Sustainable Management of a Fishery with a Strong Allee Effect

T.K. Kar and H. Matsuda
Faculty of Environment and Information Sciences, Yokohama National University, 79-7, Tokiwadai, Hodogaya-ku, Yokohama, Kanagawa 240-8501, Japan

Abstract: Traditional models of population growth assume that reducing the density will always result in the same or higher per-capita growth. This implies that populations are resilient, allowing them to recover rapidly when the factors that caused their decline are removed (e.g., fishing). However some populations experience reduced rates of survival and reproduction when reduced to very low densities. This reduced per-capita growth rate at low densities is called depensation. In this study we have considered a prey-predator model with strong Allee effect. We obtain the conditions for the existence of biological equilibrium and its stability is discussed. We have also discussed the bifurcation analysis of the model under different scenario. The bioeconomic models herein proposed, based on optimal control theory, can form a basis for more sustainable management. Mathematics Subject Classifications (2000): 34K20, 37G15, 49J15

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INTRODUCTION

The modeling of the commercial exploitations of renewable resources (such as fisheries, forestry) represents a challenging task, as it involves the nonlinear interaction of biological, economic and social components. The sustainability of this exploitation is constrained by the natural growth of the resource and overexploitation eventually leads to stock depletion and thus decreasing yields. These consequences could include fishery collapse, economic inefficiency, habitat loss or decreases in the abundance of rare species. For these reasons many authors suggest that Governments or central authorities should impose forms of regulation such as fishery regulations, either by imposing fishing restrictions, such as constant fishing efforts, or through taxation or even by simulating cooperative behavior among exploiters. However, the complexity of time evolutions of natural populations, due to nonlinear biological growth functions and the ecological complexity of interactions among species, gives rise to several difficulties in implementing suitable regulation policies that are able to combine economically and socially efficient exploitation with issues of sustainable exploitation. Indeed, these severe nonlinearities can present themselves at multiple levels and multiple ways, due to nonlinear interactions between ecological and economic components (Rosser, 2002) and present a serious challenge to policy makers. Effective fisheries management requires clear objectives supported by the best scientific advice and appropriate management actions.

The traditional, continuous time model of pure open access, based on logistic net growth, does not allow for extinction (Clark, 1990). A model where net growth exhibits critical depensation is formulated. Clark (1990) categorized the dynamics of continuous deterministic models as depensation and compensation models. The growth function is called a depensation curve if it is convex for small

Corresponding Author: T.K. Kar, Department of Mathematics, Bengal Engineering and Science University, Shibpur, Howrah-711103, India
levels of the stock. If not it is called a compensation curve. Further, if the growth rate is negative for small stock levels, we say that the resource possess critical depensation. For such process the stock will go extinct if it is reduced below a certain level. Mullon et al. (2005) studied continuous time models of a prey population under harvesting with various renewal functions (logistic, Ricker, Beverton-Holt). These models all showed 'crashes after a plateau-shaped yield under surreptitiously increasing catch levels if the renewal function was negative for stock sizes lower than a given threshold. Recent reviews by Liemann and Hilborn (2001) assert that there is a widespread evidence for critical depensation. The collapse of many fish populations of strong schoolers subject to harvesting by maximal sustainable yield is reported to be due to an Allee effect (Lande et al., 1994). Here extreme care must be taken by the practitioner.

Where renewable resource management is practiced it is generally based on the concept of Maximum Sustainable Yield (MSY), which itself is based on models of biological growth, (Clark, 1990). This is not necessarily the best management method, because the long-run consumption profile does not coincide with that of utility maximization. The resource stock under the MSY is not necessarily optimal with respect to production due to the positive relationship between productivity in harvesting activities and the resource stock size. The main problem of the MSY is economical irrelevance. It is so since it takes into consideration the benefits of resource exploitation, but completely disregard the cost operation of resource exploitation. Also we have seen that the traditional approach to fisheries management relies on single species models of population dynamics that aim to sustain harvests of commercial species. Such an approach ignores a broad suite of interactions among exploited species and between exploited species and other member of their communities. Recently, Matsuda and Abrams (2006) argued that MSY theory does not always guarantee species coexistence even for simple predator-prey systems.

One recurring aspect of many prey-predator models is that in absence of the predator the prey species grows to a carrying capacity. Also, if the predator invades, there is always a region in parameter space where the model has a positive equilibrium, implying successful invasion of the predator followed by co-existence of the prey and the predator. In regard of this issue we recall that in some cases the initial numbers of a species determine the long-term behaviour of the system. Population models with an Allee effect have this property. Now what happens when predators are introduced into the system when the prey population is in equilibrium? Three cases may occurs: first is that the predator species is not able to establish itself and it will go extinct while the prey maintains itself in the system. It is also possible to coexist both the prey and predator species. Third dramatic option is that predation invasion causes the extinction of both species. Recently, Kent et al. (2003) have shown the consequences for predators of rescue and Allee effects on prey.

THE BASIC MODEL

The resource grows due to reproduction, i.e., natural growth. It is common in the literature to assume that the natural growth function of the resource takes the form \( F(x) = rx(1-x/K) \), where \( K, r \) and \( x \) denote the carrying capacity, the intrinsic growth rate and the resource’s stock respectively. Present aim here is to generalize this function in order to capture the effect of critical depensation on the natural growth of the resource.

Taking into account the critical depensation, the net growth of the resource or population dynamics will be described by the following equation:

\[
x = F(x) = rx(1 - x/K)(x/L - 1)
\]
where L is the minimum viable population level.

The harvest function is assumed to be linear in the rate of its fishing effort E(t) and in the stock x(t), that is:

\[ h(t) = qE(t)x(t) \]

where q is the catchability coefficient which is suppose to be constant.

Using this harvesting term, we rewrite the equation for x as

\[ x = F(x) = rx(1 - x / K)(x / L - 1) - qE(t)x(t). \] (1)

Renewable resources, by definition, possess the capacity for self-regeneration, allowing humans to harvest commercially valuable goods and services in perpetuity. It has often been assumed that fishing does not impose any direct threat to the extinction as marine fish generally are very fecund and the ocean expanse is wide. However, humans often over-harvest species to near-extinction or actual collapse. The past few decades have witnessed a growing awareness that fishes can not only be severely depleted, but also be threatened with extinction through overexploitation. The collapse of the cod fishery off the east coast of Canada in the early 1990’s perhaps the most dramatic recent example of the consequences of over harvesting.

When the collapse of a resource base occur, the first and most obvious thing to look at is overexploitation of the resource. If it is known that a particular species suffers from an Allee effect, this knowledge can help prevent the collapse of a population (Coucheamp et al., 1999).

In the case of critical depensation, as E rises above a critical threshold, the fish population may be reduced to a level below the minimum viable population level L. Once this occurs, population extinction is guaranteed, regardless of future fishing activities (Fig. 1). This contradicts to the pure compensation situation (Fig. 2), in which a critical harvesting effort must be continuously exceeded for extinction to occur.

For example, fisheries managers in South Africa have estimated that their pelagic fishery faces unacceptable risks if the spawning biomass falls below one-fifth of the mean pre-exploitation level within a twenty year period (Butterworth et al., 1997).

All components in the marine ecosystem are interlinked and it is impossible to change one component without affecting everything else. Competition and prey-predator are the most common interaction for fisheries. The behaviour of the prey-predator model is known to be very sensitive to the form and parameters in the growth functions. The ecological set up of our problem is as follows. There is a prey which is harvested continuously. There is a predator living on prey. It is assumed that the harvesting does not affect the growth of the predator population directly. Thus our model becomes:

\[ \begin{align*}
  x &= rx(1 - x / K)(x / L - 1) - mx y - qE(t)x(t) \\
  y &= m o x y - dy
\end{align*} \] (2)

where m, r, and d have the usual interpretation.

Holling type II functional response probably a better description of the actual predation seen in nature but for simplicity, we assume the simplest description. It is of interest to understand the impact of the Allee effect in prey species, since there exists the possibility of extinction for both populations (predators and prey), particularly if the predator is a specialist which depends on the prey as its only resource.
Fig. 1: Yield-Effort curve for a critical depensation model MSY: Maximum Sustainable Yield

Fig. 2: Yield-Effort curve for a pure compensation model (logistic growth curve), MSY: Maximum Sustainable Yield

QUALITATIVE ANALYSIS

Here, we discuss the existence and stability of non-negative equilibria of system (2). Particularly we are interested in the interior or positive equilibrium of the system. Interior equilibrium is important for the main problem of this paper because, to control optimally we obtain the optimal harvesting effort and drive the system to the optimal equilibrium level most efficiently and the shortest time possible.

The system (2) has one possible interior equilibrium \((x', y')\), where

\[
x' = \frac{d}{mg}.
\]
Fig. 3. Phase diagram for different possibilities of $x'$. 

$$y' = \frac{1}{m} \left[ r(1 - \frac{d}{moK})(\frac{d}{mol} - 1) - qE \right]$$

$x'$ is positive but for $y'$ to be positive we must have

$$0 < E < \frac{r}{q} \left( 1 - \frac{d}{moK} \right) \left( \frac{d}{mol} - 1 \right)$$

(3)

in the region $L < \frac{d}{max} < K$  \hspace{1cm} (4)

since, $K > L$.

From the expressions of $x'$ and $y'$ we observe that $x'$ increases with $d$ and $y'$ decreases with $E$ (Fig. 3). This is natural because an increase in $d$ decreases the predator population and hence enhancing the survival rate of prey; on the other hand an increase in $E$ results the loss of food for the predator. Also we observe that as minimum viable population of prey increases, equilibrium value of predator population decreases.

Combining all these results we have the following theorem.

**Theorem 1**

The prey-predator system with harvesting described by Eq. 2 has a unique interior equilibrium $(x', y')$ for any harvesting effort $E$ with

$$0 < E < \frac{r}{q} \left( 1 - \frac{d}{moK} \right) \left( \frac{d}{mol} - 1 \right)$$

in the region $L < \frac{d}{max} < K$.

We shall now discuss the stability of the interior equilibrium point.

$(x', y')$ will be locally asymptotically stable if $x' > (K+L)/2$ and unstable if $d/max < (K+L)/2$ (All the formal derivation are given in the Appendix A). To check the non-existence of limit cycles we used
Fig. 4: Here \( x' < (K+L)/2 = 55.00 \)

Fig. 5: Here \( x' > (K+L)/2 = 55.00 \)

Bendixson Du-Lac Criterion (Appendix A). Limit cycle will not exist if \( x \) is confined in the region \( 0 < x < (K+L)/2 \) or \( (K+L)/2 < x < K \) (A.3 in the Appendix A). If \( d/m < (K+L)/2 \), the open access equilibrium will be unstable (Fig. 4). Also it is not the focus of a stable limit cycle as there is no limit cycle for \( d/m > (K+L)/2 \). As \( d/m > (K+L)/2 \), the equilibrium will be locally asymptotically stable and as there is no limit cycle so the interior equilibrium is also globally asymptotically stable (Fig. 5). Hopf bifurcation occurs when \( x' \) moves from the above of \((K+L)/2\) to the below of \((K+L)/2\). For \( x' = (K+L)/2 \), there is a stable limit cycle (Fig. 6).

From Fig. 3, we see that if the equilibrium point is \((x'_1, y')\), then it is unstable. If it is \((x'_2, y')\) then it is globally asymptotically stable and if it is \((x' = (K+L)/2, y')\) then there is a stable limit cycle exists.
Fig. 6: Here $x^* = (K + L)/2 = 55.00$

**OPTIMAL HARVESTING POLICY**

After briefly presenting the different kinds of behaviour the ecosystem here considered may exhibit, now discuss its optimal management policies. This study is aimed at not only solving the optimal harvest problem associated with the considered dynamic system but also to study the effect of critical depensation and effort tax in improving the bioeconomics of the ecosystem. It is important to stress that we give a special treatment to the solutions where the extraction rate is zero. Consequently, we have found some special cases of optimal policies that use zero extraction rates for some period of time. This kind of management policies is seldom found in the body of work in this area.

After discussing the nature of the dynamics of the system (2), now we are in a position to apply maximum principles (Pontryagin et al. 1964) to obtain the optimal harvesting policy. We need to find the path traced out by $(x(t), y(t))$ with this optimal harvesting policy so that if the population are kept along this path, we are assured of achieving the objective of the harvesting agency.

Now we consider the optimal harvesting problem with the view to maximize the objective functional

$$J = \int_{0}^{T} e^{-\beta t} (px - (c + \tau))Edt$$

s.t.

$$x = r x (1 - x/K) (x/L - 1) + mxy - qE(t)x(t)$$

$$y = mxy - dy.$$

$$0 < E < \frac{r}{q(1 - \frac{d}{m}(\frac{d}{m}L - 1) + \text{in the region } L < \frac{d}{m} < K}}.$$

$x(0) = x_0$ and $y(0) = y_0$.
\( \tau \) is the tax per unit effort and do not aim at environmental regulation. However, as Berck (1981) has shown, it increase the optimal stock and this is what leads us to consider.

Model (5) is an optimal control model with two state variables and one control variable. As per the maximum principle, the current value Hamiltonian is given by

\[
H = (px - (c + \tau)) E + \mu_1 \left[ \frac{rx}{L} - \left( 1 - \frac{x}{K} \right) - m x y - q x E \right] + \mu_2 (m x y - dy)
\]

where \( \mu_1 \) and \( \mu_2 \) are costate functions.

Clearly this is a linear control problem on infinite horizon. Hence the solution will be a combination of bang-bang and singular controls. First we study the singular solution for the optimization problem. The associated adjoint differential equations for the above problem are given by

\[
\frac{d\mu_1}{dt} = \delta \mu_1 - \frac{\partial H}{\partial x} = \delta \mu_1 - [p q E + \mu_1 \left\{ \frac{r x}{L} + \frac{1}{K} - \left( 1 - \frac{2 x}{K L} \right) \right\} + \mu_2 m x y],
\]

\[
\frac{d\mu_2}{dt} = \delta \mu_2 - \frac{\partial H}{\partial y} = \delta \mu_2 + \mu_1 m x.
\]

Now suppose E is the singular optimal control. Then using the above equilibrium solutions and after some algebra (Appendix B) we get the following equation for E:

\[
\delta (p - \frac{c + \tau}{q x^2}) - p q E - \left( p - \frac{c + \tau}{q x^2} \right) \left\{ r x + \frac{1}{L} - \frac{2 x}{K L} \right\} + \frac{m}{q} \left( p x - \frac{c + \tau}{q} \right) m x y (E) = 0
\]

(6)

Let E be a solution (if it exists) of (6). Using this value of E in the expression of \( x' \) and \( y' \), we get the optimal equilibrium.

From the point of view of ecologist managers, it may be desirable to have a unique positive equilibrium which is globally asymptotic stable, in order to plan harvesting and keep sustainable development of ecosystem. If the optimal equilibrium point falls in the region \( 0 < x < (K + L)/2 \) then it is unstable and if it falls in the region \( (K + L)/2 < x < K \), then it is globally asymptotically stable.

Now our job is to reach this optimal solution optimally from the initial state \((x_0, y_0)\). This is achieved by applying bang-bang control to the system as follows. Let us define

\[
E = \begin{cases} 
E_{as} & \text{while } S(t) = px - (c + \tau) - \mu(q x), \\
E_{sa} & \text{while } S(t) = px - (c + \tau) - \mu(q x),
\end{cases}
\]

Let T be the time at which the path \((x(t), y(t))\) generated by the bang-bang control \( E = E \) reaches the state \((x(E'), y(E'))\). Then the optimal control policy will be

\[
E(t) = \begin{cases} 
E \text{ for } 0 < t < T, \\
E' \text{ for } t > T.
\end{cases}
\]
Fig. 7: A three dimensional diagram of optimal harvesting effort and predator for different values of tax $\tau$. Parameter values are $K = 100$, $L = 10$, $m = 2$, $d = 2.5$, $p = 15$, $c = 15$, $q = 0.03$, $\alpha = 0.02$, $\delta = 0.02$

Fig. 8: Optimal path for prey and predator. Parameter values are $K = 100$, $L = 10$, $m = 2$, $d = 2.5$, $p = 15$, $c = 15$, $q = 0.03$, $\alpha = 0.02$, $\delta = 0.02$

It is often convenient to find an optimal equilibrium, i.e., the equilibrium corresponding to the optimal effort, so that the optimal path would consist of a path leading to the optimal equilibrium level as quickly as possible and then stay at that optimal equilibrium level with that optimal effort subsequently. Such an optimal policy to be practicable, it is necessary that the optimal equilibrium point be globally asymptotically stable. Here we have the two paths to reach the optimal equilibrium point. One is the most rapid approach path called the bang-bang policy and other is the singular effort policy right from $t = 0$. First one is the optimal path and the second one is the suboptimal path.

Figure 7 shows that as tax $\tau$ increases harvesting effort decreases and as a consequences predator population increases. Figure 8 shows one optimal path.
DISCUSSION

The ecological impact of overexploitation should not be underestimated, especially in models that display bi-stability, like models with strong Allee effects. In systems with strong Allee effects it is very likely that once overexploitation has occurred the Allee effect prevents any easy system recovery.

In a critical depensation model under open access or sole ownership exploitation it is possible that the fish population level will be driven to extinction. All that is required is that the optimal population level is below the minimum viable population size. If the depensation exists, fishery managers should be extremely careful because fished stocks may not recover after being fished to very low abundance, even when fishing is stopped.

It is however, clear from the studies of maximizing the present value that generally it is suboptimal to apply a positive harvesting effort at all times. Instead, the harvester should now and then allow the population to recuperate a sustainable density at which the value of the future harvesting opportunities are maximized. In this way, the Allee effect is excluded from the population and extinction in finite time is impossible for sufficiently low discount rates.

There are several extensions of this model that could be interesting research topics. One obvious extension is to introduce stochastic growth functions. Another natural extension is the harvesting effort as dynamic variable. This would make the model more interesting in a real world management setting. We leave it for future considerations.

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Appendix A

The Jacobian of the linearization of system (3) at \((x^*, y^*)\) is

\[
V(x^*, y^*) = \begin{pmatrix}
\frac{r}{L} (1 - \frac{x^*}{K}) & \frac{r}{K} \frac{x^*}{L} - 1 & -mx^* \\
\frac{r}{K} \frac{x^*}{L} & \frac{r}{L} (1 - \frac{y^*}{K}) & 0
\end{pmatrix}.
\]

The characteristic equation of \(V(x^*, y^*)\) is

\[\lambda^2 + m_1 \lambda + m_2 = 0\]  \hspace{1cm} (A.1)

where

\[m_1 = -\frac{r}{L} (1 - \frac{x^*}{K}) + \frac{r}{K} \frac{x^*}{L} - 1\]

\[m_2 = m_1 x^* y^*\]

Sum of the roots of Eq. (4) is

\[\frac{r}{L} (1 - \frac{x^*}{K}) + \frac{r}{K} \frac{x^*}{L} - 1\]

and product of the roots is

\[m_1 x^* y^*\]
For \((x', y')\) to be stable the eigenvalues must be negative if real or have a negative real part if complex conjugates. Therefore the sufficient condition for instability is

\[
\frac{\mathbf{r}x'}{L} - \frac{\mathbf{r}x'}{K} - \frac{\mathbf{r}x'}{(K - L)} > 0,
\]

which is equivalent to

\[
\frac{d}{d\sigma} > \frac{K + L}{2}
\]

(A.2)

To check the non-existence of limit cycles we shall use Bendixson Du-Lac Criterion. This criterion states that for two smooth functions \(\dot{x} = f(x, y)\) and \(\dot{y} = g(x, y)\) in a simply connected region \(D\) if there exists another smooth function \(h(x, y)\) in \(D\) such that

\[
\frac{\partial(hf)}{\partial x} + \frac{\partial(hg)}{\partial y}
\]

does not change sign in \(D\), then the system \(\dot{x} = f(x, y)\) and \(\dot{y} = g(x, y)\) has no limit cycles in \(D\).

For the system (3), let us define \(h(x, y) = 1/(xy)\).

Then

\[
\frac{\partial(hf)}{\partial x} + \frac{\partial(hg)}{\partial y} = \frac{x}{yKL}[K + L - 2x].
\]

(A.3)

The above expression will not change sign in both the region \(x < K + L\) and \(x > K + L\).

For \(x = (K + L)/2\), \(m = 0\) and hence the roots of the characteristic equation (A.1) becomes purely imaginary and they are conjugate to each other. Also we have

\[
\frac{d}{dx}(\text{trace} \mathbb{V} \big|_{x=(K+L)/2}) = -\frac{r(K + L)}{KL} = 0
\]

Hence by the Hopf-bifurcation theorem (Hassard et al., 1981), the system (2) enters into a Hopf-type small amplitude periodic solutions at the parametric value \(x = (K + L)/2\) near the positive interior equilibrium point \((x', y')\).

**Appendix B**

Formulation of the maximum principle for our optimal control problem

Now we consider the optimal control problem (5), where \(E(t)\) is the control variable and \(x(t), y(t)\) are the state variables. For many problems of economic interest, future values of rewards and expenditures are discounted, say, at rate \(\delta\), like in (5) where the term

\[
J = \int_{0}^{\infty} e^{-\delta t} \left( p_1 x(t) + (c + \tau_2) E(t) \right) dt
\]

represents the flow of total discount benefit for the fishery.

As per the maximum principle, the current value Hamiltonian is given by

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\[ H = (pqx - (c + \frac{c}{x}))E + \mu_1 \left( \frac{px}{L} - 1 \right) \left( 1 - \frac{x}{K} \right) - mcxy - qE \] + \mu_2 (mcxy - dy) \]

where \( \mu_1 \) and \( \mu_2 \) are costate functions.

Clearly this is a linear control problem on infinite horizon. Hence the solution will be a combination of bang-bang and singular controls. First we study the singular solution for the optimization problem. The associated adjoint differential equations for the above problem are given by

\[ \frac{d\mu_1}{dt} = -\delta \mu_1 - \frac{\partial H}{\partial x} = \delta \mu_1 - [pqE + \mu_1 \left( \frac{px(1 - \frac{1}{K})}{KL} \right) + \mu_2 mcxy] \]

\[ \frac{d\mu_2}{dt} = -\delta \mu_2 - \frac{\partial H}{\partial y} = \delta \mu_1 + \mu_2 mx \]

Using the maximum principle

\[ \frac{\partial H}{\partial E} = (pqx - (c + \frac{c}{x})) - \mu_1 qx = 0 \]

gives \( \mu_1 = p - \frac{c + \tau}{qx} \)

\[ \frac{d\mu_2}{dt} = 0 \Rightarrow \mu_2 = -\frac{mx}{\delta} \left( p - \frac{c + \tau}{q} \right) \]

Putting the values of \( \mu_1 \) and \( \mu_2 \) in \( \frac{d\mu_1}{dt} = 0 \), we get

\[ \delta \left( p - \frac{c + \tau}{qx} \right) - pqE - \left( p - \frac{c + \tau}{qx} \right) \left( \frac{px}{L} - 1 \right) \left( 1 - \frac{x}{K} \right) - \frac{m}{\delta} (px - \frac{c + \tau}{q}) mcxy = 0 \]

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