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The vertical distribution of eggs and larvae of mackerel (*Scomber scombrus*)

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Abstract

Results are summarised from vertical distribution sampling for eggs and larvae of mackerel (*Scombrus scombrus*) to the west of the British Isles and in the Bay of Biscay for the years 1974-1995. Early in the spawning season, in March and April, when there was no temperature stratification of the water column, eggs were found down to a depth of at least 400m. During the main period of spawning, in May and June, eggs were mostly above the thermocline in the upper 50m of the water column and generally in progressively increasing numbers towards the surface. There was a significant inverse relationship between mean depth of eggs and surface temperature. Eggs at the earliest stage of development were deeper in the water column than subsequent stages and eggs at the latest stage of development had a sub-surface peak of abundance at 10-15m depth. Larvae (2-11.9mm in length) had a similar distribution in the upper 50m of the water column in all the months in which they occurred (mostly in May and June with lesser numbers in April). There was no evidence of diel vertical migration of larvae, although in a series of samples taken in June 1995 they were more dispersed throughout the upper 50m of the water column at night than during the day when there was a sub-surface peak at 15-20m depth.

Introduction

Information on the vertical distribution of fish eggs and larvae is an essential pre-requisite for efficient sampling e.g. for stock estimation based on plankton egg surveys (Lockwood *et al.*, 1981); equally, this information is required for studies of transport and survival of eggs and larvae in relation to current systems and biological processes in the water column. In the latter context, an EU funded programme (SEFOS - Shelf-Edge Fisheries and Oceanography Studies) has been designed to study the effects of the shelf-edge current on fish stocks from Portugal through Biscay and west of the British Isles to Norway. One aspect of the SEFOS programme is an investigation of advection of the planktonic stages of mackerel (*Scomber scombrus*) and their subsequent recruitment; the present work on the vertical distribution of the eggs and larvae of mackerel is part of this study .

Spawning of mackerel (*S. scombrus*) is widespread over much of the European shelf, extending from the North Sea and west of Scotland as far south as the coasts of Spain and Portugal (Anon, 1994; Lago de Lanzós *et al.*, 1993); it is also widely distributed off the eastern coast of North America (Berrien, 1978). In European waters the highest incidence of spawning is from mid-April to mid-June at the shelf-edge and over adjacent shelf regions of the Celtic Plateau and Biscay (Anon, 1993).

Reports on the vertical distribution of mackerel eggs west of the British Isles have shown that once thermal stratification is present they are distributed mostly in the upper mixed layer above depths of about 100m (e.g. Anon, 1993; Coombs *et al.*, 1981 and 1990). A similar but more extreme restriction of eggs to the most superficial 10 or 20m of the water column has been observed for mackerel eggs in other regions where stratification is correspondingly well developed (e.g. North Sea - Iversen, 1977, Coombs *et al.*, 1981; English Channel - Southward and Barrett, 1983; east coast of North America - Sette, 1943; Lafontaine and Gascon, 1989). More limited information on depth distribution in the absence of any appreciable thermal stratification has indicated that under such conditions eggs are found at greater depths (to depths >150-200m, Walsh, 1976; Coombs *et al.*, 1981; Röpke, 1989). Larva have been reported consistently as being in the upper mixed layer (e.g. Coombs *et al.*, 1981, 1983, 1990; Lafontaine and Gascon, 1989; Röpke, 1989; Sette, 1943; Southward and Barrett, 1983; Ware and Lambert, 1985).

However, few of the above sets of results have included sufficient coverage to allow either a comprehensive description or statistical analysis of the depth distribution of eggs or larvae over the entire spawning season west of the British Isles. The purpose of the present paper is to summarise a number of studies to provide a more general description of their vertical distribution. These results incorporate some previously described data and include additional findings from more recent sampling.

Methods

Sampling was carried out at the shelf-edge and adjacent areas west of the British Isles and in Biscay between March and June on various cruises between 1974 and 1991 (Fig. 1; Table 1). A more detailed set of samples was obtained over a 33 hour period in June 1995 at a site in the Porcupine Seabight to the southwest of Ireland (Fig.1; Table 1).

All sampling was carried out using versions of the Longhurst-Hardy Plankton Recorder; Williams *et al.*, 1983; see also Pipe *et al.*, 1981) which takes a sequential series of samples along an oblique tow at a ship's speed of 3-4 knots. Filtering nets of 280μm mesh aperture were used in hauls prior to 1986 and 200μm for those subsequently. Data on the depth range over which each sample was taken and volume of water filtered, monitored by a flowmeter in the inlet cone, were recorded either by a self-contained electronics unit on the sampler frame or transmitted via a cored-cable for display and storage to a PC on the survey vessel. Additional sensors incorporated into the system included temperature (all years), salinity (1995 only) and chlorophyll *a* fluorescence (1995 only).

On completion of a haul, the sample was preserved in 4% formaldehyde solution for subsequent sorting and identification. Eggs of mackerel were staged according to the descriptions of Lockwood *et al.* (1981) and larvae measured to the nearest 0.1mm (total length). Standardised plots of vertical distribution were produced taking into account the depth range over which each sample was taken and volume of water filtered. Plots of mean distribution were then prepared using the standardised data for each haul converted to percentage occurrence down the water column (i.e. giving equal weighting to each haul). For calculation of mean depth profiles the 1995 data (which were essentially a set of replicate hauls) were treated as a single haul (including temperature data), represented by the mean distribution of each egg stage and larval group. For all hauls, only those on which 20 or more eggs or 10 or more larvae occurred for a particular egg stage or size of larvae are included.

Table 1. LHPR haul information

Haul No.	Date	Time (GMT)	Max. depth (m)	Position Lat. (N)	Position Long. (W)	S. scombrus Egg Nos.	S. scombrus Larval Nos.
74/01	10/04/74	13.06	451	55 16	12 27	16	0
74/02	13/04/74	13.00	342	51 21	13 51	19	0
75/01	06/04/75	12.50	315	51 18	14 00	32	0
75/02	16/04/75	03.08	547	55 06	10 18	25	0
75/03	17/04/75	18.12	422	54 12	13 46	154	0
75/04	21/04/75	06.00	505	58 00	10 18	98	0
77/1/01a	19/03/77	09.05	638	45 15	03 08	19	0
77/1/01b	19/03/77	10.05	638	45 15	03 08	154	0
77/1/02	21/03/77	09.24	292	46 08	04 08	164	0
77/1/03	27/03/77	17.13	434	50 40	11 15	40	0
77/2/01	08/04/77	15.50	129	48 45	06 19	17	0
77/2/02	08/04/77	16.50	129	48 45	06 19	10	0
77/2/03a	12/04/77	13.17	200	51 17	11 20	323	382
77/2/03b	12/04/77	14.17	200	51 17	11 20	49	0
77/2/04	14/04/77	03.29	384	52 45	12 18	19	0
77/2/05	14/04/77	16.01	170	53 20	13 37	136	0
77/2/06	15/04/77	19.14	680	54 45	10 35	25	0
77/2/07	17/04/77	20.55	331	55 50	09 30	135	0
77/2/08	17/04/77	21.55	400	55 50	09 30	28	0
77/2/09	22/04/77	19.40	468	58 16	09 33	121	0
77/3/01	14/05/77	01.34	119	52 15	10 54	30	0
77/3/02	16/05/77	19.40	849	50 16	11 17	238	48
77/4/01	04/06/77	07.47	818	48 15	10 39	24	0
77/4/02	04/06/77	00.05	159	48 15	10 39	38	0
77/4/03	07/06/77	20.56	578	49 16	11 51	28	0
77/4/04	09/06/77	15.24	81	51 16	07 19	20	0
77/4/05	10/06/77	08.37	185	51 16	11 23	0	12
77/4/06	11/06/77	06.23	110	52 17	11 15	24	22
78/01	11/04/78	06.00	427	56 18	09 18	111	0
78/02	11/04/78	20.07	369	55 28	09 55	102	0
78/03	13/04/78	11.40	528	56 55	09 09	417	0
78/04	20/04/78	15.17	343	57 40	09 40	355	0
78/05	20/04/78	16.17	343	57 40	09 40	63	0
78/06	21/04/78	00.47	409	58 05	09 40	652	0
78/07	21/04/78	01.17	409	58 05	09 40	86	0
78/08	23/04/78	00.30	382	58 57	07 40	50	0
78/09	23/04/78	19.49	431	59 04	07 35	39	0
80/1/01	08/04/80	13.26	142	49 43	10 31	2084	0
80/1/02	09/04/80	20.22	190	48 26	09 55	1623	1542
80/2/01	01/05/80	15.58	117	51 06	09 58	63	0
80/3/01	02/05/80	22.04	405	49 45	11 16	0	111
80/3/02	04/05/80	01.42	155	48 51	10 07	770	260
80/3/03	07/05/80	22.28	206	47 37	07 19	1890	16
80/3/04	09/05/80	10.38	274	45 14	03 06	296	0
80/3/05	10/05/80	18.39	170	44 44	02 03	190	0
80/3/06	14/05/80	10.29	155	49 11	09 30	2857	162
80/3/07	16/05/80	22.14	128	50 30	10 31	2234	27
80/3/08	17/05/80	03.21	141	50 31	10 32	1719	91
80/3/09	17/05/80	08.35	123	50 31	10 32	2519	49
80/4/01	02/06/80	08.27	191	50 19	10 45	1228	62
80/4/02	03/06/80	16.52	207	48 16	08 19	326	0
80/4/03	04/06/80	13.37	274	46 59	05 18	68	0
80/4/04	08/06/80	19.57	210	45 45	03 37	68	35
80/4/05	09/06/80	18.07	259	47 25	06 21	22	0
80/4/06	11/06/80	15.56	167	49 16	11 08	1242	237
81/01	17/05/81	09.45	205	48 55	10 56	37737	87
81/02	20/05/81	08.56	193	49 35	11 02	4769	19
81/03	21/05/81	00.01	135	49 14	10 01	321	91
81/04	21/05/81	08.05	130	49 14	07 58	22	73
81/05	21/05/81	09.05	138	49 14	07 58	17	26
83/01	09/06/83	08.46	110	49 15	11 00	1953	849
83/02	09/06/83	15.38	124	49 15	10 00	5688	47
83/03	09/06/83	20.50	124	49 15	09 00	9806	94
83/04	10/06/83	03.15	120	49 15	08 00	3146	30
83/05a	14/06/83	15.30	1003	49 45	12 00	734	91
83/05b	14/06/83	15.39	1011	49 45	12 00	580	45
83/06	15/06/83	04.47	106	49 45	10 30	2054	1425

Haul No.	Date	Time (GMT)	Max. depth (m)	Position Lat. (N)	Position Long. (W)	S. scombrus Egg Nos.	S. scombrus Larval Nos.
83/07	16/06/83	19.02	122	49 25	10 17	1744	1309
83/08	17/06/83	16.03	112	49 06	10 29	8787	521
83/09	18/06/83	11.00	595	48 15	10 30	42	0
83/10	18/06/83	18.13	33	48 15	10 30	623	29
84/01	24/05/84	23.05	102	49 15	09 30	*	1957
84/02	25/05/84	03.17	106	49 15	09 30	*	1492
84/03	25/05/84	16.16	89	49 14	09 29	*	674
84/04	28/05/84	22.40	69	49 15	10 33	*	675
84/05	29/05/84	01.15	73	49 15	10 30	*	876
84/06	29/05/84	06.19	72	49 14	10 24	*	503
84/07	29/05/84	10.22	88	49 13	10 26	*	213
84/08	29/05/84	15.17	78	49 13	10 28	*	153
85/01	12/06/85	13.15	118	49 10	09 26	1138	82
85/02	12/06/85	19.00	100	49 30	10 00	2295	30
85/03	12/06/85	21.55	106	49 55	10 22	373	39
85/04	13/06/85	08.55	109	49 24	09 53	575	66
85/05	13/06/85	11.12	113	49 20	09 46	88	88
86/1/01	23/04/86	15.20	115	48 49	10 03	1355	82
86/2/01	23/04/86	16.00	100	48 49	10 20	1875	209
86/1/02	24/04/86	12.00	170	48 51	09 54	435	0
86/2/02	24/04/86	16.04	113	49 10	09 52	172	227
86/1/03	25/04/86	12.00	151	49 03	09 48	1191	696
86/2/03	25/04/86	10.38	212	48 37	10 19	0	115
86/1/04	26/04/86	15.05	135	48 57	09 53	1220	105
86/2/04	26/04/86	07.03	222	50 57	11 22	0	1027
86/3/01	13/05/86	03.52	143	49 15	10 18	2822	0
86/3/02	14/05/86	13.06	200	50 15	11 18	119	0
86/3/03	16/05/86	23.13	154	50 50	10 52	1684	56
86/3/04	19/05/86	12.14	164	48 45	09 43	493	186
86/3/05	20/05/86	13.53	190	48 16	09 05	1094	1156
86/3/06	27/05/86	00.39	138	48 08	09 14	247	501
86/4/01	20/06/86	10.25	147	49 13	10 02	1876	340
86/4/02	26/06/86	20.53	140	50 47	10 15	956	76
86/4/03	28/06/86	18.48	132	52 48	11 16	17	283
87/01	07/05/87	22.07	116	49 00	10 04	2549	780
87/02	09/05/87	03.04	95	49 01	10 03	1512	154
87/03	09/05/87	14.27	90	49 01	10 02	1329	155
87/04	10/05/87	07.54	33	49 01	10 03	779	127
87/05	12/05/87	02.14	73	48 43	10 06	3620	410
87/06	13/05/87	01.43	77	48 43	10 07	2567	664
91/01	16/06/91	08.45	142	48 35	09 25	*	348
91/02	16/06/91	16.05	140	48 31	09 25	*	77
91/03	16/06/91	22.53	152	48 32	09 25	*	132
91/04	17/06/91	03.39	154	48 32	09 25	*	127
91/05	18/06/91	13.05	150	48 48	09 14	*	44
91/06	19/06/91	01.14	153	48 47	09 14	*	44
91/07	19/06/91	11.04	148	48 43	09 01	*	19
91/08	19/06/91	17.56	151	48 42	09 01	*	15
91/09	20/06/91	00.39	145	48 43	09 02	*	37
91/10	20/16/91	03.19	145	48 43	09 01	*	38
91/11	21/06/91	14.11	142	48 24	09 17	*	17
91/12	22/06/91	01.03	138	48 24	09 17	*	112
95/01	26/06/95	23.22	200	51 14	12 42	20	82
95/02	27/06/95	01.36	70	51 14	12 42	33	166
95/03	27/06/95	03.25	70	51 15	12 42	50	133
95/04	27/06/95	06 00	70	51 15	12 42	61	269
95/05	27/06/95	08.08	70	51 15	12 42	65	227
95/06	27/06/95	10.00	70	51 15	12 42	67	160
95/07	27/06/95	12.14	70	51 15	12 42	83	370
95/08	27/06/95	14.02	100	51 15	12 42	59	533
95/09	27/06/95	16.04	100	51 15	12 42	69	104
95/10	27/06/95	18.08	100	51 15	12 42	29	104
95/11	27/06/95	20.06	100	51 14	12 42	63	67
95/12	27/06/95	22.02	100	51 15	12 42	63	109
95/13	28/06/95	03.53	100	51 15	12 42	71	45
95/14	28/06/95	06.00	100	51 15	12 42	52	41
95/15	28/06/95	08.03	100	51 15	12 42	36	43

* not sampled for eggs

Mean depths of the vertical distributions were calculated using the formula $\Sigma f_i d_i / f_i$ where f_i and d_i are the egg and larval frequencies (%) and the mid-depth of the i^{th} depth interval respectively.

Statistical comparisons between the vertical distributions were made using both analysis of variance and non-parametric Kruskal-Wallis tests. Since both tests gave similar significance levels, only the results from the analysis of variance are presented.

Differences in the distribution of larvae by day (0600-1630hrs GMT) and night (1800-0430hrs GMT) in the 1995 samples were compared using the index of aggregation, A, based upon 'mean density' (Lloyd, 1967; see also George, 1983):

$$A = [\bar{x} + ((s^2 / \bar{x}) - 1)] / \bar{x}$$

where $\bar{x}$ and s^2 are the mean larval frequency (%) and variance respectively. Values of A<1 indicate a regular distribution, equal to 1 a random distribution and >1 an aggregated distribution.

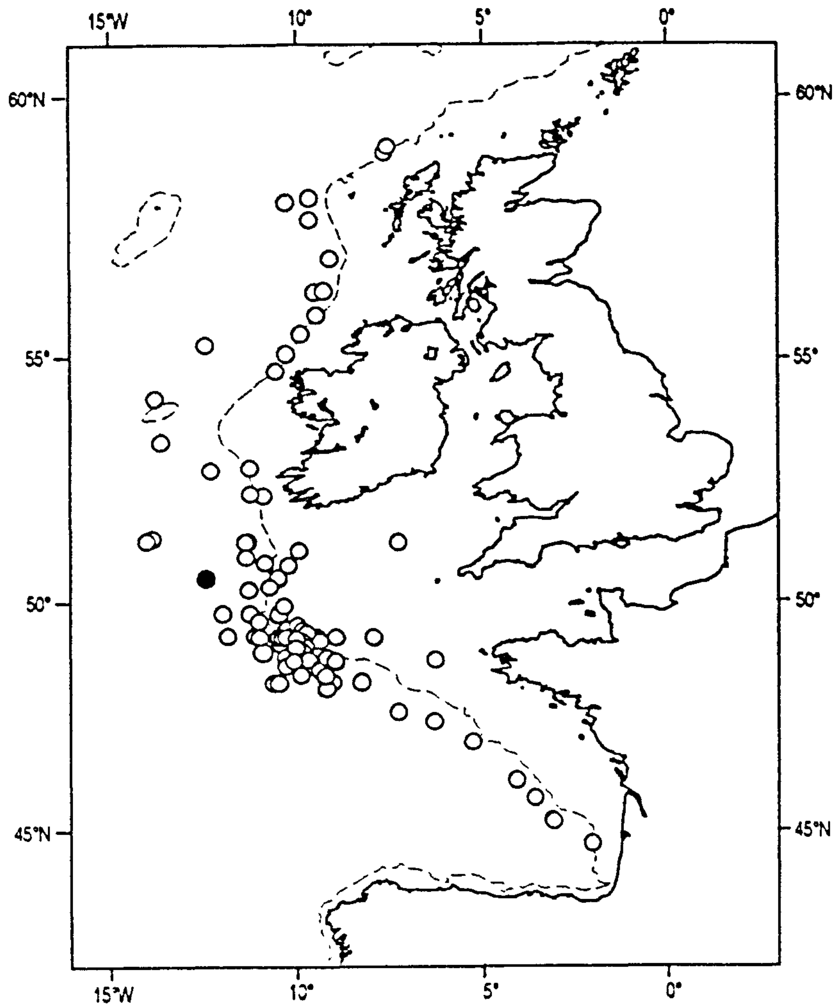

Fig. 1 Positions of LHPR hauls in the years 1974-1991 (circles) and the site of intensive sampling in 1995 (filled circle).

Results

There was a significant change ($F_{3,83}$=22.86, p=0.0001) in the mean depth of mackerel eggs over the spawning season. In March and April, eggs were distributed over a wide depth range, to at least 400m depth, while in May and June they were in shallower depths, mostly in the upper 50m of the water column (73% of eggs in the 0-50m range in May and 81.6% in June; Figs. 2 and 3). These changes in vertical distribution corresponded to the development of the seasonal thermocline, little vertical structure being evident in March and April and progressive development of stratification taking place in May and June (mean 0-50m Δt of 0.7C° and 2.8C° respectively, see Fig. 4).

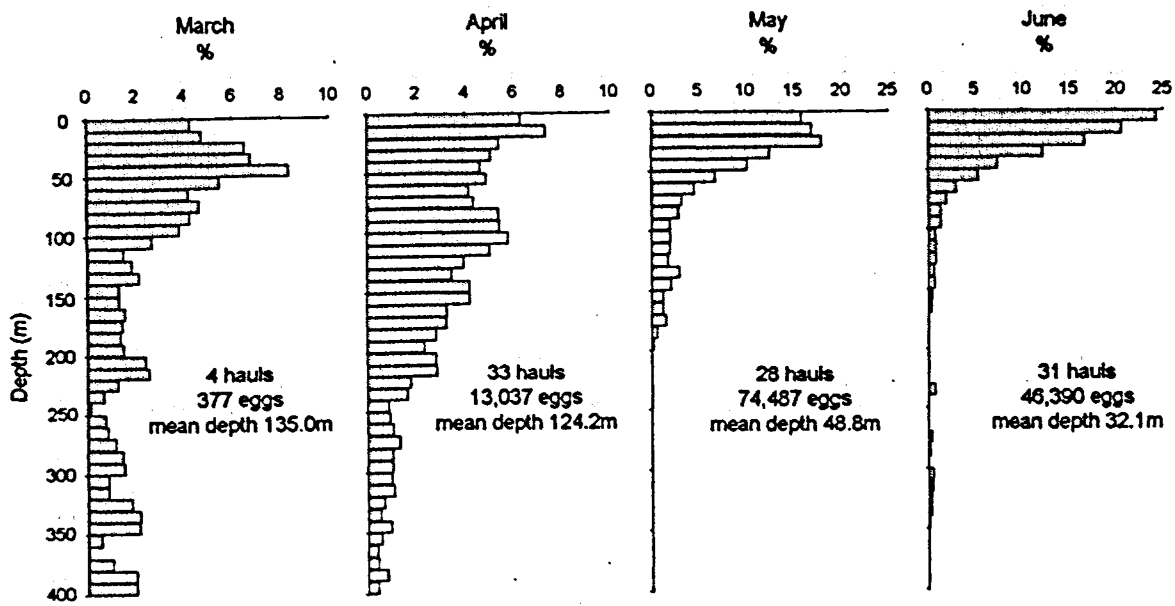

Fig. 2 Mean vertical distribution by month of mackerel eggs at all stages of development plotted by month as percentage occurrence in 5m depth intervals from sampling in the years 1974-1995. Sampling was to an individual haul maximum depth of 1011m but, for clarity of presentation, results are plotted to 400m (<2.4% of eggs in any month being taken sporadically below 400m depth).

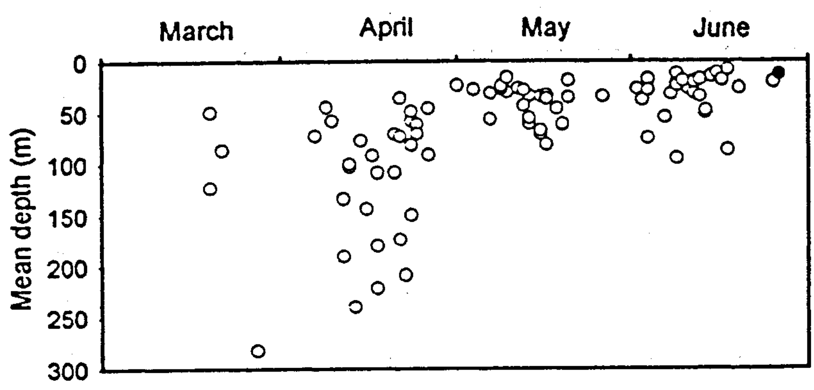

Fig. 3 Mean depth of mackerel eggs at all stages of development plotted by haul against date of sampling. The mean depth of the 1995 hauls is indicated by the filled circle.

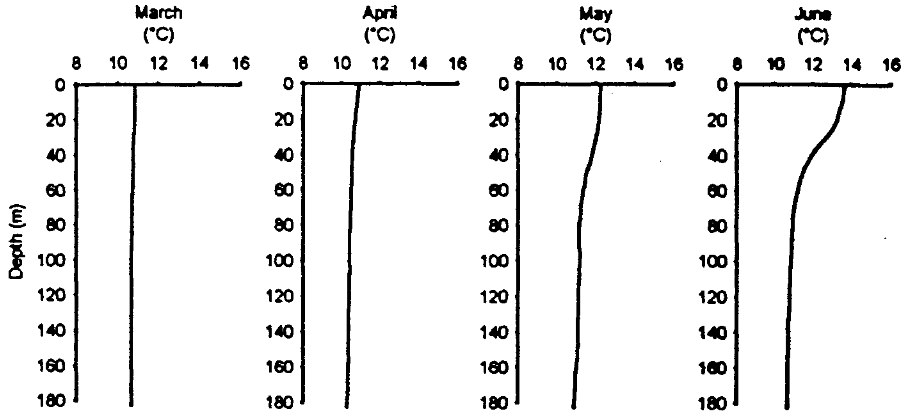

Fig. 4 Average temperature profiles by month for all LHPR hauls on which mackerel eggs were taken in the years 1974-1995.

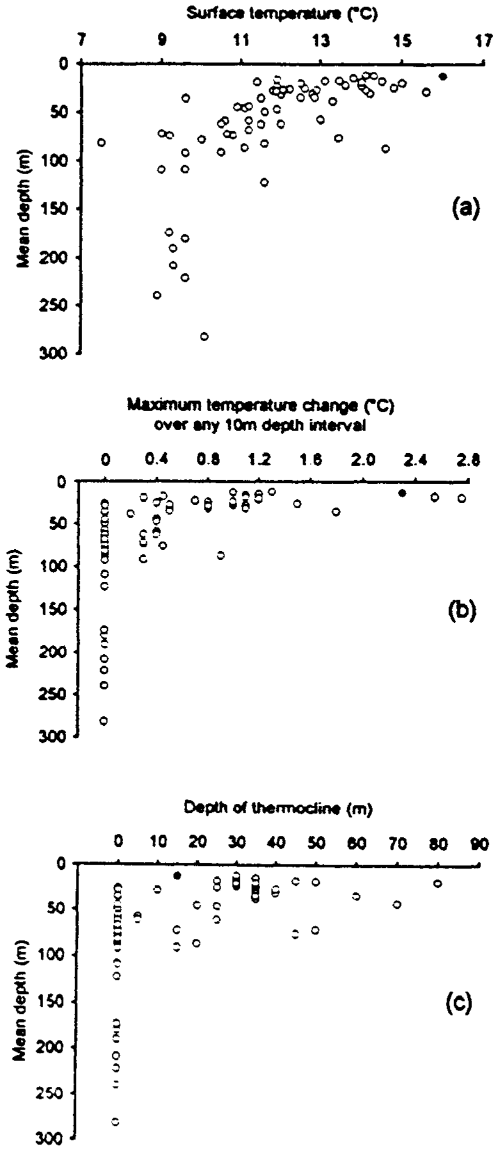

Fig. 5 Mean depth of mackerel eggs at all stages of development plotted against (a) surface temperature, (b) temperature change at the thermocline and (c) depth of the thermocline (defined as the mid-depth of maximum temperature change in a 10m depth interval). The mean depth of the 1995 hauls is indicated by the filled circle.

The relationships between mean depth of eggs and the stratification parameters represented by surface temperature, temperature change at the thermocline and depth of the thermocline are shown in Fig. 5. These indicate a progressively shallower occurrence of eggs with an increase of surface temperature (Fig. 5a) compared to a more stepwise reduction in depth of eggs for even small changes of temperature across the thermocline (<1C°, Fig. 5b), irrespective of the depth of the thermocline (Fig. 5c).

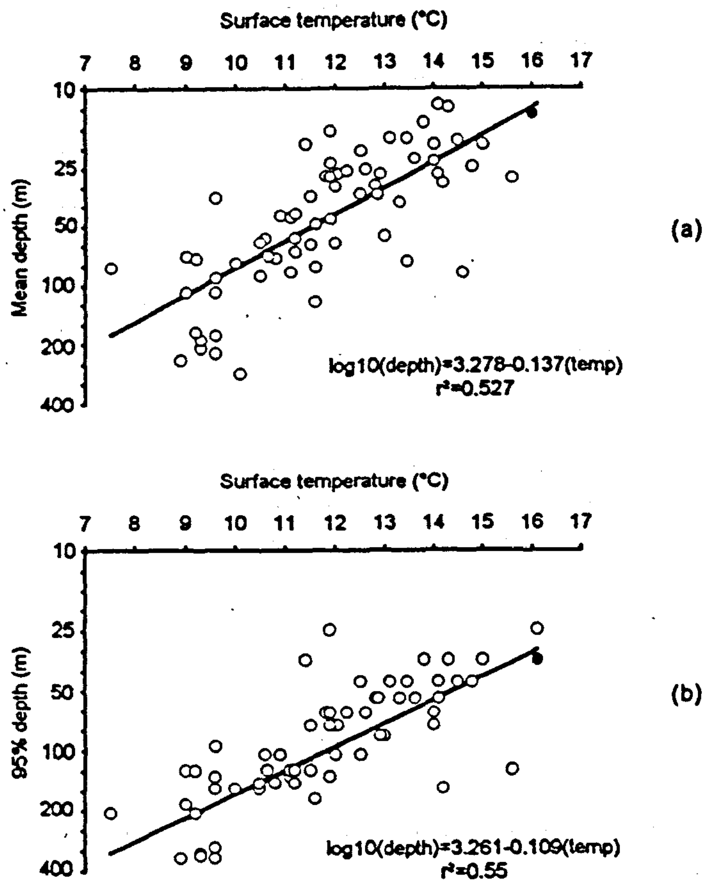

Fig. 6 Regressions of log10 transformed depth values against surface temperature for (a) mean depth of eggs at all stages of development and (b) for 95% of eggs at stage 1 of development.

A linear relationship between mean depth of mackerel eggs and surface temperature was obtained by the logarithmic transformation of mean depths (Fig 6a). The association with surface temperature was significant ($F_{1,64}$=80.2, p=0.0001) explaining 56% of the variation in mean depth. Addition of wind speed (squared) was not significant ($F_{1,48}$=0, p=0.98).

There was no clear pattern in changes of vertical distribution between consecutive egg stages during March and April. However, during May and June when the majority of eggs were in the upper 50m of the water column, paired comparisons showed stage 1 eggs were significantly deeper in the water column than those at stage 2 of development ($F_{1,97}$=4.17, p=0.044). Although changes in mean depth between stages 2 and 5 were not significant, an overall pattern in change of depth distribution was evident, this showing a movement towards the surface from stage 1 to stage 2 and then a subsequent deepening of the distribution to give a sub-surface peak of abundance at 10-15m depth by stage 5 (Fig. 7).

For practical purposes, the above results indicate that in order to sample 95% of eggs at stage 1 of development (as used in surveys for stock estimation e.g. Lockwood *et al.*, 1981; Anon, 1994), the variation in required depth of sampling would be from a depth of 243m at a surface temperature of 8°C reducing to 33m at a surface temperature of 16°C (Fig. 6b).

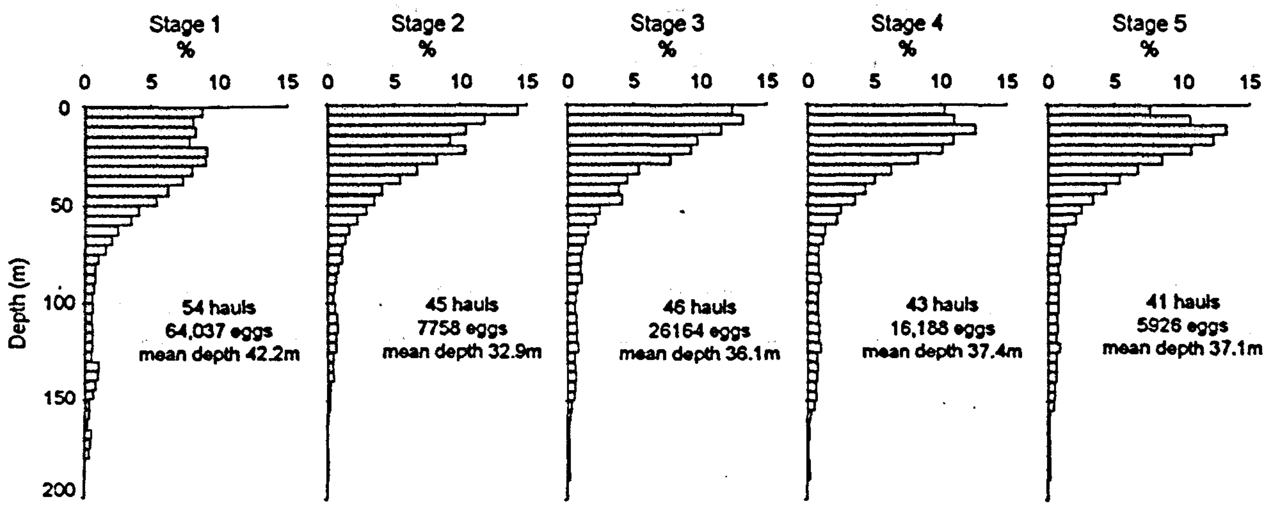

Fig. 7 Mean vertical distribution by stage of development for mackerel eggs plotted as percentage occurrence in 5m depth intervals from sampling in May and June in the years 1974-1995. Sampling was to an individual haul maximum depth of 1011m but, for clarity of presentation, results are plotted to 200m (<1.4% of eggs of any development stage being taken below 200m depth).

Most mackerel larvae were taken in May and June (47.1% and 37.0% of the total), few in April (15.9%) and none in March. There were no consistent patterns in vertical distribution between months or sizes of larvae (Table 2), all results have therefore been combined. The resulting overall distribution of larvae was similar to that for the eggs in June and July, with 84% of larvae in the upper 50m of the water column above the seasonal thermocline (Fig. 8 cf. Fig. 7; Fig. 4). In this combined set of results (1974-1995) there was little evidence of a significantly higher concentration of larvae at any specific depth in the upper 50m of the water column.

Table 2. Mean depth (m) of mackerel larvae.

Month	Larval size (mm)				
	2-3.9	4-5.9	6-7.9	8-11.9	2-11.9
April	46.33	26.45	23.52	-	38.12
May	38.00	29.05	30.01	28.88	33.83
June	37.95	31.87	31.36	42.88	32.70
All months	38.54	29.79	29.64	35.50	33.64

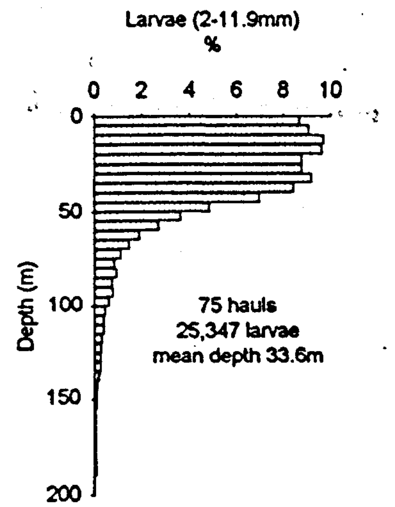

Fig. 8 Mean vertical distribution of mackerel larvae plotted as percentage occurrence in 5m depth intervals from sampling in April, May and June in the years 1974-1995. Sampling was to an individual haul maximum depth of 1011m but, for clarity of presentation, results are plotted to 200m (no larvae being taken below 200m depth).

No consistent diel changes in vertical distribution of larvae were evident in the combined data for 1974-1995, either by size or month. Examination of the results from the more coherent day/night sequence of sampling in 1995 showed little variation in mean depth of larvae (2-11.9mm in length) between day and night ($F_{1,13}$=4.01, p=0.07; Figs 9 and 10). However, larvae were more dispersed at night (A=1.61) than during the day (A=2.34) when they were aggregated about a 15-20m depth of maximum abundance with none occurring in the 0-5m depth interval (Fig. 9).

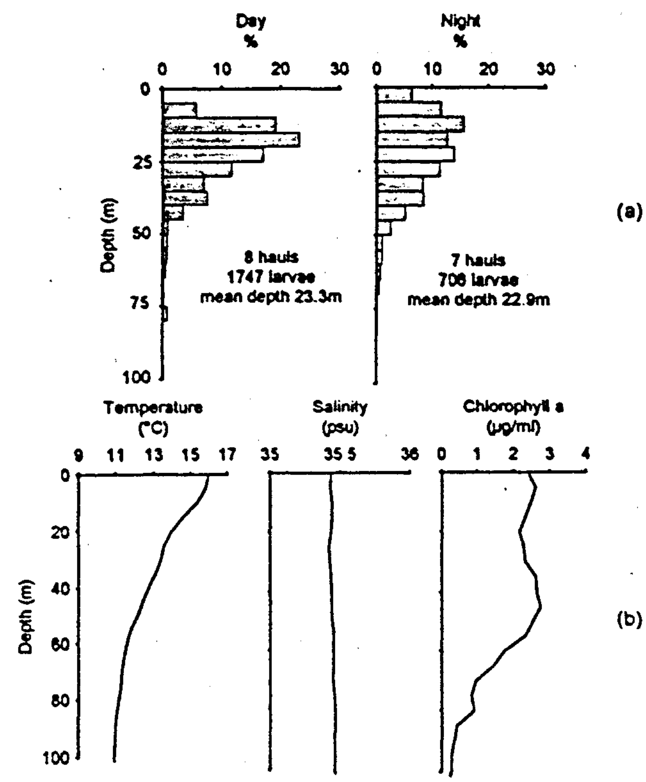

Fig. 9 Mean vertical distribution of mackerel larvae plotted as percentage occurrence in 5m depth intervals from sampling in June 1995. Day hauls were those taken between 0600hrs and 1630hrs and night hauls those between 1800hrs and 0430hrs (GMT). The mean temperature, salinity and chlorophyll *a* profiles for the hauls are plotted below.

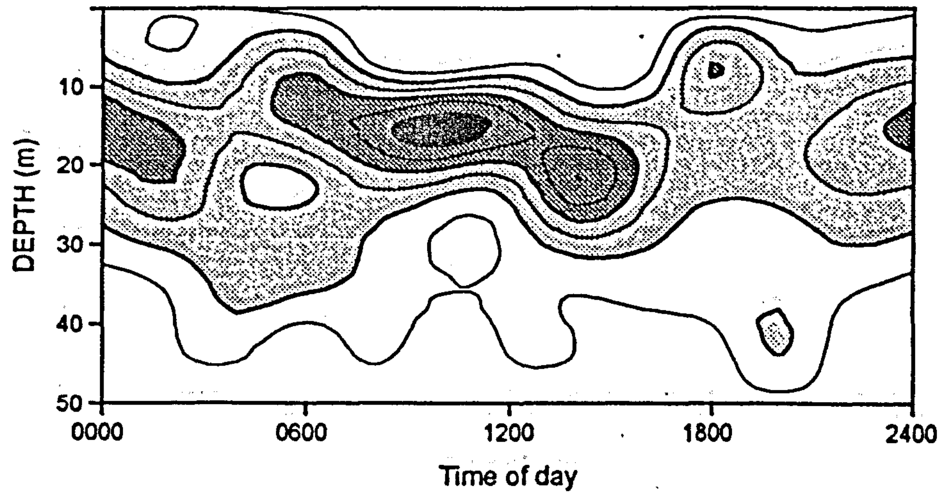

Fig. 10 Contoured distribution of mackerel larvae at 2-11.9mm in length in the upper 50m of the water column from sampling on 15 LHPR hauls in 1995. The figure was constructed using the percentage occurrence of larvae in 5m depth strata on each haul plotted at the time of day each haul was taken. Contours are drawn at intervals of 5% occurrence and filled at progressively darker shades from the 10% contour.

Discussion

The observed relatively near-surface distribution of mackerel eggs and larvae, at least in May and June, is typical of ichthyoplankton in general (e.g. Conway *et al.*, in press; Boehlert *et al.*, 1985). The deep distribution of eggs observed in March and April (>200m depth) is less common and usually confined to habitually deep-water species, or those found at depth during the spawning season (e.g. halibut, *Hipploglossus hippoglossus*, Haug *et al.*; 1986; blue whiting, *Micromesistius poutassou*, Coombs *et al.*, 1981).

Eggs of mackerel have near neutral buoyancy for most of their development (Coombs, *et al.*, 1990). Consequently, their distribution will mostly result from some combination of the depth of spawning and mixing effects (Sundby, 1983) over the embryonic development time of about 4 to 10 days (Lockwood *et al.*, 1981). Since wind mixing is greater in March and April than later in the spawning season, it is expected that eggs would be dispersed deeper in the water column in these months. However, eggs in the initial stages of development are represented as equally as those at later stages at depths >200m in March and April, therefore it is possible that a proportion of spawning does take place in the deeper layers of the water column. In May and June, when the thermocline has developed, the egg distributions indicate that spawning is entirely in the upper mixed layer, mostly at depths above about 50m. Depth-stratified trawling for adult mackerel found a similar restriction of spawning females to the near-surface layers (Anon, 1993, 1994).

The above results are consistent with other reports showing the restriction of eggs of *S. scombrus* to the mixed water above a pycnocline (e.g. Southward and Bary, 1980; Southward and Barrett, 1983; Anon, 1993). The most extreme concentration of eggs in the upper 10m or 20m of the water column is found above strong thermal and salinity stratification in the North Sea and off the east coast of North America (Sette, 1943; Iversen, 1977; Lafontaine and Gascon, 1989). Similar relationships between the distribution of eggs and thermal structure are reported for *S. japonicus* off California (Ahlstrom, 1959) and in Japanese waters (Motoda, 1955; Kishida, 1988). In all areas there is only a relatively small amount of mackerel spawning before seasonal stratification and correspondingly few reports of their vertical distribution under such conditions; both Walsh (1976) and Röpke (1989) indicate that, as in the present work, before any significant thermocline is established a considerable proportion of eggs may occur below depths of at least 100-170m.

Reports from other sampling (Röpke, 1989) in the same spawning area west of the British Isles have shown similar changes in depth distribution of mackerel eggs by stage of development as found in the present study; that is, a deeper and more dispersed distribution during early development, nearer to the surface during the middle stages and an increase in mean depth towards the end of development. Equivalent patterns have also been observed for the shallow distributions of mackerel egg stages above well-developed thermoclines in the western North Atlantic (Sette, 1943; Iversen, 1977; Lafontaine and Gascon, 1989) and for eggs of other species elsewhere (e.g. walleye pollock, *Theragra chalcogramma*, Kendall *et al.*, 1994). The increase in density of fish eggs and consequent deeper distribution down the water column towards the end of development is a common feature for pelagic eggs of many species (e.g. Alderdice and Forrester, 1968; Coombs *et al.*, 1985), including *S. japonicus* in Japanese waters (Motoda, 1955; Kishida, 1988). However, measurements of the specific gravity of mackerel eggs have shown generally lower values towards the end of development (Coombs, 1990) which would tend to lead to a shallower depth distribution prior to hatching.

Previous reports from sampling to the west of the British Isles have described a qualitative relationship between the vertical distribution of mackerel eggs and development of the seasonal thermocline (Coombs *et al.*, 1981). Off the eastern coast of North America, Ware and Lambert (1985) demonstrated a relationship between the exponential decline in egg numbers at the surface and the temperature gradient in the top 5m of the water column. In the present paper the clearest relationship is between the mean depth of eggs and surface temperature, rather than with the degree of stratification at the thermocline, since even a small amount of stratification has a marked restriction on the depth of the eggs (Fig. 5). This relationship is derived from data in the sampled area (Biscay and west of the British Isles) and might be less valid for extrapolation to other areas with different cycles of temperature change.

Estimation of the stock size of the mackerel to the west of the British Isles relies, in part, on the results of the plankton surveys for eggs at stage 1 of development (Lockwood *et al.*, 1981). The current recommended procedure (Anon, 1994) is to sample to 200m depth or 20m below a thermocline of 2.5C^{O} or more. Based on the analysis of the relationship between depth of eggs and temperature parameters in the present paper, the above recommendations are unlikely to lead to any significant under-sampling of eggs. The small proportion below 200m at the lowest surface temperatures of <9^{O}C (Fig. 6b) are found early in the season when spawning intensity is low; sampling to much greater depths when egg concentrations are low is unlikely to be justified when balanced against the opportunity to sample more stations over a wider area. Consideration of the relationship between mean depth of eggs and degree of stratification at the thermocline (Fig. 5b) suggests the criterion of a minimum temperature change of 2.5C^{O} before reducing the depth of sampling is, perhaps, too stringent. Taking into account surface temperature (Fig. 6b) rather than temperature change at the thermocline is a better guide for setting the sampling depth.

Fish larvae are generally more restricted in vertical range than are eggs, often with sub-surface peaks of abundance (e.g. Boehlert *et al.*, 1985; Conway *et al.*, in press). Most reports on the vertical distribution of mackerel larvae from both sides of the North Atlantic show their occurrence in the upper water column (Sette, 1943; Ware and Lambert, 1985; Lafontaine and Gascon, 1989; Röpke, 1989; Fig. 8). The ontogenetic movement of larger larvae towards the surface (Ware and Lambert, 1985; Lafontaine and Gascon, 1989) was not seen in the present set of data, although the combination of results from a widespread series of hauls and the relatively few larger larvae taken, would not highlight any such pattern. Similarly, the sub-surface peak in abundance of larvae, as noted by Lafontaine and Gascon (1989), was only clearly evident in the 1995 results, these being derived from a single set of hauls all taken under the same environmental conditions.

Many fish larvae, including those of mackerel, exhibit diel vertical migration, reflecting behavioural responses to preferenda of physical or biological stimuli such as light, temperature or food availability (Sette, 1943; Kendall and Naplin, 1981; Ware and Lambert, 1985; Röpke, 1989). Such migratory behaviour tends to develop only with the increased locomotory capability of mackerel larvae >6mm in length (Ware and Lambert, 1985). Additionally, the direction of migration of mackerel larvae was not the same in all studies. Röpke (1989) showed a movement of larvae towards the surface at night, in agreement with some limited observations by Sette (1943). Conversely, Ware and Lambert (1985) described a movement away from the surface at night and Lafontaine and Gascon found no day/night difference in the distribution of larvae. Therefore, it is not unexpected that the relatively small larvae (91.4% of all larvae <5.9mm in length) taken under a wide variety of conditions in the present study, showed little evidence of diel vertical migration. Results from the 1995 set of hauls showed a dispersion of mackerel larvae at night (Fig. 9) suggesting a locomotory capability which might be expressed in directed migration under certain conditions.

Overall, the results from the present study, with respect to considerations of larval drift, show that larvae of mackerel in the main area of spawning in Biscay and the Celtic Sea are mostly in the wind-driven surface Eckman layer to a depth of about 50m.

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