A Minimal Model for Plankton Dynamics in Shallow Coastal Lagoons – Chilika Lagoon, A Case Study

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ABSTRACT
In the present study, a mathematical model (NPZD) based on the four compartments Nutrient (N), Phytoplankton (P), Zooplankton (Z) and Detritus (D), is proposed for understanding the ecology of shallow coastal lagoons. Model is simulated for the two cases of detritus link with the system: i) through remineralization and ii) through remineralization and palatability of detritus to zooplankton. Numerical experiments show that the growth rate and nutrient input are the main controlling factors and provide the critical parameters for which the system is stable. Addition of detritus to NPZ model is found to change the dynamics of the system significantly. Remineralization rate is found to be more crucial than palatability of detritus to zooplankton. As a case study, the model is applied to Chilika Lagoon ($19^0 28$'N-$19^0 54$'N and $85^0 06$'E-$85^0 36$'E), the largest lagoon on the east coast of India. A fine tuning of model parameters was done in order to validate the model with observations.

Keywords: NPZD ecological model, Nutrients, Plankton, Detritus, Chilika Lagoon.

1. INTRODUCTION

Shallow coastal lagoons are highly productive systems with large concentrations of species like algae, plankton and fish. They are also nutrient rich since they accumulate most anthropogenic/man-made pollutants and are liable to become eutrophic. Limiting eutrophication processes and their effects is essential for limiting the economic damage to aquaculture and tourism industries. Understanding the processes which affect the plankton population can prove to be very helpful in planning control strategies for coastal environment management. Along with direct measurements made *in situ* and satellite information for plankton it is essential to construct models which, when validated with observed data can be used for prediction of the marine ecosystem structure.

There has been a lot of advancement in modeling the dynamics of the flow in lagoons, estuaries and coastal areas but modeling the ecology of the natural aquatic environments is relatively new. There are several difficulties in building up an ecological model, firstly, because the ecological models do not have a prescribed starting point in terms of standard equations and, secondly, because the variance associated with any set of data is usually very much greater than the mean. A simple and common ecological model, known as NPZ (Nutrient-Phytoplankton-Zooplankton) model, is based on only three primary dependent systems: phytoplankton, herbivorous zooplankton and the nutrient system [1–4]. More species or further complexities are included depending on the need for more realistic simulations.

Models used to simulate the dynamics of the ecosystem range from the most basic NPZ to more complex formulations that include more than one compartment at each trophic level, their size structure, dissolved organic material, detritus and bacteria [5–6]. In our previous paper [7] we used a three-compartment model (NPZ) to explain the seasonal variability of plankton in coastal lagoons. The present paper is motivated by the need to include the detritus component which can play a significant role in the plankton dynamics of shallow coastal lagoons where the supply of nutrients from the benthic region can be very important [5, 6, 8–11]. Unlike the ocean environment where much of the detritus may sink out of the mixed layer, in a shallow basin, the dead organic matter may be in the photic zone itself and there may be a close interaction between the materials at the bottom and the water column.

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Also, detritus is recycled by the remineralization process and is converted into nutrients thus adding to the nutrient content of the water body. In order to study the role of detritus cycling in coastal eco-dynamics, a four compartment NPZD [Nutrient-Phytoplankton-Zooplankton-Detritus] model is proposed. Several numerical experiments followed by sensitivity analysis are made for the general model. Finally, the model is used to study the ecology of Chilika lagoon ($19^0 28$'N-$19^0 54$'N and $85^0 06$'E-$85^0 36$'E), the largest brackish water lagoon in India.

In the next section, the mathematical formulation of the model is presented. Details of numerical experiments and parameter sensitivity are given in section 3. In section 4, the model is validated with data from Chilika Lagoon. The study area, its physical, dynamical and ecological characteristics as well as the need for studying the dynamics of its ecosystems are also explained. Finally, important conclusions based on the study are given in section 5.

2. MODEL FORMULATION

A mathematical model (NPZD) based on the four compartments (Nutrient (N), Phytoplankton (P), Zooplankton (Z) and Detritus (D)) is proposed for understanding the ecology of shallow coastal lagoons. The interactions between the compartments are outlined in Figure 1. The arrows indicate flow of matter between different compartments. The model equations are

$$\frac{dN}{dt} = -\frac{\alpha(t) N P}{K_N + N} + rP + \phi D + \left[\frac{m}{H(t)}\right] N_1(t) + \frac{Q}{V} N_2(t) \tag{1}$$

$$\frac{dP}{dt} = \frac{\alpha(t) N P}{K_N + N} - rP - \left[\frac{p_1 P}{A}\right]\left[\frac{c(A - A_0) Z}{K_Z + A - A_0}\right] - \left[\frac{\mu P}{K + P}\right] P \tag{2}$$

$$\frac{dZ}{dt} = \left[\frac{e\,c(A - A_0) Z}{K_Z + A - A_0}\right] - g \times Z \tag{3}$$

$$\frac{dD}{dt} = \left[\frac{\mu P}{K + P}\right] P - \phi D + \left[\frac{p_1 P}{A}\right]\left[\frac{(1-e)\,c(A - A_0) Z}{K_Z + A - A_0}\right] - \left[\frac{p_2 D}{A}\right]\left[\frac{e\,c(A - A_0) Z}{K_Z + A - A_0}\right] \tag{4}$$

All the parameters along with their units and ranges are given in Table 1. Units of N, P, Z and D are in μg/l and time unit is in days. The parameterization used in choosing the terms in equs (1) - (4) is explained in sections (2.1) - (2.4).

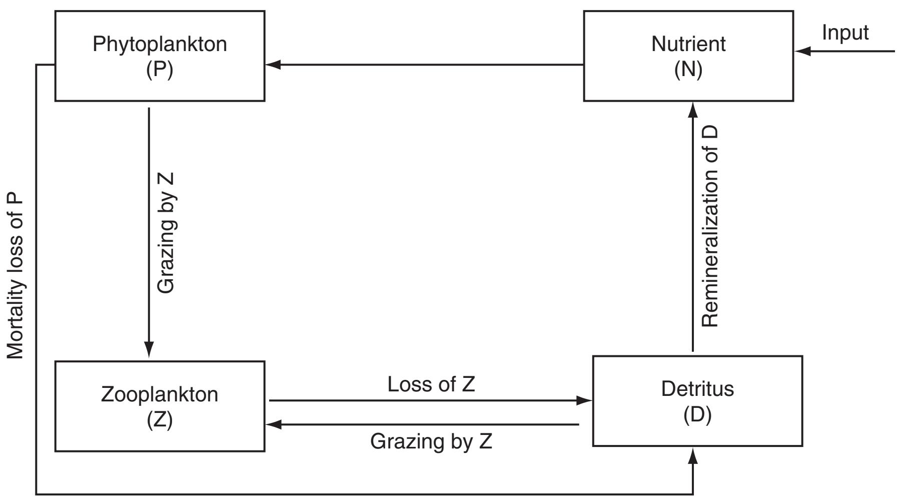


Figure 1. Schematic diagram of the model variables: Nutrient (N), Phytoplankton (P), Zooplankton (Z) and Detritus (D) in ecosystem. Arrows indicate the flow of matter through the system.

Table 1: Parameter values used in the model

Parameters	Symbols and units	Range based on numerical experiments	Assigned Values at site A_1	Assigned Values at site A_2	Assigned Values at site A_3
Phytoplankton coefficients					
Amplitude of annual growth rate oscillation	b_1 (d^{-1})	0.004-0.017	0.017	0.01	0.008
Loss rate of P due to metabolic and respiration loss	r (d^{-1})	0.1-0.2	0.18	0.12	0.135
Half saturation constant for Nutrient uptake by P	K_N (μg/l)	10-15	14	10	10
P mortality rate	μ (d^{-1})	0.028-0.05	0.028	0.03	0.03
P mortality half saturation constant	K (μg/l)	10-20	20	15	13
Zooplankton Coefficients					
Assimilation efficiency	e	0.5-0.85	0.81	0.83	0.76
Grazing rate	c (d^{-1})	0.045-1.4	0.073	0.052	0.06
Grazing half saturation constant	K_Z (μg/l)	10-30	19	18	22
Relative grazing preference for P	p_1	1	1	1	1
Relative grazing preference for D	p_2	0.1-0.7	0.42	0.42	0.42
Grazing threshold	A_0 (μg/l)	6-12	8.0	10	11
Zooplankton Loss rate	g (d^{-1})	0.015-0.035	0.028	0.03	0.03
Detritus coefficients					
Detritus remineralization rate	Φ (d^{-1})	0.004-0.2	0.035	0.06	0.06
Nutrients coefficients					
Nutrient source	N_1(μg/l)	90-200	150.89	107.95	91.25
Depth	$\bar{H}$(m)	1.5-2.5	1.5	2.0	2.5
Vertical diffusion rate	m (md^{-1})	0.03-0.09	0.045	0.045	0.053

2.1. Phytoplankton

Equ (2) represents the rate equation for Phytoplankton whose growth is mainly controlled by light and nutrient concentration. Its biomass decreases due to grazing by zooplankton and its natural mortality.

2.1.1. Growth Rate

The first term $\dfrac{\alpha(t)N}{K_N+N}$ represents average daily light limited specific growth rate of phytoplankton. $\dfrac{N}{K_N+N}$ (Holling type II) represents nutrient limitation with half saturation constant K_N. Observations of the lagoon ecosystems suggest seasonal variability with pronounced spring/summer maximum in primary production. The sudden dip in the algal biomass after a peak is partly due to the depletion of the available nutrients. In this model, following Steffen et al. [12], the phytoplankton growth rate $\alpha(t)$ is prescribed to change periodically over a period of a year in order to implement annual changes of temperature and light, i.e.,

$$\alpha(t) \quad = \bar{\alpha} - b_1 \cos\left[\frac{2\pi t}{360}\right] \tag{5}$$

where $\bar{\alpha}$ is calculated using the formulae proposed by Smith [13] and recommended by Jassby and Platt [14] and Evans and Parslow [1]. This rate is based on different values of the low light photosynthetic slope, maximum photosynthetic rate and light attenuation by phytoplankton. More details are given in [1]. 'b_1' is the amplitude of the annual growth rate oscillation.

2.1.2. Loss Rate

r(d^{-1}), represents decrease in phytoplankton biomass due to metabolic and respiration loss. This term is recycled into the system and contributes to add to the nutrients.

2.1.3. Grazing Rate

A Michaelis-Menten equation is used to parameterize the effect of food levels on zooplankton grazing rate. The zooplankton grazing on phytoplankton and detritus is parameterized as $\left[\frac{p_1 P}{A}\right]\left[\frac{c(A-A_0)Z}{K_Z+A-A_0}\right]$ and $\left[\frac{p_2 D}{A}\right]\left[\frac{c(A-A_0)Z}{K_Z+A-A_0}\right]$ respectively. A is a measure of total food perceived by the zooplankton defined as

$$A = p_1 P + p_2 D. \tag{6}$$

p_1 and p_2 are the preferences of zooplankton for P and D respectively. Even if one of the food components decreases, the food will be grazed provided the other component is abundant. A_0 is the grazing threshold applied to total food. c is the grazing rate and K_z is the half saturation constant for grazing (same values fixed for both the food components).

2.1.4. Mortality Rate

Phytoplankton natural mortality follows Michaelis - Menten kinetics and is defined as $\left[\frac{\mu P}{K+P}\right]P$ (Holling type II). μ is the specific mortality rates and K, is the mortality half saturation constant.

2.2. Zooplankton

Equ (3) represents the rate equation for Zooplankton. The first term represents total (P and D) zooplankton grazing and the second corresponds to loss term by its natural and predator mortality. Zooplankton has two alternate food sources P and D with different palatabilities, p_1 and p_2. Since, zooplankton can not assimilate the whole grazed food, the parameter *'e'* representing the assimilation efficiency (same value is assigned for both P and D) is introduced. The parameterization involved in this term is already explained in 2.1.

2.3. Nutrients

Equ (1) is the rate equation for nutrients. The first term represents loss in nutrient concentration due to uptake by phytoplankton. Second term is increase in concentration due to metabolic and respiration loss of phytoplankton. ϕD, represents addition of detritus due to remineralization, ϕ being the remineralization rate. $\frac{mN_1(t)}{H(t)}$, is addition of nutrient into the system through vertical diffusion through sediments at depth $H(t)$, where $N_1(t)$ is sediment nutrient concentration and m is the vertical mixing rate (metres per day). The depth is set to vary with time to account for the seasonal variability and it is parameterized as

$$H(t) \; = \bar{H} - b_2 \cos\left[\frac{2\pi t}{360}\right] \tag{7}$$

where $\bar{H}$ is the average depth for the whole year. 'b_2' represents amplitude of annual depth of oscillation.

The last term, $\frac{Q}{V}N_2(t)$, calculated as the product of flow rate and concentration of nutrients brought by the river flow and divided by the volume of the region [15], represents addition of nutrient in the system through river runoff. Q is freshwater flow of river, V is the volume of the region and N_2(t) is external loading of nutrients with river runoff through that region. In general, nutrient load refers to total amount of nutrients (mostly nitrogen or phosphorus) entering the water from runoff, groundwater, or the air during a given time. Further, using the annual mean and the seasonal amplitude of the nutrient load, its seasonal variability is parameterized [16] as

$$\frac{Q}{V}N_2(t) = \text{Annual mean } + \text{ seasonal amplitude} \times \cos\left(\frac{2\pi t}{365} - \text{phase}\right) \tag{8}$$

2.4. Detritus

It is important to write a distinct rate equation for detritus in a model for shallow lagoons. Phytoplankton mortality is the main source for the formation of detritus but, the unassimilated part of phytoplankton which is not grazed by zooplankton also goes into this compartment. The remineralization of detritus by bacteria recycles a part of the material back to the system. Accordingly, taking into consideration the foregoing discussion, equ (4) is framed as the rate equation for detritus. The first term represents increase in detritus concentration due to the mortality loss of phytoplankton, second term the loss term due to remineralization and the third term the increase in concentration due to addition of unassimilated part of phytoplankton. The last term represents loss term due to grazing by zooplankton.

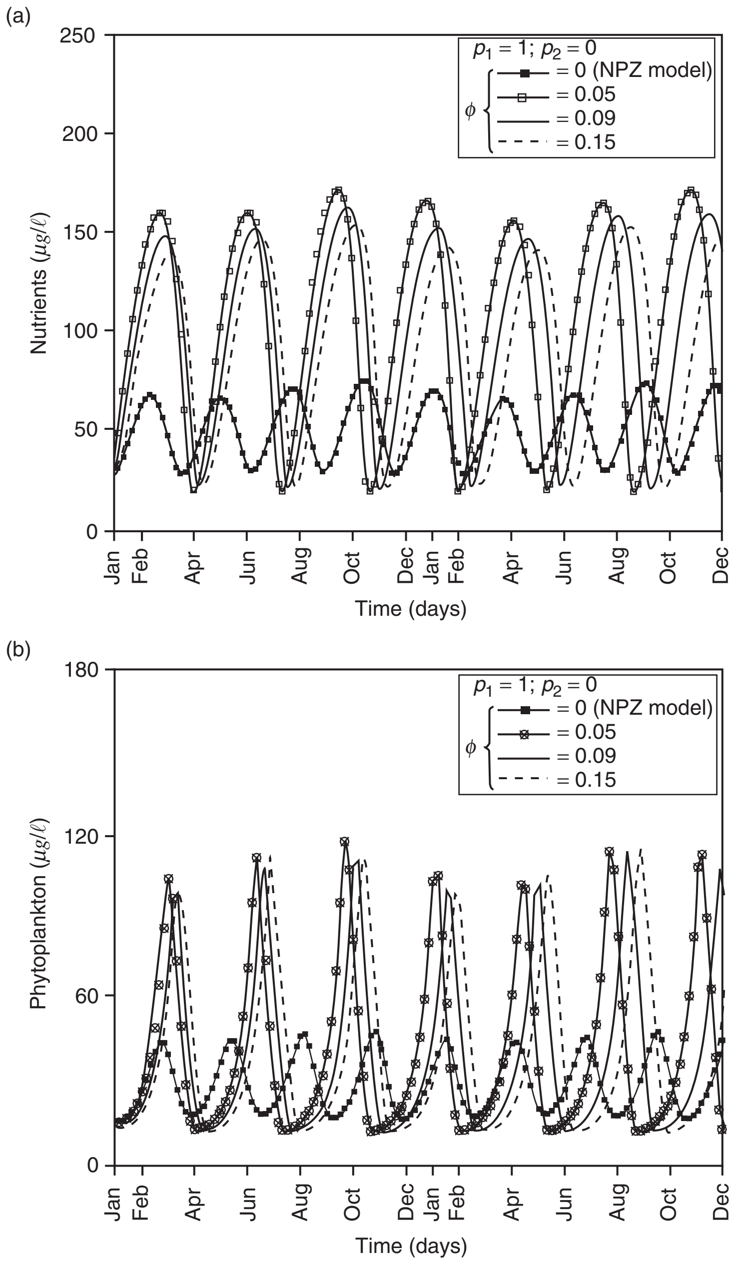
3. NUMERICAL EXPERIMENTS

An ecosystem model is largely dependent on the values of the parameters used in the model equations. Consequently, with a change in values of the parameters, a model can exhibit different dynamics. In view of this, based on the model's response to changes in their values, the parameters can be classified as critical or non-critical. Changes in the environment parameters, particularly light, nutrient availability, depth and factors like palatability associated with grazing are the controlling parameters for the non linear oscillations or distinct seasonal patterns and periodicity in plankton distribution.

The numerical experiments and sensitivity analysis help to determine the sensitivity of the model to changes in parameters and help to evaluate the behaviour of model's compartments. In the present study, 21 biological parameters are used in the model. Through the sensitivity analysis, it was found that the light limited growth rate ($\alpha(t)$), half saturation constant for nutrient uptake (K_N), m the vertical mixing rate, p_i the palatability, grazing rate (g) and $N_1(t)$ the amount of the nutrients entering into the system are the most sensitive parameters in the model. The ranges of parameters are taken from the literature [1, 5, 8, 10, 12] and could be fixed for the specific cases. For a constant value of the light limited growth rate (α), the annual plankton distribution shows periodicity with equal amplitude, whereas, dependence of α on time (equ 5) introduces bimodal oscillation. Except the parameters whose values are taken from the literature, all other parameters i.e. $\alpha(t)$, r, K_N, m etc. were varied to test the sensitivity of the results to the parameters. The ranges fixed finally are also included in Table 1. The model was run for a long time (10 years). After every 2/3 years, the profiles were found to be repeated. Changing the initial condition did not have any impact.

One of the main objectives of this paper is to study the effects of including a distinct equation for detritus compartment in the model as an improvement over the usual NPZ model. In view of this, our numerical experiments carried out with constant values of α and depth and fixed values for rest of the parameters, addressed two distinct cases: M1 and M2. M1: The detritus component gets into the food web only through remineralization. In other words, phytoplankton is the only preferred food for zooplankton and the grazing preference p_2 of zooplankton for detritus is zero. M2: Both detritus and phytoplankton are grazed by zooplankton in addition to the detritus component getting into the food web through remineralization. The two cases are discussed below:

Case M1: With $p_2 = 0$, P is the only preferable food for Z. It can be inferred from equs (1–4) that remineralization is the only contributor to linking the detritus compartment with the rest of the compartments. The loss of detritus due to remineralization is converted into utilizable nutrient thus increasing the nutrient concentration. Addition of nutrients provides more favourable condition for the phytoplankton growth and hence that of zooplankton. Figures 2(a)-(d) show the seasonal distribution of N, P, Z, D respectively for two consecutive years (for $p_1 = 1$, $p_2 = 0$ and ϕ varied alone). Since $p_2 = 0$, the only link of the detritus compartment with the rest of the equations (equs. (1) - (3)) is through non-zero values of the remineralization parameter ϕ. The range of values of ϕ found in the literature [5, 10] is between 0.04 and 0.2. When ϕ increases through small values, $(0 < \phi < 0.08)$ there is significant



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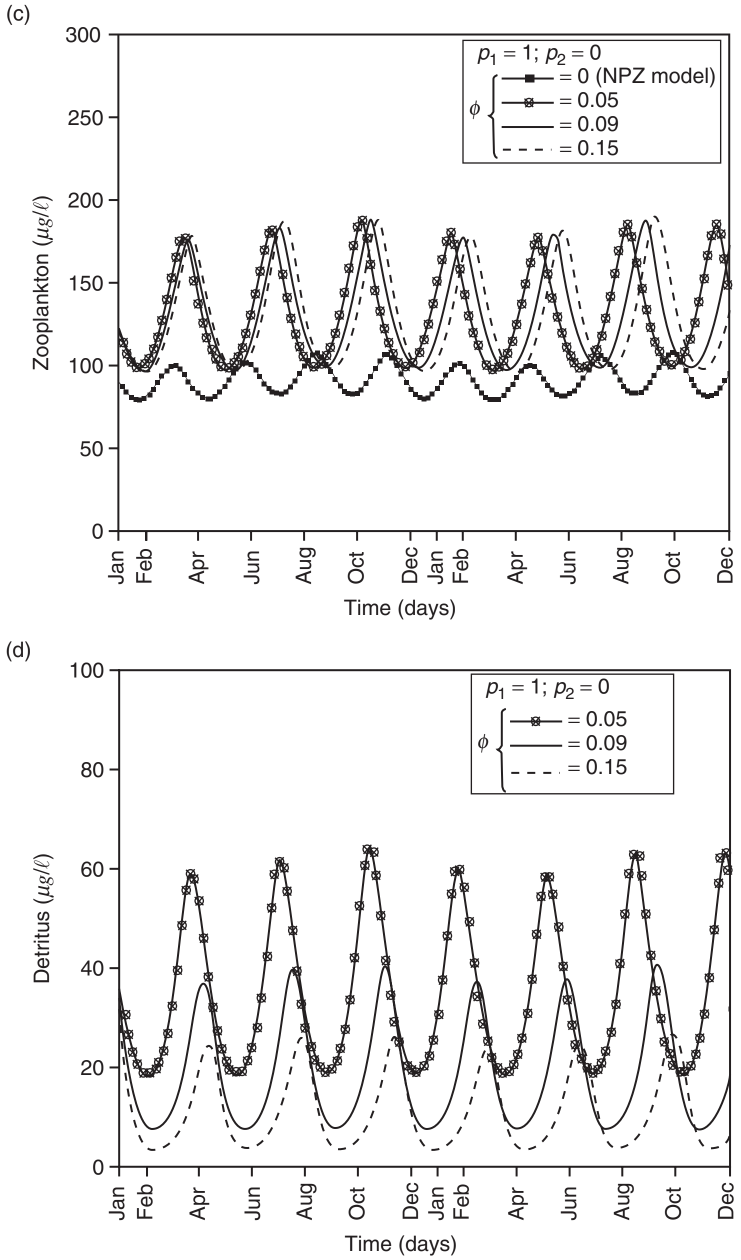


Figure 2. Seasonal variation of (a) Nutrients, (b) Phytoplankton, (c) Zooplankton and (d) Detritus with time ($p_1 = 1$, $p_2 = 0$ and ϕ varied).

increase in amplitude, peak width and length of seasonal cycles. For $0.08 < \phi < 0.2$ the system stabilises with almost uniform amplitude. There is a phase lead in nutrient distribution (Figure 2(a)) followed by those of phytoplankton (Figure 2(b)) and zooplankton (Figure 2(c)). As expected, detritus decreases with increasing values of ϕ (Figure 2(d)) since much of it is lost to nutrients due to remineralization.

Case M2: Figures 3(a)-(d) show the seasonal distribution of N, P, Z, D respectively for two consecutive years with $\phi = 0.05$ and $p_1 = 1$ and p_2 varied. When zooplankton palatability for detritus is introduced into the model through non zero values of p_2, the nutrient level goes down (Figure 3(a)) and phytoplankton too is reduced (Figure 3(b)) due to less availability of nutrients since some of detritus is directly consumed by the zooplankton. On the other hand, there is increase in Z distribution (Figure 3(c)) due to increase in value of p_2. The phase lead of nutrient distribution over those of phytoplankton and zooplankton observed in the previous case are found in this case as well. Overall the model is found to be more sensitive to ϕ than p_2.

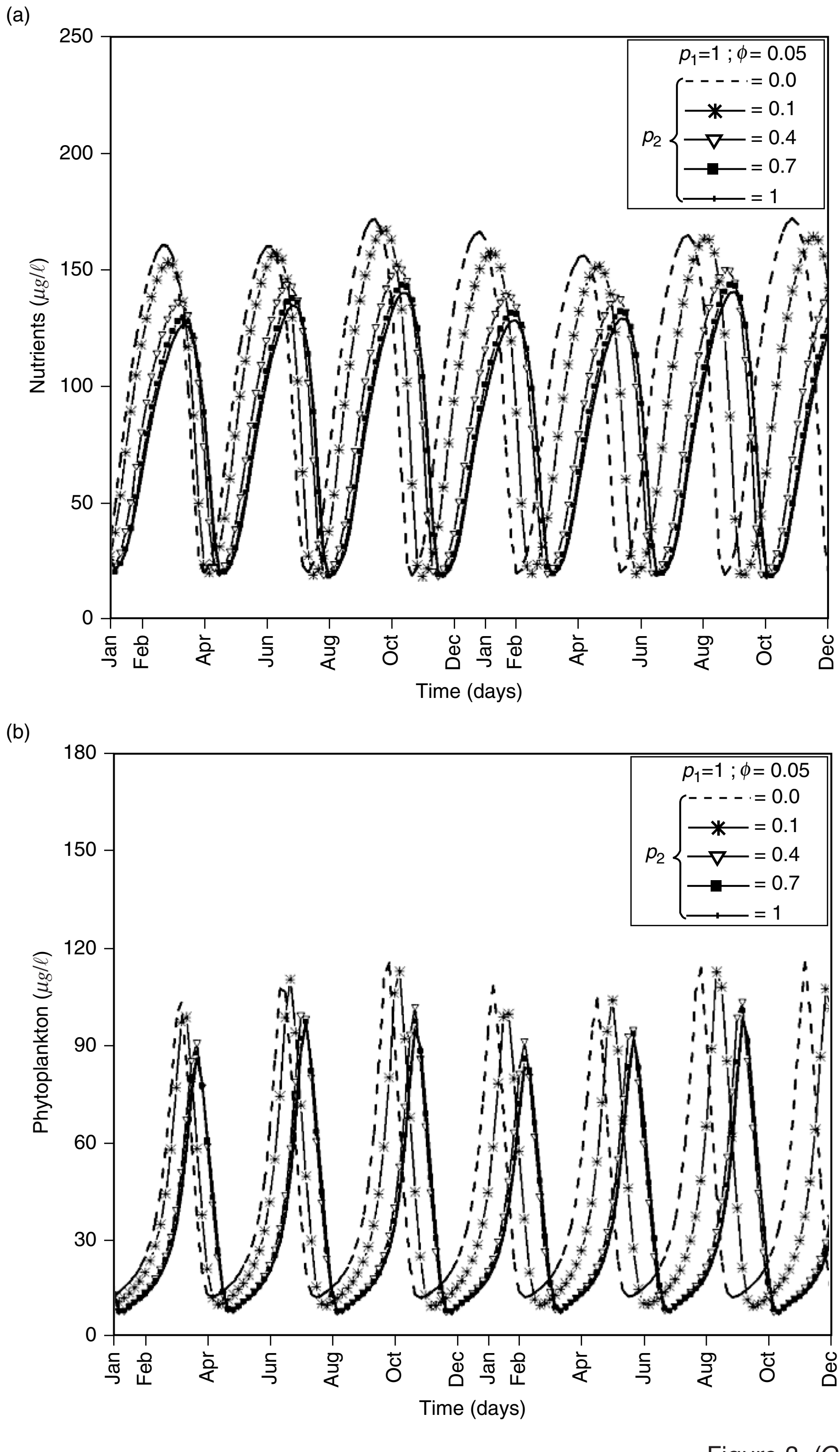


Figure 3. (*Continued*).

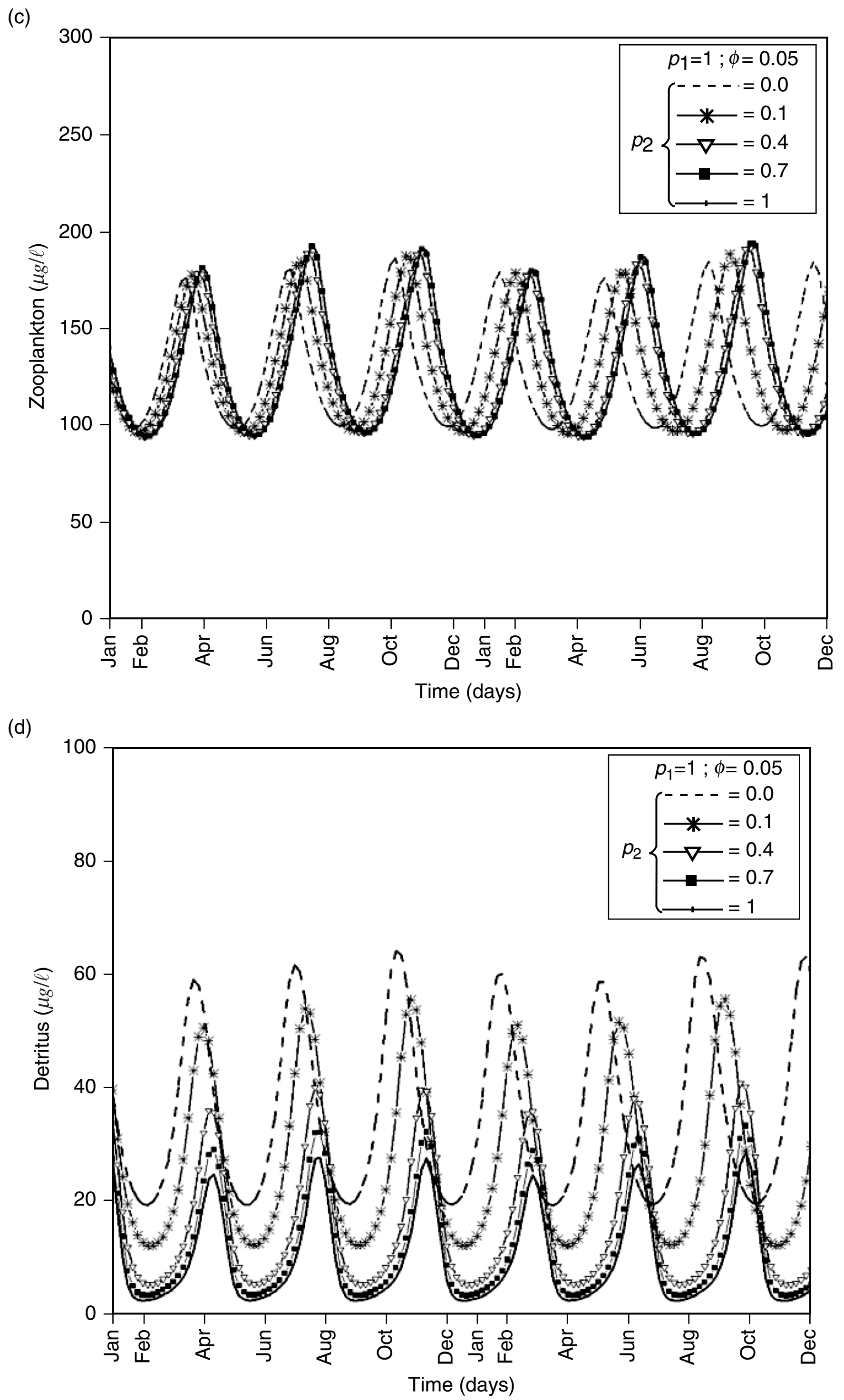


Figure 3. Seasonal variation of (a) Nutrients, (b) Phytoplankton, (c) Zooplankton and (d) Detritus with time ($\phi = 0.05$, $p_1 = 1$ and p_2 varied).

4. CASE STUDY – CHILIKA LAGOON

In this section, the mathematical model developed in section 2 is utilized for the analysis of the annual seasonal cycles of plankton, nutrient and detritus in Chilika lagoon ($19^0$28’N-$19^0$54’N and $85^0$06’E-$85^0$36’E) (Figure 4), the largest brackish water lagoon on the east coast of India. On account

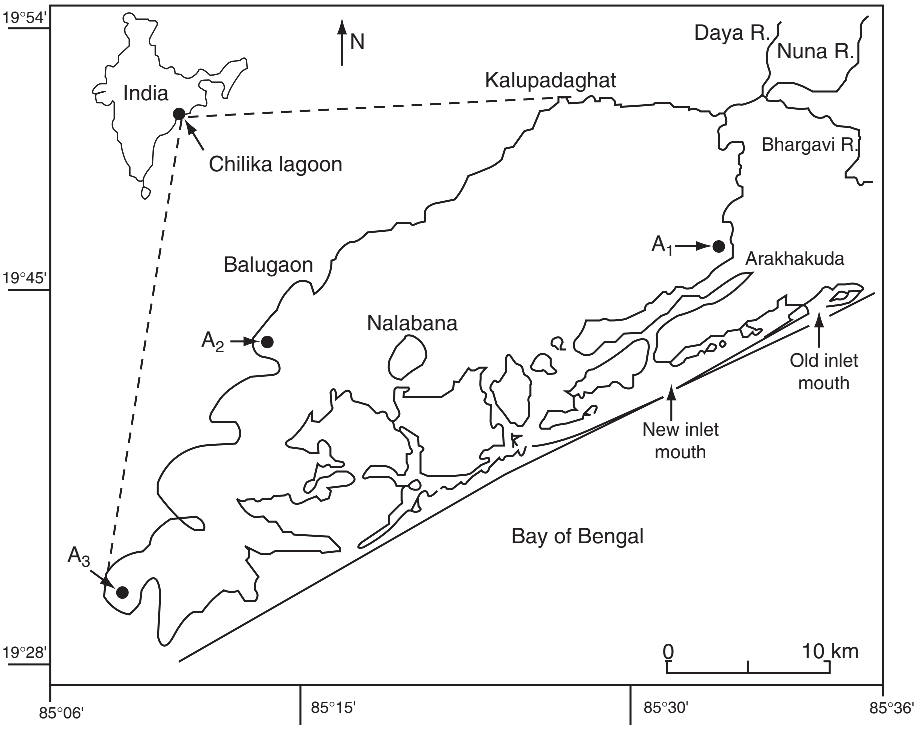


Figure 4. Map of Chilika lagoon.

of its rich biodiversity and socio-economic importance, it was designated a 'Ramsar site'-a wetland of international importance in 1981. The lagoon was added to the list of Ramsar sites in danger (the Montreux record in 1993), but following some years of innovative and exemplary remedial efforts by the Indian Government, (opening of a new mouth on 23rd September 2000 at a distance of 17 km from the existing mouth) the ecological character of the lagoon was restored and it was removed from the Montreux record on 11 November 2002 (www.chilika.com). The interest and thrust in studying the hydrodynamics and ecology of the lagoon is due to the increasing threat to it in the form of siltation, choking of the mouth connecting the lagoon to the sea, eutrophication, weed infestation, salinity changes and decrease in fishery resources [17]. A brief description of the study area and the observed data are given in sections 4.1 and 4.2 which are followed by an analysis of the ecosystem seasonal dynamics in section 4.3.

4.1. Description of The Study Area

The water spread area of the lagoon varies from 906 to 1165 km^2 during the summer (March-May) and monsoon (June-September) respectively. 52 rivers/rivulets drain enormous freshwater into the lagoon with significant load of nutrients and suspended matter. The discharge in pre-monsoon season (April-May) is $3.1 \times 10^6 m^3 d^{-1}$ and during monsoon, it is $166.8 \times 10^6 m^3 d^{-1}$ [18]. The lagoon experiences seasonal variability in the depth throughout the year and varies between 1-3.5 m. The depth is mainly controlled by the amount of freshwater influx in monsoon and tidal ingress during summer. The lagoon is separated from Bay of Bengal by a sand bar 60 km in length and width varying from 100 m to 1.5 km.

4.2. Plankton Characteristics and Description of Observed Data in Chilika Lagoon

In the present study, three specific sites: A_1 (Panaspada); A_2 (Barakul); A_3 (Rambha) (Figure 4) are chosen in the different regions of the lagoon. The choice of these sites is due to the fact that they have distinct hydrographical characteristics such as depth, salinity etc., nutrient concentrations and nutrient loading with river runoff.

The lagoon receives maximum discharge of floodwaters from the rivers and its distributaries near A_1 where it is very shallow. Site A_2 is influenced by both freshwater and marine water and is in the brackish water region. The lagoon is deepest in the neighbourhood of A_3 where it receives least amount of freshwater. The freshwater discharge due to northwestern and northeastern rivers in the northern region (near A_1) of the lagoon during monsoon and pre-monsoon seasons is approximately $157.81 \times 10^6 m^3 d^{-1}$ and $3.11 \times 10^6 m^3 d^{-1}$ respectively. In central (near A_2) and southern (near A_3) region during monsoon season discharge is approximately $6.23 \times 10^6 m^3 d^{-1}$ and $2.76 \times 10^6 m^3 d^{-1}$ respectively.

Nutrient dynamics in Chilika is mainly controlled by the addition of river runoff (June-July) and depletion caused due to uptake by phytoplankton (April-May) with maximum in rainy season and minimum in summer. More nutrient concentration was observed in A_1 where the effect of freshwater is more. Figures 5(a), 6(a) and 7(a) show the observed nutrient distribution [19] in the three sites.

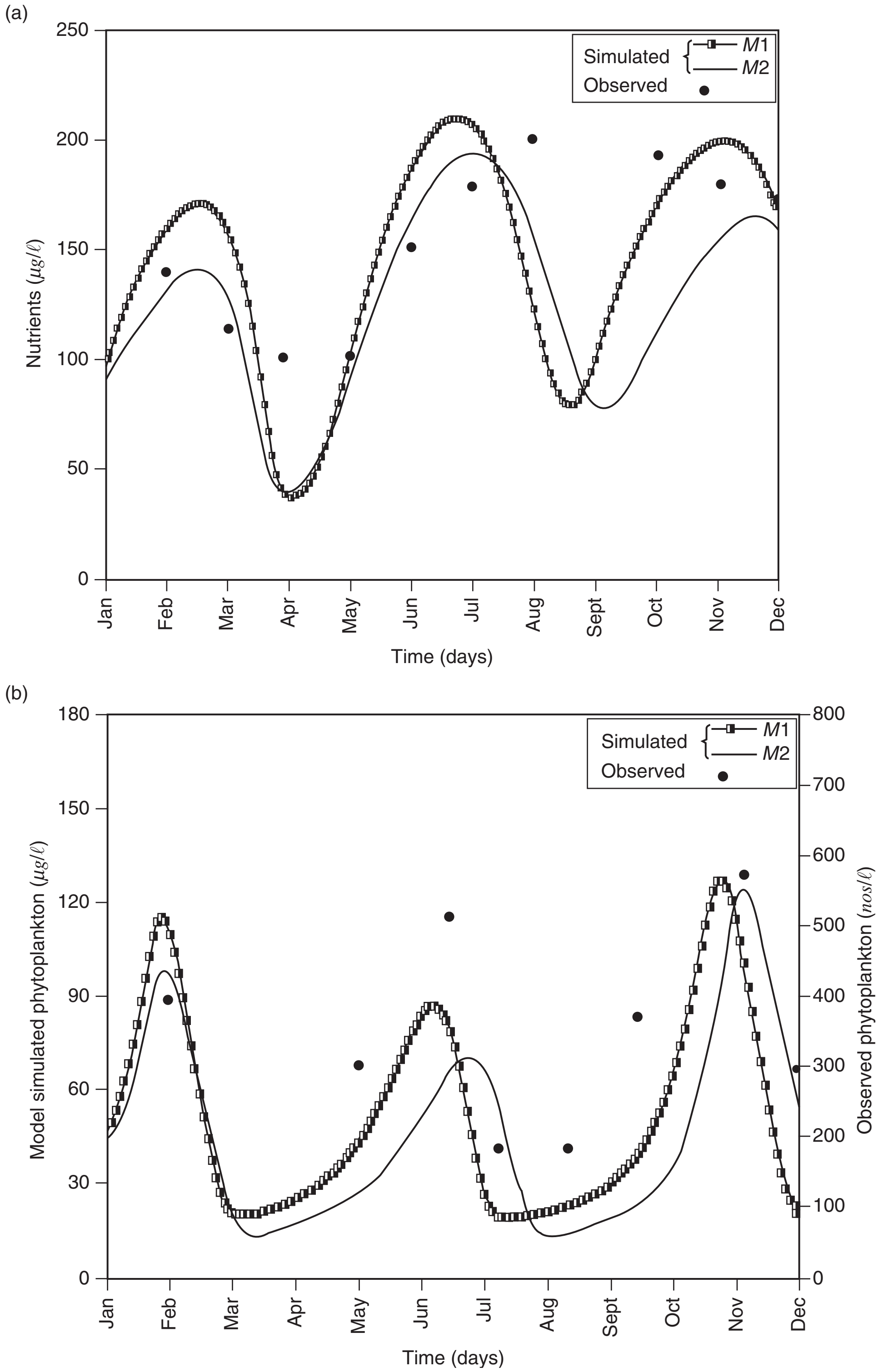
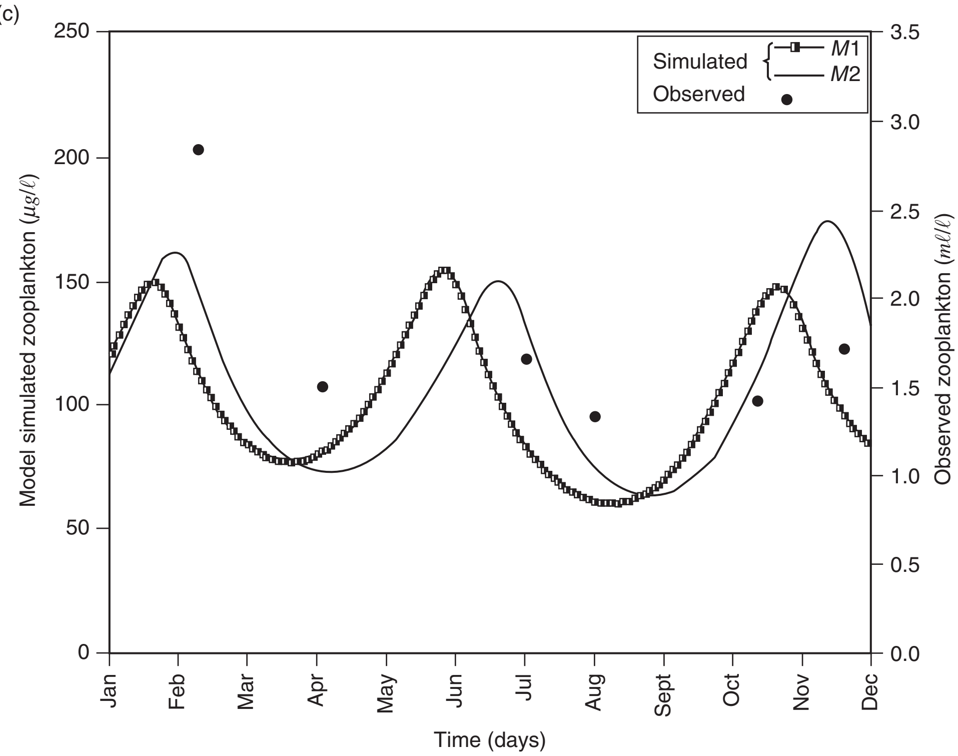


Figure 5. (*Continued*)

(c)



(d)

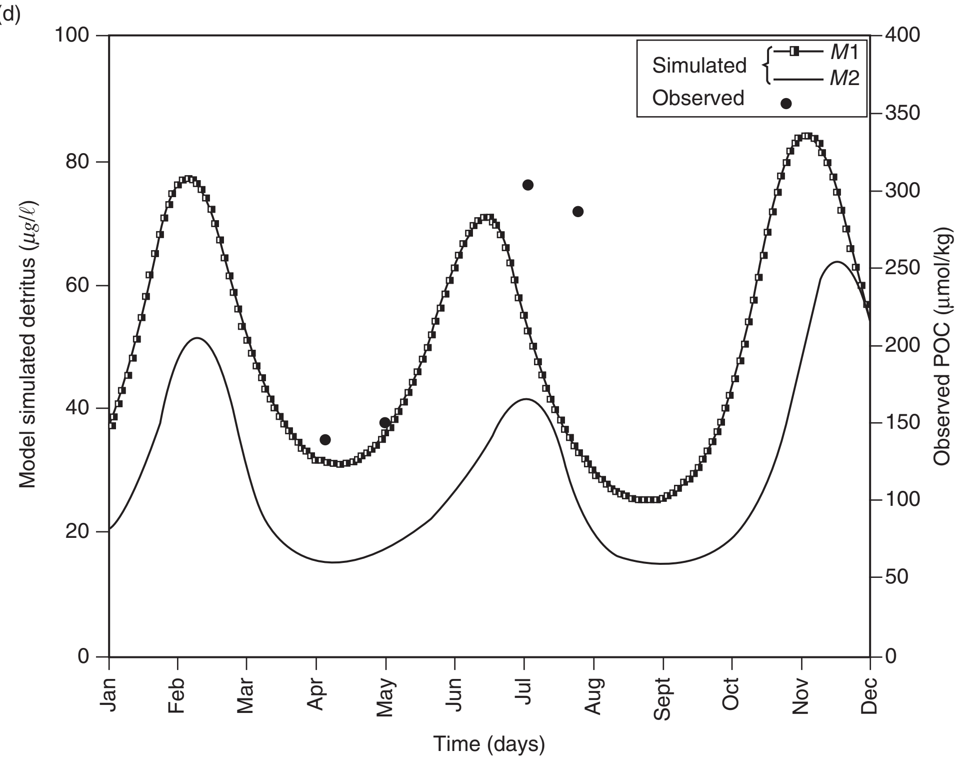


Figure 5. Annual distribution of (a) Nutrients, (b) Phytoplankton, (c) Zooplankton and (d) Detritus for M1 and M2 at site A_1.

The total biomass of phytoplankton is observed to be highest in A_3 followed by A_2 and it is lowest in A_1. The annual seasonal cycles of phytoplankton distribution show bimodal oscillations at site A_1. The observed data of phytoplankton [19] is given in Figures 5(b), 6(b) and 7(b), and data for zooplankton [20] is given in Figures 5(c), 6(c) and 7(c).

Direct measurement of detritus is quite difficult because maximum living biota coincide with it. In the absence of exact data for detritus, we have used the data for particulate organic carbon (POC) to represent detritus. The observed data of POC includes organic matter of dead organism, excretion and egestion of living organism etc. (autochthonous) and also sediment transpiration with river discharge (allochtonous). The data [18] for 2005 is available for pre-monsoon and monsoon seasons. POC concentration is high during monsoon in the neighbourhood of A_1 due to major river runoff suggesting allochthonous sources as major concentrators. Near A_3, POC concentration is high during pre-monsoon period suggesting autochthonous sources as major concentrators. Consequently, during the monsoon period, allochthonous sources dominate, whereas, during the pre-monsoon period, autochthonous sources dominate as concentrators of POC in the lagoon. Although the data is patchy, it helps to estimate the approximate concentration of detritus in the lagoon.

The observed values of phytoplankton are available as numbers per litre, for zooplankton it is in ml/l, for nutrient it is in µg/l and for POC it is in µmol/kg, whereas our model simulated results for all are obtained as µg/l. Hence, at the moment, our objective is to validate our numerical model with a qualitative comparison with the observed data.

4.3. Analysis of the Seasonal Variation of the Ecosystem Based on the Model Validation and Range of Values for the Parameters

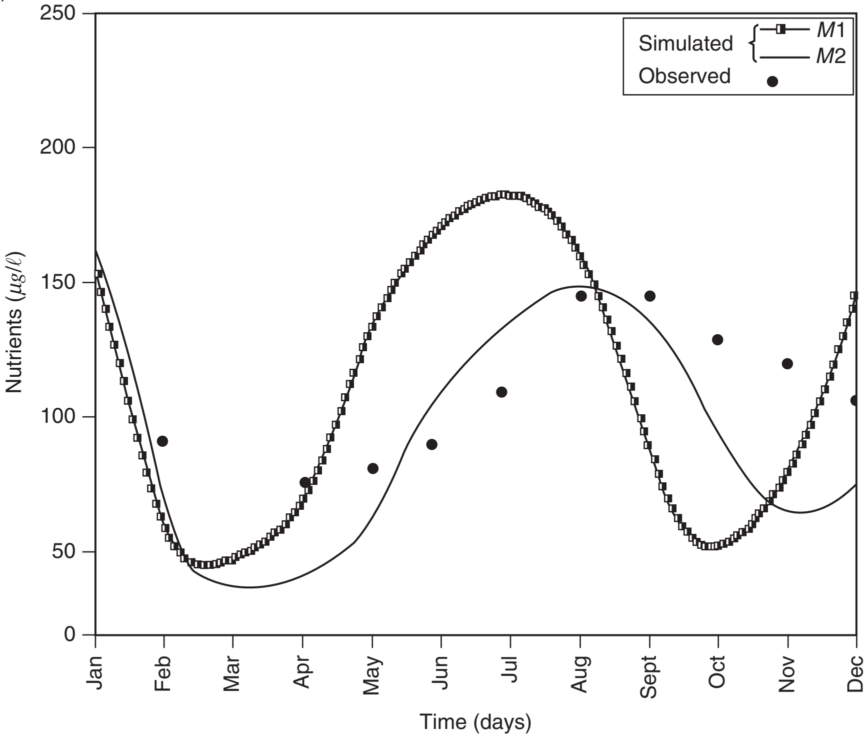
Parameters which required tuning in order to validate the model results were: r, K_N, m, c, K_Z, A_0, K, e, ϕ and g. Following our numerical experiments where we tested the sensitivity of the model to the linkage of detritus with rest of the system, we ran the model for the two cases M1, M2. M1: $p_1 = 1$, $p_2 = 0.0$ (i.e. remineralization is the only contributor which links detritus with the rest of the equations); and for case M2 : $p_1 = 1$ and $p_2 = 0.42$ (i.e. D links with the system through two processes : remineralization (ϕ) of D and palatability (p_2) of D to Z).

Model results for N, P, Z and D at site A_1 along with the observations are depicted in Figures 5(a) - (d). The observed values of the annual nutrient concentration show that concentration is high in February, June- August and October- November (Figure 5(a)). Model simulated results for both the cases studied capture well the peaks found in February as well as June-August, but the values are slightly underestimated during September-November. Nutrient concentration is lower in M2 because, with remineralization of D, it is also grazed by Z. Model results for phytoplankton seasonal cycles for both cases are able to capture the observed peaks, in February and October-November (Figure 5(b)) but they failed to capture accurately the second peak in June. Like nutrient, the peaks of phytoplankton distributions have lower amplitude in M2 and the results are more close to observations. Model results could capture the three distinct peaks of zooplankton distribution (Figure 5(c)). There is more abundance of zooplankton population in M2 and this increase in zooplankton population is due to more availability of food in the form of detritus. Detritus seasonal cycles follow the trend of phytoplankton (Figure 5(d)). Detritus concentration increases after the depletion of phytoplankton due to its natural mortality. It is seen that model results for nutrient, phytoplankton and zooplankton are better validated with observed data for M2.

The model results along with observed data for site A_2 are depicted in Figures 6(a)-(d). It is observed that nutrient concentration is high in monsoon and post-monsoon (October-November) seasons and highest in August-September. An increase in phytoplankton biomass which is observed in June-July for both is reproduced by the model. Zooplankton seasonal cycles based on M1 show two peaks, in March and the other in September-October, whereas, for M2 peaks are in March and October-November (Figure 6(c)). Model results of M2 underestimate zooplankton population in June and could not capture the June peak. Detritus seasonal cycles (Figure 6(d)) are seen to follow the trend of phytoplankton. Like A_1, model results for nutrient, phytoplankton and zooplankton based on M2 for A_2 are validated better with observations.

The model results along with observed data for site A_3 are depicted in Figures 7(a)-(d). It can be seen that they are very well validated with observations and could capture the peaks found in monsoon and post-monsoon periods. The highest concentrations are observed during June-August. April –May are seen to be the months of a rapid depletion of nutrients (Figure 7(a)). It is seen that phytoplankton seasonal cycles have the maximum amplitude in June-July (Figure 7(b)). February and September are seen to be months of a depletion of phytoplankton. Model results underestimate phytoplankton population in October- November. It is seen that zooplankton population shows three distinct peaks in March, June and October (Figure 7(c)). Model results could capture the two peaks in March and October (M2) but results for zooplankton seasonal cycles are underestimated by M1. Detritus seasonal cycles follow the trend of phytoplankton seasonal cycles (Figure 7(d)). Like A_1 and A_2, model results for nutrient, phytoplankton and zooplankton based on M2 at A_3 are validated better with observations.

(a)



(b)

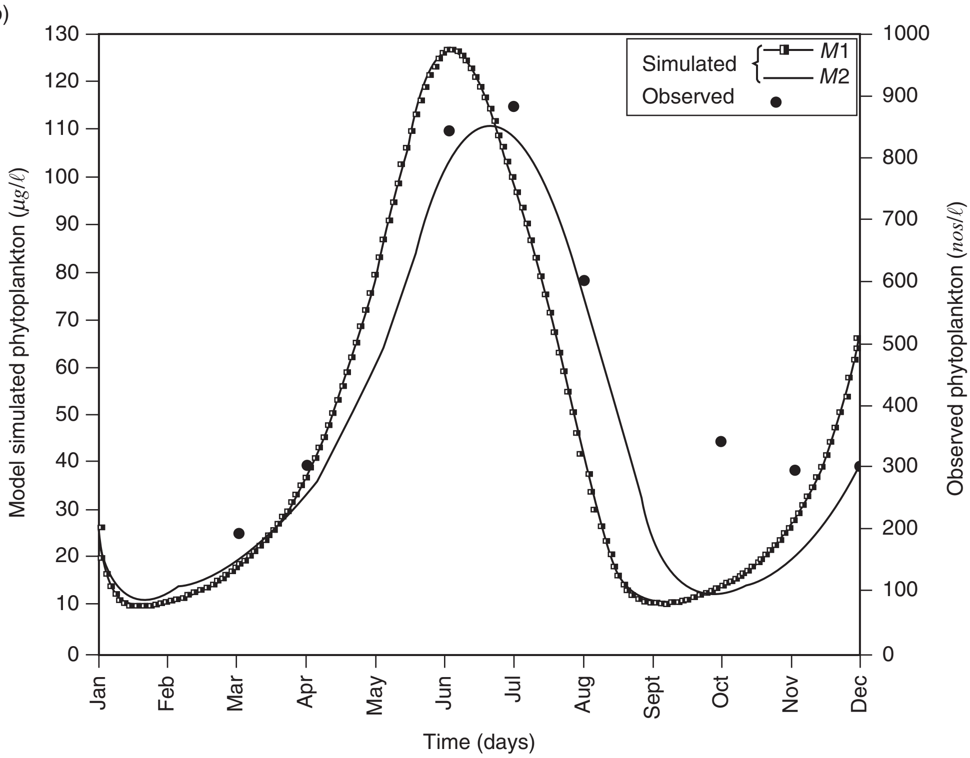
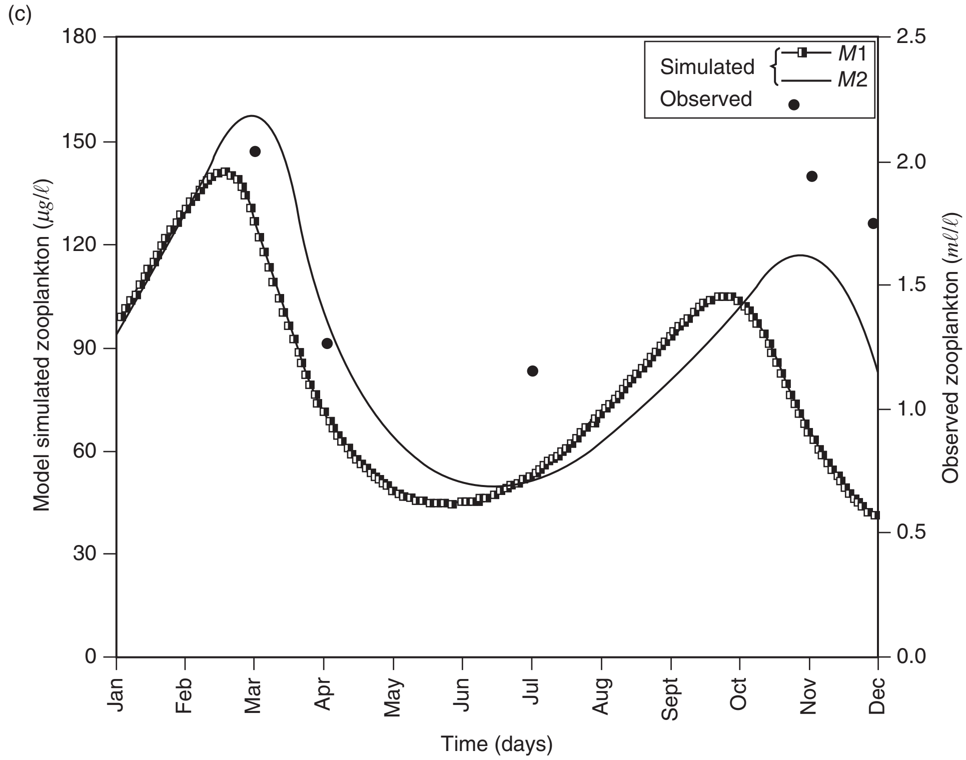


Figure 6. (*Continued*)



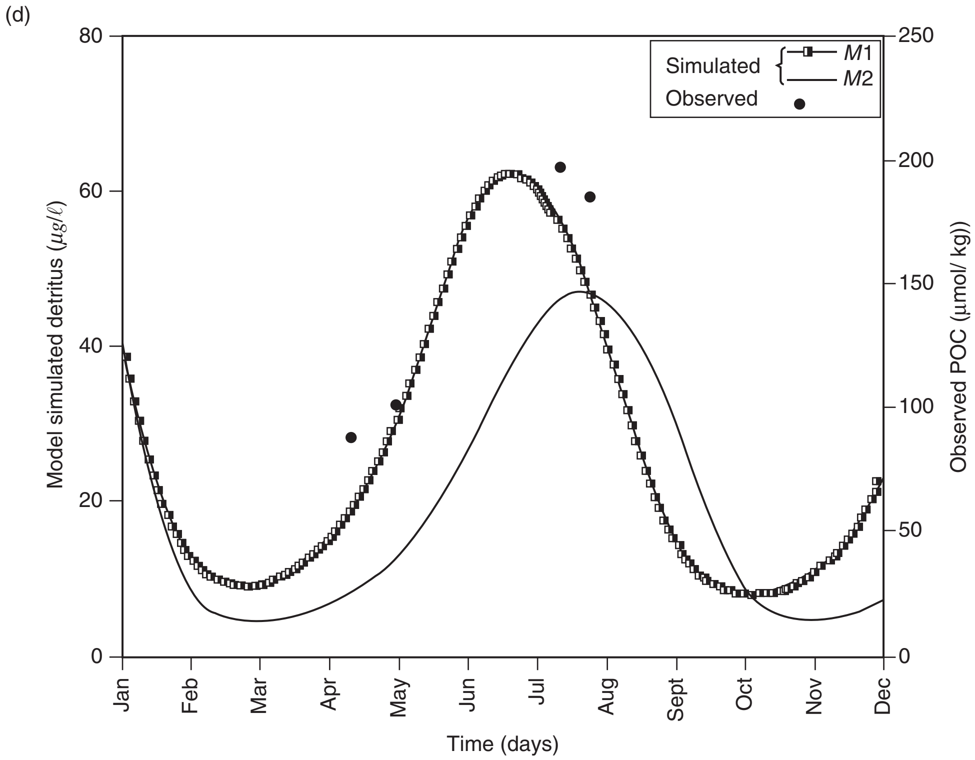


Figure 6. Annual distribution of (a) Nutrients, (b) Phytoplankton, (c) Zooplankton and (d) Detritus for M1 and M2 at site A_2.

4.3.1 Sensitivity Analysis

For the validation of the model results with available data, a fine tuning of parameters involved in the model are required. The sensitivity of the model to changes in the parameters in all the sites is similar. So, we discuss below the analysis only for site A_1. Through sensitivity analysis, it was found that the growth rate and nutrient input are the most effective parameters in controlling plankton distribution. Since the growth rate is expressed as a product of different terms (equ (2)), an individual discussion about the relative importance of each of the terms is required. The parameter involved in the nutrient limited growth rate is K_N. Increase of K_N, above the specified range (>15) results in a decrease in plankton. Another critical parameter for plankton is the loss rate due to metabolic and respiration loss 'r'.

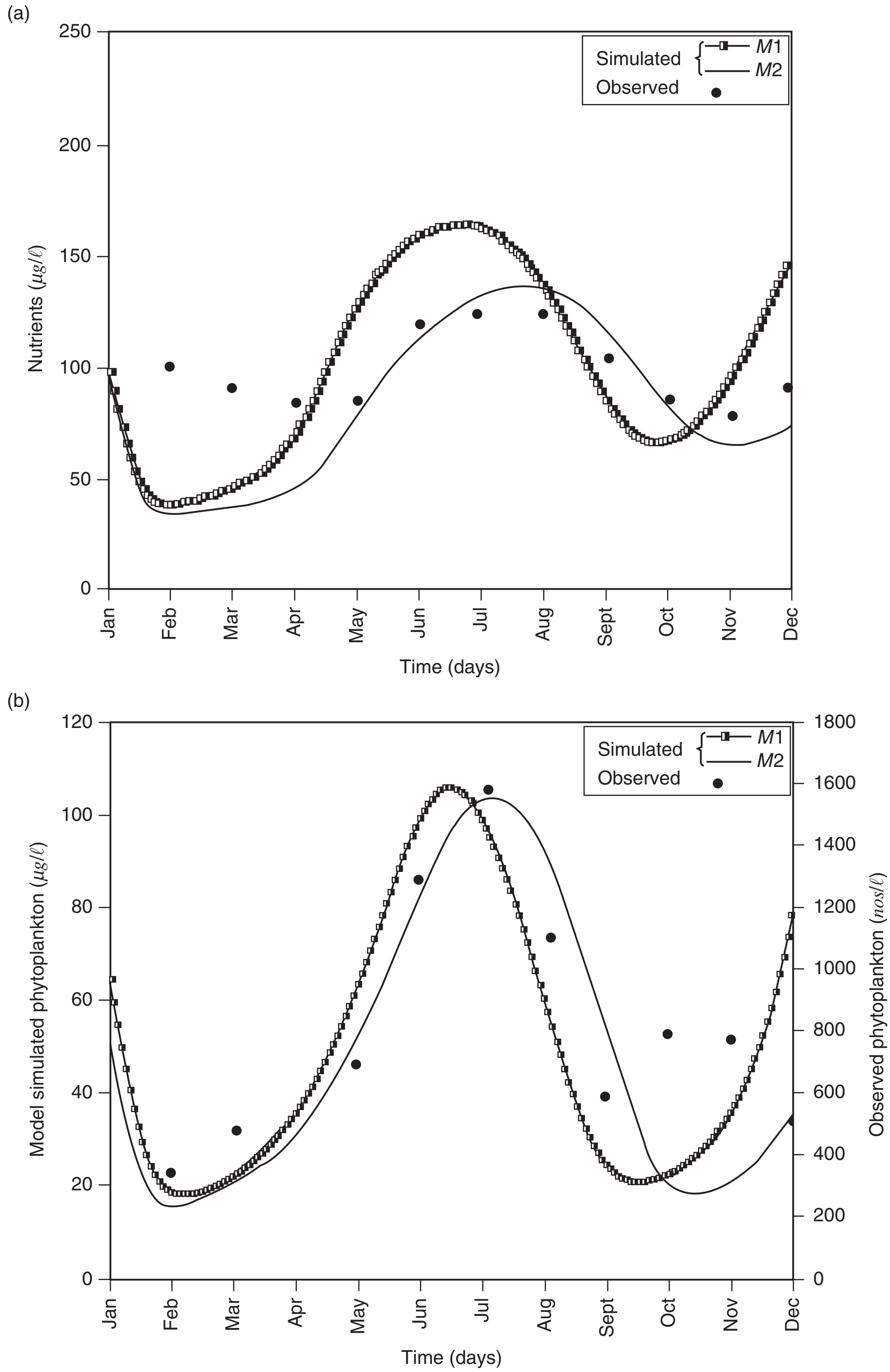


Figure 7. (*Continued*)

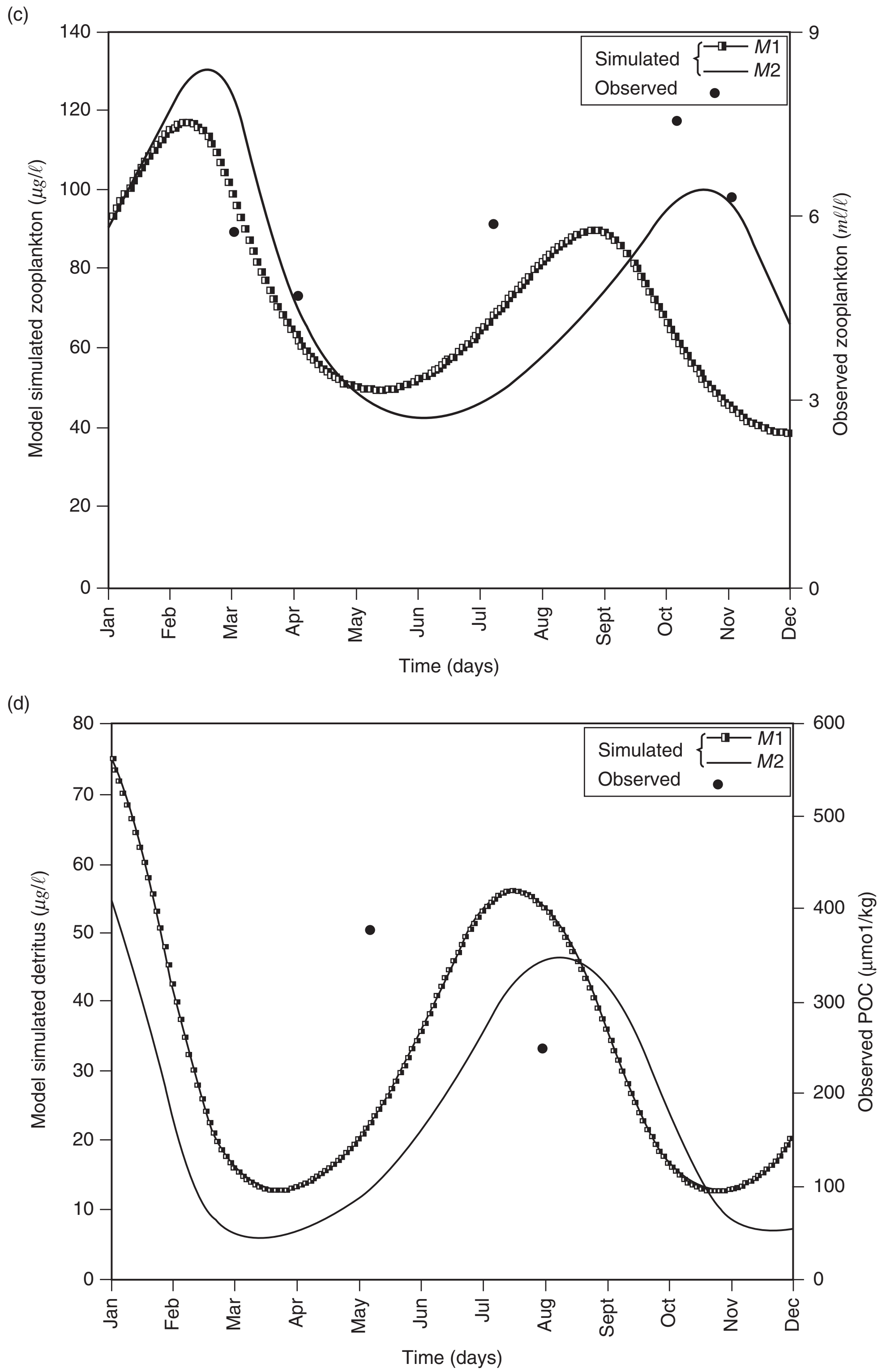


Figure 7. Annual distribution of (a) Nutrients, (b) Phytoplankton, (c) Zooplankton and (d) Detritus for M1 and M2 at site A_3.

Since respiration rate is a sink for phytoplankton, increase in *r* leads to a decrease of plankton and value for *r* is (0.18). Lower values of m (< 0.04) result in lesser nutrients entering the system leading to a lower plankton productivity. Changes in '*e*' affect the system in the same manner as c. Decreasing A_0 results in an increase of zooplankton and increasing A_0 (> 12) leads to their extinction. Decreasing K_Z (<17) results in the increase of zooplankton. Increasing *g* (> 0.033) leads to a decrease in zooplankton.

Increasing '*c*', the grazing rate leads to a decrease in phytoplankton and increase in zooplankton but, increasing *c* above a specified value (>0.077) leads to the instability of the system. As in our earlier paper [7] we have done a local stability analysis and found the range of values for the parameters for the system to be stable. The range of parameter values is listed in Table 1.

5. CONCLUSION

Our model simulation results show that addition of detritus to NPZ model changes the dynamics of the system significantly. It is seen from numerical experiments that the amount of nutrient entering into the system and growth rate (α(t)) of phytoplankton play an important role in controlling phytoplankton growth. The numerical experiments give a range of values of critical parameters for system/model to be stable. Model results predict a significant increase in amplitude, peak width and length of seasonal cycles of N, P, Z distribution with increasing values of remineralization rate (ϕ). With remineralization of detritus adding to its usual food phytoplankton, there is significant increase in zooplankton distribution and the length of its seasonal cycles increases. Model predicts that linkage of detritus to the system by the remineralization rate (ϕ) is more effective than palatability (p_2) of detritus to zooplankton. In other words, increasing p_2, beyond a certain range does not have any effect on the results. The model is tested for Chilika lagoon at the three specific chosen sites in the different region of the lagoon. The model simulated results for phytoplankton are very well validated with observations when the feed back of detritus into the system is through both the processes of remineralization and palatability of detritus to zooplankton.

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