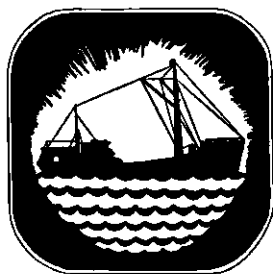


# **INTERNATIONAL COMMISSION**

for the

**NORTHWEST ATLANTIC FISHERIES**



Special Publication No. 1

## **SOME PROBLEMS FOR BIOLOGICAL FISHERY SURVEY**

and

## **TECHNIQUES FOR THEIR SOLUTION**

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Lionel A. Walford

Background for Discussion

Most of the various species of fishes with which this Commission is concerned are trans-oceanic. Few of them are confined to the western side of the Atlantic. Those of greatest interest to the Commission are characterized as bottom dwellers of the banks, yet none of them live wholly on the bottom. Certain ones rise to upper levels diurnally; all are pelagic in early life, in some instances for several months. During that time they drift in the ocean currents far from the places where they were spawned.

Thus, it seems unlikely that the populations of fishes on any bank are quite independent of those on other banks. Studies that have been made in a few localities indicate that the spawning grounds, the dispersal of young, and the distribution and migrations of adults do follow definite average patterns. At the same time there are evidently fairly consistent differences in physical characteristics of the fishes composing the populations of different banks. If these differences are inherited there must be some mechanisms by which the young return to their points of origin in order to replenish their parent stocks. Otherwise, judging from the direction of the currents in which the eggs and larvae drift, few stocks replenish themselves; many of them, if not most, must depend on the spawning of neighboring or even far distant stocks. Understanding of these mechanisms of replenishment and of the identity and degree of independence of stocks is essential to scientific direction of North Atlantic fisheries in order to attain maximum utilization.

To reach this understanding requires studying each species of interest as a whole, throughout its range. So far, research on cod, haddock and redfish in the North Atlantic has been very uneven, being intensely pursued in certain localities and neglected in others. Even in the most studied areas, some essential lines of research have been neglected. If the Commission is to achieve its purposes, the research programs in the Convention Area must be strengthened. This cannot be accomplished by simply agreeing to "cooperate" and "exchange information" about the work which the several member countries happen to be currently engaged in. It can be accomplished only by substantially enlarging programs -- increasing their size and their scope. This enlargement should be according to a plan of truly international collaboration, designed by this Commission and recommended to its members.

It is true that this Commission is bound to focus its attention on the problems of its Convention Area. Nevertheless, it is very much to its interest to see that its research programs and those carried on by European countries east of the Convention Area should fit together, so as to produce most econo-

mically and adequately all of the information which both sides need.

At the Fifth Annual Meeting, held at Ottawa in June, 1955, this Commission endorsed the recommendation of its Committee on Research and Statistics, that an interim technical meeting should be held in a European country, to which scientists of both sides of the Atlantic would be brought together to (1) specify the absolutely essential information needed for predicting the effects of various fishing intensities on stocks of various sizes and various biological properties; (2) to assemble American and European fishery scientists engaged in North Atlantic problems in order to compare, by working together with actual materials, their practices in field and laboratory techniques, to learn where important differences exist, and to determine how these differences can best be resolved; (3) to discover gaps in research programs now being carried on in the North Atlantic; and (4) to suggest how these gaps might best be filled.

The Commission accepted the invitation of the French delegation to hold the meeting in Biarritz, France. In preparation therefor, the Committee on Research and Statistics drew up nine subjects for discussion; these were modified in subsequent correspondence between the Chairman, Executive Secretary and members. On each of these subjects the Chairman appointed a Convenor to lead the discussion of the whole Committee, or, as necessary, to organize a working party of specialists to meet separately to consider assigned problems, study demonstration materials together, compare techniques of measurement and interpretations of materials, develop conclusions and prepare a report thereon to the whole Committee. The convenors were further asked to recommend for publication documents especially prepared for this meeting.

#### Subjects for Discussion

The following subjects are listed in the order in which they were first proposed:

- I. The problem of sampling oceanic stocks which are partly demersal, partly pelagic (e.g. redfish and cod) and whose distribution differs with size and age, and which are fished by diverse techniques and by diverse countries. Develop a plan of sampling the fishery stocks of the Convention Area, and of collating and analysing the samples.  
C. C. Taylor, Convenor (vice J. L. Hart).
- II. A special study of the characteristics of the catches of the salt cod fleet.  
W. R. Martin, Convenor.

- III. Devise means of reducing the time required to obtain data necessary for making assessments of stocks, especially those required as the basis for a program of conservation. S. J. Holt, Convenor (vice R. J. H. Beverton).
- IV. To make the best use of the scientific talent, arrange that men with special skills are most effectively used for the needs of the whole Commission. This may require allocating tasks and materials.  
L. A. Walford (Discussion Leader on this topic in meeting with whole Committee).
- V. Assess the effects of the haddock mesh regulation in Sub-area 5.  
H. W. Graham (Discussion Leader on this topic in meeting of whole Committee).
- VI. Comparison of European and North American techniques of measuring nets, of reading ages of fish and of studying growth.  
B. B. Parrish, Convenor.
- VII. Differentiation of fish stocks.  
C. E. Lucas, Convenor.
- VIII. A review of knowledge about the Atlantic halibut.  
G. Rollefson (Discussion Leader on this topic in meeting of whole Committee).

The reports of these working parties follow the general conclusions below.

#### General Conclusions

Throughout the discussions at Biarritz the Committee and its working parties emphasized the fundamental purpose of the Commission, i.e., to determine how to scientifically increase the production of fish and to maintain it at its highest sustained yield. At the heart of the questions which the Committee considered was the problem of how the information needed to achieve this purpose could be obtained most quickly and cheaply. To this end each working party looked particularly for short cuts in the various technical processes that go into determining maximum sustainable yields. The working parties have suggested a number of ways to save labor and improve the efficiency and accuracy of operations, but they found no quick, easy, cheap method of determining the maximum sustained yields. There is no substitute for collecting enough of the right kind of data for every species of fish of interest. To try to

make do with any less is false economy.

The Committee emphatically affirmed the principle that the foundation of all biological fishery studies must be a full, accurate reporting of statistics on the catches (not just the landings) of all species, specifying not only the quantity caught, and the place and mode of capture, but also the composition of the catches by length, weight, age, sex, and when possible, by racial stock. The Commission should publish such detailed statistics. Besides the information which commercial fishing vessels must furnish, the desired detailed reporting necessitates representative sampling of the catch throughout the Convention Area. This sampling cannot be haphazard, but must be designed to take into account the existence of different stocks of fish, the selectivity of different kinds of gear, the variations in the habits of different sizes and ages of fish, and variations in the distribution of fishing effort. In general, the sampling as carried on now is far below the minimum needs of the Commission. If only one thing were to be done now for the scientific research programs by the ten member nations of this Commission, it should be to improve the sampling of their commercial fisheries so as to provide accurate data on sizes and ages of fish composing the catches of their fleets and the stocks of fish in the sea. This is especially needed in Subareas 1 and 3 where sampling programs are particularly deficient. These areas are of greatest importance in the production of cod. Recent changes in emphasis from one kind of fishing gear to another have so increased the rate of catching young cod as to threaten the supply of the relatively large-sized fish which are required by the salt cod industry. It is, therefore, essential that those countries engaged in the salt cod industry should substantially increase the number of biologists and assistants sampling the catches of their fleets at sea as well as the landings ashore so as to maintain a constant watch for changes that do occur.

In order to combine the biological statistics from the samples which the various countries collect, it is essential that all measurements of fish should be comparable. The working parties found that methods do differ widely, and therefore, measurements are not comparable in many instances. It was agreed that a sub-committee should be appointed at the 1956 Annual Meeting to study the problem of standardizing measurements, and to draw up a conversion table for lengths obtained by different methods. To provide the materials for carrying out this assignment, it was decided that each country should submit to the Executive Secretary a report on its method of measuring fish length, along with a description of the devices used. The Committee asked that the Executive Secretary collate this material and prepare a working report for the use of the sub-committee on measurements at the 1956 meeting.

There was much discussion on the question of whether fish could be measured by some mechanical means. It was the consensus of the group that this

is more a matter of cost than of feasibility. The Executive Secretary was asked to request F. A. O. to make a suitable inquiry into the engineering problems and probable cost of producing such a device.

There is more to combining samples than merely measuring the fish by a standard procedure and totalling the results. The individual samples must be appropriately weighted, in one way to reflect accurately the populations of fishes in the sea, and in another way to reflect the total commercial catch. To design a system of sampling and of combining samples requires special study. Putting a system into effective practice once it is developed will require coordination of all sampling by the member countries.

The discussion showed that a manual on techniques of sampling and on designing sampling systems, written in non-mathematical language for the use of biologists and their assistants is urgently needed. Dr. Kesteven reported that the F. A. O. has commissioned Mr. Gulland to prepare such a manual for general use, which can be enlarged, as necessary, to meet the requirements of this Commission. Members of the Committee pledged their cooperation in this project, and agreed to supply statistical data and examples of problems, such as Mr. Gulland may request, to help him develop a comprehensive manual. The Committee commends F. A. O. for fostering this project, and urges that the manual be published as promptly as possible when the manuscript is completed.

The Committee calls attention to one obvious limitation in the commercial catch statistics; they give no information on the abundance of year broods before entrance into the fishery, and hence cannot be used for predicting fluctuations. For this it is necessary to sample the pre-commercial sizes by research vessels. If this is to be done, however, special provision must be made for it. Where research vessels are operating in the Convention Area, special time should be allotted for the purpose; but such arrangements alone will not suffice to cover the whole area, for research vessel facilities are far from adequate to fulfill the Commission's purposes. One of the most important statistics needed for following changes in abundance of fish populations, and their relation to fishing pressure, is the age composition. The working parties have made a number of recommendations for research designed to improve the consistency and to test the accuracy of age determination by scales and otoliths. These include research to test ways of minimizing the labor required for age determination, and to devise substitute methods where scales and otoliths are not usable.

Adequate sampling is basic; so also is adequate knowledge of what it is we are sampling; each of these is necessary to the other; improvement in one leads to improvement of the other. The importance of this was forcibly

brought out in the conference, for the Committee was continually faced with the problem of defining stocks; and in several instances it transpired from the discussions that differences of opinion and differences in the interpretation of data resulted from the fact that the members were talking about different varieties of the same species of fish. These evidently differ in all sorts of ways, such as growth rate, maximum size attained (therefore, age and size composition of the population), habits, fecundity, etc. It is generally accepted that the various species in the North Atlantic are not homogeneous entities, but are composed of an unknown number of units which are variously called stocks, communities, cohorts, races, sub-populations, etc. It is not possible with present knowledge to define these units precisely or to know what mechanisms keep them apart, or whether they are permanent, self-sustaining and genetically peculiar, or whether they are wholly the creatures of the environment. All studies and conservation actions relating to North Atlantic sea fishes depend on definition of these units of population. This requires close cooperation of member countries in making comparable measurements and counts of body parts of specimens collected in the samples; furthermore, it requires making special provision in the budgets of research programs, not only for the collection of the necessary data, but for their analysis, a phase of research which is often neglected in the planning. It is unlikely that stocks can be diagnosed by any single feature; consequently, it will probably prove necessary to work several in combinations, including proportions of body parts, counts of repeated structures, blood types, and chemical composition of body tissues.

In examining the research programs which the member nations conduct in the Convention Area, the Committee finds that they are particularly deficient with respect to redfish and halibut. Redfish is one of the species of greatest interest to the Commission, and likely to increase in commercial importance. Because of certain apparent peculiarities in the life history of the redfish, the effect of overfishing may appear suddenly and disastrously. This species is one of the most difficult to study, resisting most of the classical techniques of fishery research. Important though it is, difficult though it is to study, probable though the serious ultimate depletion seems in the light of accepted information, none of the member countries put enough effort into research on this species to provide even the barest information necessary for prescribing conservation measures. The Committee, therefore, urges the Commission to give particular attention to the program of redfish research recommended below.

Halibut is not of much commercial importance to all the member nations. Yet it occurs throughout the Convention Area. It seems peculiarly vulnerable to undue fishing pressure, and, judging from experience in the Pacific Ocean, is remarkably responsive to a proper regulation of fishing rate. There are



serious obstacles that would make restoration of Atlantic halibut stocks difficult. If these difficulties could be overcome, this species might yield substantially higher quantities of sea food. Very little effort goes into research on halibut at present. This Committee, therefore, asks that the Commission consider the desirability of recommending to the member nations provision for more research.

The Committee recommends that special emphasis continue to be placed on cod research, as indicated elsewhere in this discussion. It recommends further that the United States continue its careful study of the effects of the mesh regulation on the populations of haddock in Subarea 5.

In addition to these recommended research programs on particular species which involve acquiring certain classically prescribed information, -- such as rate of growth, for example, -- certain lines of study must be pursued which apply to all fishes sharing the same environmental system. For example, oceanographic research is necessary to delineate the currents, follow their fluctuating courses, and determine how they and the various properties of the water affect the dispersal and survival of eggs, larvae and adults. Trans-Atlantic oceanographic research for the specific purpose of increasing our understanding of fishery matters has been largely neglected in the past. To collect necessary information on this subject requires the full use of every available facility, including research vessels, commercial fishing vessels, trans-oceanic passenger and freight liners, weather ships, Texas towers, drifting buoys, etc. Sorting and identifying plankton, and analyzing the data collected from all these sources, for fishery purposes, requires adequate shore staff, for which hardly more than token provision is now made.

Much attention was given, in several of the working parties, to the effects which various factors of the environment have on the growth, physical characteristics, behavior and survival of larvae and young fish. Some parts of this great and important complex of problems can best be studied by carefully designed observations at sea. Others can be attacked only by laboratory experiments, which require special facilities providing for absolutely controlled conditions. Here is another field of research for which provision is not made in any of the programs in the Convention Area.

A good deal of study on the selectivity of fishing gear should be continued. Working Party VI pointed out a number of problems relating to selectivity of nets, to the techniques of measuring meshes of nets, and to the properties of materials composing nets. Every encouragement should be given to people engaged in net studies in the various countries to coordinate the planning and execution of their work, to exchange information, and to discuss their results.

The collection of data on sizes and ages of fish, and on intensity of fishing effort, is not an end in itself. This information must all be analyzed and synthesized statistically in order to determine the effects which various levels of exploitation have on the numbers, lengths, weights and ages of fish composing a given stock, and on the relative abundance of the various species inhabiting a given environment. The balance among all of these elements of fish populations is constantly changing in response both to changing conditions of environment and to changing habits of fishermen and techniques of fishing. All of this necessitates providing special staffs to process and study current data in accordance with established techniques. In addition, however, there are many unsolved problems in population dynamics, as pointed out by Working Party III, for which special developmental research is needed. The lines of research suggested by this group should lead to improving the accuracy of present methods, and to sharpening our knowledge of the precise kinds of data needed. Such research should demonstrate how the judicious use of mathematical models, which need yet to be developed and tested, can provide satisfactory working estimates of relations between various levels of fishing intensity and characteristics of catches. For this kind of research, at least one team of statisticians should be set up in the Convention Area to devote their full time to the task. There is no single piece of research which could offer so much for so little cost.

A most critical lack in fishery research is manpower. All delegates reported difficulty in recruiting young men to fill fishery research posts. Students in colleges where courses in aquatic biology are offered, are choosing chemistry, engineering and medicine in preference. The Committee urges the Commission to make a special inquiry into the causes of this condition and means of correcting it.

The following sections give a fuller reporting on the discussions, conclusions and recommendations of the several working parties at the Biarritz meetings.

THE PROBLEM OF SAMPLING OCEANIC STOCKS WHICH ARE  
PARTLY DEMERSAL, PARTLY PELAGIC, WHOSE DISTRIBUTION  
DIFFERS WITH SIZE AND AGE, AND WHICH ARE FISHED  
BY DIVERSE TECHNIQUES AND BY DIVERSE COUNTRIES.

Convenor's Report, Clyde C. Taylor \*

Among the stocks of fish in the ICNAF area which present peculiar sampling problems, either because of their biological characteristics or because of the diversity and distributions of fishing, are the redfish and the cod. Two questions were posed to the working party: (1) what information is required, and (2) how can this information be obtained on an international basis? The working party was asked to keep in mind that two major objectives of sampling are to provide information adequate to demonstrate changes in abundance and the effectiveness of the recruitment of year classes.

The working party recognized early in its discussion that an intelligent sampling program depends in large measure on the type of population model it is necessary to apply to the individual peculiarities of a stock. For this reason, Working Party I combined with Working Party III to consider jointly: (1) the requirements of a population model for interpreting the dynamics of populations partly demersal, partly pelagic, fished in various parts of their range by different types of gear; (2) the kind of sampling program best suited to provide efficiently the information required for applying such a model.

The papers presented at the symposium on sampling held at the 1954 meeting of the International Council for the Exploration of the Sea (Problems and Methods of Sampling Fish Populations. Rap. et Proc.-Verb., 141, Pt. 1, 1956) were circulated to members of the working party, and a review prepared by Beverton and Parrish, was given by Mr. Parrish. The group commended the fundamental principles presented in the papers of this Symposium and these principles were considered as a background in the further discussions.

A paper of major interest to the working party, "Sampling of semi-oceanic stocks of fish", was presented by Mr. Gulland. (See Papers and Discussions Working Party III). Mr. Gulland pointed out that in order to make use of data from commercial vessels, it is necessary to know (a) the total catch by all methods of fishing from each area and depth, (b) the total effort which, if in mixed units, would need to be expressed in homogeneous units, (c) the composition of the catch with respect to size and age, from which growth and morta-

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\* Dr. John Hart, Director of the Atlantic Biological Station, St. Andrews, New Brunswick had been appointed convenor of this working party and although he was unable to attend the Biarritz meetings, the success of the discussions was owing, in large measure, to his planning and efforts.

lity estimates could be made; and that insofar as the catch might not be representative of the true population sampled, it would be necessary to know (d) to what extent the effective fishing intensity varied with size and age and this would require having samples of size and age from all sections of the fleet.

Dr. Templeman presented data on the distribution of redfish on the Grand Banks and in the Gulf of St. Lawrence. The points brought out by Dr. Templeman's talk which were especially pertinent to the problem of sampling were as follows: Apart from spacial variations, there are variations in the catches from different depths, fish being taken at all depths between 50 and 500 fathoms. There is a gradual decrease in catches below 300 fathoms. The sex ratio varies with season, and in March and April females do not appear abundant at any depth. Spawning occurs in May and June, and sometimes as late as July. The size distribution varies with depth and it is not known for certain whether or not the fish mix to any degree between depths. The presence of certain parasites at certain depths and their absence at other depths suggests little, if any, vertical mixing.

Diurnal variations in catches of redfish show generally a midday maximum, so that any organized sampling program would have to take this into account. Another sampling problem arises from the fact that the fishermen generally work within a restricted range of depth; therefore the population outside this range is not adequately sampled.

Mr. Fleming presented information on the size distribution of cod on the east coast of Newfoundland from 1950 to 1953 and drew attention to the relation between sizes caught and method of capture. There was a general tendency for the size composition to increase with increasing depth of water.

Mr. Rollefson gave an account of the arctic cod in the Barents Sea. Fairly lengthy migrations are made to the Lofoten Islands where a large fishery exists on spawning fish. Statistics are available from 1860 on the numbers and weights caught.

Mr. Taylor presented data on diurnal variations in catches of several species in the Gulf of Maine and on Georges Banks. The data were obtained during round-the-clock trawling operations, using a 1 1/2-inch (stretch) mesh liner. Two types of diurnal variations were recognized in the data. The first, typified by the redfish and haddock, shows a midday maximum and a midnight minimum. The second type (some skates and flatfishes) shows a midday minimum and a midnight maximum. The silver hake and some other species show no significant diurnal trends.

RECOMMENDATIONS

1. In sampling oceanic stock being fished by several types of gear, the working party considers the following statistics essential:

(A) Total catch by species, subarea, and type of gear. Subarea of capture should, at the minimum, separate areas containing independent stocks. (These minimum statistical requirements are now generally met in the ICNAF area, with the possible exception that information on independence of stocks may be in question for some species).

(B) Effort data for each type of gear, expressed in standard units. This is especially important where each gear selects differently from the population as in the Lofoten cod fishery. The working party pointed out that in some situations, one type of gear fishing the species representatively might provide adequate data and that the reporting of the effort of this type of gear alone would allow some diversion of sampling time to other problems. (Since efficiency varies from vessel to vessel using the same type of gear, it is desirable to set up standards for the various vessel categories to which the performance of individual vessels may be compared. Thus total effort by all types of vessels may be expressed in terms of standard units. For example, 100 days fishing by an otter trawler of 150 gross tons is not likely to be equivalent to 100 days fishing by an otter trawler of 200 gross tons. At the present time, no country is reporting effort data to ICNAF in standard units).

2. The working party emphasized the importance of continued studies examining the amount of sampling necessary for determining age and size composition. Such studies frequently save many man-hours by improving the efficiency of the sampling procedure.

3. Where growth and recruitment are well known, the group recommended the use of age-length keys so that less time need be placed on age determination, permitting the collection of more length data. It was suggested such age-length keys be shared by countries fishing the same areas. Where growth rates are known to vary considerably, the working party cautioned that individual cases must be carefully studied before applying such keys.

4. The group recommended the collection of weight as well as length information to reveal the operation of density-dependent factors. Recognizing the manpower problem involved, the group recommended investigation of the

possibility of bulk weighing plus individual measuring. The possibility of using dry otolith weight instead of fish weight was suggested as a better indicator of fish condition than body weight.

5. The working party recommended that research vessel time devoted to sampling the pre-exploited ages of fish be increased wherever possible. The importance of measuring abundance as early in life as possible, especially prior to commercial exploitation, was stressed, since such measurements are not only useful for predictive purposes but also may provide invaluable information on the influence of natural factors on brood strength and on the magnitude of natural mortality.

6. With regard to sampling problems in the redfish fishery, the working party considered present hypotheses concerning the biology and distribution of this species to be inadequate for the purpose of interpreting the observed facts in terms of an intelligent sampling program. The working party considered that:

- (A) All methods of investigating redfish, however unlikely, should be explored.
- (B) Collection of data on catch and effort by area and depth should be continued, together with other concomitant observations now in progress.
- (C) Special surveys should be made at all depths redfish inhabit.
- (D) A high priority should be given to the development of tagging methods as the technique most likely to reveal the requirements of a sampling program.

## CHARACTERISTICS OF THE CATCHES OF THE SALT COD FLEET.

Convenor's Report, W. R. Martin.

In the ICNAF area cod is by far the most important species; cod landings amount to two-thirds of the total groundfish landings. Three-quarters of these cod are salted. It is accordingly of great importance that the Commission give close attention to the salt-cod fishery.

Fishing Equipment

Cod for salting are caught in the Convention Area by many widely different methods: pound nets, traps, jigs, baited hand lines, baited long lines, otter trawls and pair trawls. To handle these different types of gear many different types of fishing boats are employed: small rowing and motor boats for fisheries near the shore, and larger long liners, dory schooners and otter trawlers for fisheries offshore.

Inshore fisheries. Greenland's shore fishery in Subarea 1 is carried on with jigs, baited hand lines, long lines and pound nets. Rowing boats 12-26 feet in length and motor boats 26-30 feet in length are used. The fishing season extends from July to October in the northern part of Greenland (1A) and from April to October in the southern part (1E, 1F).

Canada has the largest inshore cod fishery in the Convention Area. This fishery is conducted in Subareas 2, 3 and 4.

In Subarea 2, with traps, jigs and hand lines, using motor boats 25-35 feet in length, fishing is from June to September (2H, 2J).

In Subarea 3, the season extends from May to November in the east Newfoundland area (3K, 3L) using traps early, and hand lines and long lines throughout the fishing season. In southwestern Newfoundland (3P) fishing with lines continues throughout the year. Motor boats 20-55 feet in length are used in these fisheries, with those 35-55 feet in length being equipped with power haulers for long lining.

In Subarea 4, the fishery is by trap, hand line and long line. In the Gulf of St. Lawrence area the trap fishery is centered mainly in 4R and 4S, with line fishing predominating more to the west. The season in the Gulf extends from June until October. Outside the Gulf the fishery from Nova Scotia is mainly with hand lines and long lines and the season extends throughout the year. Motor boats used are from 25-60 feet in length, with those from 35-60

feet being used for long lining with power haulers.

In recent years, both in Greenland and Canada, there has been an increase in the number of motor boats used in the fishery. In Canada the use of power haulers has increased the efficiency of the long line fishing.

Offshore fisheries. In the offshore fisheries for cod for salting, landings are made by otter trawlers, dory schooners; long liners, and pair trawlers, in decreasing order of importance.

Otter trawlers. The largest fleets of otter trawlers are operated by France, Portugal, and Spain, the ships ranging in size from about 900 to 1,400 gross tons. These trawlers usually arrive in Subareas 3 and 4 each year in February and fish in Subareas 4, 3, 2 and 1 as the season advances. Most of these ships make two or three trips during the February to December fishing season. A small fleet of large-sized otter trawlers from Italy also fished in these Subareas during the past few years. Fleets of otter trawlers from Iceland, Denmark (Faroes Is.), Norway, Germany and the United Kingdom (ships mainly around 500-700 gross tons) fish each year in Subarea 1 from April to November.

Dory schooners. Portugal has the most important dory schooner fleet; a small number fish entirely in Subarea 3 and the others fish in Subareas 1 and 3. These dory schooners make only one trip each year; their season is from June to September in Subarea 1, and from April to October in Subarea 3.

Canada has a small, but decreasing, dory schooner salt-cod fleet which fishes from March to October, primarily in Subarea 3. These ships generally make three salt-fishing trips each year.

In Subarea 1, Denmark (Faroes Is.) carries on a small fishery by schooners..

Long liners. The only offshore long line fishery for cod is in Subarea 1. A Norwegian fleet of long liners ranging between 100 and 500 gross tons fishes from April to September. Denmark (Faroes Is.) operates a small fleet of long liners in Subarea 1 during the same season.

Pair trawlers. Spain is the only country operating pair trawlers in the Convention Area. These fish in Subarea 3 mainly during the summer months but their season extends from about March until October.

In the offshore fishery, in a move toward more efficient fishing, practically all otter trawlers are now fitted with depth-recorders; many have



TABLE I - Selectivity of gear used in the salt-cod fishery

Country	Otter Trawling	Line Fishing
	Cod-end Mesh Size *(mm)	Size of Hooks (Mustad)
Canada		11 (a) 14-17 (b)
France	120-125 (about)	
Portugal	110-115	14-15 (b)
Spain	90-127 (1)	
	89-101 (2)	
	110-131 (3)	

\* As measured with ICNAF or Scottish gauge. (1) Measurement of first cover for one section of fleet using double cod-ends. (2) Measurement of second cover for a second section of fleet using triple cod-ends. (3) Pair trawler cod-end (no cover). (a) Hand line. (b) Long line.

Loran and Radar for more accurate navigation; many have radio-telephones for communication, and many are now being fitted with sonar equipment to aid in detecting the presence of fish schools. Many of the dory schooners are now fitted with similar equipment. In the long lining fleets more ships are now using power haulers than in previous years.

#### Statistics of Landings

The following countries, listed in decreasing order of importance of landings, participate in the salt-cod fishery in the Convention Area: Canada, Portugal, France, Spain, Denmark, Norway, Iceland and Italy. The order of importance of subareas producing salt-cod is 3, 1, 2 and 4.

Recent trends in the salt-cod fishery may be summarized as follows:

1. The Canadian salt-cod fishery has been declining. Schooners have been reduced to very small numbers. The bank fishery for salt-cod has been replaced by an otter trawl fishery for fresh groundfish.
2. The Portuguese salt-fishery has been increasing. Schooner landings, which exceeded those of otter trawlers until 1949, have now levelled off while otter trawler landings have continued to increase.
3. The French salt-fishery has fluctuated greatly. It virtually disappeared

during both world wars and during the depression in the "thirties". French dory schooners have been completely replaced by large otter trawlers which catch more cod for salting than any other otter trawl fleet.

4. The Spanish salt-fishery has grown steadily from 1927 except for a ten-year wartime decrease beginning in 1936. Recent developments have included (a) large catches of haddock for salting; (b) an increasing fleet of large otter trawlers; and (c) a salt-cod fishery in Subarea 3 by pair trawlers.

5. The Danish salt-fishery has increased sharply during recent years. The shore fishery from Greenland has increased, and the Faroese schooner and trawler fishery developed quickly following the last war.

6. The Norwegian salt-fishery gained prominence after 1948. The development of a pelagic line fishery for large cod is the major factor responsible for the increased landings. A few otter trawlers have also contributed to the Norwegian catch.

7. The Icelandic fishery became important in Subarea 1 in 1951.

8. An Italian fishery by a few large otter trawlers has contributed to salt-cod landings since 1950.

TABLE II - Landings of salt-cod for 1953  
(thousands of metric tons round fresh)

	Canada	Denmark	France	Iceland	Italy	Norway	Portugal	Spain	Total
Otter trawlers (1)									
- very large -	-	-	109	-	12 (3)	-	116	67	304
- large -	-	18	-	9	-	2	18	-	29
Pair trawlers -	-	-	-	-	-	-	-	43	43
Dory schooners (2)									
- very large -	-	-	-	-	-	-	109	-	109
- large 9 2	-	2	-	-	-	-	-	-	11
Long liners -	10	-	-	-	-	40	-	-	50
Inshore boats 161 23	23	2	-	-	-	-	-	-	186
TOTAL	170	53	111	9	12	42	225	110	732

(1) For details of otter trawler sizes refer to section on fishing equipment. (2) Very large dory schooners - 250 to 1,200 gross tons. Large dory schooners - 100 to 250 gross tons. (3) 1954 data.

Recent changes in the salt-cod fishery may be summarized as follows:

1. There has been a post-war increase in the landings from the Convention Area. This is largely due to increased fishing in Subareas 1 and 2. In Subareas 3 and 4 the total cod production has been maintained at a high level.
2. There has been a sharp increase in the landings by otter trawlers; about half the salt-cod landings were taken by otter trawls in 1953. Line fishing from dory schooners has become relatively less important.

#### Abundance of Cod

Abundance indices are available for some salt-cod fisheries in Subareas 1 to 4. In Subarea 1 favorable climatic conditions have resulted in the production of a series of very large year-classes of cod. In Subarea 2 cod abundance has not changed appreciably during the past 25 years. In Subarea 3 catch per unit of effort has increased with increased efficiency of fishing methods, but abundance indices have not changed significantly during recent years. In some years favorable hydrographic conditions concentrate cod along the Newfoundland coast and in those years landings increased. In Subarea 4 cod indices of abundance have decreased since the last war as a result of a decline in the numbers of large cod.

There is good evidence that the large salt-cod fishery can be increased substantially from the present level of production. Post-war developments of otter trawl and pair trawl fisheries, recent introduction of pelagic long lining in Subarea 1 and deep water long lining in Subarea 3, both for large cod, and finally the known, but little-fished, cod stocks of Subarea 2 all support the conclusion that the cod fisheries in Subareas 1, 2 and 3 can be increased.

#### Sizes of Cod Captured

The decreasing relative importance of line fishing and the increasing importance of otter trawling have resulted in a reduction in the sizes of cod taken from the Convention Area. Since large cod are of special interest to the salt-fish industry, because of greater market demand and higher value, it is important to study the relation between landings of small and of large cod. If the proportion of large cod in landings could be increased, it is possible that fishing effort and total production of cod could be increased. In-

TABLE III - Recent observations on sizes of cod taken by different gears

	Gear	Subdivision	Length Range cm	Mode cm
Canada	Trap	3L	35 - 95	53
	Hand line	3L	35 - 105	63
	Long lines	3L	40 - 120	65 - 68
	Dory schooners	3, 4	50 - 140	65
Portugal	Dory schooners	1D	55 - 100	67
	Otter trawlers	1C	40 - 90	70
		2J	32 - 70	52
Spain	Otter trawlers	3L	38 - 83	60
		3N	32 - 71	52
		3O	44 - 83	63
		4V	41 - 74	50

creased long-term total production is the aim of the Commission.

#### Conversion Factors

New studies of conversion factors for landed weights of salt-cod provided data which conform with the conversion factors tentatively accepted by the Commission in June, 1955. Preliminary data were presented on conversion factors for landed lengths of salt-cod to lengths of round fish.

#### Biological Observations

Some of the highlights in biological observations presented in papers and charts to the salt-cod working party are listed below:

1. Dr. Hansen (Denmark) presented a figure showing the decreasing growth rate in recent year-classes as compared with that found in Greenland in the "twenties". An earlier age of maturity has also been observed. Good year-classes continue to appear frequently at Greenland and catches have accordingly continued at a high level. Some recent signs of a return to a period of low landings have been observed.

2. Dr. Rodriguez (Spain) reported on recent studies of cod taken by Spanish otter trawlers from the southern Grand Bank. The 1949 year-class has predominated in the catches and the modal sizes taken have increased from 43 to 60 cm. during the period 1953 to 1955.
3. Dr. Rojo (Spain) reported on discards of cod at sea by Spanish trawlers, showing wastage by numbers to be 0.5 to 37 percent. He also presented data on catch per unit of effort for cod and haddock, showing that Spanish trawlers concentrate either on cod or haddock.
4. Dr. Ancellin (France) presented an interesting chart describing the seasons fished by French otter trawlers in the various ICNAF subdivisions.
5. Dr. Ruivo (Portugal) presented valuable information on conversion factors, sex ratios and age composition.
6. Growth rate studies by Canada, Denmark, Portugal and Spain were considered and good agreement was observed for areas where two countries sampled the same stock. Great variation in growth rate was observed throughout the Convention Area. The fastest growth rates have been found on the southern Grand Bank and at Greenland; the slowest growth was observed at Labrador, and along the east coast of Newfoundland.

#### Proposed Research Program

##### 1. Statistics

- (a) The Commission has made outstanding progress with the collection and publication of statistics of landings. It is believed that these statistics are approaching adequate detail and accuracy for Commission purposes, and that increased energy in this field is not required.
- (b) Studies of available log-book records of past fishing are needed in order to allocate landings of cod by subarea of capture and by fishing effort.
- (c) Studies of factors for converting weights of cod as landed to round weights have reached the point of diminishing returns; all material should now be reviewed. It is proposed that research in this field should now be directed to studies of conversion factors for lengths as landed to total lengths as caught.

## 2. Sampling

- (a) Progress has been made with the study of sizes of fish caught and landed, but it is proposed that work in this field should be increased. Consideration might be given to the publication of size compositions as well as statistics of catches in ICNAF publications. The basic data should include detailed information on fishing ground, depth, and selectivity of gear fished (mesh or hook size). These data should be grouped for publication. In order to advise the Secretariat on such grouping of data, the proposed cod symposium in June, 1956 might give consideration to division of stocks, and to horizontal and vertical movements of cod in relation to sex and size.
- (b) Sampling can be improved by shore sampling of landings taken from localized areas. Landings by pair trawlers and by dory schooners might be studied in this way. Such sampling would require length conversion data (see 1 (c) above).
- (c) Sampling at sea must be continued in order to sample trips which move from one area to another, and in order to assess differences between sizes caught and sizes landed. Observers should move from vessel to vessel for sampling.

## 3. Gear selection

- (a) Studies of mesh selectivity should be extended to nets with double cod-ends.
- (b) Mesh selection data for otter trawls should be studied in relation to the selectivity of other gears such as pair trawls, hand lines, long lines, pound nets and traps.

## 4. Population dynamics

- (a) Studies of recruitment, growth, and mortalities must be pursued in order to determine optimum size for first capture and optimum fishing intensity for each stock.
- (b) It is of special interest to study the possibility of increasing total production by providing for increased proportionate catches of large cod.

## 5. Prediction

- (a) A number of basic biological studies must be continued in order to

predict changes in the commercial fishery e.g. (I) studies of abundance of pre-recruits from egg, larval and small-fish surveys; (II) studies of the factors controlling year-class strength; (III) studies of changes in growth rate, maturity, and conditions factors; (IV) studies of distribution in relation to such factors as depth and temperature; (V) studies of efficiency of different baits in relation to analysis of indices of abundance.

List of Contributed Papers  
(not included in this volume)

- |                  |                                                                                                                                                                                                                                                    |
|------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Ancellin, J.     | - La Campagne de Pêche morutière des Chalutiers Français dans l'Atlantique N. W. en 1954. (1 chart)                                                                                                                                                |
| Fleming, A. M.   | - Characteristics of Canadian (Newfoundland) salt-cod fleet.<br><br>- Landings, sizes, and growth of cod caught by Canadian (Newfoundland) salt-cod fleet. (8 charts)                                                                              |
| Hansen, P.       | - Special study of the characteristics of the catches of the Greenland salt-fish fleet.<br><br>- Changes in growth rates of year classes in Greenland waters. (1 figure)                                                                           |
| Martin, W. R.    | - Characteristics of the fishing and landings by the Canadian dory schooner salt-fishing fleet. (12 charts)                                                                                                                                        |
| Rodriguez, D. O. | - Report on the cruise carried out by the Spanish vessel "Cierzo" in the waters off Newfoundland, June-July, 1955.<br><br>- Short history of the Spanish cod-fishery.<br><br>- Conversion factors (Subarea 3, " <u>Cierzo</u> ", June-July, 1955). |
| Rojo, A.         | - Total capture of cod and haddock; catch                                                                                                                                                                                                          |

per unit of effort; and haddock sizes taken by ten Spanish trawlers, 1955 (graphic presentation).

Ruivo, M.

- Conversion factors for cod. Portuguese investigations in Subareas 1 and 3 in 1955.



POPULATION DYNAMICS: DEVISE MEANS OF REDUCING THE TIME REQUIRED TO OBTAIN DATA NECESSARY FOR MAKING ASSESSMENTS OF STOCKS, ESPECIALLY THOSE REQUIRED AS THE BASIS FOR A PROGRAM OF CONSERVATION.

Convenor's Report, S. J. Holt.

### Introduction

The Working Party received eleven written contributions giving either general comments or analysis of particular aspects of our problem. These papers were not presented formally during our sessions, but were circulated in advance of the meetings and studied with reference to particular aspects of the subject as these were being discussed.

It was indeed most unfortunate that Mr. R. J. H. Beverton, whose preparatory work was eventually such an important factor in the development of our discussions, was unable to be present at the meeting. We were, however, fortunate in having, by correspondence, the benefit of the thought that he had given to the problem set to the Working Party, and his assistance in preparing the final draft of this report. It should be mentioned, finally, that before the meeting Mr. Beverton had corresponded with Dr. W. F. Thompson who, though he did not send a formal contribution, raised several important points in his letters, the substance of which has, I think, been incorporated in this report.

All meetings were held jointly with Working Party I and it was decided that the discussions on population dynamics should precede those on sampling problems. Although there was a reciprocal relation between the two subjects, it was felt that the greater need was to define first the population properties for the estimation of which adequate sampling procedures need to be devised.

The group considered first the types of assessment that are needed, then how these may be made in a wide variety of possible situations with respect to type of fishery and type of data available. It was then discussed how the desired information might be obtained, or used, more efficiently, and time saved also by:

- (a) defining situations in which it is safe to make recommendations for action (e.g. beneficial increase in mesh size, reduction of fishing intensity, etc.) when only certain limited data are available;
- (b) improving the choice of priorities in research;

- (c) supplementing - - or substituting other kinds of information for - - the usual time series (e.g. annual statistics of catch and fishing effort), the rate of accumulation of which cannot be hastened.

#### Types of Population Assessment

- (a) Rough appreciation of the present state, or condition, of a fishery, the principal question being whether the fishing is having any significant and measurable effect on the size or composition of the stock, and if so, whether the catch being taken is in general a large or small proportion of the potential steady catch.
- (b) More detailed diagnosis of the present state of a fishery, and predictions of the probable long-term effects on the characteristics of the catch of various sustained changes in the amount or selectivity of fishing.
- (c) Assessment of changes from year to year in observed characteristics of catch and population to supplement a diagnostic assessment of type (b) above, and to detect any unexpected changes that may occur. A particular need is to establish as soon as possible whether or not a given regulative measure is having the predicted result.

#### Information Needed on the Fishery

The group concluded that the method of assessment used in evaluating the effect of changes in either (or both) the amount or kind of fishing must be capable of giving information about the following characteristics:

- (a) the total weight of the catch;
- (b) the catch per unit fishing effort;
- (c) the composition of the catch, especially by species and size of fish;
- (d) the partition of the catch between different parts of the whole fishery (e.g. between different kinds of vessels or gear, or between fleets of different nations).

### Examination of Historical Changes in a Fishery

In the past much study has been devoted to methods of determining the state of a fishery from long series of data on annual catch and fishing effort. There has been some success in this, but the group did not consider that total catch, and perhaps not even catch per unit effort, could provide a very sensitive measure of changes in fish stocks. The group recommends that greater attention should be given to methods of using other characteristics of the catches (e.g. species composition, sex ratio, average size or range of size of fish) to indicate changes in the stocks, and hence point to possible effects of fishing. The need for long time-series might also be reduced by comparing, over relatively short time periods, changes in stocks of the same species in different areas, or in stocks of different species in the same area. However, the group considered that such methods could do little more than guide future research, and could not lead to firm conclusions about the expected quantitative results of changes in either fishing or natural conditions.

It is well known that observation of the consequences of large changes in fishing effort, such as have occurred during and after the two world wars, can give good indications of the general effect of fishing on the stock and hence of the possibility of improving catches by adjustment of fishing effort or selectivity of the gear. It was suggested that advantage might also be taken of such changes as rapid alterations in the type of fishing gear used.

### Information Needed to Diagnose the State of a Fishery

The group considered that for this purpose the most powerful analytical method is the development of mathematical models of fish populations, into which may be fed information relating to real populations and their structure, the predictions made of the magnitude of changes in characteristics of the catch with changes in the amount and selectivity of the fishing. Some models are, however, less efficient than others. In particular it was felt that those models in which only the gross magnitude of stock, and of catch and effort, were related by a simple theory of population growth, were of limited application. The results obtained from them were unlikely to be sufficiently reliable or detailed to give a reasonably sound basis for practical recommendations concerning a particular fishery. A satisfactory model should at least take into account separate measures of the fishing and natural mortality rates, the growth pattern of individual fish throughout their fishable life-span and the number and age of fish recruited and the age at which they first become exposed to fishing. Methods for determining these quantities depend to a great extent upon the analysis of the age and size composition and other features of

the catch. It is important that these methods should always be developed and applied in parallel with the models in which the observed values of the mortality, growth and recruitment are to be used.

The group then considered each of the above quantities in turn, paying attention to the methods of measuring and observing changes in them; the required accuracy of measurement; and the extent to which bias in estimation, through ignorance of such factors as the degree to which catch samples are representative of the whole population, may lead to wrong diagnosis.

#### Natural and Total Mortality Estimation

There are several methods of estimating natural mortality rates and they are summarized in "Problems and Methods of Sampling Fish Populations", ICES, Rapp. Proc.-Verb. 140 (1), 1956. The basis of most methods is the estimation of total mortality and the subtraction from this of a measure of the fishing mortality. An example is the procedure of plotting yearly estimates of total mortality (usually obtained from age composition data) against some appropriate index of fishing intensity. This may give a regression line from which the total mortality when there is no fishing (i.e. the natural mortality) can be calculated. Confidence limits for the natural mortality can also be calculated and such limits may be of great usefulness for certain limiting cases outlined in a later section of this report. In practice, when such procedures are used, there is a very great scatter of points, and the error of estimation is large. This might be reduced by taking longer time series but this increases the likelihood that the period covered would include changes in the relation between fishing effort and the mortality caused (resulting from unnoticed changes in either the power of the fishing units or their spacial distribution with respect to the stock), or in the natural mortality itself. The scatter may also be reduced by improved sampling methods for age composition and more accurate estimation of effort, but there remains the possibility of year to year variation in the natural mortality. If an index of this variation could be found, it could be used to reduce the scatter, and thus shorten the time series required for reliable estimation of the average natural mortality. To do this an investigation of the causes of natural mortality and their relative importance is essential, and this would enable some rough index of the intensity of the main factors, e.g. predators or disease, to be obtained. In practice, each factor that was suspected of having an influence on natural mortality would be examined; if by taking it into account the sum of squares of deviations from the regression line of total mortality on fishing effort could be significantly reduced, then this would strengthen the conviction that that factor was indeed influential. The group therefore agreed that measure -

ment of the causative agents of natural mortality promises to improve greatly our knowledge of the dynamics of fish populations, and may reduce the time required to reach practical conclusions as to their exploitation, and therefore recommends that the Commission should encourage research on this question.

The group noted that natural mortality can be estimated also from regressions of total mortality on fishing intensity when the latter varies not only with time but also with place or with age of fish, and these methods would be useful in reducing the time required for adequate measurements.

The group agreed that in principle as many different methods of estimation as possible should be used, drawing on the widest variety of kinds of data. Cross-checking the results obtained by different methods (including tagging where this is possible) gives a means of minimizing the time needed to come to a firm conclusion. Natural mortality is the most difficult of the vital rates in a population to measure and it may often be the most critical in assessing the effects of changes in the fishing. To enable a variety of methods to be used, the group recommends that the collection of the necessary data should be as complete as possible over all sections of the fishery; such data should include weight caught (including fish rejected at sea), fishing effort; and the species, sex, size and age composition of the catches. Various types of changes in these characteristics of the catch can in certain different circumstances give information about the natural mortality. Development of methods for this purpose should be pursued, and attention paid to the comparison of natural mortality rates and their variation with age and between different stocks, either of the same or different species.

#### Growth Estimation

When the age of individual fish can be determined, then growth is easily measured to the accuracy required in the diagnosis of the state of a stock. The most important aspect of growth variation is its dependence upon the abundance of the stock. Regression methods are again useful in estimating the magnitude of the density dependent effect. As with natural mortality, regressions corresponding to variations in space as well as in time might be useful, but need to be tried with care. Similarly, the variance about the regression line might be reduced by allowing for measured differences in environmental factors such as food abundance, even if only a rough index of them can be obtained. Surveys of available food would in any case be essential in any attempt to study the density dependence of growth rate by regional comparisons. In addition, sensitive measures of the recent rate of growth of a fish should be sought to supplement information on food availability. The

variation in the weight-length relation (condition) may be useful, and it is suggested also that such measures may be found by detailed examination of anisometric growth; relative growth of otoliths (which may differ in fish of the same length and weight but different ages), and of eggs and gonads were mentioned as examples that might repay closer study.

Attention was drawn to the possible use of pond experiments in the study of growth variation. Even though the rates of growth observed under such conditions do not necessarily correspond to those attained naturally, an estimate of the possible range of variation might be obtained and this would be useful in certain circumstances. The group therefore recommends that consideration be given to the possibility of increasing knowledge of growth by direct study of the natural food populations and experimental study of growth variations in fishes, and their causes. Development of techniques for valid comparison of growth of different species or stocks, by distinguishing variations due to feeding from inherent variations, is desirable.

When age itself cannot be determined, measures of growth increment and relative age (see below) are still useful. The former may sometimes be obtained by tagging and it has been suggested that an idea of the latter may be obtained from the appearance of the fish. Instances were given of changes in the relative sizes of certain external structures or features of the fish indicating relative age, and it is recommended that further studies of this matter should be made. However, the group felt that collateral evidence of growth rate would usually be required and that great care would have to be taken to ensure that the feature used as an index of relative age did not vary greatly with such factors as temperature and food supply, and also that observed differences in appearance were not of taxonomic significance.

#### Estimation of Recruitment

To obtain directly an absolute value for the number of fish annually recruited to a stock presents very great difficulties, but if data on growth, the fishing and natural mortalities and the total catch are available, the number of recruits can readily be computed. Much can be done also with a simple proportional index of recruitment, obtained, for example, as the catch per unit effort of fish at the recruitment age or size. It is very important to know whether recruitment is significantly dependent upon the size of the mature population from which the recruits are derived, and if so, the general form of the relationship. It may be necessary to know whether there is at some high level of stock density an inverse relation, that is, the number of recruits decreasing with increasing stock size, but usually, in cases where regulation

is in force or contemplated, the stock size maintained might be expected to be less than that giving maximum recruitment. Then an assumption of independence, when in fact there may be some unknown degree of direct dependence, may be an acceptable procedure because it will lead to an under-estimate of the expected effects of changes in either amount or selectivity of the fishing. (The group felt that to under-estimate the effect was less undesirable than over-estimating it because then there would be no danger of encouraging regulation in a situation when it would not in fact be beneficial).

In attempting to identify the relation by plotting indices of recruitment against indices of egg-production, or size of mature stock, over a period of years, the observed points are again liable to have a wide scatter, making it necessary to deal with time series as long as the statistics will allow. If, however, there had been a long-term trend in the conditions for larval survival, the result might be an associated change in both recruitment and egg production and when observed values of these were plotted against each other they may show a relation which would be mistakenly interpreted as one of cause and effect. It is therefore particularly important to find means of reducing scatter and thus allow effective analysis of data referring to shorter periods of time. In considering methods of reducing the scatter the group considered that a less variable index of recruitment may be obtained by suitable use of data obtained throughout the whole fishable life-span of a group of recruits. The scatter might also be reduced by studying the form of the survival curve during the pre-recruit phase, especially in identifying stages at which large density-independent mortalities occur. This is essentially a sampling problem.

It was agreed that a useful technique is to follow through from the early life of a particular group of fish which were hatched together and subject to particular environmental factors, and thus possibly having identifiable meristic characters. At the same time there is a complementary need for study of long-term trends in environmental factors thought to affect larval survival.

The particular importance of having an adequate index of recruitment when regulation of gear selectivity is considered, or changes in gear evaluated, was emphasized. Ideally this index should be obtained at an age before the fish are exposed to any of the gears considered.

#### Growth and Survival Interaction

It is possible that growth and survival rates (both on the average and with respect to variations between individuals in a brood) may sometimes be in-

versely related. Although it is not thought that this phenomenon will cause appreciable errors in use of simple models that do not take the effect specifically into account, the effects being compensatory, nevertheless some further attention should be paid to this and other similar relations between what are usually considered to be independent factors. Another example would be the possible relation in some cases of high recruitment to fast growth in the pre-recruit phase, so that there is a rapid growth through a size range in which the young are particularly vulnerable to some cause of mortality.

#### Population Estimates from Limited Data

The group paid much attention to the value of analytical models when information on critical factors such as natural mortality is lacking or poor. It was generally agreed that there were several situations in which a proper understanding of the properties of simple models, with constant parameters of growth, mortality and recruitment, can permit useful conclusions to be drawn about the expected direction of changes in size or composition of the catch following changes in the amount of selectivity of the fishing even when data on the necessary parameters are somewhat inadequate. There is need for further examination of these possibilities but some special cases are mentioned below. It cannot be too strongly emphasized, however, that the shortcut methods suggested are for use in special cases and in making particular kinds of decisions with regard to a fishery, and their application can be no more than a temporary measure pending a comprehensive and detailed study of the stock and fishery in question.

1. If only the growth rate and total mortality are known then it is possible to calculate a value of the natural mortality, such that if the true value is above it, then an increase in fishing intensity or selectivity (mesh size) will give an increased steady catch. When the relative growth rate is high and the upper limit of size is being rapidly approached, there may be cases when this calculated value of natural mortality is close to zero and well below the value of natural mortality usually found in similar stocks. There may also be some collateral evidence that the minimum possible value of the natural mortality is above this calculated value.

Conversely there is another value of natural mortality such that provided the true value is less than that value, then there will be an increase in steady catch following a reduction in effort or mesh size. Evidence that the true natural mortality is below this second calculated value may come from the lowest values of the total mortality coefficient observed over a period of time for a fishery in which the effort has fluctuated widely (allowance being made



for extreme values occurring due to sampling errors). Information on total mortality in virgin stocks, or soon after exploitation began, may delimit the natural mortality even better. In such conditions the growth rate may be abnormal, but will probably indicate a lower limit to the changes expected in growth rate when the stock is fished.

It was pointed out incidentally that data obtained before or soon after a commercial fishery develops are exceptionally useful and that special steps should be taken wherever possible to ensure that such data are obtained in the greatest detail.

The group recommends that calculations should be made and diagrams prepared of these upper and lower values of natural mortality for a wide range of total mortality, growth rate and age at recruitment, as an aid to diagnosis of the condition of the stocks.

2. If the average weight of fish in the catch, the weight at which fish enter the exploited phase, and the ratio of fishing mortality to total mortality are known, it can be determined whether the steady catch will increase or decrease following a change in the selectivity of the gear. Even if the fishing mortality or total mortality are not separately measurable, their ratio might be estimated by simple marking experiments, and determined even by those experiments in which the exact number and size of fish released is unknown (as might occur with tagging by detachable hooks). Such experiments will tend to under-estimate the ratio, but this direction of error is such that it is still possible to identify situations in which it would be advantageous to increase the size at first capture.

As in 1 above, there may be other evidence on the possible limits of fishing and natural mortality such that a firm conclusion may be reached as to whether an increase or decrease in age at first capture is desirable. The group recommends that the ratio of the weight in the exploited phase to the average weight in the catch should be explicitly calculated. When the selectivity is optimal for the actual fishing effort being made, this ratio is equal to the ratio of fishing mortality to total mortality. The aforesaid calculation should be compared with the observed ratio of the fishing to the total mortality, for any fishery for which mesh or other corresponding regulation might be contemplated.

3. When considering the direction of change as in 1 and 2 above, the change in density of stock will be small near to the observed situation, so that as a good approximation the possibility of density-dependent changes in the vital rates may be neglected. However, calculations could be made of the limits of the rate of density-dependent change which, if exceeded, would invalidate

conclusions based upon the behaviour of simple models with constant parameters.

In all the above cases, similar arguments can be applied to the direction of change in catch per unit effort and certain indices of the composition of the catch, such as average length or weight of fish.

4. The length composition of the catch has sometimes been used instead of age composition, when the latter is not available, to give indices of mortality. The procedure is simple if, during most of the fishable phase of the life span, the growth in length of the fish can be considered as approximately linear (for example, as determined from marking experiments, moulting of crustacea, etc.), since a linear relative age scale can be established. There is, however, a need to develop corresponding methods for using length (or weight) compositions in cases where a more realistic, non-linear, representation of growth (i.e. a steady increase in length with age, towards an upper asymptote) is necessary or desirable, and it is recommended that this problem should be investigated.

5. Special problems arise when there is a bias in the determination of age of fish, as for example may occur when there is uncertainty in the interpretation of the nucleus, or of intermediate rings in a scale or otolith. However, if both mortality and growth rates are determined from the same data of "age" composition, assessments may sometimes be attempted before the true method of age determination has been established. Thus consistent differences of one or more years (i.e. reading a fish of age  $x$  as  $x + k$ ) still give correct values for mortality, and since the error in the location of the growth curve on the age-axis is exactly compensated by the error in the estimation of age at first capture, the resulting catch curves are identical. Thus conclusions concerning the state of the stock are unaffected by such an error in age-determination. The same is true for errors of a constant multiple or fraction (i.e. reading a fish of age  $x$  as  $kx$ ). This will be precisely equivalent to expressing mortalities, growth and age at first liability to capture in terms of the same unit of time, equal to  $1/k$  years. The resulting calculations concerning the state of the stock are unaffected by such errors provided that such calculations were concerned only with steady-state conditions; predictions could not be made, for example, of year to year changes following a change in fishing intensity or mesh size, during the period before a new equilibrium was established, because the results of the calculations would depend critically on the number of age groups represented in the accumulated stock. It was emphasized that real evaluation errors would be introduced if other kinds of data are used for measuring either the mortality or growth rates. For example, data from marking experiments would refer to the true time scale. Since one important general conclusion of our meeting was the need to use and compare

results of several methods for determining population parameters, it is clear that the necessity to refer readings to a true absolute age scale could not be long postponed. Nevertheless our discussions served to bring out the point that errors in thinking about dynamics of populations (for example, attempts to judge the condition of a stock and its possible response to fishing from consideration of growth or mortality rates separately) may at times have greater significance than bias in the techniques of obtaining data. In view of the insufficiency of our knowledge of the basic processes determining ring formation in hard structures, which limits our certainty in age reading (especially with respect to variation of bias in reading with age itself), the group recommends that investigations should be made of the extent to which various kinds of undetected bias (especially contraction of the time-scale at high age) may be expected to lead to important errors in evaluating stocks. The results of such studies would perhaps help also in planning investigations of the bases of age determination methods of the kind discussed by Working Party VI.

6. Frequently fishing is carried out on only part of what is believed to be the geographical or depth range of a unit stock, but it is not known what fraction the part is of the whole, nor what is the rate of interchange of fish between fished and unfished areas. Preliminary calculations show that at least in some circumstances important errors are not introduced by treating the fished part of the stock, as reflected in the composition of the catch, as if it were independent of the unfished part. Discussions of this problem showed that there is some useful work to be done in analysing the errors of evaluation which might arise if calculations are based upon simple models of independent populations with constant vital rates when it is known that the real situation departs, but to an unknown extent, from the simple assumptions. It is suspected that the simple models give answers valid for practical purposes when there is a considerable degree of departure, provided that the parameters are computed from the data in the analogous way to that in which they are applied to the model to give assessments. Clearly any errors would increase as fishing intensity or selectivity departs markedly from the initial observed values, and sometimes even the direction of change of catch characteristics may not be correctly predicted. However, it has already been shown that the simple models can sometimes be applied to complex situations of spacial variation of fish concentration and fishing to give valid predictions, provided the distribution pattern of the fishing in relation to that of the stock does not greatly change. The group recommends that further studies of this general problem of the extent to which simple models can give useful working answers in complex situations should be made. Other such situations are the fishing of the same stock by gears having different selectivities, the simultaneous capture by the same gear of species having similar mortalities or growth characteristics, and fisheries based upon migrant stocks, whose presence in the fished area may be only transient.

At the same time it is of the greatest importance to continue to develop methods of analysing patterns of movement (especially offshore movements and general movements between deep and shallow water) and detecting or predicting the existence of stocks outside the fished area. No one method is sufficient and the group recommends that attention should be paid to methods of interpreting marking experiments carried out for this purpose, variations in morphometric and meristic characteristics (for which frequency distributions of measures or counts are of equal, if not greater, importance than the mean values), and data of catch, effort and composition of catches by as small areas as possible.

7. It was confirmed that there are as yet no special methods for assessing the effects of variation in the accessibility of the stock other than the most detailed and persistent study of as much of the stock and as many of the possibly significant environmental factors as can be dealt with. However, even when such basic data are available, there remains a need for satisfactory analytical techniques. It was suggested that a useful start had been made in studying how fluctuations in availability can be analysed in terms of deviations from an expected regression of apparent mortality on fishing effort.

#### Effect of Discrete Stocks on Population Assessment

Insufficient attention has been paid to the criteria by which it is decided that an observed population may be considered as effectively a homogeneous unit stock. Something has been said earlier of cases in which, even though the limits of the stock are unknown, some evaluation can be made, but the full implications of such procedure are not well understood. It is suggested that differences in reaction to fishing, particularly in fishing mortality, of two stocks whose degree of interdependence is unknown, might be useful as a means of differentiation, and that errors in such methods might be of little importance in evaluation. It seems likely that when there is doubt as to the allowable procedure, the correct catch curve will lie between that based on an assumption of homogeneity and the sum of those based on complete independence. This problem is part of the larger question of determining the practical significance of any observed inter-relations between different stocks, and the group recommends that further studies of this matter should be made.

#### Methods for Estimating and Predicting Annual Population Changes

The group agreed that this aspect of our work is in urgent need of system-

atic development. The basic data for this purpose are catches and their location, their species, age, size and perhaps other composition, and standard measures of fishing effort and its distribution by area. Methods are available for making year by year estimates of growth and total mortality. These should be further employed and refined, but the group recommends also that close study should be made of the expected dependence of various characteristics of annual catches on possible kinds of changes in fishing or particular environmental factors. The more sensitive of them might then be used for testing whether or not regulative measures are having the expected effects, and for detecting unexpected changes in the stocks.

With regard to information on fishing operations, the most important points to watch for are changes in fishing power of the fishing units which would bias fishing intensity statistics, changes in selectivity with changes in gear, and changes in the distribution of the fishing in space or time which might change the effective fishing intensity or the effective selectivity of the gear. Unfortunately the group did not have time to discuss these points in detail, and no other specific recommendation can be made.

In connection with regulations it is perhaps commonplace that research programmes have to be planned integrally with them in order to check as quickly as possible any important factors that may not have been understood or measured adequately before regulative action was taken.

The group agreed that the simple population models at present used do not use data as efficiently as may be possible; in processing data to obtain average values of various parameters, and to eliminate effects of sampling and similar errors, much potentially useful information regarding the variability of the stock and the fishery may be unused. Steps should be taken to correct this situation by continuing the development of models that make full use of all estimates of population parameters and which can also incorporate a wide variety of data relating to environmental factors. The group emphasized that in this work continued reference must be made to the available data referring to particular stocks of fish, and to the particular factors which have, in each case, been shown to be significant in modifying the characteristics of the stock, and hence of the catch. It was at the same time pointed out that improvement of the methods of analysing data would sharpen the already urgent need for more rapid processing and dissemination of detailed commercial statistics and basic sample data such as length compositions.

#### Number of Annual Series of Data Required for Assessments

A view was put forward that by a carefully planned and sufficiently com-

prehensive qualitative and quantitative analysis of the stock during two consecutive years, and including also tagging experiments, both the mortality between the individual age-groups, and their growth, can be obtained. If such investigations are possible then calculations of the change in catch per recruit, resulting from a change in fishing intensity or selectivity, can be made. However, it was thought generally that although this may be so in ideal circumstances, the conditions necessary for success are rarely fulfilled in practice.

#### Desirability of Standard Terminology and Notation

The group discussed at some length the question of notation in studies of the dynamics of fish populations. It was agreed that it is most desirable to establish standard symbols for the elementary quantities that are most frequently manipulated in the mathematical models that are being increasingly used for the evaluation of fisheries. The chief considerations when examining possible systems of notation are:

- (a) the possibility of expressing the relevant formulae in a simple and compact form which is easy to write, type and print;
- (b) the advantage of similarity of different measures being reflected in similarity of their symbols;
- (c) the desirability of arranging that relations between different measures are not unnecessarily obscured, for example by using an extra symbol for a simple function of other symbols;
- (d) the extent of conflict with the established notation of mathematics and statistics, and perhaps other sciences;
- (e) the extent of departure from present usage.

Bearing these in mind, the group listed the quantities for which it was considered standard symbols were required at present; there are certain important differences in the definitions both of these and also of the quantities for which special notation is not yet required, and the names used for them by various workers. Knowing that FAO Fisheries Division is working on a dictionary of terms used in fisheries biology, the group recommends that FAO be asked to circulate proposed definitions of the fundamental terms used in studies of population dynamics to research workers on this subject in member countries of ICNAF, to receive comments and suggestions and make available a reference list of these definitions.

It was thought desirable that in any acceptable notation distinction should be made between true population values and sample estimates or measures of the causative factors (e.g. between fishing mortality and fishing effort). This can most conveniently be done by using lower case letters for the latter, or, when this is for other reasons undesirable, to indicate sample estimates by a circumflex accent or an underline.

A list of terms and symbols is appended. These symbols are almost all in common use, and the group recommends that the Committee should consider proposing the adoption of these symbols by workers in the ICNAF region, and especially in submitting documents to the Commission for discussion at meetings or for publication.

The detailed considerations which guided the group's recommendation for individual symbols, as they arose in discussion, were as follows:

1. Mortalities. The choice for this group of symbols lay essentially between two distinct sets, used characteristically by Ricker, and by Beverton and Holt. Both sets of symbols have been used extensively in the literature and are in general use among substantial groups of research workers. Some clash with existing usage is therefore inevitable. Considering the symbols for the instantaneous rates, the group believed that the symbols  $p$  and  $q$  conflicted with the established statistical usage as probabilities (in particular  $q$  is in general equal to  $1 - p$  and also added confusion can arise because mortality coefficients have a probabilistic interpretation), and therefore recommends the use of  $F$  and  $M$ , following Beverton and Holt.

2. Numbers and weight of fish in catch and stock. The group considered that the symbols recommended for these quantities were the most suitable, and these did not depart significantly from any well established usage.

3. Fishing effort and fishing intensity. The group strongly recommended that distinct symbols should be used for a crude measure of fishing effort, e.g. the number of boats operating, which has rather greater economic than biological significance, and the best measure of the effective fishing (that is, effective in generating a fishing mortality rate in the fish population) calculable from the available data, the effective overall fishing intensity. The latter would include the standardization of fishing effort, and corrections for its geographical distribution relative to the fish. The symbol  $f$  has been widely used for both these quantities, but more generally -- at least implicitly -- for the latter. Because also of the close connection with the instantaneous fishing mortality coefficient, for which the group recommended  $F$ , and of which the fishing intensity may be considered an index, the group recommended  $f$  for fishing intensity and a similar symbol,  $g$ , for any crude measure of fishing

effort.

4. Ratio fishing intensity/fishing mortality. The group considered that by its nature a lower case letter was essential for this quantity. However, there were serious objections to all the lower case letters used in the literature consulted, and the group therefore recommended the use of  $q$  as approximating to a present use of  $Q$ . It was felt that in any likely context there would be little confusion with the use of  $q$  as a probability.

5. Age and recruitment. The group considered that while a clear distinction should be made between age at recruitment to the exploitable phase, and age at which a fish is first liable to capture by the gear in use, such distinction could be well made by the use of suffices. The group recommended the use of  $t_r$  and  $t_c$  respectively.

6. Suffices. With the development of more detailed population analysis, increased use has been made of suffices to denote the values of parameters referring to a particular age of fish during a calendar year or at a particular time. The group felt that while not as essential as the standardization of the other symbols given in the appendix, a consistency in the use of symbols is greatly desirable. A suggested notation is given.

7. Other symbols. The group considered the possibility of recommending other standard symbols, particularly in regard to marking experiments and growth studies. They felt, however, that for these applications it is not yet clear which are the exact quantities for which standard symbols are needed. It is recommended, however, that workers in these fields should pay more attention to the use of a consistent notation. They also considered that the essential preliminary to a standard notation is a precise definition of each concept for which a symbol would be required, and that advantage would come in, thus eliminating the present necessity to define terms anew in each contribution to fish population dynamics.

#### General Conclusions

The group did not feel that any definite statements could be made as to the absolute time required to make assessments in particular cases with any given accuracy. However, during our discussions certain general principles emerged. These are detailed below, with the recommendation that the Committee consider whether they might help to guide the planning of investigations of stocks in the ICNAF area.



1. The trend of research is increasing emphasis on the detailed analysis of the structure of exploited fish populations, in order to understand the rates of the separate processes of reproduction, growth and mortality, with a view to deducing expected general changes in the populations with changed conditions. The eventual aim is, however, once these processes are understood, to return as far as possible to simple but well founded methods of stock evaluation, and devise sensitive measures of stock changes.

2. It is highly desirable that as many methods as possible be used to estimate each vital rate, to provide checks on the value obtained and to bring to light unsuspected sources of error or bias in any one method. It is important that the relative accuracies of the different methods be determined under varying conditions and, if possible, confidence limits established. There is also an urgent need for means of assigning some measure of precision to predictions of changes in catch characteristics expected to result from changes in fishing. To do this effectively will require direct observation of the important natural factors that may disturb the predictions, and a procedure for allowing for as many of these factors as possible in the calculations. It would be an essential part of such a procedure that year by year estimates would be made of the rates of growth and mortality, and an index of recruitment. In addition, more efficient methods are required for determining which of the factors external to the stock, considered a priori as relevant, do in fact have significant effects.

3. The group considered the general question of reducing the variance in sample data from which vital rates are to be estimated. There should be a dual approach to this problem by the improvement of sampling methods, and by seeking very much more knowledge of the inherent variation among the fish and the actual causative and controlling factors in recruitment, growth and mortality. The biological studies should preferably be made with the definite aim in mind that the results will be incorporated in equations describing the dynamics of the population. Concerning the reduction of time to make assessments, it was concluded that time could be saved proportionately with the extent to which a wide variety of different kinds of data could in this way be brought to bear on each problem.

4. The group was impressed by the importance of taking into account some estimate, no matter how rough, of all the vital rates, in assessing the condition of a fishery. Arguments that have been based, for example, on observations simply of a slow or fast growth rate, are especially misleading, and we have seen that, paradoxically, strongly biased estimates of growth and mortality can in certain situations (where the bias is of the same kind in both estimates) be more useful than an accurate estimate of either one of these rates alone.

5. The group considered that insufficient attention has been given to the distinction between true vital rates in the population and the estimates of those rates from samples, and examination of the theoretical relation between the true and estimated values. It is most important that the procedures in computing parameters from data be complementary to the calculation of predicted catch characteristics from the parameter values. If this practice is followed rigorously it will often be possible to make approximate evaluations when complete information is unobtainable.

6. It seems that the basic principles of those methods for estimating vital rates that depend on analysis of changes in catch characteristics or other quantities with time (for example, the plotting of annual values of total mortality against the corresponding values of fishing intensity to estimate the fishing and natural mortality rates separately), can be applied equally to differences with sex and age of fish or with location, and perhaps also with species. This offers important opportunities for saving time in evaluation and for increasing confidence in conclusions. Development of these comparative methods is most desirable.

7. Much of the emphasis during the discussions was on the determination not of particular quantities such as the "maximum sustainable yield", nor even of absolute values of catch at different levels of fishing or with gears of different selectivities, but of direction of change in steady catches, their composition, and the catches per unit effort, with changes in the fishing intensity and selectivity. The group was then concerned with the topography, near the point of observation, of diagrams in which the important catch characteristics are plotted simultaneously against measures of the two independent variables of fishing mortality and age or size at first liability to capture by the gear. Some results of examining this topography have been mentioned, but there is much more to be done along these lines, including the analysis of situations where one or other kind of information is lacking, by considering the limiting possible values of the unknown parameters. This approach to stock assessment presents also new problems in graphic presentation of the results.

8. The group paid some attention to the importance of measurements of fishing effort. There has been in recent years much refinement of measures of effort and intensity for biological purposes, with the aim of getting values that are proportional to the fishing mortality caused in the stock, but these are not necessarily more useful for economic evaluation than the earlier crude measures. Although accurate fishing intensity statistics will always be essential, values of fishing intensity to relate to mortality, when a stock is being fished by a number of different types of vessel and gear, can be obtained from effort statistics of some homogeneous part of the whole fleet that covers a fairly large proportion of the fished area. These statistics can be used to

convert the catches of the whole fleet to give values of total effective efforts. It is desirable to explore further the possibilities of using such a method, as a way of overcoming some of the difficulties of converting effort statistics for different parts of the fleet (especially those using gears having differing selectivities) to standard units. If, eventually, "sample" methods of the kind described can be used to minimize the work involved in producing routine statistics of standard fishing intensity, then more attention could be paid to securing the very desirable wide sample coverage for species, sex, size and age composition of the catches, and also to obtaining the wide range of data on the different phases of the fishing operations necessary to develop the measures of real total fishing effort (including, for example, manpower, time of travel to and from fishing grounds, turnaround at port, loss of fishing time at sea through various causes, etc.) necessary for a full understanding of a fishing industry.

9. The group recognized the especial importance to this subject of good definition of concepts, terminology and notation.

#### SPECIFIC RECOMMENDATIONS

The group recommends:

1. That greater attention should be given to methods of using characteristics of the catches such as species composition, sex ratio, average size and range of size of fish, to indicate changes in the stocks and hence point to possible effects of fishing.
2. Encouragement of research on the causes of natural mortality in fish stocks, and their relative importance.
3. Collection and prompt tabulation and dissemination of statistical data on fishing effort, total catches (including fish rejected at sea), and their species, sex, size and age compositions, over all sections of a fishery and broken down by as small areas and time intervals as practicable.
4. Consideration of the possibility of increasing knowledge of growth by direct study of the natural food populations and by experimental study of growth variations in fishes and their causes; development of techniques for comparison of growth in different stocks, or of different species.
5. Further study of the significance of the external appearance of fishes in indicating their relative ages.

6. Further study of the problem of relating egg production to subsequent recruitment, and of the environmental influences on larval mortality.

7. Further attention to the possible interdependence of the rates of mortality and growth in fish stocks.

8. Further examination of the possibilities of drawing useful conclusions about the expected direction of changes in the size or composition of the catch, following changes in the amount or selectivity of fishing, even when the available data are inadequate for full analytical treatment.

- (a) As an aid to diagnosis of the condition of stocks that calculations should be made, and diagrams prepared, of upper and lower values of natural mortality such that if the true natural mortality, though unknown, is between these values then certain conclusions can be drawn as to the probable effects of changes in the amount or selectivity of fishing. These calculations should cover a wide range of values of total mortality, growth rate and age at recruitment.
- (b) Calculation of the ratio of the weight of individual fish at entry to the exploited phase to the average weight of fish in the catch, and comparison of this ratio with the observed ratio of the fishing to the total mortality for any fishery for which mesh or similar regulation might be contemplated.
- (c) Investigation of the problem of using length and weight compositions of catches more extensively as a substitute for age composition in assessment of fish stocks.
- (d) Investigation of the extent to which undetected bias in age determination may be expected to lead to important errors in assessing stocks.
- (e) Further study of the general problem of the extent to which simple population models can be used to represent complex situations without important errors being made in predicting the effects of changes in the amount or selectivity of fishing on the catch and its various characteristics.
- (f) Attention to methods of interpreting variations in morphological and meristic characters, data on effort, catch and catch composition, and marking experiments, for the purpose of analysing patterns of movement in fish stocks and of detecting or predicting the existence of stocks outside the fished area.

9. Further study of the practical significance, in evaluating stocks of a greater or lesser degree of interdependence between them, and development of methods for determining the degree of interdependence.

10. Close study of the expected dependence of various characteristics of the annual catches on possible kinds of transient or sustained changes in fishing or particular environmental factors, with the object that the more sensitive of these characteristics might be used for testing whether or not regulative measures are having the expected effects, and for detecting unexpected changes in the stocks.

11. Continuing the development of population models that can make full use of all estimates of population parameters and which can also incorporate a wide variety of data relating to environmental factors.

12. That FAO be asked to circulate proposed definitions of the fundamental terms used in studies of population dynamics to research workers in member countries of ICNAF, to receive comments and suggestions on these and to make available a reference list of these definitions.

13. That the Committee should consider proposing the adoption of the appended notation as a standard for workers in the ICNAF region and especially in documents submitted to the Commission for discussion at meetings or for publication.

14. That the Committee consider whether certain general principles which emerged during the discussions of the Working Party might help to guide the planning of investigations of stocks in the ICNAF area. The suggestions related to:

the importance of detailed analysis of the structure of exploited fish populations;

the use of several methods to estimate mortality and growth rates and the development of means for assigning measures of precision to predictions of changes in catch characteristics expected to result from changes in fishing;

the improvement of sampling methods and complementary biological studies of the causative and controlling factors in recruitment, growth and mortality;

the development of methods of using the differences between fish or stocks of different kinds or ages or in different places, as well as changes in

stocks with time, to estimate the vital rates;

emphasis on the estimation of the direction in which, and by how much, the catch will change with a given kind of change in the fishing, rather than the estimation of particular theoretical quantities such as the "maximum sustainable yield";

the importance of catch statistics and of measurements of fishing effort;

and definition of concepts, terminology and notation.

#### RECOMMENDED NOTATIONS

Instantaneous total mortality coefficient	Z
Instantaneous fishing mortality coefficient	F
Instantaneous natural mortality coefficient	M
Annual fraction surviving (survival rate)	S
Observed annual fraction surviving	s
Total number of fish in the exploitable phase of the stock	N
Total weight of fish in the exploitable phase	P
Number of fish in the catch	C
Weight of fish in the catch	Y
Number of recruits entering the exploitable phase	R
Fishing effort	g
Effective overall fishing intensity	f
The ratio between the best index of effective overall fishing intensity, and the resulting instantaneous fishing mortality coefficient	q
Length	l, L
Weight	w, W
Age at entry to the exploitable phase	$t_r$
Age at entry to the exploited phase (i.e. first liability to capture)	$t_c$
Length at entry to the exploited phase	$l_c$
Suffix denoting the value of a parameter:	
at a particular time	t
relating to a particular age of fish	n
during a particular year	x
Parameters of equations describing growth of fish:	
use preferably the symbols adopted by the author of the particular equation, if these do not conflict with the above symbols.	
E.g. $L^\infty$ $W^\infty$ and K in von Bertalanffy's equation.	

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\* Paper not published in this volume.

Holt, S. J.

- The evaluation of fishery resources  
by the dynamic analysis of stocks,  
and notes on the time factors in-  
volved.



R. J. H. Beverton and J. A. Gulland.

A key factor influencing the planning of fish population research is the extent to which fishing is influencing the stock. One possible method of obtaining information on this involves estimation of the magnitudes of fishing and natural mortality. This contribution is concerned with the estimation of mortality, and the use of these data for purposes of assessment, when only a part of a stock is fished.

### Introduction

The use of theoretical models is now an accepted technique in the study of the dynamics of exploited fish populations. It is recognized that any theoretical model must, in some respects, be a very much simplified representation of reality, and consequently the conclusions drawn from such models are treated with due caution. What is sometimes rather less obvious is that certain of the parameters contained in the model are themselves abstractions, in the sense that they cannot be measured by direct observation but have to be estimated by means of assumptions similar to those on which the model itself is based. Of special importance in this connection are mortality rates, and in reviewing the methods available for mortality estimation, Beverton and Holt (1956) have stressed the fact that mortality rates cannot be estimated unless, in effect, a model is set up to represent what are thought to be the processes of death in the population and their dependence on causal factors including, in particular, the fishing activity.

The main source of information on mortality in exploited fish populations is the size and age composition of the catch, and the way in which these properties vary with the magnitude and characteristics of the fishing activity. In what may be termed the simple theory of fishing, the structure of the catch is taken as representative of that of the population, and mortality rates are assumed to be constant with respect to age. These assumptions are unavoidable if there is no information to prove them false as is often the case; and, of course, if they are indeed true then mortality estimation is straightforward.

There are two main factors which may cause these assumptions to be invalid. One is differential selectivity of the fishing gear for fish of different sizes, or a tendency of the fleet to concentrate its activity on certain sizes of fish in preference to others (see Beverton and Holt, *ibid.* for some examples). The other is partial "coverage" by the fleet of the whole population, i.e. as distinct from preferential concentration on fish of certain sizes. The instances of this which have been examined so far appear to be restricted to seasonal

fisheries for migratory species, where it is referred to as "partial availability". Examples are the California sardine fishery (Widrig, 1954) and the British Columbia herring fishery (Tester, 1955); and in such cases partial availability is manifest as high variability of apparent mortality rates measured between adjacent years.

Partial coverage exists, however, in some degree, in nearly every fishery, whether seasonal or continuous, even if it means only that part of the population is more heavily fished than the remainder. Beverton and Holt have put forward the concept of an "effective overall fishing intensity",  $\tilde{f}$ , to provide a measure of fishing effort which, in these circumstances is proportional to the true fishing mortality coefficient in the whole population.

The question remains, however, whether this true fishing mortality coefficient would be correctly estimated by random catch sampling when there is partial coverage; and, if not, then what kind of errors are likely to be involved and what effect they would have when making assessments. We have begun a theoretical study of this problem, and some preliminary results are reported here.

#### Methods

An analysis of the relation between fishing effort and the apparent fishing mortality coefficient estimated from catch samples where partial coverage exists, must take some account of the process of interchange or mixing of fish between various parts of the whole area containing the fish population. This is a phenomenon about which relatively little is known and measurement of which involves considerable practical difficulties. We are therefore attempting to delimit the problem by examining the properties of theoretical models in which part of the population is covered by the fleet and which incorporate a mechanism of interchange of fish between the fished and unfished parts. Our procedure is to compute, for a range of conditions, the apparent mortality rates that would be estimated from catch samples taken from the fished area, and then to use these estimates to assess the state of the population by means of simple yield equations which assume complete coverage of the population by the fleet. The resulting picture is then compared, in each case, with the true yield curve which represents what would actually happen in the case in question.

It is, of course, unlikely (though not impossible) that the particular numerical results thus obtained would be applicable to any actual fishery. But we believe that examining, for a range of theoretical cases, the consequences of making just those assumptions (e.g. complete coverage) which are often un-

avoidable in practice through lack of information, can at least indicate the broad range of conditions where the simple theory is most likely to break down. The conclusions may therefore serve as a guide both to the interpretation of past data and the most effective planning of future research.

As an example of this principle we may mention two extreme cases which need no elaborate theory for analysis. These are: (a) when the rate of interchange between the fished and unfished areas is very rapid, and (b) when interchange is very slow. In the former case, catch samples taken from any part, however small, of the stock will give estimates of the true mortality rate in the whole population. In the latter, catch samples will give only the mortality rate in the fished area, but this, because of the slow rate of interchange, can be treated independently of the remainder. In either event, using these mortality estimates in simple yield equations will give correct assessments of the change in yield to be expected from any postulated change in fishing effort.

#### The Theoretical Model

From the foregoing it will be seen that the important cases are those in which the rate of interchange is neither very fast nor very slow. The mathematical treatment of interchange which we have used is that developed by Beverton and Holt (1957). This is based on the assumption that the rate of movement of fish out of a specified area can be defined by an instantaneous coefficient called the transport coefficient and denoted by  $T$ . The value of  $T$  depends on the intrinsic rate of dispersion of fish and also on the size and shape of the area to which it refers, in fact, on its perimeter to area ratio. This method can be regarded as an approximation to the much more complex theory of random dispersion which has been employed by Skellam (1951), and some preliminary studies have shown that the approximation is likely to be a satisfactory one in most cases.

The basic differential equations defining the balance between the numbers of fish in adjacent parts of the whole area, one of which (a) is fished and the other (b) unfished, are:

$$\frac{dN_a}{dt} = - (F + M + T_a) N_a + T_b N_b \quad . . . . . (1)$$

$$\frac{dN_b}{dt} = - (M + T_b) N_b + T_a N_a \quad . . . . . (2)$$

In this pair of equations  $F$  denotes the fishing mortality coefficient in the fished area (a), and  $T_a$  and  $T_b$  denotes the respective transport coefficients. The

value of the natural mortality coefficient  $M$  is assumed the same in both areas and is taken as 0.1. If  $R_a$  recruits enter area (a) at a certain age, and  $R_b$  recruits enter (b) at the same age, the solution of (1) and (2), giving the number present in each area at any subsequent age  $t$ , is:

$$N_a = R_a e^{-pt} \left( \cosh qt - \frac{(F + T_a - T_b) \sinh qt}{2q} \right) + \frac{R_b T_b (\sinh qt) e^{-pt}}{q} \dots (3)$$

$$N_b = R_b e^{-pt} \left( \cosh qt + \frac{(F + T_a - T_b) \sinh qt}{2q} \right) + \frac{R_a T_a (\sinh qt) e^{-pt}}{q} \dots (4)$$

where  $p = \frac{1}{2}(F + T_a + T_b) + M$

$$q = \sqrt{\frac{(F + T_a - T_b)^2}{2} + T_a T_b}$$

Computing these equations for integral values of  $t$  gives the age composition of fish in the fished area, as would be measured from catch samples obtained by a non-selective gear.

We describe here the results of two cases only; no final conclusions can be drawn from these alone, but they serve to illustrate the procedure we adopt and the kind of results that can be reached. In each case we assume a uniform density of recruitment throughout the area, so that the values of  $R_a$  and  $R_b$  are in the ratio of the sizes of the areas (a) and (b). The rate of interchange used is that which, when areas (a) and (b) are equal, gives values  $T_a = T_b = 1$ . This means that if fish were initially present in one area only, and were removed as soon as they entered the other area, about 65% would cross the boundary in a year. The difference between the two cases lies in the way in which an increase in fishing effort in area (a) is manifest. Thus in case (i) we assume that a constant fraction (1/5) of the whole area is fished and that increasing effort has the effect of increasing the fishing intensity (and hence the true fishing mortality coefficient) in the fished area. In case (ii) we assume the converse, that is, an increase in effort causes the fished area to increase but leaves the fishing intensity and true fishing mortality coefficient in the fished area unchanged.

### Results

Case (i). Fig. 1 shows the age compositions plotted on a logarithmic scale

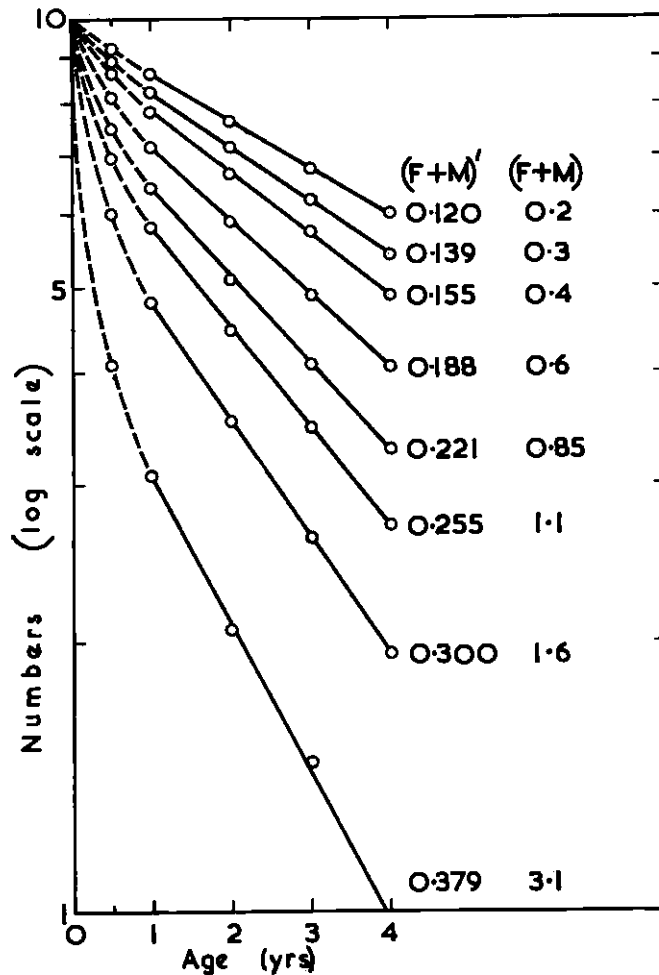


Fig. 1. Hypothetical examples of age compositions of catches obtained by fishing a small constant fraction of a stock with various fishing intensities [case (i)]. The apparent total mortality coefficients  $(F + M)'$  deduced from the slope of the catch curves are tabulated in the left-hand column of figures; the true coefficients in the fished area are shown in the right-hand column.

that would be obtained from catch samples for various values of true total mortality coefficient  $(F + M)$ , as would result from increases in fishing effort. It will be noted that they are curved during the first year of life, when depletion

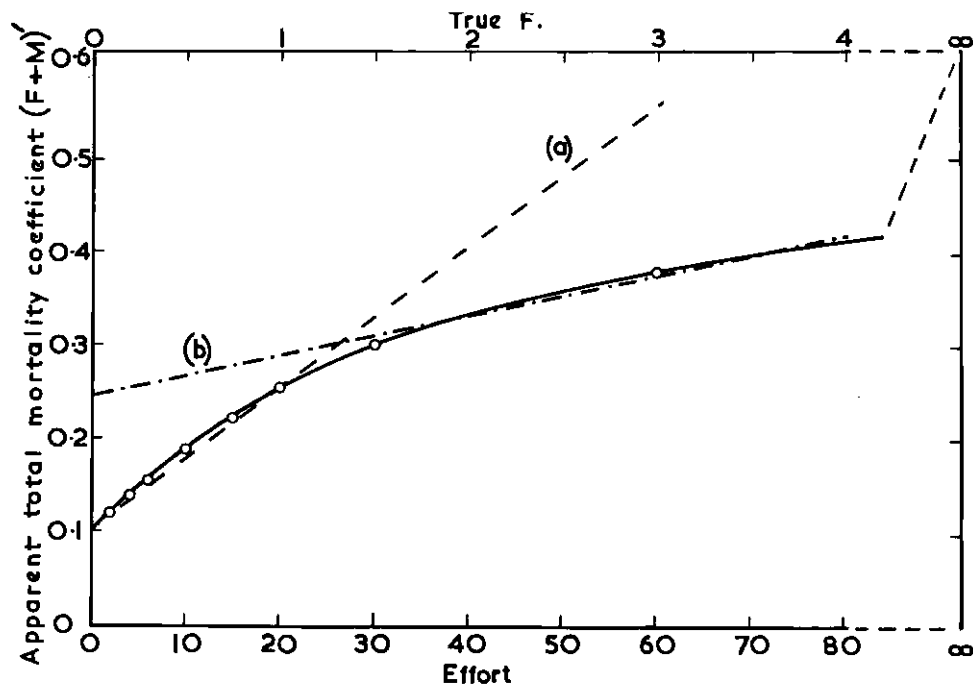


Fig. 2. Relation between apparent total mortality coefficient  $(F + M)'$  from Fig. 1 and fishing effort, for case (i). Two possible linear regressions are shown by broken lines; (a) as might be fitted to data up to 30 units of effort, (b) to data above 30 units of effort.

exceeds replenishment from the unfished area. After about a year, however, a steady-state is achieved, and thereafter the catch curves fall very close to a straight line in every case; certainly, if these were actual data there would be no hesitation in interpreting them as linear. Their slopes give the estimates of apparent total mortality rate  $(F + M)'$  listed in the left-hand column of figures; these, it will be noted, are all very much less than the true values in the right-hand column, although both sets of estimates increase together.

We now suppose that the relation between these estimates of apparent total mortality coefficient  $(F + M)'$  and the corresponding fishing effort is examined, in order to obtain an estimate of  $M$  alone. On the simple theory of mortalities this relation should be linear, the intercept on the Y-axis providing the estimate of  $M$  (see Beverton and Holt, 1956 Widrig, 1954 and Tester, 1955). Fig. 2 (full line) shows the value of  $(F + M)'$  plotted in this way against arbitrary units

of effort, the latter being such that 100 units of effort applied to the whole area would generate a fishing mortality coefficient of unity. It will be seen that the relation is curvilinear and tends to an asymptotic value as effort tends to infinity; this asymptote is, in fact, the value of  $(T_b + M) = 0.6$ , since with an infinitely high effort the structure of the catch (except initially) is determined only by the rate of transport from that area and the natural mortality rate.

We now have to decide how the data shown in Fig. 2 would be interpreted in practice, remembering that observed points are likely to have considerable scatter. If a sufficient range of effort has been experienced it might be possible to detect curvilinearity; more probably it would be thought that a linear regression would give a satisfactory representation of the data, especially as linearity would be expected from simple theory. Suppose, for example, that efforts up to only 30 units had been experienced; the regression drawn might then be that shown as (a) in Fig. 2. This passes through an intercept of 0.1, thus giving a correct estimate of  $M$ ; but it also implies that over the range of effort from 0 to 30 the fishing mortality coefficient ( $F'$ ) increases from zero to about 0.2. In fact, the true value of  $F$  in the fished area increased from 0 to 1.5. Suppose, nevertheless, that this range of  $F'$  (0 to 0.2) and an  $M$  of 0.1 are used in a simple yield equation (e.g. Beverton, 1953) to compute a yield-effort curve\*; the result is that shown by the broken curve in Fig. 3 (a). Now the true yield curve in these circumstances, calculated from the theoretical model described above for the range of true  $F$  from 0 to 1.5, but with otherwise identical parameters, is shown in Fig. 3 (a) by the continuous curve. It is seen that the two are very similar, and evidently, in this case, a true enough picture would be obtained by proceeding throughout on the assumption that the fishery did, in fact, cover the whole population.

A very different result is obtained, however, if it is supposed that only the upper range of fishing efforts, i.e. from 30 to 60 units, had been experienced. Over this range the apparent total mortality coefficient  $(F + M)'$  increases only slowly, and a regression fitted to data, such as that shown by the broken line (b), would give a larger intercept than before. In this case it would seem that the fishing mortality coefficient  $F'$  was no larger than about 0.15 even when 60 units of effort are applied, and that the natural mortality coefficient had a value of about 0.25. The simple yield curve that would be constructed in this case is shown by the broken curve of Fig. 3 (b), together with the true yield curve (full line) which is, of course, identical to the full line (a) of Fig. 3 (a). There is now marked divergence between the true and the predicted yield curves, and the false conclusion would be drawn from the latter that the yield from the fishery

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\* The parameters used are those derived for North Sea plaice, which serve as well as any for the present purposes, although this fishery is not one in which partial availability is important.

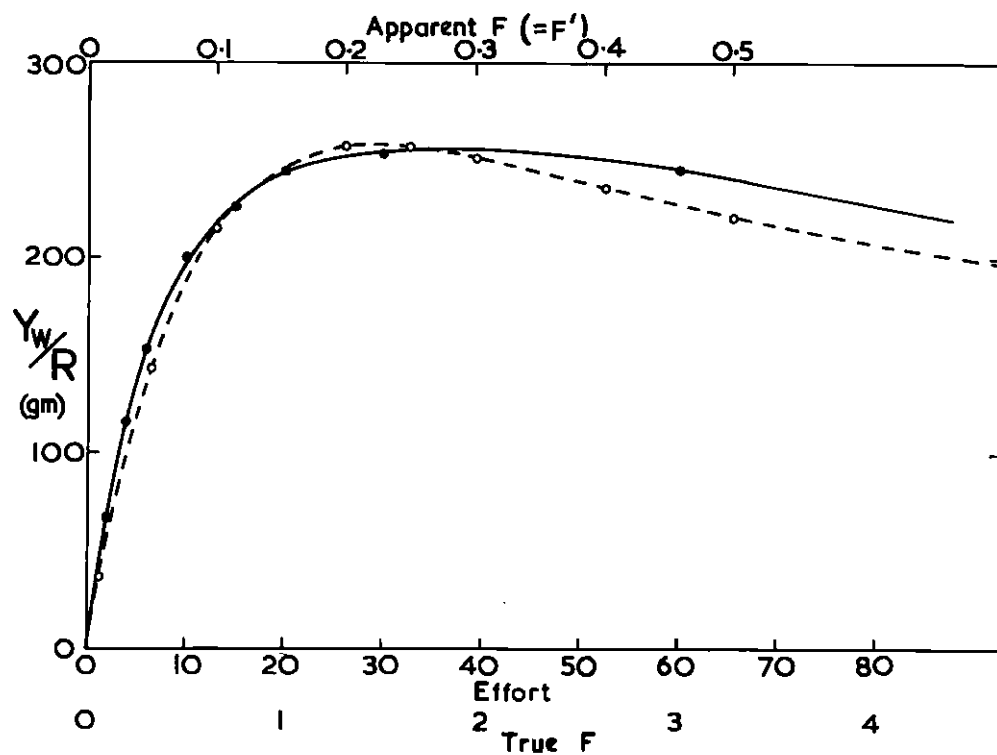


Fig. 3 (a). Relation between equilibrium yield per recruit and fishing effort for case (i). The broken line is the yield curve obtained by assuming that the whole of the stock is fished, using the relation between fishing mortality and effort defined by regression (a) of Fig. 2 ( $M = 0.1$ ). The full line shows the "true" yield curve in these circumstances, which takes account of the interchange of fish between the fished and unfished parts of the stock. It will be noted that the two curves are of similar shape.

could be increased by further expansion of effort; in fact, the yield would fall with efforts greater than about 30 units.

Case (ii). For this we maintain the true fishing mortality coefficient  $F$  in the fished area at a constant value of 3.0, this relatively high value serving to emphasize any discrepancies between predictions from simple theory and the true course of events. Increases in effort have the effect only of increasing the size of the fished area, the same arbitrary units of effort being used as in Case (i).



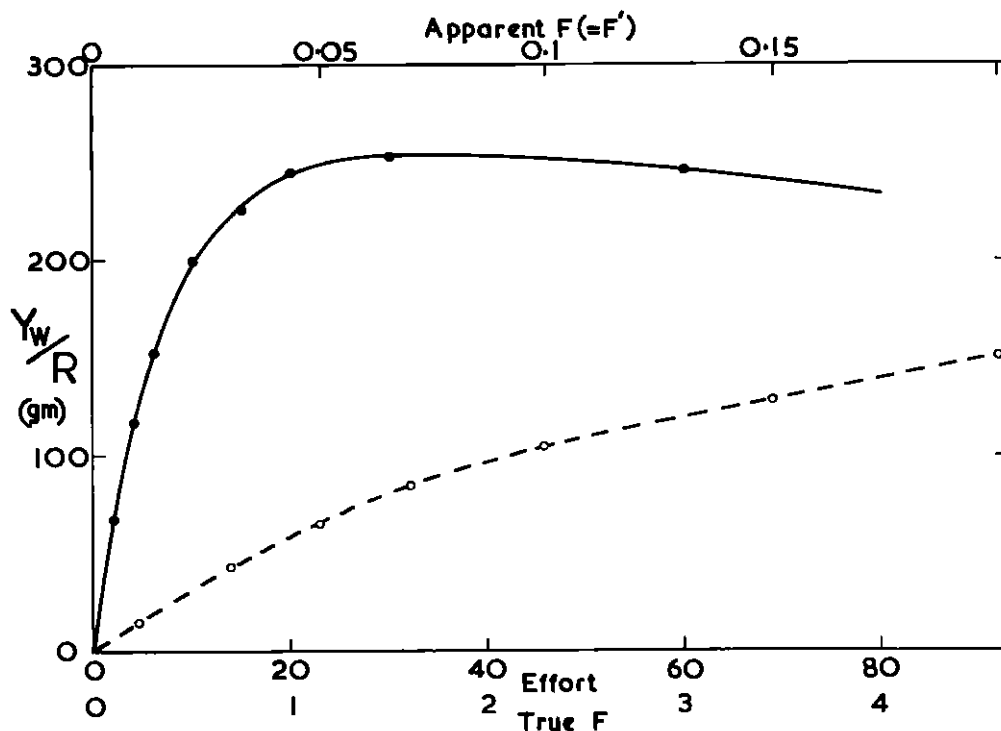
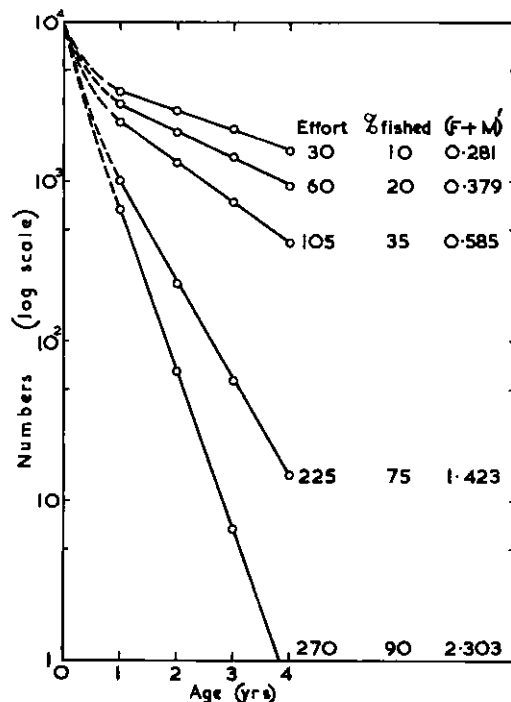


Fig. 3 (b). Relation between equilibrium yield per recruit and fishing effort for case (i). This is similar to Fig. 3 (a) except that the broken line is the yield curve obtained from the relation between fishing mortality and effort defined by regression (b) of Fig. 2 ( $M = 0.25$ ). As in Fig. 3 (a), the full line shows the "true" yield curve, and in this case the two differ considerably.

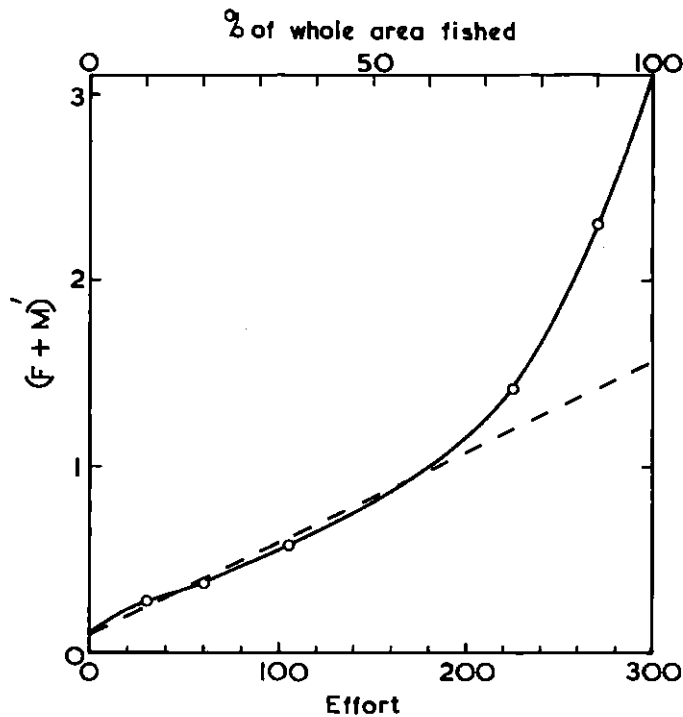
Fig. 4 shows the age compositions for various fishing efforts, the corresponding percentage which the fished area is of the whole being tabulated alongside. The shapes of these catch curves are broadly similar to those of Fig. 1, being effectively linear after the first year of life. The apparent total mortality coefficients  $(F + M)'$  estimated from the slopes of the catch curves are given in the last column of figures. The plot of  $(F + M)'$  against effort is shown in Fig. 5. The actual relation is indicated by the continuous line and is quite different from that of Fig. 2; in particular, the curve terminates at an effort of 300 units, since at this point the whole of the area is fished and the value of true  $F$  is 3.0. Here also the observed  $(F + M)'$  equals the true value (3.1).



**Fig. 4.** Hypothetical examples of age compositions of catches obtained when the result of increasing effort is to increase the fished fraction of the stock, the fishing intensity in the fished area remaining constant [case (ii)]. The apparent total mortality coefficients  $(F+M)'$  deduced from the slope of the catch curves are shown in the right-hand column of figures.

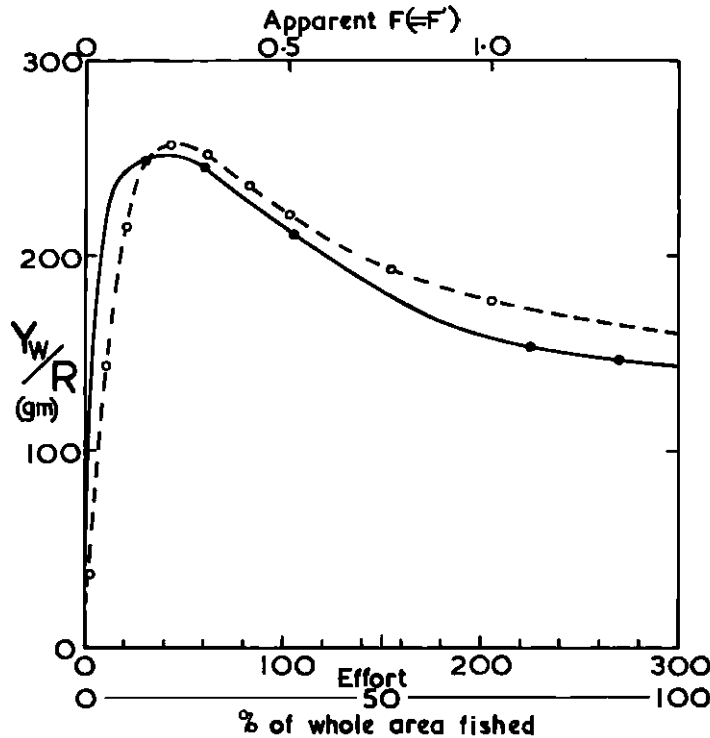
The practical interpretation of the relation between apparent total mortality coefficient and effort depends on the range of effort covered by the data. If efforts up to only some 150 units had been experienced (i.e. up to one half of the whole area is fished), the data would be well represented by a linear regression as shown, giving a correct estimate of  $M$  of 0.1. Using this value of  $M$  and the relation between  $F'$  and effort defined by the regression, gives the predicted yield-effort curve shown by the broken curve of Fig. 6. The true yield-effort curve for this case is shown by the continuous line, and it is seen that the agreement is close.

If catch samples were available only for efforts between 150 and 300 units, i.e. when more than half the area is fished, estimates of apparent total morta-



**Fig. 5.** Relation between apparent total mortality coefficient  $(F + M)'$  from Fig. 4 and effort, for case (ii). Where up to 60% of the whole area has been fished, the data would be adequately represented by the regression shown by the broken line. Where between 60% and 100% of the area has been fished, the relation is markedly curvilinear.

lity coefficient  $(F + M)'$  would increase more rapidly than the effort. Thus, attempting to fit a regression over this range of effort would give a negative intercept which would, obviously, be unacceptable. The only possible conclusion would be that the relation between mortality and effort expected from simple theory had broken down -- which is correct. But it is quite possible that the cause of this breakdown would be wrongly diagnosed unless, of course, the change in area fished was known and its implications understood. For example, the rapid increase of  $(F + M)'$  with effort towards the right-hand side of Fig. 5 might be thought due to incorrect measurement of effort; or it might be assumed that a gradual increase in the natural mortality rate had occurred during the period when the fishing effort had been increasing. Even more con-



**Fig. 6.** Relation between equilibrium yield per recruit and fishing effort for case (ii) [broken line] assuming that the whole of the area is fished, and using the relation between fishing mortality and effort defined by the linear regression of Fig. 5. The full line shows the "true" yield curve, taking account of partial availability, the two being of the same general shape.

fusing would be the result of attempting to relate the estimates of  $(F + M)'$  to the fishing intensity, i.e. the effort per unit area, which remains constant throughout. Yet such a procedure is correct if fishing is always spread over the whole population and it is the latter which is increasing its living area.

#### Interpretation

This is best presented for each case separately with reference to the

appropriate relation between apparent total mortality coefficient  $(F + M)'$  and effort, i.e., Figs. 2 and 5 respectively.

We first recapitulate the definitions  $F$  and  $F'$ , namely:

$F$  = the true instantaneous fishing mortality coefficient in the fished area, which measures the local rate of depletion due to fishing.

$F'$  = the apparent fishing mortality coefficient as estimated from the age-structure of catch samples taken from the fished area.

and add a third, namely:

$\tilde{F}$  = the effective overall fishing mortality coefficient. This defines the ratio which the catch is of the whole population. When applying the simple theory it is implied that  $F'$  is, in fact, an estimate of  $\tilde{F}$ .

Case (i), Fig. 2. A small constant fraction of the whole area is fished with a range of efforts (and hence of values  $F$ ).

- (a) On the left-hand side of Fig. 2,  $F$  is small compared with the rate of interchange between the fished and unfished areas. Hence the effect of fishing is spread fairly evenly through the whole population, and  $F'$  is nearly proportional to  $\tilde{F}$  and of roughly the same magnitude, although very much smaller than  $F$ . Hence also  $F'$  is roughly proportional to effort, and substantially correct results are obtained from the simple theory (Fig. 3a).
- (b) On the right-hand side of Fig. 2,  $F$  is large compared with the rate of interchange, and the structure of the catch is determined largely by the rate of immigration into the fished area. Hence  $F'$  is no longer proportional to  $\tilde{F}$ , the natural mortality rate is overestimated, and the simple theory breaks down (Fig. 3b).

Case (ii), Fig. 5. Varying fractions of the whole area are fished with a high constant fishing intensity.

- (a) On the left-hand side of Fig. 5 the fished area is a relatively small fraction of the whole, and  $F$  is large compared with the rate of interchange. This is the same situation as in Case (i) (b) and, as in that case, the structure of the catch is determined mainly by the pattern of immigration from the unfished area. Now, however, an increase in effort at once reduces the contribution of immigration, because it reduces the size of the unfished part of the population relative to the fished.

Thus the value of  $F'$  responds to an increase in effort [unlike Case (i) (b)], and also reflects a similar change in  $\tilde{F}$  sufficiently well for the simple theory to be applicable (Fig. 6).

- (b) On the right-hand side of Fig. 5, the fraction which the unfished area is of the whole is being rapidly reduced by a given incremental change in effort, and as a consequence  $F'$  is rapidly increasing to take on the same value as  $F$  when the whole area becomes fished. Over this range when  $F'$  is increasing rapidly it is not proportional to effort, and the simple theory breaks down.

### Conclusions

We must now see whether these kinds of results, obtained as it were by experimentation with theoretical models, can be of any practical use in population research.

It would seem possible to draw certain general conclusions even from the limited investigations presented here. One is that application of simple theory is most likely to break down when a relatively small fraction of a population is heavily fished. In these circumstances, the tendency will be to overestimate the natural mortality rate, which may perhaps lead to the conclusion that more fishing would produce a greater yield whereas, in fact, the opposite would be true. Where increases in the fishing effort have also increased the fished fraction of the population, application of simple theory is likely to give more correct assessments of the reaction of the population to fishing; or perhaps to give results which are obviously unacceptable (e.g. a negative natural mortality rate). It may be noted that the value of  $F$  assumed in Case (ii), 3.0, is perhaps higher than would usually be found in practice; values below about 1.0 were found to give results which were adequately represented by simple theory throughout the range of effort.

Qualitative deductions of this kind are of some help, and more comprehensive results than are given here may enable certain fisheries to be classified into those to which simple theory can, or cannot, be safely applied, even without further information.

The many intermediate cases of partially fished stocks require, however, a more specific appreciation. The key factors are evidently the relative magnitudes of the local fishing rate ( $F$ ) and the rate of interchange of fish between the fished and unfished areas; while the existence of a large reserve of fish supplying immigrants to the fished area, and the effective amount of that immigration,

is indicated by the extent to which the local fishing rate exceeds the estimate of mortality from catch samples.

It might be possible, by means of tagging experiments in the fished area combined with catch sampling, to estimate these factors well enough, in quite a short time, to establish whether simple theory can be safely applied. This can certainly be done in theory, and provided that tagging techniques can be used, this procedure would probably give much quicker results with far less expense than attempting to measure the true abundance and structure of the whole stock by experimental fishing surveys outside the fished area even if this were practicable.

Finally, we would mention again the importance, when simple theory is applied to complex situations, of adhering consistently to the same simplifying assumptions both when estimating parameters from data and also when using those estimates in the theoretical model for assessment. In those instances above where simple theory is found to give adequate representation of reality, both the mortality estimates and the model in which they are used are unreal, but they are each unreal for the same reasons and to roughly the same degree. The same applies to the mechanism of interchange on which the models described here are based; this is obviously a simplification of what would be found in practice, but the possibility of error is much reduced by designing tagging experiments to measure the effective interchange based on the same assumptions.

There is, of course, no question that the methods described here can ever provide, in themselves, a complete understanding of the dynamics of a partially fished stock, for which it is essential to have information on the abundance and structure of the unfished part, and, in the long run, on the exchange between the fished and unfished parts. The relevance of this contribution is that it gives examples of ways in which useful working answers can sometimes be obtained when information available falls far short of what, ideally, would be considered necessary.

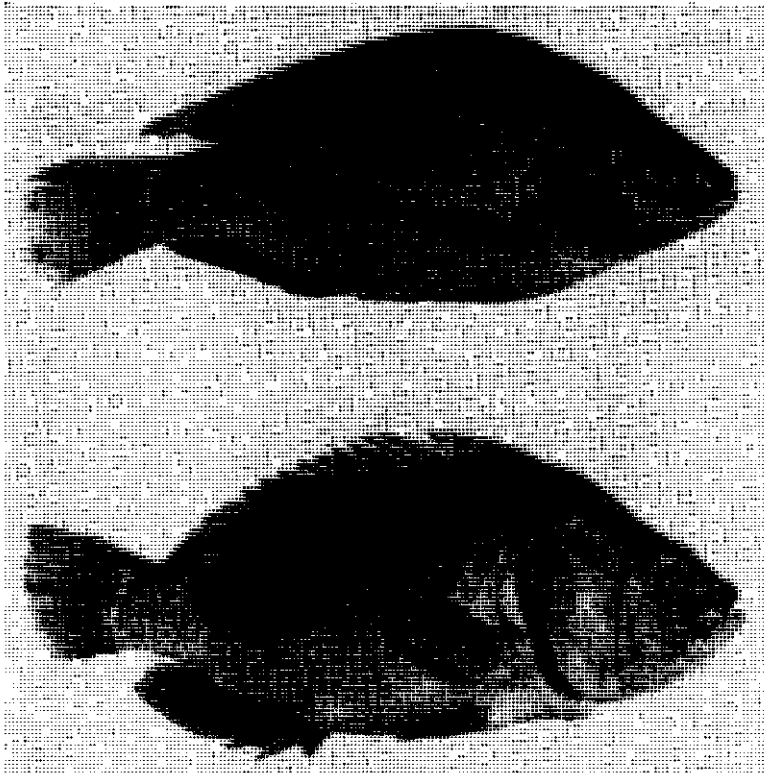
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Michael Graham.



**Fig. 1.** Tilapia esculenta. Above: A, yield 1250, catch per effort 5, younger. Below: B, yield 100, catch per effort 25, older.

Two similar gulfs of the Victoria Nyanza over 150 miles apart, separated by deep water and connected only by a long meandering coastline, each contained a population of Tilapia esculenta Graham (Fig. 1). The Kavirondo Gulf sustained a commercial fishery using gill-nets for fish typified by Specimen A: yield 1250 fish per night. The Emin Pasha Gulf sustained only an indigenous fishery using basketwork traps catching fish typified by Specimen B: yield, say 100 fish per night. Specimen B is obviously older than Specimen A. Experimental fishing in each gulf gave the average number per net per night: Kavirondo Gulf 5; Emin Pasha Gulf 25 (actually 27) and 25 was the catch per unit effort remembered for the early years in the Kavirondo Gulf.

There may be other areas in the world where, provided a comparison with virgin stock can be found, a diagnosis of a decline in catch per effort, as due to less growth and survival rather than to less reproduction can be reached very quickly and easily.

(Graham, Michael: The Victoria Nyanza and its Fisheries, pp. 10-12, Figs. 37-39, 43-45: Crown Agents, London, 1929)

J. A. Gulland.

Author's Abstract.

In a recent paper Widrig (1954) drew attention to considerable confusion in the notation used in fish population studies. Hardly any measure has had the same symbol attached to it by all workers, and up to four different symbols have been used for the same measure. The present meeting would be a suitable occasion to agree on some uniform system. The suitability of a system of notation may be judged by the manner in which it fulfils certain conditions, some of which are:

- (i) The relevant formulae can be expressed in simple and compact form, which is easy to write, type and print. (The need for easy typing makes Greek letters rather undesirable).
- (ii) Similarity between measures is reflected in the notation, e.g. capital and lower case letters for the same measure in population and sample, adjacent letters in the alphabet for similar measures.
- (iii) Relationships between measures are not obscured, e.g. an extra symbol used for a simple function of other symbols, or widely different letters used for similar measures.
- (iv) The new notation fits in with the established notation of mathematics and statistics.
- (v) The new notation differs as little as possible from the system at present in use.

A table is given of the notation used by the following authors:

Ricker, W. E. (1948).

(I have also consulted the MS of the revised version).

Beverton, R. J. H. and S. J. Holt (1957).

Parrish, B. B. and R. Jones (1953).

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Each quantity is then discussed in turn, and a standard system of notation is suggested.

J. A. Gulland.

The sampling problem as considered in this paper will be mainly concerned with the information obtainable from the activities of commercial fishing vessels. Such information regarding the size and composition of the catch, and the amount of fishing, may permit estimates to be made of the relative size and composition of the stock; also, in certain circumstances, of the absolute size of the stock, and the mortality caused by the fishing. These estimates, used with a suitable theoretical model will enable prediction to be made of the effect of any changes in the fishery, e.g. size limits or mesh regulations. In a simple fishery the catch may be a random sample of the stock (except, of course, for fish below marketable size), and also the catch per unit of fishing effort may give an undistorted index of the density of fish. Hence, samples of the catch for size or age composition give the composition of the stock, and catch per unit effort gives the size of the stock. This simple theory has, of course, been applied to many fisheries, and developed to cover uneven special distribution of fish or fishing [e.g. Beverton and Holt (1957), Beverton and Parrish (1956), Widrig (1954), and the need for proper calibration of fishing effort (e.g. Beverton and Parrish, Gulland (in press))].

In many fisheries the relation of catch per unit effort to density (i.e. fishing effort to mortality caused) does not remain constant from place to place, or from month to month: even when on the same density of fish a standard unit of fishing effort will give varying catches. For such fisheries the systems of weighting by areas will not serve to give an undistorted estimate of density of overall fishing effort [c-f equations (2.2) and (2.4) of Gulland (1955)]. However, for any given level of stock abundance, the mortality caused, and also the effective fishing effort, will be in proportion to the total catch. If then there exists some section of the fishery for which, either directly, or through subdivisions by area and time, the catch per unit provides a consistent measure of stock abundance, this catch per unit effort, combined with a knowledge of the total catch gives the total effort. Many of the factors affecting the catchability of the fish, e.g. food, temperature, depth, shoaling, spawning, etc., vary widely from place to place, and from month to month, but are likely to be much the same at the same place and date from one year to the next. Thus, though for a fishery as a whole the catch per unit effort may be a poor index of stock abundance, it is probable that within one or more sub-divisions the catch per unit effort will give a good index of abundance, though the scale, i.e. the ratio of catch per unit effort to abundance will be different for each sub-division. The indices from different sub-divisions, if more than one gives a satisfactory index, may be best combined by expressing each as a percentage of the catch per unit effort in some standard year or years, as in the example in the following table. The sub-divisions used are here considered as being two seasons e.g. spawning and feeding.

Year	Catch Per Unit Effort					1955 as % of		
	1950	1951	1952	1953	1954	Mean	1955	50-54 mean
Season A	205	100	170	310	215	200	248	124
Season B	395	190	355	600	460	400	504	126

If the indices from the two seasons are given equal weight then the index of abundance for 1955 is 125. This procedure is, for suitable weighting, equivalent to standardizing the efforts in the two seasons. In the example the unit of effort in season A is half as effective as that in season B. The procedure for estimating an index of density and the total effort in all seasons in the terms of the unit of effort in season A, is set out in the table below:

	Catch (Tons)	Effort (Days)	"A" Effort	C.P.E.	"A" Effort
Season A	248	100	100	248	
Season B	1,008	200	400	252	
A + B	1,256	300	500	251.2	
Total	2,512				1,000

It is implicit in the above calculations that all the catches in the calculations come from a single stock, and that they are similar as regards size and age composition. The reason for the first consideration is of course obvious, and the separation of races or stocks is usually resolved during an early stage of a fishery investigation, but in an area of partial mixing of two or more stocks, e.g. the central North Sea for the herring, the racial analysis of commercial catches may form an important part of a regular sampling program.

The need for age analysis of the commercial catch is not apparent in certain models of fish populations, in which the population is treated as a single entity; e.g. Graham's sigmoid curve, and more recently Schaeffer (1954). However, such models, though useful, particularly when data are limited, are by their nature unsuited to deal with such age or size specific measures as mesh regulations, size limits etc. For these the analytic method typified by Beverton and Holt (1957) are necessary. For such models the age and size analyses of the commercial catches give essential information on growth, and, if the catches are representative of the population, on total mortality rates and year-class strengths. If the catch is not representative of the population then, paradoxically, the age-analysis of the catch becomes more important. For such

a fishery the fishing mortality coefficient ( $F$  of Beverton and Holt) cannot be considered as constant for all ages; the variation from age to age may be difficult to determine, but it is likely to necessitate two sets of data, the true age composition of the population, and the age composition of the catch. Beverton and Holt have dealt fully with the case of simple mesh selection, considered either as taking place abruptly at one length, or over a range of lengths. For most important species the mesh selection characteristics of otter trawls are fairly well established, so that knowledge of the mesh size in use determines the form of the variation of  $F$  with length (or age). The length composition of the stock will be the same as that of the catch above the selection band, and also may be estimated, with caution, for lengths where the percentage retained by the nets is less than 100, but is known. The theory for trawl mesh selection may be readily extended to other gears whose physical properties entail a differential rate of capture, which rates may be readily determined experimentally e.g. long-lines (hook-size) or gill-nets (mesh-size).

Differential capture may also arise from variable distributions of different sizes of fish, e.g. for spawning, the effects of which often cannot be determined by direct experiment, or be expressed by a simple selection factor for each size-group. If, however, we denote by  $N_n$  the abundance of fish of age  $n$  (or of length  $n$ ), and  ${}_iY_n$ ,  ${}_iF_n$  the catch, and mortality caused by gear  $i$  on this age-group, and  $Y_n$ ,  $F_n$  the total catch and fishing mortality, then:

$${}_iY_n = {}_iF_n N_n$$

$$\sum {}_iY_n = Y_n$$

$$\sum {}_iF_n = F_n$$

If now, for some sub-division,  $j$ , of the fishery, the catch per unit effort of fish of age  $n$  is proportional to the abundance of that age,

$$\text{i.e. } {}_jd_n = K_n N_n$$

where  ${}_jd_n$  is the catch per unit effort of fish of age  $n$  and  $k_n$  is constant for all years.

This gives an index of abundance and of fishing effort on fish of age  $n$  which are valid for any year. If further  $k_n$  is the same for all ages ( $=k$ ), which is equivalent to the sub-division  $j$  having the same age composition as that of the stock, then:

$$F_n = k \frac{Y_n}{{}_jd_n}$$

and this gives the fishing effort for any age, or year, in the same scale. The

and this gives the fishing effort for any age, or year, in the same scale. The method is readily extended, as previously, to allow for stratification of sub-division j, and for the combination of valid indices of age-group abundance from two or more sub-divisions of the fishery.

The discussion so far has assumed that any information required is readily available and known to any desired degree of accuracy. This is in practice far from being true. The principal data required are:

1. Total catch.
2. Total effort.
3. Structure of catch divided by:
  - (a) Stock or race.
  - (b) Position of capture, with corresponding effort.
  - (c) Type of gear.
  - (d) Size and age composition.

Of these the total catch may reasonably be expected to be known exactly, though a little adjustment may be necessary to put the landed weight into terms of weight as caught. Data on method of capture, effort -- usually not in standard form -- and position of capture (at least within limits), are likely to be known fully. However there remains a considerable body of information that can only be obtained by some sampling system. The problem of designing such a system, so as to obtain the necessary information to a desired degree of accuracy in the most efficient manner, has generally received little attention in fishery research. Recent statistical analysis of the sampling of English trawl catches for age and length have shown how the accuracy may be nearly doubled for the same sampling effort (Gulland 1955), and taking into account previous modifications, the accuracy of the original sampling system has been increased several hundred percent. The sampling procedure that is actually most efficient is likely to vary from fishery to fishery, but the underlying principles of statistical sampling remain the same. Probably suitable statistical analysis could vastly increase the efficiency of most sampling programs in fishery research. Besides such adjustments in the sampling of one type of information, e.g. length composition, the accuracy of the information as a whole may be greatly improved by a redistribution of sampling effort between various types of information. For instance the 1953 Statistical Bulletin of ICNAF contains complete information on total catches, and nearly complete information on total effort (though in a wide variety of units) and distribution of catch and effort by major areas. No information on age composition is given in the Statistical Bulletin, though considerable data on size and age composition are collected as part of the research program of several countries.



These data obviously vary greatly in accuracy and the accuracy of the final estimates, e. g. of mortalities, or of year-class abundance, depends mostly on that of the weakest link. Improved accuracy in the final estimate will only be obtained by strengthening this link; in the case of ICNAF statistics this link is probably the age and length composition of the catches, and possibly also lack of accurate data of catch and effort for some section of the fishery i.e. at a particular restricted time, place and method, which gives an unbiased estimate of stock density. Implicit in such a redistribution of sampling effort is the knowledge of the final estimates (of mortalities, etc.) needed, and the methods of obtaining them. A change in method may require a new series of data, which in turn requires a different sampling method. The sampling methods needed for any fishery cannot therefore be discussed in detail without a full understanding of the method of population analysis to which the resulting data are to be applied.

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THE EVALUATION OF FISHERIES RESOURCES  
BY THE DYNAMIC ANALYSIS OF STOCKS, AND  
NOTES ON THE TIME FACTORS INVOLVED.

77

S. J. Holt.

1. To devise means of reducing the time required to assess fish stocks, it may be fruitful and, in view of the present active development of several methods of analysis, (see e.g. Schaeffer 1956) opportune, to re-examine the aims of this work, and the definitions of the concepts involved. The aims are, I believe, to develop methods of evaluating fishery resources and then to determine, for a given time and situation, what action is appropriate to increase the economic production from those resources.

Although arguments have been advanced for defining fishery resources as whole eco-systems, rather than as populations of commercially valuable fish, (Kesteven and Holt, 1955), it is an important characteristic of present methods that we begin by analysis of particular parts of those eco-systems. The unit fish stock is, for this purpose, selected as a part of the resource susceptible to separate treatment. The stock is thus considered as a partial system, and the procedure is to attempt to link this with the other elements of the eco-system -- that is, the environment of the stock -- considering each relation in turn.

2. The fundamental attributes of the unit fish stock that we seek to describe are:

- (a) its identity as an independent population; its general location; and the bounds of its distribution.
- (b) the behaviour exhibited by the individuals or schools composing it, e.g. changes of habitat at certain stages in the life history, migrations within the general area of distribution, local movements in response to various stimuli, and other forms of activity.
- (c) its magnitude.

The time factor might be considered in studying all three attributes, but in this note I wish to draw attention only to what seem to be important aspects of the last mentioned, since I believe this is the one for which the reduction of time in analysis can most profitably be discussed.

The appropriate measure of magnitude of a unit fish stock to use when considering it as an element in a resource system is not obvious. The chief requirements of a suitable measure are comparability of values as between different stocks, and a consistent relation to the catch obtainable from the stock

under well-defined conditions.

Clearly population size itself (standing crop, or biomass) is not adequate, since the standing crops of different populations of the same size may give completely different catches. The catch, being the integral of a rate of activity over a certain time period, is more closely related to the production (turnover) of living organic material, but whereas this might provide a rough index of resource potential, it is not entirely suitable when we study the fish populations themselves in detail. For example, production is a quantity that itself varies with the fishing activity, as also does the specific productivity (fractional turnover rate, or the rate of production per gram of standing crop).

3. A measure having many advocates, and to a certain extent established by being written into several international treaties, is the "maximum equilibrium (or sustainable, or sustained) catch".

The term "equilibrium" has been used in fishery theory in several ways, but in general there is an implication of stability either of a fish stock or of a fishing industry. Now a stock may be stabilized at any level of size within wide limits, and the possibilities within a given economy of stabilizing the level of operation and production of a particular industry are equally wide. In both cases, external constraints -- on the one hand, for example, the amount and kind of fishing and on the other the economic conditions outside the industry setting costs and prices -- may determine the particular equilibrium attained.

"Maximum equilibrium catch" may therefore mean either the greatest sustained catch that a stock can give, or the greatest catch that can be taken whilst allowing economic equilibrium, according to whether the fish stock or the fishing industry is the system the dynamics of which are under consideration. It has frequently been assumed that it is economically possible and desirable, or at least not economically undesirable, to take the greatest amount that the stock can sustain, but this proposition needs critical examination.

Equilibrium of a unit fish stock is here understood to mean a condition in which the weight of fish removed from the population, by capture of some and "natural" death of others, is on the average equal to the weight added through supplementation of numbers of fish by recruitment and increase in size of individual fish by growth. Such a condition is better referred to as a steady-state.

It is a characteristic, though not an invariable, property of animal populations or communities that they are able to attain steady-states within a wide range of external conditions, and it has been usual in the field of population

dynamics as with analogous physical problems to consider first the population as an "open" system in steady-state and then to examine the consequences of departures from this state.

Trends to or from particular steady-states may or may not be reversible. Reversibility would, for a fish stock, mean that if a change in the intensity of fishing caused a movement away from a steady-state, then a further change back to the original intensity would result eventually in the stock regaining the original steady-state. There are indications that this is generally true for several marine fish stocks, the most conclusive evidence being the effects of temporary cessation during wartime of fishing on depleted stocks.

Russell (1931) has given us a symbolic statement of the relation between stock size and the various additions to and removals from the stock. His axiomatic equation in fact describes a fish stock as an open system and it can give simple expression to the steady-state condition. It has been recognized that while this cannot as it stands be used to assess the state of the stocks, and the needs for corrective measures, it nevertheless represents a starting point for a working formulation of the sustained catch problem.

4. The most important variable, the relation of which with steady catch we need to discover, is the "amount of fishing". The most direct method, if a long series of commercial fishery statistics is available, is to pick out several periods during each of which the intensity of fishing and the catch were fairly constant for long enough to make possible the assumption that a steady-state was set up during each period. The average annual catch for each period is then plotted against the corresponding fishing effort. Graham (1951) has remarked that the statistics alone are usually insufficient to give a coherent graph and he gives examples in support of this from what are generally considered to be well studied fisheries.

In an attempt to interpret the limited data, some further assumptions may then be made concerning the general shape of the required curve relating equilibrium catch to fishing effort. A device that has been employed is to fit the Verhulst-Pearl logistic curve to the available data. Graham (1935) was able to do this using observations of the relation of war-caused changes in the amount of fishing to changes in the catch and the catch per unit effort from North Sea trawl fisheries. Although the validity of his assumption, that the total growth of all demersal fish populations in the area can be represented by the logistic function, cannot be tested directly, it has been accepted as a not unreasonable first approximation. Since the natural growth curve is certainly sigmoid -- whether or not it is a symmetrical logistic -- the stock will have a maximum rate of increment at some intermediate stock size when the inflexion is reached; the argument is that a maximum equilibrium catch will be

obtained when the stocks are, by fishing, kept at the level of that inflexion.

5. One difficulty in developing this method further is that -- equilibrium catch being considered only as a function of a gross measure of population size -- no account can be taken of changes in the age composition of the stock that inevitably result from changes in fishing intensity.

Schaeffer (1953) has recently attempted to make fuller use of series of annual catch and effort statistics to investigate the behaviour of fish populations when they are being exploited. His method is essentially the analysis of the fluctuations in the series for the purpose of predicting steady-states. The growth potential, and hence the steady catch that could be taken from a stock of a size equal to the average stock size in a particular year, is estimated as the algebraic sum of the actual catch in that year, and the difference between the stock size at the beginning of the year and at the end of it.

Schaeffer plotted figures for "equilibrium catch" obtained in this way against catch per unit effort for the Pacific halibut and Pacific pilchard stocks. His figures indicate that, for both species, the "equilibrium catch" increases with increasing stock size over the observed range. It is possible to fit a logistic function to data treated in this way but the scatter of points is so great that no useful estimate can be made of the stock size that would give the "maximum equilibrium catch". In fact, the data give almost no sign even of the existence of a peak in the curve. They could, however, be taken as evidence that, for the situations examined, a reduction in fishing would result in an increased average catch, provided it were also shown that the stock abundance is largely controlled by the fishing intensity.

6. A fundamental objection to the above method is that no knowledge is obtained of the extent to which the year to year changes in stock size are on the one hand the result of mortality and growth within the stock and on the other due to the recruitment of new individuals into the stock. The recruitment in a particular year can hardly be regarded in general as a simple function of the stock size in that same year. It is, for all species but those having a life span of less than one year, a function of the stock size during an earlier period at the beginning of which the new year class was spawned.

To illustrate the errors of interpretation that may arise if these facts are neglected, it is sufficient to consider the case where fishing is very intense but highly selective, only the larger fish being caught. In this situation the catch-per-unit effort may be an index of the size of the part of the stock being exploited, but this bears no simple relation to the total size of the population. Yet it is the growth of fish before recruitment which in this case determines the steady yield. Analysis of the North Sea plaice stock shows that, even

where these fish, having a possible life-span of over 20 years, become liable to capture on the average soon after they are three years old, rather more than a half of the stock growth from which the catch is derived occurs before recruitment.

Such considerations remind us that man rarely, if ever, exploits the whole of a population of fish, but rather selects only individuals within a certain range of size and age which constitute the available stock, and frequently only a readily accessible fraction of these. For further development of fishing theory, this distinction between total, fishable, and fished populations must be fully recognized and the relations between them taken into account. Fundamentally, the fished stock from which the catch comes cannot be treated as a self-reproducing unit having at any given time a potential for growth which is a function mainly of its size at that time; this potential is essentially a complex function of stock size and composition at the time and of the size and composition of the total population during some previous period.

7. The above discussion leads us to consider another approach to the maximum catch problem. It has frequently been pointed out that there is a best age at which to harvest a particular crop. For cultivated stocks this best age may be that for which the net gain is at a maximum and after which the cost of, for example, continued feeding, may be greater than the value of the additional growth. For wild fish stocks, the best age is considered to be that at which a particular year class reaches its greatest total weight, after which the losses by natural mortality are greater than the summed growth increments of the survivors. In marine fisheries it is not possible to capture all the fish at a particular age, so that in practice it is best to start catching fish when they are rather younger; how much younger depends upon how intense is the fishing -- the harder and more effective the fishing, the longer the fish can be left to grow before one tries to catch them.

Allen (1953) has discussed the best legal size limit of fish, for any particular rate of fishing. From his theorem, we may deduce that the weight of an individual of the size at which it is best to start fishing is equal to the average weight of the fish in the catch multiplied by the ratio of the fishing mortality rate to the total mortality rate in the stock. However, like Russell's equation, this formula defines a steady-state situation, a posteriori, but does not provide a means of prediction.

8. To unify these two approaches to conservation problems -- i.e. consideration of the best fraction of the stock to remove annually and of the best age at which to catch the fish -- the analytical methods developed by Baranov (1918) and several other workers since are necessary. These depend essentially upon the construction of mathematical models containing coefficients

which describe the factors of migration and recruitment, growth and mortality, and causing the removals from and additions to a fish stock mentioned in (3) above, and the relations between these factors. The various models put forward (e.g. Ricker, 1944; Tester, 1953; Tanaka, 1954; among others) have differed from each other principally in the shape of the curve used to describe growth of the individual fish, and the characteristics of each model depend to a considerable extent upon the accuracy with which the particular growth function used reproduces the general features of fish growth. When it has been a realistic one, these models have frequently shown a peak in the curve of steady yield against fishing intensity. When, however, the rate of natural mortality is high in relation to the overall growth rate, or when the dependence of growth rate of individuals on the population density is taken into account, then the curve may have no peak, but may instead approach an asymptote. Again, when the size at which fish are first liable to capture is increased, then the maximum is found to occur at a higher fishing intensity and the peak of the curve becomes less pronounced. Eventually a size is reached for which the peak disappears and the curve becomes asymptotic.

9. A clue as to a suitable measure of stock magnitude is found by considering the nature of fishing activity from the biological point of view. It has two characteristic properties -- amount, and selectivity -- especially with regard to the sizes and ages of fish taken, but also to species, sex and other attributes. We have seen that much work on the theory of fishing has considered only the former characteristic, though sometimes, especially when workers have been concerned with the management of fisheries by mesh regulation and the imposition of size limits, the selectivity of the gear for certain size classes of fish has been the main consideration.

In fact, both characteristics have always to be treated simultaneously in any acceptable theory of fishing. Doing so leads inevitably to a three-dimensional representation of the relation of steady catch to the fishing activity, but this may be shown in a two-dimensional diagram by the device of plotting contours of catch against the two axes of amount of fishing, and selectivity of fishing. One such representation is the steady-catch isopleth diagram (Beverton, 1953; there referred to as a yield-isopleth diagram) which is obtained by calculation from an equation containing parameters representing the recruitment, growth, and mortality rates of fish in a stock, and which refers to a fishery based on a stock with an annual recruitment which is effectively independent of the size of the spawning population, a constant natural mortality that can be represented by an exponential curve, and an invariant growth pattern of the individual fish conforming to von Bertalanffy's equation.

In that diagram were plotted not values of characteristics of the fishing activity itself, but the equivalent biological parameters, so that there are illus-



trated the inherent properties of the stock itself, as exhibited under the influence of a particular kind of fishing operation, trawling in the example given. It is found that for trawling operations the most useful parameters are the instantaneous coefficient of fishing mortality,  $F$  (which is conveniently proportional to the fishing intensity expressed in standard terms), and the age at first liability to capture by the gear,  $t_c$ , (which is primarily a simple function of the size of mesh in the trawl cod-end).

10. Similar procedures can be followed for dealing with hook and line and other types of fishery, but there is a further difficulty in reconciling the alternative catch-isopleth diagrams that might be drawn for a particular stock with the possibility of being exploited by different types of gear, for which the relations of selectivity to size of fish are different. With a trawl or other "bag" net such as a seine, the fishing mortality coefficient is, to a first approximation, constant for all fish above a certain age at first capture, this age being determined either by the pattern of recruitment or by the size of mesh, Rollefson's (1953) and other data indicate, however, that for hook and line gear the instantaneous fishing mortality coefficient may vary in a curvilinear manner (possibly exponentially) with age of fish. The same is undoubtedly true of gill and trammel nets. In general the mortality coefficient is some function -- but probably usually a rather simple function -- of the size or age of fish; each kind of fishing unit has a characteristic function and for trawls this is of the simplest possible kind. It is possible to define an amount and selectivity of one kind of fishing (say trawling) that will result in the same sustained catch and have roughly the same effect on the stock magnitude as any given amount and selectivity of another kind of fishing such as lining with a particular size of hook. An isopleth diagram referring to a certain kind of method can therefore be transformed to an equivalent one for some standard fishing method, and it is convenient to take trawling as the standard.

In this way standard exploitation conditions can, for the purposes of resource appraisal, be defined in biological terms so that the steady catch may be used in deriving a basic measure of magnitude.

11. The procedures of drafting an isopleth diagram and subsequent operations could be simplified in several ways, including some standardization of methods of observation and presentation of data, compilation and critical review of data on special subjects such as growth of fish, mathematical approximation, and short cuts in computation and plotting.

Other summary curves indicating certain aspects of the contour pattern may be drawn on isopleth diagrams of steady catch. The most important is the eumetric fishing curve, showing the best selectivity of the gear for each particular fishing mortality and from which may be deduced the eumetric catch

curve giving the maximum steady catch as a function of the amount of eumetric fishing. For the complementary line, shown dotted in Fig. 2 (Page 88), adjustment of selectivity is considered to be limited for technical or other reasons, and for each age at first liability to capture the best fishing mortality is imposed. On this curve lie all points of "maximum sustainable catch" obtained when only the variation of amount of fishing is considered as a factor governing catch.

The horizontal line in these diagrams marks the age of recruitment. Below this line fish are not accessible to the kind of gear under consideration and could only be caught, if at all, by adopting entirely different methods.

12. In the present context, the most important characteristic of eumetric catch curves is that they are asymptotic, the greatest steady catch being obtained only with infinitely intense but very selective fishing, that is, when all fish can be caught as soon as they reach a certain best age. I propose to call this asymptotic steady catch the potential yield. This definition differs to some extent from previous usage, "catch" and "yield" in marine fisheries having usually been treated as synonymous. However, it is useful, as we shall see, to distinguish the two quantities, and this is in keeping with the distinction made between "harvest" and "yield" in agricultural and forestry science. The potential yield is in fact that quantity which could be taken by ideal cropping methods; in marine fisheries this includes the use of gear of optimum selectivity, and highly efficient capture operations. The amount by which catch falls short of potential yield is a measure of the absolute efficiency with which the harvesting operation is being conducted; this means efficiency of organization and control, of course, as well as technical efficiency. I suggest that the assessment of potential yield in the above sense is the correct focus for work on evaluation of fishery resources, though this must of course be linked with biological production at different levels in the ecosystem of which the fish stock is part, and with the practical requirements of exploitation at the present time. Having measured potential yield, we may on the one hand examine the factors limiting the catch in relation to the potential yield, and on the other hand the means of increasing the potential yield itself in relation to the rate of organic production by the stock, by, for example, transplantation, predator control and other forms of intervention in the resource system.

13. Using the simple equation given by Beverton for a trawl fishery we may derive expressions for two quantities which are sufficient to define a eumetric catch curve. One of these is the initial slope of the curve, which might be called the responsiveness of the stock, and it is given by:

$$Q = R \cdot W^\infty \sum_{n=0}^{n=3} [1 - \exp. \{- (M + nK)\}] \exp. \{-nKt_r\} a_n / (M + nK)$$

where R = Annual recruitment

$W^\infty$  and K = Parameters of von Bertalanffy's equation for growth in weight

M = Instantaneous coefficient of natural mortality

$t_r$  = Age of fish at recruitment

L = Fishable life span and  $a_0, a_1, a_2$  and  $a_3$  are +1, -3, +3 and -1 respectively. When L is large and  $t_r$  small, as may often be assumed, this approximates to:

$$Q \approx 6RW^\infty K^3 / \text{Prod.}_{n=0}^{n=3} \{M + nK\}$$

The other quantity is the asymptote, the potential yield, and it is:

$$Y = 27RW^\infty K^3 M^{M/K} \exp. \{Mt_r\} / (M + 3K)^3 + M/K$$

Rearrangement show that the potential yield per recruit is, when expressed as a fraction of the asymptotic weight,  $W^\infty$ , a simple function of the ratio  $K/M = i$ , thus:

$$y = Y \cdot \exp. \{-Mt_r\} / RW^\infty = 3i^3 / (3i + 1)^3 + 1/i$$

This function is plotted in Fig. 1 on logarithmic scale to show the relative effects on the potential yield of proportionate changes in the ratio  $K/M$ . It will be seen that as this ratio increases (by increase in K or decrease in M) the yield can be improved relatively more effectively by increases in  $W^\infty$  or R. Such considerations might assist in evaluating alternatives of say transplantation and predator control.

The weight of the individual fish at age  $t_y$ , when the brood attains its maximum aggregate weight, is given by:

$$W_{t_y} = W^\infty [K / (K - M/3)]^3$$

The relation between the quantities Y and Q can be represented by the empirical equation:

$$C_u = Y [1 - \exp. \{-2QF/Y\}] / [1 + \exp. \{-2vQF/Y\}]$$

where  $C_u$  is the eumetric steady catch, and v is a constant lying between zero

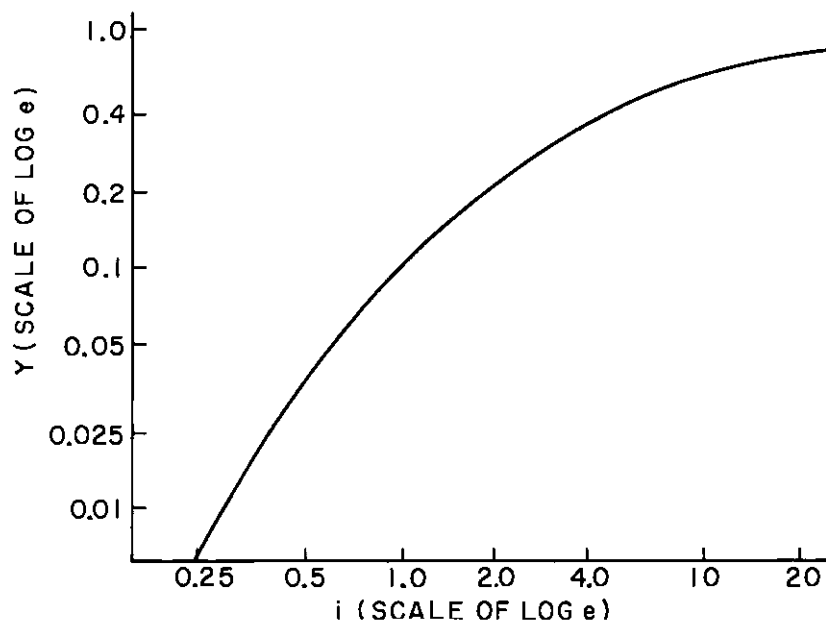


Fig. 1. Potential yield per recruit per gram asymptotic weight ( $y$ ) as a function of the ratio ( $i$ ) of the growth parameter,  $K$ , to the natural mortality coefficient,  $M$ .

and unity.

The equations for  $Y$  and  $Q$  contain only parameters referring to the recruitment, growth and mortality of fish in the stock, all of which factors are measurable. For this population model these parameters have been assumed to be constant, and if, for example, the growth rate were strongly dependent on the stock density, the deductions might be invalid. This first approximation might, however, be taken as a working basis from which to develop more comprehensive methods of estimation, and it seems to help in sorting out concepts, identifying the necessary types of data, and linking widely different kinds of observation. The advantage of using terminology and methods that are applicable equally to marine and to inland resources, and to cultural practices as well as to simple exploitation of wild stocks, might also be borne in mind.

14. We now consider the relations between potential yield, and organic production and harvest. The annual production of the fishable stock is equal, under steady-state conditions, to the total weight of fish dying in each year (in absolute terms) and the ratio of potential yield to this production is given by:

$$\sum_{n=0}^{n=3} a_n \left( \frac{M}{M+3K} \right)^{n+M/K}$$

$$\sum_{n=0}^{n=3} a_n \left[ \left( \frac{M}{M+3K} \right)^{n+M/K} \cdot e^{-(M+nK)t/r} \right] \left[ 1 - \frac{M}{M+nK} \cdot e^{Mt/r} \right]$$

Such an expression relates yield to production at this particular trophic level, and, through transfer factors, to production at other levels, so that ecological data can be integrated with the detailed studies of commercially exploited fish populations.

15. Turning now to the significance of the potential yield in putting the magnitude of the catch into perspective, we may again consider the isopleth diagram for steady catch. A simplification can be made by selecting the contour line passing through the observed value of the steady catch, which means that the diagram shall be drawn with reference to a given set of data defining an observed initial situation. On one side of this line lies improvement of catch, on the other side, decrease.

The other principal characteristics of the catch that have been identified as significant in relation to conservation problems, and to the exploitation program generally (see report of the UN Technical Conference on the Conservation of the Living Resources of the Sea, Rome 1955) are the catch per unit effort, and certain indications of "quality", notably the average size or age of the fish, and in certain cases, the species composition of the catch. Isopleths of these quantities expressed in biological terms, e.g. the ratio  $C/F$  and the average weight of fish in the catch ( $\bar{W}$ ), can also be drawn on the same diagram, again choosing for preference the particular isopleths passing through the reference point. The diagram is, by their intersection, cut into segments in some of which there is universal improvement in all catch characteristics, and in others universal detriment; whilst in other segments one characteristic is improved to the detriment of one or both other characteristics.

An example is given of this procedure (Fig. 2), the material being taken from Beverton and Holt (1956) and referring to the plaice stock of the North Sea. The curve for average weight of fish, used as an index of quality almost coincides in this case with the lower part of the curve for amount of catch. The eumetric line and its complement are shown to indicate relief on the diagram, and the potential yield is marked in.

Such diagrams can provide the basis for technical and economic evaluations by suitable transformation of the co-ordinates. Thus,  $F$  is proportional to standard fishing intensity, and catch and effort can be converted to value and cost to obtain curves for net economic gain. Diagrams for different stocks may be compared to show conditions under which returns from more

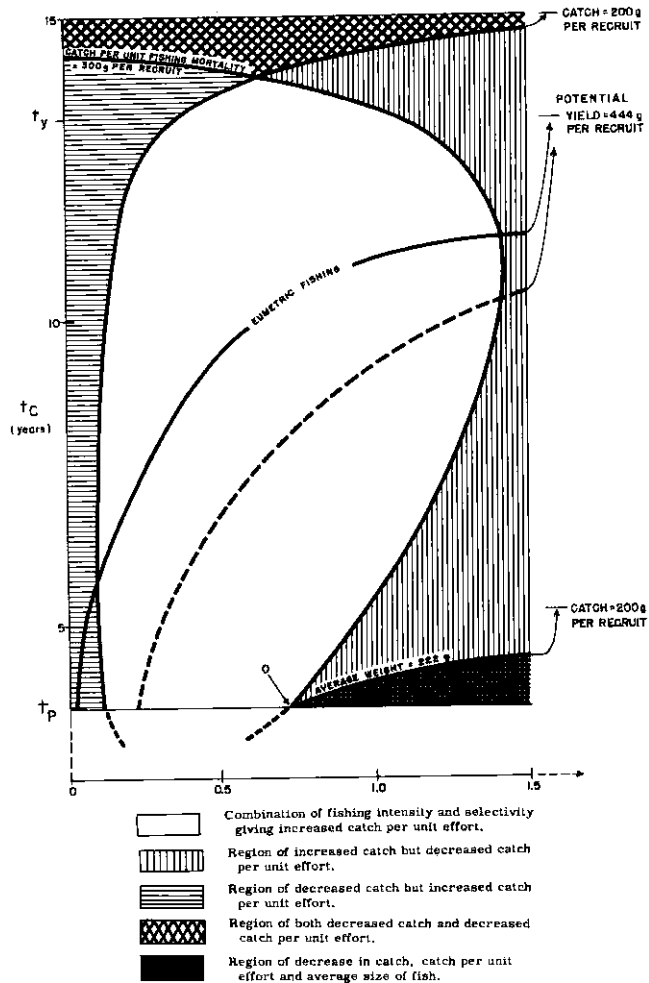
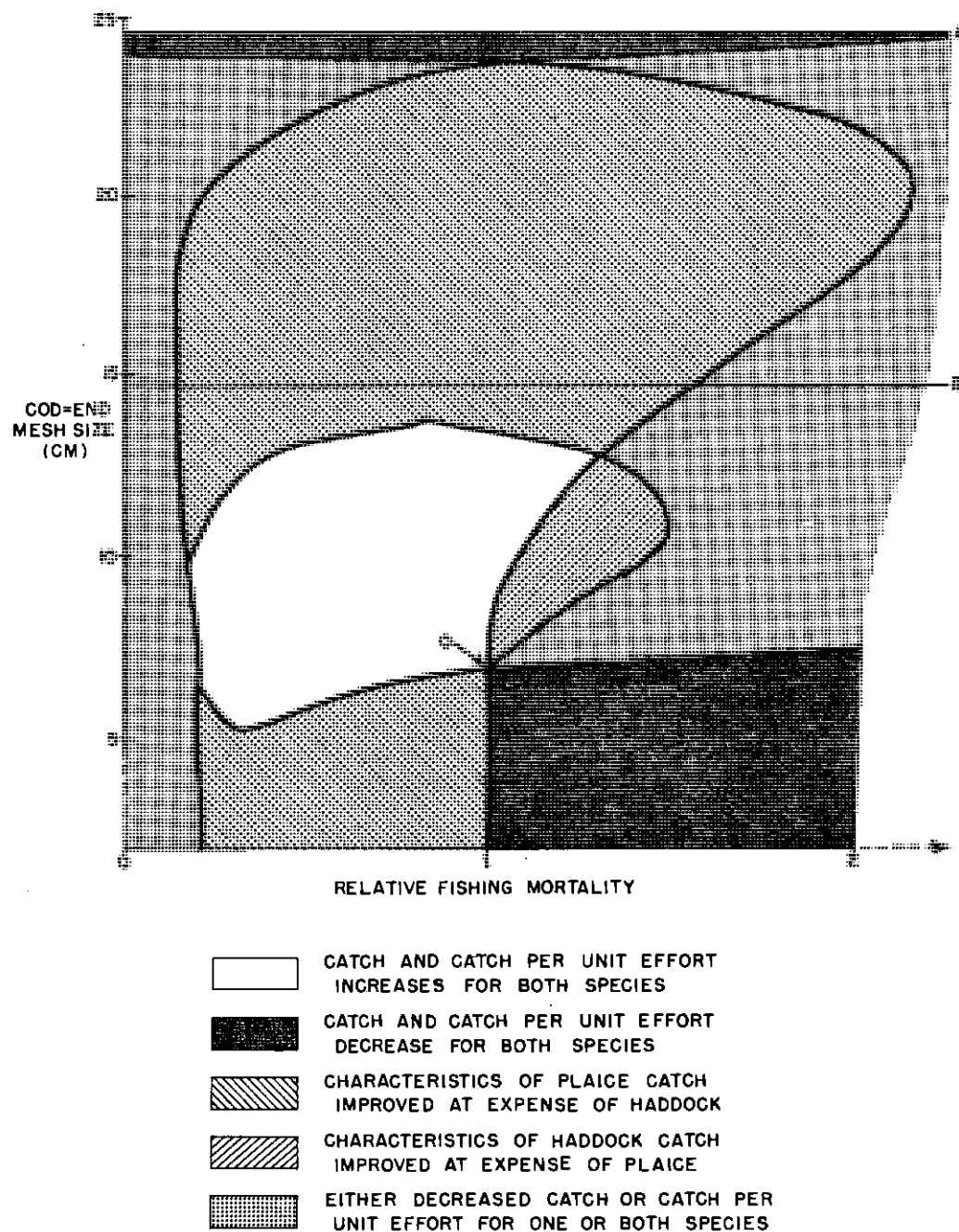


Fig. 2. Evaluation diagram for North Sea plaice.

valuable species begin to decline in relation to less valuable species, and diagrams for different types of fishing, can be compared by superposing them directly or after transformation into cost-value diagrams. They thus serve to reduce to simple terms the essential information about the magnitude of the exploited stocks that is obtainable from the records of fishing operations and catch, and from special research projects.

16. Similar presentations for mixed populations of two or more species are



**Fig. 3.** Combined evaluation diagram for North Sea plaice and haddock.

complicated but not different in principle.

Consideration of the situation where more than one species is taken by the same gear provides an example of this procedure, and incidentally illustrates the practical value of distinguishing potential yield from catch. Fig. 3 shows a combination diagram for both plaice and haddock in the North Sea. Since the relation between cod-end mesh size and  $t_c$  is different for the two species, the scale of the selectivity axis has for both been transformed to mesh size. The fishing mortality coefficient is expressed in relative instead of absolute terms, so that the two reference points of observed state, O, coincide at unity. In this case the catch and catch per unit effort lines only have been plotted, and they cut the diagram into several sectors showing different degrees of advantage or disadvantage. Not all possible combinations are distinguished here, certain groups of segments having been blended to show the general pattern more clearly. The significant feature is that although each stock has a characteristic potential yield, in practice it would not be sound policy to attempt to manage the fishery to obtain these yields - - this could only be done if species selective gears could be used. This conclusion would indeed be even more obvious if we had plotted curves for, say, sole, a valuable fish which escapes more easily through large meshes. However, it will be seen that there is a considerable area (white on the diagram) within which there is scope to improve both characteristics of the catches of both species. The extent by which the catches obtained under such conditions fail to reach the combined potential yield of the two stocks can provide an objective index by which could be judged the value of special innovations, either in species-selectivity of gear, or in the tactics of fishing so as to catch preferentially one species or another at times or places when they are segregated.

17. I suggest that, given the identification of a unit stock, we might restate the principal aims of studies in stock dynamics as:

The measurement of potential yield, as a standard for comparison with catches to characterize the general status of a fishery; and the determination of the topography of an evaluation diagram in the region of the point characterizing the present situation of an industry.

The leading questions then become "Is the catch a large or small proportion of the potential yield of that stock?" and "In what direction, and at approximately what rate, will the important characteristics of the catch change with changes (in either direction) of the amount and/or the selectivity of fishing?" To answer them, standard methods of assessment need to be worked out, comparable, for example, with the systems for routine assessment of forest increment. At present, much time is absorbed in trying to devise means



of dispensing with such empirical measurements by using only time series of catches and of fishing effort, and a minimum of other information. It will surely be agreed that catch and effort data, no matter with what precision they are obtained, are not sufficient alone. The various methods seem to differ mainly in the kinds of other experience brought to bear on the problem, and in the manner in which this is done. This experience may be expressed in the form of broad theories, such as that of logistic growth, based on studies of populations other than the fish stock in question; or it may consist of physiological or other observations than bio-demographic ones on the stock in question or similar stocks. In any case, the time taken to make a reliable evaluation will vary inversely with the success gained in applying other kinds of data to this purpose. For example, suppose it is necessary to know with a certain precision the growth rate of fish in a stock. Von Bertalanffy's equation might be fitted to age-weight data and  $K$  and  $W^\infty$  calculated. But if at least the order of magnitude of  $K$  is known from physiological experiments on that species, then fewer observations would be needed to find  $W^\infty$  with the same precision. If the physiological experiments were backed up by comparative studies of related species, the situation would be even better. Much depends upon the efficiency with which past experience is accumulated and digested and statistical population studies developed in close relation with other kinds of biological work.

18. Not only are data on catch and effort insufficient by themselves but they may not even be the most important of the array of data required to assess resources. There seems no reason why the potential yield of a stock could not be measured before it is exploited. To find the relation between catch and potential yield, effort data is not indispensable; but to fix points and gradients on evaluation diagrams it seems essential. If the methods of processing catch and effort data to compute particular parameters are the best (i.e., statistically the most efficient) that can be devised, then since we cannot increase the rate at which these kinds of data are produced, we can only try to reduce the sources of variability in them by seeking relevant information of a different kind. By the same reckoning, we may improve the testing of, for example, the effects of regulation, or predictions of future events, by paying attention not so much to fluctuations in catches as to changes in quantities such as mortality rates.

The prediction problem is essentially the estimation of steady-state conditions from data referring usually to a limited period of time, and to transient situations. There are at least two ways of attempting this. Suppose it is required to predict the change in growth rate of fish that may be expected with change in population density caused by some sustained adjustment in the amount or kind of fishing. The fluctuations in growth rate occurring over a long run of years might be correlated with fluctuations in relative stock size,

and then the presumption made that for steady-state situations and different average stock levels the same regression lines will apply. Predictions could be made in a much shorter time from controlled experiments on food utilization of that particular species of fish, but the research effort required for this might well be greater. Some field test would have to be applied, and this would include measurement of available food. By appropriately combining the two approaches, the time required to reach a conclusion on which action might reasonably be based could be minimized.

19. In the above paragraph a distinction has been made between total time and research time. As a guide for discussion, the research can be considered in three phases:

- (a) Collection and tabulation of data.
- (b) Calculation of population parameters.
- (c) Computation and presentation of evaluations in the form of diagrams, tables, etc.

The time factor in (a) has been discussed by Gulland (1955) in terms of sampling methods to reduce labour and bias and to increase accuracy. The relative extents to which effort can be reduced further by improved instrumentation, by international collaboration in reducing overlapping work, or filling in gaps in knowledge, and by standardization of practices, also demand examination.

In phase (b) the various parameters can be considered in turn.

**Mortality rates:** The requirements in measuring these were discussed in detail in papers presented to the ICES Special Meeting on Sampling, 1954. One of the chief problems is standardization of fishing intensity measures such that catch-per-unit intensity is a valid index of stock density. With refinement of procedures of measurement the concept of catch-per-unit effort is losing the economic significance it once had. Definitions of effort should be stabilized to recognize this, and Ricker's term effective effort used for that which is directly and simply related to the induced fishing mortality.

The time required for natural mortality estimation might be reduced by discovering the causes of mortality and their incidence, e.g. by measurement of morbidity rates, and using the results to reduce the variance in regressions of total mortality (from age-composition) on fishing intensity.

**Growth:** If there could be agreement to present growth data in a standard

form, then much labour in analysis could be avoided. Von Bertalanffy's equation gives, apparently, a means of separating density-dependent and density-independent processes, of estimating parameters from data varying from year to year, of comparing stocks, and of making extensive use of physiological and ecological data. A systematic analysis of the available growth data to permit comparison between related stocks could reduce substantially the time required in future investigations.

Recruitment: The urgent need is for a method of examining the dependence of the number of recruits on the size of the stock which spawned them, other than by regression over a period of many years of varying stock size, because the apparent fluctuations in survival of pre-recruits are so great. If the sources of variance can be reduced by bringing in other kinds of related information, such as some index of relative favorability of the environment in different years, the time period could be shortened (see Kesteven 1947).

In phase (c) it would seem to be more economical of effort, and perhaps more useful, to think in terms of slopes on response surfaces rather than curves of catch under varying conditions. This seems to be proving a very useful approach to the analogous problem of determining optimum conditions for industrial chemical reactions (Box, G. E. P., 1954). Means of estimating yield and slopes on the "reaction surface", by special experiments comparable with Allen's method for determining eumetric points, might therefore be worked out.

20. Lastly, standardization of terms and symbols would simplify work and should not, at this stage, be difficult to achieve.

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E. D. Le Cren.

1. Introduction

The current and logical trend in the study of the dynamics of fish populations is towards the detailed analysis of vital rates and the construction of theoretical models to describe the inter-relationships between these vital rates and the effect of fishing upon them. Unfortunately, as the models are made more complex, in the effort to make them more realistic, they require more basic data and better estimates of the vital rates. Both the collection and analysis of these data take more time and, further, it is necessary to collect data from a longer time series in order to reduce the effect of annual variability. For the efficient management of a fishery, however, it is necessary both to have good assessments of the status of the population in relation to the fishery and to be able to obtain these assessments as quickly as possible. It is thus necessary to improve the assessments that can be made and at the same time to reduce the time required. There seem to be four main lines of attack. These are:

- (a) The development and refinement of existing methods of making "rough appreciations" of the status of fish populations, and perhaps the discovery of new methods.
- (b) The finding of quicker and more direct ways to estimate the vital rates, and in particular,
- (c) The devising of ways of reducing the complications due to natural fluctuations; and
- (d) The development of analytical methods and theoretical models until they can either indicate short-cut methods that require the minimum of factual data, or can be simplified again around those factors that have been shown to be most relevant.

It is impossible in a short paper to deal fully with all four approaches, and some have been discussed at length elsewhere; I wish merely to enlarge upon a few aspects which appear to me to be particularly profitable for attack.

2. Methods of Rough Appreciation

Some features of fish populations can be fairly easily and quickly ascer-

tained from relatively few samples taken over a short period of time and can be interpreted to give some assessment of population status. Many of these features rely on the usual differences between unexploited or lightly exploited populations, and those being heavily fished. Lightly exploited or unexploited populations are generally dense - yielding high catches per unit fishing effort, the fish are usually old on the average, large in size, slow in growth rate and have the heavy-boned and heavy-headed appearances of old slow-growing fish. Heavily fished populations, on the other hand are usually sparser, yielding low catches per unit effort, and consist mostly of small, young, fast-growing fish.

Thus data on such population features as appearance, size distribution and average size, average age, and growth rate can often be used to make good guesses on the general level of exploitation of a population, especially if there is a considerable amount of similar data from other populations of the same species for comparison. Statistics on catch, fishing effort, and catch per unit effort, can often yield fair guesses of total population and total mortality rate, though the analysis of catch age data becomes rather complicated and cannot really be considered a method of rough appreciation.

All the above features, however, are subject to influence by factors other than rate of exploitation, and population density may in some environments be kept low by such factors as unfavourable conditions for the survival fish leading to low rates of recruitment, or unusually high growth rate on rich feeding grounds. The interpretation of these features, in terms of the status of the population in relation to exploitation by a fishery, can therefore be risky and inaccurate; it does however have the advantage that it can be made quickly, and rough appreciations in two or three months may be more valuable than more careful and accurate appreciations that take ten years to make. The risk involved in rough appreciations grows less as general background information on the species accumulates, and so all such information is of value. Further fundamental research may, too, discover other features of fish populations that can be rapidly and easily determined and yet yield sensitive measures of their state of exploitation.

### 3. The Estimation of Vital Rates

Most of the analyses of the dynamics of exploited fish populations depend upon the estimation of vital rates such as recruitment, growth and mortality. Much research and ingenuity has been applied to the making of these estimations, but it remains one of the most difficult problems for the fishery biologist, and especially so when time is limited. The estimation of mortality rates and their division into rates of natural and fishing mortality are particularly



difficult and time consuming. Most estimates so far made for commercial fish populations have relied upon data on catches, effort, and age-distribution, collected over a period of several years, and the estimation of natural mortality in particular may require estimates of total mortality for years or groups of years when fishing effort varied markedly. Such reliance on variations with time in fishing effort (or other factors it may be desired to use as independent variables) has two great disadvantages: (1) other environmental factors have a habit of changing with time and (2) usually several years are involved in making the primary observations.

It would seem desirable then to investigate other ways of estimating mortality and other vital rates; ways which do not rely so much on variations in factors with time. Some such methods have been reviewed or suggested recently by Beverton and Holt (1956). For example, it may be possible to make use of variations in fishing effort on different age-groups, different sub-stocks or different sexes within one stock over a fairly short period of time. There are also the possibilities of marking experiments, estimation of the total stock from egg densities, and estimation of the area "swept" by the fishing gear as alternatives to, or in combination with, data from catch samples. Many of these methods have been tried on actual samples from marine and freshwater fisheries and although the application of some of them may be confined to rather special situations it would appear that several of them are capable of development and wider application and use.

#### 4. Natural Fluctuations

One main difficulty in estimating vital rates is the introduction of errors caused by natural fluctuations. Natural fluctuations about a long-term constant average in such rates as recruitment, natural mortality, growth and migratory behaviour complicate the estimation of these rates and widen the confidence limits of forecasts. Most fishery biologists probably spend a lot of their time adjusting data to allow for some natural fluctuation or waiting for a year-class of "average" strength to appear. Sometimes a correlation with hydrological or other factors can be found and used to adjust or forecast. Such correlations can, however, be found only from a long series of data, and, unless data from one situation can be safely applied to another, are of little use when time is short. There is obvious scope here for more fundamental research on such correlations and on ways in which effects of such natural factors can be avoided or allowed for. In general, all variations in data which are not due to random error should be analyzed to provide useful information instead of having to remain as a large contribution to the total error of the estimate for which the data were primarily collected. Unfortunately the investigation of possible im-

portant factors and their correlation with variations in data from natural sources is inevitably a tedious and unrewarding research. Its success depends largely on finding the important environmental factors and having sufficient data on them of a type that can be tested against the population variations. For populations of marine fish this would seem to involve much work on their basic biology, especially in the pre-recruit stages, and on the hydrology of the area they inhabit.

- (a) Recruitment. Variation in recruitment is probably the largest problem, and one that becomes more important in heavily fished and therefore younger stocks. That wide fluctuations in the number of recruits is a common phenomenon in fish stocks has been known for a long time, but little is yet understood about the causes of these fluctuations. Although variations in the growth-rate of young fish can cause variations in the age of recruitment and thus the numbers of recruits, the rate of recruitment to a fished stock usually depends upon the number of recruits available. This in turn will depend upon the number of parent fish, the number of eggs they lay and the subsequent survival of the young stages up to the recruit stage. Occasionally correlations have been found between numbers of spawners and numbers of resultant young fish but usually no such correlation occurs; (sometimes the higher individual fecundity of the larger fast-growing fish in a sparse population may tend to compensate for the lower density of spawners). In most fish populations, and especially those of species that lay a large number of eggs, survival in the larval and young stages appears to decide the strength of the brood at the age of recruitment. Although some density-dependent mortality may operate at extremes of population density, brood survival is normally quite independent of the numbers of young fish or adults. Evidence is accumulating however, that in many cases the survival of a brood and its strength when recruited depends upon chance climatic and hydrological factors. Once such factors, or others that are closely correlated, can be identified and measured there will be hope both of making forecasts of some of the major fluctuations in recruitment and of making allowances for their effect when assessing population status. At the same time research should be intensified on methods of quantitatively sampling the pre-recruit stages so that indices of future recruitment can regularly be made. Much more research is also needed into the whole aspect of the survival of larvae and young fish and the natural mechanisms controlling population numbers.

Some of the complications due to fluctuations in year-class strength can be avoided if the analyses and models are designed in terms of separate year-classes followed through the fishery and estimates made

on a "per recruit" basis. Later observations of the actual year-class strength can then multiply up these data in terms of the sum of all the year-classes in the stock at any one time.

- (b) Natural mortality. Very little is known, either, about natural mortality in the post-recruit stages. It is a difficult parameter to estimate and is usually determined by the subtraction of fishing from total mortality. Although post-recruitment mortality is unlikely to be nearly as variable as that in the pre-recruit stages, there is almost no evidence to suggest whether or not significant short-term fluctuations occur. Data from some fisheries do suggest, however, that quite large changes in natural mortality can occur over a period of years, and as predation may be an important cause of mortality, fisheries for predators or alternative prey-species may have some influence. At present, little can be done in analyses of population dynamics except assume that natural mortality is fairly constant. Better ways of estimating it and fundamental knowledge about its incidence and causes would be very valuable.
- (c) Growth-rate is easier to estimate with fair accuracy and is less subject to fluctuation, though year to year fluctuations and long term changes have been observed. Short term fluctuations have been correlated with hydrological factors such as temperature and inverse correlations with population density have frequently been recorded. For example analysis of growth rates of the perch (Perca fluviatilis) over twenty years in Windermere show first, an increase in growth rate concurrently with a decrease in population density, and second, a very high correlation between summer surface water temperature and growth with year to year fluctuations of up to  $\pm 45\%$ . The two variables of population density and temperature could account for nearly all the variation in growth-rate (Le Cren, unpublished data). Further research on variations in growth-rate may yield fairly simple relationships between growth and some of the more important influencing factors so that "corrections" or "allowances" can be made for fluctuations in one factor while investigating another; e.g. correcting for annual variations in temperature when studying long-term changes in growth-rate.
- (d) Migrations and behaviour. Fisheries dependent on migrations to bring the fish to the fishing area or into the gear may be profoundly affected by changes in behaviour. At present so little is known about the factors influencing such migrations that nothing can be done to forecast such changes or allow for their effects on estimates of the vital rates. Measures of fishing effort or the intensity of fishing using gear that

depends upon the behaviour of the fish to make its captures may be more variable than methods of fishing where the fish plays a passive role.

As information on the influences of hydrological and other conditions on the survival, growth and behaviour of fish populations grows, more use can be made of such relationships to allow for chance year-to-year variations and fluctuations when estimates of population parameters are being made. Provided reliable correlations can be found, there is little risk in putting them to use without waiting for knowledge of the exact mechanism of the correlation. There remains, on the other hand, the influence of longer-term and intra- and inter-specific factors. There is evidence that significant changes in survival, growth rate and the balance between populations of different species, can occur naturally, or at any rate, independent of the effects of a fishery, and that it may be very important to recognize such changes without the need for detailed long-term study. (The fisheries of the Great Lakes of North America provide some good examples of such changes of which the spread of the sea lamprey (Petromyzon marinus) provides the most spectacular example. (Hile 1954). Unfortunately there seems no easy way short of detailed long-term investigation to recognize such natural changes and to distinguish them from the effects of fishing.

##### 5. Analytical Methods and Theoretical Models

It is likely that the further development of analytical methods and theoretical models of the population dynamics of exploited fish populations will yield valuable improvements in the understanding of the whole subject. If such understanding is to have important and widespread practical application it will, however, be necessary for the elaborate theoretical models to be simplified to their essentials. The models should be used to investigate the possible effects of variations in the various parameters and environmental factors in order to assess their relative importance under a variety of likely situations. Such theoretical investigations might well lead to the dismissal of many parameters and factors as being of only minor importance or likely to cancel out each other's effects, and so lead to concentration on those of greatest relevance.

A further step would be the development of the comprehensive analytical and theoretical investigations towards the discovery of simple measures of assessment that might then be applied in practice. Such simple measures would be features of the populations similar to those described in Section 1 as

methods of rough appreciation, but would differ by being based on a fairly profound analysis and understanding of the situations involved, rather than on superficial and empirical investigations. (As an analogy one might instance the use of the blood sugar test in the medical diagnosis of diabetes; a test that is simple yet reliable and based on an understanding of the nature of the disease rather than on a knowledge of its superficial symptoms). Tables of reference could be set up for such measures and for other relevant basic parameters so as to simplify and speed up the collection and analysis of data. As it is unlikely that it will ever be possible in practice to collect all the hydrographic, biological and statistical data ideally desirable for year-by-year assessment of the status of fish stocks, prior theoretical investigation and planning would seem to be essential. The theoretical analyses and model building must eventually lead not only to a deeper understanding of fish population dynamics but also to methods of assessment that can simply and speedily be put into practice where resources for sampling and analysis may be limited.

## 6. Summary

Some aspects of the problems of speeding up the assessments of the status of exploited fish populations are briefly discussed and reviewed. Emphasis is laid on: (1) the possibilities of developing and refining methods of rough appreciation, (2) the development of quicker and better methods of estimating the vital population parameters especially by avoiding the need for data from long time series, (3) the investigation and elimination of errors arising from natural fluctuations in population parameters, and (4) the development of analytical models as to yield simple diagnostic measures of the degree of exploitation, suitable for rapid and routine use in practice.

## References

- |                                                 |                                                                                                                                                                                               |
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TO MAKE THE BEST USE OF THE SCIENTIFIC TALENT, ARRANGE THAT MEN WITH SPECIAL SKILLS ARE MOST EFFECTIVELY USED FOR THE NEEDS OF THE WHOLE COMMISSION. THIS MAY REQUIRE ALLOCATING TASKS AND MATERIALS.

L. A. Walford.

Considering all the reports of the groups working at Biarritz along with those working at Halifax before the 1956 Annual Commission meeting, it is clear that a wide variety of fishery problems exist in the Convention Area. Many of these relate to the processes of fishing, to the effects of fishing on the stocks, and to the selectivity of fishing gear; many more relate to the biology of the various species of fishes and to the effects which the vagaries of environment have on abundance and distribution. To attack these problems requires research by a number of different kinds of specialists, for example, in fishery biology, bio-statistics, paleontology, microbiology, parasitology, biochemistry, oceanography, animal psychology, mechanical engineering, electronics. It requires, too, considerable special equipment, for example, research vessels, apparatus for observing sea temperatures and for collecting sea water, plankton and fish at desired depths; aquaria for all sorts of purposes including the experimental rearing of young fish; the study of behaviour, testing of fish tags, etc.; mechanical aids such as computing machines, statistical card systems, etc. which are required for the mathematical analyses so intimately a part of fishery research.

In planning research programs for the Convention Area and in judging the needs of men, material, and equipment, therefore, certain inescapable facts must be faced. The Convention Area is large (nearly one million square miles); the hydrographic conditions of the environment are exceedingly complex; the fisheries in the area are among the most valuable in the world (over four billion pounds); knowledge about the fishery resources varies greatly from one sub-area to another (within a subarea from one zone to another), and from one species to another; the amount of research varies, geographically within the Area, and among the countries belonging to the Convention.

There are other inescapable facts: no part of the Convention Area is biologically isolated; very few problems are entirely local in scope. Fishery research is costly. It requires possessing and operating seagoing vessels, the employment of scientists and assistants, the collection, processing and analysis of masses of data. We are living in a period when scientific personnel is in great demand, so that competition for them is keen. Consequently it is necessary that the member countries plan their research programs carefully, so as to cover their tasks adequately, while using their men and facilities most prudently and effectively.

No fishery problem is ever static. The weather, the hydrography, consequently all the conditions of environment, are continually changing. So, also, are the technologies of fishermen. The populations of people in all of the member countries are increasing and the demands for fish must increase apace. Thus the problems of fully utilizing the sea resources in this part of the ocean are likely to grow in complexity and are not likely to be solved in a hurry. Therefore, it is important in planning not to think of present conditions, but of needs far into the future. The Commission cannot hope to establish a fully developed research program at once, but must content itself now with laying a solid foundation so that the more difficult problems of the future can be met with enough of the right kind of knowledge. Wherever it is mutually beneficial, the members should share research facilities; wherever possible, they should expand their several programs to fulfill the Commission's function.

The Committee made many recommendations in the course of its discussions. Some of these relate to techniques of research and need not be recounted here. Recommendations which must be particularly brought to the Commission's attention, however, are the following;

#### A. Statistics and Sampling

- A.1 In studying all the research needs of the Convention Area the Committee on Research and Statistics unanimously agreed that the highest priority should be assigned to collecting and reporting statistics and to sampling the catches of their fleets.
- A.2 Certain member countries should expand their collection of statistics to bring them up to the level of ICNAF requirements. This they should do by the use of log books, interviews of captains and sampling of their fleets.
- A.3 All countries should collect and report to the Commission records of the quantities, species and sizes of fish discarded at sea. This information should be based on log book records supplemented by observations and measurements made at sea.
- A.4 Quantities of statistical data on catches, sizes of fish, etc. exist among the member countries (for example in log books), but are not fully accessible to workers because they are not published, or are not in a comparable form. These data should be collected and published. The Secretariat has undertaken this task, but must have the co-operation of all members.
- A.5 The sampling of fish caught: to determine the lengths, ages, and



weights of fish caught is generally inadequate. For all member countries, the sampling of the catches of cod (the most important of all species in the area) is inadequate; for some countries it is completely lacking.

- A.6 Samples of commercial catches landed ashore can be obtained in large numbers at relatively low cost, and these should be taken wherever sampling can be referred to specific stocks of cod. Samples of landings do not give a complete picture of catches, for large quantities of cod may be discarded at sea. It is, therefore, important to sample catches at sea, moving from vessel to vessel in order to assess differences between sizes caught and sizes landed. Each country should send observers to sea on commercial vessels for this purpose. At least two observers should be employed for sampling at sea on commercial vessels by each of the governments carrying out substantial fishing in the Convention Area (Canada, France, Portugal and Spain). Portugal and Spain have already taken steps to meet this requirement. Other countries, such as Denmark and Norway, which carry on substantial exploitation should sample correspondingly at sea. If sampling by member governments cannot be so expanded, the Commission should set up a joint program of sampling commercial catches. This would involve employment of observers and charter of vessels. It should be avoided until other methods of sampling are fully explored.
- A.7 For each species sampled, each country should report to the Secretariat the sizes, ages, weights and sexes of fish sampled, by place and time of capture. The Commission should publish these statistics.
- A.8 These additional statistics will considerably increase the load on the Secretariat, and it would, therefore, be necessary either to increase the assistance given to the Biologist-Statistician or to reduce the work required to produce the Statistical Bulletin with its present contents. The latter could be achieved by mechanizing the tabulating operation, (perhaps by the use of IBM machines) and if this proved possible, the burden of the proposed additional compilations would also be greatly lessened.

#### B. Research Vessels and Laboratory Equipment

Many of the recommendations by this Committee require special equipment, which is necessary to carry out the research which the Commission must require.

- B.1 As many observations of a special and technical nature must be taken systematically at sea, the need for research vessels working in the Convention Area is great. For example, fishing for young fish to assess strength of year groups and sampling of stocks by fishing in unfished areas are necessary tasks which can only be done from research vessels. The number of research vessels being operated in Subareas 2, 3 and 4, should be increased and the programs of these vessels, their schedules of operations and the techniques of their observations and collections should be co-ordinated by group planning among the members in order to obtain the most efficient use of the ship time available.
- B.2 Since research vessel operations are costly and scarce, every opportunity should be taken to make use of fishing vessels, patrol ships and any other ships which traverse or spend time in the Convention Area so as to obtain samples of plankton, information on water temperatures and, where possible, data on the fish stocks. Automatic collecting devices and recording instruments should be used wherever possible so as to minimize the need of technical personnel.
- B.3 The Committee has begun taking inventory of all facilities for obtaining meteorological and hydrographic data and for collecting plankton samples systematically in the Convention Area.

Many of the research projects which are in this Committee's long range plan will require experimental laboratory facilities which are not now available to scientists of member countries. Much can be learned by rearing of larvae and young fish in aquaria, where the conditions of temperature, food and chemical composition of the water can be manipulated to define requirements of normal growth and survival. Tests of tagging methods and studies of physiology, disease, and behaviour of adults can be conducted in large tanks. Such studies are needed to provide the basis for observations at sea and to define the causes of natural mortality. They cannot be undertaken, however, if the necessary equipment is lacking.

#### C. The Need for Frequent Meetings of Scientific Personnel

The healthy program of the scientific work of the Commission depends upon planning conferences among scientists. To this end it is imperative that ample opportunity be given the scientists of all Convention Countries to meet together whenever the need arises.

The whole Committee on Research and Statistics may need to meet at intervals between annual meetings as it did at Biarritz. The Scientific Advisers

to Panels may find it necessary to meet to investigate the problems related to particular subareas as the Advisers to Panels 3, 4 and 5 have done in the past. Scientists working on special problems such as population dynamics or mesh measurement should have opportunity to meet frequently to develop or compare techniques, to interchange ideas and information so that the scientific work of the Commission can progress in an orderly manner without overlap and unnecessary duplication. It is uneconomical for the scientists of each country to work separately. It is acknowledged that transatlantic travel is expensive, but frequent conferring of scientists of the Convention Countries is essential if the Commission is not to set up its own scientific staff.

The Committee has prepared a long range plan of researches for the Commission. This should be re-examined and revised at frequent intervals as the countries increase the amount of their participation and as the results of their labours emerge.

The extra commitments which have been outlined in this report have been carefully considered as essential for advising the Commission on the course to pursue in order to obtain the optimum constant yield from its area. If the new program is accepted and attempted with present resources we should fail by attempting too much. It is therefore useful to relate the effort and resources needed to carry out the additional investigations. The comparison may be most usefully made by a rough computation which compares the annual current expenditure on research in the Commission area with extra expenditure involved in the new work. The estimates are as follows:

Current program - \$ 1,272,000.

New work - 476,500.

It will be seen that if the recommendations of the Biarritz Meeting are to be effectively followed up, an increase of expenditure of about 37% will need to be found for the total annual current expenditure of the nations concerned in the Commission's work. This increased percentage will not, of course, be the same for each country but may vary according to its particular interest and the extent to which it is already undertaking research.

Some indication of the participation of the different Member Countries in the fisheries of the Commission area is given in the following table:

## 1956 Landings in thousands of metric tons.

Country	Cod	Haddock	Redfish	Halibut	Total
Canada	353	84	26	3.4	466
Denmark	53	-	-	-	53
France	111	-	-	-	111
Germany	29	-	7	-	36
Iceland	9	-	7	-	16
Italy*	12	-	-	-	12
Norway	42	-	-	0.8	43
Portugal	225	-	-	-	225
Spain	110	32	-	-	142
U. K.	3	1	-	0.2	4
U. S. A.	15	73	69	0.1	157
Total	962	190	109	4.5	1265

\* Estimate based on 1954 Landings.

## EFFECTS OF HADDOCK MESH REGULATION IN SUBAREA 5.

Herbert W. Graham.

The history and present status of the regulation was reviewed by H. W. Graham. The Committee re-examined the need for regulation, the scientific basis upon which the decision was made to increase the age of first capture of Georges Bank haddock, the basis for selecting 4 1/2 inch mesh, and the research program set up to assess the effect of the regulation.

From the report submitted the Committee noted that the 4 1/2 inch mesh is releasing small sizes of haddock precisely as had been predicted. The discard of unmarketable size has been reduced to practically nothing. The Committee also noted that the large mesh nets are more efficient in the capture of larger sizes of haddock so that, unless the fleet is fishing on large concentrations of scrod haddock, there is a distinct benefit derived from the use of the larger net.

It was observed that the real test of the value of delaying captures of the small fish lies in comparing year-class yields before and after regulation, and that doing this requires continued use of some vessels with the old small mesh gear. The 1952 year-class is the first large brood to be used in the assessment of the conservation value of the regulation. A preliminary measure on relating yield of this year-class may be ready for the June meeting of this Committee.

The Committee congratulated the United States for its success in maintaining the research program endorsed by the Commission in 1951 realizing that considerable difficulties must be met in continuing a program which involves special co-operation of the fishing fleet.

The Committee re-affirmed its original recommendation that a program designed to assess the effect of the regulation be rigidly adhered to. Toward this end it urges that every effort be made to continue the group of licensed vessels so that a satisfactory abundance index of two-year-old fish can be maintained, an index which is essential to the assessment of the effects of the regulation on the population of haddock.



COMPARISON OF EUROPEAN AND NORTH AMERICAN TECHNIQUES OF MEASURING NETS, OF READING AGES OF FISH AND OF STUDYING GROWTH.

Convenor's Report, B. B. Parrish.

The attendance at the various sessions of the working party varied widely during the course of the meeting. Some of the sessions were attended by a large part of the whole Committee while others (e.g. the net study meetings) were attended by a small number of participants. Two meetings were held jointly with other working parties, one with Working Party VII to discuss speciation in redfish, and one with Working Party I to discuss methods used in growth studies.

Scope and Procedure of Working Party

Topics covered: The following topics were covered in the eight sessions held by the working party:

A. Biological problems:

- (1) Methods of measuring and recording lengths of fish.
- (2) Methods of age determination of cod, haddock and redfish.
- (3) "Racial" investigations of redfish (jointly with Working Party VII.
- (4) Methods used in growth studies, with special reference to the use of skeletal structures (jointly with Working Party I).

B. Net and mesh problems:

- (1) Methods of mesh measurement.
- (2) Shrinkage of net material.
- (3) Mesh selection experiments.

General considerations: The working party centered its attention chiefly on:

1. Examining the features of the present methods used by different workers in the ICNAF area.
2. Comparing the results obtained by these different methods, assessing their accuracies and relative merits, and highlighting the chief problems and difficulties associated with each.

3. Determining possible lines of investigation for resolving the most important problems and difficulties.
4. Seeking agreement on standardization of methods wherever practicable.

Throughout the proceedings, emphasis was placed on the importance of "economic" considerations in the choice and application of methods, and of possible ways in which greater mechanization of routine methods might be effected.

Time did not permit a complete treatment of all aspects of the wide range of methods discussed by the working party. Discussions on some topics had to be restricted within narrow limits, and some interesting and important facets of the main topics had to be overlooked. In particular, growth and mesh selection problems were dealt with only briefly.

Proceedings: Throughout its deliberations, the working party centered attention on the exchange of data, views and ideas by informal discussion. In accordance with a request made in advance of the meeting, a number of written contributions on various topics dealt with by the working party were available to members, and most of which had been circulated in advance of the meetings. These were not formally read by the authors during the proceedings but their contents, together with other material presented during the course of the proceedings, provided the subject matter on which discussion and debate were centered. A list of the written contributions for the various topics dealt with by the working party are given at the end of this report.

The following report gives a brief summary of the main items discussed by the working party, and the conclusions and recommendations arrived at for each major topic.

#### 1. Methods for Obtaining Fish Lengths

Consideration was given to the following main aspects of this subject:

- (1) The choice of length dimension.
- (2) The methods used by different workers in making and recording measurements.
- (3) Standardization and mechanization of measuring and recording methods.

Each of the workers on the main ICNAF species -- cod, haddock, halibut



and redfish -- first described the length dimension used by them in routine length measuring and then outlined the method adopted for taking these measurements. This revealed that present practices differ both as to the precise length dimension measured and to the methods used in measuring and in recording the data. Some workers measure fork or "median fin" length, while others measure total length either with the caudal fin in its natural position or with the lobes drawn together in the midline. No workers reported using "standard length". Whilst most workers adopt the simple measuring board in making measurements, some use an "offset" scale and others not, and some read the lengths always to the nearest whole length interval, while others read to the length interval below.

The discussion indicated clearly that there are important differences between the length measuring procedures adopted by different workers on the same species, and between different species, and it was recognized that for some species, the differences might be large enough to invalidate the pooling of length frequency data. Perhaps most important of all, it was evident that workers were not aware of the various length dimensions and recording practices adopted, or of the magnitude of the differences between their recorded results.

It was agreed that comparability of length frequency data for each species studied throughout its range of distribution was very desirable and that steps should be taken to ensure that they should be made so. However, it was also recognized that complete standardization of the whole measuring procedure might prove difficult to put into effect. For example, a worker might be reluctant to break with the traditional length dimension and method of measuring and recording in his country. Earlier attempts in the ICES area at complete standardization of length measuring methods had failed largely for this reason. Thus, while the need for standardization of measuring procedure was fully endorsed in principle, it was felt that, until some definite decision could be reached on its practicability, steps should be taken to achieve comparability of length frequency data in other ways. It was agreed that this could be accomplished without complete standardization by the use of conversion factors, relating one length dimension with another. It was also felt that there was an urgent need for all workers to know precisely the dimensions and measuring methods used by all other workers on each species of fish. It was agreed that details of the methods used should accompany all reports and publications involving length frequency data.

The problem of the choice of length dimension was considered in some detail. It was generally agreed that the choice must be governed primarily by scientific considerations, but that practical considerations such as "ease and speed of handling" must be taken into account. Such considerations, for ex-

ample, will usually tip the balance of choice in favour of "total" rather than "standard" length if there are no other grounds governing the choice. It was generally agreed that the universal use of some measure of "total" length for the main species was due mainly to practical considerations. Discussion revealed that little was known about the differences in scientific result which might be derived from different length dimensions. In particular, insufficient evidence was available for making decisions regarding the relative merits of "standard" and "total" length, on scientific grounds. It was generally agreed that the answer might differ according to the nature of the investigation. The "efficiency" of the relationship between length and weight was suggested as a criterion against which to judge the merits of these measurements. In view of the large practical advantages of using "total" length rather than "standard" length all workers present considered there were no firm grounds for changing the present general routine practices of measuring "total" length, but it was felt that investigations should be instituted to arrive at more comprehensive data on which a decision could ultimately be made. It was recognized that the decision might not be the same for all species or for all types of investigation.

Length measurements are taken in very large numbers by all fishery workers throughout the world, and as investigations develop there is a growing need for larger and larger masses of length data. The total cost of this routine operation is therefore very formidable and measures for increasing the overall efficiency of the operations, both as regards the speed and cost, must be given serious consideration. The possible introduction of mechanical measuring and recording devices was considered in some detail. A possible form which an apparatus for measuring and recording length and weight might take was outlined by Dr. Kesteven. It was clearly evident that mechanization of this sort was feasible, and that, providing the apparatus could be constructed at a reasonable cost and would be able to withstand the rough handling which is inevitable under field conditions, it would be of substantial help in current fisheries investigations. The working party felt that funds should be made available for a full-scale investigation of this type of project to be made by qualified technicians. Dr. Kesteven pointed out that FAO might be able to help in initiating such a project.

Conclusions: It was unanimously agreed by the members of the working party that all length data for a species, compiled by different workers in different countries, should be comparable and readily exchangeable between workers. In principle, this is best accomplished by the adoption of a standardized system of length measurement in which the dimension to be measured, the method of measurement and the system of grouping and recording the data are defined in clear terms. However, it was recognized that this may not be easy to adopt in practice, and would necessarily take time to achieve. As an immediate measure, therefore, it was agreed that all workers should record in reports

and publications details of their measuring methods at the present time. Meanwhile, attempts should be made to assess the practicability of standardization of length measurement by ICNAF workers, to determine for each species which length dimension is the best to use for general routine investigations, and to arrive at conversion factors relating one length dimension to another.

### RECOMMENDATIONS

The following recommendations were drawn up for passing on to the Research and Statistics Committee:

1. Standardization of length dimension and method of measurement is desirable in principle.
2. Workers should define length dimensions and the grouping system in precise terms in publications.
3. The relations between different length dimensions should be investigated for all species and factors should be made available for converting one dimension to another.
4. Detailed investigations should be conducted to determine for each species which dimension is most appropriate in scientific work.
5. Attempts should be made to introduce mechanization in length and weight measurements of fish, and facilities and funds should be provided for a detailed study of this problem by skilled technicians.

### 2. Methods of Age Determination

The working party considered the methods used, the major difficulties and problems involved and the general accuracy in age determination of the three species cod, haddock and redfish. In addition to the presentation of data and the exchange of views and ideas in the meetings of the working party, considerable time was spent by the chief workers in practical demonstrations of the methods and material and in comparisons of their criteria of age interpretation. The following remarks summarize the most important points revealed by these deliberations.

- (a) Cod - Discussion centered chiefly on the methods used in age interpreta-

tion of cod from otoliths. No workers present used the scales for age determination of any but the youngest age categories. It was discovered that all ICNAF cod workers used the same general method of otolith examination, i.e. the low-power examination of the broken or cut surface of the otolith in reflected light.

Mr. Rollefson demonstrated in detail the essential features of this method, and emphasized the importance of the distribution of the light for easy and accurate recording. He showed that some shading of the surface of the otolith was desirable, and he demonstrated how, with the appropriate lighting arrangement, the zones could be interpreted. He urged all otolith workers to experiment with the lighting arrangement when commencing reading. Mr. Rollefson also emphasized the importance of a rigorous training schedule for otolith reading technicians, and he reported that in Norway all technicians recruited for this work were subjected to a thorough eye and general medical examination.

The method of distinguishing the spawning zones of cod otoliths was also demonstrated by Mr. Rollefson, who indicated how a study of the distribution and nature of the zones in the otolith gave important information on ecological differences between groups of cod in neighbouring areas.

No major difficulties in age determination by the method were mentioned by the workers present, and it was generally felt that it provided a sufficiently accurate method for all purposes.

While the otolith gives an accurate measure of the age of cod, difficulties sometimes arise in obtaining samples of otoliths, particularly from market sources, where cod are often landed in a headed state. For this reason, English workers had studied the uses of cod fin rays for age determination. Data were presented by Mr. J. A. Gulland of a comparison between age readings determined from dorsal fin rays and from otoliths. These results showed that fin rays can be used with reasonable efficiency for fish less than 6-7 years, but that for older fish the fin ray assessments gave progressively lower age readings than the otoliths. It was agreed that the fin ray could not be regarded as an efficient substitute for the otolith in cod age analysis, but it might be of use in age readings of young cod in situations where otoliths are unobtainable.

The importance of "Petersen's method" of determining age composition of large samples of cod length data was stressed, particularly in situations where large samples of otoliths could not be obtained or where facilities for reading large samples were not available.

RECOMMENDATIONS

The following recommendations were drawn up for passing to the Research and Statistics Committee:

1. The working party recommends that the otolith age reading technique, developed and perfected in Scandinavia, should be adopted by cod workers, and that each worker should examine possible improvement in the method by modifications of the lighting system.
2. Attempts should be made by all cod workers to incorporate in the otolith analysis the discrimination of spawning zones, as described by Mr. Rollefson.

(b) Haddock - Two skeletal structures are in general use in age reading of haddock; the scale and otolith. Discussion in the working party was centered on the differences in results obtained from these two structures, and on the relative efficiencies of each.

Dr. Templeman presented haddock length frequency data from Subarea 3 and their age compositions obtained from scales, and showed that the scale readings fitted well with the dissection of the length frequency data, and revealed the presence of a dominant year-class passing through the fishery. It was abundantly clear that the scale reading method provided an efficient means for obtaining the overall age composition of the catch. Dr. Templeman reported some difficulties in age reading from scales, particularly amongst older haddock because of frequent occurrences of check rings, but provided the reader was familiar with the material, efficient interpretation was possible. Dr. Templeman stressed the importance of a thorough knowledge of the biology of the species in the area under investigation, and he observed how, from a detailed examination of the scale structure, "check" rings can be distinguished from true winter rings.

Data on differences in age reading of haddock from Subareas 3, 4 and 5 obtained from scales and otoliths were presented by North American workers (Kohler, Templeman, Clark and Jensen), and of haddock from the Barents Sea by Parrish. These data indicated general agreement, but with some random variation between the two methods for fish less than 6-7 years of age, and illustrated a progressively greater and more systematic discrepancy for the older ages, for which the otolith gave the higher readings. The European material in particular indicated wide divergence of result for haddock older than 8 years. Mr. Parrish also demonstrated the same discrepancy in age reading of North Sea herring from scales and otoliths, and also showed a

greater consistency between otolith readings taken by different workers than between scale readings.

Mr. Saetersdal showed that otolith age readings of young Norwegian haddock agreed better with the age composition as determined by Petersen's method than did scale readings. This he attributed to a total lack of zone formation in the scales of some haddock, whereas in the otolith these zones were always formed. He mentioned also the greater ease in counting the outer zones in the otoliths of mature haddock. Thus, otoliths are now always used in the Norwegian haddock age investigations, the method employed being the same as that used for cod. However, scales are still taken for use in growth investigations. Mr. Saetersdal demonstrated how, as with cod, spawning zones can be recognized in the haddock otolith.

General discussions revealed that haddock workers are divided on the issue of choice of skeletal structure for age determination. It was generally acknowledged that the otoliths gave more accurate and consistent readings over the whole age range, but that in some areas, particularly where the stock is composed principally of young fish, the scale provides satisfactory results and is preferred because of the greater ease in obtaining the material and greater speed in handling. It was agreed that in some investigations a compromise, involving the use of scales for young fish and otoliths for older fish, might be appropriate.

The data presented in the meeting showed that haddock workers should not become complacent about their methods of age determination, particularly the workers using scales, and it was suggested that they should undertake rigorous checks of their results against other methods. Staining techniques were suggested as a possible aid in increasing the efficiency of reading age from scales.

#### RECOMMENDATION

The following recommendation was passed on to the main Committee:

All haddock workers should undertake to examine their methods of age reading critically, including comparisons between scales and otoliths. Wherever possible checks of the readings obtained with their current methods should be made with other data.

(c) Redfish - The current controversy concerning the interpretation of age of redfish was one of the main topics considered by Working Party VI. This pro-

blem was discussed during three sessions and a fourth meeting was held jointly with Working Party VII to discuss the "speciation" problem. Much time was also spent by the interested workers in studying otoliths and other material brought to the meeting.

Current views are divided as to the rate of growth of the main body of redbfish, Sebastes marinus in the North Atlantic; Dr. Kotthaus claims a relatively fast rate of growth while Mr. Kelly and other workers claim the contrary. The working party examined the basic features of the methods used by these workers and the data presented on this important subject. It set out to determine whether the differences in growth rate claimed by these workers could be attributed to real biological differences in the stocks of Sebastes on which their respective investigations have been based or whether they could be attributed, at least partially, to differences in age interpretations by the two groups of workers.

The methods of investigation and the results obtained by Dr. Kotthaus were first examined. Dr. Kotthaus presented a written contribution outlining the main arguments underlining his general thesis. These are essentially as follows:

1. The otoliths of Sebastes when viewed, in a whole state, under low magnification contain a large number of distinguishable narrow zones interspersed between distinct wider zones. These thin zones do not represent true winter zones and must be discounted when reading the age of the fish.
2. A consequence of reading the narrow zones is an unreasonably slow rate of growth, an unreasonably high age of first maturity (reaching an age of 17 years in some instances) and a wide range of ages reaching first maturity each year.
3. In general, the length frequencies of the commercial catches from the north-east Atlantic fishing grounds do not conform with the hypothesis of extremely slow growth in Sebastes.

For these reasons, Dr. Kotthaus had adopted the method of counting only the wider zones on the otoliths which, providing the whole otolith was viewed under low magnification, could be readily distinguished from the narrow zones.

Mr. Kelly then presented the alternative viewpoint. Photographs of Sebastes otoliths taken from fish in the Northwest Atlantic were presented, all of which showed clearly defined "winter" zones and between which no sound reason for discounting some and counting others could be found. These readings indicated a very slow rate of growth in Sebastes. The method used by

Mr. Kelly in viewing the otoliths is the same as used by Dr. Kotthaus, except in the large specimens when he examines the broken surface as in the cod investigations. Photographs of specimens of small Sebastes from the Gulf of Maine were also presented and were used to illustrate the small increase in size of Sebastes throughout the year.

Data, relevant to the subject, were also presented by other members of the working party. Dr. Lucas presented a series of length frequency data taken by Scottish research vessels off the southwest coast of Iceland and around the Faroes over a number of years. These data revealed great consistency between the length frequencies from month to month and from year to year, and the Icelandic data showed two main modes, at 20-22 cm and 35-40 respectively. No interpretation of these data was put forward but the view was expressed that the two modes might belong to the two species, S. viviparus and S. marinus respectively.

Dr. Templeman presented length frequency data of a group of small Sebastes, caught in Hermitage Bay off the south coast of Newfoundland over a period of years. Very small changes in length frequencies were recorded over the period, the increase in mode being from 7 to 11.5 cm between December 1953 and 1955. During this time no smaller group of fish appeared in the catches which suggests that these fish were completing their second year of growth in 1955. Dr. Templeman also provided extensive scale material for inspection.

Photographs of otoliths of S. marinus, and S. viviparus, prepared in Norway, were presented by Mr. Rollefson and he claimed that it was impossible to discriminate between the two types of zones as claimed by Dr. Kotthaus. The Norwegian age interpretations agreed substantially with Mr. Kelly's.

Further information on the interpretation of Sebastes otoliths was presented by Dr. Fridriksson. He cited examples of Sebastes otoliths on which up to 70 winter zones could be counted, and he was forced to regard Sebastes as a very slow growing fish.

Discussion of these data revealed clearly that the differences between the growth rates of S. marinus as claimed by Dr. Kotthaus and Mr. Kelly and other workers were due, at least in part, to differences in the interpretation of otolith zones. It was claimed by a number of members present that they could see no sound justification for the basis of discriminating between the multiplicity of zones present, as practised by Dr. Kotthaus. It was revealed that conformity of interpretation was possible between groups of biologists when the criteria used by Mr. Kelly were adopted, but not so when attempts were made to discriminate between zones. The view was also expressed that



there was no a priori justification for not accepting a slow rate of growth for Sebastes, and it was not unreasonable for the incidence of first maturity to be spread over a wide range of years. The cod was cited as an example in which such was the case.

The characteristics of the commercial fisheries for Sebastes were discussed in the light of the two current growth hypotheses. A general feature of these fisheries is that down to at least 400 metres the bulk of the commercial catch is composed of fish less than 60 cm in length. This length corresponds with an age of 7-8 years according to Dr. Kotthaus' interpretation, and of 25-30 years by the "slow growth" workers. Clearly, unless the Sebastes population is subject to such heavy mortality that the total life span is reduced to 8-10 years, for the fast growth hypothesis to be acceptable large quantities of Sebastes must move out of the exploited areas or must undergo a change in vertical distribution and escape the fishing gear. Furthermore, these fish would be expected to reach a very large size. It is known that the S. marinus population extends to depths greater than those fished intensively at present, and Sebastes of sizes up to 70-80 cm are caught, but there is no evidence at present that large concentrations of "giant" Sebastes exist. On the other hand, on the basis of the slow growth hypothesis, it is not unreasonable to expect the length composition of the population to taper off at 60-65 cm corresponding with ages of 25-30 years; under these circumstances no very great concentrations of older and larger Sebastes would be expected to exist. In this case, large untapped reservoirs of younger Sebastes would be expected, from which the present fished stocks are derived.

The importance of the growth hypotheses in assessing the present state of the Sebastes fisheries was stressed and it was agreed that caution must be exercised in interpreting observed trends in yield and in catch per unit effort of the Sebastes fisheries.

Possible lines of research for resolving the age interpretation problem were discussed. Four possibilities were considered:

- (a) Tagging.
- (b) Rearing of young Sebastes.
- (c) Exploratory fishing to discover untapped reservoirs of Sebastes or concentrations of "giant" fish.
- (d) Exchange of material between Sebastes workers, and use of alternative interpretation techniques.

### RECOMMENDATIONS

The following recommendations to the Research and Statistics Committee were made following discussions of these projects:

1. German workers should undertake to tag S. marinus experimentally by the "hook" methods; Danish workers should attempt to tag S. viviparus in the Faroes area, and S. marinus in the west Greenland area; Norwegian workers should look into the possibilities of tagging Sebastes off the Norwegian coast; and North American workers should attempt tagging experiments.
2. Rearing experiments with young Sebastes in aquaria should be attempted by Norwegian and German workers, and by other workers if opportunity and facilities are available.
3. Exploratory fishing expeditions should be made by United States workers to seek out reserve stocks of Sebastes. Attempts should also be made to study the vertical distribution of Sebastes with underwater television.

At the conclusion of the meeting all Sebastes workers were asked to make an intensive and critical review of their age interpretation techniques and wherever possible to seek other sources of information against which to check the bases of their age analyses.

On several occasions during the meetings information was presented which illustrated substantial differences in growth rate between stocks of Sebastes in different parts of the North Atlantic. These differences are greatest between S. viviparus and the two possible subspecies of S. marinus, but there are also differences between the growth rates of the main subspecies of S. marinus in different areas. It was recognized, therefore, that there is a major "racial" problem for Sebastes as well as the age interpretation problem, and it was agreed that Working Party VI should join with Working Party VII to discuss this important problem in detail. The discussions and recommendations on this aspect of the Sebastes work are contained in the report of Working Party VII.

### 3. Growth Study Methods

An important method for studying growth in fish is the taking of length

measurements on skeletal structures and calculating the total length of fish at the ends of successive years of life. The scale has been used most extensively in this work but otoliths and opercular bones have been used by some workers.

An essential to the correct application of this method is an accurate knowledge of the form of the fish length to skeletal length relation. When this relation is proportional, the fish length estimates can be made by use of the simple proportionality formula, but if it departs from proportionality, then errors in the estimated total length will result from using the proportionality formula unless corrections are applied. The errors will be progressively greater as the calculations are made from progressively larger (older) fish. This will result in biased estimates of growth and apparent differences in mean length (known as Lee's Phenomenon) of fish at any age. It is clear, therefore, that a knowledge of the general form of this relation is very important in the application of this method of growth study and in using it to study real changes of a population with age. Not until it is known that inherent bias has been eliminated can "Lee's Phenomenon" be used as an indication of real changes in the stock with age.

The occurrence of "Lee's Phenomenon" for North Sea haddock and northern North Sea plaice was demonstrated by Mr. Jones. He showed that the estimated lengths at the end of the first year of life decreased substantially when they were calculated using the proportionality formula for scale measurements taken from successively older and larger fish. Detailed analysis of the relation between scale length and fish length showed, however, a curvilinear relation, which requires the use of corrections to the length estimates using the proportionality formula. When these were applied, the magnitude of the differences between calculated lengths was reduced but not eliminated, which suggested that there were real changes in the composition of the stock with age, due either to biological factors or differential rates of mortality amongst the faster and slower growing fish.

Mr. Saetersdal demonstrated a linear but not proportional relation between scale length and fish length in the Norwegian haddock and he showed how, when the correct calculation formula was used in a homogeneous population of young haddock, "Lee's Phenomenon" was not evident in the estimated lengths of haddock at the end of their first year of life. He then showed how with older fish the phenomenon was experienced and could probably be explained on the basis of a range of ages of first maturity throughout the population.

Mr. Boerema outlined the relation between otolith length and fish length of plaice in the southern North Sea and showed a linear relationship. A linear relation between otolith length and fish length had also been recorded for her-

ring by Dutch workers. He pointed to some difficulty in interpreting the point on the otolith of plaice to which measurements should be taken due to possible changes in the widths of the outermost complete hyaline zone.

Means of reducing the time taken in making growth calculations by this method were also discussed, and Dr. Kesteven outlined the essential features of an apparatus by which the estimated fish length can be read off directly.

Discussion of the data showed that lengths calculated from measurements of skeletal structures could provide very important biological information on the ecology of fish populations providing it was known that there was no inherent bias due to the formula used in length calculations. It was recognized, therefore, that the value of this method depended on an accurate knowledge of the fish length to skeletal length relation. It was agreed that all work using this method should be preceded by a study of the fish length to skeletal length relationship for the fish stock under investigation. It was evident from data presented at the meeting that different stocks of a species might give rise to different relationships. A talk on growth studies of the Georges Bank haddock was also given by Mr. C. Taylor to the whole Committee at the end of this meeting. (See Papers and Discussions).

#### RECOMMENDATION

The following recommendation was passed to the Committee:

The working party emphasizes the importance of a knowledge of the relation between the fish length to skeletal structure length in the use of skeletal structures in growth investigations, and it recommends that this relation should be established for all stocks of each of the species for which the method is employed.

#### 4. Net Measuring and Mesh Selection Methods

The deliberations of the net-study group were centered on various facets of the problem of mesh measuring in the ICNAF area in relation to both experimental work and the enforcement of the mesh regulations. The question of standardization of mesh measuring procedures between the ICNAF and the Permanent Commission areas was considered. The importance of shrinkage in mesh measurement was also dealt with, and a short time was spent in discussing techniques for obtaining mesh selection data. A number of contribu-

tions presented at the meeting of this group are appended.

The discussions of the working party were directed towards the following main questions:

- (1) What is the best and most practical mesh dimension to adopt in both experimental and enforcement work?
- (2) What is the most appropriate and reliable method of measurement?
- (3) What distribution of measurements over the net is most appropriate in experimental selection work and in enforcement measures?

(1) The best and most practical mesh dimension: The group first considered the criteria which govern the choice of mesh dimension in both experimental and practical enforcement work. It was agreed that the most appropriate dimension was the one which gives the simplest and most consistent relationship with the selection properties of the net.

The appropriateness of the present "internal longitudinal stretched mesh dimension" was then reviewed in the light of this criterion. It was agreed that a major advantage of this dimension was that experiments conducted on both sides of the Atlantic revealed a fairly consistent linear relation between it and the 50 percent release length for a number of species of fish over a fairly wide range of mesh sizes in the cod-end of manila trawls. This permitted selection factors relating mesh size and 50 percent release length to be calculated. Further advantages were the relative ease of obtaining rough measurements quickly and its suitability for conversion to any other required dimension.

There are, however, possible disadvantages to this dimension. It has been shown in a number of experiments in the ICNAF and European areas that the "selection factors" using this mesh dimension vary with the type of material used in the cod-end. It is necessary, therefore, to consider whether greater consistency in the selection factors for different materials might be obtained with other mesh dimensions. It is possible also that the differences between the values of the selection factors for different species of fish might be smaller with another dimension.

Discussion of this problem showed that little is known of the relations between selection and other mesh dimensions and it was agreed that for the present the "internal longitudinal stretched dimension" should remain in use both for experimental mesh selection work and as the basis for enforcement of the mesh regulations. The group agreed, however, that experiments should be

conducted to provide the necessary information from which choice of the most appropriate dimension can be made.

### RECOMMENDATIONS

1. The "internal longitudinally stretched mesh dimension" should remain in use for the time being both for experimental mesh selection work and as the basis for enforcement of the mesh regulations.
2. Investigations should be made to determine other relevant dimensions which might replace the existing dimensions. The following lines of study are suggested:
  - (a) A thorough study of existing relevant mesh measurement information.
  - (b) Measurements should be made of different mesh dimensions of cod-ends made of different materials, and for which the selection characteristics are known. Dimensions suggested are: The internal longitudinally stretched mesh, various "diamond" dimensions, the "square" dimensions, and the circular diameter. These dimensions should be measured under a variety of pressures, using suitably constructed gauges.
  - (c) Selectivity experiments should be conducted at sea using a wide range of mesh sizes for cod-ends made of different materials, with the mesh dimensions measured on the basis of results obtained under (b).

(2) Mesh measuring methods: It was stressed at the outset that for practical enforcement purposes a method of measurement must be adopted which is easy and quick to apply and which is reasonably free from large operator bias. It was agreed also that if possible the method adopted in experimental work should be the same as that used in routine enforcement work, or where this is not adopted the relation between the measurements obtained in the two systems should be known.

The methods of mesh measurement at present adopted for routine checks of the mesh regulations in the ICNAF and Permanent Commission areas were briefly described by the members present. These methods differ in a number of important respects. Whereas in the ICNAF area regulations, a standard gauge exerting a standard insertion pressure, is prescribed, in the Permanent Commission area no such rigid measuring procedure is specified, and in consequence a number of different measuring systems are employed.

The view was expressed by a number of members representing countries with fishing fleets regularly visiting the ICNAF and Permanent Commission mesh regulation areas that if possible standardization of the measurement procedures in the two areas should be effected, particularly as regards the type of gauge used and the number and distribution of measurements prescribed. It was generally acknowledged that such standardization was desirable in principle, but it was recognized that there might be formidable practical obstacles to overcome in effecting complete standardization in these procedures. It was agreed, however, that early steps should be taken to standardize the method of measurement for experimental work in the two areas, and that the question of standardizing the system of measurement in the mesh regulation procedures should be looked into.

The problem of the most appropriate pressure to use in mesh measuring was considered in detail. The results of deliberations on mesh measuring methods held at the meeting of the Comparative Fishing Committee of ICES in 1955 were made known to the group. These were as follows:

- (1) Standardization of the pressure used in mesh measurement was desirable.
- (2) A longitudinal pressure of 3-4 kg between opposite knots was considered satisfactory for measurement of meshes of cod-ends made of manila, sisal and hemp.
- (3) Greater accuracy and consistency in measurement will be obtained with a gauge which exerts a longitudinal force directly rather than at right angles to the mesh.

These conclusions had been combined in a recommendation to be passed to the Permanent Commission.

The relative merits of the "longitudinal" pressure gauge and the vertical pressure gauge as used at present in the ICNAF area were considered by the group. Demonstrations of different models of these gauges were given. Results of comparative measurements using these two types of gauges on manila cod-ends were given in a contribution by Mr. Parrish, and similar data were presented to the working party for heavy manila cod-ends by Dr. McCracken. Whereas Parrish's data showed that the longitudinal pressure gauge gave the smallest variation in readings between different observers, McCracken's data showed that with the heavier twines the Scottish longitudinal gauge did not give greater consistency than the vertical pressure wedge gauge. Dr. McCracken showed that for the heavy twine cod-ends (50/4) comparability between values of mesh size obtained with vertical and longitudinal gauges was

obtained with pressures of 12 and 10 lbs. respectively.

After long discussion of the available data, and the practical considerations which govern the choice of design of measuring gauge, it was agreed that while the longitudinal pressure gauge was preferable in principle, there was insufficient evidence available at present to warrant a recommendation that the standard vertical pressure gauge used in the ICNAF regulations should be changed. It was considered, however, that experiments to determine the equivalent pressures between present designs of vertical and horizontal gauges should be made. It was also felt that the task of designing a suitable horizontal pressure gauge should be undertaken by experts.

The principle underlying the choice of pressure for the ICNAF "vertical" wedge gauge was discussed and found to agree with the ICES principle, i.e., straightening of the twine without tightening the knots.

The results of studies on the choice of pressure were provided in contributions by Mr. Boerema, Dr. von Brandt and Messrs. Bedford and Beverton. They showed that the critical pressure to apply could probably be gauged with reasonable accuracy from the observed rate of change in mesh size with increasing pressure.

It was agreed that the critical amount of pressure to be applied in measurement differs for different materials. It is less for nets made from fine cotton twine than from the heavier sisal and manila twines. It was evident that at present the appropriate equivalent pressures were not known for all of the wide range of material now used in the construction of trawls and seines, and it was agreed that experiments should be conducted to obtain these pressures.

The possibility of using an appropriate "pressure difference" when measuring meshes of nets made of different materials was considered in order to compensate for their differences in mesh selectivity. It was considered that this matter should be looked into.

The group discussed a proposal made in a contribution by Dr. Went that for practical enforcement purposes measurement practice should revert to the simple "yardstick" or "meterstick" multiple mesh measurement system. This proposal was made on the general grounds that the present trend towards precision measurement with expensive and relatively complex gauges was inadvisable from practical and legal points of view. The group felt that it was unable to comment on the legal aspects of the matter, but from data presented by Mr. Parrish showing a wide range of variation in the relation between "yardstick" and gauge measurements, it was not possible to recommend the



adoption of this proposal. It was agreed, however, that Dr. Went's general warning was very pertinent and that more experiments should be conducted to determine the relation between the "yardstick" and gauge measurements.

#### CONCLUSIONS AND RECOMMENDATIONS

1. The use of standard pressure gauges is recommended in both experimental and enforcement work in the ICNAF area.
2. Gauges applying a constant "longitudinal" pressure are better in principle than the "vertical" pressure gauges.
3. At present insufficient evidence is available to recommend an alternative gauge to the "vertical" pressure gauge used in the ICNAF regulations, but it is recommended that efforts should be made to design a satisfactory longitudinal gauge.
4. Experiments to determine the appropriate "longitudinal" pressures for measuring meshes of nets made of all materials, and especially of materials other than manila, sisal and hemp, should be made.
5. Standardization of the mesh measuring methods in experimental work should be attempted, and where this is not possible conversion factors for different methods should be worked out.
6. The possibility of standardizing the mesh measuring procedures used in the ICNAF and Permanent Commission areas should be carefully examined.

(3) Selection of meshes to measure: The group agreed that the choice of the part of the cod-end over which measurements should be taken was of importance since it is generally found that there are changes in mesh sizes from one part of the cod-end to another. The group discussed published and unpublished data relating to these problems at considerable length. Mr. Clark reported that American experiments showed that when catches are moderate most of the cod-end escapement is through its after half, but with large hauls the upper part of the cod-end was also involved in the selection process. These results agreed with data published by Cassie in New Zealand.

It was clear from the data available that the part of the cod-end most concerned in the mesh selection process varied according to the size of the catch and the species of fish in the catch. Some experimental data showed that, for

some species, parts of the net other than the cod-end played an important part. It was agreed, however, that much more experimental work should be done to determine the part played by different parts of the net, and by different sections of the cod-end. In particular, the part played by the underside of the cod-end in mesh selection should be investigated further as this had an important bearing on the rig which should be adopted in "covered net" mesh selection experiments as well as on the distribution of mesh measurements.

It was agreed in principle by the group that the mesh measurements taken both in experimental mesh selection work and in routine checks of commercial cod-ends under the mesh regulations should be made only in the parts of the net, or the cod-end, through which the fish escape in significant quantities, but it was recognized that these parts could not be specified with precision at the present time.

The differences between the routine practices adopted in the ICNAF and Permanent Commission mesh regulations were discussed. Whereas the ICNAF regulations rigidly specify the measurement of complete rows of meshes from the top to the bottom of the cod-end, the Permanent Commission regulations do not specify which meshes will be measured. The appropriateness of the ICNAF procedure was discussed in the light of the existing data and in view of the agreed principle that measurements should be made only in those parts of the net (or cod-end) which contribute significantly to the selection process. It was concluded that, at present, there was insufficient available evidence to recommend any change in the present practice.

#### RECOMMENDATIONS

1. Research should be carried out to determine which parts of the trawl and seine, and which sections of their cod-ends, contribute most significantly to the release of fish.
2. At present, no changes should be made in the prescribed distribution of measurements in the ICNAF regulations, but a review of their appropriateness should be made in due course in the light of results from the above recommendation.

#### 5. Shrinkage of Net Material

The relevance of the shrinkage problem to the routine practices applied

in the enforcement of mesh regulations was first discussed. The group acknowledged that the most important question which it raised was whether "dry" measurements could be used as a basis for judging whether the "wet" measurements would comply with the mesh size prescribed by the regulations. This depended on there being a consistent shrinkage factor, relating the "dry" and "wet" mesh sizes.

Data were presented by Dr. von Brandt showing the relation between the diameter of the spool used in the construction of trawl cod-ends and the shrunken longitudinal mesh size for different materials. These data showed that there was considerable variation between the "spool" and "shrunken" sizes for different materials. Mr. Clark presented United States data on this subject and outlined the method of net certification used in the Subarea 5 regulations. This procedure was based on there being a recognized "dry" - "wet" mesh size conversion factor, which had been determined experimentally.

Experiences of a number of members of the group indicated that in practice there is a considerable variation in the change of mesh size from the dry- unused to the wet-used state, but that at present there are not sufficient precise data available to determine its magnitude. It was agreed that studies should be made of the changes in mesh size of commercial cod-ends within the ICNAF area, and these results should determine whether consistent conversion factors can be determined. The group agreed that certification of cod-ends was a desirable practice in principle, but recognized that its adoption should be governed by the results of such studies.

It was evident that, while a number of workers had investigated some aspects of net shrinkage, particularly those made of the heavier materials, manila and sisal, little was known about the extent of the change of mesh size in other materials. It was agreed, therefore, that more research on this subject should be carried out by workers in the ICNAF area.

#### RECOMMENDATION

There is a need for a thorough discussion of all existing data on shrinkage in natural and synthetic materials, and of the changes in mesh sizes of nets with use. It is recommended that considerably more research be directed to shrinkage problems and that the results of these researches be presented at a symposium to be held at a future date and subsequently published.

## 6. Mesh Selection of Fish

The group had time for only a very brief superficial coverage of this important topic. The items discussed were:

- (1) The most efficient rig to be used in "covered net" mesh selection experiments.
- (2) Factors causing variability in mesh selectivity. The rigs of the covers used by a number of workers present were described and the relative importance of the different features of the rig was discussed. The following features were considered of importance:
  - (a) The size of the cover relative to the cod-end.
  - (b) The position and method of attachment of the cover at the top and bottom of the cod-end.
  - (c) Covering the under side of the cod-end.

It was evident from the descriptions given that there are differences between the rigs used by different workers, and differences of opinion as to the importance of one or more of the features listed above. It was acknowledged that the importance of each of these features might differ for different species of fish and for the characteristics of the gears and fishing methods adopted in different countries and regions. The group felt that there was room for much more detailed experimental work on the rig of the cover from which the importance of different features could be determined, and it was agreed that this subject should be considered in much greater detail at a future date when more experimental data were available. The group recommended that experiments should be made to test the effects of using different rigs of cover with particular attention being given to the features outlined above.

The factors, other than mesh size, which influence the selectivity of trawls and seines were briefly discussed. It was evident from available experimental data that there is quite a wide variation between the results of experiments conducted in different areas at different times with different gears and under different fishing practices. It was felt that a number of different factors might play an important part, but that current data did not permit a comprehensive assessment of the most important ones. It was decided again that more experimentation was necessary before these influences could be thoroughly assessed, and it was agreed that the results of this work should be considered in greater detail at a future date.

It became evident during these discussions that a large quantity of un-

published experimental data have been accumulated in different countries which might, when analyzed completely, throw light on the importance of different factors affecting selectivity.

#### RECOMMENDATIONS

1. Studies of the possible factors bringing about variations in mesh selectivity should be carried out, with particular attention being paid to the following factors:
  - (a) Method of rigging the cover.
  - (b) Effect of catch size.
  - (c) Effect of towing time.
  - (d) Effect of towing speed.
  - (e) Differences between materials.
  - (f) Amount of escapement through different parts of the net and the cod-end.
  - (g) Effect of variations in fish shape in different areas and seasons.
2. The group stressed the importance of doing this work in conjunction with the mesh measuring work, and recommended that there should be close liaison between all workers in this field in order that the work can be accomplished in the most efficient manner.
3. The group recommends that the results of these researches be presented by the experts at a symposium to be held at some time in the future.

#### Concluding Remark

The discussions of the many problems concerning mesh measurement and mesh selection convinced the members of the Net Study Group of the desirability of constant close liaison between workers on both sides of the Atlantic. The group considers that this meeting has been of very great importance and benefit to those present and it recommends that more opportunities to meet and exchange data and ideas should be provided in the future.

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- Parrish, B. B. - Some notes on methods used in fishery research. 151

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G. L. Kesteven.

1. I have understood the purpose of the present meeting to be to make some contribution to systematization of the program of fishery biology (its theory, its methods and its schedule of operations) so that the science should most quickly and effectively produce the results expected of it, namely to establish such understanding of the aquatic resources as will assist man to make most efficient use of them. I have then understood one of the purposes of Working Party VI to be to discuss available instrumentation and that which may be required, for the purposes of this program.

2. Generally speaking, the selection of instruments depends upon the following considerations:

- (1) The nature of the measurements or observations to be made.
- (2) The accuracy required.
- (3) The speed with which individual observations should be made.
- (4) The circumstances under which the instruments are to be used.
- (5) The expenditures permissible on the instruments themselves and on the persons who will use them.

It is useless to discuss instrumentation without discussing in some detail the foregoing considerations.

3. In fishery biology it is perhaps useful to recognize certain fundamental distinctions. First the distinction between research operations concerned with a species and those concerned with a fishable stock or exploited population. While the former are concerned with a species in the more or less classic sense and involve physiology, autecology, and so forth, the latter are concerned essentially with biodemographic problems. Fishery biology has been concerned chiefly with the latter type of operation and it is chiefly toward these that this paper is directed. However, it is important that the dependence of the latter on and its relations with the former should be kept clearly in mind; it seems likely that the program of observations and hence the instrumentation of fishery biology will be significantly affected in the future by this consideration.

4. The other basic distinction bearing upon the problem of instrumentation is that between individual and population characteristics. While certain of the latter are simple functions of the sum of individual values (e.g. mean) others are complex functions, while still others can scarcely be regarded as any function of a sum of individual values. Different measurements and observations may be required for each, and certainly the observation schedules differ.

5. Within the program of biodemographic studies for fishery biology, we are concerned with the following elements:

- (1) Identification of unit populations (racial investigations). (That this is an operation not only of initial identification of a population unit but requiring, at times, continuing confirmation of this identification, is of some significance to the program).
- (2) Description of the structure of the population (composition with respect to age, size, sex and other characteristics).
- (3) Measurement of the properties of the population (its potentials for growth and reproduction and its response to factors causing mortality).
- (4) Description of the behaviour of the population.

6. As a preliminary to carrying out such a program, the following logical steps must be taken:

- (1) Precise determination of the objectives of the observational program with respect to the preceding elements.
- (2) Selection of the necessary observations. This stage includes decisions such as: which characteristics are critical for the establishment of identity? which characteristics most accurately indicate the growth? and so forth.
- (3) Stipulation of the reference that must be made to external factors or internal processes likely to affect the particular characteristics being measured.
- (4) Definition of the accuracy with which the individual measurements and observations must be made the precision with which the population values should be estimated.
- (5) Definition, on the basis of the preceding step, of the frequency with which the measurements and observations must be made, having regard for the sources of variance indicated in (3).

7. This paper is concerned with the apparatus and methods required in biodemographic operations, for making and recording measurements of various characteristics of individual fish and chiefly with the measurement of dead fish, although certain of the methods are applicable to live fish.

8. The purpose is to examine the availability and suitability of apparatus and methods to meet the particular needs of fishery biologists engaged in biodemographic studies, more particularly in order to consider whether available methods are adequate for these needs and, if not, along what lines development might be sought. It is not concerned with the selection of characteristics for measurement, with the precision desired in the results, or with the equipment

and methods of statistical treatment and presentation of the data obtained. Obviously, the former make demands upon the instruments whilst the latter place limitations, both of which must be accommodated in the instrument design. But, in considering the adequacy of available methods, we are concerned with the accuracy and speed with which the selected measurements can be made, and whether methods in normal use, offer a capacity sufficient to meet the statistical requirement of the fishery biologist in sampling large populations. It has been impossible to make a sufficiently thorough examination to lead to any definite conclusions; at the most we present some ideas, and attempt to show how some of the problems might be attacked, and the lines along which further development might be sought.

#### The Basic Measurements and Observations

9. A schedule of measurements and observations made in fishery biology and of the principal instruments employed as follows:

(1) Linear measurements:

- (a) of the whole length of the fish, such as total length, standard length or fork length;
  - (b) of various partial dimensions of the fish, such as length of the head, the abdomen, the tail, etc.;
  - (c) of the height and thickness of the body of the fish;
  - (d) of the girth of the fish at various points.
- (a-d) Tapes and rules (celluloid strips), measuring boards, calipers.

(2) Volumetric measurements: Of the whole fish or of part of it - balances.

(3) Measurements of weight and density: Of the whole fish or of part of it - balances.

(4) Enumeration of meristic characters, fin rays, scales, vertebrae, gillrakers: X-Ray apparatus.

(5) Estimation of number of ova: Microscope, balances and volumetric apparatus.

(6) Determination of age and calculation of intermediate lengths: Scale projectors.

10. In the above schedule, no reference has been made to the normal dissecting apparatus of the biologists which is used so extensively, for instance, in the work on vertebrae, nor is reference made to the normal laboratory apparatus, such as, flasks, basins, etc. required for the examination of stomach contents, preparation of vertebral specimens, and so forth.

#### Discussion of Individual Operations

11. Linear measurements: For our purposes, these measurements fall into three principal classes. First, those (chiefly the total length) which can be made with apparatus to some degree mechanized and involving simple measurement of the distance between two parallels. Second, those measurements (such as breadth and width and of parts of the body) for which it is customary to use calipers. Third, the difficult measurements which involve the use of tapes for measuring distances along contours of the body and for measurement of girth.

12. The greatest attention has been paid to the first type of measurement for which there is a range of equipment, generally described as measuring boards. The simplest type of measuring board consists of a flat piece of wood into whose surface is let a scaled rule and at whose beginning is set a headpiece. Modifications have been made to cope with the problems of parallax. The first precaution is to ensure that the fish lies straight along the measuring board and some boards are provided with special guides to ensure this. The second problem is to ensure that the measurement is made through the central axis of the fish, lying between the tip of the snout and the centre of the caudal fork. This is of some significance in bulky fish, such as tuna. The third problem is to avoid parallax error in the final measurement. To overcome this the most successful improvement has been a mirror at the back of the board adjacent to the measuring scale and a sliding bar carrying a sighting wire so that the reflection of the wire, the wire itself, and the tip of the tail or other part being measured, when brought into juxtaposition, assure that the wire is in the correct position, and then, the wire and its reflection are brought into conjunction with the appropriate point on the scale (Thompson, 1916). This type of apparatus was most successfully developed for the measurement of small fish, notably clupeoids. Hart (1936) described a modification which permitted discard of the mirror; he reported that the use of the mirror brought eye fatigue.

13. The order of accuracy of the measurements and of the cost of obtaining that accuracy in terms of additional time must then be considered. This question has been discussed notably in papers in the Journal du Conseil (for exam-

ple, the correspondence of Thompson and Edser), but relatively little attention has been paid to the cost of obtaining the accuracy required.

14. The accuracy required in these individual measurements depends on the precision required in the population values. The latter consideration is the chief determinant of sample size and frequency. It has generally been felt that samples should be large and numerous. Gulland (1955) has discussed the matter from the statistical point of view which, it seems to me, still calls for complementary contribution from the biologist's viewpoint. However, this may be, various devices have been adapted by which to increase sample size and frequency, the simplest device being the use of the celluloid strip (Wollaston, 1928, but also see Thompson, 1929). In this method a very simple board is made with headpiece but generally without a measuring scale, a celluloid strip being tacked to the board in place of the scale. The fish is placed on the board and consequently on the celluloid strip and a hole is punched in the celluloid strip by means of an awl, either at the caudal fork or at another point of body length. By this means, marked as holes in the celluloid strip, several hundred fish can be measured for length in a short time. The celluloid strip is, of course, identified as to species, time and place of capture and other relevant information. The method has certain technical disadvantages, such as the risk that a number of holes may become superimposed or a hole may be enlarged by multiple punching, so that the number of fish represented by such a hole cannot be determined. Of greater significance, however, is that only a length frequency diagram is obtained and detailed information concerning each individual fish cannot be recorded.

15. Means have been sought (e.g. Hodgson, 1939) to increase the information to be drawn from a set of operations. Various methods have been adopted to increase the speed of the recording operation. It seems possible to employ modern electrical equipment to achieve all the principal objectives of this work, namely, samples as large and as frequent as required with measurements as accurate as possible (or necessary), plus the ability to record multiple sets of information concerning each individual fish. I have it in mind that it should be possible to construct a measuring board more or less along exactly the same lines as the clupeoid board which has the mirror, and to connect this to a recording unit in such a way that when the fish is on the board and the pointer is moved to the appropriate position, a circuit is completed and the length automatically recorded. In such an apparatus it would be a simple matter to automatically record some code number corresponding to the information concerning time and place of sampling and other relevant information about species, methods of catch and so forth. It should be possible also to refine the board to accommodate fish of all sizes so that not only would it vary in the scale it would cover and the units in which it would record (millimetres, centimetres, half-centimetres, and so on) but also could be adjust-

able so that for larger fish it would measure only above a fixed artificial baseline whose length would be exceeded by all the fish of the sample. Such a piece of apparatus could be used also for other linear measurements. For example, in the case of measurements which have to be made with calipers, the points of the calipers could be placed on the measuring scale, the pointer then moved accordingly and the circuit completed. Provided arrangements were made either for an established sequence of measurements, or for the recording of a code for the identification of each measurement, it would be possible to record any schedule of partial linear measurements.

16. Measurements of weight: For measuring weight, the principal requirements are first that the balance be robust and the working parts protected as far as possible from salt water and other corrosive agents, an important consideration particularly for market sea-board measuring. Second, that the movement of the balance be damped to speedily reach a rest point. These matters have received the attention of scale manufacturers and it is only necessary that the research institution indicate the range of weight to be measured and the accuracy with which the measurements must be made. However, the third consideration relates to the speed of operation and the number of measurements that can be taken in a unit of time and; again, it seems that fishery biologists need a balance connected, like the measuring board described above, to a recording unit in such a way that when the fish or its part is on the balance a circuit is closed when the rest point is reached, the weight indicated by the balance would then automatically be recorded. For many species of fish, such an apparatus would require a two or even three-stage operation, since the magnitude of the whole fish so far exceeds the magnitude of parts such as the liver, gonad and stomach content.

17. The compound fish measuring unit: I envisage, then, a unit for use in large-scale measuring operations at markets, processing plants and on board research and fishing vessels, which would combine the foregoing features. It would consist of a coding keyboard which could send to a recording unit a series of signals indicating the sample serial number and any information concerning time and place of sampling, etc. that ought to be included directly in the record. Other information also could be coded such as sex, gonad condition and feeding condition of the fish. The second unit would be the measuring board, the third unit the balance. The fourth unit would be the recording unit.

18. Objection has been offered to this idea on the grounds that the present arrangements with market measurers give a sufficient number of samples, each of sufficient size, in which the individual fish are measured with sufficient accuracy and detail and that, further, the practical circumstances place limitations on the operations compared with which the speed and capacity of an electrified unit would be out of all proportion. If these views are correct, then

there is obviously no need for such an apparatus, but I venture to question whether the matter has been sufficiently thoroughly examined. It seems to me that if every refrigeration plant can afford to install automatic continuous recording thermometers, often in quite complex form, it is not unreasonable that the fish measuring operations at permanent observation points should be similarly equipped. This, of course, is only an intuitive argument but I believe that thorough examination of the considerations listed in paragraph 2, in conjunction with a thorough review of the program as indicated in paragraphs 5 and 6, would show that some advance in the instrumentation for fishery biology is urgently required. A further argument which may be offered is to invite comparison between physical and biological systems in respect to their complexity and their variability. The current capacity of oceanographic instrumentation vastly exceeds that of the biological to a degree that must make it extremely difficult to make full use of the oceanographer's account of environmental systems; it is urgently necessary that the biologist should increase the sensitivity of his measurement of the fish populations.

19. Meristic counting: Measurements in this category include the enumeration of vertebrae, of spines and rays of fins, of scales (either as number of rows of scales or as number of scales within each row) and of gillrakers. There are two sources of error in this counting. First in the correct identification of the elements to be counted, especially of the vertebrae, and particularly in those species in which anomalous vertebrae occur. Second in the mental operation of the counting itself. Various techniques are employed to expose the elements that are to be counted, such as the preparation of vertebral columns by techniques involving boiling, or a simple (butchering) operation to expose the vertebrae. In the case of embryos and young fish it is possible to stain the vertebrae and fin rays with alizarin (Tåning, 1927, Gray, 1929, Hollister, 1934, Raitt, 1935). A method which appeals as being cleaner, offering more speed and also as giving better means of identifying elements to be counted is the use of X-ray apparatus. However, this still leaves the possibility of error in the counting operation itself and also leaves the problem of securing greater speed in this counting without loss of accuracy. A possibility that occurs to me in this connection is that one might have a pointer whose tip would travel along the image given by the X-ray, and whose proximal end would be connected with a kind of ratchet so that the pointer would be moved past one notch of the ratchet for each identified vertebra; the movement of the ratchet would at the same time effect the counting of the vertebrae. In this way, the mind of the observer would not be divided between the task of identifying the vertebrae and that of remembering the number reached in the count.

#### Reading and Measurement of Scales, Otoliths and Other Structures

20. Scales: It is unnecessary here to discuss the principles by which the

scale reading permits determination of the age of an individual fish. However, it is important to make the distinction between age determination and the calculation, by interpolation, of the size of the fish at various points in its life history. It is true that these operations are related and that very often the former depends on the latter for confirmation by way of collateral evidence derived from the Petersen curve analysis method and other similar work.

21. For the simple determination of age, the question of accuracy arises only in connection with identification of the markings on the scale, which, however, is not a problem of instrumentation. There is an instrumental problem in connection with the speed of the operation, and various techniques have been devised to facilitate the handling of scales for their storage and for their handling during the reading operation. In the earliest work, scales were mounted on microscope slides, generally in jelly solution, sometimes with cover slips and sometimes without. There is no doubt that with large scales this method not only presents difficulties in mounting but also optical problems of curvature of the surface carrying the markings. Furthermore, jelly-mounted scales were by no means permanent and often were difficult to handle under the microscope. Tubb and Proctor (1941) described a handy clamp which certainly permitted speedy action and was suitable for small, flat scales, but it was inconvenient for large scales. As a solution to these problems, Nesbit (1934), referring to Lea's (1918) method of securing collodion impressions of the surface of fish scales, described a technique of making impressions of the scale on celluloid strips, the impression being made by putting pressure on the scale against the celluloid strip under a special clamp.

22. For calculation of intermediate lengths, there are several instrumental problems, the first of which is to facilitate the measurement of the dimensions of the scale without loss of accuracy. Various models of scale-projector have been designed and used extensively. The simplest form is a vertical projector with the projector itself above, held on a stand, and throwing an image on a sheet of paper on the table. Excellent models have been prepared in which the projector is in a horizontal position throwing its image on a vertical screen (e.g. Van Oosten, 1923). Van Oosten, Deason and Jobes (1934) designed an apparatus in which the projector was in vertical position with its image thrown first on to an obliquely placed mirror from which it was thrown on to a sloping ground-glass screen. The whole apparatus was arranged somewhat like a convenient writing desk, of which the ground-glass screen was the working surface. With all these types of apparatus a clear image of the scale can be obtained, and the measurements of the scale dimensions can be made directly. I am unable to discuss the optical properties of these apparatuses, nor their mechanical advantages or disadvantages for focusing.

23. However, there then remained the second instrumental difficulty, namely



of converting these scale dimensions into corresponding length measurements of the fish. Various forms nomogram have been designed for this purpose, and in the apparatus of Van Oosten, Deason and Jobes a nomogram could be arranged on the ground-glass screen. Kesteven and Proctor (1941) fitted a horizontal projector with a movable screen so that by moving the screen to the appropriate position the image of a scale could in its appropriate dimension be made equal to the length of the fish from which the scale had been taken. They were working with Mugil cephalus, for which it was established that a straight line relation existed between scale size and fish length, in which, therefore, the intermediate dimensions of the scale correspond to the intermediate dimensions of the fish; the image being projected upon a metric scale, with the nucleus at zero, the intermediate lengths could then be read from this scale directly. This technique presents no difficulty as long as the scale-dimension/fish-length relation is linear, even if there should be an intercept. However, if the relation is other than linear, some transformation must be made. This could be effected by the use of a nomogram device combined with the movable screen, or a simple table of corrections could be prepared.

24. Otoliths and other hard structures: While in principle the use of these structures is the same as the use of scales, the technical problems of preparing and reading these structures are much more difficult and, it seems, not yet overcome. Tåning (1938) describes some simple apparatus to facilitate preparation of the otoliths. I have heard of other apparatus for the same purpose developed in other laboratories and of simplification of the methods of handling. However, the operation still remains arduous and its reliability perhaps not great.

#### Discussion

25. The point which seems of principal interest at the present stage concerns the sensitivity of the methods employed by fishery biologists in measuring the characteristics and properties of the fish populations under study. The present paper is not intended to examine this question but rather to indicate how the resolution of the problem of instrumentation may call for answers in the broader field. It is obvious that instruments can be obtained to make measurements with almost any degree of accuracy that might be demanded. It is then a matter for the general theory to indicate the practical order of accuracy that should be sought. It is questionable whether, with modern apparatus, there is any need to make a compromise between the order of accuracy that should be sought and the speed with which observations should be made. The next important question then relates to the design of the sampling program and the demands which this program makes in terms of sample size and frequency. The answer to this question will chiefly determine the shape of future instrumentation. It is my impression that for the accurate measurement of changes in the structure

and properties of fish populations the sampling programs should be greatly expanded to fill a much larger frame, and longer sequences, and that in order to make this possible a much higher degree of mechanization is required.

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B. B. Parrish.

## I. GENERAL

Fishery research is a field in which relatively few basic methods of investigation can be used, especially in long-term studies requiring large numbers of observations; this is true particularly of fishery biology. Many of the techniques used today were developed comparatively early in the history of the science, and have remained relatively unchanged. It is of great importance, therefore, that the subject should be examined critically by groups of interested workers at the present time, in order that the merits and shortcomings of at least some items of current methodology can be fully assessed, and any possible avenues for improvement and standardization can be discovered.

### Factors Affecting Choice of Method of Investigation

The factors and circumstances which govern the choice of method vary enormously from one field of research to another, from one investigation to another, and from one place and time to another, so it is not possible to make sweeping generalizations concerning the merits or shortcomings of any method without detailed consideration of the particular circumstances in which the investigation is conducted. However, there are a number of factors which have to be considered whenever a method is under consideration, either at the planning stage of an investigation or whenever a new technique is recommended. These are as follows:

- (1) Objective and scope of the investigation.
- (2) The desired accuracy of the result of the investigation.
- (3) The basic accuracy of the method.
- (4) The quantity of material to be handled, and its accessibility.
- (5) Technical skill required in applying the method.
- (6) Availability of resources in manpower (including a skill component), money and equipment.

The appraisal of possible methods for an investigation in the light of these factors, not only permits the choice of the most accurate method, but also al-

lows the worker to assess their economics and to arrive at a compromise between accuracy of end result and total cost. This aspect of the problem is of particular importance in long-term investigations in which a method is used in a routine way on large quantities of material. Economic circumstances may sometimes shift the balance of choice from a more accurate method to a less accurate one.

A particular feature of the economics of methodology which perhaps is not considered sufficiently seriously in the fishery research field, is the relation between initial capital outlay and subsequent cost of investigation. The subject of mechanization in some routine methods of investigation is a case in point. It is probable that, with sufficient initial outlay, electronic apparatus could be designed which would undertake the tasks of measuring and recording length and weight of fish, would read and record ages from scales or otoliths and would count vertebrae. Would the cost of developing and constructing such apparatus be justified? Only an objective appraisal of the basic factors listed above could provide the answer to this question.

The various factors and considerations outlined above will apply most forcibly to those long-term investigations for which there is a range of investigatory techniques from which a choice can be made. Some investigations will arise for which there is only one possible technique, in which case many of the above considerations must be ignored. However, even with such investigations, it is always desirable that the economic aspects of the technique should be borne in mind in order that the stimulus for the development of new techniques shall be maintained.

The foregoing remarks may serve as a background for the discussions concerning the particular fishery research methods which this special ICNAF working party has been asked to consider, and in its deliberations the working party should aim particularly to answer, for each of its projects, the following main questions:

- (1) Which of the methods at present in use is basically the most accurate and reliable?
- (2) Should a less accurate but more easily applied method be adopted universally in the light of practical circumstances?
- (3) Along what lines should research and development in methodology be directed?
- (4) To what extent is standardization of methods desirable and how can it be brought about?

The particular projects which the working party has been asked to consider are: methods of mesh measuring and methods of obtaining mesh selection data; methods of length measurement; methods of age determination, and methods used in growth studies. An attempt is made in the following paragraphs to highlight some of the most important issues and methodological problems concerning each of these topics.

## II. METHODS OF MESH MEASURING

### General

This subject has gained a position of prominence following the introduction of international mesh regulations. An essential task preparatory to the introduction of such regulations is to determine a simple and consistent relation between the primary variable, the fish selected by the mesh, and some mesh dimension (which can be quite arbitrary) of the fishing gear. Almost all work on mesh measuring has been carried out in accordance with this objective. It must be recognized that for this purpose, no account need be taken, at least initially, of the mechanism of selection, and the mesh dimension chosen for measurement need not be the one related most logically to it. However, a more detailed examination of the selection mechanism and a more careful consideration of specific mesh dimensions may become necessary if inconsistencies arise in the relationship between fish dimension and mesh dimension, particularly between different types of gear or between different types of material in the same type of gear.

A number of different mesh dimensions have been used in the course of many years of mesh measuring work. These include: the length of a "bar" (the length of twine between two knots of a mesh); the circular diameter of the mesh, the diagonal of the "square" mesh; a diagonal of the "diamond" shaped mesh and the distance between opposite knots of the mesh when it is pulled tight lengthwise. The last of these is the one which has been generally adopted internationally, at least for trawls and seines, and most of the mesh measuring techniques developed in recent years have been evolved for measuring it.

The questions for detailed consideration are:

- (1) Is this the best dimension to adopt?
- (2) If so, what is an acceptable definition of it and what are the main difficulties and snags which have to be overcome in developing a method

of measurement?

- (3) What is the best way (simplest and most accurate) of taking the measurements?

Some of the factors and/or results of experimental work which are of importance in answering these questions are as follows:

- (1) Experiments on both sides of the Atlantic using a fairly wide range of mesh sizes show a simple linear relationship between this dimension of the cod-end mesh of trawls and seines and the 50 percent retention length for a number of species of fish.
- (2) The dimension is independent of knot size, at least when measured directly, but, with some methods of measuring it, it is not independent of the flexibility and elasticity of the twine.
- (3) The relationship between the selection characteristics and this mesh dimension is not constant for cod-ends made of all types of twine. (Lucas et al 1954; Graham et al 1954; Boerema 1954; Margetts 1955).
- (4) Difficulties arise in defining the dimension precisely, and in arriving at a consistent and practical method of measurement.

It is clear from (1) that this dimension is satisfactory as a basis for applying mesh regulations as a conservation measure at least for a fishery which utilizes only one type of gear, but (2) - (4) indicate that it presents a number of practical problems. Chief of these is the difficulty in obtaining a consistent measure of the dimension which is independent of measurer's bias and which is related most closely to the selection ogive. The source of this difficulty is in defining the degree of tightness of the twine when readings are taken. It is well-known that a wide range of readings for a mesh can be obtained when different forces are exerted between the opposite knots of the mesh (von Brandt 1955 (i); Boerema 1954; Bedford and Beverton 1955). In consequence, a precise definition of the dimension, and the degree of tightness is required, and a method of measurement developed, which provides consistent readings, free from measurer's bias.

This problem, tackled energetically in Europe in recent years, was the subject of discussion in the Comparative Fishing Committee of ICES in 1955. (Subject matter contained in papers by von Brandt 1955 (i); Bedford and Beverton 1955; Parrish, Jones and Pope 1955; and Boerema 1954).

The main views expressed and conclusions reached at the meeting can be



summarized as follows:

- (1) This dimension is a satisfactory one to use as a basis for mesh regulations.
- (2) The definition of the dimension, used in the 1946 Overfishing Convention, and the present system of measurement, used in enforcing European mesh regulations, lack precision and lead to difficulties and inequalities in the enforcement measures.
- (3) The inconsistencies and inequalities in the present system of measuring and enforcement would be reduced greatly by the use of measuring gauges which provide a constant longitudinal tension between opposite knots of the mesh at each measurement.
- (4) The tension to apply will depend on the exact definition arrived at for the mesh dimension, but if this is taken as "the distance between opposite knots when the mesh is fully elongated longitudinally, but with no tightening of knots or elastic stretching of the twine", then for sisal, manila and hemp twines a longitudinal force of 3-4 kg. is an appropriate standard.
- (5) Greater accuracy and consistency in measurement will be obtained with a gauge which exerts a longitudinal force directly, rather than at right angles to the mesh.
- (6) The standard longitudinal force, consistent with the above definition of the mesh dimension, will vary from one type of twine to another: twines made from cotton and synthetic fibres will, for example, probably require smaller forces than the heavier twines. The appropriate standard for the lighter twines has not yet been determined.

As a result of these discussions, the Comparative Fishing Committee drew up the following recommendations to pass to the Permanent Commission of the Overfishing Convention:

"It is recommended that the attention of the Permanent Commission be drawn to the facts that, in mesh measurement, greater consistency will be achieved by gauges developing a direct and constant longitudinal pressure of about 3 kg. Such gauges would be adequate for measuring manila, sisal and hemp cod-ends. Some gauges of this type have already been developed."

### Types of Gauges

Results of comparative mesh measuring experiments using different types of gauges suggest that the most consistent readings are taken with gauges which develop a constant longitudinal force directly, and not one normal to the mesh, (Bedford and Beverton 1955; Parrish, Jones and Pope 1955), but as yet this type of gauge has not been introduced on a large scale in routine mesh measuring for mesh regulation enforcement purposes.

### Other Considerations

(1) Differential selection and related mesh measuring problems. One of the most important results of postwar mesh selection work has been to show the difference between the selectivity of gears having cod-ends with the same mesh size but made of different materials. This has resulted in the concept of the "light" trawl, meaning trawls made of cotton and hemp, whose selectivity has been found to be higher (at least for some species of fish) than the "heavy" trawls made of manila or sisal. These results show that there is some factor other than mesh size which brings about this difference. This factor is not known at present, but is generally thought to be related to "flexibility".

It is worth considering, therefore, whether a new system of measurement should be introduced which takes into account not only the linear mesh dimension but also the other features of the mesh which affect selectivity. The adoption of such a method would perhaps eliminate the need for introducing a number of different mesh sizes for different gear and twine types in a complex fishery (as in the North Sea at the present time) so as to ensure equal selectivity amongst all gear items. The chief difficulty in debating such new possibilities is the lack of precise information on the nature of the "other factors", but it may be possible to resolve some of the outstanding problems on this subject.

(2) Number and distribution of measurements. An important component of the problem of mesh measuring is the number and distribution of measurements required on each occasion that measurements are taken. In cod-end mesh selection work, the objective is to determine with as great an accuracy as required the average mesh size of that part of the cod-end over which selection operates.

The number of meshes to measure will depend, of course, on the range

and statistical distribution of mesh size over the selective part of the cod-end, and the acceptable limits of accuracy of the estimate. While the number to measure can be easily determined once the required accuracy and the range and statistical distribution of the mesh sizes are known, there is insufficient knowledge concerning which part of the cod-end is most involved in the selection process. At present little is known about the selection process, although some recent films have added to our knowledge. It is probable that escapes usually take place more over the lower (distal) part of the cod-end than over the upper part, but this will vary according to the size of the fish and the catch and the rig and method of working the gear. This problem is of little importance if there are no major changes in mesh size throughout the length of the cod-end, but it is of considerable importance when there are such changes, particularly if they are fairly systematic. This does appear to be so in trawl cod-ends, which, with use, tend to have larger meshes at the lower end.

(3) Shrinkage of net material. While this problem is not of consequence in deliberations on the technique of measuring, it is of great consequence in the general administration of mesh regulations. Accurate measures of the extent of the shrinkage, on wetting, of nets made of different materials are required in order that the correct mesh size will be applied when in use.

Experiments by a number of workers in different parts of the world have shown that almost all new nets made of natural fibres shrink when immersed in water, and that this shrinkage is partially or completely reversible on drying (e.g. Parrish 1950; Ellis 1951 (1)). This shrinkage is particularly marked in nets made of manila and sisal, but is also evident in cotton seines. Therefore, in enforcing a mesh regulation it is of great importance that measurements undertaken on the commercial fleet by enforcement officers should be made either in the dry or the wet state. In practice the wet state is usually specified since this is the condition of the net when in use, but on many occasions it is not easy to obtain measurements of a thoroughly wetted net on board ship, and in many cases "dry" measurements are taken. While this problem is easy to resolve on paper, it is not easy in practice, when manpower resources at the landing ports are small and the fleets large. It is a matter for investigation whether a consistent conversion factor from the wet to the dry (through damp) mesh size can be obtained and be used in judging the "legality" of dry (and damp) nets.

### III. METHODS USED IN MESH SELECTION EXPERIMENTS

The foundations on which any mesh regulation is based are the results of mesh selection experiments giving the values of the selection parameters, for

the species of fish concerned for a range of mesh sizes used in the gear. Therefore, the responsibility placed on the experimental methods is formidable and it is of the greatest importance that these methods should be subjected to the closest scrutiny.

Two experimental methods have been used almost exclusively for obtaining the basic selection data for trawls and seines; the covered net method and the alternate haul method. Each of these methods has its strong adherents amongst current fishery workers, so it is appropriate that their merits and shortcomings should be considered carefully with a view to improving and standardizing the experimental method.

#### Covered Net Method

In this method the cod-end (or other parts of the gear in question) is covered with a loose bag of small meshed netting in which fish, passing through the cod-end (or other part), are retained, so that data of the numbers of each size category of fish retained in and escaping from the cod-end are obtained. The accepted merits of the method are as follows:

- (1) Each haul made with the gear constitutes a single experiment.
- (2) It is the only method (apart from direct observation) which gives the absolute escapes from the part of the net in question.
- (3) Results obtained by this method are independent of the catching efficiency of the gear.
- (4) It is the only method (other than direct observation) which provides data for studying the effect on selectivity of such factors as size and composition of the catch, duration of haul, speed of towing, etc.
- (5) It provides information on the condition of the escaping fish.
- (6) It provides data on escapes from any chosen part of the gear; e.g. cod-end, baitings, etc.

These merits are impressive and give to this method many advantages over the less direct "alternate haul" method. It is, however, subject to one major criticism; this is the possible "masking effect" of the cover. Davis (1934) drew attention to this defect when he obtained lower values of percentage escapes with the "covered net" method than with the "alternate haul" method.

This he attributed to a reduction in the flow of water through the cod-end by the presence of the cover and a consequent reduction in the total numbers of escapes through the cod-end. An alternative explanation could be a return of fish back into the cod-end from the cover.

#### Alternate Haul Method

The essential feature of the "alternate haul" method is simply to fish two nets of different mesh size either side by side on two ships of comparable size and power, or alternately on the same ship, and to compare the length frequencies of fish caught in each. Another method, known as the "trouser trawl" method, which may be regarded as a modification of the alternate haul method, is to divide a net or cod-end longitudinally with different mesh sizes in each half, and to compare the length frequencies of fish in the two parts.

The chief merits of the alternate haul method are:

- (1) There is no cover to mask the flow of water (and fish) through the net or otherwise change the performance of the gear.
- (2) It is particularly suitable for use on commercial fishing vessels operating under normal fishing conditions over long periods of time.
- (3) It is the only method which gives a practical estimate of the profit or loss to a fisherman of a change in mesh size.

The criticisms which are aligned against this method are, however, numerous. First, it only gives the total differences in catch between the nets or cod-ends of different mesh sizes; they do not necessarily represent the effects of mesh selection only. Secondly, the results are not independent of the catching capacity of the gear. This has proved a serious difficulty since in general an increase in mesh size, at least in the cod-end, has been found to increase the overall catching capacity of the net. Some methods of correcting for this increased efficiency have been used (Herrington 1935; Beverton and Holt, 1955), but it is not clear that the correction factors are applicable over the whole size range. This criticism cannot be aligned against the "trouser trawl" method, which should be independent of this factor, but a number of other snags have been associated with it, chief of which is a bias in the numbers of fish entering the two legs of the trouser. However, this method has not received such detailed attention as the more conventional "alternate haul" one and it is worthy of more active consideration.

Third, the data obtained with the alternate haul method do not give the absolute selection ogive for either of the mesh sizes unless that of the smaller mesh is known already. However, an interesting method of computing the absolute ogive from the ratios of length frequencies obtained by the alternate haul method has been developed by Beverton and Holt (1955).

The most important question which arises from the above remarks is: "Is the masking effect of the cover a common feature of the "covered net" method and is it sufficiently large to invalidate selection data obtained by this technique?"

In recent years experiments have been conducted by a number of workers to investigate the extent of this masking (Parrish 1950 (ii); Parrish and Pope 1951; Clark 1952; Cassie 1955). The general conclusion reached by these workers is that masking is generally of small extent and does not invalidate the results of such experiments, especially when the cover is large compared with the cod-end and has substantial "flow". Work by Cassie on the design and rigging of the cover is of particular interest; he found evidence of considerable masking when the cover fitted closely over the cod-end, but absence of masking when the size of the cover was increased and was hung loosely from the baitings and belly of the trawl.

Despite the convincing results of the experiments referred to above there are a number of examples of apparent masking (e.g. Davis), and it is probable that the phenomena associated with masking will arise under some circumstances and may depend on such factors as, the size and composition of the catch, the time during the tow when the different size categories enter the cod-end, the rig of the net and the cover, and the speed and duration of the tow. At present, relatively little is known about the effect of these and other factors, and more detailed experiments, including photography and underwater observation, should be conducted to test them. In particular, more information is needed on the best size and rig of cover to use, and especially on the importance of covering the underside of the cod-end.

#### Factors Affecting Cod-End Mesh Selectivity

A common feature of the results of mesh selection experiments is the considerable variation in the values of the selection parameters for a particular mesh size in covered net experiments with a particular gear. While much of the haul to haul variation must be attributed to the complex of random factors which give rise to variability in biological experiments, other sources of variation indicate that factors associated with the gear and the method of

fishing, other than mesh size, influence its mesh selectivity.

One of the most important of these factors the material from which the net (cod-end) is constructed has been mentioned already under methods of mesh measuring. Experiments have shown that cotton seines and trawls made of cotton and hemp, the so-called "light trawls" (and cotton cod-ends attached to a trawl of heavier twine) release larger fish (particularly of roundfish species) than do trawls made of sisal and manila. (Lucas et al 1954; Graham 1954; Boerema 1954; Margetts 1955). This difference in selectivity must therefore be associated with some characteristic of the material from which the cod-end is made (at least for trawls; the difference in selectivity between seines and trawls could be due to differences in the method of working the gear). The underlying causes of these differences are as yet unknown. A difference in "flexibility" between the "heavy" and "light" materials, resulting in differences in the rigidity of the meshes when fishing, has been advanced as a likely explanation; but there are other possibilities. Much more experimentation will undoubtedly follow in the next few years, both to test the differential selectivity between other net materials, particularly the synthetic fibres, and to investigate the underlying causes. The question of differential selectivity between single and double braided cod-ends is one worthy of particular attention. At present, it is probable that this phenomenon is of greater concern in the ICES area than in the ICNAF one, but it is a subject of fundamental importance warranting active investigation.

Apart from this well established selectivity factor, there are a number of other possible sources of variation in selectivity which warrant further investigation. Prominent amongst these are: length of tow, towing speed, direction of tow relative to water currents; size and rig of gear (all components), method of gear handling; size and composition of catch, and characteristics of the fishing locality. So far as the writer is aware there are few experimental data available at present from which to assess their possible effects. Some preliminary experiments and analyses have been carried out by the Marine Laboratory, Aberdeen, with a view to assessing some of them; e.g. duration of tow, direction of tow, and size and composition of catch. Results from experiments comparing selectivities for different durations of tow have been conflicting; one experiment gave significantly higher values for the selection parameters with long tows (3 hours) than with short ones (1 hour), but two others gave values which were not significantly different. The effect of direction of tow relative to the tidal currents has also been tested in a preliminary way, but no conclusive results have been obtained.

Results given by Cassie (1955) on the effect of total catch size and composition on selectivity are of interest. He found that increase in the size of catch did not reduce the percentage escapes, but that in fact a "plug" of fish in the

cod-end improves the selective action. He found, however, that some kinds of seaweeds may reduce the escapes considerably if present in the cod-end in sufficient quantities.

#### Escape from Other Parts of Net, and Changes in Efficiency with Mesh Size

The above remarks refer to the various factors affecting cod-end mesh selection, which, it has been mentioned, can be studied exclusive of selection by other parts of the gear, or the whole gear, by the covered net method.

Selectivity of any other parts of the net can be studied in the same way. A number of such experiments, to test the escapes of fish from the wings, square and baitings of the trawl, have been made by a number of workers. In experiments conducted at the Marine Laboratory, Aberdeen, small meshed "pockets" have been attached to the outside of the net on the wings, square and baitings (Ellis 1951 (ii)). These experiments have indicated that escapes of the more "demersal" species - haddock, cod and the flatfish species are relatively small from the upper parts of the trawl (despite a larger mesh size than in the cod-end), but that there are considerable escapes of the more "pelagic" species, especially herring and some small gadoid species, from the square and baitings. However, more experiments are needed to test the magnitude of the escapes from these parts of the net with changes in mesh size in them and in the cod-end.

One important result which has emerged from the application of the "alternate haul" method, is the increase in efficiency (catching capacity) of the trawl with increase in cod-end mesh size. This result was obtained by Davis (1934) in his "Shields" experiment, and it has also been demonstrated very convincingly for ICNAF Subarea 5. Like the differential selectivity phenomenon of "light" trawls, this phenomenon has been convincingly demonstrated, but no confirmed explanation of its cause has been given. In view of its close connection with the mesh selection problem discussion of its magnitude and explanation is warranted.

#### Mesh Selection by Gill Nets

The above discussion of experimental methods and the results of their application applies to the two most important demersal gears - trawls and Danish seines - but another, highly selective net, the gill net, also warrants consideration.



Extremely few quantitative data are available concerning the selection parameters of this gear, chiefly because of experimentation difficulties. It is not possible to use the "covered net" method with this type of gear and hitherto all data have been obtained by the application of variants of the "alternate haul" method. The two methods used are: (1) to fish gill nets of different mesh sizes together in the same fleet or in neighbouring fleets of nets, and (2) to fish gill nets against another type of gear (trawl, ring-net, purse seine) on the same population of fish at the same time. It is difficult to obtain accurate quantitative data from both methods because of the large net-to-net and haul-to-haul differences in catch of most pelagic species (see von Brandt 1955 (ii)) and because of the difficulties in ensuring that two gears such as the gill net and the trawl, etc. fish the same population of fish, and in knowing the relative fishing capacities of such gears.

Some new and improved method of studying the selective properties of gill nets is urgently required. Possibilities worthy of detailed discussion are the use of small-scale aquarium experiments, continuous observation in the field by cine photography (possibly ultra-violet or infra-red) and the liberation of tagged fish of known size distribution in the vicinity of the gear.

In this brief survey of mesh selection, emphasis has been laid mainly on those aspects which relate to the methods of obtaining the selection data. Therefore many important facets of the subject have been omitted: the escape mechanism, the theoretical derivation of the selective ogive, the changes in ogive parameters with changes in mesh size (particularly its slope) and the hydro-dynamics of the gear components in action are all important aspects of the subject which contribute to a full understanding of the selection process.

#### IV. METHODS USED FOR LENGTH MEASUREMENT, FOR AGE DETERMINATION AND IN GROWTH STUDIES

Methods for measuring total length, weight and age of fish are fundamental in fishery biology. A breakdown of the fish population into length (or weight) and age-groups is necessary at some stage in almost all investigations, especially in life history studies, and studies of population dynamics. Whereas in the former it may suffice to know the length and age compositions only roughly, in the latter accurate measures of them are required for estimating mortality, for measuring recruitment and for studying growth. These important investigations, therefore, demand of the methods a high degree of accuracy and freedom from bias. Also, in view of the large variations in length and age compositions of the populations in space and time, large numbers of observations must be taken in the course of a year. Thus, economic considerations must

play an important role in the choice of methods, particularly since they must be applied in a routine way for long periods. This applies particularly to the choice of methods for age determination, which cannot usually be carried out in the field, and in consequence, considerations of methods embrace not only the process of reading the age but also of the collection and preparation of the raw material.

### Length Measurement

Measurement of total length of fish presents relatively few "technique" problems. The length can be measured rapidly and with sufficient accuracy for most purposes by placing the fish on a suitably mounted graduated scale and measuring the length from the tip of the snout to the extremity of the caudal fin. There are, however, some circumstances in which this simple, customary method is difficult to operate or is not sufficiently accurate for the investigation in hand. As a result, some modifications of this simple process have been introduced by some workers and are in general use today.

One feature of the simple method of measurement, which may prohibit its use under some field conditions, is that for rapid work two workers are required, one to measure the fish and the other to record the measurements. This may prove a serious difficulty when, for example, large numbers of measurements are made on board commercial fishing vessels, especially small ones. A modification of the simple method has been introduced by a number of workers, to meet this difficulty. This modification, described by Buchanan-Wollaston (1928) dispenses with the reading and recording processes at the time of handling the fish, and instead a mark or pin-prick is made against the total length on waterproofed paper or thin plastic placed under each fish: a fresh piece of paper or plastic can be used for each fish, or large numbers of lengths can be recorded together. As well as reducing the number of workers required, this method is rapid (except when separate paper or plastic strips are used for each fish) and allows the worker to use both hands for handling the fish. It also eliminates the "personal" errors in reading and recording the lengths under field conditions. There are, however, disadvantages of this method which weigh against its general adoption. First, the measuring and recording work is done in two stages instead of one with the customary method. Secondly, unless separate strips of paper or plastic are used for each fish, or each mark is labelled (which largely negates the "speed" advantage) lengths cannot be assigned to individual fish. This feature usually limits its application to investigations in which only the overall length composition of a population is required. However, it may be a valuable method to use along with another method of measurement, e.g. in the use of length-age keys for age de-

termination.

It is well known that "personal" errors in reading and recording large numbers of length measurements may arise when the customary method is used under field conditions and may, if accuracy is an important feature, result in biased length data. Also, if measurements other than total length are required, it is difficult to obtain accurate measurements by this method. These factors have also led to the adoption of refinements of the method designed to reduce the personal errors in reading the length. They mostly take the form of specially designed measuring trays on which the measuring scale is placed at some distance from the fish, and the length is read with the aid of a pointer. When this pointer is suitably constructed, accurate readings of dimensions other than total length can be taken (e.g. Hiatt and Hamre 1945). The importance of adopting refinements such as this in routine length measuring will depend upon the magnitude of the personal errors which arise with the simple method. It is probable that these are sufficiently small in routine measuring to be ignored for most purposes, but for some dimensions, e.g. "standard", or "fork" length they may be large enough to warrant the adoption of suitable refinements.

The actual length dimension which should be measured in biological studies has been the subject of considerable discussion amongst fishery biologists (e.g. Royce 1942; Ricker and Merriman 1945; Carlander and Smith 1945; Hile 1945). The lengths used to include the standard length, fork length and total length, and their relative merits have been considered in detail in the above papers. Total length is undoubtedly the easiest to measure, and it is probably adequate for use in most investigations, but as yet little detailed analysis of these different dimensions in relation to the objective and accuracy of the investigations has been made for many of the important commercial fish species.

#### Age Determination

Methods of determining the ages of fish have been the centre of attention by fishery biologists from the earliest stages of development in fisheries research, and today they rank amongst the best known and most important of all fishery research tools. In the course of progress in fishery research a number of different methods have been evolved for determining age, and, as in other fields, the choice of method is governed by a number of factors.

The methods in use today can, for the present purpose, be divided into two groups: those which give the age of individual fish, and those which give

only the age composition of large samples of fish. The second group cannot be used in investigations in which age is related to other characters of individual fish, but they may on the other hand be quicker to apply, and therefore may be preferable, in investigations in which only the age structure of the fish population is required (e.g. in some population studies). Therefore, in assessing the relative merits of different methods of age determination, special account must be taken of the objectives of each investigation in which the age data are to be used.

The two main methods of determining age are as follows:

- (1) By the analysis of length frequency data; generally known as Petersen's method.
- (2) By counting the number of periodic rings or zones on certain skeletal structures, the chief of which are scales, otoliths, opercular bones, vertebrae and fin rays.

#### Petersen's Method

The great merit of Petersen's method is that it is a very economic method to use since only length measurements have to be taken, and the laborious and costly process of age interpretation from scales, otoliths, etc. is avoided. It is important to consider, therefore, whether sufficient use is made of this method in present day investigations.

The principles underlying the method are as follows:

- (1) The lengths of the individuals of each age-group in a population of a species of fish having a single restricted spawning season are approximately "normally" distributed.
- (2) Growth is such that the modes of the length distributions of successive age-groups in a sample taken from the population are separated along the length axis.

Whenever these conditions are satisfied completely in a fish population, Petersen's method can be used to give accurate measures of its age composition. However, this is seldom the case in practice, and the applicability of the method will depend on the extent to which the length data satisfy these ideal conditions. A departure from the ideal may be the result of a number of factors, prominent amongst which are:

- (1) The "non-normality" of length frequency data for the constituent age-groups, due to prolongation of the spawning seasons, the mixing of growth types, and selection by the sampling gear.
- (2) The progressive reduction in growth rate with age and so greater overlapping of length frequencies of successive age-groups amongst the older age classes.
- (3) The difficulty in gauging the age of the smallest length group and of ensuring that all age-groups are represented in the samples.

These difficulties are prohibitively great for applying Petersen's method for accurate age determination of a species such as herring in some areas where fish of different growth types, derived from different spawning groups, share the same habitat. They are, however, less great in species with a single spawning season and a more prolonged and rapid growth history (e.g. cod, halibut and haddock), and the applicability of the method will be governed more by the difficulties listed under (3) than the more fundamental ones, particularly when use is made of modern statistical techniques for dissecting polymodal data (Harding 1949; Cassie 1954). These difficulties may be prohibitive in the initial stages of investigation, but may become less formidable as information on the biology of the species, and the selectivity of the sampling gear accumulates. Thus, it is often possible to replace, either completely or partially, the more laborious scale or otolith method by Petersen's method, after the early exploratory phase of the investigation. Many workers today utilize Petersen's method on large samples of length data together with smaller check samples of scales or otoliths. This is the basis of the growing use of length-age keys in routine age determination (Gulland 1955).

In some investigations, of course, Petersen's method is the only possible way of obtaining the age structure of the population. This applies to those species of fish, found mostly in the warmer regions, whose skeletal structures have no recognizable annual rings or zones, or on which a number of similar rings or zones are formed annually. It is sometimes relatively easy to determine the age of the younger year-classes from skeletal structures, but not the older ones, and in these instances Petersen's method can be supplemented by these data for the smaller sizes; other check data can also be obtained from the results of tagging experiments, and from aquaria experiments.

#### Use of Skeletal Structures

The general validity of methods of determining age from the periodic

markings on certain of the skeletal structures of fish was established early in the present century, and since that time this method has become an accepted routine in many fishery investigations. The annual expenditure of time and money on the use of those methods and their application in routine age analysis is probably greater than for any other single laboratory method, and it is of the greatest importance therefore that constant attention should be paid to the possible ways in which the methods can be improved, their accuracy increased and their cost reduced.

The magnitude of the problems in applying these methods today varies enormously from species to species and area to area. For some species in some areas accurate age determinations can be obtained quite quickly and simply from scales or otoliths, and the main avenues for improvement are in increasing the speed and reducing the cost of the method; for other species, however, there are still major problems and differences of opinion in interpreting the rings and zones on these structures. Here, the immediate problems may be quite specific and formidable, and the avenues for resolving them will possibly lie in a vigorous search for confirmatory data from other sources; in extensive comparisons between different skeletal structures; in modifications in the method of inspection (e.g. in microscopy) and in comparing and contrasting the material and results with other workers. Three species to which these important problems apply at the present time are the Atlantic hake (see Bagenal 1954), the Atlantic halibut and redfish.

For a large number of other species the problems associated with the use of skeletal structures for age determination lie between the two extremes given above. Thus, the method is used with varying degrees of precision and confidence for the main Atlantic species of gadoid (cod and haddock), of clupeoids (herring, sprat and pilchard), of Salmonids (salmon and trout) and of Pleuronectids (plaice and flounder) and other flatfishes, but, for most of them, problems associated with the choice of skeletal structure, with their collection, preparation and mounting, and with ring or zone interpretation, still arise and warrant active consideration. Aspects of these problems, relating particularly to cod and haddock are:

- (1) The relative merits of scales and otoliths in age determination of cod and haddock.
- (2) The potentialities of other skeletal structures: e.g. fin rays and opercular bones.
- (3) The accuracy of the methods at present in use.
- (4) Methods of preparation and examination of scales, otoliths, etc.

(5) The histology and physiology of ring and zone formation.

The question of accuracy is of particular interest. It is impossible to measure the absolute accuracy of any of the methods, but, by extensive comparisons of results obtained by different workers using the same and different methods, an assessment can be made of which method is the most accurate. Results of such comparisons have been published (e.g. Saetersdal 1953), and the most consistent and important result which they have shown is that the otolith gives the more reliable readings for the older age classes. This is also demonstrated in extensive comparisons, made by the writer and his colleagues, of age readings of North Sea herring using scales and otoliths. An example of one such comparison is given in Table I. These results show good agreement between independent otolith age assessments over the whole age range, but a considerable difference in assessment between the scale and otolith assessments for fish more than 7 years of age.

These examples are given to emphasize the importance of extensive comparative work in gauging the relative merits of different skeletal structures for age determination, and to indicate the possible extent of the difference in age assessment between different structures. While they point to the otolith method as the more accurate for age determination of a number of important species, there are practical difficulties and disadvantages associated with it due chiefly to the greater cost and time taken in their collection and preparation for microscopic examination. Therefore, in age determination of some species (e.g. haddock and herring) it may be profitable to use the scale method for the younger age classes and the otolith method for the older ones. In the North Sea haddock investigations, the scale method is satisfactory for the whole population because of its young age structure.

These methods of age determination are based on the recognition of seasonal changes in the form and composition of the skeletal structures, and the ease and accuracy in applying the methods depend on the extent of the seasonal changes and their regularity. At present very little is known of the basic chemistry and histology of these changes or the physiological processes which control them, and it is important that the working party should discuss current information on these processes and should consider any possible ways of studying them.

The chemical and histological changes associated with zone formation in otoliths are particularly interesting since two, as yet unresolved, explanations have been put forward. Immerman (1908) associated the sequence of opaque and hyaline zones with periodic changes in the deposition of inorganic material, while Hickling (1931) associated them with changes in the arrangement and density of the organic constituents. It is perhaps fortunate that a knowledge of

TABLE I. Comparisons between age readings\* of North Sea herring from otoliths (Readers A and B) and scales (Readers C and D).

Age	A	Otolith Readings			Scale Readings					
		B			C			D		
		Agree- ments with A	Differences from A		Agree- ments with A	Differences from A		Agree- ments with A	Differences from A	
			Higher	Lower		Higher	Lower		Higher	Lower
2	7	7	-	-	7	-	-	7	-	-
3	3	3	-	-	2	1	-	2	1	-
4	8	8	-	-	8	-	-	6	-	2
5	2	2	-	-	2	-	-	2	-	-
6	1	1	-	-	1	-	-	1	-	-
7	5	5	-	-	3	2	-	4	1	-
8	6	6	-	-	2	1	3	2	1	3
9	4	4	-	-	3	-	1	1	-	3
10	6	5	-	1	2	-	3	0	-	5
11	-	-	-	-	-	-	-	-	-	-
12	2	2	-	-	2	-	-	0	1	1
13	2	2	-	-	0	-	2	0	-	2
14	1	0	-	1	0	-	1	0	-	1

\* These age readings were taken independently by four experienced workers (A and B in otolith reading, C and D in scale reading). This sample was selected at random from the daily samples received at the laboratory for routine analysis.

these changes and the physiological processes controlling them is not essential for the successful use of these structures for age determination, but it is probable that clearer understanding of them would lead to easier interpretation and a reduction of many current difficulties.

### Growth

Growth is manifested as an increase in size of an organism and, as such, is best measured in terms of its volume or weight. However, accurate weighings are not easily made at sea and fish are often landed at the markets in a gutted or headed state; in consequence, growth of marine fishes is usually determined from length data. In those instances where a knowledge of growth in weight is required (e.g. in population studies), the length data are trans-



formed to weight with the aid of a weight-length relationship, determined from relatively small samples of lengths and weights.

The methods used in growth studies in marine investigations fall into three main groups:

- (1) By tracing the seasonal and annual increase in mean or modal length of successive age-groups in the population. This is the method usually employed; it is a "population" method which gives only the average growth characteristics of the fish population.
- (2) By taking measurements on skeletal structures. This method gives growth data for individual fish, but again it is costly and time consuming to apply on a large scale. However, it is an extremely valuable method to use in growth studies of species which are difficult to sample representatively over the whole or part of their age range.
- (3) By measuring the increase in length of tagged fish between liberations and recapture. This like (2) provides growth data for individual fish, but it has many limitations; it is costly to apply on a large scale; the growth data are usually obtained over relatively short intervals; and growth of tagged fish may not be representative of the untagged population. In consequence, this method is seldom used as a primary source of growth data, but it provides data to supplement those obtained in other ways.

The basic problems and difficulties associated with the use of methods included under (1) are essentially the same as those associated with the methods of measuring length and determining age and the accuracy with which these methods can be applied will be governed largely by the accuracy of the methods of age determination. These problems have been mentioned in the previous section and will not be considered further here. However, a number of important problems arise in the application of the second group of methods, and these are worthy of detailed consideration. The validity of these methods depends on the relationship between the growth in length of the fish and the growth of the skeletal structures, and not until this relationship is known can accurate estimates of the annual growth increments be made. The investigation of this relationship is, therefore, the starting point for all growth studies using these methods.

The skeletal structure most used in these back calculations of length is the scale, and the relationship between fish length and scale length (measured from the centre or nucleus to the periphery) has been investigated for a number of species of fish (e.g. Lea 1910; Lee 1912; Segerstråle 1933; Hile 1941;

Saetersdal 1953). The relationship between fish length and otolith length has also been determined for a few species (Hickling 1933; Saetersdal 1953).

The results of these investigations vary widely. Some workers have concluded that the relationship is linear, of the form  $L = BS$  or  $L = A + BS$  (where  $L$  = fish length;  $S$  = scale (otolith) length;  $A$  and  $B$  are constants) while others have obtained curvilinear relationships. Unfortunately, the form of this relationship is fundamental to the application of these methods, because on it will depend the form of the final calculation of intermediate length. If the relationship is of the form  $L = BS$ , the intermediate lengths can be calculated from successive measurements made on the scales or otoliths by simple proportion using the well-known formula  $L_t = L \frac{S_t}{S}$  (where  $L_t$  = length of fish at

time  $t$ ,  $S_t$  = length of scale (or otolith) at time  $t$ ,  $S$  = total length of scale and  $L$  = total length of fish), but if the relationship is of the form  $L = A + BS$ , errors in calculating the intermediate lengths will arise using the simple proportionality formula and the true values are given by a different expression, of the form  $L_t = L \frac{S_t}{S} + A (1 - \frac{S_t}{S})$ . In these circumstances the errors in the

values of intermediate lengths obtained by simple proportion, will depend on the magnitude of the second term in the above expression, and this will increase in size (age) of the fish (more precisely with increase in size of scale) and will give rise to the well-known phenomenon of apparent change in growth rate. If the relationship is curvilinear, then a more complex expression will result.

Further difficulties arise if the relationship changes at one or more points over the range of lengths examined. Whenever such changes are experienced, accurate growth calculations can only be made by applying corrections to the calculated intermediate lengths.

It is clear from these remarks that an accurate knowledge of the form of this relationship is required before this method can be applied with confidence in growth investigations. Therefore, it is essential that the initial experiments to establish its form should be as exhaustive as possible; particular attention should be paid to the variations in the relationship for scales taken from different parts of the body, so that, in the routine application of the method, they can be selected from the appropriate body region.

Once this basic relationship has been established, the application of the method in growth studies is relatively straightforward, and various methods are used in making the measurements and calculating the intermediate lengths. With most of these methods the intermediate length data are obtained in two stages; measurements are first taken on the projected scale or otolith, (with

otoliths, photographs may be more appropriate), and the calculations of intermediate lengths are then made, usually with aid of a nomogram or mechanical device (e.g. Lea 1910; Hile 1950). However, this procedure is time consuming and some attention has been paid to the development of techniques for combining these two processes. Kesteven and Proctor (1941) describe an apparatus which can be used with scales to give the values of intermediate lengths directly, and which increases appreciably the speed with which large quantities of material can be handled.

While these considerations govern the validity and accuracy of this group of methods, its applicability is also affected by other factors, most of which also affect the accuracy of age determination; indistinct annual rings or zones; the presence of false rings, crowding together of rings and variations in the time at which rings and zones are laid down are examples. However, despite them, this method has proved of great value in growth studies of some species of fish, particularly in some life history studies.

In view of the problems and difficulties mentioned above, further attention should be paid to the chief difficulties in applying this method in growth studies of those species with which the Commission is most concerned. Particular questions worthy of special consideration are:

- (1) What is the correct form of the relationship between fish length and scale (otolith, etc.) length for each species?
- (2) Which is the most accurate and reliable skeletal structure to use, and which dimension of each gives the most consistent results?
- (3) From which region of the body should scales be taken in applying this method?
- (4) By what means can the processes of measurement and calculation be combined, and the speed of applying the method be increased?

#### Summary

In this brief review of the methods used in some of the more important fishery research investigations, an attempt has been made to highlight the chief topics which have a bearing on the accuracy and the overall efficiency of the methods. Its purpose is to focus attention on the more important issues which the working party under Item 6 of the Commission's agenda should discuss, and on which a free exchange of ideas is especially warranted. As well as aiming to increase accuracy and efficiency, the working party should, wherever possible, attempt to arrive at standardization of method and termi-

nology, especially for those investigations of a long-term routine nature conducted concurrently by a number of independent workers.

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### Introduction

In the study of any animal population the ability to know the age of individual animals is an extremely powerful tool. For many species of fish this knowledge is possible through examination and counting of annuli appearing on the scales, otoliths or other parts of the fish, though for some species marked discrepancies occur between the ages as estimated by different observers (Hiyama et al 1953). For the Arctic stocks of cod the aging method generally used has been the examination of the split otolith (Rollefsen 1933), and this has given good agreement between different observers (Fridriksson et al 1933). For the English investigations on the composition of the commercial landing, however, it was considered undesirable to split open the head of the fish to obtain the otoliths, and accordingly, following the method used by Boyko (1950), the first two rays from the first dorsal fin were cut off involving no apparent mutilation of commercially valuable fish and used for age determination. On board the research vessel "Ernest Holt" both otoliths and fin rays were normally taken from the fish sampled. In order to compare ages determined from fin rays with those based on otoliths, and also to compare ages obtained by different observers, a series of experiments were carried out with a number of observers making estimates of the ages of the same sample of fish, using fin rays and otoliths independently.

### Experimental Design

Fin rays and otoliths from 290 fish chiefly from the Bear Island area caught by the "Ernest Holt" throughout the year, were placed separately in numbered packets, the numbering for fin rays being different from that for otoliths. The only information, other than the otolith or fin ray itself, available to the observer was the time of year at which the fish was caught. The otoliths had already been read once during the routine analysis of the samples, and the sample was chosen with regard to these preliminary readings so as to include fish of all ages, up to about 20, and also of the three main otolith types, Western, Western-Split and Eastern, described by Trout (in preparation). Five observers read both fin ray and otolith samples, and two other observers the otolith, but not the fin ray samples. The sheets on which each observer's age-determinations were recorded, were collected on the conclusion of each sample, so when reading the fin rays, his previous readings of the otoliths could not serve as a guide or vice versa though because of the difference in numbering such a guide could only be a general one, and not serve

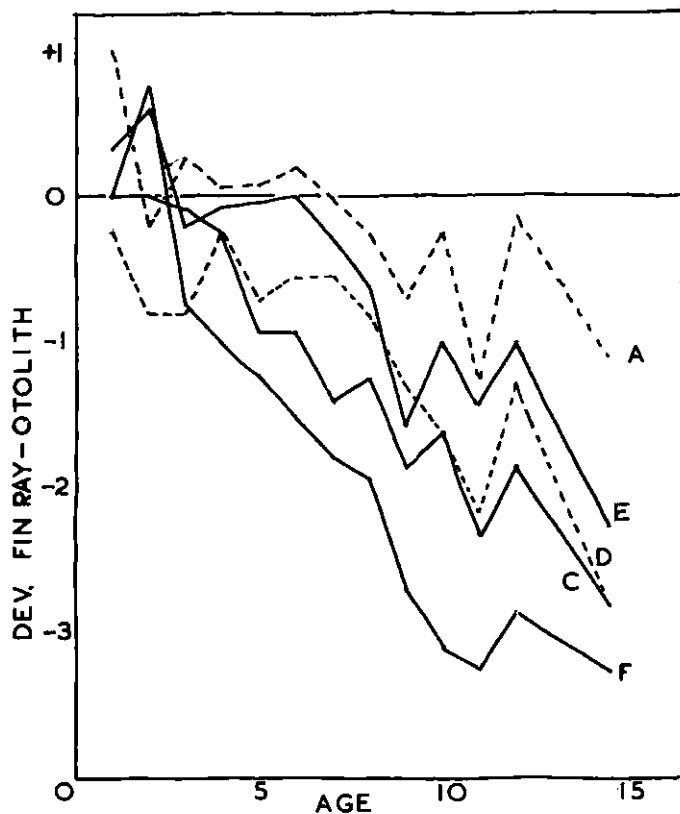
to aid in the age-determination of an individual fish. On the results of these readings a further sub-sample of 50 was chosen from the original 290 and the fin rays and otoliths, after being placed in packets renumbered from 1 to 50 were read again. These chosen fish were generally those for which there had been most disagreement among the ages as estimated from the otoliths, as it was expected that a re-examination of these would give most information about the variation between different readings by the same observer.

#### Differences Between Otolith and Fin Ray Ages

The apparent age-distributions of the initial sample of 290 fish, as obtained by the two methods by each observer are given in the appended Table VI. On first examination the distributions both as regards observers and methods, appear remarkably similar, with a modal age of about 6 or 7. However, there are important points of difference, the fin ray distribution possessing more younger fish, particularly for some observers, e.g. F, and in particular having very few of the oldest fish. For instance the estimated numbers of fish over 12 years of age for the seven sets of otolith readings are 34, 34, 30, 27, 33, 32, 29, and for the five sets of fin ray readings 10, 21, 9, 6 and 10. Therefore, at least for these older fish, observers using fin rays must seriously under-estimate the age relative to those using the otoliths. This effect is also shown in Figure 1. For this diagram only those fish are shown for which at least five out of the seven estimates using otoliths agree, thus providing a fairly definite "otolith age". For all fish of a given "otolith age" the average deviation of the "fin ray age" as determined by each observer was calculated and is plotted in the diagram, the last point on each curve, plotted at 14.5, corresponding to the average deviation of all fish with an "otolith age" greater than 12. All the curves slope downwards, indicating a progressive under-estimate of the age, though there is considerable difference between observers, e.g. for fish with an "otolith age" of 8, observer F. has an average deviation of nearly 2 years (an average "fin ray" age of 6) while A only deviates by 0.25, an average of 7.75.

A further difference between the ages obtained from otoliths and fin rays lies in the degree of agreement between observations on the same fish by different observers. In Table I are shown the number of fish for which all observers reading the otoliths (or fin rays) agreed on the age, and the number for which two, three or more different estimates of the age were made.

If the degree of agreement within each method were the same, there should be a smaller proportion of agreement for the 7 observers reading the otoliths compared with only 5 reading the fin rays, and correspondingly more fish giv-



**Fig. 1.** Deviations of the age of cod as estimated by several observers using fin rays from the mean age as determined by otoliths.

ing several different ages. The fact that the reverse is true shows that there is considerably more agreement between observers when reading otoliths than when reading fin rays. These results are not of course by themselves sufficient to indicate which, if either, of the two estimated ages is the true age. Evidence that the "otolith age" is reasonably correct is provided by the year-to-year age composition, as obtained from otoliths, of several of the northern stocks of cod. In these, outstanding year-classes can be followed through, often over a large number of years; for instance, the 1922 and 1924 year-classes at Iceland (Jónsson 1954), and the 1937 year-class at Lofoten (Rollefsen 1954). If there was any considerable progressive bias in the age as estimated from the otoliths, such following of good (and bad) year-classes would be im-

TABLE I. Agreement between observers of the estimated age using otoliths or fin rays.

	Otoliths (7 Observers)	Fin Rays (5 Observers)
All observers agree	86	45
2 different estimates	109	70
3 different estimates	64	130
4 different estimates	20	70
5 or more different estimates	11	13

possible, though there remains a slight possibility of a consistent error of one or more years, perhaps in the reading of the nucleus. The use of fin rays for regular age-determination of stocks of cod will result in a marked underestimate of the numbers of older fish. Hence mortality rates will be markedly over-estimated, and the growth-pattern distorted, so that the results are definitely unsuitable for detached population analysis. However if all that is required is to find say the approximate average age in a population, then fin rays may be satisfactory.

#### Differences Between Observers' Estimations of Age

For each fish the seven independent otolith readings are sufficient to establish an average, or majority otolith age which can be used as a standard for comparing the estimates obtained by any single observer, whether using otoliths or fin rays, and which probably does not differ greatly from the true age. The results of such comparisons are shown in Table II.

This table may be used to provide a reasonably objective measure of the ability of any observer. The difference between the sum of the positive and negative deviations is a measure of an observer's "bias" in age-determination, and the sum of all deviations is a measure of his "variance". From Table II it may be seen that when reading fin rays all observers were subject to considerable bias and variance. When reading otoliths, the "variances" of the seven observers were very similar and all were quite small. The number of agreements using otoliths varied between 194 and 223, out of a possible 290, i.e. between 67% and 77%. The single observer, D, whose variance using otoliths was appreciably larger than the others for otoliths, though still much smaller than any for fin rays, had no previous experience of age-determination

TABLE II. Deviations, from the majority otolith age, of age as estimated by individual observers.

Observers are minus majority otolith age	Reading otoliths							Reading fin rays				
	A	B	C	D	E	F	G	A	C	D	E	F
6	1	-	-	1	-	-	-	-	-	-	-	-
5	-	-	-	1	-	-	-	1	-	-	-	-
4	-	-	-	1	-	-	1	2	-	2	1	-
3	3	-	-	2	-	-	-	5	-	4	2	2
2	5	10	3	4	-	-	9	10	3	7	8	1
1	24	46	19	13	32	15	36	54	11	28	46	9
0	214	219	211	194	223	216	219	103	52	52	94	32
-1	38	19	48	55	27	51	22	82	81	87	73	71
-2	8	-	9	8	6	8	-	18	79	63	33	80
-3	1	-	-	3	1	-	1	6	28	28	15	46
-4	-	-	-	6	-	-	-	6	12	6	7	19
-5	-	-	-	1	1	-	-	1	5	7	3	15
-6	-	-	-	-	-	-	1	1	5	2	4	6
-7	-	-	-	1	-	-	-	-	4	2	-	4
-8	-	-	-	-	-	-	-	-	-	-	-	1
-9	-	-	-	-	-	-	-	-	-	-	-	2
-10	-	-	-	-	-	-	-	-	-	-	1	1
Sum of + deviations	49	66	25	42	32	15	58	102	17	62	72	17
Sum of - deviations	53	19	66	116	47	67	31	171	434	382	261	620
Sum of all deviations	102	85	91	158	79	82	89	273	451	444	333	637

in any fish, and it is worth noting that his deviations from the mean were most marked in the first batch of 66 otoliths examined, though no comparisons were made until all the otoliths were read. Two of the other observers, C and G, had good experience in reading plaice otoliths, but none in age determination of cod, while the remaining four had experience in reading cod otoliths and fin rays. Despite this difference in experience with cod otoliths, there seems to be no difference in the variance of the observers, nor is there any marked difference in bias of experienced and inexperienced readers. Comparison of

the bias of each observer when reading otoliths shows that, relative to the majority reading, all but observer A, and possibly E, show a significant degree of bias, though the amount of bias is small. Of the many possible pairings of observers, there are very few in which one of the pair does not read significantly higher, or lower, than the other, though the difference, even in extreme cases (B and D) averages less than half a year. That this is not due to each observer having his own interpretation of each individual otolith is shown in Table III, which gives the results of the check reading of 50 selected difficult otoliths. The table gives the number of times the second reading of each observer agreed with the original reading of himself, and other observers, and also with the average age of the original readings. (Observer G did not read the check sample).

TABLE III. Number of agreements (possible 50) between pairs of age determinations by observers of the same cod otolith.

Observer for second reading	Observer for first reading							Average
	A	B	C	D	E	F	G	
A	<u>25</u>	21	17	20	17	22	13	25
B	23	<u>27</u>	17	15	19	18	17	24
C	16	20	<u>15</u>	12	20	16	23	21
D	20	18	22	<u>19</u>	23	20	19	25
E	15	18	18	15	<u>24</u>	21	24	21
F	25	26	23	25	26	<u>29</u>	20	36

The italic figures in the leading diagonal give the number of agreements between the two estimates by the same observer. These are not very much higher than the number of agreements between different observers, and are less than the number of agreements between the check readings, and the majority age of the original readings. Only two observers had more than 50% agreement between their two readings.

Table III may be compared with Table IV, which gives the corresponding results for the repeated readings of the fin rays of the sample of 50 fish. The number of agreements for the fin rays are considerably lower than for the otoliths despite the fact that the sample of 50 fish was chosen to include several for which there had been marked disagreement between observers on the first reading of otoliths. The two sets of readings of the same 50 otoliths and fin rays by the same observer are also compared in Table V, which gives the difference between the two readings. Four of the observers have, for the oto-

TABLE IV. Number of agreements (possible 50), between pairs of age determinations on the same cod fin ray.

Observer for second reading	Observer for first reading				
	A	C	D	E	F
A	<u>8</u>	21	18	16	16
C	5	<u>19</u>	13	8	12
D	13	18	<u>17</u>	17	13
E	11	10	15	<u>24</u>	10
F	2	15	6	6	<u>17</u>

liths, a symmetrical distribution with the check reading where it differs, being equally likely to be above or below the original reading. Observer C was aware, after having completed his check sample, that he had altered his interpretation of the nucleus, thus adding one year to the estimate of the age; this has produced a nearly symmetrical distribution displaced one year to the left. The other observer, D, who had an apparent bias between his ten sets of otolith readings was the man with no previous experience of otolith reading, and whose original readings, as shown in Table II, tended to be below the general average. The greater age of the second estimates may be due to the correction of this bias on second time reading.

Of the fin ray distributions in Table V, two (A and C) show a large and highly significant bias, and two others (D and F) a slight bias; also, when a repeated reading was made of another sample of 50 fin rays, observer E had a large bias, his second reading averaging nearly  $3/4$  of a year younger than his original reading. None of the observers were conscious that they had altered their standard when examining the check sample. This general inability to obtain consistent results with fin rays is of course further reason to use some other method of age-determination. In contrast, using otoliths all observers obtain reasonably consistent and similar results.

The results for otoliths have shown, in Tables II - V, remarkable similarity between observers, even in the degree of scatter about the central values. This of course is consistent with the otolith providing an objective measure of the age of a fish. The lack of difference between experienced and inexperienced workers is probably due to the lack of knowledge of the true age of a fish, against which a man could learn to correct his mistakes. The most serious discrepancy between observers is the small biases apparent in Table II. The source of some of these is known to be a consistent difference in interpretation of certain types of otolith. For instance about a fifth had a very small "sum-

TABLE V. Frequency distribution of the difference between two independent estimates by the same observer of the age of the same otolith (or fin ray).

Difference: Second reading minus first	Reading otoliths						Reading fin rays					
	A	B	C	D	E	F	A	C	D	E	F	
8	-	-	1	2	-	-	-	-	-	-	-	
7	-	-	-	-	-	-	-	-	1	-	1	
6	-	-	-	-	-	-	-	-	-	-	-	
5	-	-	-	2	1	-	-	-	1	-	1	
4	-	-	-	1	-	-	-	-	1	1	-	
3	1	-	4	2	-	-	-	1	1	4	-	
2	6	4	7	4	2	1	-	-	4	4	2	
1	5	10	21	14	10	15	7	-	9	6	6	
0	26	27	15	19	25	29	8	19	17	24	17	
-1	5	7	1	4	9	4	19	18	10	6	12	
-2	4	1	-	2	3	1	13	4	3	2	5	
-3	2	1	-	-	-	-	2	-	1	1	3	
-4	1	-	-	-	-	-	-	-	1	1	1	
-5	-	-	-	-	-	-	-	3	-	-	1	
-6	-	-	-	-	-	-	1	2	-	-	-	
-7	-	-	-	-	-	-	-	-	-	-	1	
-8	-	-	-	-	-	-	-	-	-	1	-	
-9	-	-	-	-	-	-	-	-	-	-	-	
-10	-	-	-	-	-	-	-	-	1	-	-	
Not known	-	-	-	-	-	-	-	3	-	-	-	
Mean	-.06	+.12	+1.04	+1.00	+.08	+.22	-1.00	-1.00	+.26	+.06	-.52	

mer" ring after the first "winter" ring, which usually only observer 3 counted as a separate year. See Trout's paper for this meeting. So long as such otoliths form only a small part of the population, so that the bias between observers is as small as in the sample discussed (which is probably typical of Arcto-



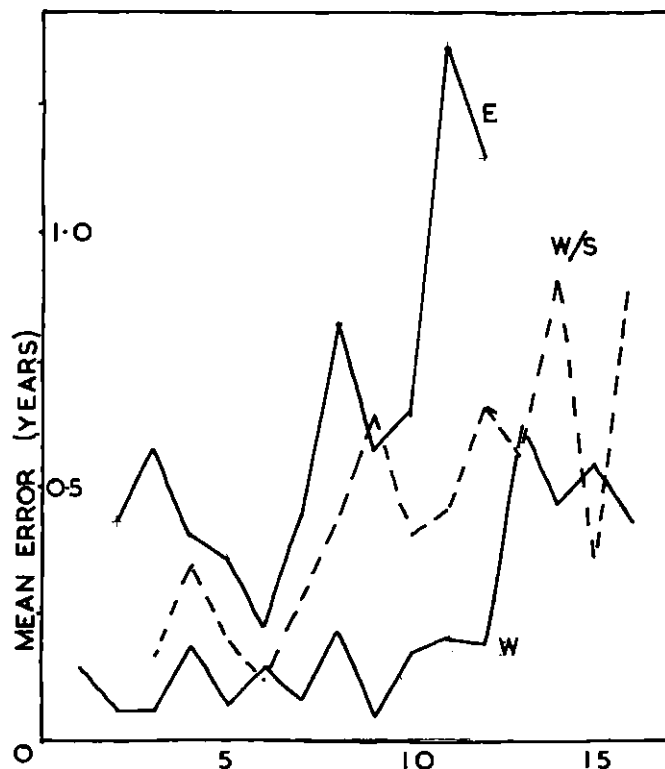


Fig. 2. Change in the deviation from the majority otolith age with age, distinguishing the three otolith types (West, West-Split and East).

Norwegian cod) then the age-determinations by any observer can be accepted as an objective measure of the age of the population. However, as will be shown, even within one stock, otoliths vary considerably in the accuracy with which they can be read. Thus it would be dangerous in some other stock to accept the age-distributions of two independent observers as being strictly comparable without direct comparisons on the same sample of otoliths.

#### Changes in the Degree of Error with Age and Type of Fish

The relative difficulty in reading each otolith may be assessed by summing the deviations of the individual estimates of the seven observers from the

TABLE VI. Apparent age distribution of the sample of cod as estimated by various observers.

Observer	Estimated from otoliths							Estimated from fin rays				
	A	B	C	D	E	F	G	A	C	D	E	F
Age												
0	-	-	-	-	-	-	-	-	-	4	-	-
1	6	4	4	6	5	6	5	3	4	7	4	17
2	5	7	9	7	7	9	7	7	7	13	5	16
3	20	17	24	23	18	23	14	16	27	26	19	31
4	19	19	20	19	23	17	21	26	39	26	25	42
5	30	30	24	36	31	28	27	30	46	33	38	51
6	34	35	37	40	34	39	34	34	33	39	38	49
7	47	40	46	42	44	43	44	42	46	34	42	22
8	32	33	30	25	30	35	39	33	21	23	33	21
9	18	22	18	14	20	16	17	26	20	31	27	11
10	17	15	18	18	13	10	18	16	15	20	16	7
11	15	20	16	18	19	19	16	15	12	13	14	8
12	13	13	13	16	13	13	18	18	4	8	16	5
13	13	12	13	10	15	16	12	8	2	3	6	5
14	11	9	9	4	5	5	7	5	3	5	2	1
15	3	9	3	5	9	7	5	6	1	1	1	1
16	5	2	3	5	1	2	3	1	-	-	-	1
17	1	2	2	1	1	1	-	-	-	1	-	-
18	-	-	-	-	2	-	1	-	-	-	-	1
19	-	-	1	-	-	-	1	-	-	-	-	-
20	1	1	-	-	-	1	-	1	-	-	-	-
21	-	-	-	1	-	-	-	-	-	-	-	-
?	-	-	-	-	-	-	1	2	9	2	2	-

"average" age; i.e. if the seven estimates are 5, 5, 6, 6, 6, 7, 8, the majority age is 6, and the sum of the deviations 5. Dividing this score by seven will give an approximate estimate of the average error of the observers for that otolith; actually it is a biased estimate, being too low because the majority age is not independently known, but has to be estimated for each age of fish and type of otolith, and the results are plotted in Figure 2. For each type of otolith the error increases with age, as might be expected, and there is a wide difference between types. For the Western type the error is very small for fish below about twelve years with an average of less than two disagreements among the seven observers. For the Eastern type there is considerable disagreement among even the young fish. This increasing error with age will

have an effect on the estimates of mortality obtained from the observed age-distribution; the extent of this bias can be estimated from Gulland's (1955) equation 1.26, if it is assumed that the errors are equally likely to be above and below the true age. For example, the average errors of the Western type ages 10, 11 and 12, read from the curve, are .21, .25 and .29 approximately.

$$\begin{aligned}\text{Thus: } a_{10} &= b_{10} = .105 \\ a_{11} &= b_{11} = .125 \\ a_{12} &= b_{12} = .145\end{aligned}$$

and taking a value for the survival rate of 50%, we have that the survival rate from 10 to 11 years, will be over-estimated by a factor of 1.01 i.e. by 1%.

For the Eastern type, we have similarly that the survival rate will be over-estimated by a factor of 1.026. This is of course greater than the bias for the Western type, but still cannot be considered very serious.

#### References

- |                                                                          |                                                                                                                                                                       |
|--------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------|
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John R. Clark.

Consistency tests of scale readers were conducted in conjunction with a study of the validity of age determination of haddock by scales.

A sample of 101 young haddock from Georges Bank were read by two experienced scale readers. The results are shown below:

		<u>Scale Reader A, Ages</u>						
		2	3	4	5	6	7	
Scale Reader	2	78	2					
B, Ages	3	2	7	1				
	4			10				
	5							
	6					1		
	7							

The two readers agreed in 95 out of 101 comparisons. Such high agreement (94%) is due to the low age of the fish in the samples. A similar comparison for older fish is summarized below:

		<u>Scale Reader A, Ages</u>						
		4	5	6	7	8	9	
Scale Reader	4	41	2					
B, Ages	5		33	1				
	6		4	5	2			
	7			1	5	1		
	8					4		
	9						1	

Scale readers A and B agreed in 89 out of 100 comparisons, (89%). The two readers had worked closely together previous to these tests and had naturally arrived at similar methods of age interpretation. Tests conducted between readers without previous experience in reading scales yielded agreement ranging from 36 percent for old fish to 78 percent for young.

A test of comparability of duplicate readings by individual scale readers was also made. In the two samples discussed above, a series of 50 duplicate samples were prepared. The samples were so arranged that the reader could not identify the duplicated samples. The results of the tests for the first sample are shown below:

Scale Reader A		Scale Reader B	
1st Reading		1st Reading	
	2 3 4 5 6 7		2 3 4 5 6 7
2	37 3	2	36 2
3	4 1	3	2 5
4	5	4	5
Duplicate 5		Duplicate 5	
Readings 6		Readings 6	
7		7	
8		8	1
9	1		

Both scale reader A and B agreed in all but 5 cases out of 51 (90%) between first and duplicate readings. The disagreements involved the same fish for each reader in three cases. Four of the five disagreements between readers discussed in the first part of this paper were involved in the disagreements between these first and second readings; the scales of the fish had indistinct markings.

Another opportunity for testing scale readings was afforded when scale reader A mistakenly read one of the routine age samples a second time. The two sets of readings were compared with the following results:

First Reading	
	1 2 3 4 5
1	1
2	14 1
3	4 127
4	7 15
5	2

The first and second readings agreed in 159 out of 171 cases (93% agreement), but the sample was of very young fish. The test is considered particularly valid because the reader did not know he was testing himself.

In all the above tests only one reading deviated by more than a single year.

Albert C. Jensen and John R. Clark.

This study was undertaken to determine if the periodic markings considered to be annuli are actually formed at the rate of one per year. The pattern of marginal growth of haddock scales thus was examined to determine the variation in the proportion of fish with "winter" and "summer" marginal scale growth.

Scales were collected during a five-year period (1950-1954) to include years of varying brood strength and growth characteristics. Twenty samples from large haddock and twenty samples from scrod were collected in the last week of each month, from the Northern Edge of Georges Bank. Scales from 2338 fish were examined, of which, approximately six percent were illegible because of regeneration or erosion of the edge and therefore rejected, leaving a total of 2208 usable scales.

The age was determined for each fish and the type of circuli at the margin of the scale was recorded. The terms summer growth and winter growth are often used to describe broad circuli and narrow circuli. However, broad circuli are formed on the scale during a short period of rapid growth, occurring in the late spring and early summer. Narrow circuli are formed during a long period of slow growth occurring from late summer to early spring. Despite these facts it is convenient to characterize these bands as "summer" and "winter" growth. Summer growth is readily recognizable, since the summer circuli are much more widely spaced than winter circuli. The commencement of winter growth is often difficult to recognize as the distance between the winter circuli narrows down gradually from the preceding summer growth. Thus, it is not always obvious whether summer-type growth is just being completed or whether winter growth is starting at the edge of a scale. In winter-type circuli the cell-like structures which make up each circulus are heavy-walled and are characterized by a partially occluded lumen. The annulus used for haddock age determinations is the zone of winter circuli.

Annuli are most sharply defined in the scales of fish 2, 3 and 4 years old. These rapidly growing young haddock produce numerous circuli and the difference between summer growth and winter growth is very marked. In fish 5 years old and older the seasonal change is not as sharply defined. The data are presented in Table I and Figure 1 for each month by individual age-groups and for all age-groups combined.

Narrow circuli are not formed exclusively during the cold months or winter season since some fish with narrow, winter-type circuli were found in every month of the year. In addition, individual fish were found with broad, summer-type growth in each month in each age-group. The proportion of fish

TABLE I. Proportion of scales with summer growth at margins; from haddock of various ages.

	<u>Jan.</u>	<u>Feb.</u>	<u>Mar.</u>	<u>Apr.</u>	<u>May</u>	<u>June</u>	<u>July</u>	<u>Aug.</u>	<u>Sept.</u>	<u>Oct.</u>	<u>Nov.</u>	<u>Dec.</u>	<u>Total</u>
<u>2-Year-Olds</u>													
No. of fish	31	1	1	29	40	55	50	63	54	52	31	36	443
No. with summer growth	0	0	0	15	32	53	28	6	0	1	0	0	
Percentage	0	0	0	51.7	80.0	96.4	56.0	9.5	0	1.9	0	0	
<u>3-Year-Olds</u>													
No. of fish	58	47	50	43	33	50	68	55	79	83	68	56	690
No. with summer growth	2	0	0	6	15	43	34	5	13	11	0	2	
Percentage	3.4	0	0	13.9	45.5	86.0	50.0	9.1	16.4	13.2	0	3.5	
<u>4-Year-Olds</u>													
No. of fish	28	65	55	46	48	42	52	35	46	30	49	29	525
No. with summer growth	2	4	0	5	17	28	36	12	12	2	3	5	
Percentage	7.1	6.1	0	10.8	35.4	66.7	69.3	34.3	26.1	6.7	6.1	17.2	



TABLE I. Proportion of scales with summer growth at margins; from haddock of various ages.

(continued)	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
<u>5-Year-Olds</u>													
No. of fish	23	44	21	33	27	29	11	15	14	11	18	20	266
No. with summer growth	4	0	2	4	9	14	5	7	3	2	1	6	
Percentage	5.7	0	9.5	12.1	33.4	48.3	45.5	46.6	21.4	18.2	5.5	30.0	
<u>6 Years and Older</u>													
No. of fish	33	38	46	46	40	21	15	12	7	3	12	14	284
No. with summer growth	3	2	1	0	12	4	8	4	2	0	1	0	
Percentage	9.1	5.2	2.2	0	33.4	19.0	53.3	33.3	28.6	0	8.3	0	
<u>All Ages Combined</u>													
No. of fish	173	195	173	197	188	197	196	180	200	179	178	155	2208
No. with summer growth	11	6	3	30	85	142	111	34	30	16	5	13	
Percentage	5.8	3.4	1.7	15.2	45.2	72.1	56.6	18.8	15.0	8.9	2.8	8.4	

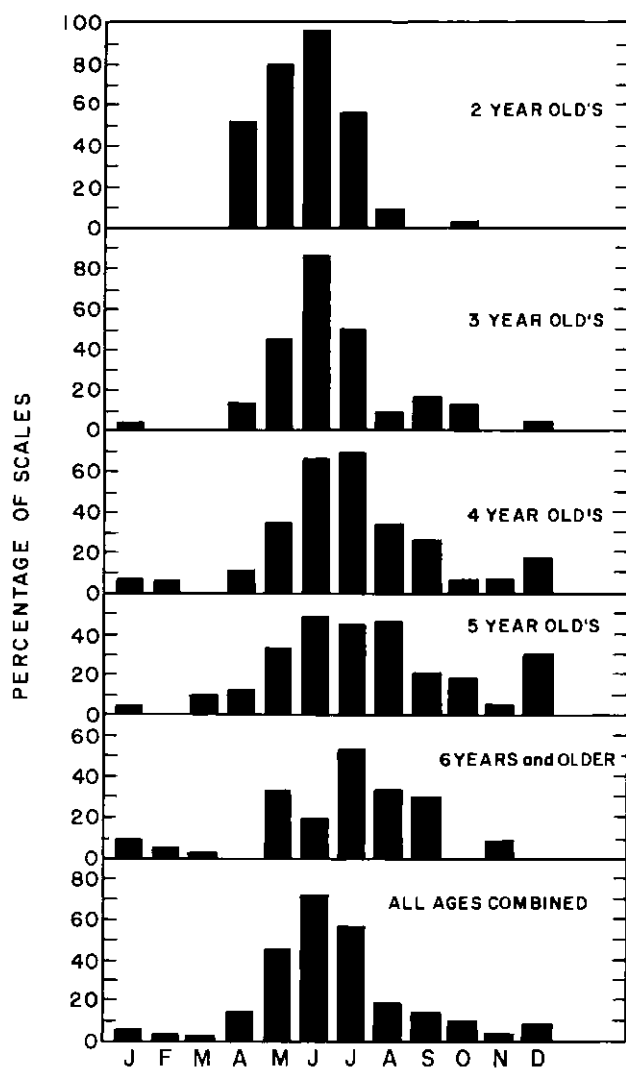


Fig. 1. Percentage of haddock with summer growth on the scale margins.

with each type of scale margin varies regularly with season, winter-type growth predominating from August through April and summer-type growth predominating from May through July. This pattern is apparent for all ages

but it is particularly pronounced for the youngest fish.

The predominance of summer-type growth at the scale edge during May-July and its nearly complete absence during the winter months confirms the belief that these zones are annual in formation and that their use in age interpretation is valid.



A. C. Kohler, W. Templeman,  
John R. Clark and A. C. Jensen.

Authors' Abstract.

A preliminary comparison of haddock scale and otolith readings was carried out by the St. John's and St. Andrews laboratories in 1950. Scales from Subareas 3 and 4 fish were read at St. John's while corresponding otoliths were read at St. Andrews. For a total of 576 individuals 464 (81%) of the corresponding readings agreed. The majority of disagreements were found in readings for old fish, with a tendency towards lower scale than otolith age readings for these individuals.

Further comparisons were made in 1952, 1953 and 1954 for haddock from Subareas 4 and 5. Scales from these fish were read by United States biologists at Woods Hole and the otoliths by St. Andrews personnel. In a total of 764 comparisons 476 (62%) were identical. The lower percentage of agreement for this group of readings led to a more detailed analysis of the data arising from them.

Otoliths gave higher readings in 180 cases of disagreement while scales gave a higher reading in 108 cases. A more detailed examination of the data indicated that up to about 8 years of age disagreement between scale and otolith age readings was usually random. Over this age in the majority of cases of disagreement otolith readings were higher than scale readings.

Random disagreement in scale and otolith readings for fish up to about 8 years of age is mainly due to different interpretations of the periodic markings in scales and otoliths. Weak annulus-like formations corresponding in the scale and otolith may be interpreted as "false checks" by one method and as true annuli by the other. Above 8 years, it appears that the outer annuli are more easily distinguished in the otolith than in the scale; thus the tendency for higher age readings for otoliths in older fish.

Summarization and comparison of age and length data from the two methods indicate that random error in the methods has little effect on growth calculated from the data. However, mortality rates and apparent dominance of year-classes can be affected.

It is believed that the scale method of age determination is satisfactory for stocks of haddock that are for the most part under 9 years of age, as in ICNAF Subarea 5. For older, slower-growing stocks, such as are found in Subarea 4, the otolith method will probably give more accurate results.



G. Saetersdal.

#### Reliability of Age Readings

In a special investigation carried out some years ago for the purpose of testing the zone formation in otoliths and scales of young haddock, Saetersdal (1953), monthly samples were collected from one locality during a three-year period.

The number of zones were compared with the length frequency distribution of the samples (the Petersen method of age determination). The comparison showed that the Petersen method and the otolith readings gave nearly identical results, showing the correct age, while a minority of the scale readings were false and differed from these two methods.

The false scale readings were most probably caused by a total lack of zone formation in a minority of one year-class in a particular growth season. In this season the mean growth of this year-class was unusually poor.

The opaque growth zone formed in the otoliths of the fish with the false scales in this season was found to be very narrow.

It is, however, not believed that the occurrence of false scales is a regular phenomenon in young fish. But this, perhaps unique, experience suggests that the otolith is a more sensitive recorder of the age of the fish than the scale.

This view is sustained by the results of several comparisons of otolith and scale readings in older age groups of gadoids. Thus Rollefsen (1933) has found that it is often not possible to discern the zones formed in the outer parts of the scales of the "skrei", while the corresponding otolith zones are particularly distinct.

Schmidt (1955) had the same experience when studying the otoliths and scales of saithe, *Gadus virens* L., from the Icelandic and Norwegian stocks. In the arctic haddock I have found that the outer zones of the otoliths of the mature fish are far more distinct and easier to identify than those of the scales; in old fish the outer scale zones may be entirely lacking.

#### The Spawning Zones

Since Rollefsen's (1933) discovery of the specific character of the zones

formed in the otoliths of the mature cod, this type of spawning zone has been found and also applied in the study of several other fish populations such as Icelandic cod, Greenland cod and Icelandic and Norwegian saithe.

In the case of the arctic haddock it is not a difficult task to demonstrate that a specific type of zone is formed in the otoliths of the mature fish. The first spawning zone may, however, be difficult to identify in first time spawners. In such cases negative deduction must be used: if no second spawning zone is present and the fish is found to be mature by the state of the gonads, it is classified as a first time spawner.

Essential information concerning the dynamics of the mature part of the population may be gained from the spawning zone analysis. Rollefson and others have shown how recruitment, age at first maturity and total mortality can be estimated. In growth studies it may also be essential to be able to split the observations into spawning classes, because maturity results in size segregation of the total population.

#### Growth Calculations from Scales

Since Lea in 1910 introduced the scale method into the growth investigations of the herring the method has been used and discussed by a great number of workers.

One of the most well-known objections to the reliability of this method was put forward by Lee (1912) and is known as Lee's phenomenon of apparent change of growth rate. Lee found that "with increasing age the groups of fish all show a decreasing rate of growth in the calculated values for each year of their lives".

Lee's phenomenon has been found in a number of fish species. Lea (1913) was of the opinion that this discrepancy was caused by selective sampling. Several other explanations have also been offered, but I think it may be said that this question has never been finally settled. A discussion of the reliability of the scale method is therefore still of actual interest.

Some contributions to such a discussion were obtained by the author when applying the scale method in the study of the growth of the arctic haddock. In efforts to "check" the calculations many authors have made use of a simple comparison of growth calculations and empirically known data of the mean length of age groups. Generally this is not a sound procedure since it leaves no room for a selective change in the population sampled. In the young imma-



ture fish such comparisons may, however, still be permissible.

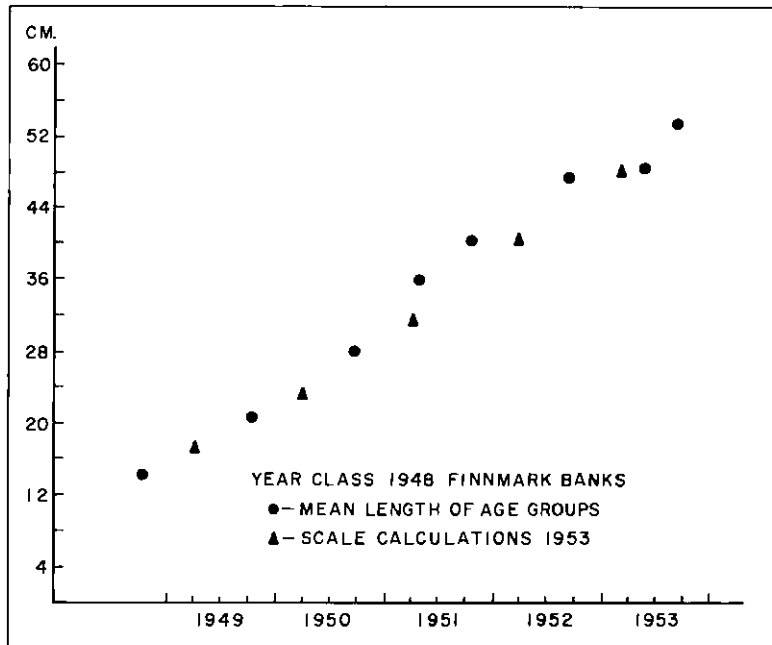
The formula used in the following calculations is based on a rectilinear regression between scale size and fish length, the line intercepting the l-axis one cm from the origin. The formula thus is:  $l = \frac{L - 1}{S}s + 1$  cm.

TABLE I. Mean values of calculated  $l_1$  compared with "empiric" mean lengths of samples from the first period of growth stagnation. 1948 year-class, Brandsfjord. (l in cm).

Calculated:	Sample No.	Date	N	$l_1$	$\sigma$
	66	24/11-49	61	16,27	0,917
	77	18/1 -50	72	16,38	1,081
	81	20/3 -50	43	16,22	1,241
	99	24/6 -50	37	16,35	1,033
	104	30/8 -50	27	16,35	1,468
	119	5/12-50	11	16,36	1,109
Empiric:	Sample No.	Date	N	$l_1$	$\sigma$
	25	29/1 -49	162	16,31	1,016
	26	19/2 -49	189	16,24	1,064
	27	14/3 -49	188	16,26	0,961
	28	27/4 -49	169	16,27	0,928
	48	8/6 -49	402	16,24	0,966

Table I shows a comparison of the mean calculated  $l_1$ 's in six successive samples of young stages of the year-class 1948 and the empiric mean lengths of samples of this year-class during the first period of growth stagnation. There is no significant difference between any of these values.

Unfortunately it was not possible to follow this year-class further in this locality. But another set of observations also comprising this year-class is available from the Finnmark banks. In Figure 1, the mean lengths of samples of age groups are compared with the calculated mean  $l$ -values based on scale measurements of some samples from the autumn 1953 (5 year old fish). The calculated values have all been referred to April 1st because studies of the



**Fig. 1.** Comparison of mean lengths of Finnmark haddock of various age groups compared with calculated mean l-values.

growth rhythm have shown that this date approximately covers the end of the annual season of growth stagnation.

The agreement between the two sets of symbols in Fig. 1 is convincing. Obviously there is no room for Lee's phenomenon in this material.

In order to follow this year-class a little further, we must consider the maturity of the arctic haddock. Only a small part (10-20%) of the fish matures at the age of five, but approximately 3/4 of the six-year-old fish have reached maturity. The mature fish emigrate from the Finnmark banks in winter and apparently do not return to this particular area.

The 1948 year-class at the Finnmark banks was thus only little affected by maturity until the winter 1953-54, but at this time a large part of the population emigrated to the spawning area farther south on the Norwegian coast.

TABLE II. Mean calculated  $l_{1-6}$  of the 1948 year-class of haddock in North Norway from scale measurements.

	$l_1$	$l_2$	$l_3$	$l_4$	$l_5$	$l_6$	$l_t$
Finnmark May 1953 Immature N:1044	17.33	23.99	31.76	39.93			48.14
Finnmark Aug./Oct. 1953 - Immature	17.43	23.92	31.87	40.16	48.02		53.38
Rostbank Spring 1954 Mature							
♀ 1st - time spawners	17.41	24.03	32.27	41.14	50.30		57.38
♀ 2nd - time spawners	18.38	26.07	34.41	44.52	53.10		58.66
♂ 1st - time spawners	16.95	23.37	31.54	39.93	48.57		55.27
♂ 2nd - time spawners	17.24	24.60	32.63	41.58	50.21		56.13
Finnmark Oct. 1954 Immature N:57	16.19	22.70	30.30	37.95	46.12	53.63	57.98

Table II shows the results of the growth calculations carried out on the immature 1948 year-class at the Finnmark banks in the spring and autumn of 1953. As it appears the values are nearly identical.

In the spring of 1954 some scale samples were obtained from the spawning stock at the Rostbank outside the Lofoten Islands. The growth calculations from these samples cannot be directly compared with those of the Finnmark population since the mature fish originate from a much larger area within which subpopulations with different growth rates probably exist.

But when classifying the observations according to sex and age at first maturity, some very interesting general features appear, see Table II. When comparing the  $l_5$ 's of the different classes it is seen that the maturity results in a definite size segregation of the fish. The males mature at a lower mean size than the females. And both in the males and in the females the part of an age group maturing in a certain year is a segregation of the larger fish.

This relation between maturity and growth rate has been found in many fish populations. But Table II reveals that the entire growth histories of the

various categories are different from  $l_1$  onwards. This means that the size segregation occurring during the years in which a year-class reaches maturity will affect all the values of the growth calculations carried out on the remaining immature part of the year-class.

In full accordance with this expectation are the results of the last growth calculations carried out on the 1948 year-class in the Finnmark area based on samples of immature fish from the autumn of 1954. These data are given at the bottom of Table II. All the values are from one or two cm below those of 1953.

This is actually a case of Lee's phenomenon: an apparent decrease in the calculated growth figures with increasing age. But the facts are fully explained by the size segregation occurring in the population during maturity.

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- |                          |                                                                                                                              |
|--------------------------|------------------------------------------------------------------------------------------------------------------------------|
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G. C. Trout.

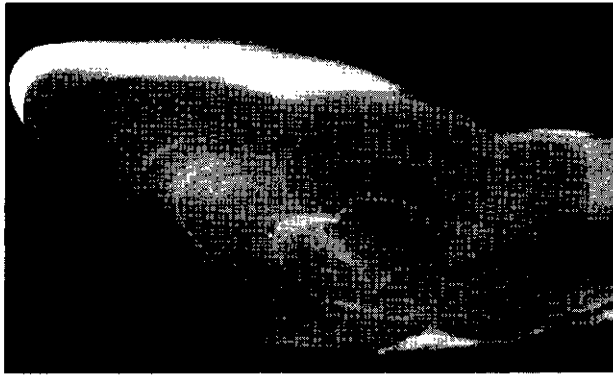
With the increasing application of age-length keys to mass length data for estimations of age compositions (Gulland 1955), it is essential that the age determinations of the smaller key samples should be carried out by the most accurate method. For gadoid populations where the mean age is high, the otolith has been shown to give a more consistent age reading than the scale, whilst other skeletal structures are unsuitable for the large samples, normally required for population studies, because of the time required in their preparation (Menon 1950). Otoliths are therefore used currently at Lowestoft for the cod of the Barents Sea, Greenland, Iceland and North Sea and for haddock of the Bear Island area. The method of viewing is that developed by Rollefson, namely, "fracture and side illumination", under a low power binocular microscope.

Hake otoliths viewed by this method are, if anything, even less clear than when read by transmitted light, whilst for the smaller whiting otolith, light transmitted through the whole otolith is entirely satisfactory.

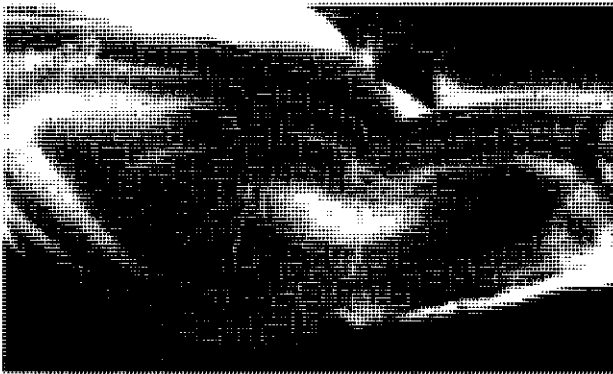
The cod of the North Atlantic and adjacent seas may be divided into "oceanic" and "local" stocks -- their separation being related primarily to the depths of their habitats. This affects the otolith very early in life; thus, the oceanic forms, the "Skrei" of the Barents Sea and the cod of Iceland and Greenland, have large nuclei, (Plates 1, 3 and 4) representing a pelagic phase of between 5 and 7 months, whilst normally, local stocks have small nuclei. The North Sea cod (Plate 2) has a pelagic phase of up to 2 1/2 months (Graham and Carruthers 1926).

Now in the Barents Sea and Greenland (Cape Farewell) cod otoliths, the nucleus constitutes the bulk of the first year growth. Frequently, however, in the Spitsbergen Bank area of the Barents Sea, the first year also includes a very narrow opaque zone, the so-called "autumn zone", separated from the nucleus by a check ring and assumed to be laid down in the new, bottom habitat, after the pelagic phase and before the hyaline winter ring.

The small nucleus of the local cod otolith, on the other hand, is followed by a wide hyaline check ring in some Norwegian Coastal cod (Rollefsen 1933 and Dannevig 1933) but in the North Sea cod this is narrow and sometimes difficult to see (Plate 2). The autumn zone, however, is very wide and frequently merges into the second year's opaque zone without much evidence of a hyaline or "winter" zone. A difference in texture of opaque material normally delimits the autumn zone in these cases and on occasion the opaqueness may be limited to the areas situated near the "points" of the viewed face. If, however, the autumn zone is followed by a normal winter ring (hyaline), it is pos-



1

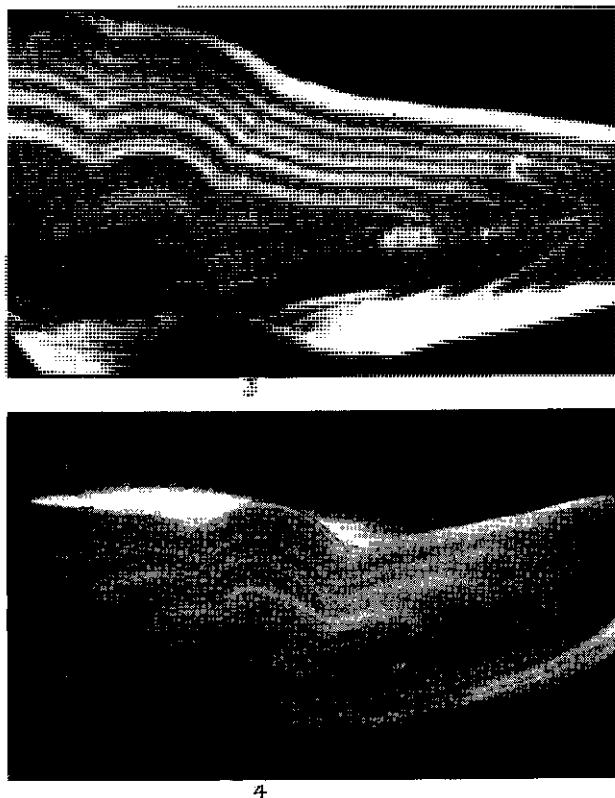


2

Plates 1 - 2. Sections of cod otoliths; explanation in text.

sible that, during early age determinations this wide autumn zone may be counted as one complete year. Thus when aging samples of a species from several major areas and habitats, correct interpretation of the structures within the early part of the otolith's growth is fundamental to accurate age determinations and criteria for aging one population may not necessarily be applicable to another.

In every sample of otoliths there are normally some about which there can be little doubt as to age. Measurement of the width of their successive years' zones (Trout, 1954) will provide a valuable guide for the more difficult otoliths. A small number of otoliths - say 20 - is adequate (Figure 1 - Table I). This



Plates 3 - 4. Sections of cod otoliths; explanation in text.

would then prevent a proportion of under-estimates of age which arise when two coalescing opaque zones are counted as a single year's growth owing to the absence of a clearly defined "winter" ring.

Such a growth curve, arranged as a curve of incremental widths, will also prove helpful when it becomes necessary to decide how many and which super-numerary zones or "split" rings, should be grouped together and included in one year's growth (Plate 3).

Before the nature of these "split" rings is discussed briefly, it is necessary to attempt an explanation of the physiology of the otolith and the cause of

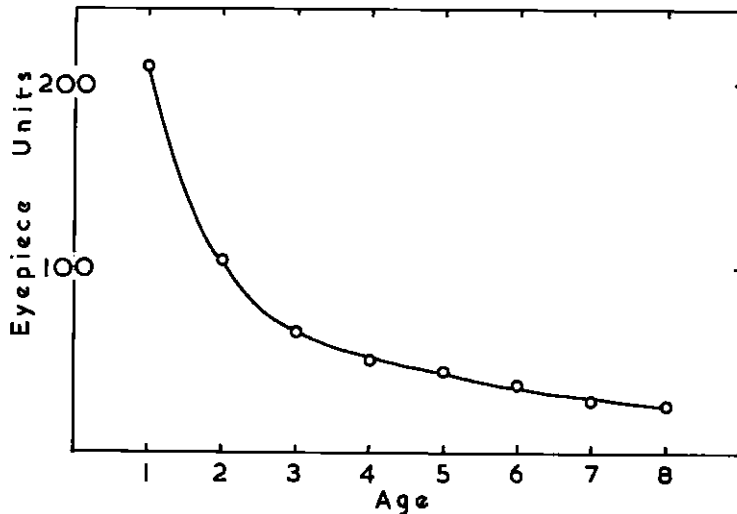


Fig. 1. Mean curve of otolith animal increments from 20 Barents Sea haddock.

the alternation of opaque and hyaline zones. This explanation is put forward from observations in the field and not from tank experiments.

For the Barents Sea material (Trout, in preparation) there is coincidence of heavy feeding and opaque zone formation. The parallel growth of fish and otolith has already been pointed out (Trout, 1954). There is an annual depth cycle for the cod on both sides of the Spitsbergen Bank, which shows them to be in water of 100-120 fathoms and less between late June and October -- the period when the greater proportion of the otoliths are laying down their opaque material and when the smallest percentage of empty stomachs is found. The opaque and hyaline zones are well marked, the latter being typically wide. There is only a short heavy feeding period of less than five months.

For the S. E. Barents Sea the cod's depth cycle is smaller in amplitude but there is a longer period during which the cod are at these or shallower depths. Zatsepin and Petrova (1939) have described the long feeding period of these cod. Their otoliths exhibit, typically, winter rings so narrow that they are difficult to determine (Plate 1). There is thus strong circumstantial evidence that opaque zone formation is associated with the period of heaviest feeding.



TABLE I. Measurements of random samples of 20 Barents Sea haddock otoliths (Axis A) in micrometer eyepiece units.

Fish No.	Year	1	2	3	4	5	6	7	8
1		212	309	371	427	476	505	-	-
2		215	349	434	482	517	556	583	600
3		216	283	356	413	458	-	-	-
4		221	292	357	405	452	486	511	528
5		217	282	338	398	441	482	504	517
6		205	293	343	392	429	473	513	548
7		205	282	347	394	-	-	-	-
8		216	305	352	397	441	478	505	-
9		223	318	379	415	454	487	514	535
10		195	294	346	401	435	476	515	543
11		201	349	417	476	529	567	594	619
12		199	342	436	495	541	559	607	654
13		213	329	387	427	458	480	504	514
14		208	331	401	-	-	-	-	-
15		221	302	356	418	-	-	-	-
16		199	316	381	421	448	485	517	534
17		173	301	351	405	453	-	-	-
18		207	309	385	432	462	-	-	-
19		219	336	399	444	497	532	-	-
20		216	343	431	487	525	559	580	601
No. of obs.		20	20	20	19	17	14	12	11
Mean		209	313	378	428	472	509	537	563
Increments		209	104	65	50	44	37	28	26

"Split" opaque zones are typical of the otoliths from the east side of the Spitsbergen Bank, East Spitsbergen and Cape Farewell, Greenland. In these three areas the shallower water, entered during the feeding season, is cold, being respectively the Bear Island Polar, the East Spitsbergen and the East Greenland Currents. Entry into the cold water appears to cause a physiological check.

In certain of the S. E. Barents Sea otoliths a well defined "summer check" ring may be found, which may be more readily visible than the true winter

(hyaline) ring, for which it could be mistaken.

It follows, therefore, that in addition to the essential data of catch of a sample, the general biology of a stock is required to be known as soon as possible in order to interpret otolith structure with certainty. This may take time and in the meanwhile certain criteria used for the preliminary age determinations may prove unsound in the light of later knowledge. Such an example led to Dannevig's rejection (1925, 1933) of the terms "summer" zone, for the opaque zone and "winter" zone for the hyaline zone of the Skagerrak cod otolith. On the assumption that the opaque zone is associated with the active feeding period, as in the Barents Sea cod, one must wonder whether the cod population described by Dannevig has a reversed or winter feeding season, and a summer season of low intensity feeding, in order to explain the anomalous otolith structure. Saetersdal (1953) points to several other intermediate examples and the general impression is that other anomalies may be explained on this basis.

There are several difficulties of interpretation still encountered in Barents Sea samples, as follows:

- (a) A final interpretation is required of the structure earlier considered by the writer (1954) (and referred to by Gulland for this meeting) as a suppressed second year ring. At the lower range its width approaches that of an autumn zone and if wrongly interpreted may result in an error in age of one year. Thus the biology of the early years of the Barents Sea cod requires further elucidation.
- (b) The year 1955 was typified in some samples from the Spitsbergen Bank by an extremely narrow and pale opaque zone, completed before the end of October (Plate 4). In fact in some October samples this zone was already surrounded by a wide hyaline zone -- certainly not a "split", as in subsequent samples no further opaque material was laid down. This could be confused in later years with a spawning zone, if care were not taken to check closely (i) the width of the previous hyaline zone, which is wide before the first spawning (opaque) zone, and (ii) the texture of the opaque zone (Rollefsen 1935). This could cause future errors in assessing spawning potential of year-classes affected by -- apparently -- a poor feeding period (Bückmann 1931). Similar narrow opaque zones occurred in 1946, 1947 and 1948.
- (c) In the market samples, which form the bulk of the age material, it is impossible to distinguish a virgin spawner by otolith alone, until after mid-August or even later, when the opaque zone, delayed by maturing gonads, begins to be laid down. This knowledge is important to

population studies when a measure of spawning recruitment is required and there appears to be no direct solution during age analyses.

- (d) Otoliths from the S. E. Barents Sea still present difficulties in that successive opaque zones cannot be separated with certainty. Their aging must be, in part, subjective, based on experience and not rigid criteria.

Although the otolith has proved to be a valuable and reasonably accurate guide in age determination a better understanding of the structure and the growth patterns of the otoliths of all food species will improve interpretation and accuracy. A blind counting of "rings" can only bring confusion and doubt upon the method.

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George F. Kelly and Robert S. Wolf.

Authors' Abstract.

The age and growth of Sebastes marinus was studied in the Gulf of Maine for several years to determine (1) the number of pairs of hyaline and opaque zones formed in the otoliths during each year; (2) the age at which the first annulus is completed in the scales and otoliths; and (3) the rate of growth and age composition.

About 2000 small redfish from 2 to 15 cm in length were periodically collected in otter trawls on the bottom at a single station throughout a period of eighteen months. A study of the growth of these fish and of the concurrent changes in the otoliths showed that a single pair of hyaline and opaque zones was formed at the edge of each otolith during a year.

A review of all available plankton samples of pelagic redfish larvae collected during the past fifty years in the Gulf of Maine gave sufficient data to fit together the growth of the pelagic larvae with that of the smallest fry trawled from the bottom. In this area spawning occurs from late April to early September. The larvae grow quickly to a length of 15 to 20 mm before commencing to settle to the bottom. The movement to the bottom begins in late August and continues into October. The young fish grow to an average length of 50 mm by the end of December. The first hyaline zone is formed in the otoliths during the period from November through March of the first winter. The young fish are between 5 and 9 months of age when the first annulus is completed in the scales and otoliths.

The ages of nearly four thousand fish were estimated from examination of the otoliths. The fish in the commercial landings generally ranged from 5 to 20 years of age with a few older. The average growth was less than 2 cm per year; ten-year-old fish averaged 27 cm whereas twenty-year-old fish averaged 36 cm in length. The evidence from the present study clearly shows the Sebastes of the Gulf of Maine to be a very slow growing stock.



Adolf Kotthaus.

In 1939 when I began investigating the European redfish, almost nothing was known about the biology of this species. At first I tried to get information about age and growth. This proved to be difficult because the otoliths are not so clearly marked as are those of other commercial fishes. Instead of more or less distinct summer and winter rings, a great number of very thin and narrow rings occur, which generally cannot be counted exactly; in some instances rings of the usual appearance can scarcely be distinguished, especially in otoliths from the deep sea redfish ("Tiefenbarsch") of the "Rosengarten" fishing ground.

Despite these difficulties, I started counting these rings, as far as possible, with the aid of a microscope enlarging about 15 to 20 times, and with transmitted light. The results were surprising in several respects, if every ring is assumed to be an annual one. For example, a fish measuring 25 cms would have been 9 to 12 years old; another fish 35 cms 12 to 17 years old; and a fish of commercial length (45 cms) 15 to 26 years old. Consequently, the mean annual growth would amount to about 1.5 to 2.5 cms. Such extraordinary slow growth is known for no other fish species reaching the same length as the redfish (80 to 90 cms). Moreover, a fish spawning for the first time at a length of about 35 cms would have to be not less than 12 to 17 years old. This also would be in contrast to the age at first spawning usually encountered in other species, namely 4 to 6. Finally, if the body length at time of formation of the first annual ring, i.e., at the end of the first year of life, is calculated from the otoliths, we get values of about 2.5 to 3.5 cms. This, however, is most improbable for Jensen (1922) has shown that young redfish reach a length of 27 to 49 mms in September of their first year of life. Furthermore, from recent German investigations we know that in September and October, young redfish 3 to 5 cms, were found in considerable masses in the stomach of cod from Greenland waters. Doubtless these small fishes are born in spring of the same year. Although Jensen uses the term "larvae" for these small fish, I believe the larger ones at least are no longer larvae.

By studying length data in successive seasons Ad. S. Jensen l.c. assumed quite a different rate of growth, as shown by the following table:

Time		Length
May	- first year	7. to 9 mms
June	- " "	12 to 30 mms
Sept.-Oct.	- " "	27 to 49 mms
Winter	- " "	47 to 69 mms
End	- " "	95 to 130 mms
End	- second year	195 to 300 mms
End	- third year	310 to 420 mms



**Fig. 1.** Age readings of otoliths of redfish.

(a) 18 cm, Gr. II, Iceland-Greenland-ridge, 13-6-55. (b) 20 cm, Gr. II. (c) *S. viviparus*, 20 cm, Gr. V; Iceland NE-coast, 4-7-55. (d) 33 cm, Gr. III, Greenland W-coast, 2-8-55. (e) Deep sea redfish, 44 cm, Gr. V, Iceland-Faroes-ridge, 11-1-55. (f) 46 cm, Gr. V, Iceland SW-coast, 21-1-55. (g) 45 cm, Gr. V, Iceland-Greenland-ridge, 13-6-55. (h) 42 cm, Gr. V, Iceland NW-coast, 26-6-55. (i) 40 cm, Gr. VI, Spitsbergen, 25-5-55. (j) 43 cm, Gr. VI, Iceland NW-coast, 26-6-55. (k) "Tiefenbarsch" 46 cm, Gr. VI3, Iceland-Faroes-ridge, 6-4-55.



This growth rate is similar to that observed in other fishes.

From these considerations it was evident to me that it was not reasonable to count each visible ring as a true annual ring.

I found it most satisfactory to study the otoliths with a low power lens (5 to 7 x magnification), and illuminated by a microscopic lamp. This permitted viewing the whole object at once. Under this low enlargement we can see that several of the narrow elementary rings come together to form more or less distinct translucent or opaque bands or zones. A similar picture obtains in other species, for example the Adriatic sardine (Clupea pilchardus), where in the first year 2 to 4 secondary rings are laid down, which easily may be erroneously taken as true annual rings, especially before the end of the first year of life when they cannot yet be compared with a true ring; likewise in the plaice (Pleuronectes platessa) from the Horns Reef area in the North Sea; and in Drepanopsetta platessoides from deeper waters, whose otoliths have an internal structure very much like that in Sebastes. Furthermore the formation of broader bands composed of several elementary rings is clearer as the habitat of the specimen investigated becomes shallower. Otoliths from Drepanopsetta living above 180 m have very distinct annual rings in which only at higher enlargement the single components can be distinguished.

From these facts I concluded that in Sebastes also, only the more or less marked bands or zones, consisting of several elementary rings, can be considered as true annuli. Of course direct proof of the correctness of my conception would be possible only by following growth in marking experiments or by direct observation of redfish living in an aquarium. But we cannot do either at present. Consequently I have tried to prove the correctness of my interpretation by means of circumstantial evidence. This is dealt with in a paper published in 1952 so that it is not necessary to repeat the full particulars. Only the main items need be summarized here:

1. All redfish otoliths - from all fishing grounds - show more or less the above-mentioned bands or zones.
2. In otoliths, bones, or scales of the same fish, we always find the same number of broad bands, even where the single secondary rings are not distinguishable.
3. The single age-groups based on the counts of these bands correspond with modes in the length frequency curve, as shown in the material collected on a research cruise to the Norwegian coast in spring 1938.
4. The mean lengths of the single age-groups in the mentioned material

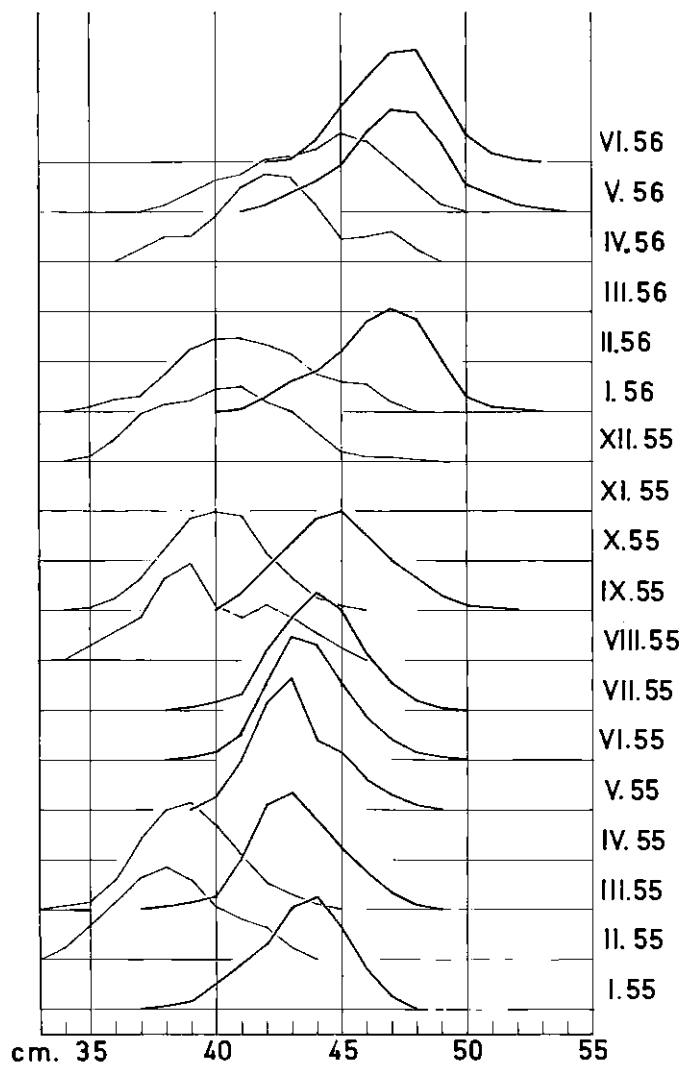


Fig. 2. Growth of redfish year-class 1952 from January 1955 to June 1956. "Marinus" type, Iceland, SW. Coast, bold lines; "Mentella" type, Iceland-Faroes Ridge, thin lines.

was calculated as follows:

Age I = 17.2 cms, II = 22.2 cms, III = 34.2 cms, IV = 39.1 cms, V =

43.8 cms, VI = 49.0 cms.

These figures are probably somewhat too high for the I and III groups and somewhat too low for the II group, since the small specimens up to nearly 30 cms were not caught representatively.

There are some further observations confirming my view:

1. In general, single rings in otoliths are clearly visible only in younger fish up to age group III. The broad annual zones are composed mostly of three translucent and three opaque thin elementary rings. In a few cases, especially within the first band, we can count 4 and in older fishes sometimes only 2 secondary rings. A similar regularity could not be expected if each visible ring were a true annual one. It might well be that these secondary rings are formed as a result of regular migrations, connected with changes in food supply, within the year. I may add that in otoliths from the American redfish, each annual zone is composed in general of two translucent and opaque rings; occasionally we find one or three rings.
2. Last summer we examined on "Anton Dohrn" redfish catches from Icelandic waters for age and level of maturity; we observed that all immature specimens belonged to age-groups I to III (according to my method of interpretation); those which were to spawn during the next season (ranging from about 30 to 40 cms) belonged to age-group IV. Only some of the larger of these belonged to age-group V. All mature fish were five or more years old. If each single ring signified a year of life, we would have been obliged to conclude that redfish spawn at intervals of 3 to 4 years; but this seems to be quite out of the question because fish develop gradually to first maturity and then ordinarily spawn annually.
3. Observations on a few otoliths of small fishes showed that in general one elementary ring outside the last visible distinct winter ring is present in May and June; there are two in late summer, and three at the turn of the year as far as it is possible to generalize the results from the relatively small amount of material investigated.

In order to bring further evidence to bear on our interpretation, it would be valuable to take an annual age census of a stock in which certain poor or rich year-classes could be traced from year to year. Thus far we have not succeeded in accomplishing this. There are strong fluctuations in age composition of the population on any one fishing ground, even during one year, which seem to have nothing to do with the composition of the total stock but are

brought about by what might be called a fluctuating migration.

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Birger Rasmussen.

In both S. marinus and S. viviparus the external appearance of the otoliths is quite similar. But if we study the polished surface of a transversal section of the otoliths in both species, it becomes apparent that we have to deal with two separate types of fish. The otoliths differ in the internal design of the hyaline and opaque zones. In the accompanying figures are shown some transversal sections of the otoliths of the two fishes. All otoliths have been magnified to the same degree.

As regards S. viviparus we may say that the zones are smoothly rounded and form broad ribbons which continue almost unchanged forward to the tip of the otolith. The opaque zones are separated by well defined hyaline zones.

In the S. marinus the opaque zones are more irregular, and they become more narrow in the ventral part towards the tip of the otolith in comparison with the otolith of S. viviparus. Furthermore, in S. marinus the opaque zones do not give the clear cut picture found in the otoliths of S. viviparus. In S. marinus the hyaline zones are not always definitely segregated and they are ordinarily broken through by narrow opaque secondary zones. The otoliths of S. marinus are therefore more difficult to read than those of S. viviparus.

I have not attempted to give a complete definition of the differences between the otoliths of the two related species of fish. Referring to the pictures it might perhaps be summarized thus:

The internal design in the otolith of S. viviparus gives a more symmetric and well-formed picture than do the otoliths of S. marinus, and they are easy to distinguish as two separate types.

Only preliminary investigations on the age and rate of growth of the two species have as yet been carried out by the present author. However, the work done on otoliths has made it clear beyond doubt that both species have uncommonly slow rates of growth, and they can become very old. Referring to the pictures of the otoliths of S. marinus and S. viviparus the difference in the two species should be quite clear.

The otolith of S. marinus 18 cm long shows an age of 6 years. The specimen 43 cm long is 20 years old. This gives a mean growth-rate of about 3 cm the first 6 years. Between the 6th and the 12th year the mean growth is about 2.5 cm yearly, and between 12 and 20 years 1.2 cm yearly.

The otoliths of S. viviparus indicate a growth during the first 7 years of about 1.8 cm yearly. From 7 to 18 years of age the mean annual growth is

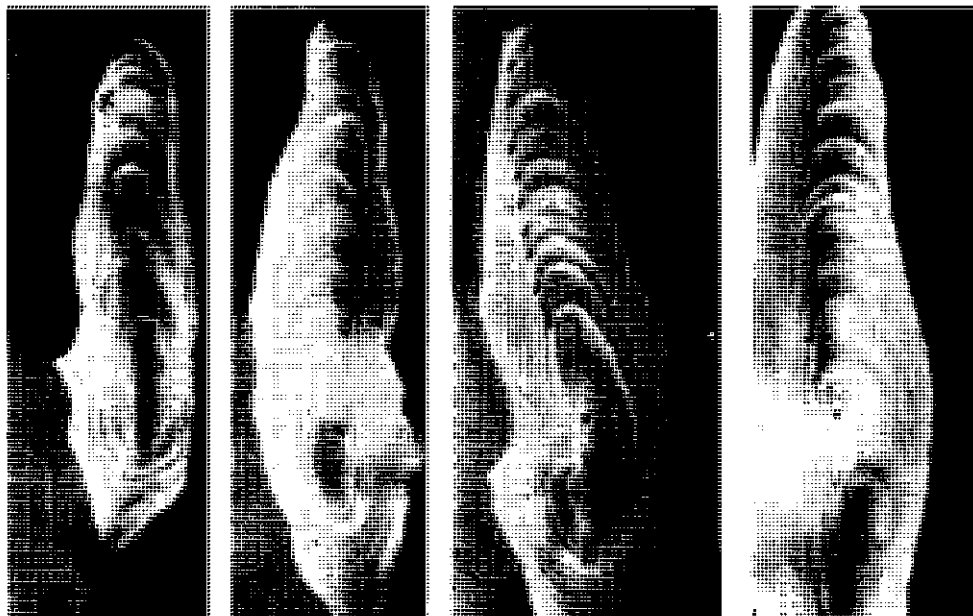


Fig. 1. Otoliths of *Sebastes marinus*, from left to right; 18.1 cm -  $\sigma$  - 6 yrs.; 25.5 cm -  $\sigma$  - 9 yrs.; 33.5 cm -  $\sigma$  - 12 yrs.; 43.0 cm -  $\sigma$  - 20 yrs.

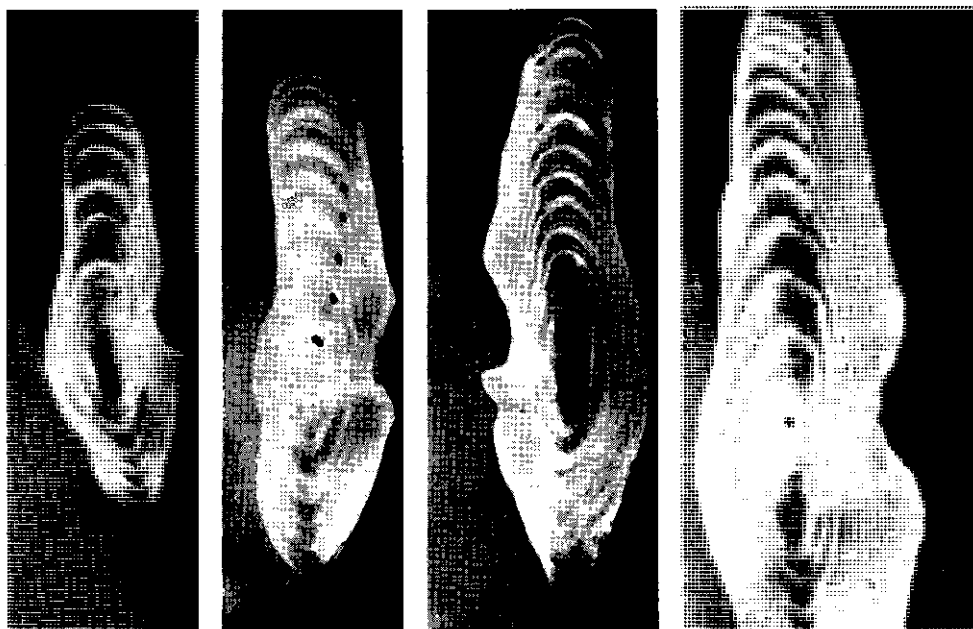


Fig. 2. Otoliths of *Sebastes viviparus*, from left to right: 12.3 cm -  $\varphi$  - 7 yrs.; 15.0 cm -  $\varphi$  - 9 yrs.; 17.1 cm -  $\sigma$  - 11 yrs.; 26.8 cm -  $\varphi$  - 18 yrs.

about 1.3 cm.

These figures are only indicative. It is, however, apparent that *S. marinus* and *S. viviparus* differ totally in regard to rate of growth, and that *S. marinus* grows about twice as fast as *S. viviparus*. Compared to other ordinary food fishes both species of *Sebastes* have a very slow growth.





E. J. Sandeman.

(Author's Abstract, presented by W. Templeman).

A group of young redfish, Sebastes marinus (L.), was found in Hermitage Bay on the south coast of Newfoundland in December, 1953. This group of fish, well isolated in length from the larger fish which comprised most of the catch, has been followed during research cruises in 1954 and 1955.

The group has shown the following total lengths, chin to mid-fork:

<u>Date</u>	<u>Average length cm</u>	<u>Length range cm</u>	<u>Number of fish</u>
December, 1953	7.1	6.0- 8.3	22
June, 1954	8.1	6.4- 9.2	125
September, 1954	8.8	7.9-10.2	70
December, 1954	9.0	7.5-10.6	172
April, 1955	9.6	8.2-11.4	218
June, 1955	10.6	8.6-12.9	207
August, 1955	11.3	9.0-13.3	316
November, 1955	11.8	9.3-13.9	1,041

A preliminary study of the scales and otoliths of these fish shows that at least 90 percent of the fish forming the above group were of the same year-class. Those fish with scale ages showing an incomplete first year in December, 1953, showed 1+ years in December, 1954, and 2+ years in November, 1955.

The annual nature of the growth rings, and the relation of the scales and the appearance of the edges of the scales to the year and date of capture, were demonstrated by a series of photographs from the samples taken in the above months.

Only three fish of definitely more recent year-classes, than that represented predominantly in the group of small redfish first captured in 1953, have been caught in the hundreds of sets from December, 1953 to December, 1955. This indicates that in this area complete failure of redfish year-classes can and does occur.



LEE'S PHENOMENON OF "APPARENT CHANGE IN GROWTH-RATE" 229  
WITH PARTICULAR REFERENCE TO HADDOCK AND PLAICE

R. Jones.

The determination of the growth of individual fish by back calculations from their scale measurements has been practised for many years. References include Lea 1910, 1913, 1929, 1938, Lee 1912, 1920, Mottram 1916, Huntsman 1918, Nall 1930, Dannevig and Høst 1931, Watkin 1933, Robertson 1936, Fry 1943, Schuck 1949, Hile 1950, Lowry 1951, and many others. The method is a useful aid to growth studies, provided the "back calculated" curves give an unbiased representation of the true growth curves of the fish concerned. Owing to the "phenomenon of apparent change in growth-rate", however, the validity of the method is suspect and is in fact dependent on the way in which this phenomenon is interpreted. Suppose, for instance, that several year-classes have been sampled and their lengths when one year old calculated from the scales. Then, the "phenomenon of apparent change in growth-rate" refers to the fact that in many instances the older year-classes appear to have been smaller when they were one year old than the younger ones. Since the older year-classes would have started life earlier than the younger ones, such a trend in their calculated first year sizes makes it appear as though there had been an increase in growth-rate during their early years of life. However, although this might sometimes be the explanation of the phenomenon, it is not always possible to account for it in this manner.

According to Lea 1913, the first person to mention this phenomenon was Sund 1911, who demonstrated it in a sample of sprats from the south of Norway. Lee 1912 showed that it occurred in herring, haddock and trout. Robertson 1936 demonstrated it in the sprat and an excellent example for the herring is given by Watkin 1933. There are several instances in which the phenomenon was not recorded (e.g. Nall 1930, for sea trout, and Saetersdal 1953, for haddock).

Explanations of the Phenomenon

Unless the existing evidence is due to chance, the simplest explanation of the phenomenon is that there was an increase in growth-rate prior to the collection of each sample. This would account for an observed decrease in the back calculated first year sizes of successively older year-classes. This is unlikely and certainly does not explain the decrease in the calculated first year sizes of a brood during successive years of its life. The data in Table I show how the calculated first, second and third, etc. year sizes of plaice decreased in a number of year-classes as they grew older. This result is quite independent of any change in the growth-rate of the year-classes concerned.

TABLE I. Back calculations of plaice sizes (ls). (Supplied by Mr. J. N. Lamont of this laboratory).

## Firth of Forth (Kirkcaldy Bay)

Age	5+	6+	4+	5+	3+	4+	2+	3+	1+	2+
1 <sub>1</sub>	7.5	7.3	7.9	8.0	8.2	7.7	8.8	8.7	11.0	9.9
1922 1 <sub>2</sub>	14.2	13.7	14.2	14.4	1924	16.6	14.0	1925	16.4	15.7
Brood 1 <sub>3</sub>	20.9	19.6	Brood	21.7	21.4	Brood	22.7	20.1	Brood	-
1 <sub>4</sub>	26.4	24.8	27.7	26.8	-	-	-	-	-	-
1 <sub>5</sub>	31.3	29.6	-	-	-	-	-	-	-	-

## St. Andrews Bay

Age	3+	4+	2+	3+	1+	2+	3+	1+	2+	1+	2+	3+
1919 1 <sub>1</sub>	6.8	6.7	1920	8.7	8.0	1921	10.8	9.6	8.1	1922	7.6	6.7
Brood 1 <sub>2</sub>	12.7	11.7	Brood	18.1	16.6	Brood	-	16.8	13.6	Brood	-	Brood
1 <sub>3</sub>	20.0	18.0	-	-	-	-	-	-	-	-	-	-

## St. Andrews Bay (continued)

Age	1+	2+	3+	4+	1+	2+	3+	1+	2+
1924 l <sub>1</sub>	9.5	9.6	8.0	-	1925	9.0	8.0	8.2	1926
Brood l <sub>2</sub>	-	16.7	-	13.9	Brood	-	15.4	15.1	Brood

## East of Inch Keith

Age	4+	5+	3+	4+	2+	3+
1 <sub>1</sub>	8.3	8.0	7.4	7.7	10.0	9.3
1923 1 <sub>2</sub>	15.2	15.8	1924	14.6	13.9	1925
Brood 1 <sub>3</sub>	22.3	21.7	Brood	21.0	20.5	Brood
1 <sub>4</sub>	28.0	27.1	-	-	-	-

In order to make back calculations from the scales, it is necessary to suppose that the growth of a fish and the growth of its scales is related in some easily calculable way. Generally, it has been supposed that the growth of a fish and its scales is proportionally or at least linearly related, although Fry 1943, for example, has considered a relationship of the form  $y = bx^n$  for several species of fish. Sherriff 1922 attempted to show that a parabolic fish-length/scale-length relationship was more appropriate than a linear one in the herring, by showing that the sum of squares of deviations from the best fitting quadratic were less than from the best straight line, fitted by the method of least squares. It is obvious, however, from the figures that the reduction in the sum of squares due to the quadratic term is non-significant so that it may be concluded that a straight line fitted the data quite adequately. Thompson (1923, 1929) gave illustrations of fish-length/scale-length relationships in North Sea and Iceland haddock. Straight lines and quadratic curves were fitted to these data and in each instance the reduction in the sum of squares due to the curvilinearity of the regressions was significant at the 1% level.

When the fish-length/scale-length relationship is proportional, the length of a fish at some previous age ( $t$ ) is given by:

$$l_t = \frac{L S_t}{S} \quad . . . . . 1$$

where  $L$  and  $S$  are the lengths of the fish and the scale respectively,  $l_t$  is the calculated length at age  $t$  and  $S_t$  is the length of the scale up to the  $t$  winter ring. If the fish-length/scale-length relationship is linear but of the form  $L = a + bS$  (where  $a$  and  $b$  are constants), then (1) must be replaced by:

$$l_t = \frac{L S_t}{S} + a \left(1 - \frac{S_t}{S}\right) \quad . . . . . 2$$

For a quadratic relationship such as that demonstrated from Thompson's data,  $L = a + bS + cS^2$  (where  $a$ ,  $b$  and  $c$  are constants), and the back-calculated lengths are given by:

$$l_t = \frac{L S_t}{S} + a \left(1 - \frac{S_t}{S}\right) - cS_t (S - S_t) \quad . . . . . 3$$

The wrong use of the simple proportional formula (1) instead of (3) would lead to under-estimates of the calculated length ( $l_t$ ) by an amount:

$$a \left(1 - \frac{S_t}{S}\right) - cS_t (S - S_t) \quad . . . . . 4$$

For example, analysis of the North Sea haddock data given by Thompson (1922) gave values of  $a$  and  $c$  equal to  $-0.62$  and  $-0.82$  respectively. The fish-lengths were measured in centimetres and the scale-lengths in millimetres. Approximate scale sizes corresponding to different ages are given in Table II, along

TABLE II. Estimated errors in calculated North Sea haddock lengths when it is assumed that the fish-length/scale-length relationship is proportional instead of curvilinear.

Age	Scale length (S) (mm)	$S_1$	$S_2$	Error in calculated lengths (cm)	
				$l_1$	$l_2$
2	1.5	1.1	1.5	-0.20	0
3	2.0	1.1	1.5	-0.53	-0.46
4	2.3	1.1	1.5	-0.78	-0.76
5	2.6	1.1	1.5	-1.03	-1.09

TABLE III. Values in lengths  $l_s$  (cm) and scale sizes  $S_s$  (arbitrary units) calculated from various samples of haddock.

Age	NE Faroe Oct. 1950		NE Faroe Dec. 1950		NW Faroe Nov. 1951		NE Faroe Oct. 1950		NE Faroe Dec. 1950		NW Faroe Nov. 1951	
	$l_1$	$S_1$	$l_1$	$S_1$	$l_1$	$S_1$	$l_2$	$S_2$	$l_2$	$S_2$	$l_2$	$S_2$
2	14.08	73.58	14.12	389	15.91	3.24	27.50	139.65	27.19	747	30.87	6.27
3	13.09	73.21	13.36	368	14.86	3.21	27.11	138.11	27.14	745	28.38	6.12
4	12.85	73.11	-	-	14.14	2.91	24.09	136.70	-	-	27.84	5.68
5	-	-	12.71	345	-	-	-	-	-	-	-	-
6	-	-	12.71	353	13.95	3.09	-	-	-	-	25.09	5.55

TABLE IV. Values of  $l_s$  calculated from a sample of Faroe haddock landed on the Aberdeen Fish Market - February 1953.

Age	$l_1$	$l_2$	$l_3$	$l_4$	$l_5$	$l_6$	$l_7$	$l_8$	$l_9$	$l_{10}$	Mean Length
3	14.78	27.12	-	-	-	-	-	-	-	-	41.00
4	14.21	26.42	38.87	-	-	-	-	-	-	-	49.51
5	13.82	25.82	41.20	48.20	-	-	-	-	-	-	55.18
6	13.67	28.25	40.12	48.76	54.48	-	-	-	-	-	58.99
8	14.86	27.38	37.00	48.00	55.12	60.96	65.12	-	-	-	68.20
9	12.89	23.83	35.15	43.39	50.34	56.07	61.24	65.05	-	-	68.09
10	10.90	23.08	34.50	43.30	48.87	54.16	58.36	62.23	64.97	-	66.97

TABLE V. Haddock samples from Great Fisher Bank - November 14, 1910. (Data from Lee 1912).

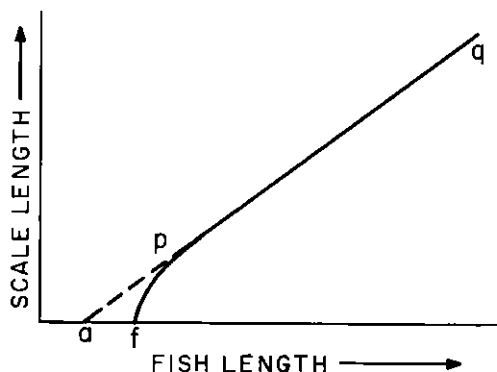
Age	$l_1$	$l_2$	$l_3$	$l_4$	$l_5$	$l_6$	$l_7$	Average Length of each Brood
2+	18.3	29.4	-	-	-	-	-	31.2
3+	17.6	30.4	40.4	-	-	-	-	41.9
4+	16.6	26.7	35.8	44.3	-	-	-	46.4
5+	15.1	22.9	30.7	38.1	46.1	-	-	48.9

with the errors calculated from (4) above.

The use of equation (1) instead of (3) under-estimates the calculated  $L_1$ 's and  $l_2$ 's, and the error increases with the age of the fish (more precisely with the size of the scales). The rate of decrease from Table II is 0.28 cm per year for the  $L_1$ 's and 0.36 cm per year for the  $L_2$ 's. A similar result was obtained from the analysis of the Iceland haddock data (Thompson 1929). For comparison, actual rates of decrease in haddock calculated lengths were calculated from the data in Tables III, IV and V.  $L_1$ 's decreased at rates varying from 0.55 to 0.60 cm per year. The corresponding  $L_2$ ' figures were 0.58 to 1.57 cm per year. Failure to allow for curvilinearity in the fish-length/scale-length relationships is therefore insufficient to account entirely for the observed rate of decrease of the calculated lengths with age.

Frequently it has been thought that the coefficient "a" in equation (2) should correspond to the length of a fish at an age when the scales were first laid down. This, however, is not so. In the adult fish the body is covered by overlapping scales. At the moment of formation the centres of these scales can be regarded as tiny points scattered through the skin. Therefore, for the first few weeks after formation, these scales will have to grow very rapidly if they are ever to overlap one another. In fact, during this period they must grow faster than the body itself. Once the scales are fully formed the degree of overlapping of adjacent scales can be expected to remain approximately constant so that once the scales are overlapping, the growth of the scale, relative to that of the fish, must decrease very greatly, otherwise they would soon outgrow the fish itself. Thus the fish-length/scale-length relationship must take the form shown in Figure 1. For purposes of calculation, it is the intercept "a" that is required.

In Table III are given haddock scale measurements up to the first ( $S_1$ ) and second ( $S_2$ ) winter rings respectively. In each case the mean scale length is



**Fig. 1.** Relationship fish-length/scale-length; *f* represents the length of the fish when the scales are laid down, whilst the portion *pq* represents the part of the relationship after the initial rapid growth by the scale.

smaller for the older age-groups, a tendency that was also described by Thompson 1922. This too, will account to some extent for the decrease in calculated lengths with age. There are two possible explanations for the decrease in scale sizes. The first is that the early formed part of the scale shrinks during the life of a fish but, although this is a possibility, there is no evidence to support it. Lea 1913 determined that the mean distance between the ridges on the scales of herring and showed that there was no tendency for these to decrease in older year-classes.

A second possible explanation for the phenomenon in the herring was proposed by Lea 1913, when he suggested that there was a segregation of fast and slow growers according to their state of maturity. If the slow growers were later in maturing than the fast growers, and if, as they matured, a further component of the slow growers mingled with the faster growers each year, then the  $L_1$ 's of these mature fish would have become progressively smaller.

The application of this theory to haddock presents a number of difficulties. In the first place, there is no evidence of a segregation of mature and immature fish of the same age except perhaps at the spawning season. It might be supposed therefore that either:

- (a) Fishing activities during the spawning season are principally concentrated on the fast growing mature fish. Consequently, later in the



year, when both mature and immature fish shoal together again, the decrease in the numbers of fast growers will have been proportionately greater than that of the slow growers in any one brood. Each year's survivors will therefore tend more and more to be those fish that started life as slow growers, rather than as fast growers. This explanation can only be applied over that range of ages during which the fish mature. Raitt 1936 has shown that 95% or more of North Sea haddock mature by the time they become four years old and yet in Tables III, IV and V the phenomenon is clearly shown in fish exceeding this age.

- (b) Alternatively, it may be supposed that there is an ever present tendency for fast growing fish to die off more rapidly than the slow growers. This certainly happens to the haddock during its second year of life when the size of a year-class is such that the largest individuals are retained in commercial fishing nets, but the smallest can still escape. For a short period therefore the fast growers will be eliminated at a greater rate than the slower growers but this can only account for a decrease in the  $L_1$ 's from age one to age two. Amongst the older fish a selective mortality rate could be a natural phenomenon due possibly to a difference in metabolic rate between fast and slow growers, or it could be due to a behaviour difference on approach of the trawl, as was suggested by Thompson 1922.

If some individuals have persistently different chance of survival from others of the same age, it is relevant to calculate just what differences in mortality rate are necessary to explain the phenomenon. Only if this is reasonable, can this explanation be regarded as likely. Theoretical considerations are dealt with in the appendix where it is assumed that the distribution of  $L_1$ 's at any age is normal and that the instantaneous rate of mortality of an individual is related to its  $L_1$  value by the formula:

$$\text{total instantaneous mortality rate} = a + b L_1 \quad . . . . . 5$$

where  $a$  and  $b$  are constants, so that for every estimated increase in the  $L_1$  value of an individual its mortality rate will increase by an amount equal to  $b$ .

From these assumptions it is shown that the annual decrease in the mean of the  $L_1$ 's is simply  $b\sigma^2$ , where  $\sigma^2$  is the variance of the  $L_1$ 's. For example, in Table VI is shown a mean annual decrease in haddock  $L_1$ 's of 0.55 so that:

$$\begin{aligned} b\sigma^2 &= 0.55 \\ \text{and therefore } b &= \frac{0.55}{\sigma^2} \end{aligned}$$

$\sigma^2$ , the variance of the  $L_1$ 's, was 3.4, so that  $b = 0.16$ .

Therefore, for every centimeter increase in the  $L_1$  value of an individual there should be an increase of 0.16 in its total instantaneous rate of mortality. For two individuals with  $L_1$ 's differing by four times their standard deviation (i.e. 7.3 cm), there would have to be a difference of 1.2 in their respective mortality coefficients.

TABLE VI. Showing the estimated range in mortality rates of individuals having values of  $l$ 's differing by four times their standard deviation (from haddock data in Table IV).

	Observed decrease in calculated lengths (d)	Variance of lengths $\sigma^2$	$b = \frac{d}{\sigma^2}$	Standard Deviation ( $\sigma$ )	Range = $4\sigma b$	Adjusted Range*
$l_1$	0.55	3.4	0.16	1.84	1.2	0.6
$l_2$	0.58	7.6	0.076	2.76	0.8	0.3
$l_3$	0.73	12.7	0.057	3.56	0.8	0.3
$l_4$	0.98	18.5	0.053	4.32	0.9	0.4
$l_5$	1.40	25.5	0.055	5.05	1.1	-

\* The figures in this column were calculated after the observed decreases in the calculated lengths had been adjusted to allow for the curvilinearity in the fish-length/scale-length relationship.

TABLE VII. As in Table VI, but from haddock data in Tables III and V.

	Observed decrease in calculated lengths (d)	Variance of lengths $\sigma^2$	$b = \frac{d}{\sigma^2}$	Standard Deviation ( $\sigma$ )	Range = $4\sigma b$	Adjusted Range *
$l_1$	0.60	3.4	0.18	1.84	1.3	0.7
$l_2$	1.57	7.6	0.21	2.76	2.3	1.8
$l_3$	4.85	12.7	0.38	3.56	5.4	5.0
$l_4$	6.20	18.5	0.34	4.32	5.9	5.3

\* See footnote to Table VI.

TABLE VIII. As in Tables VI and VII, but from plaice data in Table I.

	Observed decrease in calculated lengths (d)	Variance of lengths $\sigma^2$	$b = \frac{d}{\sigma^2}$	Standard Deviation ( $\sigma$ )	Range $= 4\sigma b$
$l_1$	0.42	2.27	0.19	1.51	1.1
$l_2$	0.76	3.58	0.21	1.89	1.6
$l_3$	1.22	4.78	0.26	2.19	2.3
$l_4$	1.13	6.94	0.16	2.63	1.7
$l_5$	1.70	13.28	0.13	3.64	1.9

This form of calculation can be extended to the  $L_2$ 's,  $L_3$ 's, etc.; and it is to be expected that the difference in mortality rates of individuals having a range of back calculated lengths of four times their standard deviations will be much the same. The results of these calculations for haddock and plaice are shown in Tables VI-VIII. For the haddock data in Table IV, the calculations in Table VI gave reasonably consistent results, suggesting that at any age, two individuals differing in length by four times the standard deviation of the lengths at that age, would be subject to instantaneous mortality rates differing by approximately 1.0. The remaining haddock (Tables III and V) and plaice (Table I) data were less consistent (Tables VII and VIII). Also, the range in mortality coefficients was rather high, being 5.9 in one instance, which seems highly improbable. Therefore, in order to explain the phenomenon of apparent change in growth rate in haddock and plaice by postulating a greater mortality rate amongst fast growers than slow growers, the range of mortality rate would have to be improbably large. For the herring, Watkin 1933 gives some relevant data. The rate of decrease in the  $L_1$ 's was 0.41 cm per year and the variance of the  $L_1$ 's was 5.35 cm<sup>2</sup>. From these figures it is found that the difference in mortality rates of two individuals with lengths differing by four standard deviations (9.25 cm) would have to be 0.7, which is not so unlikely.

Amongst the explanations so far advanced for haddock, failure to allow for a curvilinear fish-length/scale-length relationship, and the possibility that fast growers die off at a greater rate than slow growers has been suggested. Neither explanation alone was sufficient to account for the phenomenon, but it is interesting to consider whether both together can do so. Assuming that a curvilinear fish-length/scale-length relationship is generally applicable to the haddock, the decrease in  $L_1$ ,  $L_2$ , etc. due to failure to account for this is:

	$L_1$	$L_2$	$L_3$	$L_4$
Rate of decrease cm/yr.	0.28	0.36	0.42	0.50

When these figures were subtracted from the corresponding figures in the first columns of Tables VI and VII, new figures for the rates of decrease of the  $L_1$ 's,  $L_2$ 's, etc. were obtained which were supposedly due to the differential mortality effect alone. The ranges of mortality rates were then calculated as before and these are shown in the last columns of Tables VI and VII. The ranges in mortality rate in Table VI were reduced to quite reasonable values (mean 0.4) although those in Table VII were still improbably large. In this instance, therefore, it is likely that other factors were playing an important part. Certainly the observed rates of decrease of the  $L_1$ 's,  $L_2$ 's, etc. seem exceptionally large, particularly in the case of Lee's data (Table V) in which the calculated  $L_3$ 's, for example, had decreased from 40.4 to 30.7 cm over two age-groups.

#### APPENDIX

Let us suppose that individuals with different  $l_1$ 's have different probabilities of survival and that at some arbitrary age the mean  $l_1$  is equal to  $L$ . It will be supposed that groups of individuals decrease in number exponentially but at different rates according to their individual values of  $l_1$ .

Thus, instead of assuming a total instantaneous mortality coefficient of  $Z$  for all individuals we will suppose that it is linearly related to the  $l_1$  values thus:

$$Z = a + b l_1 \quad \dots \dots 5$$

where  $k$  and  $b$  are constants.

Let the distribution of  $l_1$ 's about the mean  $L$  be normal with variance  $\sigma^2$ . Then the frequency distribution at time  $t_1$  will be given by:

$$F(l_1/t_1) = \frac{N_1}{\sigma \sqrt{2\pi}} e^{-\frac{(l_1 - L)^2}{2\sigma^2}} dl_1 \quad \dots \dots 6$$

where  $N_1$  is the total number in the particular age class at time  $t_1$ .

The probability of survival of an individual until some later time  $t_2$  will, by definition, be equal to:

$$e^{-(a + b l_1) (t_2 - t_1)}$$

so that the frequency distribution of  $l_1$ 's at time  $t_2$  will become:

$$F(l_1/t_2) d l_1 = \frac{N_1}{\sigma \sqrt{2\pi}} \exp - \left[ \frac{1}{2\sigma^2} (l_1 - L)^2 + (a + b l_1) (t_2 - t_1) \right] \dots 7$$

This can be simplified to:

$$F(l_1/t_2) d l_1 = \frac{N_1 S}{\sigma \sqrt{2\pi}} \exp - \frac{1}{2\sigma^2} [l_1 - (L - \sigma^2 b(t_2 - t_1))]^2 d l_1 \dots 8$$

$$\text{where } S = \exp - [a + b L - \sigma^2 b^2(t_2 - t_1)] (t_2 - t_1) \dots 9$$

From (8) it is seen that the distribution is still normal with variance  $\sigma^2$ , but that the mean has decreased from  $L$  to  $(L - \sigma^2 b(t_2 - t_1))$ .

Therefore the annual decrease in the mean of the  $l_1$ 's is simply:

$$b\sigma^2 \dots 10$$

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Clyde C. Taylor.

Growth rates compiled from back-calculated data present a particular problem in the dynamic analysis of fish stocks. If Lee's phenomenon is present in any degree, each age at capture provides an apparently different growth rate. In view of this and the fact that the cause of Lee's phenomenon remains a subject of speculation, its nature in the Georges Bank haddock was investigated.

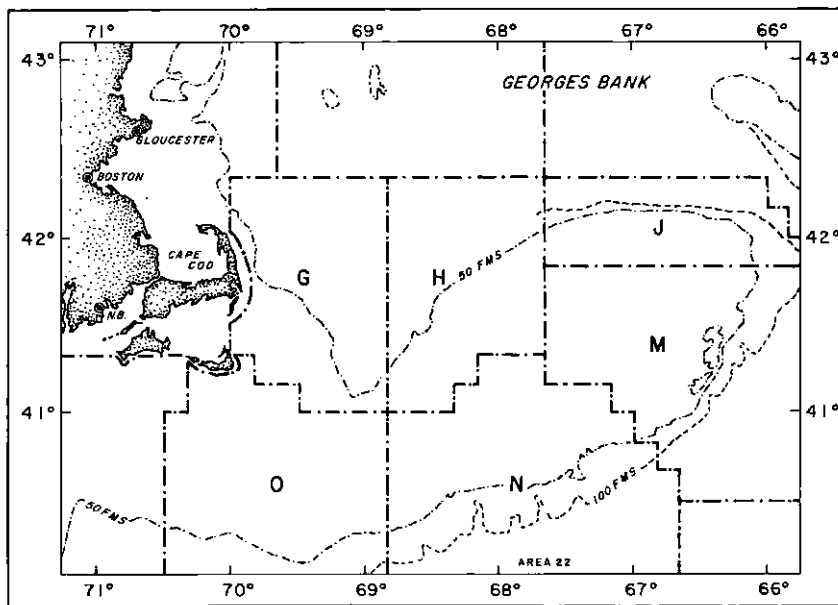


Fig. 1. Statistical subareas of Georges Bank (shaded area).

Over the period 1931 to 1947, scales from over 6,700 haddock, ranging in age from 3 to 6 years, were read and back-calculated lengths determined. The samples from each of the six subareas of Georges Bank (Figure 1) are presented in Table I. The extent of Lee's phenomenon in these data is apparent in Tables II and III.

It has frequently been suggested that the apparent change in growth rate with age at capture arises from the selective removal by the fishing gear of the larger and faster growing fish. If this is true, the phenomenon should

TABLE I. Number of fish by subarea and age at capture from the six subareas of Georges Bank (Figure 1).

Age	G	H	J	M	N	O	Totals
III	277	262	719	1295	143	-	2696
IV	305	188	740	1028	57	11	2329
V	158	146	311	511	46	19	1191
VI	66	66	140	181	28	19	500
Totals	806	662	1910	3015	274	49	6716

TABLE II. Back-calculated lengths, ages 1 - 6, of haddock captured at ages 3 - 6, Subarea J, Georges Bank.

Age of capture	Calculated Fork Length, 1931-1947						No. of fish
	1	2	3	4	5	6	
III	19.5	33.9	44.1	-	-	-	719
IV	18.6	32.3	42.3	49.6	-	-	740
V	18.2	31.1	41.0	48.7	54.4	-	311
VI	17.7	30.5	40.0	47.8	53.5	57.7	140

TABLE III. Back-calculated lengths, ages 1 - 6, of haddock captured at ages 3 - 6, Subarea M, Georges Bank.

Age of capture	Calculated Fork Length, 1931-1947						No. of fish
	1	2	3	4	5	6	
III	19.8	34.1	44.3	-	-	-	1295
IV	18.9	32.7	42.8	50.1	-	-	1028
V	18.3	31.8	41.8	49.1	54.5	-	511
VI	18.2	31.3	41.1	48.6	54.2	58.5	181

disappear in data arranged so that fish of different ages of capture have common growth rates.

As a criterion of growth rate, the fish were classified by length at age one ( $L_1$ ). Having thus classified the fish, the average length at each subsequent

age to the age at capture was calculated.

The results of these calculations for Subarea M are shown in Table IV which shows that Lee's phenomenon is not eliminated by using  $L_1$  as a criterion of classification. The table indicates that the criterion of classification is satisfactory, for clearly the smaller  $L_1$ 's grew at a slower rate at every age.

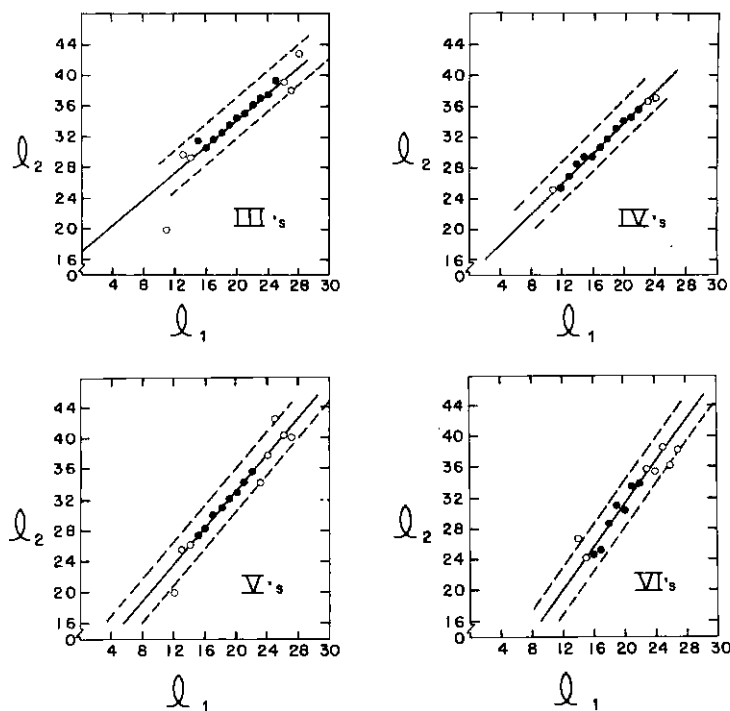
TABLE IV. Average calculated fork length at each age for fish captured in Subarea M, 1931-1947, between the ages of 3 and 6, for  $L_1 = 14$  to  $L_1 = 26$  cms.

Age at capture	$L_1$	$L_2$	$L_3$	$L_4$	$L_5$	$L_6$	No. of fish
3	14	29.17	40.75	-	-	-	12
4	14	28.38	38.96	47.08	-	-	26
5	14	26.67	37.47	46.93	53.00	-	15
6	14	27.60	39.40	48.80	54.80	58.80	5
3	15	30.97	41.72	-	-	-	32
4	15	28.49	39.00	47.13	-	-	79
5	15	27.87	38.09	45.82	51.60	-	55
6	15	27.09	36.55	44.24	50.21	55.15	33
3	16	31.37	42.13	-	-	-	67
4	16	29.67	39.80	47.33	-	-	94
5	16	29.14	39.07	46.61	52.23	-	57
6	16	29.30	39.70	46.80	52.20	56.35	20
3	17	31.65	42.39	-	-	-	109
4	17	30.82	41.18	48.57	-	-	141
5	17	29.73	39.56	47.20	53.00	-	71
6	17	29.00	38.43	46.81	52.52	57.28	21
3	18	32.46	43.22	-	-	-	169
4	18	31.86	42.24	49.76	-	-	136
5	18	31.23	41.32	48.55	54.18	-	73
6	18	31.68	41.77	49.27	54.68	58.86	22
3	19	33.34	44.01	-	-	-	187
4	19	33.29	43.64	51.21	-	-	134
5	19	32.78	42.80	50.09	55.65	-	55
6	19	32.68	42.86	50.04	55.54	59.50	22

TABLE IV. Average calculated fork length at each age for fish captured in Subarea M, 1931-1947, between the ages of 3 and 6, for  $L_1 = 14$  to  $L_1 = 26$  cms.

(continued)

Age at capture	$L_1$	$L_2$	$L_3$	$L_4$	$L_5$	$L_6$	No. of fish
3	20	34.26	44.45	-	-	-	215
4	20	33.52	43.22	50.38	-	-	117
5	20	34.02	43.55	50.53	55.81	-	47
6	20	32.81	42.90	50.48	56.19	60.14	21
3	21	35.12	44.95	-	-	-	175
4	21	34.68	44.45	51.39	-	-	101
5	21	35.38	45.56	52.38	57.10	-	39
6	21	36.22	45.44	52.22	57.67	61.56	9
3	22	35.74	45.58	-	-	-	135
4	22	35.88	45.40	52.39	-	-	77
5	22	36.10	45.63	52.20	56.98	-	40
6	22	35.80	45.80	52.70	57.40	61.70	10
3	23	36.27	45.58	-	-	-	88
4	23	36.70	46.56	53.31	-	-	54
5	23	36.95	46.48	52.95	57.81	-	21
6	23	35.00	44.14	51.71	57.14	61.43	7
3	24	37.71	46.89	-	-	-	63
4	24	37.92	46.81	53.35	-	-	26
5	24	37.17	46.58	52.92	57.92	-	12
6	24	39.33	48.33	54.33	59.33	63.33	3
3	25	38.24	47.67	-	-	-	21
4	25	38.75	47.94	53.44	-	-	16
5	25	38.12	47.13	53.50	58.00	-	8
6	25	38.67	47.33	53.67	58.67	62.33	3
3	26	38.91	47.00	-	-	-	11
4	26	39.63	48.13	54.63	-	-	8
5	26	38.83	47.67	53.67	57.67	-	3
6	26	41.00	51.00	55.00	62.00	66.00	1



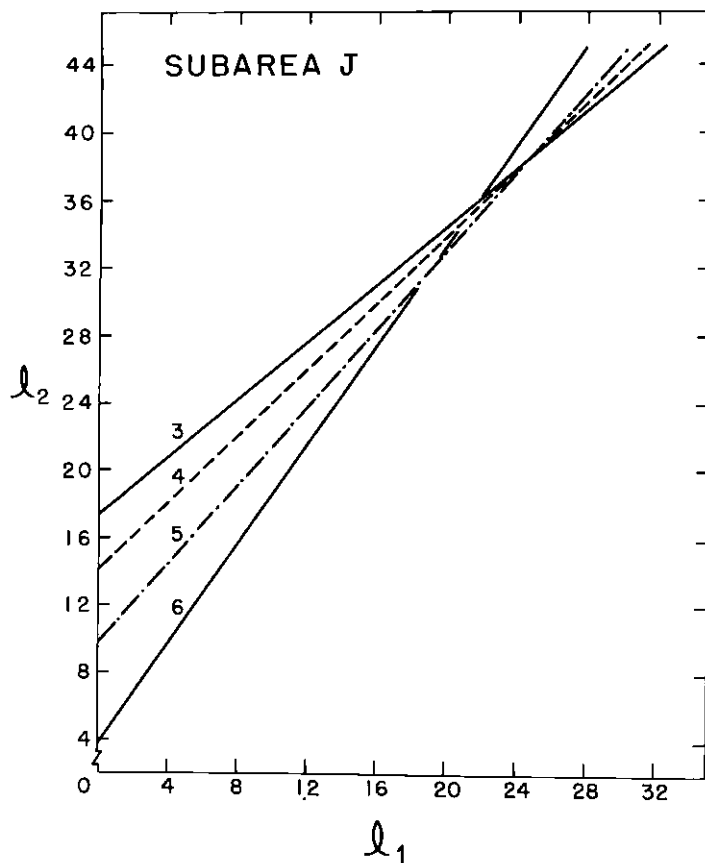
**Fig. 2.** The regression of  $l_2$  on  $l_1$  for ages of capture three to six. Solid dots are mean values; open dots are means based on less than 10 fish. The regression lines are fitted to the data for all fish (Table II) and not to the means.

Table IV reveals a new phenomenon, corroborated by the data for sub-areas other than Subarea M; a progressive change in the magnitude of Lee's phenomenon with increase in  $L_1$ , greatest for the smaller sizes, becoming progressively less until, for the larger  $L_1$ 's, the fish which grew the largest during their first year of life, it appears to occur in a reverse form.

This unexpected finding tends to upset most of the hypotheses which have been advanced to account for Lee's phenomenon. It seems, for example, to completely eliminate scale shrinkage with age, for if this hypothesis is to remain tenable, the scales must shrink differentially with length at age one, not shrinking at all for some sizes, and expanding for certain fish.

At the same time, the hypothesis that Lee's phenomenon comes about

from selective removal by the fishing gear of the larger, faster-growing fish is now subject to some doubt, for the phenomenon appears most marked among the very fish which have clearly grown the slowest and which have, presumably, a greater probability of survival to older ages.



**Fig. 3.** The regression lines of Figure 2 tend to intersect at a common point.

The regressions of  $L_2$  on  $L_1$ ,  $L_3$  on  $L_1$ , etc., are found to be linear (Figures 2, 3 and 4) for each age of capture, the regression lines tending to intersect at a common point (Figures 3 and 4). Figures 3 and 4 show why Lee's phenomenon becomes progressively less with increasing  $L_1$  and why its occurrence in reverse form should be expected beyond the point of inter-

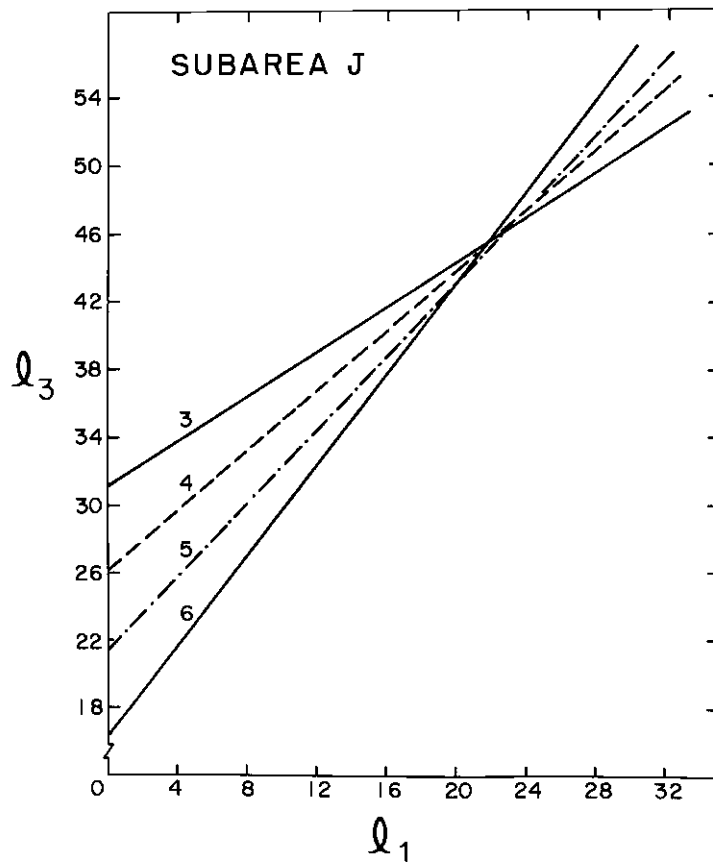


Fig. 4. The regression of  $l_3$  on  $l_1$  for ages of capture three to six. Beyond the point of intersection, Lee's phenomenon will occur in reverse form.

section.

Fitting the regression (Walford, L. A., Biol. Bull. 90, (2), 1946):

$$L_{n+1} = aL_n + b \quad (1)$$

to the data for each  $L_1$ -group and age of capture, then determining the parameters of the Bertalanffy growth equation:

$$L_t = L_\infty (1 - e^{-K(t - t_0)}) \quad (2)$$

where  $L^\infty = \frac{b}{1-a}$

and  $a = e^{-K}$

it is observed that the growth parameters change systematically with  $L_1$  and age at capture. To analyze the significance of these changes, it was desired to define a life span, since  $L^\infty$  itself has no special significance in this respect. Equation (2) cannot be solved for  $t_0$  when  $L_t$  equals  $L^\infty$ , so the concept of  $A_{.95}$  was devised.  $A_{.95}$  is the value of  $t$  in equation (2) when 95 percent of  $L^\infty$  has been attained. Solving (2) for this value of  $t$ , one obtains:

TABLE V. Growth parameters of equation (2) and equation (3) for haddock from Subarea M for ages at capture 3 - 6, together with the estimated life span,  $A_{.95}$ .

Age at capture	$L_1$	a	b	L	K	$A_{.95}$
Three	12	.7589	18.57	77.02	.2759	11.24
	16	.7390	19.12	73.26	.3025	9.96
	20	.7157	19.90	70.00	.3345	8.95
	24	.6912	20.88	67.62	.3695	7.92
	28	.6625	22.19	65.75	.4117	6.86
Four	12	.7778	16.66	74.98	.2511	12.24
	16	.7497	17.88	71.43	.2881	10.52
	20	.7207	19.34	69.24	.3275	9.11
	24	.6895	21.10	67.95	.3718	7.90
	28	.6565	23.19	67.51	.4208	6.82
Five	12	.8011	15.17	76.27	.2218	13.75
	16	.7629	16.96	71.53	.2706	11.14
	20	.7230	19.10	68.95	.3243	9.18
	24	.6806	21.68	67.88	.3848	7.61
	28	.6365	24.67	67.87	.4512	6.46
Six	12	.8080	14.43	75.16	.2132	14.25
	16	.7748	16.33	72.51	.2552	11.90
	20	.7404	18.52	71.34	.3006	10.06
	24	.7046	21.08	71.36	.3501	8.39
	28	.6644	24.16	71.99	.4089	7.13



$$A_{.95} = \frac{2.996}{K} + t_0 \quad (3)$$

where  $K$  and  $t_0$  are parameters of (2).

Table V shows how, for each age of capture and selected  $L_1$ 's, the values of the parameters of equations (1) and (2) change. The last column of Table V shows that  $A_{.95}$  declines with  $L_1$  at all ages at capture, the rate of decline being much more marked at the older ages.

The  $A_{.95}$ 's in Table V lead one to conclude that if they actually represent life spans, then necessarily there has to be a different kind of mortality curve associated with each. If one makes the not unusual assumption that the mortality associated with these curves operates at a uniform rate over the life span, then Lee's phenomenon is automatically introduced into any distribution of sizes approaching normality at age one. If it is supposed that the distribution of sizes at age one is normal, the distribution of later ages becomes positively skew.

The regressions of  $L_n$  on  $L_1$ , once determined, are sufficient to reproduce Lee's phenomenon in the observational data but they do not explain it. The combination of these regressions is, in fact, Lee's phenomenon itself, looked upon in a new light.

The application of differential mortality rates, varying with  $L_1$ , to a normal distribution of sizes at age one produces a change in the apparent growth rate with age at capture. The change calculated in this way is not as great as that actually observed in the haddock data. This suggests that selective removal of sizes by fishing gear is a contributing factor. At the same time, the hypothesis of a kind of "physiological mortality" operating independently of fishing can account for observations of Lee's phenomenon in unfished stocks. The absence of Lee's phenomenon in certain fish stocks suggests that the range of sizes at age one is near a point of intersection such as that shown in Figure 3, in which event the phenomenon would not be observed.

Analysis and interpretation of these results is continuing. If Lee's phenomenon is not an artifact inherent in the scale method of age determination in fishes, the characteristics of growth revealed in the analysis of the haddock data ought to be found in other species. Examination of shellfish growth data suggests that a change in apparent growth rate with age must occur in some species; but, except in one instance, published material in a form suitable for completing the analysis and confirming this hypothesis is lacking.



A. von Brandt.

Measuring Methods

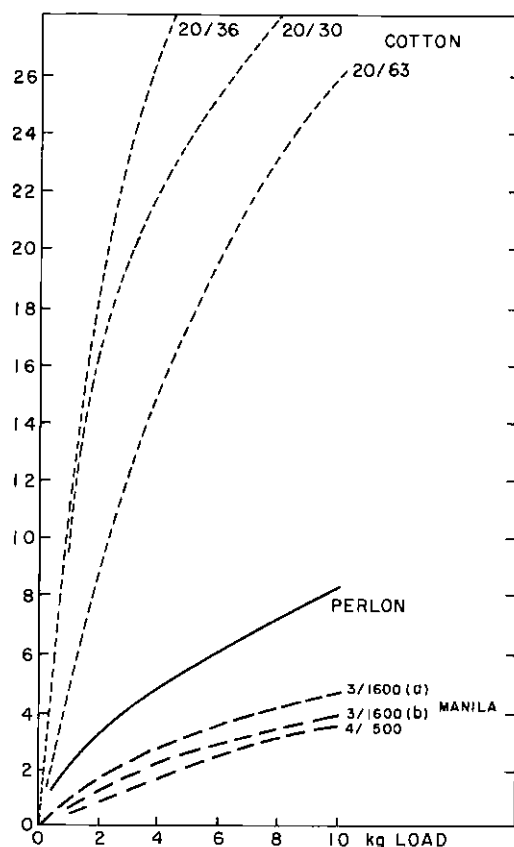
Four methods for determining the size of mesh are generally used in fisheries:

- (1) Stating the circumference of the meshing gauge (stick, spool) used for braiding the net. This method is particularly preferred by net manufacturers.
- (2) Measuring the distance from knot center to knot center, either with knots in juxtaposition or with opposite, diagonally stretched meshes. These methods are mainly used in practical fishing. Sometimes the distance from several knots (for instance, 5 knots = 2 meshes) is taken as measure for the mesh-size.
- (3) Fixing the circumference of a plate-gauge or peg which can be inserted into a mesh; and
- (4) Counting the number of knots of stretched meshes of a prescribed length.

The International Commission for the Northwest Atlantic Fisheries as well as the London Convention of 1946 have decided to determine the mesh-size by inserting a plate-gauge. Only in that way can the interior circumference of the mesh be determined, which is alone essential.

Considering the Net Manufacturers' Wishes

The net-maker should be informed about the relations existing between the results of the measurements of meshes with a plate-gauge and the circumference of the spool. Only then he will be in a position to manufacture meshes of the sizes corresponding to the measuring method employed. Numerous former works proved that the results of the measurements vary depending on the measuring method adopted. Therefore it would be desirable in experiments with varying mesh-sizes, always to know the circumference of the meshing-gauge (spool) used for knitting the net, in case it is not used as the measuring instrument.



**Fig. 1.** Load-elongation curves for various net materials. The figures of the ordinate give the elongation-percentage. The full line marked PERLON indicates plaited twine made of continuous "PerlON" 117 kg.

#### Linear Measurement of Textiles

Generally speaking, the methods of mesh measuring mean linear measurement of a twine. There does not exist any standard prescription for a linear measurement of textile twines or cords anywhere in the world, which does not require the tested material to be stretched. Usually for stretching the weight of 100 m. of twine is taken as a basis, sometimes substantially more. The

reason for that prescription is that textiles are not rigid, but are capable of more or less extension, depending on the material, and also on its method of manufacture. We use, for making net twines, fibres which stretch little, like manila, sisal and hemp; also, fibres which stretch moderately like, for instance, cotton, and those which stretch greatly like some of the new man-made fibres. However, the processing, in particular the twisting and plaiting of these materials may alter the stretching qualities to a varying degree.

Figure 1 gives a so-called load-elongation diagram of several net twines. It demonstrates how much the net twines of different type stretch with a load of up to 10 kg. The tension is given as percentage figures. If the length of the twine is to be measured, it must at least be stretched into a straight position; with elastic material the linear measurement may possibly be adversely affected. The same danger also exists when the interior circumference of the mesh is measured with the plate-gauge. The sides of the meshes must be more or less stretched for that purpose.

#### The Pressure Gauge

The use was therefore suggested of a fixed pressure when using the plate-gauge. This is particularly necessary if the nets are made of coarser material. With nets made of thin twines the meshes can be stretched diagonally without any difficulty, whereas it cannot be done without a certain force for all types of trawl nets made of manila or sisal.

For the purpose of measuring the interior circumference under a prescribed pressure, pressure-gauges have been developed which are either pushed into the mesh, vertically towards the surface of the net, or which operate with longitudinal pressure, e.g. the mesh will be stretched by a certain force into its longitudinal direction. The latter method resembles much more the actual conditions than the procedure mentioned first. Parrish, Jones, and Pope (1955), moreover, were able to prove that the measurements carried out by several persons with a longitudinally operating measuring instrument resulted in more congruous results than by the other method. However, for our investigations we used the pressure-gauge pushed vertically into the mesh (Figure 2), as this is a relatively simple and cheap instrument. Any fisherman, any net manufacturer should be in a position to procure such a measuring instrument to enable them to control their own nets.

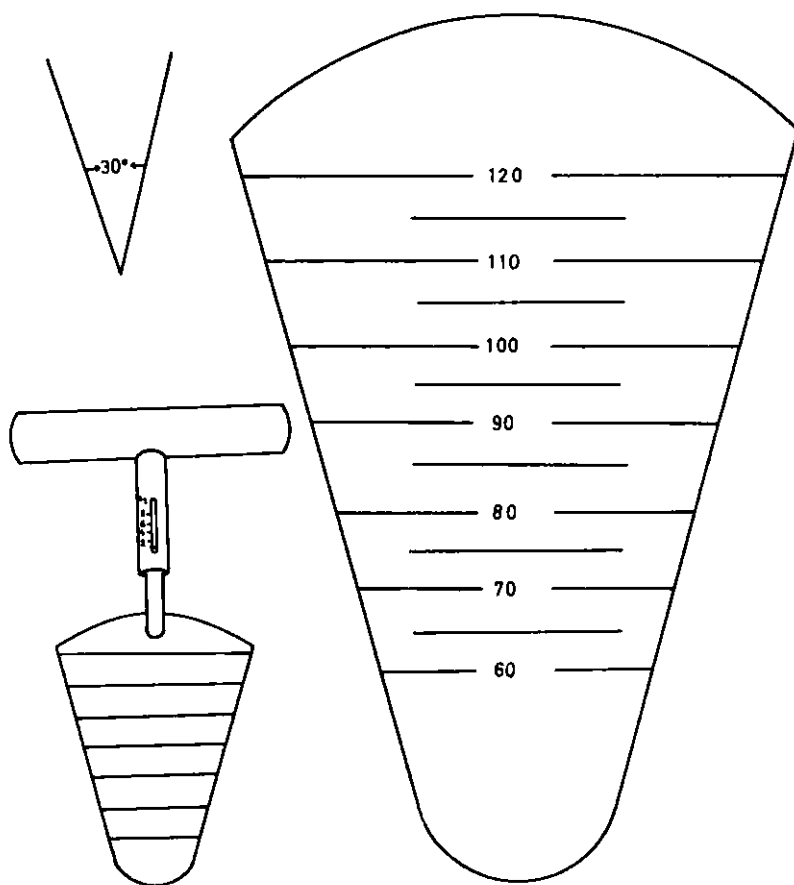


Fig. 2. The pressure gauge. Right: the plate with scale in mm.  
Above: the 30° angle of the tapering of the plate.

#### Degree of the Measuring Pressure

The pressure gauge used for our own measurements permitted use of several degrees of pressure, i.e. 2, 4, 6 and 8 kg. The differences in the mesh sizes resulting from the various pressures of 2 to 8 kg. (4.4 - 17.6 lb.) can be rather considerable. This refers also to nets made of material with lower tension like manila. Figure 3 shows the mesh sizes resulting from a pressure of 2 to 8 kg. with three wet nets made of manila net twines (4/600, 3/900 and 3/1600, as per the numeration used in Germany for manila net

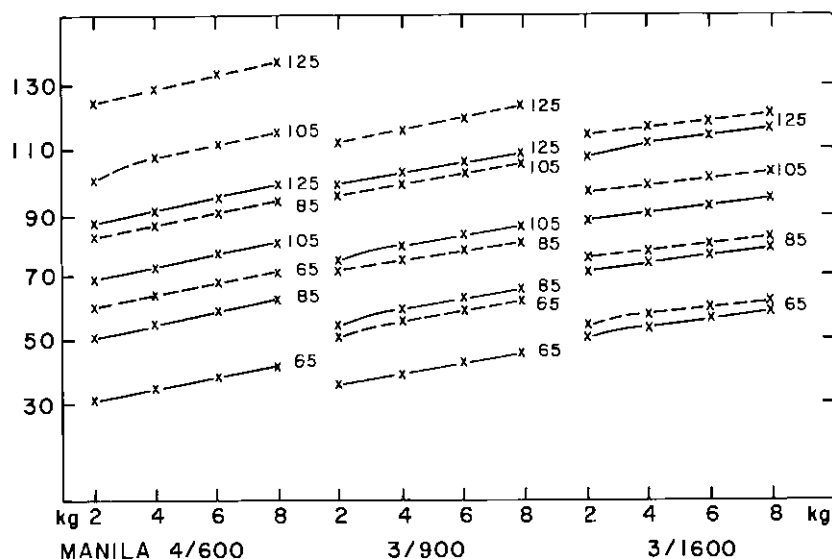
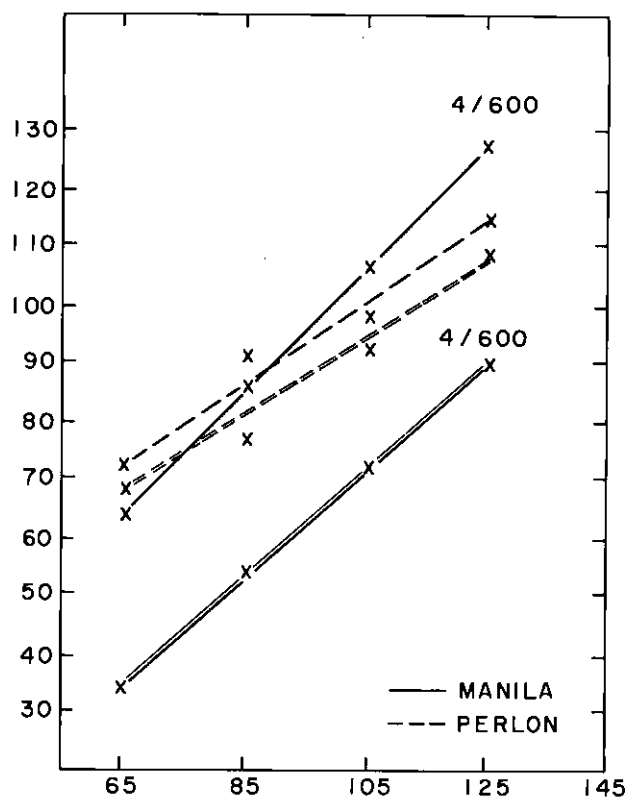


Fig. 3. Mesh sizes (mm) resulting from a pressure of 2 - 8 kgs. for three manila nets. (4/600, 3/900 and 3/1600). The figures off the lines indicate spool circumference in mm. Broken lines - single twines; solid lines - double twines.

twines, giving at first the number of the twines and then the metres per kg.), not yet used in fisheries, which has been made of single (---) or double twines (-----) by means of spools of various circumferences (65, 85, 105 and 125 mm = 2 9/16, 3 3/8, 4 1/8 and 4 15/16 in.). Thus the following sizes of mesh were found with manila 4/600 braided with a spool of 85 mm:

Pressure	2	4	6	8 kg.
Single	82	86	88	92 mm
Double	50	55	59	63 mm

Sisal or manila net twines have a small tension. Perlon, however, can have a relatively great tension. That can be seen from a comparison between a manila twist (4/600) with a breaking strength of 150 kg. and a plaited "Perlon" of 117 kg. at a measuring pressure of 4 kg. (Figure 4). It is not possible to compare any net twines, but only those which can be exchanged for fishing purposes. This refers to the two twines mentioned.



**Fig. 4.** Mesh sizes of manila and perlon nets (single and double) resulting from a pressure of 4 kgs. Ordinate - mesh sizes in mm; abscisse - spool circumference in mm.

Circumference of spool	Manila 4/600		Plaited "Perlon"	
	Single	Double	Single	Double
65 mm	64	34	72	69
85	86	55	91	77
105	107	53	97	94
125	128	90	114	109

Single-braided manila produces a mesh which approximately corresponds to the circumference of the spool, but that does not occur with double-knitting (double



line in Figure 4). With "Perlon" the differences between the circumference of the spool and the resulting meshes are not so great, but the meshes of 80/110 mm in size, which are important to us, are for double twine also smaller than they should be according to the circumference of the spool, although the measuring was done with a pressure of 4 kg.

The varying reaction of the meshes to the effect of the measuring pressure must also influence the selection or the escapement index of the trawls. No matter, whether the strength of the fish forcing itself through the meshes, or the water-pressure on the towed trawl is concerned, these forces will effect a smaller or greater extension of the meshes, always depending on the material. If therefore the mesh measurement has to be carried out with a certain pressure because of the specific material, one should try to choose a measuring pressure, the degree of which is determined by the fishing technique. Unfortunately, that presents the greatest difficulty.

Always we try to choose a sufficiently high measuring pressure, so that with a new, unused but wet, net the result corresponds to the spool employed (von Brandt, 1955, 1). Thus the greatly varying tension of the material which must already become apparent when the net is knitted by hand, but probably even with the machine-made net, might be adjusted. It proved, however, in particular with the double-knitted manila twists generally used for trawls, that this would require so great a pressure (sometimes more than 20 kg. = 44 lb.) that it could not possibly be used for measuring the meshes.

One might also use a measuring pressure resembling that acting upon the cod-end during fishing. Bedford and Beverton (1955) had the impression that the true working tension may be rather low. Schärfe 1955 found during his measurements at the seam between the rear part of the net and the so-called tunnel, that a load of 3 - 5 kg. (6.6 - 11 lb.) acts upon the individual sides of a mesh. Unfortunately, no such measurements have been made as yet with the cod-end. The load during the fishing would probably not be greater. Greater loads on the cod-end occur when the catch is hauled aboard. But at that time the fishes have scarcely any opportunity to escape.

The Northwest Atlantic Convention provides that the size of mesh shall be determined under a pressure of not less than 10 lb. (= 4.5 kg.) and not more than 15 lb. (= 6, 8 kg.). Boerema 1954 found that in his mesh size estimations the force put on the gauge was about 4 kg. (= 8, 8 lb.). Parrish 1955 suggested that the force should be so great, that it stretches the mesh without extending the twines. For the normal meshes in the cod-end of a trawl a pressure of 6 - 8 lb. (= 2, 7 to 3, 4 kg.) is intended. Bedford and Beverton (1955) were using for their mesh measurements, like Parrish, a direct-pull method of elongating the meshes. This was recorded after one minute had

elapsed from the moment when the weights were attached. They proposed a load of about 6 lb. (= 2, 7 kg.) as a standard load for mesh measurements. Cassie 1955 found in his investigations on cod-ends of manila that the 10 lb. (= 4, 5 kg.) weight was by far the most satisfactory one for giving a comparable degree of stretch of all types of trawl twist.

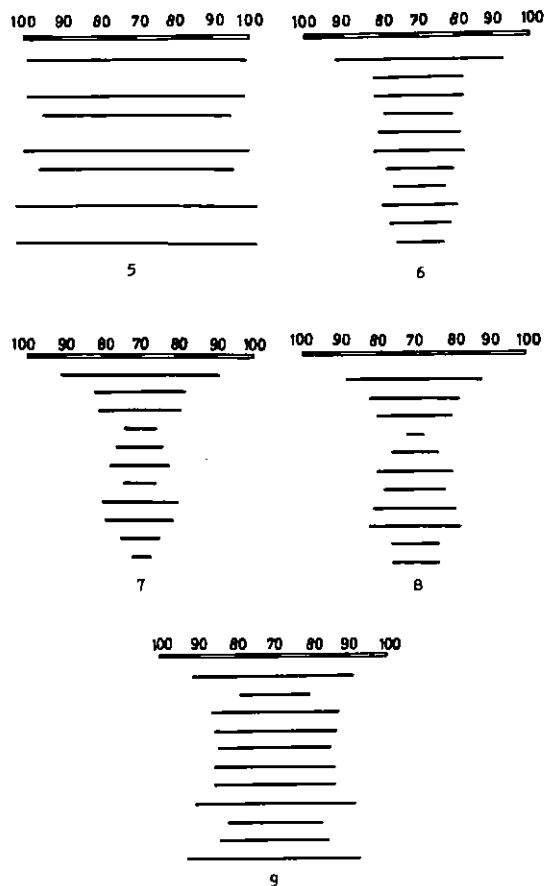
We ourselves suggested a pressure of 4 kg. (= 8, 8 lb.) for our investigations on cod-ends (von Brandt, 1955, 2). For, if many measurements have to be carried out, they should not be too difficult. When comparing the pressures proposed by the several authors for mesh-measurements, it seems that all of them reach approximately the degree which, according to previous investigations, corresponds to the pressure acting upon the cod-end meshes during fishing.

#### Changes of Meshes in the Cod-End

It is impossible to measure all meshes when controlling the cod-end; a selection must be made. Generally, the meshes to be measured are chosen at random. It is a well-known fact, that the meshes shrink in water. When the net is then used, the originally loose knots draw tight and the meshes may get larger again. But that does not occur uniformly in the cod-end. Apart from the fact that this development is influenced by the quantity of fish caught, it even varies within the cod-end. Clark 1952 has carried out measurements in 4 sections of a cod-end. Converted from inches to millimeters the following figures were obtained.

	Rear part of the cod-end			Fore part of the cod-end	
	1	2	3	4	Average
New, dry	130	130	133	130	130 mm
After 3 hauls	108	105	98	98	102
" 16 "	113	108	102	97	105
" 25 "	113	108	100	100	105
" 28 "	114	106	100	98	105

These figures show, that the part of the cod-end near the belly stretches less than the rearmost part. Cassie 1955 explains this as follows: When the catch is being lifted on board, the netting is particularly tightly strained between the top of the catch and the lifting strap, while above the strap the netting is hanging slack. Cassie concludes that for this reason it is desirable that a sys-



Figs. 5 - 9. Changes during fishing in size (mm) of meshes of a manila haddock cod-end from fore part to rear part, reading from top to bottom. Further explanation in text.

tematic rather than a random method of sampling mesh size should be used, so that all the different parts of the cod-end will be proportionally represented.

Our own measurements were made in the following way: On a double-knitted manila cod-end lateral series of 10 to 20 meshes in one row across the netting were measured, always interrupted by a series of 5 mesh rows and then the average figure for each row was computed. The following figures show the results in mm:

Figure 5) with a new, dry and unused cod-end, knitted with a knitting wood of 110 mm, double manila;

Figure 6) after the first haul;

Figure 7) after the fifth haul; and

Figure 8) after the tenth haul.

Thus the meshes shrink and stretch to a considerably varying degree. The largest meshes were at the edge, where the cod-end is attached to the tunnel, not at first at the end. That was due to the fact that the short term trial fishing produced only small catches. Ten hauls produced only a total output of approximately 100 baskets. Therefore a cod-end of the same design and made of the same material ("sister-net") was measured after having taken about 3,000 baskets (Figure 9). These measurements show 3 maxima: The first again near the edge towards the tunnel, the second at the splitting strap. Here a protective cloth was attached to the net, the third maximum is in the terminal meshes. Here too, as with Clark's measurements, the original mesh size was in no case attained.

If new nets are put into the water, they get smaller by shrinking. During fishing a pressure acts upon the net. This varies greatly when the catch is

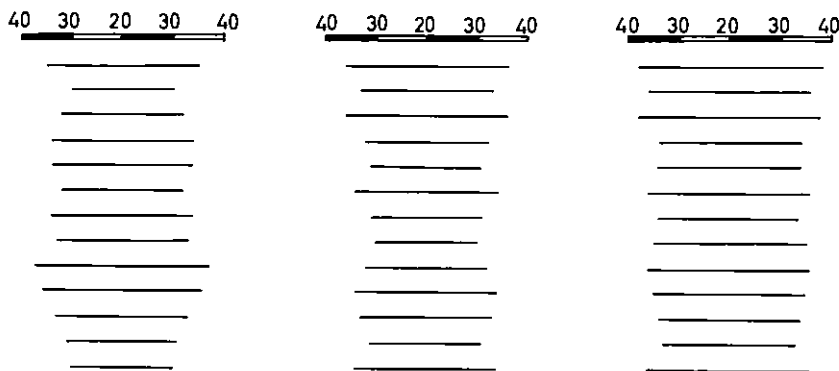


Fig. 10. Changes during fishing in size (mm) of meshes of a manila herring cod-end from fore part to rear part, reading from top to bottom. Left - cod-end after initial hauls, dry; centre - after 22 hauls (74 baskets); right - after 44 hauls (708 baskets).

lifted on board. Wherever that pressure is very great, as in the fore part of the cod-end near the tunnel, over the splitting strap, and at the rearmost part of the cod-end, the meshes will stretch.

The example shown here refers to a trawl for haddock, etc. With a herring trawl with smaller meshes and made of finer manila twines, the differences were not so great (Figure 10). The figure indicates, however, at the same time, that the meshes can always get larger during fishing, e.g. they do not remain constant. It is desirable that the changes of the mesh-sizes in the cod-end be further studied, beginning with the new dry net. These continued measurements are the basis for exact results in investigations on the selectivity of a net. If the measuring methods are not uniform and if not all changes in the mesh-sizes are considered, it will be difficult to establish useful standards of mesh-sizes.

In order to adjust the differences, it was proposed for the practical control of the mesh-size of cod-ends in Germany to measure one full row of nearly 50 to 60 meshes with a pressure-gauge of 4 kg. parallel to the long axis of the cod-end. In this way it is hoped, to detect all irregularities better than by selecting the meshes at random or measuring the mesh-rows across the cod-end netting, and to obtain a good average value for the cod-end mesh-size.

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Arthur E. J. Went.

The control of mesh size is now one of the most important methods used for the conservation of fish stocks. The actual measurement of the mesh of nets is, therefore, of considerable importance and in recent years the attention of many fishery scientists has been devoted to what, I may call, the precision measurement of the mesh of nets. Under the International Fisheries Conventions of 1937 and 1946 the measurement of nets was to be by means of a flat gauge of the required breadth and thickness. The mesh of the net had to be such that the gauge "shall pass through it easily when the net is wet". At first sight this would appear to be a simple means of measuring a net but the operative word is "easily". Every person measuring the net would, of course, interpret the word "easily" in his own way. Some would, on one extreme, merely attempt to push the gauge lightly into a mesh and, if it did not go in, that mesh would be deemed too small. Others would give it slight pressure and still others would use such force that the twine of the mesh would become unnaturally stretched.

This difficulty of defining the word "easily" in the 1937 and 1946 Conventions was fully realized when the International Convention for the North-West Atlantic Fisheries was drawn up and the pressure needed to insert the gauge into a mesh was defined. At one meeting of the Permanent Commission set up under the International Fisheries Convention of 1946 the question was discussed and an ingenious piece of apparatus produced by our Netherlands' colleagues was demonstrated to members. Subsequently other interesting and complicated pieces of apparatus were exhibited at a special meeting of the International Council for the Exploration of the Sea in Copenhagen in October, 1955. The persons who have designed these spring loaded gauges are to be congratulated on their ingenuity but one wonders if in devising these instruments the main point of mesh control has not been lost sight of and forgotten.

The purpose of measuring the meshes of a net is to ascertain if a net conforms to a definite standard. If the control of the mesh of a net is to be really effective we must have the co-operation of our fisherman. Fishermen of today are skilled in their trade but one cannot expect them to appreciate the niceties of the situation, as far as nets are concerned, if a precision instrument is necessary to determine whether or not a net conforms to the regulations. But not only have we to convince the fishermen - we must also if necessary convince the Judge of the Court to which an alleged offender is brought for contravening the regulations. Is this Judge likely to convict an offender, or if he convicts him, is he likely to impose a heavy penalty, for an offence which requires the use of a precision instrument for its detection. Speaking of Ireland I think it would be difficult to get a conviction if it should emerge in evidence that contravention could only be detected by the use of a precision instrument,

similar to those already demonstrated to us from time to time. In brief, I consider that meticulous measuring of individual meshes by precision instruments is too far removed from practical reality.

What then is the alternative? In my opinion the alternative is to return to the metre or yard stick. I know that this raises a number of important issues. For example, for any given "lumen" of a mesh the number of rows to the metre or yard will depend mainly on the twine used in the manufacture of the net. Are we not likely, however, to get virtually the same conservation effect by defining the number of rows per metre or yard for, say, two groups of nets based on the material from which they are made, somewhat on the lines of the Permanent Commission's tentative definition of a "light trawl". Could we not, for example, fix a minimum of X rows per metre or yard for nets made from manila or sisal twine and Y rows per metre or yard for nets made from other materials. The value of Y would presumably be greater than X. On balance the proper values of X and Y would probably produce, in practice, approximately the same conservation effect as the present and, I think I am justified in saying, cumbersome methods. Indeed the variation between the two methods, i.e., the metre or yard stick and the flat gauge, might well be less than those between the different methods now used by the various countries adhering to the International Fisheries Convention of 1946. I need only refer briefly to paper P. C. 4/45 (Item 9) circulated at the September 1955 meeting of the Permanent Commission in which the differences in the tolerance allowed in measuring nets was shown to range from a small tolerance in the case of Norway and up to 50% tolerance in the cases of a number of other countries. Some experiments would, of course, be necessary to establish the pressure needed to take out the natural twist in the twine of the nets before they are measured. To do this the simplest way from the practical point of view would be to place a portion of the net on some solid holdfast and attach a weight of say 10 or 20 kilos. (Simple experiments would show what weight should be adopted) and then count the number of rows per metre of that part of the net under tension.

What could be simpler and more effective? The method is capable of being understood by any fisherman and the Courts will find no difficulty in appreciating the difference between illegal (undersized) nets and those of legal size. Those persons who have the responsibility of measuring nets would no longer have to be supplied with an expensive precision instrument and they could carry out their work much more speedily. I would, therefore, strongly appeal for a return to this simple method of measuring nets and, in doing so, I would emphasize that I do not regard precision instruments for scientific work as unnecessary, merely that they are undesirable for the practical enforcement of the minimum size of the meshes of nets.



## DIFFERENTIATION OF FISH STOCKS

Convenor's Report, C. E. Lucas.

During the course of the discussion, the working party welcomed the attendance of Dr. Kesteven from time to time and took opportunity to discuss with him the use of some biological terms. In particular, however, this working party was asked to consider:

- (1) The importance of planktonic stages to the division or intermingling of groundfish stocks.
- (2) The identification of stocks in general.

Subsequently, a joint meeting was arranged with Working Party VI (Research Methods) to discuss:

- (3) The species and varieties of redfish.

Communications were solicited in advance for only the first of these topics, and eight papers were circulated before the working party met. It was fortunate that some of these concerned aspects of both (1) and (2) while two later contributions were presented at the meeting specifically on item (2). Many valuable comments were made on these two subjects during the course of the discussions, arising from experience and work in progress on both sides of the Atlantic Ocean and elsewhere. Relevant recommendations are set out below. Finally, a valuable, if indeterminate discussion was held on the different groups of redfish, giving rise to the last recommendation below.

The working party met on 5th to 7th March, and again on 9th March for a review of their recommendations to the Standing Committee on the Research and Statistics. It seems necessary to say, however, that so closely were the subject matters of this and other working parties linked that topics of significance to this party were often being discussed elsewhere and vice versa. It was very right that this should have been so, even though it had the consequence that it was not always easy to secure for these meetings sufficient of the experts on different aspects of stock differentiation for the meetings to be fully representative. Indeed, it may even be that this was in itself an important symptom. Although the identification of stocks, involving a clear knowledge of characteristics and distribution of species (and subordinate categories), lies at the root of fishery research, many disciplines are necessary for such determinations. At times, it seemed clear that the appropriate experts were very properly concerned with the discussion and resolution of technical problems before attempting to say more about species and stocks. Nowhere was

this more evident or more necessary than in relation to redfish.

As a basis for discussion notes were circulated by the Chairman setting out some of the principal considerations which have been, or may be, used from time to time in attempting to decide whether the fish in a particular fishery could be regarded as a unit stock, and/or how far they may mingle with fish of another group or groups of the same species. An adjusted and approved copy is the last section of this party's report. A unit stock was seen as a group of fish which is not known, at present, to be mixing with others, either during their planktonic\* stages or later in life; the haddock of the North American banks and those of the North Sea are good examples of stocks which are not known to mix, but it is not always so easy to decide whether the fish of a particular ground can be so differentiated. The concept seems to be a fundamental one in fishery research (in population dynamics, etc.), although it is recognized that a group might reasonably be regarded as a unit stock for practical purposes even though it is known that an insignificant proportion of its members may intermingle with others of the species.

It seems fair to say that, despite the body of knowledge represented by the contributions, and the considerable work and experience which lay behind them, the principal feeling at most stages in the discussions was that we need to know much more about the fish in the Commission's area - - both about apparently familiar aspects of the lives of fishes, and about research fields where only a tentative start has recently been made - - if our knowledge of the fisheries in that area is to be placed on sure foundations. The following points attracted particular attention and recommendations were made concerning them:

- (1) Discussion inevitably centered on the considerable distances over which fish may drift during their planktonic stages, and the significance of this recruitment for the differentiation of stocks. The stimulating suggestion was made that sometimes the duration of the planktonic phase might be prolonged, as in some other planktonic organisms, particularly if circumstances are not suitable at the normal stage of development for assuming the demersal habit. In association there is the available evidence, and the apparently logical necessity if the stock is to persist in that area, for the return of the adults in due course and their assembly for reproduction over the spawning grounds. It became clear that some of the problems cannot be solved until there is much more detailed knowledge of the habits, physiology and biochemistry of commercial fish during both their planktonic and

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\* This term should be used in preference to the term "larval" used in the working papers as a convenient code for this subject of the working party.

free-swimming life. Particular interest was shown in the possibility of fish being "conditioned" to the environmental circumstances under which they existed as eggs and larvae, so that they might conceivably be stimulated to "seek out" similar conditions on the approach of maturity.

It was recommended, therefore, that attention be drawn to the urgent need for (a) more work on the experimental rearing of fish from the egg stage, including investigation of their relationships in early life with their environment, and (b) more, and more exact, studies of migration and shoaling in adult fish, and particularly of those aspects of their environment to which they can (and do) react, so as to understand better the means whereby they find their way back to their spawning grounds.

- (2) Attention was drawn to our relatively scanty knowledge of the ecology of the plankton, and particularly of the distribution of the eggs and planktonic stages of commercial fish, in relation to hydrographical conditions on the Newfoundland and Labrador Banks.

It was recommended that, while systematic knowledge could best be advanced by the work of specially equipped research vessels, serious consideration should be given to the possibilities of supplementing such work with observations and samples which could be collected by the vessels of the various nations fishing those banks. Once the support and understanding of the owners and skippers had been obtained, simple and semi-automatic gear, such as the Hardy Plankton Indicator, could be used regularly with negligible interference to fishing activity.

- (3) Some of the most interesting and baffling biological problems were presented during the discussions on redfish in this and other working parties. Mr. George Kelly opened the discussion on the species and varieties of redfish in the North Atlantic, followed by Dr. Kotthaus and Dr. Tåning. Mr. Parrish kindly reported on the relevant findings of Working Party VI (Methods). It may fairly be said that the redfish present in most extreme forms many of the problems met in our studies of more familiar species such as cod and haddock. In particular (a) there is no agreement on the taxonomic status of the various "kinds" of redfish found in the North Atlantic and consequently no useful concept of unit stocks, and (b) there is not only evidence for different growth rates prevailing in different groups, but there is very wide divergence between one worker and the others in age determination within the same population and, indeed, on the same otoliths. According to the majority, the redfish grows surprisingly slowly but, according to the other worker, it grows some three or four times as

fast! Interest in the fishery for redfish is steadily increasing on both sides of the Atlantic and may be expected to increase further, so that it is essential to have reliable information about the rates of growth, and relationships between the different groups of fish on both sides of the Atlantic, if the population dynamics are to be analyzed. According to the evidence of those who believe these fish grow slowly, overfishing - - temporary or long-term, local or more widespread - - might not be distant. On the other hand, as we are still very ignorant of the distribution, spawning grounds and migrations of practically all the groups of redfish, the possibility that there may be relatively large concentrations of redfish which are not exploited (or even exploitable) cannot be ignored.

In all this, it is essential to record that, in most laboratories where redfish are studied, it is at best a part-time occupation; one biologist may be responsible for redfish studies and two or three other tasks as well. Real progress cannot be made in this way. If the Commission considers that the actual and potential importance of the redfish demand that our knowledge of its biology be placed on a sound footing, the intensity of work must be increased. Accordingly, it was recommended that funds should be made available for a very considerable increase in the skilled manpower and facilities provided to investigate redfish. Particular aspects on which more information is urgently needed are (a) morphology in relation to age, (b) growth rates, (c) migrations (horizontal and vertical), (d) occurrence and constitution of reproductive concentrations of the fish, (e) spawning places, (f) characteristics of the larvae of the different groups, (g) the subsequent drift of the young stages - - all in association with conventional hydrographic data. In addition (h) all available statistics should be examined for evidence of local and more widespread changes in abundance.

#### Considerations in Differentiating Stocks

The following considerations seem to be relevant when trying to decide whether the fish in a particular fishery can be regarded as a unit, or stock, in itself and how far it may be related to other groups or stocks of the same species. For convenience, the considerations can be set out under the headings of A, eggs, larvae and other passive stages, and B, the individually mobile and adult stages.

##### A. Eggs and larvae, etc.

- (i) First and foremost, it is necessary to determine what current sys-

tems exist over and around the spawning grounds. For example, the spawning products of the North Sea haddock would appear to be broadly conserved by the main anti-clockwise eddy in the northern North Sea, although variations among the factors governing this eddy might result in the loss of larvae from the area and, conceivable, their transference towards the area of another haddock fishery. Again, the general clockwise movement of the waters round Iceland not only causes the larvae of cod and saithe to drift appreciably from the spawning grounds but in general tends to retain them over the Icelandic shelf; although on occasion considerable numbers of cod larvae have been known to be diverted from this system and to drift toward Greenland waters.

- (ii) In general, horizontal eddy systems such as these tend to maintain the species in the area in question. In some instances, at least in theory, the same effect may even be maintained by a circulation within the vertical plane, as occurs in some truly planktonic species. Uni-lateral drifts, on the other hand, such as influence the plaice of the southern North Sea, for example, tend to carry eggs and larvae steadily away from the spawning grounds, and must logically be complemented by some other conservative system - - for example, a counter-current migration of the resulting adults for spawning purposes - - if the fishery in question is to persist, and particularly if it is truly a unit of stock in its own right.
- (iii) Related matters concern the speed and depth of the local currents, and the extent to which they are influenced more or less by local winds. Thus, both Walford and Carruthers (et al) have produced evidence suggesting that the success of broods may be considerably influenced by the variable direction and strength of winds over the area of the spawning grounds.
- (iv) In this context, the rate of development of the larvae in question (i.e. the period taken to attain the individually mobile, and ultimately pelagic or demersal phase), and the environmental factors such as temperature which govern this, are important.
- (v) Other factors vital to the success of broods and consequently to the possible transfer of larvae from the grounds of one fishery to those of another are the availability of suitable food - both immediately after the yolk sac stage, and successively as the young fish grow until and when they become demersal or pelagic. Conceivably, less tangible factors, such as the availability of dissolved organic matter, either for direct or accessory nutrition, may be concerned.

B. Mobile and adult stages.

- (i) Here, migration is concerned and considerations will vary greatly according to whether the species in question is mainly demersal (e.g. haddock and plaice) or pelagic (e.g. tuna, herring and, an extreme instance, the eel). Evidence for both spawning and feeding migrations has been produced, although much remains to be discovered about the stimuli inducing migration. Broadly speaking, there appears to be a much greater chance of intermingling between apparent "stock" of pelagic fish, and it is significant that the cod, in which stock inter-relationship has been shown to extend over thousands of miles, is essentially pelagic for a good deal of its life. Even though the major North Atlantic groups of cod may be largely individual, migrations have been traced which link those found at Newfoundland, Greenland, Iceland, Bear Island and in the Barents Sea, etc.
- (ii) Closely related is the possible existence of depth barriers. These do not seem to be very significant for the cod, perhaps because of its pelagic tendency, but the evidence suggests that they may be more important for the haddock, perhaps depending on the possibility that below certain depths haddock food is insufficiently abundant to attract or retain wandering fish.
- (iii) Again, we are also concerned with the normal environmental limits which the species can tolerate - for example, whether it is stenothermal or eurythermal, etc. On the other hand, there is evidence to suggest that, within the species, local "stocks" may have evolved different environmental tolerances (e.g. North Sea and Barents Sea cod).
- (iv) Other physiological differences may be revealed by marked differences in growth rate. Yet another may be shown by differential susceptibility to parasitization, although this feature must usually be subject to ecological control. A third arises in the hints of differences in the nature of proteins, etc. in various stocks (as shown, for example, by chromatography and electrophoresis).
- (v) Apart from such physiological differences, investigation of morphological characters has shown considerable stock differences. Examples are numbers of vertebrae, fin rays, etc., and peculiar characteristics of scales, otoliths, skull formation and even general appearance and taste. It is important to ascertain whether these differences are inherited or environmental (for example, some at least have been shown to be strongly under the influence of temperature).

(vi) On the other hand, it should be remembered that the absence of such morphological, physiological, etc. differences does not necessarily mean that two groups of fish are completely interrelated by continued admixture and interchange of individuals; they may still be quite individual.

(vii) When and where do they spawn?

Ultimately, either under A or B, we are concerned with (1) methods by which populations may intermix and (2) methods by which such intermixing may be detected.

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Angeles Alvaríño.

Author's Abstract.

Surface plankton hauls were taken by fishing vessels on the Grand Bank and St. Pierre in the spring and summer of 1955 at positions governed by the fishing requirements. Eight species of zooplankton were dealt with in addition to the larvae of Mallotus villosus and the eggs of Gadus callarias, Hippoglossoides platessoides and Limanda ferruginea.

Sagitta elegans arctica was found only in spring and only in the western part of the area. Its abundance was numerically dependent upon both daylight and temperature. Other spring species were Aglantha digitale, Melicerium companula, Themisto spp. and Clione limacina. Young of Mallotus, (20-30 mm) from the previous year's spawning also were found only in spring. The summer species included Beroe, Pleurobrachia and the eggs of G. callarias and L. ferruginea. Thysanoessa raschii and the eggs of H. platessoides were found in spring, but more abundantly in summer. Some of these organisms have special significance, for example, Melicerium, a boreal neritic species can be associated with a current from the southeast coast of Newfoundland; Pleurobrachia is extremely voracious and when abundant consumes most of the rest of the plankton; and T. raschii is an important food of the cod when feeding pelagically. The absence of cod larvae suggests that spawning here is not earlier than June.

These collections taken by fishing vessels could not be arranged to give proper coverage of the area and the author made a strong plea for special planktonic surveys to study the distribution of the planktonic stages of fish, to assess the hydrographic conditions by the distribution of plankton indicator species and to investigate possible correlation between the abundance of young fish and the plankton.



ADAPTABILITY OF THE HARDY PLANKTON  
RECORDER TO RESEARCH SHIP STUDIES

277

John B. Colton, Jr.

Author's Abstract.

Statistical studies of the quantities of plankton taken by three types of collecting apparatus: The Hardy plankton recorder, one-meter tow nets and the Clarke-Bumpus sampler. No significant difference in the catch per cubic meter of fish eggs was found; the Hardy recorder took as large a range of larval fishes as the one-meter net, a much larger range than the Clarke-Bumpus sampler, and as many fish in daylight hours as at night. It is concluded that (1) speed of tow is important for catching larval fishes; (2) a sample confined to the upper ten meters represents the distribution of fish eggs and larvae over the whole water column in the area sampled.



REPORT ON STUDIES OF FLUCTUATIONS  
OF YEAR-CLASS STRENGTH OF HADDOCK

279

John B. Colton, Jr.

Author's Abstract.

The early life history of Georges Bank haddock was studied to observe spawning and the effects of associated environmental factors, and to obtain a quantitative estimate of the relative magnitude of year-classes before entry to the fishery.

During March, April and May, 1953, three egg and larval surveys of 2-weeks duration were completed. Hardy plankton recorders were towed, at the surface and 10 meters, approximately 15,000 miles. Spawning centers were located. The drift of eggs and larvae was traced in relation to time, space, and ecological conditions. The drift of eggs and larvae was related to the circulation pattern determined from drift bottles.

The majority of larval haddock hatched from eggs spawned on Georges Bank drifted off the southern edge and presumably were lost to the fishery. Eggs and larvae from Browns Bank moved northwest into the Gulf of Maine where conditions were more suitable for survival.

Sampling of pre-ring haddock during September revealed that the majority of these fish were located on the western side of the Gulf of Maine and in the South Channel area.

On the basis of the distribution and drift of eggs and larvae, the resulting young haddock were probably the progeny of Browns Bank spawning. Thus it appears that the 1953 year-class of haddock on both Georges and Browns Bank depended upon the success of spawning and survival of haddock from the latter area.



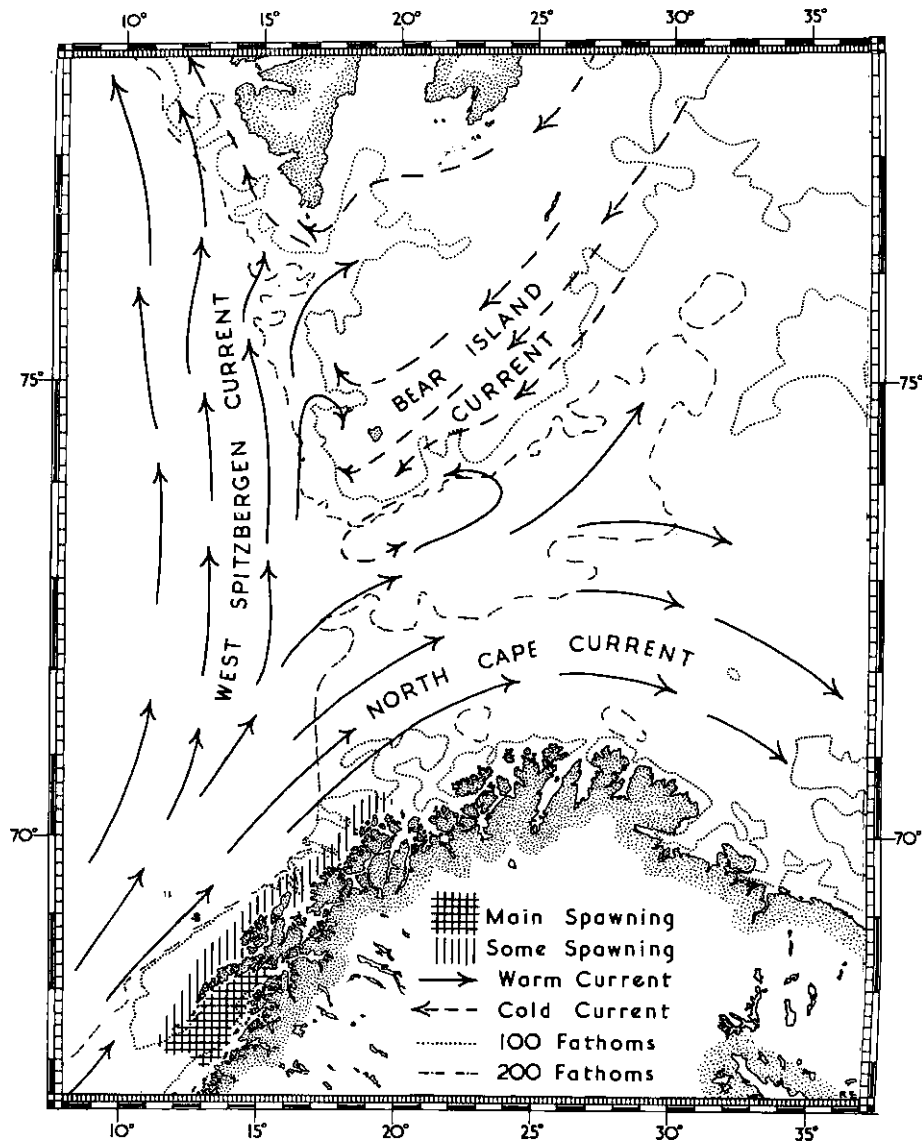
John Corlett.

Since 1949 the Research Vessel ERNEST HOLT has been working on the stocks of cod (*Gadus callarias* L.) in the western Barents Sea. In the course of this work, and incidental to the main lines of research, some information has been collected on the distribution of cod in the pelagic larval and early bottom stages and this is presented here with some additions from Norwegian work.

Figure 1 shows the main current systems in the eastern Norwegian and western Barents Seas and is based on a figure in Lee (1952). The West Spitsbergen and North Cape Currents represent extremities of the Gulf Stream system and contain "Atlantic" water of temperatures between 3°C and 8°C and salinities between 35.0‰ and 35.2‰. The Bear Island Current contains Arctic water with temperatures between -1.8°C and 1°C and salinities between 33.9‰ and 34.9‰. The mature cod of the Arcto-Norwegian stock, which cover the whole of the Barents Sea and West Spitsbergen waters in their summer feeding migrations, come together to spawn each spring off the Lofoten Islands. The main spawning is in the Westfjord, but a small amount takes place along the coast to the north. Mixed with the Arcto-Norwegian cod are some of the race of coastal cod (Rollefsen, 1933). Spawning is from late February to late April with the peak about the third week in March. The cod spawn in a band of water of temperature between 3°C and 6.5°C which is usually at a depth of 50 to 100 metres (Eggvin, 1932). The distribution of eggs and larvae round the Lofoten Islands during the spawning in recent years is given by Wiborg (1950, 1952 and 1954). Many of the eggs are carried by the surface

TABLE I. Data on which Figure 2 is based.

Year	Ship	Area	Net	Stations	
				Total	Positive
1901	MICHAEL SARS	68°N to 70°N.	Dahl Net	14	5
1949	ERNEST HOLT	West of Bear Island	1 m. Stramin	15	3
		North Cape Current	1 m. Stramin	2	2
1951	ERNEST HOLT	East and West of Bear Island	1 m. Stramin	17	0
1952	ERNEST HOLT	70°N to 74°N.	1 m. Silk	15	2
1953	JOHAN HJORT	Norwegian Coast	Clarke-Bumpus	-	-



**Fig. 1.** Surface currents and cod spawning areas in the eastern Norwegian Sea and western Barents Sea.

currents out of the Westfjord and into the northgoing current along the coast, while others are carried out into the fjords among the islands.



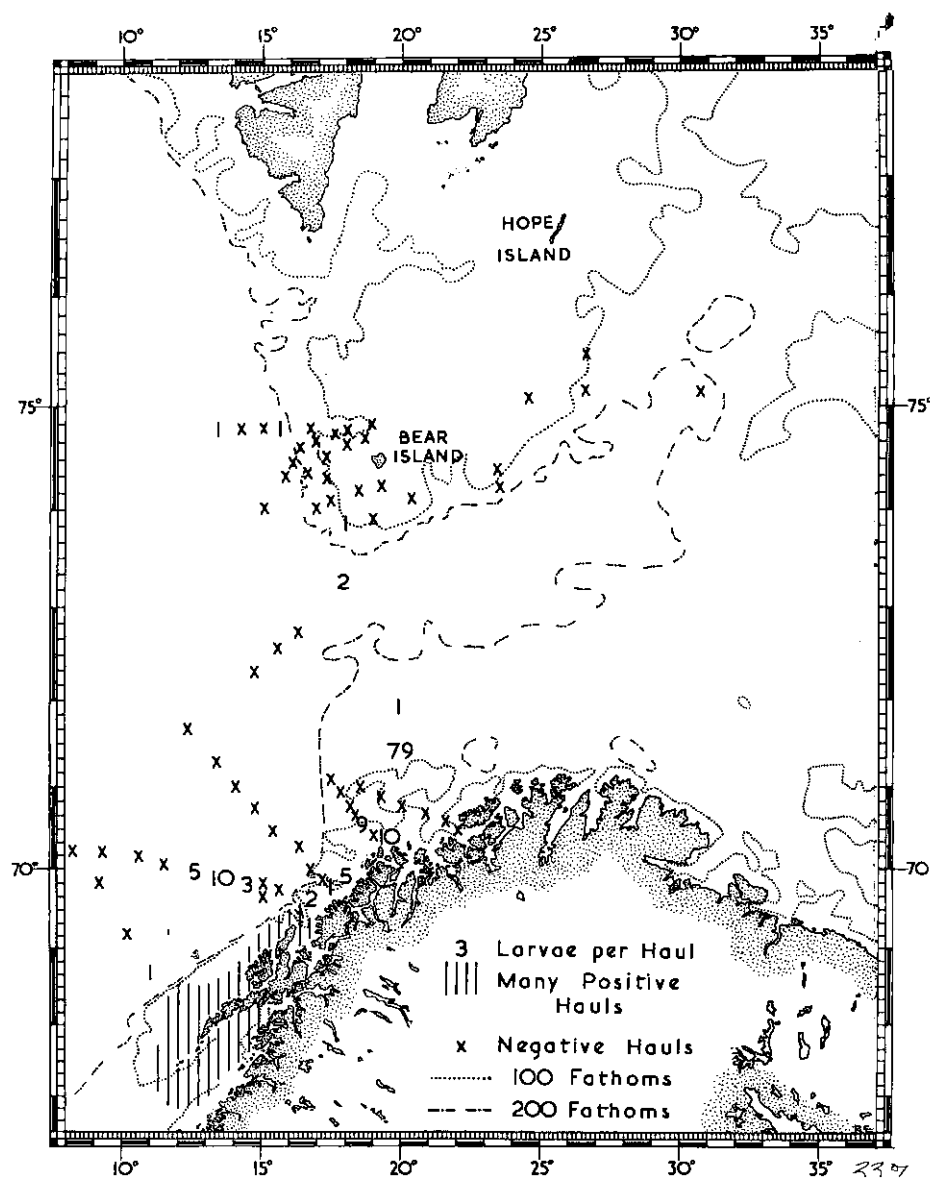


Fig. 2. Cod larvae from plankton nets in June 1901, 1949, 1951, 1952 and 1953 (see Table I).

Figure 2, showing the distribution of pelagic cod larvae in June, is a composite picture based on records from the ERNEST HOLT and from Damas (1909) and Wiborg (1954). (See Table I). The nets used on the ERNEST HOLT

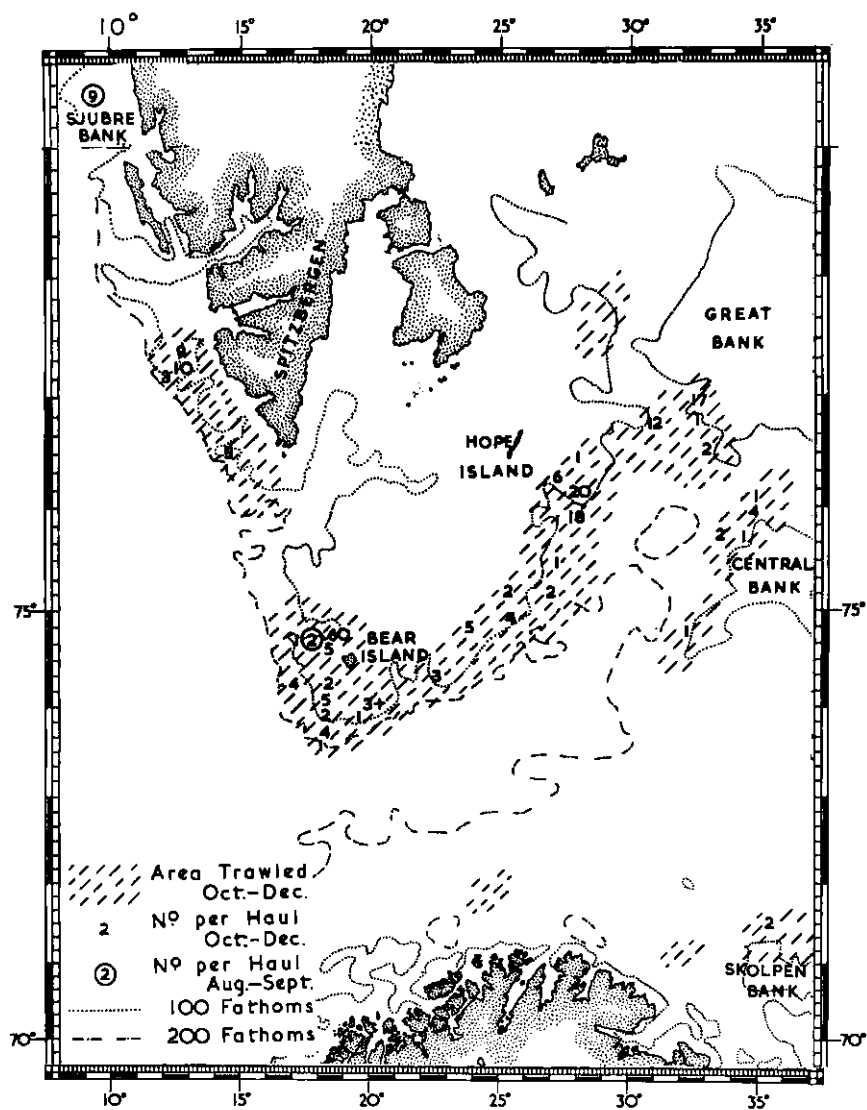


Fig. 3. Group "0" cod from the bottom. Autumn 1950, 1951, 1953 and 1954 (see Table II).

were not intended for catching fish larvae, which were taken incidentally with

the plankton catches. Probably some of the larvae were strong enough swimmers by this time to escape the nets. However, the chart serves to show that by June the larvae are in the West Spitsbergen and North Cape Currents, being carried northwards and eastwards into the Barents Sea; some have travelled as far as the latitude of Bear Island, 420 miles from the Westfjord.

Figure 3 shows the distribution of codling between five and nine months old caught by the ERNEST HOLT from 1950 to 1954 in "cod-end covers". The cover is made of shrimp netting of 80 to 90 rows to the yard and measures about 8 ft. by 5 ft.; it is laced to the back of the cod-end to sample fish escaping from the main meshes and has been used on most hauls since August, 1950. Table II gives details of the hauls in which Group "0" codling were taken. Very few were taken in August and September; it is probable that most of the larvae had not reached the bottom in these months, and possible that they were small enough to escape through the shrimp netting. Most of the Group "0" codling were caught in October, in depths between 60 and 160 fathoms on the banks west of Spitsbergen, from northwest of Bear Island round

TABLE II. Data on which Figure 3 is based.

Year	Month	Area	Positive Stations	Total Larvae	Mean Length (cm)
1950	August	West of Bear Island	1	2	7.2
	October	West and south of Bear Is.	8	23	11.25
1951	September	Northwest of Spitsbergen	1	9	9.3
	October	West of Bear Island	3	65	10.6
		West of Spitsbergen	4	27	12.4
	December	Skolpen Bank	1	2	-
1953	October	East and southeast of Hope Island	8	26	10.0
	November	Southeast of Bear Island	1	1+	-
1954	October	East of Bear Island and Hope Island	7	69	10.5
	Nov.-Dec.	East of Bear Island	4	9	10.9

to east of Hope Island, and on the Great and Central Banks east of Hope Island in 33° to 35° East. The distance from the Westfjord to the Sjubre Bank, northwest of Spitsbergen, where nine larvae were caught in August, 1950, is 720 miles, and to the station on the Great Bank where 17 were caught in October,

1954, is 680 miles. Thus the products of the spawning in the Westfjord in spring are distributed over the feeding grounds of the western Barents Sea by autumn. Also, it is known that many larvae are carried into the southern and eastern Barents Sea and others are in the north Norwegian fjords. Trout (1954) estimates that about 25% of the Bear Island population live in the fjords for the first one to two years.

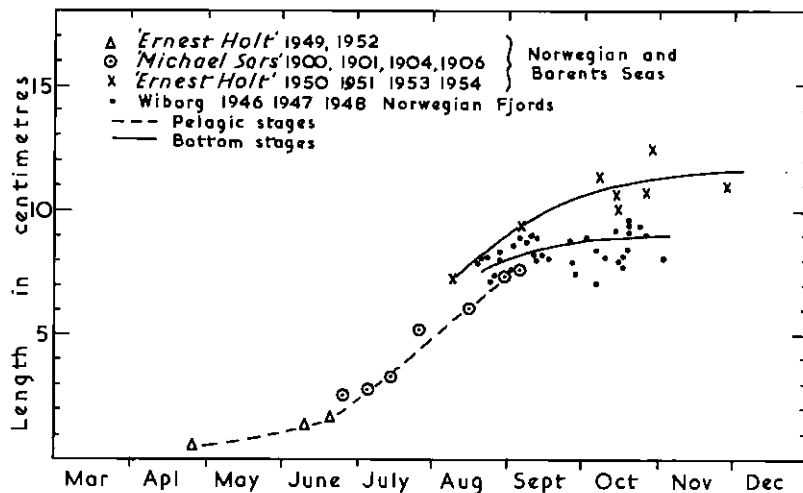


Fig. 4. Growth of Arcto-Norwegian cod in the first year.

In Figure 4 the growth curves are taken from the ERNEST HOLT data (see Table II), and from Damas (1909) and Wiborg (1949). Wiborg's hauls are in "deep" water in the fjords and so probably refer to the Arcto-Norwegian stock as the young of the coastal race of cod are said to live in shallow water. The graph shows the better growth of the bottom stages in the Barents Sea when compared with the fjords.

In Figure 5 the growth in several North Atlantic areas is compared with those in Figure 4. The curves were drawn by eye through data from various sources and years; for the North Sea, Graham (1926 and 1929); for Iceland, Saemundsson (1923) and Tåning (1943); and for West Greenland, Hansen (1949). The vertical break in the curves between pelagic and bottom stages is attributed by Graham (1926) to the plankton nets taking only the smallest and weakest swimmers and to the largest larvae going to the bottom first. Spawning in the North Sea, at Iceland, and in the Westfjord is in March; but the time and size at which the larvae reach the bottom differs. In the North Sea it is

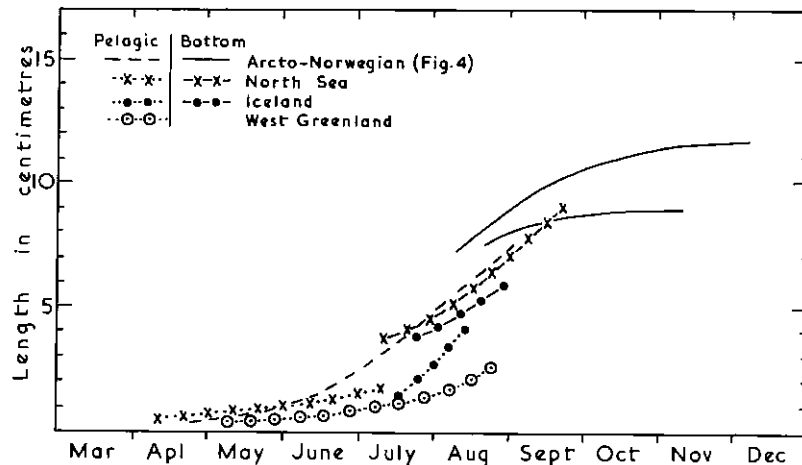


Fig. 5. Growth of first year cod in various areas.

in early July at about 3.5 cm, at Iceland in early August and about 4.5 cm, and in the Barents Sea in late August and September at about 7.5 cm. In West Greenland waters spawning is in May, and by mid-August the larvae are only 2.5 cm long and are said to be seeking the bottom. Two of the factors which affect the length of larval life are the water temperature and the depth to which the larvae have to go to reach the bottom. Those with the longest pelagic life, such as the Arcto-Norwegian stock (which are in coldest water and go deepest) have the best chance of wide dispersal.

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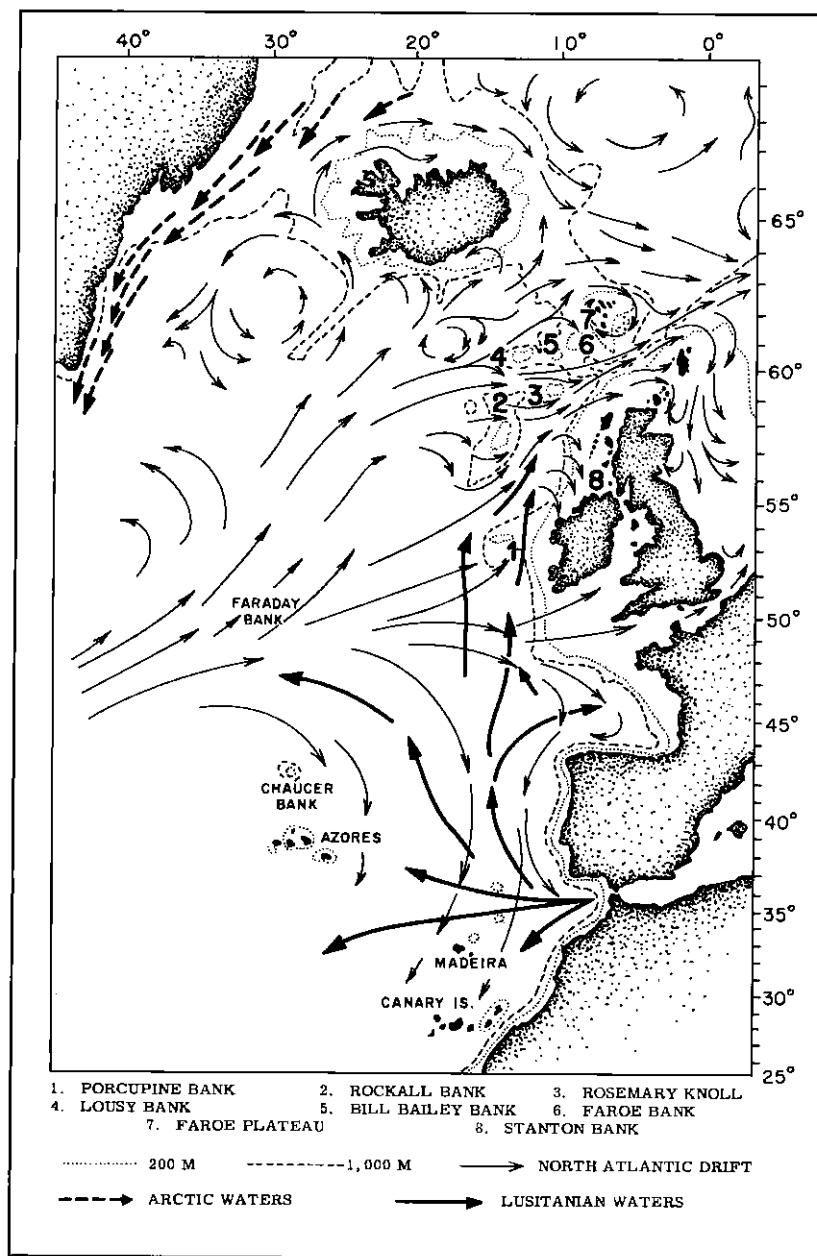
J. H. Fraser.

Introduction

In a consideration of the effect of drift on the distribution of the planktonic stages of fish certain factors need emphasis. In addition to the obvious such as the currents themselves, their direction, speed, volume, physical and chemical character, we have also to consider the spawning localities of the fish and the distance between these and the possible settlement areas, and the time factor in the life history of the fish - how long it can spend in its various stages as a transportable organism. Other factors may be critical in certain circumstances, such as the amount and type of food supply available for each stage of the organism under consideration; the micro-chemical composition of the water may have to be correct within very close limits to enable the larvae to thrive, or for their food to thrive. Predators may vary in abundance according to environmental conditions that may not be in any way limiting to the fish themselves. The strength and direction of the local wind during the appropriate months has a great influence on brood survival and on the final areas of distribution of the larvae, (Walford 1938; Carruthers, Lawford and Veley 1951; Carruthers, Lawford, Veley and Parrish 1951; Veley 1951; Chase 1955).

A study of the plankton associated with the water movements concerned can give much information that is of value in considering this topic. It can supplement the hydrographer's picture of the currents themselves, and where a marked change in the specific content occurs the progress of the boundary can give a reliable indication of speed. Plankton indicator organisms can be used to define separate water masses at different depths and, of course, the plankton samples yield direct information about the whereabouts and numbers of the fish eggs and larvae and their food supply.

The current systems on the eastern side of the north Atlantic have been fairly well plotted by the hydrographers - e.g. Helland-Hansen and Nansen, 1909; Jacobsen, 1929; Tait 1930-37, 1934, and 1957; Vallaux, 1936; Herman and Thomson, 1946; Einarsson and Stefansson, 1953, Tulloch, in the press; etc. etc. A composite figure is reproduced here as Figure 1 and has been taken from various sources including some unpublished data from the cruises of the Scottish research vessels. The spawning places and the life histories of the fish have also been worked out, and as long ago as 1909 Schmidt gave a very full and detailed account of the possibilities of larval drift over the whole area between Iceland and Spain. Since then the development of new techniques and more precise localized plankton studies has given us a much more precise



**Fig. 1.** The current systems affecting the drift of planktonic stages of fish in the northeast Atlantic.



idea of the current systems involved. This has enabled us to add some details to Schmidt's broad account and to confirm his ideas but detailed studies have not changed the broad picture he gave. The principles shown by the results of this survey in the northeast Atlantic may have application also on the western side and elsewhere, and so not be out of place at this committee.

#### The Basic Factors

The positions of the banks are important as they are, in places, shallow enough to enable certain fish to live, and sometimes also to spawn. In addition to the continental shelves around the British Isles, the Faroe Plateau and the Icelandic Shelf, the most important banks are (a) Rockall, Faroe, Lousy and Porcupine Banks with depths of less than 200 metres, and (b) Rosemary, Bligh and Hatton Banks and submarine ridges, such as the Wyville Thomson and Faroe Iceland ridges, which in places are less than 500 metres deep. It is suspected that Faraday and other deep water banks of 1000 m or over are too deep to have any significance as far as the distribution of commercial fish is concerned.

In this area of the northeast Atlantic, although the water mass is by no means homogeneous as regards depth, the upper layers are almost all moving in approximately the same direction. An oceanic flora and fauna is drifted over these banks, roughly in a northeasterly direction, but the specific content varies markedly from season to season and from year to year, and there is also a variation in speed of water transport and in the exact route taken. In some years, for example 1947, the North Atlantic Drift passes through the Faroe Shetland Channel to the Norwegian Sea with little or no inflow into the North Sea, while in other years the North Sea is strongly affected (Fraser 1952a). In some years there is a marked increase in the proportion of the Mediterranean outflow that flows northwards, so that the Lusitanian fauna which usually ceases to be apparent off the west of Ireland has been known - e.g. in 1953 - to pass on through the Faroe Channel and to reach Shetland (Fraser 1955). The speed of water movement varies considerably but it is mostly in the range of 2-6 miles per day.

The precise speeds of the water transport cannot be accurately stated for each locality as they are variable in so many ways, e.g. according to the position within the currents which are faster in the midstream, the depth, wind conditions, seasonal and annual changes. Nor is it possible to state precisely how long the planktonic phase lasts for any given species of fish, as this too is a very variable factor; it not only depends on the temperature and on other environmental conditions but there is real difficulty in defining when

this phase has passed. Too often there is a wide gap in our knowledge at just this stage; fish such as haddock disappear from the plankton collection at about 1 1/2 - 2 cm length and are found again on the bottom at 11 cm. Do they go down at 1 1/2 cm and are missed by the bottom sampling nets because they escape through the meshes, or do they remain pelagic until 11 cm but are too agile to be caught by the plankton nets? Thompson (1922) suggests the latter and Hickling (1946) suggests that haddock on Porcupine Bank take up a bottom living habit at a length of about 12 - 13 cm. Recent evidence using pelagic trawls with small mesh cod-ends adds weight to this, but the point at which they do in fact cease to be planktonic (i.e. more dependent upon drift than upon their own swimming powers) is by no means proven. For fish which are to some extent pelagic when adult such as cod, whiting, hake and *G. poutassou* Risso the end point of the planktonic phase is even more difficult to define. It is thus essential to work with some generalized figure and for this paper a 100 day period is suggested as a reasonable average for fish such as haddock, and indeed most commercial fish. Furthermore, it is debatable whether the young semi-pelagic fish could survive or not when carried out over deep water. Whiting (*G. merlangus* L.), for example, are not found over deep water by commercial fisheries, but this does not necessarily mean that they cannot survive there.

It is not necessary to give, in this paper, detailed lists of the plankton indicators, which species are recognized as characteristic of each of the water masses; but rather to use the evidence of the plankton as an indicator of the possibilities of an associated transfer of the pelagic stages of fish.

#### The Major Currents in the Area

Taking first the main inflow of the North Atlantic Drift we see (Figure 1) its broad path in the open ocean arriving near the European Shelf and splitting into two main sections, one going northeast to the Faroe Shetland Channel and the other eastwards along latitude 50°N and again splitting. The main part goes south between the Azores and the continental shelf and the other smaller part turns north along the Irish shelf to meet again the northern section which again splits to go on both sides of Rockall.

We have thus the major stream, which, since leaving the western Atlantic, has come some 3600 miles, and has crossed the mid-Atlantic ridge - the Faraday Bank area - on its way. The depths over this Bank are, however, all greater than 1000 m and mostly greater than 1500 m, and are therefore below the habitat or spawning depth of any of our normal commercial fishes. "Normal" here is, of course, important, as many species of bathypelagic and deep

water fish such as macrurids etc. would be able to spawn there and these may possibly contribute to a small extent to the commercial food catches. The total time taken for an organism, unaided by swimming, to cross the Atlantic by drift is probably some two years, and this time factor itself is enough to preclude the possibility of a successful transatlantic drift by the young of any of our normal fish. "Normal" is necessary here also, because of course the Leptocephalus of Anguilla does just this.

Looking again at the North Atlantic Drift currents, any eggs spawned in the small shallow areas round the Azores, Madeira, etc. will be carried south in the surface currents and so out of the area concerned in this paper, but larvae spawned and living in a deeper layer could be carried north in the Lusitanian stream. A survey of the life history of the important fishes, however, shows that the young of even the deep water spawning fish such as hake Merluccius merluccius (L.) and Gadus poutassou are found over deep water but mostly in the upper 200 metres.

Any transfer of fish larvae of commercial importance (except the eel) from one side of the Atlantic to the other, and in either direction, must be by easy stages, each stage involving a separate generation, and must be made by way of Greenland, Iceland, etc. and not by the North Atlantic Drift itself.

#### The Local Currents

Schmidt in 1909 dealt in a broad sense with the distribution and possible transfer of the gadoid larvae in the area between Iceland and Spain. The object of this paper is to extend and emphasize his findings with particular reference to the more local problems amongst the group of banks west and northwest of the British Isles, and to discuss the possibilities of (a) the stocks being self-contained, as opposed to (b) the interchange of larvae between the different banks, or (c) their dispersal to be lost to stock. Each of the banks of this area has, or has had, its fishery - trawl or line or both - and it is therefore of economic importance to understand any possible relationships between the stocks on the banks, or between the banks and the continental shelf.

In some areas horizontal eddy (Orton, 1937, Redfield, 1939, 1941) is held to account, at least in part, for retention of plankton over a local area. Vertical diurnal migration can also play its part, as, for example, when the organisms at the surface at night are drifted in one direction and in the daytime are returned by deeper currents running in the opposite direction. Convection currents can have a similar effect (Boden, 1952), or plankton carried off a bank by cascading water may be returned to it by migration into the surface current

(Boden and Kampa, 1953). In the area concerned, the southerly flowing boreal water is over 1000 m, often 2000 m depth, which is perhaps too deep for diurnal migration, but this deep water keeps to the deeper channels between the banks and could not return organisms over the banks even if they descended into it.

Although the general trend over this area is northerly there appear to be indications of surface reversal at times west of Ireland, taking drift bottles southward from liberations made on the routes to Weather Ships I and J from the Clyde. This may be due to a superficial cyclonic eddy system west of Ireland (Tait 1952) and may be an unusual emphasis on the eastern dispersal towards the Irish continental shelf where a southern swing can be regarded as normal (see Figure 1). Such a southerly tendency was particularly marked in 1950 and 1951 (Tait 1952, Cooper 1952a). Such a reversal should not have any very marked effect on whether the products of spawning on the actual bank at Rockall are retained there or not but might well affect the final area of distribution of products lost from Rockall Bank. A further possible exception to this northerly trend is in cascading waters, and Cooper 1952a suggests that the water at Rockall often has a suitable temperature and salinity to form a cascade. He pictures this as southflowing along the edge of the continental shelf at some 1200 m depth, and he suggests that this mechanism might assist in the survival of warm water plankton organisms that otherwise might have been drifted further north and east. This cascading is, of course, at its height in winter and should therefore be not much less than its peak at the season of maximum egg production, thereafter falling off in intensity as the larvae grow older.

The evidence we have so far from Scottish investigations would indicate that whereas Stomias, Myctophum, Maurolicus, Bathylagus, Nansenia and other bathypelagic fishes have very marked diurnal migrations, the pelagic stages of gadoids have a much smaller range and remain scattered as to depth in the upper 100 metres or so during daylight but concentrate into a narrower sub-surface band at night.

#### The Faroe Plateau

Of all the banks mentioned in this paper the only one that has been given serious attention in the problem of stock conservation or dispersal is the Faroe Plateau - the shelf surrounding the Faroe Is. - particularly by Saville (in press) for haddock. It is the largest of the banks considered here and it is an area of considerable importance for the spawning of haddock, cod and saithe (Gadus virens L.); and to a lesser extent for whiting (Gadus merlangus L.)

plaice (Pleuronectes platessa L.), lemon sole (P. microcephalus Donavan) and herring, as well as for a number of non-commercial species.

The region was fairly intensively sampled by Scottish research vessels in the spring months of the years 1950-53 inclusive with a view to investigating the planktonic phase of the haddock. Although a certain amount of data was collected relevant to other species, only haddock have been considered in any detail. The area is the centre of a fishery of some importance to Scottish and English fishermen, chiefly for haddock and cod. In 1951 Scotland's share of the haddock catch - approximately a half of the total for the area - amounted to 140,000 cwt. The water around the Faroe Is. is in a relatively static eddy system compared with the surrounding water and it maintains its own plankton population which is quite different from the typical oceanic character of the outside area (Fraser 1939, Hansen 1955). It contains an abundance of mero-planktonic organisms which have part of their life cycle as attached adults or bottom living species, and it also contains neritic holoplanktonic organisms. For example, the dominant Chaetognath is Sagitta elegans, a species associated with mixed oceanic and coastal waters, and this species is rare in the purer oceanic water off the plateau. Medusae of Bougainvillia, Aurelia, neritic copepods and larvae of inshore decapods are abundant on the plateau whereas the surrounding water contains the Chaetognaths Sagitta serratodentata, S. maxima and Eukrohnia hamata, medusae such as Cosmetira and Laodicea, Siphonophora, Thaliacea and other typical oceanic species. This plankton population amply confirms the hydrographic picture of a circulatory system round the islands (Tait 1934) and as this is adequate to retain a typical fauna it can also retain sufficient of the fish fry to maintain the stocks.

This has indeed been worked out in detail by Saville, whose investigations have shown that haddock spawn at Faroe from early March to mid-May with a peak intensity around the first week of April. Within the four years of his programme the variation in the beginning and end of the spawning season amounted to no more than a few days and could hardly be considered as significant.

As stated by Schmidt (1909) eggs of the haddock are to be found practically everywhere around Faroe. Saville found that the density distribution is however far from uniform - on every cruise during the spawning season three or four centres of high egg density occurred, outside which the numbers taken were small. These centres of egg density showed a marked constancy from year to year. The area centred to the north of the islands was clearly marked in all of the four years, whilst that in the Nolsó Bank grounds and that to the west of Myggenaes were clearly demarcated in every year except 1951 when the survey was rather too late to sample the main spawning peak. The existence of these distinct spawning loci was confirmed by the areas of greatest

density of mature haddock during the spawning season from the catches of commercial trawlers. It is noteworthy that each of these centres of spawning is situated near the edge of the shelf where the products would seem particularly vulnerable to displacement over the adjoining deep water; little or no spawning occurs close to the islands.

For each of the four years of the investigation an assessment was made of the total production of haddock eggs within the area. These assessments varied from  $50 \times 10^{11}$  in 1953 to  $70 \times 10^{11}$  in 1951 and are in reasonable agreement with an estimate of the comparative spawning potentials of the adult stocks of those years as gauged from commercial catches.

Unfortunately, the cruises were in all years too widely spaced in time to attempt to trace in real detail the drift of eggs and larvae from the spawning places. In April the larvae were still present as small dense patches which could be related to the spawning centres, but thereafter a gradual dispersion occurred so that by June larvae were scattered practically all over the shelf - a result compatible with a cyclonic eddy system around the islands as postulated by Tait (1934) for this area. Only in 1950 was the picture rather different. In that year the normal pattern of events prevailed up to May although the larvae in that month were more concentrated on the southeastern portion of the shelf than in other years. By June haddock larvae were very scarce and those few which were taken were found along the edges of the shelf preponderantly on the eastern side. Carruthers and his collaborators (1951) in the North Sea, and Walford (1938) and Chase (1955) on Georges Bank, have shown the importance which wind induced drift may assume in determining the fate of the planktonic stages of various fish stocks. In the light of these results Saville examined the wind conditions at Faroe in relation to the scarcity and distribution of haddock larvae there in June 1950. The records showed that in that year the westerly wind component was unusually strong in the months of March, April and June compared with the other three years of this investigation. It appears possible that this prevalence of winds from the west may have resulted in the loss of the bulk of the larvae spawned in the Faroe region in 1950 by drifting over the deep water to the east.

The distribution of larvae suggests that in normal years they are retained within an eddy system around the islands but exceptionally, as in 1950, they may be displaced off the Faroe shelf perhaps by the agency of persistently strong winds from one quarter. Saville finds support in other aspects of his data. An attempt was made to estimate the mortality rates of the haddock spawning products during the planktonic stage by following homologous groups from cruise to cruise in each of the four years. These rates were on the whole fairly consistent in the years 1951-53 with mortalities of about 10% per day from eggs to early larvae and 4% per day during the post-larval stage.

These mortalities are comparable with those found for similar stages of other species of fish in other areas, and taken in conjunction with the fact that the broods derived from them were in the benthic phase at least up to the normal strength, they would not seem consistent with any major loss of planktonic stages from the area by mass transport. In 1950 the results of the mortality calculations were rather different. Those eggs spawned in early March of that year showed a reduced mortality for this stage of 5% per day. The eggs spawned in April however - by far the greater part of the annual production - showed an egg mortality consistent with that of the other years at 10% per day; but the larvae derived from those between May and June suffered depletion at the rate of 10% per day also - more than twice the rate found for this stage in the other years. The significance of this observation is borne out by the subsequent rather poor showing of this brood in the demersal stage.

Saville (1956) used the numbers of larvae caught in June in the area as the basis of an index of larval abundance in that month to relate to the subsequent assessment of recruitment to the years brood from trawl catches. The larvae caught in this month covered a wide size range and the mean size varied somewhat between years. To give an adequate comparison between years the numbers caught in each year were, from a knowledge of the mortality and growth rates, first converted to the equivalent number at a standard size and then to the mean number at this size below 10 sq. metres of surface. The numbers obtained in this way for the years 1950, 1952 and 1953 were 1.2, 2.4 and 2.7 respectively. (This could not be done for 1951 because there was no June cruise in that year). Jones (1951) and Jones and Main (1953, 1954) give estimates of the density of haddock in their first year of life at Faroe for these year broods as being 228, 488 and 495 respectively. It will be seen that there is a very satisfactory degree of agreement in the relationship between these years in the two sets of data. Saville suggests that, in these years at least, after June no appreciable loss of haddock larvae from the area occurred.

The conclusions to be drawn from these four years' work at Faroe can perhaps best be summarized thus: Haddock spawn at Faroe between March and mid-May in three small distinct areas situated towards the edge of the shelf. In normal years (1951-53) the subsequent course of events is a gradual dispersion of the products of these spawnings within the eddy system leading by June to a generalized distribution of the larvae all over the Faroe plateau. During this period they undergo a gradual depletion at rates comparable with those found for the planktonic stages of fish in other areas and compatible neither with a significant gain from an external source nor with a major loss of those spawned within the area. The larval abundance in June within the area is proportional to the subsequent abundance in the first year of demersal life so that no significant loss or gain can occur thereafter. The course of events in 1950 showed spawning in the normal centres but by May the larvae

had become largely concentrated on the southeastern side of the shelf and by June were markedly scarce, the few which were taken being distributed preponderantly on the eastern edge of the shelf. The mortality pattern followed more or less the normal course up to May but between May and June it was at more than twice the "normal" rate and the brood was subsequently below normal abundance in its first year of benthic life. This year was one of unusually prevalent westerly winds and all aspects of that year's data can perhaps best be explained by ascribing them to a gradual easterly displacement of the spawning products off the shelf and over the deep water to the east under the influence of these winds.

There is evidence, of course, of loss of plankton as well as of fish fry. Wiborg (1955) has demonstrated a drift of Temora, Evadne and Podon from the Faroes to 65°N, and Evadne from thence to Jan Mayen and Norway. Hansen (1955) has traced this water movement and plankton dispersal not so much by the actual species present as by the proportions of the species from one area to another.

#### The Other Outer Banks

The remainder of the banks which have not been so well investigated can now be considered, and it is perhaps reasonably logical to consider them in geographic order in the direction of the main currents, i.e. from SW to NE. Porcupine Bank has a fishery for hake, witch (Pleuronectes cynoglossus L.) and ling (Molva molva L.), and some haddock are caught there, though this is a fishing which has declined in recent years. The plankton in this region shows that part of the Mediterranean outflow, as a Lusitanian stream, flows on either side of the bank, but over the bank itself there is little or no Lusitanian influence, but only the oceanic waters of the North Atlantic Drift. This accounts for the slightly lower bottom temperature quoted by Hickling (1946) on the bank compared with that in the deeper water between the bank and the Irish coast. No evidence of a surface eddy has been seen in the plankton but Cooper and Vaux (1949) and Cooper (1952a) suggest a possible transmission of cascaded water from there towards the continental shelf, and Cooper figures this water between the North Atlantic Central water and the Gibraltar water. Eggs and larvae from any spawning on Porcupine Bank will therefore be carried N or NNE with a tendency to be taken on to the continental shelf off the N. W. of Ireland (some 200 miles) or Stanton Bank north of Ireland (some 300 miles); or they may possibly be taken by cascaded water SE to the continental shelf off the S. W. corner of Ireland (some 300 miles), but there does not seem to be much chance of them reaching the Rockall Bank area even though it is only about 250 miles away. Adopting the suggested figure of a 100 day planktonic phase,



and with speeds of 2-3 miles per day both the continental shelf and Stanton Bank are within the possibility of reach. Larvae of non-pelagic fish carried off the bank but not dispersed to the east will have little chance of survival.

It would thus seem that maintenance of the stock of fish on Porcupine Bank must be by young or adult migration from the Irish continental shelf, to which the bank is connected by a wide area of 250-300 metres depth. The present evidence indicates that this depth is not the unsurmountable barrier to adult haddock that Raitt (1939) suggested, and it should not be a barrier to the migrations of young fish still in the pelagic (not planktonic) phase. On the other hand, Hickling (1946) stated that his data "gave some reason for believing that the haddock on the Porcupine form to a large degree a self-contained stock, though doubtless with much exchange with the haddock of the Irish coast". His data are based on the abundance of marketable fish on the bank compared with similar depths to the east of the bank and on growth rates which indicate that fish on the rich feeding ground of the bank have lived there since first going to the bottom at 12-13 cm. The probability that Porcupine Bank haddock go to the bottom at a different length from those on the Irish shelf in itself suggests that they have either been feeding in an area of richer plankton or that they have migrated in the post-planktonic stage. Hickling suggests that as the two dominant brood years of haddock over the period investigated were 1938 and 1942 the latter have been produced by the spawning of the 1938 brood on the bank. There is evidence to suggest, however, that a successful new brood is not so much dependent upon the number of spawning females as on environmental factors (Parrish 1950). It thus could be that the 1942 haddock brood on Porcupine Bank is correlated with conditions which encouraged a more successful migration of the pelagic stages before they sought the bottom. It is obvious, then, that there is much to learn and much to discuss and that neither of these two theories can be regarded as the complete answer.

Rockall Bank, the next to consider, is a large area, some 60 x 30 miles of which have depths of less than 200 metres, shelving fairly steeply to the east but rather more gently on the other sides. There is thus a fairly big trawling area surrounded by a large area too deep for trawling but suitable for lines. On it we have a trawl fishery for haddock, etc., and a line fishery for halibut, ling, etc., but little or no hake fishery (Hickling 1928). Rockall Bank acts as a divide for the North Atlantic Drift which splits with a main branch to the north and a smaller branch to the south which then turns north along the east side to join the main branch further north. The Lusitanian stream, when it persists so far is usually confined to the east side, but is occasionally found also to the west. It is here still below the North Atlantic Drift and is unlikely to take part in any initial transport of fish larvae from Rockall. The Atlantic water is mainly in streams in the upper layers on both sides of the bank, but off the edge. Thus the plankton on the bank, although oceanic in character, is

not of the same constitution as in the streams, and it shows evidence that there is relatively static water there, probably in the form of a local eddy. It is just such conditions as these that Cooper envisages as ideal for winter cascading. If this does in fact occur here some eggs and larvae would be carried down the slopes into deeper water, either remaining in the cascaded Rockall water and so being lost - this water probably moves very slowly in the channels - or by migration finding their way into the Lusitanian or Atlantic water and so being transported north and east towards the Faroe Shetland Channel, with chances of dispersal over the Scottish continental shelf or on to Rosemary Knoll. There is however a good chance that they will remain in the eddy system. The products of a spawning on the west or southwest of the bank in particular will be slowly carried over the south of the bank, along the east side and so be retained in the stock, journeys of up to 200 miles without leaving the bank could well be involved thus giving time for the eggs to hatch and for the larvae to reach the demersal stage. This suggests that, although an indigenous fish population at Rockall could maintain itself, it is periodically likely to suffer a serious loss by egg and larvae being drifted away, and that there is little chance of larvae from elsewhere adding to the stock. The channel depths between Rockall and the continental shelf exceed 2000 m and between Rockall and Rosemary Knoll are 1500-2000 m. This is almost certainly too great for any general migration of adult fish, except deep water or pelagic species, so that the stocks of fish such as haddock on Rockall Bank are probably self-contained. (Young haddock 4-10 cm have been taken on Rockall as late as July, and it seems reasonable to suppose that these have in fact been spawned on the Bank). Such a theory receives support from the quality of the haddock themselves which are soft-fleshed and recognizable as Rockall fish by those accustomed to handling them.

Rosemary Knoll. The next banks of any size to consider are Lousy Bank and Rosemary Knoll. Rosemary Knoll is the deeper of the two and topographically the more isolated. It has a line fishery of no great importance for deep water fish such as ling, halibut and tusk (*Brosme brosme* (Müller)). The depths are mostly between 500 m and 700 m and it is surrounded by water of over 1000 m and reaching almost 2000 m in depth. From its position it could be assumed to be a possible area of reception of stock of relatively deep water fish such as tusk and ling from Rockall, but it would appear to be too deep to support a haddock population. Any haddock drifted from Rockall in this direction will therefore be irretrievably lost unless they can make the 400 mile journey to Faroe Bank or the Faroe Plateau, or be carried in the easterly surface dispersal to the Scottish continental shelf as previously suggested.

Lousy Bank about 200 miles north of Rockall and 170 northwest of Rosemary Knoll has depths of less than 200 m. It would seem that the main North Atlantic Drift passes to the south of Lousy Bank and on towards the Faroe

Shetland Channel whilst another branch continues NE to the north of Lousy and towards the NW of Faroe. The deeper channels north and south of Lousy Bank have their bathypelagic fauna which is absent in the water on the bank so that there is little evidence of upwelling on the edge, but the surface Atlantic flows over it more or less uninterrupted and without an eddy. The conditions for cascading are thus not so likely to be reached there as on Rockall. There is a large eddy to the north of the stream north of Lousy and it might be remotely possible for larvae from a spawning on this bank to be carried round in it and returned some two months later, but this would appear to be far too chancy a route to suggest that it could be of any significance in maintaining a spawning population of fish on the bank.

Lousy Bank is, however, connected through a relatively shallow trough to Bill Bailey Bank and Faroe Bank, the depths of this trough being 500-600 metres, and it is therefore probable that the stocks on Lousy Bank are recruited from Faroe Bank across this trough. At one time it was thought (Thompson 1922, Raitt 1939) that this is too deep for haddock migrations but it is now considered to be within their limits as longliners get haddock from depths of 200-250 fm (500 m). The main drift of fry from any spawning at Lousy Bank would be directed into the Faroe Shetland Channel with slight dispersal possibilities to Faroe Bank (300 miles) and rather greater possibilities to the triangular area of the Scottish continental shelf between Shetland, Orkney and the Butt of Lewis, 200-300 miles. Speeds of 6-10 miles per day in the Faroe Shetland Channel are fairly normal, exceptionally reaching 14-15 miles per day and up to 20 miles per day in stream currents (Tait 1957) so that distances of 600 miles or more, and so into the northern North Sea itself, are possible.

Bill Bailey and Faroe Bank. Taking these two, and the small associated banks, as one, there is a large area shallower than 300 m which in part of Faroe Bank is less than 100 m in depth. Both lining and trawling are carried out here and there are populations of cod, haddock, ling, tusk and halibut. Although the plankton over these banks is oceanic there is a marked change in the number of oceanic species both to the north and to the south, which suggests that the main streams bypass the area and that flow across there is much reduced, but nevertheless that it is a flow and not an eddy. Fry will thus be lost to these grounds by drift towards the east and southeast into the Faroe Shetland Channel, with dispersal possibilities on to the Shetland grounds (250 miles) and also on to the Faroe Plateau; they have little chance of being retained in their original area. Recruitment can be assumed by adult migrations from the Faroe Plateau, for although the channel has a strip of over 500 m depth this strip is very narrow and does not reach 500 m at the northern end.

There is evidence, therefore, as far as the young of commercial demersal fish are concerned, that of these banks only Rockall and Faroe Plateau can

be considered with certainty as self-supporting; Porcupine Bank doubtfully so while there is little chance of young fish from spawnings on the other banks remaining to grow into adults. There is a possibility however that fry drifted from these banks will not be entirely lost, though it is certain that many will. From Porcupine Bank larvae might eventually be able to settle on the Irish continental shelf or Stanton Bank; from Rockall on the Scottish continental shelf, and from Lousy Bank, Bill Bailey and Faroe Bank on the Faroe Plateau or Shetland.

This is confirmed to some extent by the presence of small larval haddock taken in the oceanic plankton collections over deep water, i.e. away from their spawning grounds, and by the presence of larger young fish, at about the limits of the pelagic phase - up to 11 cm - taken in pelagic trawls in the Faroe Shetland Channel and over banks such as Bill Bailey Bank, where it seems most unlikely that the fry could remain for several months. Henderson (1953) also reports gadoids (other than G. poutassou and other deep water forms) 30 -50 miles outside the 100 fathom line.

From a direct commercial aspect it is doubtful if the drift of fry from one of these banks to another or on to the continental shelf will be of sufficient magnitude to affect the normal stocks except under special conditions, but there may be other considerations. For example the effects of an unfortunate series of disastrous brood years in a small isolated population might be saved by quite a small replacement from outside - indeed it is by some such way that these populations must have been started. The soft condition of the isolated Rockall haddock has been mentioned; the causative factor is not known, but it seems connected with the isolation of the stock. Further, isolated stocks could be subject to a different degree or type of parasitism, and there is evidence to support this in the distribution of Grillotia erinaceus, a parasite of the halibut, where there is a different degree of parasitism in the southern, central and northern banks (B. B. Rae - personal communication). The parasitism of the gadoids may be worth investigating from this point of view, and might produce useful evidence towards indicating possible stock relationships on the various banks.

#### Oceanic Fish

Considering now those fish which are more oceanic in character, we find a different situation, primarily because of the greater depth range acceptable as an environment to the adults. Gadus poutassou, for example, is common in the Mediterranean and throughout a wide area off the edge of the continental shelf from there to the Norwegian and Barents Sea, Jan Mayen and S. W.

Iceland. It is a fish which is to a high degree pelagic in the upper or middle layers over great depths (Schmidt 1909). Its spawning is also widespread in deep water, but would appear to be much more dense in the southerly part of this range and in early spring. Henderson (1953) found the young larvae, 5-10 mm in length, in numbers in the Rockall area, but distinctly more numerous over the centre of the passage east of Rockall than over the bank or west of it. He also found them west of Ireland, again just off the edge of the shelf. These findings suggest a northerly drift from a more southerly spawning at the edge of the shelf and not in or over the deeps of the North Atlantic, and thus confirm Schmidt's theories. The drift of larvae of G. poutassou in 1955 was investigated by the Scottish research vessel "Scotia". The results showed that the larvae first followed the path suggested by Henderson, i.e. from the south, and most abundantly east of Rockall, and thence northward splitting into two branches, the one penetrating the Faroe Shetland Channel and the other passing northwards to the west of Faroe crossing the Faroe Iceland ridge to the Norwegian Sea. In 1955 the oceanic water responsible for the drift of the young poutassou was densely populated with salps - as Schmidt (1909) had also found - and the distributions of these two organisms coincided over the area investigated so closely that it would be reasonable to assume that the final distribution of the salps would represent the possible distribution of the poutassou. "Possible" is here used instead of "probable" as two factors must be taken into consideration; that the salps in 1955 reproduced enormously within the area so that the increased population would be able to cover a wider area, and that as the young fish become older they will more and more cease to be drifted as their swimming powers increase. This distribution would take them, in 1955, well into the North Sea, Norwegian Fjords, S. W. Iceland and Jan Mayen.

It seems certain, in view of this distribution, that stocks of G. poutassou in the Norwegian Sea, Iceland, Faroe, Shetland, northern North Sea, etc. could be derived largely, if not entirely, from southern spawnings. As this drift varies from year to year the northern stocks of adult poutassou will be dependent upon this factor in addition to those normally operating on recruitment from eggs and larvae.

Although the northerly stocks of G. poutassou are fished only incidentally to other commercial fisheries they are of great importance as food for hake, and Hickling (1928) goes so far as to suggest an association of high catches of hake with the spawning of G. poutassou. There is a definite fishery for them in the Mediterranean and off the Iberian coasts. The Iberian stocks would also seem to be derived from a distant spawning, in fact from roughly the same area as the northerly stocks, i.e. the edge of the deep water extending from the west of Ireland to the north of the Bay of Biscay. Though it is not yet known, it could be that both stocks are derived from the same spawning ground,

the eggs from the southern part being drifted south and from the northerly part being drifted north by the branches of the North Atlantic Drift. If spawning is in deeper water, and not in surface or sub-surface waters, the Lusitanian stream would disperse the fish towards the north until they arrived at a suitable position for the North Atlantic Drift to have the dominant directive force, the end result being similar.

This southern stream in the Bay of Biscay towards the Iberian waters is probably also responsible for the small stocks of haddock and saithe which are occasionally found there. There is no evidence of any spawning of either of the species there and it also seems unlikely that their presence is due to adult migrations.

Whereas the young of most Gadoids have a rather short planktonic life that of Gadus poutassou is prolonged, and indeed there is probably no sharp break between the planktonic young stage and the free-swimming adult which is also partly pelagic. It is thus possible for this species to be carried the long distances suggested, and that the whole NE Atlantic stock is of the same race; with the probable exception of the Barents Sea stock (Boldovsky 1939) which does not seem to fit the Atlantic data and so may be a separate self-contained community, or derived from a spawning area not yet found (Henderson 1957).

The hake is another gadoid with a deep water spawning at the edge of the continental shelf, but in this species the planktonic stage is shorter, so that although the first general distribution is likely to follow that of G. poutassou the final dispersal is much less dependent upon drift than on migration and is therefore less widespread. There is no evidence of hake spawning at Faroe or Iceland, but there is a spring spawning off the Irish coast and a summer spawning off the North of Scotland (Hickling 1928). Following the lead of G. poutassou there should be scope for the larvae to be drifted to the SW of Iceland, but because of the shorter planktonic stage young hake have never been found there although older fish have been taken on rare occasions (Saemundsson 1949). It can be assumed that these were adult migrants. Hake are, however, occasionally abundant in the deep water east of Shetland; as the distances are so much less, these could possibly be associated with the north Scottish spawning grounds, but the situation is complicated by adult migrations, and Hickling (1928) considers them to belong to a self-contained stock.

Unpublished work on Gadus esmarkii in the Irish Sea area by Gokhale, and in the northern North Sea area by Mason, suggests that this species leaves its feeding grounds in these areas and migrates to spawning grounds in the spring to the north of Ireland or west of Orkney and Shetland. The young are then gradually drifted back, and are found at 5-6 cm length in the northern North Sea in September and as far south as east of the Firth of Forth in November

and December.

So far, fish which can be drifted only in their young stages have been considered, but it is perhaps worthwhile to call brief attention to the effect of currents on the distribution of adult fish (omitting for this paper the true pelagic fish), even though few of them are of commercial importance.

A fish that perhaps deserves special mention here is Capros aper which Cooper (1952b) has regarded as a possible indicator of a special type of water movement. This fish has its normal habitat in the yellow coral area of marine canyons 200-500 metres depth. Strong on-slope winds cause vertical oscillations and these may produce a violent eagre or bore in the canyon which could dislodge Capros to be distributed on the shelf. When this happens numerous Capros are to be found out of their normal habitat; the odd few fish that are often to be found do not suggest such an occurrence.

Fish like the Scopelids, Stomias and marine salmonids such as Nansenia are known to have extensive diurnal vertical migrations and are found in the water layers at 200-500 metres during the day and in the surface layers at night. Fish such as these are partly dependent on currents for their distribution at all stages of their life, but because of the great depth range and tolerance will be affected by the deeper currents as well as those in the upper layers. It might here be appropriate to raise the question of whether or not fish, which so far as we can ascertain are quite out of touch with the bottom, can appreciate a slow, relatively homogeneous movement of the whole water mass in which they live. Can such fish "make use of" a current or swim contranatanly?

Finally, and without going into details, the currents are responsible for the distribution of those unusual occurrences of species out of their normal habitat. Fish generally recorded as "rare fish" can often be regarded as indicators of the distribution of a particular type of water mass. Whether these fish are drifted or swim along the currents is, again, a debatable question, varying perhaps from one extreme to another between fish such as the sun fish (Mola) and other relatively quiescent fish, to tunny which is certainly not "drifted" into the North Sea and Skagerak.

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Author's Abstract \*

Size at maturity and meristic characters of redfish from the Gulf of St. Lawrence are intermediate between those of the Gulf of Maine and the more northern European areas. Redfish are abundant in the Laurentian Channel in the region southeast of Seven Islands, but scarce west of this. The narrow size range (33 to 41 cm) of the large, mature redfish taken in the Gulf of St. Lawrence is due to a southerly drift of larvae away from the spawning area, to an accumulation of old, mature fish, and to a differential distribution by sizes. The last is considered to be of primary importance. The availability of redfish on the bottom shows seasonal variations and catches were largest in the autumn. Redfish feed off the bottom and the dominant food for the sampled areas was the bathypelagic euphausiid Meganyctiphanes norvegica. Smaller catches of redfish at night in bottom trawls are attributed to vertical movements.

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OBSERVATIONS ON SUPPOSED INTERMINGLING OR A CERTAIN CONNECTION BETWEEN SOME STOCKS OF BOREAL AND SUBARCTIC DEMERSAL FOOD FISHES OF THE EASTERN AND WESTERN ATLANTIC. 313

Å. Vedel Tåning.

The question concerning an exchange or connection between fish stocks of the eastern and western Atlantic must be somewhat more restricted than the title indicates. We will here consider only marine teleosts, and none of the true archibenthal and abyssal species which have a certain natural possibility of transatlantic dispersion. On the other hand, although we exclude pelagic fishes (these, too, having a great possibility of transatlantic dispersion), it will be natural just to mention the herring because it is intimately connected to the shelf during the spawning period. A perusal of a synopsis of North Atlantic fish species will show, however, that we ought to exclude all oceanic fish species, pelagic or demersal.

The review comprises especially the boreal and subarctic food fishes because the (very few) arctic species have a rather continuous distribution from the east Continent to the west continent. The tropical-subtropical demersal food fish fauna, in turn, includes very few species common to the eastern and western Atlantic, because the isolation dates back to very ancient times and the current systems are unfavourable for transportation of pelagic fry with a very rapid development as tropic and subtropic species generally have. Only a few representatives are for instance common to the mediterranean-lusitanian (-Mauretanian) and the subtropical West-Atlantic subregions: e.g. Red Porgy (Pagrus pagrus), the Bluefish (Pomatomus saltatrix), and probably the Wreck fish (Polyprion americanus), but these may, however, enjoy long pelagic periods, which would explain their exception of character. A present day important interchange is however not likely.

The typical boreal food fishes common to the eastern and western Atlantic are the following: cod (Gadus callarias), haddock (Melanogrammus aeglefinus), coalfish (Pollachius virens), cusk (Brosme brosme), halibut (Hippoglossus hippoglossus), witch (Glyptocephalus cynoglossus) and cat or wolf fish (Anarhichas lupus). Nearly all of these are known to be able pelagic migrants; there is also the pelagic coastal bank herring (Clupea harengus) and the lumpsucker (Cyclopterus lumpus). As a general rule the mediterranean-boreal fish species, which have their southern boundary in the Mediterranean proper, are only exceptionally able to cross the Atlantic, obviously because their temperature demand during certain stages of development cannot generally be satisfied along the only available communication route, viz. the submarine North Atlantic Transversal Ridge from the British Islands to arctic Canada.

It is obvious that the re-establishment of the west-Atlantic boreal fish fauna after the Glacial Epoch took place from the east-Atlantic stocks of boreal

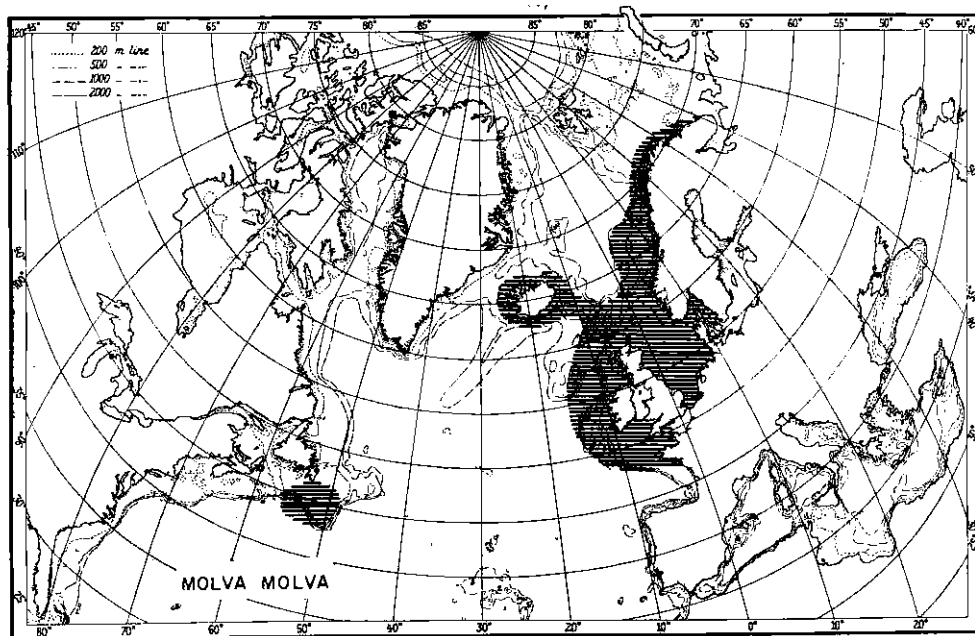


Fig. 1. Distribution of Ling *Molva molva* (L.).

and mediterranean-boreal fishes, and that the American boreal fish-fauna was much more reduced then than now, both qualitatively and quantitatively. It seems likely, however, that the recovery of this American boreal fish-fauna is still progressing. In recent years some few eastern boreal or mediterranean-boreal species have been for the first time recorded from the western Atlantic. The ling (*Molva molva*) was recently recorded from Newfoundland (Templeman and Fleming 1954), though it has not yet, as far as I know, been found as adult in Greenland waters nor as postlarva in the western Denmark Strait. (The specimens recorded from West-Greenland by Jensen (1948) as this species are *Molva dipterygia dipterygia*). The Blue Whiting (*Micromesistius poutassou*) was first recorded from the western Denmark Strait by Thor Iversen (1936); then it was found by Dr. Paul Hansen in southern West-Greenland in 1947, and it is now recorded from Georges Bank by Bigelow and Schroeder (1955). These specimens differ in no characters from the east-Atlantic specimens. It is reasonable to look upon such a conquest as caused by the present climatic change though other factors may as well be involved, e.g. a prolonged pelagic larval life, and the semi-pelagic life of the adult. It remains possible, but not likely, that the species was missed by all previous East-American ex-



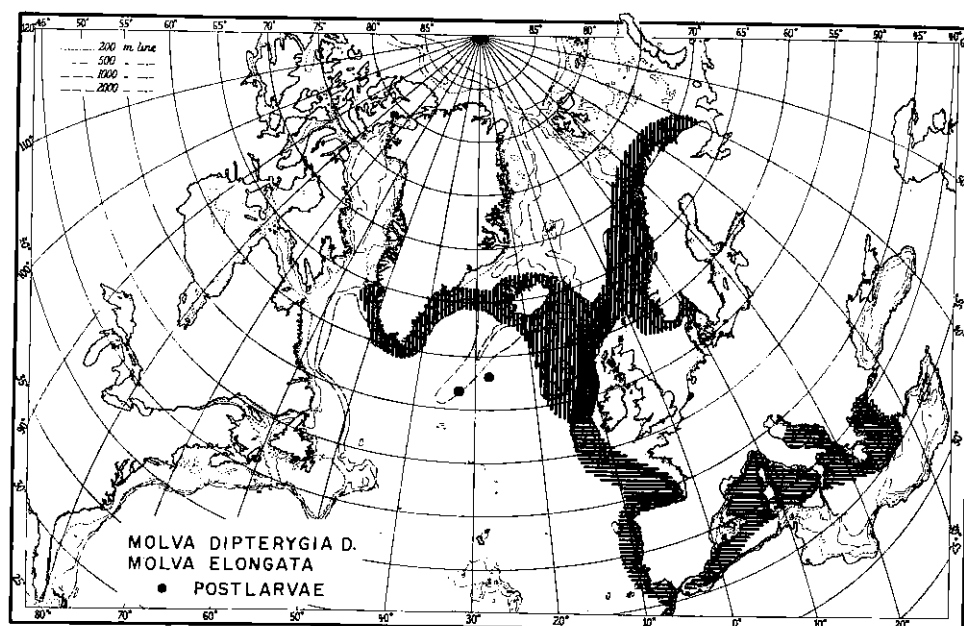


Fig. 2. Distribution of the Ling species Molva dipterygia d. (Penn.) and Molva elongata Risso.

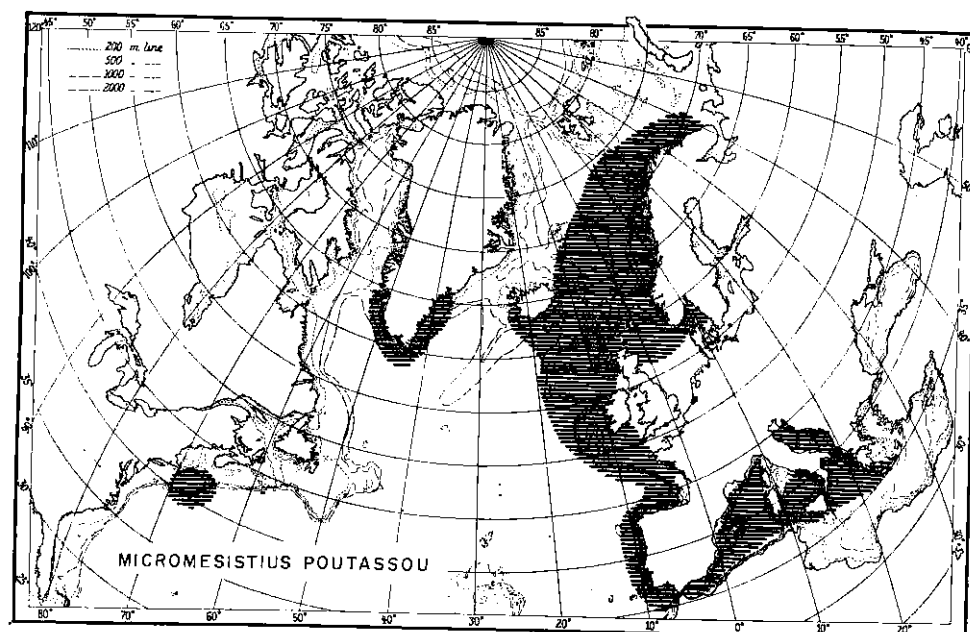
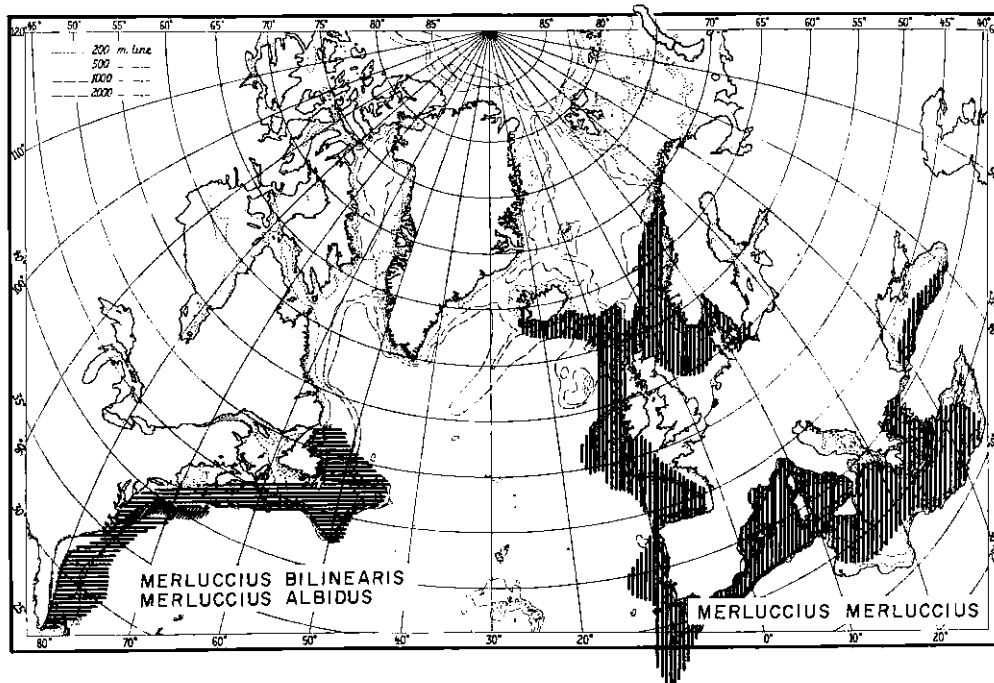


Fig. 3. Distribution of Blue Whiting Micromesistius poutassou (Risso).



**Fig. 4.** Distribution of the Hake species Merluccius bilinearis (Mitchill) M. albidus (?) and M. merluccius (L.).

peditions. It should also be stressed here that this genus (Micromesistius), Urophycis, Gaidropsarus, and Merluccius are the only Gadid-genera which have been able to disperse to the southern hemisphere, owing to some special advantages for long distance dispersal.

Other finds are also in favour of a present-day emigration to the west over the northern highway. Some species previously unknown from Iceland waters have been found there during the present warm period, e.g. some other East-Atlantic Gadids, Gadiculus argenteus thori and Pollachius pollachius.

Furthermore, the modern conception of the hake-question of American Atlantic waters is of interest in this connection. The species known previously from these waters, Merluccius bilinearis, is a rather divergent relative to the European M. merluccius. Recently however Ginsburg (1954) and Bigelow and Schroeder (1955) have shown that a "new", previously overlooked species, is also found here and is very common; this species is much more closely

related to the European species than M. bilinearis (I would prefer to call it a geographical race of M. merluccius). Ginsburg thinks that Mitchill's M. albidus (described 1918) was this species.

Similar distribution and probably similar dispersion from east to west in a favourable climatic period, (possibly after the Glacial Epoch?) is shown by some other mediterranean-boreal species, e.g. the angler fish, Lophius piscatorius, with its American partner (L. americanus), and the Black bellied rose-fish (Helicolenus dactylopterus), which as far as we know does not differ from its progenitor in the East. The factors which have permitted (and still permit?) such emigration may be those mentioned: prolonged pelagic larval stages, semi-pelagic tendency of adults, and favourable climatic conditions on the northern highway.

Species or even genera with a boreal pattern of distribution, which do not possess such advantages, have not been able to emigrate. This is the case for instance with nearly all species belonging to the Pleuronectiformes, of which only very few (e.g. the Dab, Limanda limanda) have closely related east American partners. Only three species of this group are common to the eastern and western region, viz. the halibut and the witch (Glyptocephalus cynoglossus), as well as the Long Rough Dab (Hippoglossoides platessoides) which, however, is rather more subarctic than boreal, and is split into an eastern and a western race (limandoides and platessoides).

Turning now to consider the possibilities of a migration or drift from the West-Atlantic region to the East-Atlantic region, it is obvious that the hydrographic conditions are rather adverse to transport of demersal boreal species. The eastgoing branch of the Labrador-current (mixed with Atlantic current water) might transport subarctic and certain boreal species, if the distance between the shelf in west and east were not so great, but any appreciable change is rather incredible. Probably pelagic larvae of halibut may be able to cross the distance, and also redfish (which, however, are pelagic or semi-pelagic also as adults). Two West-Atlantic boreal ground-fish have, however, carried out a transatlantic migration on a small scale, namely the squirrel hake (Urophycis chuss) to the waters west of Ireland, and the white hake (U. tenuis) to the Iceland and Greenland area (Saemundsson's Phycis borealis, described in 1913, is evidently this species). We do not know if the crossing is carried out by the white hake as postlarva or as adult, but most likely as postlarva.

The Atlantic current proper is, as we know, a conveyor of several sub-tropic fishes to European waters from Gibraltar to the northern seas (sail fish (Istiophorus americanus) and many other oceanic species). Its importance for the transport of eel-larvae is well known; less well known is the fact that

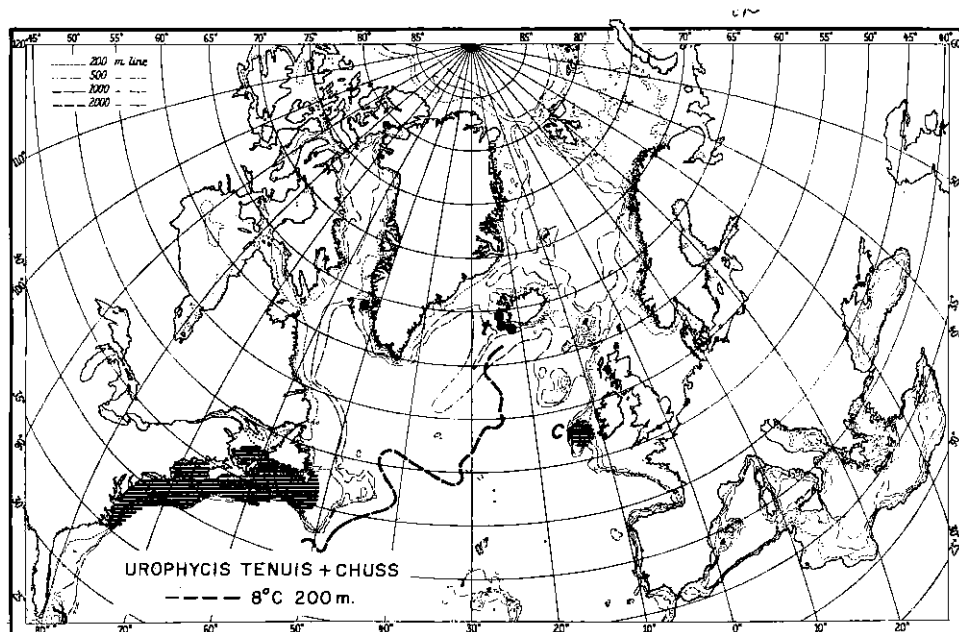


Fig. 5. Distribution of White Hake - Red Hake *Urophycis tenuis* (Mitchill)  
- *U. chuss* (Walbaum).

the larvae of the American eel may also go astray with this current to Europe. There is, however, no evidence of transport of demersal ground fish of sub-tropic origin to the east.

The preceding information has now given us a general view of the characteristics which the species of ground-fish had to possess if transatlantic transport was to have been possible in some earlier period, or must possess if still feasible. We may emphasize the following as most important:

- (1) The species should belong to the boreal (and subarctic) group of fish; less successful are species of the mediterranean-boreal group, probably because the latter species require a somewhat higher temperature during the period of propagation.
- (2) Species with a prolonged pelagic postlarval life are favoured during the passive drift over considerable distances with the prevailing oceanic currents.

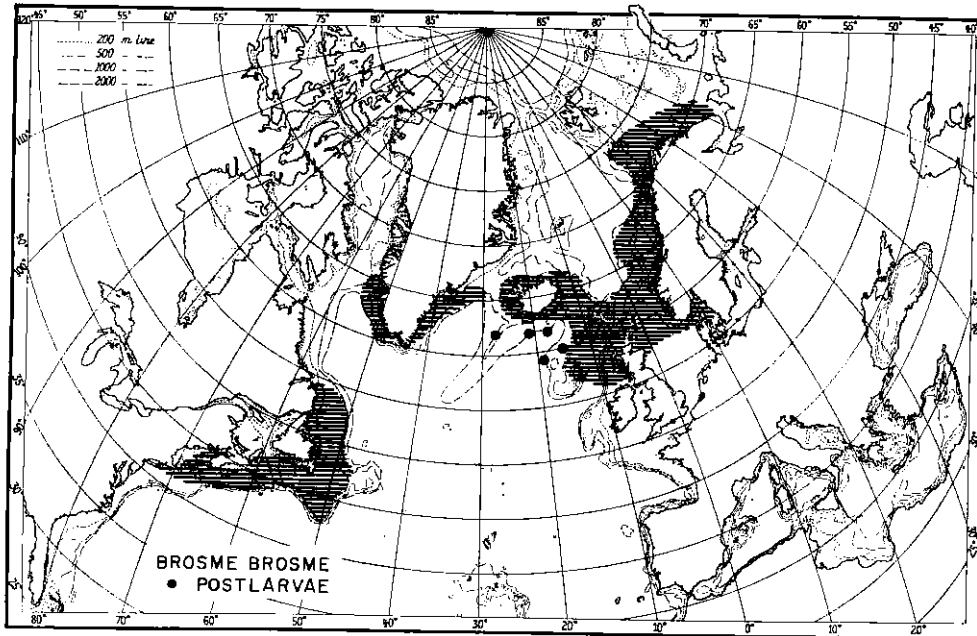


Fig. 6. Distribution of Cusk *Brosme brosme* (Müller).

- (3) Species with a tendency to pelagic habit as adults are more successful than continuously demersal species.

It cannot be denied that the conclusions drawn from faunistic data in the preceding pages are rather hypothetical, and that more facts are badly needed. Actual observations on migration or drift of the species involved over very great distances are very scarce, although from the northern highway we possess some more detailed information; we will consider these a little closer to see how far we are entitled to adopt some of our conclusions or whether the misgivings connected with some of the hypotheses compel us to reject them as of no or little value. Some other topics ought, however, first to be mentioned.

Even if the direction and speed of the currents which may carry fry westwards on the northern highway are advantageous, it is difficult to prove that fry met with on the route will survive to settle in favourable surroundings. We know far too little about the longevity of fry which have drifted off the coastal banks. Is a prolongation of the pelagic stage possible, for instance, as happens with some invertebrates which to a certain degree continue life until the

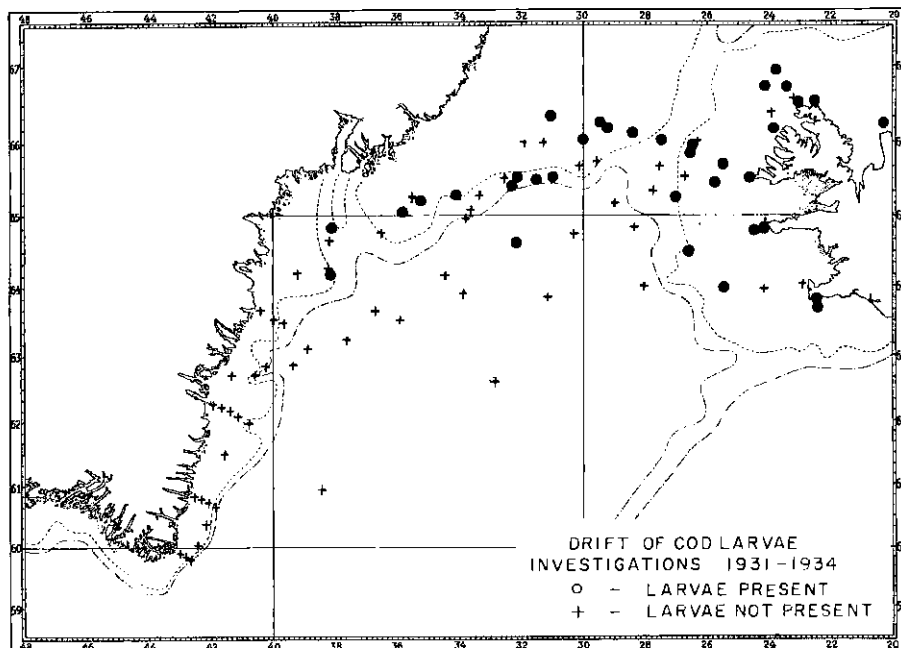


Fig. 7. Observations of larvae of Cod *Gadus callarias* L. in the area between Iceland and East Greenland, 1931-34.

water, bottom, etc. have the qualities required for their metamorphosis?

It is obvious that great alterations have occurred in the distribution of the northern fish fauna during the present warm period. This is probably caused by the drift of fry to uninhabited new areas or the immigration of adult or adolescent stages to these areas. Such a drift or immigration hypothesis suffers, however, from a shortcoming difficult to disprove. There may have been an insignificant, overlooked perennial stock living locally in such an apparently uninhabited area which, during the improved climatic conditions, may have prospered rapidly. Among invertebrates examples of this are not rare.

When, as in recent years, we have records of several species either as new in the West-Greenland area or increasing rapidly there in number, it is very difficult to determine whether this is caused by a new immigration from the Iceland area or whether an insignificant perennial stock has flourished owing to improved conditions. A comparison of the meristic characters of the

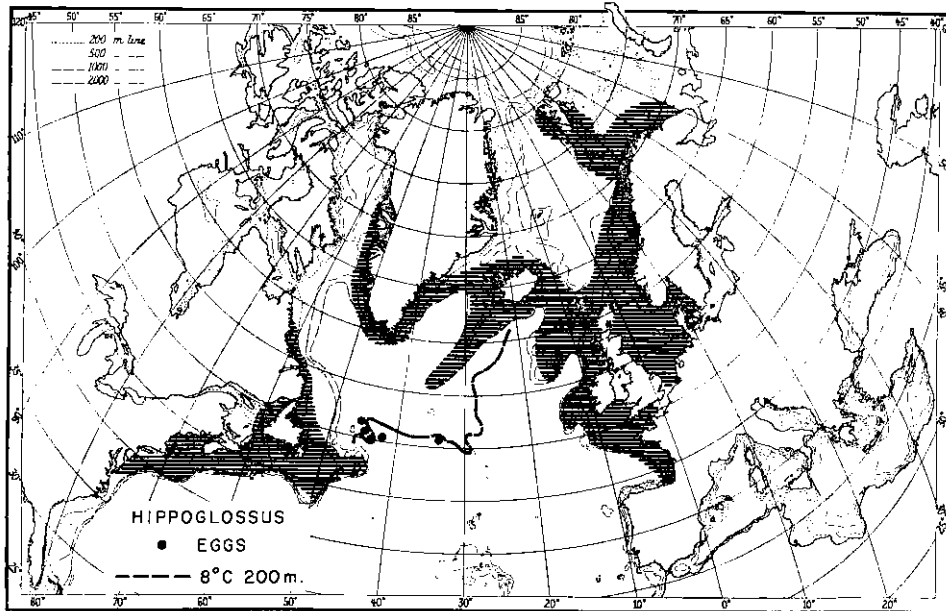


Fig. 8. Distribution of Halibut Hippoglossus hippoglossus (L.).

Iceland and the Greenland stocks of fish cannot show the origin of the new stock because we now know that even an important difference may arise during one or two generations from a change of temperature during an early embryonic period.

As new to the West-Greenland fish fauna, or at any rate only recorded from the area once or twice during the last century (e.g. in some one of the earlier warm periods about 1820 or 1870), we may (from the late Ad. S. Jensen and Dr. Paul M. Hansen) mention the following teleosts: Blue Whiting (Micromesistius poutassou) - Coalfish (Pollachius virens) - Haddock (Melanogrammus aeglefinus) - Blue Ling (Molva dipterygia dipterygia) - Torsk or Cusk (Brosme brosme) and Witch (Glyptocephalus cynoglossus). Moreover we may mention the following boreal or subarctic species, which have increased very much and have spawned in the area or have spread northwards along West-Greenland: Cod (Gadus callarias) - Halibut (Hippoglossus hippoglossus) - Redfish (Sebastes marinus) - Herring (Clupea harengus) - Spotted Catfish (Anarhichas minor) and Capelin (Mallotus villosus).

The essential thing, therefore, is to determine whether, for some of the

species mentioned, a transport of fry or immigration of adult or adolescent stages from the Iceland area actually has occurred, or whether an insignificant perennial stock has been revealed as the result of the increased fishery on cod.

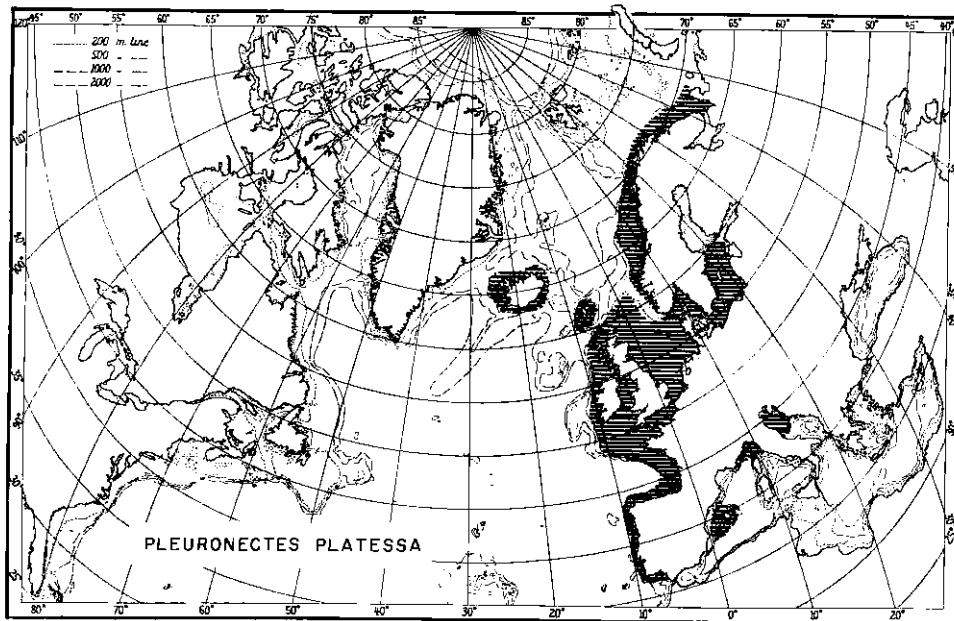
For most of the species we can only conjecture because adequate investigations or experiments are lacking. One species, viz. the cod, is however an exception, and the results for this species allow us to draw some conclusions about other species, which support the view we have gained through the faunistic studies. But we will, however, meet several new questions which we are unable to answer at present.

We possess the following results as proof of an interchange between the cod-stocks of Iceland and Greenland:

- (1) When marking started in the twenties on cod off the west coast of Greenland it was soon followed by recaptures on the Iceland spawning grounds, and in the early thirties especially many recaptures were obtained. More than 70 percent of the emigrants from Southwest-Greenland turned up in Icelandic waters. Migration of marked cod on a food-migration from Iceland to West-Greenland was also demonstrated but on a much smaller scale. The interchange was, however, proved. Later, when the stock off Greenland increased owing to increase in temperature, the importance of this interchange declined, evidently because a special West-Greenland stock of cod eventually was established. We are, however, unable to prove whether this stock was descended from emigrated Iceland cod or from a perennial small endemic Greenland stock.
- (2) The next question was, whether fry born on Iceland spawning grounds could drift over the Denmark Strait to East-Greenland and, even farther, to West-Greenland. During fishing experiments in 1931 and the following years we were able to show that a drift of fry occurred in some years to East-Greenland, and in all probability many fry also reached Southwest-Greenland, but conclusive proof is still lacking. The very rich stock of adolescent cod in Southwest-Greenland, and the great return-migration from there to Iceland, indicate however that Iceland fry actually reach this part of Greenland in great quantities. The question then became somewhat confused, however, when cod in some years was observed spawning off the southeast coast of Greenland. Nor could a study of the meristic characters settle this question.

Though an interchange of adult cod over these rather great distances has been proved, it is apparent that even for this well investigated species we are





**Fig. 9.** Distribution of Plaice *Pleuronectes platessa* L.

rather uncertain concerning some points of the exchange, especially the extent and importance of the drift of fry.

About the last link in the emigration to the west, viz. the migration between Greenland and Labrador, etc., we know practically nothing. It is likely that this distance is the most difficult for the migrating adults and drifting fry to cover, even during the present warm period. A single marked cod, tagged on the important spawning ground off Iceland, has been recaptured at Newfoundland, but the route of this fish is of course unknown (did it pass West-Greenland or did it take a more direct route?). Furthermore only one or two cod marked off Newfoundland have actually migrated to Greenland (according to Dr. Paul M. Hansen), and consequently it seems that at present any interchange there must be of a very slight extent.

There is, however, evidence that an emigration from the Iceland-Greenland cod-centre to the east is slightly greater than that from Greenland to Labrador; a few cod marked off West-Greenland and off South- and Northeast-Iceland have been recaptured at the Faroes, Norway and North Russia. A passive or active

emigration on a small scale has accordingly been proved here, and such long-distance migrations may be of some importance for the re-establishment of a cod stock in remote areas under special conditions.

From the facts obtained on cod dispersal we are entitled to deduce that other species with a similar distribution and of similar habits and environmental demands may behave in a similar way.

When, for instance, we have records of halibut postlarvae on the route between Iceland and East-Greenland, have records of halibut eggs in the mixed water north of Flemish Cap, have proved that young marked halibut about 3 years old are able to migrate from the Faroes to Iceland, and know that adult halibut migrate to about 1000 metres depth outside the continental shelf for spawning, it seems permissible to conclude that this species is able to intermingle across the northern part of the Atlantic. But the dimensions of this interchange seem outside human judgment.

The case must be similar to that applying to several other of the boreal species considered, but most of them have been studied too little to provide sufficient facts on migration, drift, etc.

On the other hand, it seems justifiable to expect that species which appear to have a distribution favourable for an east to a west migration but which differ considerably in habits and environmental requirements from the group of fish mentioned, are not likely to extend their boundary further to the west; these include several *Pleuronectiformes*, e.g. plaice (*Pleuronectes platessa*); Grey Gurnard (*Trigla gurnardus*), etc.

It is difficult to be sure that the slight interchange between east and west, and vice versa, of several boreal species is of actual significance to the fishing industry, except for the interchange of cod between Greenland and Iceland, which is evidently of primary importance. Detailed knowledge of such changes would be of special value to the fishing industry if and when the present warm period declines.

The displacement from east to west of fish stocks during long geological periods, and also the minor displacement from west to east, are of course of great importance in the long view, and will continue to be of importance during all great fluctuations of the climate of the earth, but it seems that the present slight intermingling must be of very limited importance to the fishery on both American and European fishing grounds.

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H. J. Aurich.

The large changes in the distribution and size of the stocks of some marine fishes and other animals, observed during the last decades, are of two kinds: (1) increase or decrease of the stocks (the term stocks here used for natural spawning communities), exceeding the usual fluctuations; (2) displacement of species to regions which they had previously not occupied.

At the present stage of our knowledge, there is universal agreement that these changes are caused by a change of climate. At the same time, very little is known as to how these variations in the environment can affect the size and distribution of the stocks.

Let me try to analyze the changes which the stocks of some summer spawners in the southern North Sea have suffered during the last years. Since at least 1948 - there are no observations during the war and the first years thereafter - we observed an intensive spawning of the pilchard (Clupea pilchardus) in the southern North Sea such as had not occurred before World War II. At the same time, the spawning of the anchovy (Engraulis encrasicolus), common sole (Solea vulgaris), horse-mackerel (Caranx trachurus), and mackerel (Scomber scombrus) had also risen noticeably.

The increase or the displacement of the spawning stocks may be due to:

- (1) Amelioration of the conditions of development resulting from the climatic change. Probably this is true for the common sole, which is a sedentary fish in the North Sea except during limited migrations to the feeding grounds or hibernation places.

Likewise, the strengthening of the spawning of horse-mackerel and mackerel could be explained by an increase of the stocks caused by improvement of the condition for life. But, this interpretation falls in the case of pilchard which does not appear in the southern North Sea before 1948-49; possibly in the case of the anchovy too, the spawning of that species was restricted mainly to the Zuider Zee. The sudden rise in the frequency of eggs and the considerable extension of the spawning area from the southwestern North Sea to the Baltic Sea since 1948, could hardly be due wholly to a fluctuation or to a trend.

- (2) Passive drift of pelagic stages by currents. This is without importance considering the short developmental period of the eggs during the summer months (2-3 days).

TABLE I. Average and maximum frequencies of eggs per square meter.

	1902 - 1930		1948 - 1954		
	Average	Maximum	Average	Maximum	
Pilchard	0	0	220-430	300-1100	east-Friesian area
Anchovy	2-10	24	270-640	300-1000 (1949:3885)	southern North Sea except the Zuider Zee.
Common sole	10-14	15-35	30-80	100-357	east- and north- Friesian area east 6°E
Horse-mackerel	5-15	77	200-390	300-850 (1951:2520)	east-Friesian area east 6°E
Mackerel	10-50	100-190	50-220	100-444 (1952:1716)	southern North Sea

Furthermore, Table II reveals that since 1948 the spawning has maintained approximately the same intensity and geographical extension.

TABLE II. Medium frequency of eggs per square meter. Average of all stations yielding more than  
 20 eggs per sqm : common sole  
 50 " " " : mackerel  
 100 " " " : pilchard, anchovy and horse-mackerel.

	1949	1950	1951	1952	1953	1954
Pilchard	(50)	226	236	387	250	430
Anchovy	644	342	270	303	274	264
Common sole	34	35	45	30	35	77
Horse-mackerel	(312)	279	421	219	387	355
Mackerel	-	74	129	221	(50)	149

(The values in brackets are uncertain, owing to the small number of catches).

- (3) Active immigration of mature fish. With the exception of the common sole all the other species mentioned above are typical migratory fish, entering the southern North Sea only to spawn there. Obviously in 1948 special hydrographic conditions must have existed which strengthened this immigration, and which furthermore induced an invasion of species which do not usually occur in the southern North Sea. It is of interest that the invasion of pilchard in 1948-49 was accompanied by an unusual appearance of cuttlebones (Sepia officinalis) and living stalked barnacles (Lepas fascicularis) on the north Friesian coast.

Although these special conditions did not occur in every subsequent year in the same manner, the intensity of spawning remained at about a level as shown in Table II. We must therefore assume that from this one single invasion, the old North Sea stocks became augmented, and that in the pilchard, a new subpopulation became established, which sustained itself.

To test this assumption it will be necessary to know the factors governing migration and spawning behaviour. Very little is known about this for sea fishes but, judging from bird migration, the following course of reactions is suggested:

- (1) In connection with the maturation of the gonads, which depends on the sum of heat received during hibernation time since hatching, internal factors (hormones) activate the migration drive.
- (2) The onset of migration may be a function of time, i.e., might take place at a particular stage of maturation, or it might be stimulated by variation in the temperature of the environment, as has been shown for Salvelinus (White 1941).
- (3) Which direction the fish take on their migration is determined, on the one hand by their reaction norm, i.e., the innate manner of directing their movements in a given field of stimulation; on the other hand by the external orientation field. The orientation may be a topotaxis, or it may result from trial and error movements (phobotaxis in Kühn's classification of the types of orientation).
- (4) Egg-laying and fertilization probably are not a function of time and temperature only, like maturation; rather they may be triggered by external stimuli. For example Calanus, according to Marshall & Orr (1953), is capable of laying at the beginning of its spawning period, but does not do so until the spring diatom blooming, i.e., when the food supply becomes adequate.

- (5) Finally, the whole migration cycle must be completed by return of the spent fish and the recruits from this spawning ground to the place of hibernation.

Obviously a variation of the factors conditioning the egg-laying and fertilization or the return cannot have caused the sudden invasion observed in the 1948 season. On the contrary, a premature maturation and release of the migration, due to rising temperatures at the hibernation places, could induce the migration and guide the fish beyond their usual spawning places in the English Channel, where spawning conditions were not yet favorable, as far as to the North Sea. Moreover, considering the changes in the distribution of the water masses in the entrance of the Channel (Russell, 1940, 1947) we must take into consideration a change of the orientation field also.

To conclude, I should like to emphasize the provisional and hypothetical nature of the interpretation given above, which is offered merely as a working hypothesis for verification by future research.

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A. M. Fleming.

Author's Abstract.

In the Newfoundland and Labrador region two measures, the number of vertebrae and the degree of infestation of cod by the nematode Porrocaecum are useful in showing the existence of subdivisions in the stocks of cod.

Vertebral Count Averages: Along the coast of Labrador and the east coast of Newfoundland averages of vertebral number range from 54.0-54.6. Cod of the northern edge of the Grand Bank have vertebral averages similar to those of the east coast cod.

On the southeastern portion of the Grand Bank averages range from 52.1-52.9, and averages on the central portion of the Bank are similar.

From the low averages of the southeastern region there is an increase westward along the southwest edge of the Grand Bank to averages of 53.3-53.6 on St. Pierre Bank.

Cod with such low vertebral averages as 52.8-53.0 exist in the southwest and western coastal regions of Newfoundland. From the northern part of the west coast toward the Strait of Belle Isle, averages gradually increase to the east-coast type.

Porrocaecum infestation: The larval form of the nematode Porrocaecum is found in cod flesh in the Newfoundland area. The adult occurs especially in the stomach of the harbour seal, Phoca vitulina. The largest colonies of this seal exist around the west and southwest coastal regions of Newfoundland with smaller numbers occurring in other parts. A high correlation exists between the distribution in abundance of the harbour seal and the degree of infestation of the cod by the nematode Porrocaecum.

Parasitization is high around the west and southwest coasts of Newfoundland where the largest numbers of harbour seals are found, low in other coastal areas where only small numbers of seals are present and extremely low in the offshore areas.



THE IDENTIFICATION OF HADDOCK STOCKS  
BASED ON VERTEBRAL ENUMERATION.

333

John R. Clark.

Author's Abstract.

The average number of vertebrae in haddock varies significantly from one bank to another over the range of the species. It also varies significantly from one year-class to another, being correlated with the temperature of the water during the time of spawning.

Analysis of available data indicates very little, if any, intermingling between banks.



VARIATIONS IN BODY PROPORTIONS OF REDFISH FROM THE 335  
GULF OF MAINE, NOVA SCOTIAN BANKS AND THE GRAND BANKS.

George F. Kelly and T. W. Martin.

Redfish are found abundantly in deep waters adjacent to most of the fishing banks in the North Atlantic Ocean that are north of the Gulf Stream and south of the Arctic waters. Taxonomically the bulk of these fish are classed as Sebastes marinus with lesser numbers of Sebastes viviparus in certain eastern areas. Differences are known to exist between fish collected from various fishing grounds of the North Atlantic. Most of these differences are of the type that may be associated with ecological differences such as temperature, depth, length of day or latitude. It is possible, however, that the variations are genetic and are difficult to detect.

The first phase of this study was a comparison of meristic characteristics of small samples of redfish from fifteen areas between the Gulf of Maine and the Barents Sea. The range of variation in the number of fin spines, fin rays, scale rows and gill rakers was almost identical for fish from all areas. The classic description of Sebastes marinus, based on the gross examination of meristic characteristics, applied equally well to redfish from all regions. These preliminary results indicated the need of a systematic study of the nature and magnitude of variations in the morphology of the redfish stocks of the North Atlantic.

There are no published accounts of systematic morphological studies of the Sebastes group in the Atlantic. The most recent taxonomic study (Travin 1951) was not sufficiently critical to define the limits of sub-specific variations. His conclusions regarding a new species of redfish, Sebastes mentella, were criticized by Andriyashev (1953) who relegated the form to a sub-specific status. Travin's data were not presented in a form that could be compared with material from other parts of the Atlantic. Under these circumstances, a study of Sebastes from the western Atlantic would have no basis for comparison with the Sebastes from the eastern regions. It was therefore necessary to limit the present study to the redfish stocks of the western Atlantic, and to confine racial comparisons to this area.

The study was planned to include all redfish stocks found within the boundaries of statistical areas XIX, XX, XXI, and XXII of the North American Council of Fishery Investigations system of area designation. Initially, each identifiable concentration or homogeneous group of redfish would be considered a separate stock. Some groups could later be combined if they appeared to be homogeneous. Each group would be identified by the alphabetical designation of the statistical subarea in which it is located.

Four widely separated subareas were selected for a pilot survey of the

entire region. Subarea 19 A in the Gulf of St. Lawrence, 20 D on the Grand Banks, 21 H on the Nova Scotian banks and 22 E in the Gulf of Maine were selected and all of the collected data from the areas were assembled.

The work of Matsubara (1943) on the Scorpaenidae of Japan was used as a guide in the choice of body parts that were likely to show variations. The following measurements were taken:

- Fork length
- Standard length
- Maximum body depth (base of 1st dorsal spine to base of ventral fins)
- Head length (tip of jaw to posterior edge of opercle flap)
- Horizontal diameter of orbit
- Interorbital width
- Length of pectoral fin
- Length of jaw appendage
- Length of maxillary (maxillary plus premaxillary)

These measurements were compared in regression calculations of the following relationships:

- Standard length/Body depth
- Standard length/Head length
- Standard length/Length of pectoral fin
- Standard length/Diameter of orbit
- Head length/Diameter of orbit
- Head length/Interorbital width
- Head length/Length of maxillary
- Head length/Length of jaw appendage
- Head length/Body depth
- Length of maxillary/Length of jaw appendage
- Diameter of orbit/Interorbital width

No conclusions have been drawn from the study as the racial comparisons are not yet complete. However, the trend of the data is indicated. The red-fish stocks of the New England - Newfoundland regions appear to be virtually homogeneous in all characteristics examined except that of the diameter of the orbit and the interorbital width. There are small visible differences in all comparisons of the regression slopes between areas. However, all relationships except those involving the orbit show little variation and may prove to be drawn from the same population. The fish from area 19 A showed the orbit relationship to be different from that in the other three areas. There is evidence that two groups of fish, a large-eyed and a small-eyed group, are present in the Gulf of St. Lawrence. Further study of this area is planned

for the summer of 1956 to determine the range of gradation between the extremes and the extent to which the variations in eye size may be correlated with water depth or temperature.

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## REVIEW OF KNOWLEDGE ABOUT THE ATLANTIC HALIBUT

G. Rollefson.

The papers presented and the following discussions revealed that on both sides of the Atlantic:

1. The young halibut seems to be heavily taxed by gear used for other species.
2. The halibut stocks seem very sensitive to fishing activity.

The discussion brought out that there are considerable difficulties in saving the young halibut from being caught incidentally in other fisheries. It was emphasized, however, that it was important to find means of avoiding unnecessary diminution of the recruitment of the stock.

The importance of an increased knowledge of the biology of the halibut was stressed and it was recommended that:

1. A long-term program of research of the Atlantic halibut should be framed.

Due to the fact that the stocks of halibut seem so susceptible to taxation by the fishery, it was recommended that:

2. A constant watch of changes in fishing method and fishing effort should be kept.

List of Contributed Papers

Rasmussen, B.	A short review of the history of the halibut fishery in the Davis Strait.	*
Rasmussen, B.	Tagging of halibut.	*
McCracken, F. D.	On the biology and fishing of the Canadian Atlantic halibut.	*

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\* Paper not published in this volume.





1. The first part of the document is a list of names and dates, which appears to be a record of some kind. The names are written in a cursive script, and the dates are in a more formal, printed style. The list is organized into two columns, with names on the left and dates on the right. The names are: John Smith, James Brown, and William Jones. The dates are: 1812, 1813, and 1814. The list is followed by a section of text that is also written in cursive. This text appears to be a description of the events that took place during the period covered by the list. It mentions the names of the individuals listed and describes their actions and the circumstances surrounding them. The text is written in a clear, legible hand, and it provides a detailed account of the events. The final part of the document is a short paragraph that summarizes the information presented in the list and the text. It states that the list is a record of the events that took place during the period covered by the list, and it provides a brief description of the events. The document is a valuable historical record, and it provides a detailed account of the events that took place during the period covered by the list.