Math 636 - Mathematical Modeling

Discrete Modeling II
More Population Models

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Outline

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

Sockeye Salmon Populations

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

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

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

Sockeye Salmon Populations

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

Ricker's Model

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

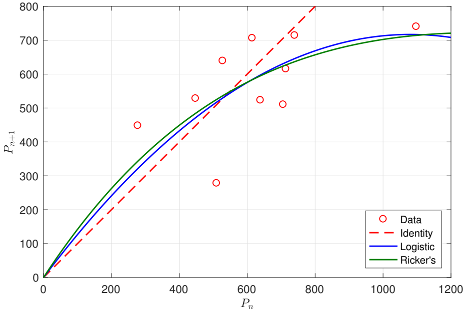
$$P_{n+1} = R(Pn) = aP_n e^{-bP_n}$$

  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

Model Updating Functions

The **Skeena River** popuation 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

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

Least Squares Fit

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

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

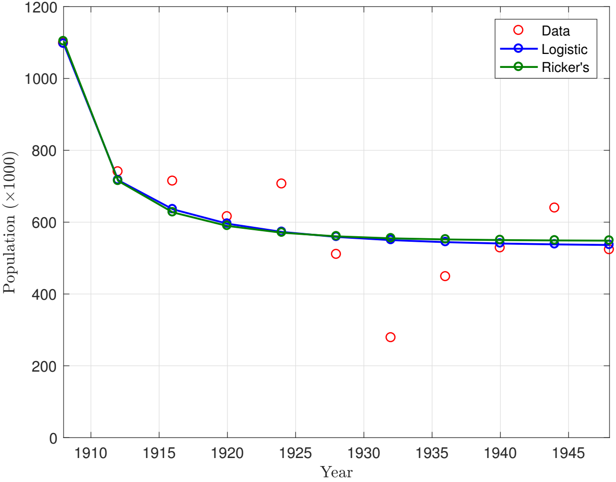
The data for P_{n+1} vs. P_n is entered with an initial parameters

```
p0 = [a,b]:
p1 = fminsearch(@sal_ric,p0,[],pndata,pn1data)
```

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

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***)



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

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**.

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.

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***

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.

Analysis of the Ricker's Model

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

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

- 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

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

- 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

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

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.

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,

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

Example of the Logistic Growth Model

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.

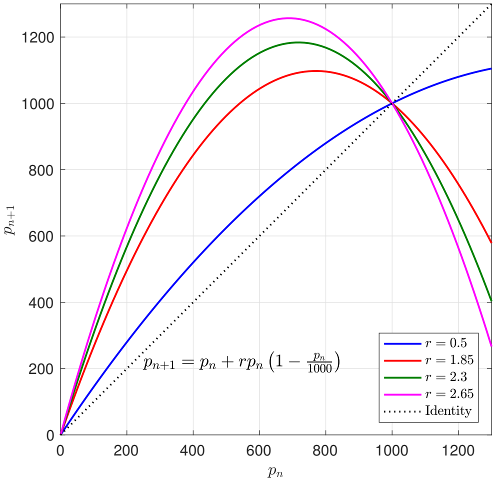
Example of the Logistic Growth Model

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***

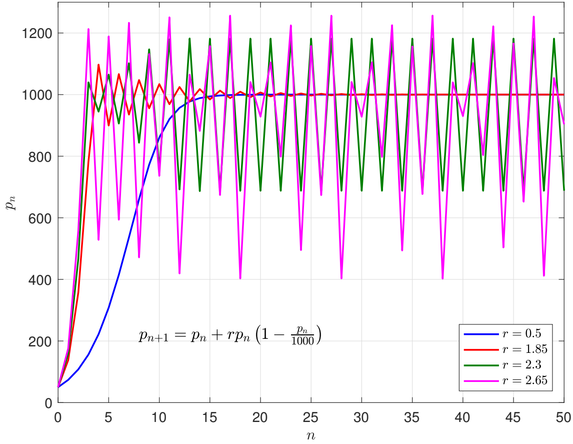
Example of the Logistic Growth Model

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



Example of the Logistic Growth Model

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***

MatLab for Logistic Growth Example

```
n = 0:50;
pnr1(1) = [50]; pnr2(1) = [50];
pnr3(1) = [50]; pnr4(1) = [50];
for i= 1:50
    pnr1(i+1) = 1.5*pnr1(i) - (0.5/1000)*pnr1(i).^2;
    pnr2(i+1) = 2.85*pnr2(i) - ...
        (1.85/1000)*pnr2(i).^2;
    pnr3(i+1) = 3.3*pnr3(i) - (2.3/1000)*pnr3(i).^2;
    pnr4(i+1) = 3.65*pnr4(i) - ...
        (2.65/1000)*pnr4(i).^2;
end

plot(n,pnr1,'b-','LineWidth',1.5);
hold on
plot(n,pnr2,'r-','LineWidth',1.5);
plot(n,pnr3,'-','color',[0,0.5,0],'LineWidth',1.5);
plot(n,pnr4,'m-','LineWidth',1.5);
```

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

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

Study of a Beetle Population 1

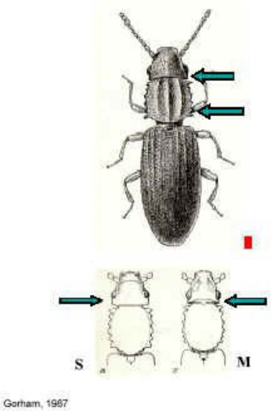
Study of *Oryzaephilus surinamensis*, the saw-tooth grain beetle

- 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

Study of a Beetle Population 2

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



Study of a Beetle Population

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)

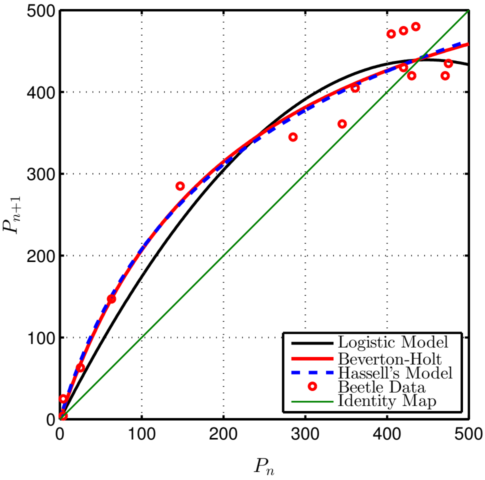
$$P_{n+1} = \frac{3.010\, P_n}{1 + 0.00456\, P_n}$$

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

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

Study of a Beetle Population

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



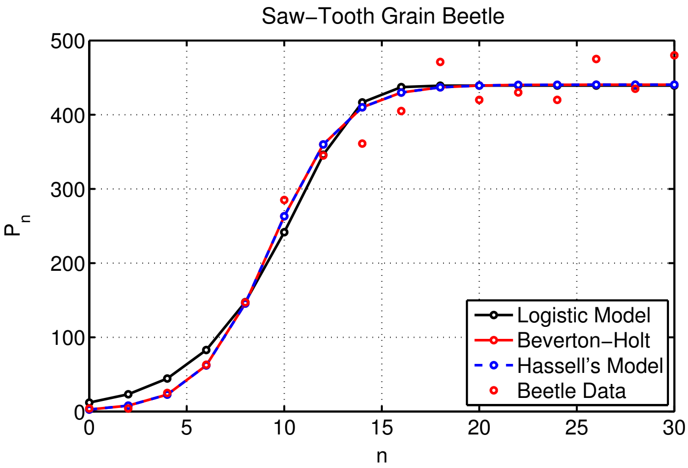
Study of a Beetle Population

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



Study of a Beetle Population

- 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.

Study of a Beetle Population

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***.

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.

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.

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.