

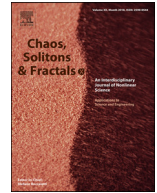


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Impact of fear effect on plankton–fish system dynamics incorporating zooplankton refuge

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ABSTRACT

In this paper, we analyze the impact of anti-predator behavior due to fear effect (K) and zooplankton refuge (r_1) on a 3-D plankton–fish dynamical system involving phytoplankton, zooplankton, and fish species. We assume that zooplankton species have developed defense mechanisms against fish predation. The fear of fish predation altered anti-predator defenses, which affects the growth of the fish population. On the other hand, zooplankton refuge reduces fish induced mortality of zooplankton and plays a significant role in controlling phytoplankton growth. The density of fish species is suppressed in the presence of high refuge and the anti-predator response of zooplankton. It is determined that K and r_1 can influence not only plankton–fish demography but also induce some mechanism to terminate planktonic blooms. Our mathematical study reveals that the low level of fear can stabilize the system dynamics in the presence of high rate of zooplankton refuge. Moreover, the low rate of zooplankton refuge can exclude complexity from the plankton–fish ecosystem in the presence of strong anti-predator responses of zooplankton. We have established the existence of all feasible biological equilibria and derived the conditional local and global stability of the given system around it. The Hopf-bifurcation analysis is carried out by considering K and r_1 as bifurcation parameters. The direction of bifurcating solutions is also determined using the centre manifold arguments. Numerical simulation is carried out to substantiate our analytical findings.

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1. Introduction

Analyzing the mechanism of the plankton–fish interaction in the marine ecosystem is a fascinating branch of research in ecology and evolutionary biology. There are two different approaches for understanding the impact of a predator on prey in predator–prey interactions, one of them is the direct killing [1–3] and another one is an indirect approach [4,5]. The indirect approach is based on the fear of predation caused by anti-predator behaviors of prey. Most of the research in mathematical ecology observed the direct predation of prey by predators. But, some experimental studies prove that apart from direct predation, fear of predator in prey species is also very significant to change their behavior and physiology [6]. Sometimes prey species are forced to change their preferable habitat, grazing areas, and reproductive zone due to predation risk

of predator population, which affects their long-term survival and fecundity rate. Recent analytical and experimental studies [2,7–18] on wolves, birds, elk, snowshoe hares, and dugongs have observed that fear of predation affects the prey–predator dynamics in different ways. Some species sacrifice their desirable living places, few alter foraging behaviors, while others experience psychological changes and population reduction. The experimental work carried out by Suraci et al. [19] has demonstrated that the predation rate of different species of crabs reduces due to the fear of large carnivores and increases their population. Wang et al. [20,21] have investigated that the cost of fear played a vital role in the growth of the prey population. They have observed that low levels of fear can induce multiple limit cycles and high levels of fear stabilize the system. Das et al. [22] proposed a stochastic mathematical model with the available additional food for the predator and studied that the high fear in prey species results in low predation and extinction of the predator population.

The phenomenon of prey refuge is interconnected with the fear factor as prey species hide physically due to fear of predation. In

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the real world, predators are not always successful in catching and killing prey species as they are often avoided by the refuge, like sea birds have nesting colonies on islands, and the semiaquatic animals, like mouse-deer, may use bodies of water as a refuge, etc. [23–26]. The prey refuge terms in mathematical models [25–29] make these models more realistic and are highly significant in the field of biomathematics. Zhang et al. [36] have determined the impact of anti-predator behavior of prey under the fear of predators with a Holling-type-II prey-predator model incorporating a prey refuge. They have investigated that the predator population extinct due to large prey refuge, but high fear cannot induce extinction of the predator population.

The study of plankton species is one of the hot spots in ecological sciences. Refuge-rich coral reefs contain a full 25% of ocean species, even though such reefs make up just 0.1% of the ocean’s surface area [33,34]. Bertolo et al. [31] have observed in their experimental study that the zooplankton refuge reduces fish induced mortality and phytoplankton growth in lakes. The experiment study [32] has proved that the zooplankton refuge increases the rotifer biomass and phytoplankton diversity. On the other hand, it decreases the phytoplankton biomass ($P < 0.05$), but do not affect the copepod biomass. Sharma et al. [30] have observed that zooplankton species follow vertical migration due to fear of predation by fish. The researchers [30–32] have studied the impact of zooplankton refuge and fear of fish predation among zooplankton species on plankton dynamics, separately. To the best of our knowledge, it is the first attempt to study the simultaneous impact of fear effect and zooplankton refuge on the plankton-fish dynamics. Thus, our present study explores the significance of the defense mechanism developed by zooplankton against fish predation for the co-existence of the plankton-fish ecosystem. We have proposed a plankton-fish mathematical model consisting of the biomass of Phytoplankton ($P(t)$), Zooplankton ($Z(t)$), and Fish ($F(t)$), respectively. The organization of our manuscript is as follows; In Section 2, a mathematical model of the given plankton system is proposed with certain assumptions. The boundedness and positivity of the plankton system are discussed in Section 3, followed by extensive stability analysis in Section 4. The existence of a Hopf-bifurcation and its direction is carried out in Section 5 and Section 6, respectively. All the analytical findings are validated in Section 7, followed by a conclusion in Section 8.

2. The mathematical model

To study the impact of fear and zooplankton refuge on the plankton-fish dynamics, we consider a three-dimensional mathematical model consisting of the biomass of phytoplankton ($P(t)$), zooplankton ($Z(t)$), and fish ($F(t)$) species at time t with the following assumptions.

$$\begin{cases} \frac{dP}{dt} = rP\left(1 - \frac{P}{K_1}\right) - \frac{\beta_1 P}{(a+P)}Z \\ \frac{dZ}{dt} = \frac{\beta_2}{(1+KF)} \frac{\beta_1 P}{(a+P)}Z - \delta_1 Z - \frac{\gamma(1-r_1)ZF}{(b+(1-r_1)Z)} \\ \frac{dF}{dt} = \frac{c\gamma(1-r_1)ZF}{(b+(1-r_1)Z)} - \delta_2 F \end{cases} \quad (1)$$

- The phytoplankton species grow logistically where the zooplankton species depend on the phytoplankton population for their growth and predate them with Holling-II functional response. The growth rate of zooplankton is taken as $\beta_2 G_1(K, F)$ where $G_1(K, F) = \frac{1}{1+KF}$. Here, $G_1(K, F)$ satisfy the following properties.
 - $G_1(0, F)=1$, in the absence of fear factor, there is no reduction in zooplankton species reproduction rate.
 - $G_1(K, 0)=1$, in the absence of fish species, there is no reduction in zooplankton’s reproduction.

Table 1
Biological conversion of parameters.

Parameter	Biological conversion
r	Intrinsic growth rate
K_1	Carrying capacity
β_1	Maximal ingestion rate of zooplankton
a	Half saturation constant
β_2	Conversion rate of $P(t)$ for the growth of $Z(t)$
K	Level of Fear in zooplankton
δ_1	Natural death rate of zooplankton
γ	Maximal ingestion rate of fish
r_1	Rate of zooplankton refuge
b	Half saturation constant.
c	Conversion rate of $Z(t)$ for the growth of $F(t)$
δ_2	Mortality rate of fish

- $\lim_{K \rightarrow \infty} G_1(K, F) = 0$, the growth rate of zooplankton species becomes zero due to a massive increase in anti-predator behavior.
- $\lim_{F \rightarrow \infty} G_1(K, F) = 0$, the growth rate of zooplankton species becomes zero when fish population is very large.
- $\frac{\partial(G_1(K, F))}{\partial K} = \frac{-F}{(1+KF)^2} < 0$, the growth of zooplankton species decreases due to increase of anti-predator behavior.
- $\frac{\partial(G_1(K, F))}{\partial F} = \frac{-K}{(1+KF)^2} < 0$, the growth of zooplankton species decreases due to increase in fish population.
- The fish species graze zooplankton with Holling-II functional response where $(1 - r_1)Z(t)$ is the amount of zooplankton population available for fish ($r_1 \in [0, 1]$). The growth rate of fish is taken as $cG_2(r_1, Z)$, where $G_2(r_1, Z) = \frac{\gamma(1-r_1)Z}{(b+(1-r_1)Z)}$. The function $G_2(r_1, Z)$ satisfies the following properties.
 - $G_2(r_1, 0)=0$, fish species extinct in absence of zooplankton species.
 - $\lim_{Z \rightarrow \infty} G_2(r_1, Z) = \gamma$, growth rate of fish species depends on its maximal ingestion rate due to huge increase in zooplankton population.
 - $\lim_{r_1 \rightarrow 1} G_2(r_1, Z) = 0$, growth rate of fish species become zero due to huge increase in zooplankton refuge.
 - $\frac{\partial(G_2(r_1, Z))}{\partial r_1} = \frac{-bZ\gamma}{(b+(1-r_1)Z)^2} < 0$, the growth of fish species decreases due to increase in zooplankton refuge.
 - $\frac{\partial(G_2(r_1, Z))}{\partial Z} = \frac{\gamma b(1-r_1)}{(b+(1-r_1)Z)^2} > 0$, the growth of fish species rises due to increase in zooplankton population.

The biological interpretations of all parameters are given below in Table 1.

3. Dynamical properties of system

3.1. Positivity and boundedness

Theorem 3.1. All the solutions of the plankton fish system (1) lie in the positive octant

$$\Sigma = \{(P, Z, F) \in \mathbb{R}_+^3, P(0) > 0, Z(0) > 0, F(0) > 0\} \text{ and its non negative solutions are uniformly bounded in } \Lambda = \{(P, Z, F) \in \mathbb{R}_+^3, 0 < P(t) < K_1, 0 < Z(t) < a_2, 0 < F(t) < a_1\}.$$

Proof. The equations of system (1) can be written as,

$$P(t) = P(0)e^{\int_0^t (r(1 - \frac{P(s)}{K_1}) - \frac{\beta_1}{(a+P(s))}Z(s)) ds}$$

$$Z(t) = Z(0)e^{\int_0^t (\frac{\beta_2}{(1+KF(s))} \frac{\beta_1 P(s)}{(a+P(s))} - \delta_1 - \frac{\gamma(1-r_1)F(s)}{(b+(1-r_1)Z(s))}) ds}$$

$$F(t) = F(0)e^{\int_0^t (\frac{c\gamma(1-r_1)Z(s)}{(b+(1-r_1)Z(s))} - \delta_2 F(s)) ds}$$

Thus, $P(t) > 0$, $Z(t) > 0$, and $F(t) > 0$ whenever $P(0) > 0$, $Z(0) > 0$, and $F(0) > 0$. Therefore, all the solutions of the plankton fish system (1) lie in the positive octant Σ .

Further, we claim that all non negative solutions are uniformly bounded in the octant Λ

$$\left\{ \begin{aligned} \frac{dP}{dt} &\leq rP(t)\left(1 - \frac{P(t)}{K_1}\right) \text{ implies } 0 < P \leq K_1. \\ \frac{dF}{dt} &\leq -(\delta_2 - c\gamma)F(t), F(t) \leq a_1(e)^{-(\delta_2 - c\gamma)t} \\ \text{as } t \rightarrow \infty, \text{ we have, } &F(t) \leq a_1, \text{ for } \delta_2 > c\gamma. \\ \frac{dZ}{dt} &\leq \beta_2\beta_1 \frac{1}{(1+KF(t))} \frac{P(t)}{(a+P(t))} Z(t) - \delta_1 Z(t), \\ \frac{dZ}{dt} &\leq \beta_2\beta_1(1)(1)Z(t) - \delta_1 Z(t), \\ \text{as } 0 < F(t) < a_1 & \\ \text{implies } 1 < 1 + KF(t) < 1 + Ka_1, & \\ 1 > \frac{1}{(1+KF(t))} > \frac{1}{1+Ka_1} \text{ and } \frac{P(t)}{(a+P(t))} < 1, & \\ \frac{dZ}{dt} &\leq -(\delta_1 - \beta_2\beta_1)Z(t) \\ \text{and so } Z(t) \leq a_2(e)^{-(\delta_1 - \beta_2\beta_1)t} & \\ \text{as } t \rightarrow \infty, \text{ we have, } Z(t) \leq a_2, & \\ \text{whenever } \delta_1 > \beta_2\beta_1. & \end{aligned} \right.$$

Therefore, all the solutions of the given plankton system are lie in the octant,

$$\Lambda = \{(P, Z, F) \in R_+^3, 0 < P(t) < K_1, 0 < Z(t) < a_2, 0 < F(t) < a_1\}.$$

4. Stability analysis

In this section, we analyze the local stability of the given dynamical system around various biologically feasible equilibrium points.

4.1. Existence of equilibrium states

Lemma 4.1.1. *The zero equilibrium $U_0(0, 0, 0)$ and the predator free equilibrium $U_1(P_1, Z_1, F_1) = (K_1, 0, 0)$ always exist.*

Lemma 4.1.2. *The fish free steady state $U_2(P_2, Z_2, F_2) = (\frac{a\delta_1}{(\beta_1\beta_2 - \delta_1)}, \frac{ra\beta_2(K_1\beta_1\beta_2 - \delta_1(K_1+a))}{K_1(\beta_1\beta_2 - \delta_1)^2}, 0)$ exists if $\beta_1\beta_2 > \delta_1$ and $K_1\beta_1\beta_2 > \delta_1(K_1 + a)$.*

Lemma 4.1.3. *The positive interior equilibrium point $U_*(P_*, Z_*, F_*)$ exists under the following conditions,*

(i) $r_1 < 1$, and $c\gamma > \delta_2$, (ii) $0 < r_1 < 1 - \frac{\beta_1\delta_2b}{ar(c\gamma - \delta_2)}$, and (iii) $\delta_1(a + P_*) < \beta_1\beta_2P_*$.

Proof. We obtain $Z_* = \frac{b\delta_2}{(1-r_1)(c\gamma - \delta_2)}$ from third equation of (1), which exists if $r_1 < 1$, and $c\gamma > \delta_2$ hold good. Now, substituting Z_* in first equation of (1), we obtain $I(P) = rP^2 - r(K_1 - a)P - rK_1a + \frac{\beta_1K_1\delta_2b}{(1-r_1)(c\gamma - \delta_2)}$. Which has a positive root P_* , if $I(0) < 0$ i.e. $0 < r_1 < 1 - \frac{\beta_1\delta_2b}{ar(c\gamma - \delta_2)}$. Further, using Z_* and P_* in second equation of system (1), we get $I(F) = F^2 + N_1F + N_2$, Where $N_1 = \frac{\delta_1K(b+(1-r_1)Z_*) + \gamma(1-r_1)}{\gamma(1-r_1)K}$, $N_2 = \frac{\delta_1(a+P_*)(b+(1-r_1)Z_*) - \beta_1\beta_2P_*(b+(1-r_1)Z_*)}{\gamma K(a+P_*)(1-r_1)}$. Then $I(F)$ admits a positive zero F_* if $I(0) = N_2 < 0$ i.e. $\delta_1(a + P_*) < \beta_1\beta_2P_*$.

4.2. Local stability

The main motive of this subsection is to determine the suitable mechanism to find out the different ranges of occurrence of planktonic blooms and its possible control.

Lemma 4.2.1. *The zero equilibrium state U_0 is unstable as r is the positive eigen value of the corresponding variational matrix.*

Lemma 4.2.2. *The predator free steady state U_1 is locally asymptotically stable (LAS) if $K_1 > \frac{\delta_1 a}{\delta_1 - \beta_1\beta_2}$.*

Lemma 4.2.3. *The fish free feasible point U_2 is LAS if $\delta_2 > \frac{c\gamma(1-r_1)Z_2}{(b+(1-r_1)Z_2)}$ and $r < \frac{2rP_2}{K_1} + \frac{\beta_1 a Z_2}{(a+P_2)^2} + \delta_1$.*

Lemma 4.2.4. *The equilibrium point U_* is LAS if $(H_1): A_1A_2 - A_3 > 0$ and $A_i > 0 \forall i = 1, 3$ hold true. Where $A_1 = -(a_{100} + b_{010} + c_{001})$, $A_2 = -a_{010}b_{100} - c_{010}b_{001} + b_{010}c_{001} + a_{100}b_{010} + a_{100}c_{001}$, and $A_3 = a_{100}c_{010}b_{001} + a_{010}b_{100}c_{001} - a_{100}b_{010}c_{001}$.*

Proof. The variational matrix M_* of the positive interior equilibrium U_* is given by,

$$M_* = \begin{bmatrix} a_{100} & a_{010} & 0 \\ b_{100} & b_{010} & b_{001} \\ 0 & c_{010} & c_{001} \end{bmatrix}$$

Where $a_{100} = r - \frac{2rP_*}{K_1} - \frac{a\beta_1Z_*}{(a+P_*)^2}$, $a_{010} = -\frac{\beta_1P_*}{(a+P_*)}$, $b_{100} = \frac{\beta_1\beta_2aZ_*}{(1+KF_*)(a+P_*)^2}$, $b_{010} = \frac{\beta_1\beta_2P_*}{(1+KF_*)(a+P_*)} - \delta_1 - \frac{b\gamma(1-r_1)F_*}{(b+(1-r_1)Z_*)^2}$, $b_{001} = -\frac{\gamma(1-r_1)Z_*}{(b+(1-r_1)Z_*)} - \frac{\beta_1\beta_2KP_*Z_*}{(1+KF_*)^2(a+P_*)}$, $c_{010} = \frac{(c\gamma(1-r_1)bF_*)}{(b+(1-r_1)Z_*)^2}$, and $c_{001} = \frac{(c\gamma(1-r_1)Z_*)}{(b+(1-r_1)Z_*)} - \delta_2$.

The characteristic equation of the variational matrix M_* w.r.t. U_* is

$$\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = 0 \tag{2}$$

Where

$$A_1 = -(a_{100} + b_{010} + c_{001}), \quad A_2 = -a_{010}b_{100} - c_{010}b_{001} + b_{010}c_{001} + a_{100}b_{010} + a_{100}c_{001}, \quad \text{and} \quad A_3 = a_{100}c_{010}b_{001} + a_{010}b_{100}c_{001} - a_{100}b_{010}c_{001}$$

Now, using Routh-Hurwitz criterion, M_* has negative eigen values or eigen values with negative real parts if (H_1) holds true around U_* . □

4.3. Global stability

Lemma 4.3.1. *If the condition $\delta_1 > \beta_1\beta_2$ is satisfied, then the predator free steady state $U_1(K_1, 0, 0)$ is globally asymptotically stable (GAS).*

Proof. We define a positive definite function V_1 as,

$$\left\{ \begin{aligned} V_1 &= P - K_1 \log\left(\frac{P}{K_1}\right) + Z + \frac{1}{c}F, \\ \text{After some simple calculations we get,} \\ \frac{dV_1}{dt} &= -\frac{r}{K_1}(P - K_1)^2 - \frac{\beta_1Z(P-K_1)}{(a+P)} - \delta_1Z \\ &\quad - \frac{\delta_2}{c}F + \beta_1\beta_2Z \frac{1}{(1+KF)} \frac{P}{(a+P)}, \\ &\leq -\frac{r}{K_1}(P - K_1)^2 - \frac{\beta_1Z(P-K_1)}{(a+P)} - \delta_1Z \\ &\quad - \frac{\delta_2}{c}F + \beta_1\beta_2Z(1)(1). \\ &= -\frac{r}{K_1}(P - K_1)^2 - \frac{\beta_1Z(P-K_1)}{(a+P)} \\ &\quad - (\delta_1 - \beta_1\beta_2)Z - \frac{\delta_2}{c}F. \end{aligned} \right.$$

Thus, $\frac{dV_1}{dt} < 0$, under the given hypothesis and by using Lyapunov-LaSalle theorem U_1 is GAS

Lemma 4.3.2. *The fish-free steady state $U_2(P_2, Z_2, 0)$ remains globally asymptotically stable if the following conditions (i) $\frac{r}{K_1} - \frac{\beta_1Z_2}{(a+P_2)(a+P_2)} > 0$ and (ii) $(1 + KF) - \beta_2 > 0$ hold true.*

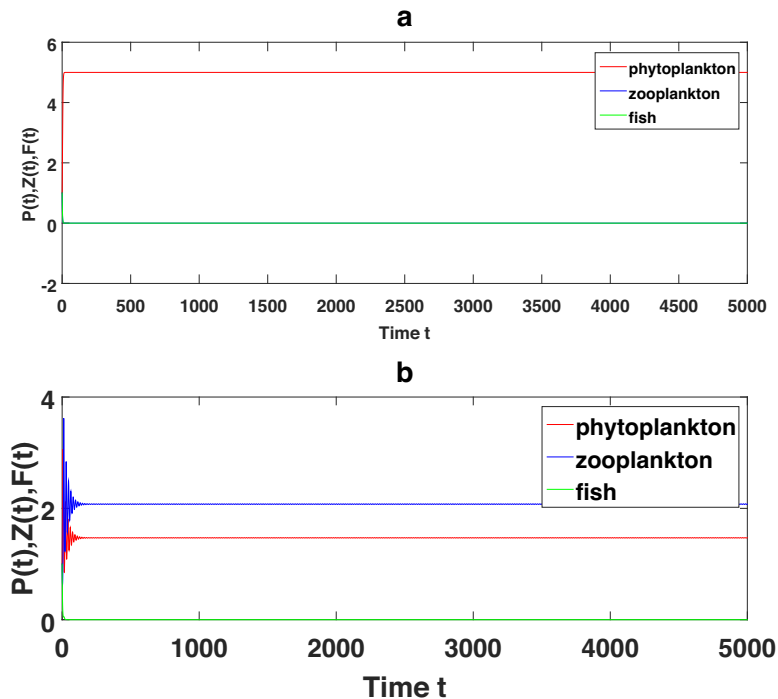


Fig. 1. Existence of equilibrium points U_1 (Fig. a) and U_2 (Fig. b).

Proof.

$$\left\{ \begin{aligned} & \text{Define } V_2 = P - P_2 \log\left(\frac{P}{P_2}\right) + Z - Z_2 \log\left(\frac{Z}{Z_2}\right) \\ & + \frac{(Z-Z_2)F}{cZ}, \text{ After simplifying, we get,} \\ & \frac{dV_2}{dt} = -\left(\frac{r}{K_1} - \frac{\beta_1 Z_2}{(a+P)(a+P_2)}\right)(P - P_2)^2 \\ & - \left(\frac{(1+KF-\beta_2)\beta_1}{(1+KF)(a+P)} - \frac{\beta_1 \beta_1 P_2}{(1+KF)}\right)(Z - Z_2)(P - P_2) \\ & - \left(\frac{\beta_1 \beta_1 P_2 KF(a+P)}{1+KF} + \frac{\delta_2 F}{cZ}\right)(Z - Z_2). \end{aligned} \right.$$

Therefore, $\frac{dV_2}{dt} < 0$, which proves that U_2 is conditionally G.A.S. (using Lyapunov-LaSalle theorem). \square

Lemma 4.3.3. The given system remains GAS around $U_*(P_*, Z_*, F_*)$ under the following conditions; $f_1 = \frac{r}{K_1} - \frac{\beta_1 Z_*}{(a+P)(a+P_*)} > 0$, $f_2 = \frac{\beta_1}{(a+P)(a+P_*)} - \frac{\beta_1 \beta_2}{(a+P)(1+KF)} + \frac{\beta_1 \beta_2 P_*}{(a+P)(a+P_*)(1+KF_*)} > 0$, $f_3 = \frac{\beta_1 \beta_2 P_* K(a+P_*)}{f_1} - \frac{c\gamma(1-r_1)}{(b+(1-r_1)Z)} + \frac{c\gamma(1-r_1)^2 Z_*}{(b+(1-r_1)Z)(b+(1-r_1)Z_*)} > 0$, $f_4 = \frac{\gamma(1-r_1)a_1}{b+(1-r_1)a_2} - \frac{\gamma(1-r_1)F_*}{b+(1-r_1)Z_*} > 0$.

Proof. To prove the global stability of the system around U_* , we have to construct a Lyapunov function. Define a positive definite function V as, $V = P - P_* \log\left(\frac{P}{P_*}\right) + Z - Z_* \log\left(\frac{Z}{Z_*}\right) + F - F_* \log\left(\frac{F}{F_*}\right)$,

After some simple calculations, using given hypothesis, and theorem 3.1 we get, $\frac{dV}{dt} \leq -f_1(P - P_*)^2 - f_2(Z - Z_*)(P - P_*) - f_3(Z - Z_*)(F - F_*) - f_4(Z - Z_*)$,

Thus, $\frac{dV}{dt} < 0$, which prove that the function V in the interior of the positive octant is a Lyapunov function. Hence the theorem. \square

5. Hopf-bifurcation analysis

In the previous section, we have determined the local and global stability of the system under certain conditions. Now, in this section, we will focus on the occurrence of Hopf bifurcation with respect to fear effect (K).

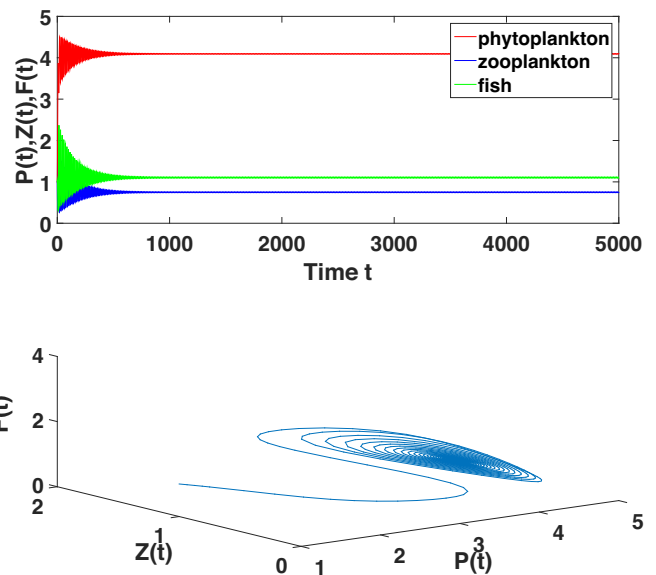


Fig. 2. Convergence of the system about U_* at $K = 0.3$.

Lemma 5.1. The dynamical system enters into Hopf-bifurcation around the interior point U_* as K passes through its critical value K^* under the following conditions,

1. $A_i(K^*) > 0, i=1,3, A_1(K^*)A_2(K^*) - A_3(K^*) = 0$,
2. $(A_1(K^*)A_2(K^*))' \neq (A_3(K^*))'$,

Proof. We consider K as a bifurcation parameter, the given plankton system shows excitability if there exists a critical value K^* of K such that $A_1(K^*)A_2(K^*) - A_3(K^*) = 0$. Thus, the characteristic Eq. (2) must have of the following form at $K = K^*$,

$$(\lambda^2(K^*) + A_2(K^*))(\lambda(K^*) + A_1(K^*)) = 0 \tag{3}$$

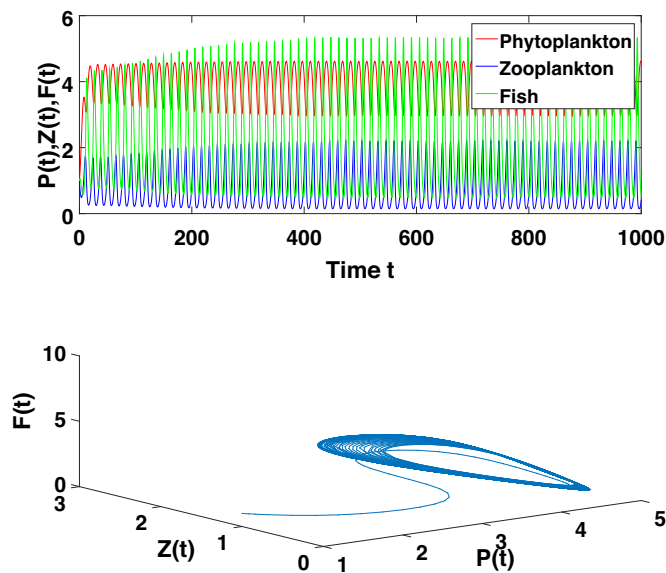


Fig. 3. Occurrence of a hopf-bifurcation at $K = 0.01$.

which clearly have roots $-A_1(K^*)$ and $\pm i\sqrt{A_2(K^*)}$. But, in general, $\lambda_1(K) = u(K) + \nu(K)$, $\lambda_2(K) = u(K) - \nu(K)$, and $\lambda_3(K) = A_1(K)$. Substituting values of $\lambda_i, i = 1, 2$ in (7) and calculating the derivatives, we get

$$\begin{cases} L_1(K)u'(K) - L_2(K)v'(K) + L_3(K) = 0 \\ L_1(K)u'(K) + L_2(K)v'(K) + L_4(K) = 0 \end{cases} \quad (4)$$

where $L_1(K) = 3u^2(K) + 2A_1(K)u(K) + A_2(K) - 3v^2(K)$, $L_2(K) = 6u(K)v(K) + 2A_1(K)v(K)$, $L_3(K) = u^2(K)A_1'(K) + A_2'(K)u(K) + A_3'(K) - A_1'(K)v^2(K)$, $L_4(K) = 2u(K)v(K)A_1'(K) + A_2'(K)v(K)$. Taking $u(K^*) = 0$ and $v(K^*) = \sqrt{A_2(K^*)}$, we obtain

$$L_1(K^*) = -2A_2(K^*), \quad L_2(K^*) = 2A_1(K^*)\sqrt{A_2(K^*)}, \quad L_3(K^*) = A_3'(K^*) - A_1'(K^*)A_2(K^*)$$

$$L_4(K^*) = A_2'(K^*)\sqrt{A_2(K^*)}$$

Solving (4) for $u'(K)$, we get

$$(u'(K))_{K=K^*} = -\frac{L_2(K^*)L_4(K^*) + L_1(K^*)L_3(K^*)}{L_1^2(K^*) + L_2^2(K^*)} = \frac{-(A_1(K^*)A_2(K^*))' - A_3'(K^*)}{2(A_1(K^*)^2 + A_2(K^*))} \neq 0 \text{ (using given hypothesis).}$$

It implies, $[(\frac{d(u)}{dK})]_{K=K^*} \neq 0$.

Therefore, the transversality condition holds true, which results in the occurrence of Hopf-bifurcation at $K = K^*$. □

6. Direction of bifurcating solutions

In this section, following along the lines of Hassard et al.[35], we shall derive the explicit formulae for determining the direction of bifurcating solutions at critical value $K = K^*$ about U_* . After some simple calculations, we can easily find the expressions

$$\mu_2, \beta_2, \text{ and } T_2 \text{ as, } c_1(0) = \frac{\{g_{20}g_{11} - 2|g_{11}|^2 - \frac{g_{02}|^2}{3}\}}{2\omega_0} + \frac{g_{21}}{2}, \mu_2 = -\frac{Re\{c_1(0)\}}{\alpha'(0)}, \beta_2 = 2Re\{c_1(0)\}, \text{ and } T_2 = -\frac{Im\{c_1(0)\} + \mu_2\omega'(0)}{\omega_0}$$

Where $g_{20} = 2(\gamma_1^1\bar{V}_1 + \gamma_2^1\bar{V}_2 + \gamma_3^1\bar{V}_3)$, $g_{02} = 2(\gamma_1^3\bar{V}_1 + \gamma_2^3\bar{V}_2 + \gamma_3^3\bar{V}_3)$, $g_{11} = \gamma_1^2\bar{V}_1 + \gamma_2^2\bar{V}_2 + \gamma_3^2\bar{V}_3$, $g_{21} = 2(\gamma_1^5\bar{V}_1 + \gamma_2^5\bar{V}_2 + \gamma_3^5\bar{V}_3)$

The values of all variables in g_{ij} s are given in Appendix 1.

Theorem 6.1 i. The parameter μ_2 helps to check the direction of the Hopf-bifurcation: If $\mu_2 > 0$, the Hopf bifurcation is supercritical and for $\mu_2 < 0$, the Hopf bifurcation is subcritical. ii. The

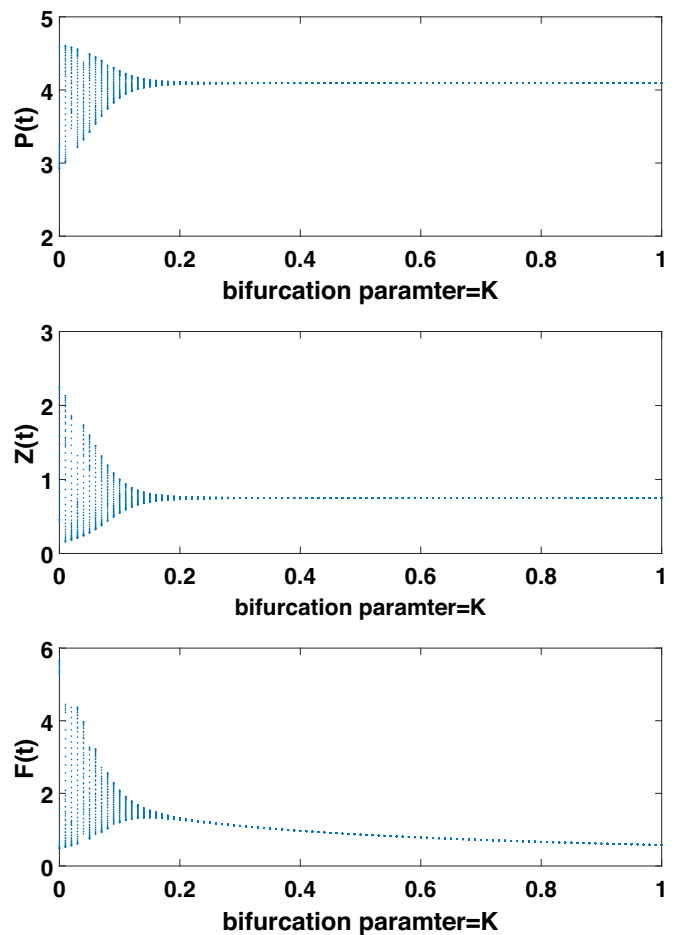


Fig. 4. Bifurcation diagram w.r.t. K at $r_1 = 0.12$ in $[S_3]$.

parameter β_2 investigates about the stability behavior of bifurcating periodic solutions: If $\beta_2 < 0$, the bifurcating periodic solutions are orbitally asymptotically stable and unstable for $\beta_2 > 0$. iii. The parameter T_2 determines the period of the bifurcating periodic solutions: If $T_2 > 0$, the period increases and decreases for $T_2 < 0$.

7. Numerical simulation

Now, we perform the simulations using MATLAB software to determine the behavior of the given plankton system by taking hypothetical parameters. We have chosen the following three suitable set of parameters to substantiate our analytical findings;

$[S_1]: r = 0.5, \beta_1 = 0.1, a = 4, \beta_2 = 1, \delta_1 = 2, \gamma = 1.42, b = 5c = 3.02, \delta_2 = 0.5, K_1 = 5, r_1 = 0.8, K = 7.$

$[S_2]: r = 0.5, \beta_1 = 1.1, a = 5, \beta_2 = 2, \delta_1 = 0.5, \gamma = 1.42, b = 5, c = 3.02, \delta_2 = 0.5, K_1 = 5, r_1 = 0.8, K = 0.5.$

$[S_3]: r = 0.5, \beta_1 = 1.1, a = 5, \beta_2 = 2, \delta_1 = 0.5, \gamma = 1.42, b = 5, c = 3.02, \delta_2 = 0.5, K_1 = 5, r_1 = 0.12, K = 0.3.$

7.1. Verification of analytical results

(i) For the set of parameters $[S_1]$, the predator-free steady state $U_1(5, 0, 0)$ exists and remains stable as long as (I) and (II) hold good:

(I). The corresponding eigen values of the variational matrix at U_1 are $-0.5000, -1.945$ and -0.5000 . (II). The stability condition given in Lemma 4.2.2, i.e. $K_1 > \frac{\delta_1 a}{(\delta_1 - \beta_1 \beta_2)}$ ($5 > 4.2105$) is satisfied.

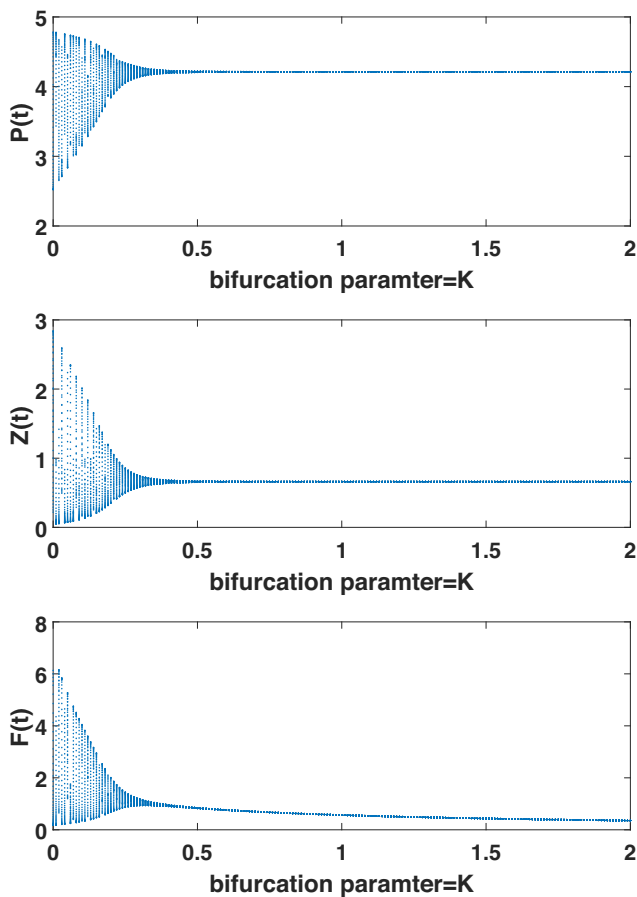


Fig. 5. Bifurcation diagram w.r.t. K at $r_1 = 0$ in $[S_3]$.

Table 2
Impact of prey-refuge in co-existence of species (using $[S_3]$).

r_1	Phytoplankton	Zooplankton	Fish
0.12	4.1023	0.7456	1.0891
0.23	3.9488	0.8618	1.1385
0.35	3.7219	1.0093	1.1825
0.43	3.5046	1.1527	1.1818
0.53	3.0870	1.4052	1.1123
0.66	1.9071	1.9413	0.4401
0.68	1.5193	2.0649	0.0577
0.69	1.4718	2.0805	0.0000

(ii) Now, for the set of parameters $[S_2]$, the fish free equilibrium $U_2(1.4741, 2.0764, 0)$ exists and remains stable as long as (III), (IV), and (V) hold good:

(III). The existence conditions given in Lemma 4.1.2, i.e. $\beta_1\beta_2 > \delta_1$ ($2.20 > 0.5$) and $K_1\beta_1\beta_2 > \delta_1(K_1 + a)$ ($11 > 6$) hold true. (IV). The eigen values of the variational matrix M_* at U_2 are $-0.033182743587021 \pm 0.367861279432523i$, and -0.17113671832296 . (V). The given dynamical system is LAS around U_2 , as the conditions given in Lemma 4.2.3, i.e. $\frac{c\gamma Z_2(1-r_1)}{(b+(1-r_1)Z_2)} < \delta_2$ ($0.3289 < 0.5$) and $r < \frac{2rP}{K_1} + \frac{a\beta_1 Z}{(a+P)^2} + \delta_1$ ($0.5 < 1.0673$) are clearly satisfied. Fig 1(a-b) shows the stable behavior of the given plankton system around U_1 and U_2 .

(iii) Simulating the given system using $[S_3]$, the positive interior equilibrium state $U_*(4.1023, 0.7456, 1.0891)$ exists and stable (see Fig. 2) due to (VI), (VII) and (VIII).

(VI). The existence conditions as stated in Lemma 4.1.3 i.e. $r_1 < 1$ ($0.12 < 1$), $c\gamma > \delta_2$ ($4.2884 > 0.5$), $0 < r_1 < 1 - \frac{\beta_1\delta_2 b}{ar(c\gamma - \delta_2)}$ ($0 <$

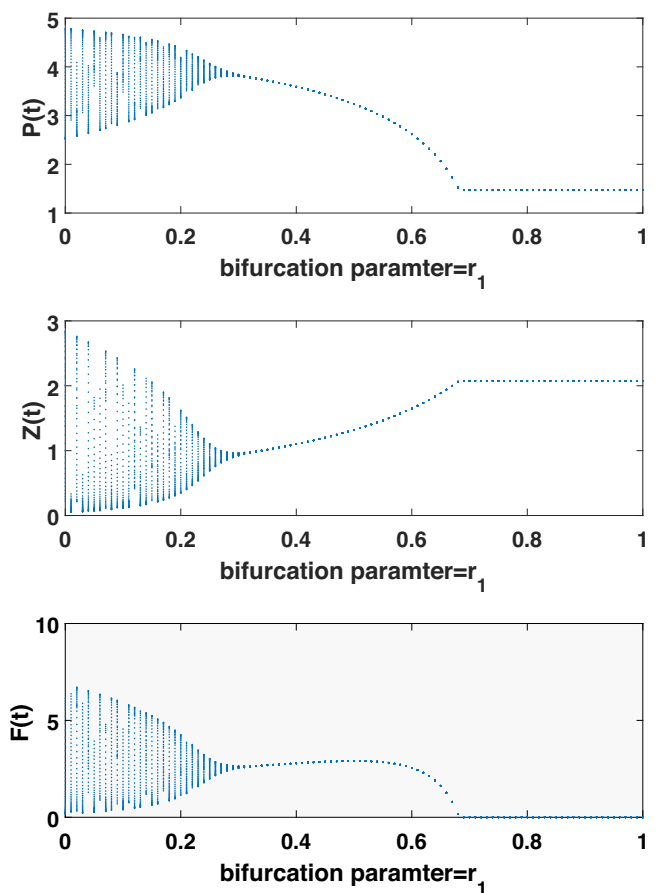


Fig. 6. Bifurcation diagram w.r.t. r_1 at $K=0$ in $[S_3]$.

Table 3
Impact of prey-refuge in co-existence of species in absence of fear affect ($K = 0$) (using $[S_3]$).

r_1	Phytoplankton	Zooplankton	Fish
0.12	4.0928	0.7499	2.2205
0.23	3.9462	0.8570	2.4351
0.35	3.7298	1.0013	2.6728
0.43	3.5015	1.1666	2.8309
0.53	3.0893	1.3989	2.8970
0.66	1.9067	1.9427	1.2722
0.68	1.5198	2.0590	0.1665
0.69	1.4709	2.0811	0.0000

$0.12 < 0.4193$), and $\delta_1(a + P_*) - \beta_1\beta_2P_* = -18.9202841 < 0$ are evidently satisfied. (VII). The eigen values of M_* at U_* are -0.3285 and $-0.002971542311705 \pm 0.458426514380385i$. (VIII). The feasible state U_* is LAS as Hypothesis given in (H_1) , i.e. $A_1A_2 - A_3 = 0.001902088495885 > 0$, $A_1 = 0.334476969230327 > 0$, and $A_3 = 0.069045896485326 > 0$ is satisfied.

(iv) The global stability of the given system around all steady states is also derived in Lemma 4.3.1 to Lemma 4.3.3 under certain conditions (see Fig. 10).

(v) Now, taking $K = 0.01$ in the set of parameters $[S_3]$, we obtain the interior equilibrium state $U_*(4.0928, 0.7499, 2.1271)$ and the stability determining eigen values are -0.3285 and $\pm 0.4584i$. The existence of real negative and purely imaginary eigen values confirms the occurrence of a Hopf-bifurcation around the positive interior equilibrium point U_* , as shown in Fig. 3. The necessary and sufficient condition for the existence of Hopf-bifurcation is also satisfied as $[(\frac{d(u)}{dK})]_{K=K^*} = 3.286624943598784e - 06 \neq 0$.

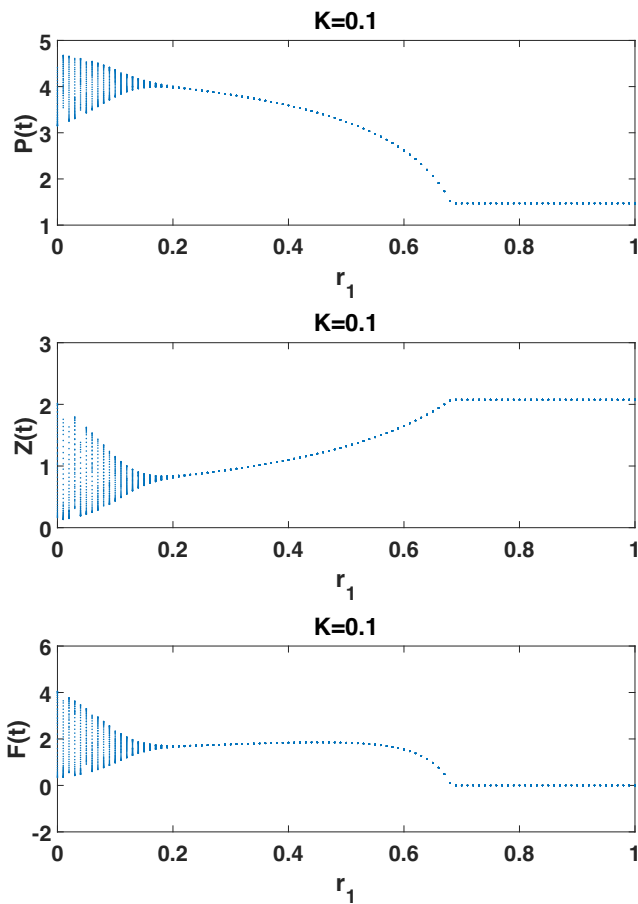


Fig. 7. Bifurcation diagram w.r.t. r_1 at $K = 0.1$ in $[S_3]$.

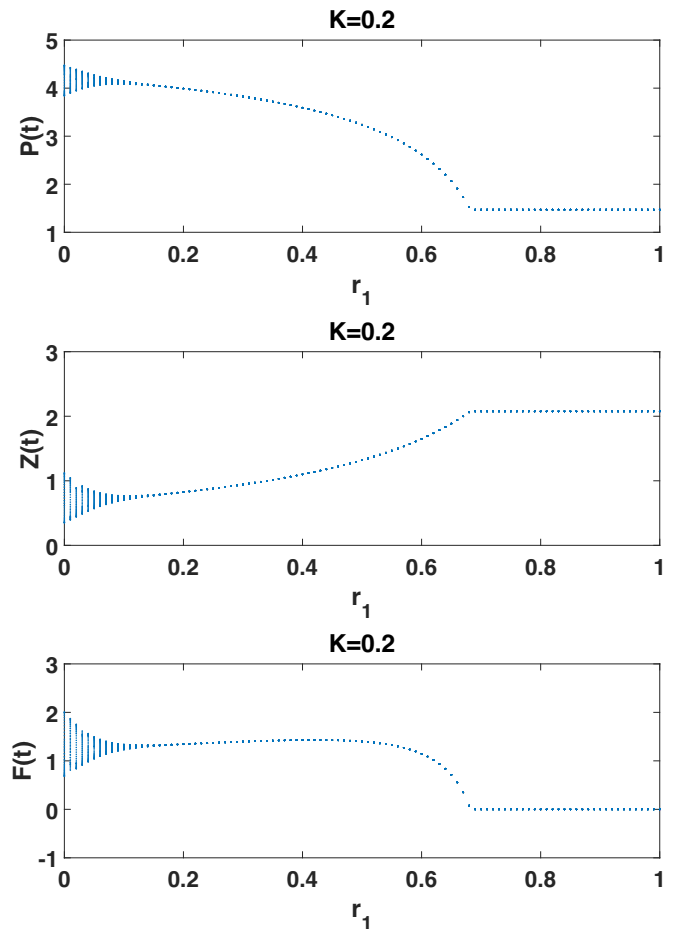


Fig. 8. Bifurcation diagram w.r.t. r_1 at $K = 0.2$ in $[S_3]$.

Thus, the given dynamical system remains stable for $K < K^*$ and enters into Hopf-bifurcation with the occurrence of periodic solutions at $K = K^*$. Next, the quantities which determine the stability of bifurcating periodic solutions are calculated as; $c_1(0) = -0.167642494742557 - 23.132383581057173i$, $\mu_2 = 1.534845440183449e + 03$,

$T_2 = 51.405296846793720$, and $\beta_2 = -0.335284989485114$. It shows that the Hopf-bifurcation is supercritical, bifurcating periodic orbits are stable and increase as T_2 increases.

7.2. Role of zooplankton refuge in co-existence of plankton-fish ecosystem (using $[S_3]$)

In this subsection, we investigate the influence of zooplankton refuge on the given plankton-fish dynamics.

[X_1]: The results of Table 2 show that the zooplankton refuge (r_1) can reduce densities of prey (phytoplankton) and top predator (fish) population but increase the zooplankton population. As the rate of zooplankton refuge rises from 0.12 to 0.69, the density of zooplankton population increases from 0.7456 to 2.0805. In contrast, the level of phytoplankton and fish population decreases from 4.1023 to 1.4718 and 1.0891 to 0, respectively. It implies that high rate of zooplankton refuge can induce the extinction of the top predator. These results are in line with the experimental results obtained by [31,32].

[X_2]: We have observed from Tables 2, 3, and Fig. 9 that if zooplankton refuge (r_1) increases gradually, the density of top predator (fish) is higher in the absence of fear effect ($K=0$) than in its presence ($K=0.3$).

Table 4

Role of r_1 and K in termination of planktonic blooms (PBs) (using $[S_3]$).

K	Occurrence of PBs	Termination of PBs
0	$0 < r_1 < 0.3$	$r_1 \geq 0.3$
0.1	$0 < r_1 < 0.2$	$r_1 \geq 0.2$
0.2	$0 < r_1 \leq 0.1$	$r_1 \geq 0.1$

[X_3]: Table 4 exhibits various levels of r_1 and K for the occurrence and termination of planktonic blooms. At $K=0$, the planktonic blooms occur for $0 < r_1 < 0.3$ as K increases from 0 to 0.1, the interval of occurrence of plankton blooms reduces to $0 < r_1 < 0.2$ (see Fig. 6 and Fig. 7). If fear effect K rises from 0.1 to 0.2, this interval shrinks to $0 < r_1 \leq 0.1$ (Fig. 8). These findings reveal that the low level of prey refuge can terminate planktonic blooms in the presence of high fear effect.

7.3. Role of fear effect in co-existence of plankton-fish ecosystem (using $[S_3]$)

The fear of top predator among zooplankton species also plays a vital role in the dynamics of given model system.

[X_4]: It is determined from Table 5 that the fear of top predator has a little bit impact on the population densities of prey, although it affects the density of top predator fish. As K increases from 2 to 150, fish population decrease from 0.3555 to 0.0065 (the result matches with [36]). It shows that the biomass of the fish population decreases due to the unavailability of prey, as zooplankton

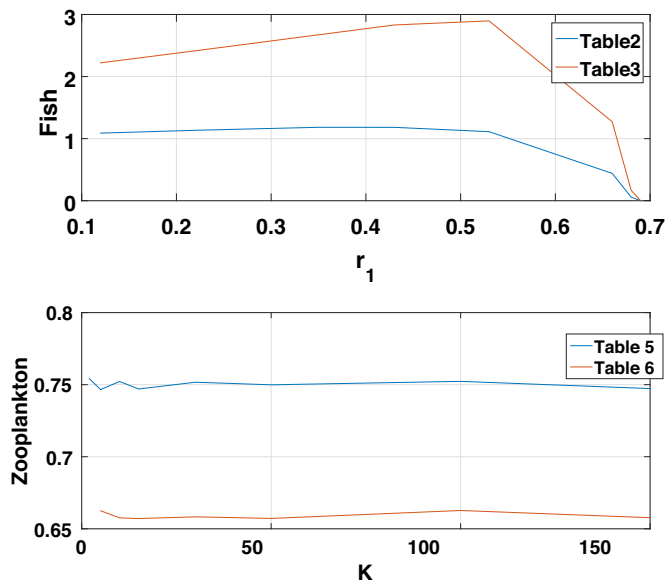


Fig. 9. Level of survival of fish species w.r.t. r_1 (Table 2) and (Table 3) and zooplankton species w.r.t. K (Table 5) and (Table 6).

Table 5
Impact of fear effect in co-existence of species (using $[S_3]$).

K	Phytoplankton	Zooplankton	Fish
2	4.0904	0.7542	0.3555
5	4.0954	0.7466	0.1685
10	4.0927	0.7522	0.0901
15	4.0949	0.7470	0.0619
30	4.0931	0.7517	0.0317
50	4.0909	0.7499	0.0194
100	4.0919	0.7523	0.0097
150	4.0941	0.7473	0.0065

species migrate from the place where they perceive high predation risk.

[X_5]: On comparing Tables 5 and 6, it is noted that if K increases continuously the density of zooplankton is high in presence of zooplankton refuge ($r_1 = 0.12$) than in its absence ($r_1 = 0$) (see Fig. 9).

[X_6]: We have also observed that the low level of fear effect in zooplankton species can terminate harmful algal blooms if the rate of zooplankton refuge is very high as Figs. 4 and 5 exhibit that the system shows excitability with the occurrence of planktonic blooms in $0 < K < 0.2$ at $r_1 = 0.12$ and in $0 < K < 0.4$ at $r_1 = 0$ and remains asymptotically stable with the termination of these blooms beyond these intervals.

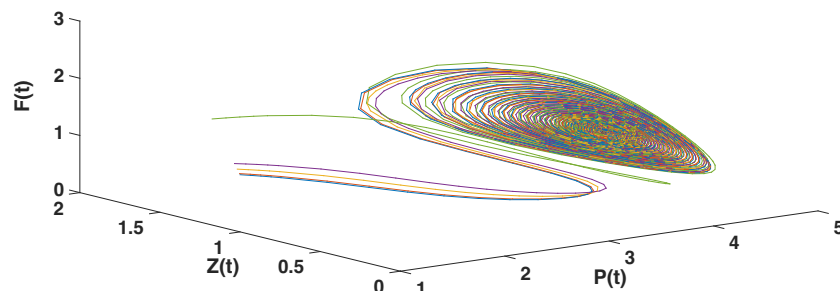


Fig. 10. Occurrence of global stability corresponding to different initial conditions $[1,1,1]$, $[1.01,1.01,1.01]$, $[1.05,1.05,1.05]$, $[1.1,1.1,1.1]$, and $[1.5,1.5,1.5]$ around $U_*(4.1023, 0.7456, 1.0891)$.

Table 6
Impact of fear effect in co-existence of species in the absence of zooplankton refuge(using $[S_3]$).

K	Phytoplankton	Zooplankton	Fish
2	4.2085	0.6649	0.3544
5	4.2086	0.6625	0.1714
10	4.2120	0.6576	0.0927
15	4.2146	0.6571	0.0632
30	4.2116	0.6583	0.0328
50	4.2136	0.6572	0.0199
100	4.2105	0.6627	0.0100
150	4.2123	0.6577	0.0067

8. Conclusion

In this study, a plankton-fish dynamical system is formulated through a defense mechanism adopted by zooplankton due to the fear of top predator (fish) in the marine ecosystem. The main motive of the present work is to investigate the influence of zooplankton refuge and fear effect on the co-existence of the plankton-fish ecosystem. Mathematically, we determine the local and global stability analysis of all the steady states of the given dynamics. The plankton system exhibits a Hopf bifurcation with the occurrence of periodic oscillations in the range $0 < K < 0.2$ and remains asymptotically stable by ruling out periodic solutions beyond it (Fig. 2 to Fig. 4). It is also observed that the Hopf-bifurcation is supercritical, the bifurcating periodic solutions are stable with increasing periods. Ecologically, we have shown that the fear effect and zooplankton refuge has the following impacts on the dynamics of the model system:

(1) The zooplankton refuge increases their biomass gradually and induces extinction of its predator (fish): as r_1 increases from 0.12 to 0.69, the density of zooplankton population increases from 0.7456 to 2.0805 and biomass of fish species decreases from 1.0891 to 0 (these results agree with experimental studies [31,32]). It is also observed that if zooplankton refuge (r_1) increases gradually, the density of fish population is higher in the absence of fear effect ($K = 0$) than in its presence ($K = 0.3$) (see $[X_2]$).

(2) The fear of top predator has a little bit impact on the population densities of prey, but it affects the density of top predator fish (see Table 5). As fear effect K increases from 2 to 150, fish population decrease from 0.3555 to 0.0065 (the result matches with [36]). Thus, the high level of fear effect cannot induce the extinction of the predator fish population. Moreover, if K increases continuously, the density of zooplankton is high in presence of zooplankton refuge ($r_1 = 0.12$) than in its absence ($r_1 = 0$) (see $[X_5]$).

(3) The results of $[X_3]$ suggest that zooplankton refuge induces some mechanism for controlling the planktonic blooms in the presence of a high fear effect. It is also observed from $[X_6]$ that

the low level of fear effect K can terminate planktonic blooms in the presence of high zooplankton refuge.

Thus, it can be concluded that the present ecological model exhibits various intervals of zooplankton refuge and fear effect for maintaining the sustainability and co-existence of the plankton-fish ecosystem.

Declaration of Competing Interest

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

CRedit authorship contribution statement

Rajinder Pal Kaur: Software, Formal analysis, Writing - original draft. **Amit Sharma:** Software, Conceptualization, Methodology, Writing - review & editing. **Anuj Kumar Sharma:** Supervision.

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Appendix A

$$\vec{V}_1 = \frac{\zeta_4 + (\zeta_6 \zeta_3 - \zeta_4 \zeta_5)(1+k)}{\zeta_1 \zeta_4 - \zeta_2 \zeta_3} + i \frac{\zeta_3 + (\zeta_5 \zeta_3 - \zeta_4 \zeta_6)(1-k)}{2(\zeta_1 \zeta_4 - \zeta_2 \zeta_3)}$$

$$\vec{V}_2 = \frac{-\zeta_2 + (\zeta_2 \zeta_5 - \zeta_1 \zeta_6)(1+k)}{2(\zeta_1 \zeta_4 - \zeta_2 \zeta_3)} + i \frac{-\zeta_1 + (\zeta_5 \zeta_1 - \zeta_2 \zeta_6)(-1+k)}{2(\zeta_1 \zeta_4 - \zeta_2 \zeta_3)}$$

and $\vec{V}_3 = k_3$, Where

$$\zeta_1 = a_{010}b_{001} - a_{001}b_{010}, \zeta_2 = a_{010}\omega_0, \zeta_3 = c_{100}b_{001} - c_{001}b_{100}, \zeta_4 = b_{100}\omega_0, \zeta_5 = a_{100}b_{010} - a_{010}b_{100} - \omega_0^2, \zeta_6 = -a_{100} - b_{010}$$

$$\gamma_1^1 = (a_{200}q_1^2), \gamma_1^2 = 2a_{200}q_1\bar{q}_1 + a_{110}(q_1\bar{q}_2 + q_2\bar{q}_1), \gamma_1^3 = a_{200}\bar{q}_1^2 + a_{110}\bar{q}_1\bar{q}_2, \gamma_1^5 = \frac{(a_{300}q_2^2\bar{q}_1 + a_{210}(q_1^2\bar{q}_2 + 2q_1\bar{q}_1q_2) + a_{120}(q_2^2\bar{q}_1 + 2q_1\bar{q}_2q_2))}{6}, \gamma_2^1 = b_{200}q_1^2 + b_{020}q_2^2 + b_{002}q_3^2 + b_{011}q_3q_2 + b_{101}q_1q_3 + b_{110}q_1q_2, \gamma_2^2 = 2b_{200}q_1\bar{q}_1 + 2b_{020}q_2\bar{q}_2 + 2b_{002}q_3\bar{q}_3 + b_{110}(q_1\bar{q}_2 + q_2\bar{q}_1) + b_{101}(q_1\bar{q}_3 + q_3\bar{q}_1) + b_{011}(q_2\bar{q}_3 + q_3\bar{q}_2), \gamma_2^3 = b_{200}\bar{q}_1^2 + b_{020}\bar{q}_2^2 + b_{002}\bar{q}_3^2 + b_{110}q_1\bar{q}_2 + b_{011}\bar{q}_2\bar{q}_3 + b_{101}\bar{q}_1\bar{q}_3, \gamma_2^5 = \frac{b_{300}q_2^2\bar{q}_1 + b_{030}q_2^2\bar{q}_2 + b_{003}q_3^2\bar{q}_3 + b_{210}(q_1^2\bar{q}_2 + 2q_1\bar{q}_1q_2) + b_{120}(q_2^2\bar{q}_3 + 2q_2\bar{q}_2q_3) + b_{102}(q_1\bar{q}_3^2 + 2q_1\bar{q}_3q_3) + b_{012}(q_2\bar{q}_3^2 + 2q_2\bar{q}_3q_3) + b_{111}(q_1q_2\bar{q}_3 + q_1q_3\bar{q}_2 + q_3q_2\bar{q}_1)}{6}, \gamma_3^1 = c_{020}q_2^2 + c_{011}q_3q_2, \gamma_3^2 = 2c_{020}q_2\bar{q}_2 + c_{011}(q_2\bar{q}_3 + q_3\bar{q}_2), \gamma_3^3 = c_{020}\bar{q}_2^2 + c_{011}\bar{q}_2\bar{q}_3, \gamma_3^4 = \frac{c_{030}q_2^2\bar{q}_3 + c_{021}q_2^2\bar{q}_3}{6}, \gamma_3^5 = \frac{c_{030}q_2^2\bar{q}_2 + c_{003}q_3^2\bar{q}_3 + c_{021}(q_2^2\bar{q}_3 + 2q_2\bar{q}_2q_3)}{6}, q_1 = a_{010}b_{001}, q_2 = -b_{100}c_{001} + \omega_0, q_3 = -b_{100}a_{010} + a_{100}b_{010} - \omega_0^2 - \omega_0(a_{100} + b_{010}), Where $a_{200} = -\frac{2r}{k_1} + \frac{2a\beta_1 Z_*}{(a+P_*)^3}$, $a_{300} = \frac{-6a\beta_1 Z_*}{(a+P_*)^4}$, $a_{110} = \frac{-\beta_1 a}{(a+P_*)^2}$, $a_{210} = \frac{2\beta_1 a}{(a+P_*)^3}$, $b_{200} = \frac{-2\beta_1 \beta_2 a Z_*}{(1+K F_*)(a+P_*)^3}$, $b_{300} = \frac{6\beta_1 \beta_2 a Z_*}{(1+K F_*)(a+P_*)^4}$, $b_{020} = \frac{2b\gamma(1-r_1)^2 F_*}{(b+(1-r_1)Z_*)^3}$, $b_{030} = \frac{-6b\gamma(1-r_1)^3 F_*}{(b+(1-r_1)Z_*)^4}$, $b_{002} = \frac{2\beta_1 \beta_2 K^2 P_* Z_*}{(1+K F_*)^3(a+P_*)}$, $b_{003} = \frac{-6\beta_1 \beta_2 K^3 P_* Z_*}{(1+K F_*)^4(a+P_*)}$, $b_{110} = \frac{\beta_1 \beta_2 a}{(1+K F_*)(a+P_*)^2}$, $b_{101} = \frac{-\beta_1 \beta_2 a K}{(1+K F_*)^2(a+P_*)^2}$, $b_{011} = \frac{-\gamma b(1-r_1)}{(b+(1-r_1)Z_*)^2} - \frac{\beta_1 \beta_2 P_* K}{(1+K F_*)^2(a+P_*)}$, $b_{210} = \frac{-2\beta_1 \beta_2 a}{(1+K F_*)(a+P_*)^3}$, $b_{201} = \frac{2\beta_1 \beta_2 K a Z_*}{(1+K F_*)^2(a+P_*)^3}$, $b_{021} = \frac{2b\gamma(1-r_1)^2}{(b+(1-r_1)Z_*)^3}$, $b_{102} = \frac{2\beta_1 \beta_2 a Z_* K^2}{(1+K F_*)^3(a+P_*)^2}$, $b_{012} = \frac{2\beta_1 \beta_2 P_* K^2}{(1+K F_*)^3(a+P_*)}$, $b_{111} = \frac{-\beta_1 \beta_2 a K}{(1+K F_*)^2(a+P_*)^2}$, $C_{020} = \frac{-2c\gamma(1-r_1)^2 b F_*}{(b+(1-r_1)Z_*)^3}$, $C_{030} = \frac{6c\gamma(1-r_1)^3 b F_*}{(b+(1-r_1)Z_*)^4}$, $C_{011} = \frac{c\gamma(1-r_1)b}{(b+(1-r_1)Z_*)^2}$, $C_{021} = \frac{-2c\gamma(1-r_1)^2 b}{(b+(1-r_1)Z_*)^3}$.$$

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