Calculus for the Life Sciences

Lecture Notes – Nonlinear Dynamical Systems: Part 1 – Logistic Growth

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Outline

Introduction

Discrete Growth Models

- The Discrete Malthusian growth model shows exponential growth
- Most animal populations grow exponentially soon after settling
- With population growth, crowding pressure decreases the growth rate
  - Space and resource limitation
  - Toxic build up

Yeast Study [1]

Growing Culture of Yeast: Classic study by Carlson in 1913

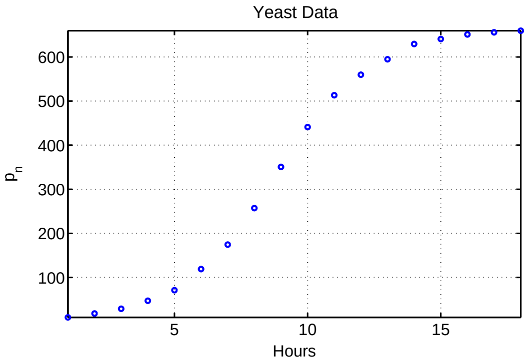
Time	Population	Time	Population	Time	Population
1	9.6	7	174.6	13	594.8
2	18.3	8	257.3	14	629.4
3	29.0	9	350.7	15	640.8
4	47.2	10	441.0	16	651.1
5	71.1	11	513.3	17	655.9
6	119.1	12	559.7	18	659.6

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



Discrete Growth Models 1

Discrete Dynamical Growth Model

There are two standard forms for **discrete population models**

One form uses a **growth function**, $G(p_n)$

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

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

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

- An **iterative map** – the population at the $(n+1)^{st}$ generation depends on the population at the n^{th} generation
- The function $F(p)$ is called the **updating function**
- The graph of the updating function
  - The $(n+1)^{st}$ generation is on the vertical axis
  - The n^{th} generation is on the horizontal axis
  - Usually want **identity map** to find **equilibria**

Logistic Growth Model

Logistic Growth Model

- Malthusian growth uses a linear updating function and grows exponentially without bound
- Most populations have a decreasing growth rate due to crowding effects
- This is the **Logistic Growth model**

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

- This equation has the Malthusian growth model with the additional term $-rp_n^2/M$
- The parameter M is called the **carrying capacity** of the population

Logistic Growth Model 2

Behavior of the Logistic Growth Model

- The Logistic growth model shows complicated dynamics – shown by ecologist May (1974)
- There is **no exact solution** to this discrete dynamical system
- Given the **Logistic Growth model**

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

  - There are **equilibria** at 0 and M
  - The parameter r has restricted values ($r < 3$) with more complex behavior for higher values of r

Yeast Study

Logistic Growth Model for Carlson Yeast Study

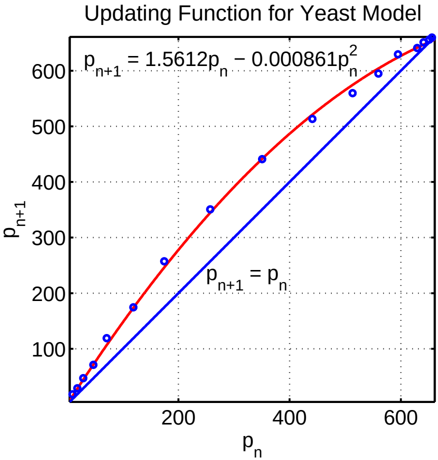
- **Logistic Growth model** has form

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

- Use successive data values to obtain p_{n+1} and p_n
- The first two points are $(9.6, 18.3)$ and $(18.3, 29.0)$ with others found similarly
- The graph of the data is fit with the best quadratic passing through the origin

Yeast Study

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



Yeast Study 3

- Recall the **logistic growth model** has the form

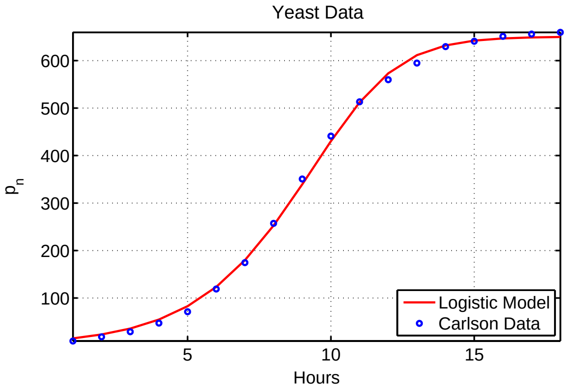
$$p_{n+1} = p_n + rp_n\left(1 - \frac{p_n}{M}\right)$$

- The best fitting model to the yeast data is

$$p_{n+1} = 1.5612\,p_n - 0.000861\,p_n^2 = p_n + 0.5612\,p_n\left(1 - \frac{p_n}{650.4}\right)$$

Yeast Study

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



Equilibria

Consider the **general discrete dynamical model:**

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

Study the **qualitative behavior of discrete dynamical equations**

- The **first step in any analysis** is finding **equilibria**
- This is simply an **algebraic equation**
- An equilibrium point of a discrete dynamical system is where there is no change in the variable from one iteration to the next
- Mathematically, $p_e = F(p_e)$
- Geometrically, this is when $F(p)$ crosses the **identity map**

Equilibria for Logistic Growth Model

Consider the **logistic growth model:**

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

If $r > 0$, then equilibria satisfy

$$\begin{aligned} p_e &= p_e + rp_e\left(1 - \frac{p_e}{M}\right) \\ rp_e\left(1 - \frac{p_e}{M}\right) &= 0 \end{aligned}$$

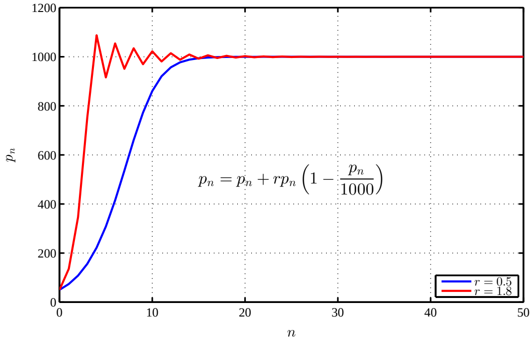
Thus, $p_e = 0$ or $p_e = M$

The equilibria for the Logistic growth model are either

- The **trivial solution** $p_e = 0$ (no population) or
- The **carrying capacity** $p_e = M$

Logistic Growth Model Simulation 1

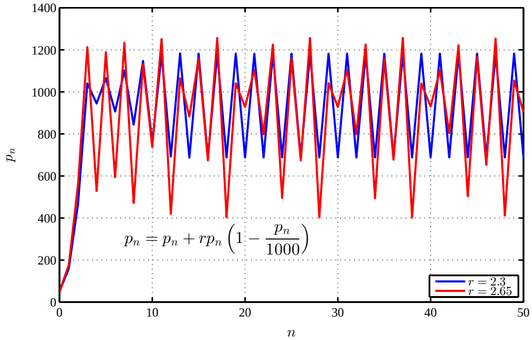
Simulation of the **logistic growth model**



- Simulation for $r = 0.5$ monotonically approaches carrying capacity
- Simulation for $r = 1.8$ oscillates and approaches carrying capacity

Logistic Growth Model Simulation 2

Simulation of the **logistic growth model**



- Simulation for $r = 2.3$ oscillates about equilibrium (Period 2)
- Simulation for $r = 2.65$ oscillates chaotically about equilibrium

Stability of Logistic Growth Model 1

Stability of Logistic Growth Model

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

- **Equilibria** are easy to find, but **behavior** of the model varies dramatically as shown by simulations above
- The **derivative** of the **updating function** $f(p)$ finds local behavior of the discrete dynamical system near an equilibrium point

Stability of Logistic Growth Model 2

Consider the **Trivial Equilibrium**, $p_e = 0$

- Since $f(p) = p + r\,p(1 - p/M)$, the **derivative** is

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

- At $p_e = 0$, the derivative satisfies

$$f'(0) = 1 + r$$

  - r positive implies solutions growing away from $p_e = 0$
  - When the population is small, there are plenty of resources and the population grows (**exponentially**)
  - Near $p_e = 0$ solutions behave like **Malthusian growth**

Stability of Logistic Growth Model 3

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

- Since the **derivative** is

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

- At $p_e = M$, the derivative satisfies

$$f'(M) = 1 - r$$

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

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**

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
- If $1 < r < 2$, then the solution of the discrete logistic model **oscillates about the equilibrium**, $p_e = M$, but the solution **asymptotically approaches** this equilibrium
- 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 of the Logistic Growth Model 1

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

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

We examine this model for $r = 0.5$, 1.5, and 2.3

- Find all the equilibria for this model
- Determine the behavior of the solution near these equilibria
- Sketch a graph of the updating function and the identity map $p_{n+1} = p_n$
- Simulate the model, starting $p_0 = 50$ for 50 iterations

Example of the Logistic Growth Model 2

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

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

the equilibria are $p_e = 0$ (**extinction**) and $p_e = 1000$ (**carrying capacity**)

Stability Analysis requires the derivative

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

Since $F'(0) = 1 + r > 1$, it follows that $p_e = 0$ is an **unstable** equilibrium with solutions **monotonically growing away**

Example of the Logistic Growth Model 3

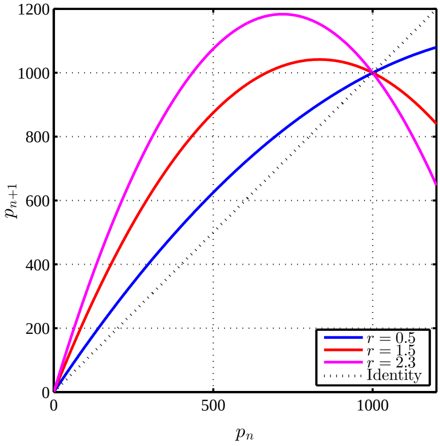
At the **carrying capacity equilibrium**, $p_e = 1000$ the derivative satisfies:

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

- When $r = 0.5$, then $F'(1000) = 0.5$.
  - $p_e = 1000$ is a **stable** equilibrium with solutions **monotonically approaching** it
- When $r = 1.5$, then $F'(1000) = -0.5$.
  - $p_e = 1000$ 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**

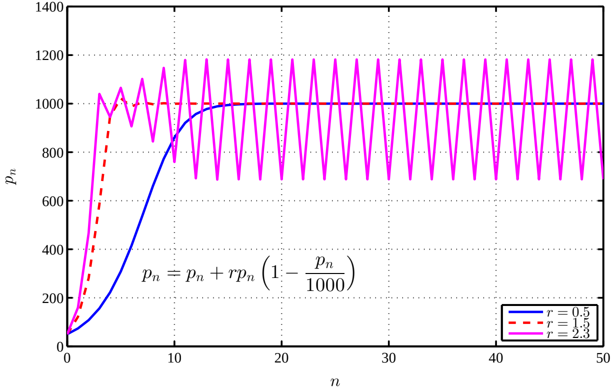
Example of the Logistic Growth Model 4

Graphing the updating function



Example of the Logistic Growth Model 5

Simulation of the Logistic growth model



Shows **classic S-curve** of population growth

U. S. Census with 3 Growth Models 1

U. S. Census with 3 Models - Models simulated with the census data from 1790 to 2010 and parameters fit

- Malthusian growth model

$$P_{n+1} = 1.1460\, P_n, \qquad P_0 = 16.35$$

- Nonautonomous growth model with n in decades after 1790

$$P_{n+1} = (1.2960 - 0.009672\, n) P_n, \qquad P_0 = 6.307$$

- Logistic growth model

$$P_{n+1} = f(P_n) = P_n + 0.2244\, P_n \left(1 - \frac{P_n}{451.8}\right), \qquad P_0 = 8.576$$

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U. S. Census with 3 Growth Models 2

Malthusian growth model

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

- Least squares best fit to census data

$$P_n = P_0(1+r)^n = 16.35(1.1460)^n$$

- The average growth over U. S. census history is $r = 0.1460$ per decade with best $P_0 = 16.35$ M
  - The sum of square errors is 2875.5
  - 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

U. S. Census with 3 Growth Models 3

Nonautonomous growth model

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

- Best least squares fit to census over U. S. history is

$$P_{n+1} = (1.2960 + 0.009672\, n)P_n \quad \text{with} \quad P_0 = 6.307$$

- This assumes a linear growth starting around 30% per decade and declining about 1% per decade
- Sum of square errors is 326.8 with P_0 being high
- This model matches the census quite well, but model difficult to analyze mathematically

U. S. Census with 3 Growth Models 4

Logistic growth model

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

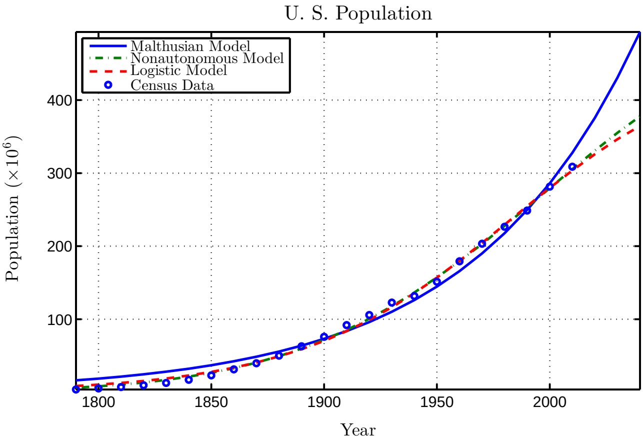
- Least squares best fit to census data

$$P_{n+1} = P_n + 0.2244\,P_n\left(1 - \frac{P_n}{451.8}\right) \quad P_0 = 8.576$$

- The growth rate is $r = 0.2244$, and carrying capacity is $M = 451.8$
- The sum of square errors is 557.4 with P_0 being high
- This model matches the census data only slightly worse than the nonautonomous model, but easier to analyze

U. S. Census with 3 Growth Models 5

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



U. S. Census with 3 Growth Models 6

Logistic Updating Function

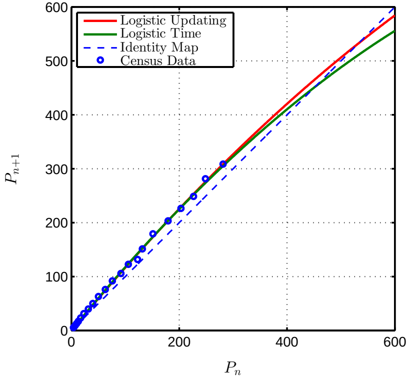
- Direct fitting of the logistic time series to data can be numerically unstable
- Finding the quadratic updating function uses stable numerical routines
- Find P_n and P_{n+1} by taking successive pairs of census data
- This fit differs from direct time series with

$$P_{n+1} = P_n + 0.2047\,P_n\left(1 - \frac{P_n}{532.6}\right)$$

U. S. Census with 3 Growth Models

Graph of the Logistic Updating function

Graph shows U. S. census data, quadratic for best updating, quadratic for best time series, and identity map



U. S. Census with 3 Growth Models

Logistic Updating function for U. S. census data

- Both logistic updating functions follow the census data very closely
- The equilibria occur at the intersections of the updating functions and the identity map
  - Fitting the time series gave $P_e = 0$ and 451.8
  - Fitting the updating function gave $P_e = 0$ and 532.6
- The slope of the updating function at a point of intersection determines the stability of that equilibrium
  - With $f'(0) > 1$, both models have $P_e = 0$ as **Monotonic Unstable**
  - With $0 < f'(M) < 1$, both models have $P_e = M$ as **Monotonic Stable**

U. S. Census with 3 Growth Models

Summary: Future Projections

- The Malthusian growth model is simple but simulates poorly for the entire history of the U. S.
- Nonautonomous growth model
  - Tracks poorly at first (poor P_0), but only a few percent error over the last few decades
  - Model fails to account for high recent immigration and higher birth rates in immigrant communities
  - Model predicts population increases to a maximum near 450 M around 2100, then declines
- Logistic growth model
  - Tracks poorly at first (poor P_0), but only a few percent error over the last few decades
  - Model predicts population increases to carrying capacity of 451.8 M, asymptotically (using smallest SSE)

Cobwebbing 1

Consider the **discrete dynamical model**

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

In the **Linear Discrete Dynamical Model section**, we showed a graphical method to view the local dynamics of this model called **cobwebbing**

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**

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

produces an equilibrium

- The process of **cobwebbing** shows the dynamics of this discrete dynamical model
- Start at some point p_0 on the horizontal axis, then go vertically to $f(p_0)$ to find p_1
- Next go horizontally to the line $p_{n+1} = p_n$
- 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

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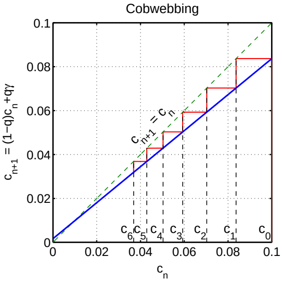
Cobwebbing – Breathing Model Example

Cobwebbing – Breathing Model Example

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

Cobwebbing – Quadratic Example

- Breathing model has a simple **linear updating function**
  - Unique equilibrium
  - Monotonic dynamics
- **Quadratic updating function** allows complicated dynamics
  - Logistic growth model is a quadratic dynamical model
  - Have observed monotonic, oscillatory, and chaotic dynamics
  - Show oscillatory dynamics for

$$p_{n+1} = 3\,p_n(1 - p_n)$$

    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

Cobwebbing – Quadratic Example

Cobwebbing – Quadratic Example