Extinction Transition on a Pie

Nadav M. Shnerb

Department of Physics, Judea and Samaria College, Ariel, Israel 44837

(March 21, 2022)

Extinction transition of bacteria under forced rotation is analyzed in pie geometry. Under convection, separation of the radial and the azimuthal degrees of freedom is not possible, and the linearized evolution operator is diagonalized numerically. Some characteristics scales are compared with the results of recent experiments, and the “integrable” limit of the theory at narrow growth region is analyzed.

The time evolution of bacterial colonies on a petri-dish has been studied recently both theoretically and experimentally [1-3]. The colony is relatively simple biological system, and its basic component, an individual bacterium, involves only “elementary” biological processes like diffusion, food consumption, multiplication, death and perhaps some interaction like chemotaxis. Studies with some bacteria strains have reported a wide variety of complex pattern formation, in most cases due to competition for food resources and chemical interaction. With uniform, not-exhaustible background of nutrients and without the presence of mutations and chemical signaling, these simple strains are suppose to invade a region of nutrient rich agar in the form of a front propagating with some typical velocity, known as the Fisher front [3-4].

Biological problems of colony growth in inhomogeneous environment and under forced convection has been modeled recently by Nelson and Shnerb [5] and by Dahmen, Nelson and Shnerb [6]. These studies have focused on the spectral properties of the linearized evolution operator, which becomes non-Hermitian in the presence of convection [10]. An experiment designed to test these predictions, has been carried out recently by Neicu et al [4].

In the experiment, a colony of Bacillus subtilis bacteria is forced to migrate in order to “catch up” with a shielded region on the the petri-dish, where all the other parts of the dish are exposed to an ultra violet (UV) light, which (under the experimental conditions) makes the unshielded bacteria immotile. It was assumed that the adaptation of the bacterial colony to the moving shielded region has nothing to do with information processing or mutual signaling in the colony, but is attributed solely to the combined effect of “dumb” diffusion of individual bacteria and the larger growth rate under the shelter. Theoretically, it was predicted that the adaptation of the colony to the moving environment falls as the drift is faster than the Fisher front velocity, and in this case the colony lags behind the shelter and an extinction transition takes place.

In order to get the essence of the theory, let us consider a one-dimensional example, where bacteria are diffusing on a line parametrized by x, and are subject to some environmental heterogeneity which implies fluctuating growth rate. If the bacteria diffuses, multiply and are forced to migrate with some convection velocity v, the differential equation which describes the evolution of the colony is,

\[ \frac{∂c}{∂t} = D \frac{∂^2 c}{∂x^2} + v \cdot \frac{∂c}{∂x} + a(x)c - bc^2. \]  (1)

where \(a(x)\) is the local growth rate. When the hostile environment outside the “oasis” causes the immediate death of any bacteria, and inside the oasis there is some positive growth rate,

\[ a(x) = \begin{cases} a & 0 \leq x \leq x_0 \\ -\infty & \text{elsewhere.} \end{cases} \]  (2)

If there is no drift, the linearized version of this problem is equivalent to the (imaginary time) evolution of quantum particle in an infinite potential well, and is determined by the eigenvalues of the evolution operator, which gives a colony localized on the oasis if it has some minimal width (which scales like the width of the Fisher front), \(x_0 > \pi \sqrt{D/a}\). The introduction of a drift term into (1) is compensated by the “gauge” of the evolution (Liouville) operator eigenfunctions

\[ \phi_n = \sin(n\pi x/x_0) \rightarrow e^{±ix/2D} \sin(n\pi x/x_0) \]  (3)

together with the eigenvalues “rigid” shift

\[ \Gamma_n(v) = \Gamma_n(v = 0) - \frac{v^2}{4D}. \]  (4)

The theory, thus, predicts an extinction transition as all the eigenvalues of (4) becomes negative, i.e., as \(v_c = 2\sqrt{aD} - O(1/x_0)\), which is the Fisher velocity [12]. Right above the extinction transition, only the largest growth eigenvalue (the “ground state”) is positive, hence the nonlinear interaction between eigenmodes [the term \(-bc^2\) in (4)] are suppressed at the transition, and the analysis is focused on the ground state of the linearized operator.

In the experiment [4], part of a petri-dish was shielded from the UV source, and then this shield was given a constant angular velocity with respect to the petri-dish.
The corresponding convection velocity $v(r) = \omega r$ was chosen to interpolate between zero (at the rotation axis) and about $2 \omega$ at the edge of the dish. It turns out that the colony indeed fails to keep rotating with the shield at about half the radius. On the other hand, the velocity profile for the bacterial density $c(r, \omega)$ does not equilibrate on the time scales of the experiment ($\sim 3$ days). In this paper, I consider the differences between the one dimensional system [3] and the actual experimental setup. In particular, the two-dimensional nature of the experiment and the effect of radial diffusion are considered explicitly.

In order to capture the essential physics using the simplest geometry, the same extinction transition is considered on a pie, i.e., a section of the two dimensional disc [See Fig. (1)]. Although the shielded region of the experiment [3] was not in that shape, it turns out that even in this simple geometry there is a coupling between the radial and the azimuthal degrees of freedom, and the spectrum becomes “chaotic” when convection takes place. The results for this case are, accordingly, relevant also to the more complicated geometry of the experiment.

The basic equation for the bacterial growth problem on a non-uniform substrate, in the absence of mutation and chemical interactions, is [3]:

$$\frac{\partial c(x, t)}{\partial t} = D\nabla^2 c(x, t) + a(x)c(x, t) + v \cdot \nabla c - bc^2.$$  \hspace{1cm} (5)

With no convection and homogeneous, positive $a$ this equation supports Fisher long propagation with velocity $2\sqrt{Da}$. The experimental front propagation corresponds to $D \sim 10^{-6} \text{cm}^2/\text{s}$ and $a \sim 10^{-3}/\text{s}$. The Fisher velocity is of order $0.1 - 1 \mu\text{m}/\text{s}$, as has been found experimentally.

The Fisher width, which is the characteristic scale of spatial correlations in their system, is $\sqrt{D/a} \sim 10^{-2} \text{cm}$, much smaller than the petri-dish radius of few centimeters.

In cylindrical geometry, Eq. (3) takes the form,

$$\frac{\partial c(r, \theta, t)}{\partial t} = D\nabla^2 c(r, \theta, t) + a(\theta)c(r, \theta, t) + v \cdot \nabla c - bc^2,$$  \hspace{1cm} (6)

FIG. 1. Pie geometry: the growth rate in the shaded region is $a$, while any bacteria outside this area are dying instantly due to the UV light. The shaded region is then rotated at angular velocity $\omega$.

and for rotating petri-dish the convection term is [1],

$$v \cdot \nabla c = \omega \frac{\partial c}{\partial \theta}.$$  \hspace{1cm} (7)

Pie geometry is defined by,

$$a(\theta) = \begin{cases} a & 0 \leq \theta \leq \theta_0 \\ -\infty & \text{elsewhere} \end{cases},$$  \hspace{1cm} (8)

i.e., we have absorbing boundary conditions [14]:

$$c(r, \theta_0, t) = c(r, 0, t) = 0.$$  \hspace{1cm} (9)

As for the boundary conditions on the petri-dish edge at $r = R$, it is reasonable to take Von-Neumann boundary and to impose the no-slip condition on the bacterial density at the surface. However, the data [3] seems to indicate extinction of the colony at the edge of the dish. This is perhaps due to the fact that the width of the boundary layer (which is expected due to the no slip condition) is about the Fisher width, which has been shown above to be very small. Accordingly, we further simplify the problem by using,

$$c(R, \theta, t) = 0.$$  \hspace{1cm} (10)

Dropping the term $-bc^2$ at Eq. (3), one has the linearized evolution operator, and for the no-drift ($\omega = 0$) case, the density of bacteria at time $t$ is given by:

$$c(r, \theta, t) = \sum_{m,n} A_{m,n} e^{a_{m,n} \theta} \phi_{m,n}(r, \theta),$$  \hspace{1cm} (11)

with the eigenstates of the evolution operator,

$$\phi_{m,n}(r, \theta) = \eta_{m,n} J_{\frac{m \pi \theta}{\theta_0}} \left(\frac{R}{\sqrt{D/T_{m,n}}} \right) \sin \left(\frac{n \pi \theta}{\theta_0}\right),$$  \hspace{1cm} (12)

where $\eta_{m,n}$ is normalization factor

$$\eta_{m,n} = \frac{2}{R \sqrt{\theta_0} J_{\left|\frac{m \pi \theta_0}{\theta_0}\right|}} \frac{1}{J_{\left|\frac{m \pi \theta_0}{\theta_0}\right|} + 1 \left(\frac{R}{\sqrt{D/T_{m,n}}} \right)}.$$  \hspace{1cm} (13)

and the constants $A_{m,n}$ are determined by the initial density distribution $c(r, \theta, t = 0)$. The eigenvalues of the Hermitian problem are:

$$\Gamma_{m,n} = D \left(\frac{j_{m \pi \theta_0}/R}{R}\right)^2,$$  \hspace{1cm} (14)

where $j_{m \pi \theta_0}/R$ is the m-th zero of the corresponding Bessel function.

2
Let us get an order of magnitude estimate for the time scales which are relevant to the experiment \cite{4}. The characteristic times needed for the “ground state” to control the system is given by the typical difference between two eigenvalues. In our case, since the first zeroes of the Bessel functions are of order 1, the times involved are \( \sim \frac{R}{D} \). For an experimental system with \( R \sim 0.01 \) m and \( D \sim 10^{-10} m^2/s \), the typical relaxation times are \( O(10^6 \text{sec}) \sim 11 \text{ days} \), which is larger than the typical time of the actual experiment.

Now I look at the non-Hermitian case, where \( \omega \neq 0 \). Unlike its Cartesian analogy \cite{8,9}, no simple gauge solves the problem, and separation of variables is impossible. Spanning the space of normalizable functions by a set of Hermitian eigenstates, the perturbative term \( \omega \partial_\theta \) mixes both quantum numbers \( m \) and \( n \). The matrix elements of the convection term are:

\[
\langle n, m | \omega \cdot \partial_\theta | k, l \rangle = 2 \omega R^2 \gamma_{nmkl}.
\]

where \( \gamma_{nmkl} \) is:

\[
\gamma_{nmkl} = \begin{cases} 
0 & \text{if } k + n = \text{even} \\
\frac{2kn}{n^2-k^2} \eta_{n,m} \eta_{k,l} I_{nmkl} & \text{if } k + n = \text{odd}
\end{cases}
\]

and

\[
I_{nmkl} = \int_0^1 \frac{J_0^m(j_m \pi/\theta_0 y)}{J_0^m(j_m \pi/\theta_0 y)} \frac{J_0^l(j_l \pi/\theta_0 y)}{J_0^l(j_l \pi/\theta_0 y)} y \, dy.
\]

In order to get the eigenvalues and eigenfunctions at finite angular velocity one should diagonalize the full non-Hermitian Liouville operator, and the extinction transition takes place as the ground state (smallest) eigenvalue, \( \Gamma_{1,1} \), becomes larger than the growth rate \( \alpha \) on the pie.

As the rotating system is not integrable, it should be studied numerically using some computer diagonalization of the linearized evolution operator. Essentially, one should look at the ground state of this operator, since this state dominates the system close to the extinction transition.

This numerical analysis, however, may lead to erroneous results if the continuum limit is not taken carefully. In the most general case, a discretized version of a model with local growth rate and hopping between sites may be realized numerically as a matrix, where the growth rates are the coefficients on the diagonal and the hopping process gives the off-diagonal terms. As any hopping term is positive semi-definite, the only negative terms are the local growth rate, and for any finite matrix, by adding an appropriate multiplication of the unit matrix, one may get a positive semi-definite matrix with the same eigenvectors. Perron-Frobenius theorem \cite{13} then implies that ground state should be a nodeless, positive eigenvector. There is a simple physical interpretation to this result: since the ground state dominates the system at long times, and the number of bacteria should not become negative, Perron-Frobenius theorem should hold. Diagonalizing numerically the evolution operator, one may get a ground state with nodes, which is physically impossible.

FIG. 2. Contour Plot of the bacterial density at \( \theta_0 = \pi \). (upper panel) \( \frac{D}{\Gamma_1 R^2} = 0 \), (middle) \( \frac{D}{\Gamma_1 R^2} = 10 \) and (lower panel) at \( \frac{D}{\Gamma_1 R^2} = 30 \).
\[ R^2/D = 0 \]

\[ R^2/D = 10 \]

\[ R^2/D = 30 \]

FIG. 3. First 100 spectral points \( \text{Im}(\Gamma R^2/D) \) vs. \( \text{Re}(\Gamma R^2/D) \) at \( \theta_0 = \pi \). (upper panel) : \( \omega R^2/D = 0 \), (middle) : \( \omega R^2/D = 10 \) and (lower panel) at \( \omega R^2/D = 30 \).

In order to solve this problem one should carefully take the discrete limit of the continuum theory. For our case, as \( \theta \) is discretized to quanta of \( \Delta \theta \), the hopping rate due to diffusion becomes \( D/(r^2 \Delta \theta^2) \) and the hopping rate due to the drift is \( \pm \omega/\Delta \theta \). In order to avoid the (physically impossible) negative hopping rates, one should keep \( \Delta \theta \) small enough. If the effective discretization is given by \( \Delta \theta = \theta_0/n \), one should truncate the matrix \( [11] \) only as

\[ n \sim \frac{\omega R^2 \theta_0}{D} \]  

(18)

Although (18) seems to indicate that the numerical diagonalization of (15) becomes simpler as \( \theta_0 \to 0 \), this, in fact, is not the case. As the eigenvalues of the unperturbed problem are related to the zeroes of the corresponding Bessel functions, and the rotation operator admits matrix elements only between eigenvalues related to Bessel functions of different order, it is much simpler to diagonalize \( [13] \) as \( \theta_0 \gg 0 \). As \( \theta_0 \to 0 \), the higher \( m \) zeroes of any Bessel of order \( n \) are smaller than the \( m = 1 \) zero of the \( n + 1 \) state and the condition (18) implies the diagonalization of an infinite matrix. Accordingly, I present here the numerical results for the case \( \theta_0 = \pi \). This situation does not coincide with the experimental conditions at \( [4] \), but there seems to be no prevention to perform the same experiment with large shielded area.

In Fig. (2), contour plots of the ground state for different angular velocities are shown. One may identify clearly the large deviations from the ground state from its shape at \( \omega = 0 \). The largest 100 spectral points for any case are shown in Fig. (3).

FIG. 4. Highest eigenvalue, \( \Gamma_0 \), in units of \( D/R^2 \), as a function of the angular velocity of the dish. The extinction transition takes place as this eigenvalue is larger than the growth rate inside the pie, \( a_{D/R^2} \), as has been found above.

\[ \begin{align*}
\end{align*} \]
Let us show now how to get a problem equivalent to (1,2) on a rotating petri-dish. In order to do that, the geometry should be taken on a narrow shell as in Fig. (5), i.e., the boundary conditions are,
\begin{align}
c(r, \theta_0, t) &= c(r, 0, t) = 0.
\end{align}
with $\Delta R = R_2 - R_1$. In the limit $R_1 \to \infty$ at constant $n$, the asymptotic expansion of the Bessel functions $J_\nu$ and $Y_\nu$ at large argument gives the eigenfunctions of the unperturbed Liouville operator,
\begin{align}
\phi_{m,n}(r, \theta) &\approx \frac{(\Gamma_{n,m}/D)^{1/4}}{\Delta R R_1 \theta_0} \sin\left(\frac{m\pi r}{\Delta R} + \alpha_n\right) \sin\left(\frac{n\pi \theta}{\theta_0}\right),
\end{align}
where the phase $\alpha_n$ ensures the boundary conditions at $R_1$ and the eigenvalues, $\Gamma_{n,m} = D \frac{n^2 \pi^2}{\Delta R}$, are independent of $n$. The matrix elements of the operator $\omega \partial_\theta$ are given by
\begin{align}
\langle n,m \mid \omega \partial_\theta \mid k,l \rangle &= \omega \delta_{m,l} \gamma_{nk},
\end{align}
with
\begin{align}
\gamma_{nk} &= \begin{cases} 
  k + n = \text{even} & 0 \\
  k + n = \text{odd} & \frac{2\pi n}{\pi^2 - k^2} 
\end{cases},
\end{align}
where the approximation
\begin{align}
\sqrt{R_1} \int_{R_1}^{R_2} \sin\left(\frac{m\pi r}{\Delta R} + \alpha_n\right) \sin\left(\frac{l\pi r}{\Delta R} + \alpha_k\right) \sqrt{r} \, dr \\
\sim \sqrt{R_1} \int_{R_1}^{R_2} \sin\left(\frac{m\pi r}{\Delta R} + \alpha_n\right) \sin\left(\frac{l\pi r}{\Delta R} + \alpha_k\right) \, dr
\end{align}
for $\frac{\Delta R}{R_1} << 1$ has been used. Accordingly, for any $m$ sector, both the diagonal and the off diagonal matrix elements are identical with the corresponding one dimensional problem, and the results should be the same.

In conclusion, the mathematical problem which corresponds to the experiment by [4] has been found to be non-integrable, and no simple gauge transformation connects the eigenvectors of the static and the dynamic problems. The actual critical velocity and ground state properties have to be studied numerically, and the limit of very narrow sector ($\theta_0 \to 0$) involves diverging numerical load. The time scales needed for the ground state to dominate the system are larger than the duration of the actual experiment, and this explains the observed inequilibrium.

I wish to thank A. Kudrolli, D. R. Nelson and K. Dahmen for helpful discussions and comments.

[1] E. Ben-Jacob et al., Nature 368, 46 (1994).
[2] J.-I. Wakita et al., J. Phys. Soc. Japan 63, 1205 (1994).
[3] E. O. Budrene and H. C. Berg, Nature 376, 49 (1995).
[4] T. Neipp, A. Pradhan, D. A. Larochelle and A. Kudrolli, cond-mat/0001023, Phys Rev. E (in press).
[5] J. D. Murray, Mathematical Biology (Springer-Verlag, New York, 1993).
[6] R. A. Fisher, Ann. Eugenics 7, 353 (1937).
[7] A. Kolmogoroff, I. Petrovsky and N. Piscounoff, Moscow Univ. Bull. Math. 1, 1 (1937).
[8] D. R. Nelson and N. M. Shnerb, Phys. Rev. E 58 1383 (1998).
[9] K. A. Dahmen, D. R. Nelson and N. M. Shnerb, cond-mat/9807394 (Jour. of Mathematical Biology, in press).
[10] See also: N. Hatano and D.R. Nelson, Phys Rev. Lett. 77, 570 (1996); J. Feinberg and A. Zee, Phys. Rev. E 59, 6433 (1999).
[11] For a discussion of rotating quantum systems see: M. Abraham, B. Galanti and Z. Olami, Phys. Rev. A 54, 2659 (1996); M Abraham and Z. Olami, Physica A 233, 503 (1996).
[12] For detailed discussion of the numerical instabilities which characterized the analysis of non-Hermitian problem like that see: S. C. Reddy and L. N. Trefethen, SIAM Jour. Appl. Math. 54, 1634 (1994); K. A. Dahmen, D. R. Nelson and N. M. Shnerb, in Statistical Mechanics of Biocomplexity, D. Reguera, J. M. G. Vilar and J. M Rubi (Eds.), (Springer, Berlin, 1999).
[13] See, e.g., F. R. Gantmacher, The Theory of Matrices (Chelsea Publishing Company, New York, 1974).
[14] These boundary conditions are exact if any bacteria becomes immotile at the UV light. This corresponds to the actual experiment - A. Kudrolli, private communication.