Discrete-Time Models

Malthus, logistic and Ricker models

Computational Biology

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Discrete-time models

Let x_n, $n \in \mathbb{N}_0$, be a quantity at the n-th measurement or after n time steps.

We are concerned with a sequence of quantities

$$x_0, x_1, x_2, x_3, \ldots$$

Examples: x_n may represent:

- the size of a population in year n;
- the proportion of individuals in a population carrying a particular allele of a gene in the nth generation;
- the number of cells in a bacterial culture on day n;
- the concentration of oxygen in the lung after the n-th breath;
- the concentration in the blood of a drug after the n-th dose;
- ...

What does it mean to build a discrete-time model?

Discrete model: is a rule describing how x_{n+1} depends on x_n (and potentially also on $x_{n-1}, x_{n-2}, \ldots, x_0$).

Consider the case where x_{n+1} depends on x_n

$$x_{n+1} = f(x_n).$$

- This equation is called discrete-time equation or difference equation, and f is called the updating function or map.
- Given some initial condition x_0, the resulting simulated sequence

$$x_1 = f(x_0), \quad x_2 = f(x_1), \quad x_3 = f(x_2), \quad \ldots$$

is called an orbit of the map.

Discrete Malthus' model

$$f(x_n) = rx_n, \quad \text{with } r > 0$$

- Let N_n be the size of a population at time n
- Discrete Malthus' model

$$N_0 \text{ given}, \quad N_{n+1} = rN_n \quad \Rightarrow \quad N_n = r^n N_0$$

corresponds to a geometric growth/decay with ratio r.

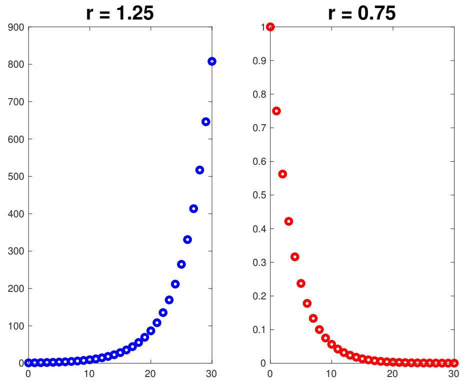

Figure: Geometric growth ($r > 1$); geometric decay ($r < 1$).

Malthus' model: example

- Let the probability of any given individual dying between censuses (the per capita mortality) be d, and let the average number of birds of any given individual in the same time period (the per capita production or reproduction) be b.
- Discrete Malthusian model:

$$N_{n+1} = (1 + b - d)N_n = rN_n,$$

where $r = 1 + b - d$ is called (net) growth ratio.

- The model is not very realistic for most populations nor for long times but it has been used (with some justification) for the early stages of growth of certain bacteria.

Discrete logistic model

Example: *Paramecium aurelia* is a single-celled organism that abounds in standing water tanks. It was studied by Gregory Gause in 1932 (see [1]).

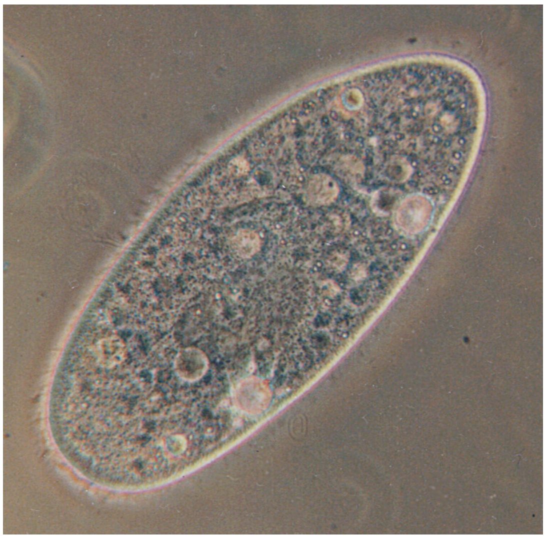

Figure: *Paramecium aurelia*.

Paramecium aurelia data

Day	Mean density	Day	Mean density
0	2	13	513
1	-	14	593
2	14	15	557
3	34	16	560
4	56	17	522
5	94	18	565
6	189	19	517
7	266	20	500
8	330	21	585
9	416	22	500
10	507	23	495
11	580	24	525
12	610	25	510

Table: Growth of *Paramecium aurelia*. Here, density is the number of individuals per 0.5 cm^3 (data taken from Gause [1]).

Define the discrete logistic model

- Let p_n be the mean density of the population on day n.
- A good starting point for building a model for p_n:

$$\text{future value} = \text{present value} + \text{change};$$

  which translates to:

$$p_{n+1} = p_n + \Delta p_n,$$

  where $\Delta p_n = p_{n+1} - p_n$.
- Goal: find a reasonable approximation for Δp_n that reproduces the given set of data.

Define the discrete logistic model: look at the data

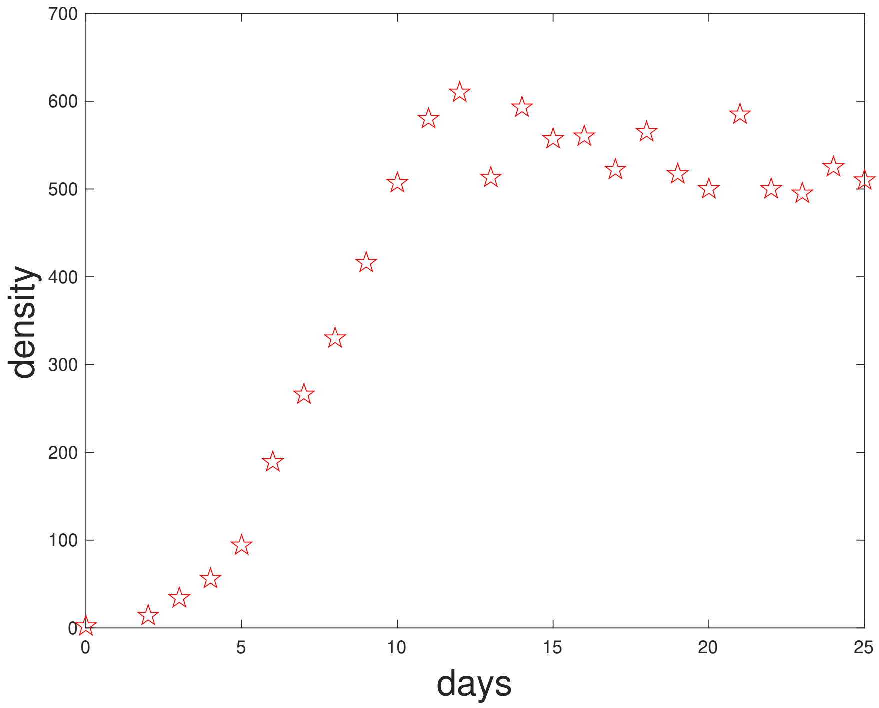

Figure: Growth of *Paramecium aurelia*.

Define the discrete logistic model: analize the data

- Initially, the population increases slowly. As time progresses, values of Δp_n increase and reach a maximum approximately halfway through the experiment.
- After that, they decrease again. We can attribute the decrease in the growth rate to intraspecific competition for nutrients and space.
- At the end of the experiment, the population appears to be leveling off when it reaches a mean density of approximately 540 individuals per 0.5 cm^3.

Define the discrete logistic model: find Δp_n

Based on observations, we can define Δp_n such that:

- is small when $p_n \approx 0$ and $p_n \approx 540$;
- is positive for $0 < p_n < 540$;
- that is negative for $p_n > 540$.

Considering

$$\Delta p_n = r(540 - p_n)p_n$$

we define a discrete logistic model for the population

$$p_{n+1} = p_n + r(540 - p_n)p_n,$$

where the parameter r remains to be determined.

Discrete logistic model: define the parameter

- In our model

$$\underbrace{p_{n+1} - p_n}_{y_n} = r\,\underbrace{(540 - p_n)p_n}_{x_n}.$$

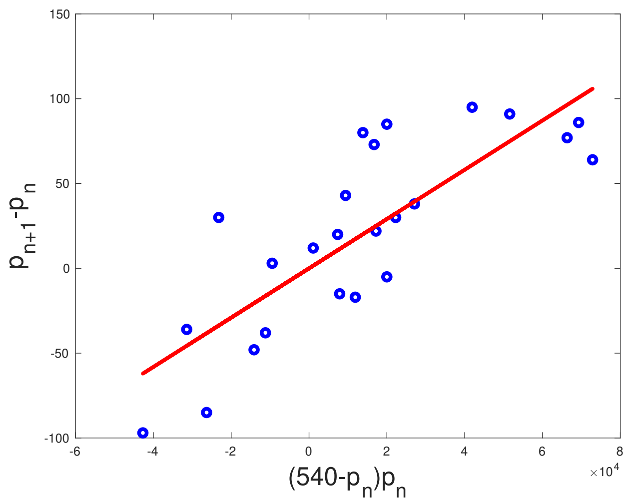

Figure: Plot of $p_{n+1} - p_n$ *versus* $(540 - p_n)p_n$.

- The slope of the line of best fit is $r \approx 0.0015$.

Discrete logistic model: validate the model

- Compare the behavior of our model

$$p_{n+1} = p_n + 0.0015(540 - p_n)p_n, \quad n = 0, 1, \ldots,$$

with the observed initial data.

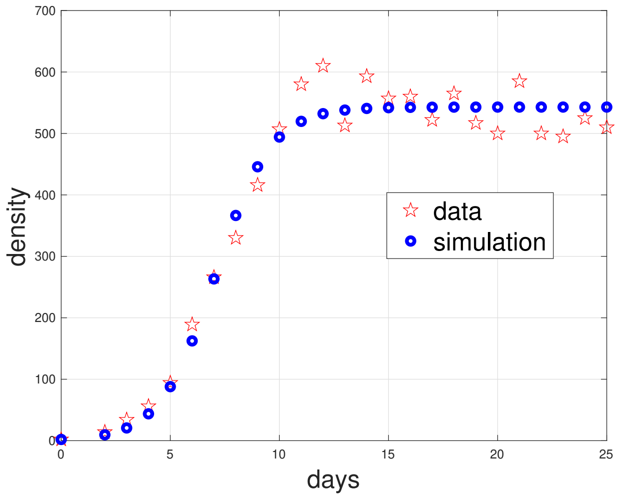

Figure: Comparison of the simulated data and the observed data.

Discrete logistic/Verhulst' model

- Discrete logistic/Verhulst' model

$$x_{n+1} = x_n + r(K - x_n)x_n = x_n + rK\left(1 - \frac{x_n}{K}\right)x_n, \quad n = 0, 1, \ldots$$

where K is the maximum population that can be sustained by the environment (the carrying capacity of the population).

- Teh discrete logistic/Verhulst' model is often written as

$$x_{n+1} = r\left(1 - \frac{x_n}{K}\right)x_n, \quad n = 0, 1, \ldots,$$

where $r = 1 + rK$ and $K = \dfrac{1 + rK}{r}$.

Other discrete population models

Ricker's population model:

$$N_{n+1} = N_n e^{r\left(1-\frac{N_n}{K}\right)}, \quad r > 0, K > 0.$$

- Constant reproduction factor e^r and a density-dependent mortality factor $e^{(-rN_n/K)}$, which is more severe the larger N_n.
- For large N_n there is a reduction in the growth rate but N_{n+1} remains nonnegative. So $N_n > 0$ for all n if $N_0 > 0$.

Other population models: replace the Malthusian equation by

$$N_{n+1} = rS(N_n)N_n.$$

- In a real population, some of the offspring produced by each adult will not survive to be counted as adults in the next census.
- $S(N_n)$ is the survival rate (depending on N_n).

Dynamics with intraspecific (within-species) competition

Same species competing for a short supply (e.g. food, space,...)

$$N_{n+1} = rS(N_n)N_n.$$

- r is the growth ratio in the absence of competition
- $S(N)$ defines the intraspecific competition function

Different ways to define $S(N)$:

- No competition: $S(N) = 1$ for all N.
- Every individual is assumed to get an equal share of a limited resource: $S(N) = 1$ for $N < N_c$ and $S(N) = 0$ for $N > N_c$, where N_c is the critical values of individuals for surviving.
- There is a limited number of units of resource and each individual which obtains one of these units of resource survives and reproduces as in absence of competition: $S(N) = 1$ for $N < N_c$, and $S(N) = N_c/N$ for $N > N_c$.

Hassell equation

- A model which exhibits all kinds of compensatory behaviour depending on the parameters is given by

$$N_{n+1} = \frac{rN_n}{(1 + aN_n)^b},$$

with $r, a > 0$ and $b \geqslant 0$; for $b = 0$ there is no competition.

- The analysis of the model is easier if we reduce the number of parameters. Defining $x_n = aN_n$, the Hassell equation becomes

$$x_{n+1} = \frac{rx_n}{(1 + x_n)^b}.$$

Homework #1

Exercise 1.1: Consider the model

$$p_0 = 2, \quad p_{n+1} = p_n + 0.0015(540 - p_n)p_n, \quad n = 0, 1, \ldots$$

1. Simulate the model and make a plot to compare the model results with the data observed by Gause.
2. Recall that the choice to use the number 540 in this equation was rather arbitrary. Try to improve the model.
3. The following Beverton-Holt model is a suitable alternative model to describe populations undergoing logistic growth

$$p_{n+1} = \frac{r}{1 + \frac{r-1}{K} p_n} p_n,$$

with $r > 0$ and $K > 0$. Fit the Beverton-Holt model to the data observed by Gause.

Homework #1

Exercise 1.2: Consider the survival of a population of whales, and assume that if the number of whales falls below a minimum survival level m, then the species will become extinct. In addition, assume that the population is limited by the carrying capacity M of the environment. That is, if the whale population is above M, then it will experience a decline because the environment cannot sustain that large a population level.

1. Let a_n represent the whale population after n years. Discuss the model

$$a_{n+1} = a_n + k(M - a_n)(a_n - m),$$

   where $k > 0$. Does it make sense in terms of the description above?
2. Sketch the graphs of a_n versus n for various initial conditions. You may assume that $M = 5000$, $m = 100$, and $k = 0.0001$.
3. The model has two serious shortcomings. What are they? Hint: Consider what happens when $a_0 < m$, and when $a_0 \gg M$.