ELSEVIER

Bionomic Equilibrium of Two-Species System. I

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ABSTRACT

The concept of bionomic equilibrium is used to obtain limits of cost per unit effort and maximum value of effort for the joint harvesting of three types of two-species systems: (1) a logistic growth model of two ecologically independent species, (2) a logistic growth model of two species that have competitive interactions, and (3) a Lotka–Volterra model of one prey and one predator. In each case, the existence of feasible bionomic equilibrium points and that of partially feasible bionomic equilibrium points are considered separately. First it is shown that cost per unit effort has both upper and lower threshold values if feasible bionomic equilibrium points occur, whereas it has only the upper threshold values if partially feasible bionomic equilibrium points occur. Further, the threshold values depend solely on the catchability coefficients, the selling prices of unit biomasses, and the parameters of the given model, namely the biotic potentials, carrying capacities, etc. Next, it is proven that for the first type of feasible point, if the cost per unit effort is kept under proper threshold values, then corresponding to each such value, the maximum value of the efforts exerted can be calculated in terms of the given parameters only. Moreover, the set of all such maximum values of the efforts for different choices of cost per unit effort is always bounded and the supremum of these maximum efforts is independent of the choice of cost per unit effort.

INTRODUCTION

Optimal harvesting of a two-species system has been considered by several authors who tried to maximize the total discounted revenue given by

$$J=\int_0^\infty e^{-\delta t}\pi(x,y,E,t)\,dt,$$

where δ is the instantaneous annual rate of discount [Wilkes 1], $e^{-\delta t}$ is the depreciation, $\pi(x,y,E,t)=(p_1q_1x+p_2q_2y-c)E(t)$ is the net revenue at time t, $E(t)$ is the total effort of harvesting subject to $0<E(t)<E_{\max}$, q_1 and q_2 are the catchability coefficients of the biomasses x

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and y, respectively, and p_1 and p_2 are the selling price of unit biomass of x and y, respectively.

The biomasses x and y are determined by suitable models:

(i) Larkin's [2] logistic growth model of two ecologically independent species is given by

$$\frac{dx}{dt} = G_1(x) \qquad \text{and} \qquad \frac{dy}{dt} = G_2(x), \tag{1}$$

where

$$G_1(x) = r_x x(1 - x/K_x), \qquad G_2(y) = r_y y(1 - y/K_y).$$

Optimal harvesting of this model has been considered by Clark [3–5].

(ii) Gause's [6] logistic growth model of two competing species is

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - \alpha xy, \qquad \frac{dy}{dt} = sy\left(1 - \frac{y}{L}\right) - \beta xy, \tag{2}$$

where r, s, α, β, K, and L are positive constants having the usual biological meanings. Joint harvesting of this model has been considered by Chaudhury [7]. Selective harvesting of this model has been considered by Clark [3,5].

(iii) A general model of one prey and one predator considered by Gibbons [8] is given by

$$\frac{1}{x}\frac{dx}{dt} = F(x,y), \qquad \frac{1}{y}\frac{dy}{dt} = G(x,y), \tag{3}$$

where F and G are smooth functions of their arguments satisfying

$$F_x < 0, \qquad F_y < 0, \qquad G_x > 0, \qquad G_y < 0, \qquad F_{xx} \leqslant 0, \qquad G_{yy} \leqslant 0,$$
$$F(x_0, y_0) = 0 = G(x_0, y_0), \qquad x_0 > 0;\ y_0 > 0;$$

$x(t)$ and $y(t)$ denote the stocks at time t of prey and predator, respectively; the subscript x or y denotes partial differentiation; (x_0, y_0) is the equilibrium point at which the species coexist. A special case of this model has been considered by Ragozin and Brown [9], where the prey has no commercial value. Hence, in this case, the predator is selectively harvested. A common prey–predator model has been considered under joint harvesting by Chaudhury [10]. It is given by

$$\frac{dx}{dt} = rx - \alpha xy; \qquad \frac{dy}{dt} = -sy + \beta xy. \tag{4}$$

Obviously, in the above process of optimization of the revenue π, first a priori knowledge of the control set $V_t = [0, E_{\max}]$ is necessary. But in the literature there is no indication of how to obtain the maximum value of the efforts. Second, when the maximum value of the efforts exists, the cost per unit effort, c, cannot remain unbounded. So limits of cost per unit effort should also be obtained, but no attempt has yet been made to determine these limits. Nevertheless, it may be mentioned that a result of Clark [4] may be put in a suitable form to obtain the upper threshold value of c for a partially feasible bionomic equilibrium point only. To make the point more clear, it is better to discuss in brief the work of Clark [3–5] in this connection.

For joint harvesting, the differential equations of the exploited system are given by

$$\frac{dx}{dt} = G_1(x) - q_x Ex, \qquad \frac{dy}{dt} = G_2(y) - q_y Ey, \tag{5}$$

where

$$G_1(x) = r_x x(1 - x/K_x), \qquad G_2(y) = r_y y(1 - y/K_y),$$

with the restrictions $r_x/q_x > r_y/q_y$ [3,4] and $r_x/q_x < r_y/q_y$ [5]. Here the same effort is applied to both species. The fishing mortalities are $f_x = q_x E$ and $f_y = q_y E$, which are different due to different catchability coefficients q_x and q_y. In this case, the nontrivial equilibrium points are given by

$$\frac{G_1(x)}{q_x x} = \frac{G_2(y)}{q_y y} = E. \tag{6}$$

The locus of all such equilibrium points, $L = 0$, is given by

$$G_1(x)/q_x(x) = G_2(y)/q_y y. \tag{7}$$

The line of zero revenue is

$$p_x q_x x + p_y q_y y - c = 0 \qquad [\pi = 0]. \tag{8}$$

Clark defined a bionomic equilibrium point as the point of intersection of $L = 0$ and $\pi = 0$ provided it lies in the positive quadrant of the xy plane. Obviously, for the attainability of such bionomic equilibrium points, E must be positive, although that has not been stated explicitly. However, what is more important is that, with the help of the above concept, Clark [3] was able to reach the conclusion "The fishery remains viable even though one of the valuable species x and y is ultimately fished out." His reasons are as follows.

The nontrivial dynamic equilibrium point of the unexploited system given by (1) is $B_0 = (K_x, K_y)$. As E increases, taking positive values starting with $E = 0$, the variable points (x, y) on $L = 0$ satisfy $x < K_x$ and $y < K_y$. Clark noted that there are two possible positions of bionomic equilibrium points, namely B_1 (where x and y are both positive) and B_2 (where $x > 0$, $y = 0$, $\pi > 0$) (see Figure 1). Although point B_2 is not a common point of $L = 0$ and $\pi = 0$, still it has been taken as a bionomic equilibrium point because the revenue is positive at

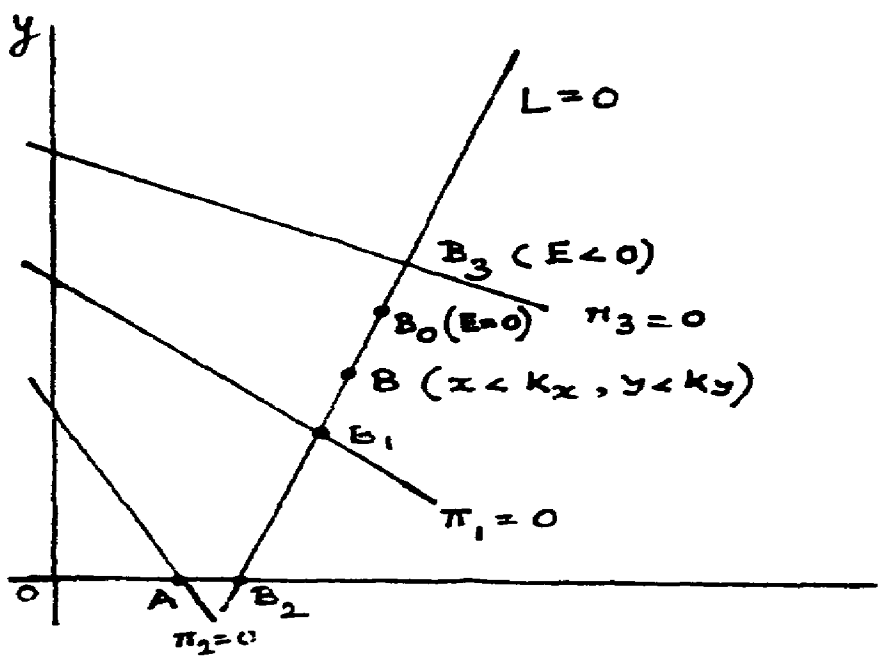

FIG. 1.

this point, so the fishery will remain viable with one species only. At point $B_2 = (x, 0)$, $x = K_x[1 - (r_y/q_y)/(r_x/q_x)]$. Under the hypothesis that $r_x/q_x > r_y/q_y$, x is positive. Also, for the point $A = (x, 0)$, $x = c/p_x q_x$. Naturally, for $\pi > 0$, the required condition is

$$(c/p_x q_x) < K_x\left(1 - \frac{r_y/q_y}{r_x/q_x}\right). \tag{9}$$

We simply remark that this condition may be put in the form

$$0 < c < p_x q_x K_x\left(1 - \frac{r_y/q_y}{r_x/q_x}\right).$$

Thus an upper threshold value of c can be found for which B_2 is feasible.

It is observed that when a bionomic feasible point B_1 occurs in place of B_2, exploitation becomes meaningful for any effort for which dynamic equilibrium points lie between B_0 and B_1 on $L = 0$. The reason is that π becomes negative as soon as dynamic equilibrium points on $L = 0$ cross B_1, and this is practically useless. The next problem, therefore, is to find threshold values of c for which a biömetric equilibrium point like B_1 occurs in place of B_2. It is expected that the required condition is

$$c \geqslant p_x q_x K_x\left(1 - \frac{r_y/q_y}{r_x/q_x}\right)$$

because, as remarked by Clark, the alternative possibility for the occurrence of B_2 is that of $B_1 = (x, y)$, $x > 0$, $y > 0$. But, in our analysis, we have shown that this is not true. In fact, the bionomic equilibrium point has been just the point of intersection of $\pi = 0$ and $L = 0$ in the positive quadrant of the xy plane, so the violation of condition (9) alone cannot stop the occurrence of points like $B_3 = (x, y)$, $x > 0$, $y > 0$, where $E < 0$. Thus the whole analysis of optimal harvesting may fail at this stage. In fact, this is the crucial point that is found missing in the whole literature. Further, this has led subsequent workers to obtain incorrect results in this connection. For example, we may consider [10]. Chaudhury and Ray considered the harvested model given by

$$\frac{dx}{dt} = rx - \alpha xy - q_1 Ex; \qquad \frac{dy}{dt} = -sy + \beta xy - q_2 Ey. \tag{10}$$

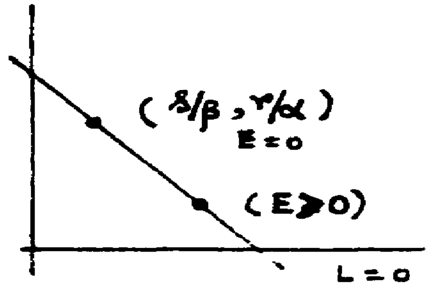

FIG. 2.

For this model, the nonnull equilibrium point is

$$(x, y) = ((s + q_2 E)/\beta, (r - q_1 E)/\alpha).$$

The line of dynamic equilibrium points is given by

$$L: \quad (\beta/q_2)x + (\alpha/q_1)y = (s/q_2 + r/q_1).$$

The line $L = 0$ starts at $(x, y) = (s/\beta, r/\alpha)$, where $E = 0$. Obviously, $E < r/q_1$ to ensure $y > 0$. As E increases, the line $L = 0$ takes the form given in Figure 2. Chaudhury and Ray denoted by (x_∞, y_∞), $(x_\infty, 0)$, and $(0, y_\infty)$ the equilibrium points as shown in Figures 3, 4, and 5, respectively. They obtained conditions for the existence of bionomic equilibrium points like (x_∞, y_∞). But these conditions are not true. In fact, we have proved in our theorem 3, page 122 that, for this model, only partially feasible $(x_\infty, 0)$ exists as a bionomic equilibrium point.

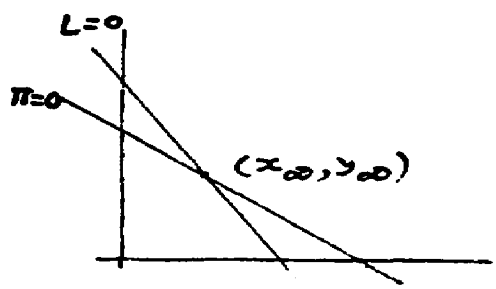

FIG. 3.

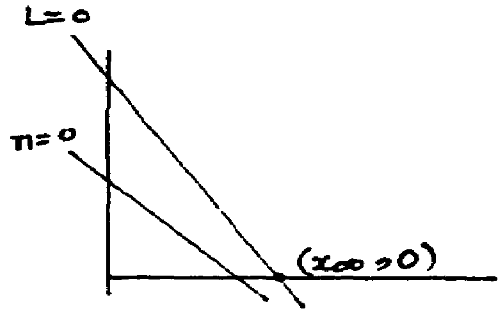

FIG. 4.

Next, let us consider [7]. In this case, the harvested model is given by

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - \alpha xy - q_1 Ex, \qquad \frac{dy}{dt} = sy\left(1 - \frac{y}{L}\right) - \beta xy - q_2 Ey, \tag{11}$$

where r, s, α, β, K, and L are positive constants having the usual biological meanings. In this case, the conditions for the existence of (x_∞, y_∞) have not been obtained. However, conditions for $(0, y_\infty)$ have been found to be

$$\text{(a)} \quad \frac{s}{q_2} > \max\left(\frac{r}{q_1}, \alpha L q_1\right) \qquad \text{or} \qquad \text{(b)} \quad \frac{s}{q_2} < \min\left(\frac{r}{q_1}, \alpha L q_1\right)$$

and

$$\text{(c)} \quad \frac{s}{q_2 L} - \frac{\alpha}{q_1} \geqslant \min\left[\left(\frac{p_2 q_2}{c}\right)\left(\frac{s}{q_2} - \frac{r}{q_1}\right), \left(\frac{p_2 q_2}{p_1 q_1}\right)\left(\frac{\beta}{q_2} - \frac{r}{K q_1}\right)\right]$$

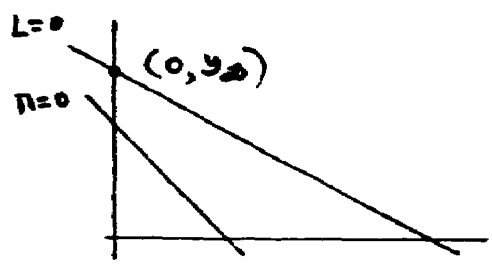

FIG. 5.

or

(d) $$\frac{s}{q_2 L} - \frac{\alpha}{q_1} \geqslant \max\left[\left(\frac{p_2 q_2}{c}\right)\left(\frac{s}{q_2} - \frac{r}{q_1}\right), \left(\frac{p_2 q_2}{p_1 q_1}\right)\left(\frac{\beta}{q_2} - \frac{r}{Kq_1}\right)\right].$$

But these conditions are not sufficient, as they cannot ensure that E is positive at the point $(0, y_\infty)$. Similarly, the corresponding conditions for the existence of $(x_\infty, 0)$ are also found to be insufficient.

Our motivation in this paper is precisely to discover the threshold values of the cost per unit effort beyond which exploitation becomes impossible and the maximum value of the effort, which determines the feasible domain of the control parameter necessary for optimization.

For the purpose of joint harvesting, three types of models of the two-species system, with suitable restrictions on the parameters, are given in the next section. In the following sections, these models are analyzed. Limits of cost per unit effort, as well as maximum effort or the supremum of the maximum values of the efforts, as the case may be, are obtained in respective cases. The Appendix contains three theorems that cover all the results concerning the three models. These theorems have also been proven in detail. Further, the Appendix also contains some examples that are formed by suitable choice of parameters of the given models. With these examples, the results of the aforesaid theorems have been verified. The concluding section makes some observations and points out some open problems.

FISHERY MODELS OF TWO-SPECIES SYSTEM UNDER JOINT HARVESTING

MODEL I. LOGISTIC GROWTH MODEL OF TWO ECOLOGICALLY INDEPENDENT SPECIES

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - q_1 Ex, \qquad \frac{dy}{dt} = sy\left(1 - \frac{y}{L}\right) - q_2 Ey, \tag{12}$$

with either of the restrictions

(a) $r/q_1 > s/q_2$ or (b) $r/q_1 < s/q_2$,

where x, y are the biomasses, r, s are the biotic potentials, K, L are the carrying capacities; and q_1, q_2 are the catchability coefficients.

MODEL II. LOGISTIC GROWTH MODEL OF TWO SPECIES HAVING COMPETITIVE INTERACTIONS

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - \alpha xy - q_1 Ex, \qquad \frac{dy}{dt} = sy\left(1 - \frac{y}{L}\right) - \beta xy - q_2 Ey, \tag{13}$$

with any one of the following four restrictions:

(a) (i) $r < \alpha L$, $s < \beta K$, and $sq_1 < rq_2 < \beta K q_1$;
(ii) $\alpha L < r$, $\beta K < s$, and $\alpha L q_2 < sq_1 < rq_2$;
(b) (i) $r < \alpha L$, $s < \beta K$, and $rq_2 < sq_1 < \alpha L q_2$;
(ii) $\alpha L < r$, $\beta K < s$, and $\beta K q_1 < rq_2 < sq_1$;

where r, s, K, and L are positive constants having the usual biological meanings and $\alpha > 0$, $\beta > 0$ are coefficients of interspecies competition.

MODEL III. LOTKA–VOLTERRA MODEL OF ONE PREY AND ONE PREDATOR

$$\frac{dx}{dt} = rx - \alpha xy - q_1 Ex; \qquad \frac{dy}{dt} = -sy + \beta xy - q_2 Ey, \tag{14}$$

where r is the growth rate of the prey x, s is the rate at which the predator dies out in the absence of the prey, α is the amount of prey consumed by unit predator in unit time, and α/β is the fraction of the energy consumed from the biomass αx for the predator reproduction.

COST PER UNIT EFFORT AND MAXIMUM EFFORT

DEFINITION 1

Let $L = 0$ denote the locus of all nontrivial dynamic equibrium points of a two-species system under joint harvesting with the same effort applied to both species, and let $\pi = 0$ denote the zero profit line. Then a *feasible bionomic equilibrium point* is defined as the point of intersection (x, y) of $L = 0$ and $\pi = 0$ if $x > 0$, $y > 0$ and the total effort E at (x, y) is positive. It is denoted by (x_∞, y_∞).

DEFINITION 2

Let $L = 0$ be defined as above. A *partially feasible bionomic equilibrium point* is defined as the point of intersection of $L = 0$ with one of the coordinate axes, provided the nonzero coordinate of that point is positive and both E and π are positive at that point. It is denoted by $(x_\infty, 0)$ or $(0, y_\infty)$ if $L = 0$ intersects the x axis or the y axis, respectively.

THEOREM 1

Let the combined harvesting of the two-species system be given by Model I. Then under restriction (a),

(i) (x_∞, y_∞) *is a feasible bionomic equilibrium point if and only if*

$$Kp_1q_1(1 - (sq_1/rq_2)) < c < (Kp_1q_1 + Lp_2q_2) \tag{15}$$

and $E_{\max}$ values are given by

$$x_\infty = K[1-(q_1/r)E_{\max}]. \tag{16}$$

where

$$x_\infty = \frac{K[csq_1 + Lp_2q_2(-sq_1 + rq_2)]}{sKp_1q_1^2 + rLp_2q_2^2} \tag{17}$$

and c takes values given by (15). Further, the set of all such $E_{\max}$ values for different choices of c given by (15) is bounded and

$$\sup(E_{\max}) = s/q_2. \tag{18}$$

(ii) *$(x_\infty, 0)$ is a partially feasible bionomic equilibrium point if and only if*

$$0 < c < Kp_1q_1(1-(sq_1/rq_2)). \tag{19}$$

In this case,

$$E_{\max} = s/q_2. \tag{20}$$

Again, under restriction (b).

(iii) *(x_∞, y_∞) is a feasible bionomic equilibrium point if and only if*

$$Lp_2q_2(1-(rq_2/sq_1)) < c < (Kp_1q_1 + Lp_2q_2), \tag{21}$$

where $E_{\max}$ values are given by (16) and (17) and c takes values given by (21). Further, the set of all $E_{\max}$ values for different choices of c given by (21) is also bounded, and

$$\sup(E_{\max}) = r/q_1. \tag{22}$$

(iv) *$(0, y_\infty)$ is a partially feasible bionomic equilibrium point if and only if*

$$0 < c < Lp_2q_2(1-(rq_2/sq_1)). \tag{23}$$

In this case,

$$E_{\max} = r/q_1 \tag{24}$$

THEOREM 2

Let the combined harvesting of a two-species system be given by Model II. Then under (a)(i) and (b)(ii),

(i) *(x_∞, y_∞) is a feasible bionomic equilibrium point if and only if*

$$\frac{Lp_2q_2(rq_2 - sq_1)}{L\alpha q_2 - sq_1} < c < \frac{sKp_1q_1(L\alpha - r) + rLp_2q_2(K\beta - s)}{\alpha\beta KL - rs}, \tag{25}$$

and $E_{\max}$ values are given by

$$x_\infty = \bar{x} - \frac{K(\alpha L q_2 - s q_1) E_{\max}}{\alpha\beta K L - rs}, \tag{26}$$

where

$$\bar{x} = \frac{Ks(\alpha L - r)}{\alpha\beta K L - rs}, \tag{27}$$

$$x_\infty = \frac{K[L p_2 q_2 (r q_2 - s q_1) - c(\alpha L q_2 - s q_1)]}{K p_1 q_1 (s q_1 - \alpha L q_2) - L p_2 q_2 (K\beta q_1 - r q_2)}, \tag{28}$$

and c takes values determined by (25). *Further, the set of all such $E_{\max}$ values for different choices of c given by* (25) *is bounded and*

$$\sup(E_{\max}) = \frac{s(\alpha L - r)}{\alpha L q_2 - s q_1}. \tag{29}$$

(ii) $(0, y_\infty)$ *is a partially feasible bionomic equilibrium point if and only if*

$$0 < c < \frac{L p_2 q_2 (s q_1 - r q_2)}{s q_1 - \alpha L q_2}. \tag{30}$$

In this case,

$$E_{\max} = \frac{s(\alpha L - r)}{\alpha L q_2 - s q_1}. \tag{31}$$

Similarly, under both restrictions (a)(ii) *and* (b)(i),

(iii) (x_∞, y_∞) *is a feasible bionomic equilibrium point if and only if*

$$\frac{K p_1 q_1 (r q_2 - s q_1)}{r q_2 - K\beta q_1} < c < \frac{s K p_1 q_1 (\alpha L - r) + r L p_2 q_2 (K\beta - s)}{\alpha\beta K L - rs}, \tag{32}$$

$E_{\max}$'s are given by (26)–(28), *and c takes values determined by* (32). *Further, the set of all such $E_{\max}$'s for different choices of c given by* (32) *is bounded, and*

$$\sup(E_{\max}) = \frac{r(K\beta - s)}{K\beta q_1 - r q_2}. \tag{33}$$

(iv) $(x_\infty, 0)$ *is a partially feasible bionomic equilibrium point if and only if*

$$0 < c < \frac{K p_1 q_1 (s q_1 - r q_2)}{K\beta q_1 - r q_2} \tag{34}$$

and

$$E_{\max} = \frac{r(K\beta - s)}{K\beta q_1 - rq_2}. \tag{35}$$

THEOREM 3

Let the combined harvesting of two species be given by Model III. Then $(x_\infty, 0)$ is a partially feasible bionomic equilibrium point if and only if

$$0 < c < (p_1/\beta)(sq_1 + rq_2) \tag{36}$$

and

$$E_{\max} = r/q_1. \tag{37}$$

Further, neither (x_∞, y_∞) nor $(0, y_\infty)$ is bionomically feasible.

CONCLUSION

For system I with restriction (a), it follows from (15) and (19) that (x_∞, y_∞) and $(x_\infty, 0)$ are not simultaneously feasible. Further, $(0, y_\infty)$ is not at all feasible, as

$$y_\infty = L(1 - (rq_2/sq_1)) < 0 \qquad \text{at } (0, y_\infty).$$

Similarly, (23) and (21) indicate that for system I with restriction (b), (x_∞, y_∞) and $(0, y_\infty)$ are not feasible simultaneously. Further, $(x_\infty, 0)$ is not at all feasible, as

$$x_\infty = K(1 - (sq_1/rq_2)) < 0 \qquad \text{at } (x_\infty, 0).$$

It may be similarly remarked that no two of (x_∞, y_∞), $(x_\infty, 0)$, and $(0, y_\infty)$ are simultaneously feasible for system II. Finally, for system III, the only feasible bionomic equilibrium point is $(x_\infty, 0)$.

Further, it may be observed that for all the models, whenever $(x_\infty, 0)$ or $(0, y_\infty)$ is a partially feasible bionomic equilibrium point, $E_{\max}$ is given by a value that is independent of the choice of c. But whenever (x_∞, y_∞) is a feasible bionomic equilibrium point, $E_{\max}$ is different for different choices of c. However, in all such cases, $\sup(E_{\max})$ always exists, and it is independent of c.

Thus, it may be concluded that it is a threshold value of c that matters most in a fishery problem. Unless c is kept under proper threshold values, feasible or even partially feasible bionomic equilibrium points do not occur. This leads to nondetermination of $E_{\max}$ or

$\sup(E_{max})$, as the case may be. As a result, optimization of revenue becomes meaningless.

From the aforesaid nature of feasibility of bionomic equilibrium points, it is very natural to point out the following open problems.

(i) Does there exist a model where (x_∞, y_∞) and $(x_\infty, 0)$ are bionomically feasible simultaneously? If so, what is $E_{max}/\sup(E_{max})$?

(ii) Does there exist a model where (x_∞, y_∞) and $(0, y_\infty)$ are bionomically feasible simultaneously? If so, what is $E_{max}/\sup(E_{max})$?

(iii) Does there exist a model where (x_∞, y_∞) is bionomically feasible but E_{max} does not exist?

APPENDIX

PROOF OF THEOREM 1

The revenue function is

$$\pi = (p_1 q_1 x + p_2 q_2 y - c)E. \tag{38}$$

The dynamic equilibrium point of the unexploited system is $(\bar{x}, \bar{y}) = (K, L)$. The dynamic equilibrium point of the exploited system is $(\tilde{x}, \tilde{y})$, where

$$\tilde{x} = K(1 - (q_1 E/r)), \qquad \tilde{y} = L(1 - (q_2 E/s)). \tag{39}$$

$$\tilde{x} > 0, \qquad \tilde{y} > 0 \qquad \text{if } E < \min(r/q_1, s/q_2); \tag{40}$$

$$\tilde{x} < \bar{x}, \qquad \tilde{y} < \bar{y}, \qquad \text{for all } E > 0. \tag{41}$$

The line of dynamic equilibrium points is given by

$$L\colon \quad \frac{r}{Kq_1}x - \frac{s}{Lq_2}y + \left(\frac{s}{q_2} - \frac{r}{q_1}\right) = 0; \tag{42}$$

$$x_\infty = \frac{K[csq_1 + Lp_2 q_2(rq_2 - sq_1)]}{sKp_1 q_1^2 + rLp_2 q_2^2}; \tag{43}$$

$$y_\infty = \frac{L[crq_2 - Kp_1 q_1(rq_2 - sq_1)]}{sKp_1 q_1^2 + rLp_2 q_2^2}. \tag{44}$$

Case (a). $x_\infty > 0$, by hypothesis; $y_\infty > 0$ if

$$c > Kp_1 q_1(1 - (sq_1/rq_2)). \tag{45}$$

For feasibility of (x_∞, y_∞), E should be positive, and hence we must get $x_\infty < \bar{x}$, $y_\infty < \bar{y}$, the condition for which is

$$c < Lp_2 q_2 + Kp_1 q_1. \tag{46}$$

So (x_∞, y_∞) is bionomically feasible if and only if (15) holds. Furthermore, $E_{\max}$ values are given by (16). Also, in such a case, $E < \min(r/q_1, s/q_2) = s/q_2$. Next, for the feasibility of $(x_\infty, 0)$, we have $x_\infty = K(1-(sq_1/rq_2)) > 0$, by hypothesis. At the point $(x_\infty, 0)$,

$$E = (s/q_2) > 0. \tag{47}$$

Now, at $(x_\infty, 0)$,

$$\pi > 0 \qquad \text{iff } c < Kp_1q_1(1-(sq_1/rq_2)).$$

Hence, $(x_\infty, 0)$ is a partially feasible bionomic equilibrium point if and only if (19) holds. Further, $E_{\max}$ equals the value of E at $(x_\infty, 0)$ or s/q_2. Again, $(0, y_\infty)$ is not feasible, as at that point $y_\infty = L(1-(rq_2/sq_1)) < 0$. Hence, from (47) it follows that $\sup(E_{\max}) = s/q_2$ when (x_∞, y_∞) is feasible.

Proof of case (b) follows similarly.

PROOF OF THEOREM 2

Using the notations of Theorem 1, we have

$$\bar{x} = \frac{Ks(\alpha L - r)}{\alpha\beta KL - rs}, \qquad \bar{y} = \frac{Lr(K\beta - s)}{\alpha\beta KL - rs}; \tag{48}$$

$$\tilde{x} = \bar{x} - \frac{KE(L\alpha q_2 - sq_1)}{\alpha\beta KL - rs}, \qquad \tilde{y} = \bar{y} - \frac{LE(K\beta q_1 - rq_2)}{\alpha\beta KL - rs}; \tag{49}$$

$$\tilde{x} > 0, \quad \tilde{y} > 0 \qquad \text{if } E < \min\left(\frac{s(L\alpha - r)}{L\alpha q_2 - sq_1}, \frac{r(K\beta - s)}{K\beta q_1 - rq_2}\right); \tag{50}$$

$$\tilde{x} < \bar{x}, \quad \tilde{y} < \bar{y} \qquad \text{under restrictions (a) and (b);} \tag{51}$$

$$L: \quad x\left(\frac{\beta}{q_2} - \frac{r}{q_1K}\right) + y\left(\frac{s}{Lq_2} - \frac{\alpha}{q_1}\right) + \left(\frac{r}{q_1} - \frac{s}{q_2}\right) = 0; \tag{52}$$

$$x_\infty = \frac{K[Lp_2q_2(rq_2 - sq_1) - c(\alpha Lq_2 - sq_1)]}{Kp_1q_1(sq_1 - \alpha Lq_2) - Lp_2q_2(K\beta q_1 - rq_2)}; \tag{53}$$

$$y_\infty = \frac{L[Kp_1q_1(rq_2 - sq_1) + c(K\beta q_1 - rq_2)]}{Lp_2q_2(K\beta q_1 - rq_2) + Kp_1q_1(\alpha Lq_2 - sq_1)}. \tag{54}$$

For cases (a)(i) and (b)(ii), $y_\infty > 0$. Further, $x_\infty > 0$ if

$$c > \frac{Lp_2q_2(rq_2 - sq_1)}{L\alpha q_2 - sq_1}. \tag{55}$$

For cases (a)(ii) and (b)(i), $x_\infty > 0$. Further, $y_\infty > 0$ if

$$c > \frac{Kp_1q_1(sq_1 - rq_2)}{K\beta q_1 - rq_2}. \tag{56}$$

In all cases, $x_\infty < \bar{x}$, $y_\infty < \bar{y}$ if

$$c < \frac{sKp_1q_1(\alpha L - r) + rLp_2q_2(K\beta - s)}{\alpha\beta KL - rs}. \tag{57}$$

Therefore, under restrictions (a)(i) and (b)(ii), (x_∞, y_∞) is a feasible bionomic equilibrium point if and only if (25) holds. Similarly, under restrictions (a)(ii) and (b)(i), (x_∞, y_∞) is a feasible bionomic equilibrium point if and only if (32) holds. Further, $E_{\max}$ values are determined by (26)–(28). Moreover, $E_{\max}$ depends on values of c given by (25) for cases (a)(i) and (b)(ii) and values of c given by (32) for cases (a)(ii) and (b)(i). But in all cases, whenever (x_∞, y_∞) is a feasible bionomic equilibrium point,

$$E < \left(\frac{s(L\alpha - r)}{L\alpha q_2 - sq_1}, \frac{r(K\beta - s)}{K\beta q_1 - rq_2} \right).$$

It now follows that for cases (a)(i) and (b)(ii), $(x_\infty, 0)$ is not partially feasible. However, $(0, y_\infty)$ is a partially feasible bionomic equilibrium point if and only if (30) holds. In this case $E_{\max}$ is given by (31). Further, when (x_∞, y_∞) is feasible, $\sup(E_{\max})$ is given by (29). Similarly, under (a)(ii) and (b)(i), $(0, y_\infty)$ is not partially feasible. However, $(x_\infty, 0)$ is a partially feasible bionomic equilibrium point if and only if (34) holds. In this case, $E_{\max}$ is given by (35). Further, for feasible (x_∞, y_∞), $\sup(E_{\max})$ is given by (35).

PROOF OF THEOREM 3

Using the notations of Theorem 1, we have

$$\bar{x} = \frac{s}{\beta}, \qquad \bar{y} = \frac{r}{\alpha}, \qquad \tilde{x} = \frac{1}{\beta}(s + q_2E), \qquad \tilde{y} = \frac{1}{\alpha}(r - q_1E). \tag{58}$$

Obviously,

$$\tilde{x} > 0 \quad \text{and} \quad \tilde{y} > 0 \qquad \text{if } E < r/q_1. \tag{59}$$

Again,

$$\tilde{x} > \bar{x}, \qquad \tilde{y} < \bar{y}. \tag{60}$$

$$L: \quad \frac{\beta}{q_2}x + \frac{\alpha}{q_1}y = \frac{s}{q_2} + \frac{r}{q_1}. \tag{61}$$

$$x_\infty > 0 \quad \text{and} \quad y_\infty > 0 \qquad \text{if } c < \min(A, B) \quad \text{or} \quad c > \max(A, B), \tag{62}$$

where

$$x_\infty = \frac{p(rq_2 + sq_1) - \alpha c}{q_2(\beta p_2 - \alpha p_1)}, \qquad y_\infty = \frac{p(rq_2 + sq_1) - \beta c}{q_2(\alpha p_1 - \beta p_2)}, \tag{63}$$

$$A = \frac{\beta p_2^2(rq_2 + sq_1)}{\alpha^2 p_1}, \qquad B = \frac{\alpha p_1^2(rq_2 + sq_1)}{\beta^2 p_1}. \tag{64}$$

Now, $x_\infty > \bar{x}$ if $c < C$, and $y_\infty < \bar{y}$ if $c > C$, where

$$C = \frac{1}{\alpha\beta}(\alpha s p_1 q_1 + \beta r p_2 q_2). \tag{65}$$

It follows from (65) that (x_∞, y_∞) is not bionomically feasible. $(0, y_\infty)$ is not feasible because as $E = -(s/q_2) < 0$ at the point $(0, y_\infty)$.

$(x_\infty, 0)$ is a partially feasible bionomically equilibrium point if and only if (36) holds. Further, in this case, $E_{\max} = r/q_1$.

SPECIAL CHOICE OF PARAMETERS IN FISHERY MODELS

Model I

Case (a). $r = 3$, $q_1 = 2$, $p_1 = 3$, $K = 1$; $s = 1$, $q_2 = 1$, $p_2 = 4$, $L = 2$.

(i) For feasibility of (x_∞, y_∞), $2 < c < 14$. Let $c = 6$; then $E_{\max} = 5/6$, $\sup(E_{\max}) = 1$, so, $E_{\max} < \sup(E_{\max})$.

(ii) For partial feasibility of $(x_\infty, 0)$, $0 < c < 2$ and $E_{\max} = 1$.

Case (b). $r = 1$, $q_1 = 1$, $p_1 = 3$, $K = 1$; $s = 3$, $q_2 = 2$, $p_2 = 4$, $L = 2$.

(iii) For feasible (x_∞, y_∞), $16/3 < c < 19$. Let $c = 7$; then $E_{\max} = 36/41$, $\sup(E_{\max}) = 1$. Thus $E_{\max} < \sup(E_{\max})$.

For partially feasible $(0, y_\infty)$, $0 < c < 16/3$ and $E_{\max} = 1$.

Model (II)

Case (a)(i). $\alpha = 1$, $r = 1$, $q = 1$, $p = 3$, $K = 2$; $\beta = 2$, $q = 2$, $p = 4$, $L = 3$. For feasibility of (x_∞, y_∞), $24/5 < c < 84/11$. Let $c = 6$; then $E_{\max} = 3/13$ and $\sup(E_{\max}) = 2/5$, so $E_{\max} < \sup(E_{\max})$.

For partial feasibility of $(0, y_\infty)$, $0 < c < 24/5$ and $E_{\max} = 2/5$.

Case (a)(ii). $\alpha = 1$, $r = 5$, $q_1 = 1$, $p_1 = 1$, $K = 1$; $\beta = 2$, $s = 8$, $q_2 = 2$, $p_2 = 1$, $L = 1$. For feasible (x_∞, y_∞), $1/4 < c < 46/19$. Let $c = 2$; then $E_{\max} = 8/11$, $\sup(E_{\max}) = 15/4$. Thus $E_{\max} < \sup(E_{\max})$.

For partially feasible $(x_\infty, 0)$, $0 < c < 1/4$ and $E_{\max} = 15/4$.

Case (b)(i). $\alpha = 1$, $r = 1$, $q_1 = 2$, $p_1 = 3$, $K = 2$; $\beta = 2$, $s = 1$, $q_2 = 1$, $p_2 = 4$, $L = 3$. For feasible (x_∞, y_∞), $12/7 < c < 60/11$. Let $c = 3$; then $E_{\max} = 9/32$, $\sup(E_{\max}) = 3/7$. Thus $E_{\max} < \sup(E_{\max})$.

For partially feasible $(x_\infty, 0)$, $0 < c < 22/17$ and $E_{\max} = 3/7$.

Model III

In this case, (x_∞, y_∞) is not feasible, so $E_{\max}$ is independent of c. Hence, there is no need to find $\sup(E_{\max})$ and compare it with $E_{\max}$.

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