Solution, Exercise 1, Dynamic Systems

Modelling Biological Systems, BIOS13

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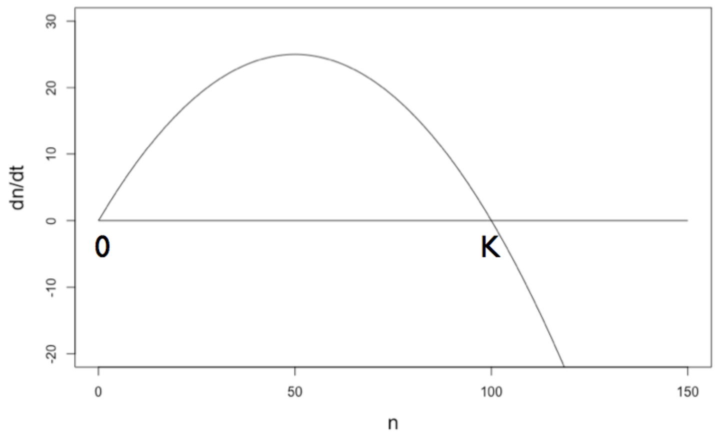
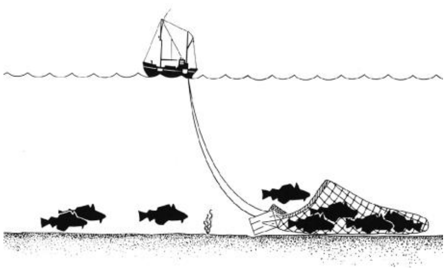
1. Consider the logistic equation that we discussed in the lecture:

$$\frac{dn}{dt} = r_0 n(1 - n/K)$$



It describes the growth of a single population with some density dependence, i.e. there is an upper bound to how large the population can become.

Now let's assume the population is harvested somehow (fishing, hunting, picking, …). The harvest is of a '*constant effort*' type, which means the number of harvested individuals per time unit is proportional to population size. In other words, the number of harvested individuals per time unit can be written *hn*, where *h* is a parameter representing the harvesting effort (the number of hours per season, or the number of fishing vessels, or something like that).



1a) Write a modified growth equation that takes harvesting into account

All we need to do is subtract the harvesting *hn* from the total population growth rate:

$$\frac{dn}{dt} = r_0 n\left(1 - \frac{n}{K}\right) - hn$$

1b) Find the new equilibrium

When is the growth rate zero?

$$\frac{dn}{dt} = r_0 n \left(1 - \frac{n}{K}\right) - hn = 0$$

$$n \left(r_0 \left(1 - \frac{n}{K}\right) - h\right) = 0$$

The last expression on the left-hand side is a product of two factors. One of them has to be zero.

Solution 1 (called the 'trivial' solution) : $n = 0$

Solution 2:

$$r_0 \left(1 - \frac{n}{K}\right) - h = 0$$

Which solves to: $n^* = K\left(1 - \frac{h}{r_0}\right)$

1c) At what values of h does the population go extinct?

The equilibrium solution from previous exercise gives us some clues. As long as $n^* > 0$ we can assume the population will not go extinct. How much harvesting is required for $n^* = 0$?

$$K\left(1 - \frac{h}{r_0}\right) = 0$$

We can assume $K > 0$ and just solve:

$$1 - \frac{h}{r_0} = 0 \Leftrightarrow h = r_0$$

Conclusion: The population will go extinct if $h \geq r_0$.

1d) Confirm that the new equilibrium is stable, if it is positive.

To analyse the stability we need the derivative of the function dn/dt at the equilibrium:

$$\frac{dn}{dt} = f(n) = r_0 n \left(1 - \frac{n}{K}\right) - hn$$

$$f'(n) = [product\ rule] = r_0 \left(1 - \frac{n}{K}\right) + r_0 n \left(-\frac{1}{K}\right) - h$$

It is at this point a good idea to resist the urge to simplify the above expression. We are now supposed to insert the equilibrium point $n = n^* = K\left(1 - \frac{h}{r_0}\right)$ and thus calculate the derivative at that point. However, when calculating the equilibrium point in (1b) we started with the equation $r_0\left(1 - \frac{n^*}{K}\right) - h = 0$ and solved for n^*. So that equation still holds, and consequently the two blue terms in the expression for $f'(n)$ above will cancel out once we substitute $n = n^*$. This simplifies the calculation a lot and we get:

$$f'(n^*) = r_0 n^* \left(-\frac{1}{K}\right) = -r_0 \frac{n^*}{K} = -r_0 \frac{K\left(1-\frac{h}{r_0}\right)}{K} = -(r_0 - h)$$

Here, the green expression actually is more informative than the simplified blue expression (again, simplifying as much as you can is not always the best way to go). The two parameters r_0 and K are by assumption positive, and n^* should also be positive (or there is extinction). It follows that $f'(n^*)$ is always negative and the equilibrium is always stable. The same conclusion can be drawn from the blue expression, but one has to keep in mind that $h < r_0$ to prevent extinction.

1e) The *yield* per time unit is simply *hn*. What is the yield at equilibrium?

The yield, i.e. the total harvest, at equilibrium becomes:

$$Y = hn^* = hK\left(1 - \frac{h}{r_0}\right)$$

1f) At what value of *h* is the yield maximized?

The expression for *Y* above expresses the yield as a function of the harvest effort *h*:

$$Y(h) = hK\left(1 - \frac{h}{r_0}\right)$$

We are now supposed to maximize this function with respect to *h*. Taking the derivative and solving for zero gives:

$$Y'(h) = K\left(1 - \frac{h}{r_0}\right) + hK\left(-\frac{1}{r_0}\right) = K\left(1 - \frac{h}{r_0} - \frac{h}{r_0}\right) = K\left(1 - \frac{2h}{r_0}\right) = 0$$

$$h = \frac{r_0}{2}$$

Is this a maximum? I calculate the second derivative to make sure:

$$Y''(h) = K\left(-\frac{2}{r_0}\right) < 0$$

The second derivative is negative, which means we have at least a local maximum. It should also be global since there are no other points where $Y'(h) = 0$, which means the slope can not change sign anywhere else. Once $Y(h)$ starts going down (above $h = r_0/2$) it will never go up again. As another piece of evidence, we also know that $Y(0) = 0$ (no harvest if no harvesting effort) and $Y(r_0) = 0$ (see 1c). In between these points we get

$$Y\left(\frac{r_0}{2}\right) = \frac{r_0}{2} K\left(1 - \frac{r_0/2}{r_0}\right) = \frac{Kr_0}{4}$$

which is the maximal (equilibrium) harvest. Note that one can harvest more than this, but that would in the long run lead to extinction. The yield above is the *Maximal Sustainable Yield*.

1g) How is the return to equilibrium affected by *h*?

The return time is calculated as

$$T_R = -\frac{1}{f'(n^*)} = -\frac{1}{-(r_0 - h)} = \frac{1}{r_0 - h}$$

We can see that increasing h will increase T_R. Indeed, as $h \to r_0$ we get $T_R \to \infty$.
Conclusion: The more we harvest, the longer the return to equilibrium after a disturbance.

2. Let's try running some simulations in R

2a) As a first exercise, plot the growth function as dn/dt vs. n (see figure in exercise 1).

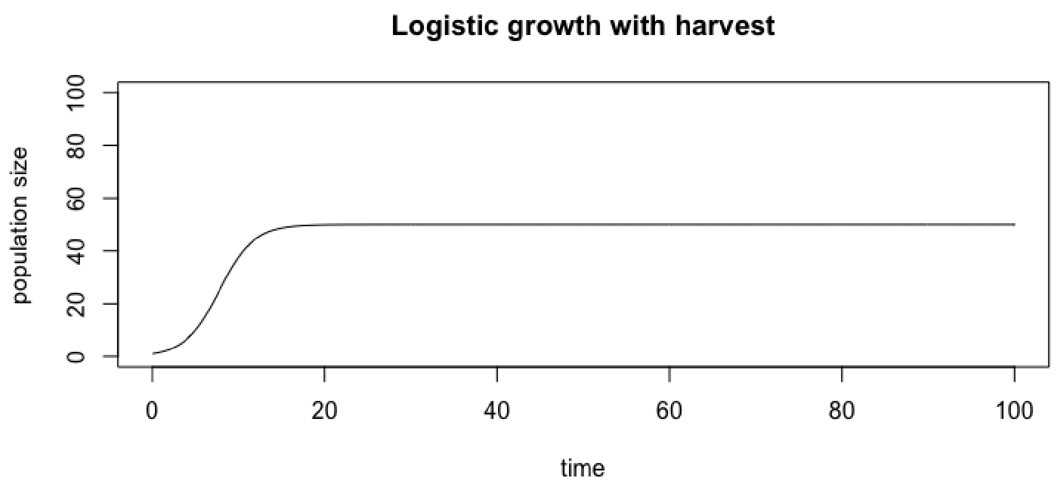
This is a matter of plotting a function, nothing else. How do you plot a function? Well, set up a vector of x-values, calculate the corresponding y-values, call the plot function, and you're done. Here we go:

```
# Script to plot growth function, dn/dt

# A few parameter values (arbitrarily chosen):
K <- 100
r0 <- 1
h <- 0.5 # should be less than r0

# A vector of n-values:
n <- seq(0, K, length.out = 100)
# The growth function (population growth rate):
dndt <- r0*n*(1-n/K)-h*n

# And plot:
plot(n, dndt, type='l', ylim=c(-5,max(dndt)))
```

2b) Write an R-script that solves the differential equation from the previous exercise. Use the `ode` function of the `deSolve` package. See the lecture notes for an example. Make your script plot the result of the ode solver.

I will use the script from the lecture as a template and include the harvesting.

```
# First load the deSolve package:
library(deSolve)
# clear workspace, just in case:
rm(list=ls())

# define the growth function:
popGrowth <- function(t, n, P) {
  dndt <- P$r0 * n * ( 1 - n / P$K ) - P$h*n
  return(list( dndt ))
}

# set up a vector of time-points for the output:
timevec <- seq( 0, 100, by=0.1 )

# we need a list of parameters:
P <- list( r0=1, K=100, h=0.5 )

n0 <- 1  # initial population size

# call the ode function:
out <- ode( y = n0, func = popGrowth,
         times = timevec, parms = P)

# plot the output:
plot( out , ylim=c(0,P$K), main='Logistic growth with harvest', ylab='population size' )
```



2c) Confirm, through your simulations, that the equilibrium you calculated in 1b) actually is an equilibrium, and that it is stable. In other words, confirm that a population with higher or lower density will approach this equilibrium over time.

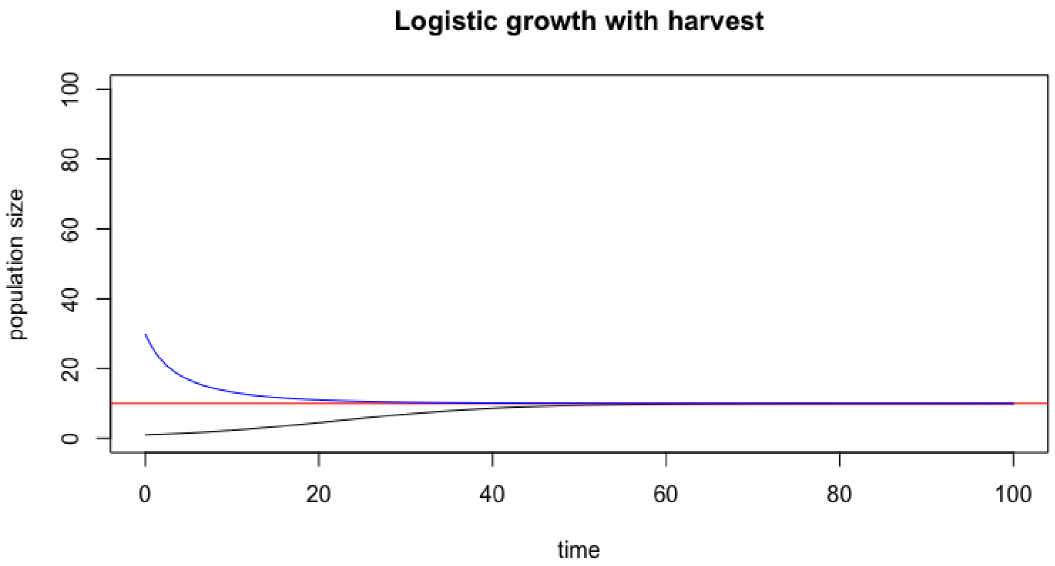
By adding a few lines to the code above we can *i*) mark the calculated equilibrium with a horizontal line and *ii*) add a second simulation that starts above the equilibrium:

```
# Calculate the equilibrium:
ne <- P$K*(1-P$h/P$r0)
# Add a line to mark it in the plot. There are several ways, I'll use the abline command here:
abline(ne,0,col='red')
# Set a new starting value, above the equilibrium:
n0 <- ne+20
# call the ode function:
out <- ode( y = n0, func = popGrowth, times = timevec, parms = P)

# Add the result to the plot:
lines( out , col='blue')
```

As you can see, the equilibrium (red) is approached both from below (black curve) and above (blue curve). It seems to be quite stable. This also confirms that our calculations underlying the red curve were correct, or, alternatively, that our program is doing the right thing. Out calculated equilibrium is the same as the equilibrium of the ode output.

2c) Confirm, again with simulations, that a higher *h* also gives slower return to equilibrium after a disturbance. Can you think of any biological implications of this?

I'll simply increase h to 0.9 and re-run the script above. New plot:



It should be clear that the return time indeed is longer, compared to the previous plot.

The biological implication is first of all that disturbances take longer to die out. This means that there is probably a new disturbance before the system has bounced back from the previous one. Taken together we get a system forever fluctuating wildly, far from equilibrium. Heavy harvesting thus means not only a low population size, but also a highly fluctuating population size, and a very high risk of extinction.