
Laboratory Manual¹

Fundamentals of Ecological Modelling

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¹This manual is under construction.

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Introduction

This laboratory manual is a compilation of the laboratories for BIOL534.

Chapter 1

Getting Started with R

1.1 Introduction

1.1.1 Learning Objectives

The primary objective of this laboratory is to get you started learning to use the R programming language and environment. Learning a new language is a process that develops with practice. Lots of practice. This lab will introduce some of the syntax and grammar for using R as well as highlight some of its capabilities.

1.1.2 What is R ?

Ellner and Guckenheimer (2006a) describe R as follows:

R is an object-oriented scripting language that combines the programming language S developed by John Chambers (Chambers and Hastie 1988, Chambers 1998) with

- a user interface with a few basic menus and extensive help facilities,
- an enormous set of functions for classical and modern statistical data analysis and modeling,
- graphics functions for visualizing data and model output.

1.1.3 Why use R ?

We will use R in this class because it is a free, powerful, rapidly developing (extensible), and relatively easy to use. Plus, it works on multiple operating systems. Finally, R has become a popular tool in biology and ecology as evidenced by the numerous discipline specific packages of functions that have been published recently (e. g. Bolker et al., 2009; Lau et al., 2013; Oksanen, 2011; Oksanen et al., 2007) and R specific ecology books (Bolker, 2008; Soetaert et al., 2008; Stevens, 2009). Thus, R is a tool that will serve our needs in this class, but it should also continue to serve your research and analytical needs long after this course.

1.2 Text Editors and Integrated Development Environments

A good **text editor** is an essential tool for programming, scientific computing, and general informatics work (see http://en.wikipedia.org/wiki/Text_editor). A text editor is used for editing plain text files, which is the format of all uncompiled programs including R scripts and functions. Notepad is an example of a basic text editor that comes with Microsoft Windows. Microsoft Word is not a text editor. Instead it is a word processing program that embeds hidden code into your documents. This code is important for word processing and page layout, but it renders Word useless as a plain text editor. Programs written in Word will generally not work.

As with all software, text editors come in multiple flavors. Some are barebones tools like Microsoft Notepad, others such as Vi and Emacs are more like Swiss army knives. The R program now comes with a general text editor to support writing R scripts. It is fairly simple to use, but (1) it is not very powerful, and (2) if you need to program for SAS or Matlab or any other language you will need a different text editor. Common text editors include Vi and Emacs.

An **Integrated Development Environment** is a software tool to assist with coding. IDEs typically include a text editor with language features like syntax highlighting and parenthesis matching, but it will also include additional tools to help practice good coding. The best IDE for R at the moment is R-Studio, which you can download for free from <http://www.rstudio.com>. I strongly recommend that you use R-Studio for your course projects.

1.3 Additional Resources

Like many computer issues, there is quite a bit of additional information about R available on the world wide web. Here are a few resources to get you started.

- R Homepage <http://www.r-project.org/>
- R Reference Card <http://cran.r-project.org/doc/contrib/Short-refcard.pdf>
- Kickstarting R <http://cran.r-project.org/doc/contrib/Lemon-kickstart/index.html>
- Getting Started with R <http://cran.r-project.org/doc/manuals/R-intro.pdf>
- Ecological Models and Data in R <http://www.math.mcmaster.ca/bolker/emdbook/>

1.4 Assignment

The instructor will introduce the R programming language and environment in class. However, programming is best learned by doing it. Therefore, following this brief introduction you will work through the introductory laboratory provided by Ben Bolker: <http://www.math.mcmaster.ca/bolker/emdbook/lab1.pdf>.

Please complete the following problems: 2.1, 3.1, 5.1, 5.3, 5.4, 8.2, 8.3, 8.4, 8.5, 8.6, and 9.2. You will need to turn in a concise summary of the problem answers.

Chapter 2

Practical Programming with R

Please see lecture notes

2.1 Introduction

This laboratory is a brief introduction to programming concepts for novice coders. At the end of the laboratory, students should be able to do the following:

- Organize computational projects
- Identify and apply programming concepts such as **loops** and **branching**
- Recognize the computational savings of vectorizing tasks when possible
- Practice debugging and problem solving skills
- Create functions in R.

2.2 Assignment

There are two parts to this assignment. First, complete problems 1, 2, 3, 4, 6, 7, 9a in [Jones et al. \(2012\)](#). Second, write an R function named “domeig” that takes as input a single vector and returns a list with components “average” (mean of the values of in the vector) and variance (the variance of the values in the vector) ([Ellner and Guckenheimer, 2006b](#)).

Chapter 3

Conceptual Modeling in the Longleaf Pine Forest

In this laboratory, the class will construct a variety of conceptual models for different aspects of ecology in the Longleaf Pine Forest on the UNCW campus. Students will practice model conceptualization.

Chapter 4

Single State Variable Models

4.1 Introduction

This laboratory exercise will provide you with experience in constructing, solving, and analyzing a single compartment (state-variable) model. This laboratory includes both the exponential and logistic growth models. Through this exercise, you will learn to encode and solve the discrete and continuous time version of the models.

4.1.1 Learning Objectives

Through your work on this laboratory, you will learn the following;

- Practice **scientific programming** in R,
- Construct two forms (discrete-time and continuous-time) of the **exponential growth** and **logistic growth** population models,
- Use **numerical approximation** techniques to estimate the solution of continuous-time differential equations (Euler and *lsoda*),
- Calculate the **error** between the numerical approximation and the true solution, and
- Apply one-at-a-time **sensitivity analysis** to determine the effect of changing model parameters.

4.1.2 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 when appropriate. Please include a copy of your programs as an appendix to the report.

The final report will be due in class on the date specified on the course website. Please email me PDF of your report and make sure to save it as “yourlastname-lab4.pdf”.

4.2 Discrete and Continuous Time Models

According to Gurney and Nisbet (1988), “A dynamic model is a mathematical statement of the rules governing change”. We can then distinguish two types of mathematical statements: an update rule that uses discrete time and a differential equation that uses continuous time.

An **update rule** describes “the relationship between the current and future state of the system”. Let N_t be the current state of the system and $N_{t+\Delta t}$ be the state after the discrete interval of time Δt . We can then write the generic update rule as

$$N_{t+\Delta t} = f(N_t). \quad (4.1)$$

This type of equation is referred to as a **difference equation**. Equations of this form are particularly suited for projecting the state of the system at regular intervals and are often used to model species that reproduce with non-overlapping generations and simultaneous reproduction, like many semelparous species. Mature adults of these organisms reproduce once and then die. For example, the checkerspot butterfly *Euphydryas editha* breeds once per year. Adults fly for a short period of time, lay their eggs near April 1, and die (Hastings 1997).

A **differential equation** specifies the rate of change of a state variable N with respect to a second variable like time t and represents a continuous change. The equations are formally defined as

$$\frac{dN}{dt} = \lim_{\Delta t \rightarrow 0} \frac{N_{t+\Delta t} - N_t}{\Delta t}. \quad (4.2)$$

4.3 Exponential Growth Population Model

In class, we discussed both the difference equation form and differential equation for of the exponential population growth model. The difference model assumes that there are non-overlapping generations, while the continuous differential model assumes births and deaths happen all the time.

4.3.1 Discrete Difference Model

Recall that we can predict the future population size with the following discrete time difference model.

$$N_{t+1} = N_t + r_d N_t \quad (4.3)$$

Where N_t is the population size now, N_{t+1} is the population size one time step into the future, and r_d is the discrete growth factor. When we factor like terms we get

$$N_{t+1} = N_t(1 + r_d)$$

and then we can let $1 + r_d = \lambda$ so that

$$N_{t+1} = \lambda N_t.$$

Note $\lambda \geq 0$ by definition.

Gotelli (2008, p. 12) showed that we can use this equation recursively to predict future population size some number of time steps into the future using

$$N_t = \lambda^t N_0 \quad (4.4)$$

where N_0 is the initial population size and t is the selected future time step.

4.3.2 Continuous Differential Model

$$\frac{dN}{dt} = rN \quad (4.5)$$

$$= (b - d)N \quad (4.6)$$

Where N is the population density (number of individuals per area), $r = (b - d)$ is the intrinsic rate of growth, b is the population specific birth rate, and d is the population specific death rate.

When considering differential equations like equation (4.2), Gurney and Nisbet (1998) suggest that “A model that uses derivatives is essentially an update rule model with very small time steps”. Differential equations are a bit more complicated to implement and use, but are often worth the investment. For example, they are better for modelling species with overlapping generations or variables that are affected continuously.

As Gotelli (2001) notes, the model in equation (4.2) tells us the instantaneous rate of population change, but it does not directly let us project the size of the population at some time in the future. To do this, we must integrate the model. We can use the rules of integral calculus to find that the exact analytical solution for the exponential growth model is

$$N_t = N_0 e^{rt}, \quad (4.7)$$

where N_t is the population density at time t , r is the intrinsic growth rate, and N_0 is the initial population density. Given N_0 , r , and t , we can now predict the future population size (making all the assumptions embedded in our model).

4.4 Logistic Growth Population Model

Recall from class that the logistic growth population model is defined as

$$\frac{dN}{dt} = rN * \left(1 - \frac{N}{K}\right) \quad (4.8)$$

where N is the size of the population, r is the intrinsic growth rate, and K is the carrying capacity.

To use this equation to project the future population size, we integrate the equation to find the following

$$N_t = \frac{K}{1 + \left[\frac{(K-N_0)}{N_0} e^{-rt}\right]} \quad (4.9)$$

Again, we can find the exact solution because the equation is integrable. What do we do when we need to find the solution to a differential equation that is not integrable?

4.5 Numerical Approximation: Euler and lsoda Algorithms

In most cases, our models will not have an exact analytical integral solution. Therefore, we will need to use **numerical approximation** techniques to estimate the solutions. The reading introduced two methods: the Euler technique and the Runge-Kutta 2 technique (Shiflet and Shiflet, 2006). These are useful for learning about numerical approximation techniques, but we will usually use a more sophisticated algorithm called *lsoda*.

4.5.1 Euler Technique

Euler’s technique is the simplest numerical method for approximating the solution to a differential equation. It is quick and easy, but it typically generates the greatest amount of error.

The method was described in detail in the reading. A quick summary of the technique is that we estimate the population size at a fixed time step from now Δt using the current population size N_t . We can summarize this as

$$N(t + \Delta t) = N(t) + (r * N(t)) * \Delta t \quad (4.10)$$

We would expect the relative error to decrease as Δt decreases, and of course this is the exact solution when $\Delta t \rightarrow 0$.

Error We can estimate the error between the exact solution and our estimated solution using the root mean sum of squared predicted (RMSEP) to compare fits. This is calculated as

$$RMSEP = \sqrt{\frac{1}{n} \sum_{i=1}^n (Np_i - Na_i)^2} \quad (4.11)$$

where Np_i and Na_i are the predicted and actual or true population values at i , and n is the number of predicted points.

4.5.2 Using lsoda

Most computer packages like R and MATLAB have more sophisticated ODE solvers built into the language. R uses a routine called *lsoda* that is included in the “deSolve” package. New R packages can be installed using the command “install.packages(“package_name”)”. Once a package is installed on the computer, you will need to load it by typing “library(package_name)”.

4.6 Tasks

Task 4.1 Discrete-Time Exponential Growth Model Projections

1. **Coding** Write a script that uses equation (4.4) to project the future population size. Hint: this can be done with either a for-loop or more efficiently using vectorization.
2. **Sensitivity Analysis** Show the effects of changing N_0 and λ . As the cognitive task is to compare the output of several models, we want to plot multiple solutions on the same graph. Create two plots. In the first plot, let $N_0 = 20$ and plot the solutions when λ takes values of $\{0, 0.5, 1, 1.5, 2\}$. In a second plot, let $\lambda = 1.25$ and plot the solutions when N_0 takes values of $\{1, 10, 50\}$. Let $t = \{0, 0.5, 1, 1.5, 2, 2.5, \dots, 25\}$.

Task 4.2 Diagram the continuous time model

Create a diagram of the continuous time exponential growth model using the Forrester symbols that we discussed in class. Make sure to clearly label each part.

Task 4.3 Plot Exact Continuous Time Population Projections

Write an R script that uses the exact solution of the differential equation (equation (4.7)) to project the future population sizes as time goes from 0 to 100. Start with $N_0 = 5$ and $r = 0.1$. Plot the solutions when r is -0.1 , 0.1 , and 1 on the same graph. What happens when you change N_0 ?

Task 4.4 Numerical Approximation using Euler and *lsoda*

In this task, you will use two numerical approximation techniques to estimate the change in population. You will first use the Euler solution with a different time steps and then you will use an “industrial strength” algorithm called *lsoda*. Given the exact solution you coded in Task 4.3, you can then compare the amount of error the different algorithms generate.

The R package *deSolve* has an ODE solver function called *ode* that will easily allow us to implement the different algorithms (and many more!). The set up to use this function is a bit tricky, so you will start your work from an existing set of programs. After making sure that the *deSolve* package is installed on your computer (use `install.packages()` if necessary), please download the following two file from the course website: [exponential.r](#).

1. Numerical integration approximation with **Euler Method**

First, read through the two program and try to understand how it works. What is the Input, Action, Output? The `exponential.r` fist defines a new R function that encodes the ODE model. Then, the file contains the code that defines the initial conditions, model parameters, and then calls the *ode* function, which requires the model function as an input argument. The run file also has the code to plot an start to analyze the results.

Second, execute the program using the default parameters. What happens? Notice that the *ode* function is initially set up to use the “method = euler” integration algorithm with a time step of $dt = 1$.

Next, change the model parameters to investigate how they alter the program function (i.e., sensitivity analysis). Please make any changes you find interesting and useful to learn about the program. Finally, try alternative values of the time step (dt) of 1, 0.1, and 0.01, and compare the approximated population trajectories to the analytically exact solution using RMSEP. You will need want to create a new R function to calculate RMSEP. What happens as dt increases? Why? What would you expect to happen in a function with dynamics like the logistic equation? Please plot all 4 solutions on the same figure.

2. Numerical integration approximation using *lsoda*

For our next task, we will use the *lsoda* routine. This is actually the default algorithm for `ode()`, so to implement it, we can remove the `method` and `hini` function parameters from the *ode* call. Using the same initial model parameterization as in Task 4.4.1, visually compare the *lsoda* solution to the exact solution and calculate the RMSEP. How does this compare to the euler solution?

Task 4.5 Diagram the model **logistic growth** model

Create a diagram of the logistic growth model using the Forrester symbols that we discussed in class. Make sure to clearly label each part.

Task 4.6 Logistic growth model population projections

Modify the R scripts you used for Task 4.4 to project the future population size of a population growing according to the logistic growth model. For your nominal runs, assume that $r = 0.1$, $N_0 = 5$, $K = 100$, and time from 0 to 100 days. Please compare the analytically exact solution of the logistic growth model (equation 4.9) to the numerical approximation with (1) the Euler solution with $dt = \{1, 0.1, 0.01\}$, and with (2) the *lsdoa* algorithm in R. Plot all 5 solutions on one graph and calculate RMSEP for each numerical approximation. Finally, describe any differences you observed in how the numerical error accumulates in this model when compared to the exponential growth model.

4.7 CHALLENGE PROBLEM: Schaffer Equation

Please complete this problem as time and your interest allow. However, not completing this problem will not count against you.

M. B. Schaefer extended the logistic model to further consider the effect of fishing on fish stocks. He assumed that fish harvest was proportional to abundance and modified the logistic equation as

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) - FN, \quad (4.12)$$

where F is the mortality from fishing pressure. Fishing mortality is often described as a function of the fishing effort E and the effectiveness q of catching and removing the fish. Thus, $F = qE$.

We know from our initial analysis of the logistic equation that in the absence of fishing, the maximum growth rate is achieved when $N = K/2$ and that the growth rate at this maximum is $rK/4$. In the fisheries context, the maximum growth rate is the maximum sustainable yield (MSY) because if we could maintain the stock at this level and harvest the production, it generates the greatest yield. The fish population size that generates the MSY is termed the maximum net productivity (MNP).

What happens when we add fishing? As long as the harvest equals the biological production, the stock will remain the same size. We can use the model (equation 4.12) to find this equilibrium population size as follows.

To find the population size at equilibrium, we first set the differential equation to zero

and solve for N^* as follows

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) - qEN \quad (4.13)$$

$$0 = rN \left(1 - \frac{N}{K}\right) - qEN \quad (4.14)$$

$$qEN = rN \left(1 - \frac{N}{K}\right) \quad (4.15)$$

$$qE = r \left(1 - \frac{N}{K}\right) \quad (4.16)$$

$$\frac{qE}{r} = 1 - \frac{N}{K} \quad (4.17)$$

$$\frac{N}{K} = 1 - \frac{qE}{r} \quad (4.18)$$

$$N^* = K \left(1 - \frac{qE}{r}\right) \quad (4.19)$$

We can now substitute this equilibrium population size into the fishing function to determine the yield (Y^*).

$$= qEN^* \quad (4.20)$$

$$Y^* = qEK \left(1 - \frac{qE}{r}\right). \quad (4.21)$$

This is a parabola with a maximum occurring at $E^* = r/2q$.

Task 4.7 How does yield change with respect to fishing effort?

As biologists and resource managers, we might want to describe how the yield changes with fishing effort. Create a plot of selected values of E versus the steady state yield Y^* (equation 4.21). Assume $q = 0.001$, $K = 100$, and $r = 0.1$.

Task 4.8 How do biological growth, the harvesting rate, and population density interact?

To better understand the relationship between the biological growth rate, harvest rate, and population density, please create a figure with two plots. In each, plot the growth rate versus population density for the logistic growth function. To each plot, add a line showing how the harvest rate (qEN) changes with population density. Recall that where these two curves intersect indicates the intersection of the equilibrium population density and its equilibrium yield. In the first plot, show a case where the population is under fished. In the second plot, show a case where the population is over fished.

Chapter 5

Ricker Model and Chaotic Dynamics

5.1 Introduction

The Ricker model is a discrete-time analogue of the continuous time logistic model. (Ricker, 1954) first formulated to model fisheries stocks. The update rule is

$$N_{t+1} = aN_t e^{-bN_t} \quad (5.1)$$

where N_t is the number of mature individuals at time t in years. Gurney and Nisbet (1998) describe their application of the model to a fishery as follows:

“We work with a time increment (Δt) of 1 year, and denote the stock of mature individuals at the census date in year t by X_t . Juveniles mature the year after their birth. Adult fish spawn once before dying and produce a maximum of $[a]$ viable recruits to the following year’s stock. Due to cannibalism on eggs by adults, the juvenile survivorship in a year when there are X_t adults is e^{-bX_t} , where b is a parameter related to the intensity of cannibalism.” (p. 27)

5.1.1 Learning Objectives

This laboratory provides you with the following:

- an introduction to the Ricker population model,
- construction of a discrete-time simulation model,
- application of sensitivity analysis for multiple model parameters and initial conditions,
- investigation of chaotic dynamics,
- practice with scientific programming in R, and
- practice communicating your ecological modeling results.

5.1.2 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 when appropriate. Please include a copy of your programs as an appendix to the report.

The final report will be due in class on the date specified on the course website. Please email me PDF of your report and make sure to save it as “yourlastname-lab5.pdf”.

5.2 Model Dynamics and Chaos

In lecture and in previous laboratories, we have primarily observed deterministic models that generate what we might call normal dynamics. A small change in initial conditions or a parameter value tends to cause a proportionally sized change in the dynamics. In this laboratory we are working with a model that generates chaotic dynamics. Gurney and Nisbet (1998) describe chaos as the “combination of non-periodic solutions and sensitive dependence on initial conditions” (p. 29). Thus, there are two characteristics that must be present in a model’s dynamics for it to generate chaotic dynamics. First, it must generate non-periodic solutions that do not damp to a specific equilibrium. Instead, the dynamics tend to revolve around one or more *attractors*, without quite reaching them. Second, the model must show extreme sensitivity to its initial conditions. This is most typically seen as wildly different predictions of variable behavior following a very small change in the initial value. An example of this is shown in Fig. 4.1.1 of the assigned reading from Otto and Day (2007).

Most models that generate chaotic dynamics only do so in selected parameter ranges. Thus, one task of the model analyst is to determine how changing the model parameters influences in model dynamics. We often ask the question: At one point does the model behavior change from the typical dynamics, to periodic dynamics, to non-periodic dynamics? Bifurcation plots like that shown in Fig. 4.1.2 (Otto and Day, 2007) illustrate these transition points or thresholds.

5.3 Laboratory Tasks

Task 5.1 Parameter Sensitivity Analysis

Your first task is to write an R script to encode the Ricker model described above using a for-loop. To begin, let $N_0 = 100$, $a = 2$, and $b = 0.001$. The nominal dynamics of this model are shown in Figure 5.1. Compare your output to these expected dynamics to ensure you have encoded the model correctly. Then, investigate how the model changes when you change parameter b . Reset b to 0.001 and explore how the behavior changes as you change a from 0.5 to about 20. What do you observe? Describe the behavior changes you see and document your observations with plots. What do you surmise is happening in this deterministic model (hint: see reading from Otto and Day (2007))? How does this compare to your solutions for the continuous time logistic equation? Next, investigate the following:

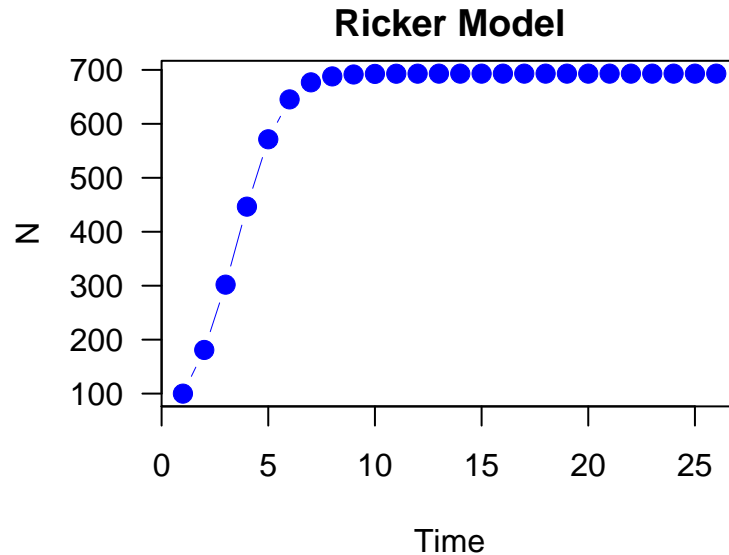


Figure 5.1: Nominal dynamics of the Ricker model with $a = 2$, $b = 0.001$, and $N_0 = 100$.

1. When $b = 0.001$, find the first value of a (to one decimal place) as you increase from 2 at which the dynamics switch from a single steady-state equilibrium, to a two cycle dynamic. Present evidence to support your discovery.
2. CHALLENGE: Given $b = 0.001$, can you find the value of a (to one decimal place) at which the dynamics change from a periodic orbit to an a-periodic orbit. Run the simulations long-enough to ensure your answer is correct. If you are able to accomplish this task, present evidence to support your discovery and explain the criteria you used to select this point.

Task 5.2 Initial Population Size Sensitivity Analysis

1. Reset your model parameters to $a = 18$ and $b = 0.001$ and now explore the effect of changing the initial population size. To start, plot the population dynamics predicted when $N_0 = 100$ and when $N_0 = 101$ on the same graph. Use a time span from 0 to 30 years. What do you observe? Try a couple of additional values.
2. Compare these initial results to the dynamics when $a = 3$, $b = 0.001$, and $N_0 = 100$ or 101 . I recommend plotting this solutions on a separate graph.
3. Exploring the “sensitivity” of the model solution to changes in parameters and initial conditions as you are doing in this laboratory is a simple form of sensitivity analysis, and is a powerful technique to learn about the functions or models you build or use.

5.4 Challenge Problem

If you have time and energy after completing the primary tasks in this laboratory, I present the following as a puzzle to challenge your analytical and programming skills.

Bifurcation diagrams like Figure 4.1.2 in the [Otto and Day \(2007, p. 118\)](#) reading are often used to describe and summarize chaotic dynamics. See if you can create a bifurcation diagram for the Ricker model.

Chapter 6

Two State Variables: Consumer–Resource Dynamics

6.1 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 $M L^{-2}$ 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.

6.1.1 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.

6.1.2 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 (μgL^{-1}).

6.1.3 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 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 the date specified on the course website. Please email me PDF of your report and make sure to save it as “yourlastname-lab6.pdf”.

Assessment There are three tasks in this assignment, each worth 25%. The quality of your report (following guidelines similar to the final project rubric) will be worth another 25%.

6.2 Two entity models with logistic space-control feedback

Table 6.1: Model variables, parameters, and their nominal values.

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	δ_1	0.001
Loss of phosphorus from phytoplankton	δ_2	0.08
Uptake (gross) of phosphorus by phytoplankton	τ_{12}	0.3
Control Parameters		
Maximum density of phytoplankton	K_2	10.0
Resource half saturation constant	k_1	0.001

6.2.1 Model Equations

$$\frac{dX_1}{dt} = C - \delta_1 X_1 - \tau_{12} X_2 \cdot f(X_2) \cdot f(X_1) \quad (6.1)$$

$$\frac{dX_2}{dt} = \tau_{12} X_2 \cdot f(X_2) \cdot f(X_1) - \delta_2 X_2 \quad (6.2)$$

Where

$$f(X_2) = \left(1 - \left(1 - \frac{\delta_2}{\tau_{12}} \right) \left(\frac{X_2}{K_2} \right)_+ \right)_+ \quad (6.3)$$

$$f(X_1) = \frac{X_1}{X_1 + k_1} \quad (6.4)$$

$f(X_2)$ is the logistic growth control function with Wiegert's correction factor, and $f(X_1)$ is a resource control function.

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 $\max(0, \bullet)$.

6.2.2 Tasks

Task 6.1.1 Draw a Forrester diagram for this system using the visual vocabulary introduced in class (see lecture notes on System Conceptualization).

Task 6.1.2 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. Figure 6.1 shows the nominal dynamics for this system with $K_2 = 2$, which you can use to verify that your model solution is working.

NOTE: What would happen if the $f(X_1)$ function were not included in equation 6.2? The $f(X_1)$ function in this model is used here to constrain the consumption rate so that the phytoplankton are unable to consume more phosphorus than is physically available. An alternative way to accomplish this task might be to use an if-then statement to turn off the consumption rate when X_1 is zero. However, in some cases this construction generates numerical errors when using the `ode` function. Thus, here we are trying to approximate a step function (0,1) using a Monod resource control function with a really small half-saturation constant. However, our focus on this task is on the effect of the space control.

Task 6.1.3 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 6.1.4 What does this model predict will happen if the phosphorus input into the system continues to increase due to increased pig farming in the watershed? With $K_2 = 10$, **change the input constant C** to simulate this change.

6.3 Two entity models with resource control

In this task we consider how a non-living resource might control the 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 in Table ?? except for the additional control parameters of the resource refuge level (α_{12}).

6.3.1 Equations

$$\frac{dX_1}{dt} = C - \delta_1 X_1 - \tau_{12} X_2 f(X_1) \quad (6.5)$$

$$\frac{dX_2}{dt} = \tau_{12} X_2 f(X_1) - \delta_2 X_2 \quad (6.6)$$

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

$$f(X_1) = \left(1 - \frac{k_1}{(k_1 + X_1)} \right)_+ \quad (6.7)$$

$$f(X_1) = \left(1 - \frac{\alpha_{12}}{X_1} \right)_+ \quad (6.8)$$

$$f(X_1) = \left(\frac{X_1^b}{X_1^b + k_1^b} \right)_+ \quad (6.9)$$

Where equation (6.7) is the *hyperbolic form of the Michaelis-Menten* equation used as a control function for resource uptake (this equation uses a $1/2$ saturation parameter), equation (6.8) is the *refuge form of the hyperbolic Michaelis-Menten* resource control, and equation (6.9) 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.

6.3.2 Tasks

Task 6.2.1 **Draw a Forrester diagram** for this system.

Task 6.2.2 Using the **hyperbolic form of the Michaelis-Menten** 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 δ_1 to 0.01. (these changes are to make the interactions as clear as possible).

- Explore the behavior as in Task 6.1.2 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.

Task 6.2.3 Using the same parameter values as before, use the **refuge from of hyperbolic** control function (equation 6.8) as the control on phosphorus uptake by phytoplankton. In this formulation, α_{12} specifies the minimum standing stock of X_1 , below which it is not available to the algae. Repeat the simulations using values for α_{12} in the range of 0 to 10 (you can do more if you are curious).

Task 6.2.4 Again using the same parameter values as in Task 6.1.2 repeat your investigations with the **generalized Michaelis–Menten functional response** shown in equation (6.9). Set $k_1 = 10$, and then explore the effect of changing b , starting with $b = 1$. Again, please present time series plots of both the state variables and the realized control functions.

Task 6.2.5 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 6.2.6 **CHALLENGE TASK** Please complete this task as time and interest allow. Recall the *bifurcation plot* used to show the changing nature of the equilibrium solutions of the Ricker model in the last lab. The x-axis of the bifurcation plot is one of the model parameters and the y-axis is the equilibrium or steady-state solution of a variable in the model. In a model exhibiting chaotic dynamics, the steady-state solution shifts from a single equilibrium to multiple values, but in a model exhibiting more simple dynamics, the steady-state solution is a single value. This challenge task is to create a plot of the model steady-state values versus a wide range of parameter values to quickly evaluate the effect of changing the model parameters on the steady-state value.

6.4 Assumptions

Task 6.3.1 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.

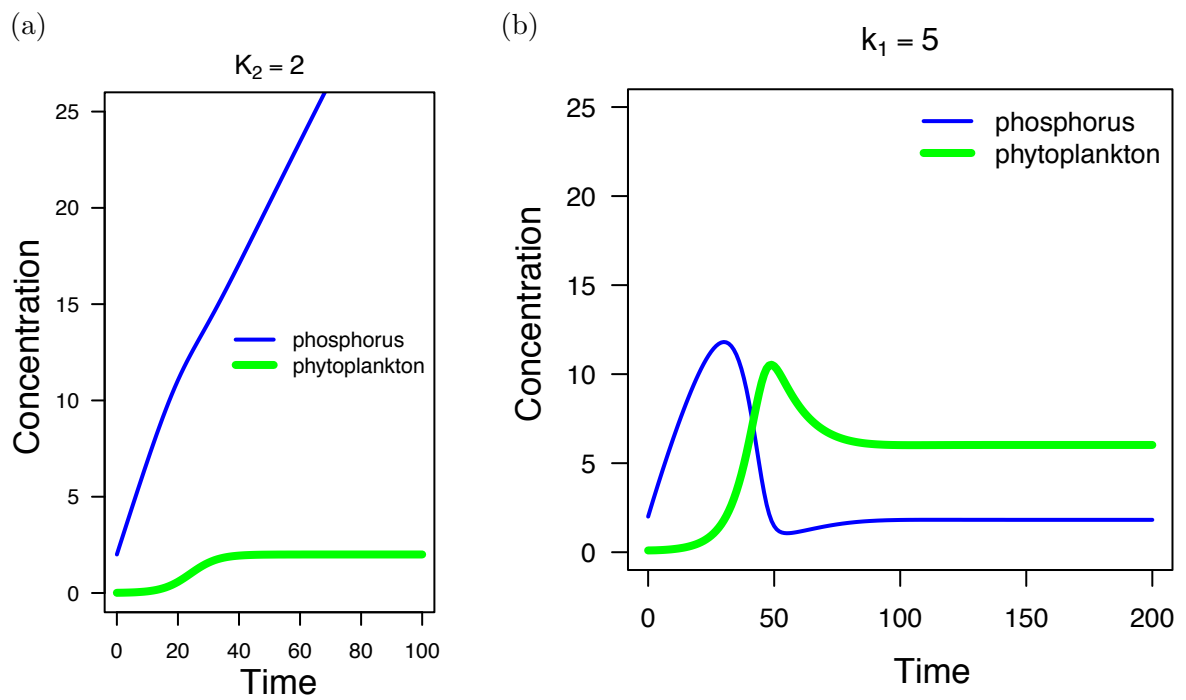


Figure 6.1: Nominal dynamics for (a) the model for Task 6.1 using the parameter values in Table 6.1 and $K_2 = 2$. and (b) Task 6.2.2

Chapter 7

Three State Variable Models

7.1 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.

7.1.1 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;
- Clearly communicate your scientific work in the form of a brief narrative report.

7.1.2 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 and the final report will be due in class on the date specified on the course website. Please email me PDF of your report and make sure to save it as “yourlastname-lab7.pdf”.

Assessment There are two tasks in this assignment, each worth 45% of the grade. The quality of your report (following guidelines similar to the final project rubric) will be worth another 10%.

7.2 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. 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 7.2 is the linear special case of the **generalized hyperbolic function**:

$$f(X_i) = \left(1 - \left(\frac{K_{ij} - X_i}{K_{ij} - \alpha_{ij}} \right)_+ \right)_+ . \quad (7.1)$$

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 7.2 is the **logistic**.

$$f(X_j) = \left(1 - w_j \left(\frac{X_j + \beta_k X_k - \alpha_j}{K_j - \alpha_j} \right)_+ \right)_+ , \text{ and} \quad (7.2)$$

$$w_j = \left(1 - \frac{\delta_j}{\tau_{ij}} \right) . \quad (7.3)$$

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 7.1. 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.

Table 7.1: 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

The equations for this model are:

$$\frac{dX_1}{dt} = C_1 - \delta_1 X_1 - \tau_{12} X_2 \underbrace{f(X_1)}_{\text{resource}} \underbrace{f(X_2)a}_{\text{space}} \quad (7.4)$$

$$\frac{dX_2}{dt} = \tau_{12} X_2 \underbrace{f(X_1)}_{\text{resource}} \underbrace{f(X_2)a}_{\text{space}} - \delta_2 X_2 - \tau_{23} X_3 \underbrace{f(X_2)b}_{\text{resource}} \underbrace{f(X_3)}_{\text{space}} \quad (7.5)$$

$$\frac{dX_3}{dt} = \tau_{23} X_3 \underbrace{f(X_2)b}_{\text{resource}} \underbrace{f(X_3)}_{\text{space}} - \delta_3 X_3 \quad (7.6)$$

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

Task 7.1.1 **Draw a Forrester diagram** of this system.

Task 7.1.2 **Simulate the model** using the parameter values defined in Table 7.1. This will be the *nominal* model dynamics to which you can compare the changes you make in the following tasks. For your reference, the expected nominal dynamics are shown in Fig. 7.1.

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 increase or decrease). Here we will investigate this last factor more closely. When given enough enrichment (nutrients entering the system, C_1),

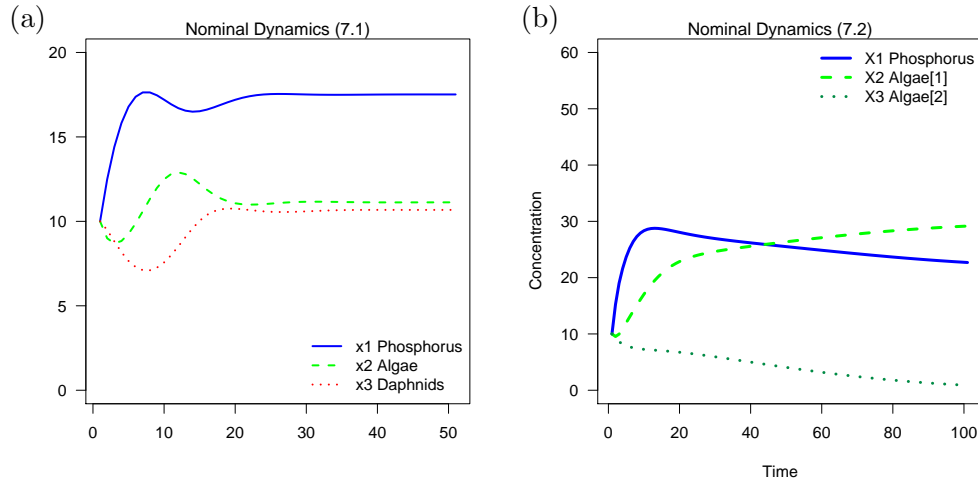


Figure 7.1: Nominal dynamics for Task 1 (a) and Task 2 (b).

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.

Task 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 alternative locally-stable steady states** depending on the starting densities (initial conditions) 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 cases the steady state value of algae is larger than the daphnids ($X_2 > X_3$), and in the other case the steady state value of daphnids is larger than the algae ($X_3 > X_2$).

Task 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 to generate two alternative stable states**. 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.

7.3 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 7.2.

Task 7.2.1 Draw a Forrester diagram the model and formulate the equations to simulate this system using what we have learned in class and the example provided in your notes;

Table 7.2: 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	τ_{12}	0.35
Max uptake of X_1 by X_3	τ_{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

7.3.1 Modes of Control

Task 7.2.2 If the model were *optimally enriched* ($X_1 > \{K_{12}, K_{13}\}$), then **what would you expect the outcome of the competition between X_2 and X_3 to be?** Why? Notice that this situation reduces to two species competing for a common resource. Thus, you should be able to use a graphical isocline analysis to predict the outcome.

This “web” model includes interspecific competition and it exhibits behavior in response to enrichment and differences in initial conditions 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.

7.3.2 Algae Adaptations

The algae parameter values and constants suggested in Table 7.2 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.

- Task 7.2.3 Which species is which? Why? What do you expect the outcome of this simulation to be? How are you making this prediction?;
- Task 7.2.4 Using the values in Table 7.2 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?
- Task 7.2.5 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.

7.4 TMP

Here are some additionally useful references:

[Blindow et al. \(1993\)](#); [Scheffer et al. \(2001\)](#); [Schröder et al. \(2005\)](#)

Chapter 8

Connecting Ecological Models with Data

8.1 Introduction

In class we talked about four specific ways in which modelers must consider and use empirical data. These include **parameter estimation**, **function selection**, **forcing or exogenous variables**, and **model evaluation**. In this laboratory, we will practice

1. using a non-linear least squares method to fit parameters to a proposed function that describes the process, and
2. using empirical observations of an exogenous variable to drive the system dynamics.

These are eminently practical skills for mathematical modelers and data analysis in general. No report is required for this laboratory.

8.2 Importing Data from Text Files

The first new issue you will encounter is that we have data stored as space delimited text files that we need to enter into R. This required using the `read.table` command. If my data file is called *data.txt* and the file is in my current working directory of R , then I would use the command as `d = read.table('data.txt')`. The R variable *d* is now a data frame in which the columns are variables and rows are observations. For example, if my text file contains the data in Table 8.1, then, `d$V1` is the first column of data.

Table 8.1: Example data

1	50	2
2	51	6
3	52	5
4	53	4

It is convenient to add column headers to your data when it is store as an ascii text file like this because it helps you remember what the variables were. If our data file has variable names on the first line, we will want to modify our command to read `d =`

`read.table('data.txt', header=TRUE)`. When you use this command on the data for this exercise, use the `str(d)` command to see how this changes the data frame.

The `read.table` command assumes that your observations are space delimited, but your data may be delimited by other markers like commas or tabs. You can add a parameter to the `read.table` command to specify the delimiter. For example, `d = read.table('data.txt', header=TRUE, sep=',')` specifies that the delimiter is a comma.

It is good practice to store your data in flat plain ascii text files. This can generally be read into a wide variety of analytical software including SAS, Matlab, and R and it is a non-proprietary format. Many biologists store their data in Excel. This can be convenient, but it often requires extra steps to extract the data for analyses beyond Excel, and you cannot open or read your data without that exact version of the Microsoft product. This might seem like a reasonable trade off today, but how much scientific data was lost because it was stored in Lotus 1-2-3 spreadsheets? Further, if you store your data in text files and perform your analysis with script based software like R you are less likely to accidentally delete or modify a cell or column of your raw data. You can import and export data from Excel as ascii text files if needed. If you just cannot give up Excel, there is a package called “xlsx” that will let you read data directly from Excel.

8.3 Fitting Parameters Using Non-Linear Least Squares

Your first task for this laboratory is to complete Exercise 9.7 in [Ellner and Guckenheimer \(2006a\)](#) *Dynamic Models in Biology* (Chapter 9, p. 297). The exercise reads as follows:

Download the data from Figure 9.5 from the book’s web site, and write a script to find least-squares parameter estimates for V and K on the untransformed scale (you should find that you duplicate the values above) and again using power transformation with $\beta = 0.5$. Do your parameter estimates for $\beta = 0.41$ indicate that trial-and-error choice of $\beta = 0.5$ was close enough?

The full text of Chapter 9 is posted on the `biol534` course website as is the `EggRatio.dat` data set.

I believe that Ellner and Guckenheimer had in mind that you would actually write a script to solve the least squares problem. This might be instructive, but R has a built in algorithm for solving non-linear least squares problems called `nls`. We will use this function. Please review the help file for this function.

In general, an `nls` call will look like the following `fit = nls(model,data,starting.values)`. When using `nls`, you must specify initial parameter values to try. Again, see the documentation for more details as well as your previous course notes.

8.4 Exogenous Data

The second task of this lab is to create a model in which the dynamics are driven by exogenous variables. For this task please use the Ross Sea data set posted on the class website.

Lets start by creating a lotka-volterra predator-prey model to simulate predation dy-

namics. Recall, that the equations for this model are

$$\frac{dN_1}{dt} = (\mu - d)N_1 - cN_1N_2 \quad (8.1)$$

$$\frac{dN_2}{dt} = bcN_1N_2 - dN_2 \quad (8.2)$$

Please select a set of parameters for the nominal simulation.

Now lets imagine that our prey is a phytoplankton growing in the Ross Sea. We would expect that its growth rate may depend on temperature. [Jørgensen and Bendoricchio \(2001\)](#) provide several possible ways of modelling the effect of temperature, but here lets select a relatively simple one, e^{a*T} . We will assume that $a = 0.06933$, which describes the non-linear effect of increasing temperature on the growth rate. I recommend you plot this function for a range of temperature values to see how the control function works. Given this, lets define $\mu = \mu_{max} * e^{a*T}$.

Now you will need to use the spline function to interpolate values to use this in your model. See the “Connecting Models to Data” lecture notes for how to do this. Then, see if you can use a monod function to model the effect of light (PUR in the data file) on the phytoplankton growth. How do these simulations compare to your nominal simulation?

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