Nonlinear Analysis: Modelling and Control, Vol. 25, No. 3, 400–416
https://doi.org/10.15388/namc.2020.25.16657

ISSN: 1392-5113
eISSN: 2335-8963

Impacts of predator–prey interaction on managing maximum sustainable yield and resilience

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Received: January 2, 2019 / **Revised:** July 7, 2019 / **Published online:** May 1, 2020

Abstract. This paper gives a broad outline of some comparative analysis of two ecological services, namely, yield and resilience of a generalist predator–prey system. Although either prey or predator species can be harvested at maximum sustainable yield (MSY) level, yet there is a trade-off between yield and resilience. When both the species are harvested simultaneously, MSY increase by changing catchabilities always increases the system resilience both in prey- and predator-oriented fishery. In particular, a prey-oriented fishery with low prey catchability gives more yield and resilience but in case of predator-oriented fishery with high predator catchability, gives more of these ecological services. Thus to get both the optimum yield and resilience, a balanced harvesting approach is needed between the prey and predator trophic levels. Throughout the analysis, we use both the analytical as well as numerical techniques.

Keywords: predator–prey, ecosystem services, maximum sustainable yield, ecological resilience, bifurcation.

1 Introduction

Harvesting has a strong impact on biological resources like fisheries and forestry, and any indiscriminate harvesting can lead to the extinction of these resources. It is unfortunate that the objectives of both high yield and stock size usually conflict with each other. We often assume that fishery has a little impact on species extinction as the resources are unlimited in a very large ocean, but in past decades, it is noticed that, due to excessive utilization of these resources, several species are threatened to extinction. Hence unless the highest priority is given to conservation of resources, there will be no economic or

[1]The author was financed by Department of Science and Technology, INSPIRE, Government of India (No. DST/INSPIRE Fellowship/2017/IF170378, dated: 12th September, 2017).
[2]The author was partially supported by the Council of Scientific and Industrial Research (CSIR) (No. 25(0300)/19/EMR-II, dated: 16th May, 2019).

social benefit. Often we come across a situation where the increase in the one ecological service results in an automatic decline to the other ecological services. Considering this trade-off between ecosystem services, researchers in recent times are giving more attention to the development of theoretical understanding between the relationship among these services. Understanding the relationship among ecosystem services and the mechanisms behind these relationships will certainly improve sustainable biological, economic and social benefits.

To avoid the extinction of resources, many scientific approaches are suggested time to time. Catch quota, lease of property rights, optimal taxation, marine reserve areas, maximum sustainable yield, nonconsumptive use of resources (e.g., ecotourism) are considered as some of the effective management tools for resources management. Ghosh et al. [8] considered a two-patch model to address the conservation effects of marine protected areas. Their study showed the positive conservation effect of marine protected areas. Paul et al. [19] addressed some economic consequences of ecotourism. It is found that ecotourism is beneficial both for revenue generation and conservation of resources. Kar [12] studied a dynamic reaction model of a predator–prey system in which taxation is considered as the control instrument. Out of these popular regulatory options, maximum sustainable yield (MSY), first originated by Schaefer [22], is considered as the most familiar management tool to harvest a resource at its maximum level in a sustainable way. It balances the over-exploitation, the removal of so much resources that the population faces danger of extinction and under-exploitation, the removal of fewer individuals than a population can withstand. This concept of MSY was first introduced in fishery management by Clark [4], and its impact on the food chain was discussed by Ghosh and Kar [5]. The use of MSY is mostly widespread in single species evaluation, and in the multitrophic context, it causes severe deterioration in the ecosystem as a whole [23]. But this classical idea of MSY is criticized by Clark [3] as it does not regard the economic factors, recruitment failure, species interaction, etc. In recent times, some influential research articles on MSY policy can be found in the multispecies system [6, 14]. The predator species may extinct due to harvesting of the prey species using MSY policy [15], but predator harvesting may be a sustainable policy, and the situation is reversed when the predators depend on alternative food sources [13]. In the case of simultaneous harvesting, it is possible to find a coexisting equilibrium to reach maximum sustainable total yield (MSTY) [13, 16].

Managing multiple ecosystem services is an important but challenging task. Among the services, ecological resilience is considered as the most important ecological service. Measuring resilience, we are able to state the different aspects of the stability of a system, whereas the stability of a system gives us only the idea about the persistence of the system near the equilibrium points. It measures the ability of a system to absorb the disturbances and get back to the natural state. After a disturbance, a system with low resilience takes longer time to return to its original state, but a system with high resilience get back quickly to its natural state. The term resilience was first introduced in the literature by Holling [9], but explaining and evaluating the system resilience is not an easy task [18]. Britten et al. [1] evaluated the time required to return to the equilibrium in the study of a community of coastal fish. They used the method proposed by Ives et al. [11], but this method is not suitable for short-lived system or oscillatory dynamics. Heish et al. [10] showed that the harvesting of a species, which is abundant in nature, increases the diversity, however, it has been noticed that the resilience of the system is reduced. Rooney et al. [21] showed that there is a negative effect of harvesting on the stability of the ecosystem. Some recent studies also showed that resilience of coral reef communities may be damaged due to fishing.

Thus from the above literature survey it is cleared to us that even though there are some influential researches either on MSY policy or resilience separately. However, due to lack of knowledge regarding the relationship among these two ecosystem services, we are wasting the opportunities to take the advantages of synergies and are at risk of incurring unwanted trade-offs. As a result, we are possibly facing dramatic and unforeseen changes in providing of ecosystem services. Such comprehension may allow manipulation of systems to diminish trade-offs, increase synergies, boost resilience and sustainable use of these ecosystem services. In addition, due to multiple levels of exogenous threats, only the MSY policy could not be a management benchmark. From this perspective we consider two ecological services, namely, MSY and resilience maximizing yield (RMY) together in a generalist predator–prey system, and to the author's knowledge, no such attempt has been made earlier. RMY is the yield obtained by maximizing resilience of the system with respect to the effort. Our main research questions are to find out the most effective way to reduce the trade-offs or strengthen the synergism of these two most important ecosystem services. Thus we develop a relationship among these two services based on individual as well as combined harvesting strategies.

The next portion of this paper is as follows. In Section 2, we discuss the model formulation and its equilibria. Sections 3 and 4 give a brief idea about the prey and predator harvesting, respectively, and their impact on resilience and MSY. Section 5 considers the combined harvesting of both the predator and prey species and its impact on yield and resilience. A brief conclusion is given in Section 6.

2 Model and it's equilibria

The most common relationship in the ecological environment is the predator–prey relationship, and here a generalist predator–prey system is proposed by a pair of differential equations as follows:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx\left(1 - \frac{x}{K}\right) - \alpha xy - q_1 Ex, \tag{1}$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = sy\left(1 - \frac{y}{L}\right) + \alpha xy - q_2 Ey, \tag{2}$$

where x and y are the prey and predator population densities respectively, at any time t. r and s are the intrinsic growth rates, K and L are carrying capacities of prey and predator, respectively. Even though this theoretical work is not a case study of a particular predator–prey system, however, krill-whale community could be a good example for the above-mentioned system [7, 17]. Each species is considered as subject to harvesting based on the catch per unit effort hypothesis. E is taken as the combined effort on both the species. q_1 and q_2 are considered as catchability coefficient of prey and predator, respectively. α is the predation coefficient, and the conversion factor is taken as unity as it does not affect the qualitative behaviour of the system but decreases the system parameters. Though the linear interaction and proportional harvesting are considered in the model, still it embodies all the key driving forces regarding the point of view of this study. Also, the combined harvesting effort is taken on the basis of the assumption that the fishermen in a particular fishery uses a specific type of trawlers, which may have different catchabilities on different trophic levels.

Equilibrium point (x^*, y^*) can be obtained by putting the variations of densities are equal to zero. Four possible equilibrium points may exist for the system. In the trivial equilibrium, both the densities are zero. Other equilibrium points are

$$\left(\frac{K}{r}(r - q_1E), 0\right), \qquad \left(0, \frac{L}{s}(s - q_2E)\right)$$

and

$$\left(\frac{K(s(r - \alpha L) + E(\alpha L q_2 - s q_1))}{\alpha^2 KL + rs}, \frac{L(r(\alpha K + s) - E(\alpha q_1 K + r q_2))}{\alpha^2 KL + rs}\right).$$

The Jacobian matrix for the above system is obtained as

$$M = \begin{bmatrix} \frac{-r}{K}x^* & -\alpha x^* \\ \alpha y^* & \frac{-s}{L}y^* \end{bmatrix},$$

where (x^*, y^*) is the coexisting equilibrium point. We denote trace and determinant of M by $T(M)$ and $D(M)$, respectively, in the whole analysis. Here

$$T(M) = \frac{-r}{K}x^* + \frac{-s}{L}y^* \quad \text{and} \quad D(M) = \left(\frac{rs}{KL} + \alpha^2\right)x^*y^*.$$

Since all the parameters are positive and the equilibrium (x^*, y^*) exists, it is easy to see that $T(M) < 0$ and $D(M) > 0$. This implies that the eigenvalues have negative real part and the system is locally stable. The real part of the leading eigenvalue is denoted by $\mathrm{Re}(\lambda_m)$.

As our aim is to harvest the resources in such a way that we can get maximum yield in a sustainable way, we maximize the yield function $(q_1Ex^* + q_2Ey^*)$ with respect to E when both the species are harvested.

Resilience, which measures the stability of a system from perturbation, is actually the time required for a system to come back to the steady state. To measure resilience, following Pimm and Lawton [20], we calculate the real part of the leading eigenvalue, i.e., $\mathrm{Re}(\lambda_m)$ and the time required to return to the equilibrium as $\tau = -1/\mathrm{Re}(\lambda_m)$. If the resilience of a system is high, then it returns quickly to the equilibrium after perturbations.

Most of the parameters are taken from Ghosh and Kar [5]. In all the cases, taking the advantage of simplicity of the model, results are shown analytically. Simulations are made only to visualize the analytical results. Parameters are chosen in such a way that the analytical restrictions are satisfied.

Table 1. Description of parameters

Symbol	Description	Value used in simulation
r	Intrinsic growth rate of prey	0.8
s	Intrinsic growth rate of predator	0.2, 0.3, 0.5, 0.8
K	Carrying capacity of prey species	2, 10, 20
L	Carrying capacity of predator species	3, 15, 70
α	The predation coefficient	0–1
q_1	Catchability coefficient of prey	0–1
q_2	Catchability coefficient of predator	0–1
E	Combined effort on both species	0–6

3 Prey harvesting

In this section, as the harvesting of only prey species is considered, we set the predator catchability coefficient equal to zero ($q_2 = 0$).

The densities at the coexisting equilibrium are

$$x^* = \frac{K[s(r-\alpha L) - Esq_1]}{\alpha^2 KL + rs} \quad \text{and} \quad y^* = \frac{L[r(\alpha K + s) - E\alpha q_1 K]}{\alpha^2 KL + rs}.$$

This equilibrium will be feasible if both $x^* > 0$ and $y^* > 0$. From $x^* > 0$ we get $E < (r/q_1 - \alpha L/q_1)$, and from $y^* > 0$ we get $E < (r/q_1 + rs/(\alpha q_1 K))$. Thus (x^*, y^*) exists, provided

$$E < \left(\frac{r}{q_1} - \frac{\alpha L}{q_1}\right) = E^x_{\text{ext}}.$$

As

$$T(M) = \frac{-r}{K}x^* + \frac{-s}{L}y^* < 0 \quad \text{and} \quad D(M) = \left(\frac{rs}{KL} + \alpha^2\right)x^* y^* > 0,$$

the system is asymptotically stable.

Now the spiral equilibrium occurs when $T(M)^2 < 4D(M)$, and the real part of the leading eigenvalue is $\mathrm{Re}(\lambda_m) = T(M)/2$. Again, if $T(M)^2 > 4D(M)$, the equilibrium point is a stable node, and the real part of the leading eigenvalue is $\mathrm{Re}(\lambda_m) = (T(M) + \sqrt{T(M)^2 - 4D(M)}\,)/2$.

A bifurcation occurs if $T(M)^2 = 4D(M)$, and the bifurcation may be spiral to node or node to spiral. $T(M)^2 = 4D(M)$ gives a quadratic equation with respect to E

$$\begin{aligned}
&\bigl[(\alpha sq_1 K - srq_1)^2 - 4\alpha^3 K^2 Lsq_1^2\bigr]E^2 \\
&\quad + \bigl[2\bigl\{sr(r-s) - \alpha sr(K+L)\bigr\}\{\alpha sq_1 K - srq_1\} \\
&\quad - 4\alpha^2 KL\bigl\{r(\alpha K + s)(-sq_1) - s(r-\alpha L)(\alpha q_1 K)\bigr\}\bigr]E \\
&\quad + \bigl[\bigl\{sr(r-s) - \alpha sr(K+L)\bigr\}^2 - 4\alpha^2 KLsr(r-\alpha L)(\alpha K + s)\bigr] = 0,
\end{aligned}$$

which determines the bifurcation effort.

The yield at equilibrium is as follows:

$$H = q_1 E x^* = q_1 E \frac{K[s(r-\alpha L) - Esq_1]}{\alpha^2 KL + rs)}.$$

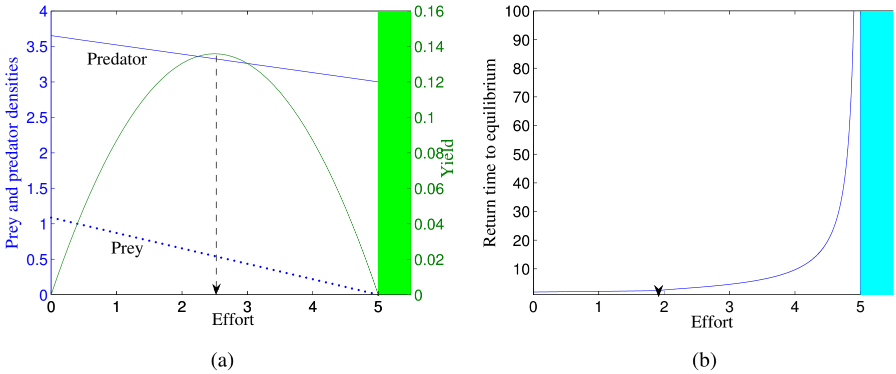


Figure 1. Consequences of harvesting of only the prey species: (a) prey and predator population densities at equilibrium and the yield (curved line): (b) the time required to return to the equilibrium of the system. Prey species goes to extinction in the coloured region. We choose the parameter set as $r = 0.8$, $s = 0.5$, $K = 2$, $L = 3$, $\alpha = 0.1$, $q_1 = 0.1$, $q_2 = 0$.

This expression is quadratic with respect to E, and hence it is possible to find an effort for which the yield is maximized. Now $\mathrm{d}H/\mathrm{d}E = 0$ gives $E = (r - \alpha L)/(2q_1)$, which is exactly half of E^x_{ext}, and $\mathrm{d}^2H/\mathrm{d}E^2 < 0$, i.e., the yield is maximized when the effort is equal to $E^x_{\mathrm{MSY}} = (r - \alpha L)/(2q_1)$.

It is also observed that both x^* and y^* are decreasing functions of E. As a result, $T(M)$ increases and $D(M)$ decreases with E. Since the real part of the leading eigenvalue is either of the forms

$$\frac{T(M)}{2} \quad \text{or} \quad \frac{T(M) + \sqrt{T(M)^2 - 4D(M)}}{2},$$

both are increasing function of E. Hence, in any situation, return time increases with the effort, and no resilience maximum yield occurs in the case of prey harvesting.

Here we consider only the value of E, which lies between 0 and E^x_{ext}. The yield curve (Fig. 1(a)) gives us some important insights into the effects of increasing effort on the prey species. We can infer from the figure that an increase of effort leads to a decrease in densities of both the species, but the prey species decreases faster in comparison to the predator species. The reason behind the occurrence of this phenomenon is the availability of another food sources to the predator species. Prey species can be harvested at MSY level as Fig. 1(a) shows that it is a sustainable policy in perspective that both the species coexist.

Now referring to Fig. 1(b), we observe that with an increase of effort from the beginning resilience decreases marginally even at the level of $E^x_{\mathrm{MSY}} = 2.5$ at which yield is maximum. For further increase of effort, resilience decreases relatively faster than earlier, and at the level where prey species goes to extinction, there is a sharp decline in the resilience. Thus, in case of generalist predator–prey system, prey species can be harvested in a sustainable way by using MSY policy with the marginal decline in resilience in compare to the unharvested system. In this case, no resilience maximum yield (RMY) occurs.

4 Predator harvesting

Here the harvesting of only predator species is considered.

The densities at the coexisting equilibrium are

$$x^* = \frac{K[s(r-\alpha L) + E\alpha L q_2]}{\alpha^2 KL + rs} \quad \text{and} \quad y^* = \frac{L[r(\alpha K + s) - Erq_2]}{\alpha^2 KL + rs}.$$

As we assume that the coexisting equilibrium of the unharvested system exists, so we consider $r > \alpha L$ throughout our analysis. Therefore the coexisting equilibrium of the harvested system exists if $E < (\alpha K + s)/q_2 = E^y_{\text{ext}}$.

As

$$\begin{aligned} T(M) &= \frac{-r}{K}x^* + \frac{-s}{L}y^* \\ &= \frac{-rs[(r-\alpha L) + (\alpha K + r)]}{\alpha^2 KL + rs} + \frac{Erq_2(s-\alpha L)}{\alpha^2 KL + rs} < 0 \end{aligned}$$

and

$$D(M) = \left(\frac{rs}{KL} + \alpha^2\right)x^* y^* > 0,$$

the system is asymptotically stable at the coexisting equilibrium. The equilibrium is spiral when $T(M)^2 < 4D(M)$, and the real part of the leading eigenvalue is $\mathrm{Re}(\lambda_m) = T(M)/2$. Again, if $T(M)^2 > 4D(M)$, the equilibrium will be a stable node, and the real part of the leading eigenvalue is $\mathrm{Re}(\lambda_m) = (T(M) + \sqrt{T(M)^2 - 4D(M)})/2$. Thus a bifurcation occurs if $T(M)^2 = 4D(M)$. This gives a quadratic equation with respect to E

$$\begin{aligned} &\left[(\alpha r q_2 L + srq_2)^2 + 4\alpha^3 KL^2 r q_2^2\right]E^2 \\ &\quad + \left[2\left\{sr(r-s) - \alpha sr(K+L)\right\}\left\{\alpha r q_2 L + srq_2\right\}\right. \\ &\quad \left.- 4\alpha^2 KL\left\{r(\alpha K + s)(\alpha L q_2) - s(r-\alpha L)(rq_2)\right\}\right]E \\ &\quad + \left[\left\{sr(r-s) - \alpha sr(K+L)\right\}^2 - 4\alpha^2 KLsr(r-\alpha L)(\alpha K + s)\right] = 0, \end{aligned}$$

which determines the bifurcation effort.

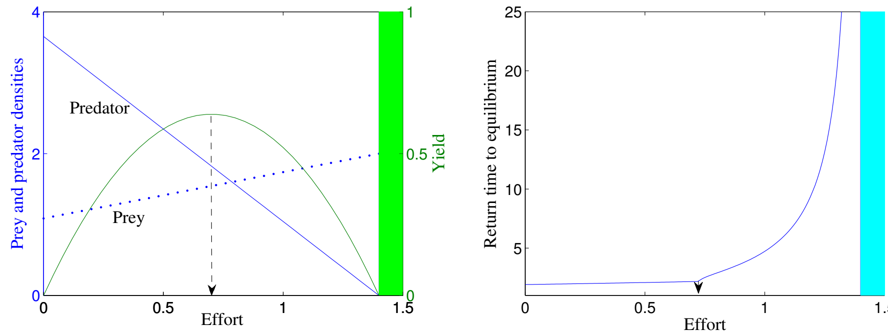
The yield at equilibrium

$$H = q_2 E y^* = q_2 E \frac{L[r(\alpha K + s) - Erq_2]}{\alpha^2 KL + rs}.$$

This expression is quadratic with respect to E, and hence it is possible to find an effort for which the yield is maximized. Now $\mathrm{d}H/\mathrm{d}E = 0$ gives $E^y_{\text{MSY}} = (\alpha K + s)/(2q_2)$, which is positive, and $\mathrm{d}^2 H/\mathrm{d}E^2 < 0$, i.e., the yield is maximized when the effort is equal to $(\alpha K + s)/(2q_2)$, which is the half of E^y_{ext}.

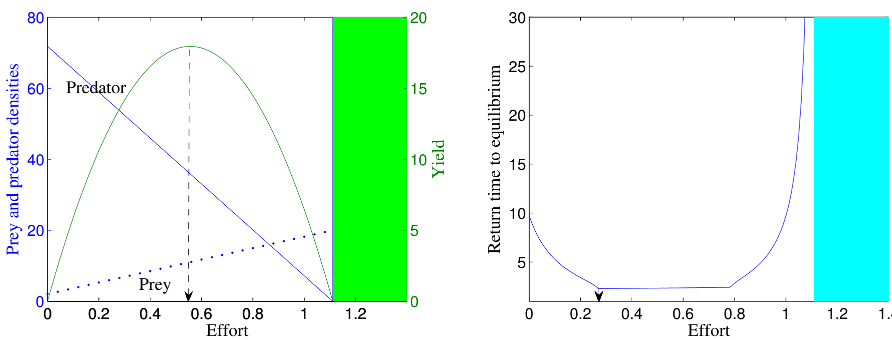
As

$$T(M) = \frac{-rs[(r-\alpha L) + (\alpha K + r)]}{\alpha^2 KL + rs} + \frac{Erq_2(s-\alpha L)}{\alpha^2 KL + rs},$$



(a) (b)

Figure 2. Consequences of harvesting of only the predator species: (a) Prey and predator population densities at the equilibrium and the yield (curved line); (b) the time required to return to the equilibrium of the system. Predator species goes to extinction in the coloured region. We choose the parameter as $r = 0.8$, $s = 0.5$, $K = 2$, $L = 3$, $\alpha = 0.1$, $q_1 = 0$, $q_2 = 0.5$.

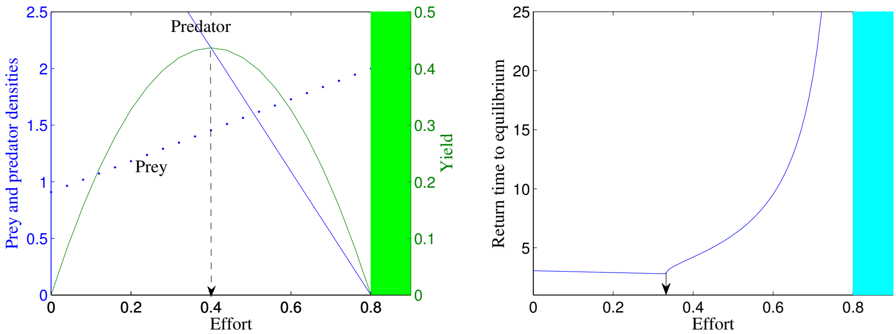


(a) (b)

Figure 3. Consequences of harvesting of only the predator species: (a) prey and predator population densities at the equilibrium and the yield (curved line); (b) the time required to return to the equilibrium of the system. Predator species goes to extinction in the coloured region. We choose the parameter set as $r = 0.8$, $s = 0.8$, $K = 20$, $L = 70$, $\alpha = 0.01$, $q_1 = 0$, $q_2 = 0.9$.

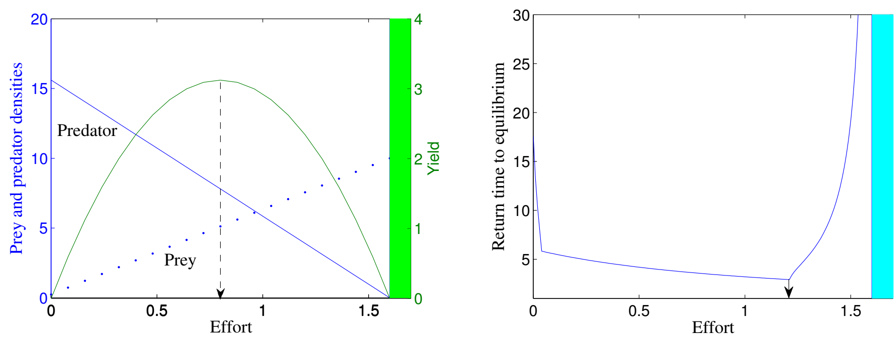
$\partial T(M)/\partial E <$ or > 0 according as $s <$ or $> \alpha L$. Depending on the above situation, we have taken two sets of parameter, which show us two different observations on the system resilience. Now we consider the two cases $s > \alpha L$ and $s < \alpha L$ separately. For $s > \alpha L$, impacts of harvesting effort on population, yield and resilience are shown in Figs. 2 and 3, and for $s < \alpha L$, those are shown in Figs. 4 and 5. We consider only those effort levels, which lie between 0 and E^y_{ext}.

Case 1: $s > \alpha L$. Next, we consider that predator species largely depends on alternative sources instead of focal prey. To include this effect, we reduce the predation coefficient and increase the carrying capacity of the predator. In Fig. 3(b), we observe that the increase of harvesting effort results in more resilient system than the unharvested



(a) (b)

Figure 4. Consequences of harvesting of only the predator species: (a) prey and predator population densities at the equilibrium and the yield (curved line); (b) the time required to return to the equilibrium of the system. Predator species goes to extinction in the coloured region. We choose the parameter set as $r = 0.8$, $s = 0.2$, $K = 2$, $L = 3$, $\alpha = 0.1$, $q_1 = 0$, $q_2 = 0.5$.



(a) (b)

Figure 5. Consequences of harvesting of only the predator species: (a) prey and predator population densities at the equilibrium and the yield (curved line); (b) the time required to return to the equilibrium of the system. Predator species goes to extinction in the coloured region. We choose the parameter set as $r = 0.8$, $s = 0.3$, $K = 10$, $L = 15$, $\alpha = 0.05$, $q_1 = 0$, $q_2 = 0.5$.

system until the spiral to node bifurcation occurs at $E = 0.79$. Thus the enrichment due to alternative sources provides a major qualitative difference in comparison to Fig. 2(b).

From both Figs. 2(a) and 3(a) we observe that with the increase of effort there is a sharp decline in predator population and increase in prey population due to reduced predation pressure on the prey species. Yield curve attains its maximum at $E^y_{\mathrm{MSY}} = 0.7$ and $E^y_{\mathrm{MSY}} = 0.55$ in Figs. 2(a) and 3(a), respectively, in the presence of both the species. Thus the MSY strategy is a sustainable policy in the perspective that both the species coexists at the MSY level.

In Fig. 2(b), from the beginning the time required to return to the equilibrium increases marginally, but after a spiral to node bifurcation at $E = 0.73$, it starts to increase rapidly. In this case, no resilience maximum yield (RMY) occurs. In Fig. 3(b), there are two bifurcation points. Spiral to node bifurcation occurs at $E = 0.79$, and the node to spiral occurs at $E = 0.26$. During the bifurcation at $E = 0.26$, the resilience becomes maximum. So resilience maximizing yield exists. As the effort at which the yield is maximized is different from the effort at which the resilience is maximized, there is a trade-off between yield and resilience, but this trade-off is not significant.

Case 2: $s < \alpha L$. In this case, also MSY exists in the presence of both the species, and MSY is attained at $E = 0.4$ in Fig. 4(a) and at $E = 0.8$ in Fig. 5(a). As far as yield is concerned, the conclusion almost remains the same as earlier. In Fig. 4(b), the return time decreases at first and after a spiral to node bifurcation at $E = 0.33$ it increases. Thus we get an effort where the return time is minimum, i.e., the system resilience is maximum. Thus, in this case, resilience maximum yield occurs. From Fig. 5(b) we observe that there are two bifurcations occurred: first, a spiral to node bifurcation at $E = 0.04$ and a node to spiral bifurcation at $E = 1.21$, but the resilience becomes maximum at spiral to node bifurcation at $E = 1.21$. Here also we observe that a trade-off is observed between yield and resilience, but predator harvesting at MSY level is more resilient than the unharvested system.

5 Simultaneous harvesting

In this section, the simultaneous harvesting of both the predator and prey species is considered. As we are interested in the coexistence of the species, we consider the coexisting equilibrium

$$(x^*, y^*) = \left(\frac{K(s(r-\alpha L) + E(\alpha L q_2 - s q_1))}{\alpha^2 K L + rs}, \frac{L(r(\alpha K + s) - E(\alpha q_1 K + r q_2))}{\alpha^2 K L + rs}\right).$$

As $r > \alpha L$ is the existence condition of the coexisting equilibrium of unharvested system, the coexisting equilibrium exists if

$$0 < E < r\frac{\alpha K + s}{\alpha q_1 K + r q_2} \quad \text{for } \alpha L q_2 > s q_1$$

and

$$E < \min\left[\frac{s(r-\alpha L)}{s q_1 - \alpha L q_2}, \frac{r(\alpha K + s)}{\alpha q_1 K + r q_2}\right] \quad \text{for } \alpha L q_2 < s q_1.$$

If $T(M)^2 < 4D(M)$, then the eigenvalues are complex, and following a perturbation, the system undergoes a dampened oscillations towards the equilibrium. In this case, the equilibrium is a stable spiral, and the real part of the leading eigenvalue is $\mathrm{Re}(\lambda_m) = T(M)/2$. Again, if $T(M)^2 > 4D(M)$, the eigenvalues are real, and following a perturbation, the system reaches the equilibrium without oscillations. This equilibrium is described as a stable node, and the real part of the leading eigenvalue is $\mathrm{Re}(\lambda_m) = (T(M) + \sqrt{T(M)^2 - 4D(M)})/2$.

A bifurcation is found to occur when $T(M)^2 = 4D(M)$, i.e., when $((r/K)x^* - (s/L)y^*)^2 = 4\alpha^2 x^* y^*$. Since x^* and y^* are functions of E, $((r/K)x^* - (s/L)y^*)^2 = 4\alpha^2 x^* y^*$ gives a quadratic equation with respect to E

$$\begin{aligned}
&\big[(\alpha r q_2 L - s r q_1 + \alpha s q_1 K + s r q_2)^2 + 4\alpha^2 K L(\alpha L q_2 - s q_1)(\alpha q_1 K + r q_2)\big]E^2 \\
&\quad + \big[2\big\{sr(r-s) - \alpha s r(K+L)\big\}\{\alpha r q_2 L - s r q_1 + \alpha s q_1 K + s r q_2\} \\
&\quad - 4\alpha^2 K L\big\{r(\alpha K + s)(\alpha L q_2 - s q_1) - s(r - \alpha L)(\alpha q_1 K + r q_2)\big\}\big]E \\
&\quad + \big[\big\{sr(r-s) - \alpha s r(K+L)\big\}^2 - 4\alpha^2 K L s r(r - \alpha L)(\alpha K + s)\big] = 0,
\end{aligned}$$

which determines the bifurcation effort.

At the equilibrium, the yield is given by

$$\begin{aligned}
H = q_1 E x^* + q_2 E y^* &= \frac{q_1 E K}{\alpha^2 K L + r s}\big\{s(r - \alpha L) + E(\alpha L q_2 - s q_1)\big\} \\
&\quad + \frac{q_2 E L}{\alpha^2 K L + r s}\big\{r(\alpha K + s) - E(\alpha q_1 K + r q_2)\big\}.
\end{aligned}$$

As this expression is quadratic with respect to E, it is possible to find an effort for which yield is maximized. Now $\mathrm{d}H/\mathrm{d}E = 0$ gives

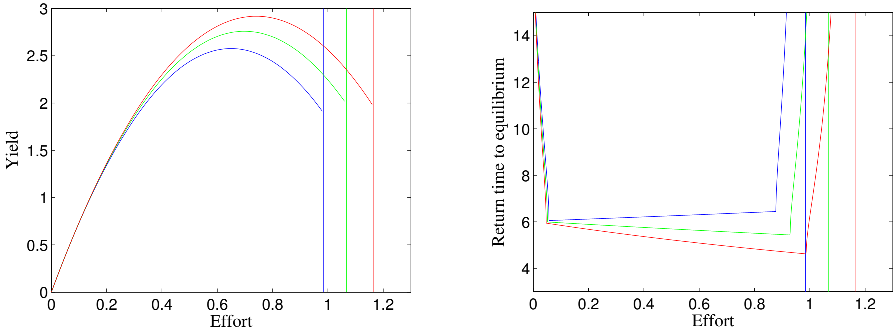
$$E_{\mathrm{MSY}} = \frac{q_1 s K(r - \alpha L) + q_2 r L(\alpha K + s)}{2(s K q_1^2 + r L q_2^2)} \quad \text{and} \quad \frac{\mathrm{d}^2 H}{\mathrm{d}E^2}\bigg|_{E_{\mathrm{MSY}}} < 0.$$

By replacing the MSY effort into the expression of yield, we get the of yield at MSY as

$$\begin{aligned}
H_{\mathrm{MSY}} &= \frac{q_1 E^{MSY} K}{\alpha^2 K L + r s}\big[s(r - \alpha L) + E^{MSY}(\alpha L q_2 - s q_1)\big] \\
&\quad + \frac{q_2 E^{MSY} L}{\alpha^2 K L + r s}\big[r(\alpha K + s) - E^{MSY}(\alpha q_1 K + r q_2)\big]
\end{aligned}$$

Figure 6 and Table 2 show the impacts of harvesting effort and prey catchability coefficient on yield and resilience. It is clearly observed that the increase of prey catchability reduces both maximum sustainable yield and resilience. As the MSY effort does not match with RMY effort, there is always a trade-off between MSY and RMY. However, MSY is always more resilient than the unharvested system, though the MSY effort approaches closure and closure to the extinction effort with the increase of prey catchability.

If we turn our attention to Fig. 7 and Table 3, it is observed that as the predator catchability coefficient increases, both the maximum sustainable yield and resilience increases. Also, as the MSY effort and RMY effort does not match, there always exists a trade-off between MSY and RMY. However, MSY is always more resilient than the unharvested system, even though the MSY effort approaches towards the predator extinction effort as the predator catchability coefficient increases.

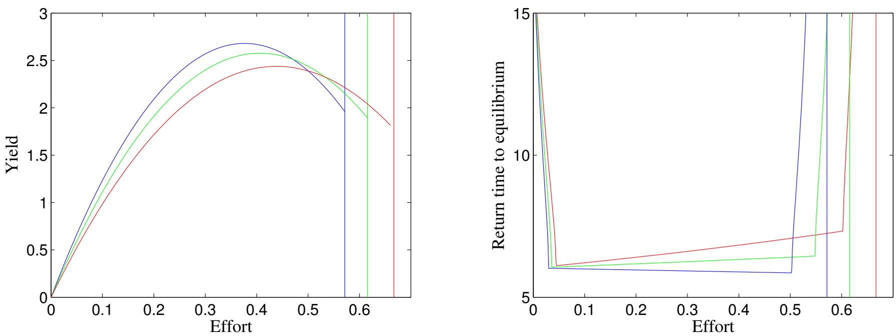


(a) (b)

Figure 6. Consequences of simultaneous harvesting with varying prey catchability: (a) yield effort curve; (b) return time to the equilibrium. The vertical lines denote the effort level at which the species goes to extinction. The parameter set is chosen as $r = 0.8$, $s = 0.3$, $K = 10$, $L = 15$, $\alpha = 0.05$, $q_2 = 0.5$ and $q_1 = 0.3$ (red), $q_1 = 0.4$ (green), $q_1 = 0.5$ (blue).

Table 2. Comparison table

q_1	MSY	E^{MSY}	E^{RMY}	E^{ext}	$E^{\text{MSY}} - E^{\text{ext}}$
0.3	2.9181	0.7408	0.9869	1.1636	0.4228
0.4	2.7590	0.6983	0.9289	1.0667	0.3684
0.5	2.5762	0.6500	0.0570	0.9846	0.3346



(a) (b)

Figure 7. Consequences of simultaneous harvesting with varying predator catchability: (a) yield effort curve; (b) return time to the equilibrium. The vertical lines denote the effort level at which the species goes to extinction. The parameter set is chosen as $r = 0.8$, $s = 0.3$, $K = 10$, $L = 15$, $\alpha = 0.05$, $q_1 = 0.8$ and $q_2 = 0.7$ (red), $q_2 = 0.8$ (green), $q_2 = 0.9$ (blue).

Table 3. Comparison table

q_2	MSY	E^{MSY}	E^{RMY}	E^{ext}	$E^{\text{MSY}} - E^{\text{ext}}$
0.7	2.4383	0.4385	0.0441	0.6667	0.2282
0.8	2.5762	0.4063	0.0356	0.6154	0.2091
0.9	2.6799	0.3763	0.5029	0.5714	0.1951

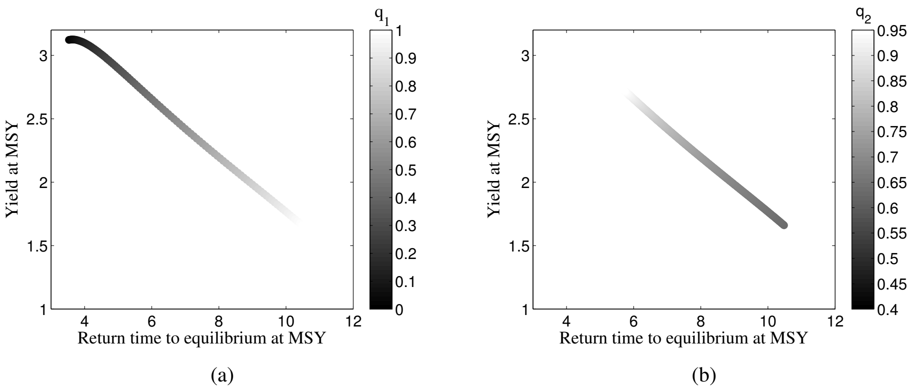


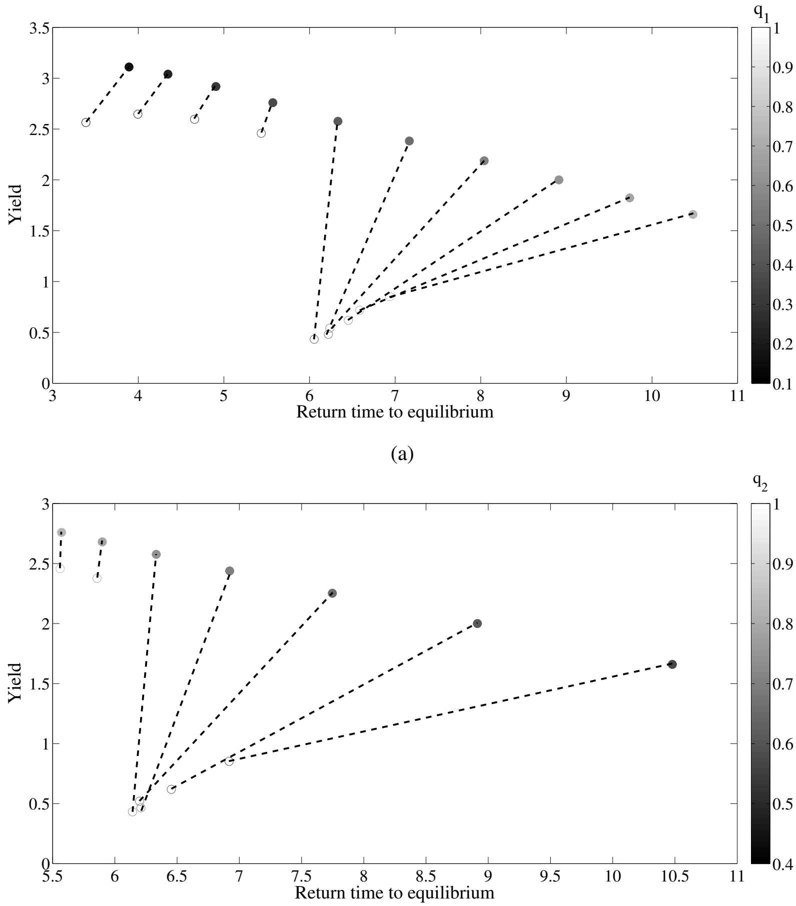
Figure 8. Synergies and trade-offs between resilience and yield at E_{MSY}. The parameters are $r = 0.8$, $s = 0.3$, $K = 10$, $L = 15$, $\alpha = 0.05$; (a) $q_2 = 0.3$ and q_1 varies from 0 to 1; (b) $q_1 = 0.8$ and q_2 varies from 0.4 to 0.95.

Drifting a little from the previous observations, we now focus our attention towards the relation between catchability and resilience. It is observed that with increasing prey catchability there is a shrinkage in the system resilience, but with increasing predator catchability the system resilience increases. From this section we can clearly conclude that the predator-oriented harvesting remains ahead of both in terms of resilience and MSY in compared to the prey-oriented harvesting.

Figure 8 shows that the increasing prey catchability decreases the yield at MSY as well as the system resilience, and the situation is reversed in the case of increasing predator catchability. This shows that the predator-oriented harvesting is more productive and more resilient, and there is no trade-off between MSY and the return time to the equilibrium, i.e., a synergy between the yield and resilience is observed in the predator-oriented harvesting.

In order to find a relation between MSY and RMY for a particular species-oriented harvesting, we go through Figs. 9(a) and 9(b). To simplify our approach, we would first confine ourselves to the effect of prey catchability on the MSY equilibria and RMY equilibria, and it is observed that with the increase of prey catchability the resilience both at RMY and MSY equilibria as well as MSY gradually decreases. Thus, in a prey-oriented harvesting, low prey catchability gives more yield and resilience. In addition, at the lower level of prey catchability, RMY gives more resilience but less yield, whereas MSY gives more yield less resilience.

Unlike what we have observed from Fig. 9(a) in case of prey-oriented fishery, from Fig. 9(b) in case predator-oriented fishery, it is observed that both the yield and resilience at MSY increases with the increase of predator catchability. In the case of RMY, resilience increases with the increase of predator catchabilty, and there is a significant change in yield in the higher side at the highest level of predator catchability. Thus a higher value of predator catchability is favourable both for yield and resilience. In addition, as there is no significant differences for MSY and RMY at the higher value of predator catchability, but as MSY gives more yield, MSY would be more favourable.



(b)

Figure 9. Connection between yield and the time required to return to the equilibrium for varying (a) prey catchability and (b) predator catchability. The change of catchability is shown using colour bar from black to light grey. For each value of catchability, filled circle and empty circle depict the MSY and RMY equilibrium respectively. The dotted line shows the equilibria between MSY and RMY. The parameter set is similar to Figs. 8(a) and 8(b), respectively.

6 Conclusion

Followed by a disturbance, a system having less resilient takes a longer time to get back to its natural state, and again suffer a new disturbance before it reaches to its original state, and aggregating of such disturbances could create a temporary state, threatening the maintenance of ecosystem services. On the other hand, due to the rapid growth of population, the main goal of fisheries management is to increase productivity. In this regard, here our focus has been on two services (the benefits that people obtain from ecosystem), namely, maximum sustainable yield and resilience. These two services are carefully chosen so as to incorporate the ever-increasing human needs keeping an eye on ecological sustainability. When we pay our attention to only one of these ecosystem services, trade-offs among the services may cause severe deterioration in them. It appears that we may be able to alter these trade-offs by focusing on the ecosystem processes that link services. While there has been substantial ecological research on some regulatory services separately, these services role in ensuring the reliability of other ecosystem services has not been systematically addressed. Managing relationships among ecosystem services can strengthen ecosystem resilience, enhance the provision of multiple services, and help to avoid catastrophic shifts in ecosystem service provision. Recently, Legović and Geček [14] studied some consequences of MSY policy in a predator–prey system, but they did not consider the resilience of the system. In fact, the impacts of ecological resilience on multi-trophic level harvesting is largely unexplored, even though it gives safeguard against global change and environmental variability.

Predator-prey interaction is important for the determination of the composition of services in a community and the dynamics of such communities. Naturally, specialist predator feeds exclusively on a single species, whereas the generalist relies on a wide variety of food sources. As the marine predators are mostly generalist in nature, we consider here a generalist predator–prey system for our study. Also, as this study is not by means of any observation or experience, our intention here is not to measure the exact quantities of population densities, ecological resilience and MSY, rather to enhance our knowledge in balancing these services. The simulations presented here should be considered from a qualitative rather than a quantitative point of view. However, numerous scenarios covering the breadth of the biological feasible parameter space were considered, and the results display the gamut of dynamical results collected from all the scenarios tested. Parameters are chosen in such a way that the conditions derived from analytical results are satisfied. Mostly, these parameters are taken from Ghosh and Kar [5].

In this paper, we have tried to find out a relationship among yield and resilience and build up three important statements:

(i) Focusing on the harvesting of only prey species, it is noticed that MSY can be achieved in the presence of both the species, but both the species at equilibrium decrease with increase of harvesting effort with the faster decrease in prey species. Since the resilience is ever decreasing, thus to implement MSY strategy, we need to give up marginal resilience.

(ii) In the case of only predator harvesting, both MSY and RMY exist. Since the efforts for maximizing yield and resilience are different, we have to compromise with the one to maximize the other, which obviously indicates the presence of trade-off between RMY and MSY.

(iii) When both the species are harvested, both MSY and resilience decrease with the increase of prey catchability in the prey-oriented harvesting, but in the predator-oriented harvesting, the situation is reversed, i.e., both MSY and resilience increase with the increase of predator catchability. This indicates that the predator-oriented harvesting is more productive and resilient, and it contradicts Bundy et al. [2], which showed that selective harvesting on lower trophic level would maximize yield and minimize ecosystem disturbance. After analyzing the effect of prey and predator catchability on MSY and RMY equilibria, the lower prey catchability and higher predator catchability is acceptable in both the sense.

Our ecosystem (especially, predator–prey systems) is more complex than the two-dimensional model that we have considered here. Moreover, linear interaction and proportional harvesting make the model more simple. However, it embodies all the leading driving forces from the point of view of this study. Even though the model is very simple, it provides some valid predictions. But in the case of such a simple model, we must restrict our prediction to refer certain key qualitative features that are robust. To make the quantitative predictions, some more elaborations are needed. Differentiation of the market value of the predator and prey trophic level can be introduced by considering the separate market prices of each trophic level. It is not explicitly considered in our model, yet different catchabilites partly capture these individual prices of different trophic levels. Still a tremendous amount of work is to be done on these ecosystem services. For example, nonlinear interaction, saturated harvesting, food chain with more than two trophic levels etc. could be interesting to study. This paper reports the first research findings on resilience when MSY is applied. This will certainly stimulate other researchers to look for resilience in connection to maximum sustainable yield in other models or in management attempts.

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