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Relationship between exploitation, oscillation, MSY and extinction

Bapan Ghosh [a,*], T.K. Kar [a], T. Legovic [b]

[a] Department of Mathematics, Indian Institute of Engineering Science and Technology, Shibpur (Formerly Bengal Engineering and Science University, Shibpur), Howrah 711103, West Bengal, India
[b] R. Boskovic Institute, POB 180, HR-10 002 Zagreb, Croatia

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ABSTRACT

We give answers to two important problems arising in current fisheries: (i) how maximum sustainable yield (MSY) policy is influenced by the initial population level, and (ii) how harvesting, oscillation and MSY are related to each other in prey–predator systems. To examine the impact of initial population on exploitation, we analyze a single species model with strong Allee effect. It is found that even when the MSY exists, the dynamic solution may not converge to the equilibrium stock if the initial population level is higher but near the critical threshold level. In a prey–predator system with Allee effect in the prey species, the initial population does not have such important impact neither on MSY nor on maximum sustainable total yield (MSTY). However, harvesting the top predator may cause extinction of all species if odd number of trophic levels exist in the ecosystem. With regard to the second problem, we study two prey–predator models and establish that increasing harvesting effort either on prey, predator or both prey and predator destroys previously existing oscillation. Moreover, equilibrium stock both at MSY and MSTY level is stable. We also discuss the validity of found results to other prey–predator systems.

1. Introduction

Human impact on natural ecosystems, especially by commercial fisheries, is diverse and accelerating. Open access fishery, over-exploitation and destructive fishing practices such as trawling are the main reasons for stock depletion. As a result, the number of marine species in danger of extinction is increasing. The proposed concept to remedy the situation is the maximum sustainable yield (MSY) policy, which is the maximum proportion that can be removed from stock over time without causing population decline below the optimum level. The MSY concept was formulated by Russell [28], Hjort et al. [13] and Graham [12]. A decade following World War II was a golden period of the concept development (see [7,25,29]; Ricker, [26]). Recently, The International Council for the Exploration of the Sea (ICES) reports that 81% of the stocks assessed are overfished and that for some stocks fishing mortality is as much as five times higher than that needed to achieve MSY. Similarly, 75 % of fish stocks in european waters are overfished [5].

In this context, the encouragement by the World Summit on Sustainable Development (Johannesburg, 2002) to apply MSY policy in ecosystems is really important. Contrary to the above advice, Walters et al. [33] have shown that the widespread application of MSY policy would, in general, cause severe deterioration in ecosystem structure, in particular the loss of top predator species. Matsuda and Abrams [20] also examine the MSY policy in various food web models and report that harvesting of a relatively few species at equilibrium causes the extinction of a significant fraction of species from the food web. Legovic [16] shows that ten out of sixteen groups of demersal fish in the Adriatic Sea have been harvested beyond MSY level. Legovic et al. [19] established that harvesting of both prey and predator towards prey MSY level causes extinction of the predator species. In the case of two or more independent populations each having logistic growth rate with approximately equal carrying capacities, Legovic and Gecek [17] conclude that MSTY (maximum sustainable total yield from both species) exists under independent efforts with the coexistence of species, but for equal harvesting effort, the species with lower biotic potential may go to extinction. Smith et al. [30] also conclude that fishing at conventional MSY level can have large impacts on other parts of the ecosystem, particularly, when they constitute a high proportion of the biomass in the ecosystem or are highly connected in the food web. Recently, Legovic and Gecek [18] concluded that species with lower biotic potential and carrying capacity may be

* Corresponding author. Current Address: Inria, Centre de Recherche Inria Sophia Antipolis, Mediterranee, BIOCORE Team, 06902 Sophia Antipolis, France. Tel.: +91 33 26684561; fax: +91 33 26682916.

E-mail addresses: keshab_bg@yahoo.in (B. Ghosh), tkar1117@gmail.com (T.K. Kar), legovic@irb.hr (T. Legovic).

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driven to extinction to reach MSTY level under equal harvesting effort, especially, if these species weakly cooperate with the rest of a mutualistic community. They also employed selective harvesting efforts on competing species [8] to reach MSTY level and observe that it does not affect the system stability character, though some populations may be too small to persist in nature. Kar and Ghosh [15] note that prey harvesting at MSY level in a prey–predator system with crowding effect among predator species may not cause any extinction. In the same work, they also assert that in a ratio-dependent prey–predator system, harvesting the prey species at MSY level does not cause extinction of the predator species. In a generalist prey–predator system, Ghosh and Kar [10] have shown that predator species can persist when prey is harvested at the MSY level. Ghosh and Kar [9] propose that prey harvesting at MSY level always becomes a sustainable fishing policy in a prey–predator system, where prey-dependent carrying capacity for predator is incorporated. Very recently, Ghosh and Kar [11] pointed out that application of nonlinear harvesting function may prevent the extinction of the predator species. Dennis [2] mentioned that a critical density is a lower unstable equilibrium in a single species model with Allee effect. Under constant effort strategy, both the lower unstable state and the upper stable state marge together and disappear for some critical effort. Hence, the yield curve has an abrupt discontinuity and population goes to extinction when the effort crosses the critical threshold. In this regard, he suggested that resource would be close to extermination when harvesting reaches the maximum level. Stephens and Sutherland [31] have shown that harvesting may cause extinction in a single species model with strong Allee effect. Kar and Matsuda [14] accurately determined the MSY at equilibrium for a single species model with Allee effect. Considering the present state of fish resources, the effect of initial population level on MSY policy remains unknown. Moreover, most of the above theoretical results are based on prey–predator systems with bilinear interaction. Therefore, effect of MSY on corresponding stocks in oscillatory prey predator systems [27,23,24,6] is also unknown.

The paper is organized as follows. In Section 2, we revisit the MSY policy based on single species logistic model. Section 3 examines the existence of MSY in a single species model incorporating the Allee effect and compares the results with that of single species logistic model. Section 4 is devoted to understanding the influence of initial population level to achieve MSY and MSTY. In Section 5, we examine whether harvesting of either prey, predator or both species creates or destroys oscillations in prey–predator systems. In addition, we establish that stock at MSY and MSTY level is stable. Finally, in Section 6, the main results are discussed in view of their applicability to other classes of models.

2. Revisiting traditional MSY

Widely studied single species mathematical model with logistic growth function and proportional harvesting [29,3] is given by:

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - qex, \tag{2.1}$$

where x is the biomass of the concerned species at any time $t > 0$, while r and K are, respectively, the intrinsic growth rate and environmental carrying capacity of the species. The harvesting function is taken as $H = qex$, where q is the catchability coefficient and e is the fishing effort. The single species model (2.1) has only one positive equilibrium K in the absence of harvesting. The rate of growth (dx/dt) is positive if the initial population level is $0 < x(t = 0) < K$ (see Fig. 1)a and negative if it is greater than K. Ultimately, the dynamic solution of the model converges to K for any $x(t = 0) > 0$.

The positive equilibrium of the exploited system (2.1) $\bar{x} = K(r - qe)/r$, exists if $e < r/q$.

The yield from the fishery at equilibrium becomes $Y = e\bar{x} = Ke(r - qe)/r$.

Our aim is to achieve the maximum sustainable yield from the system (2.1). Since the yield function is quadratic in effort, it has a single maximum at the equilibrium. MSY is obtained when the effort is $e_{MSY} = r/2q$ with equilibrium stock level $x_{MSY} = K/2$. Fig. 1b shows the variation in the biomass and the corresponding yield at the equilibrium.

Though MSY is taken at equilibrium for management purposes, the dynamic solution tends to x_{MSY} from an initial population level and will remain there for the long-term. In the present model, the dynamic solution converges globally to the equilibrium population when harvesting reaches the MSY level. Hence MSY can be achieved in the single species model with logistic law of growth. In the following section, we show that this result may not hold for the single species model in the presence of a strong Allee effect.

Remark 1. When the effort exceeds $r/2q$, the equilibrium stock becomes less than $K/2$ and the species becomes over-harvested. But over-harvested species does not necessarily mean species extinction. If instead of proportional harvesting qex, a constant yield strategy is applied to the model (2.1), the zero equilibrium disappears and a new unstable equilibrium exists. The value of the stable equilibrium is the same as that in constant effort strategy and the yield stays the same. The stable and unstable equilibria coincide with each other at MSY = $rK/4$ and all dynamic solutions reach MSY stock if initial population level exceeds $K/2$. But if the stock is overfished, i.e., $0 < x < K/2$, then constant yield $rK/4$ will drive the stock to extinction. No positive equilibrium can be found if fishermen try to achieve higher yield than $rK/4$. In this case, the model experiences a saddle node bifurcation for constant yield strategy.

3. MSY in the presence of an Allee effect

Let us consider a single species model (originally proposed by Volterra [32]) in the presence of an Allee effect (critical depensation) and harvesting. The model is given by:

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right)\left(\frac{x}{L} - 1\right) - qex, \tag{3.1}$$

where L $(L < K)$ is the population level below which the population will tend to extinction.

Fig. 2a shows the growth rate of the exploited and unexploited systems in the presence of a strong Allee effect. It is clear that the equilibrium population K of the unexploited system will be stable if the initial population level $x(0)$ is greater than $L = 20$. In the case of harvesting, the initial population level $x(0)$ must exceed 50 to obtain MSY. If the initial population level $x(0)$ lies in the range $(20, 50)$, then extinction of the population is evident at the MSY level. Hence an attempt to reach MSY may cause extinction of the population (see Fig. 2 c and d) even though the positive equilibrium exists at the effort required to achieve MSY. This phenomenon will not occur in the logistic growth model. Since the success to achieve MSY also critically depends on the initial population, MSY may or may not exist in a single species model incorporating the strong Allee effect. In the present discussion, the minimum viable population should be greater than 50 for the existence of MSY. It is also clear that MSY occurs when the stock is at $x_{MSY} = 70$, and the effort is $e_{MSY} = 1.485$. From Fig. 2a we observe that MSY occurs when growth rate is the maximum and this maximum occurs for $x_{MSY} > K/2$. In Fig. 2b the equilibrium stock and the corresponding yield are given as a function of effort