

Chapter 4:

Growth & Decay

Notes

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.

Notes

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:

$$\frac{dN}{dt} = rN \quad (4.1)$$

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 Malthus² who predicted (ca 1798) that world population would soon outgrow its resources.

²T.R. Malthus (1766-1834)

Notes

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:

$$N(t) = N_0 e^{rt} \quad (4.2)$$

i.e. (given ∞ space/ food) growth of cells is exponential.

- Note constant r can be negative or positive (i.e. decays or grows).
- For humans with α births per year & β 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.

Notes

Restricted Growth: the *Verhulst* or logistic model

- 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 .

Notes

Restricted Growth cont'd

- 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:

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

- 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.

Notes

Applications of the Model: r/K selection theory

- 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.

Notes

Applications of the Model: r/K selection theory cont'd

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).

Notes

Applications of the Model: r/K selection theory cont'd

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.

Notes

Further Applications of the Model

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

1 Spread of a Disease.

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

Notes

Further Applications of the Model cont'd

1 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 $y(t) \rightarrow \infty$ for $y(0) > M$.
- This model ignores harvesting/culling.

Notes

Further Applications of the Model cont'd

1 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

Notes

Restricted Growth cont'd

- Solving the general form of logistic growth equation Eqn.(4.3), get:

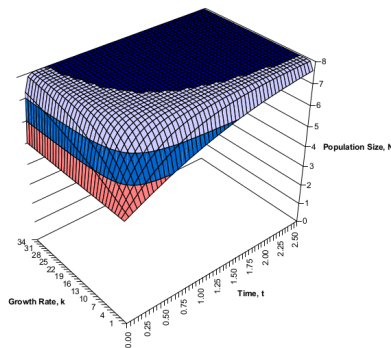
$$N(t) = \frac{K}{\left(\frac{K}{N_0} - 1\right)e^{-rt} + 1} \quad (4.4)$$

for some initial population N_0 .

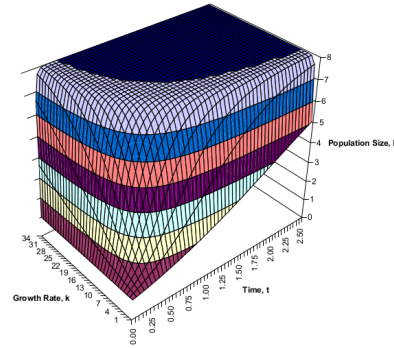
- Can see from Figs 4.1(a) & (b) that logistic growth depends qualitatively on initial population:
 - For $N_0 > K/2$, second derivative \ddot{N} is always -tive,
 - For $N_0 < K/2$ there is a period of growth which is exp'l in nature ($\ddot{N} > 0$) which then levels off ($\ddot{N} = 0$) before heading asymptotically to K ($\ddot{N} < 0$) as $t \rightarrow \infty$

Notes

Restricted Growth cont'd



(a) $N_0 > K/2$



(b) $N_0 < K/2$

FIGURE 4.1 : Logistic Growth for Different N_0

Notes

Restricted Growth cont'd

- 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:

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

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 $dy/dt = 0$):

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

Notes

Restricted Growth cont'd

- 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

Restricted Growth cont'd

- 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 $t \rightarrow \infty$.
- 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.

Notes

Restricted Growth cont'd

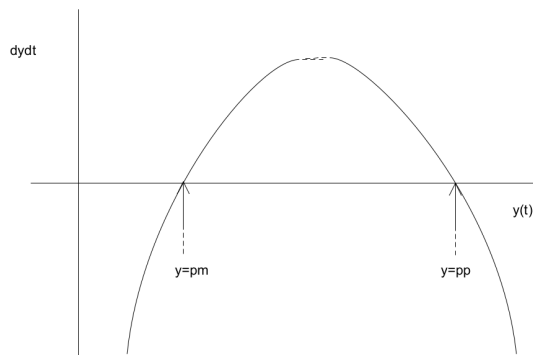


FIGURE 4.2 : $\dot{y} \text{ V } y$ for Logistic Growth with Culling

Notes

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*.

Notes


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. $\lim_{t \rightarrow \infty} N(t) = c$.
 - 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 ϵ), population will increase; if $N = -\epsilon$, population decreases further.

Notes

The Chemostat

- Logistic Growth model also used for Chemostat³
- 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.

³used to study growth of μ organisms under various lab conditions  90/117

Notes

The Chemostat cont'd

- 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.

Notes

The Chemostat cont'd

- 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 $C(t)$.

Notes

The Chemostat cont'd

- 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. α 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

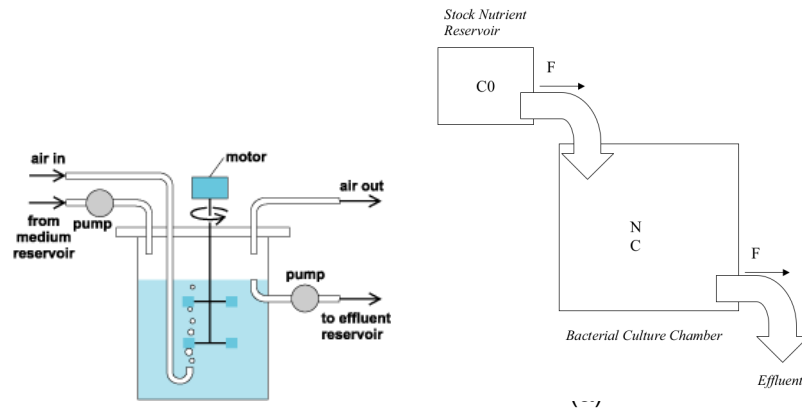


FIGURE 4.3 : Chemostat: Schematic Representations

Notes

(b)

Chemostat Parameters

Quantity	Symbol	units
Nutrient Concentration	C	mass/volume
Reservoir Nutrient Concentration	C_0	mass/volume
Bacterial population	N	mass/volume
Volume of Growth Chamber	V	Volume
Inflow/ Effluent Flow Rate	F	Volume/time

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)

Notes

The Chemostat cont'd

- Modify above chemostat eqns (4.10, 4.11) to account for influx/outflow to/from culture chamber:

$$\frac{dN}{dt} = K(C)N - \frac{FN}{V} \quad (4.12)$$

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

$$\frac{dC}{dt} = -\alpha K(C)N - \frac{FC}{V} + \frac{FC_0}{V} \quad (4.13)$$

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.

Notes

The Chemostat cont'd: Michaelis-Menten Kinetics

- 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:

$$K(C) = \frac{K_{max}C}{K_n + C} \quad (4.14)$$

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

⁴i.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)

Notes

The Chemostat cont'd: Michaelis-Menten Kinetics

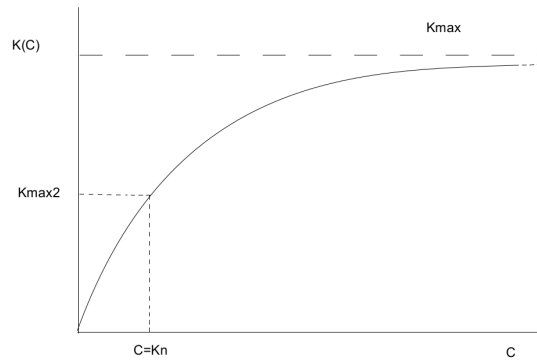


FIGURE 4.4 : Michaelis-Menten Kinetics, Eqn.(4.14)

Notes

The Chemostat cont'd: Michaelis-Menten Kinetics

- Inserting model from Eqn.(4.14) into chemostat equations Eqn.s(4.12, 4.13), to get:

$$\frac{dN}{dt} = \left(\frac{K_{max}C}{K_n + C} \right) N - \frac{FN}{V} \quad (4.15)$$

and

$$\frac{dC}{dt} = -\alpha \left(\frac{K_{max}C}{K_n + C} \right) N - \frac{FC}{V} + \frac{FC_0}{V} \quad (4.16)$$

which include no fewer than two unknowns (N, C) & six parameters ($K_n, K_{max}, F, V, C_0, \alpha$).

Notes

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:

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

& dimensionless variables:

$$\tau = \frac{tF}{V}, \quad n = \frac{N\alpha VK_{max}}{FK_n}, \quad c = \frac{C}{K_n}$$

Notes

The Chemostat cont'd: Michaelis-Menten Kinetics

- 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:

$$\text{units of } \tau = \frac{[\text{time}] \left[\frac{\text{Volume}}{\text{time}} \right]}{[\text{Volume}]} \quad (4.19)$$

rhs of which is dimensionless.

- “dimensionless” \equiv “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)

Notes

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:

$$\alpha_1 \left(\frac{\bar{n}\bar{c}}{1+\bar{c}} \right) - \bar{n} = 0 \quad (4.20)$$

and

$$-\left(\frac{\bar{n}\bar{c}}{1+\bar{c}} \right) - \bar{c} + \alpha_2 = 0 \quad (4.21)$$

where \bar{n}, \bar{c} denote the values at the steady states.

Notes

The Chemostat cont'd: Michaelis-Menten Kinetics

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

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

and

$$(\bar{n}_2, \bar{c}_2) = (0, \alpha_2) \quad (4.23)$$

- \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?

Notes

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:

$$\frac{d\mathbf{X}}{d\tau} = F(\mathbf{X}) \quad (4.24)$$

where \mathbf{X} is the vector $[n(\tau), c(\tau)]$.

- Considering close to the steady states $\hat{\mathbf{X}} = \mathbf{X} - \bar{\mathbf{X}}$ (i.e. small $\hat{\mathbf{X}}$), can say that:

$$\frac{d\hat{\mathbf{X}}}{d\tau} = \frac{d\mathbf{X}}{d\tau} = F(\hat{\mathbf{X}} + \bar{\mathbf{X}}) \quad (4.25)$$

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

$$\frac{d\hat{\mathbf{X}}}{d\tau} = \cancel{F(\bar{\mathbf{X}})}^0 + F'(\bar{\mathbf{X}})\hat{\mathbf{X}} + \cancel{O(\hat{\mathbf{X}}^2)}^0 \quad (4.26)$$

Notes

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:

$$\frac{d\hat{\mathbf{X}}}{d\tau} = \frac{d\mathbf{X}}{d\tau} = F'(\bar{\mathbf{X}})\hat{\mathbf{X}} \approx \mathbf{A}\hat{\mathbf{X}} \quad (4.27)$$

where \mathbf{A} is known as the *Jacobian* of \mathbf{F} and is given by:

$$\mathbf{A} = \begin{pmatrix} \frac{\partial f}{\partial n} & \frac{\partial f}{\partial c} \\ \frac{\partial g}{\partial n} & \frac{\partial g}{\partial c} \end{pmatrix} \quad (4.28)$$

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

$$\frac{d\mathbf{X}}{d\tau} = \mathbf{A}\mathbf{X} \text{ for } \mathbf{X} \approx \bar{\mathbf{X}} \quad (4.29)$$

Notes

Aside: Stability at Steady States cont'd

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

$$\mathbf{X}(\tau) = \sum_{i=1}^n c_i e^{\lambda_i \tau} \mathbf{v}_i \quad (4.30)$$

i.e. a linear combination of eigenpairs $(\mathbf{v}_i, \lambda_i)$ & some unknown coefficients c_i .

- For stability of equilibria (steady states) trajectories approach an equilibrium as $t \rightarrow \infty$
- Since \mathbf{X} measures proximity to our steady states, this effectively means,
- does $\mathbf{X}(t) \rightarrow 0$ for solutions of eqn.(4.27)? (Recall that \mathbf{A} is Jacobian of \mathbf{F} close to steady states).

Notes

Aside: Stability at Steady States cont'd

- Know that $c_i e^{\lambda_i \tau} \mathbf{v}_i \rightarrow 0$, iff $e^{\lambda_i \tau} \rightarrow 0$.
- But for what values of λ does $e^{\lambda_i \tau} \rightarrow 0$?
- Taking magnitudes of bothsides, get

$$\left| e^{\lambda_i \tau} \right| \rightarrow 0. \quad (4.31)$$

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

$$e^{a\tau} \sqrt{(\cos b\tau)^2 + (\sin b\tau)^2} \rightarrow 0. \quad (4.32)$$

- As term inside $\sqrt{\quad}$ is just 1, stability of solutions around steady states simply depends on real parts of all eigenvalues being less than zero.

Notes

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 $q = \det(A)$.

- 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.

Notes

Aside: Stability at Steady States cont'd

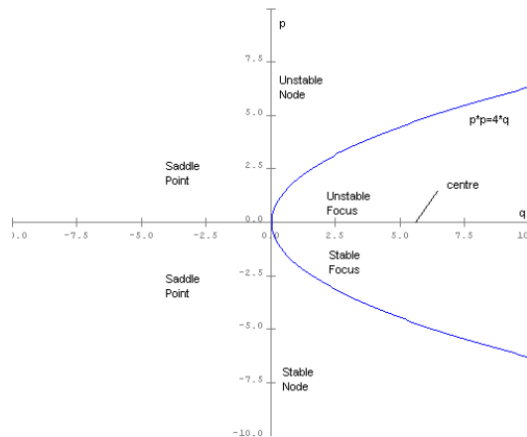


FIGURE 4.5 : Stability points on p V q

Notes

Aside: Stability at Steady States cont'd

- From Fig. 3.2, observe a number of cases:

1 λ_1, λ_2 real and distinct:

- If λ_1, λ_2 have same sign, steady state is a blue node. if $\lambda_2 < \lambda_1 < 0$, soln for $\mathbf{X} = (x \ y)^t \rightarrow 0$ in Eqn.(4.30) & it is a *stable node*. If $\lambda_1 > \lambda_2 > 0$, it is a *unstable node*.
- λ_1, λ_2 have different signs, one part of soln in Eqn.(4.30) will always go to 0 & other will go to ∞ . This is a *saddle point* singularity & is always *unstable*.

2 E-values are complex: $\lambda_1, \lambda_2 = \alpha \pm i\beta$, solns to Eqn.(4.30) are oscillatory (product of $e^{\alpha\tau}$ & $e^{i\beta\tau}$); 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.

Notes

Aside: Stability at Steady States cont'd

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

Type	Eigenvalues	Trace p , Det q
Saddle Point	different signs	$q < 0$
Stable Node	$\lambda_2 < \lambda_1 < 0$	$p < 0$ & $q > 0$
Unstable Node	$\lambda_1 > \lambda_2 > 0$	$p > 0$ & $q > 0$
Stable Focus	$\Re(\lambda) < 0$	$p^2 < 4q$ & $p < 0$
Unstable Focus	$\Re(\lambda) > 0$	$p^2 < 4q$ & $p > 0$
Centre	$\Re(\lambda) = 0$	$p^2 < 4q$ & $p = 0$

TABLE 4.2 : Stability & Matrix Properties

Notes

Aside: Stability at Steady States cont'd

- Eqn.(4.34) roots are $\lambda = \frac{p \pm \sqrt{p^2 - 4q}}{2}$, so: $\sqrt{p^2 - 4q} < p$, i.e. $p < 0$ ($\text{trace}(\mathbf{A}) < 0$) & $q > 0$ ($\text{det}(\mathbf{A}) > 0$) 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

$$\frac{d\mathbf{X}}{d\tau} = F(\mathbf{X}) = \begin{pmatrix} f(n, c) \\ g(n, c) \end{pmatrix} \quad (4.35)$$

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

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

and

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

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Notes

The Chemostat: Stability at Steady States

- So, getting back to the chemostat problem, if $\mathbf{F} = (f, g)$ 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 \mathbf{A} of \mathbf{F} (from eqn.(4.28)) is given by

$$\mathbf{A} = \begin{pmatrix} \alpha_1 \frac{c}{1+c} - 1 & \frac{\alpha_1 n}{(1+c)^2} \\ -\frac{c}{1+c} & -\frac{n}{(1+c)^2} - 1 \end{pmatrix} \quad (4.38)$$

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Notes

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:

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

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

Notes

The Chemostat: Stability at Steady States

- 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.

Notes

The Chemostat: Stability at Steady States

- So, in dimensional form, $\alpha_1 > 1$ corresponds to $\frac{1}{K_{max}} < \frac{V}{F}$.
 - As K_{max} is max bacterial repro rate with *unlimited* nutrients $dN/dt = K_{max}N$, $\frac{\ln 2}{K_{max}}$ gives doubling time τ_2 of bacterial pop'n.
 - V/F = 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 ($\tau_2 = \frac{\ln 2}{K_{max}}$), 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.

Notes

Chapter 5:

Linear & Non-Linear Interaction Models

Notes
