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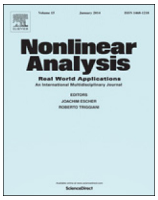

Spatiotemporal pattern formation and selection induced by nonlinear cross-diffusion in a toxic-phytoplankton–zooplankton model with Allee effect[☆]

Renji Han [a], Binxiang Dai [b,*]

[a] *School of Science, Zhejiang University of Science & Technology, Hangzhou 310023, PR China*
[b] *School of Mathematics and Statistics, Central South University, Changsha 410083, PR China*

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ABSTRACT

The spatiotemporal pattern formation and selection driven by nonlinear cross-diffusion of a toxic-phytoplankton–zooplankton model with Allee effect is investigated in this paper. We first perform the mathematical analysis of the corresponding non-spatial model and spatial model, which give us a complete picture of the global dynamics. Then the linear stability analysis shows that the nonlinear cross-diffusion is the key mechanism for the formation of spatial patterns. By taking cross-diffusion rate as bifurcation parameter, amplitude equations under nonlinear cross-diffusion are derived that describe the spatiotemporal dynamics, which interprets the structural transitions and stability of various forms of Turing patterns. Finally, numerical simulations illustrate the effectiveness of theoretical results. It is shown that the spatiotemporal distribution of the plankton is homogeneous when in the absence of cross-diffusion. However, when the cross-diffusivity is greater than its critical value, the spatiotemporal distribution of all the plankton species becomes inhomogeneous in spaces and results in different kinds of patterns: spot, stripe, and the mixture of spot and stripe depending on the nonlinear cross-diffusivity. Simultaneously, the impact of Allee effect and toxin-producing rate of toxic-phytoplankton species on pattern selection is also explored.

1. Introduction

As we know, phytoplankton are microscopic plants and primary producers at the base of the aquatic food web, floating freely near the surfaces of all aquatic environments. Zooplankton are the animals in the plankton community, of which both herbivores and predators occur, with herbivores grazing on phytoplankton and then being eaten by zooplankton predators [1]. Over many decades, marine plankton dynamics has become an important research area due to the fact that plankton act as the basis of all food chains and webs in aquatic systems and play an important role in the ecology of the ocean. Several models have been suggested

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[*] Corresponding author.
E-mail addresses: renjihan@csu.edu.cn (R. Han), bxdai@csu.edu.cn (B. Dai).

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for the investigation of plankton dynamics. However, a specific group of phytoplankton common to most aquatic ecosystems has the special physiological feature of liberating "toxic" or "allelopathic agents" harmful for the growth of other algae [2,3]. Algal toxicity is known to have a significant impact on the distribution of phytoplankton and zooplankton populations . Chattopadhyay et al. [4] proposed a mathematical model for toxic phytoplankton and zooplankton interaction and explores the role of TPP behind harmful algal blooms. The general form of mathematical model they have considered is the following nonlinear coupled ordinary differential equations

$$\begin{cases} \frac{dP}{dt} = rP(1-\frac{P}{K}) - \alpha f(P)Z, \\ \frac{dZ}{dt} = \beta f(P)Z - dZ - \theta g(P)Z, \end{cases} \tag{1.1}$$

where $P \equiv P(t)$ is the density of TPP population and $Z \equiv Z(t)$ is the density of zooplankton population at any time t with the non-negative initial condition $P(0) = P_0 \geq 0$ and $Z(0) = Z_0 \geq 0$; $r, K, \alpha, \beta, d, \theta$ are all positive constants that stand for the intrinsic growth rate, the environmental carrying capacity, the rate of predation of zooplankton on TPP population, the ratio of biomass consumed by zooplankton for its growth, the morality rate of zooplankton, the rate of toxin liberation by TPP population respectively; $f(P)$ represents the functional response for the grazing of phytoplankton by zooplankton and $g(P)$ describes the distribution of toxic substance which ultimately contributes to the death of zooplankton population. They have analyzed the above model system by taking various combinations of functional response terms. Since the pioneering work of Chattopadhyay, a growing number of biological papers on TPP–zooplankton model have been published, demonstrating the importance of this interaction [5–14].

The Allee effect describes a scenario in which populations at low numbers are affected by a positive relationship between population growth rate and density, which increases their likelihood of extinction [15–18]. Generally Allee effect is classified into two main types: Strong Allee effect (or critical Allee effect) and weak Allee effect (or non-critical Allee effect). A strong Allee effect introduces a population threshold, below which the per capita growth rate is negative and the population declines on average, and above which the per capita growth rate is positive and the population increases on average and convergence to the carrying capacity eventually [19,20]. In contrast, a population with weak Allee effect does not have a threshold to be exceeded for the population to survive [16,21,22]. Allee effect can be induced by a variety of mechanisms, including the difficulties in finding suitable mating partners, reproductive facilitation and predation, social interaction, pollen scarcity, cooperative breeding and anti-predator behavior, environmental conditioning etc (cf. [23,24], Table 1 in [25]). Allee effects are likely to occur in marine systems as suggested by Gascoigne who shows that Allee effects related to population size are also possible in large populations and metapopulations if they depend on the size of the local subpopulation rather than on the metapopulation as a whole [26]. Allee effects on subpopulation growth rate can also cause metapopulation level 'Allee effects' on a large spatial scale, with a critical number of subpopulations below which the metapopulation will go extinction [27]. Field observations by Momo [28] and Wear et al. [29] suggest that a threshold concentrations of macroalgae population is required for its cell division. This means, under excessive zooplankton, phytoplankton can experience an Allee effect. Bhattacharyya [30] considered an algae–herbivore interactions model with Allee effect on macroalgae and chemical defence. Based on the above statements, we first make the following assumptions:

- In the absence of zooplankton, the growth of single species P affected by the multiplicative Allee effect is governed by the following equation [15]:

$$\frac{dP}{dt} = rP(1-\frac{P}{K})(P-m), \tag{1.2}$$

where r is the intrinsic growth rate, K is the phytoplankton species carrying capacity and m is the threshold value satisfying $-K < m < K$. Clearly, it is called weak Allee effect if $-K < m \leq 0$ and strong Allee effect if $m > 0$. Fig. 1 depicts these two different kinds of cases.

- We also assume that the zooplankton is able to recognize the TPP populations when the toxic phytoplankton is ingested into much, and therefore it kills too much zooplankton, then the zooplankton, through some kind of chemotactic sensitivity, moves against the gradient of the TPP, and thus the zooplankton will decrease its consumption. This is modeled via a simplified non-monotonic Monod–Haldane-type functional response expressed by $\frac{P}{c+eP^2}$, which is suggested in [9].