Journal of Statistical Physics, Vol. 99, Nos. 3/4, 2000

Population Dynamics near an Oasis with Time-Dependent Convection

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Received December 10, 1999

We investigate the time evolution of a bacterial population near a favorable spot with time-dependent convection. Diffusion, growth, and saturation effects lead to a localized colony which spreads out in the surroundings. Convection by a time-dependent but spatially uniform random velocity introduces fluctuations. Equations of motion for ensemble averages are derived and compared to numerical simulations.

KEY WORDS: Biological physics; population dynamics; nonlinear dynamics; ecological pattern formation.

I. INTRODUCTION

The dynamics of populations in a disordered environment has recently aroused interest, in part because of a close analogy to the localization problem of noninteracting electrons in a random potential. A constant convective term in the linearized Fisher equation for population growth can be viewed as a non-hermitian perturbation of an Schrödinger operator. The spectrum of this time-evolution operator reveals a diverging localization length with a sharp mobility edge.(1)

This model is in fact a particularly simple example of a broad class which combines elements of fluid mechanics with population dynamics, possibly at high Reynolds number. A classic problem in fluid mechanics concerns convection and diffusion of a passive scalar contaminant by an incompressible turbulent fluid.(2) New phenomena arise if the "passive scalar" is replaced by a biological population which can multiply and

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0022-4715/00/0500-1021$18.00/0

saturate in the fluid medium, especially.if there are spatial inhomogeneities in the growth rates. Consider, for example, replacing the passive scalar by, e.g., plankton populations in the ocean.(3, 4) One might model this situation by combining the Navier-Stokes equations for an incompressible fluid with velocity $\mathbf{v}(\mathbf{x}, t)$, density ϱ_0, viscosity ν, and pressure $p(\mathbf{x}, t)$ with an equation describing transport and growth of a population density $c(\mathbf{x}, t)$,

$$\partial_t \mathbf{v} + \mathbf{v} \cdot \nabla \mathbf{v} = -\frac{1}{\varrho_0} \nabla p + \nu \nabla^2 \mathbf{v}, \qquad \nabla \cdot \mathbf{v} = 0 \tag{1}$$

$$\partial_t c + \mathbf{v} \cdot \nabla c = D \nabla^2 c + ac - bc^2 \tag{2}$$

Here, D is the diffusion constant of, say, the plankton which grow at rate a and whose population is limited by competition for limited resources by the nonlinear term $-bc(\mathbf{x}, t)^2$.

The effect of a space and time-dependent velocity field is governed by Eq. (1) corresponding to fully developed turbulence on the population dynamics described by Eq. (2) is beyond the scope of this paper. A *constant* velocity (with spatially varying growth rates) was considered in ref. 1. Here, we discard Eq. (1) and consider the effect of a velocity field $\mathbf{v}(t)$ which is random in *time* but constant in space. Such a model might be a crude approximation for the effects of turbulence on microorganisms in regions smaller than the Kolmogorov scale. We continue the discussion initiated in ref. 5 by focusing on how this time-dependent convection or "wind" affects the population near a hot spot of favorable growth rates (an oasis) surrounded by a less favorable "desert" region. We also discuss how the colony which develops is affected by a nonlinear saturation term.

The dynamics of the density of the bacterial population $c(\mathbf{x}, t)$ is governed by a generalization of the Fisher equation(6)

$$\partial_t c(\mathbf{x}, t) = D \nabla^2 c(\mathbf{x}, t) + U(\mathbf{x})\, c(\mathbf{x}, t) - bc(\mathbf{x}, t)^2 - \mathbf{v}(t) \cdot \nabla c(\mathbf{x}, t) \tag{3}$$

Here D denotes the diffusion constant and $U(\mathbf{x})$ a spatially varying growth rate. We assume that there is a single favorable spot referred to as oasis, which we take as the origin. Far away from the oasis, say for $|x| > x_0$, the growth rate is assumed to be uniform and slightly negative or zero,

$$U(\mathbf{x}) = -V_0 \leqslant 0 \qquad \text{for} \quad |x| > x_0 \tag{4}$$

which defines a region of "desert." The nonlinear term accounts for saturation effects due to competition within the species for resources. For simplicity the coefficient b is taken to be space-independent. The last term in the generalized Fisher equation describes advection by a random spatially uniform time-dependent velocity with a Gaussian statistics in time,

$$\langle v^{\alpha}(t)\rangle = 0$$
$$\langle v^{\alpha}(t)\, v^{\beta}(t')\rangle = 2\Gamma\delta^{\alpha\beta}\delta(t-t') \tag{5}$$

II. THE QUIESCENT OASIS

We first review some properties of the model without the random "wind" embodied in the velocity $\mathbf{v}(t)$, i.e., $\Gamma = 0$. For long times the density profile approaches a stationary state $c_0(\mathbf{x})$. A trivial solution is given by the extinction fixed point, namely $c_0(\mathbf{x}) = 0$. The linearized equation is sufficient to analyze the stability of this solution. Hence, the extinction fixed point is stable if all eigenvalues of the Schrödinger-like operator $D\nabla^2 + U(\mathbf{x})$ are negative. We are interested in the case where the desert is only slightly lethal, i.e., V_0 is a small parameter. Then positive eigenvalues of the growth operator correspond to bound states of the Schrödinger equation. In one dimension, on which we focus here, there is always at least one bound state, if there is a region of positive growth rates $U(\mathbf{x})$ for $|x| < x_0$.(7) Then we expect a nonzero population in the steady state and the stationary profile is given by the nontrivial solution of

$$D\frac{d^2}{dx^2}c_0(x) + U(x)\, c_0(x) - bc_0(x)^2 = 0 \tag{6}$$

For $|x| > x_0$ the potential is a constant and the differential equation is of the form of Newton's equation (x is "time" and $c_0(x)$ plays the role of a particle "position"), which can be solved by the method of quadratures. The solution that satisfies the boundary condition $c_0(|x| \to \infty) = 0$ has the form of a scaling law and is given for $|x| \gg x_0$

$$c_0(x) = \frac{3V_0}{2b}\frac{1}{\sinh^2((x + x_\pm)\sqrt{V_0/D}/2)} \tag{7}$$

where the length scales $x_\pm$ are supposed to be somewhat less than the extension of the oasis x_0 and have to be determined by matching to the solution inside of the oasis. The localization length $\xi = \sqrt{D/V_0}$ diverges as $V_0 \to 0^+$ and the colony spreads further out into the desert. For large ξ, one obtains a power law at intermediate length scales,

$$c_0(x) \approx \frac{6D}{b}\frac{1}{x^2}, \qquad |x_0| \ll |x| \ll \xi \tag{8}$$

and a crossover at $|x| \sim \xi$ to an exponential decay

$$c_0(x) \approx \frac{6D}{b\xi^2} \exp(-|x|/\xi), \qquad |x| \gg \xi \tag{9}$$

These results suggest universal behavior in the limit $\xi \gg x_0$, i.e., results independent of the details of the oasis, such as the parameters $x_\pm$. Similarly, one can convince oneself that adding higher nonlinearities, like terms $c_0^3(x)$, will not change the asymptotic results. The origin of this universality is that dimensional analysis allows only for the length scale ξ apart from scales determined from the local properties of the oasis. In the simplest case, fulfilled in one dimension, the stationary density profile far away from the oasis is governed by the single length scale ξ.

The dynamics of the population introduces a second diffusive length scale $\lambda = \sqrt{Dt}$ which grows to infinity as $t \to \infty$. An initial localized population, say $c_0(x, t=0) = 0$ for $|x| > x_0$ will spread out into the desert and approach the stationary state. For long times and distances deep in the desert we expect a scaling law

$$c(x, t) = \frac{6D}{b\xi^2} f\left(\frac{x}{\xi}, \frac{x}{\lambda}\right) \tag{10}$$

with a dimensionless function f. From the discussion of the last paragraph we already know $f(\tilde{x}, 0) = [4 \sinh^2(\tilde{x}/2)]^{-1}$, $\tilde{x} = x/\xi$. Similarly for a marginally lethal desert $V_0 = 0$, $\xi = \infty$, the stationary profile will be visible deep in the desert for distances $|x| \ll \lambda$, whereas no population is expected for $|x| \gg \lambda$. The scaling function therefore fulfills $f(0, \tilde{x}) = 1$ for $\tilde{x} = x/\lambda \ll 1$ and $f(0, \tilde{x}) = 0$ for $\tilde{x} \to \infty$.

III. RANDOM WIND

In this section we discuss the changes of the properties of the quiescent oasis when the colony is advected by a random time-dependent "wind" in d dimensions. The stochastic properties of the wind are given by Eqs. (5). The quantity of interest is the probability distribution W for the density profile $c(\mathbf{x})$ at time t. We derive the corresponding Fokker–Planck equation for the Fourier modes

$$c_{\mathbf{k}}(t) = \int_V d^d x \, c(\mathbf{x}, t) \exp(-i\mathbf{k} \cdot \mathbf{x}) \tag{11}$$

$$c(\mathbf{x}, t) = \frac{1}{V} \sum_{\mathbf{k}} c_{\mathbf{k}}(t) \exp(i\mathbf{k} \cdot \mathbf{x}) \tag{12}$$

where we use periodic boundary condition in a cubic box of volume $V=L^d$. The nonlinear time-evolution equation of the random field $c_{\mathbf{k}}(t)$ then reads

$$\frac{d}{dt} c_{\mathbf{k}}(t) = -Dk^2 c_{\mathbf{k}}(t) + \sum_{\mathbf{q}} [U_{\mathbf{k}-\mathbf{q}} - b c_{\mathbf{k}-\mathbf{q}}(t)]\, c_{\mathbf{q}}(t) - i\mathbf{k}\cdot\mathbf{v}(t)\, c_{\mathbf{k}}(t) \tag{13}$$

The probability distribution is given by

$$W(\{\varphi_{\mathbf{k}}\}, t) = \left\langle \prod_{\mathbf{k}} \delta(c_{\mathbf{k}}(t) - \varphi_{\mathbf{k}}) \right\rangle \tag{14}$$

Performing the usual steps, (see e.g., ref. 8) one derives the Fokker–Planck equation

$$\begin{aligned}\partial_t W = -\sum_{\mathbf{k}} \frac{\partial}{\partial \varphi_{\mathbf{k}}} \bigg\{ & \bigg[-(D+\Gamma)\, k^2 \varphi_{\mathbf{k}} + \sum_{\mathbf{q}} [U_{\mathbf{k}-\mathbf{q}} - b\varphi_{\mathbf{k}-\mathbf{q}}]\, \varphi_{\mathbf{q}} \bigg] W \\ & + \sum_{\mathbf{q}} \Gamma(\mathbf{k}\cdot\mathbf{q}) \frac{\partial}{\partial \varphi_{\mathbf{q}}} [\varphi_{\mathbf{k}} \varphi_{\mathbf{q}} W] \bigg\}\end{aligned} \tag{15}$$

Exact equations of motion for various moments of W can easily be derived. For example, the average of a density Fourier mode satisfies

$$\frac{d}{dt} \langle c_{\mathbf{k}} \rangle(t) = -(D+\Gamma)\, k^2 \langle c_{\mathbf{k}} \rangle(t) + \sum_{\mathbf{q}} U_{\mathbf{k}-\mathbf{q}} \langle c_{\mathbf{q}} \rangle(t) - b \sum_{\mathbf{q}} \langle c_{\mathbf{k}-\mathbf{q}} c_{\mathbf{q}} \rangle(t) \tag{16}$$

In real space one derives

$$\partial_t \langle c(\mathbf{x}) \rangle(t) = (D+\Gamma)\, \nabla^2 \langle c(\mathbf{x}) \rangle(t) + U(\mathbf{x}) \langle c(\mathbf{x}) \rangle(t) - b \langle c(\mathbf{x})^2 \rangle(t) \tag{17}$$

Suppose at time $t=0$ the time evolution starts with a small population density. Then for short times one can neglect the nonlinearity in Eq. (17) and the average density again satisfies a linear equation of the Schrödinger type. The only effect of the random wind is the replacement of D by an enhanced effective diffusion constant $D+\Gamma$. In dimension three and higher this enhancement can lead to an extinction transition.(7) Namely if the quiescent oasis possesses one or several bound states which grow in time, a strong wind leads to a Schrödinger operator with scattering states only, corresponding to a decrease of the density. Since the nonlinear saturation only suppresses growth, its neglect is justified for all times. The extinction transition for a marginally lethal desert, $V_0 = 0^+$, is accompanied by a divergent localization length. Since the eigenvalue of the last bound state $\varepsilon_0 \to 0^-$ as $\Gamma \to \Gamma_c^-$, where Γ_c denotes the critical wind strength separating survival and extinction, the localization length $l = \sqrt{(D+\Gamma)/\varepsilon_0}$ grows to infinity. Likewise the validity of the neglect of the saturation is valid for times up to the order or $t \sim 1/\varepsilon_0$ and diverges as the critical wind strength is approached from below. In one and two dimensions, there will always be at least a single bound state(7) and the localization length diverges only for $\Gamma \to \infty$.

At long times, we expect that the probability distribution approaches a nonzero stationary state for $\Gamma < \Gamma_c$, i.e., in the survival phase. Upon neglecting the second order derivative in the Fokker–Planck equation (15), i.e., all fluctuations due to the noise introduced by the wind, a solution is given by

$$W_{eq}(\{\varphi_{\mathbf{k}}\}) = \prod_{\mathbf{k}} \delta(c_{0\mathbf{k}} - \varphi_{\mathbf{k}}) \tag{18}$$

where $c_{0\mathbf{k}}$ solves the mean-field equation

$$-(D+\Gamma)\, k^2 c_{0\mathbf{k}} + \sum_{\mathbf{q}} U_{\mathbf{k}-\mathbf{q}} c_{0\mathbf{q}} - b \sum_{\mathbf{q}} c_{0,\mathbf{k}-\mathbf{q}} c_{0\mathbf{q}} = 0 \tag{19}$$

Hence in this mean field approximation one recovers the properties of the quiescent oasis with the mere replacement $D \to D + \Gamma$. We now argue that the exponents for the stationary mean-field solution are actually a lower bound. Suppose $\langle c(x)^2 \rangle \sim 1/|x|^{2\beta}$ for large $|x|$. Then Eq. (17) implies $\langle c(x) \rangle \sim 1/|x|^{2\beta-2}$ for $V_0 = 0^+$. However, $\langle c(x)^2 \rangle \geqslant \langle c(x) \rangle^2$ and therefore $2\beta \leqslant 4\beta - 4$ or $\beta \geqslant 2$.

IV. NUMERICAL RESULTS

In this section we check our theoretical results against numerical results obtained from a lattice version of Eq. (3). The population is concentrated at the sites of a hyper-cubic lattice with lattice spacing a_0 and a finite box length L. Open boundary conditions are imposed. The local density at cell i of the population is then approximated by $c(\mathbf{x}_i) = c_i / a_0^d$. Diffusion arises as the result of hopping processes between neighboring cells. The wind introduces a bias in the hopping rates. A suitable discretization of Eq. (3) is given by

$$\frac{d}{dt} c_i = \frac{D}{a_0^2} \sum_{j(i)} e^{\mathbf{v}(t) \cdot (\mathbf{x}_j - \mathbf{x}_i)/(2D)} (c_j(t) - c_i(t)) + U_i c_i(t) - \tilde{b} c_i(t)^2 \tag{20}$$

with $\tilde{b} = b/a_0^d$, $U_i = U(\mathbf{x}_i)$, and where the sum over j runs over nearest neighbors of i. In order to give the lattice version a precise meaning one has to regularize also the statistics of the random velocity. For simplicity we consider

$$\langle v^\alpha(t) \rangle = 0 \tag{21}$$

$$\langle v^\alpha(t)\, v^\beta(t') \rangle = \frac{\Gamma}{\tau} \exp\left(-\frac{|t-t'|}{\tau} \right) \tag{22}$$

A nonzero correlation time τ implies that typically the velocity at any particular time is of the order $\sqrt{\Gamma/\tau}$. Note that the local hopping bias $\exp(va_0/D) - 1$ becomes small as the lattice spacing a_0 is decreased. The continuum limit with a white noise field is recovered in the limit of first letting $a_0 \to 0$ and then $\tau \to 0$.

Numerical simulations are performed for a one dimensional chain with 1000 lattice sites. Units of length and time are taken to be a_0 and a_0^2/D, respectively. The oasis is located at the single site $x_0 = 0$, all other sites being considered as desert. A small initial population is concentrated on the oasis, whereas the desert is uninhabitated. Neglect of saturation effects, i.e., $\tilde{b} = 0$ is justified for small population densities. In order to compare to the analytical formulas one should perform an ensemble average over the different realizations of the wind. A directly accessible quantity is the time-averaged normalized population density. For $\tilde{b} = 0$ the Eq. (20) is linear. Although normalization at each time step does change the time evolution of the density profile, it takes out the trivial overall growth of the total population. Figure 1 exhibits numerical results for the time-averaged normalized population density for an oasis specified by $U_i = 0.1\, \delta_{i0}\, D/a_0^2$ and a random wind with parameters $\Gamma = D$, $\tau = 100 a_0^2/D$. The density profile far from the oasis is well represented by an exponential characterized by a decay length of $l = 40 a_0$, which is twice as large as compared to the quiescent case. The continuum description for a delta potential with a prefactor of $a_0 U_0$ yields the same value of $l = 2(D + \Gamma)/(a_0 U_0)$. The results depend only weakly on the correlation time τ. The choice of $\tau = 100 a_0^2/D$ renders the local bias $\exp(va_0/D) - 1$ a small quantity. However, this time is still short compared to the "response" time ε_0^{-1} corresponding to the eigenvalue of the bound state $\varepsilon_0 = a_0^2 U_0^2/[4(D+\Gamma)] = D/(800 a_0^2)$. Close to the oasis deviations from the continuum result are observed.

Figure 2 exhibits the time evolution of a population described by the nonlinear equation near a marginally lethal quiescent oasis. The growth rate at the oasis $U_0 = 50 D/a_0^2$ has been chosen much larger than in the last paragraph in order to achieve a small decay length of the eigenstate of the linearized equation. The details of the oasis therefore do not matter on the

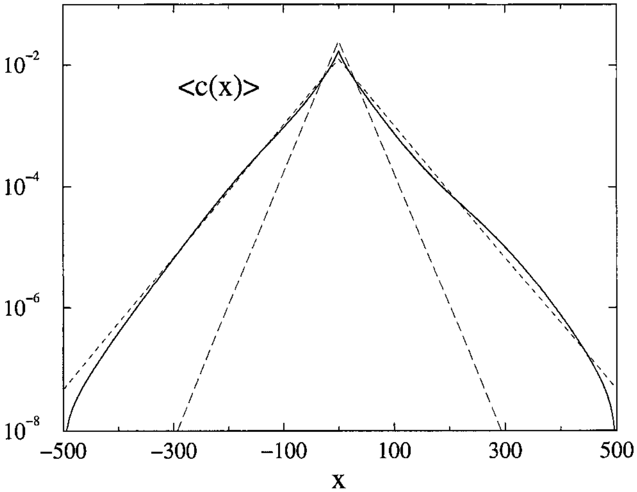

Fig. 1. Averaged normalized short-time population density $\langle c(x) \rangle$ (solid line), governed by a linearized Fisher equation with random convection in the vicinity of an isolated oasis at $x = 0$. The growth rate at the oasis spot is $U_0 = 0.1 D/a_0^2$ and the random velocity is specified by $\Gamma = 1.0 D$, $\tau = 100 a_0^2/D$. The short-dashed line is the analytic solution of the continuum model $\exp(-|x|/l)/(2l)$, $l = 40 a_0$. For comparison the same quantity $\langle c(x) \rangle$ for the quiescent oasis is plotted (long-dashed line).

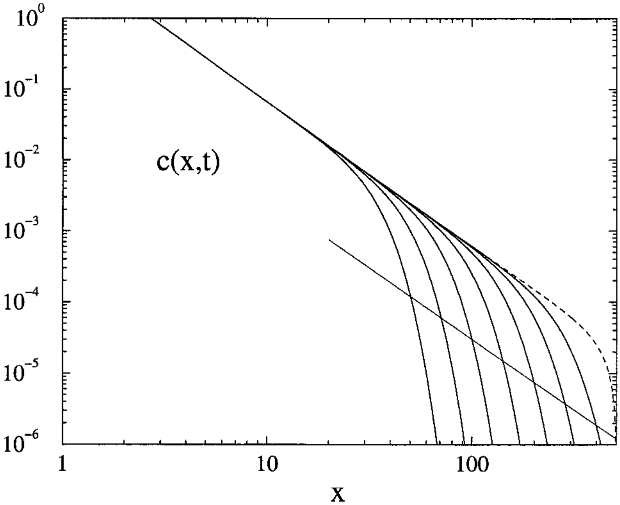

Fig. 2. Time-dependent population density, described by a nonlinear Fisher equation for the marginally lethal quiescent oasis measured in units of $\tilde{b} a_0^2/D$. The growth rate at $x = 0$ is specified by $U_0 = 50 D/a_0^2$. The thick solid lines refer from left to right to times $tD/a_0^2 = 100$, 200, 400, 800, 1600, 3200, respectively. The short-dashed lines represents the stationary density. The light solid line represents a power law proportional to $1/x^2$ and is a guide to the eye.

scales shown. Shifting curves for different times parallel to the power law x^{-2} results in a collapse of all curves on a master function. In particular one infers the exponent 1/2 which relates lengths to time $\lambda \sim t^{1/2}$.

The stationary density profile near an oasis with a random velocity is exhibited in Fig. 3. For small lethality V_0 the population spreads out far into the desert, i.e., the correlation length diverges at the same critical value $V_0^c = 0$ as in the case of a quiescent oasis. The reason is of course that the random wind merely redistributes the population locally while conserving it overall. For a neutral desert $V_0 = 0$ one observes still a power law for the stationary density profile far away from the oasis. For very large distances finite-size effects are apparent. The value of the decay exponent is compatible with the mean field $\beta = 2$ result, although the prefactor is slightly shifted. For small but nonzero lethality $V_0 > 0$ the simulation results approach exponentials for large x with correlation lengths that fulfill the scaling relation $\xi \propto 1/\sqrt{V_0}$. As can be inferred from Fig. 3, increasing the lethality by a factor of two decreases the correlation length by a factor of $\sqrt{2}$. Moreover, the prefactor is given by $\sqrt{D + \Gamma}$, i.e., the correlation length is enhanced compared a to quiescent oasis and the correction follows from the mean-field equation (19). Suppose that for large distances one can neglect $b\langle c(\mathbf{x})^2 \rangle$ compared to $V_0 \langle c(\mathbf{x}) \rangle$. The solution is then

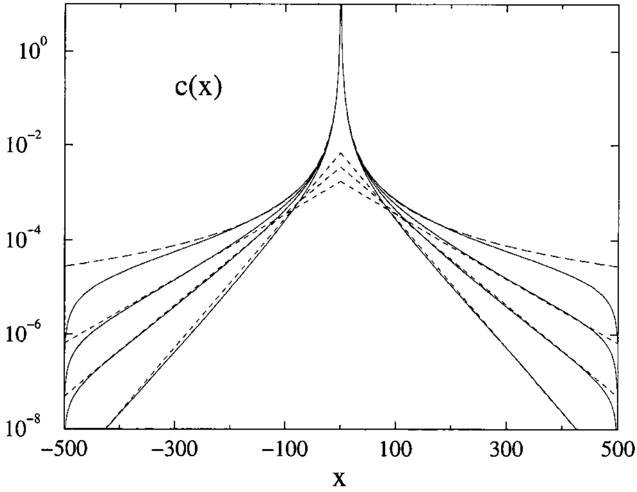

Fig. 3. Stationary density profile in units of $\tilde{b}a_0^2/D$ near an oasis at $x = 0$ specified by $U_0 = 50D/a_0^2$. The thick solid lines refer to simulations for deserts with increasing lethalities ($V_0 a_0^2/D = 0$, 0.0005, 0.001, 0.002). Parameters for the random velocity are chosen as in Fig. 1. The long-dashed line corresponds to $7/x^2$. The short-dashed curves axe exponentials $7\xi^{-2} \exp(-|x|/\xi)$ with $\xi = \sqrt{(D + \Gamma)/V_0}$.

given by $\langle c(\mathbf{x})\rangle \propto \exp(-|x|/\xi)$ with $\xi = \sqrt{(D+\Gamma)/V_0}$. The proportionality factor in turn has to be determined by matching to the critical solution, which results in $\langle c(\mathbf{x})\rangle = A\xi^{-2}\exp(-|x|/\xi)$ where the prefactor A is independent of V_0.

ACKNOWLEDGMENTS

We thank K. Dahmen and Y. Oreg for many stimulating discussions. T.F. acknowledges the support of the DFG under contract Fr 1418/1-1. D.R.N. acknowledges the support of the National Science Foundation, through Grant DMR-9714725 and the Harvard Materials Research Science and Engeneering Center via Grant DMR-9809363.

REFERENCES

1. D. R. Nelson and N. M. Shnerb, Non-hermitian localization and population biology, *Phys. Rev. E* **58**:1383 (1998); See also N. Hatano and D. R. Nelson, Vortex pinning and non-Hermitian quantum mechanics, *Phys. Rev. B* **56**:8651 (1997).
2. H. Tennekes and J. L. Lumley, *A First Course in Turbulence* (MIT Press, Cambridge, 1972); U. Frisch, *Turbulence* (Cambridge University Press, Cambridge, 1995).
3. A. R. Robinson, On the theory of advective effects on biological dynamics in the sea, *Proc. R. Soc. London A* **453**:2295 (1997).
4. R. V. Vincent and N. A. Hill, Bioconvection in a suspension of phototactic algae, *J. Fluid Mech.* **327**:343 (1996).
5. K. A. Dahmen, D. R. Nelson, and N. M. Shnerb, Life and Death near a windy oasis, *J. Math. Biology* (in press), http://xxx.lanl.gov/abs/cond-mat/9807394; See also http://xxx.lanl.gov/abs/cond-mat/9903276.
6. J. D. Murray, *Mathematical Biology* (Springer-Verlag, New York, 1993).
7. L. D. Landau and E. M. Lifshitz, *Quantum Mechanics* (Pergamon, New York, 1965), Sec. 45.
8. J. Zinn-Justin, *Quantum Field Theory and Critical Phenomena* (Clarendon Press, Oxford, 1989).

Communicated by J. L. Lebowitz