Mathematical Biology-I

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1 Linearization

$$\begin{aligned}
\frac{dN}{dt} &= I_n - r_n N - \frac{\gamma r_1 N X}{k_1 + N} - \gamma d_D D \\
\frac{dX}{dt} &= \frac{r_1 N X}{k_1 + N} - (d_1 + e_1)X \\
\frac{dD}{dt} &= d_1 X - (d_D + e_D)D
\end{aligned} \tag{1}$$

To linearize Equations (1), substitute $N = N^* + N'$, $X = X^* + X'$, and $D = D^* + D'$. Since N^*, X^* and D^* are constants, therefore, $\frac{d(N^*+N')}{dt} = \frac{dN'}{dt}$, $\frac{d(X^*+X')}{dt} = \frac{dX'}{dt}$, $\frac{d(D^*+D')}{dt} = \frac{dD'}{dt}$. The first equation of (1) becomes

$$\frac{dN'}{dt} = I_n - r_n(N^* + N') - \frac{\gamma r_1 (N^* + N')(X^* + X')}{k_1 + (N^* + N')} - \gamma d_D (D^* + D')$$

which can be written as

$$\begin{aligned}
\frac{dN'}{dt} &= I_n - r_nN^* - r_nN' - \frac{\gamma r_1(N^*+N')(X^*+X')}{(k_1+N^*)\left(1+\frac{N'}{k_1+N^*}\right)} - \gamma d_D D^* - \gamma d_D D' \\
&= I_n - r_nN^* - \gamma d_D D^* - r_nN' - \gamma d_D D' - \frac{\gamma r_1(N^*+N')(X^*+X')}{k_1+N^*}\left(1+\frac{N'}{k_1+N^*}\right)^{-1} \\
&= I_n - r_nN^* - \gamma d_D D^* - r_nN' - \gamma d_D D' - \frac{\gamma r_1(N^*X^*+N^*X'+X^*N'+N'X')}{k_1+N^*}\left(1-\frac{N'}{k_1+N^*}\right) \\
&\quad \text{(neglecting higher power of } N' \text{ in the expansion of } \left(1+\frac{N'}{k_1+N^*}\right)^{-1}\text{)} \\
&= I_n - r_nN^* - \gamma d_D D^* - r_nN' - \gamma d_D D' - \frac{\gamma r_1(N^*X^*+N^*X'+X^*N')}{k_1+N^*}\left(1-\frac{N'}{k_1+N^*}\right) \\
&\quad \text{(neglecting } N'X' \text{ as it is very small quantity)} \\
&= I_n - r_nN^* - \gamma d_D D^* - r_nN' - \gamma d_D D' - \frac{\gamma r_1(N^*X^*+N^*X'+X^*N')}{k_1+N^*}\left(1-\frac{N'}{k_1+N^*}\right) \\
&= I_n - r_nN^* - \gamma d_D D^* - r_nN' - \gamma d_D D' - \frac{\gamma r_1(N^*X^*+N^*X'+X^*N')}{k_1+N^*} + \frac{\gamma r_1 N^*X^*}{k_1+N^*}\frac{N'}{k_1+N^*} \\
&= I_n - r_nN^* - \gamma d_D D^* - \frac{\gamma r_1 N^*X^*}{k_1+N^*} \\
&\quad - r_nN' - \frac{\gamma r_1 X^*}{k_1+N^*}N' + \frac{\gamma r_1 N^*X^*}{(k_1+N^*)^2}N' - \frac{\gamma r_1 N^*}{k_1+N^*}X' - \gamma d_D D' \\
&= I_n - r_nN^* - \gamma d_D D^* - \frac{\gamma r_1 N^*X^*}{k_1+N^*} \\
&\quad - r_nN' - \frac{\gamma r_1 k_1 X^*}{(k_1+N^*)^2}N' - \frac{\gamma r_1 N^*}{k_1+N^*}X' - \gamma d_D D'
\end{aligned}$$

Since N^*, X^*, D^* is a fixed point so $I_n - r_nN^* - \gamma d_D D^* - \frac{\gamma r_1 N^*X^*}{k_1+N^*} = 0$, therefore, we have

$$\frac{dN'}{dt} = -r_nN' - \frac{\gamma r_1 k_1 X^*}{(k_1+N^*)^2}N' - \frac{\gamma r_1 N^*}{k_1+N^*}X' - \gamma d_D D'$$

as a linear equation.

The second equation of (1) becomes

$$\frac{dX'}{dt} = \frac{r_1(N^*+N')(X^*+X')}{k_1+(N^*+N')} - (d_1+e_1)(X^*+X')$$

which can be written as

$$\begin{aligned}
\frac{dX'}{dt} &= \frac{r_1(N^*+N')(X^*+X')}{(k_1+N^*)\left(1+\frac{N'}{k_1+N^*}\right)} - (d_1+e_1)X^* - (d_1+e_1)X' \\
&= \frac{r_1(N^*X^*+N^*X'+N'X^*+N'X')}{k_1+N^*}\left(1+\frac{N'}{k_1+N^*}\right)^{-1} - (d_1+e_1)X^* - (d_1+e_1)X' \\
&= \frac{r_1(N^*X^*+N^*X'+N'X^*)}{k_1+N^*}\left(1-\frac{N'}{k_1+N^*}\right) - (d_1+e_1)X^* - (d_1+e_1)X' \\
&= \frac{r_1N^*X^*}{k_1+N^*} - (d_1+e_1)X^* + \frac{r_1X^*}{k_1+N^*}N' - \frac{r_1N^*X^*}{(k_1+N^*)^2}N' + \frac{r_1N^*}{k_1+N^*}X' - (d_1+e_1)X' \\
&= \frac{r_1N^*X^*}{k_1+N^*} - (d_1+e_1)X^* + \frac{r_1k_1X^*}{(k_1+N^*)^2}N' + \frac{r_1N^*}{k_1+N^*}X' - (d_1+e_1)X'
\end{aligned}$$

Since X^*, N^* is fixed point so $\frac{r_1N^*X^*}{k_1+N^*} - (d_1+e_1)X^* = 0$, therefore, we get

$$\frac{dX'}{dt} = \frac{r_1k_1X^*}{(k_1+N^*)^2}N' + \frac{r_1N^*}{k_1+N^*}X' - (d_1+e_1)X'$$

as linear equation.

Similarly for third equation of (1), corresponding linear equation becomes

$$\frac{dD'}{dt} = d_1X' - (d_D+e_D)D'$$

Hence corresponding linearized system becomes

$$\begin{aligned}
\frac{dN'}{dt} &= -r_nN' - \frac{\gamma r_1k_1X^*}{(k_1+N^*)^2}N' - \frac{\gamma r_1N^*}{k_1+N^*}X' - \gamma d_DD' \\
\frac{dX'}{dt} &= \frac{r_1k_1X^*}{(k_1+N^*)^2}N' + \frac{r_1N^*}{k_1+N^*}X' - (d_1+e_1)X' \qquad (2) \\
\frac{dD'}{dt} &= d_1X' - (d_D+e_D)D'
\end{aligned}$$

2 Finding equilibrium point

$$\frac{dN}{dt} = I_n - r_nN - \gamma\frac{r_1NX}{k_1+N} + \gamma d_DD \qquad (3)$$

$$\frac{dX}{dt} = \frac{r_1NX}{k_1+N} - \frac{fXY}{b_1+X} - (d_1+e_1)X - g_1X^2 \qquad (4)$$

$$\frac{dY}{dt} = \eta\frac{fXY}{b_1+X} - (d_2+e_2)Y \qquad (5)$$

$$\frac{dD}{dt} = (1-\eta)\frac{fXY}{b_1+X} + d_1X + d_2Y + g_1X^2 - d_DD \qquad (6)$$

For equilibrium points of the above system, we have

$$0 = I_n - r_n N^* - \gamma \frac{r_1 N^* X^*}{k_1 + N^*} + \gamma d_D D^* \tag{7}$$

$$0 = \frac{r_1 N^* X^*}{k_1 + N^*} - \frac{f X^* Y^*}{b_1 + X^*} - (d_1 + e_1) X^* - g_1 X^{*2} \tag{8}$$

$$0 = \eta \frac{f X^* Y^*}{b_1 + X^*} - (d_2 + e_2) Y^* \tag{9}$$

$$0 = (1 - \eta) \frac{f X^* Y^*}{b_1 + X^*} + d_1 X^* + d_2 Y^* + g_1 X^{*2} - d_D D^* \tag{10}$$

From the equation (9), we get ether $Y^* = 0$ or $\frac{\eta f X^*}{b_1 + X^*} = (d_2 + e_2)$, which gives

$$X^* = \frac{b_1 (d_2 + e_2)}{\eta f - d_2 - e_2} = a \text{ (say)}$$

Now, dividing (7) by γ and then this to the rest of three equations (8)-(10) we get

$$\frac{I_n - r_n N^*}{\gamma} - e_1 X^* - e_2 Y^* = 0$$

Using the value of $X^* = a$ we get

$$Y^* = \frac{I_n}{e_2 \gamma} - \frac{e_1}{e_2} a - \frac{r_n}{e_2 \gamma} N^* \tag{11}$$

From (8), we get

$$\frac{r_1 N^*}{k_1 + N^*} = \frac{f Y^*}{b_1 + a} + (d_1 + e_1) + g_1 a, \quad \text{since } X^* = a.$$

Which can be written as

$$\frac{r_1 (b_1 + a) N^*}{k_1 + N^*} = f Y^* + (b_1 + a)\{d_1 + e_1 + g_1 a\}$$

$$or, \quad \frac{r_1 (b_1 + a) N^*}{k_1 + N^*} = f \frac{I_n}{e_2 \gamma} - f \frac{e_1}{e_2} a - f \frac{r_n}{e_2 \gamma} N^* + (b_1 + a)\{d_1 + e_1 + g_1 a\}$$

$$or, \quad e_2 \gamma r_1 (b_1 + a) \frac{N^*}{k_1 + N^*} = f I_n + e_2 \gamma (b_1 + a)\{d_1 + e_1 + g_1 a\} - f e_1 \gamma a - f r_n N^*$$

$$or, \quad r \frac{N^*}{k_1 + N^*} = c - N^* \tag{12}$$

where $r = \frac{e_2 \gamma r_1 (b_1 + a)}{f r_n}$ and $c = \frac{f I_n + e_2 \gamma (b_1 + a)\{d_1 + e_1 + g_1 a\} - f e_1 \gamma a}{f r_n}$.
Therefore, (12) gives

$$N^{*2} + (k_1 + r - c) N^* - c k_1 = 0.$$

Assuming $c > 0$, we can say that the above equation gives a unique positive root as

$$N^* = \frac{1}{2}\left[-(k_1 + r - c) + \sqrt{(k_1 + r - c)^2 + 4 c k_1} \right].$$

From (7), we have

$$D^* = \frac{r_n}{\gamma d_D}N^* + \frac{ar_1 N^*}{(k_1+N^*)d_D} - \frac{I_n}{\gamma d_D}$$

Finally, we have the interior equilibrium point as (N^*, X^*, Y^*, D^*), such that, $X^* = \frac{b_1(d_2+e_2)}{\eta f - d_2 - e_2} = a$ (say), $N^* = \frac{1}{2}\left[-(k_1+r-c)+\sqrt{(k_1+r-c)^2+4ck_1}\right]$, $Y^* = \frac{I_n}{e_2\gamma} - \frac{e_1}{e_2}a - \frac{r_n}{e_2\gamma}N^*$ and $D^* = \frac{r_n}{\gamma d_D}N^* + \frac{ar_1N^*}{(k_1+N^*)d_D} - \frac{I_n}{\gamma d_D}$, where $r = \frac{e_2\gamma r_1(b_1+a)}{fr_n}$ and $c = \frac{fI_n + e_2\gamma(b_1+a)\{d_1+e_1+g_1a\} - fe_1\gamma a}{fr_n}$.

3 Chemostat model

Consider the following model (Monod model)

$$\begin{aligned}\frac{dX}{dt} &= \mu X - DX\\ \frac{dS}{dt} &= D(S_0 - S) - \frac{\mu X}{Y}\end{aligned}$$

where $\mu = \frac{\hat{\mu}S}{K_s+S}$ and $\hat{\mu}$, D K_s & S_0 are all positive quantities.

For equilibrium point we write the system in its compact form as

$$\begin{aligned}\frac{dX}{dt} &= \frac{\hat{\mu}XS}{K_s+S} - DX\\ \frac{dS}{dt} &= D(S_0 - S) - \frac{\hat{\mu}XS}{Y(K_s+S)}\end{aligned}$$

Here $(0, S_0)$ is an axial equilibrium point and the interior equilibrium point is given by

$$\frac{\hat{\mu}S^*}{K_s+S^*} - D = 0, \quad \text{since } X^* \neq 0 \tag{13}$$

$$\text{and} \quad D(S_0 - S^*) - \frac{\hat{\mu}X^*S^*}{Y(K_s+S^*)} = 0 \tag{14}$$

From (13) we get $S^* = \frac{K_sD}{\hat{\mu}-D}$ which is positive if $D < \hat{\mu}$. Using (13) in (14) we get

$$\begin{aligned}D(S_0 - S^*) - \frac{DX^*}{Y} &= 0\\ \Rightarrow\ (S_0 - S^*) - \frac{X^*}{Y} &= 0\\ \Rightarrow\ X^* &= Y(S_0 - S^*)\\ \Rightarrow\ X^* &= Y(S_0 - \frac{K_sD}{\hat{\mu}-D})\\ \Rightarrow\ X^* &= Y\left(\frac{S_0(\hat{\mu}-D) - K_sD}{\hat{\mu}-D}\right)\\ \Rightarrow\ X^* &= Y\frac{\hat{\mu}S_0 - D(S_0+K_s)}{\hat{\mu}-D}\end{aligned}$$

Clearly, X^* is positive if $D < \frac{\hat{\mu}S_0}{S_0+K_s}$. Now if we compare two number $\hat{\mu}$ and $\frac{\hat{\mu}S_0}{S_0+K_s}$ it is clear that $\hat{\mu} > \frac{\hat{\mu}S_0}{S_0+K_s}$ as S_0 and K_s are both positive quantity. Therefore, the equilibrium point $(X^*, S^*) \equiv \left(Y\frac{\hat{\mu}S_0 - D(S_0+K_s)}{\hat{\mu}-D}, \frac{K_sD}{\hat{\mu}-D}\right)$ is a positive one if $D < \frac{\hat{\mu}S_0}{S_0+K_s}$.

Now to show the stability analysis first we obtain the Jacobian matrix at any arbitrary fixed point as

$$J(X,S) = \begin{pmatrix} \frac{\hat{\mu}S}{K_s+S} - D & \frac{\hat{\mu}K_sX}{(K_s+S)^2} \\ -\frac{\hat{\mu}S}{Y(K_s+S)} & -D - \frac{\hat{\mu}K_sX}{Y(K_s+S)^2} \end{pmatrix}$$

At the axial equilibrium point $(0, S_0)$ the Jacobian matrix reduces to

$$J(0,S_0) = \begin{pmatrix} \frac{\hat{\mu}S_0}{K_s+S_0} - D & 0 \\ -\frac{\hat{\mu}S_0}{Y(K_s+S_0)} & -D \end{pmatrix}$$

Corresponding eigenvalues are $\lambda_1 = \frac{\hat{\mu}S_0}{K_s+S_0} - D$ and $\lambda_2 = -D$. If $D > \frac{\hat{\mu}S_0}{S_0+K_s}$, then both the eigenvalues are negative which implies that the axial equilibrium point is stable. But in that case the interior equilibrium point does not exists. Once the axial equilibrium point becomes unstable then the interior equilibrium point exists, then we go for the stability analysis of that point.

Now at (X^*, S^*) the Jacobian matrix reduces to

$$J(X^*,S^*) = \begin{pmatrix} 0 & \frac{\hat{\mu}K_sX^*}{(K_s+S^*)^2} \\ -\frac{\hat{\mu}S^*}{Y(K_s+S^*)} & -D - \frac{\hat{\mu}K_sX^*}{Y(K_s+S^*)^2} \end{pmatrix} = A \text{ (say)}$$

So, the characteristic equation is given by

$$\lambda^2 - \text{tr}(A)\lambda + \det(A) = 0 \tag{15}$$

where $\text{tr}(A) = -D - \frac{\hat{\mu}K_sX^*}{Y(K_s+S^*)^2} < 0$ and $\det(A) = \frac{\hat{\mu}K_sX^*}{(K_s+S^*)^2}\frac{\hat{\mu}S^*}{Y(K_s+S^*)} > 0$. Therefore, the eigenvalues of (20) are all negative or have negative real parts, hence whenever the interior equilibrium point exists it is locally asymptotically stable.

4 Phytoplankton-Zooplankton Model

Consider the following phytoplankton-zooplankton model

$$\begin{aligned} \frac{dP}{dt} &= P(a-P) - \frac{P^nZ}{1+bP^n} \\ \frac{dZ}{dt} &= \frac{cP^nZ}{1+bP^n} - dZ^m \end{aligned}$$

where a, b c d, m & n are all positive quantities.

For $n = 2$ and $m = 1$, the equilibrium points of the system will be given by

$$P(a-P) - \frac{P^2 Z}{1+bP^2} = 0 \tag{16}$$
$$\frac{cP^2 Z}{1+bP^2} - dZ = 0 \tag{17}$$

Here $(0,0)$ is the trivial equilibrium point, $a, 0$ is an axial equilibrium point and the interior equilibrium point (P^*, Z^*) is given by

$$(a-P^*) - \frac{P^* Z^*}{1+bP^{*2}} = 0 \tag{18}$$
$$\frac{cP^{*2}}{1+bP^{*2}} - d = 0 \tag{19}$$

From (18) we get $P^* = \sqrt{\frac{d}{c-bd}}$ which is real if $c > bd$. From (19) we get

$$(a-P^*)(1+bP^{*2}) - P^* Z^* = 0$$
$$=> \quad Z^* = = \frac{(a-P^*)(1+bP^{*2})}{P^*}$$

Now, Z^* is positive if $a > P^* \implies a > \sqrt{\frac{d}{c-bd}}$. Since both the terms in this inequality are positive, then we get $a^2 > \frac{d}{c-bd}$ which implies $c > bd + \frac{d}{a^2}$. Therefore, the interior equilibrium point is given by $(P^*, Z^*) \equiv \left(P^*, \frac{(a-P^*)(1+bP^{*2})}{P^*}\right)$, where $P^* = \sqrt{\frac{d}{c-bd}}$ and which is real positive when $c > bd + \frac{d}{a^2}$.

Now to show the stability analysis first we obtain the Jacobian matrix at any arbitrary fixed point as

$$J(P,Z) = \begin{pmatrix} a - 2P - \frac{2PZ}{(1+bP^2)^2} & -\frac{P^2}{1+bP^2} \\ \frac{2cPZ}{(1+bP^2)^2} & \frac{cP^{*2}}{1+bP^{*2}} - d \end{pmatrix}$$

At the trivial equilibrium point $(0,0)$ the Jacobian matrix reduces to

$$J(0,0) = \begin{pmatrix} a & 0 \\ 0 & -d \end{pmatrix}$$

and corresponding eigenvalues are $\lambda_1 = a > 0$ and $\lambda_2 = -d < 0$, so $(0,0)$ is unstable fixed point. At the axial equilibrium point $(a,0)$ the Jacobian matrix reduces to

$$J(P,Z) = \begin{pmatrix} -a & -\frac{a^2}{1+ba^2} \\ 0 & \frac{ca^2}{1+ba^2} - d \end{pmatrix}$$

Corresponding eigenvalues are $\lambda_1 = -a < 0$ and $\lambda_2 = \frac{ca^2}{1+ba^2} - d$. Now $d > \frac{ca^2}{1+ba^2}$ implies $d(1+ba^2) > ca^2 \implies c < bd + \frac{d}{a^2}$, then $\lambda_2 < 0$, i.e., both the eigenvalues are negative which implies that the axial equilibrium point is stable. But in that case the interior equilibrium point does not exists. Once the axial equilibrium point becomes unstable i.e., when $c > bd + \frac{d}{a^2}$ then the interior equilibrium point exists, then we go for the stability analysis of that point.

Now at (P^*, Z^*) the Jacobian matrix reduces to

$$J(P^*, Z^*) = \begin{pmatrix} a - 2P^* - \frac{2P^*Z^*}{(1+bP^{*2})^2} & -\frac{P^{*2}}{1+bP^{*2}} \\ \frac{2cP^*Z^*}{(1+bP^{*2})^2} & 0 \end{pmatrix} = A \text{ (say)}$$

So, the characteristic equation is given by

$$\lambda^2 - \mathrm{tr}(A)\lambda + \det(A) = 0 \qquad (20)$$

where $\mathrm{tr}(A) = a - 2P^* - \frac{2P^*Z^*}{(1+bP^{*2})^2}$ and $\det(A) = \frac{P^{*2}}{1+bP^{*2}} \frac{2cP^*Z^*}{(1+bP^{*2})^2} > 0$. Now the stability of interior equilibrium point depends on the sign of $\mathrm{tr}(A)$. We see that

$$\begin{aligned} \mathrm{tr}(A) &= a - 2P^* - \frac{2P^*Z^*}{(1+bP^{*2})^2} \\ &= a - 2P^* - \frac{2P^*}{(1+bP^{*2})^2} \times \frac{(a-P^*)(1+bP^{*2})}{P^*} \\ &= a - 2P^* - \frac{2(a-P^*)}{1+bP^{*2}} \\ &= \frac{(a-2P^*)(1+bP^{*2}) - 2(a-P^*)}{1+bP^{*2}} \\ &= \frac{-(2bP^{*3} - abP^{*2} + a)}{1+bP^{*2}} \end{aligned}$$

Therefore, the eigenvalues of (20) are all negative or have negative real parts if $\mathrm{tr}(A) < 0$ i.e., if $2bP^{*3} - abP^{*2} + a > 0$. So, whenever the interior equilibrium point exists and if $2bP^{*3} - abP^{*2} + a > 0$ is satisfied then it is locally asymptotically stable.

The stability of interior equilibrium point can shown by choosing the following set of numerical values to the parameters such as $a = 2,\ b = 1, c = 2, d = 1$ then we see that $P^* = \sqrt{\frac{d}{c-bd}} = \sqrt{\frac{1}{2-1\times1}} = 1,\ Z^* = \frac{(a-P^*)(1+bP^{*2})}{P^*} = \frac{(2-1)(1+1\times1^2)}{1} = 2$, corresponding conditions like $c > bd + \frac{d}{a^2}$ and $a > P^*$ are also satisfied here. Now $\mathrm{tr}(A)$ becomes $a - 2P^* - \frac{2(a-P^*)}{1+bP^{*2}} = 2 - 2\times1 - \frac{2(2-1)}{1+1\times1^2} = 2-2-1 = -1 < 0$, clearly $\det(A)$ is also positive. Hence with this choice of parameters the system is locally asymptotically stable.

5 Phytoplankton-Zooplankton Model with Nutrient Recycle

Consider the following phytoplankton-zooplankton model with nutrient recycle

$$\begin{aligned}\frac{dN}{dt} &= D(N_0 - N) - aPu(N) + (1-\delta)cZw(P)\\ \frac{dP}{dt} &= aPu(N) - cZw(P) - (\gamma + D_1)P\\ \frac{dZ}{dt} &= Z[\delta cw(P) - (\epsilon + D_2)]\end{aligned}$$

where $u(N) = \frac{N}{1+N}$, $w(P) = 1 - e^{-\alpha P}$ and D, N_0, a, δ, c, α, γ, D_1, ϵ & D_2 are all positive quantities.