

Dispersal and Dynamics

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Mixing and asynchrony of interactions can be expected to stabilize the dynamics of populations. One way such mixing occurs is by dispersal, and Hastings and Gyllenberg *et al.* have shown that symmetric dispersal between two local populations governed by logistic difference equations can simplify the dynamics. These results are extended here by using a more flexible difference equation and allowing asymmetric dispersal. Although there are some instances where dispersal is destabilizing, its stabilizing effect is enhanced by asymmetry. In addition, very high dispersal rates can induce a stable equilibrium of the metapopulation despite highly chaotic local dynamics. If this equilibrium loses stability, the route to intermittent chaos can be observed. Two new conditions under which dispersal can be stabilizing are discussed. One occurs when the timing of reproduction and dispersal differs in the two patches of the metapopulation. This enlarges the asynchrony of the interactions, and simple dynamics due to dispersal are more likely. The second works by slightly adjusting dispersal rates to control chaotic dynamics. The control can replace chaos by a stable equilibrium. The evolution of dispersal rates is discussed. Since obtaining general criteria for invasion into a population with chaotic dynamics is difficult, no clear conclusions are possible as to whether evolution leads to more stable metapopulations. However, a mutant that controls chaos can invade a resident having the same local dynamics but no control mechanism, so that evolution can lead from chaos to a stable equilibrium. © 1995 Academic Press, Inc.

1. INTRODUCTION

Simple ecological models can have very complicated dynamics, as was first realized by May (1974, 1976) who showed that models for populations with discrete generations can exhibit a whole range of dynamical behavior from stable equilibria to higher order cycles and chaos. How often complex dynamics occur in natural systems is controversial; some believe that they do not occur frequently (Berryman and Millstein, 1989). One reason for this belief is that blurring the details of the interactions that induce chaos can stabilize the dynamics. Here stabilization is understood, not in the mathematical, but in the intuitive sense, as a process leading to more regular and simple dynamics. One way mixing of interactions occurs is

through spatial heterogeneity, which can be crucial in determining the dynamics of a population, and since Levins (1970) introduced it, the concept of metapopulations has become increasingly important, both theoretically and empirically (Gilpin and Hanski, 1991). In particular, dispersal in patch models can be stabilizing (Hanski, 1991; Hastings, 1991). For example, spatial heterogeneity can have a profound effect on host–parasitoid interactions, and dispersal can greatly simplify the dynamics of such systems and prevent extinctions (Hassell *et al.*, 1991; Comins *et al.*, 1992; Holt and Hassell, 1993). Similar conclusions have been reached for some predator–prey systems (Taylor, 1990).

In several recent articles the effect of spatial structure on a population with intense intraspecific competition was studied. McCallum (1992) and Stone (1993) analyzed immigration of a constant number of individuals into such a population and showed that it has a strong stabilizing effect. Hastings (1993), Gyllenberg *et al.* (1993), and Gonzalez-Andújar and Perry (1993) studied a system of coupled logistic equations and also concluded that dispersal between local populations exhibiting chaos can simplify the dynamics. To extend and complete these results is one aim of this paper. A second goal is to introduce new conditions under which dispersal can be stabilizing, and the third is to examine the evolution of dispersal rates.

In Section 2 I consider one-patch models in which a population is connected to its surroundings by migration. I show that McCallum's (1992) and Stone's (1993) results that immigration has a stabilizing effect have to be taken with some caution, for their results depend on the model chosen, and immigration can also have a destabilizing effect. On the other hand, even if dispersal is destabilizing, I show, using the ideas of controlled chaos, how small adjustments in dispersal rates can lead from chaos to a stable equilibrium.

In Section 3 I consider two patches whose populations have discrete generations and are coupled by dispersal. Hastings (1993) and Gyllenberg *et al.* (1993) analyzed systems in which the local dynamics in each patch were given by the logistic equation $f(x) = rx(1 - x)$ and dispersal was symmetric. I repeated their results using a biologically more relevant and mathematically more flexible difference equation, and I show that the stabilizing effect is enhanced if dispersal is asymmetric. This was noted by Gonzalez-Andújar and Perry (1993), but their study is rather limited and partly incorrect (see Section 3). I also show that both very high dispersal rates and asynchrony of reproduction and dispersal in the two patches are a strong stabilizing force. These results lend support to the intuitive idea that conditions which favor asynchronous mixing of interactions lead to simpler dynamics. To conclude the section I again show how metapopulation dynamics can be controlled by small adjustments in the dispersal rates, and how such self-control leads from chaos to a stable equilibrium.

In Section 4 I study the evolution of dispersal rates. In case the local dynamics exhibit a stable equilibrium the problem can be solved analytically, but for chaotic metapopulations one has to use numerical simulations. No clear-cut conclusions are possible as to whether evolution tends to simplify the dynamics. However, a mutant using a control mechanism can invade an uncontrolled resident. Thus evolution can lead from chaos to a stable equilibrium.

2. DISPERSAL AND DYNAMICS IN ONE PATCH

Consider a population with discrete generations whose dynamics are described by the one-dimensional difference equation

$$x' = f(x) = w(x) \cdot x. \quad (1)$$

Here x and x' are population densities in successive generations, and $w(x)$ is the fitness function of the population. It calculates the reproductive output per individual if the population density is x . This function is equal to the intrinsic growth rate of the population if $x=0$ and monotonically decreases to 0 as x tends to ∞ in such a way that the function f is of a humped form; it has a single maximum and also tends to 0 as x tends to ∞ . The dynamics of the population are determined by the slope of f at the equilibrium x^* , which is given by $f(x^*) = x^*$, $x^* > 0$. If $|(df/dx)(x^*)| < 1$ the equilibrium is stable. As $|(df/dx)(x^*)|$ increases above 1, the equilibrium gives way first to a stable 2-cycle, then to a 4-cycle and more generally to a 2^n -cycle. As this modulus reaches a critical value, chaos sets in. This route to chaos is described in May and Oster (1976). Note that in all the models of May and Oster (1976) and of Bellows (1981), the modulus of the derivative at the equilibrium increases with increasing intrinsic growth rate (i.e., increasing $w(0)$). Thus, the dynamics tend to be more complex for higher growth rates.

Suppose now that the population lives in a patch that is connected to its surroundings by dispersal of individuals. There are four possible basic scenarios, according to whether dispersal occurs before or after reproduction, and whether dispersal is away from the patch or occurs by migration into the patch. In the present paper I will not consider situations in which dispersal occurs before reproduction in each generation. However, I have studied that case as well, both analytically and numerically, and the results did not differ significantly from those reported here.

Dispersal is usually modeled by assuming that either a constant fraction of the population or a constant number of individuals disperses. The easiest case is when a constant fraction d of the population moves away from the

patch in each generation. If this happens after reproduction, model (1) changes to

$$x' = (1 - d) \cdot f(x) = \tilde{w}(x) \cdot x, \quad (2)$$

where $\tilde{w}(x) = (1 - d) \cdot w(x)$ is the new fitness function. Comparing with (1), we see that the effect of dispersal consists of reducing the intrinsic growth rate: $\tilde{w}(0) < w(0)$. Therefore, the effect of dispersal is to simplify the dynamics. This is a trivial but useful observation of Ruxton (1993).

More interesting is when dispersal occurs by migration into the patch. I will consider the case where a constant number of individuals is added in each generation, as introduced by McCallum (1992) and further analyzed by Stone (1993). In this case model (1) changes to

$$x' = f_c(x) = w(x) \cdot x + c, \quad (3)$$

where c is a constant > 0 . Following McCallum (1992), c could also stand for a refuge that isolates a small part of the population from density effects. Both McCallum (1992) and Stone (1993) emphasized that the dynamics given by (3) tend to be simpler than the dynamics of the original model (1). They used numerical simulations to show this, but the underlying analytical argument is very simple and goes as follows. Let x_c^* be the equilibrium of system (3). As before, the dynamics of (3) are determined by the slope of the function f_c at x_c^* . This slope is of course the same as that of f at x_c^* . Thus the dynamics of (3) are determined by the modulus

$$\left| \frac{df}{dx}(x_c^*) \right|. \quad (4)$$

It is clear that the shift of the function f induced by adding the constant c causes a shift of the equilibrium to the right. That is, $x_c^* > x^*$, where x^* is the equilibrium in the absence of migration. It follows that the effect of migration depends on whether the modulus $|df/dx|$ is increasing or decreasing at x^* . Since $(df/dx)(x^*) < 0$, $|df/dx|$ is decreasing at x^* if the second derivative $(d^2f/dx^2)(x^*)$ is positive, i.e., if x^* lies to the right of the inflection point of f . In this case dispersal will have a simplifying effect on the dynamics. It will have a contrary effect if $(d^2f/dx^2)(x^*)$ is negative. Therefore, the effect depends on the position of x^* relative to the inflection point of f .

The results of McCallum (1992) and Stone (1993) should be viewed with some caution, for they depend on the particular model chosen. Both authors primarily worked with the Ricker equation (Ricker, 1954):

$$x' = \lambda \cdot x \cdot \exp(-qx). \quad (5)$$

In this model one has $x^* = \log(\lambda)/q$, $(df/dx)(x^*) = 1 - \log(\lambda)$, and the inflection point is given by $2/q$. If x^* is unstable then $\log \lambda > 2$; hence, $2/q < x^*$ and dispersal always leads to simpler dynamics. McCallum (1992) also made some simulations with the following model, which was introduced by Maynard Smith and Slatkin (1973) and considered by Bellows (1981) to be the most generally applicable:

$$x' = \frac{\lambda x}{1 + (ax)^b}. \quad (6)$$

McCallum observed the same simplifying effect of dispersal as in the Ricker model, but this result depends on the choice of parameters. In fact, one can show that for any type of dynamics one can choose the parameters in (6) so that x^* lies to the left of the inflection point, hence, so that dispersal destabilizes the system. For example, (6) can have a stable equilibrium while dispersal leads to a 2-cycle. In such a situation dispersal enhances rather than breaks down the onset of chaos, as claimed by Stone (1993) to be the general effect of dispersal.

Even if immigration into the patch simplifies the dynamics as in the Ricker model, then, by the same token, dispersal of a constant number of individuals moving away from the patch leads to more complex dynamics. Of course, when modeling such a situation one has to make sure that the number moving away is not larger than the number present in the patch, for example by requiring that not more than a certain fraction of the population present disperses. Such threshold density-dependent dispersal out of the patch still leads to more complex dynamics in the situation considered by Stone (1993), where dispersal into the patch simplifies the dynamics. This can easily be seen by numerically simulating the Ricker model. However, using the ideas of controlled chaos, one can envisage a scenario in which such dispersal away from the patch nevertheless stabilizes the Ricker model at the equilibrium x^* . These ideas are reviewed in Shinbrot *et al.* (1993). They show how one can use the presence of chaos in a system to stabilize its dynamics with very small perturbations. This contrasts with systems that exhibit simple dynamics; to change their dynamical behavior, large perturbations are typically necessary. In an ecological and evolutionary context, controlling chaos has been described in Doebeli (1993). There I showed how small adjustments of the intrinsic growth rate can stabilize highly chaotic Ricker systems at the equilibrium density. The adjustments consist of increasing the growth rate in years of high density and decreasing it in years of low density. Since a high density means a subsequent crash, and a low density a subsequent outbreak, such adjustments tend to decrease the density fluctuations. What is interesting is that even very small adjustments are enough to stabilize the density at x^* . Similar ideas can be

used in the present situation. For the moment, I will not go into mathematical details and only will describe a recipe that works. A mathematical treatment of the ideas will be given in Section 3 for dispersal between two patches.

Suppose that $x < x^*$ in some year. Then dispersal away from the patch will decrease the size of the subsequent outbreak and thus tend to decrease the fluctuations as described above. Suppose further that the number of dispersing individuals is proportional to the difference $x^* - x$. To avoid negative population densities, we also require that not more than a certain fraction of the minimal population density x_{min} disperses in each generation. The value of x_{min} is obtained as the value of f at the maximal density x_{max} , which in turn is obtained as the value of f at the density for which the derivative df/dx is 0. The dynamics of such a system are then described as

$$x' = \begin{cases} f(x) - c & \text{if } x < x^* \\ f(x) & \text{if } x \geq x^* \end{cases} \quad (7)$$

where $c = \min(a \cdot (x^* - x), d \cdot x_{min})$. Here $a > 0$ is the proportionality factor, and $0 < d < 1$ is the fraction of the minimal population size allowed to disperse.

Using a computer and taking for f a chaotic Ricker function, one easily finds, by trial and error, values for a and d such that this system always stabilizes itself at the equilibrium x^* . In fact, d can be chosen arbitrarily small, so that in most generations the number of individuals dispersing is either 0 because $x > x^*$, or it is equal to $d \cdot x_{min}$ because $a \cdot (x^* - x) > d \cdot x_{min}$. This is similar to the case in which there is dispersal of a constant number of individuals away from the patch. Indeed, if one only applies the rule "no dispersal if $x > x^*$ and emigration equal to $d \cdot x_{min}$ if $x < x^*$," then the system does not stabilize itself and instead exhibits even more complex dynamics (i.e., larger fluctuations) than the original Ricker system. Thus what stabilizes the system is the fact that the number of individuals dispersing actually gets smaller if x is very close to x^* . Because the original Ricker system is chaotic, this will eventually happen. The phenomenon is shown in Fig. 1. Before the system gets finally trapped at x^* , dispersal is almost able to control the dynamics several times when x gets close but not quite close enough to x^* . For Fig. 1 the function f was a Ricker function, but the phenomenon that dispersal stabilizes the system in the way described can be seen for other difference equations such as (6), as long as they exhibit chaos and thus ensure that the population density gets arbitrarily close to the equilibrium in the course of time.

Note that the stabilizing effect of dispersal in this scenario is very different from the one described at the beginning of this section, although in

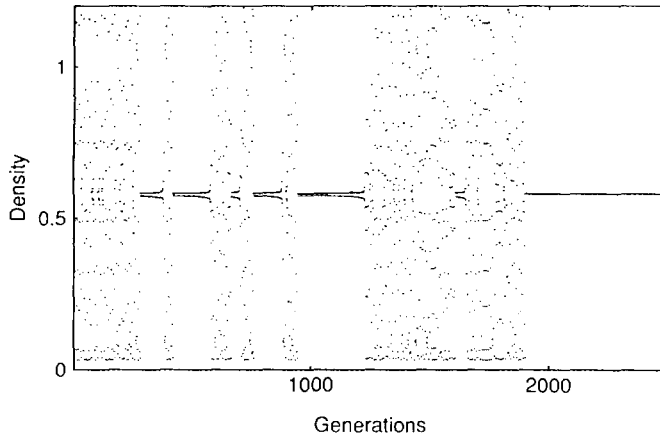


FIG. 1. Time series for the controlled system (7). The density (vertical axis) is shown in successive generations (horizontal axis). When the density gets close to the equilibrium x^* due to chaotic dynamics of the Ricker function f , the control mechanism starts to be effective. If the density was not close enough, the control only works for a while, after which the density starts to fluctuate again, but finally it is close enough to x^* and the system gets trapped there. The parameters for the figure were: $\lambda = \exp(2.9)$ and $q = 5$ for the Ricker function f , and $a = 1.38$ and $d = 0.6$ for the control mechanism (see text).

both cases dispersal is away from the patch. If a constant proportion of the population disperses, the equilibrium density changes, and if dispersal causes the new equilibrium to be stable, then a constant number of individuals will disperse in the equilibrium state. In contrast, if dispersal controls chaos, then the equilibrium density does not change, and in the equilibrium state there is no dispersal at all. Thus the two mechanisms are qualitatively very different.

3. DISPERSAL AND DYNAMICS IN TWO PATCHES

Recently, three studies modeling metapopulations that consist of two local populations connected by migration have been published. Biologically the most interesting is Hastings (1993). He assumed symmetric dispersal and the same dynamics in both patches. One of his conclusions was that dispersal can have a stabilizing effect on the dynamics. In particular, intermediate dispersal rates can lead to a stable 2-cycle despite chaotic local dynamics. This result is supported by the more formal study of Gyllenberg *et al.* (1993), who also assumed symmetric dispersal. However, in the third paper, Gonzalez-Andújar and Perry (1993) noted a stabilizing effect only when dispersal was asymmetric. They also note that very high dispersal rates can induce a stable equilibrium, but they did not have an explanation for this.

All three papers assumed that the local dynamics in each patch are given by the logistic equation $f(x) = rx(1-x)$. This model is biologically not very relevant, mainly because f is negative for large x . Moreover, the range of values of r that yield both chaos and a biologically meaningful situation is rather small, so that the use of this model to study stabilizing effects is restricted. (For example, Gonzalez-Andújar and Perry (1993) include the results from simulations they made with a value of $r = 4.2$, which is biologically meaningless since negative x -values will occur.) Hastings (1993) remarks that his results can be repeated with the Ricker equation (5). As mentioned in the previous section, this model is not generic either, and it does not exhibit the same flexibility as model (6) of Section 2, which I will use. In the first part of this section I show that simple dynamics are more likely with asymmetric dispersal and why high dispersal rates induce a stable equilibrium. I then discuss another stabilizing effect: different timing of reproduction and dispersal in the two patches also greatly simplify the dynamics of the whole system. Despite the stabilizing effect of dispersal, it is of course still possible to have chaotic dynamics for the whole system if the local dynamics are chaotic. I show how one can control chaos by slight adjustments of the dispersal rates in each generation. Such adjustments can stabilize the system at an equilibrium, similar to the situation discussed at the end of the last section.

Asymmetric Dispersal

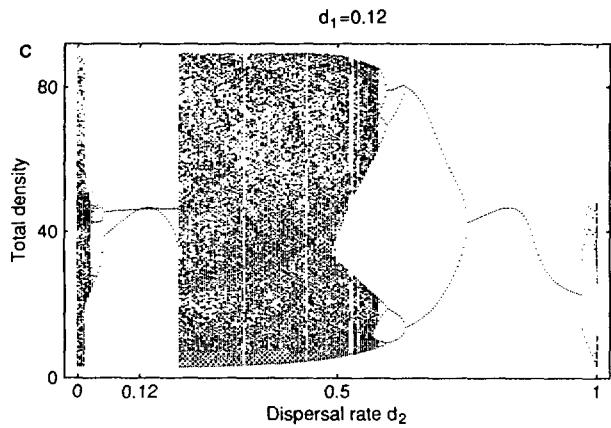
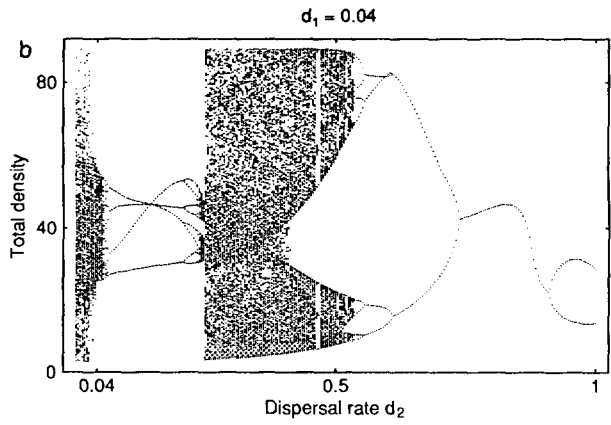
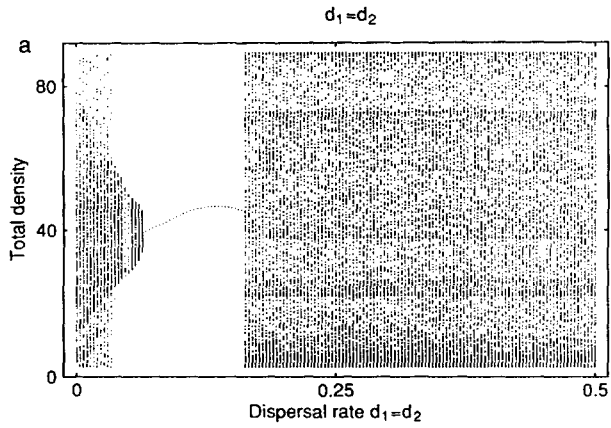
I consider a metapopulation consisting of two local populations. In each patch discrete density-dependent dynamics are followed by dispersal of a fixed fraction of the local population to the other patch. The census is made after dispersal. In the absence of dispersal the dynamics are given by $x' = f(x)$ in patch 1 and by $y' = g(y)$ in patch 2, so that the dynamics of the metapopulation are given by

$$\begin{aligned}x' &= (1 - d_1) \cdot f(x) + d_2 \cdot g(y) \\y' &= (1 - d_2) \cdot g(y) + d_1 \cdot f(x).\end{aligned}\tag{8}$$

Here $0 \leq d_1, d_2 \leq 1$ are the fractions of the populations leaving patch 1 and 2 in each generation. Both Gyllenberg *et al.* (1993) and Hastings (1993) assumed that $d := d_1 = d_2 \leq 0.5$, and for the most part they also assumed that $f \equiv g$, i.e., identical local dynamics in the two patches. One of the main results is that even if the local dynamics are chaotic, intermediate dispersal rates $d \sim 0.1-0.2$ can induce a state in which both local populations cycle between two densities. They are out of phase, so that the total density is constant (assuming that both patches are of equal size, see Fig. 2a). This 2-cycle sometimes occurs together with other locally stable cycles. The

dynamical behavior of the system then depends on the initial conditions, and the different attractors can have fractal boundaries of their basins of attraction. Somewhat in contrast to these results are those of Gonzalez-Andújar and Perry (1993), who find no stabilizing effect for symmetric dispersal (see Table 2 in their paper), only for asymmetric dispersal, i.e., when $d_1 \neq d_2$. But their study is rather limited and not very conclusive. For example, their results for the symmetric case are biased by the fact that they always used symmetric initial conditions, in which case the system stays on the diagonal $x = y$ and behaves in exactly the same way as the local populations would without dispersal. However, the result that a stabilizing effect is more likely if dispersal is asymmetric is correct. In Fig. 2 I used bifurcation diagrams to show the consequences of asymmetric dispersal. I assumed that the local dynamics are given by the function $f(x) = \lambda x / (1 + (ax)^b)$ (model (6) in Section 2), that both local dynamics are identical, and that they are chaotic without dispersal. Then, for fixed dispersal rates d_1 , the dependence of the dynamics of the system on the dispersal rate d_2 is displayed. Although chaos is common, there are windows of values of

FIG. 2. Bifurcation diagrams in which the dynamics of the total population size $x + y$ in system (8) (vertical axis) are shown in dependence on dispersal rates (horizontal axis). System (8) was first iterated long enough to eliminate transients, then plots were obtained from 200 iterations. In Hastings's symmetric model more than one attractor for simple dynamics existed for certain parameter values, so that the outcome of simulations depended on initial conditions. In the example chosen here this only happened when dispersal rates were high enough to induce a locally stable equilibrium (see text). In these cases only the equilibrium dynamics are shown in the figures. The parameters of the functions f and g in model (8) are $\lambda = 8$, $b = \frac{26}{7}$, and $a = 0.1$. These parameters imply chaos for the local dynamics in each patch. Similar patterns as shown here are observed for other parameters implying chaos. (a) Recapitulation of Hastings's and Gyllenberg *et al.*'s results for symmetric dispersal rates $d = d_1 = d_2$ between 0 and 0.5. There is a window of simple dynamics for $0.1 \leq d \leq 0.2$. For these dispersal rates the local populations move out of phase on a 2-cycle, so that the total density is constant. For the rest of the figure the dispersal rate d_1 from patch 1 to patch 2 was fixed at different values, and the dependence of the dynamics on the dispersal rate d_2 from patch 2 to patch 1 is displayed. (b) $d_1 = 0.04$. A window of simple dynamics exists for intermediate values of d_2 . The value of d_1 (indicated on the x -axis) does not lie in this window, so that symmetric dispersal results in chaos. Also, there is a window of large dispersal rates d_2 with simple dynamics. The right-hand side of this window shows the locally stable equilibrium induced by high dispersal (see text) and can be seen for all values of d_1 . (c) $d_1 = 0.12$. In the intermediate window the system now typically moves on a 2-cycle. The value of d_1 (indicated on the x -axis) lies inside this window, so that the stabilizing effect of dispersal can be seen with symmetric dispersal. In this case the total population is constant, which is seen to be a special case of a 2-cycle. (d) $d_1 = 0.175$. The window of 2-cycles gets smaller, and the value of d_1 (indicated on the x -axis) lies again outside this window, so that a stabilizing effect can only be seen with asymmetric dispersal. (e) $d_1 = 0.6$. The window of 2-cycles vanishes for $d_1 \geq 0.2$, but for large values of d_1 a new window for simple dynamics appears for low values of d_2 . Again symmetric dispersal yields chaos, but simple dynamics result, for example, for $d_2 = 0$, i.e., if dispersal occurs in only one direction.



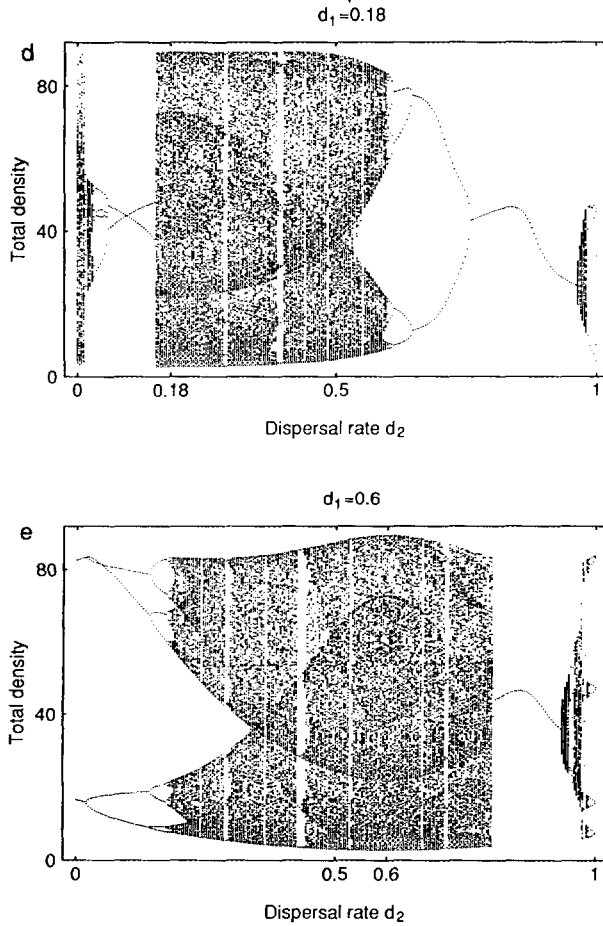


FIG. 2—Continued

d_2 for which simple dynamics occur. If d_1 is small (Fig. 2b), symmetric dispersal results in chaos, but there is a window of intermediate values of d_2 with simple dynamics. As d_1 is increased, a stabilizing effect can be seen with symmetric dispersal, because the value of d_1 lies inside a window of d_2 -values for 2-cycles. The constant total population size for symmetric dispersal is seen to be a special case of a 2-cycle. As d_1 is increased further, the stabilizing effect can again only be seen with asymmetric dispersal (Fig. 2d). For d_1 large enough (Fig. 2e), a new window of 2-cycles appears for low dispersal rates d_2 . Again chaos prevails with symmetric dispersal, but the system exhibits a simple 2-cycle if there is no dispersal in one direction at all (i.e., if $d_2 = 0$).

These results show that the stabilizing effect of dispersal is much larger with asymmetry. Hastings's (1993) and Gyllenberg *et al.*'s (1993) results are for a special case, and in contrast to their symmetric situation simple dynamics can be obtained with asymmetric dispersal for very low as well as for high dispersal rates.

Figure 2 also shows that high dispersal rates can induce equilibrium dynamics. More precisely, if one of the dispersal rates is high enough then the total population as well as the populations in each patch can approach a locally stable equilibrium. This can be shown by an analytical approximation as follows. Suppose that the local dynamics have an unstable equilibrium, and that one of the dispersal rates, say d_2 , is high. Numerical simulations show that the system can then approach a stable equilibrium, in which the population size x^* in patch 1 is approximately a fraction d_2 of the total size:

$$x^* \sim d_2 \cdot (x^* + y^*). \quad (9)$$

Also, x^* is very high, so that the reproductive output in patch 1 is near zero due to density effects:

$$f(x^*) \sim 0. \quad (10)$$

Using this and the first equation of (8) to determine the equilibrium yields

$$x^* = d_2 \cdot g(y^*). \quad (11)$$

Since $x^* = d_2(x^* + y^*)$, we have $y^* = ((1 - d_2)/d_2)x^*$, and substituting this into the last equation and using the expression (6) for g yields

$$x^* = \frac{[\lambda(1 - d_2) - 1]^{1/b} \cdot d_2}{a(1 - d_2)}. \quad (12)$$

The corresponding equilibrium density in patch 2 is then

$$y^* = \frac{[\lambda(1 - d_2) - 1]^{1/b}}{a}. \quad (13)$$

To determine the stability properties, one has to calculate the Jacobian of system (8) at this equilibrium. Note that for the function (6) one has $df/dx = (1/x - s(x)) \cdot f(x)$ with $s(x) = ab(ax)^{b-1}/(1 + (ax)^b)$. Since $f(x^*) \sim 0$, it follows that $(df/dx)(x^*) \sim 0$. Therefore, the Jacobian at the equilibrium is given by

$$\begin{pmatrix} 0 & d_2 \left[\frac{1}{y^*} - s(y^*) \right] g(y^*) \\ 0 & (1 - d_2) \left[\frac{1}{y^*} - s(y^*) \right] g(y^*) \end{pmatrix}. \quad (14)$$

Using the formula for y^* above, one sees that the dominant eigenvalue of this matrix is

$$1 - b \left(1 - \frac{1}{\lambda(1 - d_2)} \right). \quad (15)$$

The equilibrium is locally stable if the modulus of this eigenvalue is < 1 , i.e., if

$$1 - \frac{b}{\lambda(b - 2)} < d_2 < 1 - \frac{1}{\lambda}. \quad (16)$$

(Note that $b > 2$ if (6) is to have an unstable equilibrium.) This condition for d_2 is an approximation, since I used approximate equilibrium sizes x^* and y^* .

Interestingly, in such an equilibrium state the total population is much larger than the sum of the potential equilibrium sizes in each local population (Fig. 3a). At equilibrium, one of the patches has a very small population. This population serves as a source, producing many offspring in each generation, most of which move to the other patch due to high dispersal. The other patch is a sink with a large population that produces very few offspring due to density effects. In each generation the sink population gets restocked by dispersal from the source patch, and this mechanism stabilizes the whole system. This situation is very similar to the one described in Pulliam (1988), although the underlying mechanisms are quite different. In general, the source-sink equilibrium is not a global attractor, and different dynamical behaviors can be seen for different initial conditions. If the equilibrium loses stability but the dispersal rate is still high, a route to chaos that leads to intermittency can be observed; if the dispersal rate inducing a stable equilibrium is decreased, the equilibrium gives way to a stable 2-cycle. Further decrease can result in intermittent chaos (Fig. 3b). In this form of chaotic motion the dynamics are regular for most of the time, except for short intermittent periods with erratic fluctuations. High dispersal is almost able to control the dynamics and keeps the population on a 2-cycle for most of the time, but occasionally the control fails. Intermittent chaos due to sporadic failure of a control for simple population dynamics has been reported previously (Doebeli, 1993, 1994). Other forms of intermittency are shown in Mikhailov (1992) and Vandermeer (1993).

Asynchronous Dispersal

Dispersal can have an even greater stabilizing effect if the timing of reproduction and dispersal is different in the two patches. It has been noted by May *et al.* (1981) that the timing of density effects and parasitism in host-parasite systems can have a profound effect on the dynamics. A similar

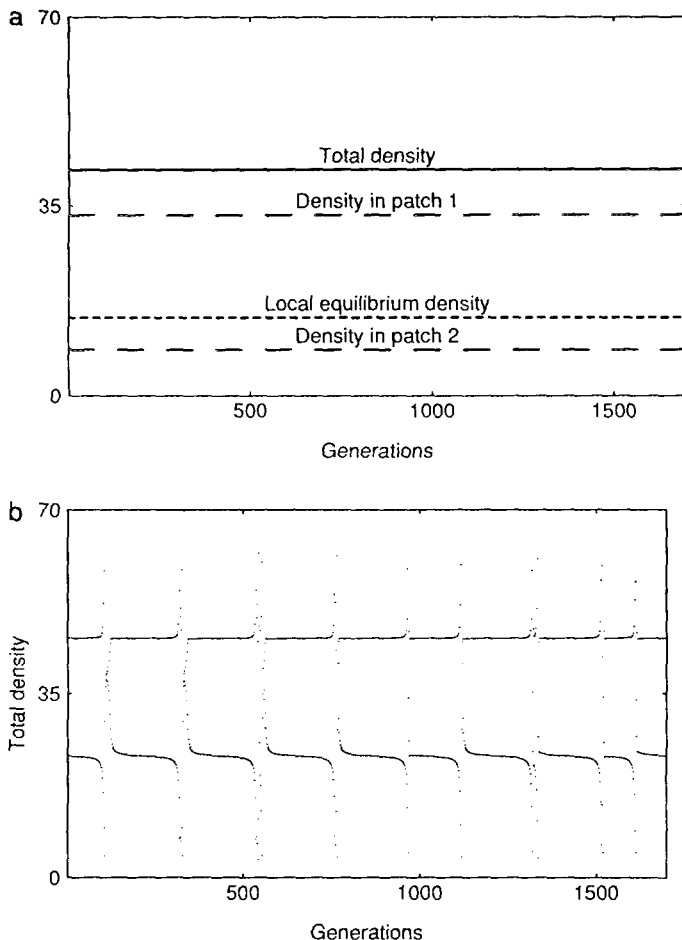


FIG. 3. Time series of the population size for high dispersal rates. The parameters for the functions f and g in (1) are $\lambda = 7$, $b = 4.9$, and $a = 0.1$. The dispersal rate d_1 is set equal to 0.4: (a) $d_2 = 0.8$. d_2 is high enough for the whole system to be stable (see text). In this state the total population size (continuous line) is much larger than the sum of the (unstable) equilibrium sizes in the two patches (dotted line). Patch 1 has a large population (upper dashed line) and is a sink (see text), while the population is low in the source patch 2 (lower dashed line). If d_2 is lowered, the stable equilibrium gives first way to a stable 2-cycle (not shown). As d_2 is further decreased, this 2-cycle is broken up sporadically by irregular fluctuations. This is shown in (b), where $d_2 = 0.754$. The total population size is displayed in successive generations. The system now exhibits intermittent chaos. The motion is regular for most of the time, except for short periods in which the control by high dispersal fails. For a theoretical treatment of the intermittency route to chaos see Schuster (1984, Chap. 3).

observation was made in Doebeli (1995a) for competition between species. In the present situation, I assume that in each generation reproduction first occurs in patch 1, followed by dispersal from patch 1 to patch 2. The patch 2 population now experiences its own density, as well as that of the newly arrived patch 1 individuals. After reproduction in patch 2, dispersal occurs from patch 2 to patch 1. If we write $f(x) = x \cdot w(x)$ and $g(y) = y \cdot v(y)$ for the local dynamics, where w and v are the fitness functions in the patches (see Section 2), the model for this system is

$$\begin{aligned}x' &= (1 - d_1) \cdot x \cdot w(x) + d_2 \cdot y \cdot v(y + d_1 \cdot x \cdot w(x)) \\y' &= (1 - d_2) \cdot y \cdot v(y + d_1 \cdot x \cdot w(x)).\end{aligned}\tag{17}$$

Figure 4 shows the dynamics of this system in dependence on the dispersal rates if the local dynamics are chaotic. In Fig. 4a symmetric dispersal is assumed, in Figs. 4b–d, d_1 is fixed at different values, while d_2 is varied continuously. For the functions f and g (resp. w and v) the same parameter values as for Fig. 2 are used. For high dispersal rates one or both local populations go extinct, but overall it is clear that the difference in the timing of reproduction and dispersal enhances the stabilizing effect of dispersal greatly. For example, for $d_1 = 0.45$, chaos only occurs for very small values of d_2 (Fig. 4d).

Controlling Chaos

To conclude this section I show how small adjustments in dispersal rates can lead to a stable equilibrium when the undisturbed system (8) exhibits chaos. To see this, write system (8) in the form

$$z' = F(z, d_1, d_2),\tag{18}$$

where $z = (x, y)$ and where I explicitly include the dependence of the system on the dispersal rates d_1 and d_2 . I assume that the system exhibits chaos for some dispersal rates \tilde{d}_1 and \tilde{d}_2 . Suppose now that the system is close to an equilibrium z^* at some point in time, so that $|z - z^*|$ is small (an equilibrium is of course a state z^* with $F(z^*) = z^*$). For parameter values d_1 and d_2 close to the nominal values \tilde{d}_1 and \tilde{d}_2 , respectively, we then have the linear approximation

$$z' - z^* = A \cdot (z - z^*) + B_1 \cdot (d_1 - \tilde{d}_1) + B_2 \cdot (d_2 - \tilde{d}_2).\tag{19}$$

Here A is the Jacobian matrix $\partial F/\partial z$, and B_1 and B_2 are the two-dimensional column vectors $B_1 = \partial F/\partial d_1$ and $B_2 = \partial F/\partial d_2$, where the partial derivatives are evaluated at $z = z^*$, $d_1 = \tilde{d}_1$, and $d_2 = \tilde{d}_2$. I assume that one can adjust the dispersal rates in each generation; a small change is made

on the basis of the value of z . More precisely, we adjust the dispersal rates according to the densities in each patch,

$$\begin{aligned}d_1 - \tilde{d}_1 &= -k_1 \cdot (x - x^*) \\d_2 - \tilde{d}_2 &= -k_2 \cdot (y - y^*),\end{aligned}\tag{20}$$

where k_1 and k_2 are constants which have to be chosen appropriately and where $z^* = (x^*, y^*)$. Thus the dispersal rate from patch 1 to patch 2 is controlled linearly by the density in patch 1, and similarly for patch 2. Substituting (20) into (19) one obtains

$$\begin{aligned}z' - z^* &= A \cdot (z - z^*) - k_1 B_1 \cdot (x - x^*) - k_2 B_2 \cdot (y - y^*) \\&= (A - C) \cdot (z - z^*),\end{aligned}\tag{21}$$

where C is the 2×2 -matrix $C = (k_1 B_1, k_2 B_2)$ (recall that B_1, B_2 are two-dimensional column vectors and that $(z - z^*) = (x - x^*, y - y^*)$). It follows that the system will approach the equilibrium z^* if the values of k_1 and k_2 are chosen such that the modulus of the dominant eigenvalue of the matrix $A - C$ is < 1 . In principle, stabilization of the system is achieved by waiting until the system gets close to z^* and then applying the perturbations (20). The closer the system is to z^* , the smaller are the perturbations needed. Typically, a chaotic attractor contains points which are arbitrarily close to an equilibrium. Thus the system gets arbitrarily close to such an equilibrium in the course of time. Therefore, in principle very tiny perturbations suffice to stabilize the system, although the smaller one allows them to be, the longer one might have to wait until stabilization occurs. This is in striking contrast to systems exhibiting regular dynamics, e.g., a cycle. To stabilize such a system at an equilibrium, large perturbations would be necessary.

While the mechanism described could be applied to a metapopulation from outside the system by artificially altering dispersal rates, it is also possible that a population has evolved to control itself by adjusting dispersal rates according to its density. For such a scenario the mechanism described is not very reasonable. Why should the population adjust dispersal rates only when it is close to an equilibrium state? A more realistic mechanism would be to apply the control law (20) at all times; i.e., not only when the density is close to z^* , but to put a limit to the magnitude of the adjustment by requiring that the change of dispersal rates is not more than a certain fraction of the nominal value. Numerical experiments show that such a mechanism also works (cf. Fig. 5a). Note that not in all

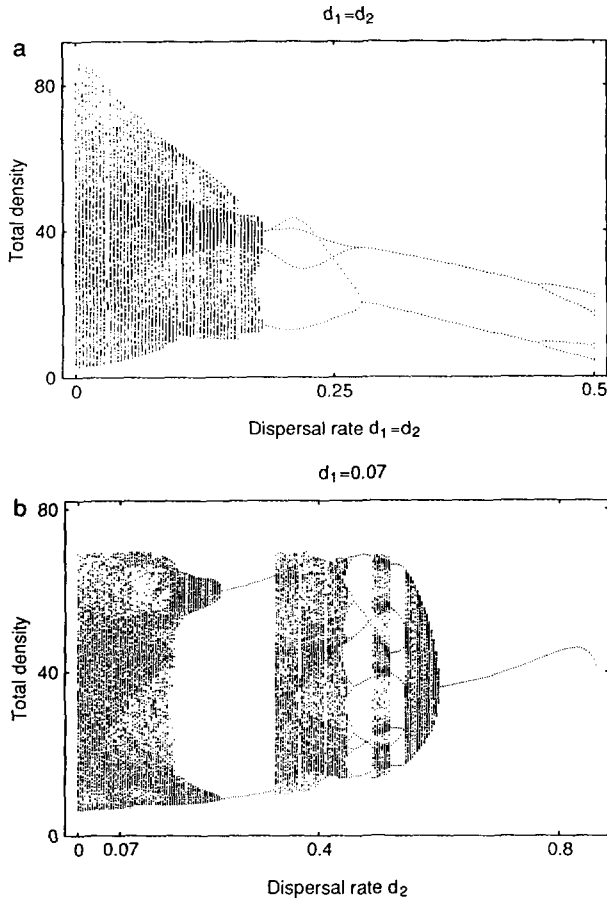


FIG. 4. Bifurcation diagrams in which the dynamics of the total population size $x + y$ in system (17) (vertical axis) are shown in dependence on dispersal rates (horizontal axis). System (17) was first iterated long enough to eliminate transients, then plots were obtained from 200 iterations. The parameters for the local dynamics in the patches were the same as for Fig. 2. Similar patterns are obtained for different sets of parameters implying chaos. For high dispersal rates one or both populations (depending on initial conditions) go extinct, and the dynamics are only displayed if this does not happen. (a) Symmetric dispersal rates, $d_1 = d_2$, between 0 and 0.5, analogous to Fig. 2a. The window for simple dynamics is larger than the corresponding window for system (8). For the rest of the figure the dispersal rate d_1 from patch 1 to patch 2 was fixed at different values, and the dependence of the dynamics on the dispersal rate d_2 from patch 2 to patch 1 is shown. (b) $d_1 = 0.07$. For low d_1 similar patterns as for system (8) with a window of simple dynamics for intermediate and one for large dispersal rates d_2 can be seen. (c) $d_1 = 0.3$. For most values of d_2 simple dynamics can be seen, in contrast to system (8), where for this value of d_1 only large dispersal rates d_2 yield simple dynamics. (d) $d_1 = 0.45$. Now only very small dispersal rates d_2 result in chaos, in sharp contrast to system (8). Hence it is clear that the stabilizing effect of dispersal is enhanced in system (17), i.e., if the timing of reproduction and dispersal is different in the two patches.

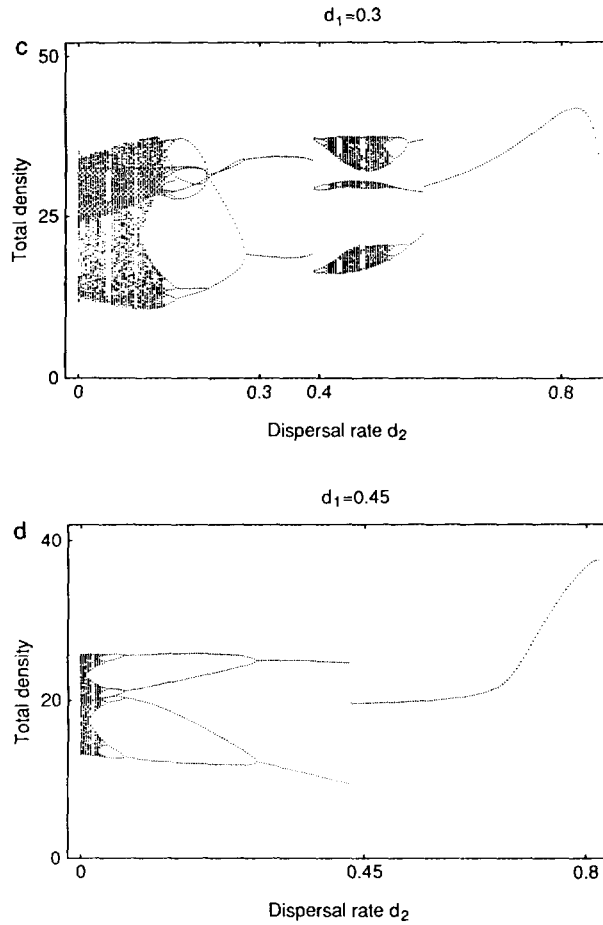


FIG. 4—Continued

cases, where the metapopulation exhibits chaos for some given dispersal rates, does there exist an equilibrium in the vicinity of the chaotic attractor. In these cases the mechanism does not work. However, other types of regular dynamics such as higher order cycles are then close to the attractor, and a similar rule can be applied to stabilize such cycles.

In Doebeli (1993) I have shown how a population can stabilize itself by small adjustments of its growth rate. If the population is a metapopulation, no intrinsic property of the local populations has to be adjusted to control chaos. Slightly altering the rates of dispersal can be sufficient. The mere presence of dispersal offers the possibility of stabilization.

4. EVOLUTION OF DISPERSAL RATES

In this section I study under what conditions a mutant with different dispersal rates can invade a resident metapopulation. I assume that the mutant has the same local dynamics and only differs with respect to dispersal rates. I write the system of the resident population in the form

$$z' = G(z) \cdot z. \quad (22)$$

Here $z = (x, y)$ is the vector consisting of the densities in the two patches and $G(z)$ is the matrix

$$\begin{pmatrix} (1-d_1) \cdot w(x) & d_2 \cdot v(y) \\ d_1 \cdot w(x) & (1-d_2) \cdot v(y) \end{pmatrix}, \quad (23)$$

where w and v are the fitness functions in the two patches. Suppose that the local dynamics in each patch exhibit a stable equilibrium and that the resulting global dynamics also have a stable equilibrium z^* . (Note that this does not necessarily follow. A counterexample can be constructed along the lines of the example mentioned in Section 2: if the equilibrium point of the function defining the local dynamics lies to the right of the inflection point of this function, dispersal can be destabilizing.) Let $w^* := w(x^*)$ and $v^* := v(y^*)$ be the values of the fitness functions at z^* . At the equilibrium, the dominant eigenvalue $\zeta(d_1, d_2)$ of the matrix

$$G(z^*) = \begin{pmatrix} (1-d_1) \cdot w^* & d_2 \cdot v^* \\ d_1 \cdot w^* & (1-d_2) \cdot v^* \end{pmatrix} \quad (24)$$

is one:

$$\begin{aligned} \zeta(d_1, d_2) = & \frac{1}{2} \{ (1-d_1) w^* + (1-d_2) v^* \\ & + \sqrt{[(1-d_1) w^* - (1-d_2) v^*]^2 + 4d_1 d_2 w^* v^*} \} = 1. \end{aligned} \quad (25)$$

To determine the evolutionary optimum for the dispersal rates, one has to calculate the derivatives $\partial\zeta/\partial d_1$ and $\partial\zeta/\partial d_2$. Using (25), we get

$$\begin{aligned} \frac{\partial\zeta}{\partial d_1} &= \frac{w^*}{4} \left[\frac{v^* - 1}{2 - (1-d_1) w^* - (1-d_2) v^*} \right] \\ \frac{\partial\zeta}{\partial d_2} &= \frac{v^*}{4} \left[\frac{w^* - 1}{2 - (1-d_1) w^* - (1-d_2) v^*} \right]. \end{aligned} \quad (26)$$

It easily follows that ζ is a global maximum, hence the resident is an evolutionary stable state, if and only if $w^* = v^* = 1$, that is, if and only if the local populations x^* and y^* are at the local equilibrium densities x_0

and y_0 (i.e., the equilibria for the local dynamics when considering the patches independently). From the equilibrium equation

$$x^* = (1 - d_1) \cdot w^* x^* + d_2 \cdot v^* y^* \quad (27)$$

it now follows that in such a state

$$d_2 = \frac{x_0}{y_0} \cdot d_1. \quad (28)$$

Thus ζ has global maxima along a line in the d_1 - d_2 -plane, and each point on this line is evolutionarily stable. For example, if the local dynamics are identical in the two patches, then each state with symmetric dispersal is evolutionarily stable. One can show that if a series of invasions leads to an evolutionary optimum, then every invasion results in the elimination of the resident, so that no polymorphism is possible. Moreover, it can be seen numerically that the total density is maximized at an evolutionary stable state. Thus the system undergoes a form of K -selection.

If the local dynamics exhibit a higher order cycle when considered alone, a similar analysis can be performed. In particular, if the dynamics in both patches are the same, then again all states with symmetric dispersal are evolutionarily stable. With numerical simulations one can check that this is also true if the (identical) local dynamics are chaotic. If the local dynamics differ general invasion criteria are hard to obtain. In principle, one has to do the following (see Metz *et al.*, 1992). Let G^m be the fitness matrix of the mutant, so that a metapopulation consisting of the mutant alone is described by $z' = G^m(z) \cdot z$. If the mutant tries to invade a resident population, it is initially rare, and the relevant component for its dynamics is the density of the resident. Therefore, the time series z_t^m of the mutant is given by

$$z_{t+1}^m = G^m(z_t^r) \cdot z_t^m, \quad (29)$$

where z_t^r is the density vector of the resident population at time t . The invasion criterion is now simply that the modulus of the dominant eigenvalue of the matrix $G^m(z_t^r)$ is on average larger than 1. If the resident undergoes chaotic fluctuations, an invading mutant has to be successful at those densities that are often attained by the resident. Thus, to obtain invasion criteria one has to know the nature of the chaotic fluctuations, and typically only numerical techniques are available. I am currently investigating how to obtain general criteria for when invasion against a chaotic resident is possible (Doebeli, 1995b). In the case considered here numerical studies yield the following result: as in the case of stable equilibrium dynamics, a difference in equilibrium densities in the two patches causes a shift of the evolutionary optima away from the diagonal.

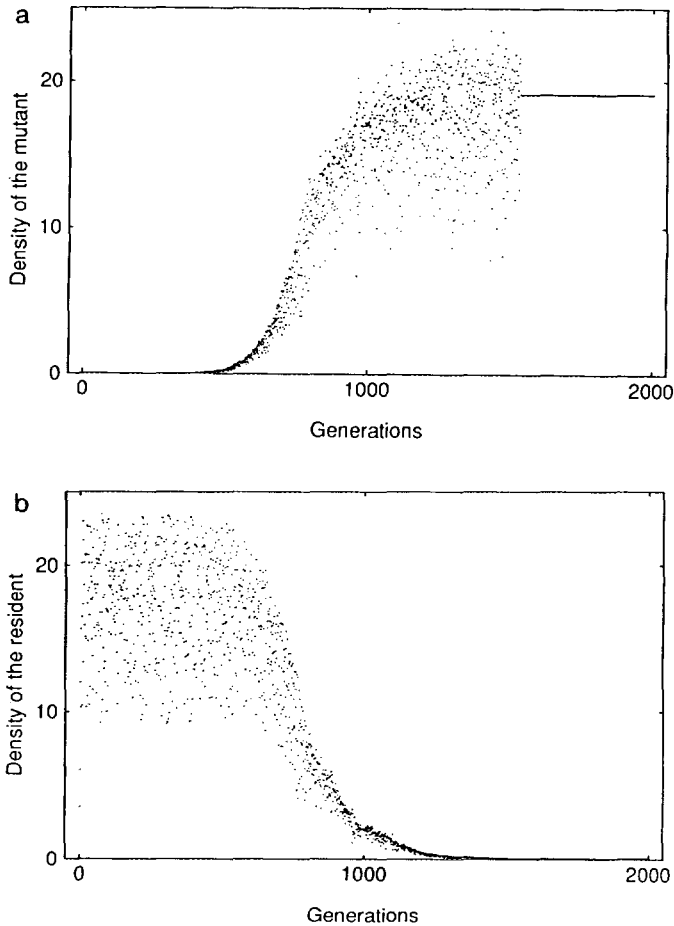


FIG. 5. Invasion of a mutant using the self-control mechanism described in Section 3 into a resident population without control. The parameters of the resident system (8) are: $\lambda = 1.7$, $b = 8.5$, and $a = 0.1$ for the local dynamics in the two patches, $d_1 = 0.1$ and $d_2 = 0.2$. The parameters for the local dynamics of the mutant are the same. The mutant's control parameters of Eq. (20) are $k_1 = 1.3$ and $k_2 = 0.6874$. The resident exhibits chaos when alone. After 200 generations a small amount of mutants is introduced. Time series of the mutant and the resident are shown. (a) The total density of the mutant increases on average. After the resident is reduced to very low densities, the control mechanism stabilizes the mutant at the equilibrium. This happens when the mutant's density gets close enough to the equilibrium. (b) The resident population first exhibits chaos and then goes extinct due to invasion of the mutant.

As in Eq. (28), the dispersal rate from the patch with the higher equilibrium density is reduced. A difference in complexity of the local dynamics causes a shift in the other direction; the dispersal rate from the patch with the more complex dynamics tends to be higher in an evolutionary stable state. Since no general criteria for invasion against a chaotic resident are available, no general conclusions can be made as to whether evolution tends to simplify the dynamics. For example, if the local dynamics are identical, evolution leads to symmetric dispersal, which may or may not have a stabilizing effect.

However, one instance where evolution does lead from chaos to a stable equilibrium is worth mentioning. It can be seen numerically that a mutant that exerts the self-control mechanism described in Section 3 can invade a resident with the same parameters but without control. Figure 5 shows how the invading mutant eliminates the resident and transforms a chaotic metapopulation into one with a stable equilibrium.

5. DISCUSSION

Dispersal leads to mixing of interactions and can therefore be expected to have a stabilizing effect on the dynamics of populations (May, 1985; Gilpin and Hanski, 1991). For example, Hastings (1993) and Gyllenberg *et al.* (1993) found a stabilizing effect of symmetric dispersal in a system of two local populations with discrete logistic dynamics. On intuitive grounds, the effect should be enhanced if the mixing of the interactions is asymmetric or asynchronous. The present study supports this idea. The results of Section 3 show that the tendency for simple dynamics is stronger with asymmetric dispersal (Fig. 2). A stabilizing effect is even more likely with asynchrony. If the timing of reproduction and dispersal differs in the two populations, simple dynamics occur for a larger range of dispersal rates (Fig. 4).

In addition, very high dispersal rates induce a stable equilibrium even if the local dynamics are highly chaotic when considered alone (Section 3). At such an equilibrium the total population density is much larger than the sum of the potential equilibrium densities in the two patches (Fig. 3a). If the control by high dispersal is relaxed, the route to intermittent chaos can be observed (Fig. 3b). In this form of "almost stable chaos" the population density behaves regularly for most of the time, except for short, intermittent periods in which it fluctuates erratically.

I have shown that by choosing the right parameters in the right model, dispersal can very well be destabilizing and lead, for example, from a stable equilibrium to cyclic dynamics (Section 2). An analogous remark was made by Ruxton (1993) for continuous time models. On the whole, however, it

seems that dispersal tends to simplify the dynamics and that this tendency is stronger under conditions of asymmetry and asynchrony. It will be interesting to try to extend these results to metapopulations with more than two patches.

For chaotic local dynamics the dynamics of the whole metapopulation can, of course, also be chaotic. The presence of dispersal then allows one to apply a control mechanism that leads to a stable equilibrium. This mechanism consists of small adjustments of the dispersal rates in each generation. The control works in one-patch models as well as in two-patch models (Figs. 1 and 5). It might be applied by an agent outside the system such as a system manager, but it is also conceivable that the individuals of a population have evolved to apply the control themselves: they might exert self-control by adjusting the dispersal rates according to their density in each generation. With the possibility of such self-control a general problem arises. If demographic parameters such as dispersal rates or equilibrium densities were measured for a population using the control mechanism they would only differ slightly from those of an uncontrolled population. Thus the two populations would be classified as the same, even though they exhibit very different dynamical behavior. This casts some doubt on methods of estimating demographic parameters to determine the dynamics of a population. (In fact, a similar observation holds for a population exhibiting intermittent chaos: if measurements were made during the long phases of regular dynamics, such a population would not be distinguished from a nonchaotic one.)

Under some circumstances a mutant using the control mechanism can invade a resident with the same parameters but without control, so that evolution can lead from chaos to a stable equilibrium (Fig. 5). A similar evolutionary advantage of controlled chaos has been described in Doebeli (1993). In general, the problem of the evolution of dispersal rates has an analytical solution only in case the local dynamics are regular. If the dynamics in the two patches are identical, symmetric dispersal rates are evolutionarily stable. Numerical simulations show that this is also true for chaotic local dynamics: if they are the same in the two patches symmetric dispersal rates evolve. For more general situations it can be seen numerically that evolution tends to favor higher dispersal rates from the patch with the more complex dynamics. It is an open problem to find general criteria describing when invasion into a resident population with chaotic dynamics is possible.

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REFERENCES

- BELLOWS, T. S., JR. 1981. The descriptive properties of some models for density dependence, *J. Anim. Ecol.* **50**, 139–156.
- BERRYMAN, A. A., AND MILLSTEIN, J. A. 1989. Are ecological systems chaotic—and if not, why not? *Trends Ecol. Evol.* **4**, 26–28.
- COMINS, H. N., HASSELL, M. P., AND MAY, R. M. 1992. The spatial dynamics of host–parasitoid systems, *J. Anim. Ecol.* **61**, 735–748.
- DOEBELI, M. 1993. The evolutionary advantage of controlled chaos, *Proc. R. Soc. London B* **254**, 281–286.
- DOEBELI, M. 1994. Intermittent chaos in population dynamics, *J. Theor. Biol.* **166**, 325–330.
- DOEBELI, M. 1995a. Phenotypic variability, sexual reproduction, and evolutionary population dynamics, *J. Evol. Biol.*, in press.
- DOEBELI, M. 1995b. Evolutionary predictions from invariant physical measures of dynamic processes, *J. Theor. Biol.*, in press.
- GILPIN, M., AND HANSKI I. (Eds.) 1991. “Metapopulation Dynamics: Empirical and Theoretical Investigations,” Academic Press, London.
- GONZALEZ-ANDÚJAR, J. L., AND PERRY, J. N. 1993. Chaos, metapopulations and dispersal, *Ecol. Model.* **65**, 255–263.
- GYLLENBERG, M., SÖDERBACKA, G., AND ERICSSON, S. 1993. Does migration stabilize local population dynamics? Analysis of a discrete metapopulation model, *Math. Biosci.* **118**, 25–49.
- HANSKI, I. 1991. Single-species metapopulation dynamics—concepts, models and observations, *Biol. J. Linn. Soc.* **42**, 17–38.
- HASSELL, M. P., COMINS, H. N., AND MAY, R. M. 1991. Spatial structure and chaos in insect population dynamics, *Nature* **353**, 255–258.
- HASTINGS, A. 1991. Structured models of metapopulation dynamics, *Biol. J. Linn. Soc.* **42**, 57–71.
- HASTINGS, A. 1993. Complex interactions between dispersal and dynamics: Lessons from coupled logistic equations, *Ecology* **74**, 1362–1372.
- HOLT, R. D., AND HASSELL, M. P. 1993. Environmental heterogeneity and the stability of host–parasitoid interactions, *J. Anim. Ecol.* **62**, 89–100.
- LEVINS, R. 1970. Extinction, in “Some Mathematical Questions in Biology” (M. Gerstenhaber, Ed.), pp. 77–107, Am. Math. Soc., Providence, RI.
- MAY, R. M. 1974. Biological populations with non-overlapping generations: Stable points, stable cycles and chaos, *Science* **186**, 645–647.
- MAY, R. M. 1976. Simple mathematical models with very complicated dynamics, *Nature* **261**, 459–467.
- MAY, R. M. 1985. Regulation of populations with non-overlapping generations by microparasites: A purely chaotic system, *Am. Nat.* **125**, 573–584.
- MAY, R. M., HASSELL, M. P., ANDERSON, R. M., AND TONKYN, D. W. 1981. Density dependence in host–parasitoid models, *J. Anim. Ecol.* **50**, 855–865.
- MAY, R. M., AND OSTER, G. F. 1976. Bifurcations and dynamic complexity in simple ecological models, *Am. Nat.* **110**, 573–599.
- MAYNARD SMITH, J., AND SLATKIN, M. 1973. The stability of predator–prey systems, *Ecology* **54**, 384–391.
- MCCALLUM, H. I. 1992. Effects of immigration on chaotic population dynamics, *J. Theor. Biol.* **154**, 277–284.
- MIKHAILOV, A. 1992. Spatio-temporal intermittency in population explosions, *Physica A* **188**, 367–385.
- PULLIAM, H. R. 1988. Sources, sinks, and population regulation, *Am. Nat.* **132**, 652–661.

- RICKER, W. E. 1954. Stock and recruitment, *J. Fish. Res. Bd. Can.* **11**, 559–623.
- RUXTON, G. D. 1993. Linked populations can still be chaotic, *Oikos* **68**, 347–348.
- SCHUSTER, H. G. 1984. "Deterministic Chaos: An Introduction," Physik Verlag, Weinheim.
- SHINBROT, T., GREBOGI, C., OTT, E., AND YORKE, J. A. 1993. Using small perturbations to control chaos, *Nature* **363**, 411–417.
- STONE, L. 1993. Period-doubling reversals and chaos in simple ecological models, *Nature* **365**, 617–620.
- TAYLOR, A. D. 1990. Metapopulations, dispersal, and predator-prey dynamics: An overview, *Ecology* **71**, 429–433.
- VANDERMEER, J. 1993. Loose coupling of predator-prey cycles: Entrainment, chaos, and intermittency in the classic MacArthur consumer-resource equations, *Am Nat.* **141**, 687–716.