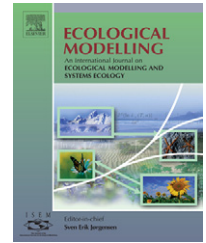


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Effect of delay on nutrient cycling in phytoplankton–zooplankton interactions in estuarine system

Kalyan Das^a, Santanu Ray^{b,*}

^a B.P. Poddar Institute of Management and Technology, Poddar Vihar, 137, V.I.P. Road, Kolkata 700052, India

^b Ecological Modelling Laboratory, Department of Zoology, Visva-Bharati University, Santiniketan 731235, India

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ABSTRACT

Phytoplankton–zooplankton interactions with delayed nutrient cycling from senescence and mortality of phytoplankton in Hooghly–Matla estuarine system are considered in this present study. Average numbers of zooplankton interacting with phytoplankton follow Poisson distribution (random zooplankton grazing). The condition for asymptotic stability of steady state is derived. The length of the delay preserving the stability is also estimated. The criterion for existence of Hopf-type small amplitude periodic oscillations of phytoplankton and zooplankton biomass is derived. Delay in the decomposition process of dead phytoplankton from senescence and other mortalities do not affect the stability of the system. All analytical results are interpreted ecologically.

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1. Introduction

Hooghly–Matla estuarine ecosystem is the largest deltaic estuarine ecosystems of the world and also regarded as one of the most productive ecosystems of the world. This estuarine complex of the tropics occupies an important place in the world map and can be categorized as “River Delta estuary” which has been advocated by Odum (1971) in addition to Pritchard's (1967) four categories of estuarine system. This system consists of several basic subsystems linked together by ebb and flow of water that is driven by the hydrological cycle (river flow) and the tidal cycles, both of which provide “energy subsidies” for the system as a whole (Ray, 1987). More than 30 species of phytoplankton and 18 species of zooplankton are recorded in this estuary (Ray et al., 2000). The litterfall from upper mangrove vegetations are the chief source of nutrients to the estuary and at the same time estuary plays an important role in the decomposition processes of the leaf

and other litters through flow and ebb tides. Lot of analytical works on the role of nutrient productions from litterfall of mangroves and their transportations to the adjacent estuary and also effect of delays on nutrient production from litterfall and transportations to the estuarine water of this ecosystem were done by many authors (Sarkar et al., 1991; Mitra et al., 1992; Sarkar and Ghosh, 1997; Mukherjee et al., 1993, 1996, 2000). Other than Hooghly–Matla estuarine system several authors performed different types of work on the interaction of prey–predator system particularly on the planktonic system in the estuarine systems throughout the globe (Gupta and Houndeshell, 1976; Kooij and Zegeling, 1996; Sugie et al., 1997; Arino and Boussouar, 2000; Litchman and Klausmeier, 2001; Bishop et al., 2006). Although Shigui (2001) handled the instability in diffusive ecological models with non-local delay effects, the present paper deals the effect of delay in different aspect of this ecosystem which is described in the following paragraph.

* Corresponding author. Tel.: +91 3463 261268; fax: +91 3463 261268.

E-mail address: sray@visva-bharati.ac.in (S. Ray).

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Senescence in phytoplankton is a natural developmental process, which may even be thought of as terminal differentiation (Finch and Schneider, 1985). It represents endogenously controlled degenerative processes leading to death; aging encompasses a wide array of passive or non-regulated, degenerative processes driven primarily by exogenous factors (Leopold, 1975). Aging does not in itself necessarily cause death but may decrease resistance to stress and otherwise increase the probability of death. The death of phytoplankton due to senescence and other causes is very important in the regulation of the system. The dead phytoplankton after decomposition is transformed into nutrients. And the major part of the dynamics of phytoplankton is controlled by nutrients (Ray et al., 2001). Decomposition process is regulated by many external factors such temperature, sunlight, chemical conditions of the water, etc. (Smith, 1982; DeAngelis, 1992). In tropics most of the time this process is very fast however, in some unfavorable conditions such as low temperature the decomposition process is delayed (Choudhury and Mahatra, 1977).

The objectives of the present work are to determine how the nutrients are regulated by the phytoplankton loss due to senescence and other deaths and also to know the effects of delay on the decomposition process of dead phytoplankton in Hooghly-Matla estuarine complex. We have also studied the effects on above conditions on phytoplankton zooplankton interactions of the system. In this paper we propose a three-dimensional model of nutrients (x), phytoplankton (y) and zooplankton (z).

2. Mathematical model

The rate equations of growth of $x(t)$, $y(t)$ and $z(t)$ may be expressed as

$$\begin{aligned} \frac{dx}{dt} &= \alpha - \delta x - \beta xy + k\gamma y \\ \frac{dy}{dt} &= y \left[\beta x - \gamma - \frac{\sigma z}{1+y} \right] \\ \frac{dz}{dt} &= z \left[\frac{\sigma y}{1+y} - \eta \right] \end{aligned} \quad (1)$$

Nutrient pool (x) is partly maintained by constant input of nutrients (α) influenced by litterfall from adjacent mangrove forest. Nutrients are also lost due to transportation by tidal wash during inflow and outflow of full and ebb tides. Phytoplankton populations (y) not only consume the nutrients but also contribute itself into nutrients after senescence and other deaths and considered another source of nutrients in the nutrient pool. Time delay is incorporated in the nutrient recycle rate after the death of phytoplankton population. Dead phytoplankton are decomposed into detritus and after re-mineralization ultimately transformed into nutrients. Therefore, constant delay parameter ($t - \tau$) is considered in the decomposition of phytoplankton population. Some fractions (k) of death phytoplankton is converted into nutrients. During conversion process detritus is one of the components. In this system detrital food chain is very prominent, the detritivores consume some portions of the detritus and therefore, the whole dead part of phytoplankton cannot be converted

into nutrients. $\sigma z/(1+y)$, is the grazing of zooplankton on phytoplankton and also the assimilation of zooplankton from phytoplankton grazing. In real ecological sense the grazing and assimilation should not be the equal always the assimilation is lesser than grazing. But for mathematical simplicity we have considered the grazing and assimilation rates are equal. After introducing the delay parameter τ in the recycling term the rate Eq. (1) of the nutrient-phytoplankton-zooplankton system with delayed nutrient recycling may be expressed as

$$\begin{aligned} \frac{dx}{dt} &= \alpha - \delta x - \beta xy + k\gamma y(t - \tau) \\ \frac{dy}{dt} &= y \left[\beta x - \gamma - \frac{\sigma z}{1+y} \right] \\ \frac{dz}{dt} &= z \left[\frac{\sigma y}{1+y} - \eta \right] \end{aligned} \quad (2)$$

where $x(0) = x_0 > 0$, $y(0) = y_0 > 0$, $z(0) = z_0 > 0$.

With initial conditions $\phi = (\phi_1, \phi_2, \phi_3)$ in the Banach space

$$C = \{ \phi \in C([- \tau, 0], \mathfrak{R}_+^3) : \phi_1(\theta) = X(\theta), \phi_2(\theta) = Y(\theta), \phi_3 = Z(\theta) \}$$

where $x(\theta) > 0$, $y(\theta) > 0$, $z(\theta) > 0$, $\theta \in [- \tau, 0]$, and τ is the non-negative constant. $\phi_i(t)$ ($i = 1, 2, 3$), are continuous bounded functions from $[- \tau, 0] \rightarrow \mathfrak{R}$. Now $\mathfrak{R}_+^3 = \{ x \in \mathfrak{R}^3 : x_i \geq 0, i = 1, 2, 3 \}$ and solution of the system (2) with initial conditions are defined on $[0, +\infty]$ and remain positive for all $t \geq 0$.

Here all the system parameters $\alpha, \delta, \beta, k, \gamma, \sigma, \eta$ are assumed to be positive. Since the growth functions are sufficiently smooth in \mathfrak{R}_+^2 , the solutions of (2) with the given initial conditions are non-negative with positive time (Hale, 1977) follows from the integral formulation of (2). Hence it is also true for the original system (Freedman et al., 1986; Gopalsamy, 1992).

The rate equations for nutrient-phytoplankton-zooplankton system without time delay are given by (1). To ensure the existence and uniqueness of the system (1), we seek the solution in $\mathfrak{R}_+^3 = \{(x, y, z) : x \geq 0, y \geq 0, z \geq 0\}$. Therefore, all the standard results on existence, uniqueness and continuous dependence on initial condition of solutions are evidently satisfied. For boundedness of solutions we state the following lemma. There exists a positively invariant box $B = \{(x, y, z) \in \mathfrak{R}_+^3 : 0 \leq x \leq \alpha, 0 \leq y \leq \alpha, 0 \leq z \leq \alpha\}$ in \mathfrak{R}_+^3 such that all solutions with non-negative initial conditions approach B as $\tau \rightarrow \infty$. Next we are interested only about the existence of the interior equilibrium of the system (1).

The interior equilibrium of (1) is given by $E(x^*, y^*, z^*)$, where

$$x^* = \frac{\alpha(\sigma - \eta) + k\gamma\eta}{\delta(\sigma - \eta) + \beta\eta}, \quad y^* = \frac{\bar{\eta}}{\sigma - \eta}, \quad z^* = \frac{(\beta x^* - \gamma)(1 + y^*)}{\sigma}$$

Clearly E is feasible if $\alpha > \delta\gamma/\beta + \eta\gamma(1 - k)/(\sigma - \eta) = \hat{\alpha}$ (say) and $\sigma > \eta$ where $\hat{\alpha} = (\delta\gamma/\beta) + (\eta\gamma(1 - k)/(\sigma - \eta))$. Thus we see that the existence of interior equilibria depend on the threshold value of external nutrient input.

Thus the interior equilibrium of (1) exists if the external nutrient input exceeded certain threshold value.

To investigate the stability of the interior equilibrium E , we compute the eigenvalues of the Jacobian matrix at this equilibrium.

The eigenvalues λ satisfies the characteristic equation

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0$$

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