Math 636 - Mathematical Modeling

Continuous Models
Logistic and Malthusian Growth

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Outline

Introduction

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- Studied ***discrete dynamical population models***
  - Have the potential to have chaotic dynamics
  - ***Closed form solutions*** are very limited
  - Qualitative analysis gave limited results
- Extend models to ***continuous domain*** – ODEs
  - Differential equations often easier to analyze
  - Allows examining populations without discrete sampling
  - Qualitative analysis shows solutions are better behaved
- Begin examining two yeast species competing for a limited resource (nutrient)

Yeast and Brewing

Competition Model: Competition is ubiquitous in ecological studies and many other fields

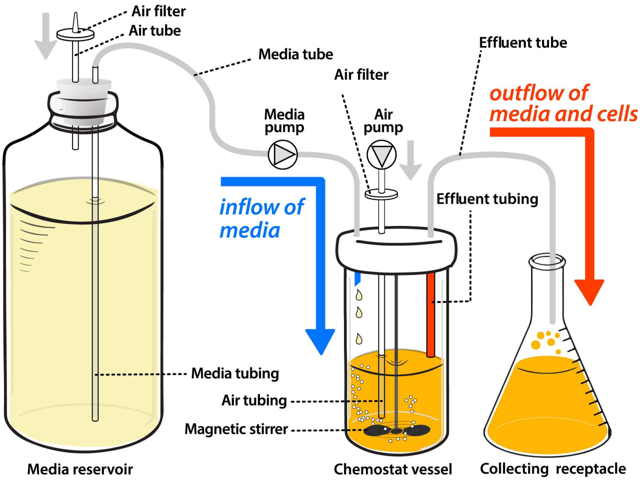
- Craft beer is a very important part of the San Diego economy
- Researchers at UCSD created a company that provides brewers with one of the best selections of diverse cultures of different strains of the yeast, *Saccharomyces cerevisiae*
- Different strains are cultivated for particular flavors
- Often *S. cerevisiae* is maintained in a continuous chemostat for constant quality - large beer manufacturers
- Large cultures can become contaminated with other species of yeast
- It can be very expensive to start a new pure culture

Chemostat Models

Chemostat Models

- A ***chemostat*** is a controlled bioreactor
  - Fresh medium (nutrient) is added continuously
  - A desired microbial culture is maintained in a static environment
  - Bioreactor has culture, nutrients, metabolic end products, and waste
  - The culture volume is maintained by removing microrganisms, end products, etc. at the same rate as nutrients enter
- Brewer's Yeast
  - Large breweries want to maintain consistent product
  - Grow their particular strain of brewer's yeast in chemostat
  - Without contamination and constant nutrient, the yeast culture exits the chemostat at a reliable concentration (***carrying capacity***)
- Hard to keep a particular culture free from contamination from bacteria and other yeast species

Diagram of Chemostat



Yeast Experiments

Yeast Experiments

- G. F. Gause[1,2] ran experiments on ***yeast cultures***
  - Rather than a chemostat, changed nutrient every 3 hours
  - Used standard brewers yeast, *Saccharomyces cerevisiae*
  - Another experiment uses a common contaminant, a slower growing yeast, *Schizosaccharomyces kephir*
  - A third experiment combined cultures to examine ***competition*** between the species
- Two repetitions were done of each experiment, and data are combined and shifted to match described conditions
- The volume measured were marks on a test tube from centrifuge and not standard units

[1] G. F. Gause, Struggle for Existence, Hafner, New York, 1934

[2] G. F. Gause (1932), Experimental studies on the struggle for existence. I. Mixed populations of two species of yeast, J. Exp. Biol. 9, p. 389

Monoculture Yeast Experiments

Monoculture Yeast Experiments

Single species culture for ***Saccharomyces cerevisiae***

Time (hr)	Volume	Time (hr)	Volume	Time (hr)	Volume
0	0.37	18	10.97	38	12.77
1.5	1.63	23	12.5	42	12.87
9	6.2	25.5	12.6	45.5	12.9
10	8.87	27	12.9	47	12.7
18	10.66	34	13.27		

Single species culture for ***Schizosaccharomyces kephir***

Time (hr)	Volume	Time (hr)	Volume	Time (hr)	Volume
9	1.27	42	2.73	87	5.67
10	1	45.5	4.56	111	5.8
23	1.7	66	4.87	135	5.83
25.5	2.33				

The much slower growing ***Schizosaccharomyces kephir*** required much longer to approach the ***carrying capacity***.

Mixed Culture Yeast Experiments

Mixed Culture Yeast Experiments

This experiment examines the competition of **2** yeast species competing for the same resource.

Time (hr)	0	1.5	9	10	18	18	23
Vol (*S. cerevisiae*)	0.375	0.92	3.08	3.99	4.69	5.78	6.15
Vol (*S. kephir*)	0.29	0.37	0.63	0.98	1.47	1.22	1.46
Time (hr)	25.5	27	38	42	45.5	47	
Vol (*S. cerevisiae*)	9.91	9.47	10.57	7.27	9.88	8.3	
Vol (*S. kephir*)	1.11	1.225	1.1	1.71	0.96	1.84	

The data show the populations increasing, but do these populations move toward an equilibrium or does something else happen with the populations?

What techniques do we have to fit models to the data?

Malthusian Growth Model

Malthusian Growth Model: The ***discrete Malthusian growth model*** has the form:

$$P_{n+1} = (1+r)P_n,$$

where P_n is the population at time n and r is the per capita growth rate.

We want change this model into a ***continuous model***.

Let $P_n \equiv P(t)$ and assume a time step of Δt, so $P_{n+1} \equiv P(t+\Delta t)$.

Assume that r is the per capita growth rate per unit time, then the ***discrete model*** becomes:

$$P(t+\Delta t) = (1 + r\Delta t)P(t).$$

This can be rearrranged to give

$$P(t+\Delta t) - P(t) = r\Delta t P(t) \qquad \text{or} \qquad \frac{P(t+\Delta t) - P(t)}{\Delta t} = rP(t).$$

Continuous Growth Model

Continuous Growth Model: The ***discrete Malthusian growth model*** was rearranged to give:

$$P(t + \Delta t) - P(t) = r\Delta t P(t),$$

so consider the limiting case as $\Delta t \to 0$,

$$\lim_{\Delta t \to 0} \frac{P(t + \Delta t) - P(t)}{\Delta t} = rP(t).$$

The left hand side is the definition of the derivative, so this equation becomes:

$$\frac{dP}{dt} = rP(t), \qquad P(0) = P_0,$$

which is the ***continuous Malthusian growth model***.

This is a ***first order linear differential equation***.

Malthusian Growth Model

Malthusian Growth Model: The ***continuous Malthusian growth model***:

$$\frac{dP}{dt} = rP(t), \qquad P(0) = P_0,$$

has the solution:

$$P(t) = P_0 e^{rt}.$$

The early stages of the yeast cultures both show this exponential growth.

How might we match this model to the first 10 hours (4 data points) of the growing culture of *Saccharomyces cerevisiae*?

There are multiple methods for fitting this model to these data.

Fitting the Malthusian Growth Model 1

The **Malthusian growth model** is given by:

$$P(t) = P_0 e^{rt},$$

and we want to fit the data (t_i, P_i):

$$(0, 0.37), \quad (1.5, 1.63), \quad (9, 6.2), \quad \text{and} \quad (10, 8.87).$$

If we are simply fitting these data to obtain an estimate on the value of r, then an algebraic fit through the first and third points is sufficient with $P_0 = 0.37$ and

$$P(9) = 0.37 e^{9r} = 6.2 \qquad \text{or} \qquad r = \ln(16.76)/9 = 0.3132,$$

which gives:

$$P(t) = 0.37 e^{0.3132t}.$$

Fitting the Malthusian Growth Model

The **Malthusian growth model**, $P(t) = P_0 e^{rt}$, is fit through the data (t_i, P_i): (0, 0.37), (1.5, 1.63), (9, 6.2), and (10, 8.87).

Frequently, ***exponential models*** are fit with the ***linear least squares best fit to the logarithm of data***:

$$\ln(P(t)) = \ln(P_0) + rt,$$

which has ***slope***, r, and ***intercept***, $\ln(P_0)$.

The ***linear least squares best fit to the logarithm of data*** gives the equation:

$$\ln(P(t)) = 0.2690\, t - 0.5034,$$

which gives the ***best continuous Malthusian growth model***,

$$P(t) = 0.6045\, e^{0.2690\, t}.$$

Fitting the Malthusian Growth Model

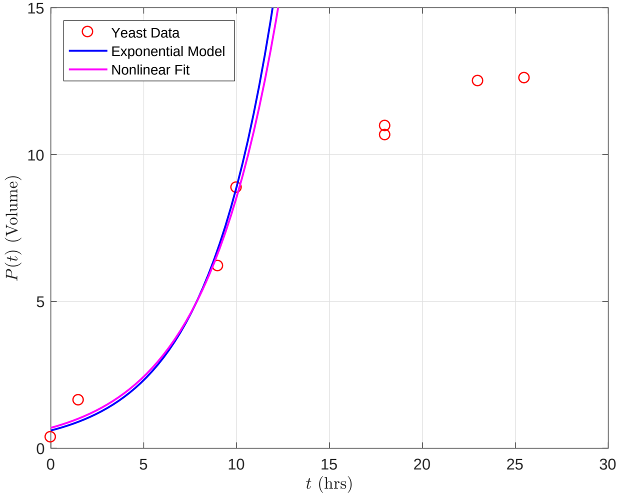
Alternately, the **Malthusian growth model**, $P(t) = P_0 e^{rt}$, is fit through the data (t_i, P_i): $(0, 0.37)$, $(1.5, 1.63)$, $(9, 6.2)$, and $(10, 8.87)$, using a ***nonlinear least squares best fit to the data***.

The ***nonlinear least squares best fit to the data*** gives the ***best continuous Malthusian growth model***,

$$P(t) = 0.6949\, e^{0.2511\, t}.$$

```
function J = yst_lstm(p, tdata, pdata)
% Least Squares fit to Logistic Growth
N = length(tdata);
yst = p(1)*exp(p(2)*tdata);
err = pdata - yst;
J = err*err'; % Sum of square errors
end
```

Fitting the Malthusian Growth Model



Logistic Growth Model

These models fit the initial data reasonably well, but are inadequate for describing the complete set of data.

- The data show a leveling off of the populations, so different models are required.
- The experiments supply a fixed amount of nutrient, so maximum population is limited.
- The ***Malthusian growth model*** simulates the early exponential growth of populations, but suppression of growth later in time is required to fit the data.
- The two data sets, ***S. cerevisiae*** and ***S. kephir***, show significantly different ***growth rates*** and ***carrying capacity***.

Logistic Growth Model

The general ***continuous growth model*** satisfies the ***differential equation***:

$$\frac{dP}{dt} = f(t, P(t)).$$

However, yeast populations should not depend on time, so the appropriate model is:

$$\frac{dP}{dt} = f(P(t)).$$

The ***Malthusian growth model*** is:

$$\frac{dP}{dt} = rP(t),$$

which has $f(P) = rP$, a linear function of P, giving the exponential growth for a solution.

Logistic Growth Model

The Maclaurin series expansion of $f(P)$ is

$$f(P) = f(0) + f'(0)P + \frac{f''(0)}{2!}P^2 + \mathcal{O}\left(P^3\right),$$

where $\mathcal{O}\left(P^3\right)$ means order P^3.

The yeast (chemostat) problem is a closed system, so when the population is at ***extinction*** or **0**, which implies:

$$f(0) = 0.$$

The ***linear term*** comes from the ***Malthusian growth***, so

$$f'(0) = r.$$

Logistic Growth Model

The population growth rate declines for larger populations, so we expect the next term in the series expansion must be negative.

In biology, this is known as ***intraspecies competition***.

Mathematically, this implies:

$$\frac{f''(0)}{2!} = -\frac{r}{M},$$

where r is from the Malthusian growth and as we'll see later M is the ***carrying capacity***.

Ignoring the higher order terms of $f(p)$ gives the ***logistic growth model***:

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{M}\right), \qquad P(0) = P_0.$$

Logistic Growth Model Solution 1

The ***logistic growth model***:

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{M}\right), \qquad P(0) = P_0,$$

can be solved using separation of variables.

Alternately, we can use Bernoulli's method. Consider

$$\frac{dP}{dt} - rP = -\frac{rP^2}{M}, \qquad \text{and let} \qquad u = P^{-1},$$

then $\frac{du}{dt} = -P^{-2}\frac{dP}{dt}$.

If we multiply the equation above by $-P^{-2}$, then

$$-P^{-2}\frac{dP}{dt} + rP^{-1} = \frac{r}{M}, \qquad \text{so} \qquad \frac{du}{dt} + ru = \frac{r}{M}.$$

The u equation is rewritten:

$$\frac{d}{dt}\left(e^{rt}u\right) = \frac{re^{rt}}{M}.$$

Logistic Growth Model Solution 2

The u equation is solved by integration, so :

$$\frac{d}{dt}\left(e^{rt}u\right) = \frac{re^{rt}}{M} \qquad \text{gives} \qquad u(t) = \frac{1}{M} + ce^{-rt} = \frac{1}{P(t)}.$$

The initial condition gives:

$$c = \frac{1}{P_0} - \frac{1}{M} = \frac{M - P_0}{MP_0}.$$

When the initial condition is inserted, a little algebra yields:

$$P(t) = \frac{MP_0}{P_0 + (M - P_0)e^{-rt}}.$$

Logistic Growth Model Solution

The exact functional form of the solution:

$$P(t) = \frac{MP_0}{P_0 + (M - P_0)e^{-rt}},$$

has **3** parameters and can be readily fit to the Gause data.

The sum of square errors formula for fitting data, $P_d(t_i)$, is:

$$J(P_0, r, M) = \sum_{i=0}^{N} \left(P_d(t_i) - \frac{MP_0}{P_0 + (M - P_0)e^{-rt_i}} \right)^2,$$

which we minimize in **Matlab** with `fminsearch`.

An ***initial guess*** for the parameters $p_0 = [P_0, r, M]$ would be to take $P_0 = P_d(t_0)$, r equal the value from the ***Malthusian growth model***, and $M = P_d(t_N)$.

Logistic Growth Model Solution

The sum of square errors code, which is used to find the best parameter fit, is:

```
function J = yst_lst(p, tdata, pdata)
% Least Squares fit to Logistic Growth
N = length(tdata);
yst = p(1)*p(2)./(p(1) + ...
    (p(2)-p(1))*exp(-p(3)*tdata));
err = pdata - yst;
J = err*err'; % Sum of square errors
end
```

The best fitting parameters come from executing `fminsearch`:
`p1 = fminsearch(@yst_lst,p0,[],tdata,pdata)`

Logistic Growth Model Solution

The best fitting parameters for ***Saccharomyces cerevisiae*** and ***Schizosaccharomyces kephir*** are given by:

$$P_0 = 1.2343, \; r = 0.25864, \; M = 12.7421,$$

and

$$P_0 = 0.67807, \; r = 0.057442, \; M = 5.8802$$

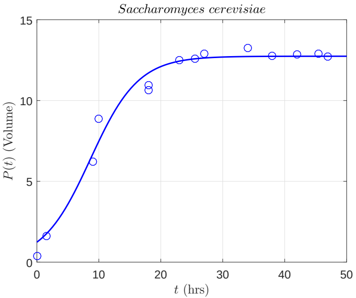
with least **SSE = 4.9460** and **SSE = 1.3850**, respectively.

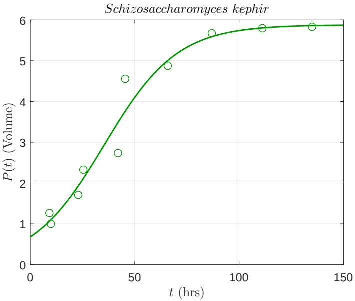
This produces the best fitting solutions:

$$P(t) = \frac{12.742}{1 + 9.323\, e^{-0.2586t}} \quad \text{and} \quad P(t) = \frac{5.880}{1 + 7.672\, e^{-0.05744t}}.$$

Logistic Growth Model Solution

The graphs of the data with the best fitting models are shown below.





Equilibria

Qualitative Analysis of ***continuous models*** provides information about types of possible behaviors of the models, such as

$$\frac{dP}{dt} = f(P).$$

It is important to learn the ***local behavior*** of the ***continuous dynamical model*** near its ***Equilibria***.

Like ***discrete dynamical models***, the analysis of continuous models with ***differential equations*** begins with finding ***Equilibria***.

Equilibria of differential equations are found by setting the ***derivative equal to 0*** or

$$f(P_e) = 0,$$

which for population models means ***no growth***.

Equilibria

For the ***logistic growth model***,

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{M}\right),$$

the equilibria satisfy:

$$rP_e\left(1 - \frac{P_e}{M}\right) = 0 \qquad \text{or} \qquad P_e = 0 \quad \text{or} \quad M.$$

Like the discrete model, the ***logistic growth model*** has the ***extinction*** or ***trivial equilibrium***, $P_e = 0$, and the ***carrying capacity equilibrium***, $P_e = M$.

We expect that locally solutions "near" the ***extinction equilibrium*** should move away and be ***unstable***, while solutions "near" the ***carrying capacity equilibrium*** should approach and be ***stable***.

Linearization

The ***local behavior*** of the ***continuous dynamical model*** near its ***equilibria*** depends on the ***linear terms*** of the function f.

Since $f(P_e) = 0$, the Taylor series expansion is:

$$f(P) = f'(P_e)(P - P_e) + \mathcal{O}\left((P - P_e)^2\right).$$

- If $f'(P_e) > 0$, then locally the solution grows exponentially (***positive eigenvalue***) and the equilibrium at P_e is ***unstable***.
- If $f'(P_e) < 0$, then locally the solution decays exponentially (***negative eigenvalue***) and the equilibrium at P_e is ***stable***.
- If $f'(P_e) = 0$, then more information must be obtained to determine the ***stability*** of the equilibrium at P_e.

Linearization 2

Stability of Logistic Growth Model: The ***equilibria*** are $P_e = 0$ and M.

The function and its derivative satisfy:

$$f(P) = rP\left(1 - \frac{P}{M}\right), \qquad \text{so} \qquad f'(P) = r - \frac{2rP}{M},$$

where $r > 0$ is the Malthusian growth rate at low density and M is the carrying capacity.

At the ***extinction equilibrium***, $P_e = 0$, we have $f'(0) = r$, which is positive and makes this equilibrium ***unstable***.

At the ***carrying capacity equilibrium***, $P_e = M$, we have $f'(M) = -r$, which is negative and makes this equilibrium ***stable***.

These results suggest that ***differential equation*** governing the ***logistic growth model*** has an initial exponential growth before moving smoothly toward the ***carrying capacity***.

Direction Field 1

Consider the general ***differential equation*** with initial value:

$$\frac{dy}{dt} = f(t, y), \qquad y(t_0) = y_0.$$

The function $f(t, y)$ provides the ***slope of the solution***.

The slope of the solution is easily found by ***computer programs*** on a grid, so the program can generate arrows showing the direction of the solution.

The ***direction field*** is this ***graphical representation*** in the y vs. t plane with arrows showing the direction of the solution.

Maple Simulation

We demonstrate the use of **Maple** for examining the ***logistic growth model*** for ***Saccharomyces cerevisiae***.

Enter the differential equation for the model:
$> de := diff(P(t),t) = 0.2586 \cdot P(t) \cdot \left(1 - \frac{P(t)}{12.742}\right);$

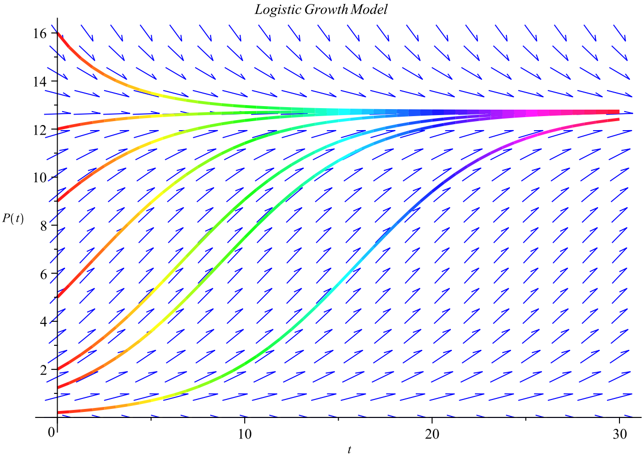
This equation is solved with the following:
$> dsolve(\{de, P(0) = 1.234\}, P(t));$

Maple can plot the ***direction field*** with any number of solutions using its package ***DEtools*** as shown below:
$> with(DEtools):$
$> DEplot(de, P(t), t = 0..30, [[P(0) = .2], [P(0) = 1.234], [P(0) = 2], [P(0) = 5], [P(0) = 9], [P(0) = 12], [P(0) = 16]], P = 0..16, colour = blue, linecolour = t, title = LogisticGrowthModel);$

(Plot appears on the next slide.)

Maple Direction Field Plot

From the previous slide, **Maple** produces the following plot:



Existence and Uniqueness

The differential equation:

$$y' = f(t, y), \qquad \text{with} \qquad y(t_0) = y_0, \tag{1}$$

with reasonable conditions on f has the ***existence*** and ***uniqueness*** of its solutions.

Theorem

If f and $\partial f/\partial y$ are continuous in a rectangle $R : |t - t_0| \leq a, |y - y_0| \leq b$, then there is some interval $|t - t_0| \leq h \leq |a|$ in which there exists a unique solution $y = \phi(t)$ of the initial value problem (1).

This **theorem** guarantees that solutions don't cross on a ***graph***.

Thus, geometrically it is easy to trace the direction of the solution from any starting point in the ***direction field***.

AutonomousDirection Field

We examine the ***direction field*** of the ***autonomous differential equation***

$$\frac{dy}{dt} = f(y).$$

In the y vs. t-plane, the ***direction field*** is constant for each value of y.

Equilibria, y_e, have slope **0** in the ***direction field***.

Between ***equilibria***, the ***direction field*** has only slopes with the same sign.

It follows that solutions ***monotonically*** go toward or away from ***equilibria***.

The ***qualitative behavior*** of the ***autonomous differential equation*** is captured in a **1D-line**, where ***equilibria*** are marked and solution directions are noted with arrows pointing right or left.

Phase Portrait 1

The ***qualitative dynamics*** of a ***scalar autonomous differential equation*** is given by a **1D-phase portrait**.

- For $\frac{dy}{dt} = f(y)$, ***graph*** $f(y)$
  - ***Equilibria*** occur when $f(y) = 0$.
  - Solutions increase when $f(y) > 0$ and decrease when $f(y) < 0$.
- When arrows of the **phase portrait** point toward an equilibrium, then it is ***stable*** and is indicated with a ***solid circle***.
- When arrows of the **phase portrait** point away from an equilibrium, then it is ***unstable*** and is indicated with an ***open circle***.
- When arrows of the **phase portrait** go in the same direction through an equilibrium, then it is ***semi-stable*** and is indicated with a ***half open circle***.

Phase Portrait

Logistic growth model

Horizontal axis is the **Phase Portrait**.

Extinction equilibrium, $P_e = 0$, is ***unstable***.

Carrying capacity, $P_e = M$, is a ***stable equilibrium***.

Positive initial conditions result in all solutions tending in time to the **carrying capacity**.