



Effects of supplying alternative food in a predator–prey model with harvesting



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ABSTRACT

In this paper, we propose a tritrophic predator–prey model with harvesting where the top-predator population is partially supported with alternative food. We report the consequences of providing alternative food to the top-predator in a top-predator harvested model. The extinction criterion for top-predator population, local stability of equilibrium points and persistence conditions are discussed theoretically. Pontryagin's maximum principle is used to characterize the optimal control of harvesting. We have derived the condition of Hopf bifurcation by varying harvesting effort. The bifurcation diagrams of the system with respect to harvesting effort in presence of alternative food are given. Our analysis shows that alternative food can prevent top-predator extinction risk at higher harvesting effort and plays a vital role for biological conservation of species.

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1. Introduction

It is now well known that most of the predators do not feed only on a single prey, but also depend on diverse prey species and are therefore involved in a complex food web interactions [1,2]. Many species are also migratory and their spatial scale much longer than the habitat occupied by some of their prey. Therefore, for these types of species, alternative prey needs to be considered to develop a realistic prey–predator system. The impact of a generalist predator not only depends on the abundance and susceptibility of the focal prey, but also on the presence and abundance of alternative prey species [3]. These additional foods are an important component of most predators (e.g., coccinellid) diet, and although they receive less attention than basal prey. In scientific literature, these foods fundamentally shape the life histories of many predator species. The availability of suitable additional food (non-prey food) in a predator prey system can have significant role on the dynamics of the system. The role of alternative prey in sustaining predator populations has been widely reported in laboratory studies and field trials examining the fecundity, feeding behaviour, extinction risk and growth rates of species subjected to diets of varying quality. In the Channel Islands, golden eagle (*Aquila chrysaetos*) predation is thought to have reduced three resident fox populations by over 95%. The review report suggested that these predators are primarily sustained by hyper abundant alternative prey species [4]. For Spiny dogfish in the North West Atlantic and Pacific hake, as spatial scale are much longer than the habitat occupied by some of their prey, alternative prey must be required as alternative source of food. Recently, the application of monoclonal antibody and molecular technology to study predation rates in the field has revealed the extent to which many predator communities rely on alternative prey before, during and after the immigration of pests into crops. Thus the dynamics of complex food web critically depend on an accurate understanding of the relative importance of direct and

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indirect effects in multi-species prey-predator system [5]. Therefore, the consequences of providing additional food to predator and corresponding effects on the prey-predator dynamics and its importance in biological control have been existing as an interesting topic to the scientists.

Recently, many biologist, researchers, and theoreticians investigated the consequences of providing additional food to predators in predator–prey systems [6–12]. Huxel et al. [6,7] reported the impact of allochthonous inputs (additional food) on the stability of a simple food web model. They assumed constant and also variable allochthonous inputs (additional food) to consumers as well as to top-predators populations. They observed that low to moderate inputs of allochthonous resources can increase species persistences. Srinivasu et al. [8] studied qualitative behaviour of a di-trophic predator–prey system in presence of additional food to the predators and discussed the effect of both high to low quality food. Sahoo and Poria investigated a disease control aspects through the provision of alternative food to predators [11]. Recently, Sahoo and Poria reported that a chaotic dynamics can be controlled by supplying additional food to predator [12].

From the point of view of human needs, the exploitation of biological resources and harvesting of populations are commonly practiced in fishery, forestry. It is important to study bio-economic models to gain insight into the scientific management of renewable resources like fisheries and forestries [13]. This is related to the optimal management of renewable resources [14,15]. To determine Governments policy to avoid overexploitation to maximize profits of commercial harvesting. It is necessary to investigate the sustainability of harvesting of populations. The above application of the field experiment motivates us to focus on the predator–prey model with harvesting. One relevant work regarding alternative food source is done by Spencer and Collie [16] establishing a model of prey-predator fish with alternative prey in presence of harvesting. Recently, many researchers [5,17] investigated harvested predator–prey system with alternative prey.

In this paper, we first consider famous Hastings–Powell (HP) [18] food chain model incorporating alternative food to top-predator population. Next, we incorporate the constant harvesting effort to top-predator population in the model. We investigate the effects of harvesting as well as the effects of supplying alternative food into the model. Our main aim is to save top-predator population from extinction in presence of alternative food. Actually, we want to control the predator population by supplying alternative food with harvesting. The section-wise split of this paper is as follows: In Section 2, the model representing the dynamics of a three species food chain in the presence of additional food top-predator with harvesting effort is constructed. In Section 3, extinction criterion of top-predator population, the local stability analysis of equilibrium points, persistence criterion of the proposed model are determined. Section 4 is devoted to find the bionomic equilibrium of the system. In Section 5, an optimal control policy of the model is determined. Hopf-bifurcation analysis is developed in Section 6. The Section 7 illustrates some of the key findings through numerical simulations. In Section 8, the different routes of continuation of the associated bifurcations are investigated with the help of the software package MATCONT [19–22]. Finally, we draw a conclusion in Section 9.

2. Model formulation

We consider the base model as Hastings and Powell food chain model [18] composed of a logistic prey (X), a Holling type II intermediate predator (Y), and a Holling type II top-predator (Z). It is, given by the following system of ordinary differential equations:

$$\begin{aligned}\frac{dX}{dT} &= R_0 X \left(1 - \frac{X}{K_0}\right) - C_1 A_1 \frac{XY}{B_1 + X}, \\ \frac{dY}{dT} &= A_1 \frac{XY}{B_1 + X} - A_2 \frac{YZ}{B_2 + Y} - D_1 Y, \\ \frac{dZ}{dT} &= C_2 A_2 \frac{YZ}{B_2 + Y} - D_2 Z,\end{aligned}\tag{1}$$

where T is time. The constant R_0 is the “intrinsic growth rate” and the constant K_0 is the “carrying capacity” of the species X . The constant C_1^{-1} and C_2 are conversion rates of prey to predators for species Y and Z respectively; D_1 and D_2 are constant death rates for species Y and Z respectively. The constants A_i and B_i for $i = 1, 2$ are maximal predation rate and half saturation constants for Y and Z respectively. In order to preserve the biological meaning of the model, the parameters are assumed to be strictly positive. Furthermore, to avoid the case where intermediate predator and top-predator cannot survive, even when their food is infinitely abundant, we assume that $A_1 > D_1$ and $A_2 C_2 > D_2$ [23] (see Appendix).

We now incorporate the constant harvesting effort E on top-predator in the model (1) and we obtain the following model:

$$\begin{aligned}\frac{dX}{dT} &= R_0 X \left(1 - \frac{X}{K_0}\right) - C_1 A_1 \frac{XY}{B_1 + X}, \\ \frac{dY}{dT} &= A_1 \frac{XY}{B_1 + X} - A_2 \frac{YZ}{B_2 + Y} - D_1 Y, \\ \frac{dZ}{dT} &= C_2 A_2 \frac{YZ}{B_2 + Y} - D_2 Z - EZ.\end{aligned}\tag{2}$$

In the model (2), we have considered a predator–prey model where top-predator depends only on intermediate predator. But recently, some authors emphasized that the presence of an alternative prey (alternative food source) [6–11] to the system may change the dynamical behaviour of the system in several ways. As an example, alternative prey can reduce the predation on intermediate predator due to predator preference for the alternative prey resource. Feeding of such multiple prey seems appropriate for fish which are predators of the larvae and juveniles of numerous fish species. Thus, the growth rate of the top-predator Z should be maximal when Y is abundant but non-zero when $Y \rightarrow 0$. Hence the model (2) can be modified to describe a partially coupled predator–prey interaction:

$$\begin{aligned}\frac{dX}{dT} &= R_0 X \left(1 - \frac{X}{K_0} \right) - C_1 A_1 \frac{XY}{B_1 + X}, \\ \frac{dY}{dT} &= A_1 \frac{XY}{B_1 + X} - A_2 \frac{AYZ}{B_2 + Y} - D_1 Y, \\ \frac{dZ}{dT} &= C_2 A_2 Z \left(\frac{AY}{B_2 + Y} + (1 - A) \right) - D_2 Z - EZ,\end{aligned}\quad (3)$$

where A is a time independent constant and its origin is the alternative resource. If $A = 1$, the top-predator depends only on the intermediate predator species and thus it is clear that the system (2) is a special case of system (3). If $A = 0$, then both the intermediate predator and top-predator population grow without any interaction and the growth rate of the top-predator is determined by alternative prey. In such case, the predation pressure on intermediate predator is completely removed and top-predator population evolves in presence of alternative food only. But such decoupled system is out of our interest. A top-predator which alternates between two sources of prey can be represented within $0 < A < 1$.

We now nondimensionalize the system (2) with $x = \frac{X}{K_0}$, $y = \frac{C_1 Y}{K_0}$, $z = \frac{C_2 Z}{C_2 K_0}$, $t = R_0 T$ and obtain the following system

$$\begin{aligned}\frac{dx}{dt} &= x(1 - x) - \frac{a_1 xy}{1 + b_1 x}, \\ \frac{dy}{dt} &= \frac{a_1 xy}{1 + b_1 x} - \frac{a_2 Ayz}{1 + b_2 y} - d_1 y, \\ \frac{dz}{dt} &= a_2 z \left(\frac{Ay}{1 + b_2 y} + c(1 - A) \right) - d_2 z - ez,\end{aligned}\quad (4)$$

where $a_1 = \frac{A_1 K_0}{R_0 B_1}$, $a_2 = \frac{A_2 K_0 C_2}{B_2 R_0 C_1}$, $b_1 = \frac{K_0}{B_1}$, $b_2 = \frac{K_0}{B_2 C_1}$, $c = \frac{C_1 B_2}{K_0}$, $d_1 = \frac{D_1}{R_0}$, $d_2 = \frac{D_2}{R_0}$, $e = \frac{E}{R_0}$. Here $a_1 = \frac{A_1 K_0}{R_0 B_1} > b_1 d_1 = \frac{D_1 K_0}{R_0 B_1}$ as $A_1 > D_1$ and $a_2 = \frac{A_2 C_2 K_0}{B_2 R_0 C_1} > b_2 d_2 = \frac{D_2 K_0}{B_2 R_0 C_1}$ as $A_2 C_2 > D_2$.

Therefore the conditions for intermediate predator and top-predator persistence become $a_i > b_i d_i$, $i = 1, 2$. The system (4) has to be analysed with the following initial conditions: $x(0) \geq 0$, $y(0) \geq 0$, $z(0) \geq 0$. In the following section we shall analyse the dynamics of the system (3) theoretically as well as numerically.

3. Theoretical study

The functions of the right hand sides of the system (4) are continuous and have continuous partial derivatives on the state space $\mathbb{R}_+^3 = \{(x(t), y(t), z(t)) : x(t) \geq 0, y(t) \geq 0, z(t) \geq 0\}$. Therefore, they are Lipschitzian on \mathbb{R}_+^3 and hence the solution of the system (4) with non-negative initial condition exists and unique. Moreover, following Cao et al. [24], it is easy to show that the state space \mathbb{R}_+^3 is an invariant domain of the system (4).

In the following section, positivity and boundedness of solution for the system (4) are established. Since the state variables x, y, z represent populations, positivity implies that they never become zero and population always survive. The boundedness may be interpreted as natural restrictions to unlimited growth as a consequence of limited resources [25].

3.1. Positive invariance

The system (4) can be written in the matrix form as $\dot{\bar{X}} = F(\bar{X})$ with $\bar{X}(0) = \bar{X}_0 \in \mathbb{R}_+^3$, where $\bar{X} = (x, y, z)^T \in \mathbb{R}_+^3$ and $F(\bar{X})$ is given by

$$F = F(\bar{X}) = \begin{pmatrix} x(1 - x) - \frac{a_1 xy}{1 + b_1 x} \\ \frac{a_1 xy}{1 + b_1 x} - \frac{a_2 Ayz}{1 + b_2 y} - d_1 y \\ a_2 z \left(\frac{Ay}{1 + b_2 y} + c(1 - A) \right) - d_2 z - ez \end{pmatrix},$$

where $F : C_+ \rightarrow \mathbb{R}^3$ and $F \in C^\infty(\mathbb{R}^3)$.

It can be shown that whenever $\bar{X}(0) \in \mathbb{R}_+^3$ such that $X_i = 0$ then $F_i(\bar{X})|_{X_i=0} \geq 0$ (for $i = 1, 2, 3$). Now any solution of $F = F(\bar{X})$ with $\bar{X}_0 \in \mathbb{R}_+^3$, say $\bar{X}(t) = \bar{X}(t, \bar{X}_0)$, is such that $\bar{X}(t) \in \mathbb{R}_+^3$ for all $t > 0$ [26].

3.2. Boundedness

Theorem 1. All solutions of the system (4) which start in \mathbb{R}_+^3 are uniformly bounded if $d_2 + e > a_2c(1 - A)$ holds.

Proof. Let $(x(t), y(t), z(t))$ be any solution of the system (4) with positive initial conditions.

Let us consider that, $w = x + y + z$,

$$\text{i.e., } \frac{dw}{dt} = \frac{dx}{dt} + \frac{dy}{dt} + \frac{dz}{dt}.$$

Using equations of (4), we have

$$\frac{dw}{dt} = x(1 - x) - \frac{a_1xy}{1 + b_1x} + \frac{a_1xy}{1 + b_1x} - \frac{a_2Ayz}{1 + b_2y} - d_1y + a_2z \left(\frac{Ay}{1 + b_2y} + c(1 - A) \right) - d_2z - ez.$$

Therefore,

$$\frac{dw}{dt} \leq -\theta(x + y + z) - (x - 1)^2 + 1,$$

where $\theta = \min\{1, d_1, d_2 + e - a_2c(1 - A)\}$, provided $d_2 + e > a_2c(1 - A)$.

Hence,

$$\frac{dw}{dt} + \theta w \leq 1.$$

Applying the theory of differential inequality we obtain

$$0 < w < \frac{1 - e^{-\theta t}}{\theta} + w(x(0), y(0), z(0))e^{-\theta t}.$$

For $t \rightarrow \infty$, we have $0 < w < \frac{1}{\theta}$. \square

Hence all the solutions of (4) that initiate in \mathbb{R}_+^3 are confined in the region $S = \{(x, y, z) \in \mathbb{R}_+^3 : w = \frac{1}{\theta} + \eta, \text{ for any } \eta > 0\}$. This proves the theorem.

Note: The condition $d_2 + e > a_2c(1 - A)$ implies that $1 - \frac{d_2 + e}{a_2c} < A < 1$. Therefore, for uniformly bounded solutions of the system (4), supply of alternative food depends on harvesting effort (e).

3.3. Extinction criterion for top-predator

Lemma 1. If $e > \frac{a_2A + a_2cb_2(1 - A) - b_2d_2}{b_2}$, then $\lim_{t \rightarrow \infty} z(t) = 0$.

Proof.

$$\frac{dz}{dt} = a_2z \left(\frac{Ay}{1 + b_2y} + c(1 - A) \right) - d_2z - ez.$$

Therefore,

$$z(t) \leq z(t_0) \exp \left(\int_{t_0}^t \left(\frac{\{a_2A + b_2a_2c(1 - A) - (d_2 + e)b_2\}y(r)}{1 + b_2y(r)} \right) dr \right).$$

Thus if $e > \frac{a_2A + a_2cb_2(1 - A) - b_2d_2}{b_2}$, then $\lim_{t \rightarrow \infty} z(t) = 0$. \square

3.4. Existence and local stability criteria of equilibrium points

The system (4) possesses following four equilibrium states:

(a) The trivial equilibrium state is $E_T \equiv (0, 0, 0)$. An eigenvalue associated with the Jacobian matrix at E_0 is 1, positive, for which E_0 is an unstable equilibrium point.

(b) The axial equilibrium state is $E_A \equiv (1, 0, 0)$. The Jacobian matrix at the equilibrium point E_A is

$$J(E_A) = \begin{pmatrix} -1 & -\frac{a_1}{1 + b_1} & 0 \\ 0 & \frac{a_1}{1 + b_1} - d_1 & 0 \\ 0 & 0 & a_2c(1 - A) - d_2 - e \end{pmatrix}.$$

The axial equilibrium point E_A is stable if $\frac{a_1}{1 + b_1} < d_1$ and $A > 1 - \frac{d_2 + e}{a_2c}$. If at least one of these conditions is violated, then $E_A(1, 0, 0)$ is unstable.

(c) The top-predator free equilibrium state is $E_P \equiv (\bar{x}, \bar{y}, 0)$, where $\bar{x} = \frac{d_1}{a_1 - b_1 d_1}$ and $\bar{y} = \frac{a_1 - (b_1 + 1)d_1}{(a_1 - b_1 d_1)^2}$. The top-predator free equilibrium point E_P exists if $a_1 > (b_1 + 1)d_1$.

We now study the stability criteria of the top-predator free equilibrium point E_P . The Jacobian matrix at E_P is given by

$$J(E_P) = \begin{pmatrix} 1 - 2\bar{x} - \frac{a_1 \bar{y}}{(1 + b_1 \bar{x})^2} & -\frac{a_1 \bar{x}}{1 + b_1 \bar{x}} & 0 \\ \frac{a_1 \bar{y}}{(1 + b_1 \bar{x})^2} & \frac{a_1 \bar{x}}{1 + b_1 \bar{x}} - d_1 & -\frac{a_2 \bar{y}}{1 + b_2 \bar{y}} \\ 0 & 0 & \frac{a_2 \bar{y}}{1 + b_2 \bar{y}} + a_2 c(1 - A) - d_2 - e \end{pmatrix}.$$

The characteristic roots of the Jacobian matrix E_P are $\frac{a_2 \bar{y}}{1 + b_2 \bar{y}} + a_2 c(1 - A) - d_2 - e$ and the roots of the equation $\lambda^2 + \sigma_1 \lambda + \sigma_2 = 0$, where

$$\sigma_1 = -\left[1 - 2\bar{x} - \frac{a_1 \bar{y}}{(1 + b_1 \bar{x})^2} + \frac{a_1 \bar{x}}{1 + b_1 \bar{x}} - d_1\right],$$

$$\sigma_2 = \left[(1 - 2\bar{x}) \cdot \left(\frac{a_1 \bar{x}}{1 + b_1 \bar{x}} - d_1\right) + \frac{a_1 \bar{y} d_1}{(1 + b_1 \bar{x})^2}\right].$$

The top-predator free equilibrium point $E_P(\bar{x}, \bar{y}, 0)$ is asymptotically stable if $\frac{a_2 \bar{y}}{1 + b_2 \bar{y}} + a_2 c(1 - A) < d_2 + e$, $\sigma_1 > 0$ and $\sigma_2 > 0$.

(d) The interior equilibrium state is $E^* \equiv (x^*, y^*, z^*)$, where $y^* = \frac{(d_2 + e) - a_2 c(1 - A)}{a_2 A - b_2[(d_2 + e) - a_2 c(1 - A)]}$, $z^* = \frac{1}{[a_2 A - b_2[(d_2 + e) - a_2 c(1 - A)]]} \left[\frac{a_1 x^*}{1 + b_1 x^*} - d_1\right]$ and x^* is the positive root of the equation $Px^{*2} + Qx^* + R = 0$ where, $P = b_1$, $Q = 1 - b_1$ and $R = \frac{a_1 \{(d_2 + e) - a_2 c(1 - A)\}}{a_2 A - b_2[(d_2 + e) - a_2 c(1 - A)]} - 1$. The positive interior equilibrium point E^* exists if $d_2 + e > a_2 c(1 - A)$, $a_2 A > b_2\{d_2 + e - a_2 c(1 - A)\}$, $\frac{a_1 x^*}{1 + b_1 x^*} > d_1$ and $Q^2 \geq 4PR$, $Q < 0$.

The Jacobian matrix at E^* is given by

$$J(E^*) = \begin{pmatrix} A_{11} & A_{12} & A_{13} \\ A_{21} & A_{22} & A_{23} \\ A_{31} & A_{32} & A_{33} \end{pmatrix},$$

where,

$$A_{11} = 1 - 2x^* - \frac{a_1 y^*}{(1 + b_1 x^*)^2}, \quad A_{12} = -\frac{a_1 x^*}{1 + b_1 x^*}, \quad A_{13} = 0, \quad A_{21} = \frac{a_1 y^*}{(1 + b_1 x^*)^2}, \quad A_{22} = \frac{a_1 x^*}{1 + b_1 x^*} - \frac{a_2 A z^*}{(1 + b_2 y^*)^2} - d_1,$$

$$A_{23} = -\frac{a_2 A y^*}{1 + b_2 y^*}, \quad A_{31} = 0, \quad A_{32} = \frac{a_2 A z^*}{(1 + b_2 y^*)^2}, \quad A_{33} = 0.$$

The characteristic equation of the Jacobian matrix E^* is given by

$$\lambda^3 + \Omega_1 \lambda^2 + \Omega_2 \lambda + \Omega_3 = 0,$$

where,

$$\Omega_1 = -[A_{11} + A_{22}],$$

$$\Omega_2 = [A_{11}A_{22} - A_{12}A_{21} - A_{32}A_{23}],$$

$$\Omega_3 = A_{11}A_{32}A_{23}.$$

It is obvious that $A_{11} < 0$, $A_{12} < 0$, $A_{21} > 0$, $A_{23} < 0$ and $A_{32} > 0$. Here $\Omega_1 = -[A_{11} + A_{22}] > 0$ if $A_{22} < 0$ and obviously $\Omega_3 = [A_{11}A_{23}A_{32}] > 0$.

Now $\Omega_1 \Omega_2 - \Omega_3 = A_{22}A_{23}A_{32} - (A_{11} + A_{22})(A_{11}A_{22} - A_{12}A_{21})$.

If $A_{22} < 0$, then $A_{22}A_{23}A_{32} > 0$, $(A_{11} + A_{22}) < 0$ and $(A_{11}A_{22} - A_{12}A_{21}) > 0$. Thus $\Omega_1 \Omega_2 - \Omega_3 > 0$.

Therefore the system (3) is locally stable at the interior equilibrium state E^* if $\frac{a_1 x^*}{1 + b_1 x^*} < \frac{a_2 A z^*}{(1 + b_2 y^*)^2} + d_1$.

Corollary 1. The system (4) is locally stable at the interior equilibrium state $E^* = (x^*, y^*, z^*)$ if $\frac{a_1 x^*}{1 + b_1 x^*} < \frac{a_2 A z^*}{(1 + b_2 y^*)^2} + d_1$.

Proposition 1. Equilibrium level of intermediate predator biomass decreases monotonically with the increase of alternative resource A if $a_2 c A < [(d_2 + e) - a_2 c(1 - A)](a_2 b_2 c + 1)$ and increases with the increase of harvesting effort e .

Proof. Differentiating y^* with respect to A we get

$$\frac{dy^*}{dA} = \frac{a_2^2 c A - [(d_2 + e) - a_2 c(1 - A)](a_2 b_2 c + 1)}{[a_2 A - b_2\{(d_2 + e) - a_2 c(1 - A)\}]^2} < 0,$$

if $a_2^2 c A < [(d_2 + e) - a_2 c(1 - A)](a_2 b_2 c + 1)$.

Now, differentiating y^* with respect to e we have

$$\frac{dy^*}{de} = \frac{a_2 A}{[a_2 A - b_2 \{(d_2 + e) - a_2 c(1 - A)\}]^2} > 0.$$

Hence the proof is completed. \square

Proposition 2. *Equilibrium level of top-predator biomass is an increasing function of additional resource A if $b_2 c < 1$, but is an decreasing function of e .*

Proof. Differentiating z^* with respect to A we get

$$\frac{dz^*}{dA} = \frac{a_2(1 - b_2 c)}{[a_2 A - b_2 \{(d_2 + e) - a_2 c(1 - A)\}]^2} \cdot \left[\frac{a_1 x^*}{1 + b_1 x^*} - d_1 \right],$$

If $b_2 c < 1$, then $\frac{dz^*}{dA} > 0$.

Again, differentiating z^* with respect to e we have

$$\frac{dz^*}{de} = \frac{-d_2}{[a_2 A - b_2 \{(d_2 + e) - a_2 c(1 - A)\}]^2} \cdot \left[\frac{a_1 x^*}{1 + b_1 x^*} - d_1 \right] < 0.$$

Hence the proof is completed. \square

Therefore, from the above Propositions, it is clear that systems biomass depends on supply of alternative resource A and harvesting effort e .

3.5. Persistence of the system

Butler et al. [27], Freedman and Waltman [28,29] developed the following definitions of persistence:

If a population $N(t)$ is such that $N(t) > 0$, then

- (i) $N(t)$ is said to be *weakly persistent* if $\lim_{t \rightarrow \infty} \sup N(t) > 0$.
- (ii) $N(t)$ is said to be *(strongly) persistent* if $\lim_{t \rightarrow \infty} \inf N(t) > 0$. Further, if $N(t) \in C$, where C is a certain class of function, then
- (iii) $N(t)$ is said to be *weakly uniformly persistent* if there exists $\delta > 0$ such that $\lim_{t \rightarrow \infty} \sup N(t) > \delta$ for all $N(t) \in C$.
- (iv) $N(t)$ is said to be *uniformly persistent* if there exists $\delta > 0$ such that $\lim_{t \rightarrow \infty} \inf N(t) > \delta$ for all $N(t) \in C$.

From biological point of view, persistence of a system means the long term survival of all populations of the system, no matter what the initial populations are. Mathematically, persistence of a system means that strictly positive solutions do not have omega (Ω) limit points on the boundary of the non-negative cone.

Theorem 2. *Let the following conditions are satisfied*

- (i) $\frac{a_1}{1+b_1} > d_1$,
- (ii) $A < 1 - \frac{d_2+e}{a_2 c}$,
- (iii) $1 + \frac{a_1 \bar{x}}{1+b_1 \bar{x}} < d_1 + 2\bar{x} + \frac{a_1 \bar{y}}{(1+b_1 \bar{x})^2 d_1}$,
- (iv) $\left[(1 - 2\bar{x}) \left(\frac{a_1 \bar{x}}{1+b_1 \bar{x}} - d_1 \right) + \frac{a_1 \bar{y}}{(1+b_1 \bar{x})^2} \right] > 0$,

and if there exists a finite number (say, n) of periodic solutions $x = \phi_r(t)$, $y = \psi_r(t)$, $r = 1, 2, 3, \dots, n$, in the xy plane, then system (4) is uniformly persistent provided for each periodic solutions of period T ,

$$\zeta_r = -d_2 - e + a_2(1 - A) + \frac{1}{T} \int_0^T \left(\frac{A a_2 \psi_r(t)}{1 + b_2 \psi_r(t)} \right) dt > 0, \quad r = 1, 2, \dots, n.$$

Proof. Let $X = (x, y, z)$ be a point in the positive quadrant and $O(X)$ be orbit through X and Ω be the omega limit set of the orbit through X . Note that $\Omega(X)$ is bounded.

We claim that $E_T \notin \Omega(X)$. If $E_T \in \Omega(X)$ then by the Butler-McGehee lemma [28] there exist a point P in $\Omega(X) \cap W^s(E_T)$ where $W^s(E_T)$ denotes the stable manifold of E_T . Since $O(P)$ lies in $\Omega(X)$ and $W^s(E_T)$ is the yz plane, we conclude that $O(P)$ is unbounded, which is contrary to the boundedness of the system.

Next $E_A \notin \Omega(X)$, for otherwise, since E_A is a saddle point which follows from the conditions $\frac{a_1}{1+b_1} > d_1$ and $A < 1 - \frac{d_2+e}{a_2 c}$, by the Butler-McGehee lemma there exist a point P in $\Omega(X) \cap W^s(E_A)$. Now $W^s(E_A)$ is the x -axis implies that an unbounded orbit lies in $\Omega(X)$, a contradiction.

Lastly, we show that no periodic orbits in the xy plane or $E_B \in \Omega(X)$. The conditions (iii) and (iv) implies that the eigenvalue values of $J(E_B)$ have negative real parts. Let $\gamma_r, r = 1, 2, \dots, n$ denote the closed orbit of the periodic solution $(\phi_r(t), \psi_r(t))$ in xy plane such that γ_r lies inside γ_{r-1} . Let the Jacobian matrix $J_r(\phi_r(t), \psi_r(t), 0)$ corresponding to γ_r is given by

$$J_r = \begin{pmatrix} F_{1x}(\phi_r(t), \psi_r(t), 0) & F_{1y}(\phi_r(t), \psi_r(t), 0) & 0 \\ F_{2x}(\phi_r(t), \psi_r(t), 0) & F_{2y}(\phi_r(t), \psi_r(t), 0) & F_{2z}(\phi_r(t), \psi_r(t), 0) \\ 0 & 0 & F_{3z}(\phi_r(t), \psi_r(t), 0) \end{pmatrix}.$$

Here $F_{3z} = -d_2 - e + a_2(1 - A) + \frac{Aa_2\psi_r(t)}{1+b_2\psi_r(t)}$. Computing the fundamental matrix of the linear periodic system, we obtain $X' = J_r(t)X, X(0) = X_0$.

We find that its Floquet multiplier in the z -direction is $e^{\int_0^T F_{3z}(t) dt}$. Then proceeding in an analogous manner like Kumar and Freedman [30], we conclude that no γ_r lies on $\Omega(X)$. Thus, $\Omega(X)$ lies in the positive quadrant and system (4) is persistent. Finally, since only the closed orbits and the equilibria from the omega limit set of the solutions on boundary of R_+^3 and the system (4) is dissipative. Now using a theorem of Butler et al. [28], we conclude that system (4) is uniformly persistent. \square

Theorem 3. Let the following conditions are satisfied

- (i) $\frac{a_1}{1+b_1} > d_1$,
- (ii) $A < 1 - \frac{d_2+e}{a_2c}$,
- (iii) $1 + \frac{a_1\bar{x}}{1+b_1\bar{x}} < d_1 + 2\bar{x} + \frac{a_1\bar{y}}{(1+b_1\bar{x})^2}$,
- (iv) $\left[(1 - 2\bar{x}) \left(\frac{a_1\bar{x}}{1+b_1\bar{x}} - d_1 \right) + \frac{a_1\bar{y}d_1}{(1+b_1\bar{x})^2} \right] > 0$,
- (v) $\left[-d_2 - e + a_2(1 - A) + \frac{a_2A\bar{y}}{1+b_2\bar{y}} \right] > 0$.

and if there exists no limit cycle in the xy plane, the system (4) is uniformly persistent.

Proof. Proof is obvious and so omitted.

4. Bionomic equilibrium

The term bionomic equilibrium is an amalgamation of biological equilibrium and economic equilibrium. The biological equilibrium of the system (4) satisfy the equations

$$\frac{dx}{dt} = \frac{dy}{dt} = \frac{dz}{dt} = 0. \quad (5)$$

The economic equilibrium is said to be achieved when the TR (total revenue obtained by selling the harvested predator z) equals TC (the total cost for the effort devoted to harvesting). At first we consider the term e to be the non-dimensional measure of the harvesting effort, p is the constant price per unit biomass, h is the constant cost of harvesting effort and ω is the economic constant. Then the economic rent (net revenue) at any time is given by

$$\pi(z, e) = TR - TC = (p - \omega ez)ez - he. \quad (6)$$

For convenience, we take p and h to be constant. So, the economic equilibrium can be obtained from the Eq. (5) and using the equation of zero profit line

$$\begin{aligned} \pi(z, e) &= 0 \text{ i.e., } (p - \omega ez)ez - he = 0, \\ \text{Therefore, } \omega ez^2 - pz + h &= 0. \end{aligned} \quad (7)$$

Therefore, using the Eqs. (5) and (7) one can obtain the feasible economic equilibrium $(\hat{x}, \hat{y}, \hat{z})$. The optimal economic rent is calculated in the next section.

5. Optimal control policy

In commercial exploitation of renewable resources the fundamental problem is to determine the optimal trade-off between present and future harvests. The emphasis of this section is on the profit-making aspect of the model. It is a thorough study of the optimal harvesting policy to optimize the profit earned by harvesting considering quadratic costs and conservation of top-predator. The prime reason for using quadratic costs is that it allows to derive an analytical expression for the optimal harvesting. It is assumed that price is a function which decreases with the increase of harvested biomass. Thus, to maximize the total discounted net revenues from the model, the optimal control problem can be formulated [31] as

$$J(e) = \int_{t_0}^{t_f} e^{-\delta t} [(p - \omega e z) e z - h e] dt, \quad (8)$$

where δ is the instantaneous annual discount rate. The problem (8) can be solved by applying Pontryagin's maximum principle subject to model (4) and control constraints $0 \leq e \leq e_{\max}$. The convexity of the objective function with respect to e , the linearity of the differential equations in the control and the compactness of the range values of the state variables can be combined to give the existence of the optimal control. Suppose e_δ is an optimal control with corresponding states x_δ, y_δ and z_δ . We take $A_\delta(x_\delta, y_\delta, z_\delta)$ as optimal equilibrium point. Here we intend to derive optimal control e_δ such that

$$J(e_\delta) = \max\{J(e) : e \in U\},$$

where U is the control set defined by $U = \{e : [t_0, t_f] \rightarrow [0, e_{\max}] \mid e \text{ is Lebesgue measurable}\}$

Now, the Hamiltonian of this optimal control problem is $H = (p - \omega e z) e z - h e + \lambda_1 \{x(1 - x) - \frac{a_1 x y}{1 + b_1 x}\} + \lambda_2 \{y(1 - y) - \frac{a_2 y z}{1 + b_2 y} - d_1 y\} + \lambda_3 \{a_2 z (\frac{A y}{1 + b_2 y} + c(1 - A)) - d_2 z - e z\}$, where $\lambda_1, \lambda_2, \lambda_3$ are adjoint or costate variables.

Here the transversality conditions give $\lambda_i(t_f) = 0, i = 1, 2, 3$.

Now, it is possible to find the characterization of the optimal control e_δ .

On the set $t : 0 < e_\delta(t) < e_{\max}$, we have

$$\frac{\partial H}{\partial e} = p z - 2 \omega z^2 e - h - \lambda_3 z$$

Thus at $A_\delta(x_\delta, y_\delta, z_\delta), e = e_\delta(t)$ and

$$\frac{\partial H}{\partial e} = p z_\delta - 2 \omega z_\delta^2 e_\delta - h - \lambda_3 z_\delta = 0. \quad (9)$$

$$\text{This implies that, } e_\delta = \frac{p z_\delta - h - \lambda_3 z_\delta}{2 \omega z_\delta^2}. \quad (10)$$

Now, the adjoint equations at the point $A_\delta(x_\delta, y_\delta, z_\delta)$ are

$$\frac{d\lambda_1}{dt} = \delta\lambda_1 - \frac{\partial H}{\partial x} \Big|_{A_\delta} = \delta\lambda_1 - \left[\lambda_1 \left(1 - 2x_\delta - \frac{a_1 y_\delta}{(1 + b_1 x_\delta)^2} \right) + \lambda_2 \left(\frac{a_1 y_\delta}{(1 + b_1 x_\delta)^2} \right) \right], \quad (11)$$

$$\frac{d\lambda_2}{dt} = \delta\lambda_2 - \frac{\partial H}{\partial y} \Big|_{A_\delta} \quad \text{Therefore, } \frac{d\lambda_2}{dt} = \delta\lambda_2 - \left[\lambda_1 \left(-\frac{a_1 x_\delta}{1 + b_1 x_\delta} \right) + \lambda_2 \left(\frac{a_1 x_\delta}{1 + b_1 x_\delta} - d_1 \right) + \lambda_3 \left(\frac{a_2 A z_\delta}{(1 + b_2 y_\delta)^2} \right) \right], \quad (12)$$

$$\begin{aligned} \frac{d\lambda_3}{dt} &= \delta\lambda_3 - \frac{\partial H}{\partial z} \Big|_{A_\delta} \quad \text{Thus, } \frac{d\lambda_3}{dt} \\ &= \delta\lambda_3 - \left[\lambda_2 \left(-\frac{a_2 A y_\delta}{(1 + b_2 y_\delta)^2} \right) + \lambda_3 \left(\frac{a_2 A y_\delta}{1 + b_2 y_\delta} + a_2 c(1 - A) - d_2 - e_\delta \right) \right] - (p e_\delta - 2 \omega e_\delta^2 z_\delta). \end{aligned} \quad (13)$$

The three Eqs. (11)–(13) are first order system of simultaneous differential equations and it is easy to get the analytical solution of the equations with the help of initial conditions $\lambda_i(t_f) = 0, i = 1, 2, 3$. Using the value of λ_3 and Eqs. (5) and (9) one can get the feasible optimum harvesting equilibrium $(x_\delta, y_\delta, z_\delta)$. Therefore the optimum economic rent or net revenue at any time is obtained using the value of z_δ from the Eq. (6). In this regard, it is important to note that we have formulated the optimal control problem considering fishing effort as control parameter. The optimal control problem is solved using a forward-backward sweep technique of 4th order Runge–Kutta method. We summarize the above analysis by the following theorem.

Theorem 4. *There exists an optimal control e_δ and corresponding solutions of the system (4) $(x_\delta, y_\delta, z_\delta)$ maximizes $J(e)$ over U . Furthermore, there exists adjoint functions λ_1, λ_2 and λ_3 satisfying Eqs. (11)–(13) with transversality conditions $\lambda_i(t_f) = 0, i = 1, 2, 3$. Moreover, the optimal control is given by $e_\delta = \frac{p z_\delta - h - \lambda_3 z_\delta}{2 \omega z_\delta^2}$.*

6. Hopf bifurcation

With variation of model parameters, qualitatively different dynamical behaviour may occur and the critical parameter values at which such transitions happen are called bifurcation points. The purpose of this study is to determine the stability of the system with the variation of different parameters of the system. We have considered e as bifurcation parameter and e_{cr} represent the critical value or the bifurcating value of the concerned parameters [32].

Theorem 5. The necessary and sufficient conditions for occurrence of Hopf bifurcation at $e = e_{cr}$ are the following

- (i) $\Omega_i(e_{cr}) > 0, i = 1, 2, 3,$
- (ii) $\Omega_1(e_{cr})\Omega_2(e_{cr}) - \Omega_3(e_{cr}) = 0,$
- (iii) $Re\left[\frac{d\lambda_i}{de}\right]_{e=e_{cr}} \neq 0, \quad i = 1, 2, 3.$

Proof. The condition $\Omega_1\Omega_2 - \Omega_3 = 0$ gives $A_{22}A_{23}A_{32} - (A_{11} + A_{22})(A_{11}A_{22} - A_{12}A_{21}) = 0$, where all A_{ij} , for $i, j = 1, 2, 3$ and Ω_i 's are given in Subsection 3.4.

Since $\Omega_2 > 0$ at $e = e_{cr}$, there exists an interval containing e in $(e_{cr} - \epsilon, e_{cr} + \epsilon)$, for every $\epsilon > 0$. Therefore, for $e \in (e_{cr} - \epsilon, e_{cr} + \epsilon)$ the characteristic equation cannot have roots containing negative real parts. For $e = e_{cr}$, we have

$$(\lambda^2 + \Omega_2)(\lambda + \Omega_1) = 0. \quad (14)$$

It has three roots namely, $\lambda_1 = +i\sqrt{\Omega_2}$, $\lambda_2 = -i\sqrt{\Omega_2}$, and $\lambda_3 = -\Omega_1$.

For $e \in (e_{cr} - \epsilon, e_{cr} + \epsilon)$, the roots of the characteristic equation are in following general form

$$\begin{aligned} \lambda_1(e) &= \eta_1(e) + i\eta_2(e), \\ \lambda_2(e) &= \eta_1(e) - i\eta_2(e), \\ \lambda_3(e) &= -\Omega_3(e). \end{aligned}$$

We now verify the transversality condition $Re\left[\frac{d\lambda_i}{de}\right]_{e=e_{cr}} \neq 0, i = 1, 2, 3.$

Substituting $\lambda_1(e) = \eta_1(e) + i\eta_2(e)$ in (14) and calculating the derivative, we get

$$\begin{aligned} M_1(e)\eta'_1(e) - M_2(e)\eta'_2(e) + N_1(e) &= 0, \\ M_2(e)\eta'_1(e) + M_1(e)\eta'_2(e) + N_2(e) &= 0, \end{aligned}$$

where,

$$\begin{aligned} M_1(e) &= 3\eta_1^2(e) + 2\Omega_1(e)\eta_1(e) + \Omega_2(e) - 3\eta_2^2(e), \\ M_2(e) &= 6\eta_1(e)\eta_2(e) + 2\Omega_1(e)\eta_2(e), \\ N_1 &= \eta_1^2(e)\Omega'_1(e) + \Omega'_2(e)\eta_1(e) + \Omega'_3(e) - \Omega'_1(e)\eta_2^2(e), \\ N_2 &= 2\eta_1(e)\eta_2(e)\Omega'_1(e) + \Omega'_2(e)\eta_2(e). \end{aligned}$$

Since $M_1(e_{cr})N_1(e_{cr}) + M_2(e_{cr})N_2(e_{cr}) \neq 0$, we have $Re\left[\frac{d\lambda_i}{de}\right]_{e=e_{cr}} = \frac{M_1N_1 + M_2N_2}{M_1^2 + M_2^2} \Big|_{e=e_{cr}} \neq 0, i = 1, 2, 3.$ and $\lambda_3(e_{cr}) = -\Omega_1(e_{cr}).$

Hence the theorem is proved. \square

A Hopf point occurs at $e = e_{cr}$ if the Jacobian matrix $J(E^*)$ has a pair of purely imaginary eigenvalues namely, $\lambda_{1,2} = \pm i\omega_0$, $\omega_0 > 0$, and no other critical eigenvalue. A Hopf point is called *transversal* if the curves of complex eigenvalues cross the imaginary axis with non-zero derivative. At the Hopf point [33], when the first Lyapunov coefficient $l_1 < 0$ ($l_1 > 0$), a family of stable (unstable) periodic orbits can be found and the equilibrium point loses its stability. Therefore, the Hopf bifurcation with first lyapunov coefficient $l_1 < 0$ ($l_1 > 0$) indicates *supercritical* (*subcritical*) Hopf bifurcation.

7. Numerical study

We perform the numerical simulation of the system (4) with the following set of parameters, most of which are taken from HP [18] model. A set of parameter values are taken as $a_1 = 5.0, a_2 = 0.1, b_1 = 3, b_2 = 2.0, d_1 = 0.4, d_2 = 0.01, c = 0.45$, which remain unchanged throughout the simulations. We examine the effects of alternative resource parameter A within $0 < A < 1$ and harvesting effort e in the system.

We first simulate the dynamics of top-predator population z for different harvesting effort e and alternative resource A in Figs. 1 and 2. From Fig. 1(a), we observe that top-predator population z extinct for harvesting effort $e = 0.01$, when no alternative resource is available. But in presence of alternative resource, we observe that the top-predator population survives for the same harvesting effort $e = 0.01$ (Fig. 1(b)–(d)). Fig. 2 depicts the dynamics of the top-predator population with harvesting effort $e = 0.015$ for different values of alternative resource parameter. From Fig. 2, it is evident that the top-predator population extinct in absence of alternative resource, but in presence of alternative resource, the top-predator population may survive in the system. Therefore, from Figs. 1 and 2, it is clear that alternative resource supply prevent the extinction risk of top-predator population in the system.

One parameter bifurcation analysis is done with respect to harvesting effort of the system 4 in absence of alternative resource (i.e., for $A = 1$) in Fig. 3. We observe from the Fig. 3 that the system has chaotic or high periodic oscillations within $0 \leq e < 0.0026$, period-2 oscillation for $0.0026 \leq e < 0.0029$, limit cycle for $0.0029 \leq e < 0.0034$, stable steady state for $0.0034 \leq e \leq 0.0067$ and extinction risk for $e > 0.0067$. Therefore, the top-predator population has extinction risk for $e > 0.0067$ without alternative resource. We now demonstrate the bifurcation diagram of top-predator population in pres-

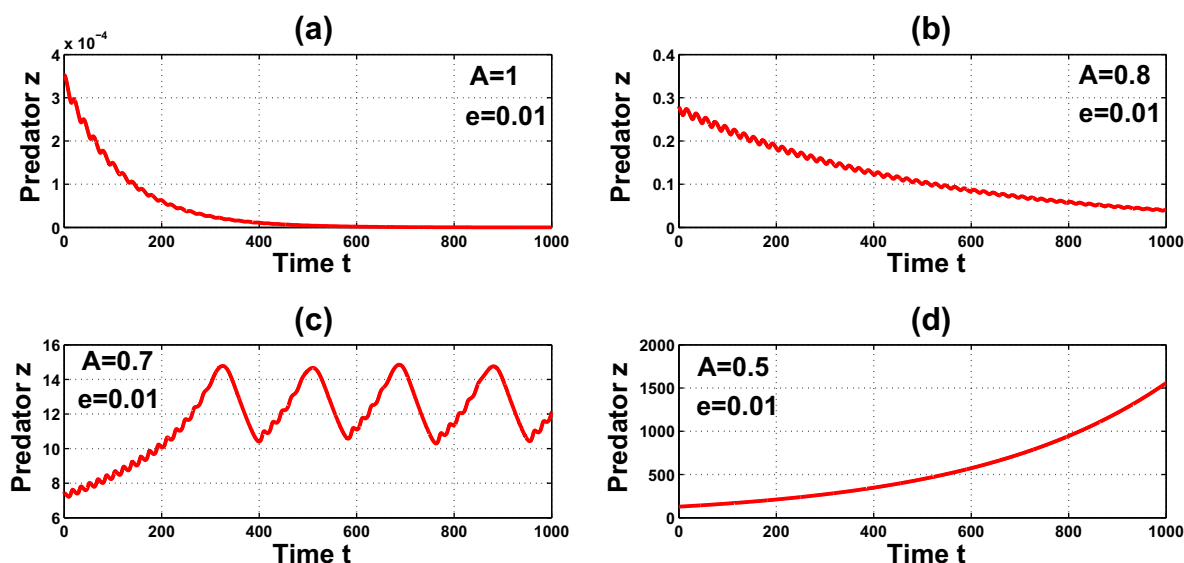


Fig. 1. Extinction risk of top-predator population (z) (a) in absence of alternative food, (b)–(d) in presence of various alternative food for constant harvesting effort $e = 0.01$.

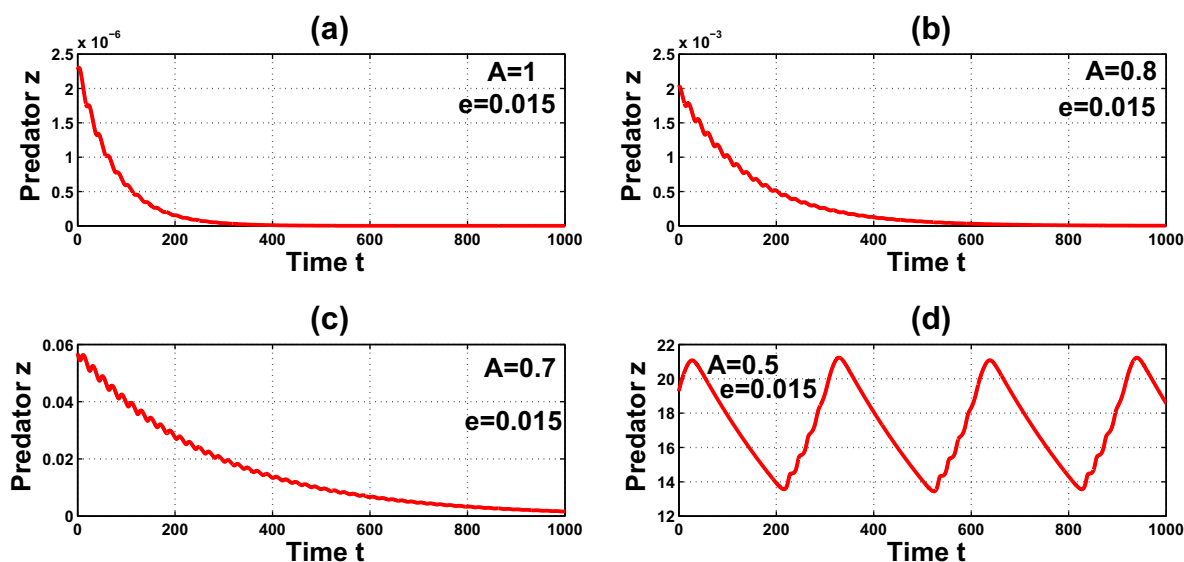


Fig. 2. Extinction risk of top-predator population (z) (a) in absence of alternative food, (b)–(d) in presence of various alternative food for constant harvesting effort $e = 0.015$.

ence of alternative resource in Fig. 4. From Fig. 4, it is evident that top-predator population survive if $e \leq 0.0095$ for $A = 0.9$, if $e \leq 0.0124$ for $A = 0.8$, if $e \leq 0.0182$ for $A = 0.6$ and if $e \leq 0.0209$ for $A = 0.5$. Therefore, for every cases there is a critical harvesting effort below that top-predator survives and above that top-predator extinct. Notice that the critical value of harvesting effort increases with the increase of alternative resource. It is important to note that dynamics of top-predator population strongly depends on harvesting effort as well as supply of alternative resource. So, we plot the dynamics of top-predator population in (A, e) -plane in Fig. 5. Fig. 5 depicts regions of chaotic or periodic oscillation, steady state and extinction of top-predator's population. Notice that in Fig. 5 the boundaries between the different dynamical regions are not perfectly distinct. Because, in Fig. 5 that the high periodic oscillations and chaotic region there are small areas. This occurs because there is some degree of sensitivity to small changes in parameter values resulting in sharp transitions between different dynamical outcomes.

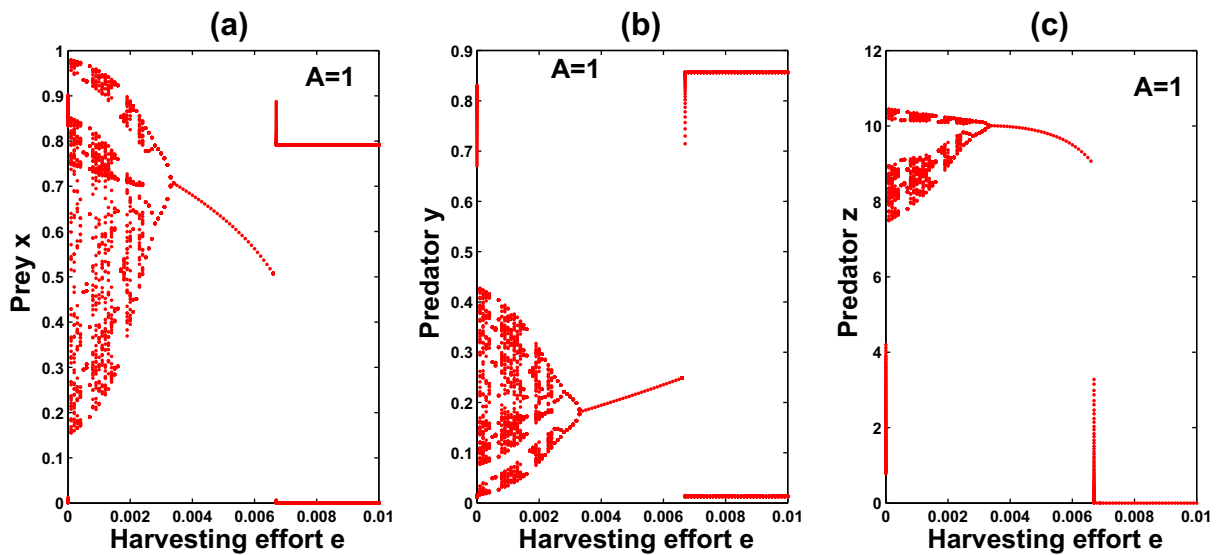


Fig. 3. Bifurcation of the system (4) with respect to harvesting effort e without alternative resource (i.e., for $A = 1$).

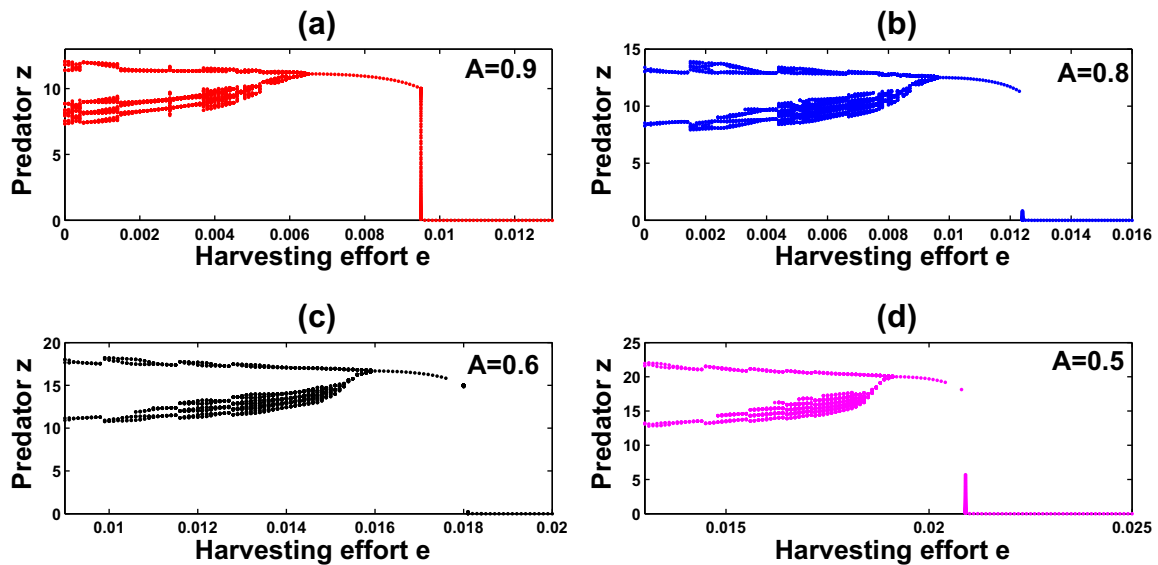


Fig. 4. Bifurcation of top-predator population (z) when harvesting effort is varying with constant alternative resource supply: (a) $A = 0.9$, (b) $A = 0.8$, (c) $A = 0.6$ and (d) $A = 0.5$.

It is obvious that the adjoint variables are directly related to the change of the value of the Hamiltonian as the time derivatives of the adjoint variables are negative of the corresponding partial derivatives of the Hamiltonian, H with respect to the state variables. We now study the nature of adjoint variables in Fig. 6. We observe that control variables $\lambda_1, \lambda_2, \lambda_3$ change significantly with time. This means that to maximize the objective functional given in 8 the rate of change of the Hamiltonian, H , should be changed according to the behaviour of adjoint variables. The effects of variation constant price per unit biomass of catch and alternative resource supply on optimal control of harvesting effort e_s on the model is described in the Figs. 7 and 8. It is evident from the Fig. 7 that for low price rate, large amount of alternative resource is required for maximum harvesting. For high price rate, optimal harvesting effort increases for small amount of alternative resource supply. Therefore, it is natural that for maximum harvesting effort, sufficient alternative resource supply is very important. However, the controllability of the fishing effort with the price per unit biomass of catch is also necessary for constant alternative resource. It is noted from Fig. 8 that when price per unit biomass of catch decreases, the consequent harvesting effort will decrease. But with the increasing time, the optimal efforts correspond to the higher price per unit biomass of catch increases more rapidly compared to the optimal efforts correspond to lower price per unit biomass of catch.

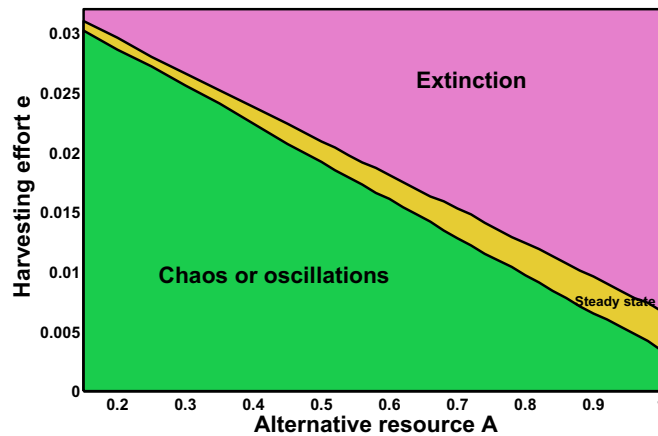


Fig. 5. Extinction region of top-predator population (z) as a function of alternative resource and harvesting effort for $a_1 = 5.0, a_2 = 0.1, b_1 = 3, b_2 = 2.0, d_1 = 0.4, d_2 = 0.01$ and $c = 0.45$.

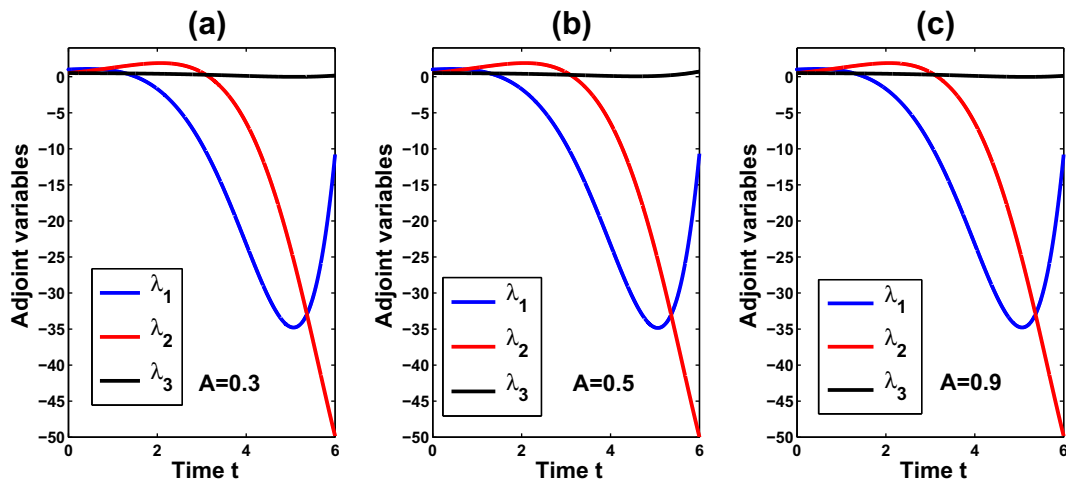


Fig. 6. Graph for the adjoint variables taking $a_1 = 5.0, a_2 = 0.1, b_1 = 3, b_2 = 2.0, d_1 = 0.4, d_2 = 0.01, c = 0.45, p = 2.5, \omega = 7.5, h = 0.1$ and (a) $A = 0.3$, (b) $A = 0.5$ and (c) $A = 0.9$.

8. Bifurcation of equilibrium and Hopf continuation

The main goal of this section is to study the bifurcation pattern of the system (4) with respect to harvesting effort e for different alternative resource parameter A . This is actually done by studying the change in the eigenvalue of the Jacobian matrix and also following the continuation algorithm. To start with we consider a set of fixed point initial solution $x_0 = 0.90582312, y_0 = 0.06745432$ and $z_0 = 5.055978$, corresponding to a parameter set of values $a_1 = 5.0, a_2 = 0.1, b_1 = 3, b_2 = 2.0, d_1 = 0.4, d_2 = 0.01, c = 0.45$, most of which are taken from Hastings–Powell model [18]. The characteristics of the limit cycle and the general bifurcation may be explored using the software package MATCONT2.5.1. In this package we use prediction–correction continuation algorithm based on the Moore–Penrose matrix pseudo inverse for computing the curves of equilibria, limit point (LP), along with fold bifurcation points of limit point (LP), period doubling (PD) and continuation of Hopf point (H), etc.

The continuation curve from this equilibrium point of the top-predator population z with harvesting effort e as the free parameter for fixed alternative resource A is shown in Fig. 9. We observe Hopf points (H), one limit point (LP), one branch point (BP) of z with the variation of e for fixed $A = 0.3, 0.5$, and 0.9 respectively in Fig. 9. For $A = 0.3$, the first Hopf point (H_1) is located at $(x, y, z, e) \equiv (1.000000, 0.000000, 14.166668, 0.053000)$ with purely imaginary eigenvalues $\pm 0.0000621646i$ and the third one being -1 . For this Hopf point the first Lyapunov coefficient turns out to be -0.06482337 indicating a supercritical Hopf bifurcation. It being negative implies that a stable limit cycle appears and the equilibrium point loses its stability. The second Hopf point (H_2) occurs at $(x, y, z, e) \equiv (0.713680, 0.179869, 16.680729, 0.060937)$ with purely imaginary eigenvalues $\pm 0.0829487i$ and the third one being -0.323779 . For this second Hopf point the first Lyapunov coefficient turns

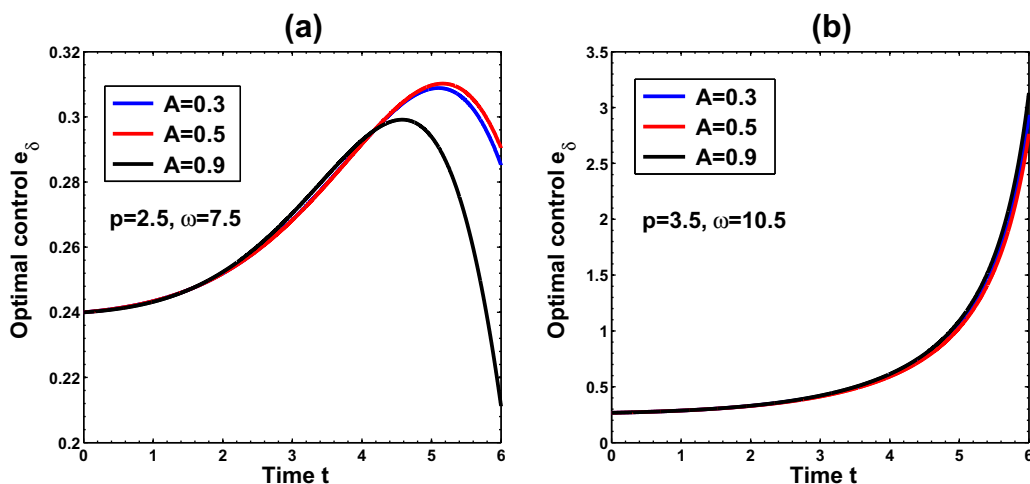


Fig. 7. Variation of optimal control of harvesting effort with the increasing time for $a_1 = 5.0, a_2 = 0.1, b_1 = 3, b_2 = 2.0, d_1 = 0.4, d_2 = 0.01, c = 0.45, h = 0.1$ and with the variation of alternative resource $A = 0.3, 0.5, 0.9$. (a) $p = 2.5, \omega = 7.5$, (b) $p = 3.5, \omega = 10.5$.

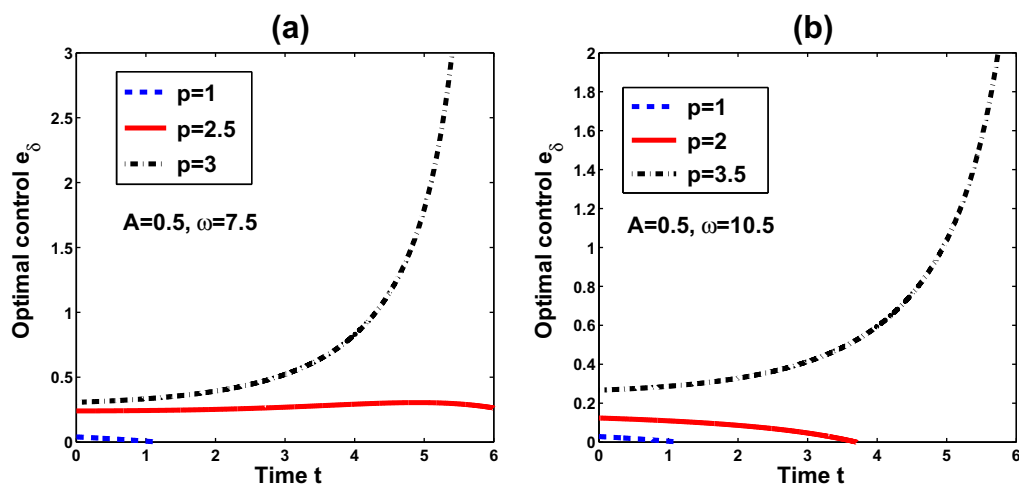


Fig. 8. Variation of optimal control of harvesting effort with the increasing time with the variation of constant price per unit biomass of catch for $a_1 = 5.0, a_2 = 0.1, b_1 = 3, b_2 = 2.0, d_1 = 0.4, d_2 = 0.01, c = 0.45, h = 0.1$ and $A = 0.5$, (a) $\omega = 7.5$, (b) $\omega = 10.5$.

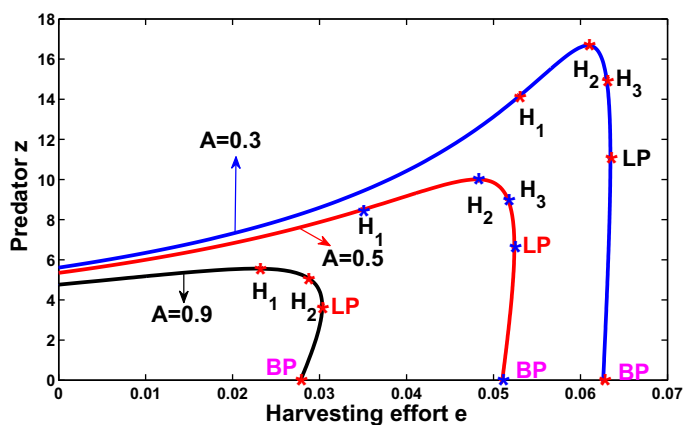


Fig. 9. Continuation curves of equilibrium with the variation of harvesting effort e of top-predator z for constant alternative resource $A = 0.3, 0.5, 0.9$.

Table 1

Parameter values of A and e at the bifurcation points in Fig. 9, together with First Lyapunov coefficients/ normal form coefficients and eigenvalues (scaled, see [33]). H_1, H_2, H_3 -Hopf point; LP-limit point; BP-branch point.

A	e	Label	First Lyapunov coefficients/normal form coefficient	Eigenvalues
0.3	0.053000	H_1	$l_1 = -0.06482337$	$-1, \pm i0.0000621646$
0.3	0.060937	H_2	$l_1 = -1.050970$	$-0.323779, \pm i0.0829487$
0.3	0.062977	H_3	$l_1 = 3.947290$	$-0.00514689, \pm i0.400839$
0.3	0.063435	LP	$a = 0.0001643415$	$0, 0.07536 \pm i0.524449$
0.3	0.062605	BP	–	$0, 0.0547368 \pm i0.518656$
0.5	0.035	H_1	$l_1 = -4.960601$	$-1, \pm i0.00005766$
0.5	0.048301	H_2	$l_1 = -1.453844$	$-0.318353, \pm i0.107578$
0.5	0.051601	H_3	$l_1 = 3.769684$	$-0.00875, \pm i0.401304$
0.5	0.052391	LP	$a = -0.0004529353$	$0, 0.075362 \pm i0.52632$
0.5	0.051008	BP	–	$0, 0.0547368 \pm i0.518656$
0.9	0.023216	H_1	$l_1 = -1.859252$	$-0.306984, \pm i0.145743$
0.9	0.028775	H_2	$l_1 = 3.418434$	$-0.0164479, \pm i0.401975$
0.9	0.030304	LP	$a = -0.001442997$	$0, 0.0753623 \pm i0.520043$
0.9	0.027814	BP	–	$0, 0.0547368 \pm i0.518656$

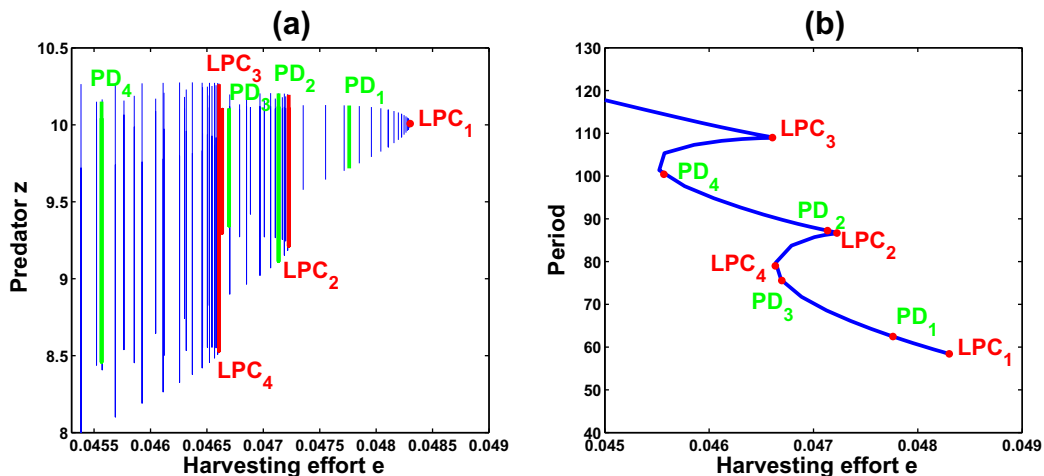


Fig. 10. (a) Family of limit cycles bifurcating from the Hopf point (H) at $e = 0.048301$ for alternative resource $A = 0.5$, (b) period of the cycle as a function of harvesting effort e .

Table 2

Periodicity and normal form coefficient of equilibrium points when harvesting effort e is varying starting from a Hopf point at $e = 0.04830140$.

e	Label	Period	Normal form coefficient
0.04830140	LPC_1	58.40594	0.01227568
0.04776136	PD_1	62.47194	-0.0009269132
0.04722546	LPC_2	86.68841	-3.483221
0.04713484	PD_2	87.24194	-0.0007307409
0.04669651	PD_3	75.55761	-0.0002355392
0.04663478	LPC_3	79.00605	0.3373427
0.04660747	LPC_4	108.9978	-6.323358
0.04556619	PD_4	100.4360	-0.00003734387

out to be -1.050970 , indicating a supercritical Hopf bifurcation. The third Hopf point (H_3) is situated at $(x, y, z, e) \equiv (0.504265, 0.249136, 15.067493, 0.062977)$. The limit point is located at $(x, y, z, e) \equiv (0.333333, 0.266667, 11.074074, 0.063435)$ with the eigenvalues as $(0, -0.07536 \pm i0.524449)$. The real part being negative, indicates that the LP is stable. A branch point BP occurs at $(x, y, z, e) \equiv (0.105263, 0.235457, 0.000000, 0.062605)$. The equilibrium bifurcation results for different alternative resource supply together with eigenvalues, first Lyapunov coefficients and normal form coefficient are listed in Table 1.

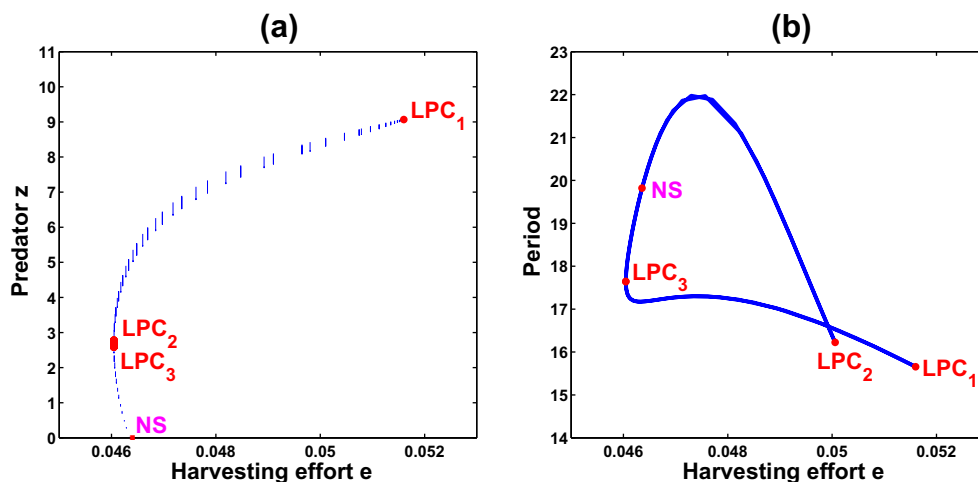


Fig. 11. (a) Family of limit cycles bifurcating from the Hopf point (H) at $e = 0.051601$ for alternative resource $A = 0.5$, (b) period of the cycle as a function of harvesting effort e .

Table 3

Periodicity and normal form coefficient of equilibrium points when harvesting effort e is varying starting from a Hopf point at $e = 0.05160091$.

e	Label	Period	Normal form coefficient
0.05160091	LPC_1	15.65692	−0.1524734
0.05005751	LPC_2	16.22452	−0.7041501
0.04604527	LPC_3	1.764316	−0.004383309
0.04635609	NS	19.82018	–

To proceed further, for supply of alternative resource $A = 0.5$, we start from the Hopf point (H_2) which is predicted in Fig. 9 as the initial point at $e = 0.048301$, and computing in backward continuation process, get a family of stable limit cycles bifurcating from this Hopf point. This phenomenon is shown in Fig. 10, where again the harvesting effort is the only free parameter. At $e = 0.048301$, we observe a LPC point with period 58.40594. At this situation two cycles collide and disappears. The critical cycle has a double multiplier equal to 1. From this it follows that a stable branch occurs after the LPC point. At $e = 0.04776136$, we get a period doubling (PD) with period 62.47194 and two of the multiplier is equal to 1. We also get another LPC and PD points at different values of e , which are listed in Table 2. One can observe LPC and Neimark–Sacker (NS) points by varying harvesting effort e starting from the Hopf point at $e = 0.051601$, presented in Fig. 9 and its results are shown in Fig. 11. We also list the bifurcation points and its periodicity in Table 3, when harvesting effort is varying for alternative resource $A = 0.5$.

9. Conclusion

A food chain model providing alternative resource (additional food) to top-predator species in a predator–prey system is proposed and analysed with constant harvesting. Choosing a suitable alternative resource A , one can reduce the predation pressure on prey as well as remove extinction possibility of top-predator population. We assume that the supply of alternative resource is not dynamic, but maintained at a specific constant level. This simplification is justified for many arthropod predators, because they can feed on plant-provided alternative food sources such as pollen or nectar, the availability of which is unlikely to be influenced by predator's consumption [34]. This model is especially important in the systems, such as caves, headwater streams, and some small marine islands, in which more energy enters the food web from alternative resource.

We have presented a systematic analysis of the model with the variation of harvesting effort in presence of suitable alternative food. From our investigation, we conclude that suitable alternative resource (A) can reduce the extinction risk of top-predator population (Figs. 1 and 2) up to some critical harvesting effort. It is also clear that one can achieve the permission to obtain higher harvesting effort for suitable supply of alternative resource (Figs. 3 and 4). Therefore, one can conclude that the extinction risk will decrease for suitable supply of alternative food even when harvesting effort is high. It seems to be one of the important result of this paper. For an example, we draw numerically a functional relationship between alternative resource and harvesting effort (Fig. 5). On the other hand, from the bifurcation analysis, we observe chaos or high periodic oscillation to steady state transition is possible by increasing harvesting effort. Therefore, chaos of a food chain model can be controlled with harvesting effort. Reasonable harvesting policies are indisputably one of the major and interesting

problems from ecological and economic point of view. Optimal harvesting policy is also derived using Pontryagin's Maximum Principle and the problem is solved both analytically and numerically. A Hopf bifurcation analysis is carried out when harvesting effort is increasing in presence of alternative resource. The bifurcation scenarios of top-predator population in presence of alternative resource is plotted in Fig. 9 when harvesting effort is varied for a considerable range. The continuation curve (LPC, PD etc.) starting from Hopf points are plotted by varying harvesting effort to identify the nature of dynamical system.

Therefore, our analysis predicts that extinction possibility of harvested species can be eliminated providing a suitable amount of alternative food to the species. We have also shown that chaos control is possible by harvesting in presence of alternative food. We have shown that biological control is possible supplying alternative food to the system. This study enables management to develop optimal harvesting strategies in presence of alternative food. Therefore, alternative food plays a very important role for biological conservation of species.

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Appendix

From the second equation of the system (1), we have

$$\begin{aligned}\frac{dY}{dT} &= A_1 \frac{XY}{B_1 + X} - A_2 \frac{YZ}{B_2 + Y} - D_1 Y, \\ &= A_1 \frac{Y}{B_1/X + 1} - A_2 \frac{YZ}{B_2 + Y} - D_1 Y, \\ &\leq (A_1 - D_1)Y - A_2 \frac{YZ}{B_2 + Y}, \text{ since } \frac{B_1}{X} + 1 > 1.\end{aligned}$$

Therefore, condition for persistence of intermediate predator (Y) is $A_1 > D_1$.

Again, from the third equation of the system (1), we obtain that

$$\begin{aligned}\frac{dZ}{dT} &= C_2 A_2 \frac{YZ}{B_2 + Y} - D_2 Z, \\ &= C_2 A_2 \frac{Z}{B_2/Y + 1} - D_2 Z, \\ &\leq (C_2 A_2 - D_2)Z, \text{ since } \frac{B_2}{Y} + 1 > 1.\end{aligned}$$

Therefore, condition for persistence of top-predator (Z) is $C_2 A_2 > D_2$.

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