AdriaMed

GCP/RER/010/ITA

Lectures notes
AdriaMed Training Course on Fish Population Dynamics and Stock Assessment
Split, 10-29 September 2001

by
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AdriaMed Technical Documents No.8
GCP/RER/010/ITA/TD-08
Termoli (Italy), December 2002
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Preface

The Regional Project “Scientific Cooperation to Support Responsible Fisheries in the Adriatic Sea” (AdriaMed) is executed by the Food and Agriculture Organization of the United Nations (FAO) and funded by the Italian Ministry of Agriculture and Forestry Policies (MiPAF).

AdriaMed was conceived to contribute to the promotion of cooperative fishery management between the participating countries (Republics of Albania, Croatia, Italy and Slovenia), in line with the Code of Conduct for Responsible Fisheries adopted by the UN-FAO.

Particular attention is given to encouraging and sustaining a smooth process of international collaboration between the Adriatic Sea coastal countries in fishery management, planning and implementation. Consideration is also given to strengthening technical coordination between the national fishery research institutes and administrations, the fishery organizations and the other relevant stakeholders of the Adriatic countries.

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For bibliographic purposes this document should be cited as follows:

Preparation of this document

This document is the final version of the Lecture Notes of the AdriaMed Training Course on Fish Population Dynamics and Stock Assessment, organised by the FAO-AdriaMed Project (Scientific Cooperation to Support Responsible Fisheries in the Adriatic Sea) in Split (Croatia), 10th – 29th September 2001.

These lecture notes aim at providing an introductory treatment of some of the basic topics of fish population dynamics and stock assessment. The notes serve as a summary of the various lectures given and as a reference guide to the methods used and the spreadsheet applications developed. Moreover, in the last chapters, multispecies and ecosystem concepts and approaches are introduced in consideration of their increasing relevance in modern fisheries management.

The lecture notes are primarily for the junior scientists participating in the AdriaMed Project component “Adriatic Sea Shared Stocks” which focuses on the appraisal of shared fishery resources of the Adriatic Sea, it can also be of interest for students and professionals of fisheries research. However, a comprehensive introduction to the theory of fishery sciences as well as of stock assessment models is outside the scope of this publication. Interested readers may find useful the literature given in Chapter 14 and Appendix III for in-depth treatment of each topic.

The document is an output of the FAO-AdriaMed Regional Project “Scientific Cooperation to Support Responsible Fisheries in the Adriatic Sea”. It is hoped that with this publication a contribution can be made to strengthen the cooperation between the fishery research institutes around the Adriatic Sea.


ABSTRACT

The AdriaMed Training Course on Fish Population Dynamics and Stock Assessment was held in Split, Croatia from the 10th – 29th September 2001. It was attended by participants from Albania, Croatia Italy and Slovenia. The main objective of the course was the enhancement of professional skills and the strengthening of scientific cooperation through joint analyses of the scientific information available on shared stocks. Furthermore, this training exercise created an opportunity for junior scientists to perform cooperative analyses and joint assessment of those species whose stocks are shared in the Adriatic Sea. A selection of methods of fish stock assessment is described in detail, with examples of calculations (based on Excel© spreadsheets, available from the publisher). Special emphasis is placed on methods based on the analysis of length-frequencies. After a short introduction to statistics and sampling, the text covers the estimation of life parameters, gear selectivity, holistic and analytical models, and prediction models. The last two chapters dealing with multispecies and ecosystem approaches are meant to serve as a conceptual background for future discussions on multi-species considerations that are increasingly relevant in contemporary fisheries research and management.
# Table of Contents

1. **The AdriaMed Training Course on Fish Population Dynamics and Stock Assessment, Split (Croatia) 10th - 29th September 2001**
   - 1.1 Background information................................................................. 1
   - 1.2 Objectives.......................................................................................... 1
   - 1.3 Methodologies..................................................................................... 2
   - 1.4 Expected Results................................................................................ 2
   - 1.5 Preparations........................................................................................ 2
   - 1.6 Contents of the course........................................................................ 2
   - 1.7 Literature used.................................................................................... 3
   - 1.8 About the lecture notes....................................................................... 4
   - 1.9 List of participants.............................................................................. 5

2. **General introduction to Stock Assessment**
   - 2.1 What is the objective of stock assessment?........................................ 7
   - 2.2 What stock assessment makes?........................................................... 7
   - 2.3 How stock assessment works?............................................................ 7
   - 2.4 Which are the tools of stock assessment?............................................ 8
   - 2.5 What is a stock?.................................................................................. 9
   - 2.6 Why the stock unit often fails?............................................................ 9

3. **Biostatistics**
   - 3.1 Basic concepts.................................................................................. 10
   - 3.2 Frequency table.................................................................................. 12
   - 3.3 Measures of dispersion and confidence intervals.............................. 12
   - 3.4 The Normal Distribution.................................................................... 14
   - 3.5 Parameter estimation.......................................................................... 16
   - 3.6 Simple linear regression..................................................................... 17
   - 3.7 Inverse regression.............................................................................. 19
   - 3.8 Functional regression analysis............................................................ 19
   - 3.9 Linear regression with two variables.................................................. 19
   - 3.10 Multi-dimensional regression............................................................ 20
   - 3.11 Non-linear regression....................................................................... 21

4. **Sampling**
   - 4.1 Accuracy and Precision.................................................................... 22
   - 4.2 Sampling designs.............................................................................. 23
   - 4.3 Sampling gear.................................................................................... 23
   - 4.4 The basic data series........................................................................ 24
     - Treatment of the sample.................................................................... 24
     - Kind of variables recorded................................................................. 26
   - 4.5 Methodology..................................................................................... 27
     - Length measurements....................................................................... 27
     - Weight measurements...................................................................... 28
     - Sex and stage of maturity.................................................................. 29

5. **Surveys**
   - 5.1 Background...................................................................................... 30
   - 5.2 Basic methodology and assumptions................................................. 31
   - 5.3 Trawl surveys.................................................................................... 31
   - 5.4 Deviations from basic assumptions.................................................. 32
6. Age and growth

6.1 Age
6.2 Length frequency analysis
6.3 Growth
6.4 Approaches to growth estimation
6.5 Growth parameters
6.6 The von Bertalanffy Growth equation (VBGF)
6.7 Estimation of parameters
6.8 Practical hints for finding the VBGF parameters K and L∞

7. Mortality

7.1 Quantitative measures of mortality
7.2 Assumptions of exponential decay model
7.3 Properties of exponential decay model
7.4 Estimation of mortality rates
7.5 Estimation of Z from catch and effort data
7.6 CPUE data from research surveys
7.7 Z from commercial fisheries
7.8 Heincke’s formula
7.9 Estimation of Z from a linearised Catch Curve
7.10 The linearised catch curve based on length data (Length converted catch curve)
7.11 The cumulated catch curve based on length composition data
7.12 Beverton and Holt’s Z-equation based on length data
7.13 Natural mortality
7.15 Formula of Alagaraja (1984)
7.16 Pauly’s Empirical formula
7.17 Rikhter and Efanov’s method
7.18 Gunderson and Dygert Method (1988)

8. Virtual Population Analysis (VPA) and Pope’s Cohort Analysis (PCA)

8.1 Model and assumptions
8.2 Iterative solution (VPA)
8.3 Pope’s Cohort Analysis (PCA)
The AdriaMed Training Course on Fish Population Dynamics and Stock Assessment, Split (Croatia) 10th - 29th September 2001

1.1 Background information

During the First Meeting of the Working Group on the Definition of Priority Topics Related to Shared Demersal and Small Pelagic Resources of the Adriatic Sea organised by the AdriaMed Project, the training requirements of each country participating in the Project were discussed.

It was clear that a general need exists for advanced level training in the application of most recent analytical methods for stock assessment. The Working Groups recognised that a large amount of data on the Adriatic fisheries resources during recent years (and also historically) have been accrued, by both scientific fish surveys and commercial catch sampling programmes, and that it had not always been possible to fully exploit this information.

Therefore, in line with the Project’s aim to strengthen the scientific co-operation around the Adriatic Sea basin and in order to support progress regarding the co-operative analysis of the available scientific information on the shared stocks, it was proposed to hold joint sessions of data analysis with the assistance of highly qualified experienced scientists within the framework of AdriaMed. The proposed activity aims at creating an opportunity for co-operative analysis and joint assessment of the common and shared stocks and at improving on the currently partial stock assessment work, often limited to the spatio-temporal data coverage of each individual data set.

Consequently, in order to prepare for future joint sessions of data analysis, a Regional Training Course on Fish Population Dynamics and Stock Assessment was organised at the Institute of Oceanography and Fisheries of Split (Croatia) from 10th to 29th September 2001.

1.2 Objectives

The overall objective is the enhancement of professional skills and the strengthening of scientific co-operation through joint analyses of the available scientific information on shared stocks. Furthermore, this training exercise created an opportunity for junior scientists to perform co-operative analyses and joint assessment of those species whose stocks are shared in the Adriatic Sea.

The objectives of the training exercise were:

- To enhance the skills of national scientists in the application of modern stock assessment methods for fish stock assessment.
- To assess the suitability of routinely collected data of each country in order to formulate technical advice for fishery management.
- To create an opportunity for co-operative analyses and joint assessments of the common and shared stocks, to improve on current partial stock assessment work, limited to the spatio-temporal data coverage of each individual set of data.
- To identify stock assessment tools that could then become common in all coastal countries. This evaluation would thus lead to the evaluation and application of the...
biological reference points for fishery management that could be appropriate for the fishery resources of the Adriatic Sea.

1.3 Methodologies

The AdriaMed training course on fish population dynamics and stock assessment particularly addresses young researchers in the region. It was structured as follows:

- The training course was attended by biologists and/or graduates engaged in fisheries or fishery related research.
- The participants were from Albania, Croatia, Italy and Slovenia.
- Experienced trainers ran the course.
- Theory was applied, using original data sets provided by the participants. Whenever possible, ad hoc Excel spreadsheet applications were created and used to run assessment models to minimise the use of existing assessment computer packages.

1.4 Expected Results

At the end of the training course, the participants were able to perform fish population dynamics and stock assessment analyses on the basis of the acquired critical knowledge and of their enhanced skills in the application of basic stock assessment and fishery resource appraisal methods. Furthermore, the participants improved their capability for co-operative analyses and joint assessments of common and shared fishery resources.

1.5 Preparations

The training course lecturers, Jeppe Kolding and Walter Ubal Giordano, met at the FAO, Rome, on the afternoon of the 15th and the morning of the 16th April 2001. An overview of the AdriaMed Project was given, together with the objectives of the course as identified by AdriaMed. The training course programme was identified and a tentative work schedule was planned and agreed upon. Course topics were considered on the basis of the CVs of the 12 participants. Logistic details relevant to the course implementation and effectiveness were discussed. Prior to the course a questionnaire was sent to all the participants (Appendix I), in order to get an overview of the background knowledge, general expectations, and data material available for each of the participants.

1.6 Contents of the course

Duration: Monday 10th to Saturday 29th September 2001

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<td>Tue 11</td>
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<td>Sampling/biostatistics</td>
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<td>Wed 12</td>
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1.7 Literature used

The following FAO manuals, made available to the participants by AdriaMed, were used during the course:


1.8 About the lecture notes

The present lecture notes are a supplement to the above course material on which they are partly based. In addition, they have been inspired by


The notes serve as a summary of the various lectures given and as a quick reference guide to the methods used and the spreadsheet applications developed. At present stock assessment is still largely based on single species methods and concepts; and this has also been the main focus of the methods taught in this course. The last chapters (12 and 13), dealing with multi-species and ecosystem approaches, are therefore more theoretical and have not been accompanied by practical exercises. They are meant to serve as a conceptual background for future discussions on multi-species considerations that are increasingly being encouraged in contemporary fisheries management.
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2 General introduction to Stock Assessment

2.1 What is the objective of stock assessment?

Stock assessment involves both a biological interpretation and the use of various statistical and mathematical calculations to make quantitative predictions about the reactions of fish populations to alternative management choices. The objective of fish stock assessment is to provide estimates of the state of the stock (size, composition, regeneration rate, exploitation level, and fishing pattern) to assure, in the long run, the self-sustainability of the stock under exploitation (Hilborn and Walters 1992). The ultimate aim is to provide biological and economic reference points to be used as guidelines for the rational management of the fishery. Traditional default objectives for a biologist have been estimation of sustainable harvest levels, such as maximum sustainable yield (MSY) and/or sustainable exploitation rates such as the optimum fishing mortality, fishing effort, and the size of fish to be caught.

2.2 What stock assessment makes?

Nowadays, stock assessment often goes further than the simple application of a general biological model. It also builds what essentially amounts to a computer simulation of the specific fishery and the resource. The resource part of the simulation is a quantitative model of the dynamics of the fish population, while the fishery part, aims at representing the harvesting process (Sparre and Venema 1998). These two components interact, producing predictions about properties of the resources under different scenarios and under different assumptions that quantify the total catch or catch by size category. In addition, more and more assessments are now incorporating the influence of abiotic variations on the stock sizes in order to distinguish between anthropogenic and natural impacts on the observed population dynamics. A comparison between predicted and observed parameters leads to an assessment of how well the mathematical model approximates the behaviour of the real source. The analyses include history of the past, determination of the present stock status, and forecasts about the future. Two essential key words are: quantitative and choices (Hilborn and Walters 1992).

2.3 How stock assessment works?

A description of a fishery consists of three basic elements:

1) The input (the fishing effort in terms of fishing gears and amount of time spent fishing)

2) The output (the amount of fish landed) as a part of the biological production.

3) The processes that describe and link the input and output (the biological processes and fishing operations).

Where input and output are normally based on observations (e.g. catch and effort statistics) and one or several mathematical model(s) represents the processes.
Furthermore, a few basic principles, considered as axioms, link the relation between fishing effort and yield:

1. In the absence of fishing effort, there will be no catch.

2. Most stocks are part of a food chain, or food web, either feeding on or giving food to other stocks, such that fishing is not the only exploiter of the system.

3. At low levels of effort the potential yield, or surplus production, of the resource is normally under-utilised.

4. At high levels of fishing effort the stock will be fished so hard that the removal of fish exceeds the regenerative capacity and the yields will start to decline. In the extreme, such a situation will eventually lead to a complete collapse of the stock and even eradication.

5. The maximum average yield, corresponding with maximum regenerative capacity of the stock, is therefore somewhere in between no effort and very high effort. Furthermore, this maximum average yield must be shared between man and other predators in a multi-species system.

6. As different stocks have different regenerative capacity rates and different size structures, the overall effort level and fishing pattern in a multi-species fishery is therefore a very complicated issue.

Putting together the pieces of this puzzle is one of the main tasks in stock assessment. In principle, any stock assessment process implies at least three components.

1) A good overview of the fishery harvesting process and the data generated.

2) Choosing or developing a model according to knowledge, assumptions and available input parameters.

3) Sound criteria to judge the goodness of fit to the data of any particular model, the biological realism, and the output parameter estimates.

Once the stock assessment is complete, technical and political choices remain. There is a distinction between assessment of biological potential and the political/social decision on how to manage the stock.

2.4 Which are the tools of stock assessment?

There are two main groups of fish stock assessment models:

- The so-called holistic, or biomass dynamic models, building on the overall stock (population) as the basic unit where individually based processes such as growth and reproduction are inherently encapsulated in the stock model. The starting point of these models are population abundance indices generated from catch and effort data
or fishery independent biomass surveys (swept area method or acoustic surveys). These models have their origin from Verhulst (1838), Graham (1935), and Schaefer (1954).

- Analytical or so-called dynamic pool models building on individual fish as the basic unit and where dynamic processes such as age, growth, mortality, and maturity are each represented by a sub-model. These models are age- or length structured and deal with a partial or the entire demographic structure of the population. They have their origin from Baranov (1918), Thompson and Bell (1934) and Beverton and Holt (1957).

### 2.5 What is a stock?

When the dynamics of an exploited aquatic resource are described and quantified, a fundamental concept is that of the “stock”. For fishery purposes the main criteria for such a concept is to identify and operate with a group of organisms that fulfil the underlying assumptions of the population models. Therefore, the definition of a stock is normally a sub-set of one particular species having the same demographic parameters (growth, natality, and mortality) and inhabiting a defined geographical area (Gayanillo and Pauly 1997).

Practically, a unit stock is an arbitrary definition of a fish population that is large enough to be essentially self-reproducing, where abundance changes are not dominated by immigration or emigration, and where members of the population show similar patterns of growth, mortality, migration and dispersal. Gulland (1983) proposed an operational definition for management purposes: a sub group of species can be treated as a stock if possible differences within the group and interchange with other groups can be ignored without making invalid the conclusions reached in the course of an assessment.

Consequently, if it becomes clear that growth and mortality parameters differ significantly in various part of the area of distribution of the species, then it will be necessary to assess the species on an area by area basis. Fish stock assessment should ideally be made for each stock separately. The results may (or may not) be subsequently pooled in a multi-species fishery. Therefore, the data must be available for each stock of each species considered.

### 2.6 Why does the stock unit often fail?

There are at least three main reasons for failing to work properly with the stock unit.

1) The full distribution area of the stock is not covered by the data collected, so that only part of the stock is considered. This is a typical example where several independent fisheries are exploiting the same stock.

2) Several independent stocks are lumped together, for example, because their areas of distribution overlap.

3) Continuous immigration and emigration of the components of one or more stocks from the fishing ground. Taking into account that most of the exploited marine resources undertake migration, an essential element to perform stock assessment is an understanding and knowledge of migration routes.
3 Biostatistics

Compared with technical man-made systems, variability is high and is an inherent characteristic in natural systems. This is especially pronounced in biological ecosystems. Describing characteristic features of organisms or their environment, effects of exploitation, treatments or external factors etc. becomes difficult due to this variation. Often, estimating and analysing variability becomes a goal in itself, since, given the high variability, analysing variation is a necessity to obtain reasonably reliable answers to the questions being asked.

The collection of material and measurements of the different variables is a major part of the total effort in most branches of science, but particularly in field sciences such as fisheries. Field work itself is both costly and time consuming, especially when it requires a survey vessel. How the data are collected and the survey is designed are extremely important because failures made in this step may invalidate the results of the entire investigation.

Hence, anyone conducting a survey or experimental investigation must consider all the common problems of sampling errors and bias (Kelly 1976, Cochran 1977, Bagenal 1978). On the one hand, there is a need for the best possible knowledge and understanding of the organisms and their environment based on previous research. On the other hand a thorough knowledge of the construction, operation and selectivity of the sampling gear is also required. Equally essential, however, is knowledge of basic statistics to be able to plan, conduct and analyse experiments and surveys in a satisfactory manner.

An example: it is impossible to measure the length of all fish in a population or even in big catches. A sample is therefore examined. Ideally, the sample is then representative of the population under investigation. Something should be said about the distribution of lengths in the population based on the information obtained from the sample.

3.1 Basic concepts

First, some fundamental concepts of the statistical sampling theory should be re-stated:

**Population:** A finite number of separate objects defined in space and time. Sometimes, due to unavoidable bias it may be necessary to differentiate between a ‘sample’ population and the real population, where the sample population consists of the objects that have an equal probability of being selected.

**Population list:** The table of the objects in a population.

**Variable:** A property measured or recorded which has one and only one value for each object in the population.
In a given population, certain parameters characterise each variable (e.g. length):

**Frequency distribution**

\[ F(x) = \frac{\text{#}x_i}{N} \]

where \( \text{#}x_i \) = No. of objects with length \( i \), and \( N \) = No. of objects in the population

**Mean**

\[ \bar{x} = \frac{\sum x_i}{N} \]

**Variance**

\[ S^2(x) = \frac{\sum (x_i - \bar{x})^2}{N - 1} \]

The variance \( S^2 \) is the sum of the squares of the deviations from the mean divided by number, \( N \), minus one.

**Standard deviation**

\( S \) or \( SD \) = the square root of the variance. \( S \) is a very usual term, since it is often interested in the variance relative to the size of the mean length. So, for that purpose \( S \) is relevant as it is the same unit as the mean.

**Coefficient of variation**

\[ CV = \frac{SD}{\bar{x}} \]

\( CV \) is the relative standard deviation (relative to the mean)

**Range**

Interval between lowest and highest value

It should be kept in mind that a parameter is a characteristic of a population, not of a sample. *Estimates* of a parameter are obtained from a sample.

In a sample of fish, for example, the length frequency sample representing the stock, is a random sample if any fish in the entire stock has the same probability of being drawn as any other. It is usually difficult to obtain pure random samples. If, for example, the juveniles are located in some nursery areas, which do not coincide with the fishing grounds from which our samples originate, the juvenile fish will be underrepresented in the samples. A similar problem is created by the selectivity of fishing gears. Samples, which are not random samples, are called *biased samples*. A feature of fish behaviour, believed to create a most serious bias, is migration. The bias must be accounted for in the analysis, and the basic methods must be modified to account for it. Some types of bias are easier to deal with than others. Bias created by migration can only be handled properly when the routes of migration are well known.
3.2 Frequency table

Sometimes, for a continuous variable such as length, it is very convenient, for treatment purposes, to arrange the sample in a table that is called a “frequency table”, by dividing the length range into a number of length intervals.

By \( j \) the index of a length group is identified, with an upper and a lower limit of length group.

\[ L(j+1) = L(j) + dL. \]

A concept that will be frequently utilised during the course is the interval size that is expressed as \( dL \). A fish of length \( x(j) \) then belongs to the length group \( j \) when

\[ L(j) \leq x(j) < L(j) + dL. \]

\( F(j) \) is the frequency of length group \( j \), or the number of fish observed in the length group \( j \). When \( L(j) \) in a frequency table is just represented by one number, it represents the lower interval limit of length group \( j \).

The midpoint of length interval \( j \) is defined as

\[ \frac{L(j) + L(j+1)}{2} \]

Statistics, such as mean, variance, etc. can be calculated the standard way by using the midpoints to represent the interval, but the precision of the calculated values will decrease with increasing intervals (\( dL \)).

3.3 Measures of dispersion and confidence intervals

The mean value is often called a statistic of location or a measure of central tendency, i.e., it is a representative value which describes the position along a given axis by which the variable is characterised. However, the mean says nothing about how the individual observations are distributed, e.g., the width of the frequency distribution. Thus, the range and the variance are needed as measures of dispersion (precision). When parameters are estimated, inclusion of estimates of dispersion is essential, since even if an estimate of the mean may be very accurate (i.e. unbiased), it can remain highly imprecise due to an extensive dispersion of the observations (see chapter on Sampling). Hence, some estimate of dispersion is needed to determine how closely our sample mean estimates the true parametric mean.

The range is a poor expression, since it is highly sensitive to single extreme values and should therefore be used with caution. The standard deviation, i.e. the square root of the variance, is preferable to the range and can often be used to estimate the so-called confidence intervals to the mean value.
The standard error \((SE)\) is the standard deviation of the means of \(N\) measurements from a population with the standard deviation \(SD\):

\[
SE = \frac{SD}{\sqrt{N}}
\]

**Note this important distinction:** The standard deviation \((SD)\) is an estimate of the dispersion of individual observations in the underlying frequency distribution, whereas the standard error \((SE)\) is a measure of the dispersion of mean values in a frequency distribution formed after a repeated estimation of means.

The standard error can be used as an indicator of the variation of the calculated sample mean. For example, let \(L_1\) and \(L_2\) be two values less than and greater than the estimated mean. If the odds are, say, 95 to 5 that the true mean \((\mu)\) lies in the interval from \(L_1\) to \(L_2\), then these values are called the 95% confidence limits. All percentage confidence limits are defined in a similar way.

In the case of the normal distribution, such confidence limits are estimated by:

\[
L_1 = \bar{x} - t(n-1) \cdot \frac{SD}{\sqrt{N}}
\]

\[
L_2 = \bar{x} + t(n-1) \cdot \frac{SD}{\sqrt{N}}
\]

Where \(t(n-1)\) are the fractiles in the "Student's t distribution" with \(n-1\) degrees of freedom. The Student's t distribution is listed in statistical tables, e.g. Sokal and Rohlf (1969) and discussed more fully in the statistical reference literature.

It is normal to choose a 95% confidence interval, which means that the probability that the mean of the population (the parametric mean) lies outside the estimated interval is less than or equal to 5%.

The estimate of the mean is, hence, normally given with the estimates of its confidence limits \((CL)\):

\[
\bar{x} \pm CL = \bar{x} \pm t(n-1) \cdot \frac{SD}{\sqrt{N}}
\]

The numeric difference between the mean and one of the confidence limits is then a measure of the dispersion and hence the precision by which the true mean has been estimated.

The confidence limits can be calculated at various level of precision, 90, 95, 99%. The higher the percentage, the higher the fractile and, therefore, the wider the interval between the lower and upper limits.
3.4 The Normal Distribution

If a variable is a so-called normally distributed, it is expected, with 95% probability, that all the observations lie between the interval

$$\bar{x} - 2 \cdot S \quad \text{to} \quad \bar{x} + 2 \cdot S$$

The mathematical expression for normal distribution is (Figure 1):

$$f(x) = \frac{N \cdot dL}{S \cdot \sqrt{2\pi}} \cdot e^{-\frac{(x-\bar{x})^2}{2S^2}}$$

Where $f(x)$ = calculated frequency, $N$ = number of observations, $dL$ = interval size, $S$ = standard deviation, $\bar{x}$ = mean length, and $\pi = 3.14159$.

![Normal distribution](image)

**Figure 1.** Normal distribution. $N=1000$, $dL=1$, $S=5$, $\bar{x} = 25$

This function will be seen many times in the courses as, for example, expressing length frequencies of fish originating from one cohort.

In fisheries sciences, there are many other types of distribution, such as lognormal distribution, negative binomial distribution and the ‘Delta-distribution’. The major difference among them is that normal distribution is symmetrical, whereas the others are skewed to various degrees. The delta distribution, for example, is used to describe the probability distribution for the catch per time unit by a trawl (see section on sampling).
The most important feature about the normal distribution is based on the so-called ‘central limit theorem’ which states:

**Central limit theorem**: In random sampling from an arbitrary population with mean $\mu$ and standard deviation $\sigma$, the distribution of $\bar{X}$ when $N$ is large (>30) is approximately normal with mean $\mu$ and standard deviation $\sigma/\sqrt{N}$

In other words, the mean value of any set of observations is (approximately) normally distributed. This result is also valid for the means of practically all distributions observed in fisheries.

For example, Figure 2 shows the highly skewed frequency distribution of 419 individual hauls from a trawl survey, and Figure 3 shows the distribution of the mean values obtained from running 2000 bootstrap estimates of the mean on the same data. Note the similarity of the Standard errors (SE) in the two figures.

**Figure 2.** Frequency distribution of 419 individual trawl hauls in 200-kg classes.
3.5 Parameter estimation

A very large part of practical stock assessment work is parameter estimation. There is a need to quantify growth, mortality, stock sizes, dynamics etc. Choosing a suitable model is one thing, Statistically relating the model to data in order to estimate the unknown variables, the parameters, is another. According to Hilborn and Walters (1992), there are three essential requirements for parameter estimation:

A formal model with parameters to be estimated.

Observed data from a population to use to estimate the parameters.

A criterion to judge the goodness of fit to the data of any particular combination of model and parameters to be estimated.

The most commonly used criteria for a goodness of fit are the least squares in which the best parameters are those that minimise the sum of the squared differences between the predicted values from the model and the observed data from the population. The sum of squares is calculated as:

$$SS = \sum (observed - predicted)^2$$
3.6 Simple linear regression

If measurements are made on two variables, x and y, it is possible to explore whether there is some relationship between the two in order to predict one from the other. Sometimes, the relationship is simple enough such that a simple linear relationship can be used, as in:

\[ y = \alpha + \beta x \]

It is a general rule that there is some variability (error) in measurements. Suppose the variable y contains measurement error but not x and that the measurements are made of n pairs of y and x values. In this fashion, one obtains a collection of measurements designated \( y_1, y_2, \ldots, y_n \) and \( x_1, x_2, \ldots, x_n \).

The model is then often written as follows:

\[ y_i = \alpha + \beta x_i + \varepsilon \]

where \( \varepsilon \) denotes the measurement error in \( y_i \).

For given values of the coefficients \( \alpha \) and \( \beta \), the deviations from the line can be computed, squared and added to obtain the sum of squares:

\[ SS = \sum_{i=1}^{n} (y_i - (\alpha + \beta x_i))^2 \]

This method of least squares estimates the coefficients (or parameters) \( \alpha \) and \( \beta \) as the values which give the smallest possible sum of squares.

It is simple to differentiate \( SS \) with respect to \( \alpha \) and \( \beta \) and to find the required minimum by solving the appropriate equation and determine where both derivatives are zero. This results in two equations with two unknowns: \( \alpha \) and \( \beta \). The solution to these equations gives estimates of the parameters. The solutions are denoted by \( \hat{\alpha} \) and \( \hat{\beta} \), to distinguish from the real parameters which are never known.

If it is assumed that \( \varepsilon \) comes from a normal distribution, it is possible to compute what sort of variability is to be expected in the estimates \( \hat{\alpha} \) and \( \hat{\beta} \). In particular, an estimate is obtained of the standard deviation of \( \hat{\beta} \). Considering the above-mentioned, this estimated standard error of \( \hat{\beta} \) by \( \hat{\sigma}_\beta \) is calculated from

\[ \hat{\sigma}_\beta = \sqrt{\frac{\sum \varepsilon_i^2}{n-1}} \cdot \frac{1}{\sum x_i^2} \]

Confidence limits for the real slope \( \beta \) are given as

\[ \hat{\beta} - \hat{\sigma}_\beta \cdot t_{n-1} < \beta < \hat{\beta} + \hat{\sigma}_\beta \cdot t_{n-1} \].

17
Linear regression is often used to examine if there is a relationship between two measurements. Then, only the significance of the relationship needs to be dealt with. If it is assumed that $\varepsilon$ comes from normal distribution, it is possible to examine whether the estimate obtained for $\beta$ is more than simply random noise.

If there is no relationship between $x$ and $y$, then $\beta$ is in fact zero. But although $\beta$ is zero, the estimate for that coefficient will not be zero, simply because of the errors in $y$. In order to examine whether there is such coincidence, a so-called t-value is computed as the ratio between the slope and its standard deviation.

When $\beta$ is zero and $\varepsilon$ is normally distributed, $t$ is subject to the so-called t-distribution. When $\varepsilon$ is not from the normal distribution, it still applies that, when there is a sufficient number of measurements, $t$ is close to having normal distribution. This means simply that when many measurements have been carried out, the probability of obtaining $|t| > 2$ is less than 5% if $\beta$ is zero.

Thus, an objective judgement is obtained as to whether there is some kind of a relationship or not. The above-mentioned t-value is computed and tested as to whether it is higher than 2 (in absolute value). Such a large t-value is improbable if there is no relationship.

The correlation coefficient ($r$) is a measure of the linear association between two quantities, both of which are subject to random variation. $r$ can be used only when both measurements are allowed to vary randomly.

$$r = \frac{\text{Cov}(xy)}{S_x \cdot S_y}$$

where $\text{Cov}(xy)$ is the covariance of $x$ and $y$ calculated from

$$\text{Cov}(xy) = \frac{1}{n-1} \left[ \sum (x_i \cdot y_i) - \frac{1}{n} \sum x_i \cdot \sum y_i \right]$$

Inserting that slope $b$ is defined as

$$b = \frac{\text{Cov}(xy)}{S_x^2}$$

the result is that

$$r = b \cdot \frac{S_x}{S_y}$$

The range of $r$ is $-1.0 \leq r \leq 1.0$ with the same sign as the slope $b$. The closer the value of $r$ gets to zero, the less association there is between the variables $x$ and $y$. 18
To test if $r$ is significantly different from 0, the 95% confidence limits for $r$ can be calculated from

$$CL(r)_{95\%} = \tanh \left[ \frac{1}{2} \ln \left( \frac{1+r}{1-r} \right) \pm \frac{1.96}{\sqrt{n-3}} \right]$$

### 3.7 Inverse regression

One of the assumptions behind linear regression analysis is that the independent variable ($x$) cannot be random. It is therefore a question if it could be possible to obtain similar results of the regression if the parameters are exchanged. This in the case both parameters are measured under the same units and with the same accuracy. In this case, the result is an “inverse regression”. Only in exceptional cases when the observation lies on the regression line ($r=1$ or $r=-1$), the same result would be obtained for the inverse regression $x = -a/b + y/b$ or $x = A + By$ where $A = -a/b$ and $B = 1/b$.

### 3.8 Functional regression analysis

One way to circumvent the problem of choosing the independent variable when both variables are random is by using the so-called *functional regression analysis*. This method estimates a slope $b'$ by the expressions

$$b' = \frac{sy}{sx} \text{ if } r > 0$$
$$b' = -\frac{sx}{sy} \text{ if } r < 0$$

and the intercept

$$a' = y - b' \bar{x}$$

Functional regression may be considered as a compromise between ordinary regression and inverse regression. In all cases, it may be seen that for all three types, the lines will pass through the mean $x$ and mean $y$.

### 3.9 Linear regression with two variables

Sometimes, there is more than one variable connected to the measurements of $y$. If, for example, $x$ and $z$ are used to explain how $y$ changes (often used in biomass dynamic models), it is possible to use the model:

$$y_i = \alpha + \beta x_i + \gamma z_i + \varepsilon$$

where $\varepsilon$ again denotes the measurement error in $y_i$.

For given values of the coefficients $\alpha$, $\beta$, and $\gamma$, the sum of squares can again be computed:

$$SS = \sum_{i=1}^{n} \left( y_i - (\alpha + \beta x_i + \gamma z_i) \right)^2$$
Again, it is possible to differentiate and solve the equations. This results in three equations with three unknowns, which are in fact rather uninteresting to solve. Most statistical kits offer reasonable methods for doing this. What is more interesting, is the fact that it is possible to test statistically whether certain coefficients in the model are zero (or something else). Let's call this the full model. If $SS$ is computed for this particular model with corresponding estimates for the coefficients:

$$SS(F) = \sum_{i=1}^{n} \left( y_i - (\alpha + \beta x_i + \gamma z_i) \right)^2$$

then this quadratic sum can be compared with the quadratic sum obtained if certain coefficients (in this case $\gamma$) are left out (or fixed to some other value):

$$SS(R) = \sum_{i=1}^{n} \left( y_i - (\alpha + \beta x_i) \right)^2$$

Obviously, $SS(R)$ is always higher than $SS(F)$ because both sums are obtained by minimising a quadratic sum, but when $SS(F)$ is computed, more coefficients are allowed to change (the coefficient for $z$ is fixed as zero when $SS(R)$ is computed). If $SS(R)$ is too high compared with $SS(F)$, then the hypothesis that the corresponding coefficient is unnecessary and the model must be rejected.

Formally, the theory that the coefficient at $z$ is zero is tested by computing:

$$F = \frac{SS(R) - SS(F)}{df(R) - df(F)} \frac{SS(F)}{df(F)}$$

where $df$ denotes the degrees of freedom in the corresponding model. Normally, $df = \text{number of measurements} - \text{number of parameters}$. In the above example, the full model has three parameters ($\alpha$, $\beta$, and $\gamma$) and, hence, $n-3$ degrees of freedom, but the reduced model has two parameters ($\alpha$ and $\beta$) and, hence, $n-2$ degrees of freedom. The computed $F$-value is then compared with tabulated $F$-values with degrees of freedom $df(R)-df(F)$ and $df(F)$. The theory that the reduced model is correct is rejected if the computed $F$-value is too high.

Exactly the same $F$-testing can be carried out on more complex theories. The full model could, for example, be in accordance with normal linear regression $y$ for $x$ and $z$, whereas the reduced model could be a hypothesis that $\alpha$ is zero and $\beta$ is 1. Thus, the reduced model contains $n$ degrees of freedom and the full model $n-2$ degrees of freedom.

3.10 Multi-dimensional regression

All the above examples can be extended in such a way that the models can contain as many variables as needed.
This is normally done by using matrixes. It is assumed that a given $y$-measurement is connected to many (e.g. $m$) $x$-values thus:

$$y_i = \alpha + \beta_1 x_{i1} + \beta_2 x_{i2} + \beta_2 x_{i3} + \ldots + \beta_m x_{im} + \epsilon_i \quad \text{where } i = 1, 2, \ldots, n$$

In this case, there is a vector of $y_i$, one for each observation, a vector of $\beta$ ($m$ of them), a vector of $\epsilon_i$ (a residual for each observation), and a matrix of $x$’s ($n \times m$). In a matrix notation the equations become:

$$Y = Xb + \epsilon$$

where $b$ is a vector of $m$ parameters which need to be estimated. The minimum of the quadratic sum is given by:

$$\hat{b} = (X'X)^{-1}X'Y$$

which gives an estimation for the coefficients. Note that $X'$ denotes a transposed matrix.

### 3.11 Non-Linear Regression

Many common models are such that they are not linear in the parameters. For example, the Ricker Stock-recruitment model is non-linear in $\alpha$ and $\beta$. Although it is possible to linearly transform the Ricker model by modelling not $R$ and $B$, but $\ln (R/B)$ and $B$, it is obvious that if recruitment is completely random, this transformation will indicate a relationship that does not exist. In this instance, there is reason to try to estimate parameters in a non-linear model.

In general, measurements are made on variables $y$ and $x$, and some function connects the measurements but the function contains unknown parameters:

$$y_i = f(x_i, \beta) + \epsilon$$

The parameters in $\beta$ may of course be as many as required but the quality of the data will determine what can be estimated with any amount of accuracy.

The simplest method is to use least squares estimation as with linear models; i.e., estimate the $\beta$ which gives the minimum value of

$$SS = \sum_{i=1}^{n} [y_i - f(x_i, \beta)]^2$$

As for linear models, it is possible to use an $F$-test to investigate the significance of coefficients in the model. This may be easily done: the first step is to compute the value of $SS$ for the full model, call it $SS(F)$, the next step is to fix those coefficients which are to be tested and the last step is to compute a new value of $SS$, by minimising the other variables to obtain $SS(R)$. The corresponding degrees of freedom are then computed and the F-value set up as above.
4 Sampling

There are two basic principles in science:

<table>
<thead>
<tr>
<th>Deduction</th>
<th>Induction</th>
</tr>
</thead>
<tbody>
<tr>
<td>&quot;the ideal world&quot;</td>
<td>&quot;the real world&quot;</td>
</tr>
<tr>
<td>= Deduce, or make, specific rules or statements from the 'general laws'. Used in mathematics</td>
<td>= Infer, or make, general rules/statements, or laws from the specific (observations). Used in statistics</td>
</tr>
</tbody>
</table>

Statistical inference = draw out information on a population based on a **sample of objects** drawn from the population:

![Diagram](image)

The sample is characterised by:

- **Variability** (spread of observations) = precision
- **Uncertainty** (bias, deviation of observed mean from true mean) = accuracy

4.1 Accuracy and Precision

![Diagrams](image)
- **Randomisation**: each object in the population has the same chance of being sampled (avoiding bias = accuracy)

- **Replication**: sampling size, measure of variability or dispersion (SD, SE, CL) (large sample = precision)

**Sampling design** is to secure randomisation and plan replication (for the desired level of precision)

Randomisation in fisheries is in practice very difficult due to:

- Selectivity of sampling gear
- Unknown spatial and temporal distribution of population
- Sampling artifacts as when catches are sorted or discarded at sea

Replication is a matter of capacity and costs

### 4.2 Sampling designs

- **Simple random sampling** (distribution homogeneous or uniform: variance \( \leq \) mean)
- **Stratified random sampling** (distribution contagious, patched with known external factors, e.g. depth: variance > mean)
- **Systematic sampling** (distribution heterogeneous without periodicity or due to unknown factors)
- **Multiple step sampling** (in the case of large variation in objects, e.g. trawl catches)

### 4.3 Sampling gear

The **choice** of the sampling gear and methodology depends on the **objectives** of the investigation:

- Which objects are to be examined and what are their characteristics and relevant properties?
- Which level of precision is desired/necessary?

Qualitative work like determining the number of species in an area requires very different data from quantitative work such as abundance estimation of a few selected species. A very high level of precision is most often associated with high costs because a very intensive sampling programme (replications) is required. A high precision is not always appropriate. If, for example, the applied methodology does not give a representative picture of the situation; i.e., the sampling is biased, then a high precision is of minor value and can even give the misleading impression of a highly accurate result.

Every sampling gear is developed and designed for specific tasks and for specific conditions and all have inherent biases and sources of error. Generally, the methods of observations in aquatic environments are rather indirect and crude. Moreover, there are some localities
(notably rocky grounds and coral reefs) which still cannot be adequately sampled. The multiplicity of the samplers described is evidence not only of these factors, but also of a general dissatisfaction with existing methods of collection.

When choosing a sampling gear, one should carefully consider the attributes and limitations of the individual gear in relation to one's objectives:

- What are the selective properties of the gear, i.e., does the gear sample the objects in the volume covered quantitatively?
- Where can it be used and how precise can it be positioned?

This relates strongly to the distribution and behaviour of the organisms to be sampled. Some may react by escaping, others by being attracted to the sampler, hence both underestimation and overestimation of abundance may result. A great problem is also that most organisms form aggregations of variable size and distribution. Thus, it is often difficult to determine which spatial resolution is appropriate. Motile organisms often also have significant diurnal behaviour patterns, which should be considered when deciding on the temporal pattern of the sampling effort.

The following practical aspects should be considered at an early stage of the work:

- How does the gear function technically and how is it operated?
- Is the gear really available at the times and places required?
- What are the costs of regular operation?
- Where can the gear be repaired and what are the costs and time required?

Final truisms (Bagenal 1978):

- Most, if not all fish capture methods are selective (species, size, etc.)
- Soundness of sampling procedure is too often assumed without being evaluated.
- There is no substitute for personal operational experience in fish capture.
- There are plenty of opportunities remaining for discovering and developing new methods.

4.4 The basic data series

Treatment of the sample

The extraction of information from the sample depends on a careful consideration of which variables to measure, in which quantities, and at which stage of the process. The simplest information about fish communities is the number of species present that are susceptible to the sampling gear. In quantitative stock assessment, one needs more than this and, normally, data on numbers, length and weight of the specimens caught are recorded. Often, more sophisticated and time consuming data like sex, maturity, age and stomach contents are
included in the sampling. The time available for fieldwork is usually limited, since running expenses may be very high, particularly when a research vessel is required. When commercial catches are sampled, short time intervals are also important in order to reduce variances induced by continuous processes during the sampling period (e.g. growth).

It is most important at the collection stage in the field to ensure that the planned sampling design is followed in order to obtain the optimal amount of data. Depending on the observed variation in the samples and/or unexpected factors influencing the data collection, it may be necessary to devote much effort to just crudely monitoring the incoming samples and adjust or alter the stratification, sampling locations etc. simultaneously, leaving the more profound processing until a later stage.

What should be recorded:

A. **Basic data**: Information on **who** took the samples and **when, where and how** the survey/sampling was conducted. This is important in all investigations and must be properly described in detail. Furthermore additional environmental information should preferably always be included to the extent possible:

- bottom topography and depths
- temperatures, salinities and oxygen
- meteorological observations

These variables are now routinely (often automatically) recorded in most fishery surveys

B. **Catch composition**: List of species and numbers and/or weight caught. Be sure to identify the species correctly and unambiguously (Taxonomic literature, FAO identification sheets). If in doubt, a sample of specimens should be preserved for later taxonomic studies. If the catches are big, one might decide to examine only a random representative sub-sample but always record the total weight and numbers. Sub-sampling, or stepwise sampling, a large trawl catch requires careful considerations on which species should be selected for total enumeration, and which should be sub-sampled and how. Due to size and morphometric differences, the individual fish are rarely randomly distributed within the catch.

C. **Individual species data**: The "classical" series includes:

- length
- weight or volume
- sex and stage of maturity
- age

These data alone provide variables which form the cornerstones of present fishery research, assessment and management. The numbers and sizes of available fish in a population (stock) determine the potentials for exploitation. Information on maturity gives important understanding about biology and reproduction for initial management and enables separation of estimates of abundance into values representing the immature and mature populations.
Where age can be determined satisfactorily, it provides a basis for estimating growth and mortality and, very importantly, year-class strength variation, all of which are essential for assessing yields and current status. Age structured models like Virtual Population Analysis (VPA) and Yield Per Recruit (YPR) require the population to be split into age groups.

Supplementary data include:
- fecundity
- stomach contents
- parasitism
- genetics
- biochemical composition (lipids, proteins etc.)
- occurrence of pollutants

**Kind of variables recorded**

- **continuous** variables (can have any value within an interval, e.g. length and weight)
- **discrete** variables (also called discontinuous or meristic, i.e. counted values in whole numbers (integers) e.g. number of eggs, fin rays, vertebrae etc.).
- **ranked** variables (e.g. stomach fullness)
- **character** variables (for attributes e.g. colour, taste, smell, visually determined maturity stages etc.)

How should the data be recorded and at which level of precision?

- All units in the International System of Units (SI).
- Level of precision, units (kg or grams, cm or mm etc) must be decided upon. Measurements are always connected with some errors: e.g. weight measurements are influenced by wind, motion, water, accuracy of the weighing device, changes of the fish by death or preservation.

How are the data to be treated/processed?

- Manually.
- Computerised processing (this requires an unambiguous coding system for recording the data in a fashion immediately readable for the computer).
- Which statistical methods to employ.

It is always wise to design the data sheets and recording routines to suit subsequent computerised processing.

- design a sheet that is simple to fill out and that does need rewriting or transformation before logging into a database.
- prepare and insert codes in the sheets. Make sure that all the codes are unambiguous. Data that are not recorded in digital units can be treated as character variables and assigned letters or numbers.
- never introduce new codes if others are already established.
4.5 Methodology

Length measurements

Why length measurements?

- length frequency distributions provide information on the demographic structure of the populations sampled.
- measuring the rate of change in length of individuals or populations are approaches to estimating growth processes.
- length is often better than age as an indicator of recruitment, maturity, and fecundity.
- in many fisheries, length is used to define legal size for harvest.

Length-measurements are easy to make but require many observations (big sample size). Therefore it must be well defined and standardised and made in accordance with previous investigations or recommendations.

There are (at least) three common standards:

- Total length (TL). (used for species with rounded or truncate tails)
- Fork length (FL). (for species with forked tails)
- Standard length (SL). (mostly used for larvae and in taxonomic studies)

There are also three different ways of measuring:

- to the nearest unit below
- to the nearest unit above
- to the nearest whole unit

The International Council for the Exploration of the Sea (ICES) recommends the first, but in all reports, it should be clearly stated which method and which measurement practice were applied. Conversion factors can be established for transforming the data from one standard to another.

Length is easily measured with a measuring board or callipers. Automatic measuring boards with direct logging capabilities through connection to a computer are available.
Causes of bias and errors:

- **Live fish**: Muscle: contractions/relaxation
- **Dead fish**: Rigor mortis
- Shrinkage from preservation.
- **Variation in measurement techniques**:
  - Spreading/folding of tail
  - Pressing of the nose into the headboard
- **Individual tendency to prefer certain numbers or approximations**.

**Weight measurements**

Why weight measurements?

- The production of a population and of the individual organism in terms of somatic growth and gonad growth is better reflected by weight changes than by information of length alone.
- Weight changes may reflect changes of the nutritional condition of the fish.
- Total weight or weight per unit area or time is the statistics normally reported in fisheries.
- Annual weight increments (growth) are significant for assessments of commercial value.

Weight is applied at different levels:

- the entire catch
- sub-units of the catch (e.g. by species)
- individual specimens

The weighing of specimens is more difficult, more inaccurate and more time consuming than length measurements. Weight can be replaced by volume (displacement volume) which is especially useful with live fish.

If the length-weight relationship is known, then the individual weight can easily be estimated in databases from length measurements.

Weighing devices:

- hanging balances or platform scales
- spring balances
- electronic balances

The choice depends on the size of the object(s), the desired precision and on the working conditions. Only hanging balances are reasonably satisfactory when working at sea in bad weather, but they are not sensitive enough for individual measurements of small fish. Generally, scale sensitivity should be about 1% of fish weight. All types of weighing devices should be calibrated periodically.
Causes of bias and error:

- external disturbance (wind, motion etc.)
- dryness or amount of water evaporated, i.e. the time the specimens have been out of water.
- stomach contents
- relative weight of inner organs (liver, gonads etc.)

Weight/length relations can be established by regression or non-linear fitting, and are important when converting length at age into weight at age. This requires a large range of data. The weight/length relations may vary seasonally and there are differences between sexes.

**Sex and stage of maturity**

Information on sex and sexual maturity are used to:

- determine current reproductive status.
- during the spawning season, determine the location of spawning grounds.
- determine size and age at first spawning.
- determine what proportion of the stock is reproductively mature/active.
- describe the reproductive cycles of species and relate them to environmental factors.
- estimate the approximate birthday of a cohort when fitting growth curves to length frequency samples.

**Sex-determinations:** Very few fish have clear external sexual dimorphism, especially in the younger stages. It is therefore necessary to dissect the fish and examine the gonads. In adult females, the eggs are readily seen in the ovaries. In adult males, the testes are typically smooth, whitish and non-granular (be careful not to confuse fat bodies with testes). In immature fish, the sex is usually not an important observation, but if needed it will often be necessary to use a dissecting microscope for determination. One should always build up experience before making routine records. Also be aware of problems with hermaphroditic species (e.g. many Labridae).

**Maturity:** These examinations are aimed at determining whether each fish is sexually immature, mature, ripe or spent. Usually a macroscopic scale is used, requiring only trained visual inspection. The criteria are based on size, location, colour and development of roe and the vascular system of the gonads and the classification is done after a key (see e.g. Kesteven 1960, Nikolsky 1963). Some experience is required and it is important that consistency is retained if several workers are involved.

For high precision or resolution, a microscopic examination is employed requiring histological preparation and perhaps staining. The classification is based on the state and size of the gametes and follicles only, also using a key. This is potentially less subjective, but of course, much more labour demanding.
5 Surveys

5.1 Background

Besides commercial fisheries statistics, the main source of information for stock assessment are fishery independent data collected by scientific abundance surveys carried out by research or commercial vessels. This type of data is now extensively used as part of the common work carried out by many regional or national commissions in managing and conserving fish stocks. Surveys were actively promoted during the exploration phase of fisheries resources in the 1970s and early 1980s, when the concept of Exclusive Economic Zone (EEZ) was adopted by the UNCLOS (United Nations Convention on the Law of the Sea). Since then, standardised scientific abundance survey data has become an important tool to estimate "indices of abundance" in the current situation and for long-term monitoring of most of the commercially important stocks.

Although the use, precision, and applicability of survey indices have increased over time, the quality of survey data has in most cases not yet been considered good enough for a "stand alone" assessment (Anonymous 1998). Normally, the indices of abundance are used to tune a VPA or other types of catch at age models (Hilborn and Walters 1992). In such models, uncertainties in the final assessment are due to the inherent uncertainties in all the models used.

The basic assumption in fisheries theory is that catch \( C \) and stock abundance, or standing biomass \( B \) are related by

\[
C = q \cdot f \cdot B
\]

where \( f \) is a measurement of the nominal fishing effort or intensity, and \( q \) is the so-called catchability coefficient (see section on Fishery Concepts). This equation can be rewritten in terms of catch per unit effort (CPUE) - which serves as the abundance index - as

\[
\frac{C}{f} = CPUE = q \cdot B
\]

For demersal fish, the abundance index obtained from bottom trawl surveys normally replaces the use of CPUE indices from the commercial fishery (Anonymous 1998). This is because commercial CPUE indices have proven difficult to utilise in a modern ever-changing industry due to changes in the catchability coefficient \( q \) (see section on Fishery Concepts). In bottom trawl surveys, catchability is kept constant by randomisation, and effort is standardised and can be set to unity, and in contrast to the commercial fishery, recruiting year classes are normally also covered by the use of small meshed cod-ends. The present state of pelagic fish stocks is normally monitored by acoustic surveys. In these surveys, trawl catches are used to identify by species the acoustic recordings and to supply information on size composition needed for converting the reflected acoustic energy to actual fish densities.
5.2 Basic methodology and assumptions

Scientific survey methods and procedures, developed to overcome our inability to directly observe underwater, are detailed in many FAO Manuals (Alverson 1971, Gulland 1975, Sparre and Venema 1998). Instrumentation and methods for monitoring gear performance have emerged in recent years, which have improved the limitations in present standard survey methodology (Anonymous 1998). The major problem with a survey is cost (Hilborn and Walters 1992).

Standard surveys are all built on simple equations where an observation parameter \( d \) is assumed to be directly related to the true density of fish \( D \)

\[
d = q \cdot D
\]  

(3)

where \( q \) is a proportionality or efficiency factor with different meanings, depending on the survey method. (Godo 1998) Surveys are sometimes conducted in which CPUE data are used to describe the assemblage of different species in any water body. However, the catchability coefficient \( q \) with a particular gear differs among most species. So, the actual abundance and composition is generally not represented in CPUE data.

The extent of standardisation varies between surveys but includes normally restrictions on vessel type and size, sampling gear, time period for the survey, procedures for launching and retrieving the sampling gear, sample treatment, and data analysis. Some of the basic assumptions are (Anonymous 1998):

I. efficiency (catchability) of the sampling gear is constant within the frames set by the standardisation,

II. all or a constant proportion of the population is available to the sampling gear over time and among surveys,

III. a fixed survey period removes seasonal variability, and

IV. when a standardisation regime is followed, temporal integrity of abundance estimates is maintained.

5.3 Trawl surveys

Bottom trawl surveys are widely used for monitoring demersal stocks when only an index of abundance is required (Sparre and Venema 1998). In this method, an estimate of the proportionality factor (catchability) is required to scale the survey estimate of abundance to absolute abundance. In general, catchability \( q \) describes how the abundance and size composition of a species differs from within the population and the survey catch (Harley and Myers 2001).

For swept area estimates, Equation (3) can be rewritten as (Anonymous 1998)

\[
d = \frac{q \cdot D}{a}
\]  

(4)
where \( a \) is the area swept by the survey trawl, and \( q \) is the catchability coefficient. If fish are also in the water column above the catching height of the trawl (the so-called trawl window, see Figure 4), Equation 4 can be written (Godø 1994)

\[
d = \frac{q_a q_e D}{a}
\]  

(5)

where the availability \( (q_a) \) gives the proportion of fish available to the trawl and \( q_e \) is the catchability of the available fish. Due to a lack of exact information, the area covered \( a \) (in Eq. 4 and 5) is often assumed to be the area swept by the trawl's wings or doors during a standard tow, and \( q_e \) is given the conservative value 1 (meaning all fish are assumed caught) or a more or less arbitrary value (Gunderson 1993). Because of the importance of this method for stock assessment, the assumptions underlying trawl surveys have been thoroughly studied in recent years (Anonymous 1998). Research has concentrated on issues relating to the trawl itself (sampling trawl geometry and performance and trawl catching efficiency) and the response of fish to the trawl.

![Figure 4](image.jpg)

**Figure 4.** Observation windows of a bottom trawl, a hull mounted acoustic transducer and a sonar. Differences in vertical distribution affect performance of the different methods. (Reproduced from Godø 1998).

### 5.4 Deviations from basic assumptions

In the following, some documented discrepancies from the basic assumptions of trawl surveys will be presented (based on Anonymous 1998).

**Abiotic factor: the trawl**

The bottom trawl is a conical net bag with a wide mouth fitted with weights on the ground-rope and floats on the head-rope. When the vessel is under way, the net is kept open by two otter boards, wooden or iron structures that are towed by the warps attached forward to their
centre. The two otter boards are connected to the net by bridles. These may be up to 200 m long and sweep the seabed over a wide area. They herd the fish towards the advancing net and so increase its effectiveness. The shape of the net varies, depending on the kinds of fish to be caught and on the types of bottom. The ground-rope may be fitted with roller gear (bobbins) so that the trawl can be used on stony bottom without being damaged. The tail end of the gear from which the captured fish are removed is called the "codend" (Sparre and Venema (1998). Otter trawl are the most widely used type of bottom trawl in commercial fisheries, and owe most of their success to the herding action of the trawl doors and sweeps used (Gunderson 1993).

During the first 20-30 years of standardised trawl surveys, the possibilities for monitoring the geometry and performance of trawls were very limited. Indirect measures of, e.g. warp angles, gave indications of the spread of the doors. But to a great extent, the integrity of survey results remained dependent on the assumption of survey consistency (Anonymous 1998). Studies by Engås and Godø (1989a) on trawl performance of cod catches and on geometry by modern acoustic trawl instrumentation have demonstrated some fundamental disagreements with the basic assumptions and shown that changes in sweeps length can drastically alter both the magnitude and size composition of the catches. Trawl geometry measures, such as wing spread and trawl height, are never constant (Godø and Engås 1989, Koeller 1991). Godø (1998) mentioned two major reasons, among others, that alter the performance of the bottom trawl:

i. The area swept by the trawl increases with depth, and hence density estimates for deep water are systematically overestimated compared with those in shallow water.

ii. Lack of stability in trawl performance, such as unstable bottom contact and error in measured tow duration, were discovered when gear performance was systematically monitored (Engås and Godø 1986, Walsh et al. 1993). Such instability is normally caused by uneven bottom conditions or by the construction or rigging of the gear itself and may contribute substantially to the imprecision of the survey indices.

Although the monitoring of trawl geometry has become standard in many surveys, there is still reluctance to change equipment or procedures to reduce its effects, for cost and operative reasons (Walsh et al. 1993). The main question for stock assessment is to what extent a change in procedures invalidates a survey time series.

It is, however, clearly documented that the original standard procedures created systematic errors in standard survey indices due to, e.g., depth dependent trawl geometry, and random errors due to, e.g., variable trawl performance (Anonymous 1998).

The catching efficiency relates the catch to the actual fish density in the area swept by a trawl tow (Eq. 4). This relationship may be a function of size and/or species. Size and species selection may occur at all stages after the fish appear within the zone influenced by the trawl; e.g. at the doors, sweeps, trawl opening and mesh selection within the trawl. Trawls are indeed very selective sampling gears. Selectivity studies of survey trawls have revealed very strong size and species dependent differences and, in particular, low efficiency for small fish. The loss of small fish occurs both by escapement under the trawl (Engås and Godø 1989a, Dahm and Weinbeck 1992, Walsh 1992, Godø and Walsh 1992, Erich 1987), and in the
sweeping zone of the trawl (Engås and Godø 1989b). When growth rates change over time, inconsistency in time-series of indices of abundance by age arises (Godø and Sunnanå 1992). Such species and size differences will, in many cases, create great uncertainty in ecosystem models that depend on survey results. Nevertheless, due to the unknown effects of selection, it is normally assumed that efficiency is independent of species and size, or at least that efficiency remains constant by species and age.

Godø (1998), in his paper on “What technologies offer to Future Fisheries Scientist”, proposes a set of technological alternatives to obtain better estimates of stock abundance by direct observations, which have been summarised and published by the Research Council of Norway (Anonymous 1998). Those technological solutions to amend biotic and abiotic constraints are presented in the following boxes 1-5 as major bottlenecks:

<table>
<thead>
<tr>
<th>Box 1: Major bottleneck</th>
<th>Box 2: Major bottleneck</th>
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<tbody>
<tr>
<td>Horizontal efficiency</td>
<td>Bottom contact</td>
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</table>
| The opening of the standard sampling trawl is 15-18 m, but the maximum area swept by the gear is the distance between the trawl doors (about 50 m). The efficiency by which the fish is herded to the opening of the trawl is dependent on the swimming capacity of a particular species, usually related to the size of the fish, its hearing and seeing capability, and its reaction to the sand cloud produced by the trawl doors. Some corrections are made today for species dependent sweep efficiency (see Dickson 1993a,b and Aglen 1996), but we still lack a full understanding and quantification of the sweeping process. New studies indicate further density dependent catch efficiency, probably related to schooling behaviour during the herding process (Aglen et al. 1997).
|                         | Selectivity and efficiency of sampling trawls totally depend on the stability of the bottom contact by the ground gear (Engås 1994). Substantial effort has been invested to improve equipment to minimise this problem (Engås and Godø 1989a). Nevertheless, due to, e.g. changing bottom conditions, perfect bottom contact under all conditions is still not obtainable. The effect of instability in bottom contact will increase when tow duration is reduced (Godø et al. 1990). Consequently, if efficiency of surveys is to be improved by shortening tow duration, there is a need for good control of bottom contact. |
| Tried solutions:        | Tried solution:         |
|                         |                         |
| • Comparative hauls with varying sweep angles | • Use acoustic trawl instrumentation (trawl height, door spread) to detect irregularities |
|                         |                         |
| • Comparative trawling with different gears | New suggested solution: |
|                         |                         |
| New suggested solutions: | • Develop a new acoustic trawl sensor to monitor bottom contact. |
|                         |                         |
Biotic factors: natural fish behaviour

The situation is complicated further by the behaviour of the target species in response to the doors and sweeplines, and variability in both of the attack angle of the sweeplines and the nature of the sand cloud when towing over different substrata (Gunderson 1993).

The natural behaviour of fish may affect trawl surveys in many ways. Few of these effects have been studied and none adequately for a quantitative assessment (Anonymous 1998). For trawl surveys, it is normally assumed that fish behave according to certain patterns, and that a standardised survey is not affected or consistently affected from year to year. Two factors, which appear to be of great importance for survey abundance time series, are variation in availability \((q_a)\) and changes in organisation structure such as schooling behaviour.

Variations in availability requires that the survey area completely brackets the geographic distribution of the target population (Gunderson 1993). It is usually necessary to sample well beyond the regions where the fish are present. For example this problem is evident for adult sizes of Merluccius merluccius in the Adriatic Sea that are not accessible to the trawl surveys or to the commercial vessels, due to migration to other geographical or bathymetrical refugium concept expressed by Caddy (1993).

An underlying assumption of trawl surveys requires that all individuals in the survey area are equally vulnerable to the sampling gear, implying that all individuals are assumed to be present in the near bottom area defined by the height of the trawl headrope. For semidemersal fishes as cod and hakes, that assumption leads to considerable bias. Migration patterns often change with size and age, resulting in significant differences in the size composition of the catches as well. Day-night inter calibration coefficients can be calculated to adjust for these effects statistically, but the high variances associated with them often make them unreliable (Gunderson 1993). For northern gadoids, this assumption potentially bias survey results strongly as exemplified for cod (Godø and Wespestad 1993). In some years, the fish are concentrated at the bottom and available for bottom trawling, while in other years much of the stock may be distributed pelagically well above the headline height of the trawl (Godø and Wespestad 1993, Karp and Walters 1994). There are additional complexities due to the uncertainty related to the effective catching height of the trawl (Aglen 1996). Substantial and varying trawl avoidance of pelagically distributed gadoids caused by ship and trawling noise has been observed (Ona and Godø 1990, Nunnallee 1991, Godø and Totland 1996). A substantial body of research on the behaviour of fish in the path of otter trawl has shown that trawl doors, sweeplines, and the mud or sand clouds they produce, present strong auditory and visual stimuli that can actually herd fish or shellfish into the path of the oncoming net (Gunderson 1993.). The problems connected to unavailability may also affect "true" demersal species, such as flatfish, since they may occur high up in water column during certain periods (Metcalfe et al. 1994).

It is well known that bottom trawl catches are highly variable, as demonstrated by repeated tows at same location (Michalsen et al. 1996). Godø et al. (1998) suggested that 5-7 trawl stations at a location were needed to stabilise estimates of density and other stock parameters for gadoids. Seasonal changes in CPUE may be independent of stock abundance as it, e.g., appears to be for the commercial CPUE of cod in the Barents Sea. CPUE seems to change.
very fast over time for unknown reasons. Periods of unexpected low catchability could be caused by unavailability. Acoustic recordings of fish in the pelagic zone would then be expected, though anecdotal information from the fishermen indicates that under such circumstances recordings of fish are scarce. If such changes in catch rates occur, independent of variation in stock level, they might also substantially affect survey indices.

**Box 3. Major bottleneck:**
Initial vertical fish distribution and availability

Since the fraction of the stock of demersal and semi-demersal species at the bottom is quite variable, both on a daily and on a yearly basis, a measured density at a specific location should be followed by an estimate of this fraction. So far, acoustic measurements have been used to compute an availability index, i.e. measuring the proportion of fish in the bottom channel of the echo integrator, 10 m high, to the total. However, the acoustic index has to this day not been integrated with the analysis of the bottom trawl data. This is because of the problems with acoustic measurements very close to the bottom and with the vertical movement of fish during trawling.

Tried solutions:
- Acoustic measurements from ships
- Computing availability for each station
- Combining density estimates from trawling and acoustics

New suggested solutions:
- Double transducer on trawl, looking upwards
- Double transducer on warp restrictor, up/down
- Extensive use of buoy - transducer during trawl passage
- Fish behaviour modelling trawl

**Box 4. Major bottleneck:**
Individual vs. schooling behaviour

It has been speculated that catchability \( (q_e) \) is affected by the internal organisation of the fish, i.e. whether the fish are distributed as single individuals or in patches or schools. Trawl surveys are considered inadequate for measuring abundance of pelagic species due to such effects. Schools react collectively and organise based on group stimuli, while individuals have a more random reaction pattern and a higher escape rate (Godø 1994, Aglen et al. 1997).

Similarly, comparisons of catches from static gears (longline and gillnets) and trawls have shown that trawls might give high catches when static gears are unprofitable and vice versa. Thus, it is quite clear that variations in fish behaviour may cause unforeseen variation in survey CPUE. Quantification of these effects on survey results and even understanding the dynamics of the problem is presently very limited.

Tried solutions:
- Trawl experiment studies of escapement

New suggested solutions:
- Use of multisampling bottom trawl to resolve the small scaled distribution of fish
- Use of silent autonomous vehicles to study small scaled distribution of fish with acoustics
Box 5. Major bottleneck:

Affected fish behavior, efficiency and availability

Fish usually react to an approaching vessel, and more so during trawling, due to the increased noise level. It is expected that fish react strongly within 100 m from the vessel and less strongly from 100 m to 300 m away. Depending on the bottom depth and the vertical distribution of the fish, the reaction can be mainly vertical, pressing the fish to deeper water towards the bottom trawl, or a combination of vertical and horizontal movements. The magnitude and pattern of this behaviour needs to be better understood. The phenomenon affects both bottom and pelagic sampling, and in particular, the consequences on the effective catching height of a bottom trawl should be clarified (Aglen 1996).

Tried solutions:
- Observations from skiff with echo sounder passed by trawling vessel
- Acoustic buoy passed by trawling vessel
- Echo sounder on ROV towed between trawl and vessel

New suggested solutions:
- Scanning sonar on trawl
- Extensive systematic studies from buoy transducer
- Application of autonomous vehicles
- Extensive acoustic tagging experiments
- Split beam and sonar tracking of individual fish response
- Modeling of fish behaviour
5.5 Organisation of a demersal trawl survey campaign

- Estimation of the Total Biomass of selected species.
- Estimation of the Total Biomass and catch rates.
- Collection of environmental and oceanographic data.
- Collection of biological data.
- Estimation of gear selectivity
- Estimation of fishing powers of fishing units.

5.5.1 Check list for the preparation of a survey

1. Information about the surveys area: topographic, atmospheric, fishermen, experiences, etc.
2. Choice of gear regarding target species selected and topographic conditions.
3. Survey design.
4. Allocation of hauls.
5. Possible numbers of hauls. Total number of days available.
   i. Travel time spent to/from selected area.
   ii. Time used for shooting and hauling trawl.
   iii. Time spent between stations.
   iv. Number of hours available per day.
   v. Migration

5.5.2 Data recorded

It depends on setting objectives.
- Log sheets are designed to summarise the **plan of activities** (distribution of duties) for the whole cruise.
- Details of individual station.
- Cover standard form summary information for each haul: vessel position, starting and ending time of hauls, total catch, sub-sampling weight, and species composition.
- Detailed information on the catch. Length, weights, sex, sexual maturation, growth.

5.6 Biomass estimated by the swept area method

This direct method for estimating stock abundance has been developed by Alverson and Pereira (1969) and is described in Sparre and Venema (1998). The swept area is the length of the path times the width of the trawl (Figure 5) and can be estimated from

\[ A = D \cdot ws, \quad D = v \cdot t \]  \hspace{1cm} (6)
where \( v \) is the velocity of the trawl over the bottom swept, \( t \) is the time the trawl is on the bottom, and \( \text{ws} \) is the wing spread of the trawl (the width of the path covered by the trawl). For estimation of the biomass, the CPUA (catch per unit of area) is used.

![Diagram of trawl swept area](image)

**Figure 5.** The swept area (reproduced from Sparre and Venema 1998).

If the exact positions at the start and the end of the haul are available (e.g. from GPS equipment), then the distance covered can be estimated in units of nautical miles (NM) by:

\[
D = 60 \cdot \sqrt{(\text{lat}1 - \text{lat}2)^2 + (\text{lon}1 - \text{lon}2)^2 \cdot \cos^2(0.5 \cdot (\text{lat}1 + \text{lat}2))}
\]

(7)

- \( \text{Lat}1 \) = Latitude at the start of the haul (degrees)
- \( \text{Lat}2 \) = Latitude at the end of the haul (degrees)
- \( \text{Lon}1 \) = Longitude at the start of the haul (degrees)
- \( \text{Lon}2 \) = Longitude at the end of the haul (degrees)

### 5.7 Stratified mean density and confidence intervals

The stratified estimator of mean density in the entire area is calculated as (Cochran 1977; Eq. 5.1, p. 91)

\[
y_{st} = \sum_{i=1}^{L} W_i y_i
\]

(8)

where

- \( L \) is the number of strata,
- \( n_i \) is the number of tows in the \( i^{th} \) stratum,
- \( y_{i,k} \) is the catch by the \( k^{th} \) tow in stratum \( i \),

(normalised to either kg/hour or t/nm\(^2\) = \( \frac{y_{i,k}}{\text{area swept}_{i,k}} \) for biomass estimates),

\[
\bar{y}_i = \frac{\sum_{k=1}^{n_i} y_{i,k}}{n_i}
\]

is the average catch in the \( i^{th} \) stratum, and

---

1 A graphic computer program developed for the NORAD/FAO R/V "Dr. Fridtjof Nansen" surveys which can calculate mean densities and confidence intervals as described in this section is available from the first author Jeppe Kolding.
\[ W_i = \frac{\text{area}_i}{\text{total area}} \] is the proportion of the survey area in the \( i \)th stratum.

The estimated variance of the stratified mean, \( \bar{y}_{st} \), is

\[ \text{var}(\bar{y}_{st}) = \sum_{i=1}^{t} W_i^2 \frac{s_i^2}{n_i}, \]  

(9)

where

\[ s_i^2 = \frac{\sum_{k=1}^{n_i} (y_{i,k} - \bar{y}_i)^2}{n_i - 1}. \]  

(10)

When \( \bar{y}_{st} \) is estimated in kg or t/nm\(^2\), then an estimate of the total biomass in the area is calculated by

\[ B = \bar{y}_{st} \cdot \text{total area} \]  

(11)

5.8 Precision of the estimates of mean density

Estimates based on the sample mean

The estimate of the standard error for each stratum mean is given by

\[ se(\bar{y}_i) = \sqrt{s_i^2}, \]  

(12)

where \( s_i^2 \) is from equation (10).

The standard error of the stratified mean (\( \bar{y}_{st} \), Equation 1), i.e. the square root of the variance of \( \bar{y}_{st} \), is calculated as

\[ se(\bar{y}_{st}) = \sqrt{\text{var}(\bar{y}_{st})}, \]  

(13)

where \( \text{var}(\bar{y}_{st}) \) is defined by Equation (9).

If the sample size is “large” enough, then the Central Limit Theorem states that each time a survey is conducted, there is a 95% chance that the true mean lies in the interval (see Cochran 1977, pp. 39-44 and Chapter 3.4)

\[ \bar{y}_{st} \pm t_{(n-1)\alpha/2}se(\bar{y}_{st}), \]  

(14)

where \( t \) is from Students t-table with (n-1) degrees of freedom and \( \alpha = 0.025 \).
**Estimates of the mean based on lognormal theory - The Pennington estimator**

Because abundance data from marine surveys usually have a large variance (much higher than the mean) and are highly skewed to the right, the sample sizes are typically not large enough; so, that Equation (2) is a valid 95% confidence interval. In fact, the confidence associated with the interval given by Equation (7) is usually much lower than 95% (McConnaughey and Conquest 1992, Conquest *et al.* 1996, Pennington 1996). A major problem with the degree of skewness is the high proportion of zero tows often observed. The development of confidence intervals is complicated by the asymmetric distribution, and the occurrence of zero catches confounds an effective normalisation transformation. Logarithmic transformation will stabilise the variance, but data will still not be normally distributed, and interpretation of re-transformed means is difficult (Pennington and Grosslein 1978).

One way to generate more precise estimates of the mean and more accurate confidence statements for skewed marine data is to base the estimators on the lognormal Delta distribution (Pennington 1983, 1996, Conquest *et al.* 1996), in which catches are divided into zero and non-zero units, followed by transformation of the non-zero values to natural logarithms. When it is found that the transformed non-zero data are approximated by a lognormal distribution (*i.e.* the logged values are normally distributed), then a more efficient estimator of mean density, $c_i$, within each stratum is given by (Pennington 1983, 1996)

$$
c_i = \frac{m_i}{n_i} \exp(\bar{x}_i) G_m\left(\frac{s_{x,i}^2}{2}\right),
$$

(15)

where

- $m_i$ is the number of sample values greater than 0 in stratum $i$,
- $\bar{x}_i$ and $s_{x,i}^2$ are the mean and variance, respectively, of the logged values of catches greater than 0, and
- $G_m(f)$ is an infinite series function of $m$ and $f$ [*for example, $m = m_i$ and $f = s_{x,i}^2 / 2$ in Equation (15)*] which is used to correct for bias in re-transformation from log to arithmetic scale and is defined by

$$
G_m(f) = 1 + \frac{m-1}{m} f + \sum_{j=2}^{\infty} \frac{(m-1)^{j-1} f^j}{m^j (m+1)(m+3) \cdots (m+2j-3) j!}
$$

(16)

The variance of $c_i$ is given by

$$
\text{var}(c_i) = \frac{m_i}{n_i} \exp(2\bar{x}_i) \left\{ \frac{m_i}{n_i} G_m\left(\frac{s_{x,i}^2}{2}\right) - \frac{(m_i - 1)}{(n_i - 1)} G_m\left(\frac{m_i - 2}{m_i - 1} s_{x,i}^2\right) \right\}
$$

(17)
**The modified Pennington estimator**

In contrast to estimates based on the sample mean (Equation 8 and 9), which are highly sensitive to a single or a few isolated high catch rates that may account for more than 50% of the total catch, Pennington’s estimator (Equation 15, and 17) is sensitive to low catch rates. These contribute little to the total catch but, when log-transformed, may give large negative values resulting in a distribution skewed to the left. In such a case, a more precise estimator of mean density within each stratum, \( \hat{\mu}_i \) (modified from Pennington 1983, 1996) is given by

\[
\hat{\mu}_i = \frac{(n_i - m_i)}{n_i} \bar{y}'_i + \frac{m_i}{n_i} \exp(\bar{x}_i) G_{nm}(\sigma_{\bar{x}_i}^2 / 2),
\]

where

- \( m_i \) is the number of sample values greater than a defined ‘cut-level’ (rather than 0 as in Equation (15) in stratum \( i \)),
- \( \bar{y}'_i \) denotes the arithmetic mean of the non-transformed values less than the cut-level, and
- \( \bar{x}_i \) and \( \sigma_{\bar{x}_i}^2 \) are the mean and variance, respectively, of the logged values of catches greater than the cut-level.

The variance of \( \hat{\mu}_i \) is given by

\[
\text{var}(\hat{\mu}_i) = \text{var}(c_i) + \left( \frac{n_i - m_i - 1}{n_i(n_i - 1)} \right) s_i^2 + \left( \frac{m_i(n_i - m_i)}{n_i^2(n_i - 1)} \right) \bar{y}'_i^2 - 2 \left( \frac{n_i - m_i}{n_i(n_i - 1)} \right) \bar{y}'_i \times c_i,
\]

where

- \( s_i^2 \) is the variance of the values less than the cut-level (Equation 10), and
- \( c_i \) and \( \text{var}(c_i) \) are Equations (15) and (17) with \( m_i \) bigger than the cut-level.

There is no single objective criterion upon which to define a cut-level bigger than zero. Basically, the logged Delta distribution should be viewed (e.g. in NANSIS GRAFER) in order to determine if it is skewed to the left and/or contains isolated small catches. As a ‘rule of thumb’ (Pennington pers. com.), the cut-level should be set as \( \max(2\bar{x}_i - x_{\max}) \), where \( \bar{x}_i \) and \( x_{\max} \) are the mean and the largest value, respectively, of the logged values of catches greater than 0.

**5.9 Stratified mean and confidence interval based on lognormal theory**

The stratified estimate of mean density (denoted by \( \hat{\mu}_{st} \)) in the entire area is calculated by replacing \( \bar{y}_i \) with \( \hat{\mu}_i \) for each stratum in Equation (8). The standard error of \( \hat{\mu}_{st} \) is obtained by substituting \( \text{var}(\hat{\mu}_i) \) for \( s_i^2 / n_i \) (which equals \( \text{var}(\bar{y}_i) \)) in Equation (9) and then

\[
\text{se}(\hat{\mu}_{st}) = \sqrt{\text{var}(\hat{\mu}_{st})}
\]
Sometimes, the \( \hat{\mu}_{st} \)-estimator is higher than the one based on the sample mean. This is because, given the sample sizes typical for marine surveys, the sample mean tends to underestimate the true mean most of the time for these highly skewed distributions (Pennington 1983, 1996, Conquest et al. 1996).

An approximate 95% confidence interval for \( \hat{\mu}_{st} \) is given by

\[
\hat{\mu}_{st} \pm t_{(n-1),se(\hat{\mu}_{st})}
\]

5.10 Estimation of maximum sustainable yield based on biomass estimates

1. Gulland’s formula for virgin stocks or poorly exploited stocks:

\[
MSY = 0.5 \cdot M \cdot B_0
\]  

(22)

where \( M \) is the natural mortality rate per year and \( B_0 \) is the virgin stock biomass

2. Cadima’s formula for exploited stocks

\[
MSY = 0.5 \cdot Z \cdot \overline{B} = 0.5 \cdot (Y + M \cdot \overline{B})
\]  

(23)

where \( Z \) it the total mortality rate per year, \( Y \) is the annual yield.
6 Age and growth

6.1 Age

Most of the variables in analytic population dynamics are defined as rates, e.g.:

\[
\begin{align*}
\text{changes in length or weight} & = \frac{dL}{dt} \quad \text{or} \quad \frac{dW}{dt} \\
\text{changes in numbers} & = \frac{dN}{dt} \\
\text{changes in biomass or yield} & = \frac{dB}{dt} \quad \text{or} \quad \frac{dY}{dt}
\end{align*}
\]

They are all values per time unit. Consequently, a measure of time, at least in relative terms, is needed. Age or relative age of the fish, by length, weight, numbers, etc., is used to determine the time scale over which the various processes have taken place. The determination of age is therefore a central prerequisite for further computations in analytical stock assessment models.

There are three approaches or methods for ageing fish, each with its particular advantages and disadvantages:

- Direct observations of individual fish, either held in confinement or from marking/recapture experiments.
- Ageing of individual fish based on annual patterns in hard structures e.g. otoliths, scales, bones etc.
- Identification of cohorts based on length frequency distributions from one or several samples representing a wide range of the population.

The first method is by far the oldest, initially described by fish culturists more than 250 years ago (Bagenal 1978). The inherent problem of this approach is the problematic extrapolation from observed values to the true population values. Cultivated or tagged fish seldom have the same growth rate as their wild or untagged relatives.

The second approach is now the preferred and most widely used method. It is based on the observation that temporal variations in the growth rate of the fish are reflected in the deposition of material in the hard parts. This leads to alternating bands or growth zones of varying transparency. In temperate waters, where the growth rates are closely correlated with the change of seasons, these bands correspond to annuli, i.e. one may count the zones, and because a set of zones is formed each year, one obtains an estimate of absolute age. Annual growth cycles are seldom as pronounced in subtropical and tropical waters, but the formation of zones may depend on other stimuli such as monsoons, river outlets, food supply, stock density, spawning, etc. These zones are often unclear, a problem that makes the method inapplicable in most cases. The discovery by Pannella (1971) of minute growth zones in many species, including tropical, with a frequency of about 360 per year, has now led to a method with which these zones are counted and regarded as daily growth zones. The
application seems very promising, but requires a good microscope and remains very labour demanding.

The third approach is based on an analysis of modes (peaks) in a length frequency distribution. Most species seem to be spawning regularly and during a relatively short period of time. If the progeny exhibit a roughly uniform growth rate, it is assumed that each mode in a length distribution represents a separate cohort. The method requires lengths of a large number and size range of fish from the population and little overlap in the sizes of fish from adjacent age groups. This last requirement is usually only met in the younger part of the population because the growth rates decrease with age, so the modes (cohorts) tend to merge. This method has been given increasing attention, partly because it is often the only alternative for tropical stocks, but also because the necessary data are easily obtained and the handling of big samples have become easy thanks to the introduction of computerised techniques.

**Definition and designation of age:**

Note the important distinction between 'age group or cohort' and 'year-class':

- **Age group or cohort** refers to the actual age in years and contains fish of the same age, regardless of the year in which they were born.
- **Year-class** refers to the group of fish produced in a particular year.(E.g. 1981-yearclass, 1982-year-class...). Hence, two fishes belonging to the same age group also belong to the same year-class. As they grow older, they will belong to progressively older age groups, but remain in the same year-class.

A consistent system is needed for designation of age, regardless of the method used for age determination. Unfortunately, there is not yet complete agreement on such a system and its terminology.

By common usage, the fish are designated by reference to annual marks:

- A fish in its first growing season belongs to age-group 0
- A fish in its second growing season belongs to age-group 1 or simply age 1 and so on.

It has been proposed and has become more or less generally accepted, that 1st January is the date in which age designation changes. This is in the northern hemisphere. In the southern hemisphere, it would correspond to 1st July.

The two first methods of ageing fish are not part of this course. In this study, only the ageing of fish from length frequency analysis will be covered.

**6.2 Length frequency analysis**

**Background.** These methods are based on the observation that the length composition of a population often exhibits modes (peaks) among the younger age groups. The particular shape
is the result of recruitment, growth, mortality and sampling (which may be biased by
selectivity or the distribution of the sampled fish).

The basic assumption underlying the statistical approaches to length frequency analysis is
that, the seasonal variations in the spawning pattern are so pronounced that the modal
distribution is equivalent to a recruitment frequency diagram. In other words, the particular
stock to be analysed must each year or season exhibit a birth frequency distribution of
approximately the same pattern and with a distinct modal shape.

The basic unit in frequency analysis are the *cohorts*, i.e. a batch of specimens of
approximately the same age that have entered the stock and which by size/age can be
discriminated from the rest of the stock. Temperate species almost always have one annual
spawning, so here the cohorts are equivalent to the year classes, and the recruitment period
and the time of maximum recruitment is easily identifiable. Tropical, or sub-tropical, species
are more complex with extended or several annual spawning seasons. Still, in most cases it is
possible to identify local maxima and minima as a result of concentrated spawning periods,
and the number and extent of recruitment periods can be defined. There may be tropical
stocks with 3, 4 or more peaks in the annual recruitment frequency, but, normally, it is
possible to determine one or two intensive periods and consider the less intensive periods as
insignificant.

The *birthday* of a single fish in a cohort is considered as a random variable within the range
of a spawning period and with the probability function approximating a normal distribution
(Gaussian distribution). It is furthermore assumed that the growth in length is a random
variable (i.e. each individual has its own set of growth parameters; \( L \), \( K \) and \( t_0 \) if the the
von Bertalanffy's growth function is adopted), but with the same probability function, i.e. a
normal distribution.

Therefore, because of different birthdays, the individuals within a cohort do not have exactly
the same age at the same time, and because of different growth, the individuals also do not
have the same length at the same age. As a result, a certain spread in lengths is expected.

Figure 6 shows eleven different life histories corresponding to eleven different sets of growth
parameters and eleven different birthdays. The figure also shows the death process. In real
populations, it will never be possible, of course, to measure all individuals and also never the
same fish more than once, but the figure shows the principles of the data collected from
samples.
Figure 6. Life histories of eleven fish.

Figure 7 shows the same situation with ten length distributions of a cohort taken at different times and measured from a bigger sample. The curve drawn through the means represents the average growth of the cohort over time. A composite length frequency distribution is in principle exactly the same situation where the separate components (distributions) are merged and each represents a separate cohort instead of one cohort followed over time.

Figure 7. Observed length distributions and growth of a cohort of *Oreochromis niloticus* (Nile tilapia) born on 3\(^{rd}\) August 1995.
To sum up: the growth of individuals from a cohort as a function of age is considered a random variable because the birthday \( t_b \) is a random variable and because the growth parameters \( (L, K, \text{and } t_a) \) are random variables. But, since it is assumed that both birth and growth parameters are normally distributed, the probability distribution of individual growth within a cohort is also normally distributed.

**The normal distribution:**

A normal distribution can be described by 3 parameters (see Excel sheet 'Normal distribution.xls'):

\[
f(x) = \frac{N \cdot dl}{SD \cdot \sqrt{2\pi}} \cdot \exp\left(-\frac{(x - \bar{x})^2}{2 \cdot SD^2}\right)
\] (1)

1) The number in the distribution \( (N) \)
2) The variance \( (S^2) \) or standard variation \( (SD) \)
3) The mean value \( (\bar{x}) \)

\( dl \) is the step length or length interval of the frequencies

In a composite length distribution, i.e. a merging of several length distributions of different cohorts, the problems are:

- To find the number of normal distributions
- To find \( N, \bar{x}, \) and \( SD \) of each distribution

This is exactly the same information that needs to be extracted from a length frequency distribution:

- How many cohorts (year classes) are represented in the sample?
- How big is the relative contribution of each cohort \( (N) \) in the sample?
- What is the mean length \( (\bar{x}) \) of each cohort?

**Methods**

There are several methods for finding the number of cohorts, their relative contribution, and the mean length of each cohort at different times in one or several composite length frequency distributions:

Visual methods
- The 'Petersen' method.
- Modal progression analysis.

Graphical methods:
- Bhattacharya method
- Cassie method
- (Tanaka method (parabola method))

Computerised versions:
- NORMSEP (FORTRAN)
• MIX (FORTRAN)
• ELEFAN I. V (BASIC)
• LFSA (BASIC)
• FiSAT (BASIC)

These and others are presently undergoing modifications and further development.

The first two are simple visual approaches, requiring only common sense in interpretation. The others are more objective attempts, in the sense that they try to apply the mathematical properties of the underlying models. Most of the methods assume a normal distribution of size at age. The advanced computerised versions are, furthermore, constraining the data set by applying the simple or seasonal Von Bertalanffy Growth Function (VBGF).

All methods require that:

• The sampling is conducted in a relatively short time span.
• The species has a spawning pattern that makes it possible to determine separate peaks of recruitment.
• Every cohort has a uni-modal distribution pattern.

Visual methods

**The Petersen method (1892).** This is the simplest, fastest but inherently also the most inaccurate of the methods. It assumes that:

• Length at age varies around a single mean value.
• Fish of the same length have approximately the same age.

Then, by simply counting the number of discernible modes and relating these to the respective lengths and frequencies, a rough estimate of the numbers and mean length of each cohort is obtained. Care must be taken that the modes in fact belong to successive age groups and not to dominating cohorts separated by more scarce broods.

**The modal progression analysis (MPA).** This is also a visual analysis, but based on a series of samples from the same population taken at known time intervals. The method is particularly applicable for short-lived species or for species which show considerable variation in cohort abundance (the method is especially useful with shrimps). When arranging the samples on the same length scale one over the other in successive order and with their relative distances proportional to the time span in sampling sessions, it may be possible to follow the progress of one or several dominant cohorts over length. By measuring or calculating the means, a direct impression of the growth is obtained. If, in addition, information of the approximate time of spawning or age at recruitment, ages to the lengths can be designated. This also applies with the Petersen method. Visual (subjective) MPA is also used for connecting mean length over time after having estimated the number of cohorts and their mean length from one of the graphical methods (e.g. Bhattacharya).
Graphical methods

**Bhattacharya method.** This method is based on:

- Assumed normal distributions of the components in a composite length frequency distribution.
- Transformation of the normal distributions into straight lines.
- Calculation of $N$, $\bar{x}$, and $SD$ by regression analysis.

A normal distribution can be transformed into a straight line by the following steps:

1) Taking the logarithms of the function value

$$\ln(f(x)) = \ln\left(\frac{N \cdot dl}{SD \cdot \sqrt{2\pi}} \cdot \exp\left(-\frac{(x - \bar{x})^2}{2 \cdot SD^2}\right)\right)$$  \hspace{1cm} (2)

By plotting these new function values against the independent value $x$, a parabola is obtained (Figure 8).

![Converting a normal distribution to a straight line](chart.png)

**Figure 8.** Converting a normal distribution (data in Figure 1) into a straight line

2) The parabola can be transformed into a straight line by calculating the difference of two adjacent function values $y = \ln(f(x+dl)) - \ln(f(x))$ and plotting this against a new independent value $z = x + dl/2$

3) The linear regression through these points has the properties that the intercept
This regression is the main element of the Bhattacharya method. When the frequencies in the length intervals \((dl)\) are assumed to be normally distributed, they are regarded as the function values. Then, by the use of the logarithms of the frequencies, computing the difference of two adjacent pairs by subtraction (i.e. \((\ln(dl+1) - \ln(dl))\)), and by plottings of the difference against the upper limit of \(dl\), a scatter diagram that can be linearised by regression is obtained. The intercept and slope of the regression line will then be an estimate of the corresponding values of the true normal distribution, approximating the frequency distribution.

In a composite length frequency distribution with several more or less overlapping normally distributed components, the procedure is to identify and calculate the relative contribution of each component step by step. In other words, one component at a time must be isolated:

1. Find the mean and variance of the first component by the above method
2. Use these figures to calculate the theoretical number of elements in each interval of the first component (this is only necessary in the overlapping length intervals of the first and second component)
3. Subtract these values from the elements in the sample, so the sample now is composed of all parts minus the first component
4. Repeat the whole procedure with the second component (which in fact now has become the 'first')
5. Repeat as long as proper identification of components is possible

Table 1 shows the calculations required for a Bhattacharya plot (Figure 9) to obtain the normally distributed components of a composite length frequency distribution.
### Table 1. Estimation of the first cohort, N1 from a composite length frequency distribution by means of the Bhattacharya method, and the total minus N1 = N2+. The arrow indicates where to start the calculation of N1 (modified from Sparre and Venema 1998).

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<td>0.00</td>
<td>50</td>
<td></td>
<td></td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>51-52</td>
<td>1</td>
<td>0.00</td>
<td>-0.69</td>
<td>51</td>
<td></td>
<td></td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

- **Column A** represents the length intervals.
- **Column B** is the frequency distribution of elements in each interval (called N1+ to indicate that it consists of the first component N1 + the rest. N1 is the component that needs to be isolated).
- **Column C** gives the logarithmic values.
- **Column D** gives the differences of the logarithmic values between two adjacent intervals.
- **Column E** gives the length against which the values of column D should be plotted (i.e. the upper limit of the smallest length group).
- **Column F** gives the calculated (theoretical) values of the differences of the logarithmic values between two adjacent intervals, obtained by insertion into the regressed line equation.
**Column G** is a back calculation to the logarithmic values of the frequencies in the first component (N1), obtained by choosing a clean value (i.e. a value where the elements are considered only to belong to N1) and adding the calculated values of the differences step-wise forward. By this, an estimate of the number of elements in each interval, which only belong to N1, is obtained.

**Column H** is the anti-logarithm of the values in column G, i.e. the frequencies of N1 now adjusted to conform to a normal distribution.

**Column I** gives the frequencies of N2+, i.e. the components of N1 have been subtracted. The idea now is to repeat the whole procedure with N2+ in order to isolate N2 and so on.

![Bhattacharya plot](image)

**Figure 9.** Bhattacharya plot corresponding to columns D and E of Table 1, and regression line estimated for the first cohort N1 with the intercept \( a = 5.33 \) and the slope \( b = -0.306 \). The calculated values of column F are obtained by inserting the independent value \( x = \) upper limit of the smallest of two adjacent length groups in the equation: \( y = a + bx \).

The points used for regression are selected on two criteria:

1. Visual inspection of the scatter diagram, identifying those points in the beginning approximating a straight line. This line corresponds to the first normally distributed component, which is interpreted as the N1 cohort. (That the straight line corresponding to N1 comes out so nicely in this example is not surprising when the length frequency histogram is considered (Figure 9), where the first component has very little overlap with its neighbouring component).

2. Also an inspection of the slope, the intercept with length axis, and the first and last point used in regression will give an indication of the mean and range of the elements.
belonging to the examined component, which can be compared to conform with the configuration of the frequency distribution.

Computerised versions of length frequency analysis:

This is only a brief superficial presentation of some of the approaches developed:
ELEFAN (Electronic LEngth Frequency ANalysis) developed by Pauly and David (1981) and with later refinements and extensions (ELEFAN I, IV). (BASIC)

LFSA (Length Frequency Stock Assessment) developed by P. Sparre (1987a) (BASIC).

The MAXIMUM-LIKELIHOOD-METHOD: NORMSEP developed by Tomlinson (1971) and later extensions and modifications by MacDonald and Pitcher (1979), Schnute and Fournier (1980) and Sparre (1987b). (FORTRAN)

FiSAT (FAO/ICLARM Stock Assessment Tools) (Gayanilo and Pauly 1997) is a package combining ELEFAN and LFSA together with additional features and a more user-friendly interface. FiSAT is presently being converted into the Windows platform.

The ELEFAN method is basically a modal progression analysis. However, if a time series of samples is not available, it can simulate a series by assuming that all cohorts follow the same recruitment and growth pattern and allocate a set of VBGF growth parameters to the sample. To estimate the set of growth parameters which best "fits" a set of length frequency data, ELEFAN I does the following (Ingles and Pauly 1984):

1. "Restructures" the length frequency sample(s) that are entered, so that small but clearly identifiable peaks are attributed a number of "points" similar to peaks based on a large number of fishes. The procedure used here essentially consists of calculating running average frequencies (over 5 length classes), dividing each length-frequency value by the corresponding running average frequency, then subtracting 1 from the quotient. A few minor adjustments are then made to prevent certain types of samples from generating biases.

2. Calculates the maximum sum of points "available" in a (set of) length frequency sample(s), where "available points" refer to points which can possibly be "accumulated" by one single growth curve. This sum is termed "available sum of peaks" (ASP).

3. "Traces" through the (set of) length frequency sample(s) sequentially arranged in time, for any arbitrary "seed" input of L∞ and K, a series of growth curves started from the base of each of the peaks, and projected backwards and forwards in time to meet all other samples of the sample set and/or the same sample repeated again and again.

4. Accumulates the "points" obtained by each growth curve when passing through peaks (positive points) or through the troughs separating peaks (negative points).
5. Selects the curve which, by passing through most peaks and avoiding most troughs, best "explains" the peaks in the (set of) sample(s) and therefore, accumulates the largest sum of points. This new sum is called "explained sum of peaks" (ESP).

6. Increases or decreases the "seeded" values of $L_\infty$ and $K$ until the ratio ESP/ASP reaches a maximum, and outputs the growth parameters corresponding to this optimum ratio.

The validity of this procedure rests on the following assumptions: Note that it does not assume normal distribution.

- That the sample(s) used represents the population investigated.
- That the growth pattern in the population is the same from year to year.
- That the VBGF describes the average growth of the investigated stock.
- That all fishes in the (set of) sample(s) have the same length at age and that therefore, differences in length can be attributed to differences in age.

The LFSA can be considered as a computer-assisted version of the Bhattacharya method, with the underlying assumption (model) that the length frequency distribution of each cohort is normally distributed. It is like ELEFAN, a package of BASIC programs, primarily intended for tropical fish stock assessment, where the emphasis is placed on the analysis of time series of length frequency samples.

The maximum-likelihood-method can also be considered as a computer-assisted version of the Bhattacharya method. The term stands for a statistical estimation procedure which uses the weighted sum of squares of deviations between the model and the observations as a measure of goodness of fit, the so-called chi-squared criterion (ELEFAN uses the ratio ESP/ASP). The basic idea is the same as for ELEFAN, to follow the progression of modes and testing a large number of alternative growth parameters and assigning values to the parameters so that the observations are given maximum likelihood. But in contrast to ELEFAN, it requires that the number of cohorts is known (which might be guessed or achieved by lumping the oldest age groups into a single group). They both produce, as output, a set of growth parameters ($L_\infty$, $K$ and $to/Ao$), and the latter, furthermore, provides the numbers and variance of the normally distributed components ($N1, N2 \ldots, S1, S2\ldots$).

**Limitations of length frequency analysis**

It is sometimes difficult to separate the components of a composite frequency distribution. This applies especially to the older parts where the overlaps become increasingly bigger. Recall that a normal distribution was characterised by the three variables: numbers, mean value and variance. Intuitively, one would expect that proper identification and resolving would become troublesome when either the mean values are lying relatively close or when increasing variance will extend the overlapping areas or a combination of both. To assess the reliability of resolving the components, a separation index has been introduced and is an automatic feature in the Bhattacharya method implemented in FiSAT.
\[ I = \frac{\overline{L}_{a+1} - \overline{L}_a}{(SD_{a+1} + SD_a)/2} \]  

(3)

Where $\overline{L}$ stands for the mean value and $SD$ for the standard deviation, $a$ and $a+1$ are two adjacent components.

When applying this separation index the general rule of thumb is:

- If the separation index ($I$) is less than 2 it is more or less impossible to properly separate the two components.

This conclusion holds for all methods, including the most sophisticated computerised versions.

6.3 Growth

Growth in its broadest sense, i.e. a change in biomass due to both change in numbers from recruitment and mortality and increment in weight, is a phenomenon of primary interest in studies concerning production of animals and plants.

The growth of a population or an individual is often represented by mathematical models describing the average change per unit of time. Well known examples are the logistic equation for population growth in numbers (see section on biomass dynamic models and section on ecological concepts) and the Von Bertalanffy Growth Function (VBGF) (Bertalanffy 1938) for individual growth in length or weight. These simple functions are often used because they, to a certain extent, correspond to a real situation, but also because they are easy to manipulate mathematically, and to combine into bigger and more comprehensive models of the systems.

Once validated age determinations have been achieved, the study of growth appears superficially to be simple, but in practice there are numerous difficulties. First, it must again be evaluated if the sampling yields representative results, taking into consideration that:

- Many fish stocks congregate in schools that are determined by sizes more than ages.
- Fishing- and natural mortality is often size selective so that the true average population growth rate might differ from the sampled individuals.

There are two types of growth to be considered:

1. Population growth in numbers or weight
2. Individual growth in length or weight
Population growth depends on the combination of natality (birth rate), mortality rate and immigrations/emigrations, and when weight is considered, also on the sum of individual growth increments.

Individual growth is within wide limits determined genetically, but is influenced by several factors:

- Food availability (quality/quantity)
- Temperature (fish are poikilotherms)
- Variable allocation of surplus energy (somatic or gonadal tissue growth and/or for locomotion and maintenance)
- Sexual differences
- Density and size distribution (hierarchical behaviour and/or competition)

The determination of growth of a single fish is therefore of little use. What is needed is some measure of mean size at age and a method of modelling or estimating the average growth rate of a species or particular stock. This is based on the assumption that although individual growth differs, there are reasonably confined limits to the range of growth rates at age in a particular habitat. Also, fish are generally considered to grow indefinitely (i.e. growth never ceases completely), but with continuously decreasing rates with age. Therefore, what is required, is a large and representative material in both numbers and age range to carry out growth calculations.

**Approaches to growth estimation**

These can be divided into nearly the same categories as age determinations:

- Direct observations from experiments of either confined or tagged/recaptured fish. Unless one is specifically dealing with cultured stocks, the first approach is questionable. The estimates are of doubtful value when extrapolating to wild stocks because of the difficulties in simulating natural conditions. The second approach must be evaluated with extreme care to insure that the actual marking method is not affecting health, behaviour or mobility. Only few of actual marking methods cause little or no retardation of growth.

- Length-at-age data. With precise and valid age determination and a large unbiased random sample, this is the most satisfactory method.

- Back calculations from analysis of hard parts, using the ratios between the lengths of fish and the spacing between the growth zones of the otoliths, scales etc. This approach is often used. It requires certain assumptions about constant iso- or allometric growth to be fulfilled.

- Estimating average length at arbitrary age from length frequency analysis (statistical) with known or assumed periodicity. This is often the only alternative when dealing with tropical or other stocks not exhibiting a regular zone pattern in their hard parts. It
is, of course, subject to the same assumptions underlying the applied length frequency analysis.

Some methods give growth of individual fish (which can be averaged), and other methods provide average growth of populations. Both are valid estimates but of different things. This should be realised and related to the objectives of the growth study when deciding on a method.

**Growth parameters**

There are several different definitions of growth expressed as rates. The simplest assumes a linear growth rate within the time interval of concern \([t_1, t_2]\). These include the following expressions:

**Absolute growth rate**: Change in weight/length per time unit, usually per year.

\[
g(t) = \frac{W_2 - W_1}{t_2 - t_1} = \frac{\Delta W}{\Delta t} \quad \text{(4)}
\]

**Relative growth rate**: Change in weight/length per time unit relative to start value in percent.

\[
g(t) = \frac{W_2 - W_1}{W_1} \cdot 100 \quad \text{(5)}
\]

**Instantaneous growth rate**: When the time interval becomes infinitely small, i.e. a differential equation.

\[
\frac{\Delta W}{\Delta t} = \frac{dW}{dt} \quad \text{when } t \to 0 \quad \text{(6)}
\]

When studying growth over shorter time intervals (less than one year), and when studying juveniles, one usually finds that the growth rate is exponential and can be expressed as an instantaneous rate as follows

\[
G = \frac{\ln(W_2) - \ln(W_1)}{t_2 - t_1} \quad \text{(7)}
\]

When this rate is multiplied by 100, it is called the **specific growth rate** and it is given in %. Eq. (7) can be transformed into an exponential growth model.

\[
W_2 = W_1 \cdot e^{G(t_2 - t_1)} \quad \text{(8)}
\]
**The Von Bertalanffy Growth Function (VBGF)**

Empirically, it is mostly observed that when length of a fish, crustacean or lammellibranch is plotted against age the result is a curve with continuously decreasing slope approaching an upper asymptote (Figure 10).

![A growth trajectory in length](image)

**Figure 10.** Example of a growth curve in length.

This is taken as an indication that the increase in length is a function of length. So when plotting the increments of length against the length with equal time intervals the result is often a scatter diagram which closely approaches a straight line (Figure 11).

![dL/dt as a function of mean length](image)

**Figure 11.** Example of a Gulland and Holt plot of growth rate against length.
Thus, one has a linear relation of growth rate in length to mean length. This can be inserted in a differential growth expression:

\[
\frac{dL}{dt} = a + b \cdot L_i
\]  \hspace{1cm} (9)

which means that the instantaneous growth rate is directly proportional to the length. If \(a\) is substituted with \(KL\) and \(b\) with \(-K\), the following is obtained:

\[
\frac{dL}{dt} = K \cdot (L_\infty - L_i)
\]  \hspace{1cm} (10)

This equation can be integrated:

\[
\frac{dL}{L_\infty - L_i} = K \cdot dt \quad \Rightarrow \quad \ln(L_\infty - L_i) = Kt + \text{const} \quad \Rightarrow
\]

\[
L_\infty - L_i = e^{-Kt} \cdot \text{const} \quad \Rightarrow \quad L_i = L_\infty - e^{-Kt} \cdot \text{const}
\]  \hspace{1cm} (11)

Let \(t_0\) be the theoretical age at which \(L = 0\), then by inserting in Eq. (11), one obtains:

\[
0 = L_\infty - e^{-Kt_0} \cdot \text{const} \quad \Rightarrow \quad \text{const} = L_\infty \cdot e^{-Kt_0}
\]  \hspace{1cm} (12)

this is used for substituting in Eq. (11):

\[
L_i = L_\infty - \left(L_\infty \cdot e^{-Kt_0}\right) \cdot e^{-Kt}
\]

or

\[
L_i = L_\infty \left(1 - e^{-K(t-t_0)}\right)
\]  \hspace{1cm} (13)

This is one version of the Von Bertalanffy Growth Function (VBGF) for length (see Excel sheet ‘VBGF-iteration.xls’).

Alternatively, as originally done by von Bertalanffy, the VBGF can be derived from bio-energetic principles where changes in weight (or production of tissue) is the difference between anabolism and catabolism

\[
\frac{dw}{dt} = H_s - kw
\]  \hspace{1cm} (14)

\(H_s\) represents the anabolism proportional with the physiological surface in a fish (as all absorption of either food or oxygen is a function of surface of the gut or surface of the gills). \(kw\) represents the catabolism which is proportional to the weight or volume as these processes are taking place intra-cellularly. Assuming the surface is proportional to the squared length and the weight or volume is proportional to the cubed length, one obtains

\[
s = pL^2 \quad \text{and} \quad w = qL^3
\]  \hspace{1cm} (15)
where \( p \) and \( q \) are constants. Using this expression for \( w \) then

\[
\frac{dw}{dt} = \frac{d(qL^3)}{dt}
\]  

(16)

which can be derived according to the chain rule of derivation giving

\[
\frac{dw}{dt} = \frac{dw}{dL} \cdot \frac{dL}{dt} = 3qL^2 \frac{dl}{dt}
\]  

(17)

Inserting Eq. (17) into (14) and substituting with (15), one obtains

\[
3qL^2 \frac{dL}{dt} = HpL^3 - kqL^3 \quad \Rightarrow \quad \frac{dL}{dt} = E - KL
\]  

(18)

where \( E = \frac{Hp}{3q} \) and \( K = \frac{k}{3} \)

This expression is the same as Eq. (9) and can be integrated as above.

**Estimation of parameters**

\( L_\infty , K \) and \( t_o \) are the three parameters that are needed to know to fit the VBGF:

\( L_\infty \) is called "L-infinity" or the "asymptotic length", representing the maximum length of an infinitely old fish of the given stock. \( L_\infty \) can be estimated from graphical plots (Ford-Walford, Gulland and Holt etc.), or it can be approximated by the mean of a selection of the biggest specimens recorded from the population, or by relation \( L_\infty \approx L_{max}/0.95 \).

\( K \) is called the "curvature parameter". It determines how fast the growth is, i.e. how fast the fish reaches its maximum size. An estimate of \( K \) is calculated from the slopes of the different graphical plots (e.g. Figure 11). Note that \( K \) is not a growth rate; it has only the unit ‘per time’. Different \( K \)'s cannot be compared when \( L_\infty \) is also different!

\( t_o \) is called "t-zero" or the "initial condition factor", It gives the start of the curve, i.e. where the theoretical length is zero. It is calculated by inserting \( L_\infty \) and \( K \) in the equation for a known length at age \( t \)

\[
t_o = \frac{1}{K} \ln \left( \frac{L_\infty - L_i}{L_\infty} \right) + t
\]  

(19)

or it can be estimated graphically from a von Bertalanffy plot.

Usually \( t_o \) is a small negative number, which is absurd in a biological sense. This is because \( L_o \) also is a problematic concept biologically when applied to the von Bertalanffy growth
model. The ontogeny of a fish is characterised by different developmental stages in the early parts of the life: egg-stage, larval-stage and metamorphosis before entering the juvenile adult form. In these early stages the VBGF does not apply and the length is, therefore, not zero at the time when the growth starts to conform to the model. But the curve must have a fixed starting point in order to operate with absolute time, and this is why it is called the initial condition factor. Therefore, regard $t_0$ as only a theoretical value, where the length-zero and time-zero have no true biological interpretations.

The VBGF parameters can also be derived from length frequency analysis where no absolute age determinations are present, but in this case the above version may not be used. The parameter time in known units has to be replaced by something else - an arbitrary age or relative age (Pauly 1984). When it is possible to split a composite distribution into some of its components, employing one of the methods described, and under the assumption that the recruitment pattern is regular, i.e. that the spawning, whether annual or sub-annual, is confined within certain specified intervals, then an arbitrary age to the first cohort $A(i)$ may be assigned. From the known sampling times, this cohort can be followed over the sampling period (modal progression analysis). A Gulland and Holt plot (Figure 11) of length increment over time (sampling interval) against length can then be performed to estimate $L_\infty$ and $K$.

Since the arbitrary age $A(i)$ will deviate from the absolute age $t(i)$ by a constant then $t_0(i)$ will deviate from $A_0(i)$ with the same constant and, hence, $A_0(i)$ is a constant. Thus, the length as a function of absolute age may as well be considered as a function of arbitrary age, and the growth equation written like this:

$$L_{A(i)} = L_\infty \left(1 - e^{-K(t(i) - A_0(i))}\right)$$ (20)

In order to use this equation to predict a length at a given time, one must somehow approximate $A_0$ to $t_0$. This is only possible if the biology of the stock is known, i.e. the development phases of progeny and the approximate recruitment time. The $t_0$ can also be estimated from maturity investigations.

In most length-based stock assessment models, however, interest lies only in relative age and not in absolute age. Further, when the time is computed of growth from $L_1$ to $L_2$, the inverse VBGF is used

$$t_L = \frac{1}{K} \ln \left(\frac{L_2 - L_1}{L_2 - L_\infty}\right) - t_0$$ (21)

Subtracting two such equations in order to find the time interval will give

$$\Delta t_{L_2 - L_1} = \frac{1}{K} \ln \left(\frac{L_\infty - L_1}{L_\infty - L_2}\right)$$ (22)

where $t_0$ is no longer used.
Practical hints for finding the VBGF parameters $K$ and $L^\infty$

As seen from Figures 10 and 11, the highest growth rates are found for the juveniles, decreasing with age/size. It is therefore important, in order to best fit a Gulland and Holt plot, that growth increments from the youngest cohorts are used. If only points from the large adult fish are used, one obtains a situation as in Figure 12, which can easily lead to inaccurate estimates of $K$.

![Figure 12](image1.png)

**Figure 12.** A Gulland and Holt plot with data points from adult fish only.

On the other hand, as seen in Figure 13, a plot with just a few data points from the juvenile part of the population will give a much more accurate estimate of $K$, when combined with a so-called forced regression where the intercept at the x-axis $= L^\infty$ is fixed (by estimating $L^\infty$ from observations on the largest fish caught, or other information).

![Figure 13](image2.png)

**Figure 13.** A Gulland and Holt plot with data points from juvenile fish only
7 Mortality

In contrast to growth and reproduction, which can be looked upon as individually based processes, the concept of mortality applies to the population level in stock assessment. The population contains unique dynamic features not shared by individuals, such as: birth rates, death rates, age structure, phenotypic plasticity, and gene pool. These attributes, which are shaped by the environment (evolution under natural selection) can be collectively summarised under the term life-history traits (Stearns 1976), and their configuration determines the resistance of the population to external disturbance and stress. The concept "life history" of a stock comprises optimally a comprehensive description of the various phases through which individuals of the population pass, i.e. from birth to maturity. This includes survival, mortality rate, fecundity and expectation of life span duration linked to the general environmental conditions. The full set of this information will provide not only a complete description of the population ecology but will, in theory, also enable one to deduce the controlling factors that determine its population dynamics.

The key parameters used when describing death are called the mortality rates. The chance of dying as a function of time, i.e. the mortality rate, is, other things being equal, closely correlated to the predictability of the environment, i.e. the frequency of random fluctuations that somehow endangers the survival of the population. The first thing to recognise is that the events that cause variation in the year-class strength in fish occur during the first year of life, because it is the youngest stage that suffers most of the mortality, Pitcher and Hart (1982) indicates:

- average adult mortality = 5 - 10 % per year
- average larvae mortality = 2 - 10 % per day

although the ranges can be much higher.

Mortality rates tend to be size specific, with rates being highest during the egg and yolk-sac stages and declining thereafter. The possible causes of the high juvenile mortality and the subsequent variations in year-class strength are an important research area in fish population dynamics. In stock assessment, mortality rates are normally considered only for the adult stages of the population, where the variation tends to be much less. Of particular importance in fisheries stock assessment - as a key input for management measures - is the level of fishing mortality that affects the stock in relation to the natural mortality.

The factors contributing to mortality can be divided into two main categories, although it must be stressed that this subdivision is purely for simplification:

- **Abiotic factors** (physical environment)
  - temperature
  - salinity
  - oxygen
  - light
  - stability and disturbances
- pollution
- **Biotic factors** (other organisms)
  - predation
  - cannibalism
  - density
  - starvation
  - competition
  - diseases

![Figure 14. Factors influencing mortality at various life stages of fish.](image)

Each of these factors has a different importance at various stages in the life cycle (Figure 14). In general, predation is considered the most natural important factor, at least at the larvae stage and older. For the adult stages, the fishing mortality is often the most important factor, often surpassing predation for heavily fished stocks.

The concept of a *cohort*, or *age-group*, was introduced in the section on Growth. All fish of a cohort are assumed to have the same age at any given time. When it is possible to age the fish, the *size-at-age* for growth estimation and *number-at-age* for mortality estimation can be observed. In the context of mortality rates, the number of survivors of a cohort as a function of *time* is a significant factor.

**Definitions:**

- The symbol $N_t$ is used to designate the *number of survivors from a cohort attaining age* $t$.

- $Tr$ is used for the time of recruitment, meaning the age at which fish enter the fishery on the fishing grounds and will probably encounter fishing gears. Thus, $N_{Tr}$ is the number of *recruits* from a cohort. Often the symbol $R$ is used to designate the recruitment ($R = N_{Tr}$).

- $Tc$ is used for the age when the cohort actually enters the fishery and and becomes catchable. $Tc$ is called the age of first capture and marks the beginning of the
exploited phase (Figure 15). The difference between $Tr$ and $Tc$ depends on the selectivity of the fishing gear.

- $Z$ is called the instantaneous rate of total mortality, the total mortality coefficient, or simply the total mortality rate.

- $F$ is called the instantaneous rate of fishing mortality, or simply the fishing mortality rate.

- $M$ is called the instantaneous rate of natural mortality, or simply the natural mortality rate.

All mortality rates are in units per time, normally per year.

As mentioned above, mortality rates are strongly size-dependent with an overall general decline in the rates as a function of size. The natural mortality of a cohort will therefore tend to decline with increasing age. In all age-based fishery models, it is possible to operate with different mortality rates at different age groups, but for practical purposes, the natural mortality rate ($M$) is normally considered more or less constant for the size/age range of the exploited part of the stock.

7.1 Quantitative measures of mortality

Over a given time interval, a proportion of the fish alive ($N_1$) at the beginning of the time interval ($t_1$) will die by various natural causes or by fishing pressures, while the rest will survive ($N_2$) until the end of the time interval ($t_2$). Mathematically, one has

$$N_1 = P + D + O + C + N_2$$

where $P, D, O$ = numbers dying from predation, diseases, and other causes, and $C$ = numbers caught by fishing. There are two ways of expressing the above-mentioned mortality:

**Relative mortality**

The most obvious and easily understood expression is represents the mortality as a fraction or a percentage of the initial number; for example, the total death rate over time interval $[t_1, t_2]$ is defined as

$$Z(t_1, t_2) = \frac{N(t_1) - N(t_2)}{N(t_1)}$$

thus, the ratio between the numbers of individuals that have left the cohort and the initial number. The closely related quantity, survival, is defined as

$$S(t_1, t_2) = 1 - Z(t_1, t_2) = \frac{N(t_2)}{N(t_1)}$$
thus, the ratio between the numbers of individuals that were present at time $t_2$ and the initial number at time $t_1$. The possible values of mortality and survival are from 0 to 1, or if expressed in percentages, from 0 to 100.

**Instantaneous mortality**

While the relative mortality rates are easily understood, they are in practise not very useful because they are difficult to work with mathematically when effects of different causes of morality are combined as in fish stock assessment (Gulland 1983). A doubling of fishing effort, for example, will not double the catch, because the additional effort will reduce the catch of the effort already fishing. It is therefore better to consider the instantaneous rates, i.e. the mortality rates applied over a very short period of time ($dt$), where the numbers in the population do not change significantly. In that case, the numbers dying from any one cause are not affected by the numbers dying from any other cause and the deaths will be proportional to the instantaneous rates. A decrease in the population numbers can then be considered as proportional to the total mortality coefficient $Z$ and written as

$$\frac{dN}{dt} = -Z \cdot N_t, \quad (4)$$

In this form, the total mortality $Z$, is then the sum of all the other coefficients, so that

$$Z = F + M \quad (5)$$

Integrating Equation (4), one obtains

$$\ln(N_t) = -Z_t + \text{constant} \quad (6)$$

or

$$N_t = N_0 \cdot e^{-Zt} \quad (7)$$

where $N_0 = \text{numbers alive at time } t = 0$.

This is the traditional model for describing mortality in a fish stock (fishing or natural causes), the so-called *exponential decay model* illustrated in Figure 15 on a cohort.
Figure 15. Basic dynamics of the decay of a cohort and corresponding symbols used in fishery models. The figure illustrates the impact of fishing to the survival rates, compared to natural decay without fishing. The line N+Catch illustrates the relative proportion of fish landed under an exploitation rate of 0.5 ($F = M$), compared to the survivors. It is important to note that the catch is much smaller than the difference between survivors with or without exploitation because the probability of dying from natural causes does not change, and the total number dying is a function of $N$.

Equations (5) and (7) are among the most basic equations in fish population dynamics. From them, expressions of the relative rates (e.g. annual) can be obtained:

$$S(t_1, t_2) = \frac{N(t_2)}{N(t_1)} = e^{-Z(t_2-t_1)}$$

and

$$Z(t_1, t_2) = 1 - e^{-Z(t_2-t_1)}$$

7.2 Assumptions of exponential decay model

Mortality as an individual process is a discrete random variable because life can only have the events dead or alive. Growth, in comparison, is a continuous variable because it can take any values within a range. The Poisson distribution is a discrete probability model useful for events occurring randomly over time when all that is known is that the average number of occurrences per time unit or space is constant.

When the time between events is completely random then the time intervals are exponentially distributed (Figure 16).
In very large populations, such as most fish stocks, it is reasonable to assume that the average mortality rate for the whole population is approximately constant over different time periods, although it may change between these periods. Although individual death is a stochastic process, the probability of dying can be considered a deterministic process, which, within short time steps, has the probability \( Z \cdot dt \). The distribution has no “memory”, because the probability of dying does not change with time. The cumulative density function

\[
f(t) = 1 - e^{-Zt}
\]
gives the probability that any individual will die within time \( t \) (Figure 17).
Any single fish has thus the probability to die of
\[ p = 1 - e^{-Zt} \] and to survive of \[ p = e^{-Zt} \]

The demographic development of the whole population \((N_t)\) can then be considered a binomial distribution \((N_0, p)\) with the statistical parameters:

\[
\begin{align*}
\bar{N}_t & = N_0 \cdot p = N_0 \cdot e^{-Zt} \\
Var(N_t) & = N_0 \cdot p \cdot (1 - p) = N_0 \cdot e^{-Zt} \cdot (1 - e^{-Zt}) \\
CV(N_t) & = \frac{SD}{\bar{X}} = \frac{\sqrt{Var(N_t)}}{\bar{N}_t}
\end{align*}
\]

In summary:

- The decrease in average population numbers can be considered as proportional to the total average mortality coefficient \(Z\), which is constant and negative within time intervals

- The exponential decay model that illustrates mortality has two parameters:
  - 1’st parameter is the starting point
  - 2’nd parameter quantifies how rapidly the curve decays (the average rate or probability of occurrences).
The rate at which something happens (mortality) is proportional to the amount that is left.

7.3 Properties of exponential decay model

If the average rate of mortality ($Z_i$) is constant in the time interval $T_i$, where $T_i = t_i - t_{i+1}$, then

1. Number of survivors ($N_{i+1}$) at the end of time interval $T_i$ is

$$N_{i+1} = N_i \cdot e^{-Z_i T_i}$$  (10)

2. Number of dead in the time interval $T_i$ is

$$D_i = N_i - N_{i+1} = N_i(1 - e^{-Z_i T_i})$$  (11)

3. Number of accumulated survivors in the time interval $T_i$ is

$$N_{ac} = \frac{D_i}{Z_i} = N_i \cdot \frac{1 - e^{-Z_i T_i}}{Z_i \cdot T_i}$$  (12)

4. Average number of survivors in the time interval $T_i$ is

$$\bar{N}_i = \frac{N_{ac}}{T_i} = \frac{D_i}{Z_i \cdot T_i} = N_i \cdot \frac{1 - e^{-Z_i T_i}}{Z_i \cdot T_i}$$  (13)

When splitting total mortality ($Z_i$) into the components of fishing mortality ($F_i$) and natural mortality ($M_i$), where $Z_i = F_i + M_i$, then

5. The number caught by fishing in the time interval $T_i$ can be expressed as

$$C_i = F_i \cdot N_{ac}$$

$$C_i = F_i \cdot \bar{N}_i \cdot T_i$$

$$C_i = E_i \cdot D_i \quad \text{where} \quad E_i = \frac{F_i}{F_i + M_i}$$  (14)

$$C_i = \frac{F_i}{Z_i} \cdot D_i$$

$$C_i = \frac{F_i}{F_i + M_i} \cdot N_i \left[ 1 - e^{-(F_i + M_i) T_i} \right]$$
7.4 Estimation of mortality rates

Estimation of \( Z \) from catch and effort data

It is possible to estimate the total average mortality rate when the number of fish in a cohort is available for two different moments in its exploited phase under the assumption that fishing and natural mortality are constant in time for certain (older) age groups. Equations (8) or (10) can be rewritten as

\[
Z_{(t_1, t_2)} = \frac{1}{t_2 - t_1} \cdot \ln \left( \frac{N_{t_1}}{N_{t_2}} \right)
\]  

(15)

For the estimation of \( Z \) with this formula, it is not necessary to know the absolute values of \( N(t_1) \) and \( N(t_2) \); only their ratio is required. This permits an estimate, \( Z \), from the CPUE data, since

\[
CPUE = q \cdot N
\]  

(16)

CPUE data from research surveys

If the CPUE data from a research survey at two different time periods where \( q \) can be assumed constant is known, and it is possible to determine the cohorts from ageing the fish, the following is obtained from Equation (16)

\[
\frac{N_{t_1}}{N_{t_2}} = \frac{q \cdot N_{t_1}}{q \cdot N_{t_2}} = \frac{CPUE_{t_1}}{CPUE_{t_2}}
\]  

(17)

Inserting this in equation (15) gives

\[
Z_{(t_1, t_2)} = \frac{1}{t_2 - t_1} \cdot \ln \left( \frac{CPUE_{t_1}}{CPUE_{t_2}} \right)
\]  

(18)

Z from commercial fisheries

In this case, the concept of an average value of CPUE over a long period must be used, where

\[
\overline{CPUE}_{(t_1, t_2)} = q \cdot \overline{N}_{(t_1, t_2)}
\]  

(19)

The mean CPUE is usually calculated as the catch of the cohort during time interval \([t_1, t_2]\) divided by the effort during that period.

Heincke’s formula

\[
Z = \ln \left( \frac{\text{CPUE}_{t_1} + \text{CPUE}_{t_2} + \text{CPUE}_{(age \ 3 \ and \ older)}}{\text{CPUE}_0 + \text{CPUE}_{t_1} + \text{CPUE}_{t_2} + \text{CPUE}_{(age \ 3 \ and \ older)}} \right)
\]  

(20)
Estimation of Z from a linearised Catch Curve

This method is based on the assumption of a ‘constant parameter system’ also called ‘steady state’. Under steady state conditions, it is assumed that all demographic variables are constant over time and over size. This means that the annual recruitment into the stock is constant, and that the overall mortality rate over the exploited part of the stock is constant. If this assumption is valid and fulfilled, then the catch in numbers-at-age over one year is equal to the catch in numbers-at-age of a cohort over its life span (Table 1). In other words, the number of survivors and the number caught would be the same for all cohorts. This is a very rigid and strong assumption, which is rarely met. However, many fishery theories and particularly long term projections, e.g. see Thompson and Bell (1934) and Beverton and Holt (1956, 1957), are in fact based on the assumption of a constant parameter system in terms of recruitment and natural mortality rates.

Table 1. Illustration of the variable and constant parameter system. The diagonal arrows represent the “true” cohorts over time, whereas the vertical arrows represent the so-called “pseudo-cohorts”. Only under an assumed constant parameter system are the pseudo-cohorts equal to the true cohorts. This means that under a constant parameter system, the development of the system during one year is equal to the development of a cohort over its life span.

<table>
<thead>
<tr>
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<td>3</td>
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<td>121</td>
<td>▼ 121</td>
</tr>
</tbody>
</table>

If an estimate of the age composition in the catch during one year is available, then a method for estimating the total mortality rate can be developed from the catch equation (Eq. 14)

\[
C_i = \frac{F_i}{Z_i} \cdot N_i \left[1 - e^{-\frac{Z_i}{T_i}}\right]
\]

by replacing \( N_i \) and rewriting the time intervals
and taking the logarithms

\[
\ln[C(t_1, t_2)] = \ln(N_{T_r}) + \ln\left(\frac{F_i}{Z_i}\right) + Z \cdot T_e - Z \cdot t_1 + \ln\left[1 - e^{-Z(t_2 - t_1)}\right]
\]  

As the first three terms are (assumed) constant, this reduces to

\[
\ln[C(t_1, t_2)] = Const - Z \cdot T_i + \ln\left[1 - e^{-Z(t_2 - t_1)}\right]
\]

where $Z t_1$ is in a linear form and only the last terms are non-linear. Various methods suggest different ways of dealing with this last term.

**Constant time intervals:**

If the time intervals are constant, e.g. one year, then the last term becomes a constant and Eq. (24) reduces to

\[
\ln[C(t_1, t_2)] = Const - Z \cdot t_i
\]

Thus, in a regression on the log-transformed catches-at-age, the slope will give an estimate of $Z$. 

**Figure 18.** Linearised catch curve with constant time intervals based on the 1980 cohort data in Table 1.
Variable time intervals

This means that \( t_2 - t_1, t_3 - t_2, t_4 - t_3 \) are not constant in the non-linear term \( \ln \left[ 1 - e^{-Z(t_2 - t_1)} \right] \).

Jones and Zalinge (1981) suggested that \( t_2 \) could take a very high value (infinity), in which case the term \( e^{-Z(t_2 - t_1)} \) would be close to 0 and the last term would also be 0 (\( \ln(1) = 0 \)). Thus, if \( C(t, \infty) \) is the catch of all fish of age \( t \) and older, a linear relationship is achieved by the so-called cumulated catch curve equation:

\[
\ln[C(t, \infty)] = \text{Const} - Z \cdot t
\]

(26)

Van Sickle (1977) and Pauly (1983) suggested that for small time intervals and since

\[ \ln[1 - e^{-x}] \approx \ln(x) - \frac{x}{2} \]

is an approximation, then using this in eqn (24) and rearranging its members gives

\[
\ln \left[ \frac{C(t, t + \Delta t)}{\Delta t} \right] = \text{Const} - Z \cdot (t + \frac{\Delta t}{2})
\]

(27)

where \( t_2 - t_1 = \Delta t \) because the intervals must be small. This is the so-called “linearised catch curve equation with variable time intervals”.

The linearised catch curve based on length data (length converted catch curve)

Using the inverse VBGF to convert lengths to relative age where

\[
\Delta t = \frac{1}{K} \cdot \ln \left( \frac{L_\infty - L_1}{L_\infty - L_1} \right)
\]

(28)

Eq. (27) can be converted into the so-called “linearised length-converted catch curve”

\[
\ln \left[ \frac{C(L_1, L_2)}{\Delta t(L_1, L_2)} \right] = \text{Const} - Z \cdot t \left( \frac{L_1 + L_2}{2} \right)
\]

(29)

This is a linear equation where \( y = \ln \left[ \frac{C(L_1, L_2)}{\Delta t(L_1, L_2)} \right], x = t \left( \frac{L_1 + L_2}{2} \right) \) and the slope is \(-Z\).

The cumulated catch curve based on length composition data

Eq. (26) can be converted to a length-based version using the inverse VBGF

\[
\ln[C(L, L_\infty)] = \text{Const} - \frac{Z}{K} \ln(L_\infty - L)
\]

(30)
where $C(L,L_\infty)$ is the cumulated catch of fish from length $L$ and above, and an estimate of $Z$ obtained from $Z = K \cdot \text{slope}$

**Beverton and Holt's $Z$-equation based on length data**

This model, developed by Beverton and Holt (1956), assumes that growth follows the VBGF, that mortality can be represented by negative exponential decay, and that $L$ is estimated from a sample representing a steady-state population.

$$Z = K \cdot \left( \frac{L_0 - \overline{L}}{\overline{L} - L'} \right)$$  \hspace{1cm} (31)

where $\overline{L}$ is the mean length of fish of length $L'$ and longer, and $L'$ is “some length for which all fish for that length and longer are under full exploitation”.

### 7.5 Natural mortality

The natural mortality coefficient, or instantaneous rate of natural mortality $(M)$, is an important, but poorly qualified parameter in most mathematical models of fish population dynamics. Normally, all other causes besides fishing are incorporated into this one parameter and is then often assumed to be a constant. Although the models do not require explicitly that $M$ is constant – it may vary in any form, our actual knowledge of the true natural mortality pattern is so poor and any direct measurements are so difficult to obtain, that for practical purposes $M$ is mostly ‘guessedimated’ and assumed constant. In particular, this last assumption is mostly not the case for natural populations. The problems of estimating the natural mortality in fish stocks have been reviewed in Vetter (1988) and Caddy (1991).

As illustrated in Fig. 14, natural mortality has several causes that may change in relative importance during ontogeny. Because dying is more certain than giving birth for any single individual (see section on ecological concepts), the natural mortality rate and pattern is one of the driving forces of evolution and consequently, the natural mortality rate has clear correlations with other life history parameters:

**$M$ is proportional to the following factors**

- Growth and therefore indirectly to the VBGF parameters $K$ and $L_\infty$
- Size or weight, which is partly a function of longevity
- Age at maturation, which is also a function of longevity
- Reproductive effort (the relative distribution of energy into gonad or somatic tissue)
- Temperature which determines the metabolic rate and therefore growth
- Environmental stability which may also affect longevity
- Intrinsic population growth rate $r$ (Malthusian factor)

There are three different approaches to estimate $M$ in fish populations (Vetter 1988):

1. Analysis of catch data from commercial fisheries, sampling programmes, or mark and recapture experiments.
2. Correlation with other life history parameters.
3. Estimation of predation from stomach content analysis and consumption experiments.

**Estimation of M from fishing data (Paloheimo 1961)**

From Eq. (5), one has that

$$M_t = Z_t - F_t = Z_t - q_t f$$

(32)

Therefore, if different estimates of \(Z\) over a wide range of efforts \((f)\) are available, a plot of \(Z\) as the dependent variable over effort as the independent will give a linear regression with \(M\) as the intercept and \(q\) (the catchability coefficient) as the slope.

Input data: Estimation of pairs of data of \(Z\) and \(f\) for a wide range of years covering different efforts.

![Estimation of M from fishing data](image)

Underlying assumptions are:

- effort is proportional to fishing mortality; \(q\) is constant (questionable)
- that mortality coefficient \(Z\) observed in between successive cohorts in exploited stocks is the sum of a constant \(M\), probability of capture \(q\), and the prevailing fishing mortality coefficient.

**Formula of Alagaraja (1984)**

If \(Tm =\) Longevity is defined as the age at which 99% of the cohort has died (corresponding to a 1% survival = 0.01) if it had been exposed exclusively to a constant natural mortality rate \((M)\), then

$$M = \frac{-\ln(0.01)}{Tm}$$

(33)

Eq. (33) can be changed to correspond to a 0.1% survival. Table 2 gives a collection of \(M\)-values for different life spans calculated at both the 1% and 0.1% survival level.
Table 2. $M$-values for various life spans ($Tm$ months and years)

<table>
<thead>
<tr>
<th>$Tm$ months</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>8</th>
<th>10</th>
<th>12</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M$ 1% per year</td>
<td>18</td>
<td>14</td>
<td>11</td>
<td>9</td>
<td>8</td>
<td>6.9</td>
<td>5.5</td>
<td>4.6</td>
</tr>
<tr>
<td>$M$ 0.1% per year</td>
<td>28</td>
<td>21</td>
<td>17</td>
<td>14</td>
<td>12</td>
<td>10.4</td>
<td>8.3</td>
<td>6.9</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>$Tm$ years</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>8</th>
<th>10</th>
<th>15</th>
<th>20</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M$ 1% per year</td>
<td>2.3</td>
<td>1.5</td>
<td>1.2</td>
<td>0.92</td>
<td>0.77</td>
<td>0.58</td>
<td>0.46</td>
<td>0.31</td>
<td>0.23</td>
</tr>
<tr>
<td>$M$ 0.1% per year</td>
<td>3.5</td>
<td>2.3</td>
<td>1.7</td>
<td>1.38</td>
<td>1.15</td>
<td>0.86</td>
<td>0.77</td>
<td>0.69</td>
<td>0.63</td>
</tr>
</tbody>
</table>

**Pauly’s Empirical formula**

Pauly (1980) made a multiple regression analysis of natural mortality (year) in 175 species on corresponding values of the VBGF parameters $K$ (per year) and $L_{\infty}$ (TL in cm) and the annual average habitat temperature $T$ (°C of the water in which the stock considered lives), giving the following empirical relationship

$$M = 0.8 \cdot e^{(-0.0152-0.279\ln(L_{\infty})+0.6543\ln(K)+0.463\ln(T))}$$ (34)

where 0.8 is an adjustment factor used for ‘schooling species’.

According to Pauly, this formula does not work for bivalves, but may give reasonable results for cephalopods and shrimps.

**Rikhter and Efanov’s method**

Taking into account the previous work of Beverton and Holt (1959), Rikhter and Efanov (1976) showed a close association between $M$ and $Tm(50\%)$, the age at which 50% of the population was mature, giving the following relationship

$$M = \frac{1.521}{Tm(50\%)^{0.72}} - 0.155$$ (34)

**Gunderson and Dygert Method (1988)**

Gunderson and Dygert related $M$ to various life history parameters for 20 stock of fish and found the highest correlation with the investment of fish in reproduction (reproductive effort) represented by the gonad somatic index (GSI)

$$GSI = \frac{\text{gonad weight}}{\text{somatic weight}}$$

and found the following empirical relationship

$$M = 0.33 + 1.68 \cdot GSI$$ (35)
8. **Virtual Population Analysis (VPA) and Pope’s Cohort Analysis (PCA)**

VPA methods require age-structured data:

- Total catch in number by age and by cohort (usually one per year)
- Estimates of natural mortality (M) by age

In addition, many of the VPA-types of models are incorporating additional information, such as:

- Abundance estimates in absolute terms, each estimate representing one or several age groups (e.g. from acoustic survey abundance estimates)
- Abundance indices, each index representing one or several age groups (e.g. from bottom trawl CPUE from research surveys)
- Effort indices (e.g. effort data from fisheries statistics)
- Mean weight by age and by year corresponding to the catch

While some or all of these elements may not be available, the total catch broken down by demographic structures (age or alternatively lengths) and estimates of natural mortality rates must be present for the VPA methods to be used.

**Output from VPA methods are:**

- Estimates of the (virtual) total population size, stock in numbers ($N$), by age and by cohort
- Population size at time of capture ($t_c$) used as index of recruitment
- Estimates of the fishing mortality by age (so-called F-array, or fishing pattern)
- Estimates of the catchability coefficient ($q$) when effort data available
- Estimates of the Spawning Stock Biomass (SSB) when mean weight by age and maturity ogive by age and year are available

Multi-species VPA can be performed when estimates of annual prey consumption are (typically obtained from stomach contents analysis from fish caught in the wild and data from laboratory experiments on digestion, evacuation rates).

The stock development is based on several processes, individually modelled or observed:

- **Growth.** ($G$) using the VGBF, or simply an age-weight vector
- **Recruitment.** ($R$) 'Output' from VPA or described as a function of the SSB (Stock-Recruitment models).
- **Fishing Mortality.** ($F$) as a process independent of natural mortality
- **Natural Mortality.** ($M$) Described either as an age dependent fixed parameter, or as a multi-species interactive process.
8.1 Model and assumptions

The Cohort model is an analytical model following a cohort in time intervals, typically by year. VPA relies on a very simple relationship for each cohort:

\[
\begin{bmatrix}
\text{Number alive at beginning of next year} \\
\text{Number alive at beginning of this year}
\end{bmatrix} = \begin{bmatrix}
\text{Number alive at beginning of this year} \\
\text{Catch this year} \\
\text{Natural mortality this year}
\end{bmatrix}
\]

The basic assumption is that the survival of the cohort during the year is governed by

\[
\frac{dN}{dt} = -N(F + M)
\]

where \(F\) and \(M\) are the instantaneous rates of fishing and natural mortality. Solving this equation for the surviving numbers of the year, one has

\[
N_{i+1} = N_i \cdot e^{-(F_i + M_i)}
\]

(2)

The total loss during the year is \(N_i - N_{i+1}\). So, the catch during the year is

\[
C_i = \frac{F_i}{F_i + M_i} (N_i - N_{i+1}) = E_i D_i
\]

(3)

also known as the Baranov (1918) catch equation. Solving Equation (2) for \(F\), one has

\[
\frac{N_{i+1}}{N_i} = e^{-(F_i + M_i)} \quad \Rightarrow \quad F_i = -\ln\left(\frac{N_{i+1}}{N_i}\right) - M_i
\]

(4)

or in logarithmic form

\[
F_i = \ln(N_i) - \ln(N_{i+1}) - M_i
\]

(5)

Substituting the equation for \(F\) (Eq.4) into the catch equation (Eq.3), one obtains

\[
C_i = \left[\frac{\ln(N_{i+1})}{\ln(N_i)} - M_i}{\ln(N_{i+1})/\ln(N_i) - M_i + M_i}\right] (N_i - N_{i+1})
\]

(6)

which simplifies to

\[
C_i = \left[1 - \frac{M_i}{\ln(N_i) - \ln(N_{i+1})}\right] (N_i - N_{i+1})
\]

(7)

Since \(Z_i = \ln(N_i) - \ln(N_{i+1})\) and \(F_i / Z_i + M_i / Z_i = 1\), it can be seen that Eq. (7) is just another expression of the catch equation (Eq. 3), but now only described in terms of numbers in the beginning and the end of the year and the natural mortality rate during the year.
8.2 Iterative solution (VPA)

Equation (7) has a transcendental meaning. It has no direct solution. It must be solved by iterative methods. Modern microcomputers make iterative solutions very easy. Newton’s method finds iterative improvements in the value of some variable $x$, which will make $f(x) = 0$. The iterative equation to find $x$ is

$$x_{\text{new}} = x_{\text{old}} - \frac{f(x)}{f'(x)}$$

where $f'(x)$ is the derivative of $f(x)$ with respect to $x$.

The derivative of eqn.(7) with respect to $N_i$ is

$$f'(N_i) = 1 - \left( \frac{Z_i - \frac{(N_i - N_{i+1})}{N_i}}{Z_i^2} \right) \cdot \frac{M_i}{Z_i^2}$$  \hspace{1cm} (8)

The following procedure (Lassen and Medley 2001), written in Visual Basic, will do the Newton iteration in a few steps. This procedure can be implemented as a Macro or Function in EXCEL to serve as a general function with three input parameters ($M_i, C, N_{i+1}$), which will return the previous stock number ($N_i$).

```vbnet
Function SolBaranov(M As Double, Ca As Double, Na_1 As Double) As Double
    Dim fx As Double, dfx As Double, Na As Double, DeltaNa As Double, Z As Double
    'calculate initial values
    Na = Na - 1 * Exp(M) 'calculate Na with no fishing
    DeltaNa = Ca * Exp(M / 2) 'calculate Pope's fishing mortality approx
    'now iterate as long DeltaNa > 0.1
    Do While Abs(DeltaNa) > 0.1 'test current accuracy
        Na = Na + DeltaNa 'add correction to Na
        Z = Log(Na) - Log(Na_1) 'calculate total mortality
        fx = (1 - M / Z) * (Na - Na_1) - Ca 'calculate the function
        dfx = 1 - (Z - (Na - Na_1) / Na) * M / (Z * Z) 'and its derivative
        DeltaNa = -fx / dfx 'calculate new correction factor
    Loop
    SolBaranov = Na 'return solution
End Function
```

**Terminal F and terminal N**

By calculating the corresponding exploitation rates ($E_i$) over the age group of the cohort, and assuming that the fishing pattern over the last 3-4 age groups should be approximately similar, an average of the 3-4 exploitation rates antecedent to $N_{\text{term}}$ can be used to estimate a new $N_{\text{term}}$ from Eq. (9) or Eq. (10) and the procedure repeated.

Normally, the last $F$, $F_{\text{terminal}}$, is estimated (typically set to 0.5). In this case the last $N$, $N_{\text{terminal}}$, can be calculated from the catch equation:
$$N_{\text{term}} = \frac{C_{\text{term}}}{F_{\text{term}} + M_{\text{term}}} \left(1 - e^{-(F_{\text{term}} + M_{\text{term}})}\right) \quad (9)$$

Alternatively, in case the last catch is a plus-group, $N_{\text{terminal}}$ can be estimated by using an estimate of the last exploitation rate ($E$) from (Sparre and Venema 1998)

$$N_{\text{term}} = \frac{C_{\text{term}}}{E_{\text{term}}} \quad (10)$$

The $N_{\text{term}}$ is used as first input to the iterative procedure of estimating the stock numbers backwards in time. During the next steps, the returned value of $N_i$ is used as new input in SolBaranov($M_i, C_i, N_{i+1}$).

Backward estimates of the fishing mortality ($F_i$) are similarly stepwise calculated from Eq. (5). The total array of $F_i$s for the cohort is a quantitative representation of the so-called fishing pattern (see Figure 19) (see Excel sheet ‘VPA.xls’).

**Figure 19.** VPA example using data from Lassen and Medley (2001) p. 78 (slightly modified by Jeppe Kolding 17/9-01). Note that the relative distribution of the fishing mortality (the fishing pattern) is also a representation of the selectivity of the fishing gear (see Chapter 11). See also Figure 15.

*Adjusting the terminal N*

By calculating the corresponding exploitation rates ($E_i$) over the age group of the cohort, and assuming that the fishing pattern over the last 3-4 age groups should be approximately similar, an average of the 3-4 exploitation rates antecedent to $N_{\text{term}}$ can be used to estimate a new $N_{\text{term}}$ from Eq. (9) or Eq. (10) and the procedure repeated.

**8.3 Pope’s Cohort Analysis (PCA)**

Pope (1972) proposed a very simple approximate solution to the Baranov equation. Pope’s Cohort Analysis is conceptually identical to VPA, but the calculation technique is simpler
and can be carried out on a pocket calculator. It is based on the approximation that the total catch is taken during a single day in the middle of the year and that only natural mortality has taken place in the full time interval. In this case, the cohort equation (Eq. 2) can be expressed as

$$N_i = \left( N_{i+1} \cdot e^{\frac{M_i}{2}} + C_i \right) \cdot e^{\frac{M_i}{2}}$$  \hspace{1cm} (11)

and $F_i$ calculated from Eq.(5).

Pope’s approximation is essentially a linear form of the transcendental catch equation. In cases of low fishing mortality, it is often a good approximation. The backward calculation started the same way as for VPA but Eq. (11) is substituted by the iterative SolBaranov function. A full description of PCA is given in Sparre and Venema (1998).

8.4 Jones’ Length Based Cohort Analysis (LBCA)

There are three approaches to decompose size groups into ages (Lassen and Medley 2001):

Using Age-Length keys (ALK)
Methods not requiring a growth model
Methods requiring a growth model

When having an Age-Length Key, the catch-at-age $i$ ($C_i$) can be determined from

$$C_i = \sum_l p_{il} \cdot C_l$$  \hspace{1cm} (12)

where $p_{il}$ = the proportion (i.e. the probability) of a fish from length group $l$ being of age $i$.

Methods not requiring a growth model rely on identifying modes in length frequency samples that are representing cohorts. Such methods are, e.g., the Bhattacharya method (see growth lecture, chapter 6) where the length frequency sample is divided into a number of normal distributions, each representing a particular cohort.

Jones’ Length Based Cohort Analysis (Jones and van Zalinge 1981) is a simple way of decomposing size groups into ages using a growth model (VBGF). In this analysis, the growth is assumed deterministic from the model and the sample is sliced up according to back-transformation of the VBGF (the inverse VBGF) where

$$\Delta t_{L_1-L_2} = \frac{1}{K} \cdot \ln \left( \frac{L_\infty - L_1}{L_\infty - L_2} \right)$$  \hspace{1cm} (13)

and Eq. (2) would be rewritten with variable time intervals as

$$N_i = N_i \cdot e^{-(F_i + M_i)\Delta t}$$  \hspace{1cm} (14)
Given the change in age over each size class ($\Delta t$), the population within each size class can be constructed in the same way as a VPA.

The method has been investigated (Addison 1989, ICES 1995a,b) with the following conclusions:

- LBCA works on a single length frequency sample assuming the population has been in steady state.
- The method is insensitive to errors in the terminal exploitation rate if $F \gg M$.
- The model is extremely sensitive to errors in $M$.
- The narrowest length interval that makes data reasonably smooth should be used. Size classes should be chosen such that $M\Delta t \leq 0.3$.
- Considerable care should be taken when only poor growth estimation is available.

Ensure that the terminal length interval (plus group) has an initial length (lower bound) of less than 70% of $L_\infty$. Any estimate of $F$ should therefore cover only the smaller size interval representing the majority of the catch.

- Estimates of abundance (stock size) should not be taken as absolute values. They should only be used as indices to reflect relative changes.

The implementation of the method is described in Sparre and Venema (1998). The output is an array of $F$ by length groups instead of $F$ by age, and the number of ‘recruits ($R$)’ refers to $L_c$ (length of first capture) instead of $T_c$ (age of first capture).

**Length Based VPA using the Cadima method**

The EXCEL spreadsheet ‘Cadima-lca.xls’ presents an implementation of the Jones’ LBCA using the computational power of modern micro-computers and an iteration algorithm suggested by Emygdio Cadima (implemented by Jeppe Kolding and Pedro Baros). It uses a ‘circular reference’ method in EXCEL such that an initial calculation of $F_{\text{terminal}}$ or $N_{\text{terminal}}$, in order to start the VPA deterministically backwards through the age/size groups, is not required.

The spreadsheet contains an initial overall exploitation rate ($E_0$) over all length groups of e.g. 0.5 (which means that $F=M$ so that $Z=2M$). The population by length groups is therefore initially back-calculated by calculating the total numbers of deaths in each length group, $(i = \Delta t = L_2 - L_1)$ from (see Eq. 3)

$$D_i = \frac{C_i}{E_0}$$

and therefore

$$N_i = N_{i+1} + D_i \quad \text{where } N_{\text{term}} = 0$$

From this initial estimate of $N_i$ by length groups, an array of $Z$, $F$ and new $E$ ($E_i,1$) are calculated where

$$Z_i = \frac{\ln(N_i) - \ln(N_{i+1})}{\Delta t}, \quad F_i = Z_i \cdot E_i \quad \text{and } \quad E_i,1 = \frac{F_i}{F_i + M_i}$$
Upon starting the iteration\(^2\), the values in the \(E_0\) column are substituted by the new \(E_i^1\) and Eq. (15) and Eq. (16) are recalculated from the new \(E_i^1\). This is the ‘circular cell reference’.

The goal is now to continue the iteration until \(E_0 \approx E_i^1\).

When \(E_0 \approx E_i^1\), the spreadsheet is ‘balanced’, which means that the observed catches are now explained by the general cohort model (Eq. 1) from the input values of \(C_i\) and \(M_i\). This is an elegant way of indirectly solving the Baranov catch equation.

\(^2\) Giving the cell ‘iterate’ a value of 1, starts the iteration. Giving the cell a value of 0 will reset the spreadsheet to the initial values.

By setting the spreadsheet to automatic calculation (under Tools/Options/Calculation) with iteration enabled and setting maximum change to e.g 0.001, the iteration will continue until \(E_0 - E_i^1 < \text{maximum change}\).
9  Predictive models

9.1 Yield per Recruit and Thompson & Bell

Long term prediction (steady state) (see Excel sheet ’Yield-per-Recruit.xls’).

The development of 1 cohort over its life:

\[ N_0 = Recruitment = R \]

**Constructing a discrete model:**

For one time interval \( i \) e.g. year:

The fraction of individuals \( S_i \) that survives from year \( i \) to year \( i+1 \) is

\[ S_i = \frac{N_{i+1}}{N_i} = e^{-Z_i} \quad \text{where} \quad Z_i = M_i + F_i \]

thus

\[ N_{i+1} = N_i \cdot e^{-Z_i} \]

The number of **deaths:**

\[ D_i = N_i - N_{i+1} = N_i \cdot (1 - e^{-Z_i}) \]

The number **caught:**

\[ C_i = D_i \cdot E_i = \frac{F_i}{Z_i} \cdot D_i \]

**Definition:** the rate of exploitation

\[ E_i = \frac{C_i}{D_i} = \frac{F_i}{Z_i} \quad (0 \leq E_i \leq 1) \]
The mean Number in time interval $i$

$$\overline{N}_i = \frac{D_i}{Z_i} = \frac{C_i}{F_i}$$

thus

$$D_i = Z_i \cdot \overline{N}_i$$

$$C_i = F_i \cdot \overline{N}_i$$

and natural deaths $= D_i - C_i = M_i \cdot \overline{N}_i$

**In summary:**

<table>
<thead>
<tr>
<th>$N_i$</th>
<th>= Recruits = given</th>
</tr>
</thead>
<tbody>
<tr>
<td>$N_{i+1} = N_i \cdot e^{-Z_i}$</td>
<td></td>
</tr>
<tr>
<td>$D_i = N_i \cdot (1 - e^{-Z_i}) = N_i - N_{i+1}$</td>
<td></td>
</tr>
<tr>
<td>$C_i = E_i \cdot D_i = F_i \cdot \overline{N}_i = \frac{F_i}{Z_i} \cdot D_i$</td>
<td></td>
</tr>
<tr>
<td>$\overline{N}_i = \frac{D_i}{Z_i}$</td>
<td></td>
</tr>
</tbody>
</table>

Now in weight (biomass):

Individual weight

![Graph showing weight increase](image)

**VBGF:**

$$L_i = L_x \left[1 - e^{-K(t-t_0)}\right] \quad \text{or} \quad W_i = W_x \left[1 - e^{-K(t-t_0)}\right]^b$$

thus

$$\overline{W}_i = W_x \left[1 - e^{-K(t_{s,i} - t_0)}\right]^b$$

and

$$\overline{B}_i = \overline{N}_i \cdot \overline{W}_i$$

$$Y_i = C_i \cdot \overline{W}_i$$
For each time interval (year\(_i\)) \(C_i, \bar{N}_i, Y_i, \bar{B}_i\) must be calculated.

Total catch in numbers: \(C = \sum_{i=1}^{n} C_i\)

Total catch in weight: \(Y = \sum_{i=1}^{n} Y_i\)

Accumulated biomass \(\bar{B} = \sum_{i=1}^{n} \bar{B}_i\)

and in numbers \(\bar{N} = \sum_{i=1}^{n} \bar{N}_i\)

Mean weight catch \(\bar{W}_{\text{catch}} = \frac{Y}{C}\)

Mean weight cohort \(\bar{W}_{\text{cohort}} = \frac{\bar{B}}{\bar{N}}\)

Biomass relative to \(B_0\) \(\%\bar{B} = \frac{\bar{B}}{\bar{B}_{F=0}} \cdot 100\)

**Steady state means:**

\[\text{The stock over 1 year} = 1 \text{ cohort over lifetime}\]

Thus

\[Y_{\text{stock (1year)}} = Y_{\text{cohort over lifetime}}\]

\[C_{\text{stock (1year)}} = C_{\text{cohort over lifetime}}\]

\[\bar{B}_{\text{stock (1year)}} = \bar{B}_{\text{cohort over lifetime}}\]

**Exploitation pattern:**

\[F_i = F \cdot s_i = f \cdot q\quad (q = \text{catchability coefficient})\]

where \(F = \) level (not depending on fish size), and \(s_i = \) relative selectivity (size dependent).

\(F_i\) is obtained from e.g. VPA, and \(s_i\) from selectivity studies or assumed.

**Objective:** Change fishing mortality by changing \(F, s_i\) or both.

Find Target Reference Points (TRP): \(F_{\text{max}}\) (max \(Y/R\)) or \(F_{0.1}\) for each scenario.

Use TRP to make management recommendations.
Calculation using EXCEL:

Input parameters (values are arbitrary examples):

<table>
<thead>
<tr>
<th></th>
<th>R</th>
<th>F_{(initial)}</th>
<th>M</th>
<th>K</th>
<th>L_\infty</th>
<th>t_0</th>
<th>a</th>
<th>b</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1000</td>
<td>0.3</td>
<td>0.5</td>
<td>0.35</td>
<td>60</td>
<td>-0.1</td>
<td>0.01</td>
<td>2.96</td>
</tr>
</tbody>
</table>

W_\infty = a \cdot I_\infty^b for input in VBGF

<table>
<thead>
<tr>
<th>i</th>
<th>s_i</th>
<th>F_i</th>
<th>Z_i</th>
<th>S_i</th>
<th>E_i</th>
<th>N_i</th>
<th>D_i</th>
<th>C_i</th>
<th>\bar{N}_i</th>
<th>\bar{W}_i</th>
<th>\bar{B}_i</th>
<th>Y_i</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0</td>
<td>F \cdot s_i</td>
<td>F_i+M_i</td>
<td>e^{-Z_i}</td>
<td>F_i/Z_i</td>
<td>R</td>
<td>N_i(1-S_i)</td>
<td>D_i E_i</td>
<td>D_i/Z_i</td>
<td>N_i \cdot \bar{W}_i</td>
<td>C_i \cdot \bar{W}_i</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>0</td>
<td></td>
<td>N_i S_i</td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>3</td>
<td>1</td>
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<td>4</td>
<td>1</td>
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</tr>
<tr>
<td>max i</td>
<td>1</td>
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<td></td>
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<td></td>
<td></td>
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</tr>
</tbody>
</table>

C = \Sigma \quad \bar{N} = \Sigma \quad \bar{B} = \Sigma \quad Y = \Sigma

<table>
<thead>
<tr>
<th>F</th>
<th>=C</th>
<th>=\bar{N}</th>
<th>=\bar{B}</th>
<th>=Y</th>
<th>%B_0</th>
<th>\bar{W}_{catch}</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.1</td>
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<tr>
<td>0.2</td>
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<tr>
<td>0.3</td>
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<tr>
<td>5</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
</tbody>
</table>

Use TABLE function in Excel:
Mark the grey area: Table with Input Column = Cell containing value of F_{init}

Draw figure(s) showing Y, \bar{B}, %B_0 and \bar{W}_{catch} as a function of F.
Determine TRP’s. F_{max} (max Y/R) and F_{0.1} (see below)
**Beverton & Holt simplification (analytical solution, continuous model):**

**Assumptions:**

“Knife edge” recruitment = same $F$ over all sizes

$M = \text{constant}$

$W = a \cdot l^3$  (isometric growth)

$l_i = L_a (1 - e^{-K(t-t_0)})$

$W_i = W_a (1 - e^{-K(t-t_0)})^3$

**Model:**

$$\frac{Y}{R} = F \cdot e^{-M(t_i-t_c)} \cdot W_a \left[ \frac{1}{Z} \left( 1 - \frac{3S}{Z+K} + \frac{3S^2}{Z+2K} - \frac{S^3}{Z+3K} \right) \right]$$

where $S = e^{-K(t_i-t_0)}$

**Derivation:**

$D = \text{total deaths} = R_e$

$$\bar{N} = \frac{D}{Z} = \frac{R_e}{Z}$$

$C = R_e \cdot E$

$$\bar{B} = R_e \cdot W_a \cdot \left[ ... \right] \quad \text{where}$$

$$\left[ ... \right] = \frac{1}{Z} \left( 1 - \frac{3}{Z+K} + \frac{3(1-C)^2}{Z+2K} - \frac{(1-C)^3}{Z+3K} \right) \quad \text{and}$$

$C = 1 - e^{-K(t_i-t_0)} = \frac{l_i}{L_a}$

$$\bar{W} = \frac{\bar{B}}{\bar{N}} = Z \cdot W_a \cdot \left[ ... \right] \quad \text{as} \quad \bar{N} = \frac{R_e}{Z}$$

$Y = C \cdot \bar{W}$
Target reference points

1) \( F_{\text{max}} = \frac{Y}{R_{\text{max}}} \)

If \( F > F_{\text{max}} \) then growth overfishing

\( F_{\text{max}} \) does not consider reproduction (recruitment overfishing).
Would \( B_{\text{max}} \) be enough for stock regeneration?

2) \( F_{0.1} = \text{where slope of } \frac{Y}{R} \text{ curve is 10\% of slope at origin} \)

\( F_{0.1} < F_{\text{max}} \)

\( B_{F_{0.1}} > B_{F_{\text{max}}} \)

\( Y_{F_{0.1}} \leq Y_{F_{\text{max}}} \)

To estimate \( F_{0.1} \):
Make a new function to the right of the Table containing \( Y/R \) values as a function of \( F \):

\[
U = 0.1 \cdot \frac{B}{R} \cdot F, \text{ as } B/R \text{ is slope at origin when } F=0
\]

This is a linear function of \( F \)

\( F_{0.1} = \text{ when } \frac{Y}{R} - U \text{ is max} \)
Constructing a discrete predictive model by length intervals

The principles are the same as for the age-based model, although a few of the equations are different due to the non-linear relationship between length and time.

For one length interval (i)

\[
\begin{align*}
N_i & \quad N_{i+1} \\
L_i & \quad L_{i+1}
\end{align*}
\]

The fraction of individuals \( S_i \) that survive from length \( i \) to length \( i+1 \) is

\[
S_i = \frac{N_{i+1}}{N_i} = e^{-Z_i \Delta t} \quad \text{where} \quad Z_i = M_i + F_i
\]

and \( \Delta t \) is the time to grow from length \( i \) to length \( i+1 \)

in case VBGF is used this interval is given by

\[
\Delta t_{L_2-L_1} = \frac{1}{K} \cdot \ln \left( \frac{L_{\infty} - L_1}{L_{\infty} - L_2} \right) \quad \text{where} \quad L_1 = L_i \quad \text{and} \quad L_2 = L_{i+1}
\]

thus

\[
N_{i+1} = N_i \cdot e^{-Z_i \Delta t}
\]

The number of deaths:

\[
D_i = N_i - N_{i+1} = N_i \cdot (1 - e^{-Z_i \Delta t})
\]

Individual mean weight in interval \( i \) is estimated from the integral over length \( i \) to length \( i+1 \) using the length-weight relationship (Beyer 1987)

\[
\begin{align*}
W_i & \quad W_{i+1} \\
L_1 & \quad L_2
\end{align*}
\]

\[
\frac{1}{w_i} = \frac{1}{(L_2 - L_1)} \cdot \frac{a}{(b+1)} \cdot \frac{(L_2 + 1 - L_1 + 1)}{(b+1)}
\]

All other equations are the same as for the age-based model.
10 **Biomass Dynamic Models**

(notes to supplement Chapter 8 in Hilborn and Walters 1992, see Excel sheet 'BioDyn-JK.xls').

Other synonymous names encountered in the literature:

- Biomass production models
- Production models
- Surplus production models
- Global production models
- General production models
- Descriptive models
- Holistic models
- "Black box" models

Basic unit is the stock (population), not the individual fish

10.1 **Basic assumptions**

- There is a maximum level that can be achieved for the biomass of the stock, the carrying capacity called $K$, $B_0$, or $B_\infty$. This feature is **density dependence**, which are not accounted for in analytical Y/R models.
- When the actual biomass is at a level below $B_\infty$, it will tend to grow towards $B_\infty$. This is an observed natural tendency for all populations.
- The specific growth rate of biomass is a function of the biomass.
- The specific growth rate always
  - is highest when $B$ is very small
  - decreases with $B$
  - is zero when $B = B_\infty$

Density dependence must be of decisive importance in nature, because, without this concept, one cannot explain the relative stability that wild populations exhibit over time (e.g. Tanner 1966, Slobodkin *et al.* 1967, Kozlowski 1980, May 1991). The population-based models are tacitly dealing with changes in the vital parameters in density dependent terms, although the process is admittedly a 'black box'. The yield-per-recruit models are dealing explicitly with age structure and mortality rates, but the birth rate (i.e. the capacity of the population to increase), and, especially in density dependent changes in loss and gain rates, are normally not incorporated. Actually, Beverton and Holt (1957, p. 24) introduced their impressive analytical work by the cautious statement that "sooner or later a more comprehensive approach will be required" and "judging by ecological experience, it seems fairly certain that 'the whole is more than the sum of its parts', and from this point of view the sigmoid curve theory remains the most successful attempt so far to state concisely and in general terms what form the reaction of a community to the exploitation of one or more of its constituent parts might be expected to take".

In general the change in biomass can be written as $\frac{dB}{dt} = G(B)$

The question then, is the choice of model, ie. $G(B)$
10.2 Models

There are 3 general functions of $G(B)$ described in the literature:

1) **Schaefer** (1954): $\frac{dB}{dt} = rB(1 - \frac{B}{B_c})$

\[
\frac{dB}{dt} = rB(1 - \frac{B}{B_c}) = r - mB \quad \text{where} \quad m = \frac{r}{B_c}
\]

2) **Fox** (1970): $\frac{dB}{dt} = rB(1 - \frac{\ln B}{\ln B_c})$

\[
\frac{dB}{dt} = rB(1 - \frac{\ln B}{\ln B_c}) = r - m\ln(B) \quad \text{where} \quad m = \frac{r}{\ln(B_c)}
\]

3) **Pella and Tomlinson** (1969): $\frac{dB}{dt} = rB(1 - \frac{B^{p-1}}{B_c^{p-1}})$

\[
\frac{dB}{dt} = rB(1 - \frac{B^{p-1}}{B_c^{p-1}}) = r - mB^{p-1} \quad \text{where} \quad m = \frac{r}{B_c^{p-1}}
\]
### Biological reference points (BRP’s):

1) **Schaefer model:**

<table>
<thead>
<tr>
<th>BRP</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum sustainable yield (MSY)</td>
<td>( \frac{r \cdot B_s}{4} \Leftrightarrow \frac{r \cdot U_s}{4 \cdot q} )</td>
</tr>
<tr>
<td>Biomass for MSY (B&lt;sub&gt;MSY&lt;/sub&gt;)</td>
<td>( \frac{B_s}{2} )</td>
</tr>
<tr>
<td>Fishing mortality rate for MSY (F&lt;sub&gt;MSY&lt;/sub&gt;)</td>
<td>( \frac{r}{2} )</td>
</tr>
<tr>
<td>CPUE for MSY (U&lt;sub&gt;MSY&lt;/sub&gt;)</td>
<td>( \frac{U_s}{2} )</td>
</tr>
<tr>
<td>Fishing effort for MSY (f&lt;sub&gt;MSY&lt;/sub&gt;)</td>
<td>( \frac{r}{2 \cdot q} )</td>
</tr>
</tbody>
</table>

2) **Fox model:**

<table>
<thead>
<tr>
<th>BRP</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum sustainable yield (MSY)</td>
<td>( \frac{m \cdot B_s}{e} \Leftrightarrow \frac{q \cdot U_s}{e \cdot q} )</td>
</tr>
<tr>
<td>Biomass for MSY (B&lt;sub&gt;MSY&lt;/sub&gt;)</td>
<td>( \frac{B_s}{e} )</td>
</tr>
<tr>
<td>Fishing mortality rate for MSY (F&lt;sub&gt;MSY&lt;/sub&gt;)</td>
<td>( m )</td>
</tr>
<tr>
<td>CPUE for MSY (U&lt;sub&gt;MSY&lt;/sub&gt;)</td>
<td>( \frac{U_s}{e} )</td>
</tr>
<tr>
<td>Fishing effort for MSY (f&lt;sub&gt;MSY&lt;/sub&gt;)</td>
<td>( \frac{m}{q} )</td>
</tr>
</tbody>
</table>

3) **Pella and Tomlinson model:**

<table>
<thead>
<tr>
<th>BRP</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum sustainable yield (MSY)</td>
<td>( r \cdot B_s \left( \frac{1}{1 + p} \right)^{\frac{1}{p + 1}} )</td>
</tr>
<tr>
<td>Biomass for MSY (B&lt;sub&gt;MSY&lt;/sub&gt;)</td>
<td>( B_s \left( \frac{1}{1 + p} \right)^{\frac{1}{p}} )</td>
</tr>
<tr>
<td>Fishing mortality rate for MSY (F&lt;sub&gt;MSY&lt;/sub&gt;)</td>
<td>( r \cdot \left( \frac{1}{1 + p} \right) )</td>
</tr>
</tbody>
</table>
10.3 Fitting the models

The major problem with biomass production models is not the models (which in biological terms perhaps are more realistic than the density independent analytical models), but finding realistic values for the parameters $r$ and $B_\infty$.

The intrinsic rate of natural increase

Usually $r$ is approximated by $r_m$ (the maximum rate of increase under specific environmental conditions) from the following basic principles: in an unlimited environment one has exponential growth

$$N_t = N_0 e^{rt}$$

and thus, when $t = T$, the mean generation time, which equals the mean age at maturation, then

$$\frac{N_T}{N_0} = e^{rT} = R_o \Rightarrow r_m = \frac{\ln R_0}{T}$$

where $R_o$ is the net reproductive rate per individual per generation. In this case, the maximum number of offspring each individual produces. $R_o$ and $T$ are in practise estimated from life history tables but, strictly, the parameter $r_m$ can only be calculated this way when the age distribution in the population is stable (Andrewartha and Birch 1954, Pitcher and Hart 1982, Krebs 1985). There are, however, only two ways for a population to develop a stable age distribution (Krebs 1985): i) either constantly growing exponentially or, ii) after having reached a constant size (i.e. when $b = d$). The first is inconsistent with the sigmoid curve theory, but is actually the definition of $r$ (being the growth rate of a theoretical population, with a stable age distribution near the origin, when $(K-N)/K = 1$). Conversely, a natural population of constant size is not unlimited ($R_o \approx 1$, e.g. Begon et al. 1990) and any observed growth, therefore, is already under 'depressive' influence of density compared to the intrinsic growth rate $r$. This indicates that the usual in situ approximations (from life tables) of $r$ by $r_m$ might be a serious underestimation or, rather, that the two values represent two fundamentally different conditions and cannot be compared.

The carrying capacity

Although $K, B_\infty$, or $B_0$ is the density dependent factor for a population in the models, its quantity (the carrying capacity) is entirely regulated by extrinsic factors, of which the

---

$^3$ It is important to differentiate between these various meanings of $r$, which often are confused or used indiscriminately in the literature (Boyce 1982). The three possible meanings are: i) the intrinsic rate of increase, which is the theoretical highest rate of increase a given population can perform, ii) the maximum rate of increase under specific environmental conditions and without density dependence and iii) the actual, or observed, rate of increase whatever limitations might be (Fenchel 1977).
population usually has little control. In addition, probably few, if any, natural animal populations utilise or occupy their environment to the carrying capacity (Andrewartha and Birch 1954, Slobodkin et al. 1967, Stearns 1977). Other species will mostly either compete for the resources or be predators. The influence of other species is also difficult to ascertain. On the other hand, if a competitor or predator is removed from the system and an expansion of other species is observed, then competition or predation is demonstrated (Levinton 1982, Deshmukh 1986). Such interactions of multi-species have been observed in the North Sea (Andersen and Ursin 1977), in the Antarctic (May et al. 1979), in the Gulf of Thailand (Pauly 1979), on West Africa (Gulland and Garcia 1984) and in many fresh water fisheries (Paloheimo and Regier 1982, Carpenter et al. 1985), where heavy fishing pressure on larger, slower growing species lead to an expansion of smaller faster growing organisms.

The models are fitted empirically from time series of observations in catch rates (CPUE) or biomass indices from bottom trawl surveys or acoustic surveys. The parameters are, therefore, indirectly estimated from the observed changes in the population abundance.

There are 3 general fitting methods:

1) Fitting under equilibrium assumptions
   (traditional method, e.g. Sparre and Venema 1998)

2) Multiple regression techniques

3) Time series fitting (non-linear iterations)
**Fitting under equilibrium assumptions**

linear regression of $C/f = CPUE$ versus effort ($f$) (see Excel sheet 'Equilib-JK.xls').

(Note that this method is no longer used, due to unlikely assumption of instant relationship between catch and biomass, and statistical dependence between $y (C/f)$ and $x (f)$).

Based on continuous models with analytical solution

**Schaefer:**

$$\frac{dB}{dt} = rB \left(1 - \frac{B}{B_\infty}\right) - \text{Catch} \quad (1)$$

**Catch:** $C = F B$ or $C = f q B$ as $F = f q$

$$\Rightarrow \quad \frac{dB}{dt} = rB \left(1 - \frac{B}{B_\infty}\right) - f q B$$

or

$$\frac{1}{B} \frac{dB}{dt} = r \left(1 - \frac{B}{B_\infty}\right) - f q \quad (2)$$

Under *equilibrium*, growth or surplus (net production) is zero

$$\Rightarrow \quad 0 = r \left(1 - \frac{B_e}{B_\infty}\right) - f q \quad (3)$$

where $B_e =$ equilibrium biomass

The equilibrium catch is then $C_e = f q B_e$, rearranging for $B_e$ and substituting in (3) gives:

$$C_e = q f \cdot \frac{B_e}{r} \cdot (r - q f)$$

or

$$C_e = q f B_\infty - q^2 \frac{B_\infty}{r} f^2 = \text{parabola} \quad (4)$$

Find max = $MSY$ by differentiation:

$$C' = q B_\infty - 2 q^2 \frac{B_\infty}{r} f \quad \text{When } C' = 0 \text{ then } f_{\text{max}} = \frac{r}{2q}$$

inserting $f_{\text{max}}$ gives:

$$C_{e(\text{max})} = MSY = \frac{r}{4} \cdot B_\infty$$

**Fitting with catch and effort data:**

$$U = CPUE = C/f = qB$$

inserting in (4) gives:

$$U_e = q B_\infty - q^2 \frac{B_\infty}{r} f_e$$

98
or \[ U_e = U_n - q \frac{U_n}{r} f_e = \text{straight line: } U_e = a - bf_e \]

Regression of CPUE = \[ U_e = C/f \] against \( f \) (note these are not independent)

Multiplying \( U_e = a - bf_e \) with \( f \) (effort) gives sustainable yield (catch) as a function of \( f \)

\[ C = f(a - bf) \quad \text{inserting } f_{\text{max}} = \frac{-a}{2b} \text{ gives:} \]

\[ C_{\text{max}} = \text{MSY} = \frac{-a}{2b} \left( a - \frac{ba}{2b} \right) = -\frac{1}{2} \cdot \frac{a^2}{b} + \frac{1}{4} \cdot \frac{b \cdot a^2}{b^2} = -\frac{1}{2} \cdot \frac{a^2}{b} + \frac{1}{4} \cdot \frac{a^2}{b} = \frac{-a^2}{4b} \]

**Multiple linear regression methods**

Walters and Hilborn (1976): based on a different form of the Schaefer model (see Excel sheet ‘Walt-Hil-JK.xls’).

Next biomass = This biomass + Surplus production - Catch

\[ B_{t+1} = B_t + rB_t \left( 1 - \frac{B_t}{B_\infty} \right) - qB_t \quad \text{where } rB_t \left( 1 - \frac{B_t}{B_\infty} \right) = \text{Schaefer} \]

and \[ B_t = \frac{\text{CPUE}_t}{q} = \frac{U_t}{q} \]

\[ \Rightarrow \quad \frac{U_{t+1}}{q} = \frac{U_t}{q} + r \frac{U_t}{q} \left( 1 - \frac{U_t}{qB_\infty} \right) - fU_t \]

Dividing by \( \frac{U_t}{q} \) and rearranging gives:

\[ \frac{U_{t+1}}{U_t} = 1 + r - \frac{rU_t}{qB_\infty} - fq \quad \Rightarrow \quad \frac{U_{t+1}}{U_t} - 1 = r - \frac{rU_t}{qB_\infty} - fq \]
this means:

$$\frac{\text{rate of change in } B}{\text{growth rate}} = \text{intrinsic growth rate} - \text{density dependent reduction in fishing mortality} = r - M_0 - F$$

Regress: $\frac{U_{i+1}}{U_i} - 1$ on $U_t$ and $f_i$. This is a multiple linear regression of the form

$$Y = b_0 + b_1 X_1 + b_2 X_2 \quad \text{where} \quad X_1 = U_t \quad \text{and} \quad X_2 = f_t$$

$$b_0 = r, \quad b_1 = -\frac{r}{qB_w}, \quad b_2 = -q \quad \Rightarrow \quad B_w = \frac{-b_0}{b_1 \cdot b_2}$$

Experience: often negative values for $r$ and $q$

Schnute (1977) transformed the Schaefer model into a similar dynamic equation by integrating the time steps over one year, giving the following multiple regression (see Excel sheet 'Schnute-JK.xls').

$$\ln \left( \frac{U_{i+1}}{U_i} \right) = \frac{r}{qB_w} \left( \frac{U_{i+1} + U_i}{2} \right) - q \frac{f_{i+1} + f_i}{2} \quad \text{where} \quad r = b_0, B_w = \frac{b_0}{b_1 \cdot b_2} \quad \text{and} \quad q = b_2$$

**Non linear time series fitting (iterations, e.g. Solver)**

Based on a different form of the Schaefer model:

Next biomass = This biomass + Surplus production – Catch

but forwarding the next biomass estimation $\hat{B}_{i+1}$ from the previous estimation $\hat{B}_i$:

$$\hat{B}_{i+1} = \hat{B}_i + r\hat{B}_i(1 - \frac{\hat{B}_i}{B_w}) - C_i$$

Estimated catch rates $\hat{U}_i$ are then calculated from

$$\hat{U}_i = \hat{q} \cdot \hat{B}_i \quad \text{or} \quad \hat{C}_i = \hat{q} \cdot \hat{f} \cdot \hat{B}_i$$

The equations are balanced by minimising the squared deviation between the estimated and the observed catch rates:

$$\text{Deviation}_i = (U_i - \hat{U}_i)^2 \quad \text{and} \quad \text{SSQ} = \sum_i (U_i - \hat{U}_i)^2$$

or

$$\text{Deviation}_i = \ln \left( \frac{U_i}{\hat{U}_i} \right)^2 \quad \text{and} \quad \text{SSQ} = \sum_i \ln \left( \frac{U_i}{\hat{U}_i} \right)^2$$
The method requires an initial estimate of the first biomass in order to be carried forward. This can be estimated from

\[ \hat{B}_1 = \frac{CPUE_1}{\hat{q}} \]

Parameters to be solved by iteration are: \( r, B^\infty, q \). Seed these (insert values) with values from an initial estimate of the parameters (may be obtained through the regression methods described above).

Iterate (using e.g. Solver) by changing \( r, B^\infty \) and \( q \) until SSQ is minimised.

Alternatively estimate \( q \) analytically from (Polacheck et al. 1993).

\[ \hat{q} = \exp \left( \frac{1}{n} \sum \ln \left( \frac{U_i}{B_i} \right) \right) \]

and iterate (using e.g. Solver) by changing \( r \) and \( B^\infty \), until SSQ is minimised.

**Auxiliary knowledge** => fix one or more of these parameters. For example, under an assumed ‘long term steady state’, an estimate of total mortality \( Z \) may be used as a substitute for \( r \) (see Chapter 12 section 3 for further explanation).

The time series fitting can incorporate independent biomass estimates (as observed values instead of estimated from the model) of from e.g. swept area method.
11 Fishery concepts

11.1 Fishing effort, catch and catch rate

An understanding of fishing effort is fundamental for assessing and managing fish stocks. Most management principles involve deciding directly or indirectly upon the amount of fishing effort \( f \) that should be applied to the stock to obtain a certain amount of catch \( C \) that is sustainable over time (Rothchild 1997). Furthermore, the most commonly used contemporary method of estimating the relative abundance of an exploited fish stock is by using the catch per unit effort \( (C/f) \) as an index of abundance.

The basic assumption in fisheries theory is that catch \( (C) \) and stock abundance, or standing biomass \( (B) \) are related by

\[
C = q \cdot f \cdot B
\]  

(1)

where \( f \) is a measurement of the nominal fishing effort or intensity, and \( q \) is the so-called catchability coefficient (defined below).

**Fishing effort**

The nominal fishing effort \( f \) is expressed in, for example, the number of fishermen, the number of boat-days, the number of meters of gill-net set, the number of hooks set, the number of pulls or shots made, etc. For fisheries data, however, it is very difficult to measure the nominal effort precisely, and, in particular, to standardise it in terms of relative fishing power. Unfortunately, due to changes in the catchability coefficient \( q \), there is no necessary fundamental relation between the magnitude of the nominal effort and the magnitude of the catch. For stock assessment purposes, there is therefore a need for a measure of fishing effort that has a constant effect upon the fish population. This measure, commonly used in the population dynamics literature, is the so-called fishing mortality.

**Fishing mortality**

The fishing mortality \( (F) \) is simply defined as the fraction of the average population taken by fishing. In other words, \( F \) can be considered as an invariant measure of effort (Rothschil 1977). \( F \) is also called the instantaneous rate of fishing mortality, i.e. the rate at which fish are dying due to fishing, and therefore expressed per time unit, usually per year. \( F \) can be measured without reference to the nominal effort, the configuration of the fishing gear, or the manner in which the gear is employed. \( F \) can be defined as

\[
F = \frac{C}{B} = q \cdot f
\]  

(2)

Although \( F \) is defined as the fraction of the average population abundance taken by fishing, and therefore intuitively should take values less than 1, it can in practice have a value of more than 1 on an annual basis for stocks with a high biological regeneration rate. This is because
the annual *productivity* for such stocks, and therefore the cumulated annual catches, can be much higher than the average standing abundance (mean biomass). These are stocks with a so-called high biological turnover, or high production to biomass ratio \( (P/B) \), which is often the case for smaller sized tropical fish species (these production concepts are further defined below).

The catch rate \((C/f)\) or Catch Per Unit of Effort \((CPUE)\) is the catch per unit of effort over a time interval and defined as

\[
CPUE = \frac{C}{f} = q \cdot \bar{B}
\]  
(3)

For scientific research surveys, or experimental fishing, effort is standardised and fishing gears kept constant in order to keep a simple relationship between catch rates and population abundance \((B)\), i.e. to minimise the inherent measurement errors and/or variations in \(f\) and \(q\). However, this so-called *fishery-independent monitoring* of stocks through scientific surveys is expensive and surveys often cannot generate the amount of data needed for the evaluation of states or changes in fish stocks or mortality rates (fishing pattern).

In many parts of the world, the main supply of information on fishing effort, catch and catch rate is through monitoring of fisheries input (fishing effort) and output (catch), i.e. through *fishery-dependent monitoring*. Long-term monitoring of fish stocks is therefore almost by necessity dependent on information obtained through the fisheries exploiting them and on the official fisheries statistical system in use. Fishery-dependent monitoring entails at least the collection of two essential parameters in fisheries statistics: catch \((C)\) and fishing effort \((f)\) and, from these, the derivation of catch-rate \((C/f)\) (FAO 1999). Catch and effort data collection systems, which address information needs for fishery management, vary in their degree of administrative and statistical sophistication, but all share the collection and maintenance of these basic parameters.

**Catchability**

Catchability \((q)\) is defined (see Eq. 3) as the relationship between the catch rate \((CPUE)\) and the true population size \((B)\). So, the unit of catchability is *fish caught per fish available per effort unit and per time unit*. Catchability is also called gear efficiency (Hillborn and Walters 1992) or sometimes fishing power, and is strongly related to gear selectivity (defined below) because it is species and size dependent. Sometimes, gear selection is simply defined as the relative change in \(q\) (Godø 1990). Therefore the fishing mortality \((F)\), as a function of the size (length) of fish, i.e. the fraction of fish caught per fish in the population, has the same shape as the gear selection curve \((S)\), but with a different value depending on the nominal effort (see Figure 19 in Chapter 7).

In other words, when effort \((f)\) is equal to 1 (unit), then:

\[
q = F = S
\]  
(4)

This means that \(q\) can conceptually be considered as the probability of any single fish being
caught. Therefore $q$ ranges between 0 and 1.

However, the probability of a fish being caught at any time depends on several factors, not only man-made, and can broadly be grouped into biological and technological factors:

1) **Biological factors** include:
   - fish availability on the fishing ground
   - fish behaviour towards the fishing gear
   - the size, shape, and external features of the fish

   where some of these factors again are dependent on season, age, environment and other species

2) **Technological factors** include:
   - Gear type, design, size, colour, and material
   - Gear position, duration, and handling
   - Experience of the fisherman

   where again these factors are dependent on biological changes

As both the unit and the different notation epitomise, the catchability coefficient (alias efficiency, or fishing power, or probability of a fish being caught), is therefore a composite and very complicated factor. Conceptually, however, ‘fish catchability’ implies primarily changes in fish behaviour (May 1984), whereas ‘fishing efficiency’ indicates changes in fishing practises (Neis *et al.* 1999) or in relative fishing power. As information on the possible causes of variation in $q$ is normally lacking, the biological and technological factors are for practical purposes normally assumed invariant of abundance, time, species, size/age, and individual skills of fishermen. However, only under this very rigid assumption can the catch rate ($CPUE$) be considered directly proportional to the stock abundance (Hillborn and Walters 1992) and be used as an index of the stock size.

Consequently, the catchability ($q$) cannot be quantified directly if catch rates are used to estimate stock sizes. The standard solution to evaluate changes in efficiency (fishing power) in a fishery over time, and with that the catchability, is, therefore, to compare catch rates from commercial and research fishing where the catchability of the research fishing is being held constant from year to year (Neis *et al.* 1999):

$$\frac{CPUE_{fishery}}{CPUE_{research}} = \frac{q_{fishery}}{q_{research}}$$

This method requires several years of data in order to detect relative changes in the efficiency of the commercial fishery. If the commercial fishing efficiency or fishing power is rising, this lag in time, before eventual changes are discovered, will lead to overestimation of stock size. (Pope 1977).
Figure 20. Fishing mortality ($F$) as a resultant of nominal fishing effort ($f$) and catchability ($q$). The number of units expresses nominal fishing effort, while catchability can be expressed by the efficiency of one unit of fishing effort.

The variability and elusiveness of the parameter $q$, and the difficulties in quantifying it, are a very important reason for the difficulties in analysing the relationship between the magnitude of nominal effort (which is also difficult to measure) and the direct effect on the regenerative capacity of the stocks. Changes in $q$, which are mostly unaccounted for, induce additional uncertainty in the parameter catch rate as an index of stock abundance, if $q$ simply varies through time. If there is a unidirectional change in $q$, as a result of, for instance, increased fishing power of a unit of effort over time, catch rates – and with that stock abundance - will be systematically overestimated. This is also an important reason why, to a large extent, fisheries science is operating with the parameter ‘fishing mortality ($F$)’ instead of the parameter ‘fishing effort ($f$)’. Unfortunately, fishing mortality is notorious for its non-comprehensibility outside the fisheries scientific community. However, in equation (2), the elusiveness of $F$, and its relationship with nominal effort and efficiency in a biological sense (i.e. the efficiency with which a fish is caught), may become somewhat less obscure when illustrated graphically (Figure 20).

11.2 Selectivity

A generally important technical measure for fishing gears is the size selectivity, which is defined as the probability of fish being retained in a fishing gear as a function of the length of the fish (Misund et al. 2002). These probabilities are often expressed as various mathematical models. A selection curve (i.e. the probability of capture plotted against the size of the fish) for trawl gears is mostly sigmoid or S-shaped, whereas bell-shaped curves are normally the case for gill-nets and hooking gears. Important selectivity measures are $L_{50}$, defined as the fish length, where the fish have a 50% probability of being retained by the gear on encounter, and the selection factor, defined as $L_{50}$ divided by mesh size in cm. In addition to the selection range which is defined as $L_{75} - L_{25}$ ($L_{75}$ is fish length where 75 % of the fish is retained, and $L_{25}$ is fish length where 25 % of the fish is retained), these parameters describe the size selection characteristics of fishing gears.
All fishing gears are species and size selective; this is not different in multi-species fisheries where one type of gear may catch a set of species, while another gear or the same gear used in a different way or different area may catch another set. This means that all fishing gears are only able to catch a certain portion of the total (multi-species) fish community present. The use of the catch rate as an index of abundance of a fish stock is therefore further complicated by the selectivity of a fishing gear. Catch rates only reflect the abundance of the fishable stock or, in other words, that portion of a fish population or fish community that can be caught by a specific gear. Catch rates can be used as an index of abundance for the total stock, under the assumption that all specimens within a (multi-species) stock at some stage during their life become part of the fishable stock.

The area of operation of a gear, the inconstant behaviour of the fish relative to the gear, and the size of the fish determine the part of a stock that can be caught by a gear. As discussed, these factors are all included in the parameter catchability. Selection may therefore differ in different areas of operation simply because of the species and sizes present on a fishing ground. For example, seines with small mesh sizes operated in shallow areas near shore that act as nursery grounds will have a higher probability of catching juvenile specimens than if they are operated further offshore, where these fish are not present. Species behaviour may change seasonally as a function of several factors such as migrations, spawning or temperature, and, by this, the probability of catching it with a certain gear. Furthermore, species may develop avoidance behaviour towards gear, which will result in a lower catchability.

Fishing gears are intrinsically associated with selectivity, and selectivity, or the impact of fishing on an ecosystem, is an essential component of a management programme (Pauly and Christensen 2001). The importance of selectivity is therefore rooted in most researchers and managers, and any non-selective capture method automatically carries the connotation of being harmful, bad, or destructive, or will at least lead to growth-overfishing seen from the traditional single-species perspective. Mesh size- and gear restrictions are therefore among the most easily applied and widely used management regulations. Consequently, most nations have imposed legislation, which bans certain gears and mesh-sizes with the aim of protecting the resource (Gulland 1982). Although many of these regulations originated from problems associated with the large scale-fisheries (Misund et al. 2002), they are often uniformly applied on all sectors. However, selectivity seems much more a problem for industrialised fisheries, which, on average, dump about 45% of their catch, while small-scale artisanal discards, on average, only 5% (Bernacsek1989), despite the fact that they mostly operate in more multi-species environments. Although numerous authors have already pointed to the problems of defining the “right” mesh-size in a multi-species fishery, the notion of regulations on selectivity still persists.
12 Ecological concepts in relation to multi-species fisheries

The following theoretical review on general ecological concepts is intended as a background for understanding multi-species considerations in stock assessment and fisheries management. Some of these concepts are used in multi-species models such as ECOPATH (Walters et al. 1997).

12.1 The regulation of populations and mortality as a key parameter

The population (stock) is the basic unit in ecology. Individual fish are born, grow and die. A fraction of these will succeed to reproduce before they die and basically they have then done their mission in terms of evolution. The population contains unique dynamic features not shared by individuals such as: birth rates, death rates, age structure, phenotypic plasticity, and gene pool. These attributes, which are shaped by the environment (evolution under natural selection), can be collectively summarised under the term life-history traits (Stearns 1976), and their configuration determines the resistance of the population to external disturbance and stress. Originally, Darwin (1859, p. 102) formulated this as: "Owing to the high geometrical rate of increase of all organic beings... the favoured forms increase in numbers,... [and] the less favoured decrease and become rare. Rarity, as geology tells us, is the precursor to extinction". However, the meaning of this process is still unknown. One suggestion is "Evolution is like a game, but where the only payoff is to stay in the game" Slobodkin (1964). Nevertheless, fishing activities is but part of many stress factors in a population, and one can understand the adaptations and life history traits of a population that cope with natural mortality factors, and one can also evaluate the effect of fishing on these stocks.

The diversity and abundance of natural populations is maintained and regulated through a series of interacting factors and associated fundamental concepts in population and community ecology such as: density dependence, compensatory mechanisms, stability and resilience which will be elaborated below. There is a distinction between internal processes that are regulated by the abundance of the population itself, such as density dependence, and external processes that are controlled by the surrounding environment and community of other species, such as compensatory mechanisms in response to disturbances, predation and competition. Density dependence, for example, is of decisive importance in nature because without this concept, one fails to explain the relative stability that populations exhibit over time, despite their innate capacity to grow geographically (e.g. Tanner 1966, Slobodkin et al. 1967, Kozlowski 1980, May 1991). On the other hand, compensatory mechanisms, or adaptive responses, are fundamental principles of evolution. Without compensatory properties, a population in a density controlled multi-species system exposed to long-term increased mortality from predation or fishing would ultimately perish. In the evolutionary game, however, internal and external processes are interacting and mutually dependent, and a clear understanding is often lacking. As a result, most theories on population and community ecology, life-histories and biomass regeneration are unfortunately rather fuzzy and difficult to interpret. Often, however, they can be reduced to show that the processes they aim to explain can be closely associated with the pattern and rate of mortality (Kolding 1994, 1997).
From an ecological point of view, therefore, mortality represents a holistic unifying concept that ‘explains’ the diversity, abundance and dynamics of populations. In essence, it is the transience of life, not life itself, that is the driving force of evolution simply because dying is more certain than giving birth. Therefore, by its focus on the role of mortality, the following treaty will define and elaborate some ecological concepts in order to possibly elucidate how the fishing pattern and increased fishing effort affect the regeneration of stocks in different ecosystems.

12.2 Production, productivity, trophic level, and density dependence

Biological production ($P$), the total amount of tissue generated in a population during a given period in time and space, is of central interest in the exploitation of renewable resources, because the yield is a fraction of this quantity.

\[ C = F \cdot \bar{B} = x \cdot P \]  

(1)

The term production, thus, includes both living and dead organisms within the time period, even if the biomass of the dead organisms does not physically exist any more. Gains in biomass are a result of individual growth, new offspring, and immigration, whereas death and emigration cause losses in biomass. 'Surplus' or net production (i.e. after natural mortality has been subtracted) is essential to any population that expands and/or yields a proportion to higher trophic levels without declining.

**Trophic level**

The concept of *trophic level* (Lindeman 1942) means grouping taxa or populations into discrete levels according to their place in a food chain, e.g. primary producers (plants and algae), herbivores, first-order carnivores, second-order carnivores, etc. This system is used to simplify the description of an ecosystem, but also to describe the interactions and efficiencies of energy transfers between trophic levels. Most models used in fisheries are single-species models with only two ‘trophic levels’, the stock and, as the only predator, the fisherman. Multi-species models, involving feeding interaction between several species or trophic levels, usually require a lot of data and are difficult to implement.

**Density dependence**

The sigmoid curve theory (Graham 1935) is describes only the change in production and biomass within a population. The theory presupposes that the regeneration of biomass, or net rate of increase, is a density dependent function of biomass ($dB/dt = g(B)$), which is dome shaped with its highest point at some intermediate level between 0 and a maximum density. It is this point that has initiated the concept Maximum Sustainable Yield (MSY). Numerous mathematical equations can produce a sigmoid curve, but the simplest model for self-regulating growth in populations is the well-known logistic equation (Verhulst 1838). Although widely criticised for oversimplification (e.g. Kozlowski 1980), it has contributed much to ecological thinking and forming of ideas, and been experimentally verified on laboratory populations of fish (e.g. Silliman and Gutsell 1958). Perhaps its greatest
applicability is in the illustration of the theory, which is best shown in its differential dome-shaped form

\[
g(B) = \frac{dB}{dt} = r_m B \cdot (1 - \frac{B}{K})
\]

(2)

where \( K = B_{\text{max}} = B_\infty \), or the theoretical carrying capacity of the environment, mainly determined by available food and space. The parameter \( r_m \) is the innate capacity or intrinsic rate of natural increase, defined as the maximum instantaneous rate of birth per individual \( (b) \), minus the minimum instantaneous rate of natural death per individual \( (d) \) under specific environmental conditions (Fenchel 1977). Logistic growth (Eq. 2) assumes that the instantaneous growth rate is decreasing proportionally with the numerical difference between \( K \) and the density \( (B) \) in relation to \( K \) (i.e. \((K-B)/K\)). Thus, the exponential growth of a population decreases as the relative saturation of the environment increases, until the asymptote \( K \) is reached and growth ceases. This means that the per capita, or actual, rate of increase \( (r) \) in the population is a linear function of density, with \( r = r_m \) at the intercept (Figure 21).

\[
r = \frac{dB}{B \cdot dt} = r_m - cB
\]

(3)

Furthermore, if it is presumed that the potential birth rate (fecundity) at the current evolutionary stage is constant (Ricker 1954, Beverton and Holt 1957) then the death rate must also be a linear function of the density, since \( d = b - r_m \). The assumption of density independent birth rate might not be true for the full range of \( r \). It is, however, generally accepted at lower population densities, and seems valid at least up to the inflection point \((K/2\) in Eq. 2) where intra-specific competition for resources starts affecting productivity (Begon et al. 1990, p. 202).

![Figure 21](image)

**Figure 21.** The linear way in which the per capita rate of increase in the logistic formula decrease density until the asymptotic \( K \) (‘carrying capacity’) is reached. Assuming density independent birth rates at lower population densities up to around \( K/2 \), the instantaneous death rate increases linearly with density in this interval. Modified from Begon et al. (1990)
Production is thus a density dependent *quantity* expressed in kilograms or tons often scaled by area or volume. Productivity is the rate or *speed* at which production is generated and is a function of both the individual biological regenerative characteristics of a particular species (the per-capita rate of increase), and the density \((B)\) of the stock. Productivity is the instantaneous rate of biomass production \(dB/dt\). In the presence of fishing the instantaneous rate of change in biomass is equal to the productivity minus the accrual rate of the yield, or combining Equations (1) and (2):

\[
\frac{dB}{dt} = g(B) - F \cdot B = g(B) - q \cdot f \cdot B
\]  

(4)  

or, in words, the change in biomass over a fixed period of time is the surplus production minus the yield:

\[
\text{new biomass} = \text{old biomass} + \text{surplus production} - \text{catch}
\]

When biomass does not change \((dB/dt = 0)\), then surplus is equal to output and a stock is said to be at an equilibrium. Reasoning along these lines has led to a set of important fishery models called surplus production models of which the Schaefer (1954) model (equivalent to Eq. 2) is an example. Another important inference is that, at any constant population size, the average total death rate \((Z)\) is equal to the intrinsic rate of increase \((r_m)\).

Productivity is also used more loosely when, for example, “changes in productivity” is related to “changes in fish yield”. What is meant in these expressions is that through environmentally driven processes, such as changes in nutrients, the productivity at different trophic levels changes, resulting in changes in fish production and, hence, fish yields. Therefore, in a changing environment, the idea of a constant carrying capacity (which is the underlying assumption for eqn. 2) is neither plausible nor necessary for conceiving density dependence or equilibrium situations. Steady state means that the actual rate of increase \(dB/Bdt = r = 0\). In a growing population \(r > 0\) and in a declining population \(r < 0\). Consequently, in nature the value of \(r\) for all non-extinct populations is fluctuating around a mean value of 0. It also implies that there will always be a set of environmental conditions at which \(r\) is positive, and a theoretical set even exists where \(r\) attains a maximal value \((r_m)\). Since \(r\) depends on the age structure in the population, it is clear that any specific value of \(r\) is only valid for a particular environment and mortality regime. The frequency and amplitude of oscillations in \(r\) must then be mainly related to the variability of the environment (the *extrinsic* factors). In fish, the change in \(r\) is dependent both on abiotic factors, such as temperature and oxygen, and biotic factors such as food and predation. Andrewartha and Birch (1954) argued that all factors limiting population growth must be considered density dependent. They grouped these in three main categories in an order of succeeding importance: i) shortage of resources like food and shelter, ii) inaccessibility of these resources in relation to the animal’s capacity of dispersal, and iii) the shortage of time when the rate of increase \((r)\) is positive. They considered the most important category, fluctuations in \(r\), to be influenced mainly by weather or predators, where, depending on the environment, it has overwhelming importance. The occurrence of intermittent short spells of optimal situations might well be illustrated by the strong year-class variation that is observed in most fisheries.
The huge variations are considered one of the biggest obstacles in fisheries modeling where, traditionally, an attempt is made to relate recruitment with stock size. Yet, stock-recruitment theory, as emphasised by Rothschild (1986), is simply a theory that attempts to account for the mortality of young fish between spawning and recruitment time. Thus, it may be generalised that there are two situations in which population size is largely determined by climate or largely determined by other animals, but where mortality is still the most important common denominator.

12.3 Compensatory mechanisms and multi-species interactions

Probably few, if any, natural animal populations utilise or occupy their environment to the carrying capacity (Andrewartha and Birch 1954, Slobodkin et al. 1967, Stearns 1977). Other species present will mostly either compete for the resources or be predators. The influence of other species is difficult to measure, although this is one of the main factors shaping evolution. On the other hand, if a competitor or predator is removed from the system and an expansion of other species is observed, then competition or predation is demonstrated (Levinton 1982, Deshmukh 1986). Such multi-species interactions have been observed in the North Sea (Andersen and Ursin 1977), in the Antarctic (May et al. 1979), in the Gulf of Thailand (Pauly 1979), in West Africa (Gulland and Garcia 1984) and in many fresh water fisheries (Paloheimo and Regier 1982, Carpenter et al. 1985), where heavy fishing pressure on larger, slower growing species lead to an expansion of smaller, faster growing organisms.

Comparing these observations with the tenets that:

- predation is believed the most important factor for natural mortality in fish (Sissenwine 1984, Vetter 1988, ICES 1988),
- adaptations tend to maximise fitness through optimal utilisation of resources (Slobodkin 1974, Stearns 1976, Maynard-Smith 1978),
- predators and prey are co-evolved (Slobodkin 1974, Krebs 1985) and,
- there is an uni-modal response of prey productivity to predator densities (sigmoid curve theory),

It is reasonable to presume that predation would 'maintain' prey populations close to their highest average production rate (Slobodkin 1961, 1968, Mertz and Wade 1976, Pauly 1979, Caddy and Csirke 1983, Carpenter et al. 1985). The argument follows simply from the sigmoid curve where the highest sustainable surplus production of the prey population ($dB/dt = \text{max} = \text{MSY}$) is also the 'carrying capacity' ($K$) of the predator population (see Figure 22 A).

The predators can in theory grow to reach $K (= \text{MSY}_{\text{prey}})$, but if they overshoot they will reduce the net prey production and, consequently, they themselves will decline from starvation. Stable 'equilibria' in such cybernetic density-controlled predator-prey relations are theoretically possible only up to the inflexion point of the sigmoid growth curve of the prey where $dB/dt$ is maximised.
Any additional mortality at this stage (as in time lagged predator-prey oscillations), however, requires a change in the life history strategy, if the prey is not to perish (Slobodkin 1974). In other words, when a population adapted to a relatively stable environment is submitted to more long-term changes in the external mortality forces, it must somehow respond by increasing $r$ (Roff 1984). This requires stress response or compensatory mechanisms (intrinsic changes) which again are related to phenotypic plasticity, a trait that is particularly prominent in fish (Stearns 1977, Stearns and Crandall 1984). Apart from anti-predator defence strategies, another strategy is to improve the average survival of the offspring either quantitatively (fecundity) or qualitatively (parental care) (e.g. Balon 1984). An example of the general importance of mortality on breeding strategies is Gunderson and Dygert's (1988) demonstration that the 'reproductive effort' (gonad-somatic weight index, GSI) had the highest correlation coefficient with natural mortality ($r^2=0.81$), compared to other life history parameters evaluated in 20 stocks of fish.
Figure 22. A simplified fish community of 3 trophic levels. Each box represents the biomass of each level (not to scale) relative to the 'virgin' biomass ($B_\infty$) of each level, under logistic conditions. Arrows indicate the flow of energy (net production) through the system. In the unexploited community (A), only the top-predator level is at the $B_\infty$ level because it gives no net production to higher trophic levels. For the lower levels, the maximum sustainable 'surplus' production (MSY) is passed on (= carrying capacity of next trophic level) so the biomass is at half $B_\infty$. In fisheries MSY=$BZ/2$, where B is the average standing biomass and Z the total mortality rate. The yield boxes in B) and C) represent the fraction of the production harvested by man under different exploitation patterns. Reproduced from Kolding (1994).
**r-K selection and size-specific mortality**

Basic ecological theory assumes that the life-history styles of all populations are to maximise the intrinsic rate of natural increase. In general, changes in the survival rate are less efficient in improving $r_m$ than in increasing the turn-over rate by decreasing the generation time ($T$), as follows from Eq. 5.

$$\frac{N_T}{N_0} = e^{rT} = R_o \Rightarrow r_m = \frac{\ln R_o}{T}$$  \hspace{1cm} (5)

where $R_o$ is the net reproductive rate per individual per generation, in this case, the maximum number of offspring each individual produces.

Empirical studies have shown that there is a strong inverse correlation between age at maturity and mortality, which can be considered as a trade-off between the advantages of being big and the probability of dying with time (Adams 1980, Gunderson 1980, Hoenig 1983, Roff 1984, Gunderson and Dygert 1988). Both Adams (1980) and Gunderson (1980) based the explanation of this phenomenon on the well-known theory of $r$- and $K$ selection. Traditionally, this theory was associated with the environmental stability, or rather the degree of 'saturation' (density) a population can reach in relation to fluctuating resources (MacArthur and Wilson 1967, Pianka 1970, 1972, Southwood *et al.* 1974, Boyce 1984). However, considering the indefinable relationship between the carrying capacity ($K$) and life history traits (Stearns 1977, Kozlowski 1980), the original interpretation of the $r$-$K$ selection is in many ways an inadequate explanation. Other authors (Murphy 1968, Schaffer 1974, Wilbur *et al.* 1974, Stearns 1977, Horn 1978) have, therefore, suggested that the different life-history styles should be considered a function of relative size-specific mortality. In essence: abiotic mortality, caused by the physical instability of the environment, is generally considered to influence the whole age structure of the population. Thus, a low-somatic and high-reproductive allocation of energy indicates that continued existence of the individual beyond the first reproduction is not profitable, due to the risk of dying from physical disturbances. On the other hand, biotic mortality (mainly predation) is considered foremost to affect the small/young individuals in a population (Cushing 1974, Ware 1975, Bailey and Houde 1989, Caddy 1991). Hence, if mortality is reduced with increasing size, it is advantageous to initially invest more in growth relative to reproduction. Empirically, this is corroborated by ‘Copes rule’, which states that in the evolution of relatively stable ecosystems there will be a tendency towards the development of larger sizes within the food-chains (Pianka 1970, Dickie 1972, Begon *et al.* 1990). In conclusion, the balance between reproduction and growth, in an optimal life history, seems determined from the relation between adult and juvenile survival (Charnov and Schaffer 1973, Horn 1978).

From this interpretation of the $r$-$K$ selection principle, then, theoretically, even for 'K-selected' species, a compensatory strategy against increased mortality on the adult stages would be to increase the turnover rate by reducing the generation time (Figure 23).
This has been corroborated by empirical studies: Power and Gregoire (1978) demonstrated that freshwater harbor seals strongly influenced the lake-trout population in a Canadian lake. By comparison with similar lakes in the same area without seals, they showed that seal predation significantly reduced the size, maturation time and abundance, but increased the relative growth rate and fecundity of lake-trout. Exploitation by man is usually strongly size selective on the larger individuals, and Estes (1979) considered this to impose an artificial $r$-selection on animals originally evolved through $K$-selection. Recently, such 'artificial evolution' has been supported by Law and Grey (1988) and Sutherland (1990). Significant reduction in age at maturity for heavily fished stocks has been observed in American plaice (Pitt 1975) and in the Northeast Arctic cod (Jørgensen 1990). Similarly, under naturally fluctuating size-specific mortality, tilapias are apparently able to adjust their mean generation time (Noakes and Balon 1982, Kolding 1993a).

To summarise so far; density, individual size, generation time, and changes in the value of these attributes over time, are all seemingly close functions of death rates in a population. The product of the first two factors gives the biomass, and the integration of biomass over time gives the production. A further condensation of biomass and production into the $P/B$ ratio directly reflects the mortality rate and vice versa.
Production processes are usually associated with the rates at which biological tissue move within trophic levels (Figure 22), and are thus dynamic quantities, which can rarely be measured directly. The environment determines primary productivity, which, depending on the number of species and network of food paths, determines the productivity at higher trophic levels. The production/biomass ratio (P/B), however, is one way of envisioning the time scale, by indicating the turn-over rate and thus the speed of the biomass regeneration. Calling the P/B ratio "the elements of synthesis", Dickie (1972) emphasised the central importance of this concept for understanding ecological and production efficiencies in relation to fishing pressure. The P/B ratio tends to decrease from one trophic level to another with distance from the primary production level, and also tends to have a general non-linear relationship with the sizes of organisms involved. This means that changes in size-composition of a population from human exploitation or predation will be reflected in the P/B ratio by a relative change in the generation time. The P/B ratio is thus an extremely useful parameter to characterise comparatively different systems, species or trophic levels within a system (see e.g. Le Cren and Lowe-McConnell 1980).

The relationship between the production rate and mean biomass was shown under more closely specified conditions by Allen (1971), who examined the P/B ratio for a number of mathematical models expressing mortality and growth. He found that for any growth model (except simple exponential), and with a simple exponential death rate, the P/B ratio is equal to the total instantaneous mortality rate (Z). Thus, the gross production per unit time, \( P = BZ^4 \), is entirely a function of the mean biomass and mortality rate. Allen (1971) also showed that if the mean generation time (T) is represented by the mean life span (this approximation implies that, on average, individuals in the population reproduce only once), and assuming simple exponential mortality, then, for any growth model, this was the reciprocal of the total instantaneous mortality rate Z, thus T = 1/Z. In other words, the reciprocal of the P/B ratio is a measure of the time it takes for the fish population to reproduce its own weight. In general, short-lived organisms, such as zoo-plankton, but also small clupeid fish such as Limnothrissa miodon, in Lake Kariba, have high rates of turnover and can regenerate the standing biomass several times per year. As biomass and production can vary over time (for instance seasonally or inter-annually) the turnover rate or P/B ratio changes as well. If such variation is caused by environmental factors or processes affecting an ecosystem but are external to it, one refers to environmentally driven processes, in contrast to human induced changes in an ecosystem, such as changes as a result of fishing.

The ecotrophic coefficient, the exploitation rate and exploitation pattern

In a fish community with several trophic levels, the amount of production, the speed at which it is generated, and the way it is dispersed through the food web, determine the amount that can be harvested by man. For fisheries management, the most important implication of density-dependent limitations to growth is that a fishery must substitute one form of mortality

\[ P = BZ^4 \]

This simple equation for defining the gross production (\( P \)) is, together with the ecotrophic efficiency (\( E \)) defined below, part of the master equation in the ECOPATH model (Walters et al. 1997).
for another, if the abundance is to remain stable, because the yield is simply the fished fraction of the total deaths. Consequently, in the traditional single-species production models, a reduction of stock size (from the theoretical $\frac{B}{g}$ at the carrying capacity $K$) is the prerequisite for increasing the 'surplus', and calculations are aimed at estimating the point of highest net regeneration rate (MSY). However, in a multi-species situation, if natural predation is already harvesting the resource close to this rate (as elaborated above), then a fishery is an additional uncompensated source of mortality and the population is driven to a collapse. Fortunately, the predation mortality is in practice simultaneously alleviated, as few fisheries focus on one single species, and the predators are also being harvested. In fact, the top levels in an ecosystem are often the first to be exploited intensively (Regier 1977, Beddington 1984). The management questions are then 1) how much of the production can be harvested (the exploitation rate), and 2) what is a rational harvesting strategy or exploitation pattern on the community, i.e. what rates should be applied to each stock. These proportions (the optimal exploitation rate and pattern) are complicated in a multi-species situation (Dickie 1972, May et al. 1979, Beddington and May 1982, Caddy and Csirke 1983). This is because the fishing mortality on one species not only will affect the target species, but will also cascade through the system by either increasing the lower trophic levels or decreasing the higher trophic levels (Figure 22). The proportion of the total generated production which can be considered as surplus, i.e. the part which is not used to maintain the population at a given level, is extremely difficult to define and, in fish stock assessments, mostly depends on the mathematical model chosen. In ecology, the ecotrophic coefficient ($E$), sometimes called ecotrophic efficiency, is defined as the proportion of the production over a period of time by trophic level (n) available as 'yield' (consumption) to the next trophic level (n+1). Dickie (1972) deduced, based on theoretical considerations, that the ecotrophic coefficient in nature is unlikely to exceed a value of 0.5 from the relationship (Ricker 1969)

$$\frac{P_{n+1}}{P_n} = E_n \cdot K_{n+1}$$  \hspace{1cm} (6)

if the ratio of production between two trophic levels (transfer efficiency) takes the conventional value of 10% (e.g. Kozlovsky 1968, and substantiated by Christensen and Pauly (1993) from 39 aquatic ecosystems) and the gross growth efficiency ($K$) has a value of 20% (e.g. Kozlovsky 1968, Jones 1982). Similarly, Heal and MacLean (1974 p. 95) concluded that the "consumption [=ecotrophic] efficiency for vertebrates preying on vertebrates may exceptionally reach 1.0, but is probably below 0.5 in most cases". In general this would imply that a maximum half of the production ($P$) is available as MSY.

In fisheries theory, the exploitation rate (also labelled E) is defined as

$$E = \frac{C}{P} = \frac{F}{Z}$$  \hspace{1cm} (7)

In principle, there is no difference between the ecotrophic coefficient and the exploitation rate if man is the only predator (interestingly, the exploitation rate in single species models also has a general recommended maximum value of 0.5, but is derived from other premises). In a multi-species fishery situation, however, the ecotrophic coefficient is the fraction that should
be shared between fishers and the fish predators, implying that the exploitation rate is lower or equal to the ecotrophic coefficient (Kolding 1993b).

The impact of fishing on a fish community can now be illustrated by combining the fisheries and ecological concepts defined above. In summary: The yield or catch is a fraction of the production and defined as $C = FB$. From the $P/B$ ratio, the production can be defined as $P = ZB$ (which shows why $C/P = F/Z$ in Eq. 7). The Maximum Sustainable Yield (MSY) = Carrying capacity of the next trophic level and has a theoretical maximum value of about half the total production, thus

$$MSY_{\text{prey}} = K_{\text{predator}} = \frac{P_{\text{prey}}}{2} = \frac{Z_{\text{prey}} \cdot B_{\text{prey}}}{2}$$ (8)

The remaining question is how to share the MSY, depending on how one wants the fish community to be composed. In the absence of other information, a conservative exploitation rate of 0.5 on top-level predators and 0.25 on lower levels could be used which means that man becomes the new top predator and otherwise share the rest fifty per cent. Such a fishing pattern will, in theory, keep the relative abundance of fish in the community unaltered, but will lower the overall biomass. The principle, together with the impact of different fishing patterns, is illustrated in Figure 22, which, for simplicity, assumes a steady state community under logistic conditions where $MSY = 0.5BZ$ at $B^*/2$. The system is closed, the primary production is finite, and it is required that the original species composition (in this case 3 stocks at 3 trophic levels) should be conserved. The general theories on co-evolution, unimodal prey-to-predator response and optimisation principles, suggest that under so-called 'virgin' conditions (Figure 22. A), the energy resource of each trophic level is defined by the maximum 'yield' from the level below. Then, the system begins to be exploited from the top level (Figure 22. B) by harvesting the MSY (i.e. reducing the 'virgin' biomass by half). This will decrease consumption by half and thus release half the 'yield' from the second level (MSY/2) for human exploitation. But, in theory no 'surplus' is made available from the first level. In Figure 22.C, exploitation starts from the bottom level. Removing a proportion of the MSY from the first level will reduce the 'carrying capacity' of the next level and thus reduce its 'virgin' steady state biomass to a new value $B^* < B$. This reduction will cascade up through the system and also affect the potential yields (MSY* < MSYn), but, in theory, the system will find a new balance under the new carrying capacities. As the lower trophic levels are having the highest productivity (highest $P/B$ ratio), the fishing pattern sketched in Figure 22.C seems the most rational solution to exploiting the whole system (i.e. maximising the output) without causing deep disturbances (Kolding 1994).

Caddy and Sharp (1986) described what they called the 'utopian', but optimal exploitation pattern, by which an ecosystem could be maintained in balance. They suggested fishing each component in proportion to the rate of natural predation, it is subjected to:

$$\frac{Y_1}{M_1B_1} = \frac{Y_2}{M_2B_2} = \frac{Y_3}{M_3B_3} \ldots = \frac{Y_n}{M_nB_n}$$ (9)

thus removing, as yield ($Y_i$), a constant proportion of the total production $P_i = M_iB_i$ for species $i = 1, 2, 3, \ldots n$. However, removing a yield must influence the production by
changing the mortality, the biomass and especially the age structure in the population. Therefore, \( Z_i \) should be substituted for \( M_i \), in which case, the relation (Eq. 9) becomes equivalent to the fishing pattern described above (except for the top predators).

In theory, due to gear selectivity, as described above, such an exploitation pattern in a multispecies community can only be achieved by employing a multitude of fishing gears. In combination, such gears can generate size-specific mortality pattern. Incidentally, in contrast with most fisheries theory based on single species considerations, such a fishing pattern should, in most systems, be highest on the smaller sizes to match the prevailing natural mortality pattern (see also Figure 22). In terms of gear selectivity, this has important consequences for most governmental legislation, which bans small mesh sizes and so-called non-selective methods.

### 12.4 Diversity, stability, resilience and regenerative capacity in different systems

Ecosystems are different from each other and have different fish communities. Are some of these ecosystems more productive or more vulnerable to fishing than others? And can some generalisations be made, based on their physical and biological attributes? The observed coexistence of several species in an ecosystem, the so-called biodiversity, and, particularly the natural regulation and maintenance of biodiversity, is theoretically a challenge (Kolding 1997). The basic unit in biodiversity is the individual species and normally the focus is on the number of species and the relative abundance and distribution of individuals within an ecosystem (the so-called *alpha* diversity). The more species, the more diverse the ecosystem, and the more one tends to value it in the prevalent contemporary cognisance. Consequently, fisheries are facing a dilemma against the drive of conserving biodiversity. For instance, FAO (1992, p. 5) wrote: "Continued high fishing intensity will contribute to a loss of biological diversity,... and this may lead to more unstable, and possibly lower, catches in the long term".

From the background assumption of “The balance of nature” (Egerton 1973), the system complexity, diversity, and environmental stability have traditionally been positively related to each other (Margalef 1968, 1969, Odum 1969). This ‘diversity-stability’ hypothesis has often led to the suggestion that highly diverse communities are particularly fragile to exploitation (May 1975, Sainsbury 1982). This conventional wisdom presupposes that the ‘goal’ or ‘strategy’ of nature is to reduce entropy (Odum 1969). “Succession generates diversity and diversity enhances stability” (Orians 1975). These notions, however, are somewhat difficult to reconcile with the overall tenet in the community ecology that: *interactions between populations are primarily negative* (competition, predation, parasitism); and symbiosis is only an exotic, and rather rare, case (Begon *et al.* 1990). On the contrary, reviews (e.g. Huston 1979, Connell and Sousa 1983, Pimm 1984) reveal that:

1) there is a continuum of temporal variability in the dynamics of most observed natural populations and communities,
2) there appears to be no evidence of multiple stable states, and
3) the more numerous the species, and the more strongly they interact, the less chance there is of stability.
Theoretical advancement in species diversity generations, notably the 'intermediate
disturbance hypothesis' (Connell 1978) and the 'dynamic equilibrium hypothesis' (Huston
1979), build on such non-equilibrium dynamic community assumptions. Both infer that
frequent but irregular disruptions are a major agent in maintaining high diversity
communities. In general, the various hypotheses for the regulation of diversity can be
grouped into so-called equilibrium and non-equilibrium models (Tonn and Magnuson 1982,
Petraitis et al. 1989, Begon et al. 1990) where selective - density dependent - predator
induced mortality belongs to the first category, whereas catastrophic - non-predictive -
density independent – environment induced mass mortality belongs to the latter. However,
common to all these hypotheses is that population reductions in the form of either selective
(predation) or non-selective mortality, (environmental disturbances) is the main mechanism
for the regulation of species numbers. The logic is that individual population densities must
be kept lower than the carrying capacity to prevent the effects of strong mutual interactions,
the so-called competitive exclusion principle (Hardin 1960). Whether the hypotheses are
based on selective mortality (equilibrium models), or on non-selective population reductions
(non-equilibrium models, both models groups predict the highest diversity to be at an
intermediate level of predation stress or disturbances, i.e. the various populations never gain
enough dominance to competitively exclude others. Basically, equilibrium models deal with
the maintenance of a steady state, while non-equilibrium models address the approach to a
steady state (Petraitis et al. 1989). But, in fact, the difference between the two groups of
models can simply be reduced to a situation where the population reductions are either
continuous or discrete (Kolding 1997). In other words, the creation and maintenance of
biodiversity can be considered regulated by the mortality pattern in the ecosystem.
Depending on the size of the selective forces and the frequency of disturbances relative to the
mean generation time, this will result in either r- (density independent) or K- (density
dependent) selection (see definition above).

The presumed positive effects of disturbances and population reductions to maintain
biodiversity, pose a theoretical paradox for fisheries because human induced stress (any
anthropogenic factor that increases mortality) is generally considered to be the main cause for
loss of biodiversity. It seems that there is a qualitative, a wholly subjective, distinction
between natural and unnatural disturbances in the current discussion of biodiversity. In
principle, there need not to be any difference between the natural mortality pattern and the
applied fishing pattern in an ecosystem. On the contrary, as elaborated above, a rational (but
perhaps utopian) exploitation in any ecosystem would be to generate a size-specific fishing
mortality (fishing pattern) that is proportional with the natural size-specific mortality pattern.
In theory, this can be done by the right combination of gears and effort. Additionally, by
observing the changes in the biomass-size spectrum of the exploited fish community, one
now has a tool for evaluating the impact of fishing on the regenerative capacity of the stocks.

It is now possible to return tentatively to the question of the positive relationship between
diversity and stability, and the relationship between stability and resilience, although the
cause-effect is not clear. These concepts, however, are deeply rooted in ecology and often
used, although the various definitions are completely muddled up in the literature (Kolding
1997). Fishing, predation, and environmental changes, all cause stress, and the capacity to
recover, persist, endure or ‘bounce back’ to a previous state is theoretically associated with
the two concepts: *stability* and *resilience*. According to one of the better known definitions (Holling 1973), stability is then "The ability of a system to return to an equilibrium state after a temporary disturbance, the more rapidly it returns and the less it fluctuates, the more stable it would be". Thus, in this definition, stability is the property of the system, and the degree of fluctuations around specific states is the result. Resilience is, according to Holling (1973), "A measure of persistence of systems and the ability to absorb change and disturbance and still maintain the same relationships and composition between populations or state variables [irrespective of relative abundance]". In this definition, resilience is the property of the system, and persistence, or the probability of extinction, is the result. In Holling's view, instability, in the sense of large fluctuations, produces a highly resilient system capable of repeating itself and persisting over time until a disturbance restarts the sequence. Thus, systems can be very resilient and still fluctuate wildly. Holling (1973) states that these two distinct properties alone define the behaviour of ecological systems. In terms of the *r*-K selection principles (in the sense of trade-off between generalised or specialised species), Holling’s definitions fulfil the usual assumptions of a relationship between *r*-selection and resilience, and between K-selection and stability. However, any measure of stability requires a time-perspective that must be seen in relation to the life span of a species, in which case the two concepts lose their meaning. A temporary fluctuating lake may be considered as a very unstable environment for long-lived species, but rather stable for daphnia and rotifers. The ambiguities in the literature between stability and resilience might thus, like the equilibrium and non-equilibrium models, simply be a matter of scale. Therefore, as described under the *r*-K selection theory and the regulation of biodiversity, the mortality rate and pattern represent the speed of regeneration against which stability and resilience should be measured. As shown in Figure 23, ‘stable’ communities have, on average, a low *r* and *Z* with a corresponding longer life-span, whereas resilient communities have a high *r* and *Z*, but a shorter life-span. What determines resilience and stability, depends on the combination of stress (continuous selective or discrete non-selective mortality) and the trade-off between the advantages of being big, or developing specialised behaviour, and the probability of dying with time. In the game of evolution, this may be formulated as: "Disturb an early succession, and it becomes an early succession. Disturb a climax community and it becomes an early successional stage that takes time to return to climax". (Horn 1974).

In summary, all the preceding ecological concepts and processes can now be generalised into two broad categories, where the environment determines the prevailing mortality pattern:

- The unstable environment characterised by discrete, density independent, non-predictive, non-selective mortality from physical changes
- The stable environment characterised by continuous, density-dependent, predictive, and size-selective mortality from the biotic community.

These two broad categories represent only extremes along a continuous axis; the stability and the instability must be seen as a time function in relation to the mean generation time of the populations. Thus, even for the ‘unstable’ environment, there are two strategies: either follow the fluctuations (boom and bust or ephemeral species) or endure the disturbances (long-lived resistant species). For the latter strategy, the unstable environment may even no longer be
unstable, but only periodic. The various concepts and biological attributes may now, for simplicity, be repeated under the two categories:

<table>
<thead>
<tr>
<th>Environment</th>
<th>Unstable</th>
<th>Stable</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mortality pattern</td>
<td>Non-selective, unpredictable, discrete</td>
<td>Selective, predictable, continuous</td>
</tr>
<tr>
<td>Density</td>
<td>Fluctuating, density independent</td>
<td>Stable, density dependent</td>
</tr>
<tr>
<td>Model assumptions</td>
<td>Non-equilibrium</td>
<td>Equilibrium</td>
</tr>
<tr>
<td>Natural selection</td>
<td>$r$-</td>
<td>$K$-</td>
</tr>
<tr>
<td>P/B ratio</td>
<td>High</td>
<td>Low</td>
</tr>
<tr>
<td>Generation time</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>Productivity</td>
<td>Fluctuating, high</td>
<td>Stable, low</td>
</tr>
<tr>
<td>Species interactions</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>Diversity</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>Vulnerability to fishing</td>
<td>Low</td>
<td>Depends on fishing pattern</td>
</tr>
</tbody>
</table>
13 Perspectives

Application of Environmental Principles into Practical Fisheries Management

Present fisheries are primarily managed on population dynamic theory based on the level of single species populations. There is some theory at the community level of biological organisation (see section 11) but very little at the ecosystem level, which is needed if ecosystem considerations are to play a role in future fisheries management. In fact, the need for precautionary management of marine resources based on ecosystem principles is now believed both obvious and crucial for fisheries. Undoubtedly, those having a realistic appreciation of species interactions have realised that management on multispecies or ecosystem basis should be a logical way to proceed. (UNESCO-SCOR-IOC 2001\textsuperscript{5}).

In this regard, there are now various initiatives for defining quantitative ecological indicators that assess marine ecosystems, promoting a sound theory to support principles for developing Ecologically Sustained Fisheries.

- 1992 **Convention on Biological Biodiversity** raised an awareness to the ecological impact of many of the high seas fisheries in the high seas and coastal zone fisheries.

- 1997 Bergen **Intermediate Ministerial Meeting of the North Sea Conference** recognised that many of the measures applied in fisheries have only been partly successful in achieving a balance between fishing effort and the available fish resources. It advocated establishing Total Allowable Catches (TAC) and the need to implement the precautionary approach in the future fisheries and environmental management in the North Sea.

The practical application of environmental principles has been discussed at length in many fora, but when it comes to the use of the concepts in practice, it has proved difficult to get agreement as to how and which measures should be taken. The critical point is which measure is necessary to ensure sustainable development without negative environmental impacts, to ensure social and economic sustainable development in harmony with the ecosystem.

Sustainable

The concept of sustainability has been embedded in fisheries literature for about half a century, at least, in the concept of maximum sustainable yield (MSY). This concept has been used for decades as a measure of fishery potential and, unfortunately, sometimes as fishery development and management targets. In the post UNCED\(^6\) era, the general concept requires explicitly that both the conditions of the ecosystem and the people living in it be either "good" or improving. There may be a number of interpretations of "goodness" (Garcia 1996). Prescott-Allen (1996) considers that "ecosystem well-being is a condition in which ecosystems maintain their quality and diversity and, thus, their potential to adapt to change and provide a wide range of choices and opportunities. Human well-being is a condition that all members of the society are able to define to meet their needs and to have a large range of choices and opportunities to fulfil their potential. A sustainable society would be able to achieve both conditions, as well as having the capacity to anticipate change and recover from eventual setbacks".

Fisheries

Aims to avoid exploitation that reduces stocks to level where recovery is difficult. The terms that are central to support the environmental principles are elaborated in the box below\(^7\)

---


**Convention on Biological Diversity (CBD)** defines “sustainable uses of component of biological diversity in a way and a rate does not lead to the long-term decline of biological diversity, thereby maintain its potential to meet the needs and expectations of present and future generations”.

**Biodiversity**: Biological diversity integrates the concept of the ecological complexes of which the organism is part. It includes diversity within and between species of an ecosystem.

**Precautionary Approach**: Lists a set of measures and procedures to prevent risk in the management of certain fisheries resources.

**Responsible**: The code of conduct sets out principles for most of the sectors involved in the fishing activities with the view “to ensure the effective conservation, management and development of living aquatic resources with due respect with the ecosystem and biodiversity”.

**Ecosystem Approach**: Reflect a holistic approach to nature and environment. Components of nature do not exist in isolation, but interact and depend on each other. This is seen in multispecies stock assessment.

### The effects of fishery on the ecosystem

- Depletion of species
- By-catch species
- Destruction of marine habitats and the marine environment by pollution and contamination

#### Ecosystem effects of fisheries

- **i) Stocks.** Sustain exploitation on surplus production bases on the basis of low risk, by application of PMP (Precautionary Management Principles). Stock depletion has serious incidences in fisheries activities rather then in ecosystems.

- **ii) Habitat.** Demersal trawling causes serious effects in bentic habitats and coastal areas.

- **iii) Pollution.** Consequences of the industrial activity and uses of harmful substances and combustible.

#### Application in fisheries research

- **i) Biological Reference Points.** Represented by $F$ to TAC in $F_{\text{max}} > F_{0.1}$ or $> F_{\text{med}}$ SS by biomass is poorly considered.

- **ii) Precautionary approach in advice.** Seeking BRP in line with realities and address statistics uncertainties.
New BRP

**B**$_{lim}$: Lowest SSB to give good recruitment. Below **B**$_{lim}$ stock threatened.

**F**$_{lim}$: Above **F**$_{lim}$ recruitment will be hampered and stock declines.

**B**$_{pa}$: Lowest SSB to give good recruitment. Above **B**$_{pa}$ stock sustained.

**F**$_{pa}$: Below **F**$_{lim}$ low level of risk.

Science and Uncertainty relating to Advice

Risk assessment and management

Hilborn *et al.* (2001) says “Risk assessment aims primarily at evaluating the consequences of various harvest strategies in terms of probabilistic statements about future trends in yields, biomass and dangers to the stock, while risk management involves finding and implementing management policies, strategies, and tactics that reduce the risk to the communities exploiting them. At best, risk assessment will tell us the appropriate probabilities and details about the consequences of various management actions, including no action. But in the end, the choice will be a gamble – how will the fishery management agency balance the risk of assured social and economic dislocation of fishery is closed against the possible longer term social economic dislocation of a fishery induced stock collapse and the biological threat of a such a collapse. Risk analysis and risk assessment do not provide better policy choices, they only evaluate them. It is therefore necessary to move from risk assessment

Precautionary Approach:

1. Acknowledges the difficulties to give advice by SSB and gives advice by F. Uncertainties quantify by statistics. i.e. observed-estimated.
2. One can never be certain that one’s perception of fish dynamics is certain. i.e. uncertainties and application of models.
3. Scientists are demanded to express and quantify uncertainties.

The precautionary approach alone cannot be a techno/scientific/bureaucratic-driven process, and if the well-being of fishing communities is not taken into account explicitly, the process will fail.

Management in line with Environmental Principles

SCOR-IOC (UNESCO)’ under its Working Group 119, on ‘Quantitative Ecosystem Indicators for Fisheries Management’ has launched the following criteria for proposals on this subject. Further information is available at [http://www.ecosystemindicators.org](http://www.ecosystemindicators.org)

1. **Constraints**

The ecosystem indicators should:

- be reasonably simple to compute and understand
- have an intuitively reasonable interpretation
- be discussed and argued in a comprehensive way (statistically, mathematically and/or ecologically)
- have some appropriate foundation in terms of an ecological theory, statistics or mathematics.
- be applicable to marine ecosystems

2. **Environmental Indicators**

Using satellite imagery (particularly in upwelling and coastal area):

- Spatial statistics of the upwelling event/region/system
- Habitat structure (heterogeneity and complexity at different scales)
- Triad indicators (i.e. how to quantify retention, concentration and production processes)

3. **Ecological Indicators**


- Multivariate methods: Ordination, Tree (Cluster Analysis), PCA (Principal Components Analysis), CA (Component Analysis) or other statistical analyses.
- Aggregated indicators of ecosystem status: size spectra,…
- Emergent property indicators: food web from mass balanced models: primary production required to sustain the fisheries, mean trophic level, transfer efficiency between exploited trophic levels, FIB index.

4. **Fisheries Indicators**

- Using catch time series: changing regimes in ecosystem dynamics (change in means and variance structure)
- Using fishing effort: characterise fishery activities, biomass distribution and catch distribution
- Using acoustic survey: characterise biomass distribution and overlap between biomass distribution and catch.
- GIS (Geographical Information System) to determine ecosystem indicators.

5. **Socio-economic Indicators**

- Ecosystem value/fisheries value, ecosystem services, economic value of non-consumptive versus consumptive uses, ecosystem health and ecosystem integrity.
14 References


Pauly, D. and David, N. (1981) ELEFAN 1, a BASIC program for the objective extraction of growth parameters from length-frequency data. *Meeresforsch*, 28 : 205-211.


Appendix I  Questionnaire sent to participants in preparation of the course

AdriaMed Stock Assessment training course in Split, September 2001
(ASSESS-2001)

Putting together the pieces of a puzzle is one of the main tasks in stock assessment. Stock assessment involves both biological interpretation, and the use of various statistical and mathematical calculations to make quantitative predictions about the reactions of fish populations to alternative management choices. The analyses include history of the past, determination of the present stock status, and forecast about the future. Two essential key words are: quantitative and choices.

Nowadays, stock assessment often goes further than applying a general biological model, to building what essentially amounts to a computer simulation of the specific fishery and the resource. The resource part of the simulation is a model of the dynamics of the fish population, while the fishery part aims at representing the harvesting and the data generating process. These two components interact to produce predictions about properties of the resources under different scenarios and under different assumptions. In addition, more and more assessments are now incorporating the influence of abiotic variations on the stock sizes. In principle, any stock assessment process implies at least three components. 1. A good overview of the fishery harvesting process and the data generated. 2. Choosing a model according to assumptions and available input parameters. 3. A sound criterion to judge the goodness of fit to the data of any particular model and the output parameter estimates. Once the stock assessment is complete, choice remains. There is a distinction between assessment of biological potential and the decision on how to manage the stock.

Questionnaire

1) What do you expect ASSESS will add to your professional background?

2) Do you consider that any specific subject/method should be specially treated during the ASSESS? Please mention only one or two subjects.

3) Give the scientific and common name of the fish species or mollusc on which you focus your research efforts.

4) What kind of fisheries data will you bring to ASSESS to be worked with during the exercises in the course? What period does it cover? Please mark only two options and add the name of the fish species treated.
   - Fisheries statistics
   - Research surveys
   - Age-length key
   - Weight–length key
   - spatial distribution and abiotic data
   - recruitment
   - migration
   - feeding
   - reproduction
5) Could you describe the reliability of your statistics fisheries data as by: historic collection process? How are they collected? How complex are they? Are they suitable to be applied in simple assessment models?

6) What kind of stock assessment model(s) are you familiar with or frequently applying in your research tasks and/or in your stock assessment? How do you estimate M and F?

7) Which kind of management regulations and target reference points are used on your fisheries? How are the fisheries monitored?

8) Can you illustrate the importance between predicted and observed data?

9) Do you consider that stock assessment is a science, and why?
Appendix II  Course evaluation by participants

**AdriaMed Stock Assessment training course in Split, September 2001**  
*(ASSESS-2001)*

**Course Evaluation**

1. How do you find the correspondence between the objectives of the course and its content

<table>
<thead>
<tr>
<th>Very good</th>
<th>Very bad</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>8</td>
</tr>
</tbody>
</table>

2. Were your expectations fulfilled?

<table>
<thead>
<tr>
<th>Very much</th>
<th>Not at all</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>4</td>
</tr>
</tbody>
</table>

3. What was your knowledge on the subjects/methods before the course?

<table>
<thead>
<tr>
<th>Very high</th>
<th>None at all</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

4. Did the course add to your knowledge on the subjects/methods?

<table>
<thead>
<tr>
<th>Very much</th>
<th>Not at all</th>
</tr>
</thead>
<tbody>
<tr>
<td>7</td>
<td>3</td>
</tr>
</tbody>
</table>

5. Did you feel that you had insufficient background knowledge to follow some subjects?

<table>
<thead>
<tr>
<th>No</th>
<th>Yes in ....mathematics, mortality</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>2</td>
</tr>
</tbody>
</table>

6. Will you be able to apply the subjects/methods in your daily work?

<table>
<thead>
<tr>
<th>Very much</th>
<th>Not at all</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>5</td>
</tr>
</tbody>
</table>

7. How do you evaluate the lectures given in the course?

*NB: One respondent had two crosses*

<table>
<thead>
<tr>
<th>Very stimulating</th>
<th>Completely boring</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>7 1 1</td>
</tr>
</tbody>
</table>

Comments (e.g. did you find some lectures especially interesting and/or particularly boring):
8. How do you evaluate the exercises given in the course?

*NB: One respondent had two crosses*

<table>
<thead>
<tr>
<th>Very stimulating</th>
<th>Waste of time</th>
</tr>
</thead>
<tbody>
<tr>
<td>4 4 2 1 1</td>
<td></td>
</tr>
</tbody>
</table>

Comments (e.g. were some exercises especially interesting and/or particularly unnecessary):

Some exercises were not necessary.

9. How do you evaluate the relative balance between lectures and exercises?

<table>
<thead>
<tr>
<th>Too many lectures</th>
<th>Too many exercises</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 3 7</td>
<td></td>
</tr>
</tbody>
</table>

10. What do you think about the scope of the course (length and content)?

<table>
<thead>
<tr>
<th>Too long</th>
<th>Too short</th>
</tr>
</thead>
<tbody>
<tr>
<td>2 1 3 4 1</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Very good</th>
<th>Very bad</th>
</tr>
</thead>
<tbody>
<tr>
<td>3 6 2</td>
<td></td>
</tr>
</tbody>
</table>

Comments (e.g. which parts were particularly good or bad):

3 weeks is too long, would have been better to split into two periods

11. Were you given the opportunity to address problems particularly relevant for you?

Yes No in ..................

11

12. Has the course given you inspiration for your future work in the field?

Yes very much No not at all

7 4

13. Has the course given you insight into the assumptions and problems associated with stock assessment methods?

Yes very much No not at all

7 4
14. Do you think there is a need for a follow up to the course/subjects at a later stage?

No  Yes in ....................

Further improvements of skills
More knowledge

15. Do you think there is a need to establish a network of research efforts between the institutions you come from?

No  Yes in ....................

Standardisation of sampling
All aspects

16. Any other comments or suggestions for improvement of the course?

- Instruct participants better in order to prepare data for the exercises
- One of the trainers should have knowledge on the Adriatic Sea and fisheries to help better understand the application of the methods in this area.
- More attention to the Adriatic region
Appendix III  Papers and material handed out to participants during the course


Caddy, J.F. and Abella, A. (1999) Reconstructing reciprocal M vectors from length cohort analysis (LCA) and commercial size frequencies of hake, and fine mesh trawl surveys over the same grounds. *Fisheries Research* 41: 169-175.


List of AdriaMed Publications

A. Technical Documents


B. AdriaMed Translations


C. AdriaMed Occasional Papers


