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The Diel Migrations and Distributions within a Mesopelagic Community in the North East Atlantic. 1. Introduction and Sampling Procedures

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CONTENTS

1. INTRODUCTION

DIEL VERTICAL migrations of planktonic animals have been studied since CUVIER (1817) described this phenomenon in fresh water Cladocera. The literature has been reviewed several times, notably by RUSSELL (1927), KIKUCHI (1930), CUSHING (1951), BAINBRIDGE (1961), BANSE (1964), VINOGRADOV (1968), LONGHURST (1976) and, most recently by PEARRE (1979). Most of this previous work described the movements of particular species or groups in isolation, and little of it was based upon systematic repeated sampling over complete diel periods.

In April 1972, NW of the Canary Islands, a series of hourly hauls was made at a constant depth over a 24 hr period. From this 24 hr series ROE (1974) analysed the diel migrations of 104 species representing 8 orders, which clearly showed the dynamic nature of the *community*. The work was, however, limited by being confined to a single depth and to a single 24 hr period, and few physical data were collected in conjunction with the biological samples. It was, therefore, impossible to determine whether or not animals behaved the same way during consecutive diel periods; whether they migrated between the same depths; whether closely related or competing species remained vertically or temporally segregated; whether deeper living migrants such as decapods and fish had optimum day depths or whether they moved up and down more or less continuously. The 24 hr series enabled feeding relationships to be analysed in conjunction with the migratory cycles of predator and prey (FOXTON and ROE, 1974; MERRETT and ROE, 1974), but this work was similarly limited as it was difficult to determine whether or not feeding occurred at other depths or times within the diel cycles.

To investigate these sorts of problems it was decided to extend the 24 hr observations by sampling four different depths for a period of 48 hr each.

The present paper serves as an introduction to the results of this 48 hr series. It describes the background of the sampling programme, the methods used and the gross results of total numbers and numbers of species. It is followed by accounts of the various groups and a statistical analysis of the total data set.

2. BIOLOGICAL BACKGROUND

Since the 24 hr series (ROE, 1974) there have been a few studies of diel migrations which have been based upon repeated samples taken over 24 hr periods. Most of these, however, have been done in shallow or near-surface waters and they have been restricted to individual species or groups, e.g. KOLESNIKOV (1973), WHITE, HEATON and SCHMITZ (1979) and ITOH, HIRATA, TANAKA, INOUE and IRIE (1979). Perhaps the most detailed has been that of ENRIGHT and HONEGGER (1977) who fished two depths for several periods of up to three consecutive days, and described the timing and speed of migration of two species of copepod (ENRIGHT, 1977; ENRIGHT and HONEGGER, 1977).

HOPKINS, FALK-PETERSEN, TAUDE and EILERTSEN (1978) examined the vertical migrations of euphausiids, chaetognaths and calanoid copepods in relation to each other and to the diel movements of sound scattering layers in a Norwegian fiord, but the only large scale oceanic sampling programme which is likely to be comparable with the present work is that carried out on the Scripps Institution of Oceanography's CLIMAX cruises (ANONYMOUS, 1974, 1975). On these cruises a considerable number of replicated samples were taken over periods of up to 10 days to depths of 600 m, but only the results for amphipods (SHULENBERGER, 1977, 1978, 1979, 1980), larval fish (LOEB, 1979) and copepods (MCGOWAN and WALKER, 1979) have been published so far.

The present sampling position was centred on 44°N 13°W. There is little information on the vertical distributions of zooplankton and nekton of this area which has been based upon systematic sampling with opening and closing nets. The first attempt was that of FOWLER in July 1900 from H.M.S. *Research* (FOWLER, 1904), and these collections (STEBBING, 1904, – amphipods and Cladocera; FOWLER, 1905a, b, 1909, – chaetognaths, Thaliacea and ostracods; HOLT and TATTERSALL, 1905, – euphausiids and mysids; WOLFENDEN, 1905, – Radiolaria; PELSENEER, 1906, – molluscs excluding cephalopods; HOYLE, 1906, – cephalopods; BROWNE, 1906, – medusae; HOLT and BYRNE 1907, – fish; KEMP, 1907, – decapods; BIGELOW, 1911, – siphonophores; and FARRAN, 1926, – copepods), remain the most complete body of information on the mesopelagic fauna of the region.

COLMAN (1962) analysed the numbers of various groups caught to depths of 1200 m by day and 4000 m by night, and the area is covered by the survey of the continuous plankton recorder (EDINBURGH OCEANOGRAPHIC LABORATORY, 1973). This survey has produced an enormous amount of data on numerous phyto- and zooplanktonic species but it is restricted to a depth of 10 m.

Similarly much of the French biological work in the Bay of Biscay is limited either to coastal areas or to shallow depths. BEAUDOUIN (1971, 1975) analysed the occurrence of various groups taken throughout the year between 100 m depth and the surface. Other workers have made general volumetric studies, (e.g. LE GALL and L'HERROUX, 1971), or have examined various individual groups, (e.g. PATRITI, 1965a, b, 1966, – siphonophores; ARBAULT and BOUTIN, 1968, – fish; ABBES, 1970, – cephalopods; ABBES and CASANOVA, 1973, –

decapods; and LAGARDÈRE, 1975, 1977, – decapods). CASANOVA (1977) analysed the zoogeography, the taxonomy and various biological aspects of the populations of several groups of mesopelagic animals between the Bay of Biscay and the west African coast. His work is the most comprehensive zoogeographic study so far undertaken in the area and includes an extensive bibliography.

Between 1968 and 1972 the Institute of Oceanographic Sciences established a line of stations at approximately 10° intervals of latitude between 11°N and 60°N along the 20°W meridian. The two nearest stations to the present position are at 53°N and 40°N where day and night vertical series were made to depths of 2000 m. ANGEL (1977a) described the distribution of ostracods from a vertical series made prior to the 48 hr series at 44°N 13°W, and later, (1977b), made some preliminary observations on the 48 hr series itself. The most recent study in this general area is that of LONGHURST and WILLIAMS (1979) who worked a section of oblique hauls with a LONGHURST–HARDY plankton recorder from off Cape Finisterre to north of 60°N.

The area has been the subject of several zoogeographic studies (EKMAN, 1953; FRASER, 1961; CASANOVA, 1977; BACKUS, CRADDOCK, HAEDRICH and ROBISON, 1977; and FASHAM and FOXTON, 1979) and finally, various oceanographic expeditions have passed through the area, including the *Valdivia* (1898–99), the *Princess Alice* and *Hirondelle* (between 1906–1914), the *Thor* (between 1908–1910), the *Michael Sars* (1910) and Wolfenden's private yacht *Silver Belle* between 1904 and 1907. The hauls made by these expeditions were sporadic and where appropriate they will be referred to in the analyses of individual groups.

3. PHYSICAL BACKGROUND

The sampling position, 44°N 13°W, lies within an area of weak and poorly defined currents which are often marked by variable wind driven surface movements – the North Atlantic Drift (HELLAND-HANSEN and NANSEN, 1926; ISELIN, 1936; DEFANT, 1961, MADELAIN, 1967; and WEGNER, 1973). FRUCHAUD (1975), FRUCHAUD-LAPARRA, LE FOCH, LE TAREAU and TANGUY (1976) and FRUCHAUD-LAPPARA, LE FOCH, LE ROY, LE TAREAU and MADELAIN (1976) have recently carried out a three year hydrographic survey of the entire Bay of Biscay region. The general homogeneity of their vertical profiles of temperature, salinity and oxygen agree with those described here. The area is, however, subject to mesoscale activity, (MADELAIN and KERUT, 1978; DICKSON and HUGHES, 1981), and there are also indications of this in our TS profiles.

This region may lie on the northern boundary of the subtropical gyre, but this is a poorly defined feature in the eastern Atlantic. Indeed, WORTHINGTON (1962, 1976) has suggested that this circulation is restricted to the western Atlantic. FASHAM and FOXTON (1979) have discussed the physical oceanography of this area in relation to the faunal zonation of decapods. They found evidence of a faunal boundary between 40°N and 53°N which they suggested may mark the northern edge of the subtropical gyre. They also described seasonal differences between 40°N and 53°N in that the shallow thermocline is permanent at 40°N but breaks down in winter at 53°N. There must be a thermal front in winter between these positions which may affect the animal distributions.

4. MATERIALS AND METHODS

The samples were taken with the I.O.S. combination midwater trawl, the RMT 1 + 8 (BAKER, CLARKE and HARRIS, 1973). Briefly this system consists of a small mouth area net of mesh

TABLE 1. SAMPLING DATA FOR THE 100 m SERIES

Station No.	Date April 1974	Haul No.	Time (GMT)	Depth Range (m)	Mean Depth (m)	Mean Temp. °C	Volume of water filtered m^3 RMT 1	RMT 8
8507#37	6	(1)	1001-1101	95-110	100.5	12.0	2876.6	31548.7
38	6	(2)	1204-1304	90-110	100.2	12.1	2797.7	33389.5
39	6	(3)	1404-1504	95-110	101.2	12.2	2711.8	34335.4
40	6	(4)	1629-1729	95-109	102.0	12.2	2711.8	34335.4
41	6	(5)	1801-1901	96-112	103.7	12.1	2843.7	32551.8
42	6	(6)	1922-2023	95-111	101.6	12.2	2778.3	34721.6
43	6	(7)	2052-2152	95-112	102.8	12.1	2892.4	30385.2
44	6	(8)	2219-2320	95-105	100.5	12.1	2912.2	32529.5
45	7	(9)	0017-0117	92-110	102.1	12.2	2676.6	34593.3
46	7	(10)	0224-0324	93-105	99.3	12.2	2767.9	33783.0
47	7	(11)	0406-0506	96-105	100.1	12.1	2797.7	33389.5
48	7	(12)	0551-0654	93-110	98.8	12.1	2880.3	35754.2
49	7	(13)	0718-0819	95-110	100.2	11.9	2778.3	34721.6
50	7	(14)	1028-1128	93-110	101.1	12.2	2797.7	33389.5
51	7	(15)	1223-1324	90-107	97.3	12.2	2778.3	34721.6
53	7	(16)	1632-1732	90-105	97.3	12.1	2613.9	34922.6
54	7	(17)	1756-1856	90-110	99.7	12.0	2545.5	35129.8
55	7	(18)	1915-2015	90-110	100.0	12.1	2822.1	32991.5
56	7	(19)	2045-2145	94-107	101.2	12.0	2797.7	33389.5
57	7	(20)	2301-0001	90-110	99.8	12.1	2676.6	34593.3
58	8	(21)	0128-0228	95-110	100.2	12.1	2613.9	34922.6
59	8	(22)	0356-0456	95-105	100.4	12.1	2643.7	34784.4
60	8	(23)	0552-0652	94-107	100.3	12.2	2711.8	34335.4
61	8	(24)	0718-0818	95-110	99.2	12.0	2643.7	34784.4
62	8	(25)	0848-0948	95-110	100.4	11.9	2876.6	31548.7
Overall Mean					100.4	12.1	2757.9	33822.1
No. Hauls		25						

Day 1 Sunrise at 0622h Sunset 1933h
Day 2 " 0621 " 1934
Day 3 " 0619

size 0.32 mm (RMT 1) combined within the same frame as a large mouth area net (RMT 8) mesh size 4.5 mm. The effective mouth areas of these nets vary with the towing speed (ROE, BAKER, CARSON, WILD and SHALE, 1980). The nets are opened and closed acoustically, and the depth of the net, the water temperature, a measure of the speed of the net through the water and the distance travelled (collectively called flow), and an indication of whether the nets are open or closed are continuously telemetered back to the ship.

TABLE 2. SAMPLING DATA FOR THE 250 m SERIES

Station No.	Date April 1974	Haul No.	Time (GMT)	Depth Range (m)	Mean Depth (m)	Mean Temp °C	Volume of water filtered m^3 RMT 1	RMT 8
8507#74	10	(26)	0910-1010	243-260	251.3	11.5	2816.9	-
75	10	(27)	1200-1300	240-260	250.7	11.5	2789.1	33512.9
76	10	(28)	1448-1548	250-260	255.0	11.6	2755.2	-
77	10	(29)	1710-1810	240-260	251.0	11.6	2843.7	32551.8
78	10	(30)	1935-2035	240-260	252.7	11.6	2884.0	31178.3
79	10	(31)	2117-2217	245-255	249.5	11.8	2735.6	34125.5
80	10	(32)	2309-0009	232-262	250.2	11.9	2755.2	33926.1
81	11	(33)	0150-0250	238-255	249.5	12.0	2718.7	34277.9
82	11	(34)	0331-0431	240-260	251.1	11.9	2891.1	30589.9
83	11	(35)	0543-0643	242-262	250.5	11.8	2728.9	34187.9
84	11	(36)	0724-0824	240-255	248.4	12.0	2545.5	35129.8
85	11	(37)	0908-1008	240-260	250.0	11.9	2827.2	32897.4
86	11	(38)	1128-1228	240-260	250.9	11.9	2789.1	33512.9
87	11	(39)	1314-1415	249-260	253.8	12.0	2921.9	32182.2
88	11	(40)	1449-1549	240-260	247.6	12.0	2863.8	32014.7
89	11	(41)	1706-1806	245-260	252.5	12.0	2789.1	33512.9
90	11	(42)	1909-2016	240-265	252.0	12.0	3187.1	36061.2
91	11	(43)	2245-2345	240-260	250.2	11.9	2568.5	35076.1
92	12	(44)	0058-0158	240-260	249.5	12.0	2774.0	33708.4
93	12	(45)	0238-0340	240-260	250.3	11.9	2790.1	35575.8
94	12	(46)	0419-0519	240-265	250.2	11.9	2718.7	34277.9
95	12	(47)	0555-0655	245-260	250.3	11.9	2789.1	33512.9
96	12	(48)	0903-1003	235-260	247.0	11.9	2755.2	33926.1
Overall Mean					250.6	11.8	2792.9	33606.6
No. Hauls		23						

Day 1 Sunrise at 0615h Sunset 1939h
Day 2 " 0613 Sunset 1940
Day 3 " 0611

To provide gross information on the vertical distributions and migrations of the animals within the area a day and a night vertical series was made between 1000 and 0 m, sampling 100 m depth layers (ANGEL, 1977a). The 48 hr series was then fished as follows.

Four depths were sampled for a period of 48 hr each. The depths were chosen partly as a result of the animals caught in the previous vertical series and partly for comparison with the 24 hr series of ROE (1974, – fished at 250 m). Tables 1–4 give details of each haul. Each haul was fished horizontally for about one hour. At each depth as many hauls as possible were

TABLE 3. SAMPLING DATA FOR THE 450 m SERIES

Station No.	Date April 1974	Haul No.	Time (GMT)	Depth Range (m)	Mean Depth (m)	Mean Temp. °C	Volume of water filtered m^3 RMT 1	RMT 8
8508#43	17	(72)	0717-0818	440-460	450.1	10.9	2885.9	28992.9
44	17	(73)	0909-1010	440-465	451.4	10.9	2910.1	28302.9
45	17	(74)	1102-1202	440-460	450.0	10.9	2888.7	29223.4
46	17	(75)	1306-1406	440-460	450.2	11.2	2884.8	28915.3
47	17	(76)	1502-1602	440-465	449.5	11.1	2871.4	28197.3
48	17	(77)	1655-1755	440-460	450.2	11.2	2888.5	30856.2
49	17	(78)	1851-1951	440-460	451.6	11.2	2843.7	32551.8
50	17	(79)	2045-2145	440-460	450.0	11.1	2892.4	30385.2
51	17	(80)	2241-2341	440-465	450.4	11.1	2892.9	30246.3
52	18	(81)	0030-0130	440-460	451.2	11.2	2888.5	30856.2
53	18	(82)	0224-0324	440-470	452.0	11.1	2854.3	32289.6
54	18	(83)	0430-0530	440-460	451.1	11.1	2888.5	30856.2
55	18	(84)	0628-0728	440-460	450.6	11.1	2888.5	30856.2
56	18	(85)	0823-0923	435-465	449.5	11.2	2891.1	30589.9
57	18	(86)	1017-1117	425-460	450.3	11.2	2891.1	30589.9
58	18	(87)	1219-1319	440-470	450.5	11.1	-	-
59	18	(88)	1415-1515	440-460	449.2	11.1	-	-
60	18	(89)	1610-1710	440-460	451.7	11.1	-	-
61	18	(90)	1808-1908	440-460	451.3	11.2	-	-
62	18	(91)	2007-2107	440-460	450.6	11.2	-	-
63	18	(92)	2158-2258	440-460	451.0	11.1	-	-
64	18	(93)	2346-0046	440-460	452.1	11.1	-	-
65	19	(94)	0133-0233	440-460	449.4	11.2	-	-
66	19	(95)	0323-0423	440-465	451.4	11.1	-	-
67	19	(96)	0530-0630	440-460	450.9	11.1	-	-
68	19	(97)	0718-0819	440-460	451.6	11.2	-	-
Overall Mean					450.7	11.1	2884.0	30247.3
No. Hauls		26						

Day 1 Sunrise 0604h Sunset 1941h
Day 2 " 0602 " 1942
Day 3 " 0600

TABLE 4. SAMPLING DATA FOR THE 600 m SERIES

Station No.	Date April 1974	Haul No.	Time (GMT)	Depth Range (m)	Mean Depth (m)	Mean Temp. °C	Volume of water filtered m^3 RMT 1	RMT 8
8508#4	13	(49)	0950–1050	590–610	600.2	10.9	2891.1	30589.9
5	13	(50)	1211–1311	590–610	599.2	10.9	2890.0	30724.0
6	13	(51)	1422–1522	590–610	601.1	10.9	2882.4	28758.6
7	13	(52)	1628–1730	590–610	599.8	10.9	2953.1	33266.6
8	13	(53)	1914–2014	580–610	599.0	11.0	2867.4	28033.2
10	13	(55)	2347–0047	590–610	600.8	11.0	2863.8	32014.7
11	14	(56)	0149–0250	586–610	600.0	10.9	2878.3	33368.1
12	14	(57)	0349–0449	590–620	600.2	10.9	2888.5	30856.2
13	14	(58)	0551–0651	590–610	602.1	11.0	2834.5	32752.4
14	14	(59)	0756–0856	590–610	598.7	11.0	2891.9	29598.8
15	14	(60)	1007–1107	590–610	598.9	11.0	2982.9	30246.3
16	14	(61)	1209–1309	590–610	597.6	10.9	2628.3	23177.3
17*	14	(62)	1416–1503	590–612	601.4	11.0	2265.0*	23135.1*
18	14	(63)	1603–1703	590–612	600.0	10.7	2891.1	30589.9
19	14	(64)	1819–1919	590–610	601.2	10.7	2892.9	30246.3
20	14	(65)	2027–2127	590–610	600.3	10.7	2891.9	29598.8
21	14	(66)	2227–2327	590–615	601.8	10.6	2884.8	28915.3
22	15	(67)	0032–0132	590–615	601.5	10.6	2893.1	29963.1
23	15	(68)	0232–0332	590–610	601.6	10.7	2872.2	31727.2
24	15	(69)	0427–0527	590–612	600.6	10.7	2836.6	27016.4
25	15	(70)	0625–0725	590–612	600.9	10.5	2863.8	32014.7
26	15	(71)	0835–0935	585–610	600.5	10.6	2854.3	32289.6
Overall Mean					600.3	10.8	2868.7	30273.7
No. hauls		22						

*excluded from mean volumes ∵ not hour tow

Day 1 Sunrise 0610h Sunset 1943h
Day 2 " 0608 " 1945
Day 3 " 0610

made within a continuous 48 hr period. The entire programme was completed within 14 days, the 100 m hauls between 6–8 April; the 250 m between 10–12; the 450 m between 17–19 and the 600 m between the 13–15. A principal aim was to examine the different times at which species migrated through the various depth layers and consequently these were sampled as discretely as possible. There was little individual variation in depth or temperature for the hauls and they are hereafter considered to have fished at 100, 250, 450 and 600 m.

The fishing behaviour of the RMT 1 + 8 has been analysed (ROE, BAKER, CARSON, WILD and SHALE, 1980) and the flow data have been converted to volumes of water fished – assuming 100% filtration by each net. This assumption is more probable for the RMT 8 than for the RMT 1, although SAMEOTO, JAROSZYNSKI and FRASER (1977) found that a rectangular mouth area net of mesh size 243 μm filtered "nearly 100%" at a speed of 4 knots. The conversion standardises the data and since the results deal mainly with relative numerical changes they are unlikely to be affected by an absolute error due to filtration rates.

The numbers of animals are expressed hereafter as the numbers caught per 1000 m^3 of water for the RMT 1 and numbers per 10,000 m^3 for the RMT 8. The flowmeter was lost during the 450 m series and there are no flow records for the latter half of this series (Table 3). To present these latter hauls in terms of a known volume of water, the mean volumes for the 450 m series have been used.

Ninety seven RMT 1 + 8 hauls were made of which one (Stn 8508#9) has been discarded since the sampled depth layer was too wide (525–610 m). Two RMT 8 hauls have not been analysed because the net failed to close properly (Stn 8507#74 and Stn 8507#76, Table 2). Station 8508#17 (Table 4) closed prematurely and the volumes of water filtered in this haul have not been used in the calculation of mean volumes filtered at 600 m.

In addition to the RMT 1 + 8 hauls a series of non-quantitative surface samples were taken at night when the combination net was fishing. These surface samples provided supplementary information on the extent and timing of the migrations of some species.

The sunset and sunrise times for each depth are given in Tables 1–4. The mean sunset and sunrise times over the entire 14 day period were 1940 hr and 0612 hr respectively. In many of the subsequent figures these mean times are indicated and night is considered to run from sunset to sunrise.

The samples were taken in a restricted geographical area within a 9.3 km radius of 44°0.5′N 12°45′W. The track charts of the ship whilst fishing are shown in Figs 1–4. During the two week period when the samples were taken the surface current was slow, averaging 0.10 knots (G. HOWE, in ANGEL, 1974), and it was therefore possible to trawl on reciprocal courses

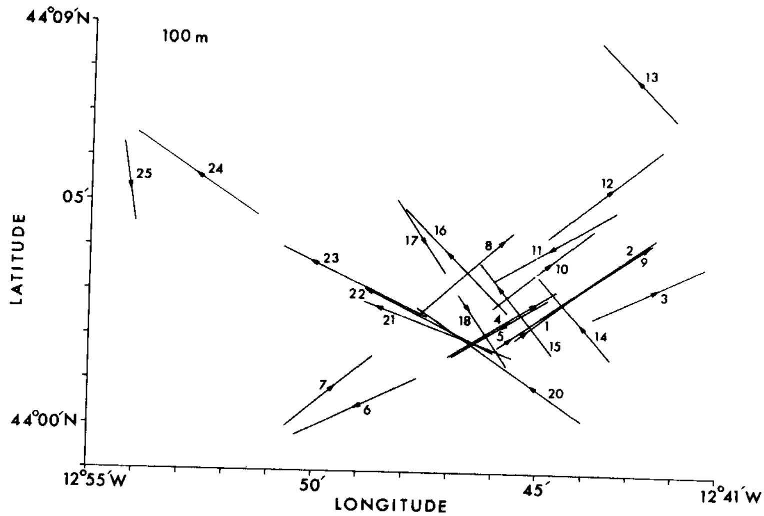

FIG. 1. Track chart of RRS '*Discovery*' whilst fishing at 100 m depth, 6–8 April. The numbers are the Haul Numbers in Table 1.

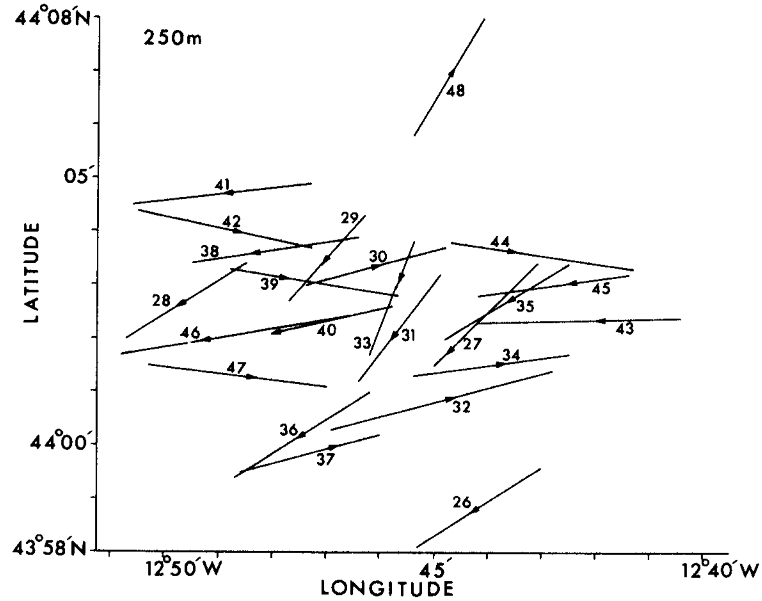

FIG. 2. Track chart of RRS '*Discovery*' whilst fishing at 250 m depth, 10–12 April. The numbers are the Haul Numbers in Table 2.

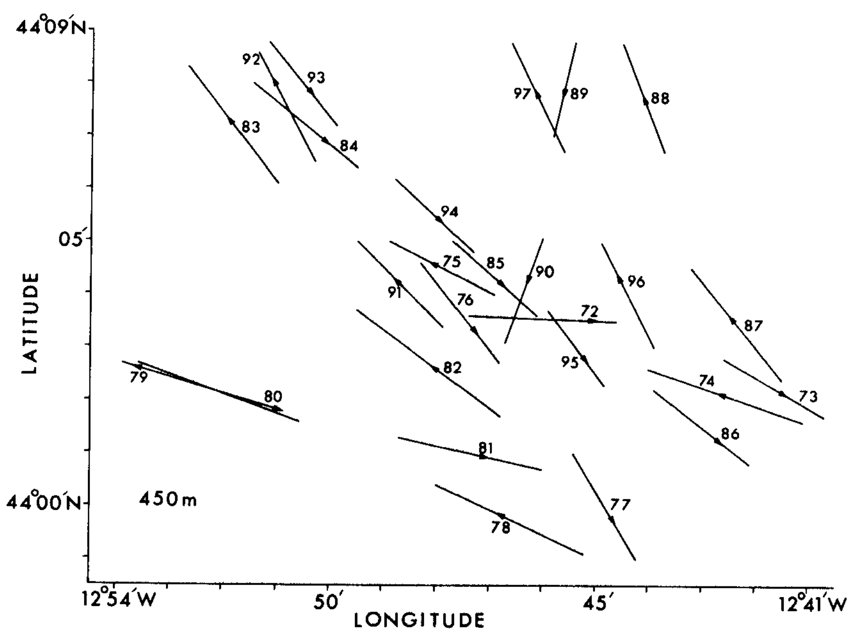

FIG. 3. Track chart of RRS '*Discovery*' whilst fishing at 450 m depth, 17–19 April. The numbers are the Haul Numbers in Table 3.

without causing great variations in fishing performance. This, in turn, enabled more hauls to be made within the 48 hr of each layer.

Eight casts were made with a Bissett–Berman S.T.D. probe between the 2nd and 19th of April (Figs 5, 6 and 7). There was little physical structure in the water column down to a depth

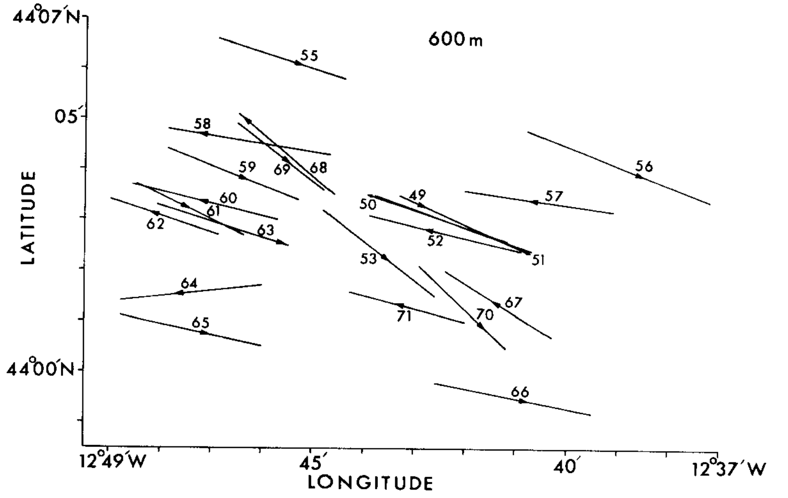

FIG. 4. Track chart of RRS '*Discovery*' whilst fishing at 600 m depth, 13–15 April. The numbers are the Haul Numbers in Table 4.

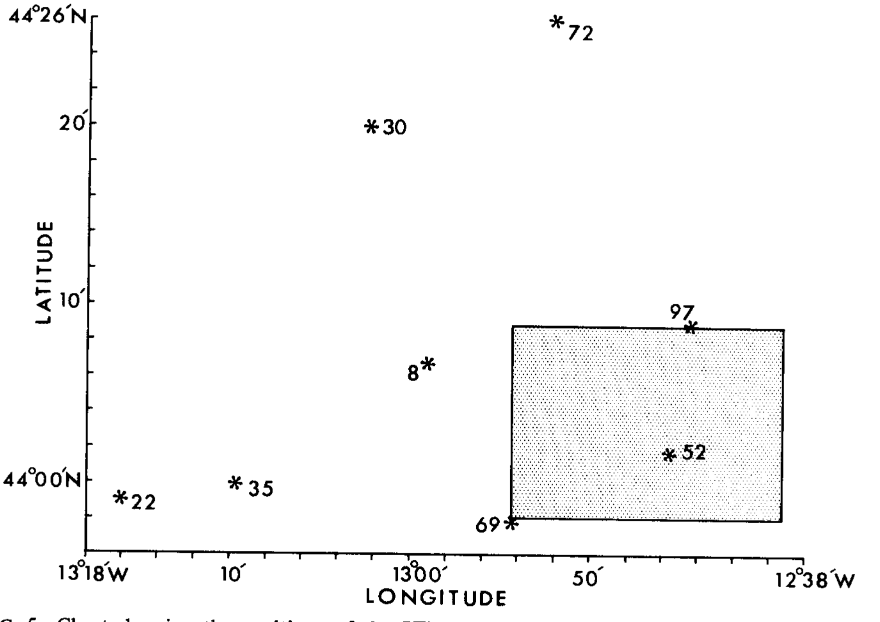

FIG. 5. Chart showing the positions of the STD casts; the numbers correspond to the station numbers in Fig. 7. The stippled region marks the area within which the biological samples were taken.

of 1000 m (Fig. 6). The surface temperature, 12.42°C, was about 0.5°C higher than at 40 m depth, suggesting the onset of stratification. The temperature decreased gradually between 40 and 980 m from 11.98 to 10.06°C. The salinity decreased from 35.699‰ at 540 m, then increased slowly to a maximum of 35.893‰ at 980 m. These slight hydrographic gradients probably had little effect on the distributions of the animals.

The TS profiles (Fig. 7) show the influence of Mediterranean water below 550 m. The

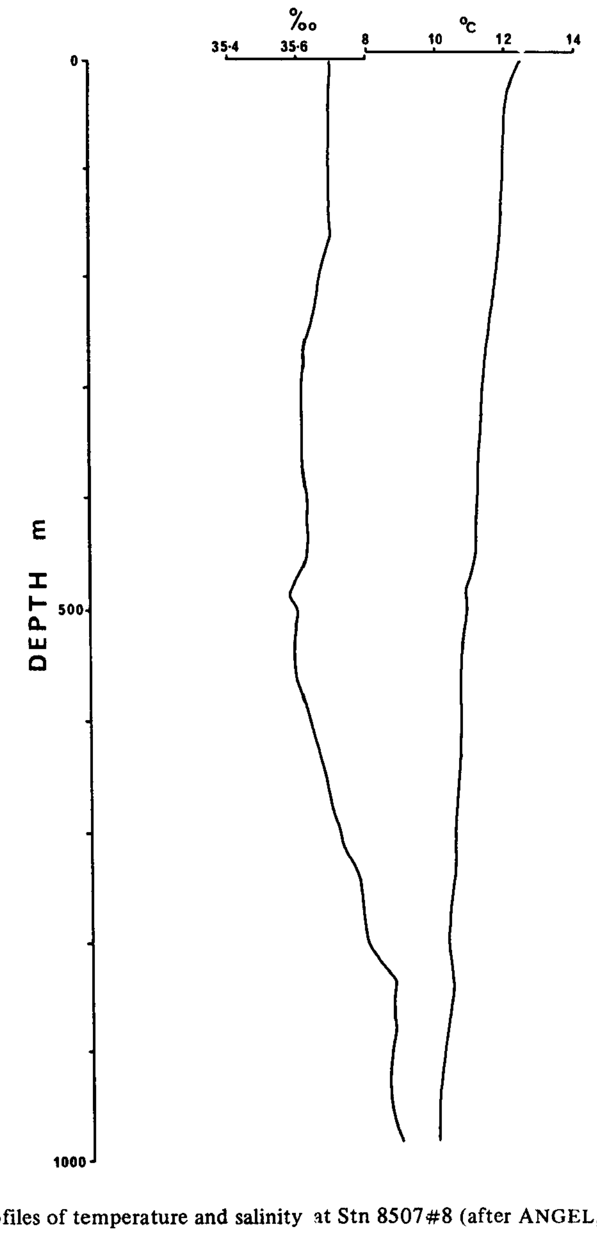

FIG. 6. Profiles of temperature and salinity at Stn 8507#8 (after ANGEL, 1977a).

depth at which this influence was first apparent varied from ca. 550 m (e.g. Dip 97, April 12) to ca. 800 m (Dip 30, April 15) and these variations may have been due to mesoscale activity (ANGEL, 1977a) so the 600 m series fished between the 13–15 April may have been subjected to mesoscale activity. It may also have been taken in the area of mixing between Mediterranean and North Atlantic water and it is therefore possible that these 600 m hauls are not directly comparable with the remaining series. There is no evidence here, however, that the fauna at 600 m was of a different provenance from that of the shallow horizons.

Ideally perhaps the type of sampling programme described here should be carried out in an

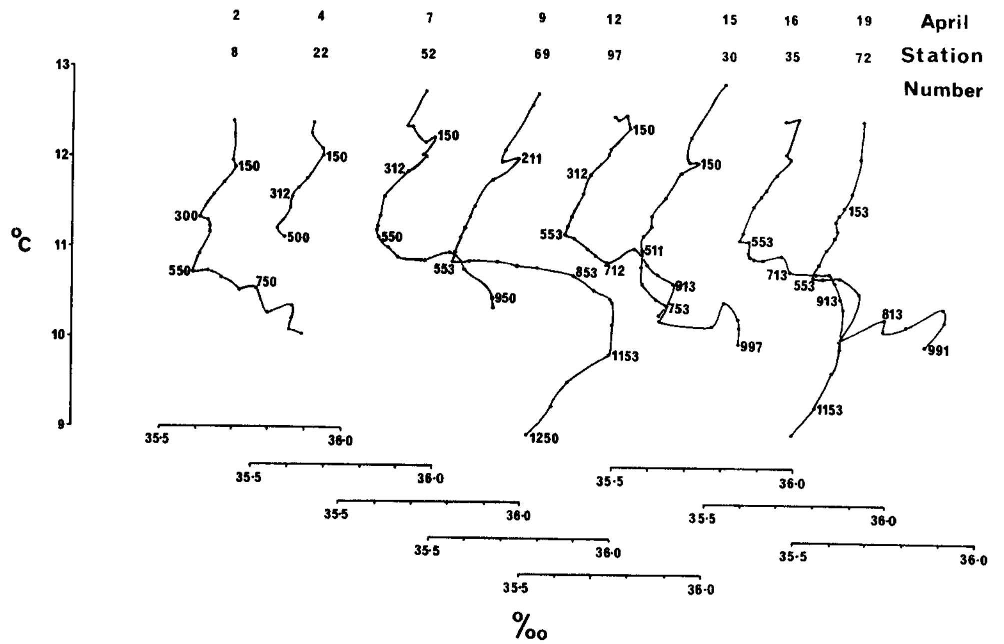

FIG. 7. TS profiles from the STD casts shown in Fig. 5. Station numbers 8, 22, 52, 69 and 97 refer to Station 8507 and numbers 30, 35 and 72 to Station 8508. The casts were made between the 2 and 19 April (after ANGEL, 1977a).

area of great stability. In this respect 44°N 13°W was not ideal, but the time scale over which these samples were taken was reasonably short (14 days) and the results are generally consistent, suggesting that any physical changes which may have occurred did not greatly affect the animal populations at this time.

A Moll–Gorczynski solarimeter was continuously monitoring the surface light intensity during this sampling programme. The resulting records are shown in Figs 8–11. On most days patchy cloud conditions predominated but the light intensity on consecutive days varied markedly. During both the 100 and 600 m series the light intensity on the first day was considerably higher than on the second (Figs 8 and 11). Conversely during the 450 m series (Fig. 10) the second day was brighter than the first. The possible effects of these variations in light intensity are discussed later.

The samples were preserved in 5% formalin and subsequently stored in a preserving fluid based upon that of Steedman (STEEDMAN, 1974). Some samples were fractioned with a Folsom Plankton Sample Splitter and the analyses of copepods and euphausiids are based upon 1/16 and variable sub-samples respectively. In the results presented later the numbers in these sub-samples have been appropriately corrected. The following groups were analysed: fish, decapod Crustacea, siphonophores, medusae and ctenophores from the RMT 8; euphausiids, mysids and amphipods from both the RMT 8 and the RMT 1; copepods and ostracods from the RMT 1. Chaetognaths were counted from the RMT 1 samples but were not analysed further.

5. DATA PRESENTATION

The numerical data derived from these analyses assumed vast proportions. They were prepared on computer punched cards and entered into the I.O.S. biological database (DOMANSKI,

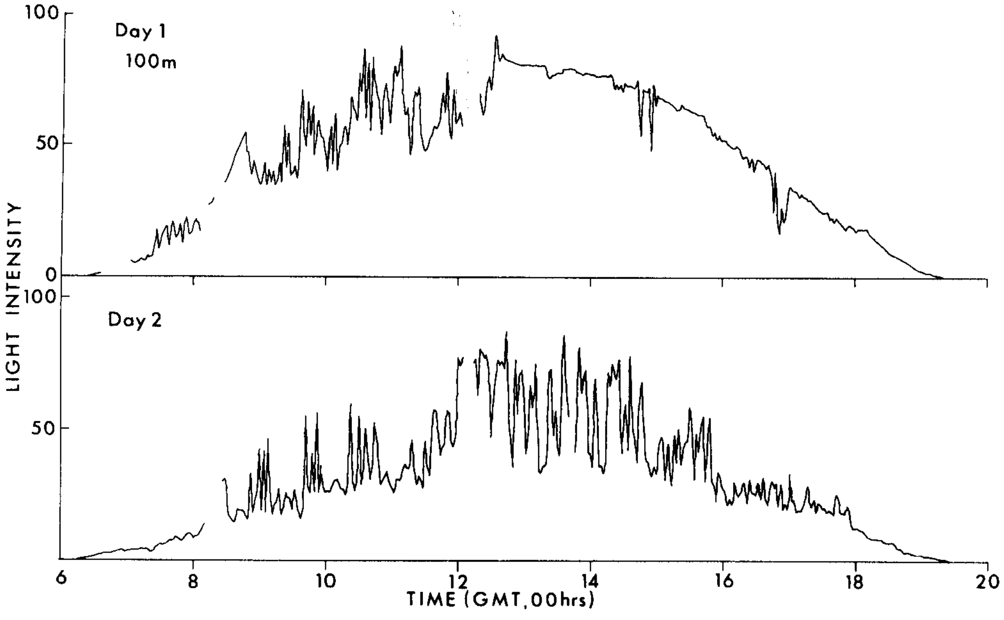

FIG. 8. Solarimeter records taken during the 100 m sampling period, 6 and 7 April. Here and in Figs 9–11 the light intensity scale is in arbitrary units and the breaks in the records are periods when the computer was otherwise engaged.

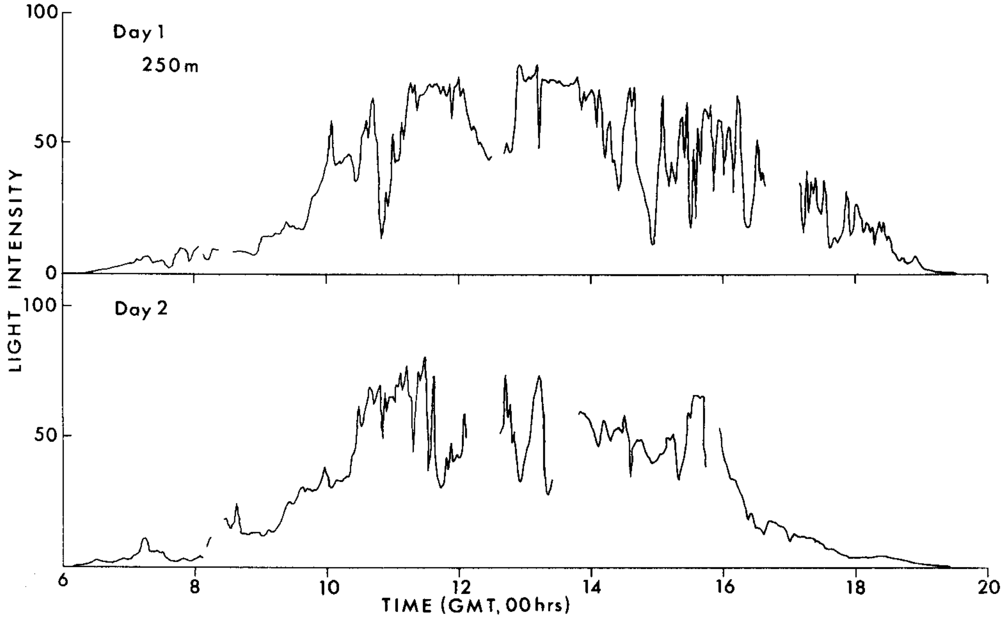

FIG. 9. Solarimeter records taken during the 250 m sampling period, 10 and 11 April.

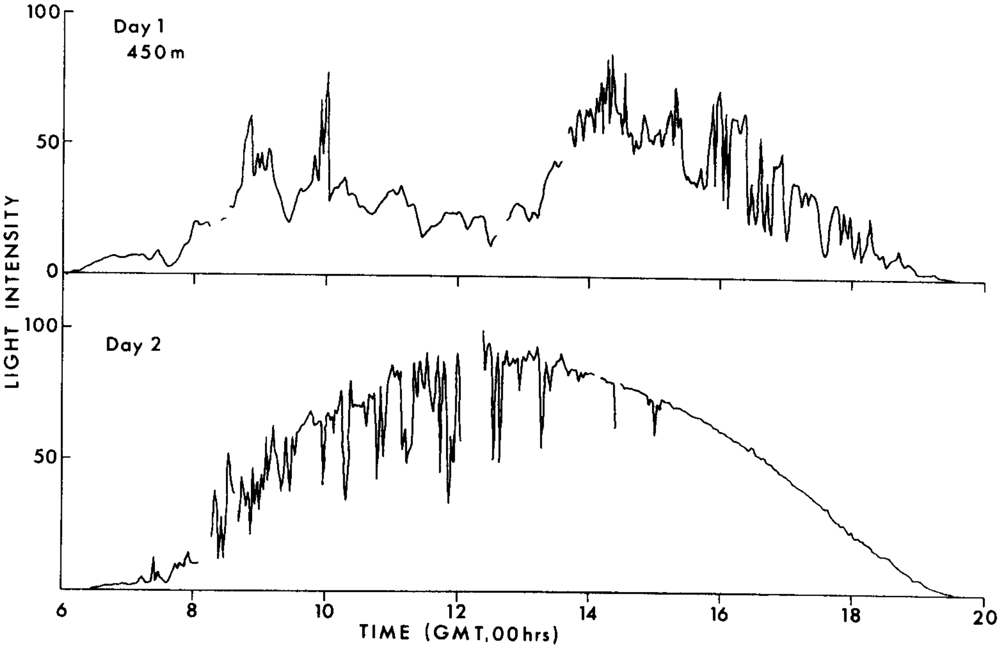

FIG. 10. Solarimeter records taken during the 450 m sampling period, 17 and 18 April.

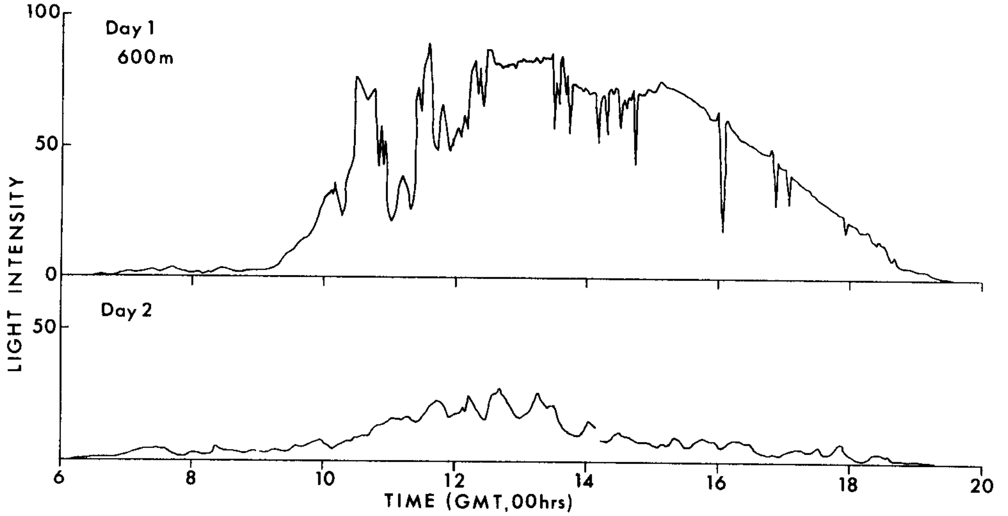

FIG. 11. Solarimeter records taken during the 600 m sampling period, 13 and 14 April.

1981). The subsequent spatial and temporal organisation of the data within the database enabled computer programmes to be used, thereby facilitating the comparative analysis of the samples.

One method of summarising the distributions of species or groups was by determining their weighted mean depths as follows:

$$\bar{D} = \frac{\Sigma n_i d_i}{n_i}$$

where d_i is the depth of a sample (i) and n_i is the numbers of individuals at that depth. This technique was first used by WORTHINGTON (1931), who applied it to freshwater plankton, and it has subsequently been employed by a number of authors, for example, GARDINER (1933), RUDJAKOV (1971) and PEARRE (1973).

To calculate the weighted mean depths the samples were first grouped into sets. Each of these consisted of one sample from each depth with each sample having a common sampling time. Figure 12 shows their construction. The first set contained the samples lying on the vertical 1000 hr axis and each sample for this set was taken at some time spanning 1000 hr. To increase the number of sets it was sometimes necessary to "move" samples when they lay close to a common sampling time but did not span it. These samples, and the sets to which they were matched, are indicated by arrows. Samples marked with an asterisk were not used because it was impossible to match them.

The construction of these sets produced rather irregular time intervals and also some gaps in the time coverage. For example no set was taken between 1230 and 1700 hr on the second day because there was no available 100 m sample. The set at 2130 hr on the first day did not have a 600 m sample. This has made the mean depths for this set artificially high for species which occurred at 600 m. When this has produced an obviously aberrant result in the plots of individual species this set has been ignored. Each mean depth calculation produces a single point and from the calculations of all the sets a profile can be drawn for the entire 48 hr period (see Fig. 15).

There are several limitations to the use of this technique in the present sampling programme. Species whose distributions extended to depths above 100 m were incompletely sampled. The mean depths of these species will therefore be artificially deep. Similarly for species which migrated to depths shallower than 100 m a part of their population will have been "lost" at night. Again, their mean depth will be artificially deep at night. Conversely species extending

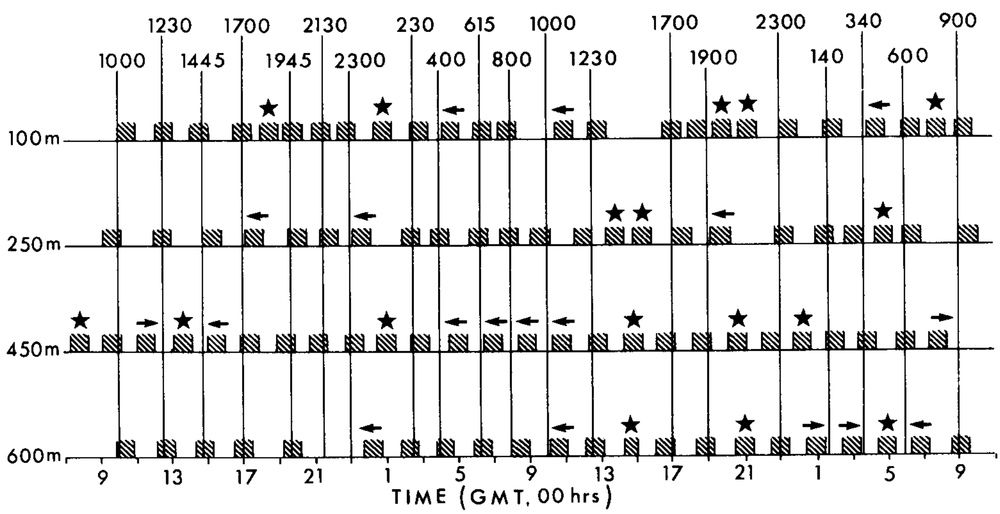

FIG. 12. The construction of the data sets used for the weighted mean depth calculations. The stars indicate samples which were not used and the arrows show samples which were "moved" into adjacent sets (see text).

to depths below 600 m will have artificially shallow mean depths. It is also possible that species which migrated in discrete layers could have been missed altogether by the relatively coarse sampling intervals – again giving spurious results.

In the present analyses data from different depths have been combined into single diel periods, although the samples were not taken simultaneously. The numerical variations of many species were so repeatable at each depth, and they were so obviously related to the adjacent depths, that this approach seems justified. In many of the subsequent mean depth profiles the distinction is made between Day 1 and Day 2. This distinction is similarly artificial since Day 1 at 100 m was not the same as Day 1 at, say, 450 m. However, the data sets for the two 24 hr periods at each depth have been treated entirely independently and the fact that they give such closely similar profiles demonstrates the highly repeatable nature of the results.

Finally it should be stressed here, as it is in the subsequent accounts of individual groups, that only regular, repeatable, diel migrations can be analysed from these samples. For such rhythmic, coherent migrations (i.e. the migrants stay together) it is possible to see sequential numerical changes in the water column. If only a small part of a population migrates at any one time, or if migrations are erratic, then these will be impossible to detect or distinguish from non-migrants (ROE, 1974; PEARRE, 1979).

6. RESULTS

The total 48 hr data from both nets at each depth has been analysed here with a simple two sample T test. A more comprehensive statistical treatment is given by DOMANSKI (1984).

6.1. *RMT 1 samples*

The total numbers of specimens per haul are shown in Fig. 13. These numbers are underestimates because some groups were not analysed, e.g. larval calanoid copepods, cyclopoids and molluscs, and others which have only been identified from the RMT 8, e.g. siphonophores, medusae and fish. It is unlikely that their addition would alter the underlying numerical trends.

The population abundance at 100 m had four peaks, one around each of the sunset and sunrise periods, but there was no significant difference between the overall numbers by day and night. These peaks are a result of the vertical migrations of animals moving through the 100 m horizon at these times. The sunset peak on the second day was larger and occurred about an hour earlier than on the first. The second day was considerably more overcast than the first and, if animals were using light to regulate their vertical position, this earlier peak may have resulted from their having shallower distributions during the second day and consequently arriving earlier at 100 m on their upward migrations.

At 250 m there was an undulating sequence with maximal abundances during the two days and minima during the nights. The overall day/night numbers were significantly different at the 99.9% level, and reflect the movements of migratory animals. Similarly the day/night numbers at 450 and 600 m were significantly different at the 95% and 99.9% level respectively.

Figure 14 indicates that the population at 450 and 600 m was less dynamic in terms of changing numbers of species than at the shallower depths, and there was no significant difference in the numbers of species by day or night. The apparent contradiction between this and the numbers of individuals is probably due to the number of partial migrants which occurred at these depths, most of whose populations migrated upwards at night but some remained behind. At 250 and 100 m the overall numbers of species by day and night were significantly

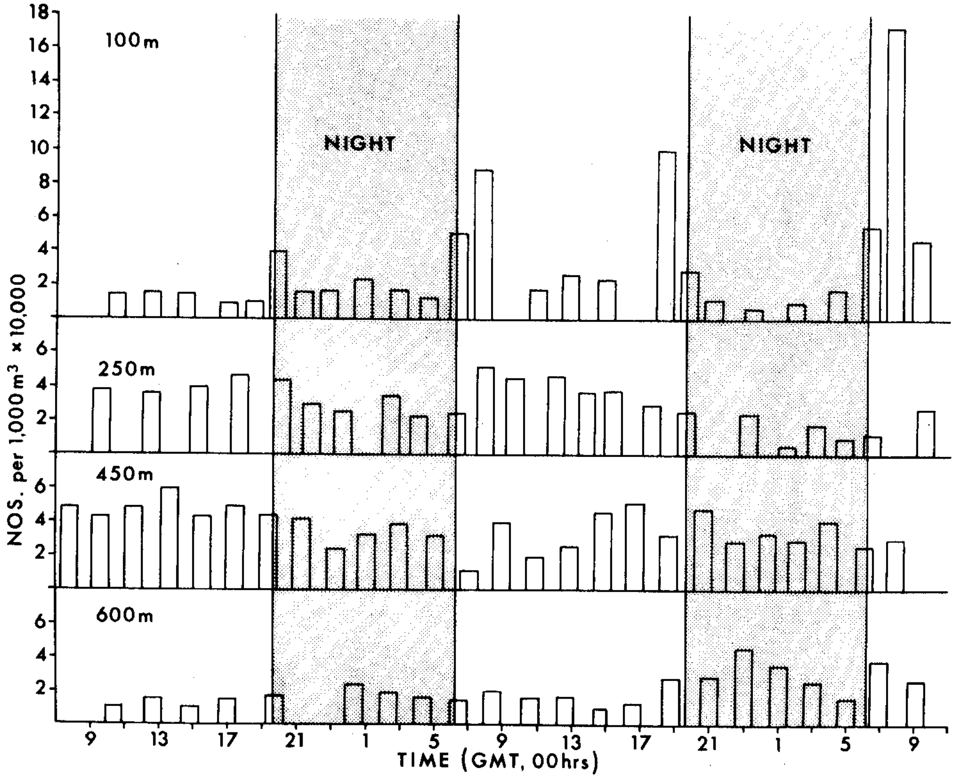

FIG. 13. The total numbers of individuals caught by the RMT 1 in each haul at each depth. The numbers are expressed as numbers per 1000 m^3 of water filtered. Here and in subsequent figures night extends from sunset to sunrise.

different at the 99.9% level. At 100 m the increase in numbers was much more abrupt and occurred much earlier on the second night than on the first. Again this may have been due to the reduced light levels on the second day.

The weighted mean depth plots for the RMT 1 catches are shown in Fig. 15. "Day 1" is the amalgamation of the first 24 hr data sets at each depth and "Day 2" the second. During the mid part of the day the population mean depth varied between ca. 310 and 370 m and was about 30 m shallower on the second day than on the first. The sharp decreases in depth around sunset and sunrise reflect the migrations of species through the 100 m depth layer at these times but the deepening in the middle part of the night is artificial. The weighted mean depth technique is obviously unsatisfactory when part of the population moves outside the sampled depth range. Many species here migrated to depths shallower than 100 m at night and consequently at least part of their populations were "lost". Copepods formed more than 90% of the total numbers caught by the RMT 1 and *Clausocalanus* spp. comprised more than 90% of the copepods. During the day *Clausocalanus* was abundant at 250 and 100 m and some of its population migrated upwards at night to depths shallower than 100 m. The consequent 'loss' of specimens depressed the depth of the population mean.

The dominance of the RMT 1 catches by a single species is unfortunate, particularly when that species migrated out of the sampled depth range. The nocturnal weighted mean depth plots are consequently artificial but the daytime ones are not. The use of this technique is

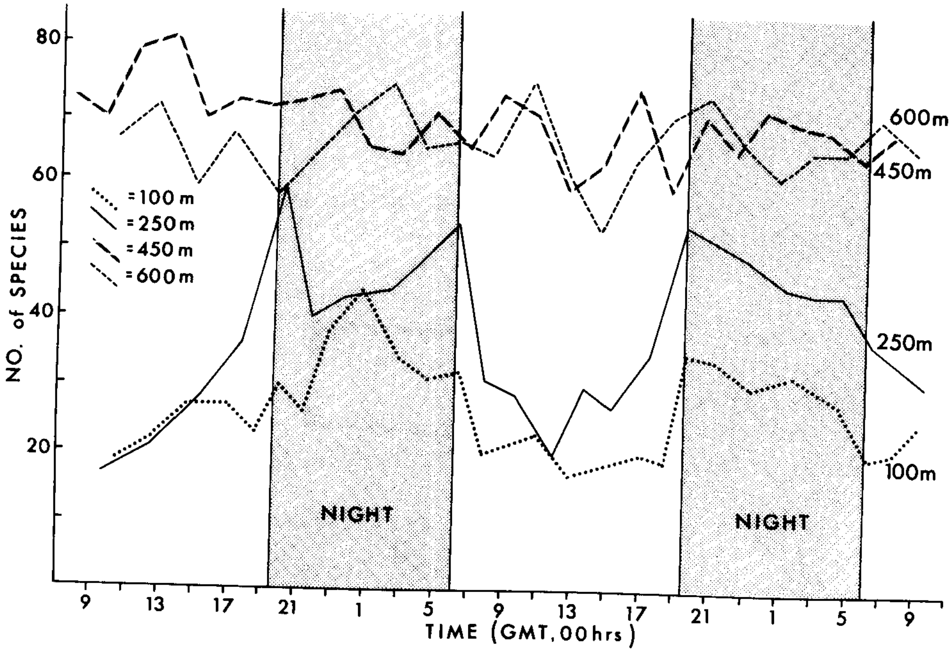

FIG. 14. The total numbers of species caught by the RMT 1 in each haul at each depth; · · · · · = 100 m; ——— = 250 m; — — — — = 450 m and - - - - - = 600 m.

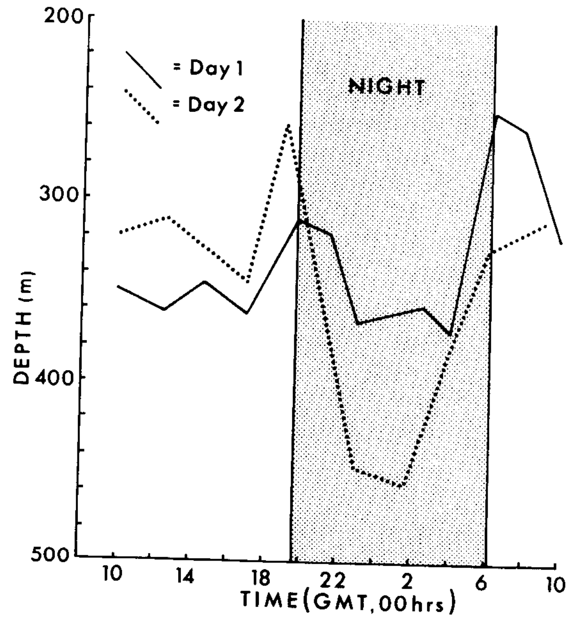

FIG. 15. Weighted mean depths for the RMT 1 samples. Data from the first and second 24 hr period at each depth has been combined to form 2 diel periods (see text); ——— = first 24 hr; · · · · · = second 24 hr.

therefore rather unsatisfactory here, but it has proved to be extremely useful in describing the distributions and migrations of numerous species and groups, and many better examples of its use can be found in the subsequent papers.

6.2. *RMT 8 samples*

The total numbers of specimens per haul, are shown in Fig. 16; again some groups have not been analysed, e.g. large chaetognaths and calanoid copepods, and consequently these numbers are slight underestimates.

Few individuals (Fig. 16) or species (Fig. 17) were present at 100 m by day. There was a marked nocturnal immigration into this depth by both individuals and species and the day/night numbers of both were significantly different at the 99.9% level. The first day series at 250 m is unfortunately incomplete, and there is no significant diel difference in the numbers of individuals because the population was dominated by the largely non-migrant siphonophores *Chuniphyes multidentata* and *Rosacea plicata*. The numbers of species were significantly greater by night.

Neither the numbers of individuals nor species had significant diel differences at 450 and 600 m. Even so, there was a continuous change in the proportions of individual species and

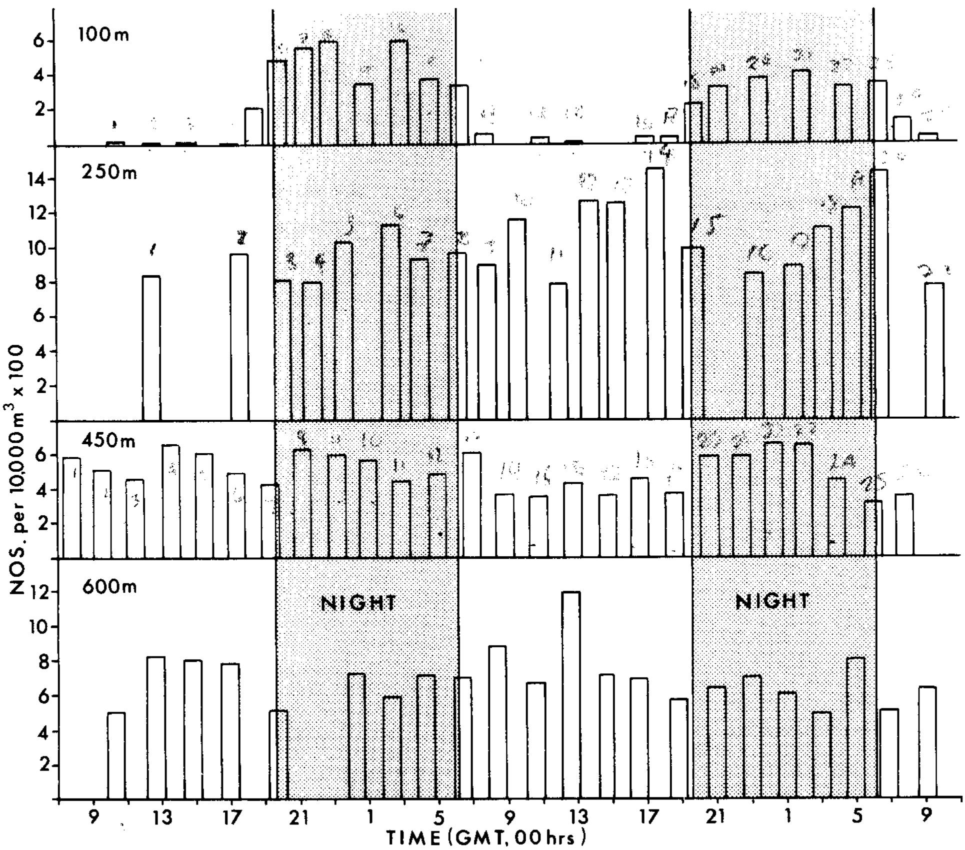

FIG. 16. The total numbers of individuals caught by the RMT 8 in each haul at each depth. The numbers are expressed as numbers per 10,000 m³ of water filtered.

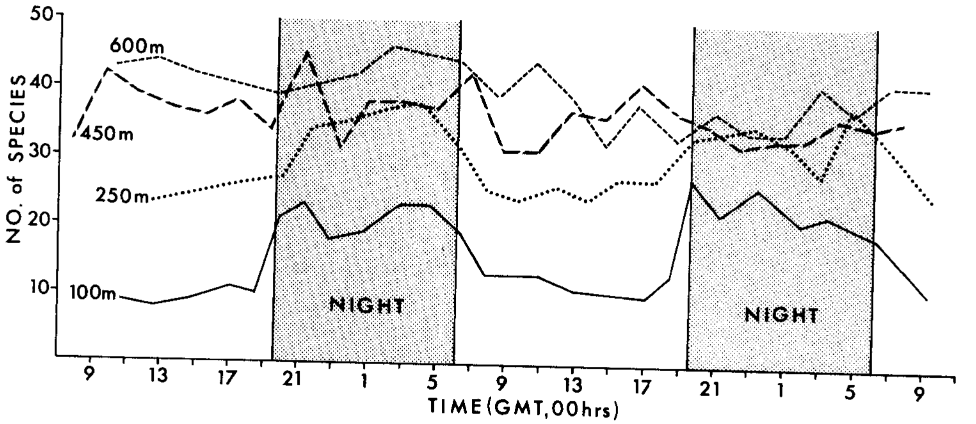

FIG. 17. The total numbers of species caught by the RMT 8 in each haul at each depth; —— = 100 m; · · · · · = 250 m; — — — — = 450 m and - - - - - = 600 m.

groups and the weighted mean depth plots for the RMT 8 populations (Fig. 18) show a distinct upward migration from day depths of ca. 450–400 m to between ca. 370–320 m at night. The amplitude of this nocturnal migration is slightly damped here because some of the abundant migrants, especially euphausiids, migrated to depths above 100 m and were consequently "lost" at night. (The weighted mean depth plot for the first 24 hr period is badly affected by missing samples, two at 250 m during the day and one at 600 m by night. The calculated points for these time sets are shown in Fig. 18 but they are obviously aberrant and have subsequently been ignored.)

The catches of both nets show greater temporal variability at 250 and 100 m than at 450 and 600 m. Many species migrated up into these depths at night but were entirely absent by day. In contrast most of these migrants left a proportion of their populations behind at 450 and 600 m during the night. The resulting deep distributional "tails" on their upward migrations

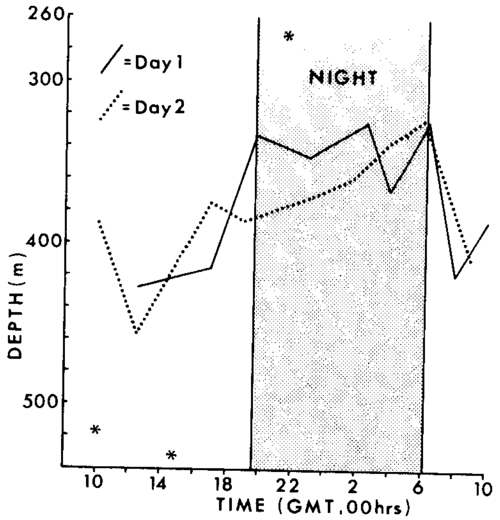

FIG. 18. Weighted mean depths for the RMT 8 samples. The asterisks mark the incomplete data sets which have been ignored (see text).

and the total absence of shallow "tails" on their subsequent downward migrations account for the apparent differences between the shallow and deep horizons. At all depths, however, the proportions of species within the populations changed continuously with time.

7. SUMMARY

(i) This paper is an introduction to a series of papers describing the diel migrations and interrelationships of a mesopelagic community in the northeast Atlantic.

(ii) The biological and physical background to the sampling area is described.

(iii) There was little physical structure in the water column to a depth of 1000 m.

(iv) The influence of Mediterranean water was detectable at varying depths between 550 and 800 m during the sampling programme. The possibility of mesoscale activity at these depths is discussed.

(v) The sampling programme is described. Using the I.O.S. rectangular midwater trawl, the RMT 1 + 8, one hour samples were taken at 4 depth horizons, 100, 250, 450 and 600 m. Each depth was fished continuously for 48 hr.

(vi) Additional non-quantitative surface samples, and surface light measurements were made throughout the RMT 1 + 8 sampling period.

(vii) 97 hauls were made and the data for fish, decapod Crustacea, mysids, euphausiids, amphipods, copepods, ostracods, siphonophores, medusae, ctenophores and chaetognaths analysed.

(viii) General results in terms of total numbers and numbers of species taken by the RMT 1 and the RMT 8 are described.

(ix) The populations at 100 and 250 m showed more diel variation than those at 450 and 600 m, but the proportions of individual species and groups changed continuously at all depths.

(x) These changes are due to diel vertical migrations. The migrations of most species only involved a part of their populations.

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