

ON THE BIOLOGY OF *CALANUS* *FINMARCHICUS*

XI. OBSERVATIONS ON VERTICAL MIGRATION ESPECIALLY IN FEMALE *CALANUS*

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(Text-figs. 1-5)

A number of different factors have been shown to affect the vertical migration of the zooplankton, among them changes in light intensity, temperature, salinity and the presence of food (see Russell, 1927; Hardy & Paton, 1947; Cushing, 1951; Bainbridge, 1953; Harris, 1953; Moore, 1958; Banse, 1959). The object of the present study was to find out whether in female *Calanus* there was any relation between vertical migration and the degree of ripeness.

When *Calanus* were taken by tow-nettings near the laboratory it was noticed that the percentage of adult females in the ripe condition was generally greater in hauls made close to the surface than in those from deep water. For example in the spring of 1953 a series of hauls was made near the surface in Fairlie Channel where the maximum depth is about 40 m, and at 60-80 m off Garroch Head a few miles away where the depth is 115 m. Throughout the period of examination there was a much higher percentage of ripe females in the shallow than in the deep hauls (Table 1, Fig. 1). The deep hauls show the progressive ripening of the females during the spring reaching a peak in percentage ripe which coincides with the spring diatom increase in the middle of March. It also coincides with the maximum number of eggs produced by laying females. In shallow water the sequence is not so obvious because of the high percentage of ripe females at the surface most of the time.

A tendency for ripe female *Calanus* to keep in the surface waters might be expected since the eggs, which are denser than sea water (Salzen, 1956), are usually found in the upper 30 m (Nicholls, 1933). In the Clyde area adults which moult from the overwintering stock of Stage V in January and February show a marked migration, and if migration to the surface for egg-laying takes place one might expect to find a difference in behaviour of females in different stages of ripeness during the spring. It is only during early spring that a good proportion of immature and medium, as well as ripe, females is certain to be found and this is therefore the best time to study their migrations.

Vertical distribution stations were worked in the spring of three years,

1953 (2 February), 1954 (16 March) and 1959 (9 February) and on each occasion hauls were taken every 3 h for 27 h. On all three occasions the weather was calm with only light airs. There was sunshine during the day, but in 1959 the sun shone only through a haze. There was bright moonlight in 1953 and 1954 but in 1959 the night was overcast and raining. Times of sunrise and sunset are shown in the figures.

The position chosen for the observations was the deep water between the

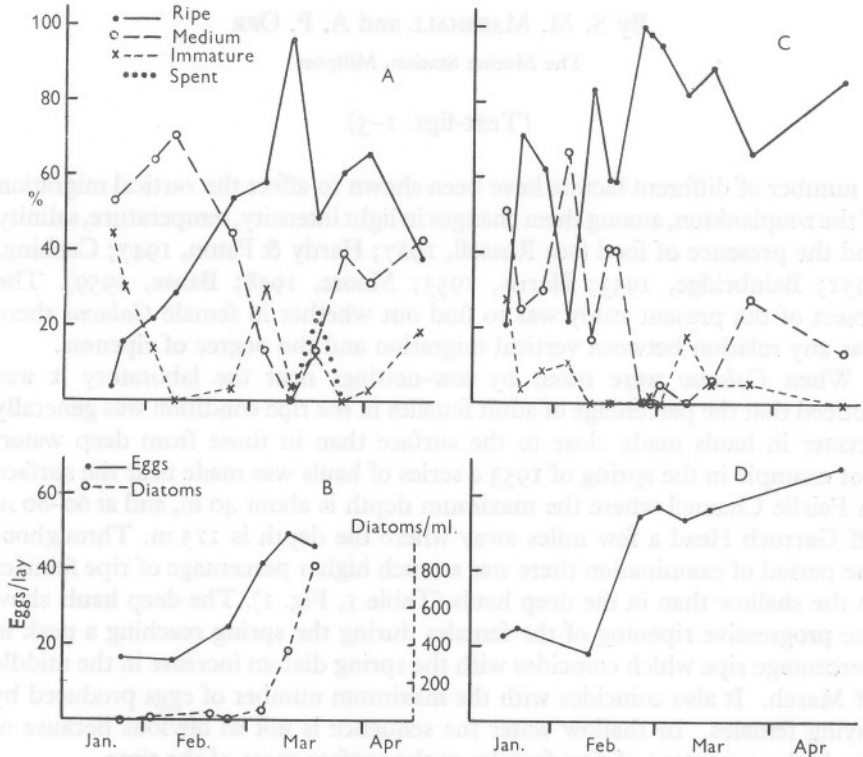


Fig. 1. Maturity of female *Calanus* in deep and shallow hauls in 1953. A and B, deep water, Garroch Head; C and D, near surface, Fairlie Channel.

south-east of the island of Bute and the Little Cumbrae. Because of the small numbers of *Calanus* present at the end of the winter, vertical hauls with a closing net would not have given sufficient numbers for studies of ripeness. Thirty-minute hauls with 50 cm diameter coarse tow-nets (26 meshes to the inch) were therefore taken simultaneously at four depths from a trawl warp to the end of which was attached a depressor (Barnes, 1951). Tows were made at a constant speed and the depth of the nets during tows checked by an Admiralty pattern depth recorder. The top net fished just below the surface, the next at 20–25 m, the third at about 45 m and the lowest net at

60-70 m. Because of the time required for hauling and untying, the deep nets were towed for a few minutes longer than the shallow on each run. There is no simple correction which can be applied for this, but the differences are unlikely to have interfered seriously with the results.

An objection to the use of horizontal tows at a small number of depths is that important differences in the concentration of organisms might be missed. If so one would expect to find changes in the total numbers from

TABLE 1. MATURITY IN SPRING, 1953

Date	No. examined	% Females				Spent	Eggs per lay	Diatoms (cells/ml.)
		Im-mature	Medium	Semi-ripe	Ripe			
Garroch Head, 60-80 m.								
2 Jan.	47	45	43	9	4	0	—	—
26 Jan.	51	31	28	26	16	0	17	0
2 Feb.	536	14	20	44	22	0	—	10
9 Feb.	51	0	22	49	29	0	16	—
19 Feb.	—	—	—	—	—	—	—	35
24 Feb.	39	3	3	41	54	0	25	0
5 Mar.	40	30	10	3	58	0	42	50
12 Mar.	25	4	0	0	96	0	50	370
19 Mar.	45	13	4	9	49	24	46	818
26 Mar.	31	0	7	32	61	0	—	—
2 Apr.	32	3	13	19	66	0	—	—
16 Apr.	32	19	34	9	38	0	—	—
Fairlie Channel, near surface								
19 Jan.	43	28	23	28	21	0	23	—
23 Jan.	56	4	9	16	71	0	25	—
29 Jan.	71	9	17	13	62	0	—	—
5 Feb.	45	11	38	29	22	0	—	—
11 Feb.	23	0	4	13	83	0	18	—
16 Feb.	87	0	2	39	59	0	—	—
17 Feb.	27	0	0	41	59	0	—	—
25 Feb.	20	0	0	0	100	0	55	—
27 Feb.	50	2	0	0	98	0	—	—
2 Mar.	21	0	0	5	95	0	58	—
9 Mar.	28	18	0	0	82	0	54	—
16 Mar.	18	6	6	0	89	0	57	—
26 Mar.	35	6	14	14	66	0	—	—
20 Apr.	14	0	7	7	86	0	68	—

top to bottom during the 27 h. There was in fact a rise in total numbers in the early evening in two of the years which may have been because of an influx from below the depth of the bottom net. Otherwise total numbers remained reasonably constant. The percentage of the total catch in different stages and states of maturity also remained fairly constant throughout.

The tow-nettings were fixed in 5% formalin and afterwards the numbers of males, females and Stage V counted in aliquot samples from each haul. When numbers allowed it at least 200 of the females were taken for staining and clearing to determine ripeness.

Three different methods of staining were tried. In the first year (1953)

the females were stained in methylene blue, dehydrated in dioxan and cleared and examined in creosote. This sometimes gave a very clear picture but the results were not consistent because the largest and ripest eggs hardly stained at all and were easy to miss. Eventually samples of this series were stained with celestine blue B (see below).

In 1954 the stain used was borax carmine and the examination was made in xylol. This method proved fairly satisfactory and the results were later checked against the celestine blue method. Staining with celestine blue B (Gray, 1958) proved the best method and was adopted for the 1959 hauls. We should like to thank Dr H. F. Steedman of the Zoology Department of the University of Glasgow for suggesting the method and for his help.

The specimens were put in a glass tube closed at the lower end by coarse bolting silk, and were washed and then stained in celestine blue B (14 ml. to 86 ml. 1% acetic acid). They were then taken through a series of alcohols and cleared in diethyl phthalate.

Unfortunately the living females especially when ripe look rather different from the fixed, stained and cleared specimens and the categories chosen, immature, medium and ripe, do not necessarily correspond exactly to those used for living material (Marshall & Orr, 1952). The eggs appear smaller and the ripe female less full of eggs. In February and March, however, the number of large eggs in a ripe female is very much smaller than it is later in the year.

The ripest eggs do not as a rule stain so heavily as the unripe, and the arbitrary criterion we have used in distinguishing the ripe from the medium is that there should be a row of these larger and paler eggs in the lower part of the oviduct (Fig. 2 c). There is no such definite criterion to distinguish the immature from the medium, but in the immature the ovary is small, the oviducal diverticula are represented by two short single rows of small eggs not extending to the front of the head and the oviducts have a single row, often discontinuous, of small eggs (Fig. 2 A). In the medium, the oviducal diverticula extend almost to the front of the head and may have more than one row of eggs each; the eggs in the oviduct are larger and pressed more closely together forming a single or a double row (Fig. 2 B). As a rule, in distinguishing the different stages, most weight was given to the appearance of the oviducts.

MIGRATIONS

A study of the vertical distribution of *Calanus* in spring has already been made for a deep station in this area (Nicholls, 1933). The four distributions, all of the same generation, within 8 weeks (although in different years), and within the same area, might be expected to resemble one another closely, but in fact they do not.

The earliest, that of Nicholls on 25 January 1932, although based on rather small numbers, shows the clearest results. Apart from this it differs from the

rest in having been done in much deeper water and with a closing net. It shows the usual pattern for the overwintering generation in which the females migrate most, in close agreement with light changes, the males migrate less, and the Stage V hardly at all.

In 1959 (9–10 February) the behaviour of females and males followed this pattern (Fig. 3 and Table 2), but the Stage V also showed a distinct migration slightly more marked than that of the males. From 9.00 to 15.00 h all stages

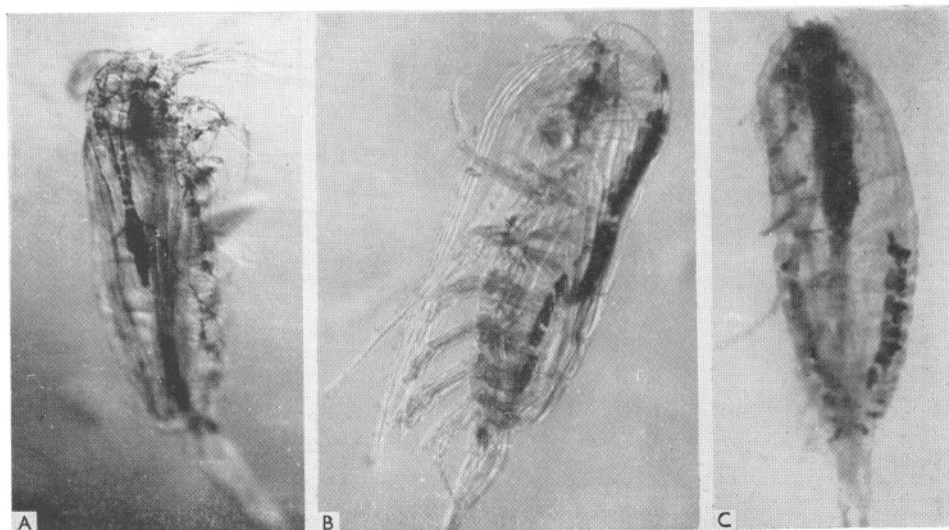


Fig. 2. Female *Calanus* stained with celestine blue. A, immature: the ovary, oviducal diverticula and right oviduct are visible. B, medium: oviducal diverticula extend farther forward and eggs are larger. C, ripe: note the two sizes of eggs in the oviduct.

were concentrated in the bottom net (62 m), but between sunset and sunrise the distribution was much more even throughout the water column with a tendency for the females to be concentrated in the upper two nets and the males and Stage V in the lower two.

In 1953 (2–3 February) the main difference was that the *Calanus* were higher in the water (Fig. 3), the highest numbers being usually in the net at 45 m in spite of clearer sunshine than in 1959. Apart from this the females showed the usual migration upwards between sunset and sunrise. This movement was less marked in the males and Stage V. All, however, behaved less regularly than in 1933 or in 1959.

In 1954 (17–18 March) the behaviour was surprisingly different. A considerable proportion of all the *Calanus* remained in the two top nets throughout the 27 h and at 9.00 and 12.00 h, the brightest hours, were even more concentrated there, a distribution quite opposite to those found earlier in

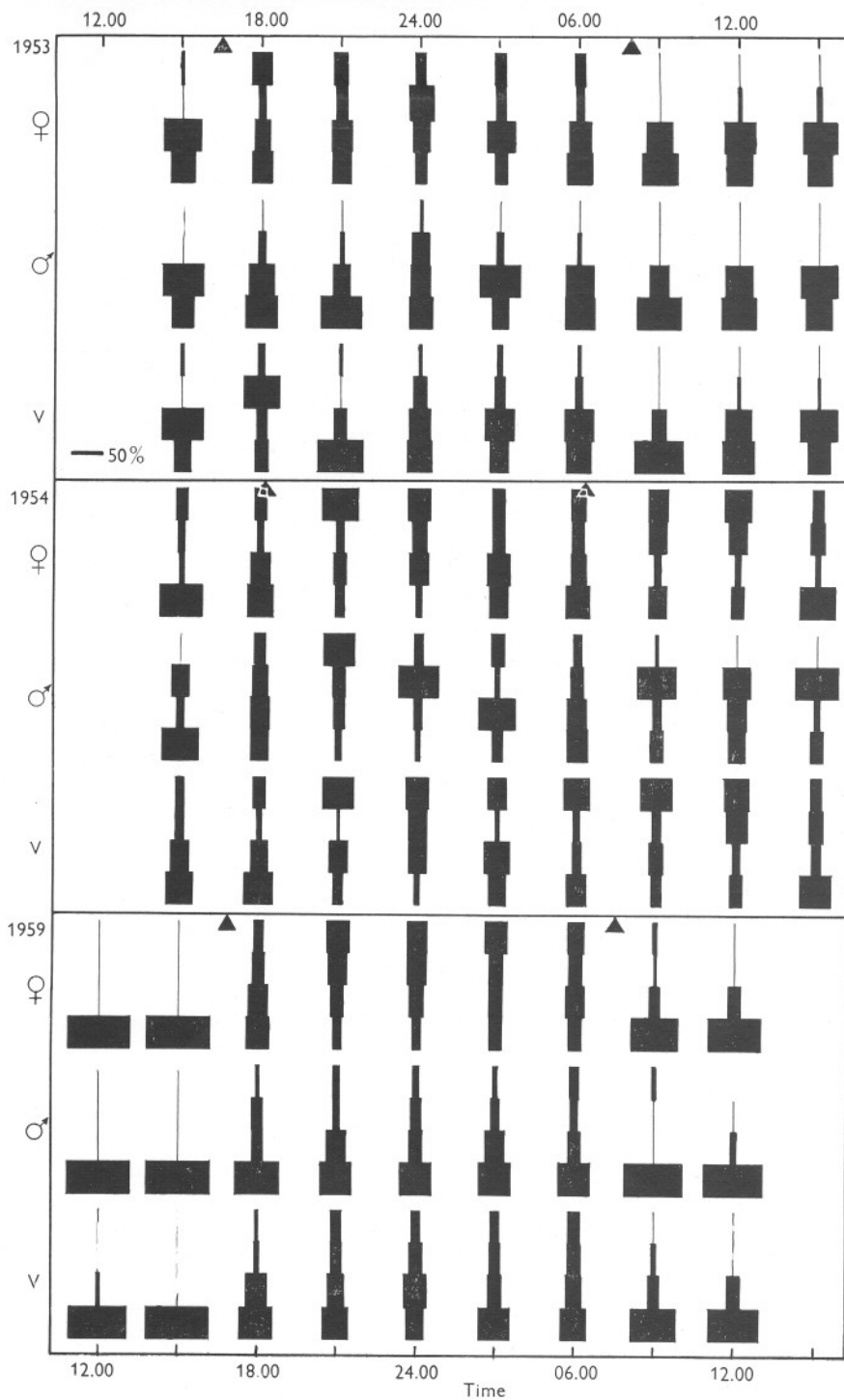


Fig. 3. Vertical distribution of male, female, and Stage V *Calanus* at four depths. The arrows show times of sunset and sunrise.

TABLE 2. VERTICAL DISTRIBUTION OF FEMALE, MALE AND STAGE V *CALANUS*

Haul	Time	2-3 February 1953						16-17 March 1954						9-10 February 1959								
		♀		♂		V		♀		♂		V		♀		♂		V				
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%			
I.	1	15.00	77	1.3	9	0.4	5	1.3	15.00	1013	23.9	2	1.4	61	13.4	12.00	13	0.3	2	0.6	0	0
	2		355	5.9	38	1.6	27	7.0		603	14.2	42	28.4	65	14.3		32	0.8	1	0.3	5	2.3
	3		3380	56.7	1480	64.4	250	65.4		359	8.5	19	12.8	133	29.3		119	2.9	3	1.0	14	6.4
	4		2150	36.1	770	33.5	100	26.2		2260	53.4	85	57.4	195	42.9		3928	96.0	302	98.1	200	91.3
II.	1	18.00	3750	32.5	80	2.2	110	10.4	18.00	547	17.9	16	18.2	46	19.2	15.00	10	0.1	6	1.0	1	0.2
	2		1400	12.1	440	12.0	600	56.5		344	11.3	21	23.9	18	7.5		55	0.6	2	0.3	4	0.6
	3		2670	23.1	1410	38.4	160	15.1		983	32.2	26	29.6	66	27.5		21	0.2	1	0.2	5	0.8
	4		3730	32.3	1740	47.4	190	17.9		1175	38.5	25	28.4	110	45.8		8990	99.1	580	98.5	650	98.5
III.	1	21.00	1690	20.7	80	2.8	20	4.0	21.00	2410	45.8	95	48.5	250	48.3	18.00	995	15.8	11	5.0	18	6.7
	2		1600	19.6	170	6.0	10	2.0		795	15.1	40	20.4	24	4.6		1150	18.2	18	8.3	23	8.5
	3		2590	31.7	780	27.4	110	22.0		1126	21.4	37	18.9	159	30.7		2024	32.1	35	16.0	89	33.1
	4		2280	27.9	1810	63.7	360	72.0		936	17.8	24	12.2	85	16.4		2134	33.9	154	70.6	139	51.6
IV.	1	24.00	602	16.6	40	3.3	14	5.7	24.00	1395	20.9	20	13.5	155	35.4	21.00	2357	36.8	61	12.6	67	18.3
	2		1385	38.1	345	28.9	55	22.5		2045	30.7	95	64.2	125	28.5		1882	29.6	57	11.8	60	16.3
	3		975	26.8	370	31.0	85	34.8		2220	33.3	20	13.5	120	27.4		1281	20.1	138	28.5	95	25.9
	4		670	18.4	440	36.8	90	36.9		1010	15.1	13	8.8	38	8.7		863	13.5	228	47.1	145	39.5
V.	1	03.00	531	17.7	26	2.3	14	8.1	03.00	925	13.1	30	20.3	75	28.0	24.00	1808	31.8	54	10.9	66	13.7
	2		468	15.6	105	9.2	29	16.8		1315	18.7	8	5.4	18	6.7		1731	30.5	83	16.7	107	22.3
	3		1390	46.4	725	63.4	80	46.2		2795	39.7	85	57.4	105	39.2		1274	22.4	109	21.9	170	35.4
	4		607	20.3	287	25.1	50	28.9		2005	28.5	25	16.9	70	26.3		869	15.3	252	50.6	137	28.5
VI.	1	06.00	673	16.4	40	2.2	13	5.3	06.00	931	22.7	18	13.3	83	40.1	03.00	2049	35.9	29	5.7	65	13.3
	2		467	11.4	110	6.0	23	9.4		951	23.2	30	22.2	26	12.6		1304	22.9	68	13.3	80	16.4
	3		1430	34.7	850	46.2	110	44.7		997	24.3	42	31.1	30	14.5		1086	19.2	152	29.9	108	22.2
	4		1545	37.5	840	45.7	100	40.6		1219	29.8	45	33.3	68	32.9		1264	22.1	260	51.0	234	48.0
VII.	1	09.00	46	1.1	13	0.7	3	1.1	09.00	1983	25.5	7	4.1	171	47.4	06.00	1491	26.9	44	15.3	59	17.3
	2		83	2.0	15	0.8	6	2.1		3167	40.7	107	62.9	52	14.4		1196	21.6	32	11.1	66	19.3
	3		1690	40.3	560	30.1	60	21.5		940	12.1	24	14.1	77	21.3		1651	29.7	62	21.6	84	24.6
	4		2370	56.5	1270	68.3	210	75.3		1694	21.8	32	18.8	61	16.9		1210	21.8	149	51.9	133	38.9
VIII.	1	12.00	132	2.2	8	0.5	7	2.3	12.00	1930	40.8	2	2.0	86	35.3	09.00	247	5.4	15	5.1	9	3.3
	2		477	7.9	60	3.6	20	6.5		1703	36.0	45	44.0	82	33.6		224	4.9	5	1.7	18	6.5
	3		3040	50.5	680	41.3	130	42.3		351	7.4	28	27.4	32	13.1		750	16.4	7	2.4	50	18.0
	4		2370	39.3	900	54.6	150	48.8		745	15.8	27	26.5	44	18.0		3356	73.3	268	90.8	200	72.2
IX.	1	15.00	150	2.6	26	2.2	4	1.9	15.00	660	15.3	5	3.9	37	16.8	12.00	13	0.3	0	0.0	3	1.0
	2		359	6.3	34	2.9	13	6.3		1348	31.2	86	66.2	47	21.4		33	0.8	4	1.0	2	0.7
	3		2960	52.1	650	55.1	120	58.0		422	9.8	12	9.2	31	14.1		697	17.6	29	7.2	63	20.5
	4		2210	38.9	470	39.8	70	33.8		1893	43.8	27	20.8	105	47.7		3220	81.3	368	91.7	240	77.9

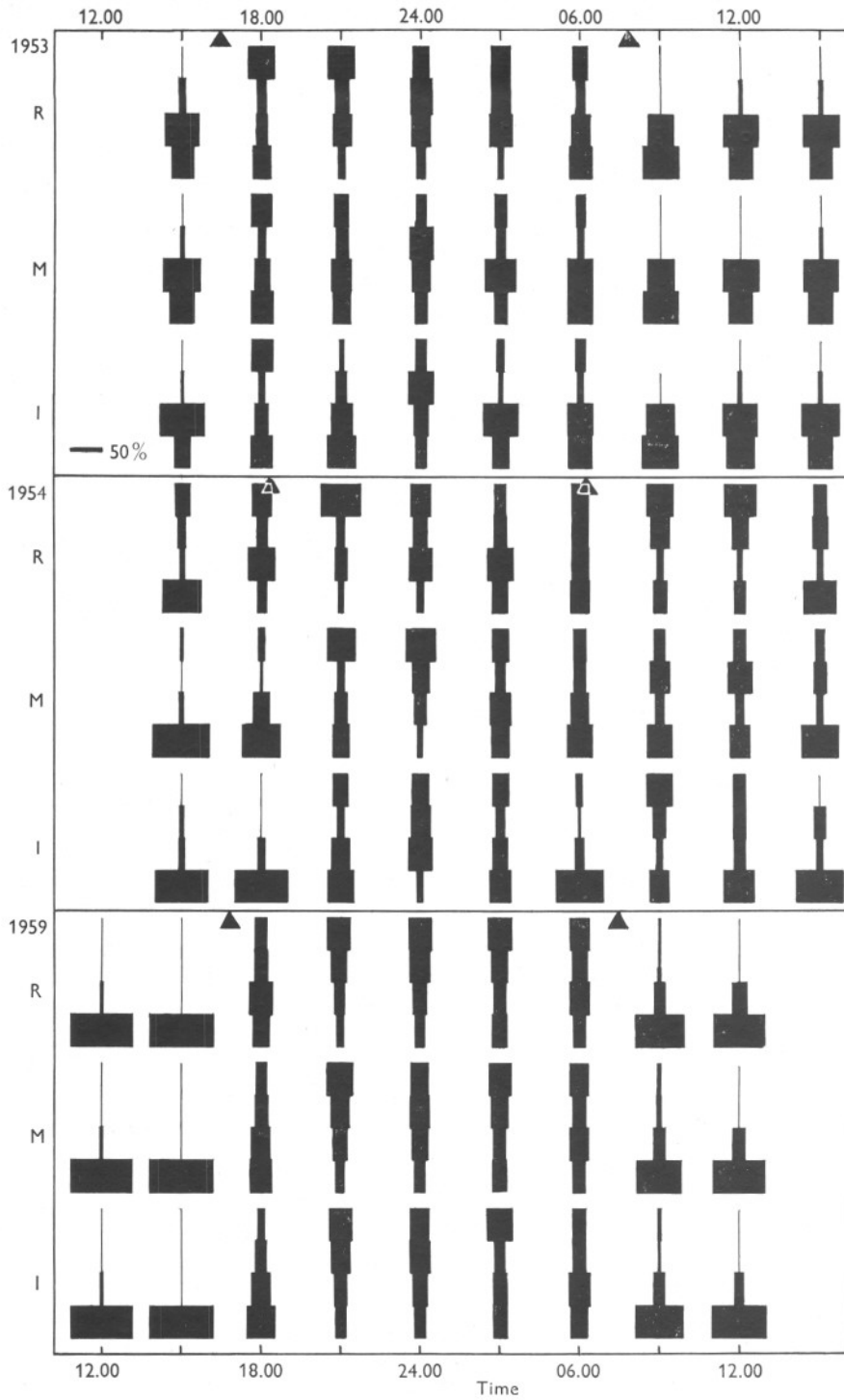


Fig. 4. Vertical distribution of ripe (R), medium (M), and immature (I) female *Calanus* at four depths.

the year. There was, however, a rise from the bottom from 18.00 to 24.00 h followed by a descent till 6.00 h and then the curious secondary rise at 9.00 and 12.00 h. At 15.00 h the distribution on the first day differed considerably from that on the second. The weather was hazy instead of clear

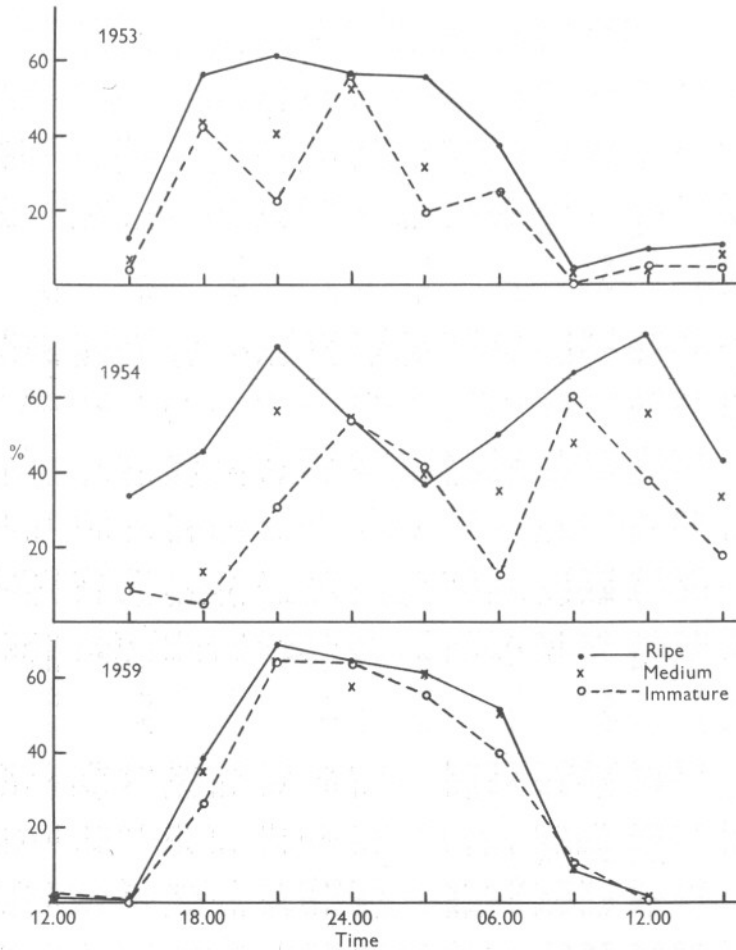


Fig. 5. Percentage of ripe and immature female *Calanus* in the two top nets.

sunshine. More of all stages were higher in the water on the second day and the males were actually richest in the second net.

Figs. 4 and 5 and Table 3 show the vertical distribution of the females when separated into three states of maturity—ripe, medium and immature. In 1953 and 1959 all resemble one another closely, but the immature show a slightly later and less marked rise and an earlier descent than the ripe. This is perhaps more clearly seen in Fig. 5, where the percentage of ripe and

TABLE 3. VERTICAL DISTRIBUTION OF RIPE, MEDIUM AND IMMATURE ♀ *CALANUS*

Haul	Time	2-3 February 1953						16-17 March 1954						9-10 February 1959								
		Ripe		Medium		Immature		Ripe		Medium		Immature		Ripe		Medium		Immature				
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%			
I.	1	15.00	9	0.9	23	0.9	6	0.4	15.00	522	21.9	31	6.6	4	1.1	12.00	5	0.3	5	0.4	3	0.3
	2		114	11.7	160	6.0	59	3.6		282	11.9	10	2.1	28	7.6		9	0.5	12	0.9	12	1.4
	3		524	53.9	1476	55.1	1143	69.9		166	7.0	17	3.6	30	8.1		57	3.0	40	3.0	25	2.9
	4		322	33.1	1018	38.0	426	26.0		1408	59.2	411	87.6	308	83.2		1837	96.3	1277	95.7	823	95.3
II.	1	18.00	818	40.1	1459	32.1	1330	33.6	18.00	435	30.1	47	9.7	16	2.7	15.00	5	0.2	3	0.1	3	0.1
	2		331	16.2	506	11.1	356	9.0		221	15.3	17	3.5	17	2.9		19	0.7	22	0.6	16	0.7
	3		339	16.6	1108	24.4	905	22.9		600	41.5	122	25.1	66	11.2		7	0.2	7	0.2	7	0.3
	4		552	27.1	1477	32.5	1363	34.5		189	13.1	300	61.7	489	83.2		2884	98.9	3734	99.2	2364	98.9
III.	1	21.00	145	6.9	773	21.6	628	39.4	21.00	1754	61.4	219	44.1	73	23.3	18.00	423	17.5	370	16.7	185	11.2
	2		321	15.4	677	18.9	355	22.3		350	12.3	61	12.3	24	7.7		506	20.9	407	18.3	253	15.3
	3		691	33.0	1144	31.9	432	27.1		531	18.6	90	18.1	86	27.4		862	35.6	680	30.6	498	30.2
	4		932	44.6	989	27.6	179	11.2		221	7.7	127	25.6	131	41.7		627	25.9	765	34.4	715	43.3
IV.	1	24.00	181	23.9	254	16.3	159	15.7	24.00	805	32.0	400	45.6	45	25.0	21.00	945	39.5	782	38.7	653	33.4
	2		250	33.1	568	36.5	412	40.8		565	22.5	234	26.6	53	29.4		702	29.4	524	25.9	603	30.9
	3		218	28.8	433	27.8	248	24.6		883	35.2	166	18.9	66	36.7		482	20.1	442	21.9	370	18.9
	4		107	14.2	301	19.3	191	18.9		259	10.3	78	8.9	16	8.9		262	11.0	272	13.5	329	16.8
V.	1	03.00	196	28.8	228	17.8	95	12.4	03.00	396	17.6	235	25.2	64	26.9	24.00	716	33.0	528	28.7	562	32.7
	2		184	27.0	173	13.5	53	6.9		430	19.1	136	14.6	34	14.3		683	31.5	528	28.7	528	30.7
	3		239	35.1	615	47.9	418	54.5		882	39.2	305	32.7	57	23.9		461	21.2	475	25.8	367	21.3
	4		62	9.1	267	20.8	201	26.2		541	24.0	256	27.5	83	34.9		310	14.3	310	16.8	261	15.2
VI.	1	06.00	195	22.7	273	14.0	161	15.0	06.00	359	25.4	133	19.2	27	8.6	03.00	791	35.6	693	33.1	576	40.3
	2		125	14.5	205	10.5	114	10.6		348	24.6	110	15.9	13	4.2		572	25.8	559	26.7	214	15.0
	3		250	29.1	735	37.6	403	37.5		343	24.2	177	25.6	43	13.7		360	16.2	398	19.0	322	22.5
	4		290	33.7	738	37.8	397	36.9		365	25.8	271	39.2	230	73.5		495	22.3	446	21.3	318	22.2
VII.	1	09.00	17	2.2	21	1.0	0	0.0	09.00	1126	39.4	168	16.5	100	40.7	06.00	557	28.4	625	29.0	317	22.0
	2		19	2.5	44	2.2	2	0.2		784	27.4	320	31.4	48	19.5		452	23.1	483	22.4	260	18.1
	3		296	38.8	867	42.4	477	44.2		298	10.4	143	14.0	25	10.2		570	29.1	607	28.1	474	33.0
	4		430	56.4	1110	54.3	600	55.6		648	22.7	387	38.0	73	29.7		381	19.4	442	20.5	387	26.9
VIII.	1	12.00	45	3.0	63	2.2	10	0.8	12.00	1140	50.3	90	17.7	34	17.9	09.00	88	4.3	88	6.1	70	6.2
	2		99	6.6	192	6.8	51	4.3		597	26.3	195	38.3	38	20.0		87	4.3	85	5.8	52	4.6
	3		802	53.2	1565	58.6	608	51.4		152	6.7	61	12.0	29	15.2		354	17.3	256	17.6	179	16.0
	4		562	37.3	994	35.3	512	43.4		379	16.7	162	31.9	89	48.6		1510	74.1	1025	70.5	820	73.2
IX.	1	15.00	62	4.1	49	1.8	7	0.7	15.00	326	19.9	109	13.2	2	1.2	12.00	5	0.4	3	0.2	5	0.4
	2		98	6.5	176	6.5	38	3.8		382	23.2	166	20.2	29	16.7		13	0.9	5	0.4	15	1.2
	3		836	55.5	1436	53.1	599	60.2		121	7.4	75	9.1	16	9.2		286	20.8	230	17.2	181	14.5
	4		509	33.8	1044	38.6	351	35.3		811	49.4	473	57.4	127	73.0		1074	78.0	1101	82.2	1046	83.8

immature in the two top nets is shown. In general the medium state females are intermediate between ripe and immature.

In 1954 the immature were concentrated in the bottom net from 12.00 to 18.00 h and showed an irregular rise in the dark with a curious dip at 6.00 h. The ripe, on the other hand, tended to concentrate at the surface even in the daylight hours and to be more evenly distributed in the dark. As before the distribution of the medium state was intermediate.

Calanus finmarchicus is the dominant form in the Clyde sea area, but during the winter an appreciable proportion of the *helgolandicus* form may be present. However their numbers were too small for a study of their diurnal migration except in the spring of 1954. The females were then much more mature than those of the *finmarchicus* form, about 90% ripe as against 70%.

The pattern of vertical migration differed from that for the *finmarchicus* in that the tendency to concentrate in the upper nets during the day was more marked. During the night, on the other hand, they were deeper than the *finmarchicus*. When the females were separated into ripe, medium and immature, it was seen that, as with the *finmarchicus* form, the ripe tended to be higher in the water for most of the time. The immature were too scarce to give reliable results.

DISCUSSION

The state of the gonad can now be added to the other factors which influence vertical migration. It is most easily distinguished in females, and it is the female which might be expected to come to the surface at night. Apart from the necessity for feeding, eggs are at this time of year laid mainly between midnight and 2.00 h (Harding, Marshall & Orr, 1951). In the early spring months before the diatoms have begun to increase in numbers these factors may not be operative. Phytoplankton is scarce and evenly distributed and, although there are often some eggs laid in February, the majority seem to be laid in March or even April. However, the hauls taken in deep water and near the surface in 1953 (Fig. 1) show that the percentage of ripe females is higher near the surface even in February.

A surprising feature of the results is the difference in migration in different years. The most unexpected difference is the behaviour of the Stage V. During the winter they are normally found in deep water, and Nicholls (1933) found that they did not migrate. We, on the other hand, have found that in all three years they migrated almost as much as the adults. Another point of interest is that the *Calanus* were deeper in 1959 than in the two other years although their behaviour was similar in 1953 and 1959.

On many occasions in 1950 and 1951 Gauld examined catches from three different depths throughout 24 h in the Clyde sea area and he says (1953): 'that only on seven of the thirteen occasions on which hauls were taken, were

the catches of the top net distinctly greater in darkness than in daylight'. This also shows how variable vertical migration may be from year to year and perhaps even from month to month.

The tendency of the *Calanus* in 1954 to remain near the surface even at noon on the second day was surprising. It almost looks as though two populations were present, a surface living and a deep living. The first generation of the year, which does live mainly at the surface, has appeared as adults in these waters as early as the middle of March and it seemed possible that there was here a mixture of the overwintering and the first generation. Had two generations been present, however, the immature should have belonged to the later surface-living rather than to the overwintering one and actually the immature were found concentrated in the bottom net from 12.00 to 18.00 h. In addition, the clearest indication of the presence of the adults of the first generation came nearly a month later, on 16 April, when the proportion of males and of unripe females rose considerably, and 30% of the latter were carrying spermatophores. An examination too of nearly 6000 measurements of the lengths of the females in the vertical distribution hauls showed that the size curve was symmetrical with no suggestion of two modes as would have been expected had the two generations been mixed.

The chief difference between the 1954 observations and those for other years is that the station was worked a month later. In 1953 and 1959 the ratio of ripe:medium:immature was about 20:50:30 while in 1954 it was 70:20:10. It is possible that the behaviour of females may show a gradual change with advancing ripeness rather than an abrupt change with the generation. The anomalous results for the females might thus be explained by the fact that the majority were ripe and were staying near the surface to lay their eggs; in this case one would have expected the Stage V and males to have behaved normally. Their distributions, however, are also anomalous although less markedly so.

Banse (1959) has stressed the importance of temperature and salinity gradients for the vertical distribution of the zooplankton. It seems improbable that here the gradients in either temperature or salinity had a measurable effect on the migrations recorded. Water samples were taken at the stations and the vertical gradient in temperature in 1959 was less than 1°C ($7.1-7.8^{\circ}\text{C}$) and in salinity less than one part per thousand ($33.15-32.57\text{‰}$). In 1959, however, the water was warmer than in the other two years (1953, $6.3-7.3^{\circ}\text{C}$; 1954, $6.2-6.9^{\circ}\text{C}$).

SUMMARY

A comparison of vertical distribution stations worked in several different years shows that the diurnal vertical migration varies considerably from one to another. The state of maturity of the females influences it in that ripe females migrate more and remain higher in the water than immature.

REFERENCES

- BAINBRIDGE, R., 1953. Studies on the interrelationships of zooplankton and phytoplankton. *J. mar. biol. Ass. U.K.*, Vol. 32, pp. 385-447.
- BANSE, K., 1959. Die Vertikalverteilung planktischer Copepoden in der Kieler Bucht. *Ber. dtsh. Komm. Meeresforsch.*, Bd. 15, pp. 357-90.
- BARNES, H., 1951. Horizontal plankton hauls. *J. Cons. int. Explor. Mer*, Vol. 17, pp. 133-9.
- CUSHING, D. H., 1951. The vertical migration of planktonic crustacea. *Biol. Rev.*, Vol. 26, pp. 158-92.
- GAULD, D. T., 1953. Diurnal variations in the grazing of planktonic copepods. *J. mar. biol. Ass. U.K.*, Vol. 31, pp. 461-74.
- GRAY, P., 1958. *Handbook of Basic Microtechnique*, 2nd ed. New York: McGraw-Hill.
- HARDING, J. P., MARSHALL, S. M. & ORR, A. P., 1951. Time of egg laying in the planktonic copepod *Calanus*. *Nature, Lond.*, Vol. 167, p. 953.
- HARDY, A. C. & PATON, W. N., 1947. Experiments on the vertical migration of plankton animals. *J. mar. biol. Ass. U.K.*, Vol. 26, pp. 467-526.
- HARRIS, J. E., 1953. Physical factors involved in the vertical migration of plankton. *Quart. J. micr. Sci.*, Vol. 94, pp. 537-50.
- MARSHALL, S. M. & ORR, A. P., 1952. On the biology of *Calanus finmarchicus*. VII. Factors affecting egg production. *J. mar. biol. Ass. U.K.*, Vol. 30, 527-47.
- MOORE, H. B., 1958. *Marine Ecology*. New York: John Wiley and Sons.
- NICHOLLS, A. G., 1933. On the biology of *Calanus finmarchicus*. III. Vertical distribution and diurnal migration in the Clyde sea area. *J. mar. biol. Ass. U.K.*, Vol. 19, pp. 139-64.
- RUSSELL, F. S., 1927. The vertical distribution of plankton in the sea. *Biol. Rev.*, Vol. 2, pp. 213-62.
- SALZEN, E. A., 1956. The density of the eggs of *Calanus finmarchicus*. *J. mar. biol. Ass. U.K.*, Vol. 35, pp. 549-54.