

Modeling migratory grazing of zooplankton on toxic and non-toxic phytoplankton

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Abstract

Migratory grazing of zooplankton between non-toxic phytoplankton (NTP) and toxic phytoplankton (TPP) is a realistic phenomena unexplored so far. The present article is a first step in this direction. A mathematical model of NTP-TPP-zooplankton with constant and variable zooplankton migration is proposed and analyzed. The asymptotic dynamics of the model system around the biologically feasible equilibria is explored through local stability analysis. The dynamics of the proposed system is explored and displayed for different combination of migratory parameters and toxin inhibition parameters. Our analysis suggests that the migratory grazing of zooplankton has a significant role in determining the dynamic stability and oscillation of phytoplankton zooplankton systems.

Keywords: Toxin-producing phytoplankton; Limit cycle; Equilibria; Non-equilibria; Stability; Density-dependent migrations; Aggregation method

1. Introduction

Toxin-producing phytoplankton (TPP) are a group of phytoplankton that have the capability of producing some toxic chemicals [1]. The dynamics of phytoplankton and zooplankton is significantly affected due to the presence of these TPP species [2,3]. In recent years, a number of studies have been conducted to investigate the effects of TPP species on the overall dynamics of phytoplankton and zooplankton [1,4–6]. In particular, to explore the dynamics of overall plankton population, Roy et al. [5] proposed and analyzed a three component mathematical model consisting of the group of non-toxic phytoplankton (NTP), toxic phytoplankton (TPP) and zooplankton. Roy et al. [5] compared their model with field data and estimated the model parameters. The analysis of their model proposed a new hypothesis for the maintenance of non-equilibrium dynamics of plankton.

A number of works have been carried out to explore the effect of dispersion or migration of species on the ecosystem dynamics [7,8]. Zooplankton species are well known for exhibiting vertical movement and other

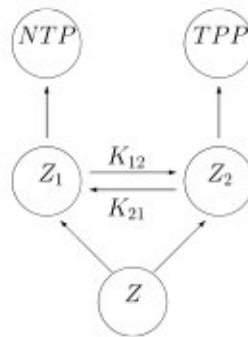


Fig. 1. Schematic diagram of zooplankton ($Z_i, i = 1, 2$) dispersal between NTP and TPP.

migratory movement in natural waters [9,10]. Although the model of [5] considered the effects of toxin inhibition on zooplankton, it lacked a realistic migratory behaviour of zooplankton species in natural waters [8]. The non-toxic and toxic phytoplankton exhibit weak interspecific competition in a common habitat [5]. On the other hand, due to their ability to move in water, zooplankton species are very likely to change their grazing activity from TPP species to NTP species or vice versa. This process would be possible by the migratory grazing of zooplankton from the TPP-dense portion to the NTP-dense portion of the common habitat and vice-versa. In our present article we incorporate these effects of zooplankton dispersal on the dynamics of a NTP–TPP-zooplankton system.

According to their activities of grazing on NTP and TPP population, we divide the entire zooplankton population into two subgroups. Let the part of zooplankton, which due to its presence in an NTP dense place graze mainly on NTP species, be denoted by Z_1 . Similarly the part of zooplankton, which due to its physical presence in a TPP dense place graze on mainly the TPP species is denoted by Z_2 . Now, due to the physical movement, the species of zooplankton which at any time belong to Z_1 category, turn to Z_2 category and vice-versa. We consider such movement at a constant rate first and then a density dependent rate. We study the behaviour of the model system taking into account the effect of the entire zooplankton species aggregated as $Z = Z_1 + Z_2$. The schematic diagram of the species interaction is given in Fig. 1.

To analyze the system we use the method of aggregation based on the central manifold theorem [11,12]. To apply the central manifold theorem we need to have: (i) a system with two time scale one is slow and the other is fast, (ii) the fast equilibrium point must be asymptotically stable, (iii) the aggregated system is uniformly bounded [13].

In the first section we consider the migration parameter to be constant and in the subsequent section we consider a variable migration. We analyze the system around the biologically feasible equilibria and discuss the overall results.

2. Formulation of the mathematical model

Extending the three-component model of [5], we formulate the model of above system (Fig. 1) mathematically under the following assumptions:

- (i) The NTP and TPP populations follow Lotka–Volterra model with intrinsic growth rates r_1 and r_2 , competition coefficients α_1 and α_2 and carrying capacity of phytoplankton K which is shared by NTP and TPP in the absence of the zooplankton.
- (ii) Zooplankton predate the NTP, TPP with Holling type-II functional response [14] in the rate w_1 , and w_2 with half saturation constant D_1 and D_2 , respectively.
- (iii) Zooplankton are divided into two subpopulation according to their activities. At an instant the zooplankton grazing on P_1 are named Z_1 and the rest of the individuals grazing on P_2 are named Z_2 . Again an individual of Z_1 which predate P_1 will be a member of Z_2 immediately when it consumes P_2 and this rate of change from Z_1 to Z_2 is denoted by K_{21} and the reverse rate by K_{12} .

- (iv) The growth rate, competition effects as well as the predation and conversion effects are much slow compared with the zooplankton migration parameter. To accommodate these difference we analyze our model using a slow-fast variable method, where the migration parameters are considered as fast variables and other demographic parameters as slow ones.
- (v) When Z_1 predate on NTP, the maximum rate of gain in Z_1 growth is ξ_1 due to predation of NTP at the rate w_1 , but when Z_2 predate TPP, the rate of inhibition in Z_2 growth is ξ_2 due to predation of TPP at the rate w_2 .
- (vi) Zooplankton are diminishing at a constant rate c .

Based on these assumptions the dynamics of NTP (P_1), TPP (P_2), NTP consuming zooplankton (Z_1), TPP consuming zooplankton (Z_2) can be written as the following system of differential equations:

$$(A) \quad \frac{dP_1}{dt} = P_1 \left\{ r_1 \left(1 - \frac{P_1 + \alpha_1 P_2}{K} \right) - \frac{w_1 Z_1}{D_1 + P_1} \right\}, \tag{1}$$

$$\frac{dP_2}{dt} = P_2 \left\{ r_2 \left(1 - \frac{P_2 + \alpha_2 P_1}{K} \right) - \frac{w_2 Z_2}{D_2 + P_2} \right\}, \tag{2}$$

$$\frac{dZ_1}{dt} = (K_{12}Z_2 - K_{21}Z_1) + \frac{\xi_1 P_1}{D_1 + P_1} Z_1 - cZ_1, \tag{3}$$

$$\frac{dZ_2}{dt} = (K_{21}Z_1 - K_{12}Z_2) - \frac{\xi_2 P_2}{D_2 + P_2} Z_2 - cZ_2, \tag{4}$$

with the initial conditions

$$P_1(0) \geq 0, \quad P_2(0) \geq 0, \quad Z_1(0) \geq 0, \quad Z_2(0) \geq 0. \tag{5}$$

3. Model 1: constant migration

The physical movement of zooplankton are much faster than their growth and interaction process. (In different context a similar phenomena has been considered [7].) Therefore the value of the parameters K_{12} and K_{21} are set much higher than the other parameters.

With this assumption we write,

$$K_{12} = \frac{k_{12}}{\epsilon}, \quad K_{21} = \frac{k_{21}}{\epsilon}, \tag{6}$$

where ϵ is a small dimensionless number and k_{12}, k_{21} are positive constants of same order of magnitude as the other parameters.

Now substituting (6) in (3) and (4) we obtain system (A) as

$$(B) \quad \epsilon \frac{dP_1}{dt} = \epsilon P_1 \left\{ r_1 \left(1 - \frac{P_1 + \alpha_1 P_2}{K} \right) - \frac{w_1 Z_1}{D_1 + P_1} \right\}, \tag{7}$$

$$\epsilon \frac{dP_2}{dt} = \epsilon P_2 \left\{ r_2 \left(1 - \frac{P_2 + \alpha_2 P_1}{K} \right) - \frac{w_2 Z_2}{D_2 + P_2} \right\}, \tag{8}$$

$$\epsilon \frac{dZ_1}{dt} = (k_{12}Z_2 - k_{21}Z_1) + \epsilon \left\{ \frac{\xi_1 P_1}{D_1 + P_1} Z_1 - cZ_1 \right\}, \tag{9}$$

$$\epsilon \frac{dZ_2}{dt} = (k_{21}Z_1 - k_{12}Z_2) - \epsilon \left\{ \frac{\xi_2 P_2}{D_2 + P_2} Z_2 - cZ_2 \right\}. \tag{10}$$

Let us now change the time scale in order to obtain a new model with a fast time scale $T = \frac{t}{\epsilon}$. To do this we write the following relations

$$\epsilon \frac{dZ_i}{dt} = \frac{dZ_i}{dT}, \quad \epsilon \frac{dP_i}{dT} = \frac{dP_i}{dT}, \quad i = 1, 2. \quad (11)$$

Substituting (11) in system (B) we get

$$(C) \quad \frac{dP_1}{dT} = \epsilon P_1 \left\{ r_1 \left(1 - \frac{P_1 + \alpha_1 P_2}{K} \right) - \frac{w_1 Z_1}{D_1 + P_1} \right\}, \quad (12)$$

$$\frac{dP_2}{dT} = \epsilon P_2 \left\{ r_2 \left(1 - \frac{P_2 + \alpha_2 P_1}{K} \right) - \frac{w_2 Z_2}{D_2 + P_2} \right\}, \quad (13)$$

$$\frac{dZ_1}{dT} = (k_{12} Z_2 - k_{21} Z_1) + \epsilon \left\{ \frac{\xi_1 P_1}{D_1 + P_1} Z_1 - c Z_1 \right\}, \quad (14)$$

$$\frac{dZ_2}{dT} = (k_{21} Z_1 - k_{12} Z_2) - \epsilon \left\{ \frac{\xi_2 P_2}{D_2 + P_2} Z_2 - c Z_2 \right\}. \quad (15)$$

3.1. Formation of aggregated one

As we see, the dynamics in system (C) are driven by two parts one of which is small perturbation. We are now interested in the fast dynamics and therefore we neglect the small terms putting $\epsilon = 0$. Now the quantities $Z(T)$, $P_1(T)$, $P_2(T)$ are invariant for the fast dynamics. So,

$$Z_1(T) + Z_2(T) = Z(T). \quad (16)$$

The fast equilibrium is thus the solution of (16) and

$$\frac{dZ_1}{dT} = k_{12} Z_2 - k_{21} Z_1 = 0. \quad (17)$$

From 16 and 17 we get,

$$Z_1^* = v_1 Z \quad \text{and} \quad Z_2^* = v_2 Z, \quad (18)$$

where $v_1 = \frac{k_{12}}{k_{12} + k_{21}}$ and $v_2 = \frac{k_{21}}{k_{12} + k_{21}}$ are intra-population frequencies. Obviously the fast equilibrium point is hyperbolically stable, i.e. asymptotically stable. Aggregating Eqs. (14) and (15) we get

$$\frac{dZ}{dt} = \left\{ \frac{\xi_1 P_1 v_1}{D_1 + P_1} - \frac{\xi_2 P_2 v_2}{D_2 + P_2} - c \right\} Z. \quad (19)$$

Therefore the aggregated model system in original time scale becomes

$$(D) \quad \frac{dP_1}{dt} = P_1 \left\{ r_1 \left(1 - \frac{P_1 + \alpha_1 P_2}{K} \right) - \frac{\bar{w}_1 Z}{D_1 + P_1} \right\}, \quad (20)$$

$$\frac{dP_2}{dt} = P_2 \left\{ r_2 \left(1 - \frac{P_2 + \alpha_2 P_1}{K} \right) - \frac{\bar{w}_2 Z}{D_2 + P_2} \right\}, \quad (21)$$

$$\frac{dZ}{dt} = Z \left\{ \frac{\eta_1 P_1}{D_1 + P_1} - \frac{\eta_2 P_2}{D_2 + P_2} - c \right\}, \quad (22)$$

where $\eta_1 = v_1 \xi_1$, $\eta_2 = v_2 \xi_2$, $\bar{w}_1 = v_1 w_1$, $\bar{w}_2 = v_2 w_2$.

3.2. Analysis and result

3.2.1. Boundedness of the aggregated system with constant migration

All solutions of (D) which originate in R_+^3 are evidently confined in the region $B = \{(P_1, P_2, Z) \in R_+^3 : \alpha_2 P_1 + \alpha_1 P_2 + Z = \frac{M}{c} + \epsilon \text{ for all } \epsilon > 0\}$. (The proof is placed in the Appendix.)

3.2.2. Equilibria

The system (D) possesses the following equilibria:

- (i) The plankton-free equilibrium $E_0 = (0,0,0)$, always exist.
- (ii) TPP- and zooplankton-free equilibrium $E_1 = (K,0,0)$, always exist.
- (iii) NTP- and zooplankton-free equilibrium $E_2 = (0,K,0)$, always exist.
- (iv) Zooplankton-free equilibrium $E_3 = (\widehat{P}_1, \widehat{P}_2, 0)$, where

$$\widehat{P}_1 = \frac{K(\alpha_1 - 1)}{\alpha_1\alpha_2 - 1}, \quad \widehat{P}_2 = \frac{K(\alpha_2 - 1)}{\alpha_1\alpha_2 - 1},$$

exists if either $\alpha_1 > 1, \alpha_2 > 1$ or $\alpha_1 < 1, \alpha_2 < 1$.

- (v) TPP-free equilibrium $E_4 = (\overline{P}_1, 0, \bar{z}_1)$, where

$$\overline{P}_1 = \frac{cD_1}{\eta_1 - c}, \quad \bar{z}_1 = \frac{\eta_1 r_1 D_1 (K\eta_1 - c(K + D_1))}{\bar{w}_1 K (\eta_1 - c)^2}$$

exists if $\eta_1 > c(1 + \frac{D_1}{K})$.

- (vi) The interior equilibrium $E^* = (P_1^*, P_2^*, Z^*)$, where

$$P_1^* = \frac{D_1(\eta_2 P_2^* + cD_2 + cP_2^*)}{\eta_1 D_2 + \eta_1 P_2^* - \eta_2 P_2^* - cD_2 - cP_2^*}, \tag{23}$$

$$Z^* = \frac{r_2(D_2 + P_2^*)(K - P_2^* - \alpha_2 P_1^*)}{k\bar{w}_2} \tag{24}$$

and P_2^* is given by,

$$\theta_1(P_2^*)^3 + \theta_2(P_2^*)^2 + \theta_3 P_2^* + \theta_4 = 0 \tag{25}$$

with,

$$\begin{aligned} \theta_1 &= \bar{w}_1 r_2 (\eta_1 - \eta_2 - c)^2, \\ \theta_2 &= -(\eta_1 - \eta_2 - c) \{ -r_2 \bar{w}_1 (K + D_1 \alpha_2) \eta_2 + (-2r_2 \bar{w}_1 D_2 + r_2 \bar{w}_1 K + r_1 \bar{w}_2 D_1 \alpha_1) \eta_1 - r_2 \bar{w}_1 c (D_1 \alpha_2 + K - 2D_2) \}, \\ \theta_3 &= \{ r_2 \bar{w}_1 D_2^2 + (-2r_2 \bar{w}_1 K - r_1 \bar{w}_2 D_1 \alpha_1) D_2 + r_1 \bar{w}_2 D_1 K \} \eta_1^2 + [-r_1 \bar{w}_2 (c + \eta_2) D_1^2 \\ &\quad + \{ (-r_1 \bar{w}_2 K + r_2 \bar{w}_1 D_2 \alpha_2) \eta_2 - r_1 \bar{w}_2 K c + 2r_2 \bar{w}_1 \alpha_2 c D_2 + r_1 \bar{w}_2 \alpha_1 D_2 c \} D_1 + 2r_2 \bar{w}_1 D_2 K (\eta_2 + 2c) \\ &\quad - 2r_2 \bar{w}_1 D_2^2 c \} \eta_1 - r_2 \bar{w}_1 D_2 c \{ (2\alpha_2 c + 2\alpha_2 \eta_2) D_1 - cD_2 + K(2\eta_2 + 2c) \}, \text{ and} \\ \theta_4 &= D_2 \{ K(-r_2 \bar{w}_1 D_2 + r_1 \bar{w}_2 D_1) \eta_1^2 - c(r_1 \bar{w}_2 D_1^2 - 2r_2 \bar{w}_1 D_2 K - r_2 \bar{w}_1 \alpha_2 D_1 D_2 \\ &\quad + r_1 \bar{w}_2 D_1 K) \eta_1 - r_2 \bar{w}_1 c^2 D_2 (K + D_1 \alpha_2) \}. \end{aligned}$$

Therefore the condition for the existence of the unique interior equilibrium point is $\theta_2 < 0, \theta_3 < 0, \theta_4 < 0$: $\eta_1 D_2 + \eta_1 P_2^* - \eta_2 P_2^* - cD_2 - cP_2^* > 0, \quad K - P_2^* - \alpha_2 P_1^* > 0$.

Now to find a interior equilibrium point we consider the following parameter set [5]:

$$\begin{aligned} r_1 &= 0.4632/\text{day}, \quad r_2 = 0.4425/\text{day}, \quad w_1 = 0.6625/\text{day}, \quad w_2 = 0.435/\text{day}, \\ D_1 &= 45 \text{ nos./lit}, \quad D_2 = 30 \text{ nos./lit}, \quad \alpha_1 = 0.002, \quad \alpha_2 = 0.001, \quad \xi_1 = 0.516, \\ \xi_2 &= 0.6, \quad c = 0.109/\text{day}, \quad K = 505 \text{ nos./lit}. \end{aligned} \tag{26}$$

For $k_{12} = 4, k_{21} = 2$, the above parameter set gives an interior equilibrium point $E^*(281.4288624, 453.0032273, 150.9466031)$.

3.2.3. Stability analysis

- (i) The plankton-free equilibrium $E_0 = (0,0,0)$ is unstable saddle.
- (ii) TPP and zooplankton-free equilibrium $E_1 = (K,0,0)$ is unstable saddle.

- (iii) NTP and zooplankton-free equilibrium $E_2 = (0, K, 0)$ is unstable saddle.
- (iv) The zooplankton-free equilibrium $E_3 = (\widehat{P}_1, \widehat{P}_2, 0)$ is an unstable saddle under the conditions,
 - (i) $\eta_1 > \eta_2 + c$, (ii) $\widehat{P}_1 > \max\left\{\frac{D_1(\eta_2+c)}{\eta_1-\eta_2-c}, \frac{cD_1}{\eta_1-c}\right\}$.
- (v) The TPP-free equilibrium $E_4 = (\overline{P}_1, 0, \overline{Z})$ is locally unstable if $\frac{\alpha}{k} \overline{P}_1 + \frac{\omega_3}{r_2 D_2} \overline{z} < 1$.
- (vi) The interior equilibrium $E^*(P_1^*, P_2^*, Z^*)$ is locally asymptotically stable with respect to the parameter set (26), which gives the eigenvalues $\lambda_1 = -0.372215$, $\lambda_2 = -0.032139 - 1.98855i$, and $\lambda_3 = -0.032139 + 1.98855i$. The real part of the eigenvalues are negative, thus the interior equilibrium is locally asymptotically stable.

3.2.4. Bifurcation diagrams and interpretation

To explore how zooplankton migration affects the dynamics around the positive equilibrium we draw bifurcation diagram, with respect to k_{12} and k_{21} .

In the Fig. 2 we observe that when $\xi_2 = 0.6$ and $k_{21} = 2$, the system settles to the stable zooplankton free equilibrium point E_3 for $k_{12} < 3.7$, all plankton co-exist for $3.7 < k_{12} < 4.15$ and the system oscillates for $k_{12} > 4.15$. In this case the critical point, i.e. the point of Hopf-bifurcation is $k_{12}^c \simeq 4.15$. If we decrease the value of k_{21} then the critical value of k_{12} decreases. Similarly, if we decrease the value of ξ_2 then the critical value of k_{12} decreases (Table 1).

In the Fig. 3 we observe that when $\xi_2 = 0.6$ and $k_{12} = 6$, the system oscillates for $k_{21} < 3$, all plankton co-exist for $3 < k_{21} < 3.4$ and settles to the stable zooplankton-free equilibrium E_3 for $k_{21} > 3.4$. In this case the critical point, i.e. the point of Hopf-bifurcation is $k_{21}^c \simeq 3$. Further simulations suggest that, for a fixed value of ξ_2 , the critical value k_{21}^c increases with increase of k_{12} (Table 2). However, for a fixed value of k_{12} , the critical value k_{21}^c decreases with increase of ξ_2 .

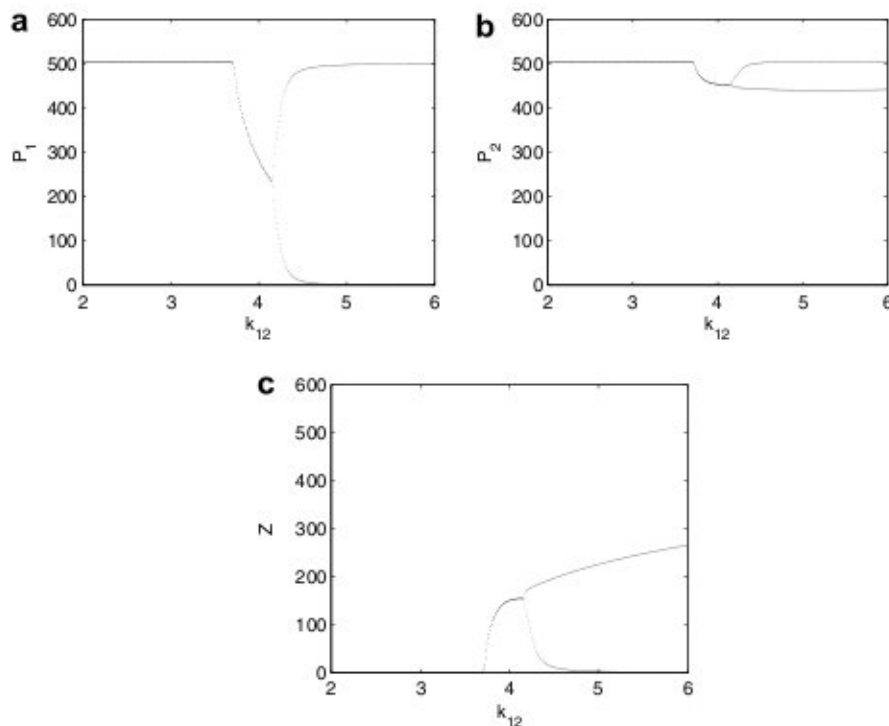


Fig. 2. Bifurcation diagram of the aggregated system (20)–(22) with constant migration has drawn taking $k_{21} = 2$, $\xi_2 = 0.6$ and $2 \leq k_{12} \leq 6$.

Table 1
Critical values of the migration parameter K_{12} corresponding to different values of ξ_2 and K_{21}

ξ_2	k_{21}	k_{12}^c
0.6	2	4.15
0.4	2	2.95
0.6	1	2.07
0.4	1	1.48

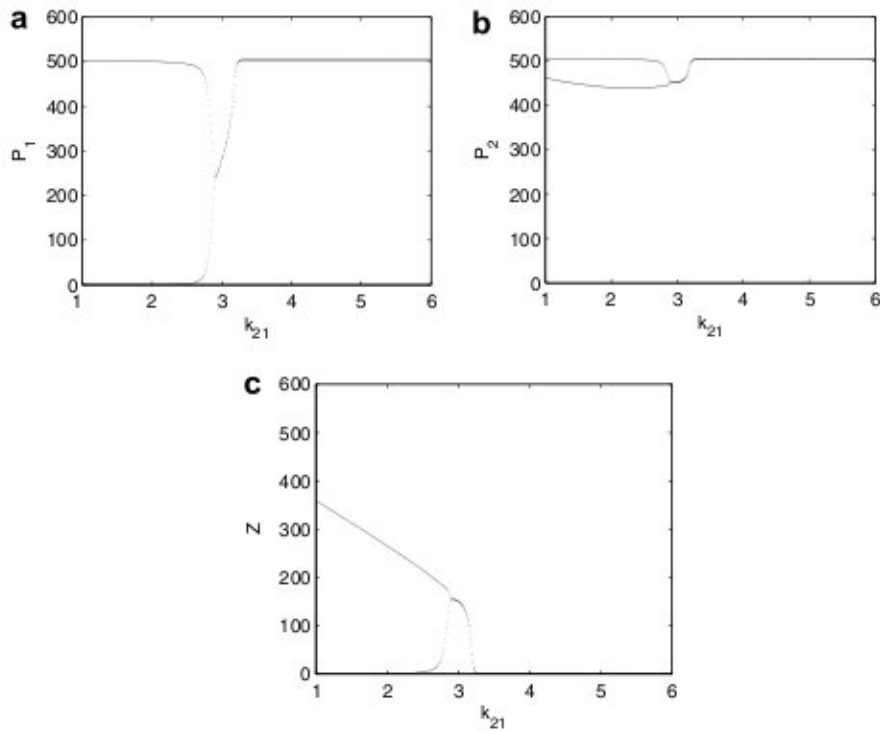


Fig. 3. Bifurcation diagram of the aggregated system (20)–(22) with constant migration has drawn taking $k_{12} = 6$, $\xi_2 = 0.6$ and $1 \leq k_{21} \leq 6$.

Table 2
Critical values of the migration parameter K_{21} corresponding to different values of ξ_2 and K_{12}

ξ_2	k_{12}	k_{21}^c
0.6	6	3.00
0.4	6	4.05
0.6	4	1.93
0.4	4	2.70

4. Model 2: Variable migration

An individual of zooplankton Z prefers to move from P_1 to P_2 when P_2 is more vulnerable and from P_2 to P_1 when P_1 is in the opposite case. Thus their migration rates are not simply constant but proportional to the density of the preferable patch. So we take

$$K_{12} = \frac{k_{12}P_1}{\epsilon}, \quad K_{21} = \frac{k_{21}P_2}{\epsilon}, \tag{27}$$

where ϵ is a small dimensionless number and k_{12}, k_{21} are positive constant of same order of magnitude as the other parameters.

With this assumption system (A) becomes

$$(E) \quad \frac{dP_1}{dT} = \epsilon P_1 \left\{ r_1 \left(1 - \frac{P_1 + \alpha_1 P_2}{K} \right) - \frac{w_1 Z_1}{D_1 + P_1} \right\}, \quad (28)$$

$$\frac{dP_2}{dT} = \epsilon P_2 \left\{ r_2 \left(1 - \frac{P_2 + \alpha_2 P_1}{K} \right) - \frac{w_2 Z_2}{D_2 + P_2} \right\}, \quad (29)$$

$$\frac{dZ_1}{dT} = (k_{12} P_1 Z_2 - k_{21} P_2 Z_1) + \epsilon \left\{ \frac{\xi_1 P_1}{D_1 + P_1} Z_1 - c Z_1 \right\}, \quad (30)$$

$$\frac{dZ_2}{dT} = (k_{21} P_2 Z_1 - k_{12} P_1 Z_2) - \epsilon \left\{ \frac{\xi_2 P_2}{D_2 + P_2} Z_2 - c Z_2 \right\}. \quad (31)$$

Fast equilibrium is thus solution of

$$\frac{dZ_1}{dT} = k_{12} P_1 Z_2 - k_{21} P_2 Z_1 = 0 \quad (32)$$

and

$$Z_1(T) + Z_2(T) = Z(T), \quad (33)$$

which gives

$$Z_1^* = \frac{k_{12} P_1}{k_{12} P_1 + k_{21} P_2} Z \Rightarrow v_1 = \frac{k_{12} P_1}{k_{12} P_1 + k_{21} P_2}, \quad (34)$$

$$Z_2^* = \frac{k_{21} P_2}{k_{12} P_1 + k_{21} P_2} Z \Rightarrow v_2 = \frac{k_{21} P_2}{k_{12} P_1 + k_{21} P_2}, \quad (35)$$

where v_1 and v_2 are equilibrium frequencies of zooplankton are no longer constant. The associated aggregated model is

$$(F) \quad \frac{dP_1}{dt} = P_1 \left\{ r_1 \left(1 - \frac{P_1 + \alpha_1 P_2}{K} \right) - \frac{\bar{w}_1 k_{12} P_1 Z}{(D_1 + P_1)(k_{12} P_1 + k_{21} P_2)} \right\}, \quad (36)$$

$$\frac{dP_2}{dt} = P_2 \left\{ r_2 \left(1 - \frac{P_2 + \alpha_2 P_1}{K} \right) - \frac{\bar{w}_2 k_{21} P_2 Z}{(D_2 + P_2)(k_{12} P_1 + k_{21} P_2)} \right\}, \quad (37)$$

$$\frac{dZ}{dt} = \frac{Z}{k_{12} P_1 + k_{21} P_2} \left\{ \frac{\xi_1 k_{12} P_1^2}{D_1 + P_1} - \frac{\xi_2 k_{21} P_2^2}{D_2 + P_2} \right\} - c Z. \quad (38)$$

4.1. Analysis and result

4.1.1. Boundedness of the aggregated system with variable migration

All solution of (D) which originate in R_+^3 are evidently confined in the region $B = \{(P_1, P_2, Z) \in R_+^3 : \alpha_2 P_1 + \alpha_1 P_2 + Z = \frac{M}{c} + \epsilon \text{ for all } \epsilon > 0\}$. (The proof is placed in the Appendix.)

4.1.2. Equilibria

The system (D) possesses the following equilibria:

- (i) The plankton-free equilibrium, $E_0 = (0, 0, 0)$, always exist.
- (ii) TPP- and zooplankton-free equilibrium, $E_1 = (K, 0, 0)$, always exist.
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- (iv) Zooplankton-free equilibrium, $E_3 = (\widehat{P}_1, \widehat{P}_2, 0)$, where

$$\widehat{P}_1 = \frac{K(\alpha_1 - 1)}{\alpha_1\alpha_2 - 1}, \quad \widehat{P}_2 = \frac{K(\alpha_2 - 1)}{\alpha_1\alpha_2 - 1},$$

exists if either $\alpha_1 > 1, \alpha_2 > 1$ or $\alpha_1 < 1, \alpha_2 < 1$.

(v) TPP-free equilibrium, $E_4 = (\overline{P}_1, 0, \bar{z}_1)$, where

$$\overline{P}_1 = \frac{cD_1}{\xi_1 - c}, \quad \bar{z}_1 = \frac{\xi_1 r_1 D_1 (K \xi_1 - c(K + D_1))}{w_1 K (\xi_1 - c)^2},$$

exists if $\xi_1 > c(1 + \frac{D_1}{K})$.

(vi) The interior equilibrium $E^* = (P_1^*, P_2^*, Z^*)$, where P_1^*, P_2^*, Z^* are the solution of the system of equations:

$$r_1 \left(1 - \frac{P_1 + \alpha_1 P_2}{K} \right) - \frac{w_1 k_{12} P_1 Z}{(D_1 + P_1)(k_{12} P_1 + k_{21} P_2)} = 0, \tag{39}$$

$$r_2 \left(1 - \frac{P_2 + \alpha_2 P_1}{K} \right) - \frac{w_2 k_{21} P_2 Z}{(D_2 + P_2)(k_{12} P_1 + k_{21} P_2)} = 0, \tag{40}$$

$$\frac{\xi_1 k_{12} P_1^2}{D_1 + P_1} - \frac{\xi_2 k_{21} P_2^2}{D_2 + P_2} - c(k_{12} P_1 + k_{21} P_2) = 0. \tag{41}$$

We solve the above system taking the set of parameters (26) and get a interior equilibrium point E^* (455.5279779, 487.2934701, 51.58329453).

4.1.3. Stability analysis

- (i) The plankton-free equilibrium $E_0 = (0,0,0)$ is unstable saddle.
- (ii) TPP and zooplankton-free equilibrium $E_1 = (K,0,0)$ is unstable saddle.

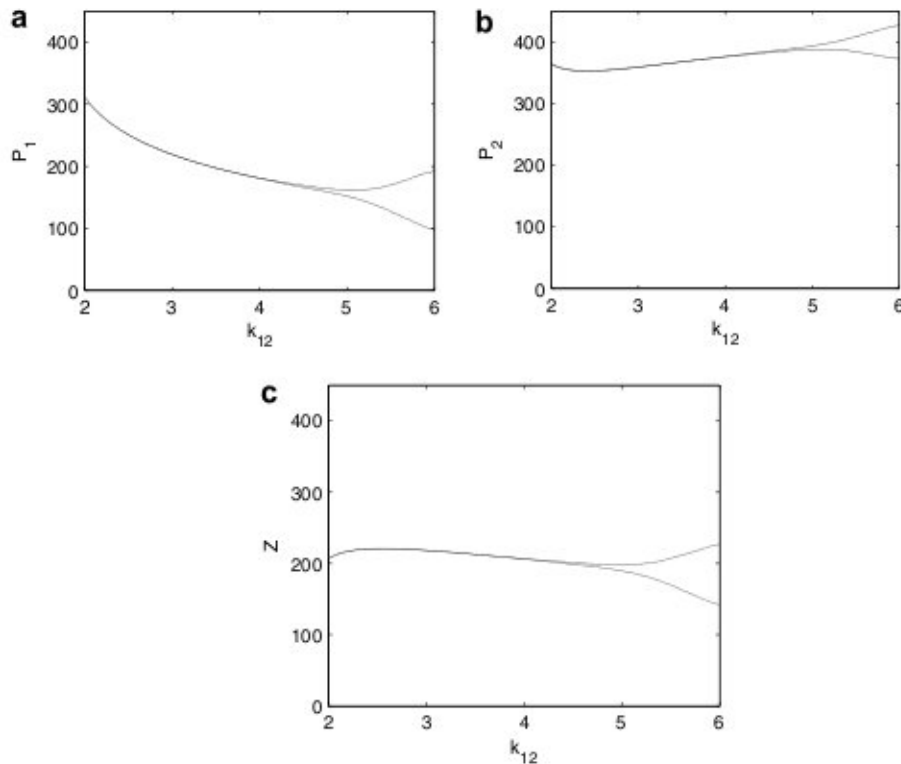


Fig. 4. Bifurcation diagram of the aggregated system (36)–(38) with variable migration has drawn taking $k_{21} = 2, \xi_2 = 0.198$ and $2 \leq k_{12} \leq 6$.

- (iii) NTP and zooplankton-free equilibrium $E_2 = (0, K, 0)$ is unstable saddle.
 (iv) The zooplankton-free equilibrium $E_3 = (\widehat{P}_1, \widehat{P}_2, 0)$ is an unstable saddle under the conditions,

$$\xi_1 k_{12} \widehat{P}_1^2 (D_2 + \widehat{P}_2) > \xi_2 k_{21} \widehat{P}_1^2 (D_1 + \widehat{P}_1) + c(k_{12} P_1 + k_{21} P_2)(D_2 + \widehat{P}_2)(D_1 + \widehat{P}_1).$$

- (v) The TPP-free equilibrium $E_4 = (\overline{P}_1, 0, \overline{Z})$ is locally unstable if $K > \frac{\alpha_2 CD_1}{\xi_1 - c}$.
 (vi) The interior equilibrium $E^*(P_1^*, P_2^*, Z^*)$ is locally asymptotically stable with respect to the parameter set (26).

4.1.4. Bifurcation diagrams and interpretation

In the case of variable migration i.e. when the migration parameters are proportional to the density of the phytoplankton we see in Figs. 4 and 5 that the model dynamics around the interior equilibrium at the estimated $\xi_2 = 0.198$ depends on the migration parameters k_{12} and k_{21} . Fixing the value of $k_{21} = 2.0$, if we increase the migration parameter k_{12} the dynamics passes from stability to oscillation through a point of Hopf-bifurcation (Fig. 4). This result suggests that if the migration parameter k_{12} is increased, the model system moves towards high amplitude oscillation. On the other hand, if we fix the value of $k_{12} = 6.0$, and increase the value of k_{21} the dynamics around the interior equilibrium passes from oscillation to stability through a point of Hopf-bifurcation (Fig. 5). This result suggests that the model system moves towards stability if the migration parameter k_{21} is high. However, given a fixed pair of values of $k_{12} = 5$ and $k_{21} = 1$, there exist a small interval of the toxin inhibition parameter $0.36 < \xi_2 < 0.37$ for which the system coexist in stable equilibrium (Fig. 6).

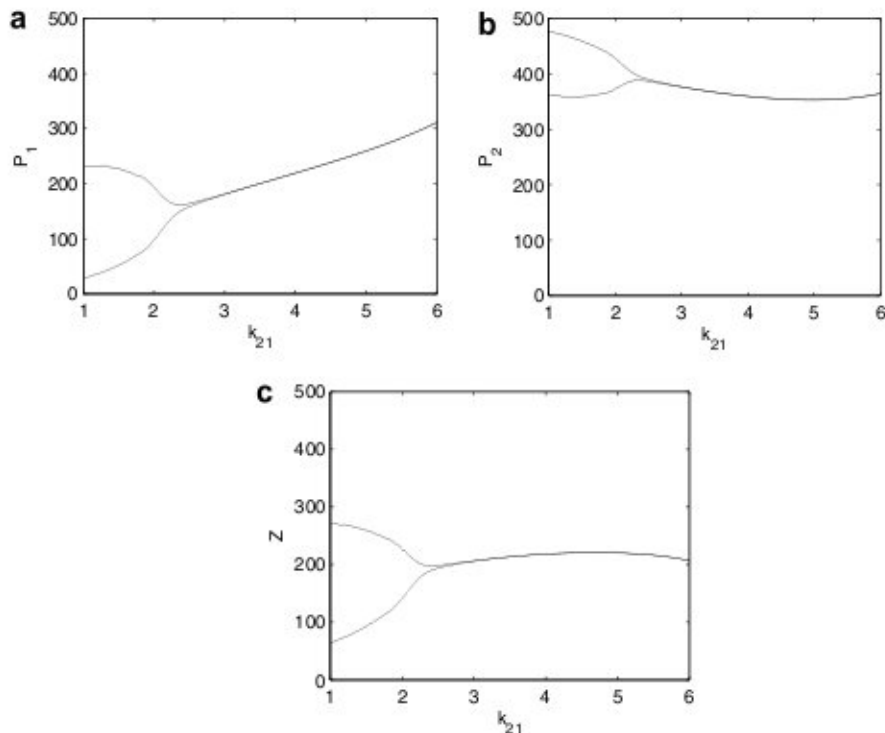


Fig. 5. Bifurcations diagrams of the aggregated system (36)–(38) with variable migration has drawn taking $k_{12} = 6$, $\xi_2 = 0.198$ and $1 \leq k_{21} \leq 6$.

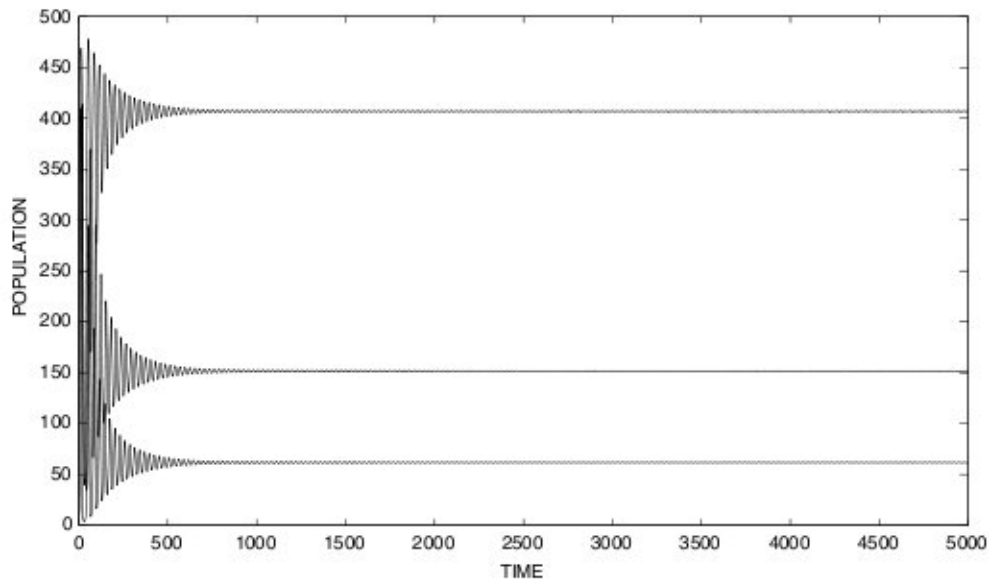


Fig. 6. Time series solution of (36)–(38) for $k_{12} = 5$, $k_{21} = 1$, $\xi_2 = 0.037$.

5. Discussion

Migratory grazing of zooplankton between NTP and TPP is a realistic phenomena unexplored so far. Through their mathematical model Roy et al. [5] have demonstrated how the toxin inhibition parameter due to TPP determines the dynamics of NTP–TPP–zooplankton systems. Extending their model, we consider the migratory grazing of zooplankton between NTP and TPP. Our analysis concentrates mainly on exploring the effects of three parameters, namely, rate at which zooplankton are migrating from NTP dense population place to TPP dense population (k_{21}), rate at which zooplankton are migrating from TPP dense population to NTP dense population (k_{12}) and the toxin inhibition parameter ξ_2 .

Zooplankton migration has been considered firstly as a constant and then as dependent on phytoplankton density. For both the cases, we have demonstrated the asymptotic dynamics of the model system around the interior equilibrium. However, this dynamics changes significantly for different combination of the migration parameters and toxin inhibition parameter. In the case of constant migration, the values of any of the migration parameters (k_{12} or k_{21}) at which point of Hopf-bifurcation occurs varies with the values of other migration parameter (k_{21} or k_{12}) and that of the toxin inhibition parameter (ξ_2). Our analysis demonstrates that for a fixed value of ξ_2 , if the migration parameter k_{12} increases, a higher value of the migration parameter k_{21} is needed for the stability of the dynamics around the coexisting equilibrium. Similarly, in the case of density-dependent migration, we find that, higher the migration rate k_{12} more likely to get dynamic oscillation, and greater the migration rate k_{21} more likely to get dynamic stability.

Biologically these results mean that, if the toxin inhibition parameter ξ_2 remains constant and the zooplankton consumes NTP more than TPP, the system is likely to exhibit oscillation, whereas, if zooplankton consumes TPP more than NTP, the system is likely to exhibit stability. These results are comparable with the study of Roy et al. [5]. They [5] demonstrated that for higher toxin inhibition parameter dynamic stability is desirable, and we find that for a constant toxin inhibition more inclination towards TPP (through migratory behaviour) leads to stability. Thus, our results establishes that along with the inhibition effects of TPP, the migratory effects of zooplankton have a great impact in determining the stability of the phytoplankton–zooplankton dynamics. We suggest that while addressing the question of plankton dynamics, the migratory grazing of zooplankton might be considered as a significant factor along with the rate parameters.

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Appendix A. The proof of boundedness of model 1

We define a function:

$$W = a_1P_1 + a_2P_2 + Z. \quad (42)$$

The time derivative of (24) along the solution of (D) is

$$\begin{aligned} \frac{dW}{dt} &= a_1 \frac{dP_1}{dt} + a_2 \frac{dP_2}{dt} + \frac{dZ}{dt} + a_1P_1 \left\{ r_1 \left(1 - \frac{P_1 + \alpha_2P_2}{K} \right) - \frac{\bar{w}_1Z}{D_1 + P_1} \right\} \\ &\quad + a_2P_2 \left\{ r_2 \left(1 - \frac{P_2 + \alpha_2P_1}{K} \right) - \frac{\bar{w}_2Z}{D_2 + P_2} \right\} + Z \left\{ \frac{\eta_1P_1}{D_1 + P_1} - \frac{\eta_2P_2}{D_2 + P_2} - c \right\} \\ &= a_1P_1r_1 \left(1 - \frac{P_1}{K} \right) + a_2P_2r_2 \left(1 - \frac{P_2}{K} \right) - \frac{a_1r_1\alpha_1P_1P_2}{K} - \frac{a_2r_2\alpha_2P_1P_2}{K} \\ &\quad + \frac{\eta_1 - a_1\bar{w}_1}{D_1 + P_1} P_1Z - \frac{\eta_2 + a_2\bar{w}_2}{D_2 + P_2} P_2Z - cZ, \\ \Rightarrow \frac{dW}{dt} + cW &= \alpha_2P_1 \left(r_1 + c - \frac{r_1}{K}P_1 \right) + \alpha_1P_2 \left(r_2 + c - \frac{r_2}{K}P_2 \right) - \frac{b_1r_1\alpha_1P_1P_2}{K} - \frac{b_2r_2\alpha_2P_1P_2}{K} \\ &\quad - \frac{a_1\bar{w}_1 - \eta_1}{D_1 + P_1} P_1Z - \frac{a_2\bar{w}_2 + \eta_2}{D_2 + P_2} P_2Z, \quad \text{provided } a_1 > \frac{\eta_1}{\bar{w}_1} > 0 \\ &\leq \alpha_2P_1 \left(r_1 + c - \frac{r_1}{K}P_1 \right) + \alpha_1P_2 \left(r_2 + c - \frac{r_2}{K}P_2 \right), \\ \Rightarrow \frac{dW}{dt} + cW &\leq \alpha_2 \frac{(r_1 + c)^2}{4\left(\frac{r_1}{K}\right)} + \alpha_1 \frac{(r_2 + c)^2}{4\left(\frac{r_2}{K}\right)} = M. \end{aligned}$$

Applying the theory of differential inequality [15] we get,

$$0 < W(P_1, P_2, Z) \leq \frac{M}{c} (1 - e^{-ct}) + W(P_1(0), P_2(0), Z(0))e^{-ct} \Rightarrow 0 < W < \frac{M}{\mu} \quad \text{as } t \rightarrow \infty.$$

Hence all solution of (D) which originate in R_+^3 are evidently confined in the region

$$B = \{(P_1, P_2, Z) \in R_+^3 : \alpha_2P_1 + \alpha_1P_2 + Z = \frac{M}{c} + \epsilon \quad \text{for all } \epsilon > 0\}. \quad \square$$

Appendix B. The proof of boundedness of model 2

We define a function

$$W = a_1P_1 + a_2P_2 + Z. \quad (43)$$

The time derivative of (24) along the solution of (D) is

$$\begin{aligned} \frac{dW}{dt} &= a_1 \frac{dP_1}{dt} + a_2 \frac{dP_2}{dt} + \frac{dZ}{dt} \\ &= a_1P_1 \left\{ r_1 \left(1 - \frac{P_1 + \alpha_1P_2}{K} \right) - \frac{w_1k_{12}P_1Z}{(D_1 + P_1)(k_{12}P_1 + k_{21}P_2)} \right\} \\ &\quad + a_2P_2 \left\{ r_2 \left(1 - \frac{P_2 + \alpha_2P_1}{K} \right) - \frac{w_2k_{21}P_2Z}{(D_2 + P_2)(k_{12}P_1 + k_{21}P_2)} \right\} \end{aligned}$$

$$\begin{aligned}
& + \frac{Z}{k_{12}P_1 + k_{21}P_2} \left\{ \frac{\xi_1 k_{12} P_1^2}{D_1 + P_1} - \frac{\xi_2 k_{21} P_2^2}{D_2 + P_2} \right\} - cZ \\
& = a_1 P_1 r_1 \left(1 - \frac{P_1}{K} \right) + a_2 P_2 r_2 \left(1 - \frac{P_2}{K} \right) - \frac{a_1 r_1 \alpha_1 P_1 P_2}{K} - \frac{a_2 r_2 \alpha_2 P_1 P_2}{K} - cZ \\
& + \frac{(\xi_1 - a_1 w_1) P_1^2 Z k_{12}}{(D_1 + P_1)(k_{12} P_1 + k_{21} P_2)} - \frac{(\xi_2 + a_2 w_2) P_2^2 Z k_{21}}{(D_2 + P_2)(k_{12} P_1 + k_{21} P_2)}, \\
\Rightarrow \frac{dW}{dt} + cW & = \alpha_2 P_1 \left(r_1 + c - \frac{r_1}{K} P_1 \right) + \alpha_1 P_2 \left(r_2 + c - \frac{r_2}{K} P_2 \right) - \frac{a_1 r_1 \alpha_1 P_1 P_2}{K} - \frac{a_2 r_2 \alpha_2 P_1 P_2}{K} \\
& - \frac{(a_1 w_1 - \xi_1) P_1^2 Z k_{12}}{(D_1 + P_1)(k_{12} P_1 + k_{21} P_2)} - \frac{(a_2 w_2 + \xi_2) P_2^2 Z k_{21}}{(D_2 + P_2)(k_{12} P_1 + k_{21} P_2)} \\
& \leq \alpha_2 P_1 \left(r_1 + c - \frac{r_1}{K} P_1 \right) + \alpha_1 P_2 \left(r_2 + c - \frac{r_2}{K} P_2 \right) \quad \text{provided } a_1 > \frac{\xi_1}{w_1} > 0, \\
\Rightarrow \frac{dW}{dt} + cW & \leq \alpha_2 \frac{(r_1 + c)^2}{4\left(\frac{r_1}{K}\right)} + \alpha_1 \frac{(r_2 + c)^2}{4\left(\frac{r_2}{K}\right)} = M.
\end{aligned}$$

Applying the theory of differential inequality we get

$$0 < W(P_1, P_2, Z) \leq \frac{M}{c} (1 - e^{-ct}) + W(P_1(0), P_2(0), Z(0)) e^{-ct} \Rightarrow 0 < W < \frac{M}{\mu} \quad \text{as } t \rightarrow \infty.$$

Hence all solution of (D) which originate in R_+^3 are evidently confined in the region

$$B = \{(P_1, P_2, Z) \in R_+^3 : \alpha_2 P_1 + \alpha_1 P_2 + Z = \frac{M}{c} + \epsilon \quad \text{for all } \epsilon > 0\}. \quad \square$$

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