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Delay-induced instability in a nutrient-phytoplankton system with flow

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In this paper, a nutrient-phytoplankton system described by a couple of advection-diffusion-reaction equations with delay was studied analytically and numerically. The aim of this research was to provide an understanding of the impact of delay on instability. Significantly, delay cannot only induce instability, but can also promote the formation of spatial pattern via a Turing-like instability. In addition, the theoretical analysis indicates that the flow (advection term) may lead to instability when the delay term exists. By comparison, diffusion cannot result in Turing instability when flow does not exist. Results of numerical simulation were consistent with the analytical results.

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I. INTRODUCTION

Plankton play an important role in ocean ecology and the climate because of their participation in the global carbon cycle at the base of the food chain [1]. In particular, phytoplankton carry out photosynthesis and form the base of the food chain in oceans, lakes, and reservoirs. However, phytoplankton blooms occur in some environments, which may lead to ecological failure and can even cause harm to humans. Hence, an understanding of the dynamic mechanism of phytoplankton becomes much more significant.

In recent years, ecologists have paid increasing attention to spatial processes in interactions among species [2–5] and have found that a variety of ecological phenomena can be modeled using partial differential equations [6]. Medvinsky *et al.* showed that modeling by reaction-diffusion equations is an appropriate tool to investigate fundamental mechanisms of complex spatiotemporal plankton dynamics [7]. Especially, pattern formation has been a major interest of many researchers. Since the pioneering work of Turing [8], pattern formation has been a common area of interest in many diverse fields of research, including chemistry [9,10], physics [11,12], biology [13], ecology [14,15], and so on.

Although some phenomena can be well explained by pattern formation in reaction-diffusion systems, flow should be considered in some cases, such as tidal currents in an algae-mussel system [16], sinking in a nutrient-phytoplankton system [17], downhill water flows in a plant-water system [18], and so on. In these cases, the systems can be described by reaction-advection-diffusion equations. Actually, the role of flow in pattern formation has been investigated recently. The formation mechanism of flow-distributed structures was discovered theoretically by Kuznetsov *et al.* [19]. Earlier, Rovinsky *et al.* [20] had indicated that the flow of species at different rate induced instability by experiment. This kind of instability is similar to the diffusion-driven one in Turing case, but it does not restrict the diffusion coefficients [20]. Thus, such a system is much more general.

Growing evidence shows that some conversion processes from one state to another in certain systems are not instantaneous, that is, time delay exists, which is an important factor affecting the dynamics of various systems. Volterra [21] considered time delay in a prey-predator system first, the result showed that a spatial distribution may possess oscillatory behavior under certain conditions. And Ott *et al.* first employed time-delayed feedback to control the chaotic behavior of a deterministic system [22]. Since then, the delay has been widely used to investigate pattern dynamics in reaction-diffusion systems, and many interesting results have been obtained [23–29]. For example, in an experimental study of delay feedback in Ref. [30], it was found that the delay could induce the emergence of a spiral wave. Although studies of the effects of delay on pattern formation are abundant in reaction-diffusion systems, such studies in advection-reaction-diffusion systems appear to be rare.

The paper is organized as follows: in Sec. II, the system with delay is introduced, and the effects of delay on the system are explored analytically. The numerical results are presented in Sec. III. Finally, the paper ends with conclusion in Sec. IV.

II. THE SYSTEM AND THEORETICAL ANALYSIS

A. The nutrient-phytoplankton system

In Ref. [31], Huppert *et al.* presented a model of phytoplankton blooms to investigate the threshold effect that a bloom would only be triggered when nutrients exceeded a certain defined level, and much better results are obtained. Here, this system is extended into a spatial one, as follows:

$$\frac{\partial N}{\partial t} = a - bNP - eN + D_N \Delta N, \tag{1}$$

$$\frac{\partial P}{\partial t} = \alpha bNP - mP - V\frac{\partial P}{\partial x} + D_P \Delta P, \tag{2}$$

where N, P are nutrient levels and phytoplankton biomass, respectively. a is a constant rate of nutrient inputs flowing

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into the system; b is nutrient uptake rate of phytoplankton; α denotes the efficiency of nutrient utilization; e and m are the mortality and loss rates of nutrients and phytoplankton, respectively; D_N and D_P are the diffusion coefficient of nutrients and phytoplankton, respectively; V is flow velocity, and $V\frac{\partial P}{\partial x}$ represents the flow that may be caused by current, wind, or other factors. All parameters are positive constants.

Although the employed uptake dynamic in this system is not Michaelis-Menten, but Lotka-Volterra, Huppert *et al.* [31] have indicated that the Lotka-Volterra term was a good first approximation to the Michaelis-Menten. And Lotka-Volterra term has received much more attention, which is used to described the population dynamics of nutrient and phytoplankton. Using the dimensionless variables in Ref. [31], and set $d_N = D_N/m, d_P = D_P/m, v = V/m$, Eqs. (1) and (2) can be written as

$$\frac{\partial N}{\partial t} = I - NP - qN + d_N\Delta N = f(N,P) + d_N\Delta N, \quad (3)$$

$$\begin{aligned}\frac{\partial P}{\partial t} &= NP - P - v\frac{\partial P}{\partial x} + d_P\Delta P\\ &= g(N,P) - v\frac{\partial P}{\partial x} + d_P\Delta P. \quad (4)\end{aligned}$$

In addition, because the conversion from nutrient uptake to reproduction in phytoplankton requires some time, delay is taken into consideration, and Eq. (4) can be rewritten as

$$\begin{aligned}\frac{\partial P}{\partial t} &= N_\tau P - P - v\frac{\partial P}{\partial x} + d_P\Delta P\\ &= g(N_\tau,P) - v\frac{\partial P}{\partial x} + d_P\Delta P, \quad (5)\end{aligned}$$

where $N_\tau = N(x,t-\tau)$, and τ is a positive constant.

B. Theoretical analysis of the system with delay

In this subsection, the effects of delay on the system will be analyzed. Based on biological reality, the objective is a nonnegative homogeneous steady state. From Eqs. (3) and (4), there always exists a homogeneous steady state, $E_0 = (I/q,0)$ under $q > 0$, and there is a unique positive homogeneous steady state, $E_* = (N_*,P_*) = (1,I-q)$ if the condition, $q < I$, holds.

Assuming τ to be small, according to the method presented in Refs. [32–34], $N(x,t-\tau) = N(x,t) - \tau\partial N/\partial t$ can be substituted into Eq. (5) to yield

$$\begin{aligned}\frac{\partial P}{\partial t} = {}& g(N,P) - \tau P f(N,P) - v\frac{\partial P}{\partial x} + d_P\Delta P\\ & - \tau P d_N\Delta N. \quad (6)\end{aligned}$$

A standard linear analysis of the stability of the uniform state to nonuniform perturbations [35] is then performed:

$$\begin{pmatrix} N\\ P\end{pmatrix} = \begin{pmatrix} N_*\\ P_*\end{pmatrix} + \varepsilon\begin{pmatrix} N_k\\ P_k\end{pmatrix}e^{(\lambda t+ikx)} + \text{c.c.} + O(\varepsilon^2), \quad (7)$$

where λ is the (complex) perturbation growth rate; $k > 0$ is the wavenumber, and $\varepsilon \ll 1$, c.c. stands for complex conjugate.

Substituting Eq. (7) into Eqs. (3) and (6), and neglecting all nonlinear terms, the characteristic matrix for the growth rate λ can be obtained as

$$J = \begin{pmatrix} \lambda - a_{11} + d_N k^2 & -a_{12}\\ -a_{21} - \tau P_* d_N k^2 & \lambda - a_{22} + ivk + d_P k^2\end{pmatrix}, \quad (8)$$

where $a_{11} = -I$, $a_{12} = -1$, $a_{21} = (I-q)(1+\tau I)$, $a_{22} = \tau(I-q)$. Obviously, $a_{11} < 0, a_{12} < 0, a_{21} > 0, a_{22} > 0$. Then the following characteristic equation for λ can be obtained:

$$\lambda^2 - A\lambda + B = 0, \quad (9)$$

where $A = \tau(I-q) - I - (d_N + d_P)k^2 - ivk$, $B = I - q + Id_Pk^2 + d_Nd_Pk^4 + (d_Nk^2 + I)ivk$.

By Eq. (9), the roots yield the dispersion relation

$$\lambda_{1,2} = \frac{A \pm \sqrt{A^2 - 4B}}{2}. \quad (10)$$

The Hopf bifurcation occurs when

$$\text{Im}[\lambda(k)] \neq 0, \quad \text{Re}[\lambda(k)] = 0 \quad \text{at} \quad k = 0.$$

Then the Hopf line can be obtained as

$$\tau_H = I/(I-q). \quad (11)$$

However, for $v = 0$, the Turing instability cannot occur because of $B > 0$. Hence, the diffusion cannot induce instability when $v = 0$.

For $v > 0$, Eq. (10) can be rewritten as

$$\lambda_{1,2} = \frac{\text{tr}_k - ivk \pm \sqrt{C + iE}}{2}, \quad (12)$$

where $C = \text{tr}_k^2 - v^2k^2 - 4\Delta_k$, $E = -2[\text{tr}_k + 2(I + d_Nk^2)]vk$, $\text{tr}_k = \tau(I-q) - I - (d_N + d_P)k^2$, $\Delta_k = I - q + Id_Pk^2 + d_Nd_Pk^4$.

To analyze the effect of flow on the system, the real and imaginary parts of the eigenvalues must be obtained as follows:

$$\text{Re}(\lambda) = \tfrac{1}{2}\left[\text{tr}_k \pm \sqrt{\tfrac{1}{2}\left(\sqrt{C^2 + E^2} + C\right)}\right], \quad (13)$$

$$\text{Im}(\lambda) = \tfrac{1}{2}\left[-vk \pm \text{sgn}(C)\sqrt{\tfrac{1}{2}\left(\sqrt{C^2 + E^2} - C\right)}\right]. \quad (14)$$

The solution is stable when $\text{Re}(\lambda) < 0$. Otherwise, the solution is unstable when one of the real parts with a finitewave number $k > 0$ is greater than zero at least.

When $\tau = 0$, by direct computation using Eq. (13), it is not difficult to find that the real parts of Eq. (12) are always smaller than zero for any $v > 0$. In other words, the flow cannot induce instability when delay does not exist. Hence, the instability is driven by delay.

For $\tau > 0$, by Eq. (13), the critical flow-induced instability condition can be obtained as

$$v_c^2 = \frac{\text{tr}_k^2\Delta_k}{(I + d_Nk^2)[\tau(I-q) - d_Pk^2]k^2}, \quad (15)$$

Obviously, when $0 < k < \sqrt{\tau(I-q)/d_P}$, Eq. (15) holds. If $v > v_c$, then the instability occurs.

Therefore, when the delay exists, the flow beyond a critical value may induce instability in a nutrient-phytoplankton system.

III. NUMERICAL RESULTS

A. Parameters and parameter space

In the previous sections, the effect of delay on the system was analyzed in detail. To study how delay and flow influence the instability of the system, numerical simulations were carried out. Before the numerical simulations are presented, the set and space of parameters will be described to show the feasibility of the theoretical results. The following parameter values were used: $I = 0.075, q = 0$, as in Ref. [31]. Therefore, the positive homogeneous steady state was $E_* = (1{,}0.075)$. The other parameters, v,τ,d_N, and d_p, will be discussed as control parameters. Noting that the diffusion of nutrients and phytoplankton is mainly induced by turbulence, and therefore set $d_N = d_P = D$.

According to Eq. (11), the Hopf line $\tau_H = 1$ can be obtained; however, τ is assumed to be small as in previous sections. Hence, the parameter τ will be discussed in the range from 0 to 1. Previous analysis has shown that instability does not occur when $\tau < \tau_H$ and $v = 0$. In other words, the occurrence of instability must be related to the speed of flow when $\tau < \tau_H$. However, an analytical expression for critical value of flow speed v cannot be obtained. In fact, it is easy to get the critical value using numerical computation when the parameters are given. Figure 1(a) presents a more indepth analysis of the relationship among three parameters v,τ, and D. It is clear from Fig. 1(a) that the system is unstable in space I, whereas the homogeneous steady state is still stable in space II. To validate this result further, the maximum value of $\mathrm{Re}(\lambda)$ was calculated, as shown in Fig. 1(b) with $v = 1.5$ and $D = 0.1$. Nonetheless, it is worth noting that $\mathrm{Re}(\lambda)$ is much larger than zero when the value of the delay τ is larger than a critical value, which means the appearance of instability and agrees with the results shown in Fig. 1(a). These results in turn confirm that all the theoretical analyses are feasible.

B. Numerical simulation

This subsection describes the numerical simulations performed to illustrate the dynamics of system Eqs. (3) and (5) in two-dimensional space. Using the Euler forward finite difference method for time integration, the time step is $\Delta t = 0.01$. For the spatial derivative, applying upwind method to the flow term, the diffusion term based on the formulas in Ref. [36], the spatial step is $\Delta h = 5/4$. The system was solved numerically in rectangular spatial grid consisting of 200×200 cells, with the flow in the y direction. It was assumed that the simulated domain was a section of a real field observation area, and therefore the periodic boundary condition was adopted in the y direction, while the zero flux boundary condition was employed in the x direction. In addition, the initial condition was considered to be spatial perturbations around the positive homogeneous steady state E_*.

The next step was to study how the delay strength τ and the flow velocity v influenced the spatial distribution. It is well known that flow is one of the important factors affecting the form of Red Tide. Figure 2 depicts the relationships among the characteristic structure of the spatial distribution, the delay strength τ, and the flow velocity v. Specifically, Fig. 2(a) shows the initial spatial distribution of phytoplankton, which is heterogeneous. In order to investigate the effects of τ and v on the spatial distribution of the phytoplankton biomass, numerical simulations of phytoplankton biomass for different values of τ and v at the same time $t = 1100$ are shown in Figs. 2(b)–2(d). By comparing Figs. 2(b) and 2(d), it is evident that the spatial distribution of the phytoplankton gradually formed into strips over time, but the maximum value of the phytoplankton biomass with $v = 2$ was greater than with $v = 1.5$. This phenomenon suggests that a large value of v can enhance the strength of phytoplankton accumulation. However, it is regretful that the change in the value of v is not much potential to influence the spatial distribution structure of the phytoplankton. Based on a comparative analysis between Figs. 2(d) and 2(c), it can be asserted that large values of the delay τ can promote the accumulation of phytoplankton because the maximum value of the phytoplankton biomass with $\tau = 0.6$ is greater than with $\tau = 0.5$ and that the width of the strip with $\tau = 0.6$ is less than with $\tau = 0.5$. These results are consistent with observations: the clusters of phytoplankton

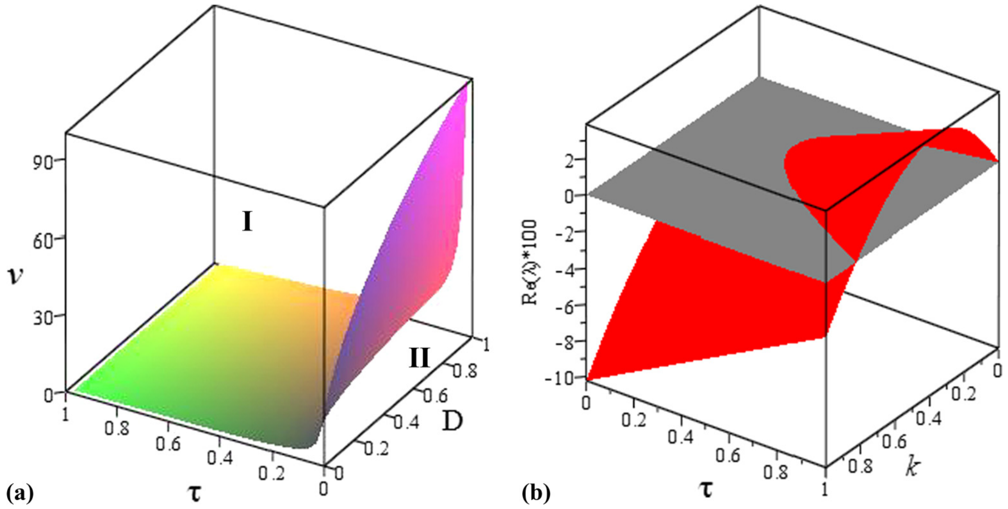

FIG. 1. (Color online) (a) Bifurcation diagram in the $v - \tau - D$ parameter space. The curved surface indicates the critical bifurcation point v_c as a function of τ and D. (b) An illustration of real part of λ, as defined in Eq. (13) for various τ, where $D = 0.1$, $v = 1.5$. The red curved surface represents the real part of λ, and the gray plane is the zero plane.

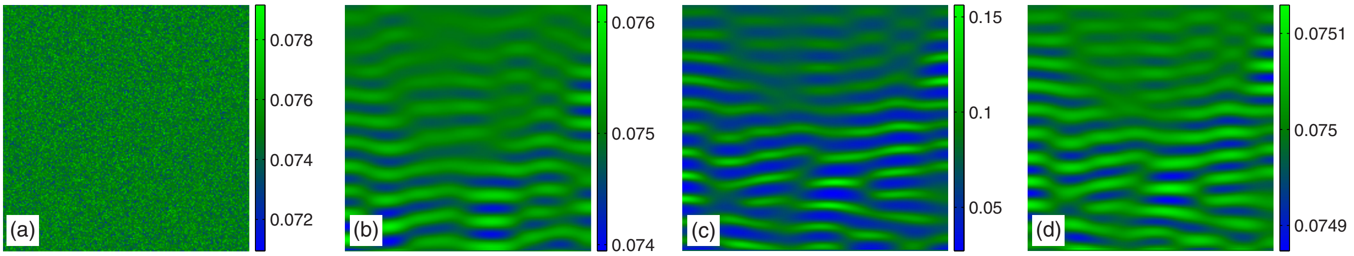

FIG. 2. (Color online) (a) The spatial distribution of phytoplankton biomass at $t = 0$; (b–d) The spatial distribution of phytoplankton biomass with $D = 0.1$ at $t = 1100$, where $\tau = 0.5, v = 2$ for (b); $\tau = 0.6, v = 1.5$ for (c); $\tau = 0.5, v = 1.5$ for (d).

become larger, and their average biomass increases. Thus, it should be stressed that the delay strength τ and the flow velocity v can seriously affect the spatial distribution of phytoplankton biomass.

For $\tau = 0$, according to the analysis in Sec. II, the positive homogeneous steady state E_* is linearly stable. This result is confirmed in Figs. 3(a) and 3(b). Figure 3(b) shows the spatiotemporal evolution of phytoplankton biomass at $x = 126.25$, and Fig. 3(a) shows the spatial distribution of phytoplankton biomass at $t = 1100$. It is obvious that the biomass eventually reaches the positive homogeneous steady state E_*. In addition, by Fig. 1(a), it can be seen that the positive homogeneous steady state E_* is stable when (τ, v, D) is in space II. For this reason, the corresponding numerical results are given, as is shown in Figs. 3(c) and 3(d), which confirm that the phytoplankton biomass indeed tends to E_*. The results of numerical simulations agree well with the analysis in Sec. II. In particular, from Figs. 2(b)–2(d), it is clear that the long-term solutions are traveling waves, in which patterns of different speed coexist. Based on the above analysis, delay can induce instability in the system directly and encourage it to form a banded pattern.

C. Analysis of sensitivity

By the previous results, it is not difficult to find that the parameters, the delay τ, and the flow velocity v can influence dynamics of system Eqs. (3) and (5). Hence, we further did an analysis of sensitivity to the parameters τ and v responsible for stability of the positive homogeneous steady state using numerical technique in system Eqs. (3) and (5). This is through changing the delay τ and the flow velocity v to observe their effects on the peak value and minimum value of population biomass. Figure 4 shows effects of the parameters τ and v on the sensitivity for the stability of the positive homogeneous steady state.

Figure 4 indicates that there is a critical value in the delay τ and the flow velocity v, respectively. When the values

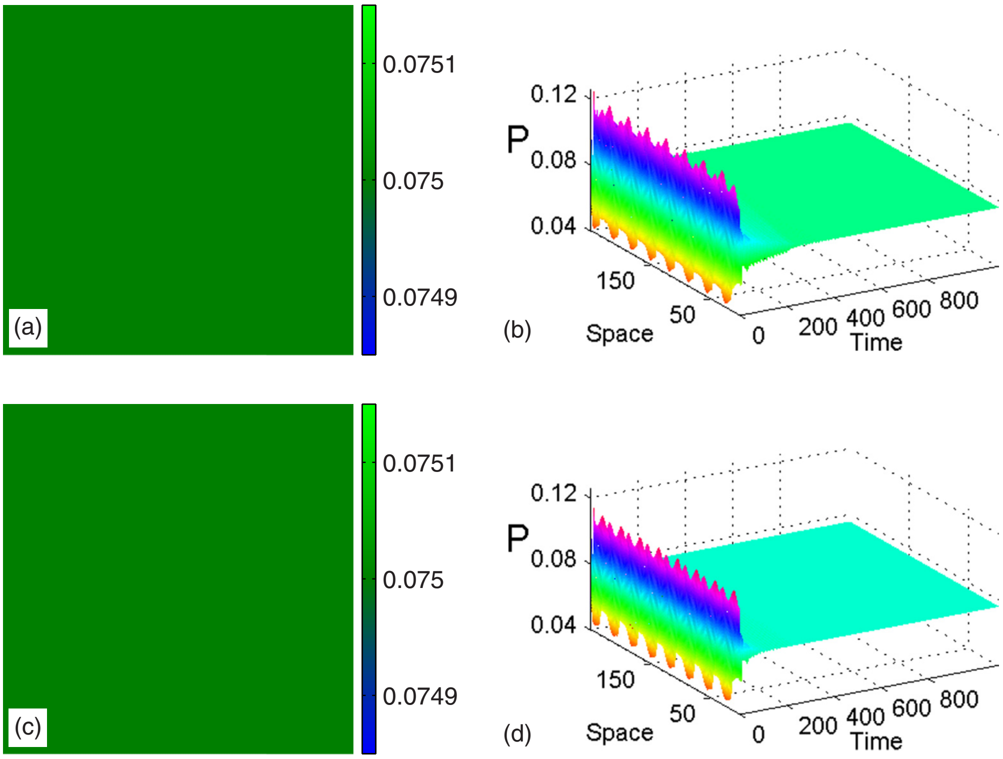

FIG. 3. (Color online) (a,c) The spatial distribution of phytoplankton biomass at $t = 1100$; (b,d) The Space-temporal evolution of phytoplankton at $x = 126.25$, where $D = 0.1$, $v = 1.5$, and $\tau = 0$ for (a,b); $\tau = 0.3$ for (c,d).

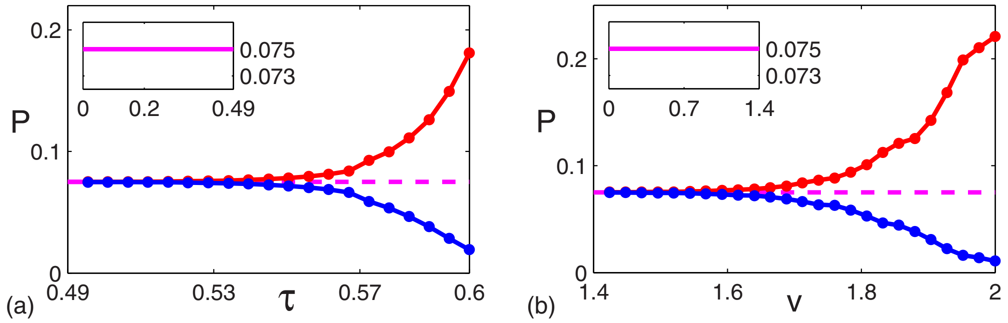

FIG. 4. (Color online) Analysis of sensitivity in system Eqs. (3) and (5) based on spatial solutions. The solid magenta lines represent the stable positive homogeneous steady state, and the dashed magenta lines represent the positive homogeneous steady state where it is unstable to spatially heterogeneous perturbations. The red lines with solid cycle and the blue lines with solid cycle represent maximum and minimum amplitude of phytoplankton biomass in the simulated domain. (a) The effect of delay on the system with $v = 1.5$; (b) The effect of flow on the system with $\tau = 0.5$.

of τ and v are less than their corresponding critical value, the positive homogeneous steady state is stable. In contrast, the positive homogeneous steady state will lose its stability. That is, with the increases of the parameter τ and v, the positive homogeneous steady state will become unstable, and the corresponding banded pattern will appear. These results show that the stability of the positive homogeneous steady state is sensitivity for variations of the parameter τ and v. In addition, it is also worthwhile to point out that the results in Fig. 4 based on system Eqs. (3) and (5) are consistent with the results obtained using approximative method in Fig. 1, this means that the method used in this paper is feasible to study the effects of time delay in advection-reaction-diffusion equations under some conditions.

IV. CONCLUSION

The system proposed in Ref. [31] has been extended in this research into a spatial one with delay, which was addressed by a couple of advection-reaction-diffusion equations with time delay. Using the approximation method described in Refs. [32–34], a spatial system with delay was investigated. The analysis focused on the effects of delay and flow on instability of the system. Simple linear analysis revealed that the positive homogeneous steady state E_* in system Eqs. (3) and (4) was locally linearly stable. However, it became unstable when time delay was present. If only flow velocity or delay was beyond some critical value, then a banded pattern could emerge. In other words, delay and flow could result in the formation of symmetry-breaking structures in the form of a banded pattern via a Turing-like instability.

A banded pattern has been obtained in others researches [4,13,14,16], and it also has been found in field observations [18,37]. In particular, in Ref. [37] the authors observed the banded distribution of phytoplankton in some seas, lakes, and rivers. These observations are very similar to our simulated results. Indeed, due to some factors such as noise, internal factors, and physical factors, etc., a constant population density may not even exist, even if uniform oscillations of cyclic population are not the case, which has been reported in Ref. [38]. In contrast, the population density may be different at different locations, while a banded pattern shows this point. Hence, the banded pattern may be a suitable explanation of a real-world natural phenomenon. Since time delay appears as an important component in bio- and ecosystem, we believe that these results of delay- and flow-induced banded pattern are likely to be important in studies of nutrient-phytoplankton systems, and the method of using the advection-diffusion-reaction equation with delay to study the evolutionary mechanism of phytoplankton such as Red Tide is feasible.

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