Bifurcation analysis: Understanding maximum sustainable yield (MSY) with the Schaefer model

A bifurcation analysis involves analyzing how population equilibria and their stability properties change in relation to a parameter such as survival rate, birth rate, or in the case of this lab fishing rates. In this lab we will analyze population models for fisheries management by graphically constructing a bifurcation analysis of two fishing strategies and to appreciate how small changes in assumptions / management scenarios can have large consequences for population dynamics, stability, and the sustainability of fisheries.

Objective: Use computer simulations in R to develop a conceptual understanding of bifurcation analyses.

Marking: each question is worth 10 points for a total of 80 points.

Introduction: Maximum sustainable yield (MSY) describes the largest number of individuals (or biomass) that can be taken from a population that retains the species stock for an indefinite amount of time (Figure 1). MSY is a particularly important topic in fisheries and other areas of resource management, where we are often interested in how many fish we can remove from a population whilst maintaining enough individuals to sustain the population for generations after generations.

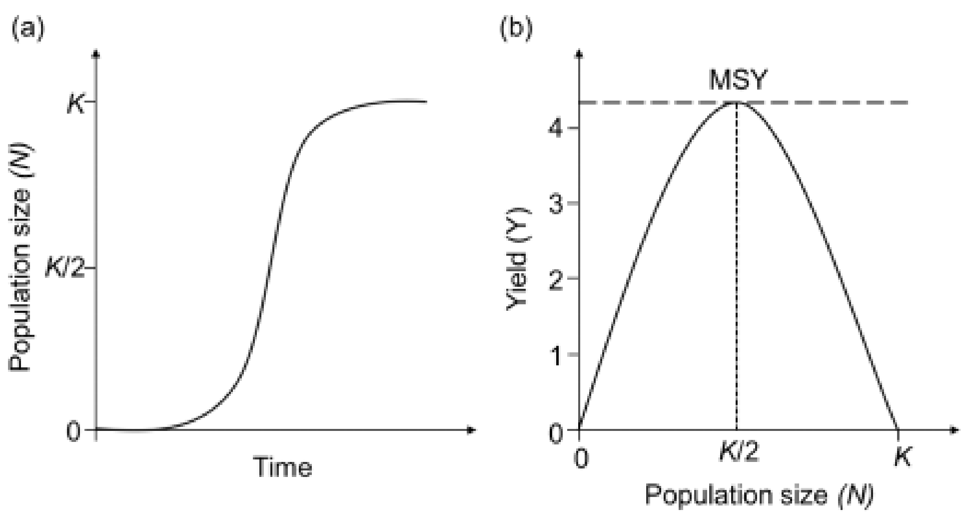

Figure 1. (a) Logistic growth model; population size (*N*) as a function of time. *K* = carrying capacity. The fastest population growth (steepest slope) of the logistic growth curve occurs at *K*/2. (b) Sustained yield (*Y*) as a function of population size (*N*). MSY = maximum sustainable yield occurs at the peak of the yield curve (where the slope of Y is zero) where the equilibrium fish population size is *K*/2 (i.e. where population growth is at its maximum).

Quantifying MSY requires an understanding of population sizes (*N*), growth rates (*r*), carrying capacities (*K*), and harvest (*H*). The Schaefer model is a well-known model in fisheries that assumes logistic growth for the fish population and a harvesting function *H(N)* that can be a function of population size:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - H(N)$$

The yield from the fishery (*Y*) is equal to the harvest function *H(N)*, and for the yield to be sustainable, the fish population must be at a stable equilibrium with the fishery. For the stable equilibrium, we set dN/dt = 0, which allows us to solve for the yield:

$$Y = H(N) = rN\left(1 - \frac{N}{K}\right)$$

The maximum sustainable yield (MSY) is the highest value of Y that is possible, and this occurs at the peak of the yield curve, where the slope of Y is equal to zero (Figure 1b). To find the number of individuals (*N*) removed that maximizes yield we find the peak in the yield curve by finding the point where the slope (*dY/dN*) is equal to zero, and solve for *N*:

$$\frac{dY}{dN} = r - \frac{2rN}{K} = 0$$

which gives

$$N_{msy} = \frac{K}{2}$$

MSY occurs when the population is at half of carrying capacity (i.e. half of the fish are gone; Figure 1b).

Part 1 – Constant Fishing Effort

We have not yet specified what the harvest function is, and this depends on the fishing strategy. One scenario is to assume that fishers exert a fishing effort e to capture the fish and so the harvest rate is proportional to the fishing effort and the abundance of fish, *H(N)* = *eN*. The model for the fish population dynamics is then

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - eN$$

which can be expressed as

$$\frac{dN}{dt} = G(N) - H(N)$$

where

$$G(N) = rN\left(1 - \frac{N}{K}\right)$$
$$H(N) = eN$$

In this model, fishers are behaving like a type I predator.

For the following simulations, let r=1, K=1000, N=1000, and e=0.3 where necessary.

Exercise 1.1: Create a plot of the growth function, $G(N)$, as a function of biomass (N) on the x-axis. Your graph should reflect that population growth equals zero when the population has 0 individuals, and when the population is at carrying capacity (K). Also identify the point of maximum population growth rate at K/2.

Hint:

#Parameters

- r<-1
- K<-1000

#Biomass
- N<-1000

#Vector to store values if G in
- G<-numeric(N)

#Initial Condition
- G[1]<-0

#Simulation

```
for (n in 1:N){
     G[n]<-r*n*(1-(n/K))
}
```

#Plotting

- NN<-seq(1,N)
- plot(NN,G,xlab="Biomass (N)",ylab="G(N)")

Exercise 1.2: On top of your graph of *G(N)* versus *N*, plot the harvest function *H(N)* starting from 0 and increasing linearly (the slope is e). Where your harvest rate meets your yield curve is an equilibrium point. Include this plot in your lab report and indicate if the equilibria are stable of unstable.

Hint:

#Parameters

- e<-0.3

#Biomass

- N<-1000

#Vector

- H<-numeric(N)

#Initial Condition

- H[1]<-0

#Simulation

- for (n in 1:N){
      H[n]<-e*n
  }

Plotting

- NN<-seq(1,N)
- lines(NN,H,)
- text(800,200,"H(N)",cex=1)

Sustainable yield occurs when the fish population is at equilibrium with the fishery (i.e. dN/dt = 0) We'll use an asterisk (*) to denote that we are solving for *N* at equilibrium when dN/dt=0:

$$0 = rN\left(1 - \frac{N^*}{K}\right) - eN^*$$

Solve for *N** in terms of the other parameters and record your finding. You should find two equilibria, one of which is zero.

Exercise 1.3: Create a diagram of the number of individuals at equilibrium (N^*) on the y-axis as a function of the harvest rate (e) on the x-axis. Indicate the stable and unstable equilibria. At what value of e does the fish population go extinct? Why?

Hint:

#Parameters

- K<-1000

#Biomass

- e<-100

#Vector
- N<-numeric(e)

#Initial Condition
- N[1]<-K

#Simulation

```
for (i in 1:e){
    N[i]=(-K*i)+K
}
```

#Plotting

- ee<-seq(1,e)
- plot(ee,N,xlab="e",ylab="N*")

Part 2 – Fishery Quota
In the previous example, we assumed that the harvest rate was a product of fishing effort and fish abundance. Instead, let's assume that managers allow an annual (constant) quota that fishers are allowed to remove from the fish population (i.e. the harvest function is a constant)

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - H$$

Exercise 2.1: Plot the relationship between $G(N)$ and N. Also plot the constant harvest H for the case where yield is less than MSY (i.e. H is independent of population size so is a horizontal line). How many points of equilibria are present? Where are these points of equilibria in relation to the MSY? Are the equilibria stable or unstable? Identify them on your graph.

Hint:

#Parameters

- r<-1
- K<-1000

#Biomass

- N<-1000

#Vector

- G<-numeric(N)

#Initial Condition

- G[1]<-0

#Simulation

- for (n in 1:N){
  G[n]<-r*n*(1-(n/K))
  }

#Plotting

- NN<-seq(1,N)
- plot(NN,G,xlab="Biomass (N)",ylab="G(N)")

- abline(h=150,lwd=3)
- text(875,170,"H(N)",cex=1)

Exercise 2.2: What is the harvest rate (*H*) at MSY? Hint: To do this, first set dN/dt = 0 and then substitute *N* with *K*/2 and then solve for H. Report your finding.

Exercise 2.3: Generate another diagram, plotting the equilibria N^* on the y-axis as a function of harvest (*H*) on the x-axis. To do this, think about how the equilibria in your graph from in 2.1 change as *H* starts at 0 and increases (no math needed). Make sure to include on your diagram the value you determined to be the number of individuals that can be sustainably removed (i.e. MSY).

Hint:

- R code is very similar to the one that you used above.

Part 3 – Compare the Fishing Strategies

Exercise 3.1: What are the implications of the two different bifurcation diagrams (i.e. constant effort in part 1 vs quota system in part 2)? Why might a constant quota system be risky for fisheries management?

Exercise 3.2: We so far considered the case of a stationary environment (i.e. population parameters are constant). However, in a non-stationary world, where r may be changing due to environmental change (natural or anthropogenic) what are the implications of the two harvesting strategies (i.e. constant effort in part 1 vs constant quota in part 2)?