Maximum sustainable yield and species extinction in a prey–predator system: some new results

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Abstract Though the maximum sustainable yield (MSY) approach has been legally adopted for the management of world fisheries, it does not provide any guarantee against from species extinction in multispecies communities. In the present article, we describe the appropriateness of the *MSY* policy in a Holling–Tanner prey–predator system with different types of functional responses. It is observed that for both type I and type II functional responses, harvesting of either prey or predator species at the MSY level is a sustainable fishing policy. In the case of combined harvesting, both the species coexist at the maximum sustainable total yield (MSTY) level if the biotic potential of the prey species is greater than a threshold value. Further, increase of the biotic potential beyond the threshold value affects the persistence of the system.

Keywords Harvesting · Combined fishing effort · Maximum sustainable total yield (MSTY) · Holling-type response function · Volterra’s first principle

1 Introduction

Growth of the human population and improvements in technology have led to unsustainable harvesting of many species. Theoretical and experimental evidence shows that exploitation of one species may cause the extinction of other species [1, 2]. In recent years, a number of fish stocks have been depleted by over-exploitation and many are in danger of extinction [3]. When individuals are removed from a population faster than the population can be

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replaced through reproduction, the population begins to decline. If the rate of exploitation is not reduced, the harvested population will eventually become extinct. In this context, sustainable harvesting practices are required for careful management of the depleted species, so that these resources are also available for our future generation.

To achieve the goal of sustainable harvesting, a balance is needed between over- and under-exploitation of renewable resources. Over-exploitation is the removal of so many individuals that the population faces danger of extinction. The detrimental effects are felt both by the exploited population and by the harvesters who may depend on this resource for their livelihoods. On the other hand, under-exploitation is the removal of fewer individuals than a population can withstand. It is therefore required to maximize the harvested yield without threatening the viability of a harvested population.

In population ecology, the maximum sustainable yield (MSY) is theoretically the largest yield (or catch) that can be taken from a species stock over an indefinite period. Existence of *MSY* in a single species population was first investigated by Schaefer [4] by using an exploitation rate based on the *catch-per-unit-effort* (CPUE) hypothesis. Sustainable fishing through the *MSY* strategy in a single species population was also considered by Kar and Matsuda [5] in the presence of the *Allee effect*. However, the *MSY* policy in a single species population faces a great challenge when it is introduced into a multispecies system, as it is unable to deal with the influence of trophic and other interactions. Legovic and Gecek [6] investigated a community of independent and logistically growing populations under a common harvesting effort. They asserted that in the case of two independent populations with approximately equal carrying capacities, *MSTY* is reached while both the populations persist. However, for a large number of independent populations, fishing to reach *MSTY* may cause the overfishing or extinction of some species. Legovic et al. [1] demonstrated that the *MSY* (*MSTY* for multispecies harvesting) policy in an ecosystem will lead to the extinction of a large number of populations and they generalized the result in a food-chain and food-web model. Recently, Legovic and Gecek [7] studied the impact of the *MSY* policy in a cooperative system and interestingly noticed that harvesting of all the species at the *MSTY* level will drive to extinction of the species with lower biotic potential and carrying capacity. The *MSY* policy also ignores the complexity in ecosystem processes because the theory uses single stock dynamic models [8]. Matsuda and Abrams [9] analyzed the *MSY* policy considering the economic components from entire food webs with an independent fishing effort for each species. They concluded that the maximum sustainable revenue (*MSR*) policy does not guarantee the coexistence of all species. Katsukawa [10] concluded that the fishing effort that achieves *MSY* has a poor performance.

The Holling–Tanner prey–predator system is one where the predator behaves like a specialist predator in a traditional prey–predator system. However, models differ from each other in different ecological aspects. The specialist predator may not survive even in the presence of focal prey in a traditional prey–predator system if the carrying capacity of the focal prey is too low [11]. In contrast, for the Holling–Tanner system, the predator species always persists in maintaining an equilibrium ratio to the prey species, even if the prey abundance is low. How the above ecological differences affect the persistence of the entire system for fishing at the *MSY* or *MSTY* level is the main theme in this research. Hence we choose the Holling–Tanner prey–predator system and compare the results with recent literature [1] for a traditional prey–predator system.

The rest of the article is organized as follows. Section 2 is a revision of previous results and techniques for a traditional prey–predator system. Formulation of the Holling–Tanner model with several response functions is explained in Section 3. Section 4 is devoted to

exhibit the impact of species harvesting at the MSY or MSTY level incorporating the Holling type I functional response. The results are generalized in Section 5 for any Holling type functional response. The main observations including the comparisons with existing literature are given in Section 6.

2 Effect of the *MSY* policy in a traditional prey–predator system

We first consider a single-species model followed by proportional harvesting due to Schaefer [4] as:

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{k}\right) - ex, \quad (1)$$

where x is the biomass of the population at any time t , r is the intrinsic growth rate, k is the environmental carrying capacity of the population and e is the harvesting effort. It is a well-established result that for model (1) the MSY occurs at $e = r/2$ and $MSY = rk/4$.

To study the consequences of the *MSY* policy in a more general framework, Legovic et al. [1] considered the following prey–predator system:

$$\begin{aligned} \frac{dx}{dt} &= rx \left(1 - \frac{x}{k}\right) - axy, \\ \frac{dy}{dt} &= axy - my, \end{aligned} \quad (2)$$

where x and y are the prey and predator biomasses at any time t . r is the constant biotic potential and k is the environmental carrying capacity of the prey. a is the predation rate and m is the natural mortality rate of the predator. This prey–predator model is simple in the sense that the predator consumes the prey population according to a linear functional response and the intraspecific competition of the predator is not taken into account. Introducing proportional harvesting to either any one species or both the species with a *combined harvesting effort*, we have the following results proposed by Legovic et al. [1]:

- (i) In any prey–predator system, fishing to reach the MSY of the prey population only will cause extinction of the predator population.
- (ii) In any prey–predator system, fishing to reach the MSY of the predator population only is unlikely to cause extinction of other species.
- (iii) In any prey–predator system subject to equal fishing efforts on both the prey and predator populations, the ultimate MSTY will be the MSY of a single isolated population composed of prey only, which means that the predator population has gone to extinction.

In the next section, we present the Holling–Tanner prey–predator system. Most of the Holling–Tanner model involves the Holling type II functional response but linear interaction is also found in Zhang et al. [12] and Hsu and Huang [13].

3 Holling–Tanner prey–predator model

In this section, we propose the following form of the Holling–Tanner prey–predator system:

$$\begin{aligned}\frac{dx}{dt} &= rx \left(1 - \frac{x}{k}\right) - \phi(x)y, \\ \frac{dy}{dt} &= sy \left(1 - \frac{y}{\lambda x}\right),\end{aligned}\quad (3)$$

where s is the biotic potential of the predator population and its carrying capacity is proportional to the existing prey size. $1/\lambda$ is the amount of prey required to support a predator at equilibrium. The function $\phi(x)$ denotes the predator response function and it is assumed that $\phi(0) = 0$, $\phi(x) > 0$ for $x > 0$. Depending upon the process of energy transfer from the resource to consumer level in ecology, many formulations of $\phi(x)$ have been developed. In the present article, we only consider four different kinds of Holling-type functional responses: (I) $\phi_1(x) = ax$, ($a > 0$), (II) $\phi_2(x) = \mu x / (L + x)$, (III) $\phi_3(x) = \mu x^2 / (L + x^2)$, (IV) $\phi_4(x) = \mu x / (L + x^2)$, where $\mu > 0$ is the maximum predation rate and L is the half-saturation constant. For more details about these response functions, we refer to Ruan and Xiao [14]. In the next section, we initiate the Holling–Tanner model with the type I functional response.

4 Effect of the MSY policy in a Holling–Tanner prey–predator system

In this section, we consider the Holling–Tanner prey–predator system with a linear functional response as follows:

$$\begin{aligned}\frac{dx}{dt} &= rx \left(1 - \frac{x}{k}\right) - axy, \\ \frac{dy}{dt} &= sy \left(1 - \frac{y}{\lambda x}\right).\end{aligned}\quad (4)$$

The coexisting equilibrium of system (4) is $\bar{R}(\bar{x}, \bar{y})$ with

$$\bar{x} = \frac{kr}{a\lambda k + r} \quad \text{and} \quad \bar{y} = \frac{\lambda kr}{a\lambda k + r}.$$

It is observed that the prey biomass at equilibrium is less than its carrying capacity and therefore it increases the possibility of the coexisting equilibrium solution to be stable, though we do not explicitly investigate the stability of the coexisting equilibrium. It is also observed that the coexisting equilibrium point is independent of the biotic potential of the predator species. However, in the following subsections we examine the impacts of this biotic potential on a single species harvesting at the MSY level and combined harvesting of both the species at the MSTY level.

The impacts of the MSY (and MSTY for the multispecies case) policy under different combinations of exploitation are discussed successively in the following subsections.

4.1 Prey harvesting

Since we consider the harvesting of the prey species only, system (4) takes the form:

$$\begin{aligned}\frac{dx}{dt} &= rx \left(1 - \frac{x}{k}\right) - axy - ex, \\ \frac{dy}{dt} &= sy \left(1 - \frac{y}{\lambda x}\right),\end{aligned}\quad (5)$$

where e is the effort employed to prey exploitation.

The coexisting equilibrium biomass of system (5) is $R_1(x_1, y_1)$, where

$$x_1 = \frac{k(r-e)}{a\lambda k + r} \quad \text{and} \quad y_1 = \frac{\lambda k(r-e)}{a\lambda k + r}.$$

It is again observed that the prey biomass at equilibrium is always less than its carrying capacity and both the prey and predator biomasses are independent of the biotic potential of the predator species as observed in system (4). Obviously, both the equilibrium biomasses reduce as the effort increases and ultimately go to extinction as the effort tends to the biotic potential of the prey species. The yield obtained at equilibrium is given by:

$$Y(e) = \frac{ke(r-e)}{a\lambda k + r}.$$

The yield function $Y(e)$ is a quadratic function of effort and has a single maximum at $e = r/2$. Hence, the MSY occurs at $e_{MSY} = r/2$ and $MSY = ek/[4(\lambda k + r)]$. Also, both the prey and predator biomasses at e_{MSY} are half of their respective biomasses found in absence of harvesting. Hence both the species can coexist even if the prey yield reaches its MSY level (see Fig. 1). It is also to be noted that the MSY in the Holling–Tanner system occurs

Fig. 1 Yield effort curve and coexisting equilibrium biomasses of the prey and predator species as functions of effort. Both the prey and predator stocks at equilibrium exist when fishing reaches the *maximum sustainable yield* level

Fig. 2 Variation of the yield curve for different biotic potentials of the prey species

at an effort level that is equal to the effort to experience *MSY* in a single species isolated fishery system (1).

It is easy to observe that a higher biotic potential of the prey species produces a larger yield as shown in Fig. 2. The effects of the variation of the predation rate on the harvested yield are shown in Fig. 3. A higher predation rate produces a lower harvested yield and *maximum sustainable yield* is achieved at the same effort level regardless of the predation rate.

From the above analysis we may state the following theorem.

Theorem 1 In Holling–Tanner prey–predator system (5), fishing of the prey species at the *MSY* level is a sustainable fishing policy.

Fig. 3 Variation of the yield curve for different predation rates

4.2 Predator harvesting

In this subsection, we consider the predator as the target species for exploitation and accordingly system (4) takes the form:

$$\begin{aligned}\frac{dx}{dt} &= rx \left(1 - \frac{x}{k}\right) - axy, \\ \frac{dy}{dt} &= sy \left(1 - \frac{y}{\lambda x}\right) - ey.\end{aligned}\quad (6)$$

The coexisting equilibrium of system (6) is $R_2(x_2, y_2)$, where:

$$x_2 = \frac{krs}{(a\lambda k + r)s - a\lambda ke} \quad \text{and} \quad y_2 = \frac{\lambda kr(s - e)}{(a\lambda k + r)s - a\lambda ke}.$$

This equilibrium exists if the biotic potential of the predator species is greater than the harvesting effort. The yield function at equilibrium is given by:

$$Y(e) = \frac{\lambda kr(s - e)e}{(a\lambda k + r)s - a\lambda ke}.$$

The yield function satisfies the following conditions:

- (i) $Y(e)$ is continuous for all $e \in [0, s]$.
- (ii) $Y(0) = 0$ and $Y(s) = 0$.
- (iii) dY/de exists for all $e \in (0, s)$.

In addition, $[(a\lambda k + r)s - a\lambda ke] > 0$ all $e \in [0, s]$.

Hence by Rolle's theorem there exists at least one point $\hat{e} \in (0, s)$ such that $dY/de|_{\hat{e}} = 0$ and hence $Y(e)$ has a maximum at $e = \hat{e}$. A possible graphical representation is shown in Fig. 4. Hence, we may state the following theorem.

Theorem 2 In Holling–Tanner prey–predator system (6), fishing of the predator species at the MSY level does not collapse the fishery.

Fig. 4 Predator stock is decreasing with effort and the yield curve exhibits a maximum value

Fig. 5 Variation of the yield curve for different biotic potentials of the prey species

The impacts of the biotic potential of the prey species and the predation rate are shown in Figs. 5 and 6, respectively. From Fig. 5 we can conclude that the lower biotic potential of the prey species gives a lower harvested yield and the required effort at MSY is higher. However, the employed effort for a lower prey biotic potential is lower in the case of prey harvesting at the MSY level. Figure 6 indicates that a smaller predation rate produces a lower harvested yield from the predator and the harvester can enjoy the MSY level with smaller employed effort if the predation rate is larger but remains in a feasible range.

Fig. 6 Variation of the yield curve for different predation rates

4.3 Both prey and predator harvesting

We now consider the combined harvesting of both the species based on the catch-pre-unit-effort hypothesis with a unit catchability coefficient. Then, system (4) becomes:

$$\begin{aligned}\frac{dx}{dt} &= rx \left(1 - \frac{x}{k}\right) - axy - ex, \\ \frac{dy}{dt} &= sy \left(1 - \frac{y}{\lambda x}\right) - ey.\end{aligned}\quad (7)$$

The coexisting equilibrium becomes $R_3(x_3, y_3)$, where

$$x_3 = \frac{k(r-e)s}{(a\lambda k + r)s - a\lambda ke} \quad \text{and} \quad y_3 = \frac{\lambda k(r-e)(s-e)}{(a\lambda k + r)s - a\lambda ke}.$$

Here the total harvested biomass from both the populations is:

$$Y(e) = e(x_3 + y_3) = \frac{ke(r-e)(s + \lambda(s-e))}{(a\lambda k + r)s - a\lambda ke}.$$

Now differentiating x_3 with respect to e , we have

$$\frac{dx_3}{de} = \frac{ks[a\lambda k(r-s) - rs]}{[(a\lambda k + r)s - a\lambda ke]^2}.\quad (8)$$

From (8) it is observed that the prey biomass at equilibrium either decreases or increases depending upon the biotic potential of both the species. Variation of the prey–predator biomass at equilibrium and existence of *maximum sustainable total yield (MSTY)* have been investigated under different situations

In addition, we address an interesting ecological phenomenon known as *Volterra's first principle* for fishing both species. Principle [15, 16] can be stated as:

'If one tries to destroy uniformly and proportionally to their numbers the individuals of the two species, the average of the number of individuals of the eaten species increases and the one of the eating species decreases'. One can easily verify this principle in the Lotka–Volterra predator–prey model.

Case I $r \leq s$.

In this case, the coexisting equilibrium exists if $e < r$. The yield curve is positive and concaves downward with respect to effort if $e(0, r)$. Obviously $dx_3/de < 0$ and it implies that the equilibrium biomass of the prey species gradually decreases. Using Rolle's theorem as discussed in Section 4.2, we can achieve *maximum sustainable total yield (MSTY)* keeping the ecological balance of both the populations (see Fig. 7). From Fig. 7 it is also clear that *Volterra's first principle* no longer works even if MSTY exists.

Case II $s < r < s/\nu$, where

$$\nu = \left(1 - \frac{s}{a\lambda k}\right).$$

Fig. 7 Yield effort curve and stock levels at equilibrium are presented

The coexisting equilibrium exists if $e < s$. Also:

$$\frac{dx_3}{de} \begin{cases} < 0, & \text{if } r \in (s, s/v) \\ = 0, & \text{if } r = s/v. \end{cases}$$

Hence, the prey population decreases as effort increases. The yield curve is positive (see Fig. 8) and concaves downward if $e \in (0, s)$. Hence fishing both species at the *maximum sustainable total yield (MSTY)* level keeps the ecological balance of both the species. Again, we observe that our result does not support *Volterra's first principle*.

Case III $r > s/v$.

In this case, the ecological meaningful equilibrium exists if $e \in (0, s)$. Now:

$$\frac{dx_3}{de} \begin{cases} = 0, & \text{if } r = s/v \\ > 0, & \text{if } r > s/v. \end{cases}$$

Fig. 8 Yield curve has a single maximum and hence MSTY can be obtained

This implies that the prey biomass increases with increasing effort. The prey biomass at equilibrium reaches its maximum value when effort reaches the biotic potential of the predator population (see Fig. 9) and our outcome agrees with *Volterra's first principle* even if MSTY does not exist.

From the above three cases we propose the following theorem for the combined exploitation of both species.

Theorem 3 *Under a combined harvesting effort on both species in Holling–Tanner prey–predator system (7), both species coexist at the MSTY level if $r < s/v$ and the predator goes to extinction if $r > s/v$.*

5 MSY (or MSTY) policy for other Holling type functional responses

In the previous section, we have studied the possible impacts of the *MSY* (or *MSTY*) policy for the Holling type I functional response. In this section, we concentrate on the other Holling-type functional responses.

Dealing with the other functional responses, increases the number of ecological parameters involved in the system and these parameters compose the equilibrium biomasses of both the species in complex form. Thus the analytical results in most of the cases are not obvious in full parametric space and complexity increases when fishing is attempted on both species. However, we draw some important conclusions based on our simulation works.

5.1 Prey harvesting

If we consider $\varphi = \varphi_i(x)$, $i = 2, 3, 4$ and harvesting on the prey species based on the CPUE hypothesis, then the coexisting equilibrium must lie on the line $y = \lambda x$. In this case, the biomasses of both species decrease with increasing effort and ultimately approach zero when the effort crosses a threshold value. The yield gradually increases as effort increases

Fig. 9 Variation of equilibrium biomasses of the prey and predator species with effort. Maximum sustainable total yield cannot be accessible

but ultimately tends to zero when both the populations tend to zero. Therefore, we have the following theorem.

Theorem 4 *In the Holling–Tanner prey–predator system with any type of response function, fishing of the prey species at the MSY level does not remove the predator population from the system.*

5.2 Predator harvesting

The coexisting equilibrium lies on the straight line $y = (\lambda/s)(s - e)x$ and therefore, it is clear that the predator species goes to extinction when $s = e$. Now y/x decreases if the applied effort increases for any Holling-type functional response. However, we cannot expect that only the predator biomass decreases and that the prey biomass remains constant or that the prey biomass increases and the predator biomass remains constant at equilibrium as the predator possesses a prey dependent carrying capacity. The fact is that the predator biomass at equilibrium decreases and the prey biomass at equilibrium increases as effort increases due to the reduction of predation pressure. Now, for a smaller effort the yield is lower even in the presence of higher standing stock of the predator and the yield becomes again lower when the effort is larger due to a lower stock of the predator. Hence, in between these two effort levels, there exists an effort for which the yield attends its maximum. Therefore, we have the following theorem.

Theorem 5 *In the Holling–Tanner prey–predator system with any type of response function, fishing of the predator species at the MSY level is a safe harvesting policy for the coexistence of the species.*

5.3 Both prey and predator harvesting

It is very difficult to present analytical results on fishing to reach the MSTY level for other types of response functions. However, we consider the following two examples to provide

Fig. 10 Equilibrium values of prey biomass, predator biomass and yield

Fig. 11 Yield effort curve and species biomasses at equilibrium. MSTY cannot be obtained but MY can be achieved if $e > 1.5$

some impacts of the MSTY policy in a Holling–Tanner prey–predator system incorporating only the type II response function.

Example 1 Suppose $r = 1.5$, $s = 1.5$, $k = 100$, $\mu = 0.9$, $\lambda = 0.5$ and $L = 1$. Then the equilibrium biomasses of both the species at equilibrium decrease with effort and ultimately go to extinction at $e = 1.5$. In this case, the *MSTY* is equal to 33.49 and it occurs at the employed effort $e_{MSTY} = 0.68$, and the corresponding equilibrium stock (x_3^*, y_3^*) becomes (38.68, 10.57). It is now straightforward to calculate that the *MSY* of the isolated prey population is equal to 37.5 with the equilibrium stock as 50. Hence, fishing at the *MSY* level on both the populations may not cause over harvesting of the prey population (see Fig. 10).

Before presenting the next example and for better understanding of our analysis we introduce the term ‘*maximum yield*’ (*MY*), which means the maximum harvested yield from the ecosystem with the extinction of at least one species.

Example 2 If we consider the prey biotic potential as $r = 6$, keeping all the other ecological parameters the same as in example 1, then the system maintains its stability but *MSTY* does not exist. Both the prey and predator stocks at equilibrium decrease as effort increases (see Fig. 11). It is also examined that such a trend remains unaltered even for a higher biotic potential of the prey species. This phenomenon never occurs in system (7). The equilibrium biomass of the predator population approaches zero as e approaches 1.5. At this effort level the prey is under harvested but *MY* can be achieved if effort is increased further. In both examples 1 and 2, *Volterra’s first principle* does not hold.

6 Conclusion

This article describes the impacts of harvesting to reach the *MSY* or *MSTY* level in a Holling–Tanner prey–predator system with different types of functional responses. Increasing the harvesting effort on the prey species reduces the equilibrium biomasses of both

species, in particular the prey biomass reduces due to harvesting and the predator biomass reduces due to lack of prey (the only food source). It is observed that harvesting of the prey species at the MSY level preserves both the species. Legovic et al. [1] proposed that in traditional prey–predator systems, fishing to reach MSY of the prey population only will cause extinction of the predator population. However, in the case of our Holling–Tanner prey–predator system, fishing of the prey species at the MSY level may be a sustainable fishing policy. Also, Walters et al. [2] showed that the widespread application of single species MSY policies would in general cause severe deterioration in the ecosystem structure, in particular the loss of top predator species. However, we observe that the predator species can survive even if the fishing reaches the MSY level on the prey species and hence we found an exception to the rule that Walters et al. [2] stated.

Next we investigated the impact of harvesting on the predator species at the MSY level for different types of functional responses and it was observed that both the species can coexist under this harvesting policy. Note that the equilibrium level of the predator species reduces with increasing effort and consequently the prey biomass increases due to lower predation pressure. These results support the previous study by Legovic et al. [1].

Legovic et al. [1] also stated that in any prey–predator system subject to equal fishing effort on both the species, the ultimate value of MSTY will be the MSY of a single isolated population composed of prey only, i.e., the predator population goes to extinction. However, two folded effects are found in our system when fishing to reach MSTY is considered from both the species in the presence of a linear functional response. Extinction of the predator species critically depends upon the biotic potentials of both the species and MSTY can be achieved if the biotic potential of the prey is less than the biotic potential of the predator. In this case both the species go to extinction as the combined effort increases, but the MSTY policy can be applicable even if the prey biotic potential is greater than the predator biotic potential (see Case II). In both the cases (Cases I and II), it is observed that the equilibrium biomasses of both the species decrease with increasing effort. Hence *Volterra's first principle* is not applicable in this situation, but MSTY cannot be accessible when the prey biotic potential crosses a threshold value (Case III) and then *Volterra's first principle* works nicely. In particular, if the functional response is of type II, then two possibilities (existence and non-existence of MSTY) are investigated in the system. However, the prey biomass at equilibrium decreases even if MSTY does not occur (see example 2). Hence fishing at the MSTY level in a Holling–Tanner prey–predator system is more likely to conserve the system species than that of the system studied by Legovic et al. [1].

From the above discussion, it is clear that fishing may not reach the MSTY level with a combined harvesting effort on both the species due to the extinction of the predator species. However, we think in the case of a generalist prey–predator system, the results may differ significantly. The recent article of Takashina et al. [17] showed the reduction of prey abundance and even extinction of the prey while both the prey and predator species are harvested at a critical effort level. Therefore it may be an interesting topic to investigate whether the prey goes to extinction or not when both the species are subjected to a combined harvesting effort at the MSTY level in case of a generalist prey–predator system. This is our next research interest for a multispecies prey–predator system.

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