

Optimal Harvesting of Ecologically Interdependent Fish Species

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The optimal exploitation of a two-species predator-prey system is considered, using Lotka-Volterra-type equations. Due to the density-dependence of ecological efficiency, both species should be harvested simultaneously over a range of relative prices. Beyond the limits of this price range, either the prey species should be utilized indirectly by harvesting the predator, or the predator should be eliminated to maximize the prey yield. Neglecting harvesting costs, the simultaneous harvest of prey and predators requires that a unit of prey biomass increase in value by being "processed" by predators. Certain results from single-species fishery models are shown not to apply to multispecies models. These are as follows: (i) Optimal regulation of a free access fishery may call for subsidizing instead of taxing the harvest of predator species. (ii) Increasing the discount rate may, at "moderate" levels, imply that the optimal standing stock of biomass increases instead of decreasing. (iii) A rising price or a falling cost per unit fishing effort of a species may raise and not lower the optimal standing stock of that species.

1. INTRODUCTION

The economics of ecologically interdependent fish species has received rather little attention in the literature. To our knowledge only two papers by economists addressing this problem have been published, one by Quirk and Smith [11] and the other by Anderson [1]. Both papers focus on the same problem, namely on comparing free-access equilibrium and social optimum. In both papers necessary conditions for optimum are derived and interpreted in rather general terms, but neither paper is very explicit on how the optimum would be affected by changes in the discount rate or the prices and harvesting costs of the different fish species involved. Questions that are not considered include the following: Does there exist a well-defined relative price of products obtained at different levels in the food chain at which harvesting should be switched from one to the other? To what extent are the results of single-species theory valid also for multispecies theory? For example, will free-access fishing effort always be excessive (excluding the case of the backward-bending yield curve; cf. [4, Chap. 1]), so that taxes or other restraining regulations will be needed? Will a stronger discounting of the future always imply a decreasing standing stock of biomass? These are the questions we endeavor to consider in this paper.

While general functional relationships like the ones used by Anderson and Quirk and Smith yield important insights, more clear-cut results must be sought at the price of introducing specific functional forms. A popular set of functions used for portraying interspecies relations is the Lotka-Volterra model. Several authors have used this model for analyzing economic aspects of multispecies systems. Clark [2] considered selective and nonselective harvesting of a two-species system. Silvert and Smith [14] derived necessary conditions for optimal exploitation of a multispecies community and considered the stability of such a situation in a Lotka-Volterra

model. May *et al.* [8] used a slightly different version of the Lotka–Volterra model to characterize the krill–whale system in the Antarctic ocean. One of their conclusions was that the optimal solution would involve a simultaneous exploitation of both species over some range of relative prices. Mendelsohn [9] considered optimal management of a stochastic system, using a discrete version of the Lotka–Volterra model. His results suggested that the optimal policy might imply depleting stocks of less valuable predator species to very low levels.

While the Lotka–Volterra model probably is not very useful for describing actual ecosystems, its attraction consists in a simple portraying of such pervasive nonlinear relations as density dependence of growth and ecological efficiency. Precisely these nonlinearities, together with density-dependent harvesting costs, would appear to distinguish the fishery from animal husbandry; the former is still essentially an advanced form of hunting, where prospects depend upon the response of a wild stock of animals, whereas the latter takes place under controlled conditions that at times resemble manufacturing. We shall use the Lotka–Volterra model extensively in this paper.

The main problem with which we are concerned in this paper is the optimal utilization of the marine food chain, but some of the results are also valid for partial predator–prey models. We begin by setting up a general multispecies model, derive the conditions for optimum, and interpret these in a familiar vein (Section 2). We then introduce the Lotka–Volterra model (Section 3) and apply the said conditions to this model (Section 4). In Section 5 we analyze the case of costless harvesting with no discounting of the future. We find that harvesting should take place at two adjacent levels in the food chain simultaneously over a range of prices of the products so obtained. The limits of this price range are characterized as follows. The species at the higher level should be eliminated when their price is so low that the lower level biomass does not increase in value by being “processed” by the higher level species. As the relative price of the higher level species increases from this “extinction level” it reaches a point where the lower level species should only be harvested indirectly by fishing the higher level species. Increasing the prey harvest marginally (from zero) then yields the same value as one would obtain from the predator fishery by increasing its food supply by the same amount. Due to the density-dependence of ecological efficiency at various levels in the food chain, these price limits do not coincide.

In Section 6 we consider harvesting costs, showing that the corrective taxes being called for to attain the social optimum with free access may turn out to be subsidies to encourage depletion of predators. In Section 7 we consider the impact of discounting the future; contrary to single-species theory a higher discount rate may, at “moderate” levels, imply an increase in the optimal standing biomass of a particular species. In Section 8 we modify the analysis of Section 7 to take account of harvesting costs. The qualitative conclusions of Section 7 are upheld, and it is shown that increasing costs per unit of effort may lower the optimal standing stock of a species, which also is contrary to single-species theory.

2. A GENERAL MULTISPECIES MODEL

Let S_i denote the stock of species i in terms of weight. Assume that the growth rate of species i can be described by a function

$$G_i(S_1, \dots, S_n). \quad (1)$$

Assume further that the cost per unit of fish caught C is a function of the abundance S of the species in question.¹ That is,

$$C_i(S_i). \quad (2)$$

Finally, let the price of fish of species i be denoted by P_i . This we shall assume constant and independent of time and the volume of catches.

Maximizing the present value of an infinite stream of rents from all species amounts to maximizing the following integral²

$$\int_0^{\infty} \left\{ \sum_{i=1}^n [P_i - C_i(S_i)] [G_i(S_1, \dots, S_n) - \dot{S}_i] \right\} e^{-rt} dt, \quad 0 \leq S_i \leq S_i^{\max}. \quad (3)$$

No population can be negative, and for all populations there is an upper limit S_i^{\max} , determined by the availability of food in the absence of predators. The maximum conditions to be derived are subject to this constraint being fulfilled. The catch rate is $G_i - \dot{S}_i$, the difference between surplus growth and the rate of change in the stock. The discount rate r is assumed to be constant over time. At the maximum the Euler equation must be satisfied. This implies

$$-\frac{\partial C_i}{\partial S_i} (G_i - \dot{S}_i) + \sum_{j=1}^n (P_j - C_j) \frac{\partial G_j}{\partial S_i} - r(P_i - C_i) - \dot{C}_i = 0. \quad (4)$$

In a steady-state solution, $\dot{C}_i = 0$ and $\dot{S}_i = 0$, and we can write (4) as

$$r(P_i - C_i) = -\frac{\partial C_i}{\partial S_i} G_i + \sum_{j=1}^n (P_j - C_j) \frac{\partial G_j}{\partial S_i}. \quad (4')$$

This has a straightforward interpretation. The left-hand side expresses the rate of return on investing the rent of harvesting an additional unit of species i . The right-hand side expresses the rate of return on leaving a unit of species i in the sea. The first term expresses the cost savings from being able to harvest from a larger fish stock. The second term is a sum of changes in the growth rate of all species resulting from augmenting the stock of species i , evaluated at the net price of fish. The changes in the growth rates are equivalent to the changes in steady-state catch rates, so that the second term on the right-hand side amounts to the value, net of costs, of the change in catches of all species resulting from changing the stock of species i . Equation (4') thus expresses equivalence between two investment opportunities, investing the rent of catching an additional fish, or leaving it in the sea for the purpose of reducing fishing costs and increasing steady-state catches.

¹This implies that costs are linearly related to fishing effort and that no crowding effects are present, so that the catchability coefficient is either constant or a function of the fish stock only. As is clear from the context, we are implicitly assuming perfectly selective fisheries in terms of species.

²Economically meaningful solutions imply nonnegativity of the quantities S_i and $G_i - \dot{S}_i$. We have omitted the more cumbersome formulation where these nonnegativity constraints are explicitly taken into account, since we shall be interested in these only as borderline cases.

3. A LOTKA-VOLTERRA MODEL OF ECOLOGICALLY INTERDEPENDENT FISHERIES

It appears that nothing very definite can be said about the management of ecologically interdependent fisheries on the basis of so general a model as the one in the preceding section. For the purpose of further analysis we shall therefore use a modified version of the Lotka-Volterra equations. A two species predator-prey model will be considered, but what we first and foremost have in mind is the transfer of biomass between levels in the food chain. We shall, for convenience, refer to these as prey and predator species, but the results may also be interpreted in terms of partial predator-prey models.

The Lotka-Volterra equations in the two-species case are³

$$\begin{aligned} G_1 &= a_1 S_1 - b_1 S_1^2 + d_1 S_1 S_2, \\ G_2 &= a_2 S_2 - b_2 S_2^2 + d_2 S_1 S_2, \end{aligned} \quad (5)$$

where a_i , b_i , and d_i are parameters. The d_i 's reflect the ecological interdependence between species, so if 1 is the lower trophic level, then $d_1 < 0$ while $d_2 > 0$. The parameter a_1 reflects the maximum relative growth rate of biomass at the lower trophic level. This will only be attained when there is no predation and the biomass approaches zero. The parameter a_2 is zero when Eqs. (5) are used for describing the growth of biomass at different levels in the food chain, but would in a partial predator-prey model be associated with other sources of food than the particular prey species being considered. The self-limiting terms $b_i S_i^2$ could depend upon a variety of factors, the outcome of which is that the maintenance needs of the biomass grow faster than the ability to acquire food as the biomass increases. For the prey species the self-limiting term would also reflect a negative feedback from its food supply, except when the prey consists of phytoplankton utilizing the flow of solar energy.

The term $d_1 S_1 S_2$ shows the loss of biomass of the prey species due to predation. This loss increases proportionally with the biomass of both species, which implies that predation is a random process and that neither saturation nor disability of predators occurs at extreme levels of food intake. The term $d_2 S_1 S_2$ shows how much

³These equations were used by Larkin [6] in a predator-prey model. The classical Lotka-Volterra equations are, in our notation,

$$\begin{aligned} G_1 &= a_1 S_1 + d_1 S_1 S_2, & d_1 < 0, \\ G_2 &= -b_2 S_2 + d_2 S_1 S_2, & d_2 > 0. \end{aligned}$$

The difference between these and Eqs. (5) is that the latter are capable of producing a stable equilibrium, while the system described by the classical Lotka-Volterra equations oscillates. Furthermore, growth of both populations in Eq. (5) is self-limiting (via $b_i S_i^2$). This is not the case in the classical Lotka-Volterra system, in which an elimination of the predator causes the prey population to explode, and the growth of the predator is limited only by the negative feedback from the prey population. Alternative amendments of the Lotka-Volterra model that also produce a stable equilibrium are possible, see, e.g., [8]. Some mathematical properties of the Lotka-Volterra model have been considered by Samuelson [12, 13]. See also Clark [2] and May [7].

TABLE I
Assumed Values of the Parameters of $G_i = a_i S_i - b_i S_i^2 + d_i S_i S_j$

	a_i	b_i	d_i	\bar{S}_i	S_i^{\max}
Level 1	1	10^{-2}	-5×10^{-2}	50	100
Level 2	0	5×10^{-2}	10^{-2}	10	10

the predator's food intake adds to its biomass, and so the predator's food conversion efficiency is $-d_2/d_1$.

Table I shows the values which we have assigned to the coefficients a_i , b_i , and d_i for use in calculations below. These values have been chosen so as to represent reasonable values of standing biomass and transfer efficiencies in the food chain.⁴ The implied food conversion efficiency of the predator species is 0.2. Various definitions of transfer efficiency in the food chain can be found in the literature.⁵ One of particular interest to us is the "ecological efficiency," which is defined as the amount of biomass removed from a particular level in the food chain, divided by the amount of biomass removed from the level below. This shows, for example, how much of the predator's food intake ends up as harvestable biomass. The ecological efficiency (EE) of the predator species in Eq. (5) is

$$EE_2 \equiv G_2 / -d_1 S_1 S_2 = -d_2 / d_1 + b_2 S_2 / d_1 S_1,$$

which is a decreasing function of the predator's biomass (note that $d_1 < 0$), the upper limit being set by the food conversion efficiency of the predator. For example, reducing the predator stock to one-half its natural equilibrium level, while leaving the prey species unexploited would give $S_1 = 75$ and $S_2 = 5$ as equilibrium values and increase the ecological efficiency of the predator from zero to 0.13, or a bit more than halfway towards its maximum value.

Since optimal exploitation of the food chain implies obtaining as valuable a product as possible and a loss of biomass is involved at every step in the chain, one might expect that harvesting ought to take place as far down as possible, except when the products obtained at higher levels are much more valuable than those further down. However, there are three nonlinearities that could modify this conclusion, implying that harvesting ought to take place at different levels in the food chain simultaneously. First, the rate of substitution between products obtained at different levels in the chain need not be constant. Second, costs per unit of biomass harvested at each level will probably increase as the biomass is depleted. Third, the ecological efficiency at each level is not constant. Here we shall deal only with the

⁴It may also be noted that the coefficients in Table I result in a stable system. The condition for stability is that the matrix $D + D^T$ be negative semidefinite, D being

$$\begin{bmatrix} -b_1 & d_1 \\ d_2 & -b_2 \end{bmatrix}$$

cf. D. G. Luenberger, "Introduction to Dynamic Systems," p. 375. Wiley, New York (1979).

⁵On different measures of transfer efficiency in the food chain, see [3] and [10].

latter two effects, as these would seem to distinguish the fishery from animal husbandry.

4. OPTIMAL EXPLOITATION IN THE LOTKA-VOLTERRA MODEL

For the purpose of applying Eq. (4') to the Lotka-Volterra model we need to consider how the cost per unit of fish caught is related to the size of the exploited fish stock. We shall assume, for simplicity, that the catchability coefficient (k) is constant. This leads to the following expression for the cost per unit of fish caught

$$C_i = \bar{c}E_i/k_iE_iS_i = \bar{c}/k_iS_i, \quad (6)$$

where E_i is fishing effort at trophic level i and \bar{c} is the cost per unit of effort. Using Eqs. (5) and (6), the maximum condition (4') becomes

$$\begin{aligned} r(P_i - \bar{c}/k_iS_i) &= (\bar{c}/k_iS_i^2)[a_iS_i - b_iS_i^2 + d_iS_iS_j] \\ &+ (P_i - \bar{c}/k_iS_i)[a_i - 2b_iS_i + d_iS_j] + (P_j - \bar{c}/k_jS_j)d_jS_j; \\ & \quad i, j = 1, 2. \end{aligned} \quad (7)$$

This condition is necessary and sufficient for maximum if the functional (3) is concave in S_i and S_j at any t . The value (V) of the integrand at time t along a steady-state trajectory is, inserting (5) and (6),

$$V = \sum_{i=1}^2 (P_i - \bar{c}/k_iS_i)[a_iS_i - b_iS_i^2 + d_iS_iS_j]e^{-rt}; \quad i, j = 1, 2. \quad (8)$$

Concavity of V implies that the matrix of second derivatives of V with respect to S_i be negative semidefinite. Evaluating the principal minors of this matrix gives the following conditions for concavity of V

$$4b_1b_2P_1P_2 > (P_1d_1 + P_2d_2)^2, \quad (9a)$$

$$-2b_iP_i \leq 0; \quad i = 1, 2. \quad (9b)$$

Since $b_i > 0$, (9b) will always be satisfied. The inequality sign in (9a) will be reversed if either P_i is high enough, but as will be shown below, (9a) is satisfied by all solutions involving exploitation of both species, as long as either r or \bar{c} equals zero.

Solving (7) for S_i gives the following nonlinear system of equations

$$S_i^2 + S_i \left[\frac{r - a_i}{2b_i} + \frac{\bar{c}}{2P_i} \left(\frac{d_j}{k_jb_i} - \frac{1}{k_i} \right) - \frac{P_id_i + P_jd_j}{2P_ib_i} S_j \right] = r\bar{c}; \quad i, j = 1, 2. \quad (10)$$

5. COSTLESS HARVESTING WITH NO DISCOUNTING

First we consider the case where $\bar{c} = 0$ and $r = 0$. Equation (10) then simplifies to⁶

$$S_1 = \frac{a_1}{2b_1} + \frac{d_1 + pd_2}{2b_1} S_2, \quad (11a)$$

$$S_2 = \frac{a_2}{2b_2} + \frac{d_1 + pd_2}{2pb_2} S_1, \quad (11b)$$

where we have normalized prices by setting $p = P_2/P_1$. These equations are represented by straight lines in the S_1, S_2 plane, as shown in Fig. 1. Letting S_2 be represented on the vertical axis, Eq. (9) implies that the line representing Eq. (11a) will always be steeper than the other.

What are the price limits within which both species will be exploited simultaneously? The lower limit, at which the value of the predator species is so low that it had better be eliminated altogether, is reached when the lines in Fig. 1 intersect on the horizontal axis. When $a_2 = 0$, as assumed in Table I, this occurs when the slope of line (11b) becomes zero. This implies $p = -d_1/d_2$. Multiplying d_1 and d_2 by $S_1 S_2$ and rewriting slightly gives

$$-P_1 d_1 S_1 S_2 = P_2 d_2 S_1 S_2, \quad (12)$$

which is easy to interpret. On the left-hand side we have the value of prey biomass eaten by the predator (cf. Eq. (5)). On the right-hand side we have the value of the growth in predator biomass resulting from this food intake. Therefore, when the price of the predator is so low that the prey biomass does not increase in value by being "processed" by the predator, the latter should be eliminated and harvesting should concentrate on the lower level in the food chain. Using the values in Table I we find that $p = 5$.

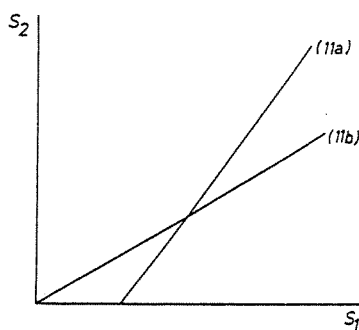


FIG. 1. Optimum biomass of prey (S_1) and predator (S_2).

⁶When $r = 0$ the integral in (3) does not converge. The objective in this case becomes one of maximizing the steady-state flow of rent, since this will always prevail over whatever transitory gains one may be able to obtain. The objective function thus becomes identical to Eq. (8). The maximum conditions are the same as (4') with $r = 0$.

The upper price limit is reached when direct harvesting of the prey ceases altogether because a more valuable product is obtained by indirect harvesting via the predator. This we may find as follows. Equilibrium without any harvesting of the prey species implies $G_1 = 0$, while the predator should be harvested so as to give maximum sustainable yield. Using $G_1 = 0$ to find S_1 as a function of S_2 (Eq. 5), substituting into G_2 , and setting $dG_2/dS_2 = 0$ gives $S_1 = 75$ and $S_2 = 5$ as equilibrium values. Using Eq. (11) we find $p = 15$, which satisfies Eq. (7).

In this special case of costless harvesting and no discounting of the future the optimal solution implies that no change in the value of sustainable biomass yield can be obtained from a marginal adjustment of the standing stock of either species. This follows from (4'), which in this special case is reduced to

$$P_i(\partial G_i/\partial S_i) + P_j(\partial G_j/\partial S_i) = 0$$

Why does not the relative price $p = 5$ constitute a clear dividing line between harvesting only the predator or the prey? As noted above, the food conversion efficiency of the predator is 20%. Therefore, when the price of the predator fish is more than five times that of the prey, the predator converts the prey biomass to a more valuable product. But food conversion efficiency represents an upper limit to the ecological efficiency of the predator. This upper limit is approached only as the predator biomass approaches zero and its "maintenance needs" vanish. But a zero standing stock yields nothing, and so harvesting the prey indirectly implies $S_2 > 0$, which reduces the ecological efficiency of the predator below its maximum theoretical level.

6. OPTIMAL EXPLOITATION WITH HARVESTING COSTS. THE CASE OF OPTIMAL SUBSIDIES

For $\bar{c} > 0$, Eq. (10) can still be simplified as above, as long as $r = 0$. Solving for S_i gives

$$S_i = \frac{2a_i b_j P_i P_j + 2\bar{c} b_j P_j (b_i/k_i - d_j/k_j) + (P_i d_i + P_j d_j) [a_j P_j + \bar{c} b_j/k_j - \bar{c} d_i/k_i]}{4b_i b_j P_i P_j - (P_i d_i + P_j d_j)^2} \quad (13)$$

Note that, as either P_i is increased such that both sides of (9a) become equal, the denominator in (13) becomes zero. Since the ecosystem cannot support infinite populations, (9a) will be satisfied by all solutions involving exploitation of both species.

As Eq. (13) is homogeneous of degree zero in P_1 , P_2 , and \bar{c} , we normalize and set $\bar{c} = 1$. This leaves us with two relative prices that determine the optimum. The availability coefficients k_1 and k_2 are potentially important determinants of the pattern of exploitation; as the ratio k_2/k_1 increases, the predator becomes cheaper to obtain, compared to the prey. We shall not pursue this question further here and set both k_i 's equal to one.

With $\bar{c} > 0$, what is the price range within which both species ought to be exploited simultaneously? For $r = 0$, Eq. (7) becomes

$$P_i(a_i - 2b_iS_i + d_iS_j) + \bar{c}(b_i - d_j) + P_jd_jS_j = 0; \quad i, j = 1, 2; \quad i \neq j. \quad (7')$$

For $S_2 = 0$ ($i = 2$) this implies $-(P_1d_1S_1 - \bar{c}d_1) = P_2d_2S_1 + \bar{c}b_2$. Multiplying on both sides by S_2 gives

$$-(P_1 - \bar{c}/S_1)d_1S_1S_2 = P_2d_2S_1S_2 + \bar{c}b_2S_2. \quad (14)$$

The interpretation of this is perhaps not as obvious as that of its counterpart in the costless case (Eq. 12), but runs along similar lines. On the left-hand side we still have the amount of prey biomass eaten by the predator, but evaluated net of harvesting costs. The first term on the right-hand side represents the gross value of the predator biomass to which the said food intake is converted. The last term on the right-hand side represents the reduction in harvesting costs resulting from increasing the predator stock from zero to a "small" S_2 . The total cost of harvesting the predator is C_2G_2 , which by Eqs. (5) and (6) is $\bar{c}(a_2 - b_2S_2 + d_2S_1)$, and so $-\bar{c}b_2$ is marginal cost with respect to S_2 . Equation (14) thus says that the predator stock should be eliminated when the net value of the prey biomass that it consumes is equal to the contribution of this food intake to the value of the predator stock plus the cost of eliminating the predator.

Since there are two relative prices that matter when $\bar{c} > 0$, the number of price limits within which both species should be harvested is infinite. Table II provides two examples. The price range within which both species ought to be exploited is of a similar magnitude as in the costless case above.

When there are harvesting costs to be accounted for, one may ask whether it might be desirable to subsidize the exploitation of predators to encourage depletion of these beyond that which an open-access fishery would bring about. The answer is affirmative; it might. Figure 2 shows how the optimal standing biomass of the two species varies with their prices. Note in particular that the optimum standing stock of the predator varies directly with its price, as long as both species are exploited. This is contrary to single-species theory where the optimum standing stock varies inversely with the price of fish. Figure 2 also shows the rent per unit of fish caught. By Eq. (6), this equals $P_i - 1/S_i$ for $\bar{c} = 1$ and $k_i = 1$. This is equal to the tax per unit of fish caught that would keep a free-access fishery in equilibrium at the optimal level of biomass. Note in particular the diagrams on the right-hand side, in which the optimal tax of predator landings is shown. If the price of predator fish

TABLE II
Price Range within which Both Species are Exploited Simultaneously ($\bar{c} = 1$)

Case I: $P_1 = 0.1$	Case II: $P_2 = 1$
$0.30 \leq P_2 \leq 1.36$	$0.076 \leq P_1 \leq 0.240$
$50 \leq S_1 \leq 73.02$	$72.38 \geq S_1 \geq 50$
$0 \leq S_2 \leq 5.35$	$5.49 \geq S_2 \geq 0$

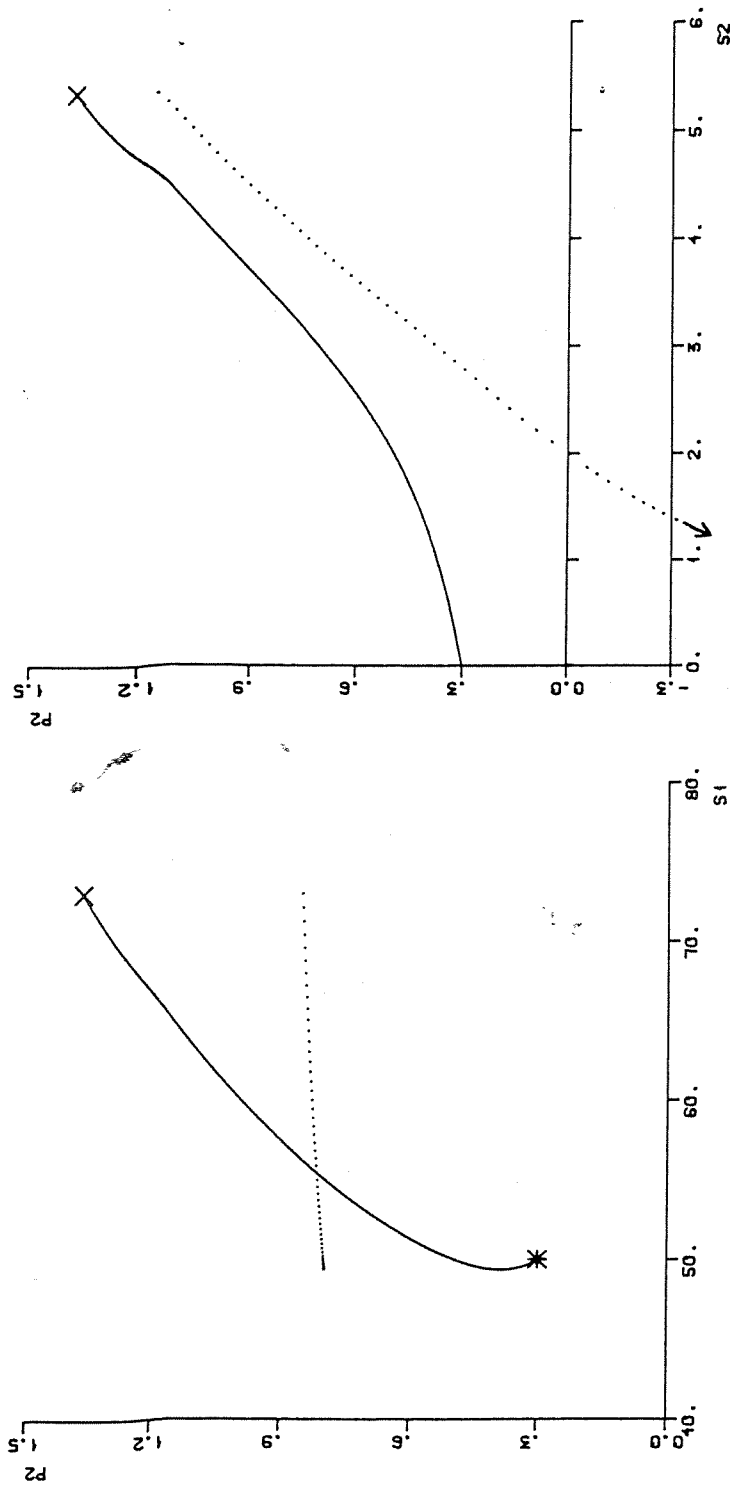


FIG. 2a. Optimum biomass of prey (S_1) and predator (S_2) as functions of predator price. Points (x) show where exploitation of prey ceases, point (*) where predator becomes extinct. Dotted lines show optimum tax per unit harvested ($P_1 - 1/S_1$), in the left half multiplied by 10. $P_1 = 0.1$.

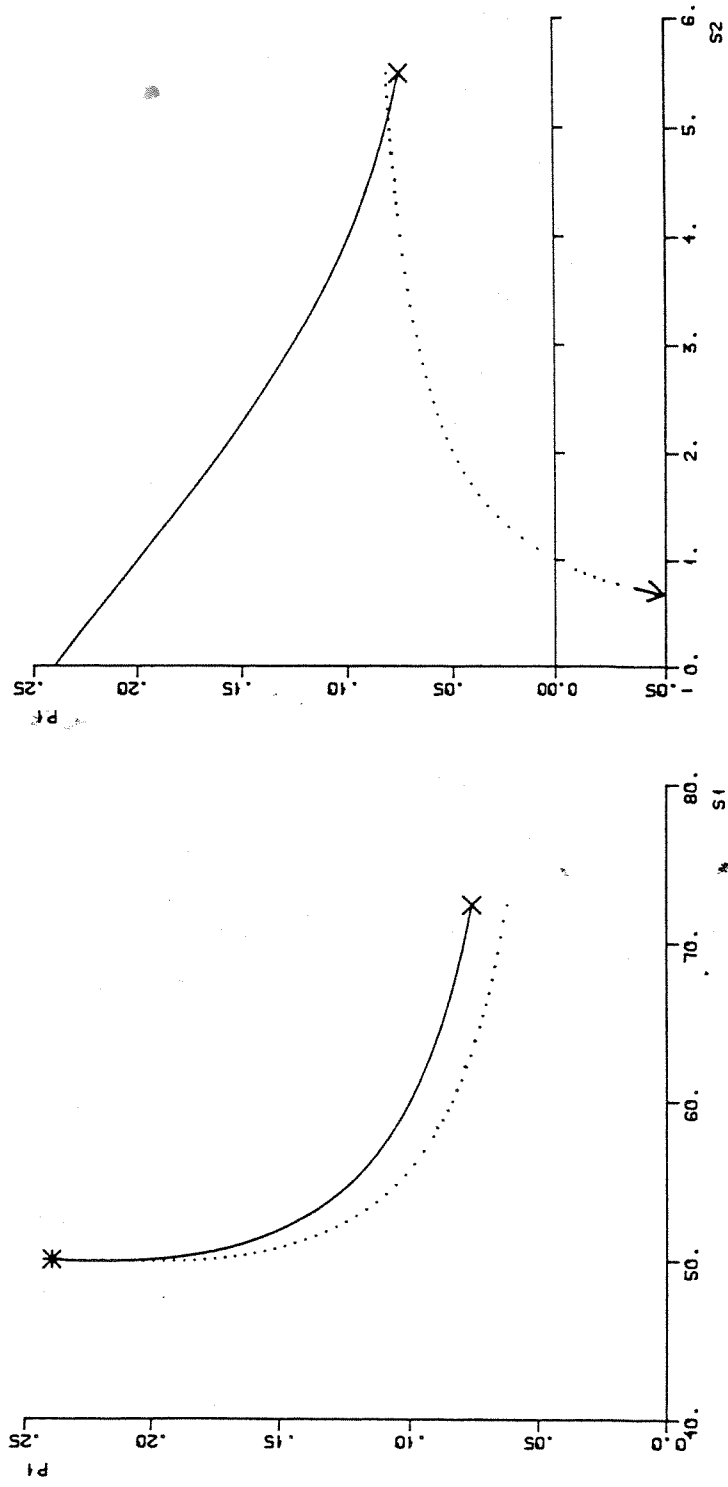


FIG. 2b. Optimum biomass of prey (S_1) and predator (S_2) as functions of prey price. Points (x) show where exploitation of prey ceases, point (*) where predator becomes extinct. Dotted lines show optimum tax per unit harvested ($P_1 - 1/S_1$), in the right half divided by 10. $P_1 = 1$.

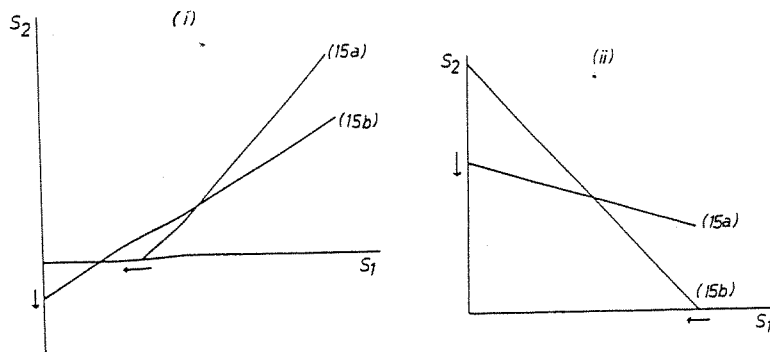


FIG. 3. Impact of discounting on optimum biomass of prey (S_1) and predator (S_2). Case (i): "efficient predator," case (ii): "inefficient predator."

falls below a certain level the harvesting of predators should be encouraged by subsidies in order to increase the harvesting potential of the prey species. Regulatory efforts in this vein have indeed been practiced for a long time, albeit not in fisheries, as bounties for killing predators of domesticated animals. Seal hunting and whaling are obvious cases where subsidies of this kind might be called for.

The optimal response of fishing effort to changes in the price of fish is for the most part in the opposite direction to the change in the standing stock. Setting the rate of surplus production (Eq. (5)) equal to the catch rate, which is $E_i k_i S_i$ (cf. Eq. (6)), gives

$$E_i = a_i - b_i S_i + d_i S_j.$$

As shown in Fig. 2, S_2 increases with P_2 (when both species are exploited) while S_1 decreases for the most part. The optimal effort devoted to the predator species (E_2) will therefore vary inversely with the price of this fish. This is also at variance with the standard result in single-species theory.

7. THE IMPACT OF THE DISCOUNT RATE ON THE OPTIMAL LEVEL OF FISH STOCKS: COSTLESS HARVESTING

The easiest case for which to analyze the impact of the discount rate on the optimal level of fish stocks is the one where there are no harvesting costs.⁷ We consider this first. With $\bar{c} = 0$ but $r > 0$ we get, instead of Eqs. (11),

$$S_1 = \frac{a_1 - r}{2b_1} + \frac{(d_1 + pd_2)}{2b_1} S_2, \quad (15a)$$

$$S_2 = \frac{a_2 - r}{2b_2} + \frac{(d_1 + pd_2)}{2pb_2} S_1. \quad (15b)$$

These equations are represented by the lines in Fig. 3. The only difference between

⁷This analysis holds as well for the more general case in which the cost per unit harvested is independent of the stock size. P then denotes price net of harvesting cost per unit.

these and the lines in Fig. 1 is the intercept with the axes, which is affected by an increasing r as shown by arrows.⁸ For the purpose of discussion, it is convenient to distinguish between two cases, depicted by the two panels of Fig. 3.

Case (i): $d_1 + pd_2 > 0$

Here the predator is an efficient converter of biomass in terms of value (cf. Sect. 5), and the lines representing Eqs. (15) have a positive slope. More forceful discounting of the future unambiguously reduces the optimal standing stock of both species. Which species is the most vulnerable candidate for "optimal elimination" depends on which line will be the first one to pass through the origin as the discount rate rises. This in turn depends on the relative size of the a_i 's. If $a_2 < a_1$, the line representing Eq. (15b) will be the first to pass through the origin, so that the predator will be eliminated before the prey. This is certainly the case in our model, as we have assumed $a_2 = 0$. In more partial predator-prey models where species 1 is not the only source of food for species 2 it is possible that $a_2 > a_1$, calling for an elimination of the prey species before the predator species.

Case (ii): $d_1 + pd_2 < 0$

In this case both lines representing Eqs. (15) have a negative slope. This case is of interest only in partial predator-prey models, as the line representing Eq. (15b) must have a positive intercept with the S_2 axis if any optimum with a positive standing stock of both species is to be obtained. As explained in Section 5, the predator would in this case be an inefficient converter of prey biomass, in terms of value. The justification for nevertheless maintaining the predator stock is then to be sought in its utilization of other sources of food, expressed by $a_2 > 0$. In this case the impact of a higher discount rate on the optimal standing stock is ambiguous; by studying the displacement of the lines in Fig. 3 it is clear that the optimal biomass of one species may increase with r . A sufficiently high r is however capable of reducing the optimal standing stock of both species to zero.

The conditions for optimal elimination of a species are a variation on a well-known theme. A replenishable resource should be depleted if it is not capable of yielding a rate of return equal to the alternative cost of capital. By Eq. (5), the marginal rate of return on investing in the stock of species i is

$$P_i(a_i - 2b_iS_i + d_iS_j) + P_jd_jS_j,$$

and thus a decreasing function of S_i . The rate of return on harvesting one unit of species i is rP_i . Setting these rates equal to one another gives, for $S_j = 0$,

$$S_2 = \frac{r - a_1}{d_1 + pd_2} \quad (i = 1), \quad (16a)$$

$$S_1 = \frac{r - a_2}{d_1 + pd_2} \quad (i = 2). \quad (16b)$$

⁸From (15) it is easily verified that (9a) will be satisfied for all finite optimal population levels, as in the previous case.

We see that (16a) is equivalent to (15a) for $S_1 = 0$. Species 1 should thus be eliminated when its marginal rate of return falls below the alternative rate of return on capital for all $S_1 > 0$. The same holds, mutatis mutandis, for Eqs. (15b) and (16b) and species 2.⁹

8. THE IMPACT OF THE DISCOUNT RATE WHEN HARVESTING COSTS ARE NOT NEGLIGIBLE

Taking fishing costs into account introduces nonlinearities; instead of the straight lines in Fig. 3 we now get curves. To economize on notation we write Eq. (10) as

$$\begin{aligned} S_i^2 + S_i(m_i + q_i S_j) &= r\bar{c}; \quad i, j = 1, 2; \\ m_i &= \frac{r - a_i}{2b_i} + \frac{\bar{c}}{2P_i}(d_j/k_j b_i - 1/k_i); \\ q_i &= -(P_i d_i + P_j d_j)/2P_i b_i. \end{aligned} \quad (10')$$

Setting $S_j = 0$ in (10') allows us to find the intercepts of the curves representing (10') with the S_1 -axis ($i = 1$) and S_2 -axis ($i = 2$), respectively. Denoting these points by S_1^* and S_2^* we find

$$\begin{aligned} S_1^* &= -m_1/2 \pm [r\bar{c} + m_1^2/4]^{1/2}, \\ S_2^* &= -m_2/2 \pm [r\bar{c} + m_2^2/4]^{1/2}. \end{aligned}$$

There are two solutions for S_i^* , one positive and one negative. Only the positive solution is of interest, however. This we may see by looking at the shape of the curves representing Eqs. (10'). Differentiation gives

$$\begin{aligned} (dS_2/dS_1)_{i=1} &= -1/q_1 - r\bar{c}/q_1 S_1^2; \\ (dS_2/dS_1)_{i=2} &= -q_2 S_2^2 / (S_2^2 + r\bar{c}). \end{aligned} \quad (17)$$

Suppose that $S_1^* < 0$. As $S_1 \rightarrow 0$, $(dS_2/dS_1)_{i=1} \rightarrow \infty$, and the curve representing (10') cannot pass into the positive quadrant. Hence only $S_1^* > 0$ is of interest. Similarly, suppose that $S_2^* < 0$. As $S_2 \rightarrow 0$, $(dS_2/dS_1)_{i=2} \rightarrow 0$, and the curve representing (10') cannot pass into the positive quadrant. Hence only $S_2^* > 0$ is of interest. The only interesting solution of (10'), therefore, is

$$S_i = -(m_i + q_i S_j)/2 + [r\bar{c} + (m_i + q_i S_j)^2/4]^{1/2}.$$

⁹Silvert and Smith assert [14] that $a_i > r$ is a necessary condition for an optimal $S_i > 0$. This is not so. Consider case (i) in Fig. 3. It is clear that both lines can intersect in the positive quadrant even if one of them has a negative intercept with the axes, which implies $a_i < r$ for one species. In Fig. 3 we have $a_2 = 0 < r$ (case (i)). In making this assertion, Silvert and Smith may have mistaken a_i for the maximum rate of return on species i , which is correct only in single-species models.

We are now ready to consider how fishing costs displace and bend the lines in Fig. 3. From Eqs. (10'), (15), and the fact that $S_i \geq 0$ we get

$$S_1 = \frac{a_1 - r}{4b_1} - v_1 \frac{\bar{c}}{4P_1} + \frac{(P_1 d_1 + P_2 d_2)}{4P_1 b_1} S_2 + \left[r\bar{c} + \left(\frac{a_1 - r}{4b_1} - v_1 \frac{\bar{c}}{4P_1} + \frac{(P_1 d_1 + P_2 d_2)}{4P_1 b_1} S_2 \right)^2 \right]^{1/2} \geq \frac{a_1 - r}{2b_1} + \frac{(P_1 d_1 + P_2 d_2)}{2b_1} S_2, \quad (18a)$$

$$S_2 = \frac{a_2 - r}{4b_2} - v_2 \frac{\bar{c}}{4P_2} + \frac{(P_1 d_1 + P_2 d_2)}{4P_2 b_2} S_1 + \left[r\bar{c} + \left(\frac{a_2 - r}{4b_2} - v_2 \frac{\bar{c}}{4P_2} + \frac{(P_1 d_1 + P_2 d_2)}{4P_2 b_2} S_1 \right)^2 \right]^{1/2} > \frac{a_2 - r}{2b_2} + \frac{(P_1 d_1 + P_2 d_2)}{2b_2} S_1, \quad (18b)$$

$$v_1 = d_2/k_2 b_1 - 1/k_1 \geq 0, \quad (18c)$$

$$v_2 = d_1/k_1 b_2 - 1/k_2 < 0. \quad (18d)$$

By comparing Eqs. (15) and (18) we see that the shift of the line representing Eq. (15a) in Fig. 3 is ambiguous, while the line representing Eq. (15b) is shifted upwards. Suppose that $v_1 \leq 0$ (the parameters in Table I imply $v_1 = 0$). Then the line representing Eq. (15a) will be displaced to the right by $\bar{c} > 0$. From Eq. (17) we see that the line representing Eq. (15a) will become steeper for any given S_1 and the other line flatter for any given S_2 , while asymptotically they will have the same slope as before. Figure 4 shows how $\bar{c} > 0$ shifts and bends the lines in Fig. 3; in case (i) ($P_1 d_1 + P_2 d_2 > 0$) the optimal standing stock of both species will increase with \bar{c} , whereas in case (ii) the stock of one species may decrease, contrary to what obtains in single-species models.

The impact of \bar{c} on the optimal stock level is ambiguous also in case (i) when $v_1 > 0$. Why this is so deserves a short comment. From (18c) we see that the likelihood of $v_1 > 0$ increases as k_2 becomes small compared with k_1 , implying that

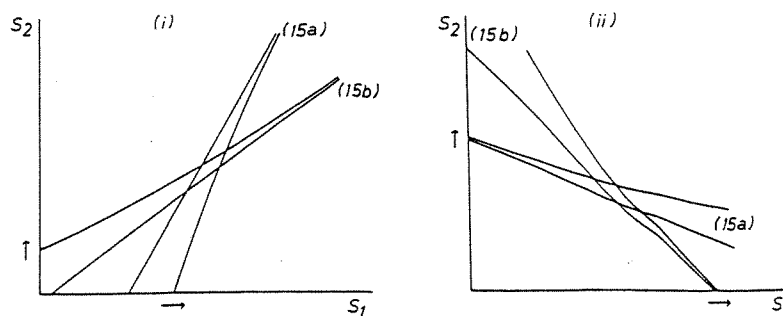


FIG. 4. Impact of harvesting cost on optimum biomass of prey (S_1) and predator (S_2). Case (i): "efficient predator," case (ii): "inefficient predator."

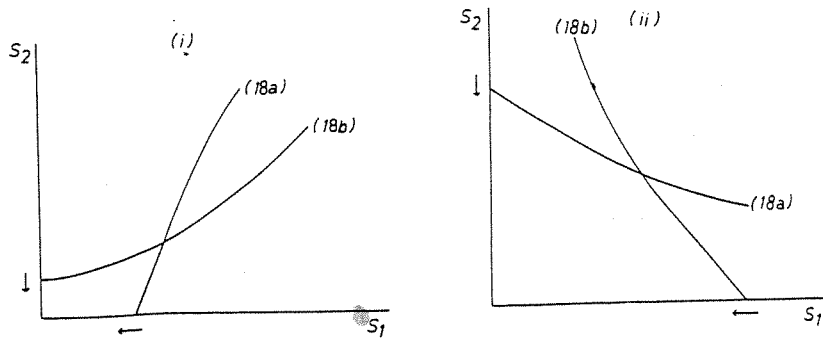


FIG. 5. Impact of discounting, at positive harvesting costs, on optimum biomass of prey (S_1) and predator (S_2). Case (i): "efficient predator," case (ii): "inefficient predator."

it becomes more costly to catch the predator compared with the prey. An increase in \bar{c} would then have a relatively large positive impact on the optimal standing stock of the predator, producing a relatively strong negative feedback effect on the optimal stock of the prey, possibly outweighing the direct positive impact of an increased \bar{c} .

The results concerning the impact of a rising discount rate that we derived for the case of zero fishing costs are, by and large, applicable for the case of nonnegligible fishing costs, but the shifts and bends of the lines in Fig. 3 are somewhat messy. Reexamining cases (i) and (ii) in Fig. 3 gives the following results, illustrated in Fig. 5. For a sufficiently large r , the intercepts of the lines representing Eq. (18) are displaced towards the origin by an increase in r .¹⁰ The slope of the line representing (18a) becomes greater, in absolute terms, for any given S_1 while that of the other line becomes less for any given S_2 (cf. Eq. (17)). In case (i) the optimal biomass of both species declines as the discount rate rises. In case (ii) we note again the possibility that the optimal level of biomass of one species increases with the discount rate,¹¹

¹⁰This may be seen as follows. Differentiating S_i partially with respect to r gives

$$\frac{\partial S_i^*}{\partial r} = -\frac{1}{4b_i} + \frac{1}{2} \left[r\bar{c} + \frac{m_i^2}{4} \right]^{-1/2} \left(\bar{c} + \frac{m_i}{4b_i} \right).$$

The right-hand side may be written as

$$(1/4b_i) \left[-1 + \frac{1}{2} \left[r\bar{c} + \frac{m_i^2}{4} \right]^{-1/2} (4\bar{c}b_i + m_i) \right].$$

As r increases, m must sooner or later become positive, and the term

$$\frac{1}{2} \left[r\bar{c} + \frac{m_i^2}{4} \right]^{-1/2} (4\bar{c}b_i + m_i)$$

will become smaller and smaller. Hence $\partial S_i^*/\partial r < 0$ for a sufficiently large r .

¹¹This happens, for example, in the borderline cases in Fig. 2 where species 2 is driven to extinction. Extinction becomes optimal at the price configurations $P_1 = 0.1$, $P_2 = 0.3$, and $P_1 = 0.24$, $P_2 = 1.0$. The quantity $(P_1d_1 + P_2d_2)$ is negative in both cases. Upon calculating the optimal biomass of the two species at these prices when $r = 0.1$, one finds that the optimal biomass of species 2 is increased from zero to 0.13 and 0.1, respectively, while the optimal level of biomass of species 1 is decreased from 50 to 44.87 and 44.99, respectively.

while that of the other species must fall. But as one species has been driven to extinction, the biomass of the other species must necessarily fall as the discount rate rises further.

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