Research Article

Single Phytoplankton Species Growth with Nonlocal Crowding Effect Caused by Chemosensory Aggregation in a Water Column

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Received 9 May 2022; Accepted 6 June 2022; Published 28 June 2022

Academic Editor: C. Rajivganthi

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In this paper, we study the existence of positive steady states for a nonlocal reaction-diffusion model which describes the growth of a single phytoplankton species with nonlocal crowding effect caused by chemosensory aggregation in a water column. Our result shows that under some conditions, the nonlocal crowding effect is effective to the existence of steady states of phytoplankton populations. Based on a key boundedness Lemma, the main result is proved by fixed point index theory and some analytical techniques.

1. Introduction

In this paper, we study the existence of positive solution for the following nonlocal problem:

\[ -u''(x) = u(x)g \left( I_0 e^{-k_1 x} \exp \left( -k_1 \int_0^x u(s) ds \right) \right) \]

\[-u(x) \int_0^L K(x,s)u(s) ds, x \in (0,L), \]

\[ u'(0) = u'(L) = 0, \]

which arises from the modeling of the growth of phytoplankton species with light and nonlocal crowding effect in a water column. In (1), \( u = u(x) \) is the population density of the phytoplankton species, and \( L > 0 \) is the depth of the water column. The first nonlocal nonlinearity on the right-hand side of (1) describes the growth of the phytoplankton species depending on light intensity at different depths, and the second nonlocal nonlinearity corresponds to the total death due to the combination of intrinsic death rate and nonlocal crowding effect caused by chemosensory aggregation. The Neumann boundary condition (2) means that the water column is closed, with no phytoplankton entering or leaving the column at the top \( x = 0 \) or the bottom \( x = L \). A more detailed explanation of the model and notations in it will be given as follows.

Our motivations to investigate above problem on the one hand stem from a kind of existing mathematical model of phytoplankton growth with light and, on the other hand, from the chemosensory aggregation behavior of phytoplankton which has never been considered in previous models. We will focus on the necessity of incorporating aggregation-crowding effect in phytoplankton individuals and its influence on the positive steady states of phytoplankton population.

Phytoplankton is microscopic plants that float in lakes and ocean waters, which form the foundation of the aquatic food chain. Most phytoplankton depend primarily on nutrients and light for growth, while a few rely entirely on light for metabolism. In eutrophic waters, where nutrients are plentiful, phytoplankton usually competes primarily for light. In [1], in order to understand the growth of phytoplankton species in eutrophication water, Huisman et al. introduced and discussed the following reaction-diffusion model for the growth of single species through numerical simulation.
proved that there exists a critical death rate where \( u \) is the death rate; critical death rate varies with other parameters conditions, Hsu and Lou also studied in detail how the corresponding steady-state problem with zero flux boundary

\[ k I \]

is the growth rate of phytoplankton as a function of light intensity

\( I = I(x, t) \) is the light intensity in accordance with Lambert–Beer law, where \( I_0 \) is incident light intensity, \( k_0 \) is background turbidity, and \( k_1 \) is the absorption coefficient of phytoplankton. \( g(I) \) is the growth rate of phytoplankton as a function of light intensity \( I = I(x, t) \). The growth rate \( g(I) \) generally satisfies

\[ g(0) = 0, \quad g'(I) > 0 \text{ for } I > 0. \]

A typical example of \( g(I) \) is the Michaelis–Menten form, and \( g(I) = ml/a + I \), where \( m \) is the maximum growth rate, and \( a \) is the half saturation constant.

The model in [1] is one of the phytoplankton mathematical models proposed and studied in recent years, and related studies on the formation of phytoplankton blooms from mathematical, experimental, and numerical perspectives can be found in [2–9] and its references. In [10], to get a comprehensive mathematical treatment of the model in [1], Du and Hsu discussed the following steady-state problem of (3) with suitable scaling:

\[ -D u'' = u \left[ g \left( e^{-k_0 x} \exp \left( -k_1 \int_0^x u(s, t) ds \right) \right) - d \right], \quad x \in (0, 1). \]

By using global bifurcation arguments, Du and Hsu proved that there exists a critical death rate \( d^* \) such that equation (5) with Neumann boundary condition (2) has a positive solution if and only if \( 0 < d < d^* \), and then, they obtained a description of the long-time dynamical behavior of the model in [1] based upon the positive steady state ([10] also considered the case of two competing species). In [11], Hsu and Lou studied the following model which is an extension of (3)

\[ u_t = D u_{xx} - vu_x + u \left[ g \left( I_0 e^{-k_0 x} \exp \left( -k_1 \int_0^x u(s, t) ds \right) \right) - d \right], \quad x \in (0, 1), t > 0, \]

where \( v \) is the sinking velocity \((v > 0)\) or the buoyant velocity \((v < 0)\). In addition to getting similar results as [10] for corresponding steady state problem with zero flux boundary conditions, Hsu and Lou also studied in detail how the critical death rate varies with other parameters \( L, v, \) and \( D \), and then, the comprehensive effect of the parameters on the persistence of a single phytoplankton species is studied. Du and Mei in [12] extended the results of [10, 11] to the model which has variable diffusion and sinking rate. In [13], the effect of photo-inhibition on the growth of phytoplankton in a single population was studied, and the results show that the model with photo-inhibition has at least two positive steady-state solutions in certain parameter ranges. In [14], by assuming that the incident light intensity and the death rate are time-periodic for single phytoplankton, Peng and Zhao established a threshold type result on the global dynamics of the model based on the basic reproduction number. In [15], Pang, Nie, and Wu introduced a local crowding effect into model (6), and they first proved the steady states in terms of the intrinsic death rate of the phytoplankton species and next investigated the asymptotic profiles of positive equilibria for small crowding rate and large advection rate. We notice that, in [15], the crowding effect of the population \( u \) at position \( x \) is assumed to only depend on the value of the population in the same point \( x \), and the interaction and competition between phytoplankton individuals at different positions are not considered.

However, according to related studies on phytoplankton population [16–19], it seems more reasonable to consider that the crowding effect depends not only on their own point in space but also depends on the population around them. Indeed, many phytoplankton (such as the dinoflagellates and more generally algae) are known to leak organic matter into the solution which forms a zone around individual cells, the "phycosphere," in which the concentration of extracellular products is higher than the surrounding concentration, see [16, 17]. On the other hand, many species of phytoplankton (algae, bacteria, and dinoflagellates) have been found to have chemosensory abilities: they can sense the chemical field generated by the presence of other particles, see [18, 19]. Thus, the released products of individual phytoplankton will attract other individuals within a certain neighborhood and finally induce aggregation behavior of phytoplankton at small scales, see [20, 21]. A corollary of this aggregation behavior is increased nonlocal competition for light and nutrients between individuals within a certain space.

Motivated by the above-described works, in this paper, we take into account the more realistic nonlocal crowding effect in the phytoplankton model and study its influence on the steady states of phytoplankton populations. To avoid some technical details, we drop the advection term and then investigate the scaled models (1) and (2).

Models (1) and (2) are an extension of the previous steady-state model discussed in [1, 10–15], and it has important significance in planktology. In (1), the first nonlocal nonlinearity is the same as in the previous model, the second new nonlocal nonlinearity corresponds to the total death due to the combination of intrinsic death and nonlocal crowding effect caused by chemosensory aggregation, and the kernel \( K(x, y) \) stands for the competition rate between individuals at position \( x \) and individuals at position \( y \). According to the previous statement on phytoplankton, the extracellular products released by a phytoplankton particle located in \( x \) may attract nearby particles located in the centered ball at \( x \) of radius \( \delta > 0 \) and then deduce a nonlocal crowding effect. Beyond the radius \( \delta \), particles cannot be usually attracted, because they are sensory-limited [21]. So, a typical form of \( K \) maybe \( K(x, y) = K_\delta(|x, y|) \) which has the following characteristics:
(H1) $K_δ(|x, y|)$ is continuous and monotone decreasing

(H2) $K_δ(|x, y|) = 0$ if $|x, y| ≥ 2$

However, in this paper, we will study (1) and (2) with more general competition kernel $K(x, y)$ that will be detailed as follows.

From a mathematical point of view, models (1) and (2) also have some new interesting features that differ from previous models. Compared to the previous steady-state problems in [1, 10–15] and other related logistic population models with one nonlocal term (see e.g., [22–31]), the appearance of two nonlocal nonlinear terms in equation (1) will cause more mathematical difficulties and make the analysis of the model particularly interesting. Under certain new assumptions on $g$ and $K$, our main result will be proved by using the fixed point index theory on cone. Although the idea is motivated by [15], significant changes are needed in the arguments due to the appearance of a new nonlocal nonlinearity, see the key boundedness Lemma 1 below which is ingeniously proved in terms of Taylor–Lagrange’s formula. Our proof will provide a new idea for studying steady-state solutions of models with multiple nonlocal terms.

The rest paper is arranged as follows: in Section 2, we give some preliminaries and prove the key boundedness result; in Section 3, we give out the main result of this paper and its proof; finally, Section 4 contains our conclusions and some problems worthy of further study.

2. Preliminaries and a Boundedness Lemma

Let $h \in C[0, L]$, we define $ψ_τ(h) = h[tg(I_0e^{-k_0} - k_1 \int_0^x h(s)ds)x] - \int_0^L K(x, s)h(s)ds + M$ where $M$ is large enough such that $tg(I_0e^{-k_0} - k_1 \int_0^x h(s)ds)x) - \int_0^L K(x, s)h(s)ds + M$.

and consequently,

$$g(I_0e^{-k_0} - k_1 \int_0^x u(s, t)ds) - \int_0^L K(x, s)h(s)ds + M.$$

Combining (10) with (4), we have

$$g(I_0) \geq g(I_0e^{-k_0} - k_1 \int_0^x u(s, t)ds) - \int_0^L K(x, s)h(s)ds.$$

We then use Taylor–Lagrange’s formula for the function $u$ at point $x_0$. For all $y \in [0, L]$, there exists $ξ ∈ (x_0, y)$ or $(y, x_0)$ such that

$$u(y) = \frac{(y - x_0)^2}{2} u(ξ).$$

Additionally, by using again (7), we obtain, for all $ξ ∈ [0, L]$

$$-u(ξ) ≤ u(ξ)\left[g(I_0e^{-k_0} - k_1 \int_0^x u(s, t)ds) - \int_0^L K(x, s)h(s)ds \geq 0 \right].$$

Let $\delta > 0$ such that $L ≥ \delta$.

Then, we define an operator $Ψ: [0, L] \times C[0, L] \longrightarrow C[0, L]$ by $Ψ_x(h) = Φ(ψ_τ(h))$, where $Φ$ is the solution operator $u = Φ(m(x))$ for the problem

$$-u(x) + Mu(x) = m(x), x ∈ (0, L),$$

$$w(0) = u(L) = 0.$$
and then,

\[-u''(\xi) \leq u(\xi) \left[ G \left( I_0 e^{-k_0 \xi} \exp \left( -k_1 \int_0^\xi u(s, t) ds \right) \right) \right] - \int_0^L K(x, s) h(s) ds \geq 0 \]

which implies that

\[-u''(\xi) \leq u(\xi) g \left( I_0 e^{-k_0 \xi} \exp \left( -k_1 \int_0^\xi u(s, t) ds \right) \right) \geq -\|u\|_{\infty} g(I_0). \tag{15} \]

Combining above inequality with (12), we have

\[u(y) \geq \|u\|_{\infty} \left[ 1 - \frac{(y - x_0)^2}{2} g(I_0) \right]. \tag{16} \]

Substituting (16) into (11), we have

\[g(I_0) \geq \int_0^L K(x_0, s) u(s) ds \geq \int_0^L K(x_0, y) \|u\|_{\infty} \left[ 1 - \frac{(y - x_0)^2}{2} g(I_0) \right] dy. \tag{17} \]

Since \(1 - \frac{(y - x_0)^2}{2} g(I_0) \geq 0\) for all \(y \in [0, L]\) according to condition (G), then (17) implies that

\[\|u\|_{\infty} \leq g(I_0) \left[ \int_0^L K(x_0, y) \left[ 1 - \frac{(y - x_0)^2}{2} g(I_0) \right] dy \right]. \tag{18} \]

Since \(K(x_0, \cdot)\) is positive in a neighborhood of \(x_0\) by the condition (ii), we deduce that

\[g(I_0) \left[ \int_0^L K(x_0, y) \left[ 1 - \frac{(y - x_0)^2}{2} g(I_0) \right] dy \right]^{-1} < +\infty. \tag{19} \]

Then, there exists \(R > 0\) such that for all \(u \in C[0, L]\) positive and \(\tau \in [0, L]\) satisfying \(u \equiv \Psi_\tau(u)\), and we have \(\|u\|_{\infty} < R\).

Our main tool is the following fixed point index theorem.

\[\square\]

**Lemma 2.** (32), Proposition 2 and (33), Theorem 2.1. Let \(F: W \rightarrow W\) be a compact, continuously differentiable operator, \(W\) be a cone in the Banach space \(E\) with zero \(\Theta\). Suppose that \(W - W\) is dense in \(E\) and \(\Theta \in W\) is a fixed point of \(F\) and \(A_0 = F(\Theta)\). Then, the following results hold:

(i) \(\text{index}_B(F, \Theta) = 1\) if the spectral radius \(\tau(A_0) < 1\)

(ii) \(\text{index}_B(F, \Theta) = 0\) if \(A_0\) has an eigenvalue greater, then 1 and \(\Theta\) are an isolated solution of \(x = F(x)\); that is, \(h \neq A_0\) if \(h \in W - \Theta\).

At last, we give a principal eigenvalue result to be used in the proof of the main result.

**Lemma 3.** (34) Let \(q(x) \in C(\overline{\Omega})\) and \(q(x) + p > 0\) on \(\overline{\Omega}\) with \(p > 0\), and let \(\sigma_1\) be the first eigenvalue of the eigenvalue problem

\[-\Delta \phi - q(x) \phi = \sigma \phi, x \in \Omega, \frac{\partial \phi}{\partial n} = 0, x \in \partial \Omega. \tag{20} \]

If \(\sigma_1 > 0\) (or \(\sigma_1 < 0\)), then the eigenvalue problem

\[-\Delta \phi + p \phi = t (q(x) + p) \phi, x \in \Omega, \frac{\partial \phi}{\partial n} = 0, x \in \partial \Omega, \tag{21} \]

has no eigenvalue less than or equal to 1 (or has eigenvalue less than 1).

**3. The Main Result and the Proof**

Our main result is as follows.

**Theorem 1.** Assume that conditions (4), (G), (i) and (ii) in Lemma 1 hold, and moreover, the function \(K\) satisfies

(i) If \(\omega \in C[0, L]\) is nonnegative and

\[
\int_0^L \int_0^L K(x, y) \omega(y) \omega(x) dx dy = 0, \text{ then } \omega \equiv 0.
\]

Then, problem (1) and (2) have a positive solution.

**Proof:** Denote \(E = C[0, L]\), \(W = \{u \in E: u(x) \geq 0, \forall x \in [0, L]\}\), then it is easy to see that \(W\) be a cone in the Banach space \(E\) with zero \(\Theta\). By Lemma 1, we can conclude that there exists \(R > 0\) such that for all \(u \in W\) and \(\tau \in [0, L]\) satisfying \(u = \Psi_\tau(u)\), and we have \(\|u\|_{\infty} < R\). We then define \(\Omega = \{u \in E: u(x) \geq 0, \forall x \in [0, L]\}\).

Obviously, \(\Psi_\tau: [0, 1] \times \Omega \rightarrow W\) is compact and continuously differentiable. Let \(\Psi = \Psi_1\), then (1) and (2) have a nonnegative solution if and only if \(\Psi\) has a fixed point in \(\Omega\).

Following from the boundedness result, for \(\tau \in [0, 1]\), \(\Psi_\tau\) has no fixed point on \(\partial \Omega\), then, by the homotopic invariance of the degree, we conclude that

\[
\text{index}(\Psi, \Omega, W) = \text{index}(\Psi_\tau, \Omega, W),
\]

\[
= \text{index}(\Psi_0, \Omega, W). \tag{22}
\]

We claim that \(\Psi_0\) has a unique fixed point \(0\) in \(\Omega\). Indeed, let \(\Psi_0(u) = u\), then

\[
\begin{align*}
-u''(x) &= -u(x) \int_0^L K(x, s) u(s) ds, x \in (0, L), \\
u'(0) &= u'(L) = 0.
\end{align*} \tag{23}
\]

Integrating the equation in (23) from 0 to \(L\) and by using the boundary value conditions, we can obtain that
\[ \int_{0}^{1} u(x) \int_{0}^{x} K(x, s) u(s) ds \, dx = 0. \] (24)

Then, by condition (iii), we get that \( u(x) \equiv 0 \). Thus, 0 is the unique fixed point of \( \Psi_{0} \) in \( \Omega \), and
\[
\text{index}(\Psi_{0}, \Omega, W) = \text{index}(\Psi_{0}, 0, W). \] (25)

Now, we show that index \( (\Psi_{0}, 0, W) = 1 \) by using Lemma 2. Let \( \Psi_{0}(0) \) be the Fréchet derivative of \( \Psi_{0} \) with respect to \( u \) at 0. For \( \varphi \in W \), let \( \Psi_{0}'(0) \varphi = \lambda \varphi \) and \( \varphi \equiv 0 \). Then,
\[
\begin{cases}
-\varphi''(x) + \varphi(L) = 0, \\
\varphi(0) = \varphi(L) = 0.
\end{cases}
\] (26)

Multiplying the above equation by \( \varphi \) and integrating from 0 to \( L \) by parts, we get that
\[
\frac{1}{\lambda} - 1 = \frac{\int_{0}^{L} (\varphi'(x))^2 \, dx}{M \int_{0}^{L} (\varphi'(x))^2 \, dx} > 0.
\] (27)

Thus, \( \lambda < 1 \) and the spectral radius \( r(\Psi_{0}'(0)) < 1 \). By Lemma 2, we have index \( (\Psi_{0}, 0, W) = 1 \), and then,
\[
\text{index}(\Psi_{0}, \Omega, W) = \text{index}(\Psi_{0}, 0, W),
\] (28)
\[
= \text{index}(\Psi_{0}, 0, W) = 1.
\]

Next, we show that index \( (\Psi, \Omega, W) = 0 \) by Lemma 2 again. Let \( \Psi(0) \) be the Fréchet derivative of \( \Psi \) with respect to \( u \) at 0. For \( u \in W \), \( \Psi(0)u = u \) is equivalent to
\[
\begin{cases}
-\varphi''(x) + Mu(x) = u(x)g(I_{0}e^{-k_{0}x}) + m(x), \quad x \in (0, L), \\
u(0) = u(L) = 0.
\end{cases}
\] (29)

We can see that \( u \equiv 0 \), that is, 1 is not an eigenvalue of \( \Psi(0) \) in \( W \). Thus, 0 is an isolated fixed point of \( \Psi \) in \( W \). Let \( \Psi(0)u = \lambda u \) and \( u \equiv 0 \). Then,
\[
\begin{cases}
-\varphi''(x) + Mu(x) \\
= \frac{1}{\lambda} \left[ u(x)g(I_{0}e^{-k_{0}x}) + Mu(x) \right], m(x), \quad x \in (0, L), \\
u(0) = u(L) = 0.
\end{cases}
\] (30)

Considering the following eigenvalue problem:
\[
\begin{cases}
-\varphi''(x) - \varphi(x)g(I_{0}e^{-k_{0}x}) = \mu \varphi(x), \quad x \in (0, L), \\
\eta'(0) = \eta(L) = 0.
\end{cases}
\] (31)

Let \( \mu_{1}(I_{0}e^{-k_{0}x}) \) be the smallest eigenvalue of (31), and let \( \mu_{1}(0) \) be the smallest eigenvalue of
\[
\begin{cases}
-\varphi''(x) = \mu \varphi(x), \quad x \in (0, L), \\
\eta'(0) = \eta(L) = 0.
\end{cases}
\] (32)

It is easy to see that \( \mu_{1}(0) = 0 \). Since \( g(I_{0}e^{-k_{0}x}) > 0 \), it follows from monotonicity of the smallest eigenvalue with respect to the weight function that
\[
\mu_{1}(g(I_{0}e^{-k_{0}x})) < \mu_{1}(0) = 0.
\] (33)

Then, by Lemma 3, the eigenvalue problem is as follows:
\[
\begin{cases}
-\varphi''(x) + Mu(x) \\
= \rho \left[ u(x)g(I_{0}e^{-k_{0}x}) + Mu(x) \right], m(x), \quad x \in (0, L), \\
u(0) = u(L) = 0.
\end{cases}
\] (34)

It has an eigenvalue \( \rho_{1} \) less than 1. Thus, it is easy to see that \( 0 < \rho_{1} < 1 \) is an eigenvalue of \( \Psi(0) \). That is, \( \Psi(0) \) has an eigenvalue greater than 1. It follows from Lemma 2 that index \( (\Psi, 0, W) = 0 \).

Since index \( (\Psi, \Omega, W) \neq \text{index}(\Psi_{0}, 0, W) \), it follows from Leray-Schauder degree theory that \( \Psi \) has at least one nonzero fixed point in \( \Omega \). That is, (1) and (2) have at least one nontrivial nonnegative solution. Moreover, by the strong maximum principle and Hopf boundary Lemma, we can show that the nontrivial nonnegative solution of (1) and (2) is a positive solution. \( \square \)

4. Conclusion

In this paper, we proved the existence of positive steady states for a nonlocal reaction-diffusion model which describes the growth of a single phytoplankton species with nonlocal crowding effect caused by chemosensory aggregation in a water column. The main feature of our model is that it captures the idea of the attraction interaction between phytoplankton due to the chemosensory behavior. This clustering characteristic in conjunction with the competition for light makes the problem become more complicated, which is manifested in the appearance of two nonlocal nonlinear terms in the model (1) and (2).

In contrast to the steady-state problem that does not account for nonlocal crowding effect such as (5) in [10], our results show that under a certain range of the growth rate depending on incident light intensity, problems (1) and (2) always have a positive solution for some positive nonlocal competitive mortality \( K \). This shows that the nonlocal crowding effect is effective to the existence of steady states of phytoplankton populations.

Note that although the existence of positive solution for steady state problem (1) and (2) has been provided in Theorem 1, the uniqueness is not known, and this also prevents us from obtaining the asymptotic profiles of the positive steady states and the longtime dynamical behavior of the model. These problems remain to be resolved in the future.

Data Availability

No data were used to support this study.
Conflicts of Interest

All authors declare no conflicts of interest in this paper.

Authors’ Contributions

YW and JW completed the main study together. YW wrote the manuscript, and XY checked the proofs process and verified the calculation. Moreover, all the authors read and approved the last version of the manuscript.

Acknowledgments

This work was supported by the NSFC (No. 12161071) and the Natural Science Foundation of Gansu Province, China (Grant no.: 21JR7RA274).

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