PHYSICAL REVIEW E VOLUME 62, NUMBER 3 SEPTEMBER 2000

Random population dispersal in a linear hostile environment

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(Received 22 March 2000)

We consider the Fisher equation and its generalization for an asocial population in a linear, hostile environment. The method of center manifold analysis is used to obtain the time-dependent solution of the former, nonlinear equation. The correct critical habitat size is obtained; in addition, the result for the steady state central density compares favorably with the exact result for relatively large population sizes (up to one half of the carrying capacity). For a model of asocial growth we obtain the expanded criteria for survival. This includes the habitat size, the population size at which positive growth begins, and also the minimum initial central density.

PACS number(s): 87.23.Cc, 02.30.Jr

I. INTRODUCTION

The Fisher equation [1] describing gene flow in a linear population and generalizations of this equation by Kolmogorov *et al.* [2] and others [3] have been extensively studied and applied to a wide variety of problems in different areas [4]. A primary focus of that work has been on the existence and stability of traveling wave solutions in an unbounded, one-dimensional domain [1–4]. This equation and some generalizations of it have been used to study population growth and dispersal, particularly to determine the minimum habitat size (critical size) required for survival when the surroundings are hostile [5,6]. Only the steady state solutions are required to determine the critical size, and for the Fisher equation, an exact implicit solution in terms of elliptic integrals, invertible to give an explicit solution in terms of a Jacobian elliptic function, was found by Skellam [5]. The description of the evolution to the steady state, and an estimate of the time required for an initial population distribution to reach this state, is a much more difficult problem. For the Fisher equation, approximate solutions based on *ad hoc* methods were found by Barakat [7] and Landhal [8].

The purpose of this paper is to present a systematic method for solving the time-dependent Fisher equation as well as some of the generalizations of this equation of interest. We consider the former equation as a benchmark example for the proposed method. This will serve the didactic function of providing a self-consistent theoretical framework that leads to a more rigorous and more generally applicable treatment than the previous *ad hoc* studies [7,8]. More importantly, the satisfactory results obtained in this context motivate application of the method to more complicated situations of interest. As a specific example, we consider a model for the random dispersal of an asocial population [6].

II. METHOD OF SOLUTION

The approach we will take is based on the center manifold theory [9,10] and the normal solution ansatz used to obtain solutions to the nonlinear Boltzmann equation [11]. The Fisher equation and its generalizations are specific examples of the general, one-dimensional single species reaction diffusion equation

$$\frac{\partial u}{\partial t}=\frac{\partial}{\partial x}D(u)\frac{\partial u}{\partial x}+F(u). \tag{1}$$

Here $u(x,t)=[n(x,t)/n_c]$ is the ratio of species population density to carrying capacity at point x in $0\leqslant x\leqslant L$ at time t, $D(u)$ is the diffusion coefficient, and the nonlinear function $F(u)$ describes the population growth kinetics. When the surroundings are hostile, as considered here, the boundary conditions are $u(0,t)=u(L,t)=0$. As we mentioned earlier, the primary focus of interest regarding Eq. (1) has been on the existence and stability of traveling wave solutions in an unbounded domain [1–3]. We are unaware of any exact solutions for a bounded domain that describe the evolution of u to a steady state.

For the Fisher equation [1] $D(u)=D=\text{const}$, $F(u)=\alpha u(1-u)$, Skellam [5] has found the exact steady state solution and the critical habitat size, but the solution involves elliptic integrals and is not particularly revealing. Approximate solutions have been determined for the time-dependent equation for the case where the initial value of u is a pure sine function [7,8]. These solutions are based on the *ad hoc* representation of the spatial dependence as a linear function [7] or a pure sine function [8]. The method that we use will provide a framework for generalizing these *ad hoc* approaches and also for resolving the difficulty that occurs when they lead to solutions that exceed the carrying capacity. The price we pay for this is that our solutions are only strictly useful when $u\ll 1$; however, we find that even when the central density at steady state is as large as one half the carrying capacity, our result is within 1% of the exact result [5]. Furthermore like the *ad hoc* solutions, our solution is expressed in terms of elementary functions, which permits a greater transparency relative to the dependence of u on the system parameters.

The normal solutions to the nonlinear Boltzmann equation [11] follow from the assumption that the distribution function $f(\mathbf{x},\mathbf{v},t)$ describing the density of atoms (or structureless

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molecules) at position **x** with velocity **v** at time *t* depends on the time only through the velocity moments $n(\mathbf{x},t)$, $\mathbf{u}(\mathbf{x},t)$, $\mathbf{P}_{ij}(\mathbf{x},t)$; i.e.,

$$f(\mathbf{x},\mathbf{v},t)\rightarrow f(\mathbf{x},\mathbf{v};n(\mathbf{x},t),\mathbf{u}(\mathbf{x},t),\mathbf{P}_{ij}(\mathbf{x},t)) \tag{2}$$

where *n*, **u**, $\mathbf{P}_{ij}$ are found by integrating $f, f\mathbf{v}, f\mathbf{v}_I\mathbf{v}_j$, respectively, over the full velocity space, e.g., $\mathbf{u}=\int d\mathbf{v}\, f\mathbf{v}$. A closely related contraction underlies the center manifold theory [9,10] and its application to the solution of nonlinear equations such as Eq. (1). Despite the fact that the principle of superposition is not applicable to nonlinear equations, a special kind of solution having this form is sought using spatial basis functions appropriate to the boundary conditions. The special property of the solution that is assumed is that the time dependence of all the coefficients beyond the first is through their functional dependence on the first coefficient. In the present context, we look for a solution to Eq. (1) of the form

$$u=\sum_{n=1}^{\infty} u_n(t)\sin(n\pi x/L), \tag{3}$$

where $u_n\rightarrow u_n[u_1(t)]$, $n>1$, reminiscent of Eq. (2). As is the case with the solution to the Boltzmann equation, the initial conditions may be such that for early times the solution obtained is not accurate (initial slip) [11]. The usefulness of this method requires that $\lim_{u_1\rightarrow 0}(u_n/u_1)\rightarrow 0$, a condition that we will show is satisfied by the solutions of Eq. (1). Since, as noted above, we consider small *u*, the solution will be well approximated outside the initial time layer by u_1. In Sec. III, we apply this method of solution to the Fisher equation and give some quantitative results.

III. SOLUTION OF THE FISHER EQUATION

The u_n can be found by substituting Eq. (3) into Eq. (1) with $D(u)=D$, $F(u)=\alpha u(1-u)$, multiplying by $\sin(n\pi x/L)$, and integrating over *x*. For $n>1$ we make use of the assumed dependence of the u_n on time through u_1 to write

$$\frac{d}{dt}u_n=\frac{\delta u_n}{\delta u_1}\frac{d}{dt}u_1=(a_n+2b_nu_1+\cdots)\frac{d}{dt}u_1, \tag{4}$$

where we have expanded $u_n=a_nu_1+b_nu_1^2+\cdots$. The equation for u_1 is

$$\frac{d}{dt}u_1=(\alpha-D\pi^2/L^2)u_1-(8\alpha/3\pi)u_1^2 + O(u_1u_2,u_1u_3,\ldots,u_2u_3,\ldots,u_2^2,\ldots). \tag{5}$$

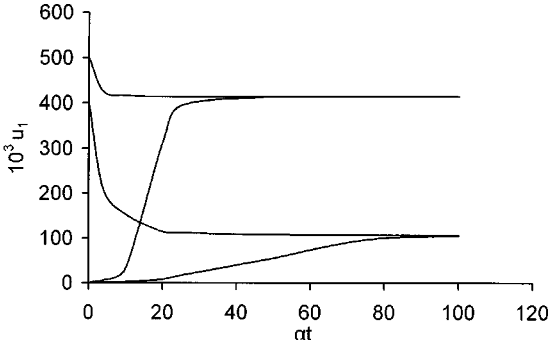

FIG. 1. Central density u_1 as a function of scaled time αt for $L/L_c=1.05\,[u_1(\infty)=0.107]$ and $L/L_c=1.25\,[u_1(\infty)=0.415]$. Two initial conditions are shown for each case.

Denoting all the terms above not explicitly containing only u_1, and similar terms of this form as "higher order," the equation for u_n, from Eqs. (4) and (5), is

$$\begin{aligned}\frac{d}{dt}u_n&=(a_n+2b_nu_1+\cdots)[(\alpha-D\pi^2/L^2)u_1\\&\quad-(8\alpha/3\pi)u_1^2+\text{higher order terms}]\\&=(\alpha-n^2\pi^2D/L2)u_n-[4\alpha/n\pi(4-n^2)]u_1^2\\&\quad\times[1-(-1)^n]+\text{higher order terms}.\end{aligned} \tag{6}$$

Equating the coefficients of u_1, u_1^2 on each side of Eq. (6), we then find

$$\begin{gathered}a_{2n}=b_{2n}=0,\quad n=1,2,3\cdots;a_n=0\\ b_n=[8\alpha/n\pi(n^2-4)][\alpha+(n^2-2)\pi^2D/L^2],\\ n=3,5,7\ldots.\end{gathered} \tag{7}$$

Equation (7) verifies that $(u_n/u_1)\rightarrow 0$ as $u_1\rightarrow 0$. Furthermore, we see that the b_n also decrease rapidly with increasing *n*. Because of symmetry, we could have expected the coefficients for even *n* to vanish; the u_{2n} do not contribute to the total population $P=\int_0^1 dx\, u(x,t)$. This means that when the initial condition is asymmetric, the solution obtained will only be good for times long enough so that the dependence on the initial condition is weak.

Subject to the above restrictions on the initial conditions, we then have

$$u=u_1\sin(\pi x/L)+\sum_{n=1} u_1^2b_{2n+1}\sin(2n+1)\pi x/L + \text{higher order terms} \tag{8}$$

where, from Eq. (5)

$$\begin{aligned}u_1&=u_1(0)(\alpha-D\pi^2/L^2)[(\alpha-D\pi^2/L^2)\\&\quad+(8\alpha u_1(0)/3\pi)(\exp(\alpha-D\pi^2/L^2)t-1)]^{-1}\\&\quad\times\exp(\alpha-D\pi^2/L^2)t.\end{aligned} \tag{9}$$

The value of the critical habitat size, $L_c=\pi(D/\alpha)^{1/2}$, is given exactly by the above result. For $L/L_c<1$ and the small values of $u(0)$ being considered here, the decay of the population is essentially exponential with a decay time of $1/\alpha[1-(L/L_c)^2]$. For $L/L_c>1$, we see in Fig. 1 that the time for an initial population to reach its steady state decreases as the initial central density increases. Also, for fixed initial central density, the time to reach the steady state decreases as the habitat size increases. Like Landhal's result for the central density [8], our result for u_1 leads to a steady state value greater than 1 when $L/L_c \gg 1$. However, the results found here are not intended to be used for values of the habitat size or initial central density so large that this can occur. Furthermore, by including additional terms in Eq. (8), the values of these variables being considered can be extended. As an example, for $u_1 = 0.5$ in the steady state, Skellam's exact result for L_c is 4.197 [5], Landhal's approximate result is $L_c = 4.031$ [8], and our result using Eq. (9) and the first two nonvanishing terms in Eq. (8) is $L_c = 4.164$. In comparing the last two results, we see that, as expected, the nonlinear dispersal equation will create new Fourier modes that are not included in the *ad hoc* solution.

In assessing how well the method of solution suggested here can be expected to work in a specific situation, the nature of the initial conditions is of particular concern. If the latter are both symmetric and roughly sinusoidal, then we expect that for the interesting case where the habitat size is close to the critical size, the results obtained will provide a good approximation for all times. The further the initial conditions deviate from the above prescription, the less trustworthy our results will be for early times. In any event, we expect that for habitat sizes not too much greater than the critical size, the steady state will be accurately described. This motivates the consideration of more complicated growth scenarios.

IV. MORE GENERAL DISPERSAL EQUATIONS: ASOCIAL POPULATIONS

We restrict ourselves here to scenarios for which Eq. (1) provides the generic template for the growth kinetics. We note first that in the case [3], when D is independent of u and $F(u) = \alpha u(1-u^N)$ that the critical length is given as before and that in the steady state $u_1(N) \propto u_1(N=1)$, but in the more interesting case [3] when $D = D_0 u$ and $F(u) = \alpha u(1-u)$, the method used here fails as the u_j are of the same order as u_1.

The case of an asocial population has been previously considered by Bradford and Philip [6], who considered general stability criteria. These authors illustrated their formal results for the special case of a sawtooth growth function. Here we consider a more general and mathematically continuous function that describes asocial growth. This requires that $F(u)$ be negative at both small and large values of u, and positive in between. The simplest possible representation of this is $F(u) = \alpha u(u^* - u)(1-u)$, $u^* < 1$.

The equation for u_1, found as before, is

$$\frac{d}{dt} u_1 = -[(D\pi^2/L^2) + \alpha u^*]u_1 + (8\alpha/3\pi)(1+u^*)u_1^2 - (3\alpha/4)u_1^3. \tag{10}$$

In steady state, the left side of Eq. (10) vanishes, and real solutions will only exist if

$$[32(1+u^*)/9\pi]^2 > (16/3\alpha)[(D\pi^2/L^2) + \alpha u^*]. \tag{11}$$

This requires both

$$u^* < 0.66, \quad L^2 > (16D\pi^2/3\alpha)(1.28 - 2.77u^* + 1.28u^{*2}). \tag{12}$$

If both of these conditions are not met, then $u_1 \to 0$ and the population does not survive. If these conditions are met, the survival of the population will depend on the initial condition. Here we will assume that the population has grown by some unknown process until, at some threshold value u_1 for the central density, the onset of asocial growth occurs, i.e., $u_1(0) = u_t$. In determining the steady state solution, we cannot restrict our attentions solely to Eq. (10) with the left side set to zero. It is not possible to determine on this basis alone, as we could for the Fisher equation, which of the possible solutions allowable by the above criteria set by Eq. (12) is ultimately realized. This can be most easily determined directly from the full equation, which we rewrite as

$$\frac{d}{dt} u_1 = -k u_1 (u_1 - r_1)(u_1 - r_2), \tag{13}$$

with $k > 0$ and where the roots $r_2 > r_1 > 0$ follow directly from Eq. (10). If $u_t < r_1$, then $(d/dt)u_1 < 0$ initially, and remains negative so that u_1 decays to zero and the population does not survive. The root r_1 is the critical minimum initial population for survival. When $r_1 < u_t < r_2$, $(d/dt)u_1 > 0$ initially, and u_1 increases until it reaches the steady state $u_1 = r_2$. The last possibility, $r_2 < u_t$, is less likely, but could conceivably occur as the result of a sudden change altering the pre-existing growth process, e.g., a changeover to food sources requiring cooperative effort. In this case, u_1 will decrease until reaching steady state at r_2.

V. SUMMARY

The emphasis here has been on illustrating the predictive ability of the method of solution described in Sec. II, particularly with regard to the parametric dependence of the critical factors that limit population growth. Despite a growing trend toward the simulation of nonlinear behavior, analytical studies can still provide a complimentary window that reveals behavior, often unexpected, as well as the underlying causes. In the case of asocial growth considered here, Eq. (10) gives a good estimate of the transient time to extinction or a finite steady state, $\tau \propto 1/[(D\pi^2/\alpha L^2) + u^*]$, that would be difficult to determine from computer studies, as well as an estimate of the initial population density survival windows and critical habitat size.

ACKNOWLEDGMENTS

I thank the faculty and staff of the Mechanical Engineering Department at Columbia University, where this work was carried out, for their warm hospitality. I also thank Ms. Kathleen Kehoe and the staff of the Biological Sciences Library at Columbia University as well as Mr. Charles Harris, Department of Pharmacology and Molecular Biology at Washington University, St. Louis, MO, for assistance with reference materials.

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