Managing Stochastic Multispecies Models*

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ABSTRACT

Qualitative properties of optimal policies for stochastic, multispecies harvesting models are described. Conditions that imply that a k-species model can be decomposed into k single species models are discussed. For a discrete, stochastic version of the Lotka-Volterra models, it is shown that finding an optimal policy can be narrowed to finding the globally optimal harvest, and to using constraints developed on the partial derivatives of an optimal policy to accelerate computations. For a discrete stochastic version of a competition model developed by Silliman, it is proven that knowledge of the globally optimal harvest is sufficient to completely describe an optimal policy. Approximate policies that are easier to solve are suggested. The results suggest that an optimal harvesting policy will tend to simplify the ecosystem—that is harvest to low levels unwanted or less valuable species.

INTRODUCTION

In a previous paper, I extended the results for stochastic, single-species, pooled-age-class harvesting models to stochastic multi-age-class models (see [4] and references cited there). These models consider a single stock or species separate from its interaction with other species. Biological systems are noted for having complex food webs, and it is desirable to examine the effects these interactions have on optimal harvesting strategies. This is particularly true when two or more interacting species are being exploited by a single fishery, or are being managed by a single controller or agency.

Let x_t (possibly a k-vector) denote the size of a stock or stocks at the beginning of period, t, z_t (possibly a k-vector) the amount harvested in period t, and $y_t = x_t - z_t$ the amount remaining at the end of period t after

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harvesting has ceased. Assume x_{t+1} is a random function of y_t, that is,

$$x_{t+1} = S[y_t, D_t],$$

where $D_1, D_2, \ldots, D_T$ are independent, identically distributed random vectors, distributed as the generic random vector D.

In each period, observing x and harvesting to y produces a return $G(x,y)$, discounted by a factor α, $0 < \alpha \leqslant 1$. Following Mendelssohn and Sobel [5], this problem can be formulated as the following system of recursive functions:

$$f_0(\cdot) \equiv 0,$$

$$f_n(x) = \max_{0 < y < x} \{ J_n(x,y) : x \in X \}, \tag{I}$$

where

$$J_n(x,y) = G(x,y) + \alpha E \{ f_{n-1}(S[y,D]) \}$$

and where the domain X is a convex set, representing the set of all possible population sizes. It is assumed that X is bounded, which is realistic, since real populations cannot be negative, nor can they be infinite.

Multispecies harvesting models have been considered to a limited extent in the literature. Quirk and Smith [6] present results for a continuous-time, deterministic Lotka-Volterra-type system, but under very restrictive assumptions. Hilborn [1] uses numerical dynamic programming to study harvesting strategies for noninteracting species that are jointly harvested.

Three types of stochastic multispecies models are analyzed in this paper. The first is a model of k noninteracting species that are jointly harvested, but whose return structure is separable. It is shown that the entire problem can be reduced to k one-dimensional problems. This result is similar to previous results in [4].

The second model is a discretized version of the Lotka-Volterra model for competing species or predator-prey systems. In this model, the growth rate for each species and all the interaction coefficients are assumed to be random variables. It is also assumed that each species is harvested, and that each species can be targeted. The first assumption can be easily relaxed; the second assumption can be relaxed if the model of "by-catches" retains all the necessary concavity properties. For example, if the by-catches are linear, then straightforward modifications to Theorem 2 can be made.

The third model is a model due to Silliman [9] based on laboratory experiments. This model is similar to the Lotka-Volterra equations, except that the interaction term is linear instead of quadratic.

1. MODELS AND RESULTS

The k-dimensional notation of Mendelssohn [4] is adapted to the k-species problem by letting superscript i denote species instead of age-class. The first model to be considered has k species that interact only in the return function. A single boat or fleet harvests k noninteracting species. Let $g^i(x^i, y^i)$ be the net benefit of harvesting species i from x^i individuals to y^i individuals. The boat or fleet may also experience costs that are independent of whether or not it harvests, but depend on the total time away from port. One possible structure for these costs is that it is proportional to a weighted sum of the total harvest sizes. This could arise if the time spent in searching for and harvesting each species is proportional to the size of the harvest from that species. Thus, the total return from harvesting is

$$G(\mathbf{x},\mathbf{y}) = \sum_{i=1}^{k} \left\{ g^i(x^i, y^i) - cw^i(x^i - y^i) \right\}, \tag{1}$$

$$c, w^i \geqslant 0 \qquad \text{for all } i.$$

The growth of each species is a random function which depends on the number of individuals of that species only, that is,

$$x_{t+1}^i = s^i[\mathbf{y}_t, \mathbf{d}_t] = s^i[y_t^i, d_t^i], \qquad i = 1, \ldots, k. \tag{2}$$

Theorem 1 states that the model described by Eqs. (1) and (2) is separable into k subproblems where each species is considered separately from all others. The advantage of this is that a k-dimensional problem can be reduced to k one-dimensional problems where the stronger results of Mendelssohn and Sobel [5] can be applied.

THEOREM 1

In the dynamic-programming problem (I), *if* $G[\mathbf{x},\mathbf{y}]$ *and* $S[\mathbf{y},\mathbf{d}]$ *are given by Eqs.* (1) *and* (2), *respectively, then the problem can be separated into* k *one-dimensional subproblems of the form*

$$f_0^i(\cdot) \equiv 0,$$

$$f_n^i(x^i) = \max_{0 < y^i < x^i} \left\{ g^i(x^i, y^i) - cw^i(x^i - y^i) + \alpha E f_{n-1}^i(s^i[y^i, d^i]) \right\}.$$

Proof. The proof follows from a similar proof in Veinott [10].   ∎

The Lotka-Volterra equations are usually represented as

$$\frac{dx^i(t)}{dt} = r^i x^i(t) + x^i(t) \sum_j a_{ij} x^j(t), \tag{3}$$

$$i, j = 1, \ldots, k, \qquad k = 2w.$$

If a_{ij} is positive, then species j is a prey of species i. If a_{ij} is negative, then species j is either a competitor or a predator of species i. (Detailed discussions of these equations and their shortcomings can be found in [3, 7, 8].)

One possible discretized version of (3) is

$$x_{t+\delta}^i - x_t^i = \delta x_t^i \left(r^i + \sum_{j=1}^{k} a_{ij} x_t^j \right), \qquad i,j = 1,\dots,k. \tag{4}$$

To include harvesting, it is assumed that a harvest of z_t^i from any species i produces a return $p^i z_t^i$ in period t, and that the transition (4) depends only on the number left after harvest, $y_t^i = x_t^i - z_t^i$. It is further assumed that each r^i, $i = 1,\dots,k$, and a_{ij}, $i,j = 1,\dots,k$, are random variables such that $r^i > 0$ with probability one, $a_{ij} > 0$ with probability one if species j is a prey of species i, and $a_{ij} < 0$ with probability one if species j is a predator or competitor of species i. The dynamic program then is

$$f_0(\cdot) \equiv 0,$$
$$f_n(\mathbf{x}) = \max_{0 < \mathbf{y} < \mathbf{x}} \{ J_n(\mathbf{x},\mathbf{y}) \}, \tag{5}$$

where

$$J_n(\mathbf{x},\mathbf{y}) = \sum_{i=1}^{k} p^i (x^i - y^i) + \alpha E f_{n-1}(\mathbf{S}[\mathbf{y},\mathbf{r},\mathbf{a}])$$

and $\mathbf{S}[\mathbf{y},\mathbf{r},\mathbf{a}]$ is given by [4].

The analysis concentrates on a modification of (5). Let

$$G(\mathbf{y}) = \alpha E \left(\sum_{i=1}^{k} p^i s^i[\mathbf{y},\mathbf{r},\mathbf{a}] \right) - \sum_{i=1}^{k} p^i y^i. \tag{6}$$

Then, as in [4, Theorem 3], there is an equivalent problem:

$$f_0(\cdot) \equiv 0,$$
$$f_n(\mathbf{x}) = \max_{0 < \mathbf{y} < \mathbf{x}} \{ J_n(\mathbf{y}) \}, \tag{7}$$

where

$$J_n(\mathbf{y}) = G(\mathbf{y}) + \alpha E f_{n-1}(\mathbf{S}[\mathbf{y},\mathbf{r},\mathbf{a}])$$

and n goes from 1 to $T-1$ if the original planning horizon is T periods. Let $\mathbf{A}_n(\mathbf{x})$ be an optimal policy function with component function $a_n^i(\mathbf{x})$.

THEOREM 2

Let $\mathbf{x}_n^*$ be the global optimum of $J_n(\mathbf{x})$ for $\mathbf{x} \in X$.

(a) *In a competitive system* (that is, $a_{ij} < 0$ with probability one for all i,j):

(i) $J_n(\mathbf{y})$ is concave for all n.

(ii) If $\mathbf{x} > \mathbf{x}_n^*$, then $A_n(\mathbf{x}) = \mathbf{x}_n^*$; if $\mathbf{x} < \mathbf{x}_n^*$, then $A_n(\mathbf{x}) = \mathbf{x}$; and

$$0 < \frac{\partial a_n^i(\mathbf{x})}{\partial x^i} < 1 \quad \text{for all } i.$$

(iii) Let I be the set of i's such that $x^i < x_n^{*i}$, and I^c the set of i's such that $x^i > x_n^{*i}$. Then

$$0 < \frac{\partial a_n^i(\mathbf{x})}{\partial x^j} < 1 \quad \text{for } i \in I, \quad j \in I \cup I^c,$$

$$-1 < \frac{\partial a_n^i(\mathbf{x})}{\partial x^j} < 0 \quad \text{for } i \in I^c, \quad j \in I.$$

(b) *In the more general system*, assume $p_i a_{ij} + p_j a_{ji} < 0$ with probability one for all i,j. Then:

(iv) $J_n(\mathbf{y})$ is pseudoconcave for all n.

(v) (i)–(iii) above are valid.

Proof. (a): $G(\mathbf{y})$ is twice differentiable. Then

$$\frac{\partial^2 G(\mathbf{y})}{\partial y^i \partial y^j} = p_i \bar{a}_{ij} + p_j \bar{a}_{ji} < 0,$$

where $\bar{a}_{ij}$ is the expected value of a_{ij}. Thus $G(\cdot)$ is concave. $S[\mathbf{y}, \mathbf{r}, \mathbf{a}]$ is concave if each $s^i[\mathbf{y}, \mathbf{r}, \mathbf{a}]$ is concave. Again, $s^i[\mathbf{y}, \mathbf{r}, \mathbf{a}]$ is twice differentiable, and

$$\frac{\partial^2 s^i[\mathbf{y}, \mathbf{r}, \mathbf{a}]}{\partial y^i \partial y^j} = a_{ij} < 0 \quad \text{with probability one,}$$

so $S[\cdot, \cdot, \cdot]$ is concave. From the usual arguments about a dynamic-programming problem "inheriting" concavity properties through time (see [5]), this implies $J_n(\mathbf{y})$ is concave, and $f_n(\mathbf{x})$ is concave and continuous. This proves (i). Claim (ii) is immediate from the concavity of $J_n(\cdot)$ and the definition of $\mathbf{x}_n^*$ as the global optimum, since the gradient of a concave function is diagonally antitone.

Claim (iii) is proven using the monotonicity of the derivative of a concave function. That is,

$$[\nabla J_n(x') - \nabla J_n(x)][x' - x] \leq 0.$$

In particular, if $x' = x_n^*$, then

$$[-\nabla J_n(x)][x_n^* - x] \leq 0.$$

Claim (iii) is essentially that if $x^i \leq x_n^{*i}$, then an optimal solution has $a_n^i(x) = x^i$, no matter what the value of the other x^j. Let δ^i be a k-vector that has value zero except at the ith component, which has value δ^i. Suppose $x^* + \Sigma_{i \in I^c} \delta^i - \Sigma_{i \in I} \delta^i$ is such that for all $i \in I^c$, $\nabla^i J_n(x^* + \Sigma_{i \in I^c} \delta^i - \Sigma_{i \in I} \delta^i) > 0$. The theorem will be true if this point is as good as any other point that decreases one or several of the species in I. Suppose not. Then

$$0 < J_n\left(x^* + \sum_{i \in I^c} \delta^i - \sum_{i \in I} \delta^i - \sum_{i \in I} \lambda^i\right)$$

$$- J_n\left(x^* + \sum_{i \in I^c} \delta^i - \sum_{i \in I} \delta^i\right)$$

$$= -\nabla J_n\left(x^* + \sum_{i \in I^c} \delta^i - \sum_{i \in I} \delta^i - \gamma \sum_{i \in I} \lambda^i\right)(\lambda) \qquad (8)$$

by the mean-value theorem, where $0 < \gamma < 1$, and λ has as its ith component λ^i. However, (8) implies

$$-\nabla J_n\left(x^* + \sum_{i \in I^c} \delta^i - \sum_{i \in I} \delta^i - \gamma \sum_{i \in I} \lambda^i\right)$$

$$\cdot \left[x_n^* - \left(x_n^* + \sum_{i \in I^c} \delta^i - \sum_{i \in I} \delta^i - \gamma \sum_{i \in I} \lambda^i\right)\right] > 0,$$

which contradicts the concavity of $J_n(x)$. Therefore the inequality in (8) must be reversed. This implies

$$0 < \frac{\partial a_n^i(x)}{\partial x^j}, \qquad i \in I, \ j \in I \cup I^c,$$

$$0 > \frac{\partial a_n^i(x)}{\partial x^j}, \qquad i \in I^c, \ j \in I.$$

To obtain the upper and lower bounds, let $z = x - y$ be the decision variable. Then parallel arguments (as in [5] or [4, Theorem 3]) yield identical inequalities for the optimal amount harvested. This yields the other bounds.

The proof has assumed the existence of the partial derivatives on the relative interior of X. However, an identical argument to [5, Corollary 4.2] proves their existence.

(b): The proof of the general model would be the same as for part (a), since $p_i a_{ij} + p_j a_{ji} \leqslant 0$ with probability one assures that $G(y)$ is concave. However, $S[y, r, a]$ is not necessarily concave, so the proof breaks down. The proof therefore is to show that $S[y, r, a]$ is a logconcave, and that an appropriate transformation of variables transforms this problem into a problem that satisfies the concavity assumptions of part (a).

For any i, and for any fixed value of r, a,

$$\frac{\partial^2}{\partial y^{i2}} \log s^i[y, r, a] = -\frac{1}{y^{i2}} - \frac{a_{ii}^2}{\left(1 + r^i + \Sigma_j a_{ij} y^j\right)^2},$$

$$\frac{\partial^2}{\partial y^{j2}} \log s^i[y, r, a] = -\frac{a_{ij}^2}{\left(1 + r^i + \Sigma_j a_{ij} y^j\right)^2},$$

$$\frac{\partial^2}{\partial y^j \partial y^k} \log s^i[y, r, a] = -\frac{a_{ij} a_{ik}}{\left(1 + r^i + \Sigma_i a_{ij} y^j\right)^2}.$$

The function $\log s^i[y, r, a]$ is concave if for any k-vector $z > 0$ we have $z \eta z < 0$ where η is the Hessian matrix of cross partial derivatives. This is equivalent to

$$-\frac{z^{i2}}{y^{i2}} - \frac{\sum\limits_{j=1}^{k} a_{ij}^2 z^{j2} + \sum\limits_{j=1}^{k} \sum\limits_{l>j}^{k} 2a_{jl} a_{ij} z^j z^l}{\left(1 + r^i + \sum\limits_{j=1}^{k} a_{ij} y^j\right)^2},$$

which equals

$$-\left(\frac{z^i}{y^i}\right)^2 - \left[\frac{\sum\limits_{j=1}^{k} a_{ij} z^j}{1 + r^i + \sum\limits_{j=1}^{k} a_{ij} y^j}\right]^2 < 0.$$

In the transformed problem (7), let $N_t = \ln x_t$, so that $x_t = \exp(N_t)$. Then the transformation becomes:

$$N_{t+1} = \log S[y_t, r_t, a_t]$$

which is concave, and the constraint set is

$$\exp(N_{t+1}) \geqslant y_{t+1} \geqslant 0,$$

which is a convex set that is increasing in N_{t+1}. Results (i), (ii), (iii) now hold for this transformed problem, and $J_n(y)$ is logconcave. However, $J_n(y)$ logconcave implies $J_n(y)$ is pseudoconcave, which is the desired claim (iv). ∎

In the competitive system, it is straightforward to show that if $\alpha p^i(1 + \bar{r}^i) < p^i$, then it is optimal to remove this species entirely at the outset. This is not necessarily true for a species that is a prey for a more valuable species, since this species has higher future value.

The usefulness of Theorem 2 is that most of the computational work is to find x_n^* for each n. Particularly on a discretized version of the model, any efficient search technique can be used to find x_n^*, which should help reduce the fabled "curse of dimensionality." A second way to increase computational efficiency is to use $A_1(x)$, the optimal policy for $G(y)$, as a near-optimal stationary policy. This can easily be calculated by any standard routine for concave optimization. It is conjectured that this will be a good approximation to a competitive system, since the less valuable species should lose value through time, as they have more of a chance of reducing the valuable species. Thus, this "myopic" policy should be a conservative policy.

For a predator-prey system, however, the approximation should be weaker, since prey species may increase in value through time. The "myopic" policy should tend to overharvest these species.

In either case, the effect of "optimal" harvesting should be to "simplify" the ecosystem, that is, reduce low-valued competitors, or low-valued predators that are not prey for any other species, to very low or zero levels. Even if these species are not harvested to zero, this increases the chance of their random extinction. Simplification of the ecosystem through harvesting places great reliance on the accuracy of the model, particularly to population ranges that have never been observed, but may come about due to harvesting. This suggests caution should be used in applying these results, since there exist few if any striking examples of the Lotka-Volterra equations explaining the behavior of a real ecosystem.

Silliman [9] performed laboratory studies on the competition between guppies (*Poecilia reticulata*) and red swordtail hybrids (*Xiphophorus maculatus* × *X. helleri*). The dynamics of each species can be described by a growth function which depends only on the size of that species and a linear interaction term. A discrete stochastic version of Silliman's model is

$$x_{t+1}^j = r^i(y_t^j, d_t^i) - \sum_{j \neq i} m^{ij} y^j, \qquad i,j = 1,2, \tag{9}$$

$$m^i \geqslant 0 \qquad \text{w.p. } 1,$$

where $r^i(\cdot, d^i)$ is concave, continuous, and nondecreasing for each d^i. The return from harvesting each species is assumed to be proportional to the amount harvested from that species, that is,

$$G(\mathbf{x}, \mathbf{y}) = \sum_{i=1}^{2} p^{i \cdot}(x^i - y^i) \qquad p^i > 0 \quad \text{for all } i. \tag{10}$$

Equation (9) is appropriate for two species competing for the same resource. Intuitively, one would expect that if we increase the number left of one species after harvesting, we will not decrease the number left of the second species. In fact, a stronger statement than that can be made.

The dynamic program (I) becomes

$$f_n(\mathbf{x}) = \max_{0 < y < x} \{J_n(\mathbf{x}, \mathbf{y})\} = \sum_{i=1}^{2} p^i x^i + \max_{0 < y < x} \{H_n(\mathbf{y})\}, \tag{11}$$

where $H_n(\mathbf{y}) = \alpha E f_{n-1}(S[\mathbf{y}, \mathbf{d}, \mathbf{m}]) - \sum_{i=1}^{2} p^i y^i$ and $S[\mathbf{y}, \mathbf{d}, \mathbf{m}]$ is given by Eq. (9). For all $\mathbf{x} \in X$, let $\mathbf{x}_n^0$ be the global maximum of $H_n(\mathbf{y})$. Theorem 3 states that an optimal policy for (11) "uncouples" the species in the sense that given $\mathbf{x}_n^0$, the optimal policy for each species depends only on its size relative to x_n^{0i}, regardless of the size of the competing species.

THEOREM 3

If for each n, $\mathbf{x}_n^0$ is a global optimum of $H_n(\cdot)$ given in (11), then for each n and all $\mathbf{x} \in X$,

$$A_n(\mathbf{x}) = \mathbf{x} \wedge \mathbf{x}_n^0,$$

where $\mathbf{a} \wedge \mathbf{b}$ denotes component-by-component minimums.

Proof. A proof similar to that of Theorem 3 in [4] shows that $H_n(\mathbf{y})$ is concave and continuous in $\mathbf{y}$ and that $f_n(\mathbf{x})$ is concave, continuous, and nondecreasing.

If $\mathbf{x} > \mathbf{x}_n^0$, then clearly $A_n(\mathbf{x}) = \mathbf{x}_n^0$, since $\mathbf{x}_n^0$ is by definition a global optimum. Otherwise, it is necessary to show that if $\mathbf{x}^1 > \mathbf{x}$, then $A_n(\mathbf{x}^1) > A_n(\mathbf{x})$.

Let $\boldsymbol{\delta}^i$ be the column vector that has zero in every coordinate except the ith, which has the value $\delta > 0$. Suppose $A_n(\mathbf{x})$ has been found for some $\mathbf{x} \in X$. Then it is clear that

$$a_n^i(\mathbf{x} + \boldsymbol{\delta}^i) > a_n^i(\mathbf{x}),$$

since if it were lower, the resulting value would have to be dominated by $A_n(\mathbf{x})$, which is feasible and by definition no less in value. It therefore

remains to show that

$$a_n^j(\mathbf{x} + \boldsymbol{\delta}^i) \geq a_n^j(\mathbf{x}).$$

At $n = 2$,

$$
\begin{aligned}
H_2(y) &= p^1 \{ aE[r^1(y^1, d^1) - m^{12}y^2] - y^1 \} \\
&\quad + p^2 \{ \alpha E[r^2(y^2, d^2) - m^{21}y^1] - y^2 \} \\
&= [\alpha p^1 E r^1(y^1, d^1) - p^1 y^1 - \alpha p^2 E(m^{21}y^1)] \\
&\quad + [\alpha p^2 E r^2(y^2, d^2) - p^2 y^2 - \alpha p^1 E(m^{12}y^2)],
\end{aligned}
$$

which is the sum of two concave functions, one of which depends only on y^1 and the other only on y^2. Therefore, at $r = 2$, it is true that:

(i) $A_2(\mathbf{x}') \geq A_2(\mathbf{x})$ if $\mathbf{x}' \geq \mathbf{x}$,

(ii) $\nabla^i H_2(y)$ is nonincreasing in y^i,

(iii) $\nabla^i H_2(y)$ is nondecreasing in y^j.

Assume as an inductive hypothesis that (i), (ii), and (iii) are valid in periods $2, 3, \ldots, n - 1$. Then at period n,

$$
\begin{aligned}
\nabla^j H_n(y) &= E \{ [\alpha p^i + [\nabla^i H_{n-1}(\mathbf{S}[y, \mathbf{d}, \mathbf{m}] \wedge \mathbf{x}_{n-1}^0) - p^i]^+](-m^{ij}) \} \\
&\quad + E \{ [\alpha p^j + [\nabla^j H_{n-1}(\mathbf{S}[y, \mathbf{d}, \mathbf{m}] \wedge \mathbf{x}_{n-1}^0) - p^j]^+](r^{j[1]}(y^j, d^j)) \} - p^j.
\end{aligned}
\tag{12}
$$

If y^i is increased, $s^i[y, \mathbf{d}, \mathbf{m}]$ is not decreased, and $s^j[y, \mathbf{d}, \mathbf{m}]$ is not increased, so by (ii) and (iii), $\nabla^i H_{n-1}$ is not increased. Since $(-m^{ij}) \leq 0$ with probability 1, then the first term is nondecreasing in y^i. Similarly, if y^i is increased, $s^i[y, \mathbf{d}, \mathbf{m}]$ is not decreased, and $s^j[y, \mathbf{d}, \mathbf{m}]$ is not increased. By (ii) and (iii), this implies $\nabla^j H_{n-1}$ is not decreased. Since by assumption $r^{j[1]}$ is nonnegative, then the second term is nondecreasing in y^i.

What has been shown is that

$$\nabla^j H_n(y + \boldsymbol{\delta}^i) \geq \nabla^j H_n(y).$$

In particular, $\nabla^j H_n(A_n(\mathbf{x}) + \gamma^i) \geq \nabla^j H_n(A_n(\mathbf{x}))$ for $0 \leq \gamma^i \leq \delta^i$. By the necessary and sufficient conditions for an optimum of a constrained concave function, this implies

$$A_n(\mathbf{x} + \boldsymbol{\delta}^i) \geq A_n(\mathbf{x}).
\tag{13}$$

To see that (13) together with (ii) and (iii) implies the theorem, note that for $\mathbf{x} \geq \mathbf{x}_n^0$ the theorem is obvious. Because of (13) and (ii) and (iii), for $\mathbf{x} < \mathbf{x}_n^0$, $\nabla^i H_n(\mathbf{x}) \geq 0$ for $i = 1, 2$; hence $\mathbf{x}$ is optimal. If $x^i > x_n^{0i}$ and $x^j < x_n^{0j}$,

then from (iii), $\nabla^i H_n(\mathbf{x}\wedge\mathbf{x}_n^0) < \nabla^i H_n(\mathbf{x}_n^0)$, which implies $a_n^i(\mathbf{x}) < a_n^i(\mathbf{x}_n^0)$. Similarly, (ii) implies $\nabla^j H_n(\mathbf{x}\wedge\mathbf{x}_n^0) > \nabla^j H_n(\mathbf{x}_n^0)$, so that $a_n^j(\mathbf{x}) = x^j$. However, increasing a coordinate at a time, it is straightforward to show that if $a_n^i(\mathbf{x}) < x_n^{0^i}$, then (13) would be violated.

The induction is complete if (i), (ii), and (iii) can be shown for period n. (i) and (iii) have already been proven; (ii) follows from concavity. ∎

An optimal policy from Theorem 3 is shown in Fig. 1, where $\mathbf{x}_n^0 = (x_n^{0^1}, x_n^{0^2})$. The policy has four regions, depending on whether or not x^{0^j} is obtainable from the present population size.

As n becomes large, $\mathbf{x}_n^0$ will tend to a single vector $\mathbf{x}^0$. If $p^1 \ggg p^2$, it is expected that an optimal policy will reduce one of the competitors to very low levels, while maintaining the more valuable species near its single-species base stock size. This "simplification" of the population dynamics is not, in most instances, a desirable feature, particularly if we have doubts that the model contains enough "richness" to accurately portray this simplified ecosystem. Extensions to more than two species are possible given similar assumptions.
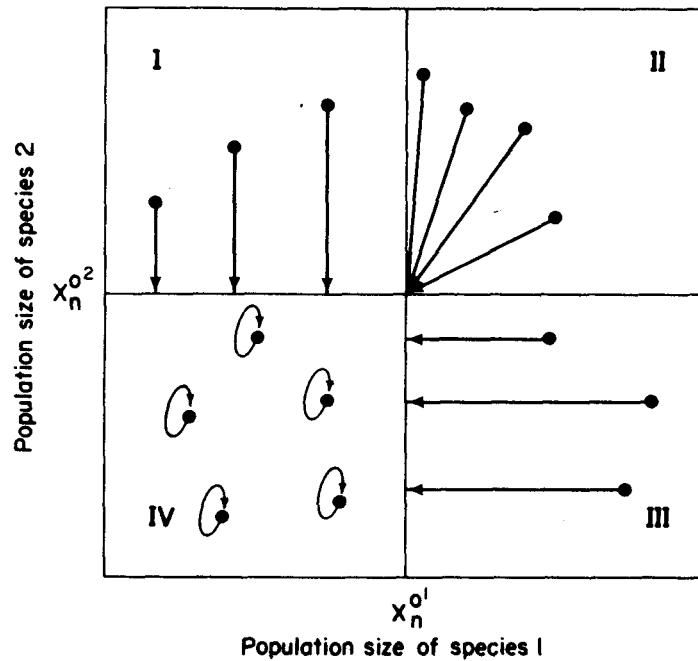

FIG. 1. Optional harvesting strategy for Silliman model at period n. In zone I, species 2 is harvested to $x_n^{0^2}$; species 1 is not harvested. In zone II, species 1 and 2 are harvested to $x_n^{0^1}, x_n^{0^2}$ respectively. In zone III, species 1 is harvested to $x_n^{0^1}$; species 2 is not harvested. In zone IV, neither species is harvested.

A simple predator-prey model analogous to the species competition model given by Eq. (9) is

$$x_{t+1}^1 = by_t^1 + m^2y_t^2 - r^1(y_t^1, d_t^1),$$

$$x_{t+1}^2 = r^2(y^2, d^2) - m^1y^1,$$

$$b, m^1, m^2 > 0 \qquad \text{w.p. 1.} \tag{14}$$

Here species 1 is the predator. It grows at a rate which is a mixture of its own population size and that of its prey, and decreases by a convex, nondecreasing function of its own population size, $r^1(y^1, d^1)$. Species 2 is the prey species. It increases by a concave function $r^2(y^2, d^2)$ and decreases by predation at a random rate m^1y^1.

Let ξ be a realization of the random variable d^1, and η a realization of b. Corollary 3 assumes that $\eta - r^{1[1]}(\cdot, \xi) < 0$ for all possible combinations of (η, ξ). This is equivalent to assuming that the predator population is nonincreasing in size without the presence of the prey. This would be true of an exclusive predator, which is not usual for fish species. However, the corollary gives insight into how harvesting will affect the ecosystem. The proof of Corollary 3 is not given, since given the above assumption, it is identical to that given for Theorem 3.

COROLLARY 3

If, in Theorem 3, S[y, d, b, m] is given by Eq. (14) instead of (9), with (d, b, m) possibly random, $r^1(\cdot, d^1)$ convex, continuous, and nondecreasing for each d^1, and $r^2(\cdot, d^2)$ concave, continuous, and nondecreasing for each d^2, then for each n and all $x \in X$, there exists an x_n^0 such that an optimal policy is given by

$$A_n(x) = x_n^0 \wedge x.$$

Similarly to Theorem 3, x_n^0 should tend to some x^0 as n gets large. If the prey species is much more valuable than the predator, an optimal policy will be to leave the predator at very low population sizes, and the prey close to a single-species optimum. If the predator is the more valuable species, then an optimal policy will tend to a prey population size that gives maximum growth to the predator. The prey should then be only a secondary or marginal component of the catch. This behavior is often observed in mixed fisheries.

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