \in (0,1]$, $t \in [0,\tau]$. Since G and g are strictly increasing, it follows from the comparison principle that $\tilde{w}(t) > w(t)$ for $t \in [0,\tau]$. Consequently, we have

$$\begin{cases}\dfrac{\partial(\tilde{v}-v)}{\partial t} \ge D\dfrac{\partial^2(\tilde{v}-v)}{\partial x^2} - d(\tilde{v}-v), & x \in (0,1),\ 0 < t \le \tau, \\ (\tilde{v}-v)(0,t) = 0,\ (\tilde{v}-v)(1,t) = (\tilde{w}-w)(t) > 0, & 0 < t \le \tau, \\ (\tilde{v}-v)(x,0) > 0, & x \in (0,1).\end{cases}$$

Then, by virtue of the strong maximum principle, we obtain that $v(x,t) < \tilde{v}(x,t)$ for $x \in (0,1]$, $t \in [0,\tau]$. This completes the proof. □

Next we derive the following boundedness lemma, and the proof here modifies the arguments in the proof of [1, Lemma 3.2].

Lemma 3.2. *Let $u(x,t)$ be the unique solution of (1.8) with the initial value $\phi \in \mathcal{C}_+$ and $\phi(x,0) \not\equiv 0$. Then there exists $C > 0$ such that $u(x,t) \le C$ for $x \in [0,1]$, $t > 0$.*

Proof. It follows from Proposition 2.1 that $u(x,t)$ is a classical solution of (1.8) for $t > \tau$ and, for $t > \tau$, $u(x,t)$ satisfies

$$\begin{aligned}\frac{\partial u}{\partial t} = & D\frac{\partial^2 u}{\partial x^2} + e^{-\gamma\tau} g\left(e^{-k_0 x - k\int_0^x u(s,t-\tau)ds}\right)u(x,t-\tau) - du \\ \le & D\frac{\partial^2 u}{\partial x^2} - du + (\max_{0\le x\le 1} g'(x))e^{-k\int_0^x u(s,t-\tau)ds}u(x,t-\tau).\end{aligned}$$

Denote $w(t) := \int_0^1 u(s,t)ds$, and consequently, we have

$$w'(t) + dw \le (\max_{0\le x\le 1} g'(x)) \int_0^1 e^{-k\int_0^x u(s,t-\tau)ds} u(x,t-\tau)dx,$$

which implies that there exists $C_1 > 0$ such that $w(t) < C_1$ for all $t > 0$.

Denote $W(t) := \max_{x\in[0,1],s\in[0,t]} u(x,s)$. If the conclusion of this lemma is not true, then $W(t) \to \infty$ as $t \to \infty$. Therefore, there exists $\{t_n\}_{n=1}^{\infty}$ such that $t_n \to \infty$ and $W(t_n) = \max_{x\in[0,1]} u(x,t_n) \to \infty$. Without loss of generality, we assume $t_n > 3\tau/2$ for any $n \ge 1$, and define $v_n(x,t) := \dfrac{u(x,t+t_n-\frac{3\tau}{2})}{W(t_n)}$. A direct computation yields

$$\begin{cases} \dfrac{\partial v_n(x,t)}{\partial t} = D\dfrac{\partial^2 v_n(x,t)}{\partial x^2} - dv_n(x,t), & \\ \qquad + e^{-\gamma\tau} g\left(e^{-k_0x-k\int_0^x u(s,t+t_n-\frac{5\tau}{2})ds}\right) v_n(x,t-\tau), & x\in(0,1),\ t>\tau, \\ \dfrac{\partial v_n(0,t)}{\partial x} = \dfrac{\partial v_n(1,t)}{\partial x} = 0, & t>\tau, \\ 0 \le v_n(x,t) \le 1, & x\in(0,1),\ t\in[0,\tau]. \end{cases}$$

Let $z(t)$ be the solution of the following ordinary differential equation

$$\begin{cases} \dfrac{dz(t)}{dt} = g(1) - dz(t), & \tau < t \le 2\tau, \\ z(\tau) = 1. \end{cases}$$

It follows from the comparison principle that $0 \le v_n(x,t) \le z(t) \le 1 + \frac{g(1)}{d}$ for $\tau \le t \le 2\tau$ and $n = 1,2,\ldots$. This, combined with the regularity theory and embedding theorem, implies that $\{v_n(x,t)\}$ is bounded in $C^{1+\alpha,\alpha}([0,1]\times[\tau,2\tau])$ for some $\alpha \in (0,1)$. Then $\{v_n(x,t)\}$ has a convergent subsequence in $C^{1,0}([0,1]\times[\tau,2\tau])$, and without loss of generality, we assume $v_n(x,t) \to v_*$ in $C^{1,0}([0,1]\times[\tau,2\tau])$. Therefore, v_* is the weak solution of the following inequalities

$$\begin{cases} \dfrac{\partial v_*(x,t)}{\partial t} \ge D\dfrac{\partial^2 v_*(x,t)}{\partial x^2} - dv_*(x,t), & x\in[0,1],\ t\in(\tau,2\tau), \\ \dfrac{\partial v_*(0,t)}{\partial x} = \dfrac{\partial v_*(1,t)}{\partial x} = 0, & t\in(\tau,2\tau). \end{cases}$$

Since $\max_{x\in[0,1]} v_n(x,\dfrac{3\tau}{2}) = 1$ for each $n \ge 1$, it follows that v_* is not identically zero. Then by virtue of the strong maximum principle (see [47, Theorem 6.43]), we obtain that $v_*(x,\frac{3\tau}{2}) \ge \delta > 0$ for $x \in [0,1]$, and correspondingly $v_n(x,\frac{3\tau}{2}) \ge \frac{\delta}{2}$ for $x\in[0,1]$ and sufficiently large n. This implies that $u(x,t_n) \ge \frac{\delta}{2}W(t_n)$ for sufficiently large n and $x\in[0,1]$, which contradicts the boundedness of $w(t)$. Therefore, there exists $C > 0$ such that $u(x,t) \le C$ for all $x\in[0,1]$ and $t > 0$. $\square$

The following result regarding the nonnegative steady state of system (1.8) is the key to the our main results on the global dynamics.

Theorem 3.3. *Assume that $d,\ D,\ k_0,\ k,\ \gamma,\ \tau > 0$.*

(i) If $d \ge d_*$, then the trivial steady state $u = 0$ is the only nonnegative steady state of system (1.8).
(ii) If $d < d_*$, then there exists $\tau_d > 0$ such that system (1.8) has a unique positive steady state $u = \phi_d$ for $0 < \tau < \tau_d$, and the trivial steady state $u = 0$ is the only nonnegative steady state of system (1.8) for $\tau \ge \tau_d$.

Proof. It is known that if $\Phi_1 \geq \Phi_2$, $\lambda_1(\Phi_1) \geq \lambda_1(\Phi_2)$ and equality holds only if $\Phi_1 \equiv \Phi_2$. Then it follows that for $\tau \in (0,\infty)$, $-\lambda_1(-g(e^{-k_0x})e^{-\gamma\tau}) < d_* = -\lambda_1(\Psi_0)$ and $-\lambda_1(-g(e^{-k_0x})e^{-\gamma\tau})$ is a strictly decreasing function of τ. Therefore, if $d \geq d_*$, then $d \geq -\lambda_1(-g(e^{-k_0x})e^{-\gamma\tau})$ for any $\tau > 0$. This, combined with [1, Theorem 2.1], implies that the trivial steady state 0 is the only nonnegative steady state of system (1.8). This completes part (i).

Noticing that $\lim_{\tau\to\infty} -\lambda_1(-g(e^{-k_0x})e^{-\gamma\tau}) = 0$, and $\lim_{\tau\to 0} -\lambda_1(-g(e^{-k_0x})e^{-\gamma\tau}) = d_*$, we see that if $0 < d < d_*$, there exits $\tau_d > 0$ such that $-\lambda_1(-g(e^{-k_0x})e^{-\gamma\tau}) > d$ for $0 < \tau < \tau_d$ and $-\lambda_1(-g(e^{-k_0x})e^{-\gamma\tau}) \leq d$ for $\tau \geq \tau_d$. Similarly, invoking [1, Theorem 2.1], we see that system (1.8) has a unique positive steady state ϕ_d for $0 < \tau < \tau_d$, and the trivial steady state 0 is the only nonnegative steady state of system (1.8) for $\tau \geq \tau_d$. This completes part (ii). □

Now based on Lemmas 3.1, 3.2 and Theorem 3.3, we obtain the following result on the global attractivity of nonnegative steady states.

Theorem 3.4. *Assume that $d,\ D,\ k_0,\ k,\ \gamma,\ \tau > 0$, and let $u(x,t)$ be the unique solution of (1.8) with the initial value $\phi \in \mathcal{C}_+$ and $\phi(x,0) \not\equiv 0$.*

(i) If $d \geq d_*$, then $u(x,t)$ converges uniformly to the trivial steady state 0 as $t \to \infty$.
(ii) If $d < d_*$, then when $0 < \tau < \tau_d$, $u(x,t)$ converges uniformly to the positive steady state ϕ_d as $t \to \infty$, and when $\tau \geq \tau_d$, $u(x,t)$ converges uniformly to the trivial steady state 0 as $t \to \infty$, where τ_d and ϕ_d are defined as in Theorem 3.3.

Proof. It follows from Proposition 2.1 and Theorem 2.2 that $u(x,t)$ is a classical solution of (1.8) when $t > \tau$ and $u(x,t) > 0$ for $x \in [0,1]$, $t > 0$. By time translation, we could assume that $u(x,t)$ is a classical solution of (1.8) when $t > 0$ and $u(x,t) = \phi(x,t) > 0$ for $x \in [0,1]$, $t \in [-\tau,0]$.

We first consider the case that $d < d_*$ and $0 < \tau < \tau_d$. Since in this case $-\lambda_1(-g(e^{-k_0x})e^{-\gamma\tau}) > d$, there exists sufficiently small $\delta > 0$ such that $d < -\lambda_1(\Phi_\delta)$ where $\Phi_\delta = -g(e^{-k_0x-k\delta x})e^{-\gamma\tau}$. Let ϕ_δ be the corresponding eigenfunction with respect to $\lambda_1(\Phi_\delta)$. Noticing that the initial value $\phi(x,t) > 0$ for $x \in [0,1]$ and $-\tau \leq t \leq 0$, we can choose $\epsilon > 0$ such that $\epsilon\phi_\delta < \min_{(x,t)\in[0,1]\times[-\tau,0]} \phi(x,t)$ and $\epsilon\phi_\delta < \delta$ for $x \in [0,1]$. Let $\underline{u}(x,t)$ be the solution of (1.8) with initial value $\underline{u}_0(x,t) = \epsilon\phi_\delta$ for $(x,t) \in [0,1]\times[-\tau,0]$. Then, for $0 < t \leq \tau$, we have

$$\begin{aligned}\frac{\partial \underline{u}(x,t)}{\partial t} =& D\frac{\partial^2 \underline{u}(x,t)}{\partial x^2} + e^{-\gamma\tau} g\left(e^{-k_0x-k\int_0^x \epsilon\phi_\delta ds}\right)\epsilon\phi_\delta - d\underline{u}(x,t)\\ >& D\frac{\partial^2 \underline{u}(x,t)}{\partial x^2} + \lambda_1(\Phi_\delta)\underline{u}(x,t) - \Phi_\delta\epsilon\phi_\delta.\end{aligned}$$

It follows that, for $(x,t) \in (0,1)\times(0,\tau]$,

$$\frac{\partial(\underline{u}-\epsilon\phi_\delta)}{\partial t} > D\frac{\partial^2(\underline{u}-\epsilon\phi_\delta)}{\partial x^2} + \lambda_1(\Phi_\delta)(\underline{u}-\epsilon\phi_\delta)(x,t).$$

Noticing that $(\underline{u}-\epsilon\phi_\delta)(x,0) > 0$, from the strong maximum principle, we conclude $\underline{u}(x,t) > \epsilon\phi_\delta$ for $0 < t \leq \tau$. Therefore, for any fixing $s \in (0,\tau)$, we have $\underline{u}(x,s+t) > \underline{u}(x,t)$ for $(x,t) \in [0,1]\times[-\tau,0]$. This, combined with Lemma 3.1, implies that $\underline{v}(x,t) < \underline{v}(x,t+s)$ for $(x,t) \in (0,1]\times[-\tau,\infty)$, where $\underline{v}(x,t) = \int_0^x \underline{u}(s,t)ds$, and hence $\underline{v}(x,t)$ is strictly increasing in t. Invoking Lemma 3.2, we see that there exists a constant $C > 0$ such that $\underline{u}(x,t), \underline{v}(x,t) \leq C$ for $(x,t) \in [0,1]\times(0,\infty)$. Then we have $\lim_{t\to\infty} \underline{v}(x,t) = v_*(x)$. Moreover, by virtue of the regularity theory and embedding theorem, we see that, for any sequence $t_n \to \infty$, $\{\underline{u}(\cdot,t_n)\}$ has a subsequence $\{\underline{u}(\cdot,t_{n_k})\}$ satisfying $\lim_{k\to\infty} \underline{u}(\cdot,t_{n_k}) = u_*$ in $C^1([0,1])$.

Taking the limit of $\int_0^x \underline{u}(x,t_{n_k})dx = \underline{v}(x,t_{n_k})$ as $k \to \infty$, we have $\int_0^x u_*(s)ds = v_*(x)$, which yields $u_* = v_*'$. Therefore, $\lim\limits_{t\to\infty} \underline{u}(x,t) = v_*'$ in $C^1([0,1])$. Note that, for any $\phi \in C_c^\infty(0,1)$,

$$\begin{aligned}\int_0^1 \underline{u}_t \phi dx = &- D\int_0^1 \underline{u}_x \phi_x dx - d\int_0^1 \underline{u}\phi dx \\ &+ \int_0^1 e^{-\gamma\tau} g(e^{-k_0 x - \int_0^x \underline{u}(s,t-\tau)ds})\underline{u}(x,t-\tau)\phi dx, \quad t > 0.\end{aligned} \tag{3.2}$$

Since

$$\underline{w}'(t) = -d\underline{w}(t) + \int_0^1 e^{-\gamma\tau} g(e^{-k_0 x - \int_0^x \underline{u}(s,t-\tau)ds})\underline{u}(x,t-\tau)dx,$$

where $\underline{w}(t) = \int_0^1 \underline{u}(s,t)ds$, we see that $w'(t)$ is uniformly continuous on $[0,\infty)$, and consequently, $\lim\limits_{t\to\infty} w'(t) = 0$. Then taking the limits of Eq. (3.2) on both sides as $t \to \infty$, we have

$$0 = \lim_{t\to 0}\int_0^1 \underline{u}_t \phi dx = -D\int_0^1 (v_*')_x \phi_x dx - d\int_0^1 v_*'\phi dx + \int_0^1 e^{-\gamma\tau} g(e^{-k_0 x - \int_0^x v_*' ds})\underline{v}_*'\phi dx. \tag{3.3}$$

Therefor, v_*' is a nonnegative steady state of model (1.8). Noticing that $v_*' \not\equiv 0$, we see from the maximum principle that $v_*' = u_d$.

Denote $\Phi_M(x) = -g(e^{-k_0 x - Mx})e^{-\gamma\tau}$ and ϕ_M is the corresponding positive eigenfunction with respect to $\lambda_1(\Psi_M)$ satisfying $\|\phi_M\|_\infty = 1$. We choose M as that in [1] such that

$$d > -\lambda_1(\Phi_M), \ \frac{1}{2} < \phi_M \le 1, \text{ and } \phi(x,t) < 2M \text{ for } (x,t) \in [0,1]\times[-\tau,0].$$

Let $\overline{u}(x,t)$ be the solution of (1.8) with the initial value $\overline{u}_0 = 2M\phi_M(x)$ for $x \in [0,1]$, $t \in [-\tau,0]$. Then, by using the similar procedure as that for $\underline{u}(x,t)$, we can obtain that $\overline{v}(x,t)$ is strictly decreasing and $\lim\limits_{t\to\infty} \overline{v}(x,t) = \int_0^x \phi_d(s)ds$, where $\overline{v}(x,t) = \int_0^x \overline{u}(s,t)ds$.

Since $\underline{u}_0(x,t) < \phi(x,t) < \overline{u}(x,t)$ for $x \in [0,1]$ and $t \in [-\tau,0]$, it follows from Lemma 3.1 that $\underline{v}(x,t) < v(x,t) < \overline{v}(x,t)$ for $x \in [0,1]$ and $t \in [0,\infty]$, where $v(x,t) = \int_0^x u(s,t)ds$. This implies that $\lim\limits_{t\to\infty} v(x,t) = \int_0^x \phi_d(s)ds$. Therefore, repeating the procedure as that for $\underline{u}(x,t)$, we can show that $u(x,t)$ converges uniformly to ϕ_d as $t \to \infty$.

Finally, we deal with the case of $d \ge d_*$ and the case of $d < d_*,\ \tau \ge \tau_d$. In these two cases, we can choose $\overline{u}(x,t)$ as that in the case of $d < d_*,\ 0 < \tau < \tau_d$. Note that 0 is the only nonnegative steady state for these two cases. Therefore, we can obtain $u(x,t)$ converges uniformly to 0 as $t \to \infty$ for these two cases. □

Remark 3.5. Here we remark that τ_d satisfies

$$-\lambda_1(-g(e^{-k_0 x})e^{-\gamma\tau_d}) = d.$$

Note that $-\lambda_1(-g(e^{-k_0 x})e^{-\gamma\tau})$ is a strictly decreasing function of τ, and satisfies

$$\lim_{\tau\to\infty} -\lambda_1(-g(e^{-k_0 x})e^{-\gamma\tau}) = 0, \ \ \lim_{\tau\to 0} -\lambda_1(-g(e^{-k_0 x})e^{-\gamma\tau}) = d_*.$$

It follows that τ_d is a strictly decreasing function of d, and satisfies

$$\lim_{d\to d_*} \tau_d = 0, \ \ \lim_{d\to 0} \tau_d = \infty.$$

Moreover, we can give a diagram to show the threshold dynamics of model (1.8) with respect to parameters d and τ, see Fig. 1.

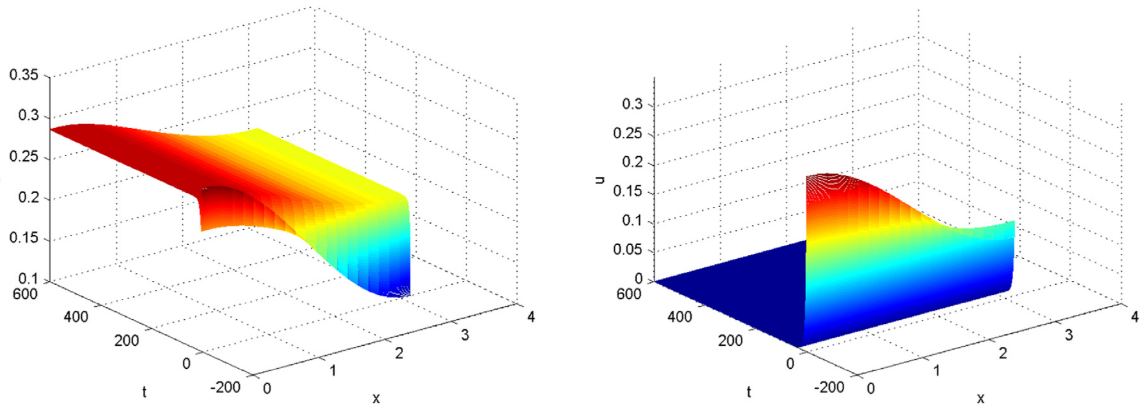

Fig. 2. The effect of delay in (1.8). Here $D = 1,\ \gamma = 1,\ k_0 = 0,\ k_1 = 1,\ d = 0.5$ and $g(x) = x$. (Left): $\tau = 0.3$; (Right): $\tau = 1$.

Finally some numerical simulations for model (1.8) are shown to support our theoretical results. Here we show numerically that: (see Fig. 2)

(i) when delay τ is small, the solution of (1.8) converges to the unique positive steady state as $t \to \infty$;
(ii) when delay τ is large, the solution of (1.8) converges to the trivial steady state as $t \to \infty$.

Therefore, the time delay can lead to population extinction but it cannot lead to temporal oscillation.

4. Discussion

Our theoretical results show that, for the large death rate case ($d \geq d_*$), the dynamics of model (1.8) is similar to the one found in [1] in the sense that there is a critical death rate d_* such that a large death rate drives the phytoplankton population to die out. This critical death rate d_* for model (1.8) is the same as the one found in [1]. But for the small death rate case ($d < d_*$), we find that there is a threshold maturation value $\tau_d > 0$ so that the population is also destined to extinction when $\tau \geq \tau_d$ and the population density $u(x,t)$ converges uniformly to the positive steady state ϕ_d as $t \to \infty$ when $0 < \tau < \tau_d$. We point out that this steady state ϕ_d also depends on the maturation time τ, and it follows from the comparison principle that $\phi_d(\tau_2) < \phi_d(\tau_1)$ if $\tau_2 > \tau_1$. This result is biologically reasonable. As the maturation time increases, the density of the phytoplankton species will decrease, and finally the species could die out. Our results also imply that the time delay cannot induce temporal oscillation for this reaction–diffusion model with nonlocal delay effect. Instead the threshold maturation value τ_d induces a global extinction of the population.

As is pointed out in [2], the phytoplankton could also sink due to their own weight. Therefore, it is natural to include the advection term in model (1.8). That is,

$$\begin{cases} u_t = Du_{xx} - \alpha u_x + e^{-\gamma\tau} g(I(x,t-\tau))u(x,t-\tau) - du, & x \in (0,L),\ t > 0, \\ Du_x(0,t) - \alpha u(0,t) = Du_x(L,t) - \alpha u(L,t) = 0, & t > 0, \\ u(x,t) = \phi(x,t) \geq 0,\ \phi(x,0) \not\equiv 0, & x \in (0,L),\ t \in [-\tau,0], \end{cases} \tag{4.1}$$

where advection a represents the sinking effects. It was shown in [2] that the dynamics of (4.1) is similar to the one found in [1] when $\tau = 0$. By virtue of the similar arguments in Section 3 and [2, Section 4], we could also prove that the dynamics of model (4.1) is similar to that of model (1.8) (here we omit the proof for simplicity). That is,

(i) if $d \geq d_*$, then $u(x,t)$ converges uniformly to the trivial steady state as $t \to \infty$.
(ii) if $d < d_*$, then there exists $\tau_d > 0$ such that when $0 < \tau < \tau_d$, $u(x,t)$ converges uniformly to the positive steady state ϕ_d as $t \to \infty$, and when $\tau \geq \tau_d$, $u(x,t)$ converges uniformly to the trivial steady state as $t \to \infty$.

Here $d_* = -\lambda_1(\Phi_0)$, where Φ_0 is defined as in (1.9), and $\lambda_1(\Phi_0)$ is the smallest eigenvalue of

$$\begin{cases} -D\psi'' - \alpha\psi' + \Phi_0\psi = \lambda\psi, & x \in (0,L), \\ \psi_x(0) = \psi_x(L) = 0. \end{cases} \tag{4.2}$$

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