Advances in Mathematics: Scientific Journal **10** (2021), no.3, 1347–1356
ISSN: 1857-8365 (printed); 1857-8438 (electronic)
https://doi.org/10.37418/amsj.10.3.22

PERTURBATION EFFECTS ON BIOMASS OF HIGHER TROPHIC-LEVEL IN PLANKTONIC ECOSYSTEMS

Ram Chandra and Anupam Priyadarshi[1]

ABSTRACT. Perturbations are well known for change in qualitative behavior of physical / bio-physical systems. Plankton systems are more vulnerable to perturbations due to rich diversity in their size, mass and traits-affinity. Phytoplankton biomass productions depends upon various factors such as nutrient uptake, excretions, mortality, mineralization and recycling processes of nutrients. In this study, we investigate dynamics of the basic compartment models consisting of nutrient (N), phytoplankton (P) and detritus (D) and we observe how perturbations change their dynamics and ecological balance. From our analysis, we observed that perturbations / heterogeneity enhance phytoplankton biomass and support coexistence in plankton ecosystems. A measurable quantity called coefficient of variation of phytoplankton (CVp) which is the ratio of standard deviation and mean of phytoplankton increases with perturbations / heterogeneity. The robust pattern of CVp and biomass with varying level of perturbations indicates that impacts of perturbations / heterogeneity cannot be ignored for intermittent phytoplankton distributed at micro-scale in plankton modeling.

---

[1] *corresponding author*

2020 *Mathematics Subject Classification.* 00A71.

Key words and phrases. Perturbations, Closure Modeling Approach, Recycling Process, Mineralization.

Submitted: 23.01.2021; *Accepted:* 07.02.2021; *Published:* 18.03.2021.

1. INTRODUCTION

Phytoplankton are microscopic, single-celled photosynthetic organisms and a key part of oceans, seas and freshwater basin ecosystems. They are the base of aquatic food systems and provide food for a wide range of sea creatures. Phytoplankton diversity affected by various factors like microbial organisms, nutrient cycling and biological-physical activities [1–3]. Phytoplankton biomass productions depend upon several constituents' factors such as nutrient uptake, excretions, mortality, mineralization and recycling processes of nutrients which influence the functioning behavior of marine ecosystem and play a vital role to maintain ecological balance [4, 5]. The death of aquatic organisms (animals and plants) and excretion, secretion and egestion from living animals (fish, zooplankton, etc.) and plants are main sources of nutrients. Nutrients are fundamental for the enhancement of phytoplankton productions and coexistence of aquatic food webs [6]. Detritus influences the availability of dissolved organic matter and nutrients (i.e., phosphorous and nitrogen) for biotic uptake. In aquatic ecosystems, the particulate matters are composed of detritus which consists of non-living biogenic material such as senescent phytoplankton, zooplankton fecal pellets etc. The nutrient content of detritus depends on the detrital source (phytoplankton community composition), age, depth, particle size and bacterial demineralization activities. Mass loss rates also known as a proxy for measure of decomposition rates depend upon the type of detritus, and on several environmental factors, such as moisture, temperature, or the presence and activity of detrivorous animals [7]. A small portion of phytoplankton biomass dies and goes into detritus compartment while remaining goes directly into nutrient compartment through respiratory process. By remineralization processes detritus converts nutrient component for phytoplankton uptake [8–10]. In this way cycling processes is going on through the plankton food web models.

Till now, the detritus cycles in nutrient-phytoplankton-detritus (NPD) systems studied based on conventional models using only first central moment approximations [3]. With advancement of new technologies, Doubell et al. [11] observed that intermittent phytoplankton is ubiquitously present at micro-scale ($<$1 mm). Later on Priyadarshi et al. [12, 13] hypothesized that micro-scale variability / heterogeneity increases higher trophic level's biomass and support plankton coexistence which is ultimately sustain for bigger diversity. Here, we investigate the impacts of higher central moments on NPD systems by using closure modelling approach [12–15] and describe how perturbation influences the dynamics of nutrient-phytoplankton-detritus (NPD) systems, particularly detritus cycling. We also interested to investigate the relationship between a measurable quantity called coefficient of variation of phytoplankton (CVp) which is defined as the ratio of standard deviation to mean of phytoplankton and perturbation in NPD systems. We found that the robust pattern of (CVp) which is positively associated with perturbation as previous finding in NP, NPZ and NPZD systems [12, 13, 16] with independent of parameter choices.

2. MODEL FORMULATION

Firstly, we develop nutrient-phytoplankton-detritus (NPD) model based on the mean-field approach i. e., considering only first central moments and ignoring the impacts of all higher central moments, also called conventional modeling. The NPD systems involve recycling processes of nutrients through respiration and mineralization processes of dead cells.

2.1. **Conventional Model.**

The nutrient-phytoplankton-detritus interactions can be described with the following system of differential equations:

$$\begin{aligned}
\frac{dN}{dt} &= -v_{\max}\frac{N}{K+N}P + M_{PN}P + M_{DN}D \\
\frac{dP}{dt} &= v_{\max}\frac{N}{K+N}P - M_{PN}P - M_{PD}P \\
\frac{dD}{dt} &= M_{PD}P - M_{DN}D
\end{aligned} \tag{2.1}$$

Here, the equations (2.1) are associated with non-negative initial conditions. The constant $V_{\max}$ represents maximum uptake rate of phytoplankton which depends on light and temperature. The phytoplankton growth function is given by Monod function $\frac{N}{K+N}$, where K is the half-saturation constant at which growth becomes half. The phytoplankton decreases through respiration, M_{PN} and mortality, M_{PD}. The loss rate, M_{DN} is used for remineralization process from detritus to nutrient. The system is conservative as $N + P + D =$ Constant $= A$.

Using the following scaled variables and dimensionless parameters:

$$n = \tfrac{N}{A}; p = \tfrac{P}{A}; d = \tfrac{D}{A}; n = 1 - p - d$$
$$m_{pn} = \tfrac{M_{PN}}{v_{\max}}, m_{dn} = \tfrac{M_{DN}}{v_{\max}}, k = \tfrac{K}{A}, m_{pd} = \tfrac{M_{PD}}{v_{\max}}, t = v_{\max}T$$

The conventional model (2.1) becomes dimensionless in following form:

$$\begin{aligned}\frac{dp}{dt} &= \frac{(1-p-d)}{(k+1-p-d)}p - m_{pn}p - m_{pd}p \\ \frac{dd}{dt} &= m_{pd}p - m_{dn}d\end{aligned} \tag{2.2}$$

2.2. **Equilibrium Point Analysis.** By equating the equations (2.2) to zero, we obtained two equilibrium points: $E_1 = (0,0)$ and $E_2 = (p^*, d^*)$, where $p^* = \frac{m_{dn}\left[1-(k+1)\left(m_{pn}+m_{pd}\right)\right]}{\left(m_{dn}+m_{pd}\right)\left[1-\left(m_{pn}+m_{pd}\right)\right]}$ and $d^* = \frac{m_{pd}}{m_{dn}}p^*$.

Theorem 2.1. *The equilibrium point* E_1 *of the conventional model* (2.2) *is stable if* $\frac{1}{m_{pn}+m_{pd}} < k+1$ *becomes saddle if* $\frac{1}{m_{pn}+m_{pd}} > k+1$, *and a saddle node bifurcation exits if* $\frac{1}{m_{pn}+m_{pd}} = k+1$.

Proof. The Jacobean of the system (2.2) corresponding to equilibrium point E_1 is:

$$J_1 = \begin{bmatrix} \frac{1}{(k+1)} - m_{pn} - m_{pd} & 0 \\ m_{pd} & -m_{dn} \end{bmatrix}.$$

From which the Eigen values are obtained by solving the corresponding characteristics equation $|J_1 - \lambda I| = 0$ as $\lambda_1 = -m_{dn}$ and $\lambda_2 = \frac{1}{(k+1)} - (m_{pn} + m_{pd})$. Now, if $\lambda_2 < 0$ i.e., if $\frac{1}{m_{pn}+m_{pd}} < k+1$ then the equilibrium point E_1 is stable. While if $\lambda_2 > 0$ i.e., if $\frac{1}{m_{pn}+m_{pd}} > k+1$ then equilibrium point E_1 is saddle having stable manifold in p -axis and unstable manifold in d-axis direction. The equilibrium point E_1 becomes non-hyperbolic and saddle node bifurcation generated if $\lambda_2 = 0$ i.e., if $\frac{1}{m_{pn}+m_{pd}} = k+1$, otherwise unstable. ☐

2.3. **Saddle-Node Bifurcation.** The existence of Saddle-Node Bifurcation around the equilibrium point E_1 is discussed in the above theorem (2.1). Here, we investigate the condition for which the interior equilibrium point E_2 goes through saddle node bifurcation in NPD system (2.2). There are several parameters associated with equilibrium point E_2 for which saddle node bifurcation may exists. Below, the condition for saddle node bifurcation around the equilibrium point with respect to parameter m_{pd} is explicitly discussed. For other parameters, similar analysis are required.

The Jacobean associated with equilibrium point $E-2$ of the model (2.2) is

$$J_2 = \begin{bmatrix} \frac{-kp^*}{(k+1-p^*-d^*)^2} & \frac{-kp^*}{(k+1-p^*-d^*)^2} \\ m_{pd} & -m_{dn} \end{bmatrix}.$$

By solving associated characteristic equation $|J_2 - \lambda I| = 0$, Eigen values are calculated. For existence of saddle node bifurcation around equilibrium point E_2, the Eigen value must be Zero i.e., $(\lambda = 0)$. The Eigen vector which satisfies the condition is:

$$J_2 \cdot \mathbf{U} = 0.$$

The corresponding Eigen vector is $\mathbf{U} = \begin{bmatrix} uu_2 \\ u_2 \end{bmatrix}$ where $u = \frac{m_{dn}}{m_{pd}}$ and $u_2 \neq 0$.

Similarly, we obtained another Eigen vector $\mathbf{V} = \begin{bmatrix} v_1, & v_2 \end{bmatrix}^T$ corresponds to Eigen value $(\lambda = 0)$ of matrix ${J_2}^T$ which satisfied the following equations:

$$\begin{bmatrix} \frac{-kp^*}{(k+1-p^*-d^*)^2} & m_{pd} \\ \frac{-kp^*}{(k+1-p^*-d^*)^2} & -m_{dn} \end{bmatrix} \begin{bmatrix} v_1 \\ v_2 \end{bmatrix} = 0$$

We get Eigen vector as follows $\mathbf{V} = \begin{bmatrix} vv_2 & v_2 \end{bmatrix}^T$ Where $v = \frac{m_{pd}(k+1-p^*-d^*)^2}{p^*k}$ and $v_2 \neq 0$. The model (2.2) can be written in the following vector form:

$$\frac{d\mathbf{X}}{dt} = \mathbf{F}(X),$$

where $\mathbf{X} = \begin{bmatrix} p & d \end{bmatrix}^T$ and $\mathbf{F} = [f \quad g]^T$. Here, f and g are RHS of the model equations (2.2). Now, from the model equations, the following is obtained:

$$\mathbf{F}_{m_{pd}}(E_2, m_{pd}) = \begin{bmatrix} -p^* \\ p^* \end{bmatrix}.$$

This is the critical condition for existence of saddle node bifurcation. Now, from the above, we have:

$$\mathbf{V}^T \cdot \mathbf{F}_{m_{pd}}(E_2, m_{pd}) = (1 - v)v_2 p^* \neq 0. \tag{2.3}$$

Hence, it satisfied the first condition of saddle node bifurcation of Sotomayor's theorem [17]. To satisfy the second condition, we have:

$$D^2\mathbf{F}(E_2, m_{pd}) \cdot (\mathbf{U}, \mathbf{U}) = \left[-\frac{u^2u_2^2k}{(k+1)^2} - \frac{4uu_2^2p^*k}{(k+1-p^*-d^*)^2} - \frac{2u_2^2p^*k}{(k+1-p^*-d^*)^3} \right].$$

From the above, the following conditions are holds:

$$\begin{aligned} &\mathbf{V}^T \cdot \left[D^2\mathbf{F}(E_2, m_{pd}) \cdot (\mathbf{U}, \mathbf{U}) \right] \\ &= -\frac{vv_2ku^2u_2^2}{(k+1)^2} - \frac{4uvv_2ku_2^2p^*}{(k+1-p^*-d^*)^2} - \frac{2vv_2ku_2^2p^*}{(k+1-p^*-d^*)^3} \neq 0. \end{aligned} \tag{2.4}$$

From equations (2.3) and (2.4), it is clear that saddle-node bifurcation exists around the equilibrium point E_2 with respect to parameter m_{pd} in the conventional NPD model (2.2).

2.4. **Numerical Verification.** For numerical verification, we assume the following parameters values (Par) and initial conditions (IC) as follows: $\mathrm{IC} : p = 0.1358, d = 0.549$ and $\mathrm{Par} : m_{pn} = 0.5, m_{pd} = 0.05, m_{dn} = 0.06, k = 0.3.$

The equilibrium point $p^* = 0.3454, d^* = 0.2878$ is gone through the saddle-node bifurcation around the parameter $m_{pd} = 0.26$. The bifurcation diagram with respect to parameter m_{pd} is drawn in the Fig. 1. The change in stability is quite clear at parameter $m_{pd} = 0.26$. Here, we present stable solution in positive direction (see Fig. 1) while unstable solutions can be produced in negative direction (not shown here). Thus, the saddle-node bifurcation exist around the equilibrium point E_2 at the parameter m_{pd}.

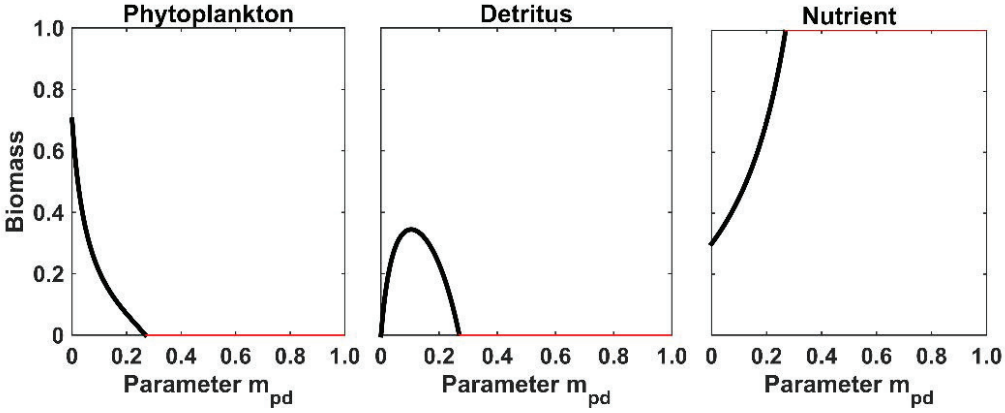


FIGURE 1. The stable solution changed at a particular point due to occurrence of saddle-node bifurcation.

3. RESULTS AND DISCUSSION

3.1. **Time Series Analysis.** Time series are drawn for two cases: i) P-dominating (P-high) and ii) P-non-dominating (P-low) at different perturbations β in the figures Fig. 2(a) and Fig. 2(b).

P-High IC: $\mathrm{p} = 0.5014, \quad d = 0.1569, n2 = 0.308, p2 = 0.0129, d2 = 0.0304, np = 0.0630, pd = 0.0198$

Par: $m_{pn} = 0.5, m_{pd} = 0.02, m_{dn} = 0.04, k = 0.8$

P-Low IC: $\mathrm{p} = 0.1358, \quad d = 0.5492, n2 = 0.0977, p2 = 0.043, d2 = 0.15, np = 0.06488, \mathrm{pd} = 0.0541$

Par: $m_{pn} = 0.5, m_{pd} = 0.05, m_{dn} = 0.06, k = 0.3$

The time series drawn in the Fig. 2(a) and Fig. 2(b) with above initial conditions and parameter sets, it is evident that P-biomass is higher in closure model than the conventional NPD model. Moreover, P-biomass increases with increase in perturbations in NPD model. The result is robust (independent of parameter choice) as same qualitative behavior is obtained for other parameter sets. It implies that intermittency enhances coexistence and support higher trophic levels.

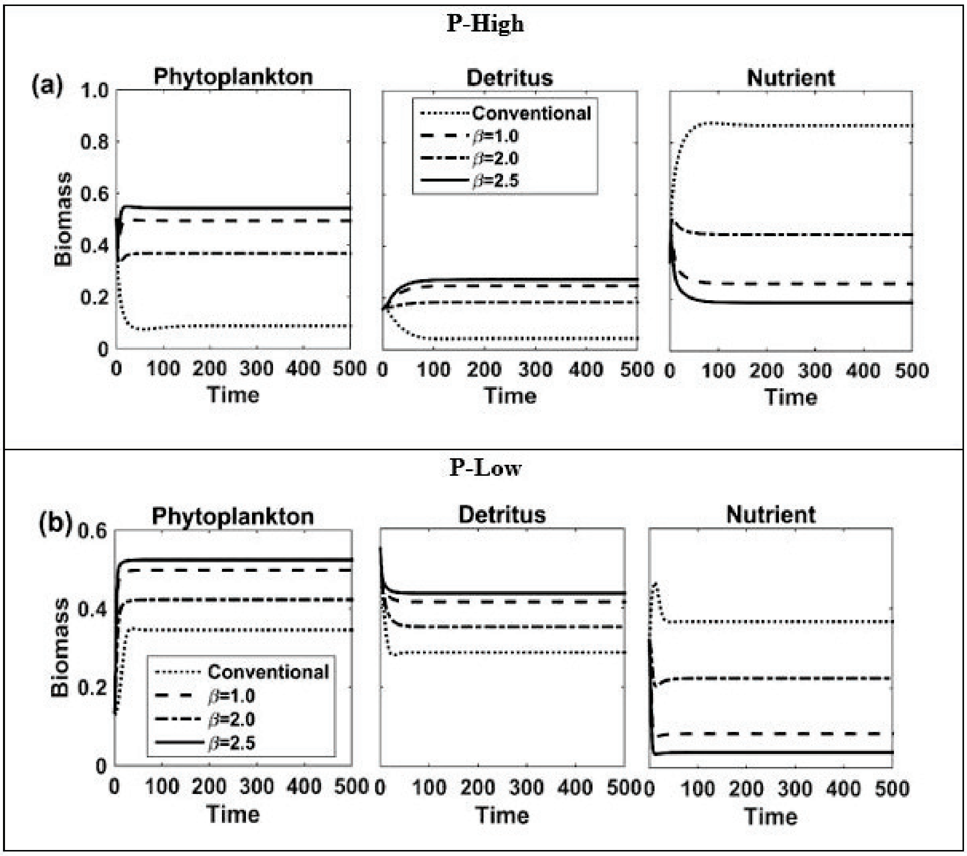
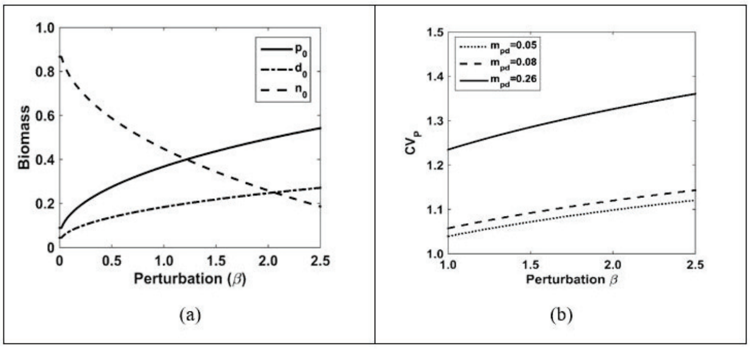


FIGURE 2. Variation in biomasses w.r.t. time for conventional and closure NPD model with increasing level of perturbation as assuming both conditions as either P-High (a) or P-Low (b).

3.2. **Perturbation's impact on biomass and CVp of phytoplankton.** Perturbation occurs in planktonic variables due to driven various processes such as physical (light variation, turbulence and advection) and biological (nutrient uptake, respiration, excretion and mineralization). Our findings show that the perturbations enhanced P-biomass while N-biomass is decreases gradually (see fig. 3(a)). The observed phytoplankton data in Fluorescence profile calibrated into mean and standard deviation and the coefficient of variations of phytoplankton CVp [11] is calculated. The NPD model for suitable parameter choice produce a similar pattern of CVp with perturbation [12]. We find that a positive association between perturbations and CVp in NPD model. The CVp increases with perturbations (see fig. 3(b)). Obtained results indicate that top-level (higher trophic level) can controls the flux of nutrients and storage of dead organic material within bottom level.



(a) (b)

FIGURE 3. **The variation over perturbation: (a) represents biomass variation and (b) represents the variation of (CVp) of phytoplankton with closure NPD model.**

CONCLUSION

The conventional way of modeling which is based on mean-field approach may be suitable for macro-scale or bigger scale but not appropriate for micro-scale spatially distributed phytoplankton. The closure modeling approach is more appropriate for micro-scale where fluctuations against the mean dominates. The flux of nutrients in water and the substantial flux of dead cell as detritus components which aggregates on lower trophic level, are controlled by turbulence or perturbation which is exerted by physical and biological processes. Using Reynolds decomposition from turbulence theory is applicable to observe the impact of perturbations on plankton ecosystem. Our findings suggest that perturbations essentially enhance the higher trophic levels biomass (P-biomass) and support coexistence. This results are consistent with perturbation and satisfied the robust pattern as previous findings. Recycling processes can extend stability and supports coexistence of planktonic species. Perturbations lead higher CVp and may sustain for greater biodiversity within planktonic ecosystems. Therefore, closure modeling approach is beneficial to understand the dynamics of planktonic ecosystem at micro-scale.

REFERENCES

[1] M.J. FASHAM, H.W. DUCKLOW, S.M. MCKELVIE: *A nitrogen-based model of plankton dynamics in the oceanic mixed layer*, J. Mar. Res., **48**(3) (1990), 591-639.

[2] C. SOLIDORO, R. PASTRES, G. COSSARINI: *Nitrogen and plankton dynamics in the lagoon of Venice*, Mar. Ecol. Prog. Ser., **184**(1) (2005), 103-123.,

[3] N.L. GOEBEL, C.A. EDWARDS, J.P. ZEHR, M.J. FOLLOWS, S.G. MORGAN: *Modeled phytoplankton diversity and productivity in the California Current System*, Mar. Ecol. Prog. Ser., **264** (2013), 37-47.

[4] P.J. FRANKS: *Coupled physical-biological models in oceanography*, Rev. Geophys, **33**(S2) (1995), 1177-1187.

[5] W. FENNEL, T. NEUMANN: *Coupling biology and oceanography in models*, AMBIO: A Journal of the Human Environment, **30**(4) (2001), 232-236.

[6] F. AZAM, T. FENCHEL, J.G. FIELD, J.S. GRAY, L.A. MEYER-REIL, F. THINGSTAD: *The ecological role of water-column microbes in the sea*, Mar. Ecol. Prog. Ser., **10**(3) (1983), 257-263.

[7] M. ZIMMER: *Detritus*, Encyclopedia of Ecology (eds S.E. Jorgensen and B.D. Fath), Elsevier (2008), 903-913.

[8] R.C. DUGDALE, J.J. GOERING: *Uptake of new and regenerated forms of nitrogen in primary productivity*, Limnol. Oceanogr, **12**(2) (1967), 196-206.

[9] C. GRENZ, J. E. CLOERN, S.W. HAGER, B.E. COLE: *Dynamics of nutrient cycling and related benthic nutrient and oxygen fluxes during a spring phytoplankton bloom in South San Francisco Bay (USA)*, Ecol. Model, **197** (2000), 67-80.

[10] N.J. ANTIA, P.J. HARRISON, L. OLIVEIRA: *The role of dissolved organic nitrogen in phytoplankton nutrition, cell biology and ecology*, Novi Sad J. Math., **30**(1) (1991), 1-89.

[11] M.J. DOUBELL, H. YAMAZAKI, H. LI, Y. KOKUBU: *An advanced laser-based fluorescence microstructure profiler (TurboMAP-L) for measuring bio-physical coupling in aquatic systems*, J. Plankton Res., **31**(12) (2009), 1441-1452.

[12] A. PRIYADARSHI, S. MANDAL, S.L. SMITH, H. YAMAZAKI: *Micro-scale variability enhances trophic transfer and potentially sustains biodiversity in plankton ecosystems*, J. Theor. Biol., **412** (2017), 86-93.

[13] A. PRIYADARSHI, S.L. SMITH, S. MANDAL, M. TANAKA, H. YAMAZAKI: *Micro-scale patchiness enhances trophic transfer efficiency and potential plankton biodiversity*, Sci. Rep., **9**(1) (2019), 1-9.

[14] S. MANDAL, H. HOMMA, A. PRIYADARSHI, H. BURCHARD, S.L. SMITH, K.W. WIRTZ, H. YAMAZAKI: *A 1D physical-biological model of the impact of highly intermittent phytoplankton distributions*, J. Plankton Res., **38**(4) (2016), 964-976.

[15] R. CHANDRA, A. PRIYADARSHI: *Impact of higher central moment approximations in system of differential equations,* AIP Conf. Proc., **1975**(1) (2018), 030023.

[16] S. MANDAL, C. LOCKE, M. TANAKA, H. YAMAZAKI: *Observations and models of highly intermittent phytoplankton distributions,* PloS one, **9**(5) (2014), 250-261.

[17] L. PERKO: *Differential equations and dynamical systems,* Springer Science and Business Media 7 (2013).

DEPARTMENT OF MATHEMATICS,
INSTITUTE OF SCIENCE
BANARAS HINDU UNIVERSITY,
VARANASI-221005, INDIA.

DEPARTMENT OF MATHEMATICS,
INSTITUTE OF SCIENCE
BANARAS HINDU UNIVERSITY,
VARANASI-221005, INDIA.
Email address: `anupam240@gmail.com`