On the Diurnal Migration of Zooplankton in Relation to the Discontinuity Layer.

By

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AS a preliminary link in the investigation of the vertical distribution of zooplankton, Prof. J. T. Ruud, of Oslo, made a series of collections in the inner part of Oslo fjord, over a complete 24-hour cycle, during the period 26.—28. June 1947. His object was to test the usefulness of his method (a combination of bathythermograph and Clarke-Bumpus plankton sampler), and he also wished to find out what importance the discontinuity layer had as a limiting factor for the vertical distribution and migration of the separate species. I am greatly indebted to Prof. Ruud for permission to use this material.

The earlier investigations on the vertical migrations of the zooplankton — after evidence for this had been obtained — were directed especially to their causes, and showed the movements to be due to changes in the intensity of light, though hydrographical factors such as temperature, salinity, oxygen content, etc. may act as limiting factors in the distribution and migration of the separate species (e.g., Bogorov 1946, Clarke 1930, 1932, 1933, Hardy 1947, Kikuchi 1930, Nicholls 1933, Russell 1927 to 1934). The discontinuity layer, with its great variations in the hydrographical factors mentioned, may be the limit of the vertical distribution of the different species and their migrations. In the Sound the discontinuity layer forms an insurmountable barrier for the larvae of bottom-living animals: if they pass this, they die (Thorson 1946). According to the biological character and the sensitivity of the separate species there are 4 possibilities:—

1. Migration from the discontinuity layer to the surface.
2. Occurrence only in the discontinuity layer.
3. Migration from deep water (or bottom) to the discontinuity layer.
4. Migration from deep water (or bottom) up to the surface.

For evidence of these points we require:—

I. A method by which we can immediately determine the depth at which the discontinuity layer lies.

II. Plankton nets towed horizontally, which can indicate the volume of water flowing through the net; and from this volume can be derived the number of species per unit of volume.

In the present investigation the bathythermograph was used for the first purpose, and the Clarke-Bumpus plankton sampler for the second.

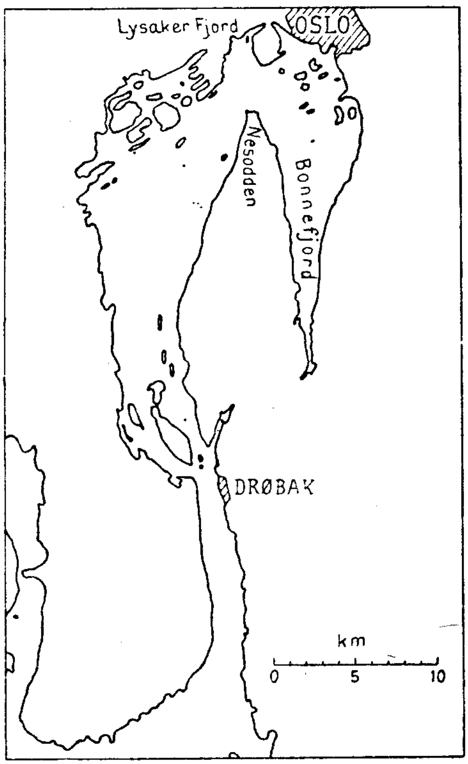

Figure 1.

Topography and Hydrography.

Two different localities in Oslo fjord were chosen for the collections — Bonnefjord on 24.—27. June and west of Nesodden on 28. June (Figure 1).

Bonnefjord is the innermost basin of Oslo fjord. The depth at the threshold in Drøbak Sound is 40 m., beyond which the hydrographical conditions are constant in the layers below 40 m. with a temperature of 6°—7°C. and a salinity of about 33 $^0/_{00}$. Furthermore, the oxygen content decreases with increasing depth so that in the deepest parts (below 150 m.) the oxygen content is very low. At several localities it is nil. The surface layers on the other hand are subject to great hydrographical change (see Braarud & Ruud 1937). The only station at which corresponding observations of temperature and salinity were made was in Bonnefjord on 24. June from 1300 to 1415 hrs.

Figure 2 shows the normal conditions at the locality and season in question. These are characterized by a high surface temperature (19°—20°C.), a marked discontinuity layer at about 10 m., with a temperature fall of about 10°C., and a constant temperature in deep water of about 6·8°C. The salinity in the discontinuity layer rises from about 20 to 31 ‰.

In Bonnefjord on 26. June at 1710, 2300 and 2330 hrs., and on 27. June at 0800 hrs., the temperature was recorded with the bathythermograph down to a depth of about 50 m., as shown in Figure 3.

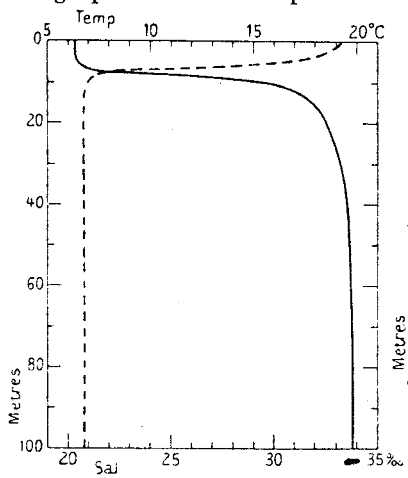

Figure 2. Distribution of temperature and salinity on 24. June from 1300 to 1415 hrs.

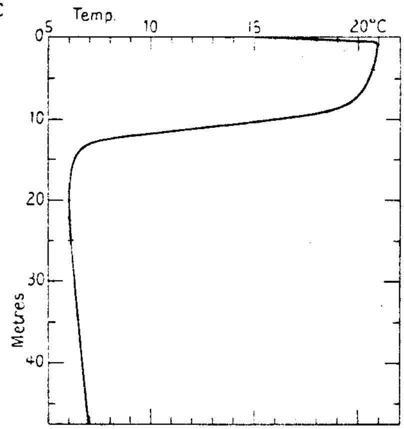

Figure 3. Temperature in Bonnefjord on 26. June at 2330 hrs.

The depth at which the net collections were made are indicated by a stroke. The uppermost depth was always 4 m., the intermediate depth was in the discontinuity layer (at 1800 hrs., 9 m.; at 2400 and 0830 hrs., 10·65 m.; and at Nesodden at 1300 hrs., 13 m.), and the lowest depth was 25 m. The surface temperature fell in the course of the night from 18·1° at 1700 hrs. to 14·7° at 0800 hrs.; with increasing depth, the temperature difference was evened out.

The discontinuity layer at 1710 hrs. was at approximately 9 m., with a very rapid temperature fall of 9·2°C. between 8·50 m. and 9·50 m., but later became somewhat deeper, with a less sharp temperature fall (at 1 m., ca. 3°C.; at 2·5 m., ca. 8°C.). At 25 m. the temperature varied between 6·3° and 6·1°C. This shows that an organism which breaks through the discontinuity layer is exposed to a temperature change of about 10°C. and a salinity change of 8—9 ‰ with a correspondingly great variation in oxygen content.

Extract from the Log Book.

Date and Hour		Locality	Weather	Depth of discontinuity layer
June	hrs.			
26.	1710	Bonnefjord	—	9 m.
26.	2330	„	cloudy, slight breeze.	10·65 m.
27.	0800	„	cloudy; slight fog; calm, slight breeze.	10·65 m.
27.	1000	„	calm, sunny.	10·65 m.
27.	1030	„	calm, sunny.	10·65 m.
28.	1300	W. of Nesodden	slight breeze, sunny.	13 m.

The depth of the discontinuity layer was determined by means of the bathythermograph. To obtain as accurate a picture as possible of the population above, within, and below the discontinuity layer in a particular hydrographical situation, three plankton samplers were attached to the same wire in the depth mentioned. At the end of the wire was hung a 30 Kg. lead weight. With the exception of the sampler used at 25 m. at 1800 hrs., which failed to close and was at once used again, all the samplers worked satisfactorily, opening and shutting in series. Complete stations were made on 26. June at 1800 and 2400 hrs., and on 27. June at 0830 hrs. (over, within, and below discontinuity layer). At 1000 hrs. two samplers were lowered to 10·65 m. at a horizontal distanee apart of 3 m. for 10 minutes. It was hoped to see in this way whether the population was quantitatively different at different places, whether the plankton occurred in clumps.

The nets used in the samplers were of No. 8 silk; the volume of water which passed through the samplers during the ten minutes varied between 3,700 and 6,300 litres.

Enumeration.

All Chaetognatha, *Meganyctiphanes norvegica*, and Hydromedusae were counted. Of the other species from one-tenth to one-hundredth part was counted, the samples being fractioned by means of Lea's plankton divider. The total number was adjusted to the number of animals per thousand litres. Unless otherwise stated, the quantities given correspond to this unit of volume.

Sources of Error.

Various errors arise during the collection of the samples so that this method is not quantitatively exact, but the results are nevertheless comparable. Clogging of the meshes may occur, e.g., in areas with great abundance of plankton or in the presence of many *Cyanea capillata*. With the width of mesh in No. 8 silk (0·17—0·12 mm. when wet) a number of small organisms are able to pass through the net, e.g., copepodite stages of *Oithona helgolandica* and all stages of *Oithona nana*. The number of these in the samples is hardly therefore representative.

The Distribution and Migration of the Various Species.

1. Species occurring chiefly in the warm surface water with the discontinuity layer as the principal boundary.

Calanus finmarchicus (Gunnerus), females. At 4 m. fewer than 10 individuals were taken at all the day stations; at 2400 hrs., however, over 1000 individuals were taken. At 25 m. numbers were fairly constant, but rose to a maximum at 0830 hrs. The same was found for the whole population of *Calanus finmarchicus*.

Number/1000 litres, 25 m.	at 1800 hrs.	at 2400 hrs.	at 0830 hrs.
Females	27	47	122
Total *C. finmarchicus*	98	143	303

During the day most individuals were found round about the discontinuity layer; their numbers decreased most rapidly the deeper the water. The upper limit for their migrations during the night probably lay between the surface and 4 m. (Fig. 4).

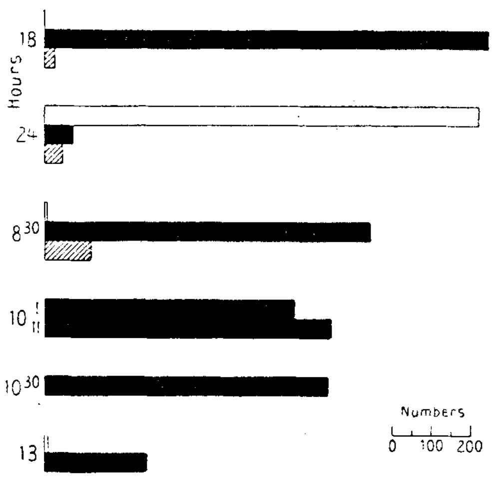

Figure 4. Number of *Calanus finmarchicus* females per 1000 litres at 4 metres (white column), in the discontinuity layer (black column), and at 25 metres (shaded column).

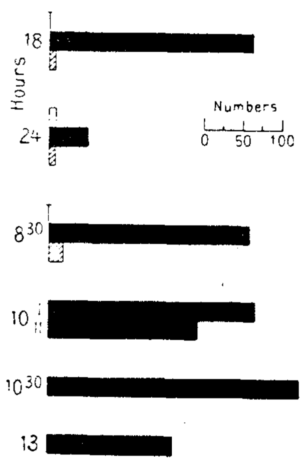

Figure 5. Number of *Calanus finmarchicus* males per 1000 litres; for signs and explanation see Figure 4.

Centropages hamatus (Lilljeborg). In the daytime this species was found around and within the discontinuity layer in large numbers. It disappeared from there at night, the maximal occurrence being in the neighbourhood of the surface. None was observed at 25 m. at any time. The adults approached nearer to the surface than the copepodite stages.

Oithona nana (Giesbrecht). Both adults and copepodites were between surface and discontinuity layer during the whole 24 hours. During the night there was a particularly large accumulation in the uppermost layers. The small population below the discontinuity layer did not seem to undergo any diurnal variation.

Podon spp. Only *Podon polyphemoides* (Leuckart) was determined, but *Podon leuckarti* (G. O. Sars) and *Podon intermedius* (Lilljeborg) are said to occur in the neighbourhood of Oslo (W i b o r g 1940). They are surface forms which migrate into the uppermost layers during the night, and are found at 25 m. in the daytime.

Evadne nordmanni (Lovén). This species is even more closely confined to the surface than *Podon*. It was not found at 25 m. Only a few were found during the day in the discontinuity layer.

2. Species occurring in or close to the discontinuity layer.

Calanus finmarchicus, males (Fig. 5). The day samples at 4 m. gave few or no specimens, and only 9 at 2400 hrs. In all samples at 25 m. the number was small but constant. In this locality the males seemed to be closely confined to the levels in and around the discontinuity layer. They migrate neither so near the surface (they probably stop between 4 m. and the discontinuity layer) nor so deep as the females. Earlier observations have shown that the males live at somewhat greater depths than the females (R u u d 1929, R u s s e l l 1934, W i b o r g 1940).

Temora longicornis (Fig. 6). For the females the upper boundary during the night lay between the surface and the discontinuity layer. The males were observed only in the discontinuity layer, and in greatly varying numbers. The females were more numerous than the males except at 1800 hrs. and 1300 hrs. The distribution of the copepodites resembled that of the males. In all samples they were fewer than the adults.

Oithona helgolandica (Claus), adults. During the day the maximum occurrence was in the discontinuity layer, but the number diminished greatly during the night. As the numbers at 4 m. were constant throughout the 24 hours, their upper boundary lay between 4 m. and the discontinuity layer. The copepodites were less mobile than the adults. The numbers at 25 m. were constant.

Sarsia tubulosa (M. Sars). In Danish waters in the summer of 1911 the highest temperatures at which *Sarsia tubulosa* was common were 9·4°C.—10·8°C. (0—8 m. in the Kattegat on 30. June) according to K r a m p 1927.

Bonnefjord; 26.—27. June 1947.

Time	Discontinuity layer Depth (m.)	t°C.	Time	Clarke-Bumpus sampler Depth (m.)	t°C.
1710 hrs.	8—10	19—8	1725—1735 hrs.	9	12·5—15
2300 hrs.	9—14	19—7	—	—	—
2330 hrs.	9—13	19—7	2348—2358 hrs.	10·65	14—15
0800 hrs.	9—13	19—8	0820—0830 hrs.	10·65	11·5—12·5

At these stations in Bonnefjord *Sarsia tubulosa* occurs only in the discontinuity layer. The figures given below give the total number of *Sarsia tubulosa* in the whole volume of water which passed through the samplers.

					at Nesodden
Time	1800 hrs.	2400 hrs.	0830 hrs.	1000 hrs.	1300 hrs.
Number	16	7	4	4	15

The distribution of *Sarsia tubulosa* seems to be determined essentially by temperature, the maximum temperature tolerable in the summer being about 15°C. In order to remain in the optimal temperature area of the hydrographical situation described *S. tubulosa* has sought to keep within the discontinuity layer the whole time. K r a m p (1915) connects the distribution with salinity. He writes, "*Sarsia tubulosa*, most abundant in the deeper strata . . . The variations from day to day of the number of individuals are very large. A connexion between these variations and the hydrographical conditions is slightly indicated, as far as a higher salinity in the lower or the intermediate water-layers seems frequently to be followed by a greater number of *Sarsia*".

A closer investigation will probably show that both temperature and salinity act as limiting factors in the distribution of *Sarsia tubulosa.*

3. Species found under the discontinuity layer and having this layer as the principal upper boundary.

Pseudocalanus minutus (Krøyer). All stages occur in the greatest numbers from 0 to 50 m. in Bonnefjord (W i b o r g 1940). In the daytime none was found at 4 m. At night for the females the principal boundary lay in the uppermost part of the discontinuity layer, whilst by far the most males were found at 25 m. and did not migrate into the discontinuity layer.

Oncaea borealis (G. O. Sars), Syn. *O. conifera* (Sars) (not Giesbrecht). Earlier investigations in Bonnefjord have shown that this species occurs most abundantly from 0 to 50 m. (W i b o r g 1940).

The principal concentration of females during the daytime lay below the discontinuity layer at 25 m. (50 m.?). During the night they migrated towards the discontinuity layer. The males and copepodites were not found at all at 4 m. nor in the discontinuity layer. They live in somewhat deeper water than the females.

Meganyctiphanes norvegica. With the exception of three adults which were found at 2400 hrs. at 25 m. (all that occurred in the sample), the following figures refer to the larval stages. All specimens were counted.

Bonnefjord; 26.—27. June 1947. Number per 1000 litres.

Depth	1800 hrs.	2400 hrs.	0830 hrs.
4 m.	1	0	0
Discontinuity layer	42	545	[illegible]
25 m.	33	1 (adult)	8.

Larval stages were found in the daytime right up to the discontinuity layer and they accumulated densely here during the night. They were not found at night at 25 m. Adults lived in the daytime below 25 m.;

at night the absolute upper boundary for these was in the lowest part of the discontinuity layer.

Chaetognatha: *Sagitta* spp. Only *Sagitta elegans* (Verrill) was determined, but according to W i b o r g (1940) *S. setosa* (J. Müller) also occurs in Oslo fjord. Formerly *S. elegans* and *S. setosa* were known by the same name, *S. bipunctata* (Quoy and Gaimard), this name now being used for a form that lives in warmer zones. *Sagitta elegans* lives mostly in waters of a fairly low salinity and temperature. In their downward migration they are accordingly stopped by high salinity, and in their

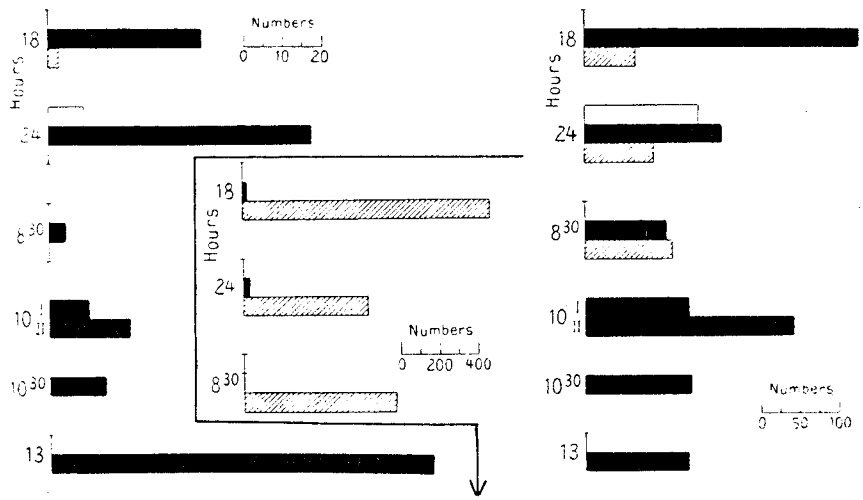

Figure 6. Number of *Temora longicornis* females per 1000 litres.

Figure 7. Number of *Oncaea borealis* females per 1000 litres.

Figure 8. Number of *Calanus finmarchicus* copepodite stage V per 1000 litres.

For signs and explanation see Figure 4.

upward travel towards the surface by higher temperatures. The younger stages, however, live in the warm surface water and are able to withstand much higher intensities of light than the older stages (R u s s e l l 1931). Probably the great increase in temperature in the discontinuity layer causes the majority of the population to remain there during the night.

Bonnefjord; 26.—27. June 1947. Number per 1000 litres.

Depth	1800 hrs.	2400 hrs	0830 hrs.	1000 hrs.	1030 hrs.
4 m.	8	11	1	0	0
Discontinuity layer	347	373	20	38	27
25 m.	22	28	41	—	—

They reached the upper boundary at about 1800 hrs. and remained in the vicinity till morning. In the daytime they were probably moving about in the lower region of the discontinuity layer.

Lensia conoidea (Keferstein and Ehlers 1860). Syn. *Diphyes conoidea*

(Keferstein and Ehlers), *Diphyes truncata* (Sars 1846), *Galetta truncata* (M. Sars 1846), *Galeolaria* (Moser 1925), *Lensia truncata* (Totton 1932).

The superior and inferior nectophores occurred separately, but were counted in pairs. They were found only at 25 m. depth. The determining factor was probably temperature. The figures mentioned below give the total number of *Lensia conoidea* in the whole volume of water passing through the samplers at 25 m.

Time	1800 hrs.	2400 hrs.	0830 hrs.
Number	30	75	24

These figures indicate a diurnal migration in the deeper strata.

Aglantha digitalis (O. Fr. Müller). The highest temperatures at which *Aglantha digitalis* was common in Danish waters during the summer of 1911 were 13·5°—13·6°C. (24—0 m. on 5. July in the Skagerak), and the highest temperatures in which it has been found are 14·1°—14·3°C. (12—0 m. on 4. July in the northern Kattegat), according to Kramp 1927. In Bonnefjord on 26. June at 2330 hrs. the discontinuity layer lay in 9—13 m. with temperatures of 19°—7°C. At 10·65 m. depth, where the sample was taken, the temperature was 14°—15°C. (see also *Sarsia tubulosa*, where the hydrographical conditions in the discontinuity layer are described).

Bonnefjord; 26.—27. June 1947. Number per 1000 litres.
(Total number in the samples in brackets.) At the stations not mentioned 0 specimens were found.

Depth	1800 hrs.	2400 hrs.	0830 hrs.
4 m.	0 (0)	0 (0)	0 (0)
Discontinuity layer	0 (0)	44 (176)	0 (0)
25 m.	0 (0)	4 (22)	0·3 (2)

In the prevailing hydrographical situation the discontinuity layer, with its rapidly increasing temperature, formed an insurmountable barrier. In the summer the maximum temperatures for the occurrence of *Aglantha digitalis* seem to be about 15°C.

4. Species on which the discontinuity layer has little or no influence.

Calanus finmarchicus (Fig. 8). Copepodite stage V. During the night the population was evenly distributed between 4 and 25 metres; it was probably distributed in this manner from the surface to below 25 m. At 2400 hrs. the relation between the numbers at 4 m. and in the discontinuity layer was 1 to 1·2; between the numbers at 4 m. and 25 m., 1·6 to 1; and between the numbers in the discontinuity layer and 25 m., 2 to 1. In the daytime the distribution did not extend appreciably above the discontinuity layer. Copepodite stage V has a more uniform vertical distribution than the adults.

Considering the total population at different depths at different periods in the 24 hours, we can see that the strongest movements occur in the uppermost water-layers, where extensive accumulations occur at night. At the same time the quantity in the discontinuity layer is reduced to one-third of the number found there in the daytime. On the other hand, the number at 25 m. remains constant (3505, 2090, 2555 individuals per 1000 litres).

The material discussed is on the whole too small to permit the drawing of general conclusions on the vertical distribution and migrations of the separate species. Most of the results obtained will only hold good in the prevailing hydrographical situation and in the season in question. Nevertheless they afford certain useful pointers for similar investigations in future.

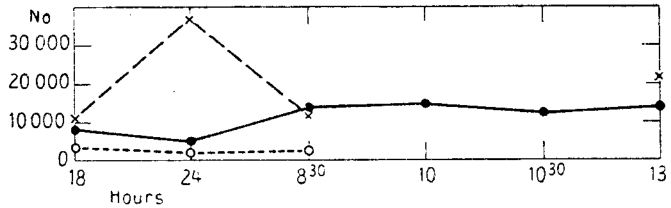

Figure 9. Diurnal variation in the total population (per 1000 litres; at 4 m. ×, the discontinuity layer ●, and 25 m. ○) at all stations.

The hydrographical data should be extended to include investigations (a) on the salinity, (b) on the oxygen content, and (c) in the daytime, on the intensity of light: to determine the factors which limit the distribution of the separate species. In a similar manner a number of Clarke-Bumpus samplers should be arranged in series at short distances from each other. In an area like that investigated, with a marked discontinuity layer at about 10 m., 5 samplers would be sufficient; 2 between the surface and the discontinuity layer, 1 in this layer, and 2 between this and 25 m. or deeper. This would give an accurate picture of the boundary areas for the several species. At the same time vertical hauls, between the discontinuity layer and the surface, and, for example, from 25 m. to the discontinuity layer, should be made in conformity with earlier practice. At the same localities at regular intervals throughout the year, full investigations should be made on the annual cycle of the separate species and their relation to the factors mentioned.

Summary.

To investigate the possible importance of the discontinuity layer as a limiting factor in the vertical distribution and migrations of the zooplankton, samples were collected from 26.—27. June 1947 from the innermost part of Oslo fjord. The position of the discontinuity layer was determined by means of the bathythermograph. Three Clarke-Bumpus samplers were kept open for ten minutes at 4 m. depth, in the discontinuity layer (9—10·65 m. depth) and at 25 m. depth. The volume of water streaming through the samplers varies from 3,700 to 6,300 litres. Investigations at the stations were made on 26. June at 1800 hrs. and at 2400 hrs.; on 27. June at 0830, 1000, and 1030 hrs. The populations were calculated per 1000 litres. The vertical distribution and migrations of the separate species proved in the main to be as follows:—

1. Species which occur mainly in the warm surface water with the discontinuity layer as its chief boundary: *Calanus finmarchicus* females; *Centropages hamatus* females, males, copepodites; *Oithona nana* females, males, copepodites; *Podon* spp. (see the text); *Evadne nordmanni.*
2. Species which occur in or near the discontinuity layer: *Calanus finmarchicus* males; *Temora longicornis* females, males, copepodites; *Oithona helgolandica* females, males, copepodites; *Sarsia tubulosa.*
3. Species found under the discontinuity layer with this layer as the chief upper boundary: *Pseudocalanus minutus* females, males; *Oncaea borealis* females, males, copepodites; *Meganyctiphanes norvegica; Sagitta* spp. (see the text); *Lensia conoidea; Aglantha digitalis.*
4. Species on which the discontinuity layer has little or no influence: *Calanus finmarchicus* copepodite stage V.

Variation in the total number of individuals in the 24 hours cycle (per 1000 l.):—

4 m. The numbers increased from 11,000 in daytime to 36,300 at night.

Discontinuity layer. The population at night was only one-third of that in daytime (this was constant at about 13,000).

25 m. The population showed no essential change (constant at about 2,500).

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