Lecture Notes for Lecture 1 of Dr. Z.'s Dynamical Systems in Biology

In biology both **differential equations** with *continuous* time, and **difference equations**, (also known as **recurrences**), with *discrete* time are very important.

A general difference equation could be very complicated, it has the format

$$x_n = F(x_{n-1}, x_{n-2}, ..., x_{n-k}) \quad , \quad n \geq k$$

where k is a finite integer, called the **order**, and F is any function with k arguments.

You are also given *initial conditions*

$$x_0 = a_0, \quad , \dots , \quad x_{k-1} = a_{k-1} \quad ,$$

for some numbers $a_0, \dots, a_{k-1}$.

In general there is no way to solve such equations, but using a computer you can compute many terms of the sequence, and look whether there is a *trend*, or limiting behavior as n goes to ∞.

If F is a linear function, then it is possible to solve them explicitly. It is then called a **linear difference equation** (or **linear recurrence**).

The general format of a linear recurrence is

$$x_n = c_1\, x_{n-1} + c_2 x_{n-2} + \ldots + c_k x_{n-k} \quad , \quad n \geq k \quad ,$$

for some **numbers** $c_1, \dots, c_k$, and again there are initial conditions as above.

Problem **1.1**: Compute x_4 of the sequence satisfying the second-order recurrence

$$x_n = x_{n-1}(x_{n-1} + x_{n-2}) \quad , \quad n \geq 2 \quad ,$$

subject to the initial conditions

$$x_0 = 2 \quad , \quad x_1 = 3 \quad .$$

Sol. to 1.1: we must first compute x_2, then x_3, and only then x_4.

$$x_2 = x_1(x_1 + x_0) = 3 \cdot (2 + 3) = 15 \quad ,$$

$$x_3 = x_2(x_2 + x_1) = 15 \cdot (15 + 3) = 270 \quad ,$$

$$x_4 = x_3(x_3 + x_2) = 270 \cdot (270 + 15)) = 76950 \quad .$$

Ans. $x_4 = 76950$.

Problem 1.2 In a certain species of animals, only one-year-old, two-year-old females, are fertile.

The probabilities of a one-year-old and two-year-old female to give birth to a new female are p_1, p_2 respectively. There were c_0 females born at $n = 0$, c_1 females born at $n = 1$. Set up a recurrence that will enable you to find the **expected** number of females born at time n.

In terms of c_0, c_1, p_1, p_2, what is the expected number of females born at $n = 4$?

Sol. to 1.2: The general recurrence is

$$x_n = p_1 x_{n-1} + p_2 x_{n-2} \quad ,$$

because at generation n there are x_{n-1} one-year-old and x_{n-2} two-year-old. We have

$$x_2 = p_1 x_1 + p_2 x_0 = p_1 c_1 + p_2 c_0 \quad ,$$

$$x_3 = p_1 x_2 + p_2 x_1 = p_1(p_1 c_1 + p_2 c_0) + p_2 c_1 = c_0 p_1 p_2 + c_1 p_1^2 + c_1 p_2 \quad ,$$

$$x_4 = p_1 x_3 + p_2 x_2 = p_1(c_0 p_1 p_2 + c_1 p_1^2 + c_1 p_2) + p_2(p_1 c_1 + p_2 c_0) = c_0\, p_1^2\, p_2 + c_1\, p_1^3 + c_0\, p_2^2 + 2\, c_1\, p_1\, p_2 \quad .$$

Ans. to 1.2: At (discrete) time $n = 4$ the expected number of females is $c_0\, p_1^2\, p_2 + c_1\, p_1^3 + c_0\, p_2^2 + 2\, c_1\, p_1\, p_2$.

How to solve Linear Recurrence Equations

To solve a linear recurrence

$$x_n = c_1\, x_{n-1} + c_2 x_{n-2} + \ldots + c_k x_{n-k} \quad , \quad n \geq k \quad ,$$

subject to initial conditions $x_0 = a_0, x_1 = a_1, \ldots, x_{k-1} = a_{k-1}$ do the following steps.

Step 1: Look for solutions of the form $x_n = z^n$, for some z. These are called **exponential solutions**.

Plug it in the recurrence getting

$$z^n = c_1\, z^{n-1} + c_2\, z^{n-2} + \ldots + c_k\, z^{n-k} \quad .$$

Dividing by z^{n-k} we get the **algebraic equation**

$$z^k - c_1 z^{k-1} - \ldots - c_k \; = 0 \quad .$$

This is called the **characteristic equation**

Step 2: Solve it, getting (in general, if you are lucky) k distinct roots, (in general complex, but sometimes they happen to be real and even integers). Let's call them $z_1, \ldots, z_k$

The **General Solution** (by the **principle of superposition**) has the **template**:

$$x_n = C_1 z_1^n + \ldots + C_k z_k^n \quad ,$$

where $C_1, \ldots, C_k$ are *arbitrary* (i.e. general) constants, **to be determined**

Step 3: Use the initial conditions to solve for these coefficients by solving the **linear system**

$$c_0 = C_1 + \ldots + C_k \quad ,$$

$$c_1 = C_1 z_1 + \ldots + C_k z_k \quad ,$$

$$\ldots$$

$$c_{k-1} = C_1 z_1^{k-1} + \ldots + C_k z_k^{k-1} \quad ,$$

Step 4: Plug-in the solutions of the above system of linear equations to the template of general equation.

Problem 1.3 Solve explicitly the recurrence equation

$$x_n = -x_{n-1} + 6x_{n-2} \quad ,$$

with initial conditions

$$x_0 = 2, x_1 = -1 \quad .$$

Sol. to 1.3: The **characteristic equation** is

$$z^2 = -z + 6$$

In other words

$$z^2 + z - 6 = 0 \quad .$$

Factorizing

$$(z+3)(z-2) = 0 \quad .$$

So the two roots are $z_1 = -3$, $z_2 = 2$.

The general solution is

$$x_n = C_1(-3)^n + C_2 2^n \quad ,$$

where C_1, C_2 are **to be determined**.

Plugging in $n = 0$ and $= 1$ using $x_0 = 2, x_1 = -1$, we get the system of two linear equations in the two unknowns, C_1, C_2:

$$2 = C_1 + C_2$$

$$-1 = -3C_1 + 2C_2 \quad ,$$

whose solution is $C_1 = 1, C_2 = 1$. Going back to the general solution we have

$$x_n = (-3)^n + 2^n \quad .$$

Ans. to 1.3: $x_n = (-3)^n + 2^n \quad .$

What to do if there are repeated roots?:

If there are

z_1 (repeated a_1 times)

z_2 (repeated a_2 times)

$$\ldots$$

z_r (repeated a_r times)

(where $a_1 + a_2 + \ldots + a_r = k$) then the **general solution** has the format

$$x_n = P_1(n) z_1^n + \ldots + P_r(n) z_r^n \quad ,$$

where $P_1(n)$ is a *generic polynomial* of degree $a_1 - 1$, $P_2(n)$ is a *generic polynomial* of degree $a_2 - 1$, $\ldots$, $P_r(n)$ is a *generic polynomial* of degree $a_r - 1$.

$$P_1(n) = C_{1,0} + C_{1,1} n + \ldots + C_{1,a_1-1} n^{a_1-1}$$

$$\ldots$$

$$P_r(n) = C_{r,0} + C_{r,1} n + \ldots + C_{r,a_r-1} n^{a_r-1}$$

and the k constants $C_{1,0}, \ldots C_{r,a_r-1}$ are determined by plugging-in.

Problem 1.4 Solve explicitly the recurrence equation

$$x_n = -x_{n-1} + x_{n-2} + x_{n-3} \quad ,$$

with initial conditions

$$x_0 = 1 \quad , \quad x_1 = 0 \quad , \quad x_2 = 3 \quad .$$

Sol. to 1.4: The **characteristic equation** is

$$z^3 = -z^2 + z + 1$$

In other words

$$z^3 + z^2 - z - 1 = 0 \quad .$$

Factorizing

$$(z+1)^2 (z-1) = 0 \quad .$$

So there two different roots, $z = -1$ that is a **double root**, and $z = 1$ that is a **simple root**.

The general solution template is

$$x_n = (C_0 + C_1\,n) \cdot (-1)^n + c_2 \cdot (1)^n \quad ,$$

in other words

$$x_n = (C_0 + C_1 n) \cdot (-1)^n + C_2 \quad ,$$

We have to find the values of C_0, C_1, C_2.

$$1 = x_0 = (C_0 + C1 \cdot 0) \cdot (-1)^0 + C_2 = -C_1 + C_2$$

$$0 = x_1 = (C_0 + C_1) \cdot (-1) + C_2 \quad ,$$

$$3 = x_2 = (C_0 + 2C_1) \cdot (-1)^2 + C_2 \cdot (1)^2 \quad ,$$

We get the system of equations

$$-C_1 + C_2 = 0 \quad , \quad , -C_0 - C_1 + C_2 = 0 \quad , \quad C_0 + 2C_1 + C_2 = 3$$

So $C_0 = 0$, $C_1 = 1$, $C_2 = 1$.

Going back to the general solution template, we have

$$x_n = (0 + 1 \cdot n) \cdot (-1)^n + 1 = (-1)^n n + 1 \quad .$$

Ans. to 1.4: $x_n \;=\; (-1)^n n + 1 \quad .$