

The Spatial Scale of Population Fluctuations and Quasi-Extinction Risk

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ABSTRACT: Using a spatially homogeneous population model with migration (random individual dispersal) and spatially autocorrelated environmental noise, we show how migration and local density regulation affect the spatial scale of fluctuations in the log of population sizes as well as the 1-yr differences in these. The difference between the squares of these two spatial scales of population fluctuations does not depend on the spatial scale of the noise but only on migration rate and strength of local density regulation. We also show how migration, local density regulation, and spatially correlated environmental noise affect the realized population process at a specific location. As the migration increases, the realized local density regulation and the expected population size increase, while the realized environmental noise decreases. This approach also enables us to analyze the dynamics of the total population size within quadrats of different sizes. The risk of local quasi extinction is strongly reduced by increasing quadrat size or migration rate, while an increase in environmental stochasticity or spatial correlation in the environmental noise increases the risk of quasi extinction.

Fluctuations in local populations often are synchronized by individual dispersal (migration) and similarities in environmental conditions depending on the geographic distance between sites (Ranta et al. 1995, 1997, 1998; Sutcliffe et al. 1996; Paradis et al. 1999). To understand population synchrony, spatial processes must be included in population models (Koenig 1998, 1999; Bjørnstad et al. 1999a, 1999b). Several approaches have been used to model spatial processes. The initial models were deterministic, in-

cluding biologically realistic features such as density-dependent migration (Levin 1992) and environmental heterogeneity (Skellam 1951). Analysis also appeared for spatial dynamics in landscapes with an explicit structure, often including stochastic environmental variation (e.g., Levin and Pacala 1997). Another approach has been to derive analytical results for simplified models with reduced or implicit spatial structure (Moran 1953; Levins 1970; Pulliam 1988). The insight gained from analysis of simple models has been the foundation for the design of several important field studies of spatial processes (see examples in Hanski and Gilpin 1997; Bascompte and Solé 1998; Hanski 1999) with important management implications (Tilman and Kareiva 1997; Bascompte and Solé 1998; Schwartz 1999).

The spatial scale of synchrony in population fluctuations influences the risk of local and global extinction (Allen et al. 1993; Bolker and Grenfell 1996; Foley 1997; Heino et al. 1997; Palmqvist and Lundberg 1998). Empirical analyses of spatial patterns in population fluctuations have revealed large interspecific differences in the spatial scale of population synchrony, even among closely related species (Hanski and Woiwood 1993; Lindström et al. 1996; Sutcliffe et al. 1996; Koenig 1998; Ranta et al. 1998; Paradis et al. 1999). In tetraonids (Ranta et al. 1998), in moths and aphids (Hanski and Woiwood 1993), and in Canadian lynx (Stenseth et al. 1999), weather is assumed to be a major factor synchronizing population fluctuations over large areas. The synchronized population fluctuations of Soay sheep (*Ovis aries*) on two neighboring islands off Scotland with no interchange of individuals provides one of the best examples of how a common extrinsic environmental factor can generate spatial autocorrelation in population dynamics (Grenfell et al. 1998). However, patterns of movement by individuals will also influence spatial patterns in population dynamics. For instance, using data on 21 butterfly species, Sutcliffe et al. (1996) showed that the population fluctuations of "mobile" species were synchronized over larger distances than the population fluctuations of "sedentary" species. Similarly, in British birds, local synchrony in population fluctuations was positively

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correlated with dispersal distance (Paradis et al. 1999). Thus, variation in migration patterns is also an important factor for interspecific differences in the spatial scaling of population synchrony. Finally, the characteristics of the local population dynamics itself (e.g., the strength of density dependence) may also affect the scaling of population synchrony (Lande et al. 1999; Bjørnstad and Bolker 2000).

The relative contribution of environmental autocorrelation, migration, and density regulation to the dynamics in space and time are poorly understood (Steinberg and Kareiva 1997; Bjørnstad et al. 1999a). However, recent analytical results derived from stochastic linear models (Lande et al. 1999; Engen 2001; Engen et al. 2002) have explained some of these empirical results and shown how environmental autocorrelation, migration, and the strength of density regulation affect the geographical scale of population fluctuations. This analytical theory is supported by extensive simulation studies (Ranta et al. 1995, 1997, 1998; Heino et al. 1997; Kendall et al. 2000; Ripa 2000). Because all these processes strongly influence local population dynamics, they should be considered when making predictions about risk of quasi extinction of local populations, that is, the probability of population decline to a certain small size within a given time (Ginzburg et al. 1982; Burgman et al. 1993).

Population synchrony, defined as the spatial autocorrelation of local population fluctuations, usually decreases with geographic distance between local populations (Bjørnstad et al. 1999a). The spatial scale of population synchrony measures the typical range of distances over which correlation of local population fluctuations is large. For the spatial autocorrelation function of the population to have a finite integral over the entire space, it must approach 0 at large distances. It may then be normalized by a constant factor to become a distribution. Lande et al. (1999) defined the spatial scale of population synchrony, say l , in a given direction, as the standard deviation of this distribution in that direction. In a linearized model with constant migration rate m , it was shown that

$$l^2 = l_e^2 + ml_p^2/\gamma,$$

where l_e is the spatial scaling of environmental stochasticity, also defined as the standard deviation, l_p is a standard deviation of the individual migration distance, and γ is the strength of the local density regulation. This result implies that even low migration rates with short-distance dispersal may greatly affect population synchrony, provided that local density regulation is weak. Engen et al. (2002) generalized this model by incorporating permanent heterogeneity in the environment affecting local population growth rates and carrying capacities.

Population synchrony often does not approach 0 at large

distances but rather some positive constant value (Bjørnstad et al. 1999a). This may be due to a common environmental variable affecting all locations. In this case, the population autocorrelation function cannot be normalized to become a distribution, and the above scaling results do not apply directly. However, we shall show that, if this constant long-distance correlation is first subtracted from the population autocorrelation function, then the same scaling results are valid for the resulting curve approaching 0 at large distances, as indicated in Lande et al. (1999).

Research workers estimate population synchrony from data on (log) population size or the yearly difference in (log) population size (Bjørnstad et al. 1999a, 1999b; Viljugrein et al. 2001). We shall see that, if there is migration, these two autocorrelation functions are generally different and greatly so if the scale of migration is large and/or the local density regulation is weak. The spatial scale of yearly differences in population size often will be practically independent of migration and local density regulation and approximately equal to the autocorrelation function for the environmental noise after subtracting the constant long-distance correlation.

Density dependence of population dynamics is a fundamental ecological concept, although no general definition seems to be agreed on (see discussion in Murdoch 1994 and Turchin 1995). Lande et al. (2002) developed a rather general definition of density dependence for a non-spatial model with age structure. In a spatial model, however, with migration between locations, the migration will itself have a density-regulating effect on the dynamics. Migration tends to smooth out population fluctuations so that local populations tend to behave like isolated populations with stronger density regulation and smaller noise. Theoretical population models generally are based on parameters describing the dynamics at local sites in the absence of migration. It is important to realize that the parameters estimated by empirically studying the population fluctuations within even small areas are not equivalent to local population parameters but are also affected by migration. Here we quantify the relations between the theoretical parameters of local dynamics and those that are estimated with migration. This is accomplished by applying the lognormal spatiotemporal model in Engen (2001) and approximating the local process by an Ornstein-Uhlenbeck process (Karlin and Taylor 1981) for log population size (for parameters used in this model, see table 1). Our model is homogeneous in space and does not account for spatial heterogeneity in habitat quality. Including spatial heterogeneity would require spatially explicit models, which cannot lead to the kind of analytical results presented here.

Using the same model, we also find approximations for

Table 1: Parameters used in model description

Parameter	Meaning
n	Population size
$X(z, t)$	Log of population size at location z and time t
\bar{r}	Mean specific growth rate
σ_e^2	Environmental variance
$r_0 = \bar{r} - (1/2)\sigma_e^2$	Long-run growth rate
γ	Strength of density regulation
M	Migration parameter
$c(z, \tau)$	Covariance function, $\text{cov}[X(w, u), X(w + z, u + \tau)]$
$c_e(z)$	Environmental spatial covariance function
$c_{\text{diff}}(z)$	Covariance function for differences
l	Scaling measures, usually with subscripts indicating the actual covariance function

the dynamics of the total population size within a given area or quadrat. The quadrats are open to dispersal with migration in and out of the area, and the spatial range of the population is assumed to go far beyond each quadrat. We analyze quadrats of different size and compute various properties of the population process within quadrats such as the realized environmental noise and strength of density dependence. Finally, we show how the time to quasi extinction (Ginzburg et al. 1982) depends on the quadrat size and spatial processes in population dynamics.

The Model

Ignoring effects of migration, a model for the annual change in population size n is

$$\Delta n = r(t)n - g(n),$$

where $r(t)$ is the specific growth rate at time t and $g(n)$ represents density regulation. If the specific growth rate fluctuates between years with mean \bar{r} and variance $\sigma_r^2(n)$, and the Δn are not too large, this process may be approximated by a diffusion with infinitesimal mean $\bar{r} - g(n)$ and variance $n^2\sigma_r^2(n)$. A simple model incorporating environmental as well as demographic stochasticity in $r(t)$ is $\sigma_r^2(n) = \sigma_e^2 + \sigma_a^2/n$. The demographic variance σ_a^2 is generated by independent individual contributions to the next generation, while the environmental variance σ_e^2 reflects environmental effects acting simultaneously on all individuals. We assume that the population is large enough to ignore demographic stochasticity and that density dependence is of the Gompertz type; that is, $g(n) = \gamma n \ln n$. The stochastic dynamics of the logarithm of population size, $X = \ln n$, can then be modeled as a diffusion

process with infinitesimal mean $r_0 - \gamma X$ and variance σ_e^2 , which is an Ornstein-Uhlenbeck process (Karlin and Taylor 1981). The parameter $r_0 = \bar{r} - (1/2)\sigma_e^2$ is the expected density-independent growth rate, and γ is the strength of local density regulation.

This model for log population density $X(z, t)$ at location z and time t may be written in the form

$$dX(z, t) = [r_0 - \gamma X(z, t)]dt + \sigma_e dB(z, t). \quad (1)$$

Here $(d/dt)B(z, t)$ is a white noise process at z , with no temporal autocorrelation, that is, the derivative of a Brownian motion (Karlin and Taylor 1981). This environmental noise has spatial correlations defined by $\rho_e(z)dt = E dB(w, t)dB(w + z, t)$. We call $\rho_e(z)$ “the spatial environmental autocorrelation.” Including density-independent migration (see appendix), Engen (2001) showed that the model remains linear if the migration rate tends to infinity and the migration distance tends to 0 so that the individual movements approach a continuous random walk in space with 0 mean and variance M per unit in each direction. An interpretation of this is that the probability that an individual migrates a distance longer than d during time t is $\exp[-d^2/(2Mt)]$. The log of population densities, that is $X(z, t)$, is normally distributed with a mean value that increases with M (Engen 2001; see appendix and fig. 4, *lower graph*). Apart from the mean of log densities, the solution is determined by the joint spatial and temporal autocovariance function $c(z, t) = \text{cov}[X(w, u), X(w + z, u + t)]$. The results are most easily expressed using the Fourier transform (Papoulis 1962) of this function (Engen 2001), which is given in the appendix.

Spatial Scaling of Population Fluctuations

Environmental conditions tend to be similar at close locations, and this similarity is likely to decrease with distance. Several empirical studies (see reviews in Koenig 1998, 1999; Ranta et al. 1998; Bjørnstad et al. 1999b) have demonstrated how this affects population synchrony, which often decreases with distance and approaches some positive constant correlation at long distances. This long-distance correlation reflects a common environmental noise term for all locations that could be generated by regional fluctuations in temperature or weather between seasons (e.g., Stenseth et al. 1999). Such autocorrelation in the environmental noise can be expressed as

$$c_e(z) = p\tilde{c}_e(z) + \sigma_e^2(1 - p), \quad (2)$$

where \tilde{c}_e approaches 0 for long distances and the constant $\sigma_e^2(1 - p)$ represents the long-distance covariance, formally

being $c_e(\infty)$. Hence, $(1 - p)$ is the long distance correlation in the environmental noise. If $p < 1$, this autocovariance function cannot be normalized to define a distribution, which means that the spatial scale defined using the standard deviation is inappropriate and must be redefined as proposed in Lande et al. (1999). It is shown in the appendix that the autocovariance function for the log of population size between local populations separated by spatial vector z and time lag τ in this model takes the form

$$c(z, \tau) = p\tilde{c}(z, \tau) + (1 - p)\frac{\sigma_e^2}{2\gamma}e^{-\gamma\tau}, \quad (3)$$

where $\tilde{c}(z, \tau)$ approaches 0 at large distances. The Fourier transform of $\tilde{c}(z, \tau)$ is given in the appendix. It follows from this that the covariance function for the between-year differences,

$$c_{\text{diff}}(z) = \text{cov}[X(w, t + 1) - X(w, t), X(w + z, t + 1) - X(w + z, t)],$$

which is simply $2[c(z, 0) - c(z, 1)]$, can be expressed as

$$c_{\text{diff}}(z) = 2p[\tilde{c}(z, 0) - \tilde{c}(z, 1)] + (1 - p)\sigma_e^2(1 - e^{-\gamma})/\gamma. \quad (4)$$

Since \tilde{c} approaches 0 at large distances, so does the term $\tilde{c}_{\text{diff}}(z) = 2p[\tilde{c}(z, 0) - \tilde{c}(z, 1)]$. We let \tilde{l}_{diff} be the scale of this function while we write \tilde{l} for the scale of $\tilde{c}(z, 0)$. Both of these scales are defined as the standard deviation in a specific direction of the distributions obtained by normalizing the functions. The components $p\tilde{c}(z, 0)$ and $2p[\tilde{c}(z, 0) - \tilde{c}(z, 1)]$ of the two autocovariances are determined by migration and local density regulation, as well as spatial autocorrelation in the environmental noise, and it is of great interest to see how these parameters describing the spatial dynamics actually affect the form of these functions. It is shown in the appendix that

$$\tilde{l}^2 = \tilde{l}_e^2 + M/\gamma, \quad (5)$$

where \tilde{l}_e is the spatial scaling of $\tilde{c}_e(z)$, while the corresponding expression for the 1-yr differences is

$$\tilde{l}_{\text{diff}}^2 = \tilde{l}_e^2 + \frac{M}{\gamma}\left(1 - \frac{\gamma}{e^\gamma - 1}\right). \quad (6)$$

Expanding the last term in a Taylor series, we find

$$\tilde{l}_{\text{diff}}^2 = \tilde{l}_e^2 + \frac{M}{2}\left(1 - \frac{1}{6}\gamma + \frac{1}{360}\gamma^3 - \dots\right), \quad (7)$$

so that, if $\tilde{l}_e^2 \gg M/2$, we have

$$\tilde{l}_{\text{diff}}^2 \approx \tilde{l}_e^2. \quad (8)$$

The coefficient of M in (5) and (6) is plotted against γ in figure 1. We see that the effect of migration M on the spatial scale of population fluctuations may be quite large when the local density regulation is weak (small γ), while the effect on the scale of the 1-yr difference is small and nearly independent of γ . If γ is small compared with 1, the ratio of the two coefficients of M is approximately $\gamma/2$. For example, with $\gamma = 0.1$, the effect of the migration on the squared scale of the 1-yr differences is only about 5% of the effect on the squared scale of the log densities. Notice also that the difference between the two squared scales,

$$\tilde{l}^2 - \tilde{l}_{\text{diff}}^2 = M/(e^\gamma - 1),$$

is independent of the environmental noise. Hence, by estimating both scales from data, we can estimate $M/[\exp(\gamma) - 1]$ even if the magnitude and spatial properties of the environmental noise are unknown.

In the appendix, we show the stronger result that $\tilde{c}_{\text{diff}}(z_1, z_2) \approx p\tilde{c}_e(z_1, z_2)$ is valid under the same condition, $\tilde{l}_e^2 \gg M/2$, and also give a more accurate second order approximation. Figure 2 illustrates that the discrepancy between the corresponding spatial correlations $\tilde{\rho}_{\text{diff}}(r) = \tilde{c}_{\text{diff}}(r)/\tilde{c}_{\text{diff}}(0)$ and $\tilde{\rho}_e(r) = \tilde{c}_e(r)/\tilde{c}_e(0)$ is quite small for realistic parameters values. The model is isotropic with Gaussian form of the environmental covariance function expressed using the distance $r = (z_1^2 + z_2^2)^{1/2}$.

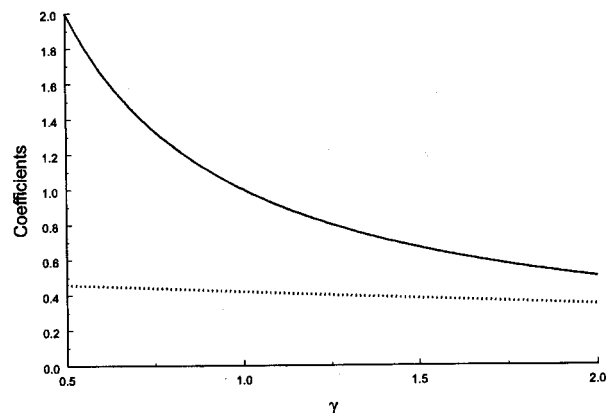


Figure 1: Coefficient of the migration parameter M in the expression for spatial scaling \tilde{l}^2 (solid line) and the scaling for the yearly differences $\tilde{l}_{\text{diff}}^2$ (dotted line) plotted against the strength of local density dependence γ .

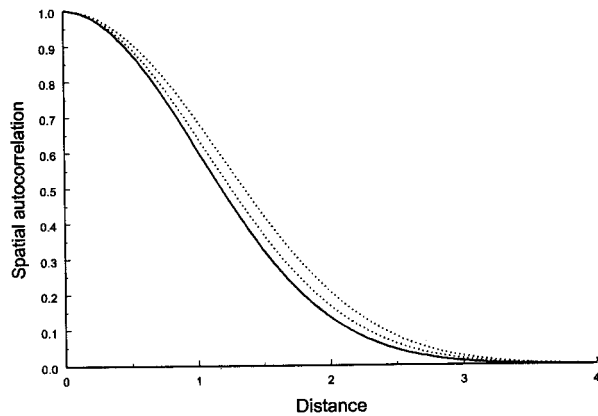


Figure 2: Environmental autocorrelation $\tilde{\rho}_e(r)$ (solid line), and the autocorrelation for the differences $\tilde{\rho}_{\text{diff}}(r)$ for migration parameter $M = 0.2$ (lower dotted line) and $M = 0.4$ (upper dotted line). The environmental autocovariance function has a Gaussian (normal) form and all functions are expressed using the distance $r = (z_1^2 + z_2^2)^{1/2}$. The other parameters are $\gamma = 0.1$, $\sigma_e^2 = 0.01$, and $\bar{l}_e = 1$.

Local Dynamics

We can compute the joint spatial and temporal autocovariance function for population fluctuations $c(z, \tau)$ as shown in the appendix. The stationary variance at a location is $c(0, 0)$ and the temporal autocorrelation function is $c(0, \tau)/c(0, 0)$. In the absence of migration, the local dynamics are given by the Ornstein-Uhlenbeck process defined by equation (1). The stationary distribution of log population density for this model is normal with mean r_0/γ and variance $\sigma_e^2/(2\gamma)$, while the temporal autocorrelation is the exponential function $\exp(-\gamma\tau)$ (Karlin and Taylor 1981). Because in the spatial model with migration the stationary distribution of log population density at a location also is normal, we may try to approximate the local process by an Ornstein-Uhlenbeck process and see how the spatial dynamics affects the local population parameters. The Ornstein-Uhlenbeck process will be a good approximation if the temporal autocorrelation function $c(0, \tau)/c(0, 0)$ is approximately exponential in time. In figure 3, we show numerical examples of this temporal autocorrelation together with an exponential approximation $\exp(-\gamma^*\tau)$. When γ^* is determined from this relation, the parameter r_0^* can be computed from the expression for the mean of log population size $r_0^*/\gamma^* = EX(z, t)$, where the expression for $EX(z, t)$ is given in the appendix. Finally, the noise of the local process, σ_e^{2*} , is determined by the expression $\sigma_e^{2*}/(2\gamma^*) = c(0, 0)$ for the stationary variance of log population density. Hence, all three parameters (r_0^* , γ^* , σ_e^{2*}) of the Ornstein-Uhlenbeck process that approximates the local process can be determined. These

three parameters, which are affected by the migration and the spatial environmental autocorrelation, we may call the locally realized rate of increase, strength of density regulation, and environmental variance. Figure 4 demonstrates how these parameters are affected by migration M for different values of the scale of the environmental noise. We see that the expected population size as well as the realized strength of density regulation increase with increasing migration, while the realized environmental variance decreases. In figure 5, we show how the expected time to quasi extinction at a location increases with increasing migration and decreases with increasing σ_e^2 .

Dynamics within Areas

The total population size in an area A is the integral of the population density $n(z, t) = \exp[X(z, t)]$ over the area,

$$N_A(t) = \int_A n(z, t) dz.$$

Using well-known properties of the bivariate lognormal distribution, we can find the joint spatial and temporal autocovariance function for $n(z, t)$, which again can be integrated over space to obtain the temporal covariance function for $N_A(t)$. For very small areas, the temporal autocorrelations within the area are all close to 1, and the stationary distribution of $N_A(t)$ is then approximately lognormal. For very large areas, most distances within the area are large, and therefore the common regional component of environmental noise that is the same at any location is the dominating one. Hence, the lognormal will

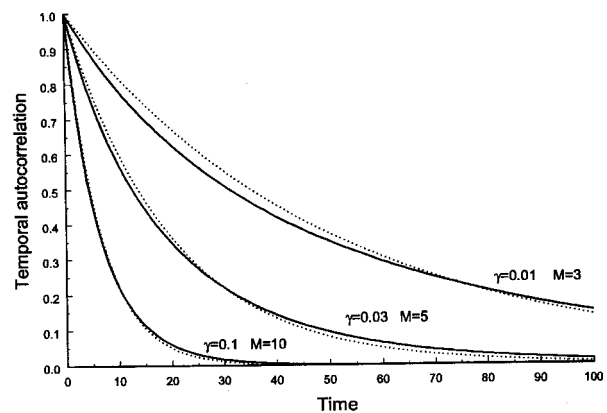


Figure 3: Temporal autocorrelation for the process at a point (solid line) and the exponential approximation (dotted line) for different combinations of γ and M . The other parameters are $\sigma_e^2 = 0.02$, $\bar{l}_e = 10$, and $p = 1$, and the environmental autocorrelation has a Gaussian form.

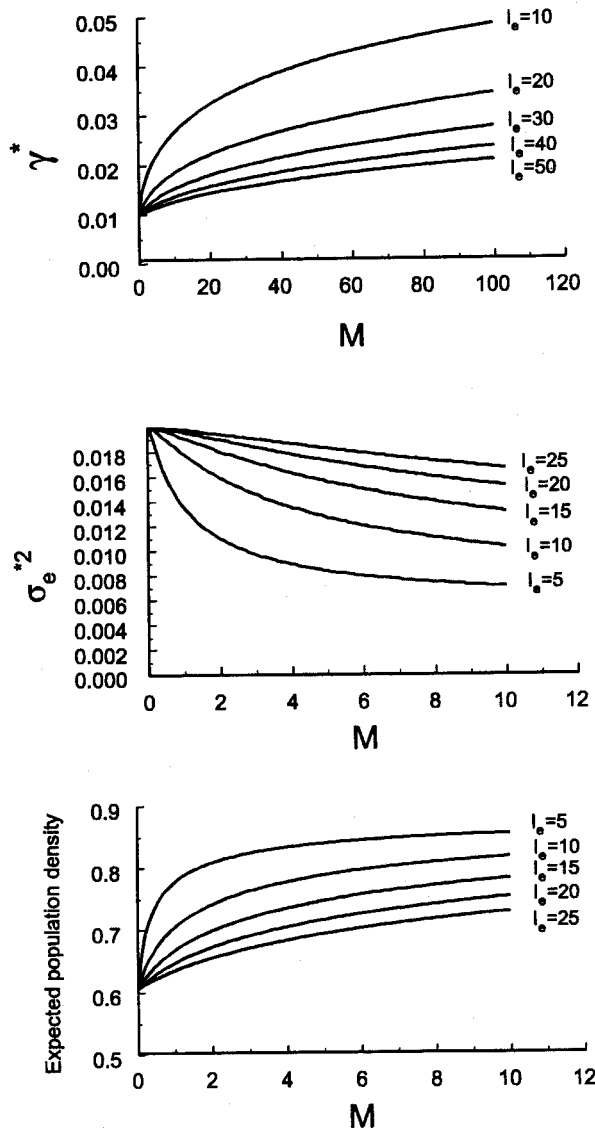


Figure 4: Local realized density regulation γ^* (*upper panel*), realized local environmental variance σ_e^2 (*middle panel*), and expected population density (*lower panel*) for different values of the scaling of the environmental noise l_e plotted against the migration parameter M . The model is the same as in figure 2 with long-distance correlation in the noise being $1 - p = 0.25$. In the absence of migration, the local strength of density regulation is $\gamma = 0.01$ and the local environmental variance is $\sigma_e^2 = 0.02$. The scales for l_e and M are not given, but since the time unit is 1 yr, the scale of M , for example, must be square kilometers per year if the scale of l_e is kilometers.

be a good approximation also for very large areas. From these considerations, we approximate the distribution of $N_A(t)$ by a lognormal for any areas of any size. The appendix shows how to compute the temporal autocovariance function for $\ln N_A(t)$ when the areas A are squares of

varying size. Then, employing the Ornstein-Uhlenbeck process as an approximation for $\ln N_A(t)$ using the same technique as for a location, we can study the dynamics of subpopulations within squares. In figure 6, we illustrate how the realized environmental variance for a square decreases with increasing quadrat size and increasing migration, and how it approaches the long-distance autocovariance in the environmental noise, $(1 - p)\sigma_e^2$ for large quadrats. The lower panel of figure 6 depicts how the expected time to quasi extinction for the quadrat increases with increasing quadrat size and migration. However, when the quadrat size measured by the length of the side exceeds about 10 times the spatial scale of the environmental stochasticity, there is relatively little increase in the expected time to quasi extinction with further increase in the quadrat size.

Discussion

When data on population sizes in space and time are available, population synchrony, the spatial autocorrelation of population size, may be estimated, either by fitting some parametric model or by a nonparametric approach (Ripley 1988; Cressie 1993; Bjønstad 1999*a*, 1999*b*). Population synchrony usually decreases with increasing geographic distance and its shape can be used to define the spatial scale of this synchrony. If population synchrony approaches a positive constant at long distances due to a regional component of environmental stochasticity, this constant should be subtracted from the population synchrony, as proposed by Lande et al. (1999), and the spatial scale of local population fluctuations should be derived

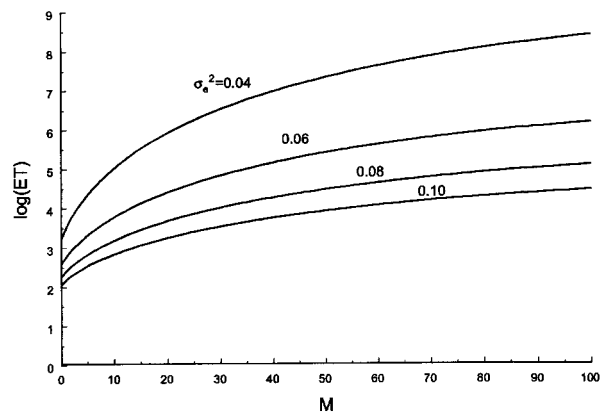


Figure 5: Logarithm (base 10) of the expected time to quasi extinction at 10% of the carrying capacity plotted against the migration parameter M for different values of the local noise σ_e^2 . The model is the same as in figure 3 with spatial scaling $l_e = 10$ and local density regulation $\gamma = 0.04$.

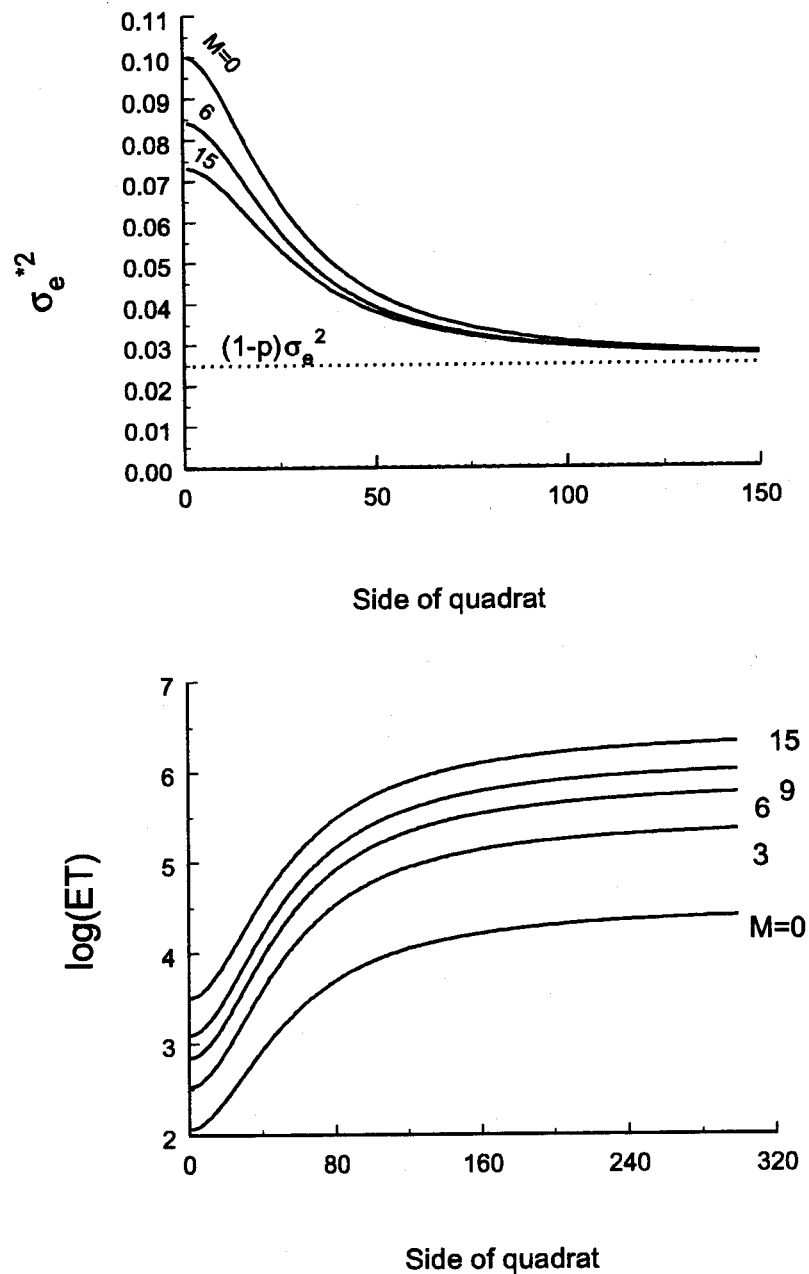


Figure 6: Realized noise σ_e^{*2} and the logarithm (base 10) of the time to quasi extinction at 10% of the carrying capacity for the total population within a quadrat plotted against the side length of the quadrat for different values of the migration parameter M . The other parameters are $\sigma_e^2 = 0.10$, $\bar{l}_e = 10$, $\gamma = 0.04$, and $p = 0.75$.

from the resulting autocorrelation function approaching 0 at long distances (Bjørnstad et al. 1999a). The important result that even small migration may have a large effect on the spatial scale of synchrony when the local density regulation is weak then also holds in the presence of regional environmental noise that often exists (Lindström et al. 1996; Sutcliffe et al. 1996; Stenseth et al. 1999).

Population synchrony is usually calculated from the observed (log) abundances or from the yearly changes in (log) abundances (Bjørnstad et al. 1999a; Viljugrein et al. 2001). For realistic values of the parameter γ expressing the strength of local density regulation, the spatial scale of 1-yr differences in local population density is expected to approximate closely the spatial scale of environmental

autocorrelation if the migration M is much less than twice the squared spatial scale of the environmental noise. This means that the spatial scale observed from the 1-yr differences is likely to reflect the spatial scale of environmental autocorrelation. We recommend that the scale for the abundances as well as for the 1-yr differences should be estimated when field data are being analyzed. If there is little difference between the two scales, we can conclude that the synchrony of the population fluctuations is not driven by migration but only by the spatial autocorrelation in the environmental noise. This may be a consequence of either a small migration or a strong local density regulation.

The concept of density regulation has been much discussed in the ecological literature. For a simple model like equation (1), the parameter γ reflects the strength of density regulation. In more complex models, for example, with a time lag longer than 1 yr, the definition of density regulation is not so obvious. Lande et al. (2002) developed a general definition of the strength of density dependence for age-structured populations. Here we have demonstrated for a spatially structured population that, if the local dynamics is approximated by the simple model (1), then the realized value of the strength of density dependence γ , which we denote as γ^* , actually increases with migration (fig. 4) so that migration has a density-regulating effect on the local dynamics that can be quantified. For spatially structured populations, γ^* is a more appropriate measure of density regulation than γ , which would apply in the absence of migration. However, the effect of migration on the population synchrony cannot be judged through estimates of γ^* obtained from studying local population fluctuations over time because γ^* is affected by migration. The influence of migration on population synchrony is determined by γ , which is different from γ^* if $M > 0$.

We also showed that migration reduces the realized local environmental stochasticity σ_e^{2*} and increases the population mean through an increase in the realized rate of increase (fig. 4). It is important to understand that, if models are fitted separately to local time series, the parameters that will be estimated are not $(r_0, \gamma, \sigma_e^2)$ but actually $(r_0^*, \gamma^*, \sigma_e^{2*})$, which we have shown may be rather different. This suggests that the impact of large-scale climate variation on local dynamics (Post and Stenseth 1999;

Sæther et al. 2000) may be more difficult to analyze than previously understood.

In addition to analyzing the local dynamics, we demonstrated how the effect of migration influenced the dynamics of the total population within quadrats of different sizes. When the environmental autocorrelation decreases toward a positive constant at large distances, the expected time to quasi extinction in a quadrat may change dramatically with the size of the area when the length of the quadrat is less than about five times the spatial scale of the environmental autocorrelation. The expected time to quasi extinction within the quadrat is practically independent of the area when the quadrat size is larger than about 10 times the scale when there is a regional component to the environmental stochasticity.

The results presented here are based on the spatially homogeneous model of Engen (2001) and are therefore not applicable for populations in a spatially heterogeneous environment. A number of scaling results including effects of heterogeneity were given by Engen et al. (2002), but in order to study local dynamics, more explicit models are required, and the kind of general analytical results found here would be difficult to obtain. Strong interaction with other species, such as predator or prey species, is not included in our model and could produce more complex spatial dynamics (Blasius et al. 1999).

All effects of migration that we have analyzed are based on the assumption that there is no cost of migration. This could be included by assuming that the local population growth rate \bar{r} decreases as migration increases. For example, Casagrandi and Gatto (1999), using a spatially implicit metapopulation model, assumed that migrating individuals were subject to an additional death rate. This would correspond to assuming that $\bar{r} = \beta_0 - \beta_1 M$ in our model. For an appropriate choice of β_0 and β_1 , one would then find that some intermediate value of M minimizes the risk of local extinction. However, for any given migration rate, all of our other results remain valid, particularly those concerning the risk of local quasi extinction as a function of area.

Acknowledgments

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APPENDIX

The Model

By adding density-independent migration to the spatial model leading to equation (1), the equation for the densities takes the form

$$dn(z, t) = [\bar{r} - \gamma n(z, t)]n(z, t)dt + mdt \int [n(z + \xi, t) - n(z, t)]p(\xi)d\xi + \sigma_e n(z, t)dB(z, t),$$

giving for the log densities

$$dX(z, t) = [r_0 - \gamma X(z, t)]dt + mdt \int [e^{X(z+\xi, t)-X(z, t)} - 1]p(\xi)d\xi + \sigma_e dB(z, t).$$

Here individuals are assumed to migrate at a rate m , and the migration distance has distribution $p(\xi)$ with 0 mean. In the limit, as m tends to infinity and the migration distance tends to 0, one can show that the Fourier transform of the autocovariance function $c(z, \tau) = \text{cov}[X(w, u), X(w + z, u + \tau)]$, that is,

$$f_\tau(\omega_1, \omega_2) = \int \int \exp[-i(\omega_1 z_1 + \omega_2 z_2)]c(z_1, z_2, \tau)dz_1 dz_2$$

takes the form

$$f_\tau(\omega_1, \omega_2) = \frac{f_e(\omega_1, \omega_2)}{2\gamma + M(\omega_1^2 + \omega_2^2)} e^{-[\gamma + (1/2)M(\omega_1^2 + \omega_2^2)]\tau},$$

where f_e is the Fourier transform of c_e and M is the migration parameter defined in the text (or see Engen 2001). From this Fourier transform, the joint spatial and temporal autocorrelations for any two locations may be computed using the formula for the inverse transform (Papoulis 1962). For an isotropic model, the inverse transform can be expressed as

$$c(z, \tau) = \frac{1}{2\pi} \int_0^\infty f_\tau(u, 0)J_0(u\sqrt{z_1^2 + z_2^2})udu,$$

where J_0 is the Bessel function of the first kind of order 0 (Abramowitz and Stegun 1972). For this isotropic case, the solution for the mean may be expressed as

$$EX(z, t) = \frac{r_0}{\gamma} + \frac{M}{4\pi\gamma} \int_0^\infty f_e(u)u^3(2\gamma + Mu^2)^{-1}du,$$

where $f_e(u)$ is the Fourier transform of the environmental autocovariance function expressed using $u = \sqrt{\omega_1^2 + \omega_2^2}$ (Engen 2001).

It can further be shown that $X(z, t)$ is a Gaussian stochastic field, which implies that the mean and the joint spatial and temporal autocorrelation give the complete description of the properties of $X(z, t)$.

General Solution for the Autocovariance Function

The Fourier transform of $c_e(z)$ given by equation (2) in the main text is

$$f_e(\omega_1, \omega_2) = pf_e(\omega_1, \omega_2) + (1 - p)\sigma_e^2\delta(\omega_1, \omega_2),$$

where \tilde{f}_e is the transform of \tilde{c}_e and $\delta(\omega_1, \omega_2)$ is the two-dimensional Dirac delta function with the property

$$\int \int g(\omega_1, \omega_2)\delta(\omega_1 - x_1, \omega_2 - x_2)d\omega_1d\omega_2 = g(x_1, x_2)$$

for smooth functions g . Hence, using the general formula for the inverse transform, the joint spatial and temporal covariance function for the log abundance takes the form

$$c(z, \tau) = p\tilde{c}(z, \tau) + (1 - p)\frac{\sigma_e^2}{2\gamma}e^{-\gamma\tau},$$

where $\tilde{c}(z, \tau)$ has Fourier transform

$$\tilde{f}_\tau(\omega_1, \omega_2) = \frac{\tilde{f}_e(\omega_1, \omega_2)}{2\gamma + M(\omega_1^2 + \omega_2^2)}e^{-[\gamma + (1/2)M(\omega_1^2 + \omega_2^2)]\tau}.$$

Further, if \tilde{f}_e is isotropic, that is, it may be expressed as a function of $(\omega_1^2 + \omega_2^2)$, this leads to

$$\tilde{c}(z, \tau) = \frac{1}{2\pi} \int_0^\infty \frac{\tilde{f}_e(u, 0)}{2\gamma + Mu^2} e^{-(\gamma + Mu^2/2)\tau} J_0\left(u\sqrt{z_1^2 + z_2^2}\right) u du.$$

The covariance function for two log abundances at the same point of time is

$$c(z, 0) = p\tilde{c}(z, 0) + (1 - p)\frac{\sigma_e^2}{2\gamma},$$

while the covariance function for the 1-yr differences in log abundance, that is,

$$\text{cov}[X(w, t + 1) - X(w, t), X(w + z, t + 1) - X(w + z, t)]$$

is

$$c_{\text{diff}}(z) = 2[c(z, 0) - c(z, 1)] = 2p[\tilde{c}(z, 0) - \tilde{c}(z, 1)] + (1 - p)\sigma_e^2(1 - e^{-\gamma})/\gamma.$$

Hence, the relevant scale for the difference is the scale of the nonconstant part $\tilde{c}_{\text{diff}}(z) = 2p[\tilde{c}(z, 0) - \tilde{c}(z, 1)]$, which has Fourier transform

$$\tilde{f}_{\text{diff}}(\omega_1, \omega_2) = \frac{pf_e(\omega_1, \omega_2)}{\gamma + \frac{1}{2}M(\omega_1^2 + \omega_2^2)} \{1 - e^{-[\gamma + (1/2)M(\omega_1^2 + \omega_2^2)]}\} d\omega_1 d\omega_2.$$

Expanding the difference between \tilde{f}_{diff} and \tilde{f}_e in Taylor series with argument $\gamma + (1/2)M(\omega_1^2 + \omega_2^2)$ and performing the inverse Fourier transform, we obtain the general formula

$$\tilde{c}_{\text{diff}}(z_1, z_2) = p\tilde{c}_e(z_1, z_2) + p \sum_{n=1}^\infty \frac{(-1)^n}{(n + 1)!} \left[\gamma - \frac{M}{2} \left(\frac{\partial^2}{\partial z_1^2} + \frac{\partial^2}{\partial z_2^2} \right) \right]^n \tilde{c}_e(z_1, z_2).$$

Using only the first term of the expansion gives the approximation

$$\tilde{c}_{\text{diff}}(z_1, z_2) \approx p\tilde{c}_e(z_1, z_2) - p\left[\frac{\gamma}{2} - \frac{M}{4}\left(\frac{\partial^2}{\partial z_1^2} + \frac{\partial^2}{\partial z_2^2}\right)\right]\tilde{c}_e(z_1, z_2).$$

For an isotropic Gaussian form of the environmental covariance function, this approximation yields

$$\tilde{c}_{\text{diff}}(z_1, z_2) \approx p\tilde{c}_e(z_1, z_2)\left(1 - \frac{\gamma}{2} + M\frac{r^2 - 2\tilde{l}_e^2}{4\tilde{l}_e^4}\right),$$

where $r^2 = z_1^2 + z_2^2$.

Scaling Results

We consider first any spatial covariance function $c(z_1, z_2)$ that is symmetric around $(0, 0)$ with Fourier transform $f(\omega_1, \omega_2)$. When dealing with the spatial scale in a given direction, say along the z_1 -axis, we assume that c can be scaled to become a distribution that has finite variance in this direction. Since the integral of $c(z_1, z_2)$ over the entire two-dimensional space is $f(0, 0)$, the relevant distribution is $c(z_1, z_2)/f(0, 0)$ with Fourier transform $f(\omega_1, \omega_2)/f(0, 0)$. Due to the symmetry, this distribution has 0 mean, and the variance along the first coordinate may simply be expressed as

$$l^2 = \left[-\frac{\partial^2 f(\omega_1, \omega_2)}{\partial \omega_1^2} f(0, 0) \right]_{\omega_1 = \omega_2 = 0},$$

which, applied to $\tilde{c}(z, 0)$, leads to the scaling result defined by equation (5) in the text. Using the 1-yr differences $\tilde{c}_{\text{diff}}(z)$ with Fourier transform \tilde{f}_{diff} we obtain equation (6).

Dynamics within Quadrats

The dynamics of the total population size in a quadrat with area A is analyzed by also approximating the log of the total population size by an Ornstein-Uhlenbeck process. Using well-known properties of the bivariate lognormal distribution, the corresponding approximation for the temporal autocovariance function for a quadrat with area A is found to be

$$c_r^*(A) = \ln \int_0^{\sqrt{2}} e^{c_r(r\sqrt{A})} f(r) dr,$$

where $f(r)$ is the distribution of the distance between two randomly chosen points in a unit square, which is

$$f(r) = \begin{cases} 2r(\pi + r^2 - 4r) & \text{for } 0 \leq r \leq 1 \\ 2r[2 \arcsin(2/r^2 - 1) + 4(r^2 - 1)^{1/2} - 2 - r^2] & \text{for } 1 \leq r \leq \sqrt{2} \end{cases}.$$

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