

fish5106stockrec Spawning stock, recruitment and production

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19. desember 2016

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Acknowledgements

MareFrame is a EC-funded RTD project which seeks to remove the barriers preventing more widespread use of the ecosystem-based approach to fisheries management.

<http://mareframe-fp7.org>

This project has received funding from the European Union's Seventh Framework Programme for research, technological development and demonstration under grant agreement no.613571.

<http://mareframe-fp7.org>

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<http://www.hi.is/>

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1 Spawning stock and recruitment

1.1 Background

Need to find limiting factors for recruitment...

- Birds: Number of sills in cliffs
- Marine mammals: Number of mature females
- etc



The recruitment process depends on many factors.

1.1.1 Details

When considering the population dynamics of any species, it is important to consider the recruitment process. How this is taken into account must depend on the biology of the species in question.

The important factors in determining recruitment vary considerably. For some bird species the number of sills on a cliff may be a determining factor for how many young can be raised in a given year. For some mammals the number of offspring is directly related to the number of mature females.

1.2 Importance of relationships

Eventually we want to describe production

- Production = Yield per recruit * Recruitment
- Can use average R to start: $\bar{Y} = Y/R \cdot \bar{R}$
- But recruitment may be related to the stock size which depends on recruitment which ...

1.2.1 Details

Recall that the task of estimating (long-term) yield, Y , for a given fishing mortality, F , has been split into estimating yield per recruit, Y/R , and the number of recruits, R , that is to say that $Y = (Y/R) \cdot R$.

The potential relationship between spawning stock size and recruitment is important since the overall production will thus not only depend on the yield per recruit but also on the number of recruits. The former analysis has provided a relatively simple answer for Y/R but the typical recruitment now needs to be investigated. If historical analysis has indicated a typical, or average, level of recruitment, \bar{R} , then this can be used to estimate the typical, or average, yield with $Y = (Y/R)\bar{R}$. This, however, only refers to conditions similar to the historical conditions where the average recruitment was observed.

If recruitment depends on how large the stock is, then another factor enters into the analysis in addition to simply considering the relative production for a fixed year-class size.

Thus, recruitment may be related to the stock size which depends on earlier recruitment which again depends on the earlier size of the stock. This leads to a circular argument which can be resolved using several different approaches. This section will focus on an equilibrium-type approach, where the emphasis is on evaluating what recruitment and stock size will correspond to a specified fishing mortality.

1.3 Checking relationships

- Now check if SSB and R are related
- Need to decide what sort of relationship should be considered
- It may not make much sense to do linear regression
- Should incorporate biological knowledge

1.3.1 Details

Having obtained a measure of the biomass which spawns each year and the resulting recruitment, it is of considerable interest to see whether some relationship can be described between these two quantities.

However, prior to simple plotting of data it makes sense to attempt to decide whether basic biological knowledge exists to specify some function or functional form to be used.

Hence one should begin by studying the recruitment process, at least in rudimentary form, to obtain some idea of plausible relationships.

1.4 The recruitment process

The recruitment process

- spawning, fertilized eggs
- larval stage, first feeding
- drift, predation
- settlement
- overwintering
- competition

1.4.1 Details

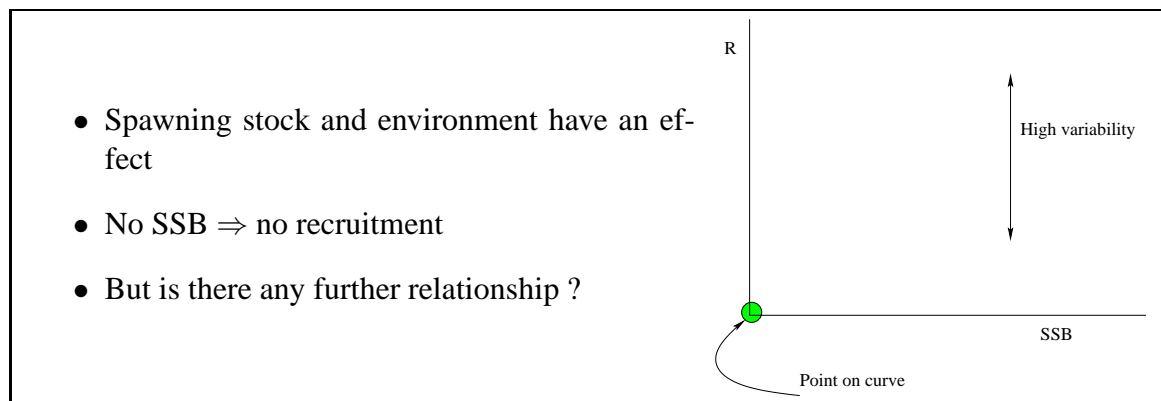
Recruitment is determined by a highly complex process which starts at spawning. The spawning stock is thus an important quantity and it is important to examine whether there are any links between recruitment and spawning stock.

In order to formulate this process in mathematical terms it is important to first visualize what factors enter the recruitment process.

The recruitment process includes several factors

- spawning
- fertilized eggs
- larval stage drift
- predation
- settlement
- overwintering
- competition

1.5 Spawning stock and recruitment

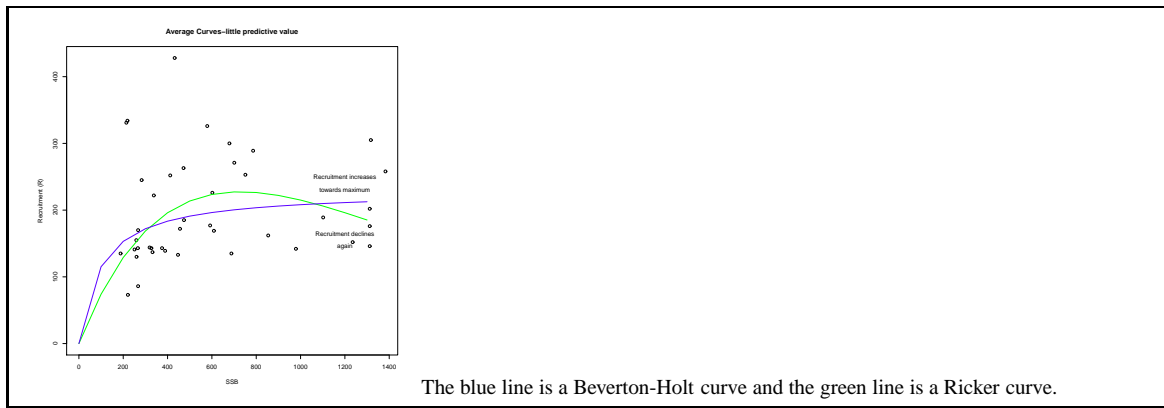


1.5.1 Details

Although complex mathematical theories may be developed on this topic, few things are clear from the outset. It is, however, clear that there will be no recruitment without a spawning stock.

It is also generally known that recruitment is quite variable and that it depends on several complex processes. Therefore it is natural to advocate a relationship which starts at the origin and increases initially as the stock size rises from zero. Actual data points would be expected to deviate considerably from this curve.

1.6 Types of trajectories



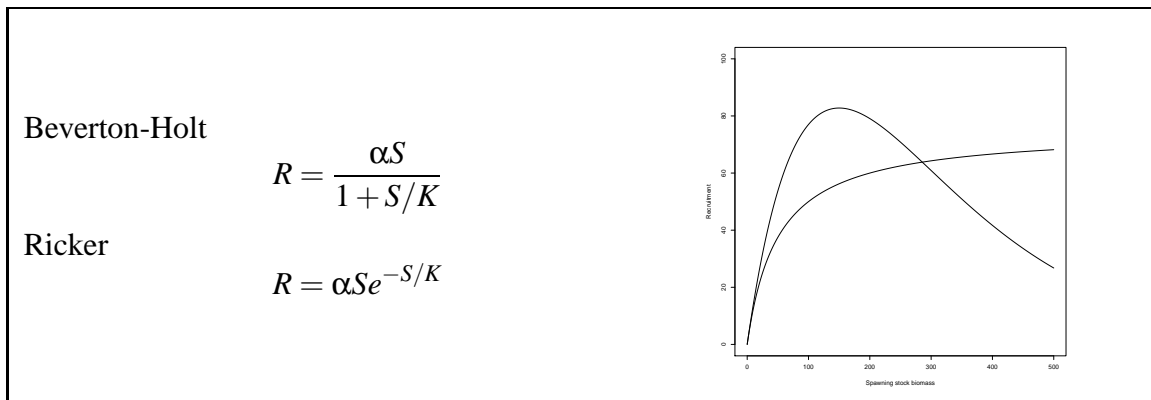
1.6.1 Details

Many models have been designed in order to explain the links between recruitment and spawning stock. The most common ones are the Beverton-Holt Model and the Ricker Model.

Note 1.1. The Beverton-Holt curve rises steadily from (0,0) but the slope becomes less steep and the curve is directed towards a specific limit when the spawning stock grows out of proportion.

Note 1.2. The Ricker curve rises up to a given maximum and then it falls and heads towards zero when there is excessive growth in the spawning stock.

1.7 Two possible trajectories



1.7.1 Details

Definition 1.1. Beverton-Holt model:

$$R = \frac{\alpha S}{1 + S/K}$$

Definition 1.2. Ricker model:

$$R = \alpha S e^{-S/K}$$

When the spawning stock has varied across a wide range, from high through low stock sizes, the simplest way to choose between these models (Beverton-Holt and Ricker) is by examining whether there is any evidence of a declining right-hand limb of the stock-recruitment function.

As it turns out, there is usually very little evidence of any changes in recruitment at large stock sizes for most stocks. For many over-exploited stocks, however, there is evidence of reduced recruitment at low stock sizes. Hence, there is usually little evidence to choose between the Ricker and Beverton-Holt models.

1.8 Recruitment and spawning stock biomass definitions

Need to define quantities

- SSB or egg production or...
- At time of spawning or ...
- Recruitment at age 0 or 1 or ...

In principle one can get SSB and R from assessment

1.8.1 Details

Note 1.3. Recruitment is simply defined as the number of fish in the youngest age group of interest. Usually this is the age group corresponding to the youngest fish in the catch.

Note 1.4. The spawning stock should correspond to the fish that reach spawning age and thus contribute to spawning. This quantity is usually measured in terms of biomass, e.g. tonnes.

In more advanced settings, the size of the spawning stock at the spawning season is used. This is computed by starting with the biomass at the beginning of the year and taking into account mortality until the onset of the spawning season.

The corresponding stock sizes are then multiplied by the proportion of mature fish in each age group and the mean weight of the age groups and the outcomes then added up to obtain the total biomass of spawning fish.

In some instances other measures are used, such as the egg biomass, or other factors are taken into account, such as the fecundity (possibly as a function of the size of females etc) or likely survival of eggs as a function of parental condition. These may be of considerable importance but will not be a part of this tutorial.

1.9 Beverton-Holt curve

$$R = \frac{\alpha S}{1 + S/K}$$

$$\alpha K = R_{\infty}$$

K =location on SSB-axis for $R_{\infty}/2$

1.9.1 Details

Definition 1.3. Beverton-Holt curve notation:

α =multiplier for prospective recruitment

K =location on the SSB-axis for $R_\infty/2$

$\alpha K = R_\infty$ =recruitment limit when spawning stock grows without bounds

In the Beverton-Holt stock-recruit relationship, the coefficients have a specific meaning. The coefficient α is a multiplier for prospective recruitment. A doubling of this coefficient results in a doubling of prospective recruitment.

On the other hand, K is a measure of location on the spawning stock axis. In the Beverton-Holt model, K is the size of the spawning stock that produces half the maximum recruitment, as becomes clear when $S = K$ is entered into the Beverton-Holt equation $R = \alpha S / (1 + S/K)$.

K =location on SSB-axis

$$\alpha K = R_\infty$$

The combined term, αK is a limit for recruitment when the spawning stock grows without limit:

$$\lim_{S \rightarrow \infty} \frac{\alpha S}{1 + S/K} = \alpha K$$

1.10 Ricker curve

Ricker Curve:

$$R = \alpha S e^{-S/K}$$

Think of this as:

- Egg production proportional to SSB
- Density dependent mortality: $-S/K$ appears as M , e.g. due to cannibalism
- K is the location of the maximum

1.10.1 Details

Definition 1.4. Ricker curve notation:

α =multiplier for prospective recruitment

K =location on the SSB-axis

αK =maximum recruitment

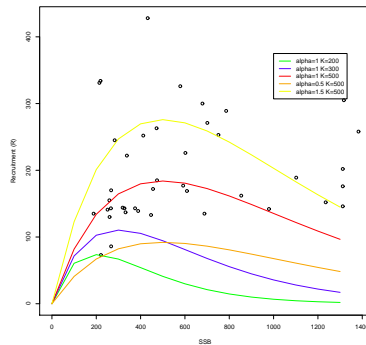
The coefficients of the Ricker curve have specific meanings. The coefficient α is a multiplier for prospective recruitment. A doubling of this coefficient results in a doubling of prospective recruitment.

The value αK denotes maximum recruitment in the Ricker Model.

K is a measure of location on the spawning stock axis.

In the Ricker Model, maximum recruitment is obtained when the spawning stock is K . This result is arrived at by differentiating R with respect to S .

1.10.2 Examples



Example 1.1. The illustration shows 5 Ricker curves. It portrays how the curves change as a function of K ($K=200, 300$ and 500 when $\alpha = 1$). The effects of a modified $\alpha = 0.5, 1$ and 1.5 when $K=500$ can also be seen.

1.11 Need for S-R curves

Need to generate recruitment when predicting medium-term effects of strategies, for example. Also to compare with Y/R to get equilibrium Y .

1.11.1 Details

Stock-recruitment curves are not normally used to predict single annual recruitment.

Need to generate recruitment when predicting medium-term effects of strategies, for example. In this case the environmental variability is added as random noise to generate variable recruitment. Also to compare with Y/R to get equilibrium Y , thought of as a long-term average, or general direction.

1.12 When to investigate S-R relationships

- What if there is no "significant relationship"?
- What does significance mean?
- Does significance=importance???
- Can a model be used if it is not "Significant"?

1.12.1 Details

There is always considerable variation in recruitment numbers for a fixed value in the spawning stock. Thus, the difference between large and small year-classes for a specific spawning stock is often considerably bigger than the difference between the lowest and highest prospective recruitment according to the recruitment curve for the period in which the spawning stock has been measured. There is a simple explanation for this: the effects of environmental factors (and possible deviations in measurements) are much greater than of the spawning stock itself at most spawning stock sizes.

This result does, however, not change the fact that **on average** we will expect smaller year-classes if the spawning stock is excessively reduced. In fact it should be obvious that curves plotted through the above-mentioned points must always be assumed to pass through the origin. For example, it makes very little sense to estimate the coefficients of a straight line through the points, since such a line might show negative recruitment for a given spawning stock or even positive recruitment where there is no spawning stock.

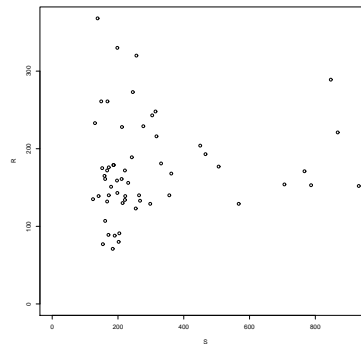
Consequently, there are always plenty of reasons to examine the links between spawning stock and recruitment. It must be emphasized that such models can not be used in order to make predictions about recruitment in a given year. On the other hand, such models give us information about the **average** recruitment and thus long-term yield potential of the stock, as is seen in other lectures.

2 Estimation methods

2.1 Estimation methods

Long-term dynamics:

- Need stock-recruitment relationship
- Can be assumed or estimated from data
- Prefer using data
- Can draw "by hand"
- Prefer objective method of fitting



2.1.1 Details

When investigating long-term dynamics of a stock, a stock-recruitment relationship needs to be used. This can be assumed or estimated from data, but of course using data is preferred to not using data.

The data can be used simply in a stock-recruitment plot to obtain guidelines on possible S-R curves. Thus, a curve can simply be drawn in "by hand", e.g. by selecting parameter values (α and K) in the Ricker curve, so that the curve passes through the point cloud.

2.1.2 Examples

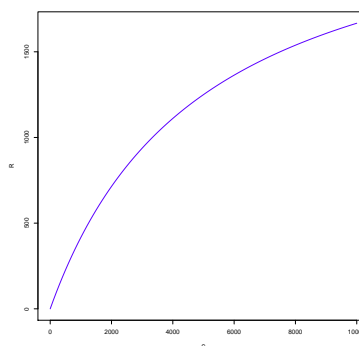
Example 2.1. Data on spawning stock and recruitment for cod in Icelandic waters are given in the following table. The data are from a Marine Research Institute publication on the state of fish stock in 1993, as used in analyses at the time (e.g. Stefansson, 1992). A few years (1952-1954) were added to the start as an attempt to obtain recruitment values for a spawning stock of a similar size. It is known that the spawning stock was large during this period and the average for the years 1955-1958 is therefore used as an approximation for the previous years.

<http://tutor-web.net/fish/fish5106stockrec/lecture20/icodsr.dat>

2.2 A predictive model

Given parameters one can "predict" recruitment

Equivalently: Given parameters one can draw an S-R curve



2.2.1 Details

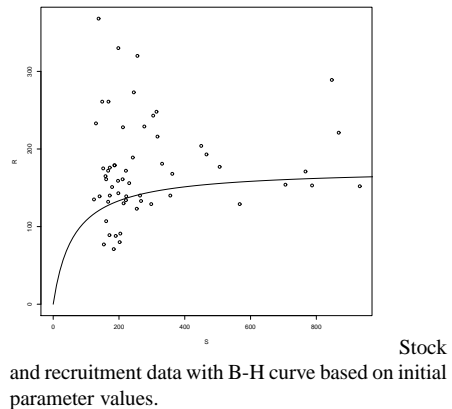
A non-linear method is preferred for estimating the parameters describing S-R curves. This is a relatively simple procedure, using either a package capable of nonlinear estimation or by using spreadsheets.

Arbitrary initial values of the coefficients are typically used as starting points. These initial values can be used to compute the "predicted" recruitment each year, \hat{R}_y , for a given spawning stock in year y .

This "predicted" recruitment is of course simply the value of the stock-recruit curve corresponding to the spawning stock biomass in the given year.

2.3 Initial values

Need to set initial values for α and K



2.3.1 Details

As a part of the estimation phase it is important to set initial values of parameters. If the estimation procedure is robust, then these are not too important. For difficult nonlinear models appropriate initial values can be quite important in order to guarantee convergence of the methods.

2.3.2 Examples

Example 2.2. For the Beverton-Holt stock-recruitment relationship the maximum (average) recruitment is $R_\infty = \alpha K$ and the value of K refers to the SSB level where recruitment is at half the maximum. Initial values should force the S-R curve to go through the point cloud and should reflect the above properties.

Choosing α and K such that the maximum theoretical recruitment is set to the average, that is to say that $R_\infty = \bar{R}$ can be used to ensure that the curve goes through the point cloud.

Commonly there is only poor evidence for a reduction in recruitment at the lowest observed SSB values. In such cases one can choose the initial value for K so that serious reductions in recruitment are only obtained well below the range of the data, e.g. such that K is half the minimum observed biomass ($K = \min_y \{S_y\} / 2$).

2.4 Measuring the quality of the model

Can use sums of squared errors:

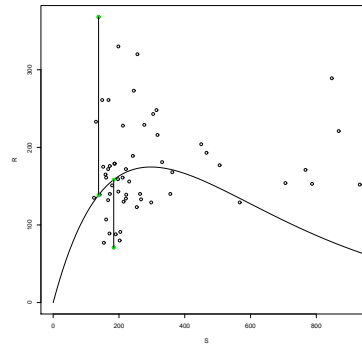
$$\sum_y [R_y - \hat{R}_y]^2$$

e.g.:

$$\sum_y [R_y - \alpha S_y e^{-S_y/K}]^2$$

$$\sum_y [\ln(R_y) - \ln(\hat{R}_y)]^2$$

Log-transformed data is often used.



Stock-recruit data for I-Cod with a potential Ricker curve. Squared residuals between the curve and observations give a measure of how well the model fits the data.

2.4.1 Details

It is now possible to compute:

$$\sum_y [R_y - \hat{R}_y]^2$$

but this quadratic sum is an indication of the (in)consistency between the model and the measurements.

At this stage it is possible to test different values of the coefficients of the model and find those values that give the lowest possible quadratic sum.

It should be noted that this is “simply” the sum of squared errors for a nonlinear model, e.g.:

$$\sum_y [R_y - \hat{\alpha} S_y e^{-S_y/K}]^2$$

which describes how well this particular model fits the data.

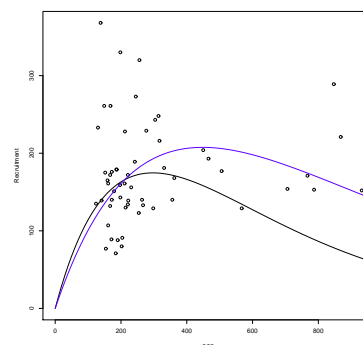
It is often more reasonable to first log-transform the data before measuring the quality of the fit.

2.5 Nonlinear estimation

Use nonlinear estimation

Get $\hat{\alpha}$ and \hat{K}

Obtain fitted curve



Stock and recruit data for I-cod (1955-2011) with fitted (blue) curve. Also shown is the curve corresponding to the initial values.

2.5.1 Details

Various numerical methods are available to simplify this search for a low value. For statistical reasons the logarithms of recruitment are more commonly used than the recruitment itself in the sum of squares.

Algorithms for numerical minimization are a standard part of many packages such as spreadsheet or statistical packages. Some care needs to be exercised since these algorithms can be quite sensitive to initial values and may not converge when the parameters are on different scales.

2.5.2 Examples

Example 2.3. The earlier data on cod in Icelandic waters can be used to obtain the best-fitting curves by minimizing the sum of squared deviations in the logarithms of recruitment. This gives the following values for the coefficients in the Beverton-Holt and Ricker functions:

	B-H	Ricker
α	2.32	0.85
K	98.5	728

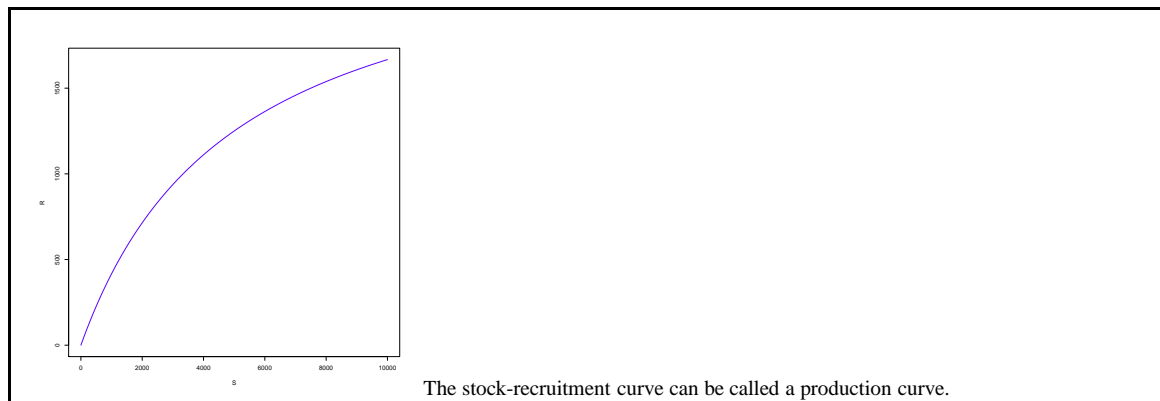
References Stefansson, G. 1992.

Ricker

Beverton and Holt

3 Production and replacement

3.1 Production

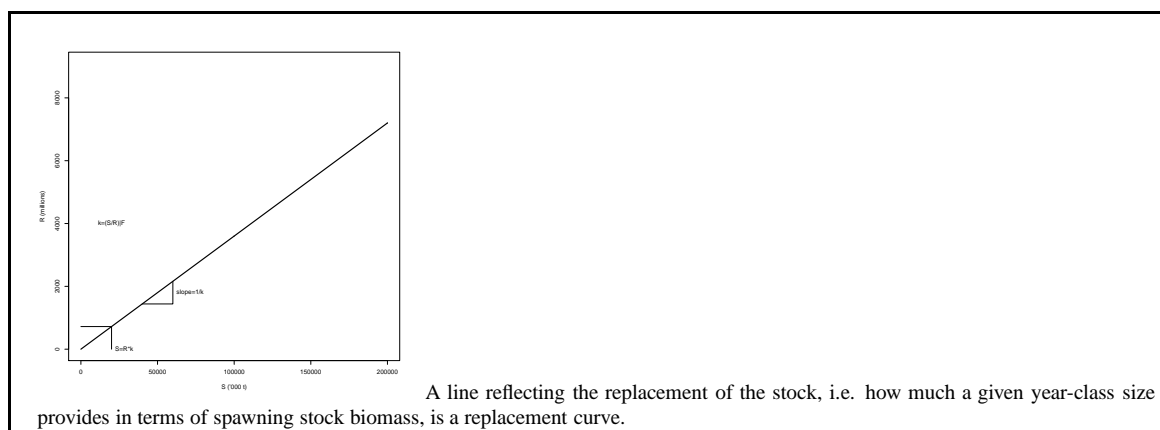


3.1.1 Details

The stock-recruitment curve is a production curve in the sense that it describes the number of recruits produced by the spawning stock.

The slope of the curve at zero is important and deserves closer examination.

3.2 Replacement



3.2.1 Details

When fishing is conducted with some specified fishing mortality rate, it is possible to compute the spawning stock biomass per recruit. Thus, each recruit will result in a contribution, $S/R = k$, into the spawning stock.

If a spawning stock of the size S produces R recruits, then the fishing mortality, F , will cause the spawning stock of these recruits to be k times R . For a fixed fishing mortality rate, the recruitment thus contributes a certain multiple of itself into the spawning stock.

3.2.2 Example

Example 3.1. A simple function can be used to compute the spawning biomass per recruit, S/R , using data (real or simulated) on natural mortality, selection at age, weight

at age, and proportion mature at age for any overall level of fishing mortality.

<http://tutor-web.net/fish/fish5106stockrec/lecture30/srcalc.r>

One of the primary purposes of computing S/R for a given fishing mortality is to use this quantity as a measure of **replacement**. The reason for the terminology is that a given number of recruits, R , will (during its lifetime) contribute

$$R \frac{S}{R}$$

to the spawning stock biomass.

Note that this equation describes SSB as a function of recruitment. If the spawning biomass per recruit for a given fishing mortality is denoted by $k = S/R$, then the slope of the replacement line is $1/k$.

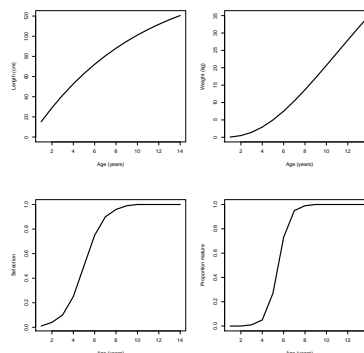
3.3 Data requirements

Need several data sets for production and replacement curves

Assessment gives the production (stock-recruit) curve

Mean weight at age, natural mortality at age, selection at age, and proportion mature at age gives spawning stock biomass per recruit

Can use simulated or real data...



Assumptions are needed...

3.3.1 Details

In order to study the behavior of the production and replacement curves, several data sets are needed.

First, in order to estimate the production (stock-recruit) curve, data on spawning stock biomass and recruitment are required. These would normally be obtained from an assessment.

Secondly, information on spawning stock biomass per recruit is needed. This information is based on a theoretical model but with data (or assumptions) on mean weight at age, natural mortality at age, selection at age and proportion mature at age.

In principle one can investigate these methods by using simulated data but of course one will eventually need real data on a particular stock. The simulations can be very useful, whether to study the theory or to see in general, what kind of response is likely, given certain natural mortality regimes, selection patterns etc.

3.3.2 Examples

Example 3.2. To generate data for simulating the production and replacement curves, one can start with simple assumptions concerning growth etc.

<http://tutor-web.net/fish/fish5106stockrec/lecture30/simdata.r>

The above simulated data is sufficient to simulate the spawning biomass per recruit.

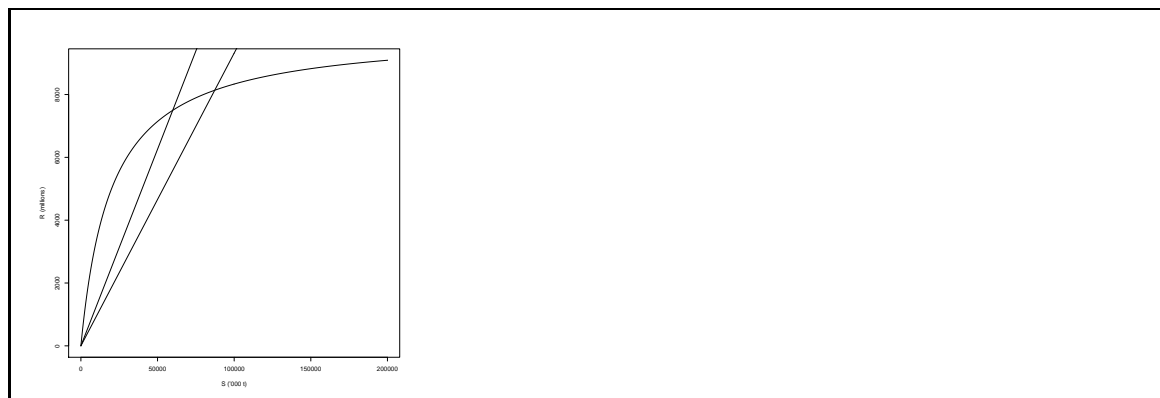
In addition, the parameters of a stock-recruit relationship need to be defined to simulate the stock-recruitment curve. This can, in principle, be done by fixing them to specific numbers

```
alpha<-0.5  
K<-20000
```

but when simulating the stock, a better alternative is to fix the collapsed fishing mortality, F_{crash} , and compute the corresponding α , from the biomass-per-recruit curve:

```
alpha<-1/srfun(selF4,M,sa,wa,pa)  
K<-20000
```

3.4 Production and replacement



3.4.1 Details

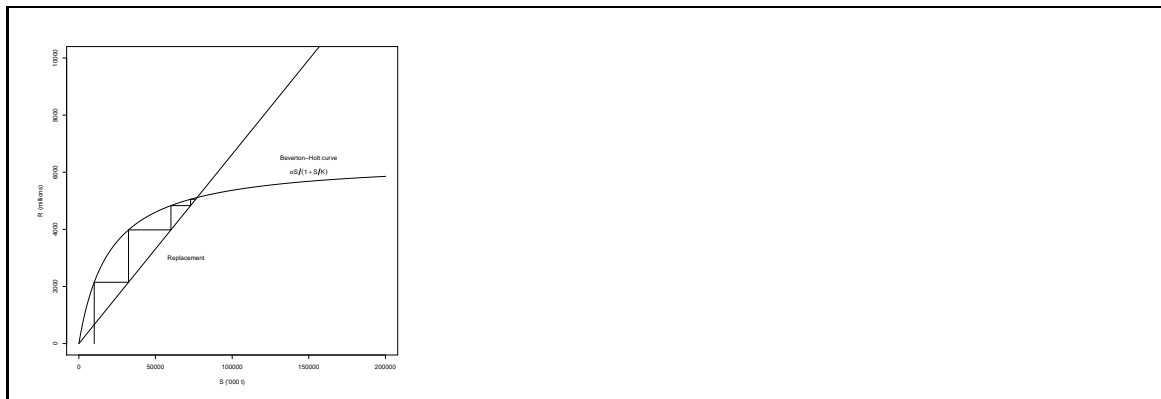
At the intersection of the two curves a theoretical equilibrium will hold.

3.4.2 Examples

Example 3.3. Given appropriate definitions of parameters, the following commands can be used to plot some production and replacement curves.

<http://tutor-web.net/fish/fish5106stockrec/lecture30/prodreplacementcurves.r>

3.5 Production and replacement: Low effort



3.5.1 Details

If a spawning stock starts at S_0 , some average level of recruitment, R_0 , will be produced, as determined by the relationship between spawning stock and recruitment. During its lifetime, a cohort of size R_0 contributes $S_1 = k * R_0$ to the spawning stock, where the constant $k = (S/R)$ is derived from the spawning stock biomass per recruit computations. S_1 then produces recruitment, R_1 , according to the relationship between spawning stock and recruitment, and so on.

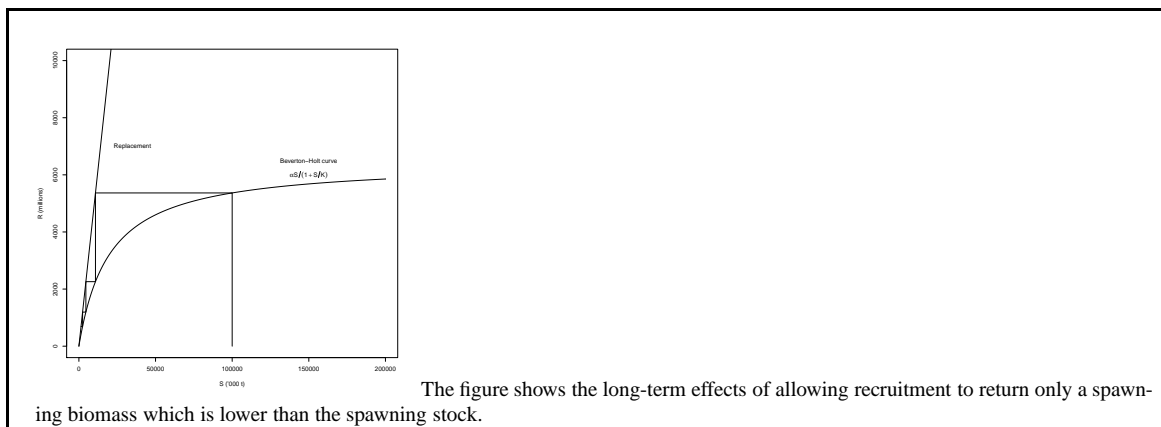
It should be noted that this ignores any time lags that occur because recruitment takes several years to enter the parental stock.

3.5.2 Examples

Example 3.4. The figure shows how a stock which starts at a certain size, thousand tonnes, seeks a certain equilibrium as the spawning stock produces a certain amount of recruits which in turn produce a certain spawning stock.

If everything has been set up then this can be generated in R using commands of the form <http://tutor-web.net/fish/fish5106stockrec/lecture30/spawningstockcurve.r>

3.6 Production and replacement: Heavy effort



The figure shows the long-term effects of allowing recruitment to return only a spawning biomass which is lower than the spawning stock.

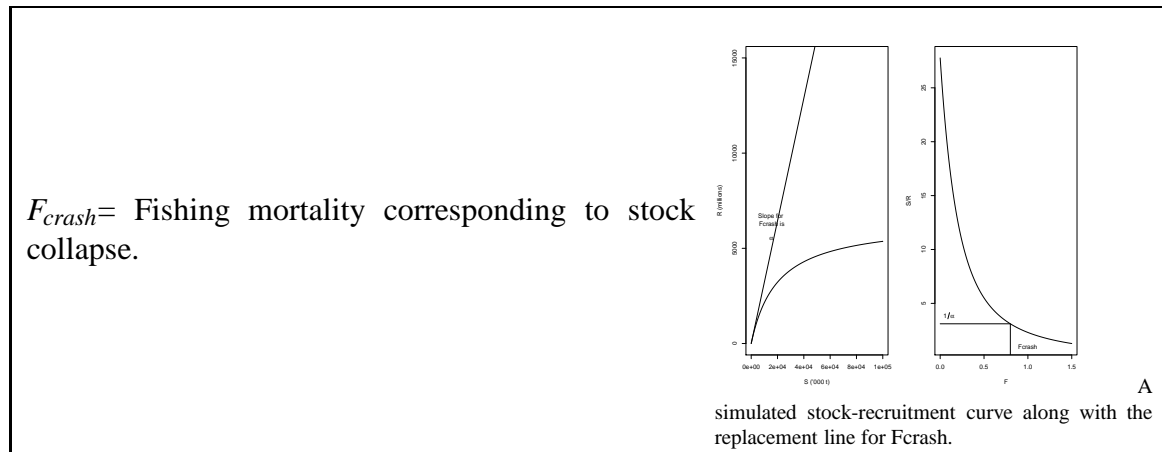
3.6.1 Details

Higher fishing mortality rates give a lower value for $k = (S/R)$ and thus more recruits are needed to counteract that mortality. A closer look reveals that the slope of the recruitment curve must be at least the same as $1/k$ if the stock is going to be able to withstand the corresponding fishing mortality. If it does not, the stock will collapse.

Note 3.1. It should be mentioned that the term "collapse" is taken to mean an average decrease in the stock which eventually leads to zero individuals.

Due to natural fluctuations this process can take a very long time and it is highly unlikely that fishing efforts will be maintained until the last fish has been caught.

3.7 Reference point: F_{crash}



3.7.1 Details

Note 3.2. The fishing mortality which corresponds to a stock collapse is denoted F_{crash} or F_{ext} .

3.8 Reference points: F_{med}

F_{med} is the fishing mortality which corresponds to the median observed slopes from data in an S-R plot.

3.8.1 Details

Many methods have been designed for assessing when a given stock is at risk. This is usually a difficult task, since it is concerned with estimating the slope of the stock-recruit curve at the origin, i.e. usually at biomass levels below those ever observed.

Note 3.3. F_{med} = the fishing mortality corresponding to the median of the R/S ratio
 F_{high} = the fishing mortality corresponding to the R/S for which only 10% of the ratios are higher
 F_{low} = the fishing mortality corresponding to the R/S for which 90% of the ratios are higher

One method is based on examining the ratio of R against S (for each year). The median of those figures denotes the typical production of the spawning stock. Therefore, the fishing mortality (F), which results in a corresponding spawning stock per recruit (S/R) should not

involve too much risk. The corresponding mortality coefficient is called F_{med} .

It is also possible to compute an R/S ratio whereby only 10% of the ratios are higher (i.e. the 90th percentile of R/S). Production of such an extent is extremely rare and it is, therefore, unlikely that the stock can withstand corresponding efforts in the long run. The corresponding mortality coefficient is called F_{high} and is often used to denote efforts likely to endanger species.

Similarly, one can compute F_{low} which is the fishing mortality corresponding to the 10th percentile of R/S . Production has been enough to sustain such a fishing mortality in 90% of all years and this is therefore very likely to be sustainable.

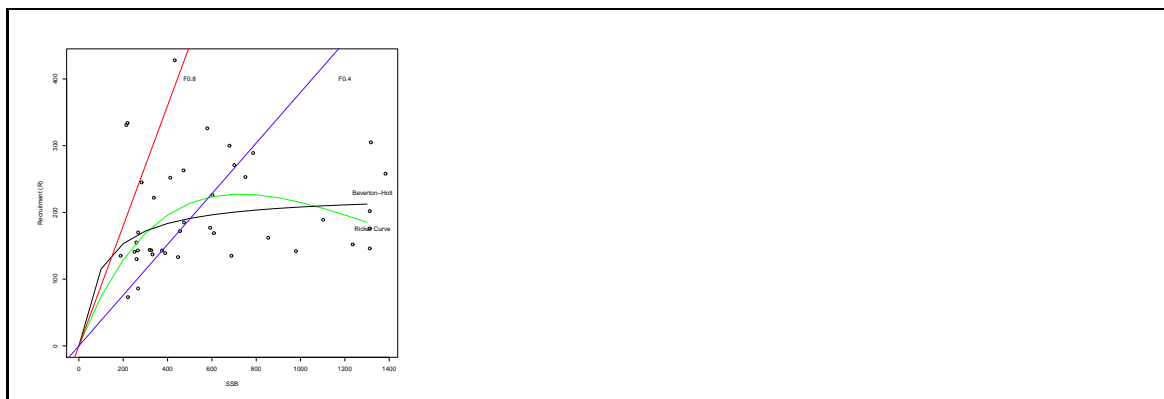
Although F_{high} is likely not to be sustainable and F_{low} is almost certainly sustainable, neither are of much interest (except possibly F_{low} when dealing with a stock which has (almost) collapsed). Rather, the interest is on a fishing mortality which is likely to provide harvests as well as likely to be sustainable.

When computing F_{med} , the procedure is as follows:

1. Take the median slope of the S/R data
 - Compute the median (S/R) for all the years in the assessment
2. Check that the units are the same as in the S/R function
 - '000 tonnes/million individuals=kg/recruit
3. Determine F_{med}
 - F corresponds to this value of S/R

It should be noted that if a stock has hardly been fished, then F_{med} will correspond to underutilization. Similarly, if the historical data used when estimating F_{med} is all on the left limb of a stock-recruit curve, then F_{med} will simply estimate F_{crash} .

3.9 Production and replacement presentation



3.9.1 Details

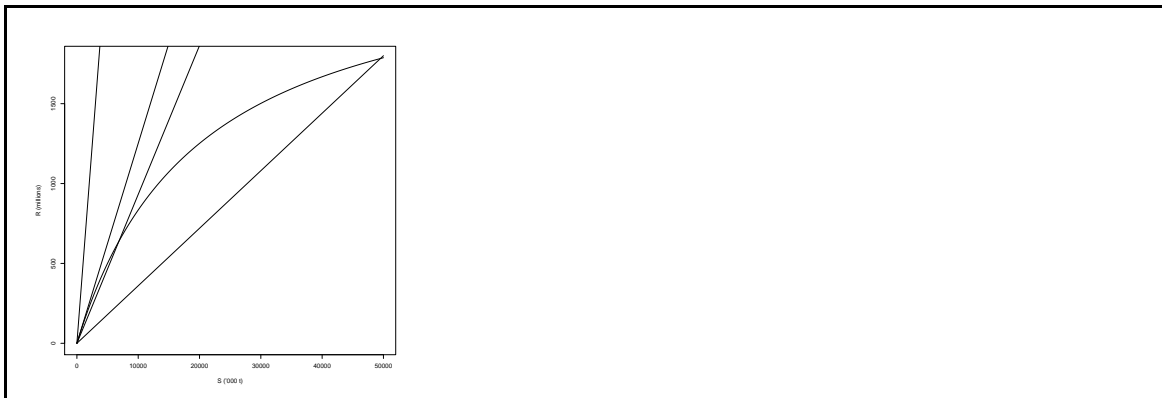
It is useful to plot the production curve (or several variants) along with several replacement lines on the same plot.

3.9.2 Examples

Example 3.5. The stock-recruitment curves based on earlier data for cod in Icelandic waters are plotted in the above figure along with two replacement curves. If the Ricker-function is used, maximum recruitment will occur in a spawning stock of just over 1000 tonnes. It is also shown that prospective recruitment decreases sharply when the stock has fallen to below 300 thousand tonnes.

Lines corresponding to F_{med} and F_{high} are plotted on the figure. The figure shows two curves which describe the possible connection between recruitment and spawning stock. The line which corresponds to F_{high} bisects the Beverton-Holt curve but not the Ricker curve. This means that if the Beverton-Holt curve is closer to the catch at F_{high} , then the stock will move towards an equilibrium in a spawning stock of just over 100 thousand tonnes, which can be expected to produce an average of 100-150 million recruits. If the Ricker curve is closer to reality, the stock will collapse if efforts are close to F_{high} . F_{high} is believed to be nearly 0.8 for the Icelandic cod. If data from the figure for the years 1955-1992 are used, it is impossible to choose statistically between the Ricker- and Beverton-Holt curves.

3.10 Spawning Stock and Recruitment - Summary



3.10.1 Details

Recruitment is a complex process which starts at spawning. Before the fry that are hatched become catchable fish, they need to find adequate food supply, avoid predators, and drift or migrate to the nursery grounds.

Mortality is extremely high during this process. It has also been discovered that there is considerably greater variability in the recruitment than in the size of the spawning stock. Consequently, general environmental factors seem to be a more influential force for determining annual year-class size, than the size of the spawning stock.

It is, however, quite clear that without a spawning stock there can be no recruitment and reasonable recruitment is highly unlikely if there is a mere handful of mature fish available. There is thus a definite connection between recruitment and the size of the spawning stock, although the existence of such a link may be very hard to "prove" since highly variable environmental factors complicate the issue.

If fishing causes such a reduction in the spawning stock that recruitment fails repeatedly or "on average", then there is no point in maintaining the same effort and hoping to get a similar catch. The stock at such high fishing mortality is simply expected to enter a downwards spiral due to repeated recruitment failure. This might take a very long time, particularly when there are intervening good years that boost recruitment. Given evidence from around the globe it is however pretty much inevitable that fishing at very high fishing mortality will eventually reduce the stock to very low levels.

3.10.2 Examples

Example 3.6. Production and replacement lines for a simulated stock. The replacement lines correspond to $F=0, 0.25, 0.35$ and 1.1 where $F_{0.1}=0.25$ and $F_{crash}=1.1$.

It should be noted that there is no built-in link between $F_{0.1}$ and $F_{crash}=1.1$; one of these describes a measure related only to growth and the other takes into account the stock-recruitment relationship.

References See Shepherd and Nicholson for Fmed.

4 Yield potential

4.1 Introduction

Y/R and S/R known for each F . Also,

$$R = \frac{\alpha S}{1 + S/K}$$

4.1.1 Details

When computations of yield per recruit, spawning stock per recruit and the relationship between recruitment and spawning stock have been completed, it is possible to compute the total yield potential of the stock in relation to different efforts (fishing mortalities).

In the following, density dependent growth and the predation of fry, or very small individuals, by young fish will be ignored. These assumptions must, however, be examined before the models are used. Notably, if very young fish are under consideration, these issues may well become important. However, for fisheries where the recruiting age is past the stage where cannibalism is important, these issues can often be ignored since they should be captured through the stock-recruitment function.

We will assume that yield per recruit (Y/R) and spawning stock per recruit (S/R) are known for each value of fishing mortality (F). This basically determines functional relationships, where Y/R is a function of fishing mortality and similarly for S/R . In some cases this is best written as $(\frac{Y}{R})|_F$ or $Y/R = g(F)$, but in most cases it is sufficient to consider Y/R for some fixed value of F and later on variable fishing mortalities.

It will also be assumed that the relationship between spawning stock and recruitment on the Beverton-Holt form has been assessed.

$$R = \frac{\alpha S}{1 + S/K}$$

4.2 The equilibrium size of the spawning stock

$S = (S/R)R$, which implies

$$\begin{aligned} S &= (S/R) \frac{\alpha S}{1 + S/K} \\ \Rightarrow 1 &= (S/R) \frac{\alpha}{1 + S/K} \\ \Rightarrow 1 + S/K &= \alpha(S/R) \\ \Rightarrow S &= K[\alpha(S/R) - 1] \end{aligned}$$

4.2.1 Details

Then things can be linked up in a relatively simple fashion. Using the Beverton-Holt stock-recruitment function, first write $S = (S/R)R$, which implies

$$S = (S/R) \frac{\alpha S}{1 + S/K}.$$

Next, cancel S to obtain

$$1 = (S/R) \frac{\alpha}{1 + S/K}.$$

and multiply both sides with the denominator, so that

$$1 + S/K = \alpha(S/R),$$

which can be solved for S and the spawning stock can be written as seen in the spawning stock equation.

Definition 4.1. Spawning stock equation for a given fishing mortality:

$$S = K [\alpha(S/R) - 1].$$

This provides the means to compute the spawning stock biomass for any given value of the fishing mortality, through the use of spawning stock biomass per recruit.

4.3 Equilibrium yield

$$Y = (Y/R)R = (Y/R) \left[\frac{\alpha S}{1 + S/K} \right].$$

4.3.1 Details

Given the equilibrium spawning stock biomass and the yield per recruit, the expected total yield corresponding to a specific fishing mortality rate can easily be derived.

Definition 4.2. Total yield by fishing mortality:

$$Y = (Y/R)R = (Y/R) \left[\frac{\alpha S}{1 + S/K} \right].$$

4.3.2 Examples

Example 4.1. Suppose the following basic definitions are stored in an R-file.
<http://tutor-web.net/fish/fish5106stockrec/lecture40/equilibrium-yield.r>

4.4 The equilibrium yield curve

The previous methodologies can be combined into the following steps:

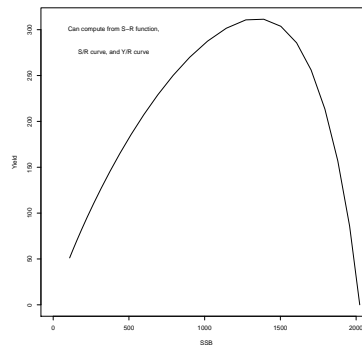
- Fix F
- Compute the yield per recruit (Y/R)
- Compute spawning stock biomass per recruit (S/R)
- Next compute S using S/R and α, K
- Finally compute R and then Y

Can do this for range of F and plot Y against F .

Maximum of this curve: MSY .

Corresponding F : F_{MSY}

Corresponding biomass: B_{MSY}



Equilibrium yield for cod in Icelandic waters (from Danielsson et al, 1996)

4.4.1 Details

The above methodology can be combined as follows. For a given fishing mortality, compute the yield per recruit (Y/R) and spawning stock biomass per recruit (S/R). The spawning stock biomass is then computed in accordance for known S/R and the coefficients in the Beverton-Holt curve. Finally, the long-term yield of the resource (Y) for this particular fishing mortality can be derived using the yield per recruit along with the number of recruits from the equilibrium spawning stock biomass.

This methodology can now be used to compute the equilibrium yield (Y) for a range of fishing mortality rates (F) and in this manner one can obtain a plot of equilibrium yield as a function of fishing mortality. This curve is commonly termed a sustainable yield curve.

Note 4.1. The biomass corresponding to the maximum sustainable yield (MSY) is denoted B_{MSY} .

4.4.2 Examples

Example 4.2. Continuing on the previous example, the following R commands will plot the entire curves for the simulated data sets.

<http://tutor-web.net/fish/fish5106stockrec/lecture40/equilibrium-yieldcurve.r>

4.5 Caveats

We assume equilibrium!

No variation is included

4.5.1 Details

It should be noted that all computations here assume that there is an equilibrium. Such an equilibrium does, of course, not exist in the sense that a real stock will tend towards such an absolute size and stay there forever.

However, these computations provide an indication of the directions or trends in stock size which would be expected under certain harvest rates.

It is easy to extend these models, for example by simulating variation in recruitment from the mean value dictated by the B-H relationship.

4.6 Other stock-recruitment relationships

Can also use the Ricker curve equation to get

$$S = K [\ln(\alpha S/R)]$$

The Cushing equation $R = \alpha S^\beta$ gives

$$S = [\alpha(S/R)]^{1/(1-\beta)}$$

4.6.1 Details

It should be pointed out that the above computations can be carried out although reference is made to other kinds of relationships between spawning stock and recruitment. If the Ricker relationship is used, the spawning stock equation for a given F changes to:

$$S = K [\ln(\alpha S/R)]$$

whereas other computations remain the same.

Definition 4.3. Cushing equation:

$$R = \alpha S^\beta$$

If the Cushing equation is used to determine recruitment then the spawning stock equation for a given F changes to:

$$S = [\alpha(S/R)]^{1/(1-\beta)}$$

4.7 Extensions

Can easily add cannibalism by juveniles

Density-dependent growth can also be included

4.7.1 Details

The effects of cannibalism can easily be added through specific equations, but biomass of young fish per recruit (J/R) must be computed in the same way as yield and spawning stock per recruit.

Taking density dependent growth into account is rather more difficult. This becomes evident in decreasing catches and spawning stock per recruit when the stock is large. A theoretical discussion of this issue was introduced by Beverton-Holt (1957) and has been tested on haddock in the North Sea.

The methods described in the previous chapter can be used to compute long-term catch projections. Given the same assumptions regarding growth, mortality, and the relationship between recruitment and spawning stock, the computations will give the same long-term results as the equilibrium-based computations above. The advantage of making long-term computations is that it gives an assessment of the total yield for the entire period, so it is possible to visualize the long-term gain of constructive measures in relation to the short-term loss of a temporary decrease in effort. There are, however, exceptions to this. Under certain circumstances, stock sizes may fluctuate so that the spawning stock, for example, oscillates around a given value and fails to reach equilibrium at the point.

5 Harvest control rules

5.1 A harvest control rule

5.1.1 Details

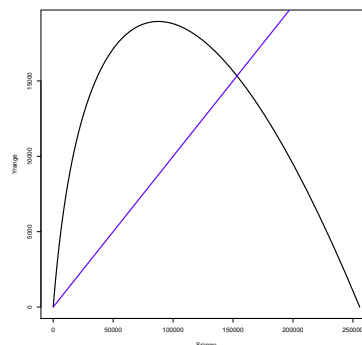
Note 5.1. A harvest control rule (HCR) is simply a formal method for determining a catch limit based on available data.

Harvest control rules could, in principle, be based on fishing mortality, stock biomass, or any other measures considered important indicators of the stock size or harvest level.

It is important to keep in mind that although the HCR can in principle be based on e.g. stock biomass, it will in reality be implemented using an estimate of the corresponding quantity, e.g. of stock biomass.

5.2 Depicting control rules

If a harvest control rule is a function of biomass, it may be depicted within the $S - Y$ plane with an equilibrium curve.



Equilibrium yield vs biomass along with HCR

5.2.1 Details

It is common practice to illustrate the HCR along with equilibrium curves.

5.2.2 Examples

Example 5.1. The simulated data can be used to draw equilibrium yield against biomass, since both are computed based on the same fishing mortalities.

Here is the complete procedure for simulating a population and drawing an equilibrium yield curve along with the HCR.

<http://tutor-web.net/fish/fish5106stockrec/lecture50/eyc-hcr.r>

5.3 Harvest control rule and equilibrium catch

5.3.1 Details

A harvest control rule could be based on a fraction of biomass. Such a harvest control rule can be plotted along with the equilibrium yield curve to indicate the long-term effects of implementing the HCR.

5.3.2 Examples

Example 5.2. The harvest control rule adopted for cod in Icelandic waters was in principle to catch 25% of the biomass each year.

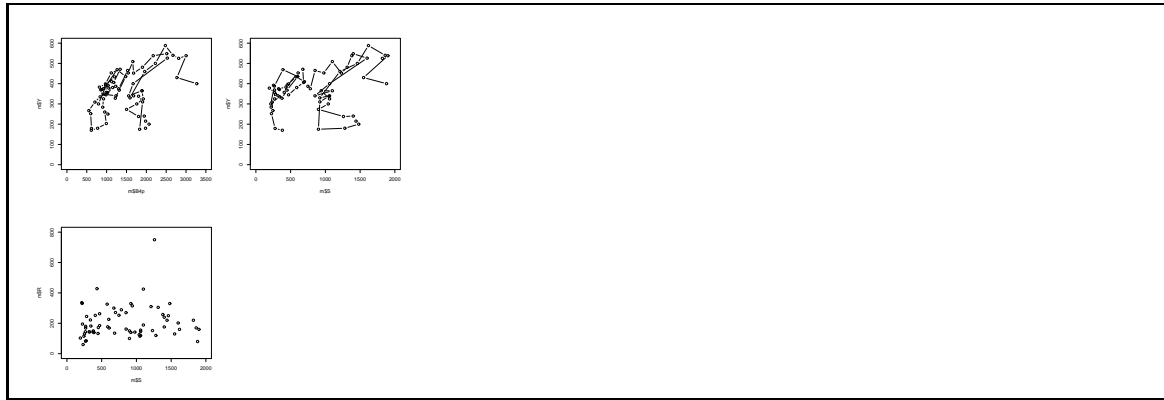
Specifically, the HCR was to be computed as 25% of the biomass of 4 year old cod or older, but taken as an average of estimates in adjacent years. Initially it was suggested that this should be an average of the current year or the previous, but later on, during the implementation phase this was changed to 25% of the average of the current year and the projection one year into the future.

As it turned out, this simple change had drastic consequences. The reason for this is related to VPA convergence, since the projection is much more uncertain than the current year's estimate. During the first 10 years of using the HCR, the estimation error (measured as a retrospective pattern) was up to 60% for this projected average.

A politically important issue at the time was that catches should not be reduced below some minimal level. This corresponds to a minimum in the HCR, indicated with the lower horizontal line.

From a theoretical viewpoint it may be important not to allow catches to exceed a certain level and this is implied with the upper horizontal line.

5.4 A case study on harvests, ICE-cod



5.4.1 Examples

Example 5.3. The adopted HCR for cod in Icelandic waters presented previously was not implemented until extensive modeling had been conducted. The modeling consisted of simulation testing of the likely performance of a range of harvest control rules.

6 Stock-recruitment functions in relation to ecological theory

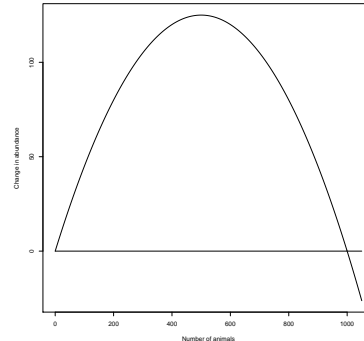
6.1 Relating ecological models to fisheries

A typical model for insects

$$N_{t+1} = N_t + rN_t(1 - N_t/K)$$

A typical model for fish

$$B_{t+1} = B_t + rB_t(1 - B_t/K) - Y_t,$$



Change in animal abundance as a function of initial state.

6.1.1 Details

Many theses have been written in ecology concerning the potential response when a species is subject to different mortality rates.

Common models in this instance are variations on a simple logistic response. If the number of animals at time t is N_t , one version of this is to project the numbers with

$$N_{t+1} = N_t + rN_t(1 - N_t/K)$$

(noting that there is no harvest) and this is of course is very similar to the corresponding production model in fisheries,

$$B_{t+1} = B_t + rB_t(1 - B_t/K) - Y_t,$$

where Y_t is harvest.

The simple models have been used to demonstrate behavior ranging from simple convergence to equilibrium through dampened oscillations, cyclic behavior to chaos.

These various types of responses have been known since 1954 in fishery science and will be shown in the following.

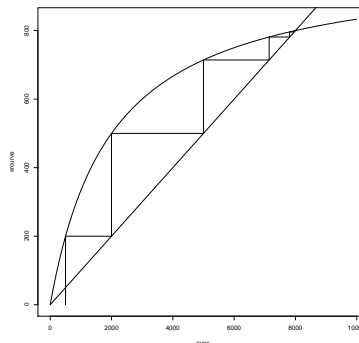
6.1.2 Examples

Example 6.1. The plot can be generated using the following R commands:

```
r<-0.5
K<-1000
x<-0:1050
plot(x,r*x*(1-x/K),xlab="Number of animals",
      ylab="Change in abundance",lwd=2,type='l')
lines(c(0,1050),c(0,0))
```

6.2 Convergence

In the case of the B-H stock-recruitment curve and low fishing mortality, the stock will converge to an equilibrium.



6.2.1 Details

Ecological models usually assume a species has only a single "age group" in the parent population and that the progeny immediately becomes the new population. The bulk biomass approaches within fisheries are of exactly the same form.

The more detailed methods which take into account age groups within a stock will of course behave somewhat differently. In addition, these models normally assume the progeny (recruits) to be related to adult biomass rather than numbers (a large fish has many more eggs than a small fish). This has not always been the case, however, and the Ricker and Beverton-Holt models can be formulated in terms of adult numbers in place of biomass, though the distinction is irrelevant for the present illustrations.

Suppose a stock generates recruitment according to a Beverton-Holt curve. Suppose further that survival into the adult population is according to a biomass-per-recruit curve for a given fishing mortality. As a first approximation, take this to be a single cohort species so

that the recruit from an adult population becomes the entire new spawning population in the following year.

If fishing mortality is too high, it is well known that the model stock will collapse. If fishing mortality is moderate, however ($F < F_{crash}$), then there is a point at which the replacement line intersects with the production curve. At this point the production is the same number of recruits as is needed to replace the stock and therefore the stock is in equilibrium. It is not hard to see that in this simple scenario the population will converge to this equilibrium, whether the initial stock size is above or below the equilibrium.

Further, the only effect of accounting for several age groups will be to smooth the transitions. The tendencies will be the same, towards the same equilibrium.

It therefore follows that in the case of the B-H stock-recruitment curve (and low fishing mortality), the stock will converge to an equilibrium.

It should be noted that this smooth and straight-forward convergence is a result of the following - when an initial stock size is away from the equilibrium, the next stock size will be closer and will stay on the same side of the equilibrium.

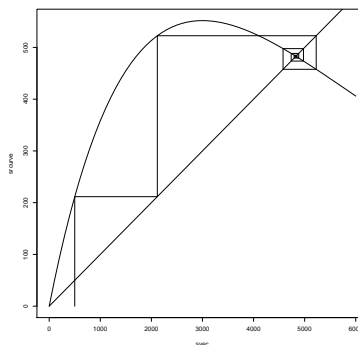
6.2.2 Examples

Example 6.2. A plot of the convergence towards an equilibrium point can be shown using the following R commands:

<http://tutor-web.net/fish/fish5106stockrec/lecture60/convergenceplot.r>

6.3 Damped oscillations

When a Ricker curve has a slight negative slope and F is low, the stock converges to an equilibrium through damped oscillations



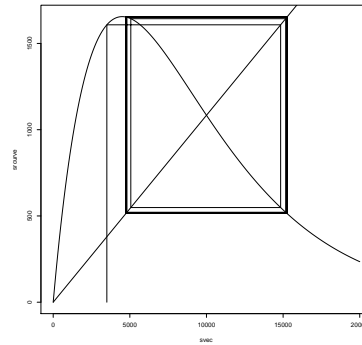
6.3.1 Details

The straight-forward convergence of the Beverton-Holt stock-recruitment relationship does not hold for other relationships. Notably, when a Ricker curve is used, the right limb has a negative slope. When the replacement line with a positive slope intersects the production curve with a negative slope, the feedback mechanism is quite different.

When a Ricker curve has a slight negative slope and F is low, the stock converges to an equilibrium through damped oscillations.

6.4 Oscillations

In specific cases the stock can simply oscillate around an equilibrium point.



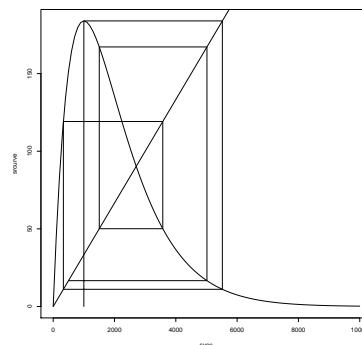
6.4.1 Details

In specific cases the stock can simply oscillate around a equilibrium point.

It should be noted that these are limiting situations and will not occur in real situations. Thus, a formal oscillation will only occur at an exact combination of parameter values. In real situations such combinations simply can not occur as the two slopes will always be different to some extent.

6.5 Chaos

When the right-hand limb of the Ricker Stock-recruitment curve has a steep negative slope, potential chaos ensues.



6.5.1 Details

A very interesting mathematical phenomenon occurs when the right limb of the Ricker curve has a steep slope. In this case strong negative feedback occurs (i.e. a large stock produces small year-classes and vice versa).

When the right-hand limb of the Ricker stock-recruitment curve has a steep negative slope, the behavior becomes unpredictable. This situation is called chaotic.

If this is to happen in a real situation, the prerequisite is to have a strongly declining right-hand limb of the stock-recruitment curve. This does not seem to happen for fish stocks.

6.5.2 Examples

Example 6.3. The figure is generated using the R commands:

<http://tutor-web.net/fish/fish5106stockrec/lecture60/chaosplot.r>

7 More general analyses of interactions

7.1 Stock and recruit analyses from indices

If you only have length and abundance data from surveys along with length-weight relationship and maturity at length, then you can generate:

- Abundance index at length
- Abundance index by length group
- Possibly index of recruitment
- Index of spawning stock biomass

This is enough for a stock-recruit plot with indices on both axes.

7.1.1 Details

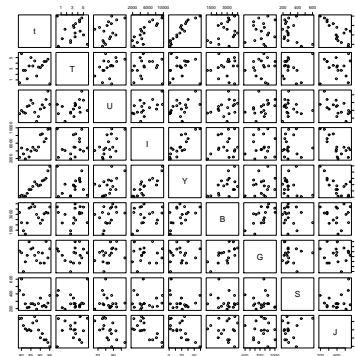
If you only have length and abundance data from surveys along with length-weight relationship and maturity at length, then you can generate:

- Abundance index at length
- Abundance index by length group
- Possibly index of recruitment
- Index of spawning stock biomass

These data suffice to obtain a stock-recruit plot with indices on both axes. Following this one can in principle fit stock-recruitment curves to the data.

7.2 Case Study: Some relationships in an ecosystem

Need to investigate the nature of relationships



7.2.1 Details

In order to decide on a framework for including species interactions, a basic understanding is needed of which interactions are important. The simplest of such analyses are pair plots and pairwise correlations.

7.2.2 Examples

Example 7.1. Consider the data file "borecol.dat" considered by Stefansson, Skuladottir and Steinarsson (1993):

<http://tutor-web.net/fish/fish5106stockrec/lecture80/borecol.dat>

The data file contains several time series of annual measurements of ecosystem variables from the arcto-boreal system around Iceland including temperature, adult and juvenile shrimp CPUE, capelin acoustic biomass estimates, cod juvenile and adult biomass estimates, and the increase in mean weight of cod from ages 4 to 5 in catches from adjacent years.

7.3 A simple predation model

Can include predation mortality in several ways, e.g.

$$\begin{aligned}N_{1,a+1,y+1} &= N_{1ay}e^{-Z_{1ay}} \\ Z_{1ay} &= F_{1ay} + M_1 + M_{2ay} \\ M_{2ay} &= \alpha_a N_{2ay}\end{aligned}$$

need to specify $\alpha...$

Same concept used by Pope and Knight to describe recruitment to one stock, affected by predation by another...

7.3.1 Details

No attempts will be made to explain general models for the predation of one species by another. Instead, a few examples will be given of how such models may be constructed. Many models are based on a simple extension of fundamental equations whereby natural mortality is divided into base mortality (M_1) and predation mortality (M_2). Then a model is designed for the predation coefficient.

An example can be taken of a model where one predator (stock 1) feeds on one type of prey (stock 2). In this case the stock equations for the prey could be set up as seen in the predation models.

Definition 7.1. Predation models:

$$\begin{aligned}N_{1,a+1,y+1} &= N_{1ay}e^{-Z_{1ay}} \\ Z_{1ay} &= F_{1ay} + M_1 + M_{2ay} \\ M_{2ay} &= \alpha_a N_{2ay}\end{aligned}$$

In this setup it is simply assumed that natural mortality due to predation is in direct proportion to the stock size of the predator. Such models are necessary to explain multi-stock effects within ecosystems, although wide-ranging research is required (for example - stomach-content samples) in order to define the nature of the effects. In some cases, the effects may be crucial but in other cases they may be fairly unimportant.

The same basic concept was used by Pope and Knight to describe recruitment to one stock, affected by predation by another. This can easily be fitted to survey data alone, as long as one can obtain an overall abundance index and a recruitment index for each species. The resulting models are simply multiple regression models where the log-recruitment of each stock is written as a function of the (log-)biomass of the various stocks. These models can correspond to Cushing or Ricker stock-recruitment models incorporating mortality.

7.4 Cannibalism by immature fish

$$R = \alpha S^\beta e^{\gamma J}$$

7.4.1 Details

A simple technique has been developed to take into account cannibalism by a species and assess the effect of this on recruitment.

Before listing such methods, it should be noted that it is not necessary to consider how much the older, mature, fish eat of young fish (or fry), because this enters directly into the stock-recruit relationship. It would, however, be interesting to assess whether there are any notable effects of the predation by immature fish.

A simple model for this was proposed by Pope and Woolner (1981), where the coefficients can be estimated using linear regression, $\ln R = \alpha + \beta \ln S + \gamma J$.

Definition 7.2. Cannibalism by immature fish:

$$R = \alpha S^\beta e^{\gamma J}$$

In this model, the term γJ enters in a fashion similar to that of the natural mortality coefficient (cf the way the parent stock enters in the exponent of the Ricker equation).

The first indication as to whether the model makes any sense at all is verified by examining whether β has a positive sign and γ a negative one. Then we need to examine whether these coefficients are significantly different from zero.

Since cannibalism may be important, although not significant due to variability, it may be necessary to examine the effects of this type of model even if the coefficients are not statistically significant. In this case certain acceptable values are either estimated or assumed for the coefficients and the effects on predictions are examined, e.g. on recruitment, catch projections, etc.