FAO Fisheries Circular, N° 701
(distribution restricted)

FIRM/C701

MODELS FOR FISH STOCK ASSESSMENT

Partial translation of the annex to the report of the
Second FAO/CNEXO Training Centre on methods for fish stock assessment

Brest (France), 26 July - 27 August 1976

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
ROME, January 1978

PREPARATION OF THIS DOCUMENT

The French original of this document contains the main lectures prepared for the two FAO/CNEXO Training Centres in fish stock assessment. These Training Centres were financed by a Trust Fund of the French Government and were held in Brest (France) in August 1973 and 1976. The English translations of the lectures presented in this version were prepared for the CIDA/FAO/CECAF Seminar on Fishery Resources Evaluation, Casablanca (Morocco), 6-24 March 1978. This Seminar was organized under the FAO/CIDA (Canadian International Development Agency) Cooperative Programme component of Project TF-INT 180 (CAN) - Assistance to the UNDP/FAO Project for the Development of Fisheries in the Eastern Central Atlantic (CECAF Project - INT/72/074). This English version does not contain the complete set of lectures presented in the French original.

W/L1452

FAO Fisheries Circular (<u>FAO Fish.Circ.</u>)

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FISHING AND ASSESSMENT OF STOCKS

by

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The assessment of fishery stocks can be seen as the application of the methods of population dynamics to stocks that are exploited by fishing. Before examining the available methods - which will be the subject here - it is important first to grasp the objectives of this discipline, i.e. to identify the nature and priorities of the information which this science is expected to supply in support of the fishing industry.

1. The Development of Fishing in the World

A quick review of the recent history of fishing and its future prospects enables us to appreciate to what extent fisheries utilize the production of life in the seas. This glance at history also shows how research problems have evolved both in time and according to the level of exploitation.

Towards the end of the last century, in the wake of the industrial revolution, conditions became ripe in the Atlantic and Northern Pacific for the fishing industry to industrialize. At that time certain technical innovations were made that greatly increased the power and efficiency of the industry at every stage of production:

- catches (otter trawls, steel hulls, steam engines),
- preservation (ice and canning processes),
- distribution (railways),
- commercialization (big outlets in the main industrial and urban centres).

Up until the second world war, this expansion was limited to the industrialized countries in the Northern Hemisphere. The demersal species were then the most sought after and production of these greatly surpassed that of pelagic species.

Starting at the end of the 1940s, two developments occurred:

- the extension of industrial fishing all over the globe as a result of the greater number of participants (USSR, Indonesia, Peru, Thailand, etc.), and the use of long-range ships capable of freezing and treating their catches on board, far from the traditional centres of consumption.

- the intensification of fishing for pelagic species (coastal and oceanic) which was facilitated by several technical innovations. Some of these improved the methods of capture (improvements to surrounding nets, refinements of pelagic trawls and acoustic detection). Others opened up new outlets (the use of fishmeal to fatten pigs and chickens).

The result was that by 1970 catches of pelagic species were twice those of demersal species, and 90% of the pelagic fish catch and half the total catch went for processing into fishmeal.

This series of innovations enabled the fishing industry to expand at a rapid rate, identical to what was achieved during the first half of the century. From 1900 to 1970 world fish production went from 4 to 70 million tons, which means that it doubled approximately every ten years. This was the highest growth rate of any food production sector and it is one of the few sectors in which production grew faster than world population. Since 1972, however, the total catch has levelled off, mainly because of the decline in the catch of a single stock: the Peruvian anchoveta. Presently, for the world as a whole, the fishing industry supplies about 10% of the animal protein consumed by man as food. The proportion is several times greater than this in the majority of the developing countries - particularly in Africa and Asia - where fish is the basic source of protein in the human diet.

Several points emerge from this brief historical survey. First of all, one can see that there are a number of prerequisites to fishery development (resources, means of capture, the ability to operate and manage the equipment, labour, systems of processing and preservation, distribution networks and markets) as well as - what is our concern - the establishment of adequate working relations among research institutes, industry and the administrative authorities. Without such working relations, in fact, even the most basic programmes and facilities cannot be exploited to their full potential. A comparison of the recent performances of various countries shows that neither in the most developed nor in the least developed countries are all the conditions mentioned above as requirements of a healthy fishing industry, fully satisfied. On the whole, conditions appear to be more favourable in the group of countries that are at an intermediate stage of development (e.g. Spain, Korea, Cuba, Indonesia, etc.).

The second point to note is that in most areas the fishing industry has developed in three stages:

- intensified fishing of traditional stocks (the most abundant, the easiest to catch and sell, those found nearest to existing markets), sometimes till a point is reached where fishing them is no longer profitable.
- fishing of unconventional species on the traditional fishing grounds (i.e. species that were of no commercial interest when traditional stocks were still abundant).
- extension of fishing activity to areas progressively farther away from the original bases. (And in these areas the first two stages are repeated.)

The steady extension of fisheries to new species and areas has brought about a dramatic change in the overall pattern of exploitation of the world's fishery resources. Whereas formerly, despite isolated cases of overexploitation, the resources of the various regions were not fully exploited, nowadays in most regions the exploitation of most species is very intense - even excessive - which calls for the urgent implementation of more and more serious measures of restraint.

2. The Nature and Distribution of Fishery Resources

For resources to be exploitable they must satisfy a certain number of conditions:

- the densities must be high enough (at least temporarily) to provide profitable catch rates.
- stocks and potential yields must be sufficiently large to justify investments and to allow catches to be maintained at a reasonable level.
- the product must be marketable. This is a condition which up to now has eliminated species at the lower trophic levels, although these are the most abundant and productive.

Due to the wide dispersal of living matter in the ocean these conditions only occasionally coincide. To appreciate this it is only necessary to compare, on a world scale, primary production (which is in the order of 150×10^9 tons/year) with the volume of marine catches (about 60×10^6 tons/year). In fact, fishing is presently viable only at a small number of productive "traps" where the production of the seas is concentrated. To illustrate the highly selective nature of fishing it is sufficient to compare the catches of the different elements of the flora and fauna to their respective biomasses. Thus as regards the flora, exploitation is very unevenly spread geographically and basically applies to just a few species of macroscopic algae, of which the harvest accounts for only one per cent of the total harvest of living matter of aquatic origin. Of the more than 20,000 species making up the world's fish fauna a mere 100 species account for over 70% of the world catch. In 1971, a single species, the Peruvian anchoveta, accounted for more than a fifth of the world's fish catch, while the seven species of anchoveta then being exploited accounted for more than a quarter of the total. (This comparison does not take into account the potential of the Argentine and the Californian anchoveta stocks whose biomasses amount to millions of tons.)

The increase in the proportion of pelagic fish in the total catch since the last world war is a measure of intensified fishing at the lower levels of the food chain. This phenomenon can even be seen in the composition of pelagic catches, where the weight ratio of phytoplankton feeders to zooplankton feeders has gone from 4/96 to 39/61 over the past 30 years. This development is the result of the greater productivity of the lower levels of the food chain. Moiseev (1972) estimated the oceanic production of zooplankton alone (i.e. not including phytoplankton) as being 13 to 15 times greater than that of the benthos consumed by exploited species, while the total weight of plankton feeders directly fished, or eaten by predators that are fished, is only 10 to 12 times greater than the total weight of exploited demersal species which feed on benthos. While the complexity of the predator-prey relationships prevents any direct comparisons, these figures do suggest that pelagic stocks are less intensely exploited than the traditional demersal stocks. This view is supported by the results of stock assessments that show coastal pelagic resources throughout the world could supply about another 15 million tons per year, while demersal stocks could not supply more than an extra 5 to 10 million tons per year.

The geographic distribution of fishing is also highly selective. Almost the entire catch is made in waters over the continental shelf (in 1971 almost the entire demersal catch and 94% of the pelagic catch), which accounts for the importance of the extent of the continental shelf as a factor in the fishery potential of a region. For example, the Atlantic and North Pacific (where the continental shelf is particularly extensive, and half the North Atlantic is less than 1 000 meters deep) supply half of the total world catch. The proportion is even higher for the demersal fish catch.

Even among neritic waters, fishery resources are unevenly spread. Upwelling regions account for around half the total potential (of conventional species) in the sea, i.e. 40 to 60 million tons out of a total which is in the order of 100 million tons (Cushing, 1972).

In fact, up to now, man has only been skimming off the cream of the oceans' total production. Is he capable of improving his performance in the near future? At present, the prospects can be considered in three groupings:

(a) As regards the traditional stocks, production probably will not increase more than 50 to 100 percent, i.e. perhaps to some 100 million tons. Considering previous rates of expansion in world fishing, such a position could be reached within the next ten years. In many regions and for the more sought after and easily utilized stocks, the achievement of this objective already depends more on the implementation of suitable management schemes than on an intensification of fishing.

(b) The development of new resources is now technically possible in some cases:

- krill (potential possibly in the region of $50 - 100 \times 10^6$ tons)
- common and oceanic squids (potential possibly between 10 and 100×10^6 tons)
- bathypelagic fish (potential $> 100.10^6$ tons).

It is likely that the development of these resources will depend less on perfecting adequate fishing and treating processes than on the possibilities of finding new outlets that are suitable both as regards quality (new products) and, above all, as regards quantities (their potential is comparable to present world production). There is no way that one can further define these prospects since the utilization of the lower trophic levels will depend on other factors that cannot yet be quantified:

- the relationship between the cost of the catch and the value of the products (increased energy costs on the one hand due to greater dispersion in the marine environment and on the other the generally lower market value of new types of products).
- the effects that exploiting these stocks may have on the productivity of traditional stocks.

(c) There is some potential in marine fish farms which at present produce a little over 5% of the world catch and could produce 20 million tons by 1985, creating some 9 million jobs. It should be noted that even if marine fish farming and fishing are in competition in certain markets for certain similar products, these two types of industry will remain independent for a long time yet as regards their sources of supply (i.e. its geographic distribution). Since the ocean and its stocks are very difficult to control fishing will remain, for a number of decades, the most suitable method of exploiting the open areas. Marine fish-farming will be concentrated especially in the narrow land/sea interface that can be more easily managed. But here it will be in conflict with other uses of the environment, notably town planning, tourism, industry and agriculture, either directly because they are competing for the same sites or indirectly because of environmental changes brought about by these different types of activity.

3. Particular Characteristics of Fishing and Fishery Resources

It would scarcely be necessary to point out that fishery resources are living, except to emphasize the importance of knowing their biology and ecology and to stress the fact that they are renewable and thus exploitable forever, but not at any rate we like (as opposed to non-renewable resources).

Above all, they are wild and thus free. Stocks, in their distribution and migrations, are unaware of the frontiers drawn by man (all marine species, even the sessile species, have at least one period in their life when they move freely). In general, therefore, they cannot be owned by individual exploiters. The latter can only enjoy the benefits of exploitation, generally in groups (however the groups may be defined). Within these groups, the fishermen compete directly for shares of the yield of the stock, which is generally limited. (Such a stock is often referred to as a freely accessible resource.)

For these reasons, it is not possible to catch fish, for example, at only a certain age and a certain predetermined size. Thus, it is not possible to catch all the members of a particular year-class at the age when the weight of the year-class is at its maximum, as can be done in the case of domestic animals raised for meat. Furthermore, in the open sea, just as in inland waters above a certain size, the environment cannot be controlled. Physiochemical conditions, nutrient salts, the composition of the associated flora and fauna (food, predators, competitors, etc.) are beyond man's control. Even in cases of extensive cultivation, there can be only partial control of the nature and degree of environmental conditions. These difficulties connected with controlling the marine environment, its inhabitants and their yield mean that the comparisons such as fruit picking versus settled agriculture, hunting versus stock breeding (i.e. between the land environment and the sea environment) are not really justified. They also explain why even though fish farming has been in existence for a long time, (the Etruscans used to culture oysters), it was, in practice, limited to immobile species (shellfish) and had to be confined to the narrow land/sea interface where at least partial control could be exercised.

Given the living and wild nature of fish stocks, the optimum rate of exploitation (and even the method, since that may determine the average age and size of the individual fish taken) cannot be chosen arbitrarily. In the long term the highest yield will be attained by maintaining the rate of exploitation at a level corresponding to the maximum rate of natural replacement of the stock; above this rate and below it there will be some decrease in the yield. The objective of stock assessments is to determine, for the various stocks, what is their maximum rate of replacement and what the pattern of exploitation[1] should be to realize it. The object of this course is to see how this can be done.

4. Investigation and Assessment of Resources

In fact, the kind of information required, and its precision, change with the intensity of exploitation of a stock (see fig. 1).

The first step, when exploitation is still light or nil, consists of identifying those resources which are most likely to support an expansion of the industry and meet the demand of the market.

Among research tasks at the various stages of fishery development, distinctions can be made according to the nature of the information being sought:

(a) Surveys aimed at directing the industry to the more interesting stocks (bearing in mind the needs and capacities of each country) so as to develop fisheries on the various stocks in the most appropriate order. This has not always been the case since fishing often develops on the basis of borrowed attitudes or methods which only rarely conform to actual requirements. Thus on the west coast of Africa trawling for demersal fish developed before seine fishing for coastal pelagic fish which better suits the needs of the region. The main goals of these surveys are to establish:

- an inventory of potentially usable stocks;
- the commercial possibilities of the corresponding catches;
- an approximate order of magnitude of potential catches, or at least a minimum limit of these potentials which can be used as a temporary ceiling for development plans.

Moreover, to arouse the interest of potential investors it is necessary to get figures on:

- estimated catches and revenues for various types of vessels and methods of fishing;
- the seasonal and areal variations in catch rates (particularly by localizing in time and space the most dense concentrations).

(b) Monitoring the state of stocks at different levels of exploitation. All fishermen know that when the number of boats exploiting a stock increases, the catch rates and individual catches decline progressively until, at a certain level, the total catch levels off (fig. 1). Any new investment will then lead to a lowering in the long term of stock abundance and catches. Since increasing fishing effort will not produce an increase in the total catch indefinitely, proper planning requires a prediction of the effects on the size and composition of the stock on the one hand, and on the yields and total catch on the other, of different increases in fishing effort.

In particular, answers must be found to the following questions:

- what proportion does the current catch represent of the potential maximum catch?
- what are the current catch rates and how will they change if fishing is intensified?

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[1] Pattern of exploitation here means the combination of the rates and modes of exploitation

- what size of fleet is required to attain the levels of production that can be envisaged?
- what will be the effects on the stock and catches of given changes in mesh size or, more generally, in the minimum size of individual fish caught?

(c) Assessment of potential maximum catch. There are, in fact, only too many examples of cases where over-optimistic estimates of potential have led to excessive investments and eventually considerable economic loss, and where the failure to take decisions to control fishing has led to serious over-exploitation of stocks and the collapse of certain fisheries. Since the control of fisheries can, in the short term, result in real hardships (reduction of investments, loss of jobs), information on the state of stocks should be sufficiently clear and precise so as to convince the decision makers. Finally, it should be noted that the potential catch rarely remains constant from one year to the next. In fact, the maximum surplus that can be fished is liable to vary from one year to the next depending on changing environmental conditions. These unpredictable fluctuations, like long-term variations, can be quite considerable for certain stocks, e.g. coastal pelagic fish. To derive the greatest benefit from them, it would be wise to take these fluctuations into account in management plans or, at least, to be in a position to cut back on fishing in the event of an abnormal drop in stock abundance. Stock evaluation, therefore, should be considered as an ongoing task where estimates are constantly being readjusted and refined.

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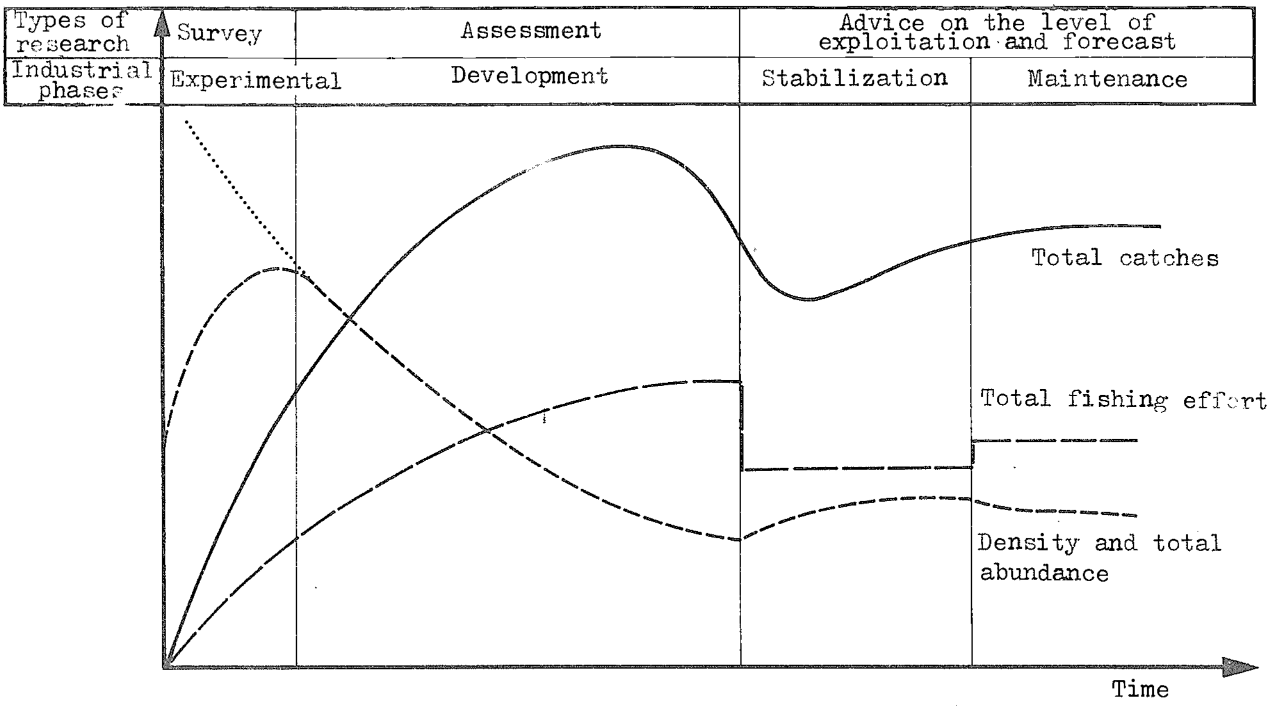

Fig. 1 - Development of a fishery
(G. Kesteven, 1973 - modified)

THE CHARACTERISTICS OF AN EXPLOITED STOCK

by

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1. Effects of fishing

In a fish stock, a number of fish is born each year. During the life of a yearclass, each year a certain percentage dies until, for some species after a few years, for others after a longer time span, all fish of that yearclass have disappeared (table 1).

Table 1 - Annual survival of 1 000 young fish at successive ages, for a long-living fish species (annual mortality 20%) and a short living fish species (annual mortality 70%)

Annual mortality %	Age 0	1	2	3	4	5	6	7	8	9	10	etc.
20	1 000	800	640	512	410	328	262	210	168	134	107	-
70	1 000	300	90	27	8	2	1					

A table can be drawn up giving the number of fish of a yearclass in the successive calendar years during its life. We can also include several yearclasses, in a scheme as table 2.

Table 2 - Number of fish surviving at each age from 1 000 young fish, for a series of successive yearclasses. Annual mortality 20%.

Year	Age 0	1	2	3	4	etc.
1959	1 000	800	640	512	410	-
1960	1 000	800	640	512	410	-
1961	1 000	800	640	512	410	-
1962	1 000	800	640	512	410	-
1963	1 000	800	640	512	410	-
etc.	-	-	-	-	-	-

If we assume that 20% of the fish die during each year of life, and that 1 000 fish were born in 1959, the figures in the rectangles in the table show the numbers from that yearclass surviving at each age. If each year the same number of fish are born, it can be seen that the numbers of each age present in one year (encircled figures) are the same as the numbers of one yearclass at successive ages during its life span (figures in rectangles). Hence the decline of numbers by age in the stock in a certain year also reflects the mortality of the fish.

Normally, the yearclass strength fluctuates from year to year. We can again construct a table in the same way as Table 2. The age composition of the stock in any one year now depends on the yearclass fluctuations, but if these are not too large will still also reflect the average decline by the mortality (table 3).

Table 3 - Number of fish at each age, with varying yearclass strength. Annual mortality 20%.

Year			Age			
	0	1	2	3	4	etc.
1959	1 000	880	960	307	410	-
1960	900	800	704	768	246	-
1961	1 300	720	640	563	614	-
1962	600	1 040	576	512	451	-
1963	1 000	480	832	461	410	
etc.	-	-	-	-		-

If a stock is exploited, each year a certain part of the fish is caught. Hence, the numbers decrease faster with age. If the numbers of survivors are set in the same scheme as the above tables, it can be seen that in any one year the stock is smaller than without fishing, and it will be smaller, the more intensive the fishery. The difference is most marked in the older fish. The heavier the fishery, the smaller the stock in the sea, and therefore also, the smaller the catch per boat. As the decrease is most marked in the older fish, the average size and age of the fish in the sea, and thus also in the catch, decreases with increased fishing. These are, in very schematic form, some of the principles of the effects of fishing on the fish stocks and the catches (table 4).

The fish stock shown in Table 4 has the same characteristic as that in Table 2 (annual natural mortality rate in the unfished state 20%). The fish of this stock is now, however, subjected to fishing, from 3 years old onwards. The fishing effort is such that the number of fish caught at each age is equal to the number dying by natural causes. At first glance it would seem that, thus, the number of fish caught during a year would also be 20% of the number present at the beginning, and that the total mortality rate would be 20 + 20 = 40% per year. This is, however, not the case, because the effects of the natural mortality and of the fishing mortality are not independent. This can be easily visualized if it is realized that some fish which would have died by natural causes later in the year if no fishing took place, now will have been caught before that time. The heavier the fishery, the lower will therefore be the percentage of fish which will die each year by natural causes. It will be shown later during this course that if two causes of mortality and simultaneously on the same stock of fish and the number of fish caught is equal to 1, 2, 3, 4. ....., n times the number of natural deaths, the annual survival rate is equal to the survival rate in the unfished stock raised to the power 2, 3, 4, 5, ..., n + 1.

For the conditions in Table 4a), where the number of fish caught is equal to the number dying by natural causes in the same time period, the annual survival rate is equal to the power 2 of the survival rate in the unfished stock (natural mortality rate 20%) if this survival rate is expressed as a fraction rather than a percentage. Thus the total survival rate under these fishing conditions is $0.80^2 = 0.64$, and the total mortality rate $1.00 - 0.64 = 0.36$ or 36%. As the numbers of fish dying by fishing and by natural causes are equal, the number of fish dying by natural causes is therefore 18%. In the same way it can be calculated that in Table 4b), where fishing is more intensive and causes twice as many deaths as the natural mortality, the number of survivors at the end of a year as the result of the combined mortalities will be $0.80^3 = 0.51$ of the initial number. Hence the total mortality is 0.49 or 49%, of which two-thirds (33%) due to fishing and one-third (16%) due to natural causes.

Table 4 - Numbers of fish at each age in the stock, and numbers caught, at different levels of fishing. The fishery catches the fish from 3-years old onwards.

(a) Total mortality rate 36%, fishing mortality equal to natural mortality

Age	0	1	2	3	4	5	6	7	8	9	10	-	Total
Stock	1 000	800	640	512	328	210	134	86	55	35	22	-	
Catch					92	59	38	24	15	10	6		244
										Average age			4.95 years

(b) Total mortality rate 49%, fishing mortality double the natural mortality

Age	0	1	2	3	4	5	6	7	8	9	10	-	Total
Stock	1 000	800	640	512	261	133	68	35	18	9	5	-	
Catch					167	85	44	22	11	6	3		338
										Average age			4.65 years

The table also shows that the total catch in numbers increases with increasing fishing, but not proportionally. If fishing effort doubles, the numbers caught are less than doubled.

All these results are rather obvious. The more intensive the fishery, the more fish caught at a relatively young age, and less and less remain to become older fish, with the result that the stock declines. All this is reflected in the catches per boat. Furthermore, the more fish caught young, the less there are to die by natural causes before they are caught, and hence the total numbers caught increase with increasing fishery. Even though these principles are simple, it is most important that they are fully understood, because these are the effects of fishing, on which stock assessment is essentially based.

So far, we have dealt with fish in numbers only. What is usually more important is the catch by weight. If we know how fast the fish grows, and thus know the weight at every age, we can convert the figures of catch in numbers into catch by weight. In order to study the relation between different levels of fishing and the catches by weight, a number of exercises are given at the end of this chapter.

From the curves obtained in these exercises, it appears that often the optimum catch by weight of a stock is obtained at an average level of fishing effort, and that at higher levels of effort the total catch does not increase, or declines again. The higher the mortality rate, the higher is the fishing effort at which the maximum catch is obtained. Again, this can be understood at closer consideration. With little fishing, the average size, and hence weight, of the fish is rather large, but few fish are caught and the total weight is low. With very heavy fishing, very many fish are caught, but all are very young when the weight per fish is low. Somewhere in between many fish are still caught, and many of fair size, resulting in a higher total weight. With high natural mortality, heavier fishing is needed to prevent too many fish dying by natural causes, and hence the optimum catch is at a higher level of effort. Similar considerations can be applied to understand the effects of changes in the age of first capture of fish.

The examples have been calculated for 1 000 fish. It is easy to understand that what happens to these 1 000 fish will happen to any other 1 000 fish of the same age, mixed with the first 1 000 in the same area. Thus, if every year 10 x 1 000, or 1 000 x 1 000, or n x 1 000 fish are born, the principles of the effects of fishing remain the same.

The above calculations were greatly simplified. For example, natural or fishing mortality may vary with age of the fish. This can easily be incorporated in the calculations which will show that the principles still remain valid. Another simplification is that it has been assumed that natural mortality, growth and recruitment remain constant, irrespective of the level of fishing. It has been shown in various species that the decline in stock size as a result of heavy fishing may lead to changes in e.g. growth or recruitment. It is clear that with a decrease in the number of larger fish in the stocks, there is less competition for food, and the egg production will also decrease. The latter does not necessarily lead, however, to a decline in recruitment as the percentage survival of the eggs and larvae may increase at lower levels of egg production. All these so-called "density dependent factors" can again be included in the calculations. The studies carried out so far in this field have indicated that whereas these factors may alter the details of the graphs and, for instance, the position of the maximum, they do not alter the overall picture of the effects of fishing.

The major purpose of this section has been to clarify, with simple examples, the general principles of the effects of fishing. The next section will explain how this knowledge can be used to evaluate the potential yield and the state of exploitation of the fish stocks.

2. Estimation of potential catches with different fleet sizes, and of state of exploitation of stocks

The calculations in the previous section have been made with simple arithmetic. Usually, it is found more convenient to use algebraic calculations, which simplify the work in more complicated situations. These matters will be dealt with in more detail in the coming weeks. Whatever the methods of calculation, it is clear that they require good information on growth, mortality and, eventually, recruitment of the fish. If such information is available, the methods can determine at what fishing mortality rate the best total catches are obtained, etc., but they do not determine the corresponding fleet size, e.g. whether 100 vessels cause a fishing mortality of, say 10 or 50% per year. However, if data on age composition and catches per boat are available for different periods with different fleet sizes fishing the stocks, it is possible to estimate what fleet size causes a moderate or intensive level of fishing. This requires, therefore, data over as many years as possible. It is in particular desirable to include in the analysis data from periods with very low levels of fishing, to get a picture of the situation when the only significant mortality is natural mortality. This requires that some sampling and statistical data collection is started in the very early stages of the fishery. Even though, at these stages, the work will not lead to immediate estimates of the available resources, they may prove to be of very great importance later when fishing has become more intensive and scientific advice is required on the needs for and methods of management of the fishery. The information on the virgin stock composition and density can never be obtained later when the fishery has developed and absence of this information makes the analysis later rather more difficult.

In many instances, however, the required detailed information on length and age-composition of the catches is not available, because of lack of funds or manpower to collect the information, impossibility of determining the age of a fish, or other reasons. If sufficient catch statistics of the fishery are available, another way of studying the problem can be applied. In the previous section the way in which fishing affects the stocks has been discussed. If data on the fleet size, the total catches and the catches per boat are available for a series of years with different levels of fishing, the catch per boat and the total catch can be plotted against the number of boats (with certain precautions and restrictions to be discussed later). The form of these curves will then more or less show what is the state of the fishery, whether it can be expected that the catch will increase at higher levels of fishing, or that fishing has already reached or passed the optimum level. For this approach statistical data are needed on the number of boats (fishing effort), broken down by size and fishing method, on the total catch for all fleets fishing the same stocks and/or on the catch per boat. Again, it is important to have these data from an early stage of the fishery onward, even though it has to be taken into account that in the first years of a fishery the catch data of a vessel are often not comparable with those of later when the gears have been developed, the fishermen have learned how to fish the species in the area, etc.

The picture given so far is a simplified one. There are many problems in estimating the various characteristics of the stocks and of fishing, and more refined models have been developed than the simple ones describes so far to allow for greater complexity. A particular aspect which should still be mentioned is that whereas the changes in the catches discusses above are those caused by fishing, there are many other causes of variation: natural ones such as those due to variations in yearclass strength, variations in catchability of the fish, or other effects of variations in the environment, changes in fishing due to market preferences, or to efficiency of the fleets, etc., sampling variation in the data. Often, these variations are more or less random, and in that case their major effect is that they cause irregular variations in the data which, if they are not too large, usually do not obscure the trends due to fishing. The changes may also, however, show a trend, e.g. a long-term fluctuation in the environment. If such a trend occurs at the same time that the intensity of fishing changes, this makes it more difficult to actually assess the effects of fishing. But whereas these difficulties complicate the work, the principles remain valid. For estimation of fish stock potentials, and of the effects of fishing on the stocks and the catches it is, therefore, essential to understand these principles.

3. Exercises characteristic of an exploited stock

I. In an unexploited stock, 20% of the fish of each age present at the beginning of each year die during the year. Growth studies have shown that the weight of the fish at each age is:

Age	0	1	2	3	4	5	6	7	8	9	10	years
Weight	0	13	37	81	147	233	325	420	512	595	650	grams

(1) Draw the curve of the number of survivors (at the beginning of each year) of a yearclass starting with 1 000 fish, as a function of age.

(2) Draw the curve of the total weight of the survivors as a function of age.

(3) At what age does the yearclass reach its maximum weight?

(4) Calculate the average age reached by the fish of one yearclass (assuming that all remaining fish die at reaching 10 years).

II. If the above stock is exploited by a fishery which starts catching the fish from 3 years old onwards with an intensity so that the numbers dying each year by fishing is equal to the numbers dying by natural mortality (total annual mortality for exploited ages is 36%):

(1) Calculate the numbers caught at each age, and draw the curve of the numbers surviving at each age.

(2) Calculate the weight of the fish caught at each age, and draw the curve.

(3) What are the number and weight of the fish caught during the whole life of the yearclass?

(4) Calculate the average age of the fish in the total catch of the yearclass.

III. Repeat exercise II for the following values:

	Total mortality per year	$\frac{\text{Numbers caught per year}}{\text{Numbers dying by natural causes per year}}$
1.	22%	0.25
2.	28%	0.5
3.	49%	2
4.	59%	3
5.	67%	4
6.	74%	5

The relation between the numbers caught and the numbers dying, given in the last column, is proportional to the fishing effort.

Plot, as a function of this measure of fishing effort, the following curves:

(1) Total number of fish caught.

(2) Total weight of fish caught.

(3) Total number of fish caught, divided by fishing effort index (as a measure of catch per unit effort).

(4) Total weight of fish caught, divided by fishing effort index.

(5) Average age of fish in total catch.

IV. Repeat exercises I, II and III for a stock in which, when unexploited 63% of the fish die each year by natural mortality, and where fishing only catches fish of one year and older, for the following values (start with 1 000 fish of 0 year):

	Total mortality for unexploited ages	$\frac{\text{Numbers caught per year}}{\text{Numbers dying by natural causes per year}}$
1.	78%	0.5
2.	86.5%	1
3.	95%	2
4.	98%	3
5.	99%	4

This species has a weight at age as follows:

Age	1	2	3	4	5	years
Weight	11.5	24.3	36.8	44.5	49.0	grams

V. Repeat exercises II and III for fisheries with different selectivity catching fish from 2nd or 5th year onwards at the indicated mortality rates.

DYNAMIC POOL MODELS

by

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1. Introduction

An exploited fish population can be thought of as a pool with continual inflows and outflows. During a year, the population in number loses some members to fishing and natural mortality and gains members as young fish recruit to it. Meanwhile, the population in weight increases or decreases according to the number and weight of the members lost and the recruits gained but also increases as individuals grow in weight. Figure 1 shows how these gains and losses might take place during a year within a stock of fish that has four age groups and therefore four size groups.

The figure shows a balance of gains and losses: recruitment compensates for losses in number due to mortality and the combination of recruitment and growth compensates for losses in weight due to mortality. The youngest age group is replaced by recruits and the older age groups are replaced by the surviving (and growing) members of younger age groups, with the result that the population at the end of the year has the same size and composition that it had at the start of the year. (Note that all members of the oldest age group die during the year, which is not entirely realistic but for practical purposes is usually an adequate way to represent the fact that all animals have a maximum lifespan.)

So long as mortality rates and recruitment remain constant, the population will repeat the processes portrayed in the figure year after year, maintaining the same size and composition and providing a catch of the same size and composition. But the steady state shown in Figure 1 is not the only one possible. If recruitment and the rate of natural mortality remained constant but the rate of fishing mortality increased, the population would eventually reach a new steady state, in which both the population and the catch would have a different size and composition, as shown in Figure 2.

In this case, even with the same annual recruitment, the standing stock is smaller in number and much smaller in weight, since the higher mortality results in low survival to the greater ages and sizes and therefore a stock consisting mostly of young, small fish. The catch in number is greater in this case because fishing removes a larger share of each group of recruits. On the other hand, since the catch consists mostly of small fish, the catch in weight is not necessarily greater and may be substantially smaller than in the previous case.

One way to realize the benefits of both cases (i.e., a fairly high catch in number of fish of a fairly large size) might be to impose the higher level of fishing mortality but only on fish above a certain size, i.e., to regulate the fishery so that small fish are not captured. This would entail some reduction of the catch in number since some small fish would be lost to natural mortality that otherwise would have been caught, but the larger average size of the fish that are caught might result in a greater catch in weight nonetheless.

Evidently the catch in weight that will be provided year after year by a stock depends in a complicated way on the level of recruitment, the rate of natural mortality, the growth schedule of the fish, the age at first capture and the rate of fishing mortality. Of these, only the last two (sometimes only the last one) can be controlled, so for management purposes the problem is to find which of all possible combinations produces the largest yield. The computations that lead to this result are the subject of this section.

Yield computations are, inevitably, laborious but two features of the dynamic pool model simplify the process considerably:

1. When a stock is in steady state (i.e., recruitment, growth and mortality are constant) the annual yield from the entire stock is equal to the yield from a single group of recruits during its entire lifespan, as can be seen in Figures 1 and 2. Another way of showing this equivalence is presented in Figure 3. Since the size and composition of the populations are the same year after year, the columns that show the size groups present at any one time can also be viewed as the progression of a single group of recruits through its life, during which individuals grow in size and decline in number, finally to extinction. In the same way, the boxes that show the catch from all the size groups present in any one year can be viewed as the successive contributions that any one group of recruits will make to the catches over the years of its life. Because of this feature of the model, it is not necessary to construct the entire stock in order to compute the annual yield; instead, it suffices to compute the total yield from a single recruit group over its entire lifespan.

2. The annual yield is directly proportional to the level of annual recruitment for any fixed combination of the other factors (growth schedule, natural mortality rate, fishing mortality rate and age at first capture). These other factors do not generally have a proportional effect but in Figures 1 and 2 it can be seen that the number of fish in each size group in each box can be doubled (or tripled, or halved) without upsetting either the balance of gains and losses or the relative composition of the stock and the catch. Only the size of the stock and the catch change, and they change in direct proportion with the change in the number of recruits. This feature makes it unnecessary to know the absolute magnitude of recruitment in order to find the best values of age at first capture and fishing mortality; instead, it suffices to find the values that maximize the yield from any arbitrary number of recruits, or more generally, the yield per recruit.

In other words, maximizing the yield per recruit maximizes the yield from the stock, a result that holds even when recruitment varies from year to year, as it usually does. In this case, the optimum values of age at first capture and fishing mortality rate do not imply a constant annual yield from the stock, but they provide the maximum yield that can be taken from the actual recruitment.

Given a knowledge of the growth schedule and natural mortality rate, then it is a straightforward computational problem to find the best values of age at first capture and fishing mortality rate according to the dynamic pool model. These values, which maximize the yield per recruit, will maximize the yield from the stock so long as one critical condition of the model is satisfied, namely, that the level of recruitment, the natural mortality rate and the growth schedule are not affected by the size and composition of the stock, which will depend on the pattern of fishing as Figures 1 and 2 show. This condition is not likely to hold at all levels of fishing mortality in any stock and some fisheries provide clear counterexamples. In particular, recruitment has decreased greatly in some stocks reduced to a small size by heavy fishing and in at least one case the rate of growth increased when the size of the stock was reduced.

Despite these counterexamples in many stocks, recruitment, growth and natural mortality have shown little systematic variation with fishing effort over a considerable range of variation in effort. For these stocks the dynamic pool model has been a reliable guide for management. The model is also useful for predicting the increase or decrease in yield that can be expected from any stock as a result of some change in age at first capture or fishing mortality rate so long as the proposed change is not very large, since a moderate change in either of these will probably not greatly affect the other factors.

It should be mentioned here that the dynamic pool model can easily incorporate relationships between recruitment, growth and natural mortality on one hand and fishing effort or stock size and composition on the other. These relationships require more involved computations but do not change the basic concept, which is the dynamic balance between gains and losses in a stock that has reached a steady state.

2. The biomass history of an unfished cohort

As the group of fish recruited to a stock in any one year (called a year-class or cohort) passes through life, its members grow in size but become progressively less numerous owing to mortality. The total weight, or biomass, of the cohort at each age is therefore the product of a decreasing function (number surviving) and an increasing function (average individual weight). In the absence of fishing, the result is usually a function with a maximum at some age: early in life, when individuals are growing rapidly, the biomass of the cohort increases despite losses to natural mortality, but as the fish age their rate of growth declines and after some age the losses to natural mortality exceed the increments due to growth, so the biomass of the cohort declines steadily.

These processes are shown numerically and graphically in Table 1 and Figure 4 with values typical of the freshwater bream Abramis brama (Backiel and Zawisza, 1968). In this example, young fish recruit to the adult stock at two years of age, the instantaneous rate of natural mortality is $M = 0.15$ and the growth schedule is as shown. It can be seen that the cohort reaches its greatest weight at an age of about eight years and declines thereafter.

The age at which biomass is a maximum is called the critical age. It is obvious that the maximum yield per recruit can be taken only be delaying fishing until the critical age and then harvesting the entire cohort at once. It is also obvious that this is impossible, since it would require an infinite fishing mortality rate. On the other hand, the biomass of an unfished cohort is often near the maximum for a few years around the critical age (in the bream example from ages seven through ten) when gains due to growth and losses due to mortality are nearly equal. Hence a yield per recruit close to the maximum can often be obtained by delaying first capture until an age somewhat less than the critical age and then harvesting most if not all of the cohort in a few years of sustained fishing thereafter. (In the case of fish with high rates of growth and natural mortality, of course, this period may be a matter of months rather than years.)

3. Methods of computing yield per recruit

For management purposes it is often necessary to compute quite precisely the yield per recruit that would be obtained with a particular age at first capture and fishing mortality rate. This precision is required because the regulatory measures called for by the computations may be a substantial burden on the government or the fishermen, so the benefits to be realized by introducing or changing regulations must be demonstrated convincingly.

The basic equation used in all computations of yield per recruit is the derivative expressing the instantaneous rate of yield from a cohort:

$$\frac{dY_t}{dt} = F_t \cdot N_t \cdot W_t$$

Where Y_t is the total yield from the cohort from the time of its recruitment to time t, F_t is the instantaneous rate of fishing mortality at time t, and N_t and W_t are the number and average weight of survivors at time t. If the mortality rates and the growth function do not change over the unit time interval following time t (in particular if F_t is a constant), then the yield from the cohort during that interval will be:

$$Y_{t+1} - Y_t = \int_t^{t+1} \frac{dY_\tau}{dt} \cdot d\tau - \int_t^{t+1} F_t \cdot N_\tau \cdot W_\tau \cdot d\tau = F_t \cdot \int_t^{t+1} N_\tau \cdot W_\tau \cdot d\tau$$

(The symbol τ replaces t in the integrands because t and t+1 are the limits of integration. Hence τ is just a different symbol for time, $t = \tau = t+1$.)

In all methods for computing yield, survivorship is represented as:

$$N_\tau = N_t e^{-(F_t + M)(\tau - t)} = N_t\ e^{-Z_t(\tau - t)}$$

There are various forms of the growth function w_τ, which among other things distinguish the different computational methods.

Once a particular growth function has been chosen it remains only to divide the life history of the fish into unit time intervals such that mortality rates and growth function parameters are constant on each interval, evaluate the successive yields from a cohort of arbitrary initial size over the sequence of intervals given particular values of the age at first capture and fishing mortality and take the sum. This sum, the total yield from the cohort over its entire lifespan, will of course be directly proportional to the arbitrary initial number R of recruits chosen for the computations. Hence the yield per recruit can be obtained either by dividing the sum by R or more simply by setting R = 1 for the computations.

A question that can arise in computing yield over the lifespan of the cohort is just how long the lifespan is. In many fish populations the rate of natural mortality is nearly constant over most of the adult period, but the oldest fish are much rarer than would be predicted from the mortality rate. Evidently natural mortality is often higher in old age among fish, as it is among humans. When one is computing yield per recruit with a single estimate of the natural mortality rate, one can suppose either that this rate persists indefinitely and the old fish die off gradually or that all survivors die at some maximum age. Since the actual course of mortality is likely to be intermediate between these extremes, the former treatment will overestimate yield and the latter will underestimate it.

In most applications, however, the difference between the two treatments in computed yield will be very small, since even in moderately fished populations the proportion of a cohort that survives to old age will be miniscule. Moreover, both treatments of mortality in old age will produce nearly the same computed difference in yield that would result from a change in the age at first capture or the rate of fishing mortality and it is this comparison that is important for practical purposes.

The remainder of this section will summarize the more common yield computations, which differ fundamentally only in the form of the growth function w_τ.

3.1 Method of Beverton and Holt

Although earlier authors presented the idea of yield per recruit and some methods for computing it, the method of Beverton and Holt (1957, 1964) is the one best known and most often used, to such an extent that the dynamic pool model is usually called the Beverton-Holt model.

In their scheme, the growth in length of fish is represented by the von Bertalanffy equation

$$L_t = L_\infty(1 - e^{-K(t - t_0)})$$

and the weight of an individual fish is assumed proportional to the cube of length:

$$W_t = aL_t^{\,3} = aL_\infty^3\,(1 - e^{-K(t - t_0)})^3$$

In the simplest case, a cohort of an arbitrary number R of members is assumed to recruit to the adult stock at age t_r and to become vulnerable to capture at age t_c (and length L_c, which for computational purposes can be taken as the mean selection length of the gear). From age t_r onward, the fish are subject to an instantaneous natural mortality rate M, and from age t_c onward to an additional instantaneous mortality rate F due to fishing. (Sometimes a maximum age t_λ is assigned, after which no fish are assumed to survive. For the reasons stated above, this approach will not be considered here; only the case $t_\lambda = \infty$ will be discussed.)

With these designations and the usual $Z = F + M$, the number R_c surviving to the age at first capture is:

$$R_c = Re^{-M(t_c-t_r)}$$

and the number N_t surviving to any age $t > t_c$ is

$$N_t = R_c e^{-Z(t-t_c)} = Re^{-M(t_c-t_r)-Z(t-t_c)}$$

The instantaneous rate of yield at age t is:

$$\frac{dY_t}{dt} = FN_t w_t$$

so the total yield from the cohort over its lifespan is:

$$Y = F\int_{t_c}^{\infty} N_t w_t dt$$

$$= F\int_{t_c}^{\infty} Re^{-M(t_c-t_r)-Z(t-t_c)}\, aL_\infty^3 \, (1-e^{-K(t-t_o)})^3 dt$$

With $(aL_\infty^3) = W_\infty$, the integrated form is:

$$Y = FRW_\infty \, e^{-M(t_c-t_r)} \left[\frac{1}{Z} - \frac{3e^{-K(t_c-t_r)}}{Z + K} + \frac{3e^{-2K(t_c-t_r)}}{Z + 2K} - \frac{1e^{-3K(t_c-t_r)}}{Z + 3K} \right]$$

Tables of yield function

Beverton and Holt (1964) have prepared tables of their yield function in terms of the three derived parameters F/Z, L_c/L_∞, and M/K. This reparameterization of the equation simplifies the tables and also shortens them, since it has been found empirically that M and K are correlated and therefore the variation of the ratio M/K is much less than the variation of either M or K among fish stocks. The authors have also explained in a preface how the tables can be used to calculate the yield for only part of the lifespan, so these tables are useful even when mortality rates or growth parameters change during the lifespan of a cohort. In fact, the tables show values of a derived quantity Y which is proportional to the yield Y. It is, however, a simple matter to calculate Y from the tabled values, as well as other quantities of interest such as mean population and biomass, mean weight in the catch, etc. Formulas for making the necessary conversions are given in Table 2.

3.2 Method of Jones

The major flow in the Beverton-Holt method is that it requires isometric growth, i.e., a strict proportionality between weight and the cube of length. In many stocks the weight of an individual is proportional to some power of length different from three and in these cases computing yield by the Beverton-Holt method will result not only in erroneous absolute yields but also in erroneous differences in yield between different ages at first capture and fishing mortality rates (Paulik and Gales, 1964).

Suppose that growth in length can be described by a von Bertalanffy curve, but that the length-weight relationship is:

$$w_t = aL_t^b$$

where b is a power different from three. The instantaneous rate of yield is then:

$$\frac{dY_t}{dt} = FN_t aL_\infty^b \, (1-e^{-K(t-t_o)})^b$$

which is easy to write but impossible to integrate. However, Jones (1957) has shown that by transformation of variables the yield can be expressed as:

$$Y = (\frac{F}{K})RaL_{\infty}^{b}\, e^{-M(t_c - t_r)} e^{(F+M)(t_c - t_o)} \int_{0}^{e^{-K(t_c - t_o)}} x^{(\frac{F+M}{K} = 1)} (1-x)^{b} dx$$

The integral is now in the form of the incomplete beta function

$$\beta\ (z;\ p;\ q) = \int_{0}^{z} x^{p-1} (1-x)^{q-1} dx$$

which has been tabulated (Pearson, 1934; Wilimovsky and Wicklund, 1963). The value of the integral can be found by entering the tables at

$$p = (F + M)/K = Z/K,\ q = b + 1 \text{ and } z = e^{-K(t_c - t_o)}$$

While this method treats allometric growth exactly, it is not often used because the exact yield cannot be computed by hand and the published tables of the incomplete beta function are in fact scarce items. When growth is markedly allometric and Jones' computation cannot be performed, Paulik and Gales (1964) have recommended that a von Bertalanffy curve be fitted to the cube root of weight at each age and this fictitious length schedule used in computations by the method of Beverton and Holt. This solution is not exact but it eliminates most of the error.

3.3 Method of Ricker

The most general and flexible computational method is due to Ricker. (He first presented it in 1945; see Ricker, 1975 for his own account.) Since this method makes no assumption about the form of the growth function, it is the simplest mathematically; for the same reason it is the most laborious computationally.

The yield from a cohort during a unit time interval is:

$$Y_{t+1} - Y_t = F \int_{t}^{t+1} N_t W_t dt$$

Whatever the form of W_t, the integral above is the average biomass of the cohort during the interval, denoted by $\bar{B}_t$. In its simplest (arithmetic) form, Ricker's method avoids the form of W_t and consequently a direct evaluation of the integral by employing the approximation:

$$\bar{B}_t = (N_t W_t + N_{t+1} w_{t+1})/2$$

That is, the average of the biomass at the beginning and end of the interval, where of course $N_t + 1 = N_t e^{-Z_t}$. The total yield is found by computing the yield on successive intervals as $Y_{t+1} - Y_t = F\bar{B}_t$ and taking the sum over the entire lifespan, which in this case must be specified.[1]

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[1] In mathematical terms, this procedure is called piecewise numerical integration by quadrature. The integral is the area under the yield curve, which is the curve representing dY_t/dt as a function of age t, which has the form $dY_t/dt = FB_t$. Quadrature means that the function B_t is approximated by drawing straight lines between the points at which w_t and therefore $\bar{B}_t = N_t W_t$ are known, rather than by assuming w_t and therefore B_t to be determined by some growth function between points. The approximation is quite accurate, regardless of the form of w_t, so long as a sufficient number of points on the curve are known. In Figure 4, for example, it can be seen that straight lines connecting the points that represent B_t at each age would lie very close to the smooth curve everywhere except in the vicinity of maximum biomass around age eight. But in this vicinity, where the absolute error of the approximation is largest, so is the area approximated, so the relative error is small over the entire curve.

Although it is an approximation, the Ricker yield computation is often more accurate than the exact forms. This occurs when the growth rate varies seasonally within the year, and for each age group the average weight is known at a few times during the year. In this case numerical integration according to the empirical growth schedule is more accurate than exact integration according to a parametric growth function, which may represent the annual growth increments quite closely but not the seasonal increments.

The major difficulty with the Ricker method, as opposed to the exact methods, is that it requires computing the partial yield during each age interval, one after the other over the entire lifespan, and taking the sum to find the yield per recruit that would be obtained with a particular combination of age at first capture and fishing mortality rate. With the exact methods this result can be obtained by evaluating a single expression. On the other hand, since the Ricker method requires a piecewise computation in any case, the labour is not increased when mortality rates vary among intervals, as is the case when the fishery is seasonal, or older fish suffer a higher natural mortality rate than younger fish, or young fish become fully vulnerable to the gear only over the course of several seasons or years.

4. Special applications

The fish of some stocks, particularly migratory ones, are caught by various gears in various places. Often the different gears are most successful in catching fish of different ages, so that in effect the fish pass through several fisheries, perhaps repeatedly, as they pass through life. In this case the effect of regulatory changes on each fishery must be considered as well as their effect on the total yield.

The exploited life history of a fish that passes through several fisheries is bound to be complicated by age-specific coefficients of catchability by each gear. Availability to each gear may vary with age as well as vulnerability. The calculation of yield per recruit to each fishery in this situation is a large job, since the lifespan must be divided into a large number of intervals and the yield to each fishery computed for each interval.

Because of the computational requirements, a computer is all but essential in applying the dynamic pool model to multi-gear fisheries. But since a computer programme that performs all the required calculations must in fact be a simulation model of all the fisheries that exploit the stock, it can rather easily be written to provide a great deal of information in addition to the total yield to each fishery under a particular set of regulations (e.g., it can provide catch per effort and mean weight in the catch in each fishery). Francis (1974), Lenarz et al. (1974) and Fonteneau (1975) described applications of the model to the fishery for yellowfin tuna (Thunnus albacares) in the Atlantic.

5. Comparison of the results given by the three methods

Tables 3a, 3b and 3c show the yield per recruit of bream for various ages at first capture and fishing mortality rates, calculated by the three methods discussed above. Growth in length was represented by the curve:

$$L_t = 42(1 - e^{-.233(t-.62)})$$

The length-weight relationship was:

$$w_t = .008142 L_t^{3.296}$$

from which $w_\infty = 1\ 823.81$. The instantaneous rate of natural mortality was $M = .15$. In the Beverton and Holt computations, the length-weight exponent was perforce taken to be 3.0 rather than 3.296, but the correct value of w_∞ was used. In the Ricker computations all survivors were presumed to die after 20 years of life.

It can be seen from the tables that, as could be expected, the values calculated by the methods of Jones and of Ricker are usually quite close, while the values calculated by the method of Beverton and Holt are in most cases substantially smaller. (In fact, the values calculated by the methods of Jones and of Ricker should be nearly identical for all values of F greater than .05. That they are not is the result of having to refer to the closest values rather than the exact values in tables of the incomplete beta integral. Even in a large table, such as that of Wilimovsky and Wicklund (1963) used here, the differences between successive entries are large and linear interpolation is not accurate, so the tabular entries frequently depart from the desired, i.e., exact, values by 10 percent or more. Nor will these deviations be consistent throughout the table. This difficulty is sufficient in itself to recommend not using Jones' method unless a computer is available to provide precise values numerically.

More important than the absolute values, however, is the fact that all three methods are in rough agreement on the best yields within any row or column of the yield table. For practical purposes, this means that any one of them would produce the same regulatory recommendation in the same conditions. As an example, if the fishing mortality rate were .4 and the age at first capture 2, all three methods predict a large increase in yield by raising the age at first capture to 6. The size of the increase is different, however: the Beverton and Holt method predicts a tripling of yield, the others only a doubling of it.

6. Yield isopleths

Often values of yield per recruit such as those in the tables are shown graphically. For any fixed value of either age at first capture or fishing mortality, the yield per recruit can be shown as a function of the other parameter, on a two-dimensional graph. To show it as a function of both parameters on a two-dimensional graph, it is customary to trace out the locus of points corresponding to the same yield for each of several levels of yield per recruit. These lines of equal yield, or isopleths, are in practice difficult to locate exactly, but they can be drawn approximately by entering the calculated yield values on a grid and interpolating between them, as shown in Figure 5.

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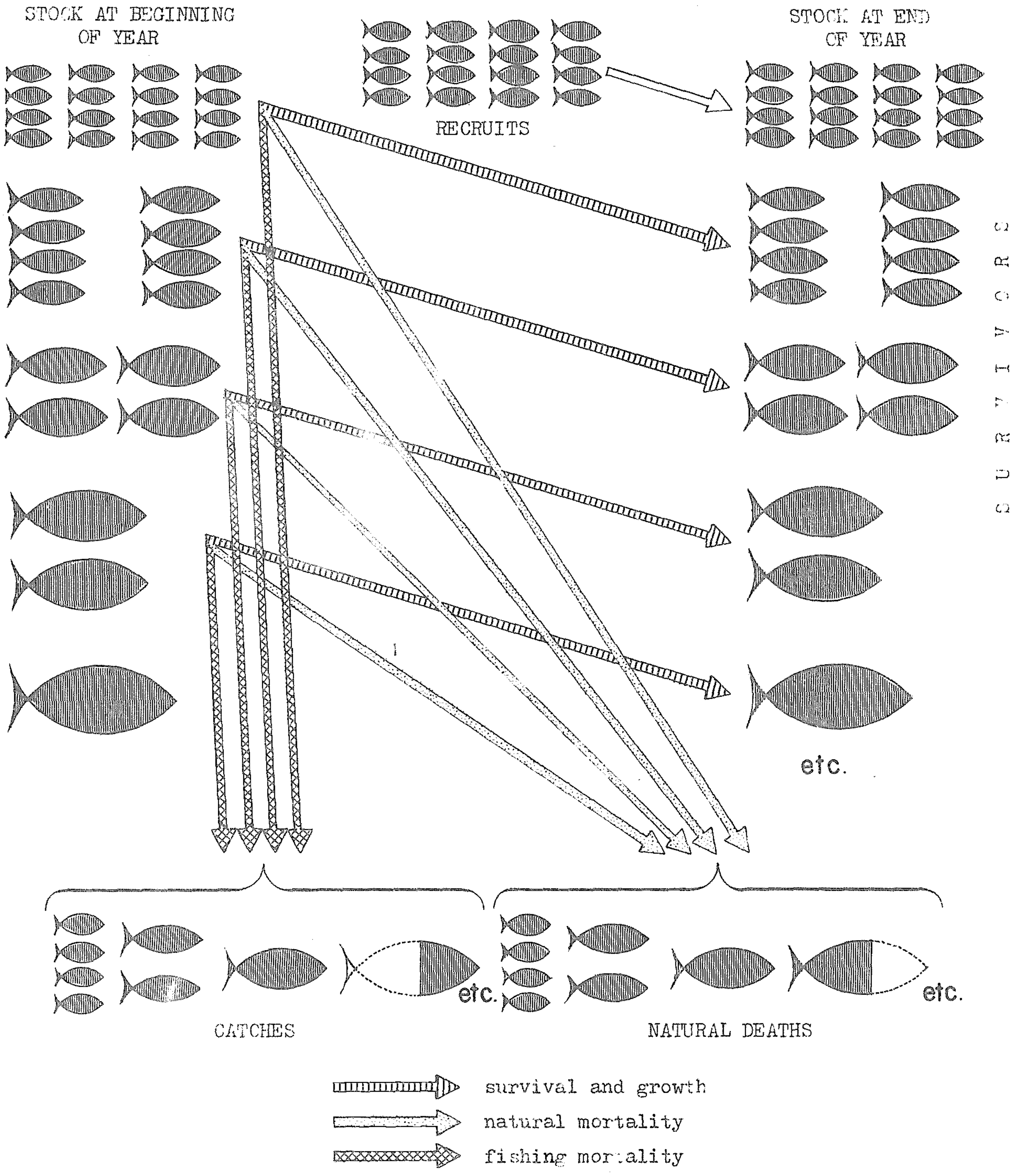

Fig. 1 - Loss and replacement of biomass in an exploited population

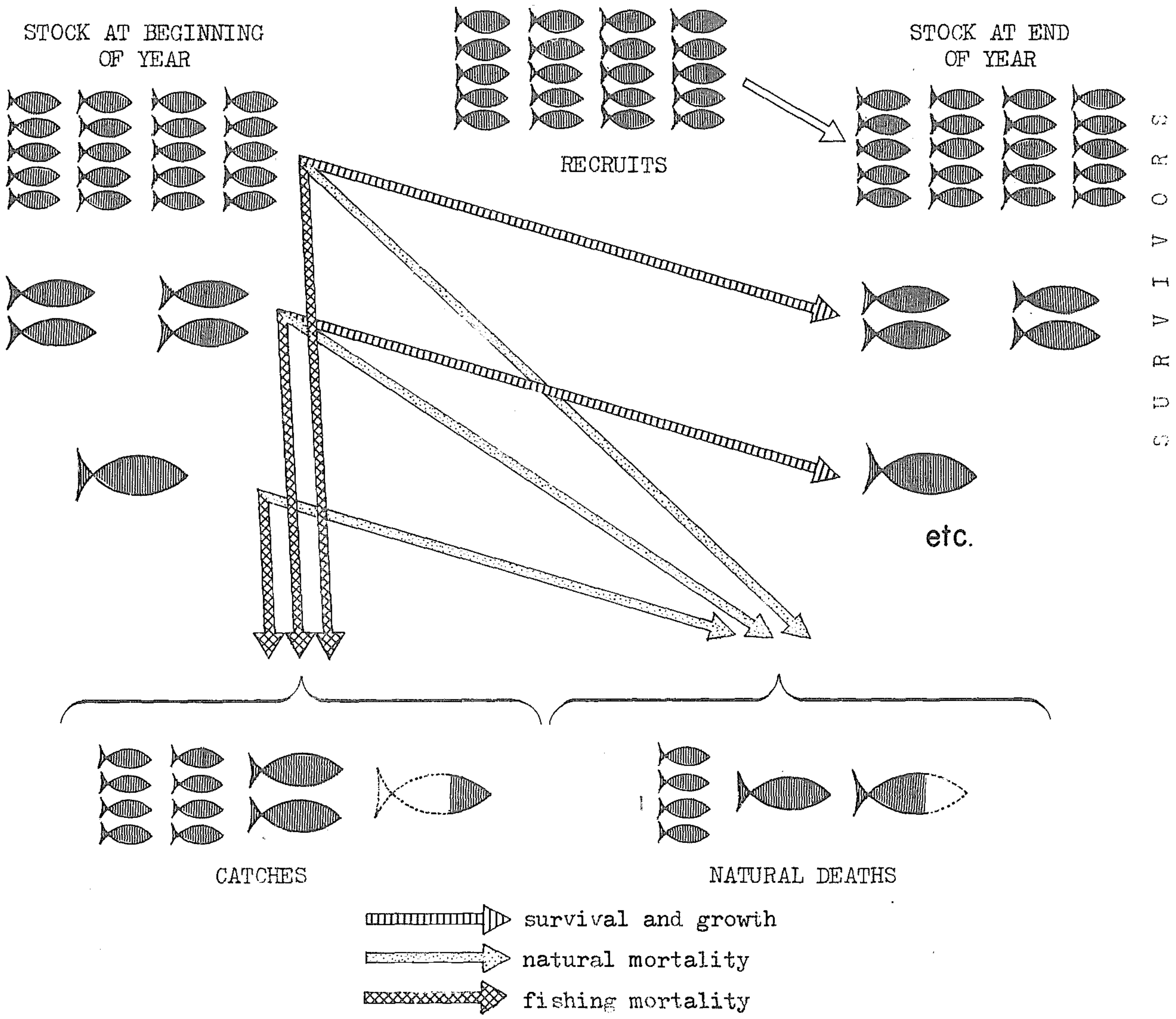

Fig. 2 - New equilibrium resulting from an increase in the rate of exploitation

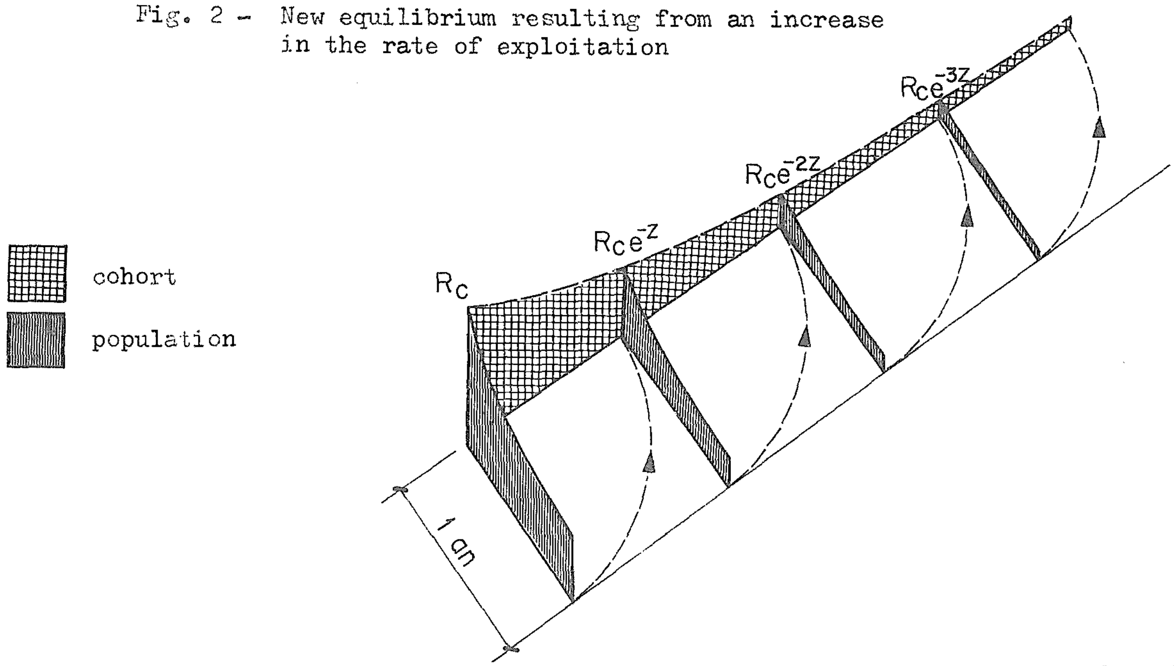

Fig. 3 - Diagram showing the equivalence of cohort abundance as a function of time and population composition as a function of age

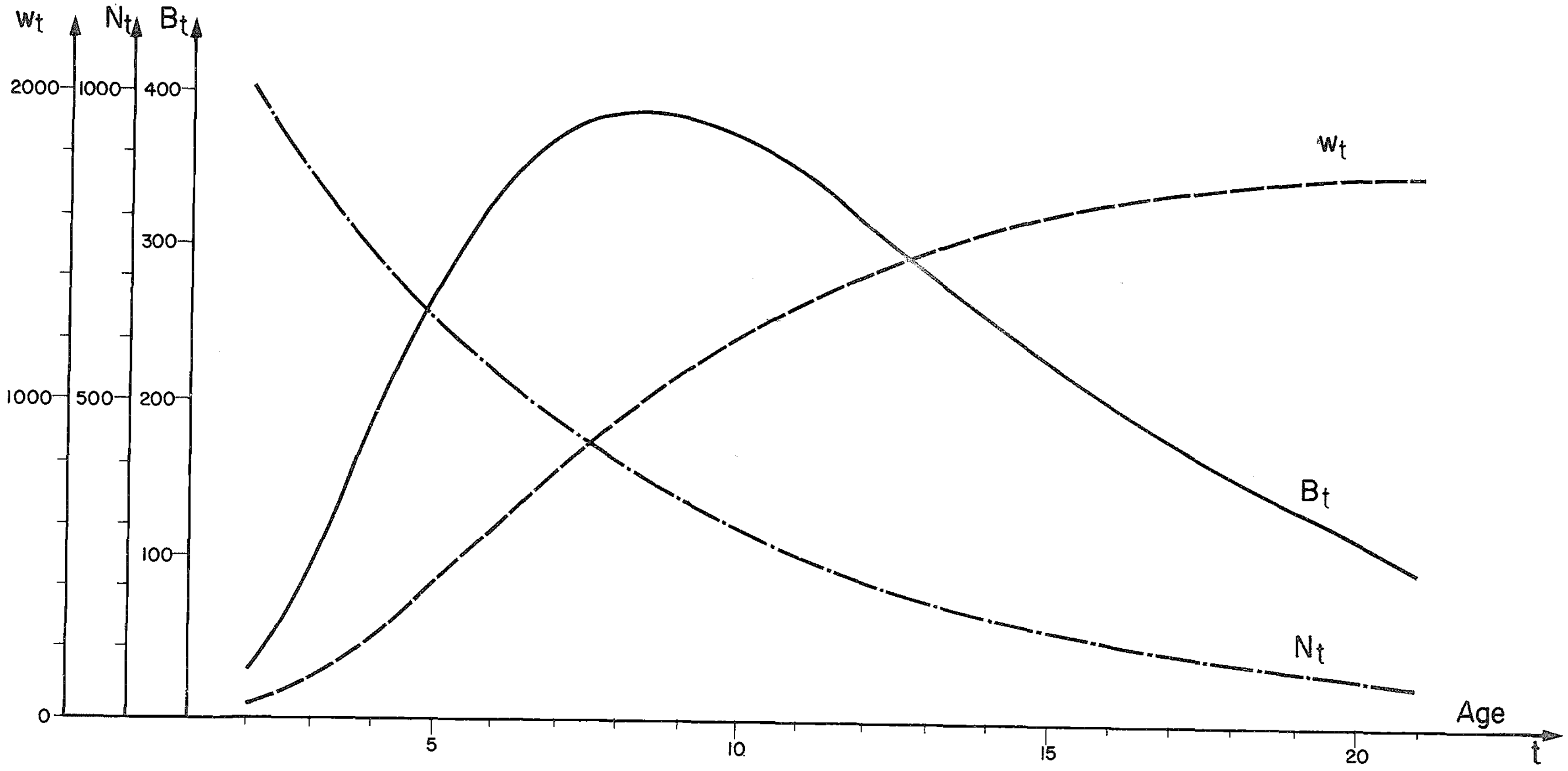

Fig. 4 - Graphical presentation of the biomass history of an unfished cohort of bream: t = age in years, w_t = average weight in grammes, N_t = number surviving, B_t = biomass in kg (data from table 1)

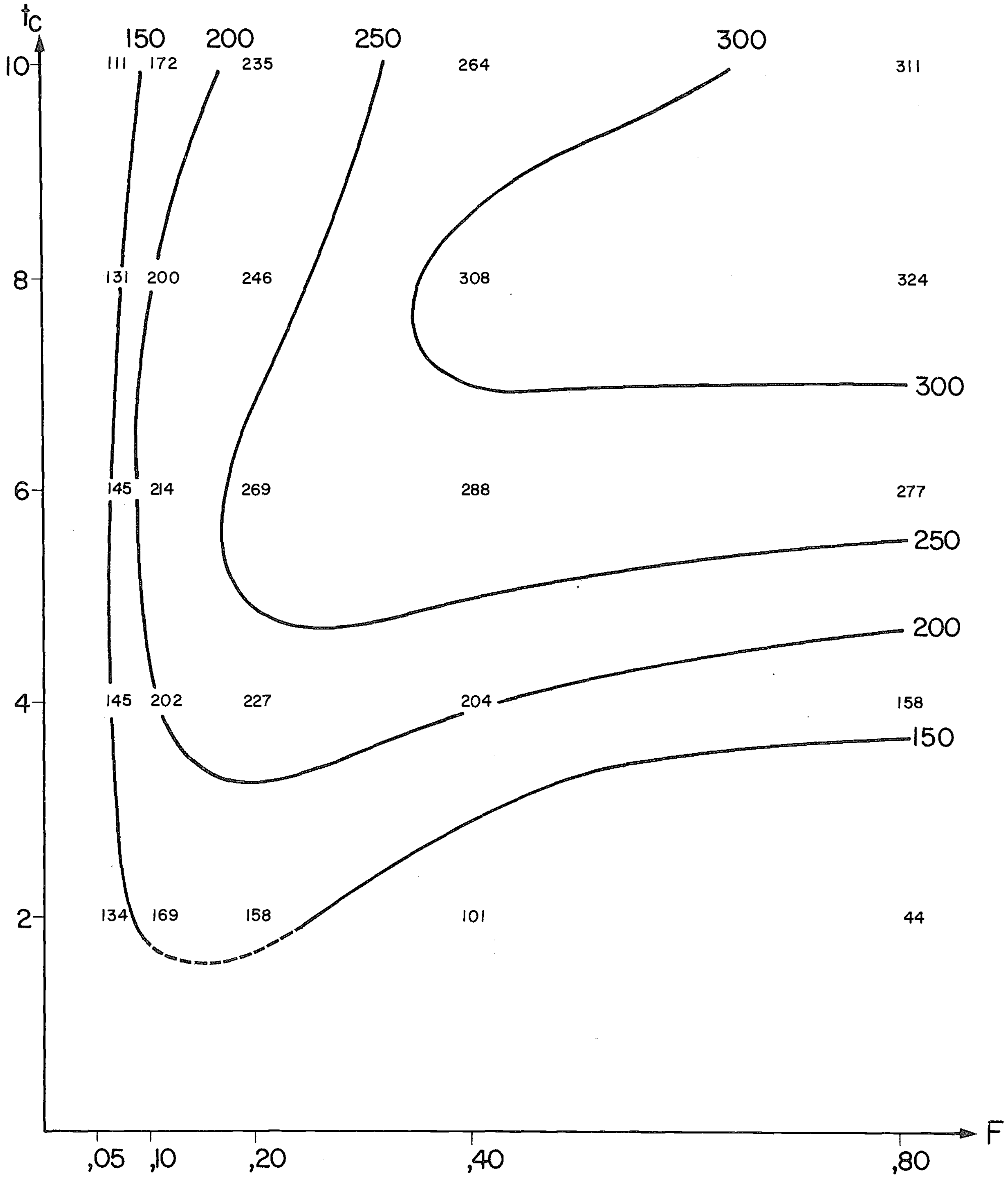

Fig. 5 - Isopleths corresponding approximately to the yield per recruit calculated by the method of Beverton and Holt (table 3a)

Table 1

Mean individual weight, number surviving and total biomass at each age of a cohort of 1 000 freshwater bream, *Abramis brama*. (Data from Backiel and Zawisza, 1968)

Age (y)	Mean weight (g)	Number	Biomass (kg)
2	25.88	1 000	25.88
3	109.49	861	94.27
4	246.69	741	182.80
5	418.94	638	267.28
6	603.63	549	331.39
7	784.08	472	370.08
8	951.86	407	387.41
9	1 101.32	350	385.46
10	1 232.31	301	370.92
11	1 341.16	259	347.36
12	1 430.98	223	319.11
13	1 508.55	192	289.64
14	1 572.17	165	259.41
15	1 621.75	142	230.29
16	1 660.31	122	202.56
17	1 695.42	105	178.02
18	1 724.16	91	156.90
19	1 740.73	78	135.78
20	1 758.80	67	117.84
(21)	(1 770.00)	(58)	102.66

Table 2

Formulas for converting from entries in the yield tables (Beverton and Holt, 1966) to quantities of direct interest

Quantity of interest	=	Value entered in tables	x	Conversion factor
Y	=	Y'	x	$R_o W_\infty$
$\bar{B}$	=	$\frac{Y'}{{}^{F}/_{M}}$	x	$\frac{R_o W_\infty}{M}$
C	=	$E(1-c)^{M/K}$	x	R_o (of Table 3)
$\bar{P}$	=	$(1-E)(1-c)^{M/K}$	x	$\frac{R_o}{M}$
$\bar{w}$	=	$\frac{Y'}{E(1-c)}\ {}^{M}/_{K}$	x	W_∞

$R_o = \frac{R}{(1-c^*)}\ {}^{M}/_{K}$ $c^* = \frac{l_r}{L_\infty} = 1-e^{-K(t_r-t_o)}$

$R_c = R_o(1-c)^{M}/_{K}$

Note: $\bar{B}$ and $\bar{P}$ are average annual values for the entire population

Table 3a

Yield in grammes per 2-year old recruit to the bream stock, calculated by the method of Beverton and Holt (t_c = age in years at first capture, F = annual instantaneous rate of fishing mortality

F t_c	0.05	0.10	0.20	0.40	0.80
2	133.78	169.07	158.31	100.67	43.77
4	145.35	201.64	227.04	203.79	157.85
6	145.34	214.38	269.14	287.97	277.15
8	131.33	200.37	265.98	308.04	324.03
10	110.61	172.05	235.40	283.93	311.38

Table 3b

Yield per recruit of bream, calculated by the method of Jones

F t_c	0.05	0.10	0.20	0.40	0.80
2	159.96	229.66	234.47	183.46	119.92
4	166.81	259.34	316.63	301.42	277.49
6	157.31	258.29	321.34	359.44	384.76
8	135.06	229.98	298.92	342.83	401.21
10	107.86	188.42	245.72	282.22	357.30

Table 3c

Yield per recruit of bream, calculated by the method of Ricker

F t_c	0.05	0.10	0.20	0.40	0.80
2	154.58	213.30	228.18	181.36	113.90
4	160.60	239.39	295.24	299.31	271.96
6	150.13	234.14	314.80	359.14	376.85
8	127.63	206.71	291.06	353.45	396.04
10	100.82	167.68	245.19	310.11	360.13

EQUATIONS FOR CALCULATING QUANTITIES OF INTEREST ACCORDING TO THE ANALYTIC MODEL OF AN EXPLOITED STOCK

by

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Definition of symbols

N_t - abundance (size in number) of a cohort at time t

$\bar{N}$ - mean abundance of a cohort during a given time interval

T - duration of a time interval

D - total number of deaths (from all causes) during a given time interval

C - catch in number during a given time interval

Y - catch in weight during a given time interval

$\bar{P}$ - mean abundance (size in number) of the entire population (all cohorts present) during a given time interval

$\bar{B}$ - mean biomass (size in weight) of the entire population during a given time interval

F - (specific) instantaneous rate of fishing mortality

M - (specific) instantaneous rate of natural mortality

$Z = F+M$ - (specific) instantaneous rate of total mortality

$E = F/Z = C/D$ - exploitation ratio (sometimes called the rate of exploitation, although this term should be reserved for the quantity $F(1-e^{-ZT})/Z$. The two quantities are of course, equal for $T = \infty$).

t_o, K, L_∞, W_∞ - parameters of the von Bertalanffy growth equation

t_r = mean age of recruitment to the stock

t_c = mean age of recruitment to the fishery (i.e., age at first capture)

R_o - abundance (size in number) of a cohort at the age of recruitment to the stock

$R_c = R'$ - abundance of a cohort at the age of recruitment to the fishery

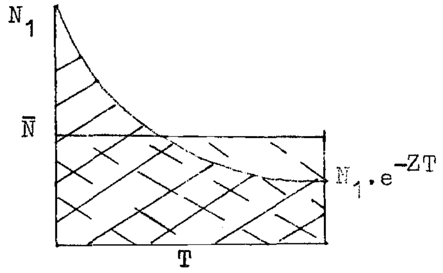
1. Equations for calculating quantities in number

- Mean abundance ($\bar{N}$), catch in number (C) and total deaths during a time interval T, given an initial abundance N_1 at the beginning of the interval:

$$\bar{N} = N_1 \frac{(1-e^{-ZT})}{ZT}$$

$$D = N_1(1-e^{-ZT}) = ZT\bar{N}$$

$$C = EN_1(1-e^{-ZT}) = FT\bar{N} = ED$$



(F, M and Z assumed constant)

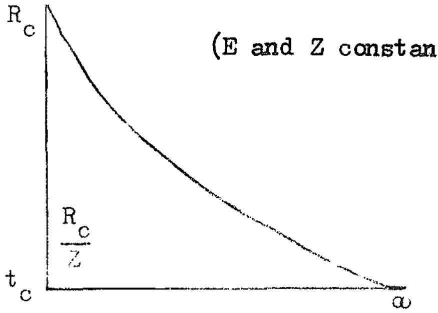
- Mean abundance ($\bar{N}$), catch in number (C) and total deaths (D) of a single cohort during its entire fishable lifespan (from t_c to $t=\infty$):

$$D = R_c$$

$$C = ER_c$$

$$\int_{t_c}^{\infty} N_t dt = R_c/Z = \text{total years lived}$$
(Life expectancy = 1/Z)

$$\bar{N} = \left[\int_{t_c}^{\infty} N_t dt\right] / \infty = 0$$



(E and Z constant)

- Mean abundance ($\bar{P}$), catch in number (C) and total deaths (D) of an entire population during one year, given an initial abundance P_1 at the beginning of the year:

$$\bar{P} = P_1(1-e^{-Z})/Z$$

$$D = Z\bar{P} = P_1(1-e^{-Z})$$

$$C = F\bar{P} = P_1\left(\frac{F}{Z}\right)(1-e^{-Z}) = ED$$

- Intial abundance (P_1), mean abundance ($\bar{P}$), catch in number (C) and total deaths (D) of an entire population in equilibrium conditions during one year:

$$P_1 = R_c/(1-e^{-Z})$$

$$\bar{P} = R_c/Z$$

$$D = R_c$$

$$C = ER_c = ED$$

R_c, F, M and Z constant

$$\Downarrow$$

Equilibrium conditions

- Equivalence under equilibrium conditions of the entire population during one year and a single cohort during its entire fishable lifespan (t_c to $t = \infty$):

Population (1 year)				Cohort (t_c to $t = \infty$)
D	=	R_c	=	D
C	=	ER_c	=	C
$\bar{P}$	=	$\frac{R_c}{Z}$	=	$\int_{t_c}^{\infty} N_t dt$

2. Equations for calculating quantities in weight

- Biomass at time t:

$$B_t = N_t w_t$$

- Mean biomass during a time interval (0, T):

$$\bar{B}_T = \left[\int_0^T N_t w_t dt\right] / T$$

The value of the integral depends on the form of the growth function w_t that is chosen. When growth during the interval can be described by an exponential function with a specific instantaneous growth rate G, that is $w_t = w_o e^{Gt}$, as in Ricker's exponential model, the integral is:

$$\int_0^T N_t w_t dt = N_o w_o \frac{(1-e^{-(Z-G)T})}{(Z-G)}$$

so, $$\bar{B}_T = \frac{B_o(1-e^{-(Z-G)T})}{(Z-G)T}$$

In the case of a population in equilibrium, the mean biomass of the population during one year is equal to the sum of the mean annual biomasses of a single cohort during its entire lifespan:

$$\bar{B} = \int_{t_c}^{\infty} N_t w_t dt$$

In the Beverton-Holt model, with

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

and $R_c = Re^{-M(t_c-t_r)}$,

$$\bar{\bar{B}} = R_c W_\infty \int_{t_c}^{\infty} e^{-(F+M)(t-t_c)} (1-e^{-K(t-t_o)})^3 dt$$

$$\bar{\bar{B}} = R_c W_\infty \left[\frac{1}{F+M} - \frac{3e^{-K(t_c-t_o)}}{F+M+K} + \frac{3e^{-2K(t_c-t_o)}}{F+M+2K} - \frac{e^{-3K(t_c-t_o)}}{F+M+3K} \right]$$

- Catch in weight from the entire population during one year:

  $Y = F\bar{\bar{B}}$

- Total production of the population during one year = $Z \cdot \bar{\bar{B}}$ (In the case of an unexploited stock, $Z=M$ and total production = $M\bar{\bar{B}}$)

- Mean individual weight of fish in the population (and catch) during one year:

  $\bar{w} = \bar{\bar{B}}/\bar{P} = Y/C$

RICKER'S EXPONENTIAL YIELD MODEL

by

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1. The model

Suppose a cohort is recruited to the fishable stock at time $t_1 = t_r$. Let N_1 denote its abundance at this time and w_1 the average weight of individuals. The total biomass of the cohort is therefore $B_1 = N_1 w_1$. After time t_1, consider the lifespan of the cohort to be divided into n intervals:

$$(t_1, t_2), (t_2, t_3), \ldots\ldots\ldots\ldots, (t_i, t_{i+1}), \ldots\ldots\ldots\ldots, (t_n, t_{n+1})$$

Let N_i, w_i and B_i denote the abundance, mean individual weight and total biomass of the cohort respectively, at time t_i.

1.1 Mortality

Between time t_i and time t_{i+1}, the instantaneous rate of fishing mortality is assumed to be constant at a level F_i, and the instantaneous rate of natural mortality is also assumed constant at M_i. Let $Z_i = F_i + M_i$ denote the instantaneous rate of total mortality, which will of course also be constant on interval i. The set of fishing mortality rates F_1, F_2, ..., F_n imposed during the n intervals forms a fishing mortality vector, which will be denoted (F_i). Similarly, (M_i) and (Z_i) will denote the corresponding vectors of natural and total mortality rates, respectively.

During the interval (t_i, t_{i+1}), the number N_t of fish that survive from time t_i to time $t > t_i$ is given by:

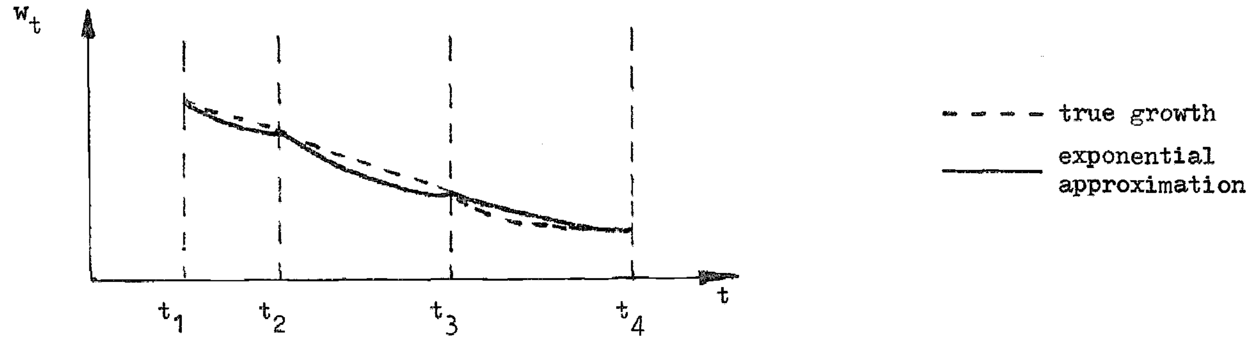
$$N_t = N_i e^{-Z_i(t - t_i)}$$

Thus, in particular:

$$N_{i+1} = N_i e^{-Z_i(t_{i+1} - t_i)}$$

Given the vector (Z_i) and the initial abundance N_1, it is therefore a simple matter to calculate N_2, N_3, ..., N_{n+1}.

Within each time interval, the function N_t is described by an exponential curve.



1.2 Growth

During the interval (t_i, t_{i+1}), it is assumed that the specific rate of growth in weight is constant at a level G_i. Let $w(t)$ represent the weight of an individual at time t during the interval (t_i, t_{i+1}). Then:

$$\frac{1}{w(t)} \frac{dw(t)}{dt} = G_i$$

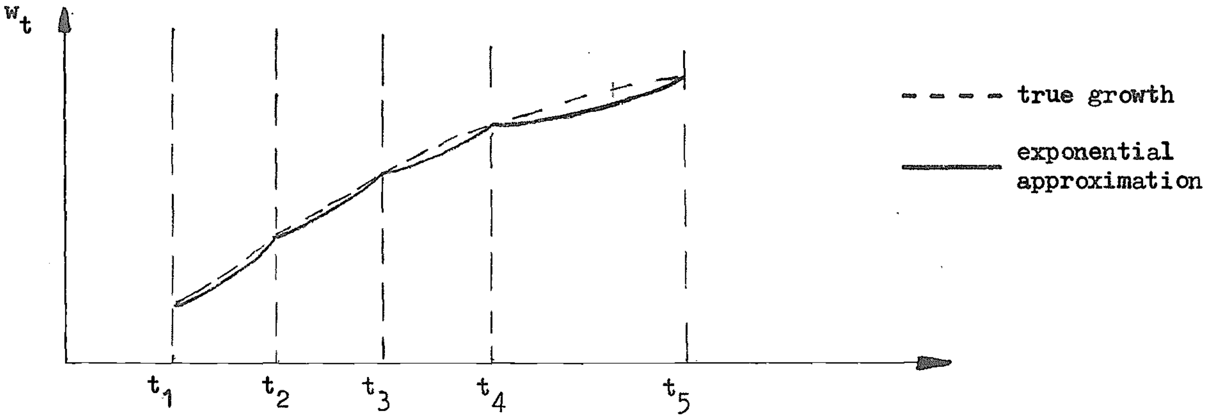
and since $w(t_i) = w_i$, it follows that:

$$w(t) = w_i e^{G_i(t-t_i)}$$

In particular, $w_{i+1} = w(t_{i+1}) = w_i e^{G_i(t_{i+1}-t_i)}$, so

$$G_i = \frac{1}{(t_{i+1} - t_i)} \quad \ln (w_{i+1}/w_i)$$

The growth in weight of an individual will therefore also be described by a series of exponential curves:



The major flaw in this description of the growth schedule is its upward concavity. As the graph shows, the true growth curve is always concave downward, while each of the exponential segments is concave upward. For this reason, one should always deal with short time intervals to minimize the error inherent in the exponential approximation.

2. Representation of the total biomass of a cohort

Let B(t) represent the total weight or biomass of the entire cohort at time t and, as above, let B_i denote $B(t_i)$. By definition, $B(t) = N(t)\, w(t)$. During the interval (t_i, t_{i+1}):

$$B(t) = N(t)\, w(t) = N_i e^{-Z_i(t - t_i)}\, w_i e^{G_i(t - t_i)}$$

or, on rearranging terms,

$$B(t) = N_i w_i e^{(G_i - Z_i)(t - t_i)} = B_i e^{(G_i - Z_i)(t - t_i)}$$

Therefore, $B_{i+1} = B_i e^{(G_i - Z_i)(t_{i+1} - t_i)}$, which is a convenient form for computation.

It can be seen from the expression above that the biomass history of a cohort will also be described by a series of exponential curves, but the direction of the concavity of each segment will depend on whether $(G_i - Z_i)$ is positive or negative. In the absence of exploitation (that is, $F_i = 0$ and therefore $Z_i = M_i$ on all intervals), the change in biomass during interval i will be described by:

$$B_{i+1} = B_i e^{(G_i - M_i)(t_{i+1} - t_i)}$$

Now if $G_i > M_i$, as is usually true for the younger age-groups, the biomass will increase. On the other hand, the biomass will decrease if $G_i < M_i$, which is usually true after a certain age since the growth rate decreases with age and mortality does not. The age at which G_i first drops below M_i is called the critical age. In the absence of exploitation, the biomass of the cohort will increase until this age is reached and then decrease until the cohort disappears entirely.

3. The catch from a cohort during its lifespan

When the fishery is in equilibrium (that is, the recruitment N_1 and the growth and mortality vectors (G_i), (F_i), (M_i) are all constant from year to year), the total catch from all the cohorts present in the stock during any one year will be equal to the total catch taken from a single cohort during all the years it is present in the stock.

3.1 Catch in number

In accordance with the model developed above, the catches from a single cohort can be computed interval by interval. Let C_i denote the number caught during the i^{th} interval. Now between time t_i and time t_{i+1}, a total of $N_i - N_{i+1}$ individuals die. The proportion of these deaths due to fishing (i.e., the proportion caught) is given by the exploitation ratio $E_i = F_i/Z_i$. Thus:

$$C_i = \frac{F_i}{Z_i} (N_i - N_{i+1}) = E_i \ (N_i - N_{i+1})$$

Since $N_{i+1} = N_i e^{-Z_i(t_{i+1} - t_i)} = N_i S_i$, where $S_i = e^{-Z_i(t_{i+1} - t_i)}$ is the fraction of the number alive at time t_i that survives to time t_{i+1}, the catch can also be represented as:

$$C_i = E_i N_i (1 - S_i)$$

However, the more useful expression for calculating catches in practice is $C_i = E_i(N_i - N_{i+1})$, since one always has to compute N_{i+1} anyway for continuing the calculations on succeeding intervals.

By simple summation, the total number caught from a cohort during its entire fishable lifespan will be:

$$C = \sum_{i=1}^{n} C_i$$

3.2 Catch in weight

Let $Y(t)$ represent the catch in weight taken from a cohort between time t_i and time t during a particular interval. And following the notation adopted for catches in number, let Y_i denote the catch in weight during the entire i^{th} interval and Y the total catch in weight from the cohort over its entire lifespan.

During the i^{th} interval, the instantaneous rate of catch in weight will be:

$$\frac{dY(y)}{dt} = F_i \; N(t) \; w(t) = F_i B(t)$$

Thus

$$Y_i = \int_{t_i}^{t_{i+1}} F_i B(t) dt$$

$$= F_i \int_{t_i}^{t_{i+1}} B_i e^{(G_i - Z_i)(t - t_i)} dt$$

$$= F_i B_i e^{-(G_i - Z_i)t_i} \int_{t_i}^{t_{i+1}} e^{(G_i - Z_i)t} dt$$

$$= F_i B_i e^{-(G_i - Z_i)t_i} \left[\frac{e^{(G_i - Z_i)t}}{G_i - Z_i} \right]_{t_i}^{t_{i+1}}$$

$$= \frac{F_i B_i}{G_i - Z_i} e^{-(G_i - Z_i)t_i} \left(e^{(G_i - Z_i)t_{i+1}} - e^{(G_i - Z_i)t_i} \right)$$

$$= \frac{F_i B_i}{G_i - Z_i} \left(e^{(G_i - Z_i)(t_{i+1} - t_i)} - 1 \right)$$

Since $B_i e^{(G_i - Z_i)(t_{i+1} - t_i)} = B_{i+1}$, this expression reduces to the simple form:

$$Y_i = \frac{F_i}{G_i - Z_i} \; (B_{i+1} - B_i)$$

The total catch in weight from the cohort is found by summation:

$$Y = \sum_{i=1}^{n} Y_i$$

Instead of following this procedure in detail, one sometimes calculates the catch in weight during an interval by multiplying the calculated catch in number by an estimated or observed mean weight at that age. This method is not rigorous, but it usually produces acceptable results and may even be preferable in cases where the error associated with the upward concavity of the exponential growth curve would be large.

3.3 Treatment of non-equilibrium conditions

When the fishery is not in equilibrium, one cannot estimate the total catch from all cohorts present in a particular year by calculating the yield from a particular cohort over its entire lifespan. Instead, for each year one must consider the cohorts present at the beginning of the year separately and apply to each the appropriate growth and mortality rates prevailing during the year to obtain the catch from each (according to the equations above), and then sum the catches from all cohorts to find the total catch for the year.

3.4 Breakdown of the catch by country or gear type

A stock can be exploited by the fleets of several countries, or by fleets using different kinds of fishing gear, and in these cases it is often necessary to calculate what share of the catch will be taken by each fleet. If there are two gears in use (e.g., pole-and-line and purse seines in the surface tuna fishery), the fishing mortality vector (F_i) will be the sum of the vectors (F_{1i}) and (F_{2i}) generated by the two gears: $(F_i) = (F_{1i}) = (F_{2i})$. To calculate the catch in weight taken by each during a particular interval, one simply calculates the total catch Y_i determined by the total fishing mortality rate F_i according to the equations above, and then allocates the catch by gear in proportion with the components of F_i. That is,

$$Y_{1i} = \frac{F_{1i}}{F_i} Y_i \quad \text{and} \quad Y_{2i} = \frac{F_{2i}}{F_i} Y_i$$

4. Alternative patterns of exploitation

The effect on catches of an increase in the age at first capture can be readily predicted by setting all fishing mortality rates to zero until that age. One can also calculate the effect of an increase in fishing effort, since this would simply increase some or all of the fishing mortality rates (F_i).

In fact, the calculations can be as detailed as is necessary to represent all aspects of the stock and the fishery, so long as there is sufficient information available to estimate the various rates. In the most general scheme, one calculates the fishing mortality rate generated by each gear type during each interval as the product of the fishing effort f_i exerted by the gear and the age-specific catchability coefficient q_{ji} of that gear: $F_{ji} = q_{ji} f_j$ where i denotes interval i and j denotes gear j. If short time intervals are used, this scheme will take account of seasonal as well as age-specific variations in catchability.

Given estimates specific to each age, season and gear, one can readily calculate the catches under any proposed pattern of exploitation. For example:

(i) Given seasonal estimates of catchability or fishing mortality, one calculates the effect of closing the fishery during part of the year.

(ii) Given gear-specific catchability coefficients, one can calculate the effect on the catches taken by each gear of change in the fishing effort of one or more gear types.

(iii) On the basis of some desirable level of fishing mortality (usually a level that gives a good yield per recruit), one can calculate various allocations of effort among gear types, seasons or countries and the corresponding division of catches.

While the Ricker model involves only simple calculations, they are numerous, and particularly in the case of non-equilibrium conditions where the short- and long-term effects of several alternative patterns of exploitation have to be worked out, the computations can be very long and arduous. But because the computations are simple, it is an easy matter to have them done automatically on even a small calculator, which not only saves time but also reduces computational errors. In fact, for practical work a programmable calculator is essential, since one almost always has to consider the effect of several alternative regulatory schemes in non-equilibrium conditions.

5. Exercise

Let the following parameters describe a given population:

t	=	2.5 an(t_r)		3.0		3.5		4.0		4.5		5.0		5.5		6.0
w_t(g)	=	100		122		182		211		258		272		324		344
M	=			= cte = 0.2												
F	=		2.0		0.0		2.0		0.0		2.0		0.0		2.0	

1. Compute the values of the parameters given in the headings of the following table:

Time intervals	G	F_i	M_i	N_i = 10 000 for $t=0$	B_i	CN_i	CP_i

Note that N_i denotes the number of the cohort at the beginning of the i^{th} interval; the same convention applies to B_i.

2. Compute the effects on the cohort when F is halved throughout its lifespan.

6. Reference

Ricker, W.E., Computation and interpretation of biological statistics of fish populations. 1975 Bull.Fish.Res.Board Can., (191):382 p.

THE EFFECT ON YIELD OF A CHANGE IN THE AGE AT FIRST CAPTURE

by

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1. Introduction

In order to estimate the change in catch to be expected from a change in fishing mortality or age at first capture according to one of the analytic population models (Ricker or Beverton and Holt), one must know all the parameters of growth, mortality and selectivity (recruitment). Other procedures have been proposed that do not require such detailed information. Allen (1953), Holt (1957) and Gulland (1961) derived expressions for the new equilibrium yield and for the yield that would be obtained immediately after a change in the fishing mortality on one or more age groups within the stock. All these methods require a knowledge of the size composition of the catch immediately before and after the change in age at first capture.

This paper presents a modification of Holt's method, which provides the same results while requiring less in the way of basic data. Before developing the method, it will be useful to review some of the equations describing the history of an exploited cohort and the effects of fishing on an entire exploited stock during one year.

2. Notation and equations

The exploited phase of a cohort is the period during which it is fished. Let:

t_1 = the age at which the cohort enters the exploited phase, i.e., the age at which it is recruited to the fishery. This will be called the age at first capture;

R_1 = the recruitment to the fishery, i.e., the number of members of the cohort surviving to age t_1;

C_1 = the catch in number from the cohort during the entire exploited phase;

E = the ratio of exploitation during the exploited phase, i.e., the fraction caught of the total number of fish that die of all causes during the exploited phase. If there are no survivors at the end of the exploited phase, the total number that died will be equal to the initial number R_1, so in this case:

$$E = \frac{C_1}{R_1} \qquad (1)$$

M, F, Z = the instantaneous rates of natural, fishing and total mortality, respectively. Here it will be assumed that these are constant throughout the exploited phase, so we have:

$$E = \frac{F}{Z} \qquad (2)$$

Also, the rate of survival during a time period of duration T will be:

e^{-MT} before the exploited phase, and

e^{-ZT} during the exploited phase

$\overline{W}_1$ = the average weight of the C_1 fish caught during the exploited phase;

Y_1 = the catch in weight from the cohort during the exploited phase. Since

$$Y_1 = C_1\overline{W}_1 \qquad (3)$$

it follows from equation (1) that

$$Y_1 = ER_1\overline{W}_1 \qquad (4)$$

3. Derivation of relationships

First consider a cohort subject to a regime of exploitation in which the ratio of exploitation E is constant and the age at first capture is t_1. These conditions define the regime, which will be designated Regime 1. If the recruitment to the fisheries is R_1, the number caught during the exploited phase will be, according to equation (1), $C_1 = ER_1$ and the catch in weight will be $Y_1 = C_1\overline{W}_1 = ER_1\overline{W}_1$. (It is assumed that the exploited phase includes all ages after t_1, so all of the R_1 recruits die in some way during it.)

Next consider a different regime of exploitation, Regime 2, in which the ratio of exploitation E is the same as under Regime 1 but the age at first capture is $t_2 \neq t_1$. In particular, suppose $t_2 > t_1$. In this case the recruitment to the fishery will be $R_2 \neq R_1$, the catch in number $C_2 = ER_2$ and the catch in weight $Y_2 = C_2\overline{W}_2 = ER_2\overline{W}_2$.

It is convenient to denote by R_k the number that survive to age t_2 under Regime 1, and similarly to denote by C_k and Y_k the catch in number and weight, respectively, of fish older than age t_2 under Regime 1. These latter two quantities can be calculated according to the equations given above, namely $C_k = ER_k$ and $Y_k = C_k\overline{W}_k = ER_k\overline{W}_k$. Figure 1 shows the decline of the number surviving in a cohort, starting with R_1 individuals at the age at first capture t_1, under Regime 1 and Regime 2.

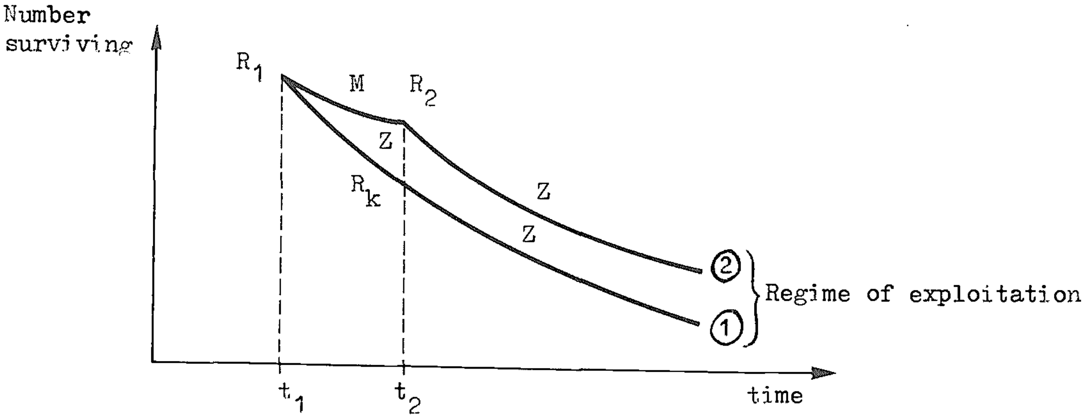

Figure 1 Effect on survivorship of a change in the age at first capture

The problem, then, is to compare Y_1, the equilibrium yield under Regime 1 to Y_2, the equilibrium yield under Regime 2, and to consider also Y_k, the yield immediately after the change in the age at first capture from t_1 to t_2.

3.1 Relationships between recruitments

As shown in Figure 1, the recruitment R_2 under Regime 2 consists of survivors from the initial R_1 to the end of the period $T = t_2 - t_1$. As the cohort is not exploited during this period under Regime 2, the rate of survival will be e^{-MT}, so

$$R_2 = R_1 e^{-MT} \tag{5}$$

The recruitment R_k also consists of survivors from the initial R_1 to the age t_2, but under Regime 1. In this case the rate of survival during the period T is e^{-ZT}, so

$$R_k = R_1 e^{-ZT} \tag{6}$$

$$\text{or} \quad \frac{R_1}{R_k} = e^{ZT} \tag{7}$$

Dividing equation (5) by equation (6), and recalling that $Z = F + M$, we find the following relationship between R_2 and R_k:

$$\frac{R_2}{R_k} = e^{FT} \tag{8}$$

Now by the elementary rules of exponents, e^{FT} can be rewritten

$$e^{FT} = (e^{FT})^{\frac{ZT}{ZT}} = (e^{ZT})^{\frac{FT}{ZT}} = (e^{ZT})^{E} \tag{9}$$

Since the exponential terms on either side of expression (9) are equal to the ratios of recruitments given in expressions (7) and (8), we can substitute the ratios for the exponential terms to obtain the following expression:

$$\frac{R_2}{R_k} = \left(\frac{R_1}{R_k}\right)^{E} \tag{10}$$

3.2 Relationships between catches in number

As stated above, the catches in number are related to the recruitments by the following expressions:

$$C_1 = ER_1$$

$$C_2 = ER_2$$

$$C_k = ER_k$$

Since the ratio of exploitation E is the same in all three cases, it is obvious that the various catches in number will be in the same ratios as the corresponding recruitments. Therefore, by substituting these catch ratios into equations (7), (8) and (10), we obtain:

$$\frac{C_1}{C_k} = e^{ZT} \tag{11}$$

$$\frac{C_2}{C_k} = e^{FT} \tag{12}$$

$$\frac{C_2}{C_k} = \left(\frac{C_1}{C_k}\right)^E \tag{13}$$

3.3 Relationships between catches in weight

3.3.1 The ratio $\frac{Y_2}{Y_k}$

Referring to equation (3), one can write:

$$\frac{Y_2}{Y_k} = \frac{C_2\bar{W}_2}{C_k\bar{W}_k} \tag{14}$$

where $\bar{W}_2$ and $\bar{W}_k$ are the mean individual weights of fish caught after age t_2 under Regime 2 and Regime 1, respectively. As the mortality rates after age t_2 are the same under the two regimes, so are the rates of survival and consequently the age compositions of the catches as well. Therefore $\bar{W}_2$ and $\bar{W}_k$ are equal, and equation (14) shows that the ratios of the catches in number and of the catches in weight are equal:

$$\frac{Y_2}{Y_k} = \frac{C_2}{C_k} \tag{15}$$

It can then be found from equation (13) that

$$\frac{Y_2}{Y_k} = \left(\frac{C_1}{C_k}\right)^E \tag{16}$$

3.3.2 The ratio $\frac{Y_2}{Y_1}$

By writing:

$$\frac{Y_2}{Y_1} = \frac{Y_2}{Y_k} \times \frac{Y_k}{Y_1} \tag{17}$$

and substituting the expression for $\frac{Y_2}{Y_k}$ from equation (16), one obtains:

$$\frac{Y_2}{Y_1} = \left(\frac{C_1}{C_k}\right)^E \times \frac{Y_k}{Y_1} \tag{18}$$

This expression is the basis of the method described below.

4. The method

If recruitment remains constant year after year and the regime of exploitation also remains unchanged, the numerical sizes of the age groups present in the population during any one year will be equal to the numerical sizes of any one cohort at the corresponding ages during the entire exploited phase (see the chapter on analytic models).

In these circumstances, C_1 and Y_1, and C_k and Y_k, C_2 and Y_2, defined above for a single cohort over its entire exploited phase, will be equal to annual catches in number and in weight from the entire population. The relationships developed in section 3 for a single cohort will therefore apply equally well to the entire population during one year. In particular, equation (18) will apply, and this is the one that provides a measure of the effect on yield of a change in regime and therefore a basis for deciding whether or not to change from Regime 1 to Regime 2.

Note that immediately after the change, the size composition of the stock will still be the one brought about by Regime 1, while the fishery will be conducted according to Regime 2. Thus recruitment to the fishery will be R_k and catches C_k and Y_k, as these were defined for a single cohort. The ratio $\frac{Y_k}{Y_1}$ therefore provides a measure of the immediate effect effect of the change in regime, while the ratio $\frac{Y_2}{Y_1}$ measures the long-term effect.

The long-term effect will be realized after a period of time equal to the duration of the exploited phase. At the end of this period, all the cohorts affected by Regime 1 will have disappeared, and the stock will have attained a new equilibrium corresponding to Regime 2.

4.1 Application

The following example is from the FAO manual on fish population analysis (Exercise 10.5.3).

The data in the table below refer to the trawl fishery for haddock around the Faeroe Islands. They give the number of fish landed by 5 cm length interval, the mean individual weight in each length group and the proportions of each length group retained by trawls with mesh sizes of 90 and 120 mm (stretched measure) in the codend.

Length (cm)	Mean weight (g)	Percentage retained 90 mm	Percentage retained 120 mm	Numbers landed (000)
25-	160	50	3	8
30-	260	80	16	314
35-	420	98	41	1 084
40-	630	100	72	1 409
45-	880	100	94	1 370
50-	1 190	100	100	952
55-	1 570	100	100	465
60-	1 760	100	100	255
65-	2 530	100	100	124
70-	3 100	100	100	73
75-	3 800	100	100	30
80+	4 600	100	100	9

In the table, the landings refer to fishing with the trawl of 90 mm mesh size. This will correspond to Regime 1, while fishing with the 120 mm net will be Regime 2. The ratio of exploitation will be taken to be $E = 0.5$.

The total catch in number under Regime 1, which we call C_1, is of course the sum of the numbers landed as given in the table. The catch in number immediately after a change to 120 mm mesh, C_k, can be found by multiplying each of the landings in the right-hand column by the ratio of the retention percentages of the 90 and 120 mm nets for that length group. The corresponding catches in weight Y_1 and Y_k are then calculated by multiplying the number landed by the mean individual weight for each length group and summing. Thus:

$$C_1 = 8 + 314 + \ldots = 6\ 093$$

$$C_k = 8 \times \frac{3}{50} + 314 \times \frac{16}{80} + \ldots = 0.48 + 62.80 + \ldots = 4\ 727.07$$

$$Y_1 = 8 \times 160 + 314 \times 260 + \ldots = 5\ 638.62$$

$$Y_k = 0.48 \times 160 + 62.80 \times 260 + \ldots = 4\ 986.80$$

and

$$\frac{Y_k}{Y_1} = 0.8844$$

$$\frac{Y_2}{Y_k} = \left(\frac{C_1}{C_k}\right)^E = e^{E\ln\left(\frac{C_1}{C_k}\right)} = 1.135$$

Immediately after the change, therefore, the catch in weight will drop to $\frac{Y_k}{Y_1} = 88.44\%$ of the catch in weight beforehand. In the long term, the new equilibrium catch with the larger mesh will be $\frac{Y_2}{Y_1} = \frac{Y_2}{Y_k} \times \frac{Y_k}{Y_1} = 1.135 \times 0.8844 = 100.38\%$ of the equilibrium catch with the smaller mesh.

In this case the gain in yield from increasing mesh size is less than one percent. Given the likely errors of estimation, this means that no significant gain at all can be achieved by a change.

4.2 Discussion

In many fisheries, small fish that are caught are often discarded at sea and not landed. In judging the economic effect of a change in mesh size, it is necessary to consider the effect on landings, not catches, but the equations on which the method presented above is based refer only to catches.

This means that, in order to judge the effect of a change correctly, one needs some knowledge of the discard pattern in the fishery. This information can be used to translate the landing data to actual catch data for Regime 1. Then the method can be applied and the calculated catches under Regime 2 can be transformed to landings under Regime 2 by applying the prevailing discard ratios.

4.3 Fishery interactions

The method can also be applied to interacting fisheries, such as the case where a single stock is exploited by two fisheries A and B, in which the age at recruitment to fishery A is ${}_At_1$ and the age at recruitment to fishery B is ${}_Bt_2$ (greater than ${}_At_1$). In this situation a change in the age at recruitment to fishery A will change the landings in both fisheries.

Calculating the absolute and relative changes in yield to the two (or more) fisheries can be very complicated, since in this case the various mortality rates and exploitation ratios can change several times during the exploited phase. Much of the reasoning presented above for the simple case can be followed, but the actual equations require a longer development that will not be given here.

5. Concluding remarks

Other methods have been used to estimate the ratio $\frac{Y_2}{Y_k}$ in the case of a single fishery. These are described in the papers cited above. In Holt's method, the ratio is given as $\frac{Y_2}{Y_k} = e^{FT}$, and in Gulland's as

$$\frac{Y_2}{Y_k} = 1 + E\left(\frac{C_1 - C_k}{C_k}\right) e^{-MT^*}$$

where T* is the difference between t_2 and the average age of the fish released (i.e., the $C_1 - C_k$ fish caught before age t_2 under the old regime).

To apply one of these methods one has to know either F (for Holt's) or T* (for Gulland's). The new method presented above does not require an estimate of T*. It does require an estimate of $E = \frac{F}{Z}$, but it is often easier to make a reasonable estimate of E than of F, since E can only vary between 0 and 1 while possible values of F can extend over a larger range.

Allen (1953) deduced the conditions in which an increase in the age at first capture would bring about an increase in yield in the long term. If W_1 is the weight at first capture and $\overline{W}_1$ the mean weight in the catch, then yield can be increased by increasing the age at first capture if $E\overline{W}_1 < W_1$. Conversely, if $E\overline{W}_1 < W_1$, the yield can be increased by reducing the age at first capture. While these inequalities show whether or not again is possible, they do not provide any measure of the long-term or short-term effect.

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COHORT ANALYSIS

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1. Introduction

The annual catches taken from a single cohort during the exploited phase (frequently called the catch vector of the cohort) can be used to calculate the abundance and fishing mortality rate of the cohort in each year, if the rate of natural mortality is known. These calculations have been carried out in various ways for many fisheries the last few years, usually because records of catch per effort could not safely be treated as indices of stock density. Fry (1949), Jones (1961), Murphy (1965), Gulland (1965), Tomlinson (1970), Pope (1972) and others have all had a part in developing these methods, which are variously referred to as virtual population analysis (VPA), cohort analysis, Murphy's method or Gulland's method. The term "cohort analysis" will be used here to the whole family of methods, all of which share the same basic principle, while the other terms such as "virtual population analysis" and "Gulland's method" will be reserved for those special cases.

Managing a fishery by limiting catch or effort can in some cases require estimates of the annual abundance and the total catch at different levels of fishing effort. Cohort analysis is often the best technique in these situations.

For clarity, it will be best first to develop the basic concepts and methods for the case of a single cohort, and then to extend these to the entire stock.

2. Symbols and equations

Let

N_i : the number of survivors in a cohort at the start of year i,

S_i : the rate of survival during year i. Thus the number surviving at the end of year i, or the beginning of year i + 1, is

$$N_{i+1} = N_i S_i \qquad (1)$$

D_i = the number of members of the cohort that die during year i,

$$D_i = N_i - N_{i+1} \qquad (2)$$

or, from (1)

$$D_i = N_i - N_i S_i = N_i(1 - S_i) \qquad (3)$$

By making a different substitution, one obtains

$$D_i = \frac{N_{i+1}}{S_i} - N_{i+1} = N_{i+1}\left(\frac{1 - S_i}{S_i}\right) \qquad (4)$$

C_i : the number caught (from the cohort) during year i

E_i : the exploitation ratio during year i, defined as the fraction, out of the total number of deaths, represented by the catches during year i, or

$$E_i = C_i/D_i \tag{5}$$

This can also be written, by substituting the expression for D_i from (3)

$$E_i = \frac{C_i}{N_i(1 - S_i)} \tag{6}$$

or, by substitution from (4)

$$E_i = \frac{C_i}{N_{i+1}} \frac{S_i}{(1 - S_i)} \tag{7}$$

$\overline{N}_i$: the average number of survivors during year i

F_i, M_i, Z_i : the instantaneous rates of fishing, natural, and total mortality, respectively, during year i, all on an annual basis, of course

$$Z_i = F_i + M_i \tag{8}$$

Assuming that the mortality rates are constant throughout the year, the following equations are true by definition

$$S_i = e^{-Z_i} \tag{9}$$

$$D_i = Z_i\overline{N}_i \tag{10}$$

$$C_i = F_i\overline{N}_i \tag{11}$$

The last two equations show that E_i can also be written as

$$E_i = F_i/Z_i \tag{12}$$

It should be noted that if the time interval used in the calculations is not one year but, say, T years (where T may or may not be a whole number), it is necessary to replace F_i, M_i and Z_i with F_iT, M_iT and Z_iT, respectively, in all the equations given above, and to redefine the subscript i as denoting one of the intervals of length T rather than a year.

3. Relationships among parameter values

Before formulating the problem and describing the method of cohort analysis, it will be useful to demonstrate for various cases that if one knows some of the parameter values for year i, one can calculate the others. The parameters in question are those defined above for year i (N_i, S_i, D_i, etc.) plus N_{i+1}, which can be considered to refer either to the end of year i or the beginning of year i+1.

3.1 Case 1 : C_i, M_i and F_i known

In this case, all the other parameters can be calculated from the following equations

$Z_i = F_i + M_i$ from (8)

$S_i = e^{-Z_i}$ from (9)

$E_i = F_i/Z_i$ from (12)

$\overline{N}_i = C_i/F_i$ from (11)

$D_i = Z_i\overline{N}_i$ from (10)

$N_i = D_i/(1-S_i)$ from (3)

$N_{i+1} = N_iS_i$ from (1)

3.2 Case 2 : C_i, M_i and N_i known

Clearly, if F_i can be obtained from these parameters, the remaining parameters can be calculated as in Case 1. To see how F_i can be found, note first that equation (6) can be written in the form:

$$\frac{C_i}{N_i} = E_i(1 - S_i) \qquad (13)$$

Substituting from equation (8), (9) and (12) gives E_i and S_i in terms of F_i and M_i, so that equation (13) becomes:

$$\frac{C_i}{N_i} = \frac{F_i}{(F_i + M_i)}(1 - e^{-(F_i + M_i)}) \qquad (14)$$

Since C_i, M_i and N_i are known in this case, the only unknown in the equation is F_i. Ways of computing the correct value of F_i will be given later (see section 7.1 below); for the moment it suffices that F_i can be found from equation (14), and then the other parameters computed as in Case 1.

3.3 Case 3 : C_i, M_i and N_{i+1} known

In this case also, an equation can be derived in which the only unknown is F_i. The correct value of F_i can then be found by the methods given in section 6, and the other parameters calculated as in the previous cases. To derive the equation, note that equation (7) can be rewritten:

$$\frac{C_i}{N_{i+1}} = E_i\frac{(1 - S_i)}{S_i} \qquad (15)$$

As in Case 2, writing E_i and S_i in terms of F_i and M_i gives the following equation in which the only unknown is F_i:

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

4. Formulation of the problem

In most cases, the problem to be solved by cohort analysis is the following:

<u>Given</u> the annual catches from a single cohort during the entire exploited phase,

<u>Given</u> the value of the natural mortality rate, assumed constant throughout the exploited phase,

<u>Given</u> for some year, the value of the fishing mortality rate,

<u>Find</u> the values of the other parameters given above for each year in the exploited phase of the cohort.

In terms of the notation given in section 1, the problem can be stated:

<u>Given</u> $C_1, C_2, C_3, \ldots\ldots$

<u>Given</u> $M_1 = M_2 = M_3 = \ldots\ldots = M$

<u>Given</u> F_i for some year i

<u>Find</u> all other parameters for each year $i = 1, 2, 3, \ldots\ldots$

5. Cohort analysis

First, note that as the problem has been formulated, C_i, F_i and M are all known for one year (year i). Therefore, as explained for Case 1 in section 2.1 above, one can directly calculate all the other parameter values for year i, including, of course, the number of survivors at the start of the year, N_i, and the number at the end of the year, N_{i+1}.

At this point one knows the number of survivors N_i at the end of the preceding year (i-1), as well as the natural mortality rate M and the catch C_{i-1} in that year. This situation corresponds to Case 3 above, so all parameter values for year i-1 can be found, and the procedure repeated for each preceding year in succession to yield the complete set of parameter values for each of the years 1, 2, ..., i.

For the following years (i+1, i+2, ...) note that for year i+1 one knows, in addition to the catch C_{i+1} and the natural mortality rate M, the number of survivors at the start of the year N_{i+1}. This situation corresponds to Case 2 above, so all parameter values can be found for year i+1 and this process repeated for each of the subsequent years to complete the solution of the problem.

6. Example

The following theoretical example will show the steps in the procedure. Let the (known) annual catch at each age from a cohort be denoted:

Age	I	II	III	IV	V	VI
Catch	C_1	C_2	C_3	C_4	C_5	C_6

Suppose that the rate of natural mortality M is known and is the same for all ages. Finally, suppose that F_4, the rate of fishing mortality at age IV, is known. The problem is then to calculate all the other parameters for the six years of the exploited phase.

The first step is to calculate all paramenters for age IV, as in Case 1 above. Thus:

$$Z_4 = F_4 + M \quad ; \quad S_4 = e^{-Z_4} \quad ; \quad E_4 = \frac{F_4}{Z_4} \quad ;$$

$$\bar{N}_4 = \frac{C_4}{F_4} \quad ; \quad D_4 = Z_4\bar{N}_4 \quad ; \quad \bar{N}_4 = \frac{D_4}{(1 - S_4)} \quad ;$$

$$\text{and} \quad N_5 = N_4 S_4$$

For age III, we now know N_4 as well as the data values C_3 and M. We are therefore in Case 3, and to find F_3 we need to determine the value that satisfies the equation:

$$\frac{C_3}{N_4} = \frac{F_3}{(F_3 + M)} \; \frac{(1 - e^{-(F_3 + M)})}{e^{-(F_3 + M)}}$$

Ways of doing so will be given later; once F_3 has been found, the other parameters for age III will be:

$$Z_3 = F_3 + M \quad ; \quad S_3 = e^{-Z_3} \quad ; \quad E_3 = \frac{F_3}{Z_3} \quad ;$$

$$\bar{N}_3 = \frac{C_3}{F_3} \quad ; \quad D_3 = Z_3\bar{N}_3 \quad ; \quad N_3 = \frac{D_3}{(1 - S_3)} \quad ;$$

$$\text{or} \quad N_3 = \frac{N_4}{S_3}$$

For age II, one now knows C_2, M and N_3, so by solving the equation:

$$\frac{C_2}{N_3} = \frac{F_2}{(F_2 + M)} \; \frac{(1 - e^{-(F_2 + M)})}{e^{-(F_2 + M)}}$$

one finds F_2, and the other parameters for age II are then:

$$Z_2 = F_2 + M \quad ; \quad S_2 = e^{-Z_2} \quad ; \quad E_2 = \frac{F_2}{Z_2} \quad ;$$

$$\bar{N}_2 = \frac{C_2}{F_2} \quad ; \quad D_2 = Z_2\bar{N}_2 \quad ; \quad N_2 = \frac{D_2}{(1 - S_2)} \quad ;$$

$$\text{or} \quad N_2 = \frac{N_3}{S_2}$$

Similary, for age I the equation to solve is:

$$\frac{C_2}{N_1} = \frac{F_1}{F_1 + M} \; \frac{(1 - e^{-(F_1 + M)})}{e^{-(F_1 + M)}}$$

and having found F_1 we can calculate:

$$Z_1 = F_1 + M \quad ; \quad S_1 = e^{-Z_1} \quad ; \quad E_1 = \frac{F_1}{Z_1} \quad ;$$

$$\bar{N}_1 = \frac{C_1}{F_1} \quad ; \quad D_1 = Z_1\bar{N}_1 \quad ; \quad N_1 = \frac{D_1}{(1 - S_1)} \quad ;$$

$$\text{or} \quad N_1 = \frac{N_2}{S_1}$$

For the ages above IV, the procedure given for Case 2 will be followed. For age V, we have C_5, M and, from the computations for age IV, N_5. The value of F_5 can be found from the equation:

$$\frac{C_5}{N_5} = \frac{F_5}{(F_5 + M)} \left(1 - e^{-(F_5 + M)}\right)$$

and knowing F_5 we can compute:

$$Z_5 = F_5 + M \quad ; \quad S_5 = e^{-Z_5} \quad ; \quad E_5 = \frac{F_5}{Z_5} \quad ;$$

$$N_5 = \frac{C_5}{F_5} \quad ; \quad D_5 = Z_5\bar{N}_5 \quad ; \quad N_6 = N_5S_5$$

That done, N_6 is known, which with C_6 and M provides the value of F_6 from the solution of:

$$\frac{C_6}{N_6} = \frac{F_6}{(F_6 + M)} (1 - e^{-(F_6 + M)}$$

and the parameters follow:

$$Z_6 = F_6 + M \quad ; \quad S_6 = e^{-Z_6} \quad ; \quad E_6 = \frac{F_6}{Z_6} \quad ;$$

$$\bar{N}_6 = \frac{C_6}{F_6} \quad ; \quad D_6 = Z_6\bar{N}_6 \quad ; \quad N_7 = N_6S_6$$

This completes the solution of the problem.

7. Related matters

7.1 Methods of solving equations (14) and (16)

These equations do not have an explicit solution because the one unknown - F_i - appears both as a linear term and as an exponent. One way to solve them is by successive approximation, and programmes for performing the iterated steps have been developed for various kinds of calculators.

Another way is to obtain an approximate value from a table prepared specifically for cohort analysis (Schumacher, 1970). There is a separate table for each value of M, and in each table the rows refer to successive values F, separated by a fixed interval, from 0.0 upward. There are several columns in each table showing, for the corresponding values of M and F, the values of E, S, (1-S), E(1-S) and E(1-S)/S. The last two, as can be seen from equations (13) and (15) are the values of C_i/N_i and C_i/N_{i+1}, respectively. To solve equation (14), therefore, one goes to the table for the appropriate value of M and scans down the column headed E(1-S) to find the value nearest to the calculated value of C_i/N_i. The row in which this value is found will show the solution F_i, and the values of the other parameters Z_i, S_i and $(1-S_i)$ as well. The procedure is similar in the case of equation (16), except that one looks for the calculated value of C_i/N_{i+1} in the column headed E(1-S)/S.

An important feature of cohort analysis is that during back calculations (i.e., successive calculation of F_{i-1}, F_{i-2}, etc. when the known value was F_i), the relative error of estimate due to any error in the starting value F_i, decreases steadily. In forward calculation, however, the relative error grows steadily and can become large after only a few intervals. Partly for this reason, one usually tries to use a starting estimate F_i at the end of the catch sequence, since most of the estimates in the sequence will then not be much affected by error in the starting value. All of the estimates in the sequence will, of course, be affected by any error in the estimate of M.

7.2 Starting the calculations from an estimate of E_i

As the problem was formulated in section 4, it was assumed among other things that the value of F_i was known for some year, usually a year near the end of the exploited phase. But other parameters that measure exploitation in some way can also be taken as the starting value for the calculations. One of these is the exploitation ratio E_i. Given an estimate of this parameter for some year, F_i, can be calculated, according to equations (12) and (8), as:

$$F_i = \frac{ME_i}{(1 - E_i)}$$

and the rest of the calculations carried out from this point as explained above.

One reason for choosing E_i over F_i for a starting estimate is that it has a smaller range of possible values, only zero to 1. When F = M, the value of E is 0.5. Hence even a rough idea such as "the stock is lightly exploited" restricts estimates of E to between 0 and 0.5. At the other extreme, if the stock is thought to be "heavily exploited", the starting value of E should be between 0.5 and 1.0.

7.3 Starting the calculations from an estimate of E_i^*, the rate of exploitation as defined by Ricker

Another parameter sometimes used as a starting value is the annual rate of exploitation E_i^* as defined by Ricker, the fraction of fish alive at the beginning of the year that are caught during the course of the year, or in the notation used here:

$$E_i^* = C_i/N_i$$

It can be noted incidentally that, by equation (13), E_i and E_i^* bear the following relationship:

$$E_i^* = E_i(1 - S_i)$$

In this case, since the estimated value of E_i^* is by definition an estimate of C_i/N_i, one is in the situation described above as Case 2 and proceeds accordingly.

7.4 Starting the calculations from an estimate of $\bar{E}_i$ (Gulland's method)

This rate of exploitation, $\bar{E}_i$, refers not to a single year but to all years in the exploited phase beginning with year i (that is i, i+1, i+2, ...). Thus $\bar{E}_i$ is the fraction of survivors alive at the start of year i that will be caught during the remainder of the exploited phase. If V_i denotes the cumulative catch from the cohort beginning with year i ($V_i = C_i + C_{i+1} + \ldots$), then E_i is defined as:

$$\bar{E}_i = V_i/N_i \tag{17}$$

When the starting value for the calculations is an estimate of $\bar{E}_i$, the first step is to calculate N_i from the equation:

$$N_i = V_i/\bar{E}_i$$

One then knows C_i, N_i and M for year i, and is thus in a situation corresponding to Case 2 above, so all the parameters for year i and the other years can be calculated.

An estimate of $\bar{E}_i$ is sometimes preferable to an estimate of F_i, especially when the exact ages of older animals are difficult to determine. In this situation one will not be able to determine the exact catch at each of the greater ages, but one will know the total catch for all those ages combined, for example beginning with age i. Then if one has an estimate of $\bar{E}_i$, along with an estimate of M and the earlier catches at age C_1, C_2, ..., C_{i-1}, one can carry out the cohort analysis (at least up to age i-1) by the methods given above.

8. Other methods

8.1 Virtual population analysis

As the problem was formulated in section 4, it was assumed that, in addition to knowing the catch in number at each age and the natural mortality rate, one had an estimate of F_i (or E_i or E_i^* or $\bar{E}_i$) for some year i. Virtual population analysis does not require an estimate of F_i because it assumes that the rate of fishing mortality is constant from year i onward, and in this case it can be calculated. Observe that by equation (17),

$$V_i = \bar{E}_i N_i \text{ and } \bar{V}_{i+1} = \bar{E}_{i+1}$$

and that, since the fishing and natural mortality rates are assumed constant ($F_i = F_{i+1} = \ldots$ and $M_i = M_{i+1} = \ldots = M$), it will also be the case that $\bar{E}_i = \bar{E}_{i+1} = \ldots$, so the ratio of the cumulative catches will be:

$$\frac{V_{i+1}}{V_i} = \frac{N_{i+1}}{N_i} \tag{18}$$

Finally, substituting from equation (1) shows

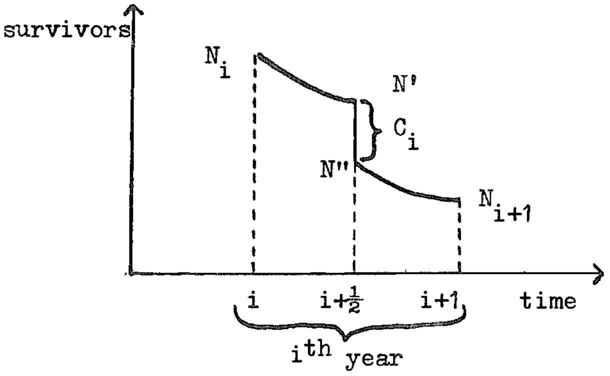
$$\frac{V_{i+1}}{V_i} = S_i \tag{19}$$

From the ratio of the cumulative catches, therefore, one can calculate the rate of survival S_i, which with the value M will provide F_i by application of equations (8) and (9). Then cohort analysis can be performed for the ages up to age i.

Equation (18) shows that under the assumption of a constant fishing mortality rate, the cumulative catches are proportional to the number of survivors at each age, and it is for this reason that the cumulative catches are called "virtual populations".

8.2 Pope's method

Pope (1972) reported an approximate equation relating the numbers of survivors at the beginning and the end of the year. This equation can be derived by treating the annual catch as if all of it were taken instantaneously in the middle of the year. In the i^{th} year, for example, which begins at time i and ends at time i+1, the entire catch is treated as being taken instantaneously at time $i+\frac{1}{2}$, as shown in the following figure.



On the graph, N' is the theoretical number of survivors at time $i+\frac{1}{2}$, calculated as though there had been no fishing between time i and time $i+\frac{1}{2}$, or:

$$N' = N_i e^{-M/2}$$

Immediately after the catch C_i has been taken, the number of survivors is $N'' = N' - C_i$. From time $i+\frac{1}{2}$ to time i+1 there is no fishing, so the number of survivors at time i+1 is:

$$N_{i+1} = N'' e^{-M/2}$$

Substituting for N'' and N' in this equation produces:

$$\begin{aligned} N_{i+1} &= (N' - C_i)\, e^{-M/2} \\ &= (N_i e^{-M/2} - C_i)\, e^{-M/2} \\ &= N_i e^{-M} - C_i e^{-M/2} \end{aligned}$$

For purposes of back calculations in cohort analysis, it is useful to rewrite this equation as:

$$N_i = N_{i+1} e^{M} + C_i e^{M/2} \qquad (20)$$

so that once N_{i+1} has been estimated, it is a simple matter to compute N_i, N_{i-1}, ... successively. Then, given the number of survivors at the beginning of each year, the annual rates of survival and fishing mortality rates can be calculated from equations (1), (8) and (9), and all the other parameters follow therefrom.

Pope found that the accuracy of the approximation (20) was quite satisfactory whenever the natural mortality rate M was equal to or less than 0.3 and the fishing mortality rates F_i were all equal to or less than 1.2.

As an example, consider the following catch data for a single cohort:

Age	I	II	III	IV	V	VI^+
Catch in number	C_1	C_2	C_3	C_4	C_5	V_6

The natural mortality rate M is known and assumed constant, and an estimate of $\bar{E}_6$ is available.

To estimate the parameters N_i and F_i at each age by Pope's method, one begins by computing $N_6 = V_6/\bar{E}_6$. Then, given N_6, one calculates N_5, N_4, ..., N_1 successively by applying equation (20):

$$N_5 = N_6e^M + C_5e^{M/2}$$

$$N_4 = N_5e^M + C_4e^{M/2}$$

$$\vdots$$

$$N_i = N_2e^M + C_1e^{M/2}$$

The annual survival rates are then $S_5 = N_6/N_5$, $S_4 = N_5/N_4$, ..., $S_1 = N_2/N_1$, from which Z_5 Z_4, ..., Z_1 and F_5, F_4, ..., F_1 can be calculated.

9. Extension to the entire exploited population

Up to this point only the calculations for a single cohort have been considered, and in fact these are very useful for studying the effects of different regimes of exploitation on the catches, biomass, etc. of a cohort over the course of its exploited phase. But it is also important to consider the exploitation of an entire population during one year. If the recruitment to the population is constant year after year, the results for the population during a single year will be the same as those for one cohort during its entire exploited phase. But this will not be true if recruitment varies. In this case, in order to determine, say, the size composition of the population at the beginning of some year, one can perform a cohort analysis for each of the cohorts present in the population during that year and then combine the results. This procedure of course requires that one know, for <u>each</u> cohort, the numbers caught at each age and the fishing mortality rate (or some equivalent parameter) for some year, as well as the natural mortality rate, which is usally assumed to be the same for all years and ages.

The situation is illustrated by the table below, which shows the composition of catches in number by age group for the period 1970–1975.

Ages / Years	I	II	III	IV	V	VI
1970	$C_{I,0}$	$C_{II,0}$	$C_{III,0}$	$C_{IV,0}$	$C_{V,0}$	$C_{VI,0}$
1971	$C_{I,1}$	$C_{II,1}$	$C_{III,1}$	$C_{IV,1}$	$C_{V,1}$	$C_{VI,1}$
1972	$C_{I,2}$	$C_{II,2}$	$C_{III,2}$	$C_{IV,2}$	$C_{V,2}$	$C_{VI,2}$
1973	$C_{I,3}$	$C_{II,3}$	$C_{III,3}$	$C_{IV,3}$	$C_{V,3}$	$C_{VI,3}$
1974	$C_{I,4}$	$C_{II,4}$	$C_{III,4}$	$C_{IV,4}$	$C_{V,4}$	$C_{VI,4}$
1975	$C_{I,5}$	$C_{II,5}$	$C_{III,5}$	$C_{IV,5}$	$C_{V,5}$	$C_{VI,5}$

In the table, the catches from the 1970 year-class are set off in boxes. An estimate of F (or some other index of exploitation) in some year must be known for each of the year-classes. When working with data from trawl fisheries, one usually tries for starting estimates for the greatest age (age VI in the table) and then back calculates to estimate the values of Z and F = Z - M in previous years, since the relative error in these estimates caused by error in the starting value will decrease steadily as the back calculations proceed.

Not all of the cohorts present in the population during the most recent year covered by the data (1975 in the table above) will have reached full recruitment, so even if an estimate of F for fully recruited age groups is available, some special treatment will be required for the youngest age groups. The application of partial recruitment factors, discussed below, provides a way of adjusting the starting estimate for these groups. Finally, some comments on predicting future catches and stock sizes are offered under the heading "Stock forecasts".

The results of a cohort analysis for data such as those in the table above are usually presented in two corresponding tables, one showing the estimates of F, and the other number of survivors, at each age in each year. These results can serve as the basic data for an empirical study of the behaviour of the stock and the fishery. The sequence of value F_i for a number of years (or other time periods) for a single cohort is usually called the F_i vector.

9.1 Partial recruitment factors

Usually the total fishing effort exerted on a stock changes from year to year as a result of changes in fleet size, fishing power or other factors. Even within a single year, a given level of fishing effort does not bring about the same rate of fishing mortality for all of the cohorts in the fishery, since there is always some variation with age in the availability or vulnerability of fish to the gear. In trawl fisheries, for example, fishing mortality is lower for small fish than for older fish that are fully recruited. Accordingly, it is customary to assume that the fishing mortality rate at each age is a fixed fraction of the fishing mortality rate of the fully recruited age groups, i.e., if F_1, F_2, F_3, ... are the fishing mortality rates at age 1, age 2, age 3, ..., and F is the fishing mortality rate at full recruitment, then the ratios F_1/F, F_2/F, F_3/F, ... remain constant from one year to the next, although total effort and therefore the actual levels of F_1, F_2, F_3, ..., F may change.

The ratios are called partial recruitment factors and their use in cohort analysis is straightforward; if for some year one has an estimate of F (for fully recruited age groups) then starting estimates for partly recruited age groups can be calculated by multiplying by the partial recruitment factors estimated for other years. Of course, partial recruitment factors may change if there is a change in gear selectivity, in stock availability, or in the temporal or spatial distribution of fishing effort with respect to the distribution of age groups.

9.2 Stock forecasting

One of the results of cohort analysis in forward calculations is the size and composition of the stock (except for the new recruits) at the end of the year, which is the beginning of the next year. To forecast the size and composition of the stock in future years, therefore, one needs estimates of the fishing mortality rates, partial recruitment factors and levels of recruitment for those years. With these, the equations used in cohort analysis provide the means to calculate, for each cohort, the number that will be caught in each year and the number that will survive to the next. If mean individual weight at age is known, then catches in weight and total cohort biomass at each age can also be computed.

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SYNTHETIC MODELS

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1. Introduction

Consider an unexploited stock of fish. During a year, its total biomass will grow by an amount equivalent to the weight of recruits that the stock receives and the growth in weight of individuals in the stock. It will decrease by an amount equivalent to the weight of fish that die of natural causes of all kinds (predation, disease, etc.). Russel (1931) described the balance of changes that occur during the year as follows:

$$B_1 - B_0 = R + G - D \qquad (1)$$

where B_0 and B_1 denote the biomass of the stock at the beginning and end of the year, respectively, and R, G and D denote recruitment, growth and mortality, respectively.

Each of the terms R, G and D on the right hand side of the equation will [illegible] affected by the environmental conditions that prevail during the year. If food is abundant one can expect that G will be relatively high and that D will probably be relatively low. Similarly, the recruitment R (as well as the other terms indirectly) will be affected, often very greatly, by the environmental conditions that prevailed at the time the recruits were spawned and immediately thereafter, that is several months or years, depending upon the life history of the species, before the recruits joined the stock.

These terms will also be influenced, and in different ways, by the size of the stock, both at the time in question and during some previous period, as well as by its demographic composition (i.e., the distribution of lengths or ages within it). The rate of growth of the biomass will always be greater in a stock containing a high proportion of young fish. As a first approximation natural deaths will be proportional to the size of the stock in number, but this proportion will doubtless be relatively greater in the case of a stock where older fish predominate. The recruitment will depend on the size of the stock some months or years before the time of recruitment (i.e., at the time the recruits were spawned) much more than on its size at the time of recruitment.

Equation (1) can be modified to take account of the effects of emigration, E, and of immigration, I, as follows:

$$B_1 - B_0 = R + G - D + I - E \qquad (2)$$

This equation provides a complete description of the factors, aside from fishing, that control the biomass of the stock. This formulation requires no assumptions, but neither does it provide a means to evaluate the state of stock or the effect of fishing on it. To do so one can proceed in either of two ways. The first, which makes use of analytical models (sometimes called structural models), consists of examining each term in the equation in detail and then formulating equations for the behaviour of each term, for example, the growth schedule of individuals and the effect on growth of food availability or of intraspecific competition. This approach usually calls for a detailed study of the stock since it requires a detailed understanding of the processes at work, and in the long term fairly exact predictions of the effects on the stock and on the catches of, for example, a given change in the pattern of exploitation.

The other approach is to consider the overall net effect of all factors that control the biomass simultaneously, i.e.,

$$\Delta B = B_1 - B_0$$

and to examine how ΔB behaves, specifically as a function of the biomass B. This approach assumes that for practical purposes the population of fish can be described in terms of its biomass only, i.e., without regard to its demographic composition. The other factors to be considered in this model, aside from the rate of natural growth ΔB (or dB/dt if one wishes to describe the continuous process rather than the absolute growth realized by the end of some fixed period), are the rate of fishing mortality F and the catch or yield Y. Synthetic models - sometimes called surplus production models or global models - describe the relationships among these quantities.

2. Behaviour of the biomass of a stock

2.1 Unexploited stock

One can suppose that in the absence of any exploitation the total biomass of a stock will not increase beyond some limiting size, determined by the amount of space and resources available, by competition, etc., that is by the carrying capacity of the ecosystem of which the stock is a part. As a first approximation one can assume that the factors determining this carrying capacity do not change systematically over time, although they may fluctuate from year to year. Consequently, the biomass of an unexploited stock will fluctuate about some mean value, and only the position of the mean will be discussed here.

Alternatively, one could suppose that the biomass B of a stock, beginning at a negligible level B = 0, would tend to increase up to its maximum level $B = B_\infty$, described above as the carrying capacity of the ecosystem for the stock. But the biomass will not grow at a constant rate. It will grow slowly when the biomass is small, more rapidly at intermediate values, and eventually it will again grow slowly as it approaches B_∞. Thus, beginning at some low value when the biomass is small, the rate, or more exactly the absolute rate of natural growth, will increase to same maximum value and decrease thereafter to 0. This implies that the absolute instantaneous rate of natural growth dB/dt will be zero when B = 0, will increase to a maximum at same intermediate level of biomass and will then decrease steadily, reaching zero when $B = B_\infty$.

Another way to describe this variation in the rate of natural growth would be to say that the specific instantaneous rate of natural growth $(1/B)\ (dB/dt)$, is some continuously decreasing function of the biomass B, generally denoted f(B). The value of this function is high when the biomass B is very small (i.e., when resources are abundant and competition is low), but it decreases steadily to zero as the biomass grows to its maximum value B_∞. Figures 1 and 2 show, in general terms, the variation of the absolute and specific growth rates with biomass.

2.2 Exploited stock

Now consider an exploited stock. Taking catches from a stock always reduces the total biomass, because it imposes an additional mortality. The biomass of an exploited stock will therefore depend on the size of the catches. If the rate of removal is higher than the stock's rate of natural growth, the biomass will decrease; if it is lower, the biomass will increase but more slowly than it would in the absence of exploitation; if the rates of removal and natural growth are equal, the biomass will remain constant. In this last case, the catch is called the equilibrium catch Y_e for that level of biomass.

At this point one can already make some general observations about the importance of equilibrium catches and equilibrium conditions of an exploited stock for fisheries management. First, one can say that for a particular stock there is no unique value of equilibrium

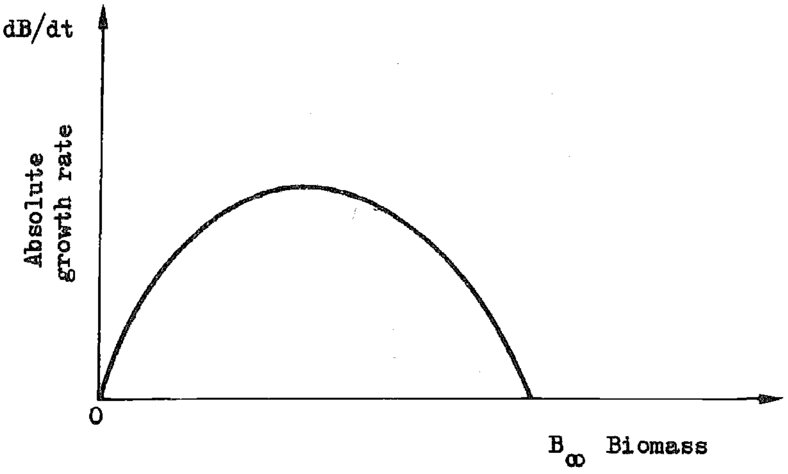


Fig. 1 - The absolute rate of natural growth of biomass as a function of biomass (in the absence of exploitation)

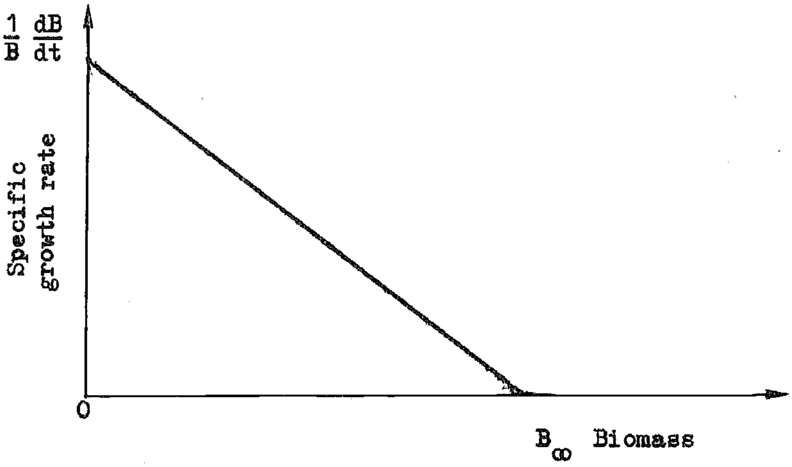


Fig. 2 - The specific rate of natural growth of biomass as a function of biomass (in the absence of exploitation)

catch. On the contrary, at each level of biomass, one can catch some quantity that will leave the biomass unchanged - the equilibrium catch, and this equilibrium catch will be different at different levels of biomass. Taking the equilibrium catch can be desirable because it maintains the biomass at a constant level. In this case one can catch the same amount year after year without causing any change in the total biomass of the stock. Second, Figures 1 and 2 show that the equilibrium catch varies with biomass. It is low both when the biomass is small and, contrary to what one might think, when the biomass is close to its maximum value (since at this level the absolute rate of natural growth is small and only a small catch can be taken without reducing the biomass). The maximum equilibrium catch can be taken when the biomass is at an intermediate level where the absolute rate of natural growth is highest.

3. Equilibrium conditions in an exploited stock

3.1 In terms of the level of exploitation (F) and the biomass ($\overline{B}$)

When a stock is exploited, the net rate of change of the biomass will depend on two components, the rate of natural growth of the stock (which will be positive) and the rate of removal by the fishery (which will be negative). Thus, for example, the specific rate of change in the biomass, $(1/B)\ dB/dt$, will be equal to the sum of the specific rate of natural growth, $f\ (B)$, and the specific rate of removal by the fishery, $-F$. Arithmetically one can write:

$$\left(\frac{1}{B}\right)\left(\frac{dB}{dt}\right) = f\ (B) - F \tag{3}$$

For a given time interval Δt, during which F remains constant, equation (3) can be written in approximate form:

$$\left(\frac{1}{\overline{B}}\right)\left(\frac{\Delta B}{\Delta t}\right) = f\ (\overline{B}) - F \tag{4}$$

where $\overline{B}$ is the mean biomass during the time interval Δt. Equation (4) gives the change in biomass ΔB as a function of mean biomass $\overline{B}$ directly:

$$\Delta B = f(\overline{B})\ \overline{B}\Delta t - F\ \overline{B}\Delta t \tag{5}$$

At equilibrium, the change in biomass ΔB will be 0, so the mathematical condition for equilibrium is:

$$f(\overline{B}) = F \tag{6}$$

From the definition of F ($= Y/\overline{B}$), and from equation (5), it follows that the equilibrium catch Y_e during a time interval Δt will be:

$$Y_e = F\overline{B}\Delta t = \overline{B}\ f(\overline{B})\Delta t \tag{7}$$

Therefore, if $\Delta t = 1$ year:

$$Y_e = B f\ (\overline{B})$$

Equations (6) and (7) show the equilibrium relationships among F, $\overline{B}$ and Y_e. The equilibrium catch given by (7) can, by means of equation (5), also be represented as a function of F. Thus, in solving equation (6) for $\overline{B}$, one would set $B = f^*(F)$ and, substituting this into (7) with $\Delta t = 1$ year, one would obtain:

$$Y_e = F f^*(F) \tag{8}$$

3.2 In terms of indices of biomass and fishing mortality

Equations (6), (7) and (8), which are fundamental for the assessment of a fishery, are usually transformed into terms of indices of biomass and fishing mortality for practical reasons. When it is measured accurately and expressed in the proper units, fishing effort X during a time interval Δt can be related to the instantaneous rate of fishing mortality F, assumed constant during the interval Δt, by the following equation:

$$F \Delta t = qX \tag{9}$$

where the constant of proportionality q is called the catchability coefficient. When Δt = 1 year, the equation simplifies to:

$$F = qX \tag{10}$$

Consequently, X provides an index of fishing mortality, F.

The index of mean biomass during the interval Δt = 1 year can be obtained by substituting the value of F given by (10) into equation (7), or:

$$Y = qX\bar{B} \tag{11}$$

or $$\frac{Y}{X} = q\bar{B} \tag{12}$$

Consequently, the catch per unit of effort Y/X is an index of mean biomass $\bar{B}$. This index will be denoted here by the letter $\bar{U}$. Therefore one can write:

$$\bar{U} = q\bar{B} \tag{13}$$

The conditions prevailing at equilibrium (6), (7) and (8) can be readily expressed in terms of the indices X and $\bar{U}$ by transposing equations (10) and (13).

4. Models

4.1 Introduction

The curves describing the absolute and specific rates of natural growth of the biomass as functions of the biomass (Figures 1 and 2) have not yet been precisely defined. Only their general characteristics have been developed. The phenomena that determine the rate of replacement within a stock as a function of its size are so complex that it is impossible to specify all the determinants of the relationship mathematically. One is therefore obliged to choose empirically, among the various functions having the general characteristics of the curves in Figures 1 and 2, the one which best fits the data at hand. The function so chosen in each case will define a particular model. Theoretically a model is thus defined by the function that relates the specific rate of natural growth f(B) to biomass B. Once the function f(B) has been chosen one can immediately specify the conditions for equilibrium.

$$F = f(\bar{B}),$$

and $$Y_e = F\bar{B} = \bar{B}f(\bar{B})$$

One can also state these equilibrium conditions in terms of indices of fishing mortality (X) and biomass ($\bar{U}$) as explained in section 3.2.

Another way to define a model is to identify empirically a mathematical relationship between $\bar{U}$ and X in equilibrium conditions. On the basis of this relationship one can infer the equilibrium condition $F = f(\bar{B})$ and, thereby, the function $f(\bar{B})$ relating the specific rate of natural growth to mean biomass.

In what follows, the first approach will be taken in presenting the models commonly used.

4.2 The Schaefer model

As explained in section 2.1, the specific rate of natural growth $f(B)$ decreases as the stock biomass decreases. As a first approximation one may suppose that the relation is linear. This was the assumption made by Graham and later by Schaefer (1954) to define their model which can thus be expressed:

$$f(B) = m - KB \tag{14}$$

When the biomass has reached its limiting value, B_{∞}, its rate of change is 0. Therefore,

$$0 = m - KB_{\infty}, \quad \text{or:} \quad m = KB_{\infty}$$

Equation (14) can thus be written:

$$f(B) = K(B_{\infty} - B) \tag{15}$$

In equilibrium conditions, $F = f(\bar{B})$ and it follows that:

$$F = K(B_{\infty} - \bar{B}) \tag{16}$$

Equilibrium conditions therefore are those that satisfy the following equations:

$$\bar{B} = B_{\infty} - \frac{F}{K} \tag{17}$$

$$Y_e = F(B_{\infty} - \frac{F}{K}) \tag{18}$$

and

$$Y_e = K\bar{B}(B_{\infty} - \bar{B}) \tag{19}$$

To express the equilibrium conditions (17), (18) and (19) in terms of indices $\bar{U}$ and X, one need only substitute into these equations the equivalents, $B = \bar{U}/q$ and $F = qX$. The equations then take the following form:

$$\bar{U} = U_{\infty} - bX \tag{20}$$

$$Y_e = X(U_{\infty} - bX) \tag{21}$$

$$Y_e = (\frac{1}{b})\bar{U}(U_{\infty} - \bar{U}), \tag{22}$$

where $b = q^2/K$

Schaefer model: $f(B) = K(B_\infty - B)$

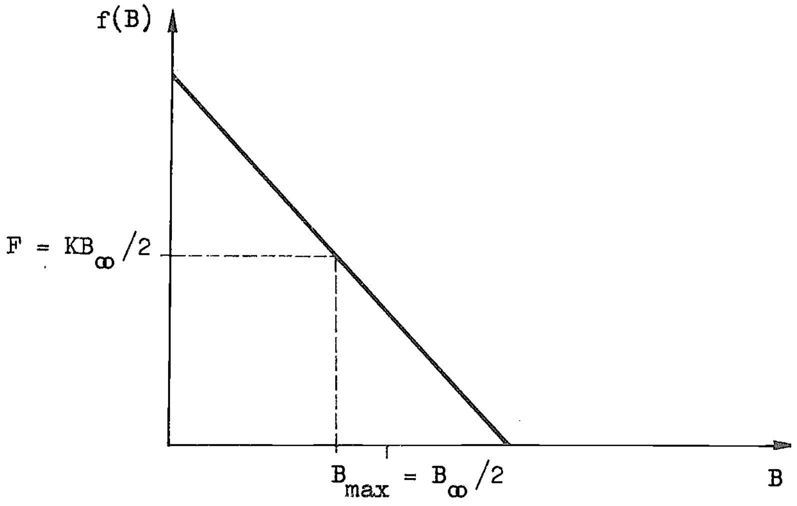
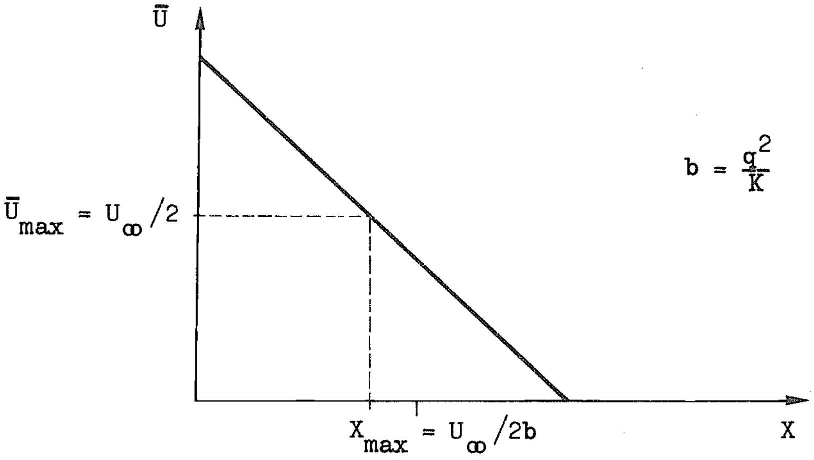


Fig. 3 - Theoretical relationship between the specific rate of natural growth f(B) and total biomass B



$b = \frac{q^2}{K}$

Fig. 4 - The relationship between the index of mean biomass and the index of fishing mortality in equilibrium conditions

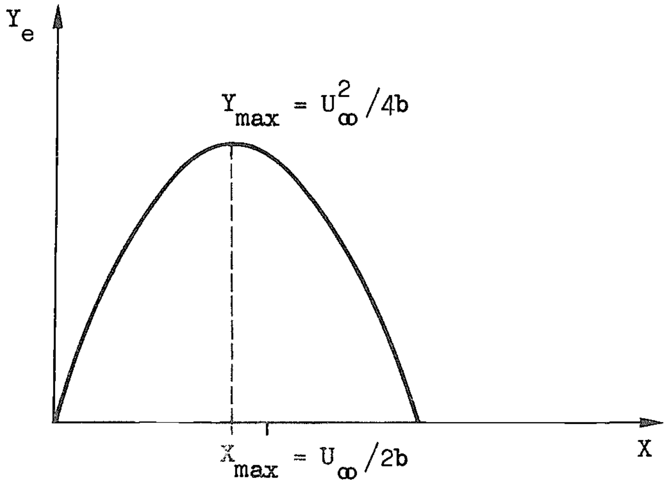


Fig. 5 - The relationship between the equilibrium catch and the index of fishing mortality, in equilibrium conditions

4.2.1 Maximum sustainable yield

One of the most important features of the equations specifying equilibrium conditions is that they provide a means of calculating the maximum equilibrium catch or maximum sustainable yield, Y_{max} (sometimes called MSY). To determine this value one sets the derivative of Y_e with respect to F (equation 18) to zero:

$$\frac{dY_e}{dF} = 0 = B_\infty - \frac{F}{K} - \frac{F}{K}$$

Consequently, the maximum sustainable yield will be taken by a value of F, denoted F_{max}, equal to:

$$F_{max} = \frac{KB_\infty}{2} \qquad (23)$$

From equation (17), one can also obtain the biomass level corresponding to Y_{max} and F_{max}, denoted B_{max}:

$$B_{max} = \frac{B_\infty}{2} \qquad (24)$$

The maximum sustainable yield Y_{max} will therefore be:

$$Y_{max} = \frac{K\, B_\infty^2}{4} \qquad (25)$$

In terms of the indices of abundance and fishing mortality, equations (23), (24) and (25) become:

$$X_{max} = \frac{U_\infty}{2b} \qquad (26)$$

$$\bar{U}_{max} = \frac{U_\infty}{2} \qquad (27)$$

$$Y_{max} = \frac{U_\infty^2}{4b} \qquad (28)$$

Figures 3, 4 and 5, which portray the relationships specified by equations (15), (20) and (21) show the most important properties of the Schaefer model. In practice, estimating the parameters of the equilibrium equation $\bar{U} = U_\infty - bX$ is basic to an assessment of a stock and a fishery. From this equation, one can easily obtain the other equations, for example, the equilibrium catch as a function of fishing effort. These equilibrium relationships make it possible to estimate the maximum sustainable yield, the corresponding level of fishing effort, the equilibrium catches that one can expect at other levels of effort, the relative abundance of the stock, etc.

4.3 Exponential model (Garrod, 1969 and Fox, 1970)

In the previous section it was assumed that as a first approximation, the specific rate of natural growth f(B) was a linear function of the biomass B. This assumption is the basis of the Schaefer model. In practice, one often observes that the data fall along a curve that is concave upward. It has therefore been proposed that an exponential function be used for fitting the observed data, i.e., a function of the form:

$$f(B) = m - K \ln B \qquad (29)$$

<u>Exponential model:</u> $f(B) = K(\ln B_{\infty} - \ln B)$

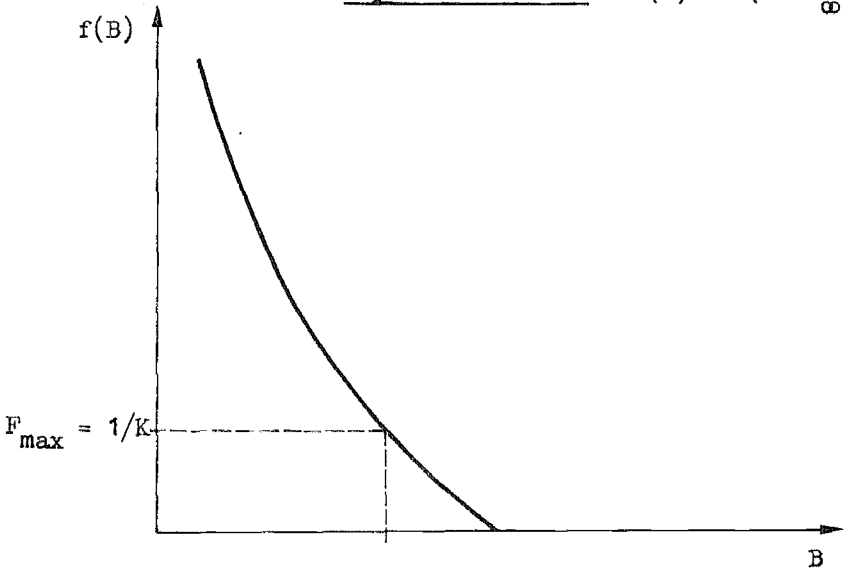


Fig. 6 - Theoretical relationship between the specific rate of natural growth in biomass and total biomass

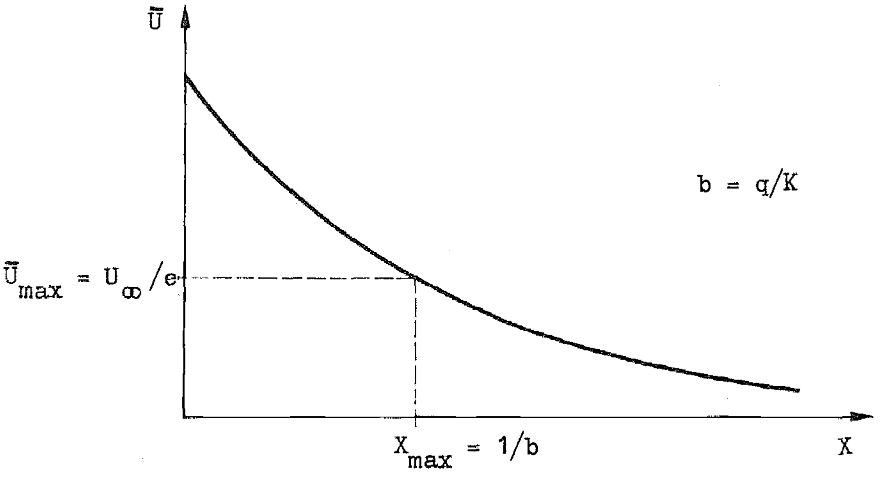


Fig. 7 - Relationship between the index of mean biomass and the index of fishing mortality, in equilibrium conditions

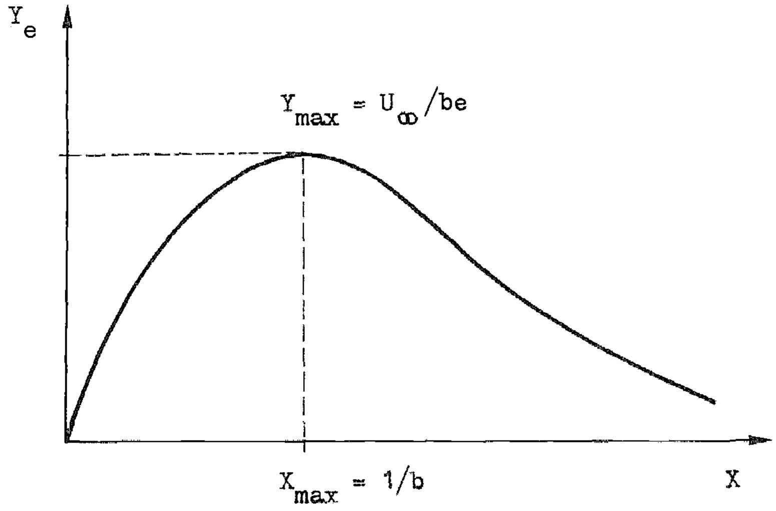


Fig. 8 - Relationship between the equilibrium catch and the index of fishing mortality, in equilibrium conditions

As was done in the case of the Schaefer model, one can then conclude that:

$$\ln B_\infty = \frac{m}{K}$$

and write:

$$f(B) = K(\ln B_\infty - \ln B) \tag{30}$$

Consequently, the conditions for equilibrium are the following:

$$F = K(\ln B_\infty - \ln \bar{B}) \tag{31}$$

or:

$$\bar{B} = B_\infty e^{-(\frac{1}{K})F} \tag{32}$$

$$Y_e = B_\infty F e^{-(\frac{1}{K})F} \tag{33}$$

$$\text{and} \quad Y_e = K\bar{B}\,(\ln B_\infty - \ln \bar{B}) \tag{34}$$

In terms of the indices $\bar{U}$ and X, these conditions are described by:

$$\bar{U} = U_\infty e^{-bX} \tag{35}$$

$$Y_e = U_\infty X e^{-bX} \tag{36}$$

$$Y_e = (\tfrac{1}{b})\bar{U}(\ln U_\infty - \ln \bar{U}) \tag{37}$$

where $b = q/K$

4.3.1 Maximum sustainable yield

The maximum equilibrium catch or maximum sustainable yield can be calculated as it was in the case of the Schaefer model, as follows:

$$\frac{dY_e}{dF} = 0 = B_\infty e^{-(\frac{F}{K})} - B_\infty (\tfrac{F}{K}) e^{-(\frac{F}{K})}$$

$$F_{max} = K \tag{38}$$

$$\bar{B}_{max} = \frac{B_\infty}{e} \tag{39}$$

$$Y_{max} = \frac{KB_\infty}{e} \tag{40}$$

Expressed in terms of the indices abundance and mortality these equations become:

$$X_{max} = \frac{1}{b} \qquad (41)$$

$$\bar{U}_{max} = \frac{U_{\infty}}{e} \qquad (42)$$

and $$Y_{max} = \frac{U_{\infty}}{be} \qquad (43)$$

Figures 6, 7 and 8, which portray these relationships, show the most important features of the exponential model.

4.4 GENPROD model (Pella and Tomlinson, 1969)

Pella and Tomlinson proposed a more general relationship between the specific rate of natural growth f(B) and the biomass B. They introduced a new parameter m to provide greater flexibility in fitting data from various fisheries to a curve of the general form they proposed. In particular they suggested an equation which can be written in the following form:

$$f(B) = K\ (B_{\infty}^{m-1} - B^{m-1}) \qquad (44)$$

This equation is a generalization of equations (15) and (30) from the models of Schaefer and of Fox.

It will be seen immediately that, in the case m = 2, this equation reduces to the Schaefer model (equation 15) and it can be shown that, when m = 1, the GENPROD model is identical to the exponential model (equation 30).

The conditions at equilibrium according to this model can be deduced as was done before; the stock is in equilibrium when:

$$F = K\ (B_{\infty}^{m-1} - \bar{B}^{m-1}) \qquad (45)$$

which is true when:

$$\bar{B} = (B_{\infty}^{m-1} - \frac{F}{K})^{\frac{1}{m-1}} \qquad (46)$$

$$Y_e = F\ (B_{\infty}^{m-1} - \frac{F}{K})^{\frac{1}{m-1}} \qquad (47)$$

$$Y_e = K\bar{B}(B_{\infty}^{m-1} - \bar{B}^{m-1}) \qquad (48)$$

<u>Genprod model</u>: $f(B) = K(B_{\infty}^{m-1} - B^{m-1})$

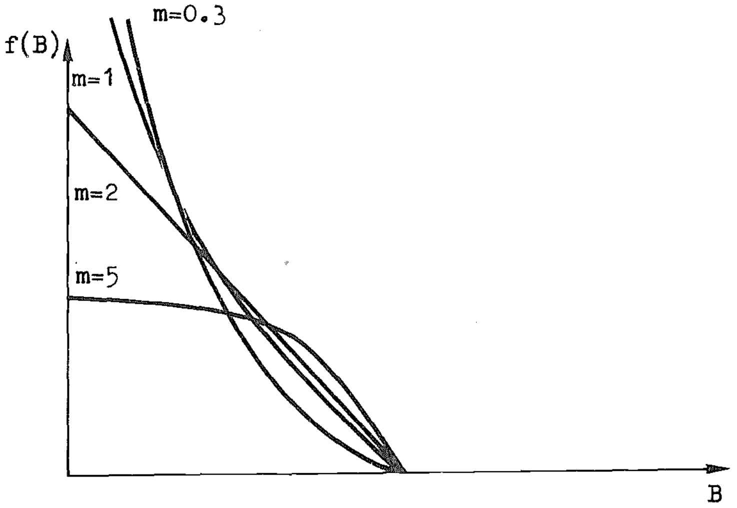


Fig. 9 - Curves showing the theoretical relationship between the specific rate of natural growth of biomass and total biomass, for selected values of m

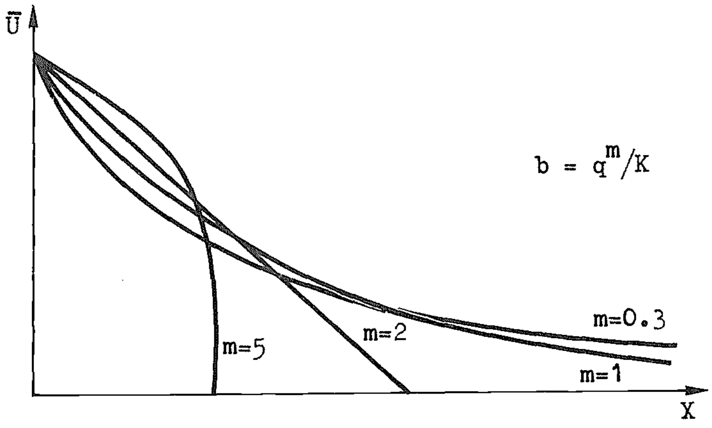


Fig. 10 - Curves showing the relationship between the index of mean biomass and the index of fishing mortality, in equilibrium conditions, for selected values of m

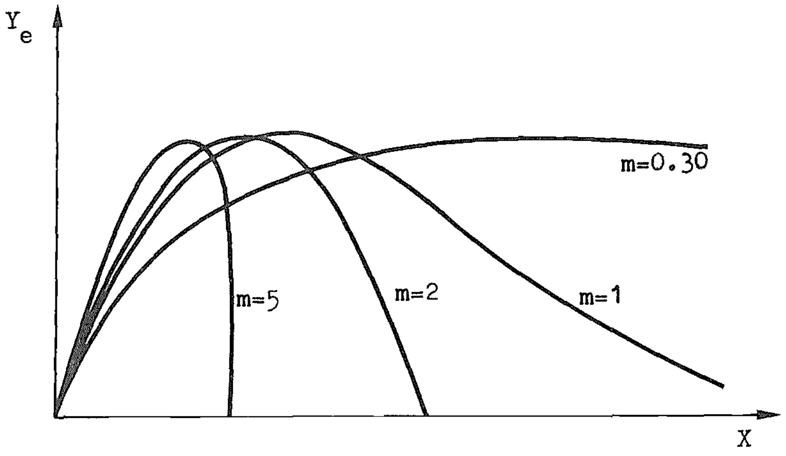


Fig. 11 - Curves showing the relationship between the equilibrium catch and the index of fishing mortality in equilibrium conditions, for selected values of m

Expressed in terms of $\bar{U}$ and X, these equations become:

$$\bar{U} = (U_{\infty}^{m-1} - bX)^{\frac{1}{m-1}} \tag{49}$$

$$Y_e = X\,(U_{\infty}^{m-1} - bX)^{\frac{1}{m-1}} \tag{50}$$

$$Y_e = \frac{1}{b}\,\bar{U}\,(U^{m-1} - \bar{U}^{m-1})^{\frac{1}{m-1}} \tag{51}$$

where $b = q^m/K$

As with the other models, the maximum sustainable yield can be determined by taking the derivative of Y_e with respect to F and setting it to 0:

$$\frac{dY_e}{dF} = 0 = (B_{\infty}^{m-1} - \frac{F}{K})^{\frac{1}{m-1}} - \frac{1}{K}\,\frac{1}{m-1}\,F(B_{\infty}^{m-1} - \frac{F}{K})^{\frac{1}{m-1} - 1}$$

Thus:

$$0 = (B_{\infty}^{m-1} - \frac{F}{K})^{\frac{1}{m-1} - 1}\;(B_{\infty}^{m-1} - \frac{F}{K}\,\frac{m}{m-1})$$

and $$F_{max} = K\,\frac{m-1}{m}\,B_{\infty}^{m-1} \tag{52}$$

$$\bar{B}_{max} = (\frac{1}{m})^{\frac{1}{m-1}}\,B_{\infty} \tag{53}$$

$$Y_{max} = K\,\frac{m-1}{m}\,(\frac{1}{m})^{\frac{1}{m-1}}\,B_{\infty}^{m} \tag{54}$$

In terms of the indices $\bar{U}$ and X, these equations are:

$$X_{max} = \frac{1}{b}\,\frac{m-1}{m}\,U_{\infty}^{m-1} \tag{55}$$

$$\bar{U}_{max} = (\frac{1}{m})^{\frac{1}{m-1}}\,U_{\infty} \tag{56}$$

$$Y_{max} = \frac{1}{b}\,\frac{m-1}{m}\,(\frac{1}{m})^{\frac{1}{m-1}}\,U_{\infty}^{m} \tag{57}$$

Figures 9, 10 and 11 show the curves corresponding to different values of m. It should be noted that in the literature this model is usually stated in a form different from equation (44) but it can be readily shown that the two forms are equivalent. Fox (1974) presented a detailed analysis of this model, of its various formulations and of its behaviour.

5. Practical applications

Usually the available data such as $\overline{B}$, $\overline{U}$ and Y do not refer to equilibrium conditions. The total catch taken during a particular period of observation (for example, 1 year) depends not only on the mean biomass and the fishing effort X exerted during this period, but also on the intensity of the exploitation to which the year classes present in the stock have been subjected previously. Therefore, before fitting the data to the equations given above it is necessary to adjust them by some method so that they will represent as nearly as possible the values that would obtain at equilibrium. Some of these methods are given below in this section (cases 1 - 5).

While one can, by use of these methods, adjust the data for the history of exploitation of the year classes present in the stock during the period in question, these methods do not take account of changes in the level of recruitment caused by changes in the size of the parent stock. By its very form, the model takes account of the effect of this phenomenon on equilibrium conditions, but in non-equilibrium conditions the effect will occur only after a lag period that depends on the life history of the stock (in particular the length of the pre-recruit period).

It can also be seen that, insofar as the basic assumption of stability in the carrying capacity of the ecosystem does not hold, there will be deviations or fluctuations in the observed values.

With these things in mind, one has to choose some mathematical function to represent the observed relationship between the specific rate of natural growth f(B) and the biomass, or an equivalent relationship. The choice of a function will be empirical: in practice one chooses the function which, among all the possible candidates, provides the best fit to the observed data. Then, by regression or another technique one estimates the parameters of the chosen equilibrium relationship giving the best fit to the scatter of points. (Ricker (1973) showed that in general it is correct to use the functional regression rather than the usual least - squares regression for fitting.) Gulland (1961) advised that fitting a curve by eye lets the researcher make use of his prior experience and knowledge of the fishery in question (such as changes in the pattern of exploitation: mesh size, discard pattern, distribution of effort in space and time, etc.). On the other hand, following an objective mechanical procedure forestalls any discussion of the subjective steps in the process, so it can be highly advantageous, for example, when working groups have to formulate management measures which will have different effects on the various parties interested in the fishery.

Case 1: Consider an exploited stock for which one knows the biomass at the beginning of each year and the total catch taken during the year for a series of years:

Year	1	2	...i..........
Biomass at beginning of year	B_1	B_2	...B_i.........
Catch during year	Y_1	Y_2	...Y_i.........

The natural growth of the biomass, ΔB_i, will be equal to:

$$\Delta B_i = B_{i+1} - B_i + Y_i$$

The observed change in the biomass ($B_{i+1} - B_i$) will thus be equal to the difference between the natural growth of the biomass during year i and the catch taken during the year Y_i. The mean biomass $\overline{B}_i$ can be approximated by the average of the biomass at the beginning and end of the year, that is:

$$\overline{B}_i = \frac{1}{2}(B_i + B_{i+1})$$

The mean specific rates of natural growth in each year can then be used to estimate the function $f(B)$:

$$f(\bar{B}_i) = \Delta B_i / \bar{B}_i$$

Case 2: Consider an exploited stock for which one knows the mean biomass and the total catch during each year for a series of years:

Year	1	2	...i...........
Mean biomass	$\bar{B}_1$	$\bar{B}_2$	...$\bar{B}_i$.........
Total catch during year	Y_1	Y_2	...Y_i.........

To estimate the mean specific rate of natural growth in this case, it is necessary to compute the natural changes in the biomass during each year. To do so, one calculates the biomass at the start of each year B_i, and from that the natural change during the year:

$$\Delta B_i = (B_{i+1} - B_i) + Y_i$$

Schaefer (1954) proposed taking the arithmetic mean of $\bar{B}_{i-1}$ and $\bar{B}_i$ as a first estimate of B_i:

$$B_i = \left(\frac{\bar{B}_{i-1} + \bar{B}_i}{2}\right)$$

In the same fashion, one can obtain:

$$B_{i+1} = \left(\frac{\bar{B}_i + \bar{B}_{i+1}}{2}\right)$$

and the two preceding equations given:

$$\Delta B_i = \left(\frac{\bar{B}_{i+1} - \bar{B}_{i-1}}{2}\right) + Y_i$$

The specific rate of natural growth of the stock at the level of biomass $\bar{B}_i$ is then:

$$f(\bar{B}_i) = \frac{\Delta B_i}{\bar{B}_i} = \frac{1}{2}\left(\frac{\bar{B}_{i+1} - \bar{B}_{i-1}}{\bar{B}_i}\right) + \frac{Y_i}{\bar{B}_i}$$

Case 3: Unfortunately it is rare that estimates of absolute abundance or biomass are available. Instead, what one usually has is values of some index of mean biomass, $\bar{U}$. If such data are available for several series of years when the stock can be considered to have been more or less in equilibrium at different levels of biomass and fishing effort, one can fit an equilibrium equation between $\bar{U}$ and X directly. For example, in the case of the Schaefer model, this equation is:

$$\bar{U} = U_{\infty} - bX$$

Consequently, if one has pairs of values $(\bar{\bar{U}}, X)$ corresponding to two or more equilibrium positions, it is possible to estimate the parameters U_∞ and b and, given these estimates, to infer the equilibrium relations (20), (21) and (22). Periods of equilibrium can be achieved when fishing effort remains at approximately the same level for a period of several years. In most cases equilibrium relations expressed in terms of the indices of abundance and fishing mortality will be sufficient for purposes of management.

Case 4: Now consider the case in which one has data of total catch Y and fishing effort X for a series of years. The index of biomass will be $\bar{U} = Y/X$. Sometimes one only knows the catch Y and an index of biomass $\bar{U}$ derived, for example, from surveys. In this case total fishing effort can be estimated as $X = Y/\bar{U}$. Thus consider the case in which one has the following data:

Year	1	2 ... i	...
Biomass index	$\bar{\bar{U}}_1$	$\bar{\bar{U}}_2 \ldots \bar{\bar{U}}_i$	...
Total catch during year	Y_1	$Y_2 \ldots Y_i$	...
Fishing effort during year	X_1	$X_2 \ldots X_i$	...

As $\bar{\bar{U}} = q\bar{\bar{B}}$ and $F = qX$, the approximation used in Case 2 above to calculate $f(\bar{\bar{B}}_i)$ can also be used here in the form:

$$f(\bar{\bar{B}}_i) = \frac{1}{2}\left(\frac{\bar{\bar{U}}_{i+1} - \bar{\bar{U}}_{i-1}}{\bar{\bar{U}}_i}\right) + \frac{qY_i}{\bar{\bar{U}}_i}$$

or $$f(\bar{\bar{B}}_i) = \frac{1}{2}\left(\frac{\bar{\bar{U}}_{i+1} - \bar{\bar{U}}_{i-1}}{\bar{\bar{U}}_i}\right) + qX_i$$

Unfortunately one cannot use this relation to estimate $f(\bar{\bar{B}}_i)$ unless one has some estimate of q. Schaefer (1956) described a technique for estimating q when a long series of data is available. Gulland (1961) proposed another method to estimate the equilibrium values; this is the subject of the next case to be discussed.

Case 5: (Gulland's method)

The consideration of Case 3 above showed that a knowledge of $\bar{\bar{U}}$ and X in equilibrium conditions makes it possible to determine the equilibrium relationships between $\bar{\bar{U}}$ and X and consequently between Y and $\bar{\bar{U}}$. Gulland suggested that when the data refer to non-equilibrium conditions, one not relate the annual values of the abundance index $\bar{\bar{U}}_i$ to the corresponding values of fishing effort X_i exerted in each year, but instead to the value of some constant fishing effort X' that would have resulted in the same mean abundance index $\bar{\bar{U}}_i$ in equilibrium. In other words, since the exploited stock, whose abundance is measured by the index $\bar{\bar{U}}_i$, is mainly composed during year i of survivors of a certain number of year classes recruited in previous years, Gulland recommended that, from the fishing efforts exerted during the previous years (which therefore determined the number of survivors in each of the cohorts exploited during year i), one calculate an equivalent constant fishing effort X' which, if it had been applied in each of the previous years, would have brought about the mean abundance observed during year i.

Gulland showed that in practice this equivalent effort X' could be approximated by the arithmetic mean of the fishing efforts applied during the year in question and a number of preceding years equal to half the duration of the exploited phase (or exploited lifespan) prevailing in the stock.

For example:

Year	1	2	3	4	5	......
Index of mean biomass	$\bar{U}_1$	$\bar{U}_2$	$\bar{U}_3$	$\bar{U}_4$	$\bar{U}_5$	......
Index of fishing effort during year	X_1	X_2	X_3	X_4	X_5	......

If, for each cohort, the exploited phase lasts 4 years (i.e., the cohort is fished out after 4 years), one would take X' as the mean of the values of X during the year in question and the two preceding years. The resulting pairs of values $\bar{U}$ and X' would then be:

$\bar{U}_5$ and $\bar{X}'_5 = \frac{1}{3}(X_5 + X_4 + X_3)$

$\bar{U}_4$ and $\bar{X}'_4 = \frac{1}{3}(X_4 + X_3 + X_2)$, etc.

The equilibrium relationship between $\bar{U}$ and X' would then be fitted to the pairs of values $(\bar{U}_5, X'_5)$, $(\bar{U}_4, X'_4)$, etc., acording to that mathematioal function which most closely conformed to the distribution of the points.

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STOCK AND RECRUITMENT

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1. Introduction

This section is concerned with relationships between the size of a fish stock and the numbers of individuals that recruit to it annually. The subject is frequently referred to using the expression "stock/recruitment relationship".

Many studies have focused attention on particular parts of the life history only, such as the larval stage. In general, however, any factor responsible for controlling the size of a population and maintaining its stability under a wide range of environmental conditions is relevant. In this context "stability" does not necessarily mean the maintenance of population size at a particular level. The populations that exist today are those that have not been eliminated during an extremely long time period. One is therefore dealing with biological systems that are not so much stable in the mathematical sense, as ones in which the probability of elimination (at least by natural causes) has been extremely small indeed.

1.1 Density-dependence and independence

The terms density-dependent and density-independent are frequently used when discussing stock recruitment relationships.

The principles are illustrated in Figure 1. This shows various relationships between hypothetical initial numbers of individuals and the numbers surviving after a given time or at a given size. The relationship shown by the line A represents the situation where the number of survivors is some constant proportion of the initial number of individuals. This is referred to as a density-independent relationship. Curve B shows a situation where the number of survivors increases indefinitely as the initial number increases. However it is not a constant proportion of the initial number. Curve C shows a situation where the number of survivors increases initially but eventually declines as the initial number is increased further. Both of the relationships B and C are referred to as density-dependent relationships. It is implicit in any discussion of population control that there is at least one stage in the life history where the number of survivors is not directly proportional to the initial number, i.e., at one or more stages in the life history a density-dependent relationship of some kind is inferred.

Biologically, the factors most likely to prevent an indefinite build-up of population biomass are:

(a) Food limitation

(b) Predation

(c) Disease

Of these, factors 2 and 3 may operate independently of food limitation or as a cause of food limitation, i.e., it is useful to distinguish between the situation in which an individual is eaten because it is weakened due to lack of food and the situation in which healthy individuals are just as liable to be eaten as weakened individuals. In the first case the number eaten will tend to be a function of the food supply as well as of the number of predators. In the second case the number eaten will depend mainly on the number of predators.

1.2 Sources of food energy

Of the various factors likely to influence the size of a fish population, food energy is one of the most important. Fish do not necessarily gather all their food energy from any one source, however, and some species exploit a series of food sources, often at various trophic levels. Figure 2 for example shows the principle sequence of food sources exploited by a North Sea haddock.

Up to a length of about 5 cm (i.e., an age of about 80 days) the principal food is herbivores such as copepods.

From about a length of 5 cm to the end of the first year of life the food comes mainly from the next trophic level (i.e., from primary carnivores such as amphipods, euphausiids, and some young fish species).

During the second year of life the fish become benthic and the food consists mainly of the smaller benthic organisms.

From a length of about 29 cm (about 2 years of age) and for the rest of the life, the food consists mainly of the larger benthic organisms and primary carnivores, including euphausiids, sandeels and small fish.

It appears therefore that juvenile haddock exploit a series of food sources before they are large enough to exploit the kind of food on which the mature biomass is largely dependent. There appears to be no reason why the food from any one, or all, of these sources might not be limiting.

1.3 A simplified life history

To reduce the problem to its simplest form it is convenient to consider the life history in two stages, each dependent on a different source (or sources) of food energy. The individuals at the moment of transition from one stage to another are usually referred to as "recruits". This term is frequently applied to the number of individuals aged 1 year. It might also apply however to the number entering the exploitable part of the stock, or to the number attaining the age of first maturity. Ecologically it would be appropriate to apply it to the number at one of the transition stages from one food type to another.

However the term "recruits" is defined, it is appropriate to consider at least two relationships. One is the relationship between the number of eggs produced by the mature stock and the subsequent number of recruits. The second is the relationship between the number of recruits and the number of eggs they can be expected to produce during the entire course of their lives.

The situation is illustrated diagrammatically in Figure 3. Figure 3.1 shows a generalized density-dependent relationship between egg production and the subsequent number of recruits. It is assumed that somewhere between egg production and recruitment, food is limiting. If egg production is increased indefinitely, a stage should eventually be reached where all individuals are likely to die.

Figure 3.2 shows a comparable relationship between the number of recruits and the subsequent egg production from these throughout the remainder of their lives. Again it is assumed that food is limited so that an indefinite increase in the number of recruits should eventually lead to a situation in which no eggs at all are produced. This relationship is given by curve B.

It is clear that equilibrium should occur at a value of egg production and a value of recruitment that satisfies both curve A and curve B. Figure 3.3 shows a simple graphical way of finding this equilibrium point. Here both curves are combined in a single diagram. Curve A is exactly as depicted in Figure 3.1. Curve B is exactly as depicted in Figure 3.2 except that the axes have been interchanged. The result is two curves which diverge initially but which eventually converge and cross over at the point marked C. The coordinates of this point define a level of egg production and a number of recruits that satisfy the relationships shown in Figure 3.1 and Figure 3.2.

The argument has been conducted in terms of numbers of eggs and numbers of recruits. To take account of growth however it would be appropriate to use other units such as the biomass of eggs and the biomass of recruits.

2. Different kinds of egg/recruit relationship

2.1 Virgin state

There are various ways of drawing A and B curves such as those in Figure 3.3 and two extreme situations are depicted in Figure 4.

Figure 4.1 shows a situation in which the B curve is practically linear at the equilibrium point C. This represents a situation in which population size is effectively limited at some stage between egg production and recruitment. It is implicit in this diagram that recruitment can never become large enough for density-dependent effects to operate during the "recruit to egg" stage of the life history.

Figure 4.2 shows the situation where it is curve A that is approximately linear at the equilibrium point C, i.e., this represents a situation where the population size is limited at some stage between recruitment and subsequent egg production. It is implicit in this diagram that egg production is prevented from ever becoming large enough for density-dependence effects to operate during the "egg to recruit" stage.

Figure 3.3 represents an intermediate situation in which both the A and B curves depart substantially from linearity at the equilibrium point C, i.e., Figure 3.3 represents a situation in which density-dependent factors play a significant part in both parts of the life history. If it is assumed that present-day species are those that have persisted for very long periods, relationships such as those in Figure 5 might, intuitively, be inferred as a first approximation, i.e., the greater the divergence of the A and B curves at their origin, the greater the potential resistance of the species to total extinction.

2.2 The effect of fishing

It is convenient to consider the effect of fishing with reference to the curves in Figures 4.1 and 4.2 separately.

Figure 6 illustrates the effect of fishing in the situation depicted in Figure 4.1 in which population size is effectively limited at the stage of egg production and subsequent recruitment.

Figure 6.1 shows the relationship between recruitment and subsequent egg production at two levels of fishing effort. Since it is assumed that there is relatively unlimited food for mature fish, changes in fishing effort would simply move the B curves up or down, i.e., for a given level of recruitment a low level of fishing effort)(curve B1) should lead to a higher egg production than a high level of fishing effort (B2). In general the effect of fishing should be to cause the B curve to move down toward the recruit axis.

Figure 6.2 shows the combination of the two B curves with the A curve. C1 is the equilibrium position when fishing effort is low, C2 is the equilibrium position when fishing effort is high. In general it is clear that the effect of fishing should be to move the point of equilibrium along the A curve toward its origin. At the same time this should be associated with a decline in egg production.

The effect on recruitment depends on the relative position of the B curves in relation to the A curve. Figure 6.2 for example shows a situation where an increase in fishing effort should increase the mean level of recruitment. Figure 6.3 on the other hand shows a situation where an increase in fishing effort should cause recruitment to decline.

It is possible that the situation depicted in Figure 6.2 is applicable to a stock in its early stages of exploitation whereas Figure 6.3 is more likely to apply to a stock that is already intensively exploited. Clearly the higher the rate of exploitation and the closer the equilibrium point is forced toward the origin, the greater the ultimate danger of a stock collapse.

Figure 7 shows the effect of fishing when the egg/recruitment relationship is of the form shown in Figure 4.2, i.e., in the situation when population size is limited at the stage between recruitment and subsequent egg production.

Figure 7.1 shows the effect of fishing on the B curve. Curve B1 represents the situation where fishing effort is low. With "X" recruits, it is supposed that food is limiting to such an extent that no egg production occurs. As fishing effort is increased it is expected that food energy should be released so that even with "X" recruits, egg production ought to be possible. The result is that an increase in fishing effort should move the B curve toward the right (B2).

Figures 7.2 and 7.3 show two possible combinations of the A and B curves. In Figure 7.2 the effect of an increase in fishing effort should be to move the equilibrium position from C1 to C2 leading to an increase in both recruitment and egg production.

In Figure 7.3, on the other hand, an increase in fishing effort would move the equilibrium position from C1 to C2 leading to a reduction in both egg production and recruitment.

It is possible that Figure 7.2 is more applicable to a stock in the early stages of exploitation whereas Figure 7.3 might be more applicable to a highly exploited stock. As before, the closer the position of the equilibrium point C to the origin the greater the danger of stock collapse.

2.3 Implications for management

The effect of fishing on levels of recruitment and egg production have important implications for management. There are three principal situations:

(a) It may happen that over a certain range of fishing effort, recruitment is approximately constant. Within this range it is expected that yields could be maximized by maximizing the yield per recruit. Management measures intended to maximize the yield per recruit would then be appropriate.

(b) In situations where recruitment is likely to change with changes in fishing effort it is more likely that maximum yields would be associated with a high level of recruitment rather than simply with high levels of yield per recruit. Management policy would then have to take recruitment, as well as yield per recruit, into account.

(c) In the situation where fishing effort is so high that egg production is below some critical level, there is always the danger of a stock collapse. Management should be prepared for this possibility and if the situation warrants it, be prepared to stop fishing entirely until there has been an adequate recovery of the stock.

2.4 Direct evidence

Numerous attempts have been made to investigate the form of the "A curve" directly. Most of these have been based on the relationship between the size of the spawning stock the subsequent number of recruits surviving to a particular age. Results tend to fall i two groups.

(a) Scatter diagrams in which the relationship between the spawning stock and the subsequent recruitment is extremely poor and frequently not statistically significant.

(b) Relationships that appear to be quite good, but that may be associated with a time series, i.e., both recruitment and spawning stock may decline steadily over a time period. In that case, however, it may not be possible to say whether the recruitment has declined because of the decline in the spawning stock or whether the spawning stock has declined because of the decline in recruitment. Alternatively both may have declined due to changes in some other factor on which both are dependent.

For one reason or another, therefore, the direct evidence has tended to be inconclusive.

It should be noted that the relationship between the size of the spawning stock and the subsequent recruitment is not necessarily the same as a relationship between actual egg production and subsequent recruitment. Large spawning stocks may be associated with low individual growth rates and fecundities, so that egg production need not necessarily be directly proportional to spawning stock size. This is a factor that has not always been taken into account and which might have contributed to inconclusive results in some instances.

2.5 Short-term variations

In practice, data relating spawning stock size (or egg production) to subsequent recruitment are necessarily collected on an annual basis. Variations can then occur due to short-term variations in the presumed underlying long-term relationships. Statistical variations in the data are also to be expected. In practice, variations due to one source or another have tended to be very large. The result is that attempts to fit theoretical curves to observed data statistically have been largely unsuccessful.

3. Theoretical considerations

Because of this, it is appropriate to consider from a theoretical standpoint how population size may be regulated at different stages in the life history.

3.1 The larval stage

For some species, the larval period has been regarded as the principal stage where population size might be limited. Biologically, important factors are:

(a) Larvae grow relatively rapidly. Their food requirements are therefore relatively large for their size, yet, being small, their capacity for searching for food is relatively small. Food limitation is therefore likely to be more critical for rapidly growing larvae than for slowly growing plankton organisms of the same size. For certain species (e.g., haddock) it has been calculated that the average density of the young stages of copepods on which the larvae feed is such that larval mortality could easily occur due to food deprivation. This species feeds on the young growing stages of copepods, the growth rate of the larvae being approximately the same as that of the copepodite. The net result is that each cohort of larvae tends to be limited for the first 1-2 months to about 3 weeks production of copepods. Copepods born earlier than this tend to be excluded as food as they tend to be too large to eat, and copepods born later tend not to be eaten, presumably because they would be so small that too many would be required to satisfy the food requirements of the larvae. A situation such as this, where individuals grow rapidly for a period on a fixed food supply, provides an effective way of limiting population size. Not all species of larvae grow at the same rate as their food however, so that limitation of numbers at the larval stage need not necessarily apply to all species. Also, even for species such as haddock where it may apply, this does not preclude the possibility of limitation of numbers at other stages in the life history.

Once haddock larvae are large enough to eat fully grown copepods, they should be able to exploit the entire production of copepods for the season, and the factors influencing survival are likely to be different.

(b) Mortality rates are believed to be high, and death is probably due to predation. It is not certain however to what extent this is due to primary predation (i.e., consumption of healthy as much as weakened individuals) or to secondary predation (i.e., consumption of weakened individuals rather than healthy ones).

(c) Many species of fish larvae appear to exploit food that occurs at a particular time in the productive cycle and sometimes mainly at a particular geographical location. It is important for survival therefore that, at the commencement of feeding, the larvae happen to be at the right place at the right time.

3.2 The stage of maturity

After maturity, growth, survival and egg production are all factors that could be influenced by food production and the size of the stock. Each genotype is presumably adapted to partition energy for survival, growth and egg production in a particular way. However, if total food energy is reduced, any one of these three factors can only be favoured at the expense of the other two. In particular, egg production is likely to then suffer either:

(a) directly, because energy is used primarily to maintain growth and survival; or

(b) indirectly, because of the reduction in growth and/or survival that would presumably occur if egg production were to be favoured in the short term.

In the long term, food limitation in the mature stage ought therefore to limit egg production.

Evidence shows that a number of species have the capacity to limit egg production directly when food is scarce. For example, egg production can be reduced by a reduction in the number of oocytes starting vitellogenesis, or by the resorption of oocytes during the maturation period. This is a factor, however, that might be more important in virgin stocks than in stocks that are subject to high levels of exploitation.

3.3 Intermediate stages

In addition to a larval food "niche" and an adult food "niche" there may be one or more intermediate sources of food energy. Some of these may be similar to the haddock larval stage, i.e., they may represent transitory food sources only suitable for individuals of a certain size, and only available for part of a year. As fish approach maturity, however, their growth rate slows down and there may be an intermediate food source that is suitable at all times of the year. To a limited extent, a large year class may then be able to improve its chances of survival by growing more slowly than average. If growth is retarded too much, however, there would be the danger of a following year class catching up in size and competing with it.

In the long term, therefore, intermediate food sources could be just as important as other food sources for limiting population size.

In addition to variations in growth rate with year class size, cannibalism also might be an important adaptation at an intermediate feeding stage, i.e.:

(a) It would be one way of reducing the competition from a following year class.

(b) At the same time, it would be taking advantage of an additional source of food energy.

3.4 Evolutionary considerations

A detailed examination of the stomach contents of North Sea gadoids shows not only that these eat different individuals throughout the course of life, but that they do so in a way that appears to minimize direct competition either with other gadoids or with other species in general. This may be done by feeding on particular organisms either in different geographical locations or at different times of the year or by feeding on different life stages of a particular species (i.e., possibly on the same species but on individuals of different sizes). It appears likely that at each stage in its life history, a gadoid is able to occupy an independent "niche" in the sense that competition with other species is avoided or reduced.

It might then be argued that in a perfectly stable environment, relationships such as those indicated in Figures 4.1 and 4.2 should not occur. Figure 4.1 for example represents the situation in which there is more than enough food for the adults whereas Figure 4.2 represents the situation where there is more than enough food for the juveniles. During the course of evolutionary time one might have expected so many sequences of feeding "niches" to have been tried by different genotypes that not only would all possible energy sources be fully utilized but that each species would fully occupy a niche at each point in its life history. This argument appears to favour relationships such as those in Figures 3.3 and 5 as the ultimate equilibrium form for all species.

In practice however it seems more probable that the ecosystem is not in a state of perfect equilibrium in this sense, but cyclical changes can occur, causing some groups of species to increase whilst others decrease, i.e., there appears to be sufficient flexibility to permit variations in the energy flow to each feeding "niche". There seems no reason in principle therefore why in the "short" term (i.e., periods possibly of the order of decades) individual species might not oscillate between alternatives such as those shown in Figures 4.1 and 4.2.

If this were so it would help to explain the lack of success so far encountered in finding a single population control process for the marine teleosts.

4. Theoretical curves

Several theoretical relationships that have been used for relating egg production to subsequent recruitment are described below. Of these, the best known and mathematically the simplest are due to Ricker, and Beverton and Holt.

4.1 The Ricker curve

The Ricker curve is given by the equation:

$$R = a N \exp - (N/N_m)$$

Where R = the number of recruits

N = the number of individuals at the beginning of the period

N_m = the initial number of individuals for which the subsequent recruitment is a maximum

a = the proportion surviving due to density-independent factors

The Ricker curve is based on the assumption that the instantaneous mortality rate is proportional to the number of individuals present initially. Thus if one is dealing with the larval stage, the initial number, (N) is the number of eggs produced (or the number of larvae at the commencement of feeding). The instantaneous mortality rate is then assumed to be proportional to this initial number.

An example of a Ricker curve is given in Table 1 and Figure 8. It is characteristically dome shaped, rising to a maximum at an intermediate value of N, and then declining.

The biological implications of the Ricker curve stem from the assumption that the instantaneous mortality rate is proportional to the number of individuals present initially. It has been suggested that this might happen if predation were primarily due to cannibalism by the adults that had been responsible for producing the eggs in the first place. A difficulty with this suggestion is that the larvae and juveniles of many species tend to be located separately from the mature adults. In individual cases other possibilities may be biologically plausible.

Characteristic of the Ricker curve is the fact that the maximum number surviving occurs when N/N_m is equal to 1.0. The proportion surviving is then 0.37. Smaller proportions surviving are possible, but only when N is greater than N_m. The significance of this is that in practice the proportion surviving during the first year of life in even moderately fecund species is very much lower than 0.37. To account for an egg/recruit relationship with a Ricker curve it is therefore necessary to assume either:

(a) that the equilibrium position is located well down the descending right-hand limb of the curve; or

(b) that the probability of survival is small because the coefficient "a" is small. This is equivalent to saying that mortality is primarily due to density-independent factors. In this case the Ricker curve, though possibly playing a part in setting an upper limit to population size, would play a relatively small part in accounting for the total mortality during the first year of life.

4.2 The Beverton and Holt curve

A rather different curve for relating egg production to subsequent recruitment has been proposed by Beverton and Holt (1957). Their formula is:

$$R = 1/(a + b/E)$$

where E is the number of eggs produced

An example is given in Table 2 and Figure 9. The characteristic of this curve is that as egg production is increased, recruitment rises toward an asymptotic level equal to 1/a.

The derivation of this curve is based on the assumption that the instantaneous mortality rate is proportional to the actual number of individuals present at any moment, i.e., it is assumed that the instantaneous mortality rate declines continuously as the number of individuals declines. This type of curve might arise if predation occurred so long as the density of the prey was above some critical level. The rate of predation might then be supposed to decline continuously as the density of prey declined.

4.3 Simulation models

More recently, attempts have been made to simulate the biological processes at work in the larval stage. One model (due to Jones 1973) simulates the situation in which a cohort of fish larvae grazes on a cohort of food organisms. The probability of a larva surviving is made a function of its probability of encounter with food. The model produces curves superficially similar in shape to Ricker curves in that survival at the end of the larval stage is a maximum at an intermediate level of egg production (or more precisely of the number of larvae at the commencement of feeding) (Figure 10).

Another model, due to Cushing and Harris, 1973, simulates the situation where larval mortality is due to the grazing of predators.

4.4 A 'flat topped' stock recruitment curve

For those species which exploit a series of food sources, before "recruitment", the "stock/recruit" relationship can be expected to be the result of more than just one biological process.

There is no reason, for example, why the stock recruitment relationship might not prove to be "flat-topped" as indicated in Figure 11. Such a curve could result if, for example, predation on juveniles operated so as to reduce their density to some critical level. Alternatively, it might result if there was competition for food and space leading to a reduction in the number of juveniles toward a particular value.

5. An example of the relationship between recruitment and subsequent egg production

Consider the situation in which there happen to be 2.81 thousands of eggs produced by each one year-old recruit. The simplest possible recruit to egg relationship that can be drawn is a straight line and this can be done on this information alone as shown in Table 3. Thus, given a thousand recruits there would be 2.8 million eggs produced. Given 5 000 recruits there would be 2 810 x 5 000 = 14 million eggs, and so on.

The relationship between recruitment and subsequent egg production shown in Table 3 is plotted in Figure 12.

Given such a relationship, it is a simple matter to determine the equilibrium level of recruitment provided one also knows the relationship between egg production and subsequent recruitment.

Some hypothetical data for this example are given in Table 4. This shows hypothetical numbers of recruits expected from given levels of egg production, and the data are plotted in Figure 13 (Curve A). Figure 13 also shows the effect of combining the two relationships.

In Figure 13 the curves intersect at a point with the following coordinates:

number of eggs = 16.5 million
number of recruits = 5 900

This example has been based on estimates of the egg production per recruit and an "egg to recruit" relationship. It illustrates the minimum amount of information needed for assessing the equilibrium level of recruitment in a stock in a situation where food for mature fish is not limiting.

6. Essential references

Beverton, R.J.H. and Holt, S.J., 1957 On the dynamics of exploited fish populations. Fish.Invest.Minist.Agric.Fish.Food G.B. (2 Sea Fish.), (19):533 p.

Cushing, D.H., 1971 The dependence of recruitment on parent stock in different groups of fishes. J.Cons.CIEM, 33(3):340-62

Ricker, W.E., 1954 Stock and recruitment. J.Fish.Res.Board Can., 11(5):559-623

6.1 Recent symposia

Recently there have been two symposia on stock and recruitment and the results have been published in the two following volumes:

CIEM, 1973 Fish stocks and recruitment. Rapp.P.-V., 164, 173

(Note this volume contains the references to Jones, 1973 and Cushing and Harris, 1973)

Blaxter, J.H.S. (ed.), 1974 The early life history of fish. The Proceedings of an International Symposium held at the Dunstaffnage Marine Research Laboratory of the Scottish Marine Biological Association at Oban, Scotland, from May 17-23, 1973. New York, Springer, 765 p.

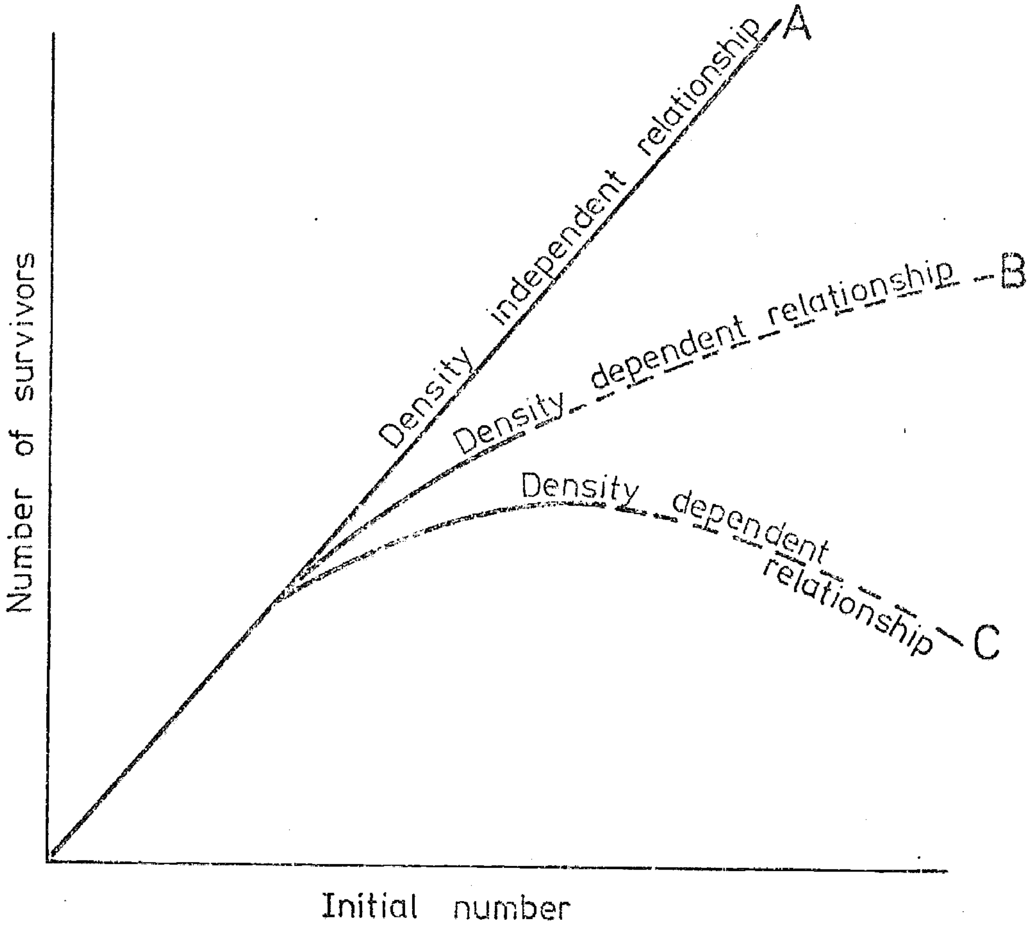
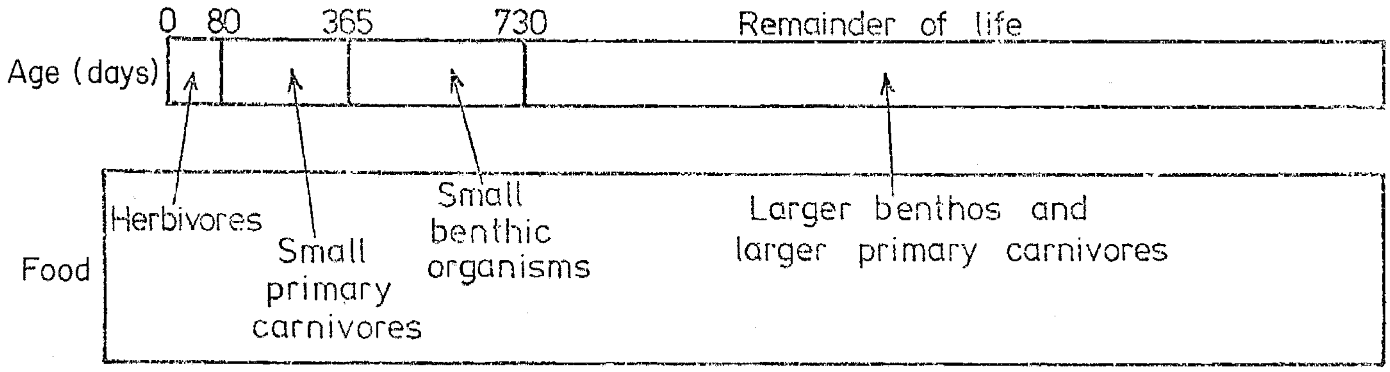


Fig. 1 - Density dependent and independent relationships



As a haddock grows it eats food organisms from various trophic levels

Fig. 2 - Haddock food resources

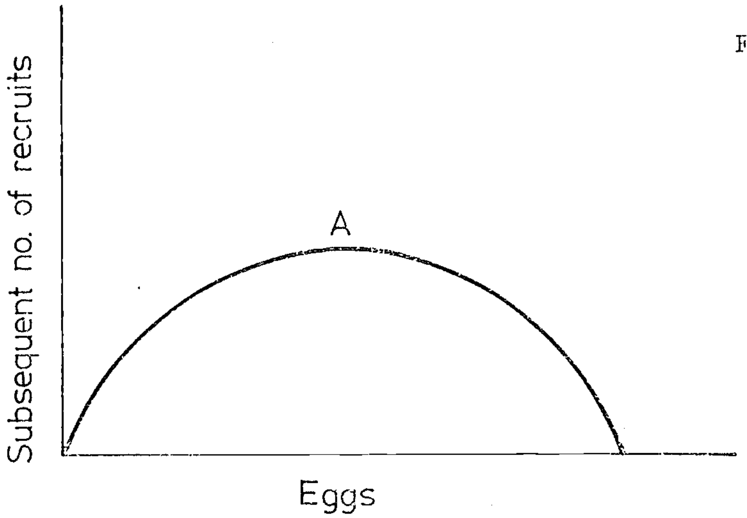


Fig. 3.1 - Egg production and subsequent recruitment

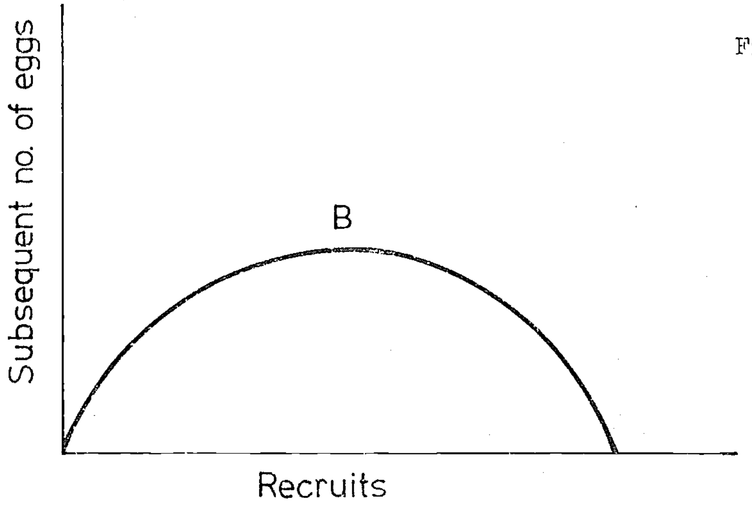


Fig. 3.2 - Recruitment and subsequent egg production

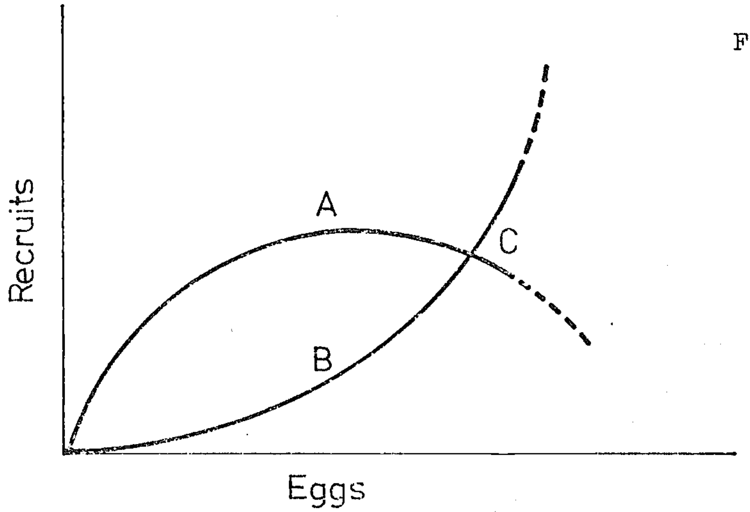


Fig. 3.3 - Finding an equilibrium point (C) to satisfy both relationships

Fig. 3 - Egg/recruitment relationship

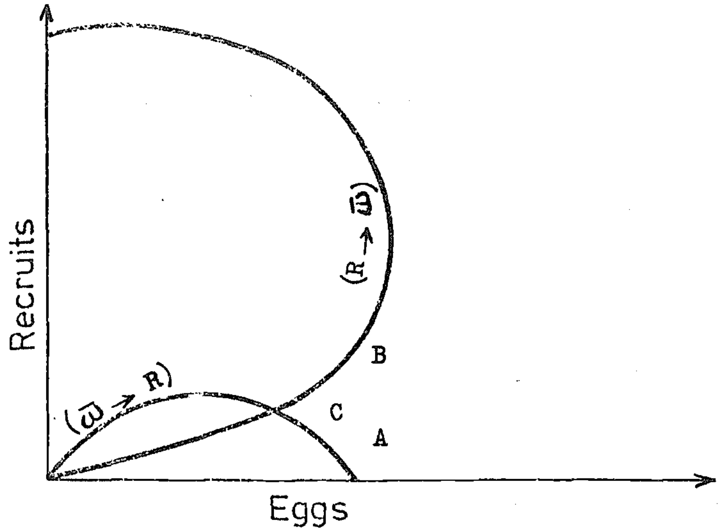


Fig. 4.1 - Population size limited at stage between egg and recruitment

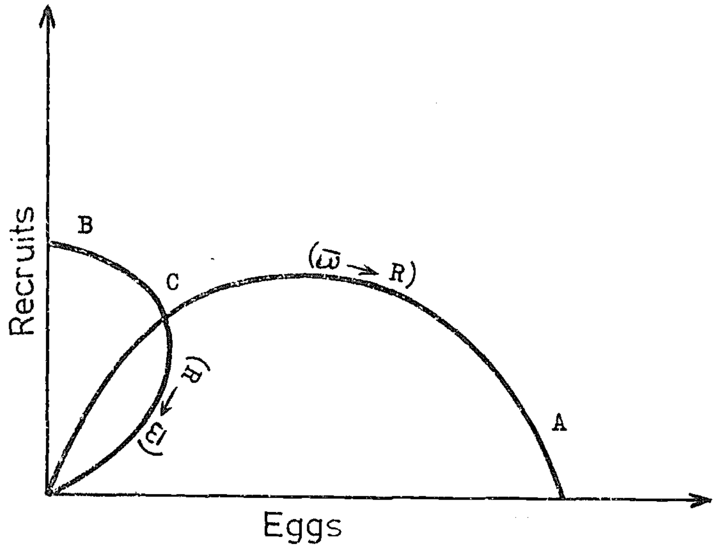


Fig. 4.2 - Population size limited at stage between recruitment and egg production

Fig. 4 - Two kinds of egg/recruit relationship

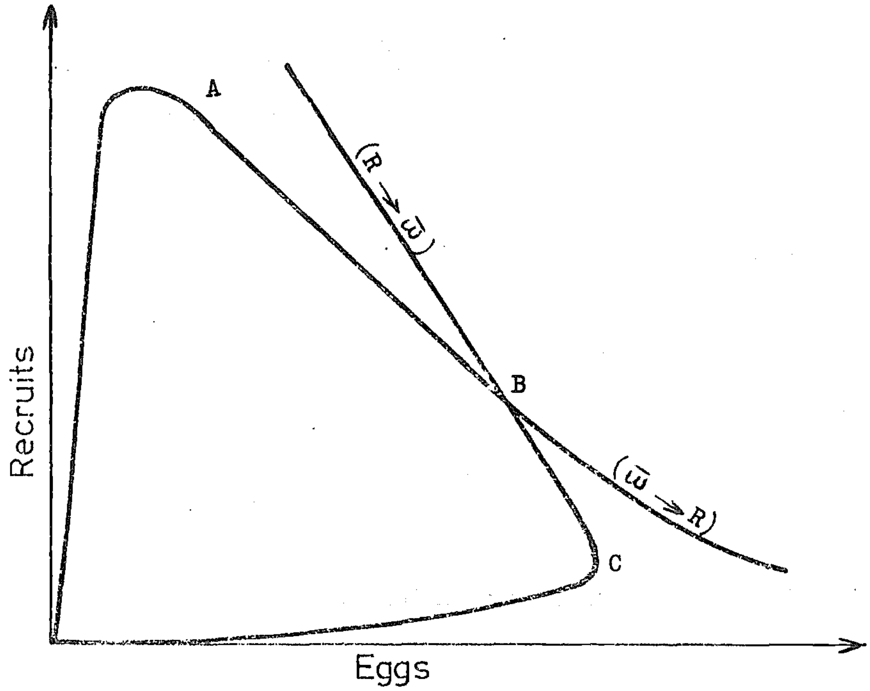


Fig. 5 - Possible egg/recruit relationships with high survival potential

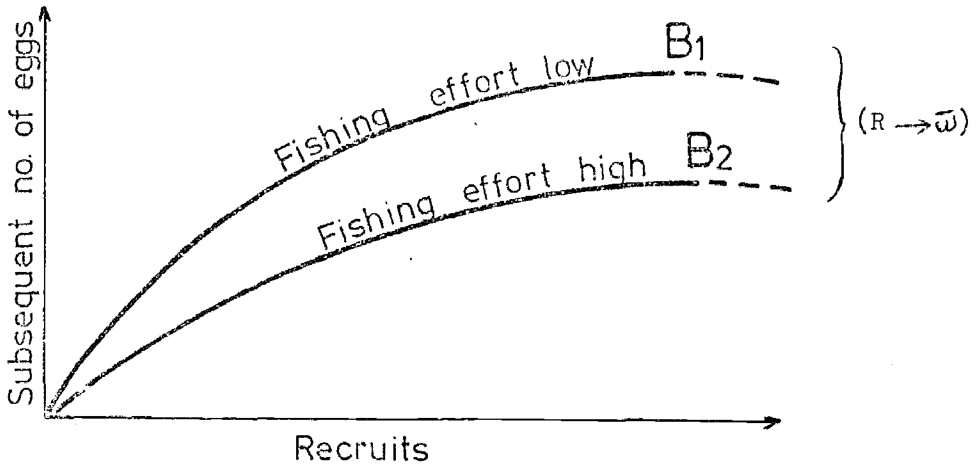


Fig. 6.1

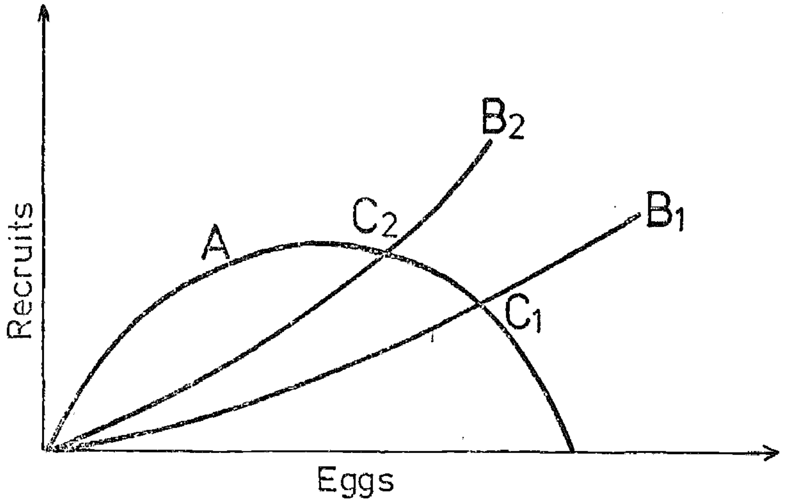


Fig. 6.2

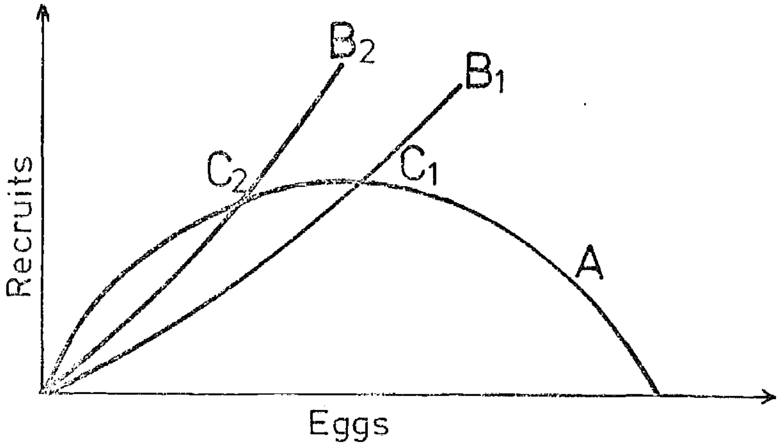


Fig. 6.3

Fig. 6 - Effect of fishing I

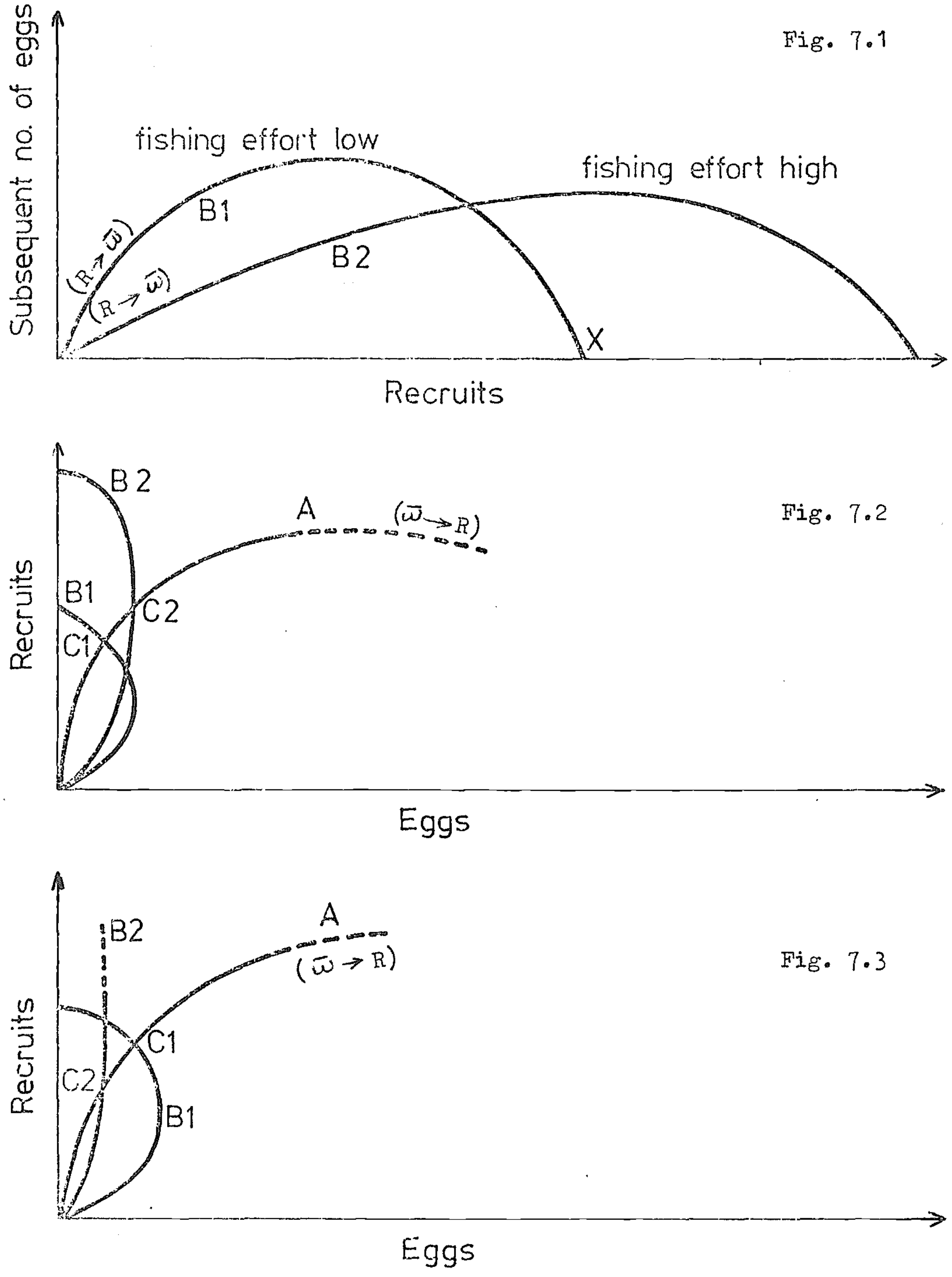


Fig. 7 - Effect of fishing II

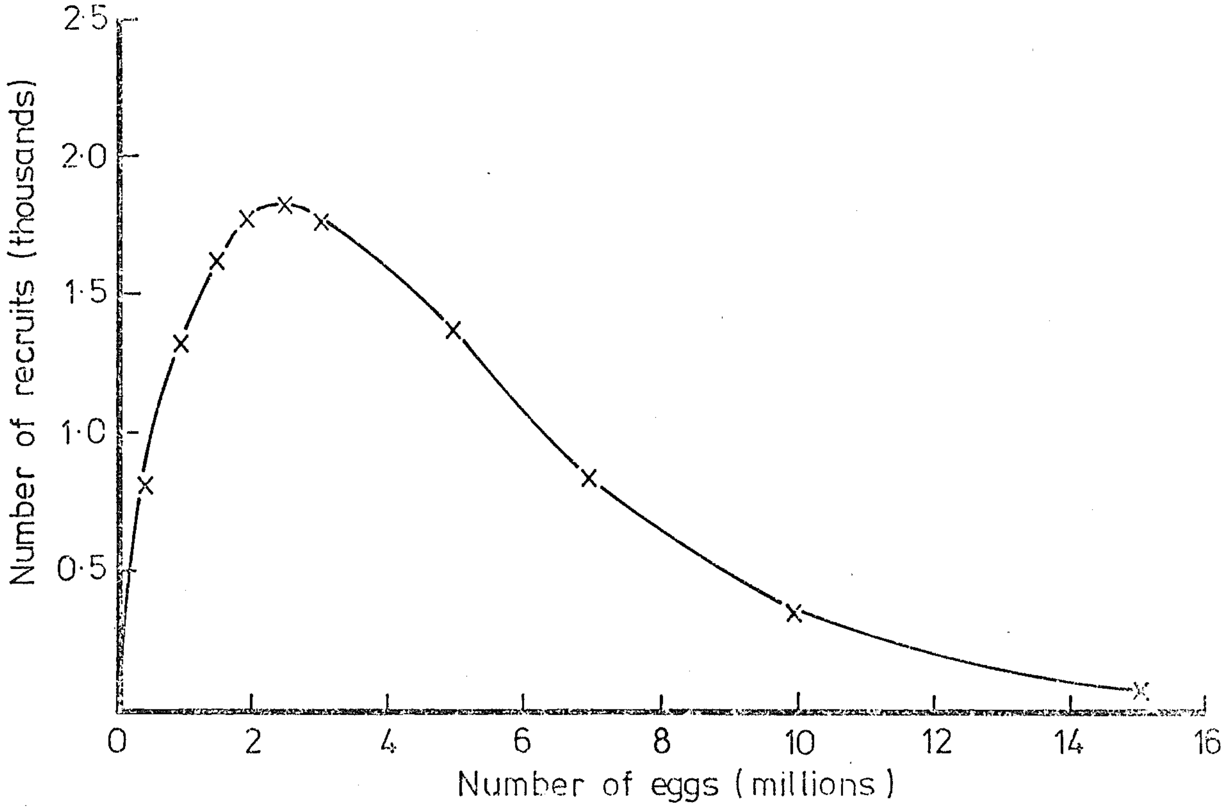


Fig. 8 - A Ricker curve is "dome shaped" leading to a maximum level of recruitment at an intermediate level of egg production (or spawning stock) size

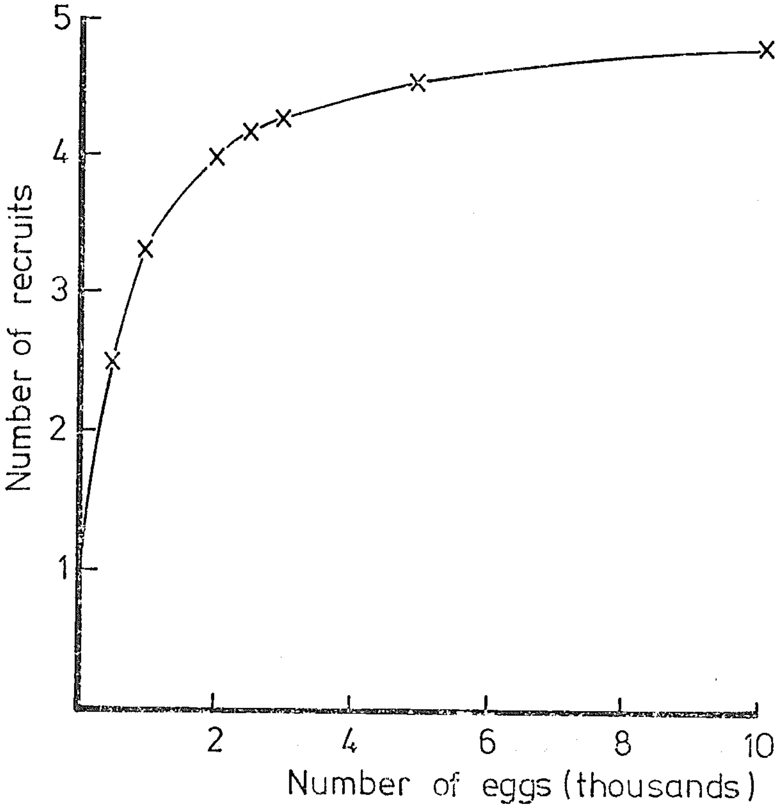


Fig. 9 - A Beverton and Holt egg/recruit curve rises towards an asymptote as egg production (or spawning stock) size is increased indefinitly

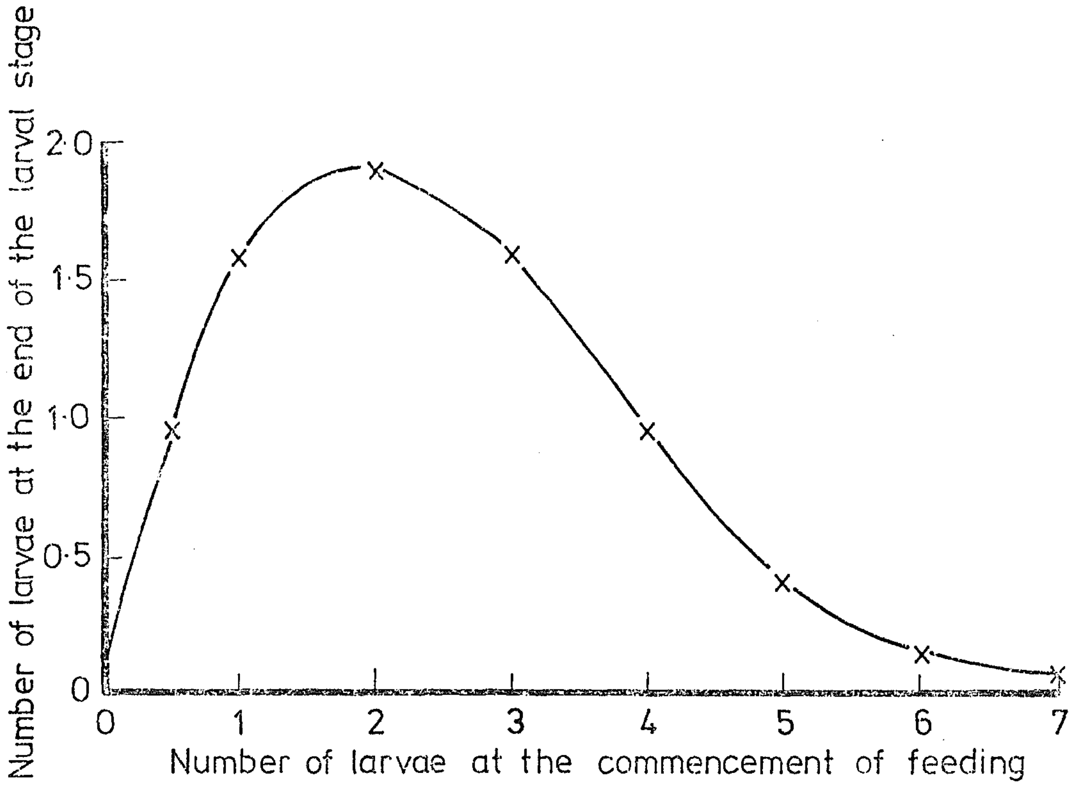


Fig. 10 - A domed shaped stock/recruit curve, superficially similar to a Ricker curve, can also be generated by supposing that larval survival is dependant on larval food abundance

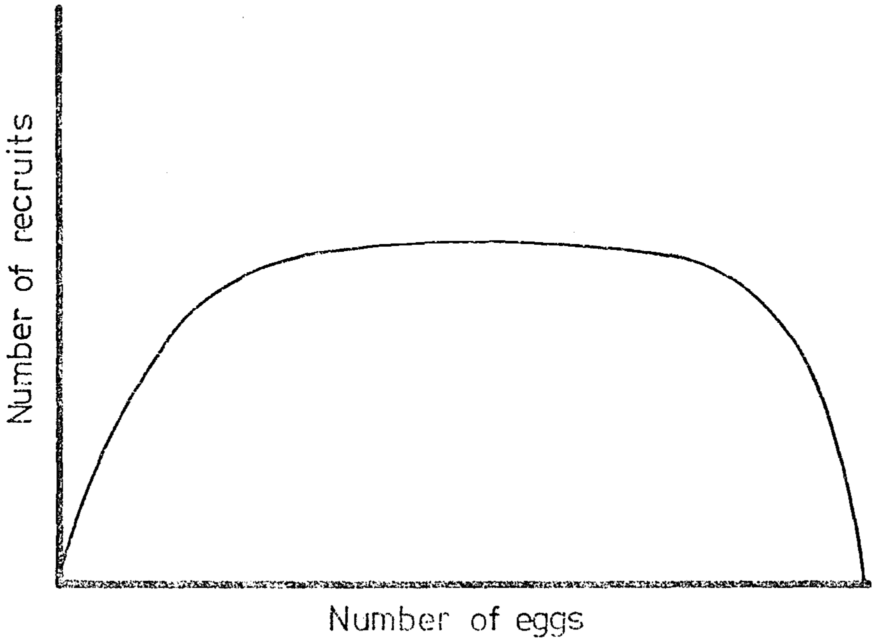


Fig. 11 - Shape of stock/recruit curve that might be expected if predation (or living space) tended to reduce the density of juveniles to some critical level

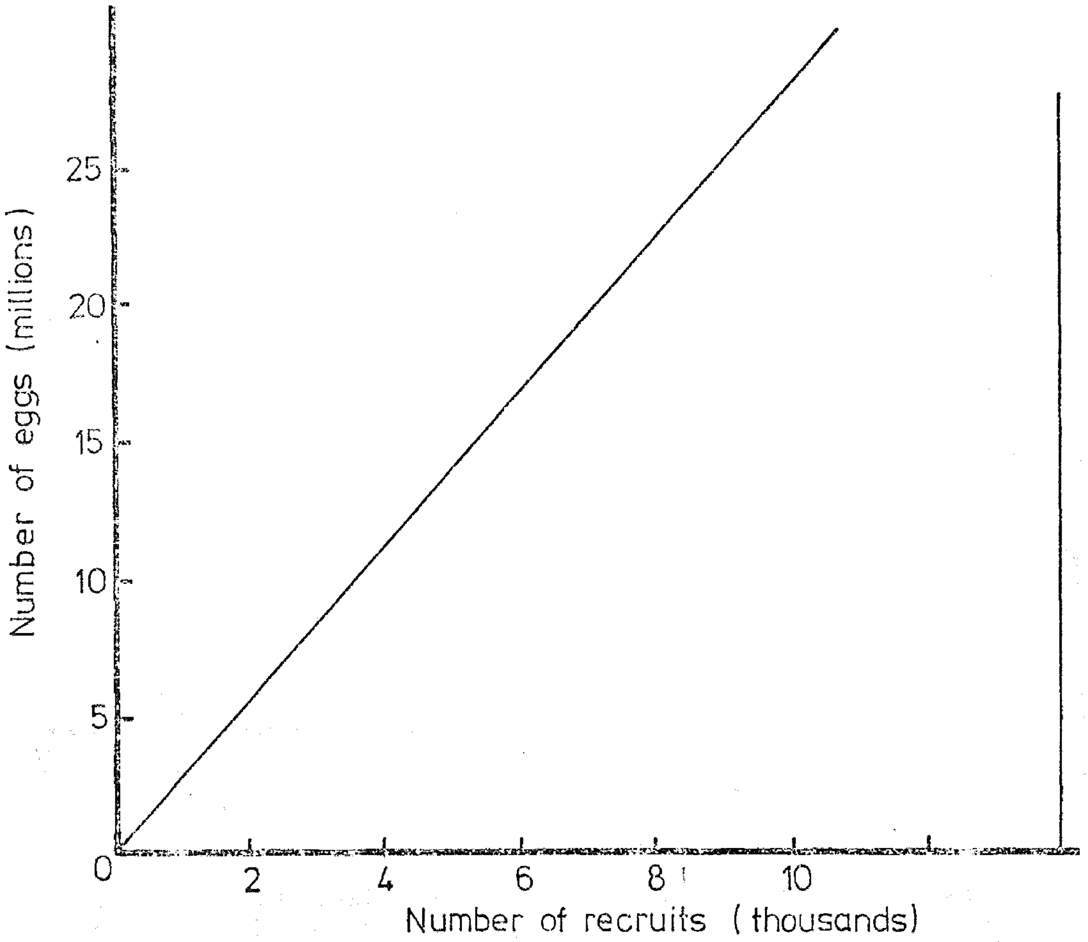


Fig. 12 - Number of eggs produced by different numbers of recruit

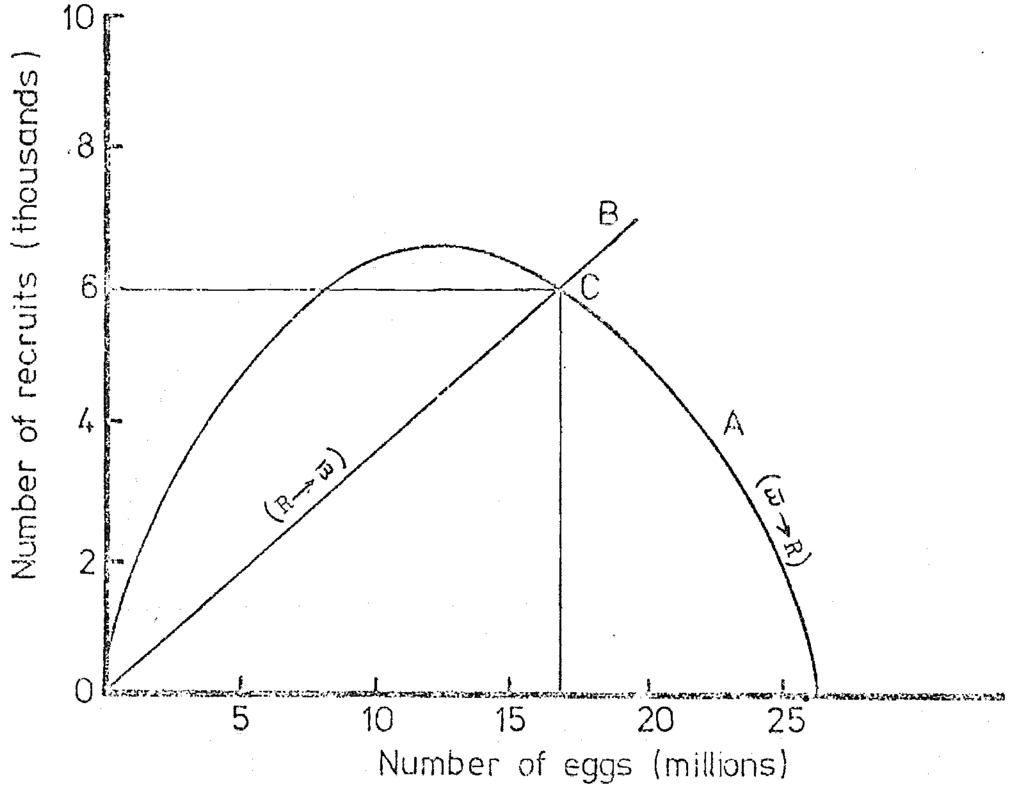


Fig. 13 - Determination of population equilibrium given: A an egg to recruit relationship and B a recruit to egg relationship

Table 1

Determination of Ricker curve

$$R = a\,E \exp - E/E_m$$

$E_m = 25 \times 10^6$ $\qquad$ $a = 0.002$

No. of Eggs E (millions)	E/E_m	$\exp - (E/E_m)$	$E \exp - (E/E_m)$	R (thousands)
0.1	0.04	0.96	0.10	0.20
0.5	0.2	0.82	0.41	0.82
1.0	0.4	0.67	0.67	1.34
1.5	0.6	0.55	0.82	1.64
2.0	0.8	0.45	0.90	1.80
2.5	1.0	0.37	0.92	1.84
3.0	1.2	0.30	0.90	1.80
5.0	2.0	0.14	0.70	1.40
7.0	2.8	0.061	0.43	0.86
10.0	4.0	0.018	0.18	0.36
15.0	6.0	0.0025	0.04	0.08

Table 2

Determination of egg/recruit curve from Beverton & Holt formula

$$R = 1/(a + b/E)$$

$a = 0.2$ $\qquad$ $b = 0.1 \times 10^3$

No. of Eggs E (thousands)	b/E	a + b/E	R (thousands)	R/E
0.5	0.2	0.4	2.5	5.0
1.0	0.1	0.3	3.3	3.3
1.5	0.07	0.27	3.7	2.5
2.0	0.05	0.25	4.0	2.0
2.5	0.04	0.24	4.2	1.7
3.0	0.03	0.23	4.3	1.4
5.0	0.02	0.22	4.5	1.1
10.0	0.01	0.21	4.8	0.5

Table 3

Hypothetical values of recruitment and subsequent egg production

Number of recruits	0	1 000	5 000	10 000
Subsequent number of eggs (millions)	0	2.8	14.0	28.1

Table 4

Hypothetical egg to recruit relationship

Number of eggs (millions)	0	5	10	15	20	25
Subsequent number of recruits	0	4 500	6 400	6 300	4 800	1 400

SEMI-QUANTATIVE METHODS OF ASSESSMENT

by

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1. Introduction

Semi-quantative methods of assessment are understood as methods of reasoning and calculation that allow us to obtain first approximations to the potential or state of exploitation of fishery resources on the basis of information that is less complete than what would be required for the standard assessment models.

In monitoring the development of a fishery, one always finds that precision, accuracy and timeliness are three interdependent qualities whose respective importance vary according to the stage of development of the fishery. Too often an excessive amount of importance is given to precision to the detriment of accuracy and especially to the need to obtain information, even if it is only approximate, at the right time (timeliness). If one realizes that, for as example as regards the variance of estimates, the need for information (and thus the cost and delays in getting it) increases much faster than any gain in precision that can be derived from it, one can see that precision can be the enemy of accuracy and, above all, of timeliness.

From this point of view, semi-quantative methods of assessment are invaluable, especially in the following three types of situation:

- when great precision is unnecessary. At the beginning, or prior to, the development of a new resource what is needed, more than anything else, is knowledge of the order of magnitude of the stock in question, or more simply, whether the stock is capable of sustaining a minimum level of catches that can be considered as the first stage of development. The time required to attain this first stage can then be used to refine the preliminary assessment;
- when information on the fishery or stock in question is hard to get (e.g. in the case of artisanal fisheries that are widely dispersed and of such small productivity that it is impossible, for practical and economic reasons, to measure production at every point);
- when assessment work has been outstripped by the expansion of a fishery and it suddenly appears urgent to adopt some form of management and plan detailed studies on the basis of whatever information can be used.

2. Interpolation and Extrapolation of Potential or Exploitation Level of a Resource

The simplest method is to use the relationships one can identify empirically between potential yield or rate of exploitation within a group of ecosystems, and certain of their physical, chemical or biological parameters (e.g. primary or secondary production). The latter will be either easy to measure or already measured since the objective is to obtain, starting from the values of these parameters, an index of the potential production or state of exploitation of resources not yet assessed. This procedure assumes that the overall masses of water taken for reference and the unit or units to be assessed only differ quantitatively in terms of the parameter or parameters chosen as indicators. In fact, the appearance of qualitative changes in the interval of extrapolation would reflect new phenomena not taken into consideration when the extrapolation was formulated. From this point of view, interpolations are clearly more certain than extrapolations.

The formulation of the extrapolation includes two stages. The first step is to check, on as large a sample as possible, the validity of the relationship between the parameter to be estimated (potential or state of exploitation), Y, and the extrapolation factor, X. The mathematical function which best represents the analogy will be determined later. As the empirical relationship shown in this way is the result of many phenomena, whose nature and role cannot be calculated, the mathematical formulation will always be simple (linear function, power, etc.).

There are various examples of this approach, such as the following.

2.1 Simple Extrapolations

Welcomme (1976) estimated the yield of African streams using previously calculated empirical relationships between the production of 18 rivers and the length of their main courses or the area of their drainages on the other. The relationships employed were in the form $Y = a X^b$, where Y is the yield to be assessed, X the index (length of river or area of the drainage) and a and b are constants estimated from the sample of 18 rivers whose yield was known.

In a similar fashion, it was possible to make a first estimate of the potential of demersal resources in the Mediterranean. An estimate of this potential was available only for stocks found along the European coasts. The current annual yield for the different geographical sectors of the Mediterranean and the corresponding areas of the continental shelf were calculated. To estimate the potential maximum yield of the African and Eastern portions of the plateau, it was presumed that maximum yield per year per unit shelf area was comparable in each pair of African-European sectors lying between the same lines of longitude, i.e. that the greatest gradient of yield would be along the East-West axis of the Mediterranean (as is suggested by the data on currents and plankton productivity). It was finally verified that figures of annual maximum yield per unit shelf area available for European coasts did not contradict this hypothesis (Gulland, 1971; Levi and Troadec, 1974).

2.2 Morphoedaphic Index (IME)

This index gives, without doubt, the best example of this type of approach. It has been perfected and applied to lacustrine ecosystems. The objective was to find an indicator, easily and quickly measured, of the approximate potential yield of a lake. To do this, various statistical techniques were used to analyse the role of various factors or groups of factors (more than 20) capable of influencing the fishing potential of a lake. Among the factors analysed were: average depth, total dissolved matter, total alkalinity, extension of shallow waters, the length of the growing season, mineral turbidity, latitude and altitude, changes in water levels, benthic and planktonic production, etc. It was found that the largest part of the variation (75% in the case of the Canadian Great Lakes where this index was first formulated) could be explained by a combination of three factors:

- climate (difficult to measure in a simple way but its influence can be eliminated by confining comparisons to lakes in a homogeneous climatic region),
- total dissolved matter,
- average depth.

It was thus possible to define a specific morphoedaphic index for a homogeneous region. This index is calculated as follows:

$$\text{IME} = \frac{\text{total weight of dissolved solid matter}^{1/}}{\text{average depth}}$$

1/ or any other equivalent measure such as conductivity or total alkalinity

The relationship between the potential fishery yield of a lake, Y, and its morphoedaphic index is usually well described (at least for the most commonly observed environmental conditions) by the function:

$$Y = a(IME)^b$$

However, in cases of particularly high salinity and shallow average depths, the actual yields may be below those predicted by such formulae (fig. 1). Such differences result from the apparence of stress phenomena among the aquatic population living in conditions where this is little current.

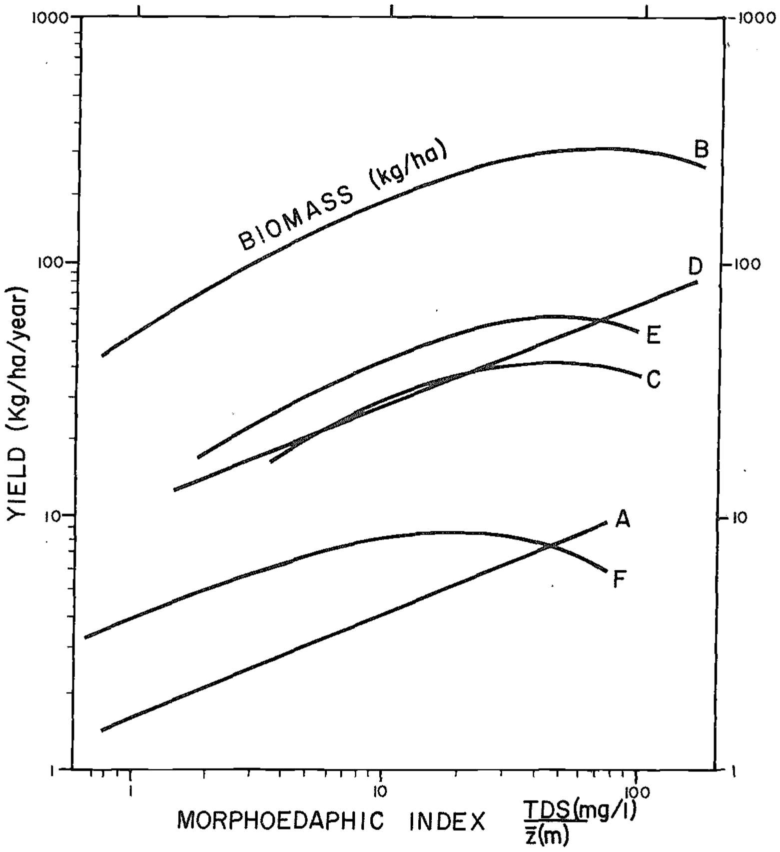

Fig. 1 - Theoretical production of 5 groups of natural lakes corresponding to different climatic conditions:
A = production curve of Northern temperate lakes in North America,
B = biomass curve of temperate reservoirs in Southern USA,
C = yield curve for the same reservoirs,
D and E = yield curves for lakes in tropical Africa,
F = yield curve for temperate lakes in Northern Finland.
(After R.A. Ryder et al., 1973)

In view of the great number of factors that determine or influence the potential yield of a given mass of water, it may seem, a priori, surprising that with such a simple formula it is possible to obtain a sufficiently valid index. In fact, in spite of its extreme simplicity and the obvious limitations of its mathematical formulation the morphoedaphic index manages to account for most of the variance observed among lakes in the same region. Confining comparisons to a single carefully chosen geographical sector greatly reduces many causes of differences, especially those due to the following:

- climate;
- methods and rates of exploitation, to the extent that, within the sector considered, economic conditions and social factors that influence exploitation are very likely to be quite similar;
- the ion composition of the total dissolved matter.

With these simplifications, the total content of dissolved salts gives a fairly good index of the water's productivity, while the average depth of the lake accounts for:

- the proportion of water present in the euphotic zone and in the peripheral zones, which are the most productive;
- the intensity of vertical flow (mixing) and thus the reutilization of nutrient salts in the food chain;
- the ease of exploitation as the shallower areas are usually the easiest to exploit.

It has been possible to check the validity of the model on a great variety of lacustrine systems such as the Great Northern Lakes of Canada, the Great Lakes of North America, the great natural and man-made lakes of Africa, the Finnish lakes, waters used for recreational fishing in California, etc. (fig. 1). It has even been used to ascertain if Loch Ness could have sufficient yield to support monsters (Sheldon and Kerr, 1972). Its performances probably derive from its very simplicity which make it very general. One can find a detailed account of the hypotheses upon which it is based as well as its applications in Ryder et al., 1974.

2.3 Discussion

This approach permits a priori assessment of the potential catch (if comparisons are made with masses of waters exploited with the same intensity) or of the state of exploitation (if comparisons are made with ecosystems of comparable productivity). It must also be stressed that in the first case one does not necessarily get the maximum potential yield. If the masses of water are not fully exploited the estimates will be too low.

The rationale of these models must be carefully borne in mind both in the design of the analysis and in the final interpretation. In general, a fishery biologist has to analyse the respective role of several factors which determine the abundance of a resource. These factors can be roughly grouped into four categories:

(a) those which depend on the pattern of fishing, i.e. the rate and method of exploitation (age at first capture, the distribution of fishing effort among the various components of a mixed species stock, etc.);

(b) the biotic capacity or natural productivity of the exploitable species in an ecosystem.

Furthermore, quite apart from fishing, stocks and environment show, over the course of time:

(c) natural variations (trends), sometimes of long term, whose causes are often not known and which can be detected only in the older fishing areas that are well documented;

(d) random fluctuations which produce a dispersion of the observations around average positions fixed by the three preceding groups of factors.

As a general rule, the fisheries biologist should be concerned above all with the first two categories (a and b) and, since his science is directed towards practical applications, especially with factors which man can control (a). His interest in natural variations (c) depends on the time scale of the estimates he is trying to formulate and the risk of their interfering with the phenomena he is studying. He will be concerned with (d) only to the extent that he can reduce the variance of his estimates by an increase in the number and extent of observations.

3. Transfer of Energy in the Food Web

One can approach the biomasses and the potential production of elements utilizable by man in an ecosystem by examining these quantities at successive trophic levels. This supposes that the trophic relationships between levels (or the components of successive levels being compared) are known both qualitatively and quantatively and that these relationships are fairly stable over time. Such a procedure, which is essential in understanding how living matter is produced in the ocean, is still difficult to apply, owing to the complexity of trophic relationships in the marine environment where successive levels of production intermingle according to ramified networks showing anastomoses and diversions in constant evolution.

The most common applications bear on the evaluation of relationships between successive trophic levels taken as a whole (primary production, secondary, tertiary). Several attempts have been made to estimate by this method the potential of resources that can be utilized by man. The range of results obtained (200 - 2 000 million tons) casts doubt on the usefulness of this approach, at least as regards the validity of results. In fact, much of the divergence among results is due to the criteria followed by the authors in defining utilizable resources. As was noted in the first course (Fishing and Assessment of Stocks), the lower limit of the levels utilizable by man depends on artificial factors (available technology, market conditions, cost of energy for capture, etc.) that are destined to change with time.

An illustration of the calculations and the difficulties that are implicit in this approach can be found in the work of Cushing (1969) on the assessment of the fisheries potential in upwelling regions. According to these assessments, half the world's fishery potential (40-60 million tons) lies in the yield of upwelling zones. If primary and secondary productions can be assessed with relative security, the energy transfer coefficients between successive levels are still little known because, on the one hand they differ among the organisms involved and, on the other hand, the higher level does not always use all the energy available to it from the lower level.

The approximate nature of this type of assessment can be illustrated by the comparison made by Paulik (1972) between estimates calculated for the same region (Peru current) by two different authors (table 1). Cushing estimated the total annual carbon fixation. He considered that this phytoplankton production was consumed by the zooplankton and by the anchovy stock, the young of which are supposed to feed on copepods and phytoplankton, and the adults mainly on phytoplankton. He assumed an energy yield of 10% per transfer. He arrived at similar conclusions by starting directly from secondary production (Cushing, 1969).

Table 1

Peru: Primary production and anchovy stock potential

Author	Fixed carbon ($t/km^2/y$) C		Area ($10^3 km^2$)		Energy yield (all transfers)		Conversion factor (live weight/C)		Annual yield of anchovy stock (10^6 tons)
Cushing (1969)	236	x	479	x	0.01 (2 levels)	x	17.9	=	20.2
Ryther (1969)	300	x	60	x	0.12 ($1\frac{1}{2}$ level)	x	10	=	21.6

Ryther, following the same procedure but with slightly different hypotheses and reasoning, arrived at final results that are practically identical. Furthermore, the two results coincide to a remarkable extent with those obtained through the classic methods of assessment which gave a total annual production of 20 million tons (10 for fishing, 9 for natural death and marine predators and 1 for consumption by guano birds) before the collapse of the fishery in 1972 and 1973. However, if we compare the successive stages of the calculations of both authors, the agreement between the results is less reassuring. The figures used by Cushing and Ryther for the area and total energy yield are quite different. Taking different areas need not be serious in itself - in taking a smaller area Ryther could have neglected a peripheral zone of low productivity. But in that case his figure for carbon fixation should have been proportionally higher than that of Cushing. So, if the estimates agree in the end, this is because the authors are using quite different values for the total energy yield!

Since the anchovy is the main user of the plankton production in the Peruvian upwelling zone, it was possible by this method to assess a well defined stock. More often, in fact, the complexity of the trophic relationships between successive levels is such that these assessment processes can only be applied to groups of fairly heterogeneous resources. Finally, it should be noted that these methods are not used exclusively for estimating the productivity of the higher levels in the food web. It has been calculated, for example, that in the virgin state whale stocks (1.0 - 1.5 million tons) consumed yearly around 50 million tons of krill. As whales are not the only consumers of krill, this figure already gives a lower limit of the potential of this resource.

4. First Evaluations of Potential Yield Starting from Biomass Measurements

A third approach that is more commonly used is to deduce the potential yield of a stock from an estimate of its biomass which can be obtained from specially organized surveys. This method has the advantage that it does not require a series of data gathered over a long period of the fishery's history. An estimate of the biomass only requires the time needed to do a survey. On the other hand, quantative surveys often require highly specialized material and human resources that are not available everywhere. Several types of surveys can be used.

Of course, only surveys which lead to estimates in absolute terms are useful here. Basically the methods listed below are used (for their description reference should be made to other sections of this course and to appropriate manuals):

(a) direct census (sessile or slightly mobile animals (shellfish, salmon, shales, etc.));

(b) surveys of eggs and larvae from which the number of spawning females can be deduced and thus the size of the parent stock;

(c) trawling surveys, to the extent that one can learn the true efficiency of the gear, i.e. the proportion (F) of the biomass present in the area swept by the trawl, that is caught by it;

(d) quantative acoustic surveys (especially for coastal pelagic species).

4.1 Relationship between Virgin Biomass and Potential Catch

The structural models give the required equations. Unfortunately assessments by surveys are especially useful for little studies and poorly documented stocks, i.e. those for which the constants in the biomass/potential conversion equations are unknown. For these situations, Gulland (1972) has proposed an approximate formula as follows:

- If $\bar{\bar{B}}_o$ is the known biomass of a virgin stock
- and Y_{max} the maximum potential of catch,
- then $Y_{max} = F_{max} . \bar{\bar{B}}_{max}$ (F_{max} and $\bar{\bar{B}}_{max}$ are unknown)

Schaefer's model immediately gives: $\bar{\bar{B}}_{max} = \frac{\bar{\bar{B}}_o}{2}$.

On the other hand, for the majority of stocks, it has been found that on approaching maximum production F is only slightly different from M[1]. With these two approximations we can write:

$$Y_{max} = 0.5 \, M \, \bar{\bar{B}}_o \qquad (1)$$

This equation can be written in the more general form:

$$Y_{max} = X . M \, \bar{\bar{B}}_o \qquad (2)$$

where the factor X corresponds to the maximum fraction that can be captured out of the biological production of a stock. This X factor can be written in the form:

$$X = \frac{Y_{max}}{M . \bar{\bar{B}}_o} = \frac{F_{max} \bar{\bar{B}}_{max}}{M . \bar{\bar{B}}_o} = \frac{F_{max}}{M} . \frac{\bar{\bar{B}}_{max}}{\bar{\bar{B}}_o} \qquad (3)$$

With this formula we can calculate the values that X can have according to the Beverton and Holt model. For this we can use the yield tables IV of Beverton and Holt (1964). These give values of Y', where Y' is defined as follows:

$$\bar{\bar{B}} = \frac{R_o W_\infty}{M} . \frac{Y'}{F/M}$$ (see the description of the yield tables)

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[1] If one assumes that the biological production of a stock remains more or less constant no matter what the level of exploitation may be, we get: $M \, \bar{\bar{B}}_o = Z \bar{\bar{B}}$. If one also takes it from Schaefer's model that $\bar{\bar{B}}_{max} \doteq \frac{1}{2} \bar{\bar{B}}_o$, we get:

$2M \doteq Z_{max} \doteq M + F_{max}$. From which we get: $M \doteq F_{max}$.

With these tables we can then directly calculate:

$$\frac{\bar{B}_{max}}{\bar{B}_o} = \frac{(Y'/F)_{Emax}}{(Y'/F)_o}, \qquad (4)$$

where the index E_{max} denotes the rate of exploitation corresponding to $\bar{B}_{max}$. To get X we only have to multiply this relationship by $(\frac{F}{M})_{max}$. Two cases have to be considered:

(a) where the age at first capture cannot be adjusted (which is most frequently the case). This case corresponds to exercise 1.

(b) where the age of the first catch can be modified. Here the calculations are not so simple as we cannot directly compare the figures of the columns in tables IV.

But in both cases we find that in practice, i.e. for the combinations c and M/K most commonly found, the values of X remain between 0.25 and 0.75 (the extreme values range from 0.17 to 0.95 which means that by using 0.5 the maximum relative error cannot exceed 3).

Cadima (unpublished) has analysed the meaning of the X factor.

Let the equations be in numbers:

$D = \Delta + C$

$D = Z.\bar{P}$

$C = E.D$ from which $E = \frac{C}{D}$

where D is the total number of deaths and Δ and C, respectively, the number of natural deaths and the number caught.

Likewise let:

- in the virgin state: $D_o = Z_o.\bar{P}_o = M.\bar{P}_o$ (5)
- at maximum equilibrium production: $C_{max} = E_{max}.D_{max}$ (6)

From the equation $D = R_c$ (in equilibrium; R_c = annual recruitment to the fishery)

we get: $D_{max} = D_o = R_c$ (7)

From the equations (5), (6) and (7) we get: $C_{max} = E_{max}.M\bar{P}_o$ (8)

Using the weight equations $Y = C.\bar{w}$ and $\bar{B} = \bar{P}.\bar{w}$, we get:

$$Y_{max} = E_{max}.\frac{\bar{w}_{max}}{\bar{w}_o}.M\bar{B}_o \qquad (9)$$

A comparison of the (2) and (9) equations shows

that $X = E_{max}.\frac{\bar{w}_{max}}{\bar{w}_o}$

4.2 Application to Assessments

To estimate a potential maximum catch by knowing the virgin biomass, it is thus sufficient to know M (equation (2)). The value of this coefficient can be determined by studying the age frequency distribution of catches made during the survey (we then get $M = Z_o$). Otherwise we take an approximate value for M by analogy with other stocks of the same species or similar species. We then try to refine the value of X starting from the yield tables and the most likely values for M/K and for $c = l_c/L_\infty$ for the stock under consideration.

If the stock is already being exploited, the above equations no longer apply. In fact, we then get for a stock at stage (1):

$$\bar{w}_1 < \bar{w}_o$$

$$E_{max} \cdot \frac{\bar{w}_{max}}{\bar{w}_1} > E_{max} \cdot \frac{\bar{w}_{max}}{\bar{w}_o}$$

$$Z > M$$

$$\bar{B}_1 < \bar{B}_o$$

Lacking anything better we can substitute M with Z in equation (2), which leads back to the assumption that the biological production of a stock ($M\bar{B}_o$ or $Z\bar{B}$) remains more or less constant for all values $\bar{B} \geqslant B_o/2$, an approximation that is justified if we accept the Schaefer's model ($F_{max} = M$) and constant recruitment.

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6. Exercises

6.1 Semi-quantative assessment of potential production of penaeid shrimp on the West Coast of Africa

(a) The yearly yield of penaeid shrimp from different fishing grounds of given surface areas is as follows:

Country	Production (tons)	Area (km^2)
Florida (from Keys to Mississipi)	10 400	16 000
Madagascar	3 200	4 000
Senegal (Cap Roxo)	1 500	1 700
Ivory Coast	1 100	1 300

Knowing that the first is over-exploited and that the other three are exploited to their optimum level, calculate yields per km^2; compare results and draw conclusions.

(b) The total area of the penaeid shrimp grounds on the West African coast has been estimated at 12 000 km^2. Assess the order of magnitude of potential yield for this region in conditions of optimum exploitation.

6.2 Gulland's approximate formula: $Y_{max} = X.M.\bar{B}_o$

Yield tables IV (p. A.42 and following) give:

$$a = \frac{\bar{\bar{B}}_E}{\bar{\bar{B}}_o} = \frac{(Y'/F)_E}{(Y'/F)_o}$$

for various combinations of $c(= \frac{l_c}{L_\infty})$ and M/K and different exploitation rates E.

Knowing that the value of (a) marked with an asterisk in the yield tables corresponds to the exploitation rates producing the highest yield (Y_{max}) for the corresponding value, calculate:

$$X = (\frac{F}{M})_{max} \cdot \frac{\bar{\bar{B}}_{max}}{\bar{\bar{B}}_o}$$

for the following (c, M/K) combinations:

M/K c	0.25	0.75	1.25	1.75	2.50	5.00
0.7			▨	▨	▨	▨
0.6					▨	▨
0.5						▨
0.4						▨
0.3						

What is the maximum relative error that can be made by taking X = 0.4 and knowing that in practice c is between 0.3 and 0.7?

6.3 Surveys

An exploratory fishing campaign has been carried out over an entire year in an area populated by a virgin stock of Atlantic pink shrimp (Penaeus duorarum). The trawl used had a headline of 16 meters. It was mounted without sweeplines. The towing speed was 2.8 knots.

The following results were obtained: area of distribution of stock = 1 850 sq. miles. Average catch (year, area) per fishing hour = 27.5 kg. Escape coefficient (estimated) = 40%.

The mortality rate for this shrimp stock is unknown, but for other stocks of the same species in similar conditions as those studied here we know that 10 to 20% of the shrimp die each month from natural causes.

(a) estimate the biomass of the exploitable stock;

(b) using Gulland's approximate formula, find an approximate value for the maximum potential yield of this stock.

The smallest shrimp caught had a total average length of 8 cm and the largest were around 25 cm. For other stocks of the same species K was estimated at around 2.0.

THE ORGANIZATION OF DATA COLLECTION AND ASSESSMENT OF STOCKS

by

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1. The need to exchange fisheries data

Since the activity of each fisherman or group of fishermen is bound to affect the catches of all others exploiting the same stock, no management plan can be drawn up until the quantities taken by all parties exploiting the same stock are known. This is why the right to fish entails the duty to keep others informed of one's actions.

The same obviously holds true for assessments. The use of assessment models - particularly global models - is possible only if one knows the value of certain parameters, including catches, for all components of the fishery for a stock. This means that for all fisheries where several fleets or groups of fishermen exploit the same stock (or stocks), the collection of data will entail not only the usual scientific and technical problems (e.g., sampling) but also difficulties of organization and coordination between the competent institutions for the various components of the fishery. Obviously the international fisheries are a case in point and that is why the compilation of national data figured very early on as being one of the prime tasks for the regional fishery bodies. The same difficulties can arise in national fisheries when a country has several research institutions working in parallel with a statistics office. In such cases a research laboratory may not have the means, nor even the administrative authority, to collect the information it needs in all the ports where catches from a particular stock may be landed.

Progress in collecting information on stocks and catches - (and, above all, in arranging for the information to be disseminated) - has been so slow that the simple lack of information on the fisheries is the reason for most of the gaps in our knowledge on the state of stocks. At present this lack of data has much more serious consequences than those resulting from deficiencies in the models or the shortage of technical expertise.

The problem is all the more crucial because the rate of exploitation is growing and growing rapidly. When catches approach the potential yield, the latter needs to be estimated with greater precision. Moreover, this precision becomes more difficult to attain since other phenomena may intervene, such as a chronic and growing deficit in recruitment, which may complicate assessment at high levels of exploitation. Finally, the faster the expansion, the less time there is available to compile and analyse the data and interpret the results. In fact, the question of data requirements in assessing stocks and fishing areas bears some resemblance to data requirements for weather forecasting. One could even go so far as to say that the smooth running of a fisheries research institution - and especially the quality of the support it is called upon to give the industry and its own administration - will, in the end, depend on the quality of the service it has set up for the routine collection of fisheries data and its dissemination to the different institutes and services concerned. Both research workers and the administrators who apportion funds and means must be made fully aware of this necessity. The value of the scientific advice that administrators can expect from their research units will largely depend on the attention they themselves have given to this essential work.

2. Data of common interest

The essential data required for assessment can be divided into the four categories given below in descending order of priority:

(a) Catches (yearly totals at least) made by the various fleets - usually identified by flag and gear - fishing the same stocks,

(b) Catch per unit effort - or better, the different measures of fishing effort and the corresponding catches - at least yearly, for all homogeneous groups of vessels (in terms of fishing power) for which such data can be gathered,

(c) Length frequency distributions (yearly summaries at least) of catches by the major fleets,

(d) Other biological data obtained through special research (prospecting surveys, growth studies, selectivity experiments, recruitment surveys, tagging, etc.).

While the data mentioned under (d) are obtained through special research, undertaken for specific purposes with the means available, the data in the first three categories can only be obtained from the continuous monitoring of the activities of commerical fleets and regular sampling of their catches. In the case of stocks fished by several fleets, the need for an exchange of data applies above all to the first three categories, with top priority being given to data on catches. In fact, such exchanges of data are absolutely necessary for determining the value of the corresponding parameters for the stock as a whole.

Although statistics of total catch, total effort and catch per unit effort refer to different parameters (production, mortality and abundance), only two of them need to be known independently (that is recorded separately), as the third can be calculated from the other two. In fact, when we have catch per unit of effort data accurately reflecting stock abundance (and this can be based on the performance of only parts of the fleets), or any other suitable index of abundance (e.g., calculated from various types of surveys), it is enough to know the total catches to deduce the corresponding total effort, or vice versa. In industrial fisheries where the catches are landed at only a few places (where they are usually recorded by the industry), it is generally easier to record landed quantities. From these, knowing the conversion factors and the discard rate, it is possible to calculate total catches in live weight. On the other hand in widely dispersed artisanal fisheries (canoe fisheries in particular), total catches are often more easily estimated by extrapolating from a random sample on the basis of, for example, the total number of fishing units (e.g., number of canoes) and the intensity of their activity in the sampled units (i.e., by estimating the total fishing effort).

Finally, it should be added that the effort devoted to data collection should correspond to the volume of the catch in each fishing area and, as a general rule, industrial fisheries should be monitored more closely than artisanal fisheries.

3. The formulation of a common statistical system (regional and national)

The data collected should refer to well defined stocks. As it is neither feasible nor necessary to analyse all the stocks in a given geographical sector, the first step will be to draw up a list of species for which separate assessments are justified. Such lists are normally prepared by all the regional committees. The selection criteria include the economic importance of the species and the fact that they are, or may be in the future, exploited by several countries. An example of such a list prepared for the Eastern Central Atlantic is given in Annex 1.

To the extent that stocks of national interest are liable to be studied by different laboratories, such lists should also be established at the national level among research institutes and the specialized statistics office. Since it is undesirable, from the operational standpoint, to use several systems at a national level which may be incompatible - at least partially - with each other, the national systems should, in practice, be drawn up by taking into account the standards which have been adopted at the regional level. For the same reason, the regional committees should consult each other periodically to make sure that the regional systems are mutually compatible. For example, this task is done for the Atlantic regions by an interagency working party (CWP)[1] whose secretariat is provided by FAO.

1/ Coordinating Working Party on Atlantic Fishery Statistics, FAO

The need to develop compatible regional and national statistical systems goes well beyond the adoption of lists of species for which efforts will be made to collect data on total catches and only this. For the statistics on each species to be referred to definite stocks, it is essential to know the geographic origin of the catches (and not just the port of landing which, when the fleets are highly mobile and capable of long trips, can lead to very erroneous conclusions). Furthermore, to have suitable fishing effort data (i.e., taking into account changes in the relative distribution of nominal effort and stocks), one will be obliged to use, in collecting data, a grid of sufficiently fine statistical areas (e.g., 1° by 1°). For these two reasons, a set of small statistical divisions should be used (Annex 2). The need for compatibility between national and regional systems mentioned before applies also to the drawing-up of these divisions.

Every fishery commission tries to get all countries that fish the stocks or geographic areas within its competence, to collect and transmit[1] data on catches, effort and corresponding catch as well as the size composition of their catches[2], according to the regulations adopted by the member countries when the regional statistical system was set up.

Furthermore, it is necessary to gather complementary information on:

(a) fishing power (fishing gear and methods, size and main characteristics of fishing boats) so that the fishing effort actually employed can be suitably measured,

(b) the mesh used, or better the selection curves corresponding to the catches of the various fleets and to their length frequency distributions.

To facilitate the transmission of data to the central office, and its processing, storage and distribution to interested bodies, there will be a need to adopt standard practices for the reporting of statistics of common interest. There will also be a need for standardization of the terms used to identify species; first at the national, and then the regional level. Annex 3 gives the rules adopted by Fishery Committee for the Eastern Central Atlantic, FAO (CECAF) for reporting length measurements. The committees will likewise fix categories of size and power, etc., of vessels in order to measure their fishing power. They will adopt the same forms for transmitting all these statistics; an example of the form used for reporting catch per unit of effort data is given in Annex 4.

4. Functions and responsibilities in the assessment and management of resources

Generally speaking, there are four stages in the activities of assessing and managing resources:

(a) the collection of basic data, its compilation and distribution,

(b) the fitting to the data of assessment models, summarizing the assessments and interpreting them in terms meaningful to administrators and fishermen. This is the stage when technical advice on the state of stocks is formulated. This advice will include the consequences for the stocks and catches (both total catches and catch rates) which can be expected, in the short and long term, under alternative management regimes,

(c) selecting management measures from the available alternatives,

(d) implementing the regulations adopted in stage (c).

---

[1] Collection and transmission are two different actions: the first is necessary, but it is not, in itself, sufficient

[2] For the selected species

Table 1 briefly analyses the division of responsibilities between regional and national bodies, as it seems will be the case in light of recent developments in the Law of the Sea. A few observations can be added to this general table:

(1) Up to now, for practical reasons, the collection and analyses of data have been considered as essentially a national responsibility. All countries engaged in exploiting the resources of a region - no matter under whose jurisdiction it falls - should participate in this work. The role of the regional committees is usually limited to defining the regional statistical system and the standards to be adopted in the collection and reporting of data, the compilation of national data and dissemination of all the data so collected to national institutes.

(2) Original work on assessment is basically the responsibility of the national research institutes. In general, the committees do not carry out such studies. Their role is more that of synthesizing national evaluations - through working parties made up of research workers from the member countries - and supplying administrators with a clear description of the general consensus which emerges concerning the state of the stocks and the probable consequences of taking various possible measures. These working parties also provide research workers with the opportunity to exchange views and compare notes, something which is essential to ensure the smooth operation and coordination of national efforts.

(3) The choice of regulatory measures will in future be the exclusive prerogative of coastal states (at least for those stocks which come under national jurisdiction, regardless of how this is defined). Since stocks in their movements and distribution are unaware of any boundaries that man may make, it is essenital, for stocks which are spread over more than one national sector, that a common plan for exploitation be agreed upon among all the coastal states involved.

(4) To the extent that the evolution of the Law of the Sea makes access to resources dependent solely on geographic jurisdiction, the adoption of any regulatory measures lies strictly with the riparian country. Implementation may, in some cases, involve noncoastal states with whom the riparian country has joined to exploit resources belonging to it.

It is clear that each country should devote to the routine collection of data and fisheries research an amount of effort which befits the present and potential importance of its fisheries (including recreational fisheries). From this it follows that not every country will be able to participate with the same intensity in the full range of research work which may be required for the proper exploitation of the fishery resources in a given region (i.e., the functions mentioned under point (2) above). Even among countries that have good research facilities, there are very few that are in a position to carry out all the biological and environmental studies that might some day be useful in developing fisheries on the resources that they possess. In the majority of cases, some specialization is inevitable. Nevertheless, the exchanges which take place, especially at meetings organized by regional committees, allow for the sharing of information and the open debate of questions without which there can be no science.

Countries with few fisheries resources and only limited means will not be able, at least for the time being, to set up research institutions. Nevertheless, the analysis of the functions entailed in stock assessment and resource management show that there are two tasks which every country should undertake:

(a) collecting basic data (as defined in paragraph 2) and reporting it to the regional body,

(b) having national expert in stock assessment and resource management take part in the regional committee's meetings and working parties. The chief function of this expert will be to assist in conveying the knowledge gained at the regional level to his own country and, on the basis of this, to draw the attention of government and industry in his country to the action they should take at the national level.

5. Conclusions

These remarks show that fisheries research cannot be fully effective without there being a network of contacts among the various national and regional institutes concerned and collaboration in data of compilation and assessment by all parties involved in the exploitation of the same stocks. Table 2 gives an outline of the type of network which has to be established. Relations will be:

- horizontal among offices working in the same fields at the national, regional and international levels,
- vertical between different activities (collection of data, assessment of stocks, formulation of scientific advice, selection of the measures to be taken and, finally, their implementation), whether at the national or regional level.

The formal establishment of a working communications network among the various national groups engaged in monitoring stocks and fisheries may take considerable time - sometimes too much time in view of the urgency of the problems - it involves decisions at a high level, institutional rivalries, etc. The creation of temporary groupings (such as *ad hoc* working groups drawn from the institutes concerned) which are set up according to the nature and urgency of specific requirements, are often the best means, in the short term, to adapt existing structures to problems as they arise.

Another conclusion to be drawn from these discussions is that the problems of organization and coordination of institutes, problems inherent in fishery research, assessment and management, are at least as important as the human and material investments in these activities.

Table 1

Functions and responsibilities in the assessment and management of resources

	National responsibility	Regional responsibility (committees)
1. (a) collect and (b) compile the information	(a) is a national responsibility; it concerns all national fleets and thus all the countries participating in the exploitation of a given stock	- definition of a regional statistical system (standards, forms)
2. assessment of stocks and formulating advice on the state of stocks	All countries and, inside the countries, all national institutions involved in assessment work for a given stock	- summarize the various national assessment work - draw up these summaries and conclusions on stock management in terms that can be understood by the national authorities and fishery industry, and by the central body of the Committee
3. selection of measures for stock management	The trend at present is for this to be the responsibility of the coastal state for stocks located in its exclusive economic zone. It is essential to have concerted action by coastal countries having stocks spread over several national sectors or by countries united by certain economic understandings	- make available a forum for the exchange of technical views and for the choice by the countries of the measures to be taken for stock management
4. implementation of regulations	The trend at present is for this to be the exclusive responsibility of the coastal state, which may admit other countries to participate in utilizing that portion of the stock inside its sector	

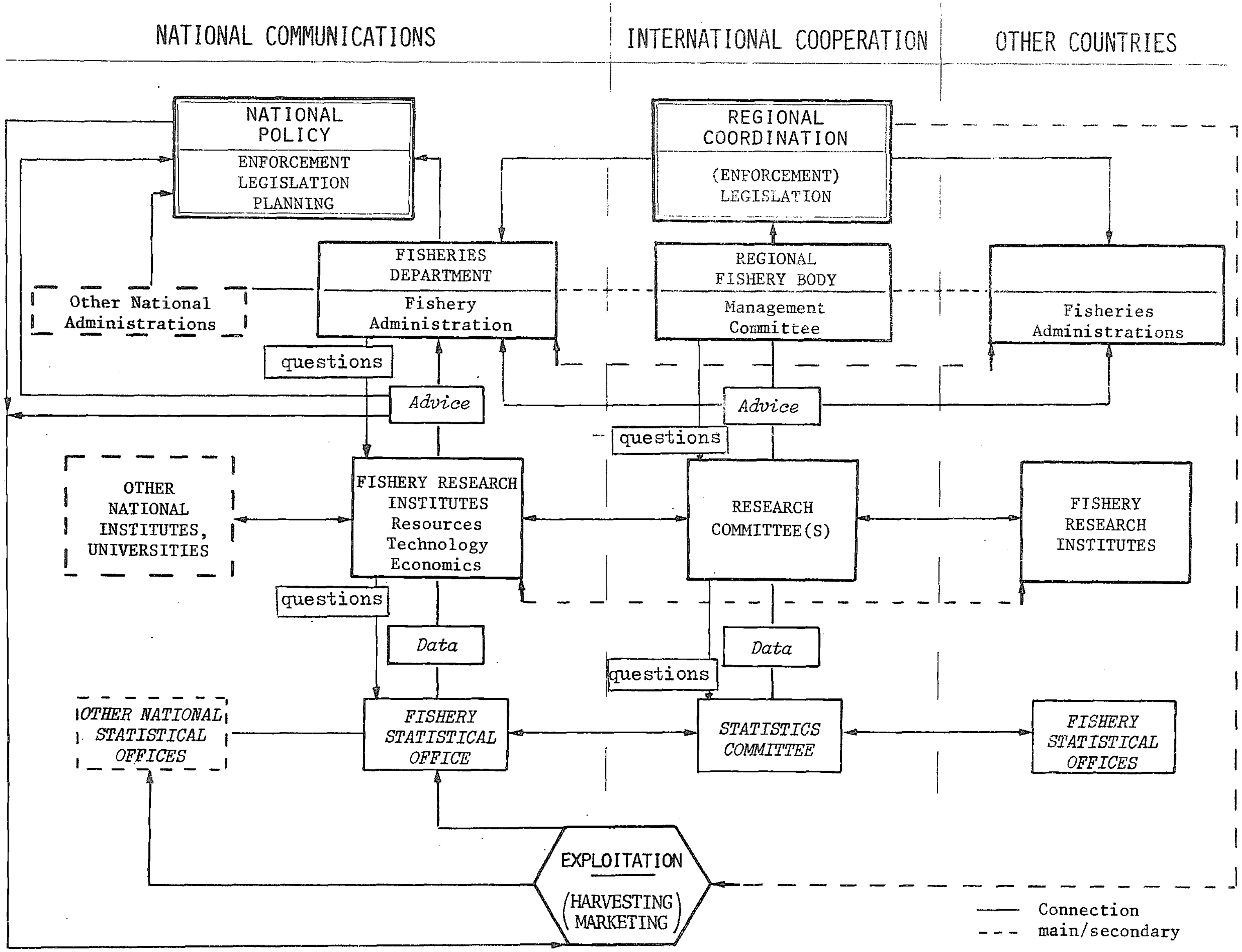


Table 2 - Theoretical flow chart showing relationships between national institutions and a regional committee with their respective functions

Table 3

A hierarchy of objectives in fisheries management, some of the measures used to achieve them, and the requirements for data, assessments and forecasting

Level	Objectives	Management measures	Data assessments and forecasts required
International Regional Fisheries Commission	Maintaining the yield from resources	International agreement on gear regulation, fishing areas and seasons, catch and fishing effort quotas	Biological data for stock assessment including annual updating of catch quotas. Some economic, social and industrial data in determining national allocations
National Fisheries Management	Development of the fishing industry and balanced growth. Maintenance of employment	Planning and assisting with investment. Subsidies. Control of prices, imports, quality	Economic data of many kinds. Assessment of size of exploitable resources and estimates of catch rates
Management of Fishing Enterprises	Maintaining employment and profitability	Improving technological efficiency and marketing of products. New investment	Evaluation of new fishing and processing methods. Short- and long-term predictions of catches and market trends

Source: Guidelines for collection and compilation of fishery statistics. FAO Fish.Tech.Pap., (148), 1975

EASTERN CENTRAL ATLANTIC

ANNEX 1

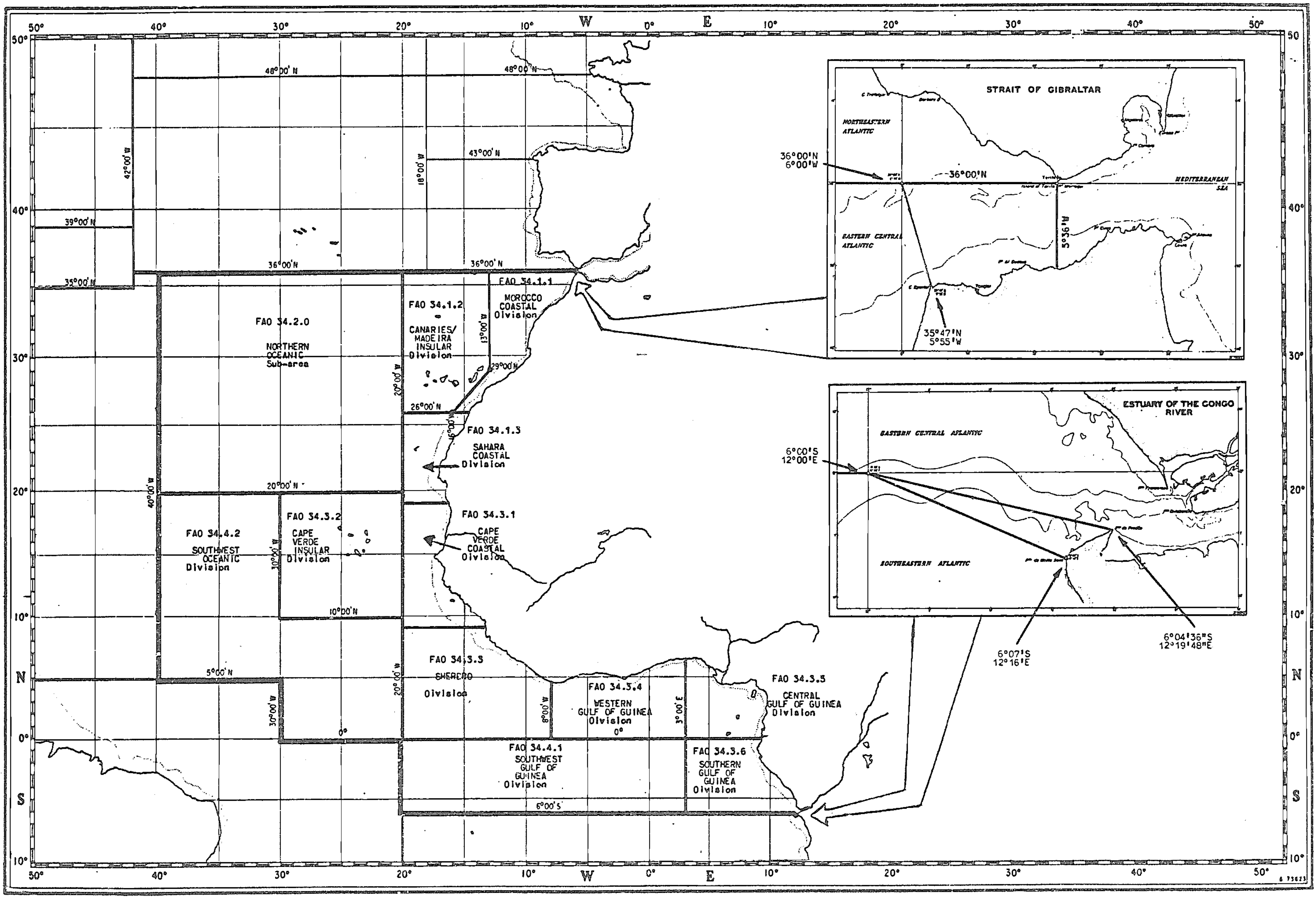
STATLANT FORM 34B - LIST OF SPECIES AND SPECIES GROUPS FOR STATISTICAL PURPOSES

Those species (occasionally species groups) for which separate statistics are required for stock assessment purposes are indicated by an asterisk.

12	TOTAL	
13	Tonguefishes = Cynoglossidae	
14		
15	Flatfishes unspecified	
16	European hake - *Merluccius merluccius*	x
17	Mauritanian and Senegalese hakes - *M. cadenati*, *M. senegalensis*	x
18	Hakes unspecified = *Merluccius* spp.	
19		
20	Sea breams - *Dentex macrophthalmus*	x
21	Sea breams - *Dentex* spp.	
22	Sea breams - *Pagellus acarne*	x
23	Sea breams - *P. coupei* (= *bellotti*)	x
24	Sea breams - *P. erythrinus*	
25	Sea breams - *Pagellus* spp.	
26	Sea breams - *Spondyliosoma cantharus*	x
27		
28	Sea breams unspecified = Sparidae	
29	Croaker - *Fonticulus elongatus*	x
30	Croaker - *Pseudotolithus senegalensis*	x
31	Croaker - *P. typus*	x
32		
33	Croakers unspecified = Sciaenidae	
34	Bigeye grunter - *Brachydeuterus auritus*	
35	Grunters - *Pomadasys* spp.	
36		
37	Grunters unspecified = Pomadasydae	
38	Jacks - *Caranx ronchus*, *Decapterus punctatus*, ...	
39	Jack mackerels - *Trachurus trachurus*, *T. trecae*	x
40		
41	Jacks unspecified = Carangidae	
42	European sardine - *Sardina pilchardus*	x
43	Flat sardinella - *Sardinella eba*	x
44	Round sardinella - *S. aurita*	x
45	Sardinellas unspecified	
46	Bonga - *Ethmalosa fimbriata*	x
47		
48	Clupeids unspecified = Clupeidae	
49	Bluefish - *Pomatomus saltatrix*	x
50	Chub mackerel - *Scomber japonicus*	x
51		
52		
53		

ANNEX 1 (continued)

	TOTAL	
54	Cutlassfish - *Trichiurus lepturus*	x
55 56 57 58	Rays unspecified = Rajidae	
59 60 61	Pink shrimp - *Penaeus duorarum* Shrimps unspecified	x
62 63	Crabs unspecified Lobsters unspecified	
64 65 66 67 68	Squids - *Loligo* spp., *Ommastrephes* spp. Cuttlefishes - *Sepia* spp. Octopuses - *Octopus* spp. Cephalopods unspecified	x x x
69 70 71	Other unspecified species	



Annex 2 - Eastern Central Atlantic (fishing area 34 - CECAF): Geographical limits of statistical sectors

ANNEX 3

CECAF: LIST OF SPECIES OF COMMERCIAL IMPORTANCE TO WHICH MAIN ATTENTION SHOULD BE GIVEN - MEASUREMENTS AND CLASS INTERVALS PROPOSED FOR LENGTH FREQUENCY DISTRIBUTION

COPACE: LISTE DES ESPECES D'IMPORTANCE COMMERCIALE A CONSIDERER EN PRIORITE - MENSURATIONS ET INTERVALLES DE CLASSE PROPOSES POUR LES DISTRIBUTIONS DE FREQUENCE

Scientific names Noms scientifiques	English	Français	Español	Measurement 1/ Mensuration 1/	Class interval Intervalle de classe
	Pelagic	Pélagiques	Pelágicos		
Sardina pilchardus	European pilchard	sardine	sardina	LT	1 cm
Sardinella aurita	round sardinella	sardinelle ronde	allacha	LF	1 cm
S. eba	flat sardinella	sardinelle plate	machuelo	LF	1 cm
Trachurus trachurus) T. trecae)	horse mackerel	chinchards	jureles	LT	1 cm
Scomber japonicus	chub mackerel	maquereau espagnol	estornino	LT	1 cm
Ethmalosa fimbriata	bonga	ethmalose		LT	1 cm
Pomatomus saltatrix	bluefish	tassergal	anjova	LT	3 cm
Trichiurus lepturus	cutlassfish	poisson-sabre	pez sable	LT	3 cm
	Demersal	Démersaux	Demersales		
Pagellus erythrinus	sea breams	sparidés (dorades, pageots, etc.)	espáridos	LT	1 cm
P. coupei (= bellotti)				LF	1 cm
P. acarne				LT	1 cm
Dentex macrophthalmus				LT	1 cm
Spondyliosoma cantharus				LT	1 cm
Merluccius merluccius) M. senegalensis)	European hake, Senegalese and Mauritanian hakes	merlu européen, merlus sénégalais et mauritanien	merluza europea, merluzas senegalesa y mauritana	LT	2 cm
M. cadenati)				LT	2 cm
Pseudotolithus senegalensis)	croakers	ombrines	corbinas	LT	1 cm
P. typus)				LT	2 cm
Fonticulus elongatus)				LT	1 cm
	Shrimp	Crevettes	Gambas		
Penaeus duorarum	pink shrimp	grosse crevette rose	gamba rosada	LT or/ou LC	½ cm 1 cm
	Cephalopods	Céphalopodes	Cefalópodos		
Octopus spp.	octopuses	poulpes	pulpos	LT or/ou/ LM or/ou WT	5 cm ?
Sepia spp.	cuttlefish	seiches	jibias	LM	2 cm
Loliginidae) Ommastrephidae)	squids	encornets	calamares	LM	?

1/ LT = Total length - longueur totale
LF = Fork length - longueur à la fourche
LC = Carapace length - longueur du céphalothorax
LM = Mantle length - longueur du manteau
WT = Total weight - poids total