

Overview: Optimisation has several applications in ecology. The most important is in finding workable compromises between wildlife conservation and industry management. The viability of wildlife populations and the human communities that exploit them is one of the foremost topics of modern applied ecology. In this practical, we will examine a specialist fishing fleet, targeting a single fish species. We will introduce the concept of maximum sustainable yield and calculate it for different types of fisheries.

## 1. The Study System

Commercial fishing offers some of the most important examples of the human exploitation of wildlife populations. Fishing fleets the world over are (or, should be) regulated for both profit and sustainability. The shape, size and rigging of a vessel as well as the fishing times and gear can determine the target species. Some fisheries specialise on one or two species, while others are generalists. In this practical we will consider a generic, specialist fishery that is strictly observed and regulated. Managers control its operation via the licences issued annually to fishing vessels. The target fish species has an intrinsic growth rate equal to 2.1 per annum and the environment's carrying capacity is  $10^5$  tonnes of fish.



Commercial fishing fleet

1. The study system

## 2. Ecological Theory

Much of the theoretical work concerning the exploitation of fish populations was developed in the 1950's by Ray Beverton and Sidney Holt. Part of the ideas discussed in their monograph "On the dynamics of exploited populations" was the **maximum sustainable yield (MSY)**, defined as the maximum amount of resource that can be harvested continuously and indefinitely.



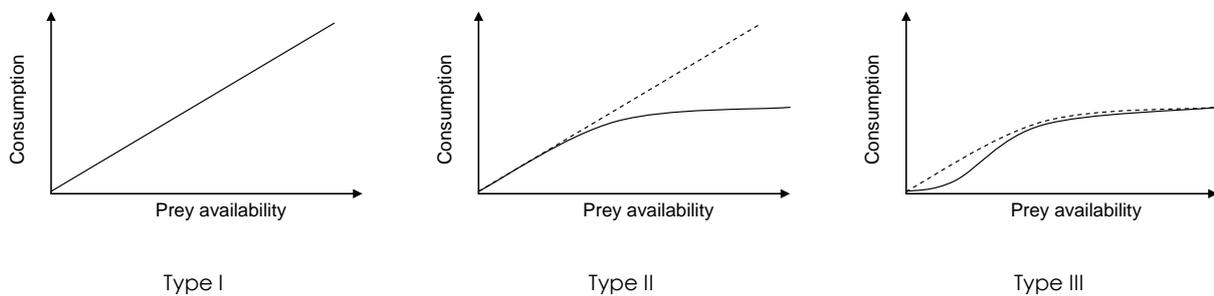
Beverton (left) and Holt (right) at work on their book, *On the Dynamics of Exploited Fish Populations*, in 1949.

2. Ecological theory

A fish stock that is increasing is, theoretically, not being harvested at full capacity. In contrast, a harvested population that is declining is overexploited. So, the sustainable yield must be an intermediate state of no change. A whole body of theory relating to the management of wild populations was based on this assumption. In fact, wildlife managers – and fisheries managers in particular – went one stage further once they realised that the theoretical value of the MSY was well below the environment's carrying capacity. So, they overexploited populations until they were reduced to this level, and then proceeded to harvest the theoretical MSY from the populations. In many cases, this was a recipe for disaster.

In general, the amount harvested comprises two things: the number of licensed vessels ( $N$ ) and the amount of fish ( $h$ ) caught by each vessel. The quantity  $N$  represents **fishing effort**. The quantity  $h$  represents the fishers' **functional response** i.e. the amount of resource (fish) taken by a single consumer (fishing vessel), in a single unit of time as a function of the availability of prey in the predator's immediate surroundings. In setting up this function, it is important to be clear and consistent about the units used to measure time, prey abundance and prey consumption: A functional response referring to annual consumption in response to overall abundance of prey is probably not a simple rescaling of the daily consumption in response to prey density measured in some fine spatial scale. Also, prey availability (and consumption) can be measured either in prey numbers or biomass.

Ecological reasoning has given rise to three main forms of functional response: A predator that can consume in proportion to prey availability has a **type I (or linear) functional response**. If prey consumption is approximately linear when prey is sparse but gradually decelerates as prey density increases, eventually plateauing at a maximum value, then the predator is said to have a **type II (or hyperbolic) functional response**. The levelling-off of the type II functional response is explained by the fact that a predator has to devote a certain handling time to each prey it consumes. Hence, although the rate of prey encounters increases with prey density, handling time remains constant. Therefore, the asymptotic rate of consumption (i.e. the plateau in the curve) occurs when the predator spends all of its time handling prey. **A type III (or sigmoid) functional response**, occurs in situations where an increase in prey density leads to an increase in the predator's searching efficiency, or a decrease in handling time.



Diagrams of the three main types of single-species functional responses.

### 3. mathematical theory

We model the growth of the fish population by a logistic model in discrete time

$$P_{t+1} = P_t + r_{\max} \left( 1 - \frac{P_t}{K} \right) P_t \quad (1)$$

If  $P_{t+1} > P_t$  the population is increasing. In theory, we should be able to harvest this surplus production for our own benefit, without any obvious risk of the population going extinct. If the total amount of fish taken each year is  $H$ , then the model becomes

$$P_{t+1} = P_t + r_{\max} \left( 1 - \frac{P_t}{K} \right) P_t - H \quad (2)$$

The amount harvested can be written in terms of fishing effort ( $N$ ) and the functional response ( $h$ ).

$$H = Nh(P) \quad (3)$$

The number of licenses is completely controlled by the managers (we have assumed no illegal fishing). The functional response of the fishers will depend on the amount of fish available, so here  $h$  is written as a function of  $P$ . The three shapes of functional response can be obtained from a single, flexible formulation for single-species functional responses proposed by Real in 1977,

$$h(P) = \frac{aP^m}{1 + atP^m} \quad (4)$$

Here,  $t$  is the fishers' handling time which sets the asymptotic value of the functional response, and  $a$  is the attack rate coefficient. Eq. (4) can take any of the commonly used forms for the FR: by setting  $m=1$  and  $t=0$ , we obtain a linear FR;

$$h(P) = aP \quad (5)$$

using  $m=1$  and  $t>0$ , we obtain a hyperbolic FR;

$$h(P) = \frac{aP}{1 + atP} \quad (6)$$

and for  $m>1$ , then the FR is sigmoid.

Combining eqs (3) and (4) gives the general harvesting term

$$H = N \frac{aP^m}{1 + atP^m} \quad (7)$$

The maximum sustainable yield ( $H_{MSY}$ ) is achieved when this population is at equilibrium, i.e. when its size (say,  $P$ ) is such that  $P_{t+1} = P_t$ .

$$P = P + r_{\max} \left(1 - \frac{P}{K}\right) P - H_{MSY} \quad (8)$$

Combining eqs (7), (8) and simplifying, gives

$$r_{\max} \left(1 - \frac{P}{K}\right) P - N \frac{aP^m}{1 + atP^m} = 0 \quad (9)$$

To find out how many licenses should be issued to achieve MSY, we solve for  $N$

$$N = r_{\max} P \left(1 - \frac{P}{K}\right) \left(\frac{1 + atP^m}{aP^m}\right) \quad (10)$$

A rather reckless management strategy might be to try and maximise the number of licenses issued. This requires us to maximise the function in eq.(10). Depending on the fishers' functional response, this task may be possible analytically, but if not, it will be necessary to carry out numerically.

## 4. R Ingredients

■ *Defining computer functions:* In computing, the term **function** has a somewhat broader definition than in mathematics, although computer functions can be used to encode mathematical functions. In general, a computer function is a self-consistent piece of code that performs a particular task. Just like a mathematical function, it usually requires some input upon which it operates to produce an output. However, unlike mathematical functions, the output generated by a particular input does not have to be unique. To fully specify a computer function, we need four components: a name for the function, the general form of the input, a description of how the function performs its task (sometimes called its "main body"), and a command to return the function's output. The appropriate syntax is:

```
function.name<-function(input)
{
  function's main body
  return(output)
}
```

Note that the main body of the function may comprise several lines of code, as we will see below, the ability to replace a multistage task by a `function.name` is the greatest advantage of **functional computing**. To illustrate the concept, let's consider the simple mathematical function  $f(x) = 5x + 7$ . The easiest way to implement this, is by first entering a value for the input and then operating on it directly:

```
> x<-4      # Assigns a value to the input
> y<-5*x+7  # Calculates the output
> y         # Prints the output
[1] 27
```

For a such a simple task, this approach is perfectly acceptable. However, for more complex tasks, that need to be performed repeatedly, it is useful to encode it as a computer function

```
f<-function(x)      # f is the name of the new function, x is its argument
{                   # Marks the start of the body of the function
  y<-5*x + 7       # Calculates the value of y on the basis of the input x
  return(y)        # Delivers the calculated output to the user
}                  # Marks the end of the body of the function
```

Note that, as soon as the first line is typed, R recognises the functional structure and expects to receive further arguments until it encounters the closing curly bracket `}`. Also, once the declaration of the function is complete, no output is produced, because no specific input has been provided. R knows that it should expect an input (here, called `x`) and it knows what to do with it once received, but it is waiting for the function to be "called". You call the function by typing its name and specifying the input, for example:

```
> f(4)
27
```

■ *Plotting mathematical functions:* R offers an overwhelming variety of options for customising graphs. These allow the production of publication-quality figures but require considerable input from the user. We will examine many of these options in later practicals. However, plotting a simple mathematical function isn't too challenging. You are required to generate a set of paired data for the independent and dependent variables, plot them and label the axes in a meaningful way. Here is an example for the function  $f(x) = 5x + 7$ , defined on the integers between -10 and 10.

```
x<-seq(-10,10,by=1) # creates sequence of values from -10 to 10 at steps of 1
y<-5*x+7            # creates list of outputs
plot(x,y, xlab="x", ylab="y") # plots y versus x and puts labels on the axes
```

■ *Working out derivatives by computer:* R can use the rules of differentiation to find the derivative of any function. The command for this is simply `D()`. You need to inform R that the argument of `D()` is a mathematical expression with the command `expression()` and you also need to specify the independent variable. You can try this with a specific polynomial like the following,

```
> D(expression(3*x^3+0.5*x^2-2*x+1), "x")
3 * (3 * x^2) + 0.5 * (2 * x) - 2
```

But you can also try it with a purely symbolic expression, like the type II functional response

```
> D(expression(a*p/(1+a*t*p)), "p")
a/(1 + a * t * p) - a * p * (a * t)/(1 + a * t * p)^2
```

This last expression is not very tidy. We can simplify it as follows:

$$\frac{a}{1+atP} - \frac{a^2tP}{(1+atP)^2} = \frac{a(1+atP) - a^2tP}{(1+atP)^2} = \frac{a}{(1+atP)^2} \quad (11)$$

Often, you may need to tidy things up after R has finished. A good way to work with complicated derivatives is to figure them out first by pen and paper and then check to see if R can come up with an expression that agrees with your result.

To calculate the derivative of a function at a particular value of its variable and for particular values of its parameters, you need to use the command `eval()`. For example,

```
> a<-3; b<-0.1; x<-100
> eval(D(expression(a*x/(1+b*x)), "x"))
0.02479339
```

■ *Numerical optimisation in R:* comes in several flavours. For example, the command `optimize()` will find the maximum or minimum of a given function in a particular domain. The following two lines retrieve the location and value of the maximum for the mathematical function  $f(t) = at / ((b+t)(T+t))$ .

```
f<-function(t,T,b,a) {a*t/((b+t)*(T+t))}
g<-optimize(f, lower=0, upper=10, a=10, b=1.3, T=0.5, maximum=TRUE)
```

Note that it was necessary to specify the domain (0 to 10) using the constraints `lower` and `upper`, the parameter values of the function (`a`, `b` and `T`) as well as the fact that we are seeking the maximum, instead of the minimum. The output is an object containing the position of the maximum (to see it here, type `g$maximum`) and the value of the function at the maximum (type `g$objective` to see it).

## 5. Practical tasks

We will calculate MSY under two different models of the fishers' harvesting performance.

- 1 Read carefully the material in sections 1-4 above.
- 2 Read through the tasks in this section.
- 3 Read through the assessment components in the next section before you carry out any tasks

Model 1: No functional response

- 4 Modify eq. (10) according to the assumption that the fishers' harvest rate is not affected by the abundance of prey (assuming there is sufficient to be taken). This is equivalent to setting  $m = t = 0$ . For this model only, assume that  $a = 2000 \text{ tonnes.y}^{-1}$ .

- 5■ Using this model, calculate analytically the derivative  $dN/dP$  using pen and paper.
- 6■ Write a bit of R code to calculate the same result by computer. Simplify the R output to make sure you have the same result as in task 5.
- 7■ Use this derivative to calculate the prey population size at which MSY is achieved.
- 8■ Calculate the number of licenses that can be issued under this model.

Model 2: Type II functional response

- 9■ Modify eq. (10) by assuming that the fishers have a type II functional response (i.e.  $m=1$ ), with parameter values  $t=0.0005$ ,  $a=0.1$ .
- 10■ Plot the functional response using fish abundances from zero to the carrying capacity.
- 11■ Plot a graph of your model from task 9. This shows the relationship between licences and equilibrium population size and will give you an idea of where the maximum number of licences is.
- 12■ Use numerical optimisation to calculate the maximum number of licenses and the corresponding equilibrium fish population. Check this against the graph of task 11.
- 13■ Can you offer an explanation for the difference in the maximum number of licenses between model 1 and model 2?

## 6. Assessment

Write a report, no longer than 3 sides of A4, that contains the following:

From model 1:

- 1■ Equation of licenses model and its derivative (tasks 4, 5 & 6).
- 2■ Report the maximum number of licenses and associated equilibrium population (tasks 7 & 8).

From model 2:

- 3■ Equation of licenses model and its derivative (task 9)
- 4■ Annotated functional response plot (task 10)
- 5■ Annotated licenses model plot (task 11)
- 6■ Report the maximum number of licenses and associated equilibrium population (task 12).
- 7■ Answer to the question in task 13.
- 8■ Attach your fully-commented code from all parts (just the code, no output)