



Modelling of phytoplankton allelopathy with Monod–Haldane-type functional response—A mathematical study

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ARTICLE INFO

Article history:

Received 4 July 2008

Received in revised form 28 October 2008

Accepted 5 November 2008

Keywords:

Phytoplankton

Zooplankton

Toxin

Functional response

Hopf-bifurcation

Chaos

ABSTRACT

In this paper, a three-tier model of phytoplankton, zooplankton and nutrient is considered and stability of different equilibrium points is analyzed along with Hopf-bifurcation around coexisting equilibrium point. Here, we have assumed toxication process as the guiding factor for bloom formation as well as its termination and this process is incorporated into our model by choosing the zooplankton grazing function as a Monod–Haldane function due to the phytoplankton toxicity. Extensive numerical simulations have been performed to validate the analytical findings and these simulation work reveal the chaotic oscillation exhibited by the model system for certain choice of the parameter values.

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1. Introduction

In aquatic ecology, the term plankton refers to the freely floating and weakly swimming organisms. There are two types of plankton, the plant species commonly known as phytoplankton which are unicellular and microscopic in size and the animal species namely zooplankton which live on these phytoplankton. Phytoplankton have a lot of utility in marine life. They play a vital role at the base of marine food chain, they also control the global carbon cycle which has a significant impact on the climate regulation. A remarkable feature associated with many phytoplankton populations is the occurrence of rapid and massive bloom formation. Such events are characterized by a dramatic sharp rise in population, up by several orders of magnitude which is shortly followed by a sudden collapse whereby phytoplankton population returns to its original low-level as if nothing had happened. This periodic nature of blooms, in the sense of rapid onset and disappearance of oscillations is a main characteristic of phytoplankton. The regular change and abrupt fluctuation of phytoplankton density within marine environment are controlled by several factors, variation of necessary nutrients, environmental forcing arising from seasonal change in environment and many others (for details, see Edvarsen and Paasche, 1998; Blaxter

and Southward, 1997). An important observation made by many researchers is that the change in population density of one species has ability to affect the growth of several other species by producing allelopathic toxins or stimulators and this is a responsible factor for seasonal change in population density of various phytoplankton species. The term ‘*allelopathy*’ was first introduced by Molisch (1937), later cited by Rice (1984) and now is defined extensively for plankton communities. According to Rice (1984), allelopathy is the effect of one plant species on the growth of other induced by releasing chemical compound into the surrounding environment and these type of chemical compounds are known as ‘*allelochemical*’ (Solé et al., 2005). Allelochemicals released by phytoplankton species has both positive and negative effects on the growth of other species.

Zooplankton population is solely dependent upon phytoplankton as their most favorable food source and a variation in phytoplankton density has a great impact on the growth of zooplankton. Blooms of harmful phytoplankton are known to affect zooplankton significantly. When blooms of such harmful species occur, the cumulative effect of all the toxins released may cause a reduction in grazing pressure of zooplankton. For example, dense assemblage of some algae such as *Phaeocystis*, *Coscinodiscus* and *Rhizosolenia* are avoided by zooplankton. Buskey and Stockwell (1993) have demonstrated in their field studies that micro- and meso-zooplankton populations are reduced during these blooms. Kirk and Gilbert (1992) reported a reduction of grazing pressure of zooplankton due to release of toxin by phytoplankton.

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Researchers have studied this issue using models that vary in complexity. Some of these models were concerned with phytoplankton–zooplankton interaction (Elser and Hassett, 1994; Tikhonova et al., 2003; Truscott and Brindley, 1994; Wilk-Wozniak et al., 2001 and references cited therein) while others include nutrient concentration into the model equations (Ruan, 1993; Jang, 2000; Jang et al., 2006; Garvie and Trenchea, 2007). A nutrient–phytoplankton–zooplankton model with generalized functional response was studied by Gard (1983). But so far as our knowledge goes the modelling of nutrient–phytoplankton–zooplankton interaction considering the effect of toxic substances released by phytoplankton species are rare except the work by Mukhopadhyay and Bhattacharyya (2006). Most of the literature considering the effect of toxic chemicals released by phytoplankton species on the grazing rate and growth of zooplankton species are of two types: (i) two-dimensional model of phytoplankton and zooplankton and (ii) three-dimensional model considering the interaction between toxic-phytoplankton–non-toxic-phytoplankton and zooplankton population. Interested readers may consult the recent review by Roy and Chattopadhyay (2007) and references cited therein for a detailed discussion in this direction.

The main objective of this paper is to consider a three-tier model of nutrient–phytoplankton–zooplankton with the usage of Monod–Haldane-type functional response to model the zooplankton grazing. Here, we are interested to study the change in dynamic behavior of phytoplankton and zooplankton interaction when there is a massive growth of phytoplankton population and toxin released by phytoplankton population affect the zooplankton grazing and survival of either species. The said process is incorporated into our modelling approach with help of Monod–Haldane-type functional response, utility and significance for the choice of such function is mentioned in the next section. The organization of the paper is as follows: Section 2 gives the description of the model and determines the equilibrium points along with some basic mathematical results. Section 3 carries out stability analysis for different equilibrium points and also investigates the possibility of Hopf-bifurcation. In Section 4, numerical simulation results are provided to substantiate the analytical findings and conclusion is drawn following ecological interpretations in Section 5.

2. Basic Model: Boundedness and Equilibria

We consider here a three-tier model of nutrient–phytoplankton–zooplankton and let $N(t)$, $P(t)$ and $Z(t)$ denote their population densities at time ‘ t ’ respectively. Also, let N_0 denote the constant supply rate of nutrient to the system while αN denotes the loss of same due to washout. We have assumed that the nutrient uptake by phytoplankton follows the Holling’s type-II functional response $\sigma(N) = (N/(k+N))$, (see Kot, 2001), which is a non-negative, increasing function that reduces to zero in the absence of nutrient. Here $k (> 0)$ is the half-saturation constant. In a recent work on toxic-phytoplankton–zooplankton model, Mukhopadhyay and Bhattacharyya (2006) assumed Holling’s type-IV functional response to model the interaction between phytoplankton and zooplankton populations, the use of such a choice has been justified as follows: ‘this type of functional response implies that for large phytoplankton density, the predation rate decreases’. Several researchers have established the fact that toxic substances released by some phytoplankton species have a repulsive effect on zooplankton and the zooplankton tries to move away from the area having thick phytoplankton density. This resembles a *group defense mechanism* for phytoplankton against zooplankton. In their modelling approach, type-IV functional response is described by the

function

$$\phi(P) = \frac{P}{(P^2/i) + P + e} \quad (2.1)$$

where ‘ i ’ and ‘ e ’ are positive parameters. The parameter ‘ e ’ can be interpreted as the half-saturation constant in the absence of any inhibitory effect and ‘ i ’ is the measure of inhibitory effect, and for large i , $\phi(P)$ reduces to a type-II functional response. Here $\phi(P)$ is a functional response in which the zooplankton’s per capita rate of predation decreases at sufficiently high phytoplankton density due to either interference or phytoplankton toxicity. This type of functional response was first introduced by Haldane (1930) in enzymology. It was then used by Andrews (1968) as a substrate uptake function. For detailed discussion in this direction, interested readers may consult the book by Kot (2001). However in this paper the toxic-phytoplankton and zooplankton population–interaction has been modelled using simplified Monod–Haldane-type functional response $\psi(P) = (P/(bP^2 + e))$, where the new parameter ‘ b ’ is defined by $b = 1/i$. Hence ‘ b ’ is also a positive parameter and can be defined as the inverse measure of inhibitory effect. The reason behind such a choice can be explained as follows: this function fits significantly well in place of the former showing similar behavior of group defense for large phytoplankton density, i.e. the repulsive effect on zooplankton due to toxicity of thick phytoplankton population can be effectively established using this functional form. For a better understanding of this hypothesis we can see the plot of the functions $\phi(P)$ and $\psi(P)$ against P with $1/i = 0.2 = b$, $e = 2$ and $0 \leq P \leq 30$ (see Section 4 for unit of P). From Fig. 1 it is clear that the basic nature of both the functional responses are similar and their values at small and high phytoplankton density are same, the only difference is the maximum value attained by the two response functions. At this position we want to remark that for large values of b the functional value of $\psi(P)$ is very small and hence the Monod–Haldane-type functional response has the ability to capture the idea that the grazing pressure of zooplankton is low when the rate of toxin released by phytoplankton is not very high, as a result the density of non-toxic phytoplankton increases significantly. Besides the choice of Monod–Haldane-type functional response, other assumptions made to form the complete mathematical model are described as follows: due to death, washout or some natural calamity, let the loss of phytoplankton and zooplankton be given by γP and ϵZ respectively while through recycling (decomposition), let $\gamma_1 P$ amount of phytoplankton and $\epsilon_1 Z$ amount of zooplankton be converted back into nutrients. Clearly, then $\gamma_1 < \gamma$ and $\epsilon_1 < \epsilon$. Also, let a , a_1 , c , c_1 denote the maximal nutrient uptake of phytoplankton, nutrient–phytoplankton conversion rate, maximal phytoplankton uptake of zooplankton and phytoplankton–zooplankton conversion rate respectively, where $a_1 < a$ and $c_1 < c$. Hence the growth rate equations of nutrient $N(t)$, phytoplankton $P(t)$ and zooplankton $Z(t)$ are given by the following system of coupled nonlinear ordinary differential equations:

$$\frac{dN}{dt} = N_0 - \alpha N - \frac{aNP}{k+N} + \gamma_1 P + \epsilon_1 Z \equiv F_1(N, P, Z) \quad (2.2a)$$

$$\frac{dP}{dt} = \frac{a_1 NP}{k+N} - \gamma P - \frac{cPZ}{bP^2 + e} \equiv F_2(N, P, Z) \quad (2.2b)$$

$$\frac{dZ}{dt} = Z \left(\frac{c_1 P}{bP^2 + e} - \epsilon \right) \equiv F_3(N, P, Z) \quad (2.2c)$$

with non-negative initial conditions $N(0) \geq 0$, $P(0) \geq 0$ and $Z(0) \geq 0$. Due to the boundedness of the functional responses, it can be easily verified that, $\lim_{(N,P,Z) \rightarrow (0,0,0)} F_1(N, P, Z) = N_0$, $\lim_{(N,P,Z) \rightarrow (0,0,0)} F_2(N, P, Z) = 0$, $\lim_{(N,P,Z) \rightarrow (0,0,0)} F_3(N, P, Z) = 0$. Also, we note that,

$$F_1(0, 0, 0) = N_0, \quad F_2(0, 0, 0) = 0, \quad F_3(0, 0, 0) = 0 \quad (2.3)$$

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