PHYSICAL REVIEW E **69**, 021908 (2004)

Extinction in population dynamics

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(Received 25 July 2003; published 26 February 2004)

We study a generic reaction-diffusion model for single-species population dynamics that includes reproduction, death, and competition. The population is assumed to be confined in a refuge beyond which conditions are so harsh that they lead to certain extinction. Standard continuum mean field models in one dimension yield a critical refuge length L_c such that a population in a refuge larger than this is assured survival. Herein we extend the model to take into account the discreteness and finiteness of the population, which leads us to a stochastic description. We present a particular critical criterion for likely extinction, namely, that the standard deviation of the population be equal to the mean. According to this criterion, we find that while survival can no longer be guaranteed for any refuge size, for sufficiently weak competition one can make the refuge large enough (certainly larger than L_c) to cause extinction to be unlikely. However, beyond a certain value of the competition rate parameter it is no longer possible to escape a likelihood of extinction even in an infinite refuge. These unavoidable fluctuations therefore have a severe impact on refuge design issues.

DOI: 10.1103/PhysRevE.69.021908 PACS number(s): 87.23.Cc, 05.65.+b, 05.40.−a

I. INTRODUCTION

Population dynamics is a venerable and important subject that has been studied thoroughly for decades [1]. Understanding ecological systems is interesting in itself, as are applications of this understanding to a large variety of important practical problems such as, for example, the spread of a virus or other disease over a host population [2], and strategies for the elimination of pests or for the protection of endangered species [3]. These examples point to the importance of the study of the extinction of populations and of the conditions that lead to extinction as well as those that protect against it.

In this paper we deal with the particular issue of *extinction*. It is well documented, and a cause of serious ecological concern, that a large number of species become extinct each year, and the literature on this topic is vast. To arbitrarily pick a few examples, the Florida Fish and Wildlife Conservation Commission maintains the state list of 117 animals currently threatened with extinction. The Florida Department of Agriculture and Consumer Services maintains a similar list of 413 plants. Each state maintains such lists, as does the U.S. Fish and Wildlife Services [4]. In most of these cases, the fear of imminent extinction is intimately tied to the small number of extant individuals *and* to the fact that their habitats are increasingly confined to smaller areas due to industrialization and development. In other words, while large unexpected catastrophic events are at times responsible for the extinction of species (most every child is aware of some version of the dinosaur extinction story), far more serious are the almost daily extinctions caused by the inevitable fluctuations associated with small numbers in restricted habitats. Our goal in this work is to provide an *analytic* assessment of the effects of these inevitable fluctuations and of the feasibility (or not) of designing habitats that are sufficiently large to provide assurance against extinction. Our interest is not to provide specific numbers for particular species, nor even to pick the most realistic and complete description that would inevitably require numerical solution. Rather, we focus on a simplified yet generic model from which we can extract new information (and some rather unexpected results) *analytically*.

The oldest population models pose relatively simple rate equations for a total population, e.g., those of the logistic variety, and typically take basic events such as births and deaths into account through appropriate rate processes. A generic example is the logistic form [5,6]

$$\frac{dX}{dt}=\mu X-X^2, \tag{1}$$

where X is a measure of the size of a population and is therefore nonnegative. The parameter μ is the difference between birth and death rates of the population, and $X=0$, μ are its steady states. All that is required for survival is that $\mu>0$. This model has had enormous impact in the biological as well as the physico-chemical literature.

Fairly early on, the possible role of fluctuations in these models was recognized and included by way of additional fluctuating terms, often in a fairly ad hoc (but at times quite appropriate) manner. The sources of the fluctuations included in this way in the earliest models were associated with variations in the *external* environment in which the population evolves, and often appeared as a fluctuation in the parameters of the equations. For example, a fluctuating birth and/or death rate in the logistic form might lead to the description [5]

$$\frac{dX}{dt}=\mu X-X^2+\xi(t)X, \tag{2}$$

where $\xi(t)$ is a zero-centered Gaussian white noise. Other sources of externally driven stochasticity such as those arising from natural catastrophes and from changes in gene frequencies [7] have also been recognized.

We make a strong distinction between externally induced stochasticity caused by environmental and other factors whose origin has nothing to do with the numbers of individuals in the population (and are in this sense controllable externally), from fluctuations that arise from the fact that populations are finite and discrete. These *internal* fluctuations can decrease only if the population increases, but this can in turn only happen if the deterministic parameters of the system are changed. For example, for the logistic model (1) the nonzero steady state populations is $X=\mu$. Internal fluctuations are associated with the fact that μ is finite (see below), a fact that can not be changed unless one can change μ itself. The role of *internal* fluctuations arising from the fact that the populations are finite and discrete has of course also been recognized, and the associated stochastic contributions to the population equations have been obtained from an appropriate expansion of a master equation [6]. Writing the logistic equation in appropriately rescaled form, one would have with $Y=X/\mu$ and $\tau=\mu t$,

$$\frac{dY}{d\tau}=Y(1-Y)+\sigma\sqrt{Y(1-Y)}\xi(t). \tag{3}$$

The parameter σ is also determined by the rates that determine μ. Note that the fluctuations in Eqs. (2) and (3) are multiplicative, thus assuring that $X=0$ is an absorbing state. If this were not so (e.g., if there were additive fluctuations), a fluctuation would be able to create a population from nothing (and might even lead to negative populations), a case not envisioned in any of these discussions.

The per capita growth rate of the population according to the deterministic logistic model (1) is

$$\frac{1}{X}\frac{dX}{dt}=\mu-X, \tag{4}$$

which clearly decreases to zero as X approaches the steady state value μ but that has a maximum as $X\to 0$. A point that was observed early on in the biological ecology literature is that this latter behavior is not descriptive of real populations in many cases, and that in fact the per capita growth rate also tends to decrease when the population becomes very small [3,8,9]. Various possible mechanisms have been discussed for this in the literature, but many of them are based on the recognition that not only the total population but also its *density* may play a crucial role in population dynamics, particularly in questions related to extinction.

More recent population models have recognized the importance of describing not only the total populations but also its spatial distribution, thereby getting a handle on density-related issues. Perhaps the easiest way of dealing with a spatial distribution is by way of reaction-diffusion equations, and indeed such studies in the biological/ecological context have a long history [10–16]. Reaction-diffusion equations describe deterministic continuous densities. Therefore, whereas they do deal with some of the density-dependence issues of great importance in the assessment of extinction probabilities, they do not in general include the other feature discussed above that is also of great consequence in these problems, namely, the effect of fluctuations. These fluctuations can again arise from a variety of internal and external sources. As noted earlier, herein we address the problem of *internal* fluctuations.

Populations are composed of discrete numbers of individuals. That populations are not continuous is particularly relevant at low densities and at low total populations. The importance of these effects has been recognized and analyzed in various ways in recent years, most prominently in works that deal with a master equation description of the population instead of a reaction-diffusion model [17,18]. These master equations are typically solved numerically and provide important information on various measures for extinction. We take a different approach to the problem, our interest lying in an analytic formulation of the problem of internal fluctuations and their consequences. On the one hand, an analytic approach necessarily requires a more narrow focus on a particular question, and therefore requires some restriction as to the range of issues that we can address. On the other hand, analytic results may provide insights that are difficult to obtain in purely numerical work.

Our specific question arises from the following situation. Suppose that a population lives in a one-dimensional bounded refuge with favorable conditions for life, while outside of the refuge the conditions are extremely harsh. A question that has been considered prominently in the mathematical literature is that of the critical size L_c of such a refuge that will guarantee the survival of the population [11,15,16], that is, the critical size beyond which the extinction probability vanishes, $P_{ext}=0$. This problem, and many generalizations of it, have been solved, but to our knowledge existing analytic solutions are based on the assumption of a continuous population. We show that accounting for the discreteness and finiteness of the population profoundly modifies the known results and may reopen an array of questions for reconsideration.

Our starting point is a master equation to describe the following scenario. In a refuge of volume V we have a population composed of a single stream of individuals called A that diffuse with constant diffusion coefficient D on a d-dimensional lattice (later d is set to unity) with lattice spacing Δx. We further suppose that the individuals reproduce by fission ($A\to A+A$) with rate constant σ_1 (sexual reproduction complicates the equations without changing our basic conclusions), they die ($A\to\varnothing$) with rate coefficient σ_2, and they compete according to the reaction $A+A\to A$ with rate coefficient λ. We suppose that $\sigma_1>\sigma_2$, because otherwise the population eventually becomes extinct with certainty. We also assume that the nutrients are homogeneously distributed so that the coefficients do not depend on the lattice site. The microscopic description of the system within the refuge is given by the master equation

$$\begin{aligned}\frac{dP(\{n_i\};t)}{dt}=\sum_i\Bigg\{&\frac{D}{(\Delta x)^2}\sum_{\{m\}}[(n_m+1)P(\dots,n_i-1,\\&n_m+1,\dots;t)-n_iP(\dots,n_i,n_m,\dots;t)]\\&+\lambda[(n_i+1)n_iP(\dots,n_i+1,\dots;t)\end{aligned}$$

$$\begin{aligned} &-n_i(n_i-1)P(\ldots,n_i,\ldots;t)]\\ &+\sigma_1[(n_i-1)P(\ldots,n_i-1,\ldots;t)\\ &-n_iP(\ldots,n_i,\ldots;t)]\\ &+\sigma_2[(n_i+1)P(\ldots,n_i+1,\ldots;t)\\ &-n_iP(\ldots,n_i,\ldots;t)]\Big\}. \end{aligned} \tag{5}$$

Here the occupation number n_j is the number of individuals at site j and $\{n_j\}\equiv(\ldots,n_{j-1},n_j,n_{j+1},\ldots)$ is the set of all occupation numbers. The index i in the sum ranges over all lattice sites and $\{m\}$ denotes the set of nearest neighbors of i. We choose a homogeneous initial condition given by an uncorrelated Poisson distribution with average population $\mathfrak{n}$ at each site:

$$P(\{n_i\};0)=e^{-\mathfrak{n}}\prod_i \frac{\mathfrak{n}^{n_i}}{n_i!}. \tag{6}$$

Outside of the refuge living conditions are assumed to be extremely harsh, represented by the addition of the process $A\rightarrow\varnothing$ with a large rate coefficient γ. In the limit $\gamma\rightarrow\infty$ (certain death outside of the refuge), we can implement this contribution by requiring that $P(\{n_i\};t)$ vanish whenever $n_k \neq 0$, where k denotes any site just beyond the refuge boundary. Thus, "harshness" is implemented as a set of boundary conditions.

Although the formulation of the master equation is straightforward, its analytic solution does not appear possible, nor does the possibility of extracting analytic moments directly from the equation. Since our goal is an *analytic* assessment of the likelihood of extinction, we turn to other methods that offer this possibility. In Sec. II we discuss the derivation of a stochastic Langevin equation whose moments can be related to those of the fluctuating population described by the master equation. In Sec. III we present criteria for survival or extinction. In this section we discuss whether a refuge can be made sufficiently large to make extinction unlikely. A summary of our results and some directions for future research are presented in Sec. IV.

II. MODEL

A. Review of the traditional mean field model

It is well known that the continuum (mean field) description of the local concentration $\rho(\mathbf{r},t)$ is the Fisher-Kolmogorov-Petrovsky-Piscunov (FKPP) equation [19]

$$\frac{\partial\rho(\mathbf{r},t)}{\partial t}=D\nabla^2\rho(\mathbf{r},t)+(\sigma_1-\sigma_2)\rho(\mathbf{r},t)-\lambda\rho(\mathbf{r},t)^2, \tag{7}$$

which has been the phenomenological starting point in a huge number of problems in physics, chemistry, and biology. In one dimension and with the refuge extending inside the interval $[-L/2,L/2]$, the equation is to be solved subject to the boundary conditions

$$\rho\left(-\frac{L}{2},t\right)=\rho\left(\frac{L}{2},t\right)=0. \tag{8}$$

For small L the only solution to this problem as $t\rightarrow\infty$ is $\rho(x,t)\rightarrow 0$, that is, the population becomes extinct. There is a critical refuge size L_c beyond which extinction does not occur and the population will be nonzero (albeit small). Since $\rho(x,t)$ is small near L_c, to find this critical value it is appropriate to linearize Eq. (7) around zero population density and solve the simpler equation [15]

$$\frac{\partial\rho(x,t)}{\partial t}=D\frac{\partial^2\rho(x,t)}{\partial x^2}+(\sigma_1-\sigma_2)\rho(x,t), \tag{9}$$

subject to the boundary conditions (8). The Fourier decomposition of the solution is given by

$$\rho(x,t)=\sum_n a_n\rho_n(x,t),$$

$$\rho_n(x,t)=\exp\left[\left(\sigma-\frac{n^2\pi^2}{L^2}D\right)t\right]\sin\left[\frac{n\pi}{L}\left(x+\frac{L}{2}\right)\right], \tag{10}$$

where $\sigma=\sigma_1-\sigma_2$, $n=1,2,\ldots$, and the a_n depend on the initial condition. Thus, all Fourier modes decrease to zero in time if and only if $L<\pi\sqrt{D/\sigma}$, leading to the conclusion that for these values of L, $\rho_n(x,t)\rightarrow 0$ when $t\rightarrow\infty$ for any n. One can therefore conclude that the critical length of the refuge is

$$L_c=\pi\sqrt{\frac{D}{\sigma}}. \tag{11}$$

That is, the population becomes extinct with certainty if $L<L_c$ and it certainly does not become extinct if $L>L_c$ (in fact, the Fourier components grow without bound in this case, but the linearized equation is then no longer valid). This result, and extensions of it, have been known for more than fifty years [10], and has served as a background for the design and analysis of refuges. Note that the linearization argument that leads to Eq. (9) is valid for any nonlinearity that can be neglected near extinction in Eq. (7), and that therefore the resulting L_c is obtained not only for this specific model [15].

B. Inclusion of internal fluctuations

The above mean field analysis does not take into account the effect of the fluctuations associated with the fact that the population is really discrete and finite. To do this short of solving the full master equation (which seems impossible), one must formulate a generalization of the FKPP model that takes the resulting fluctuations into account. Such generalizations exist in the literature in other contexts. In particular, on the basis of a beautiful theory first proposed by Doi [20], further elucidated by Peliti [21], used for the study of critical phenomena associated with bulk transitions in reaction dynamics [22], explicitly applied to a reaction-diffusion front problem by Pechekin and Levine [23], and subsequently used in a number of other contexts related to Fisher waves (see, e.g., Ref. [24]), one arrives at a stochastic differential equation for a field whose moments can be related to those of the population in the original master equation. The connection comes about as follows. The master equation Eq. (5) can be projected onto a problem in quantum field theory by the construction of an adequate Fock space. Since this calculation has been performed many times in the literature we only indicate some of the main steps. A detailed review of the procedure can be found in Ref. [22].

Consider the following operator algebra:

$$[a_i, a_j^+] = \delta_{ij}, \quad [a_i, a_j] = 0, \quad [a_i^+, a_j^+] = 0, \tag{12}$$

where a_i, a_i^+ are destruction and creation operators and the square brackets denote the commutator [21]. A state vector can be defined as

$$|\psi(t)\rangle = \sum_{\{n_i\}} P(n_1, n_2, \dots; t) a_1^{+n_1} a_2^{+n_2} \dots |0\rangle, \tag{13}$$

where $P(n_1, n_2, \dots; t) = P(\{n_i\}, t)$ is the solution of the master equation, and the sum is performed over all possible configurations of the $\{n_i\}$. The state vector obeys the imaginary time Schrödinger equation

$$\frac{d|\psi(t)\rangle}{dt} = -\hat{H}|\psi(t)\rangle, \tag{14}$$

whose formal solution is

$$|\psi(t)\rangle = e^{-\hat{H}t}|\psi(0)\rangle. \tag{15}$$

In our case the (non-hermitian) Hamiltonian is

$$\hat{H} = \sum_i \Bigg[-\frac{D}{(\Delta x)^2} \sum_{\{m\}} a_i^+ (a_m - a_i) - \lambda (1 - a_i^+) a_i^+ a_i^2 + \sigma_1 [1 - a_i^+] a_i^+ a_i - \sigma_2 (1 - a_i^+) a_i \Bigg]. \tag{16}$$

Note that we recover Eq. (5) by substituting Eqs. (13) and (16) into Eq. (14).

One introduces the Glauber state as the projection state

$$\langle S| = \langle 0| \prod_i^N e^{a_i}. \tag{17}$$

The expected values of observables $A(\{n_i\})$ can then be written as

$$\langle A(t)\rangle = \sum_{\{n_i\}} A(\{n_i\}) P(\{n_i\}; t) = \langle S|\hat{A} e^{-\hat{H}t}|\psi(0)\rangle, \tag{18}$$

where $\hat{A}$ is the operator obtained by replacing every n_i in the function $A(\{n_i\})$ by the number operator $\hat{n}_i = a_i^+ a_i$.

The steps that we do not repeat [22,23] show that this second-quantized theory can be expressed in terms of a path integral. Furthermore, from this path integral one can derive a "classical" action from which one can in turn derive the mean field continuum equation Eq. (7). If one concentrates on the path integral itself instead of moving on to the classical action, one can show an equivalence between the master equation and the following Langevin equation [22,23]:

$$\frac{\partial \psi(\boldsymbol{r},t)}{\partial t} = D\nabla^2 \psi(\boldsymbol{r},t) + (\sigma_1 - \sigma_2)\psi(\boldsymbol{r},t) - \lambda \psi^2(\boldsymbol{r},t) + \sqrt{2[\sigma_1 \psi(\boldsymbol{r},t) - \lambda \psi^2(\boldsymbol{r},t)]}\,\xi(\boldsymbol{r},t), \tag{19}$$

where $\xi(\boldsymbol{r},t)$ is Gaussian white noise with mean and correlation given by [25]:

$$\langle \xi(\boldsymbol{r},t)\rangle = 0, \tag{20}$$

$$\langle \xi(\boldsymbol{r},t)\xi(\boldsymbol{r}',t')\rangle = \delta(t-t')\delta(\boldsymbol{r}-\boldsymbol{r}'). \tag{21}$$

The multiplicative noise in Eq. (19) *must* be interpreted according to Itô. A number of crucial points must be stressed here.

(1) The field $\psi(\boldsymbol{r},t)$ is *not* the population. In fact, by itself it is not a physical quantity in this problem. Only its *moments* are related (exactly) to those of the population (see below).

(2) Because $\psi(\boldsymbol{r},t)$ is not a population, the fact that the noise in Eq. (19) can be imaginary and the value of ψ in general complex is not a difficulty. Indeed, these features simply emerge as a consequence of the exact mathematical correspondence between moments of ψ and of the population ρ and have not been introduced extraneously.

(3) The fluctuations $\xi(\boldsymbol{r},t)$ are multiplicative, Gaussian, and δ correlated, a result that emerges from the derivation (i.e., it is already inherent in the master equation) and is in no way an additional ad hoc assumption. Any modification of these fluctuations, even their interpretation, would amount to a modification of the original master equation and would therefore have to be handled with great caution.

The field ψ is the complex eigenvalue of the destruction operator, so one can relate its moments to the moments of the population density using the commutation relations Eq. (12) and the property of the Glauber state $\langle S|a^+ = \langle S|$. For the first two moments we have

$$\begin{aligned} \langle \rho(\boldsymbol{r},t)\rangle &= \langle n_i\rangle = \langle a_i^+ a_i\rangle = \langle S|a_i^+ a_i|\psi(t)\rangle \\ &= \langle S|a_i|\psi(t)\rangle = \langle a_i\rangle = \langle \psi(\boldsymbol{r},t)\rangle, \\ \langle \rho^2(\boldsymbol{r},t)\rangle &= \langle n_i n_i\rangle = \langle a_i^+ a_i a_i^+ a_i\rangle = \langle a_i^+ a_i^+ a_i a_i + a_i^+ a_i\rangle \\ &= \langle S|a_i^{+2} a_i^2 + a_i^+ a_i|\psi(t)\rangle \\ &= \langle S|a_i^2|\psi(t)\rangle + \langle S|a_i|\psi(t)\rangle \\ &= \langle a_i^2\rangle + \langle a_i\rangle = \langle \psi^2(\boldsymbol{r},t)\rangle + \langle \psi(\boldsymbol{r},t)\rangle. \end{aligned} \tag{22}$$

Higher moments can also be calculated following this procedure. Here the lattice site i is associated with the volume

$(\Delta x)^d$ around point $\boldsymbol{r}$ and we have set $\Delta x \equiv 1$ for economy of notation. These exact moment relations are the crucial mathematical connection that makes analytic conclusions possible.

As a side note we point out that the so-called stochastic FKPP equation of the form

$$\frac{\partial \rho(x,t)}{\partial t} = D\frac{\partial^2 \rho(x,t)}{\partial x^2} + \sigma_1 \rho(x,t) - \lambda \rho^2(x,t) + \sqrt{2[\sigma_1 \rho(x,t) - \lambda \rho^2(x,t)]}\xi(x,t) \tag{23}$$

cannot represent the population density either since it does not allow fluctuations around the equilibrium population density $\rho = \sigma_1/\lambda$ because the population is real, while these fluctuations do not vanish in the original discrete system. However, a connection between Eq. (23) and the original master equation Eq. (5) without the death process has recently been elaborated [6]. This connection is different from the one presented above involving the stochastic equation (19).

III. EXTINCTION PROBABILITY

A. Finite extinction probability

The mean field model for the refuge population predicts certain extinction if the refuge size $L < L_c$ and certain survival if $L > L_c$. In this section we show that the fluctuations destroy this certainty of survival, that is, that survival is in fact never guaranteed.

In the biological literature one encounters the concept of a *minimum viable population* [7,17]. There are some variations in its definition, but one that seems to be widely accepted is that a minimum viable population is the smallest isolated population having a 99% chance of remaining extant for 1000 years despite the presence of foreseeable fluctuations. Clearly one can vary the two numbers that appear in this criterion, and one certainly must for the myriad species that are currently near extinction, but, in any case, it involves a *probability of survival* in a *finite period of time*. We wish to make clear at the outset that our analytic theory is not yet developed to the point of being able to handle finite times, and we are therefore not able to implement a criterion of this sort. Instead, the theory (like the mean field prediction stated above) deals only with steady state probabilities.

That extinction is certain for $L < L_c$ is most easily shown (as is done below) by starting with the system *near* extinction and exploring the conditions that lead from there to certain extinction. First, though, one might question whether the population achieves a "near-extinction" state in a finite time. This is easily answered in the affirmative by noting that the population in the absence of competition is never lower than the population in the presence of competition, that is, that the model with $\lambda = 0$ leads to a solution that is an upper bound to our problem. In the absence of competition the contributions $\lambda \psi^2$ in the stochastic equation (19) are absent, and the description reduces to the simpler Langevin equation

$$\frac{\partial \psi(x,t)}{\partial t} = D\nabla^2 \psi(x,t) + \sigma \psi(x,t) + \sqrt{2\sigma_1 \psi(x,t)}\xi(x,t). \tag{24}$$

The mean value of ψ obeys the equation

$$\frac{\partial \langle \psi(x,t)\rangle}{\partial t} = D\frac{\partial^2 \langle \psi(x,t)\rangle}{\partial x^2} + \sigma \langle \psi(x,t)\rangle, \tag{25}$$

which is the same equation [Eq. (9)] that we solved for the deterministic case. Since $\langle \psi(x,t)\rangle = \langle \rho(x,t)\rangle$, we have the same boundary conditions as in Eq. (9). Solution (10) is a sum of exponentials that all decay when $L < L_c$, and so the population is smaller than any finite designated value at a finite time. Again, this is an upper bound for the solution in the presence of competition, so it is indeed appropriate to deal with the system near extinction since we know that such a state will be reached in a finite time.

Near extinction one can show directly from the master equation (5) that the competition term (the term proportional to λ) can be neglected. As a result, in this limit the contributions $\lambda \psi^2$ in the stochastic equation (19) can be neglected, and to find the critical refuge size one again only needs to deal with the simpler Langevin equation (24) and the associated mean value equation (25). We can thus immediately conclude that for $L < L_c$ the mean value of the population density is zero, that is, that extinction is certain. Since $\langle \psi(x,t)\rangle = \langle \rho(x,t)\rangle > 0$ for $L > L_c$, this in turn implies that extinction is certain if and only if $L < L_c$. This, however, does not tell us whether or not the extinction probability is zero for $L > L_c$ (as predicted in mean field theory). Indeed, we now show that *the extinction probability is greater than zero for any finite length of the refuge*.

It is fairly obvious that P_{ext} does not vanish if one has a finite population and thus a nonzero probability (albeit perhaps small) of a total extinction event. We will place this statement on a more formal footing. However, an arbitrarily small extinction probability is not necessarily very important since in most design problems one deals with at least some uncertainties. It is therefore useful to establish a criterion as to what constitutes a non-negligible extinction probability and what the minimal size L^* of the refuge must be to insure a probability smaller than this. Clearly, $L^* \geqslant L_c$. We will establish such a criterion and show that (depending on parameter values) the size L^* may be much larger than L_c and even infinite.

First, to establish the obvious fact that fluctuations lead to a nonzero extinction probability even for $L > L_c$, let us suppose that we begin with an infinite refuge and exclude death events $A \to \emptyset$ altogether. The population inside an interval of length L of this infinite refuge is then greater than or equal to the population inside our actual finite refuge of length L. The population density inside the finite interval of the infinite refuge in the steady state is given by the Poisson distribution

$$P(\{n_i\}) = e^{-2\sigma_1/\lambda} \prod_i \frac{(2\sigma_1/\lambda)^{n_i}}{n_i!}, \tag{26}$$

so that the probability of an unbounded realization of the process is zero. Since the integral of a bounded function over a bounded interval is bounded, we can conclude that the total population inside the interval is finite. Therefore so is the total population inside the finite refuge. Furthermore, with δ-correlated Gaussian fluctuations [26,27] any fluctuation occurs in a *finite* mean time, and therefore a fluctuation (even if rare) caused by the reaction $A \to \varnothing$ could kill the entire population in a finite time. We thus conclude that the probability of extinction is greater than zero whenever $L < \infty$. In the case of an unbounded refuge the mean value of the population density is σ/λ and is homogeneously distributed, so a local fluctuation cannot kill the population. We can summarize these conclusions as follows:

$$\begin{aligned} P_{ext} &= 1 \quad \text{if} \quad L < L_c, \\ 0 < P_{ext} &< 1 \quad \text{if} \quad L_c < L < \infty, \\ P_{ext} &\to 0 \quad \text{when} \quad L \to \infty. \end{aligned} \tag{27}$$

We can furthermore state that since the number of individuals in the population increases as the length of the refuge increases, the probability of extinction decreases monotonically and continuously as L increases continuously. Thus, consideration of the internal fluctuations drastically changes the picture; *now there is no finite size of the refuge that can be considered absolutely safe for the population*. However, we have not been able to derive the explicit functional dependence of P_{ext} on the size of the refuge.

B. An alternative criterion for extinction

As an alternative to such an explicit full solution, we propose a criterion for deciding when a population is under substantial risk of extinction, and calculate the critical size L^* of the refuge associated with this criterion. Suppose that a population density $\rho(x)$ in a refuge of length L described according to the mean field equation (7) has a maximum steady state density $M > 0$. Clearly, $L \geqslant L_c$. The maximum occurs at $x=0$, in the middle of the refuge, that is, $\rho(x=0)=M$ [15,28]. Now consider the description of this population that includes the fluctuations, and compare the average population density $\langle \psi(x) \rangle = \langle \rho(x) \rangle$ with the deterministic result $\rho(x)$. This average distribution also has a maximum at $x=0$ (see below), $\langle \psi(x=0) \rangle = M'$. We define the critical size L^* as the refuge length associated with two conditions: (1) the deterministic and stochastically obtained maxima are equal, $M = M'$; and (2) the standard deviation of the stochastic population density is equal to its mean at each x. Clearly, our idea is that a population density whose standard deviation everywhere equals its mean is in danger of extinction, and we call this a "critical population." It is not clear *a priori* that these conditions can be simultaneously satisfied, but in fact it turns out that they can. The second condition above says that for the critical population

$$\langle \rho(x,t) \rangle^2 = \langle \rho^2(x,t) \rangle - \langle \rho(x,t) \rangle^2, \tag{28}$$

or, equivalently, in terms of the field ψ, one for which

$$\langle \psi(x,t) \rangle^2 = \langle \psi^2(x,t) \rangle + \langle \psi(x,t) \rangle - \langle \psi(x,t) \rangle^2. \tag{29}$$

From Eq. (19) we obtain the following equation linking the first and second moments of ψ:

$$\frac{\partial \langle \psi(x,t) \rangle}{\partial t} = D \nabla^2 \langle \psi(x,t) \rangle + \sigma \langle \psi(x,t) \rangle - \lambda \langle \psi^2(x,t) \rangle. \tag{30}$$

Inserting Eq. (29) for the critical field then results in a closed equation for the first moment:

$$\begin{aligned} \frac{\partial \langle \psi(x,t) \rangle}{\partial t} = {} & D \nabla^2 \langle \psi(x,t) \rangle + (\sigma + \lambda) \langle \psi(x,t) \rangle \\ & - 2\lambda \langle \psi(x,t) \rangle^2. \end{aligned} \tag{31}$$

Note that the apparent irrelevance of the fluctuations in Eq. (19) other than their mean value in arriving at Eq. (31) is illusory since the relation (22) and consequently Eq. (29) are intimately connected to the precise form of the fluctuations.

In the steady state Eq. (31) reduces to a classic boundary value problem

$$D \frac{d^2 \langle \psi(x) \rangle}{dx^2} + (\sigma + \lambda) \langle \psi(x) \rangle - 2\lambda \langle \psi(x) \rangle^2 = 0, \tag{32}$$

with boundary conditions as in Eq. (9). To find L^* we multiply Eq. (32) by $d\langle \psi(x) \rangle / dx$ and rewrite the result as

$$\frac{d}{dx} \left[\frac{D}{2} \left(\frac{d \langle \psi(x) \rangle}{dx} \right)^2 + \frac{(\sigma + \lambda)}{2} \langle \psi(x) \rangle^2 - \frac{2\lambda}{3} \langle \psi(x) \rangle^3 \right] = 0, \tag{33}$$

from which it follows that

$$\frac{D}{2} \left(\frac{d \langle \psi(x) \rangle}{dx} \right)^2 + \frac{(\sigma + \lambda)}{2} \langle \psi(x) \rangle^2 - \frac{2\lambda}{3} \langle \psi(x) \rangle^3 = \text{const}. \tag{34}$$

Symmetry considerations show that the solution of this problem has only one maximum at $x=0$ [28], and since the first derivative of the solution should vanish at any maximum, we can explicitly write the constant as

$$\begin{aligned} & \frac{D}{2} \left(\frac{d \langle \psi(x) \rangle}{dx} \right)^2 + \frac{(\sigma + \lambda)}{2} \langle \psi(x) \rangle^2 - \frac{2\lambda}{3} \langle \psi(x) \rangle^3 \\ & \quad = \frac{(\sigma + \lambda)}{2} M^2 - \frac{2\lambda}{3} M^3, \end{aligned} \tag{35}$$

where M is the maximum introduced earlier. Since this maximum occurs at $x=0$, we can integrate Eq. (35) for $x>0$ to obtain

$$\begin{aligned} & x \\ & = \sqrt{\frac{D}{2}} \int_{\langle \psi(x) \rangle}^{M} \frac{dz}{\sqrt{\frac{(\sigma + \lambda)}{2} M^2 - \frac{2\lambda}{3} M^3 - \frac{(\sigma + \lambda)}{2} z^2 + \frac{2\lambda}{3} z^3}}. \end{aligned} \tag{36}$$

Taking into account that the population vanishes at the edge of the refuge we can obtain the value of the length L of the refuge as a function of the maximum of the average population density:

$$L=\sqrt{2D}\int_0^M \frac{dz}{\sqrt{\frac{(\sigma+\lambda)}{2}M^2-\frac{2\lambda}{3}M^3-\frac{(\sigma+\lambda)}{2}z^2+\frac{2\lambda}{3}z^3}}. \tag{37}$$

With the change of variables $w=z/M$ and setting $\varepsilon\equiv\lambda/\sigma$ we can rewrite this relation as

$$\sqrt{\frac{\sigma}{D}}L=2\sqrt{\frac{1}{1+\varepsilon}}\int_0^1 \frac{dw}{\sqrt{1-w^2-\frac{4}{3}\frac{\varepsilon}{(1+\varepsilon)}(1-w^3)M}}. \tag{38}$$

The steady state deterministic equation obtained by setting the left hand side of Eq. (7) equal to zero is formally identical to the critical field equation Eq. (32) with modified parameters. Since we are choosing L^* as the value where the maximum of the critical average population density is equal to the maximum of the mean field population density, the mean field model provides us with a second relation between M and L:

$$\sqrt{\frac{\sigma}{D}}L=2\sqrt{\frac{1}{\varepsilon}}\int_0^1 \frac{dw}{\sqrt{1-w^2-\frac{2}{3}\varepsilon(1-w^3)M}}. \tag{39}$$

The simultaneous solution of Eqs. (38) and (39) then leads to the value of L^* (and incidentally also of M).

The two equations reduce to the same equation if $\lambda=0$ ($\varepsilon=0$), and in this case $L^*=L_c$ and M diverges. The reason for the equality is that when the nonlinearity is not present, the total steady state population is unbounded (thermodynamic limit) and there are no fluctuations. In general, the two simultaneous equations can only be solved numerically, and the results are shown in Fig. 1.

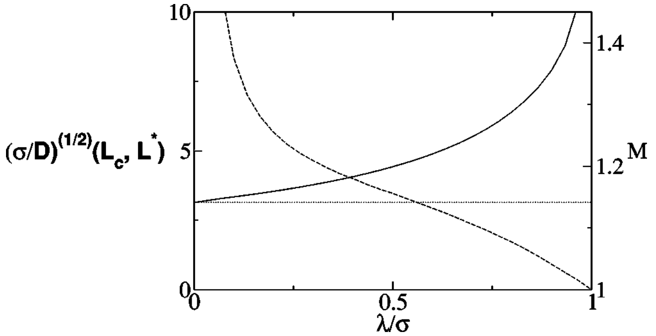

FIG. 1. Left scale: $\sqrt{\sigma/D}L_c$ (dotted line) and $\sqrt{\sigma/D}L^*$ (solid line) vs λ/σ. Note that $\sqrt{\sigma/D}L_c=\pi$ for all values of λ/σ, while L^* grows monotonically up to $\lambda/\sigma=1$, where it diverges logarithmically. Also note that $L_c=L^*$ when $\lambda=0$, and that this is the only common point of the lengths. Right scale and dashed curve: maximum M of the average population density as defined in the text vs λ/σ.

A number of important points should be noted about our results. First, L^* is indeed greater than L_c except for the single trivially coincident point when $\lambda=0$, that is, when there is no competition. Thus, according to our criterion whereby the risk of extinction is substantial when the mean and standard deviation of the population density are equal, one must increase the size of the refuge considerably beyond the deterministic refuge size to avoid this risk. Indeed, when $\lambda/\sigma=1$ the size L^* diverges logarithmically and the population density becomes uniform at density σ/λ. As λ grows beyond σ it is no longer possible to avoid considerable risk of extinction for any finite size of the refuge. The increase in M with decreasing L^* can be understood by moving from right to left in the figure: decreasing critical refuge size is associated with the requirement of a larger population (and hence a larger maximum population density) to insure against extinction. At L_c the maximum M diverges because no population, no matter how large, can be protected against extinction below this length. We can obtain an analytic expression for L^* for small values of λ/σ:

$$\sqrt{\frac{\sigma}{D}}L^*=\pi\left[1+\frac{\lambda}{2\sigma}+o\left(\left(\frac{\lambda}{\sigma}\right)^2\right)\right]. \tag{40}$$

We can also see analytically that L^* must diverge when $\lambda/\sigma=1$: at this point the two integrals for L can only be equal if they both vanish (which they do not) or if they both diverge (which they do when $M=1$).

IV. CONCLUSIONS

The main point of this paper has been to assess the effects of internal fluctuations inevitably associated with finite discrete populations on the prediction of the risk of extinction of a population in a refuge as a function of the size of the refuge. In the usual mean field deterministic model in one dimension, the population is treated as a continuum and one obtains a critical refuge length L_c such that the population becomes extinct with certainty if the length of the refuge is below this critical value, $L<L_c$, whereas survival is certain if $L>L_c$. It is well known that, as predicted by the mean field approach, the smaller the area occupied by a population, the lower are its chances for survival [29]. However, it is also known that a small size or low density of a population may also increase its chances of extinction, a feature that mean field theories do not capture [3]. Our approach deals with both of these features simultaneously through the interplay of discreteness and nonlinearity in a spatially distributed model. We have argued that the discreteness of the population and its finite size make fluctuations unavoidable, and have shown that whereas $L<L_c$ still guarantees extinction, $L>L_c$ by no means guarantees survival. While we have not been able to find an analytic expression for the survival probability as a function of L, we have focused on a sensible risk criterion for which we have found explicit results up to quadrature. Comparing deterministic and average stochastic population densities with a given maximum M, we have chosen to define a new critical length L^* as one for which the mean of the population density and its standard deviation are equal, reasoning that this variability implies considerable susceptibility of the population to extinction. We have shown that $L^* \geqslant L_c$ and, most importantly, that L^* diverges when the competition rate coefficient grows beyond that of the net growth rate of the population. For some parameter values it is possible to protect (albeit not with certainty) a population from extinction by placing it in a sufficiently large refuge, one that is certainly larger than that predicted by the standard mean field model. For other parameter values (in particular, when competition is too strong), it is not possible to evade the risk of extinction (at least according to our criterion) by enlarging the size of the refuge. Clearly, these results have serious implications for the expectations in the design of refuges.

Real physical refuges are not one dimensional, and so one might question the applicability of our results to them. This is an issue that has been addressed broadly in the literature (see, e.g., the discussion in Ref. [15]) because so many mathematical models are one-dimensional. The criteria (27) certainly hold for two and three dimensions as well, with a finite critical volume V_c that depends on geometry. If only one dimension of a refuge is small, e.g., a very long strip of land of width L, then our analysis holds exactly as presented with the extinction criterion applicable to the width. The critical radius R_c has been explicitly evaluated in terms of Bessel functions for a circular geometry [10]. If a refuge is finite in two directions or even three, e.g., a rectangular or circular or oval geometry, the detailed curves in Fig. 1 will be different, but it will still be the case that (1) the fluctuations lead to the requirement of a larger refuge than predicted by mean field theory, and (2) the critical refuge size (be it the side L of a square or a cubic refuge, or the radius R of a circular or spherical one, or even an appropriate length measure of a more complicated shape) still diverges when $\lambda/\sigma = 1$. This latter divergence can easily be shown from the equations in this paper.

Many questions still remain to be answered. For instance, an exact result for the extinction probability would clarify many issues. So would the ability to obtain time dependent solutions so as to deal with a more realistic criterion of survival over a long but finite time interval. Also, we have only considered the simplest most generic situation, whereas real systems (particularly ones not designed in the laboratory) are likely to be seriously affected by many complicating factors. Examples include the presence of convection, different boundary conditions, and spatial inhomogeneities inside the refuge. Similar questions can and should be posed when multiple species are present. In any case, in light of our results it would seem prudent to reconsider other critical size population problems to assess the effects of discreteness. As we have shown in the simple model considered here, the consequences can indeed be profound.

ACKNOWLEDGMENTS

The authors gratefully acknowledge input from J. L. Cardy. C.E. is grateful to the Department of Chemistry and Biochemistry of the University of California, San Diego for its hospitality. This work has been partially supported by the Engineering Research Program of the Office of Basic Energy Sciences at the U. S. Department of Energy under Grant No. DE-FG03-86ER13606, by a grant from the *New Del Amo Program* (U.C.M.), by the Ministerio de Educación y Cultura (Spain) through Grant Nos. AP2001-2598 and EX2001-02880680, and by the Ministerio de Ciencia y Tecnología (Spain), Project No. BFM2001-0291.

[1] J.D. Murray, *Mathematical Biology*, 2nd ed. (Springer, New York, 1993).
[2] G. Abramson and V.M. Kenkre, Phys. Rev. E **66**, 011912 (2002).
[3] F. Courchamp, T. Clutton-Brock, and B. Grenfell, Trends Ecol. Evaol. **14**, 405 (1999).
[4] http://edis.ifas.ufl.edu/BODY_CR006.
[5] W. Horsthemke and R. Lefever, *Noise-Induced Transitions: Theory and Applications in Physics, Chemistry, and Biology* (Springer-Verlag, Berlin, 1984).
[6] C.R. Doering, C. Mueller, and P. Smereka, Physica A **325**, 243 (2003), and references therein; and in *Unsolved Problems of Noise and Fluctuations: UPoN 2002*, edited by S. M. Bezrukov, AIP Conf. Proc. No. 665 (AIP, New York, 2003), p. 223.
[7] M.L. Shaffer, BioScience **31**, 131 (1981).
[8] W.C. Allee *et al.*, *Principles of Animal Ecology* (Saunders, Philadelphia, 1949).
[9] P.E. Odum, *Fundamentals of Ecology* (Saunders, Philadelphia, 1959).
[10] J.G. Skellam, Biometrika **38**, 196 (1951).
[11] N.F. Briton, *Reaction-Diffusion Equations and Their Applications to Biology* (Academic Press, New York, 1986).
[12] R.S. Cantrell and C. Cosner, J. Math. Biol. **29**, 315 (1991).
[13] O. Diekmann and N.M. Temme, *Nonlinear Diffusion Problems* (Mathematisch Centrum, Amsterdam, 1976).
[14] P.C. Fife, *Mathematical Aspects of Reacting and Diffusing Systems*, Lecture Notes in Biomathematics Vol. 28 (Springer-Verlag, New York, 1979).
[15] D. Ludwig, D.G. Aronson, and H.F. Weinberger, J. Math. Biol. **8**, 217 (1979).
[16] A. Okubo, *Diffusion and Ecological Problems: Mathematical Models*, Biomathematics Vol. 10 (Springer-Verlag, Berlin, 1980).
[17] K. Sznajd-Weron, Eur. Phys. J. B **16**, 183 (2000).
[18] K. Sznajd-Weron and M. Wolański, Eur. Phys. J. B **25**, 253 (2002).
[19] R.A. Fisher, Ann. Eugenics **7**, 355 (1936); A. Kolmogorov, I. Petrovsky, and N. Piscunov, Mosc. Univ. Bull. Math. A **1**, 1 (1937).

[20] M. Doi, J. Phys. A **9**, 1479 (1976).
[21] L. Peliti, J. Phys. (Paris) **46**, 1469 (1985).
[22] J.L. Cardy and U.C. Täuber, J. Stat. Phys. **90**, 1 (1998), and references therein.
[23] L. Pechenik and H. Levine, Phys. Rev. E **59**, 3893 (1999).
[24] E. Moro, Phys. Rev. Lett. **87**, 238303 (2001).
[25] The effects of some correlated initial conditions are discussed in J. Cardy and P-A. Rey, J. Phys. A **32**, 1585 (1999).
[26] H. Risken, *The Fokker-Planck Equation: Methods of Solution and Applications* (Springer-Verlag, Berlin, 1984).
[27] K. Lindenberg and V. Seshadri, J. Chem. Phys. **71**, 4075 (1979); K. Lindenberg and B.J. West, J. Stat. Phys. **42**, 201 (1986).
[28] B. Gidas, W.M. Ni, and L. Nirenberg, Commun. Math. Phys. **68**, 200 (1979).
[29] R.H. MacArthur and E.O. Wilson, *The Theory of Island Biogeography* (Princeton University Press, Princeton, NJ, 1967).