Solutions to Assignment #3

1. Nondimensionalize the Logistic growth equation for bacterial growth in a medium with carrying capacity K:
$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), \tag{1}$$
where r is the intrinsic growth rate of the population, by introducing dimensionless variables
$$u = \frac{N}{\mu} \quad \text{and} \quad \tau = \frac{t}{\lambda}. \tag{2}$$
Give interpretations for the scaling parameters μ and λ.

***Solution**:* Apply the Chain Rule to obtain
$$\frac{du}{d\tau} = \frac{du}{dt}\cdot\frac{dt}{d\tau}. \tag{3}$$
Next, use the equations in (2) to obtain from (3)
$$\frac{du}{d\tau} = \frac{\lambda}{\mu}\frac{dN}{dt}. \tag{4}$$
It then follows from (4) and the Logistic equation in (1) that
$$\frac{du}{d\tau} = \frac{\lambda}{\mu}\cdot rN\left(1 - \frac{N}{K}\right),$$
which can be re–written as
$$\frac{du}{d\tau} = \lambda r u\left(1 - \frac{u}{K/\mu}\right), \tag{5}$$
where we have used the equations in (2) again. We can now set
$$\lambda r = 1 \quad \text{and} \quad \frac{K}{\mu} = 1,$$
in (5) so that
$$\lambda = \frac{1}{r} \quad \text{and} \quad \mu = K.$$
Thus, μ is the carrying capacity and λ is the reciprocal of the intrinsic growth rate.

The dimensionless form of the Logistic equation is then
$$\frac{du}{d\tau} = u\,(1-u)\,.$$
$\square$

2. Consider again the chemostat model without flow in or out of a single chamber depicted in Figure 1. Proceed as in Problems 1–4 in Assignment 1 assuming this

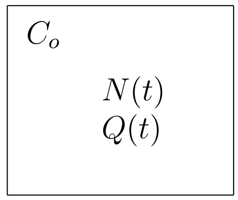

Figure 1: One–Compartment Chemostat Model

time that the *per capita* growth rate is given by the Michaelis-Menten enzyme kinetics relation

$$K(c) = \frac{rc}{a+c}, \tag{6}$$

where $c = Q/V$ is the nutrient concentration in the growth medium, to derive a differential equations for the bacterial density, $n = N/V$, and the nutrient concentration. You will need to use the yield $Y = 1/\alpha$, or the number of new cells produced in the chemostat due to consumption of one unit of nutrient.

Give an interpretation for the parameter r.

***Solution**:* Apply the following conservation principle for the number of bacteria in the chamber

$$\frac{dN}{dt} = \text{ Rate of } N \text{ in } - \text{ Rate of } N \text{ out}. \tag{7}$$

Since there is no flow in or out of the chamber, the change in the number of bacteria in the chamber has to be accounted for by the population growth according to the *per–capita* growth rate, $K(c)$. We then have that

$$\text{Rate of } N \text{ in } = K(c)N, \tag{8}$$

and

$$\text{Rate of } N \text{ out } = 0. \tag{9}$$

Combining (9), (8) and (7) then yields the differential equation

$$\frac{dN}{dt} = K(c)N. \tag{10}$$

Next, apply the conservation principle to the amount of nutrient, $Q(t)$, in the chamber,

$$\frac{dQ}{dt} = \text{ Rate of } Q \text{ in } - \text{ Rate of } Q \text{ out.} \tag{11}$$

where

$$\text{Rate of } Q \text{ in } = 0, \tag{12}$$

and

$$\text{Rate of } Q \text{ out } = \alpha K(c) N, \tag{13}$$

where α is the reciprocal of the yield, Y. Combine (13), (12) and (11) yo obtain

$$\frac{dQ}{dt} = -\alpha K(c) N. \tag{14}$$

Putting together the equations in (10) and (14) then yields the mathematical model

$$\begin{cases} \dfrac{dN}{dt} & = & K(c)N; \\ \\ \dfrac{dQ}{dt} & = & -\alpha K(c)N, \end{cases} \tag{15}$$

for the evolution in time of N and Q in the chamber.

Next, multiply the first equation in (15) by α and add it to the second equation to obtain

$$\alpha \frac{dN}{dt} + \frac{dQ}{dt} = 0. \tag{16}$$

Since α is constant and differentiation is a linear operator, we obtain from (16) that

$$\frac{d}{dt}[\alpha N + Q] = 0, \tag{17}$$

which we wanted to show.

Note that (17) implies that $\alpha N(t) + Q(t)$ is constant for all t, so that

$$\alpha N(t) + Q(t) = \alpha N(0) + Q(0), \quad \text{ for all } t,$$

or

$$\alpha N(t) + Q(t) = \alpha N_o + Q_o, \quad \text{ for all } t. \tag{18}$$

Set $A_o = \alpha N_o + Q_o$ and solving for Q in (18) to obtain

$$Q(t) = A_o - \alpha N(t), \quad \text{ for all } t. \tag{19}$$

Dividing the equation in (19) by V we obtain that

$$c(t) = \frac{A_o}{V} - \frac{\alpha}{V} N(t), \quad \text{for all } t. \tag{20}$$

Next, set $C_o = A_o/V$ and $\beta = \alpha/V$ to obtain from (21) that

$$c(t) = C_o - \beta N(t), \quad \text{for all } t. \tag{21}$$

Using (6) and (21) we then see that *per–capita* growth rate is then given by

$$K(c) = r\frac{C_o - \beta N}{a + C_o - \beta N}, \tag{22}$$

where r is the maximum *per–capita* growth rate that the medium can sustain.

Substituting the expression for $K(c)$ in (22) into the first differential equation in (15) we then obtain the following growth model for bacteria in the chamber,

$$\frac{dN}{dt} = rN\frac{C_o - \beta N}{a + C_o - \beta N}.$$

$\square$

3. The differential equation

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - p(N, \Lambda), \tag{23}$$

models a population that is subject to predation reflected in the term $p(N, \Lambda)$, which depends on the population size, N, and a set of parameters, Λ. In the absence of predation the population undergoes logistic growth with intrinsic growth rate, r, and carrying capacity, K.

In 1978, Ludwig, Jones and Holling published an article in the Journal of Animal Ecology (*Qualitative analysis of insect outbreak systems: the spruce budworm and forest*, Volume 47, pp. 315–332) in which they proposed the following constitutive equation for the predation term,

$$p(N, a, b) = \frac{bN^2}{a^2 + N^2}. \tag{24}$$

(a) Give interpretations for the parameters a and b in (24).

Solution: The parameter b is the largest possible predation rate. The parameter a is the population size for which the predation rates is half of the largest possible value. □

(b) Nondimensionalize the differential equation in (23) by introducing dimensionless variables

$$u = \frac{N}{\mu} \quad \text{and} \quad \tau = \frac{t}{\lambda}, \tag{25}$$

to obtain the dimensionless equation

$$\frac{du}{d\tau} = \alpha u \left(1 - \frac{u}{\beta}\right) - \frac{u^2}{1+u^2}, \tag{26}$$

where α and β are dimensionless parameters.

Express α and β in terms of the parameters r, K, a and b.

Solution: Apply the Chain Rule to obtain from the equations in (25) that

$$\frac{du}{d\tau} = \frac{\lambda}{\mu}\frac{dN}{dt}. \tag{27}$$

Next, combine the equations in (23), (24) and (27) to get

$$\frac{du}{d\tau} = \lambda r u \left(1 - \frac{u}{K/\mu}\right) - \frac{(\lambda b/\mu)u^2}{(a/\mu)^2 + u^2}, \tag{28}$$

where we have used the first equation in (25).

Set

$$\lambda r = \alpha, \tag{29}$$

$$\frac{K}{\mu} = \beta, \tag{30}$$

$$\frac{\lambda b}{\mu} = 1, \tag{31}$$

and

$$\frac{a}{\mu} = 1, \tag{32}$$

we then obtain from (31) and (32) that

$$\mu = a, \tag{33}$$

and

$$\lambda = \frac{a}{b}. \tag{34}$$

It then follows from (29), (30), (33) and (34) that

$$\alpha = \frac{ra}{b}$$

and

$$\beta = \frac{K}{a}.$$

Finally, substituting (29)–(32) into (28) yields (26). $\square$

4. Observe that $u = 0$ is an equilibrium point of the equation in (26). Determine the nature of the stability of this equilibrium point.

   Solution: Set $g(u) = \alpha u\left(1 - \dfrac{u}{\beta}\right) - \dfrac{u^2}{1+u^2}$ and compute

   $$g'(u) = \alpha - \frac{2\alpha}{\beta}u - \frac{2u}{(1+u^2)^2}.$$

   Then, $g'(0) = \alpha > 0$, which shows that the equilibrium point $\overline{u} = 0$ is unstable by the principle of linearized stability. $\square$

5. The equation

   $$\alpha\left(1 - \frac{u}{\beta}\right) - \frac{u}{1+u^2} = 0, \tag{35}$$

   which yields the non–zero equilibrium points of (26), cannot be easily solved algebraically.

   (a) Explain why the equation in (35) must have at least one real solution, and at most three distinct real solutions.

   Solution: After multiplying on both sides by $1 + u^2$ and simplifying, the equation in (35) can be shown to be equivalent to the equation

   $$u^3 - \beta u^2 + \left(1 + \frac{\beta}{\alpha}\right)u - \beta = 0. \tag{36}$$

   The equation in (36) is a cubic polynomial equation in u with real coefficients. Thus, it must have at least one real solution. It can have at most three distinct real solutions. $\square$

   (b) Determine conditions on α and β that will guarantee that the equation in (35) will have (i) exactly one real solution, (ii) two distinct real solutions, and (iii) three distinct real solutions.

Solution: The solutions to the equation in (35) can also be realized geometrically as intersections of the graphs of

$$y = \alpha - \gamma u \quad \text{and} \quad y = \frac{u}{1+u^2}, \tag{37}$$

where we have set

$$\gamma = \frac{\alpha}{\beta}. \tag{38}$$

Figure 2 shows a plot of the graphs of the equations in (37) obtained with WolframAlpha™ for the case $\alpha = 0.5$ and $\beta = 10$. We

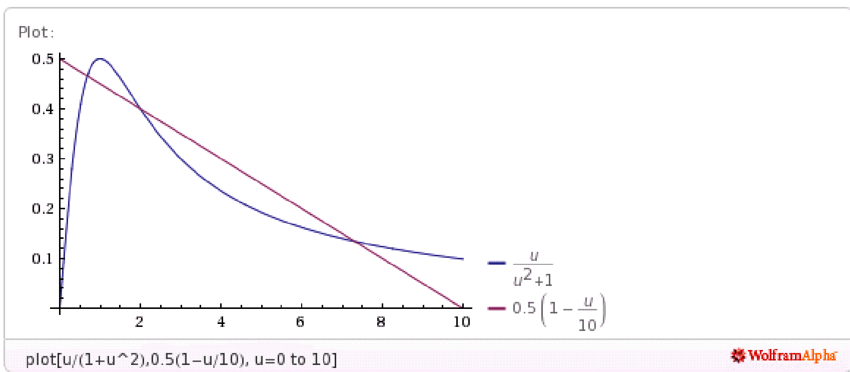

Figure 2: Plot of Equations in (37) for $\alpha = 0.5$, $\beta = 10$

see that in this case the graphs of the equations in (37) meet at three distinct points. On the other hand, for $\alpha = 0.6$ and $\beta = 10$, the graphs meet at exactly one point (see Figure 3). By varying

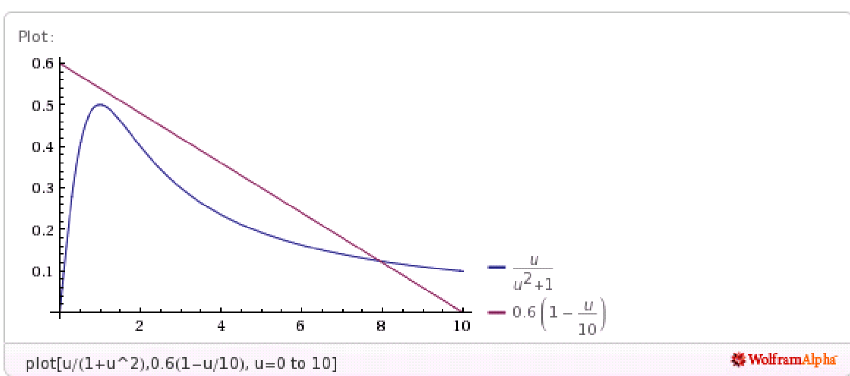

Figure 3: Plot of Equations in (37) for $\alpha = 0.6$, $\beta = 10$

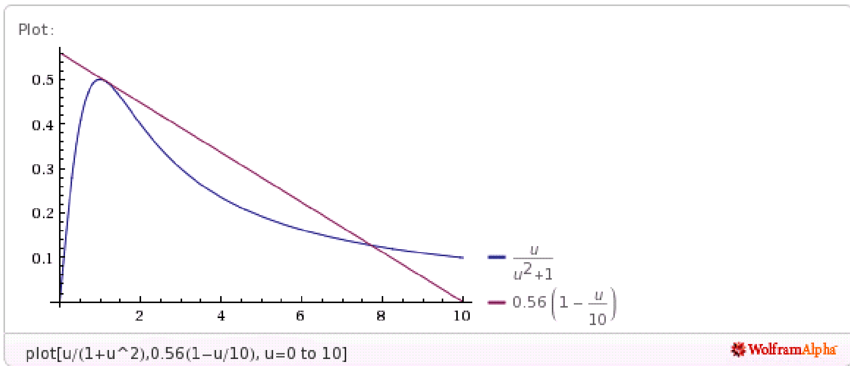

Figure 4: Plot of Equations in (37) for $\alpha = 0.56$, $\beta = 10$

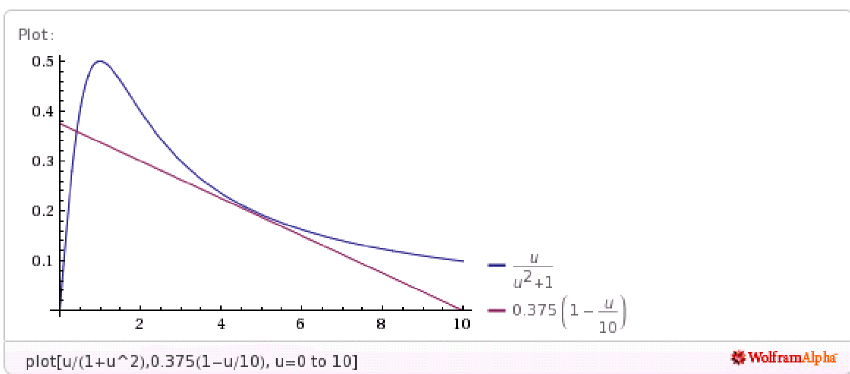

Figure 5: Plot of Equations in (37) for $\alpha = 0.375$, $\beta = 10$

α while keeping β at 10, we can make the graphs of the equations in (37) meet at exactly two points as seen in Figures 4 and 5.
We need to find conditions on α and β that will guarantee that any of the three situations depicted in Figures 2, 3 or 4 will occur.

We begin with the case in which the graphs of the equations in (37) meet at exactly two points as in Figures 4 or 5. This corresponds to the situation in which the equation in (36) has a real double root. Set

$$f(u) = u^3 - \beta u^2 + \left(1 + \frac{1}{\gamma}\right) u - \beta, \tag{39}$$

where γ is a given in 38. The cubic polynomial $f(u)$ in (39) has a double root if it has a factor of the form $(u-s)^2$, where s is a real parameter. Accordingly, its derivative

$$f'(u) = 3u^2 - 2\beta u + 1 + \frac{1}{\gamma} \tag{40}$$

will have $u - s$ as a factor.
Dividing $u - s$ into $f'(u)$ in (40) yields

$$f'(u) = (u-s)(3u + 2s - 2\beta) + s(3s - 2\beta) + 1 + \frac{1}{\gamma}. \tag{41}$$

Thus, in order for $f'(u)$ to have $u - s$ as a factor, it follows from (41) that we need to require that

$$s(3s - 2\beta) + 1 + \frac{1}{\gamma} = 0. \tag{42}$$

Next, divide $(u-s)^2 = a^2 - 2su + s^2$ into $f(u)$ in (39) to get

$$f(u) = (u-s)^2(u+2s-\beta) + \left(s(3s-2\beta)1 + \frac{1}{\gamma}\right) u - \beta - s^2(2s-\beta). \tag{43}$$

Using (42), we obtain from (43) that

$$f(u) = (u-s)^2(u + 2s - \beta) - \beta - s^2(2s - \beta). \tag{44}$$

Thus, in order for $(u-s)^2$ to be a factor of $f(u)$, it follows from (44) that we also need to require that

$$\beta + s^2(2s - \beta) = 0. \tag{45}$$

Equations in (42) and (45) express conditions on γ and β that will yield a double root for the cubic equation in (36). Solving for β in (45) we obtain the parameter β as a function of the parameter s:

$$\beta(s) = \frac{2s^3}{s^2 - 1}. \tag{46}$$

Next, use the value of β in (46) in the equation in (42) and solve that equation for γ to get

$$\gamma = \frac{s^2 - 1}{(s^2 + 1)^2}. \tag{47}$$

Combining (38), (46) and (47) we obtain the following parametric expression for α:

$$\alpha(s) = \frac{2s^3}{(s^2 + 1)^2}. \tag{48}$$

Thus, the condition on α and β that yield exactly two solutions to the equation in (36) is that the pair (β, α) lies in the curve parametrized by

$$\left(\frac{2s^3}{s^2 - 1}, \frac{2s^3}{(s^2 + 1)^2} \right), \tag{49}$$

where s is a real parameter with $s > 1$.

A parametric plot of the curve in (49) reveals that the curve has a cusp; see the graph in Figure 6 obtained through the use of WolframAlpha™. The cusp point corresponds to a value of the parameter, s, for which $s > 1$ and

$$\beta'(s) = 0 \quad \text{and} \quad \alpha'(s) = 0 \tag{50}$$

Calculating the derivatives of α and β we obtain

$$\beta'(s) = \frac{2s^2(s^2 - 3)}{(s^2 - 1)^2} \quad \text{and} \quad \alpha'(s) = \frac{2s^2(3 - s^2)}{(s^2 + 1)^3}. \tag{51}$$

Inspection of the equations in (51) shows that $s = \sqrt{3}$ solves the equations in (50). Thus, the cusp point in the graph in Figure 6 corresponds to the value of the parameter $s = \sqrt{3}$.

Hence, the curve in (49) has two branches emanating from the cusp point. The top branch is obtained as s varies from 1 to $\sqrt{3}$. It follows from (46) and (48) that, as $s \to 1^+$,

$$\alpha(s) \to \frac{1}{2} \quad \text{and} \quad \beta(s) \to +\infty.$$

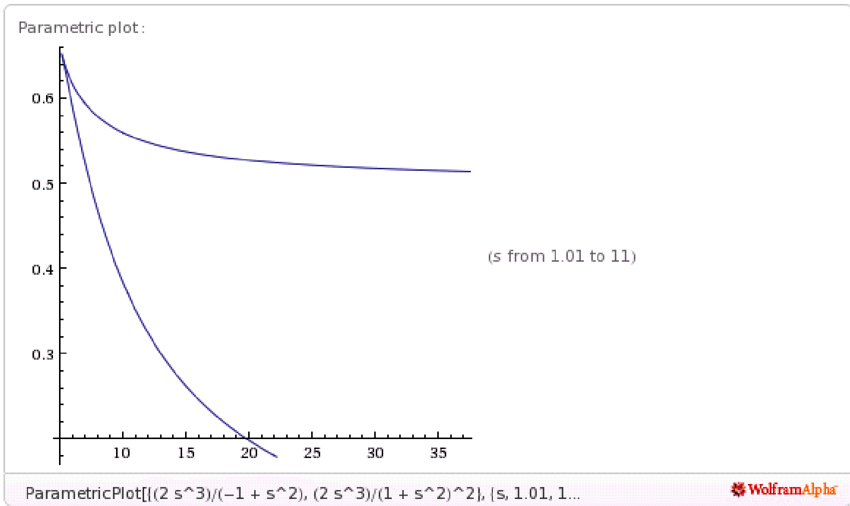

Figure 6: Parametric plot of (49) in the $\beta\alpha$–plane

The lower branch of the curve (49) pictured in Figure 6 correspond to values of the parameter s in $[\sqrt{3}, \infty)$. Note that (46) and (48) imply that, as $s \to +\infty$,

$$\alpha(s) \to 0 \quad \text{and} \quad \beta(s) \to +\infty.$$

For fixed values of β along the horizontal axis in the graph in Figure 6, values of α between the two branches yield parameter values (β, α) for which the equation in (36) has three distinct real solutions. Outside of that range, the equation in (36) has only one real solution. $\square$