Discrete Dynamical Systems

Computational Models for Complex Systems

Paolo Milazzo

Dipartimento di Informatica, Università di Pisa
http://pages.di.unipi.it/milazzo
milazzo@di.unipi.it

Laurea Magistrale in Informatica
A.Y. 2019/2020

Introduction

We will see how to define recurrence relations (or difference equations) in order to model the dynamics of systems whose state changes at discrete time intervals.

- focus on population models (birth/death of individuals)

We will see that even the simplest form of interaction between individuals can lead to the emergence of complex behaviors in the population

- chaos!

See also:
Notes on a Short Course and Introduction to Dynamical Systems in Biomathematics by Urszula Foryś
Available on the course web page

Linear birth model

Let $N(t)$ denote the density of some population at time t.

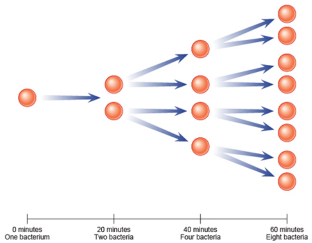
We want to construct a mathematical model able to predict the density of the same population at time $t + \Delta t$, that is $N(t + \Delta t)$.

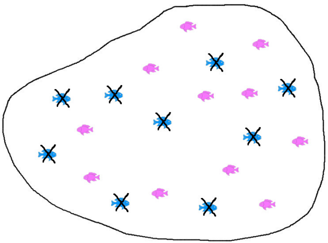
Assume that:

- all individuals are the same (no dinstinction by gender, age, ...)
- there is enough food and space for every individual
- each individual has λ children every σ time units
- there is no death in the interval $[t, t + \Delta t)$
- children do not start reproducing in the interval $[t, t + \Delta t)$

Linear birth model

Examples of populations satisfying the assumptions:





Bacteria duplication

Female fish in a big lake

In the bacteria example, in order to assume no children duplication in the $[t, t + \Delta t)$ interval, Δt has to be smaller or equal to 20 minutes.

Linear birth model

Then, the number of individuals a time $t + \Delta t$ corresponds to the number of individuals a time t, plus the number of newborns in time Δt

$$N(t + \Delta t) = N(t) + \lambda \frac{\Delta t}{\sigma} N(t)$$

where $\frac{\Delta t}{\sigma}$ describes the number of birth moments for every individual in the interval $[t, t + \Delta t)$

The equation can be rewritten as follows:

$$N(t + \Delta t) = \left(1 + \lambda \frac{\Delta t}{\sigma}\right) N(t)$$

Example: bacteria duplication

In the case of bacteria:

- duplication happens every 20 minutes, then $\sigma = 1/3$ (in hours)
- the number of children is 1, then $\lambda = 1$

Assume that at time $t = 0$ there is only 1 bacterium, after 20 minutes (1/3 hours) we have 2 bacteria:

$$N(0 + 1/3) = \left(1 + 1\frac{1/3}{1/3}\right) 1 = 2$$

Example: female fish population

In the case of fish:

- reproduction happens every 2 months, then $\sigma = 2$ (in months)
- the average number of (viable) female offsprings is 4, then $\lambda = 4$

Assume that at time $t = 0$ there is only 1 female fish, after 6 months we have 13 female fish (the mother + 12 offsprings):

$$N(0+6) = \left(1 + 4\frac{6}{2}\right)1 = 13$$

Recurrence relation of the simple birth process

From equation

$$N(t + \Delta t) = N(t) + \lambda \frac{\Delta t}{\sigma} N(t)$$

we can derive a discrete model as follows

We choose a time step (discretization step) that we consider appropriate to describe an update of the population, and we use it as Δt

- after Δt time units, newborns are considered as adults (i.e. can reproduce)

Using the notation of sequence theory, $N_t = N(t)$, we obtain:

$$N_{t+1} = r_d N_t$$

with $r_d = 1 + \lambda \frac{\Delta t}{\sigma}$ representing the (constant) birth rate.

Example: bacteria duplication

In the case of bacteria:

- a reasonable time step is 1/3 hours (since duplications happen with such a frequency)
- the birth rate turns out to be $r_d = 1 + \lambda \frac{\Delta t}{\sigma} = 1 + 1\frac{1/3}{1/3} = 2$
- indeed, the number of bacteria doubles every 20 minutes!

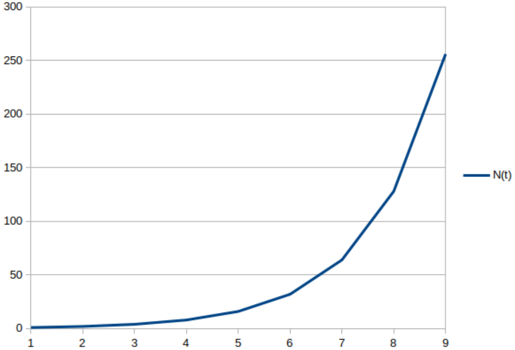
Hence, the recurrence relation is:

$$N_{t+1} = 2N_t$$

Example: bacteria duplication

Here the dynamics of the bacteria population, by assuming $N_0 = 1$:

N_0	1
N_1	2
N_2	4
N_3	8
N_4	16
N_5	32
N_6	64
N_7	128
N_8	256



Example: female fish population

In the case of fish:

- a reasonable time step is 1 year (since offsprings reach sexual maturation in one year)
- the birth rate turns out to be $r_d = 1 + \lambda \frac{\Delta t}{\sigma} = 1 + 4 \frac{12}{2} = 25$

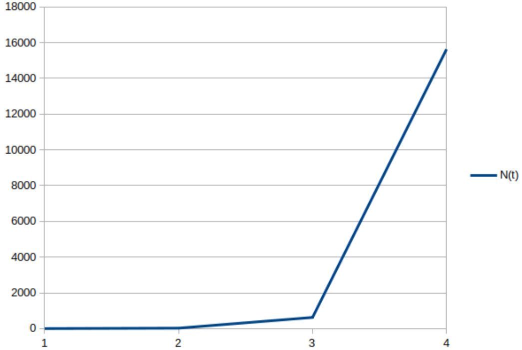
Hence, the recurrence relation is:

$$N_{t+1} = 25 N_t$$

Example: female fish population

Here the dynamics of the female fish population, by assuming $N_0 = 1$:

N_0	1
N_1	25
N_2	625
N_3	15625



General term (solution) of the simple birth process

Knowing the recurrence relation, we are sometimes able to calculate the so-called general term of the system (solution of the recurrence relation).

- It is a non-recursive definition of N_t

Let's start by calculating the first terms N_1, N_2, N_3...

$$
\begin{aligned}
N_1 &= r_d N_0 \\
N_2 &= r_d N_1 = r_d^2 N_0 \\
N_3 &= r_d N_2 = r_d^3 N_0 \\
N_4 &= \ldots
\end{aligned}
$$

It seems that $N_t = r_d^t N_0$...

This formula should be proved by using mathematical induction.

- We prove the formula (i) for $t = 0$ and (ii) for $t = k + 1$ by assuming it is valid for $t = k$.

General term (solution) of the simple birth process

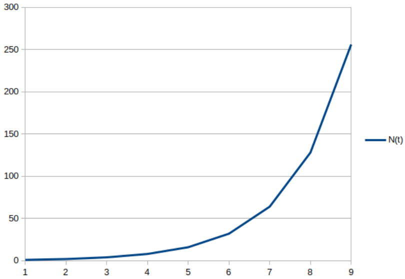
Proof of $N_t = r_d^t N_0$:

Base case. We check the formula for $t = 0$.
Checking: For $t = 0$ we obtain $N_0 = r_d^0 N_0$ that is true

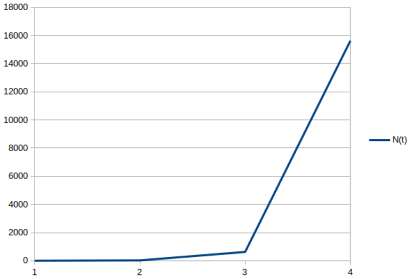
Induction case.
We assume the formula to be correct for $t = k$ and prove it for $t = k + 1$
Induction hypothesis: $N_k = r_d^k N_0$
Thesis: $N_{k+1} = r_d^{k+1} N_0$
Proof: From the recurrence relation we have $N_{k+1} = r_d N_k$. By using the induction hypothesis we obtain $N_{k+1} = r_d N_k = r_d(r_d^k N_0) = r_d^{k+1} N_0$, which proves the thesis.

General term (solution) of the simple birth process

The general term $N_t = r_d^t N_0$ tells us that the simple birth process gives rise to an exponential growth of the population over time.



Bacteria



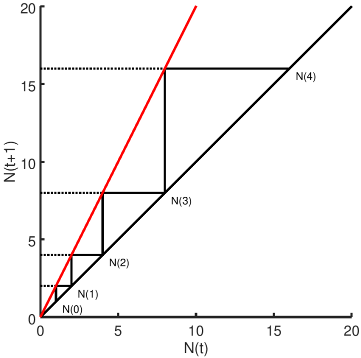
Female fish

Phase portrait

An alternative way for visualizing the trend of a recurrence relation is through its phase portrait:

- plot of the recurrence relation on the (N_t, N_{t+1}) plane
- by starting from the point (N_0, N_0) on the bisector, the other points can be obtained by "bouncing" on the curve of the recurrence relation

- in red the recurrence equation $N_{t+1} = 2N_t$
- in **black** the bisector $N_{t+1} = N_t$



Linear birth/death model

It is quite simple to extend the recurrence relation of the linear birth model in order to consider also deaths.

Assume that, on average, a constant fraction s_d of the adults die in every time step δt. The recurrence relation becomes:

$$N_{t+1} = r_d N_t - s_d N_t$$

Note that $0 \leq s_d \leq 1$, since the number of individuals which die cannot be greater than the number of individuals in the population.

Linear birth/death model

The recurrence relation can be rewritten as follows:

$$N_{t+1} = (r_d - s_d)N_t$$

Let, $\alpha_d = (r_d - s_d)$ be the net growth rate, we obtain:

$$N_{t+1} = \alpha_d N_t$$

which is a recurrence relation similar to that of the linear growth model, but with a rate α_d that is a value in $[0, +\infty)$.

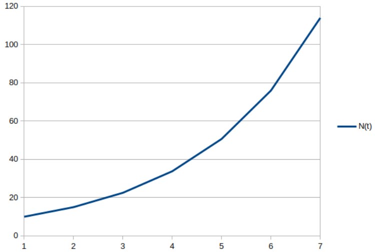
Linear birth/death model

Let's see what happens by varying α_d (assume $N_0 = 10$):

First case: $\alpha_d > 1$

for example:
$r_d = 2$
$s_d = 0.5$
$\alpha_d = 1.5$

N_0	10
N_1	15
N_2	22.5
N_3	33.75
N_4	50.625
N_5	75.937
N_6	113.906



Every Δt time units, each parent generates one offspring ($r_d = 2$) and half of the parents die ($s_d = 0.5$).

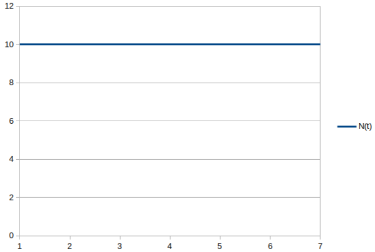
Linear birth/death model

Let's see what happens by varying α_d (assume $N_0 = 10$):

Second case: $\alpha_d = 1$

for example:
$r_d = 2$
$s_d = 1$
$\alpha_d = 1$

N_0	10
N_1	10
N_2	10
N_3	10
N_4	10
N_5	10
N_6	10



Every Δt time units, each parent generates one offspring ($r_d = 2$) and all of the parents die ($s_d = 1$).

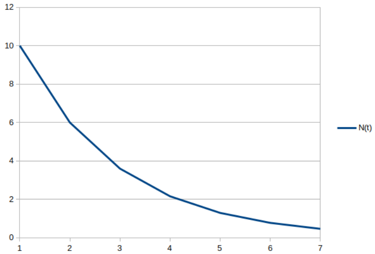
Linear birth/death model

Let's see what happens by varying α_d (assume $N_0 = 10$):

Third case: $\alpha_d < 1$

for example:
$r_d = 1.5$
$s_d = 0.9$
$\alpha_d = 0.6$

N_0	10
N_1	6
N_2	3.6
N_3	2.16
N_4	1.296
N_5	0.778
N_6	0.467



Every Δt time units, each parent generates (on average) 0.5 offsprings ($r_d = 1.5$) and 90% of the parents die ($s_d = 0.9$).

Modeling migration

The birth/death model can be easily extended to take migration into account.

In the easiest case we assume that the number of migrating individuals is positive (incoming migration) and constant in time. Then we obtain:

$$N_{t+1} = \alpha_d N_t + \beta$$

with $\beta \geq 0$ describing the constant migration rate: number of individuals entering the population every Δt time units.

The general term of this recurrence relation, for $t > 0$, is:

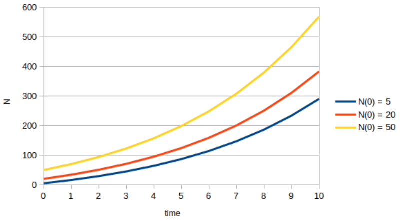
$$N_t = \alpha_d^t N_0 + \sum_{i=0}^{t-1} \alpha_d^i \beta$$

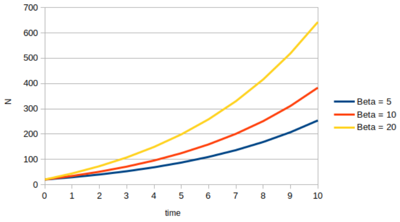
(can be proved by induction)

Modeling migration

Let's see what happens by varying α_d, N_0 and β:

First case: $\alpha_d > 1$ $(\alpha = 2)$





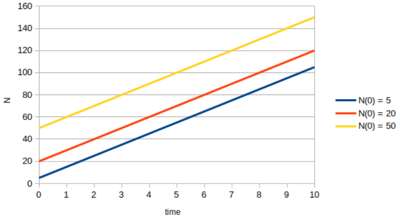
$N_0 = 5, 20, 50 \quad \beta = 10$ $\qquad$ $N_0 = 20 \quad \beta = 5, 10, 20$

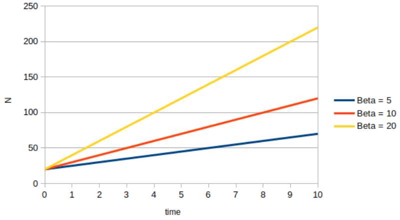
The dynamics is dominated by the birth process (exponential growth)

Modeling migration

Let's see what happens by varying α_d, N_0 and β:

First case: $\alpha_d = 1$





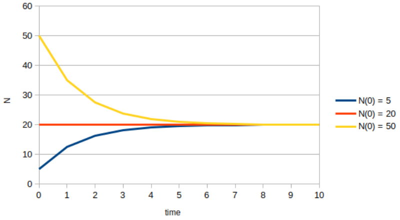
$N_0 = 5, 20, 50 \quad \beta = 10$ $\qquad$ $N_0 = 20 \quad \beta = 5, 10, 20$

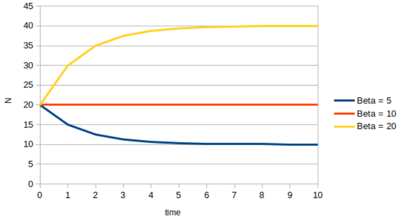
The dynamics is dominated by the migration process (linear growth).

Modeling migration

Let's see what happens by varying α_d, N_0 and β:

First case: $\alpha_d < 1$ ($\alpha = 0.5$)





$N_0 = 5, 20, 50 \quad \beta = 10$ $\qquad$ $N_0 = 20 \quad \beta = 5, 10, 20$

The population reaches a dynamic equilibrium: a stable state in which opposite phenomena compensate each other (migration compensates deaths) – independent from N_0.

Modeling migration

Let's compute the equilibrium value of N_t in the case of dynamic equilibrium:

At equilibrium we have $N_{t+1} = N_t$. By substituting N_{t+1} with N_t in the recurrence equation we obtain

$$N_t = \alpha_d N_t + \beta$$

from which we can compute

$$N_t = \frac{\beta}{1 - \alpha_d}$$

Indeed, with $\alpha_d = 0.5$ and $\beta = 10$, the population reaches

$$N_t = \frac{10}{1 - 0.5} = 20$$

independently from the value of N_0 (see previous graphs).

Interactions and non linear models

The models we have seen so far are linear

- $N_{t+1} = f(N_t)$ describes a straight line in the (N_{t+1}, N_t)-plane

Linear models describe systems in which individuals essentially do not interact

- the behavior of each individual does not depend on how many other individuals are present

An example of non-linear model is the famous logistic equation

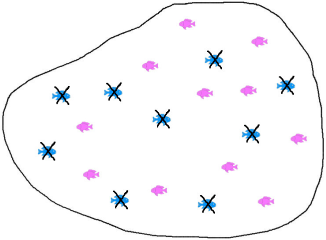
- it describes birth/death processes in which individuals compete for environmental resources such as food, place, etc.

Competition for resources is a form of interaction

- mediated by the environment

Lake fish example revisited

Let us recall the female fish example:



Assume that the resources of the lake are limited

- it offers enough food and space for a population of K female fish
- K is the carrying capacity the environment

Logistic equation

The logistic equation is defined as follows:

$$N_{t+1} = r_d N_t \left(1 - \frac{N_t}{K}\right)$$

The idea is that the birth rate $r_d N_t$ is modulated by the ratio of occupancy of the enviroment $\frac{N_t}{K}$

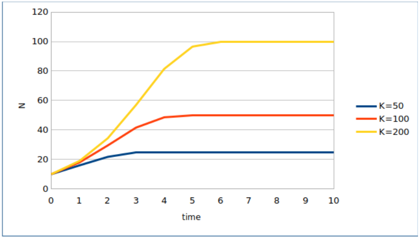
- when N_t is close to zero, we have a simple birth process with rate r_d (exponential growth)
- when N_t increases, the growth tends to stop

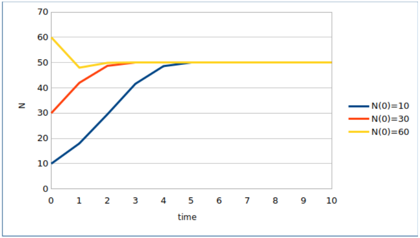
Common alternative formulation: $X_{t+1} = r_d X_t(1 - X_t)$

- obtained by dividing both terms by K, then by performing the following variable substitution: $X_s = N_s/K$

Logistic equation

Let's see what happens with $r_d = 2$, by varying K and N_0:





$N_0 = 10 \quad K = 50, 100, 200$ $\qquad$ $N_0 = 10, 30, 60 \quad K = 100$

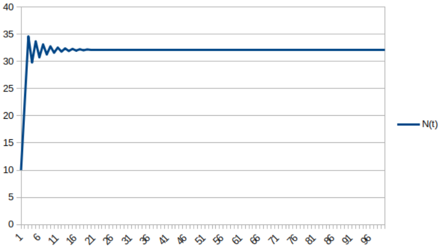
The population reaches a dynamic equilibrium representing the situation in which environment resources are fully exploited (saturation)

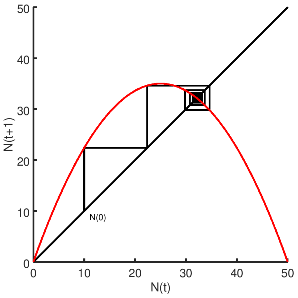
- Equilibrium is when $N_{t+1} = N_t$, that is $N_t = r_d N_t \left(1 - \frac{N_t}{K}\right)$, that is $N_t = K\left(1 - \frac{1}{r_d}\right)$

Logistic equation and periodic dynamics

It is interesting to see what happens if we increase r_d in the logistic equation.

$r_d = 2.8 \quad N_0 = 10 \quad K = 50$



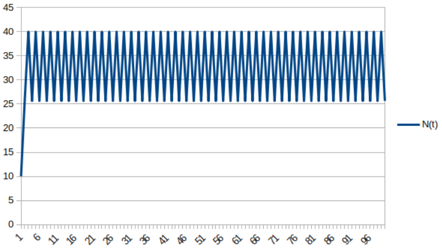


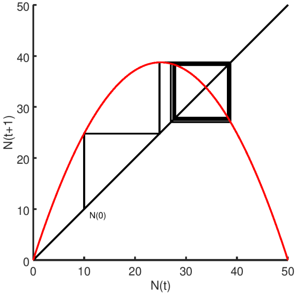
Dynamic equilibrium (after a few oscillations)

Logistic equation and periodic dynamics

It is interesting to see what happens if we increase r_d in the logistic equation.

$r_d = 3.1 \quad N_0 = 10 \quad K = 50$



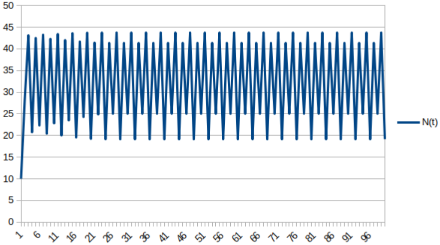


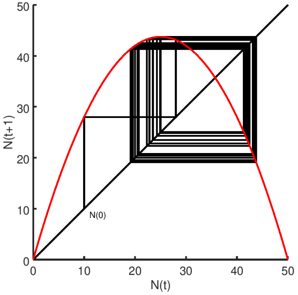
Sustained oscillations

Logistic equation and periodic dynamics

It is interesting to see what happens if we increase r_d in the logistic equation.

$r_d = 3.5 \quad N_0 = 10 \quad K = 50$



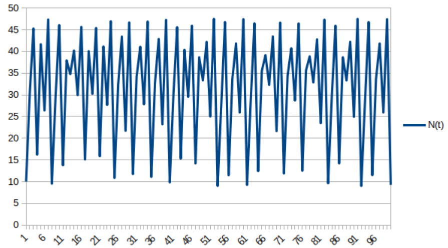


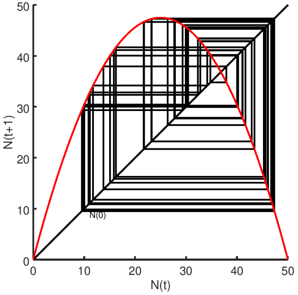
Sustained oscillations with period 4!

Logistic equation and periodic dynamics

It is interesting to see what happens if we increase r_d in the logistic equation.

$r_d = 3.8 \quad N_0 = 10 \quad K = 50$



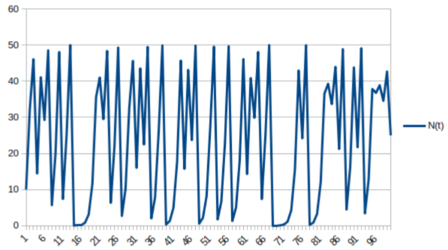


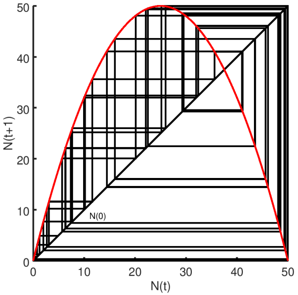
Sustained oscillations with very high period!

Logistic equation and periodic dynamics

It is interesting to see what happens if we increase r_d in the logistic equation.

$r_d = 4 \quad N_0 = 10 \quad K = 50$



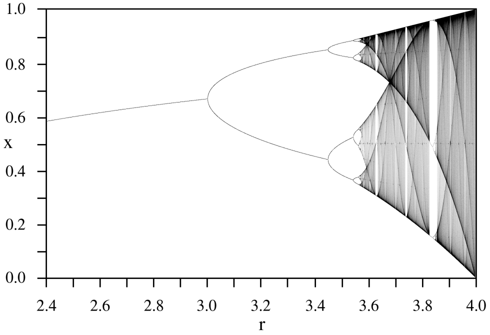


Sustained oscillations with infinite period!

- Chaotic (apparently random) dynamics

Logistic equation and periodic dynamics

This diagram (Feigenbaum's tree) describes the attractors of the logistic equation by varying r_d.



The number of attractors (and the oscillation period) doubles with an increasing rate

- The distance between consecutive bifurcation points decreases geometrically: $dist_i/dist_{i+1} \simeq 4.7$ (Feigenbaum's constant)

Systems of recurrence relations

So far we considered examples of systems described by a single variable N_t

When more than one variable has to be cosidered, we have to construct a system of recurrence equations

Let's consider also males in the fish example

- F_t models females and M_t models males
- assume a small part of males die because of fights among them (death rate s_d)

We obtain the following system of recurrence equations

$$\begin{cases} F_{t+1} = r_d F_t \left(1 - \frac{F_t + M_t}{K}\right) \\ M_{t+1} = r_d F_t \left(1 - \frac{F_t + M_t}{K}\right) - s_d M_t \end{cases}$$

where

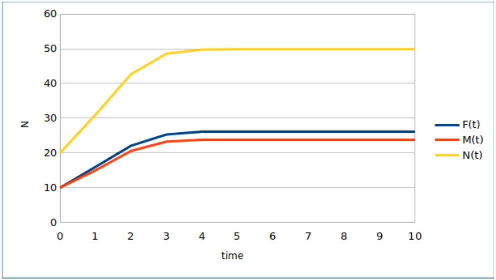
- $r_d F_t$ is used for both genders since both are generated by females
- $F_t + M_t$ describes the whole population size (to be related with the carrying capacity K)

Systems of recurrence relations

$$\begin{cases} F_{t+1} = r_d F_t \left(1 - \frac{F_t + M_t}{K}\right) \\ M_{t+1} = r_d F_t \left(1 - \frac{F_t + M_t}{K}\right) - s_d M_t \end{cases}$$

This is the dynamics of the system (with $N_t = F_t + M_t$) is:

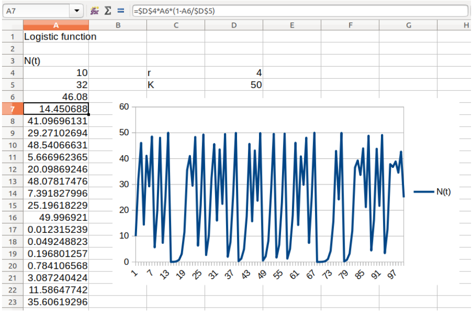
$r_d = 2$
$K = 100$
$s_d = 0.1$



Implementing recurrence relations

The implementation of (systems of) recurrence relations is quite trivial

- It can be done with a spreadsheet or with few lines of code in any programming language
- Suggestion: in the choice of the language, take plotting facilities into account...




```
N[0] = 10;
for (int t=0; t<99; t++)
  N[t+1] = r*N[t]*(1-N[t]/K);
```

Lessons learnt

Summing up:

- Recurrence relations can be used to describe dynamical systems whose state updates at discrete time intervals
  - discrete dynamical systems
- Recurrent relations are often quite easy to calculate
  - they can often be implemented by using a spreadsheet...
- Interactions among components of the modeled system lead to non-linear relations
- Even the simplest non-linear relations may lead to chaotic behaviors
- Chaos is a complex population behavior which emerges from the interaction between individuals

Limitations of discrete dynamical models

Discretization of the system dynamics may introduce inaccuracies

- recurrence equations assume that nothing happens during the Δt time between N_t and N_{t+1}
- this assumption is ok in some cases (e.g. the bacteria example)
- it is an approximation in other cases (e.g. the fish example)
- for example, usually, births and deaths can happen at any time
- smaller Δt usually correspond to more accurate approximations
- in order to increase accuracy, we should let Δt tend to 0... continuous model!

Exercise

Consider a population of adults and children. Assume that:

- the population evolves by discrete steps corresponding to 1 year
- α is the net growth rate of adults
- every year each adult generates β children
- children become adults after 3 years (this can be used to estimate the rate γ of transformation of children into adults)
- children do not die

Define a system of recurrence equations to model this adults/children population.

Think about reasonable parameters:

- in which cases the population exhibits exponential growth, dynamic equilibrium and extinction?
- is dynamic equilibrium independent from the initial values of the variables?