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A Predator-Prey Model with an Application to Lake Victoria Fisheries

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Abstract *Greater complexity in renewable resource models is achieved by acknowledging that species interact through a predator-prey relationship in which both species are harvested. The price of greater complexity is that traditional concepts, such as maximum sustained yield (MSY), have to be revised dramatically. Moreover, having chosen greater complexity, fishery biologists and other researchers must choose an explicit value for each fish, a rate of exchange of one species for every other species. Policy makers and social scientists in Tanzania, Kenya, and Uganda with a keen interest in Lake Victoria fisheries regard the resource as a tool for furthering socioeconomic goals, such as foreign exchange earnings, employment for women, and nutrition. Comparative analysis allows policy makers to understand the consequences of choosing these goals in addition to economically efficient resource use. Foreign exchange earnings, employment for women, and healthy people are other goals promulgated by Tanzania, Kenya, and Uganda in the management of Lake Victoria Fisheries. The conflicts among social goals are evident in the bioeconomic predator-prey model: a goal favoring a particular species reduces the sustainable harvest of another species. Data from Kenya are used to estimate the population dynamics equations.*

Key words Predator-prey, bioeconomic model, Lake Victoria.

JEL Classification Codes Q22, Q28.

Introduction

Lake Victoria, the second largest freshwater lake in the world, supports a rich fishery that comprises hundreds of species. Two interdependent species account for more than 88% of the harvest value in a recent, representative year. They are the Nile perch (*Lates niloticus*) and dagaa (*Rastrineabola argenticia*).

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Although perch and dagaa provide quite different service flows, not surprisingly there is no discernible integrated fisheries management policy. Perch frequently have been harvested in weights exceeding 50 kilos, pass through a relatively capital-intensive process, and are principally exported to Europe. In sharp contrast, the dagaa are basically sardines that are predated by the perch and harvested by an artisanal fishery. Dagaa are marketed locally by women and provide nutrition to a markedly undernourished population (Kulindwa, Ikiara, and Kazoora 2001).

Natural scientists have studied multiple interacting species (Larkin 1966; May 1974; Pielou 1969; Maynard-Smith 1974; Mercer 1982; and Yodzis 1994) but there has been less study of multiple species in an economic optimization framework, particularly from a bioeconomic perspective. An important exception is the development of the Ecosim model (Walters, Christensen, and Pauly 1997; Pitcher and Cochrane 2002). In this model, the objective function is a weighted linear aggregation of net present value or its log, an employment goal (jobs/value landed), a population-rebuilding target, and a measure of ecological stability. Applied applications of Ecosim we have seen exhibit linear harvest costs; that is, no stock externalities, an assumption maintained in the model presented *infra*.

Multiple-species models are not generous in the analytical results produced. Clark (1990) concludes that while optimal steady-state values often can be determined, exact solutions for the optimal path to the steady state are not known and may not exist for some problems. The simpler the model, the more likely clean results will emerge. Solow's (1976) analysis of a Volterra model is insightful, but the model has no intraspecific competition; that is, natural resource capital has no diminishing returns. Still, he concludes that even in the two-species models, there are no easily obtained qualitative results resembling those gleaned from single-species models.

Wilen and Brown (1986) make some progress in characterizing the solution to a predator-prey optimization problem. Modest success comes at the cost of assuming a unidirectional-coupled system. The lower organism enhances the growth of the upper-level organism, but the predator has no effect on the prey. This assumption seems to be rather strong and is not empirically credible for the perch-dagaa population dynamics in Lake Victoria. Ragozin and Brown (1985) established the existence of a steady state and described the unique approach to it for a predator-prey system in which only the predator species is harvested. See also Kaplan and Smith (2001) for a similar formulation to handle an endangered predator.

Sumaila (1997) formulated a predator-prey model through a "numerical procedure," applied it to the cod and capelin fishery in the Barents Sea, and compared the cooperative and non-cooperative solutions. It is a multi-cohort, age-structured model with a different predator-prey structure, so comparisons with the fisheries in this study are not directly relevant. Fischer and Mirman (1992) also compare cooperative with non-cooperative solutions in an analytical model where the population dynamics of two species are characterized by Cobb-Douglas production functions.¹ Here the emphasis is on analyzing the stability of equilibrium for alternative market structures and species interaction specifications.

Finnoff and Tshchirhart (2003) have taken a novel approach in their study of predator-prey relationships. They model a food web system with energy units acquired and consumed as prices and do comparative statics with these prices. They then add a human harvester and regulator in the applied model with the focus on the

¹ There is a literature combining predator-prey relations with spatial dimensions. See Supriatna and Possingham (1999) and references cited. The conclusions drawn bear on specific spatial features of the model assumed, so comparisons with this study are not evident.

pollock fishery. Alternative steady-state pollock populations chosen create alternative steady-state populations for the seven other species in the food web.

The analytical bioeconomic model most resembling the one developed in this paper follows Hannesson (1983), who focused on the role of the discount rate in optimal solutions and on the possibilities of extinction. Alternatively, this study focuses on the roles prices have on optimal solutions (Brown, Berger, and Ikiara 2005). This is because policy makers often pursue one or more non-efficiency objectives without understanding the more subtle ramifications of market distorting policies, which are distinct from the efficiency losses generated by the policies. Harvested perch pass through a relatively capital-intensive preparation process and are principally exported to Europe. Perch sales produce foreign exchange, a highly desired objective by those who can use instruments like export subsidies to distort the price of perch. However, there is a feedback mechanism in the predator-prey model that can cause the steady-state harvest of dagaa to decrease when the price of perch increases. Dagaa are less capital intensive and a key component of artisanal communities. Additionally, dagaa provide nutrition to a population with substantial food deficiency.

Under what bioeconomic conditions in a predator-prey model does the promulgation of one goal achieved by increasing harvest of one species (*e.g.*, increased foreign exchange earnings) cause a diminution in other socio-political success indicators related to the decrease in the harvest (increased price) of the other species? This study addresses this question by developing a dynamic model for an actual fishery. In addition, this paper further contributes to the predator-prey literature by deriving comparative equilibrium static results for all the biological and economic parameters. After computing optimal solutions, we estimate the private opportunity cost harvesters would forgo during a recovery period to achieve the socially optimal level of stocks and harvests for each species.

The Model

Perch (predator) population dynamics follows the Lotka-Volterra formulation:

$$\frac{dR}{dt} = \dot{R} = f(R) - h_1 + RD, \quad (1.1)$$

$$f(R) > 0 \text{ for } R < R_{msy}, f(R)|_{R=R_{msy}} = 0,$$

where R = the stock of perch at time t ; time subscripts are suppressed, h_1 = harvest of perch, D = the stock of dagaa, and MSY = maximum sustained yield (single stock definition).

The dagaa enter the perch population dynamics linearly. D is the effect of a unit change in dagaa on the percent growth rate of perch. Obviously, linear interaction terms between predator and prey are not the only way to characterize multi-species population dynamics but are quite common.²

² Biologists using linear interaction terms in predator-prey models include Larkin (1966) and May (1974). Clark (1990) cites and uses the Lotka and Volterra equations in his analysis of predator-prey dynamics. See also Hilborn and Walters (1992) and Walters (1986). Walters (1986) shows that in a purely biological model with no harvester behavioral response functions "an apparently minor change in functional assumptions, such as the possibility of predator-satiation of prey, leads to qualitatively different predictions" (p. 99).

Assuming the underlying population dynamics for the perch is logistic:

$$\dot{R} = r_1 R \left(1 - \frac{R}{\bar{R}} \right) - h_1 + RD, \tag{1.2}$$

where r_1 = the intrinsic rate of growth for the perch, and \bar{R} = the carrying capacity for the perch (single-stock definition). The logistic is introduced for illustrative purposes, but both biological and economic reasoning require any candidate growth function to exhibit diminishing returns.

Dagaa (prey) population dynamics are specified as:

$$\begin{aligned} \frac{dD}{dt} &= \dot{D} = g(D) - h_2 - DR, \tag{2.1} \\ \frac{dg}{dD} &> 0 \text{ for } D < D_{msy}, \quad \left. \frac{dg}{dD} \right|_{D=D_{msy}} = 0, \end{aligned}$$

where h_2 = harvest of dagaa.

Adopting the logistic form again:

$$\dot{D} = r_2 D \left(1 - \frac{D}{\bar{D}} \right) - h_2 - DR, \tag{2.2}$$

where α is a measure of the attack rate or searching efficiency of the predator. The parameters α and β are referred to as “mass action” terms. The populations interact randomly in proportion to population density as in random contacts in chemical reactions. The linear term in equation (1.2) can be written as βRD , where $\beta = (\alpha / \bar{R})$. β is a measure of how efficiently prey are converted into predator biomass. In this primitive model, it is assumed that the marginal cost of harvest is constant (perhaps 0), independent of population size. The goal in the introductory model is to maximize the present value of profit (II):

$$= \int_0^{\infty} e^{-\rho t} [P_1 h_1 + P_2 h_2] dt,$$

where ρ = the discount rate and P_i = the unit profit of harvested fish, $i = 1$ (perch), 2 (dagaa).

It is understood that harvest cannot exceed a certain maximum:

$$\begin{aligned} 0 &\leq h_1 \leq h_{1\max} \\ 0 &\leq h_2 \leq h_{2\max}, \end{aligned}$$

at any moment, an assumption made for mathematical convenience.

Forming the current value Hamiltonian for the simple maximization problem:

$$H = P_1 h_1 + P_2 h_2 + \lambda_1 [f(R) - h_1 + RD] + \lambda_2 [g(D) - h_2 - DR], \tag{3}$$

with λ_1 and λ_2 the adjoint variables for equations (1.1) and (2.1).

For a maximum of H, either we use the following bang bang controls:

$$h_1 = 0 \text{ if } \lambda_1 > P_1, \tag{3.1}$$

$$h_1 = h_{1\max} \text{ if } \lambda_1 < P_1, \tag{3.2}$$

$$h_2 = 0 \text{ if } \lambda_2 > P_2, \tag{3.2}$$

$$h_2 = h_{2\max} \text{ if } \lambda_2 < P_2, \tag{3.2}$$

or singular controls when:

$$\lambda_1 = P_1, \tag{3.3}$$

$$\lambda_2 = P_2. \tag{3.4}$$

The adjoint equations are:

$$\dot{\lambda}_1 - \lambda_1 = -\lambda_1 [f(R) + D] + \lambda_2 D, \tag{4.1}$$

$$\dot{\lambda}_2 - \lambda_2 = -\lambda_2 [g(D) - R] - \lambda_1 R. \tag{4.2}$$

In a steady-state interior equilibrium, from equations (4.1), (4.2), (3.3), and (3.4):

$$= f(R) + D - \frac{P_2}{P_1} D, \tag{5.1}$$

$$= g(D) - R + \frac{P_1}{P_2} R. \tag{5.2}$$

In equilibrium, according to the right-hand side of equations (5.1) and (5.2), the *real* marginal rate of return on each species has to earn the market rate of return (r).

It will be useful in subsequent analysis to rewrite equations (5.1) and (5.2) as:

$$= f(R) + (P_1 - P_2) \frac{D}{P_1}, \tag{5.1g}$$

$$= g(D) + (P_1 - P_2) \frac{R}{P_2}. \tag{5.2g}$$

The terms to the right of $f(R)$ and $g(D)$ arise from the predator-prey relation and can be thought of as a biological technical externality. These additional terms vanish when the species' interaction coefficients are equal to zero. Just as the traditional stock externality (unit harvest cost falls as stock increases) has economic parameters, so too does the technical externality with the common terms, $P_1 - P_2$, in

each equation. When $P_1 - P_2 > 0$, the technical externality is positive, meaning that both optimal steady-state perch and dagaa stocks are larger than for a model with independent stocks ($\lambda = 0$).

To further understand the biological technical externality, rewrite the inequality as $P_1(\lambda) = P_1 > P_2$. The left-hand side is the value of the marginal product of dagaa converted into perch. The right-hand side is the marginal cost of dagaa. When the biological technical externality is an equality, we then have the equilibrium condition for efficient factor use. When the inequality holds, the positive technical externality drives up both stocks. Moreover, it can be seen that the more inefficiently dagaa are converted into perch, the more valuable perch must be relative to dagaa for the inequality condition to hold.

Note that the technical externality is increasing in P_1 and decreasing as P_2 increases. For future reference, when:

$$\frac{P_1 - P_2}{P_2} > 0,$$

an increase in the price of dagaa (P_2) makes $P_1 - P_2$ smaller and contributes to reducing the optimal dagaa stock as a result of an increase in the price of dagaa.

Rewrite equation (4.1) for $\lambda = 0$ as:

$$\lambda_1 = \frac{\lambda_1 [f(R) + D] - \lambda_2 D}{\dots} \tag{6}$$

If the figurative owner of perch sells a unit for harvest, the rental rate of λ_1 is earned. The owner bears two future changes in perpetuity so they are capitalized by λ_1 . First is the marginal contribution of that fish to the fishery whose unit economic value is λ_1 . Second, reducing the perch stock by one unit increases the marginal productivity of dagaa by D , which is valued at its shadow value of λ_2 each period to the owner of the prey. Thus the owner of perch, in this case society in general, would gain $(\lambda_2 D)/\lambda_1$ by the diminution of perch by one unit. A parallel interpretation is obtained by rewriting the equilibrium condition for dagaa (equation 4.2).

Using the specific functional forms for the population dynamics in equations (1.2) and (2.2) in combination with equations (4.1) and (4.2) in steady state yields:

$$R = \frac{\bar{R}}{2} \left(1 - \frac{1}{r_1} \right) + \frac{\bar{R}D}{2r_1} \frac{P_1 - P_2}{P_1}, \tag{7.1}$$

$$D = \frac{\bar{D}}{2} \left(1 - \frac{1}{r_2} \right) + \frac{\bar{D}R}{2r_2} \frac{P_1 - P_2}{P_2}. \tag{7.2}$$

Equations (7.1) and (7.2) illustrate that the perch steady-state population (R) is a linear and positive function of dagaa (D), and the steady-state population of dagaa is a linear and positive function of perch, for $P_1 - P_2 > 0$.

Solving the two equations yields:

$$D^* = \frac{\bar{D} [2(r_2 - 1)r_1 P_2 + \bar{R} (P_1 - P_2)(r_1 - 1)]}{4r_1 r_2 P_2 - \bar{D}\bar{R} (P_1 - P_2)^2 P_1^{-1}}, \tag{8.1}$$

$$R^* = \frac{\bar{R}[2(r_1 - r_2)P_1 + \bar{D}(P_1 - P_2)(r_2 - r_1)]}{4r_1r_2P_1 - \bar{D}\bar{R}(P_1 - P_2)^2P_2^{-1}} \tag{8.2}$$

A sufficient condition for D^* and R^* to be optimal is for the denominators in equations (8.1) and (8.2) to be positive.

It will be useful to determine maximum sustained yield (MSY) for perch and daga. This is not a trivial determination since R_{msy} and D_{msy} are not independent. R_{msy} is not a single value but is a function of D . D_{msy} is a function of R and the analyst must choose weights which identify the importance of one species relative to the other in the maximization procedure in order to obtain a unique solution for R_{msy} and D_{msy} (Appendix 1). The solutions are based on maximizing total revenue, holding prices of the two species constant. This is in contrast to studies by Beddington and May (1980) and Flaaten (1991), who maximized the steady-state harvest of one species subject to the constraint that the harvest of the other stock equals its growth. The solutions from these early studies yield a production transformation function, which hides the quandary biologists, ecologists, and others are put in when a truly dependent multi-species fishery is considered. Now, to paraphrase Silvert (1982), biologists studying multispecies fisheries must recognize that there is a tradeoff between species. In this study, assuming that the harvest of each stock is weighted by its price, then:

$$R_{msy} = \frac{\bar{R}[2r_1r_2P_1 + \bar{D}r_2(P_1 - P_2)]}{4r_1r_2P_1 - \bar{D}\bar{R}(P_1 - P_2)^2P_2^{-1}} \tag{9.1}$$

$$D_{msy} = \frac{\bar{D}[2r_2r_1P_2 + \bar{R}r_1(P_1 - P_2)]}{4r_1r_2P_2 - \bar{D}\bar{R}(P_1 - P_2)^2P_1^{-1}} \tag{9.2}$$

The solutions to the MSY problems are just the equilibrium levels for $r = 0$. That is, $R_{msy} = R^*$ and $D_{msy} = D^*$ when the discount rate is zero. Moreover, the optimal levels of perch and daga are below MSY levels whenever (i) $P_1 - P_2 > 0$ and (ii) $r_1, r_2 > 0$. It is reasonable to assume that $r_1 > r_2$; the intrinsic rate of growth for each species is greater than the discount rate for the general case. If this is not true, then in the traditional "lumped parameter" model, with no stock externalities, when the predator-prey interaction term explicitly has been omitted, it would pay to extinguish the species because they are relatively unproductive capital. At no population level is the real rate of return greater than the return on other forms of capital. However, note from equation (5.1) or (5.2) that a positive R^* and a D^* is feasible with $r_2 < r_1$ as long as $P_1 - P_2 > 0$. Then:

$$R_{msy} - R^* = \frac{\bar{R}[2r_2P_1 + \bar{D}(P_1 - P_2)]}{4r_1r_2P_1 - \bar{D}\bar{R}(P_1 - P_2)^2P_2^{-1}} > 0, \tag{10.1}$$

$$D_{msy} - D^* = \frac{\bar{D}[2r_1P_2 + \bar{R}(P_1 - P_2)]}{4r_1r_2P_2 - \bar{D}\bar{R}(P_1 - P_2)^2P_1^{-1}} > 0. \tag{10.2}$$

³ MSY is a traditional goal in fisheries management advocated by fisheries biologists. For example, MSY is the benchmark for deciding whether a stock is overfished in the United States (Magnuson Stevens Act 1996). Management plans for every US fishery must include an assessment of MSY.

When conditions (i) and (ii) hold, positive D^* and R^* require positive denominators in equations (8.1) and (8.2), a result to be used in subsequent analysis.

Just as MSY for one species is a function, not a point, in this multispecies fishery, so, too, is carrying capacity. For example, the carrying capacity for perch is, from equation (1.2), $R = \bar{R} + (D\bar{R})/r_1$ and not the traditional \bar{R} when its growth rate of perch is zero.

Policy Analysis through Comparative Statics

New insights emerge from characterizing changes in steady-state predator-prey equilibrium due to parameter changes and, thus, are presented below. First, how does the optimal stock and harvest of dagaa or perch vary with changes in the price of each species? Such an exercise in comparative statics can be a pragmatic tool for policy analysis. Since foreign exchange is positively related to the price of perch, improving foreign exchange earnings is connected through population dynamics to changes in the optimal harvest of dagaa and, for example, its impact on nutrition levels.

The comparative statics equilibrium results for a change in the price of perch and dagaa are derived in Appendix 2 and shown in equations (11.1a), (11.1b), (11.2), and (11.3).

$$\frac{dR}{dP_1} > 0, \frac{dD}{dP_1} > 0, \quad (11.1a)$$

$$\frac{dD}{dP_2} < 0, \frac{dR}{dP_2} < 0. \quad (11.1b)$$

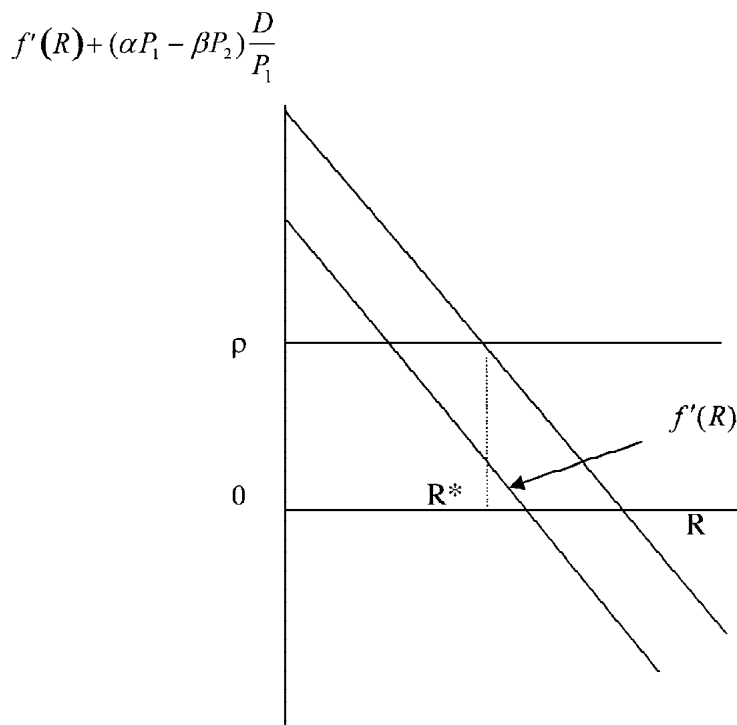
The comparative statics results here are not robust with respect to the structure of the multiple species population dynamics model. For example, see Flaaten (1991) where the species are competitive, an own harvest price increase decreases the resource stock, and an increase in the harvest price of one species increases the stock of the other.

Earlier we identified the predator-prey technical biological externality in the steady-state equations (5.1) and (5.2), where the common factor is $P_1 - P_2$. We noted that when $P_1 - P_2 > 0$, this pushed the optimal solution for R and D to the right of $= f(R) = g(D)$ (see figure 1). Thus when P_1 increases, it increases the positive technical biological externality which increases optimal R . The reasoning is the same for the positive effect of P_1 on optimal D in (5.2). The population of both perch and dagaa decrease when P_2 increases because this exogenous change decreases the positive technical biological externality. Additionally, if $R^* < (1/2)\bar{R}$,

$$\frac{dh_1}{dP_1} > 0, \frac{dh_1}{dP_2} < 0, \quad (11.2)$$

and if $D^* > \frac{1}{2}\bar{D}$, then:

$$\frac{dh_2}{dP_2} > 0, \frac{dh_2}{dP_1} < 0. \quad (11.3)$$



$$(5.1') \quad \rho = f'(R) + (\alpha P_1 - \beta P_2) \frac{D}{P_1}$$

Figure 1. Optimal Solution for Perch ($P_1 - P_2 > 0$)

For all other cases, the signs are indeterminate. It is not surprising that $(h_i/P_i) > 0$, but we have no appealing motivation for the negative sign on h_i/P_i .⁴ We know, for example, that $R^* < R_{msy}$ from equation (10.1), and if R^* increased due to an increase in P_1 in a single-species model of this type, h_1 would increase. Here the condition for $(dh_1/dP_1) > 0$ is that $R^* < 1/2 \bar{R}$ and in this model $R_{msy} = 1/2 \bar{R}$ as is the case in the single-species model (see Appendix 2). Perhaps it should be emphasized that the comparative static results here depend on the assumption of no stock externality. When $P_1 - P_2 > 0$, an increase in the discount rate decreases the stocks of both species (see Appendix 2). When $P_1 - P_2 < 0$, the sign is ambiguous (Hannesson 1983). These results are transparent by observing equations (8.1) and (8.2). Extinction is possible when the intrinsic rates (r_1 or r_2) are small and there are no enhancing positive externalities. Dagaa stocks could rise, for example, if perch stocks were fished down in response to an increase in the discount rate. The fall in R

⁴ If P_2 increases, an increase in h_2 is achieved by decreasing R and decreasing D , the latter because $G(D)$ is concave and the interaction term is linear in D . See equation (2.1). A decrease in R and D decreases h_1 . However, this explanation does not turn on the necessary condition, $R^* < 1/2 \bar{R}$, for signing $(h_1/P_2) < 0$ in (11.2). Similarly, if P_1 increases, an increase in h_1 can be achieved by increasing both R and D (equation 1.1), which then causes a decrease in h_2 (equation 2.1).

in (5.2) might require an increase in D to bring about equilibrium with an increased P .

That a price increase in one fishery leads to a steady-state decrease in the harvest of the other species is an important qualitative result. For the multispecies fishery examined in this paper, policy makers and social scientists with a keen interest in Lake Victoria fisheries regard the resource as a tool for furthering socioeconomic goals, such as increasing foreign exchange earnings, increasing women's employment, and improving nutritional levels.

Perch is a major source of foreign exchange. More than one-half the tonnage of Kenya's fish harvest is attributable to perch in recent years and in some years, more than 60% of the perch catch has been processed for export, mostly by foreign-owned firms financed by the World Bank and non-governmental organizations (Ikiara 1999). Any formal analysis or policy intervention which results in increased foreign exchange earnings through increased harvest of perch will cause a decrease in the steady-state harvest of dagaa, because an increased steady-state perch harvest and an increase in the price of perch have the same impact on dagaa harvest.⁵

Dagaa is a relatively cheap source of protein. Declining harvest of dagaa constitutes a public health concern because nearly 50% of the rural population contiguous to Lake Victoria consume less than WHO's recommended minimum of 2,250 calories per adult equivalent day (Ikiara 1999). The greatest percentage of urban people suffering food deficiency in Kenya live in Kisumu, the center of the fishing industry. More generally, protein deficiency is ubiquitous among the people living around the lake, especially children (Ikiara 1999). Shortfalls in calorie intake have public consequences, such as increased morbidity and its associated public health costs, as well as lowered mental capabilities when caloric loss is incident on children. In general, one expects that an inverse price response to a diminished harvest of dagaa (due to increased perch harvest) will cause a diminution in nutrition levels.

There will be fisheries where the inverse relationship between the harvest of two species is not easy to calculate. When $d(h_i/h_j)/d(P_i/P_j)$ cannot be signed qualitatively for the parameters in any particular setting, then clearly a quantitative analysis must be undertaken to reach any practical conclusions.

Summarized in table 1 are the comparative statics analysis for the biological parameters when $P_1 - P_2 > 0$ (Appendix 2).

Because the parameter estimates in this model do not make $P_1 - P_2$ very significantly greater than zero and λ is uncertain, the comparative static results and the discussion above should be interpreted not as iron clad prescriptive statements, but as tentative or cautionary guidelines. The problem of uncertainty is examined in greater detail in the following section.

Illustrative Solutions

The parameters for the predator-prey model were specified using data that vary from highly credible to speculative, but are the best available information. They are used to estimate the desired harvest and stock levels for perch and dagaa for Kenya. Rational management of these two fisheries should be guided by some empirical

⁵ Reviewers of an earlier draft point to several formal approaches for treating concerns about welfare weights, foreign exchange, and other outputs or inputs. Two involve alternative constructions of shadow prices to account for market imperfections. See for example, Little and Mirrlees (1974, 1991); Squire and van der Tak (1975); UNIDO (1972); or Boardman *et al.* (1996) and Layard and Glaister (1994). Policy makers in the countries riparian to Lake Victoria speak as though increasing employment of women is a matter of social justice, without revealing welfare weights (UNIDO 1972). On the moral dimension of favoring one or more groups, see Sen (1970) and Vatn and Bromley (1994).

Table 1
Comparative Statics for the Biological Parameters

	dD	dR
	+	+
	-	-
r_1		
$R > \bar{R}/2$	+	+
$R < \bar{R}/2$		
r_2		
$D > \bar{D}/2$	-	-
$D < \bar{D}/2$		
\bar{D}	+	+
\bar{R}	+	+

understanding of the biological interactions between them and the underlying economics governing them. Policy makers can differ about the management goals for the two fisheries. Fishery biologists can disagree with the biological structure and parameter estimates of the model, as can economists disagree with the economic anatomy. However, this model identifies the minimum basic data set required for applied bioeconomic analysis of the two most important fisheries in Lake Victoria.

$P_1 = \$268.13$ = the ex-vessel price per metric ton for perch (based on Kshs 80/\$);
 $P_2 = \$73.75$ = the ex-vessel price per ton for dagaa.

The prices are based on recent unpublished data developed by Ikiara and an exchange rate of 80 Kshs/\$. We assume:

$\rho = 0.03$ = the discount rate;
 $r_1 = 0.15$ = the intrinsic rate of growth for perch;⁶
 $r_2 = 0.8$ = the intrinsic rate of growth for dagaa.⁷

The species interaction coefficients are:

$\alpha = 0.0000002, \quad \beta = 0.0000006.$

While fishery biologists agree that there is a predator-prey relationship between these two most important fisheries in Lake Victoria, no research on the interaction coefficients is available. The order of magnitude of the interaction coefficients is governed by the fact that if the interaction term is larger than $1/\bar{D}$ for perch or $1/\bar{R}$ for dagaa, the predator-prey component in the dynamic population equations induces changes in the stock larger than the size of the stock. The particular values selected are based on relative values provided by fishery biologists in Lake Victoria and scaled to meet required order of magnitude values just mentioned. The conversion rate of dagaa into perch, $\beta/\alpha = 1/3$, is not much larger than the price ratio, $P_2/P_1 = 0.28$,

⁶ Personal communication with Daniel Schindler, Fisheries Sciences, University of Washington.

⁷ Personal communication with Julius Manyala, Moi University.

so the condition $P_2/P_1 > P_2/P_1$ is met, but not by a great margin. An alternative estimate of k for all prey that perch consume, not just dagaa, varies between 0.2 and 0.3 depending on the age of the perch (Moreau and Villanueva 2002).

There are no estimates for the carrying capacity parameters, but they can be estimated indirectly if there are estimates of MSY. Fishery biologists have made informed estimates of MSY, and they are presented in table 2.⁸ We will consider three cases initially.

To derive the \bar{R} and \bar{D} using the MSYs, it is necessary to assign relative weights to the species. In the first two cases, 1 and 2 in table 2, the estimated market price of each species denotes their relative importance. Case 1 assumes the high estimate of MSY for perch and Case 2 assumes the low estimate.

In Case 3 the weights for each species are equal. It may be regarded as a biological case, since many biologists are reluctant to give one species more importance than another. Also, steady-state values were derived using equations (8.1), (8.2), (1.2), and (2.2) when $\bar{D} = \bar{R} = 0$. The calculated \bar{R}, \bar{D} , MSYs, and optimal steady-state values are presented in table 2.

The magnitudes below, of course, are driven by the model assumed. A reviewer has pointed out that introducing stock externalities for perch would increase the optimal stock perhaps beyond MSY levels.

Table 2
Optimal and Calculated Fishery Values (Metric Tons)

Economic Cases		Biological Case
Case 1	Case 2	Case 3
$\bar{R} = 620,329$	$\bar{R} = 391,800$	$\bar{R} = 886,685$
$\bar{D} = 882,810$	$\bar{D} = 593,900$	$\bar{D} = 518,847$
$R_{msy} = 343,824$	$R_{msy} = 209,914$	$R_{msy} = 161,389$
$D_{msy} = 465,523$	$D_{msy} = 306,856$	$D_{msy} = 238,489$
$h_{1msy} = 55,000$	$h_{1msy} = 27,500$	$h_{1msy} = 27,500$
$h_{2msy} = 80,000$	$h_{2msy} = 80,000$	$h_{2msy} = 80,000$
$R^* = 280,272$	$R^* = 170,139$	$R^* = 382,109$
$D^* = 444,512$	$D^* = 293,843$	$D^* = 265,448$
$h_1^* = 47,963$	$h_1^* = 24,437$	$h_1^* = 52,902$
$h_2^* = 101,803$	$h_2^* = 88,770$	$h_2^* = 42,855$

⁸ Personal communication with Daniel Schindler, Fisheries Sciences, University of Washington and discussion with participants at a fisheries and forestry workshop in east Africa (Kulindwa, Ikiara, and Kazoora 2001).

Steady-state Economic Optimum and Optimum Path to the Steady State

Harvest levels were 98,280 tonnes of perch and 65,520 tonnes of dagaa in 1995, the perch harvest substantially in excess of optimal values in the above table. Using Case 2 (market price weights), which we regard as more likely than Case 3 (equal price weights) as examples (Case 3 values will be in parentheses), if we were at the economic optimum, total revenue equals \$13.1 (17.3) (tables 3 and 4) million per year or a present value in perpetuity of about \$436.6 (\$578.2) million. If we were at R_{msy} and D_{msy} , the total revenue is \$0.17 million more per year (\$4.1 million less per year). However, at R_{msy} and D_{msy} , it makes economic good sense to harvest down the stocks to R^* and D^* , earning a lump sum of \$11.6 million and put it in the bank at 3% rate of interest to capture an annual stream in perpetuity of about \$0.35 million. This strategy is a superior choice by about \$180,000 in additional revenue per year, a gain of about 1.3%. It may strike some as a little surprising that the economic optimum and the MSY solution are so close. That is because the discount rate of 3% is close to zero, which is the implied discount rate of the MSY solution, together with the fact that harvest levels are fairly unresponsive to changes in the stocks in the neighborhood of R_{msy} and D_{msy} . This result is specific to population dynamics characterized by logistic growth for typical values of the intrinsic rate (r).

Table 3
Case 2: Present Value of Revenue Streams Given Initial and Terminal Points

Path	Annual Revenue (\$ Million)	NPV (\$ Million)
Start and stay at (R_{msy}, D_{msy})	13.3	442
From (R_{msy}, D_{msy}) to (R^*, D^*)	Varies	448
Start and stay at (R^*, D^*)	13.1	437
Start and stay at 1/2 (R_{msy}, D_{msy})	9.9	330
Start and stay at 1/4 (R_{msy}, D_{msy})	5.8	194
From $(0.5 \cdot R_{msy}, 0.5 \cdot D_{msy})$ to (R^*, D^*)	Varies	407
From $(0.25 \cdot R_{msy}, 0.25 \cdot D_{msy})$ to (R^*, D^*)	Varies	380

Table 4
Case 3: Present Value of Revenue Streams Given Initial and Terminal Points

Path	Annual Revenue (\$ Million)	NPV (\$ Million)
Start and stay at (R_{msy}, D_{msy})	13.3	442
From (R_{msy}, D_{msy}) to (R^*, D^*)	Varies	512
Start and stay at (R^*, D^*)	17.3	577
Start and stay at 1/2 (R_{msy}, D_{msy})	8.5	282
Start and stay at 1/4 (R_{msy}, D_{msy})	4.7	156
From $(0.5 \cdot R_{msy}, 0.5 \cdot D_{msy})$ to (R^*, D^*)	Varies	469
From $(0.25 \cdot R_{msy}, 0.25 \cdot D_{msy})$ to (R^*, D^*)	Varies	435

Figures 2 and 3 illustrate the separatrices where:

$$\frac{dR}{dt} = 0 \text{ or } \frac{dD}{dt} = 0$$

and equilibrium levels of perch and dagaa stocks for Cases 2 and 3, respectively. Unfortunately, the two fisheries are neither at the economic optimum nor at MSY stock levels because this is a free-entry fishery. The approximate location of the two fisheries is not known. Since recent harvest levels in Kenya exceed our estimated optimum and there is widespread concern about overfishing, there is no reason to believe that the fishery is in a free-entry equilibrium at these levels. There are no stock estimates, so there is no way to know confidently where to begin the path to the steady state. Parenthetically, there is no current research agenda that would enable researchers to reliably estimate the population levels of perch and dagaa.

Suppose we start at one-half or one-fourth of MSY levels for perch and dagaa. How long does it take to reach the optimum steady-state values, and what is the present value of this policy? Starting at one-fourth MSY, it takes about 7.3 years (see figure 5) or 13.1 years for Case 3 (not illustrated) to reach the optimum which yields a present value of about \$380 (\$435) million (tables 3 and 4). Starting at one-half MSY stock levels, it takes about 3.2 (figure 4) or 9.3 years for Case 3 (not

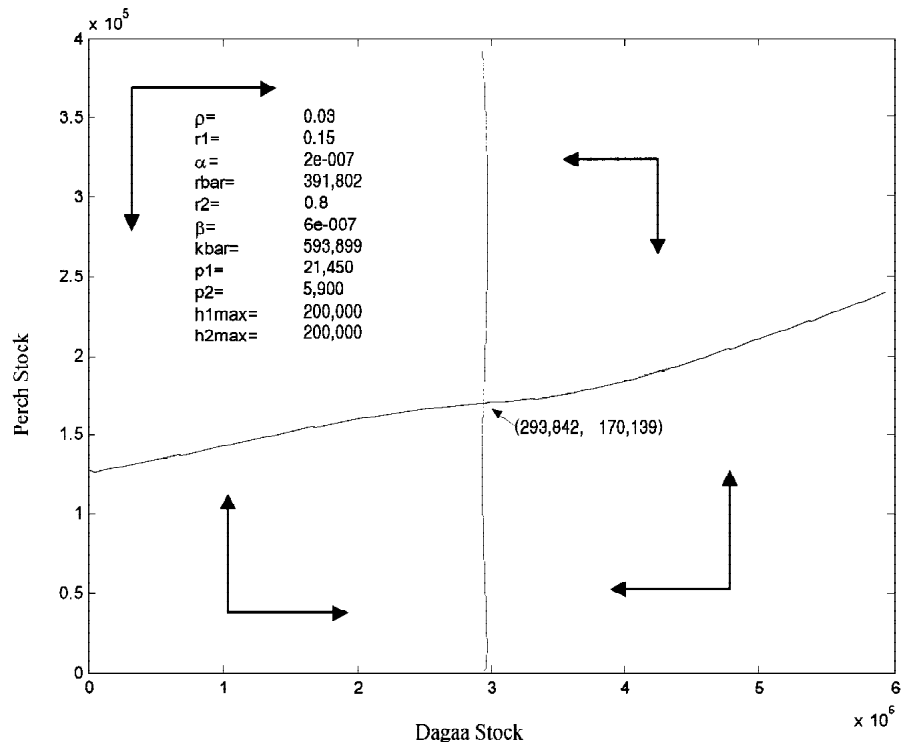


Figure 2. Case 2: Separatrices and Equilibrium

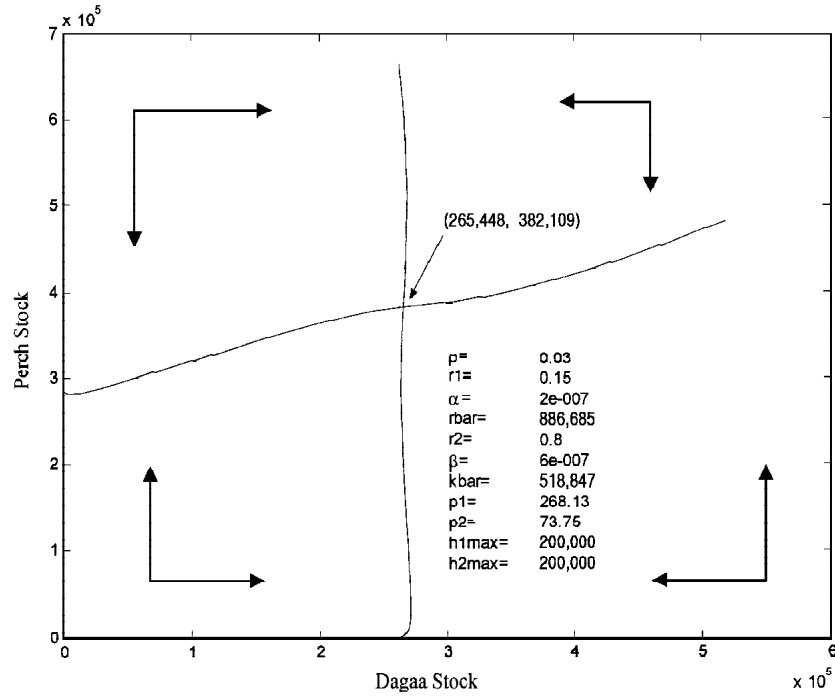


Figure 3. Case 3: Separatrices and Equilibrium

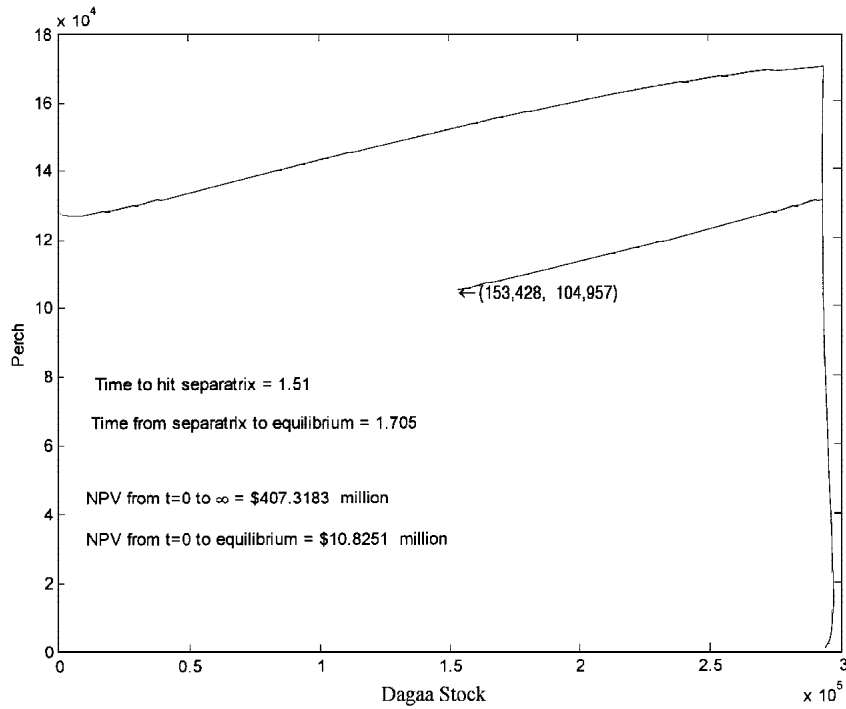


Figure 4. Case 2: Path from 1/2 MSY to Equilibrium

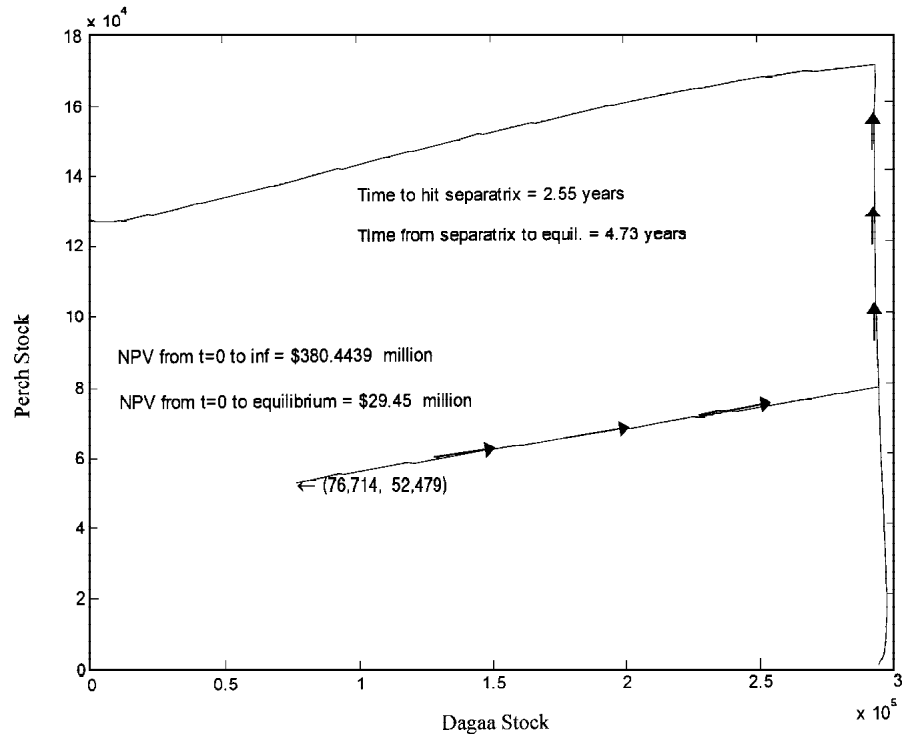


Figure 5. Case 2: Path from 1/4 MSY to Equilibrium

illustrated) to reach the optimum, which has a present value of about \$407 (\$469) million (tables 3 and 4). An interesting aspect of the solution path for this problem is that some portion of it follows the separatrix for daga.

A useful way to understand the impact of uncertainty in this model is to do some sensitivity analyses. We suppose the fishery starts at one-fourth MSY (Case 2) and calculate the elasticity of optimal net present value for the economic optimum case for an upward 1, 5, or 10% change in each of the parameters. The results are summarized in table 5.⁹ Fortunately, net present value (NPV) is inelastically responsive to all changes in the parameters except for the discount rate. More than one-half have an elasticity less than one-half in absolute terms.

Self-financing an Optimal Fishery

The World Bank, other governmental institutions, and non-governmental organizations, are in the business of making productive investments. Investing in the build-up of fish capital is an attractive option. Unfortunately, fish harvesters throughout the world are demonstrably unwilling to sit idly by while one or more

⁹ The results are computed for upward changes. The downward changes are greater than 0.03 in the elasticity estimate in only two out of 54 cases.

Table 5
Elasticity of Net Present Value

	10%	5%	1%
r_1	-1.03	-1.08	-1.12
r_2	0.33	0.33	0.33
P_1	0.77	0.77	0.77
P_2	0.23	0.22	0.23
\bar{R}	-0.18	-0.18	-0.18
\bar{K}	0.47	0.47	0.47
	0.54	0.54	0.53
	0.23	0.23	0.23
	0.72	0.72	0.71

overfished marine resources are allowed to recover. Harvester pressure not to reduce fishing is one reason why 28% of the world’s fish stocks have been depleted or nearly so (United Nations 2002). Although a handful of harvesters mainly comprise each fishery management council in the United States, the body which effectively determines fishery management policy for all harvested species, it has not been politically feasible to rationalize most fisheries. Thus, taking political feasibility into account as a necessary condition for improving the Lake Victoria fishery, probably necessitates a payment scheme to induce harvesters to temporarily leave the perch and dagaa fisheries.

Harvesters would be willing to exit if paid the loss of producers’ surplus. Consumers, in general, will be made worse off by increased prices during the interim period. However, in the absence of estimates of the demand function for dagaa, we have assumed a constant price, hence no loss of consumers’ surplus. This same assumption for perch is relatively innocuous because there are many close substitutes on the world market. Without estimates of the private supply function, g was introduced as the fraction of foregone revenues to obtain a proxy measure for lost producers’ surplus.

Without knowledge available about current stocks, suppose we start at one-half MSY levels. It takes about three years in Case 2 (figure 4) and nine years for the biological Case 3 to get to steady state and assume, for illustration, that there is no harvest during this period. Annual revenue at MSY is \$9.9 (\$8.5) million. So the opportunity cost three (nine) years from now, is:

$$\int_0^3 9.9e^{-0.03t} dt. \quad \$28.4 \text{ million} \quad \int_0^9 8.5e^{-0.03t} dt. \quad \$67 \text{ million} .$$

When both fisheries reopen, there is potential annual rental income in the amount of h_i that can be used to pay the investors, assuming they are not completely altruistic. No fishery to our knowledge has charged the full rental rate to harvesters in a managed fishery where there are tradable quotas, and it is a rare fishery for which there is any charge for the right to fish. Nevertheless, what is the annual charge (v) as a percent of revenue that would pay off the original investment?

In steady state, revenues are \$13.1 (\$17.3) million annually. So the tax revenues in present value three (nine) years from now are:

$$\int_0^3 13.1e^{-0.03(t+3)} dt = v\$400 \quad \int_0^9 17.3e^{-0.03(t+9)} dt = v\$442 \quad \text{million.}$$

Solving for v , $v = 0.07$ or 0.15 depending on the case.

Disregarding political feasibility and transaction costs, the estimated maximum charge necessary to compensate the losers in order to achieve an optimal fishery is 7% (15%) when all revenues are opportunity cost, a very unlikely case. Put another way, the *maximum* charge necessary to pay off the investment to recover fish capital is 7 or 15% of the rental rate, depending on the case. If canoes, nets, and labor in the fisheries have alternative employment opportunities, the tax rate would be less.

Conclusion

Introducing species interdependence through a predator-prey relationship is equivalent to creating a stock externality with a biological origin. When the externality shows up in the Euler equation positively, the optimal stock of a species is greater than the case where the marginal rate of growth equals the discount rate. The externality is positive when the value of marginal product of dagaa in the production of perch exceeds the opportunity cost of dagaa. When this condition holds, $(P_1 - P_2) > 0$, then the comparative statics for price changes produce unambiguous results in this particular predator-prey model.

There may be many instances where no great harm arises when two or more interdependent species are treated as though they were independent. This occurs when a and b in this model are small. However, perch and dagaa cannot be treated separately in the Lake Victoria ecosystem because they are biologically interdependent. Moreover, each species in the political arena serves very different socioeconomic objectives unrelated to efficiency (Kulindwa, Ikiara, and Kazoora 2001). Perch harvest provides foreign exchange, while dagaa harvest provides employment for women and nutrition for the undernourished population contiguous to Lake Victoria. We have provided a model illustrating when these objectives are in conflict and have to be mediated, in part, through a biological population dynamics model.

There is an interesting interdisciplinary insight that emerges from this model. The moment species' interdependence is acknowledged, the analyst must choose a rate of exchange of one species for another if there is to be a determinate solution. Economists naturally choose price weights. The choice, however made, then makes specific the otherwise ambiguous measure of MSY or carrying capacity. These concepts are functions, not points, when species are interdependent.

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Appendix 1. Calculation of Maximum Sustainable Yield

The MSY is defined as the maximum of a weighted sum, where the weights are P_1 and P_2 (in this context P_1 and P_2 are two weights and not necessarily the prices). If the weights are each set to 1, then the problem is one of maximizing sustainable harvest in tons. Alternatively, adopting an economic perspective and weighting the harvests by prices, the problem becomes one of maximizing sustainable instantaneous revenue flow.

$$\text{Maximize } P_1 h_1 + P_2 h_2 \quad (\text{A.1})$$

$$\text{over } h_1, h_2, R, D$$

$$\text{subject to } \dot{R} = \dot{D} = 0 \text{ in (1.2 and 2.1).}$$

Figures A.1, A.2, A.3, and A.4 illustrate that the MSY for a given stock is a function, not a single value. For the above problem, $r_1, r_2, P_1, P_2, \bar{R}$, and \bar{D} are taken as given. The solutions to this problem are:

$$D_{msy} = \frac{\bar{D}[2r_2r_1P_2 + \bar{R}(P_1 - P_2)]}{4r_1r_2P_2 - \bar{D}\bar{R}(P_1 - P_2)^2P_1^{-1}}, \quad (\text{A.2})$$

Maximum Sustained Yield

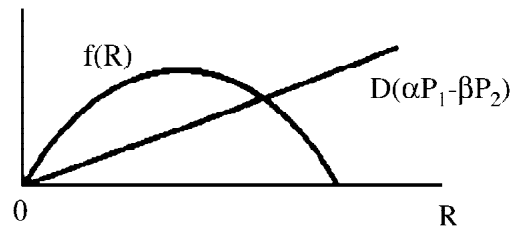


Figure A.1

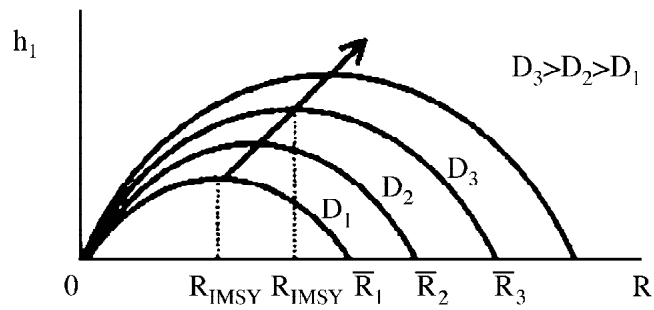


Figure A.2

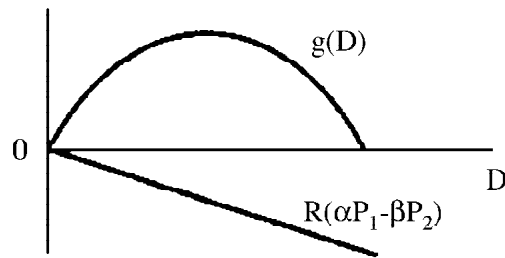


Figure A.3

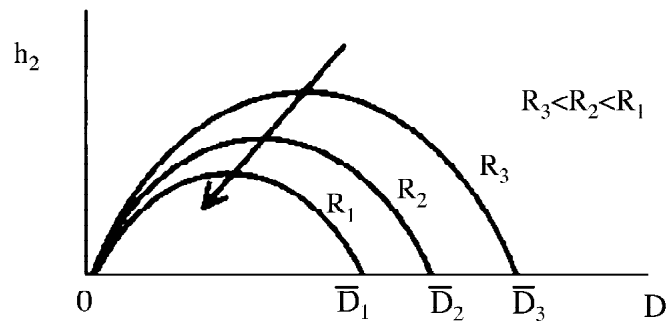


Figure A.4

$$R_{msy} = \frac{\bar{R}[2r_2P_1 + \bar{D}r_2(P_1 - P_2)]}{4r_1r_2P_1 - \bar{D}\bar{R}(P_1 - P_2)^2P_2^{-1}}. \quad (A.3)$$

Substituting equations (A.2) and (A.3) for D and R , respectively, in the harvest functions gives h_1 and h_2 in terms of the parameters values. It is therefore possible, given the MSY harvest levels, to implicitly solve for two parameter values. This method was used to solve for \bar{R} and \bar{D} given maximum sustainable harvest levels.

Appendix 2. Derivation of Comparative Statics Results

How do the optimal stocks and harvest of perch and dagaa respond to changes in the price of each species? Differentiate equations (7.1) and (7.2) with respect to P_1 :

$$\frac{D}{P_1} = \frac{\bar{D}}{2r_2} \frac{P_1 - P_2}{P_2} \frac{R}{P_1} + \frac{\bar{D}R}{2r_2} \frac{1}{P_2}, \quad (11)$$

$$\frac{R}{P_1} = \frac{\bar{R}}{2r_1} \frac{P_1 - P_2}{P_1} \frac{D}{P_1} + \frac{RD}{2r_1P_1^2}. \quad (12)$$

Substituting equation (12) into (11):

$$\frac{D}{P_1} = \frac{\bar{D}}{2r_2} \frac{P_1 - P_2}{P_2} \frac{\bar{R}}{2r_1} \frac{P_1 - P_2}{P_1} \frac{D}{P_1} + \frac{\bar{D}RD}{2r_1P_1^2} + \frac{\bar{D}R}{2r_2P_2},$$

and rearranging:

$$\frac{D}{P_1} = \frac{\bar{R}\bar{D}D}{4r_1r_2P_1^2P_2} \frac{P_2(P_1 - P_2)}{1 - \frac{\bar{R}\bar{D}(P_1 - P_2)^2}{4r_1r_2P_1P_2}} + \frac{\bar{D}R}{2r_2P_2}. \quad (13)$$

Assume $(P_1 - P_2) > 0$, which makes the numerator > 0 . Since $[4r_1r_2P_1 - \bar{D}\bar{R}(P_1 - P_2)^2P_2^{-1}] > 0$ for $R^* > 0$, the denominator is positive. Therefore, $D/P_1 > 0$.

Then, from equation (7.1):

$$\frac{R}{P_1} = \frac{\bar{R}}{2r_1} \frac{P_1 - P_2}{P_1} \frac{D}{P_1} + \frac{RD}{2r_1P_1^2} > 0.$$

Recall:

$$h_1 = r_1R - \frac{r_1}{\bar{R}} R^2 + RD, \quad (14.1)$$

$$h_2 = r_2D - \frac{r_2}{\bar{D}} D^2 - RD. \quad (14.2)$$

Differentiating equation (14.1) with respect to P_1 and rearranging terms:

$$\begin{aligned} \frac{h_1}{P_1} &= r_1 \frac{R}{P_1} - 2 \frac{r_1 R}{\bar{R}} \frac{R}{P_1} + D \frac{R}{P_1} + R \frac{D}{P_1}, \\ \frac{h_1}{P_1} &= r_1 \left(1 - 2 \frac{R}{\bar{R}} \right) + D \frac{R}{P_1} + R \frac{D}{P_1}. \end{aligned} \tag{15.1}$$

Thus, $h_1/P_1 > 0$ if $R/\bar{R} < 1/2$, and undetermined otherwise.

Differentiating equation (14.2) with respect to P_2 and rearranging terms:

$$\frac{h_2}{P_1} = r_2 \left(1 - 2 \frac{D}{\bar{D}} \right) - R \frac{D}{P_1} - D \frac{R}{P_1}. \tag{15.2}$$

Thus, $h_2/P_1 < 0$ if $D/\bar{D} < 1/2$, and undetermined otherwise.

In order to sign R/P_2 , D/P_2 , h_1/P_2 , and h_2/P_2 , begin by differentiating equations (7.1) and (7.2):

$$\frac{R}{P_2} = \frac{\bar{R}}{2r_1} \frac{P_1 - P_2}{P_1} \frac{D}{P_2} + \frac{\bar{R}D}{2r_1} \frac{-}{P_1}, \tag{16}$$

$$\frac{D}{P_2} = \frac{\bar{D}}{2r_2} \frac{P_1 - P_2}{P_2} \frac{R}{P_2} + \frac{\bar{D}R}{2r_2 P_2^2} P_1. \tag{17}$$

Substituting equation (17) into (16):

$$\begin{aligned} \frac{R}{P_2} &= \frac{\bar{R}}{2r_1} \frac{P_1 - P_2}{P_1} \frac{\bar{D}}{2r_2} \frac{P_1 - P_2}{P_2} \frac{R}{P_2} - \frac{\bar{D}R}{2r_2 P_2^2} P_1 - \frac{\bar{R}D}{2r_1 P_1}, \\ \frac{R}{P_2} \left(1 - \frac{\bar{R}\bar{D}(P_1 - P_2)^2}{4r_1 r_2 P_1 P_2} \right) &= - \frac{\bar{R}\bar{D}R}{4r_1 r_2 P_1 P_2^2} P_1 (P_1 - P_2) - \frac{\bar{R}D}{2r_1 P_1}, \\ \frac{R}{P_2} &= \frac{- \frac{\bar{R}\bar{D}R}{4r_1 r_2 P_1 P_2^2} P_1 (P_1 - P_2) - \frac{\bar{R}D}{2r_1 P_1}}{1 - \frac{\bar{R}\bar{D}(P_1 - P_2)^2}{4r_1 r_2 P_1 P_2}}. \end{aligned} \tag{18}$$

Again assume $(P_1 - P_2) = 0$ which makes the numerator negative. Since $[4r_1 r_2 P_1 - \bar{R}\bar{D}(P_1 - P_2)P_2^{-1}] > 0$ for $D^* > 0$, the denominator is positive. Therefore, $R/P_2 < 0$.

Then, from equation (17):

$$\frac{D}{P_2} = \frac{\bar{D}}{2r_2} \frac{P_1 - P_2}{P_2} \frac{R}{P_2} - \frac{\bar{D}R}{2r_2 P_2^2} \frac{P_1}{P_2} < 0.$$

Recall:

$$h_1 = r_1 R - \frac{r_1}{\bar{R}} R^2 + RD, \quad (19.1)$$

$$h_2 = r_2 D - \frac{r_2}{\bar{D}} D^2 - RD. \quad (19.2)$$

Differentiating equation (19.1) with respect to P_2 and rearranging terms:

$$\frac{h_1}{P_2} = r_1 \frac{R}{P_2} - 2 \frac{r_1 R}{\bar{R}} \frac{R}{P_2} + D \frac{R}{P_2} + R \frac{D}{P_2},$$

$$\frac{h_1}{P_2} = r_1 \left(1 - 2 \frac{R}{\bar{R}} \right) + D \frac{R}{P_2} + R \frac{D}{P_2}. \quad (20.1)$$

Thus, $h_1/P_2 < 0$ if $R/\bar{R} < 1/2$, and undetermined otherwise.

Differentiating equation (2.2) with respect to P_2 and rearranging terms:

$$\frac{h_2}{P_2} = r_2 \left(1 - 2 \frac{D}{\bar{D}} \right) - R \frac{D}{P_2} - D \frac{R}{P_2}. \quad (20.2)$$

Thus, $h_2/P_2 < 0$ if $D/\bar{D} < 1/2$, and is undetermined otherwise.

All the results, below, are derived from equations 7.1 and 7.2, and the condition for positive R^* is given in the text.

Comparative Statics wrt. ρ

$$\frac{R}{P_1} = -\frac{\bar{R}}{2r_1} + \frac{P_1 - P_2}{P_1} \frac{\bar{R}}{2r_1} \frac{D}{P_2},$$

$$\frac{D}{P_2} = -\frac{\bar{D}}{2r_2} + \frac{P_1 - P_2}{P_2} \frac{\bar{D}}{2r_2} \frac{R}{P_1},$$

$$\frac{R}{P_1} = -\frac{\bar{R}}{2r_1} + \frac{P_1 - P_2}{P_1} \frac{\bar{R}}{2r_1} - \frac{\bar{D}}{2r_2} + \frac{P_1 - P_2}{P_2} \frac{\bar{D}}{2r_2} \frac{R}{P_1},$$

$$\frac{R}{\bar{D}} \underbrace{1 - \frac{\bar{D}\bar{R}(P_1 - P_2)^2}{4r_1r_2P_1P_2}}_{>0} = -\frac{\bar{R}}{2r_1} - \frac{\bar{D}\bar{R}}{4r_1r_2} \frac{P_1 - P_2}{P_1} < 0,$$

$$\frac{D}{\bar{D}} = -\frac{\bar{D}}{2r_2} + \frac{P_1 - P_2}{P_2} \frac{\bar{D}}{2r_2} \frac{R}{\bar{D}} < 0.$$

Comparative Statics wrt. \bar{D}

$$\frac{R}{\bar{D}} = \frac{\bar{R}}{2r_1} \frac{P_1 - P_2}{P_1} \frac{D}{\bar{D}},$$

$$\frac{D}{\bar{D}} = \frac{1}{2} \left(1 - \frac{R}{r_2} \right) + \frac{R}{2r_2} \frac{P_1 - P_2}{P_2} + \frac{\bar{D}}{2r_2} \frac{P_1 - P_2}{P_2} \frac{R}{\bar{D}},$$

$$\frac{D}{\bar{D}} = \frac{1}{2} \left(1 - \frac{R}{r_2} \right) + \frac{R}{2r_2} \frac{P_1 - P_2}{P_2} + \frac{\bar{D}}{2r_2} \frac{P_1 - P_2}{P_2} \frac{\bar{R}}{2r_1} \frac{P_1 - P_2}{P_1} \frac{D}{\bar{D}},$$

$$\frac{D}{\bar{D}} \underbrace{1 - \frac{\bar{D}\bar{R}(P_1 - P_2)^2}{4r_1r_2P_1P_2}}_{>0} = \frac{1}{2} \left(1 - \frac{R}{r_2} \right) + \frac{R}{2r_2} \frac{P_1 - P_2}{P_2} > 0,$$

$$\frac{R}{\bar{D}} = \frac{\bar{R}}{2r_1} \frac{P_1 - P_2}{P_1} \frac{D}{\bar{D}} > 0.$$

Comparative Statics wrt. \bar{R}

$$\frac{D}{\bar{R}} = \frac{\bar{D}}{2r_2} \frac{P_1 - P_2}{P_2} \frac{R}{\bar{R}},$$

$$\frac{R}{\bar{R}} = \frac{1}{2} \left(1 - \frac{D}{r_1} \right) + \frac{D}{2r_1} \frac{P_1 - P_2}{P_1} + \frac{\bar{R}}{2r_1} \frac{P_1 - P_2}{P_1} \frac{D}{\bar{R}},$$

$$\frac{R}{\bar{R}} = \frac{1}{2} \left(1 - \frac{D}{r_1} \right) + \frac{D}{2r_1} \frac{P_1 - P_2}{P_1} + \frac{\bar{R}}{2r_1} \frac{P_1 - P_2}{P_1} \frac{\bar{D}}{2r_2} \frac{P_1 - P_2}{P_2} \frac{R}{\bar{R}},$$

$$\frac{R}{\bar{R}} \underbrace{1 - \frac{\bar{D}\bar{R}(P_1 - P_2)^2}{4r_1r_2P_1P_2}}_{>0} = \frac{1}{2} \left(1 - \frac{1}{r_1} + \frac{D}{2r_1} \frac{P_1 - P_2}{P_1} \right) > 0,$$

$$\frac{D}{\bar{R}} = \frac{\bar{D}}{2r_2} \frac{P_1 - P_2}{P_2} \frac{R}{\bar{R}} > 0.$$

Comparative Statics wrt. α

$$\frac{R}{\bar{R}} = \frac{\bar{R}}{2r_1} \frac{P_1 - P_2}{P_1} \frac{D}{\bar{R}} + \frac{\bar{R}D}{2r_1},$$

$$\frac{D}{\bar{R}} = \frac{\bar{D}}{2r_2} \frac{P_1 - P_2}{P_2} \frac{R}{\bar{R}} + \frac{P_1}{P_2} \frac{\bar{D}\bar{R}}{2r_2},$$

$$\frac{D}{\bar{R}} = \frac{\bar{D}}{2r_2} \frac{P_1 - P_2}{P_2} \frac{\bar{R}}{2r_1} \frac{P_1 - P_2}{P_1} \frac{D}{\bar{R}} + \frac{\bar{R}D}{2r_1} + \frac{P_1}{P_2} \frac{\bar{D}\bar{R}}{2r_2},$$

$$\frac{D}{\bar{R}} \underbrace{1 - \frac{\bar{D}\bar{R}(P_1 - P_2)^2}{4r_1r_2P_1P_2}}_{>0} = \frac{\bar{D}\bar{R}D}{4r_1r_2} \frac{P_1 - P_2}{P_2} + \frac{P_1}{P_2} \frac{\bar{D}\bar{R}}{2r_2} > 0,$$

$$\frac{R}{\bar{R}} = \frac{\bar{R}}{2r_1} \frac{P_1 - P_2}{P_1} \frac{D}{\bar{R}} + \frac{\bar{R}D}{2r_1} > 0.$$

Comparative Statics wrt. β

$$\frac{R}{\bar{R}} = \frac{\bar{R}}{2r_1} \frac{P_1 - P_2}{P_1} \frac{D}{\bar{R}} - \frac{P_2}{P_1} \frac{\bar{R}D}{2r_1},$$

$$\frac{D}{\bar{R}} = \frac{\bar{D}}{2r_2} \frac{P_1 - P_2}{P_2} \frac{R}{\bar{R}} - \frac{\bar{D}\bar{R}}{2r_2},$$

$$\frac{R}{\bar{R}} = \frac{\bar{R}}{2r_1} \frac{P_1 - P_2}{P_1} \frac{\bar{D}}{2r_2} \frac{P_1 - P_2}{P_2} \frac{R}{\bar{R}} - \frac{\bar{D}\bar{R}}{2r_2} - \frac{P_2}{P_1} \frac{\bar{R}D}{2r_1},$$

$$\frac{R}{r_1} \underbrace{1 - \frac{\overline{DR}(P_1 - P_2)^2}{4\overline{r_1}r_2P_1P_2}}_{>0} = -\frac{\overline{R}\overline{DR}}{4\overline{r_1}r_2} \frac{P_1 - P_2}{P_1} - \frac{P_2}{P_1} \frac{\overline{RD}}{2\overline{r_1}} < 0,$$

$$\frac{D}{r_2} = \frac{\overline{D}}{2r_2} \frac{P_1 - P_2}{P_2} \frac{R}{r_1} - \frac{\overline{DR}}{2r_2} < 0.$$

Comparative Statics wrt. r_1

$$\frac{R}{r_1} = \frac{\overline{R}}{2r_1^2} - \frac{\overline{RD}}{2r_1^2} \frac{P_1 - P_2}{P_1} + \frac{\overline{R}}{2\overline{r_1}} \frac{P_1 - P_2}{P_1} \frac{D}{r_1},$$

$$\frac{D}{r_1} = \frac{\overline{D}}{2r_2} \frac{P_1 - P_2}{P_2} \frac{R}{r_1}, \text{ therefore } \frac{D}{r_1} \text{ and } \frac{R}{r_1} \text{ are the same sign.}$$

$$\frac{R}{r_1} \underbrace{1 - \frac{\overline{DR}(P_1 - P_2)^2}{4\overline{r_1}r_2P_1P_2}}_{>0} = \frac{\overline{R}}{2r_1^2} \underbrace{- D \frac{P_1 - P_2}{P_1}}_{= f'(R) \text{ from 5.1' and 5.2'}}$$

$$f(R) < 0 \quad \text{if} \quad R > \frac{\overline{R}}{2}$$

$$f(R) > 0 \quad \text{if} \quad R < \frac{\overline{R}}{2}$$

$$\frac{R}{r_1}, \frac{D}{r_1} < 0 \quad \text{if} \quad R > \frac{\overline{R}}{2}$$

$$\frac{R}{r_1}, \frac{D}{r_1} > 0 \quad \text{if} \quad R < \frac{\overline{R}}{2}$$

Comparative Statics wrt. r_2

$$R = \frac{\overline{R}}{2} \left(1 - \frac{1}{r_1} \right) + \frac{\overline{RD}}{2\overline{r_1}} \frac{P_1 - P_2}{P_1},$$

$$D = \frac{\overline{D}}{2} \left(1 - \frac{1}{r_2} \right) + \frac{\overline{DR}}{2r_2} \frac{P_1 - P_2}{P_2},$$

$$\frac{D}{r_2} = \frac{\bar{D}}{2r_2^2} - \frac{\bar{D}\bar{R}}{2r_2^2} \frac{P_1 - P_2}{P_2} + \frac{\bar{D}}{2r_2} \frac{P_1 - P_2}{P_2} \frac{R}{r_2},$$

$$\frac{R}{r_2} = \frac{\bar{R}}{2r_1} \frac{P_1 - P_2}{P_1} \frac{D}{r_2} \text{ therefore } \frac{R}{r_2} \text{ and } \frac{D}{r_2} \text{ are the same sign.}$$

$$\frac{R}{r_1} \underbrace{1 - \frac{\bar{D}\bar{R}(P_1 - P_2)^2}{4r_1r_2P_1P_2}}_{>0} = \frac{\bar{D}}{2r_2^2} \underbrace{- R \frac{P_1 - P_2}{P_2}}_{=g(D) \text{ from 5.1' and 5.2'}}$$

$$g(D) < 0 \quad \text{if} \quad D > \frac{\bar{D}}{2}$$

$$g(D) > 0 \quad \text{if} \quad D < \frac{\bar{D}}{2}$$

$$\frac{R}{r_2}, \frac{D}{r_2} < 0 \quad \text{if} \quad D > \frac{\bar{D}}{2}$$

$$\frac{R}{r_2}, \frac{D}{r_2} > 0 \quad \text{if} \quad D < \frac{\bar{D}}{2}$$