Computer Lab ECFM: Population dynamics and harvesting

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Overview

In this practical you will use The Schaefer Model [1] to explore how harvesting affects population numbers and dynamics. You will be using R to explore the dynamics of the model. R is a statistical software that is very popular in especially biological sciences and can be downloaded for free. If you have not installed R and R-studio already, please see the document **"First time R user"**. R-studio is just an interface for R with many helpful utilities. It is an advantage if you know some Basic R, but you should be able to follow along this lab without any prior knowledge if you consult the **"First time R user"**. In this document R-code is text with grey background. You can copy these chunks of code to a new R-script in R-studio (instead of pasting it directly into the console because it quickly becomes hard to overview your work!). For some it might also be a repetition of calculus and algebra, and you will also practice some basic population dynamics and equilibrium theory.

There are hints for most questions **at the end of this document** if you need, and you can also look at the solutions or ask an instructor if you get stuck!

The Schaefer Model

The Schaefer model is a harvest model based on the logistic growth equation (the Verhulst model). This is a continuous-time model and the following differential equation describes the rate of change in number of individuals, N:

$$dN/dt = rN(1 - N/K) - qEN$$

where r is the intrinsic growth rate, K is the carrying capacity, q is catchability and E is harvesting effort. In this lab, N is referred to as "density" Below is some R-code to explore the population density over time in the absence of harvesting to recap the logistic growth model.

Part 1: Recap the logistic growth model without harvesting

This part is mainly to become familiar with the growth model and read in parameters that you will use later. It is recommended you do not spend too much time on this part, so essentially just copy paste the chunks of code below until you reach Question #1!

```
rm(list = ls()) # It is often a good practice to start your scrpits with this command,
# which clears the workspace (console, "calculator") from all objects.
# *Note though that if you want to start a completely clean R session you need to
# quit the program the usual way.

# Two parameters govern the dynamics of the population: the growth rate (r) and
# the carrying capacity (K).
# We can give them arbitrary values, it does not really matter here.
r <- 0.1
K <- 40
```

```r
# We also need to set the initial population density and the time range
N_ini <- 2
t <- 100

# Now we can calculate the density at the next time step!
N2 <- r * N_ini * (1-(N_ini/K)) + N_ini
N3 <- r * N2 * (1-(N2/K)) + N2
#... etc etc
```

We could repeat this iteratively, but it would be extremely tedious. This is where the loop comes in handy, which is used in programming to automate tasks. Basically, if you find yourself copy-pasting code like this, you can automate it. Here we will use a for loop. But do not worry, this lab is not about writing loops! They are just introduced so that you can get a feel of (1) how it is done (2) to explore the population dynamics.

This is essentially how you write a for loop:

```r
#for (each of these values) {
#    do the commands between the curly brackets
#}
```

Together with a feeling for indexing (basically that you can extract the "ith"-value of a vector using hard brackets):

```r
vec <- seq(1, 20, 1)
vec
```

```
##  [1]  1  2  3  4  5  6  7  8  9 10 11 12 13 14 15 16 17 18 19 20
```

```r
vec[3]
```

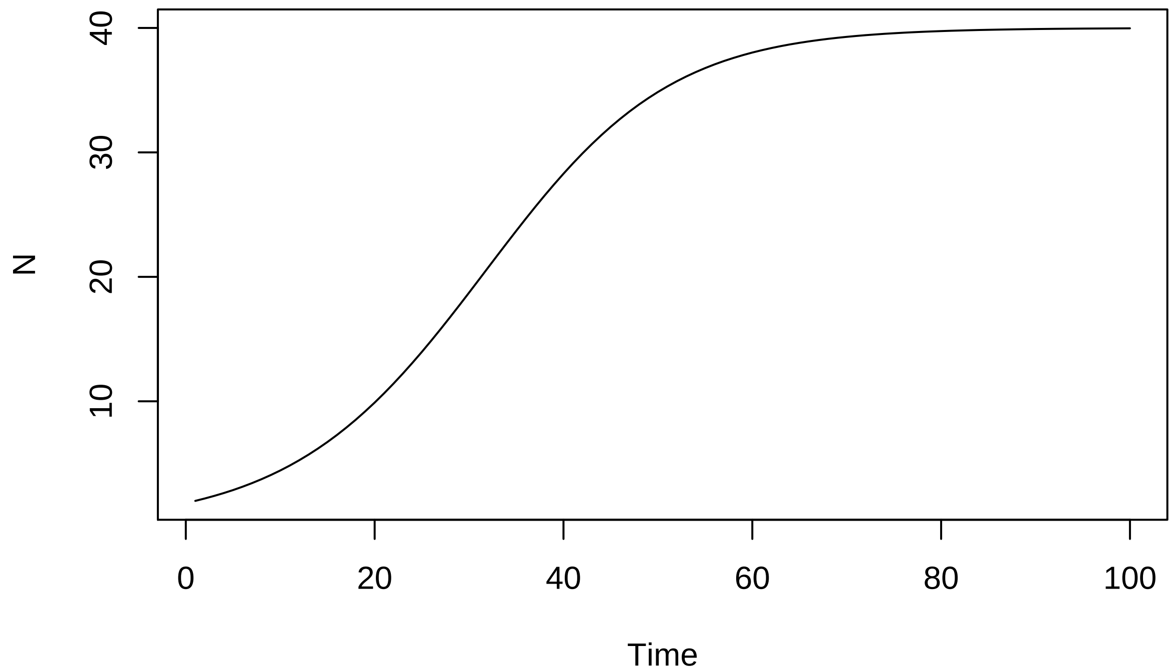
```
## [1] 3
```

... we can build a for loop to simulate the time-dynamics in density:

```r
# Create an empty vector to store the values in
N <- rep(NA, t)
N[1] <- N_ini

for (i in 2:t) {
  N[i] <- r * N[i-1] * (1-(N[i - 1]/K)) + N[i-1]
}
```

```r
# Plot how population abundance change over time
plot(y = N, x = 1:t, xlab = "Time", ylab = "N", type = "l")
```



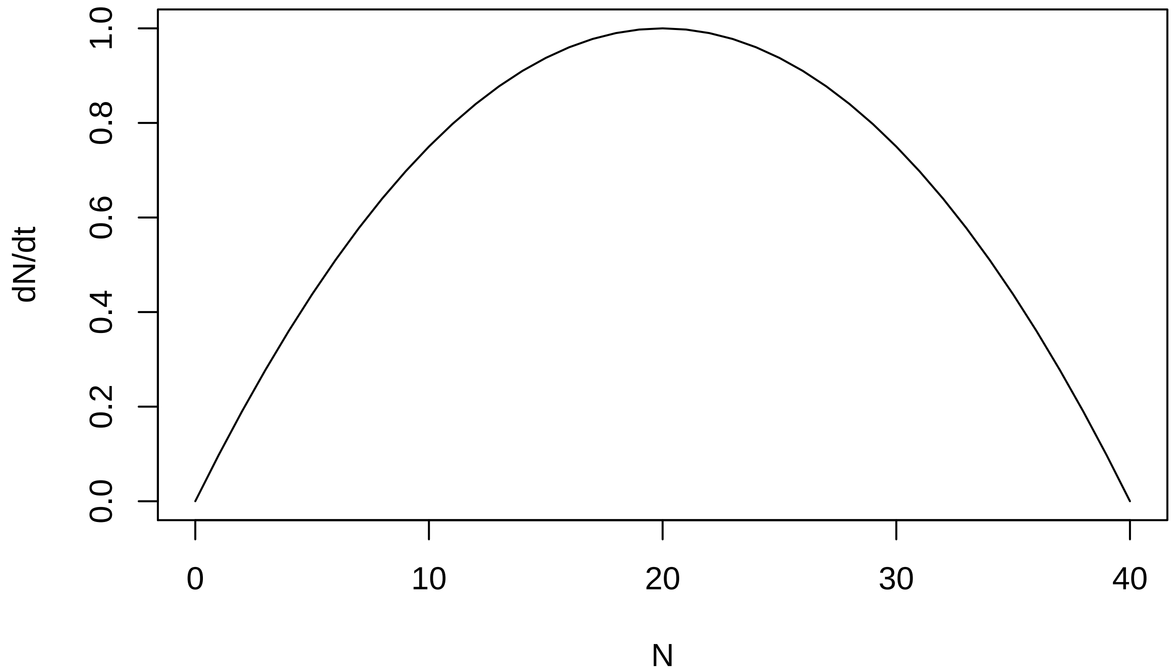
It is a bit tricky to understand exactly how density dependence works in this model. To better understand that, we can plot the population- and per capita growth rate as a function of N.

```
## We can start by creating a vector of N-values (ranging from 0 to carrying capacity):
N_vec <- seq(from = 0, to = K, by = 1)
N_vec
```

```
##  [1]  0  1  2  3  4  5  6  7  8  9 10 11 12 13 14 15 16 17 18 19 20 21 22
## [24] 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40
```

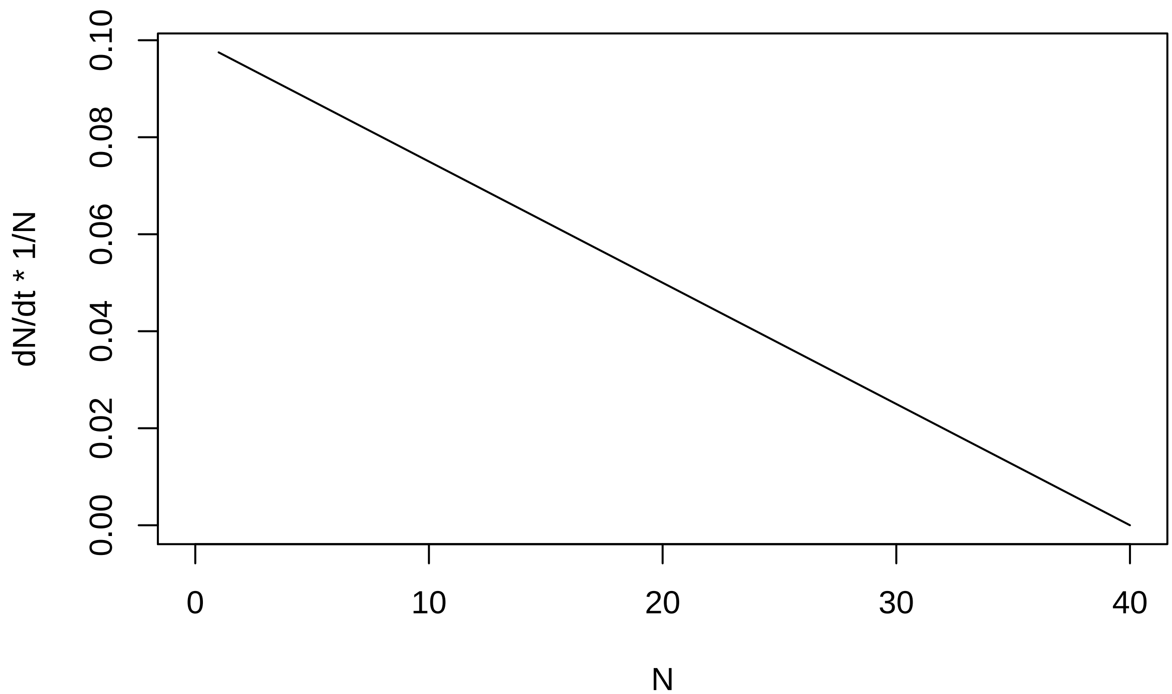
```
## Population growth rate
growth_pop <- r * N_vec * (1-(N_vec/K))

# Plot how population growth rate varies with population density
plot(growth_pop ~ N_vec, xlab = "N", ylab = "dN/dt", type = "l")
```




```
## Per capita growth rate
growth_cap <- growth_pop / N_vec

# Plot how per capita growth rate varies with population density
plot(growth_cap ~ N_vec, xlab = "N", ylab = "dN/dt * 1/N", type = "l")
```



- **Question 1:** a) How does density dependence operate in this model? b) When is the growth rate of the population highest? c) How could such density dependence occur in nature?

Part 2: Equilibrium, harvesting and bifurcations

Now let us explore the equilibrium dynamics and dynamical stability of the Schaefer model analytically and graphically. Here asymptotic stability is an important concept. An equilibrium is asymptotically stable if the system returns to it after small deviations. The density at an equilibrium is denoted $N*$.

- **Question 2:** Which are the two equilibria of the Schaefer model?
- **Question 3:** a) Can you show these equilibria graphically? Assume $q = 0.2$ (you can do this for the rest of this lab!) and $E = 0.1$. b) With this harvesting regime, what is the population density at the positive equilibrium?
- **Question 4:** What can we say about the dynamical stability of this equilibrium?
- **Question 5**: What happens to the equilibria and their stability when we *gradually* increase the fishing effort?
- **Question 6**: Plot $N*$ as a function of fishing effort, E.
- **Question 7**: a) Can you plot yield, $Y = qEN*$, as a function of fishing effort, E? b) At what effort and density is long term yield maximized? (You can give an approximate value based on the last two figures). c) How do the answers in a) and b) depend on r and K? You can look at the analytical solutions and/or redo the last two plots.

Part 3: Allee effects

In the logistic model, per capita growth rates decreases linearly with population density. However, in many cases there is a threshold density for positive growth [2], i.e. an Allee effect. In other words, there is a positive relationship between per capita population growth rate and population size at low density. We can extend the Schaefer model to account for Allee-effects like this:

$$dN/dt = rN(N/K_0 - 1)(1 - N/K) - qEN$$

- **Question 8**: What is the biological interpretation of the parameter K_0?
- **Question 9**: Plot the population- and per capita growth rate as a function of N (you can set K_0=10).

With this growth model we have an equilibrium at N*= 0 (trivial equilibrium). The non-zero equilibria are solutions to the quadratic equation:

$$r(N/K_0 - 1)(1 - N/K) = qE$$

which we obtain by equaling mortality and growth and dividing by N. Rather than solving this equation, we can explore it graphically for different fishing efforts the same way we did it before. Or, we can plot N as a function of qE:

- **Question 10**: From the above equation, plot the equilibrium density N* as a function of qE. Compare to Question #6 and explain how and why the equilibria in the two cases differ!
- **Question 11**: Plot yield as a function of fishing mortality (see Question #7). Locate the stable part of this curve. Which effort maximizes yield?
- **Question 12**: What challenges to fisheries management do Allee effects pose?

Bonus questions

- **B1**: Find the exact solution of the of the density at MSY in the Schaefer model.
- **B2**: Solve for the yield at MSY in the Schaefer model.

References

[1] Schaefer, M. B. 1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. *Bulletin of the Inter-American Tropical Tuna Commission*, 1, 25-56.

[2] PerÃ¤lÃ¤, T., & Kuparinen, A. (2017). Detection of Allee effects in marine fishes: Analytical biases generated by data availability and model selection. *Proceedings of the Royal Society B*, 284(1861), 20171284.

Hints

Question 2: Find expressions of N that leads to fishing mortality being equal to growth.

Question 4: What happens to the relationship between growth and mortality if the system is perturbed slightly to the left and right along the N-axis?

Question 5: Repeat Question #4 with higher E-values.

Question 6: Create a vector of different E-values ranging from 0-0.6 and look at the equation you found in Question #2.

Question 7: Insert the expression for the non-trivial equilibrium in the equation.

Question 9: See first part!

Question 10: Use the same N-vector you have used.

Bonus Q 1: Take the derivative of the logistic equation.

Bonus Q 2: Substitute N with K/2.