Mathematical Biology Assignment 1

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1. A boat carries N similar rowers each of whom puts in the same P power to propelling the boat

   (a) Assuming each rower occupies the same V volume of the boat, show the wetted area of the boat is $A \propto (NV)^{2/3}$ A has units $[L]^2$, NV has units $[L]^3$ since NV is the volume occupied by N rowers

   Want to find non-dimensional groupings which work, since the system will have form

$$f(\lambda_1, \lambda_2, \ldots) = 0$$

   Where λ_i are non-dimensional groupings of terms. In this case we can generate the non-dimensional grouping

$$\frac{A^3}{(NV)^2}$$

   And hence

$$A^3 \propto (NV)^2 \implies A \propto (NV)^{2/3}$$

   (b) Assuming that F_{drag} depends on the wetted area of the boat, A, its speed, U, and the density of the water, ρ, show that F_{drag} is proportional to $\rho U^2 A$ and that the rate of energy dissipation due to drag must be proportional to $\rho U^3 A$.

   Force has units $[M][L][T]^{-2}$, density $[M][L]^{-3}$, speed $[L][T]^{-1}$, area $[L]^2$ If the LHS is the quantity, and the RHS is the units (I will write F instead of F_{drag})

$$\begin{aligned}
F &= \frac{[M][L]}{[T]^2} \\
\frac{F}{\rho} &= \frac{[M][L][L]^3}{[M][T]^2} \\
\frac{F}{\rho} &= \frac{[L]^4}{[T]^2} \\
\frac{F}{\rho U^2} &= \frac{[L]^4[T]^2}{[L]^2[T]^2} \\
\frac{F}{\rho U^2} &= [L^2] \\
\frac{F}{\rho U^2 A} &= \frac{[L^2]}{[L]^2} = [1]
\end{aligned}$$

   Hence

$$f\left(\frac{F}{\rho U^2 A}\right) = const \implies F \propto \rho U^2 A$$

And the rate of energy dissipation, has same units as power: dE has units $[M][L]^2[T]^{-3}$ (energy/time)

$$\begin{aligned} dE &= [M][L]^2[T]^{-3} \\ \frac{dE}{\rho U^2 A} &= \frac{[L]}{[T]} \\ \frac{dE}{\rho U^3 A} &= [1] \end{aligned}$$

And as before we get

$$f\left(\frac{dE}{\rho U^3 A}\right) = const \implies dE \propto \rho U^3 A$$

(c) Hence show $U \propto N^{1/9} P^{1/3} \rho^{-1/3} V^{-2/9}$
From part (a), $A \propto (NV)^{2/3}$ and the power provided, NP with units $[M][L]^2[T]^{-3}$

$$\begin{aligned} dE &\propto \rho U^3 A \\ U &\propto \left(\frac{dE}{\rho A}\right)^{1/3} \\ U &\propto dE^{1/3} \rho^{-1/3} (NV)^{-2/9} \end{aligned}$$

But $dE \propto NP$

$$\begin{aligned} U &\propto dE^{1/3} \rho^{-1/3} (NV)^{-2/9} \\ U &\propto (NP)^{1/3} \rho^{-1/3} (NV)^{-2/9} \\ U &\propto N^{1/9} P^{1/3} \rho^{-1/3} V^{-2/9} \end{aligned}$$

(d) If we assume P, V are both propto body mass, is size an advantage to a rower? A rower will ideally generate the most speed, so it is an advantage if U is bigger.
If $P \propto V \propto M$ then we can sub it into the U equation

$$\begin{aligned} U &\propto N^{1/9} P^{1/3} \rho^{-1/3} V^{-2/9} \\ U &\propto N^{1/9} M^{1/3} \rho^{-1/3} M^{-2/9} \\ U &\propto N^{1/9} M^{1/9} \rho^{-1/3} \end{aligned}$$

Since the power of M is positive, yes it would be an advantage.

2. Investigate the Coriolis effect

Navier-Stokes gives

$$\rho\left(\frac{\partial \mathbf{u}}{\partial t} + 2\boldsymbol{\Omega} \times \mathbf{u} + \mathbf{u} \cdot \nabla \mathbf{u}\right) = -\nabla p + \mu \nabla^2 \mathbf{u} + \rho(\mathbf{g} - \boldsymbol{\Omega} \times (\boldsymbol{\Omega} \times \mathbf{x}))$$

Assuming the origin of the coordinate system is the centre of the Earth. Ω is 2π per 24 hours (or $7.3 \times 10^{-5} s^{-1}$) in the direction of the Earth's axis of rotation. The radius of the earth is $\approx 6,400km$. Assume the water body is a bathtub with lengthscale $\sim 1m$ and water flows $\sim 1ms^{-1}$. Take density $= 1000kg\ m^{-3}$ and viscosity $8.9 \times 10^{-4} Pa\ s$. Non dimensionalise and determine if the LHS (Coriolis acceleration) is significant (and hence if swirl direction will change depending on which hemisphere you are in)

Where $2\Omega \times \mathbf{u}$ is the Coriolis gravity term.

Let $x = L\tilde{x}$, $u = U\tilde{u}$, $t = \frac{L}{U}\tilde{t}$, $p = P\tilde{p}$ and $\mathbf{\Omega} = \frac{U}{L}\tilde{\Omega}$

$$\rho\left(\frac{\partial \mathbf{u}}{\partial t} + 2\mathbf{\Omega} \times \mathbf{u} + \mathbf{u}\cdot\nabla\mathbf{u}\right) = -\nabla p + \mu\nabla^2\mathbf{u} + \rho(\mathbf{g} - \mathbf{\Omega} \times (\mathbf{\Omega} \times \mathbf{x}))$$

$$\rho\left(\frac{U^2}{L}\frac{\partial \tilde{\mathbf{u}}}{\partial \tilde{t}} + \frac{U^2}{L}2\tilde{\mathbf{\Omega}} \times \tilde{\mathbf{u}} + \frac{U^2}{L}\tilde{\mathbf{u}}\cdot\nabla\tilde{\mathbf{u}}\right) = -\frac{P}{L}\nabla\tilde{p} + \mu\frac{U}{L^2}\nabla^2\tilde{\mathbf{u}} + \rho(\frac{U^2}{L}\tilde{\mathbf{g}} - \frac{U^2}{L^2}L\tilde{\mathbf{\Omega}} \times (\tilde{\mathbf{\Omega}} \times \tilde{\mathbf{x}}))$$

$$\frac{\partial \tilde{\mathbf{u}}}{\partial \tilde{t}} + 2\tilde{\mathbf{\Omega}} \times \tilde{\mathbf{u}} + \tilde{\mathbf{u}}\cdot\nabla\tilde{\mathbf{u}} = -\frac{P}{U^2\rho}\nabla\tilde{p} + \frac{\mu}{U\rho L}\nabla^2\tilde{\mathbf{u}} + \tilde{\mathbf{g}} - \tilde{\mathbf{\Omega}} \times (\tilde{\mathbf{\Omega}} \times \tilde{\mathbf{x}})$$

$$\frac{\partial \tilde{\mathbf{u}}}{\partial \tilde{t}} + 2\tilde{\mathbf{\Omega}} \times \tilde{\mathbf{u}} + \tilde{\mathbf{u}}\cdot\nabla\tilde{\mathbf{u}} = -\frac{P}{U^2\rho}\nabla\tilde{p} + \frac{1}{Re}\nabla^2\tilde{\mathbf{u}} + \tilde{\mathbf{g}} - \tilde{\mathbf{\Omega}} \times (\tilde{\mathbf{\Omega}} \times \tilde{\mathbf{x}})$$

$$Re(\frac{\partial \tilde{\mathbf{u}}}{\partial \tilde{t}} + 2\tilde{\mathbf{\Omega}} \times \tilde{\mathbf{u}} + \tilde{\mathbf{u}}\cdot\nabla\tilde{\mathbf{u}}) = -\frac{P\mu L}{U}\nabla\tilde{p} + \nabla^2\tilde{\mathbf{u}} + Re(\tilde{\mathbf{g}} - \tilde{\mathbf{\Omega}} \times (\tilde{\mathbf{\Omega}} \times \tilde{\mathbf{x}}))$$

Where $Re = \frac{U\rho L}{\mu}$ If $Re \to 0$ Then the Coriolis effect is negligible, i.e. we get (letting $P = U^2\rho$)

$$-\nabla\tilde{p} + \nabla^2\tilde{\mathbf{u}} = 0$$

With no curl terms. If $Re \to \infty$, then the Coriolis effect is not negligible:

$$\frac{\partial \tilde{\mathbf{u}}}{\partial \tilde{t}} + 2\tilde{\mathbf{\Omega}} \times \tilde{\mathbf{u}} + \tilde{\mathbf{u}}\cdot\nabla\tilde{\mathbf{u}} = -\nabla\tilde{p} + \tilde{\mathbf{g}} - \tilde{\mathbf{\Omega}} \times (\tilde{\mathbf{\Omega}} \times \tilde{\mathbf{x}})$$

Where $P = \frac{U}{\mu L}$

Using the given numbers: $U \sim 1$ and $L \sim 1$, $\rho \sim 1000$ and $\mu \sim 8.9 \times 10^{-4}$.

$$Re = \frac{1000}{8.9 \times 10^{-4}} = 8.9 \times 10^7$$

Which is quite large. Hence the Coriolis effect is not negligible.

3. Consider the chemical equation

$$mA + nB \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} C$$

(a) Given that the concentration c of C is

$$\frac{dc}{dt} = k_1 a^m b^n - k_{-1} c$$

Write the equations for a, b (the concentrations of A, B) The DEs for a, b are:

$$\frac{da}{dt} = -k_1 a^m b^n + k_{-1} c$$
$$\frac{db}{dt} = -k_1 a^m b^n + k_{-1} c$$

Subject to initial conditions with form $a(0) = a_i$, $b(0) = b_i$ for some a_i, b_i.

(b) Using conservation, eliminate a, and b from the equation for c

$$\frac{d(a+c)}{dt} = 0 \implies a + c = const = a_i$$
$$\frac{d(b+c)}{dt} = 0 \implies b + c = const = b_i$$

$$\begin{aligned}\frac{dc}{dt} &= k_1 a^m b^n - k_{-1} c \\ &= k_1 \left(c - a_i\right)^m \left(c - b_i\right)^n - k_{-1} c\end{aligned}$$

4. Consider Michaelis-Menten, but relax irreversibility, i.e.

$$E + S \underset{k_{-1}}{\overset{k_1}{\rightleftarrows}} C \underset{k_{-2}}{\overset{k_2}{\rightleftarrows}} E + P$$

(a) Write the set of equations for concentrations s, e, c, and p. With ICs

$$s(0) = s_i > 0, \quad e(0) = e_i = \epsilon s_i > 0, \quad c(0) = p(0) = 0$$

$$\frac{de}{dt} = -k_1 es + k_{-1} c + k_2 ep - k_{-2} ep$$
$$\frac{ds}{dt} = -k_1 es + k_{-1} c$$
$$\frac{dc}{dt} = k_1 es - k_{-1} es - k_2 c + k_{-2} ep$$
$$\frac{dp}{dt} = k_2 c - k_{-2} ep$$

With

$$s(0) = s_i > 0, \quad e(0) = e_i = \epsilon s_i > 0, \quad c(0) = p(0) = 0$$

(b) Obtain a conservation law and eliminate e from the system

$$\begin{aligned}\frac{d(e+c)}{dt} = 0 &\implies e(t) + c(t) = const = e_i = \epsilon s_i \\ &\implies e = \epsilon s_i - c\end{aligned}$$

Hence the system of equations reduces to

$$\frac{ds}{dt} = -k_1(\epsilon s_i - c)s + k_{-1} c$$
$$\frac{dc}{dt} = k_1(\epsilon s_i - c)s - k_{-1}(\epsilon s_i - c)s - k_2 c + k_{-2}(\epsilon s_i - c)p$$
$$\frac{dp}{dt} = k_2 c - k_{-2}(\epsilon s_i - c)p$$

(c) Nondimensionalise as in lectures with $\epsilon = e_i/s_i \ll 1$. Show the scaled system has 3 dimensionless parameters (give in terms of the original parameters)

Let

$$s = s_i\tilde{s}, \quad c = c_*\tilde{c}, \quad p = p_*\tilde{p}, \quad t = t_*\tilde{t}$$

(Assuming s_i for s is sensible as it is given as the IC) s equation:

$$\begin{aligned}\frac{s_i}{t_*}\frac{d\tilde{s}}{d\tilde{t}} &= -k_1(\epsilon s_i - c_*\tilde{c})s_i\tilde{s} + k_{-1}c_*\tilde{c} \\ \frac{d\tilde{s}}{d\tilde{t}} &= -t_*k_1(\epsilon s_i - c_*\tilde{c})\tilde{s} + \frac{k_{-1}t_*c_*}{s_i}\tilde{c}\end{aligned}$$

c equation

$$\begin{aligned}\frac{c_*}{t_*}\frac{d\tilde{c}}{d\tilde{t}} &= k_1s_i(\epsilon s_i - c_*\tilde{c})\tilde{s} - k_{-1}s_i(\epsilon s_i - c_*\tilde{c})\tilde{s} - k_2c_*\tilde{c} + k_{-2}(\epsilon s_i - c_*\tilde{c})p_*\tilde{p} \\ \frac{d\tilde{c}}{d\tilde{t}} &= k_1t_*s_i(\frac{\epsilon s_i}{c_*} - \tilde{c})\tilde{s} - k_{-1}t_*(\frac{\epsilon s_i}{c_*} - \tilde{c})\tilde{s} - k_2t_*\tilde{c} + k_{-2}t_*p_*(\frac{\epsilon s_i}{c_*} - \tilde{c})\tilde{p}\end{aligned}$$

p equation

$$\begin{aligned}\frac{p_*}{t_*}\frac{d\tilde{p}}{d\tilde{t}} &= k_2c_*\tilde{c} - k_{-2}(\epsilon s_i - c_*\tilde{c})p_*\tilde{p} \\ \frac{d\tilde{p}}{d\tilde{t}} &= k_2\frac{t_*c_*}{p_*}\tilde{c} - k_{-2}(\epsilon s_i - c_*\tilde{c})t_*\tilde{p}\end{aligned}$$

Let $c_* = \epsilon s_i$. The system becomes:

$$\begin{aligned}\frac{d\tilde{s}}{d\tilde{t}} &= -t_*k_1\epsilon s_i(1 - \tilde{c})\tilde{s} + k_{-1}t_*\epsilon\tilde{c} \\ \frac{d\tilde{c}}{d\tilde{t}} &= k_1t_*s_i(1 - \tilde{c})\tilde{s} - k_{-1}t_*(1 - \tilde{c})\tilde{s} - k_2t_*\tilde{c} + k_{-2}t_*p_*(1 - \tilde{c})\tilde{p} \\ \frac{d\tilde{p}}{d\tilde{t}} &= k_2\frac{t_*c_*}{p_*}\tilde{c} - k_{-2}\epsilon s_it_*(1 - \tilde{c})\tilde{p}\end{aligned}$$

Incomplete

(d) Neglect $\mathcal{O}(\epsilon)$ and smaller terms, find the leading order expression for the dimensionless complex concentration, and show that the dimensionless reaction velocity takes form

$$\frac{d\tilde{p}}{d\tilde{t}} = \frac{A_3\tilde{s} - A_1A_2\tilde{p}}{\tilde{s} + A_2\tilde{p} + A_1 + A_3}$$

We have the conservation

$$\frac{d(p + s + c)}{dt} = 0$$

Where A_i are constants

Incomplete

(e) Show that to leading order, the steady state of product and substrate concentrations (known as the Haldane relationship) is

$$\frac{\tilde{p}}{\tilde{s}} = \frac{k_1 k_2}{k_{-1} k_{-2}}$$

Incomplete

5. Consider

$$E_1 + S \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} C_1 \xrightarrow{k_3} E_1 + P$$
$$E_2 + S \underset{k_{-2}}{\overset{k_2}{\rightleftharpoons}} C_2 \xrightarrow{k_4} E_2 + P$$

(a) Write down the equations for the concentrations of S, E_1, E_2, C_1, C_2, P. Show that there are two conserved quantities and hence reduce the system to 3 equations only containing S, C_1, C_2.

$$\begin{aligned}
\frac{de_1}{dt} &= -k_1 e_1 s + (k_{-1} + k_3) c_1 \\
\frac{de_2}{dt} &= -k_2 e_2 s + (k_{-2} + k_4) c_2 \\
\frac{dc_1}{dt} &= k_1 e_1 s - (k_{-1} + k_3) c_1 \\
\frac{dc_2}{dt} &= k_2 e_2 s - (k_{-2} + k_4) c_2 \\
\frac{ds}{dt} &= -k_1 e_1 s - k_2 e_2 s + k_{-1} c_1 + k_{-2} c_2 \\
\frac{dp}{dt} &= k_3 c_1 + k_4 c_2
\end{aligned}$$

Clearly, by adding the equations,

$$\frac{d(e_1 + c_1)}{dt} = 0$$

$$\frac{d(e_2 + c_2)}{dt} = 0$$

And the p equation is redundant since

$$\frac{d(c_1 + c_2 + s + p)}{dt} = 0$$

And hence the system can reduce to

$$\begin{aligned}
\frac{dc_1}{dt} &= k_1 e_1 s - (k_{-1} + k_3) c_1 \\
\frac{dc_2}{dt} &= k_2 e_2 s - (k_{-2} + k_4) c_2 \\
\frac{ds}{dt} &= -k_1 e_1 s - k_2 e_2 s + k_{-1} c_1 + k_{-2} c_2
\end{aligned}$$

(b) Assume

$$s(0) = s_i > 0, \quad e_1(0) = e_2(0) = e_i = \epsilon s_i > 0$$

Non-dimensionalise to get a system of form

$$\begin{aligned}\frac{ds}{dt} &= -s(1+\alpha) + c_1(\mu_1 + s) + \alpha c_2(\mu_2 + s)\\ \epsilon\frac{dc_1}{dt} &= s(1-c_1) - \lambda_1 c_1\\ \epsilon\frac{dc_2}{dt} &= \alpha\left[s(1-c_2) - \lambda_2 c_2\right]\end{aligned}$$

Defining the parameters in terms of the original dimensionless parameters
By using $e_1 = e_i - c_1$ and $e_2 = e_i - c_2$ Let

$$s = s_*\tilde{s}, \quad c_1 = c_1^*\tilde{c}_1, \quad c_2 = c_2^*\tilde{c}_2, \quad t = t^*\tilde{t}$$

$$\begin{aligned}\frac{ds}{dt} &= -k_1e_1s - k_2e_2s + k_{-1}c_1 + k_{-2}c_2\\ &= -k_1(e_i - c_1)s - k_2(e_i - c_2)s + k_{-1}c_1 + k_{-2}c_2\\ &= -k_1e_is + k_1c_1s - k_2e_is + k_2c_2s + k_{-1}c_1 + k_{-2}c_2\\ &= -s(e_ik_1 + e_ik_2) + c_1(k_{-1} + k_1s) + c_2(k_{-2} + k_2s)\\ &= -se_ik_1(1 + \frac{k_2}{k_1}) + k_1c_1(\frac{k_{-1}}{k_1} + s) + k_2c_2(\frac{k_{-2}}{k_2} + s)\\ \frac{s_*}{t^*}\frac{d\tilde{s}}{d\tilde{t}} &= -s_*\tilde{s}e_ik_1(1 + \frac{k_2}{k_1}) + k_1c_1^*\tilde{c}_1(\frac{k_{-1}}{k_1} + s_*\tilde{s}) + k_2c_2^*\tilde{c}_2(\frac{k_{-2}}{k_2} + s_*\tilde{s})\\ \frac{d\tilde{s}}{d\tilde{t}} &= -t^*\tilde{s}e_ik_1(1 + \frac{k_2}{k_1}) + t^*k_1c_1^*\tilde{c}_1(\frac{k_{-1}}{k_1s_*} + \tilde{s}) + t^*k_2c_2^*\tilde{c}_2(\frac{k_{-2}}{k_2s_*} + \tilde{s})\end{aligned}$$

Letting $t^* = \frac{1}{e_ik_1}$ gives

$$\frac{d\tilde{s}}{d\tilde{t}} = -\tilde{s}(1 + \frac{k_2}{k_1}) + \frac{1}{e_i}c_1^*\tilde{c}_1(\frac{k_{-1}}{k_1s_*} + \tilde{s}) + \frac{1}{e_ik_1}k_2c_2^*\tilde{c}_2(\frac{k_{-2}}{k_2s_*} + \tilde{s})$$

Letting $c_1^* = e_i$, and $\frac{k_2}{k_1} =: \alpha$

$$\frac{d\tilde{s}}{d\tilde{t}} = -\tilde{s}(1 + \alpha) + \tilde{c}_1(\frac{k_{-1}}{k_1s_*} + \tilde{s}) + \frac{1}{e_i}\alpha c_2^*\tilde{c}_2(\frac{k_{-2}}{k_2s_*} + \tilde{s})$$

Letting $c_2^* = e_i$ gives

$$\frac{d\tilde{s}}{d\tilde{t}} = -\tilde{s}(1 + \alpha) + \tilde{c}_1(\frac{k_{-1}}{k_1s_*} + \tilde{s}) + \alpha\tilde{c}_2(\frac{k_{-2}}{k_2s_*} + \tilde{s})$$

Considering the c equations:

$$\begin{aligned}
\frac{dc_1}{dt} &= k_1 e_1 s - (k_{-1}+k_3)c_1 \\
&= k_1(e_i - c_1)s - (k_{-1}+k_3)c_1 \\
e_i^2 k_1 \frac{d\tilde{c}_1}{d\tilde{t}} &= k_1(e_i - e_i\tilde{c}_1)s_*\tilde{s} - (k_{-1}+k_3)e_i\tilde{c}_1 \\
e_i \frac{d\tilde{c}_1}{d\tilde{t}} &= (1-\tilde{c}_1)s_*\tilde{s} - \frac{(k_{-1}+k_3)}{k_1}\tilde{c}_1 \\
\frac{e_i}{s_*}\frac{d\tilde{c}_1}{d\tilde{t}} &= \tilde{s}(1-\tilde{c}_1) - \frac{(k_{-1}+k_3)}{k_1 s_*}\tilde{c}_1
\end{aligned}$$

The c_2 equation

$$\begin{aligned}
\frac{dc_2}{dt} &= k_2 e_2 s - (k_{-2}+k_4)c_2 \\
&= k_2(e_i - c_2)s - (k_{-2}+k_4)c_2 \\
e_i^2 k_1 \frac{d\tilde{c}_2}{d\tilde{t}} &= k_2(e_i - e_i\tilde{c}_2)s_*\tilde{s} - (k_{-2}+k_4)e_i\tilde{c}_2 \\
e_i \frac{d\tilde{c}_2}{d\tilde{t}} &= \frac{k_2}{k_1}(1-\tilde{c}_2)s_*\tilde{s} - \frac{(k_{-2}+k_4)}{k_1}\tilde{c}_2 \\
\frac{e_i}{s_*}\frac{d\tilde{c}_2}{d\tilde{t}} &= \alpha\left((1-\tilde{c}_2)\tilde{s} - \frac{(k_{-2}+k_4)}{k_2 s_*}\tilde{c}_2\right)
\end{aligned}$$

Using $s_* = s_i$ and $e_i = \epsilon s_i$ gives, for the c equations:

$$\begin{aligned}
\epsilon\frac{d\tilde{c}_1}{d\tilde{t}} &= \tilde{s}(1-\tilde{c}_1) - \frac{(k_{-1}+k_3)}{k_1 s_i}\tilde{c}_1 \\
\epsilon\frac{d\tilde{c}_2}{d\tilde{t}} &= \alpha\left((1-\tilde{c}_2)\tilde{s} - \frac{(k_{-2}+k_4)}{k_2 s_i}\tilde{c}_2\right)
\end{aligned}$$

And letting

$$\lambda_1 = \frac{k_{-1}+k_3}{k_1 s_i}, \quad \lambda_2 = \frac{k_{-2}+k_4}{k_2 s_i}$$

Finally gives (dropping tildes)

$$\begin{aligned}
\epsilon\frac{dc_1}{dt} &= s(1-c_1) - \lambda_1 c_1 \\
\epsilon\frac{dc_2}{dt} &= \alpha\left[s(1-c_2) - \lambda_2 c_2\right]
\end{aligned}$$

Returning to the s equation

$$\frac{d\tilde{s}}{d\tilde{t}} = -\tilde{s}(1+\alpha) + \tilde{c}_1\left(\frac{k_{-1}}{k_1 s_i} + \tilde{s}\right) + \alpha\tilde{c}_2\left(\frac{k_{-2}}{k_2 s_i} + \tilde{s}\right)$$

And letting

$$\mu_1 = \frac{k_{-1}}{k_1 s_i}, \quad \mu_2 = \frac{k_{-2}}{k_2 s_i}$$

Gives (dropping the tildes)

$$\frac{ds}{dt} = -s(1+\alpha) + c_1(\mu_1 + s) + \alpha c_2(\mu_2 + s)$$

I.e. we have the system

$$\begin{aligned}
\frac{ds}{dt} &= -s(1+\alpha) + c_1(\mu_1 + s) + \alpha c_2(\mu_2 + s) \\
\epsilon\frac{dc_1}{dt} &= s(1-c_1) - \lambda_1 c_1 \\
\epsilon\frac{dc_2}{dt} &= \alpha\left[s(1-c_2) - \lambda_2 c_2\right]
\end{aligned}$$

Where

$$\alpha = \frac{k_2}{k_1}, \quad \mu_1 = \frac{k_{-1}}{k_1 s_i}, \quad \mu_2 = \frac{k_{-2}}{k_2 s_i}, \quad \lambda_1 = \frac{k_{-1}+k_3}{k_1 s_i}, \quad \lambda_2 = \frac{k_{-2}+k_4}{k_2 s_i}$$

(c) Find leading order solutions for c_1, c_2 and hence s (technology is allowed)
To leading order, take perturbation series:

$$c_1 = c_{10} + c_{11}\epsilon + \dots$$

$$c_2 = c_{20} + c_{21}\epsilon + \dots$$

$$s = s_0 + s_1\epsilon + \dots$$

Where $\epsilon \ll 1$. The leading order system is:

$$\begin{aligned}
\frac{ds_0}{dt} &= -s_0(1+\alpha) + c_{10}(\mu_1 + s_0) + \alpha c_{20}(\mu_2 + s_0) \\
0 &= s_0(1-c_{10}) - \lambda_1 c_{10} \\
0 &= \alpha\left[s_0(1-c_{20}) - \lambda_2 c_{20}\right]
\end{aligned}$$

Solve the last two:

$$\begin{aligned}
0 &= s_0(1-c_{10}) - \lambda_1 c_{10} \\
s_0 c_{10} + \lambda_1 c_{10} &= s_0 \\
c_{10} &= \frac{s_0}{s_0 + \lambda_1}
\end{aligned}$$

$$\begin{aligned}
0 &= s_0(1-c_{20}) - \lambda_2 c_{20} \\
c_{20} &= \frac{s_0}{s_0 + \lambda_2}
\end{aligned}$$

And use in the first equation:

$$\begin{aligned}
\frac{ds_0}{dt} &= -s_0(1+\alpha) + c_{10}(\mu_1 + s_0) + \alpha c_{20}(\mu_2 + s_0) \\
&= -s_0(1+\alpha) + \frac{s_0}{s_0+\lambda_1}(\mu_1 + s_0) + \alpha\frac{s_0}{s_0+\lambda_2}(\mu_2 + s_0)
\end{aligned}$$

$$\int s_0(1+\alpha) - \frac{s_0}{s_0+\lambda_1}(\mu_1+s_0) - \alpha\frac{s_0}{s_0+\lambda_2}(\mu_2+s_0)\ ds = \int dt$$

$$\begin{aligned}\frac{1}{2}s_0^2(1+\alpha) + s_0(\lambda_1-\mu_1) + s_0\alpha(\lambda_2-\mu_2) - \alpha\lambda_2\log(\lambda_2+s_0)(\lambda_2-\mu_2)\\ -\frac{1}{2}\alpha s_0^2 + \lambda_1\log(\lambda_1+s_0)(-\lambda_1+\mu_1) - \frac{1}{2}s_0^2 = k\end{aligned}$$

$$\begin{aligned}s_0(\lambda_1-\mu_1) + s_0\alpha(\lambda_2-\mu_2) - \alpha\lambda_2\log(\lambda_2+s_0)(\lambda_2-\mu_2)\\ +\lambda_1\log(\lambda_1+s_0)(-\lambda_1+\mu_1) = k\end{aligned}$$

Where k would be obtained using $s(0)=s_i$. This is an implicit solution in s_0. Solved the integrals using `MATLAB`

```
syms s lambda1 lambda2 mu1 mu2 a
p1 = int(s*(1+a),s)
p2 =int(s*(mu1+s)/(s+lambda1),s)
p3 =int(a*s*(mu2+s)/(s+lambda2),s)
```

(d) Rescale time and find the inner solutions for s, c_1, c_2 Rescale time so that $T=\frac{t}{\epsilon}$

$$\frac{d}{dt} = \frac{\partial T}{\partial t}\frac{\partial}{\partial T} = \frac{1}{\epsilon}\frac{\partial}{\partial T}$$

Giving (to leading order) for the inner solutions:

$$\begin{aligned}\frac{1}{\epsilon}\frac{ds_0}{dT} &= -s_0(1+\alpha) + c_{10}(\mu_1+s_0) + \alpha c_{20}(\mu_2+s_0)\\ \frac{\partial c_1}{\partial T} &= s_0(1-c_{10}) - \lambda_1 c_{10}\\ \frac{\partial c_2}{\partial T} &= \alpha\left[s_0(1-c_{20}) - \lambda_2 c_{20}\right]\end{aligned}$$

And hence

$$\begin{aligned}\frac{ds_0}{dT} &= 0\\ \frac{\partial c_1}{\partial T} &= s_0(1-c_{10}) - \lambda_1 c_{10}\\ \frac{\partial c_2}{\partial T} &= \alpha\left[s_0(1-c_{20}) - \lambda_2 c_{20}\right]\end{aligned}$$

Trivially $s_0(T)=s_i$

$$\begin{aligned}\frac{\partial c_1}{\partial T} &= s_0(1-c_{10}) - \lambda_1 c_{10}\\ \frac{\partial c_1}{\partial T} &= s_i(1-c_{10}) - \lambda_1 c_{10}\\ \frac{1}{s_i(1-c_{10}) - \lambda_1 c_{10}}dc_1 &= \int dT\end{aligned}$$

Let $u = s_i(1-c_{10}) - \lambda_1 c_{10}$, $du = -\lambda_1 - s_i dc_1$

$$\frac{1}{s_i(1-c_{10}) - \lambda_1 c_{10}} dc_1 = \int dT$$

$$-\frac{1}{s_i+\lambda_1} \int \frac{1}{u} du = T + a$$

$$-\frac{1}{s_i+\lambda_1} \log(u) = T + a$$

$$-\frac{1}{s_i+\lambda_1} \log(s_i(1-c_{10}) - \lambda_1 c_{10}) = T + a \log(s_i(1-c_{10}) - \lambda_1 c_{10}) = -T(s_i+\lambda_1) + b$$

$$s_i(1-c_{10}) - \lambda_1 c_{10} = e^{-T(s_i+\lambda_1)+b} c_{10} = k_1 e^{-T(s_i+\lambda_1)} + \frac{s_i}{s_i+\lambda_1}$$

For the inner c_2 equation, the outcome is very similar:

$$\frac{\partial c_2}{\partial T} = \alpha\left[s_i(1-c_{20}) - \lambda_2 c_{20}\right] \log(s_i(1-c_{20}) - \lambda_2 c_{20}) = -Tc(s_i+\lambda_2) + a$$

$$c_{20} = k_2 e^{-Tc(s_0+\lambda_2)} + \frac{s_i}{s_i+\lambda_2}$$

The full solution could be obtained using a matching condition, but this would be difficult since the outer solution for s is implicit.