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The effect of harvesting on the spatial synchrony of population fluctuations

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ABSTRACT

Harvesting in space affects, in general, the spatial scale of the synchrony in the population fluctuations, which determines the size of the areas subjected to simultaneous quasi-extinction risk. Here we show that harvesting reduces the population synchrony scale if it depends more strongly on population fluctuations than the density dependence of the growth rate in the absence of harvesting. We show that constant and proportional harvesting always increases the spatial scale, using a theta-logistic model for density regulation. We also provide exact scaling results under harvesting for the Beverton–Holt and the Ricker stock-recruitment models that are commonly applied, e.g. in fisheries. Our results indicate that harvest in areas with large abundances should be encouraged to avoid increase of the spatial scale of synchrony in the population fluctuations that can lead to unexpected quasi-extinction of populations over large areas. Our results quantify this harvesting impact giving the resulting scales of spatial synchrony of population fluctuations. This emphasizes the importance of estimating the form of density dependence as well as the dependency of harvest upon population density of exploited populations, in order to get reliable predictions of the size of areas that can undergo simultaneous quasi-extinction.

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1. Introduction

One of the greatest contributions of harvest theory has been to provide general principles for how populations of exploited species should be managed. For example, the concept of Maximum Sustainable Yield denotes the maximum equilibrium harvest rate (Reed, 1978; Quinn and Deriso, 1999), which in a stable environment is obtained by keeping the population at the size that maximizes the population growth rate. For a logistic model of density regulation this population size is half the carrying capacity K. Another example of such a general principle is threshold harvesting, providing the optimal strategy for reduced risk of extinction or the probability of reduction in population size to an unacceptable low level in a stochastic environment (Lande et al., 1995, 1997). Although these principles have been difficult to implement in practice, they still provide important guidelines for identification of overall goals for the management strategy of exploited species.

Traditionally, harvesting theory has focused on modeling the dynamics of a single population over time. This ignores that many intensively harvested species are spread out in space and migrate over large areas. Accordingly, a central aim in obtaining a sustainable management strategy is therefore to consider the effects of harvesting at relative small geographical scales and then distribute the total quotas among sub-areas within the distributional range of the species according to some set of predetermined criteria (Lavsund et al., 2003; Cadigan et al., 2017). An additional complication introduced by space is that fishermen and hunters are often selective in their choice of areas to harvest. This may occur because of logistic constraints to access areas, management regulations (e.g. formation of reserves) or may be based on some kind of spatial harvesting strategy (e.g. by specifically visiting areas with high yields) (Ling and Milner-Gulland, 2008). Over the last decades there has therefore been increased focus on how harvest will affect interactions among sub-populations localized in different areas (McCullough, 1996; Jonzén et al., 2001; Fogarty and Botsford, 2007; Ling and Milner-Gulland, 2008; Kerr et al., 2010; Williams and Hastings, 2013; Burgess et al., 2014; Benson et al., 2015; Takashina and Mougi, 2015). This implies that the dynamics at a single location cannot be understood without including spatial aspects of the dynamics. A nice illustration has been the recent attention to formation of marine reserves as a management option (Tuck and Possingham, 2000; Gell and Roberts, 2003). General management principles for exploited species should therefore include a spatial dimension (Hilborn et al., 2003; Schindler et al., 2010; Hilborn, 2012; Benson et al., 2015).

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Spatial synchrony is a concept usually referring to the temporal covariance or correlation between two quantities, for example population densities, measured at different spatial distances (Ranta et al., 1998; Lande et al., 2003; Liebhold et al., 2004). Ignoring sampling variances the correlations are by definition one at distance zero, and in a large homogeneous area they often decrease monotonically towards zero at large distances where fluctuations are independent (Liebhold et al., 2004; Sæther et al., 2007). The spatial scale of the synchrony is a distance where correlations typically are considered to be large below that value and small at larger distances. In an isotropic model a circle with radius equal to the scale then typically is an area with rather similar population densities. Such scales can be defined in many different ways, for example where the correlation passes 0.5, $e^{-1} \simeq 0.37$ or 0.10 (Bjørnstad and Falck, 2001), but can also be expressed through the shape of the whole autocorrelation function (Engen et al., 2005). Lande et al. (1999) scaled the correlation (or covariance) function by a constant factor to produce a distribution and used the standard deviation of this distribution as a measure of spatial scale. If the correlation has an exponential form, this scale is then where the correlation equals $e^{-1} \simeq 0.37$, whereas for a Gaussian form it equals $e^{-0.5} \simeq 0.61$.

The spatial scale of the synchrony in population fluctuations is an important characteristic with important ecological ramifications to describe how population dynamics covary in space. For instance, synchronous populations tend to be more vulnerable to extinction or quasi-extinctions than populations that show spatially asynchronous population fluctuations (Heino et al., 1997; Heino, 1998; Palmqvist and Lundberg, 1998), and if the spatial scale is large, extinctions may occur surprisingly fast over large areas (Engen, 2007). Importantly, the degree of spatial scaling of the population dynamics can also be understood from basic processes affecting fluctuations in population size. This is illustrated by the model of Lande et al. (1999), who analyzed a spatial population model with spatially correlated noise, local density regulation and dispersal. Using the scale defined as standard deviation their main result is expressed by the equation

$$l_N^2 = l_e^2 + \frac{m l_f^2}{\gamma}. \tag{1}$$

Here, l_N is the spatial scale of the spatial autocovariance function for population densities, l_e is the corresponding scale for the spatial correlation of the environmental noise, m is the dispersal rate and l_f is the standard deviation of dispersal distance, while γ is the strength of local density regulation. In models with no spatial dimension $1/\gamma$ is the mean return time to equilibrium (May, 1974). An important conclusion from this analysis is that even the effect of small and moderate dispersal over small distances may be very large if the strength of local density dependence is small. A small γ makes effects of local migration spread out in space through generations, creating large areas with similar densities. If there is no dispersal then $l_N = l_e$, which is Moran's (1953) classical result.

The purpose of the present paper is to analyze how different harvesting strategies affect the spatial scale of population fluctuations. We show that harvesting may either increase or decrease the spatial scale, depending on spatial characteristics of the harvesting strategy, that is, the harvest at different locations with different population densities.

2. Dynamic population model in time and space

A general class of population models in continuous time with no spatial structure has the form

$$dN = [r - g(N)]Ndt + \sigma_e N dB(t), \tag{2}$$

where $g(N)$ is an increasing function of population size N, expressing density regulation through how it reduces the growth rate $r - g(N)$ as population size increases. The parameter σ_e^2 is the environmental noise and $dB(t)$ is the infinitesimal increment of a standard Brownian motion during time dt so that the expectation $\mathrm{E}[dB(t)] = 0$ and $\mathrm{var}[dB(t)] = dt$. The temporal variance of the noise term $N\sigma_e dB$ is accordingly $N^2\sigma_e^2 dt$. The carrying capacity K is defined so that $r - g(K) = 0$. A harvesting strategy can be defined through a harvesting rate $h(N)$, meaning that $h(N)dt$ individuals are harvested during dt. The dynamics then change to

$$dN = [r - g(N)]Ndt - h(N)dt + \sigma_e N dB. \tag{3}$$

A central focus for the harvest theory is to find choices of harvesting rates $h(N)$ that produce large mean annual yields while maintaining long-term sustainability of the harvest (Hilborn and Walters, 1992; Quinn and Deriso, 1999). Three basic harvesting strategies refer to different choices of $h(N)$: constant harvesting means that $h(N)$ is constant not depending on population density, while proportional harvesting means that the rate is proportional to N. In discrete time, quotas are the same at each time step under constant harvesting, while under proportional harvesting quotas are proportional to population density. For a given harvesting effort the yield may often be approximately proportional to density, in which case proportional harvesting is obtained in practice by choosing a fixed effort. Threshold harvesting is more conservative, choosing $h(N) = 0$ and thus stop harvesting if the density N is below a given threshold, but harvest the population down to this threshold if the density is above it. In continuous time this corresponds to $h(N)$ being zero below and infinite above the threshold (Lande et al., 1999).

A general conclusion is that constant harvesting in a fluctuating environment leads to unstable dynamics with large risk of extinction (Beddington and May, 1977). As another extreme, threshold harvesting reduces the risk of unexpected severe reductions in population size and hence represents the most sustainable approach when the population size is known (Reed, 1978, 1979; Lande et al., 1995, 1997), although temporal fluctuations in the yield will be large (Lande et al., 1997; Sæther et al., 2001).

In the absence of harvesting, Lande et al. (1999) analyzed the spatial dynamics of $N(x, t)$, the population density at location $x = (x_1, x_2)$ in the plane at time t, using the linearization at the carrying capacity which at any location and time replaces $[r - g(N)]N$ by $-Kg'(K)(N - K) = -\gamma(N - K)$, where γ is the strength of density regulation. A logistic model is defined by $g(N) = rN/K$ giving $\gamma = r$. Adding density independent dispersal at rate m to this model and writing $f(y)$ for the two-dimensional distribution of dispersal distance y for dispersing individuals, the spatio-temporal model in the neighborhood of K takes the simple linear form

$$dN(x,t) = -\gamma[N(x,t) - K]dt + mdt \int [N(x-y,t) - N(x,t)]f(y)\,dy + \sigma_e K dB(x,t), \tag{4}$$

where the integration is performed over the entire two-dimensional plane and the noise is approximated by the noise at $N = K$. The noise terms are here spatially correlated with spatial autocorrelation $\rho_e(y) = \mathrm{E}[dB(x,t)dB(x+y,t)]/dt$. This model yields stationary fluctuations of population densities with a spatial correlation $\rho_N(y) = \mathrm{corr}[N(x,t), N(x+y,t)]$. The scaling result of Lande et al. (1999) given by Eq. (1) is exact for this linear model. The spatial scale of the dispersal distance in the direction of the first coordinate is the standard deviation, the squared value being the variance $l_f^2 = \int\int y_1^2 f(y_1, y_2)dy_1 dy_2$. The scales of the environmental noise and population density are defined in the same way, with the modification that the correlation function first has to be scaled by a factor to become a distribution so

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