What Comes Around Goes Around: A Bug's Life

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1 Introduction

Many biological phenomena such as the spread of a favored gene, the population growth of species, ecological competition, and others are described by equations that contain the dominant physical processes of diffusion, convection, and a background reaction [6]. The model studied in this paper describes the limited universe of these forces and its influence on the lives and deaths one colony of photosynthetic bacteria living on an inhomogenous substrate.

Interestingly, the model reaches beyond the scope of biology to touch upon unexpected research areas in condensed matter physics, including vortices in superconductors [7] and semiconductor physics [5]. The bacteria and vortex systems are mathematically analogous, non-Hermitian models which have drawn a great deal of interest [1],[3] due to their ability to undergo a delocalization transition in their eigenfunctions. Previously such transitions were believed to be impossible in one or two dimensional systems [5].

The goal of this paper is to continue the analysis of Dahmen, Nelson, and Shnerb (DNS) [4],[2], by studying the delocalization transition in the presence of a weakly non-linear saturation term. This term represents the crowding of the bacteria due to competition or deadly concentrations of toxins from their waste.

The model is new territory for the mathematical analysis of pattern formation and population dynamics in biology. With the exception of DNS, very little work has been done on this type of inhomogenous system. Our analysis leads to the very interesting result that the dynamics of the model is governed by a differential-delay equation. This delay equation is explored with the hopes that oscillations, quasi-periodicity or chaos might arise within the physical regime of the model. A little familiarity with delay-equations and a comparison with another familiar delay-equation of mathematical biology, the Glass-Mackey delay-equation [6] , suggests a structural method to quickly predict the dynamic behavior of a subset of such equations.

Finally, several efforts are made to reasonably modify the physical system to achieve interesting dynamics. These attempts include changing the form of the non-linear saturation and the increasing the spatial complexity of the system. The former is proved to be stable, while the latter remains an open-ended question.

2 The Modified Fisher Equation

Imagine one species of bacteria living in a periodic, one-dimensional ring with coordinates in x, $0 < x < L$. Located at at the origin is an "oasis" where plentiful supplies of food and light support life. The rest of the ring is deadly to the bacteria. DNS call this region a "desert". The bacteria experience diffusion, as well as a convective drift due to a background current. They also compete with their fellow neighbors as mentioned above. This is the source of the non-linear term neglected by DNS. The equation governing this model is the Fisher equation with an extra term included to account for convection. Originally, the Fisher equation was proposed as a model for the spread of a favored gene. The modified Fisher equation is then

$$c_t(x,t) + uc_x(x,t) = Dc_{xx}(x,t) + [\beta\delta(x) - \alpha]c(x,t) - bc^2(x,t) \ , \tag{1}$$

where c(x,t) is the concentration of the bacteria. A delta function of strength β represents the oasis and the $-\alpha$ term represents the death rate of the desert. The combination of $\beta\delta(x) - \alpha$ is the spatial inhomogeniety of this particular system.

DS's biological motivation for suggesting this model was to study the effect of spatial inhomogenieties in the underlying medium. Disorder in the medium may be due to many things, including random diffusion constants, stochastic growth and death rates, or a random concentration of environimental factors such as food, toxins or illumination. Here we use the simplest choice, a random concentration of food and/or illumination.

A possible experiment suggested by DNS is to place the bacteria in a thin annular ring covered by a dark mask with a small slot cut to let light pass through. Turning the mask at a slow speed while the ring remains fixed would simulate the convection current. Currently DNS are talking with experimental biologists to do this experiment. Another practical system where this model may be applied is the circumpolar current around Anartica. It has been shown to carry photosynthetic plankton completely around the continent, with various patches of nutrient-rich upswellings supporting the plankton.

3 Linear Stability Analysis

The following section reviews the analysis of the linearized modified-Fisher equation. Here we become familiar with the delocalization transition that occurs in this biological model and with the associated behavior of the eigenspectrum. Linearizing about the fixed point $c = 0$ leads to

$$c_t(x,t) + uc_x(x,t) = Dc_{xx}(x,t) + [\beta\delta(x) - \alpha]c(x,t) \ . \tag{2}$$

3.1 Without the oasis: An example of delocalized modes

Delocalized eigenfunctions are those solutions which have a form like e^{ikx}, where k is complex and the real part is non-zero. The simplest example of a delocalization occurs if $\beta = 0$. Solutions are of the form $c(x,t) = e^{st}e^{ikx}$. Periodicity requires that k be quantized as $k = 2\pi m/L$, where m is an integer.

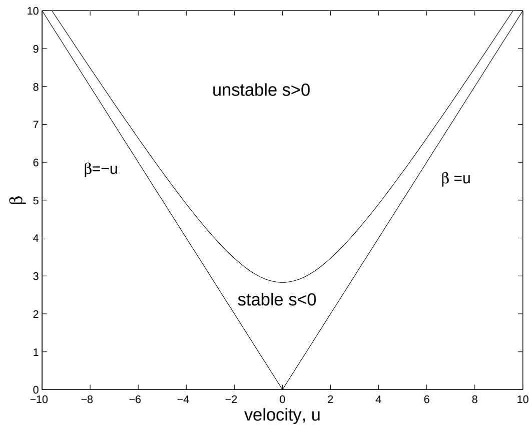

Figure 1: Regime diagram for an infinite ring

The associated dispersion relation is

$$s = -Dk^2 + \alpha - iuk \ . \tag{3}$$

The growth rate, s, is a discrete set of complex numbers. The plot of Re(s) versus Im(s) is a parabola symmetric to the real axis. Increasing the velocity u broadens the parabola. When $u = 0$, the growth rate is real. The value of α determines the stability of the eigenfunctions. The growth rate of the m^{th} eigenfunction will be positive if

$$\alpha > D\left(\frac{2\pi m}{L}\right)^2 \ . \tag{4}$$

The eigenfunction with the largest positive growth rate ($k = 0$) will dominate the system at large times.

3.2 An infinite ring

We begin the linear analysis of our system for the case of an infinite ring because it has simple analytical results which clearly demonstrate the signature of delocalization. Assume $c(x,t) = e^{st}c(x)$ to eliminate the time dependence in (1),

$$sc(x) + uc_x(x) = Dc_{xx}(x) + [\beta\delta(x) - \alpha]c(x) \ . \tag{5}$$

It may also be written as

$$c_t = \mathcal{L}c \ , \tag{6}$$

where the linear operator,

$$\mathcal{L}c = Dc_{xx} - uc_x + [\beta\delta(x) - \alpha]c \ , \tag{7}$$

generates the time-evolution of the system. When $u = 0$, the operator is Hermitian with real eigenvalues, and for strong enough disorder, all of its eigenfunctions are real and localized [2].

Using $c(x) = e^{-kx}$, a dispersion relation is found to have two roots for the wavenumber k,

$$\begin{aligned} Dk^2 + uk - s - \alpha = 0 \ , \\ k_{\pm} = \frac{-u \pm \sqrt{u^2 + 4D(s+\alpha)}}{2D} \ . \end{aligned} \tag{8}$$

Periodicity is satisfied only if the eigenfunction $c(x) = e^{-kx}$ decays as $x \to \pm\infty$. Thus we use k_+ when $x > 0$ and k_- when $x < 0$. This restriction is the equivalent of solving for only the localized eigenfunctions of this physical system, i.e. we are working in the regime where $k_{\pm}$ is real.

Using the appropriate eigenfunction to the left and right of the origin, we integrate (patch) across the delta function to acquire a value for the growth rate s:

$$\begin{aligned} D[\![c_x]\!] + \beta = 0 \ , \\ D[-k_+ - (-k_-)] = -\beta \ , \\ \Rightarrow \quad s = \frac{\beta^2 - u^2}{4D} - \alpha \ . \end{aligned} \tag{9}$$

The expression for $k_{\pm}$ (8) can now be simplified using the growth rate (9),

$$\begin{aligned} k_{\pm} = \frac{-u \pm \beta}{2D} \ , \\ \Rightarrow \quad \beta > u \quad when \ \ u > 0 \ , \\ \beta > -u \quad when \ \ u < 0 \ . \end{aligned} \tag{10}$$

The requirements on $k_{\pm}$ restrict the range of u, according to the given strength of the oasis β. We have one localized solution, although if the oasis were wider than a delta function, say a box, there would be many localized solutions.

A regime diagram (figure 1) maps the properties of this system as β and u vary. The two straight lines, $\beta = u$ and $\beta = -u$, are the boundaries which restrict $k_{\pm}$. If crossed, the eigenfunctions will be in the delocalized regime.

The marginal stability curve is the hyperbola labeled $s = 0$. As the parameters u and β tend to infinity, the marginal stability curve coincides with the delocalization transition. Inside of the hyperbola, s is positive, and thus the eigenfunctions are unstable and grow in time. Outside of the hyperbola, s is negative, and the eigenfunctions are stable and decay with time.

Larger values of α and $|u|$ shift the marginal stability curve upwards, increasing the regime of stability. This is because α is the size of the death rate; while in an infinite ring, larger velocities carry more bacteria and being carried away from the oasis is a sure death sentence in an infinite ring.

The behavior of the concentation $c(x)$ when there is positive background velocity is examined in figure (2). The plots are asymmetric due to the eigenfunction dependence on the sign of u:

$$c(x_{\pm}) = e^{\left(\frac{-u \pm \beta}{2D}\right)x} \ . \tag{11}$$

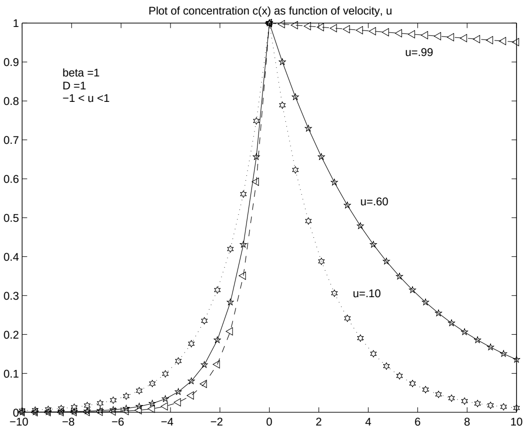

Figure 2: $c(x)$ for positive velocities

The velocity blows bacteria away from the orgin to the right, increasing their concentration in this region. To the left of the origin, the competing mechanisms of diffusion away from the oasis, and advection back into the oasis result in a thin boundary layer. If no wind or current were present, the distribution would be symmetric, decaying exponentially away from the orgin.

As the value of the velocity increases, the concentration becomes nearly constant across x because more bacteria is being blown out of the origin. For this particular example, choices for the velocity u are limited by the choice of $\beta = 1$. At $u = .99$ for instance, the eigenfunction is nearly delocalized. If we surpassed $u = 1$ we would be examing the delocalized spectrum.

The one localized mode, is unstable if

$$\beta^2 > 4D\alpha + u^2 \ . \tag{12}$$

This section has been included to introduce the problem and gain some intuition for the delocalization transition, and its dependence on the physics (D, β, u) of the system. Note that for this infinite ring case, the velocity carries the bacteria away from their haven, never returning them in time before they die. The velocity has a purely deadly effect. Thus, the inequality above, a requirement for instability, makes sense. Only if the life production in the oasis, β, is large enough to overcome the deadly effects of diffusion and convection, will the system grow in time.

3.3 A finite ring with no convective drift

We now study the linearized problem in a finite ring with no wind. When $u = 0$, (5) becomes

$$sc = Dc_{xx} + [\beta\delta(x) - \alpha]c \ . \tag{13}$$

We arrange that the unknown concentration $c(x)$ will be equal to 1 at $x = 0$. The eigenfunctions will then be of the form,

$$c(x) = (1 - A)e^{-kx} + Ae^{kx} \ . \tag{14}$$

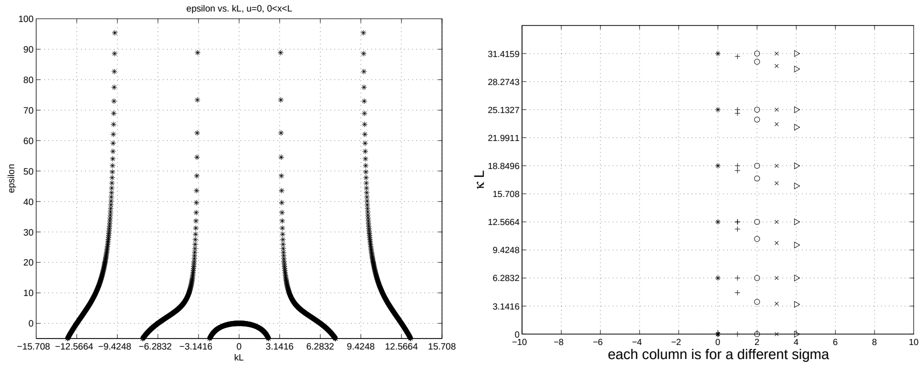

Figure 3: (a) $\sigma = \frac{\beta L}{2D}$ vs κL when $u = 0$ in finite ring (b) roots of $x(1 - \cos(x)) + \sigma \sin(x) = 0$. $* = \sigma = 0$; $+ = \sigma = 5$; $o = \sigma = 15$; $x = \sigma = 25$; $<= \sigma = 35$

Using periodicity, $c(0) = c(L)$, we find an expression for A

$$A = \frac{1 - e^{-kL}}{2 \sinh kL} \ . \tag{15}$$

Combining this result with (14), gives the expression for $c(x)$:

$$c(x) = e^{-kx} + \frac{(1 - e^{-kL})}{\sinh kL} \sinh kx \ . \tag{16}$$

Patching across the delta function gives a transcendental relation for the wavenumber k:

$$2k(1 - \cosh kL) = -\frac{\beta}{D} \sinh kL \ . \tag{17}$$

This is the same expression found for k by DNS [4], if one sets their velocity, v, equal to zero. Their result was found by solving the problem for a periodic domain with an oasis that is a finite square well, and then taking the area of the well to zero.

To study the delocalized spectrum, this expression can be neatly rewritten by letting $k = i\kappa$ and $\sigma = \beta L/(2D)$:

$$\kappa L(1 - \cos(\kappa L)) + \sigma \sin(\kappa L) = 0 \ . \tag{18}$$

In this form, we assume that the wavenumber k is purely imaginary. The spectrum may be studied graphically by plotting σ as a function of kL (see figure 3(a)). The wavenumbers k for fixed σ are found by drawing a line at one value of σ and intersecting the curves. The numerical results are plotted in 3(b) for various values of σ.

A double degeneracy exists in the solutions of the finite ring without a delta function (σ=0). This degeneracy is not reflected in 3(a) because the dispersion relation was obtained after dividing out one extra factor of $\cosh(kL)$. The degeneracy of the eigenvalues is broken by turning on the delta function strength so that $\sigma \neq 0$. As σ is increased, one of the two sets of eigenvalues moves away from the general oscillatory solutions $k = 2\pi m$ of section (3.1). As the strength of the delta function increases, the moving eigenvalues asympotote to $(2m+1)\pi$. The other eigenvalue remains fixed at these values.

None of these delocalized modes are unstable in time, although we will see in the next section, that they can be unstable when there is a strong enough wind to help blow the bacteria around the ring before they die.

One localized mode exists. The solution can be found analytically if one assumes that σ is very large so that $\cosh\sigma \approx \sinh\sigma$. In this limit, we find that $kL \to \sigma$. The localized mode can be unstable depending on the values of the parameters k and α. The dispersion relation for this system is

$$s = Dk^2 - \alpha \; . \tag{19}$$

3.4 Finite length and a constant wind: Traveling around the ring

We now explore the full linearized problem in a finite ring. The relevant partial differential equation is

$$sc(x) + uc_x(x) = Dc_{xx}(x) + [\beta\delta(x) - \alpha]c(x) \; . \tag{20}$$

We begin with the assumption of the form of the concentration $c(x)$, so that $c = 1$ at the origin,

$$c(x) = ((1-A)e^{-kx} + Ae^{kx})e^{-\frac{ux}{2D}} \; . \tag{21}$$

Applying periodicity gives an expression for the constant A

$$A = \frac{e^{\frac{uL}{2D}} - e^{-kL}}{2\sinh kL} \; . \tag{22}$$

Now, to obtain an expression for k similar to (17), we repeat patching. The $uc_x(x)$ term adds nothing new since it is zero when integrating over x; however the derivative of $c(x)$ is now more complicated due to the addition of $u/2D$ in the exponential. Using the definition, $\eta = uL/2D$ where η is the Peclet number of fluid mechanics, we find

$$2k(\cosh\eta - \cosh kL) = -\frac{\beta}{D}\sinh kL \; . \tag{23}$$

Note that if $u = 0$, it is identical to (17) as it should be. Also, if $\mathrm{Re}(k) > u$ and $L \to \infty$ the dispersion relation reduces to (9).

Given the concentration in (21), the dispersion relation is

$$s = Dk^2 - \frac{u^2}{4D} - \alpha \; . \tag{24}$$

To learn more about this new dispersion relation for k, let $k = i\kappa$ and use the definition for σ:

$$\kappa L\,(\cosh\eta - \cos(\kappa L)) + \sigma\,\sin\kappa L = 0 \; . \tag{25}$$

When k is complex, the system is best studied using a numerical algorithim to solve for

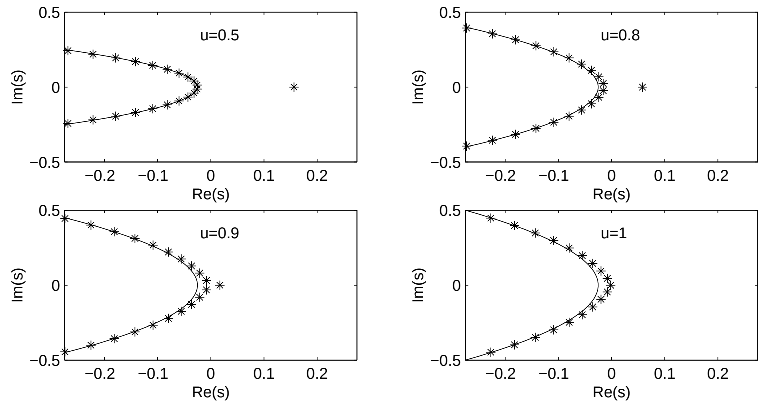

Figure 4: The movement of the localized mode into the delocalized mode with increasing velocity. Complex s is a signature of delocalization

the growth rate s. The results are very interesting. We find that the eigenspectrum is a parabola on the complex plane as it was in section (3.1), but now we also have one real eigenvalue which varies in its distance to the parabola depending on the velocity u. This is the one localized mode that accompanies the delta function. As the velocity is increased, the eigenvalue moves towards and finally onto the apex of the parabola which remains fixed. This represents the same delocalization transition we experienced in section (3.2) when we crossed the boundaries $\beta = \pm u$. Figure 4(b) shows a series of spectra with increasing velocity. Here the critical delocalization velocity, the velocity at which the real eigenvalue moves onto the parabola, is determined by a more complicated relationship between β and u which we examine in the next section.

3.5 An important limit for the finite ring with wind

Here we present a nice way to represent the delocalization transiton for a large but finite ring. This is a new addition to the analysis done by DNS.

In the limit that L is large, (23) reduces to the dispersion relation

$$e^{-L(k-\frac{u}{2D})} = 1 - \frac{\beta}{2kD} \ . \tag{26}$$

We define a parameter P, which in the limit that $L \to \infty$, is a measure of our closeness to the delocalization threshold

$$P = \frac{\beta}{u} - 1 \ . \tag{27}$$

In order to examine the complex eigenvalue spectrum, we rewrite k in terms of a complex parameter ζ,

$$k \equiv \eta[1 + P\zeta] \ , \tag{28}$$

where for eventual simplicity, ζ is

$$\zeta = 1 + \frac{x + iy}{P\eta} \ . \tag{29}$$

Then k becomes

$$k = \eta(1 + P) + x + iy \; . \tag{30}$$

Putting k (28) into the dispersion relation (26) and simplifying gives the expression,

$$e^{-P\eta} = 1 - \frac{P+1}{1+P\zeta} \; . \tag{31}$$

Making the assumption that $P\zeta << 1$, we have a final expression for ζ

$$\zeta = 1 + \frac{e^{-P\eta\zeta}}{P} \; . \tag{32}$$

Using the definitions for ζ (29, 32) and plugging it into k (28), gives a nice expression for the wavenumber

$$k = \eta[1 + P + e^{-\eta P} e^{-x-iy}] \; . \tag{33}$$

Another useful relation is obtained by combining (30, 33),

$$x + iy = \rho e^{-x-iy} \; , \tag{34}$$

where we have used the definition of ρ

$$\rho \equiv \eta e^{-P\eta} \; . \tag{35}$$

Setting real and imaginary parts equal, we have two expressions for x and y,

$$x = \rho e^{-x} \cos y \; , \tag{36}$$
$$y = -\rho e^{-x} \sin y \; . \tag{37}$$

A little maninpulation of these expressions gives the final form that we use to explore the delocalization transition,

$$x^2 + y^2 = \rho^2 e^{-2x} \; , \tag{38}$$
$$\frac{y}{x} = -\tan y \; . \tag{39}$$

Figure (5)(b) plots contours of ρ in the x-y plane. The pair of values (x, y) for each wavenumber k is found by solving

$$x = \rho e^{-x} \cos \sqrt{\rho^2 e^{-2x} - x^2} \; , \tag{40}$$

for a given ρ. The most unstable mode (the largest solution) is x_0, which is determined by $x_0 e^{x_0} = \rho$. The cooresponding y_0 is always zero, so that the most unstable model has a real eignevalue. The higher modes occur in complex conjugate pairs.

For a given value of ρ, one can draw the eigenvalue locii in the x+iy plane. It is found that when $\rho < exp(-1)$, two contour curves exist in the x-y plane, while if $\rho > exp(-1)$, only one curve exists. The associated wavenumbers k are represented as points (x, y) on the curves, corresponding to the intersections in figure 5(a). If we are in the region where

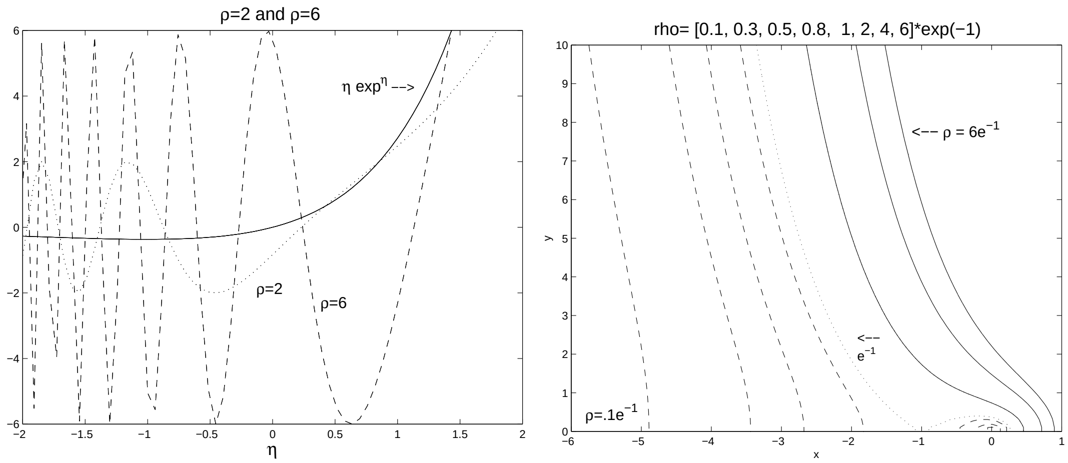

Figure 5: (a) A graphical solution of (37). The solid curve is ηe^{η} and the dashed curves show $\rho \cos\left[\sqrt{\rho^2 e^{-2\eta} - \eta^2}\right]$ for two values of $\rho = [2, 6] * exp(-1)$. (b) Eigenvalue loci obtained from (39) for various values of ρ. The dotted curve is $\rho = 1/e$ and the multi-branched dashed curves are loci with $\rho < 1/e$. The solutions obtained from the intersections of figure 5(a) can be placed on the appropriate curves above.

$\rho > exp(-1)$, the contour of ρ will be to the right of the set of half circles near the origin. An infinite set of discrete pairs of (x,y) (and thus wavenumbers k) are found along each contour in that set. If ρ <exp(-1), two curves exist, a half circle and a line somewhere to the left of the half circle. Only one pair (x_o,y_o) exists on the associated half circle, representing the one localized mode. The second curve will have an infinite but discrete set of (x,y) pairs along it, representing the the delocalized spectrum. When $\rho = exp(-1)$, we are right at the delocalization transition. This corresponds to the eigenvalue s moving onto the apex of the parabola in figure 4(b). Thus, the value of the non-dimensional parameter ρ determines at what velocity the delocalization transiton occurs, for a given β, D, L.

A similar condition restraint of the velocity like $|u| < \beta$ of the infinite ring, comes in the form of the transcendental equation

$$\rho \equiv \frac{uL}{2D} e^{(\beta - u)\left(\frac{L}{2D}\right)} < exp(-1) \ . \tag{41}$$

4 Weakly non-linear anaylsis near the delocalization transition

The goal of this work is to study the effect of the non-linear saturation term on the delocalization transition that we observed in the linear analysis. In the following sections we explore this effect in infinite and finite diameter rings.

The previous section reviewed the results of DNS and carefully studied the existance of the delocalization transition in our one-dimensional model. While DNS quickly discuss the effects of the non-linear term which represents the competition between the bacteria, they do not study it in depth. They suggest that the non-linear term is irrevelant, especially in the limit that the ring has an infinite diameter.

Here we consider the effect of the non-linear saturation term, $-bc^2$, on the delocalization transition and discuss its effects on the dynamics of our bacteria colony. The modified-Fisher equation is now examined in its entirity:

$$c_t + uc_x = Dc_{xx} + [\beta\delta(x) - \alpha]c - bc^2 \ . \tag{42}$$

4.1 Infinite ring on a windy day

We start by studying the infinite ring. We remain near to the delocalization transition represented by the lines in figure (1), by keeping β_c nearly equal to the critical beta, $\beta = u$,

$$\beta = \beta_c(1+\epsilon) \ , \tag{43}$$

where ϵ is a small parameter. We also define a slow time T and express the concentration as:

$$T = \epsilon t \ , \qquad c = \epsilon f \ .$$

Rewritten with these scalings, the adjusted equation is

$$\epsilon f_T + uf_x = Df_{xx} + \beta_c(1+\epsilon)\delta(x)f - \alpha f - b\epsilon f^2 \ . \tag{45}$$

Expanding the eigenfunction $c = \epsilon f$:

$$f = f_0 + \epsilon f_1 + \epsilon^2 f_2 + \dots \ ;$$

Substituting in the expansion of f gives:

$$\epsilon(f_{0T} + \epsilon f_{1T}) + u(f_{0x} + \epsilon f_{1x}) = D(f_{0xx} + \epsilon f_{1xx}) + \tag{47}$$
$$\beta_c(1+\epsilon)\delta(x)(f_0 + \epsilon f_1) - \alpha(f + \epsilon f_1) - b\epsilon(f_0 + \epsilon f_1)^2 \ . \tag{48}$$

The zeroth order equation in ϵ is:

$$Df_{0xx} - uf_{0x} + \beta_c\delta(x)f_0 - \alpha f_0 = 0 \ . \tag{49}$$

It is useful to write (49) in terms of the linear operator $\mathcal{L}$ (7) defined previously in section 3.2, so that

$$\mathcal{L}f_0 = 0. \tag{50}$$

The solution f_0 for this zeroth order homogeneous equation is

$$f_0 = A(T)e^{(\frac{u-\beta_c}{2D}x)} \tag{51}$$

where $A(T)$ is the time-dependent constant of the solution. This is the result we expect, since the zeroth order solution represents the eigenfunction at the delocalization transition.

The constant concentration along x is what would see when $\beta_c = u$ in figure (1). For now, we imagine that β is not quite equal to u. The first-order equation in ϵ is

$$f_{0T} + u f_{1x} = D f_{1xx} + \beta_c \delta(x) f_1 + \beta_c \delta(x) f_0 - \alpha f_1 - b f_0^2 \; . \tag{52}$$

Rewriting (52) in terms of the linear operator, $\mathcal{L}$,

$$\mathcal{L} f_1 = f_{0T} - \beta_c \delta(x) f_0 + b f_0^2 \; . \tag{53}$$

The first order eigenfunctions may be solved for from (53), using the definition of f_0 found in (51).

To find the time-dependence of $f_0 = A(T)$, we derive an amplitude equation. Using the adjoint of f_0, $f_0^\dagger$, and integration by parts, it is easy to show that

$$\langle f_0^\dagger \mathcal{L} f_1 \rangle = \langle f_1 \mathcal{L}^\dagger f_0^\dagger \rangle = 0 \; . \tag{54}$$

We may take advantage of this fact if we multiply (53) by $f_0^\dagger$ and integrate over x. The left hand side dissapears and the right hand side reduces to the amplitude equation

$$\langle f_0^\dagger \mathcal{L} f_1 \rangle = \langle f_1 \mathcal{L}^\dagger f_0^\dagger \rangle \equiv 0 = \langle f_0^\dagger f_{0T} \rangle + b \langle f_0^\dagger f_0^2 \rangle - \langle \beta_c f_0^\dagger f_0 \delta(x) \rangle \; . \tag{55}$$

Using our solution for the zeroth-order amplitude f_0 and performing the integrals results in the amplitude equation:

$$A_T = \left(\frac{\beta_c^2}{2D} \right) A + \frac{6 b \beta_c^2 A^2}{u^2 - 9\beta_c^2} \; . \tag{56}$$

This result is not unusual for a perturbative analyis of a non-linear problem, and is not of much interest except for comparison with the unique results of the next section. It is reassuring to note that if $\beta_c = u$, this amplitude equation blows up, as it should since none of the integrals we performed would have converged. The solution to (56) is found easily using the Bernoulli trick which transforms non-linear equations to solvable linear equations. As a check on this result, one may show that the analytical and perturbative energies agree at the zeroth and first orders.

4.2 Finite ring on a windy day: Part I The solution

In this section we work with the entire physical model. At the origin there is an oasis where the bacteria grows; away from the origin the bacteria struggles for life, dying at a rate α. The bacteria diffuses along concentration gradients and is advected by a constant background flow at speed u. Throughout the ring, the bacteria competes, dying if conditions become too crowded, thus adding to the the resultant death rate of the desert. Finally, the bacteria live in a finite domain with periodic boundary conditions, e.g. a ring.

The strategy here, is to expand near the delocalization threshold, as we have done for the infinite domain. It is also assumed that the ring is large, but finite. Obviously, this is not the most general consideration of the problem that can be made, but it allows one to proceed analytically. The meaning of a large domain will be discussed below.

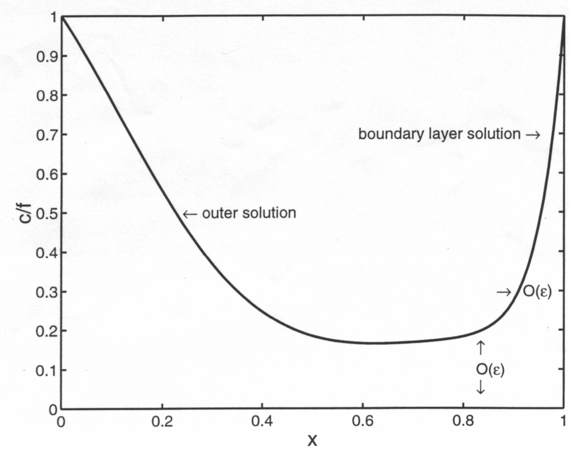

Figure 1: A schematic illustration of the boundary layer structure of the solution if $\varepsilon \ll 1$.

Figure 6: The outer and inner eigenfunctions. $\epsilon \equiv \hat{D}$

We begin by non-dimensionalizing the modified-Fisher equation with the intention of having a firm grasp of the size of each term. Non-dimensionalizing may obscure the physics, but it clarifies the relative magnitudes of terms. It is natural to scale distance with the length of the ring and to scale time with the transit time:

$$\hat{x} = \frac{x}{L}, \quad \hat{t} = t\frac{u}{L}, \quad \delta(x) = \delta(L\hat{x}) = \frac{1}{L}\delta(\hat{x}) \; . \tag{57}$$

The resulting equation is:

$$c_{\hat{t}} + c_{\hat{x}} = \frac{L}{u}\left(\frac{1}{L}\beta\delta(\hat{x}) - \alpha\right)c + \frac{D}{Lu}c_{\hat{x}\hat{x}} - \frac{Lb}{u}c^2 \; . \tag{58}$$

Several more useful non-dimensionalizations are:

$$\hat{\alpha} = \frac{L}{u}\alpha, \quad \hat{\beta} = \frac{1}{u}\beta, \quad \hat{D} = \frac{D}{Lu}, \quad \tilde{c} = \sqrt{\frac{b}{\hat{\alpha}}}\hat{c} \; . \tag{59}$$

These non-dimensionalized constants contain the physical meaning of competing effects. $\hat{\alpha}$ is the ratio of the decay rate α to the advective transit time L/u. $\hat{D}$ is the inverse Peclet number, or a measure of the strength of diffusion versus advection. Finally, $\hat{\beta}$ is a measure to the nearness of the delocalization transition. If $|\hat{\beta}| = 1$, we are at the transition.

The fully non-dimensionalized equation is

$$\tilde{c}_t + \tilde{c}_{\hat{x}} = \hat{D}\tilde{c}_{\hat{x}\hat{x}} + [\hat{\beta}\delta(\hat{x}) - \hat{\alpha}]\tilde{c} - \hat{\alpha}\tilde{c}^2 \; . \tag{60}$$

We are interested in the non-linearity near the delocalization transition, and so we expand $\hat{\beta}$ around 1. Using the non-dimensionalized diffusion coefficient $\hat{D}$ as the small parameter with which we expand, we have

$$\hat{\beta} = 1 + \hat{D}\hat{\beta}_1 \; . \tag{61}$$

When $\beta < 1$ there is a localized mode and this mode becomes delocalized if $\beta > 1$. Thus, condition (61), in which β_1 is held fixed as $\hat{D} \to 0$, ensures that the system is operating close to this delocalization threshold. β_1 may be positive or negative, putting us in either the localized or delocalized regime, as long as $\hat{D}$ is small. Small $\hat{D}$ is the equivalent to large L or large u since $\hat{D} = D/Lu$ (59).

4.2.1 The outer solution

Dropping the tildes and hats for notational simplicity, and making an expansion in the small parameter D, $c \approx c_0 + Dc_1$, (60) becomes:

$$
\begin{aligned}
(c_{0t} + \epsilon c_{1t}) + (c_{0x} + \epsilon c_{1x}) &= (\beta\delta(x) - \alpha)(c_0 + \epsilon c_1) &(62)\\
&+ D(c_{0xx} + \epsilon c_{1xx}) - \alpha(c_0^2 + 2\epsilon c_0 c_1)\ . &(63)
\end{aligned}
$$

The zeroth order equation is then:

$$c_{0t} + c_{0x} = -\alpha c_0 - \alpha c_0^2\ . \tag{64}$$

A series of tricks and substitutions are used to solve for the zeroth order concentration $c_0(x,t)$. The result is

$$c_0(x,t) = \frac{f(t-x)}{(e^{\alpha x} - 1)f(t-x) + e^{\alpha x}}\ . \tag{65}$$

Checking this expression at $x = 0$, reveals $c(0,t) = f(t)$. This implies that all higher-order terms must be zero at the origin. Meanwhile attempting to demonstrate the periodicity of the system at $x = 1$,

$$f(t) = \frac{f(t-1)}{(e^{\alpha} - 1)f(t-1) + e^{\alpha}}\ , \tag{66}$$

requires a stringent restriction of $f(t-x)$, suggesting that there is a problem at $x = 1$.

In fact, this solution is an "outer approximation", which is valid provided that $0 \le x \le 1 - \mathcal{O}(\mathcal{D})$. The failure of the outer solution at the boundary becomes apparent, if we define the restricted parameter λ,

$$\lambda \equiv \frac{e^{-\alpha}}{D}, \quad or, \quad \alpha = \log\left(\frac{1}{\hat{D}\lambda}\right), \tag{67}$$

where λ is fixed as $\hat{D} \to 0$. This means that α is large, but not very large. The parameter λ is necessary for a satisfactory asymptotic development.

In the sequel we will treat α as $\mathcal{O}(D^0)$, except when it appears in exponentials, where it is $\mathcal{O}(D^1)$. This condition means that the population which is swept away from the oasis will decay to $\mathcal{O}(D)$ on its passage through the desert before revisiting the oasis.

In the limit $D \to 0$, with β_1 and λ fixed, all details of the solution can be expressed in terms of $f(t-x)$ and simple functions of x. The form of the solution is indicated in figure (): there is a boundary layer of thickness D immediately to the left of $x = 1$.

Rewriting the zeroth order concentration c_0 in terms of λ and expanding in terms of the small parameter D, we see why the outer approximation does not satisfy the periodicity requirement. At $x = 1$, $c_0(x = 1, t)$ is:

$$c_0(x = 1, t) = \frac{D\lambda f(t-1)}{1 + f(t-1) - D\lambda f(t-1)} \; . \tag{68}$$

Expanding gives,

$$c_0(x = 1, t) \approx \frac{D\lambda f(t-1)}{1 + f(t-1)} - \frac{D^2\lambda^2 f(t-1)^2}{1 + f(t-1)} + \ldots \neq f(t) \; . \tag{69}$$

Near $x = 1$, this outer solution of the concentration of bacteria, c_0 has decayed to O(D) and thus is inappropriate to describe this region of the ring. The role of the boundary layer at $x = 1$ is to repair this failure, and so to determine the evolution of $f(t)$. This insight is the most difficult part of this asympototic expansion.

4.2.2 The boundary layer

We now turn to the "inner region", and introduce the stretched coordinate, $\xi = x/D$. In terms of ξ, equation (60) becomes

$$Dc_t + c_\xi = c_{\xi\xi} + D[\beta\delta(D\xi) - \alpha]c - D\alpha c^2 \; . \tag{70}$$

Making an expansion in D of the concentration: $c(\xi, t) \approx c_0 + Dc_1$, we arrive at an equation to solve for the zeroth order, boundary layer concentration, $c_0(\xi, t)$:

$$c_{0\xi\xi} - c_{0\xi} = 0 \; . \tag{71}$$

The solution is

$$c_0 = fe^{\xi} \; . \tag{72}$$

This solution satisfies the requirement that at $\xi = 0$ we have $c(0, t) = f(t)$, implying that all higher order terms are zero at the origin.

The first order boundary equation is:

$$c_{1\xi} - c_{1\xi\xi} = -\alpha c_0 - \alpha^2 c_0^2 - c_{0t} \; . \tag{73}$$

Solving this inhomogeneous, partial differential equation with the help of the solution $c_0(\xi, t)$ in (72), gives the expression for the first order boundary layer $c_1(\xi, t)$:

$$c_1(\xi, t) = (f_t + \alpha f)\xi e^{\xi} + r(t)(1 - e^{\xi}) + \frac{1}{2}(e^{2\xi} - e^{\xi})\alpha f^2 \; , \tag{74}$$

where r(t) is the constant of integration.

The constant $r(t)$ is found by matching the outer concentration with the boundary layer in the limit that $\xi \to -\infty$, which is equivalent to taking the limit where the boundary layer dissapears, $D \to 0$. The zeroth order boundary solution c_0 is zero, and all the terms but $r(t)$ are zero in the first order boundary layer in this limit. For the matching, the outer solution is evaluated at $x = 1$, which is appropriate in this limit, since there is no boundary current for an infinite domain. This is an example of a "switchback" - the $\mathcal{O}(D^1)$ inner solution matches the leading order outer solution.

The resultant expression for $r(t)$ is:

$$\begin{aligned} c_0(\xi &= -\infty, t) + Dc_1(\xi = -\infty, t) = c_0(x = 1, t) \\ &\Rightarrow \\ r(t) &= \frac{\lambda f(t-1)}{1 + f(t-1)} \ . \end{aligned} \tag{75}$$

The first order expression for the boundary layer concentration is then:

$$c_1(\xi, t) = (f_t + \alpha f)\xi e^{\xi} + \frac{\lambda f(t-1)}{1 + f(t-1)} \left(1 - e^{\xi}\right) + \frac{1}{2}\alpha f^2 (e^{2\xi} - e^{\xi}) \ . \tag{76}$$

Thus $r(t)$ represents a time-delay of $t - 1$. The origin of this term is interesting to note, as it will be the origin of the rest of our discussion.

As usual, an element of information has been neglected by excluding evaluation of the modified-Fisher equation at the origin. The patching condition contains this information, and can now be evaluated since we have expressions for the outer and inner solutions. This condition, obtained by integrating (70) about the orgin, is

$$c_\xi(-) - c_\xi(+) = (1 + D\beta)c(0), \tag{77}$$

where the pluses and minuses indicate evaluation to the left and right of the orgin, and thus imply whether to use the outer or inner solution. For instance, $c_\xi(+)$ is actually the outer solution to the right of the origin, $Dc(x = 0, t)$. Expanding in D gives

$$c_{0\xi} + Dc_{1\xi} - Dc_{0x} - D^2 c_{1x} = (1 + D\beta_1)[c_0(x = 0) + Dc_1(x = 0)] \ . \tag{78}$$

It is interesting to note that the zeroth order outer solution is related non-trivially to the first order boundary solution because of the role of the diffusion coeffcient D as a small parameter.

The zeroth order equation is trivially satisfied due to our choice of the constant in the solution (72). The non-trivial first order expression is:

$$c_x(x = 0, t) - c_\xi(\xi = 0, t) + (1 + \beta_1)c(x = 0, t) = 0 \ . \tag{79}$$

Differentiating the appropriate expressions of the concentration and evaluating them at $x = 0$ ($\xi = 0$) in (79) leads to a very interesting amplitude equation for f(t),

$$f_t = (\frac{\beta_1}{2} - \alpha)f - \frac{3}{4}\alpha f^2 + \frac{\frac{1}{2}\lambda f(t-1)}{1 + f(t-1)} \ . \tag{80}$$

This amplitude equation is a differential-delay equation. The rate of change of f at any time depends not only on the value of f at that particular moment, but also on the particular value of f at a specific earlier time, $t - 1$. Not suprisingly, the time-delay is 1 time-unit, or the time required for transit around the ring. Comparison to the amplitude equation for the infinite ring reveals that we have the same Ginzburg-Landau type terms, while the time-delay piece is a result of the finite-size of the ring. We note that λ is the only parameter that depends on the length of the ring L. As the ring becomes infinite in size, $\lambda \to 0$, so that the differential-delay equation reduces to the Ginzburg-Landau equation of the previous section with redimensionalization.

A good check is to verify that the first order energy obtained from (80) agrees with the analytic expression for the energy of the linear solution. The linearized version of (80) is:

$$f_t = \left(\frac{\beta_1}{2} - \alpha\right) f + \left(\frac{e^{-\alpha}}{2\sigma}\right) f(t-1) \tag{81}$$

Consistent with linearization, we assume this is an eigenvalue problem and let $f = e^{st}$. The expression for the first order energy is then:

$$s = \frac{\beta_1}{2} - \alpha + \frac{e^{-\alpha - s}}{2D} \ . \tag{82}$$

Remembering that we have non-dimensionalized our results, we work the analytic result, (23, 24), into the same form. Non-dimensionalization leads to,

$$2Dk\left(\cosh k - \cosh\frac{1}{2D}\right) = (1 + D\beta)\sinh k \ , \tag{83}$$

$$k \equiv \frac{1}{2D}\sqrt{1 + 4D(\alpha + s)} \ . \tag{84}$$

To show the equivalence, we expand k in D and drop any terms which have $e^{-(1/(2\hat{D}))}$ since they are very small.

$$k \approx \frac{1}{2\hat{D}} + \alpha + s \ . \tag{85}$$

Using this in the transcendental relation for k (81), leaves us with the expression:

$$-\frac{1}{2} + (\alpha D + sD)(e^{\alpha+s} - 1) = D\frac{\beta_1}{2}e^{\alpha+s} \tag{86}$$

Again, we consider which terms are very small. Much smaller than any of the exponential terms, sD is dropped, as is αD, since $\alpha \sim \mathcal{O}(-ln(D))$. Thus, we are left with an expression identical to the first order energy, if we rearrange the following

$$-\frac{1}{2} + (\alpha + s)De^{\alpha+s} = D\frac{\beta_1}{2}e^{\alpha+s} \ . \tag{87}$$

4.3 Finite Ring on a Windy Day: Part II The Dynamics

The next step of this analysis is obvious: we should study the stability of the steady state solutions of our amplitude equation. Before beginning this analysis, we set the tone of the rest of this project by suggesting the results that were expected.

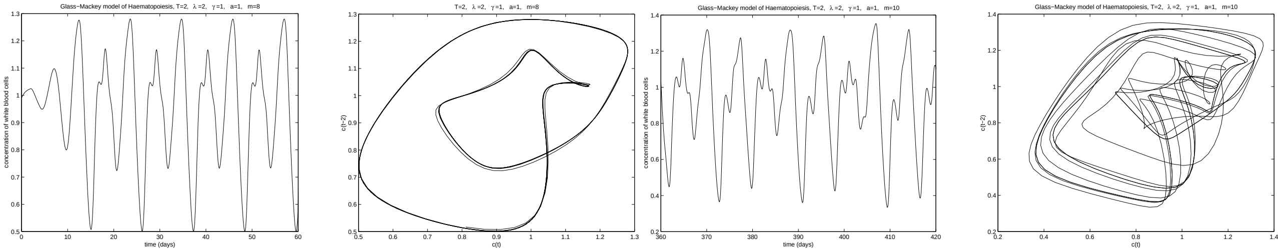

Figure 7: Periodic and chaotic behavior of the Glass-Mackey equation in various regimes (a) quasi-periodic state when m=8 (b) phase diagram, m=8 (c) chaotic state when m=10 (d) phase diagram, m=10

4.3.1 Interesting Zoology of Differential-Delay Equations

Differential-delay equations are well know for their periodic, quasi-periodic, or chaotic behaviour, with examples often arising in biology. One such system is the model suggested by Glass and Mackey [6] to describe the regulation of white blood cells. The structure of the Glass-Mackey equation is similar to our differential delay equation,

$$c_t = \frac{\lambda c(t-T)}{1 + c^m(t-T)} - \gamma c \ , \tag{88}$$

and is nearly identical to ours, if $m = 1$.

This differential-delay equation describes the change in time of the concentration of the white blood cells c_t. The rate at which cells die is proportional to c, e.g., $-\gamma c$. Meanwhile, the flux, λ of new cells produced by bone marrow, is dependent on the concentration of the blood cells at some previous set time, $t - T$ due to a delay time T in the production of white blood cells. This time delay exists because of the time costs of communciation and production. All the parameters, λ, g, m, T are greater than zero. m is a parameter determined experimentally, and if large enough, gives rise to limit cycles or chaos. See figure (7).

In our system, we deal with our first exposure to a delay-equation and thus, a potentially chaotic system. The possiblility of chaotic dynamics of the concentration of bacteria seems like a fascinating result. We examine this possibility below.

4.3.2 What about us? A stability analysis

Thus, one might begin the stability analysis of the bacteria-ring system. Perhaps the three free parameters of our system, λ, β, and α, can have both reasonable physical values and interesting dynamics. Simplifying the differential-delay equation (80) with the definitions

$$\bar{\beta} = \frac{\beta_1}{2} - \alpha \ , \quad \bar{\alpha} = \frac{3}{4}\alpha \ , \quad \bar{\lambda} = \frac{1}{2}\lambda \ , \tag{89}$$

the equation becomes

$$f_t = \bar{\beta} f - \bar{\alpha} f^2 + \frac{\bar{\lambda} f(t-1)}{1 + f(t-1)} \ . \tag{90}$$

The steady-states of (90) are found by letting $f_t = 0$ where $f(t-1) \equiv f(t)$. This leads to a cubic equation for the roots, one of which is zero, and the other two roots are obtained from

$$\bar{\alpha} f^2 + (\bar{\alpha} - \bar{\beta}) f - (\bar{\lambda} + \bar{\beta}) = 0 \; . \tag{91}$$

The roots are

$$f_{\pm} = \frac{(\bar{\beta} - \bar{\alpha}) \pm \sqrt{(\bar{\alpha} + \bar{\beta})^2 + 4\bar{\alpha}\bar{\lambda}}}{2\bar{\alpha}} \; . \tag{92}$$

Discarding the non-physical negative amplitude, we are left with two steady-states which the system may tend towards, $f = 0$ and f_0. A study of the stability is necessary to understand the dynamics. Expanding around the steady-state solutions, we use $f = f_0 + \epsilon f_1$. The delay term in (90) must also be expanded in terms of ϵ. We find that the zeroth order equation for f_0 is just the cubic equation obtained earlier. The first order differential delay-equation defining f_1 is:

$$f_{1t} = \bar{\beta} f_1 - 2\bar{\alpha} f_0 f_1 + \frac{\bar{\lambda} f_1(t-1)}{1+f_0} - \frac{f_0 f_1(t-1)}{(1+f_0)^2} \; . \tag{93}$$

It is useful to define a function N,

$$N = \frac{1}{1+f_0} \; , \tag{94}$$

$$N' = -\frac{1}{(1+f_0)^2} \; , \tag{95}$$

to rewrite (93), where $N' = dN/df_0$. Since this is a *linear* stability analysis, $f = e^s t$, which gives

$$s = \bar{\beta} - 2\bar{\alpha} f_0 + \bar{\lambda} e^{-s}(N + f_0 N') \; . \tag{96}$$

To study the growth rate s, let $s = \mu + i\omega$. (96) becomes,

$$\mu + i\omega - \bar{\beta} + 2\bar{\alpha} f_0 = \bar{\lambda} e^{-\mu - i\omega}(N + f_0 N') \; . \tag{97}$$

Direct instabilities occur when μ, the real part of s, is greater than zero. For simplicity, let $\omega = 0$ and examine if it is possible for $\mu > 0$. We can show that $\bar{\beta} = \bar{\alpha} f_0 - \bar{\lambda} N$, using the zeroth order equation, (91), so that

$$\bar{\beta} - 2\bar{\alpha} f_0 = -\bar{\alpha} f_0 - \bar{\lambda} N \; . \tag{98}$$

Using (98) we arrive at:

$$\mu - \bar{\alpha} f_0 + \bar{\lambda} N(1 - e^{-\mu}) + \bar{\lambda} e^{-\mu} N' \; . \tag{99}$$

Assuming $u > 0$, we find the expression on the right hand side to be negative for all parameters. This disproves our assumption. There can be no direct instability.

Hopf instabilities are the second possible type of linear instability. Breaking (97) up into its real and imaginary parts, squaring and combining them gives

$$(\mu - \bar{\beta} + 2\bar{\alpha} f_0)^2 + \omega^2 = \bar{\lambda}^2 e^{-2\mu}(N + f_0 N')^2 \tag{100}$$

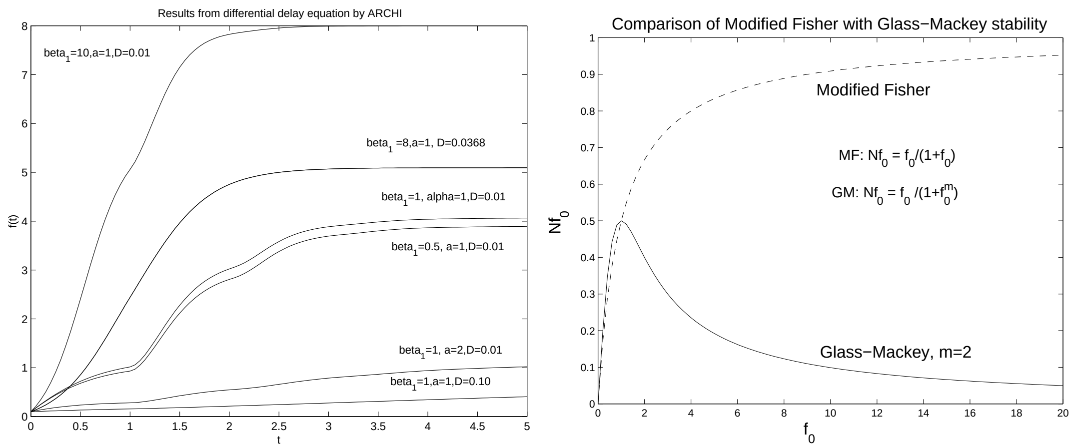

Figure 8: (a) Various steady-state solutions found numerically using ARCHI. Parameters are given with each curve. (b) Plot of Nf_0 vs f_0 of the modified-Fisher equation and the Glass-Mackey equation. The leveling off of the modified-Fisher equation prevents any instability. The negative slope in the Glass-Mackey equation is what gives it the ability to be unstable. The higher the value of the Hill coeffient, m, the steeper the slope.

For simplicity, assume $\mu = 0$, and subtract ω^2 from each side. Using (98), we have the inequality

$$(\frac{\bar{\alpha} f_0}{\bar{\lambda}} + N)^2 < (N + f_0 N')^2 \; . \tag{101}$$

If (101) is true, an instability exists. Further simplification leads to

$$\begin{array}{rcl} |f_0 N'| & > & 2N + \dfrac{\bar{\alpha} f_0}{\bar{\lambda}} \\ & \Rightarrow & \\ -\bar{\lambda}(2 + f_0) & - & \bar{\alpha} f_0 (1 + f_0)^2 > 0 \; . \end{array} \tag{102}$$

This condition is obviously impossible since $f_0, \bar{\alpha}, \bar{\lambda}$ are all positive. Thus, there are no Hopf instabilities. This system is stable – an acceptable but dissapointing result for situation represented by an equation filled with such apparent possiblity. We check these results with a numerical results, exploring some of the 3-dimensional parameter space. The two agree, as shown in figure (8(a)), which plots several numerical results. One may note that the bumpiness in the amplitude corresponds with the time delay, so that at each time unit, the slope increases until the steady-state value is reached.

4.3.3 Key to Instability: A comparison

In hindsight, it is easy to predict that our system will be stable for all parameter space, despite the freedom of three independent parameters, λ, β,and α. The hint is contained in the Glass-Mackey equation (88). Rewriting it in terms of a similar N, the N_{GM} of the

Glass-Mackey equation is,

$$N_{GM}(f_0) = \frac{1}{1 + {f_0}^m} \ , \tag{103}$$

$$N'_{GM}(f_0) = \frac{-m{f_0}^{m-1}}{(1 + {f_0}^m)^2} \ . \tag{104}$$

A similar stability analysis shows that direct instabilities are always impossible, while Hopf instabilities may exist if

$$|f_0 N'| > 2N \ . \tag{105}$$

This inequality is very similar to our the bug-ring system's inequality for Hopf bifurcations. The difference is due to the non-linear term in our amplitude equation (80). One might think that the non-linear term is what is preventing instability – that it is damping out oscillations - but comparison of these two inequalities reveal that the non-linear term only makes what is already impossible, more impossible. The stability is a result of the structure of N and N_{GM}. Plot (8)(b) shows Nf_0 versus f_0, where the slope is $X_i = N + f_0 N'$. For our system, the slope is always positive so that

$$X_1 = N + f_0 N' > 0 \ . \tag{106}$$

For Glass-Mackey,

$$X_2 = N_{GM} + f_0 N'_{GM} < 0 \ . \tag{107}$$

We see from (103) that for a Hopf instability to exist,

$$0 > X_i + N + \frac{\bar{\alpha} f_0}{\bar{\lambda}} \ . \tag{108}$$

This is impossible unless the slope, $X_i < 0$, since the other two terms are positive. And so we see that the structure of N is crucial to the stability of these types of systems.

4.4 Other possiblilities for instability

With the initial goals of this work accomplished, it is fun to continue along further lines of investigation. For instance, is it possible to modify the non-linear saturation term so that we may find a non-steady-state solution? Or what about increasing the spatial complexity? Or perhaps adding another delta function to the ring or many more, will lead to chaotic dynamics. What if the strength of the delta function(s) varies with time? The first two ideas are explored in the rest of this paper.

4.4.1 Adjusting the non-linearity

We begin with the simplest adjustment. What happens if we increase the non-linearity in the modified-Fisher equation from $-bc^2$ to $-bc^n$? Perhaps this will do something. However, it was shown that if we change the power of c to any value n, that the structure of N will be

$$N = \frac{1}{(1 + {f_0}^n)^{\frac{1}{n}}} \ . \tag{109}$$

Direct instabilities remain impossible, while this N still does not yield the negative slope N' necessary for a Hopf instability.

In fact, it appears that we must tailor a function which has a similiar behavior to the Glass-Mackey type N, so that it levels off at some lower value than it's maximum. For our system, this seems physically unreasonable.

4.5 Two delta functions and more... Does spatial complexity breed instability?

The second physically motivated suggestion, is to increase the complexity of the oasis and desert zones to acheive interesting dynamics. If one additional delta function is added to the ring, located at position a', possesing a strength β_1', while the first delta function is located at a with strength β_1, a similar analysis to section (4) leads to two coupled differential-delay equations:

$$f_t = (\frac{\beta_1}{2} - \alpha)f - \frac{3}{4}\alpha f^2 + \frac{\frac{1}{2}\lambda g(t-a)}{1+g(t-a)} \ , \tag{110}$$

$$g_t = (\frac{\beta_1'}{2} - \alpha)g - \frac{3}{4}\alpha g^2 + \frac{\frac{1}{2}\lambda' f(t-a')}{1+f(t-a')} \ , \tag{111}$$

where $\lambda = e^{-\alpha a}/2D$ and $\lambda' = e^{-\alpha a'}/2D$ In general, for independent parameters, these equations yield 8 steady-state solutions (f_0, g_0), if we count $f_0, g_0 = 0$. A study of the stability is quite complex. A few things, however can be said:

1. No direct instabilities exist, for any set parameters.
2. Equal parameters, $\beta_1 = \beta_1'$, $a = a'$, results in the amplitudes f_0 and g_0 always being equal. $(f_0 = g_0)$. This case reduces to the 1-delta function case, so there is no interesting zoology here.
3. When the parameters are not equal, f_0 never equals g_0. Stability has not been proven for this case, although numerical tests suggest that the system is stable.

The first two results are also true a system composed of n delta functions. The coupled delay-equations are straightforward to derive:

$$\begin{aligned}
f_{1t} &= \bar{\beta}_1 f - \bar{\alpha} f^2{}_1 + \frac{\bar{\lambda}_n f_n}{1+f_n} \ , \\
f_{2t} &= \bar{\beta}_2 f - \bar{\alpha} f^2{}_2 + \frac{\bar{\lambda}_1 f_1}{1+f_1} \ , \\
&\dots \\
f_{nt} &= \bar{\beta}_n f - \bar{\alpha} f^2{}_n + \frac{\bar{\lambda}_{n-1} f_{n-1}}{1+f_{n-1}} \ .
\end{aligned} \tag{112}$$

It would be nice to develop a technique to study the stability of all the steady-state solutions for 2-delta functions (and then n-delta's) which is more straightforward than the usual algebraically complex method. Perhaps this will be accomplished as our familiarity with delay-equations grow, just as the simple discovery of N made the analysis of the simplest case swifter and less convoluted.

5 Conclusion

In conclusion, the modified-Fisher equation and the delocalization transition has been studied in detail for a large ring and in the distinguished limit that λ is $\mathcal{O}(1)$. While the differential-delay equation was an unexpected result, it is an interesting property of the system which deserves more study in complex inhomogenous backgrounds. It is also suggested that a time-dependent delta function could model oscillations of illumination due to cloud cover, or the day/night cycle, as well as lead to an interesting problem with a new delay-equation. Other work may also be done in different parameter regimes, especially in the small diameter limit.

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