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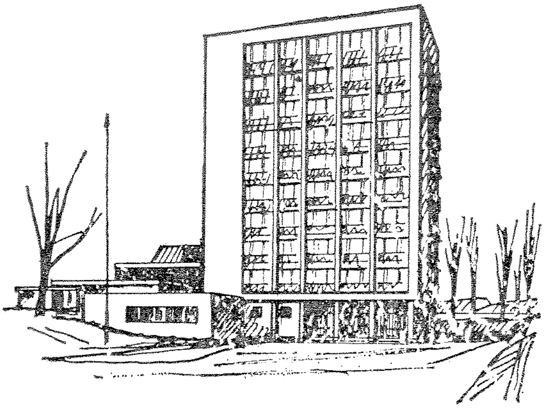

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HYDROGRAPHIC INVESTIGATIONS IN THE IRMINGER SEA IN THE YEARS 1954–1964.

By

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INTRODUCTION

The first recorded oceanographic work in the Irminger Sea was carried out in 1853 under the charge of the Danish admiral C. IRMINGER. G. DIETRICH (1957) has given a summary of all investigations made in the area since that time. From this it is evident that the main hydrographic structure of the Irminger Sea was known before the turn of the century. Later, research has concentrated on different details, but most papers dealing with the area have been based on data from only one cruise.

During the years 1959–1964 research vessels from the Institute of Marine Research, Directorate of Fisheries, Bergen, have carried out 5 cruises in the Irminger Sea. All of these took place at the same time of the year. The data collected may therefore be used for studies of annual variations.

Also, at Ocean Weather Station Alpha, in latitude 62° N, longitude 33° W, hydrographic observations have been made during 5 periods. (For convenience, Ocean Weather Station Alpha will hereafter be mentioned as Station A.) The major part of these periods also cover the same season, and altogether the data from Station A and the above mentioned cruises embrace the period from 1954 to 1964. Therefore it has been found worthwhile to examine them with regard to annual variations in the area.

MATERIAL AND METHODS

On the mentioned cruises the following numbers of hydrographic stations were worked: 27 in 1959, 23 in 1961, 46 in 1962, 58 i 1963 and 58 in 1964. In 1959 some of the observations were made in the first half of July, the remainder of the programme being carried out in the middle of August. In the years 1961–1964 all sections were worked between 15th. August and 10th. September. Fig. 1 shows the station grid in 1963 and 1964. The station grids for the other years, however, differed to some extent. The section across the Denmark Strait was worked only in 1963 and 1964. In 1959 and 1961 no section was worked off Cape

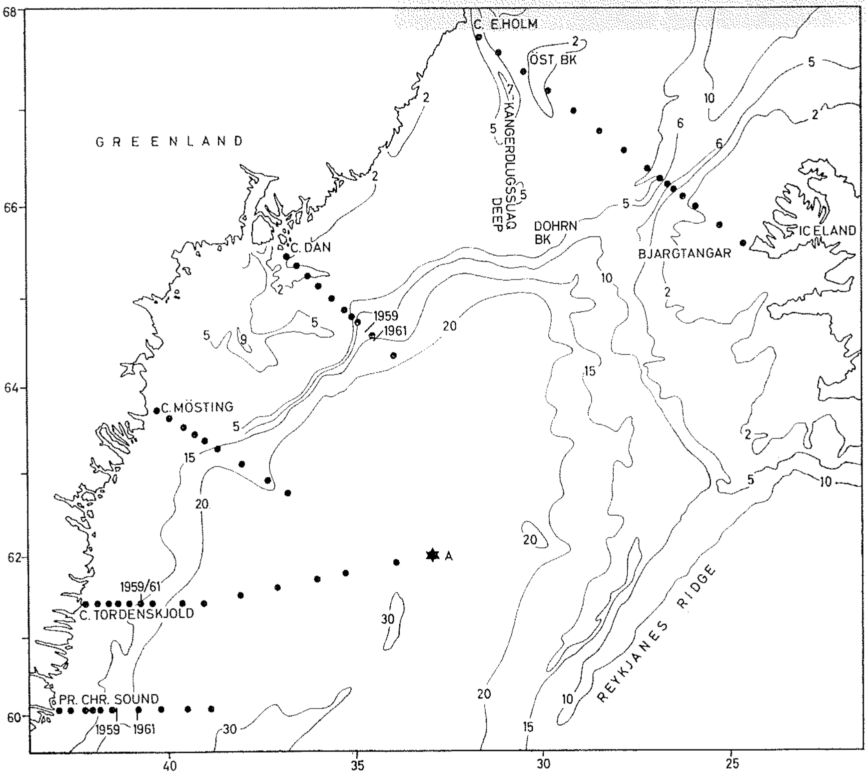

Fig. 1. Station grid for 1963 and 1964. Positions of outer stations of the sections for 1959 and 1961 are indicated. Main bathymetric features after fishery chart published by Deutsches Hydrographisches Institut, 1958. Depths in hectometres.

Møsting, and in these years the sections off Cape Dan, Cape Tordenskjold and Prince Christians Sound were shorter than in the other years. In Fig. 1 their extent is indicated by symbols in the positions of the outer stations of the sections.

On all cruises the observations were made by the usual method, Nansen reversing water bottles being used. Each water sampler was equipped with two protected reversing thermometers. No unprotected thermometers were used, but when the observations were made, the ship was always manoeuvered so that the wire was close to the vertical. At the hydrographic stations samples were usually taken at all standard depths to the bottom.

The observational work at Station A was arranged by the Institute of Geophysics, University of Bergen. The data were collected in the course of the 5 following periods when O. W. S. «Polarfront I» and O. W. S. «Polarfront II» served at the Station:

1. From 2nd July to 29 th December 1954.
2. From 3rd July 1956 to 2nd January 1957.
3. From 20th June to 16th December 1958.
4. From 21st June to 28th December 1960.
5. From 1st November 1962 to 13th April 1963.

On an average the weather ships carried out serial observations 18 times per month during these 5 periods, and altogether a total of 549 hydrographic stations were worked. At 100 of these stations samples were taken at the standard depths to 2 000 m, 346 stations were sampled at the depths 0, 50, 150, 300, 600 and 1 000 m, and at the remaining 103 stations the standard depths to 150 m were sampled.

The data from the above cruises will be available through ICES, and the data from Station A will be published by the Institute of Geophysics, University of Bergen.

THE WATER MASSES

Several different water masses enter the Irminger Sea. The more important of these are (1) Atlantic water which derives its properties in much lower latitudes, and (2) Polar water, most of which originates in polar regions.

Atlantic water is characterized by high temperature and high salinity, but in the Irminger Sea all water types with salinity above 35.00 $^0/_{00}$ are recognized as Atlantic water regardless of temperature. When entering the Irminger Sea in the region of the Reykjanes Ridge, Atlantic water exhibits salinities above 35.20 $^0/_{00}$. At Station A which is situated near the westward border of the eastern bulk of Atlantic water in the Irminger Sea, the highest salinities are about 35,18 $^0/_{00}$ with temperatures between 7° and 8° C. Off Prince Christians Sound maximum salinities usually lie between 35.05 $^0/_{00}$ and 35.10 $^0/_{00}$ and temperatures between 6° and 7° C.

Polar water is characterized by low temperature and low salinity. In the Denmark Strait values of about — 1,7° C and 33,5 $^0/_{00}$ are usually observed in its core. Further south the Polar watermass is, however, constantly eroded by mixing, and in summer the surface layer is heated by solar radiation. At this time of the year it is therefore difficult to give exact definition of Polar water in the Irminger Sea. It seems, however, practical to take 34.50 $^0/_{00}$ as the upper limit of its salinity.

Artic Bottom water is observed in the two sections across the Denmark Strait. In the deepest part of the channel through the Iceland — Greenland Ridge this shows temperatures below 0° C and salinities around 34.92 $^0/_{00}$, which are in good agreement with the accepted definition of the Artic Bottom water (Helland-Hansen and Nansen 1909).

Artic Intermediate water comes originally from a branch of the West Spitsbergen Current. According to Stefansson (1962 a) its temperature ranges from 0.0° to 2.0° C and its salinity from 34.8 $^0/_{00}$ to 35.0 $^0/_{00}$ in the area north of the Denmark Strait. In the Denmark Strait, however, this water has a greater admixture of Polar water, so that its temperatures are near or below 1° C and its salinities chiefly below 34.90 $^0/_{00}$. This is demonstrated by the T—S relation in Fig. 2. Artic Intermediate water, as defined by Stefansson, is represented by a rectangle in the Figure.

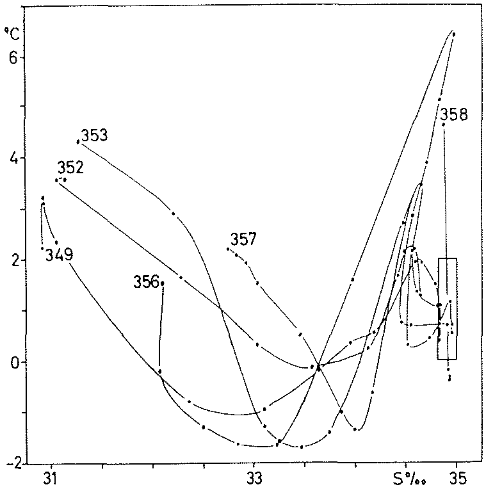

Fig. 2. T—S diagram for some stations from the section across the Denmark Strait in 1964. Arctic Intermediate Water is marked by a rectangle.

The intermediate water in the Irminger Sea forms a layer of minimum salinity at depths around 1 000 m in the central parts of the region. This water mass is characterized by a temperature of 3.5° C and a salinity of about 34.88 $^0/_{00}$ as shown by the T–S relation of observations from Station A in Fig. 3. The point of intersection of the two lines embracing the cloud of points in the Figure, indicates the characteristics of the intermediate water in 1954. Corresponding T–S diagrams for the other observational periods all give salinities slightly above 34.88 $^0/_{00}$ and temperatures between 3.45 and 3.55°C. This is in agreement with the definition given by Sverdrup, Johnson and Fleming (1946). Smith, Soule and Mosby (1937), however, have studied the intermediate water in the Labrador Sea, where it is formed, and conclude that temperatures near 3.2°C and a salinity of 34.88 $^0/_{00}$ are typical characteristics.

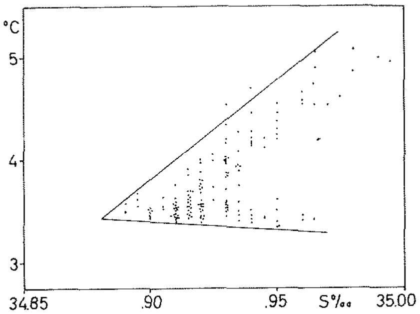

Fig. 3. T—S diagram demonstrating the characteristics of intermediate water at Station A. Observations between 400 and 2000 m depth from 1954 are plotted.

The deep water in the Irminger Sea is found at depths between approximately 1 500 and 2 500 m. It differs from the intermediate water by its higher salinity. The most saline deep water occurs at about 2 000 m depth where the salinity is significantly in excess of 34.90 $^0/_{00}$. At Station A extremely high salinities reach 34.97 $^0/_{00}$ to 34.98 $^0/_{00}$ at this depth, and the mean temperature and salinity for the 5 periods are 3.43°C and 34.943 $^0/_{00}$ respectively.

Cooper (1955), also Lee and Ellet (1965), have shown that this water mass comes from the north-eastern basin of the North Atlantic.

The bottom water of the Irminger Sea has its main source in the Arctic Intermediate water, but Arctic Bottom water is also of importance. Both these water masses overflow the Iceland–Greenland Ridge and sink to the bottom in the Irminger Sea, but Arctic Bottom water only intermittently. At the foot of the continental slope the salinities of the bottom water in the Irminger Sea are often below 34.90 $^0/_{00}$ and the associated temperatures lie between 1 and 2°C.

THE HYDROGRAPHIC SECTIONS

Between Prince Christians Sound and Cape Dan the hydrographic sections have several features in common. Polar water is always found over the shelf, while the core of the Atlantic water of the western branch of the Irminger Current is found off the edge of the shelf where it occupies the zone over the continental slope. The 34.5 $^0/_{00}$ isohaline seems to be the dividing line between Polar water and Atlantic water in this area. At the sea surface this isoline is in most cases found over the edge of the shelf.

In 1959 and 1961 the sections had only one or two stations outside the shelf, and gave little information about the Atlantic water in the western branch of the Irminger Current. In the later years, however, the sections extended farther out to sea, and off Cape Tordenskjold and Prince Christians Sound they cut through the core of Atlantic water in the western branch of the Irminger Current.

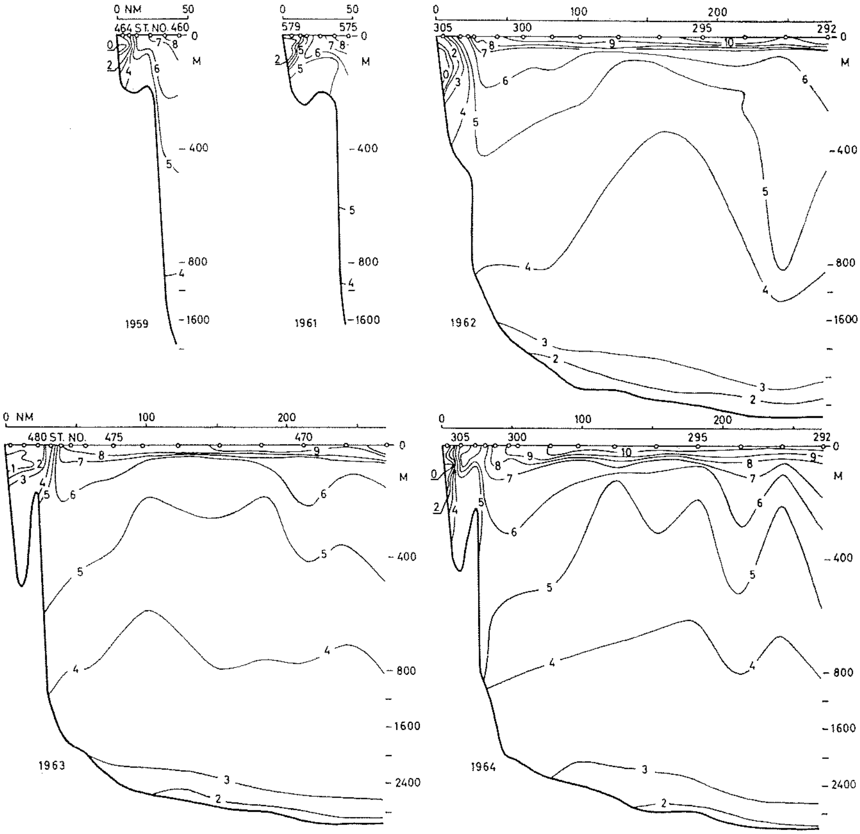

Fig. 4. Temperatures off Cape Tordenskjold in the years 1959 and 1961—1964.

The sections off Cape Tordenskjold are illustrated in Fig. 4 and 5. The lowest salinities close to the coast vary between 28.07 $^0/_{00}$ and 31.55 $^0/_{00}$ with associated temperatures between 1.65° and 3.50°C. As shown in Table 1, the lowest temperature of the Polar water is found at depths between 50 and 125 m, varying between – 0.39° and 1.58° C with salinities from 32.98$^0/_{00}$ to 33.66 $^0/_{00}$. In the different sections the width of the Polar water in the East Greenland Current is from 20 to 40 nautical miles, the 34.5 $^0/_{00}$ isohaline at the surface being found between these distances from the shore. With depth this isohaline is usually inclined to the vertical and meets the bottom on the inner part of the shelf.

Table 1. Characteristic values in the sections: minimum temperature in the Polar Water, observation depth in brackets, with associated salinity. Maximum salinity in the Atlantic water, observation depth in brackets, with associated temperature. Greatest vertical extent of the Atlantic water in the sections.

		Polar Water		Atlantic Water		
Section	Year	Min. temp. t°C	Associated sal. ‰	Max. sal. ‰	Associated temp. t°C	Vertical extent. m
Prince Chr. Sound	1959	+0.19 (30)	32.40	35.09 (150)	6.35	0 - 700
	1961	+1.22 (75)	32.36	35.11 (50)	6.46	0 - 700
	1962	-0.76 (75)	33.35	35.07 (100)	6.46	40 - 600
	1963	-0.59 (125)	33.37	35.07 (125)	6.29	60 - 300
	1964	+0.89 (75)	33.87	35.07 (150)	7.12	40 - 340
Cape Tordenskjold	1959	-0.25 (50)	33.00	35.09 (250)	5.77	0 - 630
	1961	+1.58 (75)	33.08	35.10 (125)	6.46	0 - 250
	1962	-0.39 (125)	33.34	35.06 (100)	6.51	50 - 400
	1963	+0.08 (75)	33.66	35.06 (150)	6.50	70 - 300
	1964	-0.08 (75)	32.98	35.06 (125)	6.87	0 - 400
Cape Møsting	1962	+1.34 (75)	34.07	35.08 (125)	6.47	50 - 800
	1963	+1.54 (50)	33.82	35.06 (100)	6.61	75 - 375
	1964	+0.29 (75)	33.78	35.10 (125)	7.28	60 - 500
Cape Dan	1959	-1.15 (20)	32.27	35.13 (75)	7.80	0 - 600
	1961	-0.50 (0)	28.95	35.19 (150)	7.47	0 - 650
	1962	-1.49 (50)	33.52	35.10 (150)	6.77	0 - 1000
	1963	-0.85 (30)	33.75	35.11 (200)	6.95	30 - 650
	1964	-1.52 (75)	33.43	35.15 (100)	7.76	0 - 600

The highest salinities in the Atlantic water have values from 35.06 ‰ to 35.10 ‰, and they are found at depths between 100 and 125 m. The corresponding temperatures vary between 5.8°C and 6.9°C. Table 2 shows that the mean salinity of the Atlantic water varies between 35.020 ‰ and 35.050 ‰. The highest salinity was observed in 1961, while 1962 and 1963 had the lowest values both in actual observations and in mean values. Fig. 5 shows that there was Atlantic water at the surface in the years 1959, 1961 and 1964. In the two remaining years Atlantic water was observed only at subsurface depths, its upper limit being at 50 to 100 m. The 1959 section was very short and did not reach far into the Atlantic water, but in spite of this it shows a vertical extent of the Atlantic water exceeding 600 m, the greatest extent found in any of the 5 years.

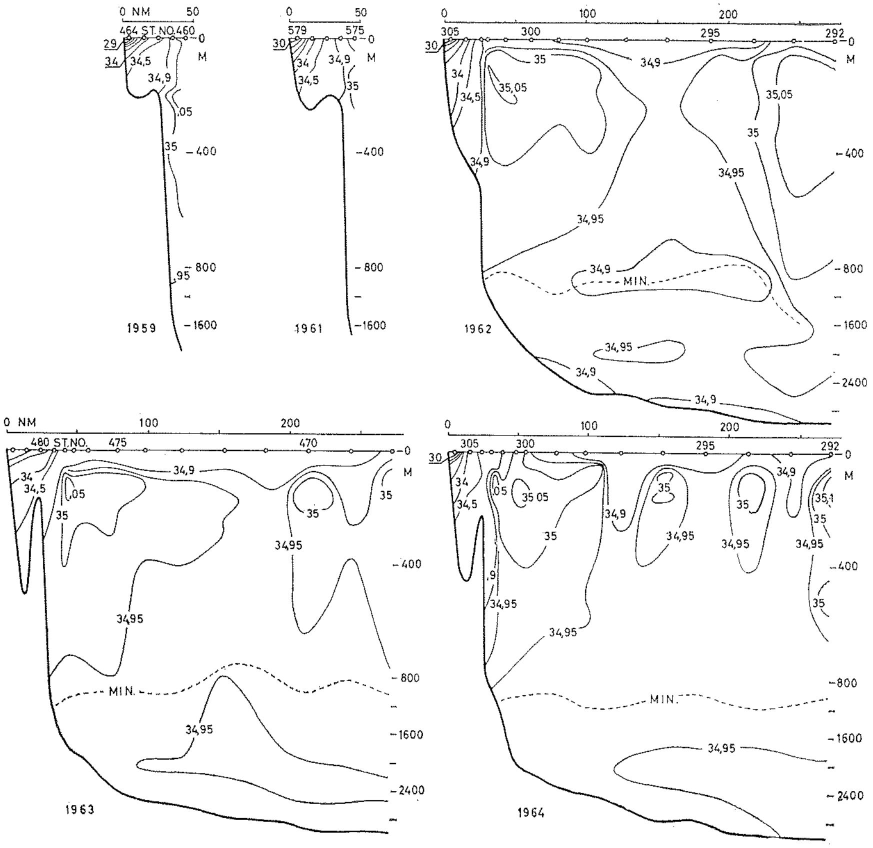

Fig. 5. Salinities off Cape Tordenskjold in the years 1959 and 1961—1964.

In the years when the sections were extended to Station A, they show that the eastward limit of the Atlantic water of the western branch of the Irminger Current is found between 100 and 115 nautical miles off Cape Tordenskjold. Farther to the east there are less saline waters

Table 2. Mean salinity of the Atlantic Water in different years and sections.

Year	Prince Chr. Sound	Cape Tordenskjold	Cape Dan
1959	35.032	35.050	35.117
1961	35.047	—	35.089
1962	35.033	35.020	35.044
1963	35.022	35.020	35.049
1964	35.032	35.032	35.051

where the salinity may decrease to values below 34.95 $^{0}/_{00}$, and even below 34.80 $^{0}/_{00}$ in the surface layer. In the eastern part of the sections Atlantic water is again observed, its extent varying much in the three sections. In 1962 when its extent was greatest, the Atlantic water was found about 60 nautical miles westwards from Station A. Vertically, its greatest extent was from 25 to 800 m depth. Salinities up to 35.07 $^{0}/_{00}$ were observed with temperatures around 6° C. In 1963 there was very little Atlantic water in the eastern part of the section, and it was observed only at two stations between 75 and 200 m depth, its salinities not exceeding 35.02 $^{0}/_{00}$. In 1964 several cores of Atlantic water were observed, and at Station A it was observed down to 500 m. At 100 m the salinity was 35.13 $^{0}/_{00}$.

In the sections from 1962, 1963 and 1964 the depth of minimum salinity in the intermediate water is marked out by a dashed line as shown in Fig. 5. On an average it was found at a depth of approximately 1 000 m. The salinity of the intermediate water showed only small variability, but in 1962 it was a little lower than in the two following years.

The deep water in the sections between Cape Tordenskjold and Station A is indicated by salinities in excess of 34.95 $^{0}/_{00}$. The sections show that its extent varies both horizontally and vertically. In 1963 and 1964 there seemed to be greater quantities than in 1962.

The lower limit of the deep water is indicated by an increase in the vertical temperature gradient. The reason for this is mixing with the colder bottom water which, from 2 500 m downwards becomes more and more dominant. As shown by Fig. 4 temperatures near the bottom were below 2°C. The influence of the bottom water was especially pronounced in the 1962 section where it exhibited salinities below 34.90 $^{0}/_{00}$ at several stations. In the other sections its salinity was about 34.90 $^{0}/_{00}$.

The sections off Prince Christians Sound and Cape Møsting show conditions which are very much the same as those in the western part of the sections off Cape Tordenskjold. A more detailed description of the distribution of temperature and salinity will therefore be omitted. The extreme values of temperature and salinity etc. in these sections are, however, given in Table 1.

The sections off Cape Dan are illustrated in Fig. 6 and 7, and minimum temperatures of the Polar water and maximum salinities of the Atlantic water are given in Table 1. From these it is seen that the lowest temperatures in the Polar water are found in the shelf area at depths between 0 and 75 m. These minimum temperatures vary between — 0.50 and — 1.25° C, and associated salinities lie between 28.95 $^{0}/_{00}$ and 33.75 $^{0}/_{00}$. Fig. 7 shows that the Polar water extends farther out to sea in this area than in the sections farther south, and there is often more

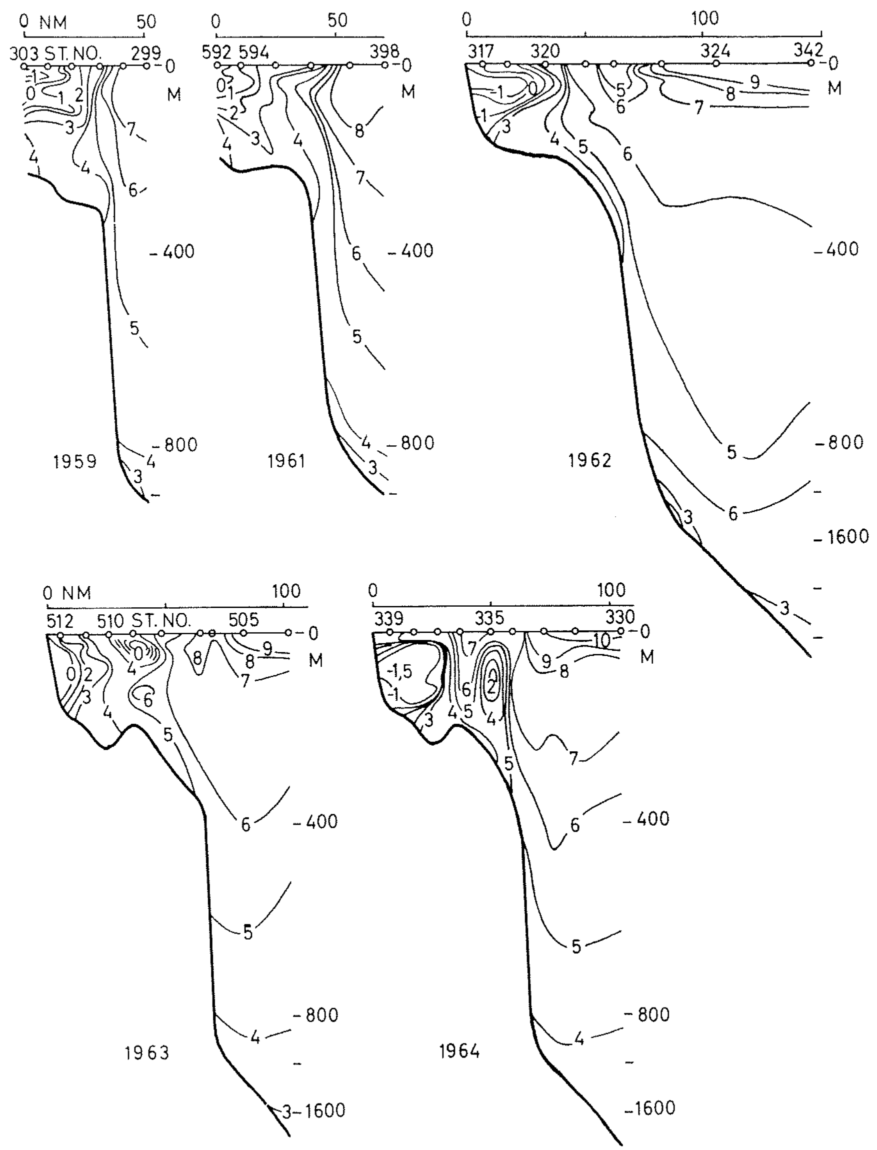

Fig. 6. Temperatures off Cape Dan in the years 1959 and 1961—1964.

than one core of cold water. In these sections the 34.5 $^0/_{00}$ isohaline meets the surface between 60 and 75 nautical miles off Cape Dan.

Compared with the sections farther south the Atlantic water has a great horizontal extent off Cape Dan, and in all the years except 1963, it reached to the surface. Because of the varying length of the sections in the different years, it is not possible to say in which year the Atlantic

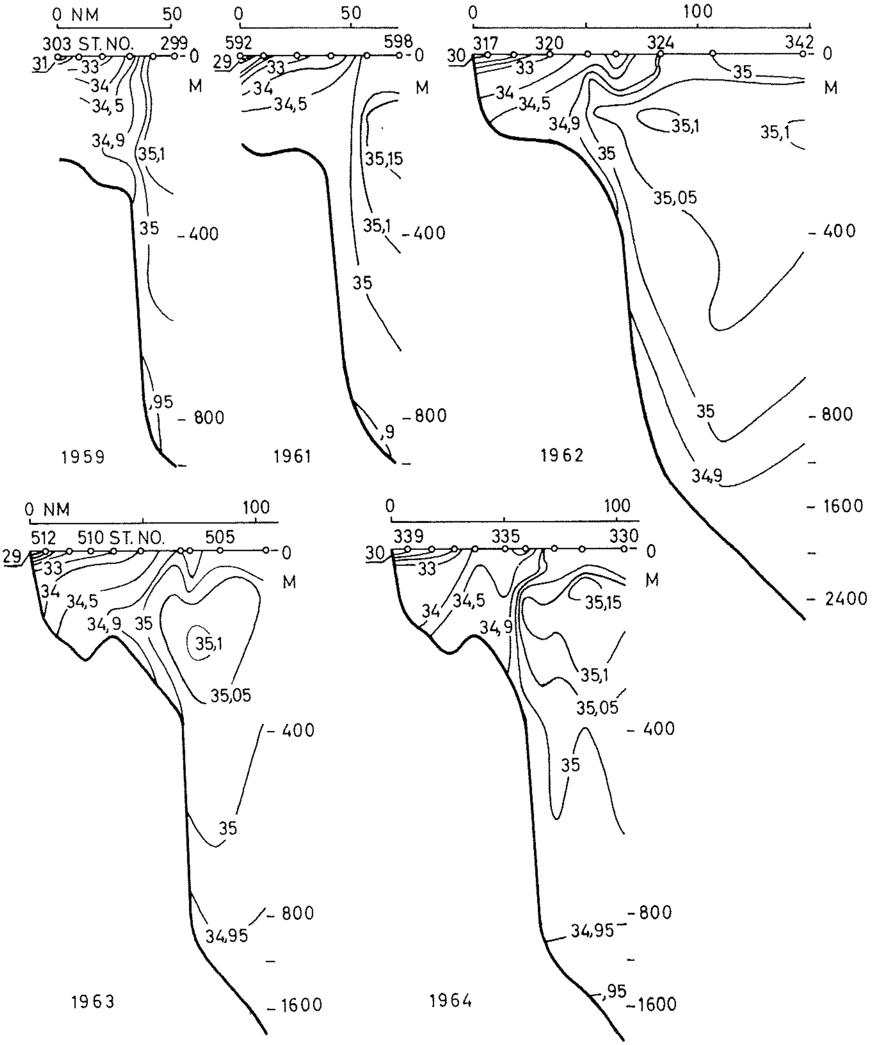

Fig. 7. Salinities off Cape Dan in the years 1959 and 1961—1964.

water had the greatest extent, but it is evident that it was smallest in 1963. As shown in Table 1, the maximum salinities of the Atlantic water vary between 35.10 $^0/_{00}$ and 35.19 $^0/_{00}$. The highest values were observed in 1961, and as shown in Table 2, the mean salinity of the Atlantic water was also high in this year.

The sections across the Denmark Strait between Cape E. Holm and Bjargtangar are illustrated in Fig. 8 which shows the section from 1964. This Figure also gives a good illustration of the conditions in 1963, which were only little different from those in 1964. In both years there were

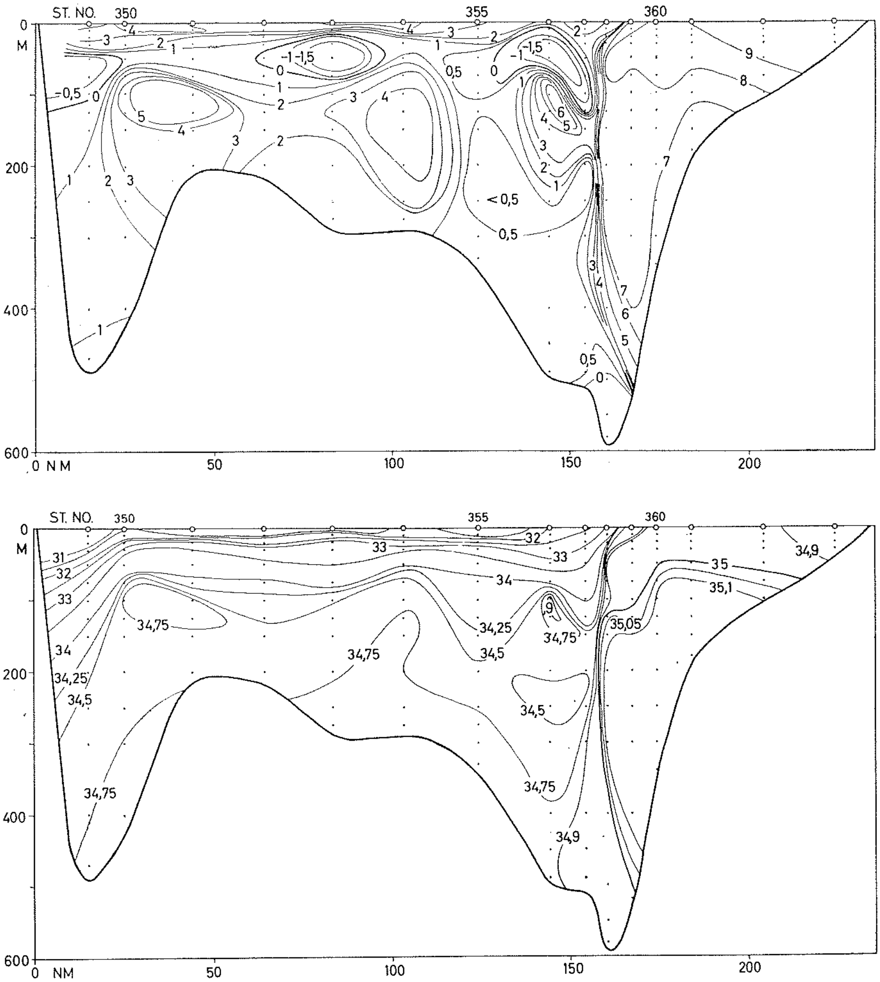

Fig. 8. Temperatures and salinities across the Denmark Strait 9.–10. September 1964.

observed three different cores of Polar water of temperature below 0° C. The most western of these was found close to the coast of Greenland. In 1963 it extended about 30 nautical miles eastwards from the coast with a minimum temperature of — 1.48° C at 75 m depth. Its vertical extent was greatest close to the coast where the temperatures were below 0° C between 30 and 150 m depth. In 1964 the corresponding core was somewhat smaller, and no temperatures below — 0.94° C were observed. In both years a second core of Polar water was observed between approximately 60 and 110 nautical miles off the Greenland coast. Temperatures near — 1.7° C were here observed at 50 m depth in both years. A third core lay over the western slope of the channel through the Iceland

–Greenland Ridge where subzero temperatures were observed down to 100 m. In 1964 the surface layer was heated to temperatures between 1° and 3° C, but in 1963 the surface temperatures were below 0° C in this area. Also here the coldest water of temperatures around — 1.7 ° C was observed at 50 m depth.

The salinity of the Polar water varied much from west to east. In the western part of the 1964 section the salinity was below 31 $^0/_{00}$, but the extreme Polar water in the middle of the Strait was of salinity about 33.5 $^0/_{00}$ in both years. West of the channel through the Iceland–Greenland Ridge the 34.5 $^0/_{00}$ isohaline was on the average found at 100 m depth. It had, however, a very wavy shape and reached a depth of approximately 200 m underneath the cores of Polar water. In the area over the sill in the channel it met the sea surface about 170 nautical miles off the coast of Greenland. In this area the Polar water and the Atlantic water lie very close to each other, and the horizontal gradients are very great. Fig. 9 shows a sea surface thermogram from 9th September 1963 which demonstrates how narrow the front between the two water masses can be in this area. As shown by the Figure, the temperature decreased from 7.9° to 2.2° C in the course of 10 minutes. According to the speed of the ship, this corresponds to a distance of hardly 2 nautical miles. The whole front had a width of approximately 18 nautical miles, and the change in temperature amounted to 8,5° C. Fig. 8 shows that this front at the westward limit of the Atlantic water goes relatively steeply toward the bottom, and the horizontal gradients seem to be great also at subsurface depths. East of the front, Atlantic water occupies the region of the eastern slope in the channel through the Iceland–Greenland Ridge and most of the Icelandic shelf area. The extremity of the Atlantic water is found just above the edge of the shelf, its temperature and salinity being 6° to 7° C and 35.13 $^0/_{00}$ to 35.14 $^0/_{00}$ respectively.

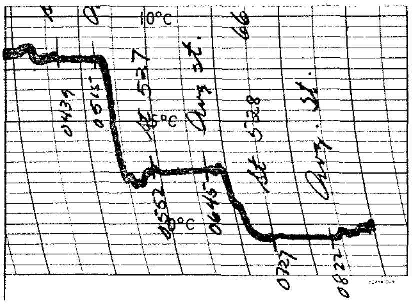

Fig. 9. Sea surface thermogram from the Denmark Strait. The sharp front between the waters of the Irminger Current and the East Greenland Current is shown.

Arctic Bottom water was in both years observed in the deepest part of the section, near the sill in the channel.

Arctic Intermediate water intruded between the Arctic Bottom water and the Polar water, and occupied the deeper water strata in the western slope area of the channel through the Icelang–Greenland Ridge.

The western part of the section crosses the Kangerdlugssuaq Deep, and in both years there was relatively warm water over the eastern slope of this deep. The salinity, which here exceeds 34.75 $^0/_{00}$, indicates an Atlantic origin of the water. HELLAND-HANSEN (1936) was of the opinion that this is a branch of the western branch of the Irminger Current, flowing northwards along the eastern slope of the Kangerdlugssuaq Deep. He also suggested that this water makes an anticyclonic circulation around the Øst Bank. This is in agreement with the sections from 1963 and 1964, because a core of warm water is also found east of the Øst Bank in these sections.

Annual variations in the sections are not easy to find as far as the Polar water is concerned. The most important reason for this seems to be that there occurs more occasional local variations within the East Greenland Current where the rough bottom topography contributes to a very turbulent flow. A consequence of this is an irregular mixing with waters from the Irminger Current in such a way that eddies bring water of Atlantic origin into the Polar water. Such a process of mixing probably takes place all the way between the Denmark Strait and Cape Farewell, but the ratio of mixing may have relatively great local variations along the current. Such local variations can then easily make confusion in possible phenomena of a scale great enough to have influence on the whole East Greenland Current and create annual variations.

Concerning the Atlantic water, on the other hand, the description of the sections brings into view annual variation in the western branch of the Irminger Current. In 1959 and 1961 the sections were rather short, and they did not reach far into the Atlantic water, but in spite of this, higher salinities were observed in these sections than i all later years. It is also obvious that the Atlantic water had a great vertical extent relative to the sections from 1962 and later. On the whole it looks as if there was much Atlantic water with relatively high salinity in the western branch of the Irminger Current in the years from 1959 to 1961. Later, the amount decreased so that only small quantities were observed in the sections from 1963. It may be useful to examine more closely these variations in the amount of Atlantic water in the Irminger Current. For this purpose the observations from Station A appear to fit well. In Fig. 10a, some of these observations are plotted in a T—S diagram, and in Fig. 10 b, observations are plotted from stations worked outside the shelf

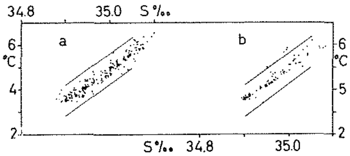

Fig. 10. T–S relation for observations off the shelf between 200 and 1200 m: a) Station A, November 1962. b) Western part of the Irminger Sea, August 1962.

area in the western part of the Irminger Sea. The Figure shows more or less the same water types at Station A as in the area of the western branch of the Irminger Current. It is therefore likely that variations in the amount of Atlantic water occuring at Station A, will also be of importance in the western part of the Irminger Sea.

VARIATIONS OF OCEANOGRAPHIC CONDITIONS AT OCEAN WEATHER STATION ALPHA

Station A lies in a border zone between two different water masses. The area between the Station and Iceland is dominated by the Atlantic waters of the Irminger Current, while the waters to the west of Station A have a more or less subarctic character. It is possible that variations in the salinity at Station A can be a consequence of the extention of the Atlantic water. If the Irminger Current carries much Atlantic water and this is extended far to the west, it might give rise to high salinity at Station A. A simple enumeration of the hydrographic stations at Station A with salinity above 35.00 $^0/_{00}$ at one or more standard depths shows great differences between some of the periods. In 1954 and 1956 Atlantic water was observed at less than 20 % of the total number of stations. In 1958 and 1960, however, salinities above 35.00 $^0/_{00}$ were observed at nearly all stations. This is suggestive of more Atlantic water in the Irminger Sea in 1958 and 1960 than in 1954 and 1956.

In order to get a better insight into the variability of temperature and salinity, isopleth diagrams have been prepared for the periods when the two weather ships served at Station A. The isopleth diagrams are based on monthly means at the standard depths. The means are produced by plotting the single observations at each particular standard depth against time, and the time axis is abscissa in the diagram. Such diagrams for 1958 are shown in Fig. 11, and the variability of temperature and salinity at the depths 0, 50, 150, 300, 600 and 1 000 m is demonstrated. For each month the means are taken from the diagrams by graphical interpolation. Such means are made for all standard depths to 2 000 m

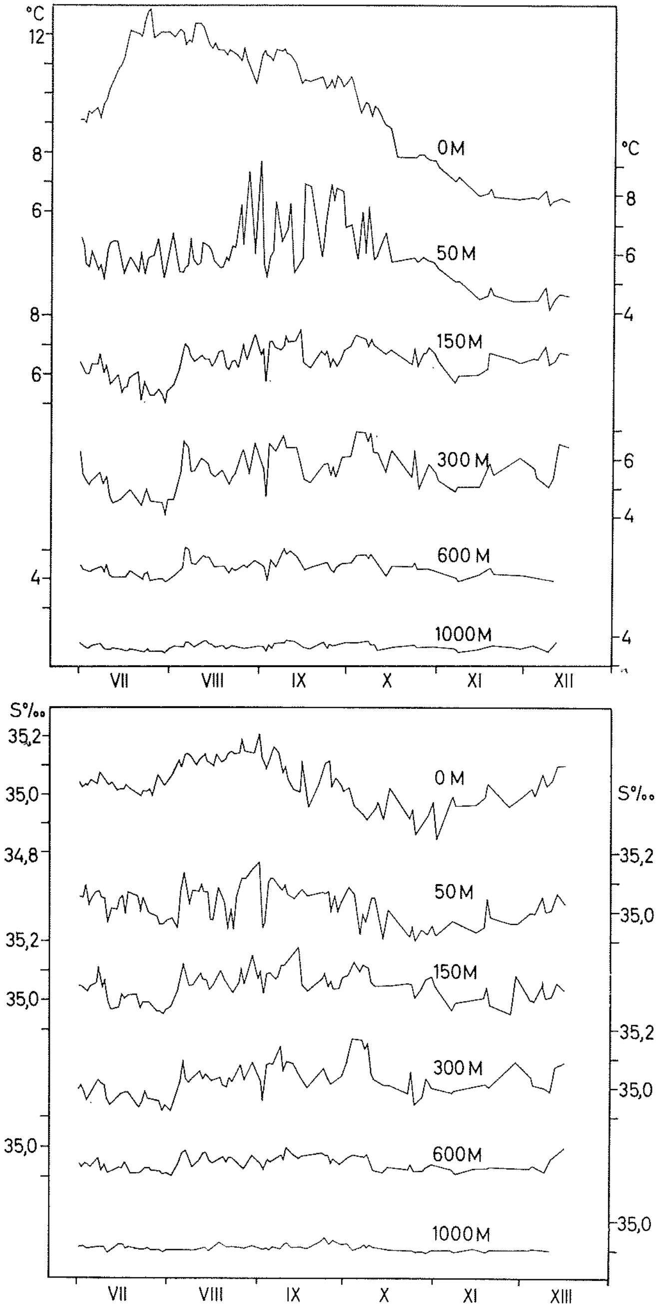

Fig. 11. Variations in temperature (upper part) and salinity at Station A during the period June-December 1958.

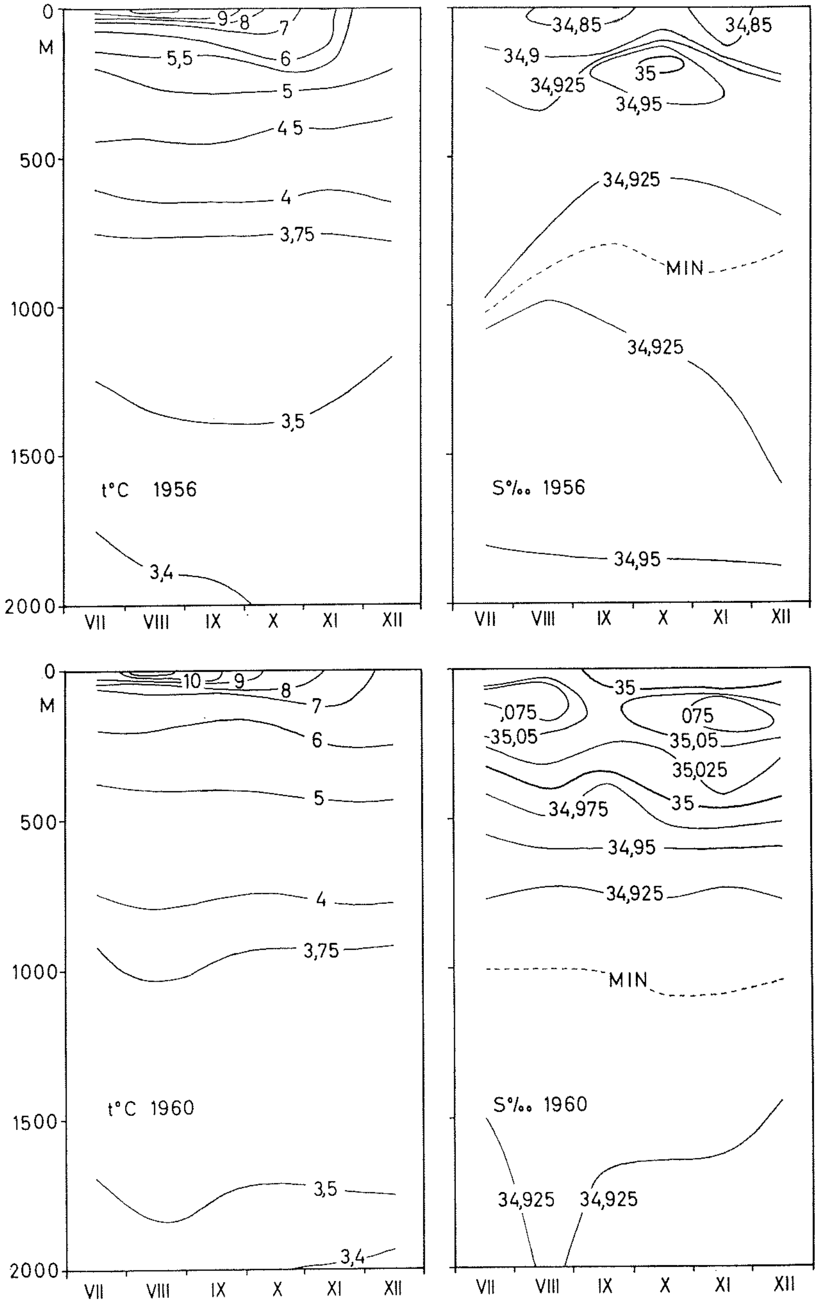

Fig. 12. Isopleth diagrams of temperature and salinity at Station A during the periods in 1956 and 1960.

for the 5 periods of observation. Isopleth diagrams for 1956 and 1960 are shown in Fig. 12. The diagrams for 1956 illustrate conditions during a period with small amounts of Atlantic water, and the diagrams for 1960 demonstrate a period when high salinities were frequently observed at Station A.

Temperature isopleths for the 5 periods show that the surface layer is warmest in August. In 1954 and 1956 the mean temperatures in the surface layer were slightly above 10° C in August, while corresponding temperatures exceeded 11° C in 1958 and 1960. A seasonal decrease is found in the upper layers so that in December the temperature was between 5° and 6° C in 1954 and 1956, and about 6.5° in 1958 and 1960. In the two former years the 6° C isotherm was found at a depth of less than 100 m during August and September, but in 1958 and 1960 the same isotherm lay between 200 and 300 m depth during these months. Even at depths as great as 2 000 m the temperature was a little lower in 1954 and 1956 than in the other years. In agreement with this the 3.5° C isotherm lay much deeper in 1958 and later periods than in 1954 and 1956.

The period in 1962/63 is not directly comparable with the other years as it does not cover the same time of year. However, at depths where the conditions are not affected by seasonal changes, the temperatures were nearly as high as in 1958 and 1960. The mean temperatures in the surface layer have their lowest values in February, near 5.5° C.

The isopleths for the salinity show that this parameter varies most in the surface layer, both from month to month and from year to year. During the periods in 1954 and 1956 the lowest salinity was observed near the surface, but in 1958 the highest salinities were found in the surface layer. Otherwise, the highest salinities are found at depths varying between 0 and 400 m. From this maximum the salinity decreases with depth to approximately 1 000 m. At this depth the intermediate water comes in, establishing an intermediate minimum of salinity as already mentioned (Fig. 3). Usually the monthly means lie a little above 34.90 $^0/_{00}$ at this depth. At greater depths the salinity increases again, and at 2 000 m the monthly means sometimes exceed 34.95 $^0/_{00}$.

At the depths where Atlantic water is found, the salinity is subject to distinct annual variations. In 1954, only the means for August at 75, 100 and 200 m were above 35.00 $^0/_{00}$, but here it is worth noting that the monthly mean at 150 m depth, which is based on a much greater number of observations, was not above 35.00 $^0/_{00}$. In 1956 the amount of Atlantic water appeared to be still smaller, as only the monthly mean for October at 200 m was above 35.00 $^0/_{00}$, but this mean is based on only 3 observations. In 1958, however, there was obviously more Atlantic water at Station A, and the mean salinity was above 35.00 $^0/_{00}$ at one or more depths in all the six months. The highest monthly mean occurred at the surface in August, and it exceeded 35.10 $^0/_{00}$. Similar conditions were found in 1960, and the isohaline for 35.00 $^0/_{00}$ lay then at depth of approximately 400 m. The highest salinities were also in this year observed in August, and the mean for this month exceeded 35.10 $^0/_{00}$ between 50 and 150 m depth.

The period in 1962/63 shows more changing conditions. The mean salinities in January exceeded 35.00 $^0/_{00}$ from the surface to 500 m depth, while February had such high values only in the surface layer. In March –April there was again Atlantic water from the surface to a depth of 300 to 400 m.

The varying conditions in the 5 periods are also easily seen in Fig. 13 which shows mean T—S relations for the periods. This Figure is based on mean values of temperature and salinity, and at each particular standard depth these values are the arithmetic mean of the 6 monthly means in the period. In some cases monthly means have not been made owing to lack of observations. In these cases interpolated values have been applied when working out the mean value for the whole period. The period in 1956 had the lowest salinity between the surface and 500 m depth. The highest mean salinities were found at depths between 50 and 300 m in 1960, but also 1958 had high values between 0 and 500 m depth.

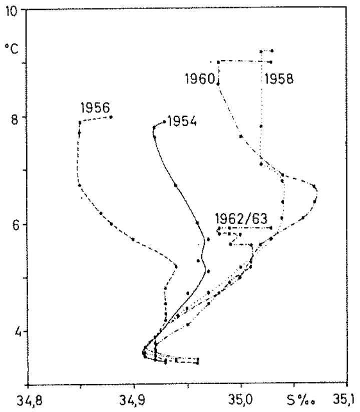

Fig. 13. Mean T–S diagram for the 5 periods of observation at Station A.

In both these years the maximum mean salinity was found at 150 m, and in 1960 it amounted to 35.07 $^0/_{00}$. In 1956 the maximum was only 34.94 $^0/_{00}$ and occurred at 200 m depth.

As a conclusion of the preceding description, it is evident that there were much greater amounts of Atlantic water at Station A in 1958–1960 than in 1954–1956. This is in agreement with the findings between the Denmark Strait and Prince Christians Sound, which also indicate much Atlantic water of relatively high salinity in the western branch of the Irminger Current 1959–1961. This is also verified by a section worked by R. V. «Dana» along latitude 62° N from the Faroes to Greenland in June-July 1959 (HERMANN 1961). This section shows Atlantic water across the whole Irminger Sea, and salinities in excess of 35.10 ‰ in the western branch of the Irminger Current. This is suggestive of an interrelation between the conditions at Station A and those in the western part of the Irminger Sea, and accordingly there should be small amounts of Atlantic water in the western part of the Irminger Sea in 1954–1956. No section from that time is involved in the data dealt with here, but good information is given by a section which was worked off Cape Tordenskjold by R. V. «Anton Dohrn» in June 1955 (DIETRICH 1957). The distribution of the salinity in this section is shown in Fig. 14, and it shows very low salinities in the western branch of the Irminger Current. The core of the current is indicated by salinities between 34.95

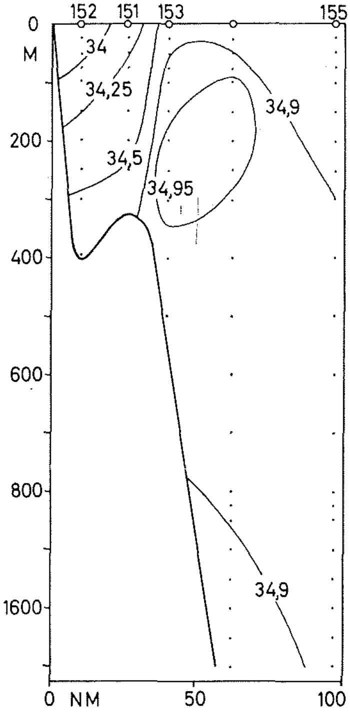

Fig. 14. Distribution of salinity off Cape Tordenskjold in June 1955. (Data from DIETRICH, 1957).

°/₀₀ and 35.00 °/₀₀. No values in excess of 35.00 °/₀₀ were observed. The conditions in July the same year are illustrated by a section worked by «Dana» along latitude 62° N (HERMANN 1957). Also this section verifies that the western branch of the Irminger Current carried only small amounts of Atlantic water in 1955. Similar conditions are also illustrated by corresponding sections along latitude 62° N from 1954 and 1956 (HERMANN 1956 and 1958).

This comparison between the observations at Station A and the sections shows that annual variations in salinity at Station A reflect similar variations in the amount of Atlantic water in great parts of the Irminger Sea. Thus there was very little Atlantic water at Station A, as in the westers branch of the Irminger Current, during the years 1954–1956. Later, the amount increased until 1959 or 1960, and after 1961 it decreased again.

RELATION BETWEEN THE WIND CONDITIONS AT STATION A AND THE AMOUNT OF ATLANTIC WATER IN THE IRMINGER SEA

It has earlier been pointed out that the bifurcation of the Irminger Current in the Denmark Strait depends on the wind conditions. HERMANN and THOMSEN (1946) write on this matter: «The fact must be presumed to be that the water under the influence of weather conditions at times all moves into the Denmark Strait, whereas at other times a considerable proportion passes the Horn and continues along the north coast of Iceland». STEFANSSON (1962a) has examined the relationship between the wind conditions and the hydrographic conditions in Icelandic waters. He concludes that the wind conditions west of Iceland may affect the influx of Atlantic water to the North Icelandic region.

Assuming that the Irminger Current annually transports approximately the same volume of Atlantic water to the area southwest of Iceland, a result of the conclution mentioned above, must be that in years with prevailing southerly winds the Atlantic water will be found close to the west coast of Iceland, and a great proportion will find its way round the Horn and flow into the North Icelandic region. In years when northerly winds are dominant, the Atlantic water will, however, extend more westwards and the greater part of it will turn around in the Denmark Strait and continue southwest in the western branch of the Irminger Current.

In order to get a better insight into this problem, the wind conditions at Station A are examined. Observations of wind force and direction are taken from the Daily Weather Report (ANON. 1953—1962) which usually gives four observations per day at 0000, 0600, 1200 and 1800 hours G. M. T. The wind force is entered in knots, and the direction to the nearest 10 degrees. The observations are plotted into central vector diagrams for each month, and summed up for every year from 1953 to 1962 inclusive. In this way the total number of knots along one line representing a certain direction, gives a measure of the quantity of wind which has been blowing from that direction during the year. This sum of wind will here be designated as accumulated wind. Since north-easterly and south-westerly winds prevail at Station A, the accumulated wind for each year is decomposed, and the components in the directions NE–SW and NW–SE worked out. In Fig. 15 the components from NE and SW are entered (thousands of knots), and it can be seen that considerable variations occur. The NE-component was smallest in 1953 and 1956 while 1960 presents the highest value. The SW-component had its greatest value in 1959, and was smallest in 1960 at the same time as the NE-component was greatest. The corresponding components from NW and SE are on the whole smaller than the components from NE and SW, and they show no variations of significance.

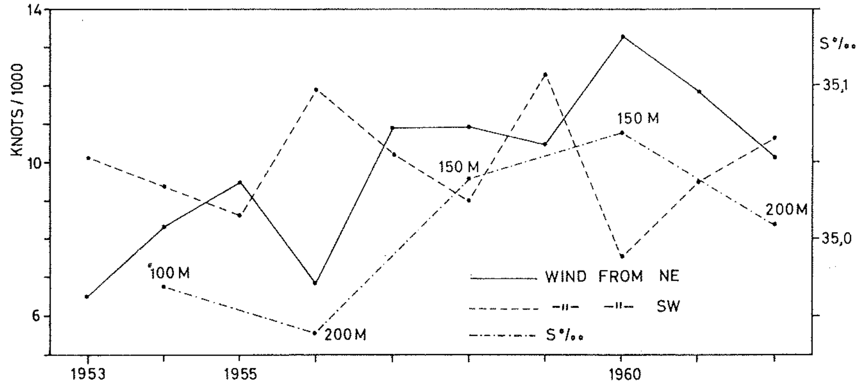

Fig. 15. Northeast and southwest components of accumulated wind (in thousands of knots) at Station A, and maximum mean salinity for each period of observation.

The highest mean salinity for each period of observation at Station A is also entered in Fig. 15. These are the maximum salinities which are entered in Fig. 13 for each period without regard to depth, except the surface. In all periods maximum mean is found at depths from 100 to 200 m. The Figure shows that the curve which represents the salinity follows rather closely the curve for the NE-component of accumulated wind. This is more clearly shown in Fig. 16 where the salinity and the NE-component are related. In this relation the points lie almost exactly along a straight line. Altogether this demonstrates a remarkably good

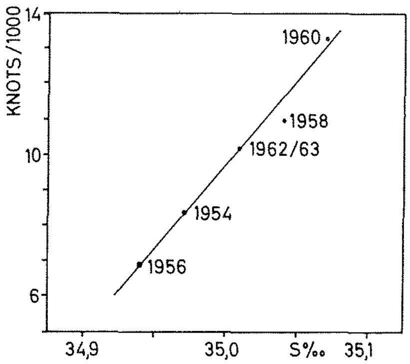

Fig. 16. Relationship between the northeast component of accumulated wind and the maximal mean salinity at Station A.

correlation between wind conditions and the salinity at Station A. It is, however, based on only 5 periods of observation and may be a matter of chance.

Following Stefansson (1962 a), the divergence of the Irminger Current in the Denmark Strait is influenced by the wind conditions, and there is good correlation between the salinities off Langanes in August and the wind conditions west and northwest of Iceland during the spring. The good relationship between the salinity and the wind conditions at Station A shows, however, that the wind plays a part also in this area. Further, the variations in salinity at Station A reflect related variations of salinity in the western branch of the Irminger Current. Consequently it looks as if the wind conditions as observed at Station A are of significance for the major part of the Irminger Sea.

If the amount of Atlantic water transported to the area southwest of Iceland is nearly constant from year to year, and low salinity at Station A indicates only that Atlantic water is lying close to the coast of Iceland, it might be expected that great masses of it should have been found near the coast and in the North Icelandic region in 1954 and 1956. In 1960, on the contrary, one might have expected to find only small Atlantic influx north of Iceland since there were high salinities at Station A and much Atlantic water in the western branch of the Irminger Current. Stefansson (1962 a) however, has shown that in 1954 and 1956 only small quantities of Atlantic water were observed in sections off Latrabjarg (Bjargtangar) compared with the years 1949, 1951, 1957, 1958 and 1959. Off Langanes the mean salinity for August between 50 and 200 m depth was in 1954 0.03 ‰ higher and in 1956 0.01 ‰ lower than the average for 15 years. For 1960 no section off Latrabjarg is available, but Stefansson (1962 b) found a pronounced influence of Atlantic water off northern Iceland in June. In a section off Siglunes higher salinities were found than in any previous year. Off Langanes the mean salinity for August between 50 and 200 m depth was 35.05 $^0/_{00}$, which is 0.10 $^0/_{00}$ higher than the average for 15 years. This shows that in 1960 there was a pronounced Atlantic influence in the western Irminger Sea as well as in the North Icelandic Irminger Current. In 1954–1956 the opposite was the case, because small amounts of Atlantic water were observed at Station A and in the western branch of the Irminger Current, and neither the sections off Latrabjarg nor the observations off Langanes indicated any great Atlantic influx to the North Icelandic region. A conclusion from this must be that the entire Irminger Current carried greater quantities of Atlantic water in the years around 1960 than in 1954–1956, so that the observed annual variation have their origin in related variations in the Irminger Current to the southwest of Iceland. The relationship between wind conditions and the salinity at Station A may consequently be regarded as a relationship between the wind conditions and the inflow of Atlantic water to the Irminger Sea. Here, however, it is not quite clear whether the wind is the generating force, or whether the wind conditions are influenced by oceanographic conditions.

If the wind is the generating force, it seems likely that it influences the divergence of the North Atlantic Current to the south of Iceland. In contrast to conditions at Station A, Atlantic water is here always present at the surface. It is therefore directly exposed to the wind stress, and in periods of prevailing north-easterly winds, relatively great amounts of Atlantic water may be forced so far to the west that more of it than usual flow into the Irminger Current. In this manner the Irminger Current may be fed with waters which otherwise, would flow into the area of the Faroe–Iceland Ridge, or into the Faroe–Shetland Channel. In such a case the increase of Atlantic water in the Irminger Current will take place at the expence of the transport to the Norwegian Current and give rise to variations in the latter opposite to those in the former current. TULLOCH and TAIT (1959) however, have shown that this flow from the area south of Iceland is not the main source of the North Atlantic Current in the Faroe–Shetland Channel. Variations in this flow will therefore probably be of little significance to the total Atlantic flow through the Channel.

Another possible reason for variations in the Irminger Current may lie in associated variations in the entire North Atlantic current. Such varying transport of Atlantic water will also include varying transport of heat, and in the area around Iceland and southern Greenland this may influence the atmospheric conditions. In such a case it is therefore possible that the oceanographic conditions give rise to the related wind conditions which are observed at Station A. If such great scale fluctuations really take place, it is likely that variations similar to those in the Irminger Current can be observed also in the other branches of the North Atlantic Current.

SUMMARY

1. The data examined consist of hydrographic sections in the western Irminger Sea and serial observations at Ocean Weather Station Alpha (Station A). The sections were worked in the years 1959 and 1961 –1964, and at station A the data were collected during 5 periods of observation in the years 1954–1963.

2. The sections as well as the data from Station A are used to give the caracteristics and extent of different water masses. The occurence of possible annual variations is also examined.

3. South of the Denmark Strait it is difficult to characterize Polar water by means of temperature and salinity, but 34.50 $^0/_{00}$ seems to be the upper limit of its salinity.

4. The intermediate water in the Irminger Sea is found at about 1 000 m depth, and T–S relations for the data from Station A show that the minimum temperature and salinity of intermediate water are 3.5° C and 34.88 $^0/_{00}$.

5. In the Denmark Strait Arctic Intermediate water exhibits temperatures near, or below, 1°C, and salinities chiefly below 34.90 $^0/_{00}$. This water mass seems to be the main source of the bottom water in the Irminger Sea.

6. The amount of Atlantic water which is carried to the Irminger Sea by the Irminger Current, varies from year to year. These variations are studied in the western branch of the Irminger Current and at Station A. In 1954–1956 only small amounts of Atlantic water were observed, but the Atlantic inflow increased until 1959–1960. During the years after 1961 the amount decreased again.

7. At Station A the wind conditions are examined, and there is a close relationship between the accumulated wind and the mean salinity in the different periods of observation.

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NORWEGIAN TAGGING EXPERIMENTS IN THE NORTH-EASTERN NORTH SEA AND SKAGERAK, 1964 AND 1965

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INTRODUCTION

Except for the ICES herring tagging experiments in 1957 and 1958 on the Bløden Ground (Aasen, Andersen, Gulland, POPP-MADSEN and SAHRHAGE 1961) no large scale tagging of herring with internal metal tags have been carried out in the North Sea. In view of the rapid development of the herring fisheries in the northern and north-eastern North Sea in the recent years, the Herring Committee of ICES (ANON. 1965) in October 1965 recommended that both internal and external tagging of overwintering herring in the north-eastern North Sea and tagging of feeding and spawning herring in the western North Sea should be carried out.

By that time the Institute of Marine Research, Bergen had already in the winter 1964 carried out one tagging experiment with internal tags in the Skagerak. Since the recommendation of the Herring Committee was passed, Norway has carried out three further experiments (November 1965, June 1966 and July 1966).

This report describes the Norwegian tagging experiments, carried out in 1964 and 1965, and considers some preliminary results that can be drawn from the recaptures up to November 1966.

MATERIAL AND METHODS

All the herring were tagged with internal steel tags and the method applied was briefly the same as described by FRIDRIKSSON and AASEN (1950 and 1952). The lengths of the herring released were recorded, and scales were taken from each fish for age determination. The taggings were performed from a small, unanchored boat. Herring were taken individually from a keep net with a dip-net, and were after tagging released directly into the open sea. The fish used for tagging were caught by purse-seine. Weather conditions were favourable during the tagging operations.

The 1964 tagging was carried out in January during a cruise of

Table 1. Norwegian tagging experiments with internal tags in north-eastern North Sea and Skagerak, 1964 and 1965 (purse-seine catch).

Date		Lib. No.	Position N	Position E	Serial number	Number of fish tagged
1964	17 Jan.	1	57°37'	06°35'	N 240501–241500	1 000
1965	5 Nov.	1	57°30'	07°20'	N 255501–256900	1 400
1965	5 Nov.	1	57°30'	07°20'	N 257001–257300	300
1965	7 Nov.	2	58°12'	10°53'	N 256901–257000	100
1965	7 Nov.	2	58°12'	10°53'	N 257301–259500	2 200
					Total	5 000

R/V «G. M. Dannevig» and a total of 1000 herring were tagged about 30 nautical miles south-west of Lindesnes (Table 1). A sample from the same catch was secured. Unfortunately no otoliths were taken and it is difficult, therefore, with certainty to classify them into autumn and spring spawners. However, it can be concluded that the herring in maturity stages VII and VIII were autumn spawners (Table 2). Further, the mean vertebral count of the herring in maturity stages I and II was 56.51, showing that most of the herring in this group were also autumn spawned fish. The herring in maturity stage IV had a mean vertebral count of 57.25, indicating that they were spring spawners. The 3-ringers (most likely the 1960 year-class of the autumn spawned fish) predominated in the sample (Table 3).

Table 2. The maturity stages of the herring in samples taken from the same catches as the tagged fish.

Maturity stage	1964		1965					
			Liberation 1			Liberation 2		
			Autumn spawners		Spring spawners	Autumn spawners		Spring spawners
	No.	%	No.	%	No.	No.	%	No.
I	27	27,0	4	4.7	1	57	60.6	1
II	14	14.0	4	4.7	1	35	37.2	–
III	3	3.0	–	–	–	1	1.1	2
IV	4	4.0	–	–	3	–	–	–
V	–	–	–	–	4	–	–	–
VI	–	–	–	–	–	–	–	–
VII	5	5.0	7	8.2	–	1	1.1	–
VIII	46	46.0	70	82.4	1	–	–	–
Total	99	100.0	85	100.0	10	94	100.0	3

Table 3. Age composition of herring in samples taken from the same catches as the tagged fish.*

Winter-rings	1964		1965								
			Autumn spawners					Spring spawners		
			Year-class	Lib. 1		Lib. 2		Year-class	Lib. 1	Lib. 2
	No.	%		No.	%	No.	%		No.	No.
0	–	–	1963	4	4.8	91	96.8	1964	–	1
1	–	–	1962	13	15.7	2	2.1	1963	1	1
2	28	30.4	1961	23	27.7	–	–	1962	3	–
3	53	51.6	1960	33	39.8	1	1.1	1961	3	–
4	2	2.2	1959	–	–	–	–	1960	1	–
5	–	–	1958	2	2.4	–	–	1959	–	–
6	2	2.2	1957	1	1.2	–	–	1958	–	–
7	2	2.2	1956	7	8.4	–	–	1957	–	–
8	4	4.3	1955	–	–	–	–	1956	–	–
8+	1	1.1	> 1955	–	–	–	–	> 1956	–	–
Total	92	100.0		83	100.0	94	100.0		8	2

*) 8 herring from the 1964 sample and 9 herring from the 1965 samples were not fit for age determinations and are omitted .

The 1965 taggings were carried out during a cruise of R/V «Johan Hjort» (HARALDSVIK 1965). The first batch (1700 herring, liberation 1) was released on 5 November, 25 nautical miles south of Ryvingen (Table 1 and Fig. 1). The herring consisted of 91.2 % autumn spawners, and the 1960 year-class predominated, followed by the 1961 year-class (Table 3). The distribution of maturity stages of the herring is shown in Table 2.

The next batch (2300 herring, liberation 2) was released on 7 November, 20 nautical miles north of Skagen (Table 1 and Fig. 1). The herring were almost entirely autumn spawned fish (97.9 %) of the 1963 year-class (Table 3). Most of these autumn spawners were in maturity stages I and II (Table 2) and the mean number of vertebrae was 56.59.

RESULTS AND DISCUSSION

THE RETURNS

In Table 4 is given a complete list of all tag returns from the 1964 experiment during the period up to 31 October 1966. Altogether 22 tags have been recaptured from this experiment, of which 14 were detected at Norwegian reduction plants, equipped with magnets. Most of

Table 4. Summary of returns from the 1964 experiment arranged according to area recovered at Norwegian plants

Area	Months																	
	1	2	3	4	5	6	7	8	9	10	11	12	Un-cer-tain	13	14	15	16	17
	1964																	
Skagerak											1 (1)		1 –					
Egersund B., Coral B.	3 (3)	1 (1)	1 (1)	1 (1)				1 (1)										
Shetland																		
Uncertain				3 –									1 –					
Total	3 (3)	1 (1)	1 (1)	4 (1)				1 (1)			1 (1)		2 –					

the tags were recaptured in the Egersund Bank-Coral Bank area. However, internal tags recovered at reduction factories cannot be allocated with certainty to a particular area and day of capture, because the tag may not reach the magnet and be recovered until some time after the herring have been caught. Notwithstanding this disadvantage it is likely that most of the tags recovered can be mapped out according to the information given by the factories, which usually know the time it takes a fish from landing until it passes through the machinery. As the fishing area of the catch reduced is known, the area of recapture can be estimated fairly well. It should be noted that only one tag of the 1964 experiment was recovered in1965, even though the yield from the North Sea and Skagerak that year was much higher than in 1964. In 1966, only 8 tags were returned up to 31 October.

Table 5 summarizes the returns up to 31 October 1966 for the two liberations in 1965. A total of 178 recoveries were returned from liberation 1, of which 141 were detected at Norwegian plants equipped with magnets. From liberation 2, 136 tags were recovered, 100 at Norwegian plants equipped with magnets. These tags were mainly recaptured in the Egersund Bank—Coral Bank area and in the Skagerak. Most of the 21 recoveries from the Skagerak were from Danish reduction factories.

and number of months after the release. The figures in brackets are number of tags equipped with magnets.

after release																		Sum
18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	Uncertain	
1965							1966											
																		2 (1)
												2 (2)		1 (1)		1 (1)		11 (11)
		1 (1)											2 (1)					3 (2)
																	2 –	6 –
		1 (1)										2 (2)	2 (1)	1 (1)		1 (1)	2 –	22 (14)

Only the recoveries from herring landed in Norway will be dealt with quantitatively, and special attention will be paid to the returns from reduction factories. However, not all the returns from factories equipped with magnets can be dealt with quantitatively due to low efficiency of the magnets and unreliable data on the catch reduced.

Before analysing the tag returns it is necessary to take into account the catch distribution and some biological characteristics of the herring caught in the Skagerak and the northern North Sea. This is important as the recaptures are used for stock size estimates, and for discussion of the movements of herring.

It appears from data published in Annales Biologiques (HARALDSVIK 1966, 1967 and 1968) that the north-eastern North Sea and the Skagerak can be regarded as the main overwintering area for the mature autumn spawned stock of the Bank herring. The north-western North Sea is considered to be the main feeding grounds for the same stock.

The recaptures, therefore, from the following periods and areas are of special interest: (1) 1 November to 31 May, Skagerak and Egersund Bank—Coral Bank and (2) 1 June to 31 October, Shetland area.

During the period 15 January to 31 May 1964 all the 6 recoveries were detected at one factory (Tables 4 and 6). Out of a total catch of

Table 5. Summary of returns from the 1965 experiment arranged according to area and month after release. The figures in brackets are number of tags recovered at Norwegian plants equipped with magnets.

Lib.	Area	Month after release												Uncertain	Total
		1965			1966										
		1	2	3	4	5	6	7	8	9	10	11	12		
1	Skagerak	11	3									1	3		18
		(6)	(2)									(1)	(1)		(10)
»	Egersund B., Coral B.		1	2			6	8	35	13	10	4	10		89
			(1)	(2)			(6)	(7)	(32)	(13)	(10)	(4)	(9)		(84)
»	Shetland								10	17	27	2			56
									(9)	(13)	(23)	–			(45)
»	Uncertain	3		2	1	2							1	6	15
		(1)		–	(1)	–							–	–	(2)
»	Total	14	4	4	1	2	6	8	45	30	37	7	14	6	178
		(7)	(3)	(2)	(1)	–	(6)	(7)	(41)	(26)	(33)	(5)	(10)	–	(141)
2	Skagerak	7	4		1	1	2			1		2	3		21
		–	(2)		–	–	–			–		(2)	(1)		(5)
»	Egersund B., Coral B.		1	3			1	16	16	24	18	5	1		85
			(1)	(3)			(1)	(16)	(16)	(24)	(18)	(5)	(1)		(85)
»	Shetland									4	6	2			12
										(4)	(4)	(2)			(10)
»	Uncertain	4	1	1	1	8	1	1	1						18
		–	–	–	–	–	–	–	–						–
»	Total	11	6	4	2	9	4	17	17	29	24	9	4		136
		–	(3)	(3)	–	–	(1)	(16)	(16)	(28)	(22)	(9)	(2)		(100)
Grand total		25	10	8	3	11	10	25	62	59	61	16	18	6	314
		(7)	(6)	(5)	(1)	–	(7)	(23)	(57)	(54)	(55)	(14)	(12)	–	(241)

34106 tons landed in the same period, 12113 tons were reduced to oil and meal at four factories equipped with tested magnets. The recapture rate was estimated to 0.54 $^0/_{00}$ returns per 1000 tons.

From June to October the same year it is likely that part of the herring

Table 6. Quantity of processed herring (tons) and number of returns from the 1964 experiment at Norwegian plants equipped with magnets, 15 January to 31 May 1964.

Factory No.	Jan.	Febr.	March	April	May	Quantity (p)	Efficiency (e)	Corrected quantity (e.p)	Returns
2	5 125.0	898.5	391.5	343.1	61.5	6 819.6*	0.95	6 478.6	6
12	233.7	567.6	199.6	546.9	27.4	1 575.2	0.94	1 480.7	–
16	56.4	502.6	189.8	170.2	–	919.0	0.93	854.7	–
31	21.3	172.7	146.9	424.0	2 034.8	2 799.7	0.80	2 239.8	–
Total	5436.4	2 141.4	927.8	1 484.2	2 123.7	12 113.5		11 053.8	6

* 953.7 tons derive from landings of foreign fishing boats in Norway.

tagged were outside the fishing area of the Norwegian fleet. Judging from Tables 7 and 8 the catches were also dominated by recruits. A lower number of returns, therefore, is reasonable during this period although only one recapture (from factory No. 2) is less than expected. From 1 November 1964 to 31 May 1965 one tag was recovered (Tables 4 and 9). Such a low recovery again was unexpected taking into account the relatively good fishery that took place in this period (Haraldsvik 1966, 1967) and since the same year-classes as in the previous year predominated in the catches. The per mille returns per 1 000 tons was estimated to only 0.01.

During the next period (1 June to 31 October 1965) one tag was recovered off Shetland. No herring were recaptured from the Skagerak and the Egersund Bank—Coral Bank area in the same period. This is also reasonable since the 1962 and 1963 year-classes made up more than 46.0 % of the herring caught (autumn spawners). Off Shetland, however, the purse-seiners exploited the same year-classes as those tagged.

In the 1965 experiment (Table 5) all the returns from 1 November 1965 to 31 May 1966 came from the Skagerak and the Egersund Bank-Coral Bank area. Pooling the number of recoveries during this period from liberations 1 and 2, a total number of 43 tags were detected at 11 factories (Table 10), giving 0,21 $^{0}/_{00}$ returns per 1 000 tons.

During the second period (1 June to 31 October 1966) the number of reduction plants processing herring increased to 16 and the returns from the Egersund Bank—Coral Bank area amounted to 137 tags, and from Shetland to 55 tags (Table 11). The recapture rates were estimated to 0.27 $^{0}/_{00}$ and 0.15 $^{0}/_{00}$ returns per 1 000 tons for the two respective areas.

Table 7. Age composition of autumn spawned herring (%) from Skagerak and northern North Sea arranged according to period, area and spawning component (number in brackets).

Period	Area	Type		Year-class									
				Autumn spawners									
		Autumn spawners	Spring spawners	1964	1963	1962	1961	1960	1959	1958	1957	1956	< 1956
1964 1 Jan.– 31 May	Skagerak, Egersund B., Coral B.	82.5 (245)	17.5 (52)				36.9	48.5	2.9	0.4	0.8	8,7	1.7
1 June– 31 Oct.	Egersund B., Coral B.	83.8 (599)	16.2 (116)			38.0	21.3	34.7	1.9	1.1	1.1	1.7	0.2
1964/65 1 Nov.– 31 May	Skagerak, Egersund B., Coral B.	92.9 (184)	7.1 (14)			12.3	30.4	52.0	0.6	0.6	1.8	2.3	
1965 1 June– 31 Oct.	Skagerak, Egersund B., Coral B.	89.7 (741)	10.3 (85)		30.3	16.3	14.0	28.2	1.4	1.3	1.9	6.1	0.1
»	Shetland	84.2 (358)	15.8 (67)			7.6	18.3	51.2	1.5	3.1	3.7	14.3	0.3
1965/66 1 Nov.– 31 May	Skagerak, Egersund B., Coral B.	91.1 (717)	8.9 (70)	0.3	46.0	16.9	9.4	21.1	0.6	0.4	1.0	4.3	0.1
1966 1 June– 31 Oct.	Skagerak, Egersund B., Coral B.	92.7 (447)	7.3 (35)	4.4	30.7	15.5	12.2	26.6	0.5	1.2	2.1	6.9	
»	Shetland	75.2 (682)	24.8 (225)	0.2	17.8	5.8	13.1	38.1	1.3	2.4	3.8	17.0	0.5

Table 8. Age composition of spring spawned herring (%) from Skagerak and northern North Sea arranged according to period, area and spawning component (number in brackets).

Period	Area	Type		Year-class										
				Spring spawners										
		Autumn spawners	Spring spawners	1965	1964	1963	1962	1961	1960	1959	1958	1957	1956	< 1956
1964 1 Jan.– 31 May	Skagerak, Egersund B., Coral B.	82.5 (245)	17.5 (52)				5.8	78.8	13.5	1.9				
1 June– 31 Oct.	Egersund B., Coral B.	83.8 (599)	16.2 (116)			1.0	3.0	72.2	7.9	10.9	4.0			1.0
1964/65 1 Nov.– 31 May	Skagerak, Egersund B., Coral B.	92.9 (184)	7.1 (14)				7.1	58.0	35.7		7.1			
1965 1 June– 31 Oct.	Skagerak, Egersund B., Coral B.	89.7 (741)	10.3 (85)		6.2	8.6	6.2	54.3	7.4	14.8	1.2		1.2	
»	Shetland	84.2 (358)	15.8 (67)				3.1	73.8	6.2	16.9				
1965/66 1 Nov.– 31 May	Skagerak, Egersund B., Coral B.	91.1 (717)	8.9 (70)		34.8	17.4	18.8	14.5	2.9	10.1	1.5			
1966 1 June– 31 Oct.	Skagerak, EgersundB., Coral B.	92.7 (447)	7.3 (35)	2.9	31.4	8.6	11.4	28.6	2.9	8.6		2.9	2.9	
»	Shetland	75.2 (682)	24.8 (225)	1.8	42.4	2.2	3.6	34.4	8.5	6.7	0.4			

Table 9. Quantity of processed herring (tons) and number of returns from the 1964 experiment at Norwegian plants equipped with magnets, 1 November 1964 to 31 May 1965.

Factory No.	Nov.	Dec.	Jan.	Febr.	March	April	May	Quantity (p)	Efficiency (e)	Corrected quantity (e.p)	Returns
2	5 439.2	4 146.2	6 517.0	570.6	678.0	337.3	4 482.3	22 170.6*	0.95	21 062.1	1
3	–	–	2 725.1	–	–	351.0	268.3	3 344.4	0.81	2 709.0	–
7	–	–	5 269.9	4 671.1	680.0	300.4	1 011.4	11 932.8	0.80	9 546.2	–
12	480.8	473.5	436.0	741.5	156.8	77.2	527.2	2 893.0	0.94	2 719.4	–
16	618.5	1 249.2	650.5	807.0	24.2	1 556.9	3 603.5	8 509.8	0.93	7 914.1	–
18	–	–	511.5	511.5	182.4	692.2	2 396.2	4 293.8	0.87	3 735.6	–
20	–	–	1 062.8	2 042.7	131.3	295.2	1 701.3	5 233.3	0.86	4 500.6	–
31	631.4	1 222.7	1 082.0	2 109.7	166.5	2 641.6	12 686.3	20 540.2	0.80	16 432.2	–
Total	7 169.9	7 091.6	18 254.8	11 454.1	2 019.2	6 251.8	26 676.5	78 917.9		68 619.2	1

* 1 602.2 tons derive from landings of foreign fishing boats in Norway.

Table 10. Quantity of processed herring (tons) and number of returns from the 1965 experiment at Norwegian plants equipped with magnets, 1 November 1965 to 31 May 1966.

Fact. No.	Eff. (e)	November			December			January			February			March			April			May		
		Corr. quant. (e.p)	Returns Lib. 1	Returns Lib. 2	Corr. quant. (e.p)	Returns Lib. 1	Returns Lib. 2	Corr. quant. (e.p)	Returns Lib. 1	Returns Lib. 2	Corr. quant. (e.p)	Returns Lib. 1	Returns Lib. 2	Corr. quant. (e.p)	Returns Lib. 1	Returns Lib. 2	Corr. quant. (e.p)	Returns Lib. 1	Returns Lib. 2	Corr. quant. (e.p)	Returns Lib. 1	Returns Lib. 2
1	0.93	2 697	–	–	–	–	–	535	–	3	–	–	–	–	–	–	1 205	1	–	3 914	3	3
2	0.95	3 913	3	–	413	1	2	1 121	2	–	34	–	–	128	–	–	1 267	5	1	4 549	1	5
3	0.81	1 420	–	–	–	–	–	305	–	–	–	–	–	–	–	–	–	–	–	893	–	–
7	0.80	1 833	–	–	240	–	–	1 198	–	–	–	–	–	–	–	–	–	–	–	4 424	1	–
12	0.94	38	–	–	–	–	–	70	–	–	58	–	–	129	–	–	124	–	–	960	–	–
16	0.93	132	1	–	–	–	–	26	–	–	–	–	–	9	–	–	210	–	–	2 991	2	4
18	0.87	300	1	–	–	–	–	79	–	–	5	–	–	–	–	–	358	–	–	1 886	–	–
20	0.86	197	–	–	–	–	–	–	–	–	–	1	–	–	–	–	133	–	–	2 786	–	–
21	0.91	44	–	–	31	–	–	46	–	–	–	–	–	–	–	–	97	–	–	2 233	–	1
31	0.80	246	1	–	–	–	–	–	–	–	–	–	–	–	–	–	123	–	–	4 395	–	–
42	0.72	116	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	236	–	–
Total		10 936	7	–	684	1	2	3 380	2	3	97	1	–	266	–	–	3 517	6	1	29 267	7	13

FACTORS AFFECTING THE RETURNS

The per mille returns of tags may be influenced by several factors, among which the following are the most important: (1) uneven dispersion of the tagged fish and the fishing effort in the area under consideration, (2) non-returns of recovered tags and losses of tags not being detected, (3) mortalitiy due to tagging, handling and bad condition of the tagged fish, (4) losses of tags from the fish by shedding and (5) losses of tags through migration.

Up to August 1965 only one factory (No. 2) has detected tags from the 1964 experiment (Tables 4, 6 and 9). It should be noted that during the first five months of 1964 the herring landed were reduced at only a few factories compared with the period from 1 November 1964 to 31 May 1965. Nevertheless, tags were expected to be found at all factories listed in Tables 6 and 9. The explanation for this bias in returns may be the failure of the tagged herring to disperse randomly. Since also the fleet obviously did not fish at random, such an uneven distribution of the returns may occur.

The herring tagged in 1965 seemed not to mix evenly during the first period (1 November 1965 to 31 May 1966) after release. Using the mean number of returns per million herring reduced as the expected number and, comparing it with the estimated number of returns per million number in each reduction plant a χ^2-test was applied. The χ^2-values obtained ($p < 0.05$) indicated that the tags were not randomly distributed between reduction plants, when pooling the returns from liberations 1 and 2. Also when excluding the recaptures during the first three months after release the distribution of the tag returns was biased ($p < 0.05$). However, considering liberation 1 separately, the returns were randomly distributed between factories ($p > 0.05$).

The non-return rate of recovered tags of cod, coalfish, haddock, halibut and catfish in Norway was estimated to be at least 4—6 % (Hylen 1963). However, it should be noted that the reward for each of these tags is N.kr. 5, whereas the reward for a herring tag is N. kr. 10. Almost all the recoveries of internal tags come from oil and meal factories, and in these plants there are only a few workers who attend to that part of the machinery where the magnets are placed. Thus, only a fairly limited number of people are concerned, and in all the plants there are placed posters with detailed instructions of what to do with the recovered tags. For this reason and the worth while reward, it is considered that the loss in Norwegian plants due to non-returns of tags recovered is probably negligible.

The returns from factories without magnets and with magnets of

Table 11. Catches of herring (tons) in the Egersund Bank—Coral Bank (Eg.) and (1 June to 31 October 1966) together with the number of

Fact. No.	Eff. (e)	June						July					
		Corr. quant. (e.p)		Returns				Corr. quant. (e.p)		Returns			
				Lib. 1		Lib. 2				Lib. 1		Lib. 2	
		Eg.	Sh.	Eg.	Sh.	Eg.	Sh.	Eg.	Sh.	Eg.	Sh.	Eg.	Sh.
1	0.93	6 627	–	8	–	7	–	6 549	78	5	–	12	–
2	0.96	8 840	47	6	–	4	–	8 900	–	5	–	9	–
3	0.77	1 702	–	2	–	1	–	1 610	31	–	–	–	–
4	0.81	2 969	–	–	–	–	–	3 804	73	3	–	1	–
7	0.80	5 764	35	3	–	–	–	5 190	161	–	–	1	–
12	0.94	941	391	–	–	–	–	765	245	–	–	–	–
16	0.93	2 416	1 079	2	–	–	–	1 499	3 274	–	1	–	2
18	0.96	1 880	1 291	2	–	–	–	1 165	4 081	–	2	1	1
20	0.86	2 381	2 093	4	–	–	–	690	2 152	–	–	–	–
21	0.91	1 729	1 616	1	4	2	–	1 248	3 019	–	3	–	–
24	0.66	1 429	3 443	–	3	–	–	7	4 093	–	1	–	–
31	0.76	2 925	2 984	2	2	2	–	147	6 566	–	1	–	–
35	0.86	1 463	1 865	–	–	–	–	–	3 378	–	1	–	–
37	0.84	–	–	–	–	–	–	–	2 199	–	2	–	–
42	0.72	68	1 437	2	–	–	–	4	2 606	–	–	–	–
43	0.94	31	2 949	–	–	–	–	–	3 549	–	2	–	1
Total		41 165	19 230	32	9	16	–	31 578	35 505	13	13	24	4

especially low efficiency are not considered for further quantitative treatment. To test the efficiency (e) of the magnets the returns from a known number of tagged fish introduced into each factory is measured (Tables 6, 9 and 11). The efficiency (e) at each factory multiplied by the quantity (p) gives the effective quantity of herring reduced.

No special test was carried out to investigate the tagging mortality in the present experiments. However, several attempts have been made to study this problem on Norwegian spring spawners (FRIDRIKSSON and AASEN 1950, 1952). These experiments indicated that the tagging mortality was negligible.

During the period 17 June to 19 September 1966 a tank experiment was carried out to test mortality of internal tagged herring. The fish were already brought to the Institute from a purse-seine catch near Bergen in autumn 1965 and were before the experiment kept in a tank. A total of 79 herring were tagged and, thereafter transferred into another tank (Table 12). Just after the tagging the herring did not shoal and refused eating for the first two days. A total of 8 herring died during the experiment, 4 of these during the first three days. When examining the

Shetland areas (Sh.) and processed at Norwegian plants equipped with magnets returns from the 1965 experiments in the two fishing areas.

August						September						October					
Corr. quant. (e.p)		Returns				Corr. quant. (e.p)		Returns				Corr. quant. (e.p)		Returns			
		Lib. 1		Lib. 2				Lib. 1		Lib. 2				Lib. 1		Lib. 2	
Eg.	Sh.	Eg.	Sh.	Eg.	Sh.	Eg.	Sh.	Eg.	Sh.	Eg.	Sh.	Eg.	Sh.	Eg.	Sh.	Eg.	Sh.
5 932	1 570	–	–	3	–	3 788	–	–	–	3	–	3 121	–	6	–	–	–
8 374	1 783	5	–	7	–	4 224	8	2	–	2	–	2 787	–	–	–	1	–
2 153	613	–	–	–	–	1 116	–	–	–	–	–	916	–	1	–	1	–
3 939	1 125	1	2	4	–	2 838	–	2	–	–	–	2 085	–	–	–	–	–
4 524	1 738	4	1	4	2	3 296	–	–	–	1	–	1 653	–	1	–	–	–
–	524	–	–	–	–	100	–	–	–	–	–	195	–	–	–	–	–
104	2 566	–	3	–	–	335	40	1	–	1	2	605	–	–	–	–	–
50	3 151	–	3	–	–	175	183	–	–	–	–	456	–	1	–	–	–
325	2 863	–	2	–	1	273	444	–	–	–	–	497	–	1	–	–	–
117	3 517	–	–	–	–	93	288	–	–	–	–	263	–	–	–	–	–
–	3 430	–	5	–	–	123	41	–	–	–	–	49	–	–	–	–	–
–	3 026	–	1	–	1	360	50	–	–	–	–	55	–	–	–	–	–
–	5 641	–	1	–	–	56	64	–	–	–	–	70	–	–	–	–	–
–	2 402	–	3	–	–	–	–	–	–	–	–	287	–	–	–	–	–
34	1 902	–	2	–	–	–	189	–	–	–	–	67	–	–	–	–	–
–	2 783	–	–	–	–	–	49	–	–	–	–	430	–	–	–	–	–
25 552	38 634	10	23	18	4	16 777	1 256	5	–	7	2	13 536	–	10	–	2	–

Table 12. Length distribution (%) of herring tagged with internal steel tags in the tank experiment.

Dimension of tag (mm)	Lenth in cm													
	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	18.0	18.5	18.5	19.0	19.5
15 x 2 x 0.5	25.0	–	12.5	25.0	15.0	35.0	10.0	–	–	–	–	–	–	–
20 x 3 x 1	–	–	–	–	1.6	4.8	27.0	22.0	23.8	6.3	4.8	3.2	3.2	3.2

dead herring and the position of the tag, apparently none of the herring had been directly damaged by the tag itself. A more likely reason for the mortality was the tagging operation, including the catching and handling of the fish. The tagging mortality was estimated to be 10.1 %.

The tank experiment showed that 4 tags (5.1 %) were lost by shedding. The wound caused by the insertion of the tag was healed after 6 weeks. Shedding tests have also been made on Norwegian spring spawners by DRAGESUND (unpublished data). According to his experiments special attention should be made to herring tagged in the immediate prespawning and spawning stages as tags were frequently found in one or both gonads. These tags are subject to a pressure during the spawning process, and consequently the shedding will be relatively high in these fish. Since the herring tagged were in a post spawning condition or immature (Table 2), the shedding rate should be compareable with that of the herring in the tank experiment.

A different way of handling the fish by the various tagging operators may affect the mortality of the tagged fish. In the present investigation all the herring tagged in 1964 were tagged by the same person, whereas the 1965 tagging was performed by three different persons. Judging from Table 13 no special difference between operators was noticed.

Table 13. Number of herring tagged and tags returned separated according to taggers (1965 experiment).

Liberation	Tagger No.	Number tagged	Returns	Rate of recapture %
1	1	850	87	10.24
»	2	850	91	10.71
2	1	750	43	5.73
»	2	750	39	5.20
»	3	300	14	4.67

Especially in open sea taggings, where herring have to be provided by purse-seiners and transferred into a keep net before the tagging can start, sometimes in unfavourable weather, the herring may soon be descaled and the condition of the fish be reduced. In two cases (Table 14) the rate of recapture was higher for the first half of release, whereas in one case it was slightly lower. However, testing the 1:1 ratio of the recaptures from the first and second half of release by applying a χ^2-test no significant differences could be found ($p > 0.05$). 98 % of the herring

Table 14. Number of returns from the first and second half of the tagged batch of each liberation.

Experiment	Number of returns from the first half of the tagged batch	Number of returns from the second half of the tagged batch	Total
1964	13	9	22
1965 (lib. 1)	105	73	178
» (lib. 2)	66	70	136

Table 15. Comparison between length (cm) at liberation for the total number of herring tagged and herring recaptured.

Length (L) at liberation (cm)	1964		1965			
			Lib. 1		Lib. 2	
	Number of fish tagged	Number of fish recapt.	Number of fish tagged	Number of fish recapt.	Number of fish tagged	Number of fish recapt.
19.0	–	–	–	–	3	–
.5	1	–	–	–	1	–
20.0	3	–	–	–	27	1
.5	2	–	1	–	59	4
21.0	14	–	1	–	190	7
.5	15	–	–	–	352	13
22.0	20	1	1	–	408	25
.5	26	–	2	–	413	22
23.0	63	2	9	–	371	28
.5	51	–	5	–	229	14
24.0	68	1	11	1	130	11
.5	63	1	9	1	61	4
25.0	84	3	15	1	14	–
.5	79	–	17	2	7	2
26.0	97	4	50	7	7	1
.5	75	1	36	1	6	–
27.0	91	3	84	11	2	–
.5	52	–	92	8	2	1
28.0	54	–	147	11	1	–
.5	41	2	105	18	2	1
29.0	24	1	181	28	–	1
.5	20	–	137	16	3	–
30.0	27	2	236	23	2	–
.5	6	–	132	7	2	–
31.0	13	–	182	15	1	1
.5	5	–	86	11	1	–
32.0	2	–	83	10	–	–
.5	–	–	25	2	1	–
33.0	3	1	29	–	–	–
.5	1	–	9	1	–	–
34.0	–	–	4	1	–	–
.5	–	–	4	–	–	–
35.0	–	–	2	–	–	–
Total	1 000	22	1 695	175	2 296	136
$\overline{L}$	25.81	26.45	29.32	29.27	22.46	22.78
s^2	5.40	6.69	4.08	3.19	1.50	2.27

landed from the North Sea and Skagerak have been caught by purse-seine. It is unlikely, therefore, to expect any selection effect due to fishing on the numbers of returns. However, the mortality of the tagged herring may be associated with the size of the fish so that the larger fish survive better than the smaller ones, or vice versa.

In Table 15 are given the length distributions at liberation of the tagged and recaptured fish, together with the means and variances. The differences between the means are small and are not significant ($p > 0.01$) according to the t-test.

Losses of tags may also take place by segregation. From Tables 7 and 8 it will be seen that mainly old herring were caught off Shetland by the purse-seiners in the summers of 1965 and 1966. It could be that after spawning the older age-groups of the tagged herring remained in this area and did not return to the Skagerak and the Egersund Bank—Coral Bank area to the same extent as the younger fish. However, this possibility can hardly explain the low rate of recapture of the 1964 experiment during the period from 1 November 1964 to 31 May 1965, since the same year-classes occurred in the catches from the Skagerak and the Egersund Bank—Coral Bank area as among the tagged fish (Tables 3, 7 and 8).

CONCLUDING REMARKS

MIGRATION

The distribution of the recaptures from the 1965 experiment clearly demonstrates a westward migration of herring tagged in Skagerak during the winter and spring (Fig. 1).

Up to 31 May 1966 no significant difference in total number of returns from liberation 1 and 2 is noticed. However, considering the recoveries from Norwegian plants only during the same period (Table 5), the number of returns from liberation 1 is somewhat higher than from liberation 2. If it is assumed that the tagging mortality in the two liberations was the same, the lower percentage of returns from liberation 2 indicates that these herring were not available for the Norwegian purse-seiners to the same extent as those from liberation 1.

The difference in number of returns for the two liberations seems even clearer when studying the recaptures during the next period, i. e. from 1 June to 31 October 1966 (Fig. 2). In June the main fishery still took place in the Egersund Bank—Coral Bank area, and the majority of the recoveries in this month derived from liberation 1. During the following two months (July and August) the Norwegian fleet was centered off Shetland and 54 herring (44 from liberation 1 and 10 from liberation 2) were recaptured in this area (Fig. 2).

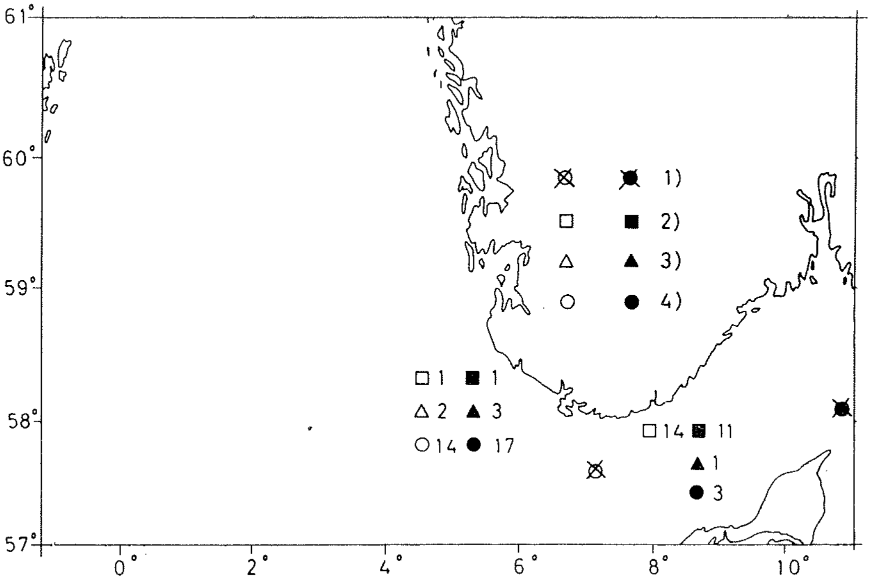

Fig. 1. Tagging localities and distribution of returns from the 1965 experiment. Open symbols refer to liberation 1 and filled symbols to liberation 2. 1) tagging localities, 2) returns November—December 1965, 3) returns January—February 1966 and 4) returns March—May 1966. The figures represent number of returns.

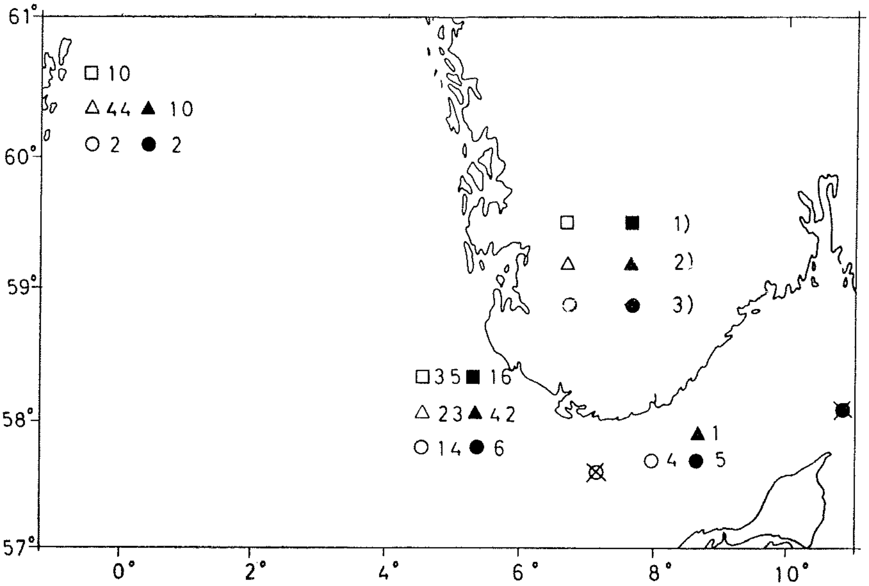

Fig. 2. Distribution of returns from the 1965 experiment. Open symbols refer to liberation 1 and filled symbols to liberation 2. 1)returns June 1966, 2) returns July—August 1966 and 3) September—October 1966. The figures represent number of returns.

At the same time part of the fleet fished in the Egersund Bank—Coral Bank area and, in contrast to the previous month most of the recoveries from this area came from liberation 2. In the next two months (September and October) most of the returns derived from the Egersund Bank—Coral Bank area, although a few tags were recaptured both off Shetland and in the Skagerak.

Judging from the figures of the per mille returns at Norwegian plants according to time and area for the two liberations (Table 16), significantly higher figures for liberation 1 are found off Shetland. The value for September-October is probably not reliable due to the difficulty in allocating all the recaptures with certainty.

Table 16. Per mille returns per 1000 tons according to time and area, the 1965 experiment.

Experiment	1965/1966	1966					
	November –May	June		July–August		September –October	
	Egers. B. – Coral B.	Egers. B.– Coral B.	Shetland	Egers. B.– Coral B.	Shetland	Egers. B.– Coral B.	Shetland
Lib. 1	0.27	0.46	0.27	0.24	0.29	0.29	–
Lib. 2	0.16	0.17	–	0.32	0.05	0.13	0.67

The same trend as off Shetland is found for the Egersund Bank—Coral Bank area except for the period July-August.

The connection therefore, between the herring appearing in the eastern Skagerak during late autumn and those present off Shetland in summer and early autumn, was not so strong as between the herring found at the western entrance of Skagerak and those off Shetland during the same period.

Comparing the age composition for the tagged herring with those fished in Skagerak and off Shetland, two possibilities may exist for the discrepancy in pattern of returns: (1) the herring in liberation 2 were dominated by Kattegat autumn spawners. These fish most likely have a feeding migration towards the Egersund Bank—Coral Bank area, resulting in many recaptures there in July-August, (2) the herring tagged in eastern Skagerak (liberation 2) consisted of Bank herring recruits, which did not migrate to the north-western part of the North Sea to the same extent as the older fish (liberation 1).

Due to the high number of vertebrae of the fish in liberation 2

(59.56) it is suggested that these herring mainly belonged to the Bank herring stock and consequently the latter explanation is the most reasonable.

STOCK SIZE

Due to the low number of recaptures of the 1964 experiment, the returns from it cannot be used for stock size assessment.

Although the requirements are only partly fulfilled for applying the returns of the 1965 experiment for quantitative assessment, they allow a tentative estimate of the stock size in the overwintering area in the north-eastern North Sea. This area is defined to cover the Skagerak and the Egersund Bank—Coral Bank and the overwintering period includes the time from 1 November to 31 May.

To adjust for losses of tags the data presented in Table 10 and the results of the tank experiment are used. Applying the figures for tagging mortality and shedding of tags obtained in the tank experiment, the effective number of tagged herring is calculated to be 3392 (1442 in liberation 1 and 1950 in liberation 2).

The losses of tags due to migration are difficult to judge from the material available. It is likely that recruits were present throughout the period in question, although the samples collected indicated that the 1963 year class was relatively less abundant from the middle of March onwards (Table 17).

Table 17. Age composition (%) of the autumn spawned herring in the samples from Skagerak—Egersund Bank—Coral Bank, 1 November 1965 to 31 May 1966.

Year-class	1965		1966						Total	
	8.11	10.12	22.1	10.3	10.3	20.4	25.5	27.5	No.	%
1964	–	1.1	–	1.2	–	–	–	–	2	0.3
-63	63.0	94.3	70.0	85.2	18.7	23.1	8.7	19.6	324	45.9
-62	31.0	4.6	11.3	3.7	11.0	24.1	18.4	29.3	119	16.9
-61	1.2	–	2.5	3.7	9.9	17.2	21.4	15.2	66	9.4
-60	3.6	–	15.0	5.0	40.6	26.4	39.8	31.5	149	21.1
-59	–	–	–	–	–	–	1.9	2.2	4	0.6
-58	–	–	–	–	2.2	–	1.0	–	3	0.4
-57	1.2	–	–	–	3.3	2.3	1.0	–	7	1.0
-56	–	–	1.2	1.2	14.3	6.9	6.8	2.2	30	4.3
> 1956	–	–	–	–	–	–	1.0	–	1	0.1
Number	84	87	80	81	91	87	103	92	705	100.0

The relative proportions of spring and autumn spawners were almost the same during the period under consideration.

The westward migration from the overwintering area to the feeding and spawning grounds in the northern and western North Sea probably started in May–June. It is reasonable, therefore, to assume that the dominant part of the autumn spawners was concentrated in the Skagerak and north-eastern North Sea during the period from November to May.

In the absence of reliable fishing effort statistics and data on local fishing intensity a reasonable estimate of the stock size in the overwintering area can be obtained using a modification of the Petersen method (AASEN, ANDERSEN, GULLAND, POPP-MADSEN and SAHRAGE 1961).

The calculated number of tags returned each month at factories equipped with tested magnets, have been plotted against the number of herring processed at the same factories in that month. From the time of tagging throughout the period up to 31 May 1966 a reduction of the effective number of tagged fish has taken place due to fishing and natural mortality. No data on total mortality of herring in the north-eastern North Sea is available, but tentative values (Anon. 1964) for the total instantaneous mortality rates ($Z_1 = 0.5$ and $Z_2 = 0.9$) have been used to estimate the effective number of tagged fish present on the fishing grounds each month. The actual number of returns have been multiplied by a raising factor $\frac{N_e}{N_i}$; N_e being the effective number tagged at release and N_i the estimated number of effectively tagged herring present in the different months calculated according to the equation:

$$N_i = N_e \, e^{-Zt}$$

The number of herring reduced at Norwegian plants according to month are obtained from samples of the catches landed at the factories. Normally three samples from each landing are taken, and the average number of herring per kg is estimated. These data have been fitted to a simple proportion line, pooling liberations 1 and 2 and, considering liberation 1 separately (Fig. 3).

Using $Z_1 = 0.5$ and pooling liberations 1 and 2 the average number of effectively tagged herring present during the period was 3 017 and the stock in million numbers estimated to be $\frac{100}{14.74}$ 3 017 = 20 454.

Converting this figure to tons the stock size has been calculated to 3.31 million tons.

For $Z_2 = 0.9$ the corresponding figures are 15 777 million numbers and 2.55 million tons.

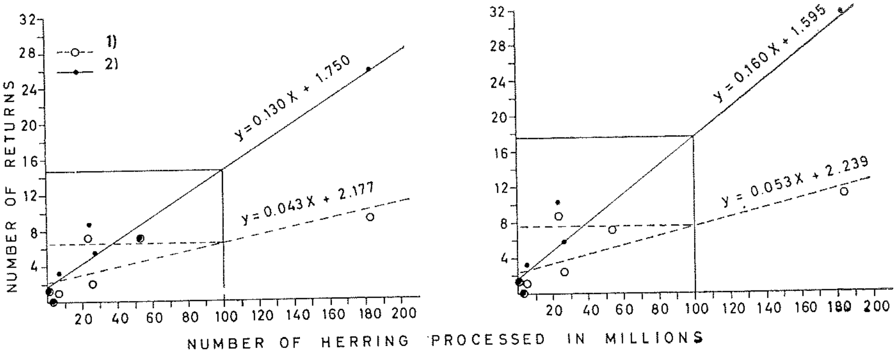

Fig. 3. Correlation between the monthly number of herring reduced at factories equipped with magnets and the estimated number of returns. Left: Z = 0.5, right: Z = 0.9. 1) liberation 1, 2) liberations 1 and 2 pooled.

Omitting liberation 2 and using $Z_1 = 0.5$, the estimated stock size in million numbers and in million tons are respectively 19 793 and 3.20, and when using $Z_2 = 0.9$ the figures are 15 565 million numbers and 2.53 million tons.

Judging from the figures no great differences in the stock size estimates are found when pooling liberations 1 and 2, and considering liberation 1 separately. Comparing the composition of the tagged herring with those obtained from samples later in the period, it is suggested that the estimates for liberations 1 and 2 pooled give the most representative values for the stock size.

In the absence of exact data on total mortality rates in the overwintering area a reasonable stock size in 1965/1966 should range between 2.55 and 3.31 million tons.

SUMMARY

1. Norwegian herring tagging experiments carried out with internal metal tags in Skagerak in 1964 and 1965 are described.
2. The returns from these taggings up to 31 October 1966 are reviewed and factors affecting the losses of tags discussed.
3. Evidence for a movement of herring from Skagerak towards the Egersund Bank—Coral Bank area and further westward to the Shetland area was found.
4. Quantitative treatment of the recaptures from Norwegian reduction plants equipped with magnets are dealt with and, tentative estimates for the stock size in the Skagerak—Egersund Bank—Coral Bank areas during the period November 1965—May 1966 are given.

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VARIATIONS IN THE QUANTITY OF ZOOPLANKTON AND THE PROPAGATION OF *CALANUS FINMARCHICUS* AT STATION "M" IN THE NORWEGIAN SEA, 1959–1966

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INTRODUCTION

The weather ship station «M» is located in the core of the North Atlantic Current at 66° N and 02° E. The hydrographic conditions are reviewed in ØSTVEDT (1955). Atlantic water masses extend downwards to 400—600 m; from about 600—1000 m the water masses are of mixed Atlantic and Arctic origin, and below 1 000 m the Norwegian Sea bottom water is found.

Zooplankton has been collected at station «M» since the summer of 1948, and a detailed analysis of the material from October 1948 to November 1949 is presented by ØSTVEDT (1955). Some aspects of the biology of copepods from station «M» were discussed by WIBORG (1955), and the variations in quantity of zooplankton from 1950 to 1958 were presented by WIBORG (1958, 1960).

The present paper reports on the quantities of zooplankton and the propagation of *Calanus finmarchicus* during the period 1959—1966.

MATERIAL AND METHODS

The present paper is based on 805 samples collected from January 1959 to September 1966, but only the 100 to 0 m samples from 1966 are included. The samples were collected in vertical hauls from depths of 25—0 m, 100—0 m, and 600—100 m with a Nansen net (diametre 72 cm, mesh size 0.2 mm) (WIBORG 1954). No samples were available from January to May 1963, and from July to December 1964, when the weatherships were stationed between Iceland and Greenland.

The zooplankton volumes were measured by the displacement method (WIBORG 1954) after removal of large coelenterates and salps, and the stage composition of *Calanus finmarchicus* was determined as described in

Lie (1965). The dominating zooplankton species were identified, but no counting or evaluation of the relative abundance of the species has been performed.

In August 1965 «Polarfront I» and in October 1966 «Polarfront II» changed to Juday nets (diametre of upper ring 40 cm, mesh size 0.2 mm) (Bogorov 1959). The sampling area of the Nansen net is 3.2 times larger than the Juday net, and the samples obtained with the Juday net were therefore multiplied by 3.2 to make the samples from the two sampling gears comparable.

The samples from the 600 to 0 m layer were assumed to represent the fauna of the Atlantic waters at station «M». However, Mosby (1950) demonstrated oscillations with an amplitude of 200—300 m in the border layer between the Atlantic water and the underlying mixed water. Samples from 600—0 m may therefore represent zooplankton from different water masses. These conditions emphasize the suggestion by Banse (1964) that zooplankton sampling should be made in relation to meaningful hydrographic parameters rather than to standard depths. However, that would require the presence of planktologists during the sampling, which was not possible at station «M».

RESULTS AND DISCUSSION

VOLUMES OF ZOOPLANKTON AT STATION «M»

Fig. 1 shows the volumes of zooplankton in the upper 100 m at station «M» as monthly means from January 1959 to September 1966. Considerable differences among the years are demonstrated; particularly 1965 and 1966 were rich and 1961 was poor in zooplankton. Similar differences among the years were demonstrated in Norwegian coastal waters (Lie 1965, 1966), where 1965 was the richest and 1961 was the poorest in zooplankton during the period 1959—1965. The coastal waters in the years 1963 and 1964 had considerably higher zooplankton volumes than in the preceding four years, but a similar pattern could not be demonstrated at station «M».

Comparisons with the earlier investigations (Wiborg 1955, 1958, 1960) indicate that the quantity of zooplankton at station «M» during 1965 and 1966 was considerably higher than in any other year since 1950.

Fig. 1 shows that the zooplankton during the first and last quarter of the year as a rule is extremely scanty in the upper 100 m. Wiborg (1955, 1958, 1960) found a slight second peak on the curves occurring in the period September—November. Similar features are also weakly indicated in Fig. 1.

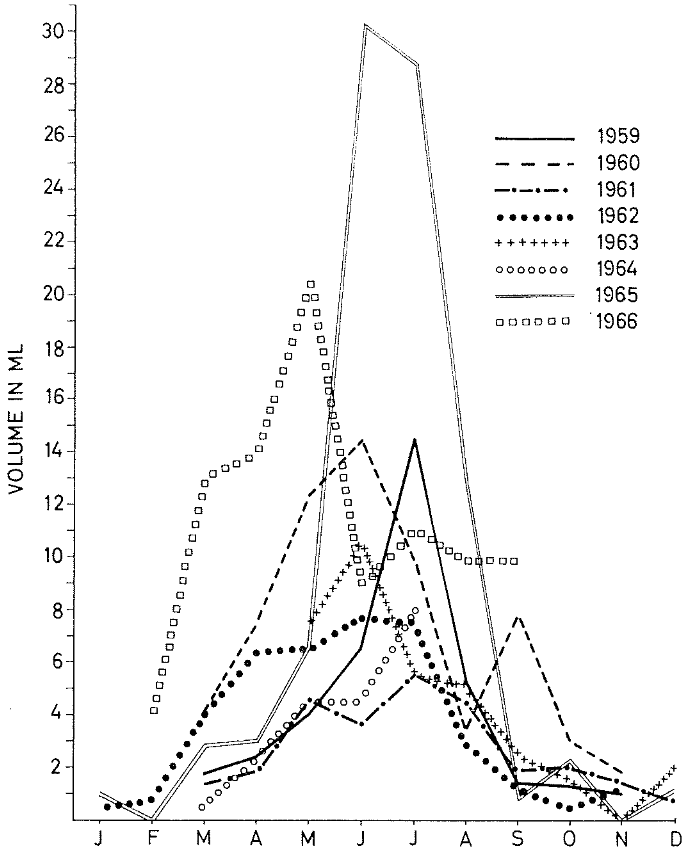

Fig. 1. Monthly mean volumes of zooplankton at station «M» in 100—0 m from 1959 to 1966.

The volumes of zooplankton in the 600 to 100 m layer are shown in Fig. 2. The volumes during December and January are somewhat lower than during the rest of the year, but the curves reveal a remarkably low variability both among monthly means and among years. About 75 % of the monthly mean volumes ranged from 5 to 13 ml.

Barnes (1949) demonstrated that a considerable portion of the plankton in vertically towed nets may be lost during the process of closing the net. The amount of zooplankton from the 600 to 100 m layer may therefore be underestimated and not directly comparable to the samples from the 100 to 0 m layer.

Beyer (1962) discussed the vertical distribution of zooplankton biomass at station «M» during 1950—1951 based on data from Wiborg (1954). He concluded that there were small seasonal variations in the biomass of the water column from 2 000 to 0 m, and he found the con-

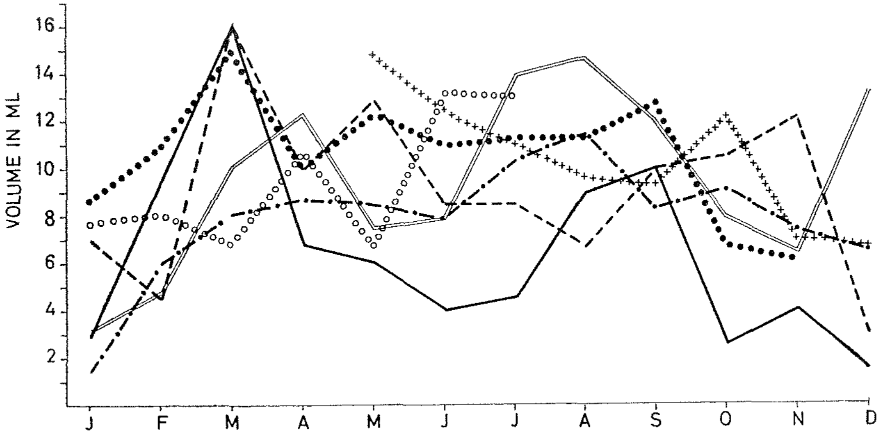

Fig. 2. Monthly mean volumes of zooplankton at station «M» in 600—100 m from 1959 to 1965. Symbols as in Fig. 1.

ditions in this respect at station «M» to be similar to the conditions in the Southern Ocean as reported by Foxton (1956). The constancy of the total biomass was explained by seasonal vertical migrations as demonstrated in Østvedt (1955), and by absorption of water by the hibernating specimens.

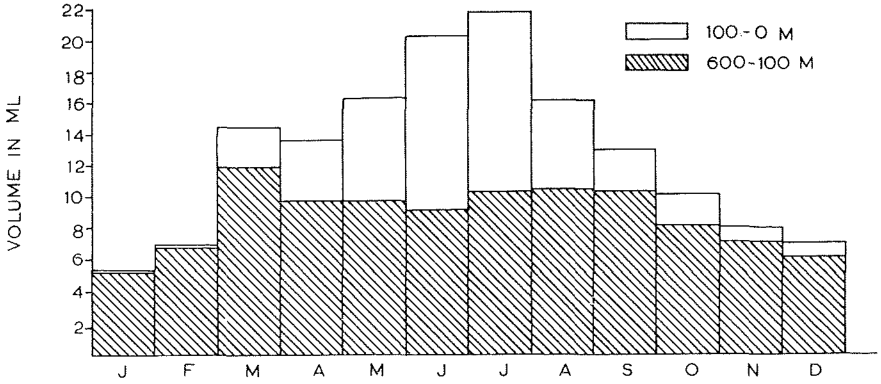

Fig. 3. Average of monthly mean volumes of zooplankton in 100—0 m and 600—100 m from 1959 to 1965.

The zooplankton volumes of the 600 to 100 m layer from 1950 to 1951 (Wiborg 1954) differ significantly from the data from the period 1959—1965. In 1950—1951 there was a maximum/minimum ratio of 6 to 1, while the ratio in 1959—1965 was about 2 to 1. The ratio for the volumes of the 600 to 0 m layer was 8 to 1 in 1950—1951, and about 4 to 1 in 1959—1965 (Fig. 3). However, as indicated in Fig. 1 and 2, the maximum/minimum ratios for individual years could be higher but, as discussed above, the variability of the 600 to 100 m layer was rather low. Wiborg (1954) found a maximum/minimum ratio in the 2 000 to 600 m layer of about 3 to 1, and during 9 months of the year from 50 % to 80 % of the total biomass was found in this layer. The large volumes and the relatively small variability of the biomass in the 2000 to 600 m and the 600 to 100 m layers tend to subdue the effect on the total biomass of the considerable variations in the upper 100 m. The zooplankton sampling in the layers deeper than 600 m was discontinued in 1959, and therefore a complete comparison with the 1950—1951 data cannot be made.

The trophic significance of zooplankton in the foodweb of marine ecosystems depends on the concentration of the zooplankton. Fig 4. shows the concentration of zooplankton as ml/m^3 for the 25 to 0 m, 100 to 25 m, and the 600 to 100 m layers, and the overwhelming superiority of the uppermost stratum is clearly demonstrated. The data from the 100 to 25 m layer are derived by subtracting the volumes in 25—0 m from the volumes in 100—0 m. Only during January—February and November—December was the concentration of zooplankton highest below 25 m depth. Fig. 4 again demonstrates the relatively small seasonal and annual variability in the density of zooplankton in the 600 to 100 layer.

When calculating the density of zooplankton in Fig. 4 it was tacitly assumed that the biomass was evenly distributed in the 600 to 100 m layer. However, Bernard (1958) found that the biomass in the deeper water masses might be highly stratified.

PROPAGATION OF calanus finmarchicus

Calanus finmarchicus was in numbers and particularly in biomass a dominating species at station «M» (Wiborg 1954, Østvedt 1955, Beyer 1962). The developmental stage distribution of *C. finmarchicus* was determined from 1962, and the data revealed insignificant differences among years. Fig. 5 shows the average monthly means of the various developmental stages during the period 1962—1966 in the 100 to 0 m samples. The majority of the females occurred in March and April, and the copepodite stages I, II, and III were found from the middle of April to the middle of June. A second peak of females occurred from July to September. The high percentages of copepodite stage V from July throughout the autumn indicate that only a part of the stock reached maturity in July-September, and the majority of the *Calanus* stock at station «M» thus had a life span of one year.

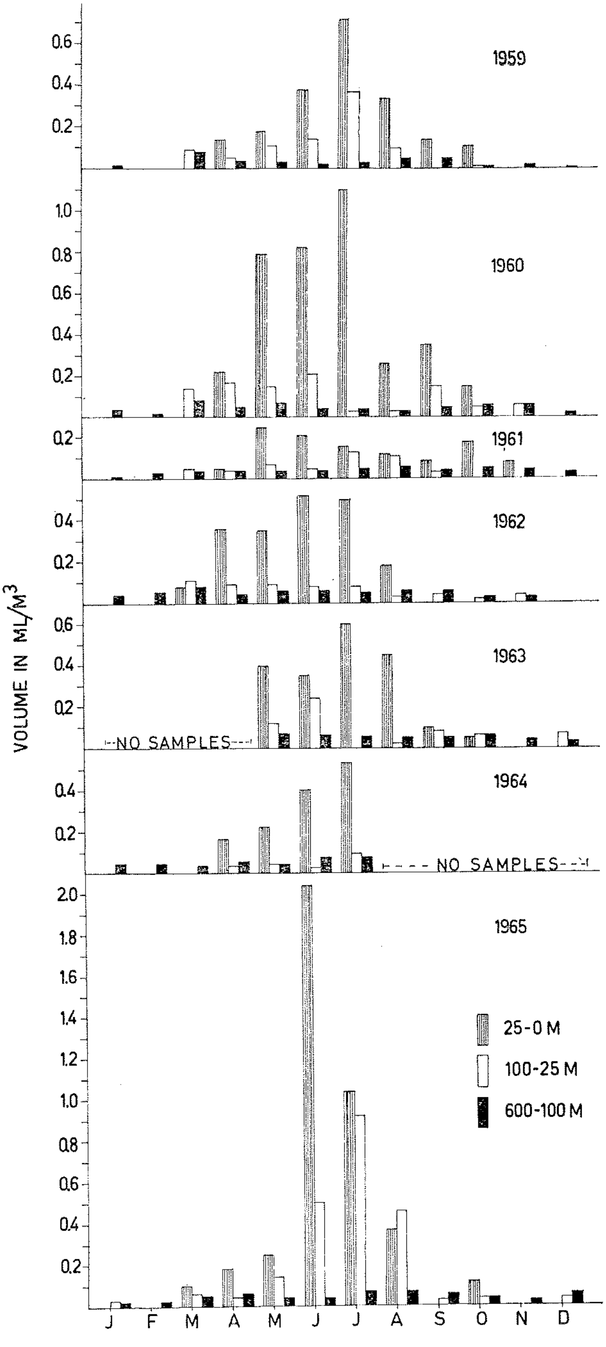

Fig. 4. Density of zooplankton in 25—0 m, 100—25 m, and 600—100 m at station «M» from 1959 to 1965.

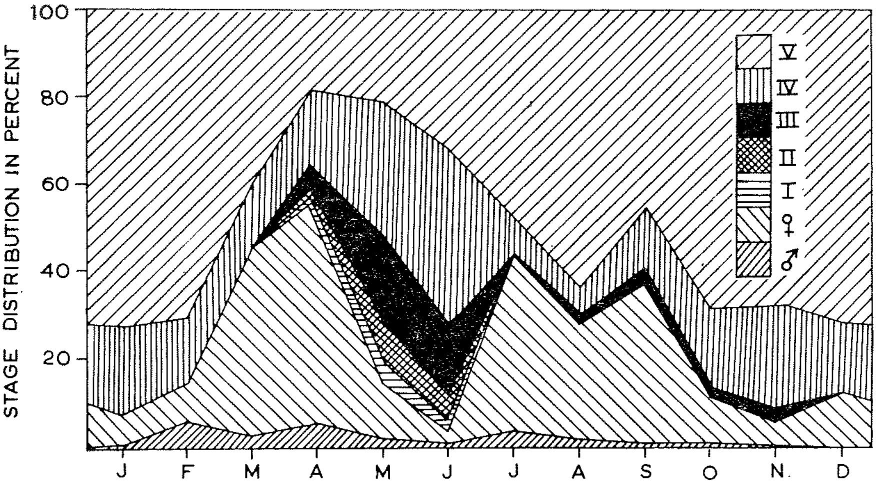

Fig. 5. Percentage distribution of males, females, and copepodite stages I—V of *Calanus finmarchicus* at station «M». Monthly mean figures 1962—1965.

These results strongly support the views on the propagation of *Calanus finmarchicus* at station «M» advocated by ØSTVEDT (1955), who also concluded that the second spawning was of minor importance. The annual variations in the developmental stage composition at station «M» and at Skrova on the northwestern coast of Norway were quite similar (LIE 1965, 1966), although the second spawning seemed to be more important at Skrova.

SUMMARY

1. From January 1959 to September 1966, 805 zooplankton samples were collected in vertical hauls from depths of 25—0 m, 100—0 m, and 600—100 m, at weather ship station «M» in the Norwegian Sea. The displacement volumes were measured, the developmental stage distribution of *Calanus finmarchicus* was determined, and the dominating species were noted.

2. Large seasonal and annual variations occurred in the volumes of zooplankton from the 100 to 0 m layer, while the volumes from the 600 to 100 m layer revealed considerable constancy. In 1965 and 1966 the plankton at station «M» appeared to be much richer and in 1961 somewhat poorer than the average for the period 1950—1966. The density of zooplankton in ml/m/ was very small in the 600 to 100 m layer while the 100 to 25 m and particularly the 25 to 0 m layer showed dense concentrations of zooplankton from April to August.

3. *Calanus finmarchicus* spawned in April and a second spawning of minor importance occurred in July—September.

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I wish to express my thanks to the meteorologists, officers and crew on the weather ships «Polarfront I» and «Polarfront II», who have collected all the material. Thanks are also due to Miss ANNLAUG HAUGSDAL and Mr. KARSTEN HANSEN for their technical assistence in measuring and sorting the samples and preparing the data for publication.

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YIELD ISOPLETHS OF THE HALIBUT, *HIPPOGLOSSUS HIPPOGLOSSUS*, IN NORTHERN NORWAY[1]

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INTRODUCTION

In late autumn and early winter halibut congregate to spawn in certain localities of the deep Norwegian fjords. Since the 1936—1937 spawning season these concentrations of fish have been exploited annually with large-meshed gill nets. These nets are usually set on the bottom between depths of 400 and 600 meters. Since the gear is highly efficient, regulations establishing a closed season and a minimum mesh size have been enforced since 1937 to conserve the stocks. There have been changes in mesh size and length of closed period, but there has never been any limitation of effort or catch.

Catches increased greatly when the gill-net fishery commenced in 1936, but they declined severely after a few years (Fig. 1). Clearly, the catches in the years 1936—1940 were in excess of the normal yield of the stocks (THOMPSON 1950) and were provided by an accumulation of large and old fish. Hostilities in 1940 to 1945 resulted in a new accumulation of fish on the grounds, and when the war ended, fishing both with gill nets and in particular with long lines was resumed on an expanded scale. Catches and stock abundance soon declined again and then stabilized. During the last 10 years they have remained at a relatively low level, and the annual yield is slightly less than 1,900 metric tons, with a value at landing of 7—8 million Norwegian krones. This pattern of stock abundance and catches was observed in the halibut fisheries of all three counties of Northern Norway, Finnmark, Troms and Nordland.

The Institute of Marine Research in Bergen, Norway, has on two occasions sponsored research on halibut. The first investigations commenced in 1936 and were stopped because of war hostilities. DEVOLD (1938 and 1943) gave the first data on catch, age composition, growth

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[1] Contribution No. 275, College of Fisheries, University of Washington.

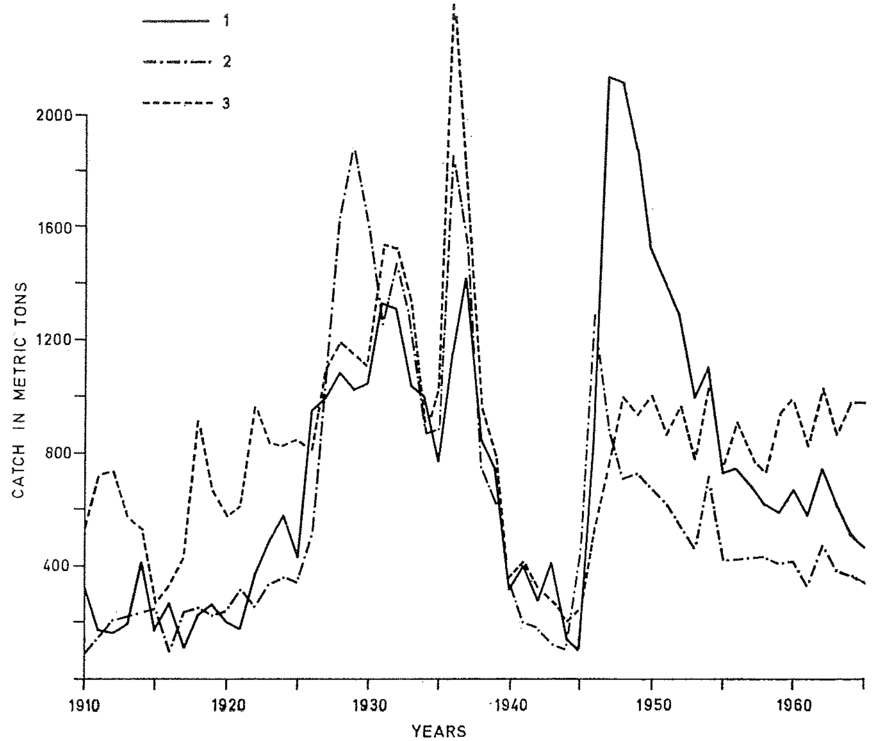

Fig. 1. Catch of halibut in Northern Norway by counties. 1) Finmark, 2) Troms, 3) Nordland.

rate and migration. In 1955 these studies were resumed and continued through 1960. Additional information was obtained by the use of experimental gill nets of varying mesh size, fished throughout the season closed to commercial fishing. The results have, in part, been published by OLSEN and TJEMSLAND (1963); but the most comprehensive account is a thesis report by TJEMSLAND (1960) in which the author attempts to establish the mesh size which will provide for the best utilization of the stocks.

The present report utilities the same basic data. There are two reasons for conducting a further analysis of the data. First, recently developed computer programs greatly facilitate the determination of growth rate and yield of a stock of fish and eliminate the previous necessity for some assumptions. Second, precise determination of the natural and fishing mortality rate, the growth rate, and above all, changes in stock abundance is not possible from existing data. These parameters are necessary to formulate a definite program for management of these fisheries so as to maintain maximum sustainable yield. A useful approach seems to be to calculate a series of yield isopleths where age at entry and fishing effort can be varied to determine intervals within which these parameters should be set to obtain a maximum yield per recruit. Another important objective is to point out areas in which further research is needed.

Analysis was performed at the Norwegian Computer Center with a Univac 1107 by the senior author, originally in preparation for a course in computer technique given at the Institute of Marine Biology at the University of Oslo, 1965—1966.

METHODS AND RESULTS

Three basic parameters are needed for any yield calculation, viz., the coefficients of the weight-length relationship for males and females; growth curves, either of length or weight, as a function of age; and mortality rates, both of natural and fishing mortality.

WEIGHT—LENGTH RELATIONSHIP

In the classical yield model developed by Beverton and Holt (1957), weight is considered a cubic function of length, primarily to facilitate manual integration. This restriction is eliminated with the use of computers. The exponent in the equation

$$W = q \cdot L^{\delta}$$

may not only be different from three, but it may also vary between male and female or between mature and immature fish.

Data on mature halibut were largely derived from catches taken with nets of 16 in. mesh. The selection range of these nets, i. e., the interval between the two «50 % selection lengths,» does not cover the size range of mature halibut. It is, therefore, reasonable to assume that the size and age composition of the catches taken with 16 in. mesh gill nets, which was the only net size used commercially prior to 1960, were biased in regard to the number of small and large fish.

The majority of the immature halibut were captured with long line. They originated from different localities in Northern Norway (Fig. 2). However, gear selection is of minor consequence since most of the size groups were represented.

Weight of the immature fish was recorded as dressed weight with the head to the nearest 10 grams, and weight of mature halibut as dressed weight without the head and to the nearest kg. Since the weight of the head represents a small fraction of total body weight in immature fish and does not influence subsequent yield calculations, the inconsi-

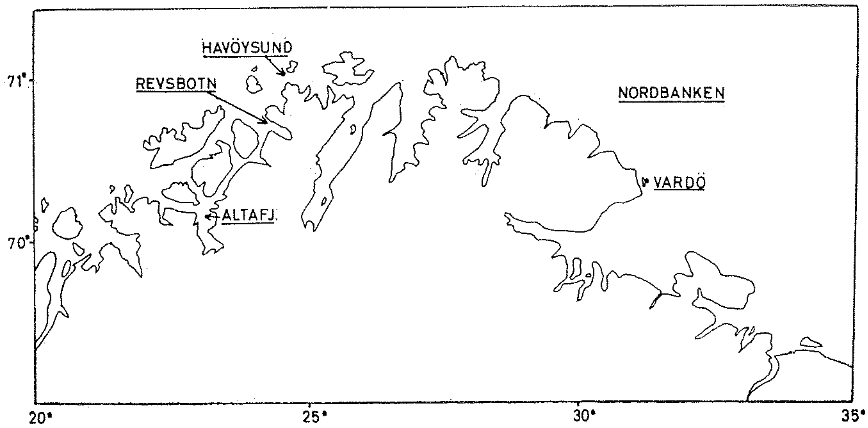

Fig. 2. Sampling localities.

stency may not be serious. Total length (distance from the tip of the head to the end of the tail) was measured to the nearest centimeter.

Table 1. Account of weight/length observations[1] on halibut, *Hippoglossus hippoglossus*, in Northern Norway.

	Location	Month	Year	Sample size	
				♂	♀
A. Immature halibut	Nordbanken	March/April	1938	65	53
	Tromsø	October	1939	383	319
	Havøysund	April	1955	59	42
	Revsbotn	May	1955	64	49
B. Mature halibut	Altafjord	Jan./Feb.	1957	990	258
	Altafjord	Jan./Feb.	1958	89	141
	Altafjord	Jan./Feb.	1959	150	162
	Altafjord	Jan./Feb.	1960	188	125

[1] An additional 744 length measurements of mature males and 93 length measurements of mature females taken at Altafjord in 1956 were used to determine growth in length.

For each of the sixteen groups of haliubt in Table 1, the two coefficients, q and δ, of the equation $W = q \cdot L^{\delta}$ were determined on the log-transformed data by linear regression. BMD program 01R (Dixon, 1965), which also permits an analysis of covariance, was used. Two hypotheses were tested: all groups have a common regression line, H_A; the different groups in the comparison have a common slope of their regression lines but with individual intercepts, H_B.

The appropriate test for hypothesis H_A is

$$F = \frac{(S_T - S_S)/(c - 1)}{S_S/(N - c - 1)}$$

where S_T is the total sum of squares around the common regression line, S_S is the sum of squares of deviations from the regression lines with common slopes, N refers to the total sample size, and c denotes the number of groups in the comparison.

For hypothesis H_B, the test is

$$F = \frac{(S_S - S_E)/(c - 1)}{S_E/(N - 2c)}$$

where S_E is the combined sum of squared deviations from individual regression lines within each group.

The results are summarized in Table 2. Hypothesis H_A was rejected consistently for all groups. Hypothesis H_B was sustained for immature males and females as well as for all mature fish combined. Although it was rejected for the mature females on the 1 % significance level, it was sustained on the 1 $^0/_{00}$ level. This was not possible for the mature males. At present it is difficult to determine whether the difference is real or whether it is an artifact caused by heterogeneity of the material and observation technique. The heterogeneity in the case of the males apparently arises from the 1958 data, which yielded a lower value than the common value given in Table 2, while the coefficients for the three other remaining years were nearly equal.

Table 2. Comparison of the regression lines of log weight/log length for different groups of halibut

Grouping	Sample size N	Regression coefficient δ	F-tests			
			Hyp. A	D.f.	Hyp. B	D.f.
All samples	3,137	3.0013	53.53**	(15, 3,120)	58.87**	(15, 3,105)
All males	1,988	2.9473	57.06**	(7, 1,979)	3.92**	(7, 1,972)
All females	1,149	3.0221	15.50**	(7, 1,140)	3.78**	(7, 1,133)
All immature halibut	1,034	3.0058	77.77**	(7, 1,025)	53.40**	(7, 1,018)
All immature males	571	2.9883	123.77**	(3, 566)	3.58	(3, 563)
All immature females	463	3.0278	57.13**	(3, 458)	0.07	(3, 455)
All mature halibut	2,103	3.2183	26.18**	(15, 2,094)	0.38	(15, 2,071)
All mature males	1,417	3.2485	40.55**	(3, 1,412)	43.39**	(3, 1,409)
All mature females	686	2.9532	11.37**	(3, 681)	4.23**	(3, 678)

** Rejection of hypothesis on the 1 % level.

For the time being it is necessary to use the regression coefficients for mature males and females determined from all data in the subsequent calculations with the reservation that later they may be modified somewhat. If one accepts hypothesis H_B, the common regression coefficient for either group can be calculated from

$$b_s = \frac{\sum_{i=1}^{c} \left[\sum_{j=1}^{n_i} X_{ij} Y_{ij} - \frac{T_i^x \cdot T_i^y}{n_i} \right]}{\sum_{i=1}^{c} \left[\sum_{j=1}^{n_i} X_{ij}^2 - \frac{(T_i^x)^2}{n_i} \right]}$$

On this basis one can determine a weight-length curve for the mature males and females. By taking the logarithm on both sides of $W = q \cdot L^{\delta}$, one obtains $\log q = \log W - \delta \log L$. Substitution of values for log L and log W yielded the results shown in Table 3.

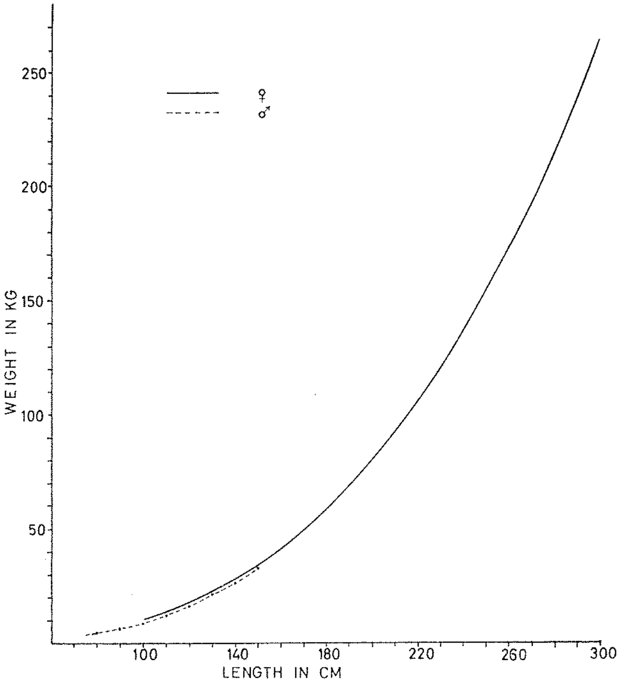

Fig. 3. Weight/length relationship of mature halibut.

Fig. 3 illustrates that despite the tremendous difference in maximal weight or length between males and females, weight as a function of length is nearly the same for males and females over the common length range, which simplifies the setting of a common lower selection size for the gill nets.

Table 3. Calculation of weight-length coefficients for mature halibut.

Sex	δ	$\text{Log}\,\overline{W}$	$\text{Log}\,\overline{L}$	$W = q \cdot L^{\delta}$
♂	3.2485	3.766	2.253	$1.295 \cdot 10^{-3} L^{3.2485}$
♀	2.9532	3.182	2.075	$2.762 \cdot 10^{-4} L^{2.9532}$

GROWTH IN LENGTH AND IN WEIGHT

A number of growth equations describe the growth of a fish as a function of age. Generally, they are derived either from the absolute or from the specific growth rate of individual fish. In observations used in this analysis age was determined from the otoliths. No backcalculations were attempted of the annual growth increments because of the great ages of the fish, which were more than 40 years for the females. Therefore, in this analysis the growth curves were derived from composite data.

SOUTHWARD and CHAPMAN (1965) applied VON BERTALANFFY'S growth-in-length curve to the Pacific halibut, *Hippoglossus stenolepis*, and found generally a very satisfactory correspondence between calculated growth increments and increments predicted from the curve itself for individual fish; but they point out that it is not certain that the average of individual growth curves will yield the same result as that derived from composite data. This condition was assumed in this analysis.

Two classes of growth curves were explored:

1. *Simple von Bertalanffy Growth-in-length Curve.*

VON BERTALANFFY (1934) first proposed the following equation to describe growth:

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

ABRAMSON'S (1965) computer program was used to estimate the parameters in the equation by a least-square technique. The method is vastly superior to methods based on the linear relationship between L_{t-1} and L_t, where errors in both variables and autocorrelation render interpretation of the results open to question. Further, all three parameters are estimated simultaneously, and the same number of observations are not necessitated for each age class. Since in this instance length at a given age was determined from actual data and not from backcalculated length data for individual fish, the method is particularly suitable.

Immature and mature fish as well as males and females were analyzed separately. The results are shown in Table 4.

Table 4. Estimated parameters for Von Bertalanffy's growth-in-length and growth-in-weight curves

Grouping	Year(s)	Sample size N	L_∞ (cm)	St. error	K	St. error	t_0	St. error
A. *Length data*								
Male, mature	1956	756	130.76	1.65	.16	.021	2.00	1.044
Male, mature	1957	1,253	131.44	1.44	.17	.019	1.85	.941
Male, mature	1956—1960	2,437	130.81	.74	.20	.012	3.68	.388
Male, mature	1957—1960	1,681	131.21	.84	.21	.014	4.21	.399
Female, mature	1956		No solution for $Z=e^{-kq}$ between .001 and .999					
Female, mature	1957		No solution for $Z=e^{-kq}$ between .001 and .999					
Female, mature	1956—1960	760	302.77	22.92	.03	.001	16.34	2.008
Female, mature	1957—1960	668	298.43	23.09	.04	.008	15.77	2.063
Male, immature	All years	—	No solution for $Z=e^{-kq}$ between .001 and .999					
Female, immature	All years	—	No solution for $Z=e^{-kq}$ between .001 and .999					
B. *Weight data*			W_∞ (kg)					
Male, mature	1957—1960	1,660	37.52	8.01	.047	.018	4.44	1.211
Female, mature	1957—1960	657	249.97	57.99	.025	.008	—2.63	.724

Mature males measured included fish from age 8 through age 31. Parameters were calculated in every case regardless of whether observations for all years were combined or observations for individual years were considered alone. Age readings are highly comparable between years; age determinations in 1956 and 1957 were made by two different people, yet the final curves for these two years are almost identical.

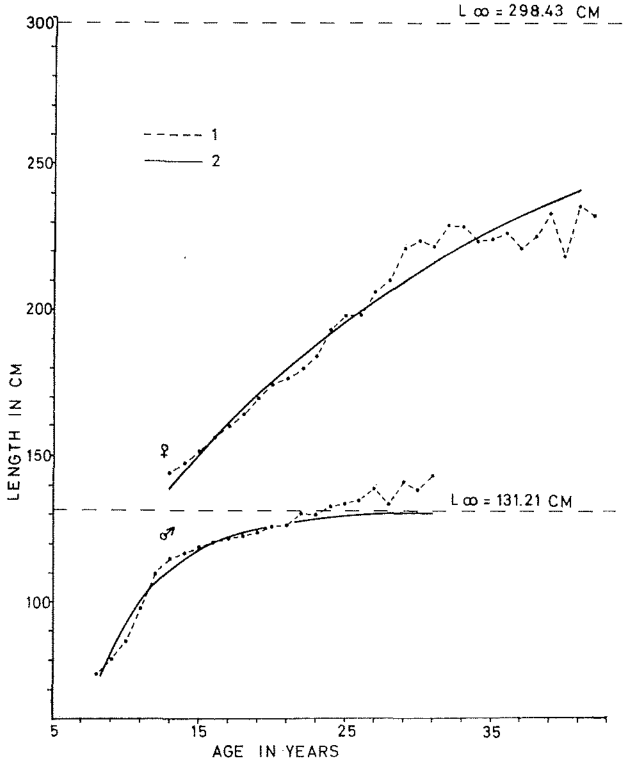

Fig. 4. von Bertalanffy's growth-in-length curves for mature halibut: female (top), and male (bottom). 1) Observed growth curve 1957—1960, 2) Estimated growth curve 1957—1960.

The estimated curve fits observed data on the males (Fig. 4, bottom), but the value of L_∞ obtained for the females is much higher than even the highest value recorded in the material examined (Fig. 4, top). The growth pattern of the two sexes differs decidedly. Mature males attain their maximum size relatively early, their growth rate retards drastically after age 12 or age 13. Mature females maintain their initial growth rate for a much longer period and retardation of their growth rate is less. The physiological difference manifested is worthy of intensive furure studies.

The question remains as to the validity of the high value determined for L_∞ for the females. The recruitment of mature females into the fishery commences at age 11 to age 13 and apparently terminates before age 20. Since only the faster growing individuals are available for exploitation at first and the samples are representative only of a restricted number of age classes, the left limb of the growth curve is inflated. The discrepancy between the calculated maximum size and the observed maximum size may be due to the females not living long enough to attain such size or the selectivity of the nets.

It is important that no solution of the equation was possible for the females when the years 1956 and 1957 were considered alone, nor for the immatures, both males and females. The latter could have been anticipated since only age classes 2 through 11 were represented, ages with a rapid, almost exponential growth pattern.

A more general form of von Bertalanffy's growth-in-length curve was calculated and plotted to incorporate data on both immature and mature halibut.

2. *Extended von Bertalanffy Growth Curve*

As discussed by Richards (1959) and Chapman (1960), a four-parameter growth equation may be obtained by starting from the general differential equation

$$\frac{dw}{dt} = H \cdot w^m - k \cdot w$$

where H and k are coefficients of anabolism and catabolism, respectively, and m is the rate of change between metabolic rate and weight. Integration of this equation with a weight-length relationship of the form $W = q \cdot L^\delta$ will lead to a von Bertalanffy equation of the following form (Chapman, 1960):

$$L_t^{1-m} = L_\infty^{1-m} - (L_\infty^{1-m} - L_0^{1-m}) e^{-K(1-m)t}$$

To estimate the four parameters L_∞, L_0, K, and m by minimizing the sum of squared deviations of observed points from estimated points is indeed a formidable task by manual methods. However, a recently developed computer program by K. J. Turnbull (1964) achieves this in a rather short time provided the growth data over the entire life span conforms to a sigmoid pattern. The solution is of the form

$$L_t = A \cdot (1.0 + B\, e^{-Kt})^{\frac{1}{1-m}}$$

Table 5. Mean lengths and weights of immature and mature halibut combined, males and females.

			♂		♀		♂		♀
Time scale t:	True age (years)	Number observations	Mean length (cm)	Number observations	Mean length (cm)	Number observations	Mean weight (kg)	Number observations	Mean weight (kg)
1	2.5	357	43.6	305	43.9	358	.82	305	.84
2	4.5	87	53.5	67	54.9	34	1.50	22	1.96
3	6.5	214	63.3	205	65.2	114	2.72	106	2.94
4	8.5	89	77.9	43	80.6	75	4.49	32	5.68
5	10.5	86	94.1	7	107.7	67	7.32	4	19.68
6	12.5	228	111.3	30	143.3	167	13.14	26	29.92
7	14.5	264	116.5	72	149.0	214	14.89	68	33.99
8	16.5	372	120.2	98	159.0	253	16.32	87	41.08
9	18.5	520	122.5	92	165.0	357	17.86	74	48.67
10	20.5	483	125.0	108	174.3	313	19.06	86	56.97
11	22.5	271	129.1	114	180.7	178	21.64	102	64.54
12	24.5	128	131.2	82	196.4	88	24.69	78	79.05
13	26.5	41	133.4	50	202.8	22	24.23	47	91.55
14	28.5	11	131.5	32	213.2	6	26.00	30	97.59
15	30.5	13	130.6	26	222.8	6	26.00	25	115.12
16	32.5			17	229.1			16	118.62
17	34.5			20	224.1			18	115.95
18	36.5			8	217.8			6	109.33
19	38.5			8	230.0			7	129.85
20	40.5			9	227.8			7	109.42

Table 6. Parameter values for CHAPMAN-RICHARD's general growth equation, rescaled.

	Scale factor	L_∞	B	K	m	K/m	K/(2m+2)	Rescales growth equation
A. Length data	1/6	21.800	30.724	.634	3.505	.181	.070	$l_t = 130.80\,[1.0 + 30.72e^{-.63t}]^{\frac{1}{1-3.51}}$
	1/10	23.810	—.095	.206	.956	.215	.063	$l_t = 238.10\,[1.0 - .095e^{-.22t}]^{\frac{1}{1-.96}}$
		W_∞ (kg)						
B. Weight data	1/1	29.388	—1.028	.222	.674	.33	.66	$W_t = 29.39\,[1.0 - 1.03e^{-.22t}]^{\frac{1}{1-.67}}$
	1/4	34.665	—.655	.186	.866	.21	.49	$W_t = 138.67\,[1.0 + .66e^{-.19t}]^{\frac{1}{1-.87}}$

The procedure consisted of finding the mean length within each of age classes 2 through 31. Because of program limitation, it became necessary to scale the lengths of the males by multiplication with a factor k = 1/6 and to average the lengths of two and two adjacent year classes. Thus the time unit t corresponds to the true age of 2.5 years with an increment of 2 years. Essentially the same was done for the females except that the timespan ranged from age 2 through age 41 and the scale factor used was k = 1/10.

The basic length data are presented in Table 5 and the parameter values are summarized in Table 6, rescaled to original values (Fig. 5). The curve for the male halibut almost follows a pure Gompertz growth curve and that of the female halibut is related more to a logistic curve. Nevertheless, the mean relative growth rate, K/m, and the weighted mean growth rate, K/(2m + 2), after the interpretation by Richards (1959), are nearly the same for the sexes.

The main interest lies in asymptotic lengths. In the case of the males there is hardly any difference from the value obtained by fitting the

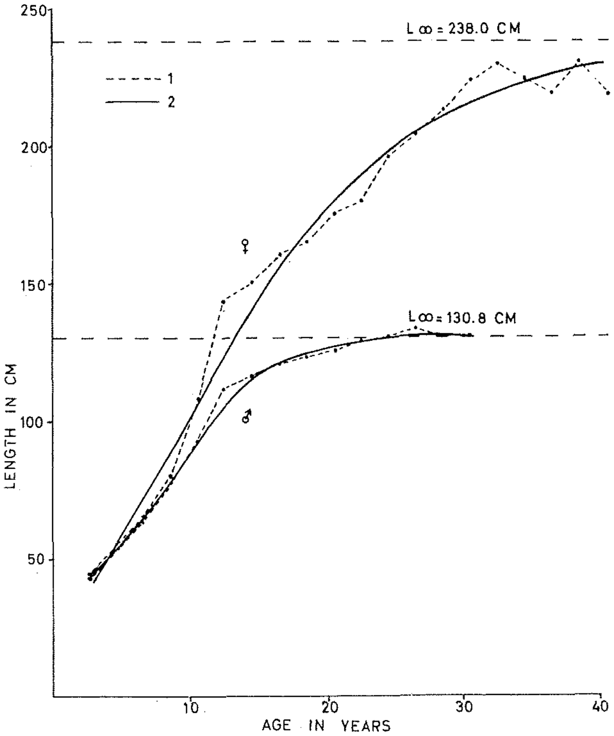

Fig. 5. Chapman-Richard's growth-in-length curve for mature halibut: female (top), and male (bottom). 1) Observed growth curve 1956—1960, 2) Estimated growth curve 1956—1960.

classical von Bertalanffy curve to the data, but in the case of the females L_∞ is about 60 cm less than the value estimated earlier. The choice between these two values can be facilitated by considering the weight data.

Growth-in-weight Curves

Since very few weight measurements were taken in 1956, the growth curve was based on data for the years 1957—1960. For the males the year classes 8 through 31 and for the females the age classes from 13 through 24 were well enough represented for the data to fit a standard von Bertalanffy growth-in-weight curve. The results are summarized at the bottom of Table 4 and illustrated in Fig 6.

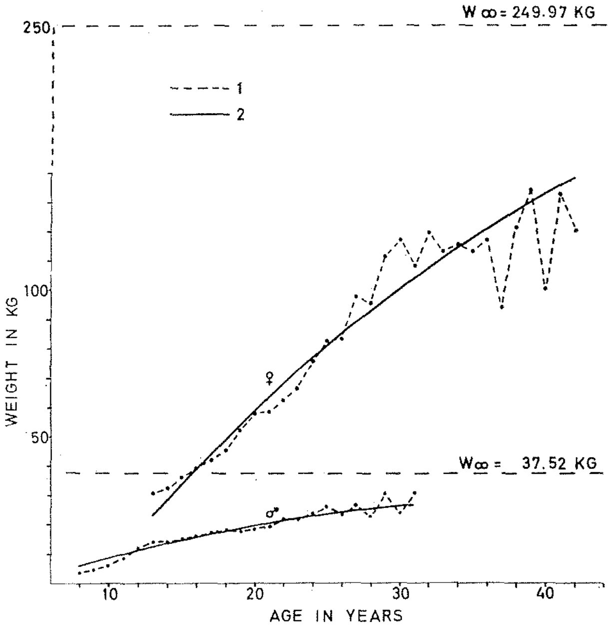

Fig. 6. von Bertalanffy's growth-in-weight curve for mature halibut: female (top), and male (bottom), 1) Observed growht curve 1957—1960, 2) Estimated growth curve 1957—1960.

The value of W_∞ for the males accords with the observed weight of the largest and oldest male halibut; but, as was the case with length, the value for the females approaches the highest weight recorded of single, exceptional individuals. It was, therefore, natural to determine the same parameter values by means of Chapman-Richard's version of the growth-in-weight curve. The results are summarized at the bottom of Table 6 and illustrated in Fig. 7.

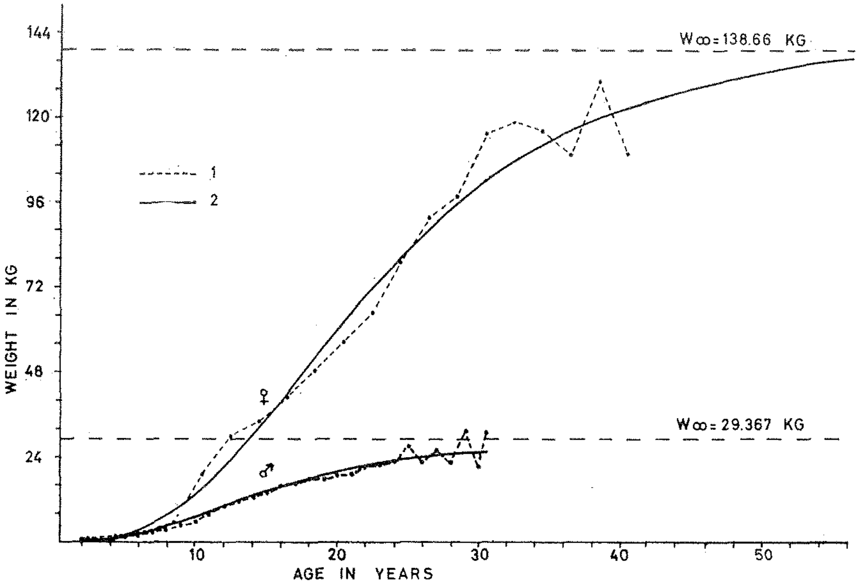

Fig. 7. CHAPMAN-RICHARD's growth-in-weight curve for mature halibut: female (top), and male (bottom). 1) Observed, 2) Estimated.

The value of m for the males equals almost 2/3, as suggested by VON BERTALANFFY (1934). The mean absolute growth rate, K/m, and mean relative growth rate, K/2(m—1), fall within the ranges given by SOUTHWARD and CHAPMAN (1965) for the Pacific halibut. Thus the two species of halibut conform to the same pattern of growth despite their widely separated ranges. The identity of the patterns is especially striking since SOUTHWARD and CHAPMAN derived their parameter estimates from backcalculated data for individual fish.

On the strength of this similarity, the values of L_{∞} and W_{∞} for the Finmark halibut derived from the generalized CHAPMAN-RICHARD's growth equation and based on average length or weight data within a year class were used in the subsequent yield calculations. The asymptotic values then conform more closely to the maximum values for length and weight usually observed. Greater precision can hardly be expected until backcalculated growth data are available for individual fish.

MORTALITY RATES

The reliability of any yield calculation depends greatly on the accurate assessment of the instantaneous natural mortality rate, M, and the applied instantaneous fishing mortality rate, F, throughout the lifespan of the fish. Very few tagging experiments have been conducted, and the observations are of little value in a separation of F and M.

The only recourse is to estimate the total instantaneous mortality, $Z = F + M$, from the composite catch curve interpreted with some caution. It is inconceivable that recruitment would remain constant in the examined halibut stock with about 30 year classes represented. However, constant recruitment is a necessary condition in any estimate of mortality from the age distribution of the total catch in one year. As an alternative one could examine changes in abundance of the same year class over the period 1956—1960 provided that the effort remained constant.

The situation is commonly encountered in practical fisheries investigations. However, with modern computer techniques yield computations can be made over a wide range of assumed values within which the true parameter values in all probability will fall. Hence, one can define an area on the yield surface encompassing the true parameter value. Frequently this suffices as a basis in formulating a rational management scheme.

The combined catch curves for males or females for the years 1956 to 1960 were analyzed in different ways by relaxing certain assumptions, as discussed by Chapman and Robson (1960) and Robson and Chapman

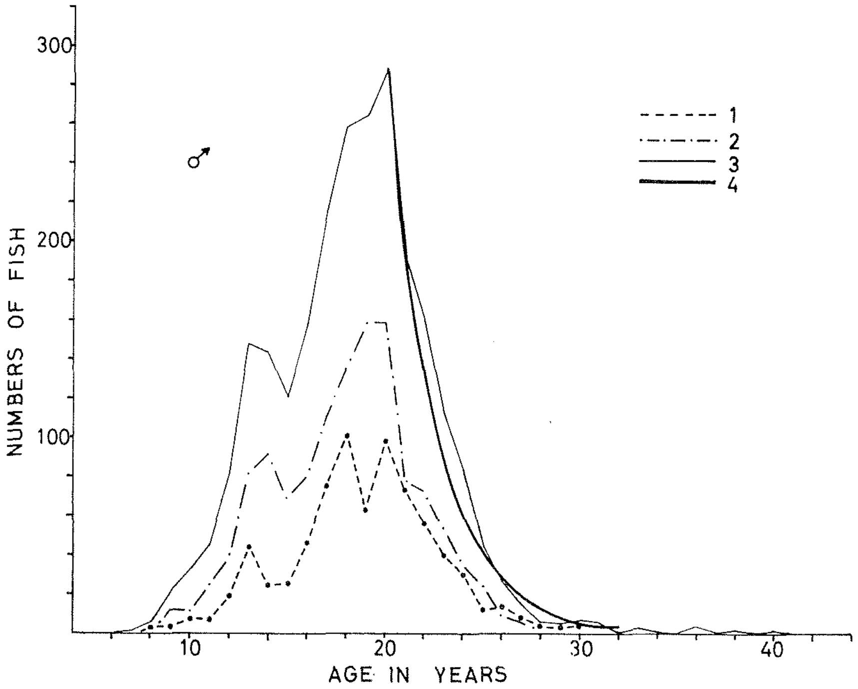

Fig. 8. Catch curves for male halibut. 1) Catch curve 1956, 2) Catch curve 1957, 3) Catch curve 1956—1960, 4) Estimated survival curve.

(1961). GALES' (1964a) computer program was used to study four alternatives:

1. calculation of total instantaneous mortality from the observed total catch curve using an age of full recruitment to the left of the peak of the catch curve,
2. testing by means of a chi-square test if the assumed age of full recruitment can be sustained, and if not, at which age this took place,
3. telescoping of the older age groups on the assumption that age determination may become progressively more difficult with increasing age,
4. exploration of segments of the catch curve to include sections with fully recruited age groups exposed to the same fishing mortality.

The catch data are depicted in Figs. 8 and 9 and the obtained Z-values listed in Table 7.

Recruitment of the males into the fishery begins in the eighth year of life, when length is about 75 cm and terminates before the twentieth year, when length ranges from 123 to 126 cm. At this age growth-in-length has been largely completed and the effect of mesh selection will not change materially with increasing age. Hence, a reasonable estimate of total mortality can be derived from the catches from age 20 on.

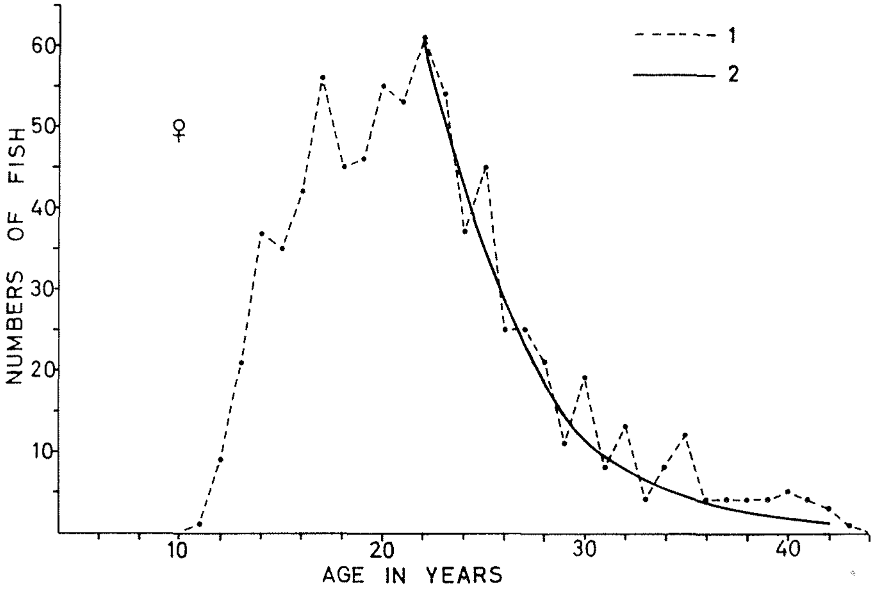

Fig. 9. Catch curve for female halibut. 1) Catch curve 1956—1960, 2) Estimated survival curve.

Table 7. Estimated total instantaneous mortality coefficients for halibut, from the original catch data and from catch data adjusted for the effect of mesh selection.

Years	Source	Z	95 % confidence interval of Z
	A. *Original catch data* ♂		
1956—60	Age at full recruitment 18 years	.30	.287 — .319
1956—60	Age at full recruitment determined to be 20 years	.39	.364 — .415
1956—60	Ages ≥ 31 combined	.39	.365 — .417
1956—60	Ages 20—28 only.........................	.38	.349 — .415
1956	Age at full recruitment 20 years	.38	.337 — .420
1957	Age at full recruitment 20 years	.45	.404 — .490
	B. *Adjusted catch data* ♂		
1956—60	Age at full recruitment 18 years	.38	.350 — .415
1956—60	Age at full recruitment determined to be 20 years	.39	.364 — .415
	C. *Original catch data* ♀		
1956—60	Age at full recruitment 17 years	.14	.128 — .150
1956—60	Age at full recruitment determined to be 22 years	.18	.165 — .204
1956—60	Ages ≥ 31 combined	.18	.160 — .202
1956—60	Ages 20—22	.23	.056 — .464
1956—60	Ages 25—29	.29	.169 — .436
1956—60	Ages 25—31	.24	.156 — .330
	D. *Adjusted catch data* ♀		
1956—60	Age at full recruitment 22 years	.16	.161 — .163
1956—60	Age at full recruitment determined to be 28 years	.18	.175 — .180

This was done, first, by setting the full recruitment age a little lower, at age 18; second, by combining the catches of all fish 31 years or more, and, third, by using only the catch vector from age 20 through age 28. In all cases the total instantaneous mortality was found to be of the same magnitude and the value of Z about .39 (Table 7).

The situation was less clear for the females. Apparently full recruitment is completed from ages 17 to 22 years, during which length ranges from 160 to 180 cm, which is in the upper selection range of the 16-in. gill nets.

The right limb of the female catch curve was first examined. With initial full recruitment at age 17, the total instantaneous mortality, Z, was calculated and the value found to be .14 (Table 7). Application of the chi-square test established the age of full recruitment at 22 years with Z = .18. The same result was obtained by telescoping all ages from age 31. Various segments of the catch curve, viz., ages 20—22, ages 25—29, and ages 25—31, yielded somewhat higher estimates, but with an associated higher variance, and broader confidence intervals (Table 7).

An attempt was made to adjust for the bias introduced by the selectivity of the gill nets. From the data on number of fish caught per length interval, OLSEN and TJEMSLAND (1963) established a set of selection curves for halibut gill nets. These were used to adjust the catch curve according to the procedure used by OLSEN (1959) for herring in Newfoundland waters. The mortality estimates derived from the adjusted data are given in Table 7. For both males and females the adjustments resulted in reduced estimates of Z, but the differences were rather small in all cases. Thus, there is a suggestion that the slope of the right-hand portions of the catch curves is too abrupt. Because of the small magnitude of this bias, the scantiness of the material from which the selection curves were derived, and the variance in the mortality estimates introduced by the adjustments, there is little reason to prefer these estimates to those derived from the original data.

In this event the total instantaneous mortality of the males may be set tentatively equal to .39; and of the females equal to .18. Assuming further that the natural mortality, M, during the exploited phase is the same for both sexes and constant from year to year, we have $F♂ + M = .39$, $F♀ + M = .18$, which gives the relationship $F♂ = .21 + F♀$, or that the instantaneous fishing mortality rate of males with the gear combination utilized was .21 higher than that for the females. It further places an upper limit of .18 on the natural instantaneous mortality.

This difference could stem from two causes. Since $F = c \cdot f$, with c as the catchability coefficient and f equal to the number of effort units, a real difference exists. But the magnitude of this difference allows for a difference in vulnerability to the gill nets between males and females caused by differences in behavior.

The right limbs of the examined catch curves represent the numbers of halibut twenty years of age or more in the catches. However, certain age groups, especially among the females, were subjected to a low fishing mortality during the years 1940—1945. Throughout their fishable lifespan these groups must have been overrepresented in the catches in relation to the younger year classes for the years studied; the younger year classes were heavily exploited by long lines after 1945. The net effect is a flattening of the right limbs of the age curves in Figs. 8 and 9. Hence, the calculated mortality rates should be considered minimum values. In the absence of suiable data for establishment of an upper bound for total mortality rate, an approximation is made in the subsequent chapter by comparing rates obtained for other stocks of halibut.

YIELD ISOPLETHS

Beverton and Holt (1957) divide the life of a fish into two principal periods. One covers recruitment to the fishing grounds and extends from time t_p to $t_{p'}$. The other includes the fishable lifespan from time $t_{p'}$ to t_λ, when the fish either die or reach a size outside the selection range of commercial gear. Throughout both periods natural mortality, M, operates and decreases the original number of recruits, R, in an exponential manner. A variable fishing mortality, F, applied either throughout the entire fishable lifespan or within preset time intervals further reduces the number of recruits.

The harvestable yield is further determined by the parameters W_∞, K, and t_0 of von Bertalanffy's growth equation and the exponent δ of the weight-length relationship. On these premises and with the notation given above, the yield from R recruits may be calculated from

$$Y_w = \int_{t_{p'}}^{t_\lambda} FRe^{-M(t_{p'}-t_p)}\, e^{-(F+M)(t-t_{p'})}\, qL_\infty{}^{\delta} \quad (1-e^{-K(t-t_0)})\delta\, dt$$

Jones (1957) and, later, Paulik and Gales (1964) have transformed this equation into an incomplete beta function and prepared a computer program to solve the Beverton and Hol yiel equation (Gales 1963). After the appropriate transformation, the equation will be

$$Y_w = (F/K)\ RW_\infty e^{-M(t_{p'}-t_p)}\, e^{(F+M)(t_{p'}-t_0)} \int_{e^{-K(t_\lambda-t_0)}}^{e^{-K(t_{p'}-t_0)}} X^{\frac{F+M}{K}-1} (1-x)^{\delta}\ dx$$

This program was utilized to construct yield isopleths for males and females individually where both $t_{p'}$, and F can be varied.

The parameter values utilized are:

t_p = 6 years
$t_{p'}$ = range 6—31 years with increments of one year
t_λ = 35 years for the males and 45 years for the females
F = range 0.0—2.0 with increments of 0.1
R = 1
M = 0.05, 0.10, 0.15

The remaining parameter values were taken from the Chapman-Richard's growth-in-weight function, some of which were substituted with data from Table 6 (Table 8). From the calculated yields, Figs. 10—11 were prepared.

Table 8. Parameter values used for yield calculation with CHAPMAN-RICHARD's growth-in-weight function

Parameter	♂	♀
$\delta = \frac{1}{1 - m}$	$\frac{1}{1 - 0.674} = 3.10$	$\frac{1}{1 - 0.866} = 7.48$
K	0.222	0.186
$t_0 = \frac{\ln B}{K}$	$\frac{0.0276}{0.222} = 0.124$	$\frac{-0.424}{0.186} = -2.279$
W_∞	29.388	138.67

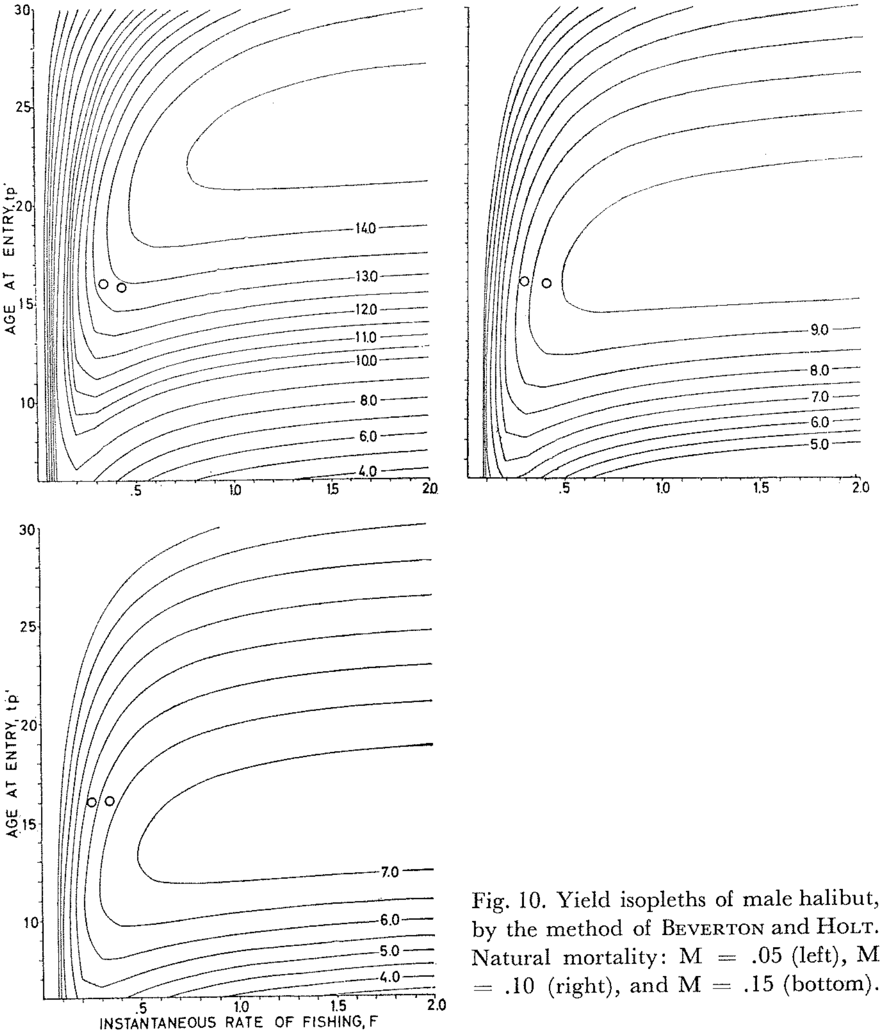

Fig. 10. Yield isopleths of male halibut, by the method of BEVERTON and HOLT. Natural mortality: M = .05 (left), M = .10 (right), and M = .15 (bottom).

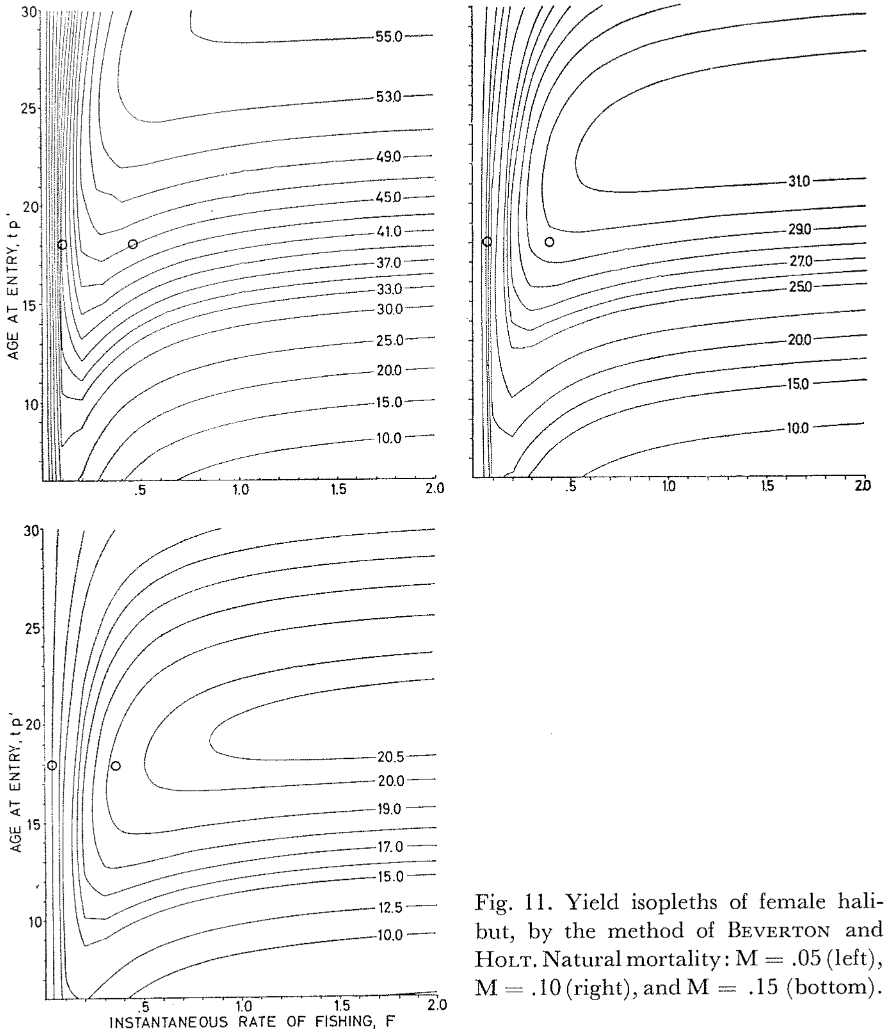

Fig. 11. Yield isopleths of female halibut, by the method of Beverton and Holt. Natural mortality: M = .05 (left), M = .10 (right), and M = .15 (bottom).

The yield isopleths have in common a very steep gradient of response surface for low fishing intensities. They all conform to the usual pattern, with the maximum yield reached at a higher age of entry, $t_{p'}$, and higher instantaneous fishing rate, F, as the natural mortality decreases. The areas of maximal yields are broad and domeshaped and vary between males and females. Therefore, they do not afford a sharp definition of optimum fishing strategy. Ideally, isopleths should be constructed for the combined yield of males and females. Since at present it is not certain that natural mortality is identical for the sexes and since the same amount of gear will not generate the same instantaneous rate of fishing on males and females, their construction must be deferred until the necessary data are available. If one assumes that males and females are recruited into the fishery in the same proportion, fishing should be adjusted largely to maximize the yield of the females.

The effect of the fishery as it is conducted today can be evaluated by assuming more than 50 % recruitment at an age of 16 years for the males and 18 years for the females, and a total instantaneous mortality, Z, of .39 for the males and .18 for the females. These lattice points are indicated by circles in Figs. 10—11.

A second set of lattice points has been drawn corresponding to a total mortality of $Z = .5$, approximately the rate estimated for the Pacific halibut (ANON., 1960). The best estimate of natural mortality, M, in the principal areas, Area 2 and Area 3, was .20. In Area 2 the best estimate of current fishing mortality, F, was .30, while in Area 3 the estimate from age composition was .25, and from catch statistics .60.

In all probability one can assume that the natural mortality is less for the halibut stock in Altafjord than for the halibut stock on the Pacific Coast of North America because of the presence of a substantial number of very old fish.

With these two points as the upper and lower bounds for total mortality, a doubling or tripling of the fishing effort will bring about only a slight increase in the yield per male recruit (Fig. 10).

The yield per female recruit increases rapidly from the lower to the upper bound of total mortality, Z. This is true for all three levels of natural mortality considered here. Beyond the upper bound an increase in fishing mortality has minor effect on the yield per recruit.

Should the natural mortality, M, be as low as .05, then the present age of entry into the fishery would be decidedly too low and a substantial increase in yield would materialize from increasing both $t_{p'}$ and F. The same would be true for the yield per male recruit although to a lesser extent.

Thus, the proper evaluation of a management program depends on the precision of the estimates of natural and fishing mortality. This is illustrated for the natural mortality in Fig. 12, where the yield is drawn as a function of $t_{p'}$ for four different values of M. Fishing mortality has been adjusted to give a total mortality of $Z = 0.39$ for the males and $Z = 0.18$ for the females. All these curves are rather flat, and a wide range of values for $t_{p'}$ around the peak will result in yields of about the same magnitude. If it is assumed that the total mortality is a precise estimate, then the yield is primarily a function of natural mortality.

It is also possible that the natural mortality rate differs between males and females; less for the females and probably decreasing with age. An

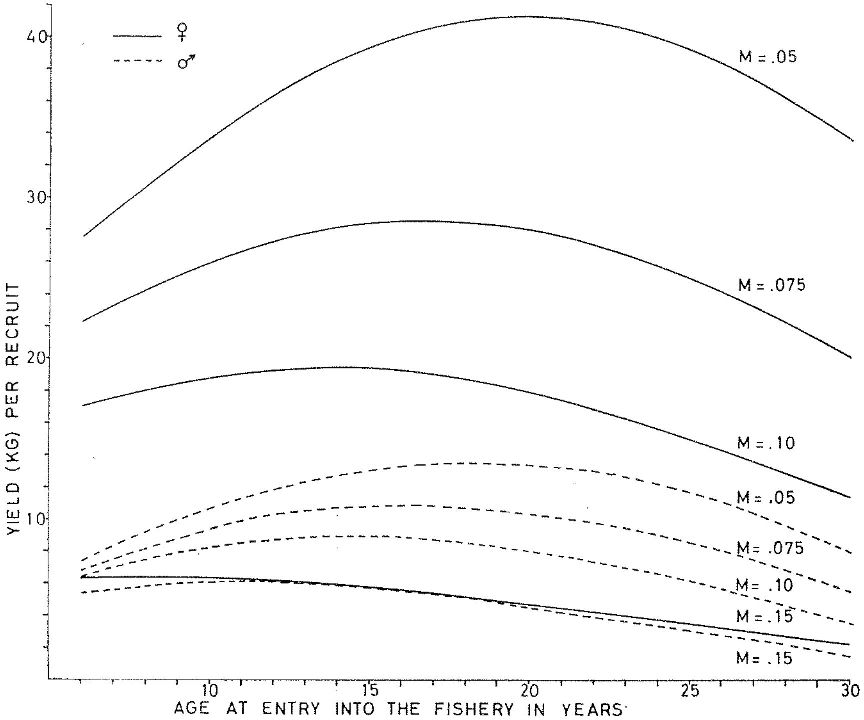

Fig. 12. Yield per female and male halibut recruit with different age at entry into fishery.

accurate assessment of this parameter should be undertaken in future investigations of these stocks of halibut. These tentative estimates serve to define the range of total mortality within which isopleths are most useful to management yield.

The preceding calculations were based on parameters obtained from a growth-in-length or growth-in-weight function fitted to observed length or weight data. A knife-edged selection of the stock was assumed despite the nature of the gear and the body proportions of the fish.

A different set of yield isopleths can be constructed after a method suggested by Ricker (1958) whereby yield is computed from the arithmetic mean of the observed weight at the beginning and at the end of each year throughout the fishable lifespan of a fish. Thus, a series of linear interpolations are made over the relatively short period of one year.

A computer grogram was prepared by Paulik and Bayliff (1967) and Gales (1964b) for this purpose. Provisions are made for introducing multipliers so that yield can be computed for any desired fishing mortality

Table 9. Mean weights and fishing rates[1] of halibut, used for computation of yield isopleths

Age	♂		♀	
	Mean weight (kg)	Instantaneous rate of fishing	Mean weight (kg)	Instantaneous rate of fishing
7	3.31	.04	5.01	.04
8	4.01	.12	6.96	.07
9	5.15	.22	7.35	.14
10	6.02	.36	32.00	.26
11	8.20	.58	28.00	.42
12	12.17	.67	30.78	.59
13	13.72	.81	32.22	.76
14	14.53	.89	35.99	.87
15	15.34	.95	39.56	.93
16	15.94	1.00	42.19	.96
17	16.62	1.00	45.14	.99
18	18.01	1.00	51.88	1.00
19	17.79	1.00	56.86	1.00
20	18.85	1.00	57.09	1.00
21	19.39	1.00	62.59	1.00
22	21.71	1.00	66.58	1.00
23	21.53	1.00	77.26	1.00
24	23.32	1.00	80.51	1.00
25	27.09	1.00	84.54	1.00
26	23.27	1.00	97.72	1.00
27	26.29	1.00	90.55	1.00
28	23.50	1.00	111.70	1.00
29	31.00	1.00	117.60	1.00
30	21.33	1.00	108.70	1.00
31	30.67	1.00	120.30	1.00
32			120.30	1.00
33			115.00	.9
34			116.50	.8
35			117.00	.7
36			101.70	.6
37			121.30	.5
38			134.30	.4
39			100.00	.3
40			138.50	.2
41			120.50	.1

[1] Multipliers for the basic instantaneous rate of fishing, F = 1.0, were initially 1. with increments of .1 to a maximum of 2.0.

for each year in the fishable lifespan of the fish. In this manner the actual recruitment curve is simulated.

The observed mean weights for males and females are listed in

Table 9. Recruitment curves were aproximated from the catch curves in Figs. 8 and 9 and also from selection curves constructed from the catches of the three sizes of experimental gill nets.

For the males, recruitment into the fishery was assumed to commence at age 7 and to terminate at age 16. This was simulated by increasing the efficiency of the basic instantaneous rate of fishing, F = 1.0, in the manner indicated in Table 9. For the females, recruitment wass assumed to commence at age 8 and to terminate at age 18. The increase in the efficiency of the fishing gear during this period simulates this prolonged recruitment.

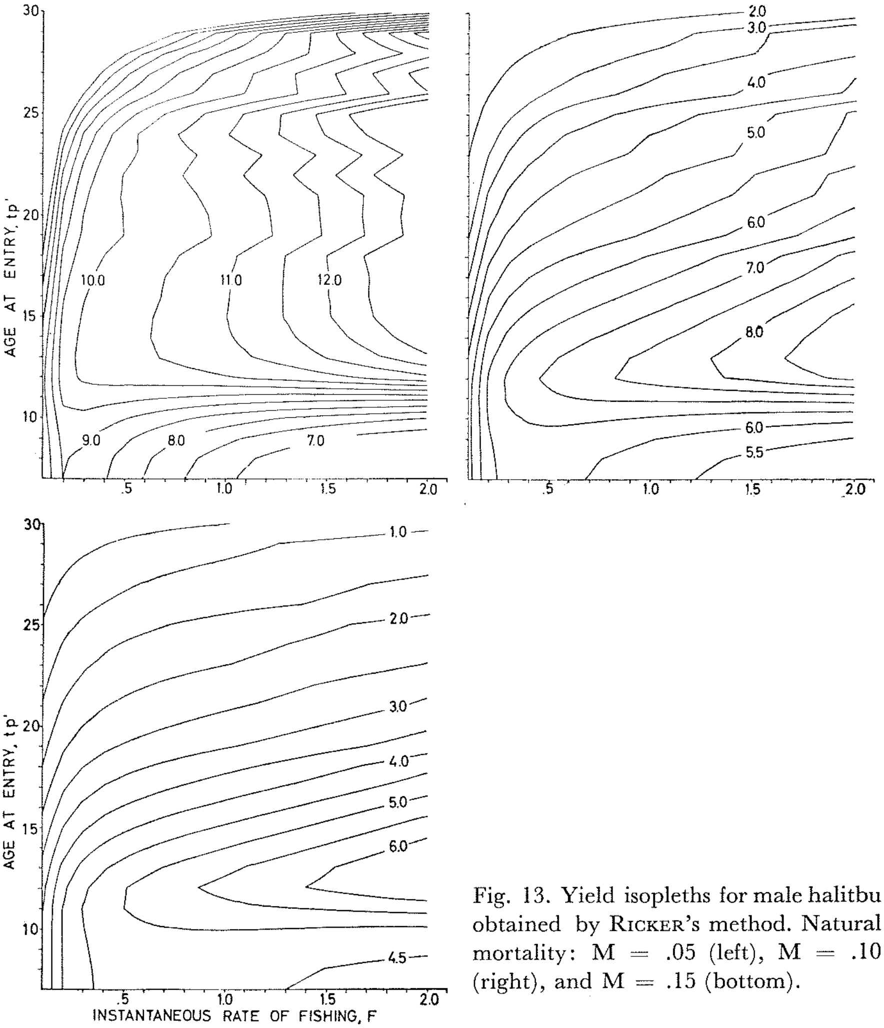

Fig. 13. Yield isopleths for male halitbu obtained by RICKER's method. Natural mortality: M = .05 (left), M = .10 (right), and M = .15 (bottom).

Gill nets place also an upper selection curve or recruitment away from the fishery. This was shown by a linear decrease in effective fishing power from age 28 to age 41 for the females, and exclusion from the fishable stock of any succeeding age classes.

The instantaneous rate of fishing at full efficiency was varied in steps from F = .1 to F = 2.0 with even increments of .1.

The age at entry into the fishery was likewise varied with even increments of one year, commencing at age 7 and ending at age 30 for the males. For the females the corresponding ages were ages 8 and 34.

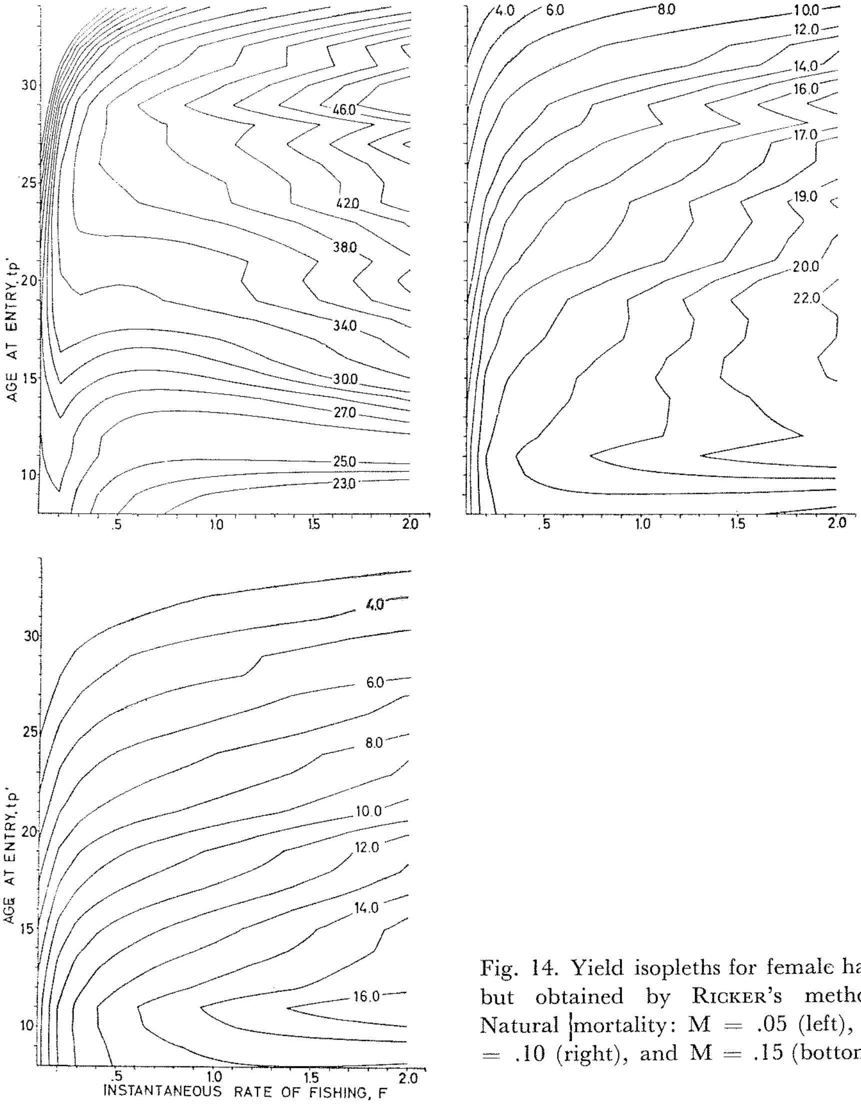

Fig. 14. Yield isopleths for female halibut obtained by Ricker's method. Natural mortality: M = .05 (left), M = .10 (right), and M = .15 (bottom).

The results are depicted in Figs. 13—14. The irregularities of the contour lines, which are especially sharp in the instance of low natural mortality, are caused by inaccuracies in observed weights. On several occasions there were recorded decreases in average weight from one year to the next, which would disappear with a larger number of observations.

The yield curves show lower over-all values than those seen in Figs. 10—11 because of the adjustment of effective fishing effort during the recruitment phase, and, in case of the females, because also of the withdrawal from the fishable stocks of the very old and large females. The response surfaces emerging in this case are somewhat different from that of the previous yield calculations. If the natural mortality, M, were in the range .10 to .15, a higher yield would be realized from both male and female recruits by increasing the fishing effort many times over the presumed present effort. The same would be true, particularly in regard to yield per female recruit, if the natural mortality were as low as .05 provided the age of entry were delayed.

DISCUSSION

The formulation of a definite strategy for management of the halibut fishery in Northern Norway should await corroborative evidence from changes in stock size as measured in catch per unit of effort. But the available material allows one to explore different possibilities.

A more precise definition of W_∞ is needed. The two computed values, one derived from von Bertalanffy's equation and the other from Chapman-Richard's formula, differ substantially. Although the latter seems to be more precise than the former on the basis of the present material, it may only hold true for the exploited stock.

There are other reasons to believe that a W_∞ of about 163 kg dressed weight is too low for the females, even if about 15 % is added to compensate for undressed weights. Larger females are frequently caught, and weights up to 333 kg have been recorded (Ehrenbaum, 1936). However, a higher value for W_∞, which only enters into the yield calculations as a multiplying factor, will only raise the values of the contour lines.

More troublesome is the uncertainty connected with the value assigned to natural mortality. The data for the present analysis were collected at a time when the fishery was intensifying, and when it was operating on stocks that had accumulated over five years. The total mortality determined from catch curves may therefore represent transitional rather than stable values. Because of the high age at entry into the fishery and the long lifespan of the halibut in Northern Norway, the period of transition must have been rather extended.

Collection of field data terminated in 1960. There is need for a reassessment of the catch curve now that the recruitment is derived from a parent population which has been fully exposed to a more even fishing pressure. At the same time a study should be made of the efficiency of different types of gill nets converted to standard units of effort. Only then can relative estimates of changes in stock size be obtained.

The present study has shown considerations essential to the rational management of the halibut stocks in Northern Norway. One is the need for a continuous set of observations on age composition and effort to obtain measure of changes in stock size. The expense involved would be relatively small compared to the possible gains. The halibut stocks in Northern Norway are to a greater extent than other stocks of fish in this area exploited by one nation only. Hence it can be regulated relatively efficiently compared with those fisheries involving many nations. Experience has demonstrated that international regulation is difficult to achieve under such conditions.

SUMMARY

1. Data on age composition, growth, and mortality rates of the halibut, *Hippoglossus hippoglossus*, collected in Finmark, 1956—1960, supplemented with data on immature halibut from various localities in Northern Norway were examined.
2. A weight-length relationship was determined separately for males and females.
3. Total instantaneous mortality rate was determined for males and females based on age composition data.
4. Yield isopleths were calculated based on a knife-edged selection curve into the fishery and also on prolonged recruitment. In the latter case variable fishing effort was applied to the age groups to simulate the recruitment into the fishery and withdrawal away from the fishable stock of the large females.
5. A precise determination of maximum length or weight, natural and fishing mortality rate were not achieved. Hence the change in yield per recruit could only be suggested as a function of age at entry into the fishery and fishing mortality.

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STUDIES ON HEMOGLOBINS AND SERUM PROTEINS IN SPRAT FROM NORWEGIAN WATERS

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INTRODUCTION

Hemoglobin polymorphism in sprat, *Sprattus sprattus* (L.), has been described by Wilkins and Iles (1966), who found three hemoglobin patterns, called «type 1», «type 2», and «type 3» (outlined in Fig. 2). Although the sprat hemoglobin patterns corresponded closely to some of the length-assosiated hemoglobin patterns in herring, no assosiation between length and hemoglobin pattern could be found in sprat, and the authors concluded that «these patterns may represent the phenotypic expression of a complex genetic segregating mechanism in this species.»

In Norwegian waters sprat is abundant in the Oslofjord and in the fjords of western Norway as far as Stad. The main sprat fisheries take place in these districts, but also at the Skagerak coast off south-eastern Norway and in the Trondheimfjord sprat is abundant enough to be of importance to fisheries.

Although spawning occurs in some fjords of south-eastern and western Norway, the sprat in Norwegian waters evidently is recruited in part from spawning grounds in the Skagerak and the Kattegat (see Dannevig 1951 for references). A correlation between catches in western Norway and the thickness of coastal water (Bakken 1966) indicates that drift of eggs and larvae with the coastal current northward along the coast is of importance for the recruitment of sprat in western Norway. Results from vertebrae counts (Dannevig 1951) indicate, however, that different shoals of sprat, even from adjacent localities, may be of different origin.

Serological methods have been applied to the problem of the population structure of sprat in Norwegian waters, and this paper deals with provisional results obtained from electrophoretic studies of hemoglobins and serum proteins. Part of the results have been briefly dealt with in preliminary reports (Møller, Nævdal and Valen 1966, Nævdal 1966).

MATERIAL AND METHODS

Blood was obtained from live sprat by cutting the tail, and collected in small glass tubes which were packed and sent on ice in thermos flasks from the sampling localities to the laboratory. There the blood was centrifuged, and the serum pipetted off.

The erythrocytes were lysed by adding destilled water, and the hemolysate was centrifuged before electrophoresis. In the first few samples (no. 1—5), heparin was used as anticoagulant, but as it appeared that hemoglobin solutions could easily be prepared also from partly clotted blood, no anticoagulant was used for the rest of the samples.

The agar-gel electrophoresis described by SICK (1965) was applied for the sprat hemoglobins. The electrophoretic run lasted for 60 minutes. Most hemoglobin analyses were made within 24 hours after the blood had been collected, but some samples had to be stored (at about 2°C) for two days before analysis. The storage did not seem to influence seriously the technical quality of the results, except that weak components tended to become stronger after storing. Two samples (no. 20 and 24) were accidentally exposed to temperatures about 10°C for one or two hours. They showed to contain several specimens with hemoglobin components of high cathodic mobility. To see whether these types excisted *in vivo* or were produced under influence of increased temperatures, experiments were carried out with storage of hemoglobin specimens at room temperatures.

Sera were subjected to electrophoresis without any initial treatment. Most samples were analysed fresh (within two days after collection), but some were stored frozen for a few days or weeks. Storage did not seem to alter the electrophoretic mobility of the proteins, but the electrophoretograms tended to become weaker and more diffuse.

Serum proteins were analysed by combined starch-/agar-gel electroresis (SICK 1965, MØLLER 1966). For determination of transferrin types, electrophoretic runs of 90 minutes were applied.

Both hemoglobin- and serum-gels were fixed in a 5:5:1 solution of methanol, water and glacial acetic acid, dried at room temperature, and then stained. Hemoglobins were stained in Amidoblack 10 B. The serum protein bands were best made visible by staining with Nigrosine, but Amidoblack 10 B could also be used. Autoradiography according to GIBLETT, HICKMAN and SMITHIES (1959), modified for this type of electrophoresis by MØLLER (1966), was carried out for identification of transferrins. Staining with o-dianisidine (peroxidase activity) was applied to detect haptoglobin/hemoglobin complexes.

Sample localities are shown in Fig. 1 and are listed in Table I together with sampling dates and the number of specimens in each sample analysed for hemoglobins and serum proteins respectively. For several specimens low consentration of proteins in the sera prevented the determination of transferrin types. Therefore the number of specimens is

Fig. 1. Sampling localities of 28 blood samples of sprat from Norwegian coastal waters.

higher for hemoglobins than for transferrins in most samples. For sample no. 9, however, working stress at the laboratory prevented analyses of all hemoglobin specimens. Unreliable results from hemoglobin samples 20 and 24 are discussed later.

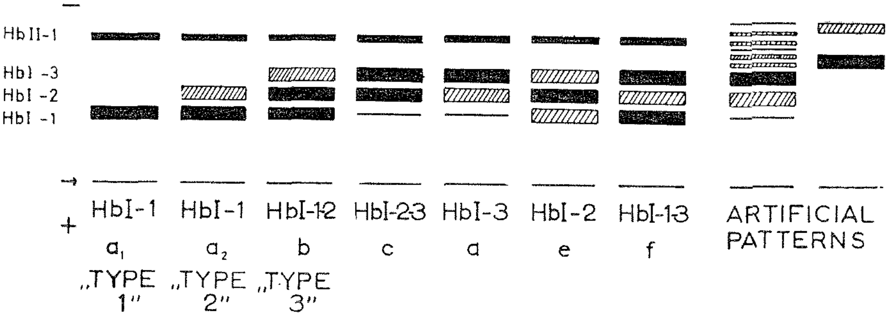
Lengths were measured for part of the material, and the age of the bulk of each sample was determined partly from size and partly from growth zones in the otholits.

RESULTS AND DISCUSSION

A. BIOLOGICAL VARIATIONS

1. *Hemoglobin*

The technique used by WILKINS and ILES (1966) allows direct comparison of results, and the three hemoglobin patterns revealed by these authors also made up the greater part of the material from Norwegian waters. In a preliminary report (NÆVDAL 1966) these patterns were called a_1, a_2, and b respectively. Other patterns were called c, d, e and f. These designations have been retained as «working names», but for a complete description of the sprat hemoglobin variations, a nomenclature similar to that used by SICK (1961, 1965) for cod hemoglobins, has been accepted.



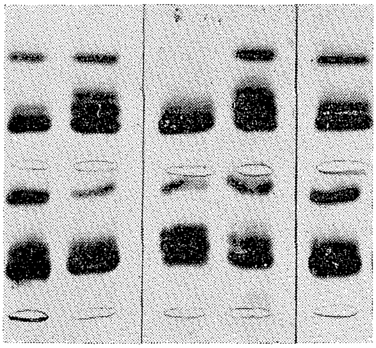


Fig. 2. Outline of hemoglobin patterns in sprat obtained by agar gel electrophoresis at pH 7.2, and photograph of electrophoretograms obtained by routine analyses. The two patterns at right were produced by heating of the specimens. Legend: Filled in bars: Strong bands. Hatched bars: Moderately strong bands. Single lines: Faint bands. Arrow indicates the point of application.

From left to right the photographed types are (in upper and lower row respectively): Hb I–1, Hb I–1–2, Hb I–1 (note the absence of the Hb II-group), Hb I–1–2, Hb I–1, Hb I–1, Hb I–2, Hb I–1 and Hb I–1.

The hemoglobin patterns (phenotypes) revealed by these studies, are outlined in Fig. 2, where also a photo of stained slides with some of the patterns is shown.

Most variations in hemoglobins were found in the slower moving group named Hb I. Three strong fractions were found to belong to this group, and these components were named Hb I–1, Hb I–2, and Hb I–3 in order of increasing cathodic mobility. One or two of these strong components were always present. All the six possible combinations were found, although some of the combinations were very rare.

Weak components were found at the positions where strong fractions were lacking. These weak components varied to some extent, and suggested several more groups of classification. However, the weak components tended to increase in strength upon storing, and it was not possible to analyse all samples immediately after sampling. Therefore classification according to weak components appeared to be less reliable, and was not applied. For the same reason, distinction between «type 1» and «type 2» of WILKINS and ILES (1966), preliminary called a_1 and a_2 respectively (NÆVDAL 1966), was also omitted because these two patterns differ only in the presence or absence of one weak component at the position of Hb I - 2. However, the weak components were present also in fresh material, and therefore probably also excist *in vivo* like the minor hemoglobin components of cod (SICK 1965). The weak sprat hemoglobin components were designed Hb I–1', Hb I–2', and Hb I–3', respectively found at the positions of Hb I–1, Hb I–2, and Hb I–3.

The hemoglobin patterns (phenotypes) were named according to which of the three main components they contained. Thus the phenotype Hb I–1 comprises the component Hb I–1 only, phenotype Hb I–1–2 comprises Hb I–1 and Hb I–2, etc. The names of the six phenotypes follow from Fig. 2.

A group of hemoglobins of somewhat greater catodic mobility, were called Hb II. The major part of the specimens contained only one strong component, named Hb II–1, in this group. This component was sometimes accompanied by a weak component (named Hb II–1') at its cathodic side. The strength of this weak component increased upon storing, and it was rarely found in fresh specimens. Therefore it probably represents denaturation products. Another component was found at the anodic side of Hb II–1 in a few specimens. This component, called Hb II—2, seemed to be stable, and probably excisted also *in vivo*. In some specimens the Hb II-group of hemoglobin components seemed to be either absent or present as a very faint band only. This occurred also in fresh specimens, and had probably nothing to do with the preservation of the samples. The variations in the Hb II-group, however, were too rare to be of any use in population studies.

Prolonged storage of the samples in the refrigerator did not result in major changes in the hemoglobin patterns, except that the minor components became stronger. After four or five days the bands became diffuse, and the patterns could not be determined. Heating of the blood, however, resulted in «new» patterns. Among specimens which had been kept at room temperatures (about 20°C) for 20 hours before reanalysis two «new» patterns, outlined to the right in Fig. 2, were found. One of these patterns comprised several bands which might vary somewhat in relative intensity, some at positions of normal hemoglobin components and some with higher cathodic mobility. It might be confused with patterns Hb I–2–3 or Hb I–3, but the weak components clearly distinguish this pattern from the normal ones. The other pattern comprised two bands, none, however, at the positions of any of the normal components.

Storage of hemoglobin specimens at room temperatures for periods of up to five hours caused no major essential changes in hemoglobin patterns, and even after 20 hours, only about half of the specimens were drastically affected.

Two samples from the Oslofjord (no. 20 and 24) contained several specimens which posessed one of the patterns which could be produced *in vitro*. These samples were exposed to a temperature of about 10°C for some hours before analysis because the ice in the thermos flasks had thawed at their arrival in the laboratory. Although considerably higher temperatures and longer time was required to produce the artificial patterns, the results of the hemoglobin analyses for these two samples seemed unreliable and were not considered.

For the greater part of the material, differences between patterns were clear, and the classification therefore fairly easy. The difference between patterns Hb I–2 and Hb I–2–3 might be less evident, and

Table 1. Distributions of hemoglobin patterns (phenotypes) in samples of sprat from western Norway and the Trondheim fjord.

Sample no.	Hemoglobin patterns						Numbers in sample	Frequency of pattern HbI–1
	HbI–1	HbI–1–2	HbI–2–3	HbI–2	HbI–2	HbI–1–3		
1	36	17	—	2	—	—	55	65.5
2	22	8	—	—	1	1	32	68.8
3	21	7	4	—	2	—	34	61.8
4	135	7	—	—	1	—	143	94.4
5	95	5	—	—	—	—	100	95.0
6	94	5	—	—	1	—	100	94.0
7	36	—	—	—	—	—	36	100.0
8	80	4	—	1	—	—	85	94.1
9	99	1	—	—	—	—	100	99.0
10	96	19	2	—	2	—	119	80.7
11	81	11	—	—	—	—	92	88.0
12	83	23	—	—	3	—	109	76.1
13	76	24	—	—	2	—	102	74.5
14	77	16	—	—	1	—	94	81.9
15	105	9	—	—	—	—	114	92.1
16	71	23	—	1	4	—	99	71.7
17	73	21	—	2	1	—	97	75.3
18	81	15	—	2	2	—	100	81.0
19	74	22	2	—	2	—	100	74.0
Total	1 435	237	8	8	22	1	1 711	83.9

the type determination of specimens with one of these patterns might accordingly be unreliable.

The material was separated into age-groups, and the hemoglobin variations were found in samples of the 0-group as well as in samples from older fishes. This supports the conclusion of Wilkins and Iles (1966) that hemoglobin patterns assosiated with age or length are not present in sprat.

Results of the hemoglobin analyses reported here support the hypothesis of genetic control (Wilkins and Iles 1966). The genetic system is still obscure, but some conclusions may be inferred from the population data presented in Table 1 and Table 2. These tables give the distributions of hemoglobin types in the analysed samples which gave reliable results.

Table 2. Distributions of hemoglobin patterns (phenotypes) in samples of sprat from south-eastern Norway.

Sample no.	Hemoglobin patterns						Numbers in sample	Frequency of pattern HbI–1
	HbI–1	HbI–1–2	HbI–2–3	HbI–2	HbI–2	HbI–1–3		
21	81	15	3	—	2	—	101	80.2
22	65	22	3	—	1	—	91	71.4
23	83	13	—	—	1	—	97	85.6
25	62	13	1	—	2	—	78	79.5
26	81	6	—	—	1	—	88	92.0
27	97	4	—	—	1	—	102	95.1
28	59	5	—	—	—	—	64	92.2
Total	528	78	7	—	8	—	621	85.0

From the distributions of phenotypes, it seems obvious that a hypothesis of three allelomorphic genes, each of which controls the strong fractions Hb I–1, Hb I–2 and Hb I–3, is not applicable. If so controlled Hb I–3 should have occurred more frequently in combination with Hb I–1 than demonstrated. However, it seems probable that the phenotype Hb I–1–2 with the strong fractions Hb I–1 and Hb I–2, represents heterozygotes with two alleles where each controls polypeptide chains in Hb I–1 and Hb I–2 respectively. Pattern Hb I–1 should then be the phenotypic expression of one of the homozygotes. The other homozygote should be expected to show a hemoglobin pattern with Hb I–2 as the only strong component. This phenotype presumably is represented by pattern Hb I–2, although the two weak fractions

Hb I–1' and Hb I–3' also occur in this pattern. With this assumption the distributions of the patterns (phenotypes) are in accordance with expected Hardy-Weinberg distributions of genotypes, and therefore the hypothesis may be correct.

It is not easy to fit the patterns Hb I–2–3, Hb I–3, and Hb I–1–3 into this hypothesis. However, transitional stages between patterns Hb I–2–3 and Hb I–2 have been noted. This finding suggests that fraction Hb I–2 is rather unstable and may be converted into Hb I–3 by environmental factors (*in vivo* or *in vitro*) or by modifying genes which perhaps act upon the recombination of polypeptide chains. Thus it seems possible that patterns Hb I–2 and Hb I–2–3, perhaps also Hb I – 3, are phenotypical expressions of the same genotype. However, if this hypothesis is correct, some samples have an excess of hypotetical homozygotes compared to expected Hardy-Weinberg distributions. The genetic basis of pattern Hb I–1–3, and also of the variations in the weak components which occurred, still is unexplained, but the possibility exsist that unknown noninherited factors may influence the hemoglobin patterns.

The variations in the Hb II-groups are also unexplained. In specimens which evidently lack this group of hemoglobins, the synthesis of the hemoglobins may be inhibited by some genetical or nongenetical factors. The Hb II–2 component may be controlled by an allele to a gene controlling the normal Hb II–1 component. These alleles must be located to another locus than the genes which control the components in the Hb I-group, because no correlation between variations in the Hb I- and Hb II-groups can be discovered.

The hemoglobin variation in sprat is rather similar to variations in the achoveta, *Engraulis ringens,* and some other clupeoid fishes in Chile (SIMPSON and SIMON SCHLOTFELDT 1966, SIMON SCHLOTFELDT and SIMPSON 1966). In these species inter- and intraspecific variation in hemoglobin patterns were found, and there was also great variations among samples caught at different localities. The intraspecific variation did not appear to be ontogenetic, but the numbers and complexity of some of the hemoglobin patterns did not permit genetic interpretation.

2. *Transferrin*

The transferrins of sprat moved towards the anode at pH 9.0, but slower than any of the other serum proteins. By autoradiography, it was shown that three bands on the sprat serum electrophoretograms represented proteins with ironbinding properties. These three bands therefore are believed to represent transferrins, and they have been named

Tf A_1, Tf A_2, and Tf B_1 in order of decreasing anodic mobility. A fourth band of still lower anodic mobility was not tested, since sera in which it occurred were not available when the tracing experiments were made. Its strength and position conforms with the transferrin bands, however, and therefore it was interpreted as a rare transferring component and named Tf B_2.

One, two, or three of the transferrin bands were present in each specimen. The transferrin patterns (phenotypes) which were found, are outlined in Fig. 3, where also a photo of some typical electrophoretograms of sprat sera is reproduced.

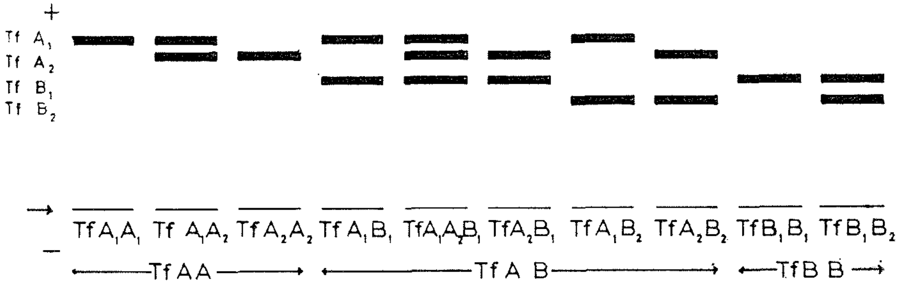


Fig. 3. Outline of serum transferrin patterns in sprat obtained by combined starch and agar gel electrophoresis at pH 9.0, and photograph of electrophoretograms obtained by routine analyses. Legend: Fig. 2.

From left to right the photographed patterns are: Tf A_1 B_1, Tf B_1B_1, Tf A_2B_1, and Tf A_1A_2.

The phenotypes got their designations according to the components they possessed, i. e. specimens with only Tf A_1, were said to belong to the phenotype Tf A_1A_1, those with both Tf A_1 and Tf A_2 to the phenotype Tf A_1A_2, those possessing both Tf A_1, Tf A_2, and Tf B_1 to the phenotype Tf $A_1A_2B_1$, etc. As shown in Fig. 3, 10 different phenotypes were found.

However, for routine analysis it proved to be difficult to distinguish between the bands Tf A_1 and Tf A_2, and therefore these two transferrins were combined and called Tf A. Tf B_1 and Tf B_2 were also combined as Tf B, since Tf B_2, which was found only in some of the samples and always at very low frequencies, did not seem to be of any value for population studies. Therefore the greater part of the material was separated into only three phenotypes, called Tf AA, Tf AB, and Tf BB.

In specimens which evidently belonged to single-component phenotypes, weak bands were often present at the positions of the other components. This was especially true for specimens belonging to phenotype Tf B_1B_1 which often had a faint band at the position of Tf A_1. Usually these components were too weak to cause any difficulty, but the faint bands varied in strength, and occasionally caused doubt about whether a specimen belonged to a double- or a single-component phenotype. However, cases of such hesitation were too few to have any great influence upon the distribution of the phenotypes and the calculated frequencies.

Transferrin variations in cod, *Gadus morhua,* have been found to be controlled by a series of polyalleles (MØLLER 1966). A similar hypothesis of co-dominant alleles each controlling one of four transferrin components, can not be accepted for the transferrin variations in sprat, because three strong transferrin components (Tf A_1, Tf A_2, and Tf B_1) occasionally were found in the same specimen. The transferrin variations in sprat therefore are more complicated than in cod and some other fishes which have been investigated (MØLLER and NÆVDAL 1966).

If the three main transferrin types, Tf AA, Tf AB, and Tf BB are considered alone, the hypothesis may be introduced that two allelomorphic genes, Tf^A and Tf^B control Tf A and Tf B respectively. The genotypes resulting from combinations of these alleles, may be called *Tf A/Tf A, Tf A/Tf B,* and *Tf B/Tf B* according to which of the alleles they possess. In Tables 3 and 4 the frequencies of the gene Tf^A, q^A, have been calculated from observed distributions of the three main transferrin types, and the observed distributions have been compared to expected Hardy-Weinberg distributions of genotypes. The tables show that for most samples there is good agreement between observed and expected distributions. Deviations have been tested by common χ^2-tests (except for a few samples where the numbers within some groups are too low, i.e. $n_{exp} < 5$).

The χ^2-values and the corresponding values for Probability show that the deviations between observed and expected distributions are not significant for any sample. The hypothesis of two allelomorphic genes therefore may be accepted to explain the main transferrin types. However, it has not yet been decided whether the subtypes are under genetical control. Tf B_1 and Tf B_2 may be controlled by two separate alleles at the actual locus, which then contain at least three alleles, Tf^A, Tf^{B1}, and Tf^{B2}, because both Tf B_1 and Tf B_2 have not been found together with Tf A in any specimen.

The fact that Tf B_2 has never been found alone also support the theory of three alleles at the actual locus, because the Tf B_2 components is so rare that the gene which eventually controls it, should not be expected to be found in a homozygotous state. The Tf A_1 and Tf A_2 components possibly are controlled by two alleles at a second locus, which influence only these two components. However, the distributions of subgroups in samples which gave the best electrophoretograms, show that there are too few hypothetical heterozygotes (Tf A_1A_2) to fit such a system. It is also possible that the subtypes depend upon noninherited factors. Consequently no explanation of the subtype variations can be given at present.

The presence of weak transferrin components in addition to the stronger components has also been demonstrated in herring (Nævdal and Haraldsvik 1966). The weak components do not necessarily exclude genetic control of the main transferrin types. However, the weak components vary in strength and are often absent, and therefore they indicate a more complicated genetic control by modifying genes or an influence by noninherited factors.

The main types, however, seem to satisfy the important claim that characteristics to be used in population studies should be genetically controlled. The corresponding gene frequencies therefore can be used to compare samples.

3. *Other serum proteins*

Outlines of some electrophoretograms of sprat sera containing some hemolysate as obtained by the combined starch-/agar-gel method at pH 9.0 are shown in Fig. 4. The hemoglobin types might also be detected by this method, which causes the Hb I-group to move towards the anode.

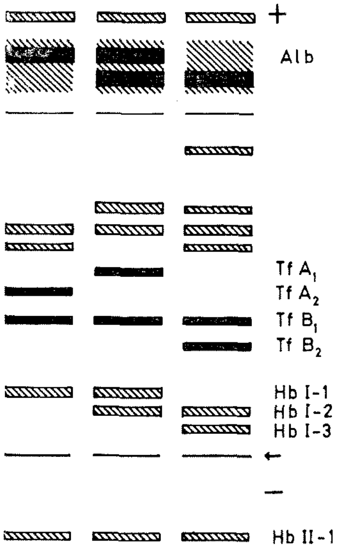


Fig. 4. Outline of sprat serum protein electrophoretograms obtained by combined starch and agar gel electrophoresis at pH 9.0. The position of the hemoglobin components are indicated. Legend: Fig. 2.

However, the agar-gel method is preferred for routine analyses of hemoglobins, since the types are revealed better and more rapid this way.

The position of the transferrin components in relation to the other serum proteins and the hemoglobins, is also shown in Fig. 4. The other serum proteins possessed a higher anodic mobility than the transferrins. In several proteins which were represented by more or less diffuse or strong bands on the electrophoretograms, individual variations were observed, and three of these patterns are shown. These bands, however, are too weak or diffuse for proper classification of the specimens, and they can therefore not be utilized in population studies.

Also in the albumin region individual variations were seen. However, the albumins did not show up as distinct bands which could be easily recognized on the electrophoretograms, and therefore also these variations were unsuitable for identification of populations. The relatively strong band which is shown in the anodic side of the main albumin components, was characteristic for sprat sera, and corresponding bands have not been found in other species (NÆVDAL and HARALDSVIK 1966, and unpublished data). Test for hemoglobin/haptoglobin complexes also gave remarkable results. Peroxidase activity was found only in the albumin region (except for the free hemoglobins), where strong, but diffuse staining with o-dianisidine was obtained. This does not agree with results for some other fish species, where well defined haptoglobin bands, not located in the albumin region, have been obtained (KOEHN 1966, NÆVDAL, unpublished data).

B. *GEOGRAPHICAL VARIATIONS*

Assuming that the hemoglobin variations are controlled genetically, attention can be turned to the geographical distribution of the samples. Frequencies (in per cent) of pattern Hb I–1 have been calculated as characteristic sample parameter and given for each sample in Tables 1 and 2.

The genetical control of the main transferrin types seems to be clear. The frequency of the gene Tf^A, q_A, has been used as characteristic parameter, and the calculated values are given in Tables 3 and 4.

Hemoglobin frequencies vary more than expected for random samples from a homogenous population, and the variation in q_A-values among samples is also considerable. However, the observed frequencies have been found from a limited and varying number of specimens within each sample, and therefore 95 % limits of confidence for the universal frequencies have been calculated.

Table 3. Observed distributions of transferrin types in samples of sprat from western Norway and the Trondheim fjord compared to expected Hardy-Weinberg distributions.

Sample no.	Transferrin groups			Numbers in sample	q_A	χ^2	Probability of worse fit
	Tf AA	Tf AB	Tf BB				
1 obs	6	24	18	48	0.38		
exp	6.9	22.6	18.6	48.1		0.40	$0.5 < P < 0.7$
2 obs	1	7	11	19	0.24		
exp	1.1	6.9	11.0	19.0			
3 obs	8	15	10	33	0.47		
exp	7.3	16.4	9.3	33.0		0.24	$0.5 < P < 0.7$
4 obs	15	64	60	139	0.34		
exp	16.1	62.4	60.5	139.0		0.12	$0.7 < P < 0.8$
5 obs	12	45	25	82	0.42		
exp	14.5	40.0	27.6	82.1		1.30	$0.2 < P < 0.3$
6 obs	11	48	36	95	0.37		
exp	13.0	44.3	37.7	95.0		0.70	$0.3 < P < 0.5$
7 obs	5	15	15	35	0.36		
exp	4.5	16.1	14.3	34.9			
8 obs	12	47	27	86	0.41		
exp	14.5	41.6	29.9	86.0		1.41	$0.2 < P < 0.3$
9 obs	14	60	61	135	0.33		
exp	14.7	59.7	60.6	135.0		0.03	$0.7 < P < 0.8$
10 obs	29	54	32	115	0.49		
exp	27.6	57.5	29.9	115.0		0.43	$0.5 < P < 0.7$
11 obs	21	44	19	84	0.51		
exp	21.8	42.0	20.2	84.0		0.20	$0.5 < P < 0.7$
12 obs	14	29	18	61	0.47		
exp	13.5	30.4	17.1	61.0		0.13	$0.7 < P < 0.8$
13 obs	8	45	34	87	0.35		
exp	10.7	39.6	36.8	87.1		1.63	$0.2 < P < 0.3$

(cont.)

Table 3 continued.

Sample no.		Transferrin groups		Numbers in sample	q_A	χ^2	Probability of worse fit
		Tf AA	Tf AB	Tf BB			
14	obs	6	27	35	68	0.29		
	exp	5.7	28.0	34.3	68.0		0.07	$0.7 < P < 0.8$
15	obs	12	40	41	93	0.34		
	exp	10.8	41.7	40.5	93.0		0.21	$0.5 < P < 0.7$
16	obs	7	47	34	88	0.35		
	exp	10.7	40.0	37.2	87.9		2.79	$0.05 < P < 0.1$
17	obs	8	33	39	80	0.31		
	exp	7.7	34.2	38.1	80.0		0.07	$0.7 < P < 0.8$
18	obs	9	29	32	70	0.34		
	exp	8.1	31.4	30.5	70.0		0.35	$0.7 < P < 0.8$
19	obs	14	38	40	92	0.36		
	exp	11.9	42.4	37.7	92.0		0.97	$0.3 < P < 0.5$
Total	obs	212	711	587	1510	0.376		
	exp	213.5	708.6	588.0	1510.1		0.04	$0.8 < P < 0.9$

A diagram of the limits of confidence is shown in Fig. 5, where the samples are arranged in geographical order. The significance of the variations in frequencies are tested by standard χ^2-homogenity tests and t-tests («Student»s tests). For calculation of χ^2-values, the number of specimens of all hemoglobin types other than Hb I–1, were combined to get sufficiently high numbers within each class, i. e. $n_{exp} > 5$. An account of the statistical test is given in Table 5. The χ^2-homogenity test of the total samples demonstrated that all samples were not drawn from one homogenous population with regard to these characteristics.

When all samples from western Norway and the Trondheimfjord were compared to all samples from South-eastern Norway by t-tests (means) and χ^2-homogenity tests (distributions), it was demonstrated that significant differences exist in the distributions of transferrin types and in the frequencies of genes supposed to control them. Corresponding differences for the hemoglobins are not significant.

According to χ^2-homogenity tests, there are significant variations in distributions of hemoglobin types within both main groups of samples.

Table 4. Observed distributions of transferrin types in samples of sprat from south-eastern Norway compared to expected Hardy-Weinberg distributions.

Sample no.		Transferrin groups			Numbers in sample	q_A	χ^2	Probability of worse fit
		Tf AA	Tf AB	Tf BB				
20	obs	16	43	30	89	0.42		
	exp	15.7	43.4	29.9	89.0		0.01	$0.9 < P < 0.95$
21	obs	18	46	27	91	0.45		
	exp	18.4	45.0	27.5	90.9		0.04	$0.8 < P < 0.9$
22	obs	14	28	26	68	0.41		
	exp	11.4	32.9	23.7	68.0		1.54	$0.2 < P < 0.3$
23	obs	12	26	17	55	0.45		
	exp	11.1	27.2	16.6	54.9		0.10	$0.7 < P < 0.8$
24	obs	12	34	10	56	0.52		
	exp	15.0	28.0	12.9	55.9		2.60	$0.1 < P < 0.2$
25	obs	12	35	23	70	0.42		
	exp	12.3	34.1	23.5	69.9		0.04	$0.8 < P < 0.9$
26	obs	16	36	32	84	0.40		
	exp	13.4	40.3	30.2	83.9		1.07	$0.3 < P < 0.5$
27	obs	13	40	34	87	0.38		
	exp	12.6	41.0	33.4	87.0		0.05	$0.8 < P < 0.9$
28	obs	10	23	19	52	0.41		
	exp	8.7	25.2	18.1	52.0		0.42	$0.5 < P < 0.7$
Total	obs	123	311	218	652	0.427		
	exp	118.9	319.1	214.1	652.1		0.50	$0.3 < P < 0.5$

The distributions of transferrin types, however, varied significantly only within the group of samples from western Norway. It appears from Fig. 5 that several samples (a. o. no. 2, 4, 9, 14, 15, 17 and 18) have low values of q_A, and these samples probably account for both the significant difference between the group of samples, and the significant variations among the samples from western Norway.

The samples from south-eastern Norway may be separated into two main groups, namely samples from the Skagerak coast and from the Oslofjord. By comparing these two subgroups of samples, the tests showed

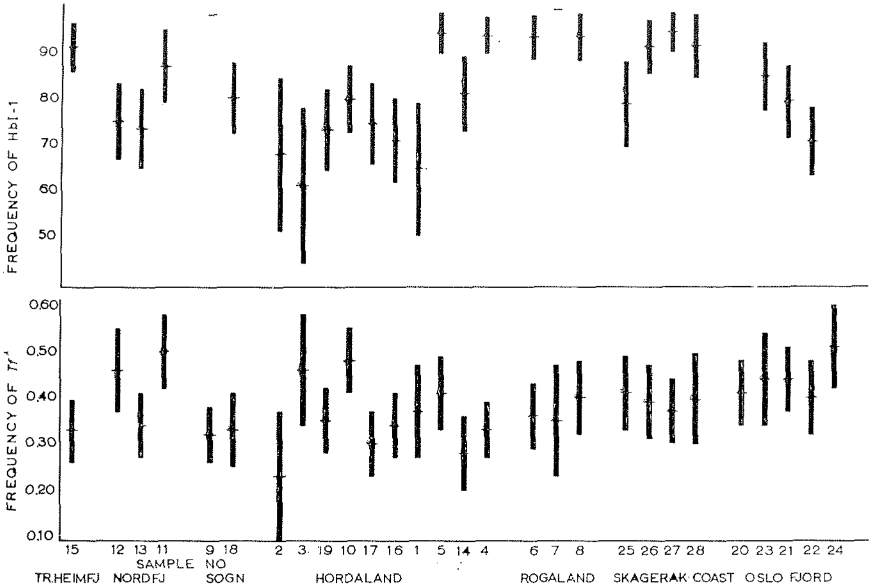


Fig. 5. Confidence intervals for the universal frequencies of Hb I–1 and for the gene Tf^A supposed to control the transferrins in the Tf A-group in sprat.

Horizontal lines mark the observed frequencies, and the vertical bars show the 95 % confidence limits. The samples are arranged in geographical order.

that the distribution of hemoglobin types vary significantly between the two subgroups of samples, whereas variation between the distributions of transferrin types is insignificant.

Further tests of the variations within each of the subgroups show that the distributions of hemoglobin types vary significantly within the samples from the Skagerak coast, but not within the samples from the Oslofjord. The distributions of transferrin types vary sligthly within both groups.

Such tests seems unnecessary for the samples from western Norway, which showed great variations, even between samples from adjacent areas (see Fig. 5). No marked geographical trend can be discovered in the variations of sample parameters, except that the samples from Rogaland all had a high percentage of Hb I–1 and nearly constant intermediate values of q_A.

The observed variations between samples are not easily interpreted. Attention may be drawn to the reliability of the type determinations. Uncertain determination of the transferrin types might be a source of error. However, cases of doubt have been tested by repeated analyses, and specimens which gave electrophoretograms of poor quality, have

Table 5. Statistical tests of significans of observed variations in distributions of hemoglobin and transferrin types of sprat.

	Hemoglobin types						Transferrin types					
	χ^2-homogenity tests			t-test of frequencies			χ^2-homogenity tests			t-tests of frequencies		
	χ^2	d. f.	P	t	d. f.	P	χ^2	d. f.	P	t	d. f.	P
Total samples	165.90	25	< 0.001				88.03	54	> 0.01 < 0.02			
Difference between samples from western and south-eastern Norway	0.45	1	> 0.5 < 0.7	0.65	1.238	> 0.5 < 0.6	10.48	2	> 0.001 < 0.01	3.13	2 604	> 0.001 < 0.01
Total samples from western Norway	133.32	18	< 0.001				66.98	36	> 0.001 < 0.01			
Total samples from south-eastern Norway	31.21	6	< 0.001				11.43	16	> 0.7 < 0.8			
Difference between samples from the Oslofjord and the Skagerak coast	14.20	1	< 0.001	3.76	574	< 0.001	2.89	2	> 0.2 < 0.3	1.61	1 168	> 0.1 < 0.2
Total samples from the Oslofjord	5.76	2	> 0.05 < 0.10				9.87	8	> 0.3 < 0.5			
Total samples from the Skagerak coast	13.15	3	> 0.001 < 0.01				1.41	6	> 0.2 < 0.3			

been rejected. Consequently, the number of specimens for which the transferrin types have been correctly determined, is low in the present material, and such cases can not explain the observed variations.

Cases of doubt are even less for hemoglobin type determinations. However, the possibility do excist that unknown non-inherited factors may influence the hemoglobin patterns, but genetic factors seem to be responsible for at least the main hemoglobin types. The variations among samples, discussed here, are based upon the main types only, and therefore these variations should be reliable.

The most likely explanation for the variations among samples is, however, that the samples have been drawn from populations which differ in their gene pool, and between which a high degree of reproductive isolation excist. The present variations may have been caused either by recruitment from separate sprat populations in the Skagerak or Kattegat, or combined recruitment from these areas with recruitments from local spawning in the fjords. Analyses of sprat from the spawning grounds in Skagerak and Kattegat must be made before further conclusions can be drawn on this subject. The present data on serological characteristics correspond fairly well with results from vertebrae counts (DANNEVIG 1951).

SUMMARY

1. A total of 2 332 hemoglobins and 2 162 sera of sprat have been analyzed by agar-gel electrophoresis at pH 7.2 (hemoglobins) and combined starch-/agar-gel electrophoresis at pH 9.0 (serum proteins). The material comprises 28 samples collected at different localities at the Norwegian coast from the Trondheimsfjord to the Oslofjord.
2. The hemoglobins were separated into several weak and strong components. Six main patterns (phenotypes) of strong components could be distinguished.
3. Intraspecific variations were also found in the serum proteins. Most of these variations appeared as presence or absence of weak bands, which were too weak or diffuse to form the basis for proper classification of specimens. However, among the serum transferrins (identitified by Fe^{59}-autoradiography) a total of ten different phenotypes were found. In most samples, individual specimens could be classified into three main combined types only.
4. The hemoglobin types did not demonstrate any relation to length or age. A hypothesis of genetical control involving two (or more) allelomorphic genes is suggested, and the observed distributions of pheno-

types coincide fairly well with expected distributions according to this theory.

5. The three main combined transferrin types seemed to be controlled by two allelomorphic genes, but all the ten types recorded could not be explained by this theory.
6. Frequencies of the most common hemoglobin type (type Hb I–1) in per cent of total number of specimens within each sample, and frequencies of the gene Tf^A supposed to control one of the components in the three main transferrin types, have been selected as characteristic sample parameters.
7. Significant variations in sample parameters and distributions of hemoglobin and transferrin types were found among the samples. No marked geographical trend could be discovered, and in some cases great differences were found among samples from adjacent areas. This implies that among the sprat in Norwegian coastal waters there exist two or more populations of different genetic composition, with a high degree of reproductive isolation.

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APPENDIX

Table I. Number of specimens analyzed for hemoglobin and transferrin types in blood samples of sprat from western Norway and the Trondheim fjord. (1—19), and south-eastern Norway (20—28). Results from samples in brackets were unreliable, and have been omitted.

Sample no.	Locality and date		Hemoglobin	Transferrin	Age
1	Håvik i Fusa Hordaland	5.X.65	55	48	1-group
2	Fensfjorden, Hordaland	15.X.65	32	19	0-group
3	Fensfjorden, Hordaland	23.X.65	34	33	0-group
4	Førdespollen, Hordaland	1.IV.66	143	139	1-group
5	Håvik i Fusa, Hordaland	6.VI.66	100	82	1-group
6	Frafjord, Rogaland	13.VI.66	100	95	1-group
7	Selvikvåg, Rogaland	13.VI.66	36	35	1+2-group
8	Krokholmane, Idsøy, Rogaland	13.VI.66	85	86	1-group
9	Simlenes, Sogn	21.VI.66	100	135	1-group
10	Grøsvik, Osterfjorden, Hordaland	2.VIII.66	119	115	2-group
11	Ryssfjæra, Nordfjord	11.VIII.66	92	84	1-group
12	Blaksæter, Nordfjord	15.VIII.66	109	61	1-group
13	Utvik, Nordfjord	16.VIII.66	102	87	1-group

Sample no.	Locality and date	Hemoglobin	Transferrin	Age
14	Nå, 14.X.66 Hardanger, Hordaland	94	68	1-group
15	Åsenfjord, 24.X.66 Trondheimsfjorden	114	93	1-group
16	Stamnes, 9.XI.66 Osterfjorden, Hordaland	99	88	0-group
17	Mostraumen, 9.XI.66 Osterfjorden, Hordaland	97	80	0-group
18	Dalsøyra, 11.XI.66 Sogn	100	70	0-group
19	Lindås, 15.XI.66 Hordaland	100	92	1+2-group
20	Måkerøy, 25.VIII.66 Oslofjorden	(87)	89	2-group
21	Son, 25.VIII.66 Oslofjorden	101	91	2-group
22	Son, 29.VIII.66 Oslofjorden	90	68	2-group
23	Slemmestad, 29.VIII.66 Oslofjorden	97	55	2-group
24	Rørvik, 30.VIII.66 Oslofjorden	(90)	56	2-group
25	Flødevigen, 1.IX.66 Aust-Agder	78	70	0-group
26	Sandnesfjord, 27.IX.66 Aust-Agder	88	84	0-group
27	Kattøya, 3.X.66 Langesundfjorden	102	87	1-group
28	Smedholmen, 3.X.66 Langesundfjorden	64	52	0-group