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Existence, uniqueness, stability and bifurcation of periodic patterns for a seasonal single phytoplankton model with self-shading effect

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Abstract

We study the existence, uniqueness, global attractivity and bifurcation of time-periodic patterns for a seasonal phytoplankton model with self-shading effect. By the comparison principle, we obtain the globally asymptotical stability of the zero solution when the principal eigenvalue λ_1 is less than zero. When $\lambda_1 > 0$, by transforming the model into a new system, we successfully prove the conjecture in previous studies on the uniqueness and attractivity of the positive periodic solution. The positive periodic pattern bifurcating from the zero solution is a very interesting phenomenon. Here we apply the Crandall and Rabinowiz's theory to prove rigorously the existence of a bifurcation point. By way of asymptotic analysis, we derive an asymptotic formula for the positive periodic pattern. Based on the solution formula, we find the linear stability of this positive pattern. Finally, we provide a numerical scheme for the calculations of the principal eigenvalue and the simulations of the solution. The simulations corroborate our theoretical analysis.

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1. Introduction

Since the pioneer work of Riley, Stommel and Bumpus [19], mathematical modeling of phytoplankton bloom has attracted considerable attention of researchers, see [1,7,8,11,12,14,18–20]. A simple convection–diffusion model was proposed by Shigesada and Okubo [20] which incorporates the sinking and self-shading effect of the phytoplankton. Let $u(x,t)$ denote the population density of plankton at depth x and time t. The original model of Shigesada and Okubo reads

$$\begin{cases} u_t = Du_{xx} - \alpha u_x + [g(I(x,t)) - d]u, & x \in (0,\infty),\ t > 0, \\ Du_x - \alpha u = 0, & x = 0,\ t > 0, \\ u(x,0) = u_0(x) \ge 0, & x \in [0,\infty), \end{cases} \tag{1.1}$$

where D is the diffusivity and α is the sinking velocity. $g(I(x,t))$ is the growth rate of the phytoplankton as a function of light intensity $I(x,t)$. Typical functions for g are given by

$$g(I) = \frac{aI}{1+bI}, \quad \text{or} \quad g(I) = b\frac{1-e^{-cI}}{c},$$

for some constants a, b and c, see also [15]. Due to the absorption of water and the self-shading effect of phytoplankton, the light intensity is modeled by

$$I(x,t) = I_0 e^{-k_0 x - k_1 \int_0^x u(s,t)ds},$$

where I_0 is the light intensity at the surface, k_0 and k_1 are two constants. The water depth is assumed sufficiently large so that another boundary condition at the bottom is added as

$$\lim_{x\to\infty} u(x,t) = 0. \tag{1.2}$$

The system (1.1)–(1.2) is a non-local convection diffusion model. If the phytoplankton is assumed to be sufficiently transparent (i.e., $k_1 = 0$), (1.1) reduces to a linear model which was investigated in [8]. Fennel in [8] found that the species attains its peak density at the vertical location where the growth rate and the death rate are balanced. When water is assumed to be sufficiently transparent (i.e., $k_0 = 0$) so that all of the light is absorbed by the phytoplankton itself, this is called a completely self-shading model. Steady-state solutions of the model were investigated by the phase plane method in [20]. When neither k_0 nor k_1 is equal to zero, the global stability of the stationary solutions were studied by way of comparison and energy method in [13].

It is interesting to study the model when the water depth is finite. In [15], Kolokolnikov, Ou and Yuan added a non-flux boundary condition at the bottom with depth L as

$$Du_x - \alpha u = 0,\ \ x = L,\ t > 0. \tag{1.3}$$

When $k_0 = 0$, the phytoplankton depth profiles and their transitions near the critical sinking velocity were studied. Depending on the sinking rate, light intensity and water depth, the plankton can concentrate either near the surface, or at the bottom of the water column, or both, resulting in a so-called “double-peak” profile. Kolokolnikov, Ou and Yuan’s study generalized the results of Shigesada and Okubo where infinite depth was considered.

When $k_0 \neq 0$, most recently, there were intensive studies for the steady state solutions of this model by Du, Hsu and Lou, see e.g. [3–6,10]. In particular, in [3,4], Du and Hsu studied the existence of concentration phenomena and their limiting profile. In [10], Hsu and Lou also pointed out that the phytoplankton forms a thin layer at the surface of the water column for large buoyant rates, and it also forms a thin layer at the bottom of the water column for large sinking rates. Precise characterizations of these thin layers were also given, see [10] for details.

In [16,17], Peng and Zhao considered that the light intensity I_0 at the surface should be time periodic due to diurnal light cycle and seasonal changes. Therefore, they studied

$$\begin{cases} u_t = Du_{xx} - \alpha u_x + [g(I(x,t)) - d(t)]u, & x \in (0, L),\ t > 0, \\ Du_x - \alpha u = 0, & x = 0, L,\ t > 0, \\ u(x,0) = u_0(x) \geq 0, & x \in [0, L] \end{cases} \tag{1.4}$$

with $I_0(t)$ and $d(t)$ to be nonnegative periodic functions. Due to the incorporation of the time-periodic functions, the model has been more practical. However, the analysis of the model becomes even more challenging. The persistence and extinction of the phytoplankton species were established in terms of a threshold value of the basic reproduction number. Most interestingly, they also presented an open question on the uniqueness of positive periodic solutions as well as a conjecture on the global attractivity of these patterns.

In this paper, we consider the following model

$$\begin{cases} u_t = D(t)u_{xx} - \alpha(t)u_x + [g(I(x,t)) - d(t)]u, & x \in (0, L),\ t > 0, \\ D(t)u_x - \alpha(t)u = 0, & x = 0, L,\ t > 0, \\ u(x,0) = u_0(x) \geq 0, & x \in [0, L], \end{cases} \tag{1.5}$$

where $u(x,t)$ represents the population density of the phytoplankton at the depth x and time t; $D(t) > 0, d(t) > 0$ and $\alpha(t)$ are all continuously differentiable T-periodic functions for some positive number T. They stand for the strength of the diffusion, the death rate of the species and the sinking effect, respectively. $g(\cdot) \in C^1([0, L])$ is a nonlinear function that describes the growth rate of phytoplankton and it satisfies

$$g(0) = 0 \text{ and } g \text{ is continuous and strictly increasing function.} \tag{1.6}$$

Moreover, the light intensity $I(x,t)$ is in the form of

$$I(x,t) = I_0(t)e^{-k_0 x - k_1 \int_0^x u(s,t)ds},\ x \in [0, L],\ t \geq 0, \tag{1.7}$$

where $I_0(t) > 0$ is a continuous T-periodic function and represents the incident light intensity, $k_0 \geq 0$ is the background turbidity and $k_1 > 0$ is the light attenuation coefficient of the phytoplankton species. The initial function $u_0(x)$ is continuous and nonnegative, and there exists a sub-interval in $[0, L]$ such that $u_0(x) > 0$. The boundary conditions show that there is no flux of phytoplankton species at the surface and the bottom of the water column. System (1.5)–(1.7) models the distribution of phytoplankton densities in a vertical water column with a cross section of one unit area and maximum depth L, see [16,17] and references therein.

We shall study the global behavior of this model. The first important and new contribution of this paper is that we obtain the uniqueness and the global attractivity of the positive periodic solution when it exists. This solves the open question as well as the conjecture in [16,17]. Furthermore, we establish a new and rigorous result on the bifurcation of the solution in terms of the death rate. Near the bifurcation point, approximate formulas for the periodic solution are derived. Based on these formulas, the linear stability of the periodic patterns is also established. Lastly, due to the occurrence of periodic light intensity, the computation of the principal eigenvalue as well as the solution is non-trivial. In addressing this challenge, we give a numerical scheme for the calculations of the principal eigenvalue and the simulations of the underlying phytoplankton model to demonstrate our theoretical analysis.

The paper is arranged as follows. In Section 2, we study the stability of the zero solution. The existence, uniqueness and attractivity of the positive periodic solution are presented in Section 3. The bifurcation and asymptotic analysis of the positive solution are showcased in Section 4. Numerical simulations are arranged in Section 5. Section 6 includes conclusion and discussion.

2. Stability of the zero equilibrium

For convenience, in this paper we denote $\mathbb{B}$ the space of all continuous functions from $[0, L]$ to $\mathbb{R}$ with the supremum norm, i.e., $\mathbb{B} = C([0, L], \mathbb{R})$. Let $Y = C([0, L], \mathbb{R}_+)$, $Y_0 = \{\phi \in Y : \phi \not\equiv 0\}$ and $\partial Y_0 = \{0\}$. Since the nonlinear term $g(I(x,t))$ satisfies the local Lipschitz condition, using the standard argument, we can prove the uniqueness and global existence of the solution $u(x,t)$ of (1.5) when the initial function $u_0(x)$ is in Y, and by the strong maximum principle and the Hopf boundary lemma, we can also know that $u(x,t)$ is positive for $(x,t) \in [0, L] \times (0, \infty)$ when $u_0(x)$ is in Y_0. Let $Q_t[u_0] = u(x,t; u_0)$ be the unique solution of (1.5). It is easy to know that Q_t is a continuously periodic semiflow on Y that follows the usual definition below.

Definition 2.1. A family of maps $\{Q_t\}_{t\geq 0}$ on the space $\mathbb{B}$ is said to be a T-periodic semiflow for some $T > 0$ provided that $\{Q_t\}$ satisfies

(i) $Q_0[\varphi] = \varphi$, $\forall \varphi \in \mathbb{B}$;
(ii) $Q_t \circ Q_T[\varphi] = Q_{t+T}[\varphi],\ t \geq 0,\ \varphi \in \mathbb{B}$;
(iii) $Q_t[\varphi]$ is continuous in (t, φ) on $[0, \infty) \times \mathbb{B}$.

The map Q_T is called the Poincaré map associated with this periodic semiflow.

In this section, we shall give conditions for the globally asymptotical stability of the equilibrium point $u(x,t) \equiv 0$ of (1.5). When $D(t)$ and $\alpha(t)$ are not constants, essentially we can follow the idea in [17] based on a taste of biological language in terms of the Basic Reproduction Number. Here however, we shall provide a short presentation only in terms of the principal eigenvalue of the corresponding linear system.

Let

$$u(x,t) = 0 + \epsilon\phi(x,t)e^{\lambda t}$$

and substitute it into (1.5). Then the coefficients to the first-order power of ϵ satisfy the following system

$$\begin{cases} \lambda\phi = -\phi_t + D(t)\phi_{xx} - \alpha(t)\phi_x + [g(I_0(t)e^{-k_0 x}) - d(t)]\phi, & x \in (0, L),\ t > 0, \\ D(t)\phi_x - \alpha(t)\phi = 0, & x = 0, L,\ t > 0, \\ \phi(x, 0) = \phi(x, T), & x \in [0, L]. \end{cases} \tag{2.1}$$

By the well known Krein–Rutman theorem [9], this problem has the existence of principal eigenvalue λ_1 with the corresponding positive eigenfunction in the domain $(0, L) \times [0, T]$. The standard stability theory of partial differential equations indicates that the equilibrium $u \equiv 0$ is locally stable when the principal eigenvalue λ_1 of (2.1) is less than zero. Furthermore, by using the comparison technique, we have the results below.

Theorem 2.1. *If $\lambda_1 < 0$, then the equilibrium $u \equiv 0$ of (1.5) is globally asymptotically stable.*

Proof. Obviously, we need only to prove that $u \equiv 0$ is globally attractive. By (1.6) and (1.7), it follows that

$$u_t \le D(t)u_{xx} - \alpha(t)u_x + [g(I_0(t)e^{-k_0 x}) - d(t)]u.$$

If a function $U(x, t)$ satisfies

$$\begin{cases} U_t = D(t)U_{xx} - \alpha(t)U_x + [g(I_0(t)e^{-k_0 x}) - d(t)]U, & x \in (0, L),\ t > 0, \\ D(t)U_x - \alpha(t)U = 0, & x = 0, L,\ t > 0, \\ U(x, 0) = U_0(x) \ge 0, & x \in [0, L], \end{cases} \tag{2.2}$$

then it is easy to know that $u(x, t) \le U(x, t)$ for $u_0(x) \le U_0(x)$. For the linear system (2.2), $\lambda_1 < 0$ implies that $U \equiv 0$ is globally attractive, and so is $u \equiv 0$. The proof is complete. □

Remark 2.1. In the case when $\lambda_1 = 0$, it is possible to develop the idea in the proof of Theorem 3.4 of [5] to obtain the global attractivity of zero solution, see also [17]. We shall leave this job into next section by applying a new technique that can also obtain the global attractivity of positive periodic pattern. This will solve the open problem raised in [16,17].

In next section, we shall study the global behavior of the solutions when $\lambda_1 \ge 0$.

3. Periodic solutions of (1.5)

By applying the idea of Theorem 2.1 in [17], it is not difficult to obtain the existence of positive periodic solution of (1.5) as well as the persistence behavior of the system when $\lambda_1 > 0$. However, here we are interested in dealing with not only the existence, but also the uniqueness and attractivity of the positive T-periodic solution of the system (1.5) which was raised as an open question in [17] and was conjectured in [16]. We shall proceed to provide a different method to handle the problem. For this purpose, by using the transformation

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

we first change (1.5) into a monotonic system as follows

$$\begin{cases} v_t = D(t)v_{xx} - \alpha(t)v_x + G(I_0(t), v) - d(t)v, & x \in (0,L),\ t>0, \\ v(0,t)=0,\ D(t)v_{xx} - \alpha(t)v_x|_{x=L} = 0, & t>0, \\ v(x,0) = \int_0^x u_0(s)ds = \varphi(x), & x \in [0,L], \end{cases} \tag{3.2}$$

where

$$G(I_0(t), v(x,t)) = \frac{1}{k_1}\int_0^{k_0x+k_1v(x,t)} g\left(I_0(t)e^{-\xi}\right)d\xi - \frac{k_0}{k_1}\int_0^x g\left(I_0(t)e^{-(k_0s+k_1v(s,t))}\right)ds. \tag{3.3}$$

Obviously, for biological reason, we need take $\varphi(x)$ as a nondecreasing and differentiable function (i.e., $\varphi'(x) \ge 0$) on $[0,L]$ satisfying $\varphi(0)=0$.

Let $\mathcal{C}^1 = \{\varphi : \varphi' \in C([0,L],\mathbb{R}) \text{ and } \varphi(0)=0\}$ with the norm

$$\|\varphi\| = \max_{x\in[0,L]}|\varphi(x)| + \max_{x\in[0,L]}|\varphi'(x)|$$

and $\mathcal{C}^1_+ = \{\varphi \in \mathcal{C}^1 : \varphi(x) \ge 0 \ \text{ for } x \in [0,L]\}$. For any $\varphi_1, \varphi_2 \in \mathcal{C}^1$, we write $\varphi_1 \le \varphi_2$ if $\varphi_2 - \varphi_1 \in \mathcal{C}^1_+$, $\varphi_1 < \varphi_2$ if $\varphi_2 - \varphi_1 \in \mathcal{C}^1_+ \backslash \{0\}$ and $\varphi_1 \ll \varphi_2$ if $\varphi_2 - \varphi_1$ is in $Int(\mathcal{C}^1_+)$, where $Int(\mathcal{C}^1_+)$ represents the interior of $\mathcal{C}^1_+$. Since we require the initial function to be nondecreasing, we define a convex subset as

$$P = \{\varphi : \varphi \in \mathcal{C}^1_+ \text{ and } \varphi'(x) \ge 0 \text{ for } x \in [0,L]\}$$

and from now on we assume the initial function of (3.2) is inside P.

Since the initial function φ is in P, the existence and uniqueness of the solution v is implied by the existence and uniqueness of u. If $\varphi \in P$, then φ' is continuous with $\varphi' \ge 0$. With φ' as the initial function of (1.5), it is easy to obtain the non-negative solution $u(x,t)$ of (1.5) for $t>0$. Returning to (3.2), we can know that $v(x,t)$ is non-decreasing in x on $[0,L]$ for any $t \in (0,\infty)$ since $v_x(x,t) = u(x,t)$ is the nonnegative solution of (1.5). This means that P is invariant under the system (3.2). Therefore, in what follows, we shall focus on the study of (3.2).

Remark 3.1. Although the boundary condition at $x=L$ is not standard, still we can provide a general existence and uniqueness result for model (3.2) with the initial function φ in a weak space $C([0,L],R)$. Using the equation, the boundary value $v(L,t)$ satisfies

$$v_t(L,t) = G(I_0(t), v(L,t)) - d(t)v(L,t). \tag{3.4}$$

Let

$$F(t, v(x,t)) = G(I_0(t), v(x,t)) - d(t)v(x,t) \tag{3.5}$$

and we are easy to know that it satisfies the global Lipschitz condition

$$\|F(t,u) - F(t,v)\| \leq k\|u - v\|$$

for some positive constant k. Define a modified Picard iteration as $v_0(x,t) = \varphi$, and

$$\begin{cases} (v_{n+1})_t = D(t)(v_{n+1})_{xx} - \alpha(t)(v_{n+1})_x + F(t, v_n), & x \in (0, L),\ t > 0, \\ (v_{n+1})(0,t) = 0,\ (v_{n+1})_t = F(t, v_n), \text{ at } x = L, & t > 0, \\ v_{n+1}(x, 0) = \varphi(x), & x \in [0, L], \end{cases} \tag{3.6}$$

for any $n \geq 0$. Note that the boundary value $v_{n+1}(L,t)$ can be worked out based on the known function $v_n(x,t)$. Thus, (3.6) is essentially a standard parabolic Dirichlet boundary value problem. Obviously, we have

$$\|F(t, v_0\| \leq \|F(t, 0)\| + k\|v_0\| \leq (1+k)m,$$

where $m = \|v_0\|$. First we can derive

$$\|v_1 - v_0\| \leq Mt$$

for some positive constant M. Set

$$M_n(t) = \sup\{\|v_n(x,t) - v_{n-1}(x,s)\| : s \leq t\}.$$

Using the technique of Green's function to re-write (3.6) into an integral equation, by induction, we can obtain

$$M_n(t) \leq \frac{Mk^n t^n}{n!}.$$

The above inequality implies that the sequence $v_n(x,t)$ converges uniformly to some continuous function $v(x,t)$. This provides the existence of the solution. The uniqueness of v can be proved by the standard contradiction argument.

To obtain the existence and stability of the positive periodic solution to (3.2), we shall use the following lemma.

Lemma 3.1. *([21], Theorem 2.3.4) Suppose that $f : P \to P$ is a continuous map. Also assume that*

(1) *f is monotone and strongly subhomogeneous;*
(2) *f is asymptotically smooth, and every positive orbit of f in P is bounded;*
(3) *$f(0) = 0$, and $Df(0)$ is compact and strongly positive.*

Then there exists threshold dynamics:

(a) If $r(Df(0)) \leq 1$, then every positive orbit in P converges to 0;
(b) If $r(Df(0) > 1)$, then there exists a unique fixed point $u > 0$ in P such that every positive orbit in $P\backslash\{0\}$ converges to $u*$,*

where $r(Df(0))$ is the spectral radius of $Df(0)$, and $Df(0)$ is the Fréchet derivative of f at zero.

The definitions of "monotone", "strongly subhomogeneous" and "asymptotically smooth" can be found in [21].

We first construct a lemma in regard to the boundedness of solutions of (3.2).

Lemma 3.2. *The solutions of the system (3.2) are bounded uniformly in x and t.*

Proof. In view of the above discussion, for any given initial function φ in P, if $v(x,t)$ is a solution of (3.2), then we have

$$v(x,t) = \int_0^x u(s,t)ds$$

where $u(x,t)$ is the solution of (1.5) with the initial function $u(x,0) = \varphi' \geq 0$. To show the boundedness of v, we only need to provide the boundedness of u of (1.5). This directly comes from the proof of Lemma 2.4 in [17] by a minor change, see also Lemma 3.2 and its proof in [5]. In other word, there exists a constant $C > 0$ such that $u(x,t) < C$ for all $x \in [0, L]$ and $t \geq 0$.

Therefore, returning to v, we have $0 \leq v(x,t) \leq M$ for $M = LC$. □

The following lemma aims to show the monotonicity of the periodic semiflow defined from (3.2).

Lemma 3.3. *Assume that $v(x,t,\varphi)$ and $\bar{v}(x,t,\bar{\varphi})$ are two solutions of (3.2) with initial functions $\varphi \geq \bar{\varphi}$. Then we have $v(x,t,\varphi) \geq \bar{v}(x,t,\bar{\varphi})$, for all $(x,t) \in [0,L] \times (0,\infty)$.*

Proof. Since $v(x,t,\varphi)$ and $\bar{v}(x,t,\bar{\varphi})$ are two solutions of (3.2), we then have

$$\begin{cases} v_t = D(t)v_{xx} - \alpha(t)v_x + G_1(k_0x + k_1v) \\ \qquad - \frac{k_0}{k_1}\int_0^x g(I_0(t)e^{-k_0s-k_1v(s,t)})ds, & x \in (0,L),\ t > 0, \\ v(0,t) = 0,\ \ [D(t)v_{xx} - \alpha(t)v_x]_{x=L} = 0, & t > 0, \\ v(x,0) = \varphi, & x \in [0,L] \end{cases} \tag{3.7}$$

and

$$\begin{cases} \bar{v}_t = D(t)\bar{v}_{xx} - \alpha(t)\bar{v}_x + G_1(k_0x + k_1\bar{v}) \\ \qquad - \frac{k_0}{k_1}\int_0^x g(I_0(t)e^{-k_0s - k_1\bar{v}(s,t)})ds, & x \in (0, L),\ t > 0, \\ \bar{v}(0,t) = 0,\ \ [D(t)\bar{v}_{xx} - \alpha(t)\bar{v}_x]_{x=L} = 0, & t > 0, \\ \bar{v}(x,0) = \bar{\varphi}, & x \in [0, L], \end{cases}$$

where

$$G_1(k_0x + k_1v) = \frac{1}{k_1}\int_0^{k_0x + k_1v(x,t)} g(I_0(t)e^{-\xi})d\xi.$$

We can define a function sequence $\{v_n\}_{n=0}^{\infty}$ inductively by the following iteration, with $v_0 = v_1 = \bar{v}(x,t)$, and

$$\begin{cases} (v_n)_t = D(t)(v_n)_{xx} - \alpha(t)(v_n)_x + G_1(k_0x + k_1v_n) \\ \qquad - \frac{k_0}{k_1}\int_0^x g(I_0(t)e^{-k_0s - k_1v_{n-1}(s,t)})ds, & x \in (0, L),\ t > 0, \\ v_n(0,t) = 0,\ \ [D(t)(v_n)_{xx} - \alpha(t)(v_n)_x]_{x=L} = 0, & t > 0, \\ v_n(x,0) = \varphi, & x \in [0, L], \end{cases} \tag{3.8}$$

for $n \geq 2$. The existence and uniqueness of $v_n, n \geq 2$ can be easily proved by a standard argument. We next prove by induction that

$$v_{n-1}(x,t) \leq v_n(x,t)$$

for $n \geq 1$.

For $n = 1$, it is true. Assume that it is true for some $n \geq 1$. We then proceed to show $v_n(x,t) \leq v_{n+1}(x,t)$.

Put $w(x,t) = v_{n+1} - v_n$. Then we have

$$w_t \geq D(t)w_{xx} - \alpha(t)w_x + h(x,t)w, \tag{3.9}$$

where

$$h(x,t) = \int_0^1 g(I_0(t)e^{-k_0x - k_1\theta v_n(x,t) - k_1(1-\theta)v_{n+1}(x,t)})d\theta.$$

Now we know that $w(x,0) = 0,\ w(0,t) = 0$ and

$$D(t)w_{xx}(L,t) - \alpha(t)w_x(L,t) = 0. \tag{3.10}$$

Combining together (3.9) and (3.10) gives

$$w(L,t)_t \geq h(x,t)w(L,t), \quad w(L,0) = 0. \tag{3.11}$$

It is easy to obtain from (3.11) that

$$w(L,t) \geq 0. \tag{3.12}$$

Now applying the maximum principle to equation (3.9), we have

$$w(x,t) = v_{n+1} - v_n \geq 0.$$

Then it follows that

$$v_{n+1} \geq v_n \geq \cdots \geq v_1 = \overline{v}(x,t), \quad n = 2, 3, \cdots. \tag{3.13}$$

Furthermore, by Lemma 3.2 and induction, it is easy to know that there exists a sufficiently large constant M satisfying

$$v_n(x,t) \leq M \text{ for all } n.$$

For (3.8), by using the standard estimate of the solution as well as its derivative with respect to the variable x ($(v_n)_x$ is uniformly bounded for all n), we can derive

$$v_n(x,t) \to v(x,t)$$

uniformly in $[0, L] \times [0, t]$, $t > 0$, for some positive function $v(x,t)$ which is the solution of (3.7). From (3.13) and the uniqueness of the solution of (3.7), we can obtain

$$v(x,t) \geq \bar{v}(x,t).$$

The proof is complete. □

Lemma 3.4. *The function* $G(I_0(t), v(x,t))$ *satisfies*

$$G(I_0(t), \lambda v(x,t)) \gg \lambda G(I_0(t), v(x,t)), \ \lambda \in (0,1), \tag{3.14}$$

for any $v \in Int(P)$.

Proof. From (3.3) it also follows that

$$G(I_0(t), v(x,t)) = \int_0^x g\left(I_0(t)e^{-k_0 s - k_1 v(s,t)}\right) \frac{\partial v(s,t)}{\partial s} ds.$$

Then, we have

$$G(I_0(t), \lambda v(x,t)) = \lambda \int_0^x g\left(I_0(t)e^{-k_0 s - \lambda k_1 v(s,t)}\right) \frac{\partial v(s,t)}{\partial s} ds$$

$$\gg \lambda \int_0^x g\left(I_0(t)e^{-k_0 s - k_1 v(s,t)}\right) \frac{\partial v(s,t)}{\partial s} ds$$
$$= \lambda G(I_0(t), v(x,t)) \tag{3.15}$$

for $v \in Int(P)$. Here we have used the fact that if $v \in Int(P)$, then $v_x(0,t) \neq 0$. The proof is complete. □

Define $\{Q_t\}_{t\geq 0}$ as

$$Q_t[\varphi](x) = v(x,t;\varphi), \forall \varphi \in P, x \in [0,L], t \geq 0,$$

where $v(x,t;\varphi)$ is the unique solution of system (3.2) satisfying $v(\cdot,0;\varphi) = \varphi$. The following lemma shows that $\{Q_t\}_{t\geq 0}$ is a monotonic T-periodic semiflow.

Lemma 3.5. *$\{Q_t\}_{t\geq 0}$ is a monotonic T-periodic semiflow on P.*

Proof. By Lemma 3.3, the map Q_t is monotonic on P for each t. We now prove that Q_t is a periodic semiflow on P in the sense of Definition 2.1. The initial condition implies that (i) is satisfied by Q_t, and (ii) follows from the existence and uniqueness of solutions of (3.2). Next, we prove (iii). It is evident that $Q_t[\varphi] = v(.,t;\varphi)$ is continuous in $t \in \mathbb{R}_+$. It remains to prove that $Q_t[\varphi]$ is continuous in φ on $[0,\infty) \times P$, that is, we will prove the following claim.

Claim. *For any $\epsilon > 0$, there exist $\delta(\epsilon) > 0$ such that if $\varphi_1, \varphi_2 \in P$ with $\|\varphi_1(x) - \varphi_2(x)\| < \delta$ for all $x \in [0,L]$, then $\|v_1(t,x) - v_2(t,x)\| < \epsilon$ for any fixed t, where $v_1(x,t)$ and $v_2(x,t)$ are solutions to (3.2) with initial functions φ_1 and φ_2, respectively.*

Let $\omega(x,t) = v_1(x,t) - v_2(x,t)$. Then $\omega(x,t)$ solves the following system

$$\begin{cases} \omega_t = D(t)\omega_{xx} - \alpha(t)\omega_x - d(t)\omega + H(x,t,\omega_1,\omega_2), & x \in (0,L),\ t > 0, \\ \omega(0,t) = 0,\ D(t)\omega_{xx} - \alpha(t)\omega_x|_{t=L} = 0, & t > 0, \\ \omega(x,0) = \varphi_1(x) - \varphi_2(x), & x \in [0,L], \end{cases} \tag{3.16}$$

where

$$\begin{aligned} H(x,t,\omega_1,\omega_2) &= G(I_0(t), v_1(x,t)) - G(I_0(t), v_2(x,t)) \\ &= \frac{1}{k_1} \int_{k_0 x + k_1 v_2(x,t)}^{k_0 x + k_1 v_1(x,t)} g\left(I_0(t)e^{-\xi}\right) d\xi \\ &\quad - \frac{k_0}{k_1} \int_0^x \left[g(I_0(t)e^{-k_0 x - k_1 v_1(s,t)}) - g(I_0(t)e^{-k_0 x - k_1 v_2(s,t)}) \right] ds. \end{aligned}$$

There are two cases to discuss.

Case 1. $\varphi_1 \geq \varphi_2$. Set $\varphi_1(x) - \varphi_2(x) < \delta$ for some $\delta > 0$ and $x \in [0, L]$. By (1.6), (1.7), for each fixed t we have

$$
\begin{aligned}
H(x,t,\omega_1,\omega_2) &\leq \frac{1}{k_1}\int_{k_0x+k_1v_2(x,t)}^{k_0x+k_1v_1(x,t)} g\left(I_0(t)\right)d\xi \\
&+\frac{k_0}{k_1}\int_0^x g'(\theta)I_0(t)e^{-k_0x-k_1v_2(s,t)}\left(1-e^{-k_1(v_1(s,t)-v_2(s,t))}\right)dx \\
&\leq B_1\omega + B_2B_3k_0\int_0^x \omega(s,t)ds \leq C_0\omega,
\end{aligned}
$$

where $B_i, i = 1, 2, 3$, are positive constants such that $g\left(I_0(t)\right) \leq B_1$, $g'(\theta) \leq B_2$, and $I_0(t) \leq B_3$, θ is located between $I_0(t)e^{-(k_0x+k_1v_1(s,t))}$ and $I_0(t)e^{-(k_0x+k_1v_2(s,t))}$ for each fixed t and $s \in [0, x]$, the constant C_0 is sufficiently large. Then, from (3.16) it follows that

$$
\begin{cases}
\omega_t \leq D(t)\omega_{xx} - \alpha(t)\omega_x + [C_0 - d(t)]\,\omega, & x \in (0, L),\ t > 0,\\
\omega(0,t) = 0,\ D(t)\omega_{xx} - \alpha(t)\omega_x|_{t=L} = 0, & t > 0,\\
\omega(x,0) = \varphi_1(x) - \varphi_2(x) < \delta, & x \in [0, L].
\end{cases}
\tag{3.17}
$$

We know that

$$
\overline{\omega} = e^{C_0t}\delta \tag{3.18}
$$

is a solution of the following ordinary differential system

$$
\begin{cases}
\overline{\omega}_t = C_0\overline{\omega},\ t > 0,\\
\overline{\omega}|_{t=0} = \delta.
\end{cases}
\tag{3.19}
$$

It is easy to verify that (3.18) is an upper solution of system (3.16). Then, we have

$$
\omega \leq \overline{\omega} = e^{C_0t}\delta. \tag{3.20}
$$

Thus, for $\forall \varepsilon > 0$, by taking $\delta = e^{-C_0t}\varepsilon$, we have

$$
\|v_1(x,t) - v_2(x,t)\| = \|\omega\| \leq \|\overline{\omega}\| = \|e^{C_0t}\delta\| = \varepsilon
$$

for each t when $\varphi_1(x) - \varphi_2(x) < \delta$ for $x \in [0.L]$. Since $v_x = u$, similarly we can use model (1.5) to show that u is continuous function of φ' for each $t > 0$. Therefore we can derive that v is continuous jointly for $(t, \varphi) \in [0, \infty) \times P$. Part (iii) in Definition 2.1 is true.

Case 2. $\varphi_1(x) \ngeq \varphi_2(x)$. Define

$$
\hat{\varphi_1}(x) = \max\{\varphi_1(x), \varphi_2(x)\},\ \hat{\varphi_2}(x) = \min\{\varphi_1(x), \varphi_2(x)\},\ \forall x \in [0, L],
$$

and let $\hat{v}_1(x,t)$ and $\hat{v}_2(x,t)$ be solutions of (3.2) with initial functions $\hat{\varphi}_1$ and $\hat{\varphi}_2$, respectively. It is clear that $\hat{\varphi}_1(x) - \hat{\varphi}_2(x) = |\varphi_1(x) - \varphi_2(x)|$ and $\hat{v}_2(x,t) \le v_1(x,t)$, $v_2(x,t) \le \hat{v}_1(x,t)$ for all $(x,t) \in [0,L] \times [0,\infty)$. Then, $|v_1(x,t) - v_2(x,t)| \le \hat{v}_1(x,t) - \hat{v}_2(x,t)$. Repeating the process of Case 1 for $\hat{v}_1$ and $\hat{v}_2$, we have that the claim also holds. Therefore, $Q_t[\varphi]$ is continuous in φ for each t in $[0,\infty)$. This indicates that Q_t satisfies (iii). The proof is complete. □

We now present the main results.

Theorem 3.6. *The following results hold:*

(a) If the principal eigenvalue λ_1 of (2.1) satisfies $\lambda_1 \le 0$, then every solution of (3.2) converges to zero;
(b) If the principal eigenvalue λ_1 of (2.1) is positive, then system (3.2) possesses a unique positive periodic solution v^* and every solution with initial function in $P \backslash \{0\}$ converges to v^*.

Proof. We will apply Lemma 3.1 to prove this theorem. It is obvious that the Poincaré map Q_T is monotone, every positive orbit of Q_T in P is bounded and $Q_T(0) = v(x,T;0) = 0$. Thus, we need only to verify that Q_T is asymptotically smooth, strongly subhomogeneous and $DQ_T(0)$ is compact and strongly positive.

For the asymptotic smoothness, since the diffusion coefficient $D(t)$ is always positive, it is easy to know that Q_T is asymptotically smooth.

Next, we will verify that Q_T is strongly subhomogeneous, that is,

$$Q_T(\lambda\varphi) \gg \lambda Q_T(\varphi), \ \varphi \in Int(P), \lambda \in (0,1), \tag{3.21}$$

where $Q_T(\varphi) = v(x,T;\varphi)$ satisfying (3.2) and $Q_T(\lambda\varphi) = \overline{v}(x,T;\lambda\varphi)$ satisfying

$$\begin{cases} \overline{v}_t = D(t)\overline{v}_{xx} - \alpha(t)\overline{v}_x + G(I_0(t),\overline{v}) - d(t)\overline{v}, & x \in (0,L),\ t > 0, \\ \overline{v}(0,t) = 0,\ D(t)\overline{v}_{xx} - \alpha(t)\overline{v}_x|_{x=L} = 0, & t > 0, \\ \overline{v}(x,0) = \lambda\varphi(x), & x \in [0,L]. \end{cases} \tag{3.22}$$

Thus, it suffices to verify $\overline{v} \gg \lambda v$. Multiplying system (3.2) by λ yields

$$\begin{cases} (\lambda v)_t = D(t)(\lambda v)_{xx} - \alpha(t)(\lambda v)_x + \lambda G(I_0(t),v) - d(t)(\lambda v), & x \in (0,L),\ t > 0, \\ \lambda v(0,t) = 0,\ D(t)(\lambda v)_{xx} - \alpha(t)(\lambda v)_x|_{x=L} = 0, & t > 0, \\ \lambda v(x,0) = \lambda\varphi(x), & x \in [0,L]. \end{cases} \tag{3.23}$$

By Lemma 3.4, from (3.23) it follows that

$$\begin{cases} (\lambda v)_t < D(t)(\lambda v)_{xx} - \alpha(t)(\lambda v)_x + G(I_0(t),\lambda v) - d(t)(\lambda v), & x \in (0,L),\ t > 0, \\ \lambda v(0,t) = 0,\ D(t)(\lambda v)_{xx} - \alpha(t)(\lambda v)_x|_{x=L} = 0, & t > 0, \\ \lambda v(x,0) = \lambda\varphi(x), & x \in [0,L]. \end{cases} \tag{3.24}$$

Comparing (3.22) with (3.24), we have $\overline{v} \gg \lambda v$.

We now verify the last condition. The linearized system of (3.2) at $v \equiv 0$ is

$$\begin{cases} v_t = D(t)v_{xx} - \alpha(t)v_x - d(t)v + \int\limits_0^x g\left(I_0(t)e^{-k_0 s}\right) v_s(s,t)ds, & x \in (0,L),\ t>0, \\ v(0,t) = 0,\ D(t)v_{xx} - \alpha(t)v_x|_{x=L} = 0, & t>0, \\ v(x,0) = \int\limits_0^x u_0(s)ds = \varphi(x), & x \in [0,L]. \end{cases} \tag{3.25}$$

Let $V(t)$ be the linear semigroup generated by (3.25) on P. Then the Fréchet derivative $DQ_T(0) = V(T)$. In view of (1.6) and (1.7), $DQ_T(0)$ is compact and strongly positive.

Furthermore, taking the derivative of (3.25) with respect to x, we have

$$\begin{cases} u_t = D(t)u_{xx} - \alpha(t)u_x + [g(I_0(t)e^{-k_0 x}) - d(t)]u, & x \in (0,L),\ t>0, \\ D(t)u_x - \alpha(t)u = 0, & x = 0, L,\ t>0, \\ u(x,0) = u_0(x) \geq 0, & x \in [0,L]. \end{cases} \tag{3.26}$$

It is easy to see that (2.1) is the characteristic equation of (3.26). If $\lambda_1 \leq 0$, then $r(DQ_T(0)) \leq 1$. By Lemma 3.1, every solution of (3.2) converges to zero. On the other hand, if $\lambda_1 > 0$, then $r(DQ_T(0)) > 1$. Again by Lemma 3.1, the Poincaré map Q_T has a unique fixed point $v^* > 0$ in P such that every positive orbit with the initial function in $P\backslash\{0\}$ converges to v^*. It means that in system (3.2) there exists a unique T-periodic solution $v^*(x,t)$ satisfying

$$\lim_{t\to+\infty} ||v(x,t) - v^*(x,t)|| = 0.$$

The proof is complete.

We shall deal with the simplified case of (1.5) when all of the light is absorbed by the plankton itself (i.e., $k_0 = 0$). System (1.5) is now called the completely self-shading model with transparent water. The main result is as follows.

Corollary 3.7. *Assume $k_0 = 0$. If all the coefficients $D > 0, d > 0$ and $\alpha \in \mathbb{R}$ are constants and*

$$d < \frac{1}{T}\int\limits_0^T g(I_0(s))ds, \tag{3.27}$$

then system (3.2) has a unique positive T-periodic solution v^* such that every solution with initial function in $P\backslash\{0\}$ converges to v^*.

Proof. Using the given conditions, (3.2) is simplified as

$$\begin{cases} v_t = Dv_{xx} - \alpha v_x - dv + \int\limits_0^{v(x,t)} g(I_0(t)e^{-k_1 s})ds, & x \in (0,L),\ t > 0, \\ v(0,t) = 0,\ Dv_{xx} - \alpha v_x|_{x=L} = 0, & t > 0, \\ v(x,0) = \int\limits_0^x u_0(s)ds = \varphi(x), & x \in [0,L]. \end{cases} \tag{3.28}$$

Then, obviously, by the proof of Theorem 3.6, it suffices to verify $\lambda_1 > 0$. The linearized system of (3.28) about the zero equilibrium is

$$\begin{cases} v_t = Dv_{xx} - \alpha v_x + [g(I_0(t)) - d]v, & x \in (0,L),\ t > 0, \\ v(0,t) = 0,\ Dv_{xx} - \alpha v_x|_{x=L} = 0, & t > 0, \\ v(x,0) = \int\limits_0^x u_0(s)ds = \varphi(x), & x \in [0,L]. \end{cases} \tag{3.29}$$

Differentiating (3.29) with respect to x leads to

$$\begin{cases} u_t = Du_{xx} - \alpha u_x + [g(I_0(t)) - d]u, & x \in (0,L),\ t > 0, \\ Du_x - \alpha u|_{x=0,L} = 0, & t > 0, \\ u(x,0) = u_0(x), & x \in [0,L]. \end{cases} \tag{3.30}$$

The characteristic system of (3.30) is (2.1) with $k_0 = 0$ and D, α and d being constants, i.e.,

$$\begin{cases} \lambda\phi = -\phi_t + D\phi_{xx} - \alpha\phi_x + [g(I_0(t)) - d]\phi, & x \in (0,L),\ t > 0, \\ D\phi_x - \alpha\phi = 0, & x = 0, L,\ t > 0, \\ \phi(x,0) = \phi(x,T),\ \phi_t(x,0) = \phi_T(x,T) & x \in [0,L]. \end{cases} \tag{3.31}$$

Now we want to find the principal eigenvalue of the above system. To this end, we can assume that the solutions of the linear system (3.31) have the form

$$\phi(x,t) = w(x)v(t), \quad w(x) \neq 0, \quad v(t) \neq 0. \tag{3.32}$$

Substituting it into (3.31), we have

$$\begin{cases} \dfrac{v_t}{v(t)} + \lambda + d - g(I_0(t)) = \dfrac{Dw_{xx} - \alpha w_x}{w(x)}, & x \in (0,L),\ t > 0, \\ Dw_x - \alpha w = 0, & x = 0, L, \\ v(0) = v(T). \end{cases} \tag{3.33}$$

Thus, there exists a constant μ such that

$$\frac{v_t}{v(t)} + \lambda + d - g(I_0(t)) = \frac{Dw_{xx} - \alpha w_x}{w(x)} = \mu.$$

Then (3.33) is equivalent to the following two systems

$$\begin{cases} Dw_{xx} - \alpha w_x = \mu w(x), & x \in (0, L), \\ Dw_x - \alpha w = 0, & x = 0, L \end{cases} \tag{3.34}$$

and

$$\begin{cases} v_t = [\mu - \lambda - d + g(I_0(t)]v(t), \ t > 0, \\ v(0) = v(T). \end{cases} \tag{3.35}$$

Solving (3.34) leads to

$$\mu = 0, \ -\frac{\alpha^2}{4D}, \ -\frac{\alpha^2}{4D} - \frac{Dk^2\pi^2}{L^2}, \ k = 1, \ 2, \ 3, \cdots. \tag{3.36}$$

Then, by (3.35), we get

$$\lambda = \mu - d + \frac{1}{T}\int_0^T g(I_0(s))ds.$$

It is obvious that the principal eigenvalue of (3.31) is

$$\lambda_1 = -d + \frac{1}{T}\int_0^T g(I_0(s))ds. \tag{3.37}$$

By (3.27), we have $\lambda_1 > 0$. Therefore, the result is true. □

Now we return to the dynamics of positive periodic solution of (1.5). Let $(v^*)_x = u^*$, where v^* is defined in Theorem 3.6. From Theorem 3.6, we have the following theorem.

Theorem 3.8. *The following results hold:*

(a) If the principal eigenvalue λ_1 of (2.1) satisfies $\lambda_1 \le 0$, then every solution of (1.5) converges to zero;

(b) If the principal eigenvalue λ_1 of (2.1) is positive, then system (1.5) possesses a unique positive periodic solution u^* such that every solution with initial function in $Y\backslash\{0\}$ converges to u^*.

Remark 3.2. The first part of this theorem agrees with our globally asymptotical stability of zero solution in section 2. The second part of this theorem answers the open question in [17] as well the conjecture in [16].

4. Bifurcation

In this section, we study the birth of positive periodic solution bifurcated from the trivial zero solution when the death rate d is less than some critical value. For simplicity, we shall assume that $D(t), \alpha(t)$ and $d(t)$ are positive constants and $I_0(t)$ is still a T-periodic function. Biologically, this means that the light strength is seasonal. Under this assumption, we suppose that $W(x,t)$ is the non-negative periodic solution to (1.5), i.e.,

$$\begin{cases} W_t = DW_{xx} - \alpha W_x + W\left(g(I(x,t) - d\right), \ x \in (0,L), \ t > 0, \\ DW_x - \alpha W = 0, \quad x = 0, L, \ t > 0, \\ W(x,0) = W(x,T), \ W_t(x,0) = W_t(x,T), x \in [0,L]. \end{cases} \tag{4.1}$$

As we already know, the stability of the trivial solution $W \equiv 0$ is determined by the following periodic eigenvalue problem:

$$\begin{cases} \lambda\phi = -\phi_t + D\phi_{xx} - \alpha\phi_x + \phi\left(g(I_0(t)e^{-k_0x}) - d\right), \\ D\phi_x - \alpha\phi = 0, \quad x = 0, L, \\ \phi(x,0) = \phi(x,T), \ \phi_t(x,0) = \phi_t(x,T). \end{cases} \tag{4.2}$$

By the Krein–Rutman theorem, problem (4.2) has a principal eigenvalue λ_1 with a positive eigenfunction. Obviously, λ_1 is a decreasing function of d. Suppose that there exists $d = d_0$ so that $\lambda_1(d_0) = 0$ with the positive eigenfunction $\phi = \phi_0$. Then we can know

$$\lambda_1(d) > 0 \text{ if } \ d < d_0; \ \lambda_1(d) < 0 \text{ if } d > d_0. \tag{4.3}$$

Thus, by Theorem 3.8, when $d > d_0$, (4.1) has the only trivial solution $W = 0$, and when $d < d_0$, there will be a bifurcated positive periodic solution. In next subsections, we shall prove that $(d_0, 0)$ is a bifurcation point and derive the asymptotic expression of the bifurcated periodic solution.

4.1. Rigorous analysis of the bifurcation

Let $\Omega_T = (0, L) \times [0, T]$, $X = L^2(\Omega_T)$ be the Hilbert space with the inner product

$$(u_1, u_2)_X = (u_1, u_2)_{L^2(\Omega_T)} = \int_0^T \int_0^L u_1(x,t)u_2(x,t)dxdt$$

for $u_1, u_2 \in X$, and

$$E = \{u : u \in C^{2,1}(\Omega_T); Du_x - \alpha u = 0 \text{ at } x = 0, L; u(x,0) = u(x,T)\},$$

which is a Banach space with the usual supremum norm. Rewrite the first equation of (4.1) as

$$D\left(e^{-\frac{\alpha}{D}x}(W)_x\right)_x + e^{-\frac{\alpha}{D}x}\left[-(W)_t + W\left(g(I(x,t) - d\right)\right] = 0$$

and define a map $\Phi : (0, \infty) \times E \to X$ by

$$\Phi(d, W) = D\left(e^{-\frac{\alpha}{D}x}(W)_x\right)_x + e^{-\frac{\alpha}{D}x}\left[-(W)_t + W\left(g(I(x,t) - d)\right)\right].$$

Then the periodic solutions of (4.1) are just zeros of this map. It is easy to see that

$$\Phi(d, 0) = 0 \text{ for all } d > 0.$$

According to the Theorem 1.7 of [2], $(d_0, 0)$ is a bifurcation point provided that

(a) the partial derivatives $\Phi_d,\ \Phi_W,\ \Phi_{dW}$ exist and are continuous;
(b) $\ker \Phi_W(d_0, 0)$ and $X/R(\Phi(d_0, 0))$ are one-dimensional;
(c) let $\ker \Phi_W(d_0, 0) = \text{span}\{\phi\}$, then $\Phi_{dW}(d_0, 0)\phi \notin R(\Phi_W(d_0, 0))$.

By verifying the three conditions above, we have the following theorem.

Theorem 4.1. *Let d_0 satisfy (4.3). Then $(d_0, 0)$ is a bifurcation point of $\Phi(d, W) = 0$ with respect to the curve $(d, 0), d > 0$.*

Proof. By a simple computation, we have $\Phi_d = -e^{-\frac{\alpha}{D}x}W,\ \Phi_{dW} = -e^{-\frac{\alpha}{D}x}$ and

$$\Phi_W(d, W)\phi = D\left(e^{-\frac{\alpha}{D}x}\frac{\partial \phi}{\partial x}\right)_x + e^{-\frac{\alpha}{D}x}\left[-\frac{\partial \phi}{\partial t} + \phi g(I_0(t)e^{-k_0x - k_1\int_0^x W(s,t)ds}) - d\phi\right]$$
$$-e^{-\frac{\alpha}{D}x}k_1 W(x,t)g'(I_0(t)e^{-k_0x-k_1\int_0^x W(s,t)ds})I_0(t)e^{-k_0x-k_1\int_0^x W(s,t)ds}\int_0^x \phi ds,$$

where $\phi \in E$. Thus, it is evident that (a) is true. Moreover, the Fréchet derivative of the map Φ at $W = 0$ is the linear operator

$$\Phi_W(d, 0) = D\left(e^{-\frac{\alpha}{D}x}\frac{\partial}{\partial x}\right)_x + e^{-\frac{\alpha}{D}x}\left[-\frac{\partial}{\partial t} + g(I_0(t)e^{-k_0x}) - d\right].$$

Set $L(d) = \Phi_W(d, 0)$. By the choice of d_0, $L(d_0)\phi = 0$ has a unique positive solution $\phi_0(x, t)$. Thus, $\dim\ker \Phi_W(d_0, 0) = 1$. Again, the adjoint system of $L(d_0)\phi = 0$ is as follows

$$\begin{cases} D\left(e^{-\frac{\alpha}{D}x}\phi_x\right)_x + e^{-\frac{\alpha}{D}x}\left[\phi_t + \left(g(I_0(t)e^{-k_0x}) - d_0\right)\right]\phi = 0, \\ D\phi_x - \alpha\phi = 0, \quad x = 0, L, \\ \phi(x, 0) = \phi(x, T),\ \phi_t(x, 0) = \phi_t(x, T). \end{cases} \tag{4.4}$$

This system has one unique solution $\overline{\phi}^* = \phi_0(x, T - t)$, that is $\dim\ker L^* = 1$, where L^* is the adjoint operator of L, which leads to $\dim X/R(\Phi_W(d_0, 0)) = 1$. Then (b) is verified.

Finally, since $\Phi_{dW}(d_0, 0)\phi_0 = -e^{-\frac{\alpha}{D}x}\phi_0$, and

$$(\Phi_{dW}(d_0, 0)\phi_0, \overline{\phi}^*)_Y = (e^{-\frac{\alpha}{D}x}\phi_0(x, t), \phi_0(x, T - t))_{L^2(\Omega_T)} > 0,$$

we know that $\Phi_{dW}(d_0, 0)\phi_0 \notin R(L)$, and condition (c) is satisfied. The proof is completed.

4.2. Asymptotic analysis of the positive solution

We now apply asymptotic analysis to study the formula of the small-amplitude solution of (4.1) bifurcated from $(d_0, 0)$. We assume

$$d = d_0 + d_1\varepsilon + d_2\varepsilon^2 + \cdots, \tag{4.5}$$

and

$$W = \varepsilon W_0 + \varepsilon^2 W_1 + \varepsilon^3 W_2 + \cdots, \tag{4.6}$$

where ε is a constant parameter satisfying $0 < \varepsilon \ll 1$. Substituting (4.5) and (4.6) into (4.1), it is easily derived that $W_0 = \phi_0$ from the first order system of ε. Up to the power of ε^2, it gives the following system

$$\begin{cases} (W_1)_t = D(W_1)_{xx} - \alpha(W_1)_x + W_1\left(g(I_0(t)e^{-k_0x}) - d_0\right) - d_1 W_0 \\ \qquad - k_1 g'(I_0(t)e^{-k_0x}) I_0(t)e^{-k_0x} W_0 \int_0^x W_0(s,t)ds, \\ D(W_1)_x - \alpha W_1 = 0, \quad x = 0, L, \\ W_1(x,0) = W_1(x,T),\ (W_1)_t(x,0) = (W_1)_t(x,T). \end{cases} \tag{4.7}$$

The first equation of (4.7) can be re-written as

$$D\left(e^{-\frac{\alpha}{D}x}(W_1)_x\right)_x + e^{-\frac{\alpha}{D}x}\left[-(W_1)_t + W_1\left(g(I_0(t)e^{-k_0x}) - d_0\right)\right] \tag{4.8}$$
$$= e^{-\frac{\alpha}{D}x}\left[d_1 W_0 + k_1 g'(I_0(t)e^{-k_0x}) I_0(t)e^{-k_0x} W_0 \int_0^x W_0(s,t)ds\right].$$

Therefore, the adjoint system of the homogeneous system of (4.7) is exactly the system (4.4). Then it has a nonnegative solution $W = W_0^*(x,t) = \phi_0(x, T-t)$. Multiplying both side of (4.8) by $W_0^*(x,t)$ and integrate it on $[0,T] \times [0,L]$, we get

$$d_1 = -\frac{\left(k_1 e^{-\frac{\alpha}{D}x} g'(I_0(t)e^{-k_0x}) I_0(t)e^{-k_0x} W_0 \int_0^x W_0(s,t)ds,\ W_0^*\right)_{L^2(\Omega_T)}}{(e^{-\frac{\alpha}{D}x} W_0,\ W_0^*)_{L^2(\Omega_T)}}, \tag{4.9}$$

which shows that $d_1 < 0$. Similarly we can proceed further to work out the formulas for $d_2, d_3, \cdots$, and the formulas for $W_1, W_2, \cdots$.

4.3. Stability of the positive periodic solution

As we already have the formula (4.6) for the positive periodic solution, we now study the stability of this solution.

Assume that the solution u of (1.5) has the ansatz $u = W + \bar{\phi}e^{\bar{\lambda}t}$. This gives rise to an eigenvalue problem around the positive solution W:

$$\begin{aligned}\bar{\phi}_t + \bar{\lambda}\bar{\phi} = D\bar{\phi}_{xx} - \alpha\bar{\phi}_x - d\bar{\phi} \\ +\bar{\phi} g(I_0(t)e^{-k_0 x - k_1 \int_0^x W(s,t)ds}) \\ -k_1 W g'(I_0(t)e^{-k_0 x - k_1 \int_0^x W ds}) I_0(t) e^{-k_0 x - k_1 \int_0^x W ds} \int_0^x \bar{\phi} ds.\end{aligned} \tag{4.10}$$

Assume further that

$$\bar{\lambda} = \varepsilon\bar{\lambda}_1 + \varepsilon^2\bar{\lambda}_2 + \cdots,$$

and

$$\bar{\phi} = \bar{\phi}_0 + \varepsilon\bar{\phi}_1 + \varepsilon^2\bar{\phi}_2 + \cdots.$$

Obviously by (4.5) and (4.6), we have $\bar{\phi}_0 = W_0$. After substituting these formulas to (4.10), we also obtain

$$\begin{aligned}D(\bar{\phi}_1)_{xx} - \alpha(\bar{\phi}_1)_x - d_0\bar{\phi}_1 + \bar{\phi}_1 g(I_0(t)e^{-k_0 x}) = \bar{\lambda}_1\bar{\phi}_0 + d_1\bar{\phi}_0 \\ +2k_1 g'(I_0(t)e^{-k_0 x})\bar{\phi}_0 \int_0^x \bar{\phi}_0 ds.\end{aligned}$$

We multiply both side by $e^{-\frac{\alpha}{D}x}W^*$ and integrate it on $[0, T] \times [0, L]$. This gives

$$\bar{\lambda}_1 = -\frac{k_1(e^{-\frac{\alpha}{D}x} g'(I_0(t)e^{-k_0 x}) I_0(t) e^{-k_0 x} W_0 \int_0^x W_0(s,t)ds, W_0^*)_{L^2(\Omega_T)}}{(e^{-\frac{\alpha}{D}x} W_0, W_0^*)_{L^2(\Omega_T)}}.$$

This means that $\bar{\lambda}_1 < 0$ and we have the stability of the positive periodic solution.

Proposition 4.2. *When $d < d_0$ and d is close to d_0, the bifurcated positive periodic solution is stable.*

5. Numerical results

In this section, we first carry out the computation of the principal eigenvalue of the system. The simulations of the solution to system (1.5) are also presented for two sets of parameters.

5.1. Numerical computations of the principal eigenvalue

For the eigenvalue problem

$$\begin{cases} \phi_t = D(t)\phi_{xx} - \alpha(t)\phi_x + \phi\left(g(I_0(t)e^{-k_0 x}) - d(t)\right) - \lambda\phi, \ x \in (0, L), \ t > 0, \\ D(t)\phi_x - \alpha(t)\phi = 0, \quad x = 0, L, \ t > 0, \\ \phi(x, 0) = \phi(x, T), \ \phi_t(x, 0) = \phi_t(x, T), \quad x \in [0, L]. \end{cases} \tag{5.1}$$

We want to show numerically how to find the principal eigenvalue. For the space $[0, L]$, we can divide it into N even intervals with $x_i = ih$ and

$$h = \frac{L}{N}.$$

We denote $\phi_i(t)$ as the value of $\phi(ih, t)$, $i = 0, 1, 2, \cdots N$. Near the left boundary $i = 0$, we can obtain

$$D(t)\frac{\phi_1 - \phi_0}{h} - \alpha(t)\phi_0 \approx 0$$

and it gives

$$\phi_0 = \frac{D(t)}{D(t) + \alpha(t)h}\phi_1.$$

Similarly we have

$$D(t)\frac{\phi_N - \phi_{N-1}}{h} - \alpha(t)\phi_N \approx 0$$

and this gives

$$\phi_N = \frac{D(t)}{D(t) - \alpha(t)h}\phi_{N-1}.$$

For the equation, we have the following systems:

When $i = 1$,

$$(\phi_1)_t = D(t)\frac{\phi_2 - 2\phi_1 + \phi_0}{h^2} - \alpha(t)\frac{\phi_2 - \phi_0}{2h} + \phi_1\left[g(I_0(t)e^{-k_0x_1}) - d(t)\right] - \lambda\phi_1; \tag{5.2}$$

when $i = 2, 3, \cdots N - 2$,

$$(\phi_i)_t = D(t)\frac{\phi_{i+1} - 2\phi_i + \phi_{i-1}}{h^2} - \alpha(t)\frac{\phi_{i+1} - \phi_{i-1}}{2h} + \phi_i\left[g(I_0(t)e^{-k_0x_i}) - d(t)\right] - \lambda\phi_i; \tag{5.3}$$

when $i = N - 1$,

$$\begin{aligned}(\phi_{N-1})_t = D(t)&\frac{\phi_N - 2\phi_{N-1} + \phi_{N-2}}{h^2} - \alpha(t)\frac{\phi_N - \phi_{N-2}}{2h} \\ &+ \phi_{N-1}\left[g(I_0(t)e^{-k_0x_{N-1}}) - d(t)\right] - \lambda\phi_{N-1}.\end{aligned} \tag{5.4}$$

Assume $\Phi = [\phi_1, \phi_2, \cdots \phi_{N-1}]^T$. We then have

$$\Phi_t = A(t)\Phi - \lambda\Phi$$

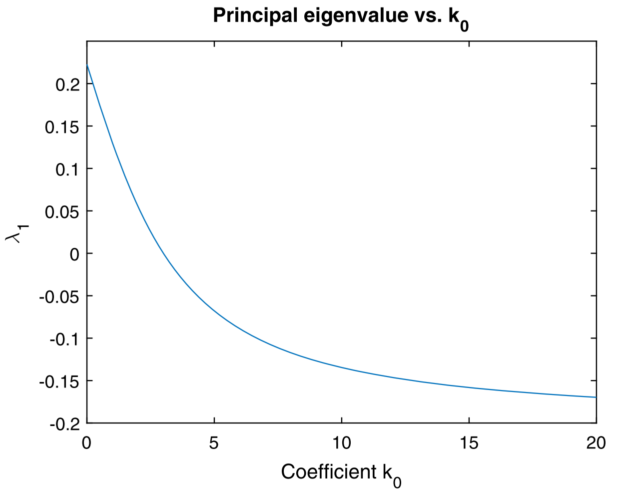

Fig. 1. Principal eigenvalues vs. k_0 in [0, 20].

and its solution

$$\Phi(T) = e^{\int_0^T (A(t)-\lambda I)dt}\Phi(0),$$

where $\Phi(0)$ is the initial data and $A(t)$ is the coefficient matrix of the system (5.2)–(5.4). Denote

$$B = \frac{1}{T}\int_0^T A(t)dt.$$

Then the eigenvalues of B are the ones of our system (5.1). We denote its principal eigenvalue as λ_1.

For a special case, we take $g(x) = \frac{x}{1+x}$, $I_0(t) = 1 + \sin t$, $D = 0.1$, $\alpha = 0.01$, $k_0 = k_1 = 1$ and $d = 0.2$, by a numerical computation, the principal eigenvalue is $\lambda_1 = 0.1303 > 0$. When we change k_0 from 1 to 10, the principal becomes $\lambda_1 = -0.1346 < 0$. When we fix all other parameters above and vary only the coefficient k_0 in the interval [0, 20], the graph of λ_1 vs. k_0 is given in Fig. 1.

It shows that the principal eigenvalue is a decreasing function of k_0 and there exists a unique value $k_0 \approx 3.5$ so that $\lambda_1 = 0$.

Remark 5.1. Similarly, it can show that λ_1 is a decreasing function of d. The corresponding curve λ_1-d is a straight line.

5.2. Numerical simulations of the plankton density solution $u(x,t)$

In this subsection, we give the numerical simulations of our system (1.5). As before, the interval $[0, L]$ is divided into N even subintervals with $x_i = ih$, $h = L/N$. Denote $u_i(t) = u(ih, t)$.

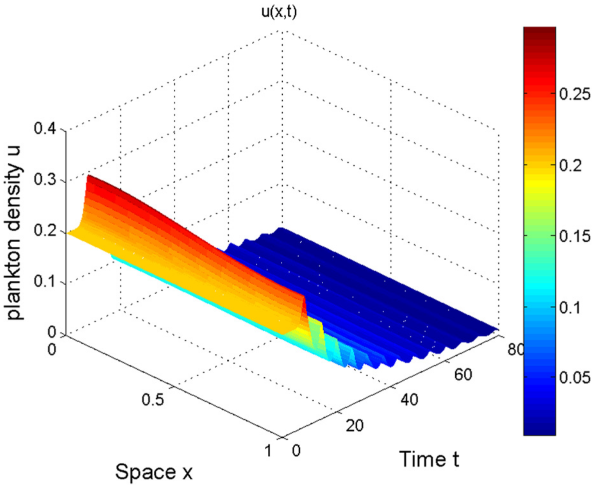

Fig. 2. Stability of the zero solution. Here $g(x) = \frac{x}{1+x}$, $I_0(t) = 1 + \sin t$, $D = 0.1$, $\alpha = 0.01$, $k_0 = k_1 = 1$ and $d = 0.365$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

For the boundary condition, we still use the same argument above to get

$$u_0(t) = \frac{D(t)}{D(t) + \alpha(t)h} u_1(t), \quad u_N(t) = \frac{D(t)}{D(t) - \alpha(t)h} u_{N-1}(t).$$

The PDE is transformed into the ODE system

$$(u_i)_t = \frac{D(t)}{h^2}(u_{i+1} - 2u_i + u_{i-1}) - \alpha(t)\frac{u_{i+1} - u_{i-1}}{2h} + u_i\left[g(I_0(t)e^{-k_0 x_i - k_1 I_i}\right],$$

where $I_i, i = 1, 2, \cdots, N$, denotes the nonlocal term

$$I_i = \int_0^{x_i} u(x,t)dx \approx \frac{h}{2}\left[u_0 + u_i + 2\sum_{j=1}^{i-1} u_j\right],$$

which can be obtained by the composite Trapezoid Rule.

The simulation, when $g(x) = \frac{x}{1+x}$, $I_0(t) = 1 + \sin t$, $D = 0.1$, $\alpha = 0.01$, $k_0 = k_1 = 1$ and $d = 0.365$ shows that the zero solution is stable, see Fig. 2. When we change the death rate to $d = 0.265$, the positive periodic solution appears and is stable, see Fig. 3. This verifies our theoretical analysis in the previous sections.

6. Conclusions and discussions

In this paper, we study the existence, uniqueness, global attractivity and bifurcation of periodic patterns for a seasonal single phytoplankton model with self-shading effect. We have assumed that the diffusion rate, the sinking or buoyant velocity and the light intensity are all seasonal.

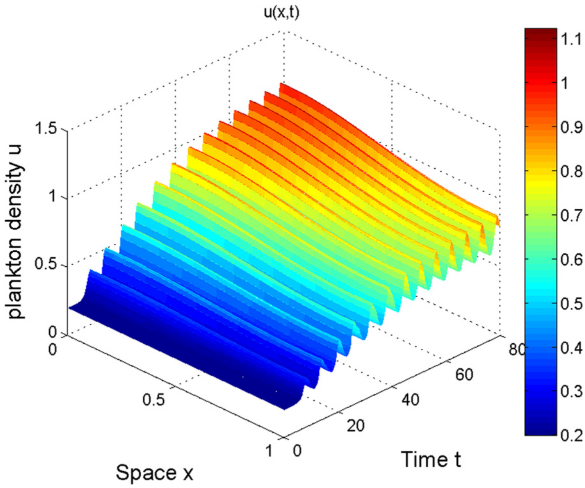

Fig. 3. Stability of the positive periodic solution. Here $g(x) = \frac{x}{1+x}$, $I_0(t) = 1 + \sin t$, $D = 0.1$, $\alpha = 0.01$, $k_0 = k_1 = 1$ and $d = 0.265$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

This also includes the case in [17] where they investigated the dynamics of plankton in terms of the basic reproduction number when the light intensity is seasonal. By the comparison principle, we obtain the globally asymptotical stability of the zero solution when the principal eigenvalue λ_1 of the corresponding linear system is less than zero. When $\lambda_1 > 0$, the uniqueness and attractivity of the positive periodic pattern were left open in [17] and also were raised as a conjecture in [16]. By transforming the model into a new system, we successfully answer the open problem and prove the conjecture in [16,17] by applying the theory of monotone system coupled with subhomogeneous property. As a byproduct, the dynamics of the bottom plankton is obtained automatically. In particular when $k_0 = 0$, it obeys a law of periodic ordinary differential equation

$$\begin{cases} \dfrac{dv(L,t)}{dt} = \displaystyle\int_0^{v(L,t)} g\left(I_0(t)e^{-k_1 s}\right) ds - dv(L,t), \qquad t > 0, \\ v(L,0) = \displaystyle\int_0^L u_0(s)ds = \varphi(L). \end{cases} \tag{6.1}$$

The positive periodic pattern bifurcating from the zero solution, when the death rate is less than a critical value, is a very interesting phenomenon. Here we apply the theory in [2] to prove rigorously the existence of a bifurcation point. When the parameter d is near this point, by way of asymptotic analysis, we derive an asymptotic formula for the positive pattern. This provides another method to compute the positive pattern. Based on this formula, we find the linear stability of this periodic pattern. Finally, for the periodic model (1.5), we provide a numerical scheme for the simulations of the solution and the calculations of the principal eigenvalue vs. the parameter k_0. Two figures are provided to indicate the solution behaviors for different parameter groups, which are in agreement with the theoretical results.

For future study, it may be challenging to study periodic plankton models with two species competing in the same environment. It is also interesting to study the stability of the numerical scheme in this paper.

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References

[1] N.F. Britton, U. Timm, Effects of competition and shading in planktonic communities, J. Math. Biol. 31 (1993) 655–673.
[2] M. Crandall, P. Rabinowitz, Bifurcation from simple eigenvalues, J. Funct. Anal. 8 (1971) 321–340.
[3] Y. Du, S.-B. Hsu, Concentration phenomena in a nonlocal quasi-linear problem modelling phytoplankton I: existence, SIAM J. Math. Anal. 40 (2008) 1419–1440.
[4] Y. Du, S.-B. Hsu, Concentration phenomena in a nonlocal quasi-linear problem modelling phytoplankton II: limiting profile, SIAM J. Math. Anal. 40 (2008) 1441–1470.
[5] Y. Du, S.-B. Hsu, On a nonlocal reaction–diffusion problem arising from the modeling of phytoplankton growth, SIAM J. Math. Anal. 42 (2010) 1305–1333.
[6] Y. Du, L.F. Mei, On a nonlocal reaction–diffusion–advection equation modeling phytoplankton dynamics, Nonlinearity 24 (2011) 319–349.
[7] U. Ebert, M. Arrayas, N. Temme, B. Sommeijer, J. Huisman, Critical condition for phytoplankton blooms, Bull. Math. Biol. 63 (2001) 1095–1124.
[8] K. Fennel, Subsurface maxima of phytoplankton and chlorophyll: steady-state solutions from a simple mode, Limnol. Oceanogr. 48 (2003) 1521–1534.
[9] P. Hess, Periodic-Parabolic Boundary Value Problems and Positivity, Pitman Res. Notes Math. Ser., vol. 247, Longman Scientific Technical, Harlow, UK, 1991.
[10] S.-B. Hsu, Y. Lou, Single phytoplankton species growth with light and advection in a water column, SIAM J. Appl. Math. 70 (2010) 2942–2974.
[11] J. Huisman, M. Arrayas, U. Ebert, B. Sommeijer, How do sinking phytoplankton species manage to persist?, Amer. Nat. 159 (2002) 245–254.
[12] J. Huisman, J. Sharples, J. Stroom, P.M. Visser, W.E.A. Kardinaal, J.M.H. Verspagen, B. Sommeijer, Changes in turbulent mixing shift competition for light between phytoplankton species, Ecology 85 (2004) 2960–2970.
[13] H. Ishii, I. Takagi, Global stability of stationary solutions to a nonlinear diffusion equation in phytoplankton dynamics, J. Math. Biol. 115 (1982) 65–92.
[14] C.A. Klausmeier, E. Litchman, S.A. Levin, Phytoplankton growth and stoichiometry under multiple nutrient limitation, Limnol. Oceanogr. 49 (2004) 1463–1470.
[15] T. Kolokolnikov, C.H. Ou, Y. Yuan, Phytoplankton depth profiles and their transitions near the critical sinking velocity, J. Math. Biol. 59 (2009) 105–122.
[16] R. Peng, X.-Q. Zhao, Effects of diffusion and advection on the principal eigenvalue of a periodic parabolic problem with applications, Calc. Var. 54 (2015) 1611–1642.
[17] R. Peng, X.-Q. Zhao, A nonlocal and periodic reaction–diffusion–advection model of a single phytoplankton species, J. Math. Biol. 72 (3) (2016) 755–791.
[18] C.S. Reynolds, The Ecology of Freshwater Phytoplankton, Cambridge University Press, Cambridge, 1984.
[19] G.A. Riley, H. Stommel, D.F. Bumpus, Quantitative ecology of plankton of the western North Atlantic, Bull. Bingham Oceanogr. Coll. 12 (1949) 1–169.

[20] N. Shigesada, A. Okubo, Analysis of the self-shading effect on algal vertical distribution in natural waters, J. Math. Biol. 12 (3) (1981) 311–326.
[21] X.-Q. Zhao, Dynamical Systems in Population Biology, Springer-Verlag, New York, 2003.