Ecological Complexity 41 (2020) 100812

Contents lists available at ScienceDirect

Ecological Complexity

journal homepage: www.elsevier.com/locate/ecocom

Dynamics of stage-structure predator-prey systems under density-dependent effect and mortality

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ARTICLE INFO

Keywords:
Stability
Routh–Hurwitz criteria
Density-dependent
Harvesting
Hydra effect

ABSTRACT

We develop a four dimensional predator-prey system in continuous time with stage-structure for both the communities. The reproduction rate of the prey and the transition rate for the predator, in our model, are assumed to be density-dependent. The stability results for the coexisting equilibrium are obtained by making use of Routh–Hurwitz criteria. Because of the density-dependent effects, numerical simulations are applied in complex situations. We observe that increasing values of the coefficients linked with density-dependent term promote the stability of the coexisting steady state. Our main focus is to understand the variation of stocks when mortality rates on different stage classes are increased. We verified that stable stock on mature predator increases with its increasing mortality rate in three different modeling frameworks. However, no such positive effect on the biomass of the immature predator occurs when immature predators are removed, culled or harvested. Therefore, we could conclude that the appearance of hydra effect on many unstructured predator-prey models is due to the mortality of the mature predator only. No hydra effect is also detected when mature prey is removed in several situations we discussed. Overall, the obtained results are new and could be interesting contribution in theoretical ecology.

1. Introduction

Mathematical models have become popular and useful to describe population dynamics in the current century. After the appearance of Lotka-Volterra model, there have been significant developments for multi-species modeling and analysis without stage and spatial structures. However, relatively less attention is paid to explore stage-structure predator-prey models. In this paper, we propose a predator-prey system with stage-structure for both the species, and investigate the dynamic modes under density-dependent effects and mortality rates.

Several articles were devoted to study the dynamics of structured populations by modeling the two stages either for prey or predator community. Some of the contribution also incorporated time delay growth factor in the structured predator-prey system. Wang and Chen (1997) developed a time delay predator-prey model with two stages (mature and immature classes) for predators and derived the condition for permanence of the system, existence of closed orbit and global stability of the unique equilibrium. The same research group (Zhang et al. (2000)) set up another model with two stages for prey community and established the results on global stability and optimal harvesting policy implemented on mature prey. A delayed model with stage-structure for both prey and predator was designed by Ma et al. (2008) and obtained the sufficient condition for the permanence of the specialist predators. Very recently Neverova et al. (2019) proposed a model with stage-structure for the prey and predator in discrete time to study the influence of inter-specific interaction. Stage structure for prey species in a predator-prey system was investigated by Liu et al. (2009) to prove the existence of singularity-induced bifurcation. Stage-structure for preys was built, combined with Beddington-DeAngelis and Holling type-IV functional responses, by Huang et al. (2010) to obtain the necessary and sufficient conditions for the permanence of the system. Liu and Wang (2011) proposed a model with stage-structure for prey where predators consumed the mature prey only. They discussed about the global stability of the coexisting steady state. Detailed Hopf-bifurcation analysis has been discussed in a recent paper by considering stage-structure for preys (Wei and

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https://doi.org/10.1016/j.ecocom.2020.100812
Received 3 July 2019; Received in revised form 23 December 2019; Accepted 5 January 2020
1476-945X/

Fu, 2016).

The above scholars mostly developed models with density-independent per capita growth rate of immature populations. More general models with density-dependent (density of mature prey class) per capita growth rate of immature prey were explored by Abrams and Quince (2005). They established the stability condition and examined the impact of predator mortality. Most of the contributions (except Ma et al., 2008; Neverova et al., 2019), including Abrams and Quince (2005), proposed predator-prey community dynamics with stages either for prey or predator. Ma et al. (2008) obtained the persistence of populations, but no discussion was provided for the existence of equilibrium, limit cycle and their stability. On the other hand, predators with single stage is proposed (three dimensional model) in Abrams and Quince (2005), which allowed to derive many analytical results for establishing local stability. In this article, we develop dynamics of predator-prey system with stage-structure for both the populations. The density-dependent term in growth function for populations are incorporated into the model. The analysis of the model can be divided into two parts: (i) The role of density-dependent effects on establishing stable steady state, and (ii) The impact of linear mortality of mature prey, mature and immature predator on stock estimation.

We first analyze the model dynamics under different inter-specific competition coefficients due to density-dependent effect in the growth term. It is observed that intra-specific competition is the effect of limited food and habitat availability among a population community. However, it produces many desirable ecological results. Kar and Ghosh (2013) have proved that intra-specific competition among predator may have a potential role to produce maximum yield from prey species. Otherwise, predator species, without intra-specific competition, surely goes to extinction. On the other hand, a global stability of the interior point is established due to the intra-specific competition among predator in a delayed Beddington-DeAngelis predator-prey model by Li and Takeuchi (2011). We focus to investigate the potential role of different types of intra-specific competition coefficients in stabilization the coexisting equilibrium.

Our conventional knowledge suggests that mortality of a species decreases its own biomass. However, theoretical (Abrams, 2015; Matsuda and Abrams, 2004; Sieber and Hilker, 2012) and empirical (Schröder et al., 2014) results, in the current decade, prove that increasing mortality can induce a positive impact on the stock of the same species. This is a paradoxical result and coined as hydra effect by Abrams and Matsuda (Abrams and Matsuda, 2005; Matsuda and Abrams, 2004). Cortez and Abrams (2016) investigated different predator-prey and food chain systems where hydra effect occur. Recently, Costa and dos Anjos (2018) established the existence of multiple hydra effect in a predator-prey system involving Allee effect and mutual interference among predators. Very recent development by Pal et al. (2019) ensures the existence of hydra effect in Rosenzweig-MacArthur type food chain with trophic level more than four. A complete scenario for stock variations has been displayed in a table for harvesting individual trophic level. There are also significant contributions on hydra effect for discrete-time single (Liz and Ruiz-Herrera, 2012) and multi-species (Neverova et al., 2018; Weide et al., 2019) community.

Predator-prey models with two stages for prey and without density-dependent term for predator species were studied by Abrams and Quince (2005). They showed that predator biomass increases at stable state when its mortality rate is increased. Schröder et al. (2014) demonstrated that hydra effect is a common feature in a stage-structured community instead of unstructured ones. Recent research based on a predator-prey system with generalist predator and stage-structure for both the populations has been conducted by Costa et al. (2017). They proved that adding more predator causes an enhancement of stable biomass for the adult prey. Clearly, the research outcomes on stage-structured models are relatively less in the context of hydra effect. Therefore, we attempt to explore stage-structure systems for examining the positive effect on stable stock due to mortality.

The paper is organized as follows: In Section 2 we propose a continuous-time predator-prey model with stage-structure for both the community. Different assumptions in developing the model are described therein. The local stability of the coexisting equilibrium, by analytical and numerical methods, are presented in Section 3. Here, we mostly focus to understand the effects of density-dependent terms on stability behavior of the coexisting equilibrium. The Section 4 is devoted to estimate the stable stock of the population when either mature prey, mature and immature predator stage are removed (harvested) by means of increasing linear mortality. The discussion along with conclusion and future perspective are provided in the last section.

2. Model

In this section we propose a stage-structure predator-prey model in continuous time. To develop the model we assume the followings:

(A) We consider that both the prey and predator have two stages: immature (younger) and mature (adult) classes. There are several studies, as reported in the Introduction section, where either prey or predator has two stage classes. In such a situation, we can think that one community evolves rapidly in comparison to the other one. For example, predator species (predatory fish) may evolve more rapidly than the prey populations (prey fish with smaller size). Because, prey fish may survive for short time and their life cycles might not be separated. Hence, considering stage-structure for predator species in models are more justified. We assume that both prey and predator evolve in the similar time scale. Hence stage-structure for both populations are incorporated into our model.

(B) It is well accepted that mature age classes are capable to reproduce offspring. Thus, reproduction rate must depend upon the existing mature class in the respective community. We assume that reproductive rate for prey (resp. predator) is density-dependent (resp. independent). On the other hand, the transfer rate for immature prey (resp. predator) to the mature stage to be density-independent (resp. dependent). The transfer rate is the only density-dependent term for predator growth in our model. Density-dependent-transition rate is plausible in many fish population dynamics as discussed by Abrams and Quince (2005). They assumed the density-dependent transition for prey populations.

(C) Only the mature predator class take part in predation and they prefer to consume only the mature prey population in our model. We modeled the predation process by the Holling-type II functional (and numerical) response (Holling, 1965). There are several studies where unstructured predator consume either immature prey (Zhang et al., 2000), mature prey (Wei and Fu, 2016) or both the stage classes (Naji and Majeed, 2016). If the size of the mature prey stages are relatively larger than immature predators, immature predator may not be able to handle mature prey. In this case, they can consume the immature prey only. On the other hand, immature prey are more easily accessible to the mature predator class, but they may not prefer the immature prey because of less nutrient value. Therefore, mature prey are in favor to the mature predator for predation. Ma et al. (2008) have assumed that mature predators only consumed the mature prey stage.

(D) We consider density-dependent mortality for mature prey populations.

On the basis of our specific axioms, the model takes the form:

$$\begin{aligned}
\frac{dx_1}{dt} &= r_1x_2(1-c_1x_2) - b_1x_1 - \mu_1x_1\\
\frac{dx_2}{dt} &= b_1x_1 - \gamma x_2^2 - \frac{\alpha x_2y_2}{h+x_2} - \mu_2x_2\\
\frac{dy_1}{dt} &= r_2y_2 - b_2y_1(1-c_2y_1) - m_1y_1\\
\frac{dy_2}{dt} &= b_2y_1(1-c_2y_1) + \frac{\beta\alpha x_2y_2}{h+x_2} - m_2y_2,
\end{aligned} \tag{1}$$

where x_1 and x_2 (resp. y_1 and y_2) are the biomass of the juvenile and adult prey (resp. predator) at any time t. The nonlinear function $r_1x_1(1-c_1x_2)$ represents the density-dependent reproductive rate for immature prey where r_1 is the maximum per capita growth rate of the adult prey and c_1 is the rate at which per capita birth rate is decreased with increased density of the adult prey. b_1 is the transition rate of immature prey to the mature class. On the other hand, $b_2y_1(1-c_2y_1)$ is referred as the density-dependent transfer rate of immature predator to adult predator where b_2 is the maximum per capita growth rate of the adult predator and c_2 is the rate at which per capita birth rate is decreased for adult class with its increasing density. μ_i's (and m_i's) are the specific death rate of the prey (and predator) stages i ($i = 1, 2$). The strength of the intra-specific competition among adult prey is indicated by γ and hence the term γx_2^2 is referred to the crowding effect among mature predator class. Holling type II functional response $\alpha x_2/(h+x_2)$ is considered for predation with α as the attack rate, β as the conversion coefficient and h as the half saturation constant.

3. Model analysis: Role of density-dependent effects

We analyze the model by determining the equilibria and establish some parameter conditions for which stability behavior of the equilibria are ensured. Note that the growth functions for immature stages are nonlinear of the state variables. Therefore, it seems difficult to investigate the model by finding the equilibria and stability conditions explicitly in term of parameters. We start our analysis for a relatively simple model configuration with $c_1 = c_2 = 0$. On later stage, simulations work would be performed to address more complex situations by considering $c_1 \neq 0$ or $c_2 \neq 0$.

3.1. Dynamics of the simple model

When we set $c_1 = c_2 = 0$, the general model is converted into

$$\begin{aligned}
\frac{dx_1}{dt} &= r_1x_2 - b_1x_1 - \mu_1x_1\\
\frac{dx_2}{dt} &= b_1x_1 - \gamma x_2^2 - \frac{\alpha x_2y_2}{h+x_2} - \mu_2x_2\\
\frac{dy_1}{dt} &= r_2y_2 - b_2y_1 - m_1y_1\\
\frac{dy_2}{dt} &= b_2y_1 + \frac{\beta\alpha x_2y_2}{h+x_2} - m_2y_2.
\end{aligned} \tag{2}$$

The above parameter choice makes the growth functions for immature stages more simpler, and hence it allows us to produce some of the results analytically.

3.1.1. Equilibria

The steady states of the model (2) are:

(i) The trivial equilibrium $S^0(0, 0, 0, 0)$. This equilibrium always exists without any parameter condition.

(ii) The predator extinction equilibrium $\bar{S}(\bar{x}_1, \bar{x}_2, 0, 0)$ with

$$\bar{x}_1 = \frac{r_1}{b_1+\mu_1}\bar{x}_2 \text{ and } \bar{x}_2 = \frac{r_1b_1 - \mu_2(b_1+\mu_1)}{\gamma(b_1+\mu_1)}.$$

The above equilibrium exists when $r_1b_1 > \mu_2(b_1+\mu_1)$.

(iii) The unique coexisting equilibrium $S^*(x_1^*, x_2^*, y_1^*, y_2^*)$, where

$$x_1^* = \frac{r_1}{b_1+\mu_1}x_2^* \text{ and } y_1^* = \frac{r_2}{b_2+m_1}y_2^*.$$

We determine x_2^* from the adult predators' nulcline. Thus, x_2^* is the positive solution of

$$\frac{r_2b_2}{b_2+m_1} - m_2 + \frac{\beta\alpha x_2^*}{h+x_2^*} = 0,$$

provided

$$r_2b_2 < m_2(b_2+m_1).$$

Finally,

$$x_2^* = \frac{Ah}{\beta\alpha - A}$$

with an additional condition $\beta\alpha > A$, where

$$A = m_2 - \frac{r_2b_2}{b_2+m_1}.$$

Since x_2^* is uniquely computed, the unique y_2^* is evaluated as the positive solution of

$$\frac{r_1b_1}{b_1+\mu_1} - \mu_2 - \gamma x_2^* - \frac{\alpha y_2^*}{h+x_2^*} = 0.$$

For the positivity of y_2^*, an essential condition $r_1b_1 > \mu_2(b_1+\mu_1)$ needs to be imposed. In fact, this restriction implies the existence of predator-free equilibrium. Therefore,

$$y_2^* = \frac{h+x_2^*}{\alpha}\left(\frac{r_1b_1}{b_1+\mu_1} - \mu_2 - \gamma x_2^*\right)$$

with

$$x_2^* < \frac{1}{\gamma}\left(\frac{r_1b_1}{b_1+\mu_1} - \mu_2\right).$$

Clearly, x_2^* is solely a function of the parameters describing the dynamics of predators, whereas x_1^* depends on parameters involved into prey and predator dynamics. It is worthwhile to recall that the equilibrium prey biomass in well known Rosenzweig-MacArthur (RM) predator-prey model without crowding effect among predators depends upon the parameters of the predators' growth function. However, in this stage-structure model, equilibrium prey biomass for both the stages depend on the parameters involved into the predator dynamics. We now derive the condition for asymptotic stability for different equilibria. The equilibrium values of the prey stage classes do not depend upon γ. However, we explore the role of this parameter in understanding stability nature for coexisting steady state.

3.1.2. Stability analysis of the steady states

The general form of the Jacobian matrix determined at arbitrary point is presented as

$$J = \begin{pmatrix}
-(b_1+\mu_1) & r_1 & 0 & 0\\
b_1 & -\mu_2 - 2\gamma x_2 - \dfrac{\alpha hy_2}{(h+x_2)^2} & 0 & -\dfrac{\alpha x_2}{h+x_2}\\
0 & 0 & -(b_2+m_1) & r_2\\
0 & \dfrac{\beta\alpha hy_2}{(h+x_2)^2} & b_2 & -m_2 + \dfrac{\beta\alpha x_2}{h+x_2}
\end{pmatrix}.$$

We find the linear stability at any equilibrium by identifying the sign of real part of all the eigenvalues obtained from the Jacobian matrix.

Stability of the trivial equilibrium

The Jacobian matrix evaluated at trivial (extinction) equilibrium is

$$J|_{S^0} = \begin{pmatrix} -(b_1+\mu_1) & r_1 & 0 & 0 \\ b_1 & -\mu_2 & 0 & 0 \\ 0 & 0 & -(b_2+m_1) & r_2 \\ 0 & 0 & b_2 & -m_2 \end{pmatrix}.$$

The stability of the extinction equilibrium can easily be determined by computing the trace and determinant values of the two block matrices. Both the block matrices have eigenvalues with negative real part if

i. $r_1 b_1 < \mu_2(b_1+\mu_1)$ and
ii. $r_2 b_2 < m_2(b_2+m_1)$.

Under the above two conditions, the extinction equilibrium is a stable node. The first condition implies that the predator extinction equilibrium $(\bar{x}_1, \bar{x}_2, 0, 0)$ cannot exist, and hence the coexisting equilibrium does exist as well (we refer to the expression of y_2^*). On the other hand, the second condition derives all the stages to extinction (i.e., non-existence of interior equilibrium). Thus the non-existence of non-trivial equilibrium is a consequence of the asymptotic stability of the trivial steady state.

Stability of the predator-extinction equilibrium

In this case, stability of $\bar{S}$ completely depends on the following block matrix

$$\begin{pmatrix} -(b_1+\mu_1) & r_1 \\ b_1 & -\mu_2 - 2\gamma\bar{x}_2 \end{pmatrix}.$$

The trace of the above matrix is negative. The determinant is given as

$$\mu_2(b_1+\mu_1) - r_1 b_1 + 2(b_1+\mu_1)\gamma\bar{x}_2.$$

However, $\mu_2(b_1+\mu_1) < r_1 b_1$ ensures the existence of the predator-free equilibrium, and hence the determinant may not be always positive. Thus for the asymptotic stability of the equilibrium

$$\bar{x}_2 > \frac{1}{2\gamma}\left(\frac{r_1 b_1}{b_1+\mu_1} - \mu_2\right)$$

must be satisfied.

Stability of the coexisting equilibrium

We assume that $J = (a_{ij})$, then a simplification of a_{44} reduces the Jacobian matrix as

$$J = \begin{pmatrix} -(b_1+\mu_1) & r_1 & 0 & 0 \\ b_1 & -\mu_2 - 2\gamma x_2^* - \dfrac{\alpha h y_2^*}{(h+x_2^*)^2} & 0 & -\dfrac{\alpha x_2^*}{h+x_2^*} \\ 0 & 0 & -(b_2+m_1) & r_2 \\ 0 & \dfrac{\beta\alpha h y_2^*}{(h+x_2^*)^2} & b_2 & -\dfrac{r_2 b_2}{b_2+m_1} \end{pmatrix}.$$

The sign of each non-zero entry is obvious. The characteristic equation corresponding to the Jacobian matrix is

$$\lambda^4 + P_1\lambda^3 + P_2\lambda^2 + P_3\lambda + P_4 = 0,$$

where

$$\begin{aligned} P_1 &= -(a_{11}+a_{22}+a_{33}+a_{44}), \\ P_2 &= (-a_{12}a_{21} + a_{11}a_{22} + a_{11}a_{33} + a_{22}a_{33} - a_{24}a_{42} - a_{34}a_{43} + a_{11}a_{44} + a_{22}a_{44} + a_{33}a_{44}), \\ P_3 &= (a_{12}a_{21}a_{33} - a_{11}a_{22}a_{33} + a_{11}a_{24}a_{42} + a_{24}a_{33}a_{42} + a_{11}a_{34}a_{43} + a_{22}a_{34}a_{43} \\ &\quad + a_{12}a_{21}a_{44} - a_{11}a_{22}a_{44} - a_{11}a_{33}a_{44} - a_{22}a_{33}a_{44}), \\ P_4 &= -a_{11}a_{24}a_{33}a_{42} + a_{12}a_{21}a_{34}a_{43} - a_{11}a_{22}a_{34}a_{43} - a_{12}a_{21}a_{33}a_{44} + a_{11}a_{22}a_{33}a_{44}. \end{aligned}$$

According to Routh–Hurwitz criteria, the coexisting equilibrium is locally asymptotically stable *iff*

$$P_1, P_3, P_4 > 0 \text{ and } P_1P_2P_3 > P_3^2 + P_1^2P_4.$$

Clearly $P_1 > 0$ always holds true. However, it seems difficult to determine the sign of the other Routh–Hurwitz conditions in full parameter space.

We have seen that one of the conditions for coexisting steady state depends on γ. We determine the values of γ numerically for the stability of the equilibrium. For simulation, we select the parameters as $r_1 = 1,\ r_2 = 0.5,\ b_1 = 0.5,\ b_2 = 0.2,\ \mu_1 = 0.1,\ \mu_2 = 0.1,\ m_1 = 0.4,$ $m_2 = 0.2,\ \alpha = 0.3,\ \beta = 0.2$
and $h = 1$. From the expression of y_2^*, we computed the threshold value for the existence of equilibrium as

$$\gamma = \frac{1}{x_2^*}\left(\frac{r_1 b_1}{b_1+\mu_1} - \mu_2\right) = 0.5866.$$

Therefore, all the stages persist when γ ∈ (0, 0.5866). Within this range we computed the values of P_3, P_4 and $(P_1P_2P_3 - P_3^2 - P_1^2P_4)$. It is observed that P_3 and P_4 are always positive, whereas $(P_1P_2P_3 - P_3^2 - P_1^2P_4)$ changes its sign. $(P_1P_2P_3 - P_3^2 - P_1^2P_4)$ remains negative within γ ∈ (0, 0.2101) and becomes positive otherwise (see Fig 1). Thus, all the stages coexist at stable steady state for all γ ∈ (0.2101, 0.5166). In particular, when $\gamma = 0.2$, the coexisting equilibrium (2.0833, 1.2500, 3.0208, 3.625) is unstable and populations experience cyclic dynamics, whereas the equilibrium (2.0833, 1.2500, 2.8646, 3.4375) is asymptotically stable when $\gamma = 0.22$. It is to be noted that the equilibrium value for mature and immature prey populations under the variation of γ are invariant. The main outcome from simulation reveals that increasing strength of intra-specific coefficient has a stabilizing effect on the coexisting steady state.

3.2. Analysis of the complex model

We investigate the impacts of varying competition coefficients involved in reproduction process for prey species and transition term for predator transition. We directly focus on the dynamic mode of the coexisting equilibrium. Deriving the expression for positive equilibrium and corresponding stability analysis are difficult. We adapted numerical scheme to compute the coexisting equilibrium and its local stability. As this model is complicated due the existence of density-dependent reproductive term for prey species and density-dependent transition term for predator growth, we explore the role of c_1 and c_2 successively. We observed that competition coefficient γ for mature predator has a stabilizing effect when it is increased. We would like to know if such stabilizing effect is likely to happen when c_1 (and c_2) is increased.

The methodology for computing equilibrium and stability criteria are the same as already been explained for simple model. We first determine the equilibrium, and then evaluate the Jacobian matrix corresponding to the complex model. Finally, we apply Routh–Hurwitz criteria to establish the stability of the equilibrium.

As a reference, we fix $\gamma = 0.15$ along with the other parameters $r_1 = 1,\ r_2 = 0.5,\ b_1 = 0.5,\ b_2 = 0.2,\ \mu_1 = 0.1,\ \mu_2 = 0.1,\ m_1 = 0.4,\ m_2 = 0.2,\ \alpha = 0.3,\ \beta = 0.2$ and $h = 1$ which are used for simple model. From Fig. 1, it is clear that the corresponding equilibrium is unstable. Now we explore the stability nature of the equilibrium when c_1 is increased. All the stage classes coexist at equilibrium when $c_1 \in (0, 0.5239)$. It is calculated that P_4 remains positive within this interval, whereas P_3 and $(P_1P_2P_3 - P_3^2 - P_1^2P_4)$ becomes positive when $c_1 > 0.055$ and 0.065, respectively. Thus, $(P_1P_2P_3 - P_3^2 - P_1^2P_4)$ plays the key role in deterring stability of the equilibrium. Fig. 2 a shows that increasing values of c_1 destroys the instability at $c_1 = 0.065$ as all the stability conditions due to Routh–Hurwitz criteria are satisfied. The populations are at non-equilibrium dynamics for smaller values of $c_1 \in (0, 0.065)$, whereas the equilibrium is stable for any $c_1 \in (0.065, 0.5439)$. Therefore, increasing competition strength among immature prey has a stabilizing effect on the system dynamics.

On the other hand, we select $c_1 = 0$ and vary c_2 under the same parameter configuration. The coexisting equilibrium remain unstable for smaller values of c_2, but gains asymptotic stability when $c_2 > 0.01$. In fact, increasing values of c_2 reduce the stock of predator biomass asymptotically. The equilibrium maintains stability for longer values of c_2 (see Fig. 2 b). Unlike the case of c_1, $(P_1P_2P_3 - P_3^2 - P_1^2P_4)$ is positive

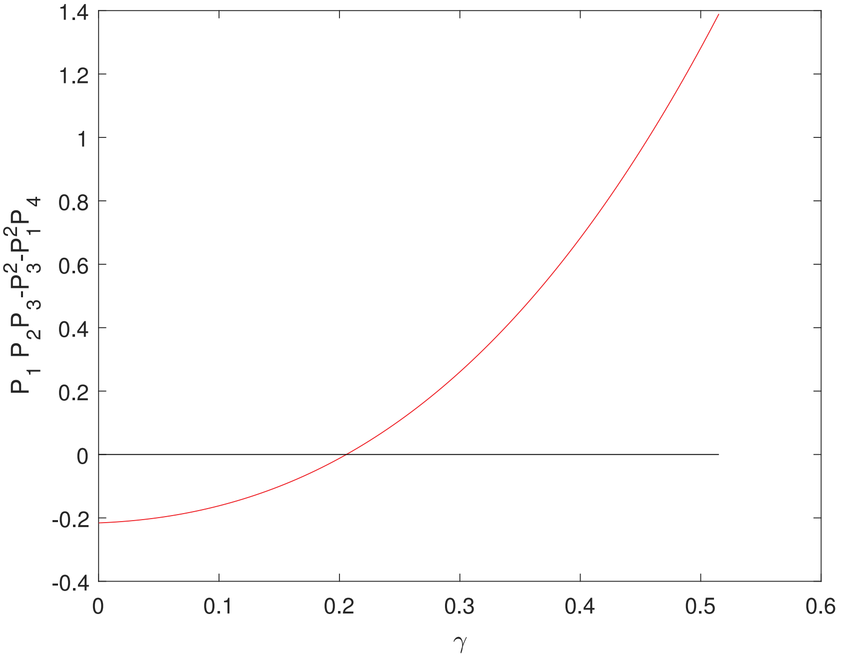

Fig. 1. The variation of $(P_1P_2P_3 - P_3^2 - P_1^2P_4)$ with respect to γ is shown. Other stability conditions are satisfied beyond the threshold value of $\gamma = 0.5866$. It concludes that higher value of competition coefficient among mature prey stabilizes the non-equilibrium dynamics to a steady state.

for $c_2 > 0.01$ and does not show much variation for larger c_2. From stabilization view point, we arrive at the same conclusion for changing c_2, as we obtain by varying c_1. It is now acceptable fact that increasing values of all γ, c_1 and c_2 together promote stability of the coexisting equilibrium as a whole.

4. Impact of mortality for mature populations

In this section, we examine if increasing mortality of the mature populations has any positive impact on biomass. Mortality rate for the predator in unstructured Rosenzweig–MacArthur model produces its higher mean density (time averaged biomass) when the populations follow cyclic dynamics. However, stock of the predator is not enhanced at stable steady state for increasing mortality rate of the predator. On the other hand, Abrams and Quince (2005) considered structured (resp. unstructured) dynamics for prey (resp. predator) species and established the hydra effect only on predator at stable steady state. We focus our investigation on the situation where stable steady stock of the target stages (mature prey, mature and immature predator) is increased due to higher mortality rate.

Economically, it is justified to harvest mature populations due to their higher market price and nutrient value. However, immature stage for predator could also be bigger in size compared to the mature prey stage. In this sense, harvesting of immature predator stage, sometimes, may be preferable as well. It is established that harvesting predator causes hydra effect when predator is unstructured (Abrams and Quince, 2005). Therefore, it would be worthwhile to examine whether harvesting mature or immature stage of predators induces hydra effect.

4.1. Simple model

First we consider the simple model where $c_1 = c_2 = 0$. From previous section, we know the equilibrium values of the mature populations as:

$$x_2^* = \frac{Ah}{\beta\alpha - A},$$
$$y_2^* = \frac{h + x_2^*}{\alpha}\left(\frac{r_1 b_1}{b_1 + \mu_1} - \mu_2 - \gamma x_2^*\right),$$

where

$$A = m_2 - \frac{r_2 b_2}{b_2 + m_1}.$$

We now determine the stock dynamics due to mortality of individual mature stages successively.

4.1.1. Removing mature predator

We estimate the variation of stocks when the mature predators' mortality is increased. The rate of change in biomass for mature prey with respect to predator mortality can be determined from the following relationship

$$\frac{dx_2^*}{dm_2} = \frac{\beta\alpha h}{(\beta\alpha - A)^2}\left(1 + \frac{r_2 b_2}{(b_2 + m_1)^2}\right) > 0.$$

Hence, harvesting mature predator leads higher density at equilibrium for both the mature and immature prey species regardless the stability mode of the system. The rate of change in biomass for mature predator is

$$\frac{dy_2^*}{dm_2} = \frac{1}{\alpha}\left(\frac{r_1 b_1}{b_1 + \mu_1} - \mu_2 - h\gamma - 2\gamma x_2^*\right).$$

Thus, maximum of y_2^* is achieved when mature prey biomass becomes

$$\hat{x}_2 = \frac{1}{2\gamma}\left(\frac{r_1 b_1}{b_1 + \mu_1} - \mu_2 - h\gamma\right).$$

Clearly, mature predator biomass at equilibrium will increase (resp. decrease) when prey biomass is inferior (resp. superior) than $\hat{x}_2$. We are mostly interested to verify if mortality leads higher density of the mature predator at stable equilibrium. Thus, we restrict our mortality rate in such a way that it cannot produce higher biomass than $\hat{x}_2$. Therefore, the critical mortality rate $\hat{m}_2$ can be found from $x_2^* = \hat{x}_2$, which yields a linear equation of m_2 as

$$\frac{Ah}{\beta\alpha - A} = \frac{1}{2\gamma}\left(\frac{r_1 b_1}{b_1 + \mu_1} - \mu_2 - h\gamma\right).$$

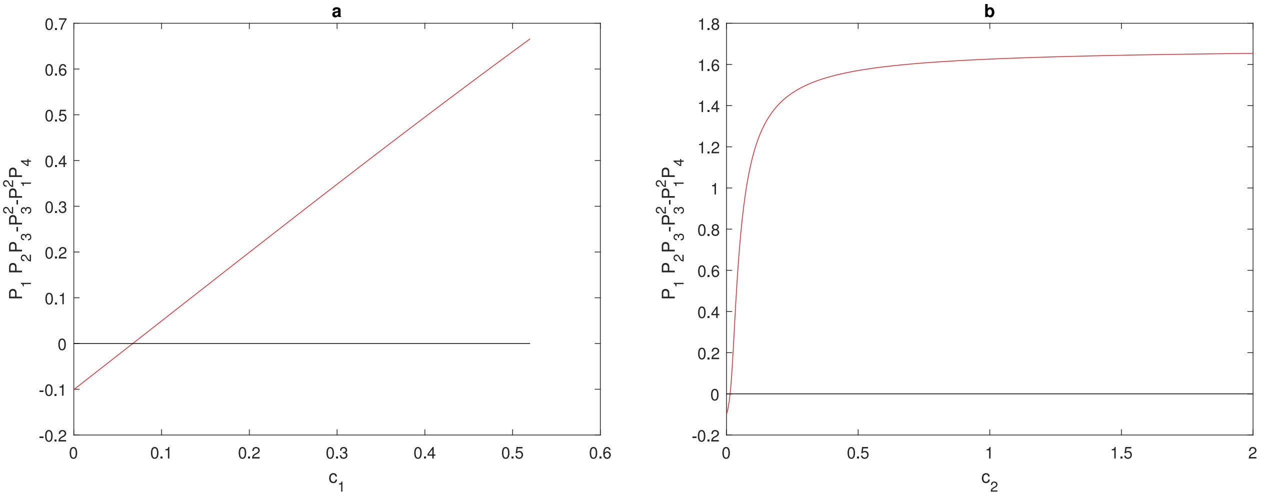

Fig. 2. (a) Change of stability due to varying c_1 with $c_2 = 0$ and (b) c_2 with $c_1 = 0$ are shown by estimating $(P_1P_2P_3 - P_3^2 - P_1^2P_4)$. Other conditions hold true within the respective range of c_1 and c_2 for which $(P_1P_2P_3 - P_3^2 - P_1^2P_4)$ is positive.

If the coexisting equilibrium is stable for $m_2 < \hat{m}_2$, biomass of the mature predator increases at stable state. Hence, a hydra effect could appear on the mature predator stage. However, it seems difficult to prove the stability nature via Routh–Hurwitz criteria analytically. We thus use simulation approach to verify the existence of such a complex phenomenon. Consider the parameter set as $r_1 = 1,\ r_2 = 5/10, b_1 = 5/10,\ b_2 = 2/10,\ \mu_1 = 1/10,\ \mu_2 = 1/10,\ m_1 = 4/10,\ \gamma = 2/10,\ \alpha = 3/10,\ \beta = 2/10$ and $h = 1$. Calculation shows that $\hat{m}_2 = 211/1050$. At this, critical equilibrium biomass are computed as

$$\left(\frac{20}{9},\ \frac{4}{3},\ \frac{245}{81},\ \frac{98}{27}\right).$$

We determine the characteristic equation corresponding to this steady state, which takes the form:

$$\lambda^4 + \frac{11\lambda^3}{5} + \frac{34831\lambda^2}{31500} + \frac{36\lambda}{4375} + \frac{54}{21875} = 0.$$

Clearly, all P_i's are positive along with

$$P_1P_2P_3 - P_3^2 - P_1^2P_4 = \frac{30631}{3828125}.$$

Therefore, the equilibrium is asymptotically stable for this critical mortality rate. We would like to recall that Rosenzweig–MacArthur predator-prey model experience Hopf-bifurcation when predator biomass achieves its maximum value, whereas no bifurcation appears for the maximum biomass in our stage-structure model.

We now want to know the stability nature of the equilibrium for a smaller mortality rate For this mortality rate, the equilibrium steady state is

$$\left(\frac{25}{12},\ \frac{5}{4},\ \frac{145}{48},\ \frac{29}{8}\right)$$

and the corresponding characteristic equation becomes

$$\lambda^4 + \frac{589\lambda^3}{270} + \frac{1459\lambda^2}{1350} + \frac{\lambda}{13500} + \frac{29}{11250} = 0.$$

The important Routh–Hurwitz condition

$$P_1P_2P_3 - P_3^2 - P_1^2P_4 = -\frac{5950493}{492075000} < 0.$$

Thus, the equilibrium is unstable. One can easily verify that the system is stable (resp. unstable) when $m \geq \hat{m}_2$ (resp. $m_2 \leq 210/1050$). Therefore, the stability threshold $\bar{m}_2$ must lie within the interval

$$\left[\frac{210}{1050},\ \frac{211}{1050}\right].$$

In fact, numerical experiment reveals that the equilibrium is unstable even if the mortality rate is in the middle of above interval.

We estimated the interval of m_2 as

$$\left[\frac{176}{1050},\ \frac{224}{1050}\right].$$

where all the stages persist. It suggests that the interval $[\bar{m}_2,\ \hat{m}_2]$, where stock of mature predator increases at stable state, is very narrow in comparison to the whole interval of mortality (176/1050, 224/1050) (where both the populations coexist). In conclusion, a hydra effect occurs in an insignificant interval when mature predator is removed. Although we are unable to explain the above fact analytically, but few other hypothetical sets of parameters reveal the same result. In addition, it is clear that non-equilibrium dynamic mode can settle down to a stable steady state once mortality rate crosses the stability threshold. Thus, increasing mortality rate has a stabilizing effect.

In the above numerical analysis, we used fractional form of the parameter values instead of decennial one. This representation does not loose any digits during the process of a series of necessary calculations. Decimal representation might not produce the exact characteristic polynomial and hence the quantities to determine stability due to Routh–Hurwitz conditions. As a result, we cannot confidently identify the narrow interval in decimal representation. However, we use decimal representation for the later situations where it does affect the qualitative analysis.

4.1.2. *Removing immature predator*

In this subsection, we examine whether harvesting of immature predator causes hydra effect over a significant range of effort. When mortality of immature predator is increased, the rate of change in biomass for the mature prey stage becomes

$$\frac{dx_2^*}{dm_1} = \frac{hb_2r_2\beta\alpha}{(\beta\alpha - A)^2(b_2 + m_1)^2} > 0.$$

Hence, both the mature and immature prey populations at equilibrium increase with the increasing mortality rate. On the other hand, the rate of change for immature predator biomass can be calculated from:

$$y_1^* = \frac{r_2}{b_2 + m_1}y_2^*$$

and

$$y_2^* = \frac{h + x_2^*}{\alpha}\left(\frac{r_1b_1}{b_1 + \mu_1} - \mu_2 - \gamma x_2^*\right).$$

Therefore,

$$\frac{dy_1^*}{dm_1} = -\frac{r_2}{(b_2 + m_1)^2} y_2^* + \frac{r_2}{(b_2 + m_1)} \frac{dy_2^*}{dm_1}.$$

Earlier we have seen that y_2^* is a nonlinear function of x_2^* and x_2^* is also a nonlinear function of m_1. Hence, finding critical value of m_1, in the form of fractional representation is difficult at which immature predator attends a maximum.

We fix the same parameter values along with $m_2 = 1/5$. It is calculated that populations persist when $m_1 \in (0.301, 0.455)$. However, numerical computations claim that all the stability conditions are satisfied at coexisting equilibrium when $m_1 \in [0.403, 0.455)$. Hence, increasing mortality promotes stability of the system.

We explore the variation of biomass for all the stages in Fig. 3 when $m_1 \in (0.301, 0.455)$. The immature predator biomass decreases at stable state with increasing mortality (see Fig. 3 b), whereas it seems from the figure that the biomass of the same stage increases when the equilibrium is unstable. We carefully (without loss of digits) determined the coexisting equilibrium at $m_1 = 401/1000$ and $m_1 = 402/1000$ as:

$$\left(\frac{5050}{2379}, \frac{1010}{793}, \frac{5693000}{1886547}, \frac{6842986}{1886547}\right)$$

and

$$\left(\frac{850}{393}, \frac{170}{131}, \frac{465500}{154449}, \frac{560462}{154449}\right),$$

respectively.

One can easily compute that the biomass of the immature predator is decreasing with increasing mortality rate between the above two values of m_1. We also calculated

$$P_1P_2P_3 - P_3^2 - P_1^2P_4 = -\frac{101166595781754842020 9}{114951500812483125000000 0} < 0$$

for $m_1 = 402/1000$.

It suggest that the equilibrium is unstable for all $m_1 \leq 0.402$. Hence, the biomass (unstable) of the immature predator decreases with its increasing mortality, at least, within the narrow range (0.401, 0.402). Therefore, no hydra effect can be appeared at stable state when immature predator is removed for $m_1 > 0.401$.

4.1.3. Removing mature prey

One can recall that the biomass x_2^* of the mature prey is independent of its mortality μ_2. Therefore, no hydra effect could be detected under its own mortality.

4.2. Complex model with $c_2 = 0$

Here we attempt to describe the results of mortality when density-dependent effects are in action on both the stages of the prey populations.

4.2.1. Removing mature predator

We have seen that a hydra effect appears in a very small range when mature predator's mortality rate is increased in the simple model. We use the same parameter set selected for describing the phenomenon of mature predator mortality in the simple model along with $c_1 = 0.3$. Then we vary the mortality rate m_2. All the stages coexist when $m_2 \in (0.1669, 0.2038)$. Fig. 4 depicts the variation of biomass for all the stages with increasing m_2. We found that all the stability criteria are met when $m_2 \in (0.17994, 0.2038)$. Therefore, populations persist at non-equilibrium (resp. stable steady) mode when $m_2 \in (0.1669, 0.177994)$ (resp. $m_2 \in (0.17994, 0.2038)$. It suggests that increasing mortality can stabilize the system. We again observed that biomass of the mature predator increases in a very small range of the mortality rate as can be seen in Fig. 4 d. Therefore, we obtain the similar phenomenon as observed in the simple model. Of course, the stability threshold is not so accurate as described for simple model, but it is plausible that hydra effect must occur.

4.2.2. Removing immature predator

We have established that mortality of the mature predator can result hydra effect, but not by the mortality of the immature predator in the case of simple model. We now check whether similar results can be obtain when immature predator is removed in the present modeling framework. We select the parameters as $r_1 = 1,\ r_2 = 5/10,\ b_1 = 5/10,\ b_2 = 2/10,\ c_1 = 3/10,\ c_2 = 0,\ \mu_1 = 1/10,\ \mu_2 = 1/10,\ \gamma = 2/10,\ \alpha = 3/10,\ \beta = 2/10$ and $h = 1$. We now choose $m_2 = 0.1805$ as it is on the range mortality where hydra effect was appeared in Fig. 4 along with $m_1 = 0.4$. The main attention is to examine if mortality of the immature predator can result a hydra effect. Computations reveal that all the populations can exist at equilibrium when $m_1 \in (0.355, 0.497)$. However, the stable coexistence is possible within the mortality interval (0.401, 0.497). It can be seen that biomass for both the prey stages are increased (Fig. 5 a and c). On the other hand, biomass of the immature predator decreases (regardless the stability behavior of the stock) with increasing mortality (Fig. 5 b). Thus, hydra effect does not appear on the immature predator stage. Therefore, we observe that likewise the simple model, no hydra effect appears on the immature predator. In addition, the hydra effect on predator populations happens due to the harvesting/ culling of the mature stage class.

4.2.3. Removing mature prey

Likewise the case of simple model the equilibrium of the mature prey stock can be determined by setting $dy_1/dt = 0 = dy_2/dt$. However, these two expressions are free from the mortality rate μ_2 of the mature prey. Hence, no hydra effect can be experienced on mature prey stage even through the immature prey possesses densit- dependent term.

4.3. Complex model with $c_1 = 0$

Finally, we consider that transition rate of immature stage to mature stage among predator possesses density-dependent function. Then we analyze the removal effects of different stage classes, and compare the results obtained so far from the above analysis.

4.3.1. Removing mature predator

First our investigations focus on removing mature predator by making use of the parameter set $r_1 = 1,\ r_2 = 0.5,\ b_1 = 0.5,\ b_2 = 0.2,\ c_1 = 0,\ c_2 = 0.1,\ \mu_1 = 0.1,\ \mu_2 = 0.1,\ m_1 = 0.1,\ m_2 = 0.12,\ \alpha = 0.3,\ \beta = 0.2,\ \gamma = 0.1$ and $h = 1$. Then the coexisting equilibrium $(10.7962, 6,\ \ 4777, 9.2126, 2.1327)$ is systematically stable. When mortality rate m_2 is increased inferior to $m_2 = 0.385$, all the stages persist. We would like to measure the equilibrium stock of all the stages when mortality is increased. It is observed from Fig. 6 a that biomass of the mature predator, at stable state, is increasing with higher mortality rate up to $m_2 = 0.219$. Further, it is decreased for $m_2 \in (0.219, 0.385)$. This observation leads to the existence of hydra effect on the mature stage of the predator. In the context of fishery science, one might attempt to catch maximum fishes of mature class. When mature predator is targeted for fishing, the obtained yield can be determined as $Y^* = m_2 y_2^*$ at the equilibrium. Apparently, one may think that maximum yield (MSY) can be achieved within a range of mortality rate m_2 where hydra effect appears. Because the stock is higher in the said range and one could think of getting higher yield. The Fig. 6 b establishes that MSY exists in a range of mortality where no hydra effect is appeared.

We have also estimated the variation of all the stages for $m_2 \in (0.12, 0.219)$ as can be seen in Fig. 7. It is interesting to note that stock of the immature predator decreases, while mature predators' stock increases with increasing mortality. However, in the case with $c_2 = 0$, biomass for both stages for predator species increases simultaneously (see Fig. 4). In the same range, biomass for both the prey classes decreases. Therefore, understanding the variation of biomass in

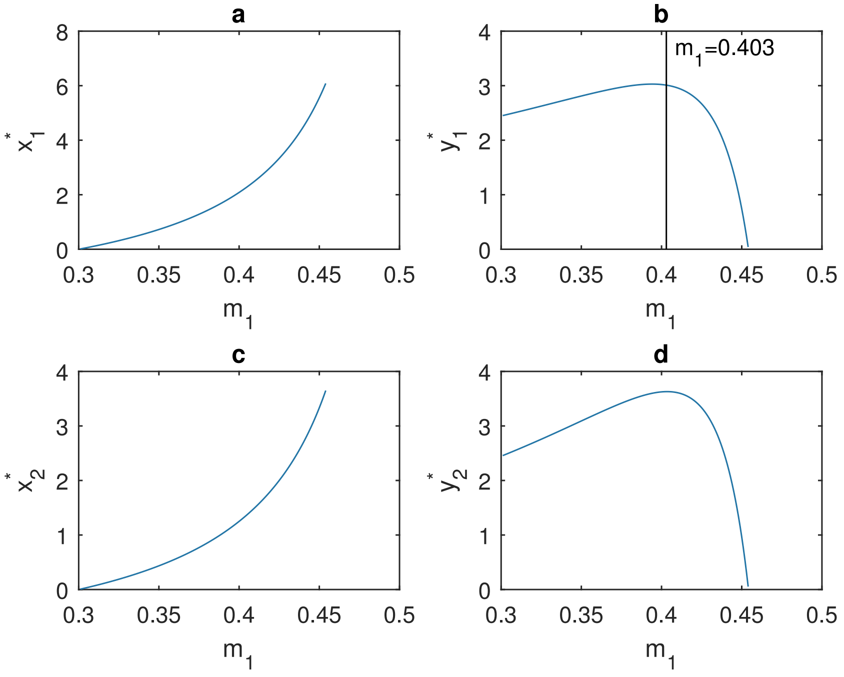

Fig. 3. The variations of prey and predator stages are shown. The stock corresponding to the stable equilibrium exists when $m_1 \in (0.403, 0.455)$. Hydra effect cannot be appeared at stable biomass on immature predator. We use the parameters: $r_1 = 1,\ r_2 = 5/10,\ b_1 = 5/10,\ b_2 = 2/10,\ \mu_1 = 1/10,\ \mu_2 = 1/10,\ m_2 = 1/5,\ \gamma = 2/10,\ \alpha = 3/10,\ \beta = 2/10$ and $h = 1$.

such a structured community is very complex. However, we have verified that stocks for both prey (resp. predator) stages increase (resp. decrease) where hydra effect does not appear (i.e., when $m_2 \in (0.219, 0.385)$.

4.3.2. Removing immature predator

We now estimate the stock of the immature predator when m_1 is varied. We fix the same parameter set used for culling the mature predator along with $m_2 = 0.2$. Populations persist at steady state when $m_1 \in (0.001, 0.479)$, but stable coexistence is possible for $m_1 \in (0.03, 0.479)$. We have shown the variation of stock for all the stages in Fig. 8. Clearly, stock dynamics with respect to mortality of the immature predator follows a very complex pattern. When $m_1 \in (0.03, 0.245)$ (resp. $m_1 \in (0.245, 0.479)$ both the stages for prey

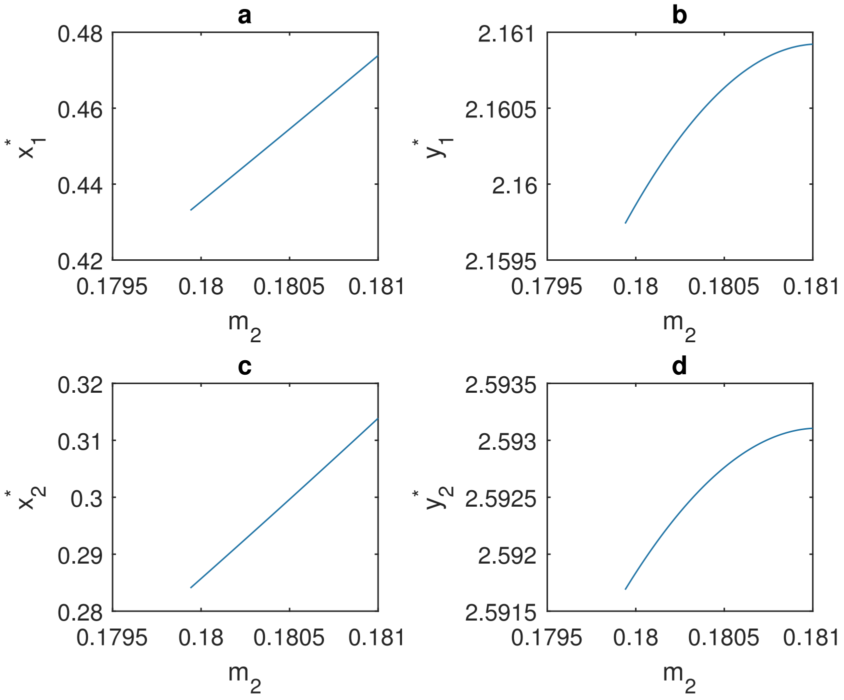

Fig. 4. The stable stocks for all stage classes are shown when m_2 is varied. Biomass of both the predator stages are increased in a small range of m_2 in comparison to the species coexistence range. (d) Shows the existence of hydra effect. We choose $r_1 = 1,\ r_2 = 5/10,\ b_1 = 5/10,\ b_2 = 2/10,\ c_1 = 3/10,\ c_2 = 0,\ \mu_1 = 1/10,\ \mu_2 = 1/10,\ m_1 = 4/10,\ \gamma = 2/10,\ \alpha = 3/10,\ \beta = 2/10$ and $h = 1$ for simulation.

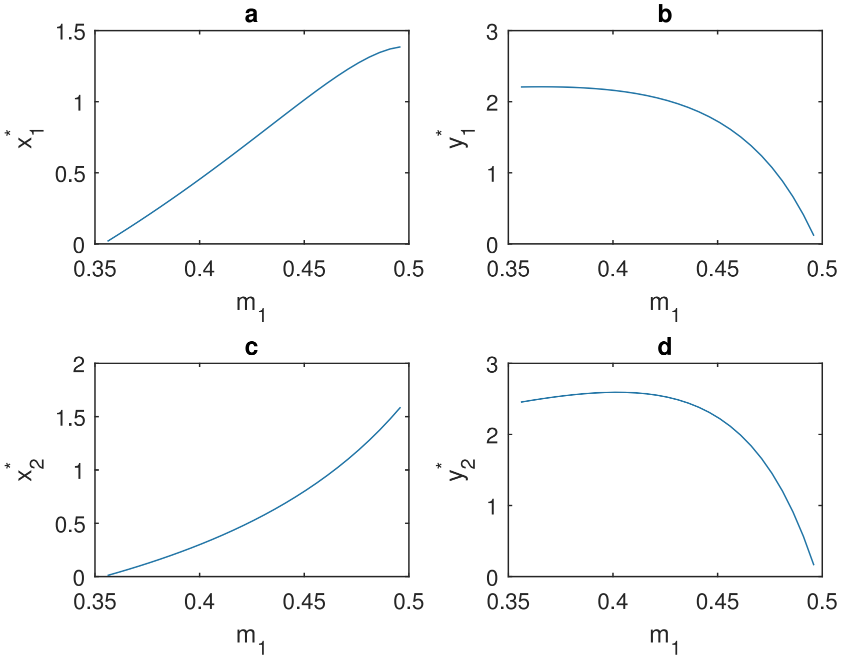

Fig. 5. The stocks for all stages are shown when m_1 is varied. The equilibrium is stable when $m_1 \in (0.401, 0.497)$. There is no positive effect on biomass for the immature predator class.

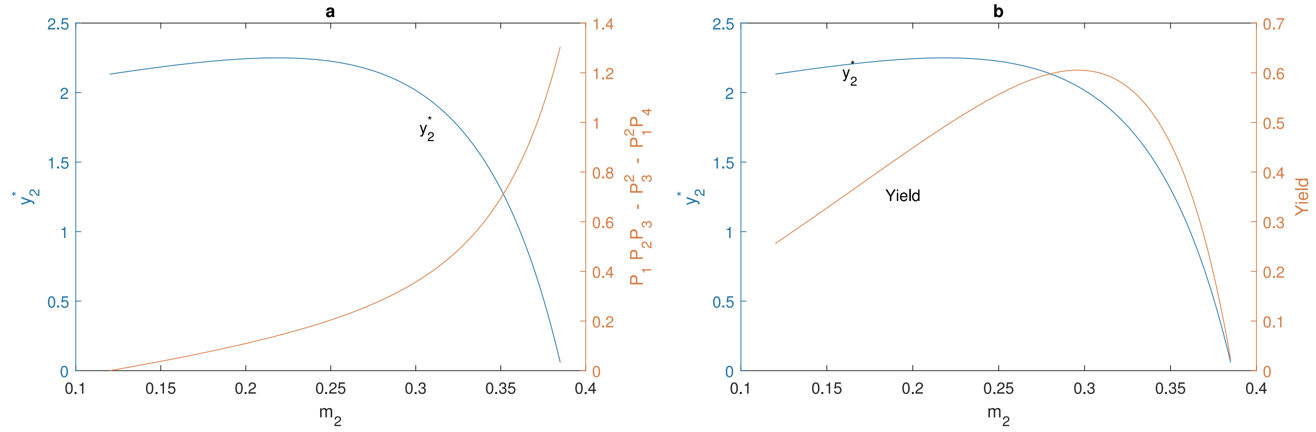

Fig. 6. (a) The biomass of the mature predator is increased for increasing values of m_2 up to certain limit and then it starts to decrease. Within the whole mortality range $(P_1P_2P_3 - P_3^2 - P_1^2P_4)$ is always positive. The other two stability conditions such as $P_2 > 0$ and $P_3 > 0$ are satisfied as well. Thus, hydra effect appears on mature predator in 40% on the effective mortality range. (b) MSY is achieved for a mortality range when stock of the mature predator is decreasing.

populations decrease (resp. increase) with increasing mortality rate as displayed in Fig. 8 a and c. However, the biomass of the immature predator linearly decreases with increasing mortality (Fig. 8 b). Therefore, no hydra effect appears on immature predator. Although the stock of the mature predator increases within $m_1 \in (0.03, 0.245)$ (Fig. 8 d).

4.3.3. Removing mature prey

In the earlier discussion, the equilibrium biomass of the prey stages were independent of mortality rate μ_2. In the current modeling framework, biomass of the prey population must be changed with mortality. A typical parameter set is chosen as $r_1 = 1,\ r_2 = 0.5,\ b_1 = 0.5,\ b_2 = 0.2,\ c_1 = 0,\ c_2 = 0.1,\ \mu_1 = 0.1,\ m_1 = 0.1,\ m_2 = 0.2,\ \alpha = 0.3,\ \beta = 0.2,\ \gamma = 0.1$ and $h = 1$. At least one feasible equilibrium exists when $\mu_2 \in (0, 0.414)$. In particular, there exist two positive equilibria when $\mu_2 > 0.15$. We observe that one of the equilibrium is stable for $\mu_2 < 0.36$; otherwise, both the equilibria are unstable for increasing mortality. Then the prey-free equilibrium (only predators survive) becomes stable for $\mu_2 \in (0.35, 0.414)$. The stable stock of all the stages are shown in Fig. 9 when $\mu_2 \in (0, 0.36)$. The biomass of both the prey stages decrease with increasing mortality on mature prey (Fig. 9 a and c).

5. Conclusion

We have built a predator-prey community model with stage-structure for both the species. Several axioms have been clarified to formulate the four dimensional model. The general model has been classified into two categories: simple model and complex model. We have studied the local stability of the equilibrium analytically for the simple model, whereas the numerical simulation has been applied for complex one. Routh–Hurwitz criteria have been used to determine the stability nature of the steady states. The main purposes of the paper were to examine (i) the effect of density-dependent term on stability and (ii) positive impacts of increasing population mortality on the stock size.

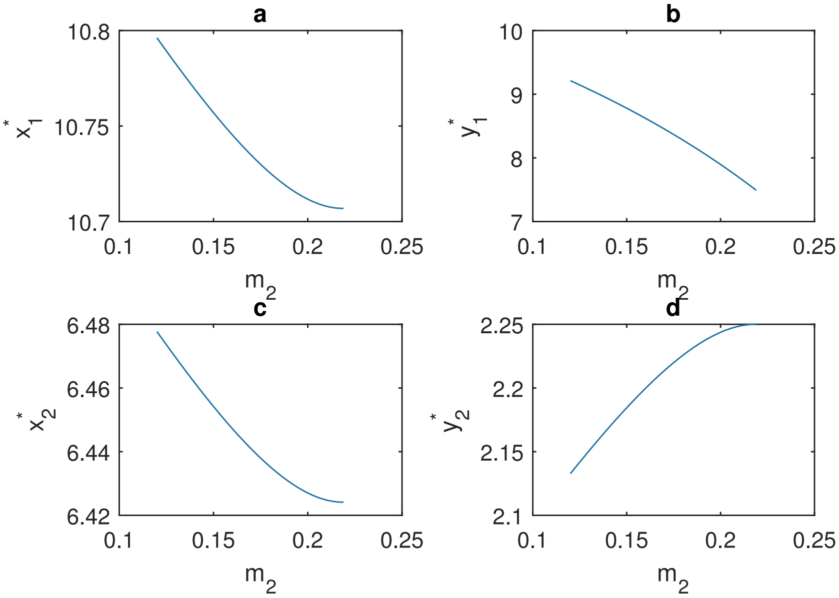

Fig. 7. The stable stocks for all the stages are shown when $m_2 \in (0.12, 0.219)$. All the stages, except the mature predator, decrease with increasing m_2.

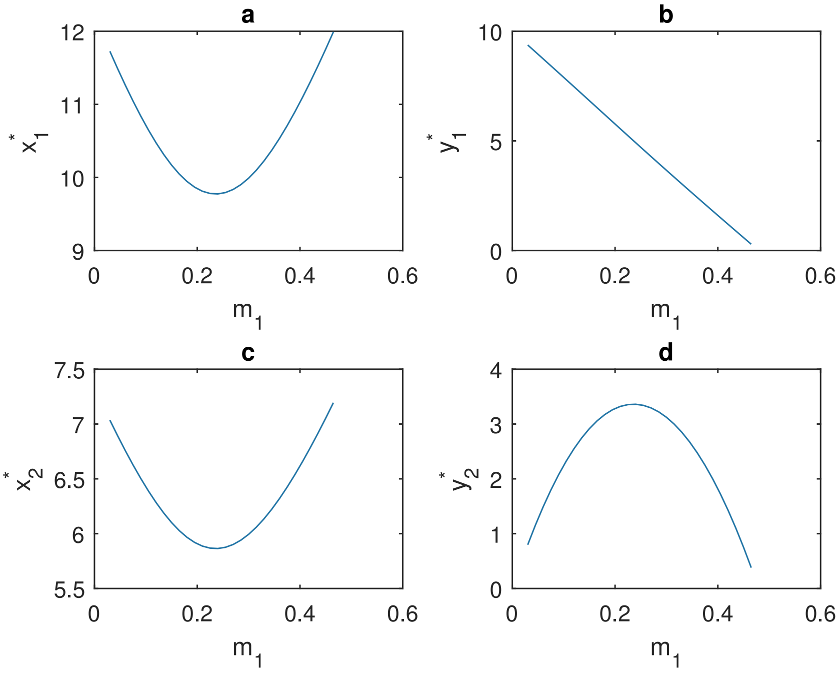

Fig. 8. The stock dynamics of all the stages, at stable equilibrium, with respect to m_1 is depicted. It reveals that hydra effect is not experienced on the immature predator class. We use the parameters as $r_1 = 1,\ r_2 = 0.5,\ b_1 = 0.5,\ b_2 = 0.2,\ c_1 = 0,\ c_2 = 0.1,\ \mu_1 = 0.1,\ \mu_2 = 0.1,\ m_2 = 0.2,\ \alpha = 0.3,\ \beta = 0.2,\ \gamma = 0.1$ and $h = 1$ for simulation purpose.

In the simple model we have observed that an unstable equilibrium, which was unstable for smaller value of intra-specific competition coefficient, could be stable for increasing value of the competition coefficient. We have also shown that increasing values of c_1 and c_1 linked with density-dependent reproduction of prey populations and density-dependent transition function, respectively, promote stability of the coexisting equilibrium. Li and Takeuchi (2011) have established the global stability of the equilibrium in a delayed predator-prey model where predator had density-dependent mortality. Thus, our results on local stability arising from density-dependent effect might be interesting from ecological view point.

We have examined the influence of linear mortality for mature age classes of both the prey and predator communities. This mortality could be treated as the harvesting in fishery science or culling of pest population from agriculture crops. First, we have studied the influence of mortality of the mature predator. A tricky method combined with analytical technique and numerical simulation have been applied effectively to understand the positive effect on mature predator's stock due to its own mortality. Our analysis revealed that stock was increased at stable state within a very narrow interval of mortality rate. Therefore, a hydra effect appears on the mature stage class of the predator species.

Several articles (see Introduction Section) established that mortality can lead hydra effect on predator population in unstructured models. We were interested to know whether such an effect arises from mature or immature predator stages. In this context, we first examined the effect on

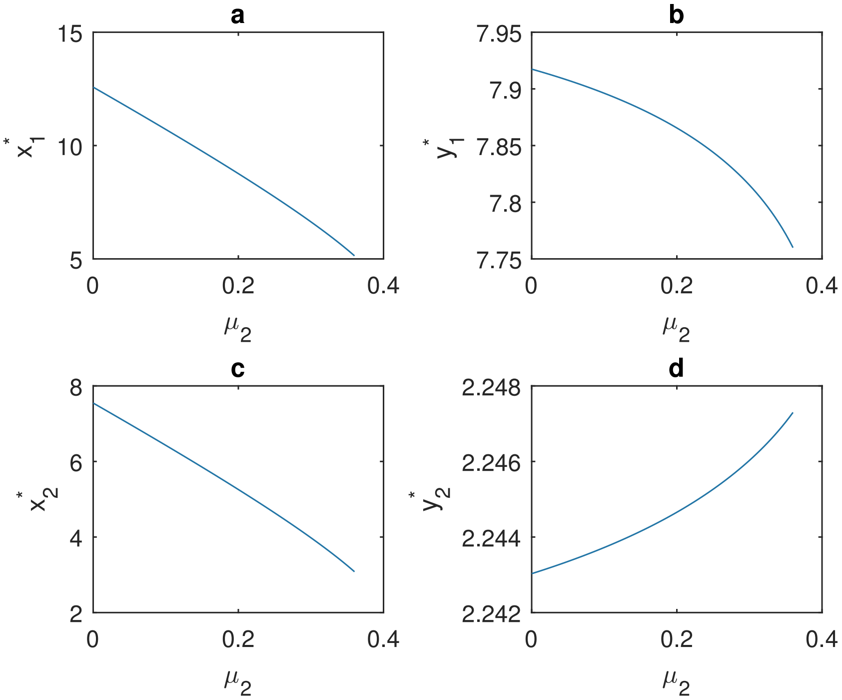

Fig. 9. The stock dynamics of all the stages, at stable equilibrium, with respect to μ_2. Clearly, biomass of the prey stages are decreasing function of μ_2. Therefore, no hydra effect is detected on the mature prey class. We choose the parameters as $r_1 = 1,\ r_2 = 0.5,\ b_1 = 0.5,\ b_2 = 0.2,\ c_1 = 0,\ c_2 = 0.1,\ \mu_1 = 0.1,\ m_1 = 0.1,\ m_2 = 0.2,\ \ \alpha = 0.3,\ \beta = 0.2,\ \gamma = 0.1$ and $h = 1$.

mortality on immature predator in the simple model. We could not detected any hydra effect on the immature predator (see Fig. 3 and the detailed analysis). The numerical techniques used without losing any digit for this finding could be interesting and effective for many other complicated situations where analytical methods cannot be applied. Here, we conclude that hydra effect on predator species is due to the positive effect of biomass on the mature predator only. We have also observed that increasing harvesting rate has a stabilizing effect on coexisting steady state in the simple stage-structured predator-prey community.

When prey populations had dentistry-dependent reproduction, mortality on mature predator had the same outcome as found for simple model. A hydra effect was identified over a small range of mortality rate on mature predator (Fig. 4). However, density-dependent function does not have any impact to induce hydra effect on the immature predator (Fig. 5). Finally, we considered the case when transition rate for predator growth was density-dependent. We have established that hydra effect had appeared on a significant range of mortality when mature predator was removed (Fig. 7). Maximum harvested biomass (MSY in the context of fishery) was achieved within an effort range where mature predator was not subjected to any hydra effect. A very complex stock dynamics was noticed when immature predator was harvested. For increasing mortality of the immature predator reduced the stocks of the prey stages and further increase of the mortality rate enhanced the stock (see Fig. 8). However, no hydra effect appears on the immature predator stage. Thus hydra effect, at stable state, is a common phenomenon on mature predator, which is unlike to happen on the immature predator in our models. Abrams and Quince (2005) have examined a stage-structure model with two stage for prey populations. The predator's dynamics was not modeled by density-dependent effect. They only reported the positive effect on biomass when mortality rate of unstructured predator was increased. Therefore, we have derived many new results in our structured model. In addition, we could not detect any hydra effect when mature prey stage was removed.

Although stage-structure model developed by ordinary differential equations reveal many interesting ecological results, structured models with time delay i.e., delay differential equations is much more accurate. Ma et al. (2008) considered time delay in the transition rate for stage-structure model of both prey and predator. Investigating such complex models could be a future perspective.

CRediT authorship contribution statement

Bapan Ghosh: Conceptualization, Methodology, Software, Formal analysis, Writing - review & editing, Project administration. **Oksana L. Zhdanova:** Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing. **Binandita Barman:** Software, Formal analysis, Investigation, Writing - original draft, Writing - review & editing. **Efim Ya. Frisman:** Conceptualization, Supervision, Project administration.

Declaration of Competing Interest

The author declare they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

Acknowledgment

This work is jointly supported by the Department of Science and Technology (DST), Govt. of India (No.: INT/RUS/RFBR/P-307) and the Russian Foundation for Basic Research (no. 18-51-45004 *IND*_a). Authors would like to thank the referees for their valuable comments and suggestions which greatly improved the quality of the content.

Supplementary material

Supplementary material associated with this article can be found, in the online version, at 10.1016/j.ecocom.2020.100812

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