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1. Introduction

For the past 25 years, staff of the Directorate of Fisheries Research at Lowestoft have been engaged in biological studies of the fish stock and recruitment problem. These studies have consisted of periodic egg and larvae surveys, aimed specifically at the plaice, *Pleuronectes platessa,* but also embracing other species occurring in the surveyed areas. Most of these surveys have been undertaken in the Southern Bight of the North Sea, but surveys have also been made in other sea areas where the intensity of plaice spawning differs from that in the Southern Bight. These areas were the Irish Sea in 1965, the central North Sea and German Bight in 1968, and the English Channel in 1968 and 1971. The specific objectives have been to determine the mechanisms operating during the planktonic phase which generate year to year variation in year-class strengths of plaice.

For 1976, it was proposed to extend these studies and to survey an area for a whole year, widening the scope of the objectives to include:

i. a general study of the distribution, mortality and drift of fish eggs and larvae;

ii. determination of the potential predation of fish eggs and larval fish;

iii. a study of the factors which determine the distribution and abundance of young fish on nursery grounds;

iv. an examination of interrelationships of fish species in the planktonic phase.

These objectives limited the choice of study area to one where:

i. the identity of the fish stocks was known or could be determined;

ii. spawning areas and nursery grounds were in close proximity;

iii. there was an appropriate mix of fish species of commercial interest;

iv. surveys could be made frequently enough with the resources available.

The final criterion restricted the choice to the North Sea. Whilst previous experience in the Southern Bight was an attraction to that area, surveys of the nursery grounds would have entailed working in an area where the Netherlands programme was well advanced. The area between the east coast of England north of the Wash and the western edge of the Dogger Bank fulfilled all the biological and logistical criteria. This area is very important to UK fishing interests because it carries an exceptional mix of fish and shellfish species of commercial importance and includes a major herring spawning ground. It is biologically interesting because it contains transition areas between central North Sea and coastal plankton communities, with associated frontal zones, and with a double peaked production cycle. No systematic plankton surveys had been undertaken in this area of the North Sea since the Flamborough line (Cattley, 1954) was discontinued in 1960, so this study will fill a fundamental gap in our basic biological knowledge of the area. Two additional attractions in favour of conducting the surveys in this part of the North Sea were that:

i. they would complement the detailed study of fishable stocks already being carried out in the area, and link with the annual young fish surveys on this coast;

ii. the annual production in this area could be compared with that shown by the more detailed studies of the spring production cycle in the Fladen Ground Experiment (FLEX) and linked with the Joint North Sea Data Acquisition Programme (JONSDAP) hydrographic survey covering the whole of the North Sea during the spring of 1976.

It was decided, therefore, to undertake a one-year intensive series of surveys of the plankton in this area of the North Sea in 1976, backed by less intensive surveys of the nursery areas in 1976, 1977 and 1978.

The primary aims of the surveys were:

i. to study the seasonal distribution and intensities of the spawnings of the more important commercial fish species;

ii. to estimate abundance and mortality in the egg and larval stages of plaice, cod, herring and any other species for which development data became available;

iii. to determine the major predators on fish eggs and larvae by examining the stomach contents of potential plankton and fish predators;

iv. to determine the course and speed of the larval drift to their nursery areas;

v. to determine subsequent recruitment, growth and mortality of the young fish.

Secondary aims, which were related to the major objectives and could be achieved simultaneously were:

vi. measurement of the standing stock of phytoplankton in terms of chlorophyll *a* and phaeophytin, identification of the major species in size and relative numbers contributing to this fluorescence, and examination of spatial, seasonal and vertical distribution and of algal succession;

vii. estimation of zooplankton biomass volumetrically and in terms of particle sizes;

viii. an investigation of fish larval feeding;

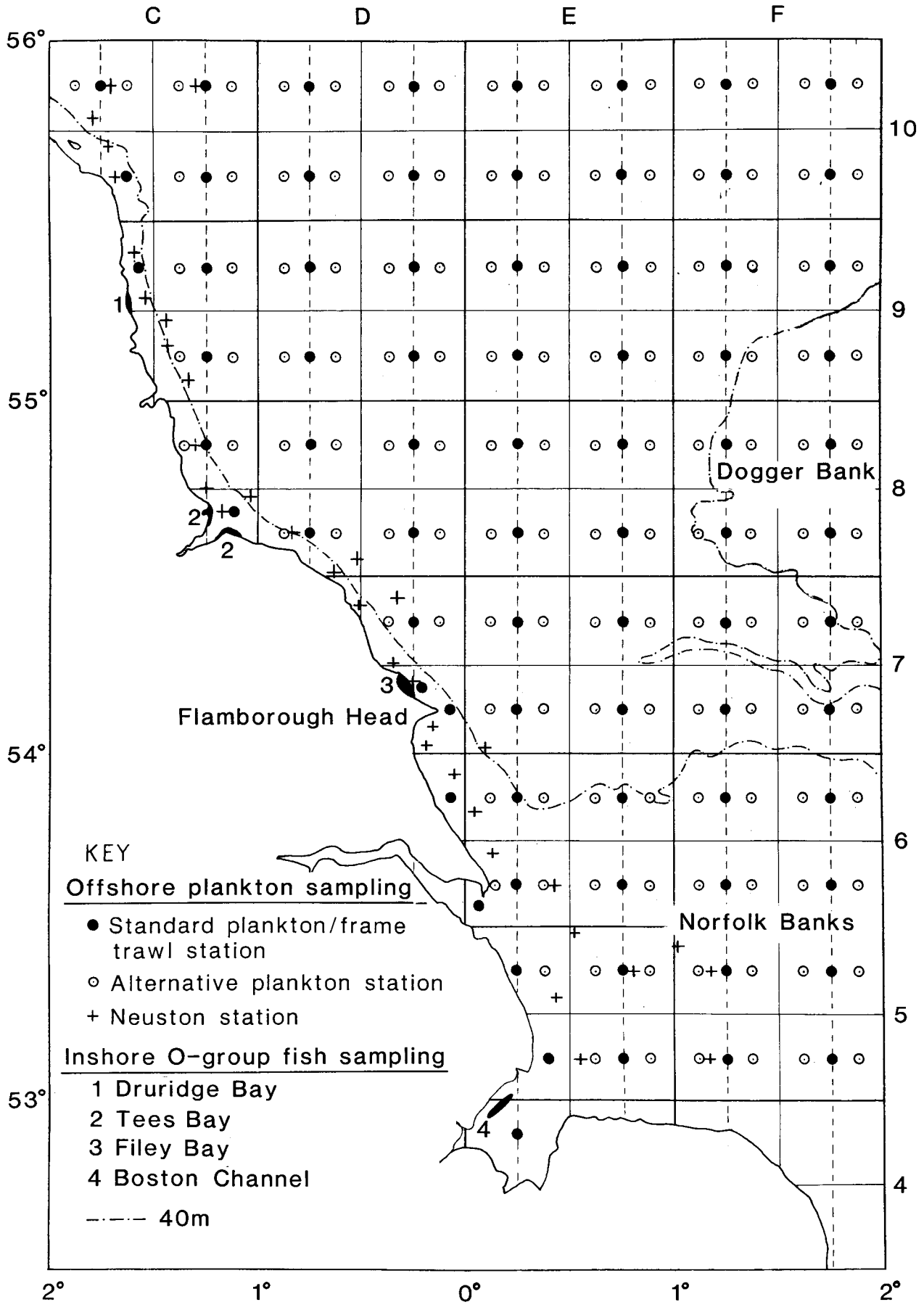


Figure 1 Grid of sampling stations off the north-east coast of England showing ICES sub-rectangles.

ix. examination of the vertical distribution of larval fish to determine when the larvae become demersal, and to assist in the interpretation of standard plankton hauls;

x. estimation of sampling errors, by taking replicate hauls and by doing small-scale replicate grids;

xi. measurement of irradiance, extinction coefficients and turbidity in the vertical water column;

xii. sampling of lobster *(Homarus gammarus)* larvae with a neuston net in areas of known occurrence of berried females.

The biological programme was to be closely supported by hydrographic observations directed towards understanding the major features of circulation in the area, and linking with the JONSDAP exercise. A complementary programme was undertaken to monitor most of the important physical and chemical properties of the sea off the north-east coast of England.

The work at sea was to be complemented by laboratory observations on the development rates of eggs and larvae of selected species; emphasis would be on ageing the larvae of plaice, cod and whiting.

2. Design of the surveys

A grid of stations based on the ICES statistical rectangles was laid down over the area from north Norfolk to 56°N and to longitude 2°E (Figure 1). Sampling points were 18 nautical miles apart longitudinally and along latitude lines 15 nautical miles apart. In the centre of this grid, to the north of the River Humber and to the south of the River Tyne, intermediate sampling points 9 nautical miles apart were designated; this central part constituted the main priority plankton sampling grid. Frame trawl hauls for young fish were to be made at selected stations whilst additional inshore stations were designated for neuston net hauls between July and November.

This survey grid was worked on twelve cruises between the end of January and the beginning of November. Seven cruises were planned for the first four months to sample cod and plaice spawnings, while the remainder, at approximately monthly intervals, were to sample summer- and autumn-spawning fish.

RV CORELLA★ undertook the first eleven of these surveys; the final survey was by RV CLIONE.

Each survey lasted approximately twelve days. This was sufficient for the grid of plankton stations to be completed once and to leave time for secondary aims not accomplished simultaneously with the plankton survey, e.g. midwater trawling for fish predators, vertical distribution studies of fish larvae and replicate plankton hauls in varying densities of fish eggs and larvae.

★ A vessel which at the time of the survey was owned by MAFF but which is no longer in service with MAFF.

3. Sampling methods and sampling gear used

3.1 Hydrographic sampling

With the exception of the moored current meter network, all the hydrographic observations were made from the vessel conducting the plankton survey.

Temperature-at-depth profiles at each sampling station were obtained from the chart records of the electronic depth gauge and thermistor sensors mounted on the plankton sampler. The thermistor used was calibrated against a secondary standard thermometer and the chart records corrected accordingly. The response time for the thermistor, as mounted on the plankton sampler, was 1.5 s for each degree centigrade over the range 2°C-20°C, which must be compared with a vertical progression of the sampler of 0.12 m s^{-1} both on shooting and hauling.

Throughout each survey the sub-surface water was continuously monitored through a stainless-steel shipboard pumping system. This pump had an intake 4 m below the sea surface and delivered uncontaminated sea water to environmental sensors set up in the ship's laboratory. The temperature, salinity, pH, dissolved oxygen and transparency sensors were mounted in a specially constructed Perspex box through which the pumped water flowed continuously.

The environmental sensors were calibrated at regular intervals during each survey: the pH, dissolved oxygen, temperature and transparency calibrations were made against known standards. For the salinometer, electronic calibration was augmented by regular, accurate salinometer measurements on water samples.

The pumped sea water supply was also used to take discrete samples at each station for subsequent salinity and nutrient salt analysis. One 250 ml sample fixed with 1 ml chloroform was taken for nitrate, nitrite and phosphate analysis and a 150 ml sample was stored in a polythene bottle and deep frozen for silicate analysis.

On five cruises from March to the end of August, discrete water samples at 5 m depth intervals between the surface and the bottom were taken, using a series of Nansen water bottle casts. These samples were subsequently analysed for total chlorophyll *a*, phaeophytin *a*, nitrate, nitrite, phosphate, silicate and salinity, and the temperature at each depth was recorded.

A solarimeter mounted at deck level, was run continuously throughout each survey, giving a chart record of total incident light energy (W m^{-2}) at the sea surface. A simultaneous record from a quantum cell, responding over the photosynthetically active range (P.A.R.) of 400 nm-700 nm wavelength, was displayed on the same chart.

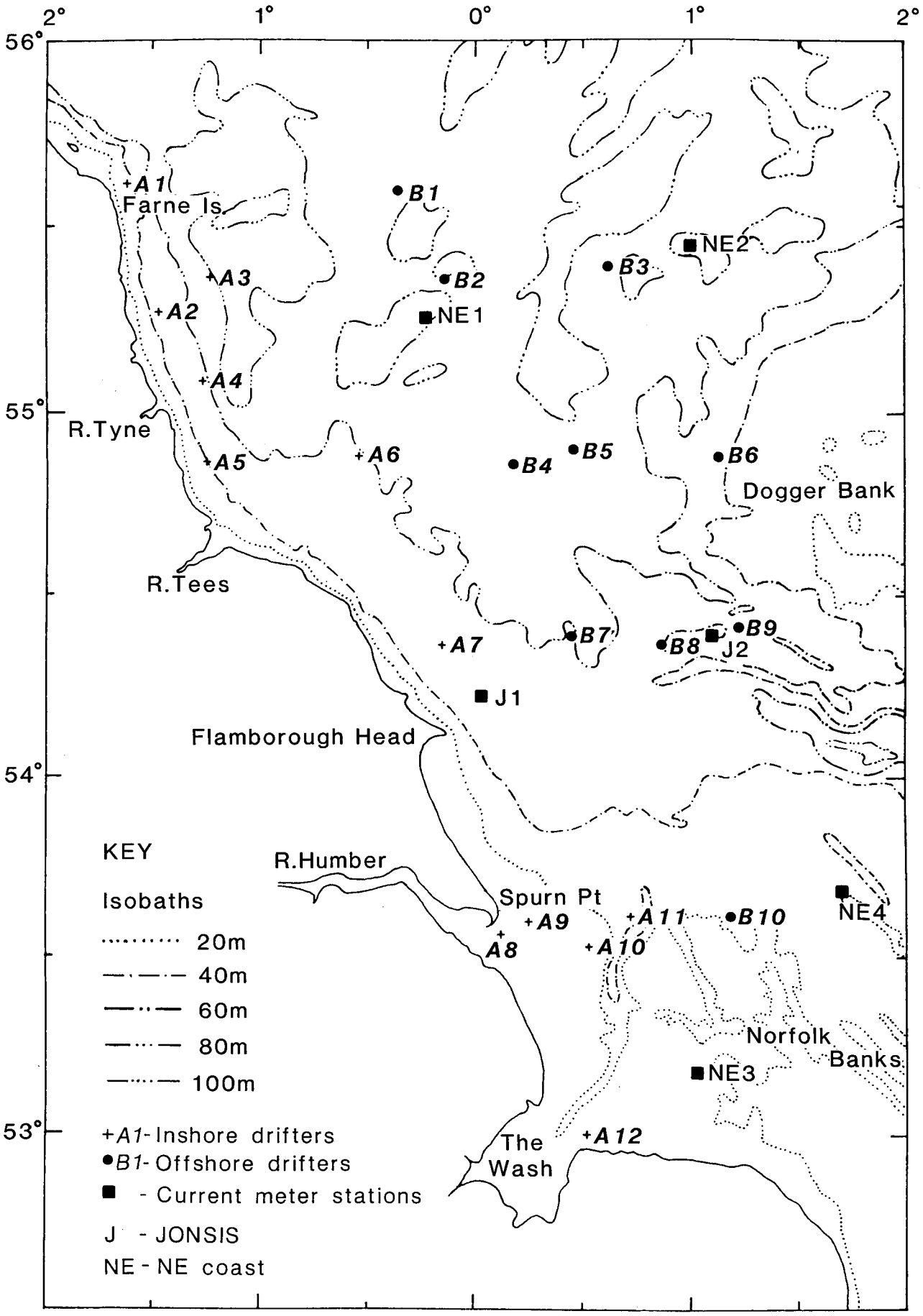


Figure 2 Bathymetric chart of the survey area, with locations of fixed current meter moorings and seabed drifter releases.

Between February and October, at each vertical distribution sampling point and at some other selected inshore and offshore positions on the survey grid, a series of quantaspectrometer observations was made. The instrument was used at 5 m depth intervals from the surface to the sea bed to give a vertical profile of light wavelength penetration over the 400 nm-700 nm P.A.R. The spectral scan thus obtained was both displayed as a chart record and integrated to give total quanta $m^{-2}s^{-1}$. Synchronised observations were made with two reference cells, one mounted adjacent to the quantaspectrometer and the other recording just below the sea surface. Selenium cells, filtered to give a $V\lambda$ response, were used as reference until August when they were replaced by quantum cells giving the same P.A.R. response as the quantaspectrometer.

Moored current meter rigs and Woodhead seabed drifters were used to study the major features of the circulation in the area. Figure 2 shows the general bathymetry of the area, the location of the six moored current meter stations and the seabed drifter release positions. Four moored stations, NE1-4, were deployed especially for these surveys, and they were suplemented by two stations, JONSIS 1 and 2 (J1 and J2), which had been in existence since January 1971 (Hill, 1971). Each station comprised a standard Lowestoft rig (Baxter and Bedwell, 1972), with two meters at stations J1, J2, NE1 and NE2, but with only one meter at the shallow water stations NE3 and NE4. Further details of the operation of these moored stations and of their data return are given in Table 1.

Table 1 Details of the data return from the moored current meter stations deployed during the north-east coast exercise, 1976

		Days deployed	Number of days of good data collected	Gross percentage
NE1	Top	273	62	23
	Bottom	273	10	4
NE2	Top	273	162	59
	Bottom	273	211	77
NE3		237	79	33
NE4		237	158	67
J1	Top	271	181	67
	Bottom	271	137	51
J2	Top	299	181	61
	Bottom	290	229	77

Between 650 and 800 Woodhead seabed drifters were released on every cruise, mainly in batches of 50 by the soluble string method (Ramster, 1965) at up to 15 of the 22 positions shown in Figure 2: the planned network of 14 release positions had to be modified on some cruises because of weather conditions and other logistical factors. The release pattern is shown in Table 2; it includes an additional release position, A4, of special interest to the local Water Authority, where 100 drifters were released when the station was occupied.

Meteorological observations were made routinely at all stations on every cruise; they included wind strength and direction, sea state and cloud cover.

3.2 Plankton sampling

3.2.1 Total phytoplankton as chlorophyll a

The same sea water source as used for hydrographic monitoring was used to deliver a continuous supply to a Turner model 10 fluorometer, specially modified to enable the standard instruments to be used for the measurements of *in vivo* chlorophyll *a* fluorescence in concentrations ranging from 0.04 to 10-15 g l^{-1} (Lincoln, 1976). As continuous monitoring of *in vivo* fluorescence of chlorophyll *a* only provides a broad picture of phytoplankton distribution, frequent calibration of the continuous measurement is required if phytoplankton standing stock is to be measured more accurately. Variability of *in vivo* fluorescence per unit chlorophyll *a* is caused by species differences, light intensity, nutrient deficiency, temperature, the presence of phaeophytin 'a' and other factors. At each plankton sampling station on these surveys, an acetone extract of chlorophyll, from a 500 ml sample of the pumped sea water, was prepared. The chlorophyll *a* fluorescence of this sample was measured using the Turner model III fluorometer fitted with a discrete sample holder. Phaeophytin 'a' fluorescence was also measured by acidification of the original extract. These calibrations (described in more detail by Lincoln, 1976) were then used, together with previously obtained calibrations of the instrument against a spectrophotometer, to convert the continuous readings into chlorophyll *a* $\mu g\ l^{-1}$. Additionally, the proportion of fluorescence attributable to the nanoplankton was obtained by measuring the *in vivo* fluorescence before and after passing part of the sample through mesh of pore size 10 μm.

3.2.2 Operation and calibration

The sampling gear used for the main surveys was the Lowestoft multipurpose plankton sampler (Beverton and Tungate, 1967). In its modified form, which was the standard for these surveys, this sampler consists basically of a 30 inch (76 cm) diameter fibreglass tube enclosing a conical nylon filtering net, 185 cm long. The mesh of the net has an aperture of 270 μm and a porosity of 46%. Water enters the net via a hemispherical nose cone with an opening of 16 inches (40.6 cm) diameter giving a 7:1 ratio of open area of net to sampler mouth opening.

Table 2 Seabed drifter release positions and dates in 1976

		Release Position											
		A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	A11	A12
		55°37′N 01°37′W	55°16′N 01°28′W	55°22′N 01°14′W	55°05′N 01°16′W	54°52′N 01°15′W	54°53′N 00°33′W	54°22′N 00°10′W	53°33′N 00°08′E	53°36′N 00°15′E	53°32′N 00°32′E	53°37′N 00°44′E	53°00′N 00°32′E
(a) INSHORE													
Release No	Date (1976)												
1	27 Jan				X								
2	28 Jan-8 Feb	X		X		X	X	X		X	X		
3	19-23 Feb	X		X		X	X	X		X	X		
4	9-15 Mar	X		X		X	X	X	X			X	
5	11 Mar				X								
6	27 Mar-3 Apr	X		X		X	X	X		X	X		
7	25 Apr				X								
8	24-29 Apr			X		X	X	X		X			X
9	11-16 May	X		X	X	X	X	X		X	X		
10	28 May-2 Jun	X		X	X	X	X	X		X	X		
11	8-13 Jul			X	X	X	X	X		X	X		
12	13-22 Aug	X		X	X	X	X	X		X	X		
13	5-13 Sep	X	X	X		X	X	X		X	X		
14	29 Sep-7 Oct	X	X	X		X		X		X	X		
15	27 Oct-3 Nov	X		X		X	X	X		X	X		
16	30 Nov				X								

		Release Position									
		B1	B2	B3	B4	B5	B6	B7	B8	B9	B10
		55°36′N 00°22′W	55°22′N 00°08′W	55°24′N 00°37′E	54°52′N 00°11′E	54°54′N 00°27′E	54°53′N 01°08′E	54°23′N 00°27′E	54°22′N 00°52′E	54°25′N 01°14′E	53°37′N 01°11′E
(b) OFFSHORE											
Release No	Date (1976)										
2	28 Jan-8 Feb		X	X	X		X	X	X		X
3	19-23 Feb		X	X	X		X	X	X		X
4	9-15 Mar		X		X		X	X	X		X
6	27 Mar-3 Apr		X	X	X		X	X	X		X
8	24-29 Apr	X	X	X		X	X	X	X		X
9	11-16 May		X	X	X		X	X	X		X
10	28 May-2 Jun		X	X	X		X	X	X		X
11	8-13 Jul		X	X	X		X	X	X		X
12	13-22 Aug		X	X	X		X	X	X		X
13	5-13 Sep	X			X		X	X		X	X
14	29 Sep-7 Oct		X	X	X	X	X	X		X	X
15	27 Oct-3 Nov		X	X	X		X	X	X		X

X indicates drifters released at positions and dates indicated.

The main sampler net was used to collect fish eggs and larvae and other macroplankton (particle size > 300 μm) including edible crab *(Cancer pagurus)* larvae. Two accessory samplers were mounted on the body of the main sampler, each one made up of a 6 inch (15 cm) diameter PVC tube with a metal nose cone with a 2 inch (5.1 cm) aperture. Each accessory sampler contained a conical nylon filtering net, 147 cm long, of mesh aperture 35 μm and porosity 16% in one sampler, and 61 μm and 26% respectively in the other. These accessory samplers were used to collect the smaller zooplankton and large diatoms and dinoflagellates. A high-speed continuous water sampler (Beverton and Tungate, 1967) was also mounted on the body of the main sampler to take an integrated water sample for small phytoplankton analysis.

An electromechanical flowmeter was fitted in the nose cone of the main sampler (Harding *et al.*, 1971), and standard mechanical flowmeters (Tungate and Mummery, 1965) at the rear of each accessory sampler. An additional mechanical flowmeter was mounted on the outside of the main sampler, operating continuously in free stream. The sampler was towed on a seven-cored electric cable armoured with a stainless-steel, load-bearing sheath. This cable was on a slip-ring cable winch, so a continuous record of water flow through the main sampling net could be displayed in the deck control room via an electronic sensor mounted on the back of the electromechanical flowmeter. The sampler was also fitted with an electronic depth gauge and a thermistor with outputs from these sensors to chart recorders in the control room. On both RV CORELLA and RV CLIONE the sampler was operated over the stern of the vessel at a towing speed of 5 knots. A Scripps depressor on a 30 cm strop was attached to the underside of the sampler immediately behind the nose cone. By paying out and hauling the cable at a constant speed, the sampler performed a shallow, oblique dive to within 2 m of the sea bed and back to the surface, thus providing an equivalent sample of each part of the water column.

Before embarking on the surveys the samplers and flowmeters were calibrated in a circulating water channel at the National Maritime Institute at Feltham (Harding and Arnold, 1971). These calibrations gave an accurate relationship between speed and volume of water accepted over the range of speeds 3-7 knots when the sampler was without a filtering net, i.e. in free flow. To calculate the actual volume filtered by each net on a sampling station, the free flow calibrated volume is adjusted by a correction factor derived from the revolutions of the flowmeter in free flow and during the sampling haul. This correction factor adjusts for the filtering net and plankton which clogs the meshes.

The revolutions per second in free flow were measured at the beginning and end of each survey, by towing the sampler without filtering nets on consecutive oblique hauls at 4, 5 and 6 knots,and the following regression of revolutions per second against speed was derived:

$y = Ax + B$, where
y = volume accepted ($1\ s^{-1}$),
x = towing speed in knots.

The constants were, for the 16 inch (40.6 cm) nose cone $A = 52.3765$, $B = 3.3784$; and for the 14 inch (35.6 cm) nose cone $A = 38.6122$, $B = 1.8668$.

To obtain the true volume filtered, the calculated volume accepted for each station is adjusted by the correction factor E obtained from:

$$E = \frac{\text{observed revolutions per second of flowmeter on the sampling station}}{\text{calculated revolutions per second in free flow at sampling station speed}}$$

in which the denominator is obtained by using the regression from the free flow calibration described above. Thus,

volume filtered = litres per second accepted in free flow x duration (s) x E.

The above method was used for the 1976 survey. Subsequent calibrations have shown that the relationship between volume filtered and revolutions per second of the flowmeter can be used with confidence for conditions of up to 75% clogging of the net. This method is independent of shipboard measurements of both distance towed and ship's speed in the range 3-7 knots, so it avoids the potential source of error inherent in measuring distance and speed accurately.

The calibration regression of the volume accepted by a 30″ sampler with a net is:

$y = Ax + B$,
where y = volume accepted ($1\ s^{-1}$),
x = revolutions of the flowmeter (metal blades) per second.

The constants were, for the 16 inch (40.6 cm) nose cone, $A = 143.6342$, $B = 9.7057$, and the regression coefficient was 0.9979

3.2.3 Collection and fixation

The samples collected at sea by the main net and by the two auxillary samplers were each washed carefully from the net into the collecting bag on the end of the net. The sample was then transferred to a glass storage jar, labelled and fixed by the addition of 40% sodium acetate buffered formalin, in the ratio one part fixative to nine parts sample plus seawater. (Preservation in buffered 4% formalin is recommended (Anon, 1984) to prevent shrinkage of fish larvae.) The fixative was lightly coloured

Table 3 Results of sub-sampling tests using 20ml and 30ml scoops

	Eggs			Larvae	
	3mm diam.	1-1.4mm diam.	1mm diam.	*Lophius*	Sandeel/ clupeids
	Actual numbers in sample				
	500	1000	450	500	500
Experiment 1					
Sample volume (S.V.) 800ml					
Aliquot volume (A.V.) 20ml					
Arithmetic mean (*)	532.93	1047.20	446.00	566.20	540.93
Standard deviation (s.d.)	54.42	130.31	41.71	74.87	54.62
Coeff. of variation (c.v.)	10.21	12.44	9.35	13.22	10.10
95% confidence interval (C.I.)	30.14	72.17	23.16	41.46	30.25
Number of sub-samples (n)	15				
Experiment 2					
S.V. 600ml					
A.V. 30ml					
*	515.67	1036.20	444.33	545.00	529.87
s.d.	55.71	86.51	27.12	56.68	63.94
c.v.	10.80	8.35	6.10	10.40	12.07
C.I.	30.85	47.91	15.02	31.39	35.41
n	15				
Experiment 3					
S.V. 600ml					
A.V. 20ml					
*	545.33	1085.20	437.33	535.07	501.20
s.d.	68.69	93.43	44.60	55.96	50.03
c.v.	12.60	8.61	10.20	10.46	9.98
C.I.	38.04	51.74	24.70	30.99	27.71
n	15				
Combined results					
*	531.31	1056.20	442.56	548.76	521.78
s.d.	59.85	104.94	37.88	63.04	57.85
c.v.	11.26	9.94	8.56	11.49	11.09
C.I.	17.49	30.66	11.07	18.42	16.90
n	45				

before use by the addition of a small quantity of eosin, to facilitate checks on the presence of fixative in a sample. Before any sorting of the main net samples, wet plankton volume was measured by displacement, to give a rough measure of zooplankton biomass. At the same time the fixative was replaced with a preserving fluid which could also be used for sample sorting (Nichols and Wood, 1978).

3.2.4 Sorting and sub-sampling

Whenever practicable, the whole main net sample was sorted for fish eggs and larvae. Sub-sampling was limited to those samples containing exceptionally large numbers of eggs or larvae. The rules for sub-sampling were:

i. that a proportion greater than one fifth was not acceptable; and

ii. that the proportion had to contain at least one hundred specimens of the appropriate group, species or devlopment stage of organisms being counted.

The device used for sub-sampling the main net sample was usually a measured scoop of either 20 ml or 30 ml: it was the only device used to sub-sample for fish eggs and larvae. The scoop was used to remove a series of aliquots from the sample made up to a known volume, (normally between 600 and 3000 ml) dependent on zooplankton biomass. The performance of the scoop was tested by an experiment in which a series of fifteen sub-samples was taken for each of three egg sizes and two larval types. A known number of each group was introduced into a general zooplankton sample which was then made up to 600 ml total volume by the addition of preserving fluid. All of the plankton sorting staff then took a series of sub-samples using both the 20 ml and 30 ml scoops. The same sample, including the returned sub-samples, was subsequently made up to 800 ml total volume and the sub-sampling routine repeated with only the 20 ml scoop. The sorting and counting of all the sub-samples was done by one person throughout the experiment, irrespective of who had taken the sub-sample. Table 3 is a summary of the results of the experiment. The coefficient of variance was greater than 12% on four occasions but, when the results are combined for the three experiments, the coefficient of variance is less than 11.5% for all groups. This analysis has shown that the errors involved in sub-sampling with the scoop, for this range of egg sizes and larvae, are acceptable at the 95% confidence interval.

Even when it was practicable to sort a whole sample, it was sometimes necessary to take aliquots of the sorted material to examine microscopically for specific identification. For example. some samples contained many hundreds of plaice eggs which could be sorted easily by eye, but for morphological staging only one hundred eggs were examined, the remainder being counted and the numbers by stage raised accordingly. Similarly, for fish eggs with no specific features other than size to aid identification, only one hundred eggs would be measured, the remainder being counted and apportioned to each size category according to the proportions in the one hundred. The polymodal egg size frequency distributions were then analysed in relation to area, time of the year and occurrence of larvae in the same sample to identify the major species present.

The Stempel pipette (Hensen, 1887) was the only other device used for sub-sampling from the main net samples. Stempel pipettes of between 1.0 ml and 10.0 ml were used to remove aliquots from which all brachyuran decapod larvae were sorted and identified. Edible crab larvae were further sorted into five zoeal and one megalopa stage, to examine their distribution abundance and stage to stage mortality (Nichols, Thompson and Cryer, 1982).

3.2.5 Vertical distribution

On selected cruises, after completing the standard grid of plankton stations, the major egg and larvae distributions could be roughly defined. The centre of these distributions was chosen as the position of a station for examination of the vertical distribution of fish eggs and larvae and of other zooplankters. The Lowestoft multipurpose plankton sampler with a net changing mechanism (Harding *et al.*, 1971) was used for these

Table 4 Dates, positions and major species of fish eggs and larvae collected by the Lowestoft multipurpose plankton sampler with changing net.

Cruise No.	Date (1976)	Position	Species														
			Sprattus sprattus	*Merlangius merlangus*	*Gadus morhua*	*Onos* spp.	*Ammodytes* spp.	*Scomber scombrus*	*Callionymus* spp.	*Limanda limanda*	*Platichthys flesus*	*Pleuronectes platessa*	*Microstomus kitt*	*Hippoglossoides platessoides*	*Nephrops norvegicus*
3	24-25 Feb	54°05′N 00°36′E	O	O	O		L			O		O			
5	11-12 Apr	54°06′N 00°40′E	O,L	O,L	O,L		L			O,L		O,L			
6	29-30 Apr	54°37′N 00°08′W		O	O		L		O	O,L		O			
8	3-4 Jun	54°51′N 01°05′W	O,L	L	L	O,L	L		O,L	O,L	L	L		L	L
11	23-24 Aug	54°22′N 00°38′W	L	O		L		L	O,L				L		L

O eggs; L larvae

studies. The sampler was deployed into four pre-selected depth bands at 4 h intervals throughout a 24 h period. Results are shown in Table 4; unfortunately, electrical failures on the sampler resulted in only five valid series being completed throughout the year.

3.2.6 Replicate hauls with the standard 30" plankton sampler

As part of the general routine on eight of the surveys the repeatability of a single sampling haul was examined to study sampling error. The sampler was fished normally for ten consecutive hauls in the same discrete body of water, and the haul to haul variance estimated. These replicate hauls were normally done in areas of high egg or larval density. The samples were processed in the normal way with the standard samples for fish eggs and larvae. Numbers of each species or stage per replicate haul were converted to numbers per square metre. The mean numbers per square metre and the coefficient of variation for each series of replicates was calculated and are presented in Table 5. These data can be used to provide an estimate of the error on seasonal production curves of eggs and larvae. The consistently high variation for both eggs and larvae indicates an unavoidable level and source of error inherent in this type of plankton sampling. It is probable that the major contributing factor is plankton patchiness. The effects of the error can be minimised by increasing the concentration of sampling points, particularly in areas of known egg and larval abundance - a concept which was incorporated into the original design of these surveys.

3.2.7 Neuston samples

A neuston net was also used on the surveys between July and November to sample specifically for lobster larvae. On the first survey, a net was used, based on the design given by Ben Yami *et al.* (1970) for a side-tracking neuston net. Its mouth opening was 1.0 x 0.25 m and its

Table 5 Results from replicate hauls made with the standard plankton sampler on selected cruises in 1976

Species and Stage		Cruise 2		5(i)		5(ii)		6		7		8		10	
		$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v
(a) Fish eggs															
Pleuronectes platessa	I	10.8	77.6	28.2	31.5			27.2	40.2						
	II	5.9	126.8	15.4	37.6			28.3	25.1						
	III	11.2	50.4	20.7	37.8			24.8	31.5						
	IV	8.8	45.1	15.4	48.7			20.9	16.0						
	V	2.5	73.6	26.5	23.6			61.5	20.2						
Mean			74.7		35.9				26.6						
Total		39.6	51.9	108.3	16.2	1.1	76.4	165.0	7.1	1.2	31.4				
Gadus morhua	I	17.8	45.9	18.8	15.2	9.8	22.5	17.5	20.4						
	II	6.3	71.7	5.8	43.5	1.8	59.4	8.3	26.2						
	III	10.9	41.4	5.2	52.8	2.2	42.8	11.0	22.6						
	IV	6.3	47.5	1.8	67.7	1.2	71.5	4.9	37.1						
	V	1.7	86.4	1.0	68.1	0.5	74.2	2.5	39.8						
Mean			58.6		49.5		54.1		29.2						
Total		43.1	29.0	32.5	22.0	15.6	20.0	44.1	15.0						
Sprattus sprattus		47.2	49.1	223.9	39.5	8.6	98.1			27.6	39.6	15.2	35.3	5.0	65.8
Callionymus spp.								8.4	24.0			4.9	30.8	2.6	57.9
Trigla spp.								3.6	26.4						
Trachurus trachurus										5.3	44.4				
Scomber scombrus														1.8	121.1
Number of replicates		10		10		10		10		10		10		10	

$\bar{x}$ mean of 10 samples; v variance expressed as a percentage.

Table 5 continued

Species and stage		Cruise 2		5(i)		5(ii)		6		7		8		10		11		13	
		$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v	$\bar{x}$	v
(b) Fish and *Nephrops* larvae																			
Pleuronectes platessa	I	0.95	80.8	3.1	62.4	0.4	129.1	8.5	28.5	0.8	88.8								
	II					1.6	61.0			2.7	64.1								
	III					0.9	65.3			0.8	82.3								
	IV											1.6	56.8						
Total		1.0	80.7	3.9	66.5	3.0	44.1	9.3	31.2	4.3	47.0	2.4	31.5						
Gadus morhua		0.5	98.2	0.5	79.5	8.4	25.4												
Merlangius merlangus						3.4	27.9					7.0	19.2			0.9	54.0		
Ammodytes spp		2.6	55.7			62.3	53.5	3.1	47.5							5.2	34.0		
Limanda limanda				0.4	118.1	195.1	29.3					3.5	61.8			8.0	29.8		
Hippoglossoides platessoides												2.4	67.1						
Microstomus kitt																1.4	51.4	2.2	56.1
Sprattus sprattus				3.2	114.3	2.2	116.3							144.1	63.2				
Clupea harengus																		11.0	31.8
Scomber scombrus														6.1	49.8				
Trachurus trachurus																1.2	66.2		
Callionymus spp.																4.8	51.6		
Onus spp.																		4.1	38.1
Arnoglossus laterna																3.9	32.2		
Nephrops norvegicus												8.9	44.5						
Number of replicates		10		10		10		10		10		10		10		10		10	

$\bar{x}$ mean of 10 samples; v variance expressed as a percentage.

filtering net was a four-panelled, nylon mesh (aperture 270 μm and porosity 46%) funnel tapering to a meshed cod-end bucket. The net was towed at 2.5-3.0 knots for approximately 10 min on each station.

On the second and subsequent surveys the net used was a 2m diameter ring net based on the net described by Southward (1970) for use as a young fish trawl. Its terylene mesh was of aperture 670 μm square (1070 μm diagonally) and porosity 45%. The conical filtering net was 6 m long ending in a bucket 20 cm in diameter. The net was towed 75 m behind the vessel which steamed at 2.5-3.0 knots with approximately 10° of starboard rudder, to keep the net out of the propeller wake. The ring frame was held at the surface by two polythene floats, one on either side ensuring that only half the frame was submerged during fishing.

The attempts to catch lobster larvae in the survey area were initially aimed at examining the sampling problems and adding to our very limited knowledge of their occurrence. Lobster larvae were found in 42 of the 168 hauls with these nets, which also provided information on the distribution of the neustonic turbot larvae. Altogether, 133 lobster larvae in all four planktonic stages were caught. The exercise was the first successful attempt to examine the temporal and spatial distribution of the larvae of *H. gammarus* (Nichols and Lawton , 1978), but the low numbers of larvae caught clearly indicated a quantitative sampling problem and a need to examine the vertical, diurnal distribution of the larval phase.

3.3 Fish sampling

Samples of fish were sought primarily in order to determine the major predators on fish eggs and larvae. A secondary, unrelated aim, was to collect specimens for metals analysis.

To identify areas within the plankton survey grid where pelagic fish were abundant, a Kelvin Hughes MS29, 50 kHz echo-sounder was run continuously. The paper record was subsequently examined to find areas where dense echo traces coincided with high numbers of eggs or larvae of plaice or cod. Fish were sampled in the selected areas using the international young gadoid pelagic trawl described by Hislop (1970). This trawl was fitted with a headline transducer connected to a Kelvin Hughes MS 44 echo-sounder on the bridge of the towing vessel, to enable the fishing depth to be controlled. Each tow consisted of fishing the net for 20 min in each of three levels: near bottom, midwater and near surface (Daan *et al.*, 1975). Tows with this trawl were made on all surveys between February and the end of August. They were made at all times of the day and night but with particular emphasis just after dawn and at dusk.

The small fish in the trawl were sampled randomly with approximately 50 fish comprising a sample of such species as sprat, herring, anchovy and sandeels. They were fixed whole in 10% buffered formalin, after injecting 4% formalin into the gut cavity of those fish more than 10 cm long. Other fish, of which the majority were whiting, gurnards and dab, were measured and the stomachs from a stratified sample comprising three fish per 1 cm length group were removed and fixed individually in 10% buffered formalin. The stomach contents were subsequently examined back at the laboratory, where all the food organisms present were recorded and an attempt made to quantify them by number and volume.

In addition to the International Young Gadoid Pelagic Trawl (IYGPT) tows, the Lowestoft 2 m^2 frame trawl was used extensively over the survey grid to sample O-group fish in their pelagic phase, thus identifying potential nursery areas. This trawl was designed to be operated both on or close to the sea bed and in midwater (Walker and Davies, 1986). It was towed at 3 knots on a single 20 mm warp, with four 6.0 m long, corner-attached, 10 mm wire bridles. After calibration of depth against warp out, using Kelvin tubes, the net was fished on double oblique tows from the surface to the sea bed and return. Catches of fish in this net were generally low, enabling the whole catch to be fixed in 10% buffered formalin and returned to the laboratory for identification and measurement.

3.4 Data processing

A list of all the stations occupied during the surveys is given in Table 6. Preliminary analysis and data processing for most of the samples collected has been completed and some of the results have already been published in many of the papers listed in the references (Section 6) of this report. Only the plankton samples have been archived; these are available for further analysis.

Table 6 Summary of the number of stations occupied and data collected during the 1976 north-east coast ichthyoplankton surveys

	Cruise											
	2	3	4	5	6	7	8	10	11	12	13	15
30-inch, high-speed plankton sampler												
– survey grid	70	100	88	102	86	93	93	100	94	124	130	116
– replicate hauls	10			20	10	10	10	9	10		10	
Surface nutrients	70	100	88	102	86	93	93	100	94	124	78	116
Changing net		7		7	7		8		8			
Neuston net								30	47	15	32	39
Pelagic frame trawl								20	57	22	28	29
Midwater trawl	3	10	4	11	12	13	16	3	5			
Nansen water bottle casts		7		7	5	5	4	2	4			
Quanta-spectrometer casts	1	3	1	8	3	3	6	2	4	2	1	
No. of seabed drifters released	700	700	650	700	700	800	800	800	800	750	700	700
Continuous monitoring nautical miles (all sensors)	1150	1200	1100	1200	1048	1200	1142	1000	1339	1800	1975	1247

The auxillary fine net samples contain the larger phytoplankters and micro-zooplankton which include, most importantly, the nauplii, copepodid and adult stages of copepods. Only the dinoflagellates from selected surveys (J.D. Dodge, personal communication) and phytoplankton from selected stations on each survey (Horwood *et al.*, 1982) have so far been examined.

4. Results

4.1 Hydrographic observations

4.1.1 Current meters

The six current meter rigs deployed in the western central North Sea between January and October 1976 formed part of a larger JONSDAP network, which was linked to a production experiment (FLEX) conducted during the spring plankton bloom on the Fladen Ground in the northern North Sea (Ramster 1977a).

The results from the six current meters have been summarised in two ways:

(a) as mean residuals for the cruise and inter-cruise periods (Figure 3);

(b) as seasonal means for winter and summer periods (Figure 4). The Hunter stream function (Hunter, 1972) was used to model the circulation for interpretation of the winter and summer vector fields (Figure 5) (Ramster, 1977b).

The winter was dominated by a persistent north-west drift north of Flamborough Head and by an anticyclonic gyre off the Lincolnshire coast (Ramster, 1977b). Analysis of the vector fields over short periods of time in March shows that there was considerable day to day variation in the residual drift due to wind speed and direction (Riepma, 1980). At that time of the year the water column is homothermal and 'en masse' movements occurred at moderate or slow velocities, for example, residual velocities of 2-3 km day^{-1} were measured.

In the marine summer on the other hand, when the deep water north of Flamborough Head was strongly stratified, the residual drift was generally offshore to the east and north-east at the surface and onshore to the west and south-west at the bottom. In shallow water south of Flamborough Head, the offshore drift was also

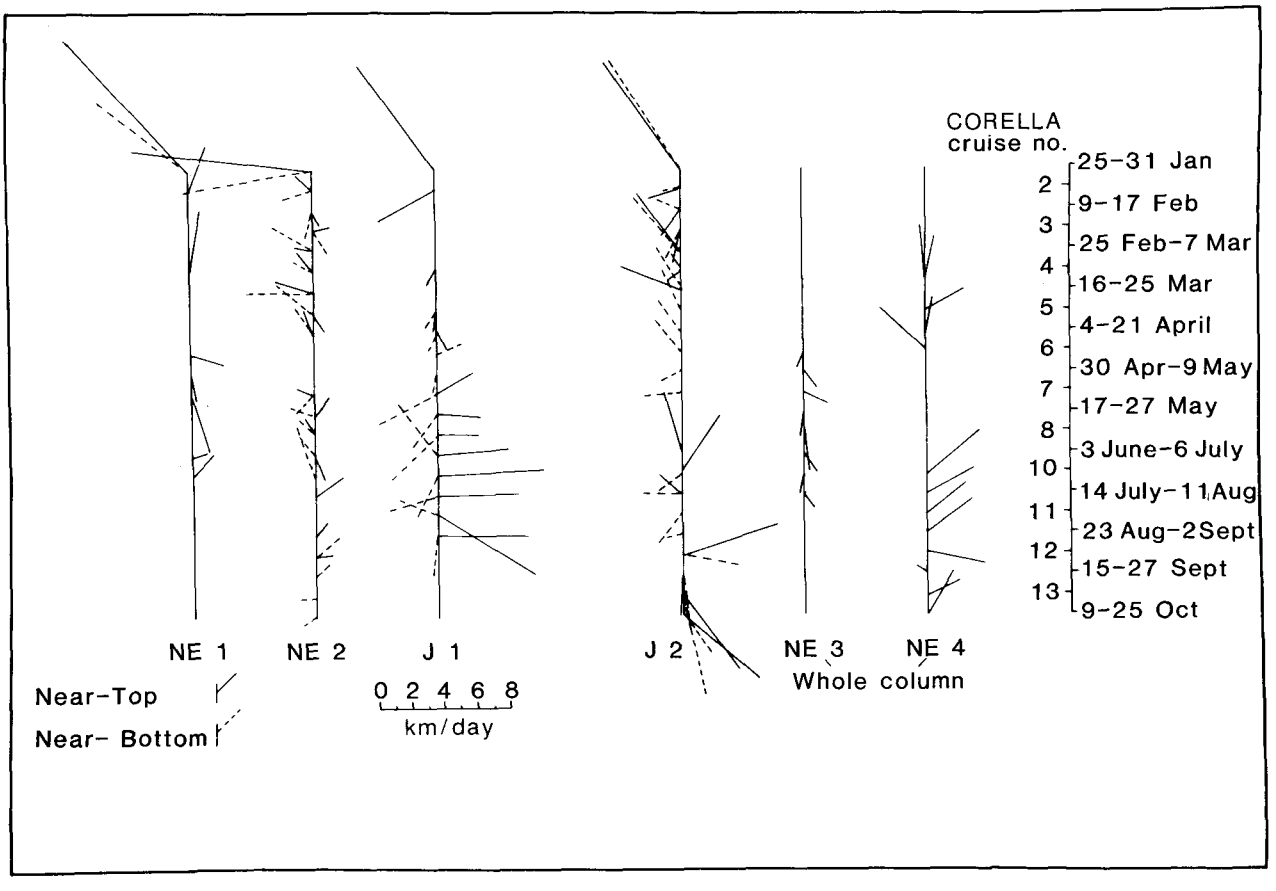


Figure 3 Mean residuals from the six moored current meter stations for the periods of the larvae surveys and intervals between surveys in 1976.

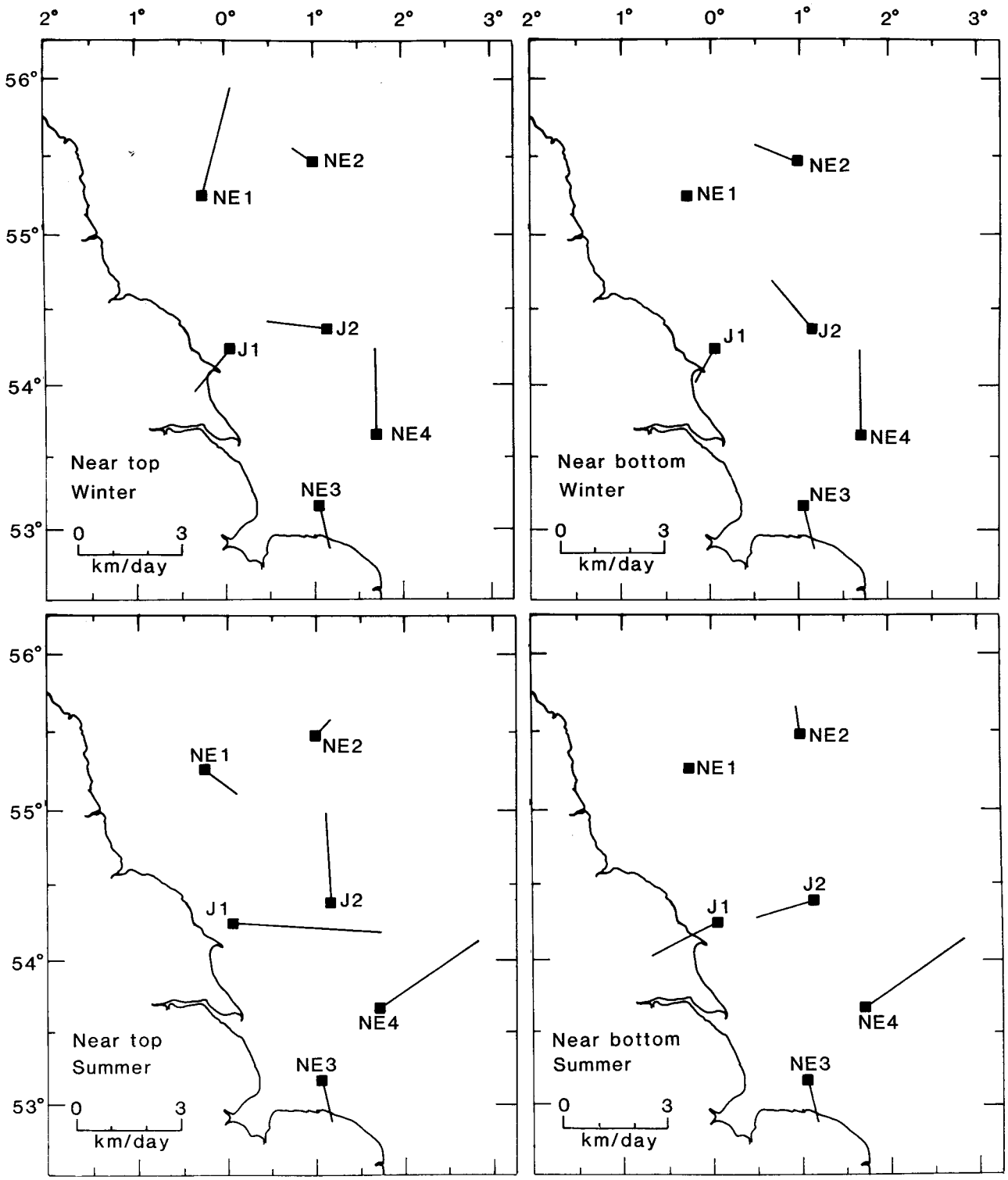


Figure 4 Seasonal mean residual drift at each moored current meter station in winter (February-April) and summer (May-September) 1976.

to the east and north-east while in coastal waters the drift was to the south and east. At that time the residual velocities were much greater over the whole region and the offshore transport of surface water resulted in a compensating onshore movement of bottom water which upwelled along the north-east coast and over the shallow Norfolk banks and the Dogger Bank. Surface residual velocities ranged from 5-8 km day^{-1} while bottom residual velocities were lower at 3-6 km day^{-1} between June and September.

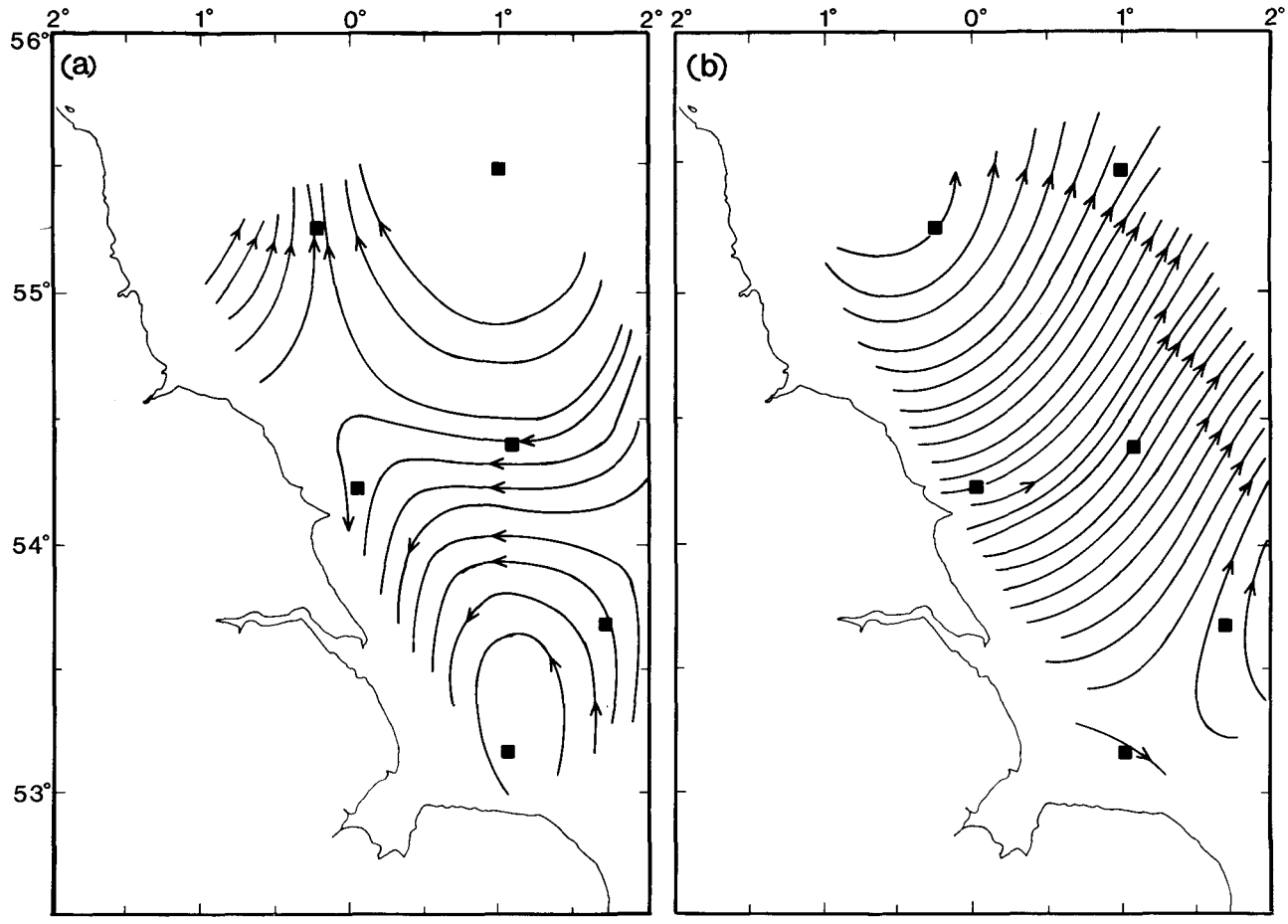


Figure 5 Model of the near-surface residual flow (Hunter/Lawrence stream function) derived from moored current meters (■): (a) in winter (February-April); and (b) in summer (May-September) 1976.

4.1.2 Seabed drifters

The principal features of the seabed drifter returns (Ramster and Jones, 1978) are illustrated in Figures 6 and 7 and are summarised as follows:

(a) returns from release stations within the coastal zone, i.e. up to 30-40 nautical miles offshore (groups A and B in Figure 2) were usually from the south-west quadrant, while returns from further offshore (group B) were usually from the east or south-east quadrants;

(b) returns from releases at each station were consistent in time and space and varied seasonally;

(c) returns from coastal regions were patchy with some zones of high incidence of return and other zones barren;

(d) beach returns from inshore station releases were most numerous in periods immediately following release, and the greatest numbers of returns were in the September-May winter period from March-August releases;

(e) drifters released offshore in February-April were not returned from beaches until 4-7 periods (see key to Figure 6) after release, whereas those from offshore in May-October reached the beaches within 1 or 2 periods after release;

(f) in general, the return patterns from most coastal station releases in February-April were different from those from coastal releases in May-October when the southerly component in drift increased;

(g) offshore, the drift changed from north-west in the early part of the year to a more southerly direction in summer-autumn;

(h) an increased speed of residual drift was coupled with the seasonal directional changes between spring and summer;

(i) a single release in November suggested a return to the February-April regime.

The seabed drifter returns indicate that there were two distinct residual regimes in the western central North Sea, corresponding to marine winter (November-April)

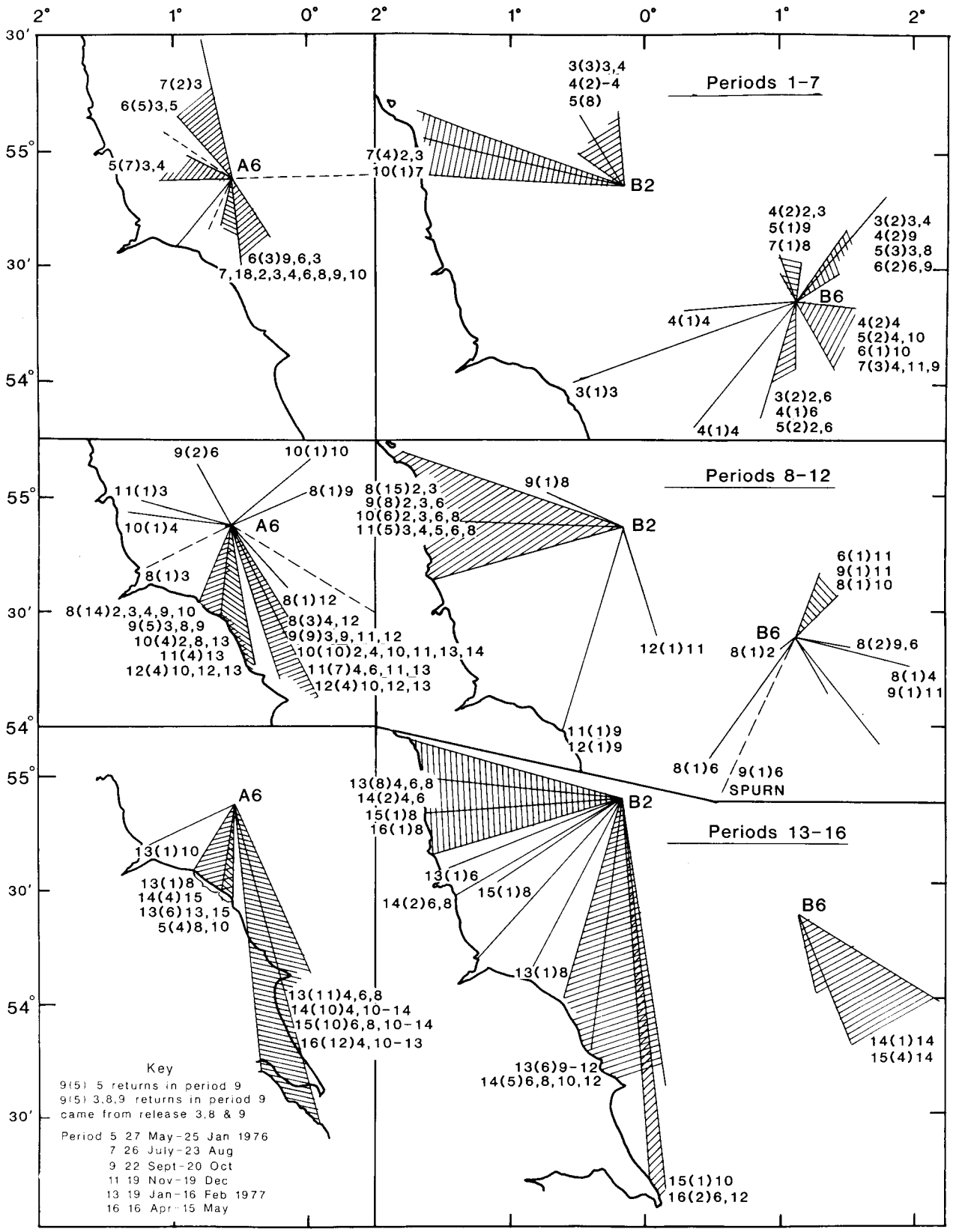


Figure 6 Seabed drifter returns from release points A6, B2 and B6, typifying results from inshore and offshore zones in 1976.

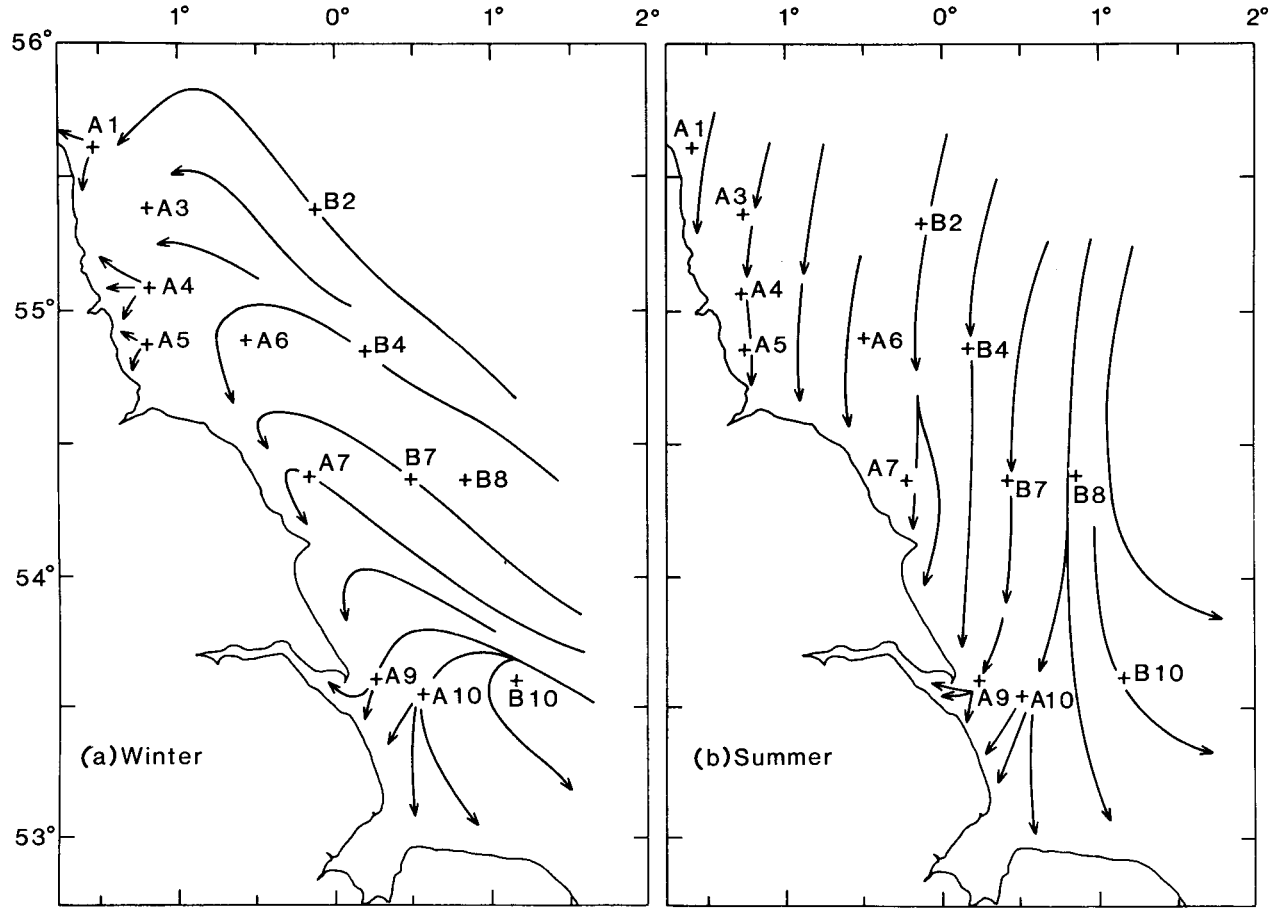


Figure 7 Deduced near-bottom circulation (from returns of seabed drifters) off the north-east coast of England: (a) in winter (February-April); and (b) in summer (May-September) 1976.

and summer (May-October) seasons (Figure 7). These seasons corresponded closely with those deduced from the moored current meter network, although the Lagrangian patterns of drift deduced from the seabed drifters do not agree completely with Eulerian drift regimes suggested by current meter data. The Lincolnshire gyre was evident in both sets of data, as was the increased velocity of residual flow in the summer months.

4.1.3 Environmental sensors and water samples

The distributions of environmental features are shown in Figures 8 and 9. In winter and early spring, the whole water mass in the survey area was mixed from surface to bottom. A tongue of warmer, highly transparent water with salinity in excesss of 34.8‰ lay offshore in the deeper water to the north of Flamborough Head ; the coastal water and water over the Norfolk banks and Dogger Bank was colder, of lower transparency and less saline. Nutrient levels were high and characteristic of the winter period: the highest values were recorded near the coast in less saline water, with particularly high values near the Humber, Tees and Tyne river estuaries. Chlorophyll *a* values were low ($< 1\ \mu g\ l^{-1}$) on the early cruises: highest values were over the Norfolk banks and Dogger Bank.

In late spring, the surface water started to warm up rapidly and a thermocline had already developed in the deeper water in April. Phytoplankton production increased and the spring bloom reached its maximum in early May and then declined in the photic zone above the thermocline in the deep water. In mixed coastal water and on the Norfolk banks phytoplankton production continued at a higher rate into the summer months.

In summer 1976, the temperature of the surface water was high - above 20°C offshore in August. The water column was strongly stratified in the deep water to the north, but usually well mixed in shallow coastal waters and over the banks. A tongue of warm water of high transparency and high salinity extended above colder, deep water in a south-westerly direction from latitude 56°N longitude 2°E to the coast at Whitby. Cold, mixed water occurred close inshore near the Farne Islands and in Filey Bay. It also extended offshore from Filey Bay for 40 nautical miles to the south-east, indicating that upwelling from the pool of deep, cold, bottom water and mixing had taken place there.

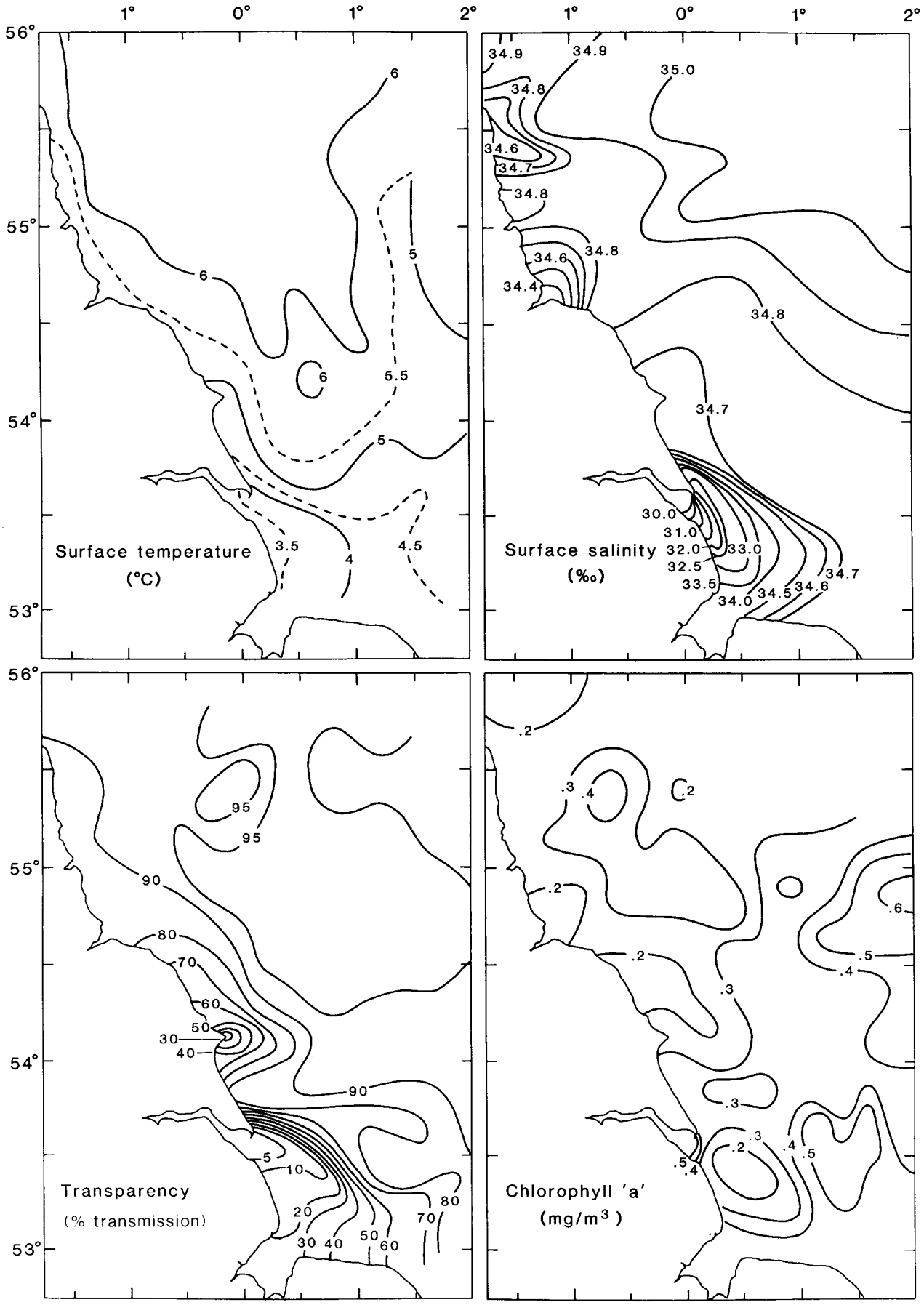


Figure 8 Spatial variation of environmental variables in the surface water off the north-east coast of England in March 1976.

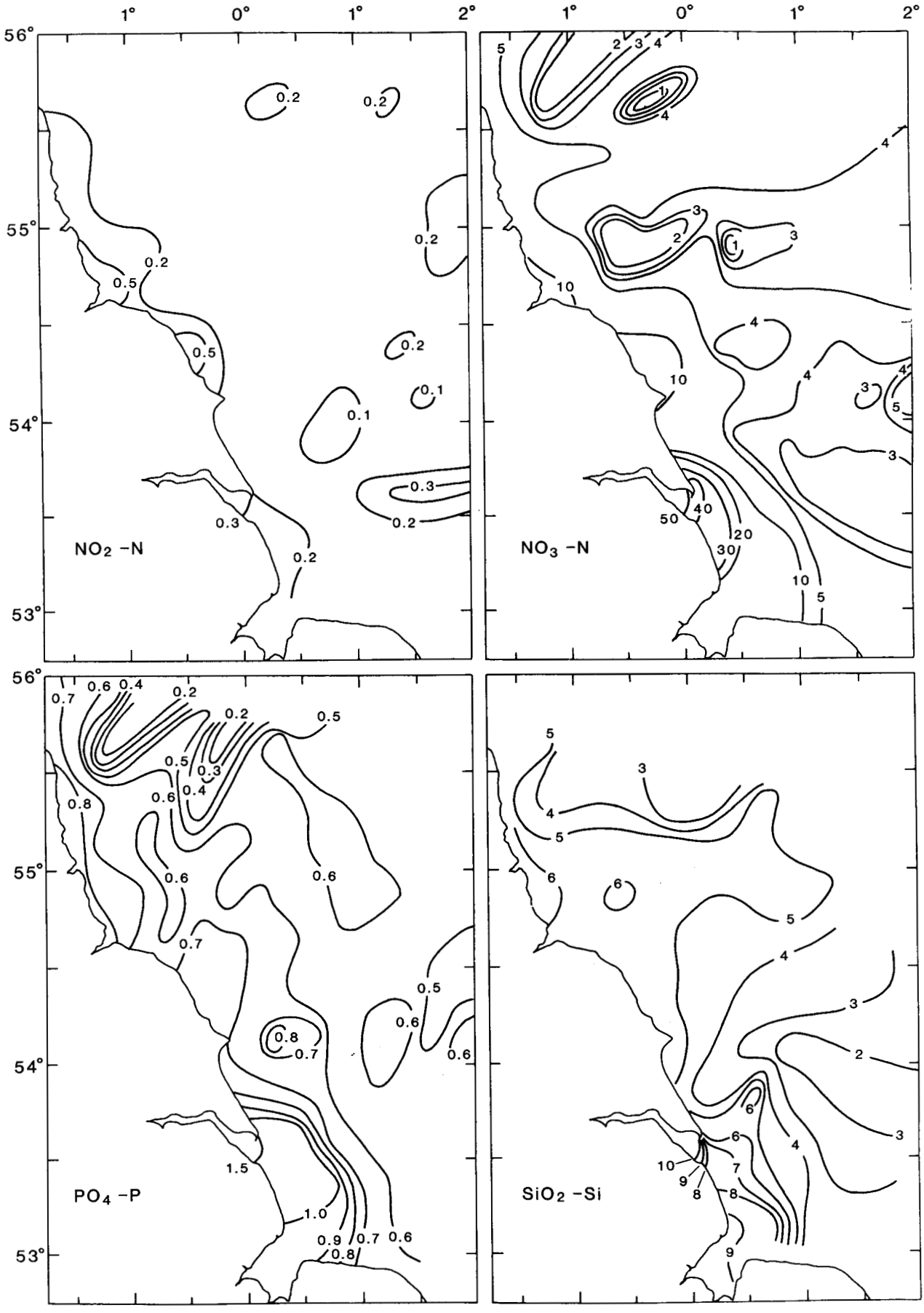


Figure 8 Continued.

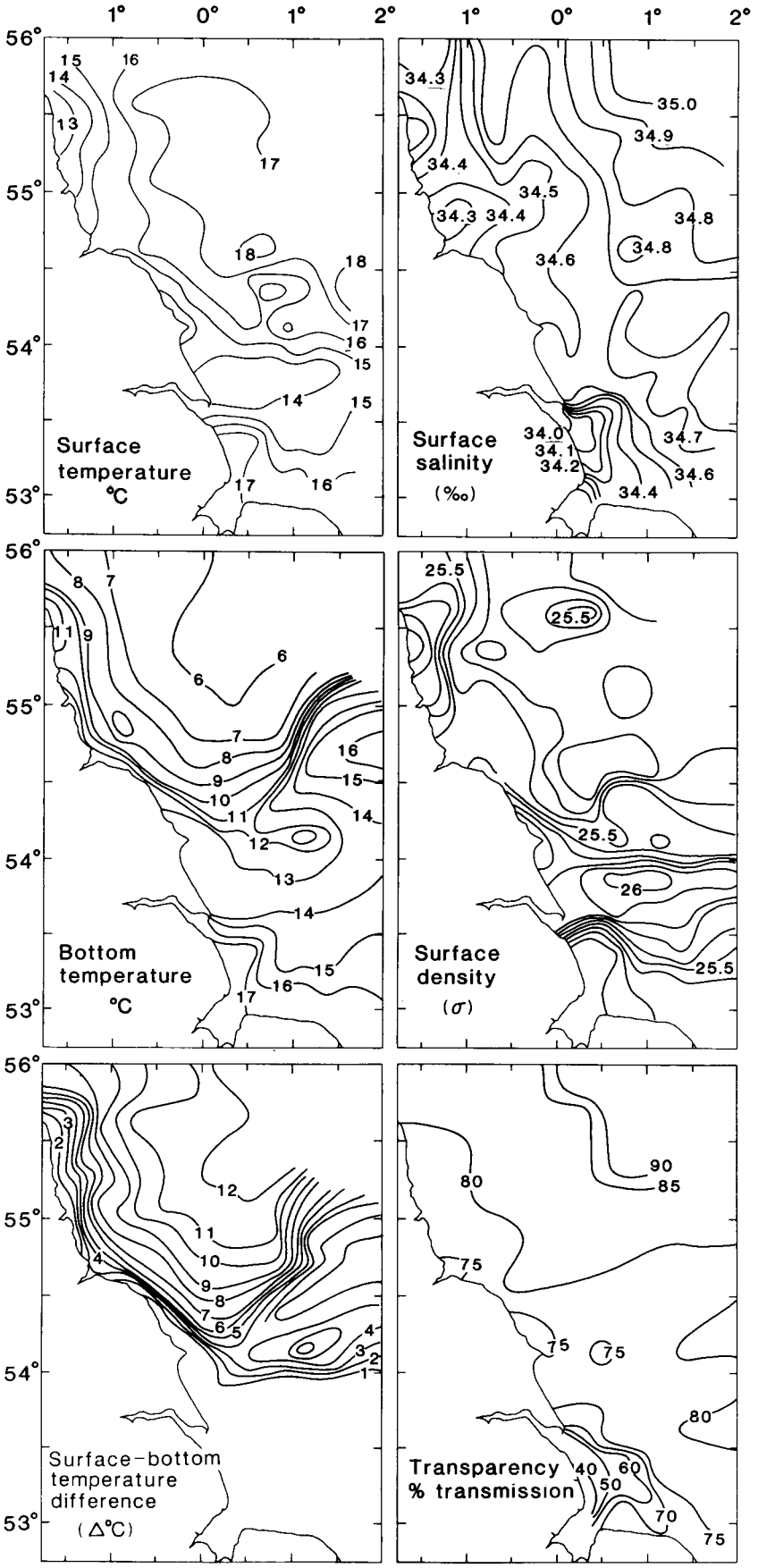


Figure 9 Distribution of environmental variables in July 1976.

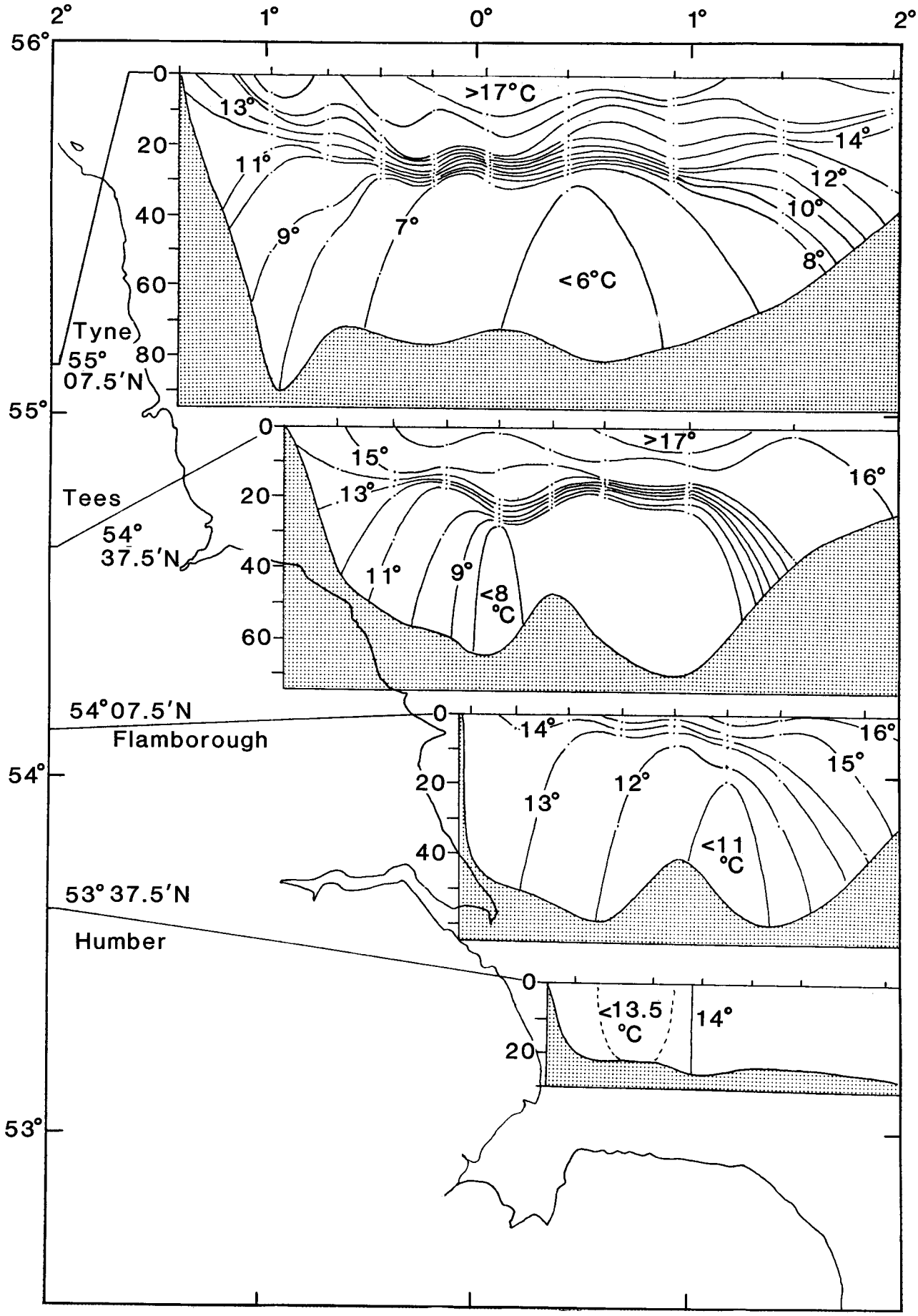


Figure 10 Transects showing the vertical temperature structure off the coast of England in August 1976.

Summer temperature sections at different latitudes showed the isotherms tilted upwards near the coast and Dogger Bank and demonstrated the existence of a strong frontal system which separated the mixed coastal and Banks waters from the stratified deep water (Figure 10). This front was 10-15 nautical miles offshore and parallel to the coast north of Tees Bay; it came much closer inshore near Whitby and continued parallel to the coast to Flamborough Head before extending eastwards along the 40 m depth contour towards the south-west corner of the Dogger Bank. Here, the front diverged into two arms, one extending eastwards to the south of the Dogger Bank, the other following the western edge of the Dogger Bank in a north-easterly direction. Infra-red photographs taken from satellites confirm the structure of this frontal system in summer (Figure 11).

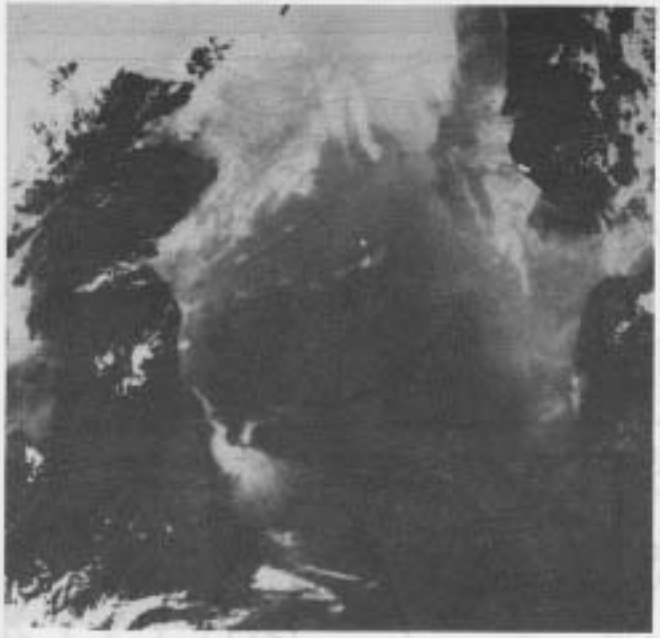


Figure 11 Thermal infra-red image from satellite, showing fronts in the North Sea in 1976.

Summer nutrient levels were extremely low in offshore surface waters, the highest values being associated with frontal mixing zones, where upwelling of nutrient-rich bottom water occurred, and with river inflows. Chlorophyll *a* levels were also highest in shallow, mixed water near the coast and on the banks, the highest values being associated with the upwelling and mixing of water masses along the front and with river inflows.

Autumn gales cooled the water column rapidly in September, so thermal stratification broke down and the frontal system moved further offshore. Mixing between surface and bottom water increased, nutrient levels were enhanced throughout the water column and a second burst of phytoplankton production occurred in the coastal mixing zones and over the deeps north of the Dogger Bank.

4.2 Biological observations

4.2.1 Chlorophyll a and phytoplankton

Phytoplankton blooms, expressed in terms of chlorophyll *a* in the surface waters, tended to be patchy throughout the area in winter and during the build-up to the spring bloom. In spring, the phytoplankton bloom extended throughout the survey area but, again, patches of high biomass indicating high production were to be found in coastal waters adjacent to river inflows and over the banks. In summer, the phytoplankton was entirely confined to coastal, mixed water but spread throughout the survey area again following the autumn overturn (Figure 12).

Examination of results, broken down into blocks of 1° E/W x 45′ N/S, shows that the seasonal pattern of primary production, as indicated by changes in chlorophyll *a* biomass, varies considerably between different locations (Reynolds, 1978). Two peaks of production, one in spring and a second in autumn, ocurred in stratified deep water to the north-east of Flamborough Head; in banks water there was an extended spring bloom, while in coastal and banks waters affected by upwelling and mixing associated with the frontal system there were one or more peaks of production in the summer months following closely after the main spring bloom.

Nutrient depletion at the surface was closely associated with the spring phytoplankton bloom. This was illustrated by Reynolds (1978) who plotted the mean concentration of silicate in each of the 1° E/W x 45′ N/S blocks against the mid-cruise date. Silicate was high in the winter and early spring but declined rapidly in the late spring to an extremely low summer level, then, following the autumn overturn, recovered to reach the high winter levels once again. The spring decline in silicate depends upon its utilisation by diatoms which dominated during the spring bloom; the autumn recovery to high winter levels of silicate indicated that silicate was not utilised to the same extent during the autumn bloom when large diatoms were less numerous.

Phytoplankton counts, made on samples taken with a fine mesh net (35 μm mesh) over deep water east of the river Tyne, were judged to represent the algal flora of the deep water mass which stratified in summer. The results of these counts have been used to describe the relative abundance and succession of phytoplankton species. The seasonal changes in abundance confirm the occurrence of two peaks for diatom abundance corresponding directly with high chlorophyll *a* values in spring and autumn, and inversely with nutrient depletion at the surface in summer. Dinoflagellates were dominant in the phytoplankton population during the summer months (Horwood *et al.*, 1982).

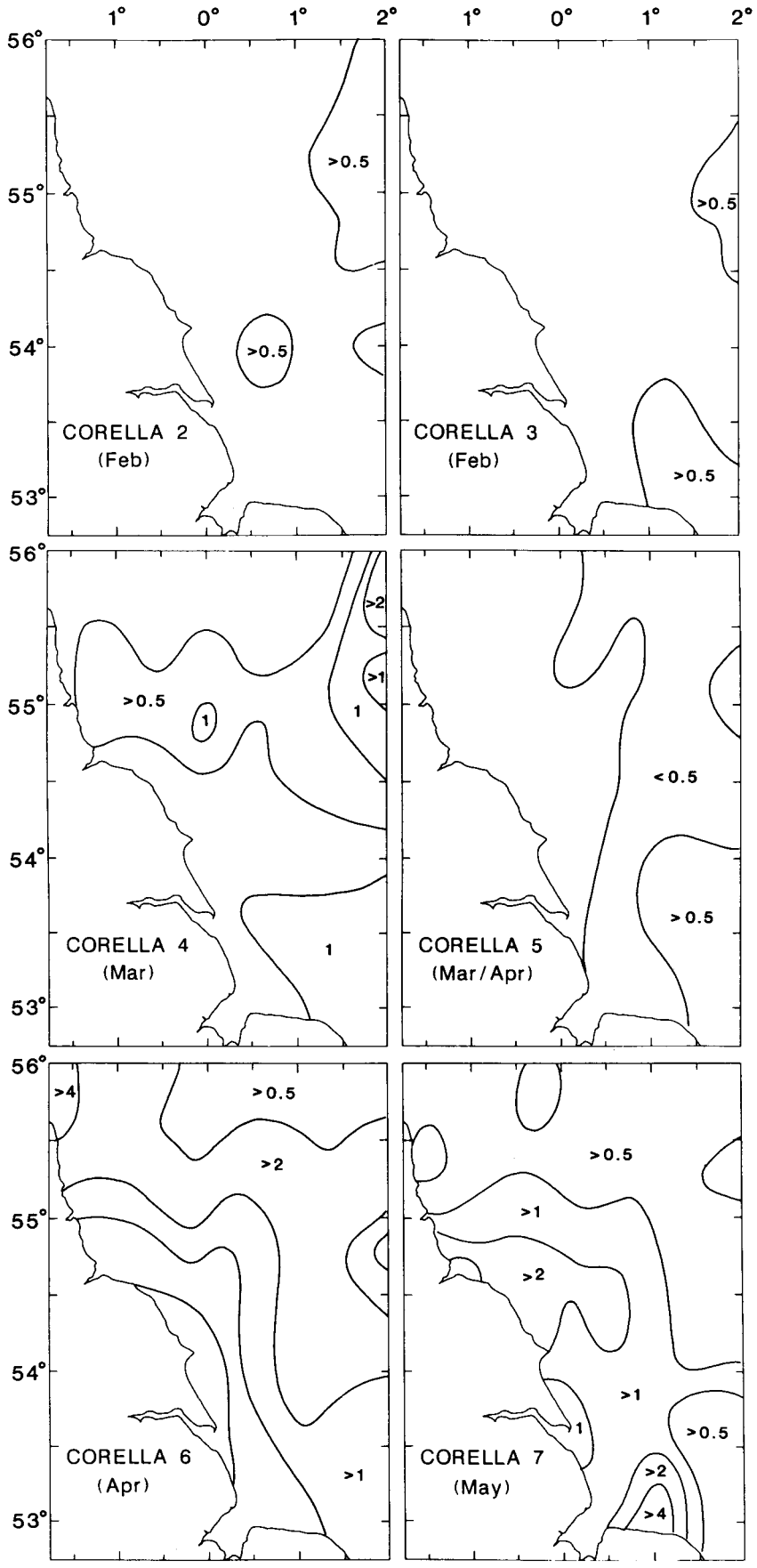


Figure 12 Distribution of chlorophyll *a* in sub-surface water on successive cruises in 1976, illustrating the seasonal variation of this parameter.

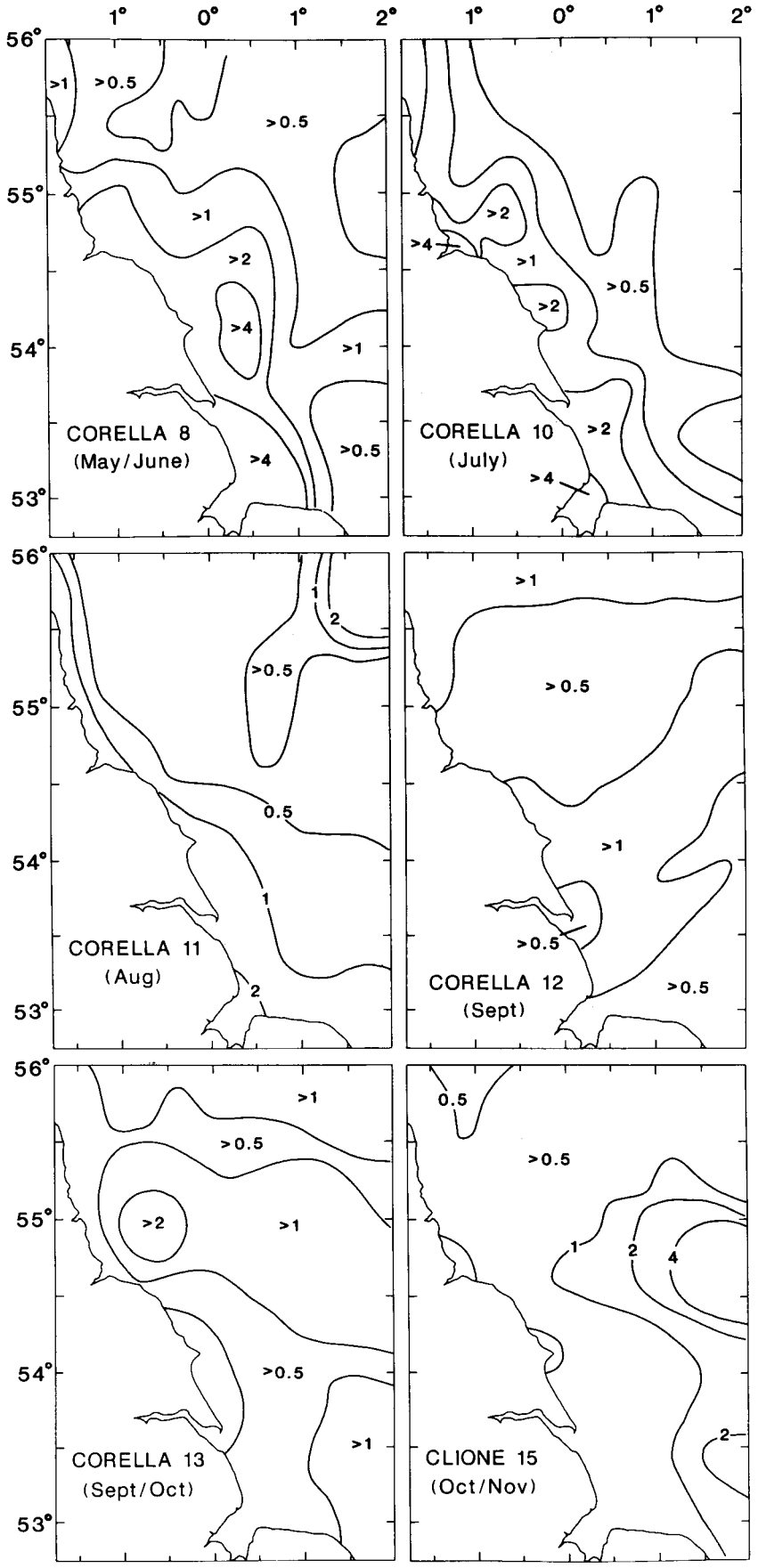


Figure 12 Continued.

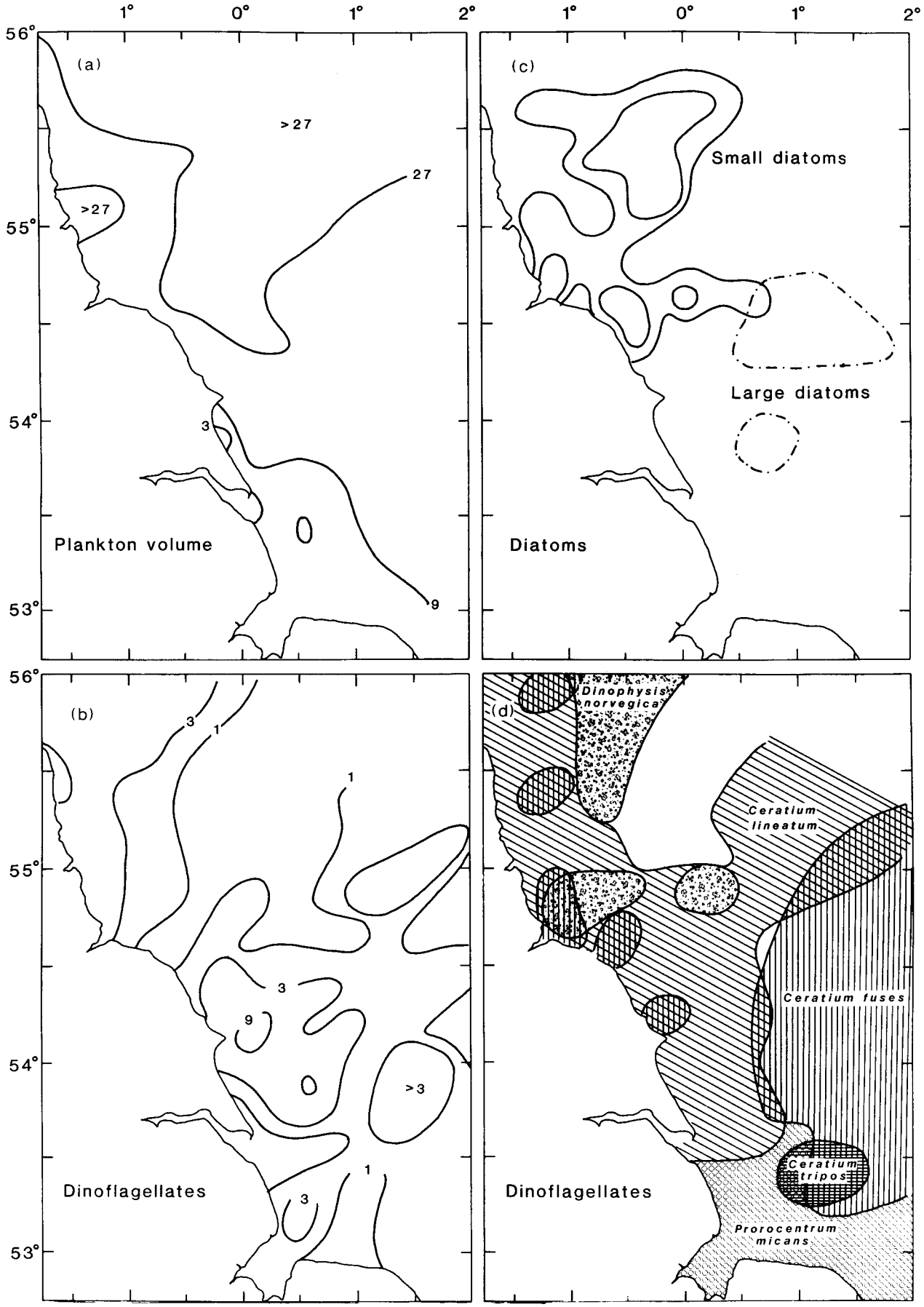


Figure 13 Distribution of planktonic organisms in August 1976: (a) plankton biomass estimated as millilitres of plankton strained by the main net; (b) numbers of dinoflagellates (millions m^{-2}); (c) numbers of large and small diatoms (millions m^{-2}); (d) main dinoflagellate species.

Spatial distributions of phytoplankton in the survey area in 1976 have so far been described only for the month of August (Figure 13). Special attention has been paid to the dinoflagellates on selected cruises (J. D. Dodge, personal communication).

4.2.2 *Zooplankton biomass*

Zooplankton biomass estimated volumetrically (see sub-section 3.2.3) was plotted on charts to illustrate the distribution of zooplankton on each cruise. The estimates of total phytoplankton biomass, derived from chlorophyll *a*, and of zooplankton biomass together with estimates of fish stock abundance, derived from records of catch-per-unit-effort in the commercial fishery have been used as indices, respectively, of primary, secondary and tertiary production in a model describing the seasonal production in this part of the North Sea,and are given in Horwood,(1982).

4.2.3 *Fish eggs and larvae*

Figure 14 illustrates the frequency distributions of fish eggs, from which species have been identified. The surveys showed that 60 species of fish spawned off the

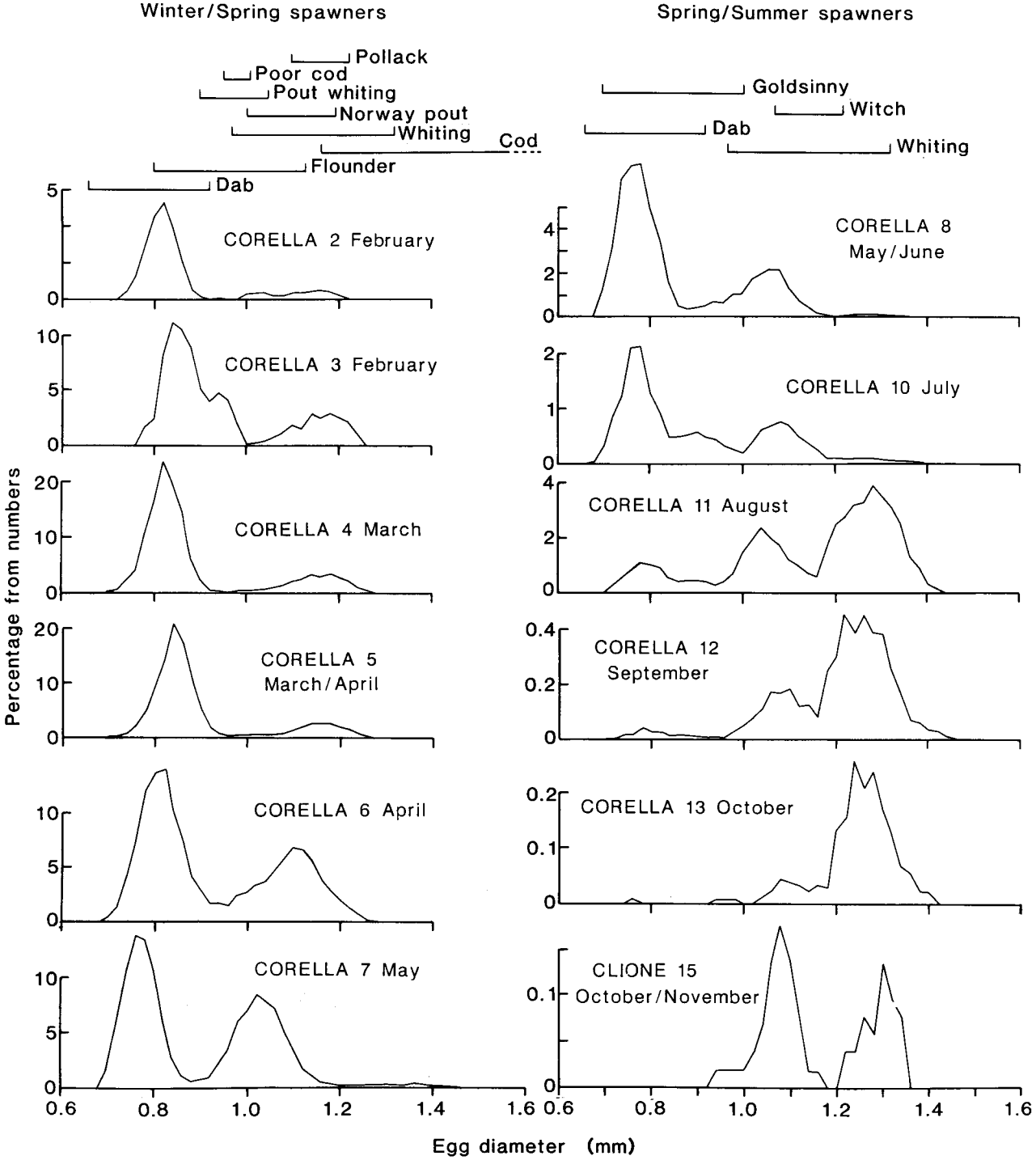


Figure 14 Size frequency distributions of measured fish eggs taken on each cruise in 1976.

Table 7 Planktonic fish eggs and larvae from the 1976 north-east coast surveys

Species	Common name	Eggs	Larvae	Months
PISCES (NEOPTERYGII)				
Isospondyli				
Clupeidae				
Sardina pilchardus	Pilchard	X		Aug
Sprattus sprattus	Sprat	X	X	Feb-Nov
Clupea harengus	Herring		X	Feb-Nov
Apodes				
Anguilla anguilla	Eel		X	Feb-Mar
Solenichthyes				
Syngnathidae				
Syngnathus rostellatus	Nilsson's pipefish		X)	Feb-Mar
			)	Aug-Nov
Entelurus aequoreus	Snake pipefish		X	Aug-Sep
Acanthini				
Gadidae				
Merlangius merlangus	Whiting	X	X	Feb-Nov
Trisopterus luscus	Pout	X	X	Feb-Nov
Trisopterus minutus	Poor cod	X	X	Feb-Nov
Trisopterus esmarkii	Norway pout	X	X	Feb-Nov
Pollachius pollachius	Pollack	X	X	May-Sep
Gadus morhua	Cod	X	X	Feb-Jul
Melanogrammus aeglefinus	Haddock	X	X	Feb-Jul
Molva molva	Ling		X	Sep
Raniceps raninus	Tadpolefish	?	X	Aug
Onos spp.	Rocklings	X	X	Feb-Nov
Percomorphi				
Serranidae				
Dicentrarchus labrax	Bass		X	Aug
Carangidae				
Trachurus trachurus	Scad	X	X	Apr-Oct
Labridae				
Ctenolabrus rupestris	Goldsinny		X	Aug-Sep
Ammodytidae				
Gynammodytes semisquamatus	Smooth sandeel		X)	
Ammodytes tobianus	Sandeel		X)	
Ammodytes marinus	Sandeel		X)	Feb-Nov
Hyperoplus lanceolatus	Greater sandeel		X)	
Trachinidae				
Echiichthys vipara	Lesser weever	X	X)	
Echiichthys draco	Greater weever		X)	Jul-Oct
Scombridae				
Scomber scombrus	Mackerel	X	X	Apr-Sep
Gobiidae				
Gobius spp.	Gobies		X	Feb-Nov
Lebetus sp.	Gobies		X	May-Nov

Table 7 continued

Callionymidae				
Callionymus lyra	Common dragonet	X	X	Mar-Nov
Pholididae				
Pholis gunnellus	Butterfish		X	Mar-Jul
Stichaeidae				
Chirolophis ascanii	Yarrell's blenny		X	Mar-May
Lumpenidae				
Lumpenus lumpretaeformis	Snake blenny		X	Mar-Jul
Triglidae				
Eutrigla gurnardus	Grey gurnard)			
Aspidtrigla cuculus	Red gurnard)	X	X	Mar-Nov
Trigla lucerna	Tub gurnard)			
Cottidae				
Myxocephalus scorpius	Bull-rout		X	Mar-Jul
Taurulus bubalis	Sea scorpion		X	Apr-Jul
Taurulus lilljeborgi	Norway bullhead		X	Aug
Agonidae				
Agonus cataphractus	Armed bullhead		X	Mar-Jul
Liparidae				
Liparis liparis	Sea snail)		X	Feb-Nov
Liparis montagui	Montagu's sea snail)			
Heterosomata				
Bothidae				
Scophthalmus maximus	Turbot	X	X	Apr-Aug
Scophthalmus rhombus	Brill	X	X	Jul-Aug
Zeugopterus punctatus	Topknot		X	Sep
Phrynorhombus norvegicus	Norway topknot	X	X	May-Oct
Arnoglossus laterna	Scaldfish	X	X	May-Nov
Pleuronectidae				
Limanda limanda	Dab	X	X	Feb-Nov
Platichthys flesus	Flounder	X	X	Feb-Sep
Pleuronectes platessa	Plaice	X	X	Feb-Jul
Microstomus kitt	Lemon sole	X	X	Feb-Nov
Glyptocephalus cynoglossus	Witch	X	X	Apr-Nov
Hippoglossoides platessoides	Long rough dab	X	X	Feb-Sep
Soleidae				
Solea solea	Sole	X	X	Apr-Aug
Buglossidium luteum	Solenette	X	X	Apr-Sep
Microchirus variegatus	Thickback sole		X	Aug-Oct
Xenopterygii				
Gobiesocidae				
Diplecogaster bimaculata	Twospot cling fish		X	Aug-Oct
Lepadogaster lepadogaster	Shore cling fish		X	Apr & Aug-Nov
CRUSTACEA				
Decapoda				
Cancer pagurus	Edible crab		X	May-Nov
Nephrops norvegicus	Norway lobster		X	Apr-Oct
Homarus gammarus	Lobster		X	Jul-Nov

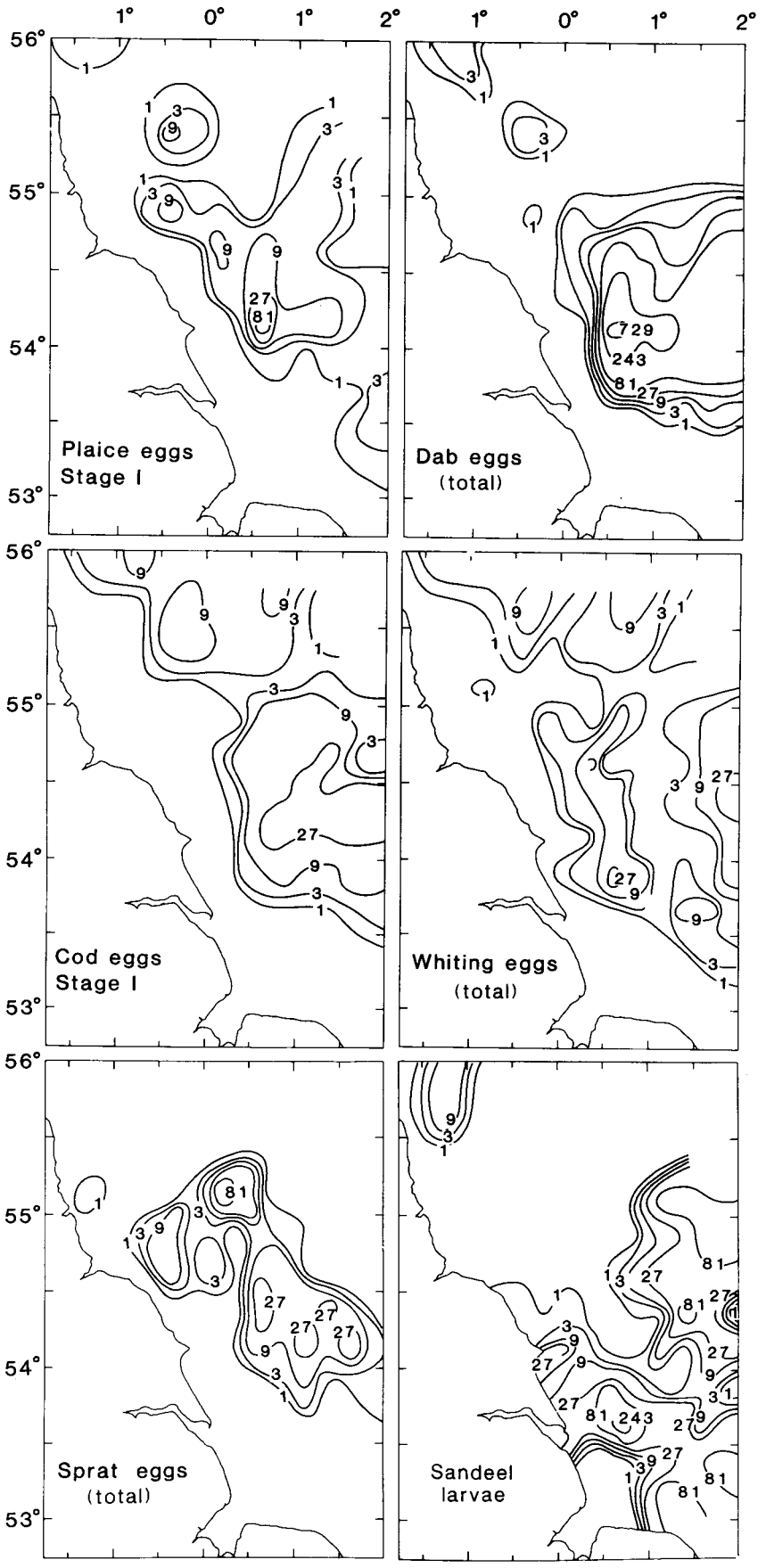


Figure 15 Distributions of fish eggs and larvae in early spring (March 1976).

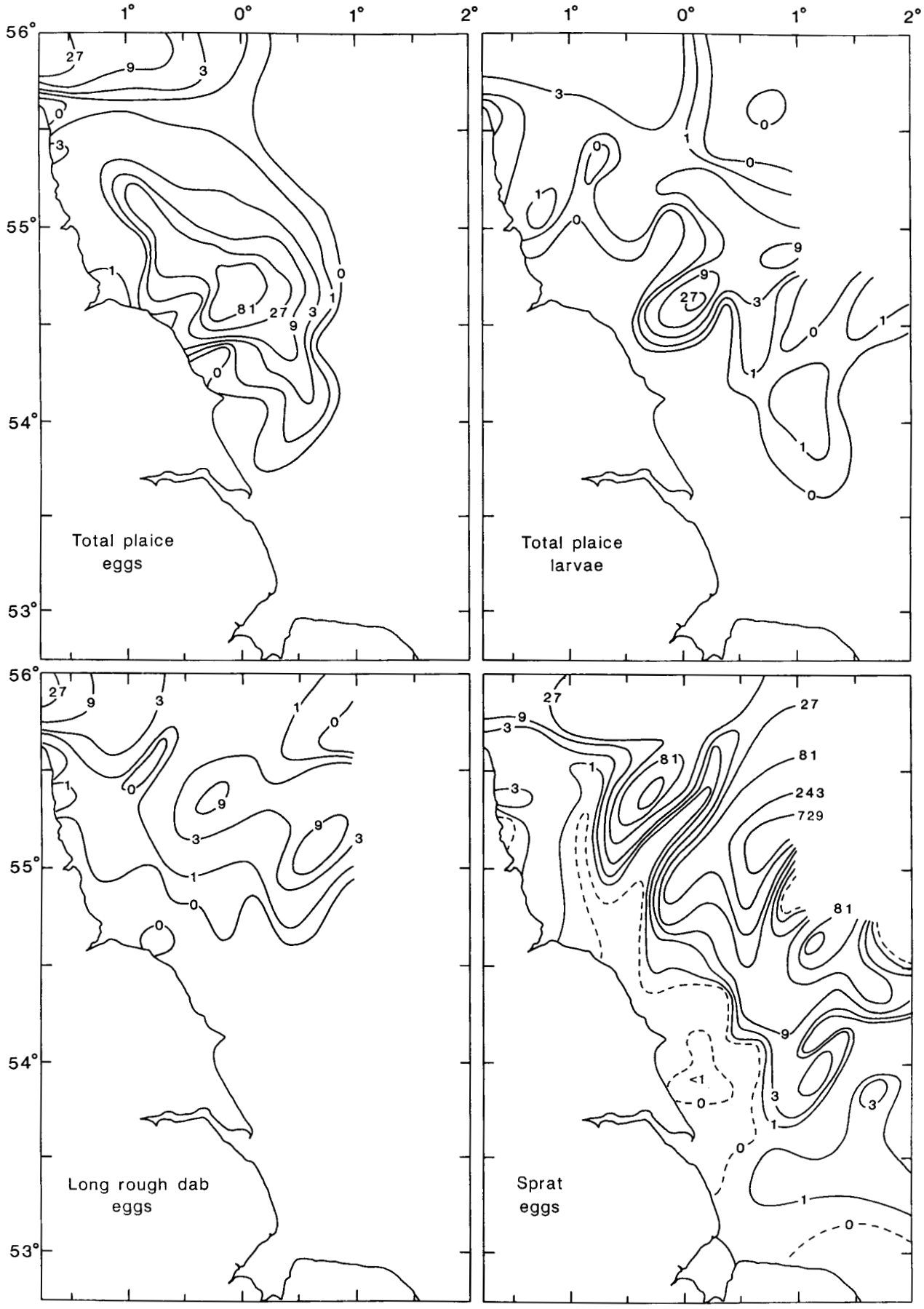


Figure 16 Distributions of fish eggs and larvae in late spring (May 1976).

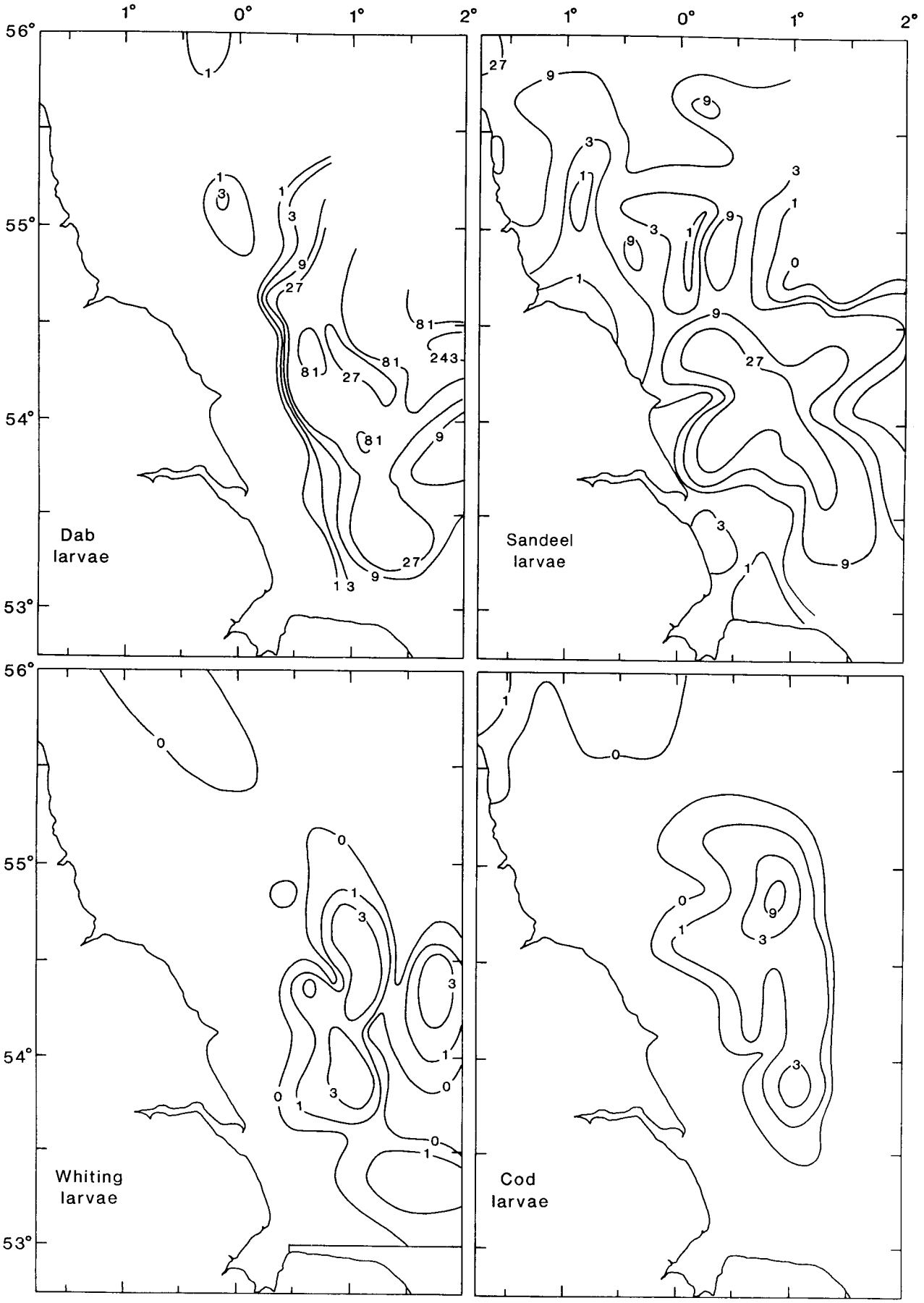


Figure 16 Continued.

north-east coast of England in 1976 (Table 7). In winter and early spring plaice, dab, whiting, cod and sprat spawned in the tongue of warm, saline and highly transparent water to the north-east of Flamborough Head, while sandeel larvae, from spawnings on the bottom in shallow water, were found distributed over the Norfolk banks and Dogger Bank and in coastal water near the Farne Islands (Figure 15). In late spring, the larvae from these offshore spawnings were abundant in the deep water north-east of Flamborough Head where newly spawned eggs of long rough dab, lemon sole, turbot, gurnard and sprat also occurred. Over the banks, sandeel larvae were scarce. Sole, sprat and scad eggs dominated in the plankton samples from the Norfolk banks (Figure 16).

Production of plaice and cod eggs and larvae was measured and mortality curves for the egg stages in January-April were constructed. The total number of eggs produced was calculated for each species from the intercepts of regression lines of $\log_e$ of the numbers

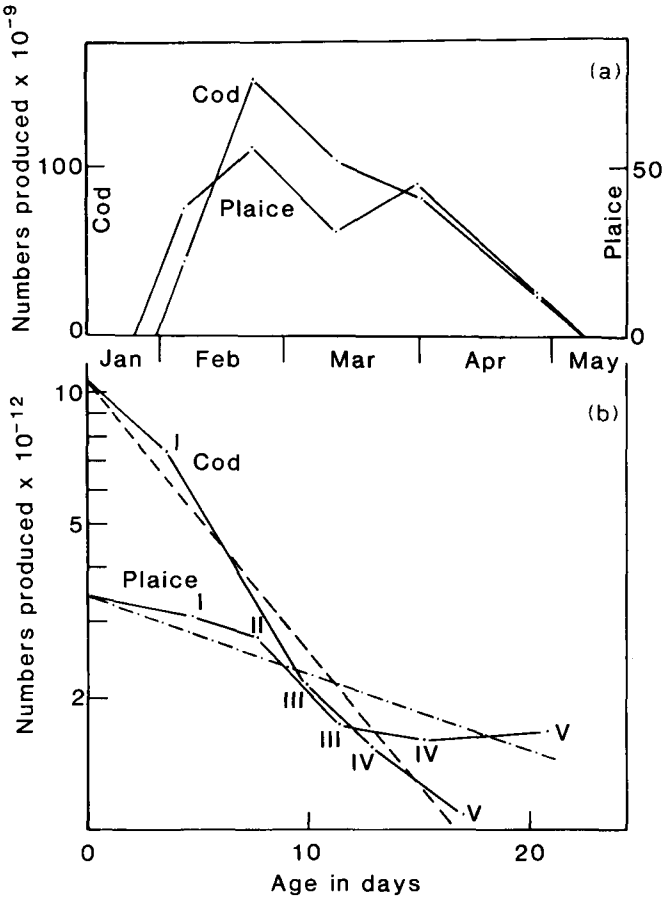


Figure 17 (a) Seasonal production and (b) mortality curves for plaice and cod eggs off the north-east coast of England in 1976. Total production of Stage 1 eggs was 7.3 x 10^{-12} for cod and 3.1 x 10^{-12} for plaice. Overall seasonal mortalities of eggs were, for cod 85.2% (Z = 0.14 per day), and for plaice 45.3% (Z= 0.04 per day).

produced in each development stage plotted against average age. This procedure gave estimates of 1.06 x 10^{13} cod eggs and 3.39 x 10^{12} plaice eggs. The mortality rate per day (Z) was estimated from the slope of the regression line at 0.14 for cod and 0.04 for plaice, equivalent to, respectively, 85% and 45% mortality between spawning and hatching (Figure 17) (Harding and Nichols, 1977).

In summer, in the deep water, the egg numbers of dab, lemon sole, turbot, brill, gurnard and sprat increased to peaks and the larvae from these summer and the late spring spawnings were dominant in the plankton. In the unstratified water south of Flamborough Head and on the Dogger Bank, sandeel larvae were again very abundant and were accompanied by larvae of sole, scad and sprat, while the egg numbers of all bank spawning species declined (Figure 18).

In late summer and autumn, the dominant species of larvae north of Flamborough Head in coastal and deep water were herring, sprat, gurnard, whiting, dab and lemon sole along with smaller numbers of Norwegian topknot, turbot and brill. Over the banks, sandeel and scaldfish were the two most abundant species. By late autumn, only the larvae of herring, sprat, whiting, gurnard, lemon sole and dab remained in the plankton and of these only herring and sprat overwintered in the plankton until the following spring (see Harding *et al.*, 1978).

Figure 19 shows that a succession of spawnings occurred throughout the year with peak numbers of both eggs and larvae occurring at different times even on the same spawning ground.

4.2.4 Crustacea

Three crustaceans of economic importance released larvae in this area of sea during the summer months: Norway lobster, *Nephrops norvegicus* (L.); edible crab, *Cancer pagurus* L.; and lobster, *Homarus gammarus* (L).

(a) *Norway Lobster.* Larvae were present off the Northumberland coast in deep waters between May and August. The location of this spawning coincides with known fishing grounds (Figure 20). Three larval development stages were sufficiently abundant in the plankton samples for seasonal production curves to be drawn and for estimates of abundance, mortality and spawning stock size to be made. Production of Stage I larvae was calculated at 5.75 x 10^{10}, equivalent to 1.64 x 10^{11} eggs laid by 7.35 x 10^{7} females and indicating a spawning stock of 5 291 t of males and females (Garrod and Harding, 1980).

(b) Edible crab. Release of larvae began in early July and continued until October with a peak in late July. Later developmental stages persisted in the plankton until November. Megalopa reached a peak in September.

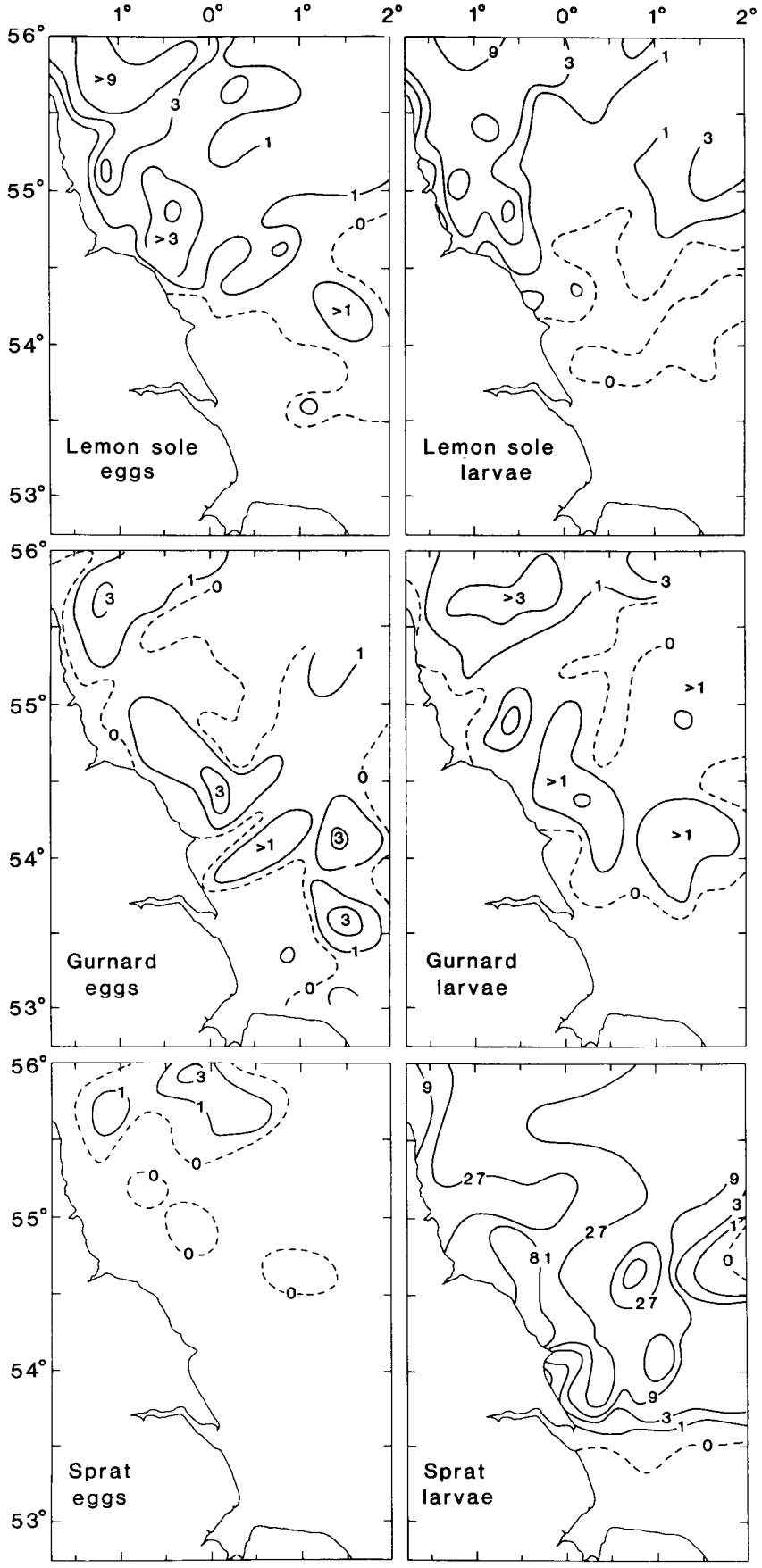


Figure 18 Distributions of fish eggs and larvae in the summer (August 1976).

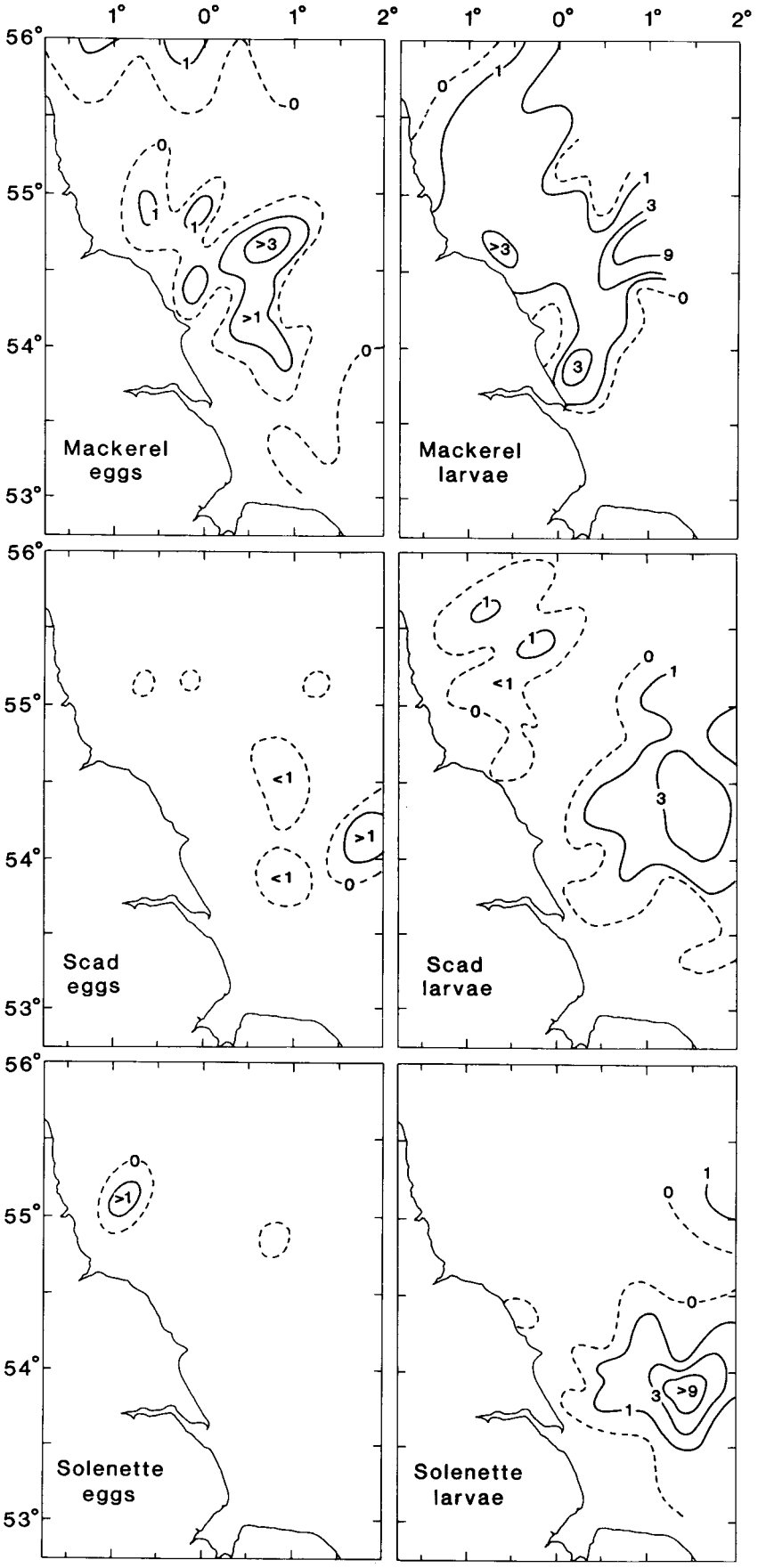
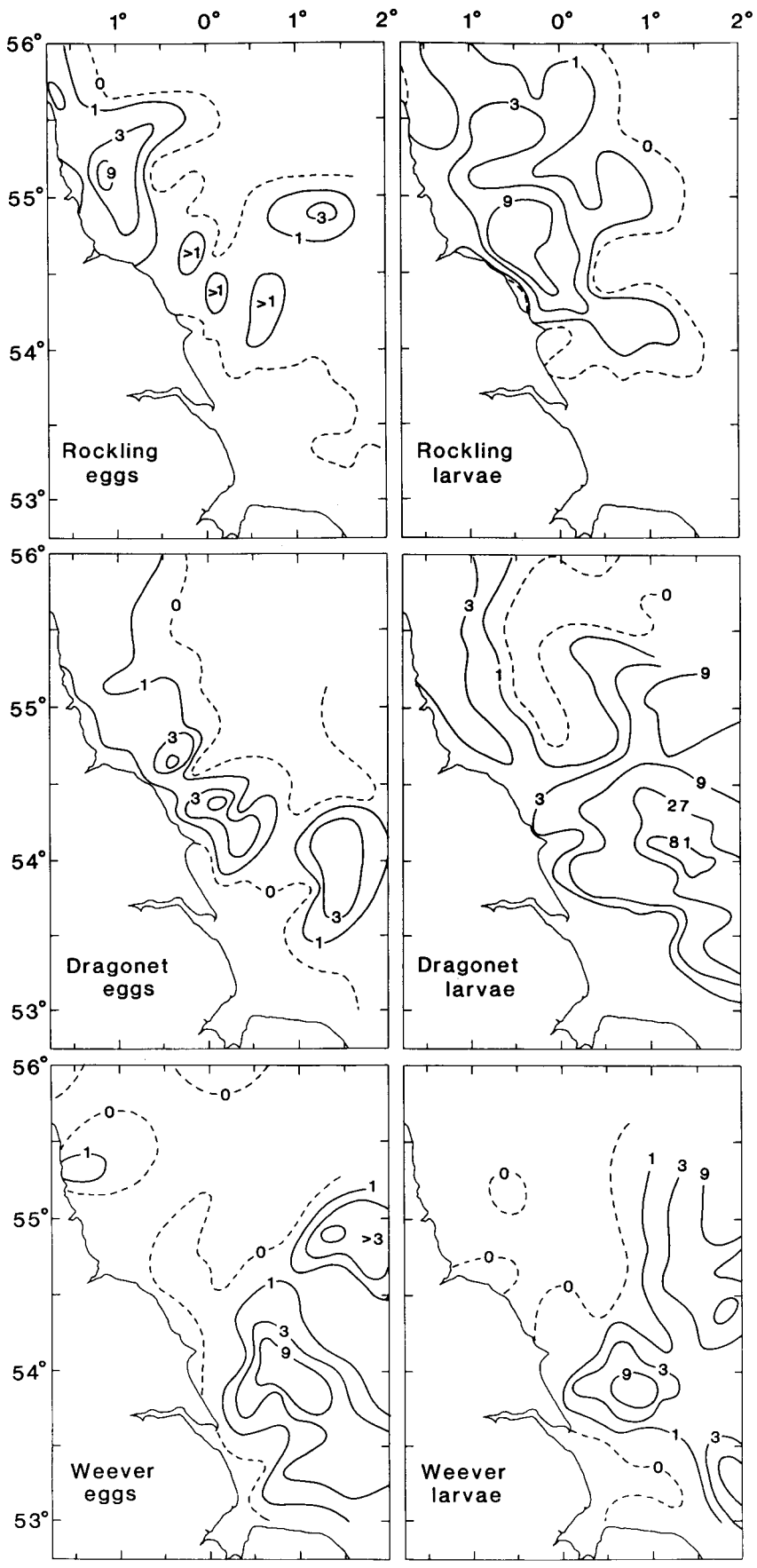


Figure 18 Continued.



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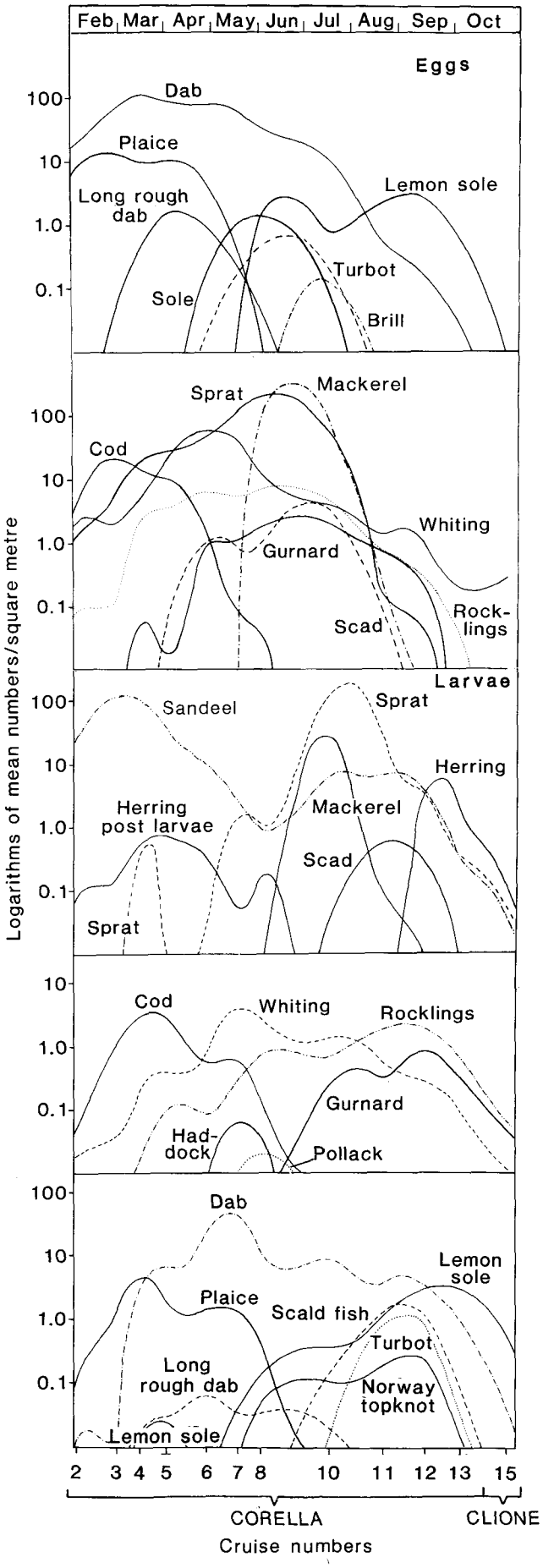

Figure 19 Seasonal variation in the abundance of fish eggs and larvae in 1976.

Releases were over a wide area. Two major hatching centres were defined from distributions of Stage I zoea: at 53°50'N, 00°55'E and at 54°25'N, 00°02'W. The western edge of another large centre of hatching was apparent on the eastern boundary of the survey area and several smaller patches of Stage I larvae were distributed over most of the area south of latitude 55°N.

The positions of the release centres were compatible with the northerly migration of mature female crabs from the north Norfolk and Yorkshire coastal fisheries but not with the previously accepted idea of an inshore hatch in spring. The subsequent movement of the patches of larvae was similar to the known pattern of water movement in the area during the summer months. Larval drift, however, cannot be shown to be wholly responsible for recruitment to the commercial fishing grounds, because the last planktonic stage was still found well offshore in many instances (Nichols, Thompson and Cryer, 1982). The movement of young crabs inshore must therefore be an active migration.
Seasonal production of Stage I larvae was estimated at 7.23×10^{12} which, based on average fecundity figures derived from previous years (Edwards, 1979), corresponds to 2 600 t of mature females. This figure is compatible with the accepted size of the fishable stock of females and with a total catch of males and females of 1 800 t from this area of sea in 1976.

(c) Lobster. Lobsters released larvae close inshore, in mixed coastal water within the limits of the local fishery for adults, in July-October. Their larvae remained within this general area throughout the pelagic phase, as shown by neuston net catches (Nichols and Lawton, 1978). Lobster larvae make diurnal migrations and may react to strong tides which are characteristic of this region (Nichols and Lovewell, 1987). Their behaviour pattern coupled with persistent onshore residual drift seemed to be sufficient to keep the larvae within the coastal belt.

4.2.5 *Vertical distribution*

Studies on vertical distribution were undertaken, using the Lowestoft changing net sampler (Harding *et al.*, 1971), on high-density patches of fish eggs and larvae. The results indicated cyclic variations in the depth distribution of both eggs and larvae over the 24 h periods studied. The changes in abundance of eggs at depth can only be attributed to mixing of the water column, which would be related to the strength of the wind and tide driving this local circulation, and to spawnings at different levels in the water column. Some developmental stages of larval fish and crustaceans and many planktonic invertebrates can change their vertical positions by swimming up or down the water column, but such a behaviour pattern could be modified by diurnal and seasonal variations in the strength of the vertical circulation and by thermal stratification.

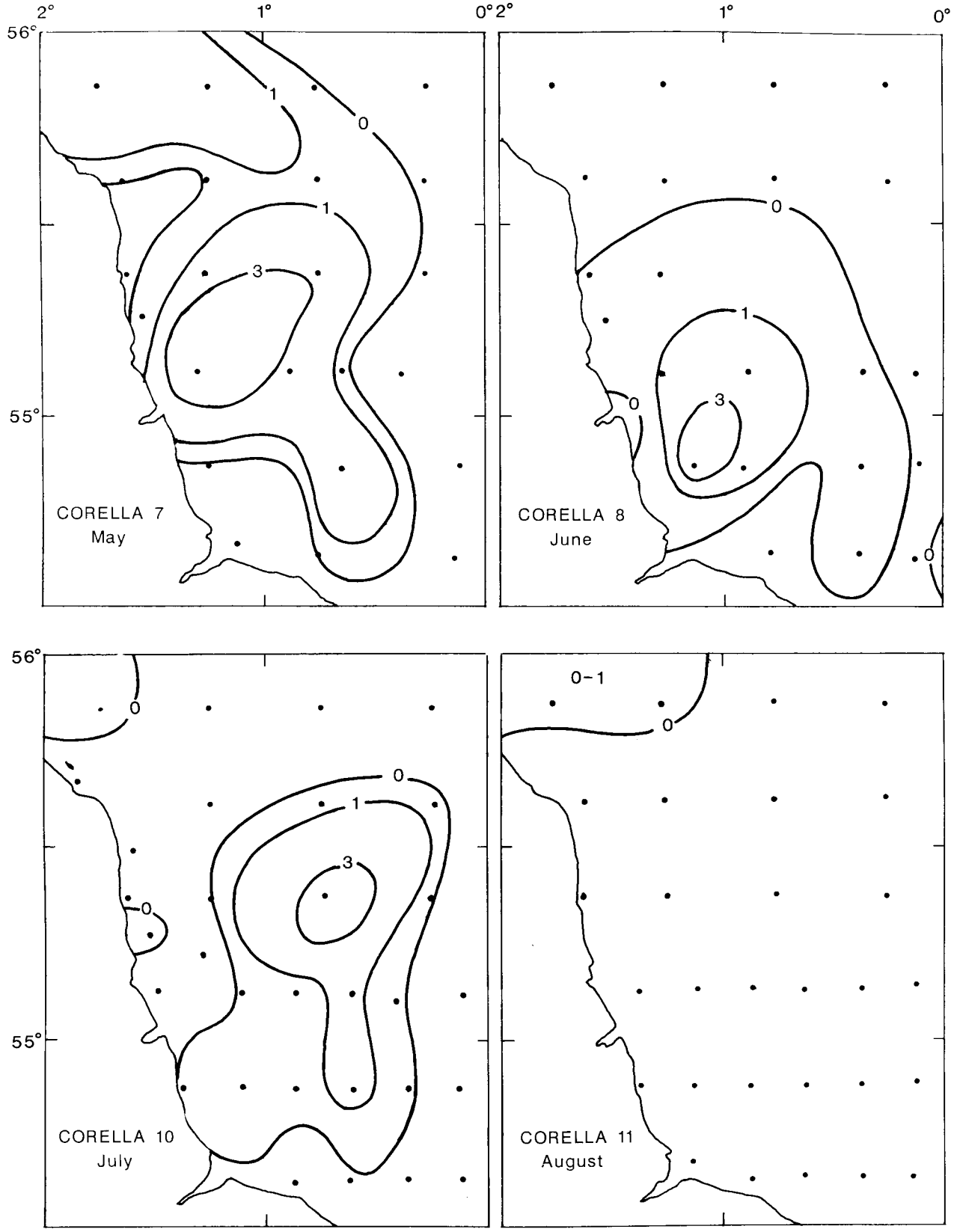

Figure 20 Distribution of Stage 1 *Nephrops* larvae on four cruises covering the main release period during 1976. • = station position.

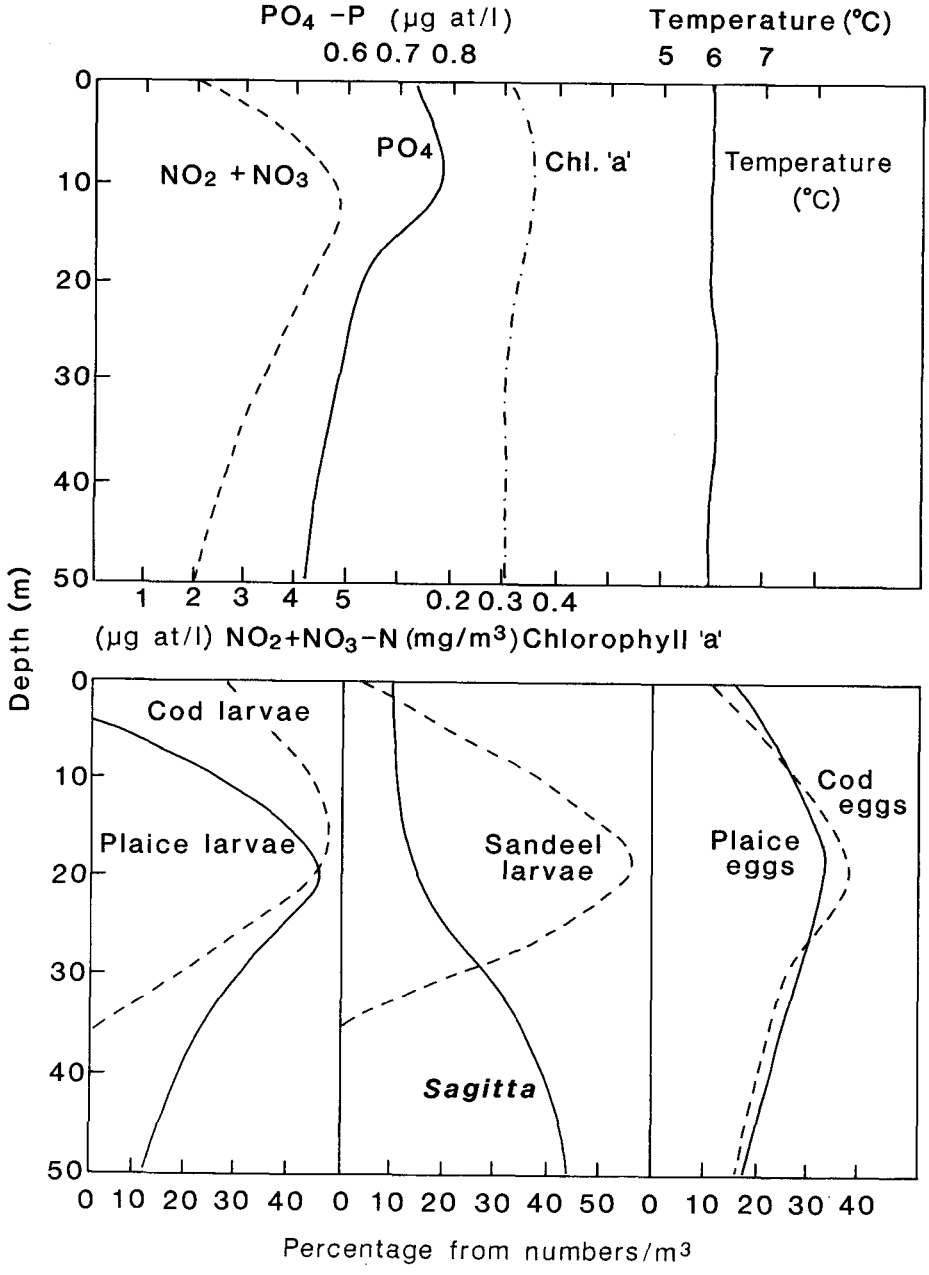

Figure 21 Vertical distribution of fish eggs and larvae in relation to environmental variables in the winter/early spring (February) 1976.

In winter and early spring when the water column was thoroughly mixed (Figure 21) there was similarity between the distributions of eggs and those of larvae, as illustrated by samples taken on 24-25 March 1976, which suggests that vertical mixing of the water column was responsible for the distribution patterns observed (Figures 21 and 22). At this season the larval population was dominated by yolk sac larvae which had just hatched and had very little swimming capacity. In contrast, arrow-worms *(Sagitta* spp.) seemed to respond to the diurnal cycle of light and darkness and were found near to the sea bed during daylight hours.

In the mid-spring, under similar environmental conditions, the eggs and early larvae of plaice still showed cyclic patterns of vertical distribution but post-larvae of plaice were found deeper in the water and showed little diurnal movement (Figure 23).

In late spring and summer, when the water column was stratified, cyclic variations in the depth distribution of fish eggs, fish larvae and crustacean larvae still occurred (Figures 24 and 25). The effect of thermal stratification was apparently nil, eggs and larvae being found throughout the water column over the 24 h sampling periods. In late spring, the vertical distribution of fish larvae varied

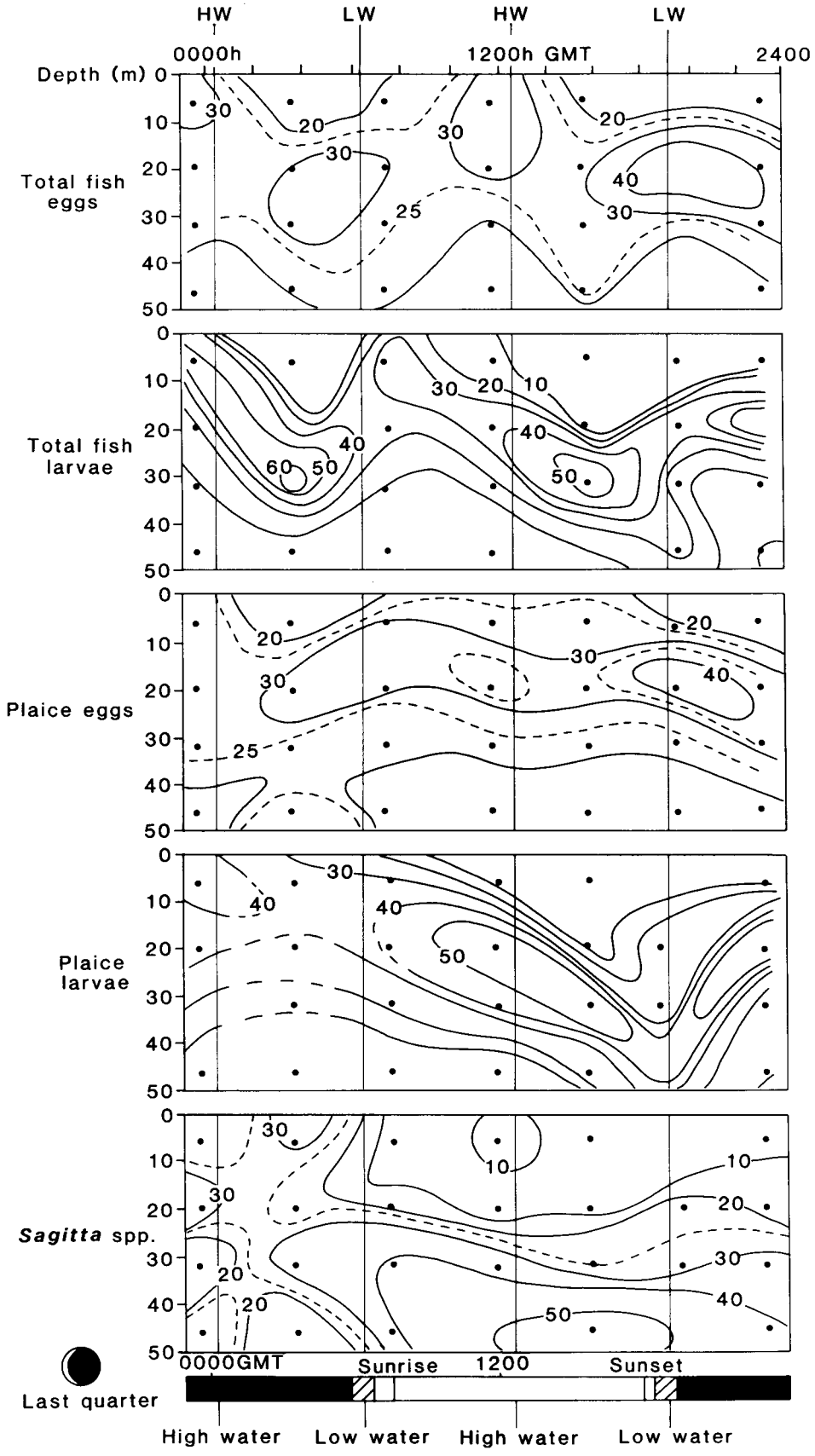

Figure 22 Vertical distribution of fish eggs and larvae in the winter/early spring (February) 1976: ▨ dawn and dusk; ■ darkness; • sampling level.

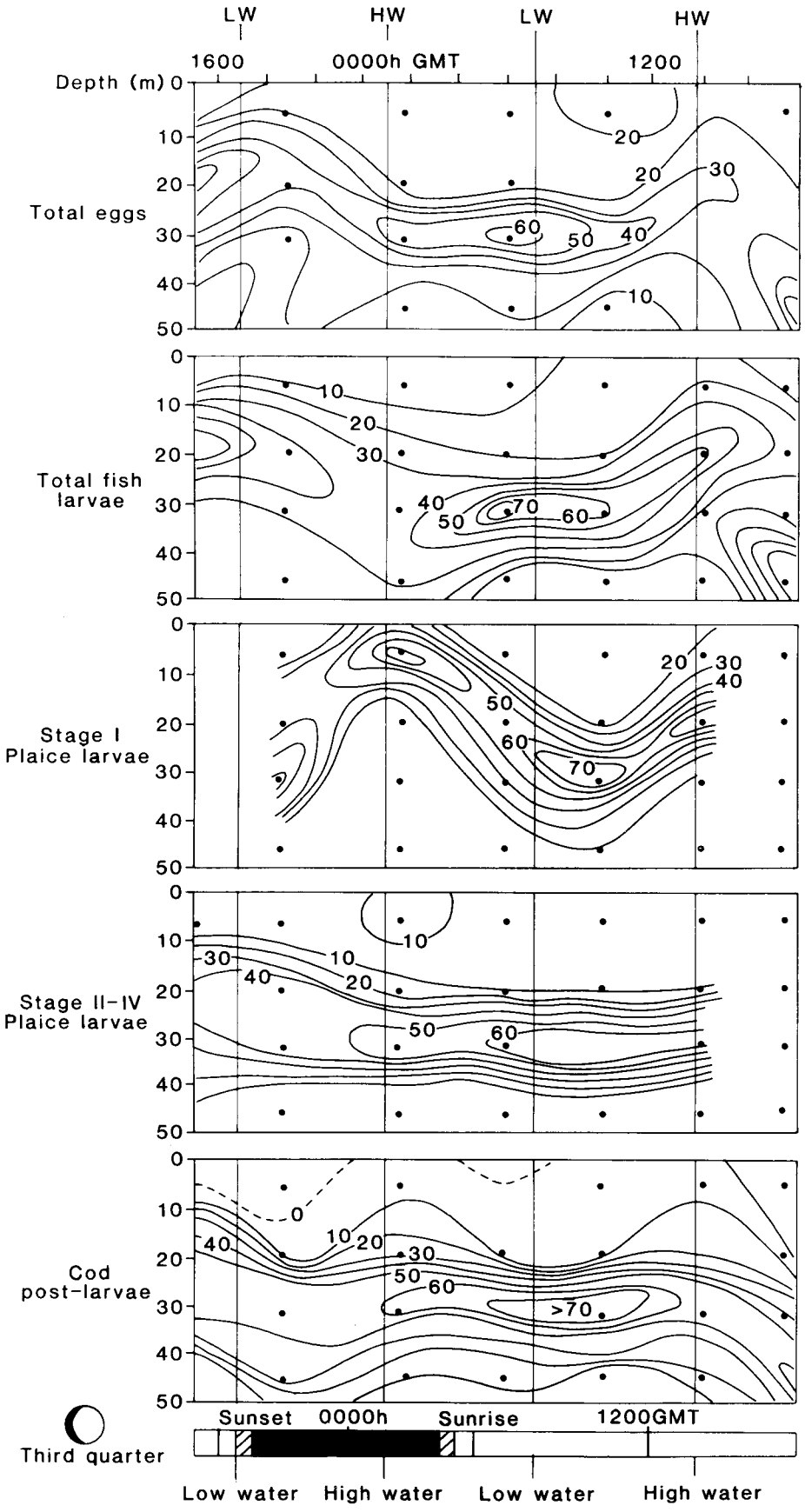

Figure 23 Vertical distribution of fish eggs and larvae over a 24 h period in mid-spring (April) 1976: ▨ dawn and dusk; ■ darkness; • sampling level.

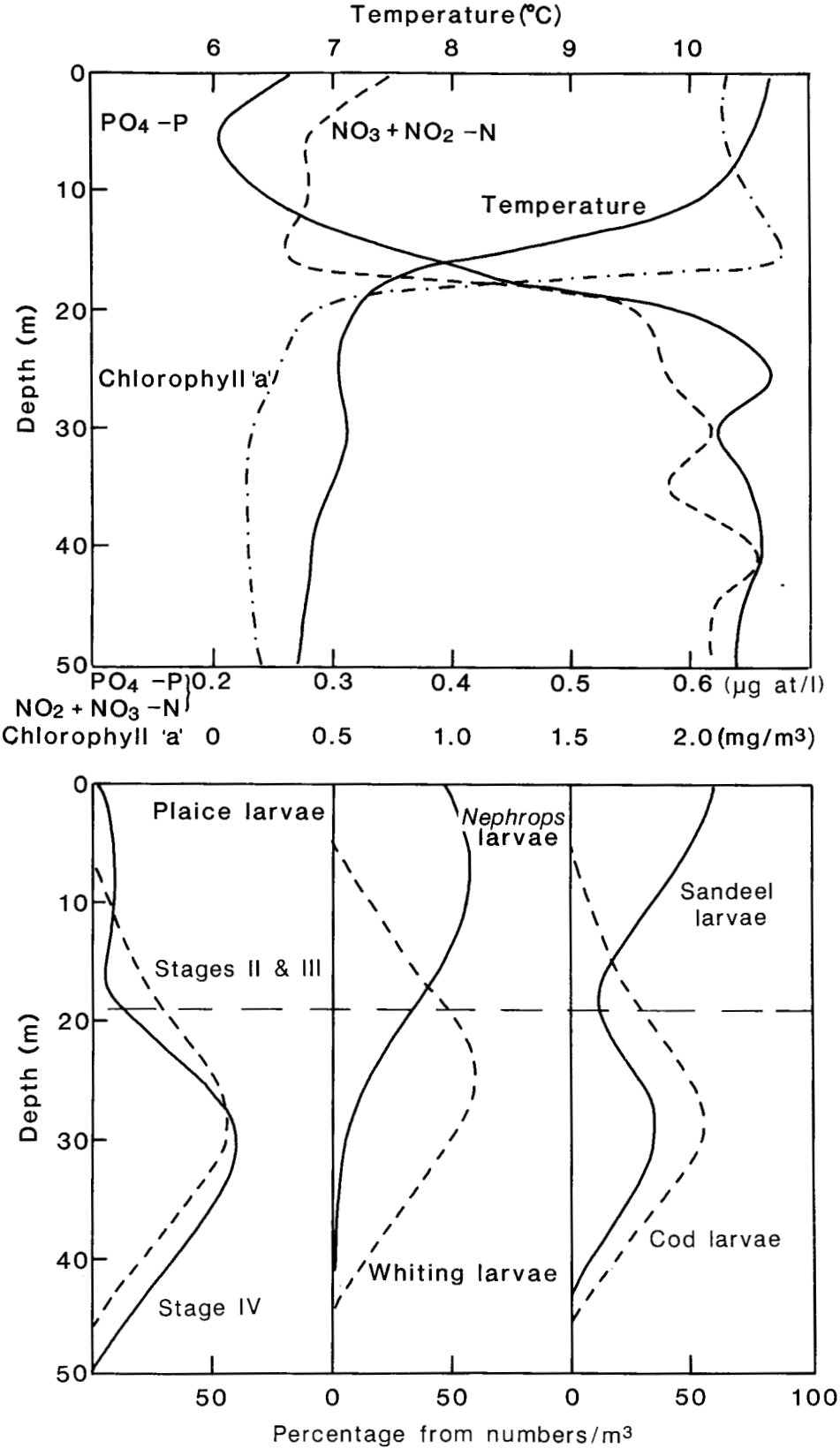

Figure 24 Vertical distribution of fish eggs and larvae and selected environmental variables in the late spring (May) 1976.

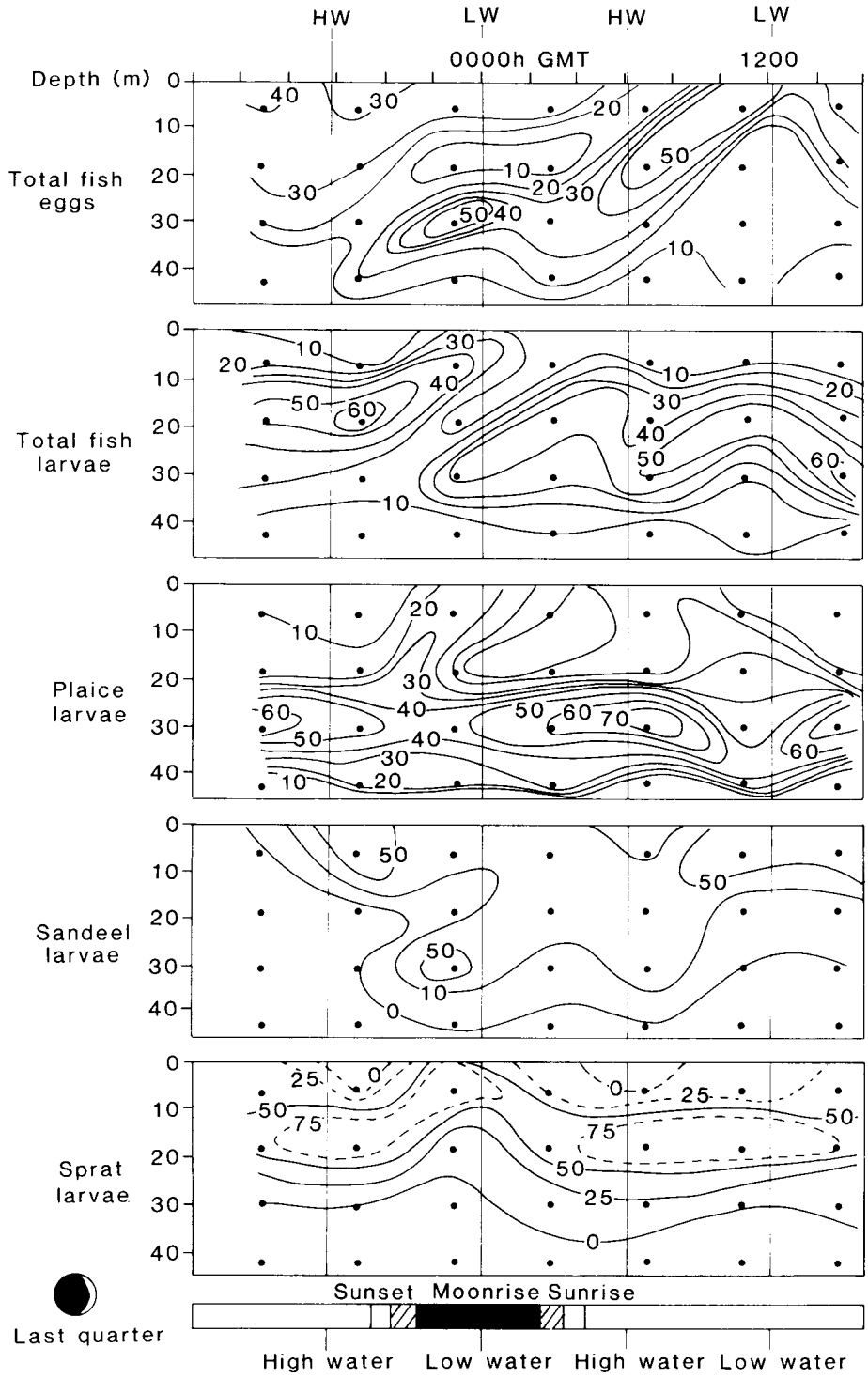

Figure 25 Vertical distribution of fish eggs and larvae over a 24 h period in the late spring (May) 1976. ▨ dawn and dusk; ■ darkness; • sampling level.

with the species and with the stage of development. Thus plaice and cod larvae, mainly at a late stage in their development, were usually below the thermocline while sprat and sandeel larvae, at an early stage of their development from recently-hatched eggs, were mostly above the thermocline throughout the sampling period. In the summer, other fish larvae were distributed to a similar pattern: size and age differences again determined the vertical stratification of sprat larvae in August (Figure 26). Only edible crab megalopa larvae showed a clear vertical migration through the thermocline in response to changing light levels (Figure 27).

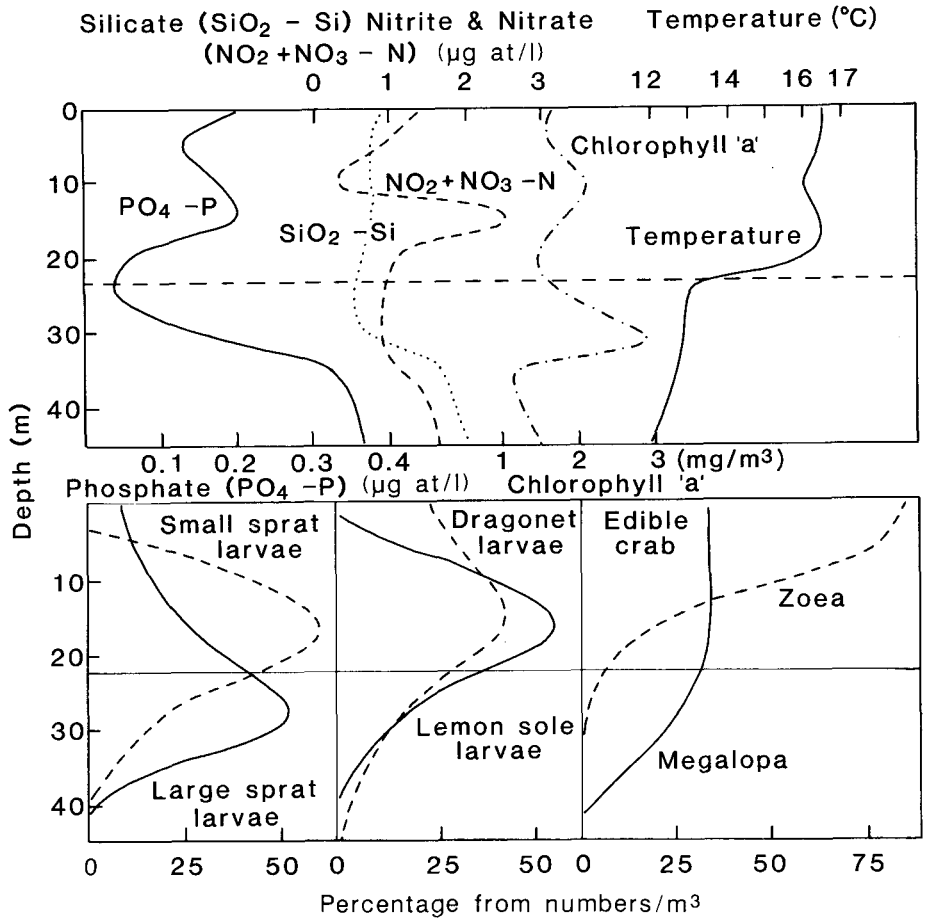

Figure 26 Vertical distribution of fish and crab larvae and selected environmental variables in the summer (August) 1976.

4.2.6. Larval drift

One of the interesting features of the summer distributions of eggs and larvae, illustrated in Figure 28, was the concentration of peak numbers near the temperature discontinuity (or front) forming the boundary between the stratified and mixed water masses. This frontal zone is a hydrographic feature characteristic of this sea area from late spring until early autumn, and may be important to the survival of pelagic fish larvae. These concentrations of eggs and larvae suggest that eggs are either spawned near the front or concentrated there by local currents. Larvae hatching from eggs spawned on either side of the front may also be concentrated there passively like the eggs, but once they are in the high concentrations of phytoplankton and zooplankton, which also develop or accumulate at this boundary, they may change their behaviour pattern to take advantage of the better feeding opportunities offered. Water movements along the front could then transport the larvae nearer to their nursery areas.

Larvae would be assisted to cross this boundary zone by:

(i) onshore–offshore movements of the frontal zone in response to tidal mixing;

(ii) turbulent eddies which develop on the boundary as a result of sheer between the water masses; and

(iii) vertical migratory movements of the larvae.

In the case of plaice larvae, which concentrate near this boundary in late spring, early stages with little swimming ability tend to be distributed near the surface, older larvae with a greater swimming capacity are found throughout the water column, while metamorphosing larvae may be found very close to the bottom with most below the thermocline and often settle on the sea bed. In thermally stratified water near the front, the older plaice larvae seem to be capable of migrating vertically through the thermocline (Figure 25). Once in the colder bottom water, they would be carried onshore to the west and south-west and thus nearer to the frontal mixing zone where metamorphosing larvae can settle out and cross to the inshore mixed water as the front moves offshore under the influence of strong tidal mixing. Alternatively, these larvae may be transported across this boundary by upwelling bottom water. Neustonic larvae such as turbot, and other larvae living in mid-water such as cod, whiting and herring, may cross the front as it erodes under the influence of tidal mixing, but could also cross in the turbulent eddies which develop on this boundary.

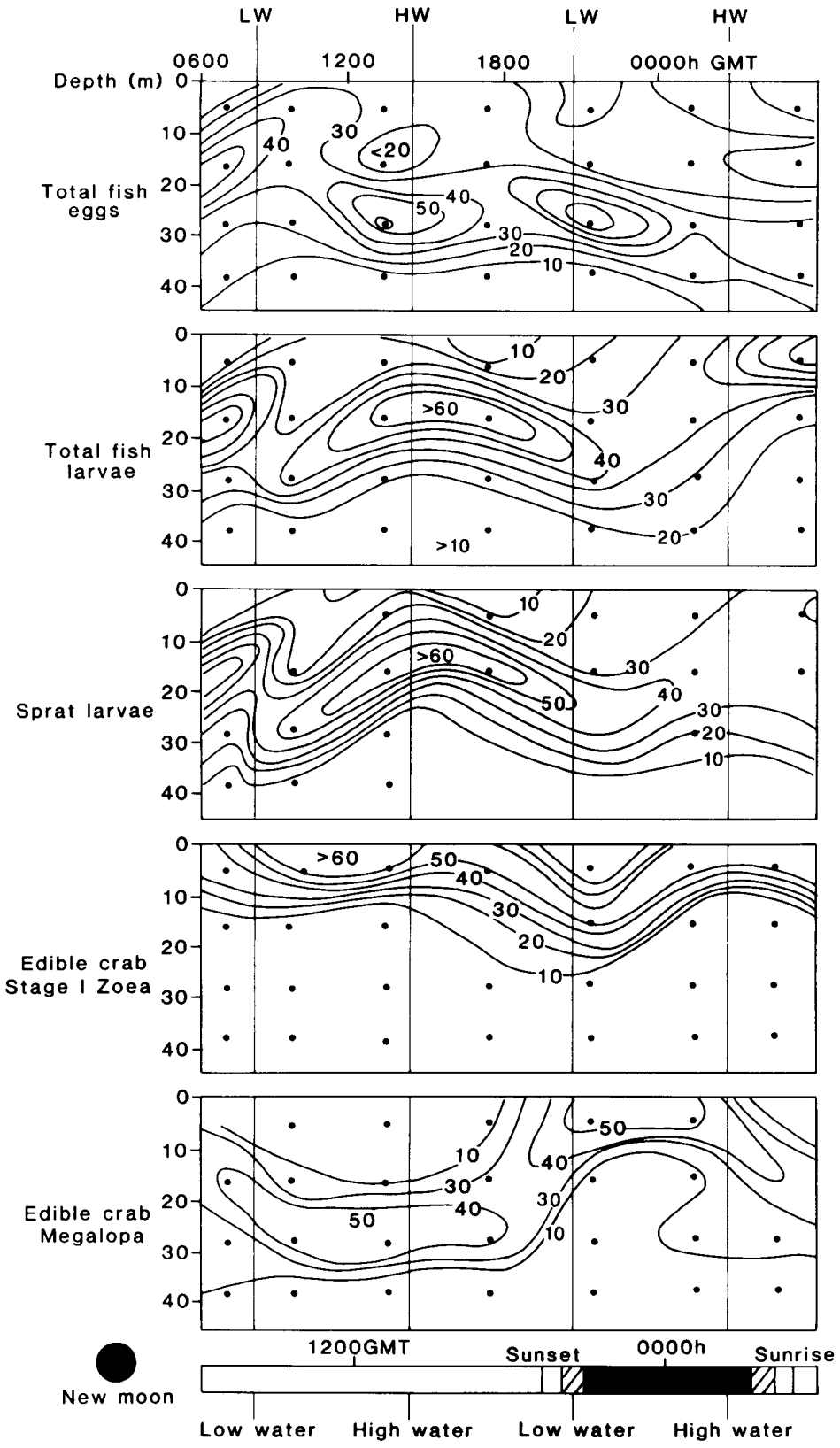

Figure 27 Vertical distribution of fish eggs and larvae and crab larvae over a 24h period in the summer (August) 1976: ▨ dawn and dusk; ■ darkness; • sampling level.

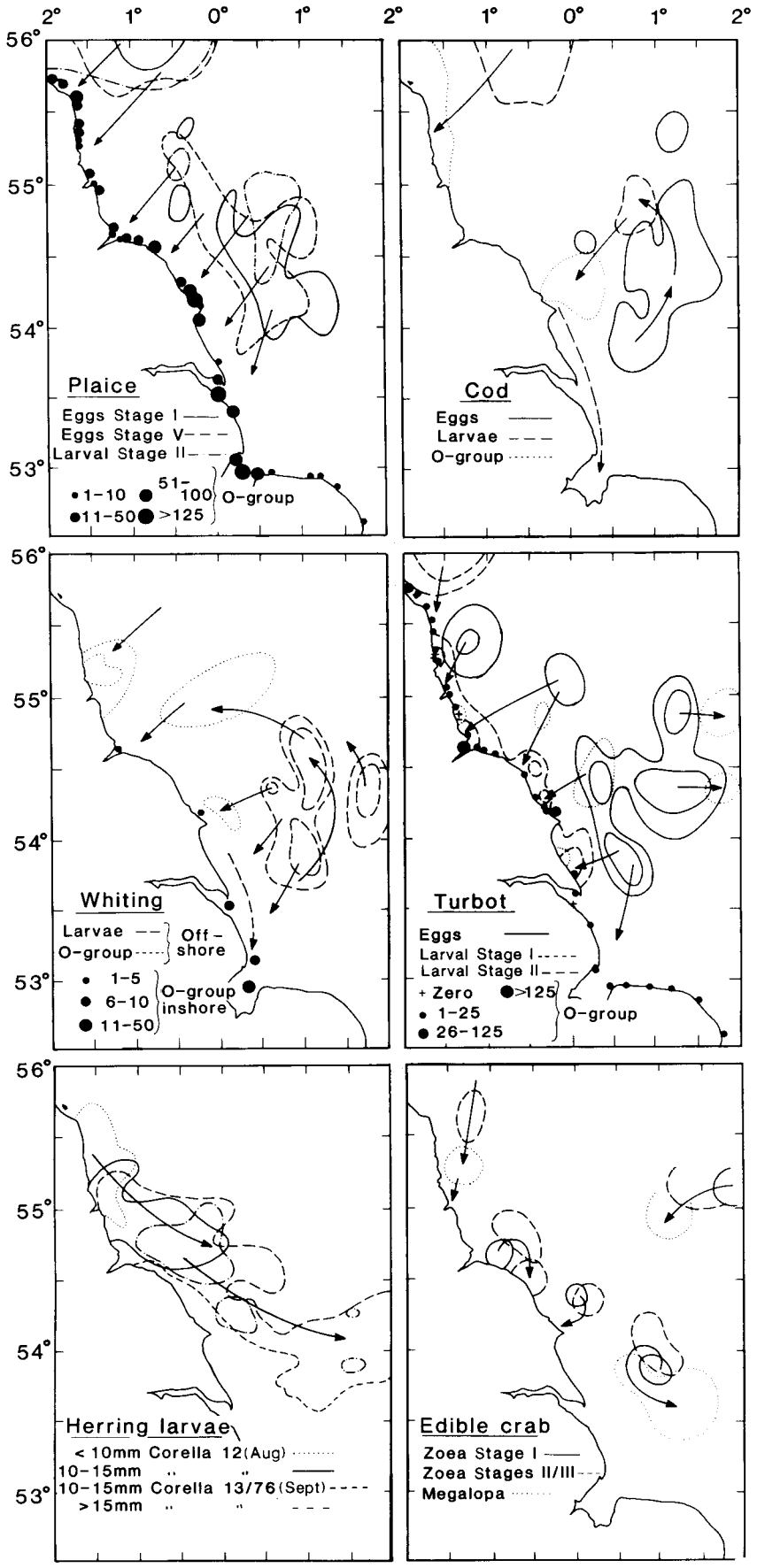

Figure 28 Larval drift deduced from distributions of different development stages of eggs, larvae and young fish or crustacea on successive cruises of 1976.

The drift of eggs and larvae to coastal nursery areas was revealed by examination of patches of developing fish eggs and larvae on successive cruises and the final disposition of O-group fish in the nursery areas (Figure 28). The pattern for winter and spring spawning plaice, cod and whiting is consistent with the residual drift measured by seabed drifters and current meters. Although turbot larvae are neustonic and their eggs and larvae are not caught in large numbers in the standard plankton sampler, the distributions of turbot eggs and larvae from the offshore surveys and of larvae taken by the neuston net served to demonstrate onshore movement towards coastal nursery beaches: Riley *et al.* (1979) have linked this migration to the frequency and strength of onshore winds.

Movements of larvae along the front were clearly shown by the distributions of herring larvae of different sizes (ages) on successive cruises. In summer, herring spawned inshore in mixed water near the Farne Islands and Whitby, and larvae were abundant in the plankton in late summer and autumn. Yolk sac larvae hatch and live near the bottom and these water movements were generally onshore. As the yolk sacs are resorbed, the larvae move up into mid-water to feed and once there they cross into the frontal zone and move offshore to the south-east along the front. In late summer and early autumn stratification broke down, the front moved further offshore and there was a general southerly movement of water down the coast as the new annual inflow started: herring larvae were entrained by these water movements and drifted towards the south-east to offshore nursery areas.

4.2.7 *Larval feeding*

A total of 8 902 larvae, belonging to twenty species from standard plankton samples collected between February and October 1976, were examined to determine their dietary preferences. Last (1980) gives details of the percentage composition of all stomach contents analysed and a description of seasonal and diurnal feeding by these planktonic fish larvae.

Table 8 Species of fish eggs and larvae found in stomachs of the ten most important fish predators

Prey organisms		Predator									
		Anchovy	*Sprat*	*Herring*	*Whiting*	*Sandeels*	*Weevers*	*Mackerel*	*Gurnards*	*Dab*	*Lumpsucker*
(a)	**Fish Eggs**										
	Pleuronectes platessa	X	X	X	X	X			X	X	X
	Others	X	X	X	X	X		X	X	X	X
(b)	**Fish Larvae**										
	Clupeidae		X	X	X		X	X			
	Gadidae			X							
	Merlangius merlangus				X	X			X		
	Gadus morhua	X	X	X	X	X					
	'Onos' spp	X		X				X			
	Ammodytidae	X	X	X	X	X		X			
	Echiichthys vipera				X						
	Scomber scombrus			X				X			
	Gobiidae			X				X			
	Callionymus lyra			X	X						
	Pholis gunnellus		X						X		
	Cottidae		X		X						
	Myxocephalus scorpius		X		X						
	Agonus cataphractus								X		
	Liparis liparis		X								
	Pleuronectidae	X		X	X	X			X		
	Limanda limanda		X		X				X		
	Platichthys flesus				X						
	Pleuronectes platessa	X			X						X
	Hippoglossoides platessoides				X						
	Indeterminate larvae	X	X	X	X	X		X			X

4.2.8 Fish predators of fish eggs and larvae

The first step towards assessing the effect of fish predators on planktonic fish eggs, larvae and young fish was to determine how frequently these planktonic organisms occurred in the diets of plankton-feeding fish. The stomach contents of 3 435 fish belonging to 27 species were examined, from trawl samples collected between March and August in the western central North Sea. Results are summarised in Tables 8 and 9 and are discussed by Garrod and Harding (1981).

The most important of the predators were known plankton feeders: anchovy, sprat, herring, whiting, sandeels and mackerel. However, the proportions of eggs, larvae and young fish found in the stomachs of most fish species differed considerably from those in the plankton. This may have been due to either selective feeding by predators or aggregation of predators on dense patches of eggs and larvae which are not detected in integrated plankton hauls (Garrod and Harding, 1981).

Table 9 Percentage occurrence of fish eggs, larvae, young fish and invertebrates in fish stomachs and in plankton samples taken near the trawl stations.

Fish predators	Prey organisms														
	Size range (cm)	*No. of stomachs examined*	*No. empty*	○ *Pleuronectes platessa eggs*	○ *Other fish eggs*	○ *Fish larvae*	○ *Young fish*	○ *Appendicularia*	*Ophiuroidea + Articlata*	*Echinodea*	○ *Chaetognatha*	⧺ *Indeterminate Crustacea*	⧺ *Indeterminate Decapoda*	*Natantia*	○ *Reptantia larvae*
* *Engraulis encrasicolus*	8-20	363	32	14.8	0.9	5.9	0.2	19.3	0	0	28.7	0.6	0.5	0	.1
* *Sprattus sprattus*	3-15	1377	159	1.9	3.1	0.2	<.1	37.5	0	0	0.2	0.4	0.8	0	0.3
* *Clupea harengus*	3-24	81	14	0.3	0	17.8	6.2	0.3	0	0	0	2.2	6.8	<.1	0.6
* *Maurolecus muelleri*	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0
+ *Merlangius merlangus*	4-32	592	47	0.5	0.2	0.8	5.0	1.0	0	<.1	0.1	2.0	5.9	0	3.2
+ *Trisopterus luscus*	21	1	1	0	0	0	0	0	0	0	0	0	0	0	0
x *Gadus morhua*	16-26	2	0	0	0	0	0	0	0	0	0	0	0	71.4	0
+ *Melanogrammus aeglefinus*	22	1	0	0	0	0	0	0	0	0	0	0	0	0	0
+ *Trachurus trachurus*	5-13	22	20	0	12.5	0	12.5	0	0	0	0	62.5	0	0	0
* Ammodytidae	3-30	394	98	0.2	3.9	1.4	0.3	40.6	0	0	0.1	<.1	0.7	0	<.1
x *Echiichthys vipera*	9-13	15	9	0	0	0	2.0	0	0	0	0	1.0	84.0	0	0
* *Scomber scombrus*	11-37	16	1	0	0.8	17.9	39.1	0	0	0	0	4.1	23.6	0	1.4
+ Gobiidae	2-5	18	14	0	0	0	0	0	0	0	0	0	0	0	0
x Callionymiidae	5-22	17	1	0	0	0	0	0	15.5	0	0	7.8	0	0	0
+ *Eutrigla gurnardus*	7-34	283	110	<0.1	0	3.0	6.7	0	0.5	0	0	9.2	12.4	25.4	8.0
+ *Agonus cataphractus*	6-10	2	1	0	0	0	0	0	0	0	0	0	9.1	0	0
+ *Cyclopterus lumpus*	4-50	4	0	28.5	15.2	3.3	0	0	0	0	0	0	14.3	0	0
Arnoglossus laterna	13	1	1	0	0	0	0	0	0	0	0	0	0	0	0
+ *Limanda limanda*	6-35	362	62	0.2	1.3	0	3.0	0	26.4	0.3	0	3.3	1.1	1.5	0.5
x *Pleuronectes platessa*	23-32	3	2	0	0	0	0	0	0	0	0	0	0	0	0
Microstomus kitt	20	1	0	0	0	0	0	0	0	0	0	0	0	0	0
+ *Hippoglossoides platessoides*	7-17	4	0	0	0	0	0	0	2.9	0	0	44.2	0	0	0
Plankton				<.1	0.7	0.1	<.1	4.4	<.1	0	0.9	0	2.7	<.1	0.4

Key
* Plankton-feeding fish
+ Semi-planktonic feeders
x Benthic feeders
○ Planktonic forms
ϕ Semi-planktonic forms
⧺ Mixture of adults and larvae

Table 9 continued

Fish predators	Prey organisms															
	Reptantia adults	○ *Euphausiacea*	∅ *Amphipoda*	∅ *Isopoda*	○ *Cumacea*	○ *Mysidacea*	∅ *Harpacticoida*	○ *Calanoida*	○ *Cladocera*	*Polychaete larvae*	*Polychaete adults*	*Bivalvia*	*Gastropoda*	*Actinaria*	*Hydrozoa*	*Other prey*
* *Engraulis encrasicolus*	0	0.4	0.2	0	<.1	0	1.5	26.6	0	<.1	<.1	0.1	0	<.1	<.1	0
* *Sprattus sprattus*	0	1.0	1.1	0	0.3	<.1	2.6	46.2	2.0	0.1	0	0.6	1.6	0	0	0
* *Clupea harengus*	0	7.8	9.6	0	0	0	0	40.2	0	0.3	5.0	0.3	2.5	0	0	<.1
* *Maurolecus muelleri*	0	7.1	0	0	0	0	0	92.9	0	0	0	0	0	0	0	0
+ *Merlangius merlangus*	0	11.6	6.7	0	0.6	0.2	1.3	53.7	1.4	<.1	0.2	0	5.4	0	0	<.1
+ *Trisopterus luscus*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
x *Gadus morhua*	28.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
+ *Melanogrammus aeglefinus*	0	14.3	85.7	0	0	0	0	0	0	0	0	0	0	0	0	0
+ *Trachurus trachurus*	0	0	12.5	0	0	0	0	0	0	0	0	0	0	0	0	0
* Ammodytidae	0	1.7	0.8	0	0.1	0	0.8	47.3	0.7	<.1	0.3	<.1	<.1	0	0	1.0
x *Echiichthys vipera*	0	5.0	0	0	0	7.0	0	0	0	1.0	0	0	0	0	0	0
* *Scomber scombrus*	0	7.1	2.7	0	0	0	0	3.3	0	0	0	0	0	0	0	0
+ Gobiidae	0	7.7	38.5	0	0	0	53.8	0	0	0	0	0	0	0	0	0
x Callionymiidae	0.8	0	17.8	0.8	7.8	0	24.7	0	0	0	0.8	7.8	16.2	0	0	0
+ *Eutrigla gurnardus*	<.1	7.1	12.6	0	9.6	0.5	3.8	0	<.1	0.5	0.5	0	0	0	0	0
+ *Agonus cataphractus*	0	0	54.5	0	27.3	0	0	9.1	0	0	0	0	0	0	0	0
+ *Cyclopterus lumpus*	0	4.8	16.7	0	0	0	0	0	0	0	0.5	0	0	0	0	16.7
Arnoglossus laterna	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
+ *Limanda limanda*	1.2	0.3	15.8	.1	5.4	0	16.8	0.8	0	0	7.8	7.6	0.6	0.2	1.1	4.7
x *Pleuronectes platessa*	0	0	16.7	0	0	0	0	0	0	0	0	83.3	0	0	0	0
Microstomus kitt	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0
+ *Hippoglossoides platessoides*	5.9	29.4	0	0	0	0	0	0	0	0	0	14.7	2.9	0	0	0
Plankton	<.1	<.1	0.2	0.1	<.1	<.1	0.7	84.0	3.3	0.5	<.1	0	1.5	0	0	<.1

4.2.9 O-group fish

The Lowestoft frame trawl was used on CORELLA cruises 6-13 and CLIONE cruise 15 to sample pelagic O-group fish: CORELLA 6,7 and 8 were confined to the inshore region within 20 nautical miles of the north-east coast of England; CORELLA 9 was an extensive survey covering a wider area of the North Sea and formed part of the International Council for the Exploration of the Sea (ICES) young gadoid survey (Daan *et al.*, 1976); CORELLA 10-13 and CLIONE 15 extended offshore to 2°E, samples being collected at selected standard plankton haul positions. Catches are shown in Table 10.

Clupeids dominated the catches from the inshore region in spring, with overwintering sprat predominant. Sprat catches declined in late spring and early summer, then recovered their dominance in late summer and autumn. Of the gadoids, only whiting was taken regularly and its largest proportions were in early summer. Amongst the flatfishes, dab was commonly caught between May and September, scaldfish appeared in the summer months, lemon sole and long rough dab were common in autumn samples, and plaice were taken in small numbers and only in July. Sandeels and gobies were the only other species to occur in significant numbers and these only during the summer months.

The data for June-October were used to determine the offshore distributions of young fish (post-larvae and O-group) before they moved to inshore nursery areas or entered the pre-adult phase offshore. They were also used to locate where the eggs and larvae drift, which may be considered to be offshore O-group nursery areas for species such as the sprat, herring, cod and whiting.

Table 10 Proportions of fish species caught with the Lowestoft frame trawl in 1976.

Species	Cruise number							
	6	7	8	10	11	12	13	15
	Number of stations occupied							
	6	6	12	16	52	23	28	29
	Positive stations							
	4	2	8	14	39	20	19	21
Myxine glutinosa				0.6		0.4		
Clupeidae (indet.)					13.0	2.6	4.8	0.4
Sprattus sprattus	99.0	47.0	79.4		20.5	27.1	61.1	52.0
Clupea harengus	0.8					5.3		
Syngnathus rostellatus						0.7	0.9	
Entelurus aequoreus					0.4			0.2
Gadidae (indet.)				1.3	0.8		0.4	0.2
Merlangius merlangus		29.4	1.4	74.5	22.9	5.6	4.8	1.2
Gadus morhua				3.3			0.4	
Rocklings				4.6	0.4	0.4		
Enchelyopus cimbrius			1.4			0.7	2.6	21.4
Trachurus trachurus					16.6	4.1	2.2	0.2
Ammodytidae (indet.)			2.7		0.4			1.0
Gymnammodytes semisquamatus					0.4			
Ammodytes tobianus							0.4	0.2
Ammodytes marinus						0.7		
Hyperoplus lanceolatus						0.4		0.2
Echiichthys vipera			1.4					
Scomber scombrus					1.6			
Gobiidae (indet.)		11.8		0.6	7.9	8.6	0.9	0.4
Pomatoschistus microps					1.6			
Pomatoschistus minutus		11.8	2.7		1.6	13.5	12.7	6.4
Callionymus lyra					0.4		0.4	0.2
Callionymus reticulatus						2.2		
Lumpenus lumpretaeformis				0.6				
Pholis gunellus					0.4			
Triglidae (indet.)					1.6	2.2	0.4	0.2
Eutrigla gurnardus							0.9	3.0
Agonus catophractus							0.4	
Cyclopterus lumpus				0.6				
Liparis liparis			1.4			0.4		
Phrynorhombus norvegicus						0.4		
Arnoglossus laterna					5.5	17.3		
Limanda limanda			9.6	8.5	1.2	6.4	6.1	1.4
Pleuronectes platessa				2.6				
Microstomus kitt	0.2				1.6			9.1
Glyptocephalus cynoglossus				1.3			0.4	2.2
Hippoglossoides platessoides				1.3	1.2	0.4		
Total number of specimens	601	17	73	153	253	266	229	496

5. Summary and conclusions

The results, obtained from the 1976 series of surveys in the sea area off the north-east coast of England, have thrown new light on the ecology of the early developmental stages in the life history of fish spawning in this region of the North Sea.

Hydrographic observations demonstrated that summer and winter regimes were very different and that the classical notion of a persistent south-easterly drift of water through the area was not entirely true. In 1976, the inshore water close to the coast always flowed to the south and east, but offshore the water movement was influenced by the strength and direction of local winds which caused reversals of flow and generated gyrals in both seasons. In summer, a strong frontal zone developed between mixed, shallow coastal and banks waters and stratified, deep water north-east of Flamborough Head.

The fish populations could be divided into two communities which spawned either in the shallow coastal and banks waters, or in the deep water which stratified in summer. A succession of spawnings occurred throughout the year by different species on the same spawning grounds. These spawnings were also linked to the seasonal movements of the water masses, to the production cycles of planktonic organisms on which larvae and young fish feed, and it is reasonable to suppose that they were associated with bottom topography and sediment type. Thus, winter spawnings of commercially important fish such as plaice and cod in the deep water produced patches of eggs and larvae which either remained stationary in a transitory winter gyral situated to the north-east of Flamborough Head or drifted slowly in a north-westerly direction towards the coast. Larvae and young fish concentrated at the boundary between shallow coastal water and the deeper offshore water, where production was high and feeding good, before migrating to inshore nursery areas. Summer spawnings in the same location also led to distributions of both eggs and larvae which were closely associated with the high production characteristic of the frontal boundary zone at that time of year. Fish which spawned in coastal waters and on the Dogger Bank and Norfolk banks produced pelagic eggs and larvae which also tended to accumulate near the frontal boundary zone. All the results indicated that circulation patterns of the water masses on both sides of the front tended to carry the eggs and larvae nearer to and along this boundary.

We suggest that mechanisms by which larvae and young fish remain near the front or cross it to reach their nursery areas are behavioural responses to the biological and hydrographical regimes found at the front. This hypothesis needs to be tested at sea through microscale surveys in three dimensions to sample the hydrography, plankton and fish communities at fronts. *In situ* sensors for rapid and continuous hydrographic observations have already been developed and used successfully to study fronts. Whilst pumps, fluorometers, particle counting equipment, camera and echo-sounders have been used to examine plankton and fish distributions, no concerted programme has yet been undertaken to investigate a front systematically, and the problems of collecting larvae and young fish quantatively in a microscale survey have yet to be solved.

The analysis of stomach contents of fish larvae and fish predators of fish eggs and larvae taken during the 1976 surveys gave valuable information on their diets. The fish larvae had varied diets ranging from phytoplankton through the various developmental stages of copepods to larval forms of molluscs. The size of the items in their diets was shown to change with their mouth gape which increased with age of larvae. Differences were observed between the diets of this larval community and the diets of larvae in the Southern Bight of the North Sea. One interesting dietary difference recorded was for plaice and sandeel larvae which fed almost exclusively on *Oikopleura dioica* in the Southern Bight but which had a more varied diet, with copepods dominant, in the western central North Sea. Pelagic fish were the most important predators of fish eggs and larvae. No fish predator occurring in significant numbers was found feeding exclusively on fish eggs and larvae. The problem of quantifying such feeding data persists; its solution requires controlled feeding experiments to determine ingestion and digestion rates. The problem of determining the abundance of fish predators also needs to be solved before the effect of predation on the mortality of eggs and larvae of fish can be assessed.

The study of the inshore nursery areas will be reported elsewhere. Although the 1976 surveys have illustrated the process in general terms, the links between larval drift and recruitment to nursery grounds have still to be described in detail.

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