Calculus for the Life Sciences
Lecture Notes – Nonlinear Dynamical Systems:
Part 2 – Other Models

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Outline

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   - Analysis of the Ricker’s Model
     - Equilibria
     - Stability Analysis
   - Skeena River Salmon Example
   - Example

3. Beverton-Holt and Hassell’s Model
   - Study of a Beetle Population
   - Analysis of Hassell’s Model
   - Beetle Study Analysis
   - More Examples
Introduction - Population Models

- Simplest (linear) model - Malthusian or exponential growth model
- Logistic growth model is a quadratic model
  - Malthusian growth term and a term for crowding effects
  - Carrying capacity reflecting natural limits to populations
  - Quadratic updating function becomes negative for large populations
- Ecologists modified the logistic growth model with updating functions that are more realistic for fluctuating populations
  - Ricker’s model used in fishery management
  - Hassell’s model used for insects
- Differentiation used in **qualitative analysis** of these models
Sockeye Salmon Populations – Life Cycle

- Salmon are unique in that they breed in specific fresh water lakes and die
- Their offspring migrate to the ocean and mature for about 4-5 years
- Mature salmon migrate at the same time to return to the exact same lake or river bed where they hatched
- Adult salmon breed and die
- Their bodies provide many essential nutrients that nourish the stream of their young
Sockeye Salmon Populations – Problems

- Salmon populations in the Pacific Northwest are becoming very endangered with some becoming extinct
- Human activity adversely affect this complex life cycle of the salmon
  - Damming rivers interrupts the runs
  - Forestry allows the water to become too warm
  - Agriculture results in runoff pollution
Sockeye Salmon Populations – Skeena River

- The life cycle of the salmon is an example of a complex discrete dynamical system
- The importance of salmon has produced many studies
- Sockeye salmon (*Oncorhynchus nerka*) in the Skeena river system in British Columbia
  - Largely unaffected by human development
  - Long time series of data – 1908 to 1952
  - Provide good system to model
- A simplified model combines 4 years
Sockeye Salmon Populations – Skeena River Table

Population in thousands

<table>
<thead>
<tr>
<th>Year</th>
<th>Population</th>
<th>Year</th>
<th>Population</th>
</tr>
</thead>
<tbody>
<tr>
<td>1908</td>
<td>1,098</td>
<td>1932</td>
<td>278</td>
</tr>
<tr>
<td>1912</td>
<td>740</td>
<td>1936</td>
<td>448</td>
</tr>
<tr>
<td>1916</td>
<td>714</td>
<td>1940</td>
<td>528</td>
</tr>
<tr>
<td>1920</td>
<td>615</td>
<td>1944</td>
<td>639</td>
</tr>
<tr>
<td>1924</td>
<td>706</td>
<td>1948</td>
<td>523</td>
</tr>
<tr>
<td>1928</td>
<td>510</td>
<td></td>
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</table>

Four Year Averages of Skeena River Sockeye Salmon
Ricker’s Model

- **Ricker’s model** – formulated with salmon populations and generally used in fish management
- **Ricker’s model** satisfies

\[ P_{n+1} = R(P_n) = aP_n e^{-bP_n} \]

with positive constants \( a \) and \( b \) fit to the data

- Consider the Skeena river salmon data
  - The parent population of 1908-1911 is averaged to 1,098,000 salmon/year returning to the Skeena river watershed
  - The resultant offspring that return to spawn from this group occurs between 1912 and 1915 and averages 740,000 salmon/year
Ricker’s Model – Salmon

- Successive populations give data for updating functions
  - $P_n$ is parent population, and $P_{n+1}$ is surviving offspring
  - Nonlinear least squares fit of Ricker’s function

$$P_{n+1} = 1.535 P_n e^{-0.000783 P_n}$$
Simulate the Ricker’s model using the initial average in 1908 as a starting point.
Summary of Ricker’s Model for Skeena river salmon

- Ricker’s model levels off at a stable equilibrium around 550,000
- Model shows populations monotonically approaching the equilibrium
- There are a few fluctuations from the variations in the environment
- Low point during depression, suggesting bias from economic factors
Analysis of the Ricker’s Model: General Ricker’s Model

\[ P_{n+1} = R(P_n) = aP_n e^{-bP_n} \]

Equilibrium Analysis

The equilibria are found by setting \( P_e = P_{n+1} = P_n \), thus

\[
\begin{align*}
P_e &= aP_e e^{-bP_e} \\
0 &= P_e(ae^{-bP_e} - 1)
\end{align*}
\]

The equilibria are

\[
P_e = 0 \quad \text{and} \quad P_e = \frac{\ln(a)}{b}
\]

with \( a > 1 \) required for a positive equilibrium
Stability Analysis of the Ricker’s Model: Find the derivative of the updating function

\[ R(P) = aPe^{-bP} \]

Derivative of the Ricker Updating Function

\[ R'(P) = a(P(-be^{-bP}) + e^{-bP}) = ae^{-bP}(1 - bP) \]

At the Equilibrium \( P_e = 0 \)

\[ R'(0) = a \]

- If \( 0 < a < 1 \), then \( P_e = 0 \) is stable and the population goes to extinction (also no positive equilibrium)
- If \( a > 1 \), then \( P_e = 0 \) is unstable and the population grows away from the equilibrium
Analysis of the Ricker’s Model

Since the **Derivative of the Ricker Updating Function** is

\[ R'(P) = ae^{-bP}(1 - bP) \]

At the **Equilibrium** \( P_e = \frac{\ln(a)}{b} \)

\[ R'\left(\frac{\ln(a)}{b}\right) = ae^{-\ln(a)}(1 - \ln(a)) = 1 - \ln(a) \]

- The solution of Ricker’s model is **stable** and **monotonically approaches** the equilibrium \( P_e = \frac{\ln(a)}{b} \) provided \( 1 < a < e \approx 2.7183 \)
- The solution of Ricker’s model is **stable** and **oscillates as it approaches** the equilibrium \( P_e = \frac{\ln(a)}{b} \) provided \( e < a < e^2 \approx 7.389 \)
- The solution of Ricker’s model is **unstable** and **oscillates as it grows away** the equilibrium \( P_e = \frac{\ln(a)}{b} \) provided \( a > e^2 \approx 7.389 \)
The best Ricker’s model for the Skeena sockeye salmon population from 1908-1952 is

\[ P_{n+1} = R(P_n) = 1.535 P_n e^{-0.000783 P_n} \]

From the analysis above, the equilibria are

\[ P_e = 0 \quad \text{and} \quad P_e = \frac{\ln(1.535)}{0.000783} = 547.3 \]

The derivative is

\[ R'(P) = 1.535 e^{-0.000783 P} (1 - 0.000783 P) \]

- At \( P_e = 0 \), \( R'(0) = 1.535 > 1 \)
  - This equilibrium is **unstable** (as expected)
- At \( P_e = 547.3 \), \( R'(547.3) = 0.571 < 1 \)
  - This equilibrium is **stable** with solutions monotonically approaching the equilibrium, as observed in the simulation.
Example 1 - Ricker’s Growth Model

Let $P_n$ be the population of fish in any year $n$, and assume the Ricker’s growth model

$$P_{n+1} = R(P_n) = 7P_n e^{-0.02P_n}$$

- Graph of the updating function $R(P)$ with the identity function, showing the intercepts, all extrema, and any asymptotes
- Find all equilibria of the model and describe the behavior of these equilibria
- Let $P_0 = 100$, and simulate the model for 50 years
Example - Ricker’s Growth Model

Solution The Ricker’s growth function is

\[ R(P) = 7P e^{-0.02P} \]

- The only intercept is the origin \((0, 0)\)
- Since the negative exponential dominates in the function \(R(P)\), there is a horizontal asymptote of \(P_{n+1} = 0\)
- Extrema are found differentiating \(R(P)\)

\[
R'(P) = 7(P(-0.02)e^{-0.02P} + e^{-0.02P}) \\
= 7e^{-0.02P}(1 - 0.02P)
\]

- This gives a critical point at \(P_c = 50\)
Solution (cont) The Ricker’s function has a maximum at

\[(P_c, R(P_c)) = (50, 350e^{-1}) \approx (50, 128.76)\]
Solution (cont) For equilibria, let $P_e = P_{n+1} = P_n$, then

$$P_e = R(P_e) = 7 P_e e^{-0.02 P_e}$$

One equilibrium is $P_e = 0$, so dividing by $P_e$

$$1 = 7 e^{-0.02 P_e} \quad \text{or} \quad e^{0.02 P_e} = 7$$

This gives the other equilibrium $P_e = 50 \ln(7) \approx 97.3$
Solution (cont) Stability Analysis – Recall

\[ R'(P) = 7e^{-0.02P}(1 - 0.02P) \]

- For \( P_e = 0 \)
  - The derivative \( R'(0) = 7 > 1 \)
  - Solutions monotonically grow away from \( P_e = 0 \)

- For \( P_e = 97.3 \)
  - The derivative \( R'(97.3) = 1 - \ln(7) \approx -0.95 \)
  - Solutions oscillate, but approach \( P_e = 97.3 \)
  - This is a stable equilibrium, so populations eventually settle to \( P_e = 97.3 \)
Solution (cont) Starting with $P_0 = 100$, the simulation shows the behavior predicted above.

\[ P_{n+1} = 7P_n e^{-0.02P_n} \]
**Beverton-Holt Model**

**Beverton-Holt Model - Rational form**

\[ P_{n+1} = \frac{aP_n}{1 + bP_n} \]

- Developed in 1957 for fisheries management
- Malthusian growth rate \( a - 1 \)
- Carrying capacity
  \[ M = \frac{a - 1}{b} \]
- Superior to **logistic** model as updating function is non-negative
- Rare amongst nonlinear models - has an explicit solution
- Given an initial population, \( P_0 \)

\[ P_{n+1} = \frac{MP_0}{P_0 + (M - P_0)a^{-n}} \]
Hassell’s Model - Alternate Rational form

\[ P_{n+1} = H(P_n) = \frac{aP_n}{(1 + bP_n)^c} \]

- Often used in insect populations
- Provides alternative to logistic and Ricker’s growth models, extending the Beverton-Holt model
- \( H(P_n) \) has 3 parameters, \( a, b, \) and \( c \), while logistic, Ricker’s, and Beverton-Holt models have 2 parameters
- Malthusian growth rate \( a - 1 \), like Beverton-Holt model
Study of a Beetle Population

In 1946, A. C. Crombie studied several beetle populations. The food was strictly controlled to maintain a constant supply. 10 grams of cracked wheat were added weekly. Regular census of the beetle populations recorded.
Study of *Oryzaephilus surinamensis*, the saw-tooth grain beetle
Data on *Oryzaephilus surinamensis*, the saw-tooth grain beetle

<table>
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<th>Week</th>
<th>Adults</th>
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<tbody>
<tr>
<td>0</td>
<td>4</td>
<td>16</td>
<td>405</td>
</tr>
<tr>
<td>2</td>
<td>4</td>
<td>18</td>
<td>471</td>
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<td>4</td>
<td>25</td>
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<td>420</td>
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<td>6</td>
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<td>12</td>
<td>345</td>
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<td>14</td>
<td>361</td>
<td>30</td>
<td>480</td>
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Updating functions - Least squares best fit to data

- Plot the data, \( P_{n+1} \) vs. \( P_n \), to fit an updating function

- **Logistic growth model** fit to data (SSE = 13,273)

  \[
P_{n+1} = P_n + 0.962 P_n \left( 1 - \frac{P_n}{439.2} \right)
  \]

- **Beverton-Holt model** fit to data (SSE = 10,028)

  \[
P_{n+1} = \frac{3.010 P_n}{1 + 0.00456 P_n}
  \]

- **Hassell’s growth model** fit to data (SSE = 9,955)

  \[
P_{n+1} = \frac{3.269 P_n}{(1 + 0.00745 P_n)^{0.8126}}
  \]
Graph of **Updating functions** and **Grain Beetle data**

- Logistic Model
- Beverton-Holt
- Hassell's Model
- Beetle Data
- Identity Map
Study of a Beetle Population

Time Series - Least squares best fit to data, $P_0$

- Use the **updating functions** from fitting data before
- Adjust $P_0$ by **least sum of square errors** to time series data on beetles
- **Logistic growth model** fit to data gives $P_0 = 12.01$ with SSE = 12,027
- **Beverton-Holt model** fit to data gives $P_0 = 2.63$ with SSE = 8,578
- **Hassell’s growth model** fit to data gives $P_0 = 2.08$ with SSE = 7,948
- Beverton-Holt and Hassell’s models are very close with both significantly better than the logistic growth model
Study of a Beetle Population

Time Series graph of Models with Beetle Data

Saw-Tooth Grain Beetle

- Logistic Model
- Beverton–Holt
- Hassell’s Model
- Beetle Data
Analysis of Hassell’s Model – Equilibria

- Let $P_e = P_{n+1} = P_n$, so
  \[ P_e = \frac{aP_e}{(1 + bP_e)^c} \]

- Thus,
  \[ P_e(1 + bP_e)^c = aP_e \]

- One equilibrium is $P_e = 0$ (as expected the extinction equilibrium)
- The other satisfies
  \[ (1 + bP_e)^c = a \]
  \[ 1 + bP_e = a^{1/c} \]
  \[ P_e = \frac{a^{1/c} - 1}{b} \]
Analysis of Hassell’s Model – Stability Analysis

Hassell’s updating function is

\[ H(P) = \frac{aP}{(1 + bP)^c} \]

Differentiate using the quotient rule and chain rule.

The derivative of the denominator (chain rule) is

\[ \frac{d}{dP}(1 + bP)^c = c(1 + bP)^{c-1}b = bc(1 + bP)^{c-1} \]

By the quotient rule

\[ H'(P) = \frac{a(1 + bP)^c - abcP(1 + bP)^{c-1}}{(1 + bP)^{2c}} \]

\[ = \frac{a(1 + b(1 - c)P}{(1 + bP)^{c+1}} \]
Analysis of Hassell’s Model – Stability Analysis

- The derivative is

\[ H'(P) = a \frac{1 + b(1 - c)P}{(1 + bP)^{c+1}} \]

- At \( P_e = 0 \), \( H'(0) = a \)
  - Since \( a > 1 \), the zero equilibrium is **unstable**
  - Solutions **monotonically growing away** from the **extinction equilibrium**
Analysis of Hassell’s Model – Stability Analysis

- The derivative is
  \[ H'(P) = a \frac{1 + b(1 - c)P}{(1 + bP)^{c+1}} \]

- At \( P_e = \left( a^{1/c} - 1 \right)/b \), we find
  \[ H'(P_e) = a \frac{1 + (1 - c)(a^{1/c} - 1)}{(1 + (a^{1/c} - 1))^{c+1}} = \frac{c}{a^{1/c}} + 1 - c \]

- The stability of the \textbf{carrying capacity equilibrium} depends on both \( a \) and \( c \), but not \( b \)
- When \( c = 1 \) (\textbf{Beverton-Holt} model) \( H'(P_e) = \frac{1}{a} \), so this equilibrium is \textbf{monotonically stable}
Beetle Study Analysis – Logistic Growth Model

\[ P_{n+1} = F(P_n) = P_n + 0.962 P_n \left( 1 - \frac{P_n}{439.2} \right) \]

- The **equilibria** are \( P_e = 0 \) and 439.2
- The derivative of the updating function is

\[ F'(P) = 1.962 - 0.00438 P \]

- At \( P_e = 0 \), \( F'(0) = 1.962 \), so this equilibrium is **monotonically unstable**
- At \( P_e = 439.2 \), \( F'(439.2) = 0.038 \), so this equilibrium is **monotonically stable**
Beetle Study Analysis – Beverton-Holt Growth Model

\[ P_{n+1} = B(P_n) = \frac{3.010 \, P_n}{1 + 0.00456 \, P_n} \]

- The **equilibria** are \( P_e = 0 \) and 440.8
- The derivative of the updating function is

\[ B'(P) = \frac{3.010}{(1 + 0.00456 \, P)^2} \]

- At \( P_e = 0 \), \( B'(0) = 3.010 \), so this equilibrium is **monotonically unstable**
- At \( P_e = 440.8 \), \( B'(440.8) = 0.332 \), so this equilibrium is **monotonically stable**
Beetle Study Analysis – Hassell’s Growth Model

\[ P_{n+1} = H(P_n) = \frac{3.269 P_n}{(1 + 0.00745 P_n)^{0.8126}} \]

- The equilibria are \( P_e = 0 \) and 442.4
- The derivative of the updating function is

\[ H'(P) = 3.269 \frac{1 + 0.001396 P}{(1 + 0.00745P)^{1.8126}} \]

- At \( P_e = 0 \), \( H'(0) = 3.269 \), so this equilibrium is monotonically unstable
- At \( P_e = 442.4 \), \( H'(442.4) = 0.3766 \), so this equilibrium is monotonically stable
Example 1 - Beverton-Holt Model: Suppose that a population of insects (measured in weeks) grows according to the discrete dynamical model

\[ p_{n+1} = B(p_n) = \frac{20p_n}{1 + 0.02p_n} \]

- Assume that \( p_0 = 200 \) and find the population for the next 3 weeks
- Simulate the model for 10 weeks
- Graph the updating function with the identity map
- Determine the equilibria and analyze their stability
Example 1 - Beverton-Holt Model

Solution - Beverton-Holt Model: Iterate the model with $p_0 = 200$

$$p_1 = \frac{20(200)}{1 + 0.02(200)} = 800$$

$$p_2 = \frac{20(800)}{1 + 0.02(800)} = 941$$

$$p_3 = \frac{20(941)}{1 + 0.02(941)} = 949.6$$

From before, the **carrying capacity** for the Beverton-Holt model is

$$M = \frac{a - 1}{b} = \frac{19}{0.02} = 950$$
Example 1 - Beverton-Holt Model

Solution (cont): The explicit solution for this model is

\[ p_n = \frac{950 p_0}{p_0 + (950 - p_0)20^{-n}} = \frac{950}{1 + 3.75(20)^{-n}} \]
Solution (cont): Graphing the **Updating function**

\[ B(p) = \frac{20p}{1 + 0.02p} \]

- The only intercept is the origin
- There is a **horizontal asymptote** satisfying

\[ \lim_{p \to \infty} B(p) = \frac{20}{0.02} = 1000 \]

- Biologically, this asymptote means that there is a maximum number in the next generation no matter how large the population starts.
Solution (cont): The updating function and identity map

Beaverton–Holt Updating Function

$p_{n+1} = B(p_n)$

$p_{n+1} = p_n$
Example 1 - Beverton-Holt Model

Solution (cont): Analysis of Beverton-Holt model

- Equilibria satisfy

\[ p_e = B(p_e) = \frac{20p_e}{1 + 0.02p_e} \]

- One equilibrium is \( p_e = 0 \)
- The other satisfies

\[ 1 + 0.02p_e = 20 \quad \text{or} \quad p_e = 950 \]

- The derivative of the updating function is

\[ B'(p) = \frac{20}{(1 + 0.02p)^2} \]
Solution (cont): Analysis of Beverton-Holt model – Since the derivative of the updating function is

\[ B'(p) = \frac{20}{(1 + 0.02p)^2} \]

- Equilibrium \( p_e = 0 \) has \( B'(0) = 20 \)
- The extinction equilibrium is unstable with solutions monotonically growing away
- The equilibrium \( p_e = 950 \) has \( B'(950) = \frac{1}{20} \)
- The carrying capacity equilibrium is stable with solutions monotonically approaching
Example 2 - Hassell’s Model: Suppose that a population of butterflies (measured in weeks) grows according to the discrete dynamical model

\[ p_{n+1} = H(p_n) = \frac{81 p_n}{(1 + 0.002 p_n)^4} \]

- Assume that \( p_0 = 200 \) and find the population for the next 2 weeks
- Simulate the model for 20 weeks
- Graph the **updating function** with the identity map
- Determine the **equilibria** and analyze their **stability**
Example 2 - Hassell’s Model

Solution - Hassell’s Model: Iterate the model with $p_0 = 200$

$$p_1 = \frac{81(200)}{(1 + 0.002(200))^4} = 4217$$

$$p_2 = \frac{81(4217)}{(1 + 0.002(4217))^4} = 43$$

These iterations show dramatic population swings, suggesting instability in the model.
Solution (cont): This model is iterated 20 times, and the observed behavior is a **Period 4 solution**

Asymptotically cycles from 163 to 4271 to 42 to 2453
Example 2 - Hassell’s Model

Solution (cont): Graphing the Updating function

\[ H(p) = \frac{81p}{(1 + 0.002p)^4} \]

- The only intercept is the origin
- Since the power of \( p \) in the denominator exceeds the power of \( p \) in the numerator, there is a horizontal asymptote \( H = 0 \)
- The derivative is

\[ H'(p) = 81 \frac{(1 + 0.002p)^4 - p \cdot 4(1 + 0.002p)^3 \cdot 0.002}{(1 + 0.002p)^8} \]

\[ = 81 \frac{1 - 0.006p}{(1 + 0.002p)^5} \]

- \( H'(p) = 0 \) when \( 1 - 0.006p = 0 \) or \( p_{max} = \frac{500}{3} \)
- There is a maximum at \((166.7, 4271.5)\)
Solution (cont): The **updating function** and **identity map**

Hassell’s Updating Function

\[ P_{n+1} = H(P_n) \]

Identity Map

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Solution (cont): Analysis of Hassell’s model

- Equilibria satisfy

  \[ p_e = H(p_e) = \frac{81p_e}{(1 + 0.002p_e)^4} \]

- One equilibrium is \( p_e = 0 \)
- The other satisfies

  \[ (1 + 0.002p_e)^4 = 81 \]

  Thus,

  \[ 1 + 0.002p_e = 3 \quad \text{or} \quad p_e = 1000 \]
Example 2 - Hassell’s Model

Solution (cont): Analysis of Hassell’s model – Since the derivative of the updating function is

\[ H'(p) = 81 \frac{(1 - 0.006p)}{(1 + 0.002p)^5} \]

- Equilibrium \( p_e = 0 \) has \( H'(0) = 81 \)
- The extinction equilibrium is unstable with solutions monotonically growing away
- The equilibrium \( p_e = 1000 \) has \( H'(1000) = -\frac{5}{3} \)
- The \( p_e = 1000 \) equilibrium is unstable with solutions oscillating and moving away from \( p_e \)