

Population Dynamics with a Refuge: Fractal Basins and the Suppression of Chaos

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We consider the effect of coupling an otherwise chaotic population to a refuge. A rich set of dynamical phenomena is uncovered. We consider two forms of density dependence in the active population: logistic and exponential. In the former case, the basin of attraction for stable population growth becomes fractal, and the bifurcation diagrams for the active and refuge populations are chaotic over a wide range of parameter space. In the case of exponential density dependence, the dynamics are unconditionally stable (in that the population size is always positive and finite), and chaotic behavior is completely eradicated for modest amounts of dispersal. We argue that the use of exponential density dependence is more appropriate, theoretically as well as empirically, in a model of refuge dynamics. © 2002 Elsevier Science (USA)

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1. INTRODUCTION

Non-linear maps have contributed greatly to our understanding of population dynamics over the past 25 years (May, 1976). The famous bifurcation diagram of the logistic map (i.e., the discrete time analog of the logistic model) encapsulates the related ideas of period doublings in steady-state populations as the reproductive rate is increased, and fully chaotic dynamics as the reproductive rate exceeds a critical value.

In more recent years, workers have utilized non-linear maps in a spatially explicit context by constructing coupled map lattices (CML) (Kaneko, 1992; Solé *et al.*, 1992). In these models, a spatial system is represented by a grid on each site of which is placed a non-linear map. The maps are coupled together to represent spatial dispersal. On varying the dispersal parameter, along with the reproductive rate, a wide range of dynamical

behavior is observed (see for example, Hassell *et al.*, 1991).

Given the complexity of CML, it is difficult to understand these different dynamical phases even qualitatively. In an attempt to unravel the complexity of spatially explicit models, we introduce here the simplest spatial generalization of a non-linear map. This is a two-site system, with density-dependent regulation at one site, and density-independent dynamics at the other. The second site is coupled to the first via dispersal. To our knowledge this model has not been studied before. There have been many studies of two-site systems, but in all cases the populations of both sites are updated under density-dependent regulation (see for example, Vandermeer (1997), and in the chaos literature Maistrenko *et al.* (1999), and references therein). A particular class of these two-site systems has been intensively studied in the context of source–sink dynamics (Hanski, 1999). A continuum version was

studied by Holt (1985) who found a globally stable equilibrium for the two-patch populations, and the bifurcation structure of a discrete version was carefully analyzed by Gyllenberg *et al.* (1996). Our model is expected to be simpler than these others, since one site has purely linear dynamics.

We have introduced our model in very general terms. In the rest of this article we shall focus on systems in which there is no reproduction or intra-specific competition whatever in the second site. We shall only consider dispersal to and from the second site, and mortality. We shall loosely describe this class of systems under the heading “refuge models” (Chesson, 1983, 1984). We shall refer to the first site (with density-dependent regulation) as the “active” site, and the second site as the “passive” site. It is well appreciated that a refuge can have profound effects on the population dynamics of the simplest model systems (see for example, Edelstein-Keshet (1988) and references therein). In spite of this, we are unaware of any previous studies of the simple refuge model outlined here. [We note, however, that a mathematical model similar to ours has recently been studied within the matrix approach to metapopulation dynamics (Vandermeer and Carvajal, 2000).]

Despite its simplicity, we expect our model to be a good starting point for the description of refuges. As an example, we consider a plant population that has an actively growing fraction and a dormant seed bank (for example, Cohen, 1966; Bosbach *et al.*, 1982; Archbold, 1989). The active fraction may be modeled in a spatially implicit manner with a non-linear map. In each cycle, the plant population will lose a certain proportion of seeds to the seed bank. In a likewise manner, the seed bank will lose a certain proportion of its seeds to germination and recruitment to the active population. In the seed bank, seeds are passive, undergoing neither growth nor death through density-dependent competition (although one expects there to be a certain density-independent attrition due to loss of viability, predation, etc.). One may also use the refuge concept for a large number of other population systems, including the well-studied example of the resting stage of eggs of microcrustaceans (Hairston, 1987; Hairston *et al.*, 1996), or long-lived adults of amphibians with strong density dependence in the larval stage (Wilbur, 1996). Another potential application of the refuge model is as a simple description of population dynamics at a range margin, where viable populations are coupled to sinks (with no density dependence).

The immediate questions that arise are: how does the refuge affect the dynamics of the active population? If there is chaos in the absence of the refuge, will the

dispersal to the refuge enhance or diminish the chaotic behavior? We make some first steps to answering these questions in this article.

In the next section, we introduce our model in the form of a two-dimensional map. We shall make certain simplifying assumptions, and present two elementary analytic observations. The remainder of the article will deal with results obtained via numerical iteration of the map. In Section 3, we study the system in which the active population has an intrinsic dynamics governed by the logistic map. We find a range of very rich behavior, but our conclusion is that the logistic map is inappropriate for use in a refuge model. In Section 4, we go on to study the exponential map. In this case, we find that a modest amount of dispersal is sufficient to remove the chaos completely from the system. We present our conclusions in Section 5.

2. THE REFUGE MODEL

We wish to consider the simplest possible model of an active population coupled to a refuge. We consider discrete time steps, with each time step consisting of two stages: birth/death and dispersal. The birth/death stage is modeled in the active population using a non-linear map corresponding to density-dependent reproduction. Only death is allowed in the refuge, with a density-independent rate μ . In the dispersal stage individuals move between the active population and the refuge with rates ε (emigration from the active site) and ε' (immigration to the active site). The reader is referred to Fig. 1 for a schematic representation of the model.

Let us denote the density of the active population at time step n by x_n , and the density of the refuge population by y_n . (We reserve the symbol t for the underlying continuous time.) The above model may then

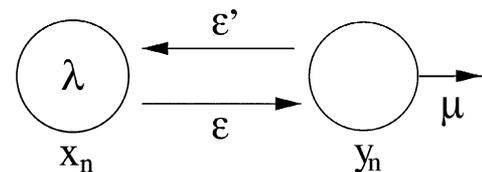


FIG. 1. Schematic illustration of the refuge model. The active population on the left (with density x_n) has internal dynamics generated by a map $f(x_n; \lambda)$. There is dispersal with rate ε from the active population to the refuge, and dispersal in the opposite sense with rate ε' . The organisms in the refuge (with density y_n) also suffer constant attrition with rate μ .

be written in the following way. For the birth/death stage we have

$$\begin{aligned}\tilde{x}_n &= f(x_n; \lambda), \\ \tilde{y}_n &= (1 - \mu)y_n,\end{aligned}\tag{1}$$

where we generally take $f(x; \lambda) = \lambda x g(x)$, such that g is a function describing the density dependence of reproduction, and λ is the reproductive rate in the absence of density dependence. For the dispersal stage we have

$$\begin{aligned}x_{n+1} &= (1 - \varepsilon)\tilde{x}_n + \varepsilon'\tilde{y}_n, \\ y_{n+1} &= (1 - \varepsilon')\tilde{y}_n + \varepsilon\tilde{x}_n.\end{aligned}\tag{2}$$

We may combine these two stages into a combined map by eliminating the intermediate populations \tilde{x}_n and \tilde{y}_n to obtain

$$x_{n+1} = (1 - \varepsilon)f(x_n; \lambda) + \varepsilon'(1 - \mu)y_n,\tag{3}$$

$$y_{n+1} = (1 - \varepsilon')(1 - \mu)y_n + \varepsilon f(x_n; \lambda).\tag{4}$$

The model is completely defined by supplying the initial population densities (x_0, y_0) .

In what follows we shall simplify the model further by (i) neglecting attrition in the refuge (i.e., we set $\mu = 0$) and (ii) taking equal dispersal rates $\varepsilon = \varepsilon'$. These choices are made purely on the grounds of simplicity, and the investigation of non-zero attrition and asymmetric dispersal are certainly worthy of future study.

The two-dimensional map now takes the form

$$x_{n+1} = (1 - \varepsilon)f(x_n; \lambda) + \varepsilon y_n,\tag{5}$$

$$y_{n+1} = (1 - \varepsilon)y_n + \varepsilon f(x_n; \lambda).\tag{6}$$

This is the form of the model we shall use for our computer experiments.

There are two equivalent ways to rewrite this map which are worthy of note. First, one may eliminate the refuge density by iterating Eq. (5) to time step $n + 2$. On substitution of Eqs. (5) and (6) one finds

$$x_{n+2} = (1 - \varepsilon)(f(x_{n+1}; \lambda) + x_{n+1}) - (1 - 2\varepsilon)f(x_n; \lambda).\tag{7}$$

Second, one may explicitly solve Eq. (6) for the refuge density in terms of the active site densities. By repeated iteration one finds

$$y_n = (1 - \varepsilon)^n y_0 + \varepsilon \sum_{m=0}^{n-1} (1 - \varepsilon)^{n-m-1} f(x_m; \lambda).\tag{8}$$

This solution may be substituted into Eq. (5) to give

$$\begin{aligned}x_{n+1} &= (1 - \varepsilon)f(x_n; \lambda) + \varepsilon(1 - \varepsilon)^n y_0 \\ &+ \varepsilon^2 \sum_{m=0}^{n-1} (1 - \varepsilon)^{n-m-1} f(x_m; \lambda).\end{aligned}\tag{9}$$

Naturally, this last expression is completely equivalent to the two-step process given in Eq. (7).

Before proceeding to the computer-aided iteration of the map, we shall make two analytic statements. The first concerns the existence of a single stable equilibrium. If we impose $y_{n+1} = y_n = y$ and $x_{n+1} = x_n = x$, it is clear from (6) that $y = f(x; \lambda)$. Substituting this into (5) immediately gives $x = y = f(x; \lambda)$. Thus, if an equilibrium exists, the active and refuge populations will be equal, and thus the effect of dispersal is irrelevant. The dynamics of the active population is unaffected by the refuge. A more subtle issue is the stability of this equilibrium. To make a detailed statement one must work with a given form of $f(x; \lambda)$. We shall just mention here that the presence of the refuge shifts the range of λ for which the equilibrium is stable, and in some cases can even change the nature of the instability from period doubling to a transition to quasi-periodicity (which will in turn give way to chaos as λ is further increased).

The second statement concerns the effect of very weak dispersal, i.e., $\varepsilon \ll 1$. The effect of weak dispersal on the active population is one of a weak perturbation, and indeed, we can see from Eq. (5) that for $\varepsilon \ll 1$,

$$x_{n+1} \approx f(x_n; \lambda).\tag{10}$$

However, the effect of weak dispersal on the refuge is a strong perturbation. We refer the reader to Eq. (8). For $\varepsilon \ll 1$, $(1 - \varepsilon)^N = \exp(-N \log(1 - \varepsilon)) \approx \exp(-N\varepsilon)$, where $N = n - m - 1$. For $N\varepsilon \ll 1$ this factor is approximately unity, while for $N\varepsilon \gg 1$ this factor is negligible. Thus, for large n , we can rewrite Eq. (8) as

$$y_n \approx \varepsilon \sum_{m:|n-m|\varepsilon < 1}^{n-1} f(x_m; \lambda).\tag{11}$$

So we are summing over $1/\varepsilon$ terms, and multiplying by ε , which essentially defines a time average. Making use of Eq. (10), we may rewrite Eq. (11) as

$$y_n \approx \langle x \rangle,\tag{12}$$

where the angular brackets indicate a time average. We expect this relation to become exact in the limit of $n \rightarrow \infty$ and $\varepsilon \rightarrow 0^+$.

This result is intuitively appealing. For weak dispersal the refuge is essentially sampling the active population, and thus for large times we would expect this sampling to lead to a refuge population which is a time average of the active population. This result is borne out by our computer experiments, reported in the following two sections.

3. DENSITY DEPENDENCE VIA THE LOGISTIC MAP

We now turn to numerical iteration of the model, as given in Eqs. (5) and (6). We shall report our results in the order in which our research progressed. The results of this section were obtained using the classical one-parameter logistic map (in which the population density is scaled to the maximum population size):

$$f(x; \lambda) = \lambda x(1 - x). \quad (13)$$

Our first investigations centered on plotting the bifurcation diagrams for the active and refuge population densities as the growth rate λ was increased, for a given value of the dispersal rate ε . This was repeated for various values of ε . Special care was taken to run the system for a long period before data were taken, to avoid including long-lived transient effects. For a very small dispersal rate of $\varepsilon = 0.0001$, the bifurcation diagram of the active site is hardly altered from its familiar form (Fig. 2a). The diagram for the refuge shows essentially a unique population density for a given value of λ (Fig. 2b), which is in accord with our result of the previous section; namely, that for small dispersal, the refuge will reflect the time average of the active population. We have confirmed this by plotting the time average of the active population, and it is practically indistinguishable from the refuge population.

For a dispersal rate of $\varepsilon = 0.1$, the range of λ over which stable dynamics exists is seen to increase, and the refuge now has a more complicated dynamics, with clearly visible period doublings and chaotic regions (Figs. 2c and d). Increasing the dispersal rate yields bifurcation diagrams for the active and refuge sites which become more and more alike, and which are identical at the symmetry point $\varepsilon = 1/2$ (in which case the bifurcation diagrams closely resemble the zero dispersal bifurcation diagram for the active site, but in which stable dynamics exist for the extended range $\lambda \in (0, 7)$).

For $\varepsilon > 1/2$ we see an abrupt change in behavior, with the period doublings disappearing. As the single equilibrium becomes unstable, the system adopts quasi-periodic behavior. This has been explicitly checked by studying trajectories. As λ is increased this quasi-periodicity gives way in turn to fully chaotic dynamics. A further increase in λ reverts the system to a 4-cycle, which then re-enters a chaotic regime via period doubling. Such transitions have previously been seen in studies of two coupled population oscillators (Vandermeer and Kaufmann, 1998). These features are especially

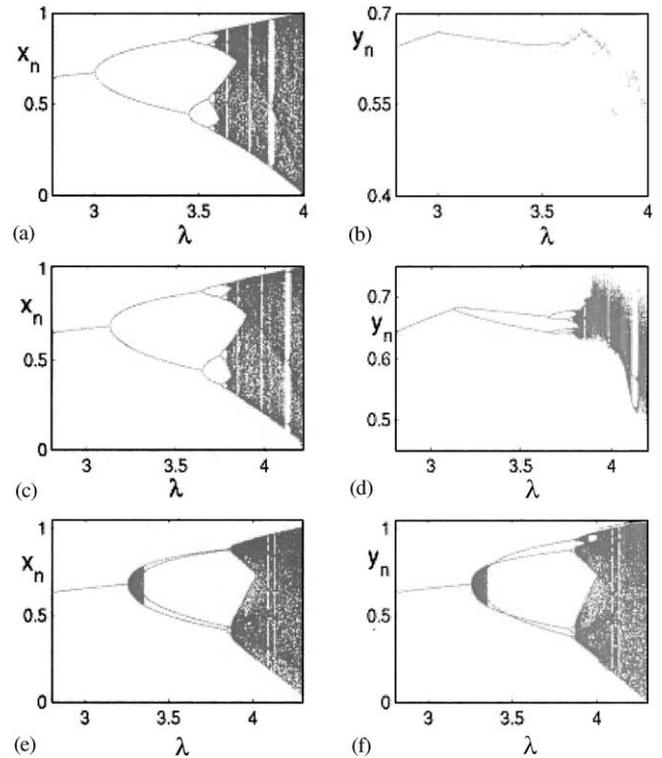


FIG. 2. Bifurcation diagrams for the active population x_n and the refuge population y_n using the logistic map; for $\varepsilon = 0.0001$ (a and b), $\varepsilon = 0.1$ (c and d), and $\varepsilon = 0.9$ (e and f).

apparent for a large value of the dispersal rate $\varepsilon = 0.9$ (Figs. 2e and f). Note how similar the diagrams are. For the largest possible dispersal rate $\varepsilon = 1$, where the populations of the active and refuge sites swap each time step, each site may be described by the pure ($\varepsilon = 0$) bifurcation diagram.

In the dynamics of the single-site logistic map, there is a finite range of λ over which the population remains bounded. In our units, this range is $\lambda \in (0, 4)$. Now that we have two parameters, we can expect that there is a region in the (λ, ε) plane, within which the populations remain bounded. We use as a criterion for bounded populations the condition that the active and refuge populations are non-negative. All of the above bifurcation diagrams were obtained with what we believed to be “generic” initial conditions $(x_0, y_0) = (0.8, 0.1)$. Using these initial conditions, we searched in the (λ, ε) plane for regions in which the populations are bounded. We found a single large region of this type, but with an extremely complicated boundary. Expanded pictures of different boundary regions show that these can be outlying peninsulas with presumably fractal features

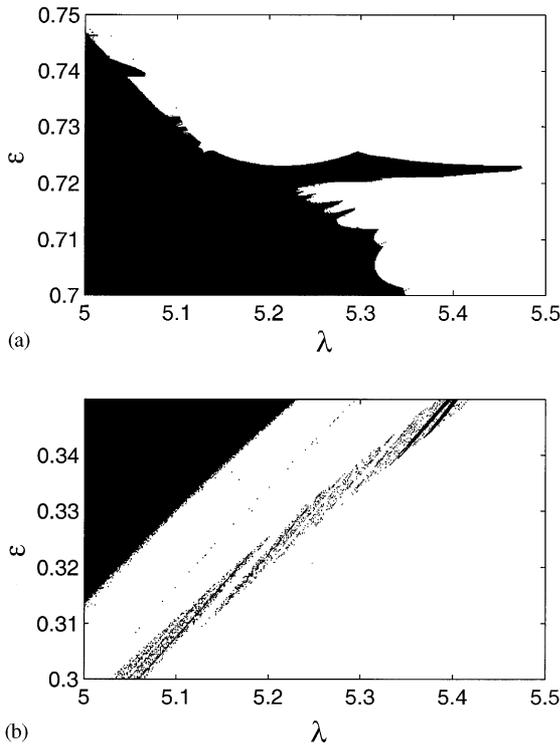


FIG. 3. Peninsulas (a) and barrier reef structures (b) in the boundary region between bounded dynamics (dark points) and unbounded dynamics (white points) in the (λ, ϵ) plane with initial conditions $(x_0, y_0) = (0.8, 0.1)$.

(Fig. 3a), or tiny disconnected islands forming a “barrier reef” structure (Fig. 3b).

Given the complexity of the region of bounded dynamics it seemed clear that we could expect these structures to change if we varied the initial conditions, and this is exactly what we found. There is in fact no “generic” initial condition for this system. We chose parameter values $(\lambda, \epsilon) = (5.3, 0.722)$ and $(5.2, 0.32)$ (which correspond to the peninsula and barrier reef structures, respectively), and looked for regions of bounded dynamics in the space of initial conditions. The results showed that these regions appear fractal (Figs. 4a and b).

For a given initial condition, and given values of (λ, ϵ) , it is simply not obvious *a priori* whether the map will lead to negative populations (and hence unbounded and unrealistic dynamics). For this reason we believe the logistic map is an inappropriate map for refuge dynamics. A reasonable model of refuge dynamics should have preferably an in-built mechanism disallowing negative population densities, or at the very least an easily determined range of parameters which lead to

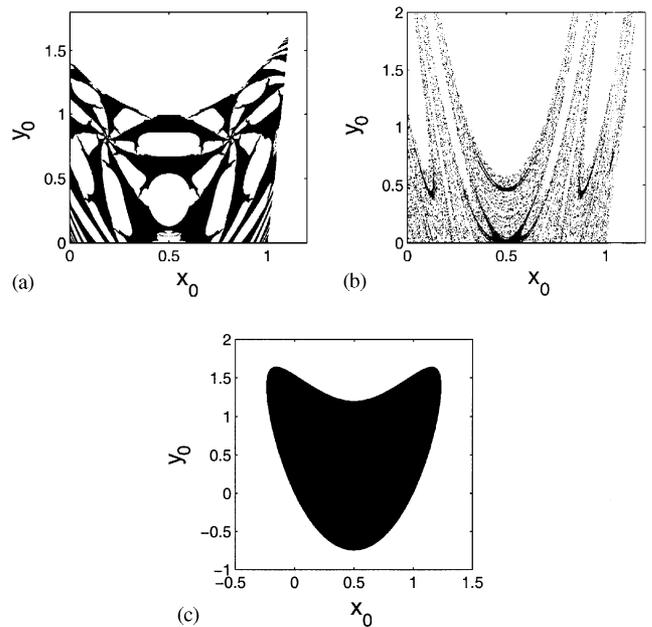


FIG. 4. Regions of bounded dynamics (dark points) in the space of initial conditions (x_0, y_0) for the parameter values (a) $(\lambda, \epsilon) = (5.3, 0.722)$ which lies near the peninsula in Fig. 3a and (b) $(\lambda, \epsilon) = (5.3, 0.32)$ which lies near the barrier reef in Fig. 3b. Panel 4(c) shows the region of bounded growth for the same parameter values as panel (a) but allowing negative population densities.

non-negative populations. The logistic map does not satisfy these basic requirements. On these grounds, one may question the use of logistic maps in more elaborate spatially explicit models, such as CML.

If we relax our requirement of bounded dynamics to demanding that the *absolute* values of the active and refuge populations remain finite, then the fractal basins become simple compact regions (Fig. 12). It is the biologically motivated imposition of non-negative population densities that generates the fractal basins.

4. DENSITY DEPENDENCE VIA THE EXPONENTIAL MAP

From our experience with the logistic map, we then chose a map which disallows negative populations. The natural choice was the exponential map, quite apart from the other compelling reason to use it; namely that it is commonly approximated in empirical observations

of density-dependent population regulation (Ricker, 1954; Wilbur, 1976).

We write this map in the form

$$f(x; \lambda) = \lambda x \exp(-x). \quad (14)$$

Note, for small x this map has the same form as the logistic map.

We first studied the bifurcation diagrams for a small value of the dispersal rate, $\varepsilon = 0.01$ (Figs. 5a and b). For intermediate values of λ we see chaotic dynamics, but for $\lambda > 65$ the chaos disappears, and the dynamics is cyclic. Note the strangely disconnected form of the bifurcation diagram (Fig. 5a). For this small value of ε , the refuge is essentially time averaging the active population. We note that the disconnected periodic

cycles seen for large values of λ are sensitive to the initial values of the population densities. However, the system is inherently stable for all values of the initial densities, in that the population number is always finite and positive.

For $\varepsilon = 0.04$ the dynamics of the active site still has a fairly substantial region of chaotic dynamics (Fig. 5c), whereas for $\varepsilon = 0.05$ the whole region gives way to 4- and 8-cycles (Fig. 5d). These clusters of stable cycles have been noted before, and the phenomenon is dubbed automonotonicity (Stone, 1993) or “period bubbling” (Vandermeer, 1997). For moderate values of the dispersal rate, $\varepsilon = 0.25$ and 0.5 , the dynamics are very simple (Figs. 5e and f). The transition from chaotic to cyclic behavior is very sharp (Figs. 5g and h). It is

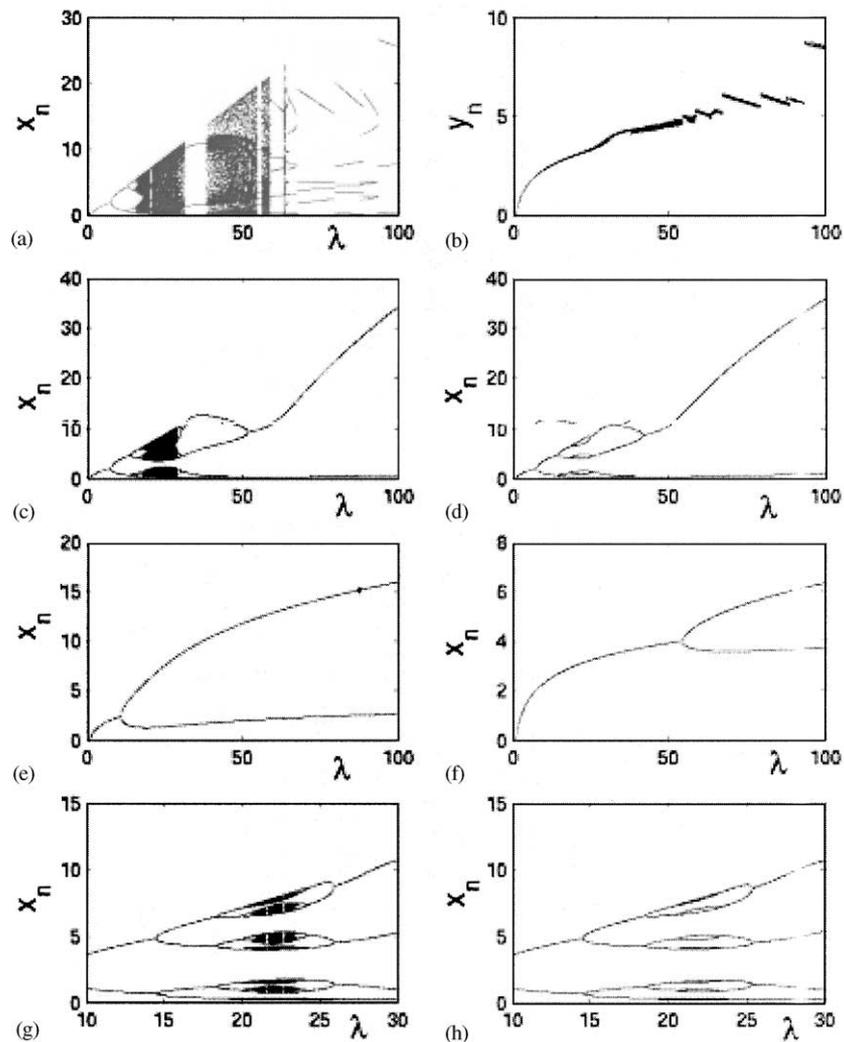


FIG. 5. Bifurcation diagrams for the active population x_n as a function of λ for the exponential map with $\varepsilon = 0.01$ (a), $\varepsilon = 0.04$ (c), $\varepsilon = 0.05$ (d), $\varepsilon = 0.25$ (e), $\varepsilon = 0.5$ (f), $\varepsilon = 0.048$ (g), and $\varepsilon = 0.049$ (h). (b) The bifurcation diagram for the refuge population y_n for $\varepsilon = 0.01$.

interesting that a modest dispersal rate of 0.05 is sufficient to remove the chaotic dynamics from this system.

5. CONCLUSIONS

We have introduced a model of an active population coupled to a refuge, as might be realized by a plant population coupled to a seed bank. We have exclusively considered symmetric dispersal rates between the two populations, and ignored attrition within the refuge. For static populations to exist, the populations of the active site and the refuge must be equal. We found that for small dispersal rate, and large times, the refuge population is static and represents a time average of the active population.

With density-dependent reproduction in the active population modeled using the logistic map, we found that the effect of dispersal led to many new features such as (i) a new route to chaos via quasi-periodic cycles, (ii) fractal boundaries between bounded and unbounded dynamics in the reproductive-rate/dispersal-rate parameter space, and (iii) fractal, and possibly riddled (Neubert, 1997), basins of attraction in the space of initial population densities. The latter, in particular, led us to seriously question the utility of the logistic map in the refuge model, since it is *a priori* unclear whether for a given choice of initial densities the dynamics will remain bounded.

Using an exponential map to model the density dependence, much of the complexity due to fractal basins and the like disappeared since this map leads to dynamics which are unconditionally stable. We found “period bubbling” for very small values of the dispersal rate, and the complete suppression of chaos for modest values of the dispersal rate (around $\varepsilon \approx 0.05$).

Our results show that the presence of a passive refuge can greatly stabilize a population that otherwise would exhibit chaotic dynamics. This effect is seen most markedly when the relationship between density and per capita reproductive success is negative exponential, rather than linear as in the classical logistic map, where negative population numbers are theoretically possible. The logistic map has also been criticized because empirical studies have shown that the majority of plants (Harper, 1977) and animals (Hassell, 1978) show non-linear density dependence of their reproductive rates.

Given the simplicity of our model, one should be careful in applying our results to real ecological

situations. However, there are a number of broad qualitative features emerging from our model which might be of relevance to real systems. First, we have seen that if the rate of dispersal between the active population and the refuge is weak, then no matter how chaotic or strongly fluctuating the dynamics in the active population, the refuge population will be static, being nothing more than a time average of the active population. This fact may play a significant role in the utility of a refuge. If a refuge is too strongly coupled to the active population, then a sustained period of stress in the active population would also drain the refuge. However, with weak dispersal, the refuge will be relatively robust over such periods, and the active population will be able to subsequently recover through immigration from the refuge.

Indeed, although the type of model we have presented largely plays a heuristic role in ecology, the “ease” with which a refuge can dampen chaotic dynamics in our model suggests that the process might be important in nature, and deserves further investigation. Many organisms are characterized by the presence of a refuge within which there is no reproduction. The most obvious examples are organisms with resting stages such as plants and their seeds, micro-crustaceans and their diapausing eggs, and many soil-transmitted pathogens. Another type of life cycle that is approximated by our theory is that characteristic of organisms with severe density dependence in the juvenile stage, but with a long-lived adult stage. Examples include many amphibians with “complex” life cycles (Wilbur, 1980).

It may be possible to infer the properties of the refuge by measurements of the active population dynamics. As we saw in Section 2, the dynamics of the model can be written purely in terms of the active population via the second-order difference equation (7). Thus, by observing the dynamics of the active population, and assuming a second-order map, one can in principle infer a value of the dispersal rate ε . If this is found to be small, one would infer the refuge population to be static, whereas if this parameter is found to be larger, then the refuge population dynamics would more closely mirror that of the active population. This may be useful in situations where one knows of the existence of the refuge, but where there is no way to empirically study its population.

Concerning future work, an important next step is to study the effect of asymmetric dispersal rates, and non-zero attrition. It is also interesting to construct a spatially explicit model of a seed bank in the depth dimension, by introducing a population density for each

soil stratum. This is equivalent to coupling an active site to a chain of passive sites, all of which are coupled via dispersal. One may then investigate the effect of the seed bank stratification on the dynamics of the active site, and, perhaps more interestingly, the depth dependence of the density profile within the seed bank. In such a model one may need to introduce the underlying continuous time t for the seed bank dynamics on grounds of realism.

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