PHYSICS 282 Spatiotemporal Biodynamics

Homework #4 (amended)

Due Wednesday Dec 11, 2024

[Note: Those not from math/physics background need not attempt problem(s) indicated by *]

1. Mutualistic interaction in the batch culture. In class, we consider the problem where a species (1) of bacteria consumes a substance A and excretes a substance B, with B being toxic to the excreting species but taken up as nutrient for growth by another species (2). Consider the case where species 1 and 2 are placed in a "batch culture" (e.g., a flask) where the substance A is provided in saturating concentration, and there is no dilution. Assume that the flask is very large so you don't have to worry about cells getting too dense. Let ρ_1, ρ_2 denote the density of the two species and n_B denote the concentration of substance B. Let the replication rate of the two species be $r_1(n_B) = r_{1,0}/(1 + \frac{n_B}{K_I})$ and $r_2 = r_{2,0}\, n_B/(n_B + K_B)$ where $r_{1,0}$ and $r_{2,0}$ are the growth rates of the two species under saturating nutrient, K_I is the half-inhibitory concentration, and K_B is the Monod constant for species 2 to grow on B. Finally, B is excreted by species 1 at rate γ per cell and the yield of species 2 growing on B is Y_B.

(a) Find the growth rate λ where the two species grow at the same rate. Find the nutrient concentration n_B^* at this steady state, and find the ratio of the two species.

(b) Show that this steady state is stable by considering what happens if the nutrient concentration is transiently different from n_B^*.

(c) Next consider the case where species 2 is absent. Let the starting density be $\rho_1(0) = \rho_0$ at time $t = 0$. Derive a relation between $\rho_1(t)$ and $n_B(t)$ by observing that $\frac{d\rho_1}{dn_B} = \frac{\dot{\rho}_1}{\dot{n}_B}$ has a simple form that can be integrated. Use the relation derived to obtain a nonlinear ODE for $\rho_1(t)$. The solution of this ODE cannot be expressed in terms of elementary functions. To see what it describes, you can solve the non-dimensionalized version of the ODE numerically, plot $\ln(\rho_1(t)/\rho_0)$ vs time. Show that behavior of the solution at small and large time are very different and obtain the approximate form numerically for these two regimes. Explain what the two regimes mean biologically. Find and rationalize the time scale $t_\times$ separating the two regimes.

[For the more mathematically inclined: show that the increase of $\rho_1(t)$ at large time is in between logarithmic and linear dependence.]

(d) Compare your answer to part **(a)** and **(c)** to assess the effect of species 2 on species 1. Explain why this effect is so different from the effect obtained in class for the same system in a chemostat.

2. Production and cross-feeding of substitutable nutrients. Consider two species of bacteria with density ρ_1, ρ_2, which generate nutrients n_A and n_B, respectively. Take these two nutrients to be substitutable. Examples could be the polymers chitin and alginate, both of which can be broken down into monomeric sugars by special (and different) enzymes. The population dynamics of this system in a chemostat can be described by the following system of ODEs:

$$\dot{\rho}_1 = (\nu_{1A} n_A + \nu_{1B} n_B) \cdot \rho_1 - \mu \cdot \rho_1,$$

$$\dot{\rho}_2 = (\nu_{2A} n_A + \nu_{2B} n_B) \cdot \rho_2 - \mu \cdot \rho_2$$

$$\dot{n}_A = \gamma_{1A} \rho_1 - \mu n_A - (\nu_{1A} \rho_1 + \nu_{2A} \rho_2) \cdot n_A$$

$$\dot{n}_B = \gamma_{2B} \rho_2 - \mu n_B - (\nu_{1B} \rho_1 + \nu_{2B} \rho_2) \cdot n_B$$

where $\nu_{i\alpha}$ are the nutrient uptake matrix introduced before, μ is the dilution rate, and γ_{1A}, γ_{2B} are the two nutrient production rates. The yield factor has been set to unity for simplification.

(a) in the limit of small μ, show that steady state solution would have $n_\alpha^* \propto \mu$ and $\rho_i \propto \mu^2$.

(b) By setting $\dot{n}_\alpha = 0$, solve for the steady state condition $n_A^*(\rho_1, \rho_2)$ and $n_B^*(\rho_1, \rho_2)$. Find the leading order dependence on ρ_1 and ρ_2 in the limit of small μ. Substitute these expression into the ODEs for ρ_1 and ρ_2 to obtain two nonlinear ODEs involving only ρ_1 and ρ_2 to the leading order for small μ.

(c) Plot the null-clines and sketch the phase flow of the ODEs obtained in part **(b)** for i) $\nu_{1A} > \nu_{2A}$ and $\nu_{2B} > \nu_{1B}$, and ii) $\nu_{1A} < \nu_{2A}$ and $\nu_{2B} < \nu_{1B}$. Describe the dynamics of the system in words for each regime, in particular, the dependence on initial densities $\rho_1(0)$ and $\rho_2(0)$.

(d) Investigate the growth phase at high densities (the runaway part of **(c)**) by assuming the nutrients have reached constant concentrations of values n_A^* and n_B^*, while the two species grow exponentially with rates λ_1 and λ_2. Find the values of n_A^* and n_B^* for i) $\lambda_1 > \lambda_2$ and ii) $\lambda_1 < \lambda_2$. Relate the resulting dynamics to the simple producer-cheater relation discussed in class and use the results derived in class to describe the parameter regime where species 1 dominates, species 2 dominates, or when either species can dominate. In the last case, what is species dominance determined by?

(e) Continuing the investigation above, we next study the case $\lambda_1 = \lambda_2$ (and refer to both as λ). Find n_A^* and n_B^* in this case and the growth rate λ in terms of the model parameters. [To simplify the algebra, you may take $\nu_{1A} = \nu_{2B} \equiv \nu$, $\nu_{2A} = \nu_{1B} \equiv \nu'$, and $\gamma_{1A} = \gamma_{2B} \equiv \gamma$.] To see whether the fixed point solution obtained here is stable, apply Tilman's analysis in the space of (n_A, n_B) for the two parameter regimes discussed in **(c)**: i) $\nu_{1A} > \nu_{2A}$ and $\nu_{2B} > \nu_{1B}$, and ii) $\nu_{1A} < \nu_{2A}$ and $\nu_{2B} < \nu_{1B}$.

(f) Summarize your findings in parts (d) and (e) by indicating the phase diagram in the space of $\left(\frac{\nu_{1A}}{\nu_{2A}}, \frac{\nu_{2B}}{\nu_{1B}}\right)$. Compare your result to the conditions derived in class for the case of essential nutrients. Discuss the differences between the two cases.

3*. Predator-Prey chase. Early on in the course (towards the end of Lecture 2), we analyzed a modified Lotka-Volterra description of the predator-prey system:

$$\dot{p} = rp \cdot (1 - p/\tilde{p}) - \nu pq \tag{1}$$

$$\dot{q} = \nu pq - \delta q \tag{2}$$

where p, q refer to the density of the prey and predator, respectively, r is the replication rate of the prey and δ is the death rate of the predator. This description differs from the original Lotka-Volterra system by the addition of the term $p/\tilde{p}$ in the growth of the prey, describing the effect of the prey's carrying capacity, $\tilde{p}$. As discussed then, the introduction of the carrying capacity breaks an accidental conserved quantity in the original Lotka-Volterra system, turning the oscillatory solution of the original system into a stable system, with $p(t), q(t)$ settling down to the fixed point p^*, q^* in the long-time limit as long as the dimensionless parameter of the system $\eta \equiv \delta/(\nu\tilde{p})$ is the below 1, i.e., if the predator's death rate does not exceed its maximal growth rate (obtained for prey at its carrying capacity).

In this problem, we will consider the spatial version of the above predator-prey system, described by Eqs. (1) and (2) with the addition of spatial diffusion term for the predator, i.e., with a term $D_q \frac{\partial^2}{\partial x^2} q$ added to the right-hand side of Eq. (2), D_q being the diffusion coefficient. The prey is considered as immobile. [Thus, the prey can be plantation and predator be herbivores.] Suppose the initial distributions are such that the two are in coexistence on the left side, i.e., $p(x = -\infty, t = 0) = p^*$ and $q(x = -\infty, t = 0) = q^*$, while on the right side, predator is absent and the prey is at its carrying capacity, i.e., $p(x = \infty, t = 0) = \tilde{p}$ and $q(x = \infty, t = 0) = 0$. Clearly as time progresses, the predator is going to advance to the right, reducing the density of the prey from $\tilde{p}$ to p^*. This is known as "wave of pursuit". You are asked to solve the propagation speed w of this wave and the shapes of the space-dependent density functions $p(x,t) = P(x - wt)$, $q(x,t) = Q(x - wt)$ during their rightward propagation. Below are some suggested steps.

(a) Make the variables dimensionless by following the scaling used on p.14 of Lecture Note, to obtain the dimensionless densities for the prey and predator, $u(\xi,\tau)$ and $v(\xi,\tau)$, respectively, for suitably scaled of the length and time scales, ξ and τ. You should end up with two dimensionless parameters: $\eta \equiv \delta/(\nu\tilde{p})$ (as introduced above) and $a \equiv \nu\tilde{p}/r$. [As explained above, we will always take $\eta < 1$.] Look for the propagating solutions, $u(\xi,\tau) = U(\xi - c\tau)$ and $v(\xi,\tau) = V(\xi - c\tau)$, by turning the two PDEs for u and v into two ODEs for U and V.

(b) Focus on the form of the propagating solutions at the leading front, i.e., for $z = \xi - c\tau \to \infty$. Assuming that the solutions extends exponentially into the asymptotic values $U(\infty) = 1$ and $V(\infty) = 0$, i.e., $U(z) \approx 1 - U_0 e^{-\lambda z}$ and $V(z) = V_0 e^{-\lambda z}$ for some coefficients U_0, V_0. Plug these forms into the two ODEs to obtain a cubic equation for λ. Analyze each of the 3 roots of λ and the associated forms of the density functions to determine a criterion for the propagation speed c in terms of the two parameters η and a. Explain how the notion of "marginal stability" can be used to fix the value of c.

(c) Next, consider the form of the density functions on the left side, i.e., for $z = \xi - c\tau \to -\infty$. Let $U(z) = u^* + u_0 e^{\kappa z}$ and $V(z) = v^* - v_0 e^{\kappa z}$, where u^*, v^* are the fixed point values of the original system. Show that for the nature of the solution depends on the value of the dimensionless parameter a: For $0 < a < a^*$ where a^* is a positive constant whose value depends on η, exponentially damped solution exist. For $a > a^*$, the solution is oscillatory. Put your results for (b) and (c) together to sketch the forms of the solutions $U(z)$ and $V(z)$ for the entire domain $-\infty < z < +\infty$.