

The Economics of Predator-Prey Harvesting

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1. Introduction

The number of species within a given habitat is often large, and the way they interact may be very complex. This applies to terrestrial as well as to marine ecosystems. Nevertheless, in most cases man utilizes just a few of the species. This is probably one of the reasons why scientists often use relatively simple models to study the population dynamics and other aspects of renewable resources. Another important reason is, obviously, that simple models are easier to analyse than complex models.

Examples of predator-prey relationships are: shark – fish (D'Ancona 1926), whale – krill (May et al. 1979), sea mammals – fish (Flaaten 1988), polar bear – ringed seal (Larsen 1986a and 1986b), wolf – reindeer (Ingold 1980) and lynx – hare (May 1974). Studies of these predator-prey systems include, inter alia, mathematical, ecological, economic and anthropological aspects of the management of the resources.

Since the seminal work by Gordon (1954), theoretical bioeconomic studies have focused on the difference between open-access harvesting and socially optimal harvesting. Multispecies analyses of these kind are to be found in Quirk and Smith (1970), Anderson (1975), Clark (1976), and Silvert and Smith (1977), all of whom

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mainly use generally formulated growth equations. Hannesson (1983) utilizes Lotka-Volterra types of growth equations from Larkin (1966) to study open-access and socially-optimal harvesting of the combined resources.

The aim of this paper is to review ecological and economic aspects of predator-prey harvesting within the framework of a simple bioeconomic model. The focus is mainly on sustainable yields and comparative statics, rather than on the dynamic behaviour of the system. In addition to this simplified approach to the ecological and economic theory of predator-prey harvesting, we will also develop the conditions under which it is possible to have an increasing optimal resource stock as a function of the social rate of discount.

In the next section we review a simple but robust predator-prey model. Open-access harvesting of the resources is studied in Section 3, and optimal management is studied in Section 4. Our findings are summarized briefly in the final section.

2. Predator-Prey Relationships

It is many years since theoretical biologists started studying ecological systems by means of mathematical models (e.g., Lotka 1925 and Volterra 1928). In the classical Lotka-Volterra model, the size of the two stocks oscillates with a period determined largely by the parameters of the model, while the amplitude is determined solely by the initial conditions (May 1981, 79). The model is "structurally unstable", meaning that the slightest alteration in the functional form of the growth equations will tip the dynamics towards a stable point or towards a stable limit cycle. Structurally unstable models are considered to have no place in biology, but nevertheless the Lotka-Volterra model highlights one of the general properties of predator-prey models, namely the propensity to oscillate.

Most two-species predator-prey models analysed in the literature can be shown to have either a stable point or a stable limit cycle (May 1981, 81). A simple model capturing the essential elements of a predator-prey system is that of May et al. (1979). In this model, as opposed to the classical Lotka-Volterra model, the growth of the prey is density dependent in absence of the predator, and the predator has a positive intrinsic growth rate. The carrying capacity of the prey is constant,² and the model has a stable point. This predator-prey model was used by May et al. (1979) particularly to discuss the Antarctic ecosystem. Maximum sustainable yield properties of this model were studied by Beddington and May (1980) and further elaborated by Beddington and Cook (1982). The latter also investigated the stability

² Larkin (1966) analyses a predator-prey model where each of the two species has its own constant carrying capacity. This expands the sustainable yield region of the system, especially for low levels of the prey stock.

properties of various harvesting regimes. Since the model is simple but still captures the essential elements of a predator-prey system, it will be used in this paper.

Let W_1 and W_2 denote the stocks of the prey and the predator, respectively. Then, the model is specified as

$$(1) \quad \dot{W}_1 = dW_1/dt = r_1 W_1 (1 - W_1/K) - a W_1 W_2,$$

$$(2) \quad \dot{W}_2 = dW_2/dt = r_2 W_2 (1 - W_2/\alpha W_1),$$

where r_1 and r_2 are the intrinsic growth rates of the respective species. K is the carrying capacity of the total system, the level to which the prey will settle in the absence of both predator and harvest.

In case of no predators, the per capita³ growth rate of the prey decreases from r_1 , for stock levels close to zero, to zero for stock levels equal to the carrying capacity. If predators exist, the per capita growth rate for the prey equals zero for a stock level lower than the carrying capacity. The presence of predators reduces the per capita growth rate in proportion to the biomass of the predator. The predation coefficient, a , tells how much the per capita growth rate of the prey is reduced per unit of the predator. Or to put it another way, a tells which share of the prey stock one unit of the predator is consuming per unit of time. The total rate of consumption is expressed in the term $a W_1 W_2$.

The predator's per capita growth rate decreases from r_2 , when its own stock level is close to zero, to zero for a stock level equal to its own carrying capacity, which is proportional to the level of the prey stock. The proportionality coefficient is α .

The equilibrium values for the prey and the predator populations, W_1 and W_2 respectively, are obtained by letting $dW_1/dt = 0$ and $dW_2/dt = 0$ in equations (1) and (2). Without harvesting there is a unique, stable equilibrium solution:

$$(3) \quad W_1^* = K/(1+\nu),$$

$$(4) \quad W_2^* = \alpha K/(1+\nu),$$

where $\nu = a\alpha K/r_1$.

It should be noticed that the intrinsic growth rate of the predator, r_2 , does not affect the equilibrium values of either of the two species. The equilibrium values of both species increase with any increase in r_1 or K , *ceteris paribus*. From (3) and (4) it follows:

³ The term "per capita" is used, even though we mean per unit of biomass.

$$(5) \quad W_2^*/W_1^* = \alpha.$$

In equilibrium, α expresses the relative size of the predator stock to that of its prey.

Even though r_2 does not affect the equilibrium values of the two stocks, it is of importance to the behaviour of the system outside equilibrium. That is, r_2 will affect the time the predator will need to reach equilibrium from a higher or lower level.

We shall now, in a simple way, introduce harvesting as a factor in the model. Suppose that the fish stocks are harvested independently with constant effort per unit of time, F_i , scaled such that $F_1 = 1$ corresponds to constant catchability coefficients equal to r_i . Then the catch rates will be

$$(6) \quad h_1 = r_1 F_1 W_1,$$

$$(7) \quad h_2 = r_2 F_2 W_2.$$

The introduction of harvesting will influence the growth rates in (1) and (2), which will be changed to

$$(8) \quad \dot{W}_1 = r_1 W_1 (1 - W_1/K) - a W_1 W_2 - r_1 F_1 W_1,$$

$$(9) \quad \dot{W}_2 = r_2 W_2 (1 - W_2/\alpha W_1) - r_2 F_2 W_2.$$

It may be useful to rewrite the variables W_1 and W_2 into a dimensionless form. Defining $X_1 = W_1/K$ and $X_2 = W_2/\alpha K$, we can rewrite equations (8) and (9) as

$$(10) \quad \dot{X}_1 = r_1 X_1 (1 - F_1 - X_1 - \nu X_2),$$

$$(11) \quad \dot{X}_2 = r_2 X_2 (1 - F_2 - X_2/X_1).$$

Recall that the dimensionless parameter ν is defined as $\nu = \alpha K/r_1$.

The equilibrium properties of this ecological system depend only on the fishing efforts, F_1 and F_2 , and ν . The dynamics additionally involve r_1 and r_2 .

The phase-diagram for the system (10) and (11) is shown in Figure 1. The isoclines are found by setting $dX_1/dt = 0$ and $dX_2/dt = 0$ in (10) and (11). This gives

$$(12) \quad X_2 = (1/\nu)(1 - F_1 - X_1) \quad \text{for } dX_1/dt = 0,$$

$$(13) \quad X_2 = (1 - F_2)X_1 \quad \text{for } dX_2/dt = 0.$$

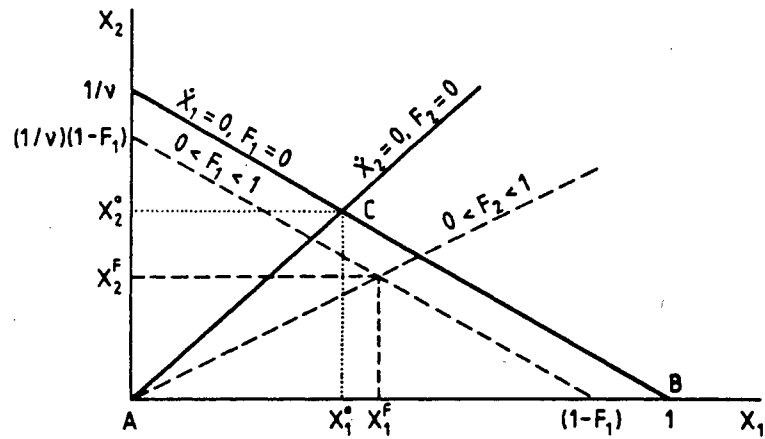


FIG. 1. The phase diagram for the predator-prey model.

If positive equilibrium levels of X_1 and X_2 , denoted by X_1^F and X_2^F , exist simultaneously, they are found where the isoclines intersect:

$$(14) \quad X_1^F = (1 - F_1) / [1 + \nu(1 - F_2)],$$

$$(15) \quad X_2^F = (1 - F_1)(1 - F_2) / [1 + \nu(1 - F_2)].$$

With harvesting taken into account relative stock size is

$$(16) \quad X_2^F / X_1^F = (1 - F_2).$$

It can be seen from (14) that only for $F_1 < 1$ will there exist a positive equilibrium value of the prey. If $F_1 \geq 1$ the prey-stock will be extinct, and so of course will be the predator, as seen from (15). The latter expression shows that only for $F_2 < 1$ and $F_1 < 1$ will the predator survive.

The equilibrium values of both species, as would be expected, increase with decreasing fishing pressure on the prey, i.e. for reduced F_1 . The larger prey stock results in an increased carrying capacity for the predator, thus implying a higher equilibrium level of the predator stock.

On the other hand, the effects on the prey and on the predator from decreased fishing pressure on the predator are the opposite of each other. From (14), the equilibrium value of the prey will decrease, and from (15), the equilibrium value of the predator will increase. The increased stock level for the predator means heavier predation on the prey, and thereby a reduced equilibrium level for the latter.

In Figure 1 the pre-harvesting stock levels of the prey and the predator are denoted by X_1^0 and X_2^0 , respectively. This figure illustrates that, in the case of harvesting, the equilibrium level of the predator will always be below its pristine level. This result is independent of whether we harvest only the predator, only the prey, or both are harvested simultaneously. On the other hand, the equilibrium level of the prey will increase with the harvesting of the predator. In Figure 1, the relative strength of the predator harvesting to that of the prey is such that the net result for the prey is a higher stock level with harvesting than without. The sustainable yield area in Figure 1 is the triangle ABC . Combinations of stock levels outside this triangle are not possible to maintain.⁴

3. Open-Access Harvesting

In the preceding section we have seen that a predator-prey system may be capable of being harvested on a sustainable yield basis for both of the species. When the species are open-access resources, we may be interested in knowing what the equilibrium levels of the stocks will be and the corresponding harvest rates. This includes the possibilities of extinction of one or both of the stocks. It is also interesting to study the dynamics of the stocks and the harvest industries to see whether the equilibrium point is reached or not.⁵ However, in this paper we shall concentrate on analysing equilibrium points by means of comparative statistics.

Given the Schaefer production function of equations (6) and (7), and assuming constant costs, c_i , per unit of rescaled effort, $E_i = r_i F_i$, the unit harvesting cost becomes

$$(17) \quad c_i(X_i) = c_i/X_i \quad (i = 1, 2).$$

The demand for each of the two species is assumed to be independent of the price of the other one and infinitely elastic with respect to its own price. Thus, p_1 and p_2 are the constant prices of the prey and the predator, respectively.

The net profit per unit of harvest under these assumptions is⁶

⁴ Essentially all deterministic two-species models will have a bounded sustainable yield area, but it need not be a triangle. The isoclines could be curves instead of straight lines, or the area could be, e.g. a quadrangle. The latter is the case for the predator-prey model designed by Larkin (1966) where the abundance of the predator has a lower limit in the absence of the prey.

⁵ Beddington and Cook (1982) have studied the stability properties of this model for various harvesting regimes, from a biological point of view.

⁶ c_i includes the alternative cost of capital and labour. That is to say that normal profit on capital and normal remuneration of labour are included in the costs. The net profit in equations (18) and (19) is therefore the pure resource rent.

$$(18) \quad b_i(X_i) = p_i - c_i/X_i \quad (i = 1,2),$$

and the total profit for each of the species is

$$(19) \quad \pi_i = (p_i - c_i/X_i)y_i \quad (i = 1,2),$$

where $y_1 = h_1/K$ and $y_2 = h_2/\alpha K$ are the normalized harvest rates of the prey and the predator, respectively.

Bioeconomic equilibrium is defined as a situation in which we simultaneously have

$$(20) \quad \pi_i = 0, \quad \dot{X}_i = 0 \quad (i = 1,2).$$

When there is zero net profit, no potential harvester has the incentive to enter the industry and no existing harvesters have the incentive to leave the business.

Let us denote the open access stock levels of the prey and the predator as X_1^∞ and X_2^∞ , respectively. From equation (19) it is seen that, unless $y_i = 0$ for either of the two species, we have the following simple expression for the open access stock levels:

$$(21) \quad X_i^\infty = c_i/p_i \quad (i = 1,2).$$

The open-access stock level of a species depends solely on the ratio of own effort cost to own price of the yield. The corresponding harvest rates are found by substituting X_i^∞ from equation (21) into the growth equations, (10) and (11). Under our assumptions, the biological parameters have no effects on the open-access stock levels. However, they will affect the harvest rates, as seen from equations (10) and (11).

Figure 2 shows the open-access stock levels derived from the ratio of the cost of effort to the price of harvest given in equation (21). The two sloping, broken lines are the corresponding isoclines for $F_1 = F_1^\infty$ and $F_2 = F_2^\infty$, and of course they intersect at the equilibrium point.

As noted above, equation (21) is valid provided that an open access solution exists with simultaneous harvest of the prey and the predator. If that is not the case, if, for example, only one of the two species is harvested at the equilibrium, the stock level of that particular species is given by equation (21). The stock level of the other species, however, has to be found in another way. We distinguish two cases: first, the case with no harvest of the predator, and then the case with no prey harvest.

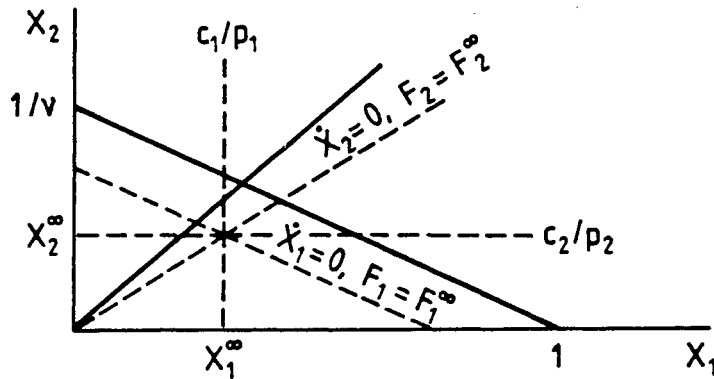


FIG. 2. Interior open-access equilibrium with simultaneous harvest of the prey and the predator.

No Predator Harvest

In general there will never be open-access harvesting of the predator if its own price is lower than the unit harvesting cost at the pristine stock level. Thus we have

$$(22) \quad p_2 < c_2/X_2^0 \Rightarrow F_2 = y_2 = 0.$$

Therefore, a necessary condition for open-access harvesting of the predator is that the ratio of the cost of effort to the price of harvest must be lower than the pristine stock level. However, this is not a sufficient condition. The following example illustrates this. If the prey is a low-cost, high-price species, as shown by $X_1 = c_1/p_1$ in Figure 3, the predator stock will be reduced below its profitability level, c_2/p_2 , and it will not be harvested at the equilibrium point (X_1^∞, X_2^∞) .⁷

Since the predator's carrying capacity is proportional to the prey stock in this model, we will always have

$$(23) \quad X_2^\infty = X_1^\infty = c_1/p_1,$$

when the predator is unharvested, i.e. when $F_2 = 0$. This is likely to happen when the prey is "inexpensive-to-catch and valuable" compared to the predator. The

⁷ If the predator had its own, constant carrying capacity, as in Larkin (1966), the chances increase that it could economically sustain a harvest even if the prey stock is reduced through harvesting.

open-access stock level of the unharvested predator depends solely on the effort cost of prey/price of prey ratio.

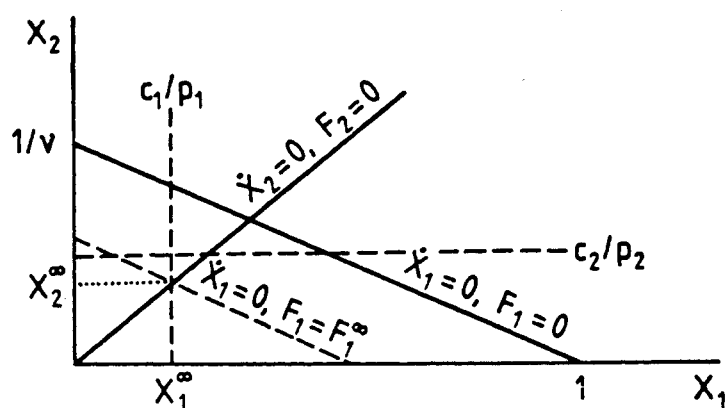


FIG. 3. Open-access equilibrium with no harvesting of the predator.

No Prey Harvest

When the prey is an "expensive-to-catch trash" species compared to the predator, the possibility emerges for this species being unharvested under open access. In this case we have

$$(24) \quad \dot{X}_1 = 0, \quad F_1 = 0.$$

Using equations (10), (24) and (21) for $i = 1$, we derive the open-access unharvested prey stock,

$$(25) \quad X_1^\infty = 1 - \nu X_2^\infty = 1 - \nu c_2/p_2,$$

when the predator is harvested. Equation (25) shows that the open-access level of the prey is a linear, decreasing function of the predator stock, which is determined solely by the predator's cost of effort – own price ratio. In other words, the unharvested prey stock is greater, the more "inexpensive-to-catch and valuable" the predator is. As seen from Figure 1, harvesting of the predator increases the prey stock. Therefore, it might well happen that a prey species which is not able to support an open-access harvest industry of its own when the predator is unharvested, can do so if the predator is harvested. This is illustrated in Figure 4 where the prey's

cost of effort – price of harvest ratio is c_1/p_1 . With $c_2/p_2 = A$ there will be no harvest of the predator-prey system, i.e. the open-access stock levels equal the pristine levels, X_1^0 and X_2^0 . If, for one reason or another, the c_2/p_2 ratio decreases from A to B , the predator becomes economical to harvest, but the prey is unharvested at the stock level X_1^B , since the equilibrium point is on the border of the sustainable yield triangle. When the c_2/p_2 ratio is further reduced to C , the predator will be harvested at the stock level X_2^C . The reduced predation pressure on the prey now makes it economical for the prey to support an open-access harvesting with the stock at the level X_1^C .

So far we have not considered the possibility of extinction. This is because the harvest function in equations (6) and (7), together with the assumption that total cost is proportional to fishing effort, imply that the unit harvesting cost in equation (17) approaches infinity when the stock approaches zero. Thus, with a constant price of harvest, the net profit per unit of harvest in equation (18) becomes negative for a positive stock level, and we have

$$(26) \quad X_i^\infty > 0.$$

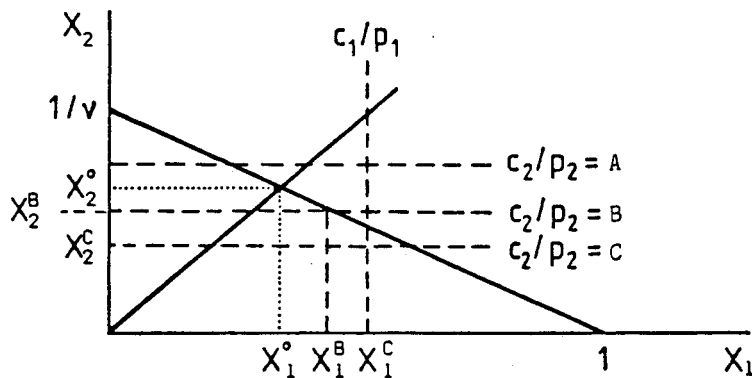


FIG. 4. Open-access equilibria with and without harvesting of the prey.

Extinction under open-access harvesting in this model only occurs either if

$$(27) \quad c_i = 0 \quad (i = 1, 2)$$

or

$$(28) \quad p_i > c_i(0) \quad (i = 1, 2)$$

for one or both of the species. The expression $c_i(0)$ is the cost of harvesting the last unit of the stock. If equation (27) or (28) is fulfilled for the predator, only this species will be extinct, while in the case of extinction of the prey, the predator will be extinct as well.

4. The Optimal Harvest

Given joint management of predator and prey, we assume that the social manager's objective is to maximize the present value of the rent from the two resources. The joint rent function is

$$(29) \quad R(t) = b_1(X_1)y_1(t) + b_2(X_2)y_2(t) = \pi_1(t) + \pi_2(t),$$

using the same notation as in the preceding section. The objective functionale is

$$(30) \quad PV = \int_0^{\infty} e^{-\delta t} R(t) dt.$$

The social manager will choose the harvest rates, the y 's, so as to maximize the present value of the rent, given the biological restrictions implied by the growth equations, (10) and (11).⁸ Rewriting the growth equations somewhat gives

$$(31) \quad \dot{X}_1 = G_1(X_1, X_2) - y_1(t), \quad 0 \leq y_1,$$

$$(32) \quad \dot{X}_2 = G_2(X_1, X_2) - y_2(t), \quad 0 \leq y_2.$$

The following notation for the first order derivatives will be used:

$$(33) \quad G_{ij} = \partial G_i(\cdot) / \partial X_j \quad (i, j = 1, 2).$$

From equations (10) and (11) we derive

$$(34) \quad G_{11} = r_1(1 - 2X_1 - \nu X_2) \geq 0 \text{ if } X_2 \leq (1/\nu)(1 - 2X_1),$$

$$(35) \quad G_{12} = -\nu r_1 X_1 < 0, \quad G_{21} = r_2 X_2^2 / X_1^2 > 0,$$

⁸ Whether one uses the effort rates, the F 's, or the harvest rates, the y 's, as the control variables, is simply a matter of convenience. In this section it is most convenient to use the latter.

$$(36) \quad G_{22} = r_2(1 - 2X_2/X_1) \geq 0 \text{ if } X_2 \leq X_1/2$$

It is now received knowledge that if an interior solution exists, there are two joint equilibrium equations that must be satisfied at the maximum (Clark 1976, 318). They are:

$$(37) \quad G_{11} + [b_2(X_2)/b_1(X_1)] G_{21} + [b_1'(X_1)/b_1(X_1)] G_1(\cdot) = \delta,$$

$$(38) \quad G_{22} + [b_1(X_1)/b_2(X_2)] G_{12} + [b_2'(X_2)/b_2(X_2)] G_2(\cdot) = \delta,$$

where $b_i'(X_i) = db_i(X_i)/dX_i$.

The economic interpretation of the result of the predator-prey analysis is quite similar to that of the single-species model. The left-hand side of equation (37) is the prey's own rate of interest, which should equal the social rate of discount, given on the right-hand side. The first two terms on the left-hand side together form the instantaneous marginal product of the species. It consists of two parts, where the direct one, G_{11} , is equivalent to the one in a single-species model. The second part is the indirect part of the instantaneous marginal product via the predator. The last term on the left-hand side of equation (37) is the marginal stock effect; that is, the cost-reducing effect an increase in the stock level of the prey has on its own harvesting.⁹ The interpretation of equation (38) is similar.

Equations (37) and (38) implicitly give the optimal equilibrium stock levels of the predator and the prey, $X_2 = X_2^*$ and $X_1 = X_1^*$, respectively.

A common economic interpretation of the singular path of single-species models can be generalized to cover the predator-prey case. Let

$$(39) \quad R(X_1, X_2) = b_1(X_1)G_1(X_1, X_2) + b_2(X_2)G_2(X_1, X_2).$$

$R(\cdot)$ is the total sustainable rent associated with a sustainable harvest at given stock levels. Then

$$(40) \quad \partial R(\cdot)/\partial X_i = b_i'(X_i)G_i(\cdot) + \sum_j b_j(X_j)G_{ji} \quad (i = 1, 2).$$

Now equations (37) and (38) can be rewritten as

$$(41) \quad (1/\delta)\partial R(\cdot)/\partial X_i = b_i(X_i) \quad (i = 1, 2).$$

⁹ Because $b_i(X_i) = p_i - c_i(X_i)$, we have: $b_i'(X_i) = -c_i'(X_i)$.

The left-hand side is often referred to as the marginal user cost, which gives the loss in present value of sustainable harvesting when the capital asset, the resource stock, is reduced by one marginal unit. The right-hand side is the net current value of harvesting the stock at the margin. In other words, optimal harvesting of the predator-prey system requires that for each of the stocks, which can be thought of as the assets of the social manager's resource portfolio, the present value of future losses from reducing the stock through harvesting should equal the current net benefits from that harvesting.

In the single-species model the optimal stock level will always be larger than the open-access level, given a positive rate of discount. This also holds for the prey in a predator-prey model. If the prey stock were below the open-access level,¹⁰ i.e. $X_1 < X_1^\infty$, equations (19) and (21) would imply $\pi_1 < 0$. The loss from harvesting the prey may be avoided simply by abolishing the harvest of this species. As shown in Section 2, this will increase the level of the prey stock, thereby increasing the carrying capacity and the surplus growth of the predator. The net profit from the harvest of the predator is therefore increased. Thus, the optimal stock level of the prey can never be below its open-access level. However, it is quite possible that the optimal predator stock level might be lower than the stock level under open-access harvesting. To see this, rewrite equations (40) and (41) for the predator:

$$(42) \quad (1/\delta)b_1(X_1)G_{12} = b_2(X_2) - (1/\delta) [b_2(X_2)G_{22} + b_2'(X_2)G_2].$$

The left-hand side of equation (42) is the loss in present value of sustainable harvesting of the prey when the predator stock is marginally increased. The right-hand side is the net gain of the combined current and present value of harvesting the predator, when the stock level of this species is marginally increased.

From equation (35) and what is said above it follows that the left-hand side of equation (42) always is negative when the prey is harvested. For the right-hand side we have that the last term in the parenthesis can never be negative, whereas the sign of G_{22} depends on the relative size of the predator stock compared to the prey stock, as shown in equation (36). When the prey is "inexpensive-to-catch and valuable", i.e. c_1 is low and p_1 is high, and the predation pressure on the prey is significant, i.e. ν is large, it can easily happen that b_2 on the right-hand side of equation (42) becomes negative. This is likely to happen when the predator is "expensive-to-catch trash", i.e. c_2 is high and p_2 is low. Then it will be optimal to reduce the predator stock below its open-access level, i.e. $X_2^* < X_2^\infty$. Private harvesters cannot be expected to harvest the predator resource at a loss. Therefore, the social manager would offer them a bounty to harvest a predator that is "expensive-to-catch trash" which preys on a species that is "inexpensive-to-catch and valuable".

¹⁰ Assuming $X_1^\infty = c_1/p_1 < X_1^0$.

It is easy to show that when the discount rate goes to infinity, the optimal stock level will approach the open-access level. If we make the reasonable assumption that $\partial R(\cdot)/\partial X_i$ is bounded, then equation (41) implies that when $\delta \rightarrow \infty$ we have $X_i^* \rightarrow X_i^\infty$, where X_i^∞ is derived from

$$(43) \quad p_i - c_i(X_i^\infty) = 0.$$

When the optimal predator stock level is below the open-access level, i.e. when $X_2^* < X_2^\infty$, then an increase in the discount rate will increase the optimal predator stock. In other words, we have shown that¹¹

$$(44) \quad \partial X_2^*/\partial \delta > 0 \quad \text{when} \quad X_2^* < X_2^\infty.$$

This result contradicts the analysis of single-species models where an increased discount rate makes it more costly to keep a large resource stock. Therefore, the optimal single-species stock is reduced when the discount rate increases. In the predator-prey model this is also the case for the prey stock, while the increase in the optimal predator stock caused by the increased discount rate helps reduce the prey to its new lower optimal stock level.¹² As noted above, a rise in the discount rate makes it more costly to keep a large prey stock; therefore a part of it is transmuted into capital in general. Another part is transmuted into predator resource capital. Thus the losses from harvesting the predator are reduced, because of the lowered unit harvesting cost and/or increased revenues.

To see how the stocks at the optimum are affected by marginal changes in prices and costs, equation (41) can be differentiated with respect to p_1 , p_2 , c_1 , and c_2 , respectively, to find the partial derivatives of the optimal stocks with respect to each of the parameters (see Flaaten 1988, ch. 7). As in the single-species model, it can be shown that the optimal level of each of the two stocks is negatively affected by an increase in the own price:

$$(45) \quad \partial X_i^*/\partial p_i < 0 \quad (i = 1, 2).$$

Also, it can be shown that

¹¹ Since the state variables in equation (41), the X_i^* s, are implicit functions of the biological and economic parameters, this result can also be found by differentiating the equation with respect to δ and solving for $\partial X_1^*/\partial \delta$ and $\partial X_2^*/\partial \delta$ (Flaaten 1988, 64–65). Such a method provides a general analysis of the effects of marginal changes in the discount rate on the optimal stocks.

¹² Hannesson (1983) asserted: "Increasing the discount rate may, at "moderate" levels, imply that the optimal standing stock of biomass increases instead of decreasing" (Hannesson 1983, 329).

It seems as if he did not notice that this only applies to the predator species.

$$(46) \quad \partial X_i^* / \partial p_j > 0$$

$$i \neq j, \text{ when } b_2(X_2) \ll 0.$$

This is to say that when the predator is a great nuisance, an increase in the price of the prey will lead to a larger optimal stock of the predator, and vice versa. The case of an increase in prey price may be explained the following way. Such a price change initially augments the value of the resource capital of the prey proportionally to the price increase. However, it pays to transform some of the increased wealth into capital in general, rewarding the social manager with the interest represented by the discount rate. This transformation may be controlled directly through harvesting the prey, or indirectly by letting the predator harvest the prey. Hence, the effect of an increased price of the prey is an increased optimal stock of the predator. The investment in the predator stock is rewarded by increased revenues and reduced harvesting cost of this species. The effects of increased effort costs are the opposite of the effects of increased prices.

So far it has been implicitly assumed that the optimal solution is an interior one. This is shown in Figures 5 and 6. In the former, the star indicates the interior solution for the case when both species are "inexpensive-to-catch and valuable". In this case both stock levels are higher at the optimum than under open access. Figure 6 illustrates the case where the prey is "inexpensive-to-catch and valuable", while the predator is "expensive-to-catch trash". In this case the optimal solution is to subsidize the predator harvest so as to reduce the stock, thereby increasing the harvestable surplus production of the prey. The star in Figure 6 indicates that it is optimal to harvest at a predator stock level below the unharvested open access level. On the other hand, the optimal level of the prey stock is higher than the open-access level of this species.

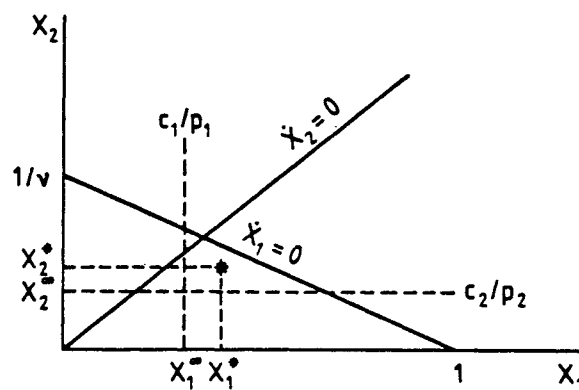


FIG. 5. Open-access and optimal interior solutions.

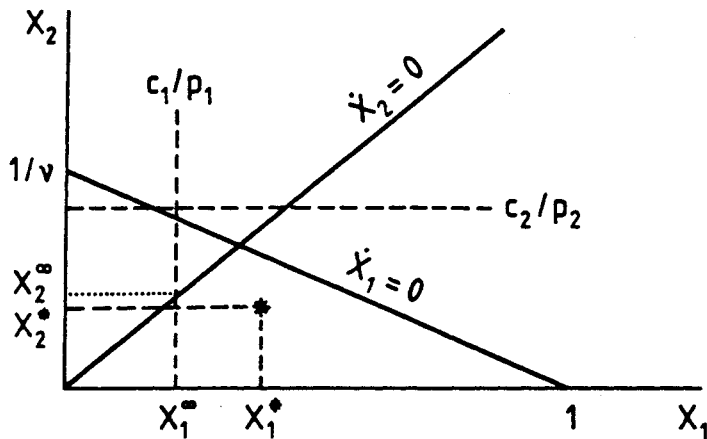


FIG. 6. Interior optimal solution and open-access solution with no harvest of the predator.

As noted above, so far the optimal solution has implicitly been assumed to be an interior one, i.e. the optimal stocks may be derived from the "golden rule" equations, (37) and (38). It is, however, possible that the optimal solution will involve no harvest of either the predator or the prey. Intuitively, it might be uneconomical to harvest the prey if it is "expensive-to-catch trash", or it might be uneconomical to harvest the predator if this species is "expensive-to-catch trash" and its predation pressure on the prey is insignificant, i.e. ν is small. The former case implies an optimal combination of stocks, indicated by the star on the prey's isocline in Figure 7, while the latter implies the combination of stocks indicated by the star on the predator's isocline in Figure 8.

To find whether the solution given by the "golden rule" equations, (37) and (38), really is the optimal solution, the following procedure may be used. First, it should be checked whether or not the golden rule solution implies positive harvest rates of both species. If it does, the solution is inside the sustainable yield triangle (ΔABC in Figure 1), and the interior solution is the solution to the maximization problem. If it does not, one of the restrictions on the harvest rates, the y 's in equations (31) and (32), becomes binding.¹³ Then it is necessary to substitute the relevant golden rule equation with the corresponding growth equation. For example, if the predator harvest rate becomes binding, the optimal steady state stocks are implicitly found from equations (32) and (33) ($y_2 = X_2 = 0$ in the former). Inserting the

¹³ Mathematical analysis of constrained optimization is found in Kamien and Schwartz (1981) and Seierstad and Sydsæter (1987). Application of the theory is found in Flaaten (1988).

optimal stock levels into the prey's growth equation, equation (31), will give the harvest rate of the prey, $y_1 > 0$. This example corresponds to what is shown in Figure 8.

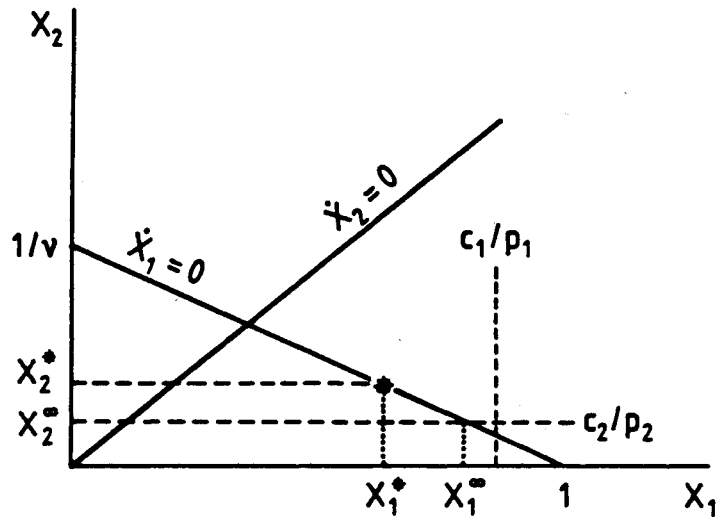


FIG. 7. Open-access and optimal stocks when the prey is "expensive-to-catch trash".

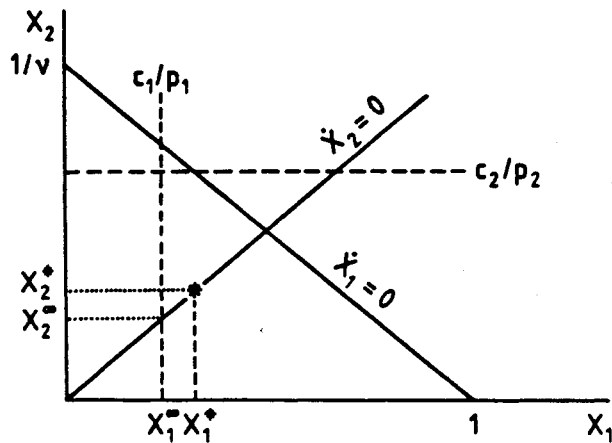


FIG. 8. Open-access and optimal stocks when the predator is "expensive-to-catch trash" with insignificant predation pressure on the prey.

5. Conclusion

In this paper we have combined a simple biological predator-prey model from May et al. (1979), reviewed in Section 2, with two economic independent harvest sectors, one for each of the species. In Section 3 we derived the equilibrium solutions of open-access harvesting of the two species simultaneously, and a corner solution with either of the species left unharvested. The ratio of cost of effort to price of harvest can be so unfavourable for both species that they are best left unharvested under an open-access regime.

Maximizing the present value of the joint economic rent from the predator and the prey may imply an interior solution with simultaneous harvest of both species, as shown in Section 4. The optimal harvest strategy could also be to harvest only the most valuable species, and leave the other unharvested. With a positive discount rate, the optimal level of the prey stock will always be larger than the open-access level. However, this need not be the case for the predator. If this species' predation pressure on the prey is significant, the predator is a low-valued species, and the prey is a high-valued species, it was shown that it may be optimal to reduce the predator stock to below its open-access level. This can be done by subsidizing the harvesters of this species.

The major finding of this paper is that the optimal predator resource stock may increase with an increase in the social rate of discount. This was shown to be the result when the predator's negative effect on the prey's growth rate is significant, the predator is "expensive-to-catch trash", and the prey is "inexpensive-to-catch and valuable".

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