

Topics covered in Ecosystem Modeling & Analysis (OCS 4410)

➤ What is a Model

- A mathematical formulation intended to represent a natural phenomenon or system
- Models can be considered to be an experimental science, since model simulations can also be used to *test the validity of the hypothesis & to generate new hypotheses*
- Models complement field work they don't replace it
- You can never build a model that replicates what is actually occurring in nature, because nature is too complex to ever be perfectly modeled, the point is to come as close as you can to the truth
- Models are the only scientific means of predicting the future

➤ Deterministic vs. Stochastic Models

Deterministic Models

- have no random variables
- a model that has only one solution, in some cases this means that the model only describes the trend.
- Their most important property is that we can predict the exact value of the variable of interest at any future time (given we know the pattern of change up to the present time)

Stochastic Models

- Contains random variables

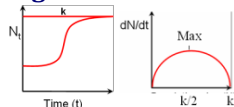
➤ Odum diagrams

- represent only energy flows, fairly implicit & simple in appearance, & relatively easy to turn into mathematical expressions
- Whatever goes into a model **MUST** come out, the model must be balanced
- Every arrow **MUST** be described as a term in a **differential equation**
- Diagrams are important when working with complex models because they have a **visual basis** for equation building, & different people can just focus on their specialties & then compile their codes to make the model

H.T. Odum's System of Generic Symbols (Energy Circuit/Systems Language Symbols)



➤ Logistic Growth



$$\frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right)$$

- Models the "S-shaped" curve of population growth which are found with **K-selected** populations (limited by carrying capacity)

➤ Difference vs. Differential equations

Difference Equations

- Equations that **recursively define a sequence**
- each term of the sequence is defined as a function of the preceding terms
- you use old values to calculate new ones
- have an **implicit** timestep

ex1. **Logistic Equation**

ex2. **Fibonacci Numbers** (1, 2, 3, 5, 8)

ex3. **Non - Overlapping Generations**

- **Euler Integration Method** with an integration step = 1

Differential Equation

- Describe **continuous systems**
- **Rates of Change** are defined in terms of **other values** in the system
- In order to solve them you must convert them into difference equations

ex1. Used to define most **physical laws**

ex2.

ex3. **Overlapping Generations**

- **Runge-Kutta** (4th order) **Integration Method** with an integration step < 1

➤ Analytic vs. Numerical Solution

Analytic Solution

- Uses calculus to solve, it is **exact**

Numerical Solution

- A numerical solution, **never exact**

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➤ Compiler

- Changes programs into applications, so that no one can see their machine code by creating stand-alone .exe files.
- Here the programs are translated in advance so that the source code is permanently converted into machine code (object code), resulting in a finished, executable program.

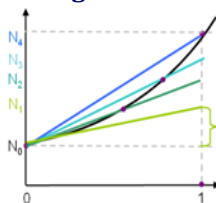
➤ Random Walk

- A term first introduced by *Karl Pearson* in 1905 to describe the formulation of a trajectory by taking successive random steps

➤ Subroutine

- Fragments of a program that are relatively self-contained.
- They perform some particular part of the work that has to be done, turned into a separate unit as part of the overall design of a larger program.
- They enable you to subdivide & thus simplify the task of creating a program.
- Begins with "SUB" & ends with "END SUB."
- Advantages: shorten & simplify source code, they're easily available for use by any program, they also need only be compiled once, not every time a program is created or revised.

➤ Runge-Kutta method



- Numerous **implicit & explicit iterative** methods for **approximating the solution of ordinary differential equations** developed in the early 1900s by German mathematicians **C. Runge & M.W. Kutta**.
- The most common is the Runge-Kutta 4th Order Method which obtains 4th order accuracy by evaluating the derivative four times in each time step: once at the initial point, twice at sample midpoints, & once at a sample endpoint; the final integration value is then derived based on these derivatives.

➤ Lotka-Volterra model & Volterra's principle

- The **simplest & most widely used model** of the **prey-predator system**
- **Volterra's Principle** : if a prey-predator system is harvested, the proportion of predators will decrease

➤ Age-structured population model

- **Principals of Age-Structured Population Modeling:**
 - 1) Birth process doesn't begin until the 1st cohort reaches reproductive age
 - 2) Reproduction only increases the size of the 1st cohort
 - 3) After 1 yr survivors from each cohort are transferred to the next higher one
 - 4) Mortality rate ↑ with ↑age → the last cohort eventually disappears from the system

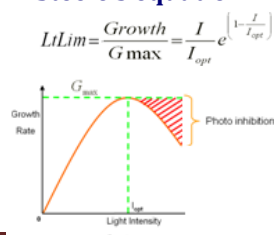
➤ Water residence time

- **Residence Time:** The average amount of time that a particle spends in a particular system
- the average amount of time a water molecule spends in a specific reservoir (atmosphere=9 days vs ocean = 3,200 years)

➤ Monod's equation

- Monod's **Hyperbolic Effect of Nutrient Concentration on Growth**: was developed to model **substrate limitation growth**
- $GROWTH = GMAX * NUTLIM = GMAX * [N / (K_S + N)]$
- One of the inherent weaknesses of the simple Monod expression is the strict implication of a single limiting nutrient
- it's usually hard to decide a priori what nutrient is most likely to become limiting, nitrogen (N), phosphorus (P), or silicon (Si)

➤ Steele's equation



- Steele developed an equation to model this **photosynthesis-light response**, where **GROWTH** is the growth rate, **GMAX** is the maximum growth rate, **I** is the incident solar radiation reduced for an average albedo of 10%, & **I_{opt}** is the optimum radiation with respect to the growth rate (or productivity) of the studied phytoplankton assemblage
- At optimum light $GROWTH = GMAX$, since **GMAX** is determined independently of from the growth-temperature equation, only the light limitation term (**LTLIM**) is required.
- This term is found by normalizing the growth equation...this is done by dividing **GROWTH** by **GMAX**

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Modeling aspects in ecology

Terminology

Population Natalty	B	The number of animals born per unit time ($B = b * N$)
Specific Natalty Rate	b	animals born per unit population per unit time ($b = B/N$)
Population Size	N	N_0 = Initial Population Size; N_t = population size at time “ t ”
Population Mortality	M	The number of animals died per unit time ($M = m * N$)
Specific Mortality Rate	m	animals died per unit population per unit time ($m = M/N$)
Population Intrinsic Growth Rate	r	This is one of the most powerful tools on the planet ($r = b - m$)
Rate of Change in Population Size	rN	Average Rate: $rN = \Delta N / \Delta t$ Instantaneous Rate: $rN = dN / dt$

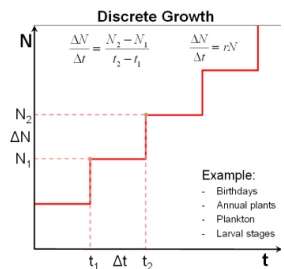
Model: a mathematical formulation intended to represent a natural phenomenon or system

Principal of Hierarchical Organization: Don't have to understand precisely how a system is structured from simpler units in order to predict how it will behave (**Odum** 1971)

Simple Population Models

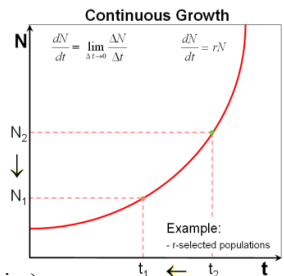
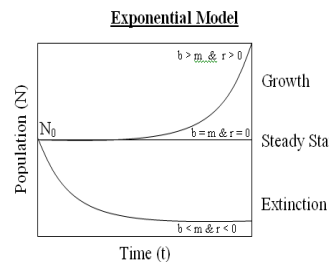
Discrete Growth Model

- Assumptions:** $N_t = N_0 * (1 + r)^t$ where $rN = \Delta N / \Delta t$
 - no immigration** (entering) or **emigration** (leaving) that will affect the population size
 - neither abiotic nor biotic factors will limit the population size
- Process:**
 - $B = b * N$; Population Natalty = (specific natalty rate)(population size)
 - $M = m * N$; Population Mortality = (specific mortality rate)(population size)
 - $r = b - m$; Population intrinsic growth rate = (specific natalty rate) – (specific mortality rate)



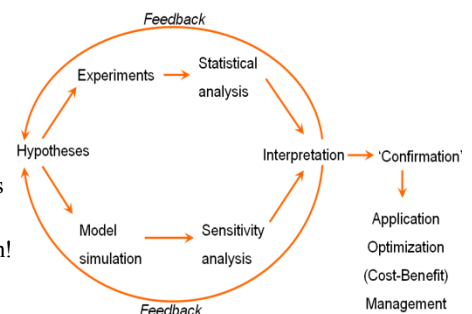
Continuous Growth Model

- Assumptions:** $N_t = N_0 e^{rt}$ where $rN = dN / dt$
 - only one species** is present → **no interspecific interactions** (biotic factors won't limit pop. size)
 - no immigration** (entering) or **emigration** (leaving) that will affect the population size
 - environmental **resources** will always remain **unlimited** (abiotic factors won't limit pop. size)
- J-curve:** describes r-selected organisms which have short life histories (such as invasive species)



The Role of Modeling in Research

- Modeling is pretty much analogous to experimental science, since model simulations can also be used to *test the validity of hypothesis* & to *generate new hypotheses*.
- For this reason models can be used to help select an environmental strategy best suited as a solution to specific problems
- Models compliment field work, they DON'T replace it!
- You can never build a model that replicates what is actually occurring in nature, because nature is too complex to ever be perfectly modeled, the point is to come as close as you can to the truth
- Mathematical models should be used to solve ecological problems, not to create them!
- Once you have a simple model, you can always make it more complex.
- The robustness of your model should reflect that of the system you are simulating
- Modeling technology is so advanced it enables us to simulate extraordinarily complex systems based on finite detail, the problem is that field studies aren't able to supply the models with the scale of information the model requires.
- Models are the **only** scientific means of predicting the future



Topics covered in **Ecosystem Modeling & Analysis** (OCS 4410)

➤ **Classes of Ecological Models**

- **Conceptual Model:** a set of scientific hypotheses about a certain biological system or biological process.
The hypotheses are based on field data or models built for a similar system.
Essentially it is a verbal description of the system of interest as well as the objectives of the model.
- **Diagrammatic Model:** a concise visual representation of the system structure & function, in the form of diagrams.
Known for modeling inputs & outputs of materials (or energy) & the importance of system components
 - **Forcing Functions (driving variables):** inputs to the system from the outside
 - **State Variables:** dynamic components of the system
 - **Transfer Functions:** flows of energy & matter between the system components
 - **Subsets (Compartments):** aggregation of certain components into larger units
- **Mathematical Model:** a mathematical formulation intended to represent a natural phenomenon or system.
Usually composed of 1 or more **differential** or **difference equations** describing the rate of change of one or more state variables
 - **System (state) Variables:** sets of numbers representing the system at any time
 - **Transfer Functions:** flows or interactions between system components
 - **Forcing Functions:** inputs to the system or factors affecting, but not affected by, system components
 - **Parameters:** constants in the mathematical expressions
- **Computer Model:** program which tells the computer to run the mathematical model
- **Empirical Model:** developed to describe a relationship, without regard for appropriate representation of processes that are operating in the real system. They are built to predict, not explain.
- **Mechanistic Model:** all important mechanisms that are underlying the system's behavior should be incorporated into the model.
They are built to explain, as well as to predict.
- **Deterministic Models:** a model that has only one solution, in some cases this means that the model only describes the trend.
Their most important property is that we can predict the exact value of the variable of interest at any future time (given we know the pattern of change up to the present time).
- **Stochastic Models:** models containing random variables (e.g. random numbers & pseudorandom numbers)
 - **Environmental Stochasticity:** aperiodic environmental variations & resulting population fluctuations
 - **Demographic Stochasticity:** describes changes in a population containing a discrete number of members, with population changes being caused by succession of individually unpredictable births & deaths

Classes of Ecological Models

Conceptual (<i>words</i>)	Mathematical (<i>equations</i>)
Diagrammatic (<i>diagrams</i>)	Computer (<i>programming language</i>)
Empirical (=Correlative) (<i>regression models</i>)	Mechanistic (=Explanatory) (<i>process oriented models</i>)
Deterministic (<i>no random variables</i>)	Stochastic (<i>random variables</i>)

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➤ Systems Ecology & Modeling

- **Systems Ecology:** the approach to ecology which uses tools & methods developed, largely in engineering, in order to study complex entities (systems)
 - **Characteristics of Systems Ecology:**
 - 1) Symbolic (modular) language
 - 2) uses fundamental ecological principals
 - 3) conservation of material, energy, & momentum
 - 4) systems facilitate discussion between people of different disciplines
- **Forrester diagrams:** represent material & information flows; more explicit & complex in appearance; hard to convert into a series of mathematical models
- **Odum diagrams:** represent only energy flows; fairly implicit & simple in appearance; relatively easy to turn into mathematical expressions
 - What ever goes into a model **MUST** come put, the model must be balanced
 - Every arrow **MUST** be described as a term in a differential equation
 - Diagrams are important when working with complex models because they have a **visual basis** for equation building, & different people can just focus on their specialties & then compile their codes to make the model

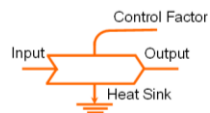
Odum Diagrams

Storage



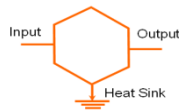
Indicates location of mass or energy storage in a system, as a balance of inflows & outflows
Used for a variety of state variables, such as water, nutrients, detritus, etc.

Interaction



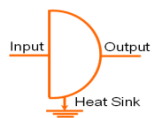
Shows interactive intersection of 2 material or energy flows, coupled to produce an outflow

Consumer



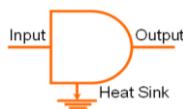
Stores energy & material.
A symbol for heterotrophic organisms & communities, such as zooplankton & bacteria.

Energy Receptor



Symbol represents the reception of energy such as sound, light, & water waves.
In this module energy interacts with cycling material producing an energy-activated state
Used, for example, to describe enzyme-substrate dynamics (Michaelis-Menten reaction).

Producer



Symbol is a combination of a 'Consumer unit' & 'energy receptor'.
Energy captured by a cycling receptor unit is passed to self-maintaining unit that also keeps the cycling receptor machinery working, & returns necessary materials to it.
The green plant is an example.

Source



Represents a source of energy or material for the system, such as the sun, temperature, fossil fuels, rain, etc. Used to denote forcing functions.

Heat Sink

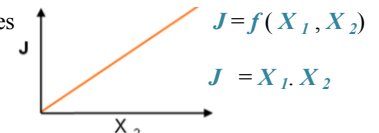


Loss of energy or matter

Work Gate (Interaction)



work gate concept is like a traffic light, it stops & goes



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➤ Modeling Process

Success of the model depends on: 1) experience of the modeler 2) availability of data 3) complexity of the model

Process: 1) Identification of the system

2) Problem definition

3) Critical decision whether or not to use the modeling approach

4) **Conceptual Model:** defines the objectives of the numerical model (depends on data availability, computing facilities, funding, etc.)

5) Boundaries of the system need to be clearly identified

6) Construct systems diagrams, showing the position of the state variables, mass storage, or energy flow

7) Identify subsystems or compartments

8) Inputs & outputs of mass & energy through all the interfaces

9) External controlling factors (e.g. light, temp., etc) must be determined to identify forcing functions that influence system dynamics

10) Chose the state variables

11) Translate into mathematical & computer forms

12) Calibration is attempted to find best accordance between computed & observed state variables, by variation of model parameters

13) Verification is a test of the internal logic of the model, does the model react as expected?

Does the model follow the law of mass conservation?

14) Final step is an iterative process, since the conceptual model will ultimately be changed if the model simulations fail to agree with real data

➤ Sample Problems

The intrinsic growth rate (r) of continuously breeding population of brown rat is 0.11/week.

Consider a population of 100 animals, living in an unlimited environment. What is the expected number of rats after a period of 1 year?

$$\begin{aligned} N_1 &= N_0 (1+r)^1 \\ &= 100 * [1 + (0.11/\text{week})(52 \text{ weeks/yr})]^1 \\ &= 100 * [1 + (5.72/\text{year})]^1 \\ &= 100 * [6.72/\text{year}]^1 \end{aligned}$$

$$N_1 = 672 \text{ rats after one year}$$

Between 1700 & 1800 A.D. the number of people on Earth increased from $6 * 10^8$ to $9 * 10^8$.

What was the average intrinsic growth rate, if we assume that the growth pattern was exponential?

$$\begin{aligned} rN &= \Delta N / \Delta t \\ &= [(9 * 10^8) - (6 * 10^8)] / [1800 \text{ A.D.} - 1700 \text{ A.D.}] \\ rN &= [3 * 10^6] / 100 \\ r &= [3 * 10^6 \text{ people/year}] / [6 * 10^8] \\ r &= 0.005/\text{yr} \end{aligned}$$

$$\begin{aligned} N_1 &= N_0 e^{rt} \\ 9 * 10^8 &= (6 * 10^8) (e^{r(100)}) \\ 1.5 &= e^{100r} \\ (r)(100) &= \ln(1.5) \\ r &= 0.00405/\text{yr} \end{aligned}$$

The size of human population on Earth was approximately $6 * 10^9$ in 1990. What is the expected number of people by the end of the year 2020, if the human population continues to increase exponentially at an average rate of 0.02/year?

Compare predictions of continuous & discrete versions of the Malthus model.

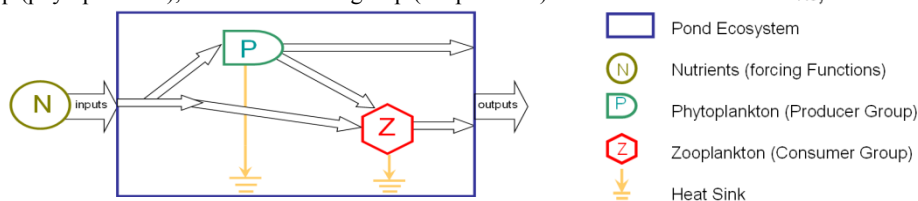
Discrete Model:

$$\begin{aligned} N_t &= N_0 (1+r)^t \\ &= (6 * 10^9) [1 + (0.02/\text{yr})]^{(2020-1990)} \\ &= (6 * 10^9) [1 + (0.02/\text{yr})]^{(30)} \\ &= (6 * 10^9) [1.02]^{(30)} \\ N_t &= 1.0868 * 10^{10} \end{aligned}$$

Continuous Model:

$$\begin{aligned} N_t &= N_0 e^{rt} \\ &= (6 * 10^9) (e^{(0.02/\text{yr})(30)}) \\ &= (6 * 10^9) (e^{0.6}) \\ N_t &= 1.093 * 10^{10} \end{aligned}$$

Using Odem symbols construct a simple model of the pond ecosystem, involving one forcing function (nutrients), one producer group (phytoplankton), & one consumer group (zooplankton).



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Equations of Change

Terminology

Carrying Capacity K

Crowding Factor $\frac{rN^2}{k}$

Steady State (equilibrium) N^* $N^* = k$ represents a stable population; while $N^* = 0$ is unstable

Numerical solution : a numerical approximation, never exact

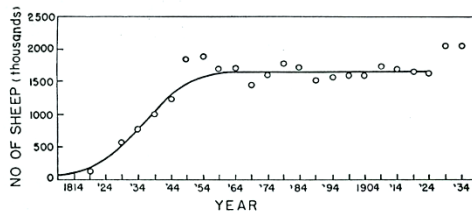
Analytic solution: uses calculus to solve, it is exact

Ecological Stability: If a population persists for a large number of generations, we can say that it is ecologically stable

Logistic Growth Model

$$\frac{dN}{dt} = rN - \frac{rN^2}{k} \quad \text{or,} \quad \frac{dN}{dt} = rN \left(1 - \frac{N}{k} \right) \quad \text{where} \quad \frac{rN^2}{k} = \text{the crowding factor} \rightarrow N_t = \frac{k}{1 + [(k - N_0)/N_0]e^{-rt}}$$

S-curve (found with K-selected populations)

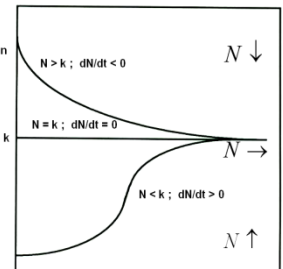


Using Derivatives to Describe Behavior of Complex Functions

$\frac{dN}{dt} > 0$	$N \uparrow$
$\frac{dN}{dt} = 0$	$N \rightarrow$
$\frac{dN}{dt} < 0$	$N \downarrow$

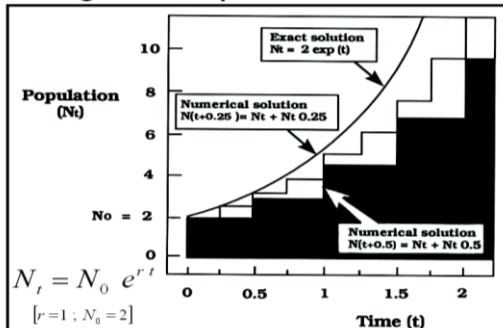
Using Derivatives to Determine Maxima and Minima of Complex Functions

$\frac{dN}{dt} = 0$ and $\frac{d^2N}{dt^2} < 0$	Maximum
$\frac{dN}{dt} = 0$ and $\frac{d^2N}{dt^2} > 0$	Minimum



	Integral Equation	Difference (Discrete)Equation	Differential (continuous)Equation
Linear Growth	$N_t = rt$ where $N = f(t)$ 	$N_{t+\Delta t} = N_t + r \Delta t$	$\frac{dN}{dt} = r$ where $\frac{dN}{dt} = f(N)$
Exponential Growth	$N_t = N_0 e^{rt}$ 	$N_{t+\Delta t} = N_t + r N_t \Delta t$	$\frac{dN}{dt} = rN$
Logistic Growth	$N_t = \frac{k}{1 + [(k - N_0)/N_0]e^{-rt}}$ 	$N_{t+\Delta t} = N_t + r N_t (1 - \frac{N_t}{k}) \Delta t$	$\frac{dN}{dt} = rN(1 - \frac{N}{k})$

Integration Steps and Model Errors



- Error is cumulative
- When building an ecosystem model, you should try to accommodate the fastest growth rate (e.g. bacteria)

Limits of Calculus

Equation	Linear Equations			Nonlinear Equations		
	One Equation	Several Equations	Many Equations	One Equation	Several Equations	Many Equations
Algebraic	Trivial	Easy	Difficult	Very difficult	Very difficult	Impossible
Ordinary Differential	Easy	Difficult	Essentially impossible	Very difficult	Impossible	Impossible
Partial differential	Difficult	Essentially impossible	Impossible	Impossible	Impossible	Impossible

ECOSYSTEM MODELING

Classification of mathematical problems and their ease of solution by analytical methods (from Hall and Day, 1990, modified after Constanza et al., 1993).

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Computers & Modeling

➤ Terminology

Absolute Machine Language	Instructions given to computers in almost incomprehensible hexadecimal codes, it's why direct programming is so difficult
Programming languages	Were created in order to write programs using relatively simple instructions
Assembly language (Object Code)	The programmer's equivalent of the computer's machine language, because each individual machine language instruction can be created in assembly language
High Level languages (Source Code)	Based on the idea of summarizing many machine language instructions into a single program command (BASIC, FORTRAN, PASCAL, C, etc.)
Application languages	(dBASE, LOTUS, etc.)
Creating computer programs	1) write the program; 2) translate the program's source code into object code using a compiler or an assembler; & last 3) convert the object code into a finished program using the link-editor
Interpreting (interpreters)	To execute any program, no matter what language its in, it must be translated into machine language. Interpreters translate programs into machine language word by word, while the program is being carried out. Since interpreters are actually performing the steps that the original program calls for, the processes is very slow & inefficient, but it is also a flexible process. The slowness is because the time is being taken up performing 2 tasks (translating the program & doing the program's work). The inefficiency is because the translation is done over & over again, each time a program step is repeated & each time the program is run. However, interpreting is very flexible since you can change, adjust, or revise a program while it is being entered into the computer.
Compiling (compilers)	Changes programs into applications, so that no one can see their machine code by creating stand-alone .exe files. Here the programs are translated in advance so that the source code is permanently converted into machine code (object code), resulting in a finished, executable program.
Assemblers	Compilers for assembly languages
Structured programming (top-down programming)	It breaks the large, hard to read & write, interrupted program listing into functional parts, each of which is developed separately, & will later make up the whole program. It is the most common (& useful) way of overcoming the problems of writing & presenting complex programs. Subroutines, Linking, & Libraries are the key components to structured programming
Subroutines	Fragments of a program that are relatively self-contained. They perform some particular part of the work that has to be done, turned into a separate unit as part of the overall design of a larger program. They enable you to subdivide & thus simplify the task of creating a program. Begins with "SUB" & ends with "END SUB." Advantages: shorten & simplify source code, they're easily available for use by any program, they also need only be compiled once, not every time a program is created or revised.
Linking (Link editing)	Making all the connections between different pieces of a program to make them work as a whole. It gathers all the parts of object code (e.g. TEST.OBJ), makes the connections between them, & produces the form that finally is ready to be run by the computer.
Libraries (object library)	A single disk file that can contain the object code for any number of program subroutines. After a subroutine is written, the program compiles the subroutine into separate, distinct object code files, & then uses a special program (LIB editor) which takes the object code & stores it in a library along with other subroutines.
QBASIC	Simplified version of QuickBASIC programming language, & includes all statements & functions found in earlier versions of BASIC. It allows for the program to be divided into SUBs & FUNCTIONS (not possible with BASIC). You write the program with an advanced screen editor that makes making changes easy. After the program is run, you will be automatically sent back to the editor so make any necessary changes.
Visual BASIC	Released in 1991, it replaced most of the QBASIC
Remark statements	All statements that begin with (') are treated as program documentation
Variables	Named memory locations that store data values; type of data used can be specified by one of the following: \$, %, &, !, #
String variables	Hold Characters : A\$, TEMP\$, etc.
Numeric variables	Hold Numbers : a, X, TEMP, temp, etc.
Simple Integers	A whole number in the range -32,768 to + 32,768. It requires 2 bytes of memory
Long integers	A whole number in the range -2,147,483,648 to + 2,147,483,648. It requires 4 bytes of memory
Single Precision floating point numbers	A real number of up to 7 digits, plus a decimal point. The range for single precision numbers is from - 3.37E+38 to +3.37E+38. If a number is too large to be represented in 7 digits the number is expressed in floating point notation rounded to 7 digits with an exponent. It requires 4 bytes of memory.
Double Precision floating point numbers	A real number of up to 16 digits, plus a decimal point. The range for double precision numbers is from - 1.67D+308 to +1.67D+308. If a number is too large to be represented in 16 digits it is converted to floating point notation. It requires 8 bytes of memory.
Arrays	An array D(N) is a set of related variables D(1), D(2)...D(N), where D is the name of the array & N is the subscript. The subscript indicates the size of an array, which must be defined by DIM statement.
Binary digit	0 or 1
Byte	1 byte = 8 bits

Topics covered in Ecosystem Modeling & Analysis (OCS 4410)

Computer Programs for Integration of Differential Equations

Terminology

Numerical Integration A straightforward techniques of calculating an incremental change in a variable & adding it to the old value of the variable. All numerical integration techniques are based on the fact that, for small incremental changes in the independent variable (Δx), the difference quotient ($\Delta y/\Delta x$) approaches the derivative (dy/dx).

Finite difference approach With small incremental changes in the independent variable (Δx), the difference quotient ($\Delta y/\Delta x$) approaches the derivative (dy/dx)

Integration Techniques Generally speaking, the more complex integration algorithms yield more stable & numerically correct results, but they take longer to run. The rule of thumb is to use the least complicated algorithm that provides stable & correct results

Euler Computationally simple; fastest for moderate step sizes. Evaluates only **one** derivative during each time step

Trapezoidal A bit more accurate than Euler.

Runge Kutta 2nd order Obtains second order accuracy. Uses a midpoint step derivative to calculate the final integration value.

Runge Kutta 4th order Obtains fourth order accuracy. This method evaluates the derivative four times in each time step: once at the initial point, twice at sample midpoints, & once at sample endpoint. The final integration value is then derived based on these derivatives.

Adaptive Obtains fifth order accuracy. The algorithm automatically

Runge Kutta 5th order takes small steps through discontinuities in the input function & large steps through smooth functions. A feature of this algorithm is that you can specify its truncation error & minimum step size.

Bulirsh-Stoer Uses rational polynomials to extrapolate a series of substeps to a final estimate. Highly accurate for smooth functions.

Model Errors

Roundoff error using single or double precision numbers to approximate infinite real numbers

Truncation Error E integration algorithm error $E = a(\Delta t)^k$

Integration algorithm order k order = number of times a derivative is evaluated in each step

Constant of proportionality a

INTEGRA A BASIC program that performs integration of ordinary differential equations, using either the Euler or Runge-Kutta (4th order) method. It was designed to run efficiently with QBasic & VisualBasic programming environments

The Euler Method	v.s.	The Runge Kutta Method 4 th Order
$\frac{dN}{dt} \sim \frac{\Delta N_0}{\Delta t} = rN_0$ <p>and $N_{t+\Delta t} = N_t + r N_t \Delta t$</p> <p>$N_1 \text{ Model} < N_1$</p>	$r = 1$ $N_0 = 2$ $m = \text{derivative}$	$m_1 = r N_0 = (1)(2) = 2$ $m_2 = r (N_0 + \frac{1}{2} m_1) = (1)[2 + (\frac{1}{2})(2)] = 3$ $m_3 = r (N_0 + \frac{1}{2} m_2) = (1)[2 + (\frac{1}{2})(3)] = 3.5$ $m_4 = r (N_0 + m_3) = (1)(2 + 3.5) = 2$ $N_1 = N_0 + m_1 = 2 + 2 = 4$ $N_2 = N_1 + \frac{1}{2} r m_1 = 4 + (\frac{1}{2})(1)(2) = 5$ $N_3 = N_2 + \frac{1}{2} r m_2 = 5 + (\frac{1}{2})(1)(3) = 6.5$ $N_4 = ?$
<p>Error Term: $\sim(\Delta t)^1$</p>	<p>Average Derivative: $m_a = \frac{1}{6} (m_1 + 2m_2 + 2m_3 + m_4) \rightarrow m_a = \frac{1}{6} (2 + 6 + 7 + 5) = 3.41$</p>	<p>Error Term: $\sim(\Delta t)^4$</p>

Topics covered in Ecosystem Modeling & Analysis (OCS 4410)

Single Population Models

Single population

An isolated group of organisms of the same species that doesn't compete with any other population for food, space, or other resources. Thus the total number of individuals (N) in a fixed region of space can only change due to natality (B), mortality (M), immigration (i), emigration (e), & harvesting (h)

Non-overlapping generations

No adults surviving to the next generation, use the Euler integration method with an integration step = 1

Difference equation:

Overlapping generations

Adults are surviving to the next generation, use the Runge-Kutta (4th order) integration method with an integration step < 1

Differential equation:

Model Structure Variation

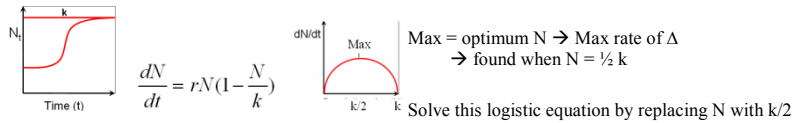
Comes from different assumptions concerning the terms bN, mN, iN, eN, & hN

Harvesting

Harvesting Questions

- 1) What's the harvesting rate that gives the maximum sustainable yield (MSY)?
- 2) What's the relationship between yield & population size?

Harvesting a Logistic Population



Specific harvest rate

$$h \quad (1/\text{time})$$

Proportional Harvesting

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right) - hN$$

of Harvested Animals

$$H \quad (\text{animals}/\text{time})$$

Constant Quota

$$\left| \frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right) - H \right.$$

Optimum Harvesting Strategy

$$N = \frac{k}{2} \rightarrow \text{Max} \frac{dN}{dt} = \frac{rk}{2} \left(1 - \frac{k}{2k}\right) = \frac{rk}{4}$$

This is the maximum harvest rate for a population with stable r & k.

$$h_{\text{opt}} = f(r) \rightarrow H_{\text{max}} = \frac{rk}{4} = h_{\text{opt}} \frac{k}{2} \rightarrow h_{\text{opt}} = \frac{r}{2}$$

If, however, r & k are fluctuating in time, then h_{opt} will be lower.

Age Structure Modeling

Principals of Age Structure Modeling

- 1) Birth process doesn't begin until the 1st cohort reaches reproductive age
- 2) Reproduction only increases the size of the 1st cohort
- 3) After 1 yr survivors from each cohort are transferred to the next higher one
- 4) Mortality rate ↑ with ↑ age → the last cohort eventually disappears from the system

Cohort

Distinct age groups

First cohort

Collective Natality rate – Mortality rate – Survival rate

Intermediate Cohorts

Inflow rate – Mortality rate – Survival rate

Last Cohort

Inflow rate – Mortality rate

Collective Natality Rate

$$NR \quad NR = b_1N_1 + b_2N_2 + \dots + b_nN_n$$

Mortality Rate of individual cohorts

$$MR_i \quad MR_i = m_i N_i$$

= (specific mortality rate)(cohort size)

Survival Rate of individual cohorts

$$SR_i \quad SR_i = (1 - m_i) N_i$$

Inflow rate from the preceding cohort

$$IR_i \quad IR_i = SR_{i-1} = (1 - m_{i-1}) N_{i-1}$$

Logistic Population in a periodically fluctuating environment (carrying capacity often varies with time due to various changes in the environment)

period	p	Period of the oscillations in k
Frequency	f	Frequency of oscillations
Angular frequency	ω	(radians/time)
Oscillating carrying capacity		Oscillating carrying capacity with an angular frequency
Scaling constant	C	Determines the amplitude of the oscillations

Topics covered in Ecosystem Modeling & Analysis (OCS 4410)

Models of Interacting Populations : Prey-Predator Interaction

➤ Population Density Fluctuations in a Prey-Predator System

- When **populations complete their growth** (& thus their **growth rate averages to 0**), population density tends to fluctuate above or below the carrying capacity
- Population density fluctuations may also result from **seasonal changes in environmental factors**, which in turn raise & lower the carrying capacity

Negative effect of population N_2 on logistic population N_1 will ↑ as the # of both species ↑

$$\frac{dN_1}{dt} = rN_1 - \frac{rN_1^2}{k} - aN_1N_2$$

= self-crowding effects

$$aN_1N_2 = \frac{rN_1^2}{k} = \text{negative effects of other species}$$

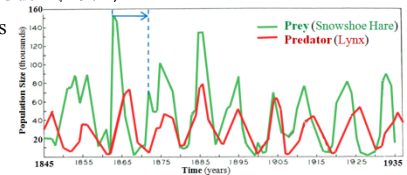
rN_1 = unlimited growth

○ 2 - Species Population Interactions (from Odum, 1971)

	Type of System	Population		General nature of interaction
		1	2	
No Significant Interaction	1) Neutralism	0	0	Population 1 & 2 do NOT affect each other
Negative (-) Interactions <i>indicates inhibition of population growth or other population attribute</i>	2) Competition (direct)	-	-	Population 1 & 2 <u>Directly</u> inhibit each other
	3) Competition (resource)	-	-	<u>Indirect inhibition</u> when common resource is in short supply
Both + & - Interactions	4) Amensalism	-	0	Population 1 inhibited, while population 2 not affected
	5) Parasitism	+	-	Population 1 (the parasite), generally smaller than the Population 2 (Prey)
	6) Predation	+	-	Population 1 (Predator), generally larger than the Population 2 (Prey)
Positive (+) Interactions <i>indicates population growth or other population attribute benefited</i>	7) Commensalism (symbiosis)	+	0	Population 1 (Commensal) benefits, while Population 2 (Host) is not affected
	8) Proto cooperation	+	+	Interaction favorable for both populations, but not obligatory (required)
	9) Mutualism	+	+	Interaction favorable to both & obligatory (is required)

○ Cyclic Fluctuations in the Population Densities of different Populations (from Odum, 1971)

- **Prey-Predator** relationship between the **Prey** (Snowshoe hare) & the **Predator** (lynx) populations
- **Snowshoe hare** has the **same cycle** but it peaks ~a year before the **lynx**
- the **lynx** population peaks every 9-10 years (9.6 av.), peaks are **followed by rapid declines**
- Thus as the **prey** population increases or decreases, so does that of the **predator**.
- **Periodicity** of ~9.6 years



○ Lotka-Volterra Model

- The **simplest & most widely used model** of the prey-predator system

Dynamics of Populations with Exponential Prey Growth	Self-Limitation of the Prey Pop. with Logistic Prey Growth
<p>Prey (N_1): $\frac{dN_1}{dt} = rN_1 - (aN_1)N_2$</p> <p>Predator ($N_2$): $\frac{dN_2}{dt} = c(aN_1)N_2 - mN_2$</p>	<p>$\frac{dN_1}{dt} = rN_1(1 - \frac{N_1}{k}) - (aN_1)N_2$</p>

Differential Equations where...

r = intrinsic growth rate of the Prey ($1/\text{time}$)

a = rate of Predation ($1/\text{predator} \cdot \text{time}$)

$(aN_1)N_2$ = exponential growth of the Prey

c = conversion rate (i.e. turning prey into predators ($\text{predator}/\text{prey}$))

m = specific mortality rate of Predators ($1/\text{time}$)

➤ Stability of the Prey-Predator System

- The **equilibrium solution** (N_1^* , N_2^*) of the **Lotka-Volterra model** is attained by finding where the rate of change equals 0.

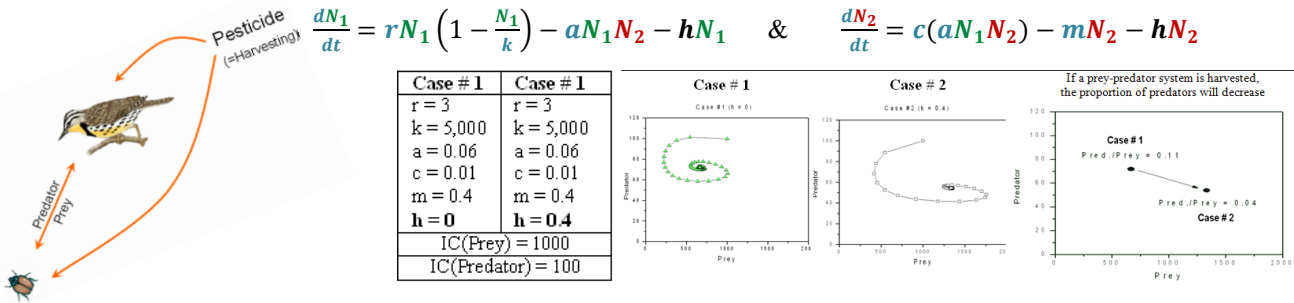
	Initial Equation with Exponential prey growth	Divide by	Resultant Equation	Equilibrium Solution
Prey Population (N_1)	$\frac{dN_1}{dt} = rN_1 - (aN_1)N_2$	N_1^*	$r - aN_2^* = 0$	$N_2^* = r/a$
Predator Population (N_2)	$\frac{dN_2}{dt} = c(aN_1)N_2 - mN_2$	N_2^*	$caN_1^* - m = 0$	$N_1^* = m/ca$

- However, the equilibrium solutions are **deterministically unstable**, because after only a small perturbation from the steady state the populations of predator & prey retain new equilibrium values

Unstable		Stable	
<p>Prey is less than wholly suitable for the maintenance of the predator population, so the predator species eventually disappears</p>	<p>Predation pressure is too high, so the prey species eventually disappears</p>	<p>2 species undergo considerable fluctuation in numbers, over time the fluctuations diminish, eventually reaching an arrangement where the mean #s of each species remain more or less stable through time</p>	<p>Following the initial fluctuations, the 2 species enter regular cycles of abundance, these cycles can persist indefinitely</p>

Topics covered in Ecosystem Modeling & Analysis (OCS 4410)

o Lotka-Volterra Model (continued...)



Parameter Estimation: the link between Data & Models

- Experimental ecologists criticize Ecosystem Modeling saying it lacks validity
- The main problem with ecosystem models is that there is incomplete information on the values of the model parameters

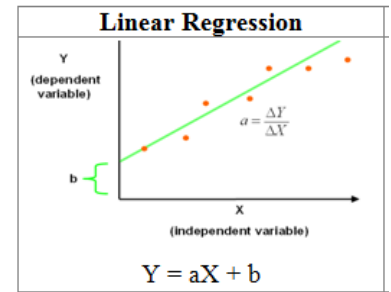
Parameter Estimation: statistical & numerical procedures that are used to obtain reasonable values for model parameters, based on existing experimental or field data, parameter estimation provides the link between the data & the model, between statistics & simulation

➤ Regression Analysis

- enables the summary & quantification of the strength of the relationship among variables
- can be used to predict new values of the dependent variables, based on observed relationships

o Simple Regression

- performs an **ordinary least squares regression** using one independent variable
- it's used to estimate the parameters of linear or selective nonlinear models
- fits a model relating one **dependent** variable (Y) to one **independent** variable (X) by minimizing the SS of the residuals for the fitted line; a & b are **Model Parameters**



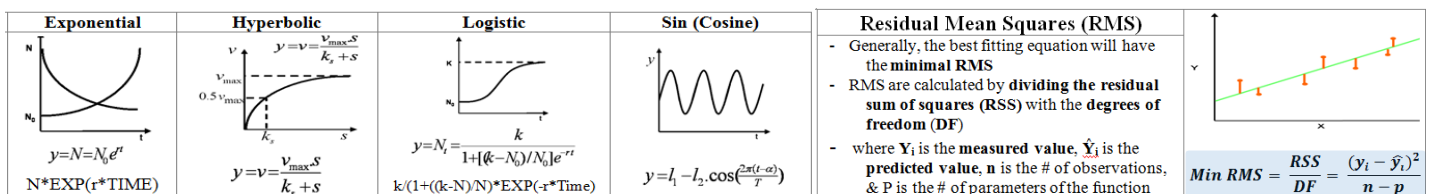
- **Linear Regression** ($y = a + bx$): easy to handle & has been used to analyze biological data
- **Multiplicative Regression** ($y = ax^b$): **linearization** is achieved through logarithmic transformation & estimating model parameters
- **Exponential Regression** ($y = e^{a+bx}$): **linearization** is achieved through logarithmic transformation & estimating model parameters
- **Reciprocal Regression** ($1/y = a + bx$): **linearization** is achieved through the reciprocal of the dependent variable
- **Multiple Regression:** performs **ordinary linear least squares regression** using **several** independent variables

o Nonlinear Regression

- produces **least squares** estimates of parameters in a **user-defined** non-linear regression model
- as a result of the common usage of Linear Regression, there has been an **overemphasis** on linear relationship
- most ecological relationships are nonlinear & therefore linearization is just an approximation with a limited slope
- analytical solutions are not available for non-linear regressions, so a **search algorithm** must be used to determine the estimates that minimize the **residual SS**
- **Marquardt algorithm:** it is a compromise between using a **straight linearization** method & the **method of steepest descent**
 - the algorithm for nonlinear regression is highly dependent upon the initial parameters, thus a great deal of care should be taken in developing the initial estimates
 - to fit data using the model of **exponential growth** ($N_t = N_0e^{rt}$) you must enter the function: $N * \text{EXP}(r * \text{TIME})$
 - This model assumes that the independent variable (TIME) contains the units of time over which the growth was measured

o Selecting types of equations to describe relationship among variables

- Developing **Empirical Models** describing **relationships** among variables is an important step in the modeling process
- The relationship between 2 variables can often be represented by several different functional forms
- an objective statistical test is needed to find the function that best fits the data



Topics covered in Ecosystem Modeling & Analysis (OCS 4410)

➤ Sensitivity Analysis

- Sensitivity Analysis provides a measure of the sensitivity of state variables to variations in the model parameters
- This analysis is usually done by changing the parameter values & observing the effects of one or more state variables of interest
- The **Sensitivity (S_{XP})** of the **State Variable ($X(n)$)**, to change in the **Parameter $P(k)$** , is defined as:

$$S_{XP} = \frac{\text{Relative change in } X(n)}{\text{Relative change in } P(k)} = \frac{\frac{\Delta X(n)}{X(n)}}{\frac{\Delta P(k)}{P(k)}}$$

- The relative change in parameters is chosen based on our knowledge of the variations to which a certain parameter may be subjected in a real system
- o Ex. the modeler estimates that variations within the 95% probability interval may account for 20% of the parameter mean value → he would probably choose to test the model by changing the parameter value for -20% & +20%.
- It's often necessary to find the sensitivity at 2 or more levels of parameter changes, because the relationship between the parameter & the corresponding state variable is rarely linear.
- This implies that it's important to know parameters with the highest possible certainty before the sensitivity analysis is carried out

➤ Parameter Estimation & Model Calibration

- **Parameter Estimation:** Parameters can often be found in the literature in the form of approximate values or intervals before these can be used in the model, the model must be calibrated (this is also true of parameters measured in the field)
- **Model Calibration:** A comparison of model results (or model predictions) with measured values.
 - During calibration several sets of parameters are tested & the various model outputs of state variables are compared with measured or observed values.
 - The parameter set that gives the best agreement between model predictions & measured data should be selected
- **Why Calibration is needed:** Characteristics of ecological models & their parameters
 - 1) most ecological parameters are not known as constraints, as are many chemical & physical parameters, thus literature parameters should be used with care
 - 2) since all ecological models are simplifications of real systems, the model structure doesn't account for every detail of the system
 - 3) by far the most ecological models are **lumped models** (a single parameter often represents the average value of several species).
 - Problem 1: because each species has its own characteristics, the variation in the species composition requires changes in the corresponding model parameters
 - Problem 2: the average of numeric characters of individual species doesn't necessarily represent the best parameter for description of the community
- Calibration procedure can help in finding a parameter that accounts best for variations in the species composition to which a community may be subjected
- Calibration can NOT be done randomly when more than a few parameters have been selected.
 - Ex. 10 parameters have to be calibrated, & 10 different values of each parameter should be tested
 - Model must be run 10^{10} times
 - if the modeler understands the variables & their relations to each other the parameters can be tested in pairs while observing the responses of the crucial state variables.
 - The model can also be broken down into a number of sub-models which can be calibrated independently

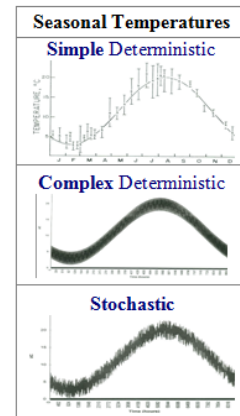
Topics covered in Ecosystem Modeling & Analysis (OCS 4410)

Description of Physical Processes in Dynamic Ecosystem Models

➤ Physical Forcing Functions

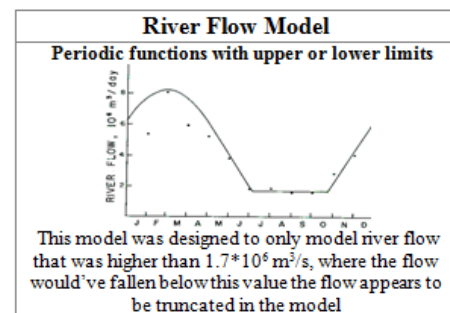
○ Temperature

- Temperature is one of the most important forcing functions affecting ecological systems
- The major variation is seasonal, though there is some diurnal & spatial fluctuations
- **Seasonal Patterns** can be closely approximated by **Sinusoidal Curves**, with simple equations to match the time of the max & min temperatures & yearly amplitudes
- Where $TEMP =$ the mean temperature in the water column ($^{\circ}C$); as the Julian day goes from 1 to 180, the cosine function changes from +1 to -1, & the temperature oscillates around the mean value of $11.5^{\circ}C$
- **Diurnal Variations** are often necessary to account for the temperature variations on different time scales



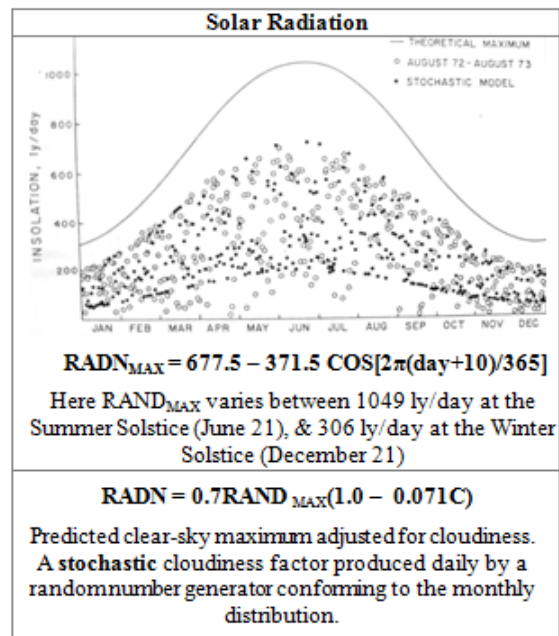
○ River Flow

- Productivity of estuaries & coastal marine ecosystems is often determined by the availability of riverine nutrients
- Riverine loads often show significant seasonal changes, which are directly coupled to changes in the water discharge
- Description of the pattern of river flow may be one of the first steps in the construction of estuarine & coastal ecosystem models
- Riverflow may also be represented by a sinusoidal function, even if its pattern is fairly complicated



○ Solar Radiation

- one of the **primary forcing functions** in models dealing with **ecosystem productivity**
- Maximum values of incident solar radiation for clear skies can be found in the literature
- Theoretical maximum of radiation received on a horizontal surface is a function of sun angle & can be calculated from the appropriate equation
- Once the maximum radiation for a certain latitude is known, it's possible to obtain a sinusoidal function that fits the theoretical clear-sky maxima & minima at solstices
- $RAND_{MAX} =$ solar radiation in langley (ly) per day ($1 \text{ ly} = 1 \text{ cal}/\text{cm}^2$); $C =$ cloud cover (in tenths)
- Stochastic cloudiness factors often over estimate the radiation & must be corrected for extinction by other atmospheric materials in addition to cloudiness (this was done by multiplying the equation for $RAND_{MAX}$ by 0.7).
- This resulted in lowering the upper radiation values by 30%.



○ Photoperiod

- Seasonal changes in the photoperiod (= number of hours of daylight) may be described by the following equation:
- $PHOTO = 0.5 - 0.125 \cdot \cos[2\pi(\text{day} + 10)/365]$
- Photoperiod (PHOTO) varies between 0.625 at the Summer solstice (June 21, 15 hrs of daylight) & 0.375 at the Winter solstice (Dec. 21, 9 hrs of daylight)

Topics covered in Ecosystem Modeling & Analysis (OCS 4410)

➤ Other Physical Processes

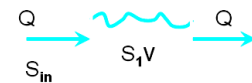
○ Exponential Decay

- A variety of physical processes (such as radioactive decay, light absorption in the water column, etc) can be approximated by a simple 1st order decay equation $\frac{dC}{dt} = -kC$; in which **C** = concentration, **k** = rate constant (1/time)
- The integral form of this equation is a well-known exponential function

○ Dilution

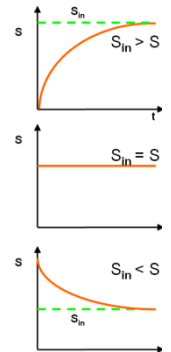
- Suppose that a high salinity seawater sample (salinity = S ppt) is kept within a constant volume container (volume = V m³)
- For the purpose of this experiment seawater was washed out of a container by a constant inflow of low salinity water (water inflow = Q m³/s; salinity of the inflowing water – S_{in} ppt), until the equilibrium is reached
- Using a simple dilution model we can predict the salinity changes within the container as a function of time

Conservative Substances



$$\frac{dS}{dt} = \text{Inflow} - \text{Outflow}$$

$$\frac{dS}{dt} = \frac{S_{in}Q}{V} - \frac{SQ}{V}$$

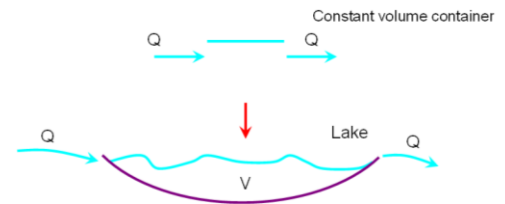


○ Behavior of Tracers in Mixed Systems

- Consider a well mixed lake of constant volume that is being contaminated by inflowing toxic substance, which could have harmful effects on the biota if threshold concentration is achieved
- The toxic substance gradually decomposes in the lake water in accordance with the first order decay reaction
- As far as the water inflow & volume of the lake remain constant, the rate of change in the concentration within the lake may be approximated by the following differential equation (see Non-Conservative Substances)
- Where C_{in} = concentration in the inflow (mg/m³), **C** = concentration in the lake (mg/m³), **Q** = water inflow rate (m³/day), **V** = the volume of the lake (m³), & **k** = the decay constant (1/day)

Non – Conservative Substances

$$\frac{dC}{dt} = \text{Inflow} - \text{Outflow} - \text{Decay} = \frac{QC_{in}}{V} - \frac{QC}{V} - kC$$

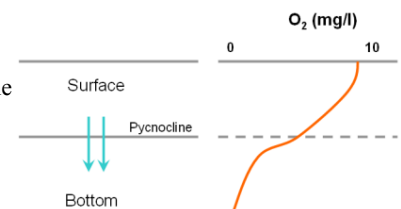


○ Diffusion

- Diffusion is one of the most important physical processes. At the molecular level, it accounts for most of the transport that takes place in water & air
- **Fick's First Law**: the mass transfer in the x direction through a unit surface is proportional to the concentration gradient
- Where **J_x** = mass flow (g/m²s), = the concentration gradient (g/m⁴), & **D_m** (m²/s, or more frequently, cm²/s) is the molecular coefficient, the negative sign shows that the direction of flux is from the higher concentration to the lower
- **Accumulation** = mass in – mass out, where the mass balance of a dispersed phase diffusing along the x-coordinate through a volumetric element of fluid

Diffusion

$$J_x = -D_m \frac{\partial C}{\partial x}, \text{ or } J_x = -D_m \frac{\Delta C}{\Delta x}$$



Topics covered in Ecosystem Modeling & Analysis (OCS 4410)

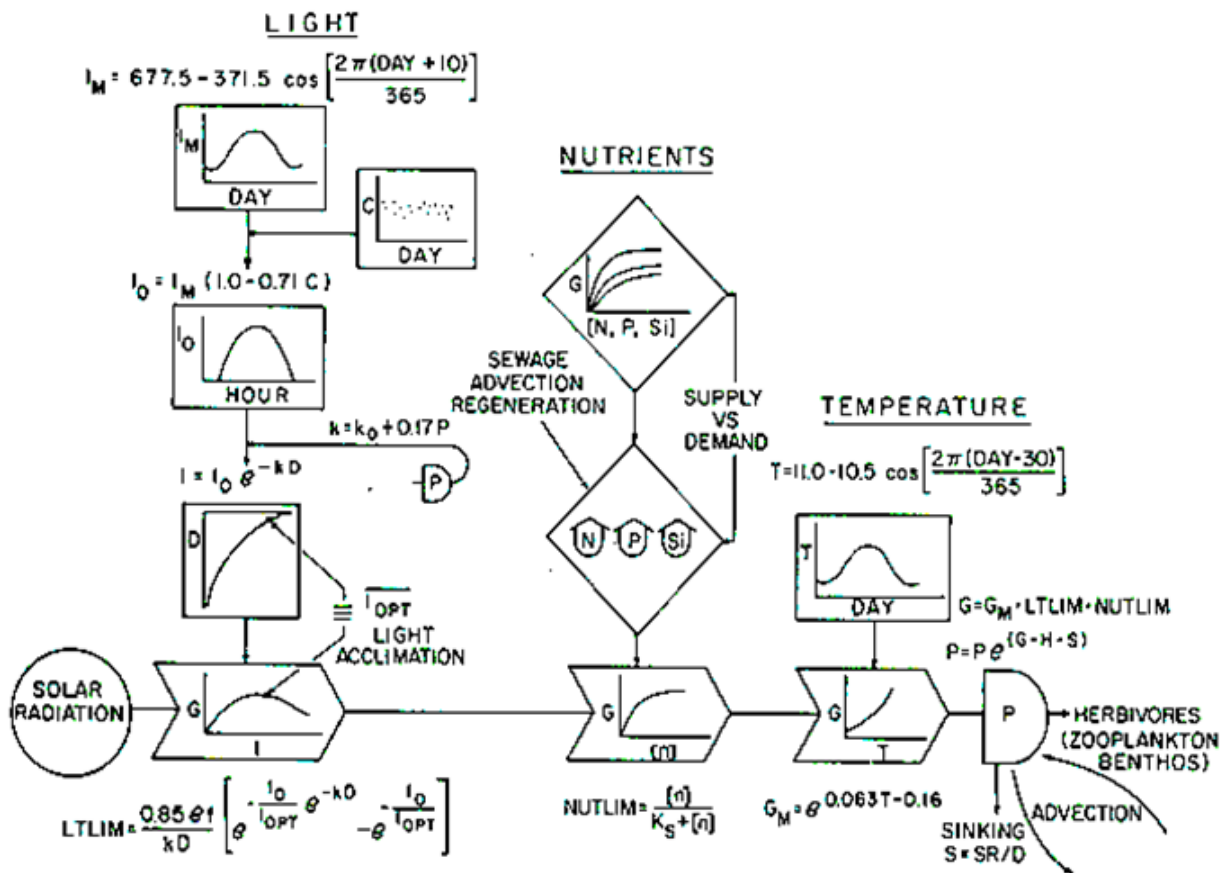
Description of Biochemical Processes

- One of the most difficult steps in the construction of ecosystem models is the mathematical description of biochemical processes
- Problem:** How do you combine the influences of several factors that are operating simultaneously into a single mathematical relationship
 - A general approach is to find the maximum rate of a certain biochemical process as a function of only one environmental factor, usually temperature
 - Once the maximum rate of change is determined, the influences of remaining factors are expressed as unit-less fractions which reduce the maximum
- Ecosystem Model complexity is often reduced by carrying out all biochemical elements of the model as a single unit (carbon, nitrogen, or energy)
- This is achieved by using conversion factors (such as those for the conversion of carbon to nitrogen, chlorophyll a to carbon, etc.)

➤ Phytoplankton Dynamics

Global equation for phytoplankton growth : $PHYTO = f(\text{Temperature, nutrients, Light}) = GMAX * NUTLIM * LTLIM$

where $PHYTO$ = phytoplankton growth rate, $GMAX = f(TEMP)$ is the temperature-dependent maximum growth rate, $NUTLIM$ = the nutrient limited term, & $LTLIM$ = the light limitation term.



Flow diagram for the phytoplankton compartment in the Narragansett Bay Model (from Kremer & Nixon, 1978). Major equations are shown with the corresponding graphical representation. A combination of the Odum and the forrester symbols is used.

○ Temperature-growth relationship (GMAX)

- **Maximum Phytoplankton Growth Rate (GMAX)** is often described s an exponential function of temperature
- **Temperature Coefficient (Q_{10})** is usually ~2
- GMAX for the global equation for phytoplankton growth model above is: $GMAX = 0.59 * e^{0.0633 * TEMP}$

Topics covered in Ecosystem Modeling & Analysis (OCS 4410)

○ Effects of nutrients

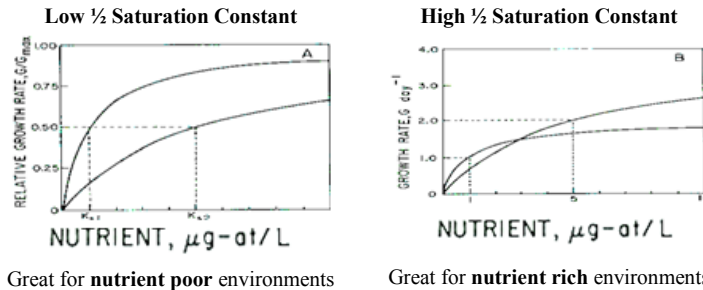
- The **hyperbolic effect** of nutrient concentration on the growth of microorganisms has long been recognized
- Increasing concentration at low levels results in a commensurate increase in growth
- At higher levels, the linear response is shifted & the increment in growth diminishes for unit increases in the nutrient

● **Monad's Hyperbolic Effect of Nutrient Concentration on Growth**

- was developed to model **substrate limitation growth**.
- It has predicted growth rate (GROWTH), which is a function of the maximum growth rate (GMAX)
- the ambient steady-state nutrient concentration (N)
- NUTLIM is a unitless fraction reflecting the degree of nutrient limitation
- characteristic 1/2 saturation constant (K_S) which is defined as the concentration at which the growth rate equals 1/2 the GMAX
- The effect of smaller values of K_S is to steepen the rate of ascent to GMAX.
- **Problem₁**: One of the inherent weaknesses of the simple Monad expression is the strict implication of a single limiting nutrient
- **Problem₂**: its usually hard to decide a priori what nutrient is most likely to become limiting, nitrogen (N), phosphorus (P), or silicon (Si)

Monad's Hyperbolic Effect of Nutrient Concentration on Growth

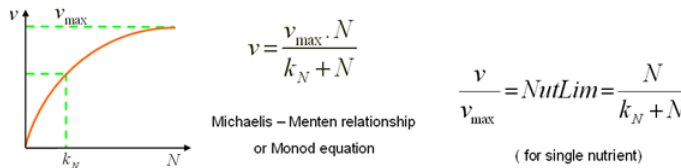
$$GROWTH = GMAX * NUTLIM = GMAX * [N / (K_S + N)]$$



Hyperbolic response of growth to a limiting nutrient for 2 different phytoplankton species
A-normalized growth rate, B-growth rate.

Although the species with the lower K_S appears to be totally dominant in the normalized presentation (A), consideration of the actual growth rates reveals that the 2nd species grows faster at nutrient levels above $3\mu\text{g-at/l}$ (B)

- **Michaelis-Menton** adapted Menton's model to be used for the **kinetics of enzymic reactions**, since the limitation results in fundamentally different levels of organization.
- This was then extended to nutrient uptake or growth since both are the result of biochemical reactions.



Limitation by Multiple Nutrients

$$NutLim = \text{Min} \left(\frac{N}{k_N + N}, \frac{P}{k_P + P}, \frac{Si}{k_{Si} + Si} \right)$$

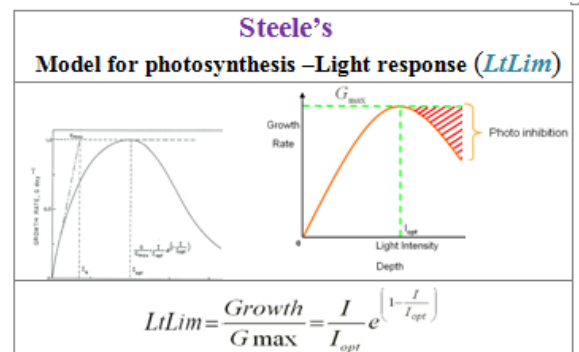
$$GROWTH = GMAX * NLIM * PLIM * SILIM$$

$$= GMAX * [N / (K_{SN} + N)] * [P / (K_{SP} + P)] * [Si / (K_{SSi} + Si)]$$

○ Effects of Light

- The derivation of a single expression for the **effect of incident radiation** on the daily growth of the entire phytoplankton population begins with the analysis of the **instantaneous photosynthesis-light response**.
- At low levels photosynthesis increases roughly proportionally to the available light, until saturation begins to flatten the response
- At higher levels **photo-inhibition occurs**

- **Steele** (1962) developed an equation to model this photosynthesis-light response, where **GROWTH** is the growth rate, **GMAX** is the maximum growth rate, **I** is the incident solar radiation reduced for an average albedo of 10%, & **I_{opt}** is the optimum radiation with respect to the growth rate (or productivity) of the studied phytoplankton assemblage
- At optimum light **GROWTH = GMAX**, since **GMAX** is determined independently of from the growth-temperature equation, only the light limitation term (**LTLIM**) is required.
- This term is found by normalizing the growth equation...this is done by dividing **GROWTH** by **GMAX**.



Topics covered in Ecosystem Modeling & Analysis (OCS 4410)

➤ Zooplankton Dynamics

- Zooplankton dynamics often require sophisticated mathematical algorithms in order to describe the conservation of mass in the grazing process, & to track development of juveniles through time.
- Copepods are the **Major herbivore** of Narragansett Bay, representing ~95% of the total population → zooplankton can be approximated by copepods in a model

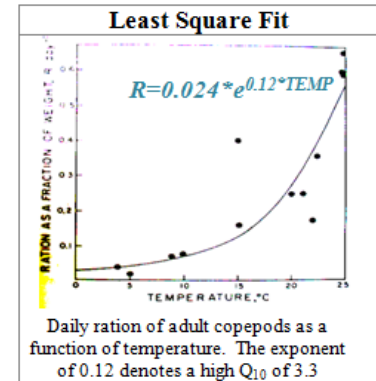
○ Food ingestion as a function of temperature

- The **daily ration** (quantity of food ingested daily) reflects the basic metabolic needs of the copepods, as well as many other organisms

- **Van't Hoff Rule:** temperature response follows an exponential relation:

$$R_{MAX} = R_{MAX0} * e^{(Q_{10}RMX * TEMP)}$$

- where **R_{MAX}** [mgC_{ingested} / (mgC_{Zoo} * day)] is the **maximum ration**
- **R_{MAX0}** is the maximum ration at 0°C
- **$Q_{10}RMX$** is the **temperature rate constant** (°C⁻¹) which is derived from the log of the physiological Q_{10}
- ex. if $Q_{10} = 2.0$, $Q_{10}RMX = (\ln 2.0) / 10 = 0.069^{\circ}C^{-1}$

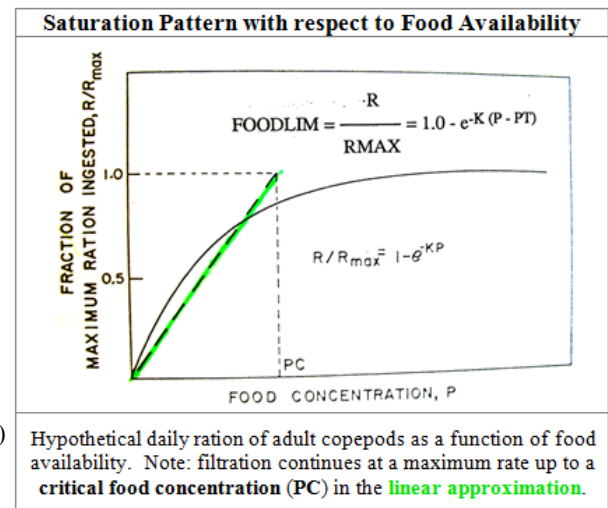


○ Regulation of zooplankton growth by the food availability

- The actual ration of copepods follows a **saturation pattern** with respect to **food availability**, which can be approximated by the rectangular hyperbola of **FOODLIM**
- where **FOODLIM** is the parameter showing the fraction of maximum ration which the measure of food limitation
- **R_{MAX}** is the **preferred ration**
- **R** is the **actual ration achieved**
- **P** is the **available food concentration**
- **PT** is the **threshold food concentration**
- **K** is the parameter determined experimentally by controlling the degree of curvature of the hyperbola

- **GRAZING = $R_{MAX} * FOODLIM$**

the rate at which the adult copepods ingest food (**GRAZING**) can be described as a function of the maximum daily ration (**R_{MAX}**) & the food availability (**FOODLIM**)



○ Respiration

- Respiration tends to decrease the assimilated ration.
- ex. in the Narragansett Bay Model, the zooplankton respiration was described as an exponential function of temperature, a Q_{10} value of 2 was chosen:
- **$RESP = RESP0 * e^{0.069 * TEMP}$**
- where **RESP** is the **respiration rate**, **RESP0** is the **respiration at 0°C**, & **TEMP** is the temperature

○ Hatching

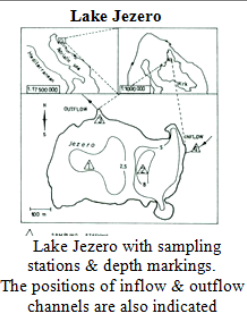
- Any excess un-respired assimilation may be used for reproduction, i.e. it enters the pool of incubation eggs
- The time required for eggs to hatch has been determined for a number of estuarine species, & can well be approximated by the exponential equation: **$H = 12.0 * e^{-0.110 * TEMP}$** where **H** is the **hatching time** (days) & **TEMP** is the temperature

Topics covered in Ecosystem Modeling & Analysis (OCS 4410)

Building & Running Ecosystem Models

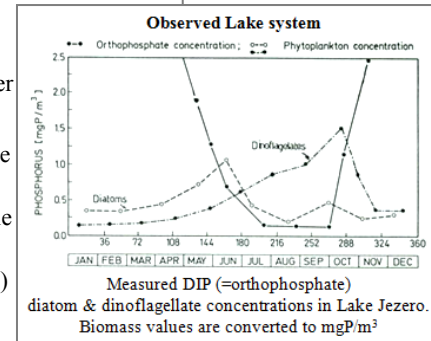
➤ Introduction

- Lake Jezero is a small accumulation on the Island of Krk in the Northern Adriatic Sea
- 10 yrs of field studies found that the primary productivity of the lake has increased over time, probably as a result of fertilizer input from the drainage area
- Since the lake is largely used for water supply, its important to know what the main factors are controlling the primary productivity since they in turn affect the quality of the drinking water



➤ Lake Characteristics

- There is only one larger stream through which drainage waters enter the lake
- The maximum inflow is during the early spring
- When the lake reaches 284 cm above sea level it begins to flow out over the barrier
- During the period of active outflow, the depth at the deepest point is ~9.5 m
- **Dissolved inorganic phosphorous (DIP)** is considered the **limiting nutrient** for the phytoplankton productivity in the lake
- Concentration of **DIP** in the **epilimnion** (layer above the thermocline) is low in the summer & high (30-60 mgP/m³) in the winter
- There are 2 dominant groups of phytoplankton in the lake: **Diatoms** (in the spring) & **Dinoflagellates** (in the late summer)



➤ Measurement Methods & Techniques

- Dissolved inorganic phosphorus was determined using a composite reagent of ammonium molybdate
- Diatom cell counts were converted into phosphorous using literature average cell-values for the dominant species & a conversion factor of 1520:1 for wet to phosphorous ratio in the plankton biomass

➤ Water Balance

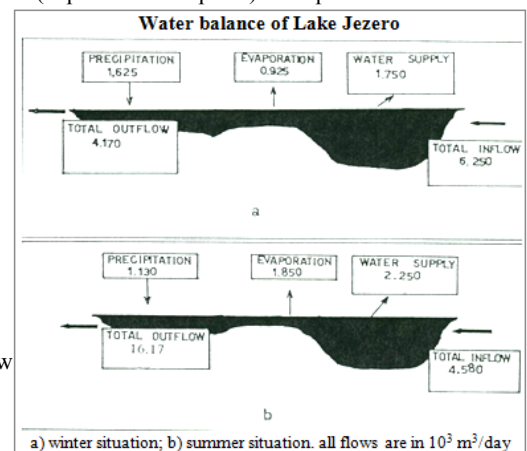
- Measurements of precipitation, evaporation, water consumption, & water level (depth at a fixed place) were performed for 2 consecutive years to calculate the water balance
- Continuous measurements of water level in the lake, carried over dry summer periods with no surface inflow, allowed an assessment of daily loss due to underground outflow

○ Winter

- Precipitation & evaporation averages over the winter period were 1.625*10³ m³/day & 0.925*10³ m³/day
- water supply was 1.75*10³ m³/day
- average runoff was 6.25*10³ m³/day
- while the total outflow was 4.17*10³ m³/day
- resulting in a water surplus of 1.03*10³ m³/day

○ Summer

- 6.74*10³ m³/day were lost due to evaporation, water supply, & total outflow
- The average total inflow was 4.58*10³ m³/day, while the precipitation amounted to an additional 1.13*10³ m³/day



➤ A Forced Michaelis-Menton based Model of Phytoplankton Dynamics

○ Model Structure

- A mathematical model was built linking the primary & secondary productivity to the main ecological factors, & thus explain the increasing eutrophication
- The model is based on the knowledge of lake ecology & growth of phytoplankton in conditions limited to 2 periodic (seasonal) factors: **light intensity & concentration of DIP**
- Most of the primary production occurs above the thermocline → the lake has been divided into 2 layers: above (**epilimnion**) & below (**hypolimnion**) the thermocline
- 4 **state variables** are monitored: DIP, diatoms, dinoflagellates, & zooplankton

○ Model Calibration

- The model was calibrated using measured flow, nutrient & biomass data.
- Physiological constraints for phytoplankton & zooplankton (e.g. max growth rates & ½ saturation constants) were adopted
- Experimentation with different time-scale integrations indicated that integration steps ≤ 1 day should be able to produce stable & accurate results during all simulation runs