

Mathematical Biology Assignment 2

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Due Date: 30th September 2020

Q1. Pheromone diffusion in a tube

We will consider the one-dimensional diffusion equation in a very long tube as a good model for the spread of pheromones, which certain ant species use as a signal for danger. Letting $u(x, t)$ be the pheromone concentration, it satisfies

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2}, \quad -\infty < x < \infty, \quad (1.1)$$

where the usual diffusion coefficient is $D = 1$ for ease. We assume this is subject to the initial condition $u(x, 0) = \alpha\delta(x)$ for some $\alpha > 0$. Other ants react to the stimulus if the concentration they perceive is 10% of α or higher, i.e. $u > 0.1\alpha$.

Part a)

From Prac Class 4, we know that the fundamental solution to this equation is

$$u(x, t) = \frac{\alpha}{2\sqrt{\pi t}} e^{-x^2/4t}. \quad (1.2)$$

To find the region of influence $-X(t) < x < X(t)$ whereby ants react to the stimulus, we simply need to use this solution and solve for $u(x, t) > 0.1\alpha$ where we can consider $t > 0$ to be fixed. Then

$$\begin{aligned} u(x, t) &= \frac{\alpha}{2\sqrt{\pi t}} e^{-x^2/4t} > 0.1\alpha, \\ \text{so} \quad e^{-x^2/4t} &> \frac{\sqrt{\pi t}}{5}, \\ \text{so} \quad -\frac{1}{4t}x^2 + \log\left(\frac{5}{\sqrt{\pi t}}\right) &> 0, \end{aligned}$$

where this quadratic has solutions

$$-2\sqrt{t \log(5/\sqrt{\pi t})} < x < 2\sqrt{t \log(5/\sqrt{\pi t})}. \quad (1.3)$$

Hence we have found the interval of influence where $X(t) = 2\sqrt{t \log(5/\sqrt{\pi t})}$. (Comments in next part).

Part b)

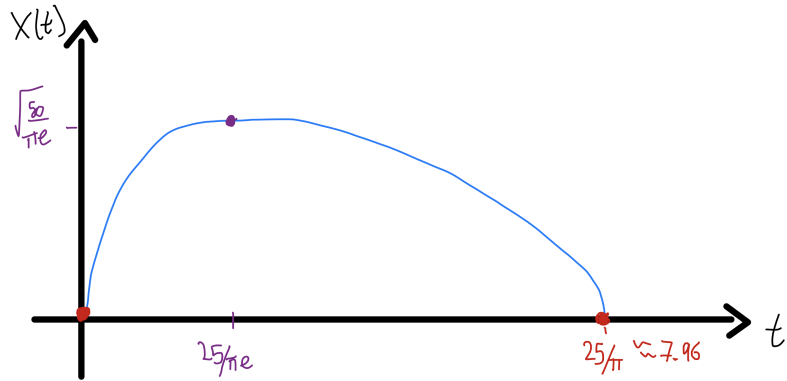


Figure 1.1: Plot of $X(t)$ on the domain for which it exists, $t \in [0, 25/\pi]$.

As we can see in Figure 1.1, $X(t)$ is only defined on a compact domain. This plot suggests that the region of influence increases dramatically soon after $t = 0$, which is conceptually quite obvious as the pheromones diffuse throughout the tube from the initial delta distribution. As the concentration flattens out for $t > \frac{25}{\pi e}$, the region eventually begins to contract on itself since too much of the pheromone concentration has been dispersed. Eventually at $t = 25/\pi$ the Gaussian $u(x, t)$ is so flat that there is no region in which the concentration is higher than 0.1α , hence $X(t) = 0$ for all $t \geq \frac{25}{\pi}$ and so the ants no longer perceive any pheromone beyond this time.

Part c)

The time T^* for which the region of influence is empty for all $t > T^*$ will satisfy $X(T^*) = 0$, as can be seen on the above plot. A quick calculation shows $X(t) = 0$ if $t \log(5/\sqrt{\pi t}) = 0$, hence either $t = 0$ (trivial) or $\log(5/\sqrt{\pi t}) = 0$. Therefore, we see that

$$T^* = 25/\pi. \tag{1.4}$$

Q2. Signal propagation in an axon

A model for signal propagation in an axon is given by

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(1-u)(u - \frac{1}{2}), \quad 0 \leq x \leq L, \quad (2.1)$$

with homogeneous Neumann boundary conditions given by

$$\frac{\partial u}{\partial x}(0, t) = 0, \quad \frac{\partial u}{\partial x}(L, t) = 0, \quad (2.2)$$

where $u(x, t)$ represents the membrane potential. We will consider steady state solutions of the given PDE, that is, where $\frac{\partial u}{\partial t} = 0$.

Part a)

In setting $\frac{\partial u}{\partial t} = 0$, we have a second order ODE in x ,

$$0 = \frac{\partial^2 u}{\partial x^2} + u(1-u)(u - \frac{1}{2}), \quad (2.3)$$

and so in setting $v = \frac{\partial u}{\partial x}$, we have a system of two first order ODEs,

$$\frac{\partial u}{\partial x} = v, \quad \text{and} \quad \frac{\partial v}{\partial x} = -u(1-u)(u - \frac{1}{2}). \quad (2.4)$$

Part b)

To find the equilibrium points, set both derivatives in (2.4) to be zero and so we clearly have three equilibrium points,

$$(u_0, v_0) = (0, 0), \quad (u_1, v_1) = (\frac{1}{2}, 0), \quad (u_2, v_2) = (1, 0). \quad (2.5)$$

To determine their stability, we first calculate the Jacobian of the system $(\frac{\partial u}{\partial x}, \frac{\partial v}{\partial x}) = (f_1(x), f_2(x))$ as in (2.4),

$$J(u, v) = \begin{pmatrix} \frac{\partial f_1}{\partial u} & \frac{\partial f_1}{\partial v} \\ \frac{\partial f_2}{\partial u} & \frac{\partial f_2}{\partial v} \end{pmatrix} = \begin{pmatrix} 0 & 1 \\ 3u^2 - 3u + 1/2 & 0 \end{pmatrix}. \quad (2.6)$$

Hence, we calculate

$$J(0, 0) = \begin{pmatrix} 0 & 1 \\ \frac{1}{2} & 0 \end{pmatrix}, \quad J(\frac{1}{2}, 0) = \begin{pmatrix} 0 & 1 \\ -\frac{1}{4} & 0 \end{pmatrix}, \quad J(1, 0) = \begin{pmatrix} 0 & 1 \\ \frac{1}{2} & 0 \end{pmatrix}. \quad (2.7)$$

Clearly all matrices have the form $\begin{pmatrix} 0 & 1 \\ a & 0 \end{pmatrix}$ for some $a \in \mathbb{R}$, which has characteristic polynomial $p(\lambda) = (\lambda - \sqrt{a})(\lambda + \sqrt{a})$ and hence eigenvalues $\lambda_{\pm} = \pm\sqrt{a}$. Therefore, we see that $(0, 0)$ and $(1, 0)$ are both unstable equilibrium points since they both have one positive real eigenvalue, whereas $(1/2, 0)$ has two purely imaginary eigenvalues and so is a centre.

Part c)

See Figure 2.1.

Part d)

Observe Figure 2.2 and notice there are annotations of three possible circles all satisfying the boundary conditions of $\frac{\partial u}{\partial x}(0, t) = v = 0$ and $\frac{\partial u}{\partial x}(L, t) = v = 0$. What we see is that there is an *infinite* number of L values that satisfy the boundary conditions, but they must be periodically constrained. We have no conditions on the behaviour of u inside the boundary, therefore meaning that a semi-circle (red), full-circle (purple) and double-circle (orange) are all valid steady state solutions for the membrane potential in our axon.

Note that, as predicted from part c), we have a centre at $(1/2, 0)$ and unstable fixed points at $(0, 0)$ and $(1, 0)$.

Part e)

Observe Figure 2.3 for possible schematic sketches of $u(x)$ based on the periodic circles in Figure 2.2. Since Figures 2.1 and 2.2 showed the trajectories in phase space as being ovallic instead of circular, the periodic functions shown will not be precisely cosine functions as they will be steeper and then flatter for different values of x such that $u(x) = 1/2$.

Most importantly, this schematic shows us how the terms in (2.3) impact the steady state of the membrane potential in the axon. In particular, the $\frac{\partial^2 u}{\partial x^2}$ term causes the diffusion of the potential from left to right. Meanwhile the $u(1-u)(u - \frac{1}{2})$ term, which will be negative when $u < 1/2$ and positive when $u > 1/2$, causes the peaks and troughs to be lifted and pushed down respectively. This is analogous to acceleration in the standard harmonic oscillator, which this equation resembles. Referring back to Figure 2.2, this corresponds to different $u(0)$ values being closer and further away from $u = 1/2$.

All in all these models show how the potential $u(x)$ is dispersed throughout axons of different lengths for steady states of the signal propagation. In the absence of the terms mentioned above, the steady state solution would merely be constant and would not contain any diffusion or periodicity, hence being unable to model how the potential rests in the axon.

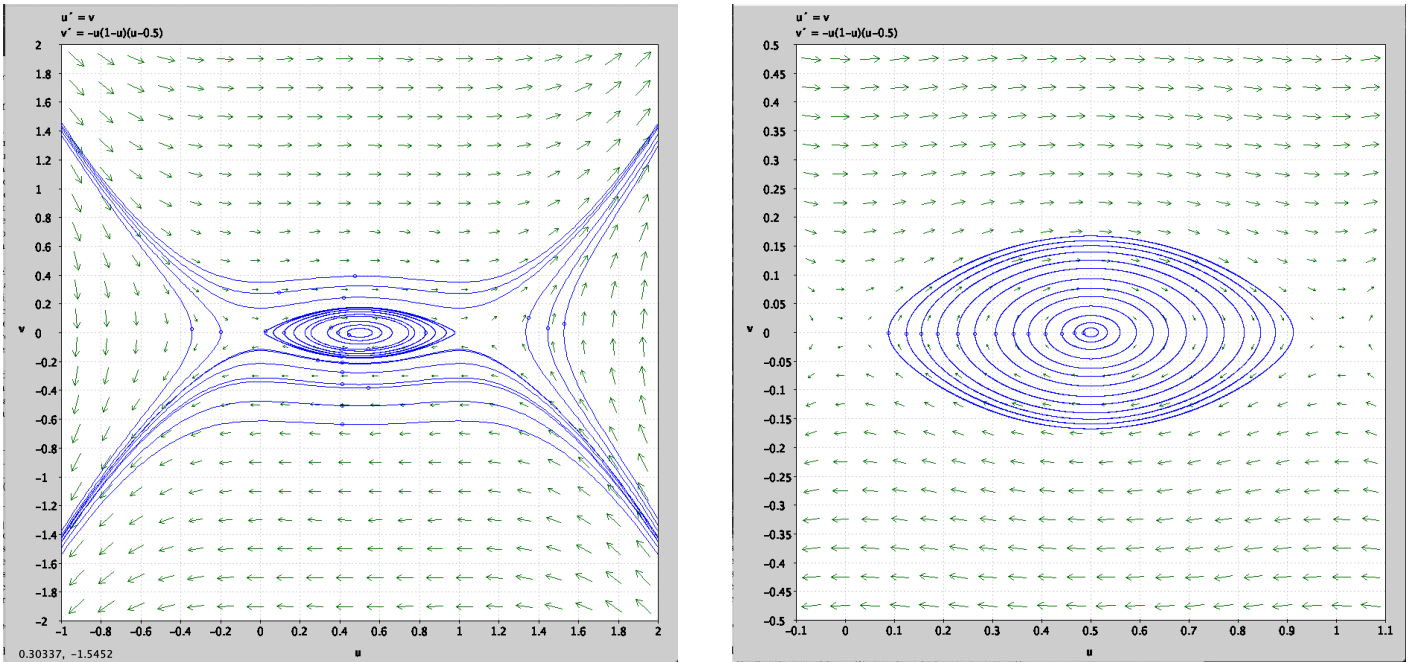


Figure 2.1: Phase plane portraits of $(u, \frac{du}{dx})$ created using `pplane8`, right hand side zoomed in a bit more to avoid precarious solutions in forbidden regions seen on the left hand side. (The left hand plot is clearly the Eye of Sauron).

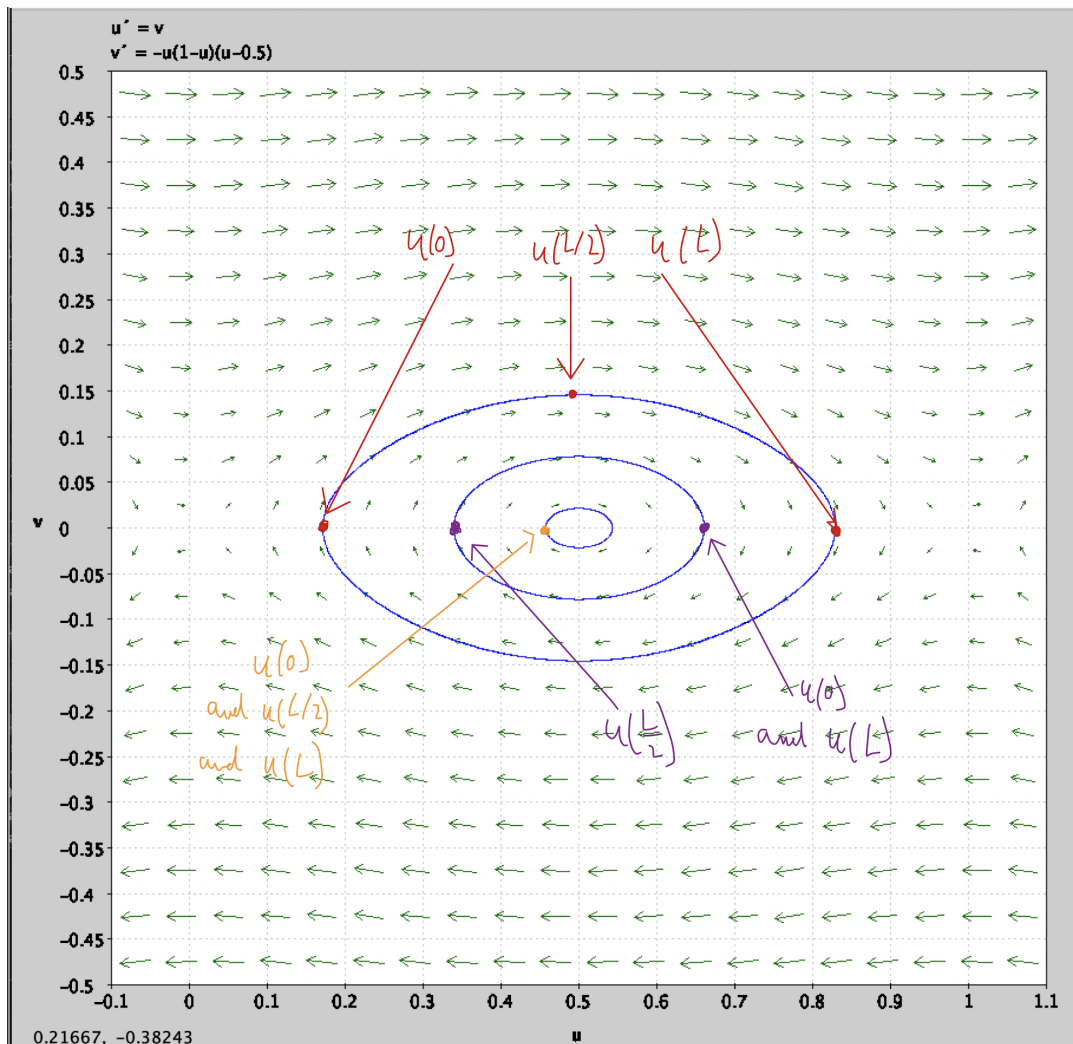


Figure 2.2: Annotated phase plane displaying three possible trajectories with different possible values of $u(0)$, $u(L/2)$ and $u(L)$ for different L values (each colour is a different L).

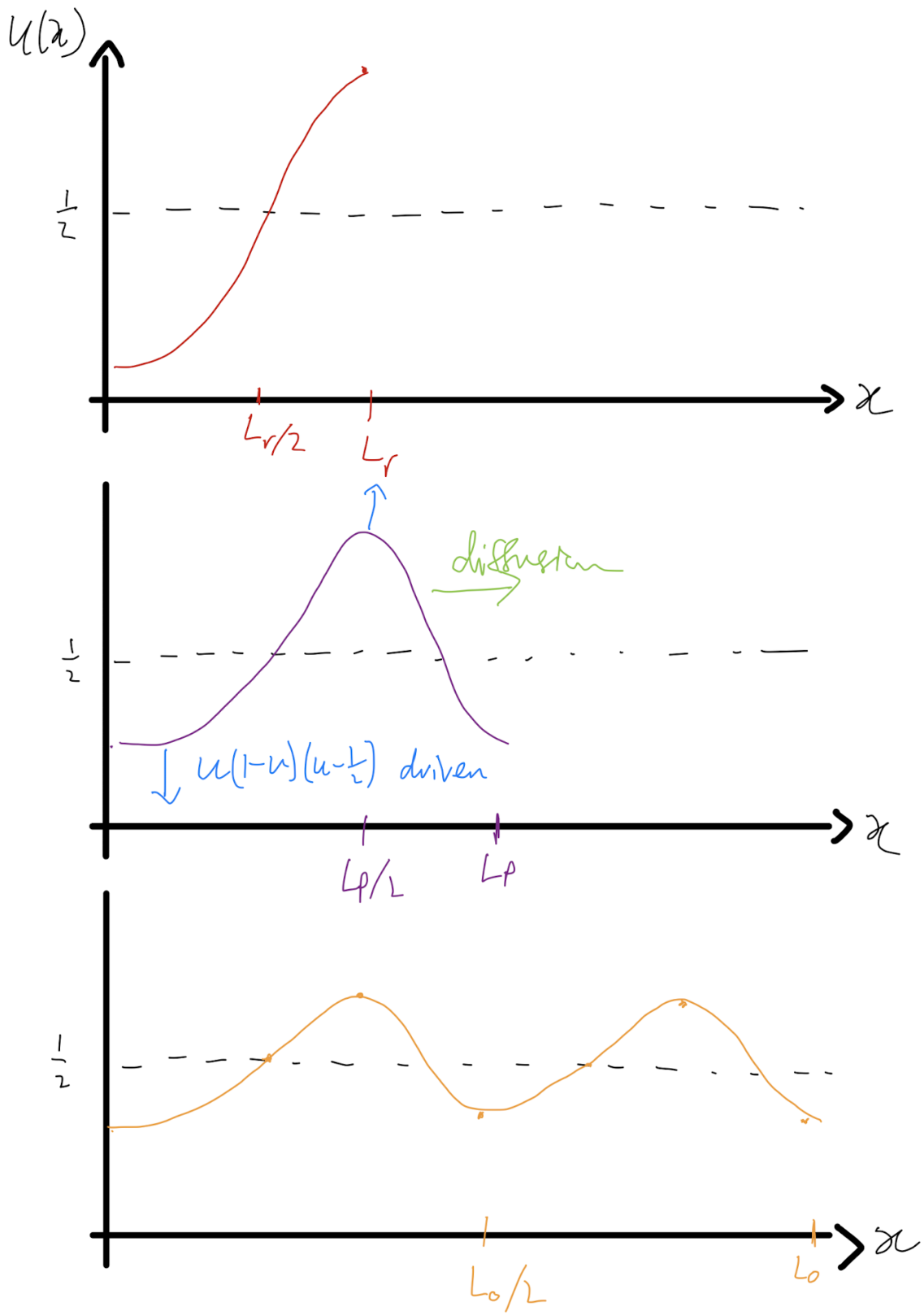


Figure 2.3: Annotated possible schematic sketches for $u(x)$ and different L values. Here we have $L_r = L_p/2 = L_o/4$.

Q3. Micro-organism chemotaxis

Travelling bands of micro-organisms, are chemotactically directed and diffusing, move into a food source - they consume food as they go. A dimensionless model of the situation is given by

$$\frac{\partial b}{\partial t} = \frac{\partial}{\partial x} \left(\frac{\partial b}{\partial x} - 2 \frac{b}{a} \frac{\partial a}{\partial x} \right), \quad \frac{\partial a}{\partial t} = -b, \quad (3.1)$$

where $b(x, t)$ and $a(x, t)$ are the bacteria and nutrient concentrations respectively. The boundary conditions for this problem are given by

$$b(x, t), a(x, t) \rightarrow 0 \text{ as } x \rightarrow -\infty, \quad \text{and} \quad b(x, t) \rightarrow 0, \quad a(x, t) \rightarrow 1 \text{ as } x \rightarrow \infty. \quad (3.2)$$

Part a)

We first note that the second equation of (3.1) states that the rate of food being eaten is proportional to the bacteria $b(x, t)$ for particular x and t values. For the first equation, the form of it is a classic continuity equation for the concentration of bacteria, with an interesting flux term (bracket), but noting that there is no source or sink term. Inside the brackets, $\frac{\partial b}{\partial x}$ is the diffusive term as we are used to in reaction-diffusion problems. The $-2 \frac{b}{a} \frac{\partial a}{\partial x}$ term is the term driving the chemotaxis - that is, it causes a flux in b away from the direction of highest b/a value. In other words, this term drives the bacteria towards the food source due to chemotaxis.

Part b)

We will look for travelling wave solutions setting $b(x, t) = B(z)$ and $a(x, t) = A(z)$ where $z = x - ct$ for a positive wave speed c . Hence we can calculate

$$\begin{aligned} \frac{\partial b}{\partial t} &= -cB'(z), & \frac{\partial a}{\partial t} &= -cA'(z), \\ \frac{\partial b}{\partial x} &= B'(z), & \frac{\partial a}{\partial x} &= A'(z), \\ \frac{\partial^2 b}{\partial x^2} &= B''(z), & \frac{\partial^2 a}{\partial x^2} &= A''(z). \end{aligned} \quad (3.3)$$

Part c)

Subbing these into the second equation of (3.1) we see that

$$A'(z) = \frac{1}{c}B(z) \quad \text{and} \quad -cB'(z) = \frac{\partial}{\partial x} \left(B'(z) - 2 \frac{B(z)}{A(z)} A'(z) \right). \quad (3.4)$$

To specify the new boundary conditions, we note that the boundary conditions must hold for all t values, and in particular for $t = 0$, so a limit in z will be equivalent to a limit in x . Therefore we have a pretty straightforward translation and our new boundary conditions are

$$B(z) \rightarrow 0, \quad A(z) \rightarrow 0 \text{ as } z \rightarrow -\infty, \quad \text{and} \quad B(z) \rightarrow 0, \quad A(z) \rightarrow 1 \text{ as } z \rightarrow \infty. \quad (3.5)$$

Part d)

Integrating both sides of the second equation of (3.4) with respect to x (where we have $dz = dx$), we now have

$$-cB(z) = B'(z) - 2\frac{B(z)}{A(z)}A'(z) + D. \quad (3.6)$$

for some constant D . Applying our boundary conditions, since $A'(z) = B(z)/c$, we see that $A'(z) \rightarrow 0$ as $z \rightarrow \infty$ and so $B(z)A'(z)/A(z) \rightarrow 0$ as $z \rightarrow \infty$ since $A(z) \rightarrow 1$. Finally, we will assume that $B'(z) \rightarrow 0$, which is reasonable to assume for our asymptotic B since this is only false in highly convoluted cases that are not physically realistic (e.g. something like $f(x) = \frac{1}{x} \sin(x^3)$ with infinitely rapid oscillations at infinity, clearly not biological). Note that this is indeed an assumption and is not a given from our boundary conditions. Hence, we see that taking limits of both sides we must have $D = 0$.

Dividing both sides by $B(z)$ and integrating, we see (where E_0, E are arbitrary constants)

$$\begin{aligned} \int -c dz &= \int \frac{B'(z)}{B(z)} dz - 2 \int \frac{A'(z)}{A(z)} dz, \\ \text{so } -cz + E_0 &= \log B(z) - 2 \log A(z), \\ \text{so } Ee^{-cz} &= \frac{B(z)}{A(z)^2} = c \frac{A'(z)}{A(z)^2}. \end{aligned} \quad (3.7)$$

Hence, again integrating both sides, we have (for arbitrary constants F_0, F)

$$-\frac{E}{c}e^{-cz} + F_0 = -\frac{c}{A(z)}, \quad \text{so } A(z) = \frac{1}{\frac{E}{c^2}e^{-cz} + F}. \quad (3.8)$$

Applying the condition $A(z) \rightarrow 1$ as $z \rightarrow \infty$, we see that $F = 1$. Taking the derivative to find $B(z)$, and noting that we can't quite remove the arbitrary constant E with our given information, we have

$$A(z) = \frac{c^2}{c^2 + Ee^{-cz}}, \quad \text{and } B(z) = \frac{Ec^4e^{-cz}}{(c^2 + Ee^{-cz})^2}. \quad (3.9)$$

Just to help with the interpretation of the equation we can reparameterise E in terms of the location of the peak of $B(z)$, denoted z_0 . With a simple calculation we see that $B(z)$ is maximised when $E = c^2e^{cz_0}$. Therefore we can finally write our equations, in terms of the arbitrary location parameter z_0 , as

$$A(z) = \frac{1}{1 + e^{-c(z-z_0)}}, \quad \text{and } B(z) = \frac{c^2e^{-c(z-z_0)}}{(1 + e^{-c(z-z_0)})^2}. \quad (3.10)$$

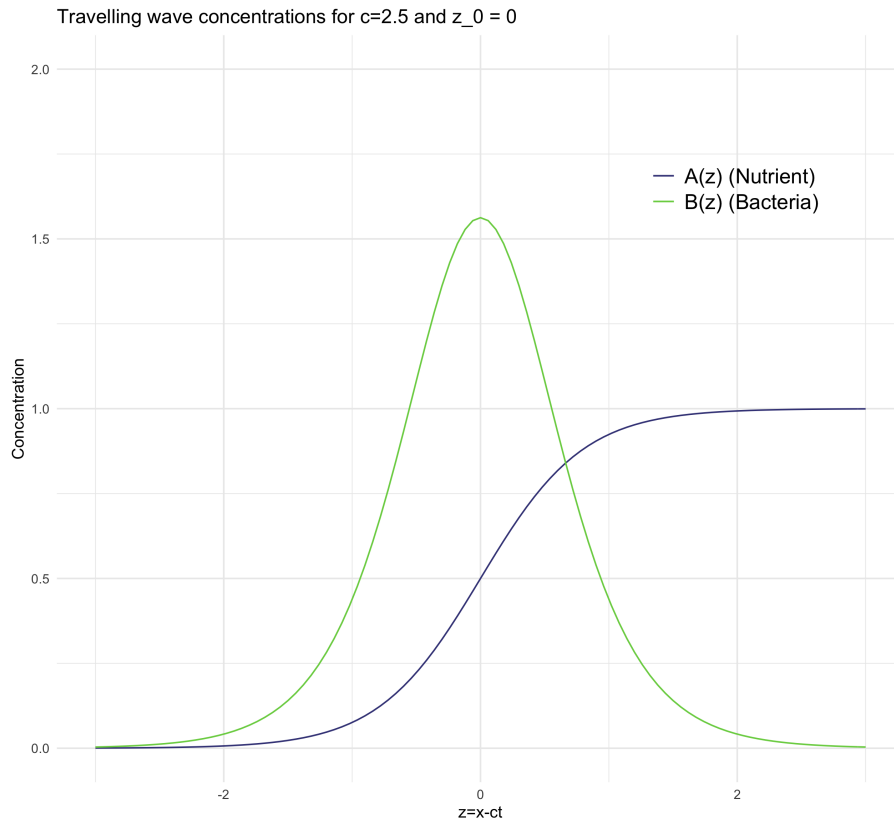


Figure 3.1: Solutions of $A(z)$ and $B(z)$ for $z \in [-3, 3]$ with $c = 2.5$, $z_0 = 0$.

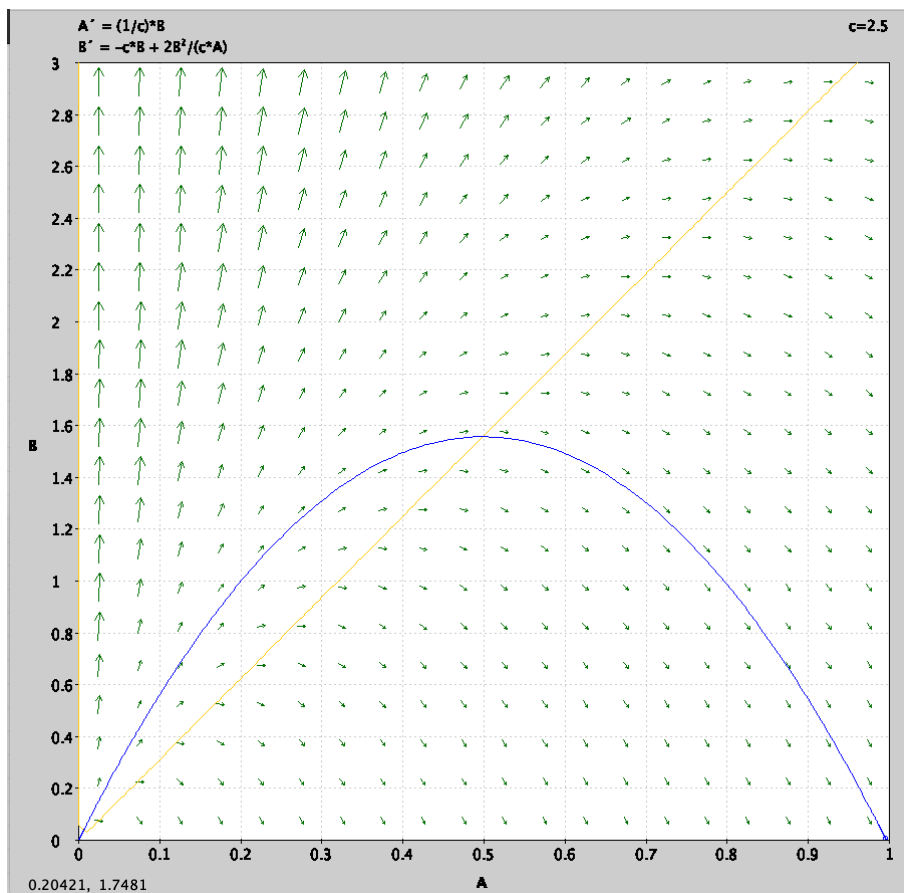


Figure 3.2: Phase plane of $B(z)$ versus $A(z)$ for $c = 2.5$.

Part e)

First, assume for simplicity that we fix a t value, say $t = 0$. Figure 3.1 shows that the bacteria move through the system as a small and highly concentrated packet (a travelling wave) about $z_0 = 0$ (which clearly looks to be Gaussian but we have shown its functional form is slightly different, in particular it has slightly heavier tails). This packet of bacteria then moves through the food from left to right, slowly degrading it as it moves along. Hence we can see it has eaten more than half of the food available for $z = x < 0$, whereas there is still a higher concentration that it will soon devour for $x > 0$. The driving terms discussed in part a) cause the bacteria to be attracted to the highly concentrated regions of nutrient.

Similarly, if we fix $x = 0$ a similar argument can be made for variation in t values, though it is clear that since $z = -ct$ in this case the z -axis of Figure 3.1 must be flipped and rescaled in order to accurately represent t . Nevertheless, we see that for as time increases from say $t = 0$ to $t = 2$ (so $z = 2$), the bacteria progressively eat most of the nutrient at the one location $x = 0$, again moving as a travelling wave.

Part f)

Putting our previous work together in a more palatable format, we can plot the following system of equations on **pplane**

$$\frac{dA}{dz} = \frac{1}{c}B(z) \quad \text{and} \quad \frac{dB}{dz} = -cB(z) + \frac{2B(z)^2}{cA(z)}. \quad (3.11)$$

Due to our imposed boundary conditions on A , that is, $A(z) \rightarrow 1$ as $z \rightarrow \infty$, there is *only one* phase plane trajectory that suits our problem - producing any others in **pplane** would have a different $A(z)$ asymptote.

The phase plane doesn't tell us much that we don't already know from the above analysis, though it does provide a useful visual guide for assessing how the concentration of bacteria relates to the nutrient for a given z value. The parabolic shape represents the fact that there are effectively zero bacteria where the nutrient is zero (as they have eaten it) and the where the nutrient is one (as they haven't moved there yet). Also, the midpoint $A = 1/2$ really does represent the location for which the bacteria are most concentrated.