Homework 1 – Linear Stability Analysis and Quasi-Stationary Approximation

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1 Linear Stability Analysis

Let us consider the following differential equation, with a boundary condition:

$$\begin{aligned} \frac{\mathrm{d}}{\mathrm{d}t} N(t) &= \mu N(t) \left(1 - \frac{N(t)}{k}\right) \equiv F(N) \\ N(t=0) &= N_0 \end{aligned} \tag{1}$$

where $\mu > 0$ is the **growth rate** and $k > 0$ is the **carrying capacity** of the system. The solution of this boundary value problem can be readily found and it is

$$N(t) = \frac{N_0 \mathrm{e}^{\mu t}}{1 + \frac{N_0}{k}\left(\mathrm{e}^{\mu t} - 1\right)}, \tag{2}$$

which is known as the **logistic equation**. Now, to perform the linear stability analysis, one has to find the stationary states of the system. These can be easily calculated by setting

$$F(N) = 0 \iff \mu N^* \left(1 - \frac{N^*}{k}\right) = 0 \iff N^* = 0 \text{ or } N^* = k$$

Let us consider a small perturbation of the stationary states $\varepsilon(t)$ with initial condition $\varepsilon(t = 0) = \varepsilon_0$. The perturbation being small means that $|\varepsilon(t)| << 1$. Thus, the system is now defined by

$$N(t) = N^* + \varepsilon(t) \implies \dot{N}(t) = \dot{\varepsilon}(t)$$

And, due to Eq (1),

$$\dot{\varepsilon}(t) = F(N^* + \varepsilon(t))$$

Linearizing the expression above simply means that we Taylor-expand it up to the first order:

$$\dot{\varepsilon}(t) = F(N^* + \varepsilon) = F(N^*) + \left.\frac{\mathrm{d}F(N)}{\mathrm{d}N}\right|_{N=N^*} \varepsilon + \mathscr{O}(\varepsilon^2)$$

Since $F(N^*) = 0$, this differential equation is trivial and its solution is

$$\varepsilon(t) = \varepsilon_0 \mathrm{e}^{F'(N^*)t} \tag{3}$$

So we have to calculate $F'(N)$ and evaluate it for $N = N^*$:

$$\frac{\mathrm{d}}{\mathrm{d}N} F(N) = \frac{\mathrm{d}}{\mathrm{d}N}\left[\mu N \left(1 - \frac{N}{k}\right)\right] = \mu\left(1 - \frac{2N}{k}\right) = \begin{cases} \mu & N^* = 0 \\ -\mu & N^* = k \end{cases}$$

Finally, by substituting these results back into Eq. (3) we obtain

$$\varepsilon(t) = \begin{cases} \varepsilon_0 \mathrm{e}^{\mu t} \xrightarrow{t\to\infty} \infty & N^* = 0 \\ \varepsilon_0 \mathrm{e}^{-\mu t} \xrightarrow{t\to\infty} 0 & N^* = k \end{cases}$$

And we conclude that $N^* = 0$ is an unstable stationary state, while $N^* = k$ is a stable stationary state. This is to be expected: the initially extinguished state quickly evolves to populated states up until it reaches the carrying capacity of the system. The latter serves as a sort of “cap” or “maximum limit” for the population, usually in terms of available resources, so if the population exceeds this amount it will not be able to sustain growth any longer.

2 Quasi-Stationary Approximation

Let us consider a consumer-resource model, where $N(t)$ is the consumer and the $R(t)$ is the resource. The general differential equations that represent such a model are

$$\begin{cases} \dot{N}(t) = [\gamma g(R(t)) - d]N(t) \\ \dot{R}(t) = \mu(R(t)) - g(R(t))N(t) \end{cases} \tag{4}$$

In the equations above, γ represents the **yield rate**, d the **death rate** of the consumer, $\mu(R(t))$ is the **growth function** of the resource, and $g(R(t))$ the **resource intake** per individual. Let us consider an **abiotic** resource and a linear intake. In this case, the expressions for μ and g are

$$\mu(R(t)) = C$$
$$g(R(t)) = qR(t)$$

where C and q are positive constants. Now, we want to perform the **quasi-static approximation** (QSA) for this system. The main idea behind the QSA is that dynamics of the resource is much faster than the dynamics of the consumer, to the point that it can be basically considered to be stationary. In mathematical terms,

$$\dot{R}(t) = 0$$

Let us perform this approximation for the second expression found in (4), we get

$$\dot{R}(t) = 0 \implies C - qR^* N(t) = 0 \implies R^* = \frac{C}{qN(t)}$$

Now, we plug this expression in equation for $\dot{N}(t)$:

$$\begin{aligned} \dot{N}(t) = [q\gamma R^* - d]N(t) = \left[\frac{\gamma C}{N(t)} - d\right] N(t) = \gamma C - dN(t) \implies \\ \implies \frac{\mathrm{d}N}{\mathrm{d}t} = \gamma C - dN \implies \int \mathrm{d}N \, \frac{1}{\gamma C - dN} = \int \mathrm{d}t \\ \implies -\frac{1}{d} \log(dN - \gamma C) = t + k \implies N(t) = \frac{\gamma C}{d} + A\mathrm{e}^{-dt} \end{aligned}$$

where A absorbs all integration constants and is determined by imposing the boundary condition

$$N(t=0) = N_0 \implies \frac{\gamma C}{d} + A = N_0 \implies A = N_0 - \frac{\gamma C}{d}.$$

In the end, in the QSA, an abiotic consumer-resource model reads as

$$R(t) = R^* = \frac{C}{qN(t)}$$
$$N(t) = \frac{\gamma C}{d}\left(1 - \mathrm{e}^{-dt}\right) + N_0 \mathrm{e}^{-dt}$$

and the corresponding stationary state is given by

$$\dot{N}(t) = 0 \implies \gamma C - dN^* = 0 \implies N^* = \frac{\gamma C}{d}$$

The model we developed so far does not take into account an important factor: Generally speaking, we cannot expect the consumers to increase their resource intake ad libitum. For instance, let us consider a monkey: If we give it just one banana, it will eat it. If we give it two bananas, chances are both bananas will be consumed. However, if we give it a million bananas, it is preposterous to assume that the monkey will eat all of them. So a more appropriate form for the individual resource intake is

$$g(R) = \frac{q_M R}{K + R}$$

which is known as the **Monod equation**. As for its parameters, q_M is the maximum intake rate per individual and K is the half-saturation constant. Indeed, notice that

$$\lim_{R \to \infty} g(R) = q_M$$

and

$$g(R) = \frac{1}{2} q_M = \frac{q_M R}{K + R} \implies R = K$$

justifying these two definitions.
Now, if we consider the QSA with the Monod equation,

$$\dot{R}(t) = 0 = C - \frac{q_M R^*}{K + R^*} N(t) \implies R^*(q_M N(t) - C) = CK \implies R^* = \frac{CK}{q_M N(t) - C}$$

Notice that if we substitute this back into the equation for $\dot{N}(t)$ we obtain

$$\dot{N}(t) = \left(\gamma \frac{q_M R^*}{K + R^*} - d\right) N(t)$$

If we unravel the fraction, we obtain

$$\frac{q_M R^*}{K+R^*} = \frac{q_M \frac{CK}{q_M N - C}}{K + \frac{CK}{q_M N - C}} = \frac{q_M \frac{CK}{q_M N - C}}{\frac{CK + q_M KN - CK}{q_M N - C}} = q_M \frac{CK}{q_M N - C} \times \frac{q_M N - C}{q_M KN} = \\ = \frac{C}{N(t)}$$

netting the result

$$\dot{N}(t) = \gamma C - dN(t)$$

meaning that the value of N^* does not change compared to what we have already seen.

2.1 Simulations

Here, we ran a few simulations to compare the results of the linear intake and the one using the Monod equation. At this point, we obtain some numerical results that have to be tested with the theory. In particular, what we can do is determining if the stationary values are consistent. For the linear intake, the stationary states are

$$N^*_{\text{lin}} = \frac{\gamma C}{d} = 10 \qquad R^*_{\text{lin}} = \frac{C}{qN^*} = 2.5$$

since we chose $\gamma = 0.8$, $C = 5$, $d = 0.4$, and $q = 0.2$. For the Monod equation intake, on the other hand, the numerical values are

$$N^*_{\text{Mon}} = \frac{\gamma C}{d} = 10 \qquad R^*_{\text{Mon}} = \frac{CK}{q_M N^* - C} = 1.6$$

as we set $q_M = 3$ and $K = 8$. The dynamics are reported in Figure 1, with the states eventually converging to their stationary values. On top of this, we display what happens if the initial value of the consumers exceeds the stationary value, while keeping the initial values of the resources. What we expect is, of course, a collapse in the population. The results of this quick analysis are shown in Figure 2, essentially proving our initial belief. Notice that the initial values of the resource was left the same in both simulations.

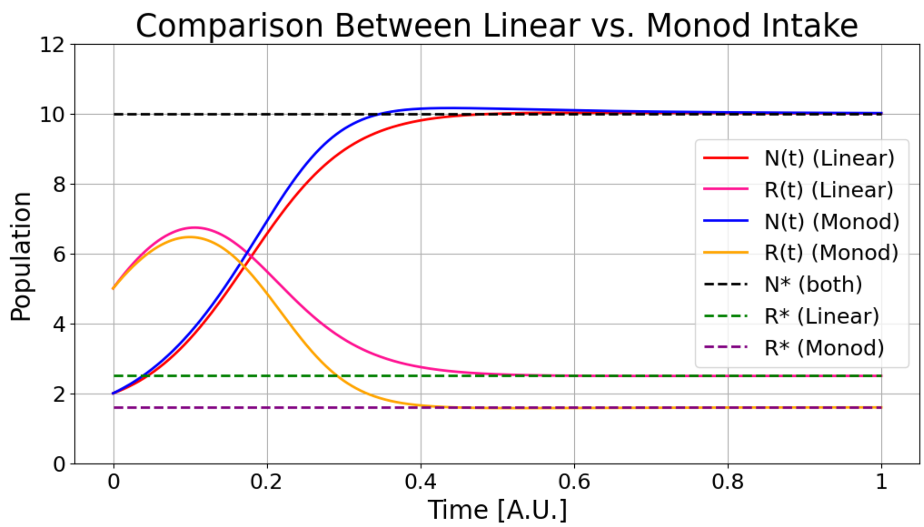

Figure 1: Comparison between the dynamics for linear and Monod intakes

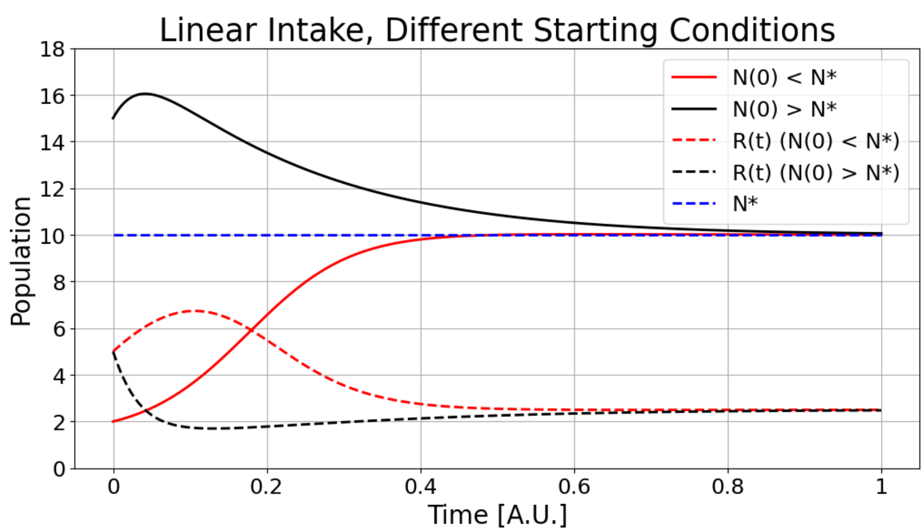

Figure 2: Dynamics with linear intake with different values for N_0.