

INSA 4BIM 2021-2022
Difference Equations and Modelling
 January the 3rd of 2022 - Duration: 1h30

Instructions

This form will be analyzed by optical reading, so please strictly respect the following rules:

- To answer, use rectangles provided below each question;
- Do not write anything outside the rectangles;
- A pre-defined number of points has been assigned to each question for a total of **23**.

All calculators are allowed, as well as an A4 sheet of paper, recto-verso, manually written and original.

Identity

Using your student card, fill in the fields below and encode your student number on the right side.

First and last names:

Student number:

<input type="checkbox"/>	0	<input type="checkbox"/>	0	<input type="checkbox"/>	0	<input type="checkbox"/>	0	<input type="checkbox"/>	0	<input type="checkbox"/>	0	<input type="checkbox"/>	0
<input type="checkbox"/>	1	<input type="checkbox"/>	1	<input type="checkbox"/>	1	<input type="checkbox"/>	1	<input type="checkbox"/>	1	<input type="checkbox"/>	1	<input type="checkbox"/>	1
<input type="checkbox"/>	2	<input type="checkbox"/>	2	<input type="checkbox"/>	2	<input type="checkbox"/>	2	<input type="checkbox"/>	2	<input type="checkbox"/>	2	<input type="checkbox"/>	2
<input type="checkbox"/>	3	<input type="checkbox"/>	3	<input type="checkbox"/>	3	<input type="checkbox"/>	3	<input type="checkbox"/>	3	<input type="checkbox"/>	3	<input type="checkbox"/>	3
<input type="checkbox"/>	4	<input type="checkbox"/>	4	<input type="checkbox"/>	4	<input type="checkbox"/>	4	<input type="checkbox"/>	4	<input type="checkbox"/>	4	<input type="checkbox"/>	4
<input type="checkbox"/>	5	<input type="checkbox"/>	5	<input type="checkbox"/>	5	<input type="checkbox"/>	5	<input type="checkbox"/>	5	<input type="checkbox"/>	5	<input type="checkbox"/>	5
<input type="checkbox"/>	6	<input type="checkbox"/>	6	<input type="checkbox"/>	6	<input type="checkbox"/>	6	<input type="checkbox"/>	6	<input type="checkbox"/>	6	<input type="checkbox"/>	6
<input type="checkbox"/>	7	<input type="checkbox"/>	7	<input type="checkbox"/>	7	<input type="checkbox"/>	7	<input type="checkbox"/>	7	<input type="checkbox"/>	7	<input type="checkbox"/>	7
<input type="checkbox"/>	8	<input type="checkbox"/>	8	<input type="checkbox"/>	8	<input type="checkbox"/>	8	<input type="checkbox"/>	8	<input type="checkbox"/>	8	<input type="checkbox"/>	8
<input type="checkbox"/>	9	<input type="checkbox"/>	9	<input type="checkbox"/>	9	<input type="checkbox"/>	9	<input type="checkbox"/>	9	<input type="checkbox"/>	9	<input type="checkbox"/>	9

1 Dynamics of a plant-herbivore model (16 points)

To study the interaction between certain plants and herbivores, Kang et al. (2008) proposed a two-dimensional discrete-time model utilizing leaf and herbivore biomasses as state variables¹. The parameter space consists of the growth rate of the host population (denoted r) and a parameter describing the damage inflicted by herbivores (denoted a). Variable $t > 0$ stands for time hereafter.

Below is the dimensionless dynamical model after normalization:

$$\begin{cases} x_{t+1} = x_t e^{r(1-x_t)-ay_t} \\ y_{t+1} = x_t e^{r(1-x_t)} (1 - e^{-ay_t}) \end{cases}$$

All parameters are strictly positive. State variables x_t and y_t have no unit.

Question 1 What happens if $x_0 = 0$ at $t = 0$?

0 0.5

If $x_0 = 0$ at $t = 0$, then $\forall t$, we will get $x_t = y_t = 0$. This statement can be proved by induction for a more formal way of doing. The biological consequence is that both populations do not growth. It is a quite obvious result (a trivial result), but it could be proved by induction in a proper way. AS a consequence, to keep the model biologically interesting, we can assume that $x_0 > 0$ and $y_0 > 0$ for the rest of the section.

¹Kang, Y., Armbruster, D., & Kuang, Y. (2008). Dynamics of a plant-herbivore model. *Journal of Biological Dynamics*, 2(2), 89101.

Question 2 Prove that, if $x_0 > 0$ and $y_0 > 0$, then $x_t > 0$ and $y_t > 0 \forall t$.

0 0.5

A proof by induction can be performed:

1. From the previous question, $x_0 > 0$ and $y_0 > 0$.
2. Let's assume that $x_t > 0$ and $y_t > 0$. Given the above equations for x_{t+1} and y_{t+1} , it immediately comes that $x_{t+1} > 0$ and $y_{t+1} > 0$.
3. We can conclude that $\forall t, x_t > 0$ and $y_t > 0$.

Question 3 Prove that $(0, 0)$ is a fixed point. Establish a linear relationship between x^* and y^* for all other fixed points. Among these fixed points, identify a limit case with $x_1^* > 0$ and $y_1^* = 0$. Specify the corresponding value of x_1^* .

0 0.5 1 1.5 2

From equation 1 of the dynamical system, it comes:

$$x^* = x^* e^{r(1-x^*)-ay^*}$$

$$\Leftrightarrow x^* \left(1 - e^{r(1-x^*)-ay^*} \right) = 0$$

$$\Leftrightarrow x^* = 0 \quad \text{or} \quad \left(1 - e^{r(1-x^*)-ay^*} \right) = 0$$

The condition $x^* = 0$ leads to $y^* = 0$.

The other condition leads to:

$$e^{r(1-x^*)-ay^*} = 1$$

$$\Leftrightarrow r(1-x^*) - ay^* = 0$$

Hence, we get a linear relationship between x^* and y^* :

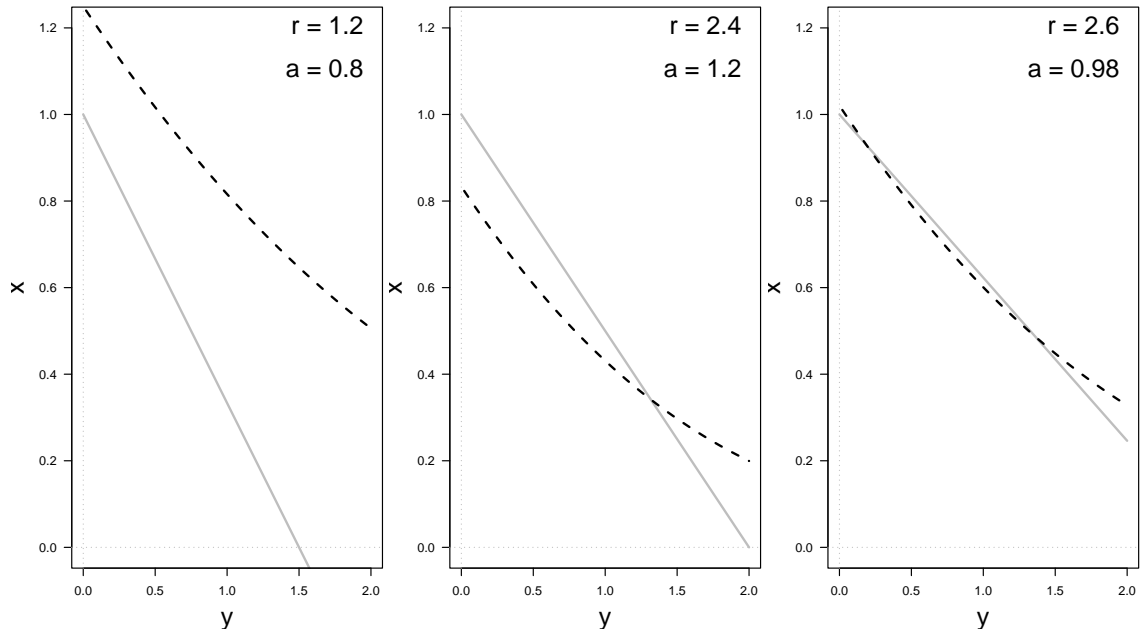
$$y^* = \frac{r}{a}(1-x^*)$$

This is a linearly decreasing function leading to The limit fixed point $(1, 0)$, with $x^* = 1$.

CORRECTION

We hereafter consider the phase plane (y, x) . Let f_1 and f_2 be the real functions defined by:

$$f_1(y) = 1 - \frac{a}{r}y \quad \text{and} \quad f_2(y) = \frac{y}{e^{ay} - 1}$$



Question 4 On the graphs above, identify the colour and/or the type of line associated with the function f_1 . Justify your answer

0 0.5 1

Grey and solid. Indeed, the function f_1 is linearly decreasing with a slope equal to $-\frac{a}{r} (< 0)$ and passes through the point with coordinates $(0, 1)$. This straight line also passes through the point of coordinates $(\frac{1}{a}, 0)$.

Question 5 What does both curves of f_1 and f_2 become when $r = 2$ and $a = 1$?

0 0.5 1

They become **tangent**, leading to only one additional fixed point. This can be proved by showing that $\lim_{y \rightarrow 0^+} f_2'(y) = -\frac{1}{2}$, that is the slope of the decreasing line equals $-\frac{a}{r}$ when $r = 2$ and $a = 1$.

CORRECTION

Question 6 What is $\lim_{y \rightarrow 0^+} f_2(y)$? Let's recall that $e^{ay} \underset{y \rightarrow 0}{\sim} 1 + ay$.

0 0.5 1

$$f_2(y) = \frac{y}{e^{ay} - 1}$$

Given that $e^{ay} \underset{y \rightarrow 0}{\sim} 1 + ay$, we get $e^{ay} - 1 \underset{y \rightarrow 0}{\sim} ay$. hence:.

$$f_2(y) \underset{y \rightarrow 0}{\sim} \frac{y}{ay}$$

So,

$$\lim_{y \rightarrow 0^+} f_2(y) = \frac{1}{a}$$

Question 7 Finally, how many fixed points may this dynamical plant-herbivore model have?

0 0.5 1

1, 2 or 3 depending on the parameter values.

Let's go back to the original system, that is in the plane (x, y) :

$$\begin{cases} x_{t+1} = x_t e^{r(1-x_t) - ay_t} \\ y_{t+1} = x_t e^{r(1-x_t)} (1 - e^{-ay_t}) \end{cases}$$

Question 8 Give the associated Jacobian matrix \mathbf{A} .

$$\mathbf{A} = \begin{pmatrix} e^{r(1-x)}e^{-ay}(1-rx) & -ax_n e^{r(1-x)}e^{-ay} \\ e^{r(1-x)}(1-rx)(1-e^{-ay}) & axe^{r(1-x)}e^{-ay} \end{pmatrix}$$

which also writes as follows:

$$\mathbf{A} = \mathbf{e}^{r(1-x)} \begin{pmatrix} e^{-ay}(1-rx) & -ax_n e^{-ay} \\ (1-rx)(1-e^{-ay}) & axe^{-ay} \end{pmatrix}$$

Question 9 Calculate the Jacobian matrix $\mathbf{A}_{(0,0)}$ at point $(x^*, y^*) = (0, 0)$. What is the stability of $(0, 0)$? What can you deduce from this result from a biological point of view?

CORRECTION

0 0.5 1 1.5 2

$$\mathbf{A}_{(0,0)} = \begin{pmatrix} e^r & 0 \\ 0 & 0 \end{pmatrix}$$

The eigenvalues of $\mathbf{A}_{(0,0)}$ are $\lambda_1 = e^r > 1$ ($r > 0$) and $\lambda_2 = 0 < 1$. This means that the dynamics is unstable on the x -axis, while it is stable on the y -axis.

Hence, $(0, 0)$ is a saddle point (unstable). Biologically speaking, this reveals that, under this model, plants can never die out.

Question 10 Calculate the Jacobian matrix $\mathbf{A}_{(1,0)}$ at point $(x, y) = (1, 0)$. Under which conditions on parameters r and a is $(1, 0)$ asymptotically stable?

0 0.5 1 1.5 2

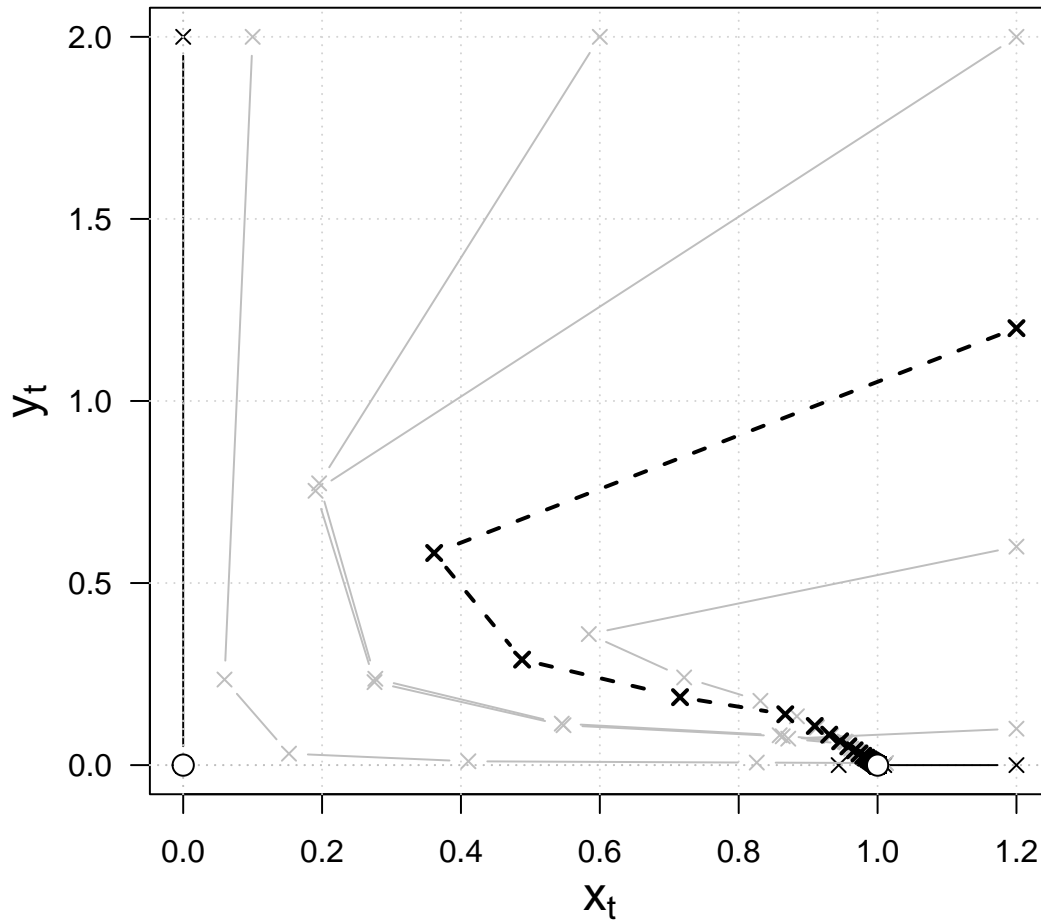
$$\mathbf{A}_{(1,0)} = \begin{pmatrix} 1-r & -a \\ 0 & a \end{pmatrix}$$

Eigenvalues of $\mathbf{A}_{(1,0)}$ are $\lambda_1 = 1 - r$ and $\lambda_2 = a$. So, point $(1, 0)$ is asymptotically stable if and only if $|\lambda_1| < 1$ and $|\lambda_2| < 1$. Given that parameters are strictly positive, this finally leads to the following conditions on parameters:

$$a < 1 \quad \text{and} \quad r < 2$$

Below is the phase portrait of the dynamical plant-herbivore model with some trajectories in the phase plane (x, y) .

CORRECTION



Question 11 What is the long-term future of both plant and herbivore populations ?

0 0.5 1

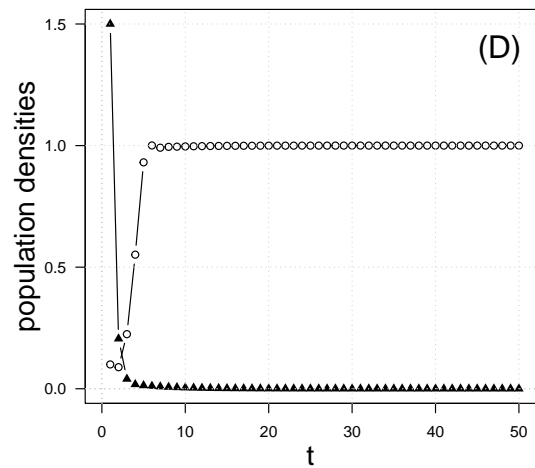
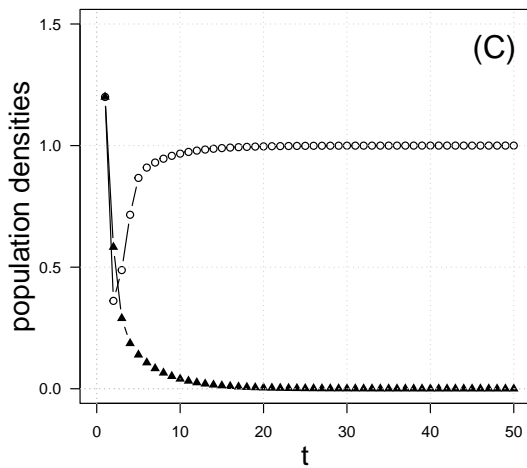
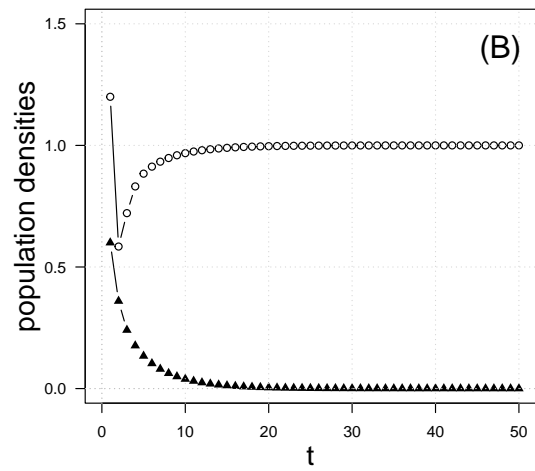
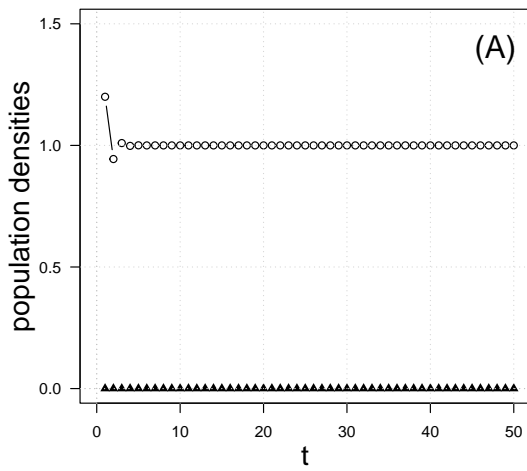
Whatever the initial conditions, except if located on the axes, all trajectories converge towards point $(1, 0)$, meaning that herbivores will always go extinct while plants will maintain at the fixed value $x^* = 1$.

Question 12 What is the particularity of the trajectory starting at point $(1.2, 0)$?

□ 0 □ 0.5 ■ 1

The trajectory starting at point $(1.2, 0)$ oscillates around the fixed point $(1, 0)$ before converging to it.

Below are some chronicle graphs.



Question 13 Which of the chronicle graphs corresponds to the dotted black trajectory on the phase portrait? Justify your answer.

0 0.5 1

The correct chronicle graph is (C), because this is the only chronicle graph starting at point of coordinates (1.2, 1.2).

2 Matrix population model for *Leptogorgia virgulata* (7 points)

Nicholas Gotelli proposed a time-invariant matrix population model to analyse the demography of *Leptogorgia virgulata*, a shallow-water gorgonian² living in the northeaster Gulf of Mexico³. He found that the average mortality and the recruitment rates were nearly balanced, so that the population growth rate, $\ln \lambda$, was close to 0.0. An elasticity analysis showed that the recruitment contributed < 5% to the measured rate of population growth. The most important component of population growth rate was survivorship, particularly of the large size classes.

Below is the life table estimated by Gotelli:

class	survival	fecundity	growth
1	0.62	0	0.16
2	0.78	0	0.1
3	0.84	0.19	0.12
4	0.86	0.19	0.11
5	0.98	0.19	0

On the basis of the R command lines and the associated outputs given at the end of this document, answer the following questions.

Question 14 Considering these monthly vital rates of recruitment, colony growth, and mortality, write the transition matrix \mathbf{M} .

0 0.5 1

$$\mathbf{M} = \begin{pmatrix} 0.62 & 0.00 & 0.19 & 0.19 & 0.19 \\ 0.16 & 0.78 & 0.00 & 0.00 & 0.00 \\ 0.00 & 0.10 & 0.84 & 0.00 & 0.00 \\ 0.00 & 0.00 & 0.12 & 0.86 & 0.00 \\ 0.00 & 0.00 & 0.00 & 0.11 & 0.98 \end{pmatrix}$$

²Une gorgone des eaux peu profondes.

³Gotelli, N. J. (1991). Demographic models for *Leptogorgia virgulata*, a shallow-water gorgonian. *Ecology*, 72, 457467.

CORRECTION

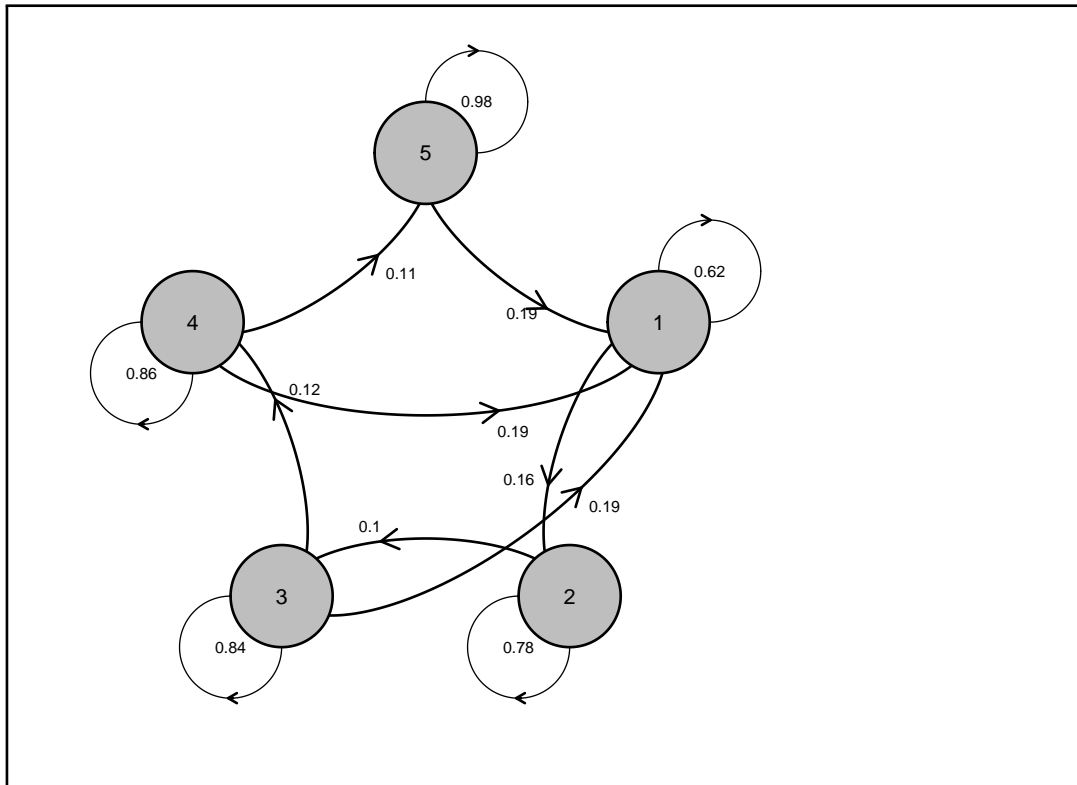
Question 15 What does the bottom-right numerical value of this matrix mean?

0 0.5 1

The bottom-right numerical value is equal to 0.98. It means that individuals entering the 5th class will stay in this class almost indefinitely (50 years on average). This can also be said as 98% of individuals in class 5 stay in class 5 from one time step to the next.

Question 16 Draw the life cycle graph corresponding to M.

0 0.5 1



Question 17 What is the final proportion of class 1 in the total population? Justify your answer.

0 0.5

$\approx 26.7\%$. This numerical value can be read on the histogram of the stable class distribution given in the R script, or directly from the eigen analysis in sub-object `$stable.stage`.

CORRECTION

Question 18 What is the numerical value of the population growth rate? Justify your answer.

0 0.5

The value is approximately 1.01 from the second graph. It is equal to 1.008533 from the eigen analysis.

Question 19 How do you interpret the R sub-object called `$repro.value`?

0 0.5

The sub-object `$repro.value` contains the reproductive values of the five classes. These are the contributions of each class from the initial condition up to the final stable distribution of classes when $t \rightarrow +\infty$.

Question 20 Given the elasticity matrix, which of the vital rates mostly influences the population growth rate? What happens if this parameter decreases of 5%

0 0.5 1

The vital rate mostly influencing λ is the survival rate of the 5th class. The corresponding elasticity value is 0.533. So, a decrease of 5% of this parameters will lead to a decrease of 0.02665% on λ that becomes equal to 0.983. This value < 1 means that the population will extinct after a certain time period.

CORRECTION

Question 21 How do you interpret the R_0 value?

0 0.5

$R_0 \simeq 1.5 > 1$ means that, for the estimated vital rates by Gotelli, the population will grow until infinity. The meaning is the same as for $\lambda > 1$.

Question 22 What does the numerical output at the very end of the R script mean?

0 0.5

The output at the very end of the R script is the generation time. The numerical value of 47.2 means that each gorgonian individual needs a little bit more than 47 months (almost 4 years) to produce a new individual.

Question 23 Can you finally confirm Gotelli's findings? Justify your answer.

0 0.5

Yes, all findings are confirmed.

R script

Matrix population model for *Leptogorgia virgulata*

INSA 4BIM 2021-2022 - Difference Equations and Modelling

January the 3rd of 2022

Load-libraries

```
library("popbio")
library("diagram")
```

Vital rates

```
vital.rates <- as.matrix(data.frame(survival = c(0.62, 0.78, 0.84, 0.86, 0.98),
                                   fecundity = c(0, 0, 0.19, 0.19, 0.19),
                                   growth = c(0.16, 0.1, 0.12, 0.11, 0)))
```

Matrix

```
M <- matrix(0, ncol = 5, nrow = 5)
M[1,] <- t(vital.rates[, "fecundity"])
diag(M) <- vital.rates[, "survival"]
M[2,1] <- vital.rates[1, "growth"]
M[3,2] <- vital.rates[2, "growth"]
M[4,3] <- vital.rates[3, "growth"]
M[5,4] <- vital.rates[4, "growth"]
```

Simulations over time

```
init <- rep(2000, nrow(M))
niter <- 100
pop <- pop.projection(A = M, n = init, iterations = niter)
# pop$lambda
```

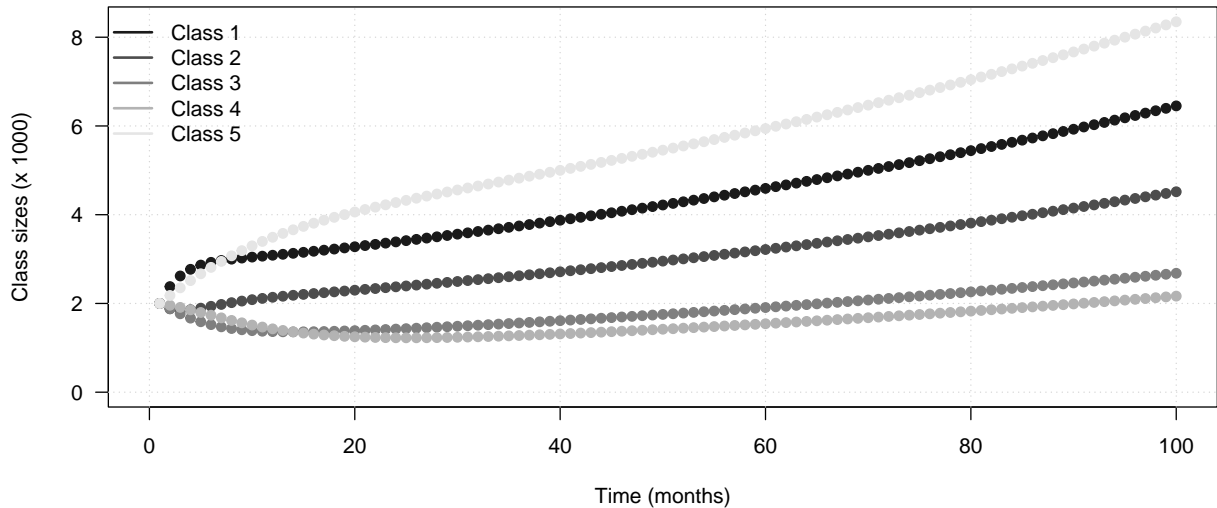
Population dynamics of each class

```
scale <- 1000
popdyn <- t(pop$stage.vectors)/scale
par(mfrow = c(1, 1))
colors <- c("gray10", "gray30", "gray50", "gray70", "gray90")
# rainbow(n = 5, start = 0.1, end = 0.9)
plot(0, 0, pch = NA, xlim = c(0, niter), ylim = c(0, max(popdyn)),
     xlab = "Time (months)", ylab = "Class sizes (x 1000)", las = 1)
grid()
```

```

for(i in 1: nrow(M)){
  points(popdyn[,i], type = "b", pch =19, col = colors[i])
}
legend("topleft", bty = "n", pch = NA, lty = 1, lwd = 2,
      legend = c("Class 1", "Class 2", "Class 3", "Class 4", "Class 5"),
      col = colors)

```

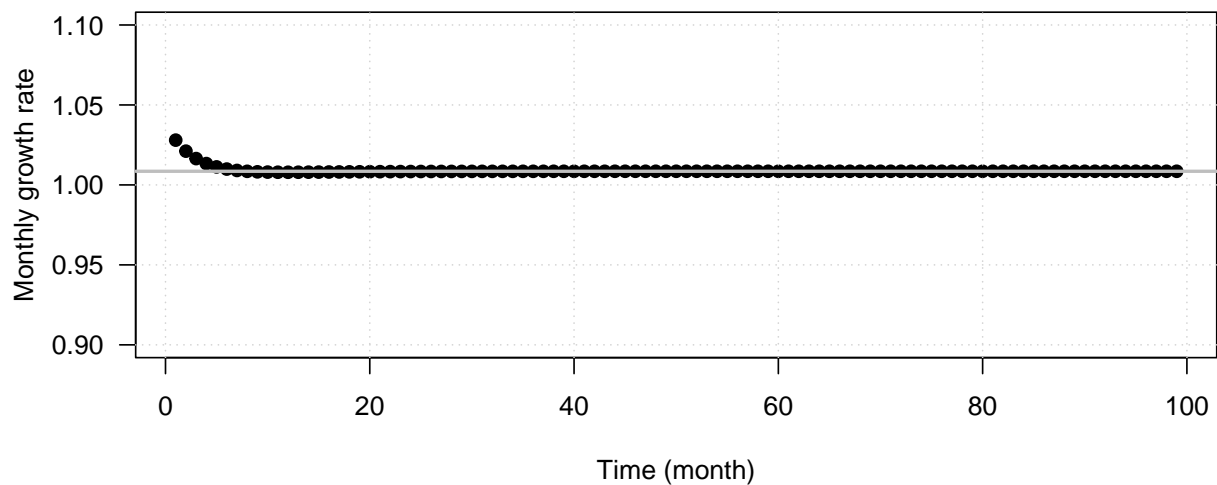


Growth rate dynamics

```

plot(1:(niter-1), pop$pop.changes, las = 1,
     pch = 19, type = "b", ylim = c(0.9, 1.1),
     xlab = "Time (month)", ylab = "Monthly growth rate")
grid()
abline(h = pop$lambda, col = "grey", lwd = 2)

```

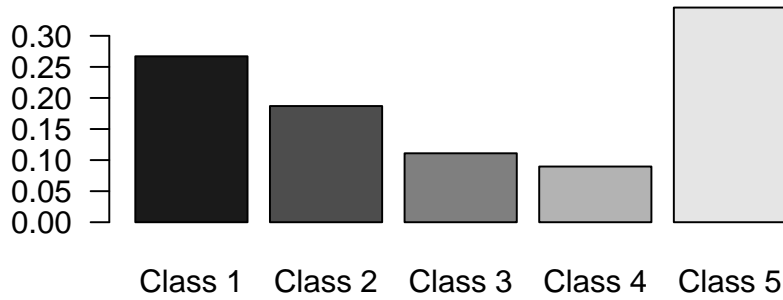


Stable age structure

```

barplot(pop$stable.stage, las = 1, col = colors,
        names.arg = c("Class 1", "Class 2", "Class 3", "Class 4", "Class 5"))

```



Demographic parameters

```
eigen.analysis(A = M)
```

```
$lambda1
```

```
[1] 1.008533
```

```
$stable.stage
```

```
[1] 0.26702070 0.18694599 0.11092551 0.08961691 0.34549089
```

```
$sensitivities
```

	[,1]	[,2]	[,3]	[,4]	[,5]
[1,]	0.06367082	0.04457709	0.02645008	0.02136907	0.08238196
[2,]	0.15461382	0.10824791	0.06422954	0.05189116	0.20005065
[3,]	0.35334346	0.24738211	0.14678564	0.11858837	0.45718158
[4,]	0.39543787	0.27685317	0.16427246	0.13271601	0.51164641
[5,]	0.42398256	0.29683781	0.17613047	0.14229612	0.54857961

```
$elasticities
```

	[,1]	[,2]	[,3]	[,4]	[,5]
[1,]	0.03914192	0.00000000	0.004982996	0.004025771	0.01552014
[2,]	0.02452891	0.08371901	0.000000000	0.000000000	0.00000000
[3,]	0.00000000	0.02452891	0.122256730	0.000000000	0.00000000
[4,]	0.00000000	0.00000000	0.019545912	0.113170101	0.00000000
[5,]	0.00000000	0.00000000	0.000000000	0.015520141	0.53305947

```
$repro.value
```

```
[1] 1.000000 2.428331 5.549535 6.210660 6.658977
```

```
$damping.ratio
```

```
[1] 1.144496
```

R_0

```
net.reproductive.rate(A = M)
```

```
[1] 1.493506
```

Generation time

```
generation.time(A = M)
```

```
[1] 47.20964
```