PHYSICS 282 Spatiotemporal Biodynamics

Homework #3

Due Monday Nov 18, 2024

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

1. Relationship between the Consumer-Resource model and population dynamics model. In class, we went over the dynamics in the chemostat. Describing the density of the organism by $\rho(t)$ and the nutrient concentration in the chemostat by $n(t)$, the CR model for the system is

$$\dot{\rho} = r(n) \cdot \rho - \mu\rho, \tag{1.1}$$

$$\dot{n} = \mu \cdot (n_0 - n) - r(n) \cdot \rho/Y \tag{1.2}$$

where $r(n) = r_0\, n/(n+K)$ is the nutrient-dependent replication rate, μ is the dilution rate of the chemostat, $n_0\mu$ is the nutrient influx, and Y is the biomass yield.

In this problem, you will derive the logistic equation which describes the dynamics of the population without referencing the nutrient,

$$\dot{\rho} = \tilde{r}\rho \cdot (1 - \rho/\tilde{\rho}), \tag{1.3}$$

and obtain the effective replication rate ($\tilde{r}$) and carrying capacity ($\tilde{\rho}$) in terms of the chemostat parameters (μ, n_0) and the physiological parameters (r_0, K, Y). Through this exercise, you will get a feel of the occurrence of "dimension reduction" (in this case, referring to a system with two degrees of freedom, $\rho(t)$ and $n(t)$ being reduced to a single degree of freedom $\rho(t)$).

(a) We shall work in a parameter region typical of chemostat operation, $\mu \ll r_0$, for which we can linearize the replication rate, taking it to be $r(n) \approx r_0 n/K \equiv \nu n$. Using this linear form of $r(n)$, express the CR equations in terms of two dimensionless variables $u \equiv n/n_0$ and $v \equiv \rho/\rho_0$ (where $\rho_0 \equiv n_0 Y$), the dimensionless time variable, $\tau \equiv n_0 \nu t$, and a dimensionless parameter, $\eta \equiv \mu/(\nu n_0)$. Sketch the two null clines and the fixed point (u^*, v^*) for $\eta < 1$ (where a nontrivial steady state with $\rho^* > 0$ exists).

(b) Expand u, v in the vicinity of the fixed point, i.e., for $u = u^* + x$ and $v = v^* + y$. For $|x| \ll u^*$ and $|y| \ll v^*$, the equation of motion can be reduced to the following linear equation

$$\lambda \binom{x}{y} = \mathcal{M} \binom{x}{y}, \tag{1.4}$$

where λ is the eigenvalue. Workout the form of the matrix $\mathcal{M}$. From $\det(\mathcal{M} - \lambda \cdot \mathcal{I}) = 0$ (where $\mathcal{I}$ is the identity matrix), solve for the two eigenvalues in term of η. In one plot, sketch how the two eigenvalues depend on η for $0 < \eta < 1$.

(c) The more negative eigenvalue (denoted as λ_{fast}) describes the decay rate of the *fast mode* and the less negative eigenvalue (denoted as λ_{slow}) describes the decay rate of the *slow mode*. For $\eta > 0.5$, what is the expression for $\lambda_{\text{slow}}(\eta)$? To find the slow mode itself, use $\lambda_{\text{slow}}(\eta)$ in the linear equation (1.4) to obtain an equation relating $x(t)$ and $y(t)$; this equation describes the slow mode. To see what this slow-mode means, re-express the equation for the slow mode in terms of $u(t)$ and $v(t)$, using the expressions for the fixed point $u^*(\eta)$ and $v^*(\eta)$. Sketch the slow-mode in (u, v) space along with the fixed point and the null clines. Next re-express the slow-mode for $u(t)$ and $v(t)$ in terms of the original variables $n(t)$ and $\rho(t)$. Can you interpret the meaning of the slow mode now?

(d) Over long time scales (after the fast mode has settled down), the two dynamical variables $n(t)$ and $\rho(t)$ collapses onto the slow mode, such that the slow mode equation becomes a constraint, and the system is effectively that of a single variable. Use this constraint to express $n(t)$ in term of $\rho(t)$, and substitute the resulting expression for $n(t)$ into Eq. (1.1) to obtain an effective equation for $\rho(t)$. Show that it is of the logistic form Eq. (1.3) and find the two parameters of the logistic equation, $\tilde{r}$ and $\tilde{\rho}$ in terms of the original parameters of the system.

(e) Comment on the range of η for which derivation of the logistic equation (part (d)) breaks down. Given that large the separation of the two time scales (λ_{fast} and λ_{slow}), the better is the derivation, what range of η is the chemostat system best approximated by the logistic equation? what are the values of $\tilde{r}$ and $\tilde{\rho}$ in this limit? Can you come up with a general explanation for why the logistic equation is a good approximation of chemostat dynamics in this limit?

2. Competition for nutrient. Two species described by densities $\rho_1(t)$ and $\rho_2(t)$ grow on the same nutrient source, of concentration $n(t)$. Suppose the growth rate of species i is given by the Monod growth law, $r_i(n) = r_{i,0} \cdot n/(n + K_i)$, the death rate is δ_i, and the nutrient influx is j_0. Find a criterion on the physiological parameters $(r_{i,0}, K_i, \delta_i)$ in order for species i to survive in the steady state.

3*. MacArthur's model of resource competition. MacArthur's model applied to 2-species (of densities ρ_1, ρ_2) and 2 substitutable nutrients (of concentrations n_A, n_B) is

$$\dot{\rho}_1 = (\nu_{1A} n_A + \nu_{1B} n_B) \cdot \rho_1 - \delta_1 \rho_1, \quad (3.1)$$

$$\dot{\rho}_2 = (\nu_{2A} n_A + \nu_{2B} n_B) \cdot \rho_1 - \delta_2 \rho_2, \quad (3.2)$$

$$\dot{n}_A = \gamma_A n_A \cdot (1 - n_A/K_A) - (\nu_{1A}\rho_1 + \nu_{2A}\rho_2) \cdot n_A, \quad (3.3)$$

$$\dot{n}_B = \gamma_B n_B \cdot (1 - n_B/K_B) - (\nu_{1B}\rho_1 + \nu_{2B}\rho_2) \cdot n_B. \quad (3.4)$$

where $\nu_{i\alpha}$ is the consumption matrix indicating the uptake preference of species i for nutrient α, δ_i is the death rate of species i, and γ_α is the generation rate, K_α is the concentration scale of nutrient α in the habitat. (The yield factor has been omitted for simplicity.)

(a) Assume the existence of a non-trivial steady state with $n_A^*, n_B^*, \rho_1^*, \rho_2^*$ all being non-zero. From $\dot{\rho}_i/\rho_i = 0$ in Eqs. (3.1) and (3.2), show that in the limit the death rate $\delta_i \to 0$, the steady state concentrations $n_\alpha^* \to 0$. Using this result in Eqs. (3.3) and (3.4), show that $\dot{n}_\alpha/n_\alpha = 0$ lead to the following equation for the steady state densities,

$$\begin{bmatrix} \nu_{1A} & \nu_{2A} \\ \nu_{1B} & \nu_{2B} \end{bmatrix} \cdot \begin{bmatrix} \rho_1^* \\ \rho_2^* \end{bmatrix} = \begin{bmatrix} \gamma_A \\ \gamma_B \end{bmatrix}$$

(b) Write down the solution of the above matrix equation for ρ_1^* and ρ_2^*. Show that the feasibility condition, i.e., $\rho_1^* > 0$ and $\rho_2^* > 0$, can be written as two conditions between the environmental parameters γ_A, γ_B, and $m_i \equiv \nu_{iB}/\nu_{iA}$, which describes the nutrient preference of species i. Plot the "ecological phase diagram" in the space (γ_A, γ_B), marking clearly the region of coexistence, and the region of dominance/extinction.

(c) For a fixed environment parameterized by $\gamma \equiv \gamma_B/\gamma_A$ (which indicates the relative nutrient availability), plot the "physiological phase diagram" in the space (m_1, m_2) by indicating which regions of this space give coexistence, and which regions give dominance of species 1 or 2.

(d) What is the 'optimal' value of m_1 that species 1 should take on to maximize its existence (i.e., survival) if it expects species 2 to take on a random value of m_2? or if it expects species 2 to take on the 'optimal' value of m_2? If the m values of both species are close to this 'optimal' value, what would be the probability that one species becomes extinct if the environmental parameter γ can take on a value within a finite range δ about a mean value, $\bar{\gamma}$ with equal probability? [Assume the environment can vary rapidly while m_i, determined by genetics, is frozen over the scale of environmental variation.] What range of m_i should each species i take on to maximize its existence in a fluctuating environment if it can coordinate with the other species which is also interested in maximizing its existence? What danger is there if the other species 'cheats'? [Note: Your response to **(d)** is not expected to be quantitative.]

4. Competition for essential nutrients. The dependence of the growth of bacterial species i on two essential nutrients A and B is given by

$$r_i(n_A, n_B) = \left[\frac{1}{\nu_{iA} n_A} + \frac{1}{\nu_{iB} n_B}\right]^{-1}$$

where $\nu_{i\alpha}$ is the single-nutrient consumption efficiency (when the other nutrient is in saturation) and n_α is the concentration of nutrient α. Unlike substitutable nutrients, the uptake of nutrient α by species i is given by $r_i \cdot \rho_i / Y_{i,\alpha}$, where ρ_i is the density of species i, and $Y_{i,\alpha}$ is the yield of species i for nutrient α. This leads to the following set of consumer-resource equations

$$\dot{\rho}_1 = r_1(n_A, n_B) \cdot \rho_1 - \mu \rho_1,$$
$$\dot{\rho}_2 = r_2(n_A, n_B) \cdot \rho_2 - \mu \rho_2,$$
$$\dot{n}_A = \mu \cdot (n_A^0 - n_A) - r_1(n_A, n_B) \cdot \rho_1 / Y_{1,A} - r_2(n_A, n_B) \cdot \rho_2 / Y_{2,A},$$
$$\dot{n}_B = \mu \cdot (n_B^0 - n_B) - r_1(n_A, n_B) \cdot \rho_1 / Y_{1,B} - r_2(n_A, n_B) \cdot \rho_2 / Y_{2,B},$$

for a chemostat-based system where μ is the dilution rate and n_α^0 is the inflow concentration of nutrient α. In this problem, you will derive the feasibility conditions for this system using Tilman's graphical approach.

(a) Without solving the equations algebraically, sketch the conditions for $\dot{\rho}_i = 0$ in the (n_A, n_B) plane. Indicate the location of (n_A^*, n_B^*) where both ρ_1 and ρ_2 are finite. On the plot, also mark the point (n_A^0, n_B^0) which is proportional to the nutrient inflow. Next, find an algebraic expression for n_A^*, n_B^* in terms of the environmental and physiological parameters. [Hint: You can first use the matrix inversion formula for n_α^{-1}.]

(b) Show the balance of nutrient fluxes at (n_A^*, n_B^*) graphically using a vector relation among the nutrient influx $\vec{J}_0$ and the consumption fluxes $\vec{J}_1, \vec{J}_2$, as done in class. Describe the condition for coexistence graphically, and write down the corresponding algebraic expression involving the constraint on n_A^0, n_B^0.

(c) Show graphically what happens if (n_A^0, n_B^0) lies outside of the constraint, and write down the algebraic expression for the steady-state concentrations n_A^*, n_B^* and densities ρ_1^*, ρ_2^* corresponding to the two types of outcomes that would arise.

(d) Describe and explain the difference of the behavior obtained here compared to the ones obtained in class for two substitutable nutrients.