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Effect of System Parameters on Plankton Dynamics: A Mathematical Modelling Approach

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Abstract: A phytoplankton-zooplankton model is proposed and analyzed as a sub-model of oxygen-plankton model. Mathematically, two coupled differential equations are considered. In this work, oxygen which is produced as a result of photosynthetic process by phytoplankton in ocean is assumed stable by keep oxygen concentration as a constant value. Basic properties of the phytoplankton-zooplankton population are detailed with analytical and numerical way under the effect of change in system parameters. In particular, effects of per-capita growth rate of zooplankton and intraspecific competition for phytoplankton on the systems' dynamical behavior are considered. To understand the system temporal structure nonspatial system is detailed. Then the spatial case is focussed with the assist of extensive numerical simulations. It is observed that the model system has rich patterns in both temporal and spatial case.

Sistem Parametrelerinin Plankton Dinamiği Üzerine Etkisi: Matematiksel Modelleme Yaklaşımı

Anahtar Kelimeler
Fitoplankton-zooplankton,
Matematiksel modelleme,
Yapı oluşumu

Özet: Fitoplankton-zooplankton modeli oksijen-plankton modelinin bir alt modeli olarak önerilmiş ve analiz edilmiştir. Matematiksel olarak, ikili diferensiyel denklem yapısı dikkate alınmıştır. Bu çalışmada, okyanuslardaki fitoplanktonlar tarafından fotosentez işleminin sonucu olarak üretilen oksijen oranı, kararlı olduğu varsayılarak oksijen konsantrasyonu sabit bir değer olarak seçilmiştir. Sistem parametrelerindeki değişim etkisi altındaki fitoplankton-zooplankton popülasyonunun temel özellikleri, analitik ve nümerik yöntemlerle detaylandırılmıştır. Özellikle, zooplanktonun büyüme hızı ve fitoplankton için tür içi rekabetin sistem davranışı üzerindeki etkileri ele alınmıştır. Sistemin zamana bağlı deişimini görmek için, mekâna bağlı olmayan sistem ele alınmıştır. Sonrasında ise mekânsal sistem, çok sayıdaki sayısal simülasyonlar yardımıyla calışılmıştır. Mevcut model sisteminin hem zamana hem de mekâna bağlı olduğu durumda zengin dinamiğe sahip olduğu görülmüştür.

1. Introduction

Mathematical modelling is based on combination of mathematics with other disciplines such as computer science, biology, physics etc. It plays an important role on exploring and understanding the underlying structure of ecological problems. For instance in biology, it provides a sensible approach when laboratory experiments are expensive or not applicable [1]. In many cases, experimental works on plankton populations usually are impossible due to its' cost and duration. Therefore, with assist of the experimental studies, mathematical modelling becomes an important way to investigate plankton dynamics. Various aspect of plankton species has a considerable place in literature. Phytoplankton and zooplankton interaction as a prey-predator system takes its place in many works [1–5].

Determination of the spatial distribution and the abundance of the organism is one of the important question in ecology [6]. Competition in species is one of the crucial factor which affects the distribution and abundance [7]. For this reason, underlying mechanism of competition is an attracting phenomenon in marine sciences. Especially, competition in plankton species is very common behavior and it can be stem from some reasons such as same resources, space etc [8, 9]. Sometimes competition can be very severe [10] and can be even results in extinction. Therefore, in this work the losses term of phytoplankton (i.e. intraspecific competition) is one of the question which need to be detailed.

Phytoplankton productivity is investigated by several researches and some fundamental works of them based

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on [11, 12]. Models on this productivity issue are presented by [13]. The model that we investigated in previous works focus on the phytoplankton productivity due to photosynthetic activity by taking into account zooplankton interaction as a prey-predator system [14, 15]. But here oxygen concentration effects on phytoplankton and zooplankton interaction is fixed to see the interaction between phytoplankton-zooplankton due to only stem from prey-predator system. So the only interaction in this system exists between zooplankton and it's prey as phytoplankton.

In this work, it is shown how intraspecific competition in phytoplankton species and the changes in maximal growth rate of zooplankton effect the dynamical behavior of the system in both temporal and spatiotemporal case. Intraspecific competition rate and the coefficient for maximum growth rate of zooplankton are determined as parameters in the given model system and these values are totally hypothetical. Note that it was not aimed here to calculate precise value of intraspecific competition rate and growth rate of zooplankton. Instead, the aim is to show how dynamical structure change with the change in these system parameters.

In view of the above, structure of the paper is as follows. In Section 2, phytoplankton-zooplankton model proposed and analyzed. In Section 3, the properties of the system are detailed by extensive numerical simulations both in terms of temporal and spatial structure. In last Section (Sec. 4), findings and its importance are focussed.

2. Mathematical Model

In this section, temporal dynamics of prey (phytoplankton) and predator (zooplankton) system is taken into account. In the present work, conceptual oxygen-phytoplankton-zooplankton model (see [14, 15] for more details) is revisited with a sub-model system. Therefore, Phytoplankton-zooplankton sub-model has the following form:

$$\frac{du}{dt} = \frac{Bo}{o+o_1}u - \gamma u^2 - \sigma\frac{uv}{u+h}, \tag{1}$$

$$\frac{dv}{dt} = \frac{\beta uv}{u+h} - \mu v. \tag{2}$$

Due to their biological meaning, all parameters are non-negative where o is the concentration of oxygen which is supplied at a constant rate at time t, u and v are the densities of phytoplankton and zooplankton, respectively. The term B is the maximum phytoplankton density per capita growth rate and o_1 is the half saturation-constant, due to limited resources, competition play an important role on shaping population size and structure. Competition is two fold; first one is competition between same species individual i.e. intraspecific competition and the second one is competition between different species, i.e. interspecific competition [16, 17]. As in Eq. (5) for the phytoplankton growth, the logistic growth equation is taken into account and intra specific competition is outlined. So, γ is density-dependent decrease in phytoplankton growth and can be assumed as intraspecific competition or self shading, h is the half saturation-abundance, β is the maximum predation rate for zooplankton on phytoplankton and the parameter μ is the natural mortality rate of zooplankton.

Considerable part of this work will use numerical simulations, dimensionless variables and system parameters should be introduced. It is considered

$$t' = t\sigma, \quad u' = \frac{u}{\sigma}, \quad v' = \frac{v}{\sigma} \tag{3}$$

and the dimensionless parameters as

$$\tilde{B} = \frac{B}{\sigma}, \quad \tilde{\gamma} = \frac{\gamma}{\sigma}, \quad \tilde{\beta} = \frac{\beta}{\sigma}, \quad \tilde{\mu} = \frac{\mu}{\sigma} \tag{4}$$

then Eqs. (5-6) take the following form

$$\frac{du}{dt} = \frac{Bo}{o+o_1}u - \gamma u^2 - \frac{uv}{u+h}, \tag{5}$$

$$\frac{dv}{dt} = \frac{\beta uv}{u+h} - \mu v. \tag{6}$$

where primes and tildes are neglected for the notations simplicity, hence all system parameters are in their dimensionless form.

First, the local dynamics of the system (5-6) is considered. It is obtained from linear stability analysis of the system:

$$\frac{Bo}{o+o_1}u - \gamma u^2 - \frac{uv}{u+h} = 0, \quad \frac{\beta uv}{u+h} - \mu v = 0. \tag{7}$$

System (5-6) has three stationary state which are the solutions of system (7): extinction state $(0,0)$, extinction of zooplankton state $(u,0)$, and coexistence state (u,v).

- The extinction (trivial) state is always exist.
- Zooplankton extinction steady state is the solutions of the system (7):

$$\tilde{u} = \frac{Bo}{\gamma(o+o_1)}, \qquad \tilde{v} = 0. \tag{8}$$

There is no restriction for the existence of zooplankton extinction state.

- The coexistence steady states of the systems are the solutions of the system (7):

$$u_\star = \frac{\mu h}{\beta - \mu}, \qquad v_\star = (u_\star + h)\left(\frac{Bo}{o+o_1} - \gamma u\star\right). \tag{9}$$

It is readily seen that for all nonnegative values of system parameters B, γ, o_1, h, β, μ and biologically meaningful region for $u > 0$ and $v > 0$, the following conditions should be satisfied.

$$\beta \neq \mu \quad \beta > \mu, \quad \text{and} \quad \frac{Bo}{o+o_1} > \gamma u. \tag{10}$$

Stationary point type depends on the eigenvalues that are the solutions of the following equation:

$$\lambda^2 - \lambda trA + detA = 0 \tag{11}$$

where A is the linearised system matrix , which is as follow;

$$A = \begin{pmatrix} \frac{Bo}{o+o_1} - 2\gamma u - \frac{vh}{(u+h)^2} & -\frac{u}{u+h} \\ \frac{\beta vh}{(u+h)^2} & \frac{\beta u}{u+h} - \mu \end{pmatrix}$$

For extinction state stability, Matrix A takes the following form:

$$det(A_{(0,0)} - \lambda I) = \begin{vmatrix} \frac{Bo}{o+o_1} - \lambda & 0 \\ 0 & -\mu - \lambda \end{vmatrix} = 0$$

the characteristic equation is

$$\left(\frac{Bo}{o+o_1} - \lambda\right)(-\mu - \lambda) = 0 \quad (12)$$

from Eq. (12) $\lambda_1 = -\mu$, $\lambda_2 = \frac{Bo}{o+o_1}$. Therefore the extinction state is always saddle, regardless what the parameter values are.
For zooplankton extinction state stability, Matrix A takes the following form:

$$det(A_{(\tilde{u},0)} - \lambda I) = \begin{vmatrix} \frac{Bo}{o+o_1} - 2\gamma u - \lambda & -\frac{u}{u+h} \\ 0 & \frac{Bu}{u+h} - \mu - \lambda \end{vmatrix} = 0$$

then the characteristic equation is

$$\left(\frac{Bo}{o+o_1} - 2\gamma u - \lambda\right)\left(\frac{\beta u}{u+h} - \mu - \lambda\right) = 0 \quad (13)$$

from Eq. (13) $\lambda_1 = \frac{Bo}{o+o_1} - 2\gamma u$, $\lambda_2 = \frac{\beta u}{u+h} - \mu$.

Therefore zooplankton extinction state can be of any type i.e. depending on system parameters.
For coexistence state stability, Matrix A takes the following form:

$$det(A_{(u_\star,v_\star)} - \lambda I) = \begin{vmatrix} \frac{Bo}{o+o_1} - 2\gamma u_\star - \frac{v_\star h}{(u_\star+h)^2} - \lambda & -\frac{u_\star}{u_\star+h} \\ \frac{\beta v_\star h}{(u_\star+h)^2} & \frac{\beta u_\star}{u_\star+h} - \mu - \lambda \end{vmatrix} = 0$$

then the characteristic equation is

$$\left(\frac{Bo}{o+o_1} - 2\gamma u_\star - \frac{v_\star h}{(u_\star+h)^2} - \lambda\right)\left(\frac{\beta u_\star}{u_\star+h} - \mu - \lambda\right) + \frac{u_\star}{u_\star+h}\left(\frac{\beta v_\star h}{(u_\star+h)^2}\right) = 0 \quad (14)$$

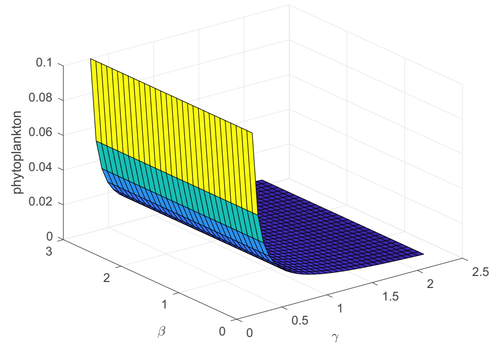
where $u_\star$, $v_\star$ is defined as in Eq. (9). The calculation of eigenvalues Eq. (14) is rather bulky. So it is not detailed here for the sake of brevity. But, to understand the underlying reason of controlling parameters choice some mathematical interpretations are needed.
Let

$$\begin{aligned} \xi &= \frac{Bo}{o+o_1} - 2\gamma u_\star - \frac{v_\star h}{(u_\star+h)^2}, \\ \kappa &= \frac{Bu_\star}{u_\star+h} - \mu, \\ \eta &= \frac{u_\star}{u_\star+h}\left(\frac{\beta v_\star h}{(u_\star+h)^2}\right). \end{aligned} \quad (15)$$

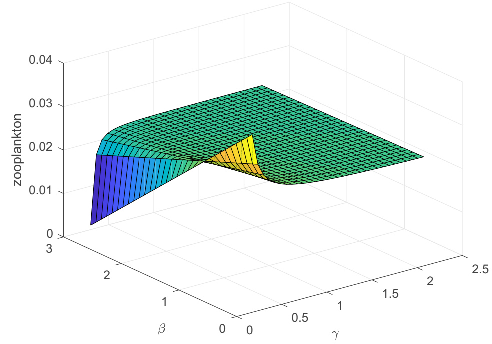
Then the eigenvalues of the system (14) are the solutions of the following equation:

$$\lambda^2 - (\xi + \kappa)\lambda + (\xi\kappa + \eta) = 0 \quad (16)$$

The stability of the system is readily depend on the choice of system parameters. For this reason, the choice of systems' controlling parameters is actually based on the mathematical approach rather than its biological meaning. Hence, stability of this equilibrium is detailed with extensive numerical simulations.



(a)



(b)

Figure 1. Steady states of phytoplankton and zooplankton vs β, γ for given ranges $(0.2 < \beta < 3)$, $(0.3 < \gamma < 3)$ and the initials are $u_0 = 0.0167$, $v_0 = 0.0123$. Other system parameters are given in the text.

To show system dynamical behavior on both spatial and nonspatial case, system parameters range should be defined under some conditions Eq. (10). Figures (1a-b) show the system steady states under the controlling parameters β and γ and keep all other parameters constant to see where phytoplankton and zooplankton have positive steady state to correspond biologically meaningful area. For chosen hypothetical values both system components satisfy positive existence state. Hence for the following numerical simulations the system parameters can be chosen from this range as it is shown in Figure (1).

3. Numerical Simulations

3.1. Temporal Distribution

In this section, nonspatial system for phytoplankton-zooplankton system is performed. In all following numerical simulations, system parameters are fixed at some hypothetical values as $B = 1.8$, $\mu = 0.1$, $h = 0.1$, $o_1 = 0.7$ and $t(time) = 1500$ and β and γ take their values from corresponding steady state figure (i.e. Fig. (1)). Note that, system parameters are selected to be compatible with the improved version of this sub-model system due to existence of oxygen in [15]. In this work our particular interest is to reveal the dynamical structure of oxygen sub-model by taking into account only phytoplankton as a main producer and zooplankton as its main consumer. The well-being of phytoplankton mainly depend on the predation rate and intraspecific competition which is detailed in model construction part. So, here, these two parameters are focussed to show systems' dynamical behavior.

Figure (2) shows the phytoplankton and zooplankton densities versus time obtained for $\beta = 0.7$ and different values of γ. For $\gamma = 0.31$ (Fig. 2a), the system develops periodic oscillations. This periodic oscillation becomes intense for the values of $\gamma = 0.6$ and $\gamma = 1.2$ (Fig. 2b) and (Fig. 2c), respectively. Further increase in γ for $\gamma = 2.1$ (Fig. 2d), after a sequence of damping oscillations phytoplankton and zooplankton densities converge to the steady state values. For this value of γ, coexistence state is stable focus. Figure (3) shows the phase plane of local population for corresponding figure (Figs. 2b-d). Here blue star shows the initial point of system tarjectories while red star show the end point of it. Figure (4) shows densities of phytoplankton and zooplankton versus time obtained for $\gamma = 1.3$ and different values of β. For $\beta = 0.3$ (Fig. 4a), densities of phytoplankton and zooplankton converge to the steady state values after some damping oscillations. But for an increase in value β ($\beta = 0.37$, Fig. 4b), the sequence of damping oscillations becomes more intense. For $\beta = 0.44$ (Fig. 4c), the system dynamics has periodical densities and it follows the stable limit cycle. Hopf bifurcation occur when β changes from 0.3 to 0.66.

The system exhibits, as a response to changes in β and γ, a succession of oscillations observed with different scale. Under the light of extensive numerical simulations performed on this model, the question should be here whether the model system satisfied the idea which is proposed by Rosenweig as 'paradox of enrichment' [18]. But in Rosenweig system, the deviation of steady state to limit cycle is a result of the change in carrying capacity in temporal scale. According to his work, further increase in carrying capacity is results in system extinction [18]. It should be noted here, the term 'paradox' is also used by several researchers to show the destabilization of ecosystem [19, 20]. But in our case, the limit cycles in different scales emerges as a result of increasing intraspecific competition or maximum predation rate. Further increase both in predation rate or competition rate results in extinction in our model system (this figures are not given here for the sake of brevity), but to reveal the destabilisation of our system is not in scope of this paper for now.

3.2. Spatial Distribution

Above numerical analysis was done for nonspatial system i.e. all species densities are distributed uniformly over space. This type of 'well-mixed' system is used in the

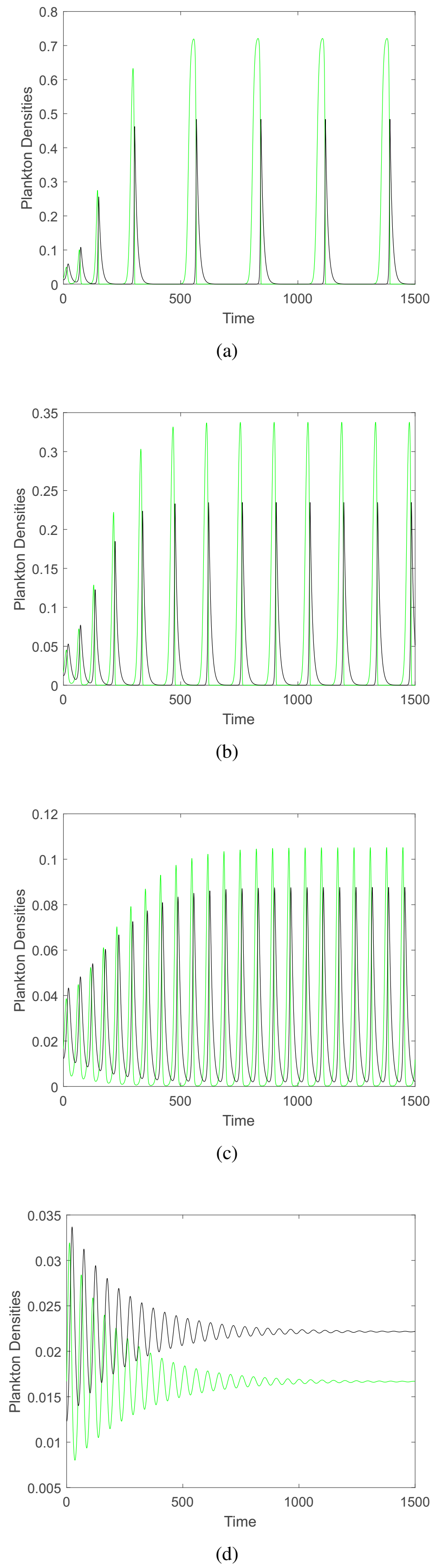
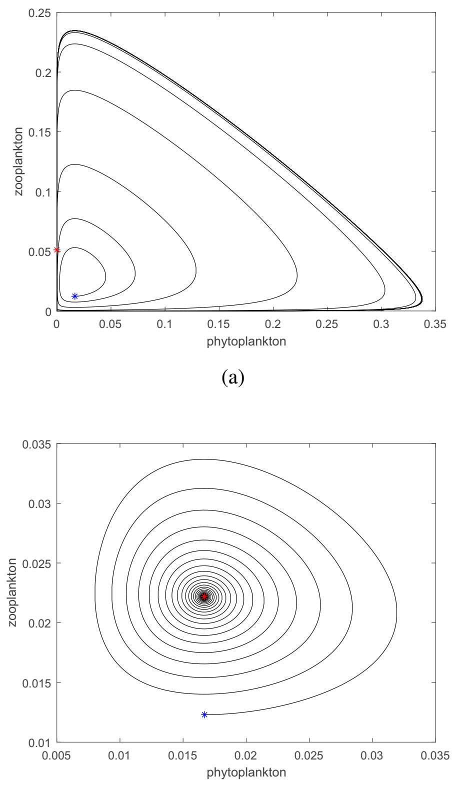


Figure 2. Densities of phytoplankton (green) and zooplankton (black) versus time obtained for fixed value of $\beta = 0.7$ for a) $\gamma = 0.31$, b) $\gamma = 0.6$, c) $\gamma = 1.2$, d) $\gamma = 2.1$ and the initials are $u_0 = 0.0167$, $v_0 = 0.0123$. Other system parameters are given in the text.



(a)

(b)

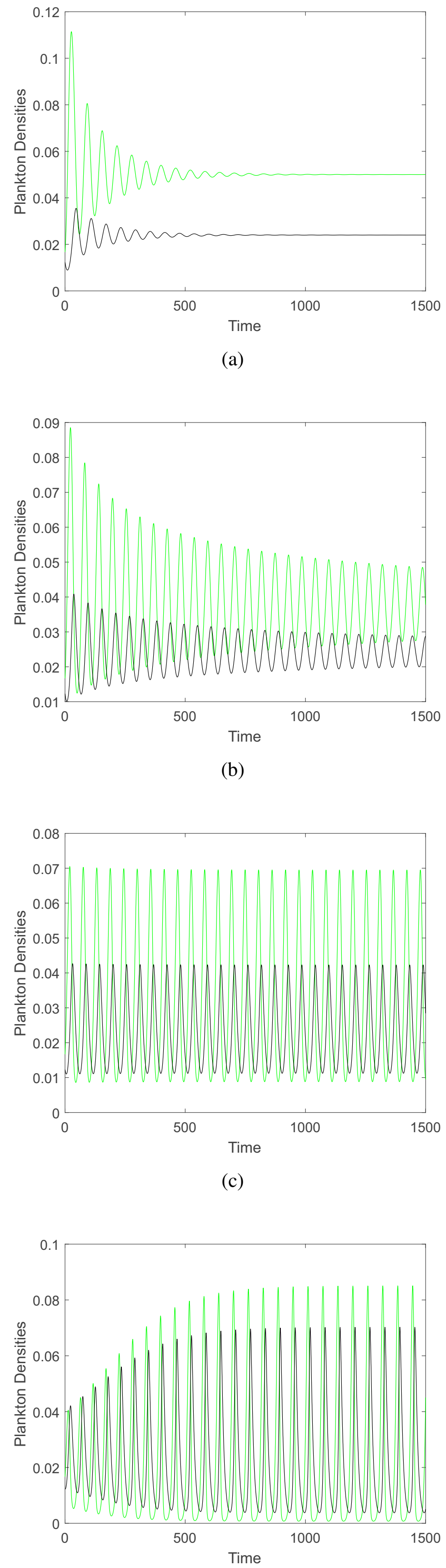
Figure 3. System trajectories for phytoplankton and zooplankton with blue star for initial point and red star for end point a) $\gamma = 0.6$, b) $\gamma = 2.1$ and the initials are $u_0 = 0.0167$, $v_0 = 0.0123$. Other system parameters are given in the text.

literature [21, 22]. But, as in observed in field researches, plankton system has ‘patchy’ distribution observed by [23]. In this section, phytoplankton-zooplankton system is considered in space by using “turbulent diffusion” approach defined as standard diffusion terms where the spatial mixing and the corresponding fluxes of matter are attributed to turbulence [24]. Actually, determining the diffusion coefficient, D, is quite a complicated issue. To consider transport of oxygen in sea water, combined action of molecular and turbulent diffusion should be taken into account. However, turbulent diffusion is much larger than its molecular value and for the spatial scale of phytoplankton dynamics (known to range from 10^{-1} to 10^{5} m) molecular diffusion is estimated to be several orders less magnitude than turbulent diffusion. Since, the model system (5-6) is a sub-model of improved oxygen-plankton system, the diffusion coefficient is assumed accordingly as in [14, 15]. For this reason, extended version of the system (5-6) is needed in terms of space which is described by following diffusion-reaction system:

$$\frac{\partial u}{\partial t} = D_1 \frac{\partial^2 u}{\partial x^2} + \frac{Bo}{o+o_1}u - \gamma u^2 - \frac{uv}{u+h}, \qquad (17)$$

$$\frac{\partial v}{\partial t} = D_2 \frac{\partial^2 v}{\partial x^2} + \frac{\beta uv}{u+h} - \mu v. \qquad (18)$$

$u = u(x,t)$ and $v = v(x,t)$ are the densities of phytoplank-



(a)

(b)

(c)

(d)

Figure 4. Densities of phytoplankton (green) and zooplankton (black) versus time obtained for fixed value of $\gamma = 1.3$ for a) $\beta = 0.3$, b) $\beta = 0.37$, c) $\beta = 0.44$, d) $\beta = 0.66$ and the initials are $u_0 = 0.0167$, $v_0 = 0.0123$. Other system parameters are given in the text.

ton and zooplankton at time t and position x. $D_1 = D_2 = D_T$ is the turbulent diffusion [25, 26]. For more details on assumption of turbulent diffusion as a coefficient for phytoplankton-zooplankton system see [1, 14]. Additionally, it should be mentioned here that, to consider appropriate scaling for the spatial coordinates as $x \to x' = x\sqrt{1/D_T}$, hence D_T is reduced from the system. Therefore, choosing $D_1 = D_2 = D_T = 1$ for dimensionless setting is in an agreement to reveal the spatial structure of the system (17-18). Also, as in its nonspatial system other system parameters are fixed ($B = 1.8$, $\mu = 0.1$, $h = 0.1$, $o_1 = 0.7$) to focus on the effect of controlling parameters β and γ.

The spatial system is considered in a finite domain $0 < x < L$ where the length of domain is defined by L. Neumann boundary conditions (zero-flux) is considered at the domain boundaries.

In this work, zooplankton distribution is considered as patch in space with uniformly distributed phytoplankton distribution [1]:

$$\begin{aligned} u(x,0) &= u_0, && (19)\\ v(x,0) &= v_0, \quad for \quad |x_i| < \varepsilon, \quad else \quad v(x,0) = 0 \end{aligned}$$

where u_0 and v_0 are the initial densities and ε ($\varepsilon = 100$) is the patch diameter. System (17-18) is solved numerically by finite difference method with the mesh steps are $\Delta t = 0.01$ and $\Delta x = 0.5$. It should be emphasized that the mesh steps are sufficiently small to get rid of any numerical artifacts.

Figure (5) shows the population spatial distribution over time obtained for the same parameter values as in Fig. (2). For Fig. (5a), different sort of oscillations arise at the wake of travelling front, and the oscillations are produced by irregular pattern. After the travelling wave leave the domain for larger time limit the domain is invaded by irregular population distribution. For an increase in γ ($\gamma = 0.6$, Fig. 2b), regular spatial distribution band is eventually displaced by the irregular spatiotemporal distribution for both phytoplankton and zooplankton. For $\gamma = 1.2$ Fig. 2c, the plateau is followed by the onset of irregular distributions in the wake of the travelling population wave behind the strongly oscillating front. For a further increase in γ ($\gamma = 2.1$, Fig. 2d), the front propagates to the right, so in the large time limit, phytoplankton and zooplankton densities converge to the spatially uniform system.

Figure (6) shows the population spatial distribution over time obtained for different values of β. For an increase in β, coexistence state connects extinction state Figs. (2c-d). For Figs. (2c-d), phytoplankton ad zooplankton densities form a narrow peak at the position of extinction and these peak values show the maximum densities for both species.

The behavior of the system under the effects of the changes in intraspesific competition and the changes in max predation rate reveal that the system has rich spatial and nonspatial structure.

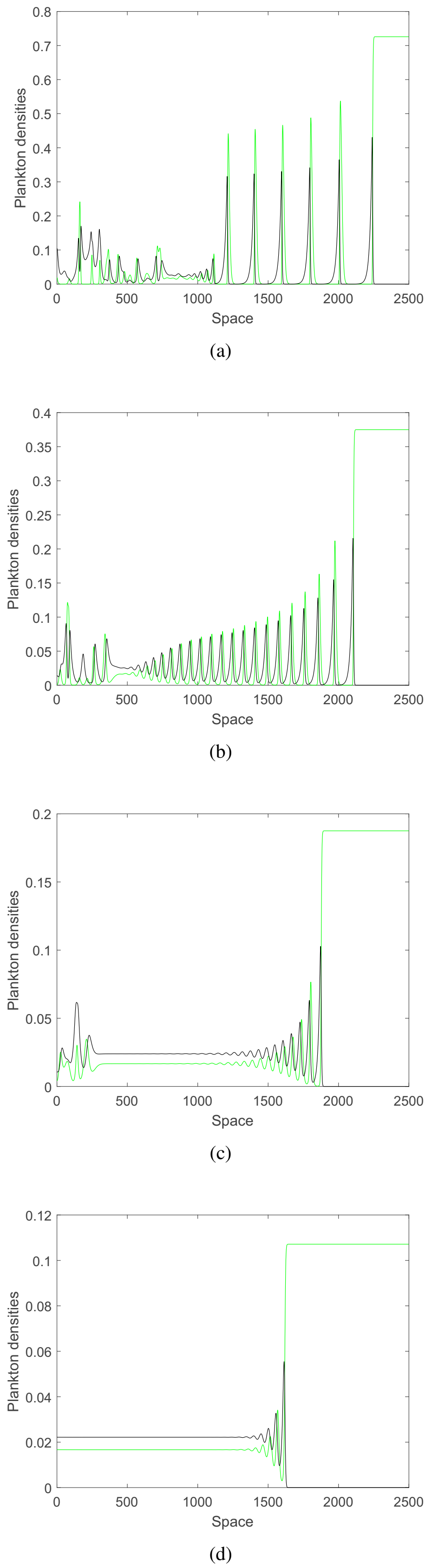


Figure 5. Distributions of phytoplankton (green) and zooplankton (black) over space at $t = 1500$ obtained for fixed value of $\beta = 0.7$ and for a) $\gamma = 0.31$, b) $\gamma = 0.6$, c) $\gamma = 1.2$, d) $\gamma = 2.1$. System initials and other parameters of the system are given in the text.

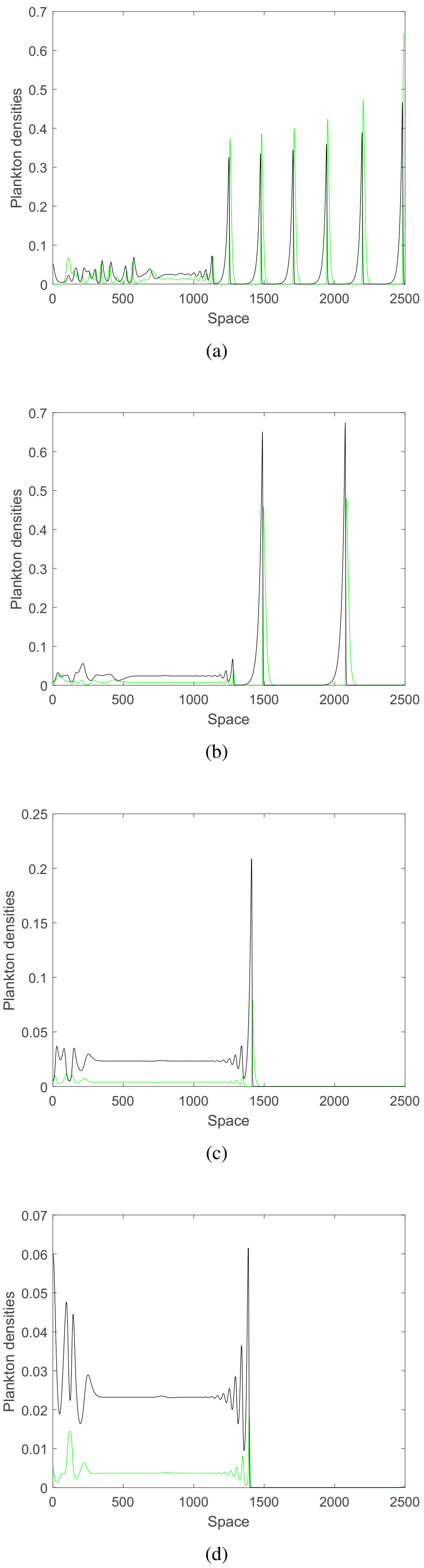


Figure 6. Distributions of phytoplankton (green) and zooplankton (black) over space at $t = 1500$ obtained for fixed value of $\gamma = 0.35$ and for a) $\beta = 0.85$, b) $\beta = 1.5$, c) $\beta = 2.6$, d) $\beta = 2.8$. System initials and other parameters of the system are given in the text.

4. Concluding Remarks

The importance of plankton dynamics in marine ecosystems have been searched for several decades. Main reason of this significant interest from researchers arises due to plankton role on constituting the base of ocean food chain [27]. A considerable progress on these researches have been focus on the understanding of the mechanisms which is relevant for plankton species. Additionally, oxygen production due to phytoplankton photosynthesis is an important phenomenon. But, there are only few studies concerned with the dynamics of the oxygen-plankton system. So, in this study by assuming oxygen variable as a constant, the dynamical behaviour of phytoplankton-zooplankton system is detailed under the effect of system other parameters. Distribution of phytoplankton and zooplankton may be driven by system parameters here these are chosen as intraspecific competition of phytoplankton and maximal growth rate of zooplankton. The mathematical model consists of two differential equations. Nonspatial version of the model is considered initially with the assumption of well-mixed spatially uniform distribution of the species. The properties of the system is revealed by analytical and numerical way. It is shown that the existence of coexistence state need some conditions which is detailed in Section 2.

Then spatially extended version of the model is considered by taking into account turbulent diffusion to explain the movement of plankton species. Note that, in order the keep in line with the use of dimensionless variables, see the beginning part of Section 2, x is changed to dimensionless coordinate as $x' = x\sqrt{1/D_T}$. It means, for the dimensionless system choosing turbulent diffusion $D_T = 1$ is not a particular choice of turbulent diffusion, but it is just a technical consequence of the change in variables. In this case the model is described by two reaction-diffusion type partial differential equations. Again in the same manner as in nonspatial case, the system has rich dynamical structure including travelling wave, population oscillation.

In this paper, it is shown that phytoplankton as prey and zooplankton as its main predator, that a nonspatial and spatial system has rich dynamical structure under the influence of the changes in system parameters. Remarkably, similar patterns - i.e. population oscillations in the wake, travelling wave - are observed in oxygen-plankton model system [28] and prey-predator system [1].

By means of numerical simulations, system parameters effect on species distribution is revealed. The revealed structure shows how the system affects the formation of dynamical structure. Note that, the results are restricted to in one-dimension, but it can be enhanced to its two-dimensions and in this case, the horizontal distribution can be seen clearly.

In conclusion, the most interesting part of the system is observed when the zooplankton maximum growth rate increase (Fig. 6), the peaks leave the domain by one by and these peaks are produced by irregular pattern. But the irregular structure is not invaded the whole domain when all the peaks are gone (see the similar succession in [28], but for the invasion is successful). These irregular structure produce oscillating population where the species has their peaks at the wake of extinction point.

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