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HARVESTING A TWO-PATCH PREDATOR-PREY METAPOPULATION

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ABSTRACT. A mathematical model for a two-patch predator-prey metapoplation is developed as a generalization of single-species metapopulation harvesting theory. We find optimal harvesting strategies using dynamic programming and Lagrange multipliers. If predator economic efficiency is relatively high, then we should protect a relative source prey subpopulation in two different ways: directly, with a higher escapement of the relative source prey subpopulation, and indirectly, with a lower escapement of the predator living in the same patch as the relative source prey subpopulation. Numerical examples show that if the growth of the predator is relatively low and there is no difference between prey and predator prices, then it may be optimal to harvest the predator to extinction. While, if the predator is more valuable compared to the prey, then it may be optimal to leave the relative exporter prey subpopulation unharvested. We also discuss how a 'negative' harvest might be optimal. A negative harvest might be considered a seeding strategy.

KEY WORDS: Fisheries, harvesting strategies, predator-prey metapopulation, seeding strategy.

1. Introduction. This paper studies optimal harvesting strategies for a two-patch predator-prey metapopulation. The dynamics of the predator-prey metapopulation is defined by four coupled difference

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equations. Optimal harvesting strategies for the metapopulation are derived using dynamic programming and Lagrange multipliers. The theory presented here is a generalization of single-species metapopulation harvesting theory developed by Tuck and Possingham [1994].

The optimal strategy for managing a dynamic renewable resource was not established until Clark [1971, 1973 and 1976], explored optimal harvesting strategies for a single-species population using dynamic programming. Clark showed that if the growth rate of the resource is less than the discount rate, then a rational sole owner maximizing the net economic gain of a resource should exploit the resource to extinction. Clark's work [1971, 1973 and 1976] has been very influential in the development of an economic theory of renewable resource exploitation and has been extended to include various economic and biological complexities (Reed [1982], Agnew [1982], Gatto et al. [1982], Clark and Tait [1982], Ludwig and Walters [1982], Chaudhuri [1986 and 1988], Mesterton-Gibbons [1996], Tuck and Possingham [1994], Ganguly and Chaudhuri [1995], Supriatna and Possingham [1998]).

Spatial heterogeneity is recognized as a factor that needs to be taken into account in population modelling in general (Dubois [1975], Goh [1975], Hilborn [1979], Lefkovitch and Fahrig [1985], Matsumoto and Seno [1995]), and in fisheries modelling in particular (Beverton and Holt [1957], Brown and Murray [1992], Frank [1992], Frank and Leggett [1994], Parma et al. [1998]). In the ocean, population patches may exist from scales of meters to thousands of kilometers and often occur in response to physical and biological processes, like advection, temperature and food quality (Letcher and Rice [1997]). The inclusion of spatial heterogeneity may change the decisions that should be made to manage a fishery (Tuck and Possingham [1994], Pelletier and Magal [1996], Brown and Roughgarden [1997]). With the inclusion of spatial heterogeneity into Clark's [1976] model, Tuck and Possingham [1994] found some rules of thumb for optimal economic harvesting of a two-patch single-species metapopulation system. One of their rules is that a relative source subpopulation, that is a subpopulation with a greater per-capita larval production, should be harvested more conservatively than a relative sink subpopulation. We define the terms 'relative source' and 'relative sink' subpopulation more precisely in the next section.

Supriatna and Possingham [1998] showed that, in some circumstances, Tuck and Possingham's [1994] single-species harvesting rules of thumb are preserved in the presence of a predator. Our previous model (Supriatna and Possingham [1998]) assumed that predation affects the predator survival. In this paper, we modify our previous model to assume that predation affects predator recruitment, that is, prey consumption primarily increases the predator population through production and survival of young rather than adult survival. The results in this paper show that the most significant rule, that we should harvest a relative source subpopulation more conservatively than a relative sink subpopulation, is robust, regardless of the biological structure of the population. We also explore the situation in which the optimal harvest for one of the populations is negative. While at first glance this appears unlikely, a negative harvest could be implemented in some cases by seeding a population.

2. The model. Consider a predator-prey metapopulation that coexists in two different patches, patch 1 and patch 2. The movement of individuals between the local populations is a result of dispersal by juveniles. Adults are assumed to be sedentary, and they do not migrate from one patch to another patch. Let the number of the prey (predator) in patch i at the beginning of period k be denoted by N_{ik} (P_{ik}) and the survival rate of adult prey (predator) in patch i be denoted by a_i (b_i), respectively. The proportion of juvenile prey and predator from patch i that successfully migrate to patch j are p_{ij} and q_{ij}, respectively, see Figure 1. Let $S_{Nik} = N_{ik} - H_{Nik} (S_{Pik} = P_{ik} - H_{Pik})$ be the escapement of the prey (predator) in patch i at the end of that period, with H_{Nik} (H_{Pik}) the harvest taken from the prey (predator). Furthermore, let the dynamics of exploited metapopulation of these two species be given by the equations:

$$N_{i(k+1)} = a_i S_{Nik} + \alpha_i S_{Nik} S_{Pik} + p_{ii} F_i(S_{Nik}) + p_{ji} F_j(S_{Njk}), \tag{1}$$

$$\begin{aligned} P_{i(k+1)} = {} & b_i S_{Pik} + q_{ii}(G_i(S_{Pik}) + \beta_i S_{Nik} S_{Pik}) \\ & + q_{ji}(G_j(S_{Pjk}) + \beta_j S_{Njk} S_{Pjk}), \end{aligned} \tag{2}$$

where the functions $F_i(N_{ik})$ and $G_i(P_{ik})$ are the recruit production functions of the prey and predator in patch i at time period k. We will assume that the recruit production functions are logistic for the remainder of this paper, that is, $F_i(N_{ik}) = r_i N_{ik}(1 - N_{ik}/K_i)$ and

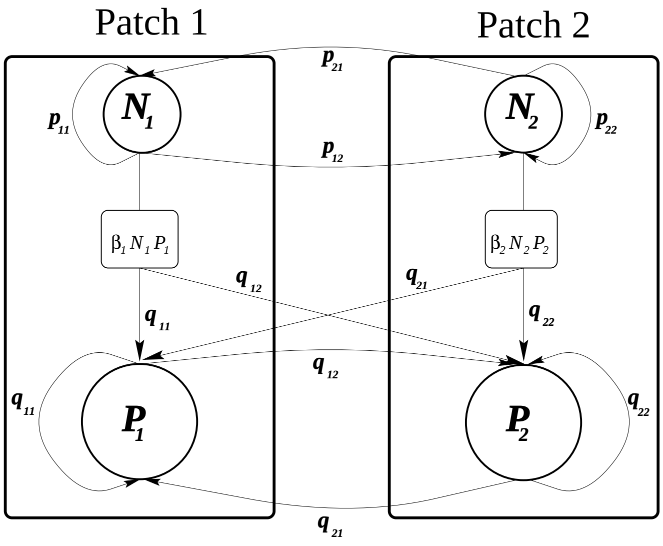


FIGURE 1. The relationships between the dynamics of the populations in a two-patch predator-prey metapopulation. The number of prey and predator are N_i and P_i, respectively. The prey and predator juvenile migration rates are p_{ij} and q_{ij}, respectively. The number of predator's offsprings in patch i from the conversion of eaten prey is $\beta_i N_i P_i$, which is distributed into patch i and j with proportion q_{ii} and q_{ij}, respectively, while some of them $(1 - q_{ii} - q_{ij})$, either die or are lost from the system.

$G_i(P_{ik}) = s_i P_{ik}(1 - P_{ik}/L_i)$, where $r_i(s_i)$ denotes the intrinsic growth of the prey (predator) and K_i (L_i) denotes the local carrying capacity of the prey (predator), with $\alpha_i < 0$ and $\beta_i > 0$.

If $\Pi_{Xi}(X_{ik}, S_{ik}) = \int_{S_{Xik}}^{X_{ik}} (p_X - c_X i(\xi))\, d\xi$ represents the present value of net revenue from harvesting subpopulation X_i in period k, where $X = NorP$, p_X is the price per unit harvested population X, c_{Xi} is the cost to harvest subpopulation X_i (it may depend on location), and ρ is a discount factor, then to obtain an optimal harvest from the fishery we should maximize net present value

$$PV = \sum_{k=0}^{T} \rho^k \sum_{i=1}^{2} \Pi_{Ni}(N_{ik}, S_{Nik}) + \sum_{k=0}^{T} \rho^k \sum_{i=1}^{2} \Pi_{Pi}(P_{ik}, S_{Pik}), \tag{3}$$

subject to equations (1) and (2), with nonnegative escapement less than or equal to the population size. We will assume $\rho = 1/(1+\delta)$ for the remainder of this paper, where δ denotes a periodic discount rate, e.g., $\delta = 10\%$.

Supriatna and Possingham [1998] used dynamic programming to obtain optimal harvesting strategies for a similar predator-prey metapopulation. They generalized the method in Clark [1976] and Tuck and Possingham [1994], and they found that in some circumstances harvesting strategies for a single-species metapopulation can be generalized in the presence of predators. Following Supriatna and Possingham [1998] we use dynamic programming to obtain optimal harvesting strategies by maximizing net present value in equation (3) and we find implicit expressions for optimal escapements $S^*_{N_{i0}}$ and $S^*_{P_{i0}}$ in the form:

$$\begin{aligned}\frac{p_N - c_{Ni}(S^*_{Ni0})}{\rho} &= (a_i + \alpha_i S^*_{Pi0} + p_{ii}F'_i(S^*_{Ni0}))(p_N - c_{Ni}(N_{i1}))\\ &\quad + p_{ij}F'_i(S^*_{Ni0})(p_N - c_{Nj}(N_{j1}))\\ &\quad + q_{ii}\beta_i S^*_{Pi0}(p_P - c_{Pi}(P_{i1}))\\ &\quad + q_{ij}\beta_i S^*_{Pi0}(p_P - c_{Pj}(P_{j1})),\end{aligned} \tag{4}$$

$$\begin{aligned}\frac{p_P - c_{Pi}(S^*_{Pi0})}{\rho} &= (b_i + q_{ii}\beta_i S^*_{Ni0} + q_{ii}G'_i(S^*_{Pi0}))(p_P - c_{Pi}(P_{i1}))\\ &\quad + q_{ij}\beta_i S^*_{Ni0}(p_P - c_{Pj}(P_{j1}))\\ &\quad + q_{ij}G'_i(S^*_{Pi0})(p_P - c_{Pj}(P_{j1}))\\ &\quad + \alpha_i S^*_{Ni0}(p_N - c_{Ni}(N_{i1})).\end{aligned} \tag{5}$$

These equations are the general form of the optimal harvesting equation for a two-patch predator-prey metapopulation. If there is no predator mortality associated with migration $q_{ii}+q_{ij} = 1$, and costs of harvesting are spatially independent, then these equations are the same as in Supriatna and Possingham [1998]. If $\alpha_i = \beta_i = 0$, then the optimal harvesting equation for a single-species metapopulation (Tuck and Possingham [1994]) is obtained. Furthermore, if there is no migration between patches, $p_{ij} = q_{ij} = 0$ for $i \neq j$, and $F'(S) = a_i + p_{ii}F'_i(S_{Ni0})$ together with $\alpha_i = \beta_i = 0$, then the equation reduces to the optimal harvesting equation for a single-species population (Clark [1976]). Although we can show that the escapements S^*_{Xi0} found by solving these implicit equations are independent of the time horizon considered, we do not show it in this paper. Consequently, due to the time independence, there is a notational change for the remainder of the paper, that is, we simply use $S^*_{X_i}$ to denote optimal escapement for subpopulation X in patch i. We discuss some properties of these escapements in the following section.

3. Results and discussion.

In this section we discuss some properties of the optimal escapements defined by equations (4) and (5). We compare the optimal escapements between the two subpopulations. For the remainder of the paper we assume that market price for the predator is higher than or equal to the price for the prey, that is, $p_P = mp_N$ with $m \geq 1$, and prey vulnerability is the same in both patches, that is, $\alpha_1 = \alpha_2 = \alpha$.

To facilitate some comparisons of the properties of our optimal escapements, we adopt the following definitions from Tuck and Possingham [1994] and Supriatna and Possingham [1998]:

1. Prey subpopulation i is a *relative source* subpopulation if its per capita larval production is greater than the per capita larval production of prey subpopulation j, that is, $r_i(p_{ii} + p_{ij}) > r_j(p_{jj} + p_{ji})$. If this is the case, then prey subpopulation j is a *relative sink* subpopulation.

2. Prey subpopulation i is a *relative exporter* subpopulation if it exports more larvae to prey subpopulation j than it imports (per capita), that is, $r_1 p_{12} > r_2 p_{21}$. If this is the case, then prey subpopulation j is called a *relative importer* subpopulation.

3. The fraction $\beta_i/|\alpha_i|$ is called the *biological efficiency* and the fraction $m(q_{ii}+q_{ij})\beta_i/|\alpha_i|$ is called the *economic efficiency* of predator subpopulation i.

3.1. Negligible costs analysis.

To simplify the analysis, the costs of harvesting are assumed to be negligible. Using these assumptions, and substituting all derivatives of the logistic recruitment functions, F_i and G_i, into equations (4) and (5), we can find explicit expressions for the optimal escapements S^*_{Ni} and S^*_{Pi}:

$$S^*_{Ni} = \frac{A_i m(q_{i1} + q_{i2})(2s_i/L_i) + C_i B_i}{\Delta_i}, \tag{6}$$

$$S_{Pi}^{*}=\frac{B_i(p_{i1}+p_{i2})(2r_i/K_i)+C_iA_i}{\Delta_i}, \tag{7}$$

provided $\Delta_i = C_i^2 - m(p_{i1}+p_{i2})(2r_i/K_i)(q_{i1}+q_{i2})(2s_i/L_i) \neq 0$, with $A_i = (1/\rho) - (p_{i1}+p_{i2})r_i - a_i$, $B_i = (m/\rho) - m(q_{i1}+q_{i2})s_i - mb_i$, and $C_i = \alpha_i + m(q_{i1}+q_{i2})\beta_i$.

It is well known, in harvesting a single-species population, that if the growth rate of the exploited population is less than the discount rate, then it is economically optimal to harvest the population to extinction (Clark [1976], Schmitt and Wissel [1985], Dawid and Kopel [1997]). This is also true in harvesting a one- or two-species metapopulation (Tuck and Possingham [1994], Supriatna and Possingham [1998]). We can show that if A_i and B_i are negative and C_i is nonpositive with $C_i > \max\{(2B_i/K_i),(2mA_i/L_i)\}$, then $\Delta_i < 0$ and all resulting escapements, $S_{N_i}^{*}$ and $S_{P_i}^{*}$, are positive. If this is the case, we can also establish the following result.

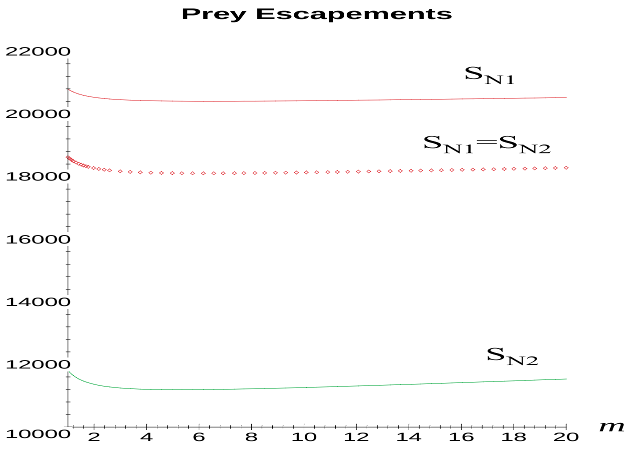
Result 1. *Assume prey subpopulation* 1 *is a relative source, that is,* $(p_{11}+p_{12})r_1 > (p_{22}+p_{21})r_2$, *while all other parameters of the prey and the predator are identical for both subpopulations. If* A_i *and* B_i *are negative, and* C_i *is nonpositive with* $C_i > \max\{(2B/K),(2mA/L)\}$, *then* (i) $S_{N_1}^{*} > S_{N_2}^{*}$ *and* (ii) $S_{P_1}^{*} \leq S_{P_2}^{*}$. *Furthermore if, in addition,* $p_{i1} \leq p_{i2}$, $q_{i1} = q_{i2}$, $S_{N_i}^{*} \leq K_i$, $S_{P_i}^{*} \leq L_i$ *with* $S_{N_1}^{*}S_{P_1}^{*} > S_{N_2}^{*}S_{P_2}^{*}$, *then* (iii) $H_{N_1}^{*} < H_{N_2}^{*}$ *and* (iv) $H_{P_1}^{*} \geq H_{P_2}^{*}$.

Result 1 suggests that if the growth rate of the populations is higher than the discounting rate $1/\rho$ (indicated by $A_i < 0$ and $B_i < 0$) and $C_i > \max\{(2B/K),(2mA/L)\}$, then we should protect the relative source prey subpopulation in two different ways: directly, with a higher escapement of the relative source prey subpopulation, and indirectly, with a lower escapement of the predator living in the same patch with the relative source prey subpopulation. Since $C_i > \max\{(2B/K),(2mA/L)\}$ can be written as $m(q_{ii}+q_{ij})(\beta/|\alpha|) > 1 + \max\{(2B/K),(2mA/L)\}/|\alpha|$, then we can interpret $C_i > \max\{(2B/K),(2mA/L)\}$ as a relatively high predator economic efficiency. Furthermore, if every escapement is less than each subpopulation's carrying capacity, lower escapement means higher harvest.

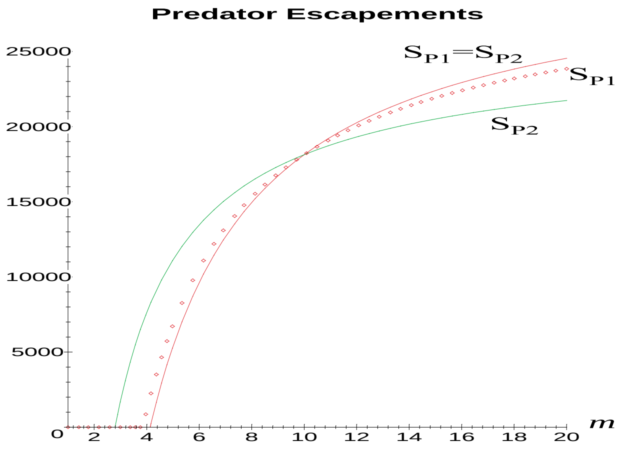
3.2. Numerical example. Let us assume that there is a two-patch predator-prey metapopulation and the prey in both patches have carrying capacities $K_1 = K_2 = 50000000$, intrinsic growth $r_1 = r_2 = 10$, and adult survivals per period are $a_1 = a_2 = 0.001$. Prey juveniles migrate with migration fractions $p_{11} = p_{12} = 0.3$ and $p_{21} = p_{22} = 0.1$, hence prey subpopulation 1 is a relative source and exporter subpopulation. Let the discount rate δ be 10%. Now suppose predators are present in both patches with intrinsic growth $s_1 = s_2 = 4$, carrying capacities $L_1 = L_2 = 50000$, and adult survival per period $b_1 = b_2 = 0.001$. Suppose the predator juvenile migration is symmetrical and high with $q_{11} = q_{12} = q_{21} = q_{22} = 0.5$. Let $|\alpha_i| = 0.000001$ and $\beta_i = 0.0000001$, that is, we assume the biological predator efficiency is 10%. Using equations (1) and (2), we can show that one of the positive equilibrium population sizes for this two-patch predator-prey metapopulation is $(\bar{N}_1, \bar{N}_2, \bar{P}_1, \bar{P}_2) =$ (36473692, 36473692, 83105, 83105). We assume harvesting begins with this equilibrium as the initial population size.

Using equations (6) and (7) and assuming the predator is 10 times more valuable than the prey, i.e., $m = 10$, we find the optimal escapement for the system $S^*_{N_1} = 20420833$, $S^*_{N_2} = 11262500$, and $S^*_{P_1} = S^*_{P_2} = 18131$ with the first period optimal harvests $H^*_{N_1} = 16052859$, $H^*_{N_2} = 25211192$, $H^*_{P_1} = H^*_{P_2} = 64973$, and the equilibrium optimal harvests $H^*_{N_1} = 24196828$, $H^*_{N_2} = 33512055$, $H^*_{P_1} = H^*_{P_2} = 56835$. As suggested by Result 1, we should harvest the relative exporter and source prey subpopulation more conservatively than the relative importer and sink prey subpopulation (in term of escapement $S^*_{N_1} > S^*_{N_2}$ and in term of harvest $H^*_{N_1} < H^*_{N_2}$). There is no difference in escapement and harvest between the predator subpopulations. This is because the predator biological efficiency is exactly the same as the inverse of m, ($m = 10$ and $\beta/|\alpha| = 0.1$). Figure 2 shows that if $0 < m < 10$, then all rules in Result 1 are satisfied. However, if m is sufficiently large, in our example if $m > 10$, these rules may be violated. This is because a large m means that a predator's economic efficiency is more than 100% or $C > 0$, see Result 1.

Figure 2 shows escapements and harvests which are plotted as functions of the ratio of predator market price to prey market price, m. The figure suggests that, in this example where the growth of the predator is relatively low ($s_i = 4$ while $r_i = 10$), if there is no difference between

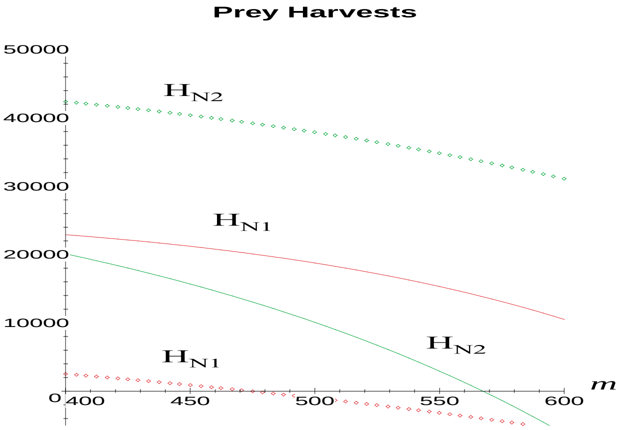


(2a)

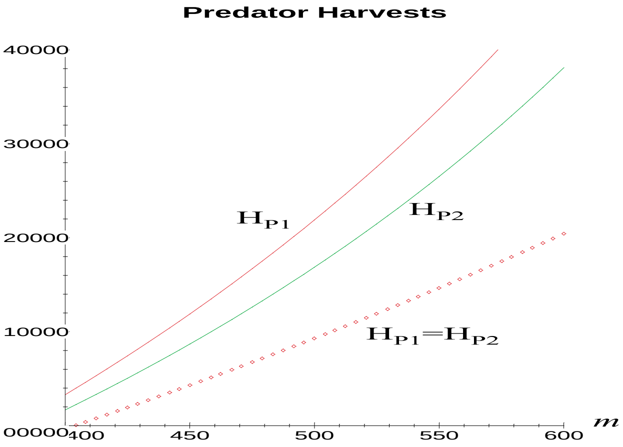


(2b) Prey numbers are in thousands.

FIGURE 2. Escapements (2a, 2b) and harvests (2c, 2d) are plotted as functions of the ratio of predator market price to prey market price m. Lines indicate results if prey subpopulation 1 is a relative source subpopulation and dots indicate results if prey subpopulation 1 is a relative exporter subpopulation.


Prey Harvests
50000
40000
30000
20000
10000
0
400
450
500
550
600
m
H_N2
H_N1
H_N1
H_N2

(2c)


Predator Harvests
40000
30000
20000
10000
00000
400
450
500
550
600
m
H_P1
H_P2
H_P1=H_P2

(2d)

the market prices ($m = 1$) then it is optimal to harvest all the predator down to extinction (upper right figure). While, if m is sufficiently large (m is approximately more than 550) then it is optimal to leave the relative sink and importer prey subpopulation unharvested, and eventually it is optimal to leave both prey subpopulations unharvested if m is even larger (lines in lower left figure). This rule is also observed for a single patch predator-prey system (Ragozin and Brown [1985]). This situation is different if there is no relative source/sink prey subpopulation. For example, if $p_{11} = p_{21} = 0.12$ and $p_{12} = p_{22} = 0.28$, then we should not harvest the relative exporter prey subpopulation (dots in lower left figure).

Furthermore, even when m is very small, if the growth of the predator is sufficiently large, then predator extinction is not optimal. For example, if $s_i = 20$ with $m = 1$, then predator optimal escapements are $S^*_{N_1} = 656$ and $S^*_{N_2} = 11096$. Predator escapement in patch 1 is less than in patch 2; this is because prey subpopulation 1 is a relative exporter and source subpopulation which should be protected by leaving less predators in that patch, see Result 1.

3.3. Dealing with negative harvest. As seen in the example above, the optimal strategy may be a negative harvest for one or more populations. A negative harvest could be interpreted as a seeding or restocking strategy. However, in many situations, such a strategy is not practical. In this case, as in single population exploitation, we can use the harvest function

$$H^*_{X_i} = \begin{cases} X_i - S^*_{X_i} & \text{if } X_i \geq S^*_{X_i}, \\ 0 & \text{if } X_i < S^*_{X_i}. \end{cases} \tag{8}$$

Another alternative is suggested by Tuck and Possingham [1994]. To avoid a negative harvest, they used the following procedure. Assume that, using the metapopulation harvesting theory, optimal equilibrium harvest for subpopulation i is negative. They set $H_{X_i} = 0$ and found a new optimal escapement from the maximization of the value function under this zero harvest constraint. We apply the same procedure if the method presented in the previous section produces a negative harvest.

A negative harvest may be optimal for the subpopulation that exports a high proportion of larvae but only contributes a low proportion of the larvae to its own subpopulation. For example, if the juvenile migration parameters for the prey in the previous example are $p_{11} = p_{21} = 0.2$ and $p_{12} = p_{22} = 0.065$ with $m = 10$, then the optimal equilibrium harvest for the prey subpopulation 2 is $H^*_{N2} = -1427582$, while all other subpopulations have a positive harvest. This strategy suggests that we should seed prey into subpopulation 2 and harvest the results from prey subpopulation 1 and both predator subpopulations. To avoid a negative harvest for prey subpopulation 2, we set $H_{N_2} = 0$ and, using the method of Lagrange multipliers, we maximize the present value in equation (3) with this additional constraint. The new equilibrium optimal escapements $S^*_{N_1}, S^*_{N_2}, S^*_{P_1}$, and $S^*_{P_2}$ satisfy equations:

$$
\begin{aligned}
\frac{(p_N - c_{N_1}(S_{N_{10}}))}{\rho} &= (p_N - c_{N_1}(N_{11}))[a_1 + p_{11}F_1'(S_{N_{10}}) + \alpha_1 S_{P_{10}}] \\
&\quad + (p_P - c_{P_1}(P_{11}))[q_{11}\beta_1 S_{P_{10}}] \\
&\quad + (p_P - c_{P_2}(P_{21}))[q_{12}\beta_1 S_{P_{10}}] \\
&\quad + (p_N - c_{N_2}(S_{N_{20}}))\left[\frac{p_{12}F_1'(S_{N_{10}})(1 - 1/\rho)}{Z}\right] \\
&\quad + (p_N - c_{N_1}(N_{11}))\left[\frac{p_{12}p_{21}F_1'(S_{N_{10}})F_2'(S_{N_{20}})}{Z}\right] \\
&\quad + (p_P - c_{P_2}(P_{21}))\left[\frac{p_{12}F_1'(S_{N_{10}})q_{22}\beta_2 S_{P_{20}}}{Z}\right] \\
&\quad + (p_P - c_{P_1}(P_{11}))\left[\frac{p_{12}F_1'(S_{N_{10}})q_{21}\beta_2 S_{P_{20}}}{Z}\right],
\end{aligned}
\tag{9}
$$

$$
\begin{aligned}
\frac{(p_P - c_{P_2}(S_{P_{20}}))}{\rho} &= (p_P - c_{P_2}(P_{21}))[b_2 + q_{22}G_2'(S_{P_{20}}) + q_{22}\beta_2 S_{N_{20}}] \\
&\quad + (p_P - c_{P_1}(P_{11}))[q_{21}G_2'(S_{P_{20}}) + q_{21}\beta_2 S_{N_{20}}] \\
&\quad + (p_N - c_{N_2}(S_{N_{20}}))\left[\frac{\alpha_2 S_{N_{20}}(1 - 1/\rho)}{Z}\right] \\
&\quad + (p_N - c_{N_1}(N_{11}))\left[\frac{p_{21}F_2'(S_{N_{20}})\alpha_2 S_{N_{20}}}{Z}\right] \\
&\quad + (p_P - c_{P_2}(P_{21}))\left[\frac{\alpha_2 S_{N_{20}}q_{22}\beta_2(S_{P_{20}})}{Z}\right] \\
&\quad + (p_P - c_{P_1}(P_{11}))\left[\frac{\alpha_2 S_{N_{20}}q_{21}\beta_2(S_{P_{20}})}{Z}\right],
\end{aligned}
\tag{10}
$$

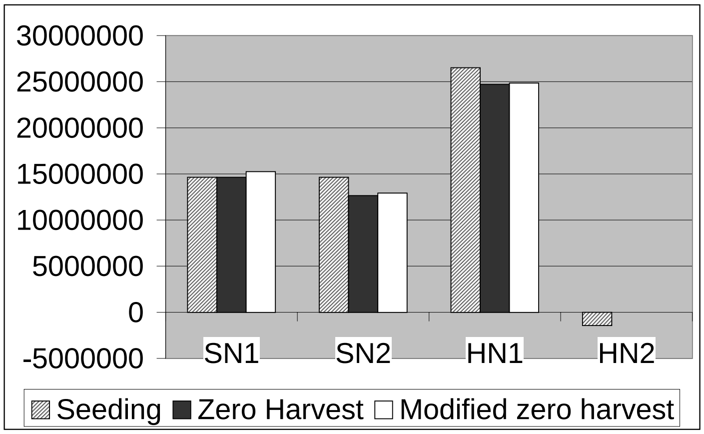


FIGURE 3a. Prey escapements and harvests.

$$\begin{aligned}\frac{(p_P - c_{P_1}(S_{P_{10}}))}{\rho} &= (p_P - c_{P_1}(P_{11}))[b_1 + q_{11}G_1'(S_{P_{10}}) + q_{11}\beta_1 S_{N_{10}}] \\ &\quad + (p_P - c_{P_2}(P_{21}))[q_{12}G_1'(S_{P_{10}}) + q_{12}\beta_1 S_{N_{10}}] \\ &\quad + (p_N - c_{N_1}(N_{11}))[\alpha_1 S_{N_{10}}], \end{aligned} \tag{11}$$

with $Z = 1 - (a_2 + p_{22}F_2'(S_{N_{20}}) + \alpha_2 S_{P_{20}})$. Solving the last three equations together with $S_{N_{20}} = N_{21}$, and assuming $Z \neq 0$, produces a nonnegative harvest for prey subpopulation 2. Figure 3 shows total profits derived from the three methods, i.e., negative harvest from (6) and (7), zero harvest from (8), and modified zero harvest from (9), (10) and (11).

If it is possible to implement a negative harvest, we find equilibrium optimal harvests are $H^*_{N_1} = 26517750$, $H^*_{N_2} = -1427582$ and $H^*_{P_1} = H^*_{P_2} = 54642$. However, if we cannot use a negative harvest in management, then using the first method (equation (8)) we find equilibrium optimal harvests are $H^*_{N_1} = 24720979$, $H^*_{N_2} = 0$ and $H^*_{P_1} = H^*_{P_2} = 52849$. Using the second method (equation (9) to (11)) we find new optimal escapements $S^*_{N_1} = 15249769$, $S^*_{N_2} = 12923857$, $S^*_{P_1} = 18131$, and $S^*_{P_2} = 16045$ with equilibrium optimal harvests $H^*_{N_1} = 24852974$, $H^*_{N_2} = 0$, $H^*_{P_1} = 50985$ and $H^*_{N_2} = 53069$, see Figure 3. If we assume the cost to put a unit of fish into the fishery is equal

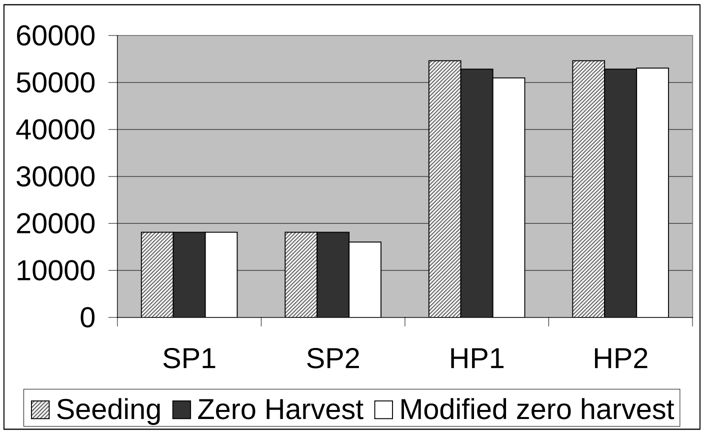


FIGURE 3b. Predator escapements and harvests.

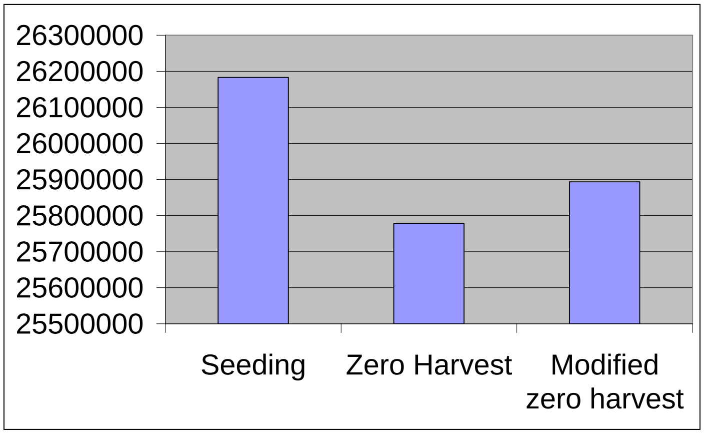


FIGURE 3c. Total profit from three different strategies. Escapements, harvests, and profits comparison for the three different methods of dealing with a negative harvest.

to the profit per unit fish from harvesting, then, neglecting all associated costs, the total revenue from the harvest is, if a negative harvest is allowable, $H_{N_1} + H_{N_2} + 10(H_{P_1} + H_{P_2}) = 26183008$ currency units. This revenue is above the revenue if we use zero harvest from either the first or second method, i.e., 25777959 from the first method and 25893514 from the second method. This suggests a negative harvest is optimal.

4. Conclusion. Harvesting strategies for a predator-prey metapopulation are established as a generalization of harvesting strategies for a single-species metapoplation. Some properties of the escapements for a single-species metapopulation (Tuck and Possingham [1994]) are preserved in the presence of the predator, such as the strategies on how to harvest relative source and sink subpopulations. We found that if there are no differences between the biological parameters of the local populations, except migration parameters, we should harvest a relative source prey subpopulation more conservatively than a relative sink subpopulation. This is the same as the rule of thumb derived from work on the single-species metapopulation (Tuck and Possingham [1994]). In addition, we should harvest the predator subpopulation living in the same patch with the relative source prey subpopulation more heavily than the other predator subpopulation.

In this paper we have discussed how a 'negative' harvest might occur. Under some circumstances our equations show that a negative harvest is optimal. A negative harvest might be considered a seeding strategy. In many situations a seeding strategy is impractical, so in this case an alternative strategy of imposing zero harvest, for the population which has a negative harvest, is the best that can be done. If it is possible to implement a negative harvest, numerical examples show that if the market price of the predator is much greater than the market price of the prey, then it may be optimal to feed the predator by seeding the prey populations, especially the exporter prey subpopulation. Numerical examples show that this strategy could increase the total net revenue compared to zero prey harvest strategies.

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APPENDIX

Proof of Result 1. Let $R = (1/\rho) - a_i$, $S = m((1/\rho) - b_i)$, $r_{im} = (p_{ii} + p_{ij})r_i$, $s_{im} = m(q_{ii} + q_{ij})s_i$.

1. If $\Delta_{S_N} = (S^*_{N_1} - S^*_{N_2})\Delta_1\Delta_2$, then using Equations 6 and 7 we obtain

$$\begin{aligned}\Delta_{S_N} &= \left(-\frac{4s_m^2}{KL}(r_{2m} - r_{1m})\right)\left(\frac{2R}{L} - C\right)\\ &\quad - \frac{2C}{L}\left(C - \frac{2S}{K}\right)s_m(r_{1m} - r_{2m})\\ &= s_m\left[\frac{2}{L}\left(C\left(C - \frac{2B}{K}\right) - \frac{4s_m R}{KL}\right)\right](r_{2m} - r_{1m}).\end{aligned}$$

Clearly, $S^*_{N_1} > S^*_{N_2}$, since $(2B/K) \leq C \leq 0$ and $\Delta_i < 0$.

2. We can prove $s^*_{P_1} \leq S^*_{P_2}$ similarly, since we have

$$\Delta_{S_p} = C\left(C\left(C - \frac{2B}{K}\right) - \frac{4s_m R}{KL}\right)(r_{2m} - r_{1m}).$$

3. Recall that equilibrium harvests are given by

$$\begin{aligned}H^*_{N_i} = \Bigg(&aS^*_{N_i} + p_{ii}rS^*_{N_i}\left(1 - \frac{S^*_{N_i}}{K}\right)\\ &+ p_{ji}rS^*_{N_j}\left(1 - \frac{S^*_{N_j}}{K}\right) + \alpha S^*_{N_i}S^*_{P_i}\Bigg) - S^*_{N_i}\end{aligned}$$

and

$$\begin{aligned}H^*_{P_i} = bS^*_{P_i} &+ q_{ii}\left(sS^*_{P_i}\left(1 - \frac{S^*_{P_i}}{L}\right) + \beta S^*_{Ni}S^*_{Pi}\right)\\ &+ q_{ji}\left(sS^*_{Pj}\left(1 - \frac{S^*_{P_j}}{L}\right) + \beta S^*_{N_j}S^*_{P_j}\right) - S^*_{P_i}.\end{aligned}$$

The difference between these two harvests, H^*_{N1} and H^*_{N2}, is

$$\begin{aligned}H^*_{N_1} - H^*_{N_2} &= (a-1)(S^*_{N_1} - S^*_{N_2}) \\ &\quad + r\Bigg((p_{11} - p_{12})S^*_{N_1}\left(1 - \frac{S^*_{N_1}}{K}\right) \\ &\qquad\qquad + (p_{21} - p_{22})S^*_{N_2}\left(1 - \frac{S^*_{N_2}}{K}\right)\Bigg) \\ &\quad + \alpha(S^*_{N_1}S^*_{P_1} - S^*_{N_2}S^*_{P_2}) \\ &< 0.\end{aligned}$$

4. Similarly, we can prove $H^*_{P_1} - H^*_{P_2} \geq 0$ if $q_{i1} = q_{i2}$.

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