

Some Features in the Migration of Cod.

By

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THE migrations of fish, hidden as they are from the eye in most cases, but showing themselves at times and places with extraordinary clearness, have from earliest times attracted the attention, not only of fishermen, but of all interested in natural phenomena, and have given rise to many theories and fantasies. The phenomena are indeed of such great biological interest, with many fascinating points regarding the behaviour of fishes, that it is easily understood why so many investigators have spent time and research on them. But, though many single problems connected with the wanderings of fish have been elucidated in the course of time, it must be admitted that a long time will pass before we have attained the deeper understanding of the main problems presented by the study of fish migrations.

The methods available for the investigation of the migrations in time and place, may be summed up under the following headings: (1) direct observation of the migrations, which in the case of sea fish can only give very limited results; (2) close study and comparison of certain meristic and other characters in races, populations, etc. (race investigations, study of scales, otoliths, etc.) to determine whether exchange takes place between different areas; these studies were expected to make a great advance in the investigation of fish migrations, but have proved to be of distinct value only in certain restricted fields; (3) the experimental method, including especially the marking of individual specimens; this likewise has its limitations, but has, for example, this advantage over the others, that the information obtained concerning the migration of individual specimens is so reliable as to be of the utmost importance in such researches.

In the following pages, using especially the cod marking experiments carried out by Danish workers in the north-western Atlantic, I shall endeavour to give an outline of the main features of the results concerning the migrations of cod, and refer, among other things, to important points in the methods of marking.

Historical remarks on marking of sea fish.

With the introduction of individual marking as a means to the study of animal migration, these investigations towards the end of last century were led into more precise, scientific lines and thus have produced considerable results, which have widened our knowledge regarding certain phases of the migration. This holds good with regard to fish and birds, as well as various other groups of animals.

With regard to freshwater fishes, from which recaptures might be expected owing to their restricted habitats, it appears that marking experiments were already carried out in the seventeenth century; the obvious case of the salmon gave rise to these primitive experiments, in which bands or the like were bound round the tail of the fish (mentioned by I z a a k W a l t o n, 1653); the marking of salmon was also undertaken later, for example, in the middle of the nineteenth century. But even in the case of the salmon and other freshwater fish the experiments did not attain a generally recognized, useful or scientific method until towards the end of last and beginning of this century.

It is of interest to note that almost the same development is shown in the marking of wild birds. After H. C h r. C. M o r t e n s e n's experiments in Jutland in 1899 and following years on the marking of birds with special rings, similar work was carried out by T h i e n e m a n n (Rossitten) and many others; but a study of past literature has revealed that various persons had already endeavoured much earlier to mark wild birds in the hope of finding them again, for example, J o h a n n L e o n h a r d F r i s c h about 1740; but it was not until M o r t e n s e n's experiments were carried out that the method was generally accepted as of use. Just as these efforts brought the marking of birds to a useful stage, the acceptance of similar methods gave rise to the marking of salt-water fish almost about the same time.

So far as I have been able to determine, T. W e m y s s F u l t o n was the first to publish a paper dealing with the sea-fish marking experiments on a scientific basis; in March to November 1888 he marked the first fishes in the North Sea, and in the following years (up to 1892) he marked in all about 4,000 specimens, including also the cod, in Scottish waters, various types of marks being used with serial numbers on them; in 1890 and 1893 he published his first results, which thus made the methods known ("Experiments on the migratory movements of seafish" and "An experimental investigation on the migrations and rate of growth of the food fishes"). A brief reference was also made to the experiments on p. 16 of the "8th Annual Rep. Fishery Board for Scotland 1889 (1890). III", where it is mentioned that marking experiments similar to F u l t o n's had also been made in Denmark; the probability is that C. G. J o h. P e t e r s e n and F u l t o n had discussed these experiments together. In 1893, after various earlier experiments, P e t e r s e n marked about 1,000 plaice in the Limfjord with marks, later to become those in general use

(Petersen's model) and in 1894 he published his first summary of these experiments ("On the labelling of living Plaice").

A few years after the experiments of Fulton and Petersen, Hugh Smith planned an extensive marking of the cod on the east coast of America (1897—1901), but these experiments, presumably owing to the place of marking (supracaudally) and possibly also to the mark used (copper and copper wire), showed no recaptures after the comparatively short period of 1½ years.

It was not until the founding of the International Council for the Exploration of the Sea, however, that the marking of sea fish became more generally used in the study of the migrations of fish, and in the years 1904—1913 considerable progress was made with the marking of economically important species. Then came an interruption until the work was taken up again after the war. Though many fish have been marked, yet these experiments, owing mainly to the limitations imposed by their cost in the case of sea fish, have dealt with far smaller numbers than the bird marking experiments undertaken in many countries, and which certainly must now amount to some millions. Of fishes only the economically important species have yet been marked to any great extent; the non-economical species, for the reason mentioned, among others, have not been the subject of any general experiments.

With regard to the cod (*Gadus callarias*), which we shall consider more closely here, about 135,000 specimens in all have been marked in the North Atlantic and adjacent waters, so far as it has been possible to determine from available publications and personal application for information. The Pacific cod, on the other hand, has not been the subject of marking experiments, so far as known.

Along the European continent from the North Sea to the Barents Sea, with their adjoining inner waters, about 15,350 have been marked, whilst an additional 20,000 or thereabout are said to have been marked recently by Russia in the Barents Sea; at the Faroe Islands about 6,850 have been marked, at Iceland (including Jan Mayen) about 8,300, and at Greenland about 10,400; lastly, on the American side of the Atlantic (Labrador, Newfoundland, Canada, and U. S. A.) about 75,000 cod have been marked.

The majority have been marked by the U. S. A. (ca. 53,500), Denmark (ca. 26,400), Russia (ca. 20,000?), Canada (ca. 12,800), Norway (ca. 10,800), and Newfoundland (ca. 8,400). In certain regions, for example, the Baltic and large parts of the North Sea far too few markings of cod have so far been made.

Remarks on the methods used in marking Cod.

It is beyond the scope of this article to describe in any detail the methods and technique of marking, but a few points may nevertheless be noted in connexion with the marking method used in the north-western areas of the Atlantic.

Both the place of attachment and type of mark have varied extremely in the marking experiments on cod in European and in American waters.

For example, attempts have been made at fixing the mark at the base of the three dorsal fins and the two anals, at the base of the caudal (both supra- and infracaudally) by means of a metal wire bound round the cauduncle, piercing the skin on the dorsal side of the fish, or passed through the gill-cover; the mark has also, in the more recent American experiments, been placed in the abdominal cavity, introduced through a slit.

The marks have been made of metal (bronze, aluminium, copper, tin, and silver) or of bone, ebonite, and celluloid, and several different types have been used. Of the types used¹), those in which a plate is

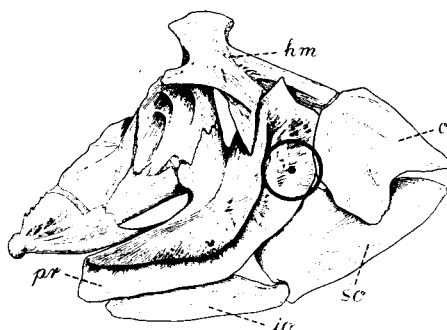


Fig. 1. Opercular bones of Cod. Supposed best position of mark in pre-operculum (*pr.*) indicated.

fixed by means of a thin metal wire (e.g., by *Fulton*, 1893, and *Hugh Smith*, 1902), have given but modest results; poor results have also been obtained from a mark of similar make to that used in marking cattle, and which was attached to the root of the caudal fin (e.g., *Schroeder*, 1931, Figs. 3—4). On the other hand, the best results have been obtained by the use of marks, often used also on other fish, consisting of two discs (of silver, bone, or ebonite) connected by means of a silver wire; in many of the experiments, where this mark has been attached to the gill-cover, the results seem to have been good, and best so long as codling have not been used. But the method of attachment has undoubtedly a good deal of importance, since the silver wire must go through a part of the gill-cover from which it cannot fall out through rubbing (see Fig. 1), whilst the two discs must be fixed pretty firmly, though not too tightly to begin with, on each side of the membrane. In Denmark from 1925 onwards we have used two ebonite discs connected by a silver wire, carefully fixed in the

¹) With regard to the many types of mark see "Journal du Conseil" Vol. VII, 1932, pp. 133—165 and *Graham* 1929.

thicker part of the gill-cover by means of a special marking needle (Tåning, 1933). For larger cod especially this method seems to be better than others which have been tried, the marks remaining attached up to 8—10 years. But it would be of advantage if experiments with marked cod were made in large aquaria, with different types of marks attached in various ways, and also for longer periods, since experiments of this kind have so far only been made to a small extent (Graham, 1929, who gives a valuable summary of the methods used in marking round fish).

Until we have reached the stage of using standard marks, which have been proved superior to all others by experiments in aquaria, for example, in regard to type, material, and method of attachment, a comparison of results from different regions will be uncertain. Provisionally, however, until more accurate data are available, we may overlook this shortcoming in the experiments, though noting that there is a most important point here in the method, which requires further clearing up.

In the investigation of migrations based on marking experiments it is clearly of the utmost importance that the marks used should remain attached to the fish for a long period, preferably throughout the whole life of the fish, from the time of marking till death. Even though we have various examples which show that marked fish can live for many years with the mark well preserved — a cod marked at East Iceland in July 1904 was recaptured at South Iceland in the spring of 1913 (cf. Sæmundsson, 1913, p. 34) and a second marked in the summer of 1926 at Kapsigdlit in Godthaab Fjord in West Greenland was retaken at the same place in the summer of 1935 — yet such individual cases should not be taken to indicate that the type of mark used will generally remain attached to the fish for the rest of its life. We know with certainty, for example, that certain marks in a very large number of cases are lost within a relatively short period (cf. Schroeder, 1930, pp. 12—14). I have felt it, therefore, as an obligation on me to determine whether the Danish cod marking experiments in northern waters have employed a method which may be considered better than those generally used hitherto. The fact, however, that we have obtained not a few recaptures up to 4—5 years after marking, and some even 8—10 years thereafter, justified the conclusion that the method must be fairly satisfactory. But even greater assurance of this is obtained from a closer examination of certain of the results from the Greenland marking experiments, which have now been carried out over a long period and thus permit of more general conclusions. As the purely technical basis of the marking experiments is of extreme importance, I may here deal more closely with this side of the matter.

The cod at West Greenland only become mature at a length of about 70 cm.; indeed, at a greater length in the case of many individuals. The migration from West Greenland to the spawning places at Iceland, which we shall discuss in more detail later, thus takes place only when

the cod have reached this length of about 70 cm. or more; but it appears that cod of 100 cm. and more do not in general migrate from Greenland to Iceland in order to spawn. The majority of the migrating cod thus fall within the lengths of 70 to 100 cm. We may now consider the distribution of the percentage recaptures of cod which have migrated to Iceland, taking account of the above-mentioned limit for mature

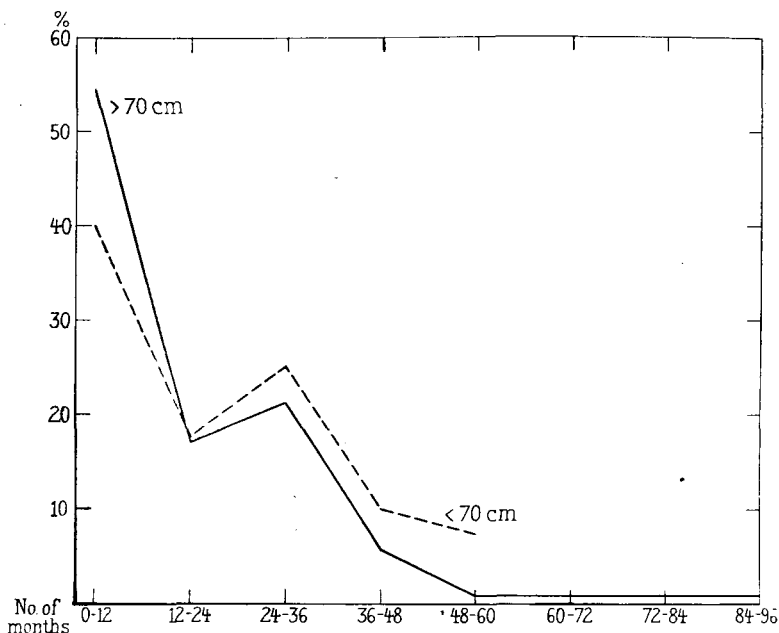


Fig. 2. Cod marked at West Greenland (1926—1933) and recaptured there. Percentage of recaptures in 12-monthly periods.

————— Curve representing Cod > 70 cm. initial length
 - - - - - " " " < 70 cm. " "

and immature fish. In all the years 1926—1933 the same method of marking has been used at Greenland, and in these years 3,595 specimens over 70 cm. have been marked, and 2,380 specimens under 70 cm.

The recaptures were distributed as shown in the following table.

Size	Number marked: West Greenland 1926—33	Number and % recaptured: West Greenland	Number and % recaptured: Iceland
> 70 cm.	3595	121 — 3.4 %	163 — 4.5 %
ca. 45—70 cm. . .	2380	41 — 1.7 %	60 — 2.5 %

As will be seen, the percentage of recaptures is lower at Greenland than at Iceland, undoubtedly chiefly due to the very different intensities of fishing at the two places; further, the percentage of cod below 70 cm. on marking, which have been recaptured, is only about half

that for the large cod, partly due to the fact that the fishermen at Greenland fish mainly for large cod and partly because the smaller cod are more liable to fall a prey to other predatory fishes and the like; perhaps also because the loss of marks is greater for this group of cod.

Closer consideration of the material with regard to the percentage distribution of the recaptures according to the time the individuals have been in the sea, gives an interesting result, as shown in Figs. 2

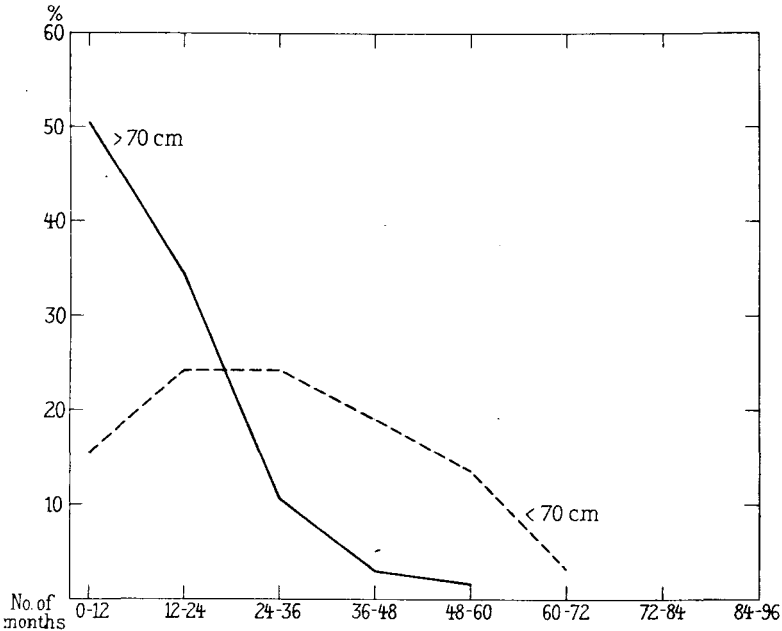


Fig. 3. Cod marked at West Greenland (1926—1933) and recaptured at Iceland. Percentage of recaptures in 12-monthly periods.

— Curve representing Cod > 70 cm. initial length
 - - - - - " " " < 70 cm. " "

and 3. The relative recaptures for each twelve months of the cod which have stayed at Greenland (Fig. 2) is almost the same for the sizes above and below 70 cm., whereas something quite different is seen in the curves for cod which have migrated to Iceland (Fig. 3). For the cod larger than 70 cm. on marking (thus mature or nearly so) we have a sharply descending curve, beginning with 50% of the recaptures within the first 12 months, after marking, then about 34% in the next 12 months, then about 10% and thereafter in the following periods only small numbers. The course of the curve for the cod smaller than 70 cm. on marking is quite different, first a rise, then for a couple of years a horizontal course and then an even fall; the cod in this group were not yet mature on marking; only in the course of the years following the marking have they become ripe in succession

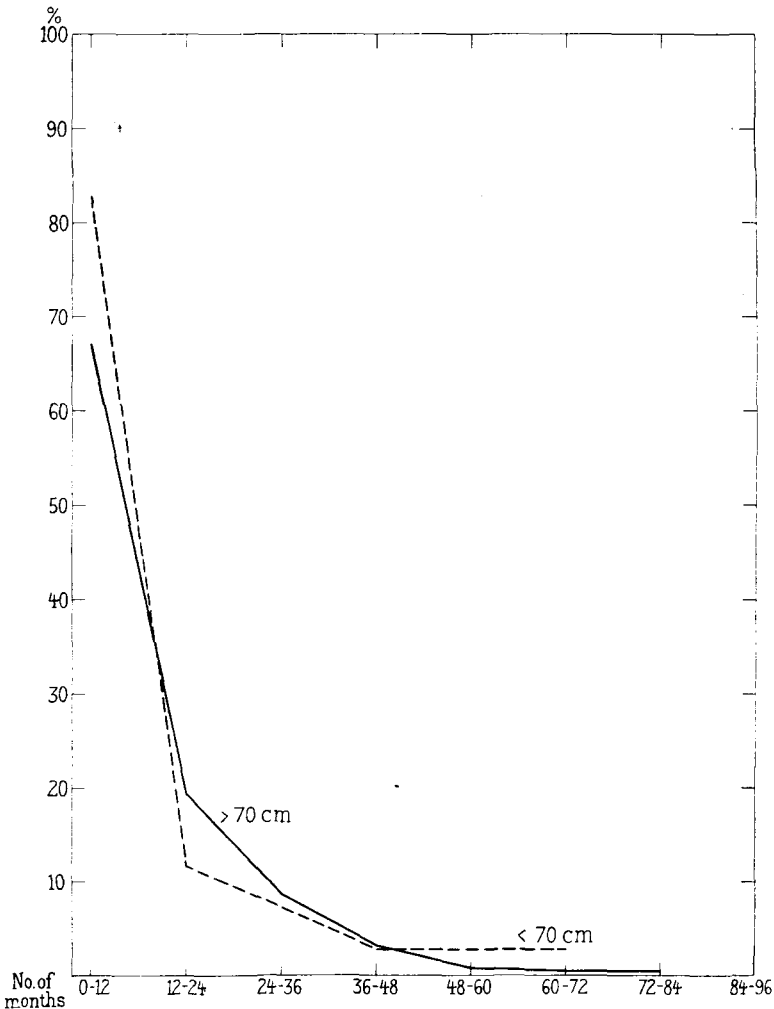


Fig. 4. Cod marked off South-West Iceland 1929—1933. Percentage of recaptures in 12-monthly periods.

— Curve representing Cod > 70 cm, initial length
 - - - " " " < 70 cm. " "

and then proceeded on the long journey to Iceland; lastly after 5—6 years this source of migrants to Iceland dries up, as the cod of this group either fall a prey to natural enemies or gradually attain the size-groups which more seldom undertake the migration to Iceland.

In the results of these marking experiments over a long series of years we have most valuable support for the conclusion that the method employed is useful. If the marks were gradually lost in large numbers, the curves for the migrants larger and smaller than 70 cm. should pursue

approximately the same course as, for example, the curves in Fig. 2; but the very characteristic difference between the two curves in Fig. 3 shows just that the marks are not lost to any great extent during the first years. Nature here, so to speak, has itself performed a laboratory experiment on a large scale, since the small fish, only as they become mature in the course of the years, leave West Greenland to appear in relatively large numbers at the spawning places of Iceland, where their larger companions are now extremely few in number, because they were already mature or very near to maturity at the time when the whole lot were marked at West Greenland.

Comparing now the curves for cod marked and recovered at Greenland with the corresponding curves for the cod marked and recaptured at Iceland (Fig. 4), we find for the latter the same gradual decrease as at Greenland for both the fish larger than 70 cm. and those smaller than 70 cm.; here naturally we do not find the interesting curve as in Fig. 3, since the small cod at Iceland are not, so to speak, kept back a number of years, like those which migrate from Greenland over to Iceland, before they make their way to the fishing grounds, but constantly run the same risk of capture as the older fish. [Of the cod marked at South Iceland in spring 10.1% of recoveries were large fish (>70 cm.) on marking, 11.8% small (<70 cm.); on the north and east coasts of Iceland the corresponding numbers for cod marked in summer were 22.5% and 26.3%.]

In this connexion also it is of interest to consider some curves showing the relative distribution for each 12 months of the recaptures in marking experiments carried out with the same methods in three widely different regions, namely, at the Faroes, Iceland and Greenland. We know that the fishing intensity is extremely different at the three places, very high at the Faroes, very low at Greenland, whereas the fishing at Iceland occupies an intermediate position in this respect. This is seen, for example, from the recapture percentages in the total, summed-up experiments since the war in these three areas; at the Faroes ca. 25%, at Iceland ca. 12%, and at Greenland ca. 6% (of which, however, ca. 3% were at Iceland). The numerous age-investigations made in the three regions also show this feature very distinctly in the age-composition of the stock of cod; at the Faroes a great decrease begins to show itself already with the 6 to 7-year-old fish, whilst the Iceland region shows large year-groups right up to 13 or 14-year-old fish, and at Greenland even older fish occur in fair numbers in the catches.

If we consider now the curves (Fig. 5) which only include material of cod larger than 70 cm. on marking, we see that these in their very different degrees of steepness clearly indicate the condition mentioned, and thus likewise afford valuable information regarding the trustworthiness of the marking method used. If, for example, we concluded that the steep fall in the curves for the Faroes indicated that the cod in the sea lost their marks in large numbers, there would naturally be no reason for not concluding that the same held good for Iceland and

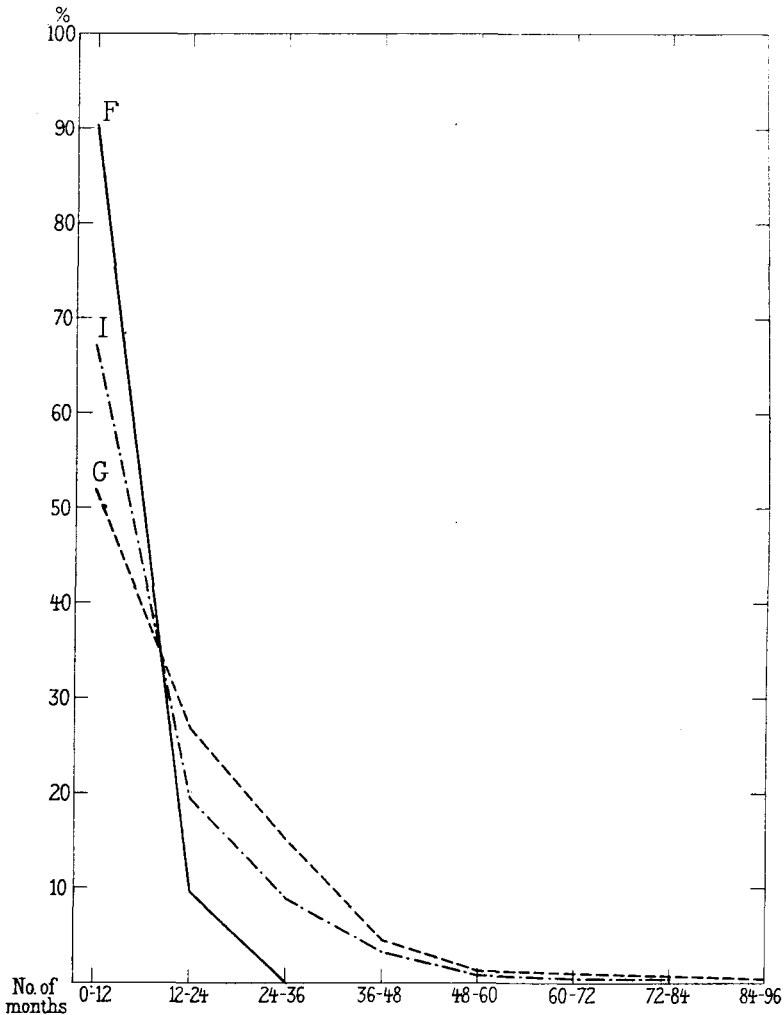


Fig. 5. Percentage of recaptured Cod in 12-monthly periods; all cod > 70 cm. initial length.

F Marking experiments at the Faroes 1927—32
 I " " " Iceland 1929—33
 G " " " Greenland 1926—33

Greenland, since the method used at these places has been quite the same. Since this is not the case, as the curves clearly show, we are entitled to conclude that the methods have been quite satisfactory and that the curves to a certain extent represent the decrease from year to year in the stocks of the respective fishing regions.

This does not mean, however, that I think the method used perfect;

far from it. We must unfortunately always reckon with the possibility that a number of the marks are lost from the fish in the sea; but I believe, nevertheless, that the method, so far as this species is concerned, is the best used hitherto.

On closer examination of the matter, however, I have obtained information regarding one of the ways in which the marks get lost, and as this is of interest from the technical side of the experiments, I may explain it.

In cod marked at Greenland it has been observed (by Paul M. Hansen) that corrosion of the silver wire connecting the two discs may occur to such an extent that the wire breaks at the middle; this corrosion occurs at the point where the wire goes through the opercular bones and surrounding tissue. Comparison of the number of such happenings in the three regions, Greenland, Iceland, and the Faroes, gave the result that great corrosion occurred almost entirely in the cod marked at Greenland.

	Number examined	weak	Corrosion moderate	strong
W. Greenland 1924—35	341	15	7	10
Iceland 1924—35	391	4	1	—
Faroes 1925—35	200	1	1	1

In plaice such a corrosion does not occur, practically speaking; among 1,135 plaice examined, which were marked at Iceland and in the North Sea, only a single case of corrosion has been observed.

In by far the great majority of cod, however, the silver wire shows not the slightest trace of having been attacked even up to 5—10 years after marking, and it should also be remarked that the corrosion is only of practical importance in the Greenland region, and even there scarcely 3 % have been so badly corroded that there is any danger of the marks being lost in this way. Here it is quite distinctly a corrosion, not of wear through friction, as the silver shows clear signs of an acid (organic or inorganic) having attacked it. The corroding process takes a long time, as the average period for which the wire, in the slightly corroded cases, has been carried in the sea, was 554 days; for the moderately corroded 809 days, and the strongly corroded wire 1,054 days. This means, therefore, that only after about 3 years is there danger of the marks being lost in a small percentage of the marked cod in this way; taken in conjunction with the fact that it is from Greenland we have the most numerous examples of the marks being borne by the cod for many years, this would indicate that the loss incurred by this means is not of much importance.

Nor does there seem to be any special concentration of the cases of corrosion at certain localities at Greenland, even though they seem to be most numerous inside the fjords and skerries; presumably the corroding substance comes from certain foods which the cod at Greenland take up perhaps locally and individually.

We have no data to show that marks attached by means of the marking needle used by us are able to work loose or break through the gill-cover, thus causing the loss of both discs and silver wire at the same time; this is probably due to the fact that we have mainly used the larger fish for the marking experiments.

Migrations in the North-West Atlantic.

The basis of our information regarding the migrations of cod within this region is mainly the marking experiments carried out during many years, and I may briefly give a summary of them.

The first marking of cod in the north-western areas of the Atlantic was undertaken by J o h s. S c h m i d t in 1904 and 1905 at East and North Iceland, as a link in his investigation of the biology of the cod at Iceland (S c h m i d t, 1907, S æ m u n d s s o n, 1913). They were continued later at North Iceland in 1908 and 1909 and in Faxø Bugt (S æ m u n d s s o n, 1913). These experiments embraced in all 1,135 marked cod, mainly the immature individuals. They showed in regard to migrations that until maturity was reached the cod remained for the most part stationary, and that none left the Iceland region; hence it was concluded that the stock of cod at Iceland might be regarded as a restricted unit.

It was not until after the world-war that marking experiments were renewed at Iceland, by S c h m i d t in 1924, and then with the help of Icelandic workers the experiments were extended to the spawning grounds at South-West Iceland; these in course of time yielded a lot of new information regarding the migrations of the stock, as these also extended to adjacent areas. In all, 7,035 specimens of cod were marked at Iceland in 1924—1936, mainly the large cod.

At the Faroes the experiments were begun in 1909, and here as also out on the Farøe Bank, 6,860 cod were marked in the years 1909—1936 (most of these experiments have been described by S t r u b b e r g, 1916 and 1933); of the cod marked at the Faroes Scotland marked 427 specimens.

When the cod fishery at Greenland became of importance in the twenties, the marking of cod was also begun there, and these experiments have yielded some of the most interesting data on cod migrations obtained by the marking method. In all 10,428 cod have been marked at Greenland; at West Greenland altogether 9,456 cod have been marked in the years 1924—1936, at East Greenland 972 cod in the years 1926—1933. Of these, 200 specimens were marked by Norwegians (T h o r I v e r s e n), whilst the experiments at West Greenland were carried out by Danish workers only (see S c h m i d t, 1933, H a n s e n, J e n s e n & T å n i n g, 1935). Finally it may be mentioned that T h o r I v e r s e n marked 113 cod at Jan Mayen in 1930.

I shall now discuss the main features of the results obtained regarding the migrations by means of the cod marking experiments referred to, and also such further information as other methods of investigation or experiments in other areas have contributed to an understanding of the migrations.

It is obvious that the results obtained from marking experiments alone can only throw a one-sided light on the migrations, since the results are entirely dependent for one thing on where, when, and in what manner a commercial fishery is carried on. Even though we know that some kind of cod fishery is carried on over nearly the whole region of distribution of the species, there is still the possibility of important information being missed with regard, for example, to the routes of migration, since the cod during the period of their pelagic wanderings may leave the restricted areas of the coastal banks and go to areas where no fishery is carried on.

Faroes.

So far as we know, the stock of cod at the Faroes makes no exchange of importance with those of neighbouring areas. Over a long period of years we have obtained the information that only two individuals marked at the Faroes have left the area, one being recorded as recaptured at the Orkneys, the other in the northern North Sea; further, two individuals marked at Iceland have been returned from the Faroes (see later), but possibly the immigration from Iceland is greater than the recaptures so far would indicate, since the marking of wandering cod has not yet been made at South-East Iceland, which lies nearest the Faroes, and from which we might imagine immigration to the islands to take place. Emigration, on the other hand, from the Faroes to the west Norwegian region has received no confirmation.

As mentioned above, *Strubberg* has made a detailed study of the marking experiments carried out at the Faroes and has shown that two-year-old cod are still very stationary, whilst the older cod wander quite a lot, probably urged thereto by the beginning of maturity; the wanderings, however, still keep to the banks round the islands and spawning occurs mostly in the area north and west of the northern islands. Between the Faroes and the Faroe Bank to the south-west there is but little exchange; cod also spawn on the Faroe Bank itself, which thus in the main houses its own stock, as the racial characters have also shown (*Schmidt*, 1930, p. 11).

The recapture percentage is very high at the Faroes, especially of small cod; in certain experiments it has been considerably over 50% (up to 75%). Consequently, the marked fish disappear completely from the catches in the course of about two years. For example, 2,363 cod were marked at the islands in 1923—1935 and of these 372 were recaptured in the first year, 194 in the second, and only 15 in the third calendar year (a total of ca. 25% recaptures). In this respect the Faroes show a marked difference from the Iceland—Greenland region,

as will be shown later, and resemble far more the North Sea in the rapid renewal of their stock.

Iceland.

The large Icelandic region, with its numerous banks, some distant from the coast, offers specially favourable conditions of life for the very abundant stock of cod, known here for hundreds of years and exploited by fishermen in recent years on an intensive scale. The

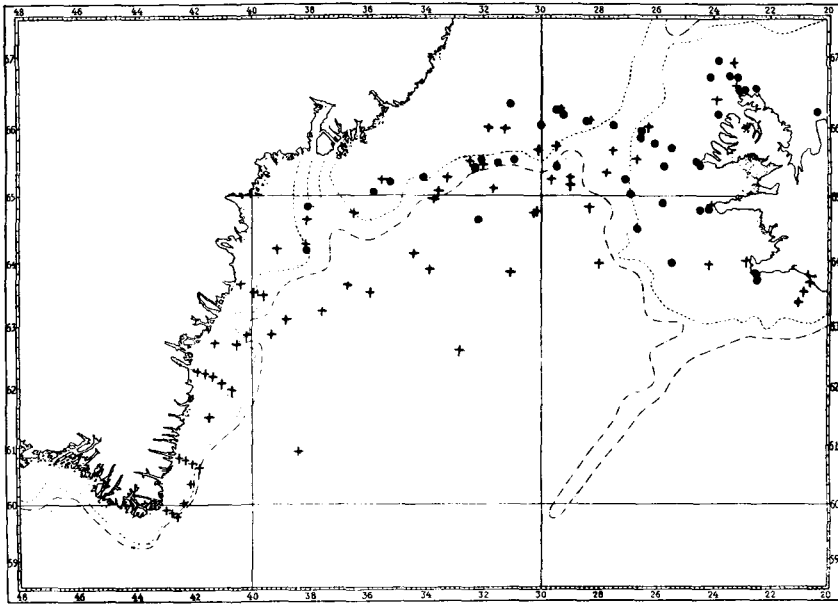


Fig. 6. Drift of Cod larvae in the Denmark Strait. Investigations 1931—34.
 ● Larvae present + no larvae

hydrographical conditions of the region are extremely well defined and are of determining influence on the life-history of the cod. Schmidt and Sæmundsson have shown this in various publications, and for the present purpose it will be sufficient to outline the main features. The south and west coasts of Iceland are washed, as known, by warmer Atlantic water, whilst the north and east coasts are washed by Arctic water; the cod spawn in spring (March—May) at certain places on the warm-water coasts, especially on the south-west; the anticyclonic current round Iceland carries large quantities of the tiny fry along the west coast to the north coast and even to the east coast, so that the fry are scattered over extensive nursery areas, where the reproduction of the cod does not occur or only to a very small extent.

As it happens, however, the whole of the water-masses on the west coast do not continue round the north coast, the so-called Irminger

Current breaking off, not only into the east-going branch along the north coast, but also into a west-going branch running from Iceland over towards East Greenland; the strength of the two branches evidently varies somewhat from year to year. Investigations since and including 1931 have shown that in certain years, especially in the month of July, large quantities of tiny cod fry are carried over towards East Greenland in the west-going branch of the Irminger Current. The chart, Fig. 6, shows where the cod fry have been found in these investigations. There are grounds for believing, therefore, that certain parts of the Greenland cod stock are brought as fry from Iceland, in the same way as the cod stock in the waters of North Norway and in the Barents Sea are partly recruited by fry from the Lofoten; this must certainly hold good for the larger part, if not the whole, of the East Greenland stock, but so far owing to various causes we have not succeeded in tracing the drift of the cod fry towards the south along the east coast down to Cape Farewell or round to the west coast, where we meet with a very rich stock of small cod in the southern districts, perhaps to a large extent of Icelandic origin. The following findings support the drift theory: spawning on a large scale of the cod at the most southerly part of West Greenland has not yet been proved; the fry cannot be brought to the most southerly part of West Greenland from the more northerly coastal banks, where spawning takes place, owing to the direction of the currents at West Greenland; racial studies have shown that the South Greenland cod resemble the Iceland stock of cod, though the characters investigated have on the whole slightly higher values¹) (Schmidt, 1930, pp. 7—8).

We must admit, however, that scientific proof of the drift of fry from Iceland to the south point and west coast of Greenland is not yet forthcoming; future investigation must determine this.

We have been obliged to dwell somewhat in detail on this early, passive wandering in the life-cycle of the cod, as it seems to form the foundation of a closer understanding of the wanderings which the marking of cod in the area have displayed.

At Iceland, as in other areas, we must make a sharp distinction between cod marked whilst still immature and those marked during the spawning period. Of the first group we have marked large numbers on the west, north, and east coasts of Iceland during a number of years; the recaptures indicate that young cod are in the main fairly stationary until the size is reached when maturity sets in; then they apparently leave the colder areas and seek the warmer Atlantic waters, which are most in evidence on the western parts of the south coast and on the west coast. Where the young cod have been marked on the last-mentioned coasts, however, they simply move out to suitable depths or at least do not undertake long migrations, since the natural conditions

¹) With our present knowledge we cannot exclude the possibility that the slightly higher values are due to the development of the tiny fry in the colder waters near Greenland during their drift from the warmer waters of Iceland to Greenland.

they need are to be found quite close to their place of growth; this is in full agreement with the experience gained with cod in many other parts of the region of distribution, both on the European and American sides of the Atlantic. The marking experiments of recent years have shown, furthermore, that West and South Iceland also attract maturing cod from far distant grounds in the north-west area of the Atlantic; for example, from Jan Mayen (Thor Iversen), from East Greenland and even from West Greenland right from Cape Farewell to Disco Bay, as will be described later. (See chart, Fig. 7.) A remarkable thing

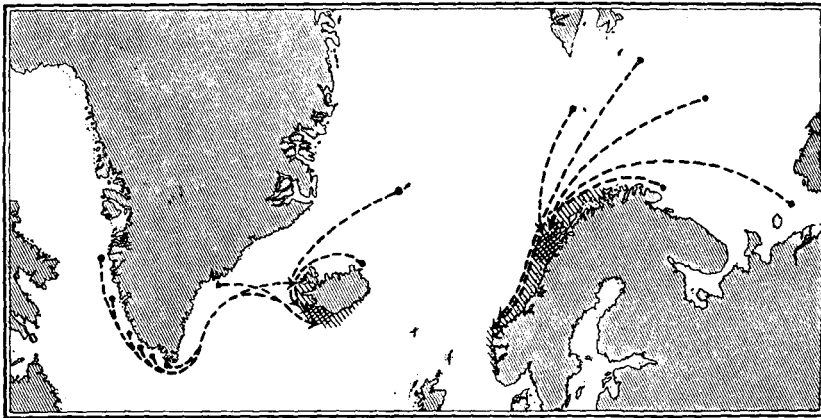


Fig. 7. Sketch of Cod migrations to spawning areas in the North Atlantic. Some few migrations given only. Principal spawning areas double hatched (South-West Iceland and Lofoten).

is that no cod marked as immature fish at Iceland have so far been recaptured outside the Iceland area. The recapture percentage of young cod marked at Iceland varies somewhat from place to place, varying between ca. 13 % and ca. 34 % in the experiments; on the whole the percentage of recaptures is lower than at the Faroes.

Of the second group of cod, namely, those marked on the spawning grounds in spring, mainly at the Westmanna Islands and on Selvogs Bank, but also at the mouth of Faxe Bugt, fully 5,000 specimens were marked in the years 1925—36; the recovery percentages for the different experiments lie usually between ca. 8 and ca. 13 % in all, thus lower than what was found for the young cod.

The following table shows the decrease in recoveries in the successive years after marking.

Number of recaptures of cod marked on the spawning grounds at South-West Iceland 1925—35 (4939 spec.)

Calendar year:	1.	2.	3.	4.	5.	6.	7.	Total
Number recaptured at Iceland.	240	120	49	22	8	2	2	443
Number recaptured outside Iceland area	10	8	2	2	1	—	—	23

Most of the cod at Iceland become mature at about 8 years old; some marked were, however, older; we can hardly expect, therefore, to follow them much longer than to the 6th year after marking, when they are 14 years old or some few years more.

The principal results of the marking experiments are thus as follows. After the spring spawning the fish spread in search of

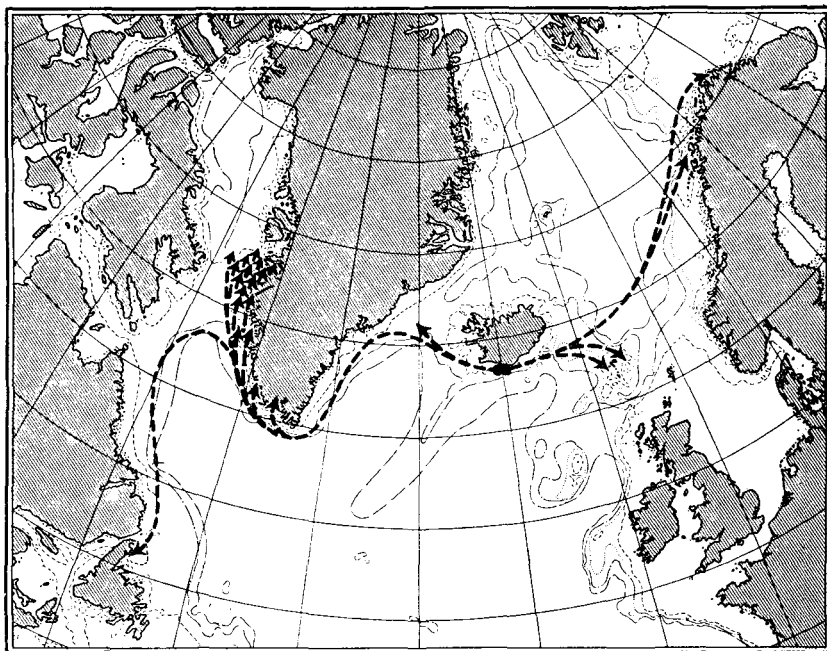


Fig. 8. Sketch of long-distance migrations of Cod marked at the spawning grounds off South Iceland. [The majority (ca. 95%) of recaptured cod from this spawning area has been reported from Icelandic waters inside the 200 metre line.]

food from the spawning places (where as elsewhere we only find a few adult fish in the summer). They move out over the coastal banks, some towards the north and east coasts where the summer fishery captures a number of the fish marked in the spring on the south-west coast. A number of the marked fish even reach much more distant localities, which means that not a few of the local stock must wander to those distant areas (see below).

The spawning time of next spring again shows at the spawning grounds mentioned a strong concentration of the marked fish, and also the succeeding springs up to the 5th or even the 6th year after marking, when a few recoveries have been reported from the principal spawning places. It may be remarked that spawning cod marked in one year at,

for example, Selvogs Bank on the south coast, may next year be retaken in the middle of the spawning time at, for example, the mouth of Faxa Bugt on the west coast, which seems to indicate that the fish do not year after year seek out exactly the same locality for their spawning, but that the natural conditions in the sea and the degree of ripeness of the fish itself determine where its spawning is to take place. This might have been supposed *a priori*, though it is difficult to prove, as the distances in question here are not greater than the fish could traverse in the course of a few days.

It is perhaps mainly of theoretical interest from the point of view of migrations to consider the specimens mentioned which have been recaptured far from the place where they were marked in the spawning time at South Iceland. The chart, Fig. 8, shows the wanderings of these individuals, though the route indicated is in no way intended to represent the actual route followed by the cod. In all, 23 individuals have been reported from outside the Iceland area, that is, about 5% of the recaptures. One of them was taken from the stomach of a Greenland shark (*Somniosus*) in the Denmark Strait, and presumably this specimen gives an indication of the route generally followed by the cod which wander to Greenland. All the others were taken during the fishing at the respective localities, and there is nothing to show that any error enters into the reports on these recaptures.

I shall not discuss here in detail the, as yet, few discoveries from Newfoundland, the Faroes, and Norway, though they indicate in a striking manner what phenomenal wanderers the cod may be in some cases, as also the importance for an understanding of the wide distribution of this species which these long-wandering individuals have, since doubtless other individuals have accompanied them. But I may briefly refer to the 17 individuals which were recaptured at West Greenland in 1930 to 1935, as they provide valuable information of general interest. We do not know whether these cod were originally of Greenland or Iceland extraction; as no juvenile cod marked at Iceland have ever been taken with certainty outside that area, it is probable that they grew up at Greenland (which does not mean that they were hatched at Greenland), and that after spawning at Iceland they have returned to Greenland. It will be very difficult to prove that such has been the case, but sooner or later it is hoped we may have means at our disposal to determine this important question. All the individuals which have made the journey are of the sizes which are known to have migrated from Greenland to Iceland, between 81 and 96 cm., one specimen of 107 cm. They were all taken at West Greenland in July—September, at a time, that is, when wandering shoals seek food along the coasts. The earliest taken was caught on 16. July; 9 were taken the same year as they were marked at Iceland, and 99 days is the shortest period from the day of marking to day of recapture; for 6 individuals the time was 108—116 days. As the route traversed must be at least between 1,000 and 1,250 nautical miles, we thus have here valuable information regarding rate of travel

of the cod in this area, even though we do not know the exact day when the migration commenced or how long the cod have been at Greenland before they were captured.

As will be seen, the average rate of travel per day lies between ca. 10—12½ nautical miles, or about 20 km. in the day. This speed approximates closely to the highest rate of travel known for cod recaptured shortly after marking at West Greenland itself (15 nautical miles or ca. 28 km. in the day); a similar rate is noted by Sund (1919, p. 63) for adult cod (Skrei) migrating away from the spawning grounds at Lofoten, namely, up to 24 km. in the day. As the cod during their wanderings away from the spawning grounds may be considered often to follow the currents near the surface, which at East Greenland, for example, run at a considerable speed, the actual movements of the fish have presumably been less than the rate indicated.

There is still one point to be mentioned regarding these emigrants, namely, that no fewer than 16 of the 23 individuals were marked in the same year at South Iceland (1931), most of them (10) even on the same ground during the same day. Of the 16 some (13) proceeded to the West Greenland banks (farthest north on these banks; see Fig. 8), 1 went to Newfoundland, 1 to North Norway, and 1 to the Faroes; the last 3 individuals mentioned have been, respectively, about 28, 38, and 28 months in the sea from the time of marking to recapture, and may thus possibly have wandered quite or partly passively with the large current-systems of the North Atlantic before they reached the places where they were recaptured.

It is a peculiar thing that the wandering impulse has affected such a large number of the cod marked on a few separate days (in addition to the example given, there are 3 other cases in each of which 2 specimens of the long-travelling cod were marked at the same time and place), and we are obliged to conclude that a purely mechanical factor influenced them and the others accompanying them out on these wide travels. Later, we shall consider this matter more closely.

In the foregoing we have been chiefly concerned with the wanderings which take the cod over great distances in their search for food; to a less extent we have mentioned the cod which do not undertake very great wanderings between two spawning periods, yet these undoubtedly comprise, according to the marking experiments, a large part of the total stock, e.g., at Iceland, though we are not yet able to estimate the scale of this. Consideration of the available data shows that the cod which undertake the food wanderings do not proceed uniformly in one direction in answer to a single stimulus or a few stimuli; on the contrary, the reaction is extremely variable with the different individuals or shoals of individuals which, for example, at the spawning grounds of South Iceland are in the stage when spawning is past and the food urge has become dominant. Some go a short distance, others farther, some even a great way (e.g., to West Greenland) in the period which lasts until certain unknown external and/or internal stimuli meet the cod in the receptive condition, when the need

to return to the spawning ground again becomes active. Our knowledge on this subject is extremely small at present; in fact, we can only guess that migrations and quantity of the food-animals, strength of the currents and the like, age of the cod and thus inclination to migrate, may be some of the factors which determine the extent of the food wanderings.

Greenland.

Along the enormous coastal stretches of West Greenland the cod has been found right from Cape Farewell at ca. 60° N. as far as ca. $72^{\circ} 21'$ N. in the Upernivik district; this area forms the extreme north-western limit in the distribution of the cod, where the stock shows great periodic fluctuations in regard to quantity and locality. During the summer and in warmer periods, like the present, the stock penetrates farther north but is periodically forced to turn south by the arctic water. The part between ca. $62\frac{1}{2}^{\circ}$ and 67° on the west coast, according to the experience so far gained, may be considered as the part of the coast where the stock has the best chance of succeeding, owing to the hydrographical conditions, even in the coldest periods, and it is therefore mainly on this stretch, in part out on the banks, in part inside the fjords, that we find some spawning. How far periods may occur in which the natural conditions offer practically a complete barrier to the reproduction of the cod at West Greenland, is not yet known, since the investigations have barely extended over 30 years, namely, from 1908, when A. d. S. J e n s e n began fishery investigations in these waters.

There is no doubt that the present warmer period has been favourable for the extension of this fish along the west coast towards the north, and this holds good also for a number of other boreo-subarctic marine animals, whilst purely arctic animals have been driven back to the north (see, for example, H a n s e n, J e n s e n and T å n i n g, 1935, pp. 13—15). As detailed records of the wanderings of the cod in this region are only available for the last 10—12 years, we have to remember that later experience from a cold period may give quite different results from those obtained up to the present; consequently, it is necessary to continue these investigations, *inter alia* the marking of cod, unbroken for a long period. In the years 1924—36 we have marked, as mentioned, 9,456 specimens of cod at about 100 localities everywhere at West Greenland from Cape Farewell to $70^{\circ} 40'$ N. both in fjords and on banks; the strenuous work of Mag. P a u l M. H a n s e n in this area has especially been of great importance. Of the marked cod, about 6% have been recaptured, more than half at Greenland and scarcely the half at Iceland.

In the following pages we shall briefly summarize the main results, so far as the migrations are concerned.

Quite a number of the cod have been found to remain stationary or only to undertake limited wanderings, and this part of the stock

includes especially the immature cod or the very large ones; among the last some have been taken even 5 years or later (up to 10 years later) on almost the same grounds as on which they were marked.

Other cod undertake somewhat longer wanderings within the West Greenland area and some apparently, especially the older cod, travel northwards as age increases to the northern bank areas round 66° to 68° N.; presumably they follow, perhaps passively, the direction of the current until the reduction in temperature calls a halt¹). Some of the cod wander from the fjords out on to the banks, and the reverse also occurs, but this exchange does not seem very pronounced and does not seem to stand closely in connexion with the reproduction of the species. A seasonal movement onto the banks, where the summer warmth is felt, and to the coastal areas has been noted quite distinctly.

The most prominent feature in the life-history of the Greenland cod is, however, that large numbers of cod leave the area entirely as maturity approaches, migrating up to a couple of thousand kilometres or more to reach the spawning grounds at West and South Iceland²). Thus, of the cod marked (1924—1935) 314 were retaken at Greenland, but no fewer than 256 at Iceland, that is, 45 % of all recaptures, which shows that myriads of cod must have emigrated to the grounds mentioned. From the time when these innumerable spawning cod leave West Greenland until they are recaptured at Iceland, they escape our observation; we do not know how they managed the journey, nor the route or depth in which they migrated, nor the rapidity with which they covered the distance, nor the exact time when the emigration begins from the several localities along the wide-stretched coastal areas of West Greenland — and still less the deeper causes of the departure, or how the fish find their way or, perhaps, feel their way on the route to the spawning grounds. Whilst the last-mentioned questions will remain long unanswered for this as for numerous other migratory species, there is a possibility that the first series of questions may be answered within not too distant a period, and we may venture already to make some tentative answers in regard to some of them.

It may be remarked, first of all, that the migration is a typical spawning migration, since it first begins when the cod are 8—12 years old and about 70—90 cm. in length, i.e., when the cod become mature. It is naturally not outside the bounds of probability that a few immature individuals may be drawn into the migration, as we know happens in the case of migrating birds. Further, it may be noted that the emigrants include but few of the really large cod over 100 cm., as the cod here as elsewhere evidently become somewhat less mobile as they grow older. It has thus been found that about 90 % of all the emigrants have a size between 70 and 100 cm.

The emigrants from Greenland to Iceland include individuals from

¹) It is remarkable that most of the migrant cod from Iceland to West Greenland were also retaken in this area (see Fig. 7).

²) As yet no cod marked at Greenland has been recaptured in the waters of Newfoundland or Labrador.

the whole coast between Cape Farewell and ca. 68° N. (almost to Disco Bay) and somewhat more from the banks and coastal waters than from inside the fjords, but this does not mean that the emigration proceeds evenly from the whole of this long distance; there is indeed a very great difference between the numbers of emigrants from the northern and from the southern districts of West Greenland. If we divide the west coast into a northern and southern area at approximately 62° N., i.e., at the extensive glacier at Frederikshaab which makes its influence felt far out to sea, we obtain the following percentages for the emigrants from the areas north and south of that point.

West Greenland	Number marked: 1924—1935	Number and percentage recapture:	
		at Greenland	at Iceland
Northern area	5640	250 — 4.4	82 — 1.5
Southern area	2860	64 — 2.2	165 — 5.8

This shows clearly that the emigration from the southern area is about 4 times as great as from the northern.

As we have seen earlier, migration also proceeds from Iceland to Greenland; consequently, since the marking at West Greenland was mainly carried out on wandering cod in the summer when the cod from Iceland¹⁾ could have arrived, it might be thought that a number of the cod marked at West Greenland had been marked after their arrival from Iceland and thus really told us nothing about the question how far cod which had grown up in the localities in question at Greenland had emigrated to Iceland. If, to clear up this question, we consider the numbers of individuals of all the emigrants marked before they became mature, we obtain some interesting results. Among the emigrants from the northern area, there were only 8 individuals below 70 cm. when marked, which were almost certainly immature fish that had not previously undertaken any long migration, whilst among the southern emigrants no fewer than 54 individuals were below 70 cm. on marking. In the northern area 1,415 cod below 70 cm. were marked, and of these only 0.6% were recaptured at Iceland, whilst in the southern area 1,491 cod of less than 70 cm. were marked and of these no fewer than 3.6% or 6 times as many as from the northern area were retaken at Iceland.

It is thus evident that the emigration to Iceland proceeds mainly from the southern area, and that as regards the cod which have grown up at West Greenland the great majority of those leaving Greenland come from the southern area, while cod of the northern area chiefly remain there. Since now, as mentioned before, there is not a little evidence that perhaps the major part of the small cod in the southern area originally came from Iceland as young fry, we reach the probable conclusion that the emigration to Iceland finds its best

¹⁾ These may originally have grown up at South Greenland.

explanation in this, that the cod return to the place where they were born in order to reproduce their species there. It is a task for the future to find support for this theory, but it agrees well with what we already know regarding the migrations in the Norwegian region, where undoubtedly the major portion of the cod which have been carried as fry away from the Lofoten northwards to Finmark and beyond, if they live long enough to reach maturity, migrate back almost to the original place to reproduce their kind.

Certain other phenomena connected with the migrations may advantageously be considered through the information provided by the marking experiments of recent years.

The marking experiments at Greenland were mainly carried out in the months of July—October, i.e., at a period when the spawning was over, and the impulse to return to the spawning grounds is not developed until late in autumn or winter. Consequently, we have never obtained from the Iceland area any recaptures in the calendar year in which the cod were marked at Greenland; the recaptures appear first in the next calendar year. This will be seen from the following summary.

Recaptures of cod marked at West Greenland 1924—35 (8500 specimens).

Calendar year:	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	Total
Number recaptured at Greenland ..	83	106	53	38	17	9	3	3	1	1	314
Number recaptured at Iceland	0	112	74	35	18	12	4	0	1	0	256

Among the Greenland cod recaptured at Iceland in the course of the years some have perhaps remained on the Iceland banks, to stay there always after their first migration; thus we see that a few "Greenland cod" have been taken at Iceland some time after the cessation of spawning, i.e., even as late as in the month of September; but in the period October—January no "Greenland cod" have been retaken at Iceland, where, however, the fishery at this time is but small. It is most likely that some of the adult cod taken at Greenland, which have spawned more than once, have several times made the journey to Iceland in order to spawn, but have again returned. Only double marking and recapture of the same individual in both areas can determine this question with certainty; and successful double marking will be an extremely difficult matter with migrating marine fish.

The earliest date for recapture of a "Greenland cod" at Iceland in the year after marking was 10. February, one "Greenlander" having reached North-West Iceland by this date, scarcely 6 months (174 days) after being marked at South Greenland; a few others were recaptured in the course of February and March, but the majority were not taken on the spawning grounds till April—May, at the height of the spawning season at Iceland. It may be noted that the emigrants were retaken on

the spawning ground at Iceland exactly at the same period as the cod marked at Iceland itself, not specially earlier or later.

We do not know exactly when the spawning cod begin the emigration at West Greenland in the autumn or winter; a few recaptures in October—November south of the places of marking on the west coast of Greenland may perhaps be taken as the first indications of a beginning of the migration to Iceland, but the material is still far too meagre to permit of any definite conclusion.

As the marking of migrating cod could not be undertaken at Greenland in the period November to April, we have but little to go upon with regard to the rate of travel during the emigration; the shortest period between the marking at Greenland and recapture at Iceland was quite 5 months (164 days) and in this period at least 720 nautical miles have been traversed (from South Greenland to South-West Iceland), giving at least ca. 7 km. per day. A few other specimens have covered the distance to Iceland at about the same rate, but the majority have apparently taken considerably longer periods, as we know nothing of the time when they started. We cannot yet say with certainty, therefore, how quickly the migration is accomplished, and the reason is not only that the marking at Greenland has not been carried on sufficiently far into the winter, but also because we do not know what route the migrating cod follow from West Greenland to Iceland. Actually we do not yet know whether the spawning migration of the cod is *contranatant* or *denatant*. Various conditions might indicate that the route is possibly from the point of South Greenland along the east coast to the ridge between Greenland and Iceland, thence over this or along its southern edge to the Iceland area itself; in favour of this is the fact, among others, that the earliest recaptures come from North-West Iceland. Along this route the migration would be against the current, *contranatant*, as is the migration in most cases of purely marine fish when they make for definite spawning grounds. If the cod from West Greenland should migrate in the same direction as certain currents which might carry them more or less passively to Iceland, then the migration would have to proceed in the currents south of Greenland and Iceland or in the southern part of the Denmark Strait. We have seen that the migration from Iceland to Greenland, with the current, may take fully 3 months; it is therefore natural that the migration in the opposite direction should take much longer (5—6 months is the shortest observed time). There is much to indicate certainly that the food migrations, which most often go with the current (*denatant*), are mainly performed in the more rapid waters of the surface layers, whilst the migration to the spawning places possibly occurs at a greater depth, where the speed of the current is reduced, and where therefore the emigrants do not meet with so much resistance. But we know very little with certainty regarding this. If it is necessary for the fish to orientate themselves in the current by means of the sense of touch or sight, we should imagine that during migration they must necessarily follow the bottom, but we have no idea what sense it is that guides

them to their goal. Observations on the behaviour of ripening and ripe cod towards different stimuli would undoubtedly be of great importance for our future investigations on their migrations. Far too few observations undoubtedly have so far been made in this field.

As already noted, the emigration of Greenland cod to Iceland must certainly embrace millions of individuals, in certain years at any rate. But it is possible that hydrographical and other factors have a great influence on the magnitude of the migration in different years, though we are unable to suggest the possibility of any periodicity. The emigration of the present period has chiefly taken place from and including the year 1930, i.e., in the period when marking experiments were carried out on a large scale at the most southerly districts of Greenland, and when at the same time the two year-classes 1922 and 1924 have shown themselves to be particularly abundant. Apparently a condition of standstill has now arrived, as none of the cod marked at Greenland in 1935 have been taken at Iceland in 1936, but it must be admitted that in 1935 the marking experiments were not carried out at that part of West Greenland from which, according to our experience, the greatest emigration takes place. The year 1936 has seen an enormous decline in the Iceland cod fishery; so far as the catch of large cod is concerned, the decrease for Iceland from 1935 to 1936 has been over one-third. To what extent there is a causal connexion between the two phenomena — emigration from West Greenland and the catch of large cod at Iceland — it is not yet possible to express any opinion, especially because, as already noted, there have not been a sufficient number of cod marked each year in the most southerly districts of West Greenland, whence, as we have seen, the greatest emigration occurs. The importance of clearing up this question, both for the fishery and for the more theoretical side of the matter, is obvious.

The following table gives a summary of the numbers of recaptures in the years 1924—1936 at Greenland and at Iceland.

Recaptures of cod marked at Greenland for each year.

	Number recaptured at		% recaptured at	
	Greenland	Iceland	Greenland	Iceland
1924	1	0	100.0	0
1925	15	0	100.0	0
1926	16	0	100.0	0
1927	16	1	94.1	5.9
1928	6	0	100.0	0
1929	9	0	100.0	0
1930	16	7	65.7	34.3
1931	32	47	40.7	59.5
1932	44	35	55.7	44.3
1933	22	57	27.8	72.2
1934	48	53	47.3	52.7
1935	58	44	56.9	43.1
1936	31	12	73.0	27.0

We have now given a brief description of the conditions at West Greenland, and, as has been mentioned, quite similar movements of the cod are found in East Greenland, namely, an emigration of the mature fish to the spawning grounds at Iceland; not a single individual has gone with the East Greenland current round to West Greenland. Altogether we have 15 recaptures of cod from Iceland marked by Danish workers and 10 marked by Thor Iversen, i.e., a total of 25 specimens which have made the journey from East Greenland (Angmagssalik district) to Iceland. These results from East Greenland need not, however, be dealt with here in detail, but I may note that the route of migration from here to Iceland is still unknown; we do not know whether the movement is towards the warmer and saltier Atlantic water which streams over from West Iceland towards East Greenland, or whether the fish follow current-systems which might carry the cod passively to South-West Iceland.

Dispersion of the cod over wide areas.

The records obtained in recent years from marking experiments of the long journeys undertaken by cod (Fig. 8) are now so numerous that we should endeavour to find a general, though provisional and hypothetical, explanation for them. The places of recovery of the cod which have started from the spawning places at Iceland, have been Greenland, Newfoundland, the Faroes, and Norway; and we may suppose that the prevailing surface-current is the power which assists the wandering cod to the distant localities at which they are recaptured; that is to say, it is not altogether due to chance that the recapture of the marked cod took place just where it did, but to the fact that during the denatant period of their life-cycle, the food migrations, the cod scatter away from the spawning areas with the prevailing currents.

It is a fortunate circumstance that for a number of years now, whilst the marking experiments were being carried on, we have also been throwing surface drift-bottles into the sea at various places round Iceland¹). Many of these have gone to the Faroes and Norway, a few to North Scotland, and one to West Greenland.

Comparing the returns of recaptured drift-bottles with those of recaptured cod from corresponding areas, we naturally find disagreement in many cases with regard to the time taken between despatch and return, but on the other hand we find some which agree precisely in this particular. I may mention a couple of cases which illustrate this point.

¹) The experiments of 1928 and 1929 were described by Tåning: Rapp. et Proc. Verb. 72, 1931, where reference is also made to some older experiments; the 1931 and later experiments have not yet been published.

From Iceland to Greenland:	
Drift-bottle from S. Iceland to SW. Greenland..	133 days
Cod from S. Iceland to SW. Greenland	109 days
From Iceland to Norway:	
Drift-bottles from E. and SE. Iceland to NW.	
Norway (near Andenes)	300—362 days
Cod from S. Iceland to Andenes (NW. Norway)	ca. 360 days
From Iceland to the Faroes:	
Drift-bottle from E. Iceland to the Faroes	97 days
Cod from S. Iceland to the Faroes	84 days
Further, a special case:	
Drift-bottles from S. Iceland to N. Scotland	832—833 days
Cod from S. Iceland to the Faroes	861 days

I mention this last case just to emphasize the possibility that certain individuals among the cod may enter the great current-systems south of Iceland and thus be carried with the surface currents from there to far distant areas, just as various bottles are carried from Iceland in one or other of the great current-systems and their drift is consequently longer than the direct route would indicate¹).

I may mention lastly that several drift-bottles thrown out in July—August between North-West Iceland and East Greenland were retaken in South-West Iceland about 200—220 days, or 6—7 months, later, after having circulated so long in the great current-system between South-West Iceland and South-East Greenland. A “migration-time” of similar duration, namely, about 210—220 days, is shown by some cod marked in September in the Angmagssalik area and recaptured the next spring at South-West Iceland, assuming that they have begun their migration to Iceland soon after the marking. Certainly the current-system in Denmark Strait has a great influence on the movements of the cod in this area, but we still know far too little of the conditions in this little-investigated area. Our knowledge of the complicated current-systems in this area is undoubtedly far too meagre to permit us to indicate with any certainty the directions taken by the drift-bottles (and so probably by cod).

So far we have but few cases showing an agreement between duration of drift of the drift-bottles and cod on migration, but I have referred to these interesting cases here to show that we must obtain more information from cod marking experiments and simultaneous use of drift-bottles.

We should also consider the question whether the process of marking may not artificially bring some of the cod up from the bottom-layers (whence they are taken almost always before marking) up to the layers where they come under the influence of the surface-currents.

¹) It may be remarked here that it is naturally very doubtful whether several of the routes marked on the chart, Fig. 8, really indicate the routes followed by the cod in question.

From our experience at East Greenland and elsewhere, we know that numbers of wandering cod come up to the surface layers, either actively or passively, where they pursue various kinds of food (crustaceans, sand-eels, capelan, etc.). Oscar Sund's extremely interesting observation of the ascent of the spawning cod from the bottom layers up to the surface during the spawning time may be referred to here, as it indicates one of the causes which possibly lead to large quantities of the cod being carried passively far afield, in contrast to those which remain on the bottom and thus appear to be less mobile.

Regarding the cod that have been one year on the spawning grounds, is it that after their food-wanderings the majority return again next year to the spawning grounds of the coastal banks, by chance, more or less passively, or perhaps led by a certain sense of direction unknown to us? Or is a large number lost to the fishery by their going to localities where a fishery is not carried on?

We have but imperfect knowledge as to the manner in which the masses of cod disperse from the spawning area. It seems, at least at certain places, as if they scatter mainly in the direction of the currents over the coastal banks; as examples of this, I may refer to the movements of the cod in North-West Norway and round Iceland, after spawning is over on the principal grounds. Quite a number of cases indicate that considerable quantities of cod on their food migrations also scatter out over the more open waters, even over great depths. The extensive fisheries of recent years in the Barents Sea and at Bear Island have shown that the cod scatter there over immense areas; further, we have a number of facts which indicate clearly that a not inconsiderable number seek their food pelagically out over great to very great depths, more or less distant from the coastal banks. Some of these records may be noted. For many years the French fishermen, using floating lines and hand-lines, and also the Faroese fishermen with hand-lines, have obtained considerable quantities of cod living pelagically north-east and east of Iceland out over great depths. Johan Hjort, Johs. Schmidt, and others have also found cod living pelagically over great depths (1000—2000 m. and more) in considerable quantities; the food they are specially seeking seems to be, *inter alia*, Schizopods and other crustaceans. The otoliths of cod as of other gadoids have been found in bottom deposits from great depths (ca. 1800 m.) and were believed to have come from specimens which had lived pelagically (A. d. S. Jensen, 1905). On the "Øst" Expedition of 1929 large quantities of cod were observed near the surface in the drift-ice area between Iceland and East Greenland (Brarud and Rud 1932). J. Charcot and Thor Iversen have found large numbers of cod of Icelandic origin at Jan Mayen, which Iversen has shown by marking experiments to migrate to Iceland to spawn and which therefore must cross the deep sea between Iceland and Jan Mayen. It is also certain that the widely migrating cod marked at Iceland, which have been recaptured in recent years at

Newfoundland, Greenland, in Denmark Strait, at the Faroes and at Norway, must have migrated over waters with depths greater than ca. 500 m. This movement of the cod out over great depths has been emphasized many years ago by Joh an Hjort. A consideration of the results from the series of marking experiments carried out during the last 10—15 years, leads us to the view that the annual decline in the cod stock in certain areas is very considerable, perhaps partly on account of this extensive pelagic dispersion of cod, at least in certain periods of their lives; in other words, a not inconsiderable part of the cod stock which scatters out from a given spawning ground, e.g., that at Iceland, or a given nursery area, is probably lost out in the open waters or elsewhere, and thus for a great part does not come within the ken of the fishermen on the banks now fished; for example, we know that the cod sometimes occur in quantities at Jan Mayen where there is no fishery.

It will be of interest here to consider the results of a series of marking experiments on the spawning grounds themselves of Iceland to see how great is the relative decrease from one year to another. In the experiments of 1929—33, a total of 3322 individuals were marked of a size greater than 70 cm., that is, undoubtedly all or nearly all spawning fish; of these, 336 specimens have been recovered, distributed as shown below in the year of marking (year 1) and following years (the great majority were taken on the spawning grounds in the years noted in the period March—May, and a few outside the spawning times later in summer).

**Number of recaptured cod (> 70 cm., initial length)
from marking experiments on the spawning grounds at South Iceland
1929—1933 (3322 cod marked)**

Calendar year:	1.	2.	3.	4.	5.	6.	7.	Total
Number	164	91	47	24	8	1	1	336
%	48·8	27·1	14·0	7·1	2·4	0·3	0·3	

The number of recaptures in the first year is probably lower than it ought to be, as several of the marking experiments were carried out in the latter half of the fishing season. In the different experiments, carried out for a number of years on the spawning grounds at South Iceland, we have found that the percentage of recaptures in the first year was only about 5 % of the total marked¹⁾; even if a number of marks are undoubtedly overlooked by fishermen, and so do not enter our records, and even if several marking experiments have been

¹⁾ E.g., of 1073 cod marked 1932 and 1934 on the spawning grounds off South-West Iceland in March (i. e., at the beginning of the fishing season) a total of 51 specimens or 4·7 % were recaptured during the year of marking.

carried out late in the spring months, which also makes the recovery percentage lower, yet the recapture figure shows that it is but a small fraction of the enormous shoals of cod which are exploited by man as they seek the spawning grounds.

From the above table it will now be seen that the number of recaptures is almost halved each whole year¹); the figures thus show, roughly speaking, that only one-half of the cod which in one year come to the spawning grounds at South Iceland, return again the following year, in addition to the new contingent of spawners and presumably quite a number of older cod which come from other areas and which have not previously been to these spawning areas.

The causes of this approximate halving from year to year may be imagined as follows:

1. marks are lost;
2. the cod die owing to (a) effort of spawning, (b) sickness or disease, (c) old age or (d) falling victims to enemies;
3. dispersion to areas where there is no fishery;
4. the fishery.

As we are considering here the relative numbers of recaptures from year to year, it is of no importance in this connexion if all the marks fished have not been delivered, since this source of error must be approximately the same from year to year. As already noted, some of the cod undoubtedly lose their marks in the sea, but, as also discussed earlier, the method of marking used must for many reasons be regarded as fairly satisfactory; during the first 3—4 years at any rate the loss of marks is hardly appreciable, since we are only dealing here with recaptures of cod marked as large individuals. The majority of the marked cod were 70 to 100 cm. long on marking, and these sizes of cod are about 6—10 years old at Iceland, and they may still as 12 to 14-year-old fish play a great part in the catches of the fishermen; thus a large number of them can appear on the spawning grounds several years after the marking. A part of the decrease is, however, due to the natural decrease with advancing age, and disease and possibly loss of strength in the act of spawning also cause some decline in numbers. The large cod here in question have quite a number of enemies, apart from man, in the Iceland area, e.g., Greenland shark, halibut, seal, etc., and these will also influence the decrease. Lastly, in accordance with various observations noted in the foregoing, the dispersion to other areas (to some extent also to the open waters) in certain parts of the region of distribution of the cod, occasions a loss of a not inconsiderable portion of the stock which in one year has visited the spawning grounds and which therefore might be expected

¹) Some few recaptures from the latest years may still come in, so that the figures for the 5th and following years may yet be increased.

to return the following year¹). Presumably, however, many of the cod which have disappeared in the open waters will sooner or later return to shallower depths, but assuredly in the case of many to areas where no fishery is carried on.

I have referred to these considerations on the dispersion of the cod after spawning, as they show that the series of continuous experiments which has now been carried on for a number of years, can afford not only direct information regarding the migrations, but also information regarding the decrease within the stock in the different areas which would be difficult to obtain in any other way. But the necessity of carrying on the marking experiments on a larger scale than hitherto must be emphasized, as also that they should be better organized and their technique improved; the marking method, as a means to the study of the migrations of this species, is far from being used as effectively as it might be.

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¹) It is commonly believed that after spawning for the first time the cod again spawns in each of the following years, at least so long as it is in possession of its full strength; this view is supported by recent Norwegian investigations in the Skagerak (Sivertsen, 1935); but the cod belonging to the northern populations should also be examined in this respect, as it is not certain *a priori* that the conditions are the same as among the southern populations.

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