Chapter 4:

Growth & Decay

Introduction

- Here, model systems with population so big (or growth so fine-grained) that continuity can be assumed.
- These continuous models give rise to *differential equations*.
- Result: no natural time delay in the models & no over-compensation of difference equations.
- Extend the logistic growth equation model above & add a culling term.
**Intro to the Topic**

Time Series

Discrete Models

Growth and Decay

**Simple Models**

- For cell population with infinite nutrients, can assume that rate of increase of cells depends on number of cells.
- Mathematically, can put this as:

\[
\frac{dN}{dt} = rN
\]  \hspace{1cm} (4.1)

for some constant of proportionality, \( r \).
- \( r \) measures average growth rate per unit time per individual (i.e. ‘2.4 children per person per life’).
- This organic growth law was named after Malthus who predicted (ca 1798) that world population would soon outgrow its resources.

\(^2\)T.R. Malthus (1766-1834)

**Simple Models cont’d**

- In real life experiments there is always a finite starting value of \( N \) at \( t = 0 \), \( N_0 \). Can show that:

\[
N(t) = N_0e^{rt}
\]  \hspace{1cm} (4.2)

i.e. (given \( \infty \) space/food) growth of cells is exponential.
- Note constant \( r \) can be negative or positive (i.e. decays or grows).
- For humans with \( \alpha \) births per year & \( \beta \) deaths, obviously

\[
r = \alpha - \beta
\]

- So population viability depends on this being positive.
- Can be shown from Eqn.(4.2) that doubling time for pop’n given by

\[
\tau_2 = \ln 2/r
\]

- So (if \( r \) is a percent) world’s population doubles itself every \( 70/r \) years.
Populations don’t grow in above manner;
Instead restrictions (on food, space, predation or any other factors) limit growth rates.
These put a limit on max sustainable population size.
This limit is called the carrying capacity of environment, $K$.
Instead of constant $r$ from Eqn.(4.1), have time dependent growth rate $\frac{1}{N} \frac{dN}{dt}$.
Eqn.(4.1) implies a constant growth rate given by $r$.

In logistic growth model, assume growth rate starts at $r$ when $N = 0$ & reach zero when $N = K$,

\[
\text{Growth Rate } \propto \left(1 - \frac{N}{K}\right)
\]

Implies growth rate decreases linearly with increasing population.
Mathematically, logistic growth model is given by:

\[
\frac{1}{N} \frac{dN}{dt} = r \left(1 - \frac{N}{K}\right)
\] (4.3)

This differential equation involves parameters $r$, $K$:
- $r$ applies to initial growth phase of a pop’n (before restrictions impact)
- $K$ imposes an upper limit on population growth.
In ecology, so-called *r/K selection theory* can be seen to widely apply. It relates to selection of traits in a species that trade off between quantity or quality of offspring. *r, K* refer to low- & high-density conditions, respectively. Terminology came from ecologists MacArthur & Wilson based on their work on insulated ecosystems. Species either *r-strategist* or *K-strategist*. This depends on selective processes shaping their reproductive strategies. Theory says that adaptation to high or low density environments involve different characteristics.

**r-selection**

In unstable environments, *r*-selection is dominates as fast reproduction is crucial. Adaptations permitting competition with other organisms are unnecessary, due to environmental volatility. Characteristic traits of *r*-selection are thought to include:

- short generation time,
- high fertility & ability to disperse offspring widely,
- early maturity onset with small body size.

Examples: bacteria, through insects (e.g. mosquitos) & weeds. Also some mammals, especially small rodents (e.g. rats).
K-selection
- In stable environments, K-selection dominates as ability to compete successfully for limited resources is crucial.
- Population sizes are typically very stable & approach max that the environment can bear.
- Differ from r-selected populations, where population numbers are more volatile.
- Characteristic traits of K-selection are thought to include:
  - long life expectancy,
  - mate choice,
  - fewer offspring but need extensive parental care to maturity
  - large body size.
- Examples: large organisms such as elephants, humans & whales.

Further Applications of the Model

As well as above, Verhulst Model has been applied to other areas:

Spread of a Disease.
- (Const) initial no. of susceptibles to infectious disease in pop'n: $K$.
- So $y$ & $(K - y)$ are no. of infectives & susceptibles after $t$.
- Chance encounters spread disease at a rate proportional to (product of) infectives & susceptibles.
- So model is $\dot{y} = ry(K - y)$
- Spread of rumors is an example of an identical model to this.
Further Applications of the Model cont’d

**Explosion/Extinction.**
- No. \( y(t) \) of crocs in a swamp satisfies \( \dot{y} = ry \)
- Here growth-decay constant \( r \propto (y - M) \) & \( M \) is a threshold population.
- Model \( \dot{y} = k(y - M)y \) gives extinction for initial populations smaller than \( M \)
- At other extreme, population explosion \( y(t) \to \infty \) for \( y(0) > M \).
- This model ignores harvesting/culling.

**Logistic Growth with Culling.**
- No. \( y(t) \) of fish in a lake satisfies a logistic model
  \( \dot{y} = (a - by)y - c \), provided fish are harvested at a rate \( c > 0 \).
- This rate \( c \) can be either constant, variable (i.e. \( c = hy \)) or involve periodic harvesting & restocking \( c = h\sin(\omega t) \).
- These models are dealt with in more detail below.
Solving the general form of logistic growth equation Eqn.(4.3), get:

\[ N(t) = \frac{K}{\left( \frac{K}{N_0} - 1 \right)} e^{-rt} + 1 \]  

(4.4)

for some initial population \( N_0 \).

Can see from Figs 4.1(a) & (b) that logistic growth depends qualitatively on initial population:

- For \( N_0 > K/2 \), second derivative \( \ddot{N} \) is always -tive,
- For \( N_0 < K/2 \) there is a period of growth which is exp'l in nature (\( \ddot{N} > 0 \)) which then levels off (\( \ddot{N} = 0 \)) before heading asymptotically to \( K \) (\( \ddot{N} < 0 \)) as \( t \to \infty \)

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Taking Eqn.(4.3) & adding a culling/ harvesting term $H$:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) - H \quad (4.5)$$

which may be non-dimensionalised (dividing through by carrying capacity, $K$), as follows:

$$\frac{dy}{dt} = ry \left(1 - y\right) - h \quad (4.6)$$

where $y = N/K$ & $h = H/K$ are non-dimensional pop'n & culling rates respectively.

- Can get steady states of this eqn (all $y$ for which $dy/dt = 0$):

$$\frac{dy}{dt} = 0 \text{ hence } -r \left(y^2 - y + \frac{h}{r}\right) = 0 \quad (4.7)$$

- Provided they meet the harvesting condition $4h < r$, both roots of Eqn 4.7:

$$y = p_{\pm} = \frac{1}{2} \left(1 \pm \sqrt{1 - \frac{4h}{r}}\right) \quad (4.8)$$

are steady states since both have the property $y = N/K < 1$.

- Note: condition $4h < r$ gives population harvesting capacity

- To find stable states of Eqn.(4.6), need to graph derivative of $y$ against $y$.

- Can look at behaviour of derivative for various values of $y$. 

- Notes
Examining the graph (Fig. 4.2), see that points $p_-$ & $p_+$ from Eqn.(4.8) demarcate areas of stability.

- For $y(0) < p_-$, population won’t grow, as $\dot{y} < 0$ for all $t$ & extinction occurs.
- For $y(0) > p_+$, $\dot{y} > 0$ & population will settle to steady state $y = p_+$.
- This follows from solving Eqn.(4.6) & examining behaviour of $y(t)$ as $t \to \infty$.
- Can see in Fig 4.2, that best culling time where $\dot{y}$ is maximal.
  - Before this population not growing at an optimal rate.
  - After this growth rate is decreasing to the steady state.
Aside: Equilibrium & Stability

- A constant solution of a differential equation is called an *equilibrium solution* or *steady state*.
- Locating/classifying steady states helps determine family of all solutions of DE equation.
- Solution to a DE of form $N(t) = \text{constant}$, because $dN/dt = 0$ is called an *equilibrium point*.

Aside: Equilibrium & Stability cont’d

- Classify steady states according to behavior of other solutions that start nearby:
  - Steady states $N = c$ is *stable* if any solution $N(t)$ that starts near $N = c$ stays near it.
  - Equilibrium $N = c$ is *asymptotically stable* if any solution $N(t)$ that starts near $N = c$ converges to it, i.e. $\lim_{t \to \infty} N = c$.
  - If an equilibrium state is not stable, it is *unstable*.
  - This means there is at least one solution that starts near equilibrium & leaves it.
  - Example is first state $N = 0$ of the Logistic Growth model with no culling (similar to Fig. 4.2, only shifted to have roots at $N = 0$ and $N = K$) Eqn.(4.3), this is an unstable state.
  - Because, if $N = +\epsilon$ (for small $\epsilon$), population will increase; if $N = -\epsilon$, population decreases further.
Logistic Growth model also used for Chemostat

For growth models so far, as nutrients are not renewed, exp’l growth is limited to a few generations.

Bacterial cultures can be kept in exp’l growth for long time with continuous culture,

Designed to relieve conditions stopping exp’l growth in batch cultures.

Such continuous culture, in chemostats, reflects bacterial growth in natural environments.

In chemostat, growth chamber is connected to a reservoir of sterile medium.

Once growth is started, fresh medium is continuously supplied from reservoir.

Fluid volume in growth chamber is maintained at constant level by an overflow drain.

Fresh medium enters growth chamber at a rate that limits bacterial growth.

Bacteria grow at same rate that overflow removes bacterial cells & spent medium.

Fresh medium addition rate affects growth rate as fresh medium contains limiting amount of essential nutrient.

Thus, chemostat relieves lack of nutrients, toxic substance accumulation, & accumulation of excess cells in culture, which initiate growth cycle's stationary phase.

Bacterial culture is maintained at relatively constant conditions, depending on nutrient flow rate.
For Chemostat, more complex model than for pure logistic growth with a limited volume of nutrient Eqn.(4.3);
As can be seen in Fig. 4.3(b), there is an inflow rate into & outflow rate from the chamber.
These latter two terms are both $F$ to conserve mass in chamber.
To start, derive logistic growth model again, for microorganism pop’n $N$, taking into account nutrient conc $C(t)$.

Can define the equations to be:

$$\frac{dN}{dt} = K(C)N = \kappa CN \quad (4.9)$$

i.e. bacteria reproducing at a rate $\propto C$, & change in nutrient conc in culture chamber:

$$\frac{dC}{dt} = -\alpha \frac{dN}{dt} = -\alpha \kappa CN \quad (4.10)$$

i.e. $\alpha$ units of nutrient giving one unit of pop’n growth.

integrating w.r.t. $t$ Eqn.(4.10) get $C(t) = -\alpha N(t) + C_0$, which, on subst’n in Eqn.(4.9), gives:

$$\frac{dN}{dt} = \kappa N(C_0 - \alpha N) \quad (4.11)$$

$\equiv$ logistic growth, Eqn.(4.3) for $r = \kappa C_0$, $K = C_0/\alpha$.  

Notes
The Chemostat cont’d

**Figure 4.3:** Chemostat: Schematic Representations

Chemostat Parameters

<table>
<thead>
<tr>
<th>Quantity</th>
<th>Symbol</th>
<th>units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nutrient Concentration</td>
<td>$C$</td>
<td>mass/volume</td>
</tr>
<tr>
<td>Reservoir Nutrient Concentration</td>
<td>$C_0$</td>
<td>mass/volume</td>
</tr>
<tr>
<td>Bacterial population</td>
<td>$N$</td>
<td>mass/volume</td>
</tr>
<tr>
<td>Volume of Growth Chamber</td>
<td>$V$</td>
<td>Volume</td>
</tr>
<tr>
<td>Inflow/Effluent Flow Rate</td>
<td>$F$</td>
<td>Volume/time</td>
</tr>
</tbody>
</table>

**Table 4.1:** Chemostat Parameters

- Note from Table 4.1 that introduce a concentration term into Eqn.(4.9).
- Must dimensionally consider $N$ as bacteria per unit volume (i.e. a pop’n density)
Modify above chemostat eqns (4.10, 4.11) to account for influx/outflow to/from culture chamber:

\[
\frac{dN}{dt} = K(C)N - \frac{FN}{V} \tag{4.12}
\]

where 2nd term on RHS is removal rate of \( N \), &

\[
\frac{dC}{dt} = -\alpha K(C)N - \frac{FC}{V} + \frac{FC_0}{V} \tag{4.13}
\]

where 2nd & 3rd terms on RHS are decrease in conc'n rate due to removal & increase due to inflow, resp.

Volume term \( V \) makes eqns dimensionally correct.

From growth rate term \( K(C) \): can see that \( K(C) \) is some limiting function of nutrient availability \( C^4 \).

Mechanism commonly adopted is Michaelis-Menten Kinetics:

\[
K(C) = \frac{K_{\text{max}}C}{K_n + C} \tag{4.14}
\]

Can see in fig.4.4 that value of \( K_n \) is nutrient conc'n needed to achieve half the maximum growth rate \( K_{\text{max}} \).

\(^4\)i.e. growth rate increases with nutrient availability only to a limiting value (determined by capacity of bacteria to reproduce themselves only at a certain rate)
Inserting model from Eqn.(4.14) into chemostat equations Eqn.s(4.12, 4.13), to get:

\[
\frac{dN}{dt} = \left( \frac{K_{\text{max}}C}{K_n + C} \right) N - \frac{FN}{V} \tag{4.15}
\]

and

\[
\frac{dC}{dt} = -\alpha \left( \frac{K_{\text{max}}C}{K_n + C} \right) N - \frac{FC}{V} + \frac{FC_0}{V} \tag{4.16}
\]

which include no fewer than two unknowns \((N, C)\) & six parameters \((K_n, K_{\text{max}}, F, V, C_0, \alpha)\).
The Chemostat cont’d: Michaelis-Menten Kinetics

- Can show (with Dimensional Analysis) that above equations reduce to:

\[
\frac{dn}{d\tau} = f(n, c) = \alpha_1 \left( \frac{nc}{1 + c} \right) - n \quad (4.17)
\]

and

\[
\frac{dc}{d\tau} = g(n, c) = - \left( \frac{nc}{1 + c} \right) - c + \alpha_2 \quad (4.18)
\]

which now only contain the (dimensionless) parameters:

\[
\alpha_1 = \frac{VK_{\text{max}}}{F} \quad \text{and} \quad \alpha_2 = \frac{C_0}{K_n}
\]

& dimensionless variables:

\[
\tau = tF/V, \quad n = \frac{NAVK_{\text{max}}}{FK_n}, \quad c = \frac{C}{K_n}
\]

Dimensional Analysis reduces it to its simplest form without dimensions.

For example, in 1st of dimensionless variables above:

\[
\tau = \frac{tF}{V}
\]

Now from Table 4.1 in dimensional form, this amounts to:

\[
\text{units of } \tau = \frac{[\text{time}]}{[\text{volume}]} \quad (4.19)
\]

rhs of which is dimensionless.

“dimensionless” ≡ “the game is half-over”, i.e. not specifying any units (e.g. minutes) for time gone but in terms of total time.

DA also has benefit of removing physical dimensions (units)
The Chemostat cont’d: Michaelis-Menten Kinetics

- Eqn.s (4.17) & (4.18) are nonlinear due to term \( nc/(1 + c) \) & thus do not have exact solutions for \( n(\tau) \) and \( c(\tau) \).
- Can, however, examine their steady-state solutions as for logistic equation, eqn.(4.7).
- Setting the derivatives \( \frac{dn}{d\tau}, \frac{dc}{d\tau} \) to zero in Eqn.s (4.17) & (4.18), get:
  \[
  \alpha_1 \left( \frac{\bar{n}\bar{c}}{1 + \bar{c}} \right) - \bar{n} = 0 \tag{4.20}
  \]
  and
  \[
  - \left( \frac{\bar{n}\bar{c}}{1 + \bar{c}} \right) - \bar{c} + \alpha_2 = 0 \tag{4.21}
  \]
  where \( \bar{n}, \bar{c} \) denote the values at the steady states.

Solving for \( \bar{n}, \bar{c} \), get two solutions:

\[
(\bar{n}_1, \bar{c}_1) = \left[ \alpha_1 \left( \alpha_2 - \frac{1}{\alpha_1 - 1} \right), \frac{1}{\alpha_1 - 1} \right] \tag{4.22}
\]
and

\[
(\bar{n}_2, \bar{c}_2) = (0, \alpha_2) \tag{4.23}
\]

- \( \bar{n}_2, \bar{c}_2 \) is a trivial solution: no bacteria left and nutrient has same conc’n as reservoir.
- For \( \bar{n}_1, \bar{c}_1 \), eqn.(4.22), clearly need \( \alpha_1 > 1 \) (no -ive conc’s) & \( \alpha_2 > 1/(\alpha_1 - 1) \) (no -ive pop’n densities)
- What is the stability of these steady states?
Aside: Stability at Steady States

- Close to steady states \((\bar{n}, \bar{c})\), assume solution behaves linearly.
- Writing the system of equations (4.17) & (4.18) as:

\[
\frac{dX}{d\tau} = F(X) \tag{4.24}
\]

where \(X\) is the vector \([n(\tau), c(\tau)]\).
- Considering close to the steady states \(\dot{X} = X - \bar{X}\) (i.e. small \(\dot{X}\)), can say that:

\[
\frac{dX}{d\tau} = \frac{dX}{d\tau} = F(\bar{X} + \dot{X}) \tag{4.25}
\]

(since \(d\bar{X}/d\tau = 0\)) which, by Taylor’s theorem, simplifies to:

\[
\frac{dX}{d\tau} = F(\bar{X})^0 + F'(\bar{X})\dot{X} + O(\dot{X}^2)^0 \tag{4.26}
\]

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Aside: Stability at Steady States cont’d

- First & last terms on rhs go to zero (first is derivative value at steady state, & last is small). So:

\[
\frac{d\dot{X}}{d\tau} = \frac{dX}{d\tau} = F'(\bar{X})\dot{X} \approx A\dot{X} \tag{4.27}
\]

where \(A\) is known as the Jacobian of \(F\) and is given by:

\[
A = \begin{pmatrix}
\frac{\partial f}{\partial n} & \frac{\partial f}{\partial c} \\
\frac{\partial g}{\partial n} & \frac{\partial g}{\partial c}
\end{pmatrix} \tag{4.28}
\]

- Have a linear system eqn.(4.27) to solve.
- For convenience, rewrite eqn.(4.27) as

\[
\frac{dX}{d\tau} = AX \text{ for } X \approx \bar{X} \tag{4.29}
\]
Aside: Stability at Steady States cont’d

- Solution of eqn system (4.29) is written as a sum:

\[
X(\tau) = \sum_{i=1}^{n} c_i e^{\lambda_i \tau} v_i
\]  

(4.30)

i.e. a linear combination of eigenpairs \((v_i, \lambda_i)\) & some unknown coefficients \(c_i\).

- For stability of equilibria (steady states) trajectories approach an equilibrium as \(t \to \infty\).

- Since \(X\) measures proximity to our steady states, this effectively means,

\[
\text{does } X(t) \to 0 \text{ for solutions of eqn.}(4.27)? \quad (\text{Recall that } A \text{ is Jacobian of } F \text{ close to steady states}).
\]

- Know that \(c_i e^{\lambda_i \tau} v_i \to 0\), iff \(e^{\lambda_i \tau} \to 0\).

- But for what values of \(\lambda\) does \(e^{\lambda_i \tau} \to 0\)?

- Taking magnitudes of bothsides, get

\[
\left| e^{\lambda_i \tau} \right| \to 0.
\]  

(4.31)

- Substituting \(\lambda = a + ib \quad (i = \sqrt{-1})\), eqn.(4.31) becomes:

\[
e^{a\tau} \sqrt{(\cos b\tau)^2 + (\sin b\tau)^2} \to 0.
\]  

(4.32)

- As term inside \(\sqrt{\cdot}\) is just 1, stability of solutions around steady states simply depends on real parts of all eigenvalues being less than zero.
Aside: Stability at Steady States cont’d

Now for a matrix $A$ given by

$$A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \quad (4.33)$$

eigenvalues are given by solutions of characteristic polynomial,

$$\lambda^2 - p\lambda + q = 0 \quad (4.34)$$

where $p = \text{trace}(A)$ and $q = \text{det}(A)$.

Roots of eqn.(4.34) are $\lambda = \frac{p \pm \sqrt{p^2 - 4q}}{2}$.

Two parameters $p, q$ thus determine stability of solution of system.

Figure 4.5: Stability points on $p$ V $q$
Aside: Stability at Steady States cont’d

- From Fig. 3.2, observe a number of cases:
  - $\lambda_1, \lambda_2$ real and distinct:
    - If $\lambda_1, \lambda_2$ have same sign, steady state is a blue node. If $\lambda_2 < \lambda_1 < 0$, soln for $X = (x\ y)^T \to 0$ in Eqn. (4.30) & it is a stable node. If $\lambda_1 > \lambda_2 > 0$, it is an unstable node.
    - $\lambda_1, \lambda_2$ have different signs, one part of soln in Eqn. (4.30) will always go to $0$ & other will go to $\infty$. This is a saddle point singularity & is always unstable.
  - E-values are complex: $\lambda_1, \lambda_2 = \alpha \pm i\beta$, solns to Eqn. (4.30) are oscillatory (product of $e^{\alpha T}$ & $e^{i\beta T}$); there are two cases:
    - If $\alpha \neq 0$ this is a focus. $\alpha < 0$ gives a stable focus and $\alpha > 0$ gives an unstable focus.
    - If $\alpha = 0$ this is a centre. In order to strictly determine stability we must examine higher order terms.

In terms of the trace and determinant $p, q$, these results are summarized in Table 4.2

<table>
<thead>
<tr>
<th>Type</th>
<th>Eigenvalues</th>
<th>Trace, Det $q$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Saddle Point</td>
<td>different signs</td>
<td>$q &lt; 0$</td>
</tr>
<tr>
<td>Stable Node</td>
<td>$\lambda_2 &lt; \lambda_1 &lt; 0$</td>
<td>$p &lt; 0 &amp; q &gt; 0$</td>
</tr>
<tr>
<td>Unstable Node</td>
<td>$\lambda_1 &gt; \lambda_2 &gt; 0$</td>
<td>$p &gt; 0 &amp; q &gt; 0$</td>
</tr>
<tr>
<td>Stable Focus</td>
<td>$\Re(\lambda) &lt; 0$</td>
<td>$p^2 &lt; 4q &amp; p &lt; 0$</td>
</tr>
<tr>
<td>Unstable Focus</td>
<td>$\Re(\lambda) &gt; 0$</td>
<td>$p^2 &lt; 4q &amp; p &gt; 0$</td>
</tr>
<tr>
<td>Centre</td>
<td>$\Re(\lambda) = 0$</td>
<td>$p^2 &lt; 4q &amp; p = 0$</td>
</tr>
</tbody>
</table>

Table 4.2: Stability & Matrix Properties
Aside: Stability at Steady States cont’d

- Eqn.(4.34) roots are $\lambda = \frac{p \pm \sqrt{\Delta}}{2}$, so: $\sqrt{\Delta} = p < p$, i.e.
  $p < 0$ (trace($A$) < 0) & $q > 0$ (det($A$) > 0) for stability.
- These latter two conditions ensure that soln’s exp’l part
  $\rightarrow 0$ as $t \rightarrow \infty$,
  i.e. conditions for stability. Hence for Stability

$$\frac{dX}{d\tau} = F(X) = \left( \begin{array}{c} f(n,c) \\ g(n,c) \end{array} \right) \quad (4.35)$$

Routh-Hurwitz Conditions at $X = (\bar{n}(\tau), \bar{c}(\tau))$ must hold:

$$\frac{\partial f}{\partial n} \bigg|_{X=(\bar{n},\bar{c})} + \frac{\partial g}{\partial c} \bigg|_{X=(\bar{n},\bar{c})} < 0 \quad (4.36)$$

and

$$\frac{\partial f}{\partial n} \bigg|_{(\bar{n},\bar{c})} \frac{\partial g}{\partial c} \bigg|_{(\bar{n},\bar{c})} - \frac{\partial f}{\partial c} \bigg|_{(\bar{n},\bar{c})} \frac{\partial g}{\partial n} \bigg|_{(\bar{n},\bar{c})} > 0 \quad (4.37)$$

The Chemostat: Stability at Steady States

- So, getting back to the chemostat problem, if $F = (f, g)$ are
given by eqn.s(4.17, 4.18):

$$\frac{dn}{d\tau} = f(n, c) = \alpha_1 \left( \frac{nc}{1+c} \right) - n$$

and

$$\frac{dc}{d\tau} = g(n, c) = -\left( \frac{nc}{1+c} \right) - c + \alpha_2$$

the Jacobian $A$ of $F$ (from eqn.(4.28)) is given by

$$A = \left( \begin{array}{cc} \frac{\alpha_1 c}{1+c} - 1 & \frac{\alpha_1 n}{(1+c)^2} \\ -\frac{c}{1+c} & -\frac{n}{(1+c)^2} - 1 \end{array} \right) \quad (4.38)$$
The Chemostat: Stability at Steady States

So at the steady state:

\[ \bar{c} = \frac{1}{\alpha_1 - 1} \text{ and } \bar{n} = \frac{\alpha_1 \mu}{\alpha_1 - 1}, \]

(where \( \mu = \alpha_2(\alpha_1 - 1) - 1 \)) given by eqn.(4.22), the Jacobian is given by:

\[ A(\bar{n}, \bar{c}) = \begin{bmatrix} 0 & \mu(\alpha_1 - 1) \\ -\frac{\mu(\alpha_1 - 1) + \alpha_1}{\alpha_1} & \frac{\mu(\alpha_1 - 1)}{\alpha_1} \end{bmatrix} \] (4.39)

For stability, as seen, trace of \( A \) must be -ive, which is true if \( \mu(\alpha_1 - 1) + \alpha_1 > 0 \) which is since \( \alpha_1 > 1 \) (no -ive conc'ns) & \( \alpha_2 > 1/(\alpha_1 - 1) \) (no -ive pop'n densities)

So a chemostat has a steady state solution (given by eqn.(4.22)) with bacteria in the growth chamber. This equilibrium will only produce biologically meaningful results subject to:

\[ \alpha_1 > 1 \text{ and } \alpha_2 > \frac{1}{\alpha_1 - 1}, \]

i.e. no -ive conc'ns and no -ive pop'n densities resp.
The Chemostat: Stability at Steady States

- So, in dimensional form, $\alpha_1 > 1$ corresponds to $\frac{1}{K_{\text{max}}} < \frac{V}{F}$.
- As $K_{\text{max}}$ is max bacterial repro rate with unlimited nutrients $dN/dt = K_{\text{max}}N \cdot \frac{\ln 2}{K_{\text{max}}}$ gives doubling time $\tau_2$ of bacterial pop’n.
- $V/F = \text{time to refill whole growth chamber volume with fresh nutrient.}$
- So if emptying time (given by $V/F \times \ln 2$ is greater than the doubling time ($\tau_2 = \frac{\ln 2}{K_{\text{max}}}$), bacteria are washed out quicker than they can reproduce.
- $\alpha_2 > 1/(\alpha_1 - 1)$ corresponds to $C_0/K_n > \bar{c}$ so max (non-dimensional) conc’n $\bar{c}$ will never be more than (non-dimensional) conc’n in stock solution.

Chapter 5:

Linear & Non-Linear Interaction Models