Calculus for the Life Sciences I

Lecture Notes – Nonlinear Dynamical Systems

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1. Discrete Logistic Growth Model
   - Introduction
   - Yeast Study
   - Discrete Dynamical Models
2. Qualitative Analysis of Logistic Growth Model
   - Equilibria
   - Simulation of Logistic Growth Model
   - Stability of Logistic Growth Model
   - Behavior of Discrete Dynamical Models
   - Examples of Logistic Growth
   - U. S. Population Models
3. Cobwebbing

Introduction

Discrete Growth Models

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  - Toxic build up

Yeast Study

1

Growing Culture of Yeast: Classic study by Carlson in 1913

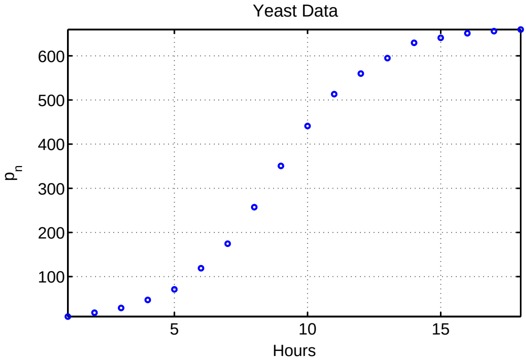
Time	Population	Time	Population	Time	Population
1	9.6	7	174.6	13	594.8
2	18.3	8	257.3	14	629.4
3	29.0	9	350.7	15	640.8
4	47.2	10	441.0	16	651.1
5	71.1	11	513.3	17	655.9
6	119.1	12	559.7	18	659.6

These data show a classic **S-shape curve**

[1] T. Carlson Über Geschwindigkeit und Grösse der Hefevermehrung in Würze. *Biochem. Z.* (1913) **57**, 313–334

Yeast Study

Carlson (1913) Yeast data: Classic **S-shape curve** with initial accelerating growth, then eventually saturation



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Discrete Dynamical Growth Model

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The population at the next time interval $(n+1)$ equals the population at the current time interval (n) plus the net growth of the current population, $G(p_n)$

Discrete Growth Models 2

Discrete Dynamical Model with Updating Function

A more general form satisfies

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  - Usually want **identity map** to find **equilibria**

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- The parameter M is called the **carrying capacity** of the population

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- Numerous applets available on the web to view behavior

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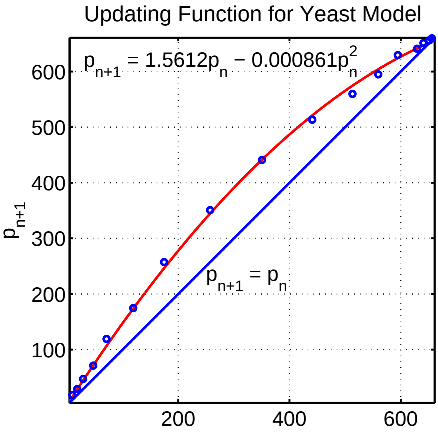
- The graph of the data is fit with the best quadratic passing through the origin

Yeast Study 2

Updating Function: Graph of best fitting **quadratic** through the origin of data, p_{n+1} vs p_n, and the identity function



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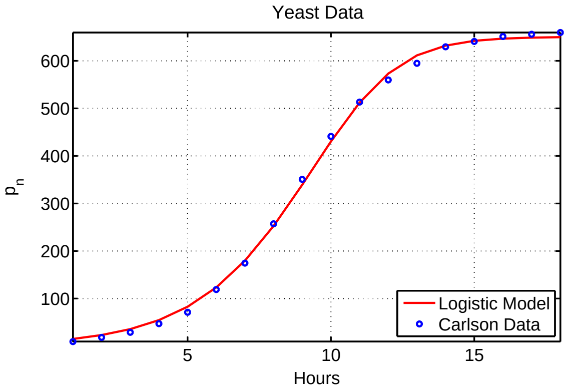
- It follows that $r = 0.5612$ and $M = 650.4$

Yeast Study 4

Simulation: The model is easily simulated and by varying the initial population to $p_1 = 15.0$, a best fit to the data is found



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- Geometrically, this is when $F(p)$ crosses the **identity map**

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- The **carrying capacity** $p_e = M$

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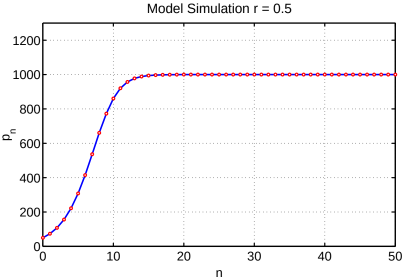
$$p_{n+1} = p_n + r p_n \left(1 - \frac{p_n}{M}\right)$$

Let $p_0 = 50$, $M = 1000$, and $r = 0.5$



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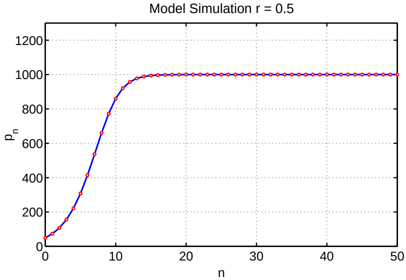

Simulation monotonically approaches carrying capacity

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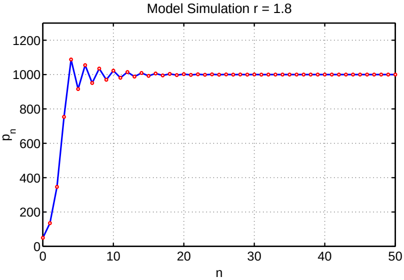

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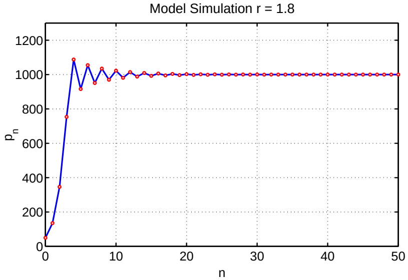

Simulation oscillates, but approaches carrying capacity

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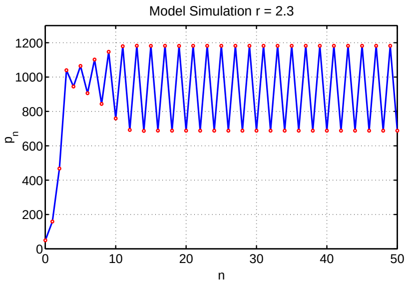

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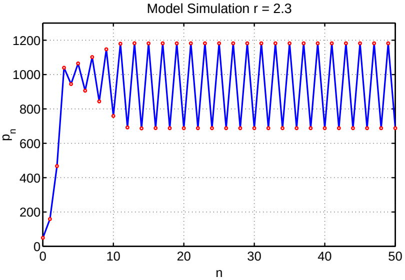

Simulation oscillates with period 2 about carrying capacity

Logistic Growth Model Simulation

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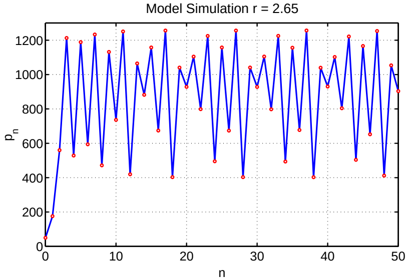

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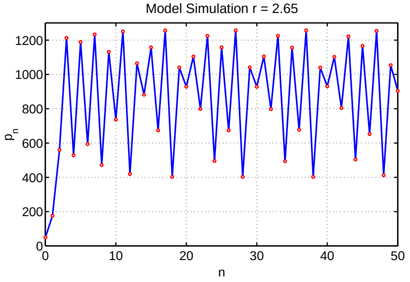

Simulation is chaotic with unpredictable results

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

- The derivative of the function $f(p)$ is valuable for determining the behavior of the discrete dynamical system near an equilibrium point

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- Evaluation of the derivative at the equilibria gives some information about the **behavior of the discrete dynamical model**

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  - Near $p_e = 0$ solutions behave like Malthusian growth

Stability of Logistic Growth Model 4

Consider the **Carrying Capacity Equilibrium**, $p_e = M$

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- There are several possible behaviors of the solution near the carrying capacity equilibrium

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  - Solutions of the discrete dynamical model oscillate about the equilibrium but move away from it
  - **The equilibrium is unstable**

Behavior of the Logistic Growth Model

Behavior of Logistic Growth Model near $p_e = M$

- If $0 < r < 1$, then the solution of the discrete logistic model **monotonically approaches the equilibrium**, $p_e = M$, which was observed for the experiment with the yeast

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- If $2 < r < 3$, then the solution of the discrete logistic model **oscillates about the equilibrium**, $p_e = M$, but the solution **grows away from** this equilibrium
- $r > 3$ results in negative solutions

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Example 1: Consider the **discrete logistic growth model**

$$p_{n+1} = f_1(p_n) = 1.3\,p_n - 0.0001\,p_n^2$$

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Solution: For the **discrete logistic growth model**

$$p_{n+1} = 1.3\, p_n - 0.0001\, p_n^2$$

the equilibria are found by substituting $p_e = p_n = p_{n+1}$

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and

$$0.3 - 0.0001\, p_e = 0 \quad \text{or} \quad p_e = 3000$$

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Solution (cont): For $f_1(p) = 1.3\,p - 0.0001\,p^2$,

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The solution monotonically grows away from this equilibrium, as expected

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At $p_e = 3000$

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The solution monotonically approaches this equilibrium

This equilibrium is **stable**

Example 1 of the Logistic Growth Model 4

Graphing the updating function

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- The p-intercepts are 0 and 13,000

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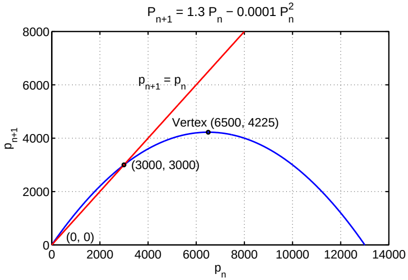

Example 1 of the Logistic Growth Model

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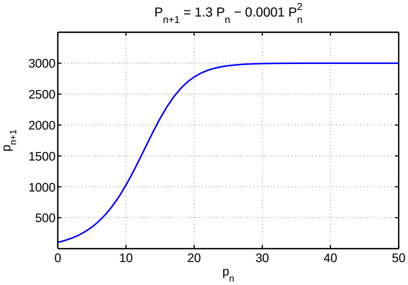
with $p_0 = 100$ for 50 iterations



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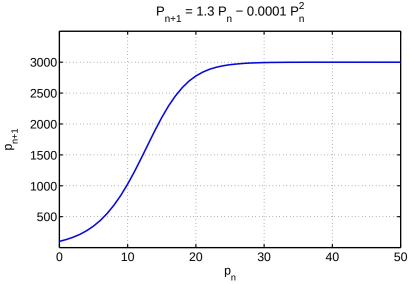

Shows classic S-curve of population growth

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and

$$1.7 - 0.0001\, p_e = 0 \quad \text{or} \quad p_e = 17,000$$

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At $p_e = 17,000$

$$f_2'(17,000) = 2.7 - 3.4 = -0.7$$

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$$f_2'(17,000) = 2.7 - 3.4 = -0.7$$

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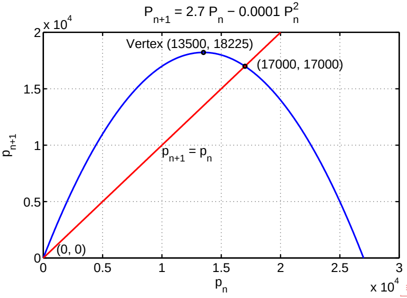

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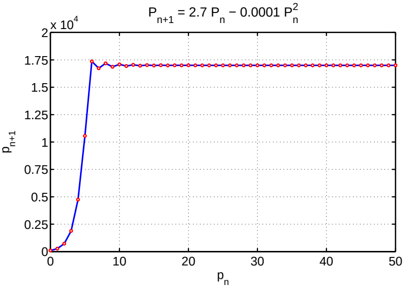

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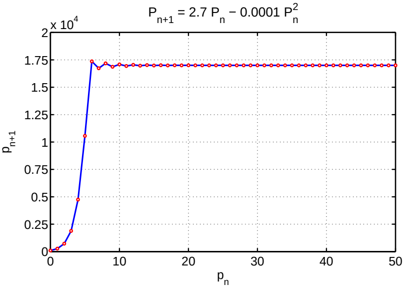

Simulation grows and overshoots the equilibrium, then oscillates toward the equilibrium

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Example 3: Consider the **discrete logistic growth model**

$$p_{n+1} = f_3(p_n) = 3.2\, p_n - 0.0001\, p_n^2$$

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the equilibria are found by substituting $p_e = p_n = p_{n+1}$

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The equilibria satisfy

$$p_e = 0$$

and

$$2.2 - 0.0001\,p_e = 0 \quad \text{or} \quad p_e = 22,000$$

Example 3 of the Logistic Growth Model 3

Solution (cont): For $f_3(p) = 3.2\,p - 0.0001\,p^2$,

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Example 3 of the Logistic Growth Model 3

Solution (cont): For $f_3(p) = 3.2\,p - 0.0001\,p^2$, the derivative satisfies

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$$f_3'(22,000) = 3.2 - 4.4 = -1.2 < -1$$

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The solution oscillates away from this equilibrium
This equilibrium is **unstable**

Example 3 of the Logistic Growth Model 4

Graphing the updating function

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Graphing the updating function

- The p-intercepts are 0 and 32,000

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Example 3 of the Logistic Growth Model 4

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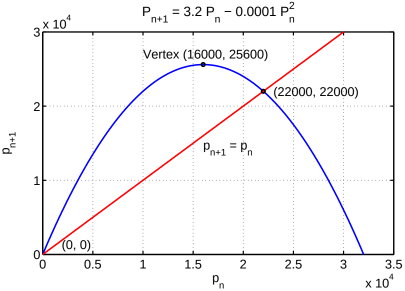
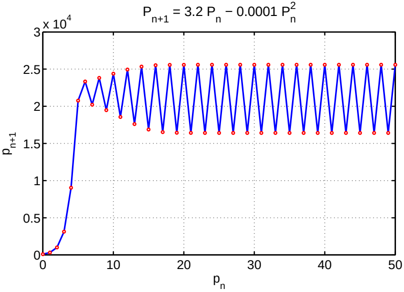


Example 3 of the Logistic Growth Model 5

Simulation of

$$p_{n+1} = 3.2\, p_n - 0.0001\, p_n$$

with $p_0 = 100$ for 50 iterations



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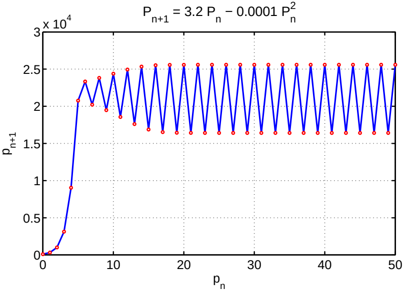

Simulation oscillates about the carrying capacity with period 2 behavior

Example 4 - Logistic Growth with Emigration 1

Logistic Growth with Emigration - Population growth may be affected by immigration or emigration

Skip Example

Consider the discrete dynamical population model

$$p_{n+1} = p_n + g(p_n) = 1.71\,p_n - 0.001\,p_n^2 - 7,$$

where n is measured in generations

Example 4 - Logistic Growth with Emigration 1

Logistic Growth with Emigration - Population growth may be affected by immigration or emigration

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- This model has a 71% growth rate per generation

Example 4 - Logistic Growth with Emigration 1

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- Logistic crowding effects are given by the term $0.001\, p_n^2$

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- This model has a 71% growth rate per generation
- Logistic crowding effects are given by the term $0.001\,p_n^2$
- 7 individuals emigrate each generation

Example 4 - Logistic Growth with Emigration 2

Logistic Growth with Emigration

$$p_{n+1} = p_n + g(p_n) = 1.71\,p_n - 0.001\,p_n^2 - 7,$$

Example 4 - Logistic Growth with Emigration 2

Logistic Growth with Emigration

$$p_{n+1} = p_n + g(p_n) = 1.71\, p_n - 0.001\, p_n^2 - 7,$$

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Example 4 - Logistic Growth with Emigration 2

Logistic Growth with Emigration

$$p_{n+1} = p_n + g(p_n) = 1.71\, p_n - 0.001\, p_n^2 - 7,$$

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- Find the p-intercepts and the vertex for $g(p)$ and graph of $g(p)$

Example 4 - Logistic Growth with Emigration 2

Logistic Growth with Emigration

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- Let $p_0 = 100$ and find the population for the next 3 generations
- Find the p-intercepts and the vertex for $g(p)$ and graph of $g(p)$
- By finding when the growth rate is zero, determine all equilibria for this model and analyze their stability

Example 4 - Logistic Growth with Emigration 3

Solution: We begin with $p_0 = 100$

$$p_1 = p_0 + g(p_0) = 100 + 0.71(100) - 0.001(100)^2 - 7 = 154,$$

Example 4 - Logistic Growth with Emigration 3

Solution: We begin with $p_0 = 100$

$$\begin{aligned} p_1 &= p_0 + g(p_0) = 100 + 0.71(100) - 0.001(100)^2 - 7 = 154, \\ p_2 &= 154 + 0.71(154) - 0.001(154)^2 - 7 = 233, \end{aligned}$$

Example 4 - Logistic Growth with Emigration 3

Solution: We begin with $p_0 = 100$

$$
\begin{aligned}
p_1 &= p_0 + g(p_0) = 100 + 0.71(100) - 0.001(100)^2 - 7 = 154, \\
p_2 &= 154 + 0.71(154) - 0.001(154)^2 - 7 = 233, \\
p_3 &= 233 + 0.71(233) - 0.001(233)^2 - 7 = 337.
\end{aligned}
$$

Example 4 - Logistic Growth with Emigration 4

Solution (cont): The growth function satisfies

$$
\begin{aligned}
g(p) &= 0.71p - 0.001p^2 - 7 \\
g(p) &= -0.001(p^2 - 710p + 7000) \\
g(p) &= -0.001(p - 10)(p - 700)
\end{aligned}
$$

Example 4 - Logistic Growth with Emigration 4

Solution (cont): The growth function satisfies

$$\begin{aligned} g(p) &= 0.71p - 0.001p^2 - 7 \\ g(p) &= -0.001(p^2 - 710p + 7000) \\ g(p) &= -0.001(p - 10)(p - 700) \end{aligned}$$

The p-intercepts are

$$p = 10 \qquad \text{or} \qquad p = 700$$

Example 4 - Logistic Growth with Emigration 4

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$$\begin{aligned} g(p) &= 0.71p - 0.001p^2 - 7 \\ g(p) &= -0.001(p^2 - 710p + 7000) \\ g(p) &= -0.001(p-10)(p-700) \end{aligned}$$

The p-intercepts are

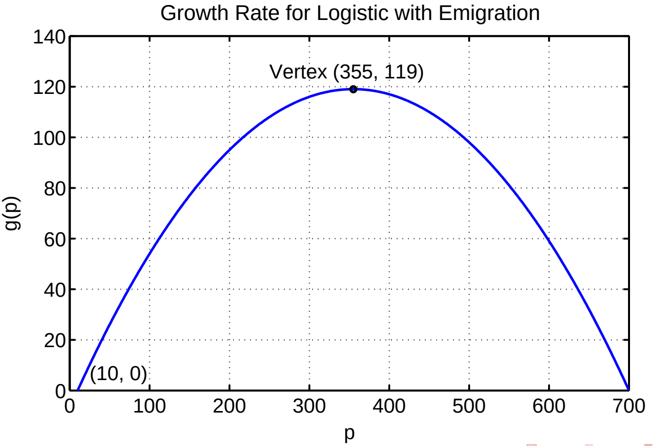
$$p = 10 \qquad \text{or} \qquad p = 700$$

The vertex satisfies $p = 355$ with

$$g(355) = -0.001(345)(-345) = 119$$

Example 4 - Logistic Growth with Emigration 5

Solution (cont): The graph of the growth function is



Example 4 - Logistic Growth with Emigration 6

Solution (cont): Equilibrium Analysis

Since the growth function $g(p)$ is zero at

$$p = 10 \qquad \text{and} \qquad p = 700,$$

these are the **equilibria**

Example 4 - Logistic Growth with Emigration 6

Solution (cont): Equilibrium Analysis

Since the growth function $g(p)$ is zero at

$$p = 10 \qquad \text{and} \qquad p = 700,$$

these are the **equilibria**

The updating function is

$$F(p) = 1.71\,p - 0.001\,p^2 - 7$$

with derivative

$$F'(p) = 1.71 - 0.002\,p$$

Example 4 - Logistic Growth with Emigration 7

Solution (cont): **Stability Analysis** With

$$F'(p) = 1.71 - 0.002\,p$$

Example 4 - Logistic Growth with Emigration

Solution (cont): Stability Analysis With

$$F'(p) = 1.71 - 0.002\,p$$

At $p = 10$,

$$F'(10) = 1.69 > 1$$

Example 4 - Logistic Growth with Emigration 7

Solution (cont): **Stability Analysis** With

$$F'(p) = 1.71 - 0.002\,p$$

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so this equilibrium is **monotonically unstable (solutions growing away)**

Example 4 - Logistic Growth with Emigration

Solution (cont): Stability Analysis With

$$F'(p) = 1.71 - 0.002\,p$$

At $p = 10$,

$$F'(10) = 1.69 > 1$$

so this equilibrium is **monotonically unstable (solutions growing away)**

At $p = 700$,

$$F'(700) = 0.31 < 1$$

Example 4 - Logistic Growth with Emigration 7

Solution (cont): Stability Analysis With

$$F'(p) = 1.71 - 0.002\,p$$

At $p = 10$,

$$F'(10) = 1.69 > 1$$

so this equilibrium is **monotonically unstable (solutions growing away)**

At $p = 700$,

$$F'(700) = 0.31 < 1$$

so this equilibrium is **monotonically stable (solutions moving toward)**

Example 5 - U. S. Census with 3 Growth Models 1

U. S. Census with Logistic Growth Model - This example uses the census data from 1790 to 2000 to compare 3 models

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U. S. Census with Logistic Growth Model - This example uses the census data from 1790 to 2000 to compare 3 models

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- Malthusian growth model

$$P_{n+1} = 1.1524\,P_n$$

Example 5 - U. S. Census with 3 Growth Models 1

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$$P_{n+1} = (1.3768 - 0.01473\, n)P_n$$

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$$P_{n+1} = f(P_n) = P_n + 0.2334\, P_n \left(1 - \frac{P_n}{411.1}\right)$$

Example 5 - U. S. Census with 3 Growth Models 2

Malthusian growth model

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Example 5 - U. S. Census with 3 Growth Models 2

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- Least squares best fit to census data

$$P_n = P_0(1+r)^n = 15.05(1.1524)^n$$

Example 5 - U. S. Census with 3 Growth Models 2

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  - The P_0 is quite high and growth only matches growth near beginning of 20^{th} century

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  - The sum of square errors is 2248
  - The P_0 is quite high and growth only matches growth near beginning of 20^{th} century
- Malthusian model isn't expected to work well over long periods of time

Example 5 - U. S. Census with 3 Growth Models 3

Nonautonomous growth model

$$P_{n+1} = (1 + k(t_n))P_n \quad \text{with} \quad P_0$$

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$$k(t_n) = 0.3768 - 0.01473\,n$$

Example 5 - U. S. Census with 3 Growth Models 3

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  - The P_0 is very close to actual 1790 census

Example 5 - U. S. Census with 3 Growth Models 3

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- Least squares best fit to census data had $P_0 = 3.77$ M
  - The sum of square errors is 543
  - The P_0 is very close to actual 1790 census
- This model matches the census quite well, but model difficult to analyze mathematically

Example 5 - U. S. Census with 3 Growth Models 4

Logistic growth model

$$P_{n+1} = P_n + rP_n\left(1 - \frac{P_n}{M}\right) \quad \text{with} \quad P_0$$

Example 5 - U. S. Census with 3 Growth Models 4

Logistic growth model

$$P_{n+1} = P_n + rP_n\left(1 - \frac{P_n}{M}\right) \quad \text{with} \quad P_0$$

- Least squares best fit to census data

$$P_{n+1} = P_n + 0.2334\,P_n\left(1 - \frac{P_n}{411.1}\right)$$

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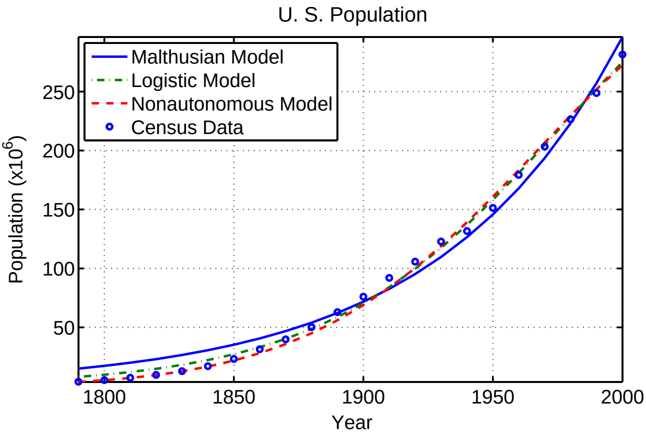
- This gives a growth rate of $r = 0.2334$ and carrying capacity of $M = 411.1$ with the best $P_0 = 8.04$
  - The sum of square errors is 479
  - The P_0 is high at 8.04 M
- This model matches the census data best of the 3 models

Example 5 - U. S. Census with 3 Growth Models 5

Graph of the 3 models and U. S. census data



Example 5 - U. S. Census with 3 Growth Models 6

Logistic Updating Function

- Direct fitting of the logistic time series to data can be numerically unstable

Example 5 - U. S. Census with 3 Growth Models 6

Logistic Updating Function

- Direct fitting of the logistic time series to data can be numerically unstable
- Finding the quadratic updating function uses stable numerical routines

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- By plotting P_{n+1} versus P_n, one can see how the data compares to the updating function for the logistic growth model

Example 5 - U. S. Census with 3 Growth Models 6

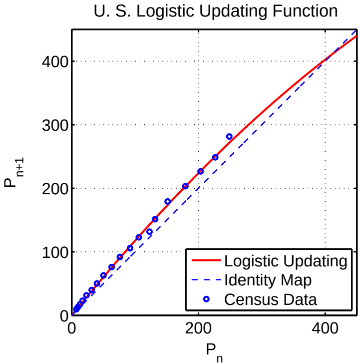
Logistic Updating Function

- Direct fitting of the logistic time series to data can be numerically unstable
- Finding the quadratic updating function uses stable numerical routines
- By plotting P_{n+1} versus P_n, one can see how the data compares to the updating function for the logistic growth model
- Find P_n and P_{n+1} by taking successive pairs of census data

Example 5 - U. S. Census with 3 Growth Models

Graph of the Logistic Updating function

Graph shows U. S. census data, quadratic for logistic model, and identity map



Example 5 - U. S. Census with 3 Growth Models 8

Logistic Updating function for U. S. census data

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Example 5 - U. S. Census with 3 Growth Models 8

Logistic Updating function for U. S. census data

- The logistic updating function very closely follows the census data except at a couple of points
- The equilibria occur at the intersection of the updating function and the identity map
- The slope of the updating function at a point of intersection determines the stability of that equilibrium

Example 5 - U. S. Census with 3 Growth Models

Logistic Updating function for U. S. census data

$$f(P_n) = P_n + 0.2334\, P_n \left(1 - \frac{P_n}{411.1}\right) = 1.2334\, P_n - 0.00056775\, P_n^2$$

Example 5 - U. S. Census with 3 Growth Models

Logistic Updating function for U. S. census data

$$f(P_n) = P_n + 0.2334\, P_n \left(1 - \frac{P_n}{411.1}\right) = 1.2334\, P_n - 0.00056775\, P_n^2$$

The **equilibria** satisfy

$$P_e = P_e + 0.2334\, P_e \left(1 - \frac{P_e}{411.1}\right)$$

Example 5 - U. S. Census with 3 Growth Models

Logistic Updating function for U. S. census data

$$f(P_n) = P_n + 0.2334\, P_n \left(1 - \frac{P_n}{411.1}\right) = 1.2334\, P_n - 0.00056775\, P_n^2$$

The **equilibria** satisfy

$$\begin{aligned} P_e &= P_e + 0.2334\, P_e \left(1 - \frac{P_e}{411.1}\right) \\ 0 &= 0.2334\, P_e \left(1 - \frac{P_e}{411.1}\right) \end{aligned}$$

Example 5 - U. S. Census with 3 Growth Models 9

Logistic Updating function for U. S. census data

$$f(P_n) = P_n + 0.2334\,P_n\left(1 - \frac{P_n}{411.1}\right) = 1.2334\,P_n - 0.00056775\,P_n^2$$

The **equilibria** satisfy

$$\begin{aligned} P_e &= P_e + 0.2334\,P_e\left(1 - \frac{P_e}{411.1}\right) \\ 0 &= 0.2334\,P_e\left(1 - \frac{P_e}{411.1}\right) \end{aligned}$$

The equilibria are

$$P_e = 0 \qquad \text{and} \qquad P_e = 411.1$$

Example 5 - U. S. Census with 3 Growth Models 10

Updating Function

$$f(P) = 1.2334\,P - 0.00056775\,P^2$$

Example 5 - U. S. Census with 3 Growth Models 10

Updating Function

$$f(P) = 1.2334\,P - 0.00056775\,P^2$$

The **derivative of the updating function** is

$$f'(P) = 1.2334 - 0.0011355\,P$$

Example 5 - U. S. Census with 3 Growth Models 10

Updating Function

$$f(P) = 1.2334\,P - 0.00056775\,P^2$$

The **derivative of the updating function** is

$$f\,'(P) = 1.2334 - 0.0011355\,P$$

At the equilibrium, $P_e = 0$,

$$f\,'(0) = 1.2334 > 1$$

Example 5 - U. S. Census with 3 Growth Models 10

Updating Function

$$f(P) = 1.2334\,P - 0.00056775\,P^2$$

The **derivative of the updating function** is

$$f'(P) = 1.2334 - 0.0011355\,P$$

At the equilibrium, $P_e = 0$,

$$f'(0) = 1.2334 > 1$$

This equilibrium is **unstable** with solutions monotonically moving away

Example 5 - U. S. Census with 3 Growth Models 11

Since the **derivative of the updating function** is

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Example 5 - U. S. Census with 3 Growth Models 11

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$$f'(P) = 1.2334 - 0.0011355\,P$$

At the equilibrium, $P_e = 411.1$,

$$f'(411.1) = 0.7666 < 1$$

Example 5 - U. S. Census with 3 Growth Models

Since the **derivative of the updating function** is

$$f'(P) = 1.2334 - 0.0011355\,P$$

At the equilibrium, $P_e = 411.1$,

$$f'(411.1) = 0.7666 < 1$$

This equilibrium is **stable** with solutions monotonically approaching the **carrying capacity**

Example 5 - U. S. Census with 3 Growth Models 12

Summary: Future Projections

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- The Malthusian growth model is simple but simulates poorly for the entire history of the U. S.

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Example 5 - U. S. Census with 3 Growth Models 12

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Consider the **discrete dynamical model**

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

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Create a graph with the variable p_{n+1} on the vertical axis and p_n on the horizontal axis

Draw the graph of the **updating function**, $f(p_n)$ and the **identity map**

$$p_{n+1} = f(p_n) \qquad \text{and} \qquad p_{n+1} = p_n$$

Cobwebbing 2

Graphically, any intersection of the **updating function** and the **identity map**

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produces an equilibrium

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- Go vertically to $f(p_1)$ to find p_2
- The process is repeated to give a geometric interpretation of the dynamics of the discrete model

Cobwebbing – Breathing Model Example

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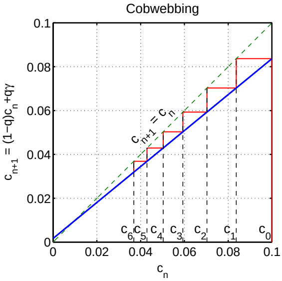
The model for a normal subject breathing an air mixture enriched with Ar satisfies the model

$$c_{n+1} = (1-q)c_n + q\gamma = 0.82\, c_n + 0.0017$$

Below reviews the cobwebbing process for this example



Cobwebbing – Quadratic Example 1

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    using a few steps of cobwebbing
  - This example has equilibria at 0 and $\frac{2}{3}$, the latter being between stable and unstable and oscillatory

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