Linked Problem Sets in *Mathematical Modeling for Epidemiology and Ecology*

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February 11, 2023

Overview

- *Mathematical Modeling for Epidemiology and Ecology* is a new Springer text by Glenn Ledder. It should be out by April.
- The book was written as a textbook for an undergraduate course and a source of problems and methods to supplement differential equations and modeling courses.
- The book features 50 sets of **linked problems**:
  - multiple problems on a single model, distributed over multiple sections.
  - All problems are accessible to students taking a first course in ODEs.
- This talk will look deeply at two of these sets.
  - I will also propose an improvement to the Turing test!

Plankton Food Web Model: Overview

- The plankton food web model appears in 4 sections:
  - 3.6 Equivalent Forms (scaling)
  - 6.1 Nullcline Analysis
  - 6.2 Linearized Stability Analysis with Eigenvalues
  - 6.3 Stability Analysis with the Routh-Hurwitz Conditions
- The problems can be further broken up for use as a multi-part project.
  - In this talk, we will break the four problems up into a total of 11 parts, each of which could be a separate assignment with a 2–3 day window.

Plankton Food Web Model: Overview

- Model components are free nitrogen F, phytoplankton (microscopic plants) P, and zooplankton (microscopic animals) Z.
  - F is a resource for P, which is prey for Z.
  - When P and Z die, their N content reenters the F pool.
- The zooplankton equation is the standard predator equation used in the Lotka-Volterra model.
- The phytoplankton equation has free nitrogen uptake and natural death instead of Lotka-Volterra's natural growth.[1]
- Total nitrogen is conserved, so we can eliminate the F equation, leaving a modified predator-prey model.

[1] NEVER use the Lotka-Volterra model! (This will be explained at the end.)

Plankton Food Web Model: Part 1 (Problem 3.6.12a)

- … free nitrogen F, phytoplankton P, zooplankton Z.

(a) Assume these mechanisms of nitrogen transfer:

1. Phytoplankton death ($P \to F$), with rate constant a.
2. Zooplankton death ($Z \to F$), with rate constant b.
3. Free nitrogen consumption ($F \to P$), with rate cFP.
4. Predation ($P \to Z$), with rate dPZ.

Write down the differential equations, using T for time.

$$
\begin{aligned}
\frac{dF}{dT} &= aP + bZ - cFP, \\
\frac{dP}{dT} &= -aP + cFP - dPZ, \\
\frac{dZ}{dT} &= -bZ + dPZ.
\end{aligned}
$$

Plankton Food Web Model: Part 2 (Problem 3.6.12bc)

(b) Show that $N = F + P + Z$ is constant.

(c) Use $N = F + P + Z$ to eliminate F from the P equation.

$$\frac{dP}{dT} = -aP \qquad + cFP - dPZ.$$

$$\begin{aligned}\frac{dP}{dT} &= -aP + c(N - P - Z)P - dPZ \\ &= \qquad \cdots\end{aligned}$$

$$\frac{dP}{dT} = P\left[(cN - a) - cP - (c + d)Z\right].$$

Plankton Food Web Model: Part 3 (Problem 3.6.12d)

(d) Nondimensionalize the P and Z equations using the reference quantities $\frac{1}{cN}$ for T, N for P, $\frac{cN}{(c+d)}$ for Z.

- $\frac{d}{dT} \to cN\frac{d}{dt}, \quad P \to Np, \quad (c+d)Z \to cNz.$

$$\frac{dP}{dT} = P[(cN - a) - cP - (c+d)Z].$$

$$(cN)Np' = Np[(cN - a) - cNp - cNz].$$

$$p' = p\left(1 - \frac{a}{cN} - p - z\right) = p(1 - \alpha - p - z)\,,$$

$$z' = \frac{d}{c}z\left(p - \frac{b}{dN}\right) = \delta z(p - \beta)\,.$$

Plankton Food Web Model: Part 4 (Problem 3.6.12e)

(e) Explain the biological significance of the parameters α and β.

$$\frac{dP}{dT} = -aP \quad + cFP \quad (-dPZ),$$
$$\frac{dZ}{dT} = \quad -bZ \quad + dPZ.$$

$$F < N \quad \rightarrow \quad cNP > cFP \quad \rightarrow \quad \alpha = \frac{a}{cN} = \frac{aP}{cNP} \leq \frac{aP}{cFP},$$

- α is the lower bound of $\dfrac{P \text{ loss from death}}{P \text{ gain from consumption}}$
- β is the lower bound of $\dfrac{Z \text{ loss from death}}{Z \text{ gain from predation}}$
- Large α is bad for P (and Z); large β is bad for Z.

Special Advantage of Linked Problems

- You can give students the full answer to one part before they do the next part.
- You can still treat linked problems as a project by having students do a final report that includes everything.

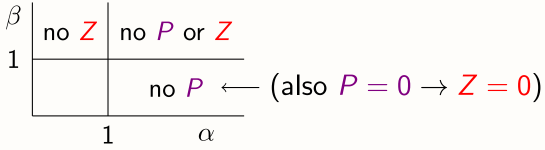
In Problem 3.6.12e, there is a much stronger statement we can make about the significance of α and β.

Plankton Model: Stronger Significance of α, β

$$\frac{dP}{dT} = -aP \qquad + cFP \qquad (-dPZ),$$
$$\frac{dZ}{dT} = \qquad -bZ \qquad + dPZ.$$

$$\alpha \le \frac{aP}{cFP}, \qquad \beta \le \frac{bZ}{dPZ}$$

- $\alpha > 1$ (ie, $1 < \alpha \le aP/cFP$): $cFP < aP$, so P can't persist.
- $\beta > 1$ (ie, $1 < \beta \le bZ/dPZ$): $dPZ < bZ$, so Z can't persist.



Plankton Food Web Model: Part 5 (Problem 6.1.8a)

(a) Determine the equilibria for the plankton population model,

$$p' = p(1 - \alpha - p - z)\,,$$
$$z' = \delta z(p - \beta)\,.$$

being careful to indicate any restrictions on existence.

- X equilibrium has $p = 0$; then $z = 0$.
- P equilibrium has $z = 0$, $p > 0$; then $p = 1 - \alpha$.
  - Requires $\alpha < 1$
- PZ equilibrium has $p > 0$, $z > 0$; then $p = \beta$, $z = 1 - \alpha - \beta$.
  - Requires $\alpha + \beta < 1$

Plankton Food Web Model: Part 6 (Problem 6.1.8bcd)

(b)-(d) Sketch the nullcline plots for $1<\alpha$, $\alpha<1<\alpha+\beta$, $\alpha+\beta<1$.

$$p' = p(1-\alpha-p-z)\,,$$
$$z' = \delta z(p-\beta)\,.$$

- z nullclines are $z=0$, $p=\beta$
- p nullclines are $p=0$, $z+p=1-\alpha$

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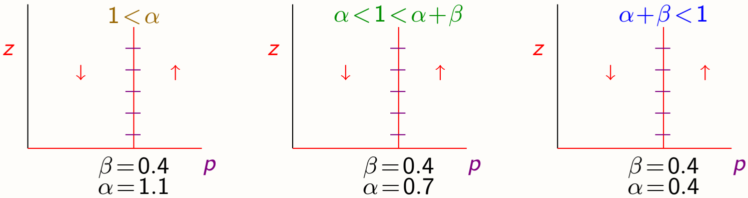
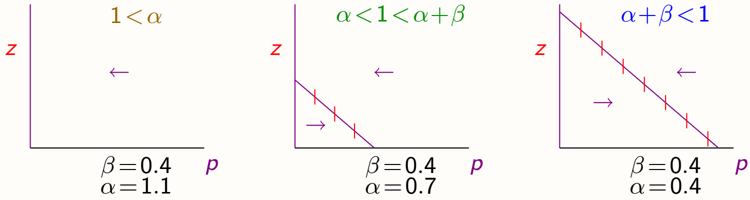


Plankton Food Web Model: Part 6 (Problem 6.1.8bcd)

(b)-(d) Sketch the nullcline plots for $1 < \alpha$, $\alpha < 1 < \alpha + \beta$, $\alpha + \beta < 1$.

$$p' = p(1 - \alpha - p - z)\,,$$
$$z' = \delta z(p - \beta)\,.$$

- z nullclines are $z = 0, \quad p = \beta$
- p nullclines are $p = 0, \quad z + p = 1 - \alpha$



Plankton Food Web Model: Part 6 (Problem 6.1.8bcd)

(b)-(d) Sketch the nullcline plots for $1<\alpha$, $\alpha<1<\alpha+\beta$, $\alpha+\beta<1$.

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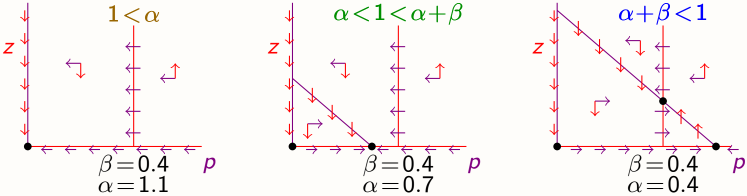
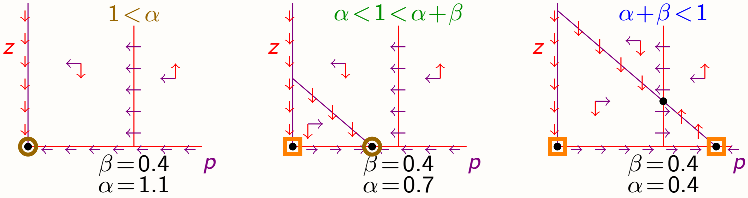


Plankton Food Web Model: Part 7 (Problem 6.1.8e)

(e) Determine any conclusions that can be drawn from the nullcline plots.



- Circles: stable (attractor in a no-egress region)
- Squares: unstable (repeller in a region)
- Coexistence equilibrium for $\alpha+\beta<1$ cannot be determined

Plankton Food Web Model: Part 8 (Problem 6.2.6abd)

(a)-(b) Determine the stability of the X and P equilibria for

$$p' = p(1-\alpha-p-z)\,,$$
$$z' = \delta z(p-\beta)\,.$$

(d) Discuss the results with reference to Problem 6.1.8.

X is $(0, 0)$	P is $(1-\alpha, 0)$

$$J_X = \begin{pmatrix} 1-\alpha & 0 \\ 0 & -\delta\beta \end{pmatrix}, \text{ stable if } 1 < \alpha.$$

$$J_P = \begin{pmatrix} -(1-\alpha) & -(1-\alpha) \\ 0 & \delta(1-\alpha-\beta) \end{pmatrix}, \text{ stable if } \alpha < 1 < \alpha+\beta.$$

(m) Results are consistent with those from nullclines.

Plankton Food Web Model: Part 9 (Problem 6.2.6cd)

(c) Determine the stability of the PZ equilibrium for

$$p' = p(1 - \alpha - p - z)\,,$$
$$z' = \delta z(p - \beta)\,.$$

using parameters $\alpha = 0.5$, $\beta = 0.25$, $\delta = 0.1$.

(d) Discuss the results with reference to Problem 6.1.8.

$$J_{PZ} = \begin{pmatrix} -0.25 & -0.25 \\ 0.025 & 0 \end{pmatrix} \quad \rightarrow \quad \lambda^2 + \tfrac{1}{4}\lambda + \tfrac{1}{160} = 0.$$

$$\lambda = \frac{-1 \pm \sqrt{0.6}}{8} < 0, \quad \text{stable.}$$

(d) Nullclines are inconclusive because $\alpha + \beta < 1$.

Plankton Food Web Model: Part 10 (Problem 6.3.5ab)

(a) [Use the Routh-Hurwitz conditions to] determine the stability of the coexistence equilibrium for the ... model

$$p' = p(1 - \alpha - p - z)\,,$$
$$z' = \delta z(p - \beta)\,.$$

(b) Discuss the results with reference to Problem 6.1.8.

- An equilibrium point is asymptotically stable iff

$$\mathrm{tr}(J) < 0, \qquad \det(J) > 0$$

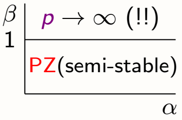
$$J_{PZ} = \begin{pmatrix} -p & -p \\ \delta z & 0 \end{pmatrix}, \quad \mathrm{tr}(J_{PZ}) = -p, \quad \det(J_{PZ}) = \delta pz.$$

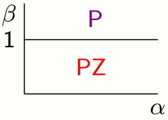
- PZ is stable whenever it exists (nullclines were inconclusive).

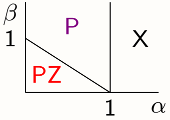
Plankton Food Web Model: Part 11 (Problem 6.3.5c)

(c) Explain the prediction the model makes for the effect of α and β (predator death rate) on the behavior of the system.

Lotka-Volterra	Logistic LV	Plankton
$p' = p(1 - z)$	$p' = p(1-p-z)$	$p' = p(1-\alpha-p-z)$







- Larger α and/or β decreases viability of zooplankton.
- Larger α can cause extinction for the whole system.
- The Lotka-Volterra results are ridiculous!!

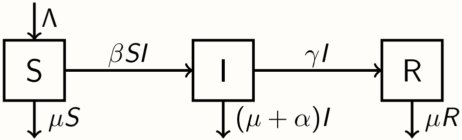
The Turing Test

- The Turing Test is intended to determine whether a machine has achieved intelligence.
- In its original form, the test is whether the machine can carry on a conversation without being identified as a machine.
- AI programs are close to passing this test, but they have clearly not achieved intelligence.
- My improved test:
  Train the AI by feeding it biology and mathematical biology writings that do not mention Lotka-Volterra.
  - Then ask it to explain why the LV model is bad.

SIR with Loss of Immunity: Overview

- We add loss of immunity to a (3D) model from the text for an SIR disease with natural death, disease-induced mortality, and fixed birth rate.
- The model appears in 3 sections:
  - 3.9 Case Study: Adding Demographics to Make an Endemic Disease Model (*development and simulation*)
  - 6.2 Linearized Stability Analysis with Eigenvalues (*disease-free equilibrium*)
  - 6.3 Stability Analysis with the Routh-Hurwitz Conditions (*endemic disease equilibrium*)

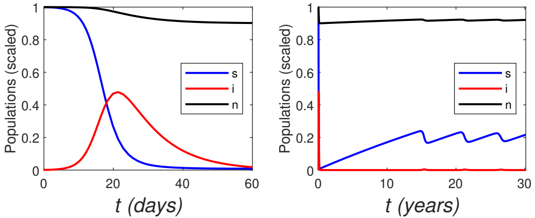
SIR with Loss of Immunity: Base Model (Example 3.9.1)



$$N' = \Lambda - \mu N - \alpha I \quad (1)$$

$$S' = \Lambda - \mu S - \beta SI \quad (2)$$

$$I' = \beta SI - \gamma I - (\alpha + \mu) I \quad (3)$$



SIR with Loss of Immunity: Problem 3.9.6ab

(a) Modify the model (1)–(3) by adding a loss of immunity term σR to the S equation.

(b) Scale the model with additional parameter $\phi = \sigma/\mu$.

$$\frac{dN}{dT} = \Lambda - \mu N - \alpha I$$

$$\frac{dS}{dT} = \Lambda - \mu S + \sigma(N - S - I) - \beta SI$$

$$\frac{dI}{dT} = \beta SI - \gamma I - (\alpha + \mu) I$$

$$\frac{d}{dT} = (\gamma + \alpha + \mu)\frac{d}{dt}; \quad N, S, I = \frac{(\gamma+\alpha+\mu)}{\mu} n, s, i; \quad \epsilon, b, d = \frac{\mu, \beta, \alpha}{\gamma+\alpha+\mu}$$

$$n' = \epsilon(1 - n) - di$$

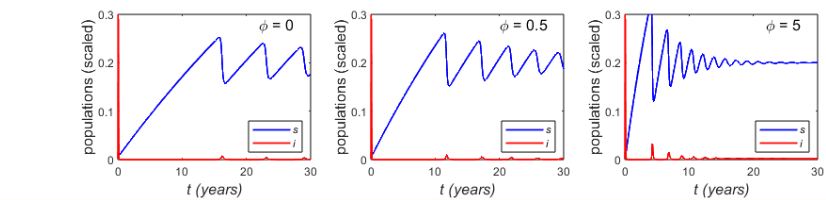
$$s' = \epsilon(1 - s) + \epsilon\phi(n - s - i) - bsi$$

$$i' = (bs - 1)i$$

SIR with Loss of Immunity: Problem 3.9.6cd

(c) Modify *ODEsim.m* to run two simulations, using the same parameters as in Example 3.9.1, with $\phi = 0.5$ and $\phi = 5$.

(d) Compare the results with those of Example 3.9.1.



- Faster immunity loss means cycles start sooner and have shorter quasiperiods with amplitudes that start larger but decay faster.

MATLAB data specification

```
% Define problem parameters

b = 3;

% Define initial conditions

s0 = 0.999;
i0 = 0.001;
IC = [s0 i0];

% Define time interval

interval = [0 10];
```

MATLAB DE specification

```
% Define the function that determines the derivatives.
%    Can use global parameters.

function dydt = rates(ttt,yyy)
    % Unpack variables
    s = yyy(1);
    i = yyy(2);
    % Calculate derivatives
    sp = -b*s*i;
    ip = b*s*i-i;
    % Assemble vector derivative
    dydt = [sp;ip];
end
```

SIR with Loss of Immunity: Problem 3.9.7abc

(a) Rescale the problem using $i = \epsilon y$.

(b) Obtain two equations relating the values n^* and y^*.

(c) Solve these equilibrium equations.

$$n' = \epsilon(1-n) - di = \epsilon(1 - n - dy)$$

- Rescaling with $i = \epsilon y$ is necessary to balance the equations.
  - Taking $\epsilon \to 0$ yields $n' \approx -di$.

$$n^* = \frac{1 + db^{-1}(\phi + 1 - b)}{1 + d\phi}, \quad y^* = \frac{(\phi+1)(1-b^{-1})}{1+d\phi}.$$

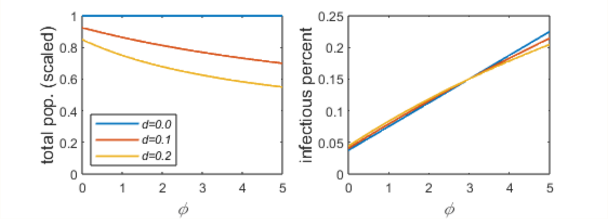
- Larger mortality decreases n^* and y^*.
- Infected fraction (y^*/n^*) increases with d if $\phi < b - 1$.

SIR with Loss of Immunity: Problem 3.9.7efg

(e) Fix $b = 4$ and plot n^* vs ϕ for $d = 0, 0.1, 0.2$. Use $0 \leq \phi \leq 5$.

(f) Repeat (e), but with y^*/n^*.

(g) Discuss what we learn from the plots of (e) and (f).



- With rapid loss of immunity, infectious percentage decreases as d increases.

SIR with Loss of Immunity: Problem 6.2.13

Determine the stability of the disease free equilibrium (1,1,0) for

$$n' = \epsilon(1 - n - dy)\,,$$
$$s' = \epsilon[1 - s + \phi(n - s) - bsy]\,,$$
$$y' = bsy - y\,.$$

$$J_{DFE} = \begin{pmatrix} -\epsilon & 0 & -\epsilon d \\ \epsilon\phi & -\epsilon(\phi + 1) & -\epsilon b \\ 0 & 0 & b - 1 \end{pmatrix}.$$

- Eigenvalues are $b - 1$, $-\epsilon$, $-\epsilon(\phi + 1)$.
  - Stable if $b < 1$.

SIR with Loss of Immunity: Problem 6.3.14

Use the Routh-Hurwitz conditions to determine the stability of the endemic disease equilibrium $\left(n^*, b^{-1}, y^*\right)$ for

$$n' = \epsilon(1 - n - dy)\,,$$
$$s' = \epsilon[1 - s + \phi(n - s) - bsy]\,,$$
$$y' = bsy - y\,.$$

- The characteristic polynomial is $P(\lambda) = \lambda^3 + c_1\lambda^2 + c_2\lambda + c_3$:

$$c_1 = -\text{tr}\, J, \quad c_2 = \sum_{k=1}^{3} \det J_k, \quad c_3 = -\det J,$$

  and J_k is the 2×2 determinant with row/column k omitted.

- The eq. sol'n is stable iff all $c_j > 0$ and $c_1 c_2 > c_3$.

SIR with Loss of Immunity: Problem 6.3.14

$$n' = \epsilon(1 - n - dy)\,,$$
$$s' = \epsilon[1 - s + \phi(n - s) - bsy]\,,$$
$$y' = bsy - y\,.$$

$$J_{EDE} = \begin{pmatrix} -\epsilon & 0 & -\epsilon d \\ \epsilon\phi & -\epsilon q & -\epsilon \\ 0 & by & 0 \end{pmatrix}, \quad q = 1 + \phi + by > d\phi.$$

$$c_1 = \epsilon(1+q), \quad c_2 > \epsilon by, \quad c_3 = \epsilon^2 by(1 + d\phi).$$

$$c_1 c_2 > [\epsilon(1 + d\phi)][\epsilon by] = c_3.$$

- The Routh-Hurwitz conditions show the EDE to be stable whenever it exists.

Shameless Self Promotion

- These linked problems and 48 other sets can be found in *Mathematical Modeling for Epidemiology and Ecology*, a new Springer text by Glenn Ledder. It should be out by April.
- All problems in the book are accessible to students taking a first course in ODEs.
- Contact me at gledder@unl.edu with questions or comments. If anyone wants to have me visit, I'm interested.