Multiple steady-states in phytoplankton population induced by photoinhibition [☆]

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Abstract

We study the effect of photoinhibition in a nonlocal reaction–diffusion–advection equation, which models the dynamics of a single phytoplankton species in a water column where the growth of the species depends solely on light. Our results show that, in contrast to the case of no photoinhibition, where at most one positive steady state can exist, the model with photoinhibition possesses at least two positive steady states in certain parameter ranges. Our approach involves bifurcation theory and perturbation–reduction arguments.
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1. Introduction

Phytoplankton are microscopic plants that float in oceans and lakes and form the base of the aquatic food chain. Since they transport significant amounts of atmospheric carbon dioxide into the deep oceans, they may also play a crucial role in the climate dynamics. Phytoplankton species typically compete for nutrients and light [4,5,16,19,28,29]. But in oligotrophic ecosystems with ample supply of light, they tend to compete only for nutrients [20,22], and in eutrophic environments with ample nutrients supply, they compete only for light [8,15]. In a water column, a phytoplankton population diffuses due to turbulent mixing caused by wind and wave actions. In many cases, phytoplankton also sinks due to its own weight.

In this paper, we consider a single sinking phytoplankton species in an eutrophic water column. Our analysis is based on a nonlocal reaction–diffusion–advection model given by Huisman and colleagues in [8,14], but the growth function $g(I)$ of phytoplankton species in the model is modified to include photoinhibition into consideration.

Photoinhibition is characterized by a decreasing rate of photosynthesis with increasing light, which occurs in many phytoplankton species that are sensitive to strong light. This phenomenon is caused by damage to the photosynthetic machinery of cells and by protective mechanisms to avoid this damage [23,27].

Without photoinhibition, the growth function $g(I)$ is generally assumed to be strictly increasing in I, representing the fact that increase of the light level I leads to better growth of the phytoplankton. In such a case this model was investigated recently through rigorous mathematical analysis in [6,7,13,21] (see also earlier work in [17,18,26] and references therein), which show that the phytoplankton population either stabilizes at a unique positive steady-state or converges to 0 as time goes to infinity, depending on whether the loss rate is below or above a critical level.

With photoinhibition, observations in many laboratory studies [10,11,24] suggest that the function $g(I)$ should be increasing before I reaches a certain critical level $I_* > 0$ where $g(I)$ has a maximum, after which $g(I)$ decreases and converges to 0 as $I \to \infty$. In a completely mixed water column, the reaction–diffusion–advection model reduces to an ODE model, and the effect of photoinhibition was studied in the recent papers [9,12]. With a growth function $g(I)$ as above, [9] demonstrates that the phytoplankton population may have two stable steady-states (one positive, the other 0), plus another unstable positive steady state, causing a bistable dynamical behavior with the phytoplankton population stabilizing at one or the other stable steady state, depending on its initial value. (The multi-species case was also considered in [9] and [12].)

In this paper, we examine the effect of photoinhibition in an incompletely mixed water column, through a single species reaction–diffusion–advection model, where photoinhibition is incorporated into the growth function $g(I)$ as described above. We show that the phenomenon of multiple positive steady-states observed in completely mixed water column persists, and their stability suggests a bistable dynamical behavior.

Multiplicity results for similar reaction–diffusion equations are usually obtained by making use of the upper and lower solution technique, combined with tools from global analysis (such as the topological degree theory or global bifurcation theory). However, such upper and lower solution techniques are difficult to apply here due to the nonlocal nature of the problem. To overcome this difficulty, apart from employing local and global bifurcation analysis, we also use a perturbation and reduction approach, which is new to this kind of nonlocal reaction–diffusion equations. It is our hope that the mathematical techniques developed here may find more applications in phytoplankton models.