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Vertical distribution of fish eggs and larvae in the Irish Sea and southern North Sea

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Fish eggs and larvae were analysed from 63 vertically stratified plankton hauls in the Irish Sea and southern North Sea. The dominant species were sprat (*Sprattus sprattus*), dragonet (*Callionymus* spp.), dab (*Limanda limanda*) and to a lesser extent rockling species, sandeel (*Ammodytes* spp.), whiting (*Merlangius merlangus*) and flounder (*Platichthys flesus*). There was little difference between species in the vertical distribution of either eggs or larvae. Most were concentrated in the upper 50 m of the water column, eggs in progressively increasing numbers towards the surface and larvae with a sub-surface peak at a depth of 10–15 m. The vertical distribution of eggs extended deeper in the water column than larvae, possibly due to some combination of eggs being spawned deeper and their passive susceptibility to turbulent mixing. There were no significant differences between day and night distributions and under mixed or isothermal conditions.

Key words: fish larvae, fish eggs, vertical distribution, Irish Sea, North Sea.

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Introduction

In temperate neritic waters, the majority of pelagic marine fish eggs are spawned at shallow depths (<50 m) and are neutrally or slightly positively buoyant (Sundby, 1991). These attributes favour hatching in the more productive surface waters. However, in European shelf waters many fish species spawn early in the year (Harding and Nichols, 1987; Nichols *et al.*, 1993), either before the establishment of a seasonal thermocline, or in areas that remain well-mixed throughout the year. This absence of water column stability may result in eggs and larvae being mixed deeper in the water column and in larvae being retained at a depth where food supply is inadequate or less suitable.

Information on the vertical distribution of fish eggs and larvae is sparse, partly due to sampling difficulties associated with their presence in generally low numbers and the specialised sampling equipment required to obtain vertical resolution (e.g. Longhurst Hardy Plankton Recorder – LHPR, Pipe *et al.*, 1981; Williams *et al.*, 1983; Multiple Opening/Closing Net and Environment Sensing System – MOCNESS, Wiebe *et al.*, 1976; pumps, Fortier and Harris, 1989). In the North Sea a few studies have provided information on the vertical distribution of eggs and larvae of individual fish species (e.g. Coombs *et al.*, 1981; Heath *et al.*, 1991; Kloppmann, 1991) or for a limited range of species (Harding and Nichols, 1987). In the Irish Sea, less sampling has been carried out for the vertical distribution of ichthyoplankton, with the descriptions being restricted to one species (Coombs *et al.*, 1992).

Between 1987 and 1990 sampling was carried out in the central Irish Sea and southern North Sea as part of a programme examining zooplankton production processes during the spring and early summer (Coombs *et al.*, 1994; Lindley *et al.*, 1994). At the same time the opportunity was taken to describe the vertical distribution of fish eggs and larvae under different environmental conditions. Results from the analysis of this material is presented here.

Methods

Zooplankton sampling

Fish eggs and larvae were sampled in the Irish Sea (Fig. 1a) and southern North Sea (Fig. 1b) using a modified

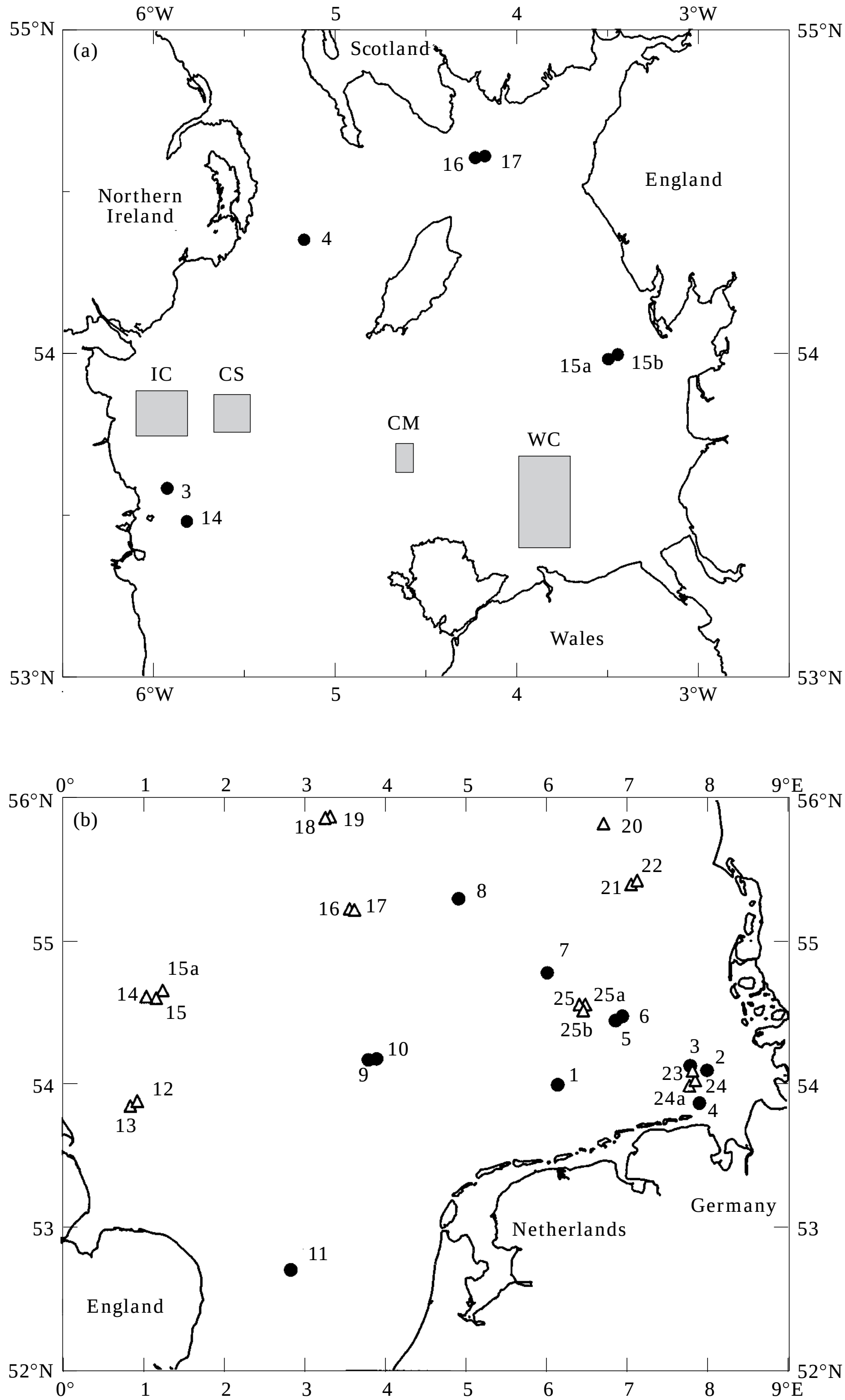

Figure 1. (a) Positions of LHPR stations in the Irish Sea; the four main sampling sites are identified as IC (Irish Coastal), CS (Central Stratifying), CM (Central Mixed) and WC (Welsh Coastal). Other haul positions are marked individually. (b) Positions of LHPR stations in the North Sea for June 1989 (●) and April 1990 (△).

LHPR sampler (Longhurst *et al.*, 1966; Williams *et al.*, 1983). This system collects plankton between two rolls of filtering gauze which are advanced at intervals inside a codend box to give a series of consecutive samples. The LHPR was towed at 3–4 knots on oblique hauls, sampling from the surface to near bottom while taking samples at intervals of 1 min, equivalent to approximately 5 m depth intervals. Mesh aperture of the collecting net and filtering gauze for all the hauls was 200 μm. Water temperature was recorded throughout the hauls and flow rate was monitored by a flowmeter mounted in the intake aperture, approximately 10 m^{-3} of water being filtered for each sample. On recovery of the sampler, the individual plankton samples were preserved in 4% borax buffered formaldehyde prepared using fresh water and subsequently sorted and analysed for fish eggs and larvae, with nomenclature following that of Russell (1976). Conductivity, temperature, depth (CTD) profiles were taken either by a Neil Brown or Guildline CTD before and after each LHPR haul.

In the Irish Sea four main sites were studied between March and June for the years 1987 to 1989 (Fig. 1a). These were: (a) a seasonally thermally stratified site of ~40 m depth close to the Irish coast, (b) a more central Irish Sea site of ~130 m depth which becomes strongly seasonally stratified, (c) a central Irish Sea, continuously mixed, isothermal site of ~70 m depth and (d) a site off the coast of north Wales of ~50 m depth, which is subject to considerable mixing. Two LHPR hauls were usually taken each time a site was visited, one at approximately midday and the other at near midnight (Table 1a). LHPR sampling was also carried out at a few additional positions in the Irish Sea as indicated in Fig. 1a.

In the southern North Sea, LHPR hauls were taken in June 1989 and April 1990 (Fig. 1b) at various times of the day and night, with some day/night pairs at the same position (Table 1b). Station positions were distributed over a wide area of the southern North Sea but with a higher concentration in the region of the German Bight; all are referred to collectively as North Sea samples. Sampling depths in the North Sea (11–67 m) were shallower than in the Irish Sea (16–125 m), reflecting differences in maximum water depth between the two areas. Further details of the environmental conditions in the two areas for the period when sampling took place are given in Coombs *et al.* (1992), Lindley *et al.* (1994) and Nichols *et al.* (1993).

Data processing

Results were used from 34 LHPR hauls (617 samples, Table 1a) in the Irish Sea and from 29 hauls in the North Sea (321 samples, Table 1b). For each individual species or group of species the vertical distribution data were processed only for those hauls on which there were a minimum of 20 eggs or 10 larvae, numbers below these levels representing sporadic occurrence only. Numbers of eggs and larvae in each haul were first standardised to give numbers m^{-3} in 5 m depth bands, using the measured volume filtered and depth range over which each sample was taken. These values were then converted to percentage depth distributions, both for comparability of presentation and to facilitate statistical analysis. Groups of hauls were combined to give overall mean depths by averaging the percentages (i.e. equal weighting being given to each haul). For comparison of depth distributions under different environmental conditions, weighted mean depth values (Roe *et al.*, 1984; Barenge, 1990) were calculated for each species or group on each haul and compared by single factor analysis of variance (ANOVA) using logarithmically transformed data where appropriate.

Results

Environmental conditions in the Irish Sea and North Sea

In the Irish Sea there is a restricted area of deep water (>100 m depth) in the west, with most other areas being <50 m in depth. There is strong tidal mixing in the shallower areas of the eastern Irish Sea (Dickson, 1987; Burkart *et al.*, 1995) and relatively low fresh water input, which is confined mainly to coastal areas in the east. These conditions were reflected in the observed hydrography. There was little thermal structure in the water column at all sampled sites in April (Fig. 2a, Table 1a). Seasonal stratification was not evident until about mid-May and had only developed to any extent by the end of May at the deep water central stratified site (0–50 m Δt of 2.5°C; Fig. 2b, Table 1a). Surface salinity at the sampled stations varied between 33.02–34.31 ppt with little observed salinity stratification (0–50 m Δs of <0.59 ppt at all stations) in any month of sampling.

The southern North Sea is largely <50 m in depth with increasing tidal mixing towards the shallower coastal areas. Relatively high levels of freshwater input can enhance stratification in coastal areas, especially in the German Bight and along the Dutch coast (Visser *et al.*, 1991). At all the sampling stations in April the water column was well mixed with negligible thermal stratification (Fig. 2c, Table 1b). During June the more coastal stations (e.g. NS1, NS3) generally showed development of a weak thermocline (0–50 m Δt of 1.2–3.9°C), while at the more offshore stations (e.g. NS6, NS8) there was a more marked development of thermal structure (0–50 m Δt of 7.2–9.6°C). On the most southerly haul (NS11), taken in the shallower water of the Southern Bight, the water column was fully mixed. Surface salinity at the North Sea sampling stations in April 1990 varied between 33.44–35.10 ppt with little salinity stratification (0–50 m Δs of <0.51 ppt at all stations). In June 1989

Table 1. LHPR haul information. The four sampling sites are IC (Irish Coast), CS (Central Stratifying), CM (Central Mixed) and WC (Welsh Coastal). Their positions are shown in Fig. 1a.
(a) LHPR haul information for the Irish Sea

Haul number	Date	Time GMT	Station position	Sampling site	Bottom depth (m)	Sampled depth (m)	Number of samples	0–50 m Δ t°C
RRS "Challenger" 29 March–19 April 1987								
IS3	2-4-87	12:28	53°35′N 05°56′W	—	52	50	22	0.1*
IS4	5-4-87	17:18	54°21′N 05°10′W	—	132	125	36	0.0
IS5	6-4-87	13:35	53°52′N 05°40′W	CS	101	100	31	0.1
IS6	9-4-87	12:38	53°53′N 05°58′W	IC	41	35	13	0.1
IS7	9-4-87	23:05	53°53′N 05°57′W	IC	41	39	13	0.1
IS8	11-4-87	12:10	53°50′N 05°28′W	CS	130	115	33	0.3*
IS9	11-4-87	23:46	53°50′N 05°28′W	CS	130	120	32	0.3*
IS11	15-4-87	12:34	53°40′N 03°59′W	WC	46	42	12	0.2
RV "Cirolana" 26 May–7 June 1987								
IS13	29-5-87	19:48	53°36′N 03°53′W	WC	42	38	12	0.6
IS14	30-5-87	15:11	53°29′N 05°49′W	—	74	73	23	1.5
IS15a	1-6-87	18:42	53°59′N 03°30′W	—	23	19	10	0.1
IS15b	1-6-87	19:00	53°59′N 03°30′W	—	23	16	10	0.2
IS16	4-6-87	13:21	54°36′N 04°14′W	—	60	47	26	0.9
IS17	4-6-87	23:42	54°36′N 04°15′W	—	56	50	20	0.9
RV "Cirolana" 9–21 April 1988								
IS18	11-4-88	23:29	53°47′N 05°49′W	IC	63	62	14	0.5
IS19	12-4-88	11:56	53°45′N 05°50′W	IC	56	50	12	0.5
IS20	14-4-88	12:09	53°51′N 05°32′W	CS	102	100	27	0.7
IS22	15-4-88	23:23	53°51′N 05°32′W	CS	108	106	24	0.3
IS23	17-4-88	12:23	53°41′N 03°59′W	WC	48	45	14	0.0
IS24	17-4-88	22:59	53°40′N 04°00′W	WC	48	40	13	0.0
RRS "Challenger" 21 May–4 June 1988								
IS25	25-5-88	00:13	53°49′N 05°33′W	CS	93	85	24	2.5
IS26	25-5-88	12:47	53°49′N 05°31′W	CS	105	100	20	2.3
IS27	26-5-88	14:51	53°24′N 03°43′W	WC	25	20	4	0.6
IS28	29-5-88	23:41	53°48′N 05°49′W	IC	47	40	12	2.2
IS29	30-5-88	12:55	53°48′N 05°56′W	IC	45	40	13	1.6
IS30	1-6-88	12:12	53°43′N 04°37′W	CM	65	60	18	0.1
RV "Cirolana" 14–29 April 1989								
IS32	19-4-89	13:05	53°29′N 03°45′W	WC	37	34	12	0.2
IS33	19-4-89	23:44	53°28′N 03°53′W	WC	38	32	14	0.1
IS34	21-4-89	12:29	53°50′N 06°06′W	IC	31	28	9	0.5
IS35	21-4-89	23:01	53°48′N 06°05′W	IC	31	28	11	0.3
IS36	22-4-89	23:09	53°45′N 05°29′W	CS	104	100	25	0.4
IS37	23-4-89	12:42	53°45′N 05°30′W	CS	107	99	22	0.4
IS39	25-4-89	12:56	53°41′N 04°35′W	CM	70	62	18	0.0
IS40	25-4-89	22:54	53°38′N 04°40′W	CM	86	85	18	0.1

*Increase in temperature towards bottom.

surface salinity was lower (30.00–33.71 ppt). Salinity stratification was greatest at the inshore German Bight stations (e.g. NS2 and NS3, 0–50 m Δs of 2.03–2.52 ppt) due to fresh water outflow. Tidal mixing at the most inshore station (NS4) prevented the establishment of any (observed) salinity stratification.

Fish eggs and larvae

The species composition and occurrence of fish eggs and larvae on LHPR hauls in the Irish Sea and North Sea are given in Table 2. In the Irish Sea, 21 species of eggs and 27 species of larvae were identified, a wider range than from the less intensive sampling in the North Sea where 15 species of eggs and 20 of larvae were recorded. Of the eggs, those of sprat (*Sprattus sprattus*), dragonet (*Callionymus* spp.) and dab (*Limanda limanda*) were the most abundant, together comprising 68% of all eggs in the Irish Sea and 92% in the North Sea. Eggs of rockling species were also relatively common in the Irish Sea (5.9% of all eggs). Larvae of *S. sprattus* (3–22 mm in length), *Callionymus* spp. (2–7 mm) and *L. limanda*

Table 1. LHPR haul information. The four sampling sites are IC (Irish Coast), CS (Central Stratifying), CM (Central Mixed) and WC (Welsh Coastal). Their positions are shown in Fig. 1a.
(b) LHPR haul information for the North Sea.

Haul number	Date	Time GMT	Station position	Bottom depth (m)	Sampled depth (m)	Number of samples	0–50 m Δ t°C
RRS "Challenger" 9–21 June 1989							
NS1	11-6-89	12:25	54°00′N 06°09′E	29	27	11	1.2
NS2	12-6-89	13:20	54°06′N 08°00′E	29	21	7	3.5
NS3	12-6-89	22:40	54°08′N 07°47′E	39	37	12	3.9
NS4	13-6-89	17:06	53°52′N 07°54′E	16	11	6	0.3
NS5	15-6-89	11:27	54°27′N 06°51′E	35	33	12	7.6
NS6	15-6-89	21:12	54°27′N 06°51′E	36	34	13	8.2
NS7	16-6-89	11:23	54°47′N 06°03′E	39	37	15	7.2
NS8	17-6-89	11:00	55°19′N 04°55′E	47	46	17	8.0
NS9	20-6-89	10:17	54°10′N 03°49′E	44	42	18	8.3
NS10	20-6-89	21:36	54°10′N 03°49′E	44	42	20	9.6
NS11	21-6-89	11:53	52°42′N 02°51′E	42	13	5	0.0
RV "Cirolana" 10–24 April 1990							
NS12	12-4-90	12:51	53°53′N 00°57′E	45	41	16	0.4
NS13	12-4-90	22:06	53°51′N 00°55′E	45	40	12	0.1
NS14	13-4-90	12:26	54°37′N 01°03′E	46	45	10	0.1
NS15	13-4-90	22:10	54°38′N 01°06′E	47	46	9	0.0
NS15a	13-4-90	22:50	54°38′N 01°06′E	43	40	9	0.2
NS16	15-4-90	12:09	55°14′N 03°34′E	26	24	6	0.0
NS17	15-4-90	22:08	55°14′N 03°37′E	27	26	6	0.0
NS18	16-4-90	12:03	55°52′N 03°16′E	69	66	19	0.3
NS19	16-4-90	21:35	55°52′N 03°17′E	68	67	16	0.3
NS20	18-4-90	22:02	55°49′N 06°43′E	39	38	11	0.1
NS21	19-4-90	11:57	55°24′N 07°03′E	30	29	8	0.1
NS22	19-4-90	21:40	55°26′N 07°06′E	30	29	8	0.1*
NS23	20-4-90	22:51	54°05′N 07°50′E	42	41	11	0.2
NS24	21-4-90	12:31	54°05′N 07°47′E	41	40	9	0.4
NS24a	21-4-90	12:45	54°05′N 07°47′E	40	34	9	0.3
NS25	22-4-90	20:14	54°33′N 06°30′E	38	37	8	0.3
NS25a	22-4-90	21:15	54°33′N 06°30′E	39	38	9	0.3
NS25b	22-4-90	21:30	54°33′N 06°30′E	39	38	9	0.2

*Increase in temperature towards bottom.

(2–17 mm) together comprised 64% of all larvae in the Irish Sea and 80% in the North Sea. Also common in the North Sea were larvae of sandeel (*Ammodytes* spp.) (6–26 mm in length; 7% of all larvae), whiting (*Merlangius merlangus*) (2–17 mm; 5.6%) and flounder (*Platichthys flesus*) (5–10 mm; 2.6%). Measurements taken make no allowance for larval shrinkage due to sample processing and preservation, but since this procedure was standardised for all hauls, shrinkage should be similar, at least within species. Typical shrinkage values for fish larvae preserved in 4% formaldehyde fall between 5 and 10% (Fox, 1996), but there are variations due to inter- and intra-specific differences and to processing routine and composition of the preservation fluid (Jennings, 1991). However, accurate length measurements were not an important component of the present study.

Vertical distribution of eggs and larvae

The variability in the mean depth distribution of the eggs between hauls was generally low, both within and between the Irish Sea and North Sea (range 13.1–22.8 m, S.E. <4.9 m; Table 3a). Exceptions were *Callionymus* spp. on stratified hauls (Δt >0.5°C) and rockling species on night hauls (S.E.s of 13.5 m and 19.7 m respectively). There were no significant differences between mean depths due to time of day ($p=0.531$–0.841) or temperature structure ($p=0.104$–0.390).

Comparable information for the more abundant fish larvae is given in Table 3b. The weighted mean depths again fell within a relatively narrow range (12.3–26.2 m) as did most standard errors which were <8.7 m, except *P. flesus* (10.6 m, but based on 3 hauls only). There were also no significant differences between hauls related to temperature structure or time of day, except *L. limanda* where there was a significant difference in the distributions between mixed (mean depth 13.5 m) and stratified conditions (mean depth 21.8 m).

Due to the similarity in depth distributions between all hauls, it was justifiable to combine all hauls for each species or group to give a description of their overall

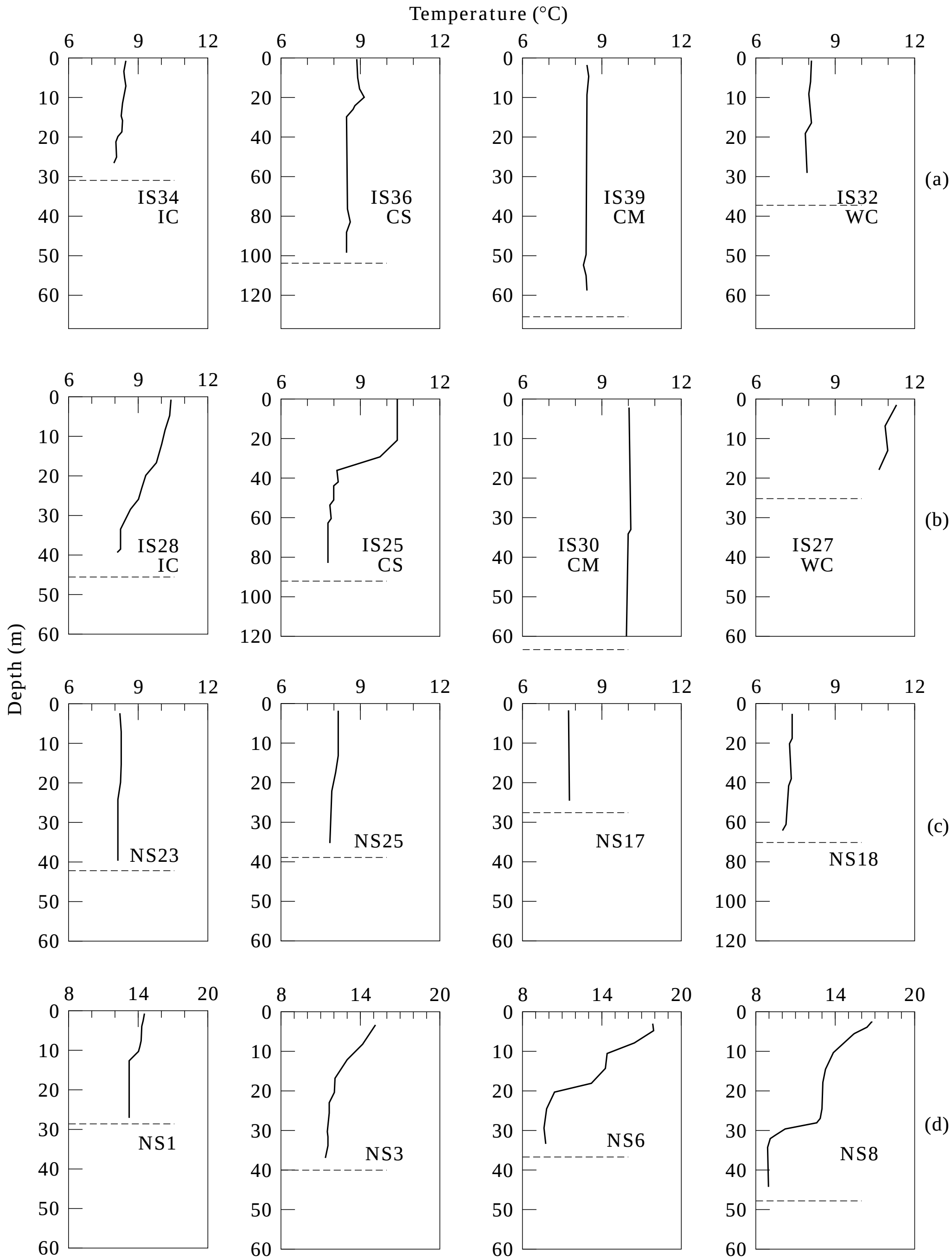

Figure 2. Representative CTD temperature profiles from the four sites, identified as IC (Irish Coastal), CS (Central Stratifying), CM (Central Mixed) and WC (Welsh Coastal), in the Irish Sea from (a) April 1989 and (b) May/June 1988 and from stations in the North Sea for (c) April 1990 and (d) June 1989. Broken lines indicate the water depth at each station.

pattern of vertical distribution. The resulting vertical distribution of eggs and larvae of *L. limanda*, *S. sprattus* and *Callionymus* spp., representing those species which were taken in higher numbers as both eggs and larvae, are plotted in Figure. 3. Their distributions were restricted mainly to the upper 60 m of the water column, with most within the top 30 m. Abundance of eggs of all three species increased towards the surface, whereas for larvae only those of *L. limanda* were most abundant at the surface, those of *S. sprattus* and *Callionymus* spp.

Table 2. Species composition and percentage occurrence of fish eggs and larvae in 34 LHPR hauls in the Irish Sea and 29 hauls in the North Sea (+ = occurrence at <0.1%).

Species	Irish Sea Positive hauls	Irish Sea Total eggs	Irish Sea % Total eggs	Irish Sea Positive hauls	Irish Sea Total larvae	Irish Sea % Total larvae	North Sea Positive hauls	North Sea Total eggs	North Sea % Total eggs	North Sea Positive hauls	North Sea Total larvae	North Sea % Total larvae
Agonus spp.	—	—	—	1	1	0.1	—	—	—	—	—	—
Ammodytes spp.	—	—	—	18	207	10.6	—	—	—	22	349	7.0
Arnoglossus laterna	1	6	0.1	2	19	1.0	—	—	—	—	—	—
Buglossidium luteum	2	2	+	5	13	0.7	5	46	0.3	4	11	0.2
Callionymus spp.	19	639	9.4	18	103	5.2	25	1631	10.4	12	186	3.8
Clupea harengus	—	—	—	1	2	0.1	—	—	—	1	1	+
Ctenolabrus rupestris	1	2	+	—	—	—	2	4	+	—	—	—
Gadus morhua	—	—	—	17	42	2.1	—	—	—	4	36	0.7
Glyptocephalus cynoglossus	—	—	—	3	6	0.3	—	—	—	—	—	—
Gobius spp.	—	—	—	13	35	1.8	—	—	—	5	6	0.1
Hippoglossoides platessoides	3	6	0.1	2	3	0.2	—	—	—	1	1	+
Limanda limanda	16	1738	25.5	22	284	14.5	27	8225	52.4	24	3170	63.9
Liparis spp.	—	—	—	6	18	0.9	—	—	—	—	—	—
Lumpenus lampretaeformis	—	—	—	3	13	0.7	—	—	—	—	—	—
Merlangius merlangus	—	—	—	15	99	5.0	—	—	—	15	277	5.6
Merluccius merluccius	1	1	+	—	—	—	2	3	+	—	—	—
Microchirus variegatus	1	1	+	—	—	—	—	—	—	—	—	—
Microstomus kitt	—	—	—	4	8	0.4	—	—	—	1	2	+
Molva molva	2	3	+	—	—	—	—	—	—	—	—	—
Mullus surmuletus	—	—	—	2	4	0.2	1	1	+	—	—	—
Pholis gunnellus	—	—	—	9	55	2.8	—	—	—	—	—	—
Phrynorhombus norvegicus	1	2	+	—	—	—	—	—	—	—	—	—
Platichthys flesus	4	7	0.1	2	4	0.2	—	—	—	6	128	2.6
Pleuronectes platessa	8	100	1.5	8	30	1.5	3	4	+	5	21	0.4
Pollachius pollachius	—	—	—	3	5	0.3	—	—	—	4	11	0.2
Rockling spp.	24	403	5.9	15	55	2.8	15	124	0.8	14	61	1.2
Scomber scombrus	6	155	2.3	—	—	—	8	139	0.9	6	38	0.8
Scophthalmus maximus	5	10	0.1	—	—	—	8	37	0.2	—	—	—
Scophthalmus rhombus	5	24	+	1	2	0.1	19	177	1.1	—	—	—
Solea solea	3	24	0.4	10	43	2.2	—	—	—	4	9	0.2
Sprattus sprattus	30	2234	32.7	25	873	44.5	20	4511	28.7	20	629	12.7
Taurulus bubalis	—	—	—	9	16	0.8	—	—	—	3	7	0.1
Trachurus trachurus	—	—	—	—	—	—	7	141	0.9	—	—	—
Trachinus vipera	—	—	—	—	—	—	2	71	0.5	—	—	—
Trigla spp.	13	116	1.7	1	1	0.1	13	39	0.2	1	1	+
Trisopterus spp.	2	3	+	7	21	1.1	—	—	—	6	15	0.3
Zeugopterus punctatus	3	5	0.1	—	—	—	—	—	—	—	—	—
Unidentified gadoid eggs	26	1346	19.7	—	—	—	27	544	3.5	—	—	—

Table 3a. Weighted mean depths and standard errors of the means for the more abundant fish eggs from all positive LHPR hauls in the North Sea and Irish Sea combined. The weighted mean depth range for all hauls, the number of hauls (n) and the probability (p) value from ANOVA analysis are also shown.

Species	Temperature structure/time of day	Mean depth (m)	Standard error	Range of mean depths (m)	n	p
Limanda limanda	Day	15.2	3.2	4.9–33.5	17	0.841
	Night	14.8	2.5	10.6–24.4	11	
	Isothermal	14.9	2.2	4.9–33.5	27	—
	Stratified	18.6	—	—	1	
	Total	15.1	2.1	4.9–33.5	28	
Sprattus sprattus	Day	14.1	3.2	4.4–28.4	20	0.698
	Night	15.1	2.2	9.3–19.9	9	
	Isothermal	15.2	3.0	5.4–28.5	19	0.390
	Stratified	13.1	3.6	4.4–19.1	10	
	Total	14.4	2.3	4.4–28.4	29	
Callionymus spp.	Day	18.4	4.9	4.9–50.1	18	0.546
	Night	16.4	3.0	10.1–26.9	12	
	Isothermal	16.3	2.1	11.2–31.4	24	0.213*
	Stratified	22.8	13.5	4.9–50.1	6	
	Total	17.6	3.2	4.9–50.1	30	
Rockling spp.	Day	14.1	9.1	8.0–27.6	4	0.643*
	Night	20.7	19.7	6.8–39.7	3	
	Isothermal	16.9	9.3	6.8–39.7	7	—
	Stratified	—	—	—	—	
	Total	16.9	9.3	6.8–39.7	7	

*Using logarithmically transformed data.

showing sub-surface peaks at 5–10 m and 10–15 m respectively.

The depth distributions of eggs of rockling species and larvae of *M. merlangus, Ammodytes* spp. and *P. flesus*, all of which were taken in moderate numbers as either eggs or larvae, are plotted in Figure 4. Eggs of rockling species, larvae of *P. flesus* and, to a lesser extent larvae of *M. merlangus* showed increased abundance towards the surface. There was some evidence of bimodality in the depth distribution of rockling eggs, possibly due to the presence of eggs of more than one species, which may also have accounted for the observed high standard error (19.7 m, Table 3a) of the mean depth. Larvae of *Ammodytes* spp. had a more even distribution down the water column, this possibly being related to the eggs being spawned demersally. Both *M. merlangus* and *P. flesus* had noticeably shallower distributions (<40 m) than other larvae taken (cf. Figs 3 and 4).

The combined distributions of all eggs and all larvae have been amalgamated in Figure 5. This figure highlights the deeper distribution of eggs (weighted mean depth of 35 m), which were taken down to the maximum depth sampled (100 m), compared to larvae (weighted mean depth of 20 m) which were restricted to depths above 55 m. Eggs were found in peak numbers at the surface while larvae have a sub-surface peak of abundance.

Discussion

There were few significant differences between the vertical distributions of different ichthyoplankton species from the Irish Sea and North Sea, either for eggs or larvae. In part, this may be due to the effects of averaging results from a number of hauls taken at different times and under different biological and hydrographic conditions.

For pelagic eggs, their vertical distribution is determined by the relationship between physical properties of the eggs, seawater density and the degree of vertical mixing of the water column (Sundby, 1991; Nissling *et al.*, 1994). The distributions observed, with increasing numbers of eggs towards the surface, is as expected for passive buoyant particles under the dominant influence of wind mixing at the surface (Sundby, 1991). The

Table 3b. Weighted mean depths and standard errors of the means for the more abundant fish larvae from all positive LHPR hauls in the North Sea and Irish Sea combined. The weighted mean depth range for all hauls, the number of hauls (n) and the probability (p) value from ANOVA analysis are also shown.

Species	Temperature structure/time of day	Mean depth (m)	Standard error	Range of mean depths (m)	n	p
Limanda limanda	Day	17.6	4.3	2.7–26.1	11	0.637
	Night	15.9	5.8	4.3–28.1	9	
	Isothermal	13.5	4.1	2.7–26.1	12	0.015
	Stratified	21.8	4.4	10.0–28.1	8	
	Total	16.8	3.5	2.7–28.1	20	
Sprattus sprattus	Day	13.7	2.7	4.9–23.2	16	0.236
	Night	16.3	3.0	9.3–24.4	10	
	Isothermal	14.4	2.4	4.9–21.2	16	0.619
	Stratified	15.4	3.9	6.7–24.4	10	
	Total	14.8	2.1	4.9–24.4	26	
Callionymus spp.	Day	14.6	4.7	5.9–24.7	7	0.350
	Night	12.3	6.7	4.1–20.2	4	
	Isothermal	13.1	8.7	4.1–24.7	4	0.789
	Stratified	14.2	3.8	5.9–20.2	7	
	Total	13.8	3.9	4.1–24.7	11	
Merlangius merlangus	Day	14.3	2.5	10.1–18.0	5	0.499
	Night	16.1	4.1	7.2–19.7	6	
	Isothermal	15.3	2.7	7.2–19.7	10	—
	Stratified	14.6	—	—	1	
	Total	15.3	2.7	7.2–19.7	11	
Ammodytes spp.	Day	19.8	3.9	11.4–26.5	8	0.143
	Night	26.2	7.2	10.2–41.8	8	
	Isothermal	23.6	4.8	10.2–41.8	14	—
	Stratified	18.4	—	15.8–21.0	2	
	Total	23.0	4.3	10.2–41.8	16	
Platichthys flesus	Day	18.7	—	—	1	—
	Night	13.7	10.6	8.2–24.3	3	
	Isothermal	14.9	7.9	8.2–24.3	4	—
	Stratified	—	—	—	—	
	Total	14.9	7.9	8.2–24.3	4	

occurrence of eggs in significant numbers in relatively deep water (>50 m depth) where wind mixing has little effect, may be attributed, in part, to tidal mixing, which is strong in many areas of the Irish Sea and possibly also to some species spawning deep in the water.

While the mean depth distributions of larvae were similar, the pattern of their distributions was variable. The vertical distribution of larvae is influenced by the same physical factors as for eggs but with the additional effects of ontogenetic and behavioural differences in response to environmental factors. There is a general feeding advantage in being distributed in the upper, more productive, layers of the water column, where food particles are present in higher abundance (e.g. Coombs *et al.*, 1992; Coombs *et al.*, 1994) and, more specifically, some studies have found the vertical distribution of larvae to be related to the depth of highest abundances of copepod nauplii (e.g. Haldorson *et al.*, 1993). Additionally, there is the influence of predation which may lead to the observed peak of larval abundance, this being the optimum balance between visual avoidance and food availability (Fortier and Harris, 1989).

The observed sub-surface peak of larval abundance may also reflect some aspect of diel migration, or net

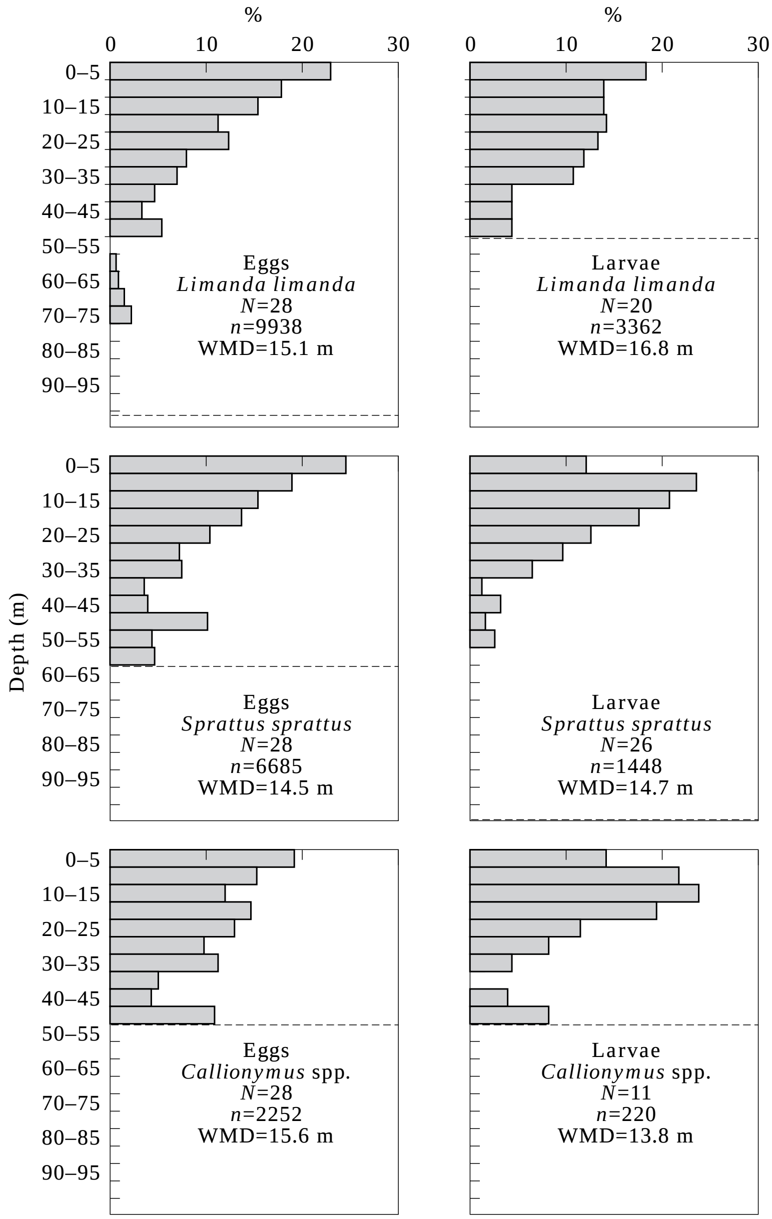

Figure 3. Vertical distribution of eggs and larvae of *Limanda limanda*, *Sprattus sprattus* and *Callionymus* spp. plotted as the mean percentage occurrence on all LHPR hauls from the Irish Sea and North Sea on each of which there were >20 eggs or >10 larvae. Also shown are the number of hauls (N) and total number of larvae (*n*) on which the distributions are based, together with the weighted mean depth (WMD) of the distributions. The maximum depth to which sampling was carried out is marked with a broken line.

avoidance in the more strongly illuminated surface layers. Although there was no direct evidence in the present study for diel migration of larvae, this can be difficult to detect unless it is synchronised amongst individuals (Pearre, 1979) and consistent over a particular size range of larvae. Röpke (1989) observed larvae of a number of species performing diel vertical migrations, but concluded that two of the species recorded in the present study (*Callionymus* spp. and *M. merlangus*) did not exhibit it. Similarly, Fortier and Harris (1989) found little difference in the diel vertical distribution of a range of fish larvae (mainly sampled within the top 40 m) except that larger larvae were sampled deeper in the water column with increasing size. Many studies have suggested that diel changes are simply a dispersal of larvae once the light stimulus disappears (Kloppmann, 1991; Leis, 1991), with the distance of dispersal being related to swimming ability. However, changes in

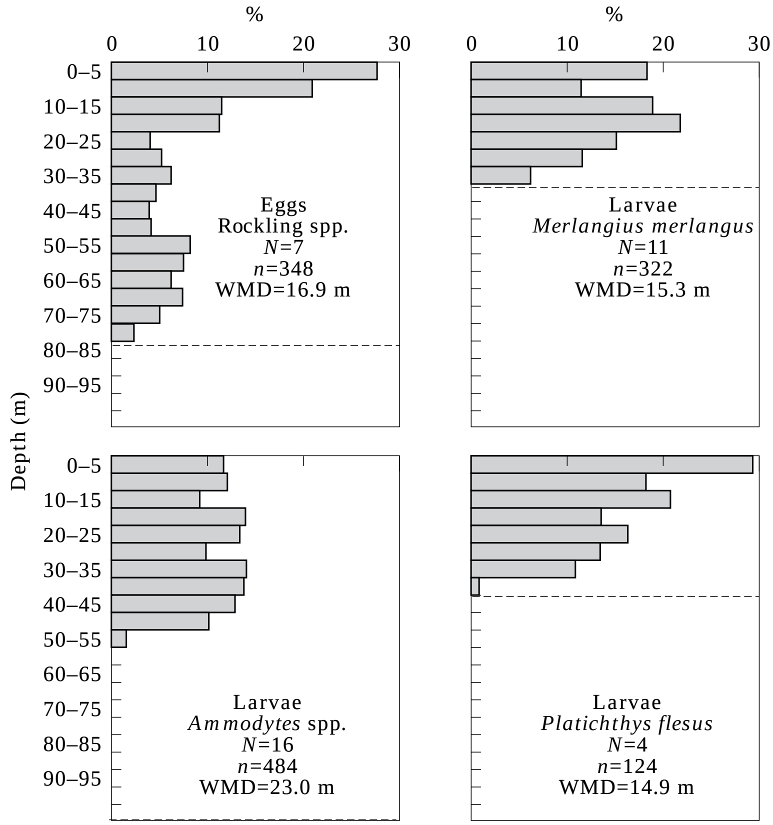

Figure 4. Vertical distribution of eggs of rockling species and larvae of *Merlangius merlangus*, *Ammodytes* spp. and *Platichthys flesus* plotted as the mean percentage occurrence on all LHPR hauls from the Irish Sea and North Sea on each of which there were >20 eggs or >10 larvae. Also shown are the number of hauls (N) and total number of larvae (*n*) on which the distributions are based, together with the weighted mean depth (WMD) of the distributions. The maximum depth to which sampling was carried out is marked with a broken line.

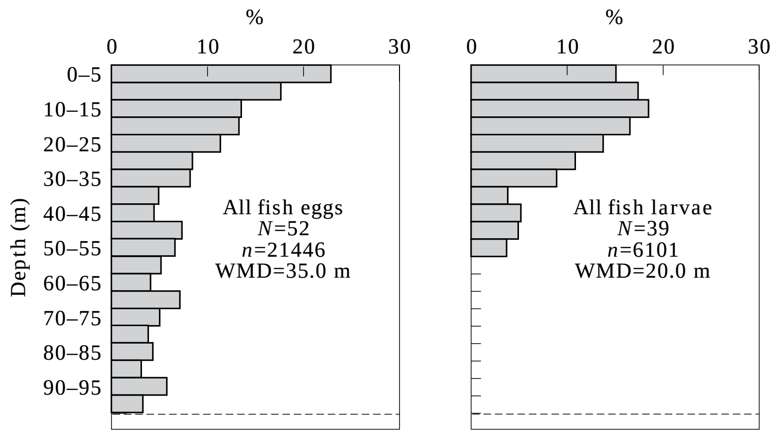

Figure 5. Vertical distribution of all eggs and larvae plotted as the mean percentage occurrence on all LHPR hauls from the Irish Sea and North Sea on each of which there were >20 eggs or >10 larvae. Also shown are the number of hauls (N) and total number of larvae (*n*) on which the distributions are based, together with the weighted mean depth (WMD) of the distributions. The maximum depth to which sampling was carried out is marked with a broken line.

vertical distribution can be difficult to demonstrate unless larvae are present in high concentrations and sampling is carried out at sufficient temporal and vertical resolution.

In the present study, there was little evidence of the influence of thermal stratification on the vertical distributions of larvae. Strong thermoclines, when present, tended to be at around 30 m depth, with the majority of larvae being above this depth irrespective of stratification. Other studies have generally shown a restriction of ichthyoplankton to the upper mixed layer (Coombs *et al.*, 1981; Boehlert *et al.*, 1985) and more rarely, under particular conditions, below the thermocline (Munk and Nielsen, 1994, for *S. sprattus* and *M. merlangus*). In the present study when a significant difference in depth distribution was noted between mixed and stratified conditions, as found for *L. limanda* larvae, the overall difference in weighted mean depth was only 8 m.

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