Harvesting creates ecological traps: consequences of invisible mortality risks in predator–prey metacommunities

PETER A. ABRAMS,1,4 LASSE RUOKOLAINEN,1,5 BRIAN J. SHUTER,1,2 AND KEVIN S. MCCANN3

1Department of Ecology and Evolutionary Biology, University of Toronto, 25 Harbord St., Toronto, Ontario M5S 3G5 Canada
2Aquatic Research and Development, Ontario Ministry of Natural Resources, Peterborough, Ontario K9J 8M5 Canada
3Department of Integrative Biology, Guelph University, Guelph, Ontario N1G 2W1 Canada

Abstract. Models of two-patch predator–prey metacommunities are used to explore how the global predator population changes in response to additional mortality in one of the patches. This could describe the dynamics of a predator in an environment that includes a refuge area where that predator is protected and a spatially distinct ("risky") area where it is harvested. The predator's movement is based on its perceived fitness in the two patches, but the risk from the additional mortality is potentially undetectable; this often occurs when the mortality is from human harvesting or from a novel type of top predator. Increases in undetected mortality in the risky area can produce an abrupt collapse of either the refuge population or of the entire predator population when the mortality rate exceeds a threshold level. This is due to the attraction of the risky patch, which has abundant prey due to its high predator mortality. Extinction of the refuge predator population does not occur when the refuge patch has a higher maximum per capita predator growth rate than the exploited patch because the refuge is then more attractive when the predator is rare. The possibility of abrupt extinction of one or both patches from high densities in response to a small increase in harvest is often associated with alternative states. In such cases, large reductions in mortality may be needed to avoid extinction in a collapsing predator population, or to reestablish an extinct population. Our analysis provides a potential explanation for sudden collapses of harvested populations, and it argues for more consideration of adaptive movement in designing protected areas.

Key words: adaptive movement; alternative states; ecological traps; extinction; harvesting; metacommunity; no-take fisheries reserves; predator–prey dynamics; protected area; risk detection; two-patch model.

INTRODUCTION

Most natural communities occur in fragmented and spatially heterogeneous environments (Leibold et al. 2004, Micheli et al. 2004). There is a growing recognition that movement within such metacommunities often has a large adaptive component (Bernstein et al. 1999, Morris 2003, Bowler and Benton 2005, Schreiber et al. 2006, Abrams 2007, Amarasekare 2008, 2010, Armsworth and Roughgarden 2008, Rowell 2009, 2010). Nevertheless, the majority of metacommunity modeling assumes random movement (Leibold et al. 2004, all but one chapter in Holyoak et al. 2005). Devising strategies for population management (exploitation or conservation) and predicting the community consequences of new invaders in metacommunities are both likely to require an understanding of the interaction between local food web dynamics and adaptive movement between habitat patches.

Manuscript received 4 January 2011; revised 15 August 2011; accepted 18 August 2011. Corresponding Editor: S. J. Schreiber.
4 E-mail: peter.abrams@utoronto.ca
5 Present address: University of Helsinki, Viikinkaari 1, P.O. Box 68, Helsinki 00014 Finland.
negative per capita growth rate. Previous work on ecological traps has not discussed harvesting as a cause of this phenomenon. Not only can a harvested patch be an ecological trap, but its attractiveness generally increases as mortality risk increases, due to the concomitant increase in food or other limiting resources. It should be noted that not all movement into sinks is maladaptive; it can be adaptive when conditions in the sink vary so that it is not always a sink, or when it provides access to, or information about other patches (Rowell 2009).

We examine the simplest food web in which the effects of undetected mortality can be studied; i.e., a predator–prey system distributed across two patches. We concentrate on predator movement because organisms occupying higher trophic levels are more likely to move between patches in metacommunities (Vander Zanden and Vadeboncoeur 2002, McCann et al. 2005, Rooney et al. 2006). Predators are also more likely to be exploited by humans (Pauly et al. 1998). Recent work shows that adaptive movement can greatly alter the population dynamics that occur with random movement in this system (Schreiber et al. 2006, Abrams and Ruokolainen 2011, Ruokolainen et al. 2011). Adaptive movement often greatly reduces system-wide variation in population densities when one of the two patches would be stable and the other would have limit cycles in isolation (Ruokolainen et al. 2011). Although the analysis presented here applies to other mortality sources that cannot be detected, we frame our discussion around human harvesting of the predator. Our results suggest that adaptive movement in circumstances with a spatially limited and undetected mortality factor often leads to alternative stable equilibria with and without the predator over a wide range of harvest rates. Increasing the harvesting rate in this scenario often leads to an abrupt collapse of the predator population, and can lead to its simultaneous and abrupt extinction from high densities in both patches.

Given that most fishing gear is designed so that fish will be unable to detect it (Kristjansson 1959, Gabriel et al. 2005), and that most predators forage adaptively using information that is available to them (Stephens et al. 2007), these results argue for a reassessment of many previous analyses of harvesting strategies for predatory fish species and of designs for protected areas. They also argue that the negative effects of novel top predators and human harvesting may often extend far beyond their immediate geographic ranges.

The Model

In most of the analysis, we assume that harvesting of predators (with population \( N_i \) in patch \( i \)) only occurs in patch 1 (the “harvested” or “risky” patch). Patch 2 could be an area that is protected or is inaccessible to harvesting; it is referred to as the “refuge.” Parameters and variables are given a subscript denoting the patch to which they apply. Because we briefly consider harvesting in both patches, we use \( H_i \) to denote the per capita harvest rate of predators in patch \( i \) in the initial formulation of the model (although \( H_2 = 0 \) in most of the analysis, and we use \( H \) without a subscript to denote the rate in patch 1). We use the categorical variable \( \varphi_i \) to denote whether the risk of harvest in a given patch can be perceived by the predator: \( \varphi_i = 1 \) if the risk from harvesting in patch \( i \) is detectable, and \( \varphi_i = 0 \) if it is not. Prey have population \( R_i \) in patch \( i \), and their per capita growth rate is a decreasing function of density, \( f[R_i] \). (Square brackets are used to denote a functional relationship.) In our numerical results we assume logistic growth: \( f_i = r_i - k_i R_i \) in patch \( i \) (prey carrying capacity is therefore \( r_i/k_i \)). Here, \( r_i \) is the maximum per capita growth rate of resource in patch \( i \), and \( k_i \) is the per capita effect of density on resource growth in patch \( i \). The predator functional response in patch \( i \) is \( g_i \), which is an increasing function of the product of the predator’s attack rate while searching \( (C_i) \) and prey density \( (R_i) \). Numerical results are obtained for both linear and Holling type-2 functional responses; in the latter case, the handling time is given by \( h \) (assumed to be identical across patches). The predator has a conversion efficiency of ingested food, \( b \), and a per capita natural mortality rate of \( d_i \) in patch \( i \). The common handling time and conversion efficiency reflect an assumption that the prey populations in each patch are phenotypically similar members of a single species. In the main analysis we assume that a predator individual has some information about conditions in both patches, either having an ability to detect conditions remotely, or by making short-duration, non-foraging visits. Thus, prey \( (R_i) \) and predator \( (N_i) \) populations in patch \( i \) change according to

\[
\frac{dR_i}{dt} = R_i f_i[R_i] - N_i g_i(C_i R_i) \tag{1a}
\]

\[
\frac{dN_i}{dt} = N_i (b g_i(C_i R_i) - d_i - H_i) - N_i M_j (W_j - W_i)
+ N_i M_j (W_i - W_j) \tag{1b}
\]

where \( M_j \) is the per capita movement rate of individuals from the currently occupied patch (first subscript) to the other patch (second subscript). \( M_j \) and \( M_j \) have an identical form; it is a nonnegative and increasing function that approaches zero as its argument becomes sufficiently negative. The argument of each movement function is the difference between the perceived fitness in the other patch and that in the currently occupied patch. Perceived fitness in patch \( i \) is

\[
W_i = b g_i[C_i R_i] - d_i - H_i \varphi_i. \tag{1c}
\]

Eq. 1c implies that the maximum perceived fitness in patch \( i \) is \( b g_i[C_i K_i] - d_i - H_i \varphi_i \), where \( K_i \) is the carrying capacity of the prey in patch \( i \) (its equilibrium density in the absence of consumption). Most of the numerical analysis will assume that the per capita movement rate from patch \( i \) to patch \( j \) is an exponential function of the
perceived fitness difference between patches. The per capita movement rate is $m$ when perceived fitness ($W$) is equal across patches. The per capita movement rate out of patch $i$ is given by

$$M_{ij} = m \times \exp[\lambda(W_j - W_i)]$$  \hspace{1cm} (1d)

where $m$ (baseline movement rate) and $\lambda$ are nonnegative constants. The fitness sensitivity parameter, $\lambda$, measures how rapidly the per capita movement rate changes with the perceived fitness difference, whereas the baseline movement rate, $m$, denotes the per capita rate of movement when the perceived fitness values of the two patches are equal. Eq. 1d has been used in several previous studies (Abrams 2000, 2007, Abrams and Ruokolainen 2011, Ruokolainen et al. 2011). Here we assume that each patch in isolation supports predator and prey in the absence of harvesting ($h(CK) > d$), so both patches have a positive $W$ at sufficiently low predator densities. In general, patches differ in one or more of the population dynamic parameters. A patch may be attractive to a predator individual because it allows a higher food intake rate (i.e., has a larger CR) or has a lower perceived mortality ($d + H0$).

Our main question is how the predator population sizes in both patches change with the per capita harvest rate, $H$, in the exploited patch ($i = 1$). We examine conditions for persistence in one or both patches and the relationship between per capita harvest rate and harvest yield (i.e., $HN$). These issues are affected by the type and level of between-patch heterogeneity and by the parameters of the movement function, Eq. 1d, which includes random movement as a special case. Alternative functional forms for population dynamics and movement are discussed briefly.

**Analysis and Results**

The first part of the analysis assumes that habitat selection is “perfect,” in that a predator individual never moves to a patch that it perceives as having lower fitness. By also assuming that the equilibrium point is stable (which is always true of an equilibrium with positive densities when the functional response is linear), we are able to derive some results analytically. This first part compares systems where the additional mortality can be perceived with those where it is invisible. The second part of the analysis uses Eq. 1d to represent movement, and adopts specific forms for prey growth functions and predator functional responses. This part has three sections: a general treatment of extinction; analysis of systems with linear functional responses; and a brief treatment of predators with type-2 responses. The main analysis treats patches that differ in the predator’s attack rate; results for heterogeneity in prey growth parameters are summarized, with more details in the Appendix.

**Part 1. Perfect movement with a stable equilibrium**

“Perfect” movement means that the per capita movement rate from patch $i$ to patch $j$ ($M_{ij}$) is zero if $W_j > W_i$. When $W_i < W_j$, then $M_{ij}$ is an increasing function of the difference $W_j - W_i$. Such a rule leads to an ideal free distribution in a stable system (Cressman et al. 2004). If $m$ is small enough and $\lambda$ is large enough, the movement function used in part 2 (Eq. 1d) can closely approximate a perfect rule. This may not produce an “ideal” outcome when fitness is not perceived accurately.

**Risk from harvesting is perceived**

We begin by considering a predator that can accurately measure and respond to the risk posed by harvesting, so that perceived and true fitness are identical. This means that patch 1 will be avoided until its prey availability is sufficiently higher than that of patch 2 to outweigh the additional harvest mortality. For systems with a stable equilibrium, this implies that the equilibrium predator populations in each patch are ultimately what they would be in isolation. There is no movement when patches have identical fitness and this is true at equilibrium, where $W_1 = W_2 = 0$. As a result, population size and harvest yield at equilibrium are unaffected by the other patch. If the harvesting effort is high enough to cause predator extinction in the exploited patch ($W_1 < 0$), individuals will not move there from the refuge (where $W_2 = 0$ at equilibrium).

**Mortality risk is not perceived**

For the rest of this section we assume that the predator does not detect the risk of harvesting ($p = 0$), and we analyze the consequences of perfect movement under this constraint. The four potential equilibrium states of the system are: (1) predators are present only in the harvested patch; (2) predators are present only in the refuge; (3) predators are absent from both patches; and (4) predators are present in both patches. We are particularly interested in determining whether two or more of these states can be locally stable in the same system (i.e., whether there are alternative attractors).

We start by finding conditions under which predators persist only in the harvested patch. This requires a net loss of individuals from the refuge when its population is near zero, which is only possible if the perceived fitness of the harvested patch is greater than that of the refuge in these circumstances. Refuge fitness with almost no predators present is $bg[C_2K_2] - d_2$, where $K_2$ is prey carrying capacity in the refuge. Perceived fitness in patch 1, $W_1 (= bg[C_1K_1] - d_1)$, must equal $H$ at equilibrium, and this must exceed the actual fitness in the refuge when it is almost empty. Therefore, a necessary pair of conditions for the predator to be present only in the harvested patch at equilibrium is

$$bg[C_2K_2] - d_2 < H < bg[C_1K_1] - d_1$$  \hspace{1cm} (2a)

where the expressions $bg[C_1K_1] - d_1$ represent the maximum fitness in patch 1. The second condition required for stability of a system with an empty refuge is that the per capita movement rate out of the refuge exceeds the maximum per capita growth rate in that
patch, as follows:

\[ M_{21}[H - (bg[C_2K_2] - d_2)] > bg[C_2K_2] - d_2 \]  

(2b)

where the argument of \( M_{21} \) is the difference in perceived fitness, \( W_1 - W_2 \). Inequality 2b is satisfied when \( 2a \) is satisfied and the movement out of patch 2, \( M_{21} \), is sufficiently large. (Because we assume "perfect" movement, \( M_{12} = 0 \) when condition 2a is satisfied.)

The second potential equilibrium only has predators in the refuge. This cannot exist under perfect movement because its existence would require that the refuge fitness at equilibrium (\( W_2 = 0 \)) be greater than the perceived fitness of the harvested patch when it has no predators. This, however, is equivalent to patch 1 being incapable of supporting any predators when \( H = 0 \):

\[ 0 > bg[C_1K_1] - d_1 \]  

(3)

which is contrary to our assumption that each patch can support predators without migration.

The third potential equilibrium is extinction of predators in both patches. This implies that prey are at their carrying capacities in each patch, and perceived fitness equals the maximum possible per capita growth rate in each patch, \( bg[C_1K_1] - d_1 \), which will be abbreviated \( W_{\text{max}} \). To observe this, set of population sizes must be locally stable. Stability is determined by the dominant eigenvalue of the Jacobian matrix of the system consisting of the two predator equations evaluated at prey populations of \( K_i \) and predator populations approaching zero. Given movement functions \( M_{ij} \), with \( M_{21} > W_{2\text{max}} \), the conditions for local stability of the extinction equilibrium are as follows:

\[ H > W_{1\text{max}} + W_{2\text{max}} - M_{12} - M_{21} \]  

(4a)

\[ H > \frac{M_{21}W_{1\text{max}} + M_{12}W_{2\text{max}} - W_{1\text{max}}W_{2\text{max}}}{M_{21} - W_{2\text{max}}} \]  

(4b)

Under perfect movement with heterogeneous patches, satisfying these conditions (4a, b) requires \( M_{21} > W_{2\text{max}} \) and \( H > W_{1\text{max}} > W_{2\text{max}} \). That is, (1) movement out of the refuge is greater than maximum growth within it; and (2) the harvest rate is greater than the maximum per capita growth rate in patch 1, which in turn exceeds the maximum per capita growth in patch 2. If \( m \) is small and \( \lambda \) is large, conditions 4a, b are also a very good approximation for the extinction conditions when Eq. 1d describes movement.

The fourth potential equilibrium has significant densities of predators in both patches. Because prey availability must be higher in the harvested patch, \( W_1 > W_2 \) when predators cannot detect harvest risk. Ideal movement then implies that \( M_{21}^* > 0 \) and \( M_{12}^* = 0 \), where the asterisks denote that the functions are evaluated at the equilibrium with positive densities in both patches. The equilibrium densities must satisfy \( N_1 = W_2N_2/(H - W_1) \). Note that there can be an equilibrium with positive densities of predators in both patches when \( W_2 > 0 \) and \( H > W_1 \). This can be shown to be locally stable under a wide range of parameter values when the functional responses are linear (addressed in the next section). The equilibrium \( N_2 \) is positive at this point, provided that \( M_{21}^* < W_{2\text{max}} \). Our previous results showed that extinction in both patches could also be locally stable when \( H > W_1 \) and \( M_{21} > W_{2\text{max}} \). These two sets of stability conditions are not contradictory because the movement rate \( M_{21} \) is a function of prey densities, which differ between these two points. The conditions do imply that the difference in perceived fitness must be smaller at the equilibrium with predators in both patches than at the equilibrium with the refuge predator population extinct. This can occur because the subsidy of predators from the refuge to the harvested patch reduces the difference in prey densities between the patches at the upper equilibrium. The potential alternative states are explored numerically below using Eqs. 1 for both linear and type-2 responses. A simultaneous collapse of both predator populations due to increasing harvest in patch 1 can occur when the equilibrium with both predator populations positive becomes unstable at an \( H \) value where the global predator extinction point is locally stable (i.e., when \( H > W_{1\text{max}} \) and \( M_{21} > W_{2\text{max}} \)).

Part 2. Numerical results for heterogeneous systems having imperfect movement (Eq. 1d)

Here prey growth is assumed to be logistic, and functional responses are either linear or Holling type-2. Parameter differences are a major determinant of the equilibrium densities in systems having random movement, because they lead to fitness differences between patches. Some parameter differences also may lead to synchrony when one or both patches in isolation are inherently cyclic (Goldwyn and Hastings 2009, Ruokolainen et al. 2011); this typically alters both the variances and mean population sizes. We illustrate most of our results for patches that differ in the predator’s attack rate, \( C \), and present other results (for differences in \( r \) and \( k \)) in the Appendix.

We begin our analysis with linear functional responses \((g = CR)\), which always produce stable systems. We then examine type-2 responses \((g = CR(1 + ChR))\), under which cyclic within-patch dynamics are possible. The numerical analyses were carried out using Mathematica 8.0.1 (Wolfram 2011). They included determination of stability of the equilibrium with high predator densities in both patches, and determination of non-equilibrium dynamics in systems with type-2 responses. Simulations used the routine NDSolve (with an AccuracyGoal setting of Infinity) for 10 000 time units, and the average population densities of cycling systems were based on the final 6000 time units. Continuation of attractors (using final parameter values to initiate the subsequent simulation following a small perturbation in one or more parameter values) was used to explore the parameter ranges under which they were locally attracting. Because movement is always bi-directional,
equlibria corresponding to extinction of predators in one patch under perfect movement become equilibria with very low densities in that patch (usually $< 10^{-6}$ for parameters used here); these will still be referred to as extinction.

Conditions for global predator extinction

Under movement rule Eq. 1d, conditions 4a, b may be evaluated numerically at the equilibrium point when functional responses are linear. Fig. 1 shows that the threshold harvesting rate, $H$, above which global predator extinction is locally stable, depends on the between-patch heterogeneity. Fig. 1 assumes that patches differ in the predator’s attack rate, $C_i$. Fig. 1A illustrates extinction conditions for a predator with a linear functional response, whereas Fig. 1B represents a similar system with a type-2 response. In both cases, as the parameter difference between patches increases, there is a sharp decline in the maximum harvest rate allowing persistence, followed by a slow increase. The initial decline in maximum $H$ reflects the loss of the ability of the refuge to persist as the difference in relative attractiveness of the two patches at low predator densities increases. Where the maximum $H$ increases with $C_1$, that rate is very close to the maximum for the harvested patch in isolation, and the refuge is close to extinction. The attractiveness of the harvested patch at low predator densities is increased by larger $m$ or $\lambda$; either of these reduces the range of parameter values allowing predator persistence (i.e., the area under the curves). Changes in baseline movement rate ($m$) or fitness sensitivity ($\lambda$) make more of a difference to persistence in the system with type-2 responses (panel B). This is largely due to the lower maximum per capita growth rate implied by this response, which reduces the maximum difference in fitness (and hence attractiveness) between patches.

Sufficient conditions for global predator persistence (which are simpler than conditions 4a, b) are given in the Appendix. When the refuge is inherently less attractive at equilibrium, it can still persist if both parameters of the movement function are sufficiently small or if there is a sufficiently small fitness difference with near-zero predator populations in both patches. The latter is most likely to be true when the two patches are similar in parameter values. Local stability of global predator extinction for a particular harvest rate is often consistent with predator persistence at that rate or a higher rate, given higher initial predator densities; examples will be provided.

Alternative states and population responses in heterogeneous systems with linear functional responses

Heterogeneity in predator attack rates.—We examine how population sizes and harvest yields change with harvesting rate when patches differ in the predators’ per capita attack rates, $C_i$. Such differences can be due to differences in the physical structure of the habitats that produce prey refuges or alter the visibility or movement ability of one or both species. We concentrate on cases in which $C_i$ is larger in the harvested patch, because this is the only situation in which harvesting in patch 1 can cause global predator extinction, given sufficiently accurate habitat choice based on perceived fitness. Fig. 2 presents two examples, both with $C_1 > C_2$; they exhibit the two types of alternative attractors that occur for this linear functional response system. In the more heterogeneous system (Fig. 2A, B), the alternative stable equilibria are high predator populations in both patches and predators only in the harvested patch. With lower
heterogeneity (Fig. 2C, D), these alternatives exist at intermediate $H$. However, at the highest levels of harvesting still admitting alternative stable equilibria (roughly $0.27 < H < 0.29$ in Fig. 2), the smaller equilibrium corresponds to global extinction. At these high harvest rates, the global predator population experiences an Allee effect: low predator densities cannot increase, but high initial numbers allow growth to the equilibrium with high densities in both patches.

For both systems in Fig. 2, equilibrium predator densities in both patches decline with increased harvesting, with predators in the refuge patch declining more rapidly. The decline in the refuge occurs because the relative attractiveness of the harvested patch increases with $H$ as prey availability increases in that patch relative to the refuge. However, the redistribution of predators involves positive feedback; at a certain value of $H$, the total productivity of predators in the refuge $(N_2^2 - d_2)$ declines because the harvest reduces density more than the per individual growth rate increases with increasing resource abundance. The resulting loss of immigrants decreases the harvested predator population, which further increases its attractiveness to individuals still remaining in the refuge. Above a threshold harvest rate, this destabilizes the equilibrium.

The result is a transition to an equilibrium where the refuge has insignificant predator density and the harvested patch has a greatly decreased predator abundance (which approximates its single-patch equilibrium). The higher attack rate in the harvested patch ensures rapid movement to that patch by those few predator individuals that move to, or are born in, the refuge.

The refuge extinction is associated with an abrupt drop in harvest yield (Fig. 2B) because the loss of immigration from the refuge greatly reduces density in the harvested patch. In Fig. 2B this occurs at a harvest rate slightly above the maximum sustained yield (MSY) point. It would clearly be preferable to harvest patch 1 at a rate lower than the MSY rate to reduce the chance of refuge extinction. The MSY per capita harvest rate in Fig. 2D is farther from the rate that causes collapse of the refuge population, but the refuge collapse is more dangerous here, as it involves a system-wide predator extinction. The example in Fig. 2 has been extended to consider higher and lower levels of heterogeneity in the

---

**Fig. 2.** Consequences of harvesting in patch 1 in a system with linear functional responses ($h = 0$) and parameters $r_i = k_i = 1$, $d = 0.025$, $b = 0.25$, $m = 0.0005$, and $\lambda = 150$. Panels (A) and (B) assume that the predator's attack rates in the two patches are $C_1 = 1.3$ and $C_2 = 0.7$; panels (C) and (D) investigate a similar system with lower patch heterogeneity: $C_1 = 1.2$ and $C_2 = 0.8$. Panels (A) and (C) show how predator populations in both patches change with harvest effort, $H$, in patch 1; $N_1$ is the solid line, and $N_2$ is the dashed line. The second attractor is given by the pair of lines at the lower right-hand side of panels (A) and (C). In panel (C), the alternative attractor consists of a small population in patch 1 and none in patch 2 for $0.22 < H < 0.275$, and extinction in both patches for $0.275 < H < 0.295$. Panels (B) and (D) show the yield from the harvest in patch 1, with the right line segment corresponding to the low-density attractor, which only exists at high harvest rates.
attack rate $C$. The range of per capita harvest rates producing alternative stable equilibria for different heterogeneities in $C$ is shown in the Appendix: Fig. A1. Given the other parameters in Eq. 2, alternative equilibria exist for $\sim 20\%$ or more of the range of harvest rates that allow persistence of the predator in at least one patch for heterogeneities ranging from $C_1 = 1.08 (C_2 = 0.92)$ to $C_1 = 1.8 (C_2 = 0.2)$. Alternative stable equilibria occur over the widest range of $H$ for low heterogeneities; this is also true of the possibility of an abrupt transition to complete extinction. Given our assumption that the harvested patch has a greater maximum per capita growth rate of predators, collapses of the refuge in highly heterogeneous systems usually occur well before $H$ is high enough to cause extinction in the harvested patch. Extinction of predators in both patches is the alternative equilibrium for the full range of $H$ values producing alternative states ($H = 0.24$ to $0.40$) when $C_1 = 1.1$, but simultaneous extinction from a state with high densities in both patches cannot occur for any $H$ when $C_1 > 1.3$.

Heterogeneity in prey growth rate parameters.— Systems with heterogeneity in the prey growth parameters can also exhibit abrupt crashes with increased harvesting and alternative equilibria over a range of harvest rates. The Appendix shows the ranges of harvest rates producing alternative equilibria for heterogeneities in the parameters $r$ and $k$, again given linear functional responses and other system-wide parameters identical to those assumed for the preceding section. Alternative states are found over a smaller range of harvest rates and a smaller range of heterogeneities in patch parameters when one of these parameters is heterogeneous than when attack rates differ between patches. Nevertheless, relatively small asymmetry in prey growth parameters results in about one-third of the range of potential harvest rates exhibiting alternative states, one involving extinction of the global population (Appendix: Figs. A2 and A3).

Predator movement parameters.— The results in Fig. 2 and the corresponding ones in the Appendix are also affected by the movement parameters $m$ and $\lambda$. When the fitness sensitivity parameter $\lambda$ becomes very small, most of the effects previously discussed disappear (if $\lambda = 0$, movement is random); see the following paragraph. A larger $\lambda$ increases movement toward an attractive sink and thus leads to a collapse of the refuge at a lower per capita harvest rate. Likewise, a larger $m$ can also reduce the per capita harvest rate at which predators go extinct in the refuge. For the example illustrated in Fig. 2C, D, the refuge (but not the harvested patch) is extinct ($< 10^{-6}$) for all $H > 0.250$, and the refuge remains extinct when its initial population is low until $H < 0.191$. Higher values of $\lambda$ allow refuge extinction to occur at lower between-patch heterogeneities, as they increase movement rates into the ecological trap. The effect of a larger baseline movement rate $m$ is similar; increasing $m$ 100-fold to 0.05 in the system used in Fig. 2C, D leads to alternative states with and without a refuge predator population for $0.193 < H < 0.235$. This is a narrower range of harvest rates with alternative states, and the attractor “without” predators in the refuge actually has a density $> 10^{-6}$ for a large part of this range (so it just manages to avoid “extinction” by the definition used here). However, there is an abrupt increase in the refuge population by more than 50-fold when $H$ is decreased from 0.193 to 0.192. The larger $m$ (0.05) means that the refuge always becomes “almost extinct” at an $H$ value lower than does the harvested patch, given the other parameters of Fig. 2C; i.e., global extinction from a situation with high densities in both patches does not occur.

Scenarios with random movement ($\lambda = 0$) that are otherwise identical to the ones just considered can sustain higher harvesting rates because the dangerous harvested patch is no longer more attractive under this scenario. Conditions 4a, b still apply, but now $M_{12} = M_{21}$; per capita movement rates in both directions are constant and equal. Very high random movement results in almost uniform predator densities across patches, so a sufficiently large $H$ will cause simultaneous extinction of both patches when it exceeds the mean per capita growth rate. However, with sufficiently low random movement, the refuge can maintain a positive predator population for any $H$. Sufficiently low per capita random movement ($M_{21} < r_2$) makes it impossible for harvesting in the exploited patch to cause system-wide extinction. Very high rates of random movement, by homogenizing the whole system, reduce the effective harvest rate by one-half. This allows predator persistence at significantly higher patch 1 harvest rates than in systems with adaptive movement and invisible harvesting risk. Fig. 3 illustrates the consequences of random movement; it is based upon a system like that considered in Fig. 2A, B except that movement is random with a per capita rate $m$ (moderate in Fig. 3A, B and high in Fig. 3C, D).

Systems with type-2 functional responses

Most predator functional responses revealed by empirical studies are saturating, and most of these are Holling type-2 (Jeschke et al. 2004). Nothing in the mechanism underlying the sudden extinctions and alternative attractors we have documented depends on linear functional responses. However, there are (at least) three aspects of systems with type-2 functional responses that seem likely to quantitatively alter the relationship between harvesting and population sizes. First, type-2 responses make it possible for the temporal mean predator population size in a homogeneous patch to increase with harvesting rate over a range of rates (i.e., a “hydra effect”; Abrams and Matsuda 2005). Secondly, saturating responses are known for producing cycles, and Ruokolainen et al. (2011) show that adaptive movement in heterogeneous two-patch systems with type-2 functional responses can result in system-wide stability in many cases when a cyclic patch is coupled to
a stable patch. In the present case, harvesting at a sufficiently high rate stabilizes the intrinsic dynamics of patch 1, which, in the presence of adaptive movement, often stabilizes the cycles arising from the predator–prey interaction in patch 2. A third property of type-2 responses is that the difference in fitness between patches is small for a wide range of prey densities, due to the common asymptote of fitness when the parameters $b$, $d$, and $h$ are similar between patches. This is likely to allow persistence of the equilibrium with high densities in both patches over a wider range of harvest rates.

Because of the increase in the number of parameters, we cannot provide a comprehensive numerical exploration of systems with type-2 responses, and confine this section to some examples that exhibit the three points outlined in the preceding paragraph. Fig. 4 compares the responses to harvesting in three different two-patch systems with type-2 functional responses ($h = 3$). With heterogeneous attack rates ($C_1 = 1.5$; $C_2 = 0.5$) and adaptive movement (Fig. 4A, B), there are two attractors when $H > 0.037$. One of these is represented by the continuation of the pair of lines that begin on the left side of Fig. 4A; these are the long-term average predator population sizes in the refuge (dashed black line) and harvested patch (solid black line). The second attractor is given by gray lines, and is characterized by predator extinction in the refuge for $H > 0.037$, and extinction in both patches for $H > 0.045$. When the system occupies the first attractor, predators in the harvested patch increase monotonically in abundance with increasing $H$ until both predator populations decline abruptly to extinction when $H > 0.049$. The long-term average yield (Fig. 4B) also increases with $H$ until it abruptly drops to zero at $H = 0.049$. If $H$ is decreased from this extinction value, predators in the refuge cannot increase when initially rare until $H < 0.037$, and at that point the equilibrium predator abundance in the refuge jumps to 90% of its unharvested density. The harvested population is able to achieve a slightly higher population density on this second attractor than on the original attractor when $H$ is close to 0.04. Predator abundance in the harvested patch increases (albeit modestly) for all levels of harvesting on the attractor that originates at $H = 0.0$. The equilibria are stable for most of the potential range of harvest rates ($H \geq 0.012$).

A system with adaptive movement that is identical to Fig. 4A, B except for having homogeneous attack rates ($C_1 = C_2 = 1$) is illustrated in Fig. 4C, D. It lacks alternative attractors and the harvested patch does not differ significantly in predator density from the unharvested patch until the harvest rate is quite high. Somewhat higher harvest yields are possible here than...
in the heterogeneous patch case, and the system as a whole is able to persist over a much wider range of harvesting rates. Fig. 4E, F represents the same system as Fig. 4A, B except that movement is random ($k = 0$). Random movement produces very different $N$ vs. $H$ curves (Fig. 4E), and a much greater maximum harvest rate (Fig. 4F; maximum $H = 0.123$) and MSY than in Fig. 4A, B. With random movement, predators in both patches increase with harvest over an intermediate range of harvest rates, where the population undergoes cycles (roughly $H = 0.02$ to 0.06).

Global predator extinction and relatively high densities in both patches exist as alternative states in many systems with type-2 responses. These alternatives generally occur in circumstances similar to those in models with linear functional responses; the widest
range of harvest rates characterized by alternative states usually is observed with low to moderate differences in attack rates. However, the fact that local fitness has a similar asymptote across patches increases the parameter space where systems with positive densities in both patches persist. The Appendix illustrates the responses to harvest in an example that is comparable to the linear-functional-response example from Fig. 2. Low heterogeneities, rather than producing alternative extinction and non-extinction equilibria, make extinction impossible under the movement parameters used in Fig. 2. Higher fitness sensitivity ($\lambda$) allows extinction from a state with high densities over a much wider range of heterogeneities and harvest rates than in the linear functional response model.

**DISCUSSION**

Our results demonstrate that whether movement is adaptive or random and whether the risk due to a mortality factor (such as harvesting) is observable are both important determinants of how a metacommunity responds to local changes in that mortality. These two aspects of movement behavior are thus important for regulating harvesting of exploited populations and for establishing reserves for species at risk. The outcomes of harvesting one patch under different types of movement and different types of between-patch heterogeneity are summarized qualitatively in Table 1. The existence of alternative states and the possibility of sudden extinction of the entire predator population are both most likely when the between-patch heterogeneity is low and movement is adaptive. Alternative states can occur with high heterogeneity, but sudden extinction of both patches is less likely in this scenario. Random movement does not produce alternative states, and, if the movement rate is low, the refuge is safe from extinction. Most previous theory examining harvesting in spatially heterogeneous environments has assumed random movement (e.g., Neubert 2003, Baskett et al. 2007, Kellner et al. 2007), and this may produce estimates of maximal or optimal harvest rates that are too high or too low if there is an adaptive component to movement. Fig. 4B and F represents a comparison where random movement produces a greater maximal yield at a larger per capita harvest rate, and the system can withstand much higher harvest rates without extinction. The risk of sudden population-wide extinction as a consequence of increased harvesting in one part of a population’s range is obviously an important consideration when identifying areas to protect. This extinction risk may occur when any spatially limited and undetected mortality factor (e.g., a novel higher-level predator) affects the focal population in the most productive areas of its range. If avoiding extinction is an important consideration, it may be optimal to harvest species in moderate- rather than high-productivity areas. Risk of sudden extinction from both patches in our models is greatest when the maximum predator per capita growth rate is only slightly larger in the risky patch than in the refuge patch. This permits relatively similar prey densities over a broad range of mortalities, so the high-mortality patch continues to be heavily subsidized by individuals from the refuge patch until harvesting is very heavy.

A few previous theoretical works have examined the consequences of harvesting in systems with adaptive habitat selection (Lundberg and Jonzén 1999, Jonzén et al. 2001, Kaitala et al. 2004). However, these articles did not model movement rates as explicit functions of fitness, most assumed discrete dynamics, and none noted the possibility of refuge collapse or alternative attractors. Some other authors who have examined habitat selection in contexts other than human exploitation have noted that maladaptive movement into sink habitats could cause extinction (Delibes et al. 2001, Kokko and Sutherland 2001, Kristan 2003, Battin 2004, Fahrig 2007; but see Rowell 2009). The first three of the preceding list of articles included analyses of models based on a single territorial species having a continuous range of territory qualities, with territories occupied based on an “ideal despotic distribution” (Fretwell and Lucas 1970). They assumed that this distribution is
achieved instantaneously when conditions change. Kokko and Sutherland (2001) and Kristan (2003) observed alternative states for some parameter values in their models. Although the underlying mechanism is rather different from the one described here, their cases of alternative states also involve attractive sinks that become more attractive as the population within them declines. In the models of Kokko and Sutherland (2001), this occurs because successively more attractive territories in the trap habitat become available as the population in that patch dies out; in our models, attractiveness increases because prey (food) abundance increases as predators are harvested in the sink patch.

Our conclusions are not restricted to the specific models just described, but more work is required to determine their applicability. We have previously investigated movement based on conditions in the current patch only (P. A. Abrams, unpublished data). Those models assumed that movement out of a patch was an exponentially decreasing function of local fitness. They had a range of outcomes similar to the Eq. 1d movement function. This is not surprising, because individuals that move to another patch will only stay there for a long time when conditions are perceived as good in the destination patch. We have also repeated most of the simulations described in the figures using a modification of Eq. 1d that caps the maximum movement rate when fitness differences become large (see Abrams and Ruokolainen 2011: Appendix). This produces only very small quantitative changes in the results we have described. Thus, refuge collapse driven by movement to a harvested ecological trap is likely to happen for a wide range of movement functions. In addition, we have considered harvesting (undetected mortality) in both patches. If the harvesting is very unequal between the patches, the preceding results are only changed slightly. Equal harvesting does not alter the difference between per capita growth rates, except via its indirect effects on the prey densities in the two patches. More crucial are the assumptions that prey do not move between patches and are not harvested in the exploited patch; changing either of these reduces the attractiveness of the harvested patch.
A variety of field observations are consistent with the models explored here. Kellner et al. (2008) note that there is considerable movement of adult individuals out of marine reserves. There is also evidence that movement affects the spatial distribution of exploited species. Harley et al. (2001) analyzed multiple harvest time series from populations of 10 exploited marine fish species to show that catch per unit fishing effort is not sensitive to real declines in population abundance. A likely explanation for this (e.g., Paloomo and Dickie 1964), is that populations became more aggregated as they decline because of adaptive habitat selection based on factors other than risk of harvest, and that fishing effort concentrates in those areas of aggregation. This account is consistent with observations (Myers and Cadigan 1995, Hutchings 1996) that the spatial distribution of northern cod (Gadus morhua) contracted significantly while its population was crashing, and that fishing fleets were attacking the remaining aggregations with great acuity (Rose and Kulka 1999). Halpern et al. (2010) review studies of marine protected areas, and suggest that movement of adults out of reserves increased the size of nearby populations, but that the effect did not extend far from the reserve. The small distance observed may have been related to the relatively small size of the reserves. Practical applications of the results presented here clearly will have to consider issues of mobility, relative sizes of harvested and refuge patches, and the relative influence of adult movement and larval transport in determining local abundances.

Ecological scenarios may be more or less complex than the predator–prey models used here. We neglected single-species models because consumer–resource models with explicit resources (i.e., prey) can show a wider range of dynamics than simple models of density dependence (e.g., Abrams 2009a, b). Nevertheless, two-patch models of single-species density-dependent growth, combined with fitness-dependent movement and invisible harvest risk, have many of the features of the predator–prey models considered here (P. A. Abrams, unpublished data); specifically, they frequently exhibit alternative attractors, one with high densities in both patches and the other with two empty patches. Continuous space (Kellner et al. 2007) and stochasticity (West et al. 2009) also have the potential to affect spatial harvesting models. We hope to consider these features in future articles.

Acknowledgments

This work was supported by grants from the Natural Sciences and Engineering Research Council of Canada. We thank A. J. Golubski and two reviewers for their advice.

Literature Cited


**Supplemental Material**

Appendix

The conditions for extinction and persistence in a model with linear functional responses, the parameter space leading to alternative equilibria in this linear response model, and the responses of populations and yields to harvesting in models with type-2 functional responses (Ecological Archives E093-027-A1).