CONTRIBUTIONS TO THE BIOLOGY OF THE MACKEREL *SCOMBER SCOMBRUS* L.

II. A STUDY OF THE FISHERY IN THE SOUTH-WEST OF ENGLAND, WITH SPECIAL REFERENCE TO SPAWNING, FEEDING, AND 'FISHERMEN'S SIGNS'

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(Plate I and Text-figs. 1–6)

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Introductory Survey

In a previous paper (Steven, 1948), brief accounts are given of three distinct mackerel fisheries that at one time existed in the south-west of England—an inshore fishery in the English Channel carried on from Plymouth, a deep-sea fishery from Newlyn, Cornwall, and an inshore fishery from Newlyn and some other Cornish ports. One of these fisheries, the Plymouth one, no longer exists. After a few years of considerable activity following the termination of the 1914–18 war, this fishery collapsed in 1924 (Table I) and came entirely to an end a few years later. The small quantities of mackerel landed at Plymouth in subsequent years have been incidental catches by vessels fishing for herrings or pilchards.

The Cornish inshore fishery took place mainly at no great distance to seaward of the northern shore of the Devon-Cornwall peninsula and was carried on chiefly by small local craft, both wind- and motor-driven; but a number of visiting east-coast drifters used also to participate, especially during January and February, when stormy weather prevented their going very far to sea in search of other shoals in deeper waters beyond the Scilly Islands (Steven, 1948,

p. 520, fig. 3). Soon this fishery too fell upon hard times and the small local craft gradually abandoned mackerel fishing. In 1931 the local Fisheries Officer reported to the Cornwall Sea Fisheries Committee that, so far as local vessels were concerned, the fishery had arrived almost at the point of extinction.

The failure of both the Plymouth and Newlyn inshore fisheries was due to a decline in the quantity of fish in nearby waters, combined with low prices which made small catches unremunerative. The fall in fishing yield in those years is clearly reflected in the mean weight of fish per landing by the local vessels engaged in the Newlyn fishery. At no time[1] from 1906 (when reliable returns first became available) until 1927 did this average fall below 10 cwt. (Text-fig. 1), and was generally much higher. But with the single exception of 1928 the 10 cwt. figure was never again reached; in fact the individual

TABLE I. QUANTITY OF MACKEREL LANDED AT PLYMOUTH, 1919–38 INCLUSIVE (IN CWT.)

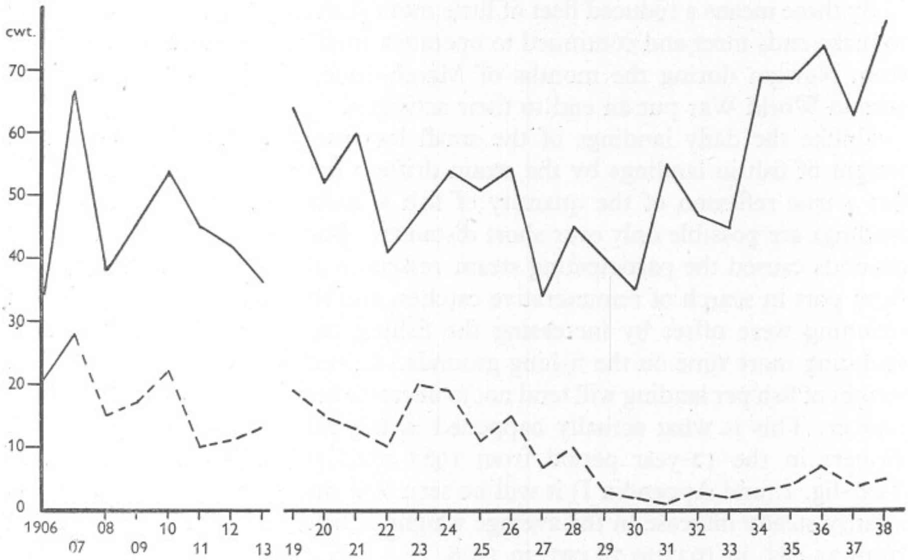
Year	Quantity	Year	Quantity	Year	Quantity
1919	**15,521**	1926	4080	1933	2200
1920	**33,618**	1927	3080	1934	1859
1921	**18,117**	1928	2582	1935	2401
1922	**18,198**	1929	3005	1936	2670
1923	**15,551**	1930	3109	1937	1669
1924	5,366	1931	3101	1938	1156
1925	5,229	1932	4709		

landings were generally less than half that amount. These weights are a reasonably accurate index of the quantity of fish available on the fishing grounds because landings by local vessels represent only one night's fishing.

Many of the steam drifters reacted to the decline in the inshore fish stocks by postponing their arrival in Newlyn until about the beginning of March in each year, when weather conditions permitted them to proceed at once to more distant fishing localities in the open sea well beyond the Scilly Islands, where better catches were to be had on different bodies of fish migrating in from the westward. But even as late as 1930 some steamers still endeavoured to obtain satisfactory catches in nearby localities in January and early February, but without success, and they worked at a loss until better weather in March enabled them to proceed to the distant grounds where better results were obtained. This was the very last year in which steam drifters fished from Newlyn as early as January. Since that time the steam-drifter fishery has opened invariably on the deep-sea grounds not earlier than the last days of February or the first days of March. But even the deep-sea grounds failed to provide satisfactory returns for all the participating craft and many of them gave up mackerel fishing altogether (Table II), their numbers falling from 90 in 1920 to 23 in 1940, the last year of normal fishing.

[1] War years excepted.

The steam drifters that did not give up fishing strove to maintain their catches at remunerative levels by working at ever increasing distances from land until eventually, from about 1927 onwards, it became the regular custom of most of the fleet to open the fishery every spring on grounds as much as 100 miles or more to seaward of the Bishop Rock (Scilly Islands) on bearings lying generally between W.N.W. and W.S.W.



Text-fig. 1. Mean weight in cwt. of mackerel per landing at Newlyn in the years 1906–38 inclusive: (——), by steam drifters; (- - - -), by local craft.

TABLE II. NUMBER OF STEAM DRIFTERS FISHING FROM NEWLYN IN THE YEARS 1920–40 INCLUSIVE

Year	No.	Year	No.	Year	No.	Year	No.
1920	90	1926	82	1931	47	1936	31
1921	60	1927	74	1932	43	1937	23
1922	80	1928	60	1933	43	1938	27
1923	80	1929	55	1934	35	1939	25
1924	68	1930	52	1935	34	1940	23
1925	87						

Daily landings from these distant grounds obviously became impossible, so the practice of preserving the fish in ice was extended and improved to enable the ships to stay at sea for more than one night at a time on each fishing trip. Single landings at the beginning of the season, therefore, came to represent as many as 4 nights' fishing.

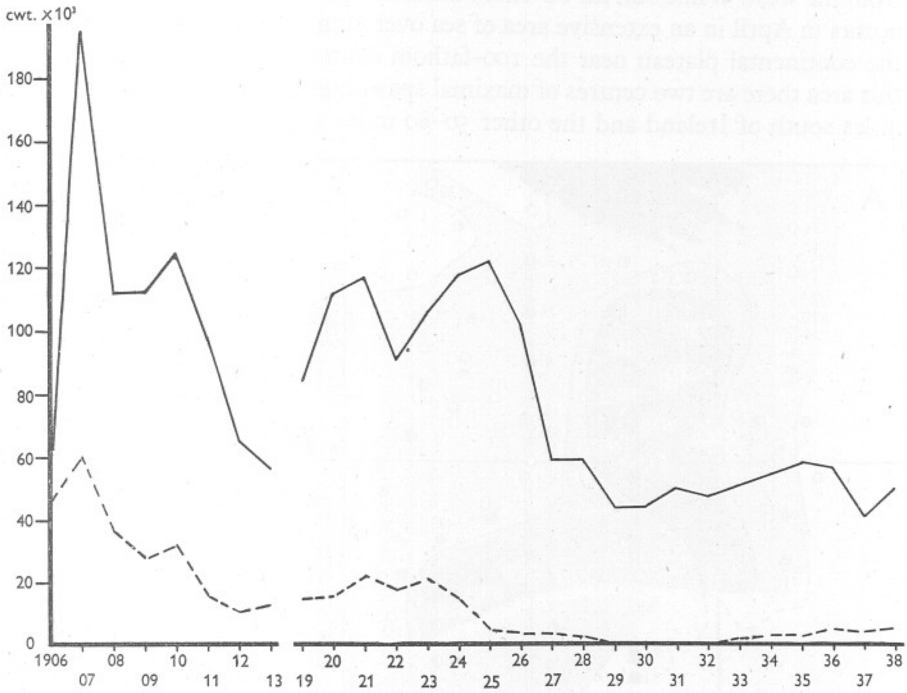
At the same time the fishing capacity of each drifter was also undergoing an important change. Before the war of 1914–18 the nets used by those craft were of a type known as 'fly nets' and had a standard size of about 20 yd. length and 5 yd. depth. On resumption of fishing after peace returned a larger 'footrope net' began to be introduced which is about 33 yd. long and just over 6 yd. deep. By about 1933 the old type had been almost entirely replaced by the new. The number of nets in each fleet remained unchanged at approximately 180. The fishing area of each drifter's fleet of nets was therefore almost exactly doubled, rising from approximately 18,000 sq.yd. to approximately 36,000 sq.yd.

By these means a reduced fleet of little more than a score of drifters was able to make ends meet and continued to operate a small deep-sea mackerel fishery from Newlyn during the months of March–June until the outbreak of the second World War put an end to their activities.

Unlike the daily landings of the small local vessels, therefore, the mean weight of fish in landings by the steam drifters from about 1927 onwards, is not a true reflexion of the quantity of fish available on the grounds. Daily landings are possible only over short distances. But scarcity of fish on nearby grounds caused the participating steam vessels to go farther and farther away from port in search of remunerative catches, and the additional costs of extra steaming were offset by increasing the fishing capacity of the nets and by spending more time on the fishing grounds. In such circumstances the mean weight of fish per landing will tend not to decrease but to increase as fish become scarcer. This is what actually happened in the Newlyn Deep-Sea Mackerel Fishery in the 12-year period from 1927 until 1938. From inspection of Text-fig. 1 (and Appendix I) it will be seen that during those years there was a fairly steady increase in the average weight of fish per steam-drifter landing from 34 cwt. in 1927 to 78 cwt. in 1938.

There was no corresponding increase in the total yield of the fishery. This, in fact, from 1927 onwards, remained remarkably constant (Text-fig. 2), because, although the mean weight per landing increased, the number of landings decreased. This decrease in the number of landings was due only in part to the increased length and duration of the fishing trips. Another and more important cause was a gradual decline in the public demand for mackerel. This is indicated by their market value on first sale (Table III), which fell steadily from 19*s*. 5*d*. per cwt. in 1929 to only 9*s*. 11*d*. in 1936. There was a slight recovery to 13*s*. 8*d*. in 1937, but another fall to 12*s*. 4*d*. in 1938.

More mackerel could have been landed by the existing fleet if the demand for them had existed; for from about 1930 onwards the skippers of steam drifters working from Newlyn voluntarily agreed from time to time to stay in port for from 1 to 3 days after each landing in order not to cause a glut of unwanted fish on a sluggish market. In some years approximately 20% of possible fishing time was lost in this way. The Statistical Tables of Sea Fisheries in England and Wales contain data covering the total landings of mackerel at Newlyn and the total number of landings by the different kinds of vessels, but no information is given either with the Tables or in the Official Reports (1906–38) concerning such changes in the fishery as have been briefly described above. Unfortunately, therefore, the official statistics concerning the Newlyn deep-sea fishery for mackerel have little or no biological significance. Important



Text-fig. 2. Total landings of mackerel at Newlyn (in thousands of cwt.) in the years 1906–38 inclusive: (——), by steam drifters; (- - - -), by local craft.

TABLE III. AVERAGE VALUE OF MACKEREL PER CWT. IN ENGLAND AND WALES FOR THE YEARS 1919–38 INCLUSIVE[1]

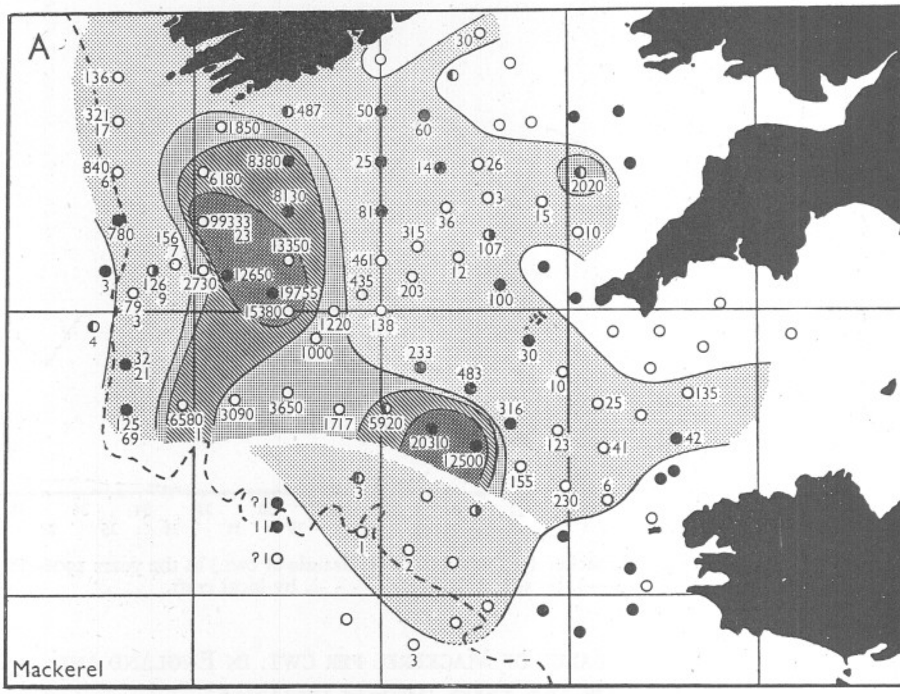
Year	Value	Year	Value	Year	Value	Year	Value
1919	39*s*. 10*d*.	1924	17*s*. 9*d*.	1929	19*s*. 5*d*.	1934	11*s*. 3*d*.
1920	15*s*. 1*d*.	1925	16*s*. 4*d*.	1930	17*s*. 9*d*.	1935	11*s*. 7*d*.
1921	21*s*. 6*d*.	1926	17*s*. 1*d*.	1931	14*s*. 7*d*.	1936	9*s*. 11*d*.
1922	16*s*. 9*d*.	1927	19*s*. 5*d*.	1932	13*s*. 9*d*.	1937	13*s*. 8*d*.
1923	15*s*. 10*d*.	1928	17*s*. 2*d*.	1933	12*s*. 3*d*.	1938	12*s*. 4*d*.

[1] From Statistical Tables of Sea Fisheries.

factors other than the availability of fish on the fishing grounds have greatly influenced both the number and size of individual landings and the total yields—factors that have not been taken into consideration during the compilation of the tables nor recorded with them.

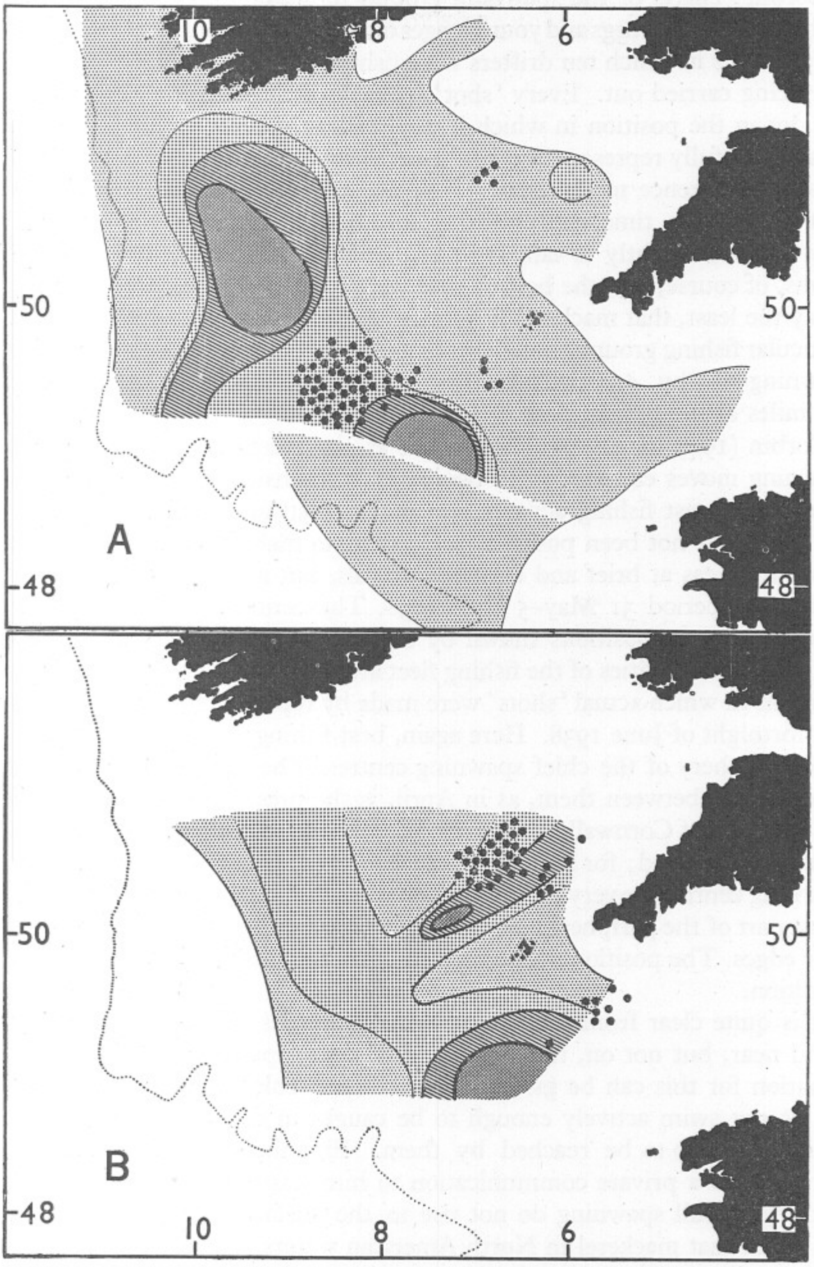
Position of the Fishing Grounds in Relation to Spawning Areas

The Newlyn deep-sea fishery takes place on fish that are moving landwards from the west. While still far off-shore most of them spawn. Heaviest spawning occurs in April in an extensive area of sea overlying the outer (seaward) part of the continental plateau near the 100-fathom contour (Corbin, 1947). Within this area there are two centres of maximal spawning intensity, one lying 40–100 miles south of Ireland and the other 50–80 miles south-west of Bishop Rock.



Text-fig. 3. Distribution of mackerel eggs (1–1000; 1001–5000; 5001–10,000; > 10,000) and young stages in the Celtic Sea in April, 1938. Reproduced from Corbin, 1938, p. 74. For further explanation see text.

The general shape and extent of those spawning areas in April 1938—a typical year—are clearly shown in Corbin's fig. 5 A (1947, p. 74) reproduced here as Text-fig. 3 (except for the omission of a coloured patch over the westernmost stations where young stages were recorded). The numerals in general refer to numbers of eggs, taken in half-hour oblique hauls with the 2 metre stramin trawl by the method described by Russell (1930, 1935). Some, however, attached to the westernmost stations, refer to the planktonic young stages—such as the lower of a pair, or single numbers outside the egg limit (*vide* the original for more exact details).



Text-fig. 4. Mackerel spawning grounds and the locus of mackerel fishing by Newlyn-based steam drifters: (A), in April, 1938; (B), in May-June, 1938. Stippling indicates density of mackerel eggs, as in Text-fig. 3.

Corbin's charts of the spawning ground for 1938 are copied in Text-fig. 4 with the number of eggs and young stages omitted, but having inserted upon them the positions in which ten drifters were fishing during the time that the survey was being carried out. Every 'shot' by each of those drifters is indicated by one dot in the position in which it was made. Fishing by those ten selected vessels was fully representative of the activities of the full fleet of twenty-seven vessels. Reference to the chart (Text-fig. 4A) clearly shows that the fishing fleet was at the time concentrating its attention upon a well-defined area between, and slightly to landward of, the two chief spawning centres. This means, of course, that the best catches were to be had there. It is remarkable, to say the least, that mackerel fishermen should so unerringly have found this particular fishing ground though quite unaware of the presence of any intensive spawning nearby, especially as these grounds lie right out in the open sea 130 miles or more from port.

Corbin (1947, p. 72) has shown that as the season advances the locus of spawning moves eastwards and decreases in intensity. At the same time the locus of greatest fishing activity also moves eastward (Steven, 1948, p. 523, fig. 4). It has not been possible in any year to make frequent surveys of the spawning areas at brief and regular intervals, but a second survey was made during the period 31 May–5 June 1938. The centres of maximal spawning were then in the positions shown by the dark stippling in Text-fig. 4B. On this chart the activities of the fishing fleet are also shown by dots indicating the positions in which actual 'shots' were made by representative ships during the first fortnight of June 1938. Here again, best fishing was found near the landward periphery of the chief spawning centres. The reason why fishing is not concentrated between them, as in April, is the presence of the Scilly Islands and the 'toe' of Cornwall in the very place where, in their absence, best fishing would be expected; for since good catches are obtained on the periphery of a spawning centre, the very best results of all should be found in a locality which forms part of the peripheries of two separate spawning grounds overlapping at their edges. The position of the highest fishing intensity in April fulfilled this condition.

It is quite clear from the fishing fleet's activities that best fishing is to be found near, but not on, the centres of maximal spawning intensity. No explanation for this can be given. The most probable reason is either that the fish do not swim actively enough to be caught in the drift nets or that they remain too deep to be reached by them. Ehrenbaum (1923, p. 5) records that Holt, in a private communication to him, expressed the conviction that mackerel in full spawning do not rise to the surface. Collins (1883, p. 277) also states that mackerel in North American waters sink during the season of reproduction and rarely appear in shoals at the surface. It should now be possible to obtain definite information on this point by investigating the spawning centres and fishing grounds with a suitable echo-sounder. Unfortunately, none was available on any of the ships with which these researches in the Celtic Sea were carried out. Arrangements are now being made for echo-sounder surveys to be carried out as soon as circumstances permit. Until this is done one can do no more than note the possibility that while spawning in deep water the fish may be either deep or relatively quiescent, or even both.

Since the fishing fleet does not catch spawning fish in the first part of the season, very few ripe mackerel arrive on the fish markets during the months of March and April. It is not until May and later that appreciable numbers of fish containing small quantities of ripe ova and sperm are landed. The explanation for this appears to be that those fish that have not yet completely spawned are now in much shallower water and cannot go down very deeply to do so. The result is that some spawning fish can now be taken in drift nets on fairly active spawning centres even though best fishing is still to be had on the periphery of such centres.

When the two inshore fisheries existed they depended on unripe fish that were in the first stages of migration to the spawning ground, i.e. they, too, worked on non-spawning populations.

Having spawned off-shore, the mackerel perform a return migration to the coast (Steven, 1948, p. 524). This return migration is not, therefore, a spawning migration as has been supposed for so long. It is simply a post-spawning anadromous migration during which the fish are actively feeding; nevertheless it cannot be said that they come inshore *in order* to feed.

The Spawning of the Mackerel

Spawning takes place throughout the Celtic Sea during the period March till July. It increases very rapidly in intensity after the start, and by mid-April reaches a peak which lasts until May. Thereafter it decreases, until by the end of July it is only very slight. In the English Channel and also in the Irish Sea this slight residual spawning continues until August and even, in some years, until September (Corbin, 1947, p. 71).

This long-drawn-out spawning season is due, in part at least, to the fact that various populations of mackerel, converging on their off-shore spawning grounds from different winter quarters, both near and far away, do not all arrive there at the same time. When spawning activity is at its greatest—in the western part of the Celtic Sea in April—fish that wintered in the English Channel are still on their way westward (Steven, 1948, p. 520, fig. 3), and not yet fully ripe. It seems possible that this spread-over may be related not only to the different lengths of the migratory journeys but also to differences in the environmental conditions, particularly of temperature, in which the fish spend the winter. According to Cooper's analysis of such temperature data as exist for these areas (Appendix II, pp. 577–81), the waters over the greater part of the Celtic Sea are isothermal down to about 120 m. and in most years have appreciably higher temperatures than those of the Hurd Deep where many if not most of the Channel mackerel spend the winter. Most of the Atlantic Slope mackerel, however, spend the winter below the 120 m. level but they, too, unless they go very deep indeed—which is unlikely—are subject to warmer conditions than the English Channel population. Observations in 1927 and 1932 reveal that the mean winter temperature along the 150 and 200 m. contours in those years was about 0·9° C. higher than the mean temperature at the Hurd Deep; only at 500 m. in 1932 and at 800 m. in 1927 (position 50° 34′ N.; 11° 17′ W.) were Hurd Deep temperatures reached. Deep-water observations are also available for 1929, but Cooper regards that year as an exceptional one. Atlantic Slope water in that year was, at 200 m. depth, 2·5–2·8° C. warmer than the Hurd Deep; even at 986 m. the Atlantic Slope water was still 0·7° C. warmer. It seems clear, therefore, that mackerel wintering on the floor of the Celtic Sea, and in considerably deeper water at the outer edge of the continental plateau, are normally subjected to appreciably warmer conditions than others that spend the winter in the English Channel. Still others wintering near the bottom in the Smalls and Saltees areas will be also subjected to temperatures at least as low as those of the Hurd Deep.

Mackerel wintering around the various banks, knolls and gullies on the floor of the Celtic Sea, and in considerably deeper water at the edge of the continental plateau, are therefore not only nearer the spawning ground but are subjected to appreciably warmer conditions during their demersal period than others that spend the winter in the English Channel and in the Smalls and Saltees areas. It seems reasonable to suppose, therefore, that it is those fish that spend their demersal period in localities near the spawning ground, where also the warmer conditions prevail, that give rise to the early intensive spawning activity, followed by others from the more distant and also colder winter localities. There is also a possibility (supported by Cooper's theory of cascading waters from the shelf area down the side of the continental slope) that there may be a concentration of planktonic food organisms—chiefly copepods—at considerable depths along certain parts of the slope in February and March, especially in colder winters. Mackerel wintering in such localities, therefore, may also be better nourished (Cooper & Vaux, 1949).

Differences in winter temperatures may also be the factors underlying the later date of maximum spawning intensity on the chief North Sea spawning ground in the Skagerrak. Here (Ehrenbaum, 1914, p. 18; 1923, p. 11) the chief maximal spawning activity takes place a month later than in the Celtic Sea. It may be significant, therefore, that North Sea mackerel spend the winter in the vicinity of the Great Fisher Bank and northwards along the Norwegian Channel at least as far as the Viking Bank where winter temperatures are in general as much as 2–3° C. lower than those found in the Celtic Sea (Appendix II).

Another important factor contributing to the great spreadover of spawning activity in both space and time is that in every individual female the eggs mature in successive batches that are spawned one after the other during an extended period, the exact duration of which is not known. Ripe translucent eggs appear in the ovary distributed widely and irregularly amongst still unripe yellowish ova in earlier stages of development. This gives rise to a peculiar speckled appearance that, for want of a better term, has been called the 'plum-pudding' stage (Le Danois, 1938, p. 22,), of which an illustration is given in Pl. I, fig. 1. These ripe ova are dehisced into the lumen of the ovary which then, on superficial examination, shows no trace of ripe eggs. Their presence can be ascertained only by opening up the ovary and examining the lumen in which a few ripe eggs will nearly always be found even after any particular batch has been shed. These must, however, be carefully looked for; a quick and superficial glance may easily miss them. An ovary that contained numerous ripe eggs in its lumen, but showed no external evidence of their presence, is illustrated in Pl. I, fig. 2. The existence of ovaries in this condition indicates that the final stages of the ripening process take place discontinuously in successive batches of eggs. Were the process a uniform and continuous one ripe eggs would always be visible externally in smaller or larger numbers throughout the whole period from the time that the first eggs ripen until the ovary is fully spent.

This mode of ripening of the eggs in mackerel ovaries is in marked contrast with the condition found in the herring, where all the eggs that are to be spawned in any one spawning season ripen more or less simultaneously, giving rise to the well-known 'mazy' condition in which large numbers of fully ripe eggs can be obtained from a single female at one time. This condition is never found in mackerel. Only a relatively small number of fully ripe eggs is ever present in a mature female at any time and a condition of easily recognized 'maziness' does not occur.

It was probably a more intimate and accurate knowledge of the ripening process in the ovary of the herring than of the mackerel that led Cunningham to make the misleading generalization (1889, p. 25): that in species of fish that swim in shoals and have pelagic and migratory habits the process of spawning is approximately simultaneous throughout the whole population in a given locality, proceeds very rapidly when once begun, and is limited definitely to one short period of the year. This generalization he wrongly applies to the mackerel in which he says: 'all the reproductive products in a given fish are matured and shed within a short space of time.'

The slightly later observations of Moore (1899, p. 5), however, are completely at variance with Cunningham's findings and in full agreement with the results of the present investigations. Moore draws attention to the fact that, in the same run of fish, individuals in very different conditions of maturity are found. The reason for this he very clearly points out to be due to the fact that 'the mackerel matures only a portion of the generation of eggs at one time', as a result of which the ovary 'becomes spotted all over, both externally and on the internal lamellae with translucent spots due to aggregations of the clear eggs'. This very early description of the 'plum-pudding' stage, and how it arises, appears not to have received from subsequent workers the attention it deserves.

Correlated with the extended spawning period in the female there is, in the male, a correspondingly long period during which ripe sperms are present in the testes. The male differs from the female in that from the time that ripe sperms first appear at the beginning of the season an appreciable amount of ripe sperm is always present until the fully spent condition is reached. As in the female, however, the quantity of ripe sexual products present in a male fish at any particular time is always relatively small. Ripe males are generally present in small numbers in commercial catches before ripe females appear in them (Table IV).

TABLE IV. PERCENTAGE OF FISH (IN COMMERCIAL CATCHES BY STEAM DRIFTERS) IN DIFFERENT MONTHS CONTAINING RIPE SPERM OR EGGS

Figures in brackets are the total numbers examined during three fishing seasons (1937–39).

	Males	Females
March	5·9 (584)	0·0 (570)
April	20·6 (569)	7·9 (625)
May	62·5 (578)	52·2 (554)
June	52·8 (625)	47·6 (464)
July	14·4 (223)	17·3 (185)

It will be seen from the table that the two sexes appear in the catches in approximately equal numbers.

FOOD AND FEEDING

Adult mackerel spend part of each year in winter quarters on or near the sea-floor in the vicinity of banks and gulleys distributed over wide areas from shallow to deep water. In the English Channel, demersal concentrations of mackerel are found hard by the Vergoyer Bank off Boulogne, and by the numerous small sandbanks near Dieppe in only a few fathoms; and along the sides of the Hurd Deep in rather more than 40 fathoms. Elsewhere in the south-western area they occur at various depths in the neighbourhood of the Smalls and Saltees, around various banks and shoals on the floor of the Celtic Sea, and even along the Continental Slope itself, where they are regularly caught by British and other trawlers in depths of well over 100 fathoms 'west of Great Sole Bank' and elsewhere, especially in late February and March.

Amongst the mackerel that winter on the bottom in the English Channel fish with packed stomachs are seldom found. On the other hand, not all of them are empty. The fish, therefore, though not feeding voraciously, are not entirely fasting.

In the Plymouth region 753 mackerel were caught by trawl on or near the sea-floor in the months of January–April during the years 1936–39. Of these 67% contained food consisting chiefly of *Nyctiphanes couchi*, mysids, small teleosts, and crangonids, but various other organisms were also represented (Table V).

It is obvious that while on or near the bottom in the English Channel the mackerel were feeding on such organisms as were suitable and available to them. By contrast, the stomachs of mackerel caught in drift nets near the surface in January have been almost entirely devoid of food. A few (just under 5% of the 138 fish examined) have contained traces of phytoplankton embedded in mucus and very occasionally traces of planktonic crustacea (copepods) have been present. Rather more plant material appears in the stomachs in February

TABLE V. PERCENTAGE OF BOTTOM-CAUGHT FISH (PLYMOUTH AREA) CONTAINING IN THEIR STOMACHS ONE OR MORE OF THE ORGANISMS LISTED BELOW

Name of organism	Percentage of stomachs in which found (to nearest whole number)
Nyctiphanes couchi	31
Mysids	26
Small teleosts	15
Crangonids	11
Polychaetes	3
Amphipods	2
Pagurids	1
Other organisms	7
Stomachs empty	33

(just over 26% of the 116 fish examined) and copepod remains were identifiable in nearly 10% of them. But, on the whole, pelagic fish caught in these months, and also in December, can be regarded as fasting. This fasting period appears to be imposed upon the fish solely by the absence of suitable food in the upper waters at this time. On or near the sea floor where food is present they do not fast, and they break their fast afterwards at any time when opportunity offers. In samples of drift-caught mackerel in early spring, most of whose stomachs are empty or contain only minute traces of food, chiefly phytoplankton, it is not unusual to find an occasional individual whose stomach is packed tightly with small pelagic fish—generally *Maurolicus pennanti*, which occur in small and localized shoals.

Bullen (1912, p. 394) is therefore correct in stating that although mackerel obtain the smaller organisms of their diet by 'filtration' the larger ones are captured by 'selective feeding'. Selective feeding has been confirmed by Damant (1921, p. 42) by direct observation in the sea. In aquarium tanks of this laboratory mackerel are fed upon fragments of squid or other suitable food which they swallow as it sinks through the water by very obvious 'visual selection'. Bullen was in error, however, in thinking (1912, p. 403) that 'when feeding upon the minor forms of the plankton mackerel are incapable of assimilating other larger prey'. The phytoplankton present in the stomachs of pelagic mackerel in early spring can have been obtained only by filtering. It is equally certain that active fishes such as *M. pennanti*, several inches in length, must have been captured by Bullen's 'selective feeding' method. There can be little doubt that mackerel obtain their food by the most profitable method depending upon the size and kind of food organisms available to them; and that, at any time of the year and wherever they may be, they fast only if there is nothing for them to feed on.

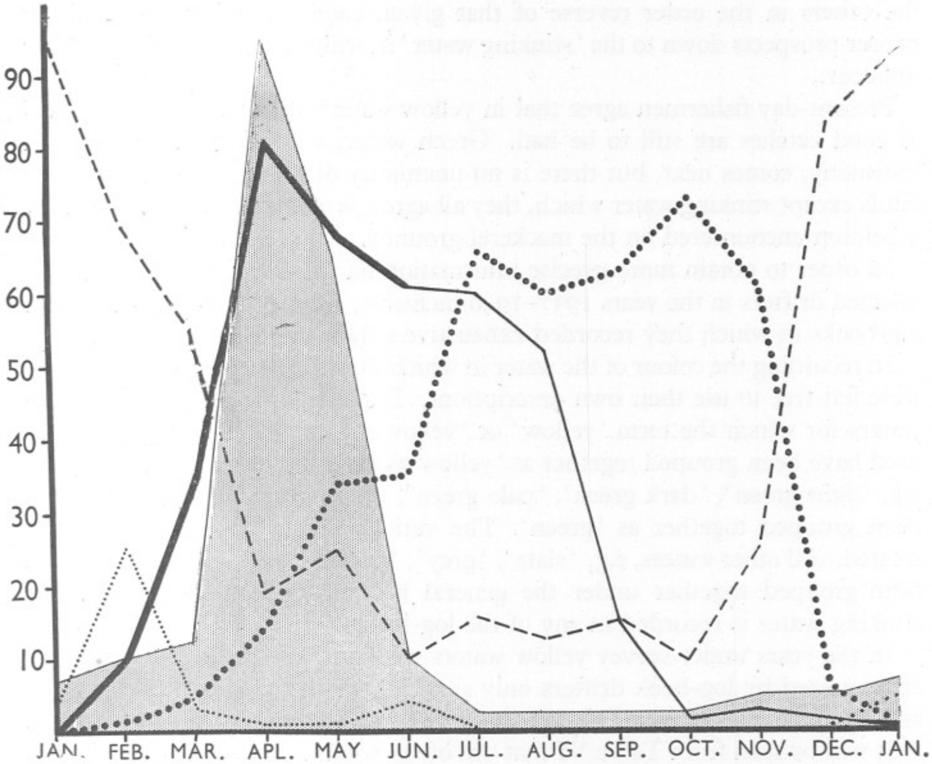
Most pelagic mackerel moving in an off-shore direction in the south-western area in the early months of the year are on migration to the spawning ground. In order to get there they leave the lower levels, where a certain amount of suitable food is available to them, for the upper layers where for a time there is practically none. The catadromous spring migration to the spawning areas is undertaken, therefore, irrespective of the presence or absence of food either at the beginning of the journey or on the way. Nevertheless, the migrating fish will at all times feed greedily if they can.

During March there is a rapid increase in the number of stomachs of pelagic mackerel containing food material—mainly copepods—and in the total quantity of food in each stomach. By the end of the month, and all through April and May, the fish feed predominantly on copepods, their stomachs being packed to bursting with these crustacea known to fisherman as 'red feed'. Although copepods predominate in the diet of the mackerel at this time a wide range of other planktonic organisms are also eaten. By about June yet another change takes place. Young pelagic stages of fish are now the mackerels' chief food, particularly *Clupea* spp., *Ammodytes* spp., and *Onos* spp. Considerable numbers of the larger crustacea also form part of the diet at this season and throughout the whole time that the fish are in shallow coastwise waters—euphausiids, mysids, the larger larvae of decapod crustacea such as *Corystes* and *Porcellana*, and even occasional pandalids, hippolytids, crangonids and similar organisms.

It will be seen (Fig. 5) that the fasting period is December—March which coincides with minimal plankton occurrence. When plankton becomes abundant the mackerel feed voraciously upon it, and continue to do so all the time that they are in off-shore waters. The change over to a predominantly fish diet, augmented with certain larger Crustacea, takes place when the mackerel have arrived back in inshore waters on their return from the spawning grounds.

Fishermen's Signs

When fishing for mackerel, especially in the Newlyn deep-sea fishery, the fishermen are influenced greatly in their choice of position for 'shooting' their nets by what are commonly known as 'fishermen's signs'. Large congregations of birds, especially diving gannets, are looked upon as good indications of the



Text-fig. 5. Diagram illustrating the changes in mackerel stomach contents in the course of one full year. The percentage of stomachs containing the chief types of food are shown thus: ......, phytoplankton; ▬, planktonic crustacea, mainly copepods; ——, non-planktonic crustacea, i.e. crangonids, pandalids, etc.; ●●●, fish; - - - -, empty stomachs. The contents over a whole month are recorded as for the mid-point of that month. Height of the stippled area indicates, in miles, on the same ordinate, the mean distance from land at which the mackerel examined were caught in each month.

presence of fish in worthwhile numbers. Even more reliance is placed upon the colour of the water. This has already been remarked upon by Bullen (1908, p. 287) who recognized five different kinds:

(i) Stinking water—water of a dull leaden colour having a recognizable and distinctly unpleasant smell.

(ii) Grey water—water similar in colour to the above but lacking the smell.

(iii) Blue water—very clear and transparent.

(iv) Green water—differing from blue water only in colour.

(v) Yellow water—turbid water of a distinctly yellow tint.

According to Bullen best catches of mackerel at that time (1906 and 1907) were generally, though not invariably, to be had in yellow water,[1] followed by

[1] This seems to have been first remarked upon by Pliny—quoted by D'Arcy Thompson (1947, p. 244)—who says: '*scombri quibus est in aqua sulphureus color*.'

the others in the order reverse of that given, each providing progressively poorer prospects down to the 'stinking water' in which mackerel are said never to occur.

Present-day fishermen agree that in yellow water[1] by far the best prospects of good catches are still to be had. Green water, according to their spoken testimony, comes next, but there is no unanimity of opinion about any other kinds except stinking water which, they all agree, is worst of all but fortunately is seldom encountered on the mackerel grounds.

In order to obtain more precise information on these and other points, ten selected drifters in the years 1937–1940 inclusive, were provided with special log-books in which they recorded exhaustive details of all their catches.

In recording the colour of the water in which they shot their nets the skippers were left free to use their own descriptions. For the purpose of tabulation all waters for which the term 'yellow' or 'yellowish' e.g. 'yellowish green', are used have been grouped together as 'yellow water'. All other shades of green e.g. 'light green', 'dark green', 'pale green', 'grass green' and the like have been grouped together as 'green'. The various 'blues' have been similarly treated. All other waters, e.g. 'slate', 'grey', 'paraffin oil', 'black', etc., have been grouped together under the general heading of 'other colours'. No stinking water is recorded in any of the log-books.

In the years under survey yellow waters were not very plentiful. They were encountered by log-book drifters only six times in 1937, eight times in 1938, and thirteen times in 1940. No yellow water was found by any of them in 1939.

It will be seen from Table VI that out of the total number of 27 shots made in yellow water during those four years no less than 21 (77·8%) yielded catches of over 10,000 fish, the average number per haul being 18,300.[2] Several catches of over 29,000 fish were made. In green water only 13·4% of the 918 catches consisted of more than 10,000 fish. In blue water, out of 183 catches only 1 had over 10,000 fish. The catches in other waters were poorer still.

It is quite clear from these log-book records that yellow water, when present, offers by far the best prospects of obtaining good catches. Yellow water is, unfortunately for the fishermen, not very plentiful, and in some years, as in 1939, may not occur at all.

Bullen (1908, p. 289) endeavoured by direct investigation to correlate the different kinds of water with the plankton present in it. Stinking water he found to be rich in phytoplankton and poor in zooplankton, but he was unable to offer any explanation of the reputed objectionable smell which he was himself unable to detect. He gave it as his opinion, though, that such an odour, if it did exist and could in fact be detected by fishermen, 'did not arise from the condition of plankton'. Long before Bullen's investigations, however, Pearcy (1885, p. 399), working near Shetland, had shown quite conclusively not

[1] Described by some Cornish fishermen as 'cow-dung water'.
[2] To the nearest hundred.

only that herrings avoid stinking water but that the odours were correlated with the presence of *Rhizosolenia shrubsolei* and *Thallassiosira nordenskioldii* with which the herring nets sometimes became so heavily coated that little slimy heaps of those organisms were formed on the deck as the nets were hauled in.

Supporting evidence that shoaling fish such as mackerel and herring avoid water heavily populated with phytoplankton, such as the diatom *Rhizosolenia* or the flagellate *Phaeocystis*, is provided by Russell (1915, p. 30) for mackerel, and by Savage & Hardy (1935) for herring. Although, therefore, stinking water has not been reported in the course of these investigations there appears to be no doubt that when it does occur poor fishing must be expected in it.

TABLE VI. CATCHES IN DIFFERENT TYPES OF WATER

Colour of water	Year	No. of shots	No. of shots having over 10,000 fish	Percentage of shots having over 10,000 fish	Average no. of fish per haul (to nearest hundred)
Yellow	1937	6	3		
	1938	8	5		
	1939		No yellow water		
	1940	13	13		
		27	21	77·8	18,300
Green	1937	230	42		
	1938	327	56		
	1939	247	30		
	1940	114	5		
		918	133	13·4	5,300
Blue	1937	88	0		
	1938	25	1		
	1939	31	0		
	1940	39	0		
		183	1	0·6	2,600
Other colours	1937	18	0		
	1938	38	0		
	1939	34	0		
	1940	32	0		
		122	0	0·0	2,000

In all other waters examined by him Bullen found zooplankton to be more plentiful than in stinking water, with phytoplankton also often present as well. In yellow water he found that phytoplankton was 'entirely absent' and that the zooplankton was confined almost entirely to three or four principal forms of which *Calanus finmarchicus* and *Pseudocalanus elongatus* were the most important.

Unfortunately, Bullen's data enable him to put forward only tentative explanations of the causes which give rise to the yellow colour and why, on the whole, yellow water is most likely to provide good catches. He quotes the 'somewhat conflicting opinions expressed by fishermen' to the effect that the coloration is due either to the presence of excrement arising from densely shoaling fish or to the abundant copepod 'feed' and adds that evidence provided by examination of certain plankton samples supports the latter view.

During the present investigations some of the skippers provided with log-books agreed also to work small townets and collect plankton samples from each position in which they shot their drift nets. They were all issued with exactly similar gear and given precise instructions for using it in such a way as to obtain reasonably comparable quantitative results. In spite of this the samples so obtained could not at first be relied upon from a quantitative point of view.

Nevertheless, their collection was continued and in due course many of the difficulties which vitiated their comparability were overcome so that some deductions could reasonably be drawn from them. These improvements arose in part because the skippers themselves found that, though by no means an infallible guide, their best catches of mackerel were generally obtained where the townet samples consisted of typical 'mackerel feed'—i.e. copepods in reasonable abundance—and they gradually learned to use the townets by standard methods for standard times in order to obtain comparable catches for their own information. It is therefore significant that, after the townets had been in use by selected skippers for one season, other skippers who at first would have nothing to do with them, asked, as a favour, to be issued with townets for their own use.

Examination of 300 samples retained as reliable, in association with the log-book records, support Bullen's finding that plankton catches in yellow water and light green water generally consisted almost entirely of copepods—chiefly *Pseudocalanus elongatus* and *Calanus finmarchicus*, with the former usually predominating both in numbers and in bulk. The largest samples of copepods also came from those two waters. These were preserved in formalin (5%) and having survived the war period have now been re-examined after an interval of more than ten years. In that time the preserving fluid in some of the jars containing copepods almost unmixed with other organisms such as *Limacina*, has acquired a yellow colour closely resembling that of the yellow waters on the fishing grounds. Certain yellow carotinoid substances from the copepods have gone into solution in the preservative fluid.

For some reason not understood, not all the copepod samples have liberated these yellow pigments into solution; but such samples, transferred into acetone, give the same tinge and depth of colour in a few months. There seems to be little doubt, therefore, that the underlying primary cause of the yellow coloration in the sea is the presence of copepods in concentrations so dense that their body pigments impart colour to the water. Such coloration will of course be augmented by their excreta in which the same pigments are present. Observation has also shown that the 'somewhat conflicting opinions expressed by fishermen' as quoted by Bullen (1908, p. 291) are probably not conflicting at all, and that the excrement produced by densely shoaling mackerel is also a contributory factor. Faecal matter expressed from mackerel is, in fact, generally of a yellowish or pinkish yellow colour. Mackerel, like most fish, tend to congregate in greatest numbers where their most acceptable food organisms are in greatest abundance (Herdman, 1913, p. 33). Both the fish themselves and their faecal matter will therefore be most plentiful in water already tinted by copepods and the effect of this will be to strengthen the yellow coloration.

In normal circumstances the distribution of copepods in high concentrations is characterized by its 'patchiness'; so also, in consequence, is the distribution of 'yellow water'. In years of unusual copepod abundance there will be an increase of yellow water in the form of more numerous patches, many of which will also cover greater areas. Since mackerel congregate in the yellow patches, the more numerous those patches are in any year and the greater their extent, the more favourable are the chances of their being found and fished in, with consequent benefit to the commercial fishery. In years of copepod scarcity the opposite will be true. This is in complete agreement with Allen's generalization (1909, pp. 396–97) that the catches of mackerel in May in the Newlyn deep-sea fishery are to some extent affected by the amount of sunshine in the same region during the previous February and March. This effect upon catches is an indirect and very interesting one. The phytoplankton crop depends, to some extent, upon the amount and intensity of sunlight in those early months. The abundance or scarcity of copepods is in turn partly dependent upon the magnitude of the phytoplankton crop upon which they chiefly feed. Copepod concentrations, being patchy in their distribution, cause mackerel to congregate in them, and those patches can be identified by the appearance of the water. *The effect of suitable amounts of sunshine in February and March is therefore to increase the number and size of the patches of sea in which good fishing is likely.* Obviously there must be a limit to this effect; for if, in any year, the conditions were so favourable that the greater part of the whole area consisted of yellow water rich in copepods there would be no localized concentrations of mackerel and therefore no improvement in the catches. Unfortunately, Bullen's statement with regard to zooplankton and the abundance of mackerel has for a very long time created a wrong impression. He states that 'the abundance or paucity of zooplankton during a certain number of years (1903–07) appears to be correlated with the greater or less abundance of mackerel'. It must clearly be understood that abundance of zooplankton cannot possibly increase the population of adult mackerel in the year in which it occurs. It is the 'catchability' of the mackerel already in existence that is affected and which may be reflected in the commercial catches.

Summary

Of the three mackerel fisheries that formerly existed in the south-west of England, only one, the Newlyn deep-sea fishery, now remains active. The fishing grounds worked by this fishery lie in the Celtic Sea as much as 100 miles to the westward of the Scilly Islands when the season opens in March,

but the distance off becomes progressively less as the season advances until, in June, when it finishes, the participating vessels are fishing close by the land. At all times best fishing is obtained on the periphery of the areas of chief spawning intensity.

The spawning season in the Celtic Sea is a very protracted one because (*a*) the fish do not all ripen and spawn simultaneously due to (i) the divergent conditions, especially of temperature, in which different groups spend the winter, and (ii) the different lengths of the migratory journeys they must make to reach the common spawning area; (*b*) in each individual female the eggs mature in successive batches that are shed one after the other over an extended period, the duration of which is not precisely known.

In the early months of the year pelagic mackerel are often found to be fasting. This is due simply to absence of suitable food in their environment at that time. The fish will always feed when food is available.

As a general rule most mackerel are caught in patches of 'yellow' water, the colour of which is caused chiefly by localized concentrations of copepods to which the fish are attracted for feeding. Copepod abundance at the height of the fishing season must be to some extent affected—indirectly through the phytoplankton—by the amount of sunshine earlier in the season. This explains Allen's correlation between early spring sunshine and commercial catches of mackerel in late spring and early summer.

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APPENDIX I

Landings at Newlyn by Local Craft (Sail and Motor) and by Steam Drifters in the Years 1906–38 Inclusive (War Years Excepted)

	Local craft			Steam drifters		
Year	No. of landings	Total quantity in cwt.	Mean weight per landing (cwt.)	No. of landings	Total quantity in cwt.	Mean weight per landing (cwt.)
1906	2159	46265	21	1850	62551	34
1907	2190	60121	28	2962	195565	66
1908	2709	36950	15	2944	112452	38
1909	1878	27549	17	2423	112189	46
1910	1476	31757	22	2281	124122	54
1911	1581	15871	10	2156	97185	45
1912	1255	13761	11	1572	65482	42
1913	806	10419	13	1537	56176	36
1919	786	15200	19	1311	84078	64
1920	1111	16470	15	2162	112683	52
1921	1721	21932	13	1963	116931	60
1922	1824	18280	10	2185	90555	41
1923	1036	20865	20	2249	106237	47
1924	750	14613	19	2182	117540	54
1925	430	4859	11	2412	122150	51
1926	290	4441	15	1888	102390	54
1927	559	3890	7	1707	58739	34
1928	273	2924	10	1301	58827	45
1929	387	983	3	1079	43670	40
1930	173	411	2	1223	43205	35
1931	77	112	1	925	50513	55
1032	202	525	3	1014	48119	47
1933	950	2321	2	1133	51223	45
1934	988	2912	3	905	55400	69
1935	694	3002	4	856	58885	69
1936	696	4547	7	777	57177	74
1937	1131	4274	4	643	40765	63
1938	935	5134	5	641	50207	78

APPENDIX II

Differences in Temperature in February of Several European Waters in which Mackerel Live

By L. H. N. Cooper, D.Sc., F.R.I.C.

In the course of these investigations into the life history of the mackerel, the question arose whether differences in temperature of the water occurred at the time of the winter minimum between, on the one hand, the Hurd Deep, and on the other, the waters south and south-west of Ireland and near the Viking Bank west of Norway.

Hurd Deep Observations

Two lines of regular surface observations cross the Hurd Deep. These lines are worked at frequent intervals by merchant ships on shuttle service between Southampton and St Malo and between Plymouth and Guernsey. No doubt there is some uncertainty in these observations, as in all surface observations from merchant ships. Down to the level of the bottom of the English Channel vertical mixing is almost certainly thorough. We have no knowledge as to how thorough it is within the trench of the Hurd Deep.

Throughout the whole period of the Irish investigations a station was regularly worked on the Southampton—St Malo line over the eastern end of the Hurd Deep at 49° 54′ N., 2° 00′ W. Occasionally this point was omitted, but the adjacent position 50° 03′ N., 1° 55′ W. differs hardly at all in temperature and on a few occasions has been used instead.

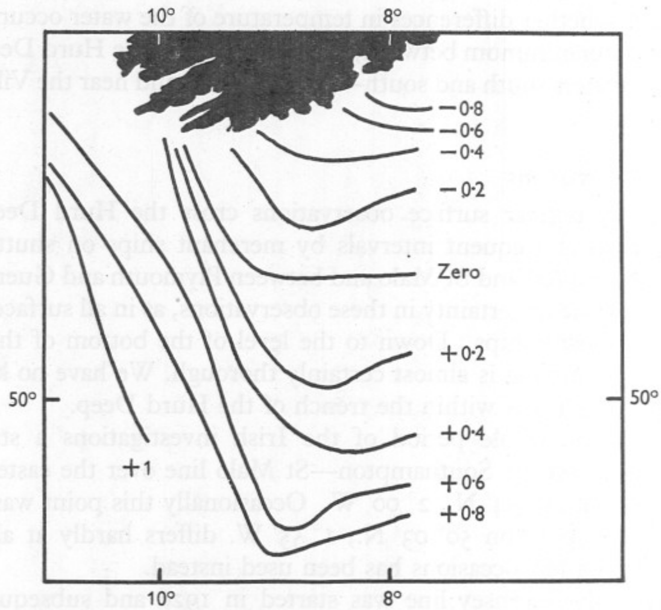
The Plymouth-Guernsey line was started in 1926 and subsequently was worked rather more frequently than the eastern line.

All data between the last January observation and 10 March have been abstracted from the *Bulletin Hydrographique* and, when necessary, graphed. The temperatures at each station about 1 and 19 February and 10 March were interpolated and the differences between the two stations evaluated. In general, the western station was the warmer, and for the eight years 1926–33, the position 49° 30′ N., 3° 02′ W. was on an average 0·4° C. warmer than the position 49° 54′ N., 2° 00′ W.

It is clear that a small temperature gradient along the length of the Hurd Deep is usual, and that the easternmost station for which most data is available lies in February over the coldest part of the trench.

Observations South of Ireland

Serial temperature observations in the Irish area have been frequently taken in February and May, but in the other winter months there are few data. The cruises were worked between 20 and 22 January in 1921 and sometime between 2 February and 10 March in the other years. In each year the mid-point in time of the Irish cruise was taken and the temperature at that time at each of the Hurd Deep positions estimated by interpolation. In the years 1926–33 the temperature of the eastern half of the Hurd Deep has been taken as the mean of these. In 1921–25, the temperatures at the easternmost position, 49° 54′ N., 2° 00′ W., have been increased by the mean correction, 0·2° C., to make them comparable with the later years.



Text-fig. 6. Differences in February temperatures between the waters south and south-west of Ireland and those at the Hurd Deep in the English Channel. Lines of equal difference—positive warmer than the Hurd Deep; negative colder than the Hurd Deep. Years 1921–33.

These Hurd Deep temperatures provide the basis line for the subsequent calculations. This temperature was subtracted from each separate Irish observation between 1921 and 1933 to give a table of differences. The mean difference at each station was then evaluated and is plotted in Text-fig. 6. Lines of equal differences were then drawn which show that the inshore water south of County Cork was colder than the Hurd Deep, and that the water south of 50° 40′ N., and west of 09° 00′ W. was warmer. The surface water above the continental slope was about 1° C. warmer.

Quite clearly the year 1929 was peculiar and so has been omitted from these calculations. Air temperatures at Scilly and Valencia were normal, whereas at Guernsey in February they were 2·7° below average. Consequently, the water over the Hurd Deep was 1·5° C. colder than the 'normal differences' for the other ten years would lead one to expect. This story concerns surface temperatures.

Bottom temperatures were also needed. The Hurd Deep surface temperatures apply to the whole water column at least down to the depth of the bottom of the English Channel adjacent to the Deep.

In the Irish area the water was almost always isothermal down to at least 120 m. Only a few stations deeper than 120 m. had been worked, namely positions *R*, *S*, *T*, *PP*, *QQ*, *RR*, and *SS* all west of 9° 55′ W., and these only in 1927, 1929 and 1932. The year 1929 has already been stated to be exceptional and it is better to use only the years 1927 and 1932 for estimating mean conditions. In these years the mean temperatures along the 150 and 200 m. contours of the shelf was about 0·9° C. higher than the temperature at the Hurd Deep. The Hurd Deep temperatures were reached at station *SS* (50° 34′ N., 11° 17′ W.) at a depth of 500 m. in 1932 and at 800 m. in 1927. In the probably exceptional year 1929, the water at the 200 m. contour was 2·5–2·8° C. warmer than at the Hurd Deep. Even at 986 m. the water was still 0·7° C. warmer.

TABLE VII

Date	Irish code letter	Position	Depth (m.)	Temp. (° C.)
10. iii. 49	*D*	50° 36′ N., 8° 04′ W.	5	9·97
		Labadie Bank	25	10·00
			60	10·00
		Sounding	*70*	—
9. iii. 49	*F*	49° 50′ N., 8° 00′ W.	5	10·30
			50	10·30
			125[1]	10·30
		Sounding	*123*	—

[1] Wire angle >45°; true depth much less than metres of wire out.

If high temperature is a factor favouring early spawning of the mackerel, those in the Celtic Sea south of 50° 40′ N. and west of 09° 00′ W. should in most years spawn earlier than those near the Hurd Deep.

The Winter of 1949 *in Waters South of Ireland*

Steven reported (3 March 1949) that the mackerel in the area south of Ireland had started spawning several weeks earlier than normal. Since at Plymouth the winter had been remarkably mild, it seemed likely that high temperatures of the water to the westward might have been associated with the early spawning. The opportunity occurred to obtain temperatures on 9–10 March along the meridian 8° 00′ W. (Table VII).

Suitable comparable temperatures had been obtained by the Irish Fisheries Service in the years 1921–22, 1924–34 and 1938, whilst surface observations are available for other years. In 1937 water as warm was present in the area of stations *D* and *F* between mid-February and mid-March, but was evidently a short-lived intrusion into a part only of the area south of Ireland. Over the whole area for the whole of the winter, the season 1936–37 was evidently markedly colder than 1948–49. Apart from this doubtful year, it is necessary to go back to 1921 to find a similar one; even that year certainly was not warmer.

It is therefore not unreasonable tentatively to correlate the abnormally early spawning of mackerel in February and March 1949 with the notably high water temperatures.

Observations on the Western Declivity of the Norwegian Channel

During winter mackerel congregate along the western declivity of the Norwegian Channel or northern extension of the Skagerrak in the latitudes of the Orkney and Shetland Islands (p. 564). In these waters a number of hydrographic stations have been worked by the Norwegian research vessels *Johann Hjort* and *Armauer Hansen* in January or February. The suitable stations worked there in 1938 and 1939 find no counterpart in simultaneous Hurd Deep observations.

TABLE VIII

Depth (m.)	Deficiency in temperature (° C.) 7. i. 37	27. i. 37
100	2·4	2·1
125	2·4	2·1
150	2·5	2·0
200	2·8	2·0
250	3·3	2·0
300	3·7	2·0

TABLE IX

Depth (m.)	Deficiency in temperature (° C.) 3. ii. 37
100	2·7
125	2·4
150	2·7
200	2·8

In 1937 on 7 and 27 January, on the parallel of latitude 60° 46′ N., the temperatures of the bottom water bathing the western declivity of the Channel were lower than the Hurd Deep mean temperatures on the same date by more than 2° C. (Table VIII).

On the parallel 59° 17′ N., on 3 February 1937, the corresponding values were as shown in Table IX.

In 1937, mackerel in these waters were subjected to temperatures about 2·5° C. lower than at the Hurd Deep.

February 1930 seems to have provided an unusually small difference in temperatures, whereas January 1931 was more 'normal' (Table X). The parallel of latitude worked in both years was 60° 08′.8N.

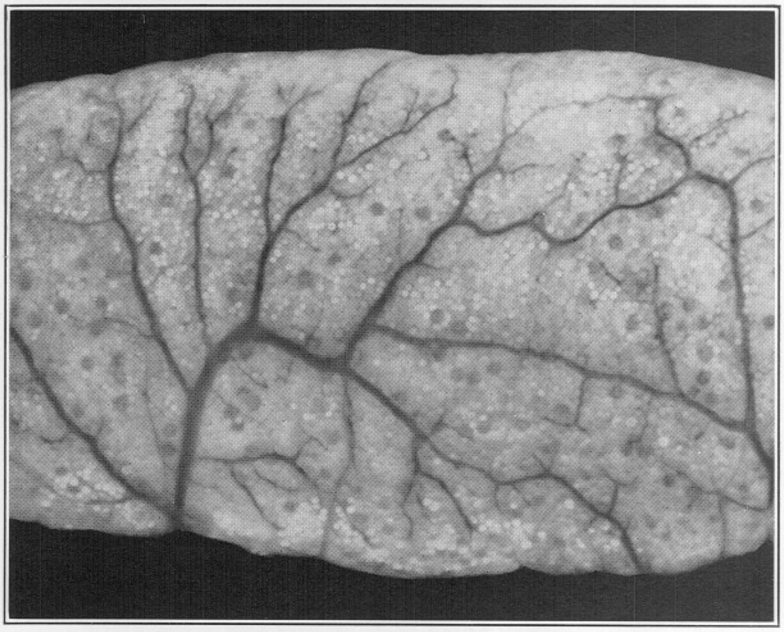


Fig. 1.

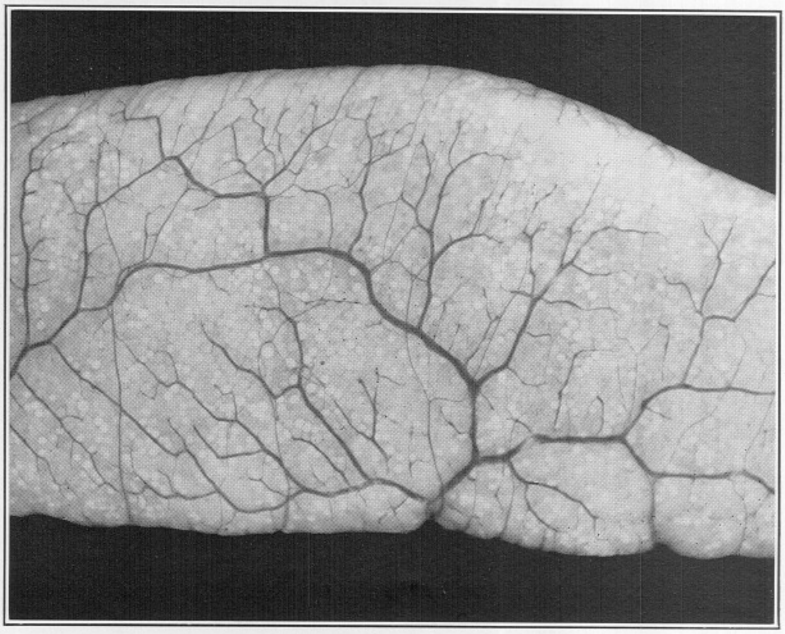


Fig. 2.

The year 1938 probably provided differences similar to 1931 and 1937.

In general we may say that the western edge of the Norwegian Channel provides temperatures 2–3° C. lower than the Hurd Deep, so that if temperature

TABLE X

Depth (m.)	Deficiency in temperature (° C.)	
	27. ii. 30	29. i. 31
100	0·3	1·9
125	0·5	2·3
150	0·5	2·0
200	0·6	2·3

controls the time of spawning, the lag in the more northern waters should be considerable.

EXPLANATION OF PLATE I

Mackerel ovary in two phases. Fig. 1, the 'plum-pudding' stage, in which the widely scattered ripe eggs appear as dark spots. Fig. 2, an ovary with ripe eggs which are not visible externally but are to be found in the lumen.