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Contributions to the Plaice  
Investigations in Norwegian Waters

By

FINN DEVOLD

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A.s John Griegs Boktrykkeri, Bergen



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## PREFACE.

The present paper contains the results hitherto arrived at during the investigations on the plaice in Norwegian waters. In earlier years investigations on the plaice were made more or less casually as the plaice fishery has played only a slight part until 20 years ago when it began to develop into a fishery of great economic importance. As the fishermen during the same period have voiced an increasing demand for protection of the plaice stock, more regular and intensive investigations had to be inaugurated also in respect of the Norwegian stock of plaice.

I wish to express my thankfulness towards the successive Fishery Directors, the late mr. ASSERSON and messrs. SALVESEN and BRYNJELSEN, and to the manager of the Research Branch, mr. BJERKAN, for the confidence shown to me in entrusting me with this investigation. At the same time I wish to render my thanks to the trustees of the Fisheries Research Fund who have granted the greater part of the necessary expenses.

My thanks are also due to mr. C. DONS, director of the Trondheim Biological Station, for submitting every year the rich plaice material collected for the hatchery of the station, and to captain BERNHARD HANSON who has supervised the collection of this part of the material.

Cordial thanks are offered my fellow-workers at the Research Branch, messrs. BJERKAN, EGGVIN, ROLLEFSEN and SUND for informations and advice on many occasions. To the last-named I am specially indebted for his never failing interest and assistance in the formal presentation of the results. The drawings were made by messrs. TH. RASMUSSEN and T. KROG. The text was translated by lector GLAMBEK and then revised by mr. SUND.

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## BRIEF SURVEY OF PLAICE FISHERY IN NORWAY.

The plaice, *Pleuronectes platessa* Lin., has long been the object of fishing in Norway. The first description of plaice fishing is found in STRØMS »Søndmørs Beskrivelse« (31), printed in 1762. STRØM tells us that the plaice was caught particularly off a number of small isles on the coast of Møre where there is a flat sandground in the sea. The fishing proved to be fairly profitable. The plaice were caught by long-lines, baited with *Arenicola marina* Lin.

O. N. LØBERG (21) describes plaice fishing in Norway in the middle of the last century. Special plaice gillnets were used at that time, of the type still used, as well as longlines baited with herring or mussels, and in shallow water also two-pronged spear. The fish were particularly taken off Sunnmøre, Lofoten and Vesterålen. The plaice were dried and shipped to Bergen. The price of dried plaice varied between 1½ and 2 »species dollar« a »våg« (18 kg) or 0,35—0,50 shillings pr. kg.

We have some historical dates regarding the plaice-fishery in the Trondheim Fjord, collected by O. NORDGÅRD (23). From these papers we can infer that there has been plaice-fishing in Norway from olden days, but only in this century it has developed to be a factor of importance in the Norwegian fisheries. The cause is the development of fresh fish export, and the introduction of the Danish seine.

The Danish seine was invented by the fisherman JENS LAURSEN VÆVER in 1848. This implement created the Danish deepsea fishing as it became successively known, and is to day probably the most important fishing implement in Denmark. In Norway it was used for the first time with success by KNUT DAHL in 1899 during fishing experiments on the coast of Helgeland on board the cutter »Motor«, captain G. M. HELGERUD. They succeeded in the course of a few days in fishing 3000 kg plaice, sold in Trondheim at 50 øre a kg. This success caused Mr. HELGERUD to continue the fishing as a commercial undertaking in Helgeland and in Lofoten from 1900. The firm O. HEGSTAD, Trondheim, started a similar activity in Lofoten from 1902. The plaice were brought alive to Trondheim in welled smacks. According to BJERKAN (2) the firm

*Blauw*, Bergen, tried plaice-fishery with Danish seine in 1904 along the coast as far as Hammerfest, but this attempt was soon given up as it fell short of the expectations. The people of Nordland, however, soon started plaice-fishing with Danish seine themselves. Fishermen from Henningsvær (Lofoten) in particular were pioneers in this domain and fishermen from Sunnmøre soon joined them, having been taught the method of fishing by Swedish smack fishers working off Ålesund.

The man, however, who has done most to spread knowledge of the Danish seine among Norwegian fishermen, was mr. M. BARCLAY, for many years secretary to »*Society for the Promotion of Norwegian Fisheries*«, later inspector of fisheries. BARCLAY wrote a very instructive article about Danish seine fishing in »*Norsk Fiskeritidende*« 1899, and in 1920 a new article treating the improvement introduced in the Danish seine fishing. Reprint of these articles were distributed among the fishermen, and BARCLAY declared himself willing to advise in purchase of the gear. At the same time the »*Society for the Promotion of Norwegian Fisheries*« provided Danish seines to be lent to fishermen.

The Danish seine requires an even bottom to fish effectively. The Norwegian Coast is, however, anything but rich in sandy flats, and those found are small. The implement works so effectively that it pretty soon will fish up most of the plaice available in such places. The fishermen therefore will have to make pauses in their fishing to allow more fish to gather. To begin with the dense accumulations of plaice resulted in fancy catches. But, as will always happen when a new, effective fishing method is introduced, the catches quickly decreased, and the fishermen had to search for new, unused fishing grounds. A few experts who went all along the coast, made fine catches and became well-to-do people. They created, however, exasperation and anxiety among the fishermen wherever they appeared.

#### *Strife about the Danish Seine.*

Protest against this new form of fishing did not wait long to be recorded. In november 1918 already the inspector of fisheries for Nordland and Troms had to send inquiries within his district to parish councils and fishermen associations asking their opinion about the Danish seine fishery (BJERKAN 2). The replies showed that a majority of them wanted Danish seines prohibited. In august 1919 mr. BJERKAN went to Lofoten where the controversy was then particularly bitter. His experiences were, however, such that he could not advise that the use of Danish seines should be prohibited, but suggested, in accordance with mr. NORDGÅRD (the late leader of the plaice hatchery in Trondheim)

that a minimum measure for plaice ought to be introduced, and protection during the time 15. March — 15. May.

The conflict about the Danish seine called forth a number of newspaper articles, public discussions and resolutions from meetings of fishermen. This proved to be the very best propaganda for the Danish seine. Everywhere it was described as a very profitable fishing-gear and opinions as to its injurious effects differed. Many fishers therefore purchased Danish seines and fitted out their boats for its use. Soon also the Danish seine slightly modified was used for »round fish« as well. The development of the popularity of the new gear is brought out by the following figures.

Table 1. *Number of Danish Seines and Round Fish Seines in Norway.*

Year	Danish seines	Round fish seines	Total
1925 .....	301	?	301
1926 .....	417	?	417
1927 .....	525	189	714
1928 .....	526	138	664
1929 .....	704	162	866
1930 .....	741	228	969
1931 .....	870	218	1 088
1932 .....	1 178	252	1 430
1933 .....	1 267	254	1 521
1934 .....	1 279	281	1 560
1935 .....	1 292	282	1 574
1936 .....	1 372	305	1 677
1937 .....	1 392	341	1 733
1938 .....	1 453	384	1 837
1939 .....	1 415	382	1 797

There are no data further back than those given in table 1.

Unfortunately exact statements of quantities given in our official statistical tables are inaccurate regarding the plaice, partly quite erroneous. On the other hand we have very exact statistics relating to the export of plaice and using these as a measure of the development of the plaice fishery we have constructed fig. 1. The figures are taken from »Norges handel«.

There was a rapid rise in the plaice export from 78 tons in 1922 to 4699 tons in 1932, then a sudden fall of more than 1000 tons in 1933. The quantity of plaice exported remained about 3500 tons till 1936 when it decreased to 2750 tons. After 1936 there has been no important change.



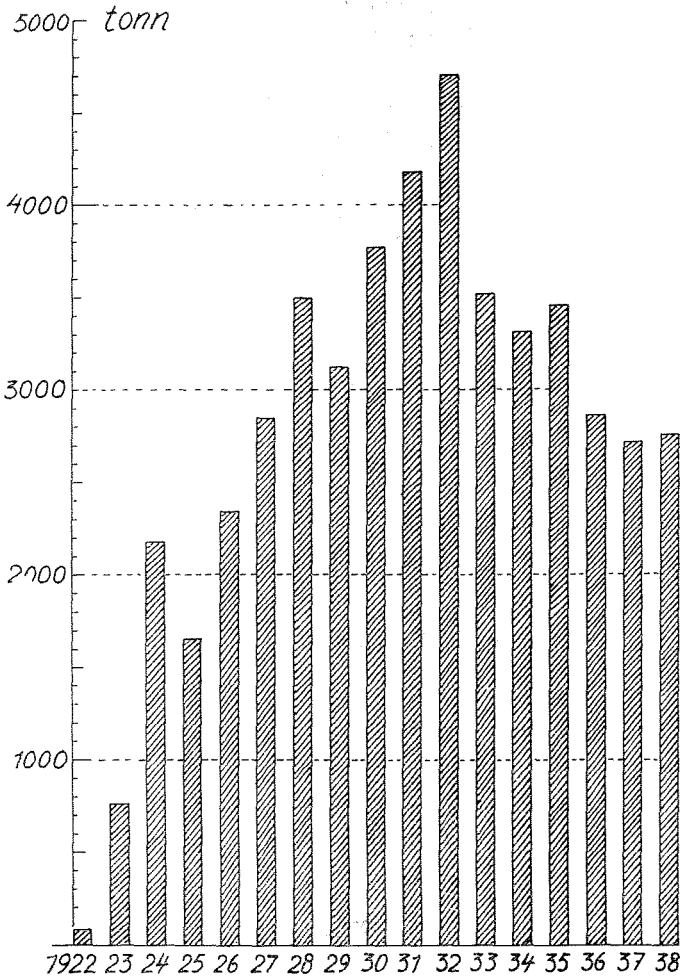


Fig. 1. Norwegian export of plaice.

*Restrictions on the Fishery.*

The Danish seine fishery was allowed to develop without any interference until 1933 when several regulations restricting the plaice fishery were introduced, viz:

1. A general prohibition to catch plaice between the 15. march and the 30. May, while the fishery of plaice with Danish seine was made unlawful during a longer season, viz. 1. March to 31. July.
2. A regulation that all plaice of total length of less than 27 cm had to thrown overboard at once.

3. Introduction of quota and other rules for the export of fresh fish to Great Britain. According to these plaice under 500 g was not to be exported.

4. Prohibition was established against export of all fresh fish, caught east of North Cape during the warmest season.

Point 2 of the act was, however, changed before it had been in force for a whole season. In an act of 6. July 1933 the general close-season was fixed as from 1. April to 15. May, while the Danish seine was prohibited between 15. March and 30. June. The size-limit of plaice exportable to Great Britain was, however, lowered to 400 gr.

These restrictions (point 1 to 4) may be responsible for most of the sudden fall, seen in fig. 1, in the quantity of exported plaice in 1933.

The fishing for halibut by means of gill-nets, starting in the autumn of 1936, which caused many of the plaice fishermen to change over to halibut fishing in the autumn season, may be made responsible for the further fall in 1936.

Thus plausible reasons can be given for the decrease in quantity of plaice caught after 1933 but the fact remains that the output pr. boat pr. day's fishing has been greatly reduced during later years. Unfortunately, our statistical data do not afford exact evidence of this.

The plaice fishery during the last 20 years has grown to be a trade of economic importance, and should be protected and carried on in a rational manner. The great number of demands for protection of the plaice, prohibition of the use of Danish seine in plaice fishing etc., has made it necessary for the fisheries administration to collect information about the plaice fishery, to gather facts about the biology of the plaice, and to make investigations as to the quantity which may rationally be caught, in other words, it has become necessary also in Norway to start plaice investigation on a broad base. Some of the results achieved till now will be dealt with in this paper.

## REVIEW OF PLAICE MARKING EXPERIMENTS IN NORWAY.

The length of the Norwegian coast with the great number of deep fjords and varying depths makes it probable that there are many different plaice populations in these waters. The earlier investigations which might be expected to give us some information about this, were, however, limited to marking experiments.

The first marking experiment of plaice in Norwegian waters was made by JOHAN HJORT in 1899. In connection with the transplantation of 23 000 young plaice from Danish waters to the Oslo Fjord HJORT had 1 400 marked. The experiment has been described by A. WOLLEBÆK (33). Only 20 recaptures were recorded from this marking experiment, and the greater number were recaptured near the spot where the plaice had been liberated. One was taken off Horten, thus having left the inner basin of the fjord where the marking had been done.

In 1908 O. NORDGÅRD (23) liberated 78 and 58 marked specimens of plaice on the 12. and 13. May resp. off Tautra in the Trondheim Fjord. Of these 30 were recaptured in the course of the 5 years following. The percentage in the first year was 18. They were all taken east of Trondheim, in the Trondheim Fjord proper.

The plaice tagged by NORDGÅRD were fished in Lofoten and carried in a well-smack to the Biological Station of Trondheim. The plaice had spawned before the marking in the basin at the newly founded hatchery at the station. The long-travels are entered in the chart fig. 2.

In the years 1924, 25, 31 and 32 P. BJERKAN (3, 4 and 6) made marking experiments at various places on the Norwegian coast. A review of these markings will be found in the following table.

The map fig. 3 shows that the coastal plaice have travelled rather far. Recaptures show that the plaice marked at the Norwegian Coast may cross the Norwegian Channel, thus having connection with the North Sea plaice.

Based on his marking experiment in Lofoten BJERKAN (6) divides the plaice into one fairly stationary mussel-eating population and one «migratory-plaice» feeding mostly on sand-eel (*Ammodytes*). Many

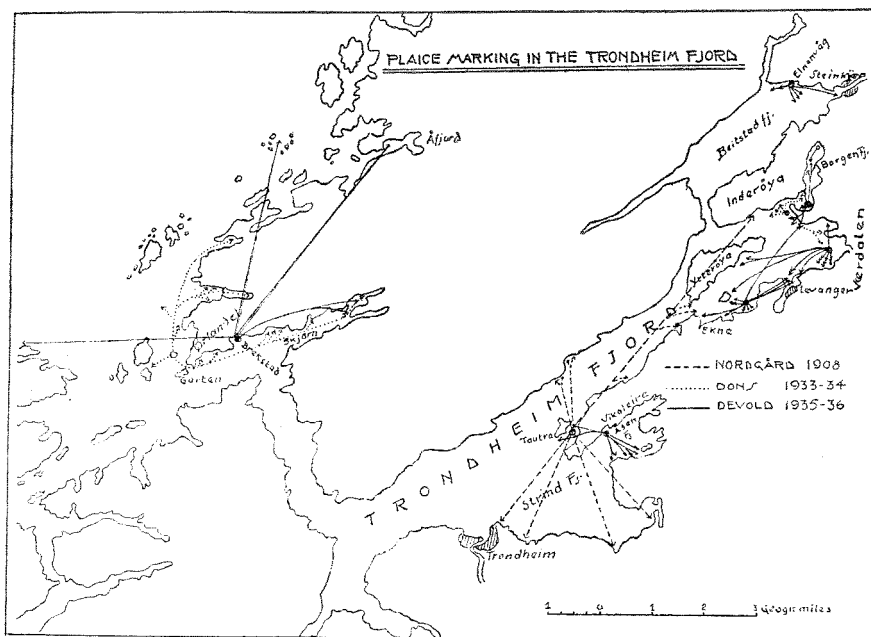


Fig. 2. Long journeys in the Trondheim Fjord.

fishermen are of the same opinion, claiming to be able to see the difference. The «migratory-plaice» is said to be slimmer, and paler in colour than the «shell-plaice». BJERKAN cites the marking experiment at Nappstømmen as an example of the stationary shell-eating population. The recaptures from this marking experiment were made near the place of liberation, and most had shell in their stomach. An important objection to this conclusion is, however, that BJERKAN in this marking experiment used only small plaice, such as the fishermen throw overboard as being too small for sale. It is a well known feature in the biology of the plaice that it is fairly stationary in the immature stage, and may start for longer travels only when ripe for spawning. The slight movement shown by the marking experiment may therefore be interpreted as nothing more than a further example that young plaice, also in Norwegian waters show less propensity for migration than the ripe fish.

In 1933 and 1934, the curator of the plaice hatchery in Trondheim mr. C. DONS, made fresh marking experiments with plaice used in the hatchery. On the 11. May 1933 500 specimens of plaice were set free at Grandeviken at the mouth of the Trondheim Fjord. Of these 123 were recaptured in the course of one year, that is 25,2 %. The places of recapture indicate very little movement. The long-travellers are entered on the chart, fig. 2.

Table 2. *Plaice marking carried out by P. Bjerkan.*

Locality	Date	Number Marked	Number Recaptures	%
N.W. of Henningsvær, Lofoten ..	20/8—24	12	0	0
N. —————	31/8—24	30	1	3,3
Ytre Steinfjord, Borge, Lofoten ..	20—22/8—24	31	3	9,7
Indre Steinfjord, Borge Lofoten ..	23/8—24	45	2	4,4
Nappstømmen, Buksnes, Lofoten	23/8—24	88	13	14,8
Nybotten, Gimsøy, Lofoten ....	15/6—25	9	2	22,3
Nordbotnene, Hasselfj., Lofoten	17—18/6—25	27	9	33,3
Laukvik, Lofoten .....	17/6—25	3	2	66,7
Nøkkelen N. of Henningsvær, Lofoten .....	18/6—25	3	1	33,3
Kilpollen, Flakstad, Lofoten ....	26/6—25	61	8	13,6
Ytre Steinsfjord, Borge, Lofoten	27/6—25	41	12	29,3
Kalkunneset, Moskenesøy, Lofoten	29/6—25	233	82	35,2
S. of Hermansdal, Lofoten	29/6—25	16	2	12,5
Horseidvika ———	29—30/6—25	121	32	26,4
Hjelbergvika ———	30/6—25	2	0	0
Tananger near Stavanger .....	10—14/1—31	91	19	20,9
—————	17—18/2—32	233	84	36,5
Ytre Tana Fjord Finmark .....	14—16/3—32	78	32	41,0
Indre Tana Fjord Finmark ....	29/3—32	41	20	48,8
Reviken, near Stat .....	6/10—32	157	60	38,2

On the 8. May 1934 100 marked plaice were liberated off Sundnes in the Trondheim Fjord. Of these 24 were recaptured within the first year (from curator DONS' manuscript).

In 1935 and 1936 the marking experiment in the Trondheim Fjord were continued by the author. Plaice were marked immediately after being captured in Danish seine at the following localities:

Table 3. *Plaice Marking in the Trondheim Fjord.*

Locality	Date	Number Marked	Number Recaptured	% Recaptures the first Year
Vikaleiret, Åsen Fjord .....	20/5—35	100	58	58
Levanger ground .....	21/5—35	100	42	42
Beitstad Fjord .....	23/5—35	100	22	21
Brekstad, Ørlandet .....	27/5—35	30	19	68
Borgen Fjord .....	26/2—36	100	44	44

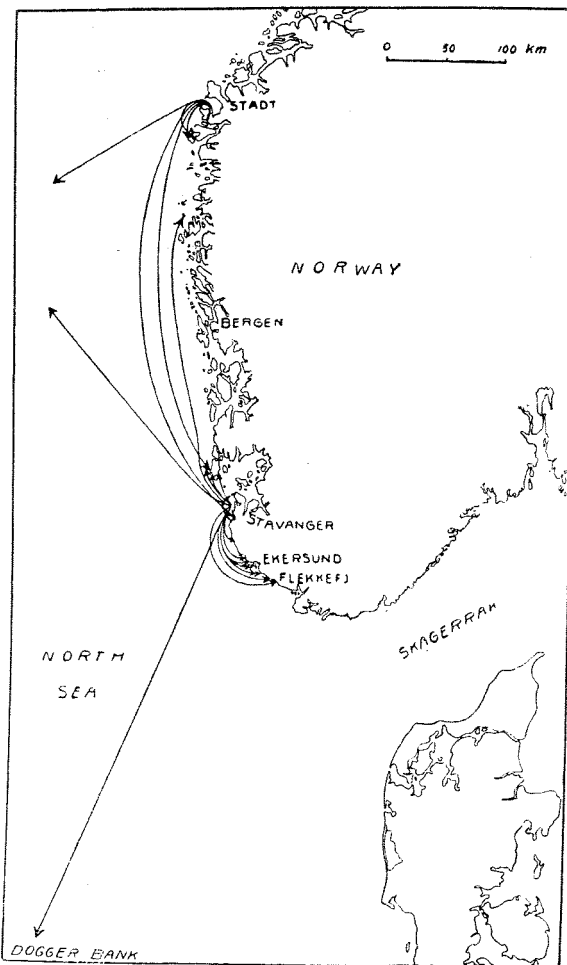


Fig. 3. Journeys from the West Coast of Norway of far-travelling tagged plaice (from Bjerkan).

By far the greater number of the recaptures were made in the same place where the fish were liberated. The long-travellers are seen in fig. 2.

A common feature of all the marking experiments made in and near the Trondheim Fjord is that none of those liberated in the fjord proper, has been recaptured outside, and none of those set free outside the Trondheim Fjord has been recaptured in the fjord. *The deep basin of the fjord near to the town of Trondheim seems to constitute a boundary between the plaice population of the Trondheim Fjord and that of the coast.* (The deep basin west of the town is devoid of plaice grounds).

In 1935 *Tromsø Museum* also started plaice investigations. SIGFRED

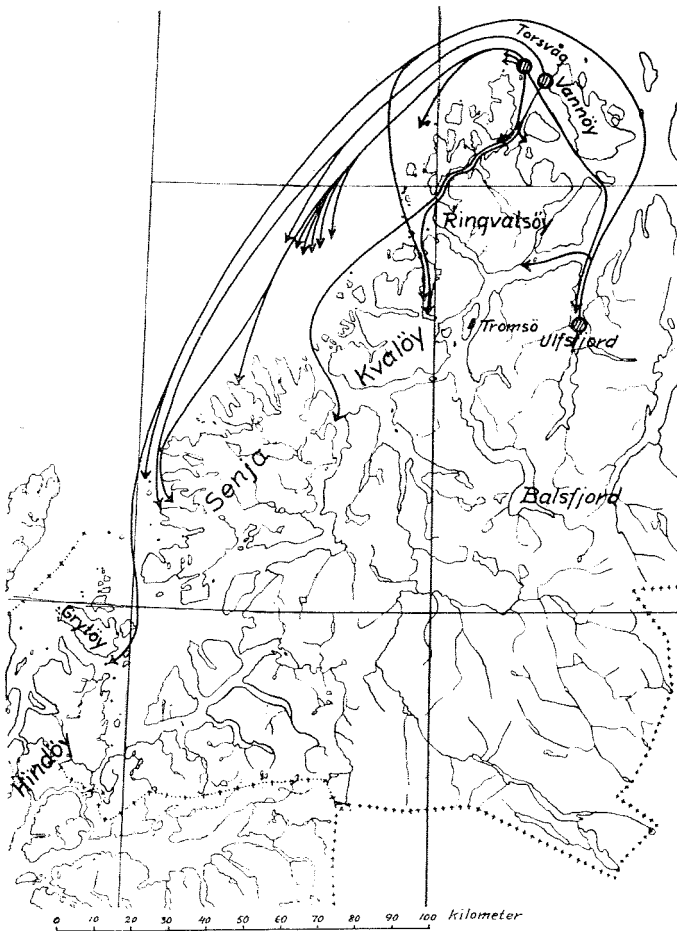


Fig. 4. Journeys of tagged plaice in N. Norway (only far-travelling specimens. — Soot-Ryen's eksperiments).

KRISTOFFERSEN, of the Museum staff, marked 186 plaice off Torsvåg between 30. Jan. and 8. Feb. and in May that same year 111 plaice were marked in the Ulsfjord. Up to Oct. 1st the following year 64 and 86 fish resp. were recaptured. Of those marked off Torsvåg 32 or 50 % of the recaptures were made more than 30 km from the plaice of liberation. In Ulsfjord, on the other hand, as much as 93 % of the recaptures were taken within a radius of one km from the place of liberation.

On the sketch-map fig. 4 are entered the long-travellers from these marking experiments. The material has been worked up by SOOT-RYEN but not yet published. SOOT-RYEN points out that the drift of eggs

and larvæ is compensated by the fact that the plaice will go south and westwards to the spawning grounds. Thus SOOT-RYEN has shown a case similar to what has been found earlier at Iceland where the plaice from N and E coast go to the S coast where spawning takes place. (SCHMIDT, SÆMUNDSON, TÅNING).

Besides the marking experiments here mentioned, plaice has also been marked by prof. dr. JOHAN T. RUUD in and near the Oslo Fjord in connection with transplantation of Danish plaice.

The Norwegian marking experiments will be dealt with in a special paper. Here is only mentioned what may throw light upon the question whether one or more plaice populations inhabit Norwegian waters. The conclusions to be drawn from these experiments are:

1. The plaice population of the West Norway waters seems to contribute to the population of the North Sea, and possibly, to receive contribution from the same.

2. The plaice in the fjords seems to be more stationary than that of the coast. An exception from this is the Tana Fjord, where a numerous population of young plaice is found off the mouth of the Tana river, and from these nursery grounds an emigration takes place to the coast and the sea outside the fjord (BJERKAN 6).

3. There seems to be neither emigration nor immigration from to the rich plaice grounds in the Trondheim Fjord.



### »RACE« INVESTIGATIONS.

To the question whether we have to reckon with a number of plaice populations in Norwegian costal waters, the marking experiments do not give definite answer. In order to get a start, if possible, towards the solution of this problem, samples from various parts of the coast have been collected with the intention to investigate the »racial« characters.

Since FR. HEINCKE in 1898 published his famous work »*Naturgeschichte des Herrings*« (12) a great number of ichthyologists of the whole world have followed his methods for definition of »races« in the various fish species. As to the plaice such investigators as CUNNINGHAM, DUNCKER, HEINCKE, Å. J. C. JENSEN, A. C. JOHANSEN, KYLE, KÄNDLER, C. G. J. PETERSEN, E. M. POULSEN, REDEKE, TÅNING o. a. have followed HEINCKES methods of dividing the species »plaice« into subspecies. In later years it is only the morphological characters which can be numerically decided at an early stage in the life of fish, which are used as a mean of distinction between various populations. It is the difference in the number of vertebræ (Vert. S.) and in the number of rays in the anal fin. (A) which are commonly used in the case of plaice.

In table 4 will be found a series of localities along the Norwegian Coast from *Jæren* to the *Tana Fjord* in Finmark, where samples of plaice have been collected for examination of Vert. S. and A.

The position of the localities will be seen on the map fig. 5. This cartogram affords a better survey than the tables. It might be seen that all localities in the Trondheim Fjord show considerably lower values than the other localities. Variations in Vert. S. along the outer coast are remarkably small. There is, however, a marked tendency in the values: off *Jæren* the number of vertebræ is fairly high,  $42,92 \pm 0,05$ . Northwards until *Vigra* it falls to  $42,77 \pm 0,07$ . From here, it remains fairly constant all the way north to *Torsvåg* in Troms, and farther north-east it rises to about 43,00. AWERINZEW (1) gives 43,15 as the number of vertebræ in plaice off the Murman Coast.

The variation found along the Norwegian Coast may, as in the case of herring (RUNNSTRØM 30), very well be explained as influenced

Table 4.

*Number of Vertebrae and Anal Fin Rays in Plaice (1935).*

No.	Locality	Date	No.	Vert. S	A
1	Tananger near Stavanger . . . .	16/12	170	42,92 ± 0,05	54,46 ± 0,10
2	Revika near Stat. . . . .	18/11	302	42,80 ± 0,03	54,29 ± 0,12
3	Vigra off Ålesund . . . . .	31/5	103	42,77 ± 0,07	53,75 ± 0,19
4	Ørlandet outs. Trondh. Fjord	27/5	64	42,65 ± 0,12	53,15 ± 0,43
5	Vikaleiret in —»—	20/5	100	42,44 ± 0,02	52,00 ± 0,17
6	Off Levanger in —»—	21/5	100	42,45 ± 0,04	51,60 ± 0,18
7	Off Sundnes in —»—	6/5	476	42,39 ± 0,03	51,84 ± 0,10
8	Rolshavn in —»—	9/4	183	42,40 ± 0,05	51,50 ± 0,17
9	Korsen in —»—	9/4	128	42,39 ± 0,06	51,50 ± 0,18
10	Off Steinkjær —»—	23/5	100	42,33 ± 0,06	51,92 ± 0,20
11	Vikna, Nord Trøndelag . . . . .	23/3	90	42,74 ± 0,08	54,27 ± 0,19
12	Rørvikbukta, Lofoten . . . . .	10/7	162	42,72 ± 0,08	53,53 ± 0,16
13	Morfjord, Lofoten . . . . .	12/7	166	42,77 ± 0,05	53,48 ± 0,20
14	Bjarkøy, Troms . . . . .	16/7	105	42,79 ± 0,06	53,22 ± 0,21
15	Torsvåg, Troms . . . . .	6/8	206	42,79 ± 0,07	53,90 ± 0,15
16	Nordlenangen, Troms . . . . .	5/8	129	42,85 ± 0,06	54,09 ± 0,20
17	Gåshopen, Sørøy, Finmark . .	2/8	119	42,84 ± 0,06	54,18 ± 0,22
18	Bukta, Alta — . .	31/7	205	42,89 ± 0,04	54,54 ± 0,15
19	N. of Sørøy — . .	2/8	51	43,00 ± 0,07	55,12 ± 0,27
20	Sandfjord near Nordkyn . . . .	26/7	64	42,97 ± 0,08	54,63 ± 0,30
21	Gulgo fjord Tana, Finmark . .	25/7	75	43,05 ± 0,08	54,81 ± 0,25
22	Off Tana River, — . .	23/7	101	42,97 ± 0,05	54,75 ± 0,17
23	Leirpollen, Tana — . .	22/7	158	43,01 ± 0,06	54,49 ± 0,17

by temperature upon the fixation of Vert. S. Table 5 is a survey of the average temperature at a depth of 4 m northward along the coast in the spring months. The temperatures have been obtained by means of sea thermographs installed in the coast-liners, and it is the monthly average temperatures based on these observations for the years 1935—38 which are entered in the table (furnished by dr. J. EGGVIN).

The spawning time of the plaice along the Norwegian Coast has not been definitely fixed, but experienced fish-merchants would, suggest mainly February for Jæren, for Trøndelag Feb.—March, in the Trondheim Fjord proper about a month later. As to the Murman Coast AWERINZEW (1) states that the first half of april is the most important time.

The main spawning time for the plaice considered and presuming that the critical period for the fixation of Vert. S. will be found in the egg stage or in the pelagic stage of the larvæ, some accordance seems to exist between number of vertebrae and temperature: a higher tempera-

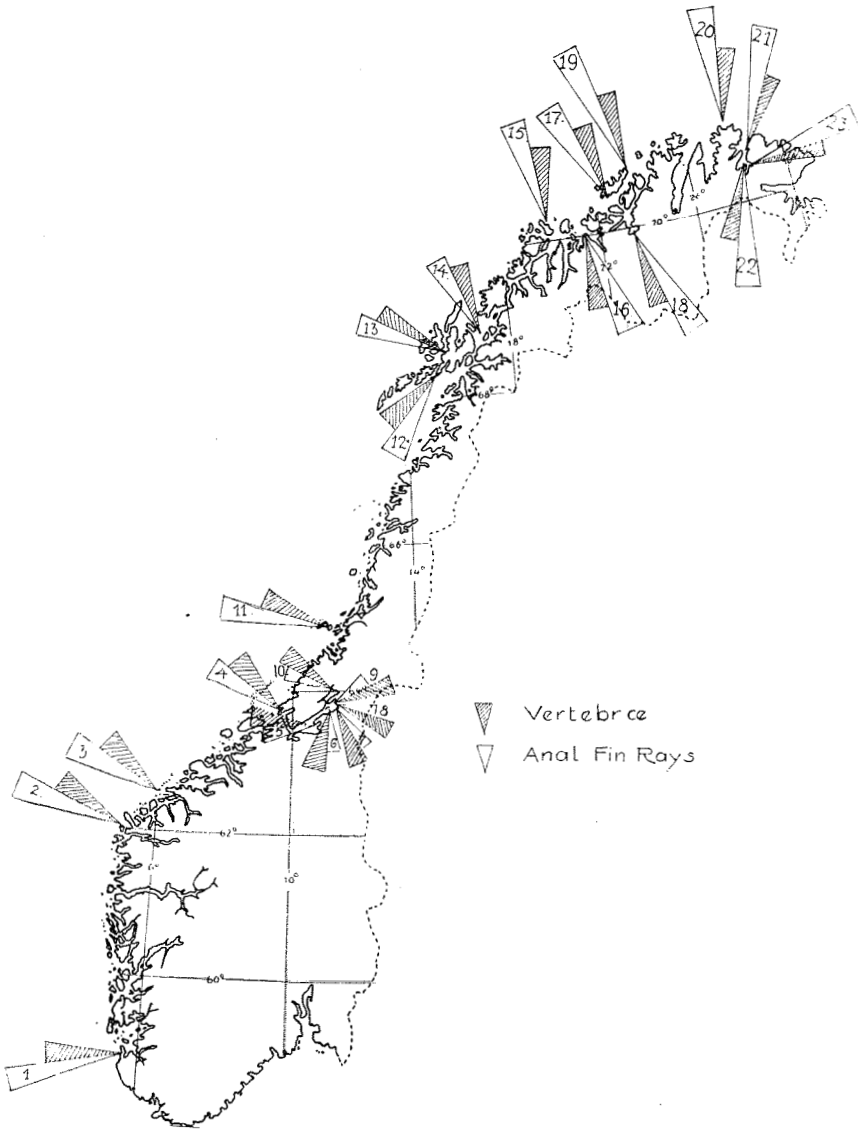


Fig. 5. Length of wedges corresponds to no. of vertebræ and anal fin rays excess of resp. 40 and 50.

Table 5.  
Average Temperature 1935—38 in 4 m Depth on the Norwegian Coast.

Locality	March	April	May
Jæren .....	3,4	4,7	8,0
Stat .....	3,9	4,4	7,8
Breisundet off Ålesund .....	3,9	4,5	7,8
Trondheim Fjord .....	4,1	4,7	7,8
Folla, Nord-Trøndelag .....	4,3	4,7	7,0
Vest Fjord .....	2,7	3,1	5,5
Vågsfjord .....	2,5	2,6	5,5
Lopphavet, Finmark .....	2,3	2,4	4,0
Off Nordkyn Finmark .....	2,7	2,8	3,9

ture apparently conditions a lower number of vertebræ, and vice versa, as shown by JOHS. SCHMIDT in the case of *Zoarces viviparus* and *Gadus callarias*.

The gradual change in number of vertebræ along the outer Norwegian Coast does not justify a division into several plaice populations.

The Trondheim Fjord is distinguished from the other localities by an extraordinarily low number of vertebræ. We will try by ordinary methods to find out whether the plaice of the fjord may be regarded as a population of its own. The coastal plaice population may be taken as represented by the samples from Vigra and Vikna, resp. 3 and 11 on the map, fig. 5. The distribution as to no. of vertebræ is shown in table 6 and fig. 6.

Table 6. Distribution as to No. of Vertebræ of Plaice. 1935.

Locality	No. of Vertebræ				
	41	42	43	44	Average
Vigra .....	1	34	56	12	42,77 ± 0,065
Vikna .....	4	29	43	14	42,74 ± 0,081
Total .....	5	63	99	26	42,76 ± 0,054
‰ .....	26	326	514	134	

The samples collected in the Trondheim Fjord the same year show the following distribution as to no. of vertebræ:

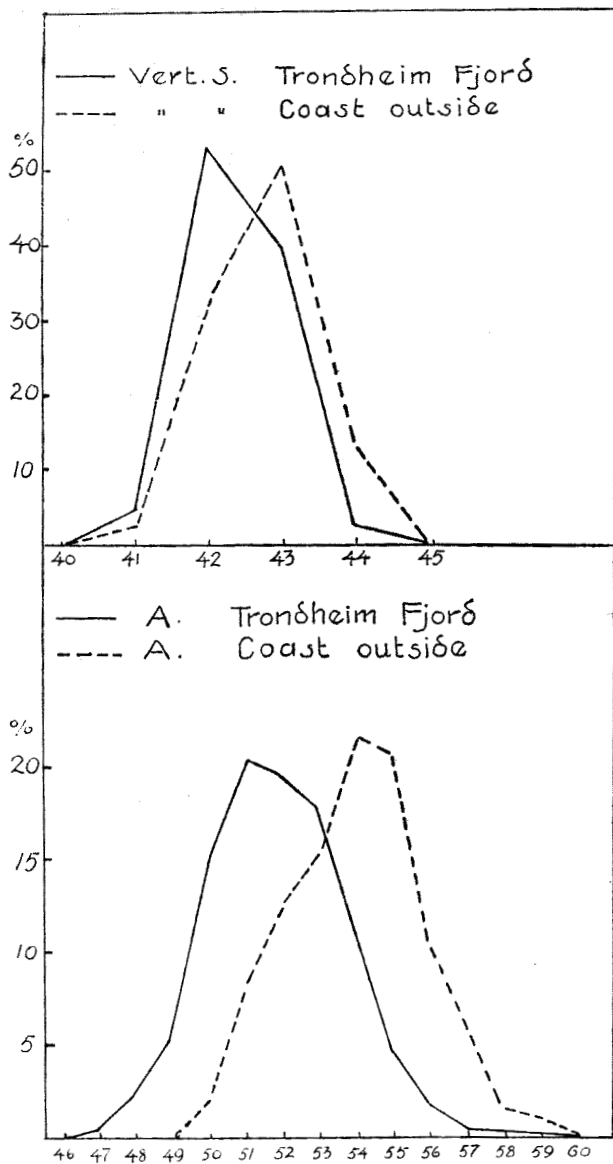


Fig. 6. Distribution of the plaice samples with regard to no of vertebrae and of anal fin rays.

Table 7.

*Distribution as to No. of Vertebrae of Plaice, Trondheim Fjord, 1935.*

Locality	No of Vertebrae				
	41	42	43	44	Average
Off Steinkjær .....	4	62	31	3	42,33 ± 0,060
Rolshavn .....	10	97	71	6	42,40 ± 0,047
Off Sundnes .....	25	249	190	9	42,39 ± 0,032
Off Levanger .....	6	49	45	4	42,45 ± 0,043
Vikaleiret .....	3	53	44	2	42,44 ± 0,023
Total .....	48	510	381	24	42,40 ± 0,016
‰ .....	50	530	395	25	

If we examine whether the average difference in number of vertebrae given in table 6 and 7 is real or not, we find:

$$\frac{D}{m_{\text{Diff.}}} = \frac{42.76 - 42.40}{\sqrt{0.054^2 + 0.016^2}} = 6.4$$

According to this there is a real difference in the number of vertebrae between the plaice population of the Trondheim Fjord and the plaice along the coast outside.

SPECIAL INVESTIGATION  
OF THE »RACIAL CHARACTERS« OF THE PLAICE.

Every winter, in the course of February, the staff of the Trondheim Biological Station are catching about 1 000 plaice with Danish seine off Sundnes in the Trondheim Fjord. The plaice are made to spawn in the hatchery of the station. After spawning in the basin of the station the plaice are again liberated in the fjord. Since the spring of 1935 these plaice, by the courtesy of the curator mr. C. DONS, have been given to the author for investigation.

In the years 1935—37 only a part of these plaices was examined as to number of vertebræ and anal fin rays, as the plan of the research aimed only at ascertaining the possibility to find out in this way if the fjord has a plaice population of its own. In the years 1938 and 1939, however, the number of vertebræ and rays has been determined in all specimens. The counts have been done by the author. The fish were boiled before counting to remove the meat in easiest way. These plaice, collected every year just before spawning-time, on their natural spawning ground or near-by, may be considered well suited for investigating variation of the »racial characters«.

As we have already seen the markings made in- and outside the fjord suggest that the fjord-deep in the outer part of the Trondheim Fjord isolates the plaice stock in the fjord proper from the stock outside, after the bottom stage has been reached. The inflow of pelagic eggs and larvæ is also probably very scanty. According to calculations made by dr. J. EGGVIN, there is an outgoing surface current in the fjord with a minimum thickness of 50 m off Trondheim. As known, the eggs and pelagic larvæ of the plaice will be found mainly in the upper layers.

Table 8 contains the result of the counts for the richer year classes, males and females separately. We may also see the distribution of anal fin rays in plaice with 41, 42, 43 and 44 vertebræ. The figures given in column X show the distribution of A in those specimens whose number of vertebræ has not been ascertained.

*Variation of Number of Vertebrae and Anal Fin Rays in the two Sexes.*

G. DUNKER (9) has devoted a very close study to *Pleuronectes flesus* from the Elbe-mouth, and has made out i. a. a real difference in A between males and females. Also in *Pleuronectes platessa* DUNKER finds a rather great difference, but not great enough to be recorded as a settled fact. The material in hand affords an opportunity to investigate the question as to plaice from the Trondheim Fjord.

Table 8. *Number of Vertebrae and Anal Fin Rays. T. B. S. 1935—38.*

	No. of Vertebrae ♂♂							No. of Vertebrae ♀♀							
	X	41	42	43	44	Sum	%	X	41	42	43	44	Sum	%	
Anal Fin Rays. Class 1925.	X	—	—	—	—	—	—	—	—	—	—	—	—	—	
	46	—	—	—	—	—	—	1	—	—	—	—	1	0,4	
	47	—	—	—	—	—	—	—	—	—	—	—	—	—	
	48	—	—	—	—	—	—	2	—	1	1	—	4	1,8	
	49	—	—	1	—	—	1	4,2	2	—	3	4	9	3,9	
	50	—	—	4	2	—	6	25,0	8	1	8	7	1	25	10,9
	51	—	—	3	1	—	4	16,7	19	1	18	8	1	47	20,6
	52	—	—	3	1	—	4	16,7	17	3	12	12	3	47	20,6
	53	—	—	2	1	—	3	12,5	16	1	10	14	—	41	17,9
	54	—	—	—	4	—	4	16,7	11	—	3	5	1	20	8,8
	55	—	—	—	1	—	1	4,2	12	—	1	8	2	23	10,1
	56	—	—	—	1	—	1	4,2	5	—	1	4	—	10	4,4
57	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
58	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
59	—	—	—	—	—	—	—	1	—	—	—	—	1	0,4	
Sum	—	—	13	11	—	24	100,2	94	6	57	63	8	227	99,8	
%	—	—	54,2	45,8	—	100	—	—	4,5	42,5	47,0	6,0	100,0	—	
Anal Fin Rays. Class 1930.	X	3	—	—	—	—	3	—	7	—	2	1	—	10	—
	46	—	—	—	—	—	—	—	1	—	1	—	—	2	0,2
	47	—	—	2	—	—	2	0,5	4	—	4	2	—	10	1,1
	48	1	1	5	3	—	10	2,3	17	2	13	3	—	35	3,9
	49	4	2	18	5	—	29	6,7	36	1	22	8	2	69	7,6
	50	5	2	39	16	1	63	14,6	70	8	48	34	2	162	17,8
	51	5	6	49	31	—	91	21,1	78	10	70	37	4	199	21,9
	52	5	2	40	35	2	84	19,5	80	2	48	54	3	187	20,6
	53	3	1	31	39	2	76	17,6	43	5	43	42	—	133	14,6
	54	1	1	25	19	—	46	10,7	25	1	26	16	1	69	7,6
	55	1	1	7	7	—	16	3,7	11	—	7	12	2	32	3,5
	56	1	—	3	8	2	14	3,2	6	—	2	1	—	9	1,0
57	—	—	1	—	—	1	0,2	—	—	—	1	—	1	0,1	
Sum	29	16	220	163	7	435	100,1	378	29	286	211	14	918	99,9	
%	—	3,9	54,2	40,2	1,7	100,0	—	—	5,4	53,0	39,0	2,6	100,0	—	



	No. of Vertebrae ♂♂							No. of Vertebrae ♀♀						
	X	41	42	43	44	Sum	%	X	41	42	43	44	Sum	%
<b>Anal Fin Rays. Class 1932.</b>														
X	4	—	—	—	—	4	—	3	—	1	—	—	4	—
47	—	—	—	—	—	—	—	—	—	2	—	—	2	1,3
48	2	1	1	—	—	4	4,3	4	1	1	—	—	6	3,9
49	1	—	2	4	—	7	7,5	5	—	3	2	—	10	6,4
50	3	—	6	2	—	11	11,8	6	2	7	3	—	18	11,6
51	8	—	9	3	—	20	21,6	12	1	11	8	—	32	20,7
52	7	—	6	3	—	16	17,2	8	—	11	7	—	26	16,8
53	5	—	4	5	—	14	15,1	11	—	15	9	—	35	22,6
54	5	—	—	6	1	12	12,9	4	1	2	6	—	13	8,4
55	2	—	—	4	1	7	7,5	4	—	4	—	1	9	5,8
56	—	—	1	1	—	2	2,2	—	—	2	2	—	4	2,6
Sum	37	1	29	28	2	97	100,1	57	5	59	37	1	159	100,1
%	—	1,7	48,3	46,7	3,3	100,0	—	—	4,9	51,8	36,3	1,0	100,0	—
<b>Anal Fin Rays. Class 1934.</b>														
X	12	—	2	4	—	18	—	—	—	1	—	—	1	—
46	—	—	0	—	—	—	—	1	—	—	—	—	1	0,4
47	—	—	2	—	—	2	0,5	—	—	—	—	—	—	—
48	1	—	3	1	—	5	1,2	1	—	2	—	—	3	1,1
49	3	1	11	5	—	20	4,7	1	—	5	1	—	7	2,7
50	9	1	24	10	1	45	10,5	3	1	15	7	—	26	9,7
51	7	1	32	28	3	71	16,5	8	1	30	16	—	55	20,8
52	14	3	39	49	3	108	25,2	10	—	19	23	2	54	20,4
53	13	2	28	36	1	80	18,6	7	1	22	22	—	52	19,7
54	4	1	23	33	1	62	14,4	7	—	8	14	1	30	11,4
55	2	1	13	9	—	25	5,8	11	—	3	12	—	26	9,7
56	1	—	1	3	1	6	1,4	5	—	—	4	—	9	3,4
57	1	—	1	2	—	4	0,9	—	—	—	1	—	1	0,4
58	—	—	—	2	—	2	0,5	—	—	—	—	—	—	—
Sum	67	10	179	182	10	448	100,2	54	3	105	100	3	265	99,7
%	—	2,6	47,0	47,8	2,6	100,0	—	—	1,4	49,8	47,4	1,4	100,0	—
<b>Anal Fin Rays. Class 1935.</b>														
X	—	—	—	1	—	1	—	—	—	—	—	—	—	—
46	—	—	—	—	—	—	—	—	—	—	—	—	—	—
47	—	—	—	1	—	1	0,9	—	—	—	—	—	—	—
48	—	—	2	—	—	2	1,7	—	1	2	—	—	3	7,3
49	—	—	2	3	—	5	4,3	—	—	3	2	—	5	12,2
50	1	—	8	10	—	19	16,2	—	—	4	3	—	7	17,1
51	—	2	16	10	—	28	23,9	—	—	2	5	—	7	17,1
52	—	—	15	7	1	23	19,7	—	1	2	7	—	10	24,4
53	—	—	8	11	—	19	16,2	1	—	2	5	—	8	19,5
54	—	—	5	8	—	13	11,1	—	—	—	—	—	—	—
55	—	—	1	4	—	5	4,3	—	—	—	1	—	1	2,4
56	—	—	—	2	—	2	1,7	—	—	—	—	—	—	—
Sum	1	2	57	57	1	118	100,0	1	2	15	23	—	41	100,0
%	—	1,7	48,8	48,8	1,7	100,0	—	—	5,0	37,5	57,5	—	100,0	—

The year-classes 1930 and 1934 are sufficiently represented in the material to be particularly well suited for the purpose. Table 10 shows Vert. S. and A in both sexes.

Table 9.

*Number of Vertebrae and Anal Fin Rays, at Sundnes, Trondheim Fjord.*

Year Class	Sex	Vert. S.	A.
1930 .....	♂♂	42,397 ± 0,029	51,823 ± 0,090
	♀♀	42,389 ± 0,027	51,423 ± 0,057
1934 .....	♂♂	42,503 ± 0,031	52,195 ± 0,086
	♀♀	42,489 ± 0,038	52,322 ± 0,110

The number of vertebrae seems to be the same in males and females of the same year-class. The 1930 year-class shows, however, a great difference in the number of anal fin rays between the two sexes, and if we examine whether the difference is real we find:  $\frac{D}{m_{Diff.}} = 3,97$ .

The difference might be explained by a personal error, a mistake in the counting, but this can be ascertained. Countings in 1935 and 1936 include a number of specimens of the 1930 year-class great enough to afford a reliable vehicle. The distribution will be found entered in table 10 and 11.

Table 10.

*Number of Vertebrae and Anal Fin Rays, Sundnes 1935, Year-class 1930*

Anal Fin Rays	♂♂ Number of Vertebrae							♀♀ Number of Vertebrae						
	x	41	42	43	44	Total	% <sub>100</sub>	x	41	42	43	44	Total	% <sub>100</sub>
47	—	—	2	—	—	2	9	—	—	1	—	—	1	5
48	—	1	2	1	—	4	17	—	—	4	1	—	5	26
49	1	—	8	1	—	10	44	2	1	9	2	1	15	79
50	1	2	25	8	1	37	156	5	3	14	9	—	31	162
51	—	4	26	20	—	50	218	8	4	18	10	2	42	220
52	1	1	20	15	1	38	166	4	1	18	18	1	42	220
53	1	1	18	21	1	42	183	5	4	11	9	—	29	152
54	1	1	15	15	—	32	139	1	1	11	3	—	16	84
55	—	1	5	5	—	11	48	1	—	3	4	1	9	47
56	—	—	1	3	—	4	17	—	—	1	—	—	1	5
57	—	—	1	—	—	1	4	—	—	—	—	—	—	—
Total	5	11	123	89	3	231	—	36	14	90	56	5	191	—

Table 11.

*Number of Vertebrae and Anal Fin Rays. Sundnes 1936, Year-class 1930.*

Anal Fin Rays	♂♂ Number of Vertebrae							♀♀ Number of Vertebrae						
	x	41	42	43	44	Total	0/100	x	41	42	43	44	Total	0/100
X	—	—	—	—	—	—	—	1	—	—	—	—	1	4
47	—	—	—	—	—	—	—	1	—	—	1	—	2	8
48	—	—	3	1	—	4	30	4	1	1	—	—	6	23
49	—	1	7	3	—	11	82	12	—	5	1	—	18	70
50	—	—	9	5	—	14	104	25	—	9	7	—	41	158
51	—	—	17	7	—	24	179	40	2	17	14	1	74	286
52	—	—	18	15	—	33	247	27	—	9	10	—	46	178
53	—	—	9	16	1	26	194	27	—	8	9	—	44	170
54	—	—	9	2	—	11	82	10	—	4	2	—	16	62
55	—	—	2	2	—	4	30	5	—	—	2	—	7	27
56	—	—	1	4	2	7	52	1	—	—	1	—	2	8
57	—	—	—	—	—	—	—	—	—	—	1	—	1	4
58	—	—	—	—	—	—	—	2	—	—	—	—	2	8
Total	—	1	75	55	3	134	—	155	3	53	48	1	260	—

The arithmetical means for A, according to counts made in 1935 and 1936 have the following values:

Table X.

Sex	Count 1935	Count 1936	Count 1935—38
♂♂	51,92 ± 0,12	51,90 ± 0,15	51,82 ± 0,09
♀♀	51,59 ± 0,12	51,53 ± 0,11	51,42 ± 0,06

We thus find the same values of A from the 1930 year-class whether the counting was made in the sample from 1935 or 1936, and the same values found by summing-up the counts 1935—38. It would be curious if an eventual error proved to be of the same kind and extent every year. During the work of counting, males and females of the various year-classes followed each other without any order, so that a systematic error can be left out of question.

The specimens were all so large that counting was easy. The difference in number of rays in the anal fin between the two sexes of the year-class 1930 of the Trondheim Fjord seems therefore to be a fact.

Fig. 7 shows the distribution of number of vertebrae and anal fin rays in males and females of 1930 and 1934 year-classes.

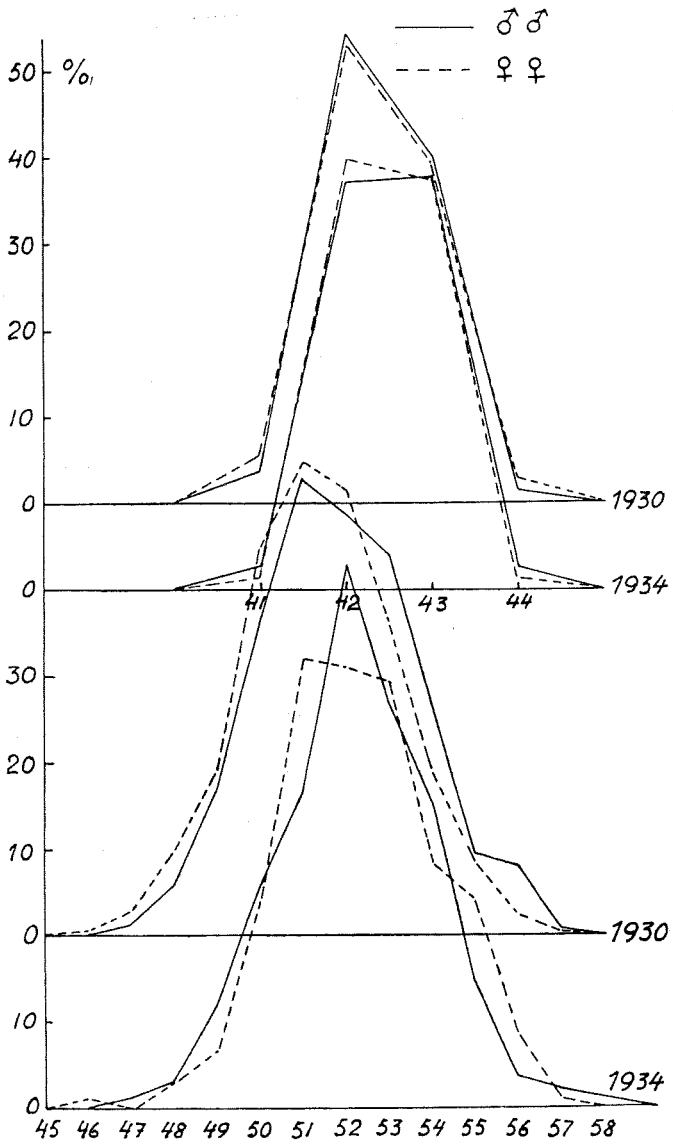


Fig. 7. Distribution with regard to no. of vertebræ and of anal fin rays of the 1930 and the 1934 year-class in the Trondheim Fjord.

The curves representing the number of vertebræ are almost identical for the two sexes within the same year-class, whilst the curves showing the distribution of anal fin ray number are shifted to the right with regard to the males of the 1930 year-class. The 1934 year-class, on the other hand, shows no real difference between the two sexes.

The conclusion of this will be: as far as the material goes there is no real difference in number of vertebræ between males and females of the same year-class of plaice in the Trondheim Fjord. The number of anal fin rays may show some difference between the two sexes of the same year-class. The difference, however, varies from one year-class to the next.

*Correlation between the Number of Vertebræ and the Number of Anal Fin Rays.*

A glance at table 8 will make it clear how the maximum number of variants moves when we compare the columns for 41, 42, 43 and 44 vertebræ. Increasing number of vertebræ corresponds to a higher number of rays in the anal fin. The range of variation is, however, rather great, so much that we may find specimens with a low number of vertebræ having a high number of rays, and vice versa. It would be possible to compute the coefficient of correlation, thus finding an expression for the doubtless positive correlation. We have, however, seen that by summing up the figures referring to males and females of the various year-classes (of which the number of specimens is great enough to show the distribution of A in plaice with 41, 42, 43 and 44 vertebræ), the material would consist of a heterogeneous mass, the permissibility of the operation thus being at best doubtful.

A computation of the arithmetical mean of A for plaice with 41, 42, 43 and 44 vertebræ from the 1930 and the 1934 year-classes, gives the following values:

Table 12.

*Correlation between Number of Vertebræ and of Anal Fin Rays.*

Vert. S	1930 Year Class		1934 Year Class	
	♂♂ A	♀♀ A	♂♂ A	♀♀ A
41	50,62	50,83	52,10	—
42	51,58	51,35	51,95	51,30
43	52,25	51,85	52,54	52,74
44	53,00	51,57	52,20	—

As to the males of the 1930 year-class there is an approximate linear increase in the number of anal fin rays with rising number of vertebræ: an increase of one vertebræ corresponds to a little less than one ray in A. In specimens with 44 vertebræ, A is low, but the average has been computed from 14 specimens only, so that the probable error is very great. As to the 1934 year-class, the number of specimens is small, the values therefore doubtful regarding specimens with 41 and 44 vertebræ.

Fig. 8 illustrates the correlation between Vert. S. and A for the 1930 year-class.

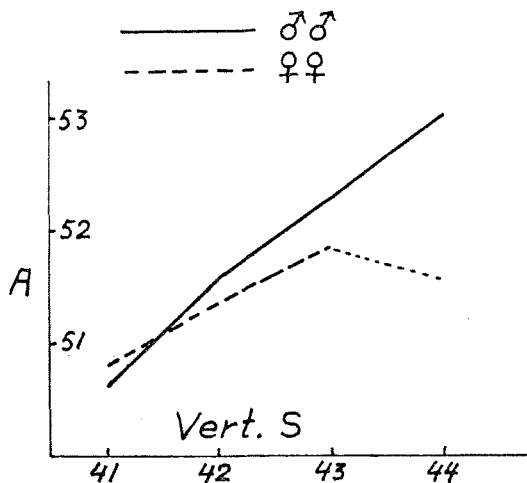


Fig. 8 Correlation between Vert. S and A.

An increase of one vertebra corresponds to a rise of about one ray in the anal fin by plaice in the Trondheim Fjord. If we compare Vert. S. and A in plaice taken at different localities, totally different relations will be found. The plaice of the Trondheim Fjord compared with that of the coast shows a difference in Vert. S. of 0,34, while the difference in A is no less than 2,46. From the literature the following values are taken (see table 13).

The plaice in the Belt Sea has about the same number of vertebræ as the plaice in the Trondheim Fjord but approximately 2 rays less in the anal fin. Further there is a difference of about one half vertebra between the population of the North Sea and that of the Baltic, and simultaneously a difference of about 4 rays.

As will be seen from the instances here given, *Vert. S. and A in the plaice vary independently from one locality to another.*

Table 13. *Number of Vertebrae and Anal Fin Rays in different Plaice Populations.*

Locality	Vert. S.	A	Source
Southern Baltic . . . . .	42,83	52,22	R. Kändler 1935
The Belt Sea + W. Baltic . . . . .	42,4—42,7	49,7—50,5	E. M. Poulsen 1938
The North Sea . . . . .	43,00	54,00	A. C. Johansen 1929
The Barent's Sea . . . . .	43,15	54,69	S. Awerinzew 1928*
Iceland . . . . .	43,14—43,58	53,73—55,5	A. V. Tåning 1929

*Number of Vertebrae and Anal Fin Rays in Plaice of various Year-classes.*

In table 8 will be found the year-classes which are represented in the material by a number great enough to give fairly reliable values for Vert. S. and A. The average computed from this table will be found in table 14 below:

Table 14.  
*Av. Number of Vertebrae and Anal Fin Rays in different Year-classes of Plaice in the Trondheim Fjord.*

Year Class	Vert S. ♂ + ♀	A ♂♂	A ♀♀
1925 . . . . .	42,53 ± 0,05		52,22 ± 0,13
1930 . . . . .	42,39 ± 0,02	51,82 ± 0,09	51,42 ± 0,06
1932 . . . . .	42,40 ± 0,05	51,76 ± 0,20	51,82 ± 0,15
1934 . . . . .	42,50 ± 0,02	52,20 ± 0,08	52,32 ± 0,11
1935 . . . . .		51,78 ± 0,17	

As to the vertebrae we find  $\frac{D}{m_{Diff.}} = 3,9$  between the 1930 and the 1934 year-classes.

*Thus a real difference in the number of vertebrae can exist between the various year-classes within the plaice population of the Trondheim Fjord.*

As to the anal fin rays we find for the males a real difference between the 1930 and the 1934 year-classes and for the females between the 1925 and 1930 year-classes and between the 1930 and 1934 year-classes.

In these cases  $\frac{D}{m_{Diff.}} = \text{resp. } 3,1, 5,6 \text{ and } 7,8.$

*Discussion.*

The plaice of the Trondheim Fjord does not receive contributions from other populations to any perceptible degree. And we find differences in the morphological characters, not only between the various year-classes, but within the same year-class a difference in number of anal fin rays for the two sexes. The difference here found can not be genotypically conditioned, but must be a result of the different hydrographical conditions to which the eggs and larvæ have been exposed. Unfortunately we have no hydrographical data covering the years in question.

A possible explanation of the difference in the number of anal fin rays shown in the two sexes of the 1930 year-class may be found in the conditions of temperature. The temperature in the upper layers can vary so much during the spring months that it may very well cause a difference in the number of anal fin rays, provided that the critical period for fixation of the number of anal fin rays is somewhat different in the two sexes. In such years where the temperature remains unchanged long enough to cover the critical period of *both* sexes no difference will be found. In other years a change of temperature may cause that one of the sexes will get a higher number of anal fin rays than the other.

ÅGE J. C. JENSEN (14) finds accordance between the temperature and the variations appearing in the number of anal fin rays in the plaice along the Jutland coast. JENSEN shows that a *high* temperature in the bottom water coincides with a *high* number of anal fin rays. The accordance, however, is not fully convincing. TÅNING (32) has shown that at the coast of Iceland, the lowest A is found in plaice living at the S. coast, and rising numbers eastwards along the N. coast, in other words, the *lowest* number of rays is found in the *warmest* water and the *highest* in the *coldest*. This seems to be direct opposition to JENSEN'S theory. JENSEN, however, explains the matter by recalling the fact that off S. Iceland the temperature increases from land towards the sea. The plaice eggs, hatched farthest from land, have in the stronger current drifted farthest, and consequently at N. Iceland those plaice grow up which have been hatched in the warmest water and, according to JENSEN, consequently have the highest number of anal fin rays. As to the plaice in Icelandic waters this explanation might hold good, but AWERINZEW(1) has found a number of anal fin rays at Murman Coast of 54,69. Further we find, as already shown, increasing number of rays in the anal fin along the Norwegian Coast from Torsvåg northwards and eastwards, together with decreasing temperature. This is difficult to explain in accordance with JENSEN'S theory. The positive correlation between



number of vertebræ and anal fin rays as shown by DUNKER, confirmed by the investigation on plaice in the Trondheim Fjord, is also adverse to JENSEN'S theory. These facts suggest that the contrary is the case. A low temperature conditions a high number of anal fin rays and vice versa.

JENSEN makes a mistake when he takes KÄNDLER'S paper »*Rassenkundliche Untersuchung an Plattfischen*« (19) to credit for his theory in writing: »Thus KÄNDLER supposes that the fact that the larger (older) plaice of the 0—Gr. on the Oder Bank in 1934 had a higher ray figure than the smaller ones is due to a development of the former at higher temperature and salinity (loc. cit. page 115)«. KÄNDLER shows in his paper that there is a positive correlation between the length and the number of vertebræ in the 0-Gr., but as to the rays in the anal fin he writes: »Diese Beziehung zwischen Körpergrösse und Wirbelzahl ist um so auffälliger, als eine ähnliche Beziehung zwischen Länge und Strahlenszahl der Analflossen *nicht* besteht«. (loc. cit. page 113).

It is thankless work to try and find the connection between the hydrographical conditions and the »racial characters« of the plaice as our knowledge of the hydrographical conditions is very limited, in particular the complicated conditions in the southern North Sea. Furthermore we know very little about what stage in the development of the plaice egg or larva is the most critical with regard to the influence of hydrographical factors on the final fixation of, f. i., the number of anal fin rays. We do not even know the time for the spawning of those eggs which will dominate the new year-class. To suppose as a matter of course that this will coincide with the maximal spawning is hardly allowable. It is most probably the food conditions of the young larvæ which decide whether a good or bad year-class of plaice shall result. The increase of the plancton in the spring must probably coincide with a great number of larvæ at the very stage when they have to begin feeding if a good year-class shall be produced. If so, it would be the hydrographical conditions in which they grow up, which eventually would have to be made the object of a closer research.

The investigation of the plaice population in the Trondheim Fjord shows that the number of anal fin rays and the number of vertebræ is subject to such great annual variations that it would be possible, by the aid of the ordinary criterions, to subsume the various year-classes under different local forms, even the two sexes of the same year-class. Of course this has nothing at all to do with facts, but shows how necessary it is, first of all, to fix the limits between which the morphological characters vary as a consequence of variable environment factors before we dare subdivide the species plaice into different races.

A most searching analysis of how the various milieu elements influence the fixation of morphological characters is offered by SIGURD JOHNSEN (18) in a short paper »*On the Variation of Fishes in Relation to Environment*«.

JOHNSEN classifies the environment elements as follows:

1. Those influencing the rate of metabolic processes (temperature, oxygen, hydrogen-ion concentration and other factors?)
2. Those influencing the egg-size (density of the medium).

We must necessarily agree with JOHS. SCHMIDT that only accurate experiments can give definite insight into the complex of factors which probably cooperate in the fixation of the »racial characters«. Thanks to GUNNAR ROLLEFSEN's discovery that the nauplius of *Artemia salina* affords food, well fitted for raising young fish, it now seems as if those problems which have been so much debated for more than hundred years, may at last be solved experimentally.

### AGE-DISTRIBUTION.

In working up our plaice material, the age has been determined by the aid of the otoliths and the interoperculum. As to the younger individuals, the otoliths may very well be used, but HEINCKES method to use the interoperculum, is the best for older plaice. From the otoliths it is difficult to discern the last year-rings with certainty in older fish. Using the interoperculum it is easy to make out the last years, but often difficult do define the close of the first. By combining age-determination by otolith and by interoperculum we may, in most cases, consider the reading as reliable.

The result of the age-investigation of the material obtained in 1935—39 from the »Trondheim Biological Station« are tabled below:

Table 15. *Age-distribution in Promille, T. B. S.*

Year	Sex	Age in Years													Total
		3	4	5	6	7	8	9	10	11	12	13	14	Older	
1935	♂♂	55	7	827	8	4	15	15	59	4	4	—	—	4	271
	♀♀	—	—	443	23	23	46	35	351	17	69	11	—	47	174
1936	♂♂	—	241	43	638	23	14	9	5	29	—	—	—	446	
	♀♀	—	84	4	581	21	18	29	27	145	22	47	6	512	
1937	♂♂	433	40	267	18	214	4	4	—	—	9	—	4	16	224
	♀♀	8	2	147	12	524	14	18	35	6	161	2	43	26	345
1938	♂♂	203	640	16	72	13	41	—	3	—	—	10	2	2	513
	♀♀	8	237	18	165	—	405	18	18	14	12	65	2	38	510
1939	♂♂	40	644	258	13	19	2	22	2	—	—	—	—	624	
	♀♀	—	112	248	30	126	9	340	5	14	16	7	70	24	569

The table shows the age-distribution of the mature fish, males and females separately. The column »Total« (number of individuals examined in the respective years) gives also the sex-proportion of the year.

A graph of the figures (fig. 9) affords a clearer understanding. It will be seen how the 1930 year-class dominates the samples from 1935 and 1936, further that the 1925 year-class also must have been

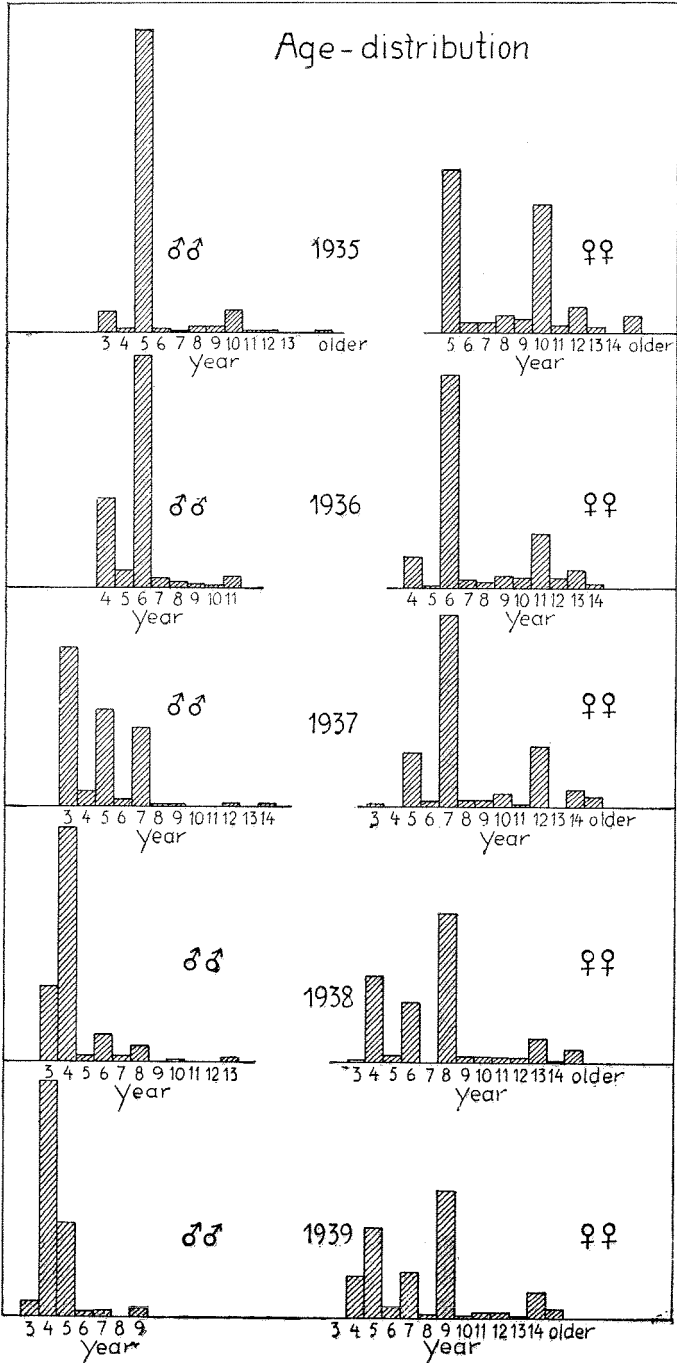


Fig. 9. Age-distribution of nature plaice in the Sundnes Area, Trondheim Fjord.

very strong. The same was ostensibly the case with the 1923 year-class, while on the other hand the year-classes 1929, 1931 and 1933 were weak.

The strong and the weak year-classes reappear in all the five years covered by this research. This seems to indicate that the material is fairly representative of the mature part of the stock, and we may therefore regard it as a fact that *there are great variations in the strength of the year-classes in the Trondheim Fjord plaice.*

*Incidence of Sexual Maturity in the Light of Age Analyses.*

The proportion between the number of males and females varies much from one year to the next. By looking at the age-distribution, table 15, we shall find a reasonable explanation. The males assert themselves in the mature stock already when three years old, whereas the females only in perceptible numbers from their fourth year. Further it is very strange how much quicker the number of males decrease than the females, the males seeming liable to a higher mortality than the females. We shall come back to this below.

The males appear in the mature stock at an age of three. At four they are more strongly represented, and reach their maximum at five. At six their number is distinctly reduced, and decreases rapidly every year thereafter.

The plaice in the Trondheim Fjord has, at an age of three years already, to a great extent, passed the minimum measure of 27 cm. The year-classes in the mature stock is therefore taxed by the fishery as well as by the natural mortality. And yet the number of individuals of mature males increases, relatively and actually from the third to the fifth year. The stock receives a greater accession from the immature males than what is necessary to counterbalance the losses. At an age of six the year-class has been reduced, and the reduction is more rapid in the seventh and eighth year. From this we can infer that *the greater part of male plaices in the Trondheim Fjord attain maturity at an age of three to six years.*

Whether the 7th year-class of males receives contributions of immatures, cannot be decided in this way. There are, however, a few immature 6-years males during spawning time in this area.

The females appear in the mature stock as 4 years old and increase in number until their 6th year. Even at an age of 7 it looks as if the contribution from the immature stock almost counterbalances the losses. *The greater part of the females plaice in the Trondheim Fjord attain maturity at an age of 4 to 7 years.*

From these data the reason is clear why the sex ratio varies so much as the samples show. It is a consequence of the variation of the strength of the year-classes, of the earlier incidence of maturity in the males and of their greater mortality.

## THE GROWTH OF THE PLAICE.

Hardly any fish has been subjected to such diligent research with regard to growth as the plaice. In spite of the fact that it has been investigated by a number of workers in various countries, it has not been possible to ascertain its average growth. The difficulty lies in procuring a representative material. A. C. JOHANSEN discovered that the larger individuals of one year-class of plaice will seek deeper water, while the more slow-growing will stay longer among the younger in shallower water. The same has also been pointed out by HEINCKE (13). As late as in 1938 BÜCKMANN and KOTTHAUS (8) came to the following conclusion with regard to plaice from the Flemish Bay and the German Bay: »Trotz der umfangreichen Untersuchungen, die gerade bei diesen Fischen durchgeführt worden sind, ist es kaum möglich das wahre durchschnittliche Wachstum in diesem Gebiet zu ermitteln«.

First of all we will try to investigate if a similar segregation goes on within the plaice-stock in the Trondheim Fjord.

The map fig. 10 gives an impression of the aspect and depth-conditions of the Borgen Fjord. The fjord is a branch of the Trondheim Fjord. It has a comparatively smooth bottom, covered with clay and mud with a rich bottom-fauna (NORDGÅRD 23). It is just outside this branch-fjord, off Sundness, in a depth of 20—40 m, that the plaice is caught, by a Danish seine, every year to be used in the hatchery of »Trondheim Biological Station«. Therefore it was of some interest to get samples from the Borgen Fjord for comparison. On the 28. Feb. 1935 183 plaice were taken off Rolshavn in a depth of 20 m. On the 9. April the same year 128 plaices were caught off Korsen in a depth of about 10 m. These samples were caught by the same Danish seine used in catching hatchery plaice off Sundnes.

The sex-composition of these samples is shown in table 16.

The females dominate the samples taken in the Borgen Fjord, whereas the males are more numerous off Sundnes. At the same time it is seen that practically all individuals off Korsen are immature, off Rolshavn 87,4 % of the females are immature, while off Sundnes the

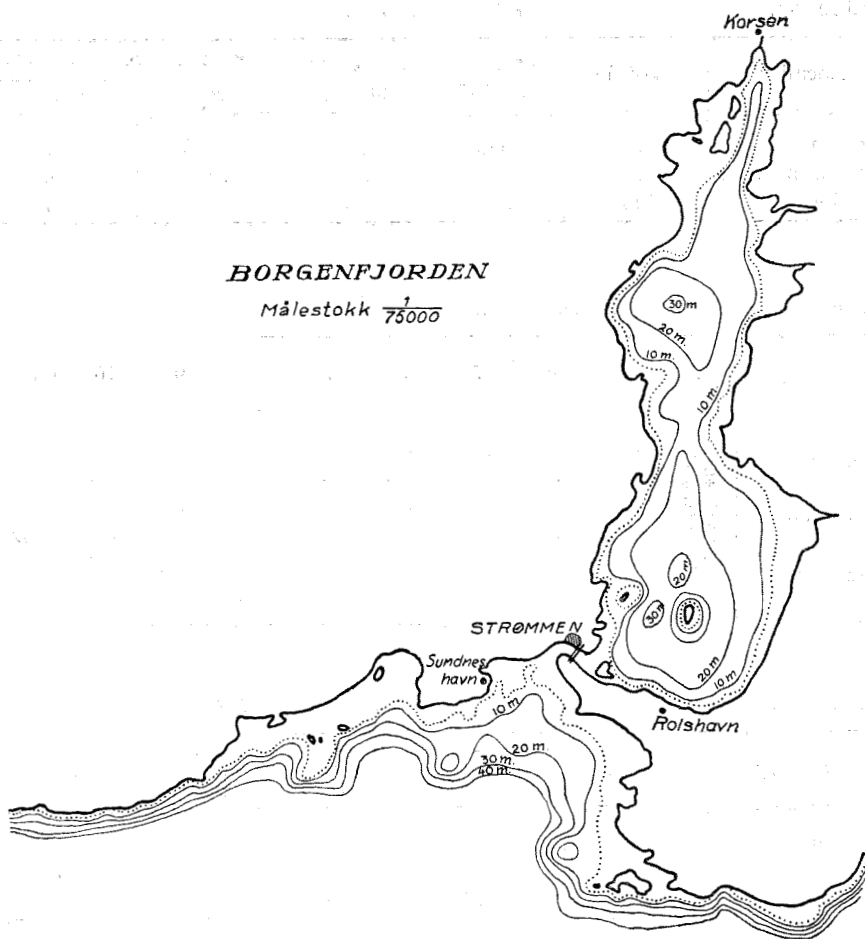


Fig. 10. Depths of the Borgen Fjord and Sundnes Area.

immatures make up 30,7 %. As to the males only 1 % of the total are immature off Sundnes.

The age-distribution is shown in table 17.

The samples from Korsen and Rolshavn are completely dominated by the 5 years' individuals, i. e. the 1930 year-class. Off Korsen also those of 3 years are well represented. The great difference found in the sex-composition of the samples is due to the 1930 year class, which alone shows the following sex-composition:

The females and also the immature of both sexes constitute a considerably higher percentage in the Borgen Fjord than outside, off Sundnes. This serves to verify that the males attain maturity at an

Table 16. *Sex-composition.*

Locality	Total	Percentage of ♂♂	Percentage of ♀♀	Percentage of Immature	
				♂♂	♀♀
Korsen .....	128	34,3	65,7	93,2	97,7
Rolshavn ....	183	14,2	85,8	53,8	87,4
Sundnes .....	1173	51,6	48,4	1,0	30,7

Table 17. *Age-distribution in ‰<sub>00</sub> 1935.*

Locality	Sex	3	4	5	6	7	8	9	10	Older
Korsen ....	♂♂	465	—	535	—	—	—	—	—	—
	♀♀	118	—	847	—	23	—	—	—	12
Rolshavn ...	♂♂	154	—	846	—	—	—	—	—	—
	♀♀	31	—	892	6	—	6	—	—	62
Sundnes ..	♂♂	52	7	828	7	7	15	15	58	10
	♀♀	17	13	600	13	13	27	20	217	80

Table 18. *Sex-compositon of the 1930 Year-class.*

Locality	Total	♂♂ %	♀♀ %	Immature Individuals in ‰	
				♂♂	♀♀
Korsen .....	95	24	76	87	100
Rolshavn ....	166	13	87	55	87
Sundnes .....	190	49	51	3	49

earlier age than the females, and suggests an emmigration of mature individuals from the Borgen Fjord.

The size-distribution of the 5 years old plaice in the three samples is shown in fig. 11. For the sake of comparison the distribution in all samples have been reduced to ‰ after being smoothed according to the formula  $b = (a + 2b + c) / 4$ , the letters a, b and c representing the number of individuals in three consecutive cm-groups. All individuals in the sample, measuring 29,5 to 30,4 cm are included in the 30 cm-group. The 31 cm-group contains those from 30,5 to 31,4 cm a.s.f.

Off Korsen the individuals of the 1930 year-class are the smallest. Off Rolshavn they are medium-sized and the biggest off Sundness. A computation of the average lengths gave as a result (the standard error multiplied by 3).



Table 19.

*Average Length in cm of the 1930 Year-class, with Standard Error.*

Locality	♂♂		♀♀	
	Av. Length	3 m	Av. Length	3 m
Korsen .....	31,2	0,8	32,0	0,7
Rolshavn .....	31,6	1,6	36,0	0,6
Sundnes .....	34,1	0,4	36,8	0,5

As will be seen a considerable difference in size exists between males and females, but there is also difference within the same sex from the various localities. *A segregation is taking place, as the larger individuals of a year-class are to be found in deeper water than the smaller.*

We might explain the slight growth off Korsen, as an effect of over-population, like what has been observed along the Jutland coast. It is, however, difficult to accept such an explanation, considering the short distance we have to do with and realizing that the whole area in which the three localities are situated, make up one undivided plaice-ground.

Completely parallel conditions are found in the Tana Fjord in Finmark. At the mouth of the river Tana there is a basin called Leirpollen. This communicates with the main fjord through a narrow channel. Samples have been captured in the Leirpollen, in the channel itself and on the banks outside. The length-distribution in these samples and in those from Korsen, Rolshavn and Sundnes is shown on fig. 12. There are many such localities among the Norwegian skerries, in bays and coves and small fjords with sandy shores where the plaice grows up, and from where it afterwards emigrates to recruit the fishing grounds. An excellent illustration of these conditions is found in BJERKANS marking experiment on the Tana banks (6). Young plaices were marked and afterwards recaptured at different localities in the fjord and even taken in trawl-catches off the coast of Finmark.

Samples taken at a certain depth from a plaice-ground may therefore give a completely wrong picture of the stock in the area. To take three localities so near each other as Korsen, Rolshavn and Sundnes we find difference both with regard to size, growth, sex-proportion, incidence of maturity and age-composition. None of the samples would give a correct idea of the stock of plaice in the area as a whole. If we should want to form an approximately correct conception of the stock, samples had to be collected from a number of localities within the area, and the various samples had to be considered in proportion to the

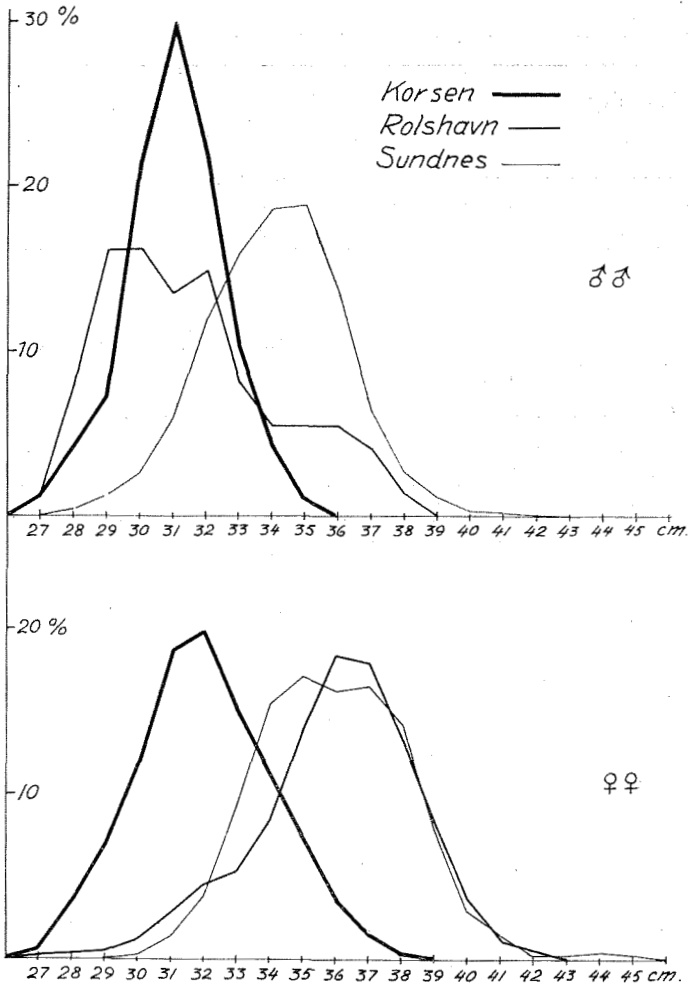


Fig. 11. Length-distribution of 5 year-old plaice from various lokalities in the Trondheim fjord.

actual number of plaice in existence at these localities. As far as our present knowledge goes, such weighting is well-nigh impossible.

Along the Norwegian coast with its most diverse depth-conditions, it is extremely difficult, if not impossible, to procure representative samples for a fairly accurate characterization of the growth of the plaice. The values found according to usual methods can only be rough approximations. But we will compute the average length of the different year-classes in the mature stock. On account of the great variation

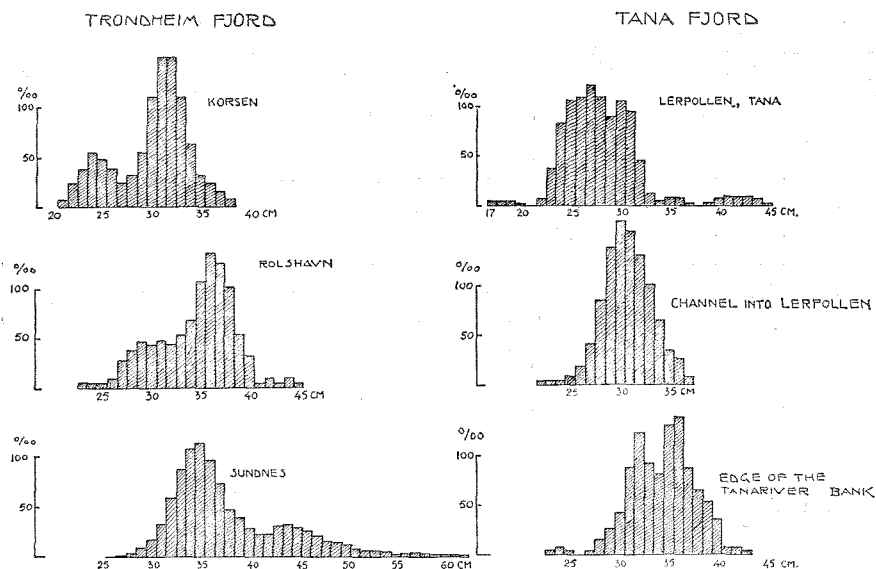


Fig. 12. Length-distribution of plaice at increasing distance from the nursery grounds (Korsen, resp. Lerpollen).

in the strength of the year-classes, the material is only sufficient to provide fairly good mean values of some of the year-classes represented. The greater part of the material from 1937 had been salted, and measurements before salting repeated after one month in salt shows a contraction of about 1 cm. Therefore, the greater part of 1937 material must be left out of account. In the table below are entered the values for the different year-classes according to computations in 1935—39.

Table 20.

*Average Length of Males, Sundnes, Trondheim Fjord.*

Age	1935		1936		1937		1938		1939		35—39	
	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n
3	30,5	15	—	—	31,3	38	32,5	103	31,4	25	32,0	181
4	—	—	35,0	107	—	—	35,1	329	33,2	404	34,2	840
5	34,1	212	35,9	19	35,7	18	38,4	8	35,4	102	34,8	419
6	—	—	36,4	289	—	—	37,7	37	36,9	8	36,6	334
7	—	—	—	—	37,7	24	38,8	5	38,1	12	38,0	41
8	35,8	5	—	—	—	—	38,4	22	—	—	37,9	27
9	37,8	4	—	—	—	—	—	—	38,9	13	38,1	17
10	39,1	17	—	—	—	—	—	—	—	—	39,1	17

Table 21. *Average Lengths of Females, Sundnes, Trondheim Fjord.*

Year	1935		1936		1937		1938		1939		35—39	
	cm	n	cm	n	cm	n	cm	n	cm	n	cm	n
4	—	—	37,8	44	—	—	37,5	124	36,4	62	37,3	230
5	37,5	78	—	—	40,0	21	41,6	10	39,1	141	38,8	250
6	—	—	39,3	301	—	—	42,4	73	40,8	17	40,0	391
7	—	—	41,2	13	41,7	61	—	—	43,0	75	43,0	149
8	42,4	8	44,5	9	—	—	44,9	211	43,0	5	44,8	233
9	45,5	6	44,3	16	—	—	50,8	9	45,0	198	45,2	229
10	45,6	58	47,7	12	—	—	47,5	6	46,3	3	46,2	79
11	—	—	49,9	74	—	—	49,4	7	50,0	7	47,7	88
12	—	—	51,6	10	49,4	32	51,8	6	48,1	9	50,0	57
13	—	—	—	25	—	—	52,1	36	48,0	4	51,6	65
14	—	—	—	—	53,3	12	—	—	50,4	39	51,4	51
15	—	—	—	—	—	—	55,3	13	—	—	55,3	13

The figures in the column »35—39« show the average length of the different year-classes, based on the material collected in the course of 5 years. The samples were taken in February and the figures are therefore supposed to represent the average lengths of mature individuals of the respective year-classes, the last years growth being finished. Fig. 13 shows the growth. In spite of the comparatively great number from which the mean values have been computed, they do not give a smooth growth-curve. The reason is that there has been an important change in the growth during the period covered by the investigation. The growth of the female plaice of the two strong year-classes 1925 and 1930 was found to have taken place at the following rate:

Table 22. *Annual Growth of Plaice, Sundnes, Trondheim Fjord.*

Year of Life	Year-Class 1930 cm	Year of Life	Year-Class 1925 cm	Calendar Year
6	1,8	11	1,6	1935—36
7	2,8	12	1,7	1936—37
8	3,2	13	2,7	1937—38

The growth increases with progressive age in both year-classes, as distinct from what has been generally experienced in plaice and other fish. The improved growth in 1938 may also be understood from fig. 14 which shows the average lengths of the males, computed from

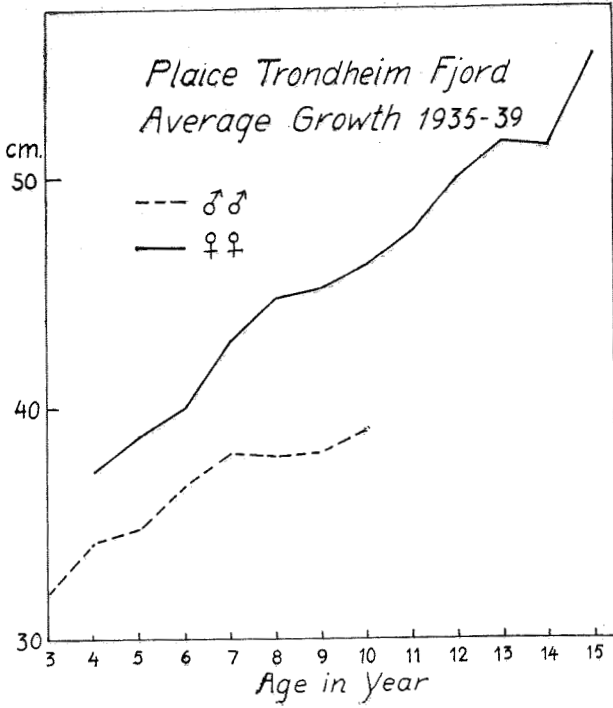


Fig. 13.

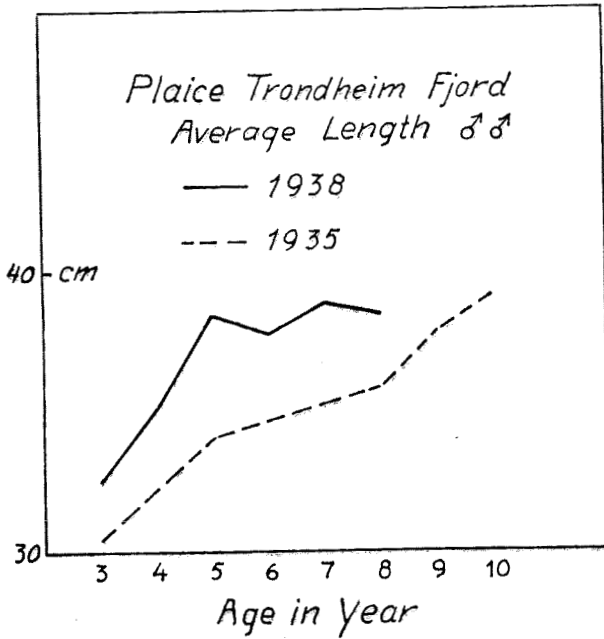


Fig. 14.

the 1935 and 1938 material. All values from 1938 lie above the corresponding values from 1935. In 1939 smaller increments were again observed.

The explanation of this matter is an improvement of the growth-conditions for the plaice in the Trondheim Fjord during the period 1935—38. In september 1934 some Sunnmøre fishermen discovered a number of grounds suitable for the Danish seine. Previously, fishing for plaice in the fjord had been carried on mainly with gill-nets. The modern Danish seine being practically unknown in the fjord. In the autumn and winter 1934—35 no less than 40 Danish-seinesmacks from other parts of the country took part in the plaice- and haddock-fishery. The fishermen of the fjord soon learnt the new methods, so that in spring 1935 already, there were 20 Danish-seine-smacks belonging to local fishermen. It may therefore be possible that intense fishing has thinned the stock and thus caused better food conditions for the remainder. The natural fluctuations in the plaice population may also be a concurrent cause. The 1931 and 1933 year-classes were very weak ones, and even that of 1932 is poor, compared to the 1930 and 1925 year-classes. In 1934 and 1935, on the other hand, we have strong year-classes again, and these begin from 1938 to assert their rights on the feeding-grounds of the mature population, and this may therefore be one of the causes that the growth decreases again from this year.

It is worth notice, however, that ROLLEFSEN (28) finds a general increase in the growth of the cod in the same years, it may thus be possible that it is not a local feature only, but may be connected with the general rise of temperature found in the whole of the northern area in this period. We will come back to this question later.

A comparison between the average lengths of the various age-groups from the Trondheim Fjord and the plaice from other localities cannot be summarily made as the plaice were caught on the spawning-ground just before spawning time. The youngest age-groups of the mature plaice therefore represent a selection of the most fast-growing within the respective year-classes. The average size of the 3—6 years groups are probable to high.

A. C. JOHANSEN (17) states the following values for the average length of the plaice in the Belt waters, based on measurements made by himself and REIBISCH (table 23).

These values are based on measurements made in the course of September, and yet we see that the highest values found within that area, lie well below the corresponding average from the Trondheim Fjord.

HEINCKE and BÜCKMANN (13) state that the lengths of the 5-group, measured in September off Heligoland, given in table 24.

Table 23. *Average Length in mm of Plaice in the Belt Waters.*

Sex	1	2	3	4	5	6	7	8	9	10	Locality
♀♀	80	165	205	240	265	270	285	300	315	330	Langeland Belt
♂♂	80	160	160	195	220	—	—	—	—	—	—
♀♀	80	165	205	240	255	270	280	290	300	310	Southern Entr. to Little Belt.
♂♂	80	160	190	205	215	225	235	245	—	—	Fehmarn Belt.
♀♀	80	165	200	225	240	250	260	270	280	290	Fehmarn Belt.
♂♂	80	160	180	190	200	210	220	230	—	—	—
♀♀	70	140	180	200	215	230	240	250	260	270	Fehmarn Belt.
♂♂	70	140	170	180	190	200	210	220	—	—	Kadet Channel.

Table 24. *Average Length in mm, Heligoland.  
September. 5-group.*

Year	♂♂ mm	♀♀ mm
1905/06	299	327
1916/18	253	280
1919	229	250
1922	234	208
1925	219	262

The highest values 1905/06 lies 6 and 7 cm resp. below the average length of the plaice in the Trondheim Fjord of the same age-group.

Å. VEDEL TÅNING (32) quotes the length of the various age-groups in Icelandic waters at a depth of 20—50 m, measured in June—August.

Table 25. *Average Length in cm of Plaice in Icelandic Waters.*

Age-group	S. Iceland	Faxa Bay	N. Iceland	E. Iceland
3	29—31	23—25	ca. 26	ca. 20
4	33—37	26—28	27—30	25—28
5	36—40	28—31	31—33	29—30
6	(35—37)	29—33	33—37	(31—32)
7	(36—44)	33—35	35—39	(35—36)

TÅNING'S values are average length of males and females together. He describes the values from S. Iceland as the highest ever observed till then. We see that the growth of the plaice in the Trondheim Fjord is, at any rate, equal to the growth in the Icelandic waters.

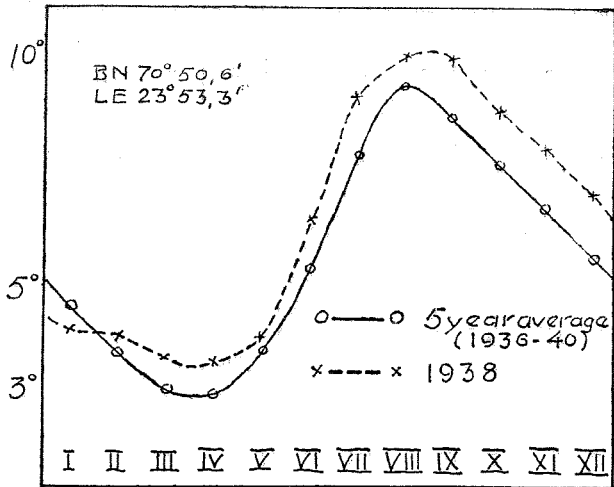


Fig. 15. Average temperature of seawater at 4 m during 1936-40 and in 1938.

Apart from the considerable better growth found in the Trondheim Fjord plaice, there are important features common to A. C. JOHANSEN'S results and those arrived at on material from the Trondheim Fjord:

1. There is a considerable difference in growth between males and females.

2. The decrease in number of males is more rapid than the decrease of females, so that the material, as to the older age groups, is insufficient for settling the average length of the males.

3. After a very rapid growth in the first years, there is a considerable reduction in the growth-rate during the years when sexual maturity sets in, afterwards the growth-rate decrease slightly with age.

According to TÅNING'S tables the conditions in Icelandic waters, apart from N. Iceland, are completely different with regard to the two first points, the males being practically of the same size as the females within the same age-group, and quite as numerous, the 7-group containing 521 males to 476 females.

Now, JOHANSEN'S and REIBISCH'S measurements were made early in this century when the plaice fishery in the Belt Sea to a great extent was carried out with gill-nets. The same is still the case in the Sundnes area in the Trondheim Fjord, — commercial fishery with Danish seine being prohibited except for catching parent fish for the T. B. S. hatchery. The gill-nets probably take an unequal toll from the two sexes. The meshes of the nets is namely calculated mainly to catch plaice of 30—40 cm length and as the females use considerably less



time in passing through these dangerous size-limits than the males, this may explain why males of older age-groups now are relatively so rare in the samples from the Sundnes region, and in the Belt Sea 35 years ago. In Icelandic waters, on the other hand, it is Danish seine and trawl which mainly are in use, and these implements catch plaice without selection in point of size over 30 cm. Why the male plaice in Icelandic water apparently, according to TÅNINGS tables, grow as fast as the females, is more difficult to explain.

The samples collected from other localities in Norwegian waters are few and therefore insufficient for computing the growth. Nevertheless we shall quote some data:

Table 26. *Average Length of Plaice in mm, Norwegian Waters.*

No. on Map. 6	Locality	Date	Age-groups							
			3	4	5	6	7	8	9	10
3.	Vigra near Ålesund . . . . .	31/5—35	307 (32)	330 (37)	379 (16)	411 (9)	430 (2)	—	—	—
10.	Beitstad Fjord. Trondheim Fj. . . .	23/5—35	368 (28)	396 (18)	400 (26)	390 (3)	453 (3)	462 (4)	470 (6)	513 (13)
19.	Sørøy in Finmark . . . . .	2/8—35	307	397 (3)	424 (21)	473 (10)	473 (8)	465 (2)	512 (2)	—
23.	Leirpollen in Tana, Finmark. . .	22/7—35	165 (38)	219 (7)	250 (2)	264 (40)	284 (42)	291 (7)	—	—

The number of individuals upon which the average length is based, has been entered in ( ), males and females taken together. The course of the values permit us to form an opinion as to the growth:

The Sørøy-grounds show a very high average length of 6 years' and older individuals. This is remarkable when we bear in mind the low temperature in which the plaice of these waters live. The fig. 15 (furnished by dr. EGGVIN) shows the temperature at Revsbotn, a little E of the place where the sample was collected. The unbroken line shows the medium temperature in 4 m depth based on termograph observations throughout the years 1936—40. The dotted line shows the same for 1938, the warmest year ever recorded. The temperature in 4 m depth seldom exceeds 10° C. normally being above 9° during one month of the year only. Deeper down the annual amplitude is smaller and the maximum temperature lower. According to ÅGE J. C. JENSEN (15) the growth of the plaice in Danish waters is fairly proportional to the temperature up to about 15° C. Consequently, we should expect to find a bad growth along the Finmark coast. As shown by BJERKAN (6) the sand-eel (*Ammodytes*) is the chief food for a great portion of the plaice in N. Norwegian waters.

Sand-eels may appear in enormous shoals along the Finmark coast, and plaice captured under such conditions, are choke-full of them. This may be the cause of the good growth, but otherwise it is a common feature found in most species of fish that the best growth is found in those individuals which live in comparatively warm water the first years, but these will attain maturity at an earlier age, and after maturity the growth decreases. Those living farther north attain maturity at a later age, thus keeping their relatively good growth longer. The plaice along the Finmark coast remain in the immature stage 2—4 years longer than f. inst. the plaice in Danish waters. The main cause of the higher average length in older year-classes in Icelandic and Norwegian waters may probably be found in this circumstance.

The bad growth which the values from the Leirpollen imply, may be connected with the fact that this cove is a typical nursery ground, where the segregation must lead to a considerably smaller difference between the average lengths of two consecutive year-classes, than the actual growth of the plaice in the cove, as found if the emigrated individuals could be included in the sample.

*A new Method in Computing the Growth of the Plaice.*

In spite of the comparatively rich material, collected every year in the Trondheim Fjord, only the strongest year-classes are sufficiently numerous to enable a fairly accurate determination of the average length of the year-classes. If a method of computing the growth might be found, similar to that applied to the herring, the progress would have been better.

ÅGE J. C. JENSEN (15) introduces such a method in trying to compute the growth of the plaice from the width of the zones in the otoliths. The method is most interesting, but, as JENSEN points out, there is no direct proportionality between the growth of the otolith and of the fish, and the computation of the length of the fish in its different years of life therefore is difficult. The performing of homogeneous measurements of the otoliths is also attended with technical difficulties.

The scales of the plaice are small and, in the case of older individuals, unsuitable for the determination of age, and consequently not to be used in the same way as the herring-scale.

The interoperculum, on the other hand, will serve our purpose better. The object is relatively large, and the winter-rings are generally discernible as distinct lines. The first year may be difficult to ascertain, but the later years are easily distinguished in most cases.

The photograph plate 1 shows an enlarged picture of the right inter-

operculum of a 5-years' old plaice about 35 cm long. Similar photographs are easily made by using the interoperculum itself as »negative« in a projection apparatus. It is best to clear up the object in acetone, so that the lines, showing the limits of annual growth, are well discernible.

It is difficult to fix the growth-center, but a very characteristic bend will be seen where the letters  $a_1, b_1, c_1, d_1$  and  $a_2, b_2, c_2, d_2$  are inscribed. Generally the distances  $a_1—a_2, b_1—b_2$  etc. are easily measured. If we adopt the same terms as those used in the case of the herring-scale, designating the distance  $a_1—a_2$  by  $v_2, b_1—b_2$  by  $v_3$  etc. we shall arrive at the following proportion (provided that proportionality exists between these lengths and the length of the plaice in the respective years):

$$\frac{v_n}{V} = \frac{l_n}{L} \text{ or } l_n = \frac{Lv_n}{V}$$

The index  $n$  indicates the year for which we will compute the length,  $l_n$  is the length in this year,  $L$  indicates the measured length of the plaice, and  $V$  corresponds to the distance  $d_1—d_2$  in our photograph,  $v_n$  is the corresponding distance on the interoperculum in the year in question.

The condition of finding the actual length of the plaice in the year we compute, is that proportionality really exists. For the purpose of ascertaining this, the distance  $d_1—d_2$  has been measured on a great number of plaices from the Trondheim Fjord, and the result are entered below in the table.

Table 27. *Total length of Plaice and Size of Interoperculum.*

Sex	V in mm	28	29	30	31	32	33	34	35
♂♂	L in mm . . . . .	340	345	360	362	379	378	396	395
	Number . . . . .	17	31	28	28	27	28	17	7
♀♀	L in mm . . . . .	—	—	—	343	363	373	382	388
	Number . . . . .	—	—	—	5	12	16	20	19

Sex	V in mm	36	37	38	39	40	41	42	43
♂♂	L in mm . . . . .	405	—	—	—	—	—	—	—
	Number . . . . .	7	—	—	—	—	—	—	—
♀♀	L in mm . . . . .	403	406	422	432	442	453	473	467
	Number . . . . .	31	23	37	23	24	10	10	5

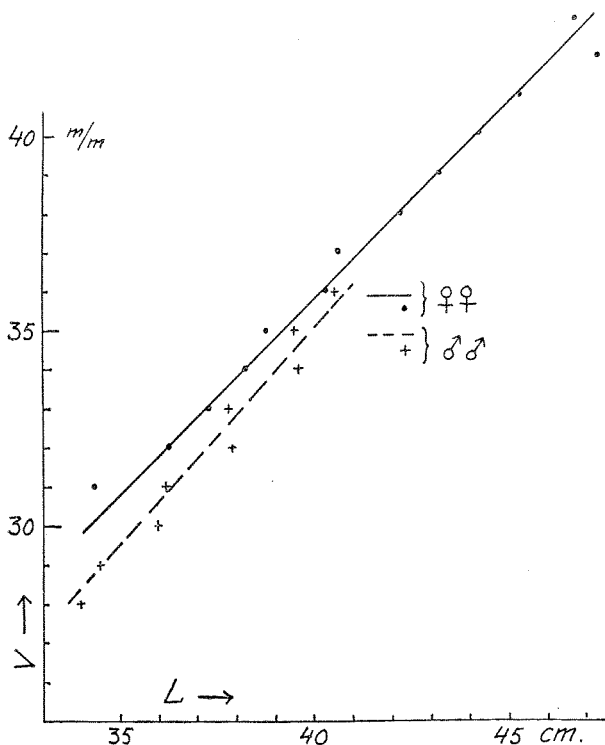


Fig. 17. Correlation between total length (L) and length of interoperculum (V).

The figures in the table were arrived at in the following way: Males and females were grouped separately according to the size of interoperculum in intervals of 1 mm, and the average total length of each group was computed, and entered together with the number of specimens in each group.

Fig. 17 illustrates the result. We see that the values are grouped as nicely as could be expected along two straight lines. The interoperculum of the females is a bit larger than that of the males, *both sexes showing a linear proportion between the size of interoperculum and the total length within the range considered.*

The measurement of the interopercula was made by placing it over a strip of mm-paper. As seen from the table 1 mm in V corresponds to 1 cm in L, the accuracy in measuring of V thus being somewhat less than the accuracy in the measuring of L. By using simple magnifying apparatus, with a magnifying power of 10, we will be able to measure V with at least the same accuracy as L.

The method looks very promising, but should be subjected to much closer trial before its efficiency can be definitely decided.

## THE SPAWNING ZONES OF THE PLAICE.

During his work on the age-determination of cod (*Gadus callarias*) by the aid of otoliths, GUNNAR ROLLEFSEN (1932) discovered that the zones in the otoliths from a certain year change in appearance. The opaque belts which in the first years make up the greater part of the growth of the otolith, change into narrow sharply defined zones, and the continued growth of the otoliths is mainly seen in the hyaline belts.

From this ROLLEFSEN inferred that a change had taken part in the life of the cod, revealing itself in this way. He suggested that the change was caused by the onset of sexual maturity. Through investigations of a great number of otoliths and ascertainment of the date, when the change took place in each of them, ROLLEFSEN succeeded in pointing out a series of facts in support of this inference.

ROLLEFSEN terms the changed outer zones in the otoliths »Spawning Zones«. By counting these it is presumably ascertained how many times each individual skrei has spawned and, the age known, it will, in all probability be possible to ascertain the age at maturity.

It proves to be very easy to see similar changes in the otoliths of the *Pleuronectids*, and even more suitable for the purpose is the interoperculum. A. C. JOHANSEN (1912) is fully alive to the fact that we can generally ascertain the onset of sexual maturity by the aid of otoliths in *Pleuronectes platessa* Lin. In his paper »Om Rødspetten og Rødspettefiskeriet i Beltefarvandet« page 25, JOHANSEN writes as follows (here quoted in Engl. translation): »When we see that the rings, from a certain point in the otolith, become distinctly narrower than the earlier rings, then we have, as a rule, an indication of the age at which the plaice attain maturity, for after the occurrence of maturity, the growth-rate declines very much. The great decline in the growth-rate, will, in some cases begin in the first period of growth already, before the attainment of maturity, in other cases only after maturity«.

O. NORDGÅRD (1913) writes in his paper: »Beretning om utklækning av guldflyndre« (23) page 84, »After the fourth ring (of interoperculum), the year-rings, as a rule, were lying close to each other. After spawning

has begun the growth declines, which was to be expected«. NORDGÅRD consequently has been aware of the fact that the occurrence of spawning could be ascertained by the aid of the interoperculum.

It is, however, ROLLEFSEN's discovery of the spawning zones in the skrei-otoliths and his recognition of the statistical value of the discovery, which has opened prospects of a far closer research into the biology and fluctuations of sexual mature fish populations.

In the material here investigated, otoliths as well as interoperculum, were used. To make such investigations much training is necessary, (as also is the case of age-determination) to attain assurance in the work. In the case of some individuals it is not possible to state safely the change after a certain age. Such individuals have been left out of account. This amounts, however, to a few percent only of the whole material.

As mentioned by JOHANSEN, the decline in growth does not always coincide with the first spawning, but may occur in the growth-period before spawning. This is what is called by ROLLEFSEN »preamble of spawning«. A plausible explanation of the fact that a decline in growth — when part of the power of growth is transferred to the development of the gonads — cannot always be traced, is that the plaice may have sought deeper water and have arrived into an environment conditioning a more rapid growth. The potential growth is reduced at the onset of sexual maturity, but the actual growth may not necessarily decrease, it may even increase, as we shall see below.

By the aid of a few pictures we shall try to show the appearance of the spawning zones on the interoperculum of the plaice.

The above sketch is a direct copy of HEINCKES illustration to show the difference in growth in plaice from the North Sea and from the Baltic. *A* shows the interoperculum of a 21 cm long male plaice from the North Sea, and *B* the same of a 21 cm long female plaice from the Baltic. The drawing has been used by many authors to demonstrate the difference in growth in these two areas, thus also in »Depths of the Ocean« by MURRAY and HJORT. As an object of demonstration to show difference in growth, it is, however not very lucky, for *A* is a drawing of the right interoperculum, and *B* of the left. (The right interoperculum always grows quicker than the left in the same individual). But the drawings are good illustrations of the interoperculum of a 3 years' old male which has not yet spawned or is in spawn for the first time, and of a 6 years' female which reached sexual maturity at an age of 3 years.

By a closer scrutiny of the appearance of the winter-rings on the interoperculum, we shall discover that generally an important difference sets in from a certain year. The first rings are not particularly distinct,

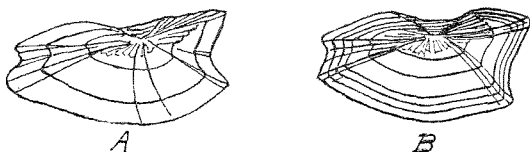


Fig. 18.

A. Interoperculum of North Sea plaice.

B. Interoperculum of Baltic plaice.

(After Heincke.)

but from a certain year the winter-rings become very prominent and broader. The first rings show a gradual transition from the winter-rings to the new growth, while from a certain year the limit of the winter-rings appear as distinct lines.

The photograph, plate 2, fig. 19, shows a portion of the interoperculum of a female plaice, 63 cm long, killed 20/4 1936 at Trondheim Biological station. It has reached an age of 21 years; the two first years are not discernible on the photograph. We can see that the third and fourth zone of stagnation are narrow and not very prominent. From the fifth, on the other hand, they become more distinct and considerably broader. By comparing this change in appearance of the winter-rings with the otoliths this change is coincident with the occurrence of the spawning zones in the otoliths. In this case the plaice is believed to have begun spawning at an age of 5. Here we see a considerable decrease in growth after the change in appearance of the winter-rings has occurred, but no »preamble of spawning«.

The photograph, plate 3, fig. 20, shows the interoperculum of a female plaice, 11 years old, killed after spawning 27/4 1936 at T. B. S. It measured 51 cm. We see the broader and heavier winter-rings from the 6th year. The growth is considerably slower from its 5th year of life, and this may be taken as a »preamble of spawning«. The change itself in the appearance of the stagnation-zones stands out more distinctly on the object itself when seen through a binocular where the picture has more depth.

Plate 4, fig. 21, shows the photograph of the interoperculum of a 10 years' female plaice, 49 cm, (29/4 1935 T. B. S.). It is supposed to have attained maturity at an age of 6. Here no »preamble of spawning« is observed, on the contrary, the growth in its 6th year seems to have been better than in the 4th and 5th. The winter-rings from the 6th year show most distinctly a changed appearance below the figures 6, 7 etc. The winter-rings, besides being broader than the earlier ones, are terminated by a marked line.

Plate 4, fig. 22, shows the interoperculum of a female plaice which had not spawned in the season 1935, as could be seen from the ovary.

It was captured at the plaice-ground off Levanger in the Trondheim Fjord 21/5 1935, at an age of 5 years. No spawning zones can be seen. Another interesting thing about this photograph is that it shows the commencement of a new growth. By examining the gonads of the plaice caught between May 20th and 27th 1935 at various localities in the Trondheim Fjord, it was easy to decide which of them had spawned during the season. In those which had spawned, the interoperculum is bordered by a marked winter-ring, whereas still immature individuals distinctly show the commencement of a new growth. We may therefore presume that *immature plaice begin the new growth at an earlier date in spring than the mature individuals.*

It is easy enough to choose a number of interopercula from the rich material which has now been collected, and show a series of photographs on which the »spawning zones« will show as plainly as on the fig. 19, but such a demonstration of model objects would not afford any evidence that the change in the appearance of the zones is actually caused by the onset of sexual maturity. By means of the pictures here reproduced we hope to have conveyed a notion of the different types which most frequently occur in the Trondheim Fjord, and to have shown the actual appearance of the change. Now we shall proceed to show how the material arranges itself when classified with regard to no. of »spawning zones«.



THEORETICAL TREATMENT.

In a few papers (5—7) GUNNAR ROLLEFSEN has described a method by which, it is claimed, the relative strength and age-composition of the stock of the skrei (*Gadus callarias*) can be foretold. M. GRAHAM (11) has criticized the method expressing his doubt whether it be theoretical allowable. Before we proceed to handle the plaice material according to ROLLEFSENS methods, we shall investigate the mathematical basis of the theory.

We shall imagine a stock of fish within a limited area where the stock can receive no contributions, and no individuals can emigrate from the stock. It is assumed that we know the age of every individual in the stock and the age at the first spawning, which occurs at the earliest at an age of 3 years, at the latest at an age of 6 years. Then we can tabulate all adult individuals of the stock in a certain year,  $p$ , in one of ROLLEFSEN'S »spawning schemes« as follows:

*The mature Stock in the Year p.*

Total Age	Age at First Spawning			
	3	4	5	6
3	C <sub>3</sub>			
4	C <sub>4</sub>	D <sub>4</sub>		
5	C <sub>5</sub>	D <sub>5</sub>	E <sub>5</sub>	
6	C <sub>6</sub>	D <sub>6</sub>	E <sub>6</sub>	F <sub>6</sub>
.	.	.	.	.
.	.	.	.	.
.	.	.	.	.
n	C <sub>n</sub>	D <sub>n</sub>	E <sub>n</sub>	F <sub>n</sub>

All individuals which have attain maturity at an age of 3, are here indicated by the letter C, and the index added shows the age of the individuals in the year  $p$ . In the same way the letter D indicates those which have attain maturity at an age of 4, E at an age of 5 etc.

Consequently, according to ROLLEFSEN's definitions:

$$\begin{aligned}
 C_3 + C_4 + C_5 + C_6 + C_7 + \dots + C_n &= \Sigma C \text{ constitute spawning-group 1.} \\
 D_4 + D_5 + D_6 + D_7 + \dots + D_n &= \Sigma D && \text{---}\rangle\text{---} && 2. \\
 E_5 + E_6 + E_7 + \dots + E_n &= \Sigma E && \text{---}\rangle\text{---} && 3. \\
 F_6 + F_7 + \dots + F_n &= \Sigma F && \text{---}\rangle\text{---} && 4.
 \end{aligned}$$

Further, all individuals which have attain maturity in the same calendar year:

$$\begin{aligned}
 C_3 + D_4 + E_5 + F_6 &= S_1 \text{ constitute spawning-class 1.} \\
 C_4 + D_5 + E_6 + F_7 &= S_2 && \text{---}\rangle\text{---} && 2. \\
 C_5 + D_6 + E_7 + F_8 &= S_3 && \text{---}\rangle\text{---} && 3. \\
 \text{etc. etc.} &&&&&
 \end{aligned}$$

It is assumed that the mortality in the course of the year is the same in all year-classes.

If the mortality is called d, then

$$d = 1 - c$$

where c is the coefficient of remanence.

After one year the stock will be composed of:

*The mature Stock in the Year (p + 1).*

Total Age	Age at First Spawning			
	3	5	5	6
3	$C_3$			
4	$cC_3$	$D_4$		
5	$cC_4$	$cD_4$	$E_5$	
6	$cC_5$	$cD_5$	$cE_5$	$F_6$
7	$cC_6$	$cD_6$	$cE_6$	$cF_6$
.	.			
.	.			
.	.			
n	$cC_{n-1}$	$cD_{n-1}$	$cE_{n-1}$	$cF_{n-1}$

Consequently we can, by the aid of the coefficient of remanence compute all components of the mature stock, with the exception of spawning-class 1, i. e. the individuals which have attained maturity during the year p to (p + 1). In our scheme for the year (p + 1) these are indicated by  $C_3$ ,  $D_4$ ,  $E_5$  and  $F_6$ .

ROLLEFSEN has shown that, maturity in the case of the cod, seems to occur according to a definite rule, namely that a certain numerical proportion exists between the number of individuals of a year-class which attain maturity at a certain age, and those of the same year-class, which attained maturity the year before.

In the case of our theoretical stock we can express this so:

$$\frac{D_4}{C_4} = \frac{D_5}{C_5} = \frac{D_6}{C_6} = \dots = \frac{D_n}{C_n} = \frac{D_4 + D_5 + D_6 + \dots + D_n}{C_4 + C_5 + C_6 + \dots + C_n} = f_{4/3}$$

$$\frac{E_5}{D_5} = \frac{E_6}{D_6} = \frac{E_7}{D_7} = \dots = \frac{E_n}{D_n} = \frac{E_5 + E_6 + E_7 + \dots + E_n}{D_5 + D_6 + D_7 + \dots + D_n} = f_{4/5}$$

$$\frac{F_6}{E_6} = \frac{F_7}{E_7} = \frac{F_8}{E_8} = \dots = \frac{F_n}{E_n} = \frac{F_6 + E_7 + F_8 + \dots + F_n}{E_6 + E_7 + E_8 + \dots + E_n} = f_{6/5}$$

From the spawning scheme in the year  $p$  we can compute  $f_{4/5}$ ,  $f_{5/4}$  and  $f_{6/5}$  and with that we have the means at our disposal to compute  $D_4$ ,  $E_5$  and  $F_6$ .

These will be:  $D_4 = f_{4/3} \cdot C_3$ ,  $E_5 = f_{5/4} \cdot D_4$  and  $F_6 = f_{6/5} \cdot E_5$ .

In other words from the mature stock in the year  $p$  we can compute all components in the year  $(p + 1)$  with the exception of  $C_3$ .

In such species of fish where a year-class successively attains maturity in the course of some years, the component  $C_3$  will be small compared to the entire stock of mature animals, and the error made by assuming it equal to the component of a year-class of normal strength will generally be insignificant. If we in our research of the immature stock beforehand knew the strength of the still immature year-classes we shall also be fairly safe in estimating the value of  $C_3$ .

Till now we have dealt with a theoretical stock where all components are known. In nature no means are available to ascertain this, but if we can procure a really representative sample of the mature stock, then the proportion between the components of the sample ( $c$ ,  $d$ ,  $e$  and  $f$ ) will be the same as the actual proportion between the components of the whole mature stock ( $C$ ,  $D$ ,  $E$  and  $F$ ).

If the total number of the mature stock in the year  $p$  is called  $T_p$ , then the actual number can be tabulated as follows:

*The Mature Stock in the Year  $p$ .*

Total Age	Age at First Spawning			
	3	4	5	6
3	$T_p c_3$			
4	$T_p c_4$	$T_p d_4$		
5	$T_p c_5$	$T_p d_5$	$T_p e_5$	
6	$T_p c_6$	$T_p d_6$	$T_p e_6$	$T_p f_6$
7	$T_p c_7$	$T_p d_7$	$T_p e_7$	$T_p f_7$
.	.			
.	.			
.	.			
n	$T_p c_n$	$T_p d_n$	$T_p e_n$	$T_p f_n$
Sum	$T_p \sum c$	$T_p \sum d$	$T_p \sum e$	$T_p \sum f$

Here is  $\sum c + \sum d + \sum e + \sum f = 1$ .

$T_p$  cannot be determined, but all the other factors we can determine from a representative sample of the stock in the year.

Provided that the mortality is constant in all year-classes, and that maturity occurs according to a definite rule, then the whole mature stock in the year ( $p + 1$ ) can be tabulated as follows:

*The Mature Stock in the Year ( $p + 1$ ).*

Total Age	Age at First Spawning			
	3	4	5	6
3	$T_p x$			
4	$\zeta T_p c_3$	$\zeta T_p c_3 f_{4/3}$		
5	$\zeta T_p c_4$	$\zeta T_p d_4$	$\zeta T_p d_4 f_{5/4}$	
6	$\zeta T_p c_5$	$\zeta T_p d_5$	$\zeta T_p e_5$	$\zeta T_p e_5 f_{6/5}$
7	$\zeta T_p c_6$	$\zeta T_p d_6$	$\zeta T_p e_6$	$\zeta T_p f_6$
.	.			
.	.			
.	.			
n	$\zeta T_p c_{n+1}$	$\zeta T_p d_{n+1}$	$\zeta T_p e_{n+1}$	$\zeta T_p f_{n+1}$

Consequently we can express the mature stock in the year  $p$

$$T_p = T_p (\sum c + \sum d + \sum e + \sum f)$$

as  $(\sum c + \sum d + \sum e + \sum f) = 1$

and in the year  $(p + 1)$

$$\begin{aligned} T_{p+1} &= T_p [x_3 + \varsigma (c_3f_{4/3} + d_4f_{5/4} + e_5f_{6/5}) + \varsigma (\Sigma c + \Sigma d + \Sigma e + \Sigma f)] \\ &= T_p [x_3 + \varsigma (c_3f_{4/3} + d_4f_{5/4} + e_5f_{6/5}) + \varsigma] \end{aligned}$$

The proportion between the stock of the year  $p$  and  $(p + 1)$ :

$$\frac{T_p}{T_{(p+1)}} = \frac{1}{x_3 + \varsigma + \varsigma (c_3 f_{4/3} + d_4 f_{5/4} + e_5 f_{6/5})}$$

The unknown total number ( $T_p$ ) of which the stock consists in the year  $p$ , is a factor in the numerator as well as in the denominator, and can be left out. *Consequently we may, from the relative number in our spawning scheme of the year  $p$ , compute the age-composition and the relative increase or decrease of the mature stock in the year  $(p + 1)$ , provided that we possess a representative sample of the stock in the year  $p$ , and that we know the mortality and the proportion of each year-class attaining maturity in each year of its life.*

#### Mortality.

The best method for computing the mortality of the mature portion of the plaice stock in the Trondheim Fjord, is that which EINAR LEA has developed with regard to the Norwegian herring-stock. LEA shows (20) that the proportion of the stock, which survives from one spawning-season to the next, may be computed from material collected through a series of years, by means of the formula:

$$\begin{aligned} \varsigma = & \frac{(b_2 + c_2 + d_2 + \dots + n_2) + (b_3 + c_3 + d_3 + \dots + n_3) + \dots +}{(a_1 + b_1 + c_1 + \dots + m_1) + (a_2 + b_2 + c_2 + \dots + m_2) + \dots +} \\ & \frac{+ (b_x + c_x + d_x + \dots + n_x)}{+ (a_{x-1} + b_{x-1} + c_{x-1} + \dots + m_{x-1})} \quad (1) \end{aligned}$$

Here is  $a_1, b_1, c_1, \dots, n_1$  in LEA's terminology the proportion which the 7 years' herring made up of the samples in the series of years  $A$  to  $N$ .

$a_2, b_2, c_2, \dots, n_2$  denote the proportion which made up by the 8 years' herring in the samples from the series of year  $A$  to  $N$ .

$a_x, b_x, c_x, \dots, n_x$  denote the proportion made up in the samples from the respective years  $A$  to  $N$  by the oldest year-class represented in the material.

Instead of using the proportion which each year-class makes up in the samples from the respective years, there are no theoretical objections

in using the proportion made up by the different spawning-classes in the samples from the different years. It is a great advantage to treat spawning-classes instead of year-classes. For LEA shows that it is necessary to exclude from the computation the year-classes which still receive contributions from the immature stock. As to the plaice from the Trondheim Fjord this means that we should have to exclude the males of all year classes younger than 7, and the females of all year-classes younger than 8 years, i. e. the most important part of the material. If, however, the proportion of the samples made up by the respective spawning-classes is made the basis of calculation, then each spawning-class constitutes a definite biological unit, which receives no more contributions from the immature stock, and consequently the entire material of mature individuals can be included in the computation.

The meaning of the different symbols in LEA'S formula, when the spawning-classes are used as a basis of computation is as follows:

$a_1, b_1, c_1, \dots, n_1$  express the proportion made up by the first time spawners of the samples in the respective years  $A$  to  $N$ .

$a_2, b_2, c_2, \dots, n_2$  express the proportion which second-time spawners make up of the samples in the respective years  $A$  to  $N$  etc.

LEA also shows that the proportion of a year-class surviving the period from one spawning season to the next, can be computed by means of the formula:

$$\epsilon = \frac{b_2 + c_2 + d_2 + \dots + n_2}{a_1 + b_1 + c_1 + \dots + m_1} \quad (2)$$

The formula expresses the proportion of the 7 years' herring which will return to the spawning grounds as 8 years' individuals in the series of years  $A$  to  $N$ . In our case it expresses the proportion of the first-time-spawners returning to the spawning grounds as secondtime-spawners.

The formula (1) and (2) for computing the coefficient of remanence can only be used on the assumption that the mortality is constant in the series in question, and further, that it is the same in all year-classes, resp. all spawning-classes. LEA shows that if the stock is decreasing, e. g. from overfishing, then the calculated  $\epsilon$  will be greater than the actual, but smaller if the stock is increasing.

THE ONSET OF MATURITY,  
STUDIED BY MEANS OF THE SPAWNING-ZONES.

Before proceeding to try the theory on the material, we shall examine whether a definite proportion exists between the number of individuals which attained maturity in a certain year, and those of the same year-class which became mature the year before. We shall examine this in those year-classes where the extent of the material permits it, by means of the spawning-zones, and try to ascertain whether any difference as to the age at first spawning is found in the various year-classes.

*The 1925 Year-class.*

As regards the males, the number of individuals of the 1925 year-class in our material, is so small that no conclusions are permissible, they had nearly died out as early as in 1935. The females, on the other hand, are richly represented in the material through all years 1935—39. The results of determining the spawning-zones in the otoliths and interoperculum are as follows:

*Onset of Maturity 1925 Year-class Females.*

Year of Sampling	Age at First Spawning						Total	Mean Age	$\sigma$
	3	4	5	6	7	8			
1935 . . . .	—	4	13	29	14	1	61	5,92 ± 0,11	0,88
1936 . . . .	—	7	19	37	11	—	74	5,70 ± 0,10	0,83
1937 . . . .	1	5	11	30	12	1	60	5,83 ± 0,12	0,95
1938 . . . .	1	4	7	17	3	1	33	5,61 ± 0,17	0,97
1939 . . . .	—	9	6	17	5	—	37	5,49 ± 0,17	1,01
1935—39	2	29	56	130	45	3	265	5,74 ± 0,06	0,93
% . . . . .	0,8	11,0	21,1	49,1	17,0	1,1			

The figures show the number of females of the 1925 year-class in which the spawning-zones can be reliably counted, and the distribution of the individuals according to age at first time's spawning. Further the average age at attained maturity has been computed from the number found for each year, together with standard error and mean deviation.

The agreement is, as will be seen, rather good. As far as can be judged from these data, maturity sets in at an age of 3—8 years, and the average age of the females of the 1925 year-class at attained maturity was  $5,74 \pm 0,06$  years.

*The 1930 Year-class.*

At the collection of the material in 1935 the 1930 year-class was 5 years old. As some individuals of this year-class seems to attain maturity at an age up to 8 years old, it will be necessary to extrapolate the number attaining maturity at the age 6—8 years according to the apparent rule of the successive maturing observed in the sample from 36—39. Only then we will be able to compare the material collected before 1938 from this year-class. Then we shall find that the age at first time spawning is distributed as shown in the following table. (Extrapolated values printed in italics.)

*Onset of Maturity, 1930 Year-class, Males.*

Year of Sampling	Age at First Spawning						Total	Mean Age	$\sigma$
	3	4	5	6	7	8			
1935 . . . .	6	79	239	<i>49</i>	<i>14</i>	<i>0</i>	387	$4,96 \pm 0,04$	0,75
1936 . . . .	18	76	157	32	<i>12</i>	<i>0</i>	295	$4,80 \pm 0,05$	0,85
1937 . . . .	0	11	27	39	1	<i>0</i>	78	$5,00 \pm 0,10$	0,71
1938 . . . .	1	3	12	14	1	<i>0</i>	31	$5,05 \pm 0,20$	0,83
1939 . . . .	0	4	7	12	1	<i>0</i>	24	$5,00 \pm 0,23$	0,84
1935—39	25	173	442	146	29	<i>0</i>	861	$4,91 \pm 0,03$	0,89
% . . . . .	3,1	21,2	54,1	17,9	3,6	0,0			

The deviations shown by the data obtained in the different sampling years, lie within the limits of the probable error, and may be ascribed to the limited material.

As to the females, we shall find in the same way:

*Onset of Maturity, 1930 Year-class, Females.*

Year of Sampling	Age at First Spawning						Total	Mean Age	$\sigma$
	3	4	5	6	7	8			
1935 . . . .	0	11	66	47	<i>16</i>	<i>0</i>	140	$5,49 \pm 0,07$	0,80
1936 . . . .	0	40	136	121	<i>39</i>	<i>7</i>	337	$5,48 \pm 0,04$	0,86
1937 . . . .	0	21	94	58	22	<i>7</i>	196	$5,54 \pm 0,06$	0,81
1938 . . . .	1	26	90	67	21	2	207	$5,42 \pm 0,06$	0,78
1939 . . . .	0	17	83	66	23	<i>0</i>	189	$5,50 \pm 0,06$	0,82
1935—39	1	115	469	359	121	4	1 069	$5,48 \pm 0,04$	0,86
% . . . . .	0,1	10,8	43,8	33,6	11,3	0,4			



The data from the different sampling years show a very good agreement. The average age of the males in the 1930 year-class at attained maturity was found to be  $4,91 \pm 0,03$  years and of the females  $5,48 \pm 0,04$  years.

*The 1932 Year-class.*

As to this year-class we can not use the material collected before 1937, as the extrapolated values in the scheme would be too many and too conjectural. According to the determinations on samples from 1937—39 we shall find in the same way:

*Onset of Maturity, 1932 Year-class, Males.*

Year of Sampling	Age at First Maturity					Total	Mean Age	$\sigma$
	3	4	5	6	7			
1937 .....	3	26	31	8	0	68		
1938 .....	1	9	23	4	0	37		
1939 .....	0	4	6	2	0	12		
1937—39 .....	4	39	60	14	0	117	$4,60 \pm 0,06$	0,65
% .....	3,4	33,4	51,3	12,0	0,0			

As to the females one is not justified in using more of the material than from 1938 and 39.

*Onset of Maturity, 1932 Year-class, Females.*

Year of Sampling	Age at First Maturity					Total	Mean Age	$\sigma$
	3	4	5	6	7			
1938 .....	1	22	44	17	1	85		
1939 .....	0	10	46	15	1	72		
1938—39 .....	1	32	90	32	2	157	$5,01 \pm 0,06$	0,70
% .....	0,6	20,4	57,3	20,4	1,3			

Accordingly, the average age at attained maturity is, in the case of males of the 1932 year-class  $4,60 \pm 0,06$  and of the females  $5,01 \pm 0,06$  years.

The agreement between the determinations from the samples collected in the different years is, as far as can be controlled, very good. There is, on the other hand, a real difference between the year-classes as *the average age at the first spawning is decreasing from the 1925 year-class and up to the 1932 year-class.* If we draw a curve showing the distribution of the relative numbers as to age at attained maturity, we shall see that the curves for the 1930 and the 1932 year class are

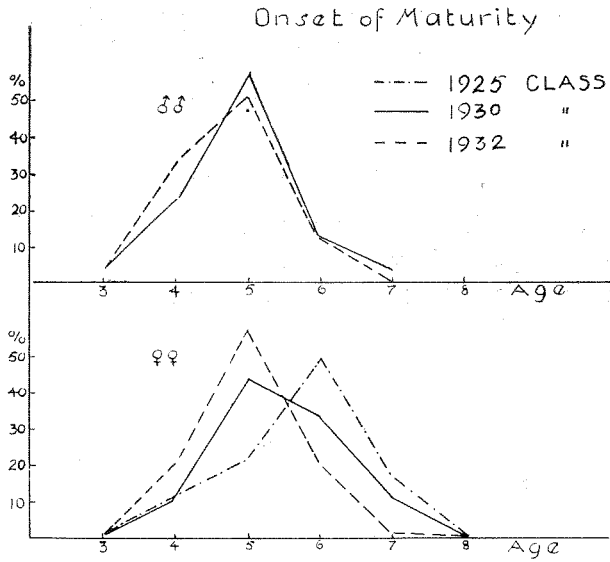


Fig. 23.

displaced to the left compared to the 1925 year-class. This applies to both sexes, as shown in fig. 23.

Thus, maturity is not reached at the same ages by the different year-classes. The *f*-coefficients computed as an average of all year-classes in the material with a view to predict the relative number of first-time spawners, may therefore show an important deviation from the real *f*-coefficients for the different year-classes producing first-time spawners in a certain year. We must know the «rule of the onset of maturity» for each single year-class to obtain a reliable result. The forecast of the number of first-time spawners, which is the same as forecasting the number recruiting the mature stock, may therefore prove somewhat problematic.

APPLICATION OF ROLLEFSEN'S THEORY  
TO THE PLAICE MATERIAL.

*Mortality.*

The material collected at Trondheim Biological Station in the years 1935—38 has been tabulated according to age and onset of maturity, based on the spawning zones. The immature individuals in the samples and those for which we can not quite reliably count the number of spawning zones have been left out. The proportion of each spawning group in each year-class is expressed in ‰ of the whole sample of males and the same for the females, as it is necessary that the two sexes are dealt with separately. The material from the different years is composed as follows:

Males.

1935							1936						
Total Age	Age at First Spawning						Age at First Spawning						
	3	4	5	6	7	Total	3	4	5	6	7	Total	
3	55	—	—	—	—	55	—	—	—	—	—	—	
4	—	7	—	—	—	7	72	169	—	—	—	241	
5	22	292	513	—	—	827	9	23	11	—	—	43	
6	—	4	4	—	—	8	41	172	354	72	—	639	
7	—	4	—	—	—	4	2	7	11	—	—	20	
8	—	—	7	7	—	14	—	2	5	7	—	14	
9	—	4	7	—	4	15	—	2	7	—	—	9	
10	—	15	26	15	4	60	—	2	2	—	—	4	
11	—	—	4	—	—	4	—	11	9	9	—	29	
12	—	4	—	—	—	4	—	—	—	—	—	—	
13	—	—	—	—	—	—	—	—	—	—	—	—	
Older	—	4	—	—	—	4	—	—	—	—	—	—	
Total	77	334	561	22	8	1 002	124	388	399	88	—	999	

		1937							1938						
Total Age	Age at First Spawning							Age at First Spawning							
	2	3	4	5	6	7	Total	2	3	4	5	6	7	Total	
2	4	—	—	—	—	—	4	4	—	—	—	—	—	4	
3	—	432	—	—	—	—	432	—	203	—	—	—	—	203	
4	—	13	27	—	—	—	40	—	99	540	—	—	—	639	
5	—	13	116	138	—	—	267	—	—	14	2	—	—	16	
6	—	—	9	9	—	—	18	—	2	18	45	8	—	73	
7	—	—	49	121	40	4	214	—	—	2	6	2	—	10	
8	—	4	—	—	—	—	4	—	2	6	23	8	2	41	
9	—	—	4	—	—	—	4	—	—	—	—	—	—	—	
10	—	—	—	—	—	—	—	—	—	2	—	—	—	2	
11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
12	—	—	—	4	4	—	8	—	—	—	—	—	—	—	
13	—	—	—	—	—	—	—	—	—	4	6	—	—	10	
Older	—	—	—	4	—	—	4	—	—	—	2	2	—	4	
Total	4	462	205	276	44	4	995	4	306	586	84	20	2	1 002	

1935

$$\begin{aligned}
 a_1 &= 55 + 7 + 513 &= 575 \\
 a_2 &= 292 + 4 &= 296 \\
 a_3 &= 22 + 4 + 7 + 4 &= 37 \\
 a_4 &= 4 + 7 + 4 &= 15 \\
 a_5 &= 7 + 15 &= 22 \\
 a_6 &= 4 + 26 &= 30 \\
 a_7 &= 15 + 4 &= 19
 \end{aligned}$$

1936

$$\begin{aligned}
 b_1 &= 169 + 11 + 72 &= 252 \\
 b_2 &= 72 + 23 + 354 &= 449 \\
 b_3 &= 9 + 172 + 11 + 7 &= 199 \\
 b_4 &= 41 + 7 + 5 &= 53 \\
 b_5 &= 2 + 2 + 7 &= 11 \\
 b_6 &= 2 + 2 + 9 &= 13 \\
 b_7 &= 11 &= 11
 \end{aligned}$$

1937

$$\begin{aligned}
 c_1 &= 4 + 432 + 27 + 138 &= 601 \\
 c_2 &= 13 + 116 + 9 + 40 &= 178 \\
 c_3 &= 13 + 9 + 121 &= 143 \\
 c_4 &= 49 &= 49 \\
 c_5 &= &= 0 \\
 c_6 &= 4 + 4 &= 8 \\
 c_7 &= 4 &= 4
 \end{aligned}$$

1938

$$\begin{aligned}
 d_1 &= 203 + 540 + 2 + 8 &= 753 \\
 d_2 &= 99 + 14 + 45 + 2 &= 160 \\
 d_3 &= 18 + 6 + 8 &= 32 \\
 d_4 &= 2 + 2 + 2 + 3 &= 27 \\
 d_5 &= 6 &= 6 \\
 d_6 &= 2 &= 2 \\
 d_7 &= 2 &= 2
 \end{aligned}$$

Females.

1935								1936							
Total Age	Age at First Spawning							Age at First Spawning							
	2	3	4	5	6	7	Total	3	4	5	6	7	8	Total	
4	—	—	—	—	—	—	—	12	72	—	—	—	—	84	
5	—	60	358	—	—	—	418	—	4	—	—	—	—	4	
6	—	11	5	5	—	—	21	—	78	266	237	—	—	581	
7	—	5	16	—	—	—	21	—	10	12	—	—	—	22	
8	—	11	16	11	5	—	43	—	10	6	2	—	—	18	
9	—	16	5	5	5	—	31	—	4	18	6	2	—	30	
10	—	22	71	158	76	5	332	—	6	8	10	4	—	28	
11	—	5	5	5	—	—	15	—	4	37	72	22	—	145	
12	5	5	43	11	—	—	64	—	10	12	—	—	—	22	
13	—	5	5	—	—	—	10	2	14	25	4	2	—	47	
Older	—	17	11	11	—	—	39	—	4	12	4	—	—	20	
Total	5	157	535	206	86	5	994	14	216	396	335	30	—	1 001	

1937								1938							
3	8	—	—	—	—	—	8	8	—	—	—	—	—	8	
4	—	2	—	—	—	—	2	10	228	—	—	—	—	238	
5	2	61	84	—	—	—	147	—	10	8	—	—	—	18	
6	—	6	6	—	—	—	12	2	43	86	33	—	—	164	
7	—	67	249	157	51	—	524	—	—	—	—	—	—	—	
8	—	6	6	—	2	—	14	2	51	176	131	41	4	405	
9	—	6	8	4	—	—	18	—	6	12	—	—	—	18	
10	—	2	12	16	4	—	34	—	8	2	8	—	—	18	
11	—	—	4	2	—	—	6	—	4	4	6	—	—	14	
12	2	10	39	63	45	2	161	—	—	8	4	—	—	12	
13	—	—	—	—	2	—	2	2	8	14	33	6	2	65	
Older	4	18	35	12	—	—	69	2	14	12	22	2	—	42	
Total	16	178	443	252	106	2	997	26	372	322	227	49	6	1 002	

In the same way as for the males we find:

1935	1936	1937	1938
$a_1 = 363$	$b_1 = 309$	$c_1 = 145$	$d_1 = 281$
$a_2 = 70$	$b_2 = 282$	$c_2 = 226$	$d_2 = 147$
$a_3 = 48$	$b_3 = 94$	$c_3 = 257$	$d_3 = 174$
$a_4 = 102$	$b_4 = 26$	$c_4 = 81$	$d_4 = 178$
$a_5 = 174$	$b_5 = 60$	$c_5 = 32$	$d_5 = 71$
$a_6 = 92$	$b_6 = 84$	$c_6 = 65$	$d_6 = 18$
$a_7 = 38$	$b_7 = 45$	$c_7 = 71$	$d_7 = 22$

Now we can compute the coefficient of remanence from LEA'S formula.

$$\zeta = \frac{(b_2 + c_2 + d_2) + (b_3 + c_3 + d_3) + (b_4 + c_4 + d_4) + \dots + (b_7 + c_7 + d_7)}{(a_1 + b_1 + c_1) + (a_2 + b_2 + c_2) + (a_3 + b_3 + c_3) + \dots + (a_6 + b_6 + c_6)}$$

The result of the computation will be:

	Coefficient of remanence:	
	Males	Females
$\zeta_{35-36}$	0,75	0,70
$\zeta_{36-37}$	0,39	0,86
$\zeta_{37-38}$	0,24	0,76
$\zeta_{35-37}$	0,57	0,78
$\zeta_{36-33}$	0,31	0,81
$\zeta_{35-38}$	0,46	0,77

The indices denote the calendar years of the material upon which the computations have been based. As will be seen, the coefficient of remanence for the males is very variable. This is caused partly by the scantiness of the material and also by the fact that the mature stock undoubtedly has changed materially through the years 1935—38. In the samples from the several years the males make up respectively 59,6, 46,3, 39,4 and 50,1 % of the mature stock. As mentioned above it is clear from LEA'S discussion that if the stock is decreasing, then the computed  $\zeta$  will be greater than the actual and smaller if the stock is increasing. The natural changes will assert themselves most distinctly in the case of males, as these die out first.

Curator DONS' marking experiment carried out in the area has been mentioned above. It gave a recapture-percentage of 24 in the course of one year. According to our computations we get an average mortality of about 38,5 %, males and females taken together. Accordingly the computed value is 14,5 % higher than the percentage of recapture. We must indeed expect a higher total mortality than the percentage of recapture in a marking experiment as the natural mortality comes in addition, and some marks probably have been lost.

#### »Maturing Factors«

It remains to compute the »maturing factors«. We may compute these on the basis of the distribution on the various age-groups and spawning-groups of all plaice examined. For example,  $f_{4/3}$  expresses the proportion between those which, according to number of spawning-zones, have attained maturity at an age of 4 years, and those which

have attained maturity at 3, and are 4 years old or older. Likewise  $f_{5/4}$  expresses the proportion between those which have been judged mature at an age of 5 years, and those considered mature at 4, and are 5 years old or more.

Then we find from the material 1935—38.

	$f_{4/3}$	$f_{5/4}$	$f_{6/5}$	$f_{7/6}$	$f_{8/7}$
♂♂	4,94	1,82	0,25	0,04	—
♀♀	20,3	2,66	0,82	0,34	0,04

*Prognosis of the Stock.*

Now, we have the means required to compute from the spawning scheme of one year the age-composition and the eventual relative increase or decrease of the stock in the following year. In our computations we shall use as coefficient of remanence in the case of males and females respectively 0,46 and 0,77.

*Computation of the Age-composition of ♂♂ 1936,  
Based on the Composition 1935.*

Maturing Factors	$f_{4/3}$ 4,94		$f_{5/4}$ 1,82		$f_{6/5}$ 0,25		$f_{7/6}$ 0,04		Observed Distribution 1935	Calculated Distribution 1936		Observed Distribution 1936
	3	4	5	6	7	Total	Total	%	%			
Age at First Spawning	3	4	5	6	7	Total	Total	%	%			
3	55	—	—	—	—	55	—	—	—			
4	25	124	—	—	—	—	149	23,0	24,1			
	—	7	—	—	—	7	—	—	—			
5	—	3	5	—	—	—	8	1,2	4,3			
	22	292	513	—	—	827	—	—	—			
6	10	134	237	59	—	—	440	67,9	63,9			
	—	4	4	—	—	8	—	—	—			
7	—	2	2	—	—	—	4	0,6	0,6			
	—	4	—	—	—	4	—	—	—			
8	—	2	—	—	—	—	2	0,3	1,4			
	—	—	7	7	—	14	—	—	—			
9	—	—	3	3	—	—	6	0,9	0,9			
	—	4	7	—	4	15	—	—	—			
10	—	2	3	—	2	—	7	1,1	0,4			
	—	15	26	15	4	60	—	—	—			
11	—	7	12	7	2	—	28	4,2	2,9			
	—	—	4	—	—	4	—	—	—			
12	—	—	2	—	—	—	2	0,3	0,0			
	—	7	—	—	—	7	—	—	—			
Older	—	3	—	—	—	—	3	0,5	0,0			
Total	—	—	—	—	—	1 001	649	100,0	99,9			

The agreement between the observed and the computed age-distribution is very good. The computation shows that the mature stock of males through the year 1935—36 has been reduced by 35 %.

*Computation of the Age-composition of ♀♀ 1936,  
Based on the Composition 1935.*

Maturing Factors		$f_{4/3}$ 20,3	$f_{5/4}$ 2,66	$f_{6/5}$ 0,82	$f_{7/6}$ 0,34	$f_{8/7}$ 0,04	Observed Distribution 1935	Calculated Distribution 1936		Observed Distribution 1936
Age at First Spawning	3	4	5	6	7	8	Total	Total	%	%
4	—	—	—	—	—	—	—	—	—	8,4
5	—	—	—	—	—	—	—	—	—	0,4
6.	—	60	358	—	—	—	418	—	—	—
	—	46	276	226	—	—	—	548	55,2	58,1
7	—	11	5	5	—	—	21	—	—	—
	—	8	4	4	1	—	—	17	1,7	2,2
8	—	5	16	—	—	—	21	—	—	—
	—	4	12	—	—	—	—	16	1,6	1,8
9	—	11	16	11	5	—	43	—	—	—
	—	8	12	8	4	—	—	32	3,2	3,0
10	—	16	5	5	5	—	31	—	—	—
	—	12	4	4	4	—	—	24	2,4	2,8
11	—	22	71	158	76	5	332	—	—	—
	—	17	55	122	58	4	—	256	25,8	14,5
12	—	5	5	5	—	—	15	—	—	—
	—	4	4	4	—	—	—	12	1,2	2,2
13	—	5	5	43	11	—	64	—	—	—
	—	4	4	34	9	—	—	51	5,1	4,7
Older	—	22	16	11	—	—	49	—	—	—
	—	17	12	9	—	—	—	38	3,8	2,0
Total	—	—	—	—	—	—	994	994	99,8	100,1

The agreement between the computed and observed age-composition for the females in 1936 is very good with the exception of the 11th year-group. The material from this year-group seems not to be representative, either the 10th year-group is over-represented in 1935 or the 11th is under-represented in 1936. We shall soon return to this. We see further that a number of 4 years individuals appear in the material from 1936. At present no means are available to predict the number of these.

According to our computations the mature stock of females should contain almost the same number in the years 1935 and 1936. Actually,



it has probably increased by about 10 % through the recruiting of the 4 years old individuals.

A computation in the same way of the stock of mature plaice in 1937, made from the material collected in 1936, will give as result:

*Agreement between Calculated and Observed (Obs.)  
Age composition 1937.*

	Males				Females			
	Obs. 1936	Calculated 1937		Obs. 1937	Obs. 1936	Calculated 1937		Obs. 1937
	‰	Number	‰	‰	‰	Number	‰	‰
2	—	5	4	4	—	—	—	—
3	241	498	432	432	—	—	—	11
4	43	46	40	40	84	—	—	3
5	639	253	220	267	4	210	217	152
6	20	21	18	18	587	3	3	8
7	14	295	257	214	22	509	523	550
8	9	9	8	4	78	17	18	3
9	4	6	5	4	30	15	15	14
10	29	4	3	0	28	24	25	39
11	—	2	2	0	145	22	23	3
12	—	13	11	8	22	111	115	169
13	—	10	—	4	0	17	18	0
Older	—	—	—	—	67	42	43	48
Total	999	1 162	1 000	995	1 001	970	1 000	1 000

As to the males, a new strong year-class has appeared, of which we have not previously had any observations, and as we have no informations about the age-composition in the immature stock, we accordingly are unable to prognosticate it. In the table has been entered the relative number of individuals corresponding to the number observed in 1937, in the case of 2, 3 and 4 years old individuals. A prediction of the mature males of 1937 would be quite misleading, unless we beforehand, through investigation of the immature stock, got knowledge of the strength of the 1934 year-class.

The 1933 year-class is a weak one, as no individuals were to be found in the material from 1936. We have calculated the percentage of the 1934 year-class from the observed number in 1937, and using this, we find a very good agreement between the computed and observed values in the case of the remaining year-classes. The mature males have, according to the computation increased in number by about 15 % from the spring 1936 until the spring 1937.

As regards the females the agreement between the values computed and observed is fairly good. The error made by leaving the three and four years' females in 1937 out of account, is just over 1 % only, and of no practical importance.

The stock of mature females has been reduced, according to the computation, by about 2 % from the spring 1936 until spring 1937.

There is, according to the computation, a slight increase in the number of males, while the number of females is practically unchanged through the year 1936—37. Now the males make up 46,3 % of the sample in 1936, while in 1937 they make 39,4 %, that is to say a reduction in number of males. But according to the computation we should have expected an increase. The explanation is likely to be found in the circumstance that the author took part in the capture of the breeding stock of fish in 1935 and 1936. These years therefore all captured plaice were taken care of, whereas, in the other years the habit was to throw overboard the smaller individuals, the interest being centred on procuring the best possible breeding stock for the hatchery. In this way also some mature individuals might have been thrown overboard, and these will in most cases be males, as they are usually the smaller. Therefore there is every reason to believe that the material from 1937 is less representative than that of the two preceding years.

*Agreement between Calculated and Observed (Obs.)  
Age-composition 1938.*

	Males				Females			
	Obs. 1937	Calculated 1938		Obs. 1938	Obs. 1937	Calculated 1938		Obs. 1938
	% <sub>00</sub>	Number	% <sub>00</sub>	% <sub>00</sub>	% <sub>00</sub>	Number	% <sub>00</sub>	% <sub>00</sub>
2	4	—	—	—	—	—	—	—
3	432	229	203	203	8	—	—	8
4	40	602	535	639	2	128	134	238
5	267	40	36	16	147	7	7	13
6	18	138	125	73	12	167	175	164
7	214	8	7	10	524	10	10	0
8	4	99	88	41	74	404	423	405
9	4	2	2	0	18	12	13	18
10	—	2	2	2	34	14	15	18
11	—	—	—	—	6	26	27	14
12	—	—	—	—	161	5	5	12
13	—	—	—	—	—	126	132	65
Older	8	4	4	14	71	55	58	42
Total	991	1 124	1 002	998	997	961	999	997

The agreement between the computed and observed values is not as good as before. As to the males the three-group in 1938 is computed from the observed proportion in 1938, the fourth and following age-groups from the material in 1937. We see that the four-group, i. e. the 1934 year-class, is computed to make up 53,5 % of the mature stock in 1938, but according to the observation it makes up 63,9 %. In the case of the females the corresponding figures are 13,4 and 23,8 %. The 1934-year-class is much stronger represented in the material from 1938 than we should expect from the calculations. This may be caused by an under-representation of the 3 years olds in the 1937 material, because the smallest individuals have been thrown overboard. But we may also assume that the better growth, which we have treated in an earlier section is followed by an precocious maturity, and that a greater percentage of the year-class therefore has attained maturity at an age of 4 years than the 1935—38 average implies.

There is also a poor agreement between the numbers computed and observed of the 13 years' individuals. It is the 1925 year-class which does not behave in the way expected. If we for the females of this year-class examine the agreement between the computed and observed values, this, in the respective years, is:

	‰ Computed	‰ Observed
1936.....	25,8	14,5
1937.....	11,3	16,1
1938.....	13,2	6,5

It is obvious that the year-class is not correctly represented in the samples. Probably there are too few of the 1925 year-class in the 1936 material, and too many in 1937.

The computation of the number of mature males show an increase of about 12 % from spring 1937 to spring 1938, and the number of mature females should be slightly reduced in the same period. This is confirmed by the sex composition in the two years, as the number of mature males in 1937 constituted 39,4 % of the sample while in 1938 they constituted 50,1 %.

Upon the whole the computation up till 1938 of the plaice stock in the Sundnes area agrees well with the observations. The diagram of the result, fig. 24, will give a clearer illustration of this than the tables. The hatched columns show the result of the computations, the open columns the observations of the same year.

*Agreement between Calculated and Observed (Obs.)  
Age-composition 1939.*

	Males				Females			
	Obs. 1938	Calculated 1939		Obs. 1939	Obs. 1938	Calculated 1939		Obs. 1939
	‰	Number	‰	‰	‰	Number	‰	‰
2	4	—	—	—	—	—	—	—
3	203	57	40	40	8	—	—	—
4	639	560	389	644	238	128	93	114
5	16	746	518	258	18	652	473	252
6	73	7	5	13	164	19	14	27
7	10	34	24	19	0	135	98	130
8	41	5	3	2	405	0	0	9
9	—	20	14	22	18	313	227	340
10	—	—	—	—	18	14	10	6
11	—	—	—	—	14	14	10	13
12	—	—	—	—	12	11	8	16
13	—	—	—	—	65	9	6	8
14	—	—	—	—	—	51	37	57
Older	16	8	5	2	42	33	24	25
Total	1 002	1 437	998	1 000	1 002	1 379	1 000	997

The agreement between the computed and observed age-distribution is poor, both as to the males and to the females. A closer investigation in order to ascertain what components in our computed and observed spawning schemes cause the disagreement, shows that it is the computation of the number of first time spawners which comes short. The maturing factors  $\frac{1}{5/4}$  used in the computation, are 1,82 and 2,66 for resp. males and females, while the factors computed from the 1939 material for the 1934 year-class are 0,16 and 1,47. Biologically this expresses that most of the males of the 1934 year-class, are mature already when 4 years old, and also that the females of this year-class have attained maturity earlier than older year-classes were observed to do.

It is shown above that the average age of the females at first spawning is lower in the 1930 year-class than in the class 1925, and the 1932 year-class still lower. The 1934 year-class shows a further lowering of the age at the attainment of maturity. (The intervening year-classes are so scarce that the number of specimens available do not allow any conclusions on this point).

Together with this precocious maturity in the later year-classes a more rapid growth is observed. A corresponding course of events has been observed in the skrei (or »Arcto-Norwegian« cod) by GUNNAR ROLLEFSEN (27 and 29). Mr. OSCAR SUND tells me that he is engaged in

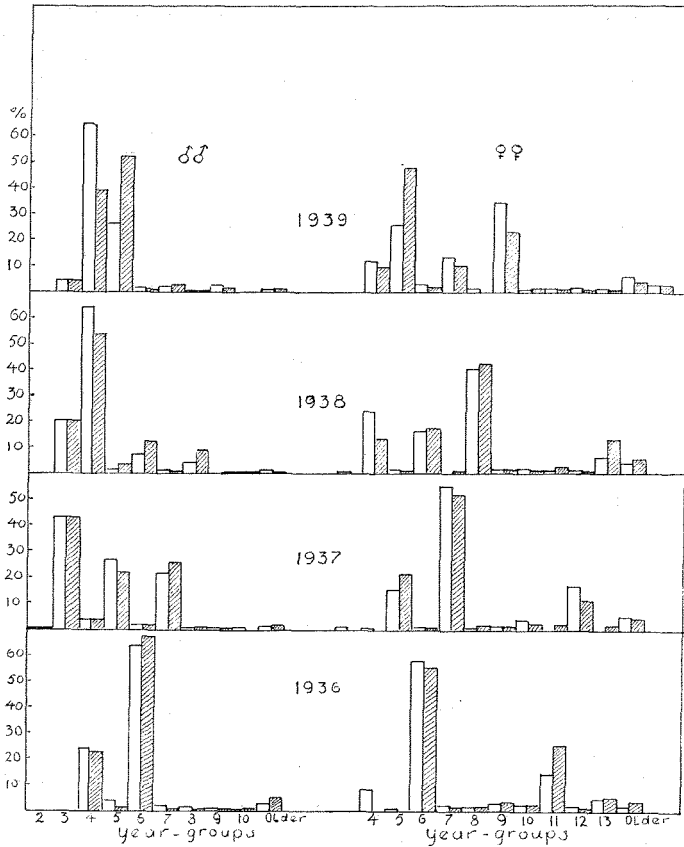


Fig. 24. Agreement between calculated (hatched columns) and observed age distribution of plaice (open columns).

scrutinizing the Norwegian herring material from the same view-point and finds a similar phenomenon as far as his research has advanced, e. g. a difference of about 1 cm between the 1930 catch and the 1938 catch of winter herring for the ages 5—10 years. In the S. North Sea the growth-rate of the plaice has increased after 1931 (BÜCKMANN 7). GILSON (10) treats the herring in the Flemish Bight and the E. part of the Channel. He shows that mature herring appear in these waters at an age of three years at the earliest. At an age of four years they are relatively more numerous. The percentage of 5-year olds is smaller and the decrease continues in the succeeding years. Thus the 1933 year-class appeared for the first time in the 1936-samples with a percentage of 15,5. If now this year-class had behaved in the habitual way, a higher percentage than the figure just mentioned were to be expected of 4-years olds in 1937. As a matter of fact, the year-class in question provided only

12 % of the number examined. GILSON (10) writes on this p. 41: »Besides that it was expected that the class 1933, just appeared with a passable initial percentage of 15,5 % and supposed to be in its augmentative stage, would also supply a passable percentage. In fact, however, this was not the case and the unusual reduction of the class 1933 in its 4th year was a surprise.« GILSON makes no attempt at explaining the phenomenon. A possible explanation is, however, that the 1933-year-class has attained maturity earlier than what is usual for the herring in these waters thus representing quite a parallel case to that made out for the plaice of the Trondheim Fjord. In 1936, most of the herring from 1933, having attained maturity when 3 years old, the remainder, maturing a year later, is insufficient to make up for the mortality.

It thus appears that the higher growth-rate and the precocity caused by it are no particularities of the Trondheim Fjord plaice, but extend in fact over wide areas and apply to the most diverse marine animals. They are found in the Barents Sea skrei which mostly feeds on fish and the larger crustaceans, and in the plaice of the Trondheim Fjord and probably also of the North Sea, living on the bottom fauna, and it appears that similar conditions are also met with in the case of the Norwegian herring tribe and the Channel herring, exclusively plankton feeders.

It may therefore be permissible to seek the cause of this widespread phenomenon in a universal improvement of the physical conditions of the sea, first of all the general rise of temperature in northern waters during later years. The period of this change appears to extend over several years, so that a scrutiny of pertinent temperature curves together with the variations observed in the age at first spawning might make it possible to get a better prediction of the constitution of next years recruit-spawners. If temperature decides early or late maturity, it seems reasonable to consider the last summer and winter temperature in the sea-area as settling the percentage of the several year-classes which are going to spawn the following spring.

ROLLEFSENS method for prediction of the next year's mature stock as to age-composition and eventual relative increase or decrease, has still, its deficiencies, which ROLLEFSEN himself has discussed (27 a, 29), but it is doubtless a step forward in getting an insight into the fluctuations of mature stocks of fish. In the case of the plaice material, we should without doubt have got a better agreement between observed and calculated values, if the samples from the different years had been as representative as possible. May be we shall have to distribute the collection of the samples over the whole of the spawning time, as it

may be possible that f. ex. younger year-classes gather on the spawning grounds at a later date than the older. A great deficiency in the material here produced is that hydrographical observations are too scanty to afford a much-needed corollary.

It is worth trying how far the method can be used for plaice populations further southwards. As to these, maturity comes at an earlier age, thus enabling a greater proportion of the stock to be taken into consideration, but at the same time the efficiency of the method depends upon the circumstance that the maturing of a year-class is distributed over some years. The method is more reliable the more spawning groups there are.

## SUMMARY.

The plaice-fishery has occupied a very humble place among the Norwegian fisheries up to 20 years ago, when it began to develop into an important industry. The reason first of all is to be found in the rapid development of the fresh-fish export in the last two decades, next it is a consequence of the Danish seine being widely introduced also among Norwegian fishermen.

The marking experiments made on plaice in Norwegian waters seem to suggest that the plaice on the coast banks are comparatively mobile, whereas the stock of the fjords are more stationary. The reason is probably to be found in the topographical features of the bottom. Depths of more than 200 m constitute no absolute hindrance on the movements of the plaice, but seem to be very restrictive. SOOT-RYEN'S marking experiment in North-Norway show that the drift of eggs and larvae in pelagic stages is compensated by the tendency of older individuals to move actively in the opposite direction.

The morphological characters suggest that the same race is found along the Norwegian coast from Jæren to Tana, but the stock of the Trondheim Fjord shows an important deviation with regard to number of anal fin rays as well as to number of vertebrae.

The number of anal fin rays seem to be so much influenced by the environment, that it must be doubted whether it is allowable for characterizing plaice populations.

Also in Norwegian waters a segregation is going on within the plaice stock, as the quickest-growing individuals within a year-class seek deeper water at an earlier age than the more slow-growing.

The plaice stock of the Trondheim Fjord has a very high growth-rate, which has increased very much during the years 1935—38.

The winter rings of the interoperculum, which show distinctly the close of each year of life may probably be used for computing the total length of plaice in its different years of life.

The otoliths as well as the interoperculum seem to reveal the age of a plaice at the onset of maturity. On the basis of such, we may,



in the same way as GUNNAR ROLLEFSEN has done for the skrei, divide the mature portion of the plaice stock into spawning-classes and spawning-groups. From these may be computed the mortality, using LEA'S formula. In the case of male plaice in the Sundnes area in the Trondheim Fjord it was found to be 54 %, the females 23 %.

The age-composition and the relative increase or decrease of the mature stock have been computed one year in advance from the number of spawning-zones, and the age-compositions thus computed show a good agreement with the observed compositions. As regard this, the year 1939 makes, however an exception. It is the first time spawners which do not enter the mature stock in analogy with the older year-classes.

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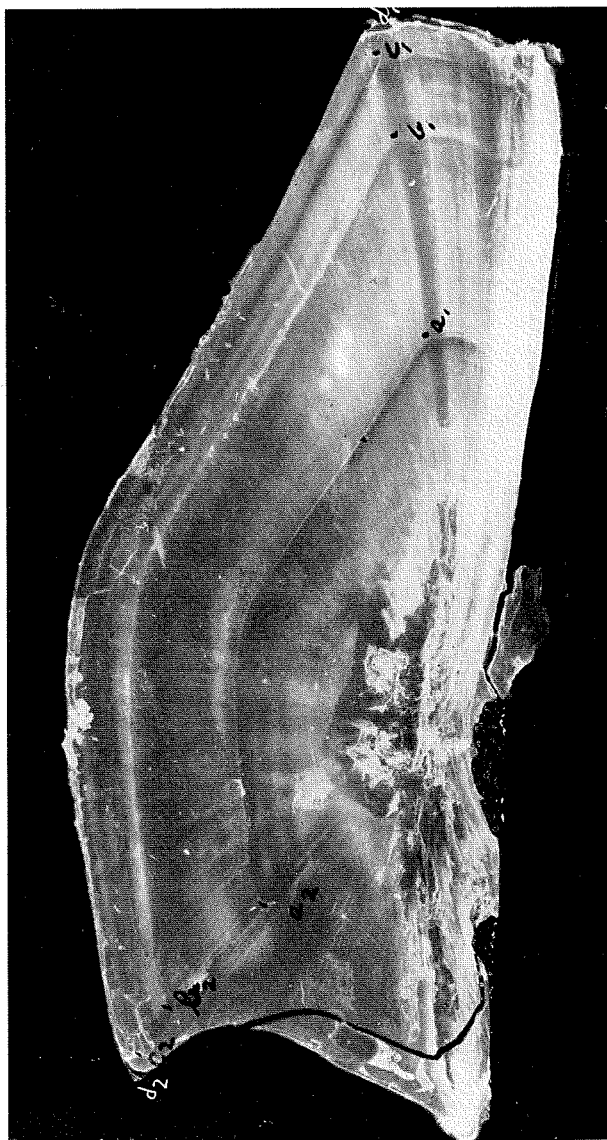


Fig. 16.

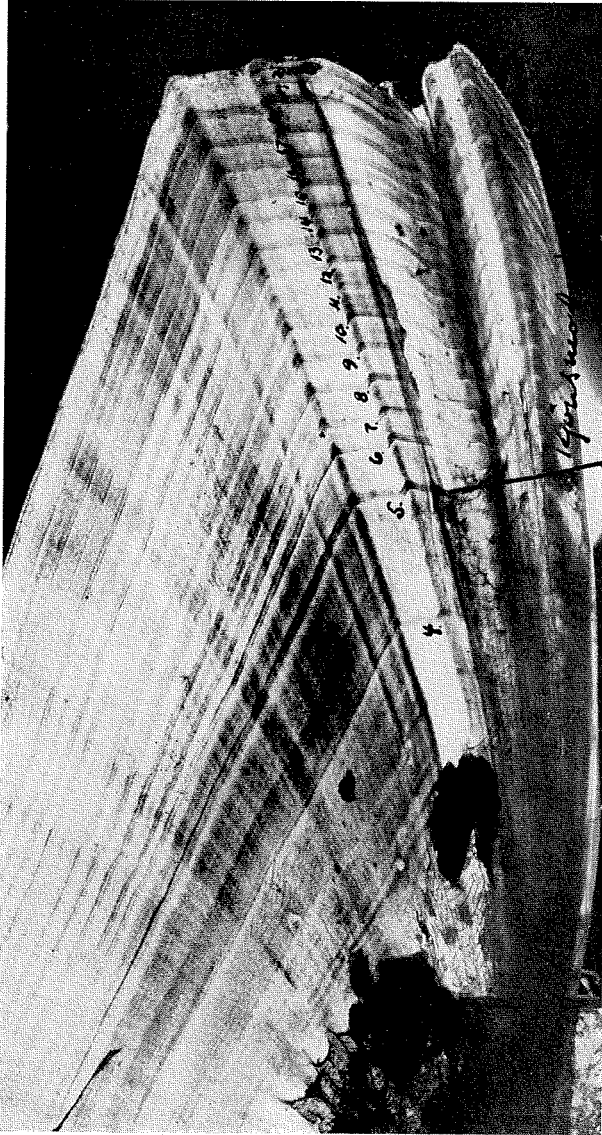


Fig. 19.

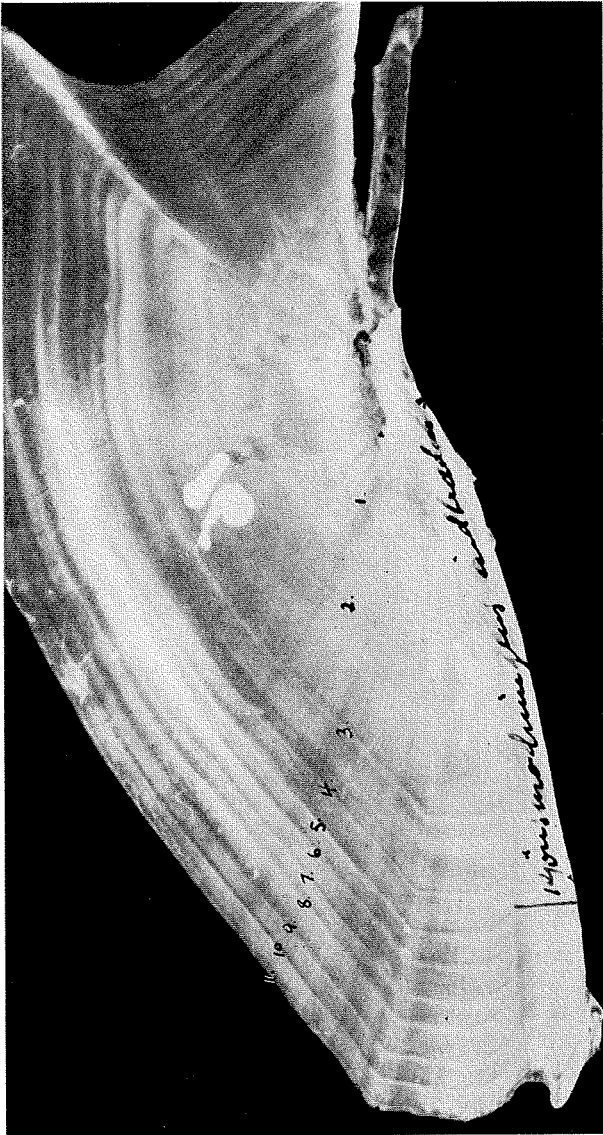


Fig. 20.

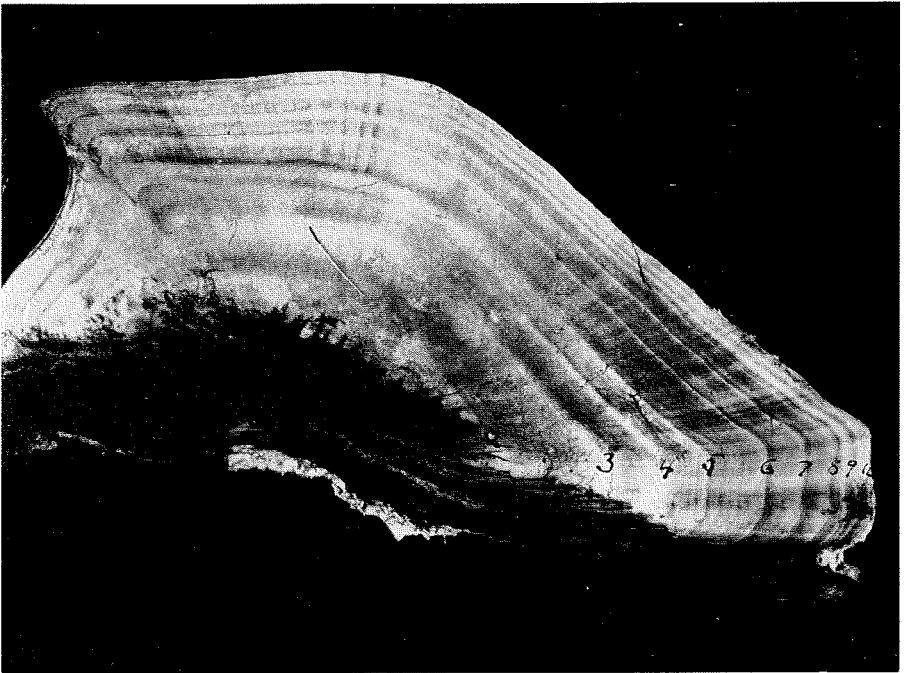


Fig. 21.

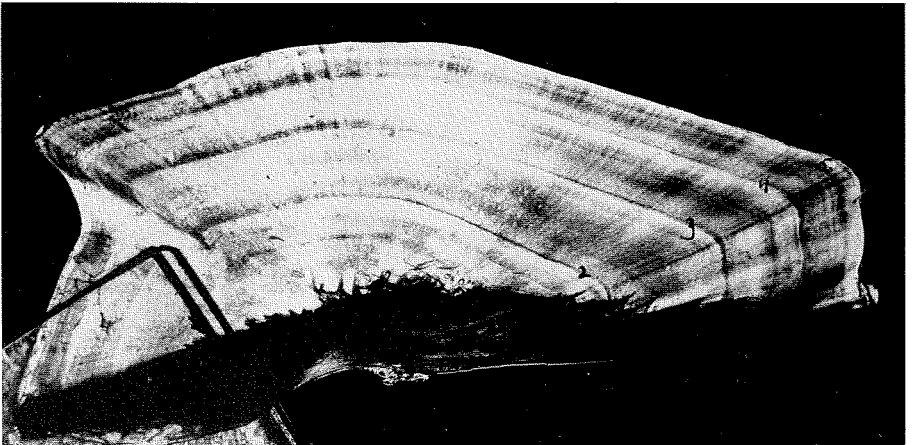


Fig. 22.