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ZOOPLANKTON IN RELATION TO HYDROGRAPHY IN THE NORWEGIAN SEA

By

KRISTIAN FREDRIK WIBORG

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A/S JOHN GRIEGS BOKTRYKKERI, BERGEN

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INTRODUCTION

The Norwegian Sea is a very interesting area both from a biological and hydrographical point of view. It is also of economic importance because of the very rich fisheries. SARS (1886) stated that there were large quantities of zooplankton on the coast banks of Norway bordering the Norwegian Sea, and an abundant life existed where cold arctic water met the temperate Atlantic water. GRAN (1902) made the first ecological study of the zooplankton in the Norwegian Sea. Later DAMAS (1905) investigated the copepods in the southern part. DAMAS & KOEFOED (1909) and STØRMER (1929) also published some data on zooplankton from the Norwegian Sea. From 1902 to 1908 the International Council for the Exploration of the Sea organized plankton investigations in the Norwegian Sea and other areas. The results were published in Bulletin Trimestriel (1910—1931). WITH (1915) reported on the copepods collected by the Ingolf expedition. RUUD (1932) discussed the plankton conditions of the whaling grounds and their relation to the ocean currents. ØSTVEDT (1955) investigated the zooplankton collected at weather station M throughout one year.

The present report is based mainly on zooplankton sampled during the cruises of vessels from the Norwegian Fishery Research Institute from 1948 to 1954. Samples taken by the meteorologists and crew of the Norwegian weather ships «Polarfront I» and «Polarfront II» at station M from 1950 to 1954 are also included.

I take this opportunity to express my sincere gratitude to the men who directed and participated in the cruises and took plankton samples, especially Messrs. DEVOLD, EGGVIN and RASMUSSEN. I am also in debt to Messrs. EGGVIN, MOSBY and RUUD who took the initiative in sampling plankton from the weather ships, and entrusted to me the material collected since 1950. To the chief meteorologists JORANGER, MADSEN, SKAAR and TØNNESSEN, and the officers and crew on board the weather ships I convey my warmest thanks for an enormous number of plankton samples, collected at all times of the year, both day and night. Finally I want to thank my assistent, Mrs. MEYER, who made a great number of measurements and prepared the drawings.

Bergen, July 1955. *Kristian Fredrik Wiborg.*

MATERIAL AND METHODS

The main part of the plankton samples was taken in vertical hauls with a Nansen net, silk No. 8, and 70 cm in diameter. During the cruises in the Norwegian Sea one haul from 200 m to the surface was usually taken at each station. In 1953 and 1954 some deep hauls were made in steps from 1000 m to the surface. The cruises were all during the summer and autumn; in 1948—1951 from the beginning of June to the end of August, in 1952—1954 from the last of May to the beginning of July

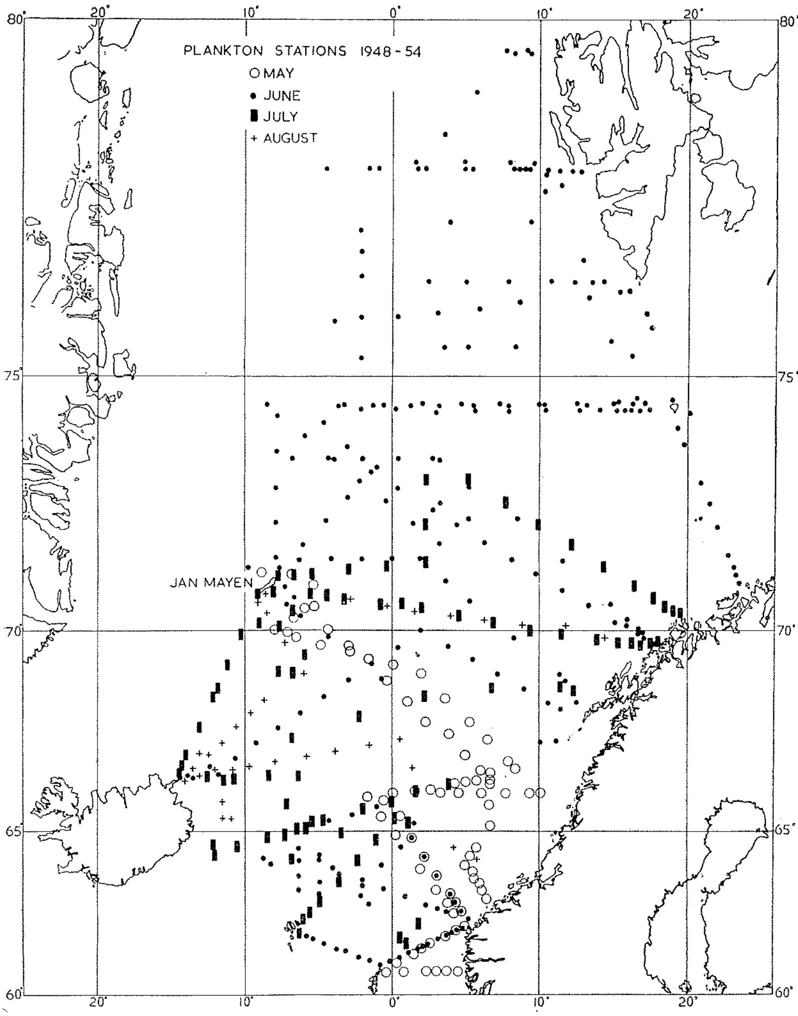

Fig. 1. Zooplankton stations 1948—1954.

(fig. 1). In 1953 a section of stations was taken in September off western Spitsbergen.

At station M, 66°N. lat., 02°E. long., a full station to 2000 m was usually worked each month, with hauls 2000—1000 m, 1000—600 m, 600—100 m, and 100—0 m. In addition, 100—0 m hauls were taken each week. From February 1953 through June 1954 the same program was also carried out at night. In addition, a haul 25—0 m and horizontal hauls with a one meter net (silk No. 0) were made once a week both day and night. The horizontal hauls were taken at the surface, lasting for half an hour at a speed of 2—3 knots. Sometimes the hauls were made while the ship lay drifting, the time then being extended to one hour. The hauls are therefore not strictly comparable. All the horizontal hauls have been adjusted to a one-hour tow.

All plankton samples were preserved in 3—5 % formalin.

Volume measurements were made by draining or displacement (Wiborg 1954). The copepods were measured using a Spencer microscope with an ocular micrometer. For *Calanus finmarchicus* and *C. hyperboreus* the enlargement used gave a scale unit of 0.097 mm, for *Pseudocalanus minutus, Metridia longa* and *M. lucens* 0.0513 mm, and for *Microcalanus pusillus, M. pygmaeus* and *Oncaea borealis* 0.0125 mm.

All measurements were taken on the metasome.

TOPOGRAPHY AND HYDROGRAPHY OF THE NORWEGIAN SEA

Helland-Hansen & Nansen (1909) based their monograph on the Norwegian Sea on the cruises of the «Michael Sars» in 1900—1904, and on observations by other workers. They defined the Norwegian Sea as the whole sea-area between Norway, the Shetland Islands, the Faroe Islands, Iceland, Greenland, Spitsbergen and Bear Island. The basin is bordered to the east, southeast and south by the Norwegian coast, the North Sea Plateau, The Faroe-Iceland ridge, the Iceland Plateau and the Iceland—Greenland ridge. The northern border is a possible ridge between Greenland and Spitsbergen. The Greenland Sea is considered a subdivision. It lies between Greenland north of 71 N. lat., Jan Mayen, and Spitsbergen.

The main currents were outlined (fig. 2). The direction of currents and water movements is greatly influenced by the bottom configuration. The main part of the water entering the Norwegian Sea from the south passes the Wyville-Thompson ridge, which has a mean depth of 470—500 m. The flow is northeastwards through the Faroe—Shetland Channel. Below 600 m is found very uniform bottom water of a salinity of 34.92—

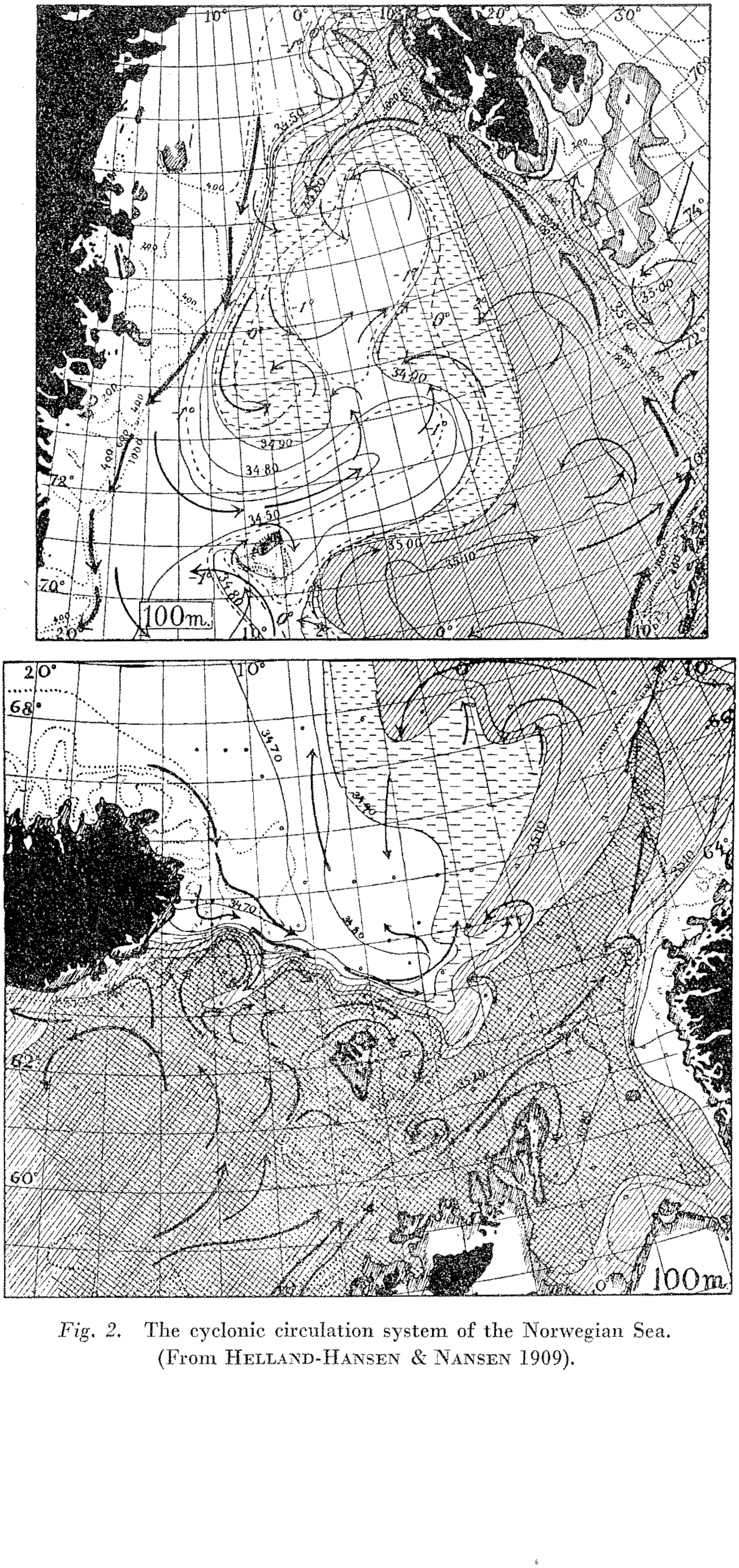

Fig. 2. The cyclonic circulation system of the Norwegian Sea.
(From HELLAND-HANSEN & NANSEN 1909).

34.94 per mille, and a temperature of — 0.94° to — 1.0°C. in the southeastern part. In the Greenland Sea the bottom water is colder than — 1.0°C. Warmer and more saline water of Atlantic origin lies on top of the bottom water. Atlantic water enters the Norwegian Sea through the Faroe-Shetland Channel and is carried northwards through the eastern part of the Norwegian Sea. A branch of the East Greenland arctic current, the East Iceland current, flows southeastwards between Iceland and Jan Mayen. The water has a low temperature and a salinity of 34.86—34.90 per mille.

A number of eddies border the Atlantic current on its way northwards, some of them stationary, such as the large cyclonic eddy in the southern Norwegian Sea. HELLAND-HANSEN & NANSEN also mentioned

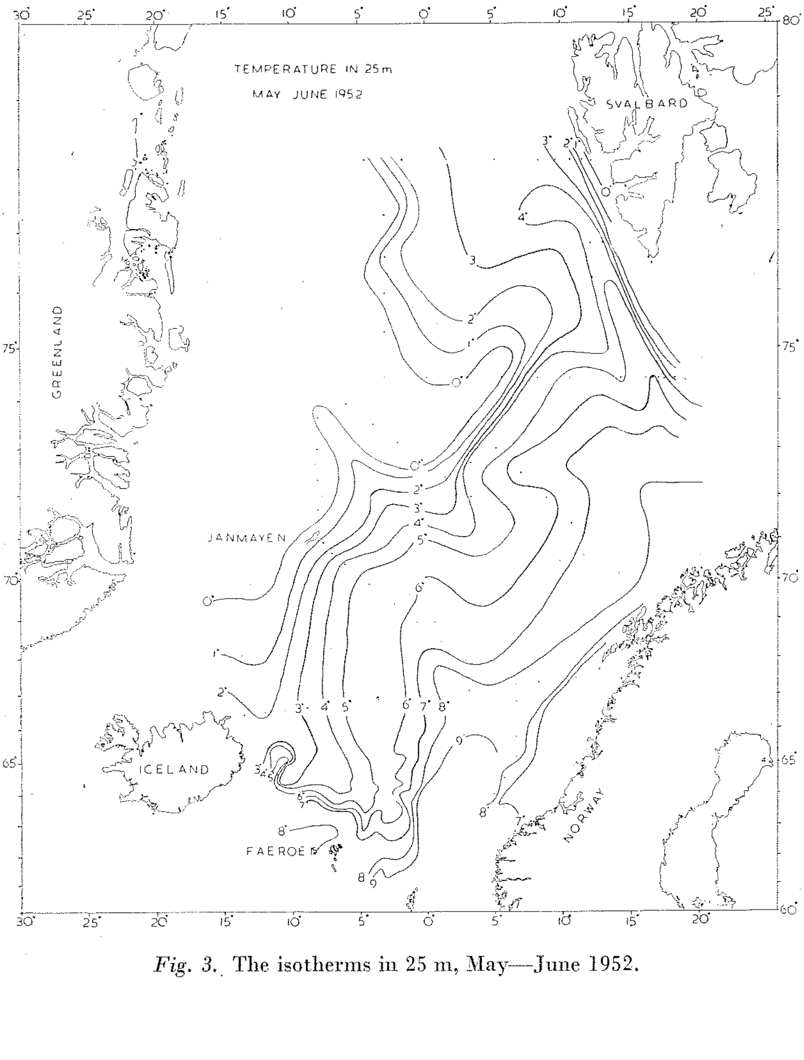

Fig. 3. The isotherms in 25 m, May—June 1952.

other areas with more or less stationary water; the boundary between the western side of the southern eddy and the East Iceland current, the axis of the cold current itself, and finally the area over the Faroe-Iceland ridge, on the boundary of the Norwegian Sea.

A branch of diluted Atlantic water runs westwards in the sea west of Spitsbergen, sinking under the polar water and forming an intermediate layer of warmer water in the Greenland Sea. This layer may to a certain extent also be supplied by minor branches of the North Atlantic current passing to the west immediately north and south of Jan Mayen. A large eddy of cold water is situated in the East Greenland current northwest of Jan Mayen, between 74° and 76° N. lat. In this area we have the so-called «Bay-Icebight» of the sealers.

HELLAND-HANSEN & NANSEN pointed out that there will be variations in the position of the currents and eddies from year to year.

Hydrographical observations were made in connection with the present investigation, and some are published (DEVOLD 1951, 1953, ØSTVEDT 1955). Some observations from station M and adjacent areas were treated (MOSBY 1950, HALLDAL 1953). The isotherms at 25 m during the summer of 1952 were traced (fig. 3). The cold tongue between Jan Mayen and Iceland is clearly evident. There is also a core of warmer water protruding into the cold area northeast of Jan Mayen. The East Iceland current was very conspicuous all the summers observations were made, except 1950, when a layer of at least 25 m of warm water covered the surface.

VOLUMETRIC DISTRIBUTION OF THE PLANKTON

The distribution of the zooplankton in the Norwegian Sea from 1948 to 1953 was plotted (fig. 4). As the material was not sufficient to give complete charts of distribution for each month, a more general picture of the distribution of plankton during the summer months has been given. When there was more than one observation from identical or neighbouring positions, the highest figure was used. The northern area, including the Greenland Sea, was only investigated during the first half of June.

The greatest concentrations of plankton are found where HELLAND-HANSEN & NANSEN stated that the water masses were more or less stationary, and in the border areas between warm and cold water. The large concentrations in the cold area are mainly *Calanus hyperboreus*, those in the warm area, with a few exceptions, *C. finmarchicus*.

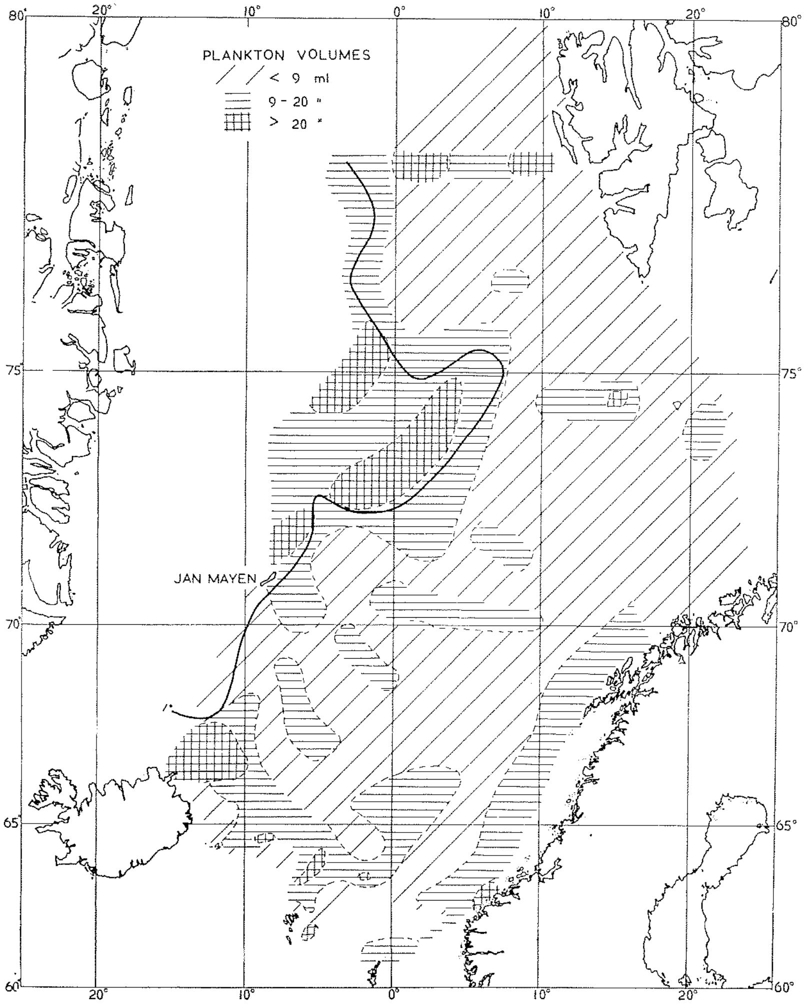

Fig. 4. The distribution of zooplankton 1948—53. Nansen net hauls.

In the southern Norwegian Sea the greatest quantities of plankton are usually found from the end of June to the beginning of August. In the Greenland Sea the maxima are assumed to occur later, probably in August. West of Bear Island, according to CORLETT (1953), there is maximum in dry weight of plankton over deep water from May to July, in shallow water in August. Hauls from the temperate part of the Norwegian Sea may therefore be regarded as fairly representative of the period of maximum abundance. A few vertical hauls in the upper 100 m off western Spitsbergen in September 1953 yielded only small quantities of plankton.

At the beginning of July 1949 the plankton was abundant between Jan Mayen and the northwestern coast of Norway. It consisted mainly of *Aglantha digitale*, except on the coast banks, where *Calanus finmarchicus* dominated. At the end of June *Aglantha* had nearly disappeared, except near the coast. In the northern cold area plankton was more abundant in June 1953.

The East Iceland current is quite rich in plankton, especially where cold water meets warmer currents and slope areas, as along the northern and northeastern shores of Iceland. In the central part of the southern Norwegian Sea there is little plankton. Gran (1902) found those areas very poor in plankton in summer and autumn, a fact he associated with the upwelling of water of Atlantic origin from deeper layers.

Ruud (1932) discussed the plankton conditions of different whaling grounds and their relation to the oceanic currents. In the Norwegian Sea whaling takes place along the slopes of the banks, where coastal water mixes with the North Atlantic current. Those places afford the largest supplies of euphausiids and copepods, and the abundance is due not only to production, but more to accumulation in backwaters. At Møre, on the west coast of Norway, there is a maximum in the catch of sei whales in April—May, coinciding with the spring maximum of *Calanus finmarchicus.* The whaling starts in coastal water where the food conditions are best, but in the course of the spring shifts to the border areas between the coastal water and the North Atlantic current, in those localities where the conditions favour the formation of backwaters and convergences with large accumulations of plankton. In Spitsbergen waters whales were once caught in the mixed layers between the cold coastal current and the warm North Atlantic current. Equally important whaling grounds were situated to the northwest of Prince Charles Foreland, where the polar water from the north forms a distinct backwater. In the areas of convergence along the edge of the ice between Spitsbergen and the Denmark Strait whalers used to catch the Greenland whales. In recent times whalers from Iceland hunted blue and fin whales there. These facts are in accord with the large concentrations of plankton in the border layers between cold and temperate water (p. 11).

Hjort (1902) studied bottlenose whaling in the Norwegian Sea. He delineated the most important areas of bottlenose whaling (fig. 5). It is clear that those areas are located where there is a maximum of plankton. This is still more apparent when a comparison is made with the quantitative distribution of the most important copepods, e.g. *Calanus finmarchicus* (fig. 18, p. 30).

In order to see to what extent the observations from the Norwegian Sea are representative for certain periods of the year, it is useful to

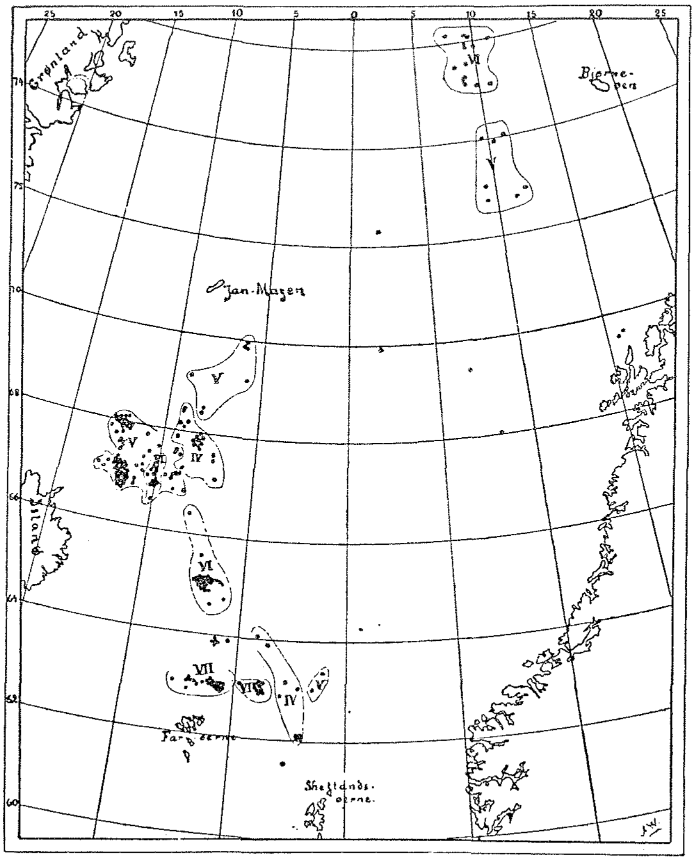

Fig. 5. Bottlenose grounds in the Norwegian Sea. (From Hjort 1902).

make a comparison with the yearly variations in plankton volume at station M. The variation of the monthly mean volumes of plankton in the upper 100 m was examined (fig. 6). In all years there was maximum volume in June, and in some years peaks in April, August and October. In 1950 the June volume was the highest, in 1953 the peak was in April. In the latter year vertical hauls in April were taken only during the night, and vertical migrations of the plankton may make this volume too great when compared with those of the other years.

It is debatable whether hauls taken during the day are representative of the quantity of plankton present. At station M, plankton hauls were taken alternately by day and night for more than one year. The variations in plankton volume in the upper 100 m and 25 m were examined (fig. 7). There was more plankton during the night than during the day in the upper 25 m, especially in April and in July. In the upper

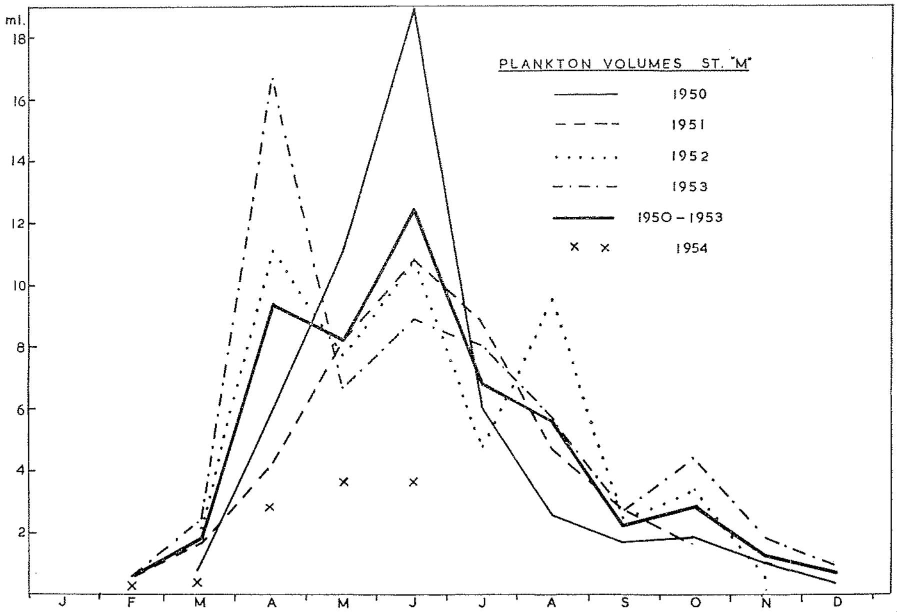

Fig. 6. Variations in plankton volume in the upper 100 m at station M in 1950—1954. Nansen net hauls, monthly mean figures.

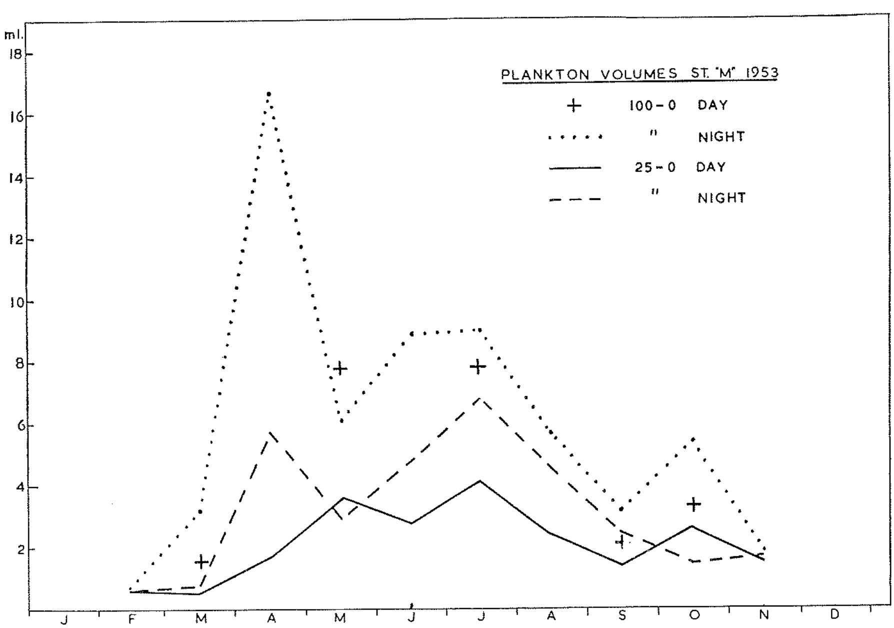

Fig. 7. Variation of plankton volumes in the upper 100 m, resp. 25 m, in day and night hauls at station M in 1953. Nansen net hauls, monthly mean figures.

100 m there was the same difference, but not so marked. As the plankton hauls during the cruises in the Norwegian Sea were usually taken from 200 m to the surface, vertical migration probably does not greatly influence the summer results.

There is, however, another problem. The larger organisms, especially the important euphausiids, usually avoid the ordinary plankton nets during the day. Euphausiids were usually taken singly. At station M,

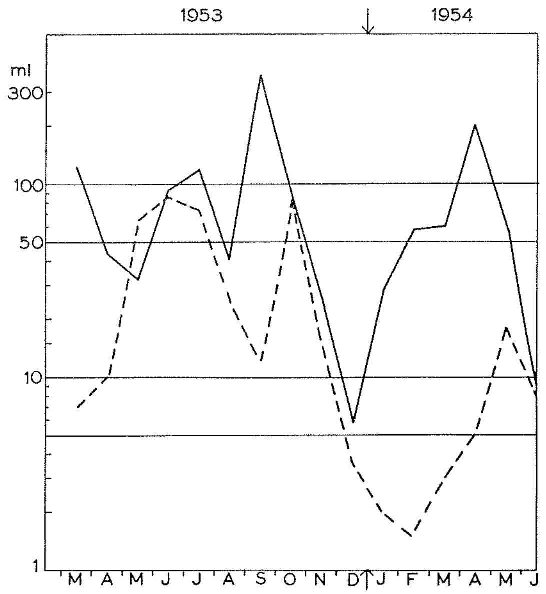

Fig. 8. Variation in plankton volume at day (broken line) and night (continuous line) in 1 hour's horizontal surface hauls with a meter net at station M in 1953—1954. Montly mean figures, and logarithmic scale.

Østvedt (1955) rarely got single adult specimens during the day. On the basis of hauls with the continuous plankton recorder, Henderson & Marshall (1944) and Glover (1952) stated that nearly all euphausiids in the Northeastern Atlantic and the North Sea had a diurnal vertical migration, being absent from the surface layers during the day. *Thysanoessa longicaudata* was the only species which occurred near the surface in daytime. One must be cautious in judging an area to be poor in zooplankton because vertical or horizontal hauls taken in daylight yield small quantities of plankton. There may possibly have been euphausiids present, which avoided the nets, or they have stayed in deeper layers.

In vertical hauls at station M, euphausiids were caught regularly in the upper 25 m and 100 m during the night, usually 2 to 10 specimens per haul, but occasionally as many as 30. *Meganyctiphanes norvegica* and *Thysanoessa inermis* were caught in almost equal numbers, but *T. longicaudata* was also taken. In May—July, only larval euphausiids were caught. In the horizontal hauls there was usually a striking difference between the day and night hauls, the latter yielding far greater volumes (fig. 8). This was often due to euphausiids taken in the night, especially during the first half of 1954. From May to August chiefly larval euphausiids were taken, and the difference in volume between the day and night hauls was not very great. The annual variation in volume was, with a few exceptions, similar to that of the vertical hauls, with peaks in June—July, and September—October.

Large shoals of euphausiids have repeatedly been observed at the surface during the night in the Norwegian Sea. Fishing boats have sailed for hours through enormous phosphorescent masses of these animals. Such shoals have also occasionally been observed during the day. On the fishing grounds of North Norway the saithe (*Gadus virens*) may chase the euphausiids so they leap above the surface. According to HJORT & RUUD (1929) large quantities of *T. inermis* were observed near Jan Mayen in August 1910.

PLANKTON REGIONS IN THE NORWEGIAN SEA

GRAN (1902) divided the Norwegian Sea horizontally and vertically into different plankton regions. In the upper 100 m he distinguished between the Asterionella-, Tripos- and Clio-regions (fig. 9). The Tripos-region included the warmest area, and was characterized by a number of species, the dominant ones being temperate-Atlantic-oceanic. They are present all the year round, with maxima in August—September. The indicator forms were *Ceratium tripos, Calanus helgolandicus, Metridia lucens, Oithona spinirostris* (GRAN: *O. plumifera*), and *Microsetella atlantica.* Boreal-oceanic forms were also found, mainly *Aglantha digitale, Calanus finmarchicus, Pseudocalanus minutus* (GRAN: *P. elongatus*), and *Oithona similis.* Neritic species and arctic-oceanic forms were also included, the latter not belonging to the region, but introduced either by vertical migrations from the deep or brought in by cold currents.

The Clio-region included the colder areas, characterized by the same plankton elements as the Tripos-region, but dominated by arctic and boreal-oceanic species, the leading forms being *Clione limacina* and *Limacina helicina* (GRAN: *Clio borealis* and *Limacina arctica*). The arctic areas could be separated as a subregion.

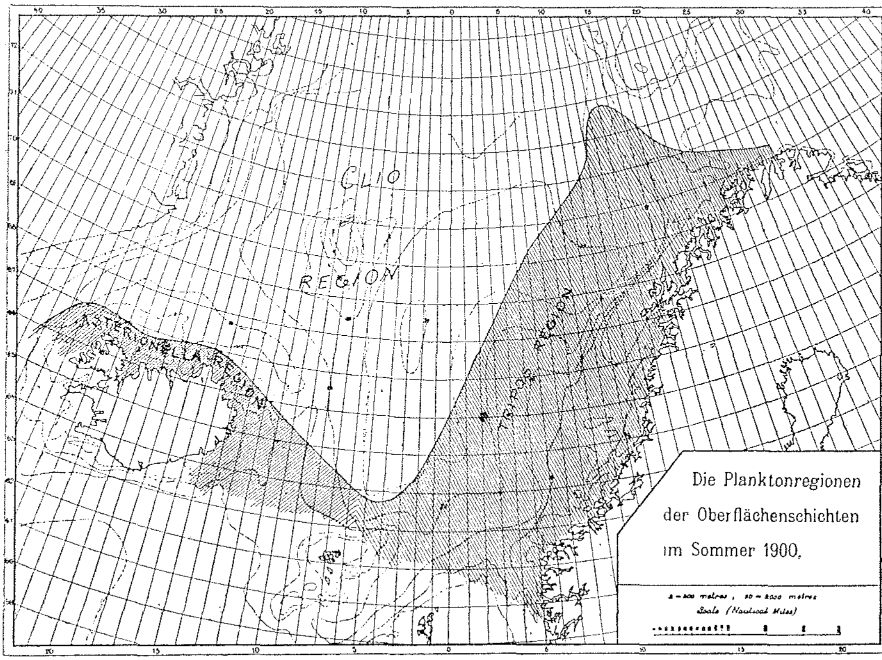

Fig. 9. Plankton regions in the Norwegian Sea. (From GRAN 1902).

The regions of the surface waters could not always be clearly distinguished from each other, and the borders might also change during the year. In the deeper waters GRAN named the upper layers above 0°C., including water of Atlantic origin, the Euchaeta-region, the cold bottom layers, the Cyclocaris-region.

GRAN considered the Norwegian Sea as a self-supporting area, distinct from the Polar and the Atlantic oceans in the composition and content of plankton, with a community of species of its own. *Calanus finmarchicus* was regarded as indigeneous to the area, but each year great numbers might be carried away into the Polar Ocean by the North Atlantic current.

DAMAS (1905) showed how *Calanus finmarchicus, C. hyperboreus* and *Pseudocalanus minutus* occurred mostly in different areas of the southern Norwegian Sea. HELLAND-HANSEN & NANSEN (1909) discussed DAMAS' results from a hydrographical view and related the occurrence of *Calanus hyperboreus* to the axis of cold arctic water (fig. 10, area 3), while *C. finmarchicus* was evidently stationary in mixed water of arctic and Atlantic origin (fig. 10, areas 2 and 4). *Pseudocalanus* was stationary in the central area, in water chiefly of Atlantic origin (fig. 10, area 1).

At station M, HALLDAL (1953) found that no influence could be traced from the area between Iceland and the Faroes (the Asterionellaregion of GRAN). However, the region to the northwest of station M (the Clio-region of GRAN) seemed to play a part in that the indicator species there, *Ceratium arcticum*, occurred at station M throughout the spring and into the summer (HALLDAL 1953, p. 33).

ØSTVEDT (1955) stated that there were great variations in the quantity and composition of the zooplankton in the upper 100 m at station M during the year. From May on the copepod stocks increased rapidly,

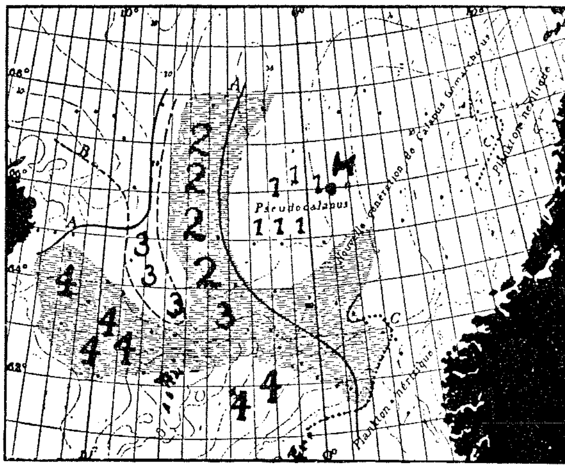

Fig. 10. The distribution of Calanidae in the southern Norwegian Sea according to DAMAS(1905, Pl. I), reconstructed by SØMME (1934). The numbers denote the areas where the different species abound. 1, *Pseudocalanus minutus* in water of Atlantic origin, 2 and 4, *Calanus finmarchicus* in mixed waters. 3, C. *hyperboreus* in arctic water. See also text.

reaching a maximum in the second half of June. *Calanus finmarchicus* and *Pseudocalanus minutus* were dominant, but *Oithona similis* was also numerous. *Sagitta* and *Eukrohnia* occasionally occurred in large numbers, while copepods and nauplii were almost completely absent from mid-June to mid-August.

On the basis of the present material an attempt is made to distinguish different plankton regions in the Norwegian Sea (fig. 11). One may broadly distinguish between a cold and a temperate area. The first includes the Greenland Sea (DAMAS & KOEFOED 1909) and can be roughly separated from the temperate area by the 1°C. isotherm at 25 m. This isotherm, based on hydrographical data from 1952, has been inserted in most of the charts. The cold area is characterized by great quantities of *Calanus hyperboreus*, but *Oithona similis* and *Oncaea borealis* are also

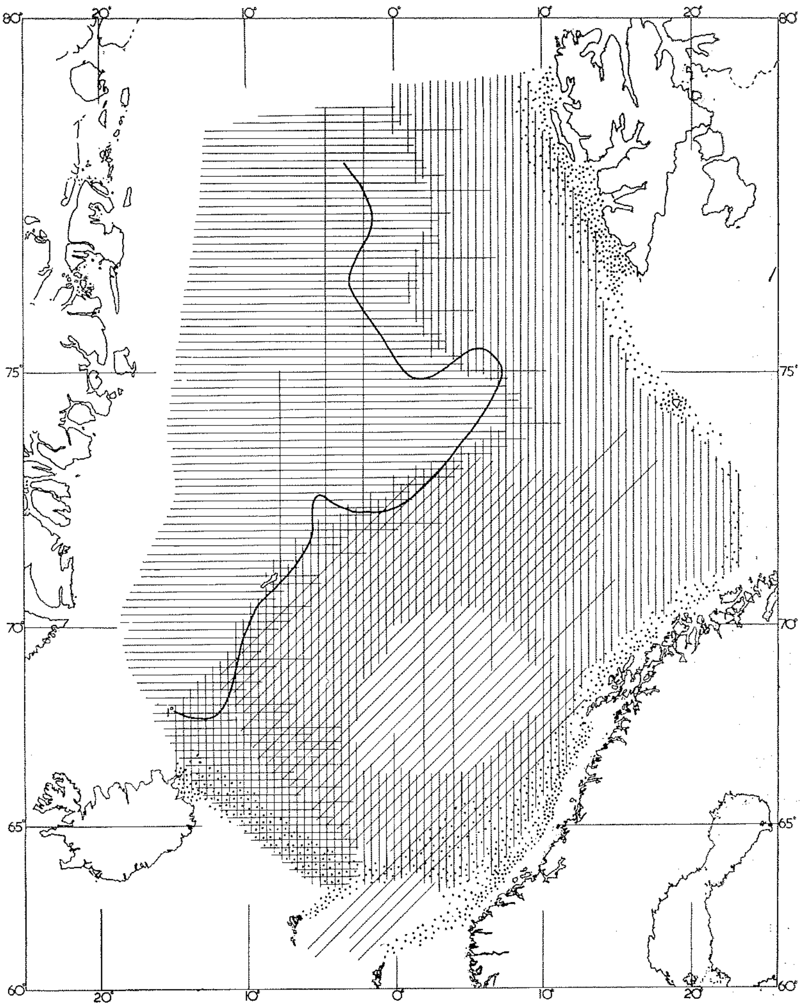

Fig. 11. Plankton regions in the Norwegian Sea. Horizontal hatching: arctic plankton. Vertical hatching: temperate water plankton. Oblique hatching: plankton of Atlantic origin. Dots: neritic plankton.

numerous, and *Pseudocalanus minutus* moderately abundant. These three copepods have their maxima of abundance in the border area along the 1°C. isotherm. Juvenile *Themisto abyssorum* and *Limacina helicina* also occur, the latter in large numbers. *Eukrohnia hamata* and *Metridia longa* are found regularly, while *Calanus finmarchicus* is scarce. It will be shown how the stocks of *Oncaea borealis, Pseudocalanus minutus* and *Calanus finmarchicus* are supplied from the temperate areas.

In the temperate part of the Norwegian Sea most of the observations have been made in the southern area. It is not easy to define the different plankton regions clearly, as the conditions are quite variable. The borders may change during the year, and also from one year to another. One may distinguish one or two regions, including the sea southeast of Jan Mayen, and the slope area from Northeast Iceland past the Faroe Islands. These areas are characterized in the same way as station M (ØSTVEDT 1955). In summer they are dominated by *Calanus finmarchicus, Pseudocalanus minutus, Oithona similis* and *Oncaea borealis,* also by *Sagitta elegans, Eukrohnia hamata,* and in the area around station M by *Aglantha digitale* and *Limacina retroversa.* The slope area includes the East Iceland current, which contains a fairly high number of *Calanus hyperboreus,* especially early in summer, when the other plankton species are scarce. Later in summer, however, the surface layers are warmed and a rich plankton is found over fairly large areas. It was shown by DAMAS (1905, Pl. I) that adult *Calanus finmarchicus* is abundant in the southeastern part of the cold tongue.

The central part of the southern Norwegian Sea is less rich in plankton than the surrounding areas. It is dominated by water from the North Atlantic current (HELLAND-HANSEN & NANSEN 1909). DAMAS (1905) characterized the central area by the dominance of *Pseudocalanus minutus.* However, the present investigation revealed that this species has its maximum of abundance in the slope area during the summer. In July the central area is dominated by large numbers of *Aglantha digitale* and *Limacina retroversa.* Copepods are scarce, apart from certain localities which may be correlated with eddy movements of the currents. The central area is not clearly separated from the slope and Jan Mayen areas.

Along the continental shelf of Norway in summer there is a very homogeneous plankton, consisting mainly of *Calanus finmarchicus* and some *Oithona similis* and *Metridia lucens,* accompanied by a number of neritic species. This type of plankton may also be found in the northern part of the Norwegian Sea off Bear Island and Spitsbergen. There is also a certain admixture of *Calanus hyperboreus,* both from the Greenland Sea and from coastal areas.

After August there is only a small number of plankton samples from the Norwegian Sea, except at station M. According to ØSTVEDT (1955) the plankton changes considerably in composition during the autumn. The most important copepods (*Calanus finmarchicus* and *Pseudocalanus minutus*) leave the surface layers, and warm-water and autumn forms become more numerous, and may be carried very far northwards with the North Atlantic current in autumn and winter.

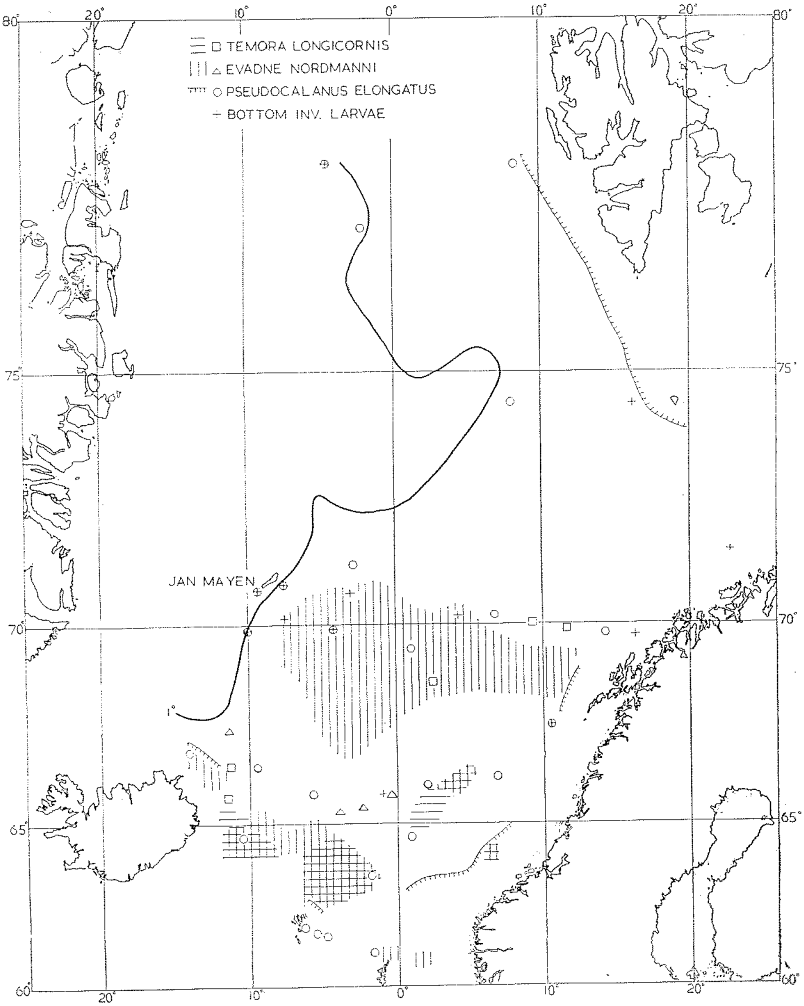

Fig. 12. Distribution of some neritic plankton species, and of *Evadne normanni* in the Norwegian Sea. The symbols denote records of single specimens.

DISTRIBUTION OF NERITIC ORGANISMS

The presence of neritic organisms in the open ocean indicates that the water masses have their origin partly in coastal areas. Pelagic organisms which have a littoral bottom stage during their development, are the most reliable indicators.

According to HELLAND-HANSEN & NANSEN (1909) the Norwegian coastal water may extend as far as 100 nautical miles from the coast in summer and autumn. DAMAS & KOEFOED (1909) have shown how *Cyanea* *capillata*, which starts its pelagic life from a littoral bottom stage, is successively carried away from the coast of Norway in July and August. ØSTVEDT (1955) found neritic organisms at station M in summer and autumn. JOHNSON (1940) used the distribution of the pelagic larvae of a crab, *Emerita analoga*, to trace water movements along the Pacific coast of the United States.

The distribution of organisms of neritic origin in the Norwegian Sea from 1948 to 1953 was plotted (fig. 12). *Temora longicornis* and *Pseudocalanus elongatus* have their main distribution in coast and bank waters, but in summer and autumn the populations may be carried some distance from the coast by the surface currents. Single individuals have been taken in distant parts of the Norwegian Sea. The main distribution of *Temora longicornis* during the summer is in good conformity with that given by FARRAN (1910). No neritic organisms were found in the Greenland Sea in summer.

Evadne nordmanni was earlier considered to be entirely neritic, and GRAN (1902) thought it might be useful as an indicator of coastal water. Recent investigations (KIELHORN 1952, reviewed by CORLETT (1953)) have, however, shown that *Evadne* may also be able to establish populations in the open ocean, far from any coast. High numbers of *Evadne* are found in summer and autumn in the coast areas surrounding the Norwegian Sea, usually accompanied by *Podon* spp. The figures of APSTEIN (1910) show similar distributions.

A concentration of *Evadne* was found in the sea between Jan Mayen and Norway (fig. 12). This occurrence seems to be related to a vortex there (c.f. p. 10), but the population was without doubt originally introduced from coastal waters. Similar distribution has been reported for planktonic algae. OSTENFELD (1913) has shown that the neritic diatom *Chaetoceros laciniosus* may be carried seawards and develop where conditions are favourable. This was confirmed by HALLDAL (1953), who found similar conditions at station M in April—May 1949.

VARIATION IN GROWTH AND SIZE IN COPEPODS

It is known that there can be great variations in growth and size within a species. In an earlier paper (WIBORG 1954) was discussed how size variations in copepods may be used to distinguish populations of different origin. GRAN (1902) stated that in the Norwegian Sea the various developmental stages of *Calanus finmarchicus* were smaller in summer and autumn than in spring, and also smaller in the southern part of the Norwegian Sea than farther north. GRAN believed that a higher temperature speeded up the development, but the individuals became smaller.

STEUER (1931) established geographical races on the basis of size variations in copepods. ADLER & JESPERSEN (1920) studied length variations of copepods during a long period of time and found that the variations were inversely correlated with the temperature during growth. Later workers have nearly all accepted the theory that temperature is the most important factor influencing growth in copepods. However, USSING (1938), followed by DIGBY (1954) believed that variations in the food conditions in the fjords of East Greenland influenced the size of the copepods, as temperature variations were slight. JESPERSEN (1939) stated that in those localities there were variations in temperature in the upper water layers, and that the greater part of the small individuals was taken in those layers.

Few workers seem to have considered the paper of COKER (1933). He reared three species of fresh-water copepods, *Cyclops serrulatus, C. viridis* and *C. vernalis* at six different temperatures, ranging from 10° to 30°C. In each culture eggs from a single copepod were used. Cultures of protozoans or algae were offered as food, and also chopped filamentous algae (*Mougeotia*).

There appeared to be a marked negative correlation between the temperature during growth and the length attained in the different developmental stages. In *Cyclops viridis* diminished food supply possibly reduced the final length of the individuals, but the effect was quite inconsiderable in comparison with the effect of a difference in temperature of 10°C. In the two other species COKER did not observe any influence of reduced food supply, but the time required for development increased considerably. If the cultures were crowded, the mortality also increased. COKER'S experiments, and the experiences of most workers studying the annual variations in size of copepods in a certain locality, seem to afford proof that temperature is the most important factor in regulation of the size.

COKER mentioned certain problems involved in the mechanism of growth in copepods. 1) Are the great variations in length usually found in a pure culture of copepods mainly caused by individual reactions to the lack of food? 2) Which part do hereditary dispositions play in the influence of the temperature on the size? That is, would two clones of the same species, reared at the same temperature, be as variable in size as the same clone, reared at 10° and 20°C? These and similar questions can only be answered by experiments.

THE QUANTITATIVE DISTRIBUTION OF SOME PELAGIC ORGANISMS IN THE UPPER LAYERS OF THE NORWEGIAN SEA DURING THE SUMMER

In this chapter I shall deal separately with the plankton animals which have their main distribution in the open ocean, or those which are of great importance both in coastal areas and in the open ocean. As most of the samples were taken in the upper 200 m, only those species will be treated in detail, which occur in some number in the upper layers or are important for the understanding of water movements or displacements of plankton populations.

Copepoda

Calanus hyperboreus Krøyer

Calanus hyperboreus may be regarded as a true arctic species, because the largest stocks are always found in arctic water. It is, however, found all over the Norwegian Sea, but in the warmer parts it is mostly confined to the deeper layers. The distribution was plotted (fig. 13). *C. hyperboreus* is abundant in the entire cold area, with a maximum in the central part. As has previously been shown by DAMAS (1905) and FARRAN (1911), *C. hyperboreus* is also moderately numerous in the East Iceland current. In spring and early summer it is spread in small numbers over nearly all the temperate parts of the Norwegian Sea.

Variations in Size

The larger specimens are found to the west of the drawn line (fig. 13) which roughly corresponds with the 1°C. isotherm at 25 m in 1952. In 1952, and to some extent in 1953, in the areas surrounded by two sinuous bends, there were quite large populations of smaller individuals. The size distributions in 1952 were plotted for all the stations and for station M (figs. 14 and 15).

According to ØSTVEDT (1955), the bulk of the population at station M is found below 1000 m. The mean length of *C. hyperboreus* at station M is intermediate between those of the cold and the temperate areas. The main peak in the size curve of stage V corresponds with that in the temperate area, the peak in the females with that of the cold area. ØSTVEDT stated that the stock of *C. hyperboreus* at station M could not be of local origin, and it seems safe to conclude that the stock is supplied from the area northeast of Jan Mayen. The possibility of transport from the coast of East Greenland to station M has also been considered, and

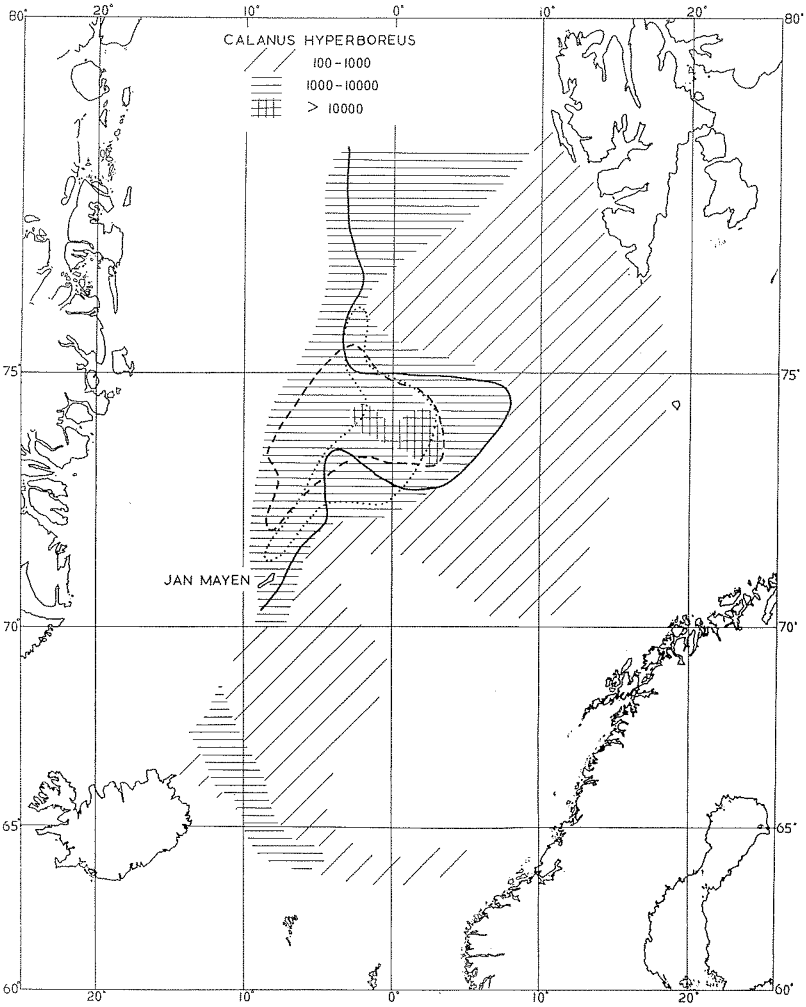

Fig. 13. The quantitative distribution of *Calanus hyperboreus* in 1948—1953. The continuous line marks the border between two populations, with smaller individuals to the east. Area limited by dots: Main distribution of the old generation 1952. Area limited by hatched line: Main distribution of the new generation 1952.

some measurements from JESPERSEN (1939) are inserted in fig. 15. *C. hyperboreus* in East Greenland fjords has a size which is intermediate between those of the two populations northeast of Jan Mayen, but as the measurements are from different years, no further conclusions may be drawn. At approximately 77° N. lat., off the coast of East Greenland, females of *C. hyperboreus* measured on an average 6.77 mm, stage V 5.28 mm (SØMME 1934).

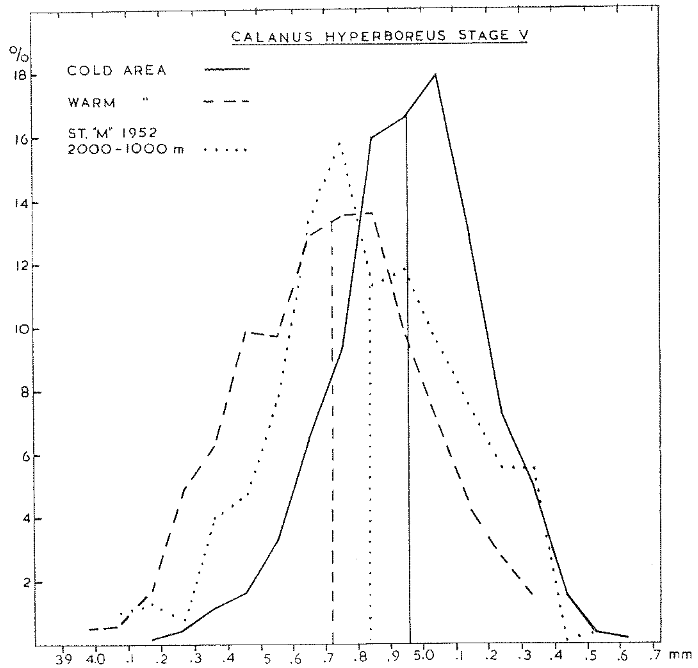

Fig. 14. Size distributions of *Calanus hyperboreus*, stage V.

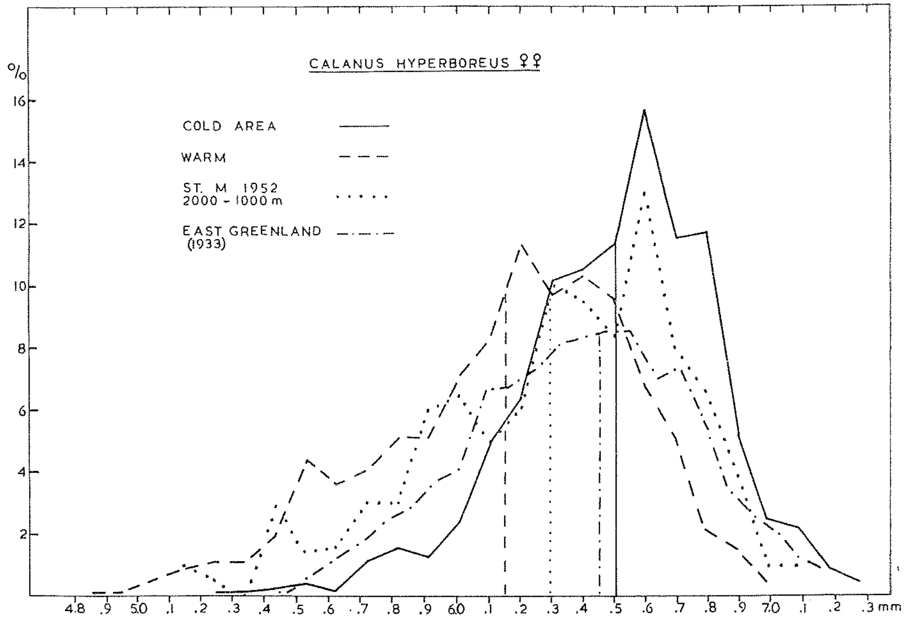

Fig. 15. Size distributions of females of *Calanus hyperboreus*. A size distribution from East Greenland has been inserted (JESPERSEN 1939).

It has been shown by JESPERSEN (1939) that *C. hyperboreus* may also vary in length with depth, the smaller individuals at higher levels. In the cold area of the Norwegian Sea almost the entire stock is found in the upper 50—100 m. At station M there has been a very good opportunity to study this problem. *C. hyperboreus* has been measured in all the plankton hauls taken during 1952 (figs. 16 and 17). There is a decrease in mean length from the deep towards the upper layers. In stage V the difference in length is slight from the 2000—1000 m to the 1000—600 m haul, while the individuals in the 600—100 m haul are considerably smaller. The females show irregular length distributions in the two upper hauls. It is difficult to explain how such length differences originate. The smaller individuals represent only a small part of the total stock at station M. As ØSTVEDT (1955) deduced spawning of *C. hyperboreus* in the upper layers in March—April, the small individuals may be of local origin. The possibility that they have been brought to station M by currents from coastal areas of Western Norway may be excluded, as the average size of stage V in Norwegian fjords is only 4.1 mm, compared with 4.5 mm at station M.

MARSHALL (1933) found an increase in size in *C. finmarchicus* with increasing depth.

Distribution of Stages

In the cold area near Jan Mayen, nauplii were the main part of the stock of *C. hyperboreus* in the first half of June 1952 and 1953. Further north- and westwards the maximum gradually changed to copepodite stage I—II, especially along the border towards temperate water. There were also peaks in the percentage of stage IV—V. This indicates that *C. hyperboreus* spawns in this area during May. In East Greenland fjords USSING (1938) found nauplii at the end of May and beginning of June, and the maximum percentage of stage I in June, II in July, and III in August.

DAMAS & KOEFOED (1909) observed spawning near East Greenland in August. They thought that *C. hyperboreus* did not spawn over the great depths of the Norwegian Sea, but only off East Greenland along the continental shelf. Northeast of Iceland they only found late developmental stages. No nauplii ocurred in the East Iceland current. In June only stages IV—VI were taken in the temperate areas of the Norwegian Sea, but north of 78°N. lat. stage III dominated.

The present material shows that from the end of June and throughout July stage III usually dominated in the East Iceland current as far as north of the Faroes, sometimes even to the Norwegian coast. In

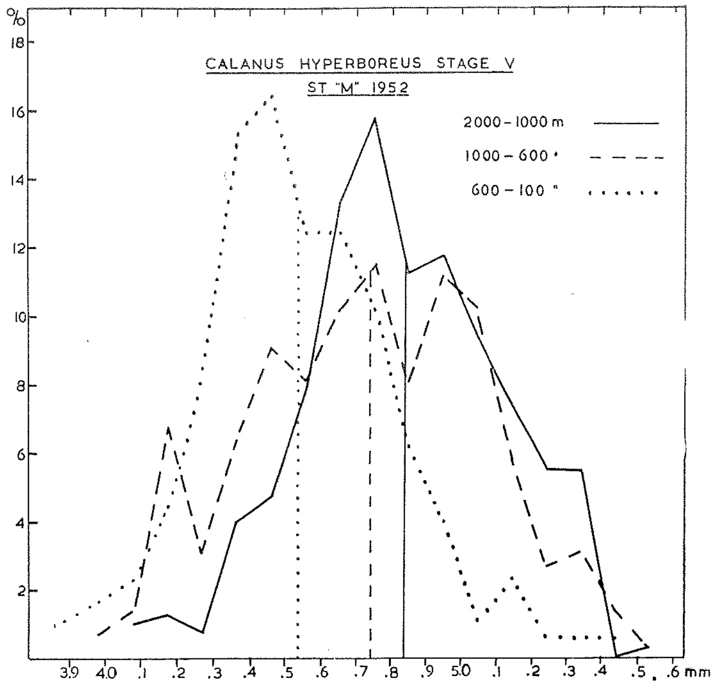

Fig. 16. Size distributions of *Calanus hyperboreus* stage V, station M, 1952.

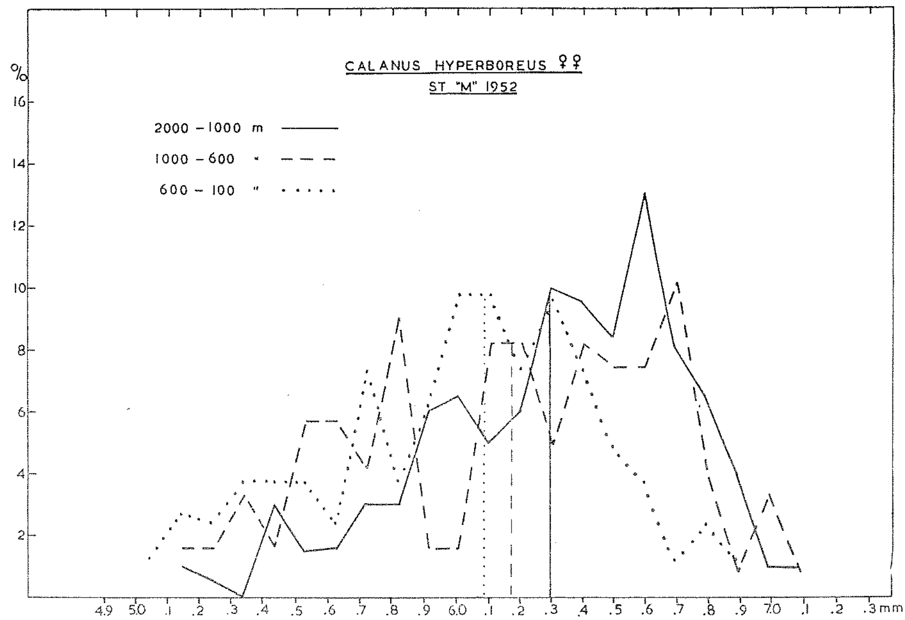

Fig. 17. Size distributions of females of *Calanus hyperboreus*, station M, 1952.

August stage III may still be dominant near Jan Mayen, but in all other parts of the temperate area stage IV is most common. There is evidently an extensive transport of *C. hyperboreus* with the East Iceland current from the cold area both before and after spawning. Most of the individuals gradually go to deeper water and are numerous in the bottom layers, as at station M. How far the bulk of the stock is carried northwards in the deeper layers cannot be stated, as there were very few deep hauls in the area outside station M.

A few copepodites remain in the upper layers and are carried northwards with the North Atlantic current. Along the western coast of Norway those individuals are distinguished from local stocks by their greater size (RUUD 1929, WIBORG 1954). Some specimens may also spread eastwards from the border areas between cold and temperate water from Jan Mayen and northeastwards. Near the shelf from Bear Island and northwards local stocks are evidently admixed.

Calanus finmarchicus (Gunnerus)

In the temperate parts of the Norwegian Sea *Calanus finmarchicus* is the dominant copepod in the plankton during spring and summer (GRAN 1902, and others). It is also abundant in the fjords of Spitsbergen and in the upper layers to the west of Spitsbergen, immediately east of the Polar current. In the Greenland Sea it is numerous in the intermediate layers (DAMAS & KOEFOED 1909).

The distribution of *C. finmarchicus* in the Norwegian Sea in 1948—1953 (fig. 18) is in good accordance with that of the plankton volumes, except in the cold area. In the area between Jan Mayen, Iceland and the Faroes the figures are mainly based on the observations from July—August 1951. Great numbers of *C. finmarchicus* were also found off the western and southern slopes of Bear Island and western Spitsbergen, and along the western and northern coasts of Norway.

In Norwegian coastal waters *C. finmarchicus* has 1—2 main periods of reproduction a year; off Møre in March and May—June, in the Lofoten area in April. Minor spawnings occur in the late summer or autumn. At station M, ØSTVEDT (1955) observed the main spawning in April, and a second of minor importance in August. In June stage IV dominated, in July—August stage V. Near Jan Mayen and Bear Island one may find a maximum of nauplii in cold water from the end of June to the middle of July, probably the first spawning of a local stock. However, in most places stage IV—V dominate during the summer months. In July 1948 females were more abundant than other stages

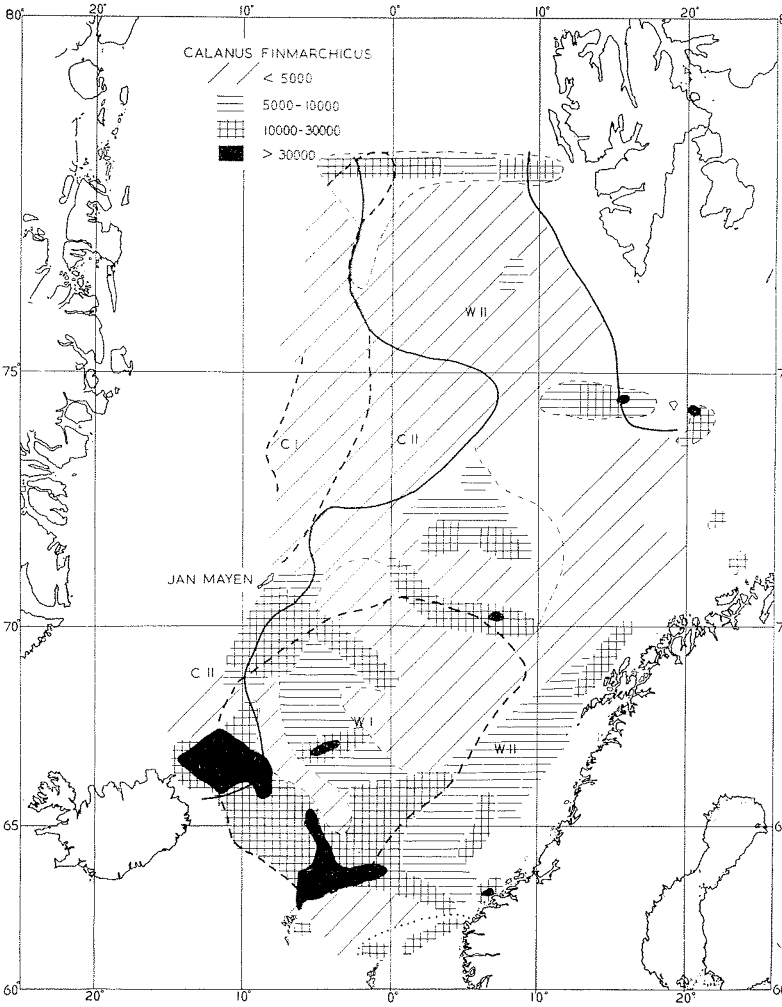

Fig. 18. The quantitative distribution of *Calanus finmarchicus* 1948—1953. Large individuals are found west of the long, and east of the short, continuous line. In the areas C I and W I, surrounded by hatched lines, the individuals are small, in C II and W II of middle size. For further explanation, see text.

between Jan Mayen and Lofoten, perhaps indicating the beginning of a second spawning. During the first half of June 1952 females dominated from Jan Mayen to Spitsbergen, following the 2°—4°C. isotherms at 25 m (fig. 3, p. 9). This was associated with quite large stocks. No nauplii were found. Similar features were observed in 1953. In the cold area stages IV—V were dominant. In the temperate area of the northern Norwegian Sea *C. finmarchicus* probably starts the spring spawning in the middle of June, in the cold area not until July—August.

The Populations of Calanus finmarchicus and their Movements within the Norwegian Sea

GRAN (1902) assumed that the Norwegian Sea was a self-supporting area as regards plankton, but that considerable quantities were carried away with currents into the Polar Ocean each year. DAMAS (1905) observed intensive spawning of *Calanus finmarchicus* in the southern Norwegian Sea, and DAMAS & KOEFOED (1909) drew attention to the importance of the spawning areas along the slopes and coastal banks of western and northwestern Norway. They further assumed that *C. finmarchicus* in the intermediate layers of the Greenland Sea had a double origin, partly deriving from the fjords and slopes of western Spitsbergen, partly from the southern Norwegian Sea, following the path of the North Atlantic current. HELLAND-HANSEN & NANSEN (1909) and DAMAS (1905) believed that *C. finmarchicus* was more or less stationary within the cyclonic system of the southern Norwegian Sea. ØSTVEDT (1955) has shown that in winter there is a large stock of *C. finmarchicus* in the deeper layers at station M, situated on the border of this cyclonic system.

In the procedure of distinguishing different populations of *C. finmarchicus* one may follow two methods; examining differences in stage composition or differences in the size distribution of the developmental stages. A very large number of females and stage V copepodites, 50—100 specimens of each per station, has been measured from nearly all the plankton hauls taken in the Norwegian Sea from 1948 to 1954.

In the middle of April 1950 a series of plankton hauls was taken from northern Norway to Bear Island (WIBORG 1954, p. 71). At all stations situated in temperate water females of *C. finmarchicus* had nearly the same mean length, 2.7 mm. At station M, the yearly size variations throughout 1950 were investigated. On some occasions there were sudden variations in the mean length within short intervals of time. It was then assumed that we had to deal with different populations which were partly local, partly brought in from other areas. They presumably came from the coast and slope areas of western Norway, and in the autumn also from the North Atlantic.

The present investigation affords further indication of the existence of at least two different populations of *C. finmarchicus* in the southern part of the Norwegian Sea. In the first half of June 1952 the females measured on an average 2.58 mm in the sea between station M and Jan Mayen, but 2.80 mm from the slope of the edge east of station M and northwards to Spitsbergen. Later in the year the average size decreased in the latter area.

The length distributions of stage V in different areas of the Norwegian Sea during the summer of 1952 were computed (fig. 19). In the temperate part the copepodites are smaller in the central southern area (fig. 18, W I) than in the Norwegian coast and slope areas, and in the middle of the sea north of 70°N. lat. (fig. 18, W II). In the Greenland Sea, *C. finmarchicus* is also of a moderate size, and two different areas, C I and C II may be distinguished, with length distributions corresponding to those in the areas W I and W II. It is clear that there is

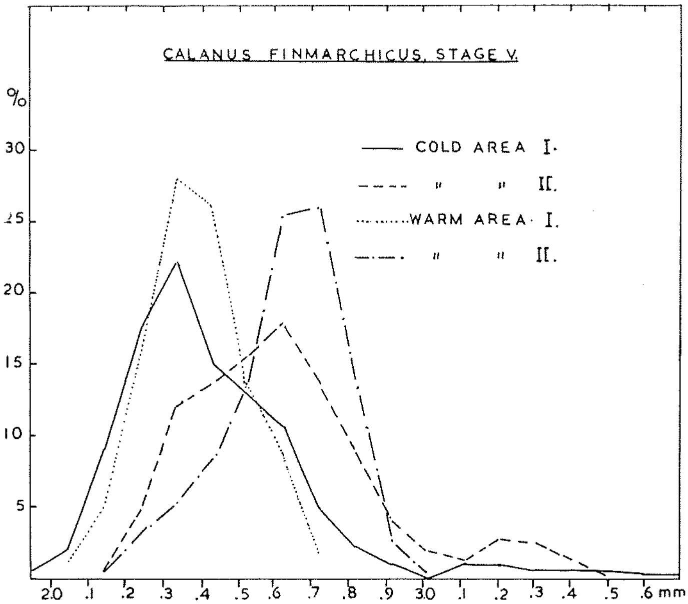

Fig. 19. Size distributions of *Calanus finmarchicus*, stage V.

a certain degree of mixing between the populations in C I and C II (fig. 19). In addition, there is a small group of large specimens of 3.0 mm or more. Similar large individuals are also found near Bear Island and Spitsbergen in cold water (WIBORG 1954, p. 72).

Mr. P. TALLANTIRE, formerly at the Fisheries Laboratory, Lowestoft, England, has been good enough to send me some measurements of *C. finmarchicus* taken in a section of stations from Bear Island and westwards at different times of the year. In June stage V measured on an average 2.80 mm, but during the late summer and autumn the mean length gradually decreased to 2.20—2.40 mm from August to April. This is in conformity with the observations from a section off western Spitsbergen in September 1953. The copepodites then had a mean length of 2.4—2.5 mm. The difference in the length distributions between the areas C I and C II may be explained as follows: The small copepodites originate in the southern part of the Norwegian Sea and/or from the summer generation hatched along the western coast of Norway in June—July. These copepodites have followed the branch of the North Atlantic current into the intermediate layers of the Greenland Sea. On their way northwards they must pass Bear Island in late summer.

On the western slope of the Bear Island bank, and from the west coast of Spitsbergen to the 2°C. isotherm at 25 m (fig. 3) large quantities of *C. finmarchicus* were taken at the beginning of June in 1952 and 1953. They were mainly stage V and females, 500—21000 specimens per haul. The population may be of local origin, as cyclonic systems are known to exist in the area (HELLAND-HANSEN & NANSEN 1909), but they may also have been introduced with the North Atlantic current from coast and slope waters of western and northwestern Norway. The larger copepodites found in area C II evidently belong to that population. They may have followed that branch of the North Atlantic current which according to HELLAND-HANSEN & NANSEN turns to the west from the Bear Island and flows into the Greenland Sea.

In 1953 and 1954 the same distribution of smaller and larger copepodites of *C. finmarchicus* was observed in the cold area as in 1952. Small females were found in the southern Norwegian Sea (fig. 18, W I). In 1952 they were also taken at 3 stations in the cold area, probably introduced in the tongue of warm water (p. 10). In 1953 and 1954 no influx of warm water could be traced in this direction, and the females taken in the cold area were all of the same size as those found in W II. It is suggested that since the moulting from stage V to adults takes place at a comparatively low temperature in the areas C I and C II, the adults will attain a «normal» size, even if the copepodites are small.

C. finmarchicus was also measured in plankton samples taken near Jan Mayen in April 1954 (fig. 20). Females and stage V were most numerous in the upper 200 m. They were nearly all of the same mean length as in the cold area in June of the same year, the smallest individuals being caught southwest of Jan Mayen (sts. 6 and 7). A small percentage of the females measured more than 3.5 mm.

It is probable that *C. finmarchicus* stayed in water of above 0°C. between 100 and 200 m. The hauls were taken from 200 m to the surface, and the temperature was usually below 0°C. in the upper 50—100 m.

HELLAND-HANSEN & NANSEN (1909) showed that the water in the intermediate layers of the Greenland Sea comes mainly from the north and penetrates southwards at least to 70° N. lat. It might therefore be of interest to see how far south it is possible to trace the population of the small and medium-sized *C. finmarchicus*.

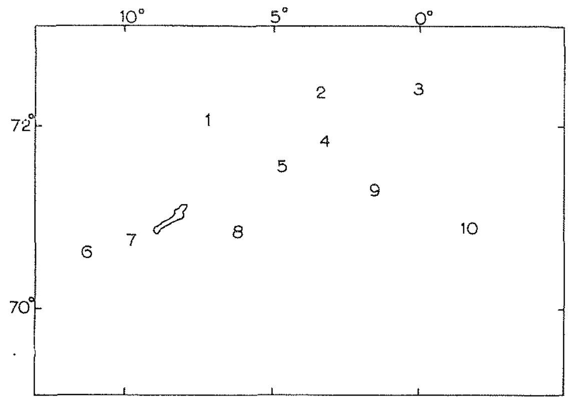

Fig. 20. Plankton stations, «Norsel» 1954.

SØMME (1934) measured some *C. finmarchicus* from a vertical haul 20—0 m off the coast of East Greenland at 76°47′ N. lat., 15°21′ W. long. The length distributions were bimodal, stage V with one main group at 2.0—3.1 mm and a few specimens measuring 3.4—3.7 mm. The females measured 2.8—3.6 mm, a few 3.9—4.2 mm. At that locality the temperatures were below 0°C. to the bottom (175 m), but at some distance the temperatures were above 0°C. from 250 m and deeper. It is likely that *C. finmarchicus* had been introduced in the intermediate layers and later migrated towards the surface.

Farther south, in the fjords of East Greenland from 74° to 70° N. lat., USSING (1938), JESPERSEN (1939) and DIGBY (1954) found bimodal length distributions of *C. finmarchicus* in summer, but there the large individuals were most numerous. JESPERSEN stated that most of the small individuals were taken in the surface layers above 0°C., the large specimens mainly in the cold intermediate layers. There was also a higher percentage of small individuals in the bottom water, which was above 0°C. The bottom water is probably of the same origin as the intermediate warm layer in the Greenland Sea. JESPERSEN did not draw any conclusion as to the origin of the small *C. finmarchicus*, but showed that they were of the same length as the individuals present in the warmer water of the Denmark Strait farther south (about 65°N. lat.). It must be considered as proved that temperature is the most important factor in determining the length of the copepods (p. 23). Therefore, it follows that the small *C. finmarchicus* found off the coast and in the fjords of East Greenland had grown up in water of a comparatively high temperature. Those found in open water and probably also in the bottom layers of the fjords, had been brought there with water from the North Atlantic current, and had their origin in the southern part of the Norwegian Sea, or off the coast of western and northern Norway.

Pseudocalanus minutus Krøyer

In an earlier paper (WIBORG 1954) the distinction of *Pseudocalanus minutus* from the neritic *P. elongatus* Boeck, as well as its identity with *P. gracilis* G. O. Sars was pointed out. *P. minutus* is more oceanic in distribution than *C. finmarchicus*. The distribution from 1948 to 1953 was plotted (fig. 21).

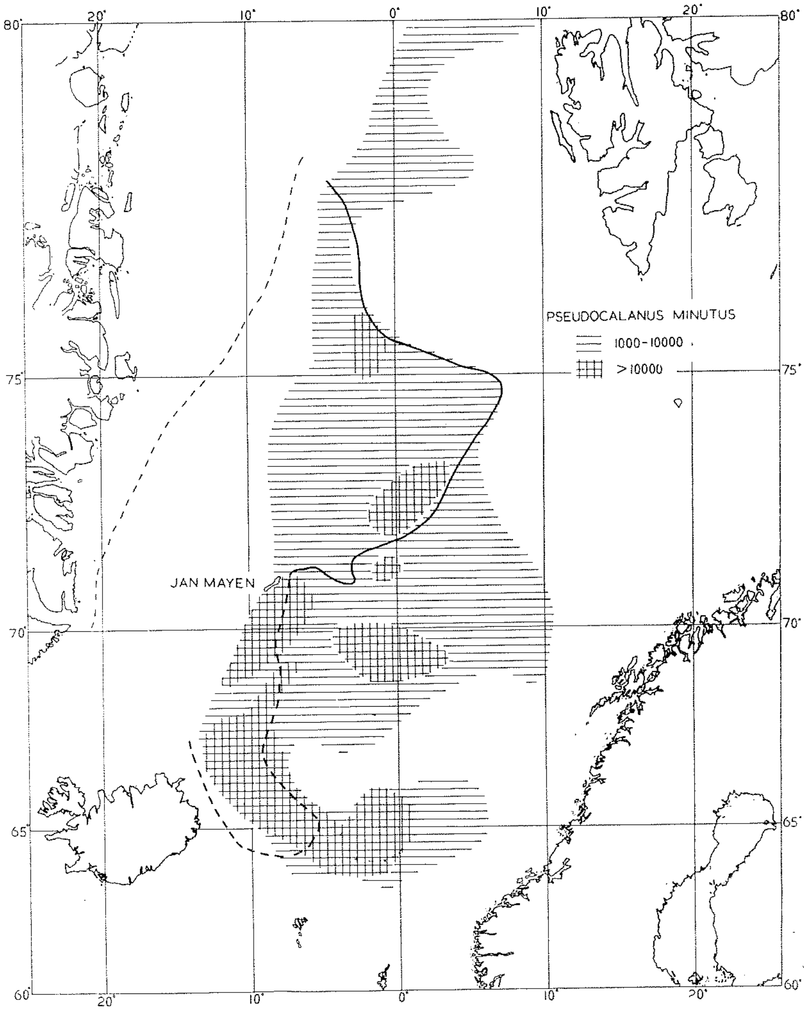

Fig. 21. Quantitative distribution of *Pseudocalanus minutus* 1948—1953. The thin, hatched line signifies the distribution to the west, according to DAMAS & KOEFOED (1909). Small individuals are found west of the continuous line, large specimens inside the area surrounded by a thick, hatched line.

Pseudocalanus minutus is also found in small numbers in the coastal areas of Norway (WIBORG 1954) and Spitsbergen, but it only occurs in quantities in the open ocean and near Jan Mayen, which can hardly be considered an ordinary coastal area. The main concentrations correspond very well with those of *Calanus finmarchicus*, but in the cold area the maximum numbers along the 1°C. isotherm are mainly caused by a large number of nauplii. The females are more uniformly distributed.

DAMAS (1905) observed the maximum of abundance of *Pseudocalanus minutus* in the centre of the southern Norwegian Sea between 0° and 10° W. long. He found little or nothing in the Iceland-Faroe area, where this investigation showed the greatest concentrations. DAMAS' observations were made at the end of May, and *P. minutus* might have a more restricted distribution at that season, correlated with the life cycle of the species. According to ØSTVEDT (1955), *P. minutus* is most numerous in the surface layers at station M during May and June. From July to the following spring most of the stock is found below 600 m. Very few plankton hauls have been taken in the area where DAMAS found a maximum of abundance, which he correlated with the presence of Atlantic water. However, it seems justified to conclude that *P. minutus* is more numerous where mixing takes place between Atlantic and arctic water. The species is very scarce in the North Atlantic current off the coast of Norway and further north in June. In September 1953 *P. minutus* was moderately abundant off western Spitsbergen between 0° and 5° E. long., in accordance with the distribution found in this investigation (fig. 21).

Variations in Size

In the Greenland Sea the females of *P. minutus* were smaller (mean length 1.08 mm) than in the temperate area of the Norwegian Sea (mean length 1.13 mm). From Jan Mayen to Iceland (the area inside the hatched line in fig. 21), closely corresponding with the East Iceland current, the largest individuals (mean length 1.20 mm) are found. The measurements from the cold area were made on material from 1952, but similar results were obtained from 1953 and 1954. The size distributions and a length curve from the coast of Spitsbergen were compared (fig. 22). Similar large females were also found near Bear Island in June 1948.

The fact that one finds the smallest individuals of *P. minutus* in the cold area must be taken as proof that the stock has been introduced from the temperate parts of the Norwegian Sea, as was found for *Calanus finmarchicus*. From station M there are measurements of *P. minutus* from all seasons of the year. In 1952 the females had nearly the same length distribution and mean length, 1.14 mm, from March to July.

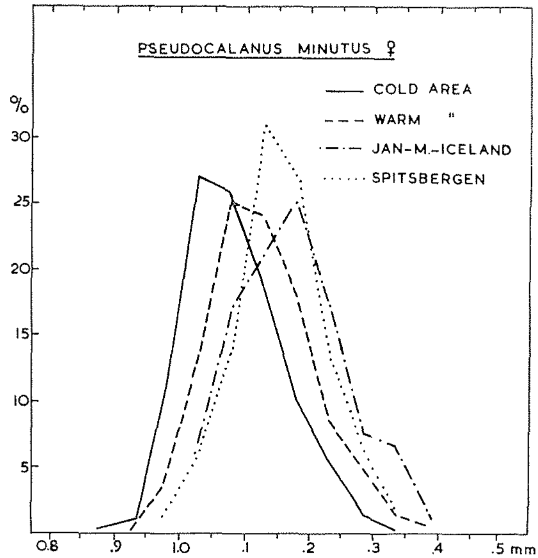

Fig. 22. Size distributions of *Pseudocalanus minutus.*

This agrees very well with the statement of ØSTVEDT (1955) that *P. minutus* has only one spawning period a year. From February to May stage V copepodites had a mean length of 1.08—1.15 mm, decreasing gradually to 1.05—1.07 mm in June and July. It is therefore assumed that the small females found in the cold area in June originate from copepodites which developed in the southern Norwegian Sea from June to August of the previous year, and were carried into the cold area with the North Atlantic current.

There are also some length measurements from the Jan Mayen area in April 1954 (table 1). Northeast of the island the females were small and the length distributions unimodal. Two or three modes were found at two stations southwest of Jan Mayen with greater mean lengths (1.13—1.20 mm). This was most clear in the 600—200 m haul at station 6 (fig. 20). This seems to indicate, as mentioned, that a local population with somewhat larger individuals may develop in the area from Jan Mayen southwestwards in the East Iceland current. But the conditions evidently vary from year to year, and sometimes there is an identical size distribution of *P. minutus* over large areas, from Jan Mayen to the coast of Norway. Off East Greenland DAMAS & KOEFOED (1909) observed two length groups of *P. minutus*, approximately corresponding to those found in the Greenland Sea and in the Jan Mayen area. As the two authors, however, were not always able to distinguish the two species of *Pseudocalanus*, this statement must be regarded with caution.

Table 1. Length Measurements of Females of *Pseudocalanus minutus*, «Norsel» 1954. Scale Unit = 0,0513 mm.

Station	Haul	17	18	19	20	21	22	23	24	25	26	27	28	n	Mean length mm
1	200—0	—	2	13	36	21	15	7	2	3	1	—	—	100	1.07
2	1000—600	—	1	5	23	31	25	9	6	—	—	—	—	100	1.09
2	600—200	—	5	18	28	27	15	4	2	1	—	—	—	100	1.05
2	200—10	—	1	11	30	27	12	11	7	1	—	—	—	100	1.08
3	200—0	—	—	6	23	25	22	12	7	4	—	—	1	100	1.10
4	600—210	1	1	17	31	28	9	6	5	2	—	—	—	100	1.06
4	200—0	—	2	7	28	29	13	12	6	3	—	—	—	100	1.10
5	1000—600	1	7	15	24	22	17	10	1	2	—	—	—	99	1.06
5	600—190	—	2	5	27	25	17	12	9	3	—	—	—	100	1.10
5	200—0	1	5	12	25	25	20	7	4	—	1	—	—	100	1.07
6	600—205	—	—	1	8	11	13	12	20	23	8	2	2	100	1.20
6	200—0	—	3	5	12	16	22	21	16	3	2	—	—	100	1.13
7	600—208	—	—	—	2	1	2	3	6	5	1	—	—	20	1.21
7	200—0	—	1	8	13	12	20	15	17	12	2	—	—	100	1.21
8	200—0	—	—	12	14	24	13	22	10	3	2	—	—	100	1.11
10		—	—	1	3	11	11	9	12	3	—	—	—	50	1.15

Some workers (JESPERSEN 1923, FARRAN 1951) have, so far as they have distinguished two forms or species of *Pseudocalanus*, considered *P. minutus* (*P. gracilis*) as a partly arctic form. The present investigation has shown that *P. minutus* is not a native of the Greenland Sea, but has been introduced from temperate areas, even if considerable spawning may take place in the border area towards warmer water. Small populations may establish themselves in local cold areas, such as near Spitsbergen and Jan Mayen, but probably they are not maintained there very long.

In West Greenland waters *P. minutus* (*P. gracilis*) is the most dominant form (JESPERSEN 1923).

Microcalanus pusillus G. O. Sars

In an earlier paper (WIBORG 1954) the validity of the differentiation between *Microcalanus pusillus* G. O. Sars and *M. pygmaeus* (G. O. Sars) was defended. The former has been considered a temperate and boreal species, the latter mainly arctic (FARRAN 1951, and others). *M. pusillus* is usually not found near the surface, except in winter (MARSHALL 1949, ØSTVEDT 1955). It is therefore to be expected that *M. pusillus* would be scarce in the plankton material from the Norwegian Sea, except in the deep hauls, and the catches cannot be regarded as representative of the distribution.

In the southern Norwegian Sea *M. pusillus* occurred rather regularly, but usually in low numbers (50—400 per haul in the upper 200—0 m). In some areas, as off East Iceland, and along the continental shelf of Norway, a haul sometimes exceeded 1000 specimens. Where Atlantic water dominated, *M. pusillus* was usually absent from the upper layers.

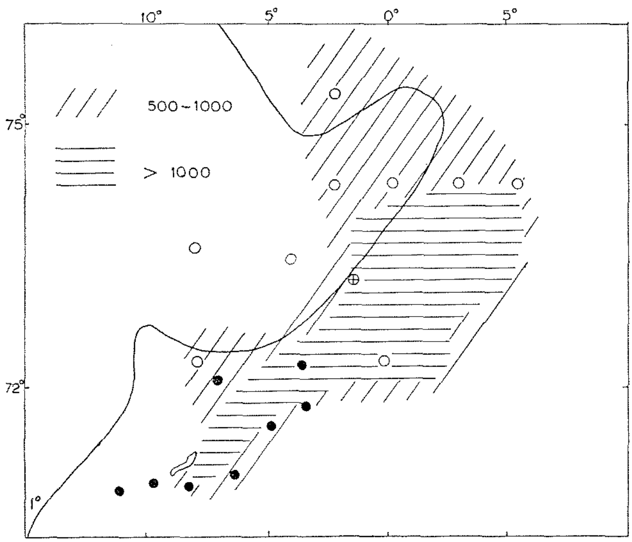

Fig. 23. Quantitative distribution of *Microcalanus pusillus* northeast of Jan Mayen in 1952—1954. Symbols indicate records of small *M. pygmaeus*. Rings: 1952, crosses: 1953, dots: 1954. The 1° C isotherm at 25 m in 1952 has been inserted in this, and the following figures.

The species was also found in the cold area in 1952 and 1953. The females were scarce (10—100 per haul), but the copepodites were sometimes quite abundant (2000 or more per haul). As adult *M. pygmaeus* were also taken in the same hauls, there is the possibility that some copepodites belonged to this species. With this reservation the distribution of *M. pusillus* in the cold area was plotted (fig. 23). Where deep hauls were made (in 1953) *M. pusillus* was concentrated in the 600—100 m hauls, as ØSTVEDT (1955) also found.

All the female *M. pusillus* were measured. In the cold area they were very scarce, but in 1952 the mean length, 0.47—0.49 mm, corresponded very nearly to that observed at station M in March—April (WIBORG 1954, p. 138). In the temperate area the females measured 0.54—0.60 mm on the average. It seems likely that *M. pusillus*, like

P. minutus, had been introduced into the cold area with the Atlantic water the previous autumn, and had reproduced very heavily the next spring, especially along the border of temperate water.

In the middle of September 1953 *M. pusillus* was very abundant in the upper 200 m off western Spitsbergen (reaching 3900 specimens per haul). Nearly all were copepodites. This observation agrees very well with the statement of FARRAN (1936) that the species was abundant at the beginning of September 80 nautical miles north of Spitsbergen. The stock had evidently been transported northwards with the North Atlantic current.

Microcalanus pygmaeus (G. O. Sars)

In arctic waters *Microcalanus pygmaeus* is said to be an inhabitant of the upper layers DAMAS & KOEFOED 1909, JESPERSEN 1934, 1939, USSING 1938 and others). As the two species of *Microcalanus* have usually been confounded, earlier statements cannot be accepted with certainty. At station M, *M. pygmaeus* is usually taken below 1000 m, but a few specimens may be found higher, even above 600 m (ØSTVEDT 1955, and the present investigation). The stock is probably not self-supporting, but gets a more or less constant supply from the Greenland Sea and possibly also from other areas, as has been assumed for *C. hyperboreus* (ØSTVEDT 1955, p. 27).

M. pygmaeus is very scarce or absent from the upper 200 m of the Norwegian Sea in summer. In the cold area only a few specimens were taken in 1952. In 1953, when deeper hauls were made, *M. pygmaeus* was common in the 600—100 m and 1000—600 m hauls.

Variations in Size

At station M there was a moderate stock of *M. pygmaeus* all year (ØSTVEDT 1955). The size variations have been discussed (WIBORG 1954). During the year the mean length of the females varied slightly from 0.71 to 0.74 mm. In June 1952, however, the length distribution in the 2000—1000 m haul was bimodal, with the main peak at 0.65 mm and only an indication of the usual peak at 0.73 mm. In the 1000—600 m haul only large individuals occurred. The same phenomenon was repeated in August. No hauls were taken below 1000 m in July. In order to investigate whether this feature was repeated each year, *M. pygmaeus* was measured from the deep hauls taken at station M in May—August of 1950, 1951, 1953 and 1954. A few small females were found in May—June 1953 and in May—June 1954. They were scarce compared to those present in 1952, but always confined to the 2000—1000 m hauls.

Table 2. Length Measurements of Females of *Microcalanus pygmaeus*, 1953. Scale Unit 0.0125 mm.

Area	Depth m	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	n	Mean length mm
NE of Jan Mayen	1000—600	—	—	—	1	—	4	2	1	—	—	3	4	4	10	13	14	6	3	2	59	0.72
—«—	600—100	6	6	8	16	13	14	4	4	2	2	—	3	—	—	—	1	—	—	—	79	0.61
W of Bear Island	1000—600	—	—	—	1	—	—	—	—	1	—	3	4	4	7	4	4	1	1	1	31	0.72
—«—	600—100	—	—	1	2	3	—	1	2	1	—	—	—	—	—	—	—	—	—	—	10	0.62
SE of Jan Mayen	1000—600	—	—	—	—	—	—	—	1	1	5	12	16	25	17	15	5	2	—	—	100	0.71
NW of Lofoten	1000—600	—	—	—	—	—	—	—	—	1	2	2	2	5	8	10	7	6	5	2	50	0.74
—«—	600—100	—	—	—	—	—	—	—	—	—	—	2	—	1	—	—	1	—	—	—	4	0.71

Table 3. Length Measurements of Females of *Microcalanus pygmaeus*, «Norsel» 1954. Scale Unit 0.0125 mm.

Station	Depth m	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	n	Mean length mm
2	1000—600	—	—	—	1	3	1	7	13	5	5	2	3	2	—	1	3	1	3	5	10	3	3	71	0.61
2	600—100	—	—	1	1	—	3	3	2	3	1	1	—	—	—	—	—	—	—	—	—	—	—	15	0.59
4	600—210	—	2	2	3	10	13	20	11	19	13	1	5	—	—	1	—	—	—	—	—	—	—	100	0.60
5	1000—600	1	—	2	1	1	4	5	3	—	1	—	—	—	2	6	3	2	5	3	4	2	—	45	0.66
5	600—190	—	1	3	7	12	10	10	17	19	6	8	1	2	2	1	—	1	—	—	—	—	—	100	0.60
5	200—0	—	—	—	—	1	1	4	3	1	2	—	—	—	—	—	—	—	—	—	—	—	—	12	0.60
6	600—205	—	—	—	2	7	7	9	15	15	19	6	5	2	4	3	—	1	—	—	2	—	—	94	0.62
7	600—208	—	—	—	1	4	4	8	11	11	8	1	4	2	—	—	1	2	3	5	6	5	1	77	0.66

The *M. pygmaeus* taken in the upper 200 m northeast of Jan Mayen in 1952 (fig. 23) all belonged to the same size group as the small females at station M, with a mean length of 0.61 mm. In 1953 only large individuals (mean length 0.72 mm) were taken in the 1000—600 m hauls southeast of Jan Mayen (table 2). No specimens were found above 600 m. In the cold area individuals of the same size were taken in the 1000—600 m hauls, but in the 600—100 m haul there were almost exclusively small individuals (mean length 0.61 mm). West of Bear Island large specimens (mean length 0.72 mm) were taken in the 1000—600 m haul, but very few small *M. pygmaeus* above 600 m. In April 1954 some plankton hauls were made near Jan Mayen. Small females of *M. pygmaeus* (mean length 0.58—0.62 mm) dominated in the upper 600 m, but in the 1000—600 m hauls small and large specimens (mean length 0.72—0.74 mm) occurred in about equal numbers (table 3). Immediately west of Jan Mayen (fig. 20, sts. 6 and 7), some large females were also found in a 600—200 m haul.

It is very difficult to give a satisfactory explanation of the variations in mean length. One may assume that the smaller individuals have developed northeast of Jan Mayen in water of higher temperature than usual for the main part of the stock. Whether such conditions are found regularly or only in certain years is not certain. Another possible explanation is that in some years *M. pygmaeus* may produce two generations, one in the early spring, another in late summer or autumn. In any case the presence of small individuals below 1000 m at station M may be taken as proof that the bottom water has been renewed. Otherwise the small individuals should have been present also above 1000 m. Further investigations are desirable, especially in deep water between Jan Mayen, Greenland and Iceland.

Metridia longa (Lubbock)

Metridia longa is very numerous in coastal waters, especially in the intermediate layers (Jespersen 1934, 1939). It also thrives in boreal areas, e.g. in the deeps of the Norwegian fjords (Runnstrøm 1932, Wiborg 1940, 1954). At station M, *M. longa* is most common below 100 m, with a maximum in the 600—100 m layer (Østvedt 1955). This also seems to be the case in other parts of the Norwegian Sea, and for this reason the present material cannot be regarded as representative. *M. longa* was taken in moderate numbers at most of the stations, usually 100—1000 specimens per haul. Minima are indicated where the North Atlantic current is of greater influence, but there the main stock will probably be found at a greater depth. The species is probably very common in the deeper layers all over the Norwegian Sea.

ØSTVEDT (1955) concluded from the occurrence at station M of copepodites of stage I—III that the main spawning took place in April—May. In the Norwegian Sea, nauplii and stage I—III copepodites have been found from June to August. In June the females were usually most abundant, then males and stage V copepodites.

Variations in Size

The females of *M. longa* were remarkably uniform in size all over the Norwegian Sea (mean length 2.65 mm, total range 2.46—2.87 mm). In the cold area the individuals were slightly larger (mean length 2.66—2.69 mm) than in the temperate part (2.62—2.65 mm), but exceptions were found. From station M we have length measurements throughout 1952. The mean length varied between 2.62 mm and 2.66 mm. Thus *M. longa* evidently grow up in the intermediate water layers which offer nearly the same temperature conditions in both the cold and warm areas of the Norwegian Sea.

For East Greenland fjords JESPERSEN (1939) gave an average length of females of *M. longa* of 2.78 mm. USSING (1938) gave 2.65 mm, but his hauls were only taken down to 50 m and there is the possibility that he only sampled a part of the stock. For some copepods, e.g. *Calanus hyperboreus*, there is a tendency for the smaller individuals to keep to the upper limit of the vertical distribution (p. 27).

Metridia lucens Boeck

Metridia lucens is usually regarded as an Atlantic species, but local stocks may exist in certain areas, e.g. the Skagerak and along the Norwegian coast (FARRAN 1911, RAE & REES 1947, WIBORG 1954). At station M this copepod is most common in water of Atlantic origin, especially in winter (ØSTVEDT 1955). In the summer months of 1948—1953 *M. lucens* was most abundant in the eastern part of the Norwegian Sea. The main distribution (fig. 24) is very similar to that given by FARRAN (1910). *M. lucens* was also present in low numbers farther north, off Bear Island and Spitsbergen, in accord with previous observations. In the deep hauls taken in 1953 and 1954 it was also recorded near Jan Mayen, but not found in the cold area northeast of the island.

During the summer of 1950 *M. lucens* was very abundant in a section from Norway to Shetland, but the number declined very rapidly in the Shetland—Faroe Channel. This indicates that a local stock had devel-

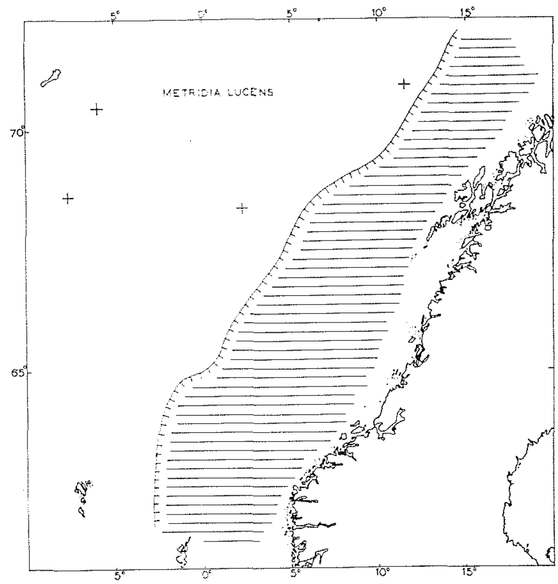

Fig. 24. The main distribution of *Metridia lucens* in the Norwegian Sea in 1948—1953. Crosses indicate single records.

opped in the area east of Shetland. Although *M. lucens* may be brought into the Norwegian Sea with the North Atlantic current, it thrives in coastal waters and may attain its greatest numbers where the Atlantic water is more or less mixed with coastal water.

Variations in Size

It has been shown that *M. lucens* varies in size from one locality to another along the coast of Norway (WIBORG 1954). Females of *M. lucens* were also measured from station M. During 1952 the mean length increased from a minimum of 1.65—1.69 mm in April—May to a maximum in July—August of 1.87 mm. Later there was a slight decrease to 1.74 mm in December, but a high figure of 1.85 mm in October. The figures were a little higher than the corresponding values off the coast of Norway in 1949—1950.

In a section from Møre to Jan Mayen, and off Bear Island the mean lengths at the beginning of June 1952 were very uniform (1.79—1.85 mm). Off the west coast of Spitsbergen *M. lucens* was more scarce and the mean length was only 1.73 mm. This indicates that *M. lucens* is constantly carried northwards with the North Atlantic current. The individuals found in the northernmost localities were transported farthest. They may belong to a generation which had grown up in the southern Norwegian Sea during the preceding autumn. Those farther south were transported for a shorter period and may belong to the spring generation, either in the southern Norwegian Sea, or in Norwegian coastal waters.

M. lucens is evidently not carried into the Greenland Sea like *Calanus finmarchicus* and *Pseudocalanus minutus.* It has been recorded from the north of Spitsbergen in 81°40′ N. lat. (FARRAN 1936), but was not found by the Belgica expedition (DAMAS & KOEFOED 1909) nor in East Greenland waters north of 61° N. lat. (JESPERSEN 1939).

Metridia nauplii have been found fairly abundant in the Norwegian Sea at a number of localities. Those present in the southern part in June and July probably belong to *M. lucens.* In contrast to *M. longa,* this species has 3 or 4 spawning periods a year (RAE 1951, WIBORG 1954).

Oithona similis Claus

Oithona similis is one of the most common copepods in northern waters, both in coastal water and in the open ocean, especially during late summer and autumn. It is most common in the upper 50 m, but present at all depths. Known as a euryhaline and eurytherm species, it is supposed to reproduce heavily most of the year.

The distribution of *O. similis* in the Norwegian Sea was plotted (fig. 25). The distribution bears some resemblance both to that of *Pseudocalanus minutus* and of *Oncaea borealis* (figs. 21 and 27), but *Oithona similis* has a more extensive distribution. The great concentrations on the frontier between cold and temperate water and in the central part of the southern Norwegian Sea are especially remarkable.

It is again stressed that the observations in the southern part were taken mainly in July and August, those in the cold area in June. In September 1953 *O. similis* was very abundant off western Spitsbergen from the coast to about 5° W. long. Along the coast of Norway there is usually a maximum in the stock in August—September, but sometimes also in May (WIBORG 1954). At station M the maximum is reached at the end of June, but there are also peaks in August and October (ØSTVEDT 1955).

Oithona spinirostris Claus

Oithona spinirostris is usually regarded as an Atlantic form, but it has been identified in the plankton of the Norwegian Sea as far as north of Spitsbergen at 81° N. lat. (FARRAN 1936). It was probably carried there by the North Atlantic current. It also occurs, though scarce, in

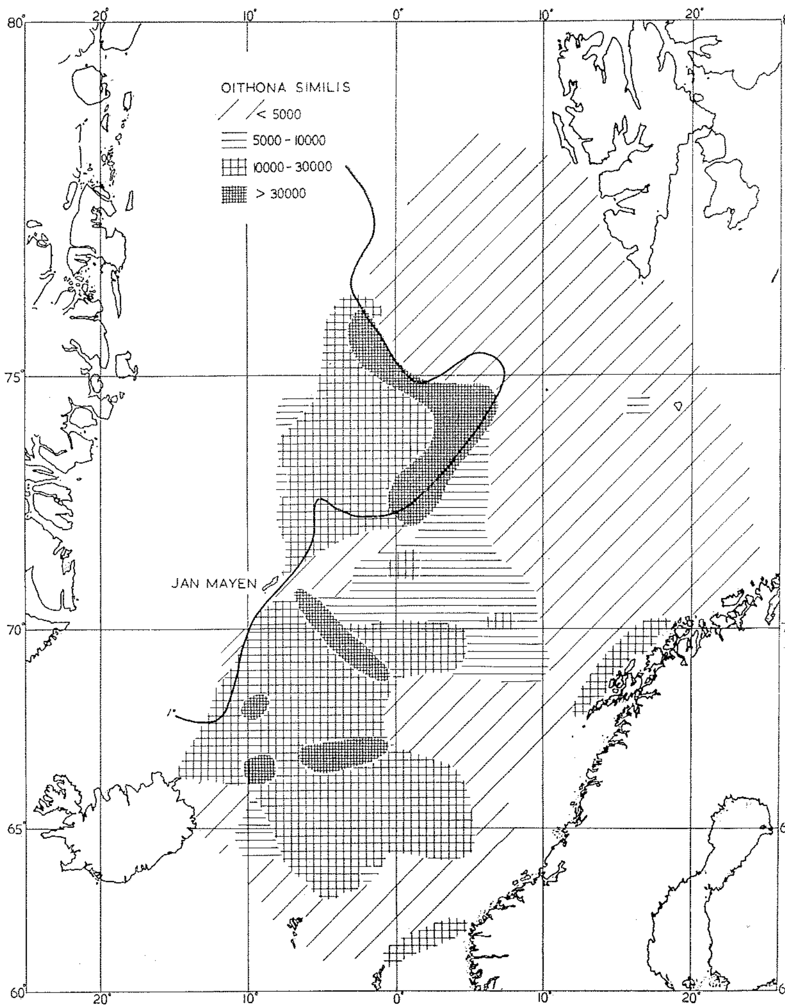

Fig. 25. Quantitative distribution of *Oithona similis* in 1948—1953.

some fjords of East Greenland (JESPERSEN 1939) and its presence there is possibly connected with the warm undercurrent from the north. At station M, *O. spinirostris* was most abundant in the 600—100 m layer, but moderately numerous in the upper 100 m i May and June (ØSTVEDT 1955).

O. spinirostris has been found in moderate numbers, usually 50—500 specimens per haul, at most of the stations in the Norwegian Sea. In the cold area it was missing in the surface layers, but was found below 100—200 m. In 1953 it was more scarce in the upper layers than in the preceding year from the Bear Island section to the northwestern coast of Spitsbergen. The areas where the stock of *O. spinirostris*

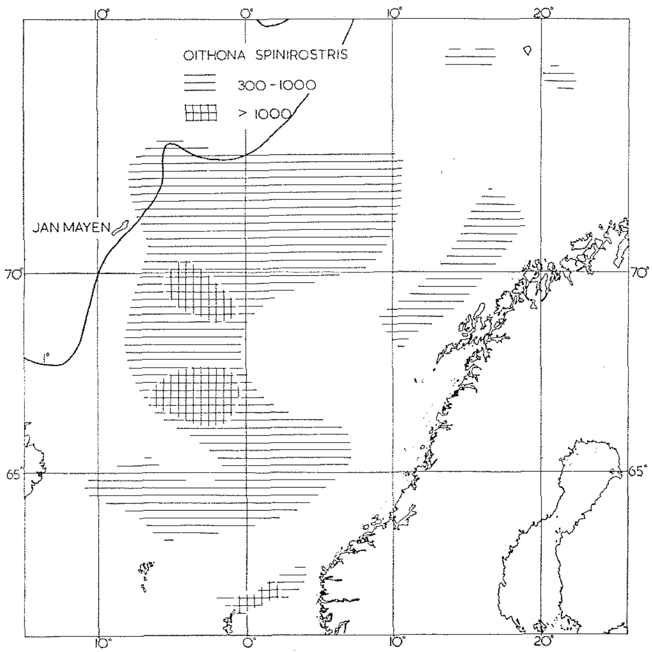

Fig. 26. Quantitative distribution of *Oithona spinirostris* in 1948—1953.

exceeded 500 specimens in the upper 200 m were plotted (fig. 26). The area of maximum abundance is mainly limited by the 4° and 7° isotherms at 50 m. Station M falls within this area. In June 1951 *O. spinirostris* was also abundant from Møre on the west coast of Norway to Shetland.

Oncaea borealis G. O. Sars

Oncaea borealis is usually found in intermediate or deep water, although it may also occur near the surface. According to JESPERSEN (1939) the species has its main distribution in colder, partly arctic areas, but it is also common in the deeper layers of some Norwegian fjords (RUNNSTRØM 1932, WIBORG 1940). At station M it is present below 100 m all the year round and especially numerous between 1000 and 600 m. In May and June a moderate stock is found in the upper 50 m (ØSTVEDT 1955). In East Greenland waters *O. borealis* is abundant near the coast in the Polar current (JESPERSEN 1939), and also numerous in the fjords in July—October (USSING 1938, DIGBY 1954).

The distribution of *O. borealis* in the Norwegian Sea in 1948—1953 (fig. 27) is very similar to that of *Pseudocalanus minutus*, but more restricted, probably because the hauls were not taken deeper than 200 m.

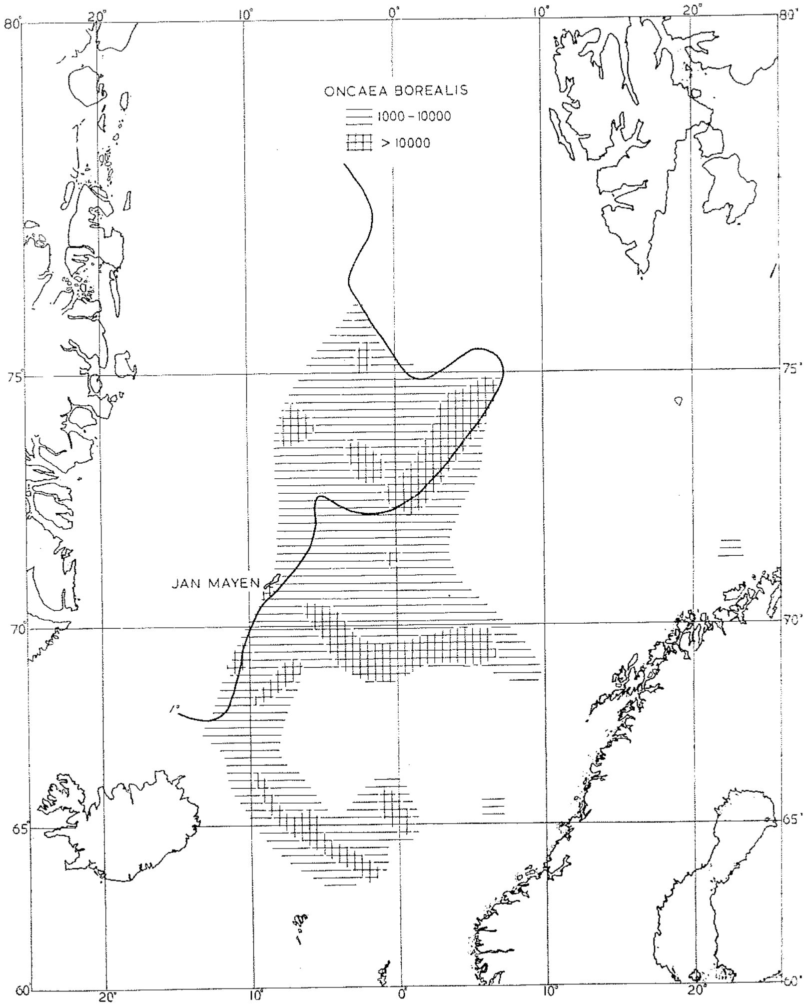

Fig. 27. Quantitative distribution of *Oncaea borealis* in 1948—1953.

Oncaea borealis was present at most of the stations, but scarce outside the hatched areas. A few deep hauls taken in 1953 revealed that in the cold area *O. borealis* was found mainly in the upper 100 m in some localities, in others between 600 and 100 m. In the temperate area the species was very scarce down to 1000 m at three stations. In September 1953 some specimens were taken in the upper 100 m off western Spitsbergen. Farran (1936) found *O. borealis* in abundance north of Spitsbergen in July.

A number of females of *O. borealis* were measured. The total range of variation was 0.425—0.525 mm. In 1952 three size groups could be distinguished. In the cold area the females were small (mean length 0.47 mm) except at two stations, where they averaged 0.485 mm, the same as southeast of Jan Mayen and north of the Faroes. In 1953 *O. borealis* was also smaller in the cold area. In September 1953 in temperate water off western Spitsbergen the females had a mean length of 0.47 mm.

In common with *Pseudocalanus minutus*, the smaller individuals of *Oncaea borealis* are found in the cold area. The reason may be that

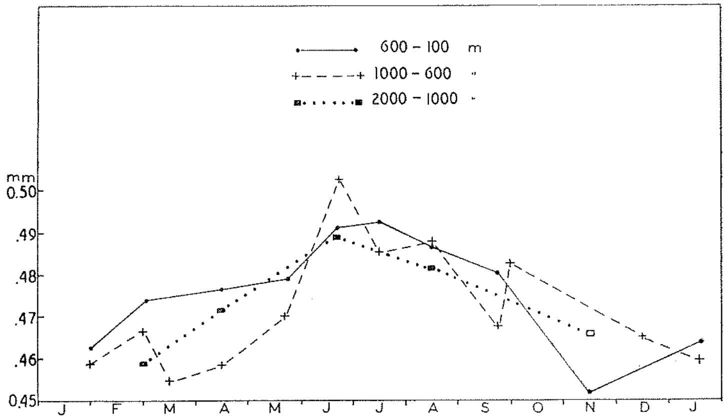

Fig. 28. Variation in mean length of females of *Oncaea borealis* at station M in 1952.

they also have their origin in the temperate areas of the Norwegian Sea. As *O. borealis* is found in numbers in the upper 100 m at station M during summer (ØSTVEDT 1955), some individuals may be carried away with the North Atlantic current, as was suggested in the case of *Pseudocalanus minutus*. The presence of small *Oncaea borealis* west of Spitsbergen in September 1953 also supports this hypothesis. It is also possible that local populations may be found in the cold area, living under similar temperature conditions in the intermediate layers.

In Scoresby Sound, East Greenland, females of *O. borealis* measured 0.42—0.54 mm, mean length 0.47—0.49 mm (DIGBY 1954).

O. borealis females taken at station M during 1952 were also measured (fig. 28). The mean length increased from January—March to a maximum in June—July, and decreased afterwards till January the following year. The size curves differ somewhat from one depth to another, but the main features are the same. If we consider the changes in mean length as percentage of the minimum length, there is an increase of 7—10 % in maximum length. For *Microcalanus pusillus* and *C. finmarchicus* this figure has been calculated as 13 % at station M. In neritic species the relative length variations can be much greater, as high as 33 % in *Pseudocalanus elongatus.*

Oncaea borealis is very abundant in the inner part of the Oslo fjord with maximum occurrence in the upper 50 m (WIBORG 1940). Below 25 m the temperature is 6°—7°C. all year and the maximum salinity is 32—33 ‰. The *O. borealis* from the Oslo fjord have been measured from two stations in July 1933 and February 1934. The mean lengths were 0.441 mm and 0.424 mm respectively, the range 0.40—0.49 mm. The smallest specimens, taken in February, had probably grown up during the autumn in water of higher temperature, those in July evidently belonged to the generation hatched in February. The occurrence of *O. borealis* in the Oslo fjord is perhaps similar to that of *Metridia longa* there, both species otherwise living in the intermediate and deep layers of the Norwegian Sea and in the upper layers of arctic seas (JESPERSEN 1939).

Other Copepods

In addition to the species treated above, other copepods were found more or less regularly.

Neritic species: *Paracalanus parvus* (Claus), *Pseudocalanus elongatus* (Boeck), *Temora longicornis* (Müller), *Centropages hamatus* (Lilljeborg), *Acartia clausi* Giesbrecht, *A. longiremis* (Lilljeborg), *Anomalocera patersoni* Templeton. *Centropages typicus* Kröyer may be included here, although it is also Atlantic.

Paracalanus parvus, Pseudocalanus elongatus, Acartia clausi and *Centropages typicus* were all abundant in a section from western Norway to Shetland in July 1950. *P. elongatus* numbered more than 70 000 specimens per haul at some stations. In the other areas of the main occurrence the different species seldom exceeded a few hundred specimens.

Temora longicornis was selected to illustrate the distribution of neritic organisms (fig. 12, p. 21). In July 1950 and 1951 *T. longicornis* was very abundant in the Iceland—Faroe area. More than 15 000 specimens per haul were taken near the slope, but abundance decreased very suddenly towards deep water.

Species of Atlantic origin: In addition to *Centropages typicus*, the following species have been recorded singly or in small numbers: *Eucalanus elongatus* Dana, in the Faroe—Shetland Channel in July 1950, *Rhincalanus nasutus* Giesbrecht off northern Norway and west of Bear Island, *Clausocalanus arcuicornis* (Dana) off Møre in June and August.

Scottocalanus securifrons (Scott) was taken at approximately 71° N. lat., 10° E. long., below 100 m. This seems to be the northermost record of this species (ØSTVEDT 1955). *Pleuromamma robusta* (Dahl) was caught singly from north of Shetland to northern Spitsbergen, always in Atlantic water.

Species of intermediate or deep layers: *Spinocalanus abyssalis* Giesbrecht, *Aetideus armatus* (Boeck), *Chiridius obtusifrons* Sars, *Gaidius tenuispinus* (Sars), *Pareuchaeta norvegica* (Boeck), *P. farrani* (With), *P. glacialis* (Hansen), *Scaphocalanus magnus* (Scott), *S. brevicornis* (Sars), *Scolecithricella minor* (Brady), *Pleuromamma abdominalis* (Lubbock) and *Oncaea conifera* Giesbrecht were all found more or less regularly, usually singly or in small numbers. *Pareuchaeta norvegica* and *Scolecithricella minor* were most common. According to GRAN (1902) the former is characteristic of the intermediate layers of the Norwegian Sea. ØSTVEDT (1955) found *Pareuchaeta norvegica* most abundantly between 600 and 100 m. The present material is therefore not representative of the distribution. The species was taken regularly in numbers of 20 to 50 per haul, but seldom above 200 m in the cold area. When deep hauls were made, *P. norvegica* was most numerous in the 600—100 m layer, but was also common below 600 m. — *Scolecithricella minor* was caught fairly often in all areas when the hauls were taken down to 200 m.

Other species: *Microsetella norvegica* (Boeck) was taken regularly in small numbers, especially in the central part of the Norwegian Sea. Because of its small size, it was not caught quantitatively in the nets.

Coelenterata

Aglantha digitale (Müller)

According to GRAN (1902), *Aglantha digitale* is indigenous to the Norwegian Sea. The adults are most common in the deeper layers. The young are sometimes very abundant near the surface and may be carried with the currents. ØSTVEDT (1955) usually found *A. digitale* below 100 m, but a large number of young individuals was taken in the upper layers in June and July.

The distribution of *A. digitale* was plotted for 1948—1953 (fig. 29). The main stock was found in the central and southern part of the Norwegian Sea. Single specimens occurred widely except in the cold area, and from Bear Island and northwards. In September 1953, 50—250 young per vertical haul were taken in the surface layers off western Spitsbergen. GRAN (1902) observed a mass occurrence of young *Aglantha* southeast of Bear Island in August. There is probably a centre of pro-

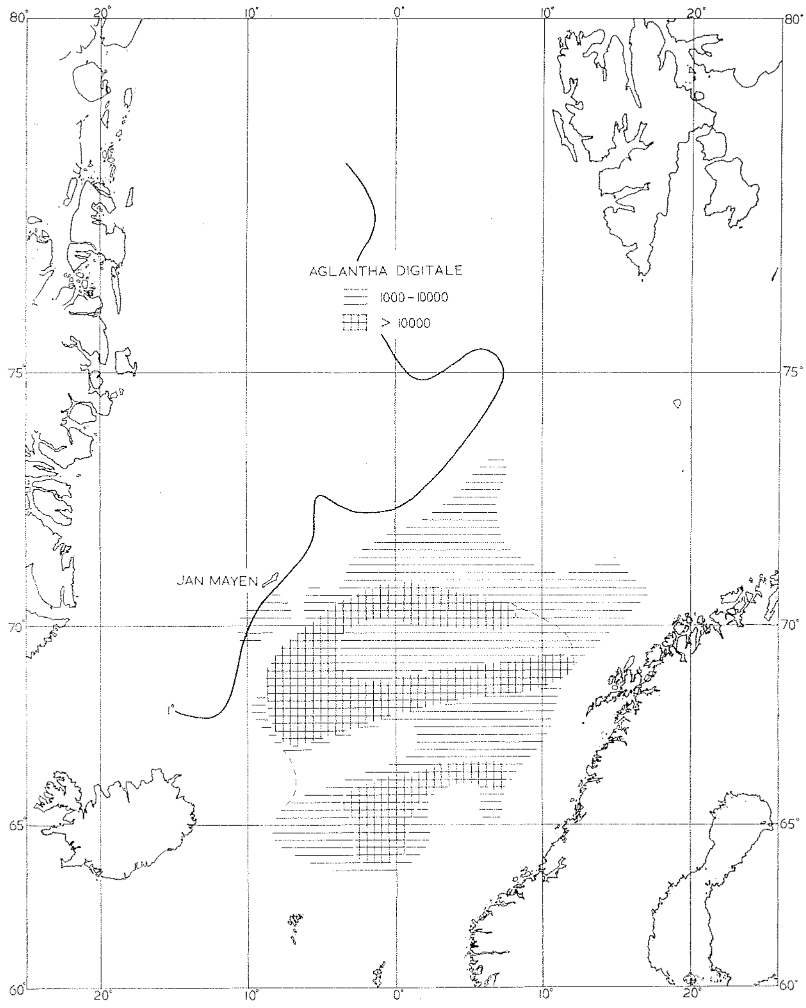

Fig. 29. Quantitative distribution of *Aglantha digitale* in 1948—1953.

pagation in the central part of the southern Norwegian Sea, from where young *A. digitale* are distributed to other areas. FRASER (1952) lists *A. digitale* together with *Sagitta serratodentata* as Atlantic species, and FRASER & SAVILLE (1949) found *A. digitale* in quantity in the Faroe—Shetland Channel in July 1948 along with Atlantic organisms. It may therefore be carried into the Norwegian Sea with the North Atlantic current. In the Denmark Strait there is another current of Atlantic water, the Irminger current. At weather station A, 62° N. lat., 33° W. long., small *A. digitale* were extremely abundant from July to October 1954.

Other Species

In July 1950 *Bougainvillea principis* (Steenstrup), *Laodicea undulata* (Forbes & Goodsir) and *Phialidium* sp. were found near the Faroes, *Cosmetira pilosella* Forbes near Shetland. *Diphyes arctica* (Chun) occurred often in the deep hauls. *Agalmopsis elegans* Sars was taken near the Faroes in July 1950, and off the coast of North Norway and west of Bear Island in June 1952.

Pteropoda

Limacina retroversa (Fleming) was usually numerous in the surface layers at station M in June—July and September—November (ØSTVEDT 1955).

The distribution in the Norwegian Sea in 1948—1953 was plotted (fig. 30). The distribution is very similar to that of *Aglantha digitale* (fig. 29), but there are also concentrations between Shetland and Norway, and off North Norway and Bear Island. In the Norwegian Sea the stock is probably supplied both from the Atlantic (PAULSEN 1910), and from nearby coastal areas. At station M the species was not taken during April—May, and an increase took plase very suddenly in June (ØSTVEDT 1955). In September 1953 *Limacina retroversa* was taken in moderate numbers immediately west of Spitsbergen. A vertical haul close to the coast yielded 22 400 small *Limacina*, probably *L. retroversa.*

L. helicina (Phipps) is an arctic species. DAMAS & KOEFOED (1909) found it in the fjords of Greenland and Spitsbergen, near Bear Island and Jan Mayen, and in the cold area of the Norwegian Sea. FRASER (1952) stated that *L. helicina* is usually taken together with *Calanus hyperboreus, Metridia longa, Oikopleura vanhöffeni* and other arctic species.

The distribution of *Limacina helicina* in the Norwegian Sea in 1948—1953 was plotted (fig. 30). Most of the individuals in the cold area were very small. Larger specimens were only taken along the coast of Bear Island and Spitsbergen. The exact distribution of *L. helicina* could not be determined, as the small individuals were not always identified to species. The boundary probably coincides with the 1°C. isotherm at 25 m.

Clione limacina (Phipps) has been taken singly or in small numbers in all areas.

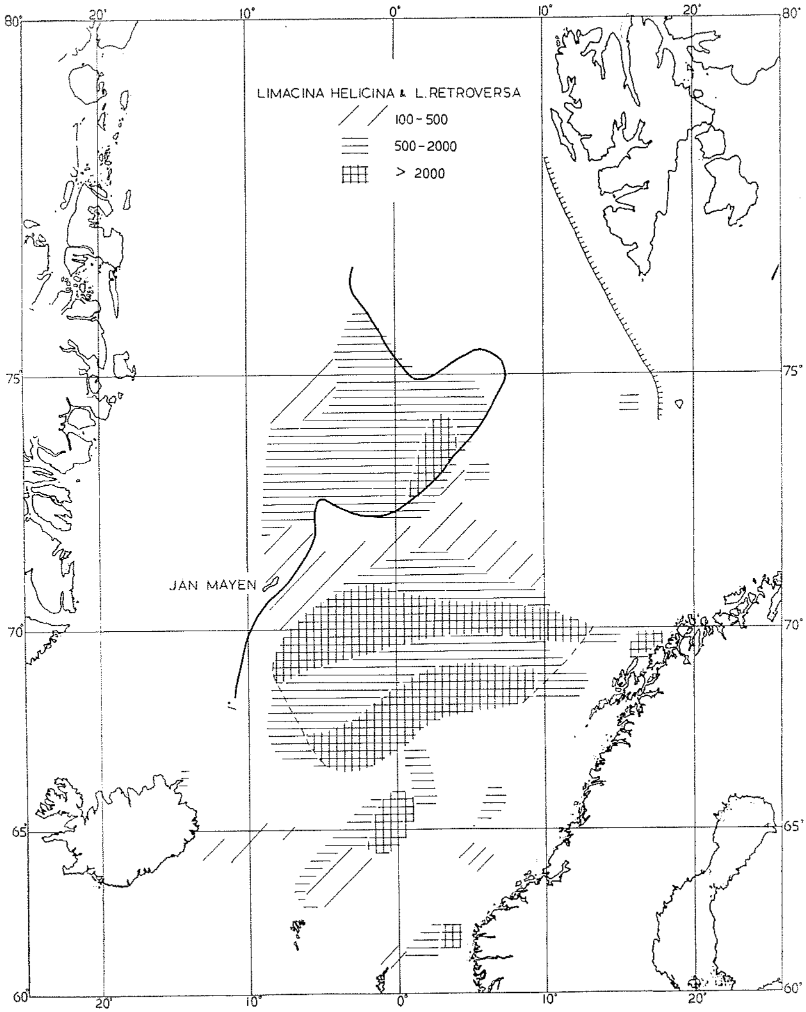

Fig. 30. Quantitative distribution of *Limacina helicina* (west of the continuous, and east of the feathered line), and of *L. retroversa* (east of the continuous line) in 1948—1953.

Chaetognatha

Sagitta elegans Verrill

According to FRASER (1952) *Sagitta elegans* can be divided into three subspecies: *S. e. elegans,* a coastal form associated with oceanic influence, found on both sides of the Atlantic; *S. e. baltica* in the Baltic; *S. e. arctica* with a boreal-arctic distribution. In the present material no distinction has been made between the subspecies, but it is assumed

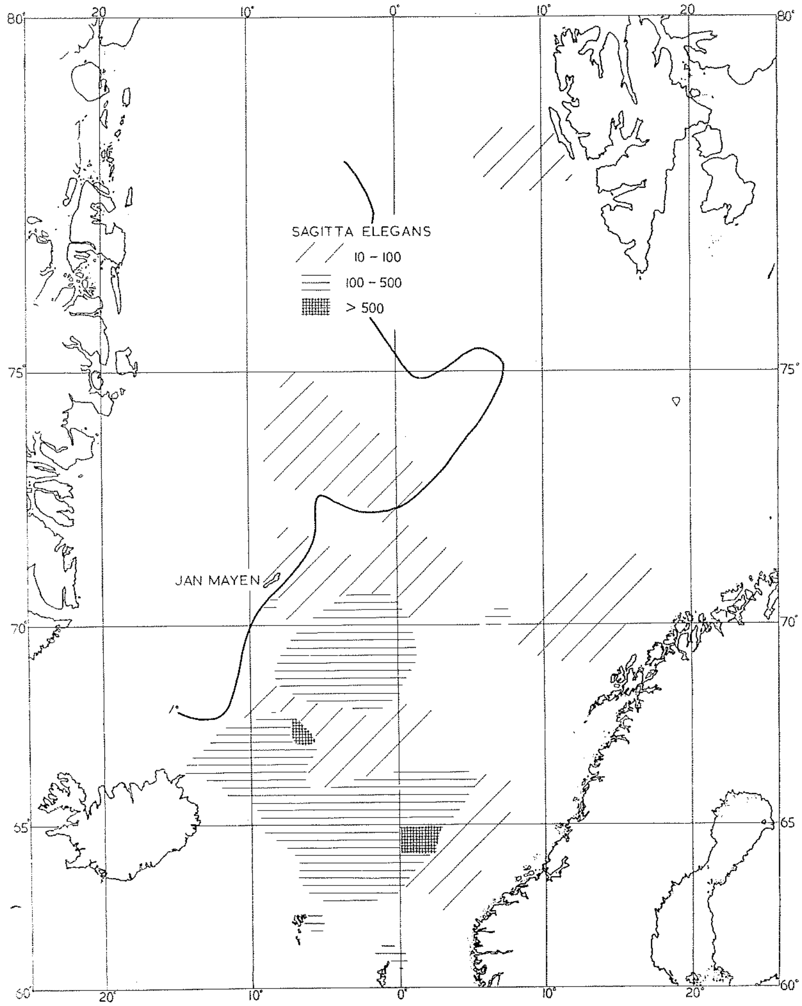

Fig. 31. Quantitative distribution of *Sagitta elegans* in 1948—1953.

that there is mainly *S. e. arctica*. At station M, ØSTVEDT (1955) found this subspecies exclusively.

The distribution of *S. elegans* during 1948—1953 was plotted (fig. 31). The main stock seems to be concentrated in the southern part of the Norwegian Sea, and few were found in the cold area. The specimens present were possibly brought in by the warm current northeast of Jan Mayen. *S. elegans* was very scarce in the deeper layers in the cold area. Off western Spitsbergen it was only taken in September 1953. Single individuals occurred all over the temperate area. At station M, ØSTVEDT (1955) found *S. elegans* in quantity in the upper 100 m only in June and July. The individuals then measured less than 10 mm and probably originated from a spawning in April—May. At other times of the year the majority was usually taken in the 600—100 m layer.

Eukrohnia hamata (Möbius)

FRASER (1952) states that *Eukrohnia hamata* is found at all depths in boreal waters, but in more temperate zones it is associated with cold water. It is usually taken with *Sagitta elegans arctica, Calanus hyperboreus, Metridia longa, Limacina helicina* and other cold water species. According to ØSTVEDT (1955) it is a permanent member of the fauna below 100 m at station M, with maximum occurrence in the 600—100 m layer. In the upper 100 m he found the highest number in June.

The quantitative distribution of *Eukrohnia hamata* in the Norwegian Sea in 1948—1953 was studied (fig. 32). In contrast to *Sagitta elegans*, *Eukrohnia hamata* is common all over the Norwegian Sea and much more numerous, especially in the colder parts, as was also found by DAMAS & KOEFOED (1909). One must remember, however, that the hauls cannot be regarded as representative of the population. The deep hauls taken in 1953 showed that the maximum occurrence was between 600 m and 100 m.

Cladocera

The distribution of *Evadne nordmanni* Lovén has already been discussed (p. 22). In coastal waters *Podon* spp. usually had the same distribution as *Evadne*. Along the Iceland—Faroe ridge a maximum of 2100 specimens per haul was taken in July 1951, but the abundance decreased very rapidly towards deep water. No specimens were found very far from shore.

Ostracoda

The ostracods belong to the intermediate and deep water layers, and are therefore not accurately represented in the material. In the cold area, and north of Bear Island, ostracods were taken quite regularly (50—400 specimens per haul) but were mostly juveniles. When deeper hauls were made, the ostracods were found almost equally distributed in the 600—100 m and 1000—600 m hauls, but never in large numbers. The maximum was 1000 specimens in the column from 1000 m to the surface. The species most often present were *Conchoecia elegans* Sars and *C. borealis* Sars, but *C. obtusata* Sars was also taken.

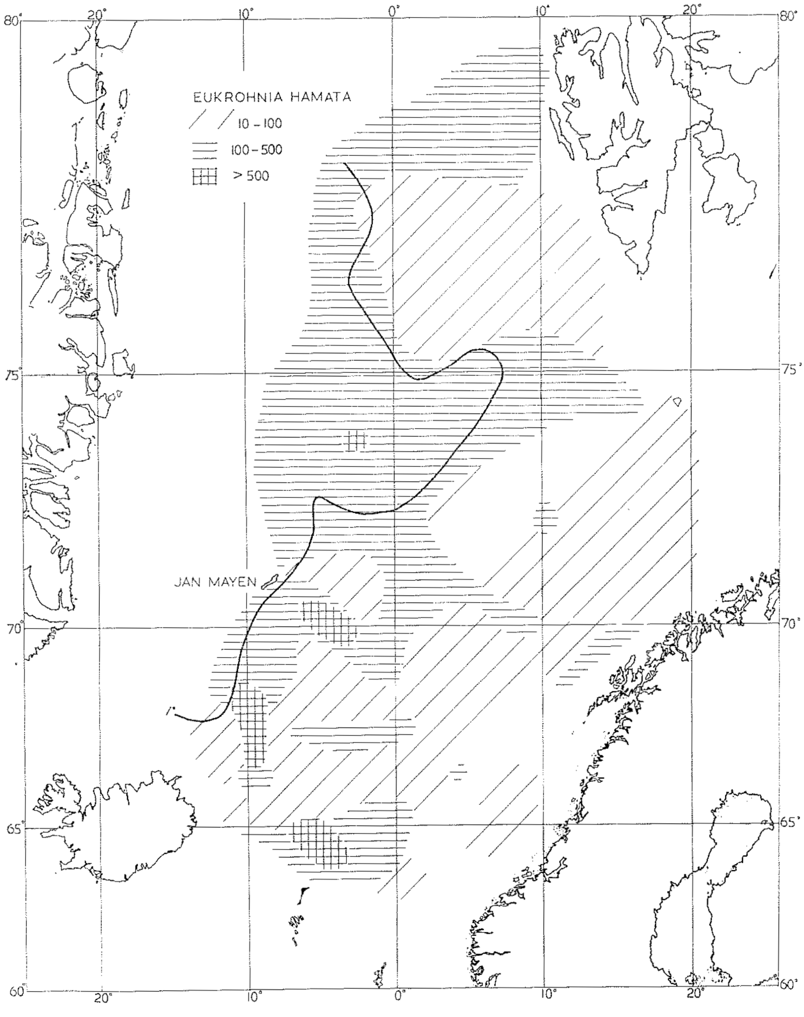

Fig. 32. Quantitative distribution of *Eukrohnia hamata* in 1948—1953.

Amphipoda

Themisto abyssorum Boeck

According to GRAN (1902) *Themisto abyssorum* is very common in the Norwegian Sea, and is characterized as oceanic-arctic-boreal, with the main distribution in water of arctic origin. Adults were mainly taken in deep water, while the young were in the upper layers. At station M, ØSTVEDT (1955) found the adults mainly below 100 m, most abundantly below 600 m. The young were common in the upper 100 m, with the maximum occurrence in April—June.

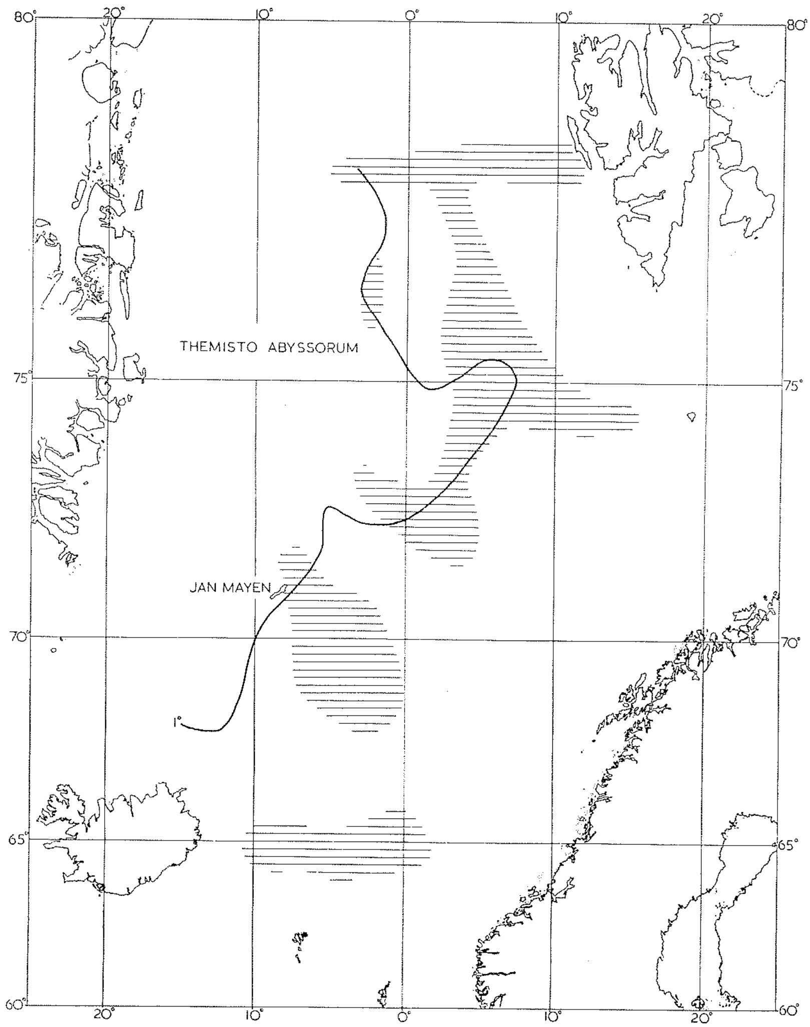

Fig. 33. Themisto abyssorum. Hatched areas indicate where the stock exceeded 100 individuals per vertical haul.

T. abyssorum was very common in the Norwegian Sea in 1948—1953. Because of the shallow hauls mainly young specimens were taken. The areas where 100 or more specimens were taken per haul, were plotted (fig. 33). In 1948—1950 the number per station varied between 4 and 160, averaging about 20—50. In the southern Norwegian Sea 250—500 specimens were taken per station in 1951. *T. abyssorum* was very abundant in the cold area in June 1952 and 1953. The numbers obtained evidently depended on whether or not one sampled after a period of reproduction.

Themisto libellula (Mandt) was caught singly at a number of localities, especially in or near the cold area.

Themisto compressa f. compressa (Goes) was found at a few stations, mainly in Atlantic water off the west coast of Norway.

Euphausiacea

As mentioned (p. 15) euphausiids are not caught quantitatively in ordinary plankton nets. Therefore only information on the occurrence of the different species will be given. In 1951 and 1952 adults of *Meganyctiphanes norvegica* (M. Sars) were taken singly off the west coast of Norway and along the Iceland—Faroe ridge. In 1953 this species was also found southeast of Jan Mayen and off western Spitsbergen at nine stations. *Meganyctiphanes* larvae were found in moderate numbers in June—July off the Iceland—Faroe ridge, north of Shetland, and off the west coast of Norway.

Thysanoessa longicaudata (Kröyer) was the most common species. Adults occurred at 65 stations, mainly in the temperate area, sometimes as many as 20—30 specimens per haul. In 1953 the species was also taken in the cold area. Larvae were fairly abundant, especially in July in the southern Norwegian Sea, but some were also taken along the continental slope of Norway and off western Spitsbergen.

Thysanoessa inermis (Kröyer) is a coastal form and the adults were mainly caught near Iceland, off western Norway, Bear Iceland and Spitsbergen at 14 stations. Eggs and early larvae were numerous on the Bear Island bank in June 1948.

Thysanoessa raschi (M. Sars) and *Thysanopoda acutifrons* (Holt & Tattersall) were both recorded from one station off Møre in August 1951.

Copelata

Five species of Copelata have been identified, namely: *Fritillaria borealis* Lohmann, *Oikopleura dioica* Fol, *O. labradoriensis* Lohmann, *O. vanhøffeni* Lohmann and *O. parva* Lohmann. The first two species are neritic.

Fritillaria borealis was found as abundant as 2000 specimens per haul northeast of the Faroes, and also abundant in the Faroe—Shetland Channel, northeast of Iceland, off the coast of North Norway and east of Jan Mayen. This species has maxima of abundance in Norwegian coast waters in April—May and July—August (WIBORG 1954).

Oikopleura dioica was taken in considerable numbers between Norway and Shetland in June 1950 and in bank water off Møre in June 1952. This species is numerous in coastal areas of Norway in June and July (WIBORG 1954).

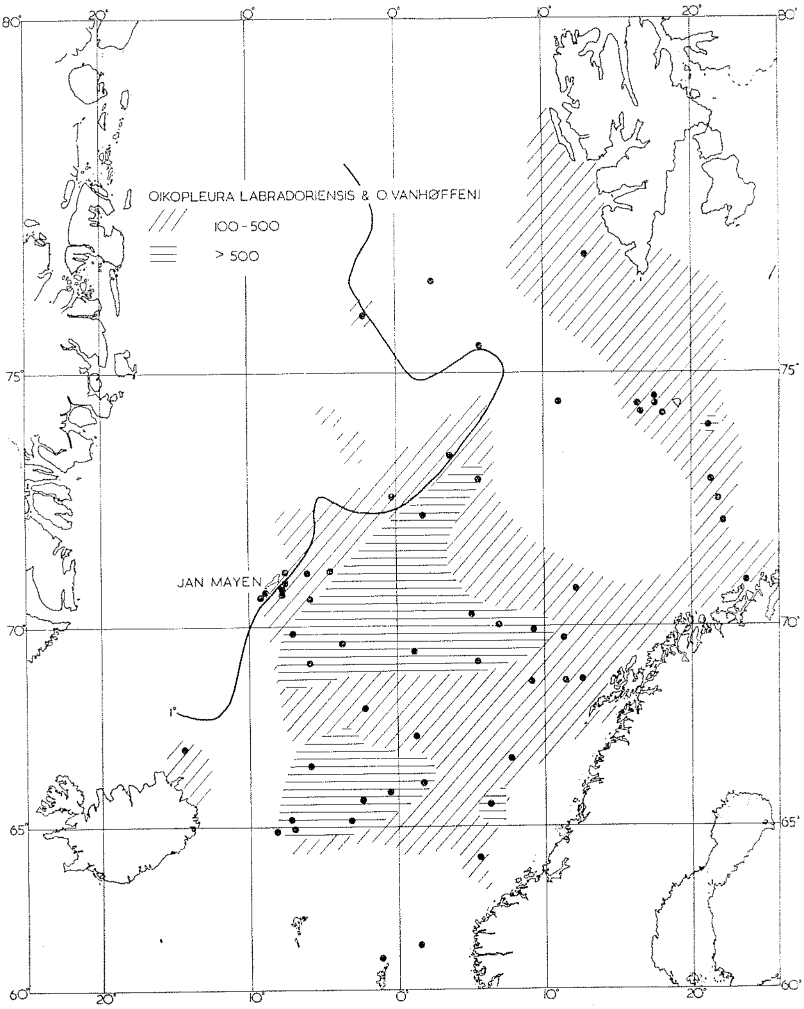

Fig. 34. Quantitative distribution of *Oikopleura labradoriensis* and *O. vanhøffeni* 1948—1953. Dots indicate records of *O. vanhøffeni*.

The distribution of *O. labradoriensis* and *O. vanhøffeni* was plotted (fig. 34). As stated earlier (WIBORG 1954) there is some doubt as to the identification of *O. vanhøffeni*. The two species were therefore not separated. There are two main areas of distribution, one in the southern part of the Norwegian Sea and another between Jan Mayen and Norway, but with a few exceptions the catch never exceeded 100 specimens per haul. In the cold area the two species are very scarce or absent, except near Jan Mayen, Bear Island and western Spitsbergen. In 1954, however, *O. vanhøffeni* was found in moderate numbers north and northeast of

Jan Mayen. It has previously been reported from Spitsbergen (DAMAS & KOEFOED 1909), the Barents Sea (LOHMANN 1901—1911), near Shetland (BÜCKMANN 1926), the Faroes (FRASER & SAVILLE 1949), and the coast of Norway (WIBORG 1954). It is therefore to be expected that *O. vanhøffeni* should be widely distributed in the Norwegian Sea.

O. labradoriensis is boreal (LOHMANN 1901—1911) and numerous in Norwegian coastal waters in June and July (WIBORG 1954). The areas of maximum density are mainly dependant on this species.

O. parva occurs along the west coast of Norway (RUNNSTRØM 1932, WIBORG 1954) and is said to belong to the deeper warmer layers of the Norwegian Sea (LOHMANN 1911). A few specimens have been found on different stations from the southern Norwegian Sea to off western Spitsbergen, all of them below 200 m.

Thaliacea

A few specimens of *Salpa fusiformis* Cuvier were taken in the Faroe—Shetland Channel near Shetland in July 1950, and some off the coast of Møre, western Norway, on 31 August 1951. As reported previously (WIBORG 1954) salps were recorded at station M in September—October 1950, but were absent in 1951—1952, when they occurred abundantly along the west coast of Norway. In 1953 salps were again taken in numbers at station M from 25 September to 4 November.

SUMMARY

A study was made of the distribution of zooplankton organisms in the Norwegian Sea during May—August 1948—1954. It is based on plankton collected in vertical Nansen net hauls in the upper 200 m. Samples taken by the Norwegian weatherships at station M during 1950—1954 were used as a supplement.

The hydrographical conditions in the area are discussed on the basis of earlier investigations, and on observations taken with the plankton samples.

The greatest concentrations of plankton were found along the slopes of the continental shelves and near the submarine ridges, in the border areas between cold and temperate water, and in or near the centres of the cyclonic systems.

During the summer, water of Atlantic origin was poor in plankton.

The most important whaling grounds correspond very well with the localities where the largest quantities of plankton were observed.

At station M, more plankton was usually taken in the upper 25 m during the night than during the day. In hauls taken down to 200 m diurnal vertical migration does not influence the quantity of plankton to any extent, except for euphausiids which usually avoid the net during the day.

One may broadly distinguish between a cold area, including the Greenland Sea, and a temperate area in the Norwegian Sea. The former is mainly characterized by *Calanus hyperboreus*, the latter by *Calanus finmarchicus*. In the temperate area the central part is dominated by *Aglantha digitale* and *Limacina retroversa* in summer.

The distribution of neritic organisms is mainly correlated with the extension of the coastal water. In summer *Evadne nordmanni* may establish a local population in the open sea between Jan Mayen and Norway.

Temperature is assumed to be the most important factor influencing growth and size of copepods.

The horizontal distribution of various plankton organisms during the summer is shown.

Calanus hyperboreus was dominant in the cold area, but also moderately abundant in the East Iceland current to the north of the Faroes. Single individuals were found all over the temperate area. Two populations can be distinguished by size distributions. The smaller individuals were found in the temperate area and in border areas between cold and temperate water.

Calanus finmarchicus was dominant in the temperate area, the distribution in general corresponding with the volumetric distribution of the plankton. Different populations have been distinguished on the basis of size distributions. The largest individuals live in coastal and bank waters from Bear Island to Spitsbergen and in the cold area, but the smaller individuals dominate in all areas. Those present in the cold area have evidently been introduced from the temperate area with branches of the North Atlantic current.

Pseudocalanus minutus is a native of the open ocean, being replaced in coastal areas by *P. elongatus*. The largest stocks were located in the southwestern corner of the Norwegian Sea, and in the border areas between cold and temperate water. *P. minutus* was scarce in the cold area. There were two or more populations. In the cold area the stock consisted of small individuals probably introduced from the temperate area the previous autumn. Some large individuals were found near Jan Mayen and on the banks from Bear Island to Spitsbergen.

Microcalanus pusillus lives chiefly between 600 and 100 m, and is distributed quite uniformly over large areas of the Norwegian Sea. The samples are not representative of the distribution. In the cold area the individuals were small and were probably introduced from the temperate area.

Microcalanus pygmaeus was mainly found in the deeper layers of the Norwegian Sea, at station M chiefly below 1000 m. In the cold area some specimens were taken in the upper 200 m. At station M the stock is probably supplied from other parts of the Norwegian Sea, and conclusions have been drawn regarding the renewal of the bottom layers.

Metridia longa was common in the intermediate and deeper layers of the Norwegian Sea. *M. lucens* was most abundant in the eastern parts, partly introduced with the North Atlantic current. The size variations of the individuals are discussed for both species.

Oncaea borealis and *Oithona helgolandica* were both similar to *Pseudocalanus minutus* in horizontal distribution. The latter were also numerous in coastal areas, especially during the autumn.

Oithona spinirostris is quite common in the intermediate layers. The area of maximum abundance is generally limited by the 4° and 7°C. isotherms at 50 m.

Aglantha digitale was mainly confined to the intermediate and deeper layers as adult form, and reproduced very heavily in June—July. The young were numerous in the upper layers in the central parts of the temperate area of the Norwegian Sea, especially between Jan Mayen and Norway. Later in the autumn they were carried farther northwards.

Limacina retroversa was similar to *Aglantha digitale* in oceanic distribution, but was also numerous in coastal areas. *Limacina helicina* was restricted to the cold areas.

Sagitta elegans was most abundant in the southwestern part of the Norwegian Sea. *Eukrohnia hamata* was common in all areas and more numerous than *Sagitta elegans*, especially in the colder parts. As the two species also live in the intermediate and deeper layers, the material is not representative of the distribution.

Ostracods were taken regularly, especially in the cold area. They live mainly in the intermediate and deeper layers.

Of the amphipods, *Themisto abyssorum* was most usual. It was found all over the Norwegian Sea, mainly as young individuals. The highest numbers were observed in the cold area.

Eggs and larvae of euphausiids were taken fairly regularly, especially in coastal and slope areas. Adult euphausiids are not caught quantitatively. *Thysanoessa longicaudata* was the species most frequently taken.

Of the copelates, *Oikopleura labradoriensis* and *O. vanhøffeni* were most numerous. There were one or two main areas of distribution in the temperate area, but the copelates were scarce or absent in the cold area. *O. vanhøffeni*, however, was taken in moderate numbers north of Jan Mayen in 1954. *Fritillaria borealis* was numerous in some coastal areas, e.g. northeast of the Faroes.

Salps were taken in the Faroe—Shetland Channel in July 1950 and off the west coast of Norway in August 1951. They were numerous at station M in September—November 1951 and 1953.

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