Optimal Harvesting for a Predator–Prey Metapopulation

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In this paper we present a deterministic, discrete-time model for a two-patch predator–prey metapopulation. We study optimal harvesting for the metapopulation using dynamic programming. Some rules are established as generalizations of rules for a single-species metapopulation harvesting theory. We also establish rules to harvest relatively more (or less) vulnerable prey subpopulations and more (or less) efficient predator subpopulations.

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1. INTRODUCTION

All marine populations show some degree of spatial heterogeneity. Sometimes this spatial heterogeneity means that modelling the species as one single population is not adequate. For example, abalone, *Haliotis rubra*, has a discrete metapopulation structure with local populations connected by the dispersal of their larvae (Prince *et al.*, 1987; Prince 1992). Brown and Murray (1992) and Shepherd and Brown (1993) argue that management for abalone should depend on the characteristics of local populations. Frank (1992) provides another example of the metapopulation structure. He points out that fish stocks, such as the cod of Iceland and West Greenland, which are separated by a large distance, and the two haddock stocks of the Scotian Shelf, are known to be strongly coupled by the dispersal of individuals. He also suggests that those stocks possess the 'source/sink' property described by Sinclair (1988) and Pulliam (1988), that is, persistence of the population in a sink habitat can be maintained by the migration from a source habitat. Source/sink habitat will be defined precisely in the next section. Furthermore, Frank and Leggett (1994) argue that the collapse of major fisheries such as North Atlantic Cod and Atlantic and Pacific Salmon, is due to the over-exploitation of the source population.

Despite the importance of spatial heterogeneity, increasing the complexity of a population model by adding spatial heterogeneity is rarely done in fishery management modeling, even for single species (Clark, 1984). Exceptions are Clark (1976), Tuck and Possingham (1994) and Brown and Roughgarden (1997) for a single species, and Hilborn and Walters (1987), Leung (1995), and Murphy (1995) for multiple species. In this paper we present a model for a spatially structured predator–prey population. We address the issues of spatial structure and predator–prey interaction, and study optimal harvesting for the metapopulation. We use metapopulation theory to describe the spatial structure of the predator–prey system. Using this approach, we obtain the optimal harvest for each local population which gives important information on how we should harvest a population if management can be specified for local populations, such as abalone.

2. THE MODEL

This section describes a deterministic, discrete-time model for a spatially structured predator–prey system. The model has similar structure and assumptions to that described in Tuck and Possingham (1994).

Assume that there is a predator–prey population in each of two different patches, namely patch 1 and patch 2. Let the movement of individuals between the local populations be caused by the dispersal of the juveniles. Predation occurs on adult prey, and larval dispersal and production are independent of the other species. Let the population size of the prey and predator on patch i at the beginning of period k be denoted by N_{ik} and P_{ik} respectively. The proportion of prey and predator juveniles from patch i that successfully migrate to patch j are p_{ij} and q_{ij} respectively (Fig. 1). If the amount of harvest taken from the prey and predator stocks in patch i at the beginning of period k are $H_{N_{ik}}$ and $H_{P_{ik}}$ respectively, let $S_{N_{ik}} = N_{ik} - H_{N_{ik}}$ and $S_{P_{ik}} = P_{ik} - H_{P_{ik}}$ be prey and predator escapements on patch i at the end of that period. These escapements determine the growth of the population after exploitation. Furthermore, let the dynamics of the exploited prey and predator population be given by the equations:

$$N_{i(k+1)} = a_i S_{N_{ik}} - \alpha_i S_{N_{ik}} S_{P_{ik}} + p_{ii} F_i(S_{N_{ik}}) + p_{ji} F_j(S_{N_{jk}}), \qquad (1)$$

$$P_{i(k+1)} = b_i S_{P_{ik}} + \beta_i S_{N_{ik}} S_{P_{ik}} + q_{ii} G_i(S_{P_{ik}}) + q_{ji} G_j(S_{P_{jk}}), \qquad (2)$$

where a_i and b_i denote the survival rate of adult prey and adult predator in patch i respectively. The functions $F_i(N_{ik})$ and $G_i(P_{ik})$ are the recruit production functions of the prey and the predator on patch i in 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 $G_i(P_{ik}) = s_i P_{ik}(1 - P_{ik}/L_i)$, where r_i and s_i denotes the intrinsic growth of the prey and predator respectively,
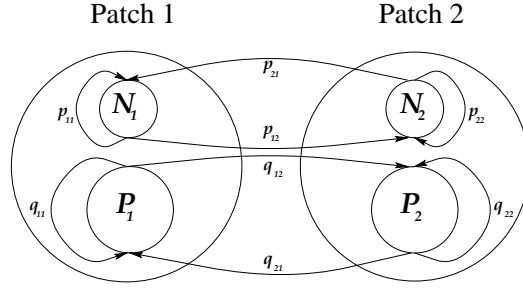
Patch 1   Patch 2

Figure 1.   The predator–prey metapopulation diagram for a two-patch model. The numbers of predator and prey subpopulations i are indicated by P_i and N_i respectively, their juvenile migration rate are q_{ij} and p_{ij} respectively.

and K_i and L_i denotes the prey and predator carrying capacities respectively, with $\alpha_i > 0$ and $\beta_i > 0$.

Using present value maximization (Clark, 1976), the objective of a sole-owner is to maximize the net revenue from harvesting each subpopulation of the prey and the predator up to the time horizon $t = T$. If Π_{X_i} represents the present value of net revenue resulting from harvesting population X in patch i, and ρ is a discount factor, then the sole-owner should maximize net present value

$$PV = \sum_{k=0}^{T} \rho^k \sum_{i=1}^{2} \sum_{X=N}^{P} \Pi_{X_i}(X_{ik}, S_{X_{ik}}) \tag{3}$$

subject to equations (1) and (2), with non-negative 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.

If there is no discount rate ($\delta = 0$) then the net revenue (3) in any period generated by escapements S_{N_i} and S_{P_i} has exactly the same value to the net revenue from the same escapements in any other periods. Hence, we only need to find optimal escapements for one period to go. The resulting revenue by applying this zero discount rate is often known as maximum economic yield (MEY). If the discount rate is extremely high ($\delta \longrightarrow \infty$) then the net revenue (3) approaches

$$PV_\infty = \sum_{i=1}^{2} \sum_{X=N}^{P} \Pi_{X_i}(X_{i0}, S_{X_{i0}}), \tag{4}$$

which is the immediate net revenue without considering the future and is maximized by optimal escapements $S^*_{X_{i\infty}}$. We use the symbol '∞' to indicate that the exploiter only cares about profit this period, which is the same as applying the large discount rate $\delta \longrightarrow \infty$. It can be regarded as an open-access exploitation.

The net revenue for a two-patch predator–prey population from the harvest $H_{X_{ik}}$ of the sub-population X_i in period k is

$$\Pi_{X_i}(X_{ik}, S_{X_{ik}}) = \int_{S_{X_{ik}}}^{X_{ik}} (p_X - c_{X_i}(\xi))d\xi, \tag{5}$$

where p_X is the price of the harvested stock X and is assumed to be constant, while c_{X_i} is the unit cost of harvesting and is assumed to be a non-increasing function of X_i and may depend on the location of the stock. To obtain the optimal harvest for a two-patch predator–prey population we define a value function

$$J_T(N_{10}, N_{20}, P_{10}, P_{20}) = \max_{0 \le S_{X_{i0}} \le X_{i0}} \left(\sum_{k=0}^{T} \rho^k \sum_{i=1}^{2} \sum_{X=N}^{P} \Pi_{X_i}(X_{ik}, S_{X_{ik}}) \right) \quad (6)$$

which is the sum of the discounted net revenue resulting from harvesting both populations in both locations up to period $t = T$. This function is maximized by choosing appropriate optimal escapements $S^*_{X_{ik}}$. Equation (6) is used recursively to obtain the value function at time $T + 1$, that is

$$J_{T+1}(N_{10}, N_{20}, P_{10}, P_{20}) = \max_{0 \le S_{X_{i0}} \le X_{i0}} \left(\rho J_T(N_{11}, N_{21}, P_{11}, P_{21}) \right.$$

$$\left. + \sum_{i=1}^{2} \sum_{X=N}^{P} \Pi_{X_i}(X_{i0}, S_{X_{i0}}) \right). \quad (7)$$

Thus the optimal escapements, $S^*_{N_{i0}}$ and $S^*_{P_{i0}}$, for a two-patch predator–prey system can be found by iterating this equation back from time T.

First, consider the net revenue in equation (6) for time horizon $T = 0$. The resulting net revenue, $J_0(N_{10}, N_{20}, P_{10}, P_{20})$, represents immediate net revenue taken from the next harvest without considering the future value of the harvest, hence the maximum value is exactly the same as the maximum value of PV_∞ in (4). We consider two cases.

CASE 1. *If the unit cost of harvesting is constant, let $c_{X_i}(X_i) = c_{X_i}$, then $p_X - c_{X_i}$ in (5) is constant. Hence, the integral in (5), and thus PV_∞ in (4), is maximized by $S^*_{X_{i\infty}}$ satisfying*

$$S^*_{X_{i\infty}} = \begin{cases} X_i & \text{if } p_X \le c_{X_i} \\ 0 & \text{if } p_X > c_{X_i}. \end{cases} \quad (8)$$

Therefore, if the unit cost of harvesting is constant and lower than the unit price of harvested stock then it is optimal to drive the stock to extinction (see also Fig. 2 for a relatively large discount rate). On the other hand, if the unit cost of harvesting is constant and greater than or equal to the unit price of harvested stock then we should not harvest the stock at all.

CASE 2. *If the unit cost of harvesting is not constant then PV_∞ in (4) is maximized by $S^*_{N_{i\infty}}$ and $S^*_{P_{i\infty}}$ satisfying $\left. \frac{\partial \Pi_{X_i}(X_{i0}, S_{X_{i0}})}{\partial S_{X_{i0}}} \right|_{S_{X_{i0}} = S^*_{X_{i\infty}}} = 0$. Differentiate the integral in (5) with respect to $S^*_{X_{i0}}$ to obtain $p_N - c_N(S^*_{N_{i\infty}}) = 0$ and $p_P - c_P(S^*_{P_{i\infty}}) = 0$. The last two equations say that optimal escapements occur if the marginal revenue equals the marginal value of cost. This condition is known as 'bionomic equilibrium' (Gordon, 1954).*

(a) Profit is maximum at (14505,9010) for discount rate 10%

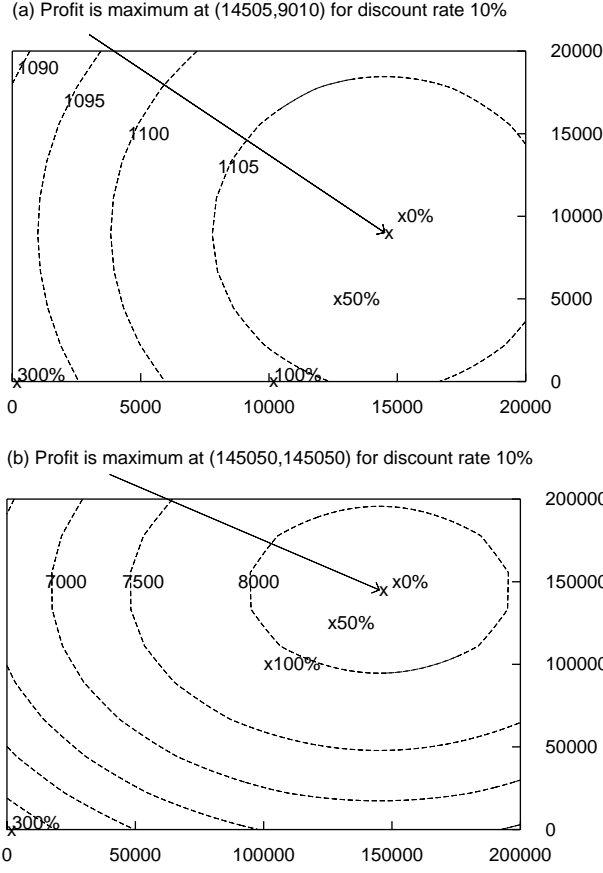(b) Profit is maximum at (145050,145050) for discount rate 10%

Figure 2. Contour plot for the profit in (3) as a function of (a) predator escapements and (b) prey escapements, calculated in millions unit with discount rate 10%. Escapements $S_{P_1} = 14{,}505$ and $S_{P_2} = 9010$ are found as the predator optimal escapements (a) and escapements $S_{N_1} = S_{N_2} = 145{,}050$ are found as the prey optimal escapements (b). The symbol '×' indicates the position of equilibrium escapements for various discount rates, e.g. ×0% indicates the position with no discount rate.

Next, to obtain the net revenue for time horizon $T = 1$ we substitute these immediate escapements into equation (7). As in the case for the time horizon $T = 0$, to maximize the revenue, we use the necessary conditions for optimality by differentiating the resulting equation with respect to escapements for the time horizon $T = 1$, that is $S_{N_{i0}}$ and $S_{P_{i0}}$. This procedure yields

$$\frac{p_N - c_{N_i}(S^*_{N_{i0}})}{\rho} = (a_i - \alpha_i S^*_{P_{i0}} + p_{ii} F'_i(S^*_{N_{i0}}))(p_N - c_{N_i}(N_{i1}))$$

$$+ (p_{ij} F'_i(S^*_{N_{i0}}))(p_N - c_{N_j}(N_{j1}))$$

$$+ \beta_i S^*_{P_{i0}}(p_P - c_{P_i}(P_{i1})), \tag{9}$$

$$\frac{p_P - c_{P_i}(S^*_{P_{i0}})}{\rho} = (b_i + \beta_i S^*_{N_{i0}} + q_{ii} G'_i(S^*_{P_{i0}}))(p_P - c_{P_i}(P_{i1}))$$

$$+ (q_{ij} G'_i(S^*_{P_{i0}}))(p_P - c_{P_j}(P_{j1}))$$

$$- \alpha_i S^*_{N_{i0}}(p_N - c_{N_i}(N_{i1})). \tag{10}$$

These equations are the general form of the optimal harvesting equation for a two-patch predator–prey population system. The escapements $S^*_{X_{i0}}$ found by solving these equations are the optimum escapements of the prey and the predator on each patch that maximize revenue provided the Hessian matrix $J''_1(S_{N10}, S_{N20}, S_{P10}, S_{P20})$ satisfies $[J''_1(S^*_X)(S_X - S^*_X)] \cdot [S_X - S^*_X] < 0$ where $S_X = (S_{N10}, S_{N20}, S_{P10}, S_{P20})$ and $S^*_X = (S^*_{N10}, S^*_{N20}, S^*_{P10}, S^*_{P20})$. It can be shown that these optimal escapements of predator–prey metapopulation are independent of the time horizon considered.

3.   RESULTS AND DISCUSSION

In this section, the optimal escapements in equations (9) and (10) are compared with the strategies in which spatial structure is ignored. The rationale for this is that we want to know how important it is to use the theory presented here for choosing optimal escapements. We consider two ways in which spatial structure can be ignored. First, the whole system can be considered a well-mixed homogeneous population. Secondly, the existence of the patches is recognized, but we assume that there is no migration of individuals between patches. Our optimal escapements from a two-patch connected predator–prey model are compared with those systems in which spatial structure is ignored.

We adopt the following definitions about the characteristics of local populations from Tuck and Possingham (1994).

1. Prey subpopulation i is a *relative exporter* prey subpopulation if it exports more larvae to the prey subpopulation j than it imports (per capita), that is $r_1 p_{12} > r_2 p_{21}$. In this case, prey subpopulation j is called a *relative importer* prey subpopulation. Relative exporter and relative importer predator subpopulations are defined similarly.

2. Prey subpopulation i is a *relative source* prey subpopulation if its per capita larval production is greater than the per capita larval production of prey subpopulation j, that is $r_i(p_{ii} + p_{ij}) > r_j(p_{jj} + p_{ji})$. In this case, prey subpopulation j is called a *relative sink* subpopulation. Relative source and relative sink predator subpopulations are defined similarly.

Optimal harvesting equations for an unconnected and well-mixed predator–prey population can be obtained from equations (9) and (10) by assigning $p_{ij} = q_{ij} = 0$ for $i \neq j$, and $p_{ii} = q_{ii} = 1, i = 1, 2$. However, if we incorrectly consider there

is no connection between subpopulations, we would measure the growth rate for prey subpopulation i as

$$r_{iu} = r_i p_{ii} + r_j p_{ji}. \tag{11}$$

If it is considered a well-mixed predator–prey system, then the per capita growth of the whole prey population is

$$r_w = (r_i(p_{ii} + p_{ij}) + r_j(p_{jj} + p_{ji}))/2. \tag{12}$$

The growth rate for the predator is measured similarly. In addition, we define the following terms:

3. Prey subpopulation i is a *relatively more vulnerable* prey subpopulation to predation if $\alpha_i > \alpha_j$. In this case, prey subpopulation j is called a *relatively less vulnerable* subpopulation.
4. Let $\alpha_i = \alpha_j$ or $\beta_i = \beta_j$. If $-\alpha_i + \beta_i > -\alpha_j + \beta_j$ then predator subpopulation i is called a *relatively more efficient* predator subpopulation. In this case, predator subpopulation j is called a *relatively less efficient* subpopulation.

3.1. *The case of negligible costs.* To simplify the analysis and obtain explicit expressions for the optimal escapements, we assume the costs of harvesting are negligible and there is no difference between the price of the prey and predator. Using these assumptions, and substituting all derivatives of the logistic recruitment functions, F_i and G_i, equations (9) and (10) become

$$\frac{1}{\rho} = a_i + (p_{i1} + p_{i2})\left(r_i - \frac{2r_i}{K_i}S_{N_i}\right) + (-\alpha_i + \beta_i)S_{P_i}, \tag{13}$$

$$\frac{1}{\rho} = b_i + (q_{i1} + q_{i2})\left(s_i - \frac{2s_i}{L_i}S_{P_i}\right) + (-\alpha_i + \beta_i)S_{N_i}. \tag{14}$$

Let $A_i = \frac{1}{\rho} - (p_{i1} + p_{i2})r_i - a_i$, $B_i = \frac{1}{\rho} - (q_{i1} + q_{i2})s_i - b_i$, and $C_i = -\alpha_i + \beta_i$. Solving equations (13) and (14) produces explicit expressions for the optimal escapements $S_{N_i}^*$ and $S_{P_i}^*$

$$S_{N_i}^* = \frac{A_i(q_{i1} + q_{i2})\frac{2s_i}{L_i} + C_i B_i}{\Delta_i}, \tag{15}$$

$$S_{P_i}^* = \frac{B_i(p_{i1} + p_{i2})\frac{2r_i}{K_i} + C_i A_i}{\Delta_i}, \tag{16}$$

provided $\Delta_i = C_i^2 - (p_{i1} + p_{i2})\frac{2r_i}{K_i}(q_{i1} + q_{i2})\frac{2s_i}{L_i} \neq 0$. In the case of $\alpha_i = \beta_i = 0$, equation (15) determines optimal escapement for a single-species metapopulation. Tuck and Possingham (1994) find some rules of thumb for harvesting a single-species metapopulation system. That is if we use single-species metapopulation harvesting theory, then:

1. A relative source subpopulation would be harvested more conservatively than a relative sink subpopulation.
2. A relative exporter subpopulation would be harvested more conservatively than if we use unconnected single-species population theory, while a relative importer subpopulation would be harvested more heavily.
3. A relative source subpopulation would be harvested more conservatively than if we use well-mixed single-species population theory, while a relative sink subpopulation would be harvested more heavily.

If A_i and B_i are negative and C_i non-positive with $C_i > \max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}$ then the escapements in (15) and (16) can be shown to be always positive. An interpretation of the condition $A_i < 0$ is that the sum of the proportion of surviving adults (that can survive to the next period a_i) and the per capita larval production (product of intrinsic growth and the proportion of juveniles that remain in the system $(p_{ii} + p_{ij})r_i$) is higher than the discount rate $1/\rho$. This is a normal situation, otherwise equations (15) and (16) may produce negative escapements, which means it is economically optimal to harvest the populations to extinction (Clark, 1976). The condition $B_i < 0$ is interpreted similarly, while C_i is non-positive with $C_i > \max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}$ interpreted as a high predator efficiency. Hence, if one of the populations has a very high adult mortality, a very small intrinsic growth, a very high proportion of juveniles lost from the system, or a very small predator efficiency then extinction may be optimal. Extinction is also observed by Horwood (1990) when only the prey species is harvested and the prey has a Beverton–Holt recruit production function.

To give a clear insight into how our predator–prey metapopulation optimal escapements differ from spatially unstructured predator–prey optimal escapements, we construct the following results. We assume the predator has a symmetric migration, that is $s_{1m} = s_{2m} = s_m$, in all results that follow.

RESULT 1. *Let one of the prey subpopulations be a relative source while all other parameters of the prey and the predator are identical for both subpopulations. We assume the prey subpopulation 1 is a relative source, that is $(p_{11} + p_{12})r_1 > (p_{22} + p_{21})r_2$. If $\alpha = \beta$, or if A_i and B_i are negative and C_i is non-positive with $C_i > \max\{\frac{2B_i}{K}, \frac{2A_i}{L}\}$, then*

$$S^*_{N_1} > S^*_{N_2} \quad and \quad S^*_{P_1} \leq S^*_{P_2}.$$

We conclude, from Result 1, that if predator efficiency is relatively high ($C_i > \max\{\frac{2B_i}{K}, \frac{2A_i}{L}\}$) 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.

The previous result allows us to compare our predator–prey optimal escapements between different patches. Up to this point, we conclude that if predator

efficiency is relatively high, then the first rule of thumb from single metapopulation harvesting theory is preserved, that is we should harvest a relative source subpopulation more conservatively than a relative sink subpopulation. To see how important and how different our predator–prey metapopulation escapements compare with the escapements which occur if we incorrectly consider the population as a spatially unstructured system, we construct the following results.

RESULT 2 (COMPARISON WITH AN UNCONNECTED TWO-PATCH PREDATOR–PREY SYSTEM). *Let $S^*_{N_i}$ and $S^*_{P_i}$ denote the optimal escapements from the predator–prey metapopulation given by equations (15) and (16), and let $S^*_{N_{iu}}$ and $S^*_{P_{iu}}$ denote the optimal escapements if we incorrectly consider the system as a system consisting of two unconnected predator–prey systems. Assume that one of the prey subpopulations is a relative exporter and also a relative source while all other parameters of the prey and the predator are identical for both subpopulations. Without loss of generality let $p_{12}r_1 > p_{21}r_2$ and $p_{11}r_1 \geq p_{22}r_2$. If A_i and B_i are negative and C_i is non-positive with $C_i > \max\{\frac{2B_i}{K}, \frac{2A_i}{L}\}$, then*

$$S^*_{N_1} > S^*_{N_{1u}}, \qquad S^*_{N_2} < S^*_{N_{2u}}, \qquad S^*_{P_1} \leq S^*_{P_{1u}}, \qquad S^*_{P_2} \geq S^*_{P_{2u}},$$

$$S^*_{N_1} + S^*_{N_2} \leq S^*_{N_{1u}} + S^*_{N_{2u}}, \qquad and \qquad S^*_{P_1} + S^*_{P_2} \geq S^*_{P_{1u}} + S^*_{P_{2u}}.$$

RESULT 3 (COMPARISON TO A WELL-MIXED PREDATOR–PREY SYSTEM). *Let $S^*_{N_i}$ and $S^*_{P_i}$ denote the optimal escapements from the predator–prey metapopulation given by equations (15) and (16), and let $S^*_{N_w}$ and $S^*_{P_w}$ denote the optimal escapements if the predator–prey metapopulation system is incorrectly considered as a well-mixed predator–prey system. If all hypothesis and assumptions of the Result 2 are satisfied and in addition if C_i satisfies*

$$C_i \left(B_i C_i^2 + \frac{3(\frac{1}{\rho} - a - r_w)s_m}{L} C_i - \frac{2B_i r_w s_m}{KL} \right) = 0,$$

then

$$S^*_{N_1} > \frac{1}{2} S^*_{N_w}, \qquad S^*_{N_2} < \frac{1}{2} S^*_{N_w}, \qquad S^*_{P_1} \leq \frac{1}{2} S^*_{P_w}, \qquad S^*_{P_2} \geq \frac{1}{2} S^*_{P_w}$$

$$S^*_{N_1} + S^*_{N_2} \leq S^*_{N_w}, \qquad and \qquad S^*_{P_1} + S^*_{P_2} \geq S^*_{P_w}.$$

Results 1, 2 and 3 are the generalizations of the rules of thumb in Tuck and Possingham (1994) for harvesting a single-species metapopulation. In addition to the rules summarized in these results, we also established rules to harvest more (less) vulnerable prey and more (less) efficient predator subpopulations. These rules are summarized in the following result.

RESULT 4. *Without loss of generality assume that the predator subpopulation 1 is relatively more efficient, that is $C_1 > C_2$, but other parameters are identical*

to subpopulation 2. If $A_1 = A_2 = A$ and $B_1 = B_2 = B$ are negative, and C_i is non-positive with $C_i > \max\{-\frac{r_m B}{AK}, -\frac{s_m A}{BL}\}$, then

$$S_{N_1}^* > S_{N_2}^* \qquad and \qquad S_{P_1}^* > S_{P_2}^*.$$

Result 4 suggests that to harvest a predator–prey metapopulation optimally, we should leave both subpopulations living in the patch with a relatively more efficient predator with higher escapements than the other subpopulations. A special case is when $\beta_1 = \beta_2$. In this case, we should leave both subpopulations living in the patch with relatively less vulnerable prey higher escapements than the other subpopulations. Similar results as in Results 1–3 can also be established if we assume the prey has a symmetric migration and one of the predators is a relative source subpopulation. We illustrate the result for this asymmetric predator migration in the following numerical example.

3.2. *A numerical example with negligible costs.* In this section, a numerical example is presented to illustrate and to compare our two-patch predator–prey optimal escapements. For the purpose of comparison, parameters for the prey and predator population are similar to those in Tuck and Possingham (1994).

Assume that the prey in both patches have carrying capacities $K_1 = K_2 = 400{,}000$, with intrinsic growth $r_1 = r_2 = 1000$ and adult survival per period $a_1 = a_2 = 0.001$. The juveniles migrate symmetrically, that is $p_{11} = p_{22} = 0.001$ and $p_{12} = p_{21} = 0.003$, hence there is no relative source/sink and exporter/importer prey subpopulation. Assume the discounting rate δ is 10%. Before the exploitation begins, it is assumed that the population is in the equilibrium state. In the absence of the predator, the unharvested population sizes for prey subpopulations 1 and 2 are $\bar{N}_1 = \bar{N}_2 = 300{,}100$. Using equation (15) with $C_i = 0$, we find the optimal escapements for the prey subpopulations 1 and 2 are $S_{N_{1s}}^* = S_{N_{2s}}^* = 145{,}050$, hence both prey subpopulations are harvested equally with first-period optimal harvests $H_{N_{1s}}^* = H_{N_{2s}}^* = 155{,}050$ and equilibrium optimal harvests $H_{N_{1s}}^* = H_{N_{2s}}^* = 224{,}900$.

Now suppose the predator (P_i) is present. Let the intrinsic growth of the predator be $s_1 = s_2 = 1000$ with the carrying capacities $L_1 = L_2 = 40{,}000$. We assume the adult survival per period of the predator is no different from the adult survival of the prey and no different between patches, hence $b_1 = b_2 = 0.001$. The predator on patch 1 is assumed to be a more relative source/exporter than the predator on patch 2, with the migration parameters $q_{11} = q_{21} = q_{22} = 0.001$, and $q_{12} = 0.003$. Let $\alpha_i = \beta_i = 0.00001$, that is we assume the predator has a high conversion efficiency. Using NAG routine c05nbf, we find one of the positive equilibrium population sizes for this two-patch predator–prey system, that is $(\bar{N}_1, \bar{N}_2, \bar{P}_1, \bar{P}_2) = (270{,}581, 205{,}331, 43{,}248, 76{,}676)$ from equations (1) and (2).

Using equations (15) and (16), we find the optimal escapement for the system $S_{N_1}^* = S_{N_2}^* = 145{,}050$ and $S_{P_1}^* = 14{,}505$ and $S_{P_2}^* = 9010$ (Fig. 2). These

escapements are the same as those of a single-species metapopulation since we have $\alpha_i = \beta_i$ for each patch. However, the optimal harvests are different. In this case, we find the first period optimal harvests $H^*_{N_1} = 125{,}531$, $H^*_{N_2} = 60{,}281$, $H^*_{P_1} = 28{,}743$, $H^*_{P_2} = 6766$, and the equilibrium optimal harvests $H^*_{N_1} = 203{,}861$, $H^*_{N_2} = 211{,}831$, $H^*_{P_1} = 22{,}775$, and $H^*_{P_2} = 38{,}784$. As expected, because there is no source/sink or exporter/importer prey subpopulation, using both methods we harvest predator subpopulation 1 more conservatively than predator subpopulation 2. In this case $H^*_{P_1} = 22{,}775$ and $H^*_{P_2} = 38{,}784$ from two-patch predator–prey escapements, while $H^*_{P_{1s}} = 1735$ and $H^*_{P_{2s}} = 25{,}715$ from single-species metapopulation escapements.

Even though the degree of predator–prey interaction is very low, that is small α and small β, optimal harvests from a single-species metapopulation and from a predator–prey metapopulation can be very different quantitatively. In general, if $C_i \leq 0$, then the optimal escapement from a predator–prey metapopulation is less than or equal to optimal escapement from a single-species metapopulation. As a result, if we use optimal escapement from a single-species metapopulation as a policy to manage a predator–prey metapopulation system, then we might under harvest the stocks. On the other hand, if we use optimal harvest from a single metapopulation, we might over harvest the prey and under harvest the predator. Next, we compare the optimal escapements and equilibrium harvests from a predator–prey metapopulation to the optimal escapements and equilibrium harvests if spatial structure is not considered in the system.

Table 1. Escapements and harvests comparison between correct and incorrect assumption with $p_N = p_P$.

PPM	$S^*_{N_1} = 145{,}050$	$H^*_{N_1} = 203{,}861$	$S^*_{P_1} = 14{,}505$	$H^*_{P_1} = 22{,}775$
	$S^*_{N_2} = 145{,}050$	$H^*_{N_2} = 211{,}831$	$S^*_{P_2} = 9010$	$H^*_{P_2} = 38{,}784$
	$S^*_N = 290{,}100$	$H^*_N = 415{,}692$	$S^*_P = 23{,}515$	$H^*_P = 61{,}559$
UPP	$S^*_{N_{1u}} = 145{,}050$	$H^*_{N_{1u}} = 211{,}831$	$S^*_{P_{1u}} = 9010$	$H^*_{P_{1u}} = 20{,}294$
	$S^*_{N_{2u}} = 145{,}050$	$H^*_{N_{2u}} = 203{,}861$	$S^*_{P_{2u}} = 14{,}505$	$H^*_{P_{2u}} = 36{,}736$
	$S^*_{N_u} = 290{,}100$	$H^*_{N_u} = 415{,}692$	$S^*_{P_u} = 23{,}515$	$H^*_{P_u} = 57{,}030$
WPP	$S^*_{N_w} = 290{,}100$	$H^*_{N_w} = 413{,}036$	$S^*_{P_w} = 25{,}346$	$H^*_{P_w} = 63{,}391$

PPM, predator–prey metapopulation,
UPP, unconnected predator–prey population,
WPP, well-mixed predator–prey population.

First, if our predator–prey metapopulation system is incorrectly considered as an unconnected two-patch predator–prey system, then the optimal escapements are found from equations (15) and (16) by replacing p_{ii}, p_{ij}, q_{ii} and q_{ij} with 1, 0, 1 and 0 respectively, and replacing $(p_{ii} + p_{ij})r_i$ and $(q_{ii} + q_{ij})s_i$ with r_{iu} given by equation (11), and $(q_{ii} + q_{ij})s_i$ is replaced by s_{iu} similarly. The resulting

escapements are $S_{N_{1u}}^* = S_{N_{2s}}^* = 145{,}050$, $S_{P_{1u}}^* = 9010$, and $S_{P_{2u}}^* = 14{,}505$. The harvesting strategy from these escapements produces optimal equilibrium harvests $H_{N_{1u}}^* = 211{,}831$, $H_{N_{2u}}^* = 203{,}861$, $H_{P_1}^* = 20{,}294$, and $H_{P_2}^* = 36{,}736$ with total harvest $H_u^* = H_{N_u}^* + H_{P_u}^* = 472{,}722$. This total harvest is less than the total harvest if we correctly use a predator–prey metapopulation escapements, that is $H^* = H_N^* + H_P^* = 477{,}251$ (see Table 1). This is because if we use unconnected predator–prey theory, we fail to recognize the exporter predator subpopulation which is important as a contributor to the other predator subpopulation. In this case, we exploit the relative exporter predator too heavily, with escapement only 9010, while the relative importer predator is harvested too conservatively with escapement 14,505. We note that there is no difference to the total harvest from the prey, and that the difference is only to the harvest from individual patches. If we use the harvesting strategy from unconnected two-patch predator–prey escapements, we over harvest the prey living in the same patch with the relative exporter predator, while the prey living in the same patch with the relative importer predator is under harvested. In conclusion, in this example, compared with the harvesting strategy from unconnected two-patch predator–prey escapements, the harvesting strategy from a predator–prey metapopulation gives a higher total harvest while it leaves the relative exporter predator a higher escapement.

Secondly, if our predator–prey metapopulation system is incorrectly considered as a well-mixed predator–prey system, then the optimal escapements are found from equations (15) and (16) by replacing p_{ii}, p_{ij}, q_{ii} and q_{ij} with 1, 0, 1 and 0 respectively, and replacing $(p_{ii} + p_{ij})r_i$ and $(q_{ii} + q_{ij})s_i$ with r_w given by equation (12), and $(q_{ii} + q_{ij})s_i$ is replaced by s_w similarly. The resulting escapements are $S_{N_w}^* = 290{,}100$ and $S_{P_w}^* = 25{,}346$. The harvesting strategy from these escapements produces optimal equilibrium harvests $H_{N_w}^* = 413{,}034$ and $H_{P_w}^* = 63{,}392$ with total harvest $H_w^* = H_{N_w}^* + H_{P_w}^* = 476{,}426$. This total harvest is less than the total harvest from the predator–prey metapopulation, that is $H^* = 477{,}251$ (see Table 1). As indicated by Result 3, using the escapement from a well-mixed predator–prey population would over harvest the relative source predator subpopulation (P_1) and under harvest the relative sink predator subpopulation (P_2), since $S_{P_1}^* = 14{,}505 > S_{P_w}^*/2 = 12{,}673 > S_{P_2}^* = 9010$.

3.3. *The case of cost inclusion.* We assume that both unit costs of harvesting C_{X_i} and market prices p_X are constant, but the costs may differ between patches and the prices may differ between species. A relatively constant unit cost of harvesting are known, for example, in the clupeoids fishery (Munro, 1992). Using these assumptions optimal escapements for both the prey and predator have exactly the same form as escapements where costs are negligible, i.e.

$$S_{N_{ci}}^* = \frac{A_{ci} Q_{ci} \frac{2s_i}{L_i} + C_{ci} B_{ci}}{\Delta_{ci}},$$

$$S^*_{P_{ci}} = \frac{B_{ci} P_{ci} \frac{2r_i}{K_i} + C_{ci} A_{ci}}{\Delta_{ci}},$$

provided $\Delta_{ci} = C^2_{ci} - P_{ci} \frac{2r_i}{K_i} Q_{ci} \frac{2s_i}{L_i} \neq 0$ with

$$A_{ci} = \frac{(p_N - c_{N_i})}{\rho} - [p_{ii}(p_N - c_{N_i}) + p_{ij}(p_N - c_{N_j})]r_i - a_i(p_N - c_{N_i}),$$

$$B_{ci} = \frac{(p_P - c_{P_i})}{\rho} - [q_{ii}(p_P - c_{P_i}) + q_{ij}(p_P - c_{P_j})]s_i - b_i(p_P - c_{P_i}),$$

$$C_{ci} = -\alpha_i(p_N - c_{N_i}) + \beta_i(p_P - c_{P_i}),$$

$$P_{ci} = p_{ii}(p_N - c_{N_i}) + p_{ij}(p_N - c_{N_j}),$$

$$Q_{ci} = q_{ii}(p_P - c_{P_i}) + q_{ij}(p_P - c_{P_j}).$$

Similar results to the four results discussed in the negligible cost analysis can also be obtained by inserting an additional subscript c into the appropriate parameters, with additional conditions such as:

1. For Result 1, the prey subpopulation 1 is a relative source subpopulation with $p_{11}r_1 \geq p_{21}r_2$ and $p_{12}r_1 > p_{22}r_2$ (or $p_{11}r_1 > p_{21}r_2$ and $p_{12}r_1 \geq p_{22}r_2$).
2. For Results 2 and 3, the marginal net revenue from the prey subpopulation 1 is lower than or equal to the marginal revenue from the prey subpopulation 2, that is $p_N - c_{N1} \leq p_N - c_{N_2}$, and its ratio satisfies

$$\frac{p_N - c_{N_1}}{p_N - c_{N_2}} \geq \frac{r_2 p_{22}}{r_1 p_{11}}.$$

4. CONCLUSION

Harvesting strategies for a spatially structured predator–prey system are established as a generalization of harvesting strategies for a single-species metapopulation. Some properties of the escapements for a single-species metapopulation are preserved in the presence of predators, such as the strategies on how to harvest a relative source/sink and exporter/importer local population. In the absence of harvesting costs, we find that if there are no biological parameter differences between local populations, the rules of thumb for harvesting a single-species metapopulation can be used to manage a predator–prey metapopulation provided the predator efficiency is high. Furthermore, we find that, in some circumstances, with harvesting costs and cost differences between patches, and price differences between species, the rules are unaltered if all costs of harvesting are independent of the size of the stocks.

In addition, we establish rules to harvest relatively more (or less) vulnerable prey subpopulations and more (or less) efficient predator subpopulations. In general, if the migrations between subpopulations are symmetric, and there is no biological variability except the vulnerability of the prey, then we should harvest a relatively less vulnerable prey subpopulation more conservatively than the other prey subpopulation which is more vulnerable to predation. A special case occurs when there is no predation in patch 1, that is $\alpha_1 = \beta_1 = 0$. In this case, patch 1 is a refuge for the prey. We find that the prey living in their refugial habitat should be harvested more conservatively than the prey living in the habitat where predation occurs. Similarly, if the only biological variability is the predator efficiency, then we should harvest the prey living in the same patch with the relatively more efficient predator more conservatively than the other prey subpopulation. Furthermore, if both prey vulnerability and predator efficiency vary between patches, unlike predator efficiency, prey vulnerability does not have any significant effect on the optimal escapements. In this case, we harvest a relatively more efficient predator more conservatively than a relatively less efficient predator. We also harvest the prey living in the same patch with the relatively more efficient predator more conservatively.

It is important to realize the limitation of the model in this paper. It ignores age-structure and only considers Lotka–Volterra predator–prey functional form. Future models should include age structure and take into account various types of predator–prey functional forms to make a more realistic model and generalize results presented in this paper.

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APPENDIX

A.1. Proof of Result 1. Recall that $B_1 = B_2$ and $C_1 = C_2$, and hence we ignore their subscripts. Let $\Delta_{S_N} = (S_{N_1}^* - S_{N_2}^*)\Delta_1\Delta_2$. Substitute escapement $S_{N_i}^*$ from equation (15) into expression $S_{N_1}^* - S_{N_2}^*$ and rearrange the result to obtain

$$\Delta_{S_N} = \left(-\frac{4s_m^2}{KL}(r_{2m} - r_{1m})\right)\left(\frac{2R}{L} - C\right) - \frac{2C}{L}\left(C - \frac{2S}{K}\right)s_m(r_{1m} - r_{2m})$$

with $R = \frac{1}{\rho} - a$ and $S = \frac{1}{\rho} - b$. Simplify the equation above to obtain

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

Clearly $S_{N_1}^* > S_{N_2}^*$, since $\frac{2B}{K} \leq C \leq 0$ and $\Delta_i < 0$. We can prove $S_{P_1}^* \leq S_{P_2}^*$ and Result 4 similarly.

A.2. Proof of Result 2. All parameters are equal except $p_{12}r_1 > p_{21}r_2$. Recall that

$$S_{N_1}^* = \frac{(R - r_{1_m}) \frac{2s_{1m}}{L} + CB}{C^2 - \frac{4r_{1m}s_{1m}}{KL}}$$

and

$$S_{N_{1u}}^* = \frac{(R - r_{1u}) \frac{2s_{1m}}{L} + CB}{C^2 - \frac{4r_{1u}s_{1m}}{KL}}.$$

Following the proof of Result 1 we obtain

$$(S_{N_1}^* - S_{N_{1u}}^*) \Delta_{1u} \Delta_1 = (r_{1u} - r_{1m}) \left(C \left(C - \frac{2B}{K} \right) - \frac{4Rs_{1m}}{KL} \right) \frac{2s_{1m}}{L},$$

where $\Delta_{1u} = C^2 - \frac{4r_{1u}s_{1m}}{KL}$, and $\Delta_1 = C^2 - \frac{4r_{1m}s_{1m}}{KL} < 0$. Since $p_{11}r_1 \geq p_{22}r_2$ and $\Delta_i < 0, i = 1, 2$, then $\Delta_{1u} < 0$. Furthermore since $r_{1_m} > r_{1u}$ and $0 > C > \frac{2B}{K}$, then we have $S_{N_1}^* - S_{N_{1u}}^* > 0$. In other words $S_{N_1}^* > S_{N_{1u}}^*$. Analogously we can prove that $S_{N_2}^* < S_{N_{2u}}^*$, $S_{P_1}^* < S_{P_{1u}}^*$ and $S_{P_2}^* > S_{P_{2u}}^*$.

Now we only need to show that $S_{N_1}^* + S_{N_2}^* \leq S_{N_{1u}}^* + S_{N_{2u}}^*$ since $S_{P_1}^* + S_{P_2}^* \geq S_{P_{1u}}^* + S_{P_{2u}}^*$ can be shown similarly. Recall that

$$(S_{N_1}^* - S_{N_{1u}}^*) = \frac{(r_{1u} - r_{1m})X}{\Delta_{1u} \Delta_1},$$

and similarly

$$(S_{N_2}^* - S_{N_{2u}}^*) = \frac{(r_{2u} - r_{2m})X}{\Delta_{2u} \Delta_2},$$

where

$$X = \left(C(C - 2B/K) - \frac{4Rs_{im}}{KL} \right) \frac{2s_{im}}{L} < 0,$$

with i is either 1 or 2. If $\Delta S_{Nu} = (S_{N_1}^* + S_{N_2}^*) - (S_{N_{1u}}^* + S_{N_{2u}}^*)$ then

$$\Delta S_{Nu} \Delta_1 \Delta_{1u} \Delta_2 \Delta_{2u} / X$$

$$= (r_{1u} - r_{1m}) \left[C^4 - (r_{2m} + r_{2u}) 4s_{im} C^2 / (KL) + r_{2m}r_{2u} 16s_{im}^2 / (K^2 L^2) \right]$$

$$+ (r_{2u} - r_{2m}) \left[C^4 - (r_{1m} + r_{1u}) 4s_{im} C^2 / (KL) + r_{1m}r_{1u} 16s_{im}^2 / (K^2 L^2) \right]$$

$$= (r_{1u} - r_{1m} + r_{2u} - r_{2m}) C^4 - 2(r_{1u}r_{2u} - r_{1m}r_{2m}) 4s_{im} C^2 / (KL)$$

$$+ (r_{1u}r_{2u}(r_{1m} + r_{2m}) - r_{1m}r_{2m}(r_{1u} + r_{2u})) 16s_{im}^2 / (K^2 L^2)$$

Since $r_{1_u} + r_{2_u} = r_{1_m} + r_{2_m}$, then the first term is zero, and the third term is equal to $(r_{1_u} r_{2_u} - r_{1_m} r_{2_m})(r_{1_m} + r_{2_m}) 16 s_{im}^2/(K^2 L^2)$. Hence we have

$$\Delta S_{Nu} = \frac{(-8 s_{im} C^2/(KL) + (r_{1_m} + r_{2_m}) 16 s_{im}^2/(K^2 L^2))(r_{1_u} r_{2_u} - r_{1_m} r_{2_m})}{\Delta_1 \Delta_{1u} \Delta_2 \Delta_{2u}} X$$

$$= \frac{(8 s_{im}/(KL)(\frac{2(r_{1_m} + r_{2_m}) s_{im}}{KL} - C^2))(r_{1_u} r_{2_u} - r_{1_m} r_{2_m})}{\Delta_1 \Delta_{1u} \Delta_2 \Delta_{2u}} X$$

Since $\Delta_i < 0$ with $i = 1, 2$, then $C^2 - \frac{2(r_{1_m} + r_{2_m}) s_{im}}{KL} < 0$. We can prove that if $p_{11} r_1 \geq p_{22} r_2$ then $(r_{1_u} r_{2_u} - r_{1_m} r_{2_m}) \geq 0$. Hence $\Delta S_{Nu} \leq 0$. This completes the proof.

A.3. Proof of Result 3. Recall that

$$S_{N_w}^* = \frac{(R_w - r_w)\frac{2 s_w}{L_w} + C_w B_w}{C_w^2 - \frac{4 Q_w r_w}{K_w L_w}} = \frac{(R - r_w)\frac{s_w}{L} + C B}{C^2 - \frac{s_w r_w}{KL}}.$$

Hence

$$\frac{1}{2} S_{N_w}^* = \frac{(R - r_w)\frac{s_m}{L} + C B}{2C^2 - \frac{2 s_m r_w}{KL}}.$$

Using Result 2 we obtain

$$S_{N_1}^* = \frac{(R - r_{1_m})\frac{2 s_m}{L} + C B}{C^2 - \frac{4 s_m r_{1_m}}{KL}} > \frac{(R - r_w)\frac{2 s_m}{L} + C B}{C^2 - \frac{4 s_m r_w}{KL}} = S_0$$

since $r_{1_m} > r_w$. Furthermore, since C is the root of $(\frac{1}{2} S_{N_w}^* - S_0)\Delta_{\frac{w}{2}} \Delta_0 = -3(R - r_w)\frac{s_m C^2}{L} - B C^3 + \frac{B r_w 2 s_m C}{KL} = 0$ then $S_{N_1}^* \geq \frac{1}{2} S_{N_w}^*$. We can prove $S_{N_2}^* \leq \frac{1}{2} S_{N_w}^*$, $S_{P_1}^* \leq \frac{1}{2} S_{P_w}^*$ and $S_{P_2}^* \geq \frac{1}{2} S_{P_w}^*$ similarly. The proof of $S_{N_1}^* + S_{N_2}^* < S_{N_w}^*$ and $S_{P_1}^* + S_{P_2}^* > S_{P_w}^*$ can be done by following the last part of the proof of Result 2.

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