Calculus for the Life Sciences I

Lecture Notes – More Applications of Nonlinear Dynamical Systems

Joseph M. Mahaffy,
⟨mahaffy@math.sdsu.edu⟩

Department of Mathematics and Statistics
Dynamical Systems Group
Computational Sciences Research Center
San Diego State University
San Diego, CA 92182-7720

http://www-rohan.sdsu.edu/∼jmahaffy

Spring 2013

Outline

Introduction - Population Models

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
  - Has a carrying capacity reflecting natural limits to populations
  - Quadratic updating function becomes negative for large populations
- Ecologists have modified the logistic growth model to make the updating function more realistic and better able to handle largely fluctuating populations
  - Ricker's model used in fishery management
  - Hassell's model used for insects
- Differentiation needed to analyze these models

Sockeye Salmon Populations 1

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
- Many salmon spawning runs have become 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 uneffected by human development
  - Long time series of data – 1908 to 1952
  - Provide good system to model

Sockeye Salmon Populations – Spawning Behavior

- Create table of sockeye salmon (*Oncorhynchus nerka*) in the Skeena river system
- Table lists four year averages from the starting year
- Since 4 and 5 year old salmon spawn, each grouping of 4 years is an approximation of the offspring of the previous 4 year average
- Model is complicated because the salmon have adapted to have either 4 or 5 year old mature adults spawn
- Simplify the model by ignoring this complexity

Sockeye Salmon Populations – Skeena River Table

Population in thousands

Year	Population	Year	Population
1908	1,098	1932	278
1912	740	1936	448
1916	714	1940	528
1920	615	1944	639
1924	706	1948	523
1928	510		

Four Year Averages of Skeena River Sockeye Salmon

Ricker's Model – Salmon

Problems with Logistic growth model

$$P_{n+1} = P_n + rP_n\left(1 - \frac{P_n}{M}\right)$$

- Logistic growth model predicted certain yeast populations well
- This model does not fit the data for many organisms
- A major problem is that large populations in the model return a negative population in the next generation
- Several alternative models use only a **non-negative** updating function
- Fishery management has often used **Ricker's Model**

Ricker's Model – Salmon

Ricker's Model

- **Ricker's model** was originally formulated using studies of salmon populations
- **Ricker's model** is given by the equation

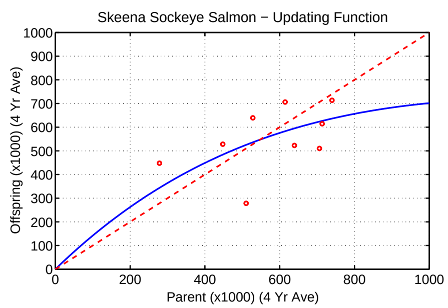
$$P_{n+1} = R(Pn) = aP_n e^{-bP_n}$$

- The positive constants a and b are 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
  - It is assumed that the resultant offspring that return to spawn from this group occurs between 1912 and 1915, which averages 740,000 salmon/year

Ricker's Model – Salmon

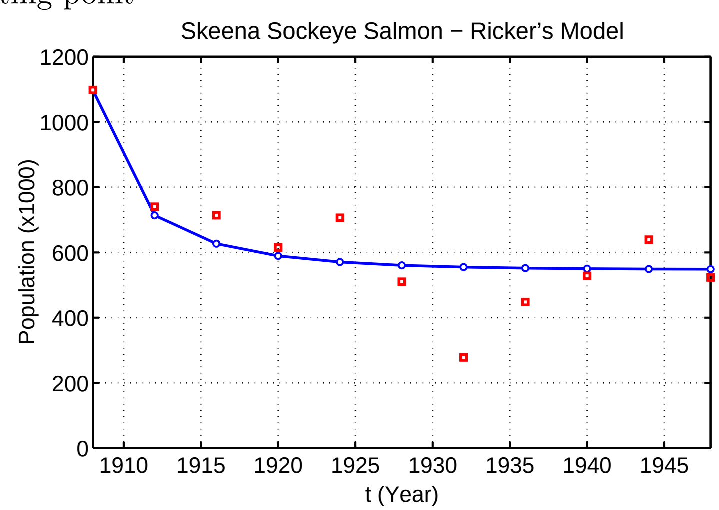
- Successive populations give data for updating functions
  - P_n is parent population, and P_{n+1} is surviving offspring
  - Nonlinear least squares fit of Ricker's function

$$P_{n+1} = 1.535\, P_n e^{-0.000783\, P_n}$$



Ricker's Model – Salmon

Simulate the Ricker's model using the initial average in 1908 as a starting point



Ricker's Model – Salmon 5

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 1

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

$$\begin{aligned} P_e &= aP_e e^{-bP_e} \\ 0 &= P_e(ae^{-bP_e} - 1) \end{aligned}$$

The equilibria are

$$P_e = 0 \qquad \text{and} \qquad P_e = \frac{\ln(a)}{b}$$

Note that $a > 1$ required for a positive equilibrium

Analysis of the Ricker's Model 2

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 3

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

$$R'(P) = ae^{-bP}(1 - bP)$$

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

$$R(\ln(a)/b) = ae^{-\ln(a)}(1 - \ln(a)) = 1 - \ln(a)$$

- The solution of Ricker's model is **stable** and **monotonically approaches** the equilibrium $P_e = \ln(a)/b$ provided $1 < a < e \approx 2.7183$
- The solution of Ricker's model is **stable** and **oscillates as it approaches** the equilibrium $P_e = \ln(a)/b$ provided $e < a < e^2 \approx 7.389$
- The solution of Ricker's model is **unstable** and **oscillates as it grows away** the equilibrium $P_e = \ln(a)/b$ provided $a > e^2 \approx 7.389$

Skeena River Salmon Example

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

$$P_e = 0 \qquad \text{and} \qquad P_e = \frac{\ln(1.535)}{0.000783} = 547.3$$

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 1

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

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

Skip Example

- 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 1 - Ricker's Growth Model 2

Solution The Ricker's growth function is

$$R(P) = 7\, P e^{-0.02 P}$$

- 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 $R(P)$

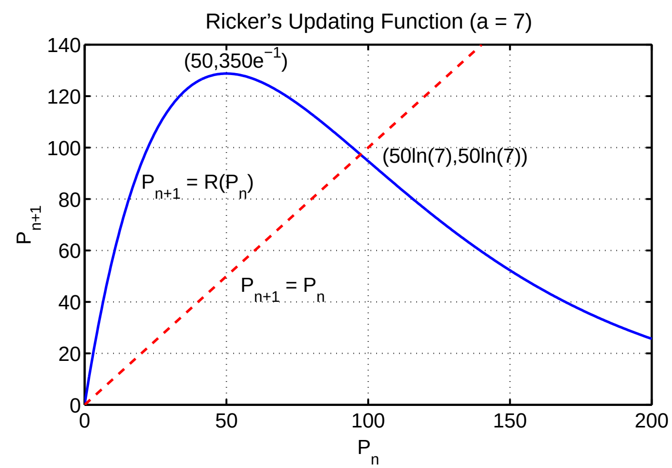
$$\begin{aligned} R'(P) &= 7(P(-0.02P)e^{-0.02P} + e^{-0.02P}) \\ &= 7\, e^{-0.02P}(1 - 0.02\, P) \end{aligned}$$

- This gives a critical point at $P_c = 50$

Example 1 - Ricker's Growth Model 3

Solution (cont) The Ricker's function has a **maximum** at

$$(P_c, R(P_c)) = (50, 350e^{-1}) \approx (50, 128.76)$$



Example 1 - Ricker's Growth Model

Solution (cont) For **equilibria**, let $P_e = P_{n+1} = P_n$, then

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

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

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

This gives the other equilibrium $P_e = 50\ln(7) \approx 97.3$

Example 1 - Ricker's Growth Model

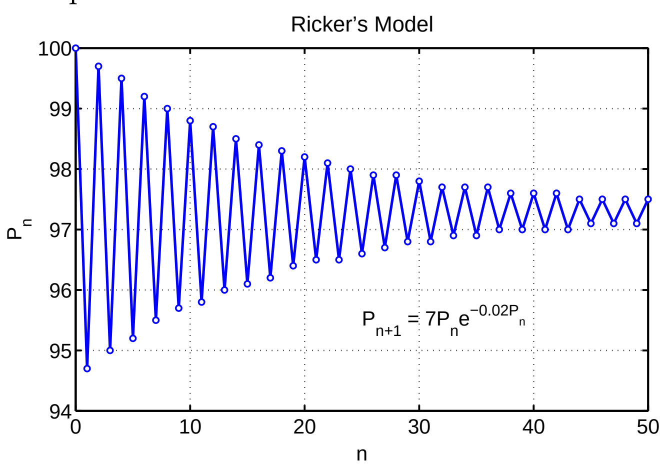
Solution (cont) Stability Analysis – Recall

$$R'(P) = 7\,e^{-0.02P}(1 - 0.02\,P)$$

- 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 $P_e = 97.3$

Example 1 - Ricker's Growth Model

Solution (cont) Starting with $P_0 = 100$, the simulation shows the behavior predicted above



Example 2 - Ricker's Growth Model

Example 2 - Ricker's Growth Model Let P_n be the population of fish in any year n, and assume the Ricker's growth model

$$P_{n+1} = R(P_n) = 9\,P_n e^{-0.02P_n}$$

Skip Example

- 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 2 - Ricker's Growth Model 2

Solution The Ricker's growth function is

$$R(P) = 9\,Pe^{-0.02P}$$

- 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 $R(P)$

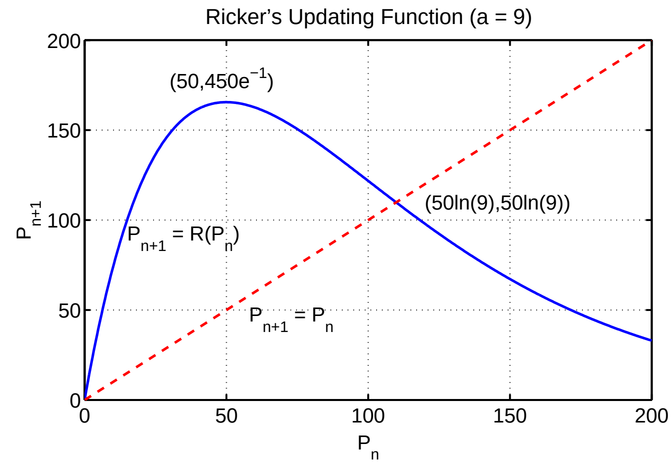
$$\begin{aligned} R'(P) &= 9(P(-0.02P)e^{-0.02P} + e^{-0.02P}) \\ &= 9\,e^{-0.02P}(1 - 0.02\,P) \end{aligned}$$

- This gives a critical point at $P_c = 50$

Example 2 - Ricker's Growth Model 3

Solution (cont) The Ricker's function has a **maximum** at

$$(P_c, R(P_c)) = (50, 450e^{-1}) \approx (50, 165.5)$$



Example 2 - Ricker's Growth Model 4

Solution (cont) For **equilibria**, let $P_e = P_{n+1} = P_n$, then

$$P_e = R(P_e) = 9\,P_e e^{-0.02P_e}$$

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

$$1 = 9\,e^{-0.02P_e} \quad \text{or} \quad e^{0.02P_e} = 9$$

This gives the other equilibrium $P_e = 50\ln(9) \approx 109.86$

Example 2 - Ricker's Growth Model 5

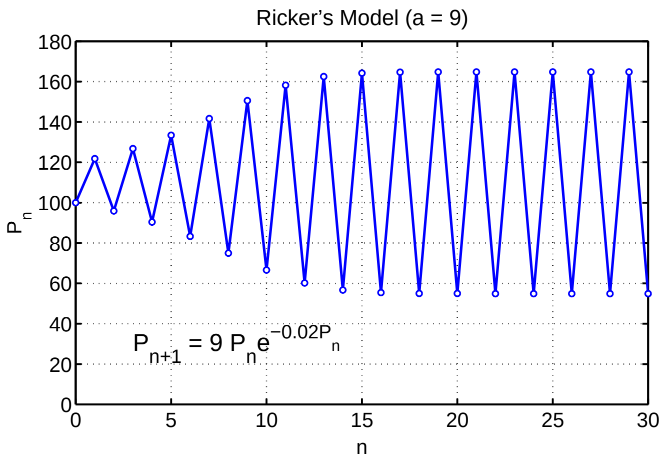
Solution (cont) **Stability Analysis** – Recall

$$R'(P) = 9\,e^{-0.02P}(1 - 0.02\,P)$$

- For $P_e = 0$
  - The derivative $R'(0) = 9 > 1$
  - Solutions **monotonically grow away** from $P_e = 0$
- For $P_e = 109.86$
  - The derivative $R'(109.86) = 1 - \ln(9) \approx -1.197$
  - Solutions **oscillate** and **grow away** from $P_e = 109.86$
  - This is a **unstable equilibrium**, and populations oscillate with **Period 2** between 55 and 165

Example 2 - Ricker's Growth Model 6

Solution (cont) Starting with $P_0 = 100$, the simulation shows the behavior predicted above



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

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

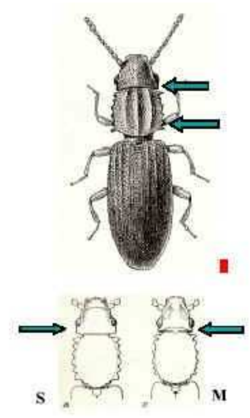
Study of a Beetle Population 1

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
- These are experimental conditions for the **Logistic growth model**

Study of a Beetle Population 2

Study of *Oryzaephilus surinamensis*, **the saw-tooth grain beetle**



Gorham, 1987

Study of a Beetle Population 3

Data on *Oryzaephilus surinamensis*, **the saw-tooth grain beetle**

Week	Adults	Week	Adults
0	4	16	405
2	4	18	471
4	25	20	420
6	63	22	430
8	147	24	420
10	285	26	475
12	345	28	435
14	361	30	480

Study of a Beetle Population 4

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)

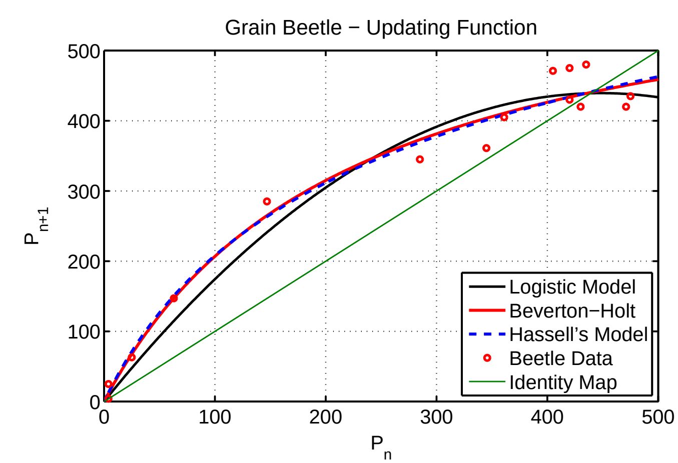
$$P_{n+1} = \frac{3.010\, P_n}{1 + 0.00456\, P_n}$$

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

$$P_{n+1} = \frac{3.269\, P_n}{(1 + 0.00745\, P_n)^{0.8126}}$$

Study of a Beetle Population 5

Graph of **Updating functions** and **Beetle data**



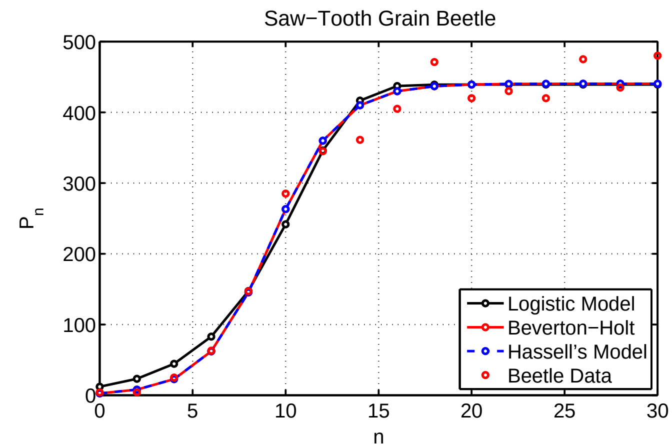
Study of a Beetle Population 6

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 7

Time Series graph of Models with Beetle Data



Analysis of Hassell's Model 1

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
$$\begin{aligned}(1+bP_e)^c &= a\\ 1+bP_e &= a^{1/c}\\ P_e &= \frac{a^{1/c}-1}{b}\end{aligned}$$

Analysis of Hassell's Model 2

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
$$\begin{aligned}H'(P) &= \frac{a(1+bP)^c - abcP(1+bP)^{c-1}}{(1+bP)^{2c}}\\ &= a\frac{1+b(1-c)P}{(1+bP)^{c+1}}\end{aligned}$$

Analysis of Hassell's Model 3

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 4

Analysis of Hassell's Model – Stability Analysis

- The derivative is

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

- At $P_e = (a^{1/c} - 1)/b$, we find

$$\begin{aligned} H'(P_e) &= a\frac{1+(1-c)(a^{1/c}-1)}{(1+(a^{1/c}-1))^{c+1}} \\ &= \frac{c}{a^{1/c}} + 1 - c \end{aligned}$$

  - The stability of the **carrying capacity equilibrium** depends on both a and c, but not b
  - When $c = 1$ (**Beverton-Holt** model) $H'(P_e) = \frac{1}{a}$, so this equilibrium is **monotonically stable**

Beetle Study Analysis 1

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 2

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 2

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

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

  - 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**

SDSU

Example 1 - Beverton-Holt Model 1

Example 1 - Beverton-Holt Model: Suppose that a population of insects (measured in weeks) grows according to the discrete dynamical model

$$p_{n+1} = B(p_n) = \frac{20\, p_n}{1 + 0.02\, p_n}$$

Skip Example

- 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**

SDSU

Example 1 - Beverton-Holt Model 2

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

$$\begin{aligned} p_1 &= \frac{20(200)}{(1+0.02(200))} = 800 \\ p_2 &= \frac{20(800)}{(1+0.02(800))} = 941 \\ p_3 &= \frac{20(941)}{(1+0.02(941))} = 949.6 \end{aligned}$$

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

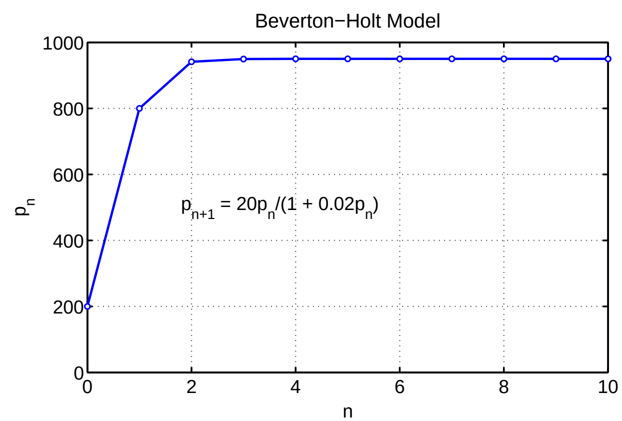
$$M = \frac{a-1}{b} = \frac{19}{0.02} = 950$$

SDSU

Example 1 - Beverton-Holt Model 3

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

$$p_n = \frac{950\, p_0}{p_0 + (950 - p_0)20^{-n}} = \frac{950}{1 + 3.75(20)^{-n}}$$



SDSU

Example 1 - Beverton-Holt Model

Solution (cont): Graphing the **Updating function**

$$B(p) = \frac{20\,p}{1+0.02\,p}$$

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

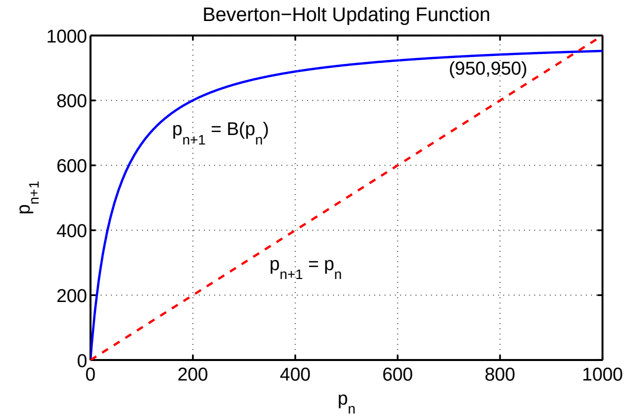
$$\lim_{p\to\infty} B(p) = \frac{20}{0.02} = 1000$$

- Biologically, this asymptote means that there is a maximum number in the next generation no matter how large the population starts

Introduction
Salmon Populations
Analysis of the Ricker's Model
Beverton-Holt and Hassell's Model
Study of a Beetle Population
Analysis of Hassell's Model
Beetle Study Analysis
More Examples

Example 1 - Beverton-Holt Model

Solution (cont): The **updating function** and **identity map**



Introduction
Salmon Populations
Analysis of the Ricker's Model
Beverton-Holt and Hassell's Model
Study of a Beetle Population
Analysis of Hassell's Model
Beetle Study Analysis
More Examples

Example 1 - Beverton-Holt Model

Solution (cont): **Analysis of Beverton-Holt model**

- Equilibria satisfy

$$p_e = B(p_e) = \frac{20\,p_e}{1+0.02\,p_e}$$

- One equilibrium is $p_e = 0$
- The other satisfies

$$1+0.02\,p_e = 20 \quad \text{or} \quad p_e = 950$$

- The derivative of the updating function is

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

Introduction
Salmon Populations
Analysis of the Ricker's Model
Beverton-Holt and Hassell's Model
Study of a Beetle Population
Analysis of Hassell's Model
Beetle Study Analysis
More Examples

Example 1 - Beverton-Holt Model

Solution (cont): **Analysis of Beverton-Holt model** – Since the derivative of the updating function is

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

- 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 1

Example 2 - Hassell's Model: Suppose that a population of butterflies (measured in weeks) grows according to the discrete dynamical model

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

Skip Example

- 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 2

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

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

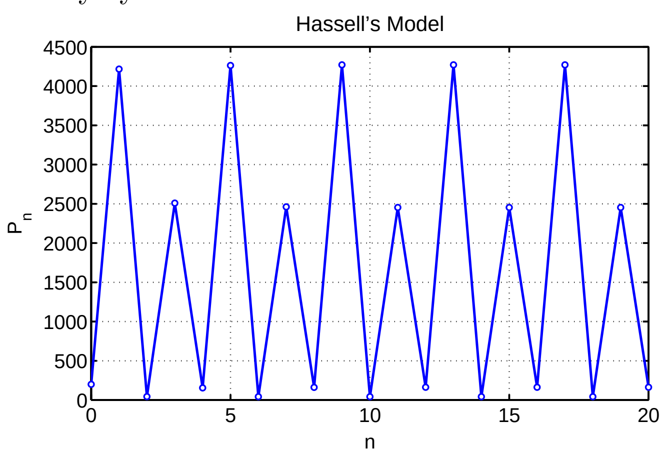
$$p_2 = \frac{81(4217)}{(1+0.002(4217))^4} = 43$$

These iterations show dramatic population swings, suggesting instability in the model

Example 2 - Hassell's Model 3

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 4

Solution (cont): Graphing the **Updating function**

$$H(p) = \frac{81\,p}{(1+0.002\,p)^4}$$

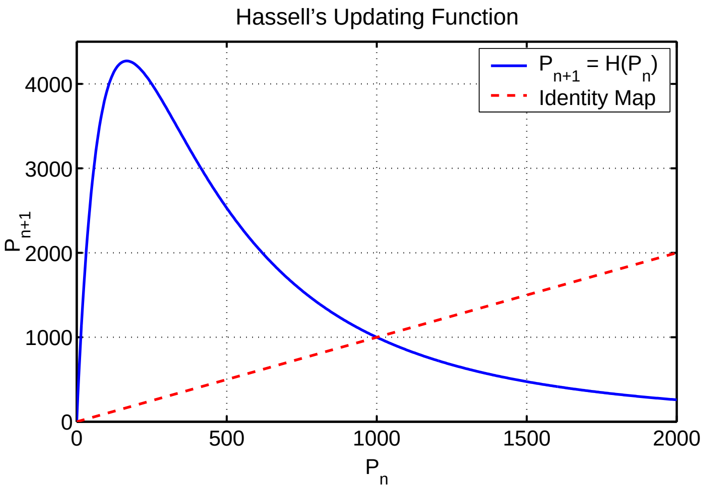
- The only intercept is the origin
- Since the power of p in the denominator exceeds the power of p in the numerator, there is a **horizontal asymptote** $H = 0$
- The derivative is

$$H'(p) = 81\frac{(1+0.002\,p)^4 - p\cdot 4(1+0.002\,p)^3 0.002}{(1+0.002\,p)^8} = 81\frac{(1-0.006\,p)}{(1+0.002\,p)^5}$$

- $H'(p) = 0$ when $1 - 0.006\,p = 0$ or $p_{max} = \frac{500}{3}$
- There is a **maximum** at $(166.7, 4271.5)$

Example 2 - Hassell's Model

Solution (cont): The **updating function** and **identity map**



Example 2 - Hassell's Model

Solution (cont): Analysis of Hassell's model

- Equilibria satisfy

$$p_e = H(p_e) = \frac{81\, p_e}{(1 + 0.002\, p_e)^4}$$

- One equilibrium is $p_e = 0$
- The other satisfies

$$(1 + 0.002\, p_e)^4 = 81$$

- Thus,

$$1 + 0.002\, p_e = 3 \quad \text{or} \quad p_e = 1000$$

Example 2 - Hassell's Model

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

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

- 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

Example 3 - Chalone Model

Example 3 - Chalone Model or Model for Cellular Division with Inhibition: A biochemical agent, **chalone**, is released by a cell to inhibit mitosis of nearby cells, preventing the over crowding of cells.
This was an early model for **cancer**, speculating that this control breaks down

$$p_{n+1} = f(p_n) = \frac{2\, p_n}{1 + 10^{-8} p_n^4}$$

Skip Example

- Let $p_0 = 10$ and find the population for the next 2 generations
- Simulate the model for 20 weeks
- Determine the **equilibria** and analyze their **stability**

Example 3 - Chalone Model

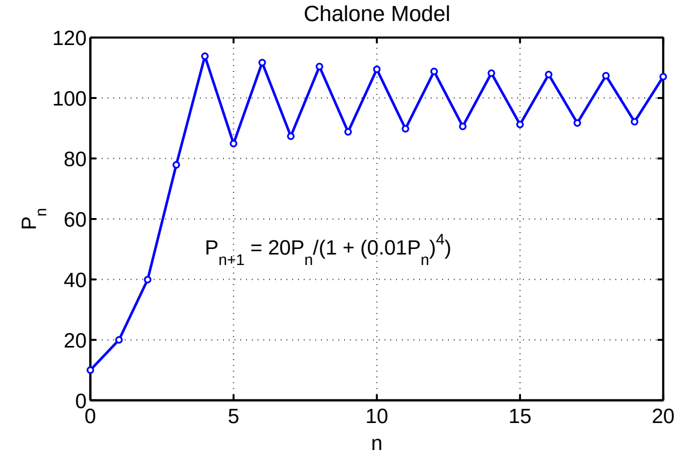
Solution - Chalone Model: Iterate the model with $p_0 = 10$

$$
\begin{aligned}
p_1 &= \frac{2(10)}{1+10^{-8}(10)^4} = 20.0 \\
p_2 &= \frac{2(20)}{1+10^{-8}(20)^4} = 39.94 \\
p_3 &= \frac{2(39.94)}{1+10^{-8}(39.94)^4} = 77.90
\end{aligned}
$$

SDSU

Example 3 - Chalone Model

Solution (cont): This model is iterated 20 times, and the model shows oscillations



SDSU

Example 3 - Chalone Model

Solution (cont): **Analysis of Chalone model**

- Equilibria satisfy

$$p_e = f(p_e) = \frac{2\,p_e}{1+10^{-8}\,p_e^4}$$

- One equilibrium is $p_e = 0$
- The other satisfies

$$1 + 10^{-8}\,p_e^4 = 2$$

- Thus,

$$p_e^4 = 10^8 \quad \text{or} \quad p_e = 100$$

SDSU

Example 3 - Chalone Model

Solution (cont): **Analysis of Chalone model** – The derivative of the updating function is

$$
\begin{aligned}
f'(p) &= 2\frac{(1+10^{-8}\,p^4) - p(4\times 10^{-8}p^3)}{(1+10^{-8}\,p^4)^2} \\
&= \frac{2 - 6\times 10^{-8}p^4}{(1+10^{-8}\,p^4)^2}
\end{aligned}
$$

- Equilibrium $p_e = 0$ has $f'(0) = 2$
- The **extinction equilibrium** is **unstable** with solutions **monotonically growing away**
- The equilibrium $p_e = 100$ has $f'(100) = -1$
- The $p_e = 100$ **equilibrium** is on the **border of stability** with solutions **oscillating** and **slowly approaching** p_e

SDSU