Salmon Model
Qualitative Analysis of the Discrete Models
Study of a Beetle Population

# Math 636 - Mathematical Modeling
## Discrete Modeling II
## More Population Models

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## Outline

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Salmon Model
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Study of a Beetle Population

Salmon Populations
Ricker's Model

## Review - Population Models

**Review - 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
- Introduced **qualitative analysis**, which always starts finding the equilibria

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Study of a Beetle Population

Salmon Populations
Ricker's Model

## 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

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Salmon Populations
Ricker's Model

Sockeye Salmon Populations                                    2

## 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
  - Damming rivers interrupts the runs
  - Forestry allows the water to become too warm
  - Agriculture results in runoff pollution

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Ricker's Model

Sockeye Salmon Populations                                    3

## 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
- A simplified model combines **4** years

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Study of a Beetle Population

Salmon Populations
Ricker's Model

Sockeye Salmon Populations                                    4

## 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

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Salmon Populations
**Ricker's Model**

Ricker's Model – Salmon

## Ricker's Model

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

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

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

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Study of a Beetle Population

Salmon Populations
**Ricker's Model**

## Model Updating Functions

The **Skeena River** population data are used to find best models.

- Successive populations give data for updating functions
  - $P_n$ is parent population, and $P_{n+1}$ is surviving offspring
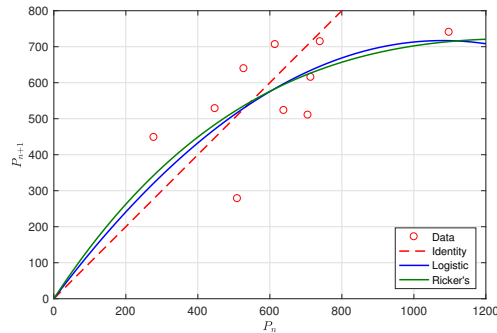


Nonlinear least squares fit of Logistic model

$$P_{n+1} = 1.3277\, P_n - 0.0006146\, P_n^2$$

and Ricker's model

$$P_{n+1} = 1.5344\, P_n e^{-0.0007816\, P_n}$$

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Study of a Beetle Population

Salmon Populations
**Ricker's Model**

## Least Squares Fit

Below is the **MatLab** function for minimizing the ***sum of square errors*** for the ***Ricker's updating function***.

```
1  function J = sal_ric(p0,pndata,pn1data)
2  % Least Squares fit to Logistic Growth
3  N = length(pndata);
4  err = [pn1data - p0(1)*pndata.*exp(-p0(2)*pndata)];
5  J = err*err'; % Sum of square errors
6  end
```

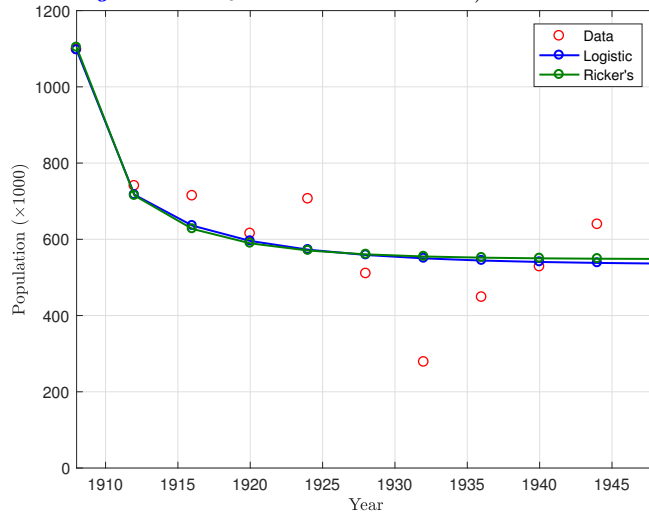The data for $P_{n+1}$ vs. $P_n$ is entered with an initial parameters
p0 = [a,b]:
p1 = fminsearch(@sal_ric,p0,[],pndata,pn1data)

A similar process is followed to best fit the ***logistic updating function***.

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Study of a Beetle Population

Salmon Populations
**Ricker's Model**

## Model Simulations

Best fitting ***logistic*** and ***Ricker's models*** are simulated and compared to data.
($P_0 = 1096.8$ for ***logistic*** and $P_0 = 1103.7$ for ***Ricker's***)

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Study of a Beetle Population

Salmon Populations
**Ricker's Model**

## Summary of Models for Salmon

### Summary of the Discrete Models for Skeena river salmon

- Both ***discrete models*** level 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

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**Qualitative Analysis of the Discrete Models**
Study of a Beetle Population
Analysis of Ricker's Model
Skeena River Salmon Example
Example of Logistic Growth

## General Discrete Dynamical Model (Autonomous)

Consider the **general autonomous discrete dynamical model:**

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

- The **first step in any qualitative analysis** is finding **equilibria**.
- Solve the **algebraic equation**

$$p_e = f(p_e).$$

- Solve algebraically or numerically.
- Geometrically, solutions are when $f(p)$ crosses the **identity map**.

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Study of a Beetle Population
Analysis of Ricker's Model
Skeena River Salmon Example
Example of Logistic Growth

## Behavior of Discrete Dynamical Model

Suppose the **autonomous discrete dynamical model:**

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

has an equilibrium, $p_e$.

- The **second step in the qualitative analysis** is taking the derivative and evaluating at the **equilibria**.
- The *qualitative behavior* depends on both the sign and magnitude of the derivative at the **equilibrium**.
- If the *sign* is positive, then solutions have a *monotonic behavior*, i.e., solutions stay on the same side of the equilibrium.
- If the *sign* is negative, then solutions have an *oscillatory behavior*, so the solution jumps across to the other side of the equilibrium.
- If the magnitude of the derivative, $|f'(p_e)| > 1$, then the *qualitative behavior* near the equilibrium is *unstable* with solutions moving away.

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**Qualitative Analysis of the Discrete Models**
Study of a Beetle Population
Analysis of Ricker's Model
Skeena River Salmon Example
Example of Logistic Growth

## Summary of Behavior of Discrete Dynamical Models

- If $f'(p_e) > 1$
  - Solutions of the discrete dynamical model **grow away** from the equilibrium (**monotonically**)
  - *The equilibrium is unstable*
- If $0 < f'(p_e) < 1$
  - Solutions of the discrete dynamical model **approach** the equilibrium (**monotonically**)
  - *The equilibrium is stable*
- If $-1 < f'(p_e) < 0$
  - Solutions of the discrete dynamical model **oscillate** about the equilibrium and **approach** it
  - *The equilibrium is stable*
- If $f'(p_e) < -1$
  - Solutions of the discrete dynamical model **oscillate** about the equilibrium but **move away** from it
  - *The equilibrium is unstable*

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Qualitative Analysis of the Discrete Models
Study of a Beetle Population
**Analysis of Ricker's Model**
Skeena River Salmon Example
Example of Logistic Growth

## 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

$$P_e = aP_e e^{-bP_e} \qquad \text{or} \qquad P_e(ae^{-bP_e} - 1) = 0.$$

The equilibria are

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

with $a > 1$ required for a positive equilibrium.

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Qualitative Analysis of the Discrete Models
Study of a Beetle Population

Analysis of Ricker's Model
Skeena River Salmon Example
Example of Logistic Growth

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

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Salmon Model
Qualitative Analysis of the Discrete Models
Study of a Beetle Population

Analysis of Ricker's Model
Skeena River Salmon Example
Example of Logistic Growth

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 $a > e^2 \approx 7.389$

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Qualitative Analysis of the Discrete Models
Study of a Beetle Population

Analysis of Ricker's Model
Skeena River Salmon Example
Example of Logistic Growth

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

$$R'(P) = 1.535e^{-0.000783P}(1 - 0.000783P)$$

- 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

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Qualitative Analysis of the Discrete Models
Study of a Beetle Population

Analysis of Ricker's Model
Skeena River Salmon Example
Example of Logistic Growth

Skeena River Salmon Example

A similar analysis is performed for the *logistic model*, where

$$P_{n+1} = F(P_n) = 1.3277\, P_n - 0.0006146\, P_n^2.$$

The equilibria are

$$P_e = 0 \qquad \text{and} \qquad P_e = 533.2$$

The derivative is

$$F'(P) = 1.3277 - 0.001229\, P)$$

- At $P_e = 0$, $F'(0) = 1.3277 > 1$
  - This equilibrium is *unstable* (as expected)

- At $P_e = 533.2$, $F'(533.2) = 0.6716 < 1$
  - This equilibrium is *stable* with solutions monotonically approaching the equilibrium, as observed in the simulation

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**Qualitative Analysis of the Discrete Models**
Study of a Beetle Population

Analysis of Ricker's Model
**Skeena River Salmon Example**
Example of Logistic Growth

## Skeena River Salmon Example

Both the *Ricker's* and *logistic models* provide very similar *updating functions* passing through the *Skeena River salmon data*.

Using these *updating functions* with the best fitting $P_0$, the *discrete dynamical model simulations* give very similar solutions.

The *carrying capacity equilibria* are separated by only a few percent with both showing the same *monotonic stability*. (The SSE for the *logistic simulation* was 120,918, while the *Ricker's simulation* was 126,428.)

Yet the large $P_n$ behavior of these models from their *updating functions* is dramatically different.

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Qualitative Analysis of the Discrete Models
Study of a Beetle Population

Analysis of Ricker's Model
Skeena River Salmon Example
**Example of Logistic Growth**

## Example of the Logistic Growth Model                1

**Example:** Consider the **discrete logistic growth model**

$$p_{n+1} = F(p_n) = p_n + r\,p_n\left(1 - \frac{p_n}{1000}\right),$$

with $r = 0.5$, 1.85, 2.3, and 2.65.

We perform a *qualitative analysis* of this model and observe the *dynamic behavior*.

From information before, we know the equilibria are $p_e = 0$ (*extinction*) and $p_e = 1000$ (*carrying capacity*).

The *stability analysis* requires the derivative,

$$F'(p) = 1 + r - \frac{2rp}{1000}$$

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**Qualitative Analysis of the Discrete Models**
Study of a Beetle Population

Analysis of Ricker's Model
Skeena River Salmon Example
**Example of Logistic Growth**

## Example of the Logistic Growth Model                2

With $F'(p) = 1 + r - \frac{2rp}{1000}$, for $p_e = 0$,

$$F'(0) = 1 + r > 1,$$

provided $r > 0$.

It follows that $p_e = 0$ is an *unstable* equilibrium with solutions *monotonically growing away*. (If the *net growth rate* is negative, the population *monotonically declines to extinction*.)

At the *carrying capacity equilibrium*, $p_e = 1000$, the derivative satisfies:

$$F'(1000) = 1 + r - \frac{2r(1000)}{1000} = 1 - r,$$

so this behavior depends on $r$.

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**Qualitative Analysis of the Discrete Models**
Study of a Beetle Population

Analysis of Ricker's Model
Skeena River Salmon Example
**Example of Logistic Growth**

## Example of the Logistic Growth Model                3

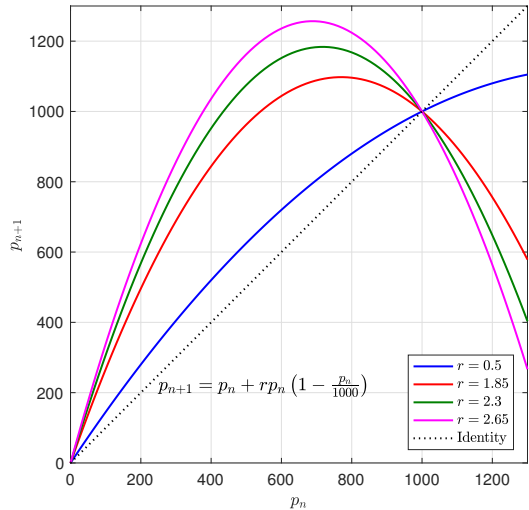Since $F'(1000) = 1 - r$, we have the following:

- When $r = 0.5$, then $F'(1000) = 0.5$.
  - $p_e = 1000$ is a *stable* equilibrium with solutions **monotonically approaching** it
- When $r = 1.85$, then $F'(1000) = -0.85$.
  - $p_e = 1000$ is a *stable* equilibrium with solutions **oscillating** and **approaching** it
- When $r = 2.3$, then $F'(1000) = -1.3$.
  - $p_e = 1000$ is an *unstable* equilibrium with solutions *oscillating* and *moving away*
- When $r = 2.65$, then $F'(1000) = -1.65$.
  - $p_e = 1000$ is an *unstable* equilibrium with solutions *oscillating* and *moving away*

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Qualitative Analysis of the Discrete Models
Study of a Beetle Population
Analysis of Ricker's Model
Skeena River Salmon Example
Example of Logistic Growth

## Example of the Logistic Growth Model 4

**Graphing the updating functions** for *discrete logistic model*



$$p_{n+1} = p_n + rp_n\left(1 - \frac{p_n}{1000}\right)$$

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Study of a Beetle Population
Analysis of Ricker's Model
Skeena River Salmon Example
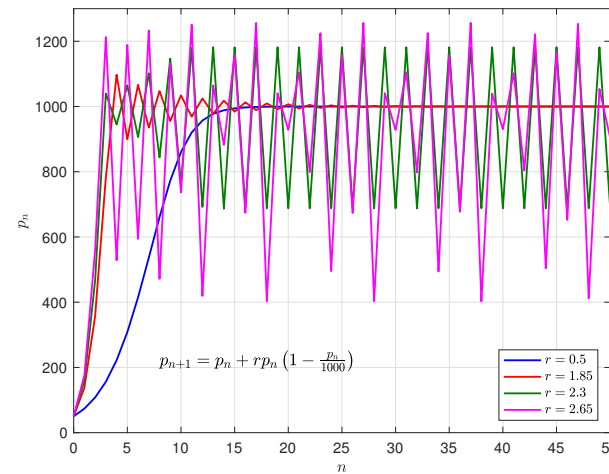Example of Logistic Growth

## Example of the Logistic Growth Model 5

**Simulation** of the *logistic growth model*



$r = 0.5$
gives *monotonic*
*classic S-curve*

$r = 1.85$
shows solution
*oscillating* toward
*equilibrium*

$r = 2.3$
gives a *period-2*
solution

$r = 2.65$
results in *chaos*

$$p_{n+1} = p_n + rp_n\left(1 - \frac{p_n}{1000}\right)$$

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Study of a Beetle Population
Analysis of Ricker's Model
Skeena River Salmon Example
Example of Logistic Growth

## MatLab for Logistic Growth Example

```
1  n = 0:50;
2  pnr1(1) = [50]; pnr2(1) = [50];
3  pnr3(1) = [50]; pnr4(1) = [50];
4  for i= 1:50
5      pnr1(i+1) = 1.5*pnr1(i) - (0.5/1000)*pnr1(i).^2;
6      pnr2(i+1) = 2.85*pnr2(i) - ...
           (1.85/1000)*pnr2(i).^2;
7      pnr3(i+1) = 3.3*pnr3(i) - (2.3/1000)*pnr3(i).^2;
8      pnr4(i+1) = 3.65*pnr4(i) - ...
           (2.65/1000)*pnr4(i).^2;
9  end
10
11 plot(n,pnr1,'b-','LineWidth',1.5);
12 hold on
13 plot(n,pnr2,'r-','LineWidth',1.5);
14 plot(n,pnr3,'-','color',[0,0.5,0],'LineWidth',1.5);
15 plot(n,pnr4,'m-','LineWidth',1.5);
```

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Qualitative Analysis of the Discrete Models
Study of a Beetle Population
Fitting the Models
Choosing Best Models
Return to U. S. Logistic Models

## Insect Populations

**Insect populations** are often seasonal or generational, making their study good for *discrete dynamical models*.

- The most common models remain *Malthusian* and *logistic growth models* (possibly with immigration or emigration).

- The *Beverton-Holt* and *Ricker's models* with their *positive updating functions* are also common:

$$P_{n+1} = \frac{aP_n}{1 + \frac{P_n}{b}} \qquad \text{and} \qquad P_{n+1} = aP_n e^{-bP_n}.$$

- *Hassell* modified the Beverton Holt model for insects, adding an additional parameter, to obtain

$$P_{n+1} = \frac{aP_n}{\left(1 + \frac{P_n}{b}\right)^c}$$

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Qualitative Analysis of the Discrete Models
Study of a Beetle Population
Fitting the Models
Choosing Best Models
Return to U. S. Logistic Models

## Study of a Beetle Population

1

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

- 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

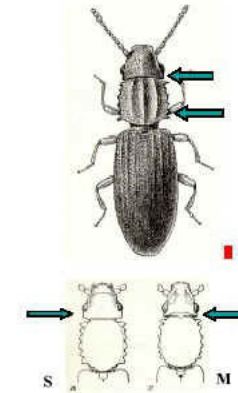- Regular census of the beetle populations recorded

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

Salmon Model
Qualitative Analysis of the Discrete Models
Study of a Beetle Population
Fitting the Models
Choosing Best Models
Return to U. S. Logistic Models

## Study of a Beetle Population

2

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



Gorham, 1987

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Qualitative Analysis of the Discrete Models
Study of a Beetle Population
Fitting the Models
Choosing Best Models
Return to U. S. Logistic Models

## Study of a Beetle Population

3

**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)

$$P_{n+1} = P_n + 0.9615\, P_n \left(1 - \frac{P_n}{439.2}\right)$$

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

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

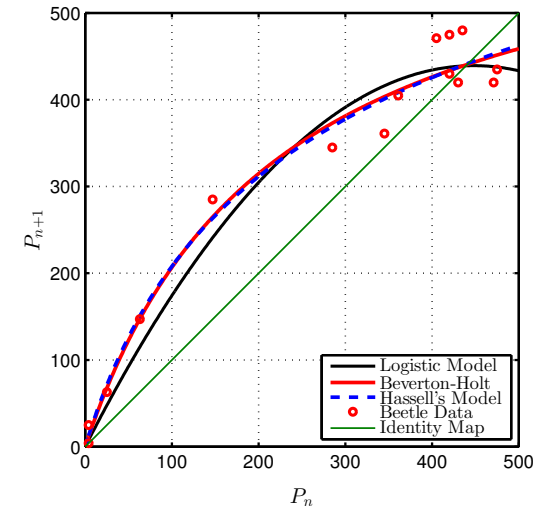- **Hassell's growth model** fit to data (SSE = 9,955)

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

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Qualitative Analysis of the Discrete Models
Study of a Beetle Population
Fitting the Models
Choosing Best Models
Return to U. S. Logistic Models

## Study of a Beetle Population

4

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

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Qualitative Analysis of the Discrete Models
Study of a Beetle Population
Fitting the Models
Choosing Best Models
Return to U. S. Logistic Models

## Study of a Beetle Population 5

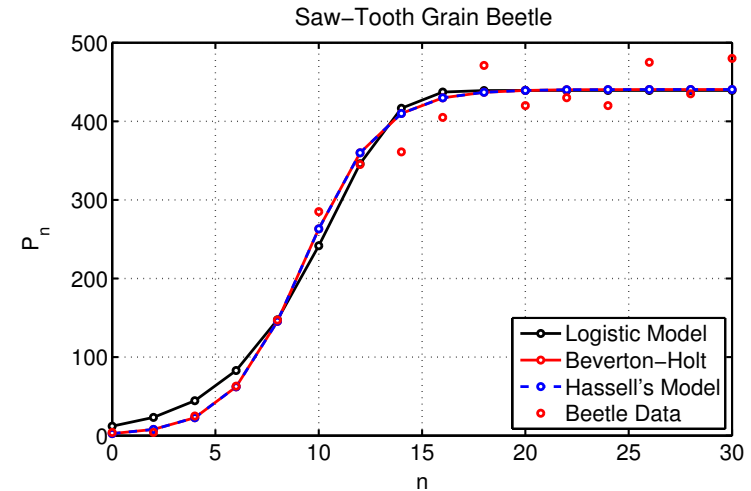**Time Series** - Least squares best fit to data, $P_0$

- 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

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Qualitative Analysis of the Discrete Models
Study of a Beetle Population
Fitting the Models
Choosing Best Models
Return to U. S. Logistic Models

## Study of a Beetle Population 6

**Time Series graph of Models with Beetle Data**



Saw–Tooth Grain Beetle

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Qualitative Analysis of the Discrete Models
Study of a Beetle Population
Fitting the Models
Choosing Best Models
Return to U. S. Logistic Models

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- The graphs of the *updating functions* and *time series simulations* show very good fit of all models presented.

- However, the *Beverton-Holt* and *Hassell's models* are clearly better according to the **SSE**.

- From a programming perspective, the curve fitting of the *updating functions* is numerically more robust, so has a larger region of stability.

- This is why often one first fits the *updating functions*, then finds the *best initial condition*.

- Trying to fit directly all parameters of the model and the initial population is a significantly more complicated computational problem, which makes it inherently less stable numerically.

- One can select various numerical algorithms to fit this highly nonlinear problem, but good initial guesses improves performance.

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Qualitative Analysis of the Discrete Models
Study of a Beetle Population
Fitting the Models
Choosing Best Models
Return to U. S. Logistic Models

## Study of a Beetle Population 8

The graphs and the **SSE** indicate that *Beverton-Holt* and *Hassell's models* and superior to the *logistic model*.

We apply the *Bayesian Information Criterion (BIC)* and *Akaike Information Criterion (AIC)* to the *time-series solutions* above:

| Model | SSE | BIC | AIC |
|---------------|-------|-------|-------|
| Logistic | 12027 | 111.5 | 155.4 |
| Beverton-Holt | 8578 | 106.1 | 150.0 |
| Hassell's | 7948 | 107.6 | 150.7 |

Since the *Beverton-Holt model* has one fewer parameter, than the *Hassell's model*, the *Information Criteria* indicate that the best choice of models is the *Beverton-Holt model*.

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Qualitative Analysis of the Discrete Models
Study of a Beetle Population

Fitting the Models
Choosing Best Models
Return to U. S. Logistic Models

## Return to U. S. Logistic Models                                           1

Previously, we found the ***best fitting logistic model*** by varying the
**3 parameters**, growth rate, $r$, carrying capacity, $M$, and initial
population, $P_0$.

The result by performing a ***least squares best fit*** to the ***time
series*** with the **census data** was:

$$P_{n+1} = P_n + 0.2245 P_n \left(1 - \frac{P_n}{451.7}\right) \qquad \text{with} \quad P_0 = 8.575,$$

which had a $SSE = 557.4$.

This least squares computation is very complex, which also means it
is more likely to be ***unstable*** and fail to converge.

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Qualitative Analysis of the Discrete Models
Study of a Beetle Population

Fitting the Models
Choosing Best Models
Return to U. S. Logistic Models

## Return to U. S. Logistic Models                                           2

For the salmon and beetle populations, we began with the population
data and considered fitting the ***updating function*** with different
models.

The population data are organized into $P_n$ and $P_{n+1}$, where a simple
curve fitting algorithm is applied to the ***updating function***.

A ***least squares best fit*** to the **census data** organized into $P_{n+1}$ vs.
$P_n$ by taking successive decades finds the ***best fitting quadratic***
below:

$$P_{n+1} = P_n + 0.20466 P_n \left(1 - \frac{P_n}{523.5}\right).$$

Subsequently, a ***nonlinear least squares fit*** to the ***time series*** by
varying only the initial condition, $P_0$, is performed, giving

$$p_0 = 10.2886 \qquad \text{with} \qquad SSE = 667.1.$$

These two least squares computations are relatively simple, which also
means the results are more likely to be ***stable*** and converge easily.

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Salmon Model
Qualitative Analysis of the Discrete Models
Study of a Beetle Population

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## General Discrete Least Squares

The computation is more stable with the two step process, but how does this
affect our model?

The graphs below show that over the range of data, the two models perform very
similarly, so it would be very hard to select which model is better.

They predict significantly different ***carrying capacities***, but neither is very
reliable given these are human populations.



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