Laboratory 7: Three State Variable Models

Bio534 Fundamentals of Ecological Modeling
Fall 2008

Introduction

In this laboratory you will construct and simulate models with three state variables. You will consider two different structures: chain and resource competition (web). This material builds on the previous laboratory exercises and provides you an opportunity to investigate several of the modeling ideas we have discussed in class.

Learning Objectives

At the end of this laboratory you will be able to

- Construct and simulate a three compartment (i.e., a three state variable) model of an ecological system;
- Draw an informative conceptual diagram of a modeled system using the Forrester symbolic vocabulary;
- Use a model system to identify the ecological relationships necessary to achieve a stable limit cycle;
- Use a model system to investigate the consequences of changing the state variables' initial conditions and define alternative stable states;
- Modify existing equations to mathematically describe a new scenario;
- Clearly communicate your scientific work in the form of a brief narrative report.

Reporting Your Work

Please describe your work in the form of a short narrative report. Include a brief introduction to the laboratory that describes both the modeling and learning objectives. It should also briefly characterize the system you are modeling and identify its boundaries. This should be followed by a task-by-task description of (1) the task, (2) the action you take, (3) the result(s) of the action (with evidence like a table or graph), and (4) an ecological interpretation of what you learned. Please conclude the report with a section in which you consider what you have learned from this laboratory. How does it relate to the other topics we have discussed in class? How might it relate to your research? What concept or task did you struggle with the most? Why? Include a copy of your programs as an appendix to the report.

We will work on this laboratory for two weeks (Oct. 23 and Oct. 30) and the final report will be due in class on **TUESDAY Nov. 4**. Please provide me with a hard copy of your report in class.

Assessment There are two tasks in this assignment, each worth 10 points each. The quality of your report (following guidelines similar to the final project rubric) will be worth another 5 points for a total of 25 points.

Task 7.1: Linear Chain

For this task you will construct a linear chain model with three compartments: (1) an abiotic resource with constant input, (2) a plant producer, and (3) an herbivorous consumer. **Structurally**, it just adds one level, the consumer, to the previous model of phosphorus–phytoplankton dynamics (Laboratory 6). For example, imagine that we introduce a population of *Daphnia* to feed on the algal compartment.

Certain combinations of parameter values in the linear-chain model can produce a situation where at least two locally-stable steady states are possible.

The functional form we will use to represent **resource control** in both this model and the one in Task 3.2 is the linear special case of the **generalized hyperbolic function**:

$$f(X_i) = \left(1 - \left(\frac{K_{ij} - X_i}{K_{ij} - \alpha_{ij}}\right)_+\right)_+ . \tag{1}$$

In this equation K_{ij} is the satiation level of j on i and α_{ij} is the refuge of i from consumption by j. Being linear, this function produces a constant change in the feedback effect for a unit change in the resource.

The functional form for **space-related control** in this model and the one in Task 3.2 is the **logistic**.

$$f(X_j) = \left(1 - w_j\left(\frac{X_j + \beta_k X_k - \alpha_j}{K_j - \alpha_j}\right)_+\right)_+ , \text{and} \tag{2}$$

$$w_j = \left(1 - \frac{\delta_j}{\tau_{ij}}\right). \tag{3}$$

Given this information, construct a linear three entity model in which the first component is an abiotic pool of phosphorus (X_1), the second is an algal consumer (X_2), and the third is a daphnid predator on the algae (X_3). This system will include the variables and parameters listed in Table **??**. Values listed with the parameters are the initial values to use for this exercise, which were chosen as both biologically reasonable rates and constants for the example system and as a set that will exhibit the range of behavior desired in response to manipulations of enrichment rate and starting densities.

The equations for this model are:

$$\frac{dX_1}{dt} = C_1 - \delta_1 X_1 - \tau_{12} X_2 \underbrace{f(X_1)}_{resource} \underbrace{f(X_2)a}_{space} \tag{4}$$

$$\frac{dX_2}{dt} = \tau_{12} X_2 \underbrace{f(X_1)}_{resource} \underbrace{f(X_2)a}_{space} - \delta_2 X_2 - \tau 23 X_3 \underbrace{f(X_2)b}_{resource} \underbrace{f(X_3)}_{space} \tag{5}$$

$$\frac{dX_3}{dt} = \tau 23 X_3 \underbrace{f(X_2)b}_{resource} \underbrace{f(X_3)}_{space} - \delta_3 X_3 \tag{6}$$

Table 1: Variables and Parameters for Task 7.1

Name & Description	Symbol	Nominal Value
State Variables and Initial Values ($X_i(0)$)		
Phosphorus	X_1	10
Algae	X_2	10
Daphnids	X_3	10
Constant Rates		
Input of available phosphorus	C_1	5
Rate Parameters		
Max uptake of X_1 by X_2	τ_{12}	0.35
Max uptake of X_2 by X_3	τ_{23}	0.5
Loss rate from X_1	δ_1	0.1
Loss rate from X_2	δ_2	0.1
Loss rate from X_3	δ_3	0.2
Control Parameters		
Refuge of X_1	α_{12}	5
Threshold response density of X_2	α_2	20
Refuge of X_2	α_{23}	5
Threshold response density of X_3	α_3	10
X_2 satiation concentration of X_1	K_{12}	20
Carrying Capacity of X_2	K_2	70
X_3 satiation concentration of X_2	K_{23}	20
Carrying Capacity of X_3	K_3	30

Notice that these equations assume that there is 100% assimilation for simplicity. How will this modeling assumption effect your work below?

7.1.1 Draw a Forrester diagram of this system.

7.1.2 Simulate the model using the parameter values defined in Table **??**. This will be the *nominal* model dynamics to which you can compare the changes you make in the following tasks.

Stable limit cycles can occur in a system for a variety of reasons including timelags (which we have not discussed), cyclic external influences, and internal system dynamics. Recall that for a limit cycle to be stable, it must represent a dynamic steady state (i.e. the cycle amplitude should not decrease). Here we will investigate this last factor more closely. When given enough enrichment (nutrients entering the system, C_1), the resource-prey-consumer system described above will cycle provided certain relationships between the top predator in the chain and its prey occur. These involve the growth rate of the algae vs. daphnids, the algal refuge from Daphnia, and the degree of crowding the daphnids can withstand without severe intra-compartmental interference competition occurring.

7.1.3 Change the appropriate parameter values in your model to produce a stable limit cycle without explicit timelags. What value of C_1 will you use? Why?

There is also an enrichment level (C_1) where the system exhibits two alteranative locally-stable steady states depending on the starting densities of both the Daphnids and Algae (no additional parameter changes need to be made). See Beisner et al. (2003) for an explanation of *alternative stable states*. In one of these steady states the prey have escaped from control by the top consumer and the standing stock of available resource is high, predator and prey densities are low. In the other, prey and predator densities are higher and the available resource is lower.

7.1.4 Starting with an enriched system (high value of C_1) and all other parameters as initially defined, explore the initial conditions necessary for this situation to develop. Think in terms of allowing the prey to escape complete predator control when the prey are started high and of being held to a low level when they are started low. Explain what you did to achieve this goal.

Task 7.2: Resource Competition

For this task, you will construct a two-competitor model in which both groups of algae utilize a single pool of available phosphorus, which will include **interspecific interference competition** in the manner we discussed in lecture and using the variables and parameters defined in Table **??**.

Table 2: Variables and Parameters for Task 7.2

Name & Description	Symbol	Nominal Value
State Variables		
Phosphorus	X_1	10
Algae$_1$	X_2	10
Algae$_2$	X_3	10
Constant Rates		
Input of available phosphorus	C_1	8.15
Rate Parameters		
Max uptake of X_1 by X_2	$\tau 12$	0.35
Max uptake of X_1 by X_3	$\tau 13$	0.2
Loss rate from X_1	δ_1	0.1
Loss rate from X_2	δ_2	0.2
Loss rate from X_3	δ_3	0.1
Control Parameters		
X2 satiation concentration of X_1	K_{12}	20
X3 satiation concentration of X_1	K_{13}	50
Carrying Capacity of X_2	K_2	30
Carrying Capacity of X_3	K_3	50
Refuge of X1 from X_2	α_{12}	5
Refuge of X1 from X3	α_{13}	10
Threshold response density of X_2	α_2	10
Threshold response density of X_3	α_3	20
Competition coefficient X_2 on X_3	β_2	0.2
Competition coefficient X_3 on X_2	β_3	0.8

7.2.1 Draw a Forrester diagram the model;

7.2.2 Formulate the equations to simulate this system using what we have learned in class and the example provided in your notes;

This competition model shows behavior with respect to enrichment and starting densities that differs in many ways from that shown by the model in Task 7.1 (recall the graphical analysis of four possibilities that we discussed in class). For example, at certain levels of enrichment the competitor model will show an effect due to starting density in that two different outcomes are possible when the winner of the competition is a factor. However, the model cannot exhibit two locally-stable states in which both competitors survive in each case.

7.2.1 Why not? What is there about the modes of control in this model such that a steady state maintained via interference competition can be observed, but flow control maintained solely by exploitative competition always leads to one winner? (Hint: this does not depend on the parameter values listed in Table **??**).

The parameter values and constants suggested in Table **??** are those that represent two distinct adaptations. If you study the values, you should be able to see that one species has attributes that make it tolerant of crowding, a good interference competitor, but slower growing than the second, which is a poor interference competitor, but has a greater growth rate and is more efficient at utilizing resources.

7.2.2 Which species is which? Why? What do you expect the outcome of this simulation to be? How are you making this prediction?;

7.2.3 Using the values in Table **??** as a start for your simulations, explore the behavior of this model. What is the nominal behavior? What happens if you alter the enrichment rate?

7.2.4 When you are satisfied that you fully understand the variation in behavior and the reasons behind it, make whatever changes you find interesting in some of the other model parameters. When you produce an interesting or unexpected result, report graphs, a brief description, and your explanation if you can suggest one. If you would like, you may substitute some of the other formulations of control functions we have discussed in class or those you have constructed to fit any particular situation, and observe the effects on the behavior of the model.

References

Beisner, B.E., Haydon, D.T., and Cuddington, K. 2003. Alternative stable states in ecology. Front. Ecol. Environ. 1: 376–382.