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ZOOPLANKTON INVESTIGATIONS FROM WEATHER SHIP M IN THE NORWEGIAN SEA, 1948—49.

WITH 25 FIGURES IN THE TEXT

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Contents.

I. Introduction.

The first ecological study of zooplankton in the Norwegian Sea was undertaken by Gran (1902) in the years 1900—1902. He found that the Norwegian Sea could be divided into regions, each having its characteristic plankton community. His description of the development of *Calanus finmarchicus* forms the basis of our knowledge of this species.

Gran's work was carried a stage further by Damas (1905), who in May and June 1904 investigated the distribution of *C. finmarchicus, C. hyperboreus* and *Pseudocalanus minutus* in the central area of the Norwegian Sea.

Farran (1910 and 1911) and Scott (1911) described the distribution of various zooplankton forms in this Sea from material collected in 1902—1908 during voyages organized by the International Council for the Exploration of the Sea.

With (1915) has given an account of the copepods collected by the Ingolf expedition, and Størmer (1929) has worked up material acquired during the voyage of the «Michael Sars» to West Greenland waters in 1924.

The zooplankton in the coastal waters round Iceland has been the subject of study by Paulsen (1906), and along the coast of West and North Norway by Ruud (1929) and Sømme (1934).

Most of the material mentioned above had been collected during the summer months and mainly from the upper layers (200—300 m.) of the sea. Our knowledge of the plankton in these layers during the winter, and of the plankton in the deeper layers, was therefore very incomplete.

Since the summer 1948 the opportunity has been afforded of collecting plankton from weather ship M, stationed in the Norwegian Sea at 66° N and 2° E. This material, assembled in the course of October 1948 —November 1949, is the subject of the present work. Material collected since 1950 has in part been collated by Wiborg (1954).

I wish to express my warmest thanks to the meteorologists, the officers and crews of the weather ships «Polarfront I» and «Polarfront II» for their untiring patience in the work of getting the samples. I am under an obligation to Dr. J. Eggvin, Professor Dr. H. Mosby and Professor Dr. Johan T. Ruud for their permission to make use of the material, and to Dr. G. L. Clarke of Harvard University for stimulating discussions.

II. Material and Methods.

The zooplankton was collected by means of a Nansen closing-net of the same kind as was used by Ruud (1929) and Wiborg (1940). It is 70 cm in diameter and made of silk, numbers 0 and 8.

Five consecutive vertical hauls were taken weekly through the following water columns: 50—0 m., 100—50 m., 1000—600 m. and 2000 (or bottom)-1000 m. These depth intervals were chosen in order to get samples from characteristic water masses. The hauls 50—0 m. and 100—50 m. would sample the surface layers, with their seasonally varying conditions. The haul 600—100 m. was to sample the core of the Atlantic current and the upper part of the transitional layers below this, while the haul 1000—600 m. was to sample the waters of mixed Atlantic and Arctic origin. The hauls below 1000 m. were expected to represent the plankton in the bottom waters. This scheme was planned on the basis of the hydrographical conditions found in October 1948 (see fig. 3).

All hauls were taken in daylight, between the hours of 0900 and 1200 Greenwich mean time, and any modifications in the distribution of the animal plankton due to diurnal vertical migrations should therefore be without significance. The samples were immediately fixed in 4 % formalin.

Table 1 shows the weekly hydrographical and biological programme carried out on board weather ship M. (according to Mosby, 1950). The hauls from 600—100 m., 100—50 m. and 50—0 m. were all undertaken on Wednesdays, while the two deepest hauls, 1000—600 m. and 2000—1000 m. were made on Tuesdays and Fridays respectively.

Table 1.

Weekly hydrographical and biological programme at M. (From Mosby 1950).

Day	Hydrography	Biology
Sunday	1 000	
Monday	1 000 + 150	
Tuesday	1 000	N. 1 000—600
Wednesday	150	N. 600—100—50—0
Thursday	2 500	F. 100—0
Friday	(1 000 + 150)	N. 2 500—1 000
Saturday	1 000 + 150	

N. = Nansen-net. F. = Phytoplankton-net.

150: Standard depths to 150 m.

2 500: Standard depths to 2 500 m.

1 000: Thermosonde to 1 000 m. and waterbottles in standard depths.

Correlation of the hydrographical observations and plankton hauls was effected only on Tuesdays. On Wednesdays, when the three hauls from the upper 600 meters were taken, hydrographical observations were carried out only to a depth of 150 m. Owing to the time required for making a haul from the 2000—1000 m. layer it was as a rule impossible to make hydrographical observations on Fridays. Only in the event of it being impracticable to get plankton hauls on that day were hydrographical observations carried out. The hauls from the deepest layers had therefore to be correlated to the hydrographical observations made on the previous day.

It was not always possible to carry out the weekly programme, especially in the winter, when the weather could be very stormy. Samples taken from irregular depths have as a rule been left out of account. Table 2 shows the number of samples taken each months which have been the subject of complete analysis.

Table 2.

Number of samples from the different depths each month 1948—1949.

Depths	Months	O	N	D	J	F	M	A	M	J	J	A	S	O	N	Total
50—0 m.	....	4	2	3	1	4	3	4	3	5	4	4	3	1	1	42
100—50 m.	....	4	2	3	1	4	3	4	3	5	4	4	3	1	1	42
600—100 m.	....	2	3	3	1	4	3	4	3	5	5	4	2	1	1	41
1 000—600 m.	....	0	3	3	1	4	2	4	3	4	5	5	4	1	1	40
2 000—1 000 m.	....	0	1	3	1	4	1	5	1	5	5	4	4	1	1	36

The samples were in general too large to admit of a counting of the total number of individuals. All large organisms, such as Chaetognatha, Euphausiacea and Medusae, were removed and counted separately. The rest of the sample was then divided by means of a Lea Plankton Divider into fractions for analysis. This apparatus and its reliability have been discussed by Wiborg (1951). Finally the whole sample was examined for species which were few in number.

The copepods were determined on the basis of descriptions by Giesbrecht (1892), G. O. Sars (1900, 1903, 1918, 1924 and 1925), With (1915) and Rose (1933). Some authors have found difficulty in separating the copepodite stages I, II and III of *Calanus hyperboreus* from the corresponding stages of *Calanus finmarchicus* (Størmer 1929, Sømme 1934 and Jespersen 1934). In this material, however, the difference in size between the corresponding stages of the two species was so great that they could easily be separated (cf. Ruud 1929). The nauplii of the genus *Pareuchaeta,* which are very characteristic, were assigned to their species, while other copepod nauplii were not. For the determination of other systematic groups use was made of the «Plankton Sheets» of the International Council for the Exploration of the Sea and Nordisches Plankton. The paper by Einarsson (1945) was found useful for determination of the Euphausiacea.

The number of individuals per meter of the haul or per cubic meter filtered by the net has not been calculated, although it should be noted that the hauls from the various levels differ in length. Relatively to haul 50—0 m. the length of the other hauls, reckoning from above, was 1 : 10 : 8 : 20.

The total number of *Calanus finmarchicus* and *Pseudocalanus minutus* in the whole water column from 2 000 m. (or bottom) to surface was found by adding together the five different weekly hauls. Sometimes the deepest haul was not undertaken, but no correction has been made on this account, as at that time of the year most of the stocks were found above the 600 m. level, and it was assumed that only a few specimens would have been found below 1000 m.

Hensen (1887 and 1901) and Lohmann (1903) have drawn attention to the variations in samples taken in vertical plankton hauls. In recent years Gardiner (1931), Winsor and Walford (1936), Winsor and Clarke (1940) and Barnes (1949) have studied these variations statistically. Barnes found the coefficient of variation of a single observation to be 35 % for a haul of moderate length (about 60 m.). In the case of very short hauls the coefficient of variation was of the order 90 %. He suggests that the variation found depends largely on variations in the volume of water filtered by the net.

Fig. 1 shows the total number of copepods per haul at the different depths from October 1948 to November 1949 taken from weather ship M. As will be seen, there is considerable variation in the numbers of individuals from week to week and from season to season. It seems just to assume that the weekly variations depend in part on variations in the volume of water filtered.

As already stated, the material collected at M. was taken from different water layers by means of vertical hauls with a Nansen closing-net. Barnes (1949) holds that significant losses in the catches occur when the nets are closed on the Nansen principle, and according to Marshall (1949) this loss may be as much as 50 % of the total catch. At M. the deep hauls were effected through much longer columns of water than those examined by Barnes. It may be assumed therefore, that the loss due to the closing of the net has been of significance only if the zooplankton was very unevenly distributed in depth. In the case of the short haul, 100—50 m., however, the error may have significance.

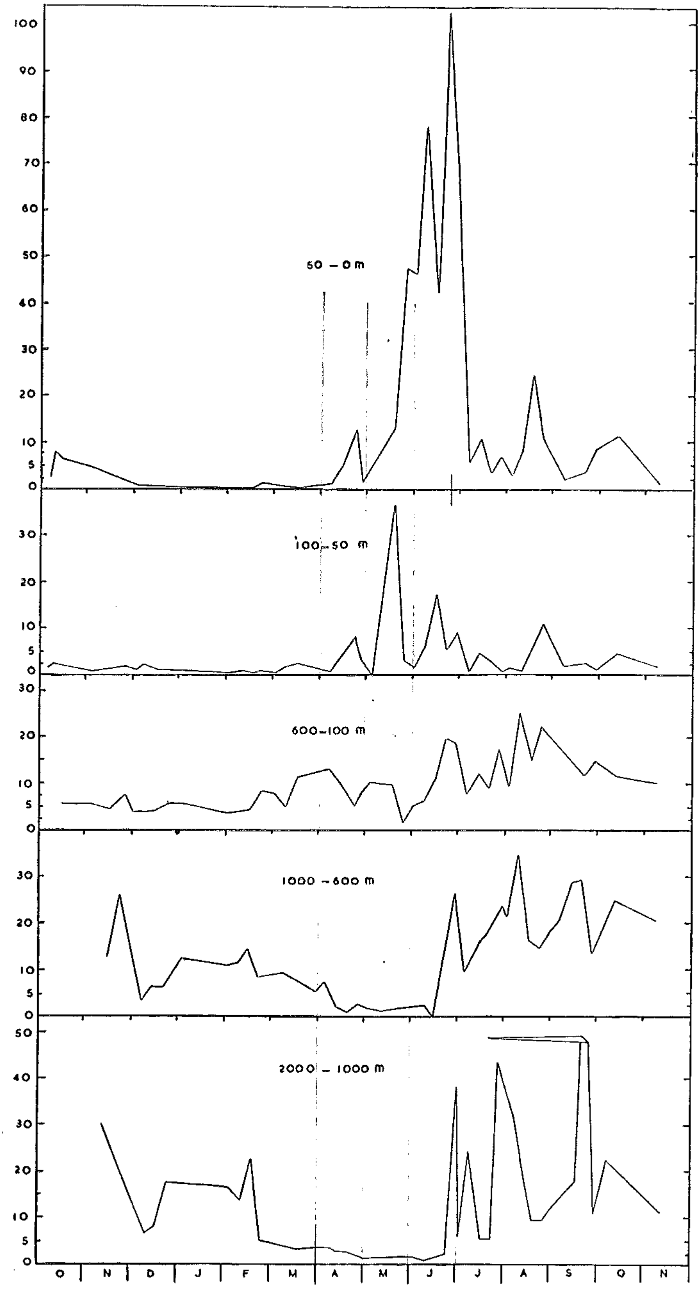

Fig. 1. Total numbers of copepods in thousands per haul at the different depths, October 1948 to November 1949.

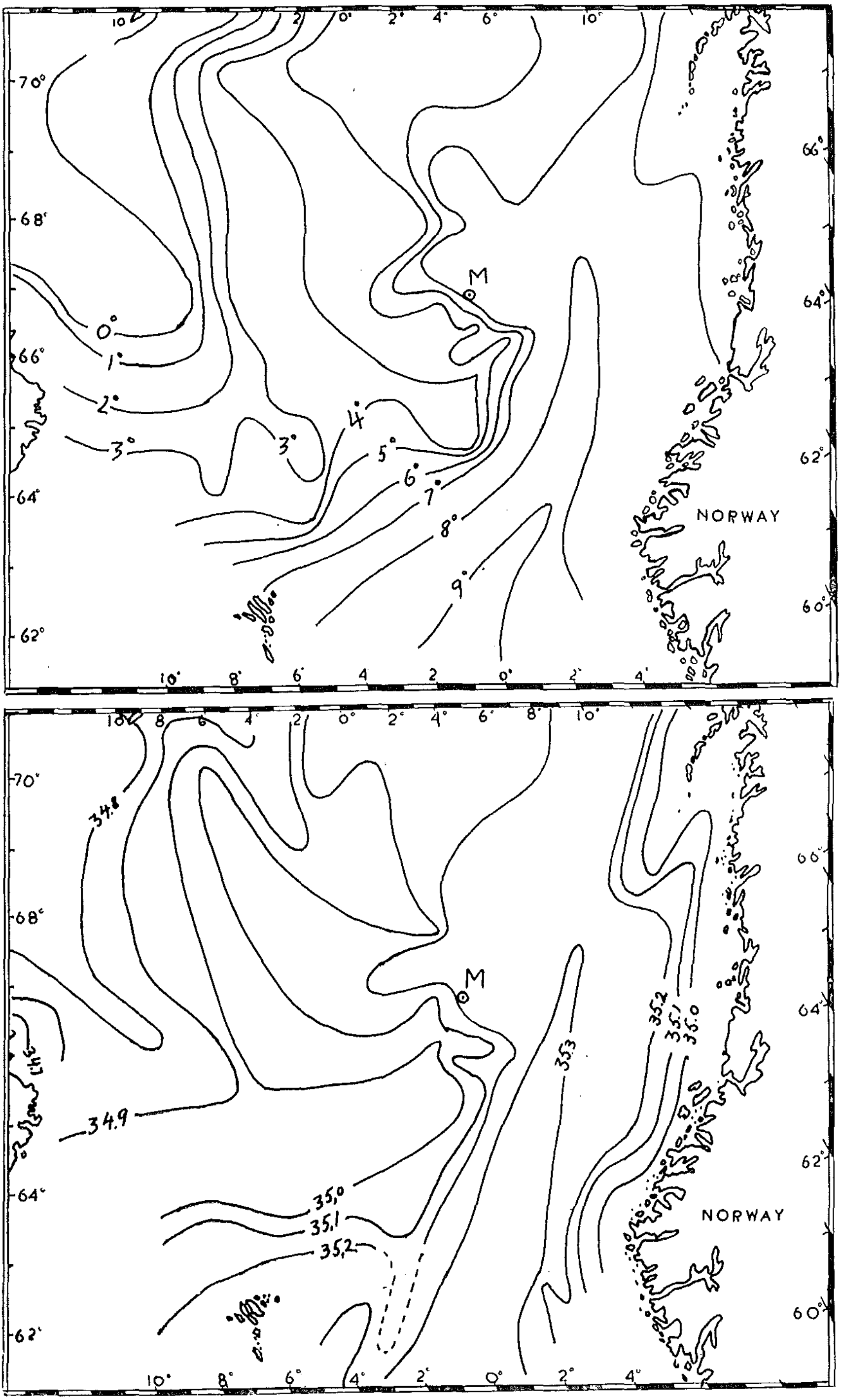

Fig. 2. Distribution of temperature and salinity at 100 m. depth in the Norwegian Sea, in the summer 1949. (After Eggvin.)

III. Topography and Hydrography of the Norwegian Sea at Station M.

The hydrography and topography of the Norwegian Sea have been described by Helland-Hansen and Nansen (1909).

Weather ship M. is stationed at 66° N. Lat. and 2° E. Long., and the vessel is allowed to drift within a square area of 10 × 10 nautical miles. The depth at the station is about 2 000 m., but the bottom slope is such that the depth within he said area may vary from 3000 to 1500 m. The station is located on the western edge of the Atlantic current (Mosby 1950) in the centre of the great cyclonic system of the Southern Norwegian Sea, described by Helland-Hansen and Nansen (1909).

By the courtesy of Dr. J. Eggvin fig. 2, showing the temperature distribution and salinity at 100 m. depth in the Norwegian Sea in the summer 1949, is given here.

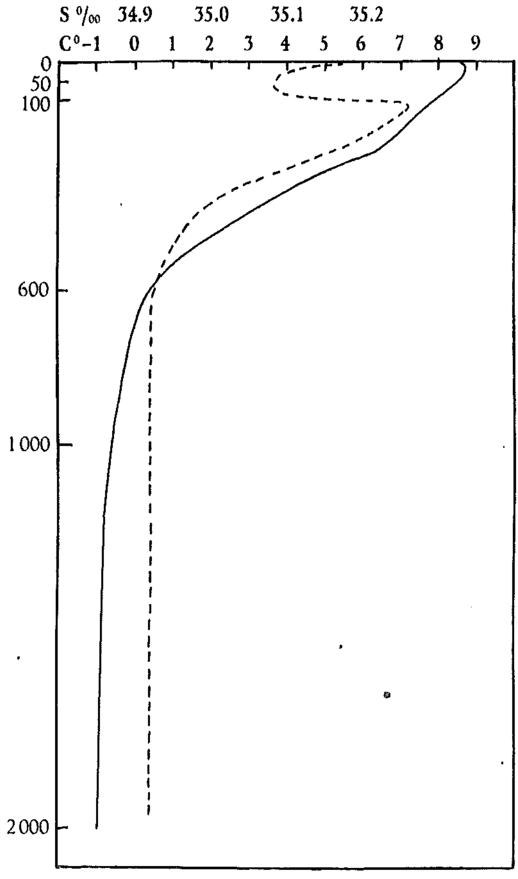

Fig. 3. The vertical distribution of temperature (——) and salinity (- - -) at station M, October 10th, 1948.

Fig. 3 shows the vertical temperature distribution and salinity on October 10th, 1948, when the collection of zooplankton samples commenced. According to Halldal (1953), breakdown of the stratification of the water masses had begun in October, and these were mixed above the thermocline, which was found at 50 m. From November to April the conditions were unstable, owing to the mixing processes, which in February extended almost down to the 400 m. level. In April stratification began to establish itself, but perfectly stable conditions did not ensue until June, from which date they lasted until November.

Fig. 4 shows the monthly mean temperature at 100 m. and at the surface. Between October 1948 and November 1949 the lowest mean temperature at the surface was 6.21° C. (March and April) and the highest 10.70° C. (August). At a depth of 100 m. the yearly amplitude was approximately 2° C.

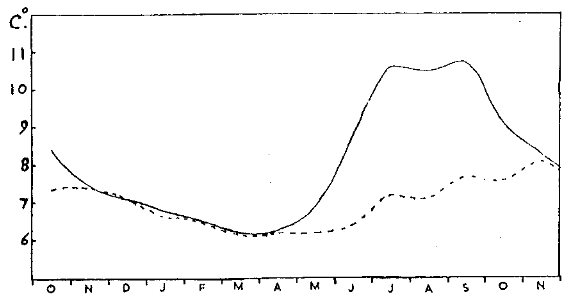

Fig. 4. Monthly mean temperatures at the surface (———), and at 100 m. depth (- - - -) from October 1948 to November 1949.

The East Icelandic Polar Current does not influence the hydrographical conditions in the upper water layers at station M, as this current sinks below the Atlantic Current at a point north of the Faroes (Tykkhelle 1947).

In the autumn there is a perceptible decrease in the salinity of the surface layers, probably due to mixing with Norwegian coastal waters having a salinity of less than 35 ‰.

In the Norwegian Sea water masses which have a salinity of 35 % or more are deemed to be of Atlantic origin. At station M 35 ‰ salinity was found to correspond to a temperature of 3—4° C. (Mosby 1950), and these figures, which signify the lower limit of the Atlantic waters, are usually found at depths of 300—400 m. — in the autumn and winter even deeper.

Mosby (1950) has observed internal waves of some magnitude all the year round, in border layers beneath the Atlantic water masses. The location of the isotherms of 3° and 4° C. varies very rapidly and with great vertical amplitude. On July 9, 1949, the isotherms moved upwards about 270 m. in less than 20 hours. The waves seem to have a duration of some 11 days and an amplitude of about 200 m.

Below the Atlantic water and down to about 1000 m. the waters are of mixed Atlantic and Arctic origin. At these depths the variations in salinity and temperature during the year are small. As will be seen from fig. 5, which gives the monthly mean temperatures at 600 m. and 1000 m., the difference between the minimum and maximum temperature was only 1° and 0.15° C. respectively.

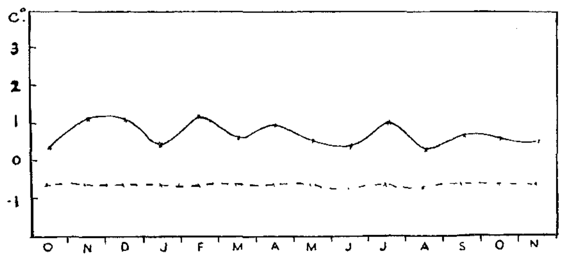

Fig. 5. Monthly mean temperatures at 600 m. (———) and 1000 m. depth (----) from October 1948 to November 1949.

Below 1000 m. the characteristic bottom water of the Norwegian Sea is found, with a temperature of — 1.0—0° C. and a very uniform salinity of 34.92 ‰. Helland-Hansen and Nansen (1909) are of the opinion that this bottom water remains practically unchanged for many years.

IV. Nature and Fluctuations of the Plankton Communities.

The species which have been identified in the zooplankton material from the M station are listed below, with indication of the depths at which they were taken (table 3). The numbers given represent the aggregates from all hauls taken at the respective depths. The list does not pretend to be complete as regards the species present in the samples, Radolaria, Challengerida and a few species from other groups not having been identified.

As will be seen, copepods were the dominant find. A total of 55 species of these were identified, the following 13 species occurring at all depths: *Calanus finmarchicus, Calanus hyperboreus, Pseudocalanus minutus, Microcalanus pygmaeus, Gaidius tenuispinus, Pareuchaeta norvegica, Scolecithricella minor, Metridia longa, Metridia lucens, Oithona similis, Oithona spinirostris, Oncaea borealis* and *Microsetella norvegica*. Nine of these species were also the most abundant. They are listed in

Table 3.
The number of individuals of each species recorded in vertical hauls taken at weather ship M during 1948—49.

Depth of hauls in m.	50—0	100—50	600—100	1000—600	2000—1000
Number of hauls	42	42	41	40	36
Number of species	35	35	67	52	64
Number of species of copepods	20	19	38	30	37
Number of species recorded in the respective hauls only	2	0	19	2	19
Coelenterata:					
Aglantha digitale (O. F. Müller)	3177	666	894	1137	234
Atolla wyvillei Haeckel	—	—	—	—	17
Beroe cucumis Fabricius	1	—	6	3	5
Diphyes arctica (Chun)	5	2	543	232	12
Lensia conoidea Keferstein & Ehlers	—	—	5	—	—
Physophora hydrostatica Forskål	—	—	2	—	—
Polychaeta:					
Tomopteris spp.	—	2	78	31	19
Phyllodocidae	—	—	9	88	71
Pteropoda:					
Limacina retroversa (Flem.)	7844	276	1663	112	—
Clione limacina (Phipps)	—	—	10	4	2
Chaetognatha:					
Sagitta elegans Verrill	125	157	178	54	3
» *maxima* (Conant)	—	—	27	5	5
» *serratodentata* Krohn	—	—	1	—	—
» *planctonis* Steinhaus	—	—	1	—	—
Eukrohnia hamata (Møbius)	315	178	4350	2716	684
Cladocera:					
Evadne nordmanni Lovén	650	10	—	—	—
Copepoda:					
Calanus finmarchicus (Gunn.)	167736	49365	163253	216919	130385
» *hyperboreus* Krøyer	1841	1461	5431	5990	47313
Rhincalanus nasutus Giesbrecht	—	—	3	8	4
Eucalanus elongatus Dana	—	—	—	1	—
Paracalanus parvus (Claus)	773	697	62	—	—
Pseudocalanus minutus (Krøyer)	136834	24488	27334	107026	202595
Microcalanus pygmaeus (G. O. Sars)	4154	11621	62530	32885	46738
Spinocalanus abyssalis Giesbrecht	—	—	1	4	145
» *magnus* Wolfenden	—	—	—	5	52
Aetideus armatus (Boeck)	3	31	70	40	—
Aetideopsis rostrata G. O. Sars	—	—	3	176	546
Pseudaetideus armatus (Boeck)	—	—	4	41	54
Chiridius obtusifrons G. O. Sars	—	—	31	36	1
Chiridiella macrodactyla G. O. Sars	—	—	—	—	2
Gaidius brevispinus (G. O. Sars)	—	—	39	282	631
» *tenuispinus* (G. O. Sars)	1	2	327	125	5

Depth of hauls in m.	50—0	100—50	600—100	1000—600	2000—1000
Number of hauls	42	42	41	40	36
Number of species	35	35	67	52	64
Number of species of copepods	20	19	38	30	37
Number of species recorded in the respective hauls only	2	0	19	2	19
Gaetanus pileatus Farran	—	—	3	3	—
» *minor* Farran	—	—	1	—	—
Euchirella curticauda Giesbrecht	—	—	1	—	—
» *rostrata* (Claus)	—	—	2	—	—
Pseudochirella pustulifera (G. O. Sars)	—	—	—	—	2
» sp.	—	—	—	—	1
Undeuchaeta major Giesbrecht	—	—	—	—	2
Pareuchaeta norvegica (Boeck)	12	93	1702	994	98
» *farrani* (With)	—	—	2	456	2657
» *bradyi* (With)	—	—	—	—	38
» *glacialis* (H. J. Hansen)	—	—	5	33	18
Scottocalanus persecans (Giesbrecht)	—	—	1	—	—
» *securifrons* (Th. Scott)	—	—	1	—	—
Scaphocalanus magnus (Th. Scott)	—	—	—	3	14
» *brevicornis* (G. O. Sars)	—	—	—	47	976
Amallothrix sp.	—	—	—	—	1
Scolecithricella minor (Brady)	38	117	1199	226	3
» *ovata* (Farran)	—	—	—	—	1
» *dentata* (Giesbrecht)	—	—	2	—	—
Temora longicornis (O. F. Müller)	570	70	1	—	—
Temorites brevis G. O. Sars	—	—	—	—	3
Metridia longa (Lubbock), stage IV, V, VI	155	1836	22315	7787	4493
» *lucens* Boeck, stage IV, V, VI	610	1357	11295	2975	138
Pleuromamma robusta (Dahl)	—	1	659	247	—
Centropages typicus Krøyer	219	130	—	—	—
Heterorhabdus norvegicus (Boeck)	1	—	85	64	20
Lucicutia longicornis (Giesbrecht)	—	—	1	—	—
» sp.	—	—	—	—	2
Augaptilus glacialis G. O. Sars	—	—	—	—	1
Candacia armata (Boeck)	—	—	1	—	—
Anomalocera patersoni Templeton	1	—	—	—	—
Acartia clausi Giesbrecht	6422	1875	727	—	—
Oithona similis Claus	129100	39210	36110	20540	9870
» *spinirostris* Claus	3580	6690	26420	9610	1360
Oncaea borealis G. O. Sars	26300	5200	18360	116730	62380
» *conifera* Giesbrecht	—	—	99	69	26
Microsetella norvegica (Boeck)	328	56	5	3	7
Parathalestris croni (Krøyer)	—	—	1	—	—
Clytemnestra rostrata (Brady)	—	—	1	—	—
Ostracoda:					
Conchoecia borealis G. O. Sars, » *elegans* G. O. Sars, » *obtusata* G. O. Sars	5	43	3366	8281	6422

Depth of hauls in m.	50—0	100—50	600—100	1000—600	2000—1000
Number of hauls	42	42	41	40	36
Number of species	35	35	67	52	64
Number of species of copepods	20	19	38	30	37
Number of species recorded in the respective hauls only	2	0	19	2	19
Isopoda:					
Nothophryxus lateralis G. O. Sars	—	—	—	—	1
Amphipoda:					
Themisto abyssorum (Boeck)	444	381	272	403	143
» *compressa f. bispinosa* (Boeck)	—	1	4	8	2
» » *f. compressa* (Goes)	—	—	5	2	—
Hyperia galba (Montague)	—	—	1	—	—
» *medusarum* (Müller)	—	—	—	—	1
Hyperoche medusarum (Krøyer)	1	—	—	—	—
Scina borealis G. O. Sars	—	—	—	1	4
» sp.	—	—	—	—	1
Cyphocaris bouvieri Chev.	—	—	—	—	1
Cyclocaris guilelmi Chev.	—	—	—	28	109
Lanceola clausi Bovallius	—	—	—	—	3
Calliosoma sp.	—	—	—	—	1
Mysidacea:					
Boremysis arctica (Krøyer)	—	—	—	—	1
Euphausiacea:					
Meganyctiphanes norvegica (M. Sars)	200	92	223	139	9
Thysanoessa longicaudata (Krøyer)	212	130	219	563	148
» *inermis* (Krøyer)	—	—	6	37	3
Euphausia krohnii (Brandt)	—	—	1	—	—
Nematobrachion boopis Calman	—	—	1	—	—
Nematoscelis megalops G. O. Sars	—	—	1	—	—
Decapoda:					
Galathea rugosa (Fabricius)	1	1	—	—	—
Hymenodora glacialis (Buchholtz)	—	—	—	35	129
Sergestes arcticus Krøyer	—	—	—	1	—
Copelata:					
Oikopleura spp.	3551	1233	1568	43	336
Fritillaria borealis acuta Lohmann	—	20	50	—	—
Pisces:					
Myctophum glaciale Reinh.	1	7	3	—	—
Paraliparis bathybii Collett	—	—	—	—	1

table 4, and their frequencies at the different depths are calculated as percentages of the total number of copepods found in all samples from these depths.

Table 4.
Frequencies of the most abundant copepod species in per cent of total number of copepods.

Depth in m.	50—0	100—50	600—100	1000—600	2000—1000
Total number	481605	146181	386396	524681	511188
Calanus finmarchicus	34.83	33.77	42.25	41.34	25.51
Calanus hyperboreus	0.38	0.90	1.40	1.15	9.25
Pseudocalanus minutus	28.41	16.75	7.07	20.40	39.63
Microcalanus pygmaeus	0.86	7.95	16.26	6.27	9.14
Metridia longa / *Metridia lucens*	0.79	3.57	10.77	2.30	0.90
Oithona similis	26.81	26.81	9.35	3.91	1.93
Oithona spinirostris	0.74	4.58	6.84	1.83	0.27
Oncaea borealis	5.46	3.56	4.75	22.25	12.20
Total	98.28	97.90	98.70	99.45	98.84

Calanus finmarchicus, Pseudocalanus minutus and *Oithona similis* are predominant in the upper water levels, 50—0 m. and 100 —50 m., representing as much as 80—90 % of the whole number of copepods. In haul 600—100 m. *Calanus finmarchicus* is still more dominant, while *Pseudocalanus* and *Oithona similis* have declined considerably in importance. *Microcalanus* and the two species of *Metridia* are fairly well represented. In hauls 1000—600 m. and 2000—1000 m. *Calanus finmarchicus, Oncaea borealis* and *Pseudocalanus minutus* are predominant in the composition of the copepod fauna. It is clear therefore that *Calanus finmarchicus* and *Pseudocalanus* are in point of number the most important of the copepods found in the plankton at station M. Of the whole number these two species constituted approximately 58 %, i.e. *C. finmarchicus* 36 % and *Pseudocalanus* 22 %. The percentages recorded by Ruud (1929) in respect of the waters along Møre in 1925—27 are very similar, namely *C. finmarchicus* 34 % and *Pseudocalanus* 17 %.

A. PLANKTON OF THE SURFACE LAYERS

Station M lies near the western border of an area which Gran (1902) termed the «Tripos region». This extends in a north-easterly direction from the Faroe-Shetland Channel, and from the Norwegian coast seawards for about 200 miles. The vertical limit of the region was reckoned by Gran as lying 100 m. below the surface.

The plankton fauna in the upper 100 m. of this «Tripos region» showed great variation in abundance and composition. By far the greater part consisted of copepods, whereof as many as 20 species were found in varying numbers. Only *Calanus finmarchicus, Pseudocalanus minutus* and *Oithona similis* were present on all occasions; these occurred in abundance. Most of the stocks of *C. finmarchicus* and *P. minutus* spend the winter in deep water, but some were found above the 100 m. limit. *Oithona similis* alone was a faithful and permanent inhabitant of the upper layers all the year round and was equally abundant even over the 50 m. line.

Some other copepods also, viz. *Acartia clausi, Paracalanus parvus* and *Centropages typicus,* were found most frequently in the surface layers, and never deeper than 600 m. They showed a characteristic seasonal variation in number, being most numerous in October—November. *Microcalanus, Metridia, Calanus hyperboreus, Oithona spinirostris, Oncaea borealis* and some other species had their main distribution below 100 m., but were found also in varying number in the surface layers, this being dependent on their seasonal vertical migration and breeding habits.

Other zooplankton species, such as *Aglantha, Limacina, Eukrohnia hamata, Sagitta elegans, Meganyctiphanes norvegica* and *Thysanoessa* may be said to be temporary members of the fauna of this region. A more detailed description of the occurrence of the various species is given in later chapters.

The seasonal variation in the composition of the plankton fauna may be illustrated by the monthly mean percentage of certain species and groups of species at the different depths. These are given in fig. 6.

In October 1948 the boreal species *C. finmarchicus, Microcalanus* and *Oithona similis* constituted some 60 % of the total number of organisms found above 100 m. *Acartia clausi, Paracalanus parvus* and *Centropages typicus,* which are probably to be regarded as southern immigrants, were also present in relatively large quantities. Other organisms than copepods formed in the same months about 28 % of the total number found in the 50—0 m. depth. This large percentage is due to *Limacina retroversa,* which was very numerous in the hauls taken on October 9th and 14th.

During the winter, December to March, the southern immigrants gradually disappeared and were almost entirely absent in February, when the plankton population in the surface layers reached its lowest ebb. In this period *Microcalanus* and *Oithona* formed 80—90 % of the communities in the surface layers. *C. finmarchicus* and *P. minutus* increased in number at the end of the winter, probably as a result of the annual vertical migration of the stocks from deeper water (cf. Chap. V).

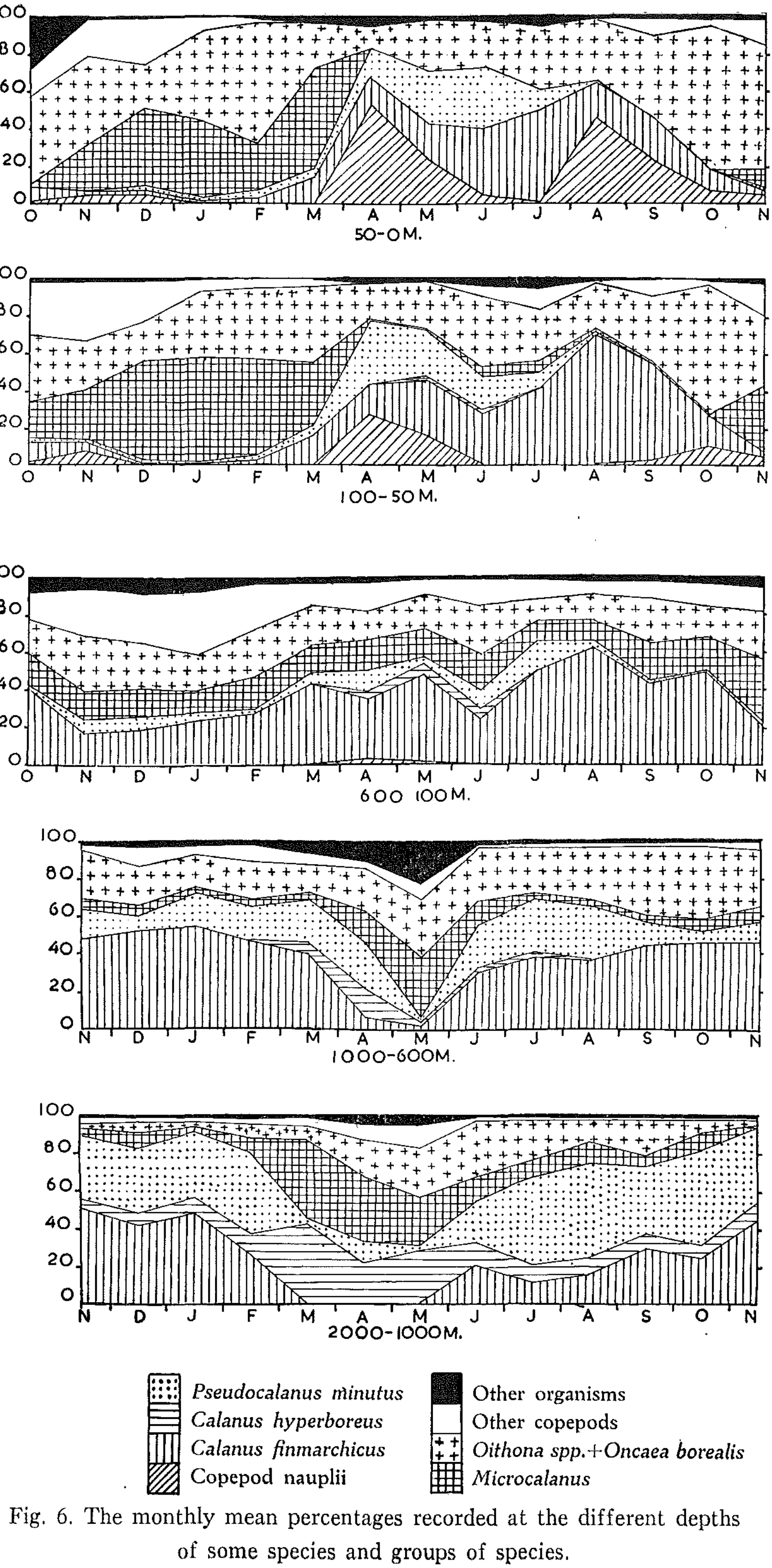

Fig. 6. The monthly mean percentages recorded at the different depths of some species and groups of species.

In April and May the vernal increase of the phytoplankton commenced (Halldal 1953) and soon showed itself in an augmentation of the numbers of *C. finmarchicus* and *P. minutus*. From May onwards the copepod stocks in the water layers above 50 m. increased rapidly, reaching a peak of 100 000 copepods in the second half of June (Fig. 1). The spring fauna in the surface layers contained only a few species, but these occurred in great abundance. *C. finmarchicus, P. minutus* and the nauplii of these and other copepods constituted 70—80 % of the population. Other authochthonous species too, viz. *C. hyperboreus, Oithona similis, Oncaea borealis* and the amphipod *Themisto abyssorum,* spawned in the spring, but these species were, in comparison with *C. finmarchicus* and *P. minutus,* only of minor importance. After the offspring of *C. finmarchicus* and *P. minutus* had developed into the copepodite stages IV and V at the beginning of June, they sank into deeper water for hibernation.

In July the numbers of the zooplankton organisms in the surface layers declined suddenly. From medio June to medio August nauplii of copepods were almost completely absent in the hauls, while on the other hand other organisms, such as *Aglantha, Oikopleura, Sagitta* and *Eukrohnia,* at times occurred in good number. These species had probably their chief spawning period then. In consequence of the mass increase of nauplii and small copepodites during the spring, these predatory organisms flourish in the summer. In the summer 1949 some neritic species, namely *Evadne nordmanni* and *Temora longicornis,* were found in the surface layers at station M.

During the autumn, August to December, a second spawning of copepods occurred. Most of the spring-spawned stock of *C. finmarchicus* had evidently descended to deeper layers when the second spawning of this species took place in the surface layers. This second spawning was, however, of minor importance compared with the spring one. In the warm surface layers in August the plankton communities gradually changed their character. Copepods of southern distribution appeared in relatively large numbers, viz. *Metridia lucens, Acartia clausi* and *Paracalanus parvus.* The two latter species were not observed in the plankton from February/March to July/August. The occurrence of these species must therefore depend upon an influx from other areas. *Limacina retroversa,* which was found in relatively large numbers in surface layers in October 1948, appeared also in the autumn 1949, but only in small numbers. A single specimen of the Atlantic species *Salpa fusiformis* was noted in the surface layer in October 1948. In 1949 it was not observed at all. In October 1950, however, it appeared again in vertical hauls taken at station M (Wiborg 1954), and swarms were also caught by the continuous plankton recorder between Bergen and station M (Rae 1951).

By the end of October 1949 the autumn forms had gradually disappeared, and *Microcalanus,* which had been totally absent in the 50 m.

layer and nearly absent in the 100 m. layer since April, was again found in the 50 m layer. At the beginning of winter *Microcalanus* and *Oithona similis* were again the dominant species in the surface layers.

B. PLANKTON OF THE INTERMEDIATE DEPTHS

Gran (1902) divided the deeper waters of the Norwegian Sea into two regions: the «Euchaeta region», corresponding to the deep layers of the Atlantic Current, and the «Cyclocaris region», corresponding to the bottom waters of Arctic origin.

The lower limit of the Atlantic water is usually found at about 300—400 m. (Mosby 1950), and the true bottom water of the Norwegian Sea is found below 1000 m. It would therefore be legitimate to distinguish between three regions — the deep layers of the Atlantic Current, the transitional waters of mixed origin, and the true bottom water.

As stated, rapid vertical oscillations have been observed in the transitional layers. According to the programme followed at station M, plankton samples were to be collected weekly by non-biologists, so that the depths which were to be explored by the vertical hauls had to be determined beforehand. The haul from 2000 m. (or bottom) to 1000 m. strained the true bottom water, while the haul from 1000 m. to 600 m. took the transitional water layers. It was clear, however, that haul 600—100 m., which was designed to fish the deep layers of the Atlantic Current, in fact in many cases fished the upper part of the transitional layers as well.

The water masses between 600 and 100 m. are mostly of Atlantic origin, and many species which have their main distribution in these depths may no doubt be considered as characteristic inhabitants of the deep water of the Atlantic Current. Gran called this region the Euchaeta region because he found the copepod *Pareuchaeta norvegica (Euchaeta norvegica,* Gran 1902) a very characteristic inhabitant there. The present material gives support to his observations. *P. norvegica* occurred at all depths, but most abundantly at 600—100 m. *Metridia lucens, Scolecithricella minor* and *Pleuromamma robusta* were also characteristic forms found in these layers. Other species of copepods which were invariably present in the hauls from 600—100 m. were *Calanus finmarchicus, Pseudocalanus minutus, Microcalanus, Oithona similis, Oithona spinirostris* and *Oncaea borealis*. Their numbers varied according to the season of the year.

As shown in the list in table 3, 67 species of plankton animals have been identified in the samples from 600—100 m., 19 of these were found only in this layer, all being Atlantic forms, the northern limits of which are usually regarded as being the Iceland-Faroe-Shetland ridge. Some of the species have not previously been recorded as present in the Norwegian Sea, namely *Lensia conoidea, Gaetanus pileatus, Gaetanus minor, Euchirella curticauda, Euchirella rostrata, Scottocalanus persecans, Scottocalanus securifrons, Scolecithricella dentata, Lucicutia longicornis, Clytemnestra rostrata, Euphausia krohnii, Nematobrachion boopis, Nematoscelis megalops, Sagittta serratodentata, Sagitta planctonis*. It may be presumed that these species penetrate into the Norwegian Sea as far as Lat. 66° N only occasionally, and as their occurrence must depend on the inflow of Atlantic water through the Faroe-Shetland Channel, it is likely to vary considerably from year to year.

Ruud (1929) and Størmer (1929) have both drawn attention to the fact that *Calanus finmarchicus* is less numerous in the central core of the Atlantic Current than in the mixed waters of the contiguous areas. If this is true also in a vertical direction, we should expect to find *C. finmarchicus* more abundant in the 600—100 m. hauls when the lower limit of the Atlantic Current occurs higher up than when it occurs lower down. In other words there should be a negative correlation between the numbers of *C. finmarchicus* in the samples from 600—100 m. and the volume of the waters of Atlantic origin.

Observations of temperature and salinity were made only down to 150 m. when the hauls from 600—100 m. depth were taken. Observations made in deeper layers on the day before or after the taking of the plankton haul could not be used for our purpose, since the hydrographical situation may change rapidly. However, the temperature (or salinity) found at 150 m. may furnish an indication of the lower limit of the Atlantic Current, and the correlation between the numbers of *C. finmarchicus* in the hauls from 600—100 m. and the temperature found at 150 m. has been tested on this assumption. In this connection the material collected during the breeding period, April to June, has been left out of account, as the population shows a different behaviour in this period than during the rest of the year. The remaining material has been divided into two portions, one covering the period October—March, the other the period July—October. It is assumed that the effect of the autumn breeding has little significance in this connection.

In respect of the period October—March the correlation coefficient between the number of *C. finmarchicus* found in hauls from 600—100 m. and the temperature at 150 m. was ascertained to be $r = .72$, with 11 degrees of freedom, giving a value for P of much under .01.

In respect of the period July—October the correlation was $r = .72$, with 8 degrees of freedom, P between .01 and .02.

From this it seems fair to conclude that the day-depth of *C. finmarchicus,* outside the spawning season, is determined by the depth of the Atlantic Current. This may serve to explain why Størmer and Ruud found *C. finmarchicus* less abundant in the core of the Atlantic Current than on either side of it, their material including only a few hauls from the transitional waters below the Atlantic Current where this is deepest. It is obvious that other factors besides temperature (or salinity) may influence the vertical distribution, for instance light intensity and the food conditions.

In the winter *C. finmarchicus* was found to be most abundant in the hauls from 1000—600 m., that is to say in the lower strata of the transitional layers. These seem therefore to be the waters preferred by *C. finmarchicus* for its hibernation, and from this centre of distribution the non-breeding population is found in decreasing number toward the waters of Atlantic origin.

Some specimens of *C. finmarchicus* were recorded in the lower part of the transitional layers (1000—600 m.) at all times, even in the spring, when most of the stock undertook a vertical migration toward the surface layers, where propagation then began. The same behaviour was observed in the case of *Pseudocalanus minutus* also. Some specimens lagged behind or did not join in the vertical spring migration. These two species, and a number of others, viz, *C. hyperboreus, Microcalanus, Pareuchaeta norvegica, Metridia longa* and *Oncaea borealis,* must therefore be regarded as whole-year members of the fauna of the deep transitional layers. But of these, only *Oncaea borealis* was at all times of the year encountered in any large number. It would seem therefore that the transitional layers are the chief centre of distribution as regards this species.

Other plankton species which were regularly met with in hauls from 1000—600 m. are: *Aglantha digitale, Conchoecia* spp., *Themisto abyssorum* and *Eukrohnia hamata.*

The list of species given in table 3 shows that *Pareuchaeta norvegica,* which Gran (1902) regards as characteristic of the deep Atlantic waters, is present in the deeper transitional layers also. As pointed out above, however, the 600—100 m. hauls often fished the upper part of the transitional layers as well as the deep Atlantic waters. Our material does not therefore provide a basis for a characterization of a distinct deep Atlantic plankton community. Species which are constantly met with in the samples from 600—100 m. are also found, but irregularly in the samples form 1000—600 m. The composition of the fauna gradually changes as one passes from the waters of the Atlantic Current downwards to greater depths. True Atlantic species disappear little by little and are replaced by deep water species from the bottom water. But two species, namely *Eucalanus elongatus* and *Sergestes arcticus* were encountered only in the 1000—600 m. hauls, and in each case only stray individuals, which seems to show that the transitional layers have no specific fauna of their own.

Gran (1902) has drawn attention to the fact that in the deep layers of the Norwegian Sea there are only slight variations in the temperature and light. We should not expect therefore to find such large seasonal variations in the plankton fauna as those observed in the surface layers.

The dominant part played by *C. finmarchicus* and *P. minutus* in the animal plankton has been emphasized above. The ascent of these species from the deep water layers in the spring, and their descent to deep water again in the summer and autumn will determine the numbers of these copepods in the several water layers. As shown in fig. 6, *C. finmarchicus* and *P. minutus* represented in the winter more than 60 % of the population in the hauls from 1000—600 m., as compared with 20—30 % in the hauls from 600—100 m. In March and April the numbers declined in the 1000—600 m. hauls (fig. 1), owing to the vertical migration of *C. finmarchicus* and *P. minutus* to the upper water layers. In May therefore *Microcalanus, Oithona* and *Oncaea borealis* were dominating the small population of copepods found in the deep transitional layers. The high percentage of other organisms than copepods in April and May was mainly due to the relatively large numbers of *Conchoecia* spp.

In the 600—100 m. hauls the number of copepods increased more or less regularly during the spring. Adult individuals of *C. finmarchicus* and *P. minutus* formed the bulk of the population.

During the summer the percentage of *C. finmarchicus* and *P. minutus* in the 1000—600 m. hauls increased rapidly, constituting in July about 70 % of the population.

Little variation was noted in the population at these depths during the autumn, except that there was a gradual decrease in he numbers of individuals. This tendency persisted throughout the winter.

C. PLANKTON OF THE DEEP WATER

Gran (1902) gave to the cold bottom layers of the Norwegian Sea the name «Cyclocaris region», because of the presence of the large amphipod *Cyclocaris guilelmi*. That this species is characteristic of the said layers is borne out by the present material. Thus *Cyclocaris* was present in nearly every haul from 2000—1000 m. and it was not found at all above 600 m.

Several copepod species, viz. *Calanus finmarchicus, Calanus hyperboreus, Pseudocalanus minutus, Aetideopsis rostrata, Scaphocalanus brevicornis, Pareuchaeta farrani, Microcalanus* and *Oncaea borealis,* were constant members of the bottom water fauna. The two latter species were, however, more abundant in higher layers. *C. hyperboreus* was most numerous in the hauls from the bottom water, and by reason of its large size gave to these a characteristic appearance. During the spring spawning season *C. finmarchicus* and *P. minutus* were present only in small numbers.

Several other organisms, for example *Hymenodora glacialis*, *Atolla wyvelli* and *Conchoecia* spp., were also characteristic forms in the cold bottom layers.

It will be seen from table 3 that 64 species have been identified in the 2000—1000 m. hauls, 19 of these were found only in this layer; most of them were rare, however, and some represented by a single specimen. From what is published concerning the geographical distribution of these 19 species, hardly any are known as specifically Arctic species. Of the copepods, *Pareuchaeta bradyi*, *Temorites brevis* and *Augaptilus glacialis* are considered to be Arctic-boreal, but stray specimens of all these species have been recorded from deep water in the Atlantic proper and from the Mediterranean Sea (*Temorites brevis*, G. O. Sars 1925).

Pseudochirella, *Undeuchaeta major* and *Scolecithricella ovata* are all definitely Atlantic species, which are found only at great depths. They have not previously been recorded as occuring in this northern latitude of the Norwegian Sea.

C. finmarchicus and *P. minutus* were found to be still more dominant in the 2000—1000 m. hauls than in the 1000—600 m. ones. As will be seen from fig. 6, these two species in some months constituted more than 70—80 % of the total number of animals collected. When therefore these species migrate from the deep layers in the spring, the composition of the plankton population becomes significantly changed. *Microcalanus* and other species then dominate in numbers if not in bulk, until the arrival of new generations of the said two species from the upper waters restores the former composition.

D. DISCUSSION

The most conspicuous feature of the zooplankton communities found at station M is the predominance of a few copepod species. The main body, as pointed out by Gran (1902) and Damas (1905), consists of autochthonous boreal species. These writers also stress the fact that the Norwegian Sea has a characteristic fauna, which is not merely a mixture of organisms of Atlantic and Arctic origin.

According to Damas, the central part of the cyclonic system existing in the southern Norwegian Sea, where weather ship M is stationed, is remarkable for its abundance of *Pseudocalanus minutus*. He draws the conclusion that this species is stationary in the area, the water masses of which were subsequently ascertained by Helland-Hansen and Nansen (1909) to be chiefly of Atlantic origin.

The material from M should be sufficient to show that *Pseudocalanus minutus* is indigenous in this part of the Norwegian Sea. During the winter it is in fact the dominant species in the deep water layers. It has only one spawning period, and if there is any immigration to the stock from other localities, where the species may have a different life-cycle, this is negligible.

On the other hand Damas found *C. finmarchicus* to be more abundant in the areas bordering the Gulf Stream. He suggests therefore that this species has its chief centre of distribution in water of mixed origin, a view which has since been supported by Ruud (1929) and Størmer (1929). From the present material it seems fair to conclude that *C. finmarchicus* also in a vertical direction is more abundant in the transitional layers below the Gulf Stream than in the Atlantic water proper, seeing that we found it's depth of occurrence in the daytime, except in the spawning period, to be dependent on the volume of the Atlantic water. It is true that our knowledge of the diurnal vertical movements of the species in this locality is limited. We do not know whether the immature or resting members of the stock migrate into the true Atlantic water at night, nor is any information available concerning their day-depth in other parts of the open Norwegian Sea.

According to Helland-Hansen and Nansen (1909), the bottom layers of the Norwegian Sea are almost stagnant. If this is so, it may be reasonably inferred that the hibernating stocks in the deep layers are not subject to any great dispersion. It is a remarkable fact, however, that even the samples taken from 2000—1000 m. depth show considerable variation both in numbers and composition from week to week. In late summer and autumn particularly, when descending movements of new broods are taking place (cf. figs. 8, 12 and 13), the numbers of *C. finmarchicus, C. hyperboreus, P. minutus* and other species may display immense weekly fluctuations. On September 28, 1949, for example, *Oithona spinirostris* and *Oncaea borealis* were totally absent in the 2000—1000 m. haul, whereas in that taken a week earlier they were numerically the dominant species. Such variation may of course be due to inequality in the distribution of the plankton. There may be some patchiness in the descending movement, but if the descent is mainly brought about by sinking, this seems hardly likely. The irregularities may also be due to errors in sampling. As has been stated earlier, the weather ship is allowed to drift in an area of ten square miles, and within this area the depth of the water varies from 1500 to 3000 m. The volume of water strained in the deepest haul will vary correspondingly. The important point is that in that case the distance of the haul from the bottom will also fluctuate. Nothing is known, however, about the influence of the bottom on the distribution of the plankton in the overlying water layers.

Regarding the movement of the deeper water layers our information is scanty. Mosby (1953) recorded velocities of 19 cm./sec. near the bottom at about 1000 m. depth in the southern Norwegian Sea. The deeper layers of this Sea are fairly well supplied with oxygen (O_2 about 82 %), which indicates either that they have been recently aerated or that the biological processes which require oxygen are inconsiderable. In the former case the velocities of the bottom layers must be greater than has hitherto been assumed (cf. Mosby's observations), in the latter case the animal population is presumably small and their metabolic processes low. The second alternative has much to say for itself, as the temperature of the water is naturally low.

Measurements of the length of *Calanus hyperboreus* carried out by Wiborg (1954) at station M and other localities in the north-west of the Norwegian Sea seem to show that the stocks of this species have grown up under similar external conditions. This is only explicable on the assumption that an undercurrent of Arctic water supplies the central area with a stock of *C. hyperboreus* and that communication between the central area and the surrounding areas is greater than implied in Damas' theory. According to Sømme (1934), this species approaches the surface for spawning purposes, which takes place in the upper water layers. It is impossible for a brood hatched in the surface layers at station M to grow up under the same external conditions as exist in the vicinity of Jan Mayen.

Length measurements of copepods found in our material of 1949 have not been undertaken, but Wiborg (1954) took measurements of *C. finmarchicus* in the material collected at station M in 1950. Fig. 7 shows the variations in the mean length of *C. finmarchicus*, stage V, found at station M in that year.

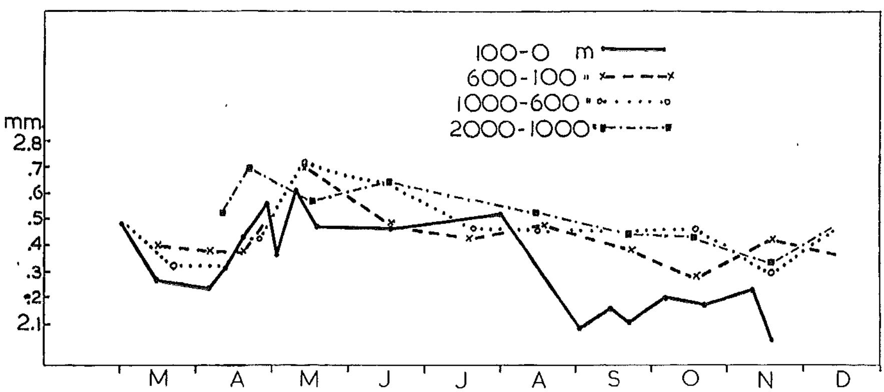

Fig. 7. Variations in the mean length of the cephalothorax of *Calanus finmarchicus*, stage V, at weather-ship M in 1950. (From Wiborg, 1954.)

It will be seen that in the spring and early summer the animals in the deep water layers and in the upper strata are of similar length. From August onwards stage V in the upper layers is distinctly smaller than that found in the deeper layers. The smaller animals, which enter the area in August and September (1950), evidently form part of another population. From their length it may be assumed that they have grown up in warmer water than the larger animals found at the same time in the deeper layers.

The population of *C. finmarchicus* which was small in length was in the autumn 1950 accompanied by an influx of *Salpa fusiformis*. On this account Wiborg suggests that the stock of small *Calanus* had been brought in from the Atlantic.

The spring-spawned generation of *C. finmarchicus* had, as mentioned, already descended to deep water in July, and the second spawning was, in 1949, of minor importance compared with the spring spawning. Thaliacea were not observed at all in the autumn 1949, but simultaneously with the spawning of *Calanus* in August and September *Metridia lucens* was found to increase in number in the upper water layers. Later on in the autumn *Acartia clausi* and *Paracalanus parvus* were also found in the hauls. When met with in the North Sea these species are regarded as indicators of Atlantic water (Rae and Rees 1947). If this applies to the Norwegian Sea, it is reasonable to assume that the stock of *C. finmarchicus* which spawned in the autumn 1949 had been brought in by Atlantic water. On the other hand the decline in the salinity of the surface layers seems to rule out such an explanation, and an outdrift of coastal waters seems more probable. Neritic species such as *Evadne* and *Temora longicornis* were also observed in June and July. In the same haul as contained *Temora* we also found *Acartia clausi* in great number. On that day the salinity in the upper 50 meters was relatively low — 35.01 ‰.

On the basis of the hydrographical observations it seems difficult to draw any certain conclusions regarding the immigration of planktonic animals from other localities. Moreover the fact must not be overlooked that the water layers may move in different directions at different velocities. As suggested by Hardy (1935), the plankton communities may be reshuffled each night, the components varying according to the extension of their diurnal vertical migration. New elements may constantly be introduced into the area by dislocations in other areas. Thus the surface layers at M will be stocked in part by fauna drifting in from the coastal areas and in part by elements coming with the Atlantic waters from the south. The southern and neritic forms, which in the course of the summer and autumn are brought to the M area, disappear almost entirely in the winter. When the spring begins, only indigenous species are found in the surface layers.

V. The Annual Vertical Migration and its Role in the Life History of Copepods.

When, at the beginning of the present century, Gran (1902) carried out his studies of planktonic copepods in the Norwegian Sea, he noticed that the stocks of *Calanus finmarchicus* in the autumn descended to deep levels for hibernation. In early spring a vertical movement in the opposite direction occurred, and the animals continued their development to sexual maturity and spawning in the surface layers. The fact of such an annual vertical migration has since been confirmed by many investigators. Sømme (1934) was the first to draw attention to its significance and to attempt an explanation of the phenomenon. During his studies of *Calanus finmarchicus* and *Calanus hyperboreus* in the Lofoten area twenty years ago he observed that the vertical movement to the surface commenced in February and March and that all stages of development in the stock participated in this migration. He inferred that the movement could not be due to the approach of maturity, and decided that the increase in light intensity was the stimulating factor.

Ussing (1938) arrived at the same conclusion in his study of the annual vertical migration of copepods in the waters of East Greenland. He too found that all stages present, stages IV, V and VI, took part in this spring migration. He agreed with Sømme that it bore no relation to approaching maturity and spawning. Reasoning from analogy with the diurnal vertical migrations and the explanations of them given by other investigators, Ussing concluded that the annual vertical migrations are governed primarily by variations in light intensity. Decreasing intensity in the autumn leads to decreasing photokinesis in the copepods, which then sink slowly to deeper levels. Increasing light intensity in the spring stimulates them to greater activity, and a positive phototaxis leads to an ascent to the surface. The assumption is that the animals are more sensitive to light in the spring than in the autumn. The light intensity which stimulates to ascent in early spring is weaker than that observed at the time of sinking. Ussing found support for this assumption in the evidence derived from experiments concerning phototaxis in copepods recorded by Rose (1925).

Use has been made of the present material for a detailed examination of the annual vertical migration.

A. CALANUS FINMARCHICUS

Fig. 8 shows the seasonal variation in the numbers of *Calanus finmarchicus* at different depths. In winter the major part of the stock was found below the 600 m. limit. The surface layers were at that time of the

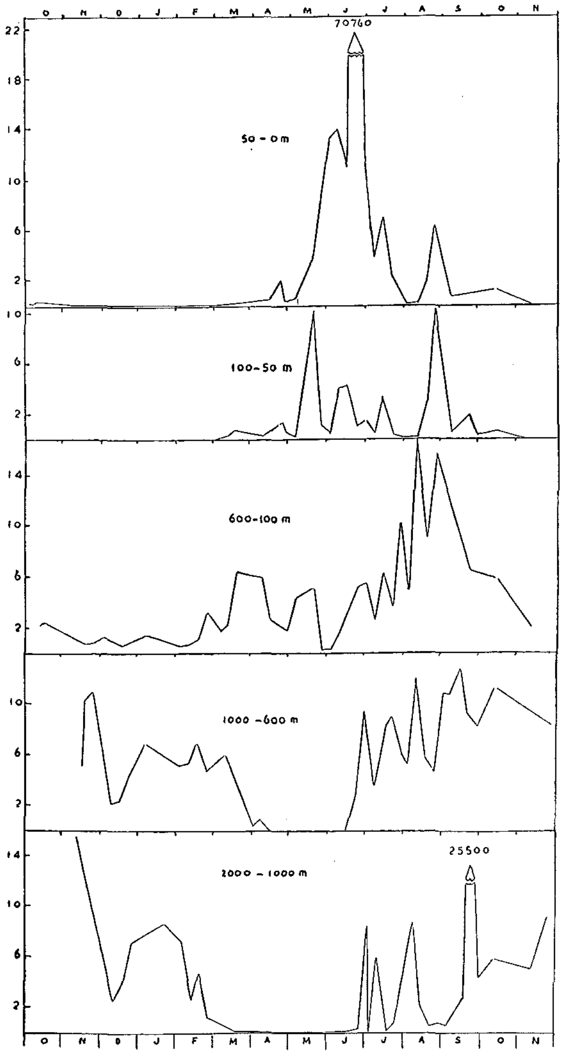

Fig. 8. Total numbers of *Calanus finmarchicus* (all stages except nauplii) in thousands per haul.

year practically void of this species, but an invasion into the upper layers began in February/March. The simultaneous decrease in numbers in the deeper layers seems to indicate that a vertical movement toward the surface was in progress. A month later, March/April, most of the species was found above 600 m., and in the course of April, May and June it had practically disappeared in depths below 600 m. From the second half of June, however, *C. finmarchicus* was again found in increasing number in the deeper layers, and by the middle of July it was abundant even below 1000 m. Thereby a cycle of annual vertical migration was completed.

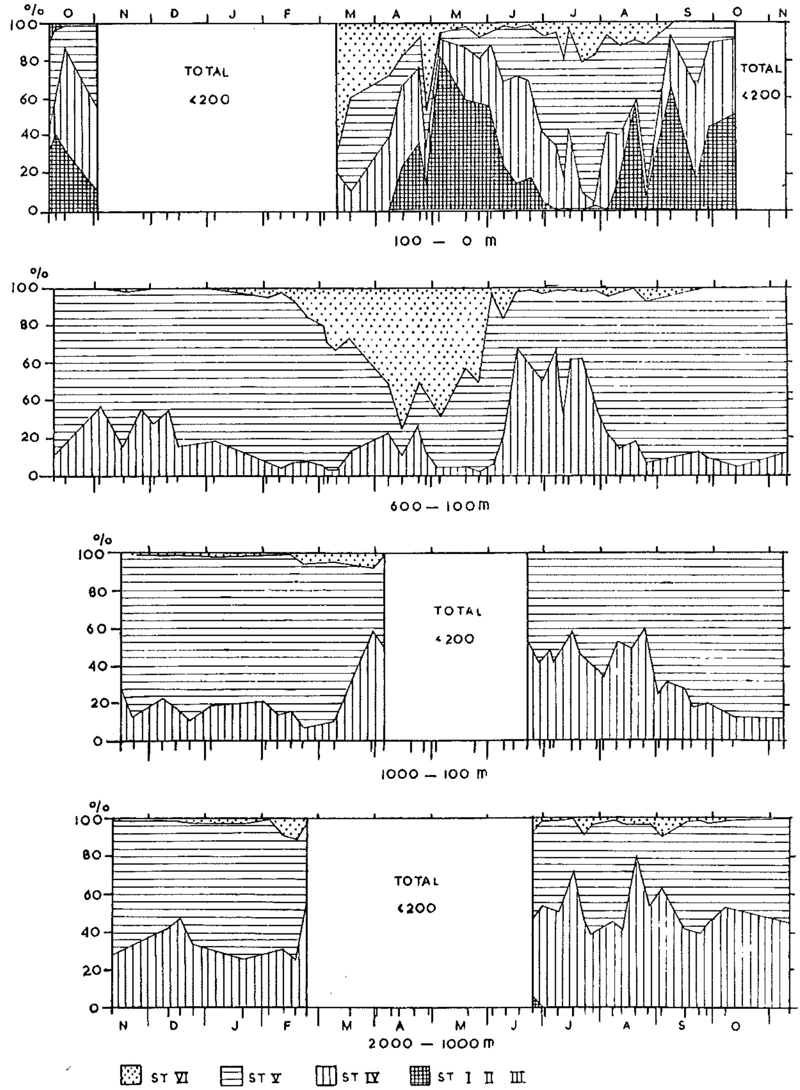

Fig. 9. Frequencies in per cent of the different stages of *Calanus finmarchicus* found in the vertical hauls at M. Where total numbers are less than 200 per haul, the diagram is left blank.

Fig. 9 shows the seasonal variation in the percentage distribution of the stages of development at different depths. The blank spaces in the diagrams cover the periods in which the hauls contained less than 200 specimens. It will be seen that in winter the stock of *C. finmarchicus* consisted mostly of copepodite stages IV and V. At the time the vertical migration upwards commenced in February/March these two stages were still dominant, but all stages present in the stock took part in the migration. This coincides with the observations of Sømme (1934) and Ussing

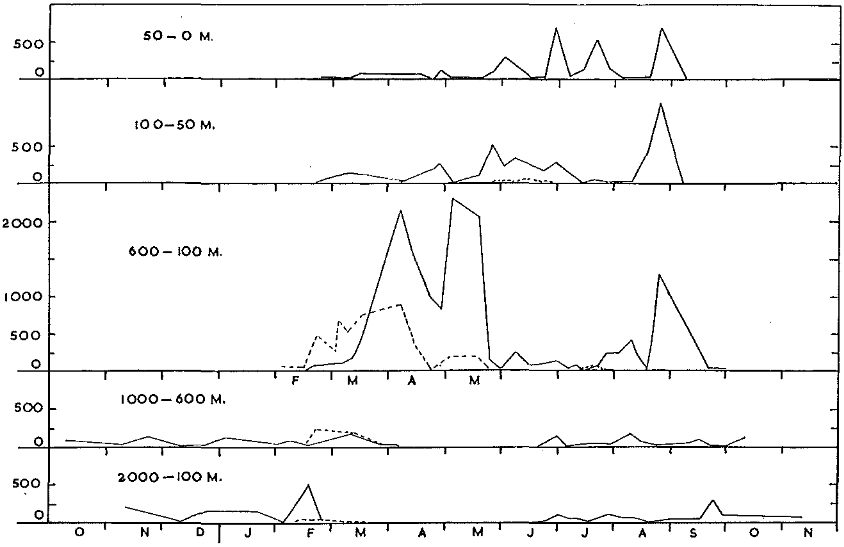

Fig. 10. Total numbers per haul of *Calanus finmarchicus,* males (- -) and females (—).

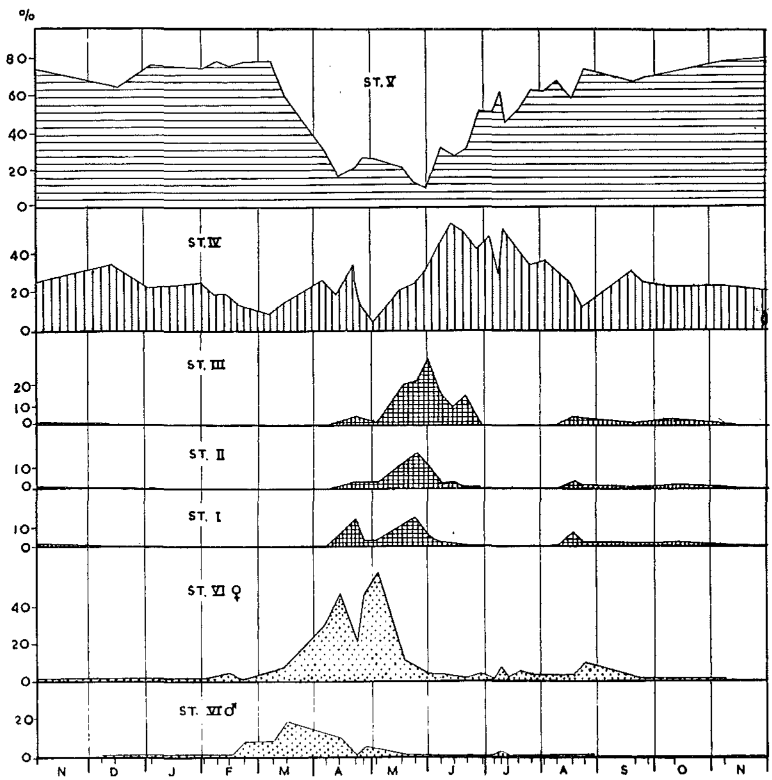

Fig. 11. Frequencies in per cent of the different stages of *Calanus finmarchicus,* calculated for the whole water-column from 2000 m. to surface.

(1938). Simultaneously with the commencement of the upward movement the percentage of adult individuals increased, especially in the 600—100 m. hauls, and in April, when the migration was completed, they were in the majority in this layer. Thus in the case of this species the moulting from stage V to sexually mature animals occurred during or subsequent to the vertical migration.

Fig. 10, which shows the seasonal variation in the numbers of males and females at various depths, bears witness to this fact.

When the vertical migration started, the number of males was found to get larger in the hauls from 600—100 m. Most of the males were found in the course of March, being at that time of the year more numerous than the females, whose numbers did not cumulate until April/May.

Fig. 11 gives the variations in the percentage distribution of the stages of development of this species in all the layers from 2000 m. to surface.

The presence of mature males and females in the hauls is often taken as a sign of spawning (With 1915, Wimpenny 1936, cf. also Marshall & Orr 1952). As stated above, the maximum number of males was found in March. Except for a sudden fall in the numbers on April 23rd, the percentage of females increased from the beginning of March to the first week in May.

The nauplii present in the samples were not determined according to species, but as *C. finmarchicus* was predominant it is reasonable to assume that most of the nauplii belonged to this species.

The total number of nauplii found in the three hauls from 600 m. to surface will be seen from table 5. (No nauplii were found below 600 m., except nauplii of *Pareuchaeta*).

The table gives the aggregate numbers occurring in the respective hauls each month. It gives likewise a frequency figure, showing the number of hauls in which the species in question was found (in this case the nauplii), divided by the total number of hauls taken at the said depth and in the said month.

In April, May and June considerable numbers of nauplii were encountered, and occurred in every haul from the 50 m. to surface layer. This abundance of nauplii coincides with the occurrence of males and females of *C. finmarchicus*.

It may be inferred from this that *C. finmarchicus* commenced to spawn in the first days of April. The large number of nauplii was followed by a peak in the percentage of copepodite stage I (fig. 11), but the following stages did not reach a peak before May. It may be that the food conditions were unfavourable for this first brood from April, the phytoplankton production being negligible until May (Halldal 1953).

The high percentage of females present in May (fig. 11), when the diatom population had increased, was succeeded by the maximum occur-

Table 5.

Copepod nauplii:

Monthly numbers and frequencies of occurrence at the different depths.

Depth in m.	Month	O	N	D	J	F	M	A
50—0	Number ..	422	340	90				10260
	Frequency .	4/4	2/2	1/3	0/1	0/4	0/3	4/4
100—50	Number ..	170	190					4460
	Frequency .	2/4	1/2	0/3	0/1	0/4	0/3	3/4
600—100	Number ..	76	70					1350
	Frequency .	2/2	2/3	0/3	0/1	0/4	0/3	2/4

(Continued)		M	J	J	A	S	O	N
50—0	Number ..	15710	18200	120	21530	3270	870	60
	Frequency .	3/3	5/5	1/4	4/4	3/3	1/1	1/1
100—50	Number ..	6940	120		60	120	470	80
	Frequency .	3/3	2/5	0/4	2/4	2/3	1/1	1/1
600—100	Number ..	375	10	100	250	50	150	
	Frequency .	2/3	1/5	1/5	2/4	1/2	1/1	0/1

rence of stages I, II, III, IV and V, the two latter stages constituting more than 80 % of the stock during the summer and autumn.

A new increase in the number of adults occurred in July/August. Owing to the abundance of copepodites stages IV and V their percentage was small, but, as will be seen from fig. 10, the actual number in August was almost as large as in the spring. The largest number of females occurring at a single station was recorded in August.

A second spawning of *C. finmarchicus* took place in August/September, which was followed by an increase in the percentage of stages I, II and III (fig. 11).

There is no means of knowing whether the adults which spawned in the summer were offspring of the adults which spawned in the spring, but if this were the case, there is a span of 3 1/2 to 4 months between two successive generations. This agrees well with what is already known concerning the life cycle of *C. finmarchicus* in Norwegian coastal waters of same latitude.

From fig. 11 it will be seen that the second spawning of *C. finmarchicus* in August/September was not so prolific as that in the spring. This is confirmed by the figures in fig. 8, which show that the numbers found in the layers over 100 m. were in July insignificant compared with those found in the deeper hauls, in which the stock consisted of copepodites in stages IV and V — evidently offspring of the spring spawning stock.

It would seem therefore that the main body of the spring-spawned generation descends to deeper waters for hibernation as early as July, thus passing through a life-cycle which covers a full year. The assumption that the animals found in the deep layers in July belong to the new generation is supported by the fact that *C. finmarchicus* was absent from the deepest hauls for three or four months, approximately the time it takes for a generation to develop from the egg to stage IV or V.

From a comparison of figs. 8 and 9 it is apparent that the descent to deeper layers began as soon as the spring generation had moulted into stages IV and V. It seems clear therefore that there is a close relation between the distribution of the various stages of development and the annual vertical migration.

It has already been stated that the second brood of *C. finmarchicus*, spawned in August/September, had no particular significance in this area in 1949. But it is reasonable to assume that the offspring of this second spawning, after the descent, mingles with the first, and that the hibernating stock will then consist of a mixed population.

B. CALANUS HYPERBOREUS

This species occurred only in small numbers, but our investigations show that its annual vertical migration is similar to that of *C. finmarchicus*.

Fig. 12 gives the seasonal variation in numbers of *C. hyperboreus* at different depths. During the winter most of the stock was found below 1000 m., at a deeper level even than *C. finmarchicus*.

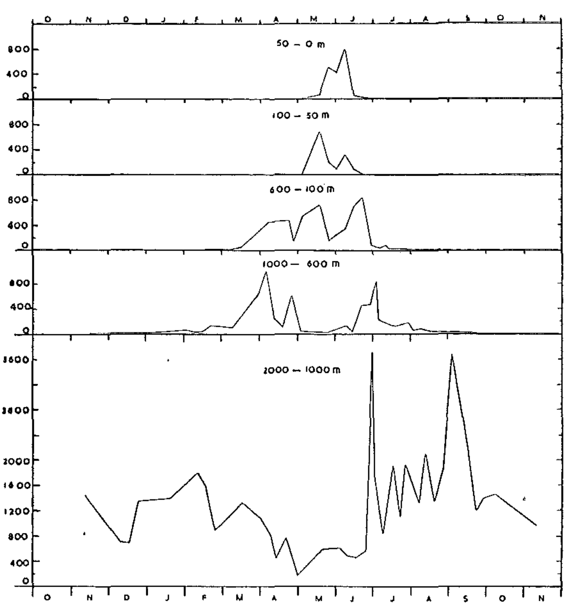

Fig. 12. Total numbers per haul of *Calanus hyperboreus* (all stages except nauplii).

From the middle of March it occurred in increasing numbers in the 1000—600 m. and 600—100 m. hauls, and in May/June also above 100 m. At the same time a lessening number in the deeper hauls was apparent.

From the records it appears therefore that the ascending movement from the layers below 1000 m. commenced medio March and terminated at the end of April. But already in July *C. hyperboreus* had practically disappeared from the hauls above 600 m., and in August almost the whole stock was again found below the 1000 m. level.

The species did not at any time disappear completely from the depths below 1000 m., but in May and June the numbers were approximately one-third of those found during the winter. This seems to show that only part of the stock migrated to the upper layers in the spring. Such segregation into two physiologically different groups has previously been noted by Sømme (1934) and Wiborg (1954) in the Lofoten area.

The distribution of the various stages of development in the winter and during the spring ascending movement does not afford any clue to the causes of this segregation.

The total numbers at the various stages are recorded in table 6. As will be seen, *C. hyperboreus* occurred only in small quantity during the year.

During hibernation the stock consisted of stages III, IV, V, and adults, and the youngest stages predominated in hauls below 1000 m. All stages took part in the ascending movement in March.

Table 6.

Calanus hyperboreus:

Monthly numbers of the various stages and frequencies of occurrence at the different depths.

50—0 m.

Stage ..	O	N	D	J	F	M	A	M	J	J	A	S	O	N
VI ♂ ..														
VI ♀ ..										1				
V									100					
IV								100	310					
III								300	540					
II								150	210					
I								30	100					
Total ..								580	1260	1				
Freq. ..	0/4	0/2	0/3	0/1	0/4	0/3	0/4	2/3	3/5	1/5	0/4	0/3	0/1	0/1

(Table 6 cont.) 100—50 m.

Stage	O	N	D	J	F	M	A	M	J	J	A	S	O	N
VI ♂ ..														
VI ♀ ..								1	9					
V								10	224					
IV								171	245					
III								210	70					
II								250	20					
I								250						
Total ..								892	568					
Freq. ..	0/4	0/2	0/3	0/1	0/4	0/3	0/4	3/3	4/5	0/4	0/4	0/3	0/1	0/1

600—100 m.

Stage	O	N	D	J	F	M	A	M	J	J	A	S	O	N
VI ♂ ..					1	4								
VI ♀ ..		2		2	7	26	82	120	256	12	4	2		4
V	1	5	1	1	10	21	425	250	452	13	3			3
IV	3	6	4	3	18	10	600	1050	364	64	2			2
III		1	1	3	4	4	425		1110	50				
II														
I														
Total ..	4	14	6	9	40	65	1532	1420	2182	139	9	2		9
Freq. ..	1/2	2/2	2/3	1/1	4/4	3/3	4/4	3/3	5/5	5/5	4/4	2/3	0/1	1/1

1000—600 m.

Stage	O	N	D	J	F	M	A	M	J	J	A	S	O	N
VI ♂ ..		5	3	2	15	5	8	3						
VI ♀ ..		16	3	5	36	81	160	24	73	95	38	13	1	5
V		34	15	16	49	47	296	26	252	175	46	6		5
IV		15	1	3	120	190	710	30	455	560	88	2		1
III ..					50	380	780	6	335	720	2			
II														
I														
Total ..		70	22	26	271	703	1954	89	1118	1530	174	21	1	11
Freq. ..		3/3	3/3	1/1	4/4	2/2	4/4	3/3	4/4	5/5	5/5	4/4	1/1	1/1

(Table 6 cont.) 2000—1000 m.

Stage	O	N	D	J	F	M	A	M	J	J	A	S	O	N
VI ♂ ..					24		10							
VI ♀ ..		80	430	100	515	200	605	90	510	779	480	385	5	100
V		390	565	300	995	335	910	220	1040	1370	970	1190	150	175
IV		460	1000	400	1875	410	1230	240	1665	2105	1900	2440	450	375
III		640	755	600	2375	380	495	45	2555	3295	3250	4350	800	325
II														
I														
Total ..		1460	2750	1400	5784	1325	3290	595	5770	7549	6600	8365	1450	975
Freq. ..		1/1	3/3	1/1	4/4	1/1	5/5	1/1	5/5	5/5	4/4	4/4	1/1	1/1

Merely from the number of individuals in the various stages of development it is not easy to determine exactly the date when spawning took place, stages III, IV, V and adult females being found the whole year round. Evidence of approaching spawning is revealed by the presence of eggs in the oviducts of females (Sømme 1934). In the 2000—1000 m. hauls several cases of this occurred in February and March, but none after the vertical migration was completed in April. In the 1000—600 m. hauls they were encountered in February, March and April, but none after May 4th.

In the 600—100 m. layer females with eggs in the oviducts were rather scarce, but they were met with in the period January 4—June 22. Females taken on April 14th were clearly in process of spawning, only a few eggs being left in the oviducts.

From these observations it seems reasonable to conclude that maturing of the sexual glands takes place in February and March, prior to or during the annual vertical migration, which fact has also been reported by Sømme (1934).

The number of males was always small — apparently the rule both in boreal and in Arctic waters (Sømme 1934). In the 1000—600 m. hauls they were found from November to May, but in the 2000—1000 m. and 600—100 m. layers they only occurred in February, March and April, that is to say during the period when the maturing of the females took place.

Copepodite stages I and II were very infrequent, being found exclusively in the uppermost 100 m. between May 18 and June 15. Sømme (1934) did not find stages I and II in the Lofoten area before the first week of April, about 1 1/2 months after the spawning.

Assuming that the time required for development from egg to stages I and II is about the same in the Norwegian Sea, the spawning at station M must have commenced in March/April, and have terminated a month later. The fact that nauplii were not encountered before the middle of April also suggests that the chief spawning activity of *C. hyperboreus* in this part of the Norwegian Sea occurs in April, just after the vertical migration.

As stated, all the stages present in the deep layers, namely III, IV, V, and VI, took part in the annual vertical migration, and in April these were found at all depths. In May, however, stage III had almost disappeared from hauls 600—100 m., while stages IV and V were found in relatively large numbers. As no spawning was observed before March/April it may be assumed that the individuals in stages IV and V which were encountered in April and May belonged to the winter stock. Males were not observed subsequent to May 3rd, and only a few females with eggs in the oviducts were found later. It is unlikely therefore that the individuals which were still in stages IV and V in April and May reached maturity in the summer or autumn 1949. The present material does not enable us to determine whether these individuals moved downwards in July for a second hibernation, which would give them a life-cycle of two or more years.

The same question applies to that portion of the stock which did not ascend in the spring and which was found below 1000 m. after completion of the vertical migration. This stock comprised individuals in stages III, IV, V and VI, the same as were found during the winter. It was impossible to determine whether females taken below 1000 m. level after April were spent, although Sømme (1934) affirms that this can easily be deduced from the swollen state of the oviducts. It seems probable, however, that the females found below 1000 m. in May and June had neither taken part in the vertical migration nor spawned. The question arises therefore whether those found below the 1000 m. level have fallen below a depth from which they can rise again, and thereby, as assumed by Ussing (1938), become lost for propagation of the stock.

C. PSEUDOCALANUS MINUTUS

This species occurred in large numbers in the material collected at station M, and its vertical migration shows similar features to that of *C. finmarchicus* and *C. hyperboreus*.

Fig. 13 shows the seasonal numerical variation of *P. minutus* at various depths. Most of the stock hibernated below 600 m., and it is apparent that the main body occupies an area lower than *C. finmarchicus*, since the proportion of *P. minutus* was greater in the 2000—1000 m. hauls.

The ascending movement commenced in March and terminated medio April. From that time until the end of June the species was almost absent from the hauls below 600 m., the majority being taken above 50 m.

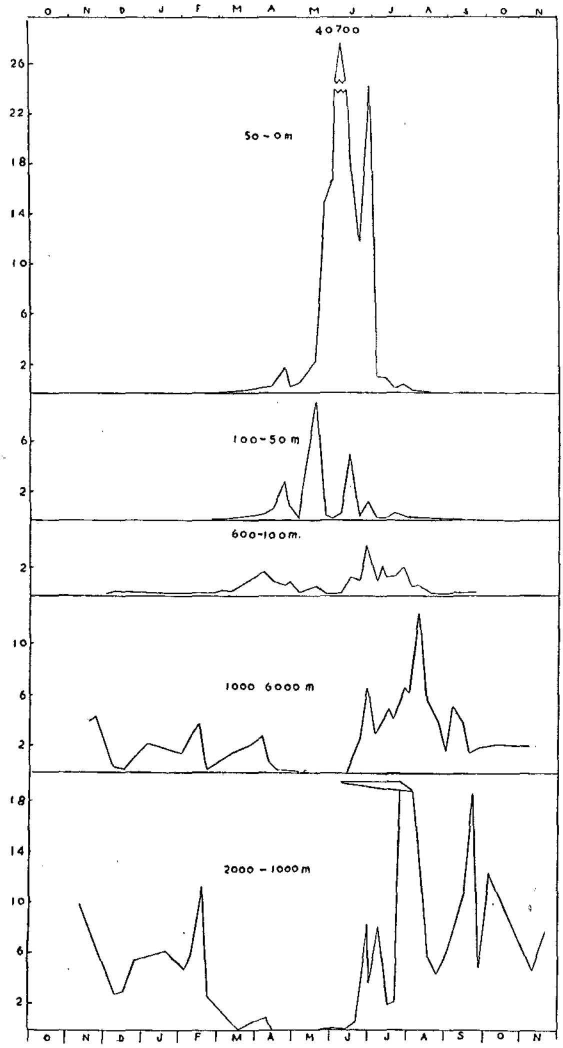

Fig. 13. Total numbers in thousands per haul of *Pseudocalanus minutus* (all stages except nauplii).

At the end of June and beginning of July the downward movement began, and in August practically the whole stock was found again below 600 m.

Fig. 14 shows the seasonal variations in the percentage distribution of the different stages of development at various depths. The hibernating stock below 600 m. consisted almost entirely of copepodites stage V. At higher levels there was a higher percentage of stage IV, but, as fig. 13 shows, the total numbers of *P. minutus* were insignificant above the 600 m. level in the winter. For calculation of the percentages in fig. 14 the numbers in the three upper layers have therefore been added together.

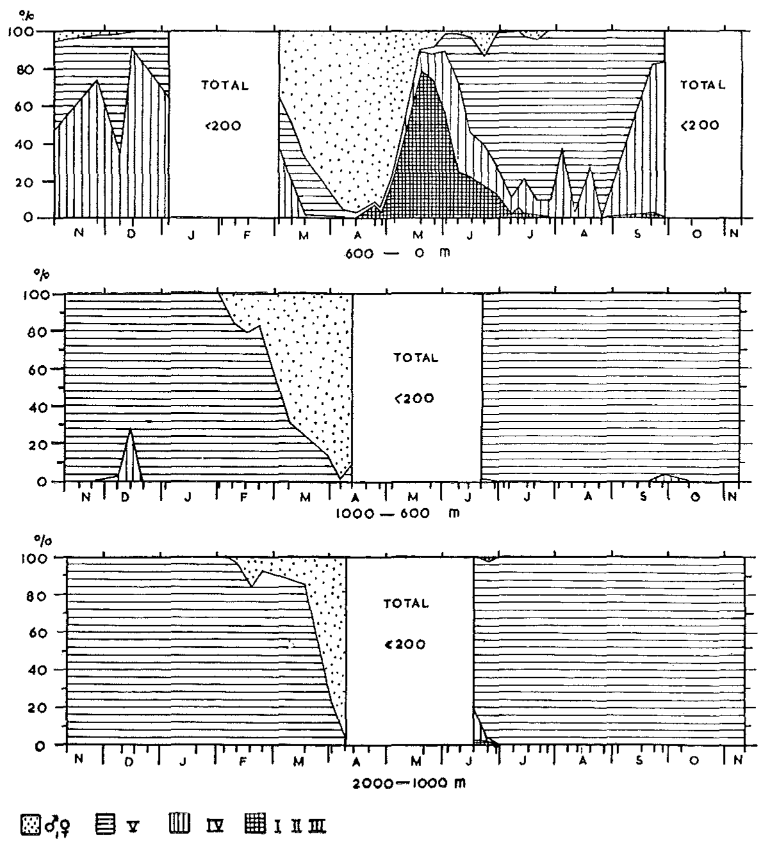

Fig. 14. Frequencies in per cent of the different stages of *Pseudocalanus minutus* found in the vertical hauls at M. Where total numbers are less than 200 per haul, the diagram is left blank.

Table 7 gives monthly figures for males and females taken in the different layers. When the ascending movement commenced, a large proportion of mature specimens were found in the two deepest layers, and when the migration ended in April sexually mature animals predominated. From this it may be inferred that moulting from stage V to mature individuals, as regards this species, occurs immediately before or during the ascent, and not, as in the case with *C. finmarchicus,* after the migration has been completed.

As in usual among copepods, the males were less frequent than the females. Approximately 23 % of the number of adults recorded during the year were males, most of them being found below 600 m.

This material, taken in the middle of the day, seems to suggests that the males did not participate in the vertical migration to the same extent as the females. If this is so, pairing must have occurred in March and April, before the migration was completed, or it may be that the two

Table 7.

Pseudocalanus minutus:

Monthly numbers of males and females taken at the different depths.

Depth in m.	Month	N	D	J	F	M	A	M	J	J
50—0	Males				4	5	21		250	
	Females ..	11	2		11	40	3155	1590	4100	75
100—50	Males					22	185	120		
	Females ..	15	3		8	100	5020	1103	680	40
600—100	Males				20	50	150			25
	Females ..	10			26	730	4200	355	60	75
1 000—600	Males				1260	825	1295	5		
	Females ..				21	2100	2260	7	27	
2 000—1 000	Males				2276	10	775			
	Females ..	80					420		40	

sexes meet at night, if the males ascend to the layers where the females are encountered.

Females were very scarce in layers below 1000 m. In the 600—100 m. hauls they were found in great numbers in April. Then they were found in abundance successively in the 600—100 m., 100—50 m. and even the 50—0 m. layers, where they were met with from medio April to end of June.

Females with egg-sacs do not normally occur in this material, but a few specimens, with a couple of eggs attached to the genital segments, did occur. Similar observations have been made in the North Sea and English Channel (Marshall 1949) and also in the Gulf of Maine (Fish 1936).

The ovigerous females were found above 600 m. only in the period April 14—June 27. Immediately prior to and during this period spawning must be presumed to have taken place.

In May and June successive stages of the new generation were found in the upper layers (cf. fig. 14), which supports the view that the main spawning of *P. minutus* occurred in April/May, immediately after the ascent.

As was seen from fig. 13, the new generation made its appearance in the 50 m. layer in May and early June, but when it had developed into stage V the descent for hibernation began.

Thus with *P. minutus* there was only a single spawning period. This appears still more clearly from fig. 15, where the frequencies of the diffe-

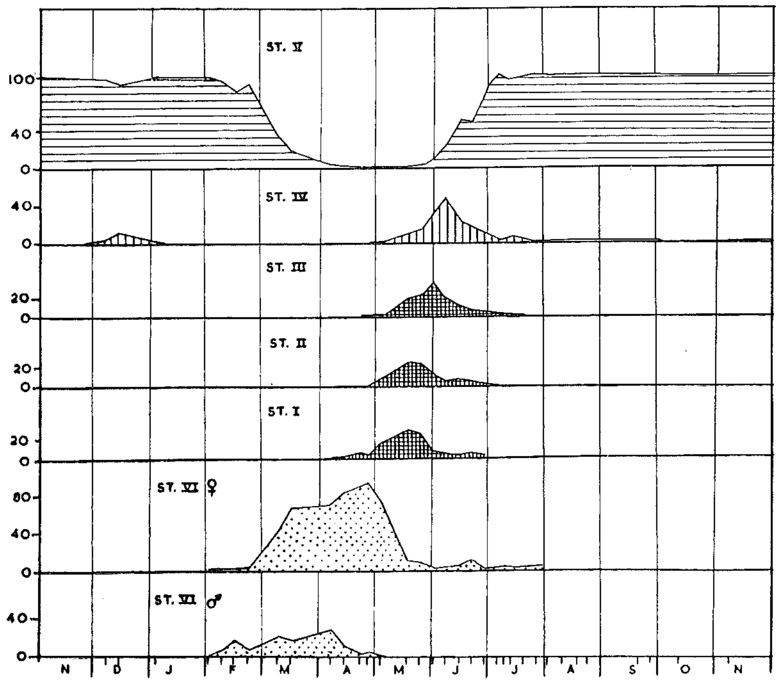

Fig. 15. Frequencies in per cent of the different stages of *Pseudocalanus minutus*, calculated for the whole water-column from 2000 m. to surface.

rent stages of development in the whole water column from 2000 m. to the surface are illustrated. From July to February/March copepodite stage V dominated the population almost entirely; the other stages, males, females, copepodite stages I, II, III and IV, followed in rapid succession during the next three or four months.

D. DISCUSSION

It is a significant fact that specimens of *Calanus finmarchicus* and *Pseudocalanus minutus* from all the water layers, even the deepest, seem to participate in the annual vertical migration. But this is not consonant with the opinion of Ussing (1938) that animals which have fallen below a depth of about 1000 m. in the Norwegian Sea must be regarded as lost for propagation of the stock, unless ascending currents happen to carry them upwards. Support for this view is only found in the behaviour of *Calanus hyperboreus*.

Mosby (1950) has recorded the existence of internal waves of considerable magnitude in the border layers underlying the Atlantic water masses, but we have no reason to suppose that there exist ascending currents of a magnitude that would suffice to sweep the depths below 1000 m. clear of *C. finmarchicus* and *P. minutus* during the spring. It there is any external factor which acts as a stimulus to the ascending movement of copepods in spring, it must be one which makes itself felt below the 1000 m. depth in the waters here under consideration.

In his discussion of the factors which influence the vertical distribution of copepods Clarke (1934, p. 538) states: "Directional movement can be caused only by gravity, light, and possibly the presence of other organisms, but other factors may have an indirect effect through modification of whatever geotropic or phototropic reactions are in operation." The effect of light on the movements of copepods is indubitable. That it is the chief factor in influencing migration is clear from the extensive studies on the diurnal migration of copepods.

As yet we have no measurements of the light conditions at station M, not even in the surface layers, but from what is known about light penetration to the deeper layers in other areas, it is doubtful whether the light is sufficiently intense in February and March to evoke a reaction in copepods living 1000 m. or more below surface. The possibility cannot, however, be entirely disregarded.

According to Sømme (1934) and Ussing (1938) the increasing light intensity in spring at the surface must be an important factor in stimulating the annual vertical migration of copepods. But Clarke (1938) has shown that changes in transparency have much greater significance for the changes in the submarine illumination than seasonal variations in the amount of daylight reaching the sea surface. According to Clarke (1939), if the extinction coefficient varies between 0.10 and 0.05, the proportion of daylight present at a depth of 500 m. will be 10^{11} times greater for the minimum value of k than for the maximum value.

No data are available concerning the seasonal variation in water transparency at station M, but assuming that the annual vertical migration is governed by light intensity, it seems fair to conclude that the fluctuations in transparency are of greater significance for this movement than the changes in daylight caused by the increasing altitude of the sun in the spring.

Watermann et al. (1939) have shown that certain crustacea in the Sargasso Sea, which in the daytime sojourn at a depth of about 800 m., undertake extensive diurnal vertical migrations. A great part of the movement seems to occur at a time when there is only starlight at the surface. Calculations based on the light penetration data indicate, however, that these animals are at some time of the day affected by light penetrating from the surface. These writers think that the vertical migration cannot be explained solely by variations in the light intensity, but as this factor is the only daily environmental variable in deep water, it may play an important part in the phenomenon. It may be that the light acts in conjunction with other factors such as temperature and gravity.

It cannot be doubted that gravity exerts a determinative influence on the vertical distribution of copepods. A positive geotaxis, or lack of a stimulus to negative geotactic movements, would lead to a sinking to lower levels, such as we observe in the autumn.

Experiments carried out by Kikuchi (1938) on the reaction of planktonic fresh-water copepods to light and gravity have shown that the species react variously to gravity. Some are indifferent or positive to gravity, both in diffused light and in darkness, at all temperatures. Others are indifferent to gravity in darkness, but when the temperature of the water is raised show temporarily a slight tendency to positive "geotropism". On the other hand Dice (1914) found that high temperature produces a tendency in *Daphnia* to positive "geotropism" and low temperature to negative "geotropism".

But whether variations of temperature affect the sign of geotropic reactions or not, this cannot be the explanation of the spring ascent of copepods at station M, as in the 1000 m. level the temperature was almost constant during the whole year (cf. fig. 5).

Although it has been proved that external factors may change the sign of geotaxis and phototaxis, the significance of the internal physiological state of the organisms has also been pointed out by several writers (Watermann et al., 1939). Physiological changes may alter the sign of geotaxis or the sensitivity to external impulses which influence the reaction to gravity.

Sømme (1934) and Ussing (1938) thought it possible that the spring ascent of copepods has no connection with their development to sexual maturity, and that it could not be related to a spawning migration. The material from station M shows, however, that the annual vertical migration of the copepods in some cases is connected with their life cycle. There is, for example, a definite relationship between the ascent of *Pseudocalanus minutus* to the surface and the moulting from stage V to sexual maturity. This suggests that the spring ascent may be compared to a spawning migration, and one may consequently seek the stimulus to the ascending movement in an internal impulse excited by approaching maturity. In the case of *Calanus finmarchicus,* where it is stages IV and V which ascend, it is more difficult to suppose that the incentive to upward movement lies in sexual development, although Marshall and Orr (1952) observed a distinct growth of the sexual glands in stage V.

It is easy to understand that the physiological changes which accompany sexual development may alter the sign of geotaxis from positive to negative, thereby inciting to ascent. Clarke (1936) has pointed out that phototactic responses cannot occur at depths where the illumination is so diffuse that its direction is no longer perceptible to the copepod. Nevertheless the intensity of the light present may affect the sign of geotaxis. It is difficult to believe therefore that light intensities in depths below 1000 m. in the Norwegian Sea in February and March can affect a phototactic mechanism, although we know that great changes in sensitivity to light may occur in copepods. The characteristic distribution of the different stages indicates that the sensitivity to light alters from stage to stage during development, and it may well be that a change in the physiology of the hibernating stages, due, for instance to starvation, appreciably increases the sensitivity to light. But this will hardly explain the upward migration from depths between 1000 and 2000 m.

In the course of their ascent the copepods will gradually come under the influence of increased light intensity, and thus the upward movement initiated by some other factor may be accelerated by a positive phototactic reaction.

It would be interesting to test by experiments on *Calanus,* which has been adapted to darkness for several months, the minimum light intensity which excites a phototactic reaction.

Sømme (1934) and others have drawn attention to the fact that the ascent toward the surface occurs at a later date in northern waters than in more southerly areas, where the spawning of the species begins earlier, synchronizing with the spring conditions of the sea. It can hardly be doubted, therefore, that light conditions have significance for the migration to the surface, but we are inclined to think that this relates to the final stages in an upward movement which is primarily excited by internal factors related to sexual development.

These questions have relevance for our understanding of the cycles of zooplankton production in the sea. For amplification of our knowledge more experimental work and further observation of the natural habitats in winter time are needed. A study of possible diurnal vertical migrations of hibernating copepods in the deeper layers would also be valuable, and might afford a clue to the understanding of the mechanism which underlies the cycle of annual vertical migration.

VI. Remarks on the Different Species.

A list of the species and their aggregate numbers in all hauls taken at the respective depths has been given in table 3. The tables below show the monthly numbers of certain species found at station M. These tables also show a monthly frequency figure, that is the number of hauls which contained the species in question divided by the total number of hauls taken at the said depth and in the said month.

Coelenterata

Aglantha digitale (O. F. Müller).

This species was the only coelenterate which occurred regularly. It was found at all depths, but most frequently in the hauls between 1000

Table 8.

Aglantha digitale:

Monthly numbers and frequencies of occurrence at the different depths.

Depth in m.	Month	O	N	D	J	F	M	A
50—0	Number ..						45	
	Frequency .	0/4	0/2	0/3	0/1	0/4	1/3	0/4
100—50	Number ..					1		
	Frequency .	0/4	0/2	0/3	0/1	1/4	0/3	0/4
600—100	Number ..	6	12	15	1	15	15	75
	Frequency .	1/2	3/3	3/3	1/1	4/4	2/3	4/4
1 000—600	Number ..		193	81	61	90	32	54
	Frequency .		3/3	3/3	1/1	4/4	2/2	4/4
2 000—1 000	Number ..		12	6	9	36		4
	Frequency .		1/1	2/3	1/1	3/4	0/1	2/5
(Continued)		M	J	J	A	S	O	N
50—0	Number ..		2730	402				
	Frequency .	0/3	5/5	4/4	0/4	0/3	0/1	0/1
100—50	Number ..		287	367	1			10
	Frequency .	0/3	4/5	2/4	1/4	0/3	0/1	1/1
600—100	Number ..	39	108	195	337	38	35	7
	Frequency .	3/3	4/5	5/5	4/4	2/2	1/1	1/1
1 000—600	Number ..	68	42	53	200	138	46	59
	Frequency .	3/3	3/4	5/5	5/5	4/4	1/1	1/1
2 000—1 000	Number ..		30	2	10	92	21	12
	Frequency .	0/1	2/5	1/5	2/4	3/4	1/1	1/1

and 100 m. Thus it seems to be a characteristic form in the intermediate water layers, as has previously been reported by Gran (1902).

The full-grown specimens were always taken below 100 m. In June and July a large number of small individuals were caught in the uppermost 100 m., mostly in the 50—0 m. layer. This mass occurrence of young ones indicates that spawning took place in the late spring or early summer.

Atolla wyvillei Haeckel.

Seventeen specimens of this bathy-pelagic medusae were taken at station M, all of them in hauls below 1000 m.

Beroë cucumis Fabricius.

Of the fifteen specimens of this ctenophore taken, only one was from the layer above 100 m.

Diphyes arctica (Chun), *Lensia conoidea* Keferstein & Ehlers, *Physophora hydrostatica* Forskål.

Diphyes arctica was found at all depths. The majority were taken, however, in the 600—100 m. hauls, it being present in nearly every sample from this depth (frequency 37/41).

The two other species of siphonophora are true warm water forms and were found only in the hauls from 600—100 m. in September and October 1949.

Polychaeta

Tomopteris spp.

The Tomopteridae found have not been identified to species. They were never taken in the 50—0 m. hauls and at no time in large numbers — at the most 10 specimens in a haul.

When found in the North Sea, where it makes a seasonal appearance, culminating in the autumn, *Tomopteris* is regarded as an indicator of water of Atlantic origin (Rae 1949). At station M it occurred chiefly in the autumn and winter. In the deep layers it was only found in the period November—February. This indicates that the presence of *Tomopteris* in the Norwegian Sea depends on the inflow of Atlantic water.

Phyllodocidae.

Some specimens of this family were taken in hauls from the depths below 100 m.

Table 9.

Tomopteris spp.:

Monthly numbers and frequencies of occurrence at the different depths.

Depth in m.	Month	O	N	D	J	F	M	A
100—50	Number ..							
	Frequency .	0/4	0/2	0/3	0/1	0/4	0/3	0/4
600—100	Number ..	3	10	5	9	12	4	7
	Frequency .	1/2	3/3	2/3	1/1	4/4	2/3	3/4
1 000—600	Number ..		2	6	3	10	2	2
	Frequency .		2/3	2/3	1/1	3/4	2/2	2/4
2 000—1 000	Number ..		3		9	7		
	Frequency .		1/1	0/3	1/1	4/4	0/1	0/5

(Continued)		M	J	J	A	S	O	N
100—50	Number ..				1			1
	Frequency .	0/3	0/5	0/4	1/4	0/3	0/1	1/1
600—100	Number ..	6	3	3	2	3	1	10
	Frequency .	3/3	2/5	2/5	1/4	2/2	1/1	1/1
1 000—600	Number ..	2	2			2		
	Frequency .	2/3	2/4	0/5	0/5	2/4	0/1	0/1
2 000—1 000	Number ..							
	Frequency .	0/1	0/5	0/5	0/4	0/4	0/1	0/1

Pteropoda

Limacina retroversa (Fleming).

In some hauls this pteropod constituted quite a large proportion of the animal stock. It was never found below 1000 m. and was most frequent in the 600—100 m. hauls. The majority occurred in the 50—0 m. layer in October and November 1948.

Limacina, like *Tomopteris,* when found in the North Sea, has usually been regarded as an indicator of water of Atlantic origin (Rae 1949). According to Rae (1950), *Limacina* has a later season in the North Sea than in the Atlantic. His material from the continuous plankton recorder suggests that in 1949 the appearance of this species in the North Sea was delayed, in comparison with 1948. At station M it was more abundant in the hauls taken in the autumn 1948 than in 1949, but the material is too scanty to admit of conclusions respecting the occurrence of *Limacina* in the said two years. Moreover, as has been pointed out by Bigelow and Sears (1939), this species is an extremely variable one, from place to place and from year to year.

Table 10.

Limacina retroversa:

Monthly numbers and frequencies of occurrence at the different depths.

Depth in m.	Month	O	N	D	J	F	M	A
50—0	Number ..	6901	280	1		1		
	Frequency .	4/4	2/2	1/3	0/1	1/4	0/3	0/4
100—50	Number ..	175	46	3			1	
	Frequency .	3/4	1/2	1/3	0/1	0/4	1/3	0/4
600—100	Number ..	481	188	380	130	135	21	5
	Frequency .	2/2	1/3	3/3	1/1	3/4	2/3	2/4
1 000—600	Number ..					111		
	Frequency .		0/3	0/3	0/1	2/4	0/2	0/4
2 000—1 000	Number ..							
	Frequency .		0/1	0/3	0/1	0/4	0/1	0/5
(Continued)		M	J	J	A	S	O	N
50—0	Number ..		300	221		60	80	
	Frequency .	0/3	3/5	2/4	0/4	3/3	1/1	0/1
100—50	Number ..		21	30				
	Frequency .	0/3	2/5	1/4	0/4	0/3	0/1	0/1
600—100	Number ..			1	1	151	100	70
	Frequency .	0/3	0/5	1/5	1/4	2/2	1/1	1/1
1 000—600	Number ..			1				
	Frequency .	0/3	0/4	1/5	0/5	0/4	0/1	0/1
2 000—1 000	Number ..							
	Frequency .	0/1	0/5	0/5	0/4	0/4	0/1	0/1

Clione limacina (Phipps).

This species, which is characterized by Gran (1902) as typical of the region of the East Icelandic Polar Current in the western part of the Norwegian Sea, was found at station M solely in layers below 100 m., and in 13 hauls only 16 specimens were observed.

Chaetognatha

Sagitta elegans Verrill

Sagitta elegans has three varieties, two of which occur in the Norwegian Sea (Russell 1939). According to Fraser (1949) *Sagitta elegans*

Table 11.
Sagitta elegans:
Monthly numbers and frequencies of occurrence at the different depths.

Depth in m.	Month	O	N	D	J	F	M	A
50—0	Number ..		3	2		1		
	Frequency .	0/4	1/2	2/3	0/1	1/4	0/3	0/4
100—50	Number ..		2	10		4		
	Frequency .	0/4	1/2	2/3	0/1	1/4	0/3	0/4
600—100	Number ..	14	10	10	3	12	11	15
	Frequency .	2/2	3/3	3/3	1/1	4/4	3/3	3/4
1 000—600	Number ..		13	3	5	19	3	
	Frequency .		2/3	2/3	1/1	4/4	1/2	0/4
2 000—1 000	Number ..							
	Frequency .		0/1	0/3	0/1	0/4	0/1	0/5
(Continued)		M	J	J	A	S	O	N
50—0	Number ..		80	38	1			
	Frequency .	0/3	2/5	3/4	1/4	0/3	0/1	0/1
100—50	Number ..		126	11	3	1		
	Frequency .	0/3	3/5	2/4	2/4	1/3	0/1	0/1
600—100	Number ..	1	13	35	41	7	3	3
	Frequency .	1/3	2/5	2/5	4/4	2/2	1/1	1/1
1 000—600	Number ..					1	2	8
	Frequency .	0/3	0/4	0/5	0/5	1/4	1/1	1/1
2 000—1 000	Number ..		2			1		
	Frequency .	0/1	1/5	0/5	0/4	1/4	0/1	0/1

elegans Verrill is found in Scottish areas in mixed oceanic and coastal waters, while *Sagitta elegans arctica* Aurivillius in the Faroe-Shetland Channel occurs chiefly in association with *Eukrohnia hamata* and *Calanus hyperboreus*. In the material from station M all the specimens which were submitted to close examination proved to be *Sagitta elegans arctica* Aurivillius.

The occurrence was never large, and the species was mostly found in the hauls from 600—100 m. Only three specimens were observed in the layers below 1000 m.

The specimens found in the layers above 100 m. were usually less than 10 mm. long, and occurred chiefly in June and July. This was probably due to spawning in late spring or early summer.

Table 12.
Sagitta maxima:
Monthly numbers and frequencies of occurrence at the different depths.

Depth in m.	Month	O	N	D	J	F	M	A
600—100	Number ..	1	1	1	2	4	3	2
	Frequency .	1/2	1/3	1/3	1/1	3/4	2/3	2/4
1 000—600	Number ..				1		2	
	Frequency .		0/3	0/3	1/1	0/4	1/2	0/4
2 000—1 000	Number ..					1		1
	Frequency .		0/1	0/3	0/1	1/4	0/1	1/5
(Continued)		M	J	J	A	S	O	N
600—100	Number ..		3	3	1	2	1	3
	Frequency .	0/3	2/5	2/5	1/4	2/2	1/1	1/1
1 000—600	Number ..			1	1			
	Frequency .	0/3	0/4	1/5	1/5	0/4	0/1	0/1
2 000—1 000	Number ..	1		1			1	
	Frequency .	1/1	0/5	1/5	0/4	0/4	1/1	0/1

Sagitta maxima (Conant).

A total of 37 individuals was encountered in the course of the year. It was mainly caught in the 600—100 m. hauls and never above 100 m. Although the material is scanty for forming an opinion, it suggests that *Sagitta maxima,* which according to Fraser (1949) is a deep water species, mostly occurs in water with a temperature above 0° C.

Sagitta serratodentata Krohn.

Fraser (1949) reports that this species mostly occurs at the surface and in the subsurface of warm oceanic water. When found in the North Sea it is regarded as indicative of the presence of water of Atlantic origin (Russell 1935, and Fraser 1937). At station M a single specimen was taken in a 600—100 m. haul in March. According to the literature this species has not previously been recorded in this northern latitude of the Norwegian Sea.

Sagitta planctonis Steinhaus.

Like the foregoing species, *Sagitta planctonis* has not previously been caught in the Norwegian Sea. At station M it was found in a haul from the 600—100 m. layer in April.

In the Scottish plankton collections this species was not recorded before 1948, when it was taken in deep water west of the Hebrides (Fraser 1949).

Table 13.
Eukrohnia hamata:
Monthly numbers and frequencies of occurrence at the different depths.

Depth in m.	Month	O	N	D	J	F	M	A
50—0	Number ..						1	
	Frequency .	0/4	0/2	0/3	0/1	0/4	1/3	0/4
100—50	Number ..						3	5
	Frequency .	0/4	0/2	0/3	0/1	0/4	1/3	2/4
600—100	Number ..	264	365	294	166	356	382	448
	Frequency .	2/2	3/3	3/3	1/1	4/4	3/3	4/4
1 000—600	Number ..		399	172	103	389	241	166
	Frequency .		3/3	3/3	1/1	4/4	2/2	4/4
2 000—1 000	Number ..		15	18	17	81	1	88
	Frequency .		1/1	3/3	1/1	4/4	1/1	5/5
(Continued)		M	J	J	A	S	O	N
50—0	Number ..		310	4				
	Frequency .	0/3	3/5	2/4	0/4	0/3	0/1	0/1
100—50	Number ..	35	98	23	3	5		6
	Frequency .	2/3	4/5	3/4	1/4	1/3	0/1	1/1
600—100	Number ..	155	599	359	485	279	154	44
	Frequency .	3/3	5/5	4/5	4/4	2/2	1/1	1/1
1 000—600	Number ..	107	192	180	221	300	100	146
	Frequency .	3/3	4/4	5/5	5/5	4/4	1/1	1/1
2 000—1 000	Number ..	3	159	71	66	119	14	32
	Frequency .	1/1	5/5	5/5	4/4	4/4	1/1	1/1

Eukrohnia hamata (Møbius).

This was the chaetognath most frequently found at station M. It appeared at all depths, and was a permanent member of the fauna below 100 m. The majority of specimens were taken in the 600—100 m. hauls.

In the layer above 100 m. *Eukrohnia hamata* occurred most frequently in June and July, consisting almost entirely of young individuals (less than 10 mm.). This indicates that spawning took place in the summer, a presumption which is supported by the fact that adults carrying eggs or larvae were observed in some hauls from depths below 600 m. in May, July and August.

Cladocera

Evadne nordmanni Lovén.

Gran (1902) established the presence of this neritic species in the Norwegian Sea during the summer, and he drew attention to the value of Cladocera as indicators of coastal water. Two hauls taken from the 50 m. layer at station M on June 29th and July 6th contained 500 and 150 individuals respectively of this species. On July 10th, 10 specimens were also found in a haul from the 100—50 m. layer. *Evadne nordmanni* can be carried to this area by currents either from the Faroe-Shetland Channel or from the Norwegian coast.

Copepoda

Calanus finmarchicus (Gunn.).

This species was caught in large numbers at all depths, even below 1000 m. The numbers varied in accordance with the annual vertical migration and the breeding periods, as stated in the chapter above.

Fig. 16 shows the distribution of the total number of *C. finmarchicus* collected in hauls from 2000 m. to surface. The curve represents the weighed mean numbers based on three successive observations. It will be seen that there was a steady decrease in the number of individuals each

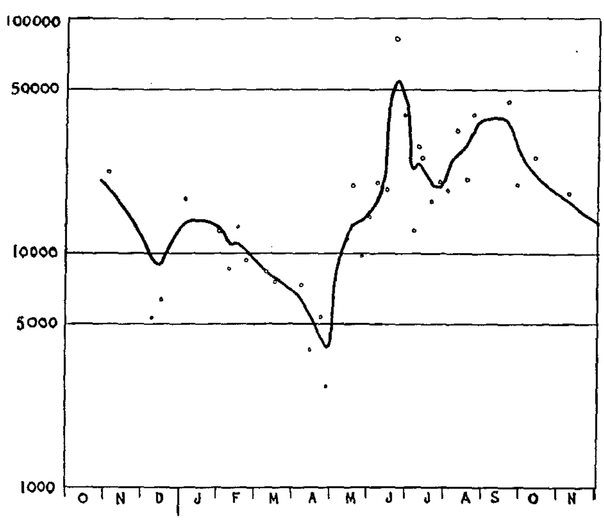

Fig. 16. The seasonal variation in total numbers of *Calanus finmarchicus*, 2000 m. to surface. (Logarithmic scale).

week during the winter, the minimum being reached in April, when the total for the whole water column was only 2700 specimens. This low figure seems to be the general rule for *C. finmarchicus* after hibernation. In Norwegian coastal waters the minimum occurs about 1 1/2 months earlier, namely medio March (Ruud 1929, and Sømme 1934).

In the middle of May the numbers of *C. finmarchicus* increased rapidly, reaching a peak in June, with approximately 80000 individuals. Another maximum was recorded in September with 38800 individuals. As has been pointed out above, these two maxima correspond to two spawning periods, one in April/May and another in August/September (cf. Chapter V A). The spring spawning was the more important, forming the bulk of the hibernating stock.

Calanus helgolandicus (Claus), which at one time was classified as a distinct species, but is now usually regarded as a more southerly form of *C. finmarchicus* (Rees 1949), has not been found in the material from station M.

Calanus hyperboreus Krøyer.

Calanus hyperboreus is an Arctic species and, according to Damas (1905), is stationary in the southern Norwegian Sea only in the area northeast of Iceland. This area has been shown by Helland-Hansen and Nansen (1909) to coincide with the East-Icelandic Polar Current.

It has already been stated (Chap. V, B, fig. 12) that *C. hyperboreus* was found in large quantities only below 1000 m., where the water masses are mainly of Arctic origin. In May and June it was also present in the layers above 100 m. In these months the maximum temperature in the upper 100 m. was 8.4° C., and the salinity varied from 35.15 to 35.29 ‰. According to Ruud (1929), this species was never found off Møre in water having a higher temperature than 7.5° C. or higher salinity than 35.00 ‰.

Sømme (1934) records the spawning of this species in water with temperature 1.5—7.5° C. At station M some spawning of *C. hyperboreus* probably occurred in April, when the highest temperature and salinity in the surface layers were 7.3° C. and 35.34 ‰ respectively. The increase of the stock in the deep layers in summer and autumn is, however, as already stated (p. 27), probably caused by an influx of *C. hyperboreus* from other spawning areas, possibly carried by an undercurrent of Arctic water.

Rhincalanus nasutus Giesbrecht.

This Atlantic species was encountered in 12 hauls during the year, usually singly. The highest number found in one haul was 4, from 1000—

600 m., in November 1948. The species was not found above 100 m., which is in keeping with earlier records from the northern waters (Jespersen 1940).

Eucalanus elongatus Dana.

A single specimen, a female, of this Atlantic copepod was observed in a haul from 1000—600 m. in November.

Table 14.

Paracalanus parvus:

Monthly numbers and frequencies of occurrence at the different depths.

Depth in m.	Month	O	N	D	J	F	M	A
50—0	Number ..	305	290	100	10	3		
	Frequency .	4/4	2/2	3/3	1/1	1/4	0/3	0/4
100—50	Number ..	235	259	135	8			
	Frequency .	4/4	2/2	3/3	1/1	0/4	0/3	0/4
600—100	Number ..		40	21		1		
	Frequency .	0/2	3/3	2/3	0/1	1/4	0/3	0/4

(Continued)		M	J	J	A	S	O	N
50—0	Number ..					10	1	54
	Frequency .	0/3	0/5	0/4	0/4	1/3	1/1	1/1
100—50	Number ..							60
	Frequency .	0/3	0/5	0/4	0/4	0/3	0/1	1/1
600—100	Number ..							
	Frequency .	0/3	0/5	0/5	0/4	0/2	0/1	0/1

Paracalanus parvus (Claus).

This species was caught for the most part in the surface layers and solely in late autumn and winter, mainly October/November. It was never found in hauls below 1000 m. and was entirely absent from the beginning of February to September. Its occurrence must therefore depend on an influx from other localities.

At station M *Paracalanus parvus* was somewhat more numerous in the autumn of 1948 than in 1949. In Norwegian coastal waters it showed similar fluctuations, being frequent in the plankton samples taken in 1948, scarce in 1949, and numerous again in 1950 (Wiborg 1954).

Pseudocalanus minutus (Krøyer).

Three forms now usually regarded as belonging to this species have been reported: *Pseudocalanus elongatus* (Boeck), *Pseudocalanus major* G. O. Sars, and *Pseudocalanus gracilis* G. O. Sars.

According to the characters described by Sars (1903), *Pseudocalanus gracilis* seems to be the dominant form in the material from station M. As the question whether these forms represent distinct species is still undecided, they are treated here as one species: *Pseudocalanus minutus* (Krøyer), following the practice of former writers (With 1915, Størmer 1929, Marshall 1949, Farran 1951 and others).

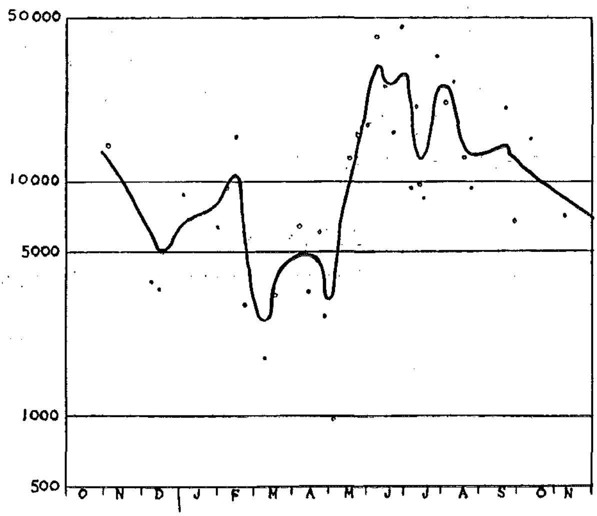

Fig. 17. The seasonal variation in total numbers of *Pseudocalanus minutus*, 2000 m. to surface. (Logarithmic scale).

Fig. 17 gives the variations in the total numbers of *P. minutus* recorded in hauls from 2000 m. to surface. The curve represents the weighed mean numbers based on three successive observations. There was a slight increase in the stock during March and April. It is unlikely that this augmentation was caused by spawning in this part of the sea, as adults dominated the stock and young copepodites were not encountered until the second half of April (cf. Chap. V, C).

P. minutus revealed only one spawning period, corresponding to the numerical increase recorded in May and June. After the maximum had been reached medio June, the numbers gradually declined in the course of the autumn and winter.

Microcalanus pygmaeus (+ pusillus) (G. O. Sars).

Two species of *Microcalanus* have been reported: *M. pygmaeus* (G. O. Sars) and *M. pusillus* G. O. Sars. Following With (1915), they have usually been regarded as one species (Størmer 1929, Ussing 1938, Marshall 1949 and others), but Farran (1951) thinks they are two forms of a variable *M. pygmaeus*.

In the present material there are two groups of *Microcalanus* distinguished by the size of the individuals. The larger form agrees well with the description given by Sars (1900) of *M. pygmaeus*. The total length of the females varies between 0.84 and 0.94 mm., the average being 0.86 (based on 150 specimens). They have relatively long antennulae. The smaller form, which corresponds to *M. pusillus* G. O. Sars, has short antennulae and the females measure 0.58 to 0.64 mm., the average length being 0.60 mm. No difference was found in the terminal spine of the natatory limbs, which agrees with With's observation.

Attempt has been made, without measuring, to assign the individuals found in the material to one or other of the two size groups, but the young copepodites were very difficult to distinguish by size, and in some cases they have undoubtedly been misplaced.

Table 15.

The vertical distribution of *Microcalanus pusillus* and *M. pygmaeus*.

Depth in m.	*M. pusillus* Number	*M. pusillus* %	*M. pygmaeus* Number	*M. pygmaeus* %
50—0	4154	4.5	—	—
100—50	11071	12.0	550	0.8
600—100	57415	62.2	5415	8.2
1000—600	13130	14.2	19757	30.0
2000—1000	6703	7.2	40035	61.0

Table 15 shows the percentage distribution of the two forms of *Microcalanus* from 2000 m. to surface. Although there may be some inaccuracies, it is clear that the larger form, *M. pygmaeus*, has its main distribution in the layers below 600 m., while the smaller form, *M. pusillus*, is most numerous in the upper layers. The latter seems therefore to belong to the fauna of the Atlantic waters, while the former apparently has its main distribution in the bottom layers.

Since the completion of this work, Wiborg (1954) has, on the basis of actual measurements, found that the two forms can be separated into two distinct groups, and he regards them therefore as distinct species.

The total numbers of the two forms of *Microcalanus* per haul at the different depths are given in fig. 18. They were found both in the surface layers and in the layers below 1000 m. From March to September they were entirely absent in the 50—0 m. layer, and in the same period they were also scarce in the 100—50 m. hauls.

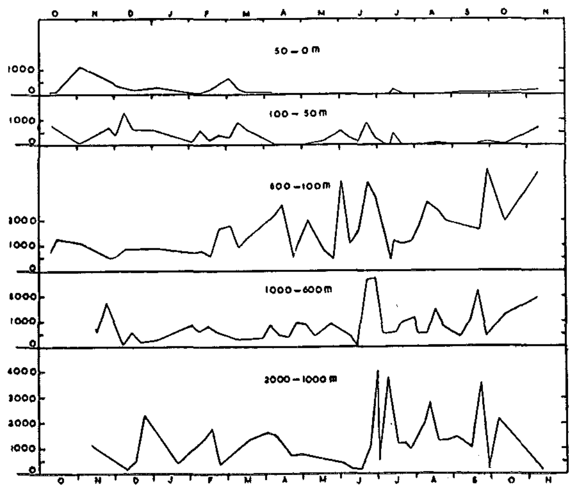

Fig. 18. Total numbers per haul of *Microcalanus pygmaeus*.

In the counts *Microcalanus* has not been classified according to the stages of development. Ruud (1929) states that the youngest stages slip through the meshes of the net, so that the highest numbers must be expected when the adults are at a maximum, possibly coinciding with the spawning. As will be seen from the figure, there was no great increase in the population during the year.

Spinocalanus abyssalis Giesbrecht.

This species was represented by a few individuals in most hauls from the 2000—1000 m. depth. Only five specimens were caught in the layers above 1000 m. *S. abyssalis* must therefore be regarded as belonging to the deep water fauna of the Norwegian Sea.

Spinocalanus magnus Wolfenden.

This, like the foregoing species, is a typical deep water form. At station M it was recorded only twice in hauls above 1000 m., while it was present in 23 out of the 36 hauls taken from deeper levels.

Aetideus armatus (Boeck).

This was taken at station M only in small quantities, and for the most part in the 600—100 m. hauls (600—100 m.: freq. 13/42). In hauls from deeper layers it was recorded once. *Aetideus armatus* was therefore mainly found in the water layers of Atlantic origin above 600 m.

Aetideopsis rostrata G. O. Sars.

This species was never taken above 100 m. and only twice above 600 m. It was recorded in 31 out of 40 hauls from 1000—600 m., and in all hauls (36) taken below 1000 m.

Table 16.

Aetideopsis rostrata:

Monthly numbers and frequencies of occurrence at the different depths.

Depth in m.	Month	O	N	D	J	F	M	A
600—100	Number ..							
	Frequency .	0/2	0/3	0/3	0/1	0/4	0/3	0/4
1 000—600	Number ..		2	1	2	4	1	45
	Frequency .		1/3	1/3	1/1	2/4	1/2	4/4
2 000—1 000	Number ..		23	35	11	79	24	62
	Frequency .		1/1	3/3	1/1	4/4	1/1	5/5

(Continued)		M	J	J	A	S	O	N
600—100	Number ..	2	1					
	Frequency .	1/3	1/5	0/5	0/4	0/2	0/1	0/1
1 000—600	Number ..	64	19	14	6	14	1	3
	Frequency .	3/3	4/4	5/5	3/5	4/4	1/1	1/1
2 000—1 000	Number ..	11	84	86	55	58	11	7
	Frequency .	1/1	5/5	5/5	4/4	4/4	1/1	1/1

The results seem to indicate that *Aetideopsis rostrata* belongs to the deep water fauna, as has also been pointed out by previous writers (Damas and Koefod 1907, Jespersen 1934).

It seems that the adult male has not yet been recorded. In the present material several male copepodites of stage V were observed, but no adult males.

Pseudaetideus armatus (Boeck).

In Greenland waters this copepod has been taken exclusively in hauls using more than 600 m. wire (*Aetideus armatus*, Jespersen 1939). Approximately the same vertical distribution was found at station M. Out of 99 specimens, only four were taken above 600 m.

Chiridius obtusifrons G. O. Sars.

A single female of this arctic-boreal copepod was found in a haul from 2000—1000 m. All the other specimens were taken in 1000—600 m. and 600—100 m. hauls — 1 male, 61 females and 5 copepodites in all.

Three females bearing egg sacs were also taken, one in January and two in June. These scanty records seem to indicate that spawning occurs in winter as well as in summer.

Chiridiella macrodactyla G. O. Sars.

Two specimens, an adult female and an individual stage V, were found in hauls from 2000—1000 m. Apart form this the species has been reported from the seas between Spitzbergen and Greenland (Damas and Koefoed 1907), from the Atlantic (G. O. Sars 1925) and from the South Pacific (A. Scott 1909), in all cases at great depth.

Gaidius brevispinus (G. O. Sars).

This copepod was a characteristic feature of the hauls from below 600 m. It was never found in hauls above 100 m., but was present in 16 out of 41 hauls from 600—100 m., invariably in small number. It was most abundant in the 2000—1000 m. hauls.

Table 17.

Gaidius brevispinus:

Monthly numbers and frequencies of occurrence at the different depths.

Depth in m.	Month	O	N	D	J	F	M	A
600—100	Number ..	2	1	1				
	Frequency .	2/2	1/3	1/3	0/1	0/4	0/3	0/4
1 000—600	Number ..		10	4	3	14	12	50
	Frequency .		3/3	3/3	1/1	2/4	2/2	4/4
2 000—1 000	Number ..		28	33	16	125	8	100
	Frequency .		1/1	3/3	1/1	4/4	1/1	5/5

(Continued)		M	J	J	A	S	O	N
600—100	Number ..	9	13	3	3	6	1	
	Frequency .	2/3	4/5	1/5	2/4	2/2	1/1	0/1
1 000—600	Number ..	46	32	26	43	31	8	3
	Frequency .	3/3	4/4	5/5	5/5	4/4	1/1	1/1
2 000—1 000	Number ..	3	74	71	83	66	14	10
	Frequency .	1/1	5/5	5/5	4/4	4/4	1/1	1/1

The distribution of adults and copepodites is as follows:

Hauls	Males	Females	Copepodites
600—100	—	35	4
1000—600	4	182	96
2000—1000	27	148	456

Adult males and females and young copepodites were caught all the year, which is an indication that spawning takes place at all seasons of the year.

Table 18.

Gaidius tenuispinus:

Monthly numbers and frequencies of occurrence at the different depths.

Depth in m.	Month	O	N	D	J	F	M	A
50—0	Number ..					1		
	Frequency .	0/4	0/2	0/3	0/1	1/4	0/3	0/4
100—50	Number ..			1				
	Frequency .	0/4	0/2	1/3	0/1	0/4	0/3	0/4
600—100	Number ..	20	31	49	26	19	10	17
	Frequency .	2/2	3/3	3/3	1/1	4/4	3/3	4/4
1 000—600	Number ..		2	13		36	26	15
	Frequency .		2/3	2/3	0/1	3/4	2/2	2/4
2 000—1 000	Number ..					1		
	Frequency .		0/1	0/3	0/1	1/4	0/1	0/5

(Continued)		M	J	J	A	S	O	N
50—0	Number ..							
	Frequency .	0/3	0/5	0/4	0/4	0/3	0/1	0/1
100—50	Number ..							1
	Frequency .	0/3	0/5	0/4	0/4	0/3	0/1	1/1
600—100	Number ..	7	43	35	34	15	10	11
	Frequency .	3/3	5/5	5/5	4/4	2/2	1/1	1/1
1 000—600	Number ..	3	3	6	6	6	5	4
	Frequency .	1/3	3/4	3/5	4/5	1/4	1/1	1/1
2 000—1 000	Number ..		1	1	1	1		
	Frequency .	0/1	1/5	1/5	1/4	1/4	0/1	0/1

Gaidius tenuispinus (G. O. Sars).

This copepod was taken at all depths, but only 3 specimens were caught above 100 m., whereas it was found regularly in the 600—100 m. hauls. Below 1000 m. it was as rare as above 100 m. *Gaidius tenuispinus* must therefore be regarded as characteristic of the fauna in intermediate depths.

Gaetanus pileatus Farran; *Gaetanus minor* Farran;
Euchirella curticauda Giesbrecht; *Euchirella rostrata* (Claus).

The published records indicate that these Atlantic copepods have not previously been taken from this northern latitude of the Norwegian Sea. At station M they were all taken in hauls from 600—100 m. in February, March and August, in the case of *Gaetanus minor* and *Euchirella curticauda* only once.

Pseudochirella pustulifera (G. O. Sars); *Pseudochirella* sp;
Undeuchaeta major Giesbrecht.

These Atlantic copepods were found in hauls from 2000—1000 m. Two females of genus *Pseudochirella* coincided with the description given by With (1915) of *P. pustulifera* (G. O. Sars). Another female of same genus has not been identified. Two copepodites, stage V, of *Undeuchaeta major* were observed.

Pareuchaeta norvegica (Boeck).

This species has been reported by Gran (1902) as typical of the deep Atlantic water layers in the Norwegian Sea. Although it was found at all depths at station M, the material clearly supports his conclusion (cf. Chap. IV, B).

The numbers of the various stages of development of *P. norvegica* and its frequency in the different months of the year, are shown in table 19.

Above 100 m. it was rather rare the whole year. About 59 % of the total number of individuals was taken in hauls from 600—100 m.

In the deeper layers the older copepodite stages were more frequent than the younger stages. Stages I, II and III were not found below 1000 m. Reports of the vertical distribution of the various stages of *P. norvegica* by other writers are rather inconsistent. Wolfenden (1904) found that the young copepodites often occurred in the surface layers, while the adults were mostly found in deeper layers, down to 500—600 fathoms. This is in accordance with the observations of Gran (1902) and With (1915). Størmer (1929) and Jespersen (1934) on the other hand found young copepodites in deeper water than the older stages. As these writers

Table 19.

Pareuchaeta norvegica:

Monthly numbers of the various stages and the frequencies of occurrence of the species at the different depths.

50—0 m. + 100—50 m.

Stage ..	O	N	D	J	F	M	A	M	J	J	A	S	O	N
VI					1	1		1					1	
V														
IV	3	2	2					1	1	2				
III ..	9	1							22	7				1
II	9	3	3		1	1			1	5		10	1	1
I	1	2	1		2	3			5	1				
N														
Total	22	8	6		4	5		2	29	15		10	2	2
Freq.	2/4	2/4	3/6	0/2	2/8	1/6		1/6	4/10	3/8		1/6	1/2	1/2

600—100 m.

Stage ..	O	N	D	J	F	M	A	M	J	J	A	S	O	N
VI	41	40	53	10	19	19	44	14	34	48	67	54	24	30
V	38	71	39	13	8	10	36	22	76	80	77	63	53	18
IV	65	18	14	13	11	1	12	11	34	50	17	21	3	3
III ..		9	13	2	3	1	3		10	4	1	3	2	10
II	1	5	6		8	5	2	1	4		1		1	20
I	1	8	1		6	8	1	11	2	2	2		1	20
N	3		1		32		20	2	54	27		1		10
Total	149	151	127	38	87	44	118	61	214	211	165	142	84	111
Freq.	2/2	3/3	3/3	1/1	4/4	3/3	4/4	3/3	5/5	5/5	4/4	2/2	1/1	1/1

1000—600 m.

Stage ..	O	N	D	J	F	M	A	M	J	J	A	S	O	N
VI		67	40	43	99	25	45	28	16	29	32	52	23	31
V		5	20	9	26	9	8	6	2	4	5	8	3	7
IV					6	4	2	3	2		4	1		
III ..						2	4	2	3		2	1		
II		2	1		1			3	2		5	1		
I					21			1				1		
N		2			29	5	95	145		2				
Total		76	61	52	182	45	154	188	25	35	48	64	26	38
Freq.		3/3	3/3	1/1	4/4	2/2	4/4	3/3	4/4	5/5	5/5	4/4	1/1	1/1

(Table 19 cont.) 2000—1000 m.

Stage ..	O	N	D	J	F	M	A	M	J	J	A	S	O	N
VI			1	1	10				26	4		4	1	
V			1	4	14				6	2			1	
IV			1		6								2	
III ..														
II														
I														
N					14									
Total			3	5	44				32	6		4	4	
Freq.			1/3	1/1	3/4				1/5	2/5		1/4	1/1	

did not distinguish between the species of the genus *Pareuchaeta,* their results are, however, bound to be inaccurate.

Nauplii, copepodites stages I—V, males with spermatophores, and females bearing spermatophores and egg sacs, were recorded at all times of the year. It is possible, therefore, that spawning takes place at all seasons of the year, as previously recorded from the Gulf of Maine (Bigelow 1926) and Norwegian coastal waters (Wiborg 1954). As a matter of fact in the 1000—600 m. hauls most of the nauplii were taken in February, April and May. Adult males and females were also present in relatively large number below 600 m. from December to March. It would seem therefore that spawning is most intense in winter and early spring.

The average number of nauplii and copepodites stages I, II and III for the whole year was small compared with the number of adults (see table 19). It is true that the animals may have a longer life as adults than in the younger stages of development, but it is more reasonable to assume that the main spawning area lies in waters south of station M and that the animals drift northwards in the course of their development. With (1915) has remarked that although this species is found in process

Table 20.

Pareuchaeta norvegica:

The vertical percentage distribution of the various stages at the different depths.

Depth in m.	Stage			
	VI ♂	VI♀	V—IV	III—II—I
50—0 + 100—50	0.5	0.3	1.2	28.2
600—100	39.3	47.6	82.5	55.6
1000—600	56.5	47.6	12.6	16.3
2000—1000	3.6	4.5	3.7	—

Table 21.
Pareuchaeta norvegica:
The number and the percentages of the two sexes of stages IV, V and VI.

Stage	Total number	Sex	Number	Per cent
VI	1078	♂	189	17.5
		♀	889	82.5
V	744	♂	362	48.6
		♀	382	51.4
IV	317	♂	150	47.3
		♀	167	52.7

of propagation in northern waters, it ought possibly to be regarded as a North Atlantic species.

It is a known fact that adult male copepods are less numerous than the adult females, but males and females in copepodite stages IV and V are equally numerous (Ussing 1938, and Marshall 1949).

Table 21 shows the percentage of the two sexes of *Pareuchaeta norvegica* in stages IV, V and VI. In stages IV and V there are about 50 % of each sex, while in stage VI the males are much fewer, being only 17.5 % of the whole number of adults.

Pareuchaeta farrani (With).

According to With (1915) this species has its main distribution in the area between Iceland, Norway, Greenland and Spitzbergen, where it is found at fairly great depths.

At station M *P. farrani* was common in hauls from layers below 600 m., but in small number at depths above 1000 m. The numbers of the various stages of development and the frequency of occurrence in the several months are shown in table 22.

Above 600 m. only two specimens were found; these are not included in the table. Of the total number in all hauls, 85 % were taken below 1000 m.

Table 23 shows the vertical percentage distribution of the various stages of development. Stage VI is almost evenly distributed between the 2000—1000 and 1000—600 m. layers. Stage V is also fairly well represented in the 1000—600 m. hauls, but of the other stages, 90 % or more are found below 1000 m. It is evident therefore that the younger stages are encountered at deeper levels than the older stages.

Of ovigerous females, 68.7 % were found in hauls from 1000—600 m., while the nauplii were taken almost entirely below 1000 m. It is probable that the nauplii, after hatching have sunk to deeper levels.

Table 22.

Pareuchaeta farrani.

Monthly numbers of the various stages and the frequencies of occurrence of the species.

1000—600 m.

Stage	N	D	J	F	M	A	M	J	J	A	S	O	N
VI	16	16	7	6	13	18	24	22	31	26	26	8	5
V	3	4	3	7	6	12	15	10	9	18	12	2	2
IV	1			1		6	13	6	6	6	3		1
III				1		7	10	11	8	8			
II		1					5	9	5	2			
I						1			1				
N		1	1			20	1						
Total ..	20	22	11	15	19	64	68	58	60	60	41	10	8
Freq. ..	2/3	3/3	1/1	3/4	2/2	4/4	3/3	3/4	5/5	5/5	4/4	1/1	1/1

2000—100 m.

Stage	N	D	J	F	M	A	M	J	J	A	S	O	N
VI	8	10	6	13	1	32	3	36	33	18	23	4	7
V	11	17	7	24	2	20	6	40	41	36	41	9	8
IV	10	24	6	39	3	59	6	42	62	72	39	14	12
III	9	22	16	54	14	86	2	44	70	59	40	13	5
II	13	21	8	71	10	103	1	30	35	21	19	10	3
I		14	1	31	8	81	40	35	24	12	85	20	2
N	6	37	7	54	4	135	90	43	113	94	86	10	2
Total ..	57	145	51	286	42	516	148	270	378	312	333	80	39
Freq. ..	1/1	3/3	1/1	4/4	1/1	5/5	1/1	5/5	5/5	4/4	4/4	1/1	1/1

Table 23.

Pareuchaeta farrani:

The vertical percentage distribution of the various stages at the different depths.

	Stages							Females with egg-sacs	
Depth in m.	VI	V	IV	III	II	I	N	%	No.
1000—600	53.0	18.3	10.0	9.4	6.0	0.6	3.2	68.7	114
2000—1000	47.0	71.7	90.0	90.6	94.0	99.4	96.8	31.3	52

Nauplii, copepodites stages I—V, males with spermatophores and females with spermatophores and egg sacs were found at all seasons of the year, so that it seems spawning occurs at any time of the year.

The number of eggs in the sac is very small. Jespersen (1934) counted their number in 20 sacs and found this to vary from 14 to 16 eggs, in one case as many as 18. In the present material the number found in 80 sacs varied from 12 to 22, the average being 16.7.

Table 24.

Pareuchaeta farrani.

The number and the percentages of the two sexes of stages IV, V and VI.

Stages	Total number	Sex	Number	%
VI	412	♂	74	18.0
		♀	338	82.0
V	365	♂	189	51.8
		♀	176	48.2
IV	431	♂	223	51.5
		♀	208	48.5

Table 24 gives the number and percentage of the two sexes of *P. farrani* in stages IV, V and VI. As in the case of *P. norvegica,* there were about 50 % of each sex in stages IV and V, while in stage VI there were 18 % males and 82 % females.

Pareuchaeta bradyi (With).

This species is rarely met with. A single female was first observed in the Norwegian Sea by With (1915). Later another specimen was reported by G. O. Sars (1925) in the material collected in the Atlantic by the Prince of Monaco. In the material from station M 30 females have been identified. Of the male, which has not previously been described, there are 8 specimens which may be assigned to this species. Their total length is 7.3 mm. It is easily distinguishable from the males of the other species of this genus by the shape of the two last joints of the exopodite of the left fifth leg.

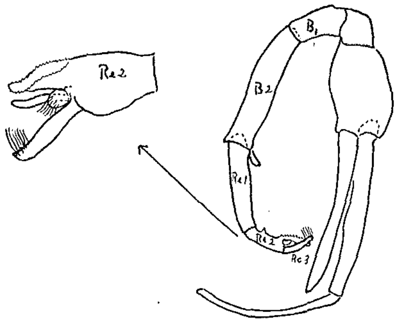

Fig. 19. *Pareuchaeta bradyi,* male: Left fifth leg. (Magnification of proximal joint abt. 10.)

Eight ovigerous females and three females with spermatophores were encountered in the period February—November. The material is rather scanty for deductions, but it would seem that the spawning period extends through the whole year, as in the case of the other two species of the genus.

The number of eggs in the sac is extremely small. Five sacs, which appeared to be full, were examined; four of these were found to contain six eggs, and the fifth eight eggs.

Pareuchaeta glacialis (H. J. Hansen).

Of this Arctic copepod 56 females were taken at station M. Only the adult specimens were identified. There were, however, some young copepodites, which could not with certainty be referred to any other species of *Pareuchaeta,* and which probably belong to *P. glacialis.*

It was commonest in the 1000—600 m. hauls, being found only occasionally above the 600 m. level. This vertical distribution agrees with what has previously been observed in the Norwegian Sea area (Damas and Koefoed 1907). Ovigerous females were encountered in November, June, July and September.

Scottocalanus persecans (Giesbrecht);
Scottocalanus securifrons (Th. Scott).

A single specimen of each of these true Atlantic species was taken in 600—100 m. hauls in October and May respectively. It is probably only an exceptional circumstance that these species penetrate as far into the Norwegian Sea as latitude 66° N.

Scaphocalanus magnus (Th. Scott);
Scaphocalanus brevicornis (G. O. Sars).

These species are typical deep water forms and were taken exclusively below 600 m. *S. brevicornis* was the more frequent, and appears to be a permanent member of the plankton fauna in the layers below 1000 m.

Amallothrix sp.

A single female, which must certainly be assigned to this genus, was taken in a 2000—1000 m. haul in November.

Scolecithricella minor (Brady).

According to Jespersen (1940) *S. minor* must be regarded as an Atlantic species, although it also occurs in specifically Arctic waters.

At station M the maximum numbers were taken in the 600—100 m. hauls, only 3 specimens being obtained in the 2000—1000 m. hauls. The evidence from this material shows therefore that *S. minor* principally occurs in water of Atlantic origin.

Table 25.

Scolecithricella minor:

Monthly numbers and frequencies of occurrence at the different depths.

Depth in m.	Month	O	N	D	J	F	M	A
50—0	Number ..	6	20	11			1	
	Frequency .	2/4	1/2	2/3	0/1	0/4	1/3	0/4
100—50	Number ..	25	7	42	2			
	Frequency .	4/4	2/2	3/3	1/1	0/4	0/3	0/4
600—100	Number ..	64	140	100	90	220	63	175
	Frequency .	2/2	3/3	3/3	1/1	4/4	3/3	2/4
1 000—600	Number ..			30		131	50	10
	Frequency .		0/3	1/3	0/1	4/4	1/2	1/4
2 000—1 000	Number ..					1		
	Frequency .		0/1	0/3	0/1	1/4	0/1	0/5
(Continued)		M	J	J	A	S	O	N
50—0	Number ..							
	Frequency .	0/3	0/5	0/4	0/4	0/3	0/1	0/1
100—50	Number ..		21			10		10
	Frequency .	0/3	2/5	0/4	0/4	1/3	0/1	1/1
600—100	Number ..	165	40	54	4	1	3	80
	Frequency .	3/3	1/5	4/5	2/4	1/2	1/1	1/1
1 000—600	Number ..	5						
	Frequency .	1/3	0/4	0/5	0/5	0/4	0/1	0/1
2 000—1 000	Number ..	1			1			
	Frequency .	1/1	0/5	0/5	1/4	0/4	0/1	0/1

Scolecithricella ovata (Farran);
Scolecithricella dentata (Giesbrecht).

These Atlantic species have not previously been reported from the Norwegian Sea. The two specimens identified as *S. dentata* were a little damaged, but the determination is thought to be correct. *S. dentata* was found in the 600—100 m. hauls taken in February and March. *S. ovata* was taken in a 2000—1000 m. haul in April.

Temorites brevis G. O. Sars.

Three females of this species were taken below 1000 m. Otherwise it is found in Arctic waters, mostly above 200 m., (G. O. Sars 1900) and in the Mediterranean, in deep water (G. O. Sars 1925).

Temora longicornis (O. F. Müller).

T. longicornis is a neritic species. At station M it was found in hauls taken in October and November 1948, mostly above 50 m., and in June 1949 from the 50—0 m. level. On the latter date, June 22, the salinity at the surface was relatively low, 35.01 ‰. In October 1948 the salinity at the surface was also rather low, probably as a result of mixture with coastal water.

This species may enter the station M area either from Norwegian coastal waters or from the Atlantic through the Faroe-Shetland Channel.

Metridia longa (Lubbock).

Fig. 20 below shows the number of specimens of this species, stages IV, V and VI, taken in each haul. The young copepodites, stages I, II and III, are not included, as they were not distinguished from *Metridia lucens* at the same stages of development.

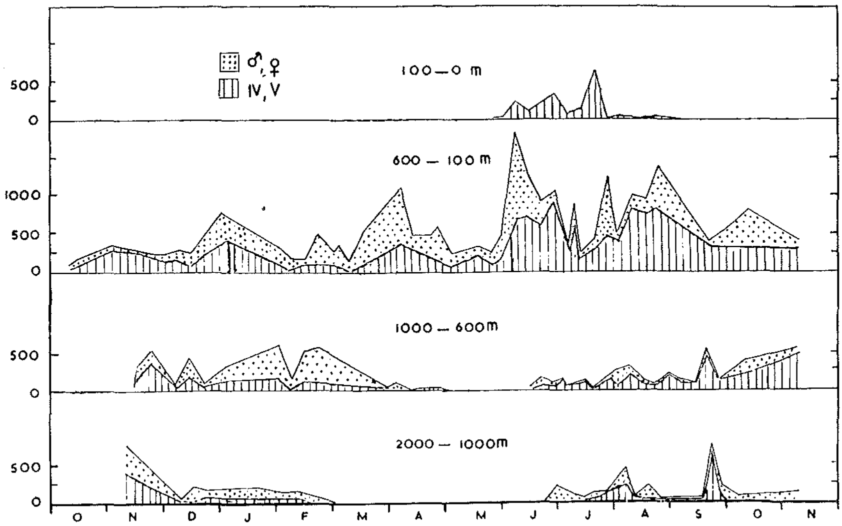

Fig. 20. Total numbers per haul of *Metridia longa*, stages IV, V and VI.

M. longa was mostly found in the 600—100 m. hauls. During the winter a considerable part of the stock was also taken below 600 m., but from April/May to July it was almost absent from these deeper layers. *M. longa* should therefore probably be regarded as belonging to the intermediate depths. The temperature in these layers varies between 0.9° and 4.0° C., and the salinity between 34.94 and 35.00 ‰. These figures are in good agreement with the ones given by Farran (1910) for the chief distribution of this species. In the waters of West Greenland, on the other hand, the main distribution is found in the 600—800 m. layer, with temperatures below 0° C. (Jespersen 1934).

Copepodites stages IV and V, adult males and females, were encountered at all depths. Table 26 shows the vertical distribution of adult males and females.

Table 26.
Metridia longa.
The vertical distribution of males and females.

Depth in m.	VI ♂ Number	VI ♂ %	VI ♀ Number	VI ♀ %
50—0	18	0.4	33	0.3
100—50	35	0.7	185	1.5
600—100	3240	65.0	7386	59.2
1000—600	1672	33.6	2191	17.6
2000—1000	11	0.2	2677	21.4

As will be seen, approximately 20 % of the females, but less than 1 % of the males, were caught below 1000 m. This seems to indicate that the females live at lower depths than the males, a result which is incompatible with observations from the West Greenland waters (Jespersen 1934) and from the White Sea (Bogorov 1932) where males were caught at deeper levels than the females.

Adult males and females of *M. longa* were encountered all the year. Of the total number of adults counted, 29 % were males and 71 % females. Only in a few hauls taken between December and January were the males found to outnumber the females.

Fig. 20 shows that adults predominated in the stock from January to June; from June to October stages IV and V were in the majority. The number of copepodites of *Metridia* spp., stages I, II and III, in each haul is shown in fig. 21.

They were taken exclusively in the uppermost 600 m. The young copepodites encountered in May and June mostly belonged to *M. longa,* while in the autumn *M. lucens* predominated. This seems to justify the

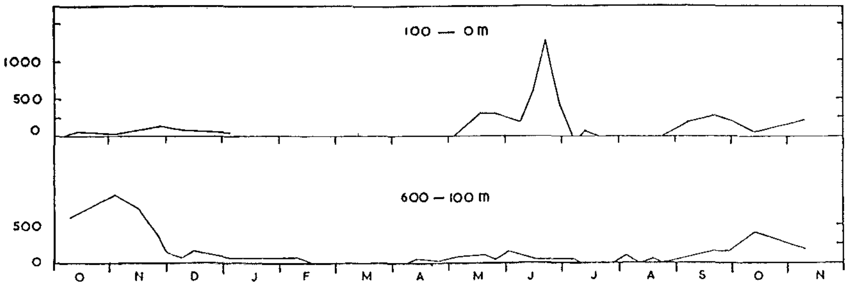

Fig. 21. Total numbers per haul of the copepodites I, II and III of *Metridia* spp.

conclusion that the main spawning of *M. longa* occurred in April/May. As some specimens of M. longa stages I, II and III were also observed in the autumn, there may have been a slight spawning at that period.

Metridia lucens Boeck.

Størmer (1929) reports that in the area between Iceland, the Faroes and Shetland *Metridia lucens* is mostly found in Gulf Stream water. At station M it was met with at all depths, but usually in small number. Fig. 22 shows the numbers of stages IV, V and VI in the hauls from the various depths.

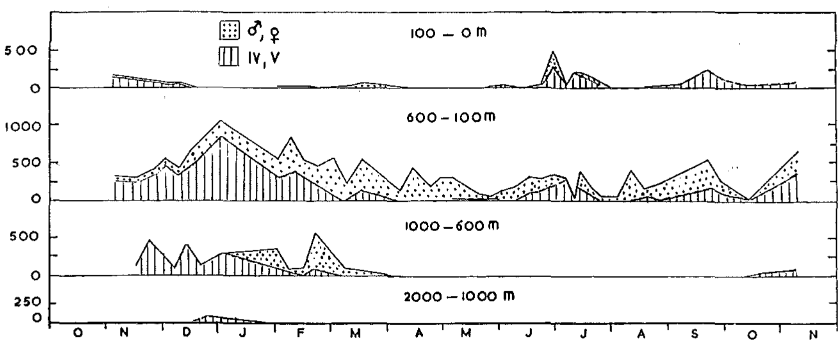

Fig. 22. Total numbers per haul of *Metridia lucens,* stages IV, V and VI.

It will be seen that *M. lucens* was scarce in hauls from the uppermost 100 m., being found with any regularity at this depth only in the summer and autumn. In the winter it occurred in all hauls from 1000—600 m., and occasionally even in hauls from 2000—1000 m. At station M, therefore, this species undoubtedly occurs in water with temperature below 0° C. But fig. 22 shows that most of the stock was taken in hauls from 600—100 m., and the hydrographical observations show that the greatest number occurred when the Atlantic water layer was deep. Thus the present material supports the view of Ruud (1929) and Størmer

(1929) that *M. lucens* has in the Norwegian Sea its main distribution in water of Atlantic origin.

In the North Sea *M. lucens* has been found to be a valuable indicator of water of Atlantic origin (Rae and Rees 1947). The species drifts into the North Sea in the autumn and winter. According to Rae (1951) something similar may occur in the Norwegian Sea. He found that in the material collected with the continuous plankton recorder between Bergen and station M in 1950 *M. lucens* did not make its appearance before late autumn. The specimens caught in January/February/March were deemed to belong to the population which had come in in the previous autumn. The present material shows that *M. lucens* was in 1949 present during the whole year. In the summer, however, the stock was very small, being found mostly below 100 m. If the distribution was similar in 1950, it may be understood why *M. lucens* was not caught in the continuous plankton recorder.

Adult males and females were caught at all depths. Table 27 shows the vertical distribution from 2000 m. to surface.

Table 27.

Metridia lucens.

The vertical distribution of males and females.

	VI ♂		VI ♀	
Depth in m.	Number	%	Number	%
50—0	11	0.6	66	1.2
100—50	27	1.5	235	4.4
600—100	1175	62.2	4910	86.1
1000—600	675	35.7	415	7.3
2000—1000			57	1.0

The males were taken at relatively greater depths than the females.

Of the total number of adults counted, 25 % were males and 75 % females. As appears from fig. 22, adult males and females were most numerous in April/May and August/September, while stages IV and V dominated the population during the winter.

A few copepodites stages I, II and II of M. lucens were caught in June and July, but they were more numerous in the autumn hauls. Spawning may have occurred in early summer, but as no increase in the number of the older stages was observed during the summer it must have been restricted, or the brood may not have survived the summer.

A slight augmentation of the stock (mainly adults) was noticeable in the autumn. These individuals in older stages of development were probably immigrants from a spawning centre in a more southerly area.

Some copepodites stages I, II and III were also present in the autumn, and it may be inferred therefore that spawning actually took place in the vicinity of station M.

On the basis of the above observations it seems safe to conclude that the local stock of *M. lucens* in this area almost dies out in the course of the winter. Some spawning may occur in May and in August/September; the autumn increase of the stock depends mainly on an influx from other spawning centres in more southerly waters.

Pleuromamma robusta (Dahl).

Along the Norwegian coast this Atlantic copepod has been encountered as far north as the Barents Sea (Manteufel 1941). At station M it was found the whole year in hauls from 600—100 m., but only once in a 100—50 m. haul and in 11 out of 40 hauls from 1000—600 m. It was most abundant in February, March and April, when several young copepodites were also present. At the other seasons of the year the specimens caught were mostly adults (of the total number, 106 were adult males, 546 adult females, and 255 copepodites).

Table 28.
Pleuromamma robusta:
Monthly numbers and frequencies of occurrence at the different depths.

Depth in m.	Month	O	N	D	J	F	M	A
100—50	Number ..						1	
	Frequency .	0/4	0/2	0/3	0/1	0/4	1/3	0/4
600—100	Number ..	15	11	33	29	117	123	145
	Frequency .	2/2	3/3	3/3	1/1	4/4	3/3	4/4
1 000—600	Number ..			3		132	90	16
	Frequency .		0/3	1/3	0/1	4/4	1/2	2/4

(Continued)		M	J	J	A	S	O	N
100—50	Number ..							
	Frequency .	0/3	0/5	0/4	0/4	0/3	0/1	0/1
600—100	Number ..	21	82	27	11	20	9	16
	Frequency .	3/3	5/5	5/5	4/4	2/2	1/1	1/1
1 000—600	Number ..	1		1	1			
	Frequency .	1/3	0/4	1/5	1/5	0/4	0/1	0/1

Centropages typicus Krøyer.

This species is usually regarded as a typically temperate form, and the northern limit of its common occurrence is probably the Faroe-Shetland Channel (Jespersen 1940).

A single specimen was taken in June at station M, but apart from this it was only recorded as present in the period October to December 1948. In all cases it was taken above 100 m. In the autumn of 1949 it was absent from the hauls, implying that it is only occasionally that it penetrates so far into the Norwegian Sea as Lat. 66° N.

Heterorhabdus norvegicus (Boeck).

A single specimen of this species was taken in a haul from the 50—0 m. layer. Apart from this it was only observed in hauls from depths exceeding 100 m., most frequently in the 600—100 m. layer (in 31 out of 41 hauls).

Lucicutia longicornis (Giesbrecht); *Lucicutia* sp.

A male of the genus *Lucicutia,* which must probably be assigned to the warm-water species *L. longicornis,* was found in a haul from 600—100 m. in February. Two females, total length 4.40 mm (2.96 + 1.44) of same genus were caught in a haul from 2000—1000 m. in August and September.

Augaptilus glacialis G. O. Sars.

A single male of this arctic-boreal copepod was taken in a 2000—1000 m. haul in February.

Candacia armata (Boeck).

When found in the North Sea this species is regarded as an indicator of water of Atlantic origin (Rae and Rees 1947). At station M one male was recorded in a haul from 600—100 m. in February. The species has previously been observed as far north as the Barents Sea (Manteufel 1941).

Anomalocera patersoni Templeton.

This surface form was found in a vertical haul from 50—0 m. in October. In the evening of the same day this copepod was observed swarming about in the surface water, and a surface haul was found to contain almost exclusively this species, and some *Thysanoessa longicaudata.*

Acartia clausi Giesbrecht.

At station M this species made a similar seasonal appearance as *Paracalanus parvus*. From October to April it was taken in every haul from the uppermost 100 m., and after the middle of November and until March it was also present in the 600—100 m. hauls. From April to August it was recorded only 4 times in hauls from 50—0 m., but otherwise it was invariable present at this depth.

Table 29.
Acartia clausi:
Monthly numbers and frequencies of occurrence at the different depths.

Depth in m.	Month	O	N	D	J	F	M	A
50—0	Number ..	2526	690	245	15	14	15	1
	Frequency .	4/4	2/2	3/3	1/1	4/4	3/3	1/4
100—50	Number ..	1112	348	312	25	34	40	
	Frequency .	4/4	2/2	3/3	1/1	4/4	3/3	0/4
600—100	Number ..		220	142	30	175	160	
	Frequency .	0/2	2/3	3/3	1/1	4/4	2/3	0/4
(Continued)		M	J	J	A	S	O	N
50—0	Number ..		2250	175	20	411	10	50
	Frequency .	0/3	1/5	1/4	1/4	3/3	1/1	1/1
100—50	Number ..							4
	Frequency .	0/3	0/5	0/4	0/4	0/3	0/1	1/1
600—100	Number ..							
	Frequency .	0/3	0/5	0/5	0/4	0/2	0/1	0/1

Oithona similis Claus.

This was one of the commonest copepods at station M, only *Calanus finmarchicus* and *Pseudocalanus minutus* being caught in larger number (see table 4).

Fig. 23 gives the numbers of *Oithona similis* taken in the hauls at various depths. The majority were caught above 50 m. and the species must be said to be a true inhabitant of the surface layers. No less than 55 % of the total number were taken in the 50—0 m. hauls, and only 5 % from depths below 1000 m.

In March, April and May *O. similis* practically disappeared from depths below 600 m. How far the increase of the stock in the uppermost

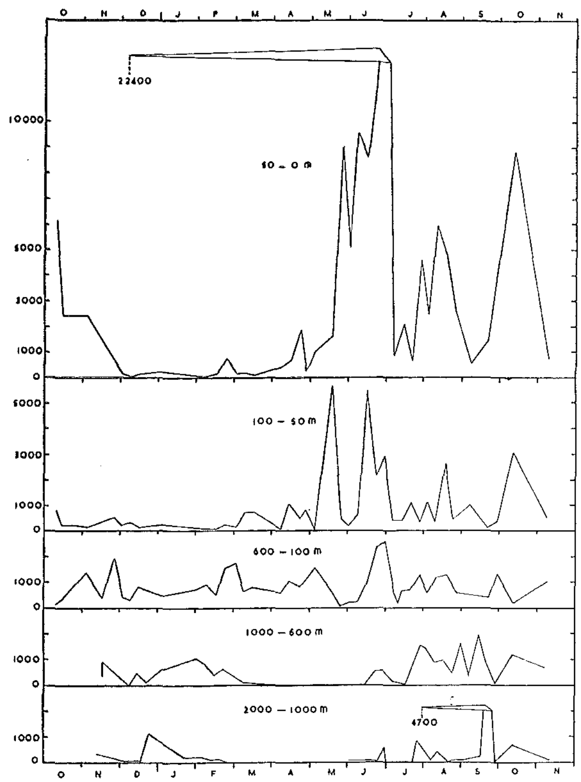

Fig. 23. Total numbers per haul of *Oithona similis.*

600 m. in the spring and summer was due to spawning and vertical migration is impossible to determine, as in the counting of the material the different stages of development have not been distinguished.

Oithona spinirostris Claus.

This species was not nearly as numerous as *O. similis*. The numbers of *O. spinirostris* in the different hauls are shown in fig. 24. It was taken

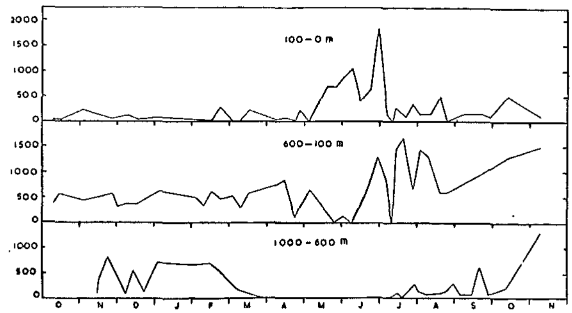

Fig. 24. Total numbers per haul of *Oithona spinirostris.*

regularly in hauls from 600—100 m., but in hauls from other depths it was on several occasions entirely absent.

Of this species 55 % were captured in the 600—100 m. hauls. The vertical distribution agrees with what has previously been noted in the southern Norwegian Sea (Farran 1911, Størmer 1929, Ruud 1929).

Oncaea borealis G. O. Sars.

This species was encountered at all depths, but in any large number only below 600 m. The number of specimens taken in the hauls at various depths will be seen from fig. 25.

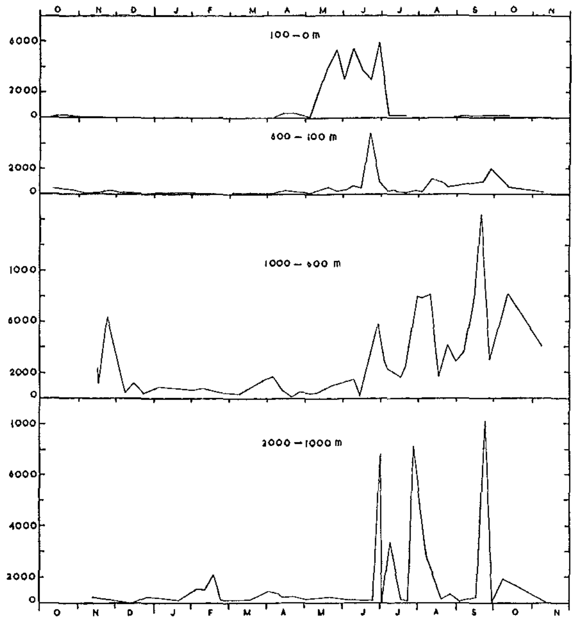

Fig. 25. Total numbers per haul of *Oncea borealis*.

About 80 % were taken in depths below 600 m., which is in agreement with earlier observations, showing that *O. borealis* mainly occur in the cold bottom water (Størmer 1929 and Jespersen 1934). In the hauls above 100 m. it was found in relatively large number only in May and June, while the maximum occurrence in the deeper layers was in the autumn.

Oncaea conifera Giesbrecht; *Microsetella norvegica* (Boeck).

Occasional specimens of these species were met with in the hauls, *O. conifera* exclusively below 100 m., while *M. norvegica* was commonest in the surface layers.

Parathalesthris croni (Krøyer) (Syn: *Halithalestris croni* (Krøyer)); *Clytemnestra rostrata* (Brady).

Single specimens of these Atlantic copepods were found in hauls from 600—100 m. in October and March respectively. *Glytemnestra rostrata* has not previously been reported from the Norwegian Sea.

Isopoda

A few specimens of parisitic isopoda were collected at station M. Except for a single specimen of *Notophryxus lateralis* G. O. Sars, they have not been identified more precisely.

Nothophryxus lateralis was found in a haul from 2000—1000 m. Of larger crustacea, 10 specimens of *Thysanoessa longicaudata* were taken in the same haul.

Ostracoda

Three species of the genus *Conchoecia* have been identified in the present material: *C. elegans* G. O. Sars, *C. borealis* G. O. Sars, and *C. obtusata* G. O. Sars. The identification was not effected at the time of counting. Gran (1902) states that these species have almost the same vertical distribution in the Norwegian Sea, where they are characteristic forms of the intermediate deep sea fauna. The monthly numbers and frequency of occurrence of *Conchoecia* spp. are shown in table 30. From this it will be seen that they were taken in nearly every haul from depths below 100 m.

Table 30.
Conchoecia spp:
Monthly numbers and frequencies of occurrence at the different depths.

Depth in m.	Month	O	N	D	J	F	M	A
50—0	Number ..					4	1	
	Frequency .	0/4	0/2	0/3	0/1	1/4	1/3	0/4
100—50	Number ..			31	1			
	Frequency .	0/4	0/2	2/3	1/1	0/4	0/3	0/4
600—100	Number ..	240	670	530	210	390	300	6
	Frequency .	2/2	3/3	3/3	1/1	4/4	3/3	3/4
1 000—600	Number ..		125	260	12	318	750	1345
	Frequency .		3/3	3/3	1/1	4/4	2/2	4/4
2 000—1 000	Number ..		320	430	300	1175	1	621
	Frequency .		1/1	3/3	1/1	4/4	1/1	5/5

(Table 30 continued)		M	J	J	A	S	O	N
50—0	Number ..							
	Frequency .	0/3	0/5	0/4	0/4	0/3	0/1	0/1
100—50	Number ..	11						
	Frequency .	2/3	0/5	0/4	0/4	0/3	0/1	0/1
600—100	Number ..	37	302	41	350	150	40	100
	Frequency .	3/3	5/5	4/5	4/4	2/2	1/1	1/1
1 000—600	Number ..	1210	800	1200	760	1300	200	1
	Frequency .	3/3	4/4	5/5	5/5	4/4	1/1	1/1
2 000—1 000	Number ..	92	505	768	735	850	450	175
	Frequency .	1/1	5/5	5/5	4/4	4/4	1/1	1/1

Amphipoda

Themisto abyssorum (Boeck).

This was the most frequent amphipod at station M. Gran (1902) regards *T. abyssorum* as an oceanic boreo-arctic species and states that it occurs in the Norwegian Sea mainly in water layers of Arctic origin. At station M. it was a characteristic inhabitant of water layers between 1000 and 100 m., with the maximum occurrence below 600 m. In hauls from the uppermost 100 m. adult specimens were extremely rare, and juveniles were found only in the summer. (Table 31.)

Ovigerous females were taken on a few occasions in February (2000—1000 m.), in March and May (1000—600 m.), and in April (600—100 m.). Larvae were most frequent in April, May and June, indicating that spawning occurred in spring or early summer, possibly in connection with an annual vertical migration.

Cyclocaris guilelmi Chevreux.

Gran (1902) found that this amphipod was a true member of the deep water fauna of the Norwegian Sea, and on the basis of this called the deepest region «the Cyclocaris region». The present material evidently supports this view. *Cyclocaris* was taken in all hauls from the 2000—1000 m. level, and was never recorded as present above 600 m. According to Sars (1900) it has been captured in the Arctic in hauls using 100—130 m. wire. He regards it as sub-pelagic in habits, at times descending to very great depths.

Other amphipods.

At station M several species of amphipods were noted in hauls from depths below 600 m. Each species was represented by only a few indivi-

Table 31.
Themisto abyssorum:
Monthly numbers and frequencies of occurrence at the different depths.

Depth in m.	Month	O	N	D	J	F	M	A
50—0	Number ..							12
	Frequency .	0/4	0/2	0/3	0/1	0/4	0/3	3/4
100—50	Number ..							70
	Frequency .	0/4	0/2	0/3	0/1	0/4	0/3	2/4
600—100	Number ..	47	15	19	3	7	14	22
	Frequency .	2/2	3/3	3/3	1/1	2/4	3/3	3/4
1 000—600	Number ..		55	14	8	31	11	16
	Frequency .		3/3	3/3	1/1	4/4	2/2	3/4
2 000—1 000	Number ..			7		13		1
	Frequency .		0/1	3/3	0/1	4/4	0/1	1/5
(Continued)		M	J	J	A	S	O	N
50—0	Number ..	150	280				2	
	Frequency .	1/3	5/5	0/4	0/4	0/3	1/1	0/1
100—50	Number ..	109	190	12				
	Frequency .	2/3	5/5	4/4	0/4	0/3	0/1	0/1
600—100	Number ..	8	21	2	76	12	21	5
	Frequency .	3/3	4/5	4/5	4/4	2/2	1/1	1/1
1 000—600	Number ..	9	8	69	94	73	10	5
	Frequency .	3/3	2/4	5/5	5/5	3/3	1/1	1/1
2 000—1 000	Number ..		14	19	29	40	16	4
	Frequency .	0/1	5/5	3/5	4/4	4/4	1/1	1/1

duals. The following have been identified: *Themisto compressa f. bispinosa* (Boeck), *Themisto compressa f. compressa* (Goes), *Hyperia galba* (Montague), *Hyperia medusarum* (Müller), *Hyperoche medusarum* (Krøyer), *Scina borealis* G. O. Sars, *Scina* sp., *Cyphocaris bouvieri* Chev., *Lanceola clausi* Bovallius, *Calliosoma* sp. (Table 3.)

Mysidacea

Boremysis arctica (Krøyer).

A single specimen was obtained in a haul from 2000—1000 m.

Euphausiacea

Meganycthiphanes norvegica (M. Sars).

According to Einarsson (1945) the chief center of abundance of

Table 32.

Meganyctiphanes norvegica:

Monthly numbers and frequencies of occurrence at the different depths.

Depth in m.	Month	O	N	D	J	F	M	A
50—0	Number ..							
	Frequency .	0/4	0/2	0/3	0/1	0/4	0/3	0/4
100—50	Number ..						1	1
	Frequency .	0/4	0/2	0/3	0/1	0/4	1/3	1/4
600—100	Number ..	35	24	6	7	15	33	18
	Frequency .	2/2	3/3	3/3	1/1	4/4	3/3	4/4
1 000—600	Number ..		9	4	9	65	29	10
	Frequency .		3/3	3/3	1/1	4/4	1/2	2/4
2 000—1 000	Number ..					2		
	Frequency .		0/1	0/3	0/1	1/4	0/1	0/5
(Continued)		M	J	J	A	S	O	N
50—0	Number ..		200					
	Frequency .	0/3	2/5	0/4	0/4	0/3	0/1	0/1
100—50	Number ..		60	30				
	Frequency .	0/3	2/5	1/4	0/4	0/3	0/1	0/1
600—100	Number ..	7	23	25	16	2	8	4
	Frequency .	3/3	4/5	5/5	4/4	1/2	1/1	1/1
1 000—600	Number ..			1		2		
	Frequency .	0/3	0/4	1/5	0/5	1/4	0/1	0/1
2 000—1 000	Number ..		4			3		
	Frequency .	0/1	1/5	0/5	0/4	1/4	0/1	0/1

M. norvegica in the Norwegian Sea lies south of latitude 65° N., and follows the slope of the Norwegian coast. From this area the larvae are carried northwards by the currents during the summer.

As will be seen from the table, *M. norvegica* was taken only in small number and most frequently in hauls from 600—100 m. In these it occurred regularly. In layers above 100 m. it was caught only in the spring and summer, and then almost exclusively as juveniles.

Although *M. norvegica* was encountered at all depths it appears from the present material that its chief resort is the deep Atlantic and transitional water layers. It should be noted, however, that the reason why adult specimens have been caught only occasionally in the layer above 100 m. may be that they have a tendency to escape the plankton nets in the daytime.

Table 33.

Thysanoessa longicaudata:

Monthly numbers and frequencies of occurrence at the different depths.

Depth in m.	Month	O	N	D	J	F	M	A
50—0	Number ..	7	3	2		1	2	
	Frequency .	2/4	1/2	2/3	0/1	1/4	1/3	0/4
100—50	Number ..	3	1					
	Frequency .	1/4	1/2	0/3	0/1	0/4	0/3	0/4
600—100	Number ..	36	17	12	5	28	53	6
	Frequency .	2/2	3/3	3/3	1/1	3/4	2/3	3/4
1 000—600	Number ..		135	34	21	216	58	
	Frequency .		3/3	3/3	1/1	4/4	1/2	0/4
2 000—1 000	Number ..		9	59	27	22		
	Frequency .		1/1	3/3	1/1	4/4	0/1	0/5
(Continued)		M	J	J	A	S	O	N
50—0	Number ..		190	7				
	Frequency .	0/3	3/5	3/4	0/4	0/3	0/1	0/1
100—50	Number ..		86	20	19	1		
	Frequency .	0/3	4/5	3/4	2/4	1/3	0/1	0/1
600—100	Number ..	2	7	22	9	4	9	9
	Frequency .	2/3	2/5	3/5	3/4	2/2	1/1	1/1
1 000—600	Number ..			1	3	37	27	31
	Frequency .	0/3	0/4	1/5	1/5	4/4	1/1	1/1
2 000—1 000	Number ..					17	5	9
	Frequency .	0/1	0/5	0/5	0/4	2/4	1/1	1/1

Thysanoessa longicaudata (Krøyer).

This species occurred regularly in the hauls from depths below 600 m. in the period November—March, but from then onwards to August it was almost entirely absent from hauls below 600 m.

According to Einarsson (1945) this species probably makes an annual vertical migration, which may be the reason why it was encountered in layers below 600 m. only in the winter. It is strange, however, that no increase in the numbers recorded in the upper layers during the spring was observed. It may be that the adult specimens escape the plankton net when hauled through the surface layers.

Eggs of euphausidae, which must probably be assigned to *T. longicaudata,* were taken in small numbers in the uppermost 100 m. during April, May and June.

Thysanoessa inermis (Krøyer).

This species was found only occasionally at station M. A total of 46 individuals were taken in 7 hauls, all from depths below 100 m. The largest catch was 26, in a haul from 1000—600 m. in March.

According to Einarsson (1945) the spawning of this species is chiefly cinfined to the coastal banks, but adults and larvae may be carried far from the coast by currents, and they are sometimes caught in great numbers in the open Norwegian Sea. The present material confirms that it must be regarded as an immigrant to the plankton fauna at station M.

Other euphausidae.

Single specimens of the following species were taken in hauls from 600—100 m. in March and July: *Euphausia krohnii* (Brandt), *Nematoscelis megalops* G. O. Sars, and *Nematobrachion boopis* Calman. According to Einarsson (1945) they must be regarded as southern visitors in the northern parts of the Atlantic.

Decapoda

Hymenodora glacialis (Buchholtz).

This large decapod was frequently caught, but only in small number, in hauls from 2000—1000 m., less frequently in hauls from 1000—600 m., and never above 600 m. A total of 164 specimens were counted in 48 hauls. In Arctic waters it may be found at the surface (Sars 1900). Ovigerous females were sometimes encountered in May and June.

Sergestes arcticus Krøyer.

A single specimen of this species was taken in a haul from 1000—600 m. in March.

Galathea rugosa (Fabricius).

Two larvae of this species were found in a sample from 100—50 m. in July and August.

Copelata

Oikopleura spp.

The copelata of the genus *Oikopleura* have not been identified to species. As appears from table 34, they were caught at all depths, but only in small number below 600 m. The largest occurrence was in the summer.

Frittilaria borealis acuta Lohmann.

This species was found in a few hauls from layers above 600 m. in October 1948 and November 1949.

Table 34.

Oikopleura spp:

Monthly numbers and frequencies of occurrence at the different depths.

Depth in m.	Month	O	N	D	J	F	M	A
50—0	Number ..	80		1				380
	Frequency .	1/4	0/2	1/3	0/1	0/4	0/3	4/4
100—50	Number ..		1	4			2	154
	Frequency .	0/4	1/2	1/3	0/1	0/4	1/3	4/4
600—100	Number ..							575
	Frequency .	0/2	0/3	0/3	0/1	0/4	0/3	4/4
1 000—600	Number ..							
	Frequency .		0/3	0/3	0/1	0/4	0/2	0/4
2 000—1 000	Number ..							
	Frequency .		0/1	0/3	0/1	0/4	0/1	0/5
(Continued)		M	J	J	A	S	O	N
50—0	Number ..	200	2000	650	20	200		20
	Frequency .	2/3	5/5	1/4	1/4	2/3	0/1	1/1
100—50	Number ..	80	945	23	4			20
	Frequency .	2/3	4/5	3/4	2/4	0/3	0/1	1/1
600—100	Number ..	77	303		312	51		250
	Frequency .	2/3	2/5	0/5	4/4	2/2	0/1	1/1
1 000—600	Number ..		26	10	5	2		
	Frequency .	0/3	2/4	3/5	3/5	1/4	0/1	0/1
2 000—1 000	Number ..		33	54	123	124	2	
	Frequency .	0/1	2/5	2/5	3/4	3/4	1/1	0/1

Thaliacea

Salpa fusiformis Cuvier.

Thaliacea were not encountered in vertical hauls at station M in the period 1948—1949, but a single specimen of the Atlantic form, *Salpa fusiformis,* was observed at the surface on October 14, 1948.

According to Fraser (1950) this species was present in the Scotch plankton collections in July and August 1949, after complete absence since 1939. Rae (1951) reports that swarms of Thaliacea were recorded by the continuous recorder between Bergen and station M in October 1950. About the same time it was reported by Wiborg (1954) as present in vertical hauls at station M.

Pisces

Myctophum glaciale Reinh.

Adults and larvae of this species were occasionally met with in hauls from the uppermost 600 m.

Paraliparis bathybii Collet.

A single specimen of this deep sea fish was taken in a haul from 2000—1000 m.

VII. Summary.

1. At station M (66° N, 2° E) in the Norwegian Sea zooplankton was collected in the period October 1948 to November 1949. The collection was effected by means of a Nansen closing-net, 70 cm in diameter, made of silk nos. 0 and 8. Five consecutive vertical hauls were taken weekly (except in stormy weather) through the following water columns: 50—0 m., 100—50 m., 600—100 m., 1000—600 and 2000 (or bottom)—1000 m. The samples were preserved in 4 % formalin. 205 samples have been subjected to full analysis. For purposes of analysis the samples were devided by a Lea plankton divider into fractions.

2. Station M is located on the western border of the Atlantic current in the central part of the great cyclonic system of the southern Norwegian Sea. In the Norwegian Sea, water masses which have salinities of 35.00 ‰ or more are deemed to be of Atlantic origin. At station M 35.00 ‰ salinity was found to correspond to a temperature of 3—4° C. (Mosby 1950), and this temperature, representing the lower limit of Atlantic water, is as a rule found at depths of about 300—400 m. Below the Atlantic water and down to about 1000 m. are layers of mixed Atlantic and Arctic water. Below 1000 m. is found the characteristic bottom water of the Norwegian Sea, with a temperature of — 1.0—0° C. and a very uniform salinity of 34.92 ‰.

3. Copepods predominated in the fauna. A total of 55 species were identified. Of these, 13 occurred at all depths, among them the following 9 being the most abundant: *Calanus finmarchicus, Calanus hyperboreus, Pseudocalanus minutus, Microcalanus, Metridia longa, Metridia lucens, Oithona similis, Oithona spinirostris* and *Oncaea borealis*. In respect of number *Calanus finmarchicus* and *Pseudocalanus minutus* were by far the most important. Of the total number of copepods in all the hauls these two species formed about 58 %, namely *C. finmarchicus* 36 % and *P. minutus* 22 %.

4. In the vertical distribution of the species it is possible to distinguish (a) plankton of the surface layers, (b) plankton of the intermediate depths, corresponding to the deep layers of Atlantic water and the transi-

tional layers of mixed origin, and (c) plankton of the deep water. In each division there is found a characteristic fauna with species which are regularly present and others which only occur as varying members of the plankton fauna. The seasonal variation in the composition of the fauna at the different depths is given in fig. 6, which shows the monthly average frequencies of certain species and groups of species. In the plankton fauna of the surface layers it is possible to distinguish four seasonal occurrences. In the winter period (December to March, inclusive) the plankton fauna was quantitatively poor. The spring period (April to medio June) was characterized by the spawning of the autochtonous species *Calanus finmarchicus* and *Pseudocalanus minutus*. In the summer (medio June to medio August) the main stock of *C. finmarchicus* and *P. minutus* left the surface layers for hibernation in deep waters. In the autumn period, extending from medio August to December, species which have their main distribution in more southerly waters drifted into the area.

The seasonal variation in the fauna of the intermediate depths and the deep water is mainly due to the annual vertical migration of *C. finmarchicus* and *P. minutus*. When these species emigrated from the deep layers in the spring, the composition of the plankton population was substantially changed, until the descent of new generations of the two species restored the previous situation.

5. The annual vertical migration and its significance in the life history of *C. finmarchicus, C. hyperboreus* and *P. minutus* are demonstrated and discussed. In winter the stock of *C. finmarchicus* consisted chiefly of stages IV and V, the majority of the population being found below 600 m. The vertical migration to the surface layers commenced in February/March and all stages present in the stock took part in this movement. Moulting from stage V to sexually mature males and females occurred during and after the migration. The spring spawning took place in April/May, and a second spawning (of minor importance in 1949) occurred in August/September. The majority of the spring-spawned generation, after reaching stages IV and V, descended to deeper layers as early as June/July, thus having a life-cycle of a full year.

In the case of *Calanus hyperboreus* the ascent from water layers below 1000 m. commenced medio March and was completed by the end of April, but only part of the stock migrated to the surface layers. All stages present (III, IV, V and VI) took part in the upward movement. Spawning probably occurred in April. In August practically the entire stock was found below 1000 m. again.

In the case of *Pseudocalanus minutus* the bulk of the stock hibernated below 600 m. Ascent commenced in March and was concluded medio April. From then on to the end of June the majority of the population was found above 50 m. In June/July the downward migration began and in

August practically the whole stock was found below 600 m. again. With this species the moulting from stage V to mature individuals occurred before or during the ascent. It had only one spawning period, in April/May, immediately after the upward movement.

The factors which govern the annual vertical migration are discussed. It is pointed out that neither ascending currents nor variations of temperature in this part of the Norwegian Sea are sufficient to explain the upward movement from depths between 1000 and 2000 m. It is concluded that light has some significance for the migration to the surface, but this relates to the final stages of an ascent which is probably initiated by internal factors to be sought in the sexual development.

6. Short remarks are made on the seasonal occurrence of the various species.

VIII. References.

(Abbreviations according to *World list of scientific periodicals published in the years 1900—1950.* 3rd ed. 1952.)

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