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Methods in Age and Growth Investigations

By
Gunnar Selmer Sætersdal
Directorate of Fisheries,
Institute of Marine Research

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A.s John Griegs Boktrykkeri, Bergen

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Preface.

The present paper deals with the results of an investigation of the methods used in age and growth determination of haddock. The work has been carried out at the Institute of Marine Research, Bergen in the years from 1948 to 1951.

I offer my best thanks to Director GUNNAR ROLLEFSEN and Mr. GUNNAR DANNEVIG for their kind advice and help. I am also greatly indebted to Mr. ERLING SØRENG, Bessaker, who has supplied most of the material, and to Mr. G. C. TROUT, Fisheries Laboratory, Lowestoft, for correcting the english text.

Introduction.

The reliability of the methods used in determining age and growth of fish is a question of prime importance in fisheries biology. Today, most investigators make use of methods which are being based on the seasonal structures in scales, otoliths or other bones of the fish. These methods were taken up during the years around the turn of the century, and their reliability has since been discussed in a number of papers. The most important contributions in this discussion have been based on material from the herring and cod investigations. In the case of the herring this applies to papers by LEA (1910, 1911, 1913, 1924, 1933, and 1938) and LEE (1912 and 1920), and in the case of the cod to papers by GRAHAM (1926 and 1929 I & II), A. DANNEVIG (1925 and 1933). and ROLLEFSEN (1933 and 1935). In many cases, however, the results obtained from such special investigations have been given a more general validity than originally intentioned, as the methods have been used without further trial in other areas and also on other fish species.

THOMPSON (1923 and 1926) discussed certain points concerning the reliability of the scales of the North Sea haddock for age and growth investigations, but in a number of other investigations from various areas scales and otoliths of haddock have been used without their applicability for the material in question having been tried. This applies to haddock investigations from Iceland by SÆMUNDSSON (1925) and THOMPSON (1928), from the Barents Sea by SUVOROV (1927) and LUNDBECK (1932), from Skagerak and Kattegat by MOLANDER (1929); from the Belt Sea by A. C. JOHANSEN (1926), and from the New Foundland area by THOMPSON (1939). A. DANNEVIG (1933) has pointed to the disadvantages of a similar uncritical use of the methods of age determination of cod from different areas: the results are uncertain and incomparable. This must apply to the growth determinations to an even higher degree. Thus it was found advisable to start the haddock investigations in Norwegian waters by studying the methods to be used in determining age and growth.

Seasonal structures have been found in several bones in the haddock. SÆMUNDSSON (1925) found especially distinct zones in sections of the claviculæ. In the present work the otoliths were preferred because they are readily sampled and because of the good results obtained in otolith readings of cod from Norwegian waters. The scales were included because they have been used in almost all previous investigations of haddock.

Material and methods.

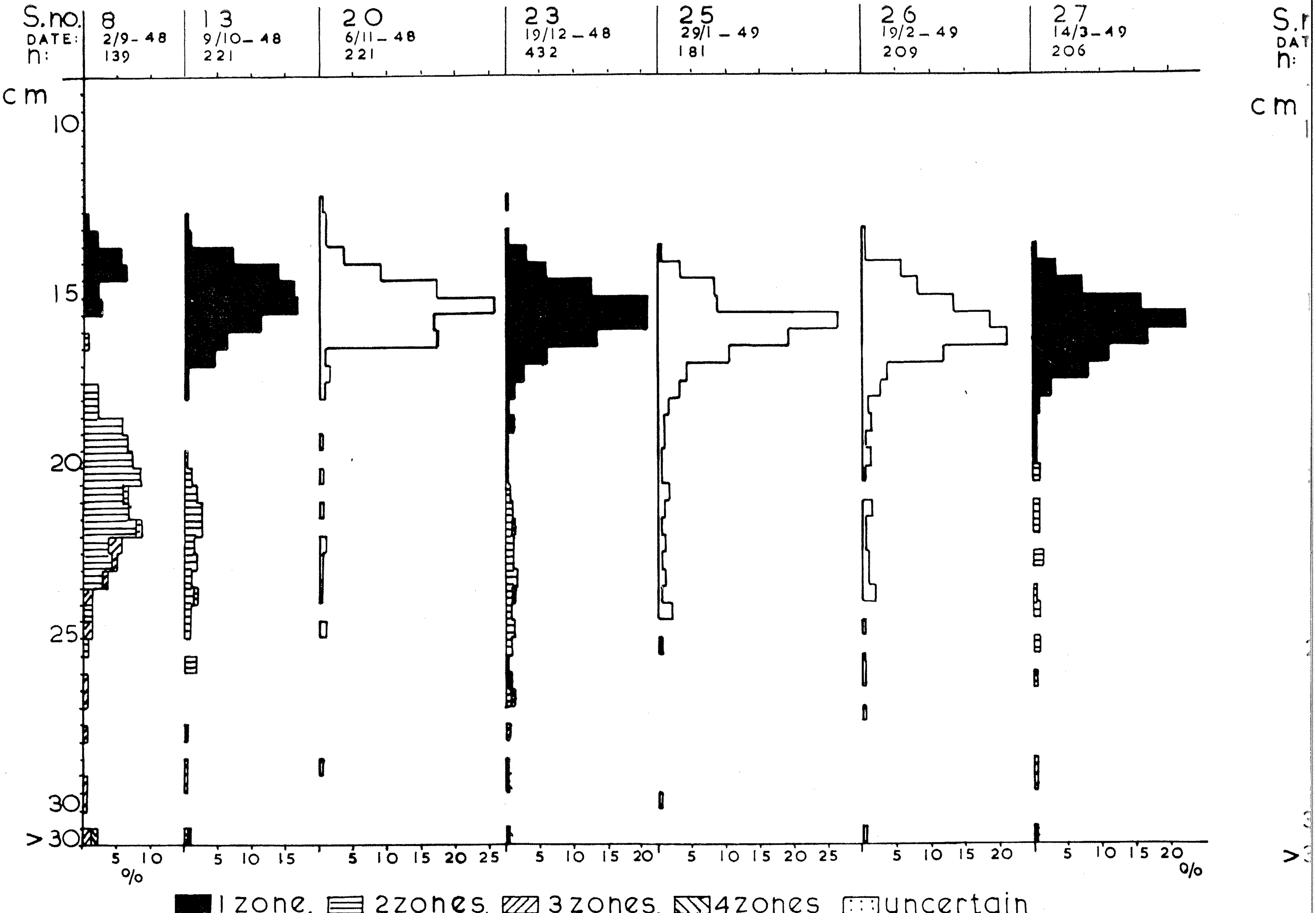
For several reasons the main part of the material consists of young fish. In the lowest age groups the Petersen method can be used as a check on other methods of age determination, and it is absolutely preferable to use young immature fish when taking a series of samples for growth estimations, the probability of selection in size, maturity etc. being less than in older fish. It was furthermore comparatively easy to obtain samples of young haddock throughout the year, as the lowest age groups are usually taken in great quantities by prawn trawlers in a number of localities along the Norwegian coast from Møre northwards to the Barents Sea.

The most important part of the material covered three years and consists of 29 samples taken with intervals of about a month from September 1948 to August 1951 by Mr. ERLING SØRENG from his prawn-trawl haules in one and the same locality: the Brandsfjord in Trøndelag at about 64° N.

The Brandsfjord is a small fjord, the inlet of which is separated only by a few skerries from the open sea. The depth of the trawling ground varies from 72 to 143 m. Outside the trawling ground there is possibly a small threshold with a depth of about 100 m.

The samples were preserved in 4 % formalin. If it is not neutralized the acidity of the formalin will decalcify the otoliths. Several methods were tried in order to neutralize the concentrated (40 %) formalin, but they were apparently without effect. When however the neutralization (with borax) was carried out on the diluted (4 %) formalin (ATKINS 1922), several months preservation left the otoliths undamaged.

The effect of shrinkage of the fish has not been considered in the length measurements. Since however the time in and the concentration of the formalin has been about the same for all the samples, the shrinkage should not influence the comparison of length data.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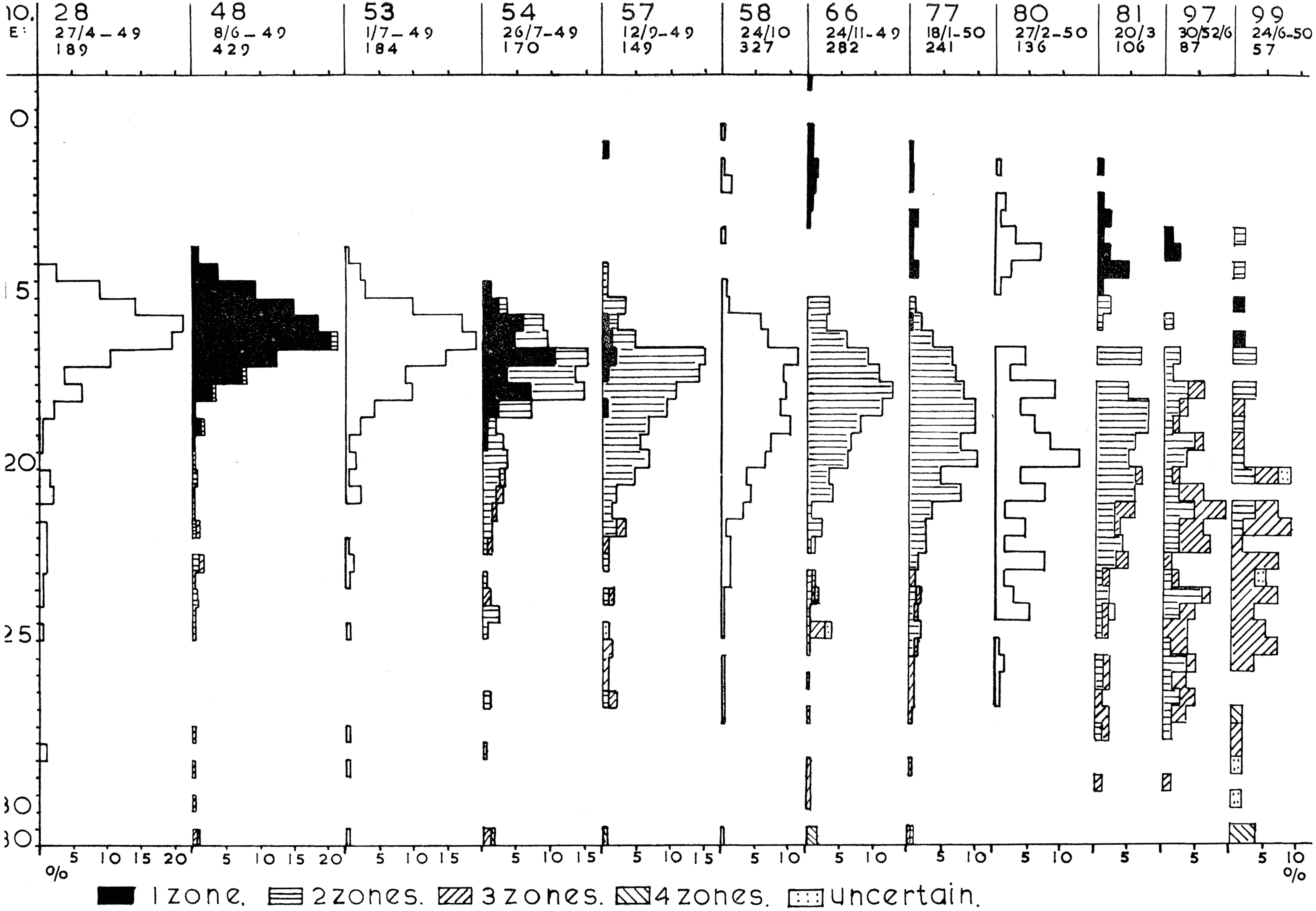
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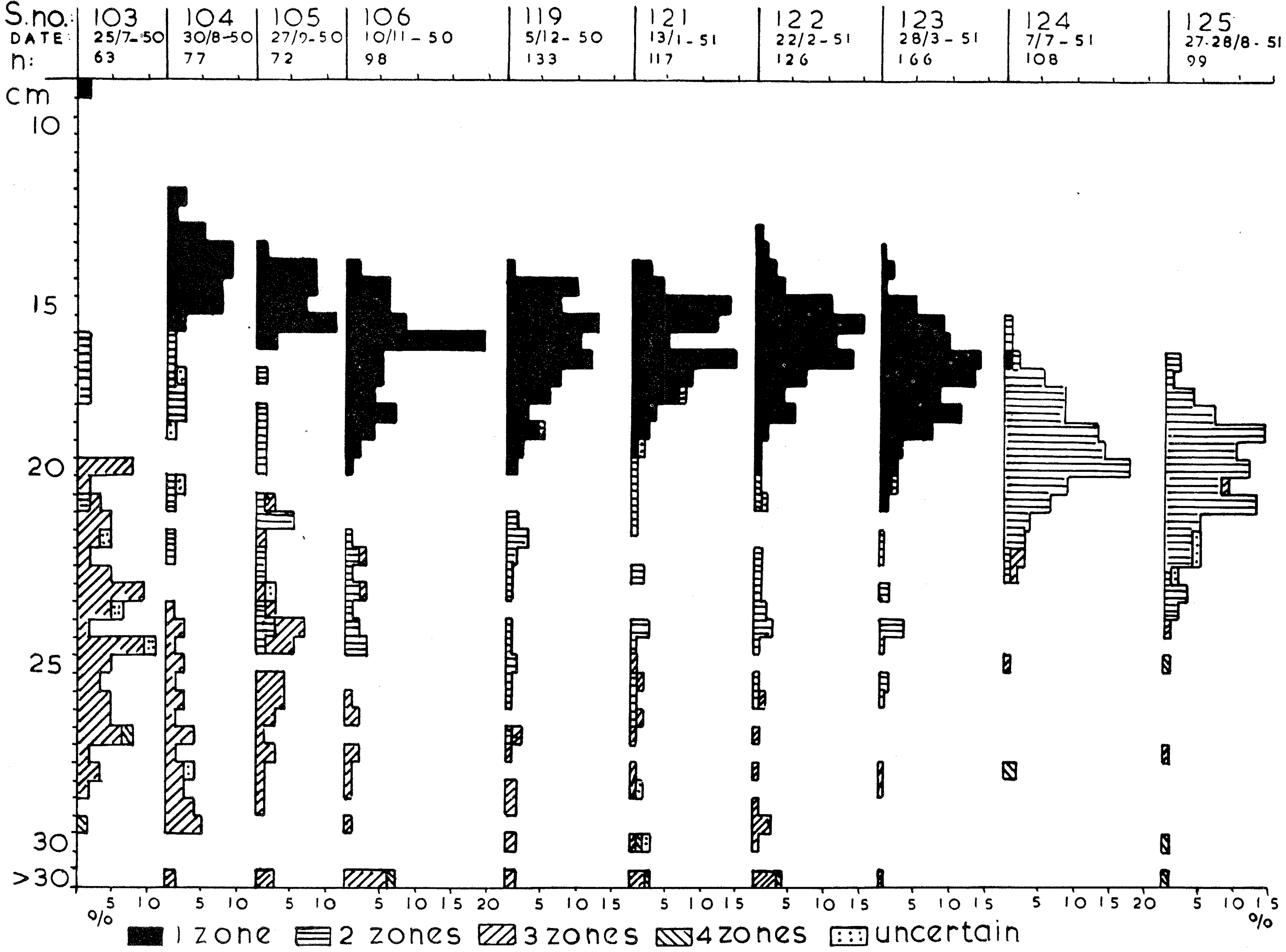
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The following procedure was used in the working up of the material. In 22 of the samples the total length of the individual was recorded on a small envelope in which both otoliths and a small sample of scales were kept. Scales could unfortunately not be secured from all samples since, in some instances, they had been completely chafed off, probably during the trawling. In order to save labour only a maximum of 150—200 such individual observations were made on each sample, the remainder of the fish were only measured for length. For the same reason individual observations were omitted in 7 of the samples, total length being the only observation taken.

In the first samples the sex of the individuals was observed, but as there appeared to be no significant differences between the growth rates of the males and the females, sex observation was, later on, only taken occasionally.

A great number of samples of both young and mature haddock from the coast of western and northern Norway and from the Barents Sea were also available. Some of these samples have been used as supplementary material in this investigation.

An important question in the evaluation of the material is the one concerning the identity of the populations from which the samples have been taken. This question is dealt with at the end of the paper.

For examination the sacculus otoliths were broken apart near the point where some indentations can be found on the edges of the median sulcus. As will be shown later, the growth center of the otolith seems to be located near this point. The broken section of one of the pieces was examined with a binocular microscope using a strong side illustration and a magnification of from 15 to 30 xx. The reading was facilitated, when necessary, by moistening the section with a mixture of glycerine and water. "Difficult" otoliths and otoliths used for growth measurements were ground with the help of a diamond disc operated by a dentists drill.

Several of the terms which occur in the literature of age determination characterizing the rings of the otoliths such as winter and summer zones, dark and light zones, are ambigous and should be avoided. In this study the following terms "opaque zones" and "hyaline zones" are used. The opaque zones will appear dark by transmitted and whitish by reflected light. The hyaline zones will appear white by transmitted and dark by reflected light. Fig. I and II (plates) show the same otolith photographed by reflected and transmitted light respectively.

For the purpose of age determination the number of opaque or hyaline zones were counted, the date of capture was compared with the known seasonal rhythm in zone formation, and from this information the age was deduced. For practical reasons the term O-group or 0 years has been used until the 31st of December, the first calendar year of life, I-group or 1 year from the 1st of January the second calendar year and so on.

For reasons which will be discussed later the scales were selected from an area near the median line in the region of the posterior part of the second dorsal fin. The first samples were treated according to the method described by GRAHAM (1929 III): bleaching the scales in peroxide and mounting them in glycerine jelly. In search for a less labourous method the procedure of taking celluloid impressions of the scales as described by NESBIT (1934) was tried. Instead of a press a roller was used. As it proved unnecessary to clean the scales before taking the impressions, this method was very laboursaving indeed. The mounted scales and the scale impressions were examined in a modified EDINGER's projection apparatus using a magnification of 30 xx.

The structure of the scales are described as zones with narrow sclerites and zones with broad sclerites. The age determination by scales was undertaken in the same way as described for otoliths. In an attempt to eliminate the personal judgement in age determination GRAHAM (1926 and 1929 I) has described a method for age determination of cod based on scale tracings. In the great majority of my scales however there could be no doubt about the number of zones, and as GRAHAM's method is rather labourous it was not used in spite of the advantages connected with it.

The use of otoliths and scales in age investigations.

According to GRAHAM (1929 I) the question whether the zone formation in otoliths and scales are annual can be checked in several ways of which 1) comparison with the Petersen method, and 2) the seasonal record of the marginal structure were best suited for the present material.

Comparison of otolith zones with the Petersen method.

In this comparison the number of zones was defined as the total number of opaque zones found. Even the first narrow trace of a new opaque zone found at the margin was counted.

Fig. 1 shows the length distribution of all the samples from the Brandsfjord, and the number of zones in the otoliths found in the examination of the whole or a representative number of fish of each sample.

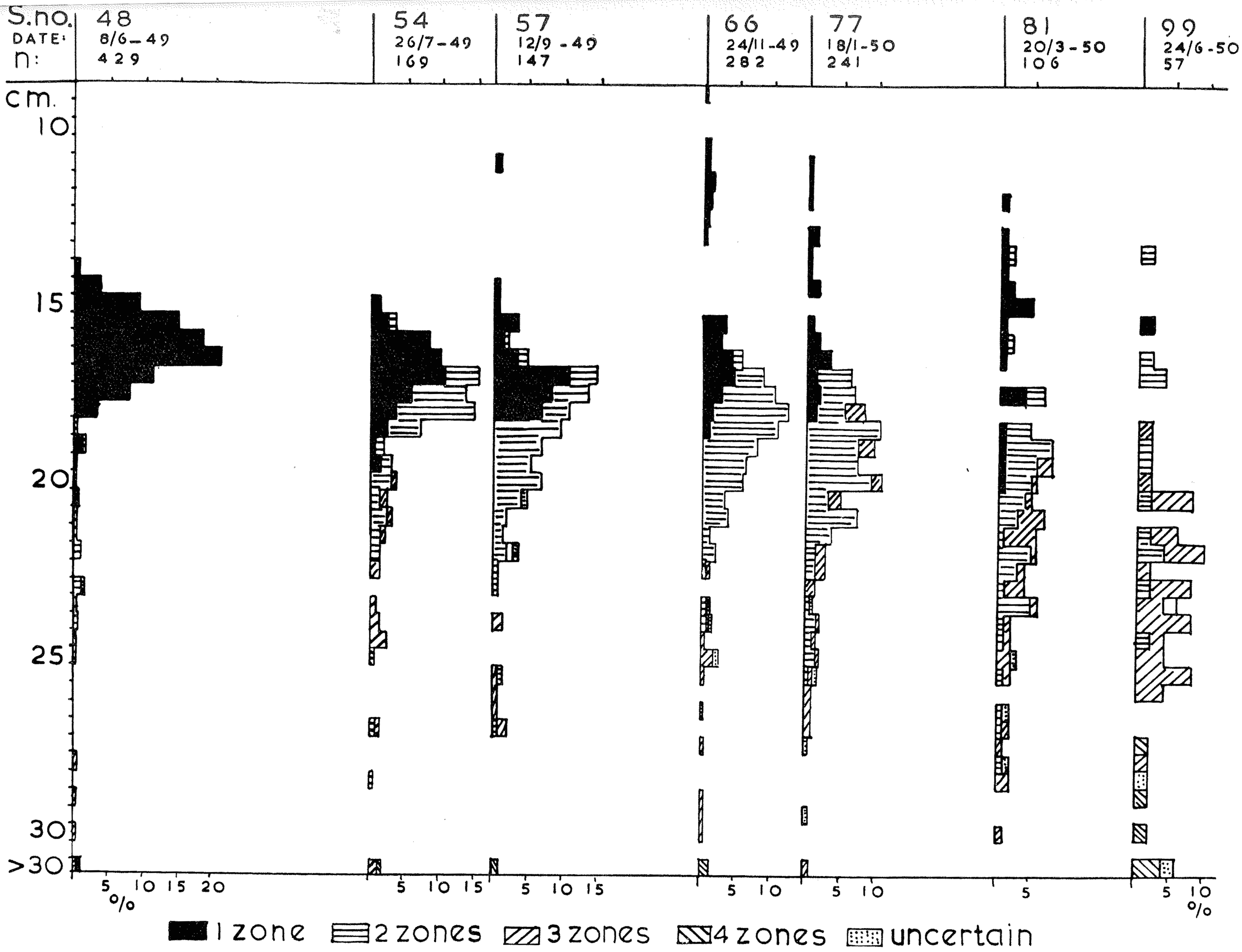

Fig. 2. The length distribution of the samples compared with the number of zones in the scales.

The blank diagrams refer to the samples in which for various reasons total length was the only observation taken.

There can be no doubt that the distinct grouping found in the length distribution of almost all of the samples in fig. 1 must be caused by different age groups. A new group of small fish appears in August—September each year (samples 8, 57, and 103). As substantially smaller haddock have not been observed anywhere in Norwegian waters at this time of the year, it may be inferred that these are the O-groups appearing in the catches for the first time.

It further follows from the diagrams that the yearclasses 1948 and 1950 were rich relative to the 1949 yearclass. The same variation in brood strength was found in a great number of samples of young haddock taken in the Norwegian coastal areas from the Brandsfjord northwards to the Barents Sea in these years (SÆTERSDAL 1952).

In most of the samples in fig. 1 the grouping in the length frequency distribution is in striking accordance with the number of zones found in the otoliths. Exceptions to this rule, such as samples 54 and 57, are easily explained by the fact that in a fish population there is a certain amount of dispersion in the time of the laying down of a new zone.

Comparison of scale zones with the Petersen method.

The number of zones in the scales was defined as the number of zones with broad sclerites found. Even a single new row of broad sclerites outside a zone with narrow ones was counted as one zone. In order to save labour sub samples were selected for scale examination from very numerous samples, taking care that the sub sample acquired the same pattern of length frequency distribution as the original sample.

In the first four samples examined, samples 8, 13, 23, and 27, there were no cases of disagreement between the number of zones found in the otoliths and in the scales, and accordingly it was considered unnecessary to give separate illustrations of these scale readings.

Fig. 2 shows the length frequency distribution and the number of zones in the scales of the remaining samples examined. In sample 48 almost all of the individuals in the length group 14—20 cm (the 1948 yearclass) have one zone in the scales. In samples 54 and 57 the same length grouping contains individuals with one zone and with two zones, obviously because some of the fish have started the formation of a new zone with broad sclerites. But this disagreement between length grouping and the number of zones in the scales persists in the following samples 66, 77, and 81. Some of the fish which according to their length, must

Table 1. *Number and percentage of the fish of the 1948 yearclass whose «scale age» was one year less than the «otolith age».*

Sample no.	Sampling dates	Number of fish investigated	Number disagreeing	Percentage disagreeing
66	24/11 1949	61	15	24 %
77	18/1 1950	72	14	19 %
81	20/3 —	82	15	18 %
99	24/6 —	37	6	17 %
104	30/8 —	27	3	12 %
119	5/12 —	11	0	0 %

belong to the 1948 yearclass have still only one zone in the scales. In sample 77 the formation of the third zone in the scale has apparently started. In this sample and in sample 81 the 1948 yearclass consists of a mixture of individuals with one, two, and three zones in the scales. In the remaining samples the number of fish belonging to the 1948 yearclass was too small to give any foundation for an age determination by the length grouping. Of the 1950 yearclass no scale readings were undertaken.

The agreement between the Petersen method for age determination and the number of zones in the scales is thus very good for the first year but not the second year of this investigation. Evidently a part of the 1948 yearclass failed to form a zone with broad sclerites in the year 1949. There was, as fig. 1 shows no corresponding lack of formation of opaque zones in the otoliths, but the opaque zones formed in 1949 were in many cases unusually narrow. Figs. III and IV (plates) shows photographs of a scale impression and the otolith of a fish from sample 77. Although very narrow the second opaque zone in the otolith is distinct. No trace of a second zone with broad sclerites can be found in the scales. And fig. V and VI (plates) are photographs of a scale impression and the otolith of a fish from sample 104, 30/8 1950, in which the otolith- and scale readings disagreed.

In many of the fish of the 1948 yearclass which did form a second zone with broad sclerites in 1949, this zone was very narrow. An example of this is shown in the photograph fig. VII (plate) of a scale impression of a fish from sample 99, 24/6 1950.

Table 1 lists the number and percentage of the fish of the different samples whose age as determined by the scales was one year less than that found by otolith readings. The decline in the percentages from sample 66 to sample 77 may be caused by a belated formation of the zone with broad sclerites in some individuals. In the last samples the numbers of fish of this yearclass were unfortunately very small.

Discussion.

As pointed out by GRAHAM (1929 I) an agreement between Petersens method and other methods for age determinations only tells that the majority of the determinations are correct. The numerous samples and the very pronounced grouping in the length frequencies of the present material, however, constitutes an unusually good basis for a comparison, and this comparison shows that the Petersen method and the otolith readings gave nearly identical results showing the correct age whilst a minority of the scale readings were false and differed from these two methods.

The seasonal record of the otoliths.

Further valuable informations on the zone formation have been obtained by recording the marginal character of the scales and the otoliths.

The observation of the marginal character of the otoliths soon showed that the opaque zones were not formed evenly and at the same time over the whole surface of the otolith. In some of the samples opaque material was found at the pointed ends of the section, the rest of the margin being hyaline. This may probably be related to the fact that it is the opaque zones which, so to speak, form the otolith. As can be seen in fig. IX (plate) the hyaline zones have about the same width in all directions of the section, whereas the opaque zones are definitely broadest in the direction of the pointed ends.

Furthermore it was observed that the zone formation at the sulcus side of the otolith in many cases seemed to be ,,out of step'' with the rest of the otolith being about half a zone ahead. Fig. VI (plate) shows an example of this. For this reason the area in and near sulcus was not taken into account when determining the marginal character.

The following system was used (partly from A. DANNEVIG 1933):

o: narrow opaque zone at margin, may be limited to the pointed ends.

O: distinct opaque zone at margin.

h: narrow hyaline zone at margin.

H: distinct hyaline zone at margin.

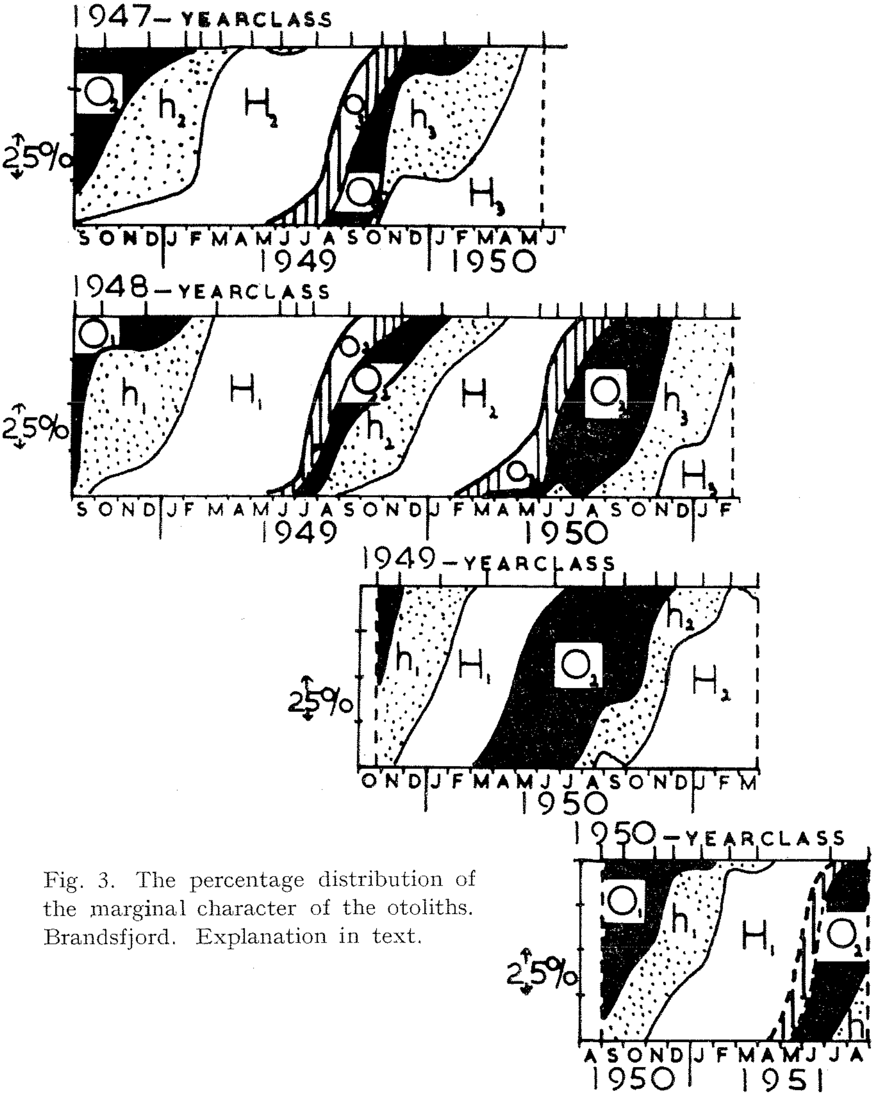

Fig. 3. The percentage distribution of the marginal character of the otoliths. Brandsfjord. Explanation in text.

An attached figure refers to the number of the zone counted from the center.

The marginal character of an otolith section is a very difficult object for a photographic plate, but it should be possible to obtain an idea of the appearance of the stages mentioned above from the following figures:

o: figures I and II. 0: figures VI and IX.

h: fig. VIII and H: fig. IV.

In order to avoid the influence of personal prejudice on the results of the determinations, the date of collection of all the samples from the first year was disguised. The later samples were worked up when they arrived.

In fig. 3 diagrams have been drawn showing the percentage distribution of the marginal character of the otoliths in samples of the yearclasses 1947, 1948, 1949, and 1950 from the Brandsfjord. To increase the clarity, a new zone appearing for the first time has been placed at the bottom of the diagram, and roughly smoothed curves have been drawn between points belonging to the same zone. The slopes of these curves show the degree of simultaneity of the zone formation in the population, whereas the areas limited by the curves will give an idea of the time spent in the formation of the various zones.

The seasonal record of the scales.

The following classification was used:

b: one or a few rows of broad sclerites at margin.
B: distinct zone with broad sclerites at margin.
n: one or a few rows with narrow sclerites at margin.
N: distinct zone with narrow schlerites at margin.

The number of the zone counted from the center was also noted.

In an attempt to follow the zone formation by means of a more exact method, the width of the second plus the third sclerites from the margin at the posterior part of the scale was measured. The outermost sclerite was omitted because it is frequently difficult to decide whether it is complete or not.

Fig. 4 shows the percentage distribution of the marginal character of the scales, and the average width and standard deviation of the second plus the third sclerite. The age determination has been based on scale readings except in the case of the minority of the 1948 yearclass in the samples 77, 81, 99, and 104 which according to the scales should belong to the 1949 yearclass. Here the otolith readings (and the Petersen method) have been used, and the fish placed in the 1948 yearclass.

A general view of the fluctuations in the marginal structures of the otoliths and scales is given in fig. 5 where all the yearclasses have been put together and the results illustrated in the usual way for the purpose of more convenient comparison with similar diagrams from other investigations.

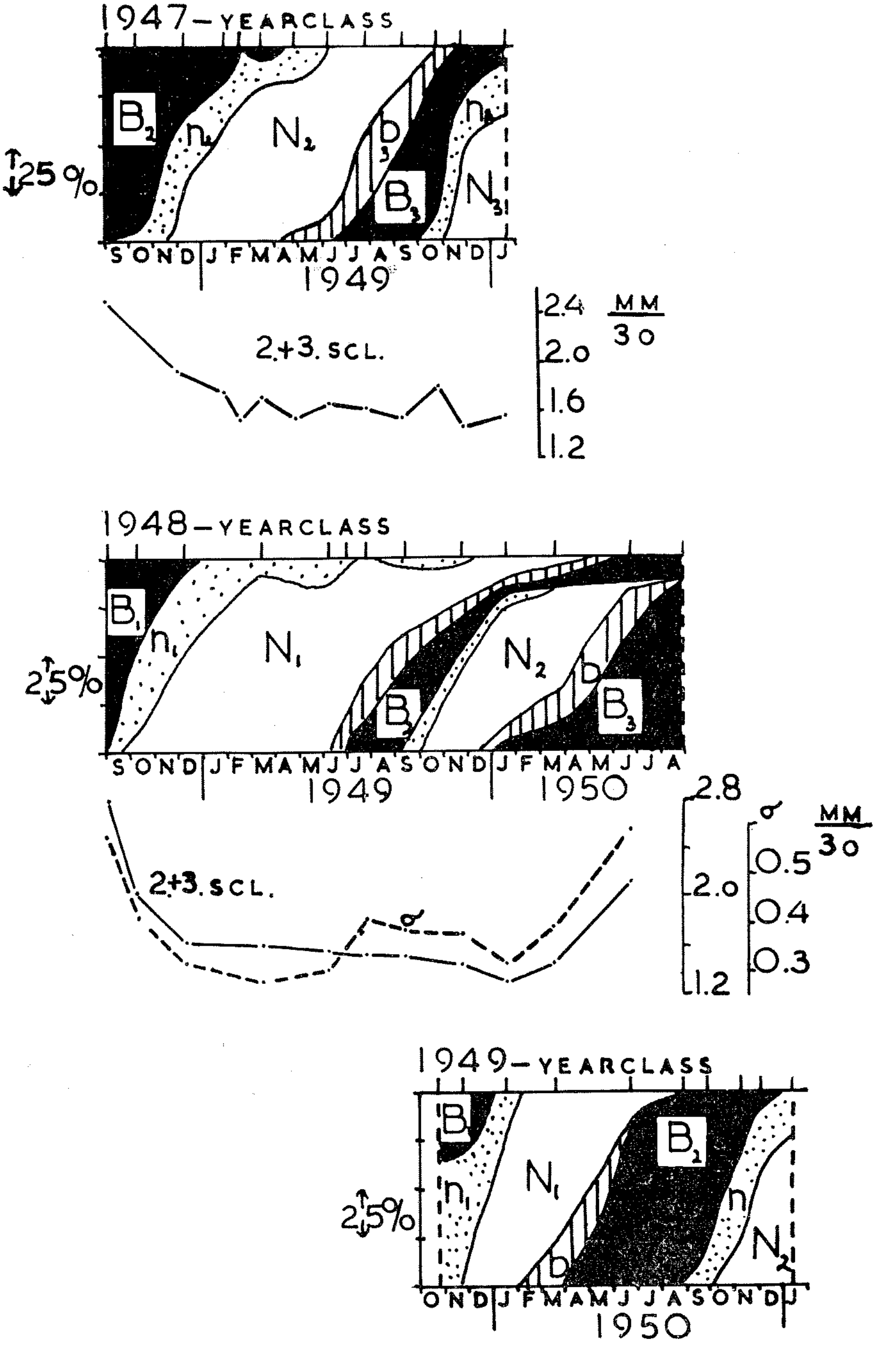

Fig. 4. The percentage distribution of the marginal character of the scales and the width of the 2nd + 3rd sclerites from the margin. Brandsfjord. Explanation in text.

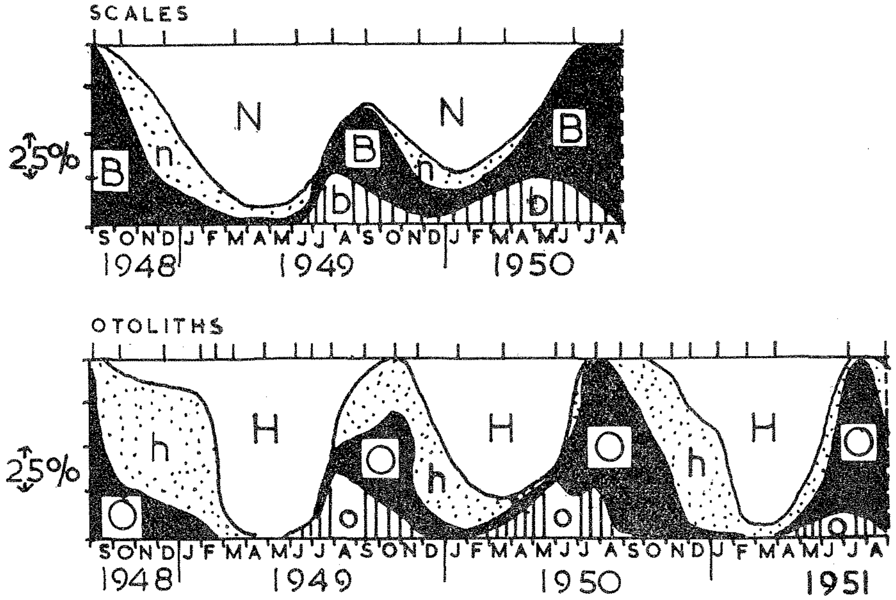

Fig. 5. The percentage distribution of the marginal character of the scales and the otoliths. All yearclasses combined. Brandsfjord.

Discussion.

According to Graham (1929 II) the seasonal record is excellent evidence on the validity of the methods provided there is a sharp turn over from one kind of marginal structure to another, that is, provided there is a high degree of simultaneity in the formation of the zones. He further says that such a sharp turn over rate has never been recorded. In Graham's (1929 I) own investigations of cod scales he found annual fluctuations in the marginal structures ranging from 0—15 % to about 90 %. He concludes that some of the scales do not follow the seasonal law of the majority, and will give misleading results when used for age determination.

But several other authors do not seem to agree with Graham in this conclusion. Both Hickling (1933), A. Dannevig (1933), and Menon (1950 I) found that the annual fluctuations in the marginal structures did not always reach 0 % and 100 %, but in spite of this they consider the fluctuations found as evidence of the validity of the methods. The main point seems to be the undisputable annual character of the fluctuations. Both Hickling and A. Dannevig are of the opinion that the deviations from the 0 % to 100 % fluctuations are caused by secondary zones which when they appear inside the margin can easily be distinguished from the true zones.

As can be seen from fig. 5 the fluctuations in the present material do not range from 0 % to 100 % every year. In the year 1949 opaque zone and broad sclerites only reach maximum values of about 65 to 70 %. The reason for these low values may be that some part of the haddock population in the Brandsfjord did not form such a zone in that year. As has been shown in a previous chapter this is probably true for a minority of the 1948 yearclass in the case of the scales. But the main cause of the unusually low maximum values in 1949 must be other than a total lack of zone formation, since this has not occured in the case of the otoliths. Turning our attention to the figures 3 and 4 it is apparent that the areas covered by the terms o and 0 and b and B are very small in 1949 for both the 1947- and the 1948 yearclass, that is the time spent in the formation of the opaque zone and broad sclerites has been short. From the diagrams most of the fish seem to have spent only two to three months on the formation of these zones, whereas each other yearclass on the whole has spent more than six months in forming comparable zones. This great spread in the time of zone formation does not necessarily reduce the value of the methods, but it demands knowledge of the season in which the zones are formed.

The reason for the abnormality in zone formation in the Brandsfjord in 1949 is probably growth stagnation caused by overcrowding. This will be commented upon in a later chapter.

On the whole there is a good agreement between the zone formation in the otoliths and in the scales. The slopes of the curves in fig. 5 indicate that there is a somewhat higher degree of simultaneity in the zone formation of the otoliths, which is a confirmation of similar observations made by A. DANNEVIG (1933) on the cod. Individual comparison of the marginal character in otoliths and scales showed that 282 of a total of 1252 observations differed in marginal character.

The seasons in which the zones are formed.

An intimate knowledge of the seasons in which the zones are formed is a condition for the proper use of the methods, a point which has been overlooked by many investigators.

From fig. 5 it appears that in the Brandsfjord hyaline zone and narrow sclerites are the dominant marginal characters in the months October—November to May—June. These periods cannot however be taken too strictly as the seasons of the formation of the zones since total stagnation in the growth of the otoliths and scales may happen. Scale measurements (see fig. 8 p. 24) indicate that such periods of stagnation in the growth of the scales did in fact occur in the present material during the seasons in which narrow sclerites dominated the margin. But it is obvious that the formation of a zone must take place some time within the season in which that kind of zone dominates the margin, and these seasons will be refered to subsequently as the time of formation of the respective zones.

In order to include areas outside the Brandsfjord the marginal character was determined in some samples of haddock from the Finnmarken banks and from the West Coast (of southern Norway) see fig. 6. These samples have not been split into yearclasses, but they consist of fish of from 1 to 8 years old. Fish older than 8 years were omitted as the determination of the marginal character is complicated by the narrowness of the opaque zones in old fish.

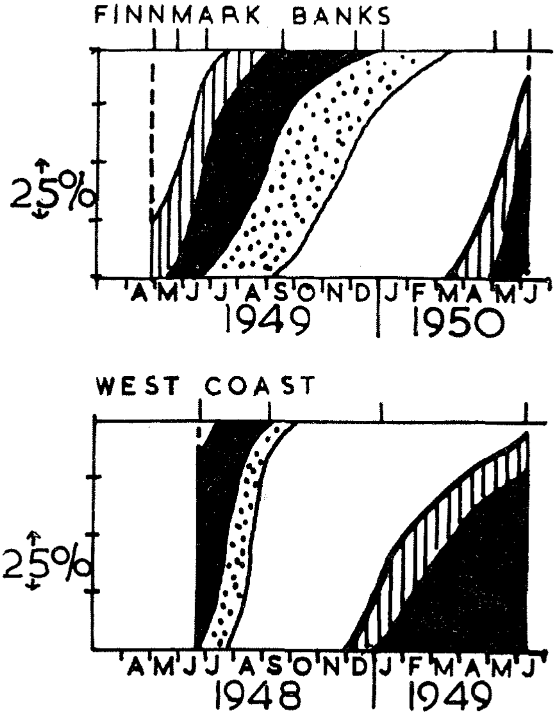

Fig. 6. The percentage distribution of the marginal character of the otoliths in samples from Finnmarkbanks and West Coast.

In Finnmark the hyaline zones seem to be laid down in the months September to May, the opaque ones mainly in June, July, and August. This is in accordance with the Brandsfjord material with perhaps a slightly longer periode spent on the formation of the hyaline zones.

The material from the West Coast is somewhat scanty, but it has been included here because there are signs of some shifting of the seasons compared with the Brandsfjord and Finnmark. Three of the samples are from the southernmost locality sampled, Ogna, the sampling dates being 23/6—48, 6/9—48, and 6/1—49. All of the fish in the sample from 6/9—48 had already completed the formation of

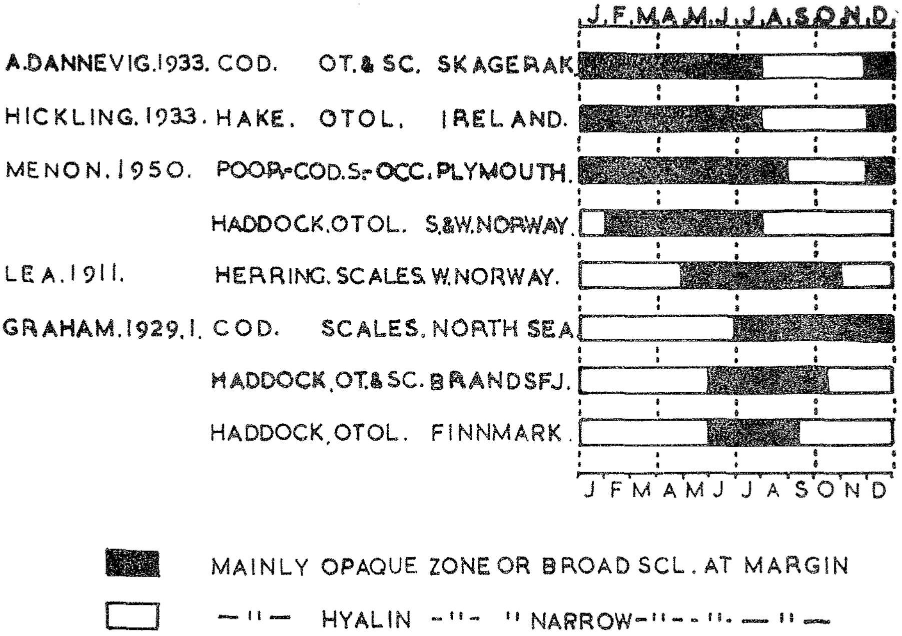

Fig. 7. Main seasons of zone formation in some fish species.

the opaque zone, and 30 % of the fish in the sample from 6/1—49 had begun the formation of a new opaque zone. Unfortunately there were no further samples from Ogna or neighbouring localities that year, but in a sample taken on 10/6—49 near Ålesund about 290 miles farther north, only 5 % still had hyaline zones at the margin. This sample is included in the diagram. In a sample from Tananger, a locality near Ogna taken on 16/1—51 7 % of the otoliths showed an opaque margin.

As can be seen from fig. 5 the seasons of the zone formation can vary more than a month from one year to another in the same locality

A comparison with the seasons of zone formation found in other investigations may be of some interest. Fig. 7 is a summary of available information. The heterogeneity of the material in respect of species, age, and maturity, and the rough simplifications made in the illustration, make discussion of the details in fig. 7 rather questionable. It seems however possible to divide the results into two main groups having almost reversed seasons of zone formation namely: fish laying down opaque zone or broad sclerites during the winter, and fish laying down hyaline zone or narrow sclerites during the winter. In all cases but one however, the last quarter of the year is dominated by hyaline zone or narrow sclerites.

Table 2. *Age determination by scales and by otoliths. Number of cases of disagreement between the two methods grouped according to otolith age and number of observations characterized as uncertain grouped according to most probable age.*

Age group	N	Disagreeing	Uncertain scales	Uncertain otoliths
0	124	0	0	0
I	481	17	7	5
II	434	54	24	16
III	68	1	2	1
IV	119	11	9	2
V	52	8	4	4
IV	12	0	0	0
VII	40	3	2	1
	1330	94 7,1 %	48 3,6 %	29 2,2 %

Fig. 7 emphasizes the importance of an intimate knowledge of the seasons of zone formation of the particular population which is being investigated.

Comparison of the reliability of the two methods

In the preceding chapters it has been shown that the zones found in both the otoliths and the scales were annual formations in the great majority of the cases.

The abnormalities in the zone formation of the 1948 yearclass in 1949 are of considerable interest. They indicate that, in the scale, a total lack of zone formation may sometimes occur. The extreme narrowness of some of the opaque zones and zones with broad sclerites formed during this season (1949) suggests that the width of these zones is a poor criterion when one is concerned with separating "secondary" zones from true annual ones.

In table 2 is listed the age distribution of those fish on which both otolith- and scale reading have been used for age determination. The number of cases in which these two readings disagreed are listed according to their "otolith age", and the number of readings which were classified as uncertain according to their most probable age. Of the 94 cases of disagreement 53 belonged to the previously discussed part of the 1948 yearclass which had irregular zone formation in the scales.

Some previous investigations have shown fairly good agreement between the number of zones in the otoliths and the scales of the cod such as Graham (1929 I) and A. Dannevig (1933), but, as is also the case in the present investigation, the material used in these comparisons was mostly derived from young fish. A. Dannevig (1933) p. 34 says: "For adult fish the two methods give divergent results, as we evidently lose sight of the zones when using the scale method". In a comparison of the otoliths and the scales of the skrei Rollefsen (1933) found in very many cases more zones in the otoliths than in the scales: "and a careful comparison of the corresponding rings in the two classes of objects made it clear that the scale rings corresponding to the outermost otolith zones were difficult to identify on the scales". In the case of the loddetorsk, the younger immature part of the same population, Rollefsen found that the scales were perhaps just as good as the otoliths.

One is temped to conclude that in the case of the haddock and cod the otolith is a more sensitive instrument than the scale, and records smaller differences in the condition of the fish than does the scale.

The use of otoliths and scales in growth investigations.

Growth-rhythm and zone formation.

One of the most striking phenomena which one meets in growth studies of fish is the periodic character of the growth showing itself as a more or less conspicuous annual rhythm. A more thorough investigation of this rhythm demands repeated length observations covering a year or more on a population or representative samples from a population. This is a cumbersome method which can not always be used. One must however, have reason to expect a close connection between the two phenomena growth rhytm and zone formation. If such a connection does exist the simple record of zone formation will provide one with valuable information on the growth rhythm.

Table 3 shows the numbers in and the average lengths of the samples of the yearclasses 1947, 1948, 1949, and 1950 from the Brandsfjord. Assuming that the samples have been taken from the same populations one may draw conclusion as to the growth of each yearclass. The growth of fish being multiplicative it should be illustrated on a logarithmic scale. In figures 8 and 9 are plotted the natural logarithms of the observations in table 3 as ordinates, the abscissa being the time. The curves have been drawn by free hand. A more explicit illustration of the variations in growth is seen in fig. 10, obtained by plotting the monthly differences from the curves in figures 8 and 9. These figures will be approximate values of the geometrical growth rates: $G = \frac{\ln l_t \div \ln l_0}{t}$ for

Table 3. *Mean length of samples of the yearclasses 1947 to 1950 from the Brandsfjord (l in cm).*

Sample no.	Date	1947		1948		1949		1950	
		N	$\bar{l}$	N	$\bar{l}$	N	$\bar{l}$	N	$\bar{l}$
8	2/9 —48	92	20,89	28	14,39				
13	9/10 -	40	22,64	173	15,29				
20	6/11 -	10	22,70	210	15,54				
23	9/12 -	47	23,38	375	15,80				
25	29/1 —49	16	22,87	162	16,31				
26	19/2 -	14	22,89	189	16,24				
27	14/3 -	15	23,17	188	16,26				
28	27/4 -	17	21,74	169	16,27				
48	8/6 -	18	22,61	402	16,24				
53	1/7 -	6	22,17	169	16,74				
54	26/7 -	27	22,80	139	17,42				
57	12/9 -	12	24,92	133	18,24	1	11,0		
58	24/10 -	10	24,80	306	18,46	9	12,11		
66	24/11 -	11	25,89	246	18,53	15	11,47		
77	18/1 —50	14	28,11	215	19,48	12	13,38		
80	27/2 -			115	20,67	21	13,71		
81	20/3 -	6	26,92	86	20,68	14	13,89		
97	30/5 2/6	7	26,79	75	22,34	4	14,38		
99	24/6 —50			44	23,24	8	16,38		
103	25/7 -			53	23,68	4	16,75	1	8,9
104	30/8 -			28	26,61	11	18,59	35	13,97
105	27/9 -			26	25,87	17	20,68	28	14,84
106	10/11 -			16	28,56	12	23,25	69	16,35
119	5/12 -			11	29,23	18	22,94	104	16,28
121	13/1 —51			10	28,65	15	22,73	87	16,14
122	22/2 -			12	29,75	13	23,31	99	16,07
123	28/3 -					14	23,82	149	17,02
124	7/7 -							102	18,96
125	27+28/8-51							89	19,66

each month. In fig. 10 curves have also been drawn showing, for monthly intervals the percentage of fish with opaque margin and broad sclerites at the margin respectively. These values have been obtained by estimation from the diagrams in figures 3 and 4.

Fig. 10 shows that the growth curve of the 1947 yearclass drops below 0 for some time. This seems to indicate biased sampling or a changing stock. The samples contained, however, small numbers of fish. There is a good agreement between the three curves of the 1947 yearclass. In the case of the 1948 yearclass the agreement is also striking except for about half a year during autumn and winter 1949—1950 where the

The 1949 yearclass shows a marked annual rhythm in growth rate closely followed by the other curves. This is also the case with the 1950 yearclass, but as there were no samples from March until July 1951 the course of the curves during this time is somewhat uncertain.

It is difficult to find a statistical means of measuring the agreement between the curves in fig. 10. The comparison is complicated by the fact that the growth rate includes two phenomena, namely: 1) the percentage of individuals in the population which have beeng growing, and 2) the amount of growth of these individuals, whereas the curves of the zone formation merely show the percentage of fish having a certain type of zone at the margin. The good agreement found in fig. 10 accordingly seems to permit the conclusion that growth and zone formation are in fact closely connected phenomena. This conclusion is supported by the results of scale measurements, see fig. 8, where average values of scale size have been plotted below the corresponding logarithmic values of average fish length.

The growth rhythm and its connection with zone formation has been discussed in several previous works. LEA (1911) found a marked annual rhythm in the growth of the II- and III- groups of herring from the west coast of Norway, the stagnation period lasting from December to March during which the "winter rings" were formed in the scales.

A marked annual growth rhythm was also found by THOMPSON (1926) in the North Sea haddock, the period of low growth rate lasting from November—December to March—April.

GRAHAM (1929 I) found close agreement between the variations in growth rate and the type of sclerites formed in his material of cod from the North Sea. There was an almost complete stagnation of growth from September—October to March, and narrow sclerites dominated the margin from January to July.

In the hake HICKLING (1933) showed that low growth rate in the autumn was accompanied by hyaline zone at the margin of the otoliths.

In an investigation of the cod from the Norwegian Skager Rack coast A. DANNEVIG (1925) found that low growth rate gave narrow sclerites, high growth rate broad sclerites. Later he examined (A. DANNEVIG 1933) growth and sclerite formation in cod kept in confinement in the sea. Sclerite curves were compared with growth curves, but there was no agreement between broad sclerite formation and growth periods.

The major part of the works referred to above, confirm that the annual growth rhythm and its close connection with zone formation are phenomena of general character in the life history of fish. As previously mentioned the agreement between growth and zone formation can be used in obtaining valuable information on the growth rhythm from records of the marginal character. In the intricate studies of growth in fish the phenomenon of growth rhythm is of great importance and deserves more attention than it has hitherto been given.

The factor or factors responsible for the growth rhythm and zone formation have been the subject of much discussion. In most cases the interest has been concentrated on limited numbers of external factors such as temperature, food etc.

The bottom temperature at the trawling ground in the Brandsfjord was recorded from June 1950 to August 1951, in most cases at fortnightly intervals. The temperature observations are plotted in fig. 11. From an inspection of the curves in figures 10 and 11 it is obvious that there is no simple relationship between temperature and growth. High temperature in the summer 1950 is accompanied by high growth rate in all of the three yeargroups 1948, 1949, and 1950. But the growth rates decrease and reach their minima at the same time as the temperature has its maximal values in mid winter. Unfortunately the temperature observations only cover about one year, but most probably the curve in fig. 11 shows the normal pattern of annual temperature fluctuation at this depth (140 m), even if the temperatures found in June and July 1951 are somewhat lower than those found in the same months of 1950.

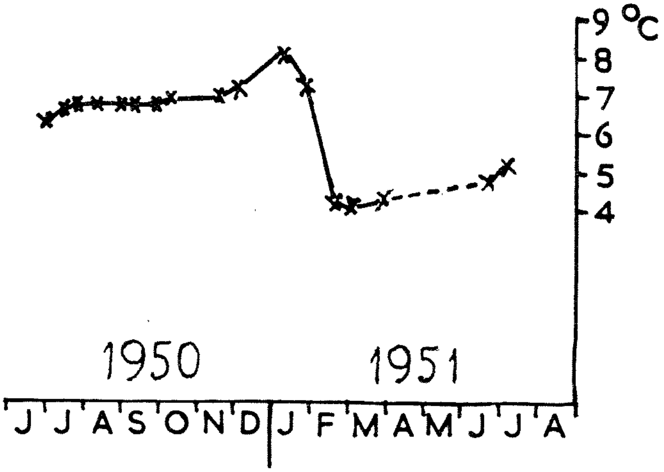

Fig. 11. Bottom temperature in the Brandsfjord at about 140 m 1950—1951.

In the herring Lea (1911) found a relationship between temperature and growth which is in the main the same as the one found in this work, the seasons of maximal values of growth rate and temperature being displaced about a quarter of a year.

Graham (1929 I) also was unable to find any obvious relationship between temperature and growth rate of young cod. In another work (Graham 1929 II) he refers some observations and experiments on factors which might effect scale structure and growth rate. The results were however in part quite contradictory, and no conclusion could be drawn.

An example of how complicated the relationship between growth rate and temperature can be, has been given by Brown (1946 III): "Two year old trout were grown in controlled environmental conditions in water of different temperature". "The specific growth rate of trout living at different constant temperatures and of those living in water of changing temperature were high between 7° C and 9° C and between 16° C and 19° C and were low above, between and below these temperatures. The existence of these two growth rate maxima may be explained by a differential effect of temperature on the amount of food eaten and the activity of the fish, the former being maximal between 10° C and 19° C the latter between 10° C and 12° C."

Another experiment carried out by the same author (Brown 1946 II) is of even greater interest in this discussion: "Two year old trout were grown in environments where the following factors were controlled: temperature, amount and intensity of illumination, rate of flow, composition and aeration of the water, quality and quantity of the food and amount of living space." Brown found that: "In spite of constant environmental conditions all the fish had an annual growth-rate cycle, with an autumn check, a spring maximum and another autumn check which coincided with maturation of the gonads when they became 3 years old." And further that: ,,The specific growth of length was directly proportional to the condition factor ($K = \frac{100.W}{L_3}$)".

These results suggest that the growth rhythm in fish is a response to an inherent rhythm which in mature fish coincides with the spawning rhythm. The hypotheses of an inherent rhythm is not a new one. It was put into words probably for the first time by Schneider (1910) in a paper on age determination of herring, and it has been supported by a number of papers since then. Thus, zones have been found in the scales of tropical fish (Schneider 1910 and Mohr 1921), and Someren (1950) reports zone formation in the scales of rainbow trout transplanted to some rivers in Kenya where the seasonal changes in the environment are insignificant. He found a high correlation between the number of spawning fish and the number of fish with a check at the margin of the scales. Zones were also formed in the scales of immature fish.

Graham (1929 I) is of the opinion that a combination of inherent rhythm and temperature is responsible for the variations in growth rates found in his material.

For the hake HICKLING (1933) was able to show close connection between the annual variations in condition, growth rate and zone formation, and the season of the maturing of the gonads. He finds that an inherent rhythm is the most probable cause of the annual variations.

In 8 different species of non-salmonide fresh-water fish from east Anglia HARTLEY (1947) found that the check formation in the scales took place in late spring and summer coinciding with the spawning season of the species.

MENON (1950 I) on the other hand was not able to find any relationship between the zone formation in the supraoccipitalia of the poor cod and condition. The hyaline zones dominated in the autumn whereas the spring was the season of spawning and low condition. However there appeared to be a rather low degree of simultaneity in zone formation in his material, thus more than 40 % of the fish had a hyaline margin throughout the spring.

In conclusion it may be said that many facts are accounted for by assuming that an inherent factor is responsible for the annual rhythm in the growth of fish. Some observations do not agree with this hypothesis, however, for example the differences found in the time of zone formation of fish populations which have approximately the same spawning season (see fig. 7). The reservations with which the comparisons in fig. 7 must be regarded have, however, been mentioned. It is also probable that the effect of the inherent factor may be modified by external factors, such as temperature, abundance of food etc. Thus overcrowding was probably responsible for the late and partly abnormal growth and zone formation of the 1948 yearclass in the year 1949 in the Brandsfjord which has been discussed above.

Growth calculations. Discussion of previous papers.

Since LEA introduced the scale method into the growth calculations of the herring in 1910 the method has been used and discussed in a great number of papers, the most important of which have been reviewed or listed in papers by GRAHAM (1929) II, MOHR (1927, 1930 and 1934), and MENON (1950 II). Here only an outline of the main problems will be given, and a few of the later papers discussed.

The main interest has centred upon the question whether the ratio between the fish length and the scale length : *k* is constant for each individual throughout its life, or at least can be illustrated by a straight line. Most investigators concerned with this problem have made use of mass observations taking large numbers of paired observations of fish and scale lengths and trying to find the functional relationship between the two sets of data. If this relationship is not a straight line passing through the origin in a cartesian coordinate system, it has been concluded that k is not constant for each individual fish throughout its life.

In determining the relationship between the two sets of data use has been made, in most cases, of the theory of correlation and regression. Lea (1933) has shown that the correlation coefficient and regression lines may give highly variable and misleading information depending upon the material used. This has also been shown by Ottestad (1934).

In a later work Ottestad (1938) discuss the question whether one can expect to find the nature of the relationship between fish growth and scale growth at all by means of mass observation. His main objection is that there is no way of making sure that the different age groups or length groups used are stages in the life history of one and the same population. On the contrary most sampling will surely be selective in one way or other. If this selection also applies to k the use of mass observation may give erroneous results. Now Ottestad shows that in Lea's material of herring from 1910 there is a positiv correlation between k and the length of the fish. The same phenomenon has been mentioned by several authors: Molander (1918), Lee (1920), and in the case of the place otoliths by Buckmann (1931): in fish of the same size, scales and otoliths of older fish will, on average, be of somewhat larger size than those of younger ones. A sampling which is selective in respect of size will in such cases give a biased distribution of k. Ottestad (1938) also draws the attention to geographical variations in k as a possible source of error.

In an attempt to find a better formula for growth calculations of herring Lea (1938) makes use of paired means of fish lenght and scale length of age groups in order to determine the relation between fish growth and scale growth. The mean points were distributed very regularly along a line of the type $\bar{l} = a + b.\bar{s}$, and he deduced the following formula $l = \frac{L}{S} \cdot s + A\,(1 \div \frac{s}{S})$, (which can also be written $l = \frac{L \div A}{S} \cdot s + A$) The constant A is determined from the equation $\bar{l} = a + b.\bar{s}$.

This formula for individual growth calculation will give mean values which will lie near the empirically determined line $\bar{l} = a + b.\bar{s}$, but this does not mean that each individual calculation is correct. Lea does not discuss the geometrical significance of his formula. It describes, however, straight lines passing through the point $l = A$ on the l-axis, their individual angle coeficient being the relation $\frac{S}{L\text{-}A}$ (see fig. 14). Thus calculations with this formula presuppose that the lines describing the relation between fish growth and scale growth for each individual fish (Lea's "individual lines") are straight in that period of the life history of the fish in which growth calculations are undertaken, and furthermore that all the lines meet in the point $l = A$ on the l-axis. It is possible that the individuals lines are straight throughout the whole or the greater part of the life of the herring, but it is unlikely that all the lines or the extrapolated straight parts of the lines should meet in one point on the l-axis. However, small differences in A will have but little influence on the results of the calculations, and as mentioned above the mean values will be correct.

Lea found a numerical value of A lying between 8 and 12 mm. He emphasizes that this quantity A has no biological significance and must not be confused with the length of the herring when the first scales are formed, which is of no consequence for this formula. In mentioning the same kind of formula Schuck (1949) also points to the fact that: „the relationship between fish and scale size during the first year is completely inconsequental to the problem of back calculation to the first annulus".

A simple arithmetic formula which can be described as a straight line in an ordinary coordinate system as the one mentioned above can be used when the growth of the two quantities are isogonic, that is when their geometric growth rates are the same (Simpson & Roe 1939). If the geometric growth rates are different, but maintain a constant ratio to each other, the type of growth is called simple heterogony, and can be described as a straight line in a logarithmic coordinate system. Le Cren (1947) using the opercular bone in growth calculations of perch arrived at the following formula: $l = L. \frac{b^{0,9202}}{B^{0,9202}}$ or $\log l = \log L + 0.9202 (\log b \div \log B)$. The ratio between the geometric growth rates 0,9202 is not very far from 1, but sufficiently so to give results differing significantly from those obtained when using an arithmetic formula.

A further complication of the method of growth calculations by means of scales arises from the fact that scales taken from different parts of the fish give different results. In the herring (Lea 1910) and the haddock (Thompson 1923) the numerical values of the computed l_1's have been shown to increase when scale sampling occurs from the head towards the tail. In a more detailed investigation of this phenomenon A. Dannevig & Høst (1931) found increasing numerical values of

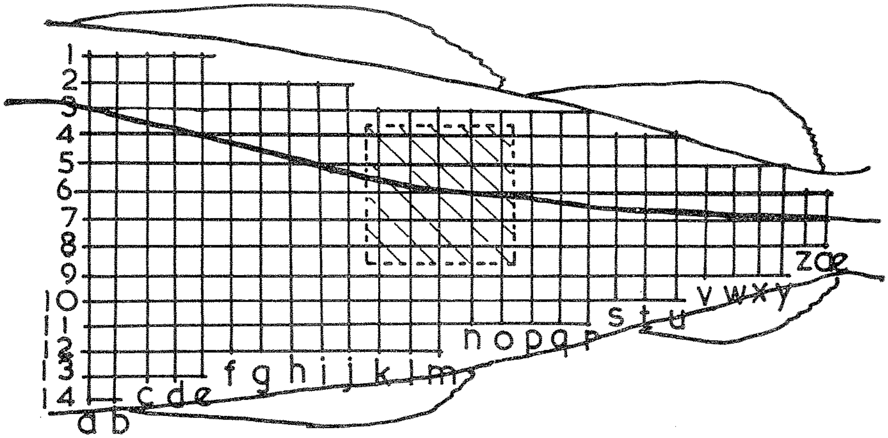

Fig. 12. Growth calculations with different scales from the same fish. Crossings of lines indicate position of the scales used. The selected area is hatched.

l_1, l_2, and l_3 towards the tail in salmon, trout, cod, coalfish, pollack, and haddock.

In order to get the best possible result of the scale measurements undertaken in this work, the following procedure was chosen:

1) An area on the fish was sought in which the variation in the computed lengths from one scale to another was small, thus improving the comparability of the individual computations.

2) Large numbers of paired observations of fish length and the length of a scale from this area were collected and a curve describing in the best possible way the relationship between these two sets of data was determined.

Scales from different parts of the fish.

In this investigation a 3½ year old fish measuring 45 cm was used. 246 scales were taken from points shown approximately by the intersections of the lines in fig. 12. In 66 of the scales the central parts were more or less blank.

Lea's simple proportion formula was used in the calculation of l_1, l_2, and l_3 on the remaining 180 scales. At least in the case of the l_1 and l_2 there was the same tendency to increase towards the tail region as found by others. By the inspection of tables and diagrams showing the calculated lengths an area was found in which the variations seemed small (hatched in fig. 12). Table 4 shows the means and standard deviations of A: all the 180 scales, B: 90 selected large and regular scales and C: the 22 large and regular scales from the selected area. The means

Table 4. *Calculations with different scales from the same fish. Mean values and standard deviations for A: all scales used, B: only large and regular scales, and C: large and regular scales in the selected area.*

	A N = 180		B N = 90		C N = 22	
	$\bar{l}$	σ	$\bar{l}$	σ	$\bar{l}$	σ
l_1	15,47	0,73	15,54	0,54	15,54	0,33
l_2	24,38	0,97	24,62	0,76	24,69	0,54
l_3	31,72	0,87	31,85	0,73	31,88	0,53

Table 5. *Calculated values of l_1 based on 10 measurements of each of 3 scales.*

1st scale		2nd scale		3rd scale	
cm	N	cm	N	cm	N
14,3	4	15,7	1	14,8	1
14,5	3	15,8	5	15,3	5
14,7	1	15,9	3	15,5	2
14,8	2	16,2	1	15,8	2
	10		10		10
σ = 0,19 cm		σ = 0,13 cm		σ = 0,27 cm	

are approximately the same in B and C, and somewhat lower in A, but the standard deviation figures reveal the advantage of using scales from the chosen area.

Some of the variations found are due to inaccuracies of observation (arising from the technique). Table 5 shows the spread in the l_1's calculated from 10 separate measurements of each of 3 regular scales. Accordingly about half the variations found in table 4 are probably caused by inaccurate observations.

Thus individual growth calculations based on one scale can never be expected to give entirely satisfactory results. The „error" will depend upon a number of factors such as age and length of the fish, quality of the scale, technique etc. When computing average values of l_1 etc. the errors will of course be smoothed out.

The relation between the growth of the fish and the growth of the scales from the selected area.

In fig. 13 paired means of scale size and fish length have been plotted. In the material from the Brandsfjord constituting the 1947 and 1948 yearclasses, the samples have been kept separate. The material from

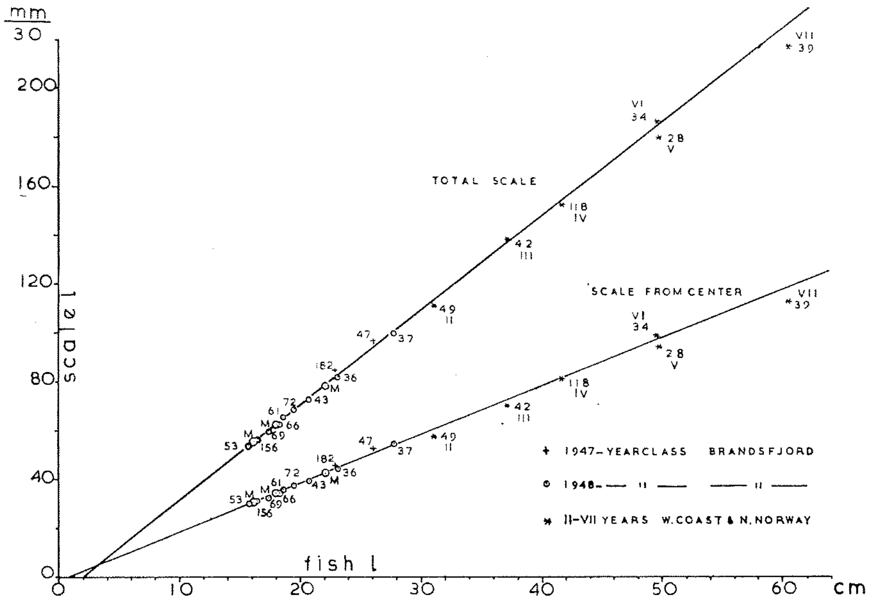

Fig. 13. Paired means of scale size and fish length. The lines have been roughly fitted to the observations of the 1948-yearclass by the help of the three mean values marked M.

the West and North Norway have been grouped according to age. Two measures of scale size have been used: total scale and scale from centre to posterior margin.

The points in fig. 13 are distributed along straight lines with a fair degree of regularity. The exact determination of the lines which are best fitted to all observations offers some difficulties, and as mentioned in a previous chapter several objections may be raised against the supposition that such lines do in fact describe the true relationship between the two sets of data. This will not be the case if the sampling has been selective in respect of k, a possibility that may arise through a correlation between k and growth rate.

The material of the 1948 yearclass from the Brandsfjord is however probably not selective in respect of growth rate, and by using this material alone the possibility of selection for k should be excluded. The straight lines in fig. 13 have been fitted to the observations of the 1948 yearclass by the help of the three means marked M.

There are no essential differences in the distribution of the points along each of the two lines. Being most convenient the use of the posterior of the scale (scale from center) should accordingly be preferred.

The two lines have interceptions of the l-axis of approximately 1 cm and 2 cm. These quantities have no biological meaning, but they prove the existence of a change in the relationship between scale growth and fish growth since no scales are formed until the fish is 3 to 4 cm.

From the regular grouping along a straight line of the paired means in fig. 13 one must be permitted to infer that the lines describing the relation between fish and scale growth in each individual are also rectilinear. The average interception of the l-axis of these individual lines is approximately 1 cm. If it is assumed that all the individual lines *meet* in the point $l = 1$ cm the formula for growth calculation is: (see fig. 14) $l = \left(\frac{L \div 1}{S} s + 1\right)$ cm.

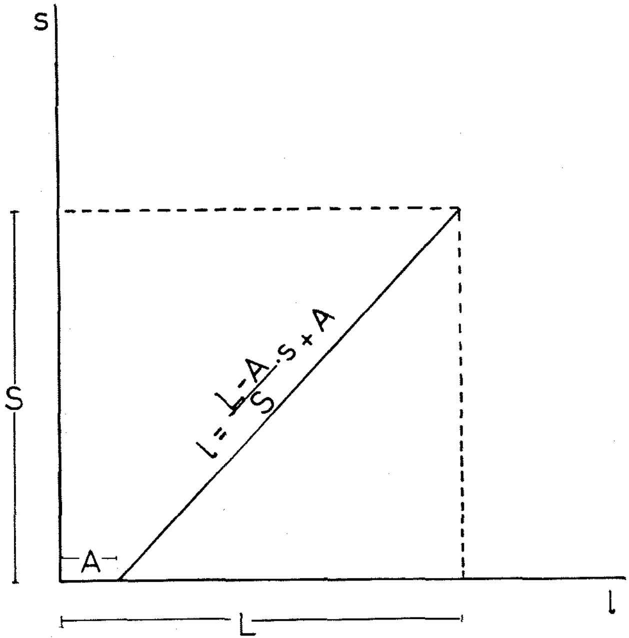

Fig. 14. Illustration of a rectilinear relationship between fish- and scale growth with a positiv interception of the l-axis and the formula to be used in such cases.

The relation between the growth of the fish and the growth of the otoliths.

In studying the structure of the hake otoliths HICKLING (1931) found that they consisted of an inorganic crystalline substance and concentric shells of organic substance which were bound together by radial fibres. The distance between the shells was fairly constant at about 2 μ, whereas their thickness varied from 1,5 μ to extreme thinness.

Table 6. *Measurements on different sections of the same otoliths (in 1/225 mm) and the corresponding calculated l-values (in cm).*

Otolith	Section	Otolith measurements						Calculated lengths				
		o_1	o_2	o_3	o_4	o_5	ot	l_1	l_2	l_3	l_4	l_5
I	1	333	402	496	509		597	21,2	25,6	29,8	32,4	
	2	330	394	464	530		602	20,8	24,9	29,3	33,4	
II	1	287	385	485	550	630	719	18,8	25,2	31,7	36,0	41,1
	2	284	377	473	547	636	747	17,9	23,8	29,8	34,4	40,1
	3	278	385	482	560	645	743	17,6	24,4	30,5	35,4	40,8
III	1	290	391	463	524		608	18,6	25,0	29,5	33,4	
	2	280	401	477	547		627	17,4	25,0	29,7	34,0	

HICKLING found that the ringed structure was caused by grouping of shells with different thickness, thick shells predominating in opaque zones, thin shells in hyaline zones.

The structure appearing in thin ground sections of haddock otoliths studied under a high magnification agrees very well with the photographs shown in HICKLING's paper. The structure can probably be interpreted as growth stages of the otolith. This then also applies to the hyaline zones. In a transverse section the growth centre can in most cases easily be found as in fig. IX (plate). In a longitudinal section there appeared to be no distinct point of centre, the structure rather implying that the otolith is initiated as a small rod. The central part is however located slightly towards the blunt end of the otolith, and it seems to be accompanied by a distinct notch in the edge of the longitudinal sulcus at the surface of the otolith. A transverse section cut near this notch will therefore show all the zones in an otolith, and will probably be the best plane on which to undertake measurements. The procedure of measurements was as follows: The otolith was broken near the point of the notch and ground down to this point. On the suggestion of Mr. G. C. TROUT of Lowestoft, a Standard Ramsden Screw Micrometer Eyepiece was used, the magnification being 25 xx, and the unity 1/225 mm. Fig. IX (plate) shows the axis of measurements and the way in which the zones and the total size of the otolith was measured.

In order to examine the variations in the resulting growth figures caused by small differences in the position of the plane of measurements in the area of the notch, this plane was varied a little within limits which might be expected in routine measurements. Table 6 shows the results of the measurements, and the calculations based on the simple proportion formula. The number of observations are too small for any statistical treatment, but from the order of magnitude of the variations found it

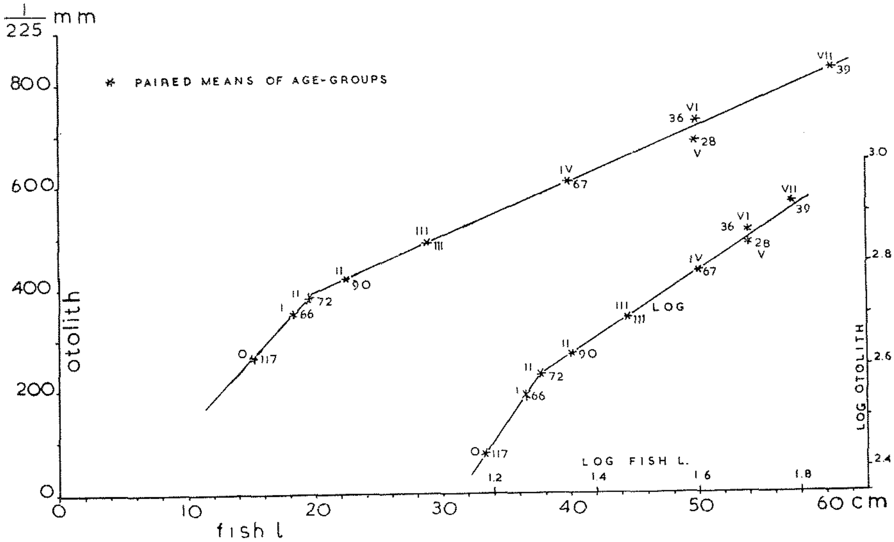

Fig. 15. Otolith measurements and fish length. The lines have been roughly fitted to the paired means. Logarithmic values to the right.

is evident that the method is not well suited for individual growth calculations. When using averages of a sufficiently large number of observations this factor of variation will be smoothed out.

In an effort to find the relationship between the growth of the otolith and the growth of the fish, the size of the otolith from the centre along the axis shown in fig. IX was measured in a number of samples. In fig. 15 the results are plotted as paired means of age groups. The points seem to be distributed along two straight lines or a curve. The shape of this curve can not be caused by a selectivity in the material as previously discussed. There is obviously no simple rectilinear relationship between otolith size as defined here and fish length. It is possible that another definition of otolith size, for instance total length, might give a rectilinear relationship. HICKLING (1933) examined the relation between total length of hake otoliths and fish length, and his curve has much the same form as the one shown here. It is thus probable that the curve in fig. 15 describe the true relation between the growth of the fish and the growth of the otolith. This relationship is not isogonic, nor can it be descibed as simple heterogony as the bend in the curve is still apparent in a logarithmic coordinat system. Apparently this is a case where the ratio between the two geometric growth rates: the coefficient of heterogony, suddenly change. Such changes are in some instances known to be coincident with important physiological events in the life of the organism such as onset of maturity (SIMPSON & ROE p. 372). The inflexion of the curve in fig. 15 corresponds to a fish length of about 20 cm. This does not agree very well with the average length of the fish attaining maturity which in the pertaining areas probably lies above 30 cm.

The complicated relationship between otolith size and fish length renders the use of otolith measurements difficult for growth calculations. It is, however, possible that by using average values of sufficiently large number of observations the method can be of some interest. As no formula can be deduced, the average values of zone widths must be used to compute the corresponding average l_1 etc. graphically from the curve itself.

There are not many papers on the use of otoliths for growth calculations. BUCKMANN (1931) has made some use of the otolith of the plaice in growth investigations of this species. He found the width of the rings to be a useful criterion of the growth conditions in the corresponding season. In the calculation of l_1 in hake HICKLING (1933) used otolith measurements. In an investigation of the poor cod MENON (1950 I) measured the length and the width of 600 otoliths, but he was not able to find any correlation between either of these quantities and the length of the fish.

Comparison of growth calculations based on the scales and on the otoliths.

There can be little doubt that the scale method is the superior of the two, giving more accurate and reliable results. It may be of some interest to examine the agreement obtained when using the two methods on the same material.

In table 7 are listed the results of three different methods of growth calculations: graphical computation based on average values of zone widths of the otoliths, graphical computation based on the scales, and calculations based on the scale formula. In the cases where the number of observations is not too small (italics in table 7) the agreement is fair.

Comparison of growth calculations and empirically known data of the average length of age groups have been used by several authors in ,,controlling'' the calculations. Generally this is not a sound procedure since it leaves no room for a change in the population sampled, but in some special cases it may prove valuable. In the Brandsfjord, the 1948 yearclass was sampled for more than two years during which time there was probably no important change in the population. In table 8 the means and standard deviations of the calculated l_1 of six samples of this yearclass are shown. For comparison the mean length and standard deviation of five samples of the same yearclass, caught during the season of the first growth stagnation are included. The greatest difference between the two sets of data is found in samples 77/26 (or 48). The difference is 0,14 cm, and this is 0,97 times the standard error of the difference and not significant. Without further statistical tests it seems permissible to conclude that all the observations in table 8 were drawn from the same population.

Table 7. *Growth calculions based on otoliths and on scales. Comparison of results. (l in cm).*

Sample No.	Date	Age gr.	N	$\overline{l}$	Otoliths graph.		Scales graph.		Scales formula	
					$\overline{l_1}$	$\overline{l_2}$	$\overline{l_1}$	$\overline{l_2}$	$\overline{l_1}$	$\overline{l_2}$
77	Br.fj. $^{18}/_{1}$–50	II	*72*	19,47	*17,1*		*16,5*		*16,38*	
104	Br.fj. $^{30}/_{3}$ -	II	*26*	27,19	*17,0*	*20,6*	*16,1*	*20,0*	*16,35*	*20,37*
48	Br.fj. $^{8}/_{6}$-49	II	17	22,59	17,2		16,1		15,97	
66	Br.fj. $^{24}/_{11}$ -	II	11	26,09	17,1	23,0	16,6	23,2	15,32	21,36
43	Vardø $^{2}/_{6}$ -	IV	*24*	37,96	*17,5*	*23,2*	*17,1*	*22,9*	*17,29*	*23,10*
83	Røstb.$^{22}/_{3}$-50	V	13	56,15	17,0	23,5	15,0	22,0	16,42	24,00
	Røstb. —	VI	12	55,86	17,1	22,2	16,1	22,6	15,30	21,40
	Røstb. —	VII	*37*	60,21	*17,1*	*23.6*	*16,2*	*23,7*	*16,28*	*24,12*

Table 8. *Mean values of calculated l_1 compared with «empiric» mean lengths of samples from the first period of growth stagnation. 1948-yearclass, Brandsfjord. (l in cm).*

Sample No.	Date	N	$\overline{l_1}$	σ	Sample No.	Date	N	$\overline{l}$	σ
66	24/11—49	61	16,27	0,917	25	29/1—49	162	16,31	1,016
77	18/1 —50	72	16,38	1,081	26	19/2—49	189	16,24	1,064
81	20/3 —50	43	16,22	1,241	27	14/3—49	188	16,26	0,961
99	24/6 —50	37	16,35	1,033	28	27/4—49	169	16,27	0,928
104	30/8 —50	27	16,35	1,468	48	8/6—49	402	16,24	0,966
119	5/12—50	11	16,36	1,109					

$d/\sigma\, d$ samples 77/26 = 0,14/ 0,144 = 0,97 method for age determination). This comparison showed that the Petersen method and the otolith readings gave nearly identical results, showing the correct age, whilst 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 the 1948 yearclass in the year 1949.

The marginal character of the otoliths and scales was recorded in a number of samples, and distinct annual fluctuations were found. In the Brandsfjord hyaline zone and narrow sclerites were the dominant marginal characters from October—November to May—June. In Finnmark the hyaline zones seemed to be laid down in the months from September to May. A few samples from more southern localities (West Coast) suggest that in these parts the opaque zones were laid down earlier in the year.

A comparison with the seasons of zone formation found in other investigations showed that great variations may occur. Therefore an intimate knowledge of the zone formation of the particular population which is being investigated is a condition for the proper use of otoliths and scales for the purpose of age determination.

The seasons of zone formation were compared with the annual rhythm in growth, and a close connection was found between these two phenomena. Opaque zones and broad sclerites were formed mainly during growth periods, hyaline zones and narrow sclerites during periods of growth stagnation. It is suggested that this agreement between growth and zone formation can be used in obtaining valuable information on the growth rhythm in fish populations from records of the marginal character.

The factors responsible for the growth rhythm and zone formation are discussed. There was no obvious relationship between the bottom temperature in the Brandsfjord and the annual rhythm in growth and zone formation. A review of some literature on this subject indicated that the most plausible cause is an inherent rhythm coinciding with the spawning rhythm in mature fish.

Some of the later papers on the methods of growth calculations are discussed. In order to get the best possible results of the scale method the following procedure was chosen by the author: 1) An area on the fish was found in which the variation in the computed lenghts from one scale to another was small. 2) Large numbers of paired observations of fish length and the size of a scale from the selected area were collected and a curve describing in the best possible way the relationship between these two sets of data was determined. This curve proved to be a straight line which intercepted the *l*-axis in the point $l = 1$ cm when being extrapolated. The formula corresponding to this relationship is: $l = \left(\frac{L \div 1}{S}.s + 1\right)$ cm.

The relation between the growth of the fish and the growth of the otoliths was found to be rather complicated and not suited for individual growth calculations. It is possible that by using average values of sufficiently large numbers of observations the method can be of some interest. The scales are, however, undoubtedly superior for the purpose of growth calculations.

In the last chapter it is shown that the populations of the various yearclasses in the Brandsfjord were nearly identical for one and up to two years after they entered the fjord. This is a point of great importance for the conclusions drawn in the previous chapters.

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PLATES

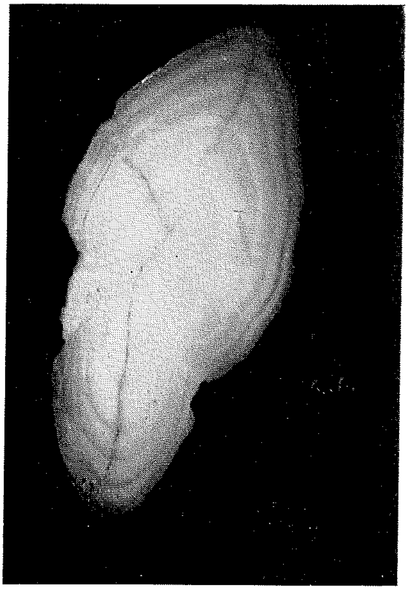

Fig. I. Otolith of a 5 year old fish (35 cm) from Karmøy 15/6 1948. Reflected light.

Fig. II. Same otolith as in fig. I, photographed in transmitted light.

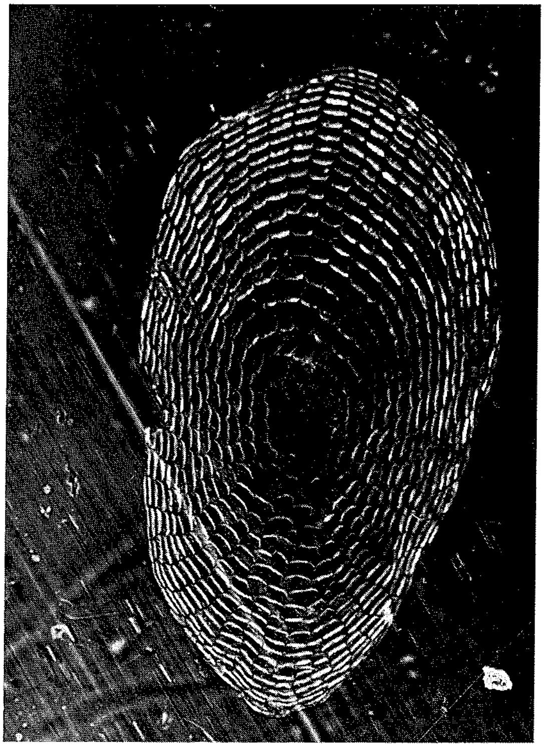

Fig. III. Scale of a fish from sample no. 77, Brandsfjord 18/1 1950. Fish length 15,5 cm.

Fig. IV. Otolith of same fish as in fig. III.

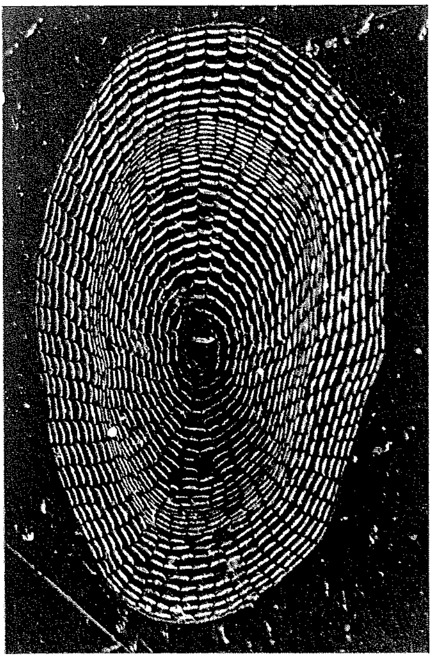

Fig. V. Scale of a fish from sample no. 104, Brandsfjord 30/8 1950. Fish length 24 cm.

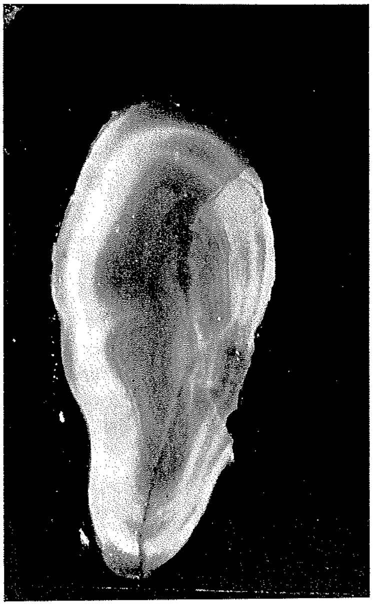

Fig. VI. Otolith of same fish as in fig. V.

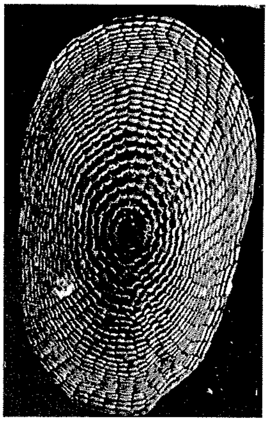

Fig. VII. Scale of a fish from sample no. 99, Brandsfjord 24/6 1950. Fish length 21,5 cm.

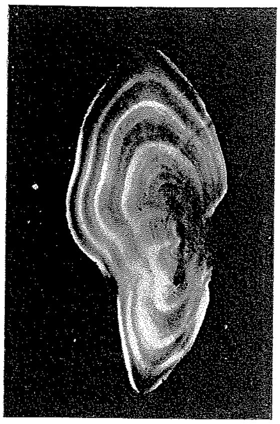

Fig. VIII. Otolith of a 3 year old fish from sample no. 10, Ogna 6/9 1948. Fish length 46 cm.

Fig. IX. Otolith of a 4 year old fish from sample no. 43, Vardø 2/6 1949. Fish length 36 cm.