BMS 1901 Calculus for Life Sciences

Week7

10/12/2020

Dr. Hsiang-yu Yuan

Study objectives

Understand per capita growth rate and logistic differential equation

Able to test equilibrium and stability and understand the phase plots

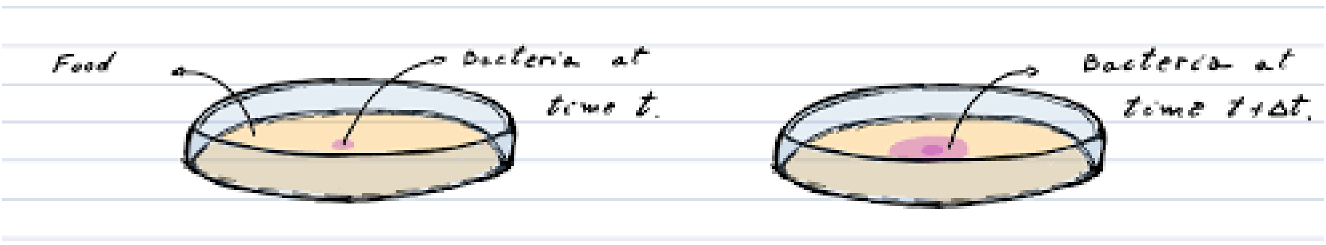
References:

Biocalculus by Stewart and Day

Chp7.1 Logistic equation

Chp1.6 Logistic difference equation

Chp7.2 Phase Plots, Equilibria and Stability



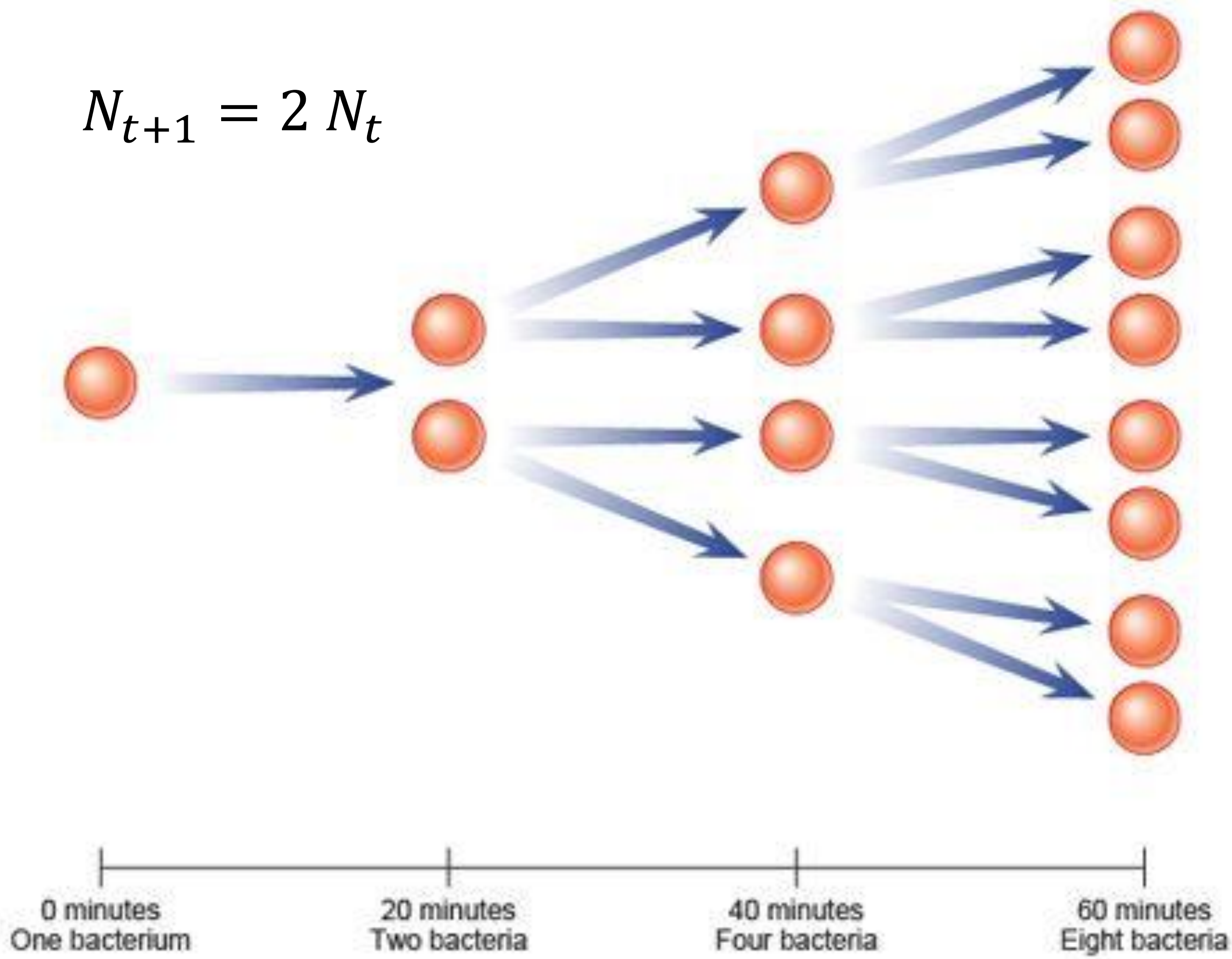
In many natural phenomena, quantities grow or decay at a rate propotional to their size.

For instance, if $y = f(t)$ is the number of individuals in a populaiton of animals or bacteria at time t, then it seems reasonable to expect that the rate of grow $f'(t)$ is propotional to the population $f(t)$.

What function can be used to model this kind of growth?

Models of Population Growth

$$N_{t+1} = 2\ N_t$$



0 minutes
One bacterium
20 minutes
Two bacteria
40 minutes
Four bacteria
60 minutes
Eight bacteria

More generally, if each cell can produce R daughters, then the difference equation

$$N_{t+1} = R\,N_t$$

relates successive and the solution is

$$N_t = N_0 R^t$$

The number R is the number of offpsring per individual and is called the **per capita growth factor**

Population Growth

- $P(t)$ is the size of a population at time t:

$$\frac{dP}{dt} = kP \qquad \text{or} \qquad \frac{1}{P}\frac{dP}{dt} = k$$

$\frac{1}{P}\frac{dP}{dt}$: growth rate divided by the population size

- **relative growth rate**
- **per capita growth rate**

Population Growth

$$\frac{dP}{dt} = kP \qquad \text{or} \qquad \frac{1}{P}\frac{dP}{dt} = k$$

- growth rate is proportional to population size
- relative growth rate is constant

(2) Theorem The only solutions of the differential equation $dy/dt = ky$ are the exponential functions

$$y(t) = y(0)e^{kt}$$

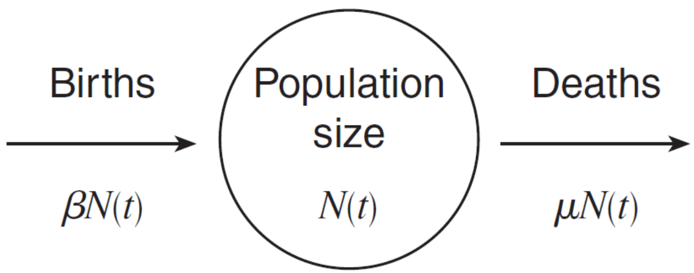
- a population with constant relative growth rate must grow exponentially

- relative growth rate appears as the coefficient of t in the exponential function Ce^{kt}.

Models of Population Growth

Recall that since the rate of change of $N(t)$, the number of yeast cells, can be written as $dN(t)/dt$, we can write

$$\text{(1)} \qquad \frac{dN(t)}{dt} = \beta N(t) - \mu N(t)$$



$$\frac{dN(t)}{dt} = \beta N(t) - \mu N(t)$$

Time (h)	Pop. size ($\times 10^6$/mL)	Time (h)	Pop. size ($\times 10^6$/mL)
0	0.200	19	209
1	0.330	20	190
2	0.500	21	210
3	1.10	22	200
4	1.40	23	215
5	3.10	24	220
6	3.50	25	200
7	9.00	26	180
8	10.0	27	213
9	25.4	28	210
10	27.0	29	210
11	55.0	30	220
12	76.0	31	213
13	115	32	200
14	160	33	211
15	162	34	200
16	190	35	208
17	193	36	230
18	190		

Models of Population Growth

Now if we define the constant *r as*

(2) $$r = \beta - \mu$$

then Equation 1 can be written more simply as

(3) $$\frac{dN(t)}{dt} = rN(t)$$

The quantity *r* in Equation 2 is called the **per capita growth rate**. It is the rate of growth of the population *per individual* in the population, such as $\frac{dN(t)}{dt}\frac{1}{N(t)} = r$.

Models of Population Growth

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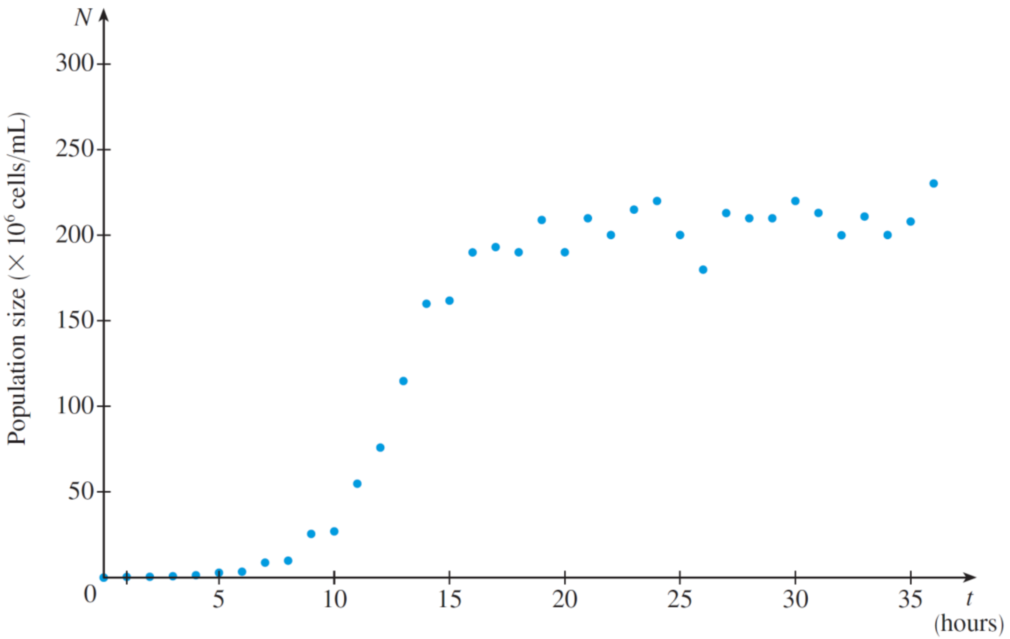
7	9.00	26	180
8	10.0	27	213
9	25.4	28	210
10	27.0	29	210
11	55.0	30	220
12	76.0	31	213
13	115	32	200
14	160	33	211
15	162	34	200
16	190	35	208
17	193	36	230
18	190		

Table 1

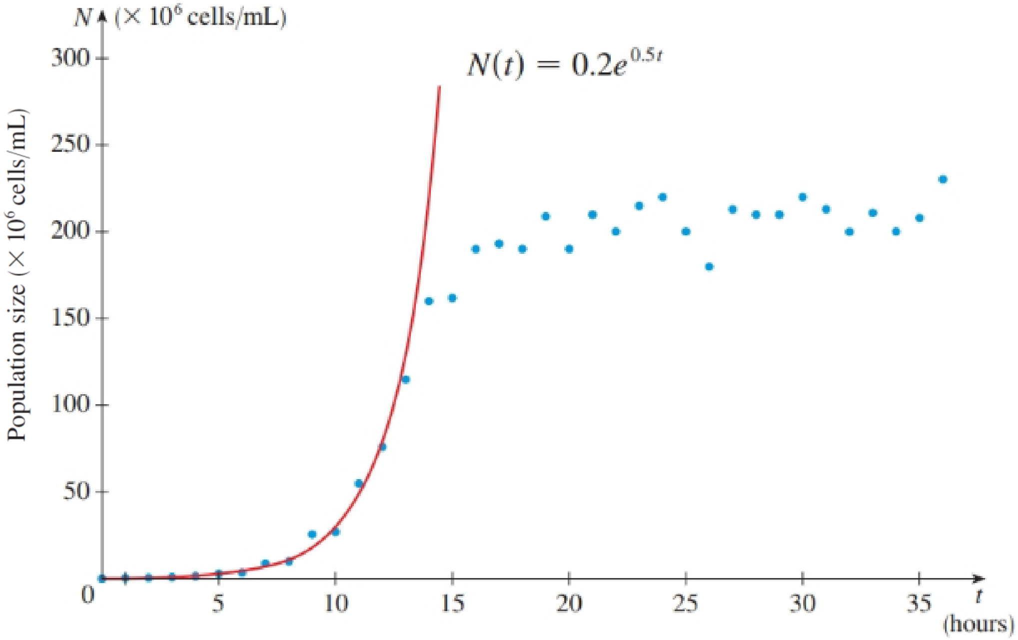


A scatter plot of the data in Table 1

Figure 1

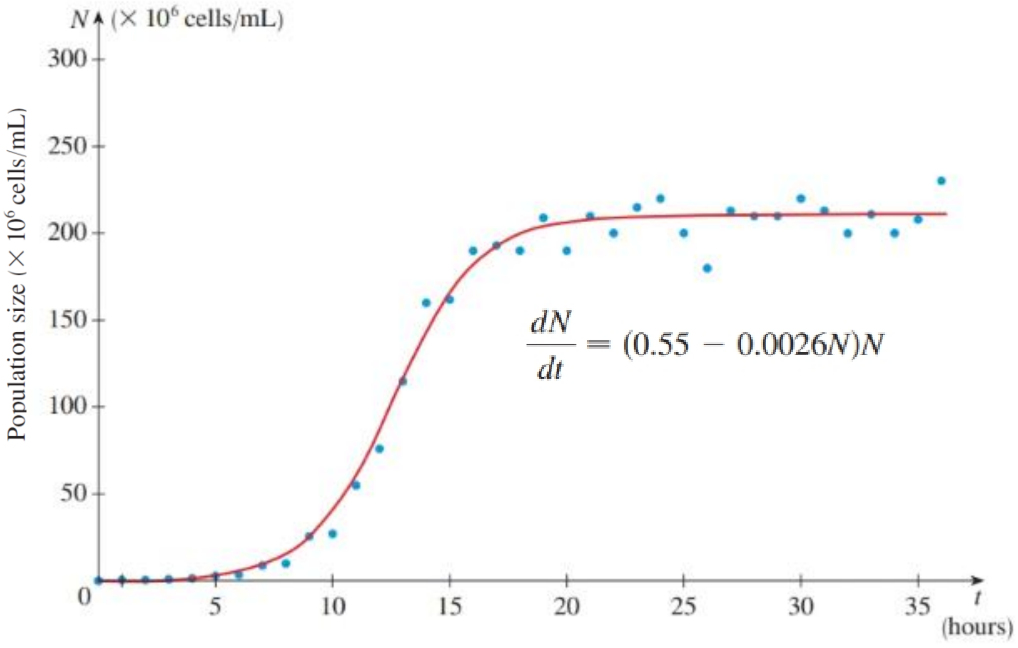
Models of Population Growth

Does the exponential curve fit data well? No, it fits well only before 13 hours.



Models of Population Growth

Does the exponential curve fit data well? Yes, it fits well for all 35 hours.



Equation 3 tells us that $N(t)$ is a function whose derivative is equal to the function itself. What function will satisfy this relationship?

Models of Population Growth

The positive constant K is referred to as the *carrying capacity*; it is the population size at which crowding and resource depletion cause the per capita growth rate to be zero.

The differential equation

$$\frac{dN}{dt} = r\left(1 - \frac{N}{K}\right)N \qquad \textbf{(4)}$$

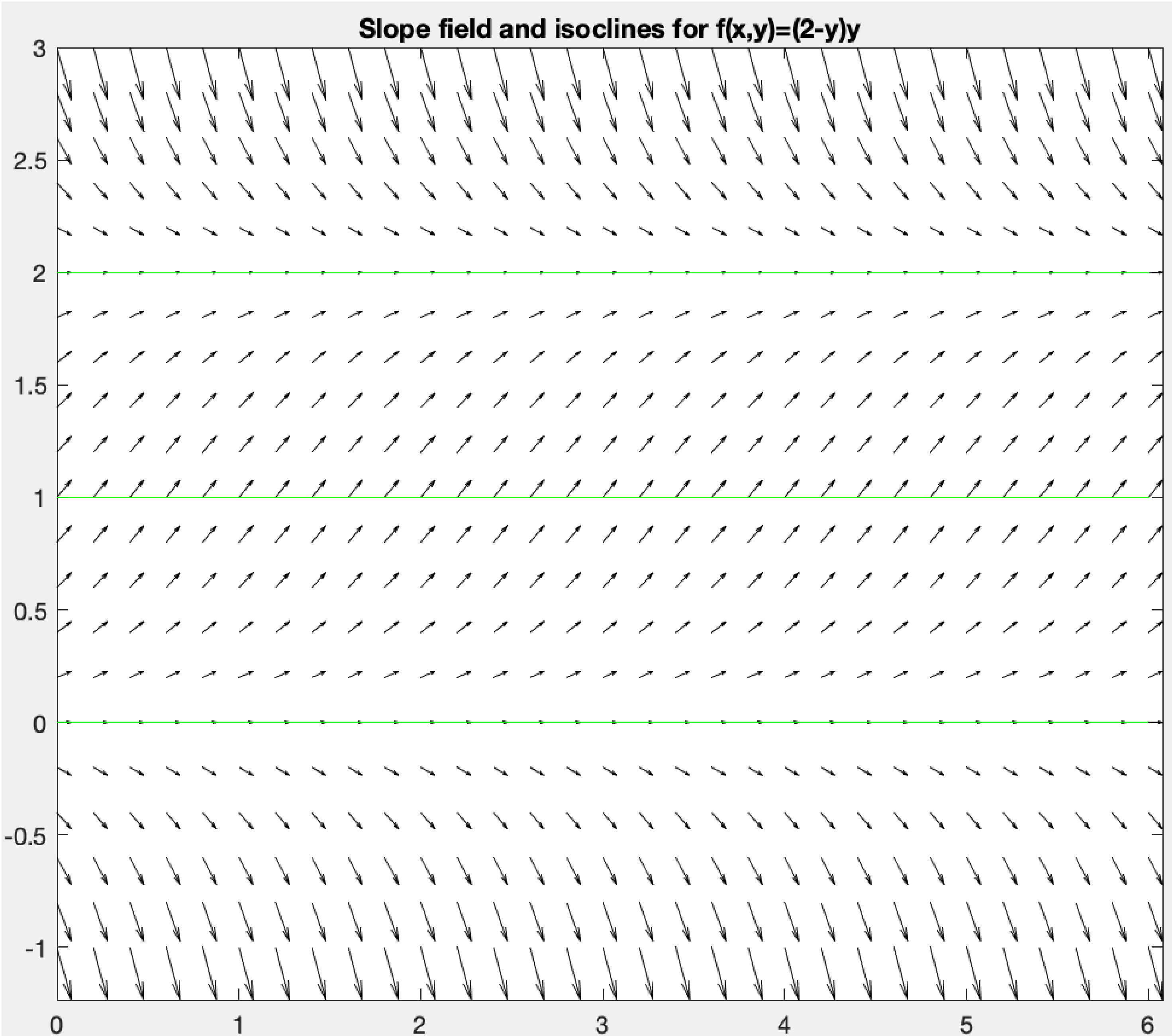
is called the **logistic differential equation,** or more simply the **logistic equation**.

Example of an autonomus system

The equation $y' = (2-y)y$ is autonomous, since the independent variable, let us call it x, does not explicitly appear in the equation. To plot the slope field and isocline for this equation, one can use the following code in GNU Octave/MATLAB

Run in matlab:

```
Ffun = @(X,Y)(2-Y).*Y; % function f(x,y)=(2-y)y
[X,Y]=meshgrid(0:.2:6,-1:.2:3); % choose the plot sizes
DY=Ffun(X,Y); DX=ones(size(DY)); % generate the plot values
quiver(X,Y,DX,DY, 'k'); % plot the direction field in black
hold on;
contour(X,Y,DY,[0 1 2], 'g'); % add the isoclines(0 1 2) in green
title('Slope field and isoclines for f(x,y)=(2-y)y')
```


Slope field and isoclines for f(x,y)=(2-y)y
3
2.5
2
1.5
1
0.5
0
-0.5
-1
0
1
2
3
4
5
6

Modelling of exponential and logistic growth

- How population ecology studies the density, distribution, size, sex ration, and age structure of populations.
- Exponential growth calculations are included along with a discussion of logistic growth.

https://www.youtube.com/watch?v=PQ-CQ3CQE3g

Phase Plots

Phase Plots

Phase plots provide a way to visualize the dynamics of autonomous differential equations, to locate their equilibria, and to determine the stability properties of these equilibria. Consider the autonomous differential equation

$$\frac{dy}{dt} = g(y)$$

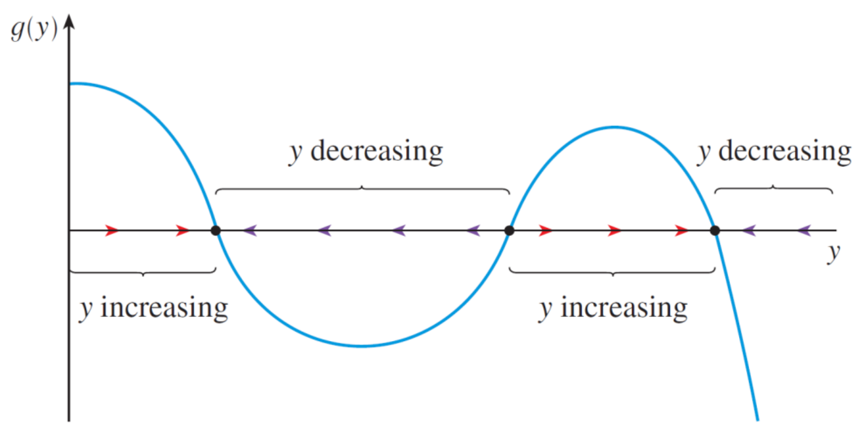
To construct a phase plot we graph the right side of the differential equation, $g(y)$, as a function of the dependent variable y.

Where this plot lies above the horizontal axis, $y'(t) > 0$ and so y is increasing. Where it lies below the horizontal axis, $y'(t) < 0$ and so y is decreasing.

Phase Plots

Points where the plot crosses the axis correspond to values of the variable at which $y'(t) = 0$.

We can use these considerations to place arrows on the horizontal axis indicating the direction of change in *y*, as shown in Figure 1.



A typical phase plot

Figure 1

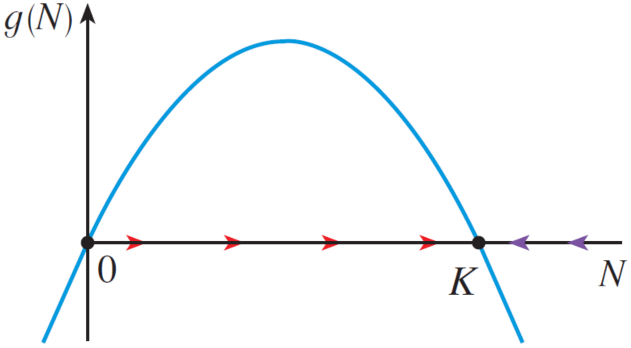
Example 1 – *The logistic equation*

Construct a phase plot for the logistic growth model $dN/dt = r(1 - N/K)N$ assuming that $r > 0$.

Solution:

We need to plot $g(N) = r(1 - N/K)N$ as a function of N. This is a parabola opening downward, crossing the horizontal axis at $N = 0$ and $N = K$.

In Figure 2 we can see that N increases when taking on values between 0 and K and decreases when taking on values greater than K.



Phase plot for logistic model

Figure 2

Example 3 – *The Allee effect*

Some populations decline to extinction once their size is less than a critical value. For example, if the population size is too small, then individuals might have difficulty finding mates for reproduction. This is referred to as an *Allee effect* after the American ecologist Warder Clyde Allee (1885–1955). A simple extension of the logistic model that incorporates this effect is given by

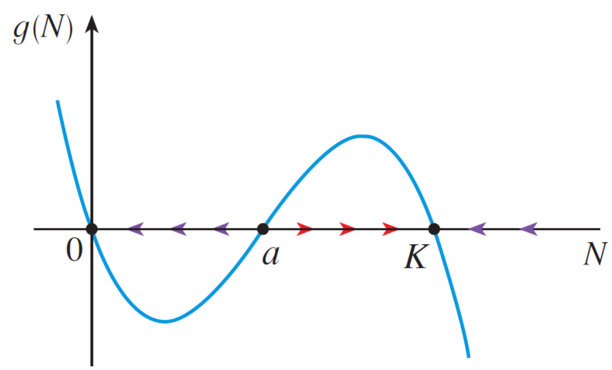
$$\frac{dN}{dt} = r(N - a)\left(1 - \frac{N}{K}\right)N$$

where $0 < a < K$. Construct a phase plot assuming that $r > 0$.

Example 3 – *Solution*

We plot $g(N) = r(N - a)(1 - N/K)N$ as a function of N. This is a cubic polynomial whose graph crosses the horizontal axis at $N = 0$, $N = a$, and $N = K$.

The graph lies below the horizontal axis for values of N between 0 and a and for values of $N > K$. [See Figure 4(a).]



(a) Phase plot for an Allee effect

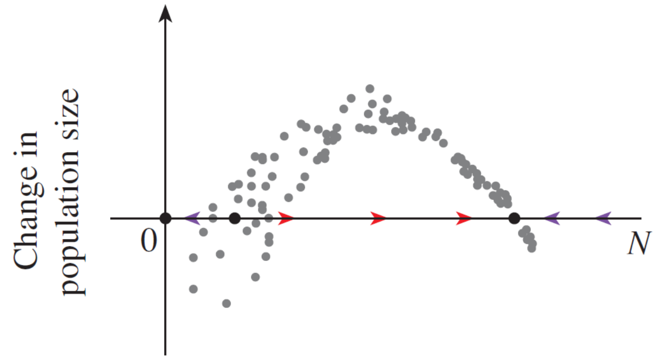
Figure 4

Example 3 – *Solution*

cont'd

Therefore N will approach 0 if it starts between 0 and a, whereas it will approach K if it starts anywhere greater than a.

Figure 4(b) displays data for the phase plot of an experimental microbial population.



(b) Data for the phase plot of a microbial population

Figure 4

Equilibria and Stability

Equilibria and Stability

Phase plots provide information about how the dependent variable changes, as well as values of the variable at which no change occurs. Such values are referred to as *equilibria*.

Definition Consider the autonomous differential equation

(1) $$\frac{dy}{dt} = g(y)$$

An **equilibrium** solution is a constant value of y (denoted $\hat{y}$) such that $dy/dt = 0$ when $y = \hat{y}$.

Equilibria are found by determining values of $\hat{y}$ that satisfy $g(\hat{y}) = 0$. They correspond to places where the phase plot crosses the horizontal axis.

Example 4 – *The logistic equation (continued)*

Show that $\hat{N} = 0$ and $\hat{N} = K$ are equilibria of the logistic growth model from Example 1.

Solution:

Substituting $\hat{N} = 0$ and $\hat{N} = K$ into the equation $g(N) = r(1 - N/K)N$ gives $g(\hat{N}) = 0$ in both cases.

In the yeast data of the earlier section, $\hat{N} = K$ corresponds to the steady number of yeast cells reached as the experiment progressed. ($\hat{N} = 0$ corresponds to the absence of yeast.)

Equilibria and Stability

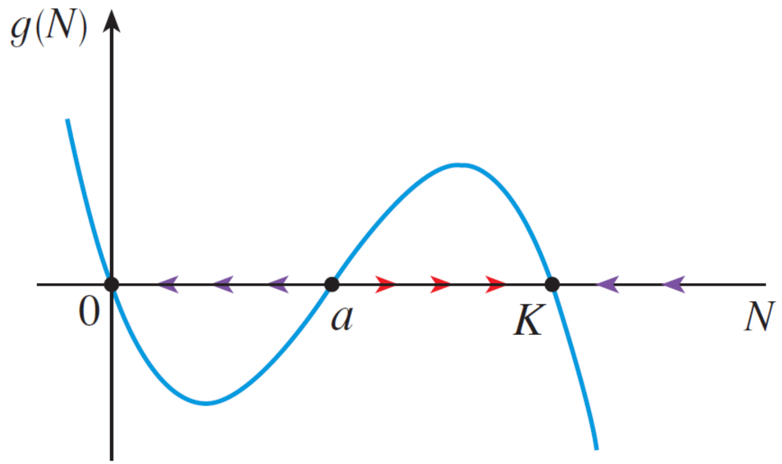
In addition to providing a way to visualize equilibria, phase plots provide information about their stability properties.

> **Definition** An equilibrium $\hat{y}$ of differential equation (1) is **locally stable** if y approaches the value $\hat{y}$ as $t \longrightarrow \infty$ for all initial values of y sufficiently close to $\hat{y}$.

An equilibrium that is not stable is referred to as **unstable**.

Example 6 – *The Allee effect (continued)*

Find all equilibria for the model of an Allee effect in Example 3 and determine their stability properties from the phase plot in Figure 4(a).



Phase plot for an Allee effect

Figure 4(a)

Example 6 – *Solution*

We need to find the values of $\hat{N}$ that satisfy the equation

$$r(\hat{N} - a)(1 - \hat{N}/K)\hat{N} = 0$$

We can see that these are $\hat{N} = 0$, $\hat{N} = a$, and $\hat{N} = K.$ These are the points at which the phase plot in Figure 4(a) crosses the horizontal axis. From the arrows on the figure we can also see that both $\hat{N} = 0$ and $\hat{N} = K$ are locally stable whereas $\hat{N} = a$ is unstable— no matter how close we start *N* to the value a, it always moves farther away from a as time passes.

Equilibria and Stability

Local Stability Criterion Suppose that $\hat{y}$ is an equilibrium of the differential equation

$$\frac{dy}{dt} = g(y)$$

Then $\hat{y}$ is *locally stable* if $g'(\hat{y}) < 0$, and $\hat{y}$ is *unstable* if $g'(\hat{y}) > 0$. If $g'(\hat{y}) = 0$, then the analysis is inconclusive.

Example 7 – *Population genetics*

Two bacterial strains sometimes feed on chemicals excreted by one another: strain A feeds on chemicals produced by strain B, and vice versa. This phenomenon is referred to as *cross-feeding*. Suppose that two strains of bacteria are engaged in cross-feeding (strain 1 and strain 2).

For a relatively simple model of cross-feeding, the frequency *p*(*t*) of the strain 1 bacteria is governed by the differential equation

$$\frac{dp}{dt} = p(1 - p)[\alpha(1 - p) - \beta p]$$

Example 7 – *Population genetics*

cont'd

where α and β are positive constants. Suppose that $\alpha = 1$ and $\beta = 2$. Then the differential equation simplifies to

$$\frac{dp}{dt} = p(1 - p)[(1 - p) - 2p] = p(1 - p)(1 - 3p)$$

(a) Find all equilibria.

(b) Determine the stability properties of each equilibrium found in part (a).

Example 7 – *Solution*

(a) Equilibria are values of $\hat{p}$ satisfying the equation

$$\hat{p}(1 - \hat{p})(1 - 3\hat{p}) = 0$$

This gives $\hat{p} = 0$, $\hat{p} = 1$, and $\hat{p} = \frac{1}{3}$.

(b) We first need to calculate the derivative of $g(p) = p(1 - p)(1 - 3p)$ with respect to p.

After some simplification we obtain

$$g'(p) = 1 - 8p + 9p^2$$

Example 7 – *Solution*

cont'd

We then need to evaluate this at each of the equilibria.

- $\hat{p} = 0$: $\quad g'(0) = 1 - 8(0) + 9(0)^2 = 1$

  which is positive, meaning that $\hat{p} = 0$ is unstable.

- $\hat{p} = 1$: $\quad g'(1) = 1 - 8(1) + 9(1)^2 = 2$

  which is positive, meaning that $\hat{p} = 1$ is unstable.

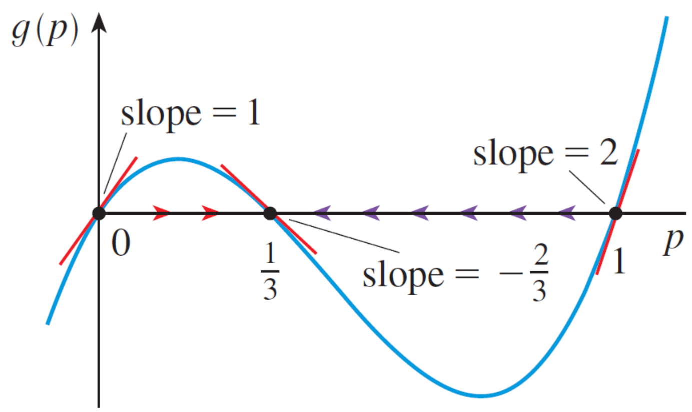
- $\hat{p} = \frac{1}{3}$: $\quad g'\left(\frac{1}{3}\right) = 1 - 8\left(\frac{1}{3}\right) + 9\left(\frac{1}{3}\right)^2 = -\frac{2}{3}$

  which is negative, meaning that $\hat{p} = \frac{1}{3}$ is locally stable.

Example 7 – *Solution*

cont'd

These results suggest that, over time, we expect the frequency of strain 1 bacteria in the population to approach $\hat{p} = \frac{1}{3}$ as indicated by the arrows in Figure 7.



Phase plot for cross-feeding model

Figure 7

Supplementary

Autonomous differential equation systems

An **autonomous system** is a system of ordinary differential equations of the form

$$\frac{d}{dt}x(t) = f(x(t))$$

where *x* takes values in *n*-dimensional Euclidean space and *t* is usually time.

It is distinguished from systems of differential equations of the form

$$\frac{d}{dt}x(t) = g(x(t), t)$$

in which the law governing the rate of motion of a particle depends not only on the particle's location, but also on time; such systems are not autonomous.

Can you think any examples of the autonomous system or non autonomous system?