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Fish stock dynamics
An adaptation of the course Fish stock dynamics
given by F. Thurow during the winter semester
1969-1970 at the Institute of Oceanography,
Kiel University

by F. Bingel, D. Brunswik, H. Grimm
C. Gehlhaar and C. John

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1971

Fish stock dynamics

An adaptation of the course "Fish stock dynamics"
given by F. Thürow
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prepared by
F. BINGEL, D. BRUNSWIK, H. GRIMM, C. GEHLHAAR and C. JOHN
1971

Translator's note: For some reason, the authors have presented their
Figures not in numerical order, and I have not
changed their order.

In the equations presented in this paper, the symbol
(.) means a multiplication; thus, $r \cdot s$ means r multi-
plied by s .

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1. Introduction

Fish population research is concerned with, and is aimed at, the development of model notions regarding the dynamics of fish stocks. The results of studies in this field represent the basis for both optimal fishing and predictions with respect to future catches, and they also reveal the efficiency of regulatory measures.

The immediate subject of this particular branch of fisheries biology is the fish stock. According to various authors, the unit stock can be defined as follows:

The stock (unit stock) is a unit of individuals of one tribe or one species, which interbreeds and maintains itself within a defined area during a certain period (season) and ^{is} subjected continuously to isolated exploitation by fishing (Bückmann, 1963; Cushing, 1968; Hempel and Sarhage, 1961; the Lowestoft Paper, 1962; and the ICNAF Paper, 1958).

The following methods are employed to distinguish between individual stocks:

- Evaluation of meristic characters;
- Biochemical studies; and
- Mark and recapture experiments.

1.1. Development of fish population research

The first paper dealing with fish population dynamics was published in 1877 by V. Hensen, who estimated the number of mature cod and plaice individuals present in both the Kiel fjord and in the Eckernförde Bay by sampling pelagic eggs. Population dynamics research received a

fresh impetus after fishermen came to realize that stocks fluctuated^u in numbers. For instance, the landings of herring from fishing off Bohus län amounted to 200,000 tons in 1896, but decreased to 20,000 tons already during 1897. That finding gave rise to the establishment of the International Council for the Exploration of the Sea (ICES).

Since the publication of Heincke's (1913) general review paper, ICES has been concerned chiefly with the survey of fish populations. A number of theories have been discussed in the course of the years proposing concepts regarding the factors causing these particular fluctuations. The value of model concepts of this type can be tested by either long-term surveys of populations or large-scale experiments. The latter approach is difficult for financial reasons. Due to these reasons, we know only the example of Pacific halibut fishing as^a large-scale experiment (Thompson, 1960), which is carried out off the shores of the USA and Canada with the aid of long lines. During the years 1913 to 1915, the maximum yields obtained there amounted to around 30,000 tons. After the catches decreased, commissioners were appointed, who determined that 40 per cent of the stock present was taken by the fishermen. Exploitation of halibut on these fishing grounds was thereupon limited by the introduction of quotas, which, at first, were filled within a period of eight months; then, within one of four months; and during the years between 1945 and 1950, within a period of one to four months, although the quota had already been increased during the later years. This halibut experiment has demonstrated that deliberate and meaningful regulations will result in changes in the stock with respect to the number of individuals present.

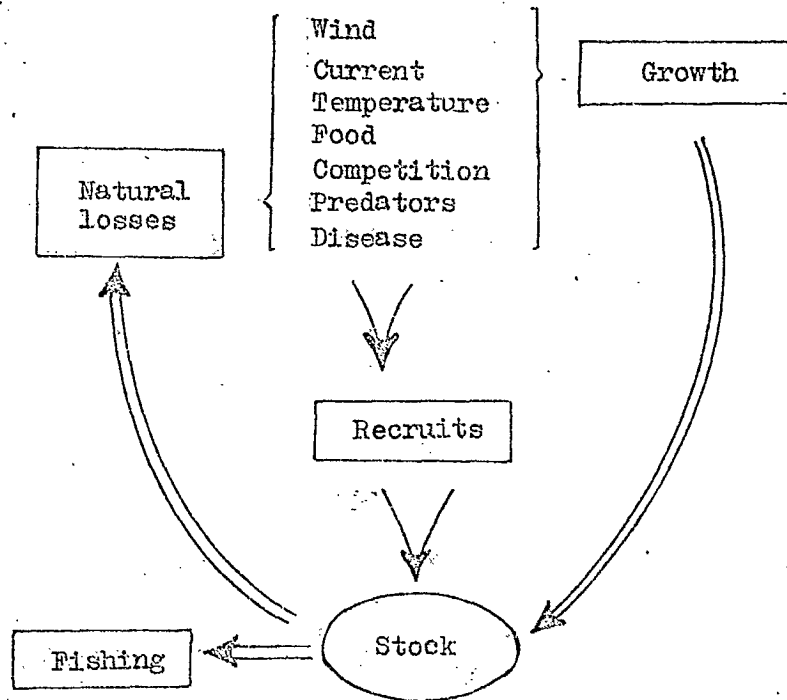


Figure 1 - Scheme illustrating factors affecting stocks of fish

Population (stock) changes are due to:

- Increase in stock weight due to growth;
- Increase in stock weight due to recruitment;
- Decrease in stock weight due to natural mortality; and
- Decrease in stock weight due to mortality due to capture.

1.1.1. The theory of overfishing (Russel, 1942)

A given stock of fish is affected by both natural mortality and mortality due to capture. Exploitation of a stock previously not exploited by fishing will lead to changes in stock structure.

Increasing exploitation by fishing

- a) changes both the age composition and the growth of the stock (we know that large individuals are less frequently captured);

- b) decreases the catch per unit of effort (i.e. the density of the stock); and
- c) results--after initial increases--in decreasing yields.

1.1.2. The thinning out theory

The following experiments have been carried out with respect to the question of correlations possibly existing between stock density and growth of individuals:

1. Henking (1922) released slow-growing Baltic Sea plaice in the North Sea and found that the rate of growth did not change.

2. On the other hand, fast-growing North Sea plaice continued to grow at a fast rate also in the Baltic Sea.

In 1916, Heincke outlined the hypothesis that the different growth rates exhibited by individual stocks were determined by genetic factors.

In his experiments concerned with transporting plaice from the mouth of the Limfjord to the interior of that fjord, Petersen (1909), on the other hand, found that the rate of growth increased after release at the latter site. Strodtmann (1935) repeated corresponding plaice release experiments in Kiel and he arrived at the following conclusions:

1. The Baltic Sea plaice exists under conditions of severe food competition and realizes only a certain fraction of its growth potential.

2. Transportation of young plaice from the Baltic Sea to the North Sea resulted in considerably improved growth. (In his experiments, Henking had used very old plaice individuals.)

The results reported by Strodtmann agree with those obtained by Hempel (1958), who demonstrated that density-dependent growth can be observed only in one- to three-year-old plaice.

During the twenties, the discussions on the effects exerted on growth were concerned chiefly with the theory of "thinning out" supported by Petersen (1909), Garstang and, initially, also by Kyle (1928). According to that theory, the catch per unit of effort will be greater if the juvenile year classes are decimated in numbers to such an extent that the individual rate of growth will increase noticeably resulting in increased total weight of the stock in question.

Russell (1932) and Bückmann (1932) have subjected that theory to critical reviews, since their respective calculations showed:

The individuals of the thinned-out stock must live within the thinned stock for two years without being subjected to exploitation by fishing before their higher individual weight (= total weight of the stock) will be greater than the total of the more numerous but smaller plaice of the original, not thinned stock. Thinning of a given stock two years before exploitation, however, cannot be realized, since it is not profitable.

1.1.3. The theory of reproduction (stock-rec^uruitment relationship)

In 1897, Holt found that the maintenance of stock size is ensured only if each individual belonging to that stock has ~~the~~ the chance to participate in spawning. According to Holt, there would then exist a direct correlation between the number of parents and the number

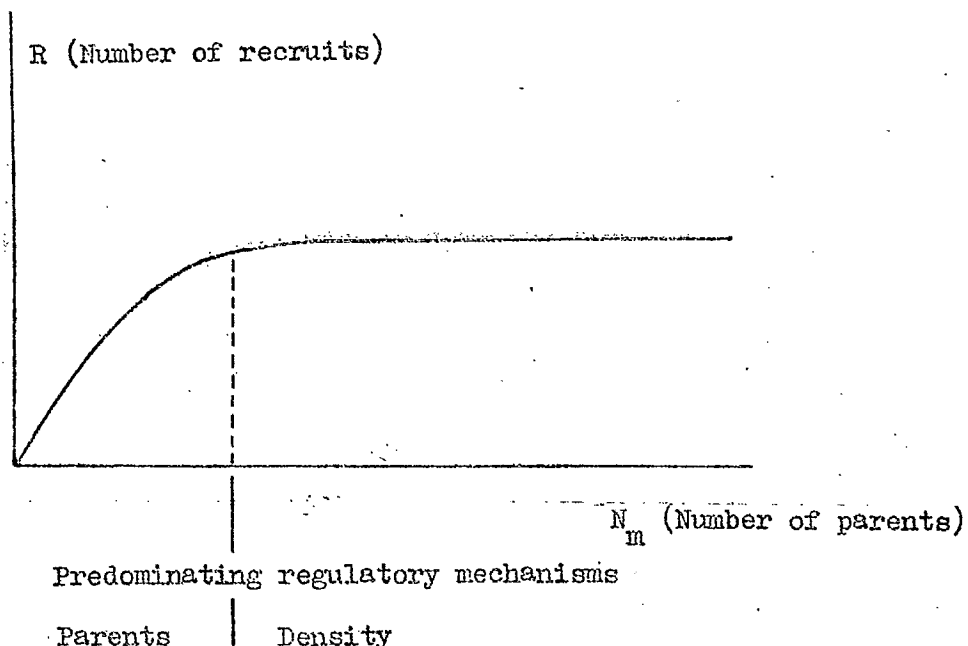


Figure 2 - Mechanisms controlling the number recruits.

of offspring. In 1968, Garrod was able to demonstrate that ^{this} correlation exists in the case of the Arcto-Norwegian cod. However, it appears that no such correlation between the number of parents and the number of offspring exists in populations of other fish species. Other factors then must play a limiting role as long as the number of eggs does not fall below a certain minimum.

1.1.4. Natural fluctuations

Fluctuations are changes in population or stock size. The large fluctuations known from the past must have had natural causes. In many cases correlations have been found to exist between the number of one-year-old individuals and the number of recruits, but not between the number of eggs and the number of recruits, and it would therefore

appear that these natural factors must have exerted their effects during the first year of life and, probably, during the first weeks of life.

Only in cases of extreme decimation of stocks can fishing activities alone be held responsible for changes in the number of individuals in a given population or stock.

1.2. Optimal fishing

In order to obtain the greatest possible long-term yield in fishing, we must institute optimal exploitation of the stock. The hypothesis of optimal fishing has been established on the basis of the following experimental results and the following model concepts.

1.2.1. The guppy experiment (Silliman and Gutsell, 1958)

The weight of the catch does not increase in a linear manner with increasing fishing effort; instead, there exists a maximum yield at a certain fishing effort, and the yield will decrease with further increase in fishing effort. The results obtained in the guppy experiment support that hypothesis: In four aquaria, guppies (Lebistes reticulatus L.) . 8 . were maintained for 174 weeks, which period of time corresponds to 58 guppy generations. Both temperature and food supply were kept constant during the entire duration of the experiment, and possible cannibalism was kept at a low level by making available protected grounds for the young within the aquaria. The biomass was determined once a week by weighing. The stock not subjected to exploitation by fishing grew up to week 60 (corresponding to 20 generations). At that point, this particular

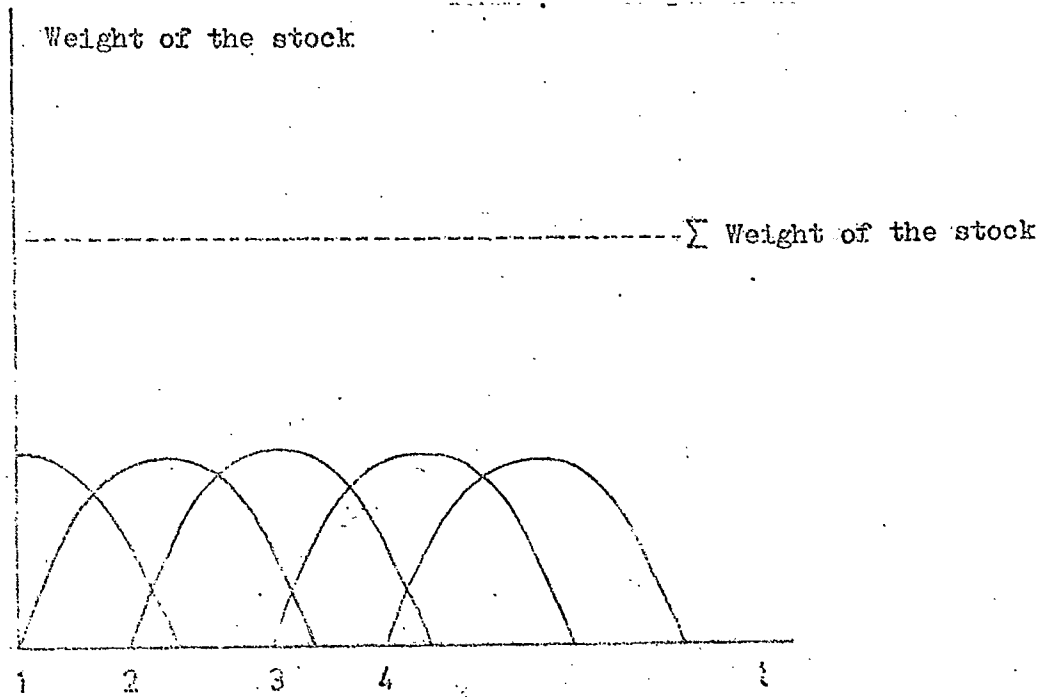


Figure 3 - Steady state of guppy stock after twenty generations

stock had reached a steady state, i.e. constant recruit levels and constant loss rates ensured the maintenance of both the age structure and biomass at a constant level.

Starting during week 40, two of the four aquaria were subjected to "exploitation by fishing" at intervals of three weeks; the juvenile individuals—as is done in the case of deep-sea fishing—were spared during these "actions". The fishing intensities, in that order, were 10, 25, 50, and 75 per cent, respectively; each higher fishing intensity was instituted always after the stock had regained its steady state. The following results were obtained in that experiment:

1. Individual growth was greater in the exploited stocks than in the unexploited ones.

2. The average age of the stocks was greatly lowered by the increased mortality due to capture (always involving the older individuals) and, perhaps, also due to the decrease of cannibalism.

3. The size of the stocks decreased with increasing fishing. At exploitation by fishing of 10 per cent, the stock decreased by about one third; at 25 per cent, by more than one half; and at 50 per cent, the stock exhibited only 20 per cent of its initial size. Fishing at the 75 per cent level led to the extermination of the stock within 21 weeks (corresponding to seven generations).

4. The following aspect is of particular importance in connection with our considerations regarding optimal fishing: Due to the above mentioned growth increase and the rejuvenation of the stock, productivity of that stock reached a maximum value with exploitation, which was situated at a fishing intensity somewhere between 25 and 50 per cent. The weight of the stock (its biomass) at that point amounted to only about one third of the initial weight (biomass) as is shown in Figure 4.

These results permit a preliminary definition of optimal fishing: The yield curve reaches a maximum at a point between exploitation at a level too low and exploitation at a level too high in intensity. Continued maintenance of maximal yields requires that recruit number, growth and losses are maintained at fairly constant levels (steady state).

The following possibilities are given for influencing the position of the steady state and, thus, for obtaining the optimal yield: Changing the minimum age of the individuals at the time of capture by modifying the mesh size, and changing fishing intensity.

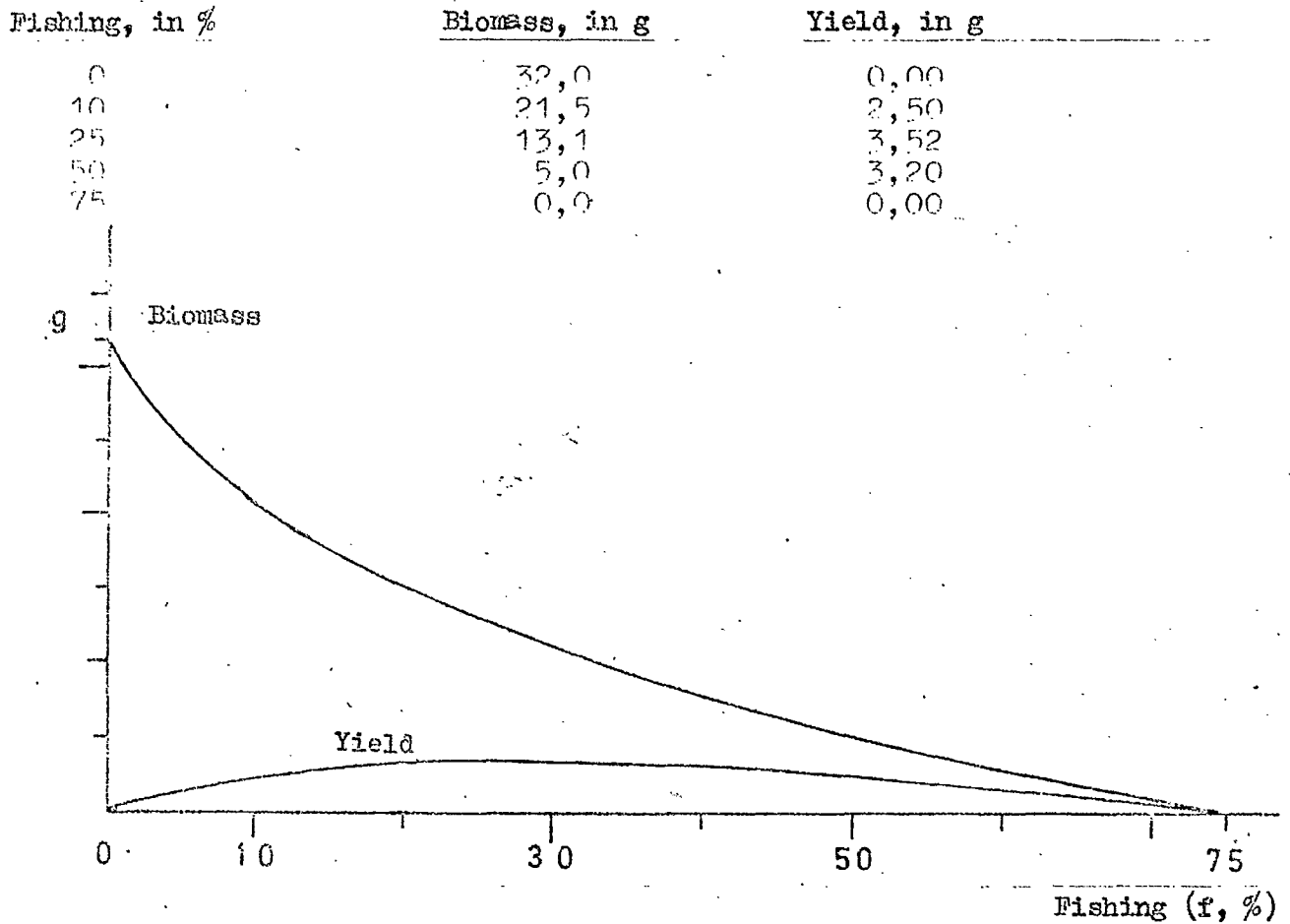


Figure 4 - Dependence of biomass and of yield upon fishing

1.2.2. The sigmoid curve (Robertson, after Bückmann, 1963; Schaefer, 1954; 1957)

The growth of a human population was demonstrated by Verhulst (1845) in the form of a sigmoid or S-shaped curve. Hjort and Ottestadt (1933) have adapted that model for use in fish population dynamics.

When an empty biotope is populated, we find that the population (or the stock) first grows in a logarithmic manner. However, starting at a certain point, the weight of the population will approximate a final

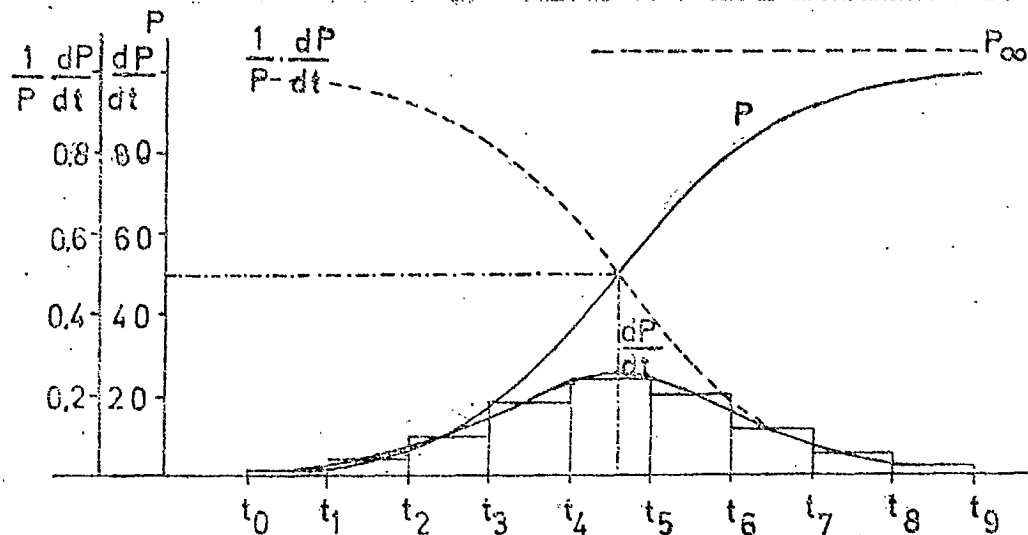


Figure 5 - Sigmoid curve. Representation of Robertson's function of Stock weight. After Bückmann, 1963.

value (P_{∞}) in an asymptotic manner. The sigmoid curve is shown in Figure 5.

The growth curve indicates the weight of a given population—excluding the effects of exploitation by fishing—at any point in time. The first derivation $\frac{dP}{dt}$ of that function gives us the rate of growth of the population in question. Population (or stock) growth is at maximum when the weight of that population amounts to one half of the maximum weight. It then follows that an optimal situation exists for exploitation by fishing when (1) exploitation is started at the point of "inflection" of the sigmoid curve (where exponential growth turns into logistic growth), (2) the stock is maintained at one half of its maximum weight, and (3) the excess stock is captured by fishing.

Growth $\frac{dP}{dt} = G \cdot P$. P is approximately constant during the log phase. G is the measure for the rate of growth.

According to the Robertson model, optimal fishing is given when . 11 .
the increase in growth at half maximal stock weight is continuously being removed by fishing.

Despite the extensions undertaken by Schaefer (1954; 1957), who added fishing intensity as a term to the Robertson model, we find that this model does not fully reflect the growth of a given stock, since changes in the minimum age of the fish at the time of capture as well as changes due to age composition (due, for instance, to changes in recruitment) are not incorporated into that formulation.

1.2.3. The yield isopleth diagram

Beverton and Holt (1957) have derived a yield equation, into which they have incorporated the parameters missing from the model constructed by Robertson and modified by Schaefer.

The correlations existing between fishing intensity, minimum age at the time of capture (t_c) and yield in unit of weight (Y) can be represented in graphic form in the isopleth diagram, in which the lines of equal yield are plotted for the two variables f and t_c . The isopleth diagram is constructed on the basis of calculations performed using the yield equation (Equation 10, further below). The curve AA' (the eumetric curve) in the isopleth diagram indicates the fishing intensity that must be applied in order to obtain a certain yield at lowest t_c (corresponding to the mesh size of the nets employed).

The eumetric curve BB' indicates the mesh size (corresponding, in turn, to the minimum age at the time of capture, t_c) that must be

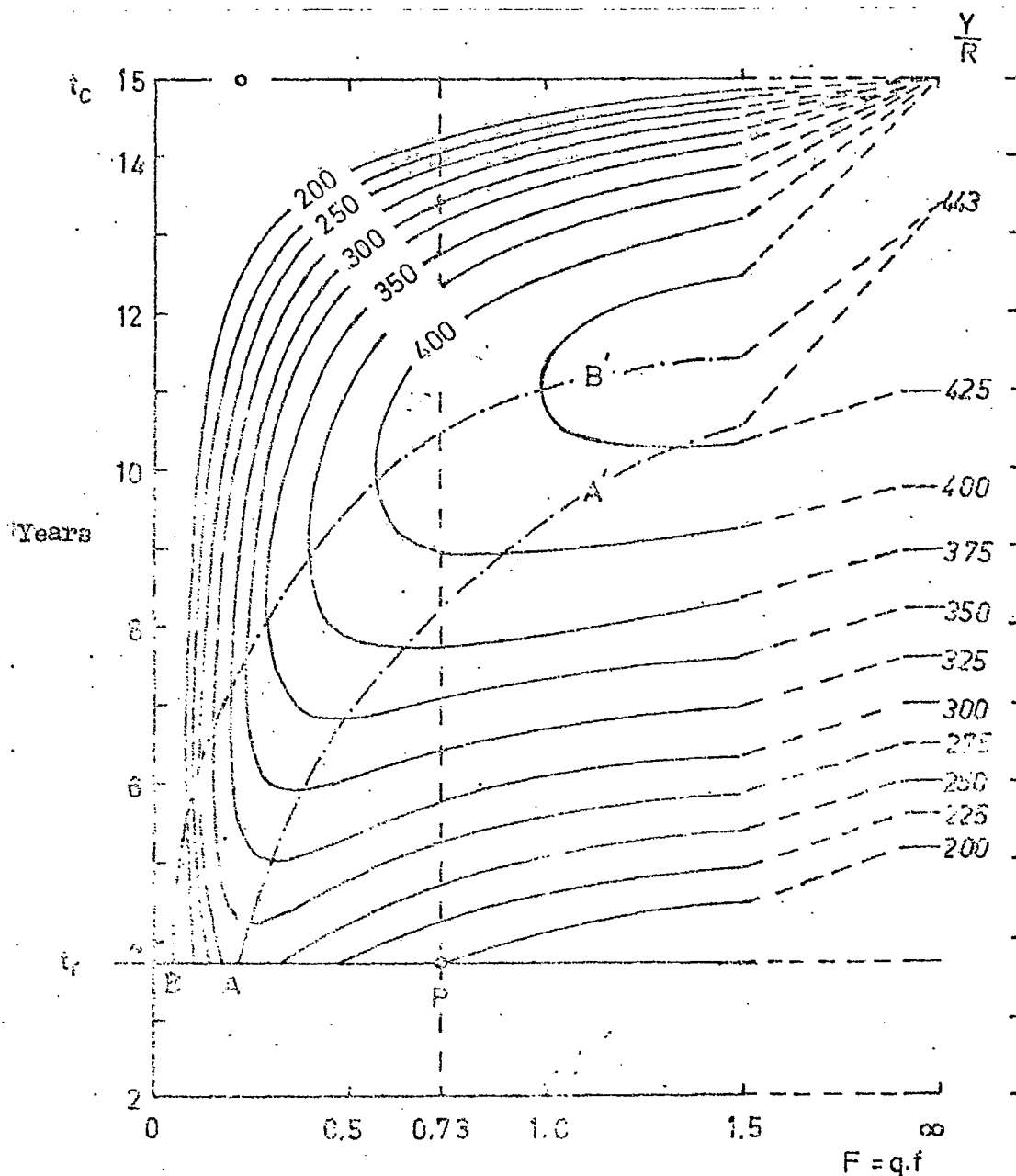


Figure 6 - Yield isopleth diagram of plaice. Yield in unit of weight per recruit as a function of fishing intensity and minimum age at time of capture.

Abscissa: Exponential coefficient of capture (mortality due to fishing), F . That coefficient contains fishing intensity in the following form: $F = q \cdot f$.

Ordinate: Minimum age at time of capture, t_c . The recruitment age of plaice, t_r , is 3.72 years, at a mesh size of 70 mm.

The numbers on the individual isopleths indicate the yield per recruit in gram. P represents the value pair for the decade 1929 - 1938. The upper and the left borders of the diagrams represent the zero line of Y/R .

employed in order to obtain a certain yield at minimal effort. This means that at this point the yield is obtained at the lowest financial expenditure.

Point P indicates the pre-war (i.e. pre-World War II) values for the North Sea plaice population for f and t_c . We will obtain the highest yield at this f if we enlarge the mesh size in a manner bringing about that the minimum age at the time of capture will be 10.5 years. The yield obtained decreases again with further increase of mesh size. We, then, realize that underfishing is indicated above the eumetric curve, and overfishing, below that curve. This particular diagram (Figure 6) thus demonstrates that pre-war fishing in that particular plaice stock was situated far in the region of overfishing. When we go ahead and proceed on along the eumetric curve in order to increase the yield, we must adjust both fishing effort and mesh size in a correlated manner.

The theoretically maximal yield along the eumetric curve is reached at an infinitely high fishing effort. Since the eumetric curve does not exhibit a maximum, we must, when defining optimal fishing, also take into consideration economical aspects in addition to minimum age at the time of capture and fishing intensity.

Optimal fishing then is given when mesh size and fishing effort are combined in a manner bringing about that the resulting yield is situated on the eumetric curve at the point where that yield is associated with the maximum economic profit.

In order to arrive at a table containing the values indicated in the yield isopleth diagram, Beverton and Holt (1957) have derived the

yield equation, which reflects the yield in units of weight of one year class in the exploited phase. The following parameters are incorporated into that equation:

- Z = the exponential coefficient of overall mortality;
- F = the exponential coefficient of mortality due to capture;
- K = the metabolic constant of the growth equation (Bertalanffy, 1934; 1938), $K = k/3$;
- W_{∞} = the maximum mean weight of the fish;
- w = the weight of one individual;
- t_0 = the theoretical value for the start of growth;
- t_c = the minimum age at the time of capture;
- t_m = the maximum age; and
- R^1 = the number of recruits present at time t_c .

In addition, the dependent variables N = the number of individuals in the population, and Y = weight of the yield, and the independent variable t are incorporated into the growth equation.

The following parameters are regarded as being constant in that equation: Z , F , M , K , W_{∞} , t_0 , t_c , t_m , and R^1 .

The biomass of a given stock is estimated using the following equation:

Equation 11

where n and U are parameters that have been incorporated because of the summation formula; they possess no analytical importance. The yield is that share of the biomass that is removed by fishing.

The yield in units of weight of a given year class during the time interval between t_c and t_m is given by the yield equation:

Equation 12

The yield isopleth diagram is constructed with the aid of that growth equation, and optimal fishing is indicated when the plots are situated on the eumetric curve of that diagram.

2. Determination of parameters

. 14 .

The parameters required for the yield equation can be assigned to the primary factors (cf. Figure 1) recruits, growth, and losses. The minimum age at the time of capture and the maximum age are summarized within the concept of "life span".

2.1. Material

In order to assign numerical values to our parameters, we must know:

- Population (or stock or tribe) density;
- Fishing effort;
- Age structure of the population in question;
- Length distribution; and
- Weight distribution.

2.1.1. Sampling

The material required for studies can be obtained by taking samples from landings or by capturing individuals for the purpose of research.

A. Landings: In general, we are unable to examine the entire material landed, i.e. we are forced to take random samples. The following aspects must be taken into consideration during sampling:

All individuals of the stock investigated should have the same chance to appear in the sample. Subjective selection during sampling must be avoided.

That can be done either by taking numerous samples or by using the method of random sampling; in the latter case, subjective selection is excluded with the aid of statistical methods (random tables, Fischer, 1948). Inhomogeneities in the stock with respect to both space and time must be taken into consideration.

Two possible sources of systematic error (bias) must be considered:

1. During the study of landed fish, we must inquire whether these fish have been caught at a single or at several fishing sites. Samples caught at a single site are not representative for a given stock.

2. The fishing method employed in each case involves selection. Due to processing on board of the fishing vessel, it is possible that certain groups are lost for scientific study. Observations on board regarding processing measures will yield an estimated value for that error, which, in consequence of that observation, is greatly reduced.

B. Research captures: Voyages to the fishing grounds for the purpose of capturing fish for study permit adequate sampling and avoid many sources of error, but they only rarely yield adequate bodies of data. Use of fine-mesh nets abolishes the greater selection of commercial

fishing. Furthermore, fishing grounds can be worked during such voyages, which are not used by commercial fishermen.

2.1.2. Measurement series

Measurement series provide indications on stock structure with respect to particular characters. Arrangement of data from such series, however, requires that one definite method is used and described in detail, so that the values obtained will be reproducible and comparable.

The standard measures of length employed in fisheries are:
Standard length, fork length, and total length.

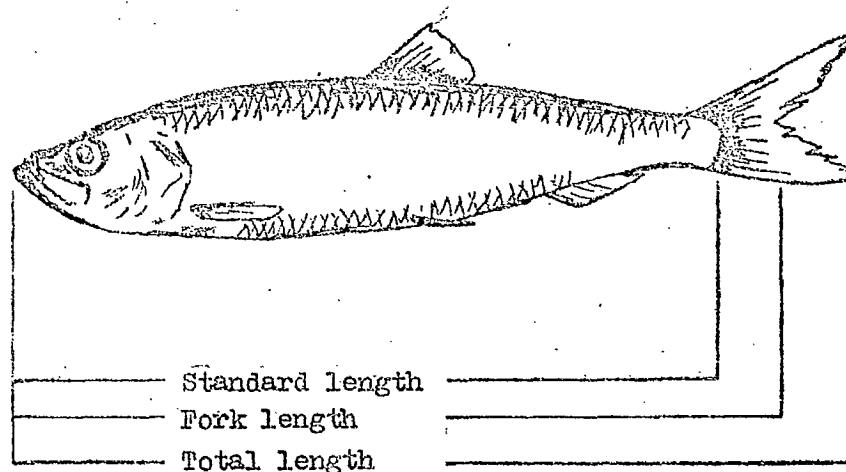


Figure 7 - Schematic representation of measures of length employed in fisheries biology

More detailed outlines on length measurements may be found, among others, in Rückmann (1929), in the FAO Manual prepared by Laevastu (1965), and in Kändler (1968).

Weight measurements can be performed only with difficulty on board of fishing vessels at sea, since scales do not work in a reliable manner during rough seas. We distinguish between the following weights:

- w_f , fresh weight (f = fresh),
- w_g , gutted weight (g = gutted),
- w_h , head-off weight (h = head off), and
- w_{fi} fillet weight (fi = fillet).

In this connection, we again refer the reader to the literature mentioned above.

2.1.3. Age composition

. 16 .

The age composition of a given population or a given stock can be determined, in some species, on the basis of length distribution within a given catch and, otherwise, on the basis of the structure of the solid tissues (otoliths, scales, and bones). These solid tissues are formed in the course of different growth stages during the summer and winter, respectively. This method, however, is difficult to use.

in tropical and subtropical areas. The Peterson method of analysing length distribution is more promising in the latter areas, and this, in particular, in species having sharply delimited spawning periods. In the latter case, we find that the extreme values will appear at regular time intervals. According to recent convention, the first day of January is regarded as the day of birth in the case of many species, since growth is either arrested or inhibited during the winter months.

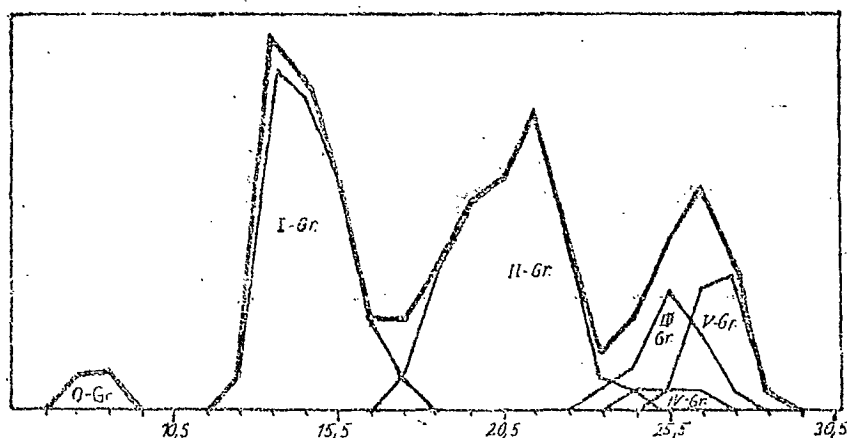


Figure 8 - Example for age determination after Petersen's statistical method. After Bückmann, 1929.

2.1.4. Yields

In cases where we wish to draw conclusions regarding the nature of catches on the basis of landings, we must remember that losses occur on board of the vessels during both sorting and packing.

The following shares of the catch are not included in the statistics kept at the deep-sea fish markets:

- a) Undersized fish thrown back into the sea;
- b) Fish sold directly by the fishermen to buyers;
- c) Fish caught by sports-fishermen;
- d) Fish processed into fish-meal, and fish used as bait; and
- e) Slaughtering offall.

The data appearing in the landing statistics under "processed fish" must be recalculated for fresh weight. That is the case, for instance, with fillet, head-off, and gutted fish. We, furthermore, must analyse the statistical categories, like herring I, II, III, etc. when considering yields. The yields obtained in different stocks (or tribes)

must be considered individually. It is furthermore possible that age group divisions differ from one landing site to the next one.

2.1.5. Fishing activities and the catch per unit of effort

The complex "fishing activities" encompasses three concepts requiring definition: Fishing effort, fishing intensity, and the catch per unit of effort.

Fishing effort

Fishing effort (g) is the effective duration of use of fishing gear and tackle. The level of fishing effort, g , depends on the number, the kind, and the time of operation during the year. We, therefore, have available different possibilities for measuring fishing effort. We can use as the unit of measure, for instance, standard trawling hours per year. Proceeding in that way, we must compute the effort of each vessel in order to arrive at comparable efforts put forward by different vessels; the effort of the individual vessel is measured against the effort put forward by an arbitrarily selected "standard ship". Individual computation is required because the catch capacity of individual ships can vary to a great extent (depending on the size of the nets, engine power, etc.)

Fishing intensity

Fishing intensity (f) is the fishing effort expended per given area

In connection with that formulation we assume uniform distribution of the individuals. It then follows that fishing intensity is proportional to the mortality due to capture:

17-2

The coefficient of catchable fish, q , has been introduced as a proportionality factor:

17 - 3

The coefficient q is determined on the basis of mark and recapture experiments (Section 2.6.2.).

However, since fish are distributed in a non-uniform manner over the large area, A , we subdivide A into sub-areas. Overall fishing intensity is calculated on the basis of the weighted total of individual intensities applied over the various sub-areas:

The catch per unit of effort

. 18 .

The catch per unit of fishing effort (C.P.U.E.), g , is expressed by the following formulation:

$$\text{Catch per unit of effort} = \frac{c}{g} = \frac{c}{fA}.$$

The catch per unit of effort represents a relative reflection of stock density. In the determination of catches per unit of effort, we

must take into consideration, above all, the power factor, since the catch capacity of individual vessels differs to a great extent. The catches per unit of effort are affected also by the different distribution of the fish during the different seasons of the year. These differences in distribution are caused, among others, by: Migration to the spawning grounds, food supply, oxygen content of the water, temperature differences, and currents. These factors together affect the overall behavior of the fish.

The power factor (PF) has been introduced in order to enable workers to compare the different catch capacities of individual fishing vessels. We assign the $PF_u = 1$ to the fishing vessel u, which has caught 100 fishes per unit of effort. The fishing vessel v has caught 80 fishes under the same conditions:

$$PF_v = \frac{80}{100} = 0.8 PF_u$$

The power factor $PF = 1$ is assigned to the fishing vessel, which has yielded the greatest number of values capable of comparison with other fishing vessels. This means that this particular vessel must have fished together with as many other fishing vessels as possible on a given fishing ground. The power factor is valid always only for the stock for which it has been determined.

Once the power factor has been determined for a series of vessels, we can go ahead and correlate that value with known vessel characteristics, like G.R.T. and H.P. In this way, we are then able to read the PF for any vessel. One example would be the linear dependence between power factor and tonnage derived by Beverton and Holt (1957) and shown in Figure 9.

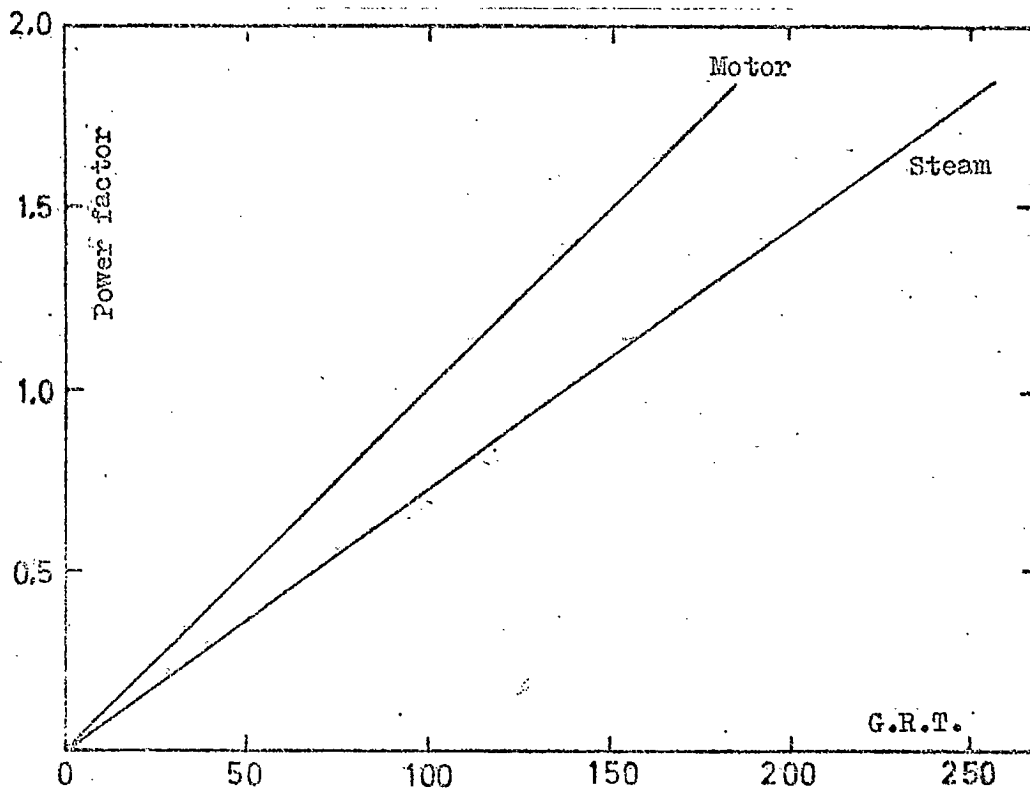


Figure 9 - Power factor in dependence upon tonnage. After Beverton and Holt, 1957

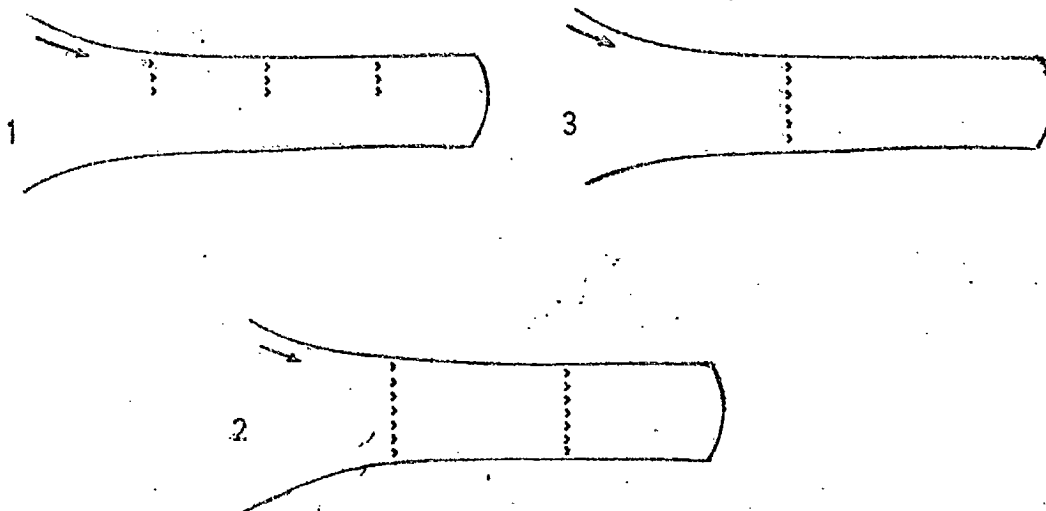


Figure 10 - Example for interactive fishing. After Beverton and Holt, 1957. Sketches 1 and 2: Interactive setting of nets. Sketch 3: Non-interactive setting of nets. → The direction preferred by fish for migrating.

We speak of heterogenous fishing in cases where a given stock is subjected to fishing using different fishing methods. In practice, we must start on the basis of yields obtained with the aid of different types of fishing gear when determining stock densities. When we then obtain the catches per unit of effort using different gear, we are given the possibility to test our respective results. The terms g and f are calculated only for one type of fishing gear.

$$\frac{\text{Total yield}}{\text{Catch per unit of effort of trawling}} = \left[\begin{array}{l} \text{Trawling} \\ \text{standard hour} \end{array} \right] = \sum g.$$

The standard trawling hour represents the hours that are required to make a certain catch in a given area while fishing only with the standard trawling net. In the determination of both the catch per unit of effort and fishing intensity, we find that factors like gear saturation, interactive fishing, and density dependence of effort play important roles.

Interactive fishing is given in cases, where, because of their particular arrangement, not all nets have the same chance to retain the same quantity of fish. This type of fishing is seen, for instance, when nets are arranged along a coast in a direction paralleling the preferred migration route of a given fish species, and the last nets, therefore, will in the end contain less fish than the ones set up in front (Figure 10).

2.2. Estimating average recruit numbers after Beverton and Holt

. 20 .

In order to estimate average recruit numbers, we must know certain parameters (t_0 , K , W , t_c , F , and M). Using equation (12) (cf. Section 3.3.) we are able to calculate Y by means of R' . On the other hand, we

can obtain R' by dividing Y (determined on the basis of fish landing data) by Y/R' . The error in that method is due to inaccuracies in the landing statistics. Additional possibilities for estimating recruitment are given by determining egg numbers and by catching larvae.

2.3. Life span

The life span of individual fish can be subdivided as shown in the following diagram:

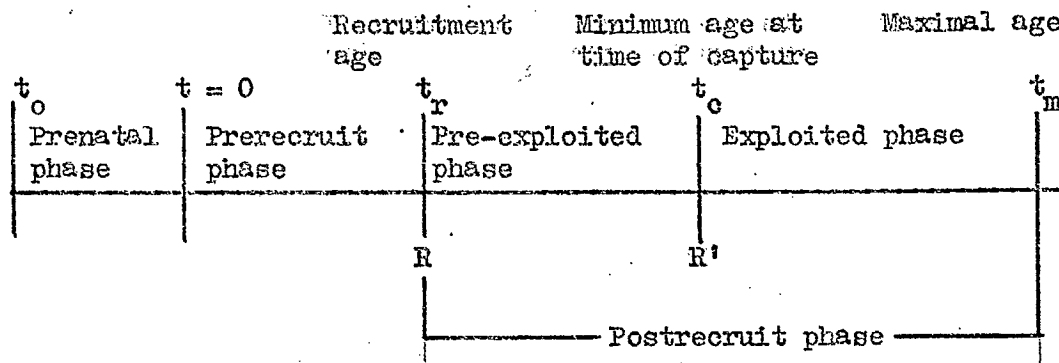


Figure 14 - Life span of individual fish

The symbols used in this diagram stand for:

- t_0 to $t = 0$ the prenatal (embryonal) phase
- t_0 the prenatal age; the theoretical value for $L = 0$ and $W = 0$, representing the probable time of egg fertilization
- $t = 0$ the time of hatching
- $t = 0$ to t_r the prerecruit phase
- t_r to t_c the pre-exploited phase; the recruits are already present in the exploited area but, because of their small size, are as yet not subjected to fishing
- t_c the mean minimum age at the time of capture
- t_m the mean maximum age; the end of the exploited phase

The exploited phase only is considered when we make use of the variable t , i.e. t is situated somewhere between t_c and t_m :

$$t_c \leq t \leq t_m$$

R represents the number of recruits having reached age t_r
 R' represents the number of recruits having reached age t_c .

. 22 .

Transition from the pre-recruit phase to the pre-exploited phase and from the latter on to the exploited phase, of course, does not take place at the same moment in all individuals. However, in mathematical determinations we make calculations using mean or average values:

The moment t_r has been reached when 50 per cent of the recruits have immigrated into the exploited area; the moment t_c has been reached when 50 per cent of the recruits have reached the minimum age for capture. "Knife-edge selection" can occur in nature when the recruits immigrate into the exploited area only after they have reached age t_c .

2.3.1. Recruiting age

Determination of the recruiting age is necessary in cases where t_r and t_c are situated close together, so that selection has started already before recruitment. Estimation of the recruiting age can be carried out in the course of great numbers of investigational catches at great numbers of stations when close-meshed nets are used. Commercial nets are not suited for that purpose because of their large mesh size.

Determination of recruiting age given recruitment from several age groups

In cases where recruitment of a given year class encompasses several years, it is evident that the individuals belonging to the

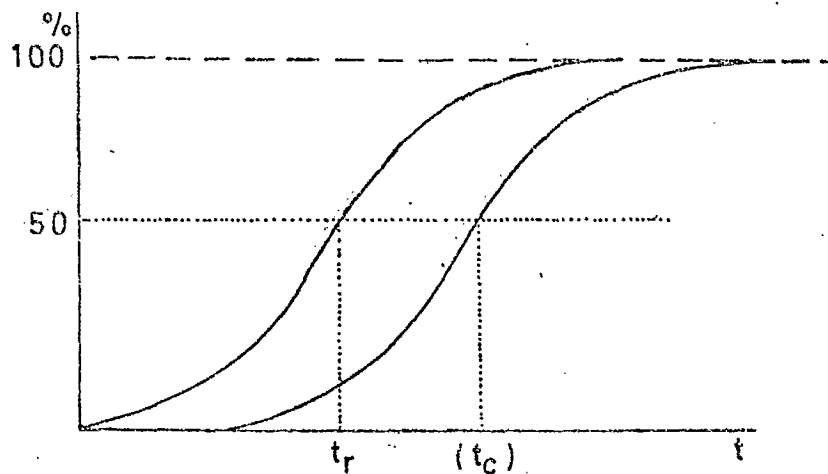


Figure 15 -- Recruitment curve showing both immigration of recruits into the exploited area and reaching of the minimum age for capture

different age groups will exhibit intervals of natural mortality that differ in length. We can construct a recruitment curve for each recruitment year of that year class. Following conclusion of recruitment involving several years, we determine the frequency percentage curves for the age groups from the recruitment curves. Once we then have calculated—separately for each age group—the number of recruits present after conclusion of recruitment, we are in a position to determine the 50-per-cent value of overall recruitment with the aid of these values and using the weighted-average method.

. 23 .

The mean recruiting age for overall recruitment is calculated on the basis of the mean recruiting age of the individual years and the corresponding recruit numbers, again using the method of the weighted average.

The number of recruits surviving following conclusion of recruitment can be determined with the aid of the following equation involving the parameters:

$\bar{N}$: mean year class strength to be determined as density from unit catch

Θ_g : age group 0 of a given year class

Θ_{g+1} : age group 1 of that year class recruiting one year later

θ_g^t : recruiting age of age group 0

$$R = \frac{\Theta_{g+r} \bar{N}_{x+r} \cdot (F+M) \cdot e^{-(F+M)\Theta_{g+r}} \cdot \left(1 - e^{-(F+M)}\right) \sum_{n=0}^{n-1} n R \cdot e^{(F+M)n} \theta_g^t}{1 - e^{-(F+M)} (\Theta_{g+r+1} - \theta_g^t)}$$

22

2.3.2. Minimum age at the time of capture, and selection

The minimum age at the time of capture is determined with the aid of the selection curve applicable to the particular fishing gear used. It is assumed in this connection that the stock in the selection area is fully recruited, since the selection curve otherwise reflects only a part of the recruits excluding the part still existing outside of the exploited area. In cases of incomplete recruitment, we therefore require both the recruitment and the selection curves, which then give us the resulting selection with the average minimum age at the time of capture.

Selection represents the percentage of length groups of fish captured among the length groups present in the area subjected to exploitation by fishing. Selection covers only the individuals already recruited.

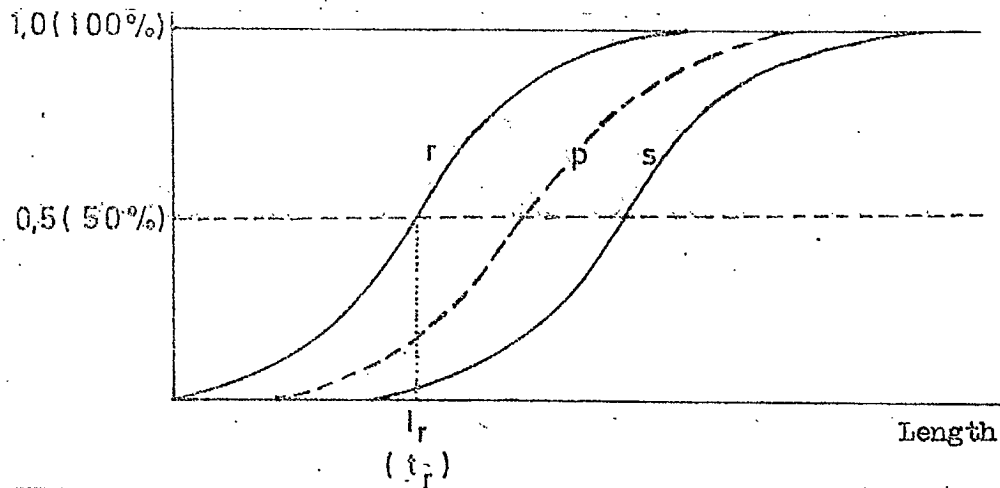


Figure 16 -- Selection curve. The recruitment curve, r ; the selection curve, s ; and the resulting selection, p . After Gulland, 1969.

Both recruitment and selection curves represent summation curves, . 24 . which indicate the shares of individuals recruited or captured, respectively, up to moment t ($=$ body length). The position of the selection curves, of course, is determined by net mesh size. In cases where the foot of the curve is situated to the right of the point indicating 100 per cent recruitment, we are dealing with a situation where fishing is performed in a fully recruited stock; in cases where the foot of that curve is situated still within the range of the recruitment curve, we are dealing with a situation where fishing is carried out only in the part of the stock already recruited (which is as yet not fully recruited).

In cases where recruitment and selection overlap, we calculate the resulting selection using the equation

$$P = r \cdot s.$$

Table 1 - Example for $P = r \cdot s$

Length	Frequency distribution of recruitment	Selection	Resulting selection
cm	r	s	$P = r \cdot s$
11	0,0	0,0	0,0
12	0,1	0,5	0,05
13	0,5	0,8	0,40
14	0,9	0,95	0,86
15	1,0	1,00	1,00

The value of t_c is determined with the aid of P. The selection curve, s, must be constructed for each type of fishing gear and tackle.

Gear selection has been studied chiefly in the case of trawling nets: The upper side of the cod end has a predominantly selective action. Three methods are used:

1. Two fishing vessels of equal catch capacity trawl the commercial net to be tested and the quantitatively catching close-mesh test net over the same fishing ground at the same time.

2. One fishing trawler moves the nets to be compared in turn. In this instance, too, the conditions are: The same are must be covered, and this at approximately the same time.

3. A close-mesh net is permitted to float behind and around the cod end being tested.

In all three methods, the worker must measure the mesh size after each catch and evaluate the catch in a quantitative manner. The values obtained during the individual catches are presented as weighted mean. The selection factor of a given net is calculated as follows:

$$\text{Selection factor} = \frac{50\% \text{ retention length}}{\text{mesh size}}$$

2.3.3. Maximum age

Determination of the maximum age, t_m , on the basis of the age of the oldest specimens present in a given catch is not permitted, because we know that these specimens are better able to escape and, therefore, are under-represented in the catch. Beverton and Holt (1957), for that reason, have recommended to insert a preliminary--assumed--value into the yield equation. In cases where the yield curves for different assumed t_m values are situated closely together, we fix t_m arbitrarily in a manner ensuring that the yield curve is not affected within the determinant regions.

. 25 .

2.4. Growth

Increase of stock biomass is due to increases in both length and weight of the individual stock members. This growth has been determined by mathematical means by Bertalanffy (1934), Ford (1934), and Walford (1933; 1946), among other authors. According to Bertalanffy, length l_t at time t represents a fraction of the final maximum length l_{∞} .

$$l_t = l_{\infty} (1 - e^{-K(t - t_0)})$$

7

Since increase in weight takes place approximately with the cube of length ($l_{\infty}^3 \hat{=} W_{\infty}$), growth with respect to weight can be expressed by the following formulation:

$$w_t = w_{\infty} (1 - e^{-K(t - t_0)})^3$$

8

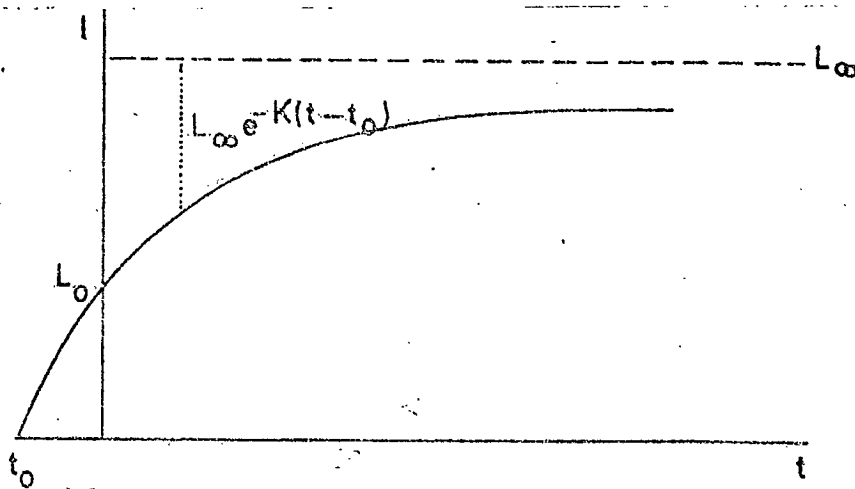


Figure 17 - Longitudinal growth after Bertalanffy's function

Increase in growth is represented by a curve corresponding to that plotted in Figure 17. K is the so-called metabolic constant (cf. Section 2.4.1.).

The Ford-Walford equation has been developed in an empirical manner following studies in the herring.

$$l_{t+1} = a + b l_t$$

10

That equation represents a straight line having its origin at "a" for $t = 0$, and the slope "b"; however, that equation describes growth in an inadequate manner at the beginning and at the end of the life span.

2.4.1. The metabolic coefficient K

K characterizes the extent of energy utilization during maintenance metabolism, that utilization being related to the final state. In population-dynamic calculations, K is assumed to be both species-specific

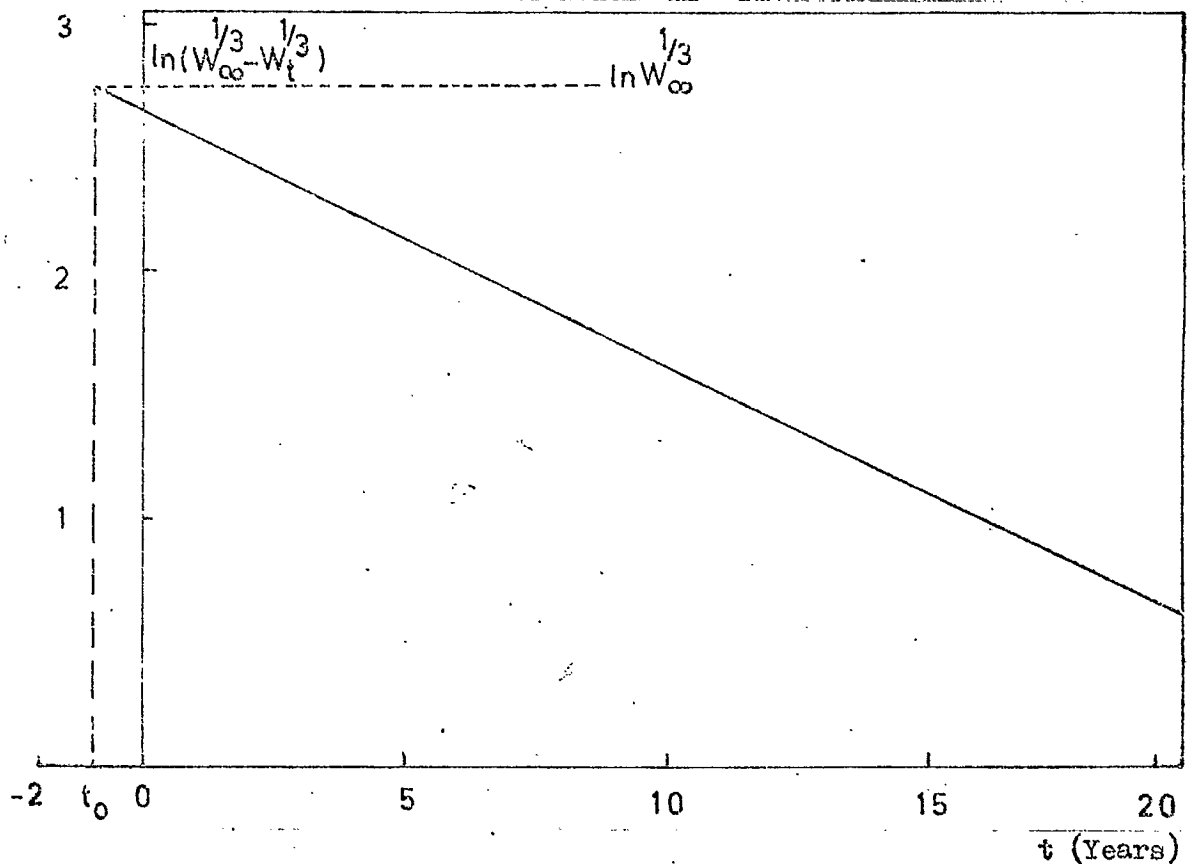


Figure 18 - Graphical determination of constants K and t_0 of Bertalanffy's function. After Bückmann.

and constant during the entire life. In the case of intermediate age groups, Beverton and Holt have demonstrated agreement between the actual and the calculated values in halibut, sole, and haddock; agreement, however, does not exist in the cases of juvenile and old groups. K , furthermore, is affected by ecological conditions like temperature, for instance. In cases of food deficiency, we find however that only W_{∞} is changed, while K remains constant. That fact has been demonstrated by Bertalanffy (1934).

Determination of K after Beverton and Holt

Using a graphical representation of $\ln \sqrt[3]{\frac{l_{\infty}}{l_t}} - \sqrt[3]{\frac{l_{\infty}}{l_t}}$,

K can be determined at t as the slope of the curve. That diagram (Figure 18), at the same time, provides a value for t_0 .

If we claim that the equations derived by Bertalanffy and by Ford-Walford, respectively, are identical (as suggested by Hohendorf, 1966), we are able to calculate the metabolic coefficient K in the following manner:

$$\ln \frac{1}{b} = K.$$

The constant b is determined with the aid of the regression technique using the Ford-Waldorf equation (cf. Section 3.2.).

2.4.2. Mean maximum length

. 27 .

The point where the course of the growth curve becomes asymptotic in character indicates the fact that the fish has reached its final length. Since the rate of growth decreases in a steady manner, we find with increasing t that the values l_t and l_{t+1} approximate the value of l_{∞} .

27-1

The length l_{∞} is obtained by projection of the point of intersection of the straight line $l_t = l_{t+1}$ with the straight line $l_{t+1} = a + b l_t$ after Ford and Walford, since we should also be able to obtain l_{∞} using the general growth equation. When we regard the growth equations

of Ford and Walford and that of Bertalanffy as being identical (cf. Section 2.4.1.), it follows that

27-2

2.4.3. Prenatal age t_0

The "prenatal age" represents a theoretical value for $l = 0$ and $w = 0$. Since the fish at the moment of hatching, $t = 0$, exhibits already a certain length as well as a certain weight, it follows that t_0 should have a negative sign.

The method for determining t_0 by graphic means has already been presented further above in Section 2.4.1. That diagram corresponds to the representation $\ln (I_{\infty} - l_t)$ at t . We are also able to calculate t_0 on the basis of the assumed identity of the different growth equations of the aforementioned authors, since we can rearrange the Bertalanffy equation in the following manner:

27-3

That equation corresponds to the form $y = c - d x$. The two constants c and d can be calculated with the aid of the regression technique using the series for the value pairs $\ln (I_{\infty} - l_t)$ and t . Since $d = K$, it follows:

27 - 4

2.5. Total losses

Fish population science must develop models for both the rate of increase of a given stock and the rate of subtraction due to death and capture. The subtracting processes are characterized by losses due to fishing activities, on the one hand, and to natural causes, on the other one; together, these losses are defined as the "total loss". We In order to recognize fluctuations, we must attempt to observe the age groups of a given year class in an individual manner. Determination of the parameters involved must be carried out using different and, if possible, independent methods in order to obtain indications regarding the accuracy of estimations.

The following methods can be used for determining total losses: . 28 .

- a) Calculations involving year class sizes;
- b) Calculations involving both average age and average length;
- c) Calculations involving the relative age composition; and
- d) Calculations involving the virtual population.

2.5.1. Calculation of total losses according to year class sizes

The catches per unit of effort (weight) are used as the measure of stock size determined at yearly intervals. The shares of the year classes are obtained on the basis of age determinations. In cases where the catch per unit of effort is available as weight, we are forced to perform recalculations.

Table 2 - An example, where catch per unit of effort $(c/g)_x = 170$ kg, and $(c/g)_{x+1} = 150$ kg.

Year x	Age class				Σ
	0	A	B	C	
Numbers, in %	<u>20</u>	<u>70</u>	<u>10</u>		100
Mean weight, in kg	<u>3</u>	<u>2</u>	<u>1</u>		
Weight, in kg	60	140	10		210
Σ numbers	16,2	56,7	8,1		81,0
Year x + 1					
Numbers, in %		<u>15</u>	<u>80</u>	<u>5</u>	100
Mean weight, in kg		<u>3</u>	<u>2</u>	<u>1</u>	
Weight, in kg		45	160	5	210
Σ numbers		10,7	57,2	3,6	71,5

The values underlined in Table 2 are known from sampling. On the basis of these weight data on the catches (per unit of effort) we arrive at the total number of individuals in the catch being assessed:

210 kg $\hat{=}$ 100 individuals
 170 kg $\hat{=}$ 81 individuals
 150 kg $\hat{=}$ 71.5 individuals

If these values are representative for the year class sizes, we are able to use the following equation:

$$Z_t = \ln \frac{N_0}{N_t}$$

3a

In the case of our example, $t = 1$, since the two samples were obtained at an interval of exactly one year. For Year Class A, we then obtain:

$$Z = \ln \frac{56,7}{10,7} = 1,67$$

In cases where the catches per unit of effort and age composition data, respectively, are available as average values for one year, the equation is written in a general manner as follows:

$$Z \cdot t = \ln \frac{\bar{N}_t}{\bar{N}_{t+1}}$$

This equation can be solved by using either iterative or semigraphical means.

Assuming that Z is equal in all age groups, total loss can be determined by graphical means. The equation:

$$\ln N_t = \ln N_0 - Z \cdot t \quad \text{cf. Equation (3)}$$

corresponds to the equation:

$$y = a - b \cdot x.$$

For the value pairs N_t and t , we calculate the constants a and b of the regression line and obtain for b the slope of the straight line corresponding to Z .

Table 3 - An example. We obtain $b = Z = 0.700$ for the following values:

$\ln \frac{C}{S}$	Age group
3,007	4
4,443	5
4,550	6
4,589	7
3,569	8
2,962	9
2,234	10
1,842	11
0,820	12+
21,423	63

We consider only age groups 6 to 12+, since the younger groups are as yet not completely retained in the nets. Recalculation into percentage values gives for Z:

$$Z = 0,700$$

$$Z(\%) = 100 (1 - e^{-Zt}) = 100 (1 - e^{-0,7 \cdot 1}) = 100 \cdot 0,503$$

$$Z(\%) = 50,3 \%$$

The annual losses, thus, amounted to 50.3% in each age group.

2.5.2. Calculation of total losses according to average age or length

. 30 .

Gulland (1969) has presented the following equation for Z using the average age (t), the average length (l), the final length (L_{∞}), the metabolic constant K, as well as the minimum age at time of capture (t_c):

30-1

The following example may serve as illustration (cod from the western Baltic Sea; average values for 1956 - 1962):

30-2

2.5.3. Determination of overall mortality on the basis of relative age composition after Lea

Lea (1929) based his calculations of overall mortality on the relative composition of spawning stocks of Norwegian spring herring, which he studied during several successive years. In these calculations, Lea compared the relative numbers of a certain year class during two consecutive years and, thus, obtained the survival rate of that particular age group during the period of time considered by him. Let a_7 and b_8 represent shares within the total catch of one and the same year class, which year class was seven years old during year "a", and eight years old during year "b" (the following year). A and B represent the numerical year class sizes in the years "a" and "b"; the survival rate then is:

30-3

The relation

$$S = 1 - Z$$

exists between survival rate S and overall mortality Z .

The unknown quantities A and B are eliminated, when we relate the survival rate of a given age group to the survival rates of a certain age group; for instance:

$$30-4$$

In this manner, we obtain the terms amenable to calculation:

$$30-5a \quad \text{and} \quad 30-5b$$

In cases where the survival rates within a stock change only to a small extent within the exploited age groups, we find that these quotients will yield values close to 1.

. 31 .

2.5.4. The virtual population

Determination of overall mortality can also be performed by using the method of the virtual population. The virtual population represents the share of a given stock made visible by fishing activities. The virtual population, thus, yields only values for the exponential coefficient of capture (i.e. mortality due to fishing activity). In cases where the exponential coefficient of natural mortality is known following employment of other methods, we are able to calculate Z by adding the values for F and M . Determination of F and M is made with the aid of a table on the basis of the virtual population.

Table 4 - Working table (M = 0.20). Excerpt from Schuhmacher, 1970.

F	Z	e^{-Z}	$\frac{F}{F+M} (1 - e^{-Z})$	$r = \frac{e^{-Z}}{\frac{F}{F+M} (1 - e^{-Z})}$
0,01	0,21	0,811	0,009	90,1
0,10	0,30	0,741	0,086	8,62
0,20	0,40	0,670	0,165	4,06
0,30	0,50	0,607	0,236	2,57
0,40	0,60	0,549	0,301	1,82
0,50	0,70	0,497	0,360	1,381
1,00	1,20	0,301	0,582	0,517
1,30	1,50	0,223	0,674	0,331

Schuhmacher (1970) has arranged a working table of that type enabling us to determine mortality due to capture (Table 4). Schuhmacher's table is based on the following equations (cf. also Section 3.9. in this connection):

$$r_n = \frac{e^{-Z_n}}{\frac{F_n}{Z_n} (1 - e^{-Z_n})}$$

36

In this equation, r_n represents the population at the end of the year expressed as a share of the annual catch; however, r_n can also be expressed as a function of the survival rate during the year "n" and the exploitation rate E_{n+1} :

$$r_n = \frac{1}{E_{n+1}} \frac{V_{n+1}}{V_n - V_{n+1}}$$

37

"F" can be read from the table if "r" is known.

2.6. Determination of F and M

In order to establish effective and economically suitable mechanisms of regulation, we must be able to divide overall mortality of a given stock into natural mortality, on the one hand, and mortality due to capture, on the other one. The following methods can be used for determining the exponential coefficients of mortality: Direct enumeration methods, mark and recapture techniques, and determination with the aid of fishing intensity and year class size data.

2.6.1. Direct enumeration

In cases where both the landings C (expressed as numbers of individuals) and the average population size $\bar{N}'$ are known, we are able to calculate mortality due to capture using the following equation (direct census or enumeration):

$$F = \frac{C}{\bar{N}'}$$

When determining the landings C , the worker must take into consideration also the losses occurring during processing of catches on board of the fishing vessels.

The population size $\bar{N}'$ can be estimated using several different methods (cf. Equation 20).

The number of females present can be calculated on the basis of both the egg numbers (integration of catches made using egg nets) and fecundity, and the total population (or stock) number can be estimated on the basis of the sex ratio (Hensen, 1887). In the case of anadromous

migrating fishes we can make counts along passes leading to the spawning sites. The catch per unit of effort, too, permits estimation of stock density.

2.6.2. Mark and recapture techniques

Mark and recapture experiments are performed in order to determine the exponential coefficient of capture (mortality due to fishing), F . These techniques, furthermore, permit determination of both fishing intensity, f , and the coefficient of catchable fish, q . Natural mortality must remain constant during the entire experiment. The exponential coefficient of overall mortality, Z , is composed of the sum of the exponential coefficients of natural mortality and of capture (mortality due to fishing):

$$Z = M + F$$

However, since marking experiments lead to a certain increase in natural losses due to marking-caused death, losses of marks or tags, and unreported recaptures, we must use in our calculations a corrected, i.e. increased value for overall mortality, Z' :

$$Z' = M' + F$$

where $M' = M + \mu$ the exponential coefficient of natural mortality in the marked stock;

μ = the loss due to marking manipulations;

N_0 = the number of marked specimens;

n_1 = the number of specimens recaptured and reported back during time interval T_1 ; and

n_2 = the number of specimens recaptured and reported back during time interval T_2 .

The recapture periods should be of equal duration:

33-1

The following equations can be used for estimating F and M' in cases where the fishing intensity, f , is both constant and equal during the courses of the two recapture periods:

Equation 29

Since N_0 , n_1 , n_2 , and T are measured in the experiment, we are able to determine in a relatively simple manner mortality due to capture, F , apart from natural mortality. Following determination of F , we go ahead and calculate the corrected natural mortality, M' .

Equation 30

. 34 .

In cases where fishing intensity, f , differed during the courses of the two recapture periods, F and M' can be estimated using the following equation:

Equation 32

[Several words appear to be missing in the original; Translator]
The coefficient of catchable fish, q , can be estimated using the following equation in cases where we are dealing with two fishing periods with constant f covering at least one year:

Equation 34

We obtain M by inserting the value for q into the following mathematical formulation:

Equation 35

Mark and recapture experiments are tainted by the following sources of error:

<u>Type of error after Ricker</u>	<u>Error</u>
<u>1.</u> Influences exerted on F	a) Incomplete reports on recaptured individuals at constant rate b) Marking-caused mortality immediately after marking has been carried out
<u>2.</u> Influences exerted	c) Marking-caused steady constant death rate d) Steady constant loss of mark or tag
<u>3.</u> Influences exerted on Z and F	e) The recaptures are not representative since the availability of marked and that of un- marked individuals differ f) The marked and the unmarked individuals are not distributed in an uniform manner

2.6.3. Determination of F and M with the aid of year class sizes and f

According to the established equation¹, $Z = M + qf$. Z is proportional to f in cases where M and q are constant. M and q can be estimated using regression techniques once a series of value pairs of Z and f has been determined.

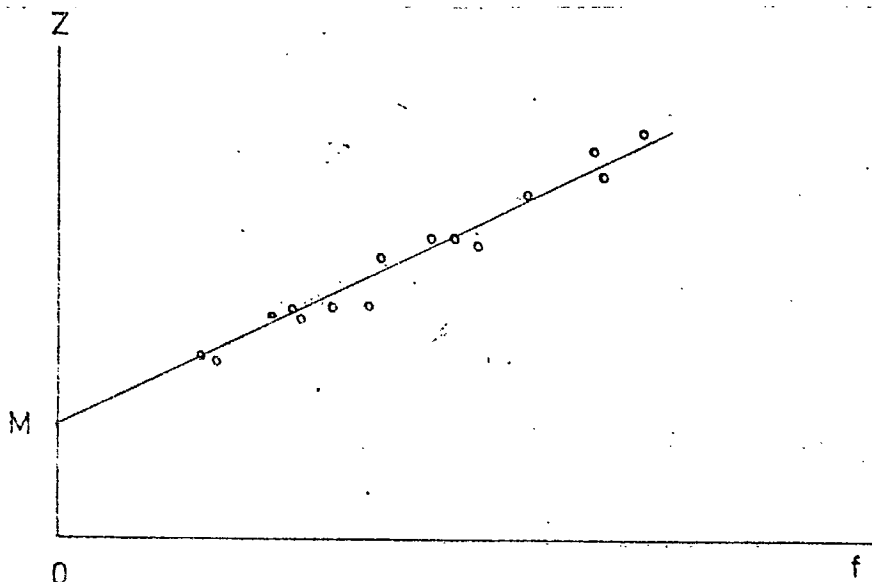


Figure 19 - Overall mortality in dependence upon f. $Z = M$ when $f = 0$. After Beverton and Holt, 1957.

The following linear equation is employed for determining Z and M:

$$Z = qf_x + M = \ln \frac{A \bar{N}_x}{A \bar{N}_{x+1}} + \ln \frac{(qf_{x+1} + M) \left(1 - e^{-(qf_{x+1} + M)} \right)}{(qf_x + M) \left(1 - e^{-(qf_x + M)} \right)}$$

23

In that Equation, both f (the fishing intensity) and $A \bar{N}_x$ or $A \bar{N}_{(x+1)}$ respectively (the catch per unit of effort, c/g) are known;

¹cf. Sections 2.1.5. and 2.6.2.

not known are q and M . Solution of the equation is obtained by iterative approximation after Beverton and Holt. The right additive term is not considering during first approximation. The constants M and q are determined using regression techniques. The values obtained in this manner are inserted into Equation (23), and this manipulation then yields more exact values for Z . With the aid of the latter, we next repeat determination of both M and q , with M and q finally remaining constant after these steps have been repeated several times.

Using the original equation of Beverton and Holt, Paloheimo, in 1961, developed a linear equation permitting determination of both F and M without elaborate iterative approximations.

$$\ln \frac{A \bar{N}_x}{A \bar{N}_{x+1}} = q \cdot \frac{1}{2} (f_x + f_{x+1}) + M$$

The regression constants M and q can be directly determined. The standard deviations of M and q are reduced by 27 to 69 per cent compared with the iterative approximation method. No improvement is obtained only in cases where q is strictly constant.

The natural mortality M can also be determined in cases where fishing has not been carried out over a relatively long period of time. That situation may arise, for instance, following discontinuation of fishing because of war activities or severe ice conditions during the winter. The relative sizes of at least one year class before and after the period of discontinued fishing must be known. The overall mortality Z

--which can be readily estimated in cases like these--equals M , since $F = 0$.

A similar procedure permits estimation of F . Consideration of the overall mortality of one year class during the course of the years of discontinued fishing gives us $Z_1 = M$. When this year class then enters the exploited phase, we are able to determine the increased overall mortality $Z_2 = M + F$. The difference between Z_2 and Z_1 equals F . These results, however, cannot be used without certain criticism, i.e. we must take into consideration the possibility that the juvenile individuals probably are subjected to increased natural mortality and, perhaps, also to an undeterminable increased mortality due to capture, so that F is probably underestimated in calculations of this type.

2.7. The yield isopleth diagram (Application of the yield equation)

. 37 .

Once the individual parameters have been determined, we are in the position to use the yield isopleth diagram for calculation.

Using an equation as complex as the yield equation (12), it is always best to compile first a working sheet in the form of tables.

Beverton and Holt (1957) have prepared a working sheet containing values for British plaice fishing (North Sea plaice).

The following parameters have been given by the latter authors:

M	= 0.10		
t _r	= 3.72 years	t _c - t _o	= 4.535 years
t _c	= 3.72 years	t _c - t _r	= 0.0 years
t _m	= 15 years	t _m - t _c	= 11.28 years
t _o	= -0.815 years		=
W	= 2867.0 g	-M(t _c - t _r)	
K	= 0.095	W e	= 2867.0 g
q	= 0.00892		= (S)

The Tables presented on the following pages are condensed after Beverton and Holt (1957).

Table 5

. 38 .

n	M + nK	U _n	$\dot{U}_n e^{-nK(t_c - t_o)}$
0	0,100	+1	+1,0000 = (T ₀)
1	0,195	-3	-1,9500 = (T ₁)
2	0,290	+3	+1,2675 = (T ₂)
3	0,385	-1	-0,2746 = (T ₃)

Table 6

	(A)	(B ₀)	(C ₀)	(D ₀)	(E ₀)	(F ₀)
n=0	F	(A)+M+nK	(B ₀) λ	1-e ^(C₀)	$\frac{(T_0)(D_0)}{(B_0)}$	$(E_0)(A)=\frac{C}{R}$
	0,00	0,40	1,1280	0,6762	6,7620	0,0000
	0,30	0,40	4,5120	0,9890	2,4725	0,7418
	0,50	0,60	6,7680	0,9989	1,6648	0,8324
	1,00	1,40	> 10	1,0000	0,9091	0,9091
	1,50	1,60	> 10	1,0000	0,6250	0,9375

n=1	(A)	(B ₁)	(C ₁)	(D ₁)	(E ₁)
	0,00	0,195	2,1996	0,8893	-8,8930
	0,30	0,495	5,5836	0,9962	-3,9244
	0,50	0,695	7,8396	0,9996	-2,8046
	1,00	1,195	> 10	1,0000	-1,6318
	1,50	1,695	> 10	1,0000	-1,1504

n=2	(A)	(B ₂)	(C ₂)	(D ₂)	(E ₂)
	0,00	0,290	3,2712	0,9620	4,2046
	0,30	0,590	6,6552	0,9987	2,1455
	0,50	0,790	8,9112	0,9999	1,6043
	1,00	1,290	> 10	1,0000	0,9826
	1,50	1,790	> 10	1,0000	0,7081

n=3	(A)	(B ₃)	(C ₃)	(D ₃)	(E ₃)
	0,00	0,385	4,3428	0,870	-0,7040
	0,30	0,685	7,7268	0,9995	-0,4007
	0,50	0,885	9,9828	0,9999	-0,3103
	1,00	1,385	> 10	1,0000	-0,1983
	1,50	1,885	> 10	1,0000	-0,1457

Table 7

(A)	(P)	(R)
F	$(E_0) + (E_1) + (E_2) + (E_3)$	$(A)(P)(S) = \frac{Y}{S}$
0,00	1,3696	0,00
0,30	0,2929	251,92
0,50	0,1542	221,05
1,00	0,0616	176,61
1,50	0,0370	159,12

The values given in column (R) are plotted against fishing intensity:

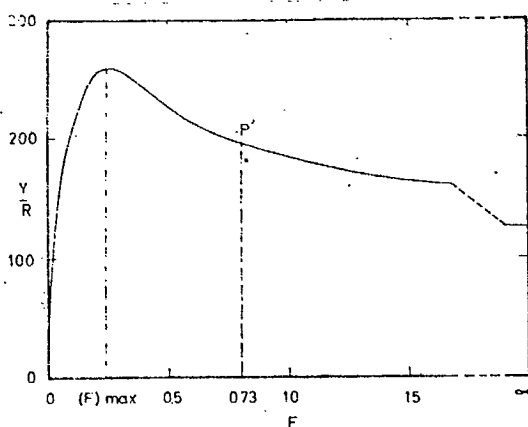


Figure 21 - Yield per recruit in dependence upon capture (mortality due to fishing). North Sea plaice: t_0 , 3.72 years; mesh size, 70 mm. After Beverton and Holt, 1957.

With beginning mortality due to capture, F , the curve at first rises steeply in order to tend gradually toward an asymptotic value with increasing F . This curve exhibits a yield maximum (yield on a weight basis per recruit), which, in shorthand, is F_{max} . In this connection, F_{max} is

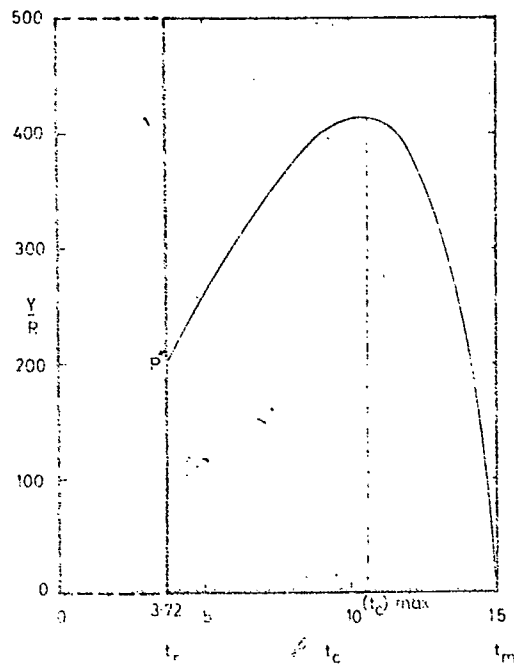


Figure 22 - Yield per recruit as a function of the mean minimum age at the time of capture, t_c , at constant $F = 0.73$

the coefficient of mortality due to capture, at which the maximal yield per recruit is attained. The asymptotic value reached would correspond to the weight exhibited by the fish at the moment that individual enters the exploited area, since the infinitely high fishing intensity has as a result that all recruits are immediately captured after reaching the exploited area.

When mortality due to fishing is kept constant at $F = 0.73$ and t_c varies, we will obtain the picture shown in Figure 22.

That curve, too, exhibits a maximum, $(t_c)_{max}$. Its origin is situated at t_r , the recruitment age, and it ends, with the value of zero, at the maximally possible minimum age at the time of capture of $t_c = t_m$.

In our outlines presented further above, we have considered yield per recruit always in dependence on only one parameter. When we now go ahead and consider all three parameters (i.e. Y/R , F , and t_c) together as variables within one diagram, we obtain the yield isopleth diagram introduced by Beverton and Holt (1957). During the construction of diagrams of that type, F and t_c are plotted on the X and Y axes, the Y/R values are assigned to the respective value pairs, and the values of equal yield are connected by lines (Figure 6).

The yield isopleth diagram then gives us the annual yield per recruit (in units of weight) as a function of F and t_c . The curves presented in Figures 21 and 22 are incorporated into the isopleth diagram. The horizontal line, $t_c = 3.72$, appearing in Figure 6 represents the corresponding part of the curve plotted in Figure 21, and the vertical line, $F = 0.73$, represents the curve plotted in Figure 22. The Point P values in Figure 6 appeared, in correspondence, in Figures 21 and 22 as Points P' and P'', respectively. Point P represents the pre-war values for British plaice fishing given by Beverton and Holt with $F = 0.73$ and $t_c = 3.72$. . 42 .

The line AA' connects the maxima of curves of the type shown in Figure 21, and it gives different values for $F_{\max}$, i.e. the F values at which the highest yields are obtained at constant t_c . $F_{\max}$ increases in each case with increasing t_c .

The line BB' connects the maxima of the curves corresponding to the Figure 22 curve; that line gives us the different values for $(t_c)_{\max}$, i.e. the t_c , at which the highest yield is obtained at constant F . The $(t_c)_{\max}$ value, too, increases with increasing F .

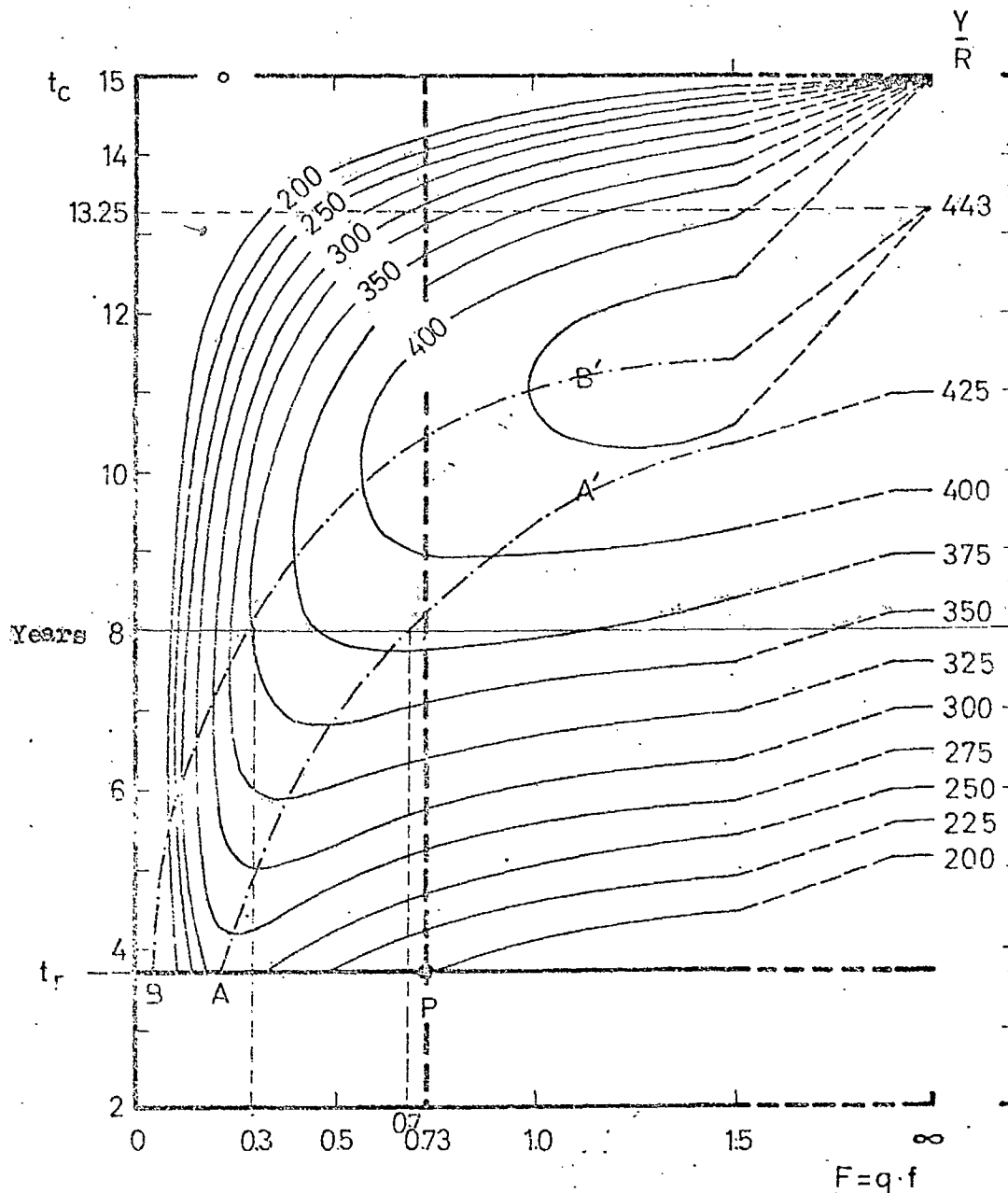


Figure 6 - Yield isopleth diagram of plaice. Yield in unit of weight per recruit as a function of fishing intensity and minimum age at time of capture

The curve BB' represents the eumetric fishing curve. Using that curve, we are able to obtain the t_c value at which we will obtain the greatest yield at a certain fishing intensity.

We will obtain optimal yields in cases where mesh size and minimum age at time of capture are combined in a manner ensuring that the yield is situated on the eumetric curve at maximal profitability.

3. The theory of fishing. Derivation of mathematical models

. 43 .

3.1. Losses

Following the models proposed by certain other authors, Beverton and Holt (1957) developed a population or stock model based on infinitesimal calculations. At a loss rate assumed to be constant, there arises a curve, on which the number of individuals, N , represents a function of time, t :

43-1

This curve exhibits a tangential slope, which is defined by the first derivation:

43-2

In this equation, Z is a constant requiring further definition. We obtain the function by integration of the first derivation, for which purpose we must perform the following mathematical manipulation:

43-3

Since we are able to integrate $\frac{dN}{N}$, we divide by N :

43-4

Constant factors are preferred:

43-5

Solution of the integral gives:

43-6

or:

43-7

Equation (3) is next subjected to delog procedures:

43-8

or:

43-9

where N_t is the number of survivors, and
 e^{-Zt} is the survival rate = S.

The slope of the curve is changed with changes in Z; Z represents .44.
the exponential coefficient of overall mortality, which is composed of
natural mortality (exponential coefficient), M, and mortality due to
capture (exponential coefficient), F.

$$Z = F + M$$

We are able to calculate Z using Equation (3a). For that parti-
cular purpose, we not require the absolute number of individuals, but
only their relative values at the beginning and at the end of the time

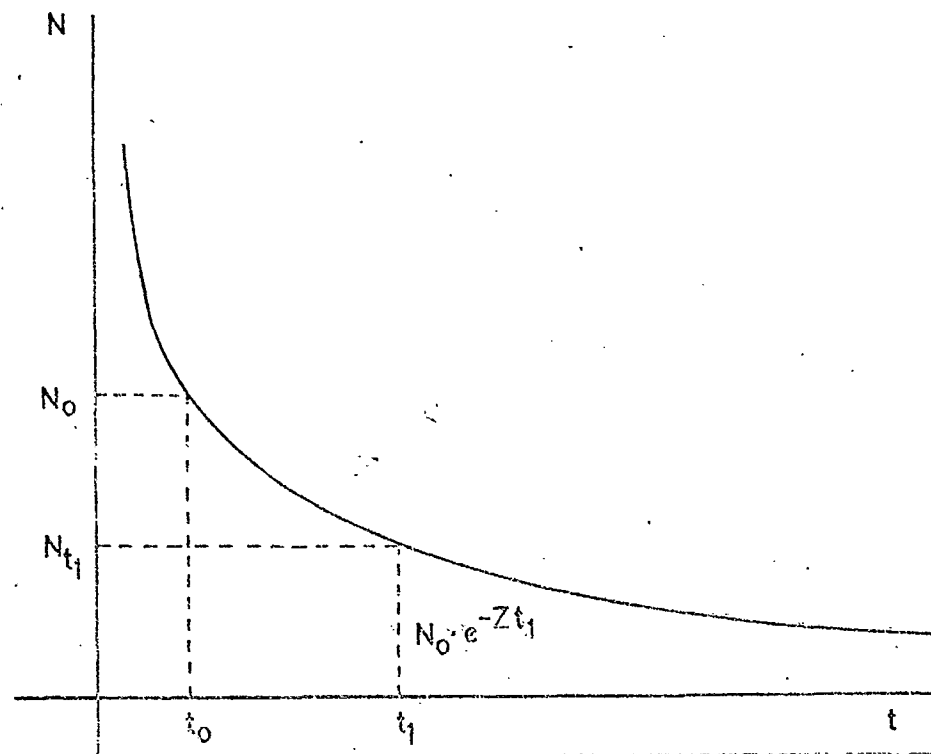


Figure 20 - Exponential decline of a stock (number of individuals) at constant annual total loss rate.

interval, t ; using these values we then form the relation

$$\frac{N_0}{N_t}.$$

Equation (5) gives us the number of individuals still present after passage of the time interval t . The following is valid in the case of Equation (5):

$$N_t < N_0 \quad \text{since} \quad e^{-Zt} = \frac{1}{e^{Zt}}$$

The number of individuals meeting death during the interval t is obtained by subtracting N_t from N_0 . We insert the value of Equation (5) for N_t :

$$N_0 - N_t = N_0 - N_0 e^{-Zt}$$

N_0 is then removed from the brackets:

. 45 .

45-1

where

45-1A

= the number of dead individuals, and

= the mortality rate.

Separate consideration of the parameters reducing the stock involves the following term for the unexploited stock:

45-2

and the following term for the loss due to capture:

45-3

In the case of very small intervals of time (with dt being infinitesimally small):

$$dN = F N dt, \text{ and}$$

$$dN = M N dt.$$

Since, furthermore, $dN = Z N dt$, it follows that the coefficients of mortality F and M must act in an additive manner:

$$F + M = Z$$

3.2. Growth

Bertalanffy's growth equation, which is based on infinitesimal calculations, permits us to obtain quantitative data on growth of populations. In connection with the growth equation we use the changes in individual weight as our point of departure: The increase in size (increases in length, volume, and weight, respectively) during the unit of time employed. The change in body mass (w) is given by the difference between the anabolic metabolic processes and the catabolic metabolic processes:

$$\frac{dw}{dt} = Hs - kw,$$

where H is the coefficient of anabolism and k is the coefficient of the substances utilized for maintenance metabolism; both coefficients are species-specific. H is proportional to the absorbing surface s , and k is proportional to the weight w of the individual. The following statements are valid during proportional growth (cf. Bertalanffy, 1951, page 277):

46-1 and

The term now reads:

46-2

We obtain the following expression with the aid of the mathematical chain rule:

46-3

We solve that equation for the differential $\frac{dl}{dt}$:

46-4

Since the quotients $\frac{Hp}{3q}$ and $\frac{k}{3}$ contain only constant values, we set

46-5 and

We then obtain

46-6

This linear differential equation contains only two integrable variables. For the purpose of integration, we separate these variables l and t :

46-7

We form the integral:

46-8

We solve this integral with the aid of substitution. We set $Z = E - Kl$ and then obtain the first derivation:

46-9

Since $\frac{dZ}{dl}$ cannot be integrated, we substitute dl as follows:

46-10

We now insert these values for Z and dl into the integral:

. 47

47 -1

We add the term $-\frac{1}{K}$ setting it in front of the integral:

47-2

The integral is solved within the limits of Z_0 to Z_t :

47-3

We again insert $Z = E - Kl$ into that equation:

or:

47-4

and multiply with $-K$:

47-5

Subjecting that equation to delog procedures, we obtain

47-6

We divide in order to eliminate the first fraction:

47-7

If t in that expression tends toward infinite, e^{-Kt} and, thus, . 48 .
also the first addend equal zero. The final length of the individual fish
is given by the expression:

48-1

We insert that value into the equation:

48-2

This equation represents the original form of Bertalanffy's function of longitudinal growth. L_{∞} is the (at an average) greatest possible final length of the individual fish, and L_0 is the length at age $t = 0$;

$K = \frac{k}{\gamma}$ is the species-specific constant of maintenance metabolism, i.e. the catabolic coefficient. In order to eliminate I_0 , we perform a calculation step related to the initial conditions, where

and

48-3

and multiply

48-4

We dissolve for I_0 :

48-5

We multiply with e^{Kt_0} :

48-6

Continuing our multiplication, we obtain:

48-7

We then return to our initial equation and insert the value obtained for L_0 :

. 49 .

49-1

We remove L_0 from the brackets:

49-2

Powers having the same base are multiplied by addition of the exponents:

49-3

This equation represents Bertalanffy's equation of longitudinal growth. Length at time t , L_t , is a fraction of the maximum final length, L_0 .

In order to obtain growth expressed as weight on the basis of that equation, we solve the relation between weight and length introduced further above in this Section for L :

49-4 , or

For time t , we, thus, obtain:

49-5

and for the final length of the individual fish:

49-6

At L_{∞} , the individual fish has reached its final weight, W_{∞} .

We insert these values into Equation (7):

. 50 .

50-1

We power with 3, and obtain:

50-2

Multiplication with q leads us to Bertalanffy's equation of growth expressed as weight:

50-3

Beverton and Holt (1957) have presented that equation in a modified form:

50-4

In the binomial of Equation (8), we substitute—for the sake of simplicity— $K(t - t_0) = m$, and we then obtain:

50-5

Following introduction of the binomial coefficient U , we obtain:

50-6

Each n in that equation corresponds to a certain U :

. 51 .

When $n = 0$, $U = 1$;

when $n = 1$, $U = -3$;

when $n = 2$, $U = 3$; and

when $n = 3$, $U = -1$.

When we now reverse the substitution performed further above:

51-1

we obtain the form of the binomial used by Beverton and Holt:

51-2

Following insertion of that binomial into Equation (8), we obtain the growth equation:

51-3

The Equations (8) and (9) indicate:

Increase in weight takes place with the third power of body length. That increase is influenced by the metabolic constant K and is limited by the final weight W_{∞} . Once we know the species-specific parameters W_{∞} , t_0 , and K , we are able to determine the weight at any point in time, t .

Following studies on herring, Ford (1932) and Walford (1946), using empirical means, have constructed the following growth equation:

51-4

This equation represents a straight line with slope b and ordinate segment a . The growth equations presented by Ford and Walford, on the one hand, and by Bertalanffy, on the other one, correspond as has been demonstrated, among others, by Hohendorf (1966) in a simple manner.

The following table of numerical values has been arranged for these two sets of equations:

Time
interval

Ford-Walford
Equation (10)

Bertalanffy
Equation (7)

52 - 1

Equations (10)A and (7)B give:

52-2

According to Equation (7)A:

52-3

that is

Equations (10)B and (7)C give:

52-4

We insert into that equation the value for a just obtained, and the value obtained using Equation (7)B for $1_{t_0} + 1$:

52-5

In analogy to $a^2 - b^2 = (a + b)(a - b)$, we can factorize $(1 - e^{-2K})$:

52 - 6

By dividing with $I_{\infty} (1 - e^{-K})$, we obtain

52-7

We have thus demonstrated that the constants a and b of the Ford-Walford Equation (10) can be expressed as follows:

52-8

On insertion of these expressions into the Ford-Walford equation, we obtain:

52-9

We replace l_t by Equation (7):

. 53 .

53-1

That expression is to be identical with Equation (7)

53-2

or:

We, thus, are permitted to regard the Ford-Walford equation as a linear recursive formula of Bertalanffy's function, and it may be used for the determination of the constants required in our calculations.

3.3. Recruitment and recruits

. 54 .

The stock is an interbreeding unit that maintains itself. The relation between adult individuals and recruits has been treated in the models proposed by Ricker (1954) and by Beverton and Holt (1957). These two models do not operate with absolute numbers of offspring, but are based on relative values. Fluctuations become evident in the equations for yield and selection, respectively.

Recruits after Ricker (dome-shaped curve)

The relations between adult stock and recruitment have been investigated by Ricker (1954) in the cases of several anadromous and a few other fish species. He obtained a pattern of asymmetric reproduction curves. Maximum reproduction occurred approximately at intermediate frequency of parents, and the branch of the curve rising to the maximum was steeper than the branch dropping beyond the maximum. Ricker (1958) has described these curves in an approximate manner using the following equation:

54-1

where

R is the number of offspring having almost reached spawning maturity;

N_1 is the number of spawners (parents);

N_r is the "parameter of self-reproduction" of the parent generation, that is the number of individuals produced in the next generation by the individuals of the present generation (replacement number of spawners);

R_r is the average number of individuals of the next generation produced by a parent generation having the size N_r ; and

N_m is the size of the parent stock producing the maximum number of offspring (spawners needed for maximum recruitment).

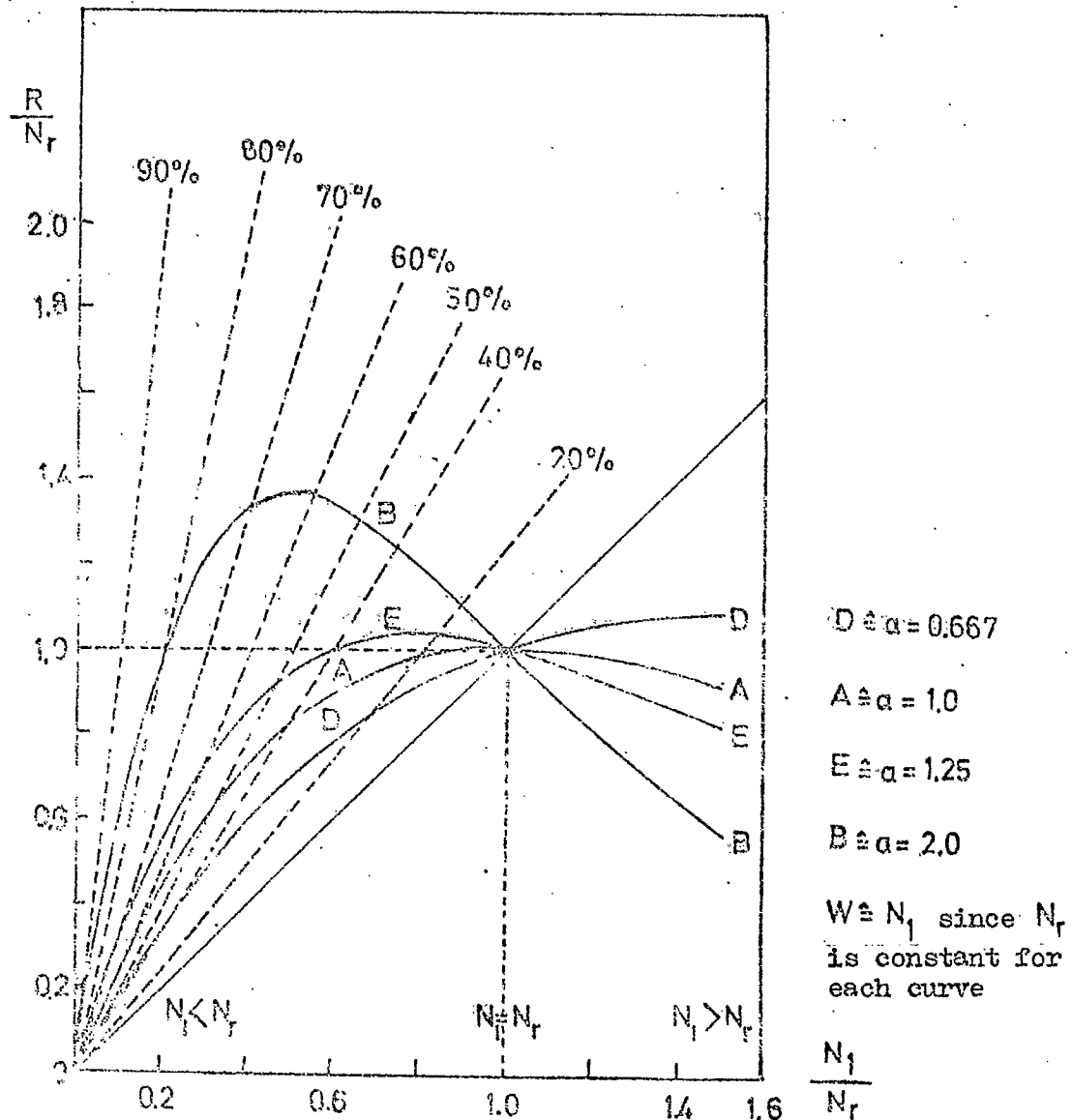


Figure 11 - Schematic representation of stock reproduction under different conditions. After Ricker, 1958

If we operate with equal units--Ricker employed as measure the egg egg numbers of the parents and the egg numbers of the next generation--then $R_r = N_r$, and the equation presented above can be simplified:

54--2

Introducing a for $\frac{N_r}{N_m}$; z for $\frac{R}{N_r}$; and W for $\frac{N_1}{N_r}$, we obtain

54 - 3

The diagram shown as Figure 11 has been plotted using different values for a , the stock-specific constant. This diagram illustrates reproduction of stocks under different conditions (family of dome-shaped curves), and demonstrates that the reproduction curve varies with different values for the constant a .

When $N_1 = N_r$, $z = 1 \cdot e^{a(1-1)} = e^0 = 1$.

All curves pass through the point $z = 1$; $W = 1$. That point is the one at which the parent generation has reached the replacement level, i.e. the number of offspring produced in the next generation is equal to the number of individuals in the present generation:

$$R_r = N_r$$

Ricker has explained the frequent deviations in reproduction curves in the following manner:

a) The dome-shaped curve is relatively flat.

That situation can be attributed to a limited supply of food. Furthermore, dispersed distribution of the stock has as a result that the density effects are not uniformly felt within the entire stock. In

the case of species exhibiting territorial behavior, we may find that the right branch of the curve proceeds horizontally due to occupancy of a limited area.

b) The right branch is relatively steep.

That situation arises in cases where the food or the oxygen supply is not adequate for a great number of individuals to undergo proper development. In extreme cases, the entire next generation may perish.

c) The dome-shaped curve is relatively steep.

That situation reflects a reduced rate of reproduction at low density. In the case of widely distributed populations, the sexes have difficulties in meeting, and predators affect small stocks relatively more markedly. That fact has been demonstrated by Naeve (1954) in the case of recruits of pink salmon (Onorhynchus gorbusha).

Recruits after Beverton and Holt

In principle, one would assume the following relations to exist between egg number and recruit number:

The recruit number = egg number times survival rate:

$$R = \text{Egg} \cdot e^{-Mt} \quad (\text{Beverton and Holt, 1957})$$

The egg number is an expression for the number of parents. The equation presented is valid only in cases of low stock density (egg number).

In reality there furthermore exists a density-dependent regulation of the number of offspring.

These two factors have been taken into consideration by Beverton and Holt in the following equation:

$$R = \frac{1}{\alpha + \frac{\beta}{\text{egg}}}$$

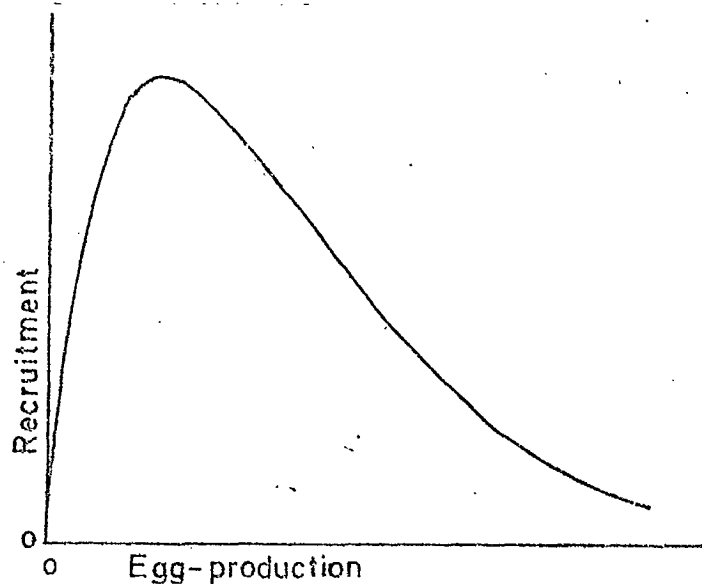


Figure 12 - Relation between egg number and recruitment at density-dependent growth of the larvae. After Beverton and Holt, 1957.

where α is the density-dependent loss rate, and
 β is the density-independent loss rate.

Discussion of that equation reveals: When the egg number tends toward infinite, we find that the quotient β/egg tends toward zero and the recruit number R tends toward $1/\alpha$. In the case of large egg numbers, we find that the recruit number is density-dependent; in that of small egg numbers, the recruit number is determined by the factor β/egg . The density-dependent mortality of pelagic stages has been demonstrated in the cases of mackerel, whitefish, pikeperch, and herring. Garrod (1968) has shown that the stock of the Arcto-Norwegian cod had been decimated to such an extent by fishing that recruitment was shifted into the region of low density dependence.

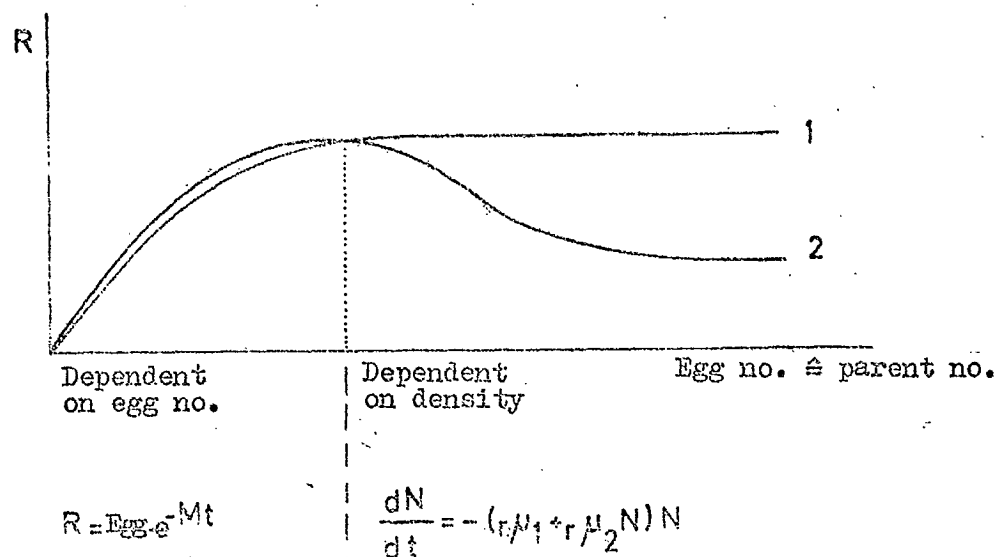


Figure 13 - Density-independent (1), and density-dependent (2) recruitment

Beverton and Holt have studied sixteen year classes of North-Sea plaice without finding correlations to exist between recruit and egg numbers.

In the most simple cases (in agreement with numerous population studies), we find that the mortality coefficient depends on the population density:

$$\frac{dN}{dt} = -(r\mu_1 + r\mu_2 N)N$$

$r\mu_2$: the density-dependent rate of larval loss
 $r\mu_1$: the density-independent rate of larval loss.

This function represents a special case of the equation:

$$\frac{dN}{dt} = -Z N$$

3.4. The yield equation

. 58 .

3.4.1. One year class during its entire life according to weight and number

The parameters required for calculating the yield of a given year class during the exploited phase are given further above in Section 1.2.3.

We define the number of recruits R immigrated into the exploited area to time t_r as N_{t_r} .

58-1

These recruits, of course, are subject to natural mortality M . At time t_c , there are still R' individuals present:

58-2

cf. Eq. (5)

The exploited phase starts at time t_c . The following equation is valid at any point in time, t ($t_c \leq t \leq t_m$):

58-3

The biomass is given by the product of the number of individuals and their average weight:

58 - 4

The yield obtained represents a part of the biomass taken by fishing from the stock.

. 59 .

Since the rate of removal by fishing is

59-1

the capture rate is:

In correspondence with Equation (2), the following equation is valid for yield on a weight basis:

59-2

We substitute Equation (11) for $N_t w_t$:

59-3

In order to perform integration, we must summarize the terms containing the variable t ; the remaining part of the equation remains constant:

59-4

We solve the integral after the formula:

59-5

We, thus, obtain

. 60 .

60-1

Following insertion of the constants, the equation reads:

60-2

The first exponent between the brackets is removed by multiplication, and we, furthermore, reduce with 60-3A

60-3B

We shift expression 60-4A appearing in that equation before the summation sign between the brackets:

60-4B

and are now able to remove 60-5A from the brackets:

60-5B

We summarize that expression to obtain Equation (12):

60-6

The yield equation (12) gives us the yield on a basis of weight of one year class during the time interval between t_c and t_m . In this connection it is assumed that K , F , M , W_0 , R' , t_c , t_o , and t_m are constant.

Management of the yield equation in the form given by Beverton and Holt is a very complex matter, since the parameters F , M , W , t_r , and t_c all appear separately. For that reason, the afore-mentioned authors have rearranged their equation, and the modified equation contains only three separate parameters, which are derived from the parameters mentioned above. The values of these three parameters have been presented in tabular form. . 61

For the purpose of their rearrangement, Beverton and Holt (1966) have employed Yield Equation (12) with the assumption that the life span of the individuals has no upper limit ($t_m \rightarrow \infty$); that manipulation has as a result that the bracketed expression equals 1:

61-1

The following relations are employed:

61-2

E is the rate of exploitation. Using that relation, we can derive:

61-3

The yield equation expression

61-4 can be rearranged as follows:

61-5

The following expression can then be derived from Bertalanffy's growth equation:

61-6

62-1

Following potentiation with n , we obtain for time t_c :

62-2

In that equation, l_c represents the length of the individual fish at time t_c (the minimum age at the time of capture).

Beverton and Holt have introduced the parameter c to replace the quotient $\frac{l_c}{l_\infty}$:

62-3

The parameter c corresponds to the average selection length, expressed as a fraction of the asymptotic length L . In analogy, the following statement is valid for the following relation

62-4

In that equation, M/K represents the ratio of the coefficients giving the relative rate of changes in number and length with age.

The expression representing the individuals still surviving at time t_c can be rearranged as follows:

62-5

A new parameter, R_0 , is introduced in that equation. R_0 represents the number of recruits present at time t_0 .

62-6

We obtain the following yield equation after inserting the relations (13), (14), (15), and (16) just derived:

. 63 .

63-1

Mathematical rearrangement of that equation gives Yield Equation (17):

63-2

We then find that only three parameters remain: E , c , and M/K , and E and c can vary only between 0 and 1. The values tabulated for that equation provide a dimension-less value Y' . In order to obtain again a suited dimension, we must multiply Y' with appropriate factors. In the case where we, for instance, wish to know the yield per recruit in grams, we will multiply that equation with:

63-3 ; following insertion of the relations (15) and (16):

63-4

The absolute amount is calculated by multiplying Y/R with the absolute number of recruits present at time t_r .

The numerical yield (C) of a given year class is derived in analogy to Equation (12). The weight is not considered in that calculation.

63-5

We integrate:

63-6

64-1

Following multiplication, we obtain:

64-2

Following reduction, we obtain Equation (18) for the numerical yield:

$$64-\frac{F}{Z} 3$$

That equation is valid during the entire exploited phase of a given year class.

Solution of that equation for $\frac{F}{Z}$ gives:

$$64-4$$

$$\frac{\text{Coefficient of mortality due to capture}}{\text{Coefficient of overall mortality}} = \frac{\text{Number of individuals captured}}{\text{Number of all individuals killed}}$$

3.4.2. One stock during one year according to weight and numbers

The Equations (12) and (18) are valid also for the yield of the entire stock within one year if the number of recruits is the same during each year under consideration.

That fact is made evident by the data presented in Table 8.

The yield of a given stock during the course of one year is exactly as high as the yield of a year class during the exploited phase, as is demonstrated in that Table using the year 1965 and the year class 1959 as example.

Table 8 - An example. The fishing rate amounts to 50%, and recruitment is constant.

Year class	Fishing year					
	1961	1962	1963	1964	1965	Total
1959	1000	500	250	125	63	1938
1960		1000	500	250	125	
1961			1000	500	250	
1962				1000	500	
1963					1000	
Total						1938

3.5. Annual mean population sizes

Both natural mortality and mortality due to capture decrease the weight of a given stock after recruitment. Frequently it is useful to determine the size of a stock at an annual average.

The mathematical formulation constructed for that purpose follows the theoretical picture of stock composition. The recruit year classes in this approach are equal in size:

65-1

(m - 1) Year classes are present during year m (Table 9) start of the first year (t_0), the stock consists of

R'_0 individuals.

At time φ ($0 \leq \varphi \leq 1$) of the first year, the number of year class 0 members present during the exploited phase amounts to

$$R'_0 e^{-Z\varphi}$$

Table 9

Years	1	2	3	4	5		m
Year classes	0	0	0	0	0		0
present		1	1	1	1		1
			2	2	2		2
				3	3		3
					4		4
							.
							.
							.
							.
							m-1

At the end of the first year, when $\phi = 1$, that number is

$$R'_0 e^{-Z}$$

At that moment, year class 1 joins the stock. At the beginning of the second year, the stocks consist of

$$R'_0 e^{-Z} + R'_1 \quad \text{individuals.}$$

At time ϕ of the second year:

$$(R'_0 e^{-Z} + R'_1) e^{-Z\phi}$$

At the end of the second year:

$$(R'_0 e^{-Z} + R'_1) e^{-Z} = R'_0 e^{-2Z} + R'_1 e^{-Z}$$

At time ϕ of the third year, the stock consists of:

$$(R'_0 e^{-2Z} + R'_1 e^{-Z} + R'_2) e^{-Z\phi} \quad \text{individuals.}$$

At time ϕ of the m -th year, the stock consists of

$$(R'_0 e^{-(m-1)Z} + R'_1 e^{-(m-2)Z} + \dots + R'_{m-2} e^{-Z} + R'_{m-1}) e^{-Z\phi}$$

individuals. Since the entire stock is covered during the m -th year, it follows--according to definition--that the entire number of individuals is N_ϕ at time ϕ : . 67 .

67-1

R' can be removed from the brackets in that equation:

67-2

By way of the total number of the [words missing in the original; Translator] in year i (integers between 0 and $m-1$), we are able to develop Equation (19):

67-3

That equation gives us the number of individuals present during year m at time ϕ .

$\bar{N}'$ is the number of individuals present at the annual average in the exploited stock:

$$\bar{N}' = \frac{\text{Total of the individuals determined in the random samples}}{\text{Number of random samples}} = \quad 67-4$$

67-5

We insert into that equation the value found for N_{ϕ} using Equation (19):

67-6

Cf. the derivation of the yield equation for the solution of this integral.

67-7

Following multiplication:

67-8

The solution of this equation reads:

. 68 .

68-1

Following multiplication:

68-2

Most of the addends between the brackets cancel one another out, and there remains as the result:

68-3

We can substitute $(t_m - t_c)$ for m , since the duration of the exploited phase $(t_m - t_c)$ covers the interval of m years.

$$m = t_m - t_c$$

Furthermore:

$$Z = F + M$$

We now obtain Equation (20), which gives us the annual mean number of individuals during the exploited phase, i.e. it gives us a value for the size of a given stock during a given year:

68-6

Division of Equation (18) by Equation (20) yields the following value for F :

68-7

In cases where both the landings C (number of individuals) and the mean population size $\bar{N}$ are known, we are able, with the aid of that equation, to calculate directly the coefficient of mortality due to capture. Sources of error using that method are found in the inaccuracies in estimating stock size and catch size, respectively.

3.6. Total losses. Extension of the first formulations.

. 69 .

Since the formulations so far presented are overly specific in nature, we are forced to extend them in order to be able to determine the desired parameters.

According to Equation (20), the annual mean year class size of year class A is:

69-1

In that equation, N_x is the number of individuals present at the start of year x .

Since mortality is not necessarily equal during each year, it follows for year $x + 1$ that

69-2

The relation of year class sizes then is:

69-3

We solve for 69-4A

69-4B

and subject that equation to delog procedures:

69-5

. 70 .

70-1

Equation (21) yields the coefficient of overall mortality.

In cases where $(F + M)_x$ and $(F + M)_{x+1}$ are approximately equal, we find that the second addend of that equation tends toward zero, and Equation (21) becomes identical with Equation (3). In these cases, Z can be calculated by inserting $\bar{N}_x$ and $\bar{N}_{x+1}$ into the equation.

70-2

3.7. Determination of the recruiting age during recruitment from several age groups

In cases where recruiting of a given year class encompasses several years, individuals of the different age groups will exhibit intervals of natural mortality that differ in length. Let us next consider the process of recruitment.

The following symbols are used in connection with these determinations:

- the age group of a year class proving the recruits
- $70-3$ the age group of that same year class recruited one year later
- the age group of that same year class providing recruits r years later

These groups exhibit the following mean recruiting ages, that is the following mean arrival times at the exploited area:

- the recruiting age of age group
- $70-4$ the recruiting age of age group
- the recruiting age of age group
- and the following numbers of individuals:

- the number of recruits of age group
- $70-5$ the number of recruits of age group
- the number of recruits of age group

Therefore:

the number of recruits of age group $71-2$ present on the average during year x . That number is smaller than ${}_0R$, since the recruits are present in the exploited area already for a certain period of time.

- $71-1$ the number of recruits of age group $71-3$ present on the average during year $x + 1$. The individuals still present of the original number ${}_0R$ as well as the since recruited ${}_1R$ individuals are included in that term.

the number of recruits of age group $71-4$ present on the average during year $x + r$.

is employed to represent the catch, c/g .

The year class in question appears for the first time in the catch during the course of year x as age group θ_p in the number R_p . In cases where all recruits are immediately subjected to complete mortality, we obtain the number of individuals present at an average during year x by using Equation (20):

71-5

The individuals present are subjected to complete fishing between the moment of recruitment t_p and the end of the year $\theta_p + 1$; t , thus, represents the difference between the age at the end of the first year and the recruitment age:

71-6

The number of individuals surviving at the end of the first year, thus, amounts to:

71-7

At the average of the second year, $x + 1$, we obtain for that recruit group:

71-8

At the average of the third year, $x + 2$, we obtain:

72-1

During the course of the second year, $x + 1$, the new recruit group, ${}_1R$, joins the first one. The average number of recruits now amounts to:

72-2

the new recruit group last year's recruit group

At an average of year $x + 2$, there remains the following number of individuals belonging to the new recruit group ${}_1R$:

72-3

The total recruit number of year $x + 2$ is increased by ${}_2R$ and then amounts to:

72-4

We solve for ${}_2R$:

72-5

We divide that equation by the left bracketed expression and multiply with $(F + M)$:

. 73 .

73-1a

In the numerator we remove 73-1b and 73-1c from the brackets:

73-2

The bracketed expression in the numerator can be reduced with the aid of a summation formula:

73-3

That expression then yields Equation (22) for the year r :

73-4

Equation (22) gives us the number of surviving recruits of a given year class after conclusion of recruitment.

In cases where we are dealing with only one age group, the subtrahend in the numerator becomes zero, since the sum becomes zero. We then obtain:

73-5

That equation again corresponds to the equation present initially . 74 .
in this Section.

The following parameters are required:

- $\bar{N}$ = representing the mean unit catch per age group
- $F+M$ = the coefficient of mortality
- θ_0 = the youngest age group determined by means of age determination; in the following example, it is 2.
- θ_0^+ = recruiting age; in the example, it is 2.45
- θ_1^+ = recruiting age; in the example, it is 3.35
- θ_2^+ = recruiting age; in the example, it is 4.33

As an example for recruitment from several age groups, we present here the values determined by the British trawler fleet between 1946 and 1948. These studies showed that, in essence, only the age groups II, III, and IV were involved in recruitment (Figure 25). Following immigration into the exploited area, the recruits of all age groups are subjected, in addition to natural mortality, also to mortality due to capture. In order to eliminate that difficulty, the juvenile individuals are given as fractions of the adult ones:

<u>No. of II</u>	during January, February, etc.
No. of VI - XI+	
<u>No. of III</u>	during January, February, etc.
No. of VII - XI+	
<u>No. of IV</u>	during January, February, etc.
No. of VIII - XI+	

In this connection, it is assumed that overall mortality is equally high in all age groups. After smoothing of the values we obtain the density relationship shown in Figure 23.

The curve in Figure 23 illustrates the increase in the number of individuals due to recruitment during the course of the summer. The

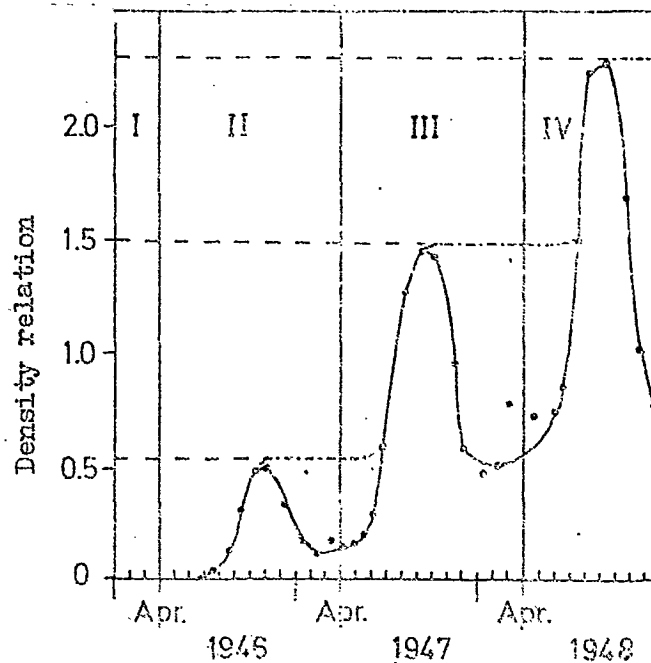


Figure 23 - Density relations between age groups II, III, and IV and age groups VI+, VII+, and VIII+, for each month, in the case of plaice. Modified after Beverton and Holt, 1957

declining branch of the curve (in evidence during the winter months) reflects the fact that during that season spawning stocks are chiefly exploited. In the case that no spawning concentrations would occur, we would find instead that the curve of the recruited individuals (age group II) remained at the 0.5 level until the arrival of age group III. Recruitment by age group III, thus, starts only at the asymptotic point at 0.5 and is concluded at the asymptotic point at 1.5. That process is repeated once more with age group IV. Figure 23, thus, makes evident the relative quantities of the recruitment groups:

Age group II	0 → 0.5
Age group III	0.5 → 1.5
Age group IV	1.5 → 2.3

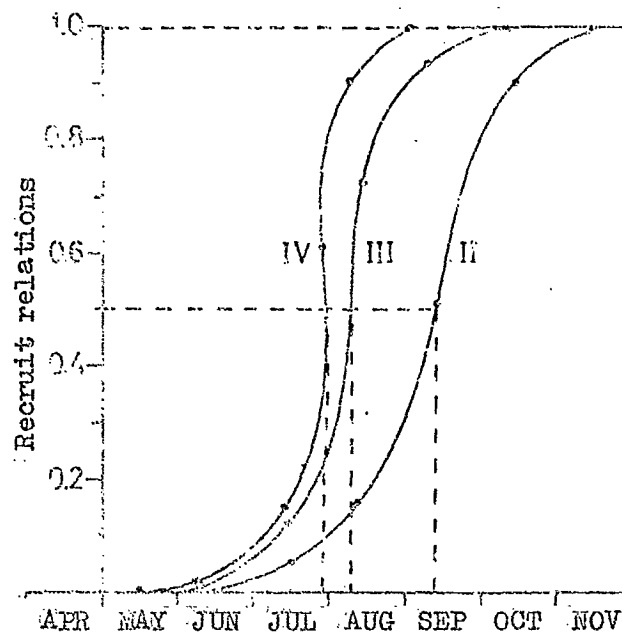


Figure 24 - Seasonal frequency percentage curve of recruitment of plaice for age groups II, III, and IV. After Beverton and Holt, 1957

These data yield the frequency percentage curves plotted in Figure 24, where the regions mentioned above have in each case been set to equal 1.0 ($1.5 \rightarrow 2.3 = 0.8 \rightarrow 1.0$).

Figure 24 shows the number of recruited individuals in the different age groups at each point in time as the proportion of the total number of individuals recruited during the season:

1. The individual curves proceed in an almost parallel manner.

The mean recruitment age, t_r , of the year class can be regarded as the weighted mean of the mean recruitment ages of the individual age groups. For that purpose we must know the relative shares of the different age groups; these shares are determined with the aid of Equation (22).

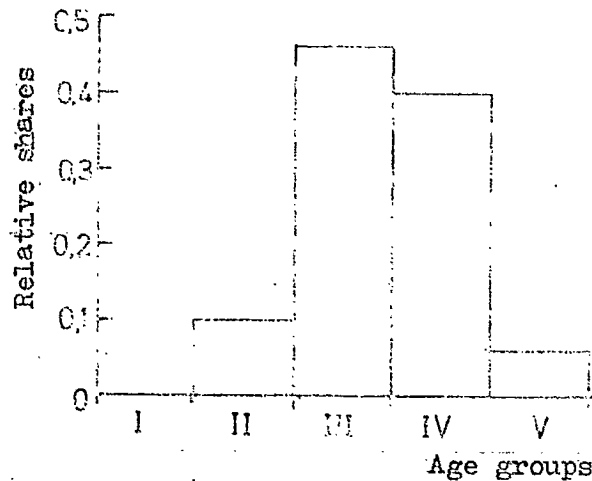


Figure 25 - Relative age distribution of recruits (plaice). After Beverton and Holt, 1957.

2. The recruitment season coincides with the period of growth.
In other words: The growth period is also the period of greatest activity.

3. The three age groups appear, with respect to chronology, in reversed order of age. That means that recruitment proceeds in a manner similar to that seen in the case of the spawning migrations, where the older individuals, too, arrive at the spawning sites before the younger ones.

The relative age distribution of the recruits is illustrated in Figure 25.

Taking into consideration also age group V, which provides a small number of recruits, we find by means of calculation that the mean recruitment age, t_r , is 3.73 years.

By adding the values presented in Figure 25, we obtain the frequency percentage curve for recruitment plotted in Figure 26 on the basis of individual length.

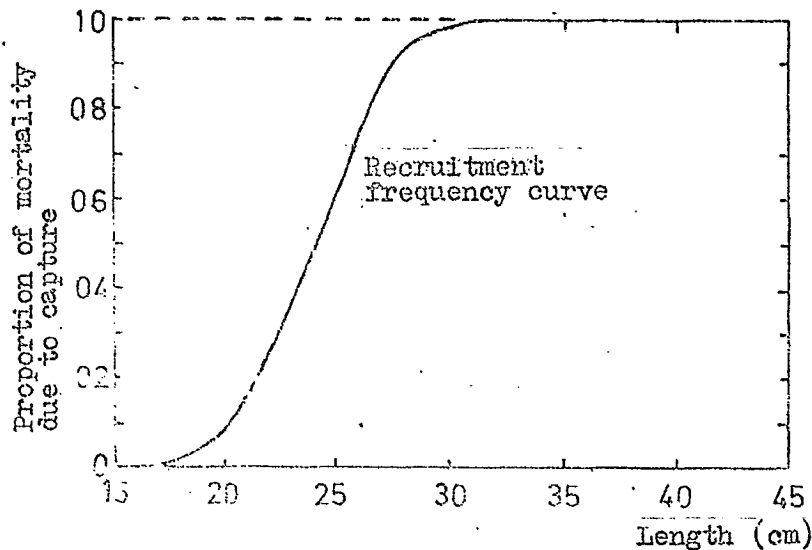


Figure 26 - Plaiice recruitment. Frequency percentage curve. Modified after Beverton and Holt, 1957.

3.8. Separation of F and M

3.8.1. Iterative approximation

The coefficients of natural mortality and of mortality due to capture, M and F, respectively, can be separated with the aid of iterative approximation using Equation (21). By inserting the relation $F = q f$ (cf. Section 2.1.5.) into Equation (21), we obtain Equation (23) for the interval of one year; the solution of that equation has been described already in Section 2.6.3.

$$qf_x + M = \ln \frac{A \bar{N}_x}{A \bar{N}_{x+1}} + \ln \frac{\left(qf_x + M \right) \left(1 - e^{-(qf_{x+1} + M)} \right)}{\left(qf_{x+1} + M \right) \left(1 - e^{-(qf_x + M)} \right)}$$

3.8.2. The Paloheimo method

. 78 .

In 1961 Paloheimo, on the basis of the Beverton-Holt formulation, developed a linear equation, which can be solved without complex iterative approximation procedures.

Paloheimo writes Equation (21) in the following form:

78-1

That equation can be solved in an approximate manner through one mathematical step, in which the second addend

78-2

is transformed into a simple relation. For Z (coefficient of overall mortality) one frequently obtains values of:

78-3

Paloheimo developed the series

78-4

and obtained

78-5

One sees:

78-6

or in a general form:

For $0.2 = Z = 1.0$. we find that the mean value of a is situated at 0.47; that value decreases with increasing Z

The value of 0.5 is adequate for practical purposes, since K is . 79 . small toward 1. By inserting Equation (24) into Equation (21), we obtain:

79-1

We again substitute $Z = q f + M$ for Z and obtain:

79-2

Following multiplication and rearrangement of the notations between the brackets, we obtain:

79-3 first eq. only!
cont →

79-3

2nd

+ 3rd eq. (25)

In this linear relation, 79-4 is plotted against
79-5

The regression constants q and M can be directly determined, and iterative approximation is no longer required. Using hypothetical examples, Paloheimo was able to demonstrate that the linear formulation yields better values for both q and M than the one proposed by Beverton and Holt following four to five iterative steps. The standard deviations were reduced by 27 to 69 per cent. No improvement could be obtained only in cases where q is strictly constant.

3.8.3. Mark and recapture techniques

. 80 .

3.8.3.1. Constant fishing intensity during the recapture period

Taking into consideration the parameters introduced in connection with marking and recapture (cf. Section 2.6.2.), the following statements are valid:

and

80-2

In the case of constant fishing intensity and equal recapture-reporting intervals, we use

80-3

We can form the quotient using n_2 and n_1 :

80-4

or:

We insert Equations (27) and (28) into Equation (26):

80-5

and solve for F:

80-6

Equation (29) is inserted into Equation (28)

. 81 .

81-1

and solved for M' :

81-2

That equation is applicable only in cases where both F and M' are constant during the recapture period.

3.8.3.2. Varying fishing intensities with time

In mark and recapture experiments, n/f is to N_0 as c/g is to $\bar{N}$:

81-3

so that we are able to substitute the expression 81-4 in Equation by

81-5

We obtain Equation (32) for the interval covered by the recapture period T_1 :

81-6

In analogy to Equation (23), q and M' are known and can be determined with the aid of iterative approximation or regression procedures, respectively, using the known value pairs of f and n . That procedure also gives us F_r , since $F_r = q f_r$.

. 82 .

The advantages of this method:

N_0 does not appear (is not known in the case of marking-caused losses) and an additional loss rate does not become effective, since the ratio numbers n_1/n_2 appear in the calculations (cf. Section 2.6.2. regarding the error after Ricker).

3.8.4. Fishing intensities during two periods with different constant values

Let us consider two-year periods α and β , respectively, with f_α and f_β , in which case $f_x = f_{x+1}$. The second addend of Equation (23) then equals zero.

82-1

Substraction

incl. the line

82-2

We solve for q :

82-3

Following rearrangement of Equation (33) for M , we obtain

82-4

and are able to calculate the coefficient of natural mortality . 83 .
by inserting the value from Equation (34) for q . Taking into consideration
the relation (31), we obtain the equations already presented above in
Section 2.6.2.

3.9. The virtual population

V_n , the virtual population of year n , is the number of individuals
of a given year class captured since the beginning of the year n up to
the disappearance of the year class (t_m). V_n can be determined by analysis
of the landings. Using the method of the virtual population, we will
demonstrate further below how, at known constant M , F and M can be determined

for each age group of the year class without that knowledge of either fishing intensity, f , or catch per unit of effort, c/g , is required. Due to the continuous changing of the power factor (PF) of the fishing vessels, determinations of both f and c/g are associated with ever increasing difficulties. The method described here is valuable for just that reason.

C_n is the number of individuals of the year class captured during the year n ;

N_n is the number of the individuals of the year class present at the beginning of the year n ;

V_n is the virtual population of the year class at the beginning of the year n ;

E_n is the $\frac{V_n}{N_n}$ fraction of individuals captured among N_n .

Following Fry (1949) and Jones (1964), Gulland (1965) has developed the following method:

The survival rate S of the year class during year n is:

83-1-2-3-

replaces

The ratio of the number of surviving individuals of the year class in question (at the end of year n), N_{n+1} , to the number of individuals captured during year n is r_n . If M is constant, r_n is a function of F . When M is known, we are able to calculate r_n values for each F value and arrange a table.

In cases where r_n can be calculated by other means, we will be able to obtain from that table the values of both

84-1 and

For that reason we will search for an additional expression for r_n :

84-2

84-3 We extend with

84-4

since $C_n = V_n - V_{n+1}$.

That expression enables us to determine r_n . In this connection we must know the value of E_{n+1} ; to obtain that value we must construct an additional equation:

84-6

since

84-7

These three expressions can be used for the determination of F and Z in each individual age group of the year class in question, if the virtual population and M are known and we, furthermore, are able to estimate an approximate value for E during the last year of life. We then proceed as follows:

. 85 .

a) We insert into Equation (37) both V_n and V_{n+1} for the year before last and the last year ($t_m - 1, t_m$) as well as the approximate value of E_{n+1} for the last year of life.

b) Using the r_n value determined in this manner, we obtain from the table

85-1

and

c) The two last values together with the approximate value of E_{n+1} are inserted into Equation (38), and we obtain E_n .

d) Using that E_n value and the known V_n value as well as V_{n-1} , we obtain r_{n-1} with the aid of Equation (37).

e) Using that r_{n-1} value and the table, we obtain

85-2 and

Any error in the estimated first value of E_{n+1} is smoothed out up to the second or third age group before last.

4. Symbols and definitions

- C Catch; capture measured in number of individuals caught
- C/g catch per unit of fishing effort
- F exponential coefficient of capture (mortality due to fishing)
- f fishing intensity; effort related to area and stock density
- g fishing effort (unit of)
- K metabolic constant in Von Bertalanffy's growth equation
- l length in cm
- l_c length at age t_c
- l_r length at the time of recruitment
- l_∞ final length of fish in Von Bertalanffy's equation
- M exponential coefficient of natural mortality
- N number of individuals in a given stock (population) or in parts of a stock
- PF power factor
- q coefficient of catchable fish; $q = F/f$
- R recruitment; the number of individuals present at time t_r
- R' number of recruits present at time t_c ; $R' = R e^{-M(t_c - t_r)}$
- s absorbing surface of a fish in Von Bertalanffy's equation
- S survival rate; $S = e^{-Z}$
- 1-S death rate; $1 - S = 1 - e^{-Z}$
- t time, measured in years; a variable
- t_c minimum age at time of capture, mean
- t_m maximum age, mean
- t_0 prenatal age in Von Bertalanffy's equation

- t_r mean recruitment age
- V virtual population; the number of individuals captured in a given year class
- w weight of an individual, in grams
- w_{t_c} weight of an individual at age t_c
- w_{∞} final weight of a fish in Von Bertalanffy's equation
- Y weight of yield; catch in unit of weight
- Z exponential coefficient of overall mortality; $Z = F + M$

Catch per unit of effort: A relative term for stock density.

Death rate: The percentage of deaths per unit of time (0 to t) compared with the number of individuals alive at time 0.

Eumetric fishing: Mean minimum age of fish at time of capture and fishing intensity are related in a manner ensuring that the catch is produced as cheaply as possible under the conditions existing.

Exploited phase: The interval during which a given year class is subjected to fishing. This interval encompasses the period between t_c , the minimum age at time of capture, and t_m , maximum age.

Fishing effort: A measure for the use of fishing gear and tackle reflecting the number of fishing voyages per year; the trawling hours per year; the number of net castings per year; etc.

Fishing intensity: The fishing effort expended per given area, measured in relation to population density per sub-area.

Optimal fishing: The point on the eumetric fishing curve indicating yield at maximum profit.

Overfishing: A state indicated when the yield in the isopleth diagram lies below the eumetric fishing curve.

Power factor: The factor used to compare the fish-catching capacity of different vessels.

Prenatal age: A theoretical value for $t = t_0$, corresponding biologically to the time of egg fertilization.

Selection: A factor reflecting the selective properties of the fishing gear used. This factor represents the percentage of length groups of fish captured among the length groups present in the area being fished.

Stock (unit stock): A unit of individuals who interbreed within a given area. This unit is subjected to uniform fishing. Dispersion, due to either immigration or emigration, is insignificant.

Survival rate: The percentage of survivors present at time t compared with the number of individuals alive at time 0.

Thinning out: A theory, according to which greater catches per unit of effort will be obtained if the juvenile year classes are decimated in numbers to such an extent that the individual growth rate will increase noticeably resulting in increased productivity of the stock.

Underfishing: A state indicated when the yield lies above the eumetric fishing curve.

Virtual population: The share of a given year class captured in the course of fishing operations.

Yield: The weight or the number of captured fish.

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