# Laboratory 5

## Building Two State Variable Models
## for Consumer–Resource Dynamics

Monday 29$^{\text{th}}$ September, 2008

## Introduction

In this laboratory you will construct and simulate two state variable models. Recall that a state variable describes the change in a measurable quantity through time and usually has units of M $L^{-2 \text{ or } -3}$. The models in this exercise are designed to give you some practice in manipulating the carrying capacities, the asymptotic resource threshold and the refuge. However, please conduct and report additional manipulations as you desire.

### Learning Objectives

At the end of this laboratory you will be able to

- Construct and simulate a two compartment (i.e., a two state variable) model of an ecological system;
- Draw an informative conceptual diagram of a modeled system using the Forrester type symbolic vocabulary;
- Use system dynamics terminology to describe and classify the behavior of both time-series trajectories and control functions;
- Perform sensitivity analysis to characterize the role of parameters in quantitative models;
- Identify the ecological assumptions of the logistic and hyperbolic control functions; and
- Distinguish between space and resource controls on compartment growth.

### Scenario

For this exercise, consider your system of interest to be the section of the Lower Cape Fear river that flows through Wilmington. Your modeling goal is to describe the ecological factors that control the phytoplankton production in the river. Your initial model will consist of two state variables: (1) an abiotic resource—a pool of phosphate ($PO_4^{3-}$)—with a constant input from upstream that is utilized by (2) a producer or consumer either controlled by some form of intraspecific crowding (logistic) or by resource limitation. We will be utilizing an ecosystem point of view.

These are continuous time, nonlinear differential equation models that are suitable for the crude description of the dynamics of a wide variety of organisms, both semelparous and iteroparous. The exercise is particularly designed so that you familiarize yourself with the characteristics of both the logistic and hyperbolic control functions, both of which can be generalized to more realistic and useful forms. Consider the bookkeeping unit of both models to be elemental phosphorus ($\mu g L^{-1}$).

### 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 explanation or interpretation of what is occurring. Please conclude the report with a section in which you consider what you have learned from this laboratory. How does it relate to the 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 and the final report will be due in class on **Oct. 14**. Please provide me with both a hard copy of your report in class.

**Assessment** There are three tasks in this assignment, each worth 5 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 20 points.

## Task 5.1: Two entity models with logistic space-control feedback

| Name | Symbol | Nominal Value |
|---|---|---|
| State Variables | | |
| Phosphorus | $X_1$ | 2.0 |
| Phytoplankton | $X_2$ | 0.01 |
| Constant Inputs | | |
| Input of available phosphorus | $C$ | 0.5 |
| Specific rate parameters | | |
| Loss from available phosphorus pool | $\delta_1$ | 0.001 |
| Loss of phosphorus from phytoplankton | $\delta_2$ | 0.08 |
| Uptake (gross) of phosphorus by phytoplankton | $\tau_{12}$ | 0.3 |
| Control Parameters | | |
| Maximum density of phytoplankton | $K_2$ | 10.0 |

### Equations

$$\frac{dX_1}{dt} = C - \delta_1 X_1 - \tau_{12} X_2 f(X_2) \quad (1)$$

$$\frac{dX_2}{dt} = \tau_{12} X_2 f(X_2) - \delta_2 X_2 \quad (2)$$

Where

$$f(X_2) = \left(1 - \left(1 - \frac{\delta_2}{\tau_{12}}\right)\left(\frac{X_2}{K_2}\right)_+\right)_+ \quad (3)$$

$f(X_2)$ is the logistic growth control function with Wiegert's correction factor.

For your first run of this model, use initial conditions of $X_1$= 2, $X_2$ = 0.01, time = 100, $\tau_{12}$ = 0.3, $\delta_1$ = 0.001, $\delta_2$ = 0.08, and $C$ = 0.5. Notice that we are assuming that 100% efficiency in the conversion of phosphate to phosphorus in phytoplankton. Recall that the $(\bullet)_+$ notation indicates that $\bullet$ is constrained to be positive. This can be accomplished in R using the maximum function as follows $\max(0, \bullet)$.

### Tasks

5.1.1 Draw a Forrester diagram for this system using the visual vocabulary introduced in class (see lecture notes on System Conceptualization).

5.1.2 Explore the behavior of this system for a few values of $K_2$ ranging from 1 to 15. Label the initial, transient, and steady states of the dynamics. Please explain the qualitative differences in the system dynamics as $K$ increases[1].

5.1.3 With $K_2 = 10$, change the input constant $C$ to explore its effect on component growth. This could represent increasing or decreasing the pollutant load from the watershed to the river.

5.1.4 Leave $K_2 = 10$ and $C = 0.5$ and increase the initial value of $X_2$ to levels 2 to 50 times the carrying capacity and note the responses. Discuss what would happen in this model at these very high initial values if you did not constrain $f(X_2)$.

## Task 5.2: Two entity models with resource control

In this task we explicitly model how a non-living resource controls growth of the consumer compartment. This is in contrast to the competition for unspecified resources represented in the logistic function or the Lotka-Volterra competition equations that we often assume to be space.

Variable and parameters are the same as above except for the additional control parameters, which are the 1/2 saturation constant ($k_1$) and the resource refuge level ($\alpha_{12}$).

### Equations

$$\frac{dX_1}{dt} = C - \delta_1 X_1 - \tau_{12} X_2 f(X_1) \quad (4)$$

$$\frac{dX_2}{dt} = \tau_{12} X_2 f(X_1) - \delta_2 X_2 \quad (5)$$

Where $f(X_1)$ can be one of several functional forms

$$f(X_1) = \left(1 - \frac{k_1}{(k_1 + X_1)}\right)_+ \quad (6)$$

$$f(X_1) = \left(1 - \frac{\alpha_{12}}{X_1}\right)_+ \quad (7)$$

$$f(X_1) = \left(\frac{X_1^b}{X_1^b + k_1^b}\right)_+ \quad (8)$$

[1]You will need to constrain the consumption rate so that the phytoplankton are unable to consume more phosphorus than is physically available. A logical way to do this would be to use an if–then statement to turn off the consumption rate when $X_1$ is zero, but this generates numerical errors with lsoda. Instead, we can set up a Monod resource control function to act nearly like a step function as $X_1$ goes to zero. Try adding $f(X_1) = \frac{X_1}{X_1 + ks}$ where $ks$ is a very small number like 0.001

Where equation (6) is the *hyperbolic form of the Michaelis–Menton* equation used as a control function for resource uptake (this equation uses a 1/2 saturation parameter), equation (7) is the *refuge form of the hyperbolic Michaelis–Menton* resource control, and equation (8) is a *generalized form of the Michaelis–Menten* equation (see lecture notes on control functions).

To visualize the change from space control to resource control, imagine that we expand the surface area (more light) with the same volume. Whereas the algae in the previous example could indeed be exposed to limitation by scarcity of a resource (when they took the standing stock of $X_1$) to zero and existed only on the continuous input), you should have noted that the response was "all or none", i.e. they increased, controlled only by the influence of whatever space control was affecting them until the space control function was relaxed enough such that the phosphorus went to zero. Then, they existed at a level set by the rate of input in the phosphorus compartment ($X_1$). Now we will explore the behavior of the system when the growth rate of $X_2$ is affected in a continuous manner by changing densities of $X_1$ (this is called *Donor Controlled*). Observe how the interactions change with the alternative response functions.

### Tasks

5.2.1 Draw a Forrester diagram for this system.

5.2.2 Using the hyperbolic form of the Michaelis–Menton equation with a 1/2 saturation parameter (where $k_1$ specifies the value of the limiting resource when the ingestion permitted is 0.5 of the maximum), set time from 1 to 200, the initial values of $X_2$ to 0.1, and $\delta_1$ to 0.01. (these changes are to make the interactions as clear as possible).

- Explore the behavior as in Task 6.1 for a few values of $k_1$ in the range of 1 to 20.
- For each scenario, plot both the time series of the compartment behaviors and the realized control function $f(X_1)$. HINT: If you calculate $f(X_1)$ in your model function as an auxiliary variable, you can then add it to your list of information to return in the *out* variable.

5.2.3 Using the same parameter values as before, use the refuge from of hyperbolic control function (equation 7) as the control on phosphorus uptake by phytoplankton. In this formulation, $\alpha_{12}$ specifies the minimum standing stock of $X_1$, below which it is not available to the algae. Repeat the simulations using values for $\alpha_{12}$ in the range of 0 to 10 (you can do more if you are curious).

5.2.4 Again using the same parameter values as in Task 6.1 repeat your investigations with the generalized Michaelis–Menten functional response shown in equation (8). Start with $b = 1$ and then explore the consequences of increasing and decreasing $b$. Again, please present time series plots of both the state variables and the realized control functions.

5.2.5 How would you classify the three resource control functions using Holling typology of functional responses? Please present plots to support your conclusion. Identify one or two ecological assumptions encoded into these functions.

## Task 5.3

Consider the structure of the models you have investigated here and the ecological assumptions they make. Briefly discuss the major assumptions and why they are or are not appropriate for our modeling objective. If you were going to make one change to the model to improve its realism, what change would you make and why?

There is no one true answer to this question. Instead, I am interested to learn how you are reasoning through the modeling problem.