ISSN 0308-5589

MINISTRY OF AGRICULTURE FISHERIES AND FOOD
DIRECTORATE OF FISHERIES RESEARCH

FISHERIES RESEARCH TECHNICAL REPORT

No. 37

A review of spawning in the North Atlantic Mackerel, *Scomber scombrus* L

P.O. JOHNSON

LOWESTOFT, 1977

The author

P O Johnson PhD, is a Senior Scientific Officer in the Fish Stock Management Division of the Directorate of Fisheries Research. He is stationed at the Fisheries Laboratory, Lowestoft.

Fish. Res. Tech. Rep., MAFF Direct. Fish Res., Lowestoft. (~~35~~ 37), 22pp.

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A REVIEW OF SPAWNING IN THE NORTH ATLANTIC MACKEREL, *SCOMBER SCOMBRUS* L

by

P O Johnson

Introduction

This paper summarises information concerning the spawning of mackerel in the North Atlantic region. It covers their spawning areas, timing and duration of spawning, levels of eggs and larval production with estimates of spawning biomass, long-term fluctuations in spawning stock levels and general relationships between spawning and hydrographic conditions.

Spawning Areas

In both European and North American waters mackerel spawning areas are mainly found within the confines of the continental shelf. In the north-west Atlantic the spawning range extends from Cape Hatteras (36°N) to the Gulf of St Lawrence and Nova Scotia coast (45°N), and occasionally to the west coast of Newfoundland (48°N), although the most importance area appears to lie between Chesapeake Bay and Cape Cod (42°N). (Dannevig, 1919; Bigelow and Welsh, 1925; Sparks, 1929; Sette, 1943; Bigelow and Schroeder, 1953.)

In European waters spawning extends from the north-west coast of Spain (43°N) to the west coast of Norway (62°N) and covers most of the shelf waters, including the English Channel, North Sea, Skagerak and Kattegat but excluding the Baltic Sea, although eggs have been reported as far as Kiel Bay. (Buchanan-Wollaston, 1911; Ehrenbaum, 1923; Nilsson, 1914; Furnestin, 1939; Le Gall, 1939; Farran, 1939; Corbin, 1947; Heegard, 1947; Fraser, 1949; Fraser and Saville, 1949; Saville, 1950; Henderson, 1954 and 1961; Kandler, 1956; Bagge, 1956; Myrberget, 1965; Lindquist, 1968 and 1970; Wallace and Pleasants, 1972; Iversen, 1973 (in Hamre, 1975 and ICES, 1974); Bainbridge, Cooper and Hart, 1974; Arbault and Lacroix, 1975; Johnson and Dawson, 1975; Walsh, 1976.)

Mackerel appear as summer visitors to Faroese and Icelandic water, but there is no evidence for spawning in these areas (Joensen and Taning, 1970; Saemundsson, 1947).

The best overall picture of spawning distribution in north European waters (excluding Biscay) is provided by the Hardy Continuous Plankton Recorder (CPR) surveys undertaken on a regular basis by the IMER Oceanographic Laboratory, Edinbrugh (Henderson, 1954 and 1961; Bainbridge *et al*, 1974; Coombs, unpubl, in preparation). The published results relate to larval distributions only, but since the larvae are predominantly small and Bainbridge *et al* (1974) present distribution charts covering the smallest stage larvae only, they should provide a best estimate for the distribution of spawning.

Figure 1 is a composite chart of the principal spawning areas and incorporates both results of the CPR surveys and evidence from other more restricted egg and larval surveys undertaken by various authors.

Mackerel Spawning in the North Sea

Ehrenbaum (1923), summarised the then available evidence for the distribution of mackerel spawning in the North Sea. Maximum egg densities were found in June-July, with major spawning areas off the south coast of Norway and in the Skagerak, with less intense spawning in the eastern half of the central North Sea, mainly between 54°N and 57°N, and northwards over the Viking Bank to about 62°N. (Most of this evidence is from the years 1901-09.) Spawning diminished towards the Southern Bight, and little was evident in the coastal waters off the east coast of England. It is of interest to compare the distribution of mackerel eggs in the Southern Bight area for June 1909 (Buchanan-Wollaston, 1911) with those recorded in June 1960 and 1962 on sprat egg surveys undertaken by the Lowestoft Laboratory (Figures 2a-c). The more extensive survey undertaken in June 1962 shows a distribution closely similar to that found in June 1909, and both the later surveys clearly show little or no spawning in the immediate coastal waters off the east coast of England.

This evidence thus suggests that, as far as the southern North Sea is concerned, the general pattern of spawning has remained much the same. The principal evidence concerning the more recent longer-term distribution of mackerel spawning in the North Sea derives from the CPR surveys, and this involves the smaller larvae, mainly under 7 mm in length, averaging about 5 mm (data supplied by Mr S H Coombs of IMER, Plymouth). However, some caution has to be exercised in drawing conclusions from the results of these surveys since the actual sampling levels are very low, and the numbers of larvae involved generally small. The recorder actually filters about 3 m^3 of water over a distance of 10 nautical miles, and this usually represents a unit sampling interval. The results have been generally presented as average densities within basic rectangles measuring 1° latitude x 2° longitude. In the

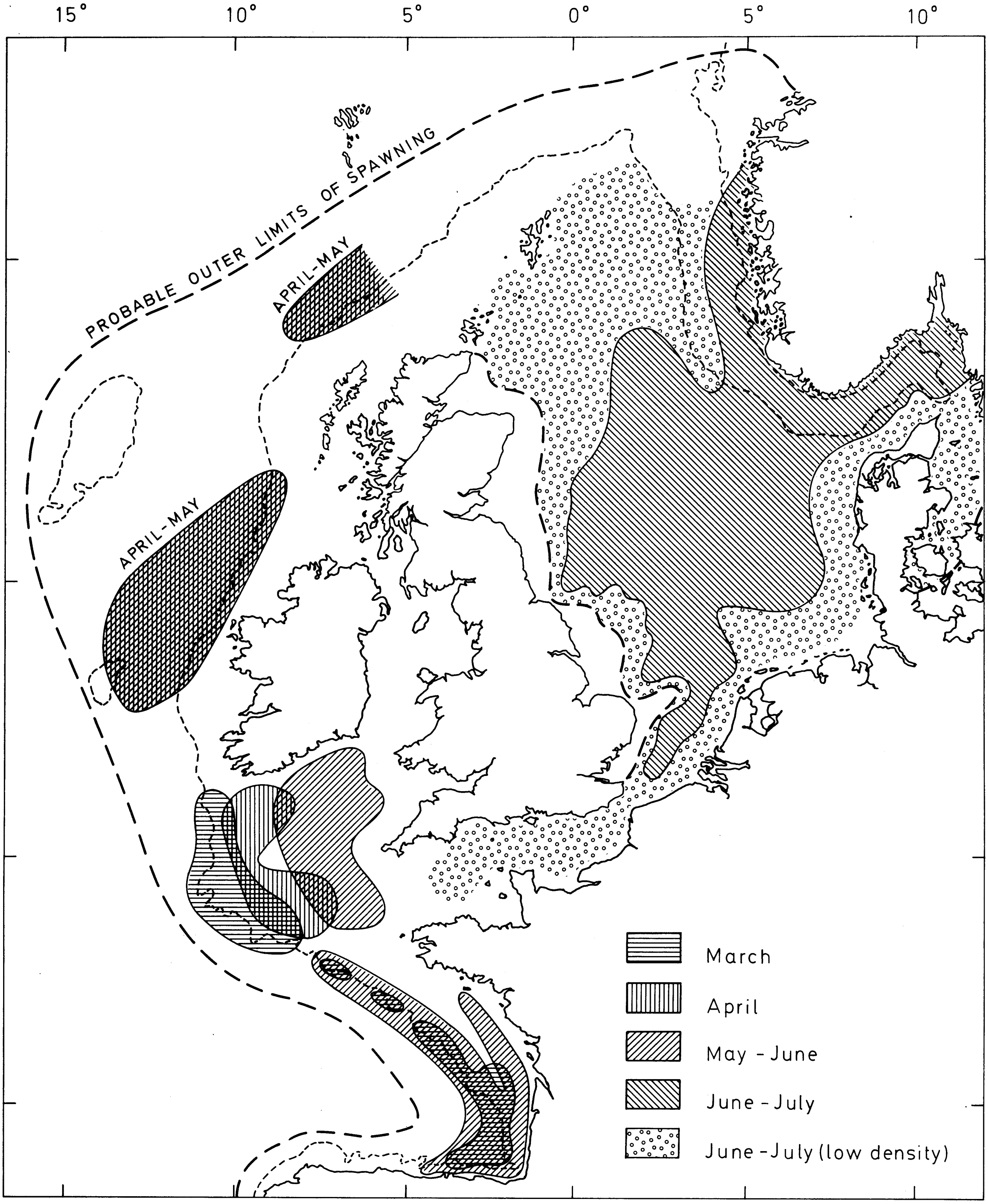

Figure 1 Principal mackerel spawning areas

North Sea those rectangles covering the main mackerel spawning areas range in size from about 12,100 km^2 in the northernmost part (61°-62°N) to around 15,000 km^2 in the southernmost part (52°-53°N).

There has also been some variation in the sampling routes used, although in the years 1938-39, and from 1950 on, most of the main mackerel spawning areas within the North Sea have been adequately traversed over the principal months of spawning, and when results are averaged and compared over sufficiently long periods, any really significant changes in general levels of abundance or patterns of distribution should emerge, (Figures 3-5).

The recorder samples at a fixed depth (about 10 m below surface) and it is thus not possible to estimate abundance in absolute terms when the vertical distribution of the larvae is unknown. However, an approximate relative

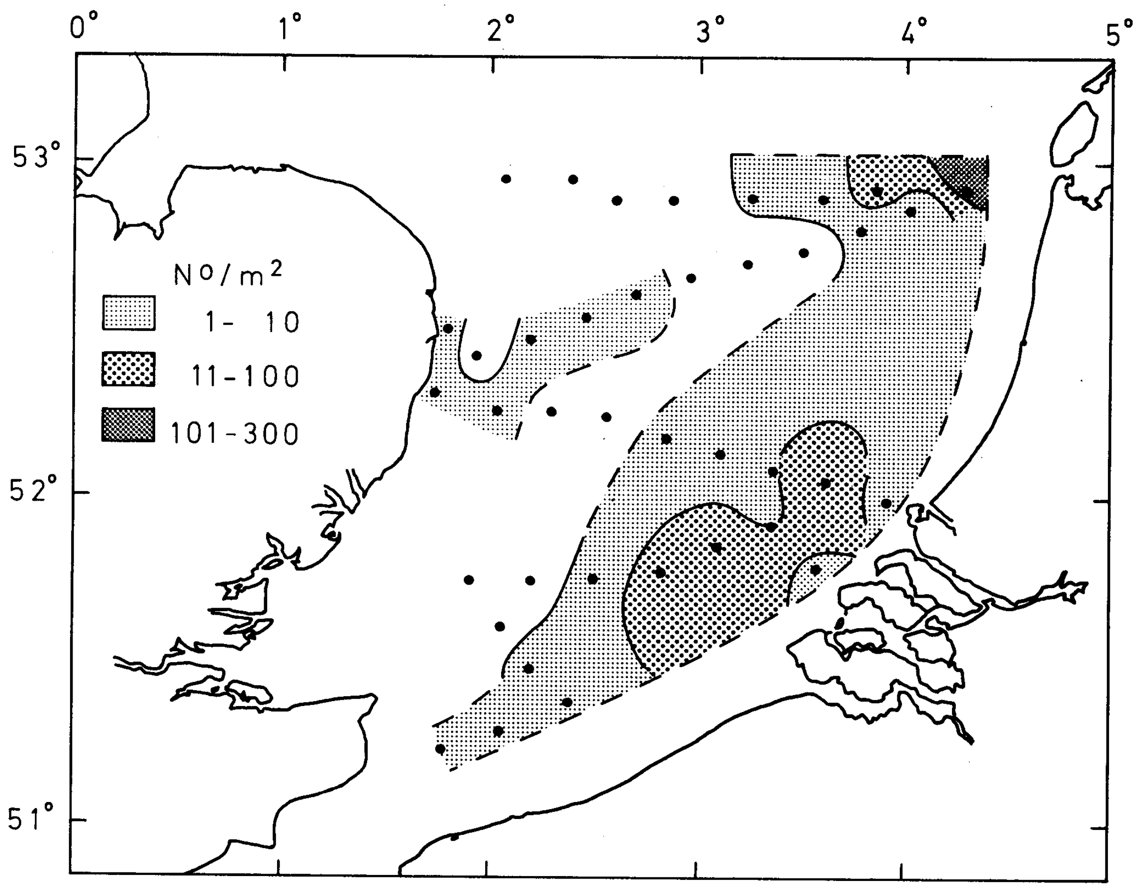

Figure 2a   Mackerel eggs, June 1909, ● indicate sampling stations

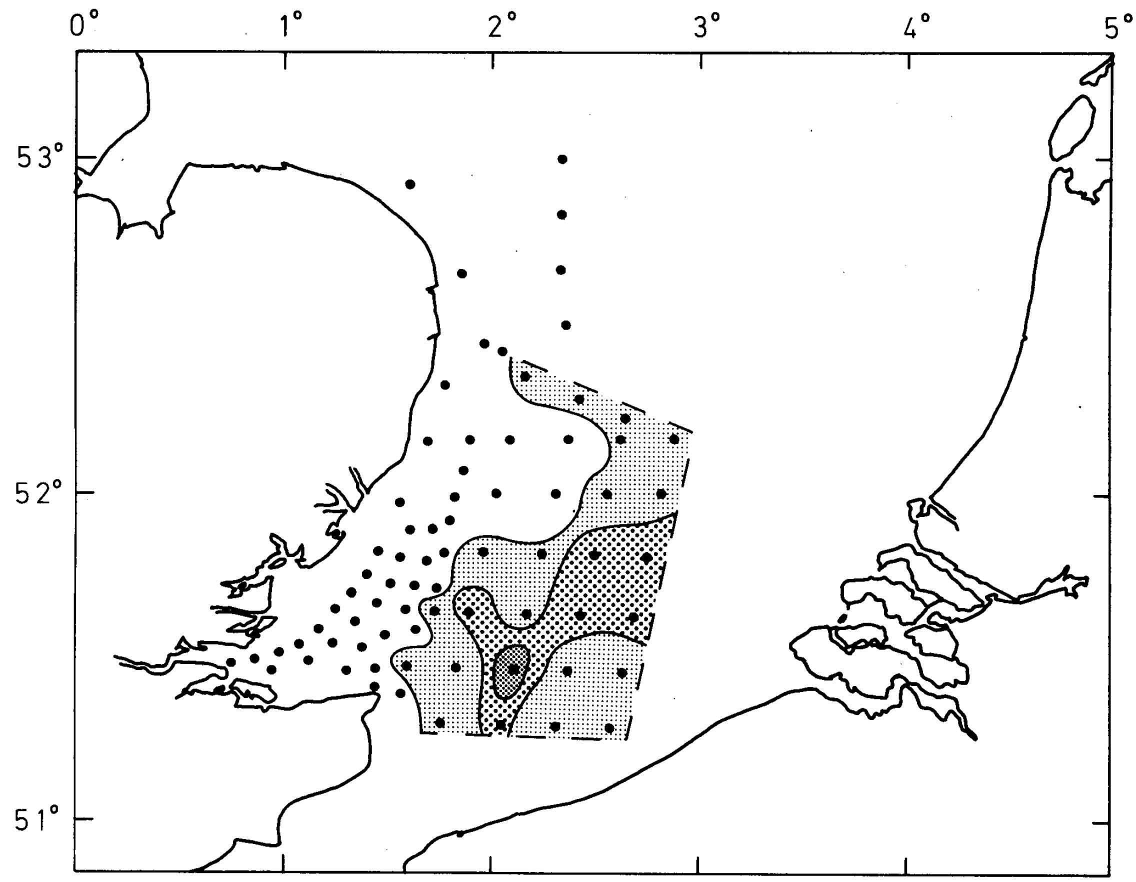

Figure 2b   Mackerel eggs, June 1960, ● indicate sampling stations

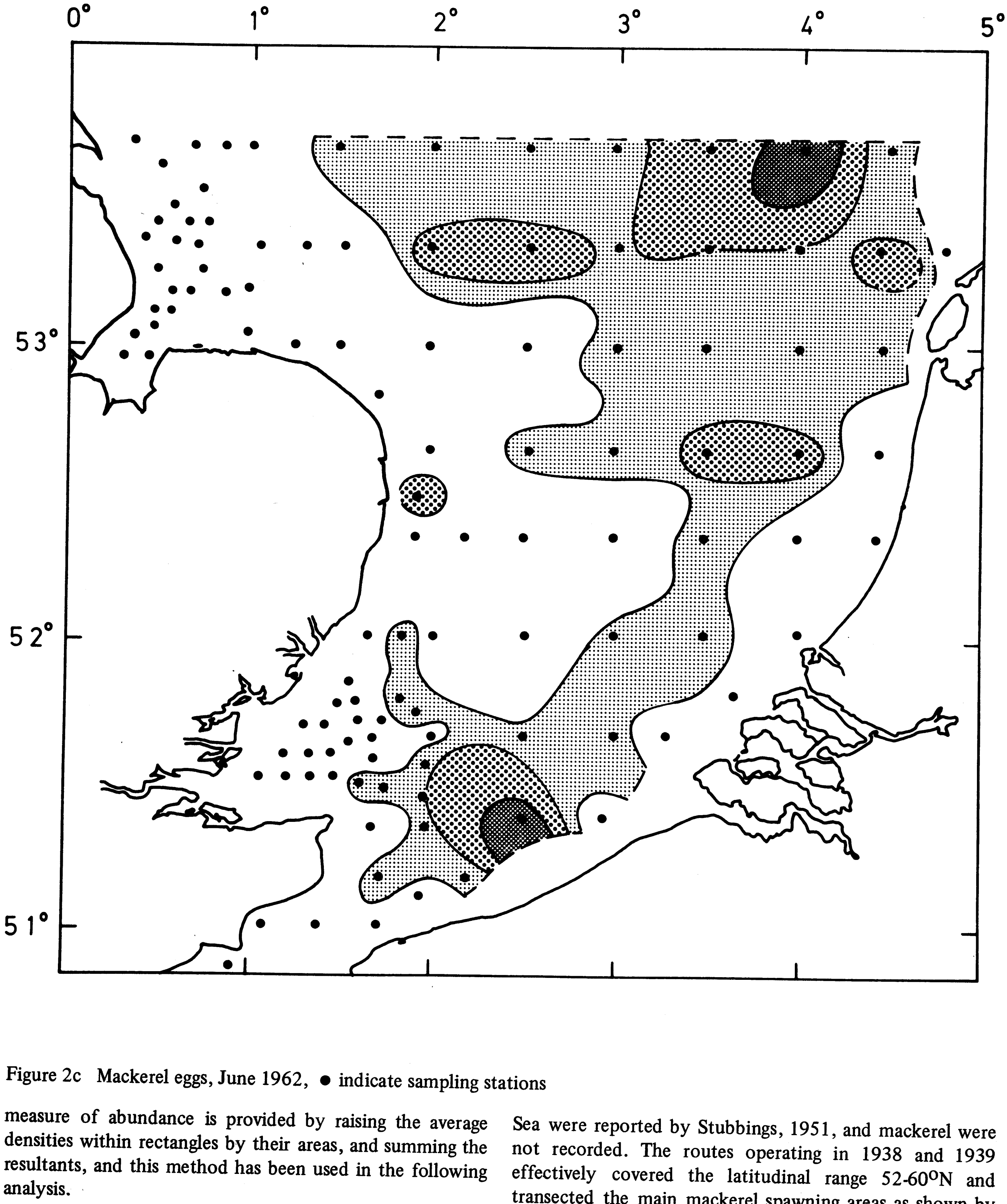

Figure 2c Mackerel eggs, June 1962, ● indicate sampling stations

measure of abundance is provided by raising the average densities within rectangles by their areas, and summing the resultants, and this method has been used in the following analysis.

Mackerel Larval Distributions as shown by CPR Surveys

1 1938-39 (Figure 3)

The results for fish egg and larval distribution in the North Sea were reported by Stubbings, 1951, and mackerel were not recorded. The routes operating in 1938 and 1939 effectively covered the latitudinal range 52-60°N and transected the main mackerel spawning areas as shown by the post-war surveys. About 19% of the larval material he examined was unidentifiable, but was considered to have been mainly pleuronectids and gadoids. The apparent lack of mackerel in these years may have been due to exceptionally low larval densities, below the sampling threshold of the gear.

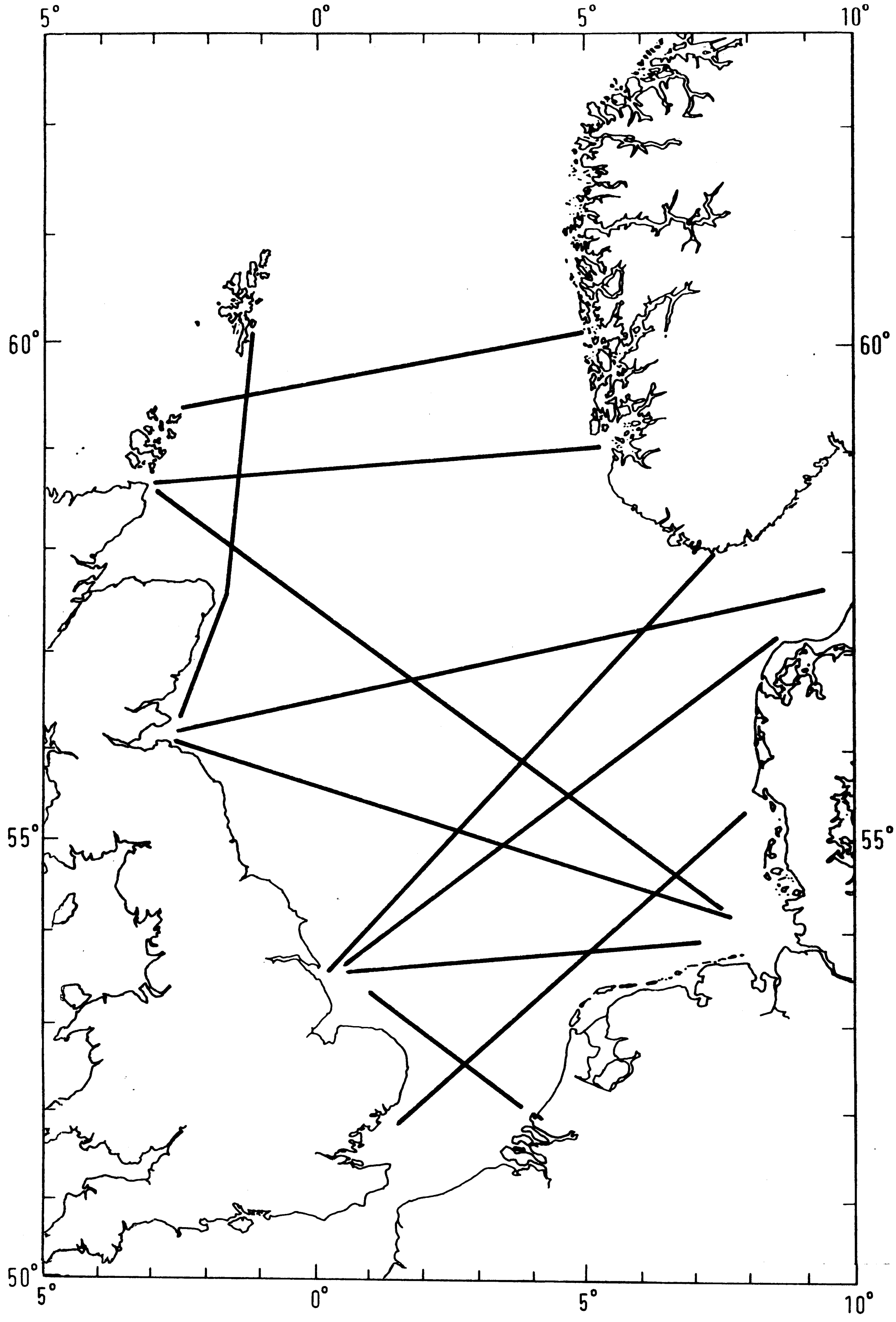

Figure 3 CPR routes, 1938-39

2 1948-56 (Figure 4)

Results for the immediate post-war years, 1946-49, are presented by Henderson, 1954. However, the routes in these years did not cover the North Sea north of about 58°N, except for a short route running from the north-east coast of Scotland to Shetland. In the years 1947 and 1948 the quantities of mackerel larvae taken in the central and southern North Sea were generally low, and mainly recorded along the route from the Firth of Forth to the Skagerak, north of 56°N. In this context it is of interest to note Fraser's (1949) chart of distribution for mackerel

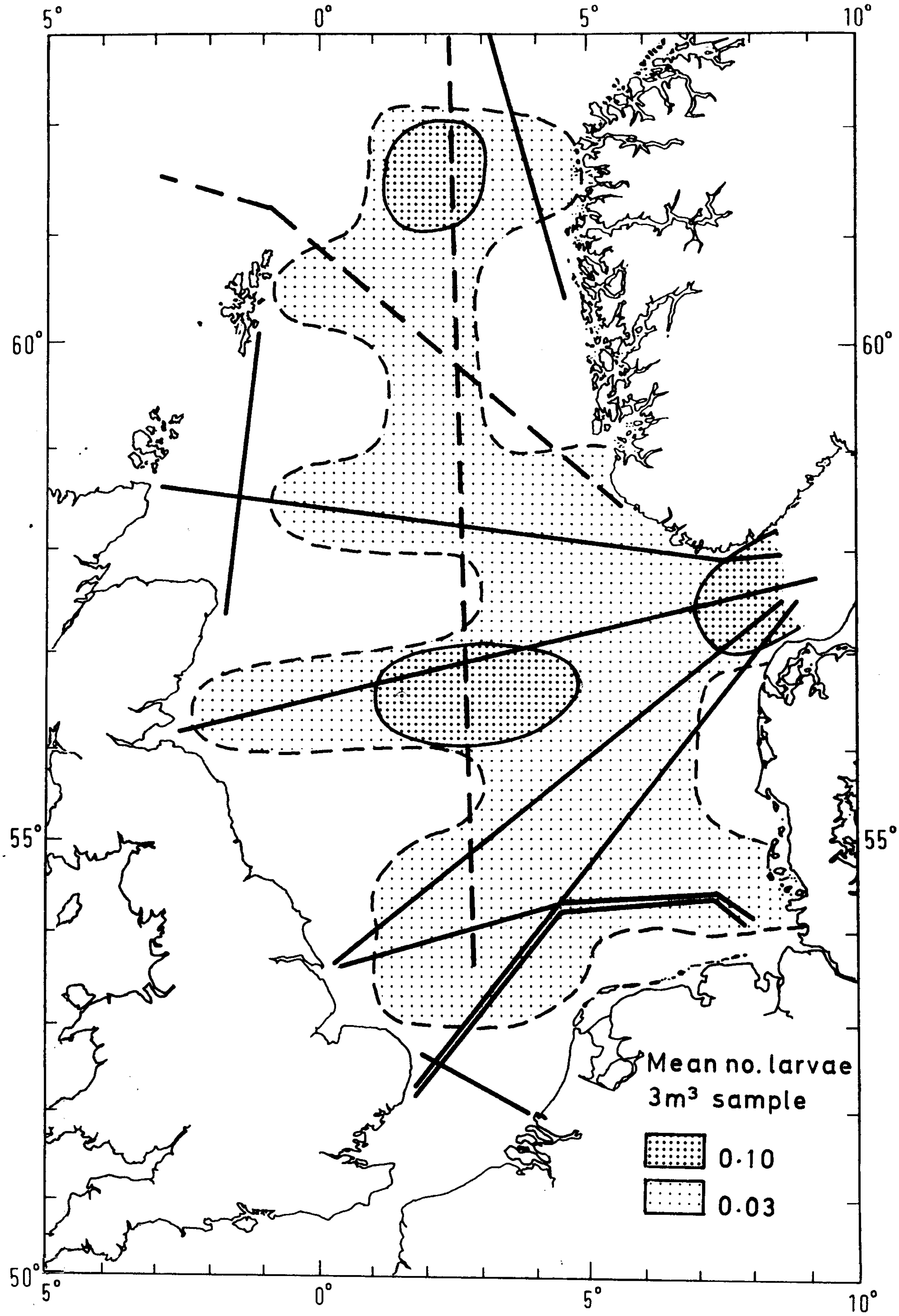

Figure 4 CPR routes, 1948-56 (with mackerel larval distribution, Henderson 1961)

larvae in the northern North Sea, in July 1947. These were 4-12 mm in length, with a modal length of 7 mm. They were found over a wide area between the Orkneys-Shetland region and west coast of Norway, from about 58°N to 61°30'N, thus falling outside the limits of the recorder survey at this time. In July 1949 a very large increase in numbers occurred, with the largest quantities along most of the route between the Firth of Forth and Skagerak, but with significant numbers also appearing in the German Bight region, mainly east of 3°E, between 54°N and 56°N. The average density of larvae in July 1949 was over ten times as great as that in the same month of the previous two years.

From 1950 onwards additional routes were established to cover the region north of 58°N, whilst the central and southern areas of the North Sea were well covered except (up to 1956) for a limited area off the north-east coast of England. Results for the 1948-56 period (Henderson, 1961) suggested three main areas of relatively high mackerel larval density, the northernmost one between 61°N and 62°N and 01°-03°E, the second in the area 56°-57°N, 01°-05°E, just north of the Dogger Bank, and the third at the entrance to the Skagerak. Larvae were also found widely distributed at a much lower density between 53°N and 62°N.

3 1958-68 (Figure 5)

The pattern of routes in this period changed slightly compared with that of 1948-56. The region immediately off the north-east coast of England was covered,

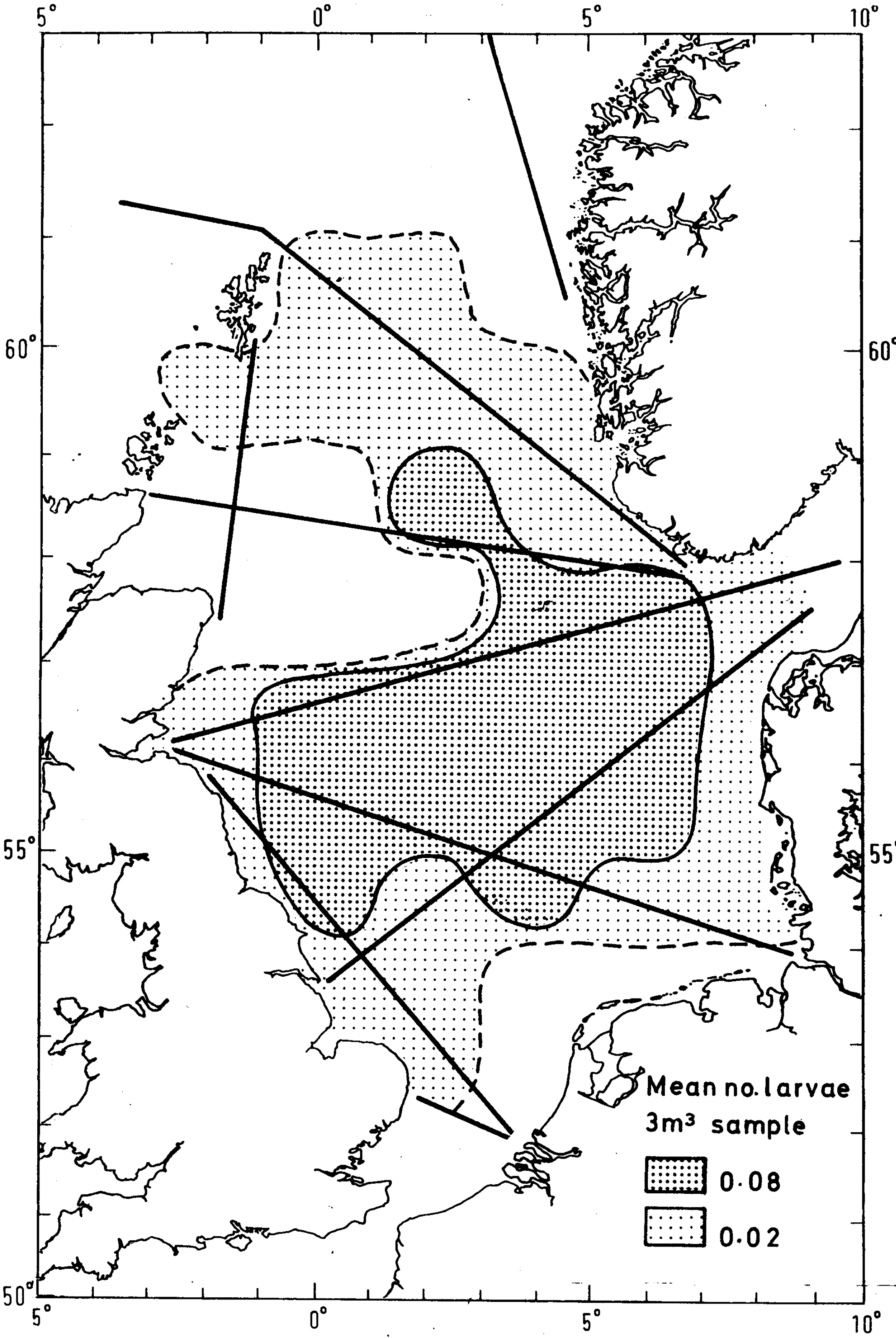

Figure 5 CPR routes, 1958-68 (with mackerel larvae distribution from Coombs unpubl chart)

Table 1

North Sea - Distributions and abundance indices* for mackerel larvae as shown by CPR surveys (1948-56/1958-68)

Range in latitude	Rectangles with larvae in both periods		Rectangles sampled in each period but with larvae in only one		Rectangles with larvae but not sampled in each period	
	1948-56	1958-68	1948-56	1958-68	1948-56	1958-68
61-62°	-	-	3.87	NIL	-	-
60-61°	0.71	1.14	-	-	-	-
59-60°	0.36	0.58	NIL	1.74	-	-
58-59°	1.10	3.49	-	-	0.15	-
57-58°	4.64	6.73	-	-	-	-
56-57°	8.61	6.99	NIL	3.48	-	-
55-56°	0.82	6.45	NIL	3.22	-	3.26
54-55°	1.53	5.08	-	-	-	3.29
53-54°	0.43	0.10	0.43	0.24	-	-
52-53°	-	-	NIL	0.09	-	-
Totals	**18.20**	**30.56**	**4.30**	**8.77**	**0.15**	**6.55**
N of 56°N	15.42	18.93	3.87	5.22	0.15	-
S of 56°N	2.78	11.63	0.43	3.55	-	6.55

For those rectangles sampled in each period

	1948-56	%	1958-68	%
N of 56°N	19.29	85.7	24.15	61.4
S of 56°N	3.21	14.3	15.18	38.6
	22.50		39.33	(0.6:1.0)

*Abundance index= Σ(mean density per rectangle x area)

(Areas of rectangles corrected for latitudinal changes and incompleteness where they intruded into land areas)

whilst the distribution of regular routes adequately covers most of the likely areas for mackerel larval distribution in the North Sea.

Results for 1958-68 (Coombs, unpublished data) show some marked changes compared with the situation in the 1948-56 period and Table 1 summarises for the North Sea the relative distributions and abundance indices by 1° latitudinal belts for mackerel larvae in the two periods. For a more precise comparison the data have been grouped into (a) rectangles sampled and with larvae in both periods, (b) rectangles sampled in both periods but with larvae in only one, and (c) rectangles with larvae but sampled in only one period.

The major change (noted by Coombs in his unpublished analysis) involves an apparent shift in abundance to the south of 56°N in the 1958-68 period. For those rectangles commonly sampled in both periods the proportion of larvae north and south of 56°N changes from a 86:14 ratio in 1948-56 to 61:39 in 1958-68. This increase mainly involves an area between 54°N and 56°N, which covers the Dogger Bank region. There was also a marked decline in abundance in the northernmost part of the North Sea (60-62°N) in the 1958-68 period. In terms of overall abundance, the estimate for the latter period was nearly double that the for former period.

A more recent assessment by S H Coombs (unpublished charts) provides a comparison of mackerel larval densities and distributions in the periods 1958-65 and 1966-73. These distributions were expressed as the sums of monthly mean larval densities in each basic rectangle within each period, and clearly show a contraction of larval distribution in the 1966-73 period within the northern North Sea, north of 58°N. South of this latitude the distribution area and relative abundance indices remained much the same in the two periods.

The Celtic Sea region

A similar analysis for the Celtic Sea is shown in Table 2. This covers an area within the limits 47°-52°N and 05°-13°W. The most notable features are (a) a very marked drop in the overall index of abundance for the 1958-68 period, this being eight times less than for the 1948-56 period, and (b) a shift in the proportion of larvae north and south of 50°N, there being relatively more in the northerly section in 1958-68, although in absolute terms there were far fewer larvae taken. Compared with the indices of abundance for the North Sea, the overall level in the Celtic Sea was nearly nine times as great in the 1948-56 period, but declined to only 0.6 that for the North Sea in 1958-68.

Period mean values derived from an annual analysis of mean larval abundance indices provided by S H Coombs for the North Sea and Celtic Sea are as follows:

PERIOD	NORTH SEA	CELTIC SEA
1948-56*	35.2	116.7
1958-68	112.5	31.3

(*1950-56 for the Celtic Sea)

These figures clearly confirm the results of the above analysis although the relative magnitudes of change differ, which is probably mainly due to differences in the methods of averaging and raising the basic data.

Table 2

Celtic Sea - (47°-52°N:05°-13°W) - Distributions and abundance indices for mackerel larvae as shown by CPR surveys (1948-56/1958-68)

Range in latitude	Rectangles with larvae in both periods		Rectangles sampled in each period but with larvae in only one		Rectangles with larvae, but not sampled in each period	
	1948-56	1958-68	1948-56	1958-68	1948-56	1958-68
51-52°	17.95	7.09	-	-	-	7.09
50-51°	59.67	7.25	NIL	0.14	-	-
49-50°	93.96	3.85	-	-	-	-
48-49°	27.70	4.54	NIL	0.76	-	-
47-48°	-	-	NIL	0.61	-	-
Totals	**199.28**	**22.73**	**NIL**	**1.51**	-	**7.09**

Indices of total abundance for rectangles sampled in both periods

	1948-56	1958-68
	199.28	24.24 (8.2:1.0)
N of 50°N	77.62	14.48
S of 50°N	121.66	9.76
% Distr	39.0	59.7
	61.0	40.3

The distribution charts for 1958-65 and 1966-73 showed little change in the overall relative abundance between the two periods, although there was some suggestion of a shift in the main distribution towards the western half of the area in the latter period.

Annual and Longer-term fluctuations in Mackerel spawning

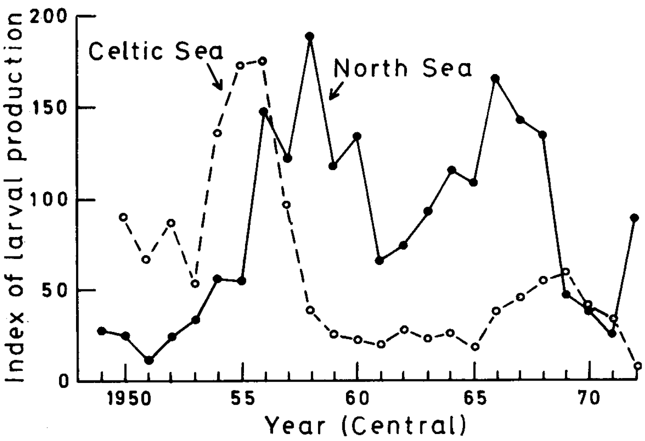

Figure 6 Mackerel larval production (CPR surveys)

The estimates of annual larval production for the Celtic Sea and North Sea for the years 1948-73 kindly supplied by S H Coombs are shown in Figure 6 as smoothed three - yearly running means of area-weighted larval production for the two areas. This shows that there have been some extreme fluctuations in both regions, and these changes have not been in-phase. The Celtic Sea showed a major peak in the 1950s; and a lesser one in the late 1960s, whilst the North Sea produced two major peaks, the first in the late 1950s and following that in the Celtic Sea, and the second just after the mid-1960s and prior to the minor peak in the Celtic Sea.

Table 3

North Sea mackerel - Annual indices of larval abundance in relation to estimated spawning stock sizes and year-class strength

Year	Smoothed index of larval density	Spawning* stock (.000 tons)	Year-class* strength at 1 year (millions)
1962	73	-	3540
1963	92	-	320
1964	114	2190	850
1965	108	2866	1418
1966	162	2692	2035
1967	142	1913	319
1968	133	1468	530
1969	46	938	3287
1970	40	445	292
1971	24	247	
1972	88	1482	

*Estimates from Hamre, 1975

Interpretation of these fluctuations may be helped by reference to Table 3, where the indices of larval production in each year in the North sea are compared with estimates of spawning stocksize and year-class strengths in the North Sea mackerel population (Hamre, 1975). The index of larval production appears to be more closely associated with spawning stock size than with year-class strength. This could be explained by the fact that most mackerel larvae taken by the CPR are small, 94-98% being below the length of 10-11 mm at which size Sette (1943) showed a critical mortality as likely to occur and so determine the resulting year-class strength.

Thus, if the CPR index of larval production provides a valid measure of spawning stock strength, then it is evident that spawning stocks appear to have undergone some extreme fluctuations in magnitude (up to 12:1) in both of the main spawning areas. Here it is of interest to note that a similar range in magnitude is shown for individual year-class strength estimates by Postuma (1972) using catch per unit effort data, and by Hamre (1975) from virtual population analysis.

The north-west Atlantic mackerel population has shown extreme fluctuations in magnitude during its long period of recorded history (Sette and Needler, 1936) and possible causes of these changes have been examined by Taylor *et al* (1957). The European mackerel fisheries, although long-established in both the Celtic Sea and North Sea, have not, until the last decade, been heavily exploited, and any fluctuations in catch could have been due either to changes in economic factors or to changes in stock strength, or to a combination of both factors.

Postuma (1972) noted a steady decline in the catch per unit effort of the Dutch trawl fishery for mackerel in the north-eastern North Sea from 1959 onwards, and this change was ascribed to a natural decline in recruitment because the downward trend was clearly established in a period when fishing mortality was very low prior to 1964. The greatly increased fishing effort from 1965 onwards may thus have coincided with a period of naturally declining population.

The larval production curve over this period (Figure 6) does not suggest a continuing and unbroken decline from 1959 onwards. It does show a marked drop from 1958 to 1961, but then enters another upwards trend peaking in 1966, and then shows a rapid decline to a minimum in 1971. The final period does coincide with that of greatly increased fishing effort in the North Sea when the catch rose from an average annual level of 92,000 tons in the 1960-64 period to 650,000 tons in the 1965-69 period. On the other hand, the low level of larval production in 1971 appears to have been the norm for earlier years (1948-53) when fishing mortality was negligible. These fluctuations in larval production do not appear to be readily linked with the longer-term temperature trends and changes in the North Sea discussed by Hill and Dickson (1975), although this aspect might merit further examination in view of the possible significance of temperature to changes in the north-west Atlantic mackerel population shown by Taylor *et al* (1957). They have also taken place against a background of a copepod production which has shown a rapidly increasing downwards trend from the late 1950s to 1973 (Colebrook, 1975).

Timing of egg and larval production

The available data on timing are summarised in Table 4. A weighted numerical estimate of timing (Index of timing) is also given in cases where sufficient quantitative monthly data are provided. This average timing was derived by weighting the equivalent calendar number for each month (applicable to the mid-point of the month) by the density in that month, and dividing the summed product by the summed monthly densities.

The earliest spawning is found over Biscay and the Celtic Sea grounds, with peak egg production in April-May and main larval production between April and June. If the average timing of larval production for the 1937-39 Celtic Sea surveys is compared with that for the 1948-67 CPR, surveys, it appears to have occurred one month earlier in the post-war period. This difference is most probably explained by the different types of netting used in the two periods. The earlier surveys were undertaken using a 2 m stramin net, which has a relatively coarse mesh (Corbin, 1947; Southward, 1970), and Sette (1943) showed by comparative tows with a 1 m finer meshed net that stramin netting was not retaining the smaller mackerel larvae. The 50% selection level was at about 7 mm and larvae were not fully retained until around 9 mm. The average lengths of larvae taken were 3.8 mm for the fine net and 10.1 mm for the stramin net. In terms of equivalent age (using Sette's conversion formula) these would have been 7.8 days and 27.8 days after spawning respectively. This represents a difference of about three weeks, which could largely account for the difference in timing noted above.

The larval production period observed off Plymouth is concerned mainly with the larger post-larval stages, since these samples were taken with a 2 m stramin net. This region is also not directly associated with the main mackerel spawning which takes place over the Celtic Sea and which occurs earlier and at a much higher intensity than over the western end of the English Channel, where spawning takes place mainly in July, The differences found in mean timing between the pre- and post-war periods are probably not significant when allowance is made for the large fluctuations in numbers taken from year to year and the fact that the type of netting and sampling technique used also changed after 1960 (Southward, 1970). The most consistent features to emerge are that post-larvae are found from May to September, with a peak in July, and that this timing is close to that in the North Sea.

The North Sea and Skagerak-Kattegat spawning period falls much later than that of the Celtic Sea and Biscay, commencing about May and continuing into August, possibly later in some years. Peak egg and larval production develop in June-July after the rapid spread of spawning over most of the North Sea in June. The CPR surveys show that the timing of larval production in the region south of 55°N is virtually identical with that in the region between 55°N and 58°N, and that the difference in timing between the North Sea and Celtic Sea is about 2½ months. The North Sea spawning is spread over a shorter time (May-August) than is the Celtic Sea spawning (March-July), with about 75% of the total larval production concentrated within the peak month of July as compared with only 46% for April in the Celtic Sea. In the north-west Atlantic region the mackerel show an earlier peak spawning period (May-June) towards the southern end of their spawning range, and a later one (June-July) towards the northern end, thus tending to overlap in timing with the Celtic Sea and North Sea populations, although closer to the latter group.

Spawning in relation to environmental factors

Bainbridge *et al* (1974) noted that in relation to plankton production cycles the peak of larval production in the Celtic Sea coincides with the spring outburst of phytoplankton, although this was not evident in the North Sea where the peak larval production period fell between the spring and autumn peaks of phytoplankton and even after the main increase in copepod populations. They concluded that, in the case of the North Sea, factors other than larval food supply must primarily determine the timing of spawning. They also pointed out that the monthly progression of the area of mackerel larval production tended to follow the pattern of warming as shown by the spread of the 10°C and 11°C isotherms over the waters of the north European shelf.

Table 4 Timing of mackerel egg and larval production in different sea areas

Mackerel

Area	Period	Egg production: Commence	Egg production: Peak	Egg production: End	Egg production: Index of Timing	Larval production: Commence	Larval production: Peak	Larval production: End	Larval production: Index of Timing	Source
Biscay (44°-50°N)	1964 - 72	End Feb	May	Jul	-	Mar	May-Jun	Aug	-	Arbault & Lacroix, 1975
Celtic Sea/Bristol Channel/W. end English Channel (48°-52°N)	1937 - 39	Mid Mar	Apr-May	Early Aug	4.73	Mar	May-Jun	Aug	5.46	Corbin, 1947
	1948 - 67	-	-	-	-	Mar	Apr-May	Aug	4.41	Bainbridge *et al*, 1974
						(CPR surveys - all larval sizes)				
Off Plymouth (50°11′N 04°13′W)	1924 - 29	-	-	-	-	May	Jul	Aug	6.80	Russell, 1930, 1935-40, 1947
	1930 - 34	-	-	-	-	Jun	Jun-Jul	Sep	6.71	1969, 1973.
	1935 - 39	-	-	-	-	May	Jul	Aug	6.67	Russell & Demir, 1971
	1946 - 49	-	-	-	-	Jul	Jul	Aug	7.38	Corbin 1948-49, 1951
	1966 - 71	-	-	-	-	Jun (Post-larvae)	Jul	Sep	7.24	
North Sea										
(i) S. of 55°N	1948 - 67	-	-	-	-	Jun	Jul	Aug	7.12	Bainbridge *et al*, 1974
(ii) 55°-58°N	1948 - 67	-	-	-	-	Jun	Jul	Aug	7.10	
						(CPR surveys - all larval sizes)				
(iii) Mainly E. of 4°E	1901 - 09	May	Jun-Jul	Aug	-	-	-	-	-	Ehrenbaum, 1923 (summarising results from various sources).
(iv) Mainly S. of 54°N	1959 - 62	May	Jun-Jul	Aug	-	Jun	Jul	Aug	-	Unpubl. data from Lowestoft surveys.
Skagerak/Kattegat										
(i) Mainly E. side (59°-56°N)	1911 - 1912	Jun	Jul	Aug	-	-	Jul	-	-	Nilsson, 1914
(ii) *Mid-Kattegat/ Northern belts*										
(a) Mid-Kattegat	1929 - 41	May	Jun-Jul	Oct	6.47	-	-	-	-	Heegard, 1947
(b) South Kattegat		May	Jun	Oct	6.26	-	-	-	-	
(c) North Belts		May	Jun	Aug	6.38	-	-	-	-	
(iii) *Skagerak*	1957 - 59	May	Jun	(Jul)*	-	May	Jun	(Jul)*	-	Myrberget, 1965

Table 4 (contd)

Area	Period	Egg production: Commence	Peak	End	Index of Timing	Larval production: Commence	Peak	End	Index of Timing	Source
(iv) *Skagerak/ Northern Kattegat*	1962 - 63	May	Jun	(Jul)*	-	May	Jun	(Jul)*	-	Lindquist, 1968, 1970.
N.W. Atlantic										
Cape Hatteras-Cape Cod (36°-42°N)	1926 - 32	Mid Apr	May-Jun	(Jul)*	-	End Apr	Jun	(Jul)*	-	Sette, 1943
Gulf of Maine (42°-44°N)	1926 - 32	May	Jun	(Jul)*	-	-	-	-	-	Sette, 1943
Gulf of St Lawrence	1915	May	Jun-Jul	Aug	-	-	-	-	-	Dannevig, 1919
Nova Scotia coast (44°-45°N)	1922	May	Jun-Jul	Aug	-	-	-	-	-	Sparks, 1929

(*Surveys did not extend beyond July).

Several other authors have suggested that differences in the timing of movements and spawning in mackerel are temperature-linked. For example, Sette (1950) examined the appearance and disappearance of mackerel in relation to sea temperatures in various localities along the American coast and concluded that there was a lower limiting temperature of 7.8°C which could act as an effective barrier to dispersal in the spring months. This level of temperature restriction might apply in the case of mackerel overwintering in the northern North Sea, but is much less likely for those overwintering along the western European shelf and in Biscay where minimum winter temperatures are usually in excess of 10°C south of Ireland and do not fall much below 9°C to the north of Ireland.

Steven (1949) suggested that the extended period of spawning shown by mackerel in the Celtic Sea, and the difference in timing of spawning compared with the North Sea, could be related to differences in the winter temperature regimes experienced by fish in their overwintering areas and to differences in the lengths of migration routes between the overwintering and the spawning areas. This possibility was investigated by Cooper (1949) who examined the temperature levels during February in various known overwintering localities for mackerel. These included the Hurd Deep, western half of the Celtic Sea, and the edge of the Viking Bank west of Norway. In the Celtic Sea the water was found to be isothermal at this time of year down to a depth of at least 120 m, and this also applied for the Hurd Deep. A comparison between these two areas showed that the average temperature levels in February were such that mackerel overwintering to the south of 50°40'N and west of 09°00'W would experience temperatures 0.2-0.8°C above those in the Hurd Deep area, and this might be sufficiently great to account for the earlier onset of spawning in mackerel in the western part of the Celtic Sea. By contrast, the February temperature levels along the western edge of the Norwegian Deep Water were generally 2-3°C lower than those the the Hurd Deep, and this finding might be associated with the much later spawning in the northern and central North Sea. Steven (1949) also noted that in 1949 mackerel to the south of Ireland began spawning in February, several weeks earlier than normal for this area, and this he related to the exceptionally mild winter which resulted in higher than average water temperatures.

The mackerel encounters fairly wide ranges of temperature and salinity throughout its spawning range in the North Atlantic and probably meets the most extreme conditions in the Skagerak and Kattegat where hydrographic conditions are very complex (Svansson, 1975). In this region eggs have been found in water of temperature 6-18°C and salinity 16.0-35.0°/oo, although the majority were usually within the limits 11-14°C and 25.0-31.5°/oo. (Nilsson, 1914; Myrberget, 1965). Nilsson (1914) also maintained that the lower salinity level for successful development of the eggs was about 26°/oo. The opposite extreme for salinity is met with in the Celtic Sea where, in the months March to July, the average salinity over the main mackerel spawning areas was found to be in the range 34.5-35.6°/oo and the temperature in the range 10.0-15.5°C (Corbin, 1947). In Biscay in the months of March and May, most spawning took place within the temperature range 11.0-14.0°C (Arbault and Lacroix, 1975).

In the North Sea most mackerel spawning takes place in salinity levels between the above extremes. Surveys undertaken in June and July by the Lowestoft laboratory and covering most of the southern and central North Sea as far north as 57°30'N have shown most eggs to be within a salinity range of 33.0-35.2°/oo and a temperature range of 10-15°C.

Finally, on the American coast spawning grounds Sette (1943) found that nearly 92% of all the eggs taken in May and June 1932 were from water with a temperature range of 9-14°C, whilst Bigelow and Welsh (1925) noted a range of 8-16°C temperature and 31.9-33.0°/oo salinity for mackerel eggs in the Gulf of Maine.

The general conclusion to be drawn from these diverse results is that spawning seems more closely limited by temperature, with an optimal range of 10-15°C, rather than by salinity (26.0-35.6°/oo).

Estimations of spawning biomass

The available spawning data are mostly very incomplete in time and area and are thus not suitable for estimating spawning stock size by the usual method from a total egg production curve. In the case of mackerel the situation is further complicated by the serial nature of its spawning. Earlier estimates of total fecundity (Moore, 1899; Bigelow and Welsh, 1925), suggested that a 'medium' sized female could produce 360,000-450,000 eggs over its total spawning period, although only 40,000-50,000 would mature and be shed at any one time. This represents about 1/9th of the potential total fecundity, and if all the eggs are to be shed, indicates nine distinct spawnings during the season.

If total potential fecundity is proportional to body weight, then it might reasonably be assumed that the average number of ripe eggs released per unit of body weight is also proportional. The average batch size is unknown, and it would obviously be difficult to determine this by direct observation since in ripe fish (maturity stage 6) where the largest eggs ($>$ 0.9 mm diameter) do form a discrete group, one cannot be certain that at the time of capture the fish had not already shed some of its ripe eggs, particulary if the spawning act is completed in a fairly short time. Prior to this stage of maturity the largest egg groups are not sufficiently differentiated to allow one to identify them as a discrete ripening batch. The average batch size is also dependent on the number of individual spawning operations per fish during the season, and this might vary depending on environmental conditions such as the available food levels.

However, it might also be assumed that the proportion of the total potential fecundity likely to ripen and be 'simultaneously' released by an individual would be the same, whether it were a large, medium or small fish. Further, if the recovery interval between the release of successive batches were of the same order as egg development time (5-7 days during the peak spawning period) then such a relationship should assist continuity of egg production by the spawning population. Thus, if nine discrete batches were released, then the time taken to complete spawning by an individual fish would be nearly 2 months, which is well within the period of 4-5 months for egg production in the sea. Staggering of spawning in time beyond the basic individual fish limit would then arise due to asynchronous ripening of fish within the population. Reasonable assumptions have thus had to be made, and the 'batch' method attempts to establish a direct relationship between the total eggs and the spawning biomass necessary to account for this number of eggs. This also avoids the problem of determining the size distribution of fish within the spawning population and enables the assessment of the weight of spawning population from individual 'one-off' surveys. Such estimates are likely to be minimal ones and of an 'instantaneous' nature applicable only to the relatively limited period of time covered by each survey.

Integration in time to produce a seasonal egg production curve would involve the use of assumptions for most of the material available at least as far-reaching as those above. This approach was attempted by Walsh (1976) using data from the Celtic Sea 1938-39 surveys, and he outlines the problems encountered. There also remains the problem of egg resorption (Macer 1976), even when one has adequate material for the construction of a total production curve, and can use a total potential fecundity/weight relationship.

More recent estimates on total fecundity (Macer 1976) agree with the earlier values, and show a linear relationship between fecundity and $(\text{length})^3$, and hence a relatively constant fecundity per unit body weight irrespective of total size. Using the basic regression established by Macer, a conversion factor for raising total eggs to equivalent spawning biomass was derived as follows.

The basic weight/length relationship used was that for the months of January and February in fish from Cornish waters when they are taking little or no food prior to spawning. The total fecundity per unit body weight over the length range 28-45 cm was then found to average 886 eggs per gram. Assuming that the batch size averages 1/9th of this leads to a 'batch' fecundity per unit body weight of 98.4 eggs per gram. However, for the purpose of raising to total spawning biomass, allowance must be made for the males, and here the sex ratio was assumed to be 50:50. Steven (1949) produces some evidence for this in the Celtic Sea. The use of this ratio reduces the 'batch' fecundity estimate to 49.2 eggs per gram of male plus female and this is equivalent to a 'batch release' of 49.2×10^6 eggs per ton of spawning fish.

A correction factor now has to be applied to allow for mortality in the egg stage, since the eggs sampled on any particular occasion will represent the cumulative product of spawning over a period of days determined by the development time for the eggs. Sette (1943) showed that at 11°C the average time to hatching was about seven days, with a mortality rate of 5% per day, resulting in 70% survival between spawning and hatching. Thus, if the egg production rate has been maintained at a fairly constant level over the period prior to sampling, then the average age of eggs in the sample should be about 3.25 days. The number of eggs sampled would thus have to be raised by a factor of 1.2 to allow for mortality in the development period. This further reduces the 'batch' fecundity per unit body weight to 34.36 eggs per gram, or 34.36×10^6 eggs per ton of spawning fish. This was the value used as a conversion factor for the surveys analysed. This method could obviously be refined in many respects, but should provide at least order of magnitude estimates of spawning stock sizes, particularly when individual surveys have been undertaken around peak spawning and a high proportion of the mature population is actively spawning. Where the data were presented as numbers per 'standard' haul problems arose in converting much of them to standard numbers under a square metre. Where sufficient subsidiary details were provided the data were converted to comparable reference densities by making various assumptions.

The Celtic Sea surveys undertaken in 1937-39 posed further difficulties in assessing the spawning population. The sampling procedure used was not likely to have sampled to a depth greater than 50 m (Corbin, 1947; Russell, 1926; 1930) over an area where the average depth is usually within the range 120-140 m, and if eggs were present below this level they would obviously not have been accounted for. Evidence from a number of sources (Nilsson, 1914; Sette, 1943; Myrberget, 1965) suggests that the majority of mackerel eggs would be present in the top 50 m or even less, but these observations were made in the Skagerak/Kattegat and off the American coast, areas typified by pronounced vertical stratification of the water column. Walsh (1976) produces evidence from hauls made over deep water to the west of Scotland in April-May 1967, to show that on average 60% of the mackerel eggs were found within the top 50 m. More recent evidence (Coombs, pers. comm) from samples taken with a Longhurst-Hardy plankton recorder in April 1974 and 1975, showed mackerel eggs present to depths exceeding 300 m over deep water off the shelf to the west of the British Isles. Overall, about 50% of the eggs were found in the top 50 m and 75-80% within 100 m of the surface. The density/depth profiles (sampling was carried out in 10 m steps) showed considerable variation in detail between stations, but typically an exponential decline in numbers from the surface maximum downwards.

Another feature of these surveys which could have led to an underestimate of egg numbers involves the relatively coarse stramin netting used. The measurements made on this type of netting by Southward (1970) showed across-mesh values of 0.7-1.2 mm (average 0.9 mm) and diagonal values 0.9-1.5 mm (average 1.2 mm). If these are compared with the dimensions of mackerel eggs, which range in diameter from about 1.0-1.4 mm and average 1.18 mm in both European and American waters (Buchanan-Wollaston, 1911; Ehrenbaum, 1923; Bigelow and Welsh, 1925; Sparks, 1929), there seems a distinct possibility that a proportion of eggs could have been lost through the netting.

An additional aspect likely to lead to an underestimate of spawning biomass when assessing it from individual surveys is that the proportion of the total adult population actually spawning during the relatively limited period of each survey is unknown. Steven (1949), provides some evidence from samples taken by drift net in the Celtic Sea for the months March-July, 1937-39, to show that the average proportion of ripe running fish in any one month did not exceed 52% for females and 62% for males. On the other hand, Nilsson (1914) produces figures to show that in the eastern Skagerak up to 90% of the fish sampled were ripe running during the peak spawning period, although his sampling was rather limited in time and area. Nevertheless, the apparently greater proportion of North Sea mackerel becoming ripe simultaneously during peak spawning could be a reflection of the relatively shorter and more intense spawning shown by this population compared with that of the Celtic Sea.

A final problem, common to most of the surveys analysed, was due to the survey grid's incompletely covering the spawning area. In some instances a correction could be applied for this by rounding-off or by an arbitrary completion of open contours.

Results for all the surveys covered are summarised in Table 5. They relate to the Skagerak/Kattegat, North Sea, English Channel, Celtic Sea, Bay of Biscay and American coast spawning areas.

In the case of some surveys, eg Biscay, the published form of the data (usually as contoured density charts) did not allow a full analysis, and the results from these are included in Table 5 in a more abbreviated form.

A comparison of the maximum densities in each area shows that the highest levels (236-269 eggs per m^2; 6.9-7.8 tons spawning fish per km^2) were recorded from the Inner Skagerak/Kattegat surveys of June 1962 and 1963, followed by the North Sea surveys in June 1972 and the American coast surveys in May-June 1932 (150-165 eggs per m^2; 4-5 tons per km^2). Peak levels recorded on the Celtic Sea and Biscay surveys were considerably less (42-72 eggs per m^2; 1-2 tons per km^2), whilst the lowest levels (4-11 eggs per m^2; 0.1-0.3 ton per km^2) were recorded in the English Channel and southern North Sea.

The estimates of spawning stock biomass show a considerable range in magnitude, although, for reasons outlined earlier, they are likely to be very conservative ones, particularly for the 1937-39 Celtic Sea surveys.

The largest estimates arise from the North Sea surveys undertaken in June-July 1972, where the combined total exceeds 1 million tons, which is of the same order of magnitude as Hamre's (1975) spawning stock estimate of 1,482 x 10^3 tons for 1972. A comparison of the estimates from Iversen's surveys undertaken in the northern North Sea in June-July 1971 and 1972 shows that the spawning stock in this area more than doubled between the two years, and this also agrees with Hamre's estimate of a large stock increase at this time, mainly due to recruitment of the very successful 1969 year class. Another interesting festure of these two surveys is that the total area of spawning did not show a comparable increase, the reduced stock of 1971 covering much the same area as the greatly increased stock in 1972.

Raised maximum estimates for the 1937-39 Celtic Sea surveys were similar in each year, ranging from about 213,000 to 285,000 tons, although these were probably considerable underestimates and might well be doubled. Walsh (1976) used a total egg production method to assess the Celtic Sea spawning stock for the years 1938-39 from results of the surveys reported by Corbin (1947). He concluded that his estimates of between 105,000-287,000 tonnes were unrealistically low and discusses possible reasons for this, together with the difficulties arising in handling the data available. The survey undertaken in this region in May-June 1967 covered only a portion of the total likely spawning area for this time of year, and a raised spawning stock estimate of 106,000 tons could probably also be doubled.

The Skagerak/Kattegat spawning population in the 1962-63 period appears to have fallen in the range of 100,000-150,000 tons, although these surveys did not adequately cover the Norwegian side of the Outer Skagerak, where there was some evidence for even higher egg densities at that time.

The average estimate for the Biscay stock in the peak spawning month May over the period 1964-72 was about 75,000 tons, the maximum estimate being 135,500 tons for May 1966.

Walsh (1976) also provides estimates for the strength of the relatively unknown component of mackerel spawning stock to the west and northwest of the British Isles (52°30' - 60°00'N, shelf to 17°W). These fall within the range 164,000-220,000 tons for April-May 1967.

The peak estimates for the American coast surveys were about 325,000 tons which compares with Sette's (1943)

Table 5 Mackerel Spawning

Celtic Sea Surveys (Basic data from Corbin, 1947)

Period	No of stations with eggs	Mean egg density (No/m^2)	S.E.	% MSE	I/K	Spawning area (Km^2)	Sampling intensity (Km^2/Sta)	Total eggs (x10^{-9})	Minimal spawning tonnage	Tons/Km^2
Apr 1937	19	57.6	21.5	36.52	2.92	34,067	1,793	1,963.6	57,148	1.68
May 1937	15	14.9	6.2	41.49	3.12	38,544	2,570	575.8	16,758	0.43
Jul 1937	7	0.4	0.2	47.22	2.06	14,634	2,091	5.6	163	0.01
Apr 1938	62	42.5	17.5	41.19	12.67*	115,546	1,864	4,910.7	142,919	1.24
Jun 1938	24	44.7	15.3	34.14	3.17	56,721	2,363	2,537.1	73,839	1.30
Jul 1938	20	2.3	0.9	40.28	3.91	47,344	2,367	106.5	3,100	0.65
Mar 1939	6	0.2	0.1	47.83	1.50	13,907	2,318	3.3	96	0.01
Apr 1939	69	45.0	11.8	26.16	5.07	156,107	2,262	7,017.0	204,220	1.31
Jun 1939	28	54.8	11.3	20.70	1.25	118,225	4,222	6,477.5	188,519	1.59
South Ireland/Bristol Channel (Basic data from Wallace and Pleasants, 1972)										
May-Jun 1967	43	58.8	15.9	27.03	3.37	43,660	1,015	2,569.0	74,767	1.71
Western half English Channel (06°30' W - 02°00' W)										
May-Jun 1967	39	11.0	3.2	29.12	3.52	39,958	1,025	438.3	12,756	0.32
Jul 1968 (06°W - 02°W)	13	3.8	0.9	23.07	0.45	15,788	1,214	59.5	1,732	0.11
Eastern half English Channel (02°00' W - 01°30' E)										
May-June 1967	8	3.5	1.1	32.40	0.62	9,763	1,220	34.2	995	0.10

(*This exceptionally high value was mainly due to a single station where very large numbers were caught, excluding this reduces I/K to 4.06)

Table 5 (contd) Mackerel Spawning

North Sea Surveys

Area/Period	No. of stations with eggs	Mean egg density (No/m²)	S.E.	% MSE	I/K	Spawning area (Km²)	Sampling intensity (Km²/Sta)	Total eggs (x10⁻⁹)	Minimal spawning tonnage	Tons/Km²
Southern area (51°00' - 53°00'N; coast - 03°00'E) (Basic data from Lowestoft surveys unpublished)										
Jun 1960	24	14.2	5.4	37.65	3.88	5,560	232	79.0	2,299	0.41
(51°00' - 53°40'N; 01°30'E - 05°00'E)										
Jun 1962	38	9.5	2.1	22.21	1.86	30,350	799	286.8	8,347	0.28
South-Western area (52°30' - 54°40'N; 00°00' - 03°00'E)										
Jul 1961	72	51.9	18.8	36.17	10.82	22,108	307	1,146.5	33,367	1.51
Jun 1972 survey (Basic data from Johnson and Dawson, 1975)										
Sector										
E Scotland	6	44.9	27.5	61.18	3.54	7,815	1,303	351.1	10,218	1.31
Gut-Fisher bank	19	171.2	48.1	28.10	1.63	36,499	1,921	6,247.2	181,816	4.98
Jutland	14	103.4	35.0	33.83	1.80	24,790	1,771	2,564.3	74,630	3.01
NE England	24	165.1	40.0	24.25	1.50	24,819	1,034	4,098.1	119,269	4.81
Dogger	24	145.1	34.7	23.89	1.45	39,703	1,654	5,760.1	167,640	4.22
German Bight	26	62.3	14.7	23.65	1.38	36,399	1,400	2,375.0	69,121	1.90
Wash	6	6.6	2.5	37.86	0.81	5,257	876	34.4	1,001	0.19
Southern Bight	21	39.4	14.4	36.44	3.18	34,556	1,646	1,362.5	39,654	1.15
Overall	140	107.0	12.9	12.05	2.05	209,838	1,499	22,792.7	663,349	3.16

Northern area (57°00' - 60°00'N) (Basic data from Iversen, 1973)

Period	Mean egg density (No/m²)	Spawning area (Km²)	Total eggs (x10⁻⁹)	Minimal spawning tonnage	Tons/Km²
Jun-Jul 1971	71.4	109,552	7,820.2	227,596	2.08
Jun-Jul 1972	154.3	116,994	18,052.1	525,381	4.49

Table 5 (contd) Mackerel Spawning

Swedish surveys - Skagerak and Kattegat (Basic data from Lindquist, 1968)

Area/Period	No. of stations with eggs	Mean egg density (No/m^2)	S.E.	% MSE	I/K	Spawning area (Km^2)	Sampling intensity (Km^2/Sta)	Total eggs (x10^{-9})	Minimal spawning tonnage	Tons/Km^2
(i) Inner Skagerak/Kattegat (entrance)										
Jun 1962	62	269.3	41.2	15.30	1.47	12,764	206	3,437	100,029	7.84
Jun 1963	66	236.4	35.0	14.79	1.47	13,386	203	3,164	92,084	6.88
(ii) Outer Skagerak (Danish half, Hantsholm - The Skaw)										
Jun 1962	23	202.4	86.6	42.75	5.14	4,890	213	990	28,812	5.89
Jun 1963	30	63.0	31.0	49.15	0.72	9,392	313	592	17,229	1.83
New England Shelf Surveys 1932 (Basic data from Sette, 1943)										
May 2-6	17	82.6	25.9	31.31	1.82	76,823	4,519	6,346	184,691	2.40
9-16	19	164.6	72.6	44.08	4.55	67,982	3,578	11,190	325,669	4.79
19-23	16	150.4	76.4	50.78	5.59	54,944	3,434	8,264	240,512	4.38
24-28	18	160.0	62.7	39.18	3.26	70,218	3,901	11,235	326,979	4.66
Jun 1-4	11	58.4	29.8	50.90	3.91	47,223	4,293	2,758	80,268	1.70
6-8	8	40.6	23.1	56.92	3.68	45,792	5,724	1,859	54,104	1.18
16-19	5	57.3	21.8	38.01	0.83	26,835	5,367	1,538	44,761	1.67

Biscay surveys (Data from Arbault and Lacroix, 1975)

Average values for March (1966, 1969, 1970 and 1971)
and May (1964, 1966, 1968, 1969, 1970, 1971 and 1972)

	Mean egg density (No/m^2)	Spawning area (Km^2)	Total eggs (x10^{-9})	Spawning tonnage	Tons/Km^2
Mar 44-46°N	59.1	12,191	720.5	20,969	1.72
46-48°N	44.8	1,463	65.5	1,906	1.30
48-50°N*	NIL	-	-	-	-
Overall	57.5	13,654	786.0	22,875	1.68
May 44.46°N	72.5	21,991	1,594.3	46,399	2.11
46-48°N	35.4	25,360	897.7	26,126	1.03
48-50°N*	13.3	5,635	74.9	2,180	0.39
Overall	48.5	52,986	2,556.9	74,705	1.41

(* Sampling grid very limited in this sector) estimate of about 276,000 tons using a different method. In this context it is of interest to note that the catch of mackerel in the north-west Atlantic attained a peak of 420,000 tons in 1973, and averaged 354,000 tons per year over the period 1970-74, (FAO Yearbook 1974 (39)). However, the spawning stock estimates refer only to the component spawning off the American coast and do not include the spawning areas north of the Gulf of Maine, where Sette considered there might have been a further equivalent quantity. The relative magnitude of the mackerel stock in the north west Atlantic in 1932 was also unknown, the fishery had by then entered a decline after a peak in the late 1920s (Taylor, *et al*, 1957).

Summary

In European waters three main mackerel spawnings are known, these being in the Bay of Biscay, Celtic Sea and North Sea (including the Skagerak). They appear to be fairly discrete in area, and also in time in the Celtic Sea and North Sea. There is also some evidence for a further wide spawning area to the west and north-west of the British Isles, extending from the Porcupine Bank to Rona, north of the Hebrides, although the relative importance of this region to the spawning production of the north European mackerel is not yet fully assessed.

Spawning commences eariest in Biscay and the Celtic Sea (February-March), lasts until July, and peaks in April-May. It is much later in the North Sea, where it starts about mid-May, extends until August, and peaks in June-July. Spawning takes place over a wide range of salinity (25.0-35.6°/oo) but a more restricted range of temperature (10-15°C).

In more recent years the North Sea appears to have supported the largest population but the balance between this area and the Celtic Sea has shown some considerable changes in the period 1948-73. Within these two areas there have also been large oscillations in spawning stock size, which have not been in phase between areas, and which between extremes have shown a 12:1 change in magnitude.

Acknowledgement

I would like to thank MR S H COOMBS, IMER, PLYMOUTH, for making available a considerable amount of unpublished data from the CPR surveys, which were of great value in compiling this review.

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