LECTURES IN FISH POPULATION
DYNAMICS

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CONTENTS

INTRODUCTION

Population dynamics is the science describing the forces acting
on an animal population and how the population react to these
forces.

Within general ecology we study population dynamics with the
purpose of increasing our understanding of the forces and
interactions in an ecosystem. Within fisheries biology our
goal is more specific. We want to study population dynamics
to be able to predict what will happen to a population, or
a stock as we usually call it, when it is subjected to specific
external forces. If we can predict what will happen, we may
also be able to lead the development in the direction we want.

"What will happen" to the stock means:
1) What will the size of the stock be, i.e. what will
   be its recruitment, growth and mortality.
2) What will be the structure of the stock, i.e. age
   and size composition etc.
3) What will be the yield, or in other words net
   production.

"External forces" here means:
1) Natural forces:
   a) biotic environment (other stocks who can be
      prey, predators or competitors).
   b) abiotic environment (temperature, currents etc.).
2. Human activities. Here fishery is our main concern,
   but pollution etc. can also fall in this group.

A simple drawing can illustrate what we are talking about.
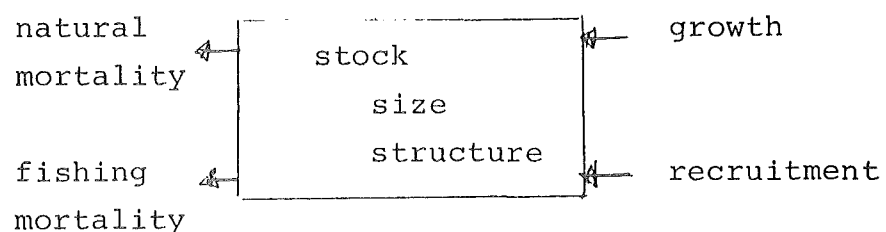
This drawing gives the simplest possible picture of how a stock can increase or decrease in size.

In addition to those factors mentioned, immigration and emigration could be included. We can also subdivide the factors mentioned by i.e. splitting natural mortality into death caused by old age, by deseases by spawning stress, by being eaten etc. We could also take growth and show how it depends on temperature, on food available and on the stock structure (e.g. age composition).

We can go on like this and make the picture more and more complicated, but simultaneously it will give an increasingly good picture of what is really going on in the nature.

A drawing like the one we showed above is a <u>model</u>, but when we tal about models in population dynamics we usually think of mathematical models.

A mathematical model could be anything from the simple equation relating weight and length of a fish

$$w = al^b$$

when w is the weight of fish, l = length, a, b = coefficients

to the complicated sets of differential equations used in an ecosystem model.

Basically there are two reasons for making models:

1. They can help us to <u>understand</u> the nature, because they can help us to select some few important factors and leave out the rest. By <u>simulation</u> we can find out which factors are important and how they influence the system.
2. They can help us to make <u>predictions</u> Instead of trying and failing with various exploitation patterns we can use a model to compute what is the best selection under a given set of conditions.

When making a model we want it to

     1) be as simple as possible

     2) fit the realities as closely as possible

     3) be as general as possible.

These demands can never be fulfilled simultaneously, and
we always have to make a compromise between them.

To make the model simple is important because of the compu-
tations involved, although with a large computer, this pro-
blem can be overcome. But if we want to use the model to
get a deeper understanding of the nature it is important that
it is not too complex. A complex model with many parameters
also takes a lot of data to be fitted.

It is Obvious that the model should fit nature as closely
as possible, but as a closer fit usually means larger com-
plexity this will set . the limits for how far we should go.

We must always consider

     1)   what we want to use the model for

     2)   how accurate answers we need and

     3)   which data we can base it on before we decide
           how simple and how well fitted to reality the
           model should be.

It is also obvious that we want the model as general as
possible, but again the complexity will usually set the
limits.

The models we use in population dynamics can be grouped in
several ways:

They can first be divided in

     1) deterministic models and

     2) stochastic models

A deterministic model will give an estimate, i.e. a point,
a line or even a multidimentional surface, sometimes with
an estimate of fiducal limits. A stochastic model gives a
probability distribution. In population dynamics determinis-

tic models have been used almost exclusively, although
in recent years stochastic models have been introduced
especially in situations where there is a large random
variation.

We can also group models as

1) analytical and
2) descriptive.

An analytical model aims to explain, and analyse what is
going on in nature. A descriptive model shows an empirical
relation. The distinction between these two types is not
absolute. The von Bertelanffy growth equation (see GROWTH)
was originally evolved from physiological hypothesis, and
could therefore be classified as analytical. Today, we use
it, however, because it shows a good empirical fit to age-
length relation of fish, i.e. as a descriptive model.

We can also group models according to their use, i.e.

growth models
recruitment models
stock models
ecosystem models.

In the present course we will mainly be concerned with
population models of exploited fish stocks.

Two general types of population models are commonly used.

1) Surplus Production models, often referred to as
descriptive population models
2) Dynamic Pool models, usually referred to as
Analytic stock models.

In the surplus production models the stock is the basic
unit subjected to the simple laws of population growth as
developed by Volterra (1931) and Leslie (1957). Fishing
acts as a predator in a predator/prey system. Graham made
a model of this type in 1939 and the most well-known one
was described by Schaefer in 1954.

In the dynamic pool models the individuals are the basic
units, and the stock size is a function of number of in-
dividuals recruited to the stock, and their growth and mor-
tality. The fishery is considered an additional mortality
factor. Baranov (1918) first used these principles in fish
population dynamics. Later Ricker (1948, 1958) has developed
models of this kind. The model presented in the classical
work of Beverton and Holt (1957) is, however, the most
applied model today.

We have also multi-stock models which could either be an
extention to one of the two types of models decribed above,
or they could be based on other approaches.

When we want to use a population model we should ask two
questions.

    1)   What do we want to get from the model?

    2)   Which data can we put into it?

Usually we want to get estimates of stock production which
can be used to give advice for optimal management of the
stock in question. Generally the analytical model gives
the best and most reliable results, but they also have a
greater demand for input data, and usually it is the avail-
able input data which will decide which model we can use.

A descriptive model only uses data on catch and effort. An
analytical model also needs data on age, growth and mor-
tality, and for many stocks, these data are not readily
assessable. For a proper management we also need estimates
of stock size and recruitment.

Mathematical modelling of populations has two sides: the
biological and the mathematical and to make a model input
from both sides is needed. The biologists must first pre-
sent information or hypothesis on the mechanisms and laws
which are operating. The mathematician must describe it in
mathematical language and find analytical or numerical ways
of solving the equations involved. Then the biologist must
supply data so that the parameters of the model can be fitted.

Then the model must be tried. If it gives results which does not deviate significantly from reality the model can be accepted and used for prediction.

If a significant deviation is found three questions must be asked:

1) Are the biological assumptions underlying the model correct?
2) Are important factors left out?
3) Are the parameters correctly estimated?

As in all hypothesis testing, it is important to use a new set of data for testing a model, not the same data as those used for parameter fitting. The mathematical and statistical sides of model making are, however, beyond the scope of this course.

STOCK

Fish are separated into species and races but these taxonomic
categories are usually not adequate for population dynamics.
We require an ecological unit which should be both a) homogeneous
and b) self-contained. Such a unit is called a "stock".

There are many definitions for the concept of stock. In 1960
ICNAF, ICES and FAO defined it this way:

> "A stock is a relatively homogeneous and self-contained
> population whose decrease by emigration and increase by
> immigration are insignificant in relation to the growth
> and mortality rate".

This definition is not particularly stringent. There are terms
such as "relatively homogeneous" and "insignificant in relation
to". However, in practice this definition is useful as it
gives room for the important quality of sound judgement.

In 1971 Gulland put forward a definition which states:

> "A stock is a self-contained and self-perpetuating group
> without mixing from outside the group, and for whom the
> biological characteristics and the effect of fishing are
> uniform. Such a stock will also be a genetic unit".

However, the value of requiring genetic isolation when deter-
mining what is a stock for fisheries biology is still in doubt.
The important point is that the unit one chooses should be
useful in practice. A definition given by Gulland (1969) made
this point very clear:

> "A group of fish can be regarded as a stock when the
> results one obtains from assessment and other population
> dynamics studies which regard the group as a stock do

not differ significantly from reality".

This method of looking at the problem can be very useful when it is difficult to determine what should be considered as a stock.

Determination of stock membership

Usually one cannot pick up a fish and say which stock it belongs to. A sample is usually taken and the distribution of one or more characteristics is examined to determine stock membership. We shall look at some of the types of characteristics which can be of use in this context.

1. Morphological characteristics - i) morphometric, "characteristics which can be measured", for example the eye diameter of Norway haddock or the ratio between carapace length and overall length of shrimp; or ii) meristic, characteristics which can be counted, such as the number of vertebrae in herring.

    A disadvantage of these morphological characteristics is that they vary not only between stocks but also between age groups, yearclasses etc.

2. Physiological characteristics - a typical example is growth patterns, which are used to differentiate stocks in both herring and cod. Most often otoliths are used since this is where an individual's growth history is written down.

    Spawning time is also an important characteristic and can be used to distinguish between autumn-spawning and spring-spawning stocks of herring.

3. Biochemical characteristics - when speaking of bio-chemical characteristics one thinks primarily of blood types and serum proteins but a long list of other characteristics can also be used. These latter are of increasing significance in recent years since they have the advantage of not being influenced by

the immediate environment, in contrast to vertebrae counts and growth patterns.

4. Ecological characteristics - this group is not uniform and contains such traits as behaviour, age distribution, degree of parasitic infestation etc. In practice these methods are not commonly used but a few of them, such as degree of parasitic infestation, have given promising results.

Tagging experiments can often give a clearer picture of the divisions between stocks. Using mackerel as an illustration (Fig. 1) we see that it has spawning grounds in the North Sea and west of Ireland. Fish from both spawning grounds have feeding areas north of Shetland. The degree of interchange between these two groups while they are in the feeding area will determine whether we can separate them into two stocks or not. If we tag fish on the two spawning grounds, the outcome will approach one of two extremes:

   i) all fish tagged at one spawning ground are found again in the same area
   ii) fish tagged at one spawning ground appear at both areas with equal frequency

As in most other corresponding situations, one finds neither of these extremes in mackerel. Thus the deciding factor is how one interprets the phrase "insignificant exchange" in the definition of stock.

In most cold and temperate regions a stock will usually have a spawning ground, a nursery ground and a feeding ground (Fig. 2). The fish usually swim against the current from the feeding ground to the spawning ground. From there the eggs and larvae will drift to the nursery ground whereas the adults will swim back to the feeding area.

In addition to these grounds a stock may also have an overwintering area, a feeding ground for young fish etc. It can be the migration from the nursery ground to the feeding area which constitutes recruitment. It is important to

note that the migration pattern is intimately linked with the currents. This is essential for transportation of the larvae from the spawning grounds to the nursery grounds.

More than one stock may spawn in the same geographical location, as in Lofoten where two types of cod spawn - the coastal cod and Norwegian-Arctic cod. In much the same way the Finnmark coast and the Barents Sea are nursery grounds for a large number of species.

That which is normally regarded as a single stock may have several feeding areas. Norwegian-Arctic cod, for example, has a feeding ground near Bear Island (Bjørnøya) and one eastward in the Barents Sea. Fish from these two territories display a few differences in growth patterns but are considered as one stock for practical purposes.

The distribution and migration patterns of a stock are not fixed - the Atlanto-Scandian herring has changed its migration pattern several times in the last twenty years.

In our waters the stock structure is clear for most species but there are important exceptions. We know that both winter- and summer spawning capelin exist but we are unable to differentiate these stocks by anything other than spawning season.

There are also examples where the stock structure is well known but several stocks are placed together for practical assessment.   Such is the case with herring in the North Sea - it is known that several stocks exist but although they are not completely independent units it has proven both difficult and impractical to regulate each stock separately because they are fished simultaneously.

Plaice in the North Sea possess similar problems.

If we leave our waters and go to tropical and subtropical regions, much less   is known about the stock structure nor do we find familiar migration patterns.

During récent years, some information on stocks and their distribution and migration in tropical areas have, however, been collected.

We can look at North-West Africa as an example. Fig. 3 and 4 show the geographical and temporal distribution of upwelling. Fig. 5 shows the distribution of <u>Sardinella</u> <u>aurita</u> in the same area. The adult fish seem to have a migration pattern following the upwelling. They spawn, however, in several positions, and there are no distinct spawning areas and feeding areas. The nursery areas on the other hand are distinct, and the juveniles also are at least partly separated from the adult stock. It could also be noted that the adult stock is closer to the shore during the cold than during the hot season.

In coral reef fishes we find a completely different picture. The adult fish stay constantly in the reef where they first settled, but the eggs and larvae are usually pelagic and it seems that they join a general pool of pre-recruits which could settle in any reef which they are led to by the currents. Therefore one reef can usually not be regarded as a stock unit.

The data available are insufficient for drawing general conclusions but it seems that usually
1) the adult has less regular migration patterns in tropical than in temperate waters.
2) the spawning grounds are not as distinct.
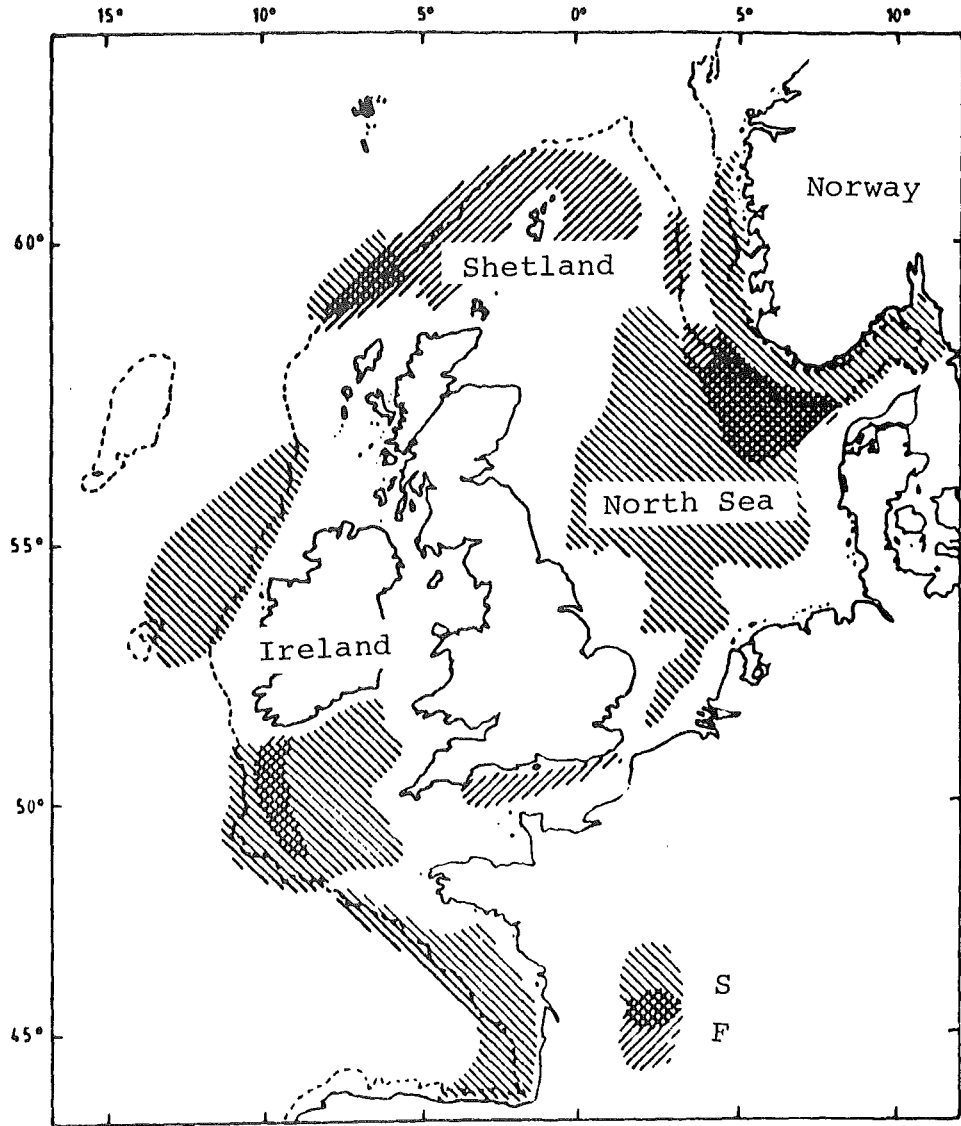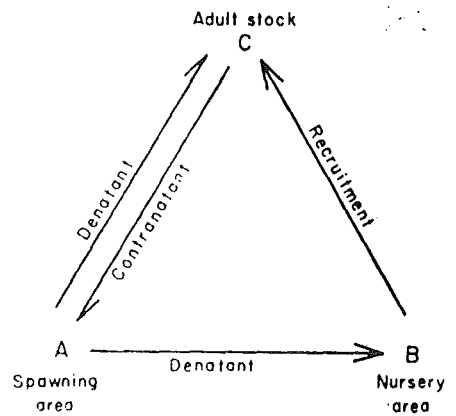3) the larvae and juveniles have a more shallow and more coastal distribution than the adults.

Fig.1. Spawning (S) and fishing (F) areas for mackrell.

Fig.2. Fish migrations can usually be reduced to a simple triangular pattern, with the spawning area, nursery area, and adult stock at the three corners.
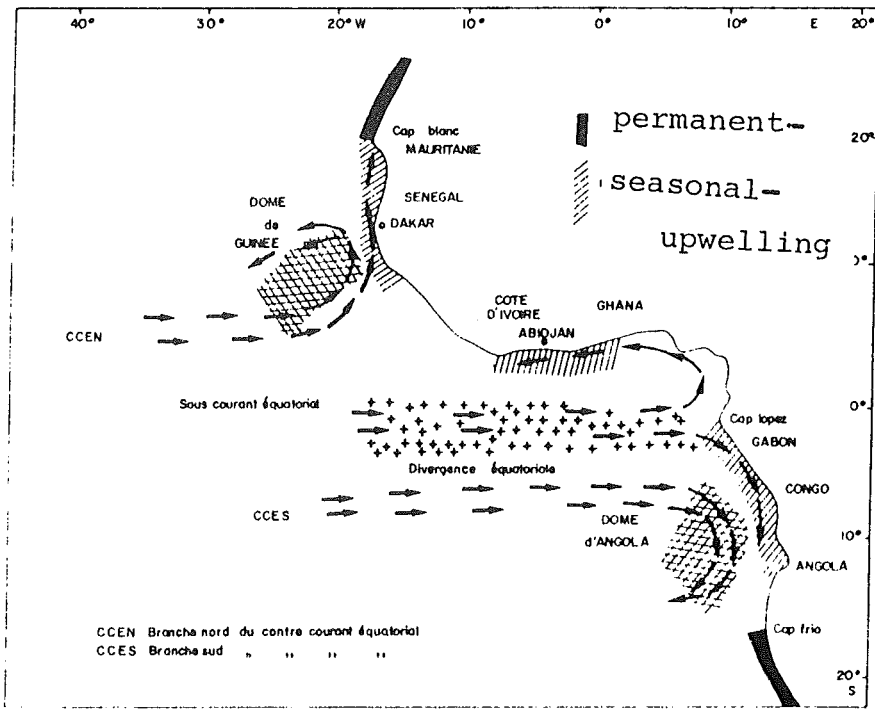
Fig.3. Production systems off west Africa (From Voituriez and Herbland, 1982)

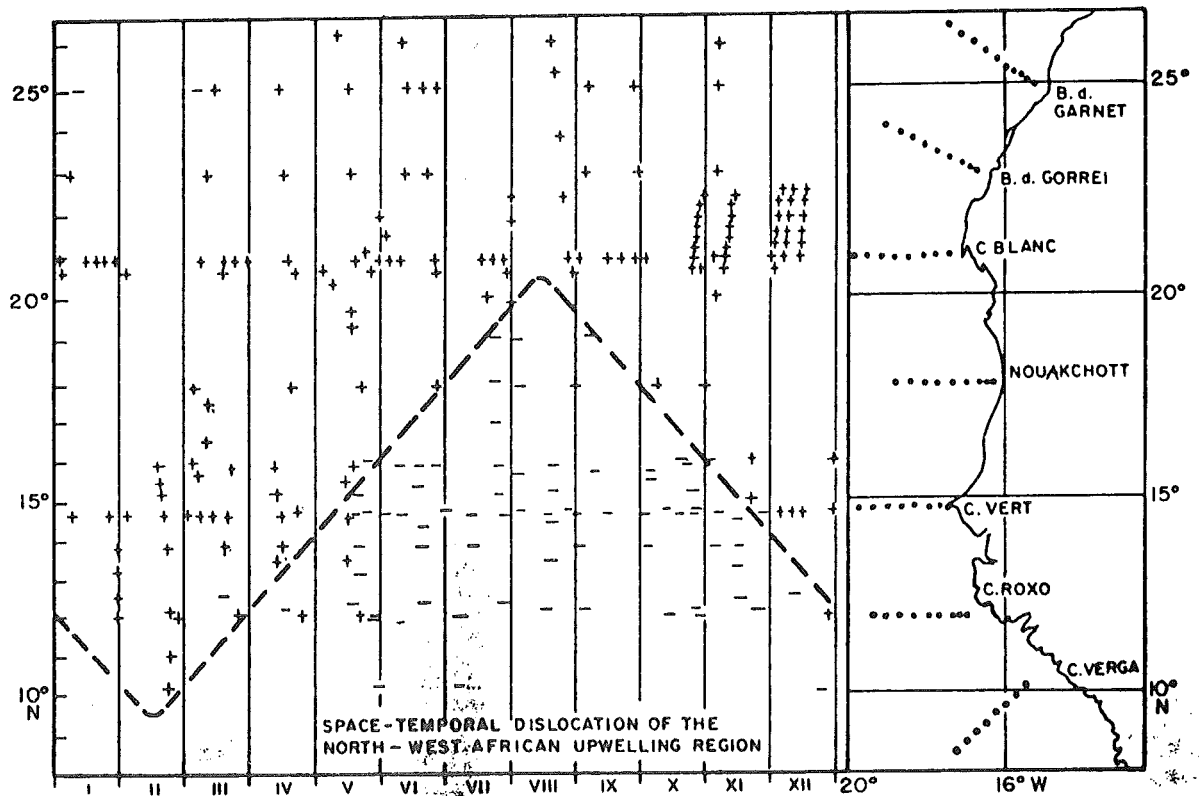
Fig.4. Seasonal variation of upwelling along the Northwest African coast (from Schemainda and Nehring, 1975). The plus signs indicate the presence of upwelling, and the minus signs indicate the absence of upwelling.
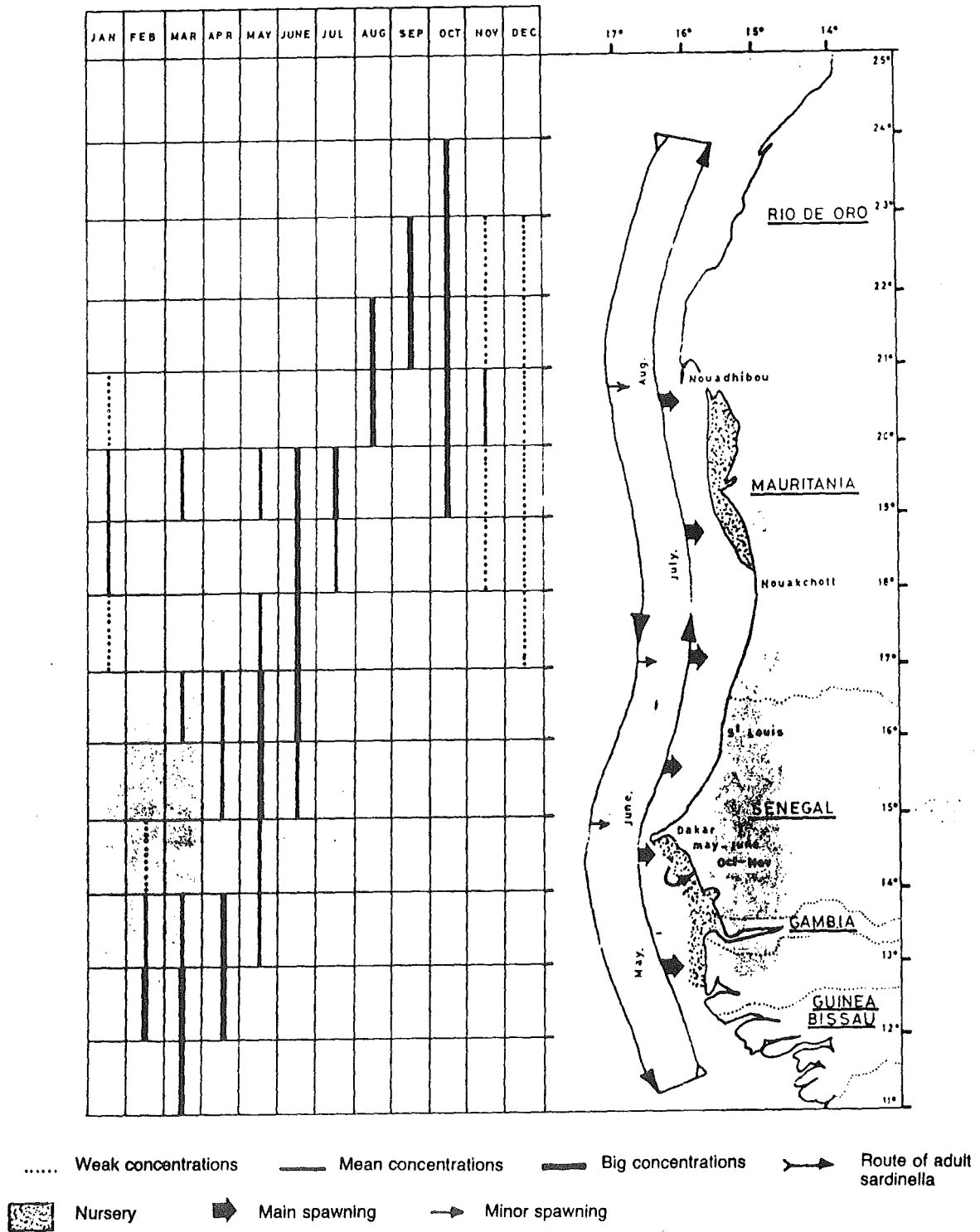
...... Weak concentrations   ——— Mean concentrations   ●—● Big concentrations   ➤—➤ Route of adult sardinella

▨ Nursery   ➡ Main spawning   → Minor spawning

Fig.5. Migration pattern of Sardinella aurita.
(From Boely, Chabanne, Freon and Stequert 1982)

GROWTH

The term growth can be used in two contexts in population dynamics

1. population growth i.e. change in the size of the population, usually the difference between the rates of natality and mortality
2. individual growth i.e. change in the size (lenght, weight etc.) of an individual.

Growth can be both positive and negative. Here we will take up the concept of individual growth.

Unlike the higher vertebrates, a fish will continue to grow throughout its life. Growth in length will go toward an asymptote but it will not usually stop completely nor will it become negative (Fig. 1). This growth rate is most often highest when the fish is young and decreases with time, usually exhibiting a sharp decrease when the fish becomes sexually mature. This applies to fish of short life cycles in particular.

Usually there are seasonal variations in the growth rate - in temperate waters growth is often high in summer and low in winter. These variations are critical for the annual rings found in otoliths and other hard structures (bones,scales, etc.).

Weight also approaches an asymptote. A typical growth curve for weight has a turning point i.e. is S-shaped (Fig. 1). Weight can display large seasonal fluctuations and, as in mackerel, may decrease in winter (Fig. 2).

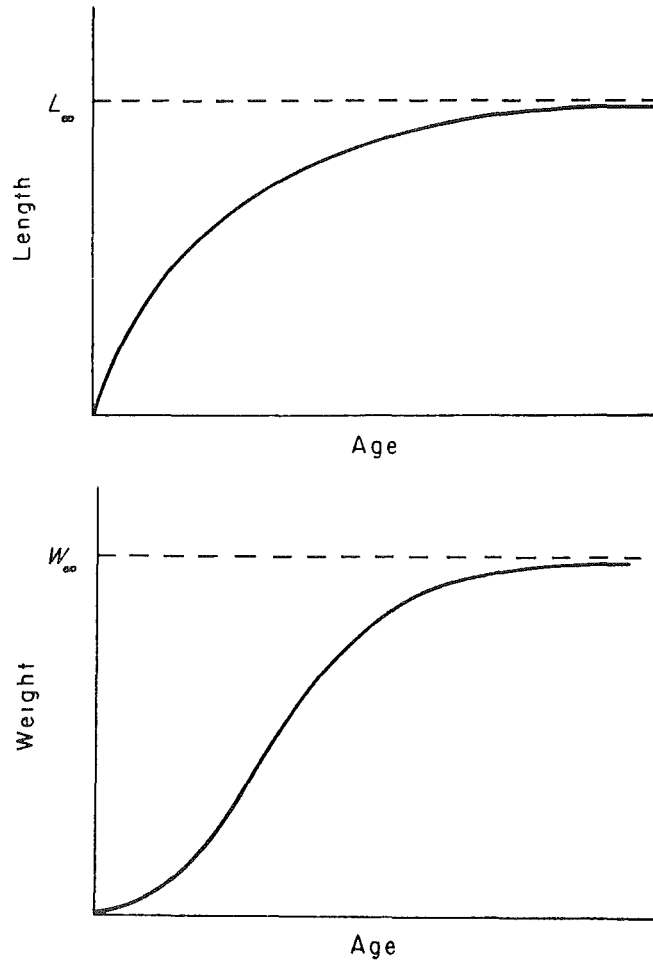Growth is often divided into

a) somatic growth
b) gonad growth

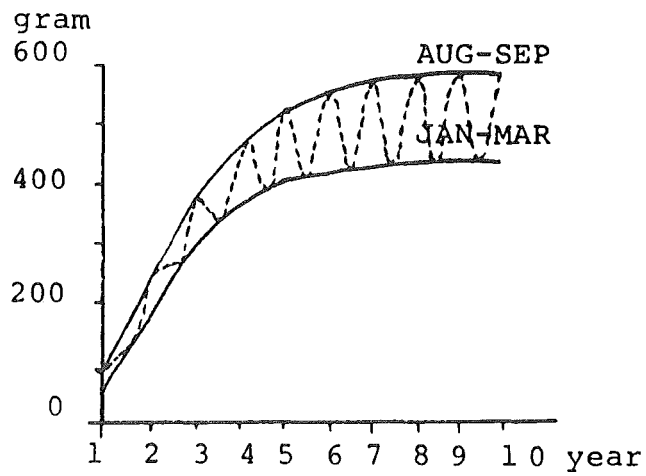Fig. 1. Typical patterns of growth in length and weight of fishes

Fig. 2. Growth of mackerel (Scomber scombrus).The broken line shows the seasonal fluctuations in weight.

In many species the somatic growth slows down or almost ceases when maturation is reached and the gonads start growing fast.

Length (l) and weight (w) can be related using the expression

$$lgW = a' + b \log l \text{ or}$$
$$W = a \, l^b$$

The regression coefficient b is often used as a measure of fish condition. Usually it is close to 3. In mature fish there are cyclical changes, i.e. b > 3 during gonad development and b < 3 after spawning.

In growth studies we are usually concerned with growth rates, that is increase in weight or length per unit time:

$$\frac{W_2 - W_1}{t_2 - t_1} = \frac{dW}{dt}$$

If the time period considered is small the rates can be expressed as instantaneous rates.
We can use

$$\text{absolute growth rates } \frac{dW}{dt}$$

$$\text{or relative growth rates } \frac{1}{W} \frac{dW}{dt}$$

In principle, the growth of fish can be determined in three different ways:

1. measuring the length of the same individual at several points of time
2. estimate from the average length of fish of a known age
3. back calculation of growth from marks in the otoliths, scales etc.

The first method is of little practical use in fishery biology, so we shall instead examine the second and the third one.

Usually when the fish have a limited spawning period, as it is nor-
mally in temperate waters, the number of eggs hatched per unit
time will approximate a normal distribution. After hatching,
samples will show the larvae to have a normal distribution in
length (Fig.3a).

A group of fish born in the same time interval is called a
cohort. In temporate waters this is equivalent to a year class
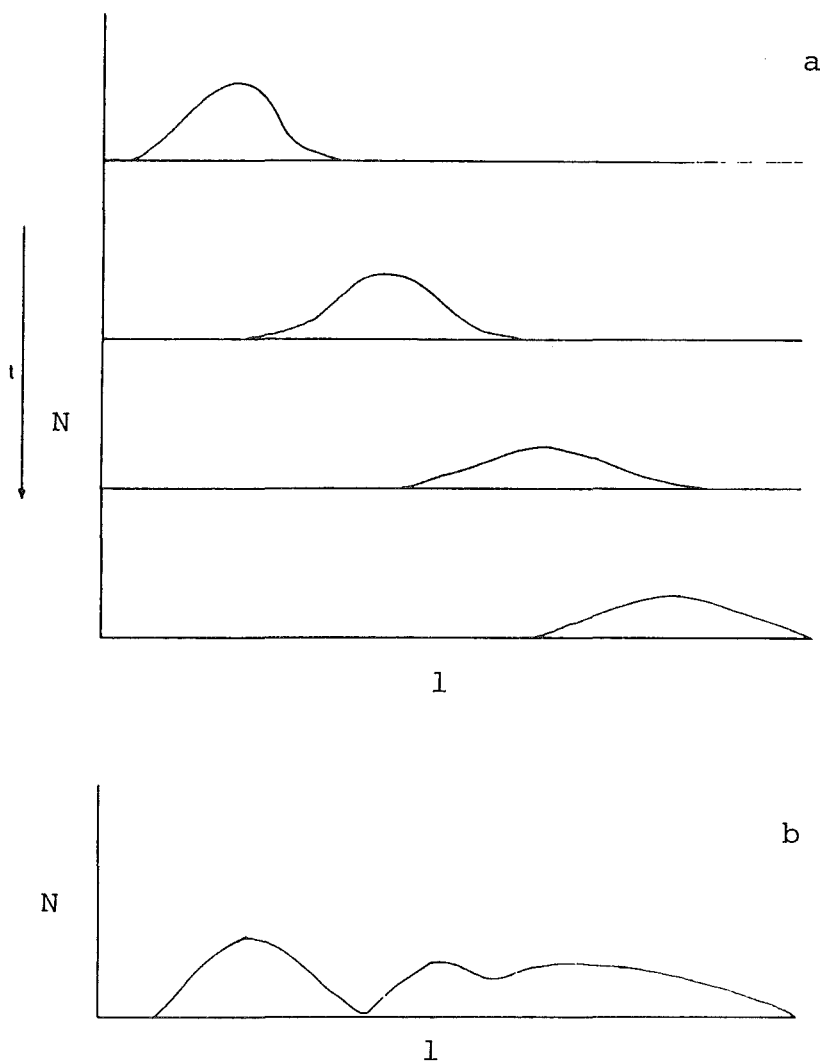whereas, in tropical regions, there can be several cohorts per
year.

Fig. 3. a : Size distribution of a cohort at four diferent
times. b : Sample obtained if the cohorts occure simulta-
nously.

Some individuals grow slowly and some quickly. Therefore the range in length will increase and the variance becomes larger but generally the length of a cohort will continue to be normally distributed.

If we sample a population containing the cohorts shown in Fig. 3 we get a sample like that of Fig.3b. This arises by summing the individual length distributions.

If we have such a sample and wish to calculate the growth, we must try to split the length distribution into its components. The first cohort can easily be distinguished but to separate out the second cohort we must use various statistical methods which assume a normal distribution (see for example Bagenal and Tesch 1978). Cohorts 3 and 4 overlap to such a large degree that they are not easily distinguishable with the above methods. Thus it becomes necessary to determine the age of the fish before proceeding further.

If we can separate the different components of a length distribution as shown in Fig.3b and we know the time interval between them (usually 1 year in boreal waters, but often shorter in tropical ones) we can use this for growth calculations.

If we have two or more collections with a known time interval between them we can calculate growth by examining the shift in the peaks. This is actually a parallel to the first method but instead of following an individual we follow a cohort.

The growth can be illustrated like in Fig. 4 . The growth curve should go through the means of the length distributions in the samples but the length distributions in our samples will not always reflect those of the population.

If we catch fish by trawl the smallest fish will easily slip through the mesh and thus be under-represented. We will also get an overestimation of the mean length of the youngest age group and possibly inadequate representation of the largest group since they can easily avoid the trawl. Thus the mean length of the oldest year classes can be underestimated (Fig. 4).
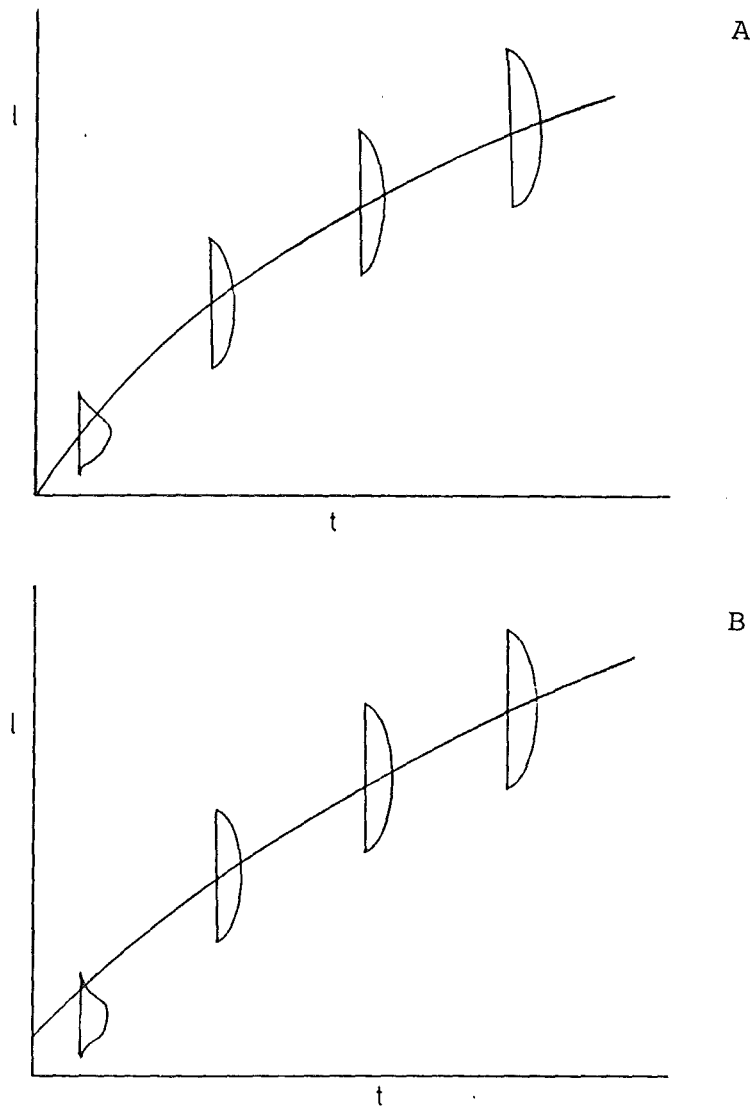
Fig. 4. A: Size distribution and growth curve for a fish population. B: True size distribution and growth curve based on samples overestimating the size of the smallest cohorts

Before going further we will briefly look at a mathematical model for growth. The most popularly used equation for describing growth in fish is von Bertalanffy's growth curve:

$$l_t = L_\infty (1 - e^{-K(t - t_o)})$$

Here L_∞ is the asymptotic length the fish go toward and t_o is the age at which the length would have been 0 if growth followed von Bertalanffy's equation. Both these values are

mathematical parameters and say little about biology. L_∞ also doesn't need to correspond particularly well to the fishes' actual maximum length. K is an expression for growth rate. We shall return to the derivation of this equation and how it can be fitted to the data.

If we go back to the samples taken with selective gear, we see that this will lead to an underestimation of K and L_∞ and give a negative t_o with relatively high value. A large negative t_o should always be interpreted as an indication that something is wrong, even if there are many other causes beside sampling error for such a result.

One of the other possible causes of a negative t_o is selective mortality where the smallest fish of each age groupe have the greatest chance of dying. This can occur when predation is the most important cause of death,but as we shall see later, mortality in an overfished population may more often be selective for larger individuals.

One should also note that the less the youngest age-group is represented in the material, the less is the reliability of the estimate of t_o. An underrepresentation of young fish will most often result in negative t_o even if there is no selectivity.

Along with gear selectivity, behavioural differences between quick-growing and slow-growing individuals can give variations in the growth calculations.

Back calculation of growth

If the ratio between the fish length and some dimension of otoliths, scales or other parts showing cyclical marks is known, this can be used for back calculation. Annual, monthly or daily marks can be used, and the ratio makes it possible to calculate the fish length at the time when a given mark was formed (Fig. 5).
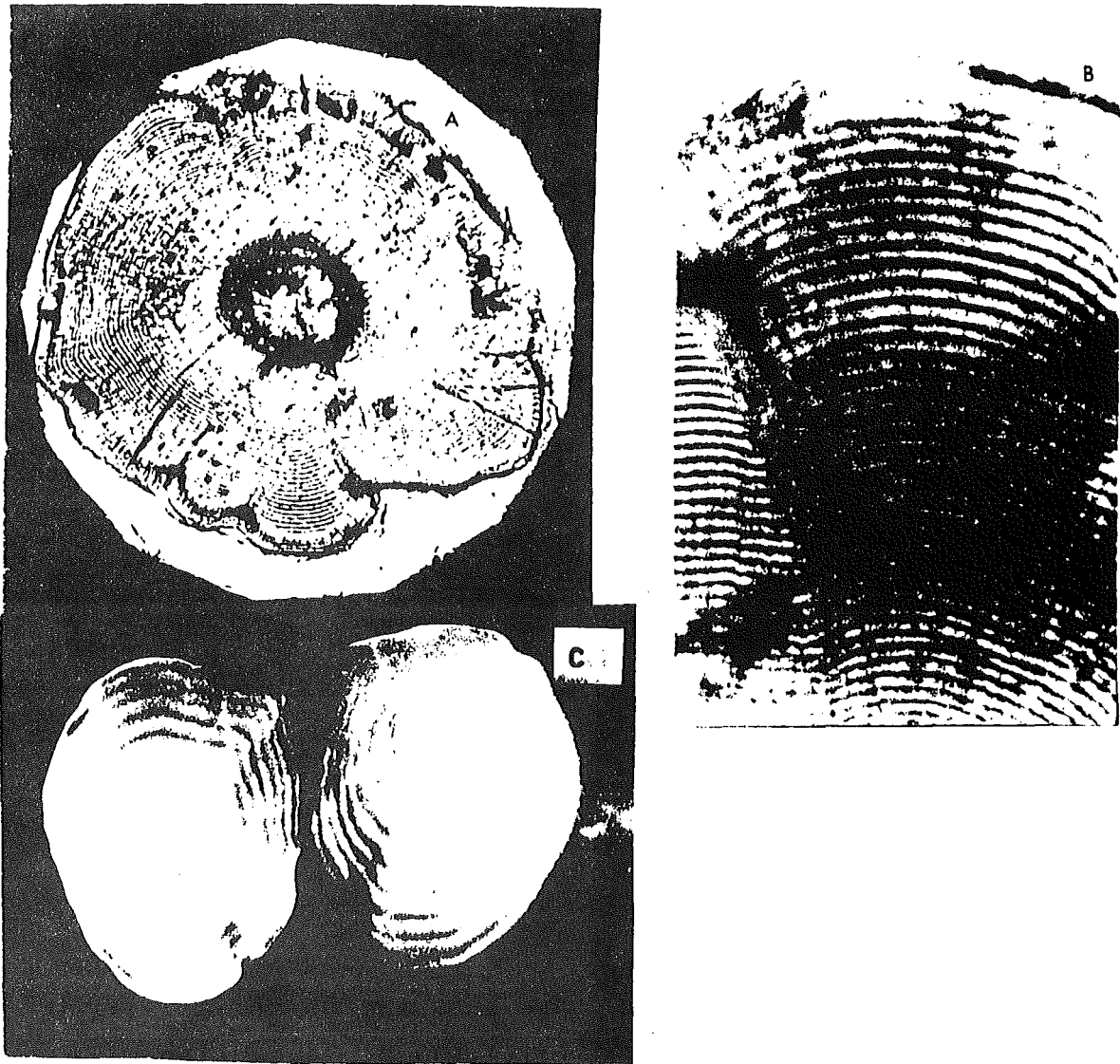
Fig. 5. Otoliths showing growth zones. A and B: Daily growth rings in Benthosema fibulatum (From Gjøsæter et al. 1984). C: Annual rings in Hippoglossoides platessoides (From Isaksen 1977).

The following procedure could be used:

1. Measure fish length and diameters, radii or another simply measurable dimension in otoliths, scales, vertebrae or other structure where cyclical marks are found. A wide range of fish lengths should be used.

2. Plot corresponding values and fit a regression. If a simple regeression cannot be fitted, try to measure another dimension.

3. Measure the diameters (or other dimensions) of annual or daily marks, and use the regression to calculate the fish length when this ring was formed.

Lee's phenomenon:

Fish caugth at older age often gives a lower back-calculated length for a given age than fish caught at a younger age. This is called Lee's phenomenon.

Possible causes are of three different types:

a) Technical - Use of incorrect scale:body relationships in back-calculation of growth.

b) Biassed sampling - Where fish of different sizes are not represented in samples of scales or otoliths in propor- tion to their abundance. Usually it is the smaller fish of an age-group that appear in samples less frequently than larger ones. The reason may be either that the samp- ling gear in use catches large fish more effectively, or the larger fish may have a different distribution or habits - often associated with the fact that more of them are mature and so take part in migrations or spawning manoeuvres that make them more easily caught.

c) Selective mortality - Where the mortality rate among the larger fish of an age-group is different from that among the smaller. Size-selective mortality may arise either from natural mortality factors, or (when fishing is a significant source of mortality in the population) from differing catchabilities of fish of different sizes.

Selective mortality, unlike the other two causes of Lee's phenomenon is a property of the fish population rather than of the technique.

In a situation with sampling error the back calculated lengths are usually close to the true lengths at age than those derived by direct observations.

When there is a Lee's phenomenon caused by any of the other factors listed above, the direct observations are usually closest to the truth.

Growth variations between species

Maximum length in fish varies from 2-3 cm (Gambusia holbrookii)
to many meters (Rhincodon typus) and the time needed to reach
this length varies from a few months to many years.

Expressed as the constant K in von Bertalanffy's growth
equation, the growth rate varies from around 0.05 (Acipenser)
to approximately 5 (Benthosema fibulatum and Rastrelliger
kanagurta).

There seems to be a negative correlation between growth rate
expressed by K and the maximum length L_∞ when the latter is
about 30 cm or less (Fig. 6). There seems to be little correla-
tion for larger species.

Often there is a positive correlation between L_∞ and the
age a fish may reach. Tropical fish typically have a more rapid
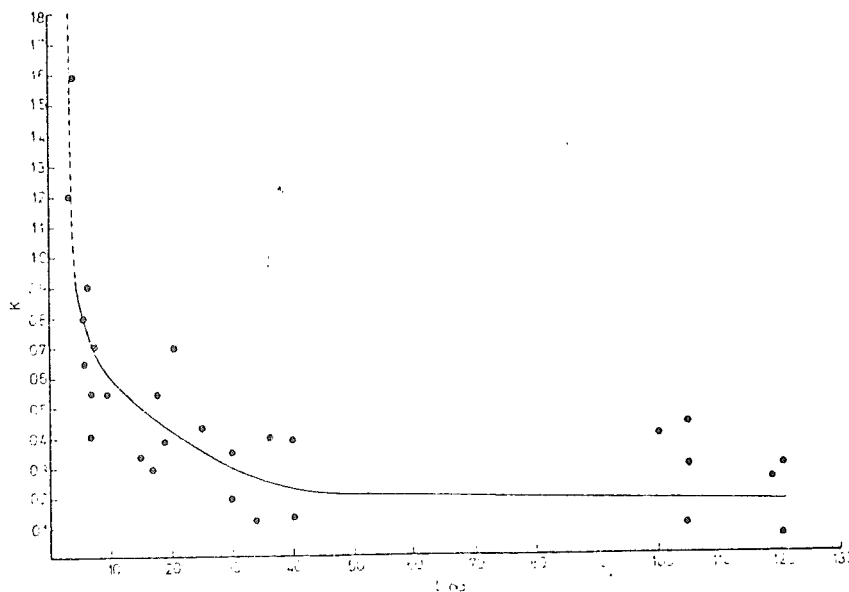rate of growth than fish from temperate or cold waters.

Fig. 6. Relationship between K and L_∞ (From Beverton and
Holt 1959)

Growth variation within species

There can be large variations in growth within a species as well. These variations can be of a geographical or temporal nature and may have many causes.

Some growth curves of northern lantern fish can illustrate how great variation can be (Fig. 7). Here L_∞ varies, within a limited area and over a relatively short time, between 70 and 87 mm; K varies between 0.20 and 0.45 and t_o between +0.3 and -0.6. If one looks at specimens of the same species from Canadian waters, they show a growth pattern similar to that found in western Norway. On the other hand, in the Meditterranean the species have a maximum length of 30-40 mm. K is not known exactly, but seems to deviate little from that of northern waters.
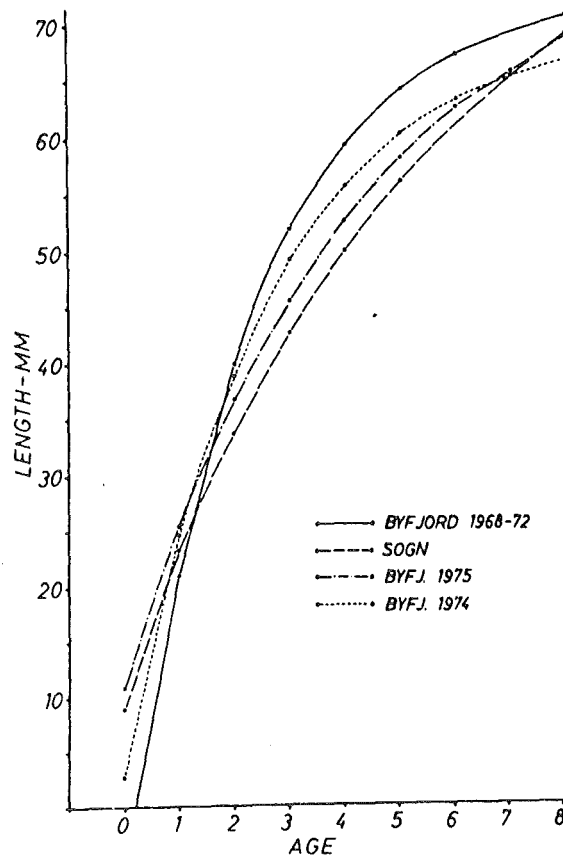

Fig. 7. Growth of <u>Benthosema</u> <u>glaciale</u> in Norwegian waters (From Gjøsæter 1973)

For cod in the Northern Atlantic K varies between 0.06 and 0.40, L_∞ varies between 65 and 120 cm (Fig. 8).
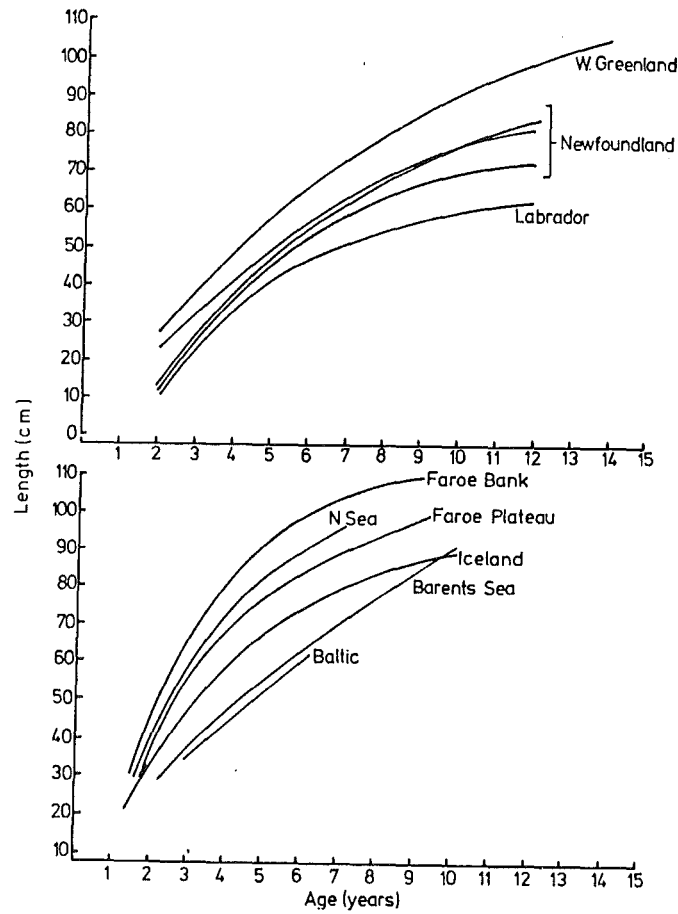

Fig. 8. Growth curves of North Atlantic cod.

In addition to geographic variations in growth, one often finds variations from year to year. Fig. 9 shows how the growth of plaice in the North Sea has varied from 1935 to 1968. Such temporal changes in growth may be connected to hydrographic conditions or to density dependent factors such as food supply. Both these factors appear to work their strongest influence on young year-classes. We will come back to this.
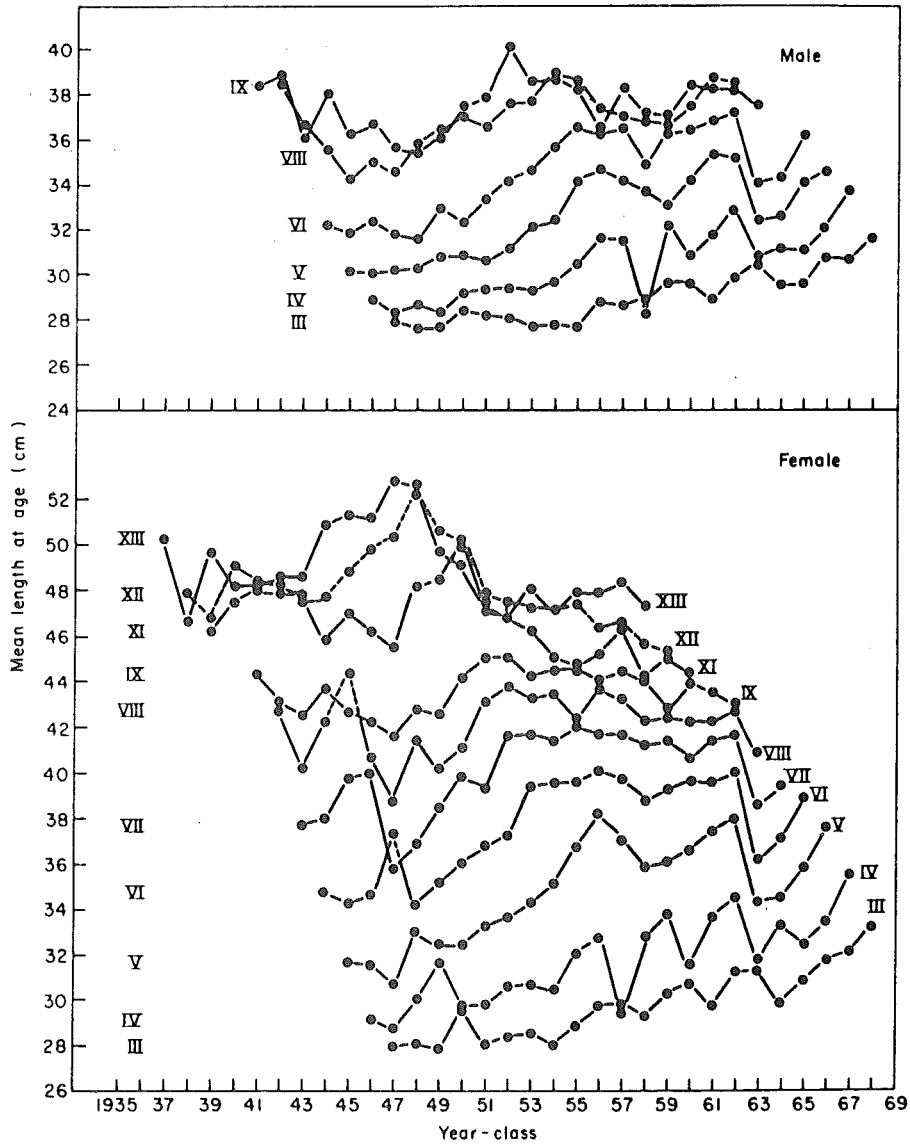
Fig. 9. Changes in growth of plaice, as shown by the trends in mean length of fish of each age in year-classes between 1935 and 1969

Not all the food taken is available for growth. The rate at which fish grow dependes on the amount of ingested food (I), the amount excreted (E), and on metabolism (M).

I = E + M + G

The amount excreted and the metabolism is found to vary little
in fishes, therefore growth rate depends mainly on the ingested
food amount (Pitcher and Hart 1983). An example of this is
given by them taken from the experiments done by Brett et al.
(1969) on sockeye salmon fingerlings. Three main ration sizes
are defined (Fig. 10), a) the maintenance ration - which is food
just sufficient to keep the metabolism of the fish going with
nothing to spare for growth, b) optimum ration which produces
maximum growth rate per unit of food. This amount of ration is
important from the point of view of economy, c) and the maximum
ration which produces highest growth rate.

Some other factors are also known to influence the growth rate.
These are:

1) temperature
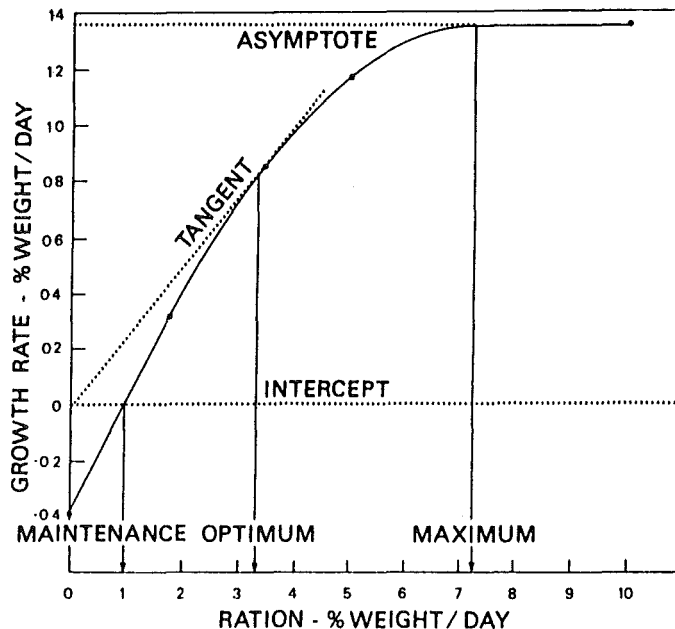2) hierarchical behaviour
3) genetic
4) maturity
5) density

Fig. 10. Growth rate as a function of ration size in
Sockeye Salmon. The tangent to the curve defines the
point of maximum growth (From Pitcher and Hart 1983)

Temperature

Investigations have shown that both von Berterlanffy's
coefficients $(K, L_{\infty}$, will be effected by the temperature
(Fig. 11).

Experiments on <u>Cypridon macularius</u> (Kinne 1960) showed that this
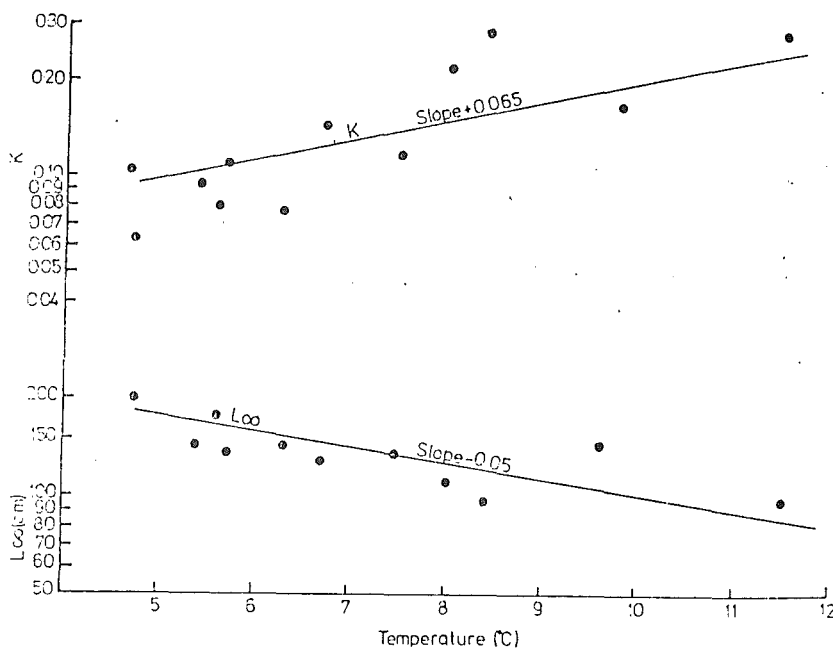species showed maximal growth rate at an optimum temperature
(Fig. 12).

Fig. 11. Relationship between L and temperature and K and
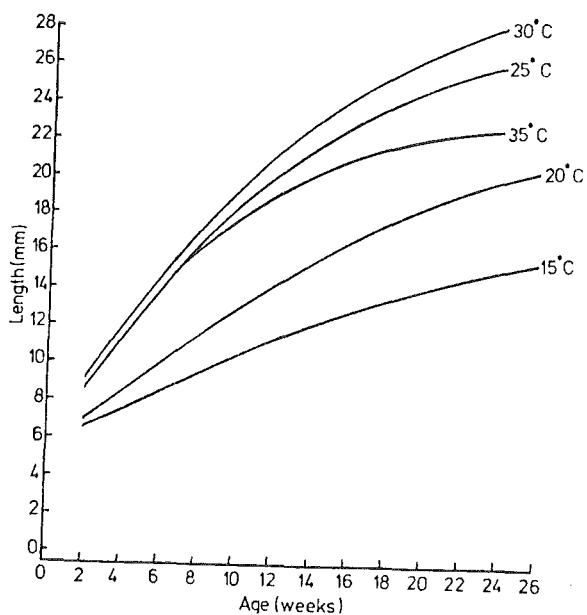temperature (From Jones 1976)

Fig. 12. Growth curves for <u>Cyprinodon macularius</u> at different
temperatures (From Kinne 1960).

Maturity

When a fish begins to mature the energy that has been used for growth will be required for the developing of the maturing gonad. Growth will also be influenced by the spawning migrations of fishes. Pitcher and Hart (1983) propose that the fish produce excess of material during the period of somatic growth and store it in the body to be later used for gonadal growth. An example of this is shown by the experiments of Canadian pike by Diana and Mackay (1979) (Fig. 13).

They observed that although female production was twice as high as male production (from May - March), expressed annually both sexes produced similar amounts of somatic tissue. Immature pike grew extremely fast in their first year of life, passing all energy into somatic growth.
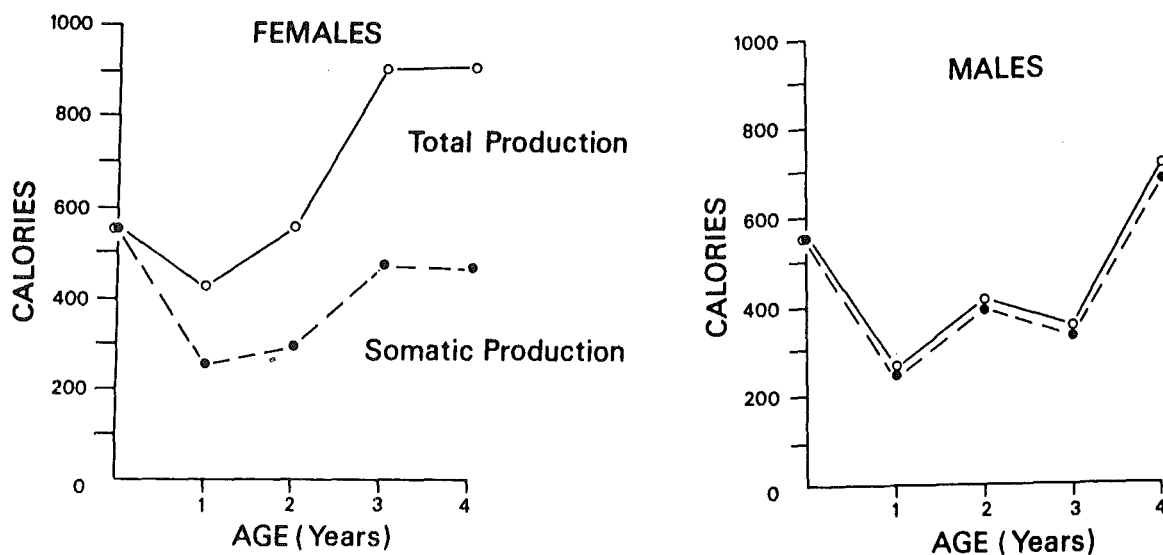

Fig. 13. Total and somatic production by Pike from Lac Ste Anne, Canada. (From Pitcher and Hart 1983).

Density dependance

Growth of fishes has been compared at different densities in
lakes and culture ponds (Cushing 1981). Reduction in the
specific growth rate of trout fry with increased density were
observed by LeCren (1965) (Fig. 14).
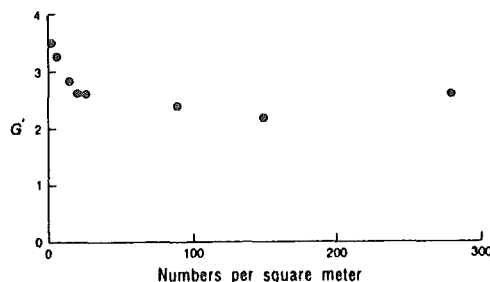
Fig. 14. Reduction in growth rate with increased density
of trout fry (From Cushing 1981).

Iles (1974) explains growth depensation as a density dependent
indicator. If two individuals compete for a single food
particle, the odds are heavily in favour of the larger one. He
categorizes two types of competition which can occur at higher
densities:

a) Intra year class competition - lies within a yearclass
b) inter year class competition - occur between yearclasses
   and is always in favour of older fish and against new
   yearclasses.

Intra year class competition is applied to stocks which
produce a large number of zygotes, e.g. clupeiods. In this type
of competition death of one individual increases chance of
another (density dependent feed back) (Fig. 15 A).

Inter year class competition - applies in general to species
where there is no abrupt ecological transition as fish grow
older and larger, e.g most demersal species. In these types of
competition the older ones are directly competing with the
young - even cannibalizing (Fig. 15 B).
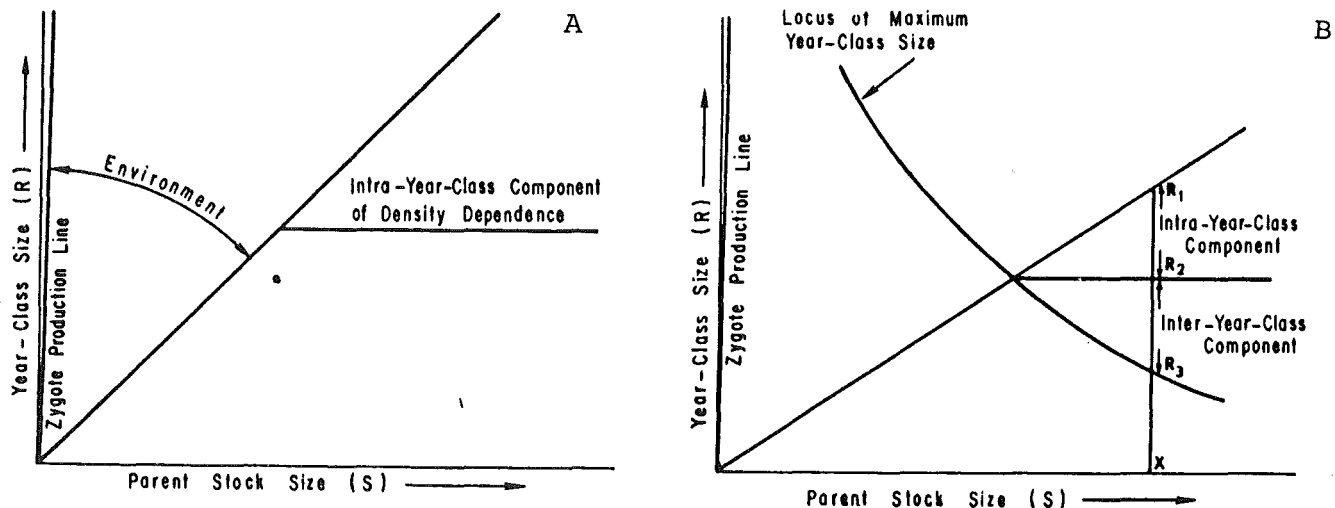
Fig. 15. Models for intra-cohort (A) and inter-cohort (B) density dependence (From Iles 1980)

Von Bertalanffy's growth curve

We return now to von Bertalanffy's growth equation and will look at how this can be adapted to the available data.

One can arrive at this growth equation from two starting points. Von Bertalanffy assumed that growth was the difference between anabolism and catabolism and, further, that anabolism was proportional to surface area and catabolism proportional to weight:

$$\frac{dw}{dt} = H_s - Kw$$

By replacing w with l^3 and s with l^2 we get

$$\frac{dl}{dt} = H - Kl$$

This can be transformed to $l_t = L_\infty (1 - e^{-k(t-t_o)})$

The other possible starting point is to assume that length increase is linearly related to length

$$\frac{dl}{dt} = K (L_\infty - l)$$

For integration we write

$$\frac{dl}{L_\infty - l} = K \, dt$$

therefore

$$- \lg (L_\infty - l) = K \, t + \text{konst.}$$

or $\quad L_\infty - l = e^{-Kt} \cdot \text{konst.}$

or $\quad l = L_\infty - \text{konst.} \, e^{-Kt}$

If we define t_o as the age at which $l_t = 0$ we get

$$0 = L_\infty - \text{konst.} \, e^{-Kt_o}$$

$$\text{konst.} = L_\infty \, e^{Kt_o}$$

subsequently

$$l_t = L_\infty - L_\infty \, e^{Kt_o} \, e^{-Kt}$$

or $\quad l_t = L_\infty (1 - e^{-K(t - t_o)})$

If we have data from a period with an equal time interval (T) in between, we can write

$$l_{t+T} = L_\infty (1 - e^{-K(t+T - t_o)})$$

subtract

$$l_t = L_\infty (i - e^{-K(t - t_o)})$$

to result in

$$l_t + T - l_t = L_\infty \, e^{-K(t - t_o)} (1 - e^{-KT})$$

or $\quad l_{t+T} - l_t = (L_\infty - l_t)(1 - e^{-KT})$

We can now plot $l_{t+T} - l_t$ to get a line with slope coefficient $1 - e^{-KT}$ (Fig. 16).

Also $l_t = L_\infty$ when $l_{t+T} - l_t = 0$ i.e. the first has reached its maximum length when it no longer grows.
Usually T is set to equal 1 (one year, one month or whatever scale we wish to use).
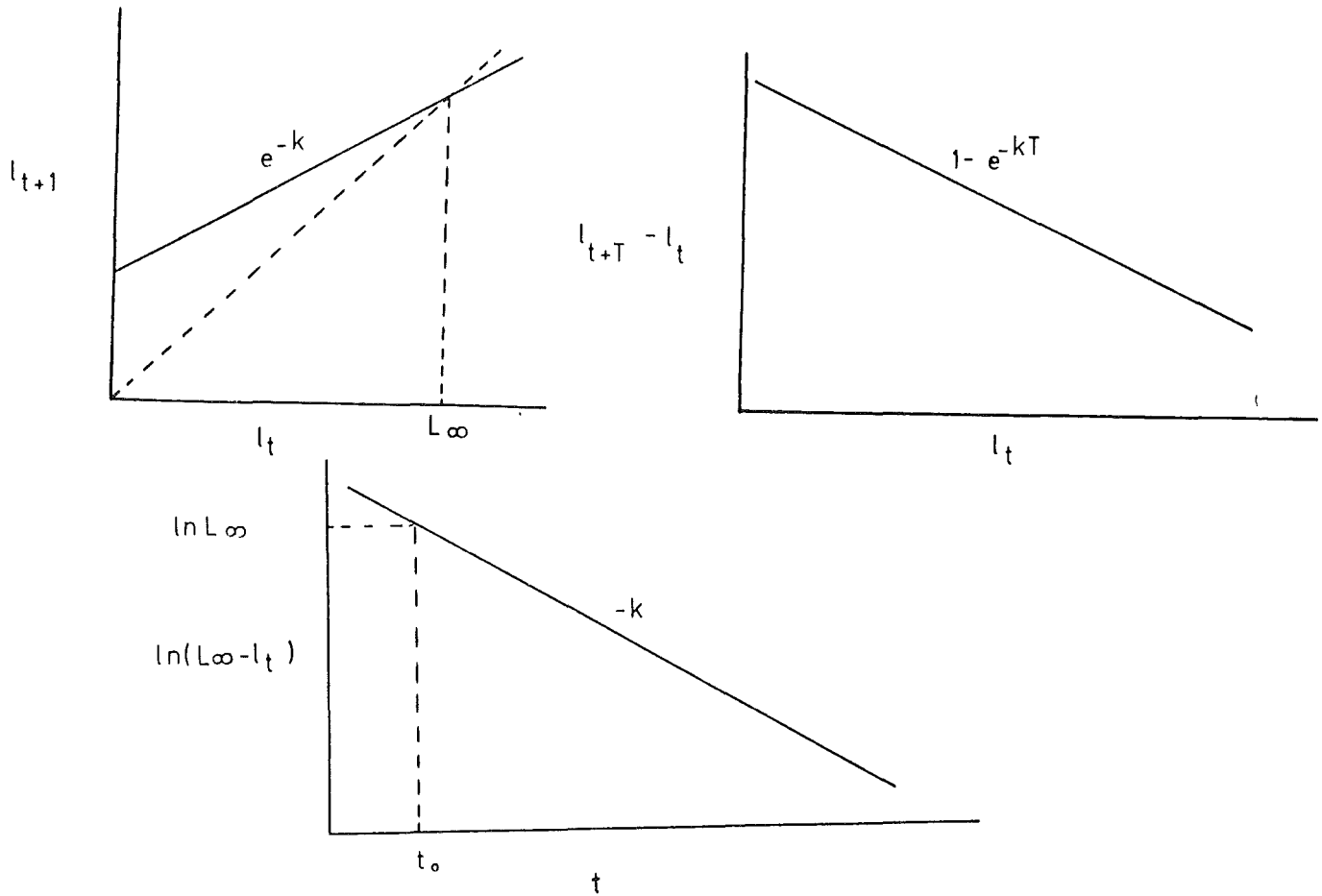
Fig. 16: Plots used to fit von Bertalanffy's growth curve.

The last equation can also be given in an alternative form

$$l_{t+T} = L_\infty (1 - e^{-KT}) + l_t e^{-KT}$$

If we make $T = 1$ and plot l_{t+1} against l_t we get the so-called Ford-Walford diagram. Here the slope constant is e^{-K} and L_∞ is reached when $l_{t+T} = l_t$ i.e. when the line cuts diagonally through the axes (Fig. 16).

These plots give us an estimate of K and L_∞. The only thing lacking is t_o. In this case we can apply a method described by Beverton and Holt (1957):

Given $l_t = L_\infty - L_\infty e^{-K(t-t_o)}$
we take its logarithm $\ln (L_\infty - l_t) = \ln L_\infty + K t_o - Kt$

By plotting $\ln (L_\infty - l_t)$ against t we get a line with slope coefficient $-K$ which goes through a point with the coordinates $(t_o, \ln L_\infty)$ (Fig. 16).

The methods we have seen here are simple and can be used without advanced aids.

Several computer programs have been developed which can accommodate von Bertalanffy's growth curve and which also calculate the variance of the parameters. These programs can give greater accuracy than the simple methods we have looked at but most often the largest source lies in sampling and the added accuracy of the computer calculations is not always realistic.

The above mentioned methods require a fixed time interval between samples and that all samples be given equal weight regardless of the number of fish. This particular problem is solved in the more advanced methods but, in most practical cases, this will have limited value.

When using growth data in models of population dynamics it is often weight and not length that concerns us. It can be shown that:

$$wt = W_\infty (1 - e^{-K(t - t_o)})^3$$

where W_∞ is found by the relation

$$W = al^b \quad \text{where} \quad b \quad \text{is often near 3.}$$

If we wish to apply von Bertalanffy's growth curve directly to weight data, it can best be done by employing $W_t^{1/3}$ and using the same method as for length.

Growth equations for multiple population models

Von Bertalanffy's growth curve is good as an empirical description of the course of growth of a fish but if one wishes to model an ecosystem one requires equations where growth is also a function of what the fish eats. Andersen and Ursin (1977) constructed a model which takes this into consideration.

We begin with this equation

$$\frac{dw}{dt} = Hw^m - Kw^n$$

This equation says that growth is the difference between the energy that comes in and that which goes out. Incoming energy can be described as

$$\frac{dR}{dt} = f\,h\,w^m$$

where R is food consumed, w is body weight, f is the feeding level ($0 \leq f \leq 1$) and h is a food assimilation coefficient. h is a function of many things, including temperature.

Of the food eaten, a portion β is absorbed. That which goes in is therefore

$$\beta\,\frac{dR}{dt} = \beta\,f\,h\,w^m$$

Outgoing energy can be devided into two types of loss

1. loss due to feeding and assimilation (feeding catabolism) $a\beta\,\dfrac{dR}{dt}$

2. loss due to processes independent of the fish's eating (fasting catabolism) $K\,w^n$.

This all becomes $\quad a\,\beta\,\dfrac{dR}{dt} + K\,w^n = a\,\beta\,fhw^m + Kw^n$

a is possibly a function of feeding level and K a function of temperature.

From this we get

$$\frac{dw}{dt} = (1 - a)\,\beta\,\frac{dR}{dt} - Kw^n =$$

$$(1 - a)\,\beta\,fhw^m - Kw^n$$

From an ecological viewpoint, feeding level f is the most

interesting component of this expression. f depends on the
available food Φ and the relationship

$$f = \frac{\Phi}{\Phi + Q}$$

where Q is a species specific constant (as suggested) Φ
is the quantity of food organisms, B = WN multiplied by a
factor G_b which expresses how well-suited these prey are
as food for the organism under investigation

$$\Phi = \Sigma G_b \; W_b \; N_b$$

G_b initially appears to depend on the size of the prey in
relation to the size of the predator but the preferances
for demersal or pelagic organisms, for certain colours etc.
can also be important.

MORTALITY

In fisheries biology mortality means removal of individuals
from the stock. Mortality can therefore be divided into
mortality sensu stricto and emigration. According to the
commonly used definition of a stock unit the emigration
should, however, be of minor importance compared to other
stock regulating factors.

The real mortality can also be grouped in various ways,
i.e. as

    1.   Natural mortality

        a) due to predation
        b) due to starvation
        c) due to diseases or pollution
        d) due to spawning stress
        e) due to old age

    2.   Mortality due to fishing

The relative importance of these sources of mortality
varies. Usually predation is supposed to be the most im-
portant factor, at least in small fishes. For the top pre-
dators, however, other sources must be more important.
Spawning stress is important, i.e. in Salmonidae most
individuals die after spawning, but it is probably of
some importance in other fish groups too (see e.g.
Andersen & Ursin, 1977).

Mortality is usually expressed as instantaneous rates of
change, i.e. $\frac{dN}{dt}$
where N is number and t time.

In practical fish stock assessment and management mortality

.

is usually considered constant from recruitment to maximum age.

This implies that one individual has a constant chance of dying during a unit of time.

This can be expressed as

$$\frac{dN}{dt} = -ZN$$

To integrate this differential equation, it can be written in form (using arbitrary points N_o, t_o)

$$\int_{N_o}^{N_t} \frac{dN}{N} = \int_{t_o}^{t} -z \; dt$$

$$\log_e \left(\frac{N_t}{N_o}\right) = -z \, (t - t_o)$$

$$\frac{N_t}{N_o} = e^{-z(t - t_o)}$$

$$N_t = N_o e^{-z(t - t_o)}$$

where N_o, N_t are fish in numbers at time o and t respectively. Then number at time t (N_t) can be expressed as

$$N_t = N_o e^{-z(t - t_o)}$$

This is a basic equation used in fishery biology for expressing the mortality of a fish.

If M is the instantaneous natural mortality coefficient, the rate at fish are dying due to natural causes;

$$\left(\frac{dN}{dt}\right)_M = -MN$$

If F is the instantaneous fishing mortality coefficient,
the rate at fish are dying due to fishing;

$$(\frac{dN}{dt})_F = -FN$$

If Z is the total instantaneous mortality coefficient,

$$(\frac{dN}{dt})_{F+M} = -(F+M)N = -ZN$$

In a very short time interval the deaths due to fishing
will be equal to FNdt, natural deaths MNdt, and total deaths
ZNdt, therefore

$$F + M = Z$$

I.e. instantaneous mortality coefficients are additive, and
this is one of the reasons that they are preferred to abso-
lute rates or percentages.

An important task of fishery biologists is splitting total
mortality coefficient Z into its components M (natural
mortality coefficient) and F (fishing mortality coefficient).

It is usually most convenient to estimate Z (total mortality
coefficient), therefore it is considered first.

Methods of estimating the total mortality coefficient.

1.

The total mortality can   be measured in a steady state
by the average age and length in the exploited population,
which will, if the fishery is not selective, be the same
as in the catch. If the ages and lengths of entry into the
exploited phase, and the averages in the catch, are t_c, l_c,
$\bar{t}$, and $\bar{l}$ respectively, the following expressions for Z can
be readily derived (cf Beverton and Holt, 1956).

$$Z = \frac{1}{\bar{t} - t_c} \quad ; \quad Z = \frac{K(L - \bar{l})}{\bar{l} - l_c}$$

where K, L are the constants in the von Bertalanffy equation.

2. Construction of catch curves

A catch curve is a plot of natural logarithm of fish numbers against their age, where Z (total mortality coefficient) is the slope with sign changed, of the decending part of the curve (Ricker, 1975). The number present is usually not known. What we have at hand is catch data which can be used as an index of abundance. In the case of different fishing efforts acting in obtaining the catch, catch per unit effort (C.P.U.E.) is used as an index of abundance (Fig. 1).

$$N_t = N_o e^{-Zt}$$

$$\ln N_t = \ln N_o - Zt$$

In short lived species, first step should be to make an attempt to smooth out the recruitment pulses. This is done by pooling the data, obtained at regular intervals during a period of one year.

Since the growth of fish in length is not linear, and generally slows down as length increases, there is a tendency for the older size groups to contain more age groups than younger size groups. Gulland (per.comm.) in Pauly (1982) suggests this to be compensated for by dividing the number of fish in each size group (cm-class) by time it takes the fish to grow through size group (Δt). The catch curve equation thus becomes

$$\log_e \left(\frac{N}{\Delta t}\right) = \log_e N_o - Zt$$

where t is the age corresponding to the midlength of
each class. Δ t = time needed for the fish to grow
through each length class.
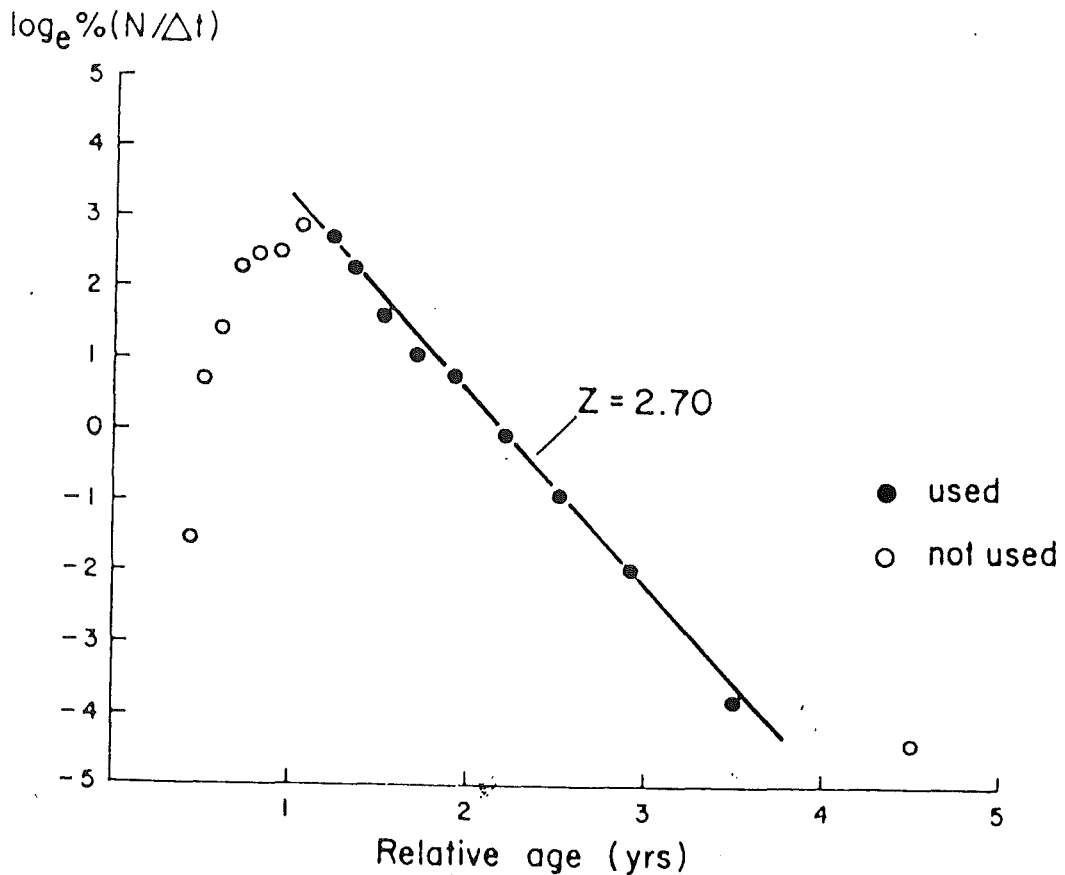
Fig. 1. A length-converted catch curve. The term "relative
age" refers to the fact that t_o is set equal to zero when
converting length to age. Note that for the computation of
Z, one point, too far to the right was omitted, along with
the ascending part of the curve (see Pauly, 1982).

Identification of biased points is important in fitting
the catch curve. Only the points really belonging to the
descending part of the curve, and contained within a rea-

sonable age span are used. The scattered points in the ascending part of the curve, in younger ages are due to incomplete recruitment and are therefore not included in the catch curve (Fig. 1). Few individuals which are close to L_∞ (asymptotic length) should also be excluded as it can generate unrealistic high ages.

Estimation of natural mortality

This is a parameter very difficult to estimate. Natural mortality estimates of tropical fish have been obtained from estimates of total mortality in stocks known.

It has been estimated from a time series of values of Z (total mortality coefficient) from the stock and plotted against their corresponding values of f (fishing effort), with M been obtained from the intercept of the lines fitted to these data (Ricker, 1975) (Fig. 2).

$$Z = M + F$$
$$Z = M + q \ f$$

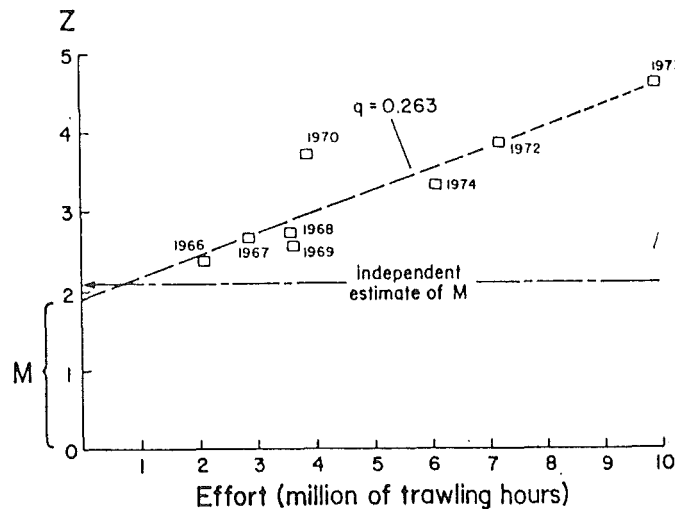q = catchability coeff. of the gear in question
f = fishing mortality.

Fig. 2. Example of plot of total mortality on effort for a tropical stock (Selaroides leptolepis, Gulf of Thailand) (From Pauly,1982).

This method also provides an estimate of q. Once the M is estimated, it is possible to get the value of fishing mortality too.

Tropical multispecies stocks are often exploited, while time series of Z and effort are generally not available. Therefore estimation of M for tropical fish stocks have so far been a difficult task.

Pauly (1982) described a method of estimating natural mortality coefficient from a knowledge of growth para- meters of a given stock (L_∞ asymptotic length, L_∞ asymptotic length and K growth constant) and of its mean environmental temperature.

The empirical relationship obtained by him is described as

$$\log_{10}M = 0.0066 - 0.279 \log_{10}L_\infty + 0.6543 \log_{10}K$$
$$+ 0.4634 \log_{10}T$$

M = exponential rate of natural mortality
L_∞ = asymptotic length
T = mean annual temperature in Celsius

An important feature in this method is that reliable estimates of M can be obtained, independently of estimates of Z. In Fig. 2 independent estimate of M is obtained by using this method.

Although natural mortality is usually considered as inde- pendent of age, recent research has shown that this is not so.

Fig. 3 shows the natural mortality as a function of age for cod (Gadus morhua) from the Barents Sea (Tretyak, 1983).
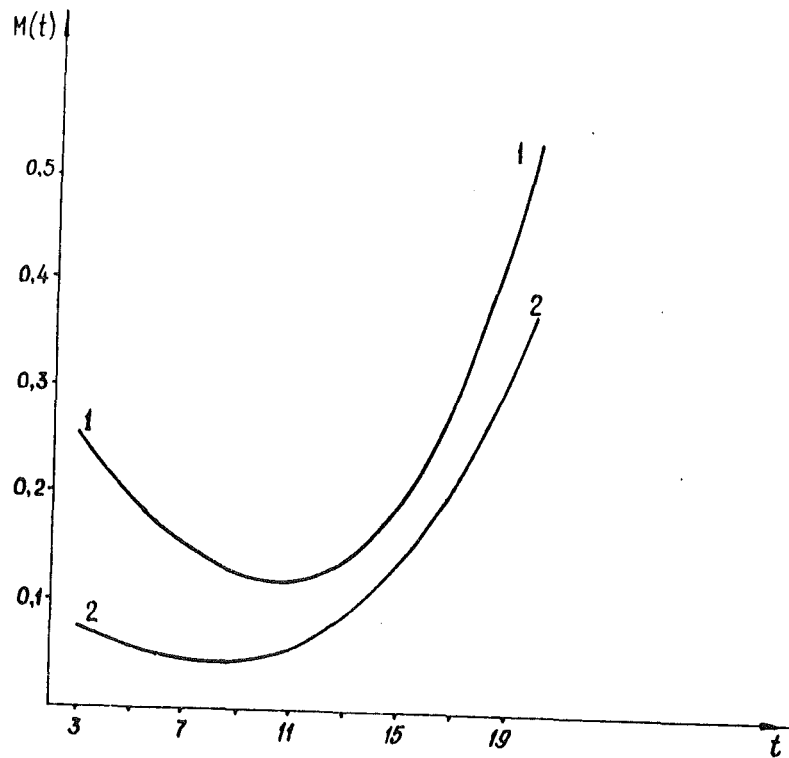
Fig. 3. Change in natural mortality rate of Arcto-Norwegian cod with age under different age composition of catches and various values of parameters $\bar{t}_s$, M_{tm} and t_e: 1 - mean age composition of catch for 1946-1950, $\bar{t}_s$=10.5 yrs, M_{tm}= 0.12, t_e=30 yrs; 2 - mean age composition of catch for 1976-1979, $\bar{t}_s$=7.9 yrs, M_{tm}=0.06, t_e=30 yrs.

The curve for 1946-50 shows the situation when the stock size was large. The high mortality among young fish (< 10 years)is probably due to cannibalism and other means of predation. The increased mortality in old fish could be due to old age and spawning stress (cod reach maturity at an age of 8-11 years).

The curve for 1976-79 shows the mortality during a period with very low stock size. There is a general reduction in

mortality, which could be considered a density dependent effect. Due to heavy exploitation the number of older fishes were most strongly reduced. This may have caused reduced cannibalism and so explain why the mortality of the youngest age group shows the most pronounced reduction.

The situation in other species may be similar to that of cod, but due to the great difficulties in estimating natural mortality even when it is considered as a constant makes it difficult to reveal age dependent or density dependent variation.

Munro (1974) found evidence that natural mortality rate (M) reduces in exploited communities, whereas it increases in some species in unexploited communities. The total mortality rate appears to be lower in the exploited areas than in the unexploited areas (Fig. 4).
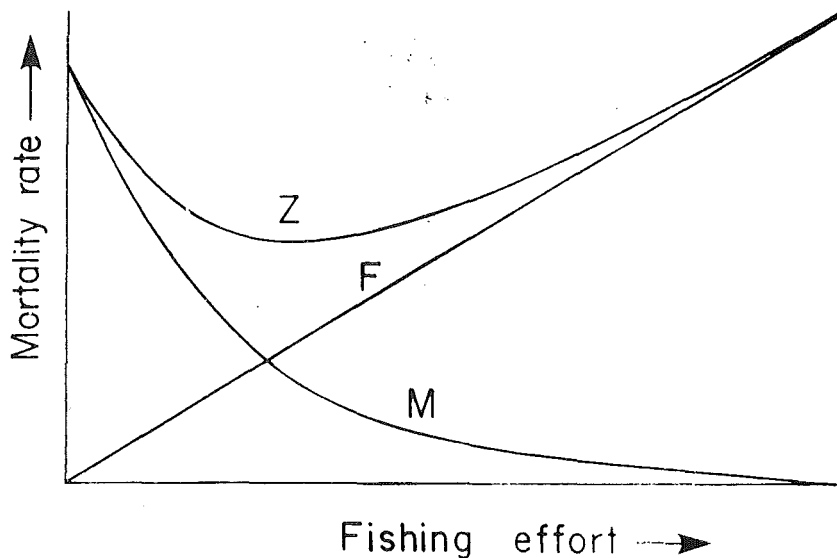

Fig. 4. Theoretical interrelationships between natural mortality rate (M), fishing mortality rate (F) and total mortality rate (Z=F+M) which will exist if natural mortality rates in an exploited community decline as a result of concurrent exploitation of predatory species and given the assumption that natural mortality rates are proportional to predator biomass (from Munro 1974).

Estimation of F (fishing mortality coefficient).

Fishing mortality could be estimated by numerous methods. Some of the main methods often used are

1) direct observations
2) swept area
3) marking
4) estimates of total mortality if natural mortality data are available
5) VPA

None of the methods are entirely satisfactory. Therefore it is best to obtain independent estimates of F by using several methods. Marking experiments are one of the best known methods of estimating fishing mortality and therefore dealt in detail here.

Estimation of F by tagging.

In this method we assume that the tagged fish are subjected to constant fishing and natural mortality rates. These are the same as in the natural untagged population.

If the initially tagged number of fish is N_o, then the number alive at time t (N_t) is

$$N_t = N_o e^{-Zt} = N_o e^{-(F+M)t}$$

rate of tagged fish being caught

$$\frac{dn}{dt} = FN_t = FN_o e^{-(M+F)t}$$

where n is the number of tagged fish recaptured.

The total number of returns from t=o, the time of tagging up to the time T is therefore obtained by integrating.

$$\int_0^{T} \frac{dn}{dt}\, dt = \int_0^{T} FN_0 e^{-(F+M)T}\, dt = \frac{FN_0}{F+M}\left[1-e^{-(F+M)t}\right]$$

If the returns are grouped in time intervals of length T, naumber caught at time r

$$rT = N_0 \frac{F}{F+M}\,(1-e^{-(F+M)rT})$$

naumber caught at time r + 1

$$(r+1)T = N_0 \frac{F}{F+M}\,(1-e^{-(F+M)(r+1)T})$$

number caught between (r+1)t and rt is $= n_r$

$$n_r = N_0 \frac{F}{F+M}\,(1-e^{-(F+M)(r+1)T}) - N_0\frac{F}{F+M}(1-e^{-(F+M)rT})$$

$$n_r = N_0 \frac{F}{F+M}\,(1-e^{-(F+M)(r+1)T} - 1 + e^{-(F+M)rT})$$

$$n_r = N_0 \frac{F}{F+M}\,(-e^{-(F+M)(r+1)T} + e^{-(F+M)rT})$$

$$n_r = N_0 \frac{F}{F+M}\, e^{-(F+M)rT}\,(1-e^{-(F+M)T})$$

$$\log_e n_r = -(F+M)rT + \log e \left\{\frac{FN_0}{F+M} \times (1-e^{-(F+M)T})\right\}$$

By plotting $\log_e n_r$ against r, a straight line is obtained (Fig. 5). Slope of the line gives $-(F+M)T$. The intercept is equal to

$$\log_e \frac{FN_0}{F+M}\left\{1-e^{-(F+M)T}\right\}$$

Since (F+M) is known from the slope, and N_0, the initial number of tagged fish is known, F the fishing mortality can be calculated.
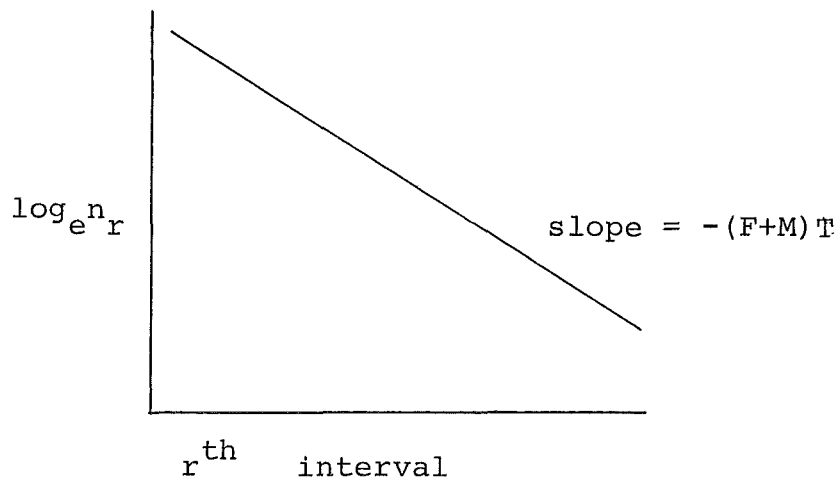
Fig. 5. Relationship between $\log_e n_r$ and the rth time interval.

The assumptions made are not often fulfilled. Deaths of fish immediately after tagging, incomplete records of tags recaptured, non-random mixing of tagged and untagged fish and change in vulnerability to fishing due to tagging may influence the results.

Estimating survival rates.

If the number alive at time t is N_t, and at time t+1 is N_{t+1}, then

$$N_{t+1} = N_t e^{-(F+M)(t+1 - t)}$$

where F is the fishing mortality coefficient and M is the natural mortality coefficient.

$$\frac{N_{t+1}}{N_t} = e^{-(F+M)}$$

$$\ln\left(\frac{N_{t+1}}{N_t}\right) = -(F+M)$$

$$S = \text{survival rate} = \frac{N_{t+1}}{N_t} = e^{-(F+M)}$$

Here we assume the two year classes to be equal size at recruitment. The error from this source can be reduced by taking average survival estimates for a series of ages.

$$S = \frac{N_1 + N_2 + - - - - -}{N_0 + N_1 + N_2 + - -}$$

Chapman and Robson (1960) found that the best estimate of S is the maximum likelihood expression, which is given as

$$S = \frac{T}{\Sigma N + T - 1}$$

where

$$T = N_1 + 2N_2 + 3N_3$$

$$\Sigma N = N_0 + N_1 + N_2 + - - - -$$

Density dependence

Le Cren (1965) showed that mortality was also density dependent. The more individuals the more competition for food, living space, etc., and the number of deaths will be higher. He showed that growth and mortality are linked in such a way that numbers are reduced to match the density of the available food (Fig. 6).
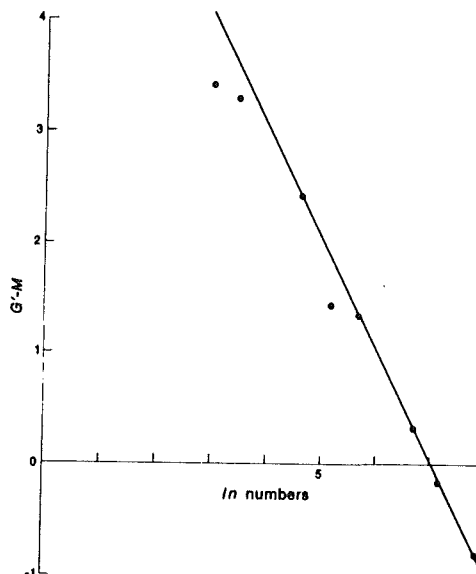
Fig. 6. The relationship between the difference between specific growth rate (G') and specific death rate (M) and the logarithm of density in numbers. Data from Le Cren, 1965, from Cushing and Harris, 1973).

Fig. 7 shows the relationship between growth rate and death rate of fish larvae of plaice, haddock, and mackerel.
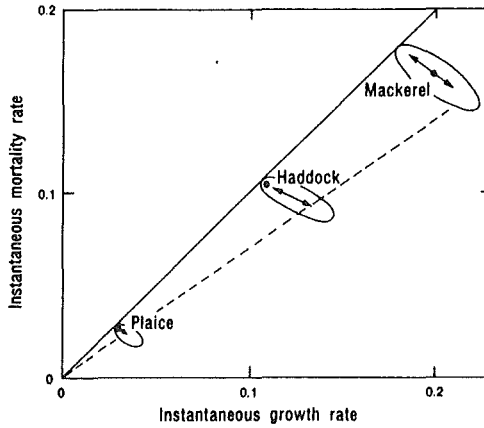
Fig. 7. The dependence of the mortality rates of larvae on their growth rates, comparing plaice, haddock, and mackerel. (Cushing 1981, adapted from Ware 1975).

Faster growing plaice larvae experience lower mortality rate than the slow growing haddock and mackerel larvae.

When food is abundant fish larvae grow quickly through the predatory fields (Fig. 8) and suffer less mortality than if food is scarce.
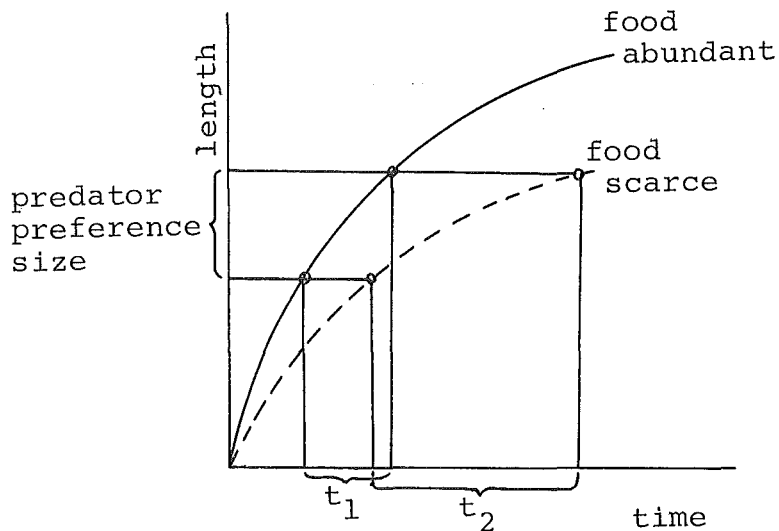
Fig. 8. Relation between growth rate of fish larvae and the time period they are vulnerable to a given predator (predator field).

t_1 predator field for the faster growing larvae
t_2 "   "   "   " slow   "   "

Cushing and Harris (1973) showed that such mechanisms could generate density dependent growth and density dependent mortality.

RECRUITMENT

Recruitment can be defined as the addition of new members to a group. In fishery biology we usually mean admission to the fishable part of the stock.

In this sense of the word recruitment does not mean the number of fish hatched but rather the number of fish which join the fishable part of the stock. This can occur when young fish migrate from the nursery grounds to the adult grazing grounds (e.g. many flounder species), when they descend to the bottom (e.g. shrimps) or by altering their behaviour in some form. However, it usually means that they can be caught by conventional fishing gear.

There is therefore a close correlation between gear selectivity and recruitment. We will not delve into gear selectivity here, instead we will briefly explain what it is. If we have a fish stock where all the size groups are represented within the same area and have similar behaviour, the use of a gill net to catch the fish will allow the very small ones to slip through the mesh and the very large ones will not be caught. The result would be a selection curve with almost normal distribution.

However, the selection curve we are most interested in is that for trawl. In this case the smallest slip through whereas those fish over a given size will be caught. Sometimes the result will be skewed because the largest may manage to swim away from the trawl but this is of little practical significance. In early stock models a selection length was usually chosen to equal the length at which 50% of the fish are caught, assuming that all the smaller fish escape and all the larger fish are captured (knife-edged selection). This is not always necessary any more because the computers presently in use can easily treat any selection curve.

We will also note that age at recruitment t_r is normally

set equal to the lowest possible practical selection length. As we will see later, the one used in practice is called t_c (c for catch).

Recruitment to the studied fish stocks can vary by up to a factor of 100 or more from one year to the next (Table 1). The natural mortality also leads to a reduction in numbers from the egg stage to the age at recruitment of the order of 10^3 to 10^7. Regulation of this requires very finely tuned mechanism.

Even though the relationship between parent stock and recruitment is one of the most critical factors in the regulation of a fishery, it is still not sufficient information to formulate a satisfactory model to predict recruitment.

Table 1.   Recruitment variation in North Sea fishes 1963-1975. Numbers adjusted to a value of 100 for the most outstanding year class of each species. "Ratio" is the ratio between the numbers in the strongest and weakest year classes. After Ursin (1979b).

Year Class	Gadoids					Flatfishes		Clupeids		Sandeel	Mackerel	
	Cod	Haddock	Whiting	Saithe	Norway Pout	Plaice	Sole	Herring	Sprat	Sandeel	Mackerel	
1963	52	1	14	17	4	100	100	100			10	
1964	49	1	26	23	6	29	21	53			26	
1965	70	2	30	18	.5	28	11	47			43	
1966	63	12	37	50	7	25	11	66	59		62	
1967	20	100	100	51		21	18	65	62		10	
1968	19	6	33	55	2	27	9	36	37		16	
1969	82	2	30	29		32	26	78	41		100	100
1970	100	14	33	29	45	25	6	62	20	100	9	12
1971	18	21	68	30	7	20	14	41	19	21		17
1972	35	4	90	40	16	62	19	19	46	47		4
1973	31	21	63	100	100	40	18	47	91	28		15
1974	51	40	92	27	38	25	7		100	86		11
1975	27	9	37	50	18	37	22		79	41		4
Ratio	6	100	7	6	200	5	17	5	5	5	11	25

Ricker (1975) set up a few points which a stock(P)- recruitment(R) model should fulfill:

1. the curve must pass through the origin, i.e. no parents will result in no recruits
2. the curve should not reach the abscissa with large parent stocks, i.e. irrespective of the size of the parent stock, recruitment will not be eliminated
3. the relative recruitment (R/P) should decrease with increasing P
4. the recruitment must be larger than the parent stock at some level of parent stocks' size.

A great number of models can be constructed from plausible biological regulatory mechanisms which fulfill these requirements. We shall primarily examine two such classical models without stating which of the two is better.

1. Ricker's recruitment model.   In his work in 1954 Ricker laid the foundation for modern investigation of the stock-recruit relationship. He developed an equation which states, in its simplest form,:

$$R = A \, P \, e^{-B \, P}$$

where R is the number of recruits, P is the parent stock size. A is the coefficient of density independent mortality and B the coefficient of density dependent mortality (Fig.1).

This model can be expressed also by the equation

$$\frac{R}{R_r} = \frac{P}{P_r} \, \exp \frac{P_r}{P_m} \, (1 - \frac{P}{P_r})$$

where R_r is the number of recruits which replaces the stock P_r - i.e. the point of equilibrium. P_m is the stock size which gives maximum recruitment.
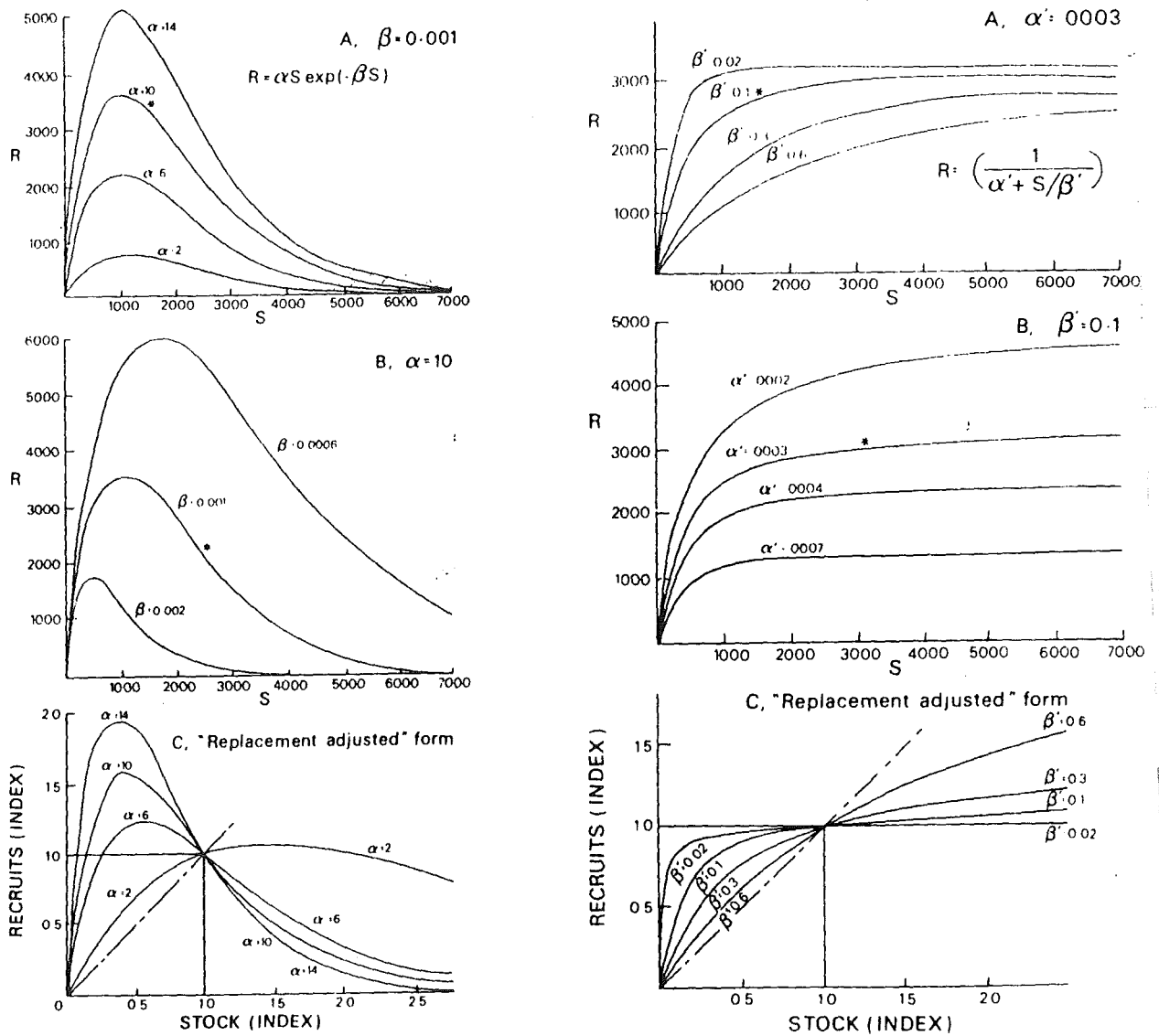
Fig.1. Ricker (left) and Beverton & Holt (right) stock-recruitment curves. (From Pitcher and Hart, 1982)

This equation was first used on salmon where almost all the fish die after spawning. In this case the R_r replacing P_r has a clear biological significance. Most other species have several yearclasses in the spawning stock and R_r has little meaning.

By deriving equation (1) we get $(1 - BP)\, Ae^{-BP}$ and we see therefore

$$P_m = \frac{1}{B} \qquad\qquad R_m = \frac{A}{Be}$$

When Ricker developed this model, the biological assumption was that the density dependent component of mortality is caused by cannibalism. This is probably not applicable to marine fish stocks. However, if one assumes that the fish larvae are more vulnerable to predation if they get less food, then the same model can be applied (Cushing 1977).

2. Beverton and Holt's recruitment model. - Beverton and Holt (1957) assumed that recruitment was governed by the density dependent mortality. If the mortality for eggs and larvae is proportional to the number alive at any given time and the mortality subsequently decreases continually with the number of individuals, this can give a relationship in the form of:

$$R = \frac{1}{a + \frac{b}{P}}$$

where a and b are constants (Fig.1).

Unlike to the Ricker curve, this model does not give a maximum and recruitment approaches an asymptote when P increases.

A curve of Ricker's type appears to be best when 1) cannibalism (consumption of larvae by the adult fish) is an important regulating mechanism or 2) when increased density results in slower growth of the larvae through the stages most vulnerable to predation or other types of mortality or 3) when there is a time lag in the reaction of predators such that one can observe overcompensation for initially high densities of larvae.

Beverton and Holt's type of curve is assumed best when there is a maximum carrying capacity due to food supply or space or when there can be immediate and constant predator pressure.

Table 2.   Some attributes of r- and K-selected fishes
(From Lowe - McConnell, 1977).

Dominant type of selection:	'r' (fecundity)	'K' (resource use efficiency)

Where found	upwelling zones
	estuaries
	continental shelf off
	  large river mouth
		coral and rock reefs
		littoral/benthic zone of
		  African Great Lakes

Dominant groups of fish	pelagic
	clupeoids and their
	  predators
		demersal
		acanthopterygian (spiny-
		  rayed) and eel-like forms

Diversity of fauna	less diverse with dominants	very diverse lacks dominants
Seasonality of environment	fluctuates with seasonal influx of nutrients varies from year to year	very stable throughout year very stable year to year
Environmental cover	lacking fish school	plentiful many territorial and solitary fish

Schooling	prey-fish school, often
	  with diurnal migrations
		many fish school on reef
		  by day, dispersing away
		  from reef to feed by night

Growth	fast	slower and variable
Longevity	prey-fish have short life cycles	many have long life cycles some with sex change
Reproduction	pelagic eggs, numerous no parental care protandry in polynemids	breeding displays, pairing often parental care protogyny in serranids and cleaner wrasse
Production/ Biomass ratio	high	lower

Food sources	specializations to use foods
	  at low trophic levels, or to
	  feed on fish which do so
		adaptive radiations to use a
		  great variety of foods, but
		  species specialize and
		  may be stenophagous

Competition for food	may respond to increased
	  nutrients by increased
	  population size
		appears to be little

Competition for living space	appears to be little,
	  not territorial
		very great
		many territorial
		diurnal/nocturnal change-
		  over

Effect of predation	leads to uniformity ? restricts speciation	leads to aspect diversity ? promotes speciation

A curve of the Ricker type can only occur when the mortality
in some way is dependent upon the _initial_ density, i.e. on the
number of eggs spawned or the number of parents producing these
eggs as in the case of cannibalism.

A curve of the Beverton and Holt type occurs when the mortality
depends on the _current_ density of larvae only.

To further study the characteristics of the two types of curves
it is useful to have a look at the logistic equation

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

where N is stock size, K is carrying capacity or maximum stock
size and r is the intrinsic rate of increase (see Descriptive
stock models).

This equation can be used to illustrate two strategies of
stock growth.

The so-called r-strategists can produce a lot of offspring and
quickly fill up an empty niche. In a highly variable environ-
ment, i.e. an environment with changing carrying capacity
they can easily adjust their number. They can also quickly
colonize new habitats.

K-strategies reproduce more slowly. They are adapted to stable
environments where it is important to persist and out-compete
rivals.

The following relations have been derived.

Ricker curve $\qquad\qquad A = e^{r} \qquad B = \frac{r}{K}$

Beverton and Holt curve $\qquad b = e^{-r} \qquad a = (1 - e^{-r})/K$

The density-dependent parameters of the two types of curves
therefore show the following relation

$$A = \frac{1}{b}$$

From this Erberhardt (1977) concluded that the Ricker type
of curves describe the recruitment in a typical r-selected
species. These have a rapid population growth. They frequently
overshoot the carrying capacity, K, and then oscillate about
that level.

The higher the hump is, the greater will the oscillations be.
It has been shown that stocks having a Ricker curve with high
hump is less susceptible to extinction than stocks with lower
humps.

Beverton and Holt's type of model typically describes a
K-selected species where the population tends to remain near
the level of the carrying capacity. These models cannot
generate oscillations in the same way as the Ricker type of
models do.

Adaptation of the data

There are several methods with which to fit these models
to the actual data. Here we will illustrate two simple
graphic methods:

1. Ricker $$R = APe^{-BP}$$

$$\frac{R}{P} = Ae^{-BP}$$

If $\ln \frac{R}{P}$ is plotted against P we get a straight line
with intercept equal to $\ln A$ and a slope of $-B$.

2. Beverton and Holt $$R = \frac{1}{a + \frac{b}{p}}$$

$$\frac{1}{R} = a + \frac{b}{p}$$

If $\frac{1}{R}$ is plotted against $\frac{1}{P}$ this gives a straight line with
intercept a and slope (direction coefficient) b.

From a statistical viewpoint, neither of these methods are satisfactory since the variables are not independent but it would require too much to get into more advanced methods here.

For tropical stocks Pauly (1982) suggested the following method to get indirect estimate of recruitment which next can be used to fit a P/R - curve:

1. Estimate growth and natural mortality
2. Compute Y/R for each year
3. Divide Y/R into the catch to get number of recruits

Several of the assumptions which this method is based on (will be treated later) are obviously violated by using this procedure. However, the result might give a first approximation.

Depensatory recruitment curves

All the curves we have looked at till now have been compensatory i.e. $\frac{R}{P}$ has increased when P has decreased. There are situations which imply that this is not always the case. Instead, imagine a depensatory curve (Clark 1974, Gulland 1977). The important characteristic here is that at small values of P, $\frac{R}{P}$ will decrease with decreasing P i.e. relative natural mortality increases (Fig.2)

In species which form schools it is reasonable to expect such depensatory effects when predation is heavy. Schooling is, of course, a means to avoid predation and, within certain limits, the effectiveness of the school increases with school size. Possibly just such a mechanism is the reason why herring stocks are so vulnerable to total collapse during intensive fishing.
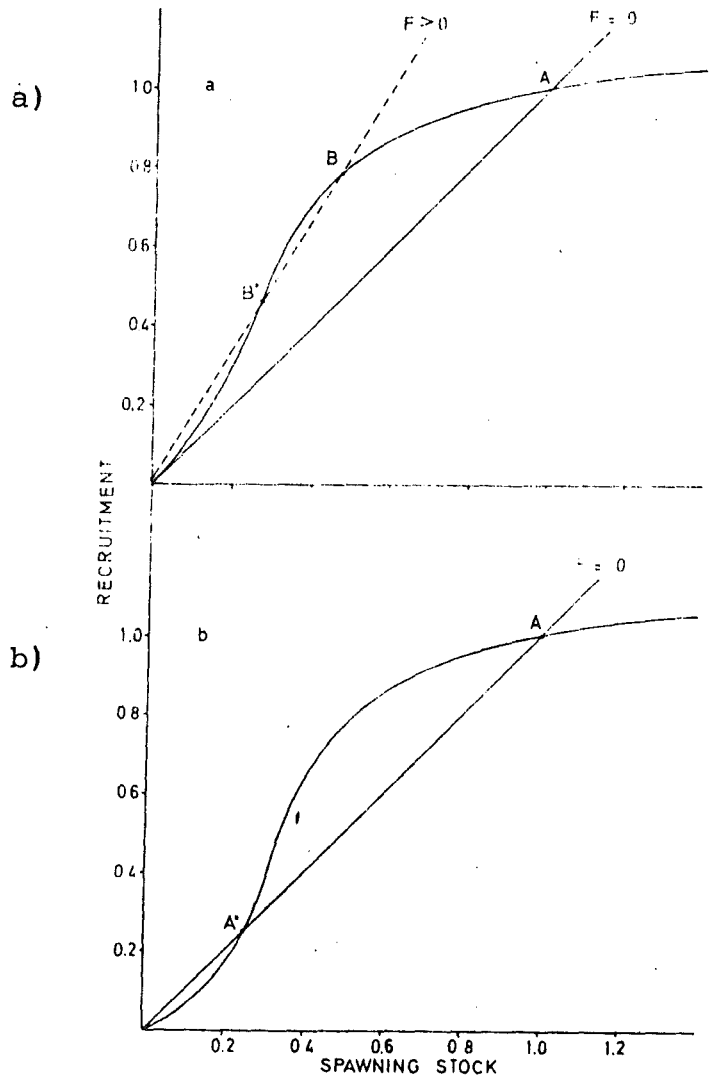
Fig.2. Depensatory stock-recruitment curves. The straight
lines are the compensation line for fishing mortality
F = O and F > O. a non-critical depensation. b critical
depensation (From Ulltang, 1980).

Examples of recruitment curves

Some typical recruitment curves for tropical fish are
shown in Fig.3. Most of them show the great scattering
of points so characteristic to R/P curves also from temperate
waters.

They offer some evidence, however, that a Ricker type of
curve gives a better fit than a Beverton and Holt type.
Some of the curves have a very high hump suggesting great
fluctuations in stock size, but also lower susceptibility
to overfishing than stocks with lower humps.

All these curves should, however, be regarded as pre-
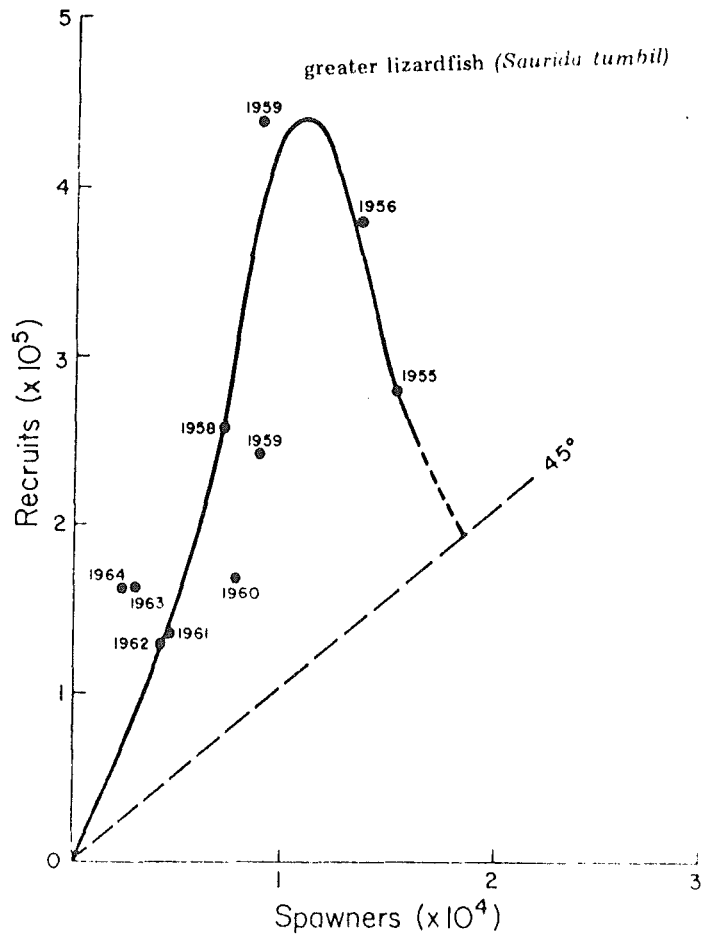liminary, and the conclusions drawn are tentative only.

Fig. 3. Stock-recruitment relationship for some tropical
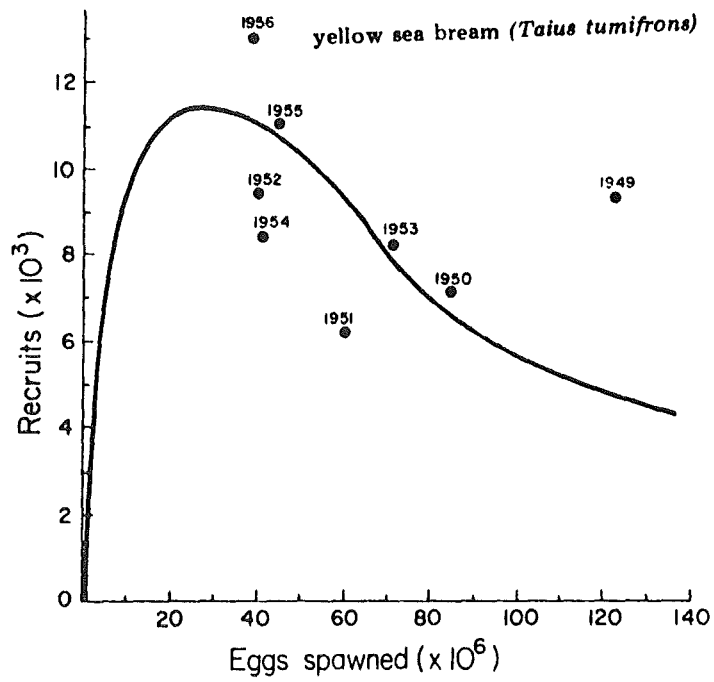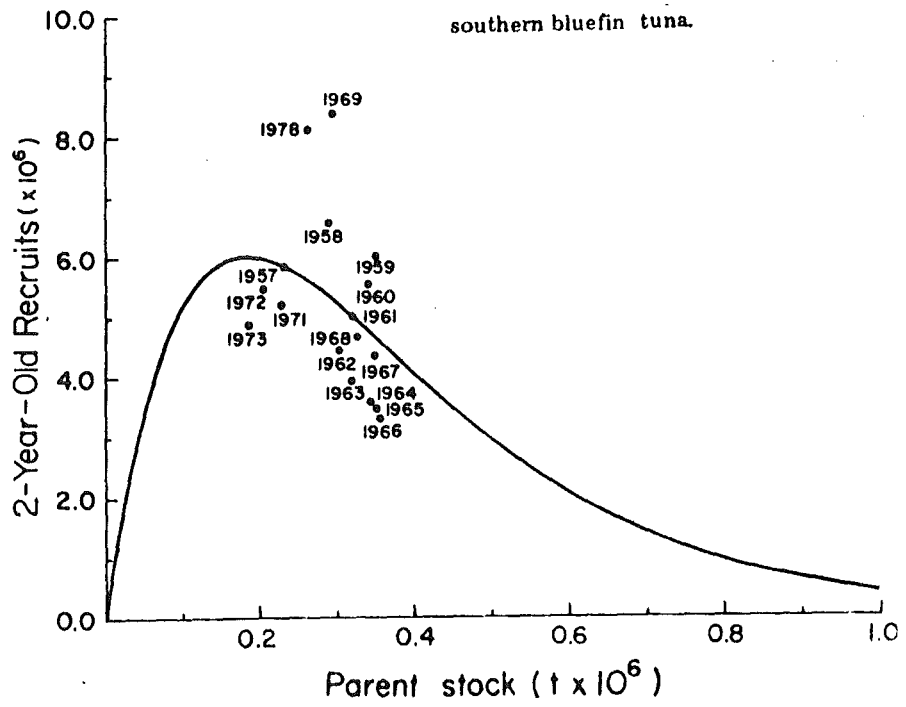fish stocks. (from Murphy 1982)

southern bluefin tuna.

yellow sea bream *(Taius tumifrons)*

Fig. 3. cont.

Recruitment pattern

The temporal recruitment pattern of a fish is a function of

     1)   spawning season

     2)   survival of larvae and juveniles

Even with a continuous spawning, the recruitment can be concentrated to one or more distinct seasons.

Sharp (1980) used the concept "recruitment windows" which were open only during brief periods. These periods could be related to hydrography, availability of food and possibly to presence of predators.

It has i.e. been shown that several fish species from the northern Indian Ocean have recruitment periods matching with the monsoonal system. (Pauly and Navaluna, 1983)

Although it seems likely that spawning will be concentrated to those seasons where the larvae have a fair chance of surviving, there is in fact very little evidence to prove this. Some data for maturity and recruitment pattern for Sardinella gibbosa from Sri Lanka may be taken as evidence for coinciding spawning and recruitment pattern (Fig. 4).

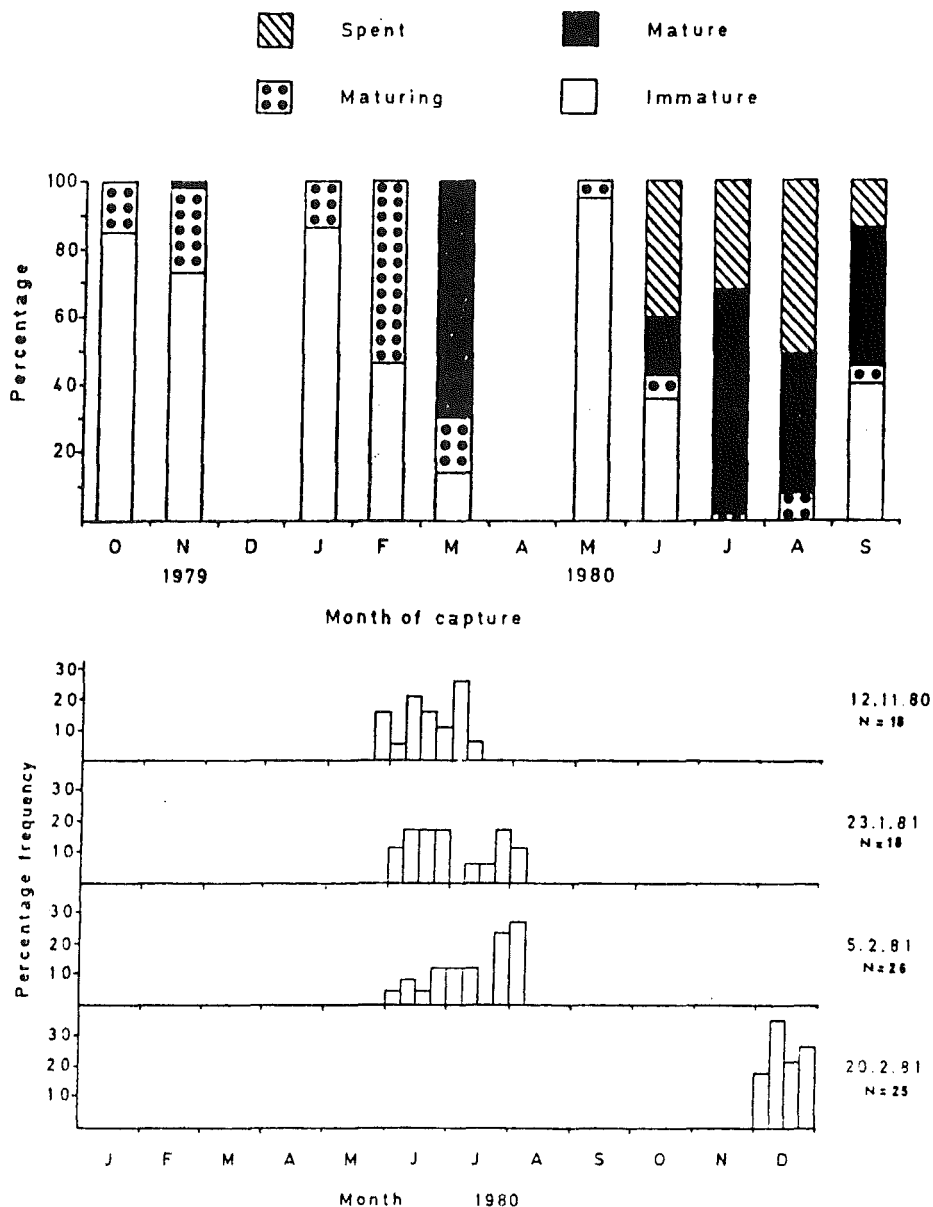Recruitment patterns for some tropical fish stocks are given in Fig. 5.

Fig. 4. Gonad cycles indicating spawning periods in
Sardinella gibbosa from Sri Lanka (upper) and birth-
dates of the same species as calculated from daily growth
rings in the otoliths (lower). Dates given at the right-
hand side indicate when the samples were taken. (From
Dayaratne and Gjøsæter, 1984)
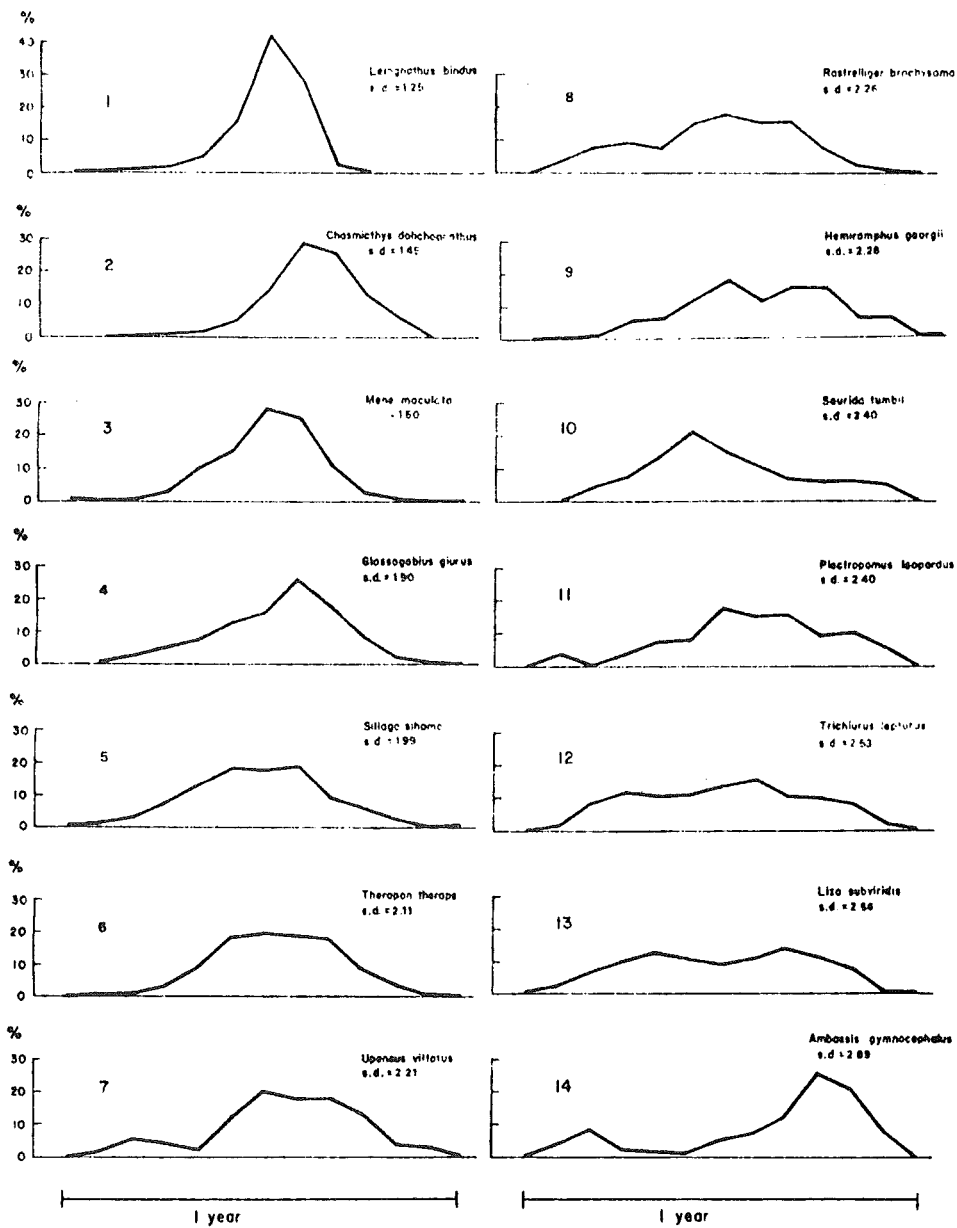
Fig. 5. Recruitment patterns in 14 stocks of fishes whose growth parameters were estimated by means of ELEFAN I. Note increase in standard deviation from *Leiognathus bindus* (s.d. = 1.25) to *Ambassis gymnocephalus* (s.d. = 2.89), with corresponding shift from 1 to 2 recruitment seasons. Source of length-frequency data: Balan 1967 (1), Goeden 1978 (11), Tamura and Honma 1977 (2), Marquez 1960 (4) and Ziegler 1979 (3, 5, 6, 7, 8, 9, 10, 12, 13, 14). (From Pauly 1982)

ANALYTICAL MODELS.

The starting point of this type of model is the individual fish, compared to the Schaefer type of model which regards the total stocks as the basic unit.

In a stock the whole life span can be divided into periods. For each period the number alive, the number caught, the number dying of natural causes, and the number surviving to the beginning of next period can be calculated, and the yield in weight can be calculated if the number caught and the mean weight of individual fish is known.

This process can be calculated mathematically. The parameters of the stock concerned are given below.

N_t = number of fish at age t

W_t = average weight of fish at age t

R = no. of recruits, or no. of fish alive at time t_r

M = instantaneous natural mortality coefficient

F = instantaneous fishing mortality coefficient

We first consider a time period before fishing operates. If

t_r = age at recruitment

t_c = age at capture

then

$$t_r < t < t_c$$

the number alive at time t, N_t, can be given as

$$N_t = R\, e^{-M(t-t_r)}$$

The number alive at first capture, R', can be given as

$$R' = R\, e^{-M(t_c-t_r)}$$

Therefore

$$N_t = R'e^{-(F+M)(t-t_c)}$$

$$N_t = R\, e^{-M(t_c-t_r)-(F+M)(t-t_c)}$$

The yield in weight is proportional to fishing mortality (F), stock size in number (N_t) and mean weight of an individual at age t ($\overline{W}_t$).

The yield in weight caught in a short interval

$$\frac{d\,y}{d\,t}t = FN_tW_t$$

$$d\,y_t = FN_tW_t dt$$

The total weight caught throughout the life span of a cohort (t_c = age at first capture, t_λ = maximum age) is then

$$Y = \int_{t_c}^{t_\lambda} FN_tW_t dt$$

W_t can be expressed in the form of von Bertalanffy's growth equation

$$W_t = W_\infty (1-e^{-k(t-t_o)})^3$$

where k is the growth constant of the species concerned. This equation can be written as

$$W_t = \left[1 - 3e^{-k(t-t_o)} + 3e^{-2k(t-t_o)} - e^{-3k(t-t_o)}\right] W_\infty$$

$$W_t = W_\infty \sum_{n=0}^{3} u_n e^{-nk(t-t_o)}$$

$$u_o = 1, \quad u_1 = -3, \quad u_2 = 3, \quad u_3 = -1$$

therefore yield can be expressed

$$Y = \int_{t_c}^{t_\lambda} F \cdot R'W\, e^{-(F+M)(t-t_c)} \sum_{n=0}^{3} u_n e^{-nk(t-t_o)} dt$$

writing $t-t_o = (t-t_c)+(t_c-t_o)$ and rearranging

$$Y = FR'W_\infty \sum_{n=0}^{3} u_n \int_{t}^{t_\lambda} e^{-(F+M+nk)(t-t_c)} \cdot e^{-nk(t_c-t_o)} dt$$

Integration gives

$$Y = FR'W_\infty \sum_{n=0}^{3} \frac{u_n}{F+M+nk} e^{-nk(t_c-t_o)} (1-e^{-(F+M+nk)(t_\lambda-t_c)})$$

If t_λ is sufficiently large, the last term can be neglected. The yield equation becomes

$$Y = FR \; e^{-M(t_c-t_r)} \; W_\infty \sum_{n=0}^{3} \frac{u_n e^{-nk(t_c-t_o)}}{F + M + nk}$$

Recruitment is unknown and often variable and therefore difficult to estimate. Therefore the yields are normally calculated as yield per recruit.

$$Y/_R = Fe^{-M(t_c-t_r)} \; W_\infty \sum_{n=0}^{3} \frac{u_n e^{-nk(t_c-t_o)}}{F + M + nk}$$

This model assumes that the stock is in equlibrium condition, and that recruitment is independent of parent stock size.

The Beverton and Holt model gives the yield of one year-class throughout its life. If the stock is in equlibrium and the recruitment is constant, it can easily be shown, as in the following example that the same result can be obtained by looking at the yield from all year-classes caught during a particular year.

| | YEAR | | | | | |
	1976	1977	1978	1979	1980	
1976	1000	800	400	300	100	4
1977		1000	800	400	300	3
1978			1000	800	400	2
1979				1000	800	1
1980					1000	0

The 1976 year-class throughout its life span.

Year-classes 1976-1980 present in the fishery in the year 1980.

Variation of population and catch characteristics with fishing
mortality (F).

Fig. 1 shows the variation of annual yield in weight per re-
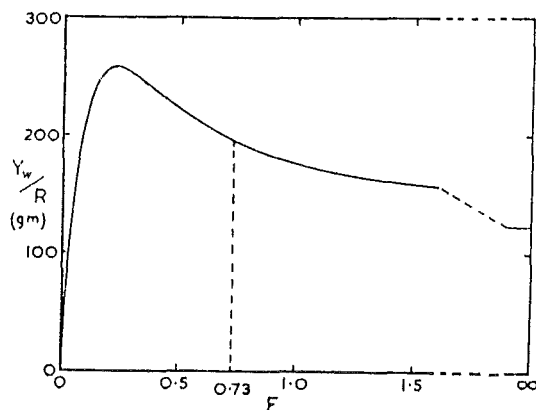cruit of plaice with fishing mortality under equlibrium con-

Fig. 1. Plaice: Yield against fishing mortality, 70 mm. mesh.
(Steady yield per recruit,Y_W/R, as a function of fishing mor-
tality coefficient F, with t_c=3.72 yrs. The vertical broken
line at F=0.73 indicates the point on the curve corresponding
to the pre-war fishing intensity, a procedure that is follo-
wed in subsequent diagrams where relevant. An important fea-
ture of this curve is that it has a maximum at a value of F
considerably less than the pre-war value). (From Beverton and
Holt 1957).

By examining the shape of yield curve (Y/R) Vs fishing morta-
lity (F) we can see that

1) The curve starts at the origin - that is yield is zero
   when fishing mortality is zero.

2) As F increases from 0 ——> so does Y/R very rapidly at
   first though at a continuously decreasing rate.

3) If t_c < $t_{crit.}$ a maximum value of the yield (Y/R) is
   reached at a certain value of fishing mortality. ($t_{crit.}$
   is the age when the year-class has its greatest biomass).

4) Thereafter the curve decends comparatively slowly with the slope decending towards an asymptotic yield as

F ——————> ∞ . This $^Y/_R$ corresponds to weight at recruitment.

It must be remembered that this curve relates to equilibrium yields and gives no information on the actual changes in yield in <u>time</u> with changes in fishing mortality.

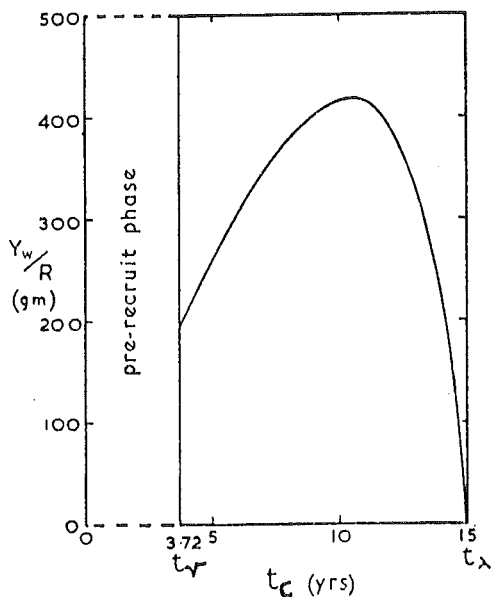<u>Variation of population characteristics and catch characteristics with t_c.</u>

Fig. 2. Plaice: Yield against mesh, pre-war fishing intensity. (Yield per recruit,Y_W/R, as a function of mean selection age, t_c , with F=0.73. The maximum of the curve occurs at a value of t_c considerably above that for a 70 mm. mesh (3.72 yrs.) (From Beverton and Holt 1957).

The curve begins at age t_c at which fish enter an exploited stage. The curve reaches zero at a value of t_c = t_λ , implying that the mesh size is too large to catch any fish during their life span.

We can consider variation in yield simultaneously with F and t_c. This is called the yield isopleth diagram.

Since there are two variables present, this diagram is drawn by plotting F and t_c on x and y axes respectively and by drawing lines through numerically equal values of yield. In this way a form of contour map - which is referred to as "isopleth diagram", is constructed (Fig.3).
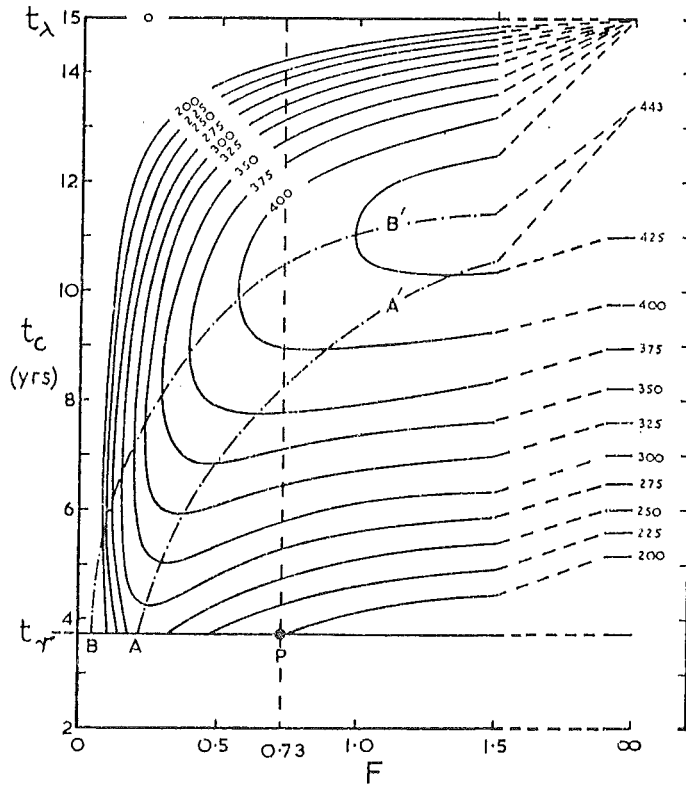

Fig. 3. Plaice: Yield isopleth diagram. (This shows the steady yield obtained from any combination of F and t_c . Contours are of yield per recruit at intervals of 25 gm. The top and left hand borders of the diagram are the zero contour of Y_W/R. The line AA' joins the maxima of yield-mortality curves, while the line BB' joins the maxima of yield-mesh curves. The point P indicates the pre-war values of F and t_c). (From Beverton and Holt 1957).

Sections parallel to the F axis at various levels of t_c show that F_{max} (the value of F given the highest Y/R for a given t_c) increases as t_c increases, and the curves of yield with respect to F at these higher values of t_c become flatter, the maxima eventually disappear (Figs.3 and 4). The changes of F_{max} with different values of t_c is shown by AA' line.
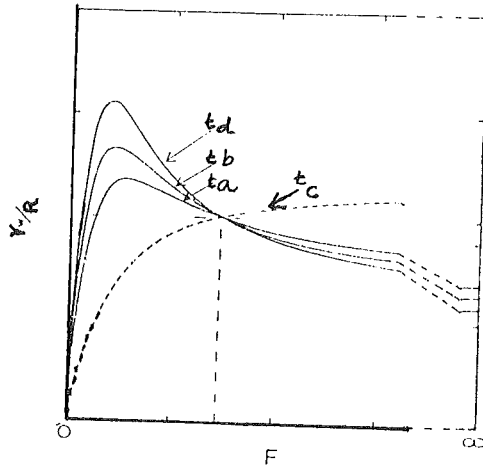

Fig. 4. Different values of age at capture (t_c) on yield fishing mortality curves. $t_a < t_b < t_d < t_c$

In the yield/isopleth diagram given for plaice - by Beyerton and Holt (195⅗) - the maximum possible yield is obtained when $F \longrightarrow \infty$ and $t_c = 13.35$ (where AA' and BB' lines meet). This is the age at which the total weight of year-brood is at its greatest (which is referred to as critical age, Fig. 5).

The BB' line joins the maxima of yield - t_c curve (Fig. 3). Sections parallel to the t_c axis show that Y/R first increases with F and then decreases. The value of t_c max increases with F as does F_{max} with t_c.
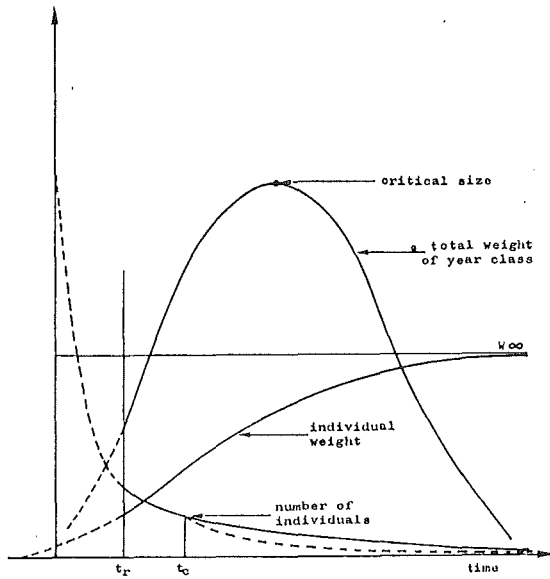
Fig. 5. Changes in numbers and weight of a year-class of fish during its life. (From Gulland 1969).

Variation of other characteristics:

1) Natural mortality (M)
2) Growth constant (k)

1) Effect of different M values on Y_W/R Vs F curve.

Fig. 6. Plaice: Effect of different natural mortalities on yield-fishing mortality curves. (Yield per recruit, Y_W/R, as a function of F with t_c =3.72 yrs., taking M=0.05, 0.10, 0.15, and 0.50).(From Beverton and Holt 1957).

As M value increases the $^Y W/_R$ value decreases, but the curves have the same general shape. With higher values of M (0.50) the maximum in the yield curve no longer occurs within the working range of F (Fig. 6).
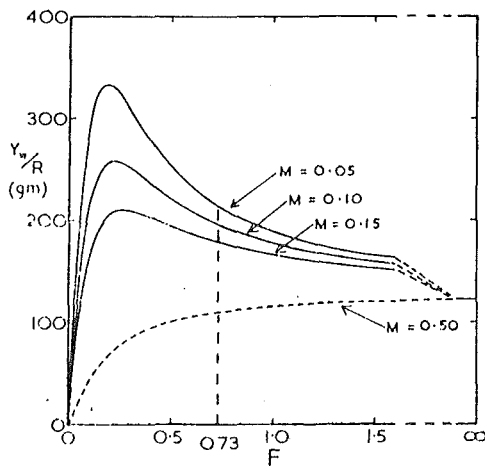
1b) Effect of different M values on $^Y W/_R$ Vs t_C curve.
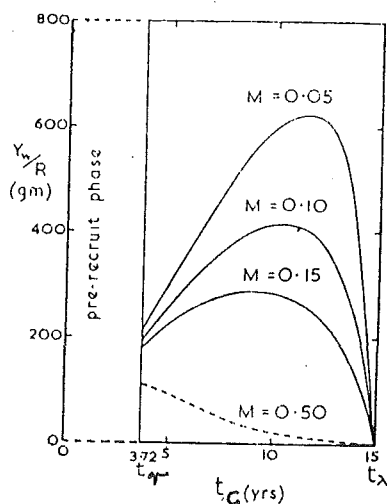
Fig. 7. Plaice: Effect of different natural mortalities on yield-mesh curves. (Yield per recruit, $^Y W/_R$, as a function of t_C with F=0.73, taking M=0.05, 0.10, 0.15 and 0.50 respectively). (From Beverton and Holt 1957).

Taking the same range of M as before, and considering the effect of M on $^Y W/_R$ curves against t_C, we can see that the level of the curve and $t_{c\ max}$ decreases as M increases (Fig. 7).

2. Effect of k - von Bertalanffy growth parameter - on $^Y W/_R$ Vs F curve.

Large changes in k have to be made before noticeable differences in the shape of yield curves are caused (Fig. 8a). The level of the curves differ greatly which is due to the difference in weight of individual fish in the exploited phase (Fig.8b).
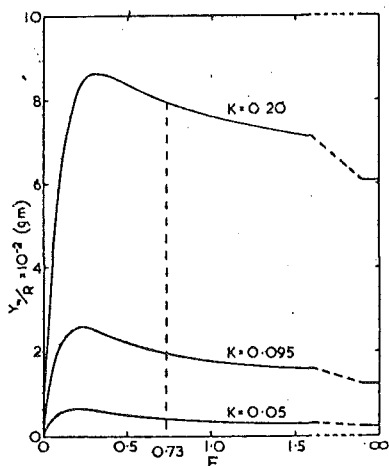
Fig. 8a. Plaice: Effect of different growth rates on yield-fishing mortality curves. (Yield per recruit, $^Y W/_R$, as a function of F with t_c =3.72 yrs. taking K=0.05,0.095 and 0.20 respectively).(From Beverton and Holt 1957).
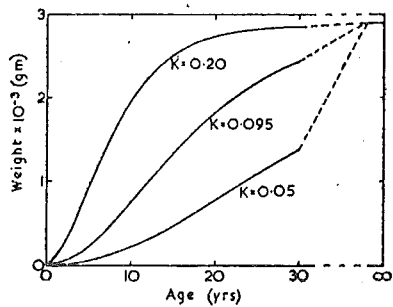
Fig. 8b. Plaice: Curves of growth in weight given by the values of K used in Fig. 8a. (In each case W_∞ and t_o have their usual values, i.e. 2867 gm. and 0.815 yrs. respectively).(From Beverton and Holt 1957).

Variations in some other parameters with F and t_c.

1. Biomass against F.

Fig. 9. Plaice: Biomass against fishing mortality, 70 mm. mesh.(Biomass per recruit of the exploited phase, $\overline{P}'_W/R$ (proportional to catch per unit effort) as a function of fishing mortality coefficient F with t_c =3.72 yrs. With a 70 mm. mesh this is also the curve of biomass of the whole post-recruit phase, since in these circumstances $t_r = t_c$).(From Beverton and Holt 1957).

Biomass P_W/R decreases continuously from a finite value at F = 0, rapidly at first and then flattening to an asymptote at zero as F $\longrightarrow \infty$ (Fig. 9).

For plaice $t_r = t_c$; therefore this curve is the same as that of annual mean biomass of the whole post recruited phase. $\overline{P}_W/R$ as a function of F for haddock where $t_c > t_r$ will be as shown in Fig. 10.

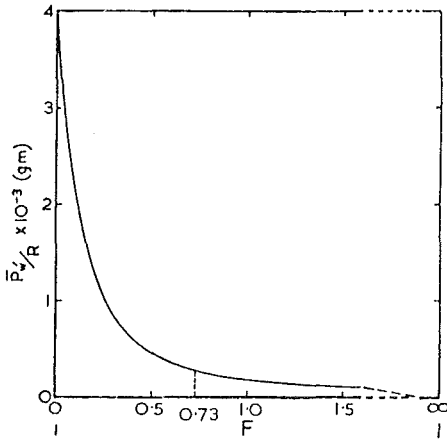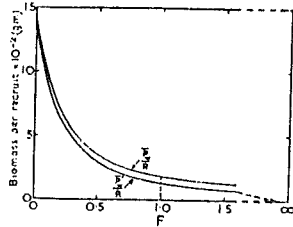Fig. 10. Haddock: Biomass against fishing mortality, 70 mm. mesh. (Biomass per recruit of exploited phase, $\overline{P}'_W/R$ (proportional to catch per unit effort) and total biomass per recruit, $\overline{P}_W/R$, as functions of F with t_c =1.83 yrs.)(From Beverton and Holt 1957).

2. Mean weight and length against F.
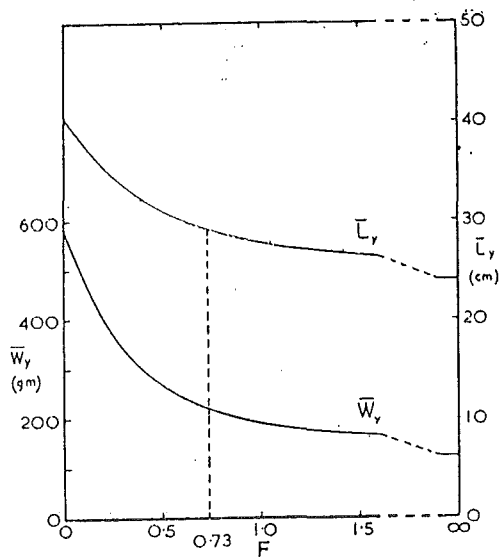
Fig. 11. Plaice: Mean weight and length against fishing mortality, 70 mm. mesh. (Mean weight, $\overline{W}_y$, and length, $\overline{L}_y$, of fish in the catch as functions of F with t_c =3.72 yrs.) (From Beverton and Holt 1957).

The average weight of fish of the catch $\overline{W}_y$ also decreases continuously from a finite value at F = 0 to an asymptote

as $F \longrightarrow \infty$. This asymptote is the mean weight of fish at age t_r; it is the same Y_W/R at $F = \infty$ (Fig. 11).

The mean length of fish in the catch varies in a similar way (Fig. 11).

Variation of biomass with age at recruitment (t_r), in the total biomass per recruit $(\overline{P}_W/R)$ phase, and of the exploited phase $(\overline{P}_W'/R)$.

The behaviour of $\overline{P}_W/R$ with respect to t_c is very different from that with respect to F (Fig. 12).
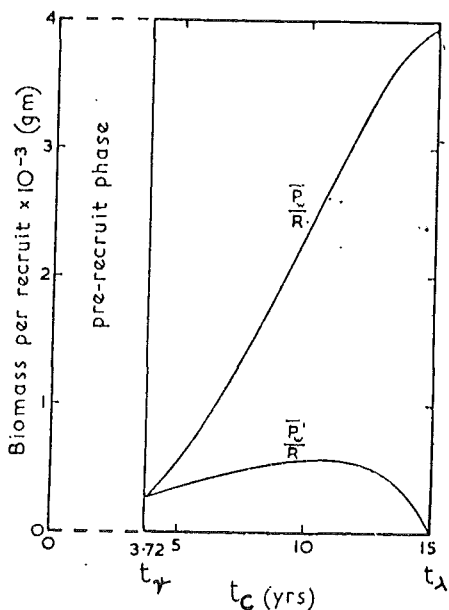
Fig. 12. Plaice: Biomass against mesh, pre-war fishing intensity. (Biomass per recruit of the exploited phase, $\overline{P}_W'/R$, and total biomass per recruit, $\overline{P}_W/R$, as functions of t_c with $F=0.73$).(From Beverton and Holt 1957).

When $t_r = t_c$ as in the case of the plaice, $\overline{P}_W/R = \overline{P}_W'/R$. But as t_c is increased, the values of $\overline{P}_W'/R$ raises to a maximum (Fig. 12), and then falls to a zero as t_c approaches t_λ. This is because, with t_c very close to t_λ, the exploited

phase is only a very small fraction of the total population. But the total biomass per recruit $\overline{P}_w/R$ increases continuously to a finite value. The biomass at $t_c = t_\lambda$ is the same as when $F = 0$ in Fig.9. (Refer Beverton and Holt 1957 for more details).

Simultaneous variation of biomass (of the exploited phase and total biomass) with F and t_c.

In Fig. 13a we can see that $\overline{P}_w'/R$ decreases with F at all values of t_c. This decrease is least when t_c is large.
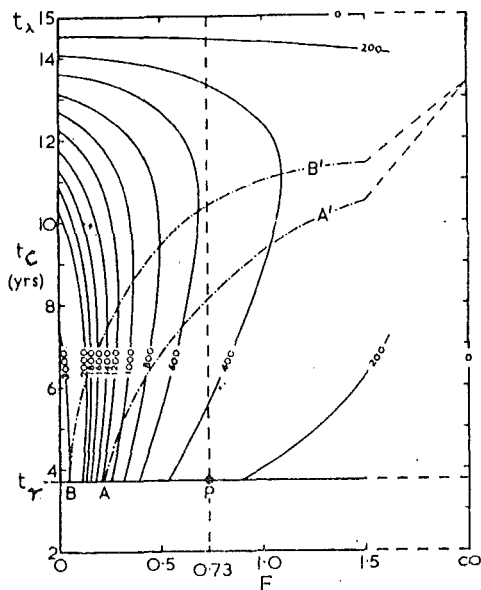
Fig. 13a. Plaice: Isopleth diagram for biomass of exploited phase. (Contours are of $\overline{P}_w'/R$ (proportional to catch per unit effort) at intervals of 200 gm.(except the highest). The top and right-hand borders of the diagram are the zero contour of $\overline{P}_w'/R$. The lines AA' and BB' are drawn from Fig. 3, and the point P indicates the pre-war values of F and t_r .) (From Beverton and Holt 1957).

The variation in $\overline{P}_w/R$ with t_c depends however on values of

F (Fig. 13b). At very low fishing intensities $\overline{P}_w/R$ decreases as t_c increases, but at higher values of F a maximum occurs.
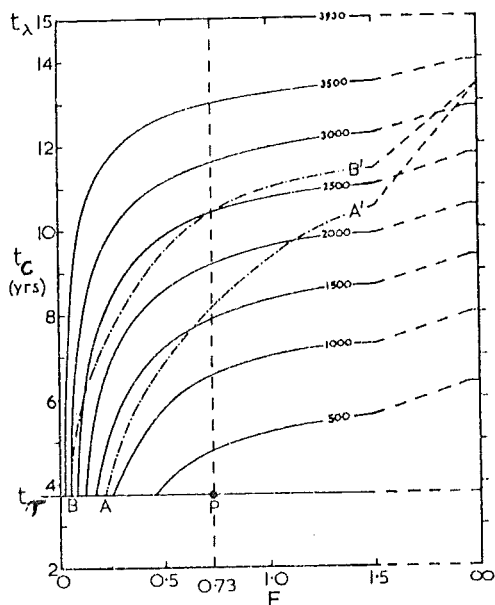
Fig. 13b. Plaice:Isopleth diagram for total biomass.(Contours are of $\overline{P}_w'/R$ at intervals of 500 gm. The top and left hand borders of the diagram are the contour for maximum possible biomass, i.e. in the virgin stock. The lines AA' and BB' are drawn from Fig. 3, and the point P indicates the pre-war values of F and t_c).(From Beverton and Holt 1957).

Immediate effects of regulation.

Regulation of fishing intensity (f).

Transitional phases following a decrease in (f).

In Fig. 14 it is seen that

a) during the first year following the change in fishing intensity (f) there is a big and nearly proportional drop in yield.

Fig. 14. Plaice: Transitional phase following a reduction in
fishing intensity. (Annual yield (open histogram, left hand
scale) and catch per unit effort (shaded histogram, right
hand scale) during transitional phase following a reduction
of fishing intensity to half the pre-war level in one stage,
i.e. a sudden change in F from 0.73 to 0.37). (From Beverton
and Holt 1957).

    b) the yield has recovered to its original value in this
       case by the 3rd transitional year and the loss made up
       in this case after 7 years have passed.

    c) although new steady state is not theoretically reached
       until λ^{th} year (in this case the 11th year), the chan-
       ges occurring after about the sixth year are very small.

By a stepwise reduction of fishing intensity (f) (Fig. 15) it
is seen that

    a) the yield does not decrease as much as in the first
       case.

    b) it takes a longer period to reach equilibrium.

In both the above examples, the catch per unit effort (cpue)
increases throughout the transitional phase. This is s general
characteristic, however the reduction in fishing intensity is
made.
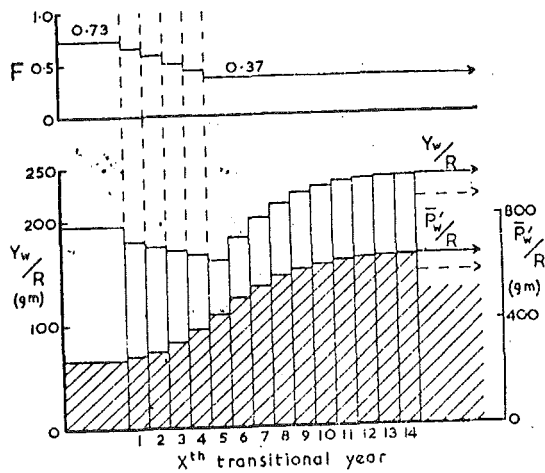
Fig. 15. Plaice: Transitional phase following a series of reductions in fishing intensity. (Yield and catch per unit effort following a reduction in fishing intensity to half the pre-war level in five equal stages at yearly intervals, i.e. a change in F from 0.73 to 0.37 in steps of 0.073). (From Beverton and Holt 1957).
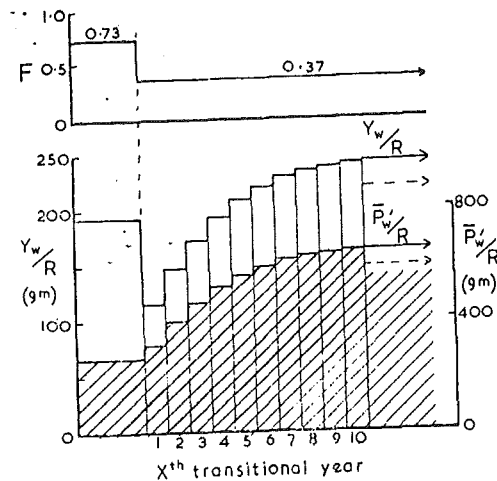
Transitional phases following an increase in (f).
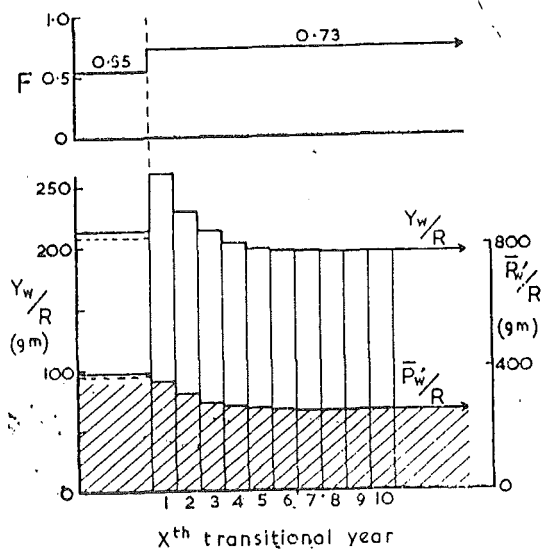
Fig. 16. Plaice: Transitional phase following an increase in fishing intensity. (Yield (open histogram, left hand scale) and catch per unit effort (shaded histogram, right hand scale) following an increase in fishing intensity from 75% of the pre-war level to the pre-war level, i.e. a sudden increase in F from 0.55 to 0.73.

a) In the example of plaice the fishing intensity is increased from 0.55 to 0.73. The yield is increased initially.

b) After some years (in this case 3 years afterwards) the yield falls back to its original level (Fig. 16).

c) Initial gains are lost after 7 years have elapsed and the final level of yield is lower than initial level. In this case c/f is continuously decreasing.

This illustrates one of the main features to be found in the unregulated fisheries, namely that as exploitation has intensified, increase in vessel or gear efficiency has brought only temporary improvements.

Mesh regulation.

An increase in mesh size from 70 mm to 134 mm in plaice (Fig. 17) have the following effects

Fig. 17. Plaice: Transitional phase following an increase in mesh. (Yield and catch per unit effort following a sudden increase in mesh from 70 to 134 mm. as shown at the top of the diagram. This increase in mesh is equivalent to a change in t_c from 3.72 to 5 yrs.) (From Beverton and Holt 1957).

a) A drop in yield is followed by the increase in mesh size.

b) The original level of yield is attained after some period, in this case 3 transitional years (when reducing f it took 5 years to reach the original level).

c) The loss is made up within the 5th year in this example (compared to 9th year when reducing f).

Note that cpue falls at first due to the fact that when mesh is increased small fishes are let pass trough, but after some time cpue increases again because small fishes are allowed to grow.

Changes in mesh-size could also be done stepwise. In this case the initial loss of yield following each change is less, but it takes longer period to recover to its original level (Fig. 18).
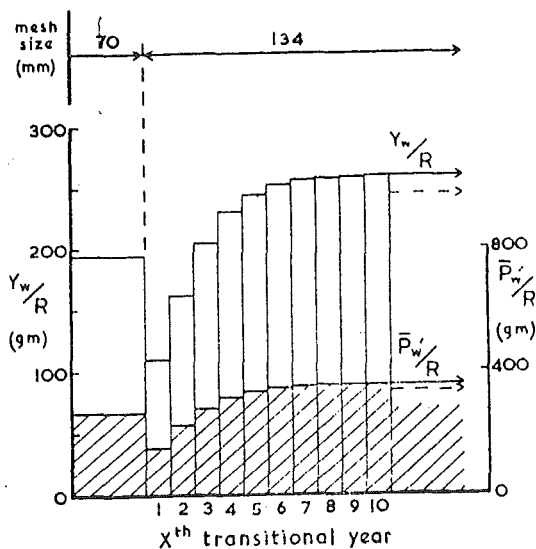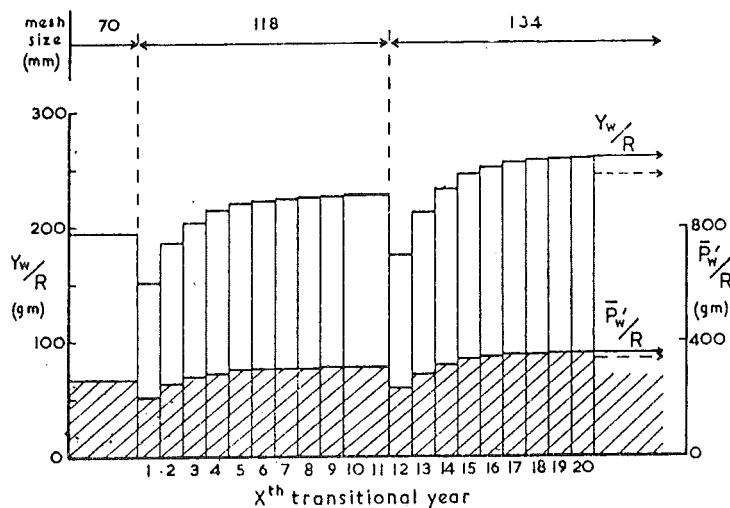

Fig. 18. Plaice: Transitional phase following two increases in mesh size. (Yield and catch per unit effort following increase in mesh from 70 to 118 mm. followed by a further increase from 118 to 134 mm., as shown at the top of the diagram. Each of these changes is equivalent to an increase in t_c' of 0.64 yrs.) (From Beverton and Holt 1957).

VIRTUAL POPULATION ANALYSIS

Virtual population was originally defined by Fry(1957) as the sum
of fish belonging to a given year class present in the water at any
given time that are destined to be captured in the fishery.
Presently the common meaning of VPA is a stepwise process developed
by Gulland(1965) to calculate N- population at each age, F- instant-
aneous fishing mortality for a year class.

The following data should be available to calculate these

      1. Knowledge of catch in number at each age
      2. M (natural mortality)
      3. an estimate of N or F in the final year considered.
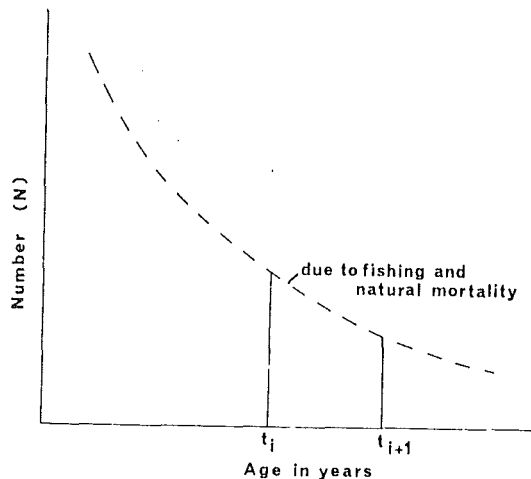
The number in a given year
class reduces due to natural
mortality and fishing (Fig.1)

We are used to go from t_i
to t_{i+1}, but in VPA we go the
other way.

Fig.1.The number of fish of a
      year class alive at time t.

Gulland's VPA is based on the following equations

$$(1) \quad N_{i+1} = N_i e^{-(F_i+M)}$$

$$(2) \quad C_i = N_i \frac{F_i}{F_i+M} (1-e^{-(F_i+M)}$$

where

      i = index for the year i
      C_i = catch in numbers
      N_i = the size (in numbers) of the year class at the
            beginning of the year i
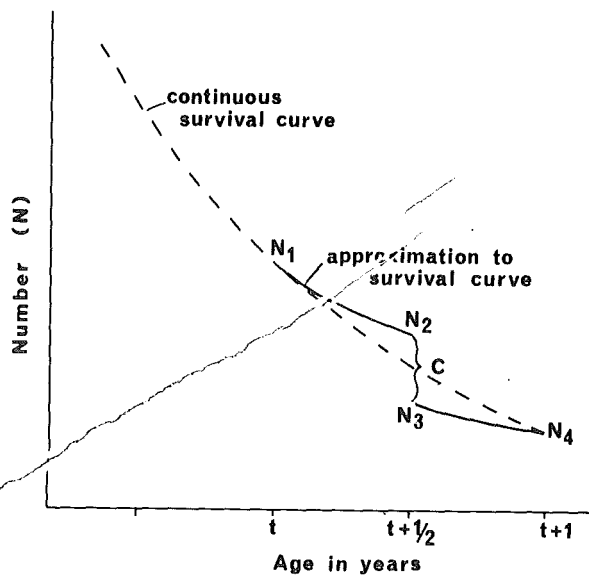
Fig. 3. Approximation to continuous survival curve assumed in cohort analysis (N = number in sea, C = number caught).

Here

$$N_2 = N_1 e^{-\frac{M}{2}} \rightarrow N_1 = N_2 e^{+\frac{M}{2}}$$

$$N_3 = N_2 - C$$

$$N_4 = N_3 e^{-\frac{M}{2}} \rightarrow$$

Therefore

$$N_4 = N_1 e^{-M} - C \cdot e^{-\frac{M}{2}} \quad \text{or}$$

$$N_{t+1} = N_t e^{-M} + C_t e^{\frac{M}{2}}$$

But we want to go the other way.

Then we can easily show:

$$N_t = N_{t+1} e^{M} + C_t e^{\frac{M}{2}}$$

F_i = instantaneous rate of fishing mortality on a per year basis.

M = instantaneous rate of natural mortality on a per year basis.

$$(3) \quad \frac{N_{i+1}}{C_i} = \frac{(F_i+M)\, e^{-(F_i+M)}}{F_i\,(1-e^{-(F_i+M)})}$$

The input data is a list of catch in number by year and year class (Fig. 2a).

Based on this we can calculate the size of a year class (Fig. 2b), and the corresponding fishing mortality (Fig.2c). The framed F in Fig. 2c are guessed.

We do the calculations for one year-class at the time. That is, we follow a diagonal row as indicated in the figures.

Guess F_t, give C_t and M.

So calculate N_{t+1} from (3)

$$\frac{N_{i+1}}{C_i} = \frac{(F_i+M)\, e^{-(F_i+M)}}{F_i\,(1-e^{-(F_i+M)})}$$

It is not difficult to calculate N_i. The problems arise when we want to calculate F. F has to be solved numerically either by reference to tables or by iteration. Either methods make the calculations somewhat laborious.

To overcome these problems Pope (1972) proposed a step function (instead of the usual exponential curve) by assuming that catch of each age group is taken exactly half way through each year (Fig. 3). It is an approximation to Gulland's (1965) virtual population analysis which is usable up to the values of M = 0.3 and F = 1.2 (Pope, (1972).

a \ y	year						
	74	75	76	77	78	79	80
0	$\boxed{C_{0,74}}$	$C_{0,75}$	$C_{0,76}$	$C_{0,77}$	$C_{0,78}$	$C_{0,79}$	$C_{0,80}$
1	$C_{1,74}$	$\boxed{C_{1,75}}$	$C_{1,76}$	$C_{1,77}$	$C_{1,78}$	$C_{1,79}$	$C_{1,80}$
2	$C_{2,74}$	$C_{2,75}$	$\boxed{C_{2,76}}$	$C_{2,77}$	$C_{2,78}$	$C_{2,79}$	$C_{2,80}$
3	$C_{3,74}$	$C_{3,75}$	$C_{3,76}$	$\boxed{C_{3,77}}$	$C_{3,78}$	$C_{3,79}$	$C_{3,80}$
4	$C_{4,74}$	$C_{4,75}$	$C_{4,76}$	$C_{4,77}$	$\boxed{C_{4,78}}$	$C_{4,79}$	$C_{4,80}$
5	$C_{5,74}$	$C_{5,75}$	$C_{5,76}$	$C_{5,77}$	$C_{5,78}$	$\boxed{C_{5,79}}$	$C_{5,80}$
6	$C_{6,74}$	$C_{6,75}$	$C_{6,76}$	$C_{6,77}$	$C_{6,78}$	$C_{6,79}$	$\boxed{C_{6,80}}$
7	$C_{7,74}$	$C_{7,75}$	$C_{7,76}$	$C_{7,77}$	$C_{7,78}$	$C_{7,79}$	$C_{7,80}$

(age)

Fig. 2a

	74	75	76	77	78	79	80	81	82	83
0	$\boxed{N_{0,74}}$	$N_{1,75}$	$N_{1,76}$	$N_{1,77}$	$N_{1,78}$	$N_{1,79}$	$N_{1,80}$	?	?	
1	$N_{1,74}$	$\boxed{N_{1,75}}$	$N_{1,76}$	$N_{1,77}$	$N_{1,78}$	$N_{1,79}$	$N_{1,80}$	?	?	
2	$N_{2,74}$	$N_{2,75}$	$\boxed{N_{2,76}}$	$N_{2,77}$	$N_{2,78}$	$N_{2,79}$	$N_{2,80}$	?	?	
3	$N_{3,74}$	$N_{3,75}$	$N_{3,76}$	$\boxed{N_{3,77}}$	$N_{3,78}$	$N_{3,79}$	$N_{3,80}$	?	?	
4	$N_{4,74}$	$N_{4,75}$	$N_{4,76}$	$N_{4,77}$	$\boxed{N_{4,78}}$	$N_{4,79}$	$N_{4,80}$	?	?	
5	$N_{5,74}$	$N_{5,75}$	$N_{5,76}$	$N_{5,77}$	$N_{5,78}$	$\boxed{N_{5,79}}$	$N_{5,80}$	?	?	
6	$N_{6,74}$	$N_{6,75}$	$N_{6,76}$	$N_{6,77}$	$N_{6,78}$	$N_{6,79}$	$\boxed{N_{6,80}}$	?	?	
7	$N_{7,74}$	$N_{7,75}$	$N_{7,76}$	$N_{7,77}$	$N_{7,78}$	$N_{7,79}$	$N_{7,80}$	?	?	

Fig. 2b

	74	75	76	77	78	79	80	81	82	83
0	$F_{0,74}$	$F_{0,75}$	$F_{0,76}$	$F_{0,77}$	$F_{0,78}$	$F_{0,79}$	$\boxed{F_{0,80}}$	F_0^*	F_0^*	
1	$F_{1,74}$	$F_{1,75}$	$F_{1,76}$	$F_{1,77}$	$F_{1,78}$	$F_{1,79}$	$\boxed{F_{1,80}}$	F_1^*	F_1^*	
2	$F_{2,74}$	$F_{2,75}$	$F_{2,76}$	$F_{2,77}$	$F_{2,78}$	$F_{2,79}$	$\boxed{F_{2,80}}$	F_2^*	F_2^*	
3	$F_{3,74}$	$F_{3,75}$	$F_{3,76}$	$F_{3,77}$	$F_{3,78}$	$F_{3,79}$	$\boxed{F_{3,80}}$	F_3^*	F_3^*	
4	$F_{4,74}$	$F_{4,75}$	$F_{4,76}$	$F_{4,77}$	$F_{4,78}$	$F_{4,79}$	$\boxed{F_{4,80}}$	F_4^*	F_4^*	
5	$F_{5,74}$	$F_{5,75}$	$F_{5,76}$	$F_{5,77}$	$F_{5,78}$	$F_{5,79}$	$\boxed{F_{5,80}}$	F_5^*	F_5^*	
6	$F_{6,74}$	$F_{6,75}$	$F_{6,76}$	$F_{6,77}$	$F_{6,78}$	$F_{6,79}$	$\boxed{F_{6,80}}$	F_6^*	F_6^*	
7	$\boxed{F_{7,74}}$	$\boxed{F_{7,75}}$	$\boxed{F_{7,76}}$	$\boxed{F_{7,77}}$	$\boxed{F_{7,78}}$	$\boxed{F_{7,79}}$	$\boxed{F_{7,80}}$	F_7^*	F_7^*	

Fig. 2c

mortality increases both types of errors are reduced.
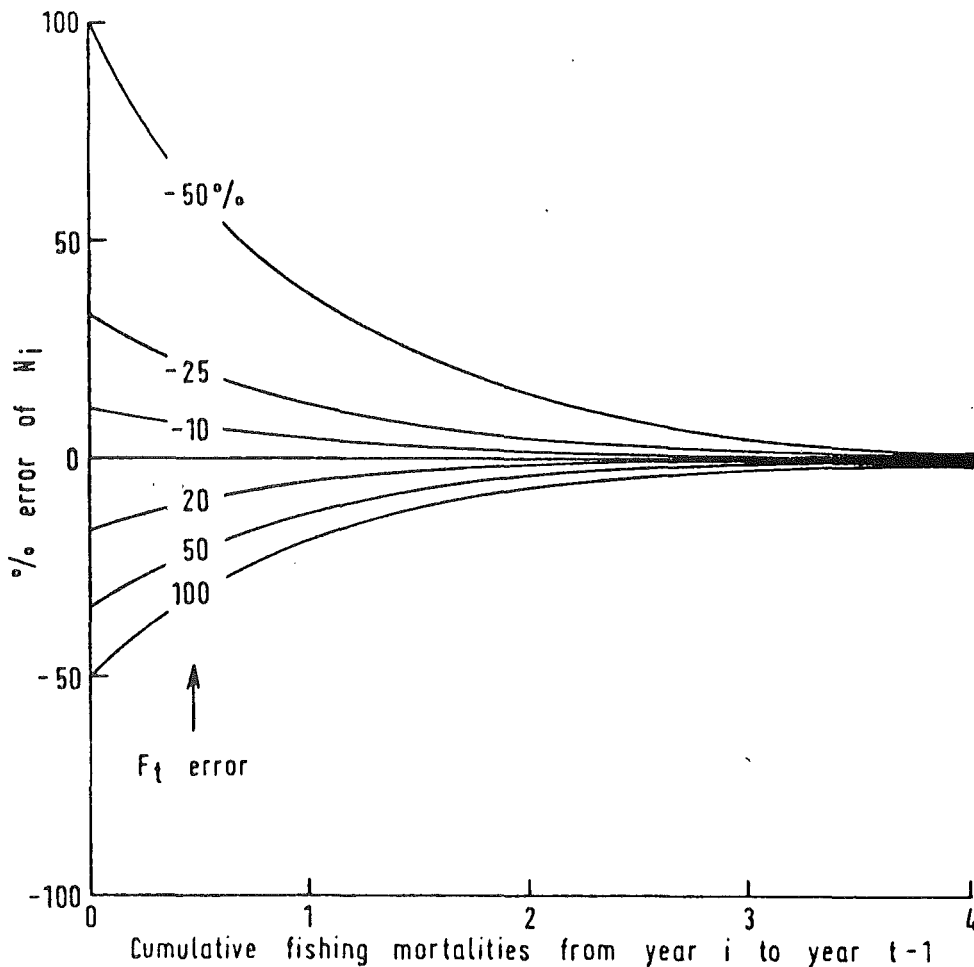
Fig. 4. Graphs of the percentage error in N_i due to incorrect values of F_t plotted against the cumulative fishing mortalities from year i to year t-1 (Pope, 1972).

Example. If F_t was overestimated by 100 % from a year class and the cumulative fishing mortality was equal to 2.0, then the percentage error in N_i would be -7% and the percentage error on F_i would be +7%.

If, however, F_t was underestimated by 50 % and the cumulative fishing mortality was equal to 2.0 then the percentage error in N_i would be at the most +14% and the percantage error in F_i would be -14%.

when we take N_{t+1} as present. This means that we consider a year class from the last year it is present in the catches and work-out backwards in time. As in the Gulland's VPA N_{t+1} has two possible forms. In the first form C_{t+1} refers to as the catch in year t+1 only, in this case

$$N_{t+1} = \frac{C_{t+1} \cdot Z_{t+1}}{F_{t+1}(1-e^{-Z_{t+1}})}$$

The second form of N_{t+1} is when C_{t+1} refers to catch in year t+1 and subsequent years. This is usually the case with a completely fished year class. Then

$$N_{t+1} = \frac{C_{t+1} \cdot Z_{t+1}}{F_{t+1}}$$

We also need a fomula to calculate the F_t
We can use

$$N_{t+1} = N_t e^{-(F+M)}$$

or

$$e^{-(F+M)} = \frac{N_{t+1}}{N_t}$$

Therefore

$$-(F+M) = \ln \frac{N_{t+1}}{N_t}$$

or

$$F = \ln \frac{N_t}{N_{t+1}} - M$$

If we start at age 6 we can go backwards as follows:

$$\boxed{N_5} = N_6 \cdot e^M + C_5 \cdot e^{\frac{M}{2}}$$

$$\boxed{N_4} = N_5 e^M + C_4 \cdot e^{\frac{M}{2}}$$

$$N_3 = N_4 e^M + C_3 \cdot e^{\frac{M}{2}}$$

The difference between Gulland's VPA and Pope's cohort analysis can be seen from Table 1 where the results of both methods are compared. It can be seen that in no case

Thus provided that F_t can be estimated within this range and provided that cumulative fishing mortality is greater than 2.0, the error in the estimates of N_i and F_i should be small enough for most uses.

If, however, the cumulative fishing mortality is small, which is the case when the number of recruits to a year class is estimated from the catches of partially recruited age groups, then the accurate estimation of N_i and F_i will require the accurate choice of F_t.

Table 2 shows the results of cohort analysis for the 1956 year class of Arcto-Norwegian cod (Pope, 1972) This assumes that the true values of M and F_t are 0.3 and 0.8 respectively. The percentage error in N_i and F_i when F_t is overestimated by 100% and underestimated by 50% is also shown. (These errors were computed by running the data with appropriate values of F_t and are therefore precise).

Table 2. The percantage of N_i and F_i when F_t is overestimated by 100% and when F_t is underestimated by 50% for the 1956year-class of the Arcto Norwegian cod, with M=0.3 and when the true value of F_t=0.8 (Pope,1972).

Age (years)	$N_i \times 10^{-6}$	F_i	Cumulative F_i	% error when F_t is taken as 0.4		% error when F_t is taken as 1.6	
				in N_i	in F_i	in N_i	in F_i
12	0.2	0.8000[a]	—	+ 68.66		- 32.27	
11	1.1	1.3670	1.3670	+ 17.50	- 26.44	- 8.22	+ 22.21
10	3.2	0.7806	2.1475	+ 8.02	- 10.77	- 3.77	+ 6.07
9	8.5	0.6747	2.8222	+ 4.08	- 5.50	- 1.92	+ 2.82
8	22.2	0.6570	3.4792	+ 2.12	- 2.91	- 0.99	+ 1.43
7	71.2	0.8657	4.3449	+ 0.89	- 1.40	- 0.42	+ 0.67
6	200.1	0.7333	5.0782	+ 0.43	- 0.63	- 0.20	+ 0.29
5	413.6	0.4261	5.5043	+ 0.28	- 0.35	- 0.13	+ 0.16
4	672.0	0.1854	5.6897	+ 0.23	- 0.22	- 0.11	+ 0.16
3	944.7	0.0405	5.7302	+ 0.22	- 0.25	- 0.10	+ 0.25
2	1278.2	0.0024	5.7326	+ 0.22	- 0.00	- 0.10	+ 0.00
1	1726.6	0.0007	5.7333	+ 0.22	- 0.00	- 0.10	+ 0.00

[a] Assumed.

It can be seen that these percentage errors are similar, but in general smaller than their estimates in Fig.4 .

do the estimates given by the two methods differ more than
2 % (Pope, 1972).

Table 1. Comparison of the results of virtual population
analysis and cohort analysis. Arcto-Norwegian
cod, 1956 year-class, M=0.3 (Pope,1972)[?].

Age (years)	Fishing mortality, F_n			Population, $N_i \times 10^{-6}$		
	Virtual population analysis	Cohort analysis	% error	Virtual population analysis	Cohort analysis	% error
12	0.8000[a]	0.8000[a]		0.2	0.2	
11	1.3400	1.3670	2	1.1	1.1	0
10	0.7826	0.7806	–	3.1	3.2	2
9	0.6768	0.6747	–	8.3	8.5	2
8	0.6582	0.6570	–	21.7	22.2	2
7	0.8636	0.8657	–	69.6	71.2	2
6	0.7341	0.7333	–	195.6	200.1	2
5	0.4289	0.4261	1	405.5	413.6	2
4	0.1874	0.1854	1	660.2	672.0	2
3	0.0411	0.0405	1	928.5	944.7	2
2	0.0024	0.0024	–	1256.4	1278.2	2
1	0.0007	0.0007	–	1697.1	1726.6	2

[a]Assumed.

Errors in N_i and F_i can be introduced by the incorrect
choice of F_t and sampling errors in C_i.

These two sources of errors are investigated in detail
by Pope (1972)

(1) Incorrect choice of F_t.

Fig. 4 shows percantage error of N_i against the cumulative
fishing mortality from year i to year t-1.

It can be seen that underestimation of F_t results in esti-
mates of N_i which are too large and estimates of F_i which
are too small, whereas overestimating F_t has the reverse
effect. It can also be seen that as the cumulative fishing

(2) Incorrect choice of M.

The effect of an error in M depends on how F_t is derived.
If Z is estimated i.g. by a catch curve and F_t is taken as
Z_t-M then an error in M will give a similar error in F.
The error in N will be

$$\frac{\widehat{N}_t}{N_t} = \frac{F_t}{\widehat{F}_t} = \frac{Z_t - M}{Z_t - \widehat{M}}$$

($\widehat{N}$, $\widehat{F}$, and $\widehat{M}$ are estimated values, N, F, and M true values).

If Z is constant, the error will be constant, and the re-
lative change in stock size from year to year will be correct.

If Z varies, the relative changes in stock size will also be
in error, but usually the error will be small, and smaller
the higher F is compared to M.

For a more detailed discussion of the effects of error in M
Ulltang (1977) should be referred.

DESCRIPTIVE STOCK MODELS

A descriptive stock model or a surplus yield model as it is
often called, regards the stock as a unit, following the
simple laws of population growth and where a fishery acts
as a predator in a predator/prey system.

To visualize how a surplus yield model works imagine we
put a few fishes into a pond. They will grow and reproduce.
The increase both in number and biomass will be faster and
faster, following an exponential curve. After some time
there will, however, be competition for food and space, and
the growth will decrease. When the carrying capacity of the
system is reached, the stock size will stabilize or show
more or less regular cycles around the maximum value often
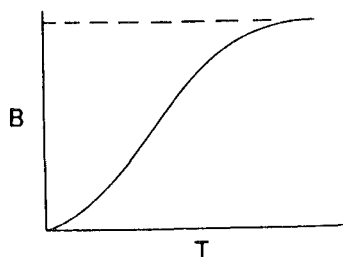called B_∞ or K (Fig. 1).

Fig. 1. Growth of biomass as a function of time. The
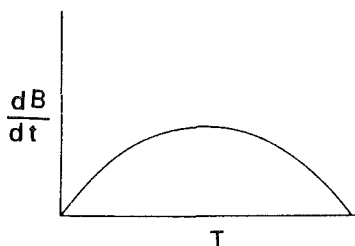asymptote represent the carrying capacity.

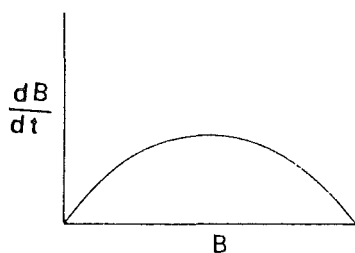Fig. 2. Net growth of biomass as a function of time.

Fig. 3. Net growth (production) as a function of biomass.

We can get the net growth per unit of time by differenti-
ating the curve in Fig. 2. This will give a parabola with
no growth for t=0 and when $B=B_\infty$, and a maximum growth for
some intermediate value.

If we look at stock size as the independent variable in-
stead of t we can look at the relation between $\frac{dB}{dt}$ and B
(Fig. 3).

This shows that a stock gives the highest net production
at some intermediate level. With the formulas most fre-
quently used maximum net production is obtained when
$B= \frac{B\infty}{2}$.

When we exploit a stock we usually want to take the net
production. If we take more, the stock will decrease, if
we take less the stock will increase.

If we start to exploit a virgin stock with stock size
B_∞ then the net production is near zero. If we take
$Y= \Delta B_1$ the stock size will decrease with this amount and
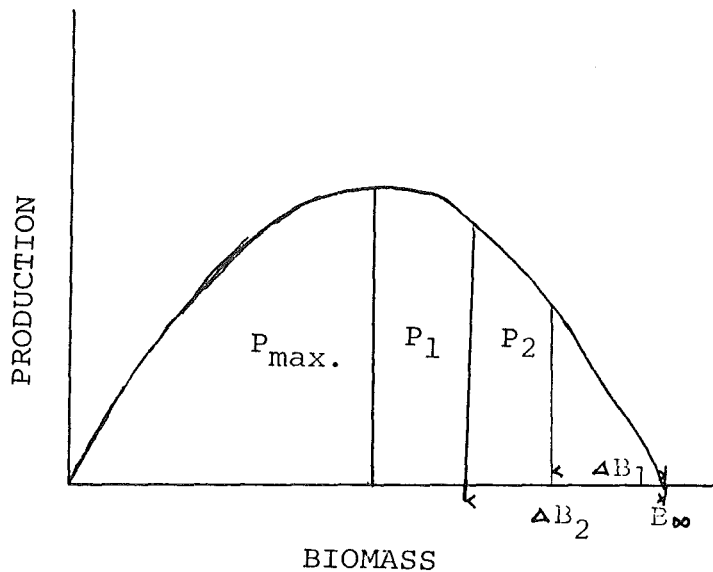we will get a production P_1 (Fig. 4). Next year we can

Fig. 4. Biomass and production of an exploited stock. For
explanation see text.

take $Y=P_1$ and the stock will stabilize at the size $B\infty - \Delta B_1$, or we can take $Y=P_1 +\Delta B_2$. Then the stock size will decrease again, and the new production will increase again, and the new production will be P_2.

We can go on taking more than the production till the stock size reach $\frac{B\infty}{2}$ and the net production P max. If we allow the stock to stabilize at that level we get the highest possible equilibrium yield (MSY). If we go on taking more than the production, the stock size will decrease below $\frac{B\infty}{2}$ and then the production will decrease too.

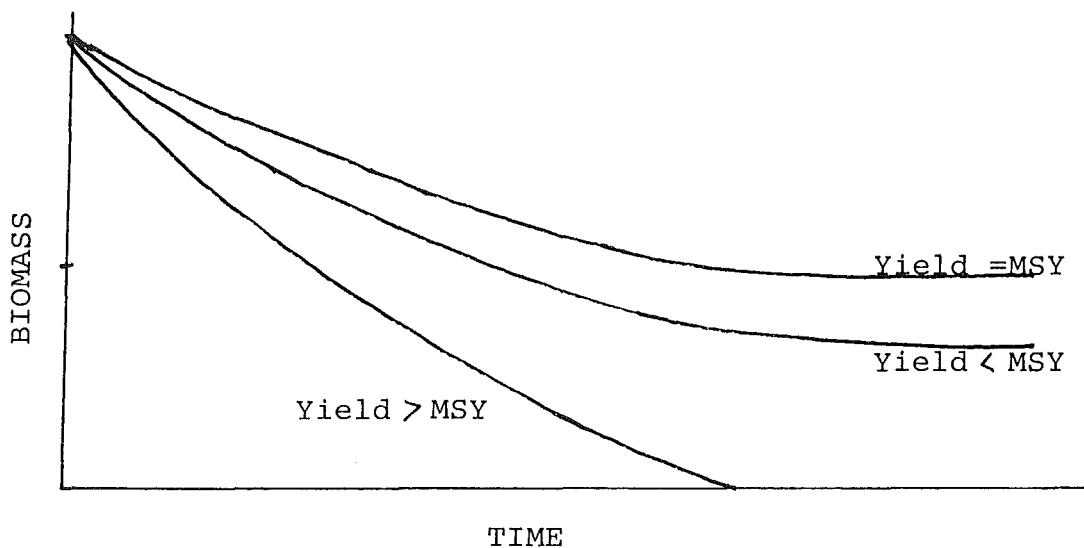The relation between stock size, yield and time is illustrated in Fig. 5.

Fig. 5. Biomass and yield as a function of time for three levels of annual yield.

We can get an equilibrium yield at any level below MSY, but not above that level. It should be noted that the same equilibrium level can be obtained for two levels of B. Usually it is advisable to keep to the left of the value giving MSY, as that gives the highest catch per unit of effort, and it also stabilizes the stock.

The change in biomass can be written

$$\frac{dB}{dt} = G(B)$$

In the Schaefer model this function is taken as

$$G(B) = Bk \frac{B_\infty - B}{B_\infty} = Bk \left(1 - \frac{B}{B_\infty}\right) \tag{1}$$

where B_∞ is the maximum biomass under equilibrium and k is a constant. This equation describes the <u>logistic</u> growth curve.

If there is a fishery we should substract a function H(f). This function could be FB=fqB where F is instantaneous rate of fishing mortality, f is fishing rate and q is a catchability coefficient.

Then we have

$$\frac{dB}{dt} = Bk \left(1 - \frac{B}{B_\infty}\right) - fqB \tag{2}$$

or

$$\frac{1}{B} \frac{dB}{dt} = k \left(1 - \frac{B}{B_\infty}\right) - fq \tag{3}$$

Under conditions of equilibrium the growth is zero and the equation becomes

$$0 = k \left(1 - \frac{B_e}{B_\infty}\right) - qf \tag{4}$$

where B_e is the equilibrium biomass.

As

$$Y = FB = fqB$$

the equilibrium yield is

$$Y_e = fqB_e$$

or

$$Y_e = qf \frac{B_\infty}{k} (k-qf)$$ (5)

To find the maximum value of the equilibrium yield the equation (5) can be differentiated giving

$$f = \frac{k}{2q} \quad \text{and} \quad Y_{e\ max} = \frac{k}{4} B_\infty$$ (6)

Equation (5) gives a parabola and if we have an equilibrium situation this can be fitted by plotting catch per unit effort against f

$$u = \frac{Y}{f} = qB$$

An equilibrium situation is, however, rare in practical fisheries and then we must use other methods.

Schnute (1977) gives a good method for fitting the model in non-equilibrium situations. We shall use a method described by Walter (1975) as this is easy to understand, and easy to use without having a computer.

From equation (2) and (4) we can find

$$B_e = B + \frac{1}{aB} \frac{dB}{dt}$$ (7)

where $a = \frac{k}{B_\infty}$

Therefore, looking at a short time interval

$$U_e = U + \frac{q}{aU} \frac{\Delta U}{\Delta T}$$ (8)

where ΔU is change in catch per unit effort over the period ΔT.

By integrating eq. (2) and substituting U = qB we can derive the equation

$$U_e = U_i + \frac{q}{a} \left(\frac{U_{i+1} - U_i}{U_{i+1}} \right) \tag{9}$$

where the index refers to year.

Walter (1975) shows that $U_e < U_{i+1} < U_i$

therefore, as a first approximation we can use U_{i+1} instead of U_e.

Using eq. (5) and introducing $a = \frac{k}{B\infty}$ we get

$$Y_e = qf \frac{1}{a} (k - qf)$$

or $\quad U_e = q \frac{1}{a} (k - qf) \tag{10}$

Therefore we can plot

$$U_{i+1} = A - Cf_i \tag{11}$$

where $A = \frac{kq}{a}$ and $C = \frac{q^2}{a}$ $\qquad$ (11a, 11b)

This gives us two equations and three unknown.

There are several ways to proceed. One is to derive the equation:

$$\frac{U_{i+1} - U_i}{U_{i+1}} = \alpha (A - U_i - Cf_i) \tag{12}$$

The mathematics behind it is somewhat complicated, and Walter (1975) should be consulted for details.

Equation (12) gives a line through the origin with slope α.

We can now find:

$$k = \alpha A \quad q = \alpha C, \quad a = \alpha^2 C \quad \text{and} \quad \alpha = \frac{a}{q} \tag{13}$$

Walter (1975) also shows that

$$U_e = U_{i+1} \left(1 + \frac{U_{i+1} - U_i}{U_i \, e^{\frac{a}{q} U_{i+1}} - U_{i+1}} \right) \tag{14}$$

The procedure of fitting the Schaefer model to non-equilibrium data is then:

Plot U_{i+1} against f_i and fit a straight line (eq. 11). This gives estimates of A and C (eqs. 11a, 11b).

Insert A and C into equation (12), and plot. This gives an estimate of α.

By using equation (14) we can now estimate U_e for each year, and this can be plotted against f_i to give the final estimate of A and C in equation (11).

As we have seen

$$Y_{max} = \frac{k}{4} B\infty = \frac{k^2}{4a}$$

for $\quad f = \frac{k}{2q}$

or $\quad Y_{max} = \frac{A^2}{4C} \quad$ for $\quad f = \frac{A}{2C}$

The Schaefer model can be regarded as a special case of
the more generalized production model

$$\frac{1}{B} \frac{dB}{dt} = a - bB^{m-1}$$

introduced by Pella and Tomlinson (1969).

When $m=2$ this model reduces to the Schaefer model. If
$m>2$ the sustainable yield versus effort has its maximum
to the left of $\frac{B_\infty}{2}$. The catch per unit effort versus
effort curve is concave.

When m approaches 1 we get the Fox (1970) model:

$$\frac{1}{B} \frac{dB}{dt} = a \left(-\ln \frac{B}{B_\infty}\right)$$

For this model we get MSY for a stock size smaller than
$\frac{B_\infty}{2}$.

MULTISPECIES MODELS

Most of the models presently used in management of
fisheries are considering fish stocks as independent
units. In fisheries based on single species, and which
do not bring the biomass of the species concerned too far
down, these models have given reasonable results.

When several species are taken in the same fisheries
these models are, however, not sufficient.

We should always expect two types of interactions:

Technological interactions:

That means that when we fish for one species, one or
more other species are also caught in appreciable
amounts.

Biological interactions:

This means that two or more species compete for food or
space, or that there is a predator - prey relationship
between them. These interactions may change with the
stage of the fish. E.g. the larvae of species A and B
may compete for food, while fry of A may be food for
adult B etc. Therefore, a fishery changing the stock
size of one species will also change the living con-
ditions of other species.

Some examples of covariance in abundance of fish stocks,
probably caused by interaction are shown in Figs. 1 - 3.

Several types of ecosystem models are used, and they
show different levels of complexity:

1. Simple regression models

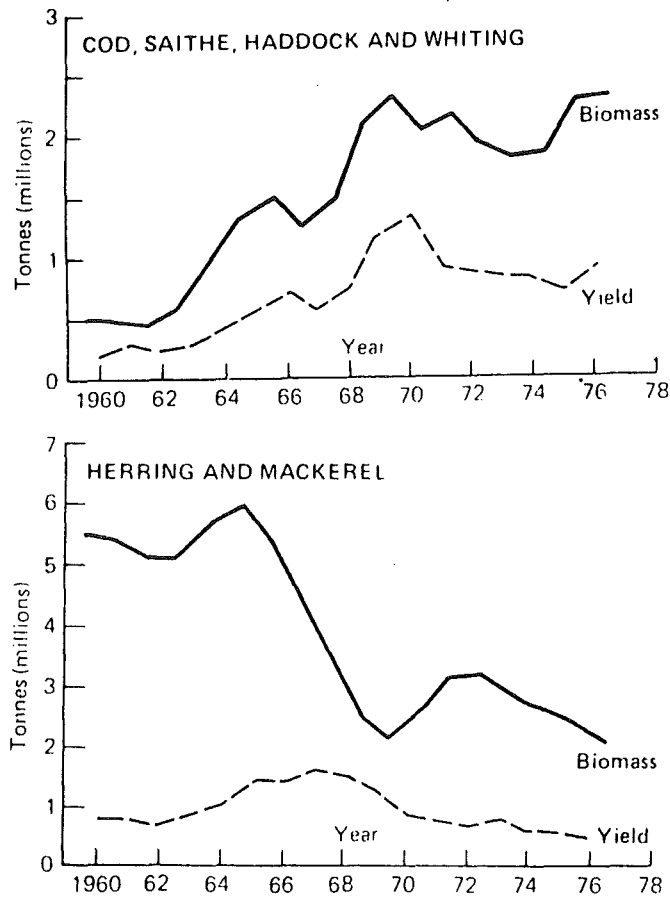This type of models has mainly been used for lakes and

Fig.1. Biomass and yield of pelagic and demersal fishes
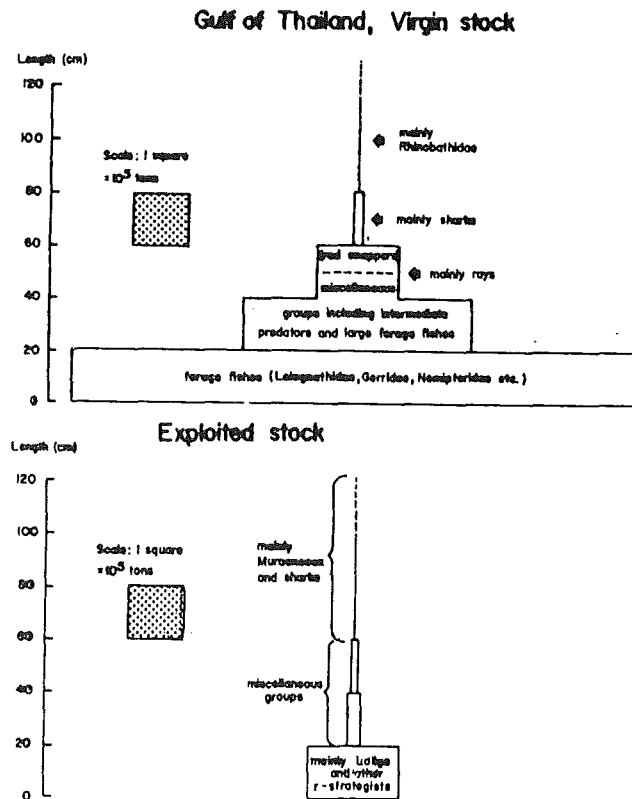in the North Sea (From Ursin 1979)

Fig. 2. Size distribution of virgin and exploited stocks in the
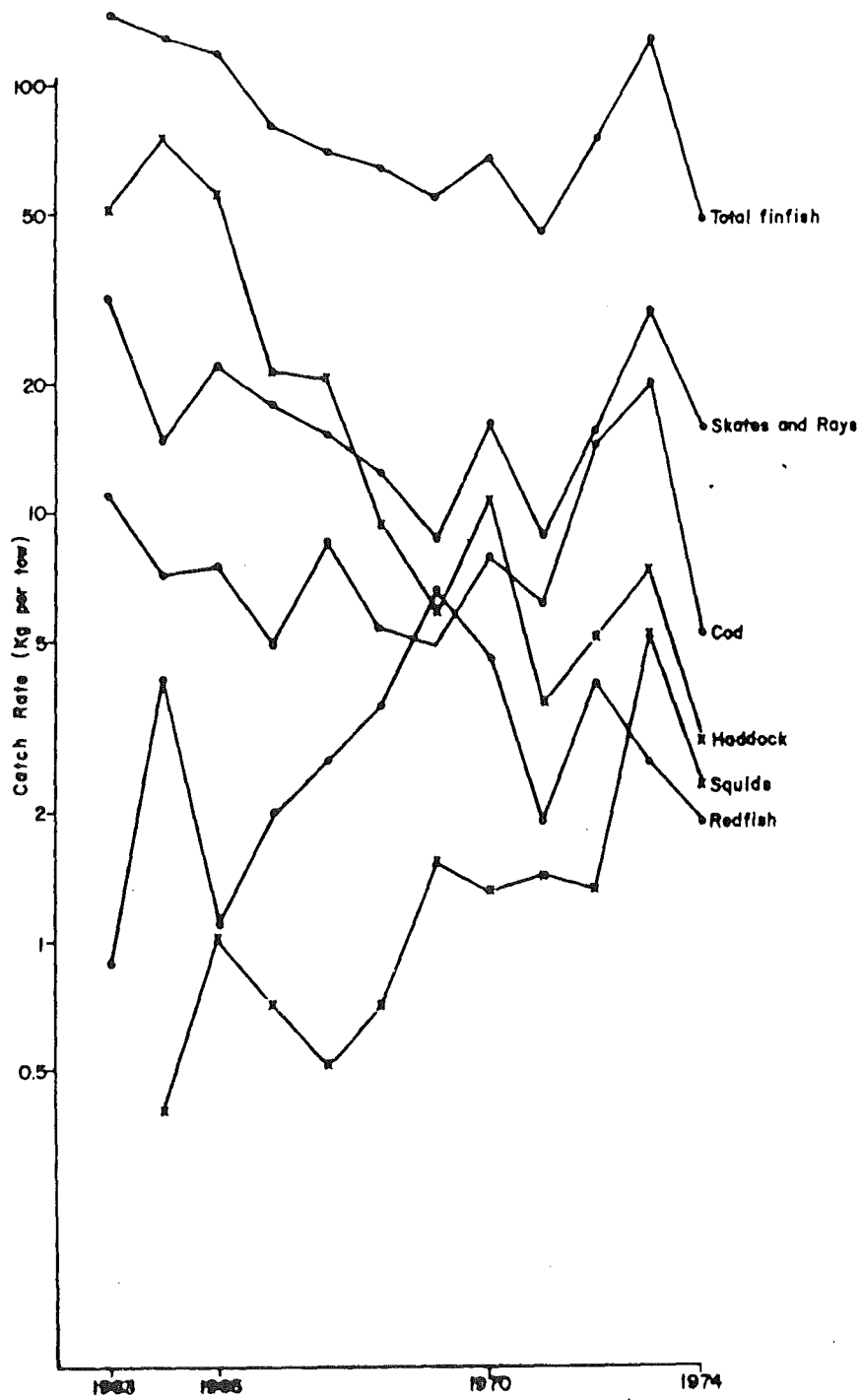Gulf of Thailand. (From Pauly 1979)

Fig. 3. Abundance of some important stocks on George
Bank (From Anon. 1978)

reservoirs. Based on some lakes studied in details, a regression of fish yield on depth, primary production and other factors are made. Based on a regression like this potential yield in other lakes can be estimated when some other variables are known. An example is shown in Fig. 4. More details about such models are given by Anon (1978) and Jones (1982).

2. Multispecies surplus production models

These are descriptive models giving the interaction as positive or negative factors without explaining the mechanisms. These models, which will be treated in more details, are mathematically simple. But the task of parameter estimation is overwhelming if many species are included. A more detailed description of this type of model is given by Pope (1976) and Kirkwood (1982).

3. Menu type models

These models are based on a description of who eats whom. A matrix of the probability that one species will be eaten by another species are used to simulate the biomass variations in the stocks involved. Models of this type have been used by e.g. Riffenburg (1968) and Agger and Nilsen (1972).

4. Multispecies dynamic pool models

Multispecies extentions of the Beverton and Holt model and of VPA belong to this group. The most important feature of these models is the description of growth and mortality as a function of the biomass of prey and predator species. Models of this type are described by e.g. Andersen and Ursin (1977), Pope (1979) and Helgason and Gislason (1979).
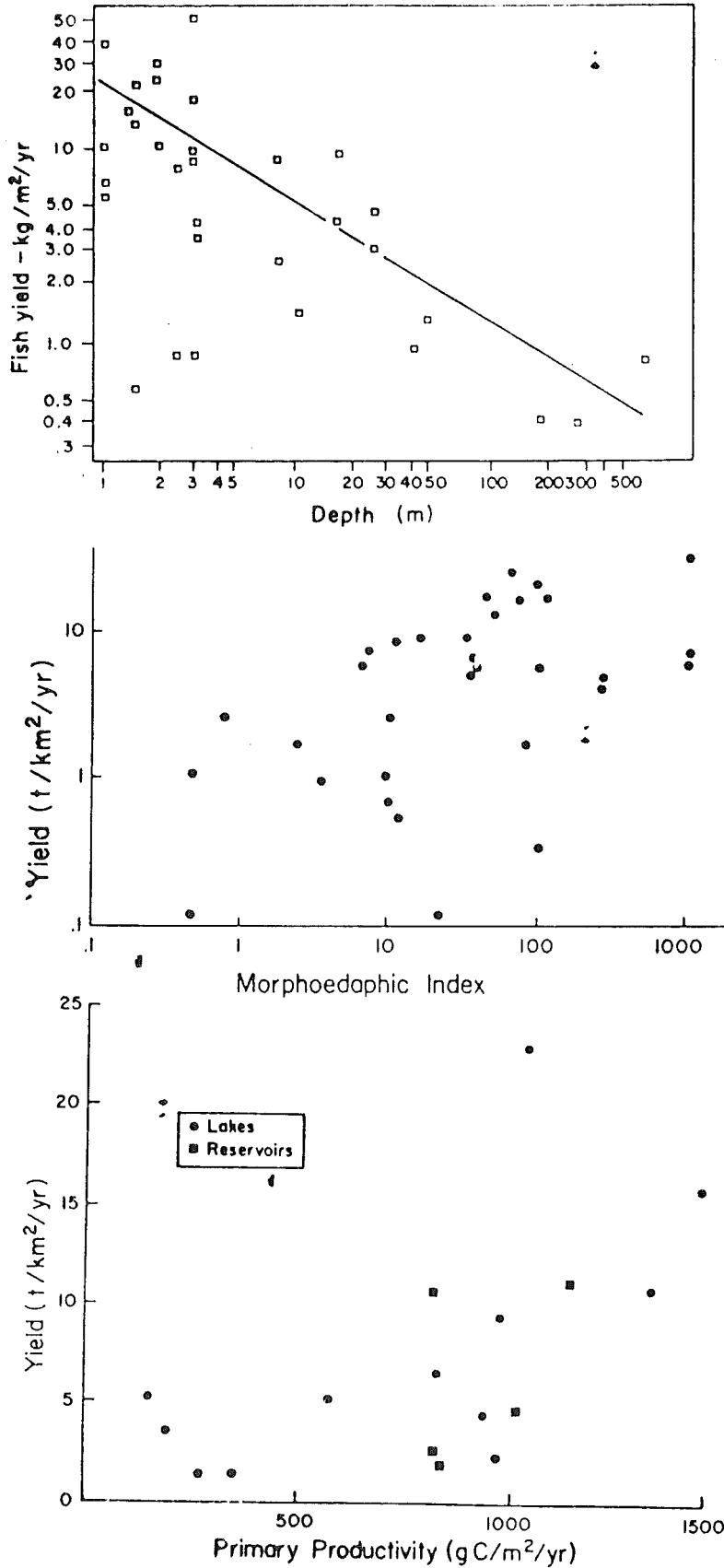
Fig. 4. Examples of regressions of yield on various environmental factors (From Jones 1982, Marten and Polovina 1982)

5. Ecosystem models

These models are aiming at a description of the eco-
systems and the fish stocks are treated as a part of
this. As in the menu type models the food consumption
is an important part of these models, too, but other
parts of the ecosystem is also incorporated. Models of
this type have been described by Laevastu and Favorite
(1978) and Laevastu and Larkin (1981).

Which type of model one should choose depends on the
type of data available, on the expertice and on the
computer facilities available and on the purpose of
modelling.

Multispecies surplus production models

The simplest way of extending this approach to a multi-
species situation is to consider the usual Schaefer
equation:

$$\frac{1}{B}\frac{dB}{dt} = k\ (1 - \frac{B}{B\infty}) - qf \qquad (1)$$

as describing the changing in the total biomass of all
species combined.

This approach has been used by several authors (for a
review, see Anon, 1978). Generally these overall
Schaefer models seem to fit the data better than the
sum of Schaefer models fitted to the single species.

Only further research can tell why, but the following

explanations have been suggested:

1)   Total biomass react in a simpler way to over-
        all fishing effort than do   the individual
        stocks.

2)   The better fit is simply a result of the aver-
        aging process.

3)   The overall biomass/overall effort fit is an
        artifact of the fitting process or of changes
        in the fisheries.

In spite of the fairly good results obtained in several
situations, this approach has been criticized e.g. by
Pauly (1979). And there seems to be good biological
basis for this criticism, which mainly falls within two
groups:

1)   Fishes, except some top predators as tuna and
        sharks, are preyed upon by other fishes, and are
        therefore giving a "yield" to these predators,
        i.e. they are not at the $B\infty$ level. (This point
        applies to all Schaefer models.)

2)   As stocks of different size, growth and pro-
        duction will have different yield/effort relation-
        ships (Fig. 5), on common yield/effort curve is
        only an abstraction.

The second way of extending the Schaefer model is to in-
clude an explicit term to account for interaction.

We can look at a simple two-stock system:

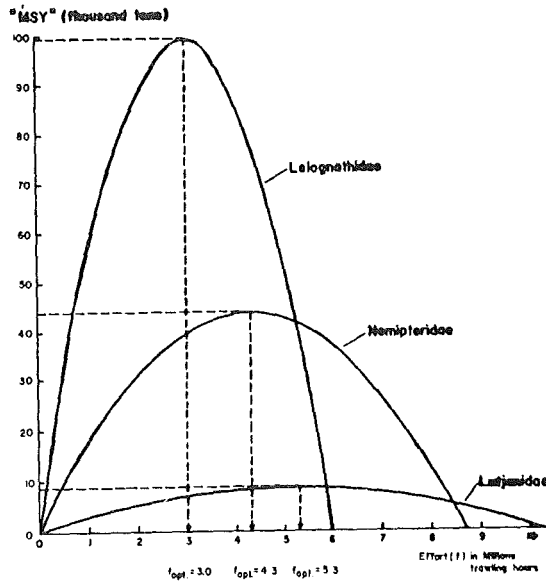$$\frac{1}{B}\frac{dB}{dt} = a - bB - cP - qf_B \tag{2}$$

Fig. 5. Yield and effort for thre fish families from the
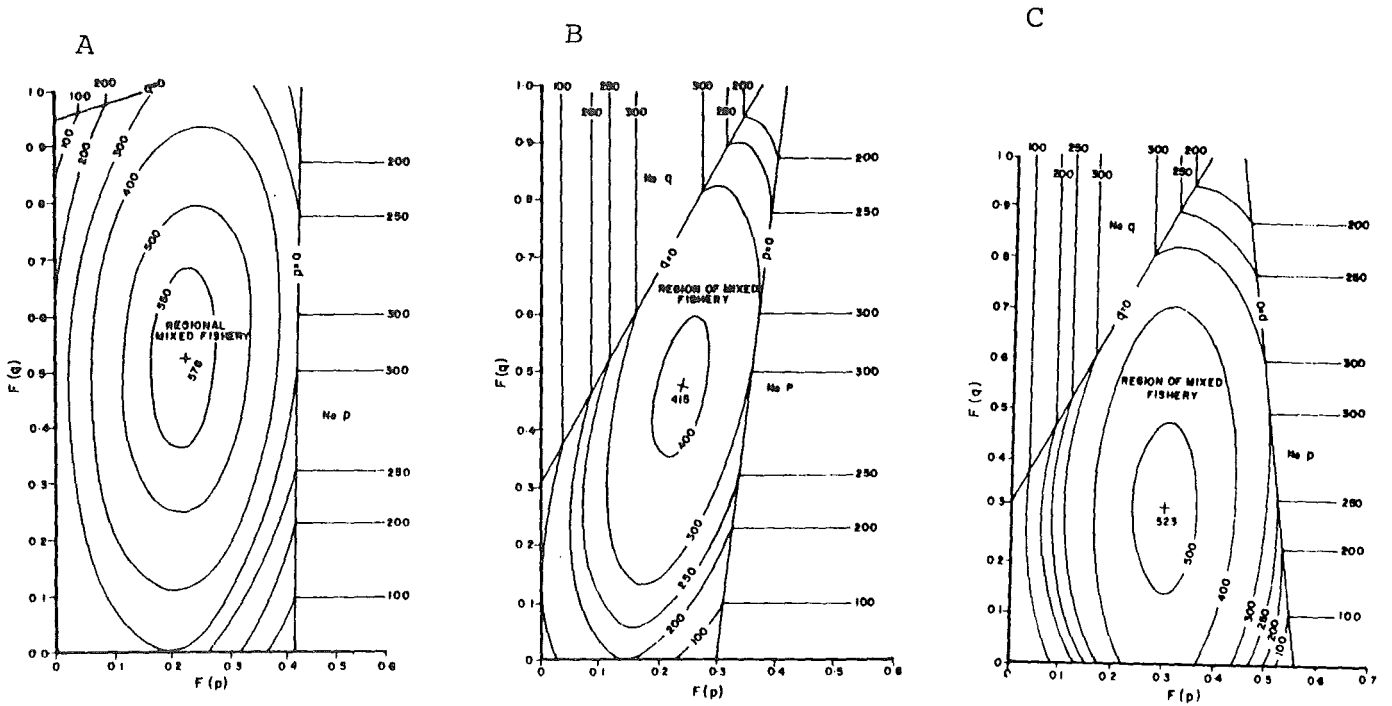Gulf of Thailand (From Pauly 1978)

Fig. 6. Yield-isoplet diagrams for two species with
A: weak competition
B: strong competition
C: one is predator on the other
(From Anon. 1978)

$$\frac{1}{P} \frac{dP}{dt} = a' - b'P - c'B - q'f_p \tag{3}$$

To account for real interaction, a timelag should be in-
cluded, but let us assume that equations (2) and (3) de-
fine the steady state (when $\frac{dP}{dt} = \frac{dB}{dt} = 0$).

When c and c' has the same sign it means that one stock
increases when the other one decreases, i.e. a situation
with competition. If we change sign on one of the c, we
can simulate a predator/prey system.

Equations (2) and (3) could be extended to contain any
number of stocks. The number of parameters which has to
be fitted becomes, however, overwhelming if the number
of stocks is larger. For two stocks 8 parameters are
needed, for 4 stocks 24 and for 6 stocks 48 parameters.
(Parameters = $(n + 1)^2 - 1$)

Therefore we shall analyse the two-stock situation only.
As $Y = fqB$ we can write

$$Y_B = aB - bB^2 - c\ BP \tag{4}$$

$$Y_p = a'B - b'P^2 - c'\ BP \tag{5}$$

or $\quad Y = Y_B + Y_p = aB + a'P - bB^2 - b'P^2 -$

$$(c + c')\ BP, \tag{6}$$

Therefore, a diagram of total yield as function of the
size of the two stocks will give concentric ellipses.
Similarly, Y as a function of fishing mortality of the
two stocks will give concentric ellipses:

$$Y = AF_p + A'F_B + CF^2_B + C'F_p^2 + DF_B F_p \tag{7}$$

Fig. 6 shows how the diagram looks in a situation with

low competition, one with strong competition, and one
with a predator/prey situation. The straight lines in-
dicate when one of the stocks are eliminated.

Several conclusions can be drawn from the diagram.
First it is clear that whether interaction is present
or not the contours of equal yield gives ellipses centered
on the maximum yield of the system.

Therefore, as long as no stock becomes zero any fishery
which develops with the fishing mortalities on its
various component stocks in equal proportion, i.e. pro-
gressing along the straight line in the F_B, F_p plane,
will have a parabolic yield curve. These yield curves
will, however, give a lower maximum than the curve go-
ing through the joint maximum point. The effort re-
quired to achieve the maximum will in general also be
different.

If we know all the parameters of the model, finding
the maximum yield would be a question of solving the
following equations for the populations of the various
stocks (P).

$$\frac{\delta Y}{\delta P_1} = 0, \quad \frac{\delta Y}{\delta P_2} = 0, \quad \frac{\delta Y}{\delta P_3} = 0,$$

For a two-stock model we could get:

$$\frac{\delta Y}{\delta P_1} = a_1 - 2b_1 P_1 - (c_1 + c_2)P_1 = 0 \tag{8}$$

$$\frac{\delta Y}{\delta P_2} = a_2 - 2b_2 P_2 - (c_1 + c_2)P_2 = 0 \tag{9}$$

This will give maximum Y for

$$P_1 = \frac{a_1 2b_2 - a_2(c_1 + c_2)}{4b_1 b_2 - (c_1 + c_2)^2} \tag{10}$$

$$P_2 = \frac{a_2 \, 2b_1 - a_1 \, (c_1 + c_2)}{4b_1 b_2 - (c_1 + c_2)} \qquad (11)$$

So , what can we do if we don't know a, b and c for the stocks involved? Let us assume that we can vary the ratios of the efforts applied to different species so as to achieve certain desired population biomasses. Then it will be interesting to see the effect of reducing the biomass of each stock to half its virgin biomass. If there were no interaction, this would obviously give the overall maximum yield of the system.

Generally, for two stocks the ratio of the yield when P_1 and P_2 are $\frac{P_{1\infty}}{2}$ and $\frac{P_{2\infty}}{2}$ to maximum overall yield is

$$1 - \frac{(c_1 - c_2)^2}{4b_1 b_2 - 4c_1 c_2} \quad : \quad 1 \qquad (12)$$

Therefore, if the interaction terms are equal the ratio will be 1 : 1. Also if c_1 and c_2 are small compared to the parameters b_1 and b_2 the ratio will be close to 1 : 1. Interaction terms with opposite signs, will give great deviation (i.e. predator/prey situations). (see Fig. 6)

In conclusion it seems that aiming at a biomass for each species which are about half a level of virgin stock size seems to be a good first approximation to maximize the yield.

If one species is a predator on the other, the predator should be brought to a level below half P_∞ while the prey should be reduced less.

Usually maximum yield should not be the only goal for fishery management and for the purpose of higher stability and conservation, and also to get a higher catch per unit effort it has been recommended to keep the stocks around $2/3 \, P_\infty$ instead of reducing them to $1/2 \, P_\infty$.
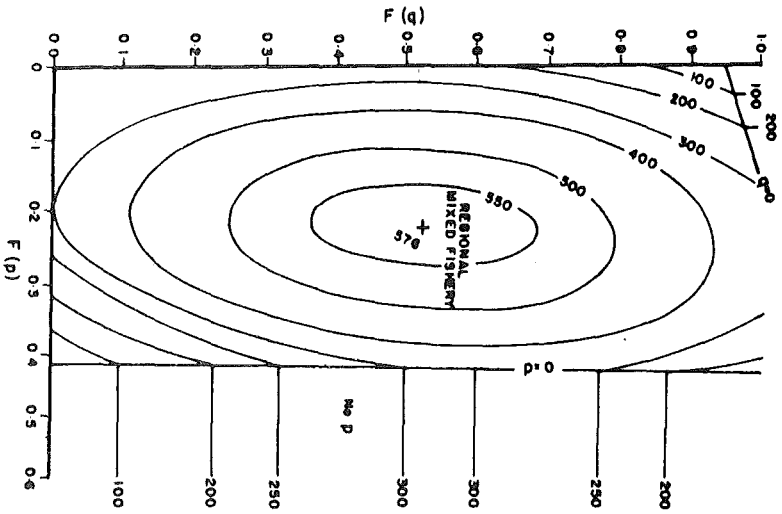
Fig.6 Yield-isopleth diagram
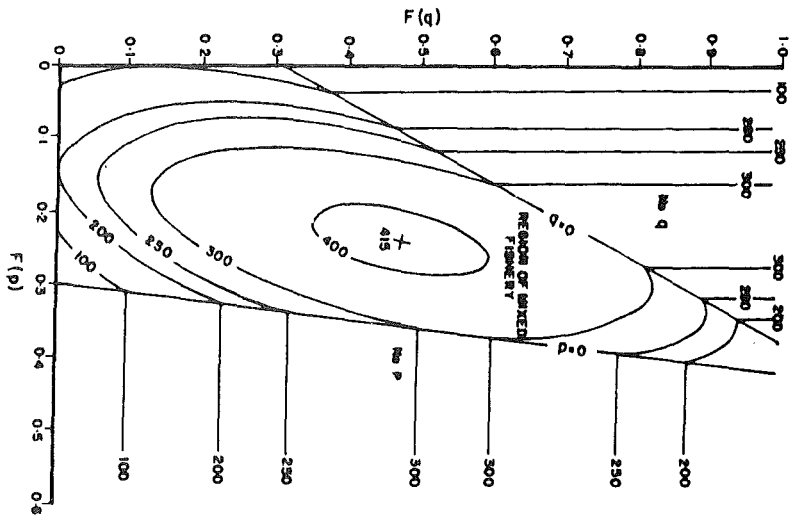for two species with
weak composition

Fig.7 Yield-isopleth diagram for
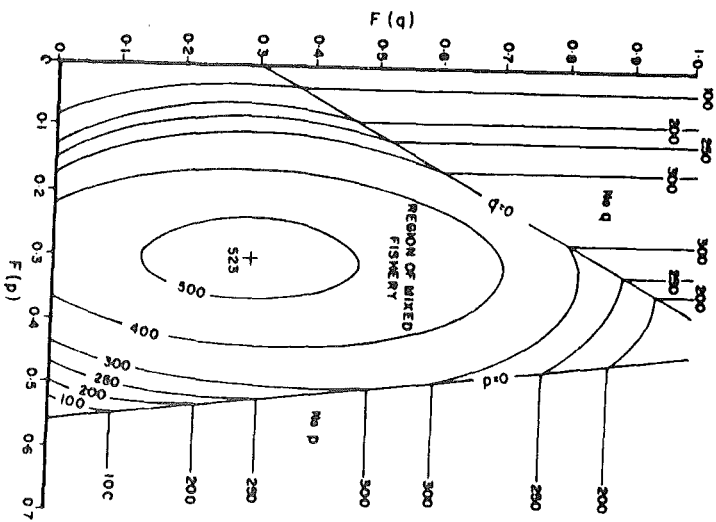two species with strong
competition

Fig.8 Yield-isopleth diagram for
two species, one the prey
of the other

USE OF EGG AND LARVA DATA FOR CALCULATIONS OF SPAWNING
STOCK SIZE IN FISH

Determining the stock size is one of the fundamental
exercises in fishery biology, both when working with well-
regulated commercial stocks and when searching for new
resources.

A series of methods are at our disposition. The most
important of these can be classified into the following
system:

      i)   calculations from catch per unit effort
     ii)   tagging experiments
   iii)   acoustic investigations
    iv)   calculations from egg and larva data

All these methods have their advantages and disadvantages
so it cannot be stated that one method is generally best.

We shall examine only the last of these methods, the
estimation of stock size from egg and larva data, taking
into account the principles for the method and the
biological background. Thereafter we shall look at the
methods of calculation and finish with some examples of
their application particularly for new resources.

It is assumed that a female of a given size spawns a
known number of eggs per unit time (usually per year).
Practically speaking, nearly all eggs are fertilized and
a certain amount - usually the majority - develop into
larvae. At the larval stage mortality is high and variable.
From the fingerling stage up to adulthood mortality
decreases and becomes constant. Thus if one takes as a
starting point the number of eggs or young larvae it is
possible to back-calculate to the size of the parent stock.
Thereafter one can directly estimate the size of the next
generation.

The principle of stock calculations from egg and larva data is therefore given in its simplest form. The number of eggs and larva produced is estimated, and devided by the number of eggs spawned per female to produce the number of females in the spawning stock.

$$P = \frac{E}{F} \qquad \frac{\text{eggs produced}}{\text{fecundity}}$$

By also considering the sex ratio in the spawning stock the total stock size may be estimated. This method was first employed by Hansen and Apstein in 1897 in an attempt to estimate the plaice stock in the North Sea. The method met strong opposition and was largely ignored until the middle of the present century.

In 1956 Beverton and Holt wrote that egg surveys were probably the best method with which to estimate stock size. Nonetheless the method still seems to be comparatively poorly recognized by most fishery researchers, despite work presented at a meeting of the International Congress for the Exploration of the Seas in 1980 and a symposium at Wood's Hole in early 1979 indicating an increase in use and popularity.

When looking at the biological basis of the method it is natural to begin with fecundity. This is a relatively simple point when dealing with total spawners who lay all their eggs over a short period of time each year. Fecundity, defined as the eggs to be laid in the coming spawning season, can be easily measured in mature fish which are easily distinguishable by their size.

The problem becomes much larger when dealing with partial spawners. A range of egg sizes can be found in the ovaries (Fig. 1) and it is very difficult to determine the number of eggs to be spawned in a given period. Much work has been done on this problem but the conclusion seems to be that it is necessary to conduct basic studies on the ovaries and course of spawning for every single species one wishes to work with.
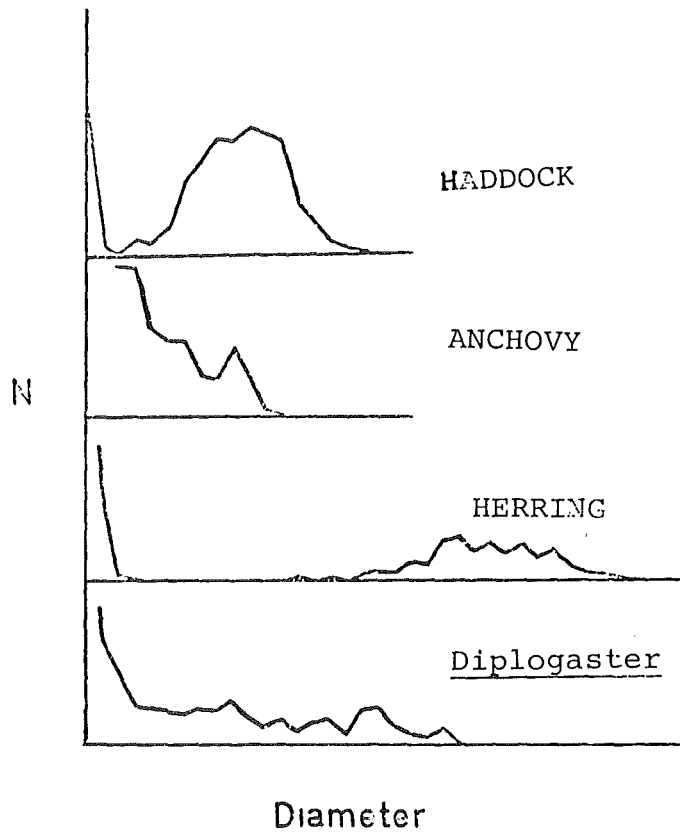
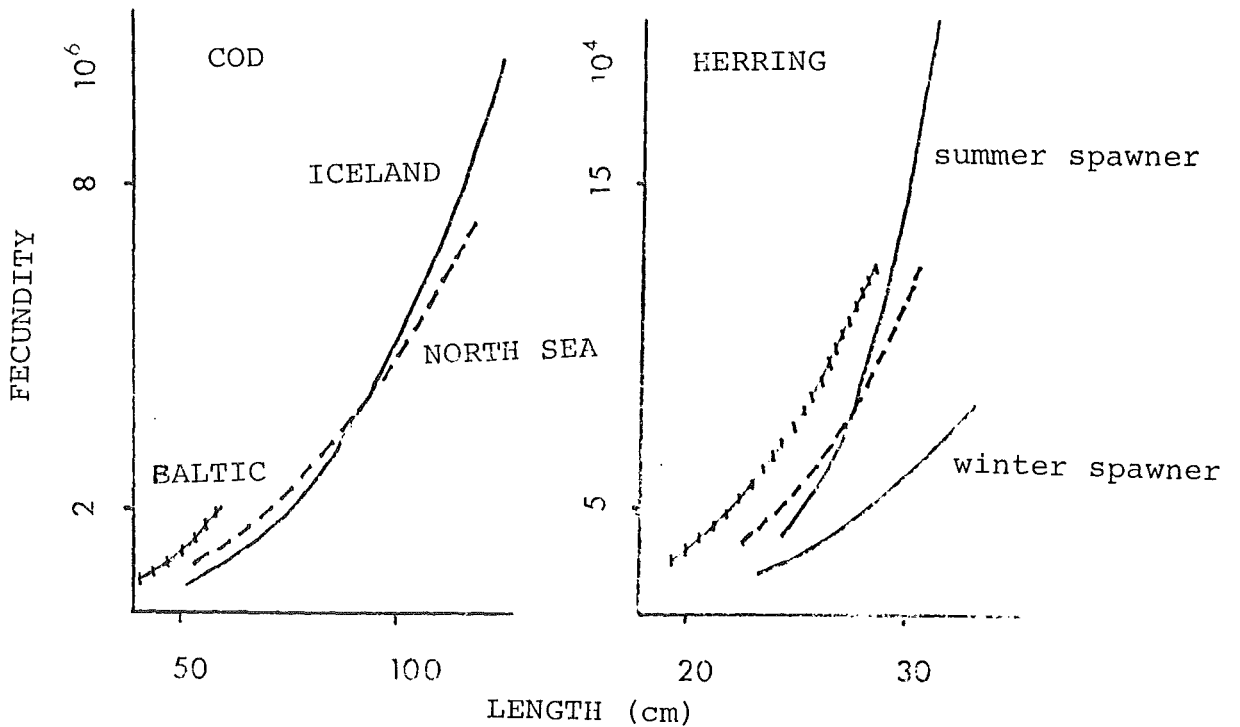Fig.1. Size-frequency distribution of ovarial eggs of some partial- and total-spawners.

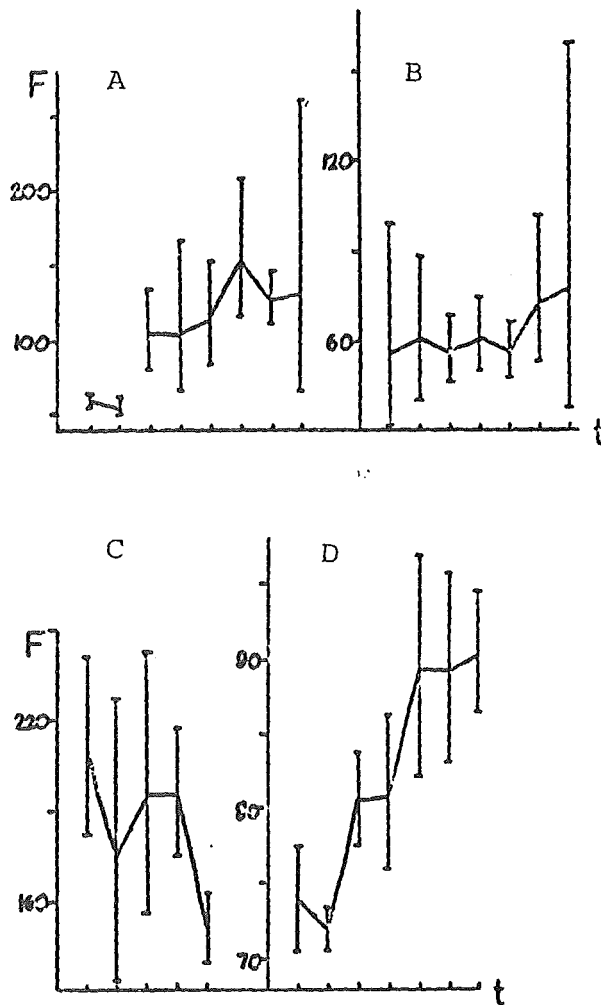Fig. 2. Fecundity of some stocks of cod and herring.

Fig. 3. Annual variation in mean and range of fecundity of
A: Plaice, B: Long rough dab, C: Witch and D: Perch.

In practice only a few fish will be measured for fecundity
and the total egg production of the stock will be calculated
from the relationship between fecundity and length or weight.
Figure 2 illustrates that this relationship can vary greatly
between stocks within a species. As a rule the relationship
is reliable but there are exceptions such as herring and
other clupeids where there seems to be no correlation
between fish length and egg number.

There are also many confounding variables. For example it
has been shown for a number of species that food availability
and stock density have considerable influence on fecundity.
Thus, fecundity is a parameter which cannot be measured
once and considered constant. Fig. 3 shows the calculated
fecundity and its range for different species of fish. For
the sake of efficiency, fecundity was estimated from a fish
of average size for each species.

So the eggs are spawned. The per cent fertilized is usually
near 100% for marine fish and therefore the next factor to
be considered is mortality at the egg stage. Here it becomes
necessary to distinguish between pelagic and demersal eggs.

For pelagic fish a mortality of between 2 and 10% per day
seems to be normal in boreal waters. In the tropics it may
be much higher - a mortality rate of about 25% per day has
been reported for sardines off California. However, because
of the much shorter incubation times, the total mortality
in tropical waters is not necessarily any greater than in
colder waters. It must also be remembered that sampling
problems make all such estimates of mortality very uncertain.

For species with demersal eggs such as capelin and herring
mortality generally seems to be much lower. For herring a
mortality rate of 1 - 10% during the entire incubation time
is common and capelin usually have less than 25% mortality.
The thickness of the egglayers may be a critical factor for
survival of herring whereas this seems to be of little
importance for capelin. If one uses larvae as the basis for

estimates, such a correlation between egglayer thickness and mortality can result in a systematic underestimation of the size of large yearclasses since these often lay the thickest deposits.

The low values given for capelin and herring do not include mortality due to predation. For capelin, Sætre and Gjøsæter have shown that predation usually plays a subordinate role. Nonetheless it is clear that haddock and pollack can consume a significant amount of the eggs laid by the individual stocks of herring.

Mortality at the larvae stage is more difficult to survey. The concept of critical period has stood central in the debate. May (1974) went through the available data and concluded that there was insufficient evidence to either prove or disprove the hypothesis. It remains a fact that larval mortality is high and variable but is probably lowest in the period where the larvae are still nourished by the yolksac.

During an investigation of plaice in the North Sea, Bannister et al. (1974) found that larval mortality was of the same order as egg mortality, that is, 2 - 10% per day. Dragesund and Nakken showed that herring larvae had a mortality rate of almost 20% per day during the first 14 days. All such estimates, however, are in the meantime considered unreliable because of the undetermined significance of "selection".

We have now looked briefly at the relationship of parent stock to number of eggs or larvae found in the sea at a given time and shall go over to examine the sampling problems involved. These can be separated into three categories:

1. variation and systematic error in conjunction with the individual samples
2. variation due to integration over an area
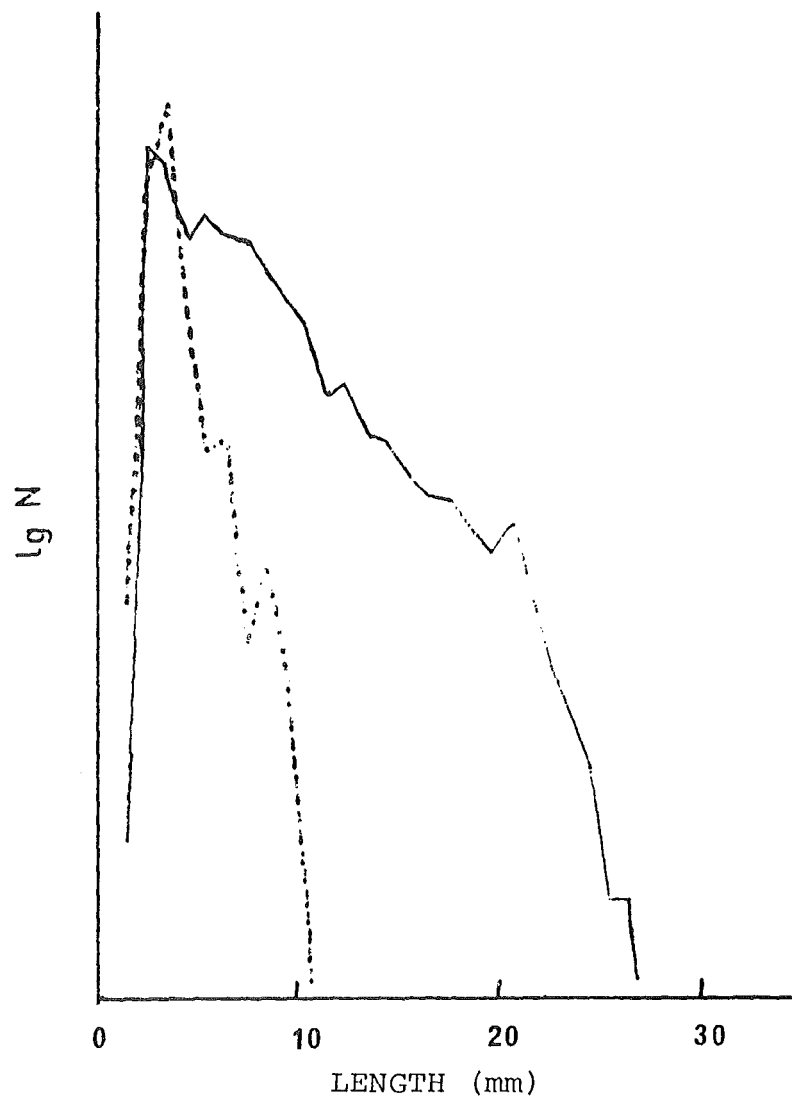3. variation due to integration over time.

Fig. 4. Number of larvae caught in a plankton
net (━ ━ ━ ━) and in a seine net (━━━━).

In addition to these points we can include variation due to age determination and the rate of larval development.

Many investigators have researched just how representative a plankton tow is to the quantity of eggs or larvae in the watermass it sampled. But because so many factors interact it is difficult to achieve an unambiguous result.

The problem has a technical side: what percentage of the available water is filtered by the equipment under differing conditions and how great is the probability that an egg or larva of a given size can escape the equipment or slip through it? This is dependent on the shape of the gear, the rate of tow, the towing angle (vertical, horizontal or oblique) and the type of plankton found in the locality etc.

Modern plankton gear usually has good filtering capabilities - in any case, when the clogging problem is not too great. However, avoidance is a serious problem, especially for larva sampling.

Figure 4 shows the catch in a specially constructed seine net and in a plankton haul. There is a great difference in the length distributions caught by the different gears, especially during daylight. These data refer to Engraulis larvae but can be presumed to be relatively representative of other species also.

Clearly the perfect plankton gear does not exist. In the handbook "Standard techniques for pelagic fish egg and larva surveys" published by the FAO in 1977, the use of Bongo nets is generally recommended but this is certainly not the last word on this topic.

The distribution of eggs and larvae in space and time is of fundamental significance to the sampling program. We will first examine spatial distribution:

Spatial distribution is a complex problem but eggs and larvae will usually be spread so that they can be representatively sampled from one depth interval. Thus the spatial

distribution becomes a distribution along a plane.

Fish eggs and larvae are not evenly spread throughout a water mass. Usually the sampling will give a distribution with patchiness   i.e. a small per cent of the samples will contain a large per cent of the total eggs and larvae. The younger the stage under observation the more obvious this becomes.

Smith (1973) dealt with this phenomenon relatively deeply in sardines. He points out that the fish spawn in schools, resulting in a patchy distribution of newly-spawned eggs. Around such nucleii of freshly spawned eggs is an area devoid of eggs, into which the eggs will soon diffuse and create a corona around the tight nucleus. This diffusion will eventually result in a more even distribution. For sardines, Smith found that the nucleii could have a diameter of tens of meters whereas the corona could fluctuate from one hundred meters to several hundred meters.

Other distributions exist for other species, despite certain common characteristics. It is therefore recommended that the distribution be investigated for each species and life stage concerned before making assumptions based on a given distribution.

If one wishes to use common statistical methods for various types of hypothesis, one must know the distribution of the data. If the theoretical distribution is known, it becomes possible to evaluate the number and size of the samples one should take.

In "Standard techniques for pelagic fish egg and larva surveys" it is recommended that the distribution fulfill the following requirements:

1. has patchiness, $s > \bar{m}$
2. has 0 observations
3. goes toward Poisson distribution for low values of $\bar{m}$
4. $\bar{m}$ and s^2 are not assumed to be independent

A negative binomial distribution fulfills these requirements
and is sufficiently flexible to be adapted to many circum-
stances.

The variance and median are related as in the expression

$$s^2 = \bar{m} + \frac{\bar{m}^2}{K}$$

where K is the expression for the degree of patchiness in
the distribution. There are also examples of log normal
distributions being used but these assume that the 0 - obser-
vations are ignored.

If the distribution is strongly skewed, the transformation

$$x^1 = \log (x + a)$$

may be used, where "a" is often made equal to 1. The object
is to make the data fit the requirements of the most common
statistical analyses such as analysis of variance, t-tests
etc. Thus the transformation can normalize the data and
stabilize the variance.

For mackerel eggs, Ulltang (1978 note) showed that the best
result would be obtained by setting a = 0 and ignoring
the 0 - observations. This illustrates the significance of
evaluating the transformation to be used in each case
instead of using one formula uncritically. In many cases
such transformations are unnecessary because non-parametric
statistics can be used to test the hypothesis.

Suppose we have a series of stations sampled on a cruise
which we consider synoptic. We have estimates for the
number of larvae per square meter of surface at each station
and the next step is to integrate them over the whole area.
Three methods can usually be applied:

1. averaging all the stations within an area or
    subarea. If the stations are randomly distributed,
    this method will give a result free from systematic
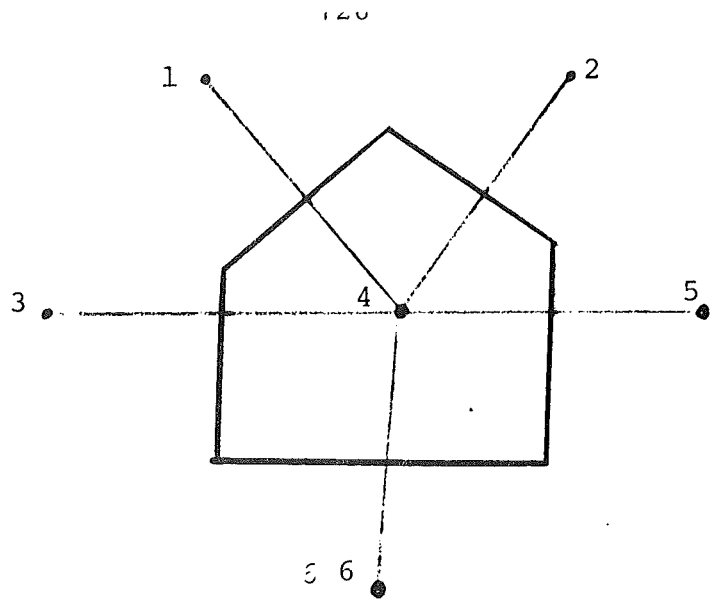   error

Fig. 5. Construction of polygon for estimating size of area representative for station 4. The figures indicate station numbers.
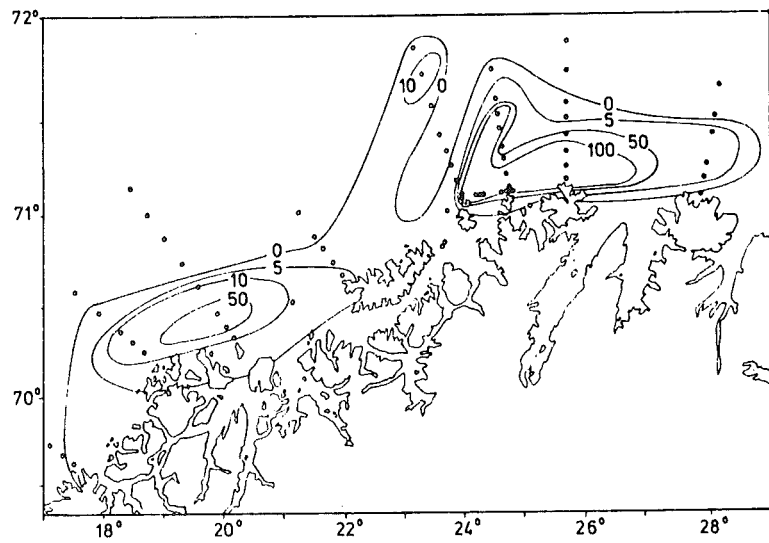

Fig. 6. Example of station grid and isolines to estimate larval abundance of Capelin.

2. weighting each station by the area of a polygon which arises from the drawing of perpendiculars through the midpoints of transects between each station and the surrounding stations. This method corresponds to linear interpolation between each station and its surrounding area. Sætre and Gjøsæter have developed a computer program using integration of this type to calculate the number of capelin larvae. (Fig. 5)

3. the third and most used method is to draw iso-metric lines between the stations and measure the area contained. Usually these lines are drawn by rule of thumb but Buchanan-Wollaston (1923, 1926) developed a graphical method, enabling the lines to be plotted objectively. (Fig. 6)

Sette and Ahlstrom (1948) used all of these methods to estimate egg production in Pacific sardines. The difference in results was insignificant when compared to the other sources of error. In other cases the differences can be larger especially if the stations were chosen with knowledge of the probable location of most of the larvae (this renders the first method inapplicable).

If there are no estimates of the number of eggs on the spawning grounds over a series of time intervals, then the next problem becomes to calculate egg production over time. Here there are two possible methods:

1. surveys which cover the entire spawning period, allowing integration over time as well as over area

2. constructing a spawning curve to indicate the proportion of the stock's total egg production spawned at any given time. Thus back-calculation from the number of eggs found at any given time will lead to the total egg production. Such a spawning curve can be constructed from gonad studies or by regular sampling of representative stations. (Fig. 7, 8)
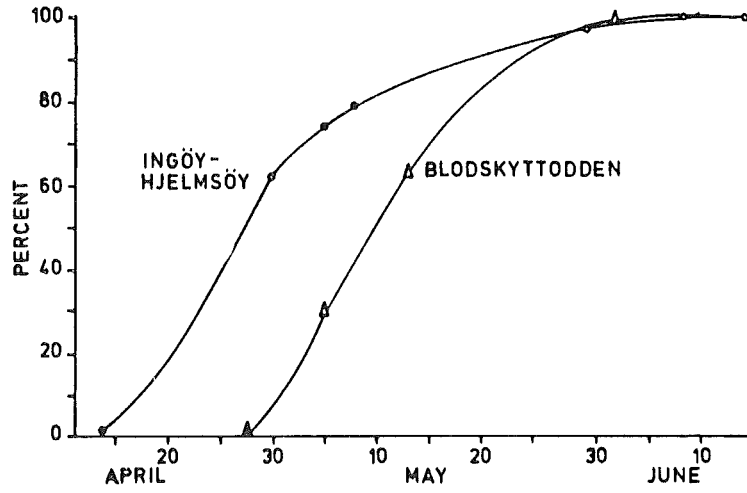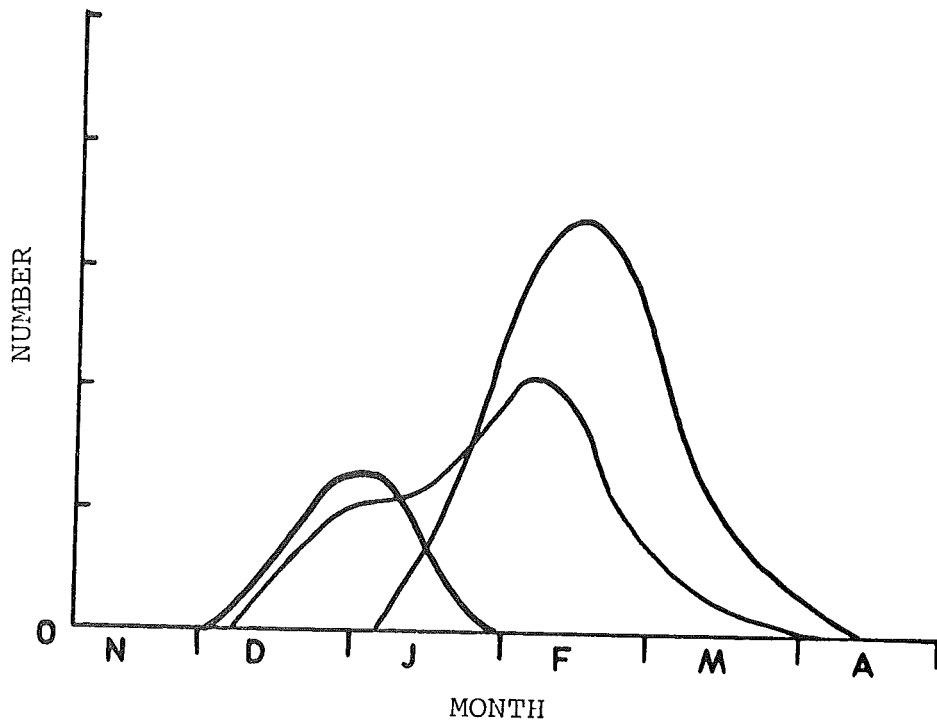
Fig. 7. Cumulative hatching curves for Capelin

Fig. 8. Spawning curves for Herring from A: English Channel, B: Southern Bight and C: Southern North Sea.

As we shall see later the hatching curve can be applied in a corresponding manner.

Some researchers have assumed that the course of spawning follows a normal distribution or a parabola and have adjusted such functions to their data. The useable calculation of the time integral can be aided by a theoretical curve, particularly if there is a long period between successive cruises.

Irrespective of which method is chosen, the presumption is that one knows how long the stages under study will last in the ambient temperature regiones. Age determination on the egg can be accomplished through the degree of development of the embryo. Ageing becomes somewhat more complicated for larvae but yolksac size seems to be a reliable determinant (in capelin, for instance). Daily rings in the otolith may also be used but are far too time consuming for a routine investigation. Counting the number of eggs up to three days old will correspond to three days production.

An interesting application of theoretical distributions in time and space is found in the work of Bagge and Muller from 1977. They studied cod eggs in Bornholm Basin but on some of the cruises the spawning grounds were only partially covered. Thus they assumed that there was a spawning center and that the eggs were normally distributed around this. On this basis a computer adjusted a two-dimensional normal distribution to the data. They also constructed a mathematical model which presumed that the spawning intensity followed a parabola throughout the season as well as a model which illustrated the hatching and mortality of the egg stage.

A number of investigations have been conducted to determine the best division of effort when one has a limited amount of ship time. Saunder English (1964) studied flounder eggs in Puget Sound and found that coverage over time - i.e. repetitive surveys - were most important, followed by coverage of area and finally by the grid density of stations per survey. Taking many stations in the same position gave

the least reduction in the variance. Of course, these con-
clusions cannot be directly applied to other species or
areas but it is probable that they correspond to many
situations.

We can summarize what we have said thus far in the formula

$$P = \frac{1}{FS\ (1 - Kd)} \int \oint \frac{Eij}{\bar{d}}\ d\ A\ dt$$

where P is the parent stock, Eij is the number of eggs
at station i on cruise j, K is the egg mortality per
day and d is the number of days the eggs are in the stage
under investigation. $\bar{d}$ is the median age of the eggs,
F is the fecundity and S is the sex ratio of the spawning
stock.

Generally this is applied to pelagic eggs but can also be
used on larvae with a few simple modifications.

When working with fish with demersal eggs the problem of
sampling becomes somewhat different. To illustrate a solution
we will go through a method that Sætre and Gjøsæter described
in 1974 to estimate the size of the capelin stock:

Capelin lay eggs wich are well mixed with the sand and
gravel on the bottom at depths between 25 and 50 meters.
The incubation time is about one month.

The following data are prerequisite for the method:

1. localization of the spawning ground - this is
    done by grabs
2. calculation of the number of eggs e spawned on
    one of these spawning grounds B. This is done
    primarily by scuba divers
3. calculation of the number of larvae l younger
    than d days old hatched from this spawning
    ground at the time t
    $_1$

    4.   calculation of the number of larvae L younger than d days old hatched from the entire spawning ground at time t_2

    5.   construction of a hatching curve for the entire area and for spawning ground B.

The number of eggs spawned on ground B can be expressed as

$$e = \frac{1}{a_1 \, (1 - K_1) \, (1 - K_2) \, (1 - K_3)}$$

where l is the larvae younger than d days old at time t_1, a_1 is the proportion of all hatched larvae from this spawning ground which are from 0 to d days old at time t_1. K_1, K_2 and K_3 are respectively egg mortality, hatching mortality and larva mortality up to time of sampling. Systematic sampling error during the larva collection is included in K_3.

In a similar manner we can apply this relationship

$$E = \frac{L}{a_2 \, (1 - K_1) \, (1 - K_2) \, (1 - K_3)}$$

where E and L are eggs and larva number for the entire spawning ground or, more precisely, a part of that area.

If one assumes that mortality and sampling error are similar for both the well-investigated part of the spawning ground and for the rest of the spawning ground, the relationship can be expressed as

$$\frac{E}{e} = \frac{L \, a_1}{l \, a_2}$$

and the parent stock size becomes

$$P = \frac{L \, e \, a_1}{F \, S \, l \, a_2}$$

where F is the fecundity and S the sex ratio of the
spawning stock.

Determination of the stock size of unconventional resources
can, in principle, be carried out with the aforementioned
methods. However, in practice, we often run into problems
which make it necessary to perform a simplification.
Typical of such problems are:

    1.   incomplete knowledge of the fecundity and
        spawning course of the species in question

    2.   use of larva data instead of egg data because
        eggs are difficult to identify or the eggs
        cannot be found

    3.   the cruises are often planned with other aims
        and sampling grid is seldom optimal in both
        time and location.

The best one can do in such cases often is to create a
relative measure. If the larval production is larger in one
area than in another, it may be assumed that the parent
stock is also larger.

Useful indicators of this can be found by comparing species
which have similar fecundity and spawning course. As an
example, we shall examine some data from the Gulf of
California published by Ahlstrom and his coworkers in 1971:

At the larval stage the following proportion was found:
      Gonostomatids   22%
      Myctophids   16%
      Clupeids   14%

Among the Gonostomatids the dominant species was
Vinciguerria lucetia and we will look a little closer at
this. This fish has an average weight of approximately 0.7 g
and a fecundity around 430 eggs per gram. The area investi-
gated was 10^{12} m^2.

The number of Vinciguerria larvae per haul showed large

fluctuations. I have calculated the arithmetic mean for the period to be 95 larvae m^{-2} surface. By doing the same for Sardinops one gets an average of 14 larvae m^{-2} surface. There usually was about seven times as many Vinciguerria larvae as Sardinops larvae.

If we temporarily disregard egg and larva mortality we can perform a loose evaluation. If we now consider the larval abundance in June 1957 260 m^{-2}, we can calculate the number of fish needed to produce these larvae:

$$\frac{260 \cdot 10^{12} \cdot 2 \text{ g}}{430} = 1.2 \cdot 10^{12} \text{g} = 1.2 \cdot 10^{6} \text{ tons}$$

If we accept the mean larval density previously calculated and assume that the larvae are catchable for a week and that each fish spawns twice a year (something revealed by gonad studies) we get

$$\frac{95 \cdot 10^{12} \cdot 2 \cdot 52 \text{ g}}{430 \cdot 2} = 11 \cdot 10^{6} \text{ tons}$$

This entails quite a few assumptions but now we have an idea of the size order of the stock.

We can also use another method - on the basis of the egg tally (not the larva) from the cruise, Ahlstrom and his coworkers calculated the Sardinops stock to be 48.000 tonnes in February 1956, 505.000 in April 1956 and 74.000 in February 1957. If we assume that Sardinops and Vinciguerria produce larvae at the same rate, we can estimate the amount of Vinciguerria to between 0.2 and 1.2 million tonnes. There were much fewer Vinciguerria larvae found on these three cruises than average, indicating that the result can be close to that expected from the direct calculations.

What we have looked at so far are methods to get an absolute measure for stock size but often a relative measure will suffice. Thus if one has a few years of estimates of egg production and stock size from other methods - such as back calculations from virtual population analyses - it is

possible to establish a regression which can be used to predict absolute stock size.

This method has several advantages. If the fecundity, mortality and equipment selectivity are constant from year to year these will no longer be sources of error. However, it is still vitally important to have adequate data to create a picture of the entire course of spawning in time and space.

The determining factor is that the material is collected each year at relatively the same time and place of spawning. Nonetheless, the sampling effort saved can be considerable and it is probable that the results obtained by these relative methods are satisfactory. The assumption is that one has data from enough years to give a reasonably good regression.

We have hitherto said very little about the confidence intervals around the estimates we are making. The main reason for this is the lack of literature on this topic. Furthermore the models found in the literature are concerned only with the variance of the number of eggs found in the sea. I think there are no satisfactory treatises of the variance due to rate of development or age determination of the stages under investigation.

Even without taking this last source of error into consideration, it seems that the confidence intervals are usually more than 50% of the stock estimates.

The determination of (parent) stock size from egg and larva data will therefore not give particularly high precision in the estimates. I will, however, conclude that the method is useful, both as a supplement to other methods and where other estimates are not available.

USE OF PROBABILITY PAPER TO ANALYSE NORMAL DISTRIBUTIONS

If we plot the cumulative frequencies of a normal distribution on a probability paper we get a straight line. The crossing of 50% gives us the mode of the distribution.

If we add several distributions, we get a line with an inflection-point corresponding to each of the crossing points between two distributions (Fig. 1).

Harding (1949) described a method for analysing the normal distributions which are representing the components of a polymodal distribution. The method was refined by Cassie (1954) and the following gives a short account for his method.
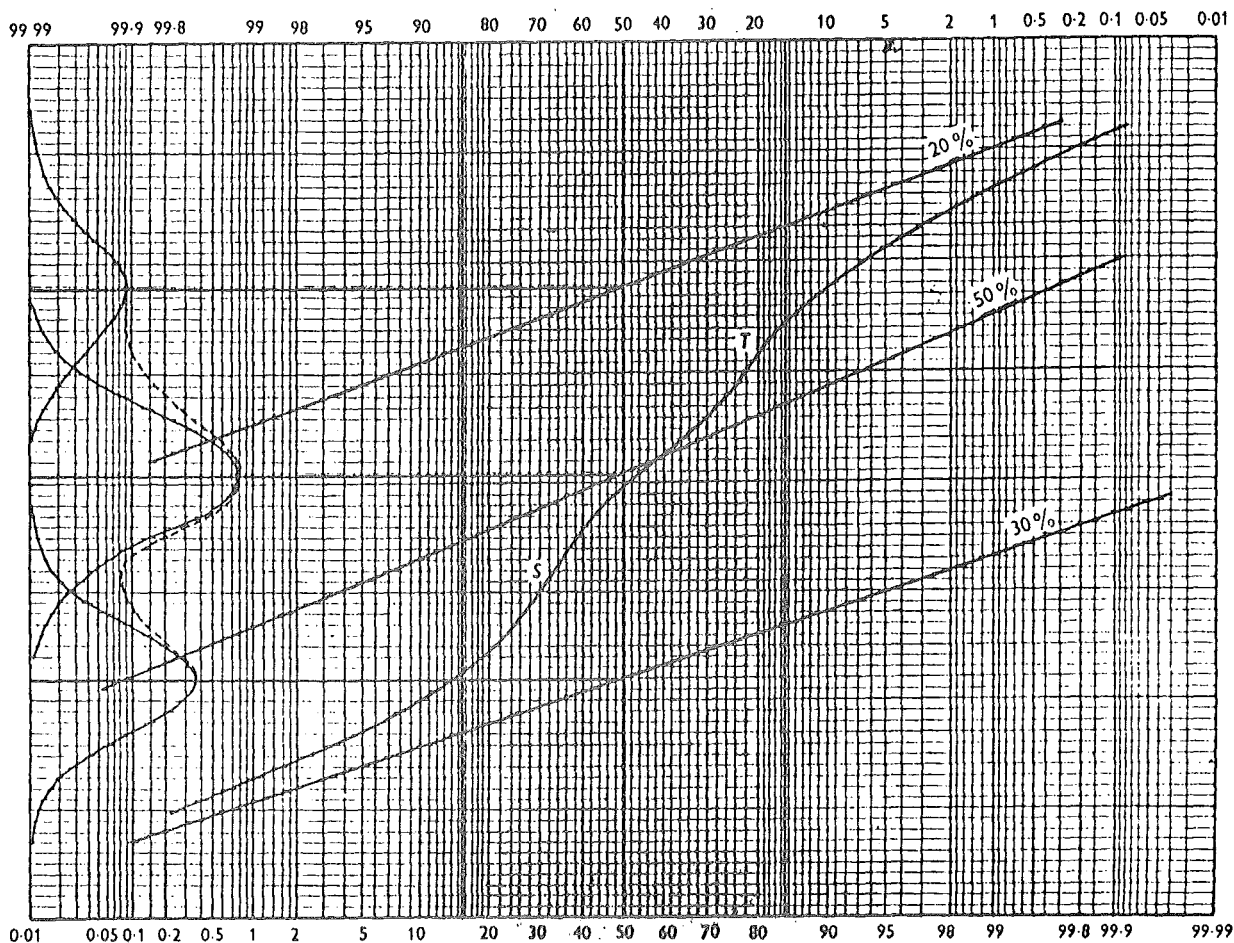
Fig. 1. A three-modal normal distribution split into its components.

Take the size distribution of a fish, and plot the comulative frequency distribution (the circles in Fig. 2.).

Find the inflection points. This may take some experience, and some trial and error may also be envolved.

In Fig.2 the following inflection points were found:

10%, 66%, 91% and apparently 98.6%.

The segments of the curve is supposed to represent the 0, 1, 2, 3 and 4 year old fish respectively.

Fig. 2. A comulative frequency distribution split into its normal components. For explanation, see text.

The percentage of each age group is:

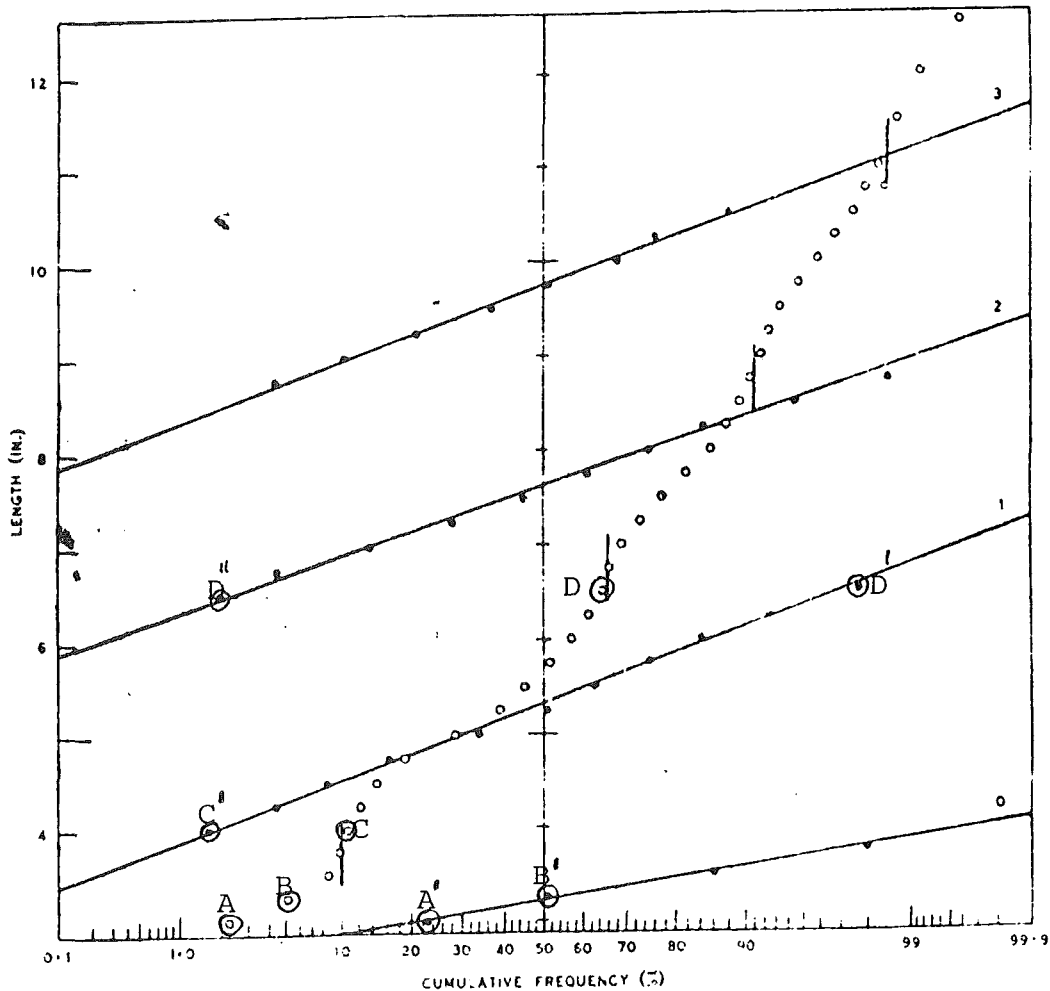|			
0	10%	-0%	= 10%
1	66%	-10%	= 56%
2	91%	-66%	= 25%
3	98.6%	-91%	= 7.5%
4	100%	-98.6%	= 1.4%

The 0-group show probably little overlap with older fish, and should be analysed first.

The first point A represents 2.3% of the whole distribution, i.e. 2.3% of the fish has the size corresponding to this point or smaller.

We want to find the proportion of the 0-group fish who has this size or smaller:

$$2.3\% \quad \frac{100}{10} = 23\%$$

as the 0-group represents 10% of the total sample. This is marked A'.

The next point B gives

$$5.0\% \quad \frac{100}{10} = 50\% \quad \text{giving point B'.}$$

We can go on like this and construct the line marked 0 in Fig. 2.

Next we look at point C representing 10.9% of the whole sample. Subtracting the 10% accounted for by the 0-group we get 0.9% which is the commulative frequency of the 1-group which is smaller than C.

Therefore this point represent

$$0.9\% \quad \frac{100}{56} = 1.6\% \quad \text{of the 1-group.}$$

As we go on there will be an increasing overlap between 1 and 2, and the points we fit using this procedure will be expected to lay to the right of the curve 1.

Therefore we have to modify the method. Take point D corresponding to 64.8%. This point corresponds to point D" representing 97.0% of the I-group.

The percentage of the total represented by the 1-group will then be

$$97\% \quad \frac{56}{100} = 54.3\%$$

To this we must add the 10% represented by the 0-group. Therefore, point D represents 64.8%. Of this 0- and 1-group represents 54.3% + 10% = 64.3%.

Therefore, 64.8% − 64.3% = 0.5% represents the II-group.

The point D' for the II-group line is then

$$0.5\% \quad \frac{100}{25} = 2.0\%$$

Summary of the method.

Using the left limb of a component to construct the percentage distribution for that component.

A.   If there is no overlap with lower components:

  1. Read percentage from the comulative curve: (P)

  2. Subtract the percentage of all lower components (L)

  3. Calculate the percentage within the component studied:

$$p = (P-L) \quad \frac{100}{c_i}$$

   (c_i is the percentage of the component in question in the whole sample).

  4. Plot p values to get a straight line.

B.   When there is overlap between C_1 and C_2.

1. Read the percentage P from the comulative curve.

2. Find the corresponding percentage P_1 from the component 1-curve.

3. The percentage of the total represented by this component will be T

$$T = P_1 \ \frac{C_1}{100}$$

4. Subtract T and L from P.   P-L-T represent the percentage of component C_2 (as percentage of the total material).

5. Calculate the corresponding point on the component 2 curve:

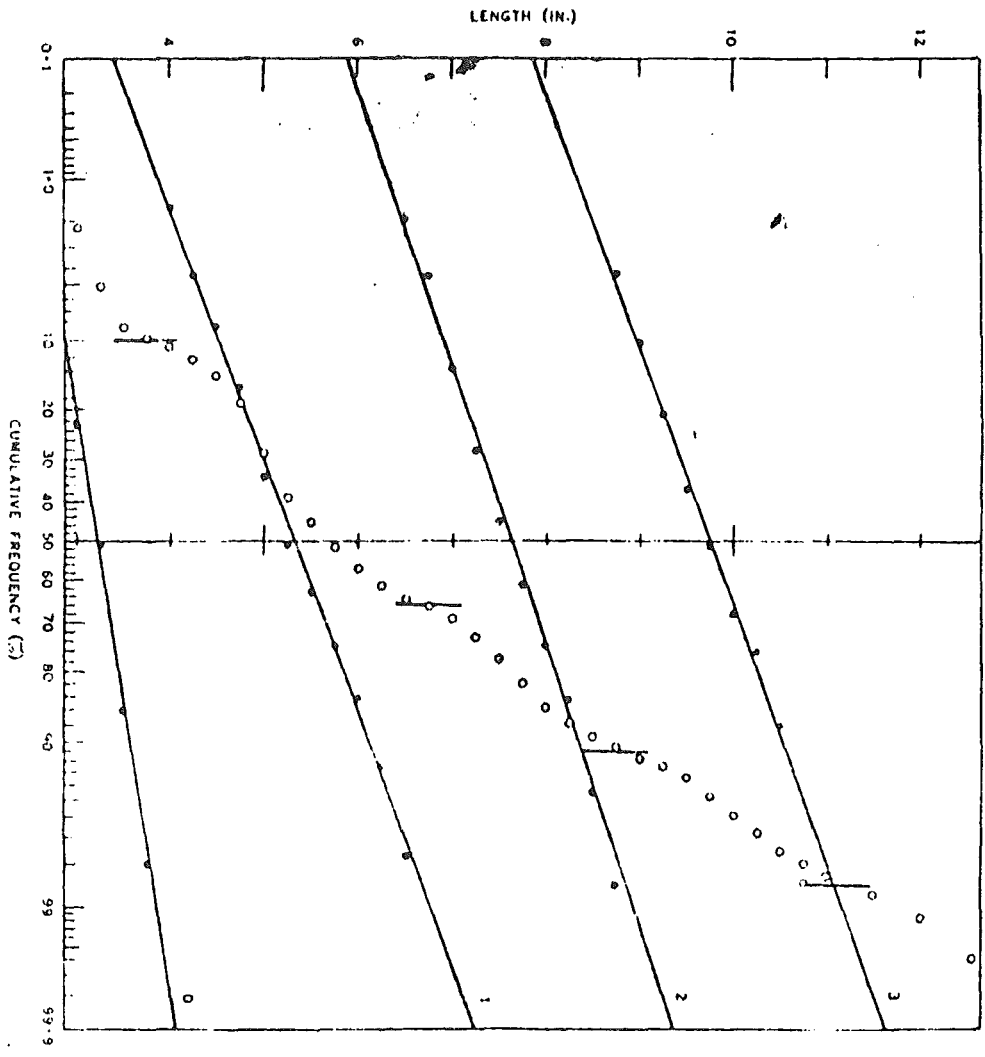$$P_2 = (P-L-T) \ \frac{100}{C_2}$$

Fig. 1.—Cumulative percentage length distribution of 256 snapper.

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