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Spatial structure has a paramount influence on population dynamics. This has until recently been neglected in harvesting theory. In this paper, we demonstrate how source-sink and habitat selection theory can provide guidance for harvesting spatially structured populations. We also show how harvesting can affect the spatial distribution of the exploited resource, which has consequences for the design of protected areas. This implicit treatment of space is complemented by a spatially explicit predator-prey model. It turns out that harvesting of the prey and/or the predator species in one patch in space sometimes has effects on the other species outside the harvested patch. We stress the importance of considering how realistic the representation of the spatial dimension has to be in population management.

Key words: Harvesting, population management, predator-prey dynamics, reserves, seasonality, spatial dynamics

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During the last two decades, we have seen a rapidly growing interest in the spatial dimension of population dynamics (Kareiva 1990, Tilman & Kareiva 1997, Turchin 1998, Bascompte & Solé 1998, Bjørnstad, Ims & Lambin 1999, Hanski 1999) and an increased understanding of how organisms respond to patterns and processes at various spatial scales (Levin 1994, Mangel 1994). Theoretical ecologists have demonstrated how complex patterns can arise in spatially extended populations (Hastings 1990, Kareiva 1990), even though the environment itself is homogeneous. It is also widely recognised that most environments are spatially structured and we know from habitat selection theory (Rosenzweig 1991, Sutherland 1996) that individuals should and do respond to such environmental heterogeneity.

Despite the strong emphasis on spatial aspects in theoretical ecology and the evidence for the importance of spatial structure in natural populations (Wiens, Stenseth, van Horne & Ims 1993), most harvesting theory is built on the assumption of continuously distributed populations in uniform environments (notable exceptions are Bisonette 1997, and short sections in Quinn & Deriso 1999). There have been, however, a few recent attempts to inject harvesting theory with spatial ecology (see references in Quinn & Deriso 1999), e.g. metapopulation dynamics (Tuck & Possingham 1994, McCullough 1996, Supriatna & Possingham 1998, Cooper & Mangel 1999), source-sink dynamics (Lundberg & Jonzén 1999a, Tuck & Possingham 2000) and habitat selection theory (MacCall 1990, Lundberg & Jonzén 1999b). One may argue that the spatial aspects of harvesting theory is still premature. In practice, however, spatial regulation has a long history in conservation and management of terrestrial systems (e.g. Leopold 1933) and is receiving an immense interest also among contemporary scientists and managers (Joshi & Gadgil 1991, McCullough 1996). This trend towards spatial control of harvested populations as an alternative or complement to quotas and temporal restrictions is most obvious in fisheries management (e.g. Botsford, Castilla & Peterson 1997).

In this paper, we will put harvesting theory in a spatial context, exemplifying how the concepts of habitat selection theory and source-sink dynamics can guide our understanding of the spatio-temporal dynamics of exploited populations. On one hand, we are interested in how to harvest spatially structured populations, but on the other hand we are also interested in how harvest *per se* may affect the spatial distribution of the exploited resource. That may have great implications on how to use reserves as a management tool. Finally, we will simulate an exploited predator-prey system in a spatial setting, highlighting the potential indirect effects of biological interactions and the spatial dimension.

Source-sink dynamics

Although notoriously difficult to document (Watkinson & Sutherland 1995, Diffendorfer 1998), sources and sinks are integral parts of the landscape of any organism (Sæther, Ringsby, Bakke & Solberg 1999). The whole idea behind the source-sink theory is that although certain habitats are very poor in terms of survival and reproduction, they may nevertheless be used by a species. In fact, long-term average abundance in a sink habitat may exceed the one in a source (defined as a habitat where the population would have a positive equilibrium population density in the absence of emigration or immigration; Pulliam 1988). More formally, the situation can be illustrated by a very simple population model where we let S be the density in the source habitat and N the density in the sink. The rate of change in the respective habitat can now be expressed as (Lundberg & Jonzén 1999a):

$$\frac{dS}{dt} = rS\left(1 - \frac{S}{K}\right) - eS + dN - h_S S \qquad (1)$$

$$\frac{dN}{dt} = eS - mN - dN - h_N N \qquad (2).$$

In the source, the population grows logistically where r is the maximum *per capita* growth rate and K the carrying capacity. Individuals migrate from the source to the sink at a rate e and from the sink to the source at a rate d. The only net input into the sink is the individuals immigrating from the source. Since mortality exceeds reproduction in the sink, the population decreases intrinsically at a rate m. Lande (1987) has also developed a similar model under assumptions similar to those of Pulliam (1988). Because we are interested in the harvesting of such a spatially subdivided population, we also introduce harvesting in the source, h_S, and in the sink, h_N. Lundberg & Jonzén (1999a) showed the outcome of an attempt to optimise the harvest in the above situation. It turns out that under the assumptions specified above, two principal situations emerge. To optimise the maximum sustainable yield (MSY), either 1) the sink should be harvested at optimal rate and the source be left alone, or 2) if the sink is a very poor habitat and there is little back migration into the source, the sink should be harvested at maximum rate and the source at its optimal rate (Fig. 1A,B). Note that here we have defined 'optimal' in its narrowest sense. An optimal harvest rate is a value of h that maximises the product of the harvest rate and the corresponding equilibrium population density. Thus, this measure only maximises yield and takes no other

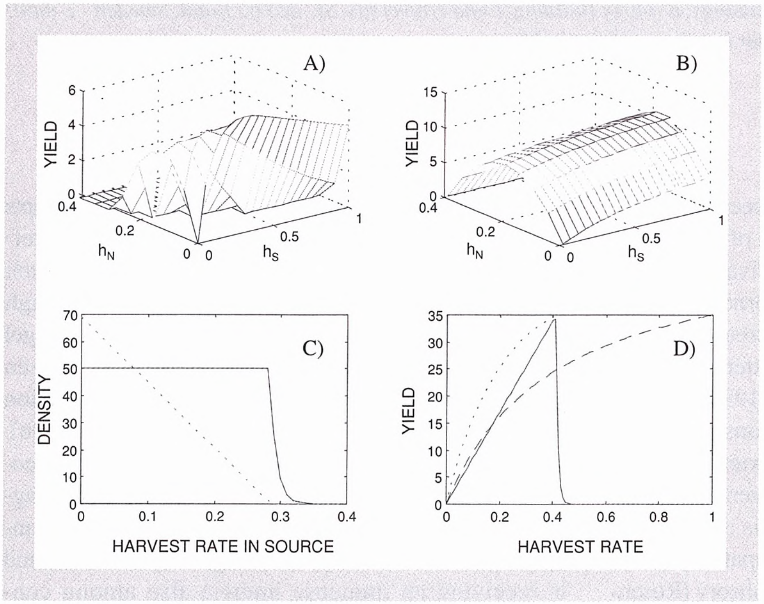

Figure 1. Yield as a function of the harvest rate in the source (h_S) and in the sink (h_N). The results are based on Equations 1 and 2. In A), the optimal strategy is to harvest the sink only, and the yield is given by $Y_N = \left(\frac{K(d+m)}{4rd}\right)\left(r - \frac{em}{d+m}\right)^2$ (r = 0.4; K = 100; m = 0.1; e = 0.4; d = 0.2). In B), the source should be harvested at its optimal harvest rate, and the sink at the maximum rate. The yield functions for the source and the sink are given by $Y_s = \left(\frac{K}{4r}\right)\left(r - \frac{em}{d+m}\right)^2$ and $Y_N (h_N \rightarrow \infty) = \frac{eK(r-e)}{r}$, respectively (r = 0.5; K = 100; m = 0.75; e = 0.1; d = 0.001). In C), the equilibrium population density in the source (–) and the sink (---) is given for different harvest rates in the source. The parameter values of Equations 3-5 are $\lambda_S = 1.4$; $\lambda_N = 0.7$ and u = 50. In D) the yield in relation to harvest rate for indiscriminate harvest (the same rate in both source and sink), or harvest in only the source or the sink is given. The parameter values of Equations 3-5 are $\lambda_S = 1.7$; $\lambda_N = 0.7$ and u = 50. Subfigures A) and B) are from Lundberg & Jonzén 1999a.

factors (e.g. long-term persistence or economic revenues) into consideration.

The above scenario is of course overly simple. It shows, however, that spatial heterogeneity dramatically changes both the potential harvest (yield) and the possibilities for the population to persist under exploitation. To further illustrate the problem, we now let the habitat use and migration between habitats be a little different. The model follows from Pulliam's (1988) original model for source-sink dynamics. We now let the migration from the source to the sink be density-dependent in such a way that there is a threshold density in the source below which there is no migration. One example of such a situation would be in territory holding animals, when migration out of a habitat occurs when all territories are occupied. If the source population is below the threshold, there is no migration and the sink goes deterministically extinct. Should the population density in the source exceed that threshold, the surplus emigrates to the sink. The dynamics of the system can then be expressed as:

$$S(t+1) = S(t)\lambda_s(1-h_s) - M(t) \qquad (3)$$

$$N(t+1) = [N(t)\lambda_N + M(t)](1-h_N) \qquad (4),$$

where S and N are the population densities in the source and sink, respectively, λ_i is the *per capita* population growth rate in the respective habitat (where $\lambda_N < 1$ by definition), and h_i is the respective harvest rates. M(t) is the time-dependent emigration rate from the source and is expressed as:

$$M(t) = S(t)\lambda_s - u \qquad (5),$$

where u is the threshold population density in the source when emigration starts to take place.

We can now imagine that we apply any of the following harvesting strategies: harvest in the source, harvest in the sink, and harvest in both habitats. The results of these strategies are illustrated in Figure 1C,D. Note that for a low harvest rate in the source, the equilibrium density is larger in the sink than in the source (see Fig. 1C). The optimal harvest rate in the source, resulting in MSY, is the value of h_N, denoted h_N^*, and is the rate which reduces the population size to the threshold value (u). Hence,

$$h_N^* = \frac{\lambda_N - 1}{\lambda_N} \qquad (6).$$

When only the sink is harvested, no optimal harvest rate exists and the sink should be harvested at maximum rate. Interestingly, harvesting in the sink results in a higher yield for a wide range of harvest rates.

Harvesting and habitat selection

Not all spatial heterogeneity is manifested as sources and sinks. The resource matching across habitats of different qualities is, however, a ubiquitous phenomenon, often generalised in the framework of Ideal Free Distribution (IFD) theory (Fretwell & Lucas 1972, Sutherland 1996). If for the sake of general argument, we avoid the important discussions about deviations from the 'Ideal' (that individuals have full information about the resource distribution and make rational decisions) and 'Free' (that all individuals are free to choose and without fitness costs) in the theory, we can simply say that the expected distribution of individuals in the population across habitats should be such that fitness is equalised, i.e., it should not be profitable for an individual to move to an alternative habitat at equilibrium. This process of habitat selection may have interesting and important ramifications for harvesting. One example is the possible effects of reserves on the harvesting decisions and effects on the exploited populations. Not least in marine fisheries has the idea of no-take areas (e.g. marine reserves) become much emphasised (Lauck, Clark, Mangel & Munro 1998).

Suppose now that we distinguish between two habitats in the landscape or part of the ocean. If we denote the total area A and the fraction of that area set aside as a reserve c, then we have two habitats with the areas (1-c)A and cA, respectively. Let the habitats be characterised by two parameters; the maximum *per capita* population growth rate, λ_i, and the strength of the density-dependence, a_i. The change in population density in the two habitats can now be expressed as:

$$X_1(t+1) = X_1(t)\lambda_1\exp(-a_1X_1(t)) \qquad (7)$$

$$X_2(t+1) = X_2(t)\lambda_2\exp(-a_2X_2(t)) - hX_2(t) \qquad (8),$$

where X_i is population density in the respective habitats, and h is the harvest rate in the area outside the reserve (Lundberg & Jonzén 1999b). According to the IFD theory, the *per capita* growth rates in the two habitats should be the same at equilibrium. Under that condition the equilibrium densities in the two habitats can be solved. Noting that $X_1 \equiv N_1/(cA)$ and $X_2 \equiv N_2/((1-c)A)$, where N_i is population size, we can now calculate the proportion of the total population that is occupying the reserve as follows:

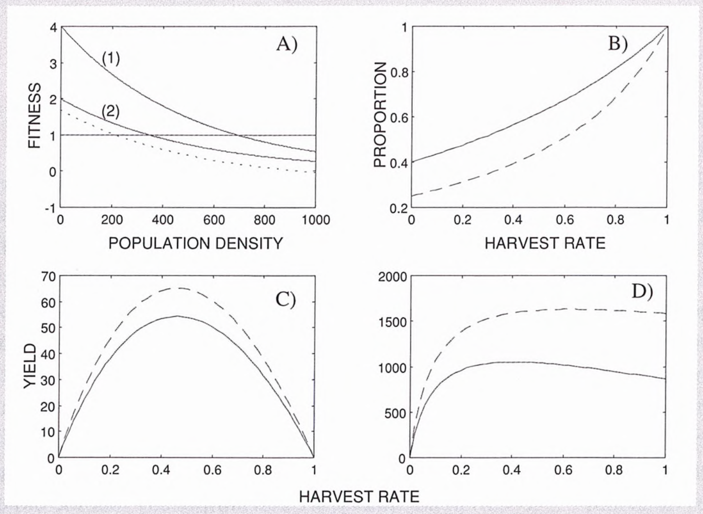

Figure 2. Fitness as a function of population density (A) for two habitats, 1 and 2, without harvesting (–). When the fitness lines cross the horizontal line, fitness is equal (and equal to unity) across habitats and the ideal free distribution is obtained. When the harvest rate is 0.3 in habitat 2, fitness decreases for all densities (---). In B) the proportion of the population found in the reserve is expressed as a function of the harvest rate outside the reserve according to Equation 9. The parameter values are c = 0.25; $a_1 = a_2 = 0.002$; $\lambda_1 = 4$ and $\lambda_2 = 2$ (–); $\lambda_1 = \lambda_2 = 2$ (---). In C) the yield is expressed as a function of the harvest rate outside the reserve when there is no spill-over and 25% (–) or 10% (---) of the total area is protected. The other parameter values are $a_1 = a_2 = 0.002$; $\lambda_1 = 4$ and $\lambda_2 = 2$. In D) the yield is expressed as a function of the harvest rate outside the reserve when 25% of the total area is protected and 5% (–) or 25% (---) of the recruitment in the is exported to the outside. The other parameter values are $a_1 = a_2 = 0.002$; $\lambda_1 = 4$ and $\lambda_2 = 2$. The figure is from Lundberg & Jonzén 1999b.

$$\frac{N_1^*}{N_1^*+N_2^*} = \frac{a_2c \ln(\lambda_1)}{a_2c \ln(\lambda_1) + a_1(1-c) \ln(\lambda_2/(1+h))} \qquad (9)$$

(Lundberg & Jonzén 1999b). Figure 2 summarises the main results of this exercise. Note 1) that optimal harvest rate (with respect to MSY) does not change with the fraction set aside as reserve (c), nor with the quality of the reserve, and 2) that the size and the quality of the reserve affect the possibility of protecting a large proportion of the population. Hence, large fitness hotspots may be needed for satisfactory protection.

The above results apply to situations where there is a cost-free and continuous flow of individuals across the reserve border. If there is a net migration in either direction, i.e. if the pure IFD does not apply, things will change. Imagine, for example, that the recruits within the reserve are partly exported to the outside and that only mature individuals are harvested. Lundberg & Jonzén (1999b) showed that under such circumstances, the optimal harvest rate actually changes somewhat depending on the design of the reserve (fraction allocated to the reserve and its quality relative to the harvested areas; see Fig. 2).

Although the habitat selection models used here may have little resemblance to real management situations, they nevertheless further elucidate the problem of spatial heterogeneity in harvesting theory. This is true also for situations where habitat heterogeneity is created as a management tool (e.g. reserves).

Indirect spatial effects of harvesting

The question where to allocate the harvesting efforts becomes further complicated if we assume large-scale migration between reproductive areas. Let us imagine that a population is distributed across a number of more or less distinct subareas connected by migrating individuals. Each subarea has its own population renewal process and the migration among subareas is proportional to local current population density. Let us further assume that the species in question coexists in the subareas with its predator who is entirely dependent on it as a prey. We can now express the full dynamic system, with the prey density, N_i, and the predator density, P_i, as:

$$N_{t+\varepsilon,i} = f(N_{t,i}) - f(N_{t,i},P_{t,i}) - h^N \cdot N_{t.i} \qquad (10)$$

$$P_{t+\varepsilon,i} = g(N_{t,i},P_{t,i}) - g(P_{t,i}) - h^P \cdot P_{t.i} \qquad (11)$$

$$N_{t+1,i} = N_{t+\varepsilon,i} + M(N_{t+\varepsilon,i},N_{t+\varepsilon,j}) \qquad (12)$$

$$P_{t+1,i} = P_{t+\varepsilon,i} + M(P_{t+\varepsilon,i},P_{t+\varepsilon,j}) \qquad (13).$$

The local dynamics of the prey in subarea i (Equation 10) is a function of density-dependent renewal, $f(N_{t,i})$, mortality due to predation, $f(N_{t,i},P_{t,i})$, and harvesting, where h^N is the harvested proportion. Similarly, the local dynamics of the predator (Equation 11) is a function of growth from the predation upon the prey, $g(N_{t,i},P_{t,i})$, a density-dependent mortality, $g(P_{t,i})$, and harvesting. The local dynamics are then followed by migration of both species, and the net immigration into area i is added to the local density (Equations 12 and 13). If we assume that a constant proportion m^X of the population migrates, and that the exchange of individuals between two subareas depends upon the distance between them, the net migration of each species (X equals N or P) to subarea i can be expressed as:

$$M_{t+\varepsilon,i} = m^X \cdot \sum_{j=1,i\neq j}^{n} \left(X_{t+\varepsilon,j} \cdot \frac{e^{-c \cdot d_{ij}}}{\sum_{j=1,i\neq j}^{n} e^{-c \cdot d_{ij}}} - X_{t+\varepsilon,i} \right) \quad (14),$$

where d_{ij} is the distance between subareas i and j, and c is a parameter scaling the distance dependence, with high values of c corresponding to high mortality during migration and thus a small fraction of successful migrants. For this analysis we used Ricker-dynamics for the local prey renewal, predation with a type II functional response and Beverton-Holt type density-dependent mortality in the predator. With these assumptions, Equations 10 and 11 take the form

$$N_{t+\varepsilon,i} = N_{t,i} \cdot e^{r\cdot(1-l\cdot N_{t,i})} - \frac{a \cdot N_{t,i} \cdot P_{t,i}}{1 + a \cdot b \cdot N_{t,i}} - h_x \cdot N_{t,i} \quad (15)$$

$$P_{t+\varepsilon,i} = P_{t,i} + g \cdot \frac{a \cdot N_{t,i} \cdot P_{t,i}}{1 + a \cdot b \cdot N_{t,i}} - \frac{P_{t,i}^2}{s + P_{t,i}} - h_y \cdot P_{t,i} \quad (16),$$

where r is the intrinsic growth rate, $^1/_l$ the carrying capacity, a the predator attack rate, b the predator handling time of a prey, g the energy conversion ratio for the predator, s reflects the degree of density dependence of the predator mortality, and h is the harvested proportion. In this two-species system we can now explore the influence of migration between subareas on the effects of harvesting.

We applied harvesting of the prey species in only one out of four subareas to study the effects on the yields of the predator in all subareas. The subareas were randomly located as points in two dimensions and numbered from the 'northernmost' area (subarea 1) with increasing distance to subsequent subareas (such that subarea 2 is the one closest to subarea 1, subarea 3 is the second closest and subarea 4 the most distant). The results, illustrated in Figure 3, highlight three important aspects of migration for population management. First, migration of either or both of the species cause harvesting to have effects on yields outside the harvest subarea being exploited (see Fig. 3B,C). The reduction of predator yield is, naturally, largest in the harvested subarea (subarea 4 in Figure 3), and declines with distance from this subarea (see Fig. 3B). Secondly, harvesting can affect even non-migratory species in other areas, if these interact with a migratory species (see Fig. 3B). Thirdly, the significance of these indirect spatial effects of harvesting depends upon the mobility of the two species. When only the prey is migrating, the subareas are affected quite differently by harvesting in one subarea (see Fig. 3B). With a migratory predator species, however, these differences decrease and the reduction in the yields is fairly similar in all subareas (see Fig. 3C,D). Thus, as migration and species interactions cause harvesting to have effects beyond the immediate area

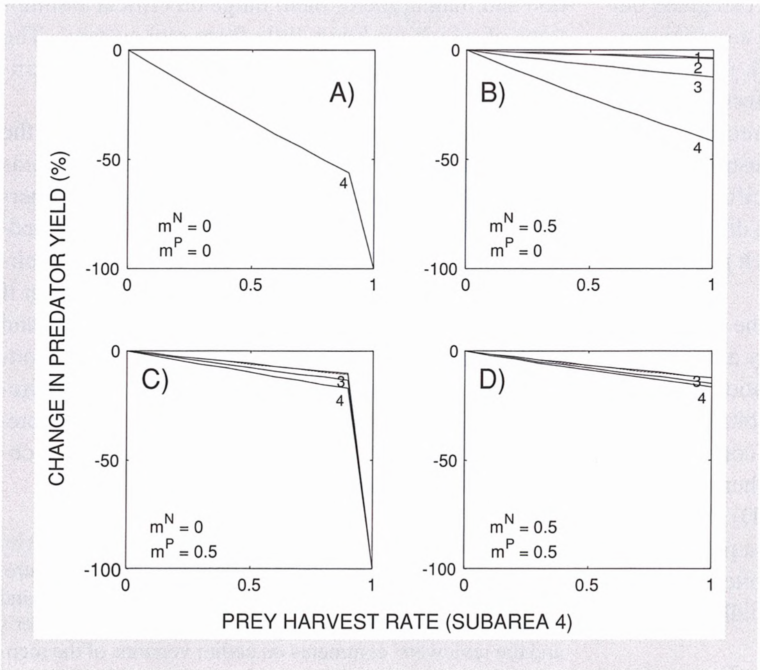

Figure 3. Effect of increased prey harvest rate in one subarea (subarea 4) on the yield of the predator in all subareas, for different rates of prey and predator migration. The results are based on Equations 10-16. In A), when neither of the species is migratory ($m^N = 0$, $m^P = 0$), harvesting only reduces the predator yield in the same subarea (4). With migration of either the prey (B; $m^N = 0.5$, $m^P = 0$), the predator (C; $m^N = 0$, $m^P = 0.5$), or both (D; $m^N = 0.5$, $m^P = 0.5$), the predator yield is reduced in all subareas. The reduction is largest in the harvested subarea (4) and declines with distance (numbering of subareas corresponds to the distance between areas, with subarea 3 being closest to subarea 4, subarea 2 second closest and 1 the most distant). With a migratory predator (see subfigures C and D) the yield reductions differ less between subareas than with only a migratory prey (B). The parameter values used are r = 1.5, l = 0.01, a = 0.75, b = 7.5, g = 0.1, s = 15, c = 0.1, and $h^P = 0.3$ in all subareas.

and species being harvested, explicit considerations of space and movement may be necessary when deciding on where and how much to harvest.

Discussion

Historically, ecologists have simplified their work by treating abundance and distribution as separate topics (Turchin 1998). Hence, temporal dynamics take place in a uniform environment and the distribution is simply a snapshot at a given point in time. Naturally, the problems of abundance and distribution are intertwined by the movements of individuals, and current theoretical work has emphasised the importance of having a spatio-temporal world-view in ecology (e.g. Tilman & Kareiva 1997, Turchin 1998). It is not clear, however, when and how the spatial dimension should be included in population management, and what the marginal benefit of such a spatial resolution would be (e.g. Sæther, Ringsby, Bakke & Solberg 1999).

In this paper, we have demonstrated how simple source-sink and habitat selection theory can guide our thinking about population harvesting in a spatial context. We have learned from source-sink models that optimal harvest strategies are strongly affected by habitat characteristics, and that failure to recognise this spatial structure is suboptimal and puts sustainability at risk. The interplay between habitat-specific dynamics and the migration of individuals between different habitats is the key to understanding how such populations are to be managed.

The source-sink models are based on the assumption that the *per capita* risk of being killed by a hunter or a fisherman does not affect individual migration decisions. This assumption is challenged in the habitat-selection models, where harvesting has fitness-consequences and individuals are trying to distribute themselves according to the ideal free distribution (IFD). As soon as the harvest rate varies in space, there is a potential for a change in the distribution of the exploited resource, an idea deserving more attention in both wildlife and fisheries management.

In both source-sink and habitat-selection models, space is implicitly represented. This simplification may be valid in many situations (Roughgarden 1997), but without an explicit consideration of space we do not know how much we can reduce the complexity, and the risk of over-simplification remains elusive. In our last example, we studied a predator-prey interaction in a spatially explicit model. With a number of simplifying, albeit reasonable, assumptions we highlighted that harvesting of migratory populations can have effects beyond the immediate area being harvested. Furthermore, the mobility of the two species determines the significance of the indirect effects of harvesting. Such indirect spatial and trophic effects can be crucial for where to allocate harvesting efforts, and with a spatially explicit model their significance can be evaluated. The problem in all spatial modelling is, of course, that the results are strongly contingent on assumptions about spatial scale, landscape structure, dispersal mechanisms and local versus global demographic and stochastic processes. Therefore, we caution against over-interpretations of such modelling results. We do think, however, that such simplified exercises may help us identify targets of more detailed studies and underscore less apparent problems in natural systems. The source-sink model, for example, shows that if the landscape is structured roughly as assumed, then harvesting decisions (and other population management) may be full of surprises notwithstanding the management objectives. The spatial and trophic indirect effects indicated in our last example also show that such effects may indeed be real, but also that the direction and magnitude of them hinge on critical assumptions of which we know little from real systems. The modelling results indicate that such knowledge is crucial.

In conclusion, our results clearly indicate that the spatial dimension can dramatically change our ideas about how to manage exploited populations. Furthermore, some effects, e.g. local extinction, can only be studied if the spatial dimension is included. Under what circumstances population management would do better if we based our decisions on analyses of spatial data and models is, however, still uncertain. This can only be sorted out by comparing the outcome and the data requirements of models of varying complexity. The theories presented in this paper can hopefully provide some ecological guidance for that urgent task.

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