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UNDER LEDELSE AF LAUGE KOCH

THE BIOLOGY OF SOME IMPORTANT PLANKTON ANIMALS IN THE FJORDS OF EAST GREENLAND

BY

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WITH 27 FIGURES IN THE TEXT

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PREFACE

During the Danish Three-Year Expedition to Christian X's Land (East Greenland) 1931—34 under the leadership of Dr. LAUGE KOCH collections of plankton were made regularly, about every fortnight, from fixed stations, thus in 1931—32 at Ella Island by Dr. G. THORSON and in 1932—33 at Eskimonæs by mag. sc. H. MADSEN. The present paper has been worked out chiefly on the basis of these collections, and I take the opportunity to thank the two gentlemen for having handed over to me their valuable material.

In the summer of 1933 I was myself a member of the expedition on board the s. s. *Godthaab*, from which zoological and hydrographical investigations were made, and I had thus the opportunity to make a number of observations in the field which have afterwards been of great use to me during the preparation of the present work. For this opportunity to become aequainted by personel inspection with the fauna of the fjords of East Greenland I wish to express my thanks to the leader of the expedition, Dr. LAUGE KOCH.

For permission to use the Zoological Laboratory I thank the former leader of the laboratory Professor AD. S. JENSEN.

To Dr. P. JESPERSEN and Dr. E. STEEMANN NIELSEN I am indebted for valuable help in various questions concerning the literature.

Finally I wish to express my gratitude to Professor A. KROGH and Professor R. SPÄRCK for the interest they have taken in my work and for good advice given me during the preparation of the present paper.

INTRODUCTION

Through the expeditions of the last half century the zooplankton of the Arctic seas has been thoroughly investigated both as regards the stock of species and the distribution of these species. At the same time a large number of observations have been made on the biology of the different species, especially in regard to their periods of reproduction and stages of development, and it has been quite empirically ascertained what depths these species prefer.

That nevertheless our knowledge of the biology of the plankton animals of the Arctic is rather incomplete, is due in the first instance to the fact that the material has mostly been collected on summer trips. This means that samples from the winter time are lacking to a great extent, and the biology of the Arctic plankton animals during the winter is thus partially unknown. From Greenland waters only one investigation with samples from all seasons of the year was available, viz. that of the DRYGALSKI Expedition to Little Karajak Fjord 1891—93 (see VANHÖFFEN, 1897).

This investigation brought to light several interesting observations; however, comparable countings are not available for the individual species of copepods, which constitute the main quantity of the animals, the copepods having been counted *en bloc*. Furthermore, the vertical plankton hauls are derived from different depths and are thus not comparable in themselves. The available material, collected from fixed stations in East Greenland by means of uniform hauls from uniform depths, therefore, should provide a possibility of furnishing fresh information in various respects of the biology of the Arctic plankton animals.

The presentation of the problems in the present work must differ somewhat from that of a corresponding work concerning Danish waters. The material is given once for all, and only such information has been obtained as can be derived from this given material. Questions which might be solved at home by verification experiments, must here be left open, or the solution must be given in the form of a hypothesis.



Fig. 1. East Greenland from about 70° to 74° 30′ N. lat.

Accordingly we cannot ask: What questions should be solved? but: What information can the material supply about the biology of these animals? As a consequence, the investigation of the common species will take up the greater part of the space, while the less common species will be treated quite briefly. The purpose is to give as thorough a report as possible on the biology of the common species.

Some few of the species mentioned have been subjected to very careful investigations in boreal seas. This is especially true of *Calanus finmarchicus*, about which a copious literature is available, which, however, it would take us too far to recapitulate here. In the following only such papers will be mentioned as may serve to elucidate the biology of the species in Arctic seas. Of other thoroughly investigated species may be mentioned *Calanus hyperboreus* (SØMME, 1934) and *Sagitta elegans* (RUSSELL, 1932—33). As is well known, however, experience of the biology of a species in one water cannot be immediately transferred to the same species living under other external conditions.

MATERIAL

The material which has been at my disposal consists of about 1000 vertical plankton hauls taken during G. THORSON's wintering on Ella Island in 1931—32, about 500 secured by H. MADSEN at Eskimonæs in 1932—33, and 40 hauls made by the Greenlander BENJAMIN SAMUELSEN at Ella Island in the autumn of 1932. The hauls were taken by means of a hand plankton net from a depth of 50 m to the surface and from 25 m to the surface; as to the few samples from October, 1931, however, the depths are 30 and 15 m. The samples were taken at intervals of about two weeks, from 10 to 50 samples each time. The winter samples were taken through a hole in the ice. The depth of the water at the place where the Ella Island samples were taken, was precisely 50 m, so that the deep samples were hauled through the whole water column from the bottom to the surface; the result has been that a number of animals which live at or in the bottom have been included in some of the samples. However, these species will not be treated in detail here. Two kinds of plankton gauze were employed, a very fine gauze (No. 12), which collected even the smallest nauplii, and a somewhat coarser one (No. 3), which for instance allowed nauplii of *Oithona similis* to pass through.

The material from Ella Island was fixed in 96 per cent. alcohol. The samples from Eskimonæs were fixed partly in alcohol, partly in 4 per cent. formol and partly in trichlorous acetic acid, sometimes in connection with formol. The latter fixations have proved to be more suitable than fixation by means of alcohol for *Appendicularia* and *Chaetognatha*, which are very poorly preserved in alcohol. On the other hand the great majority of the animals, viz. the *Copepoda*, have been excellently preserved in alcohol. A considerable number of the samples were counted and provisionally determined while the animals were alive by G. THORSON and H. MADSEN. By pouring the samples from one receptacle to another a number of the individuals are unavoidably lost and moreover a number of animals succumb during fixation. Hence some items of information are exclusively due to the above-mentioned

counts, since it has been impossible to find these animals again in the samples.

These counts are of importance for another reason, too. Owing to a lack of glasses several samples taken on the same day were poured into one glass, by which some individuals were lost; but the original number is found in the tables. As regards the *Copepoda*, no attempt at a determination was made in the counts; however, by a proportional calculation it is possible to arrive at the original number of the individual species.

Only pure plankton species will be treated below; the bottom animal larvæ have already been thoroughly treated by THORSON (1933, 1936).

As regards the quantitative comparability of the samples it may be said that the same species may be assumed to be collected in a number which depends to a great extent on the number in which it actually occurs in the water column in question. As to the absolute number of the species, however, it can only be said that the number found is a minimum number. As to the proportionate frequency of the species we must express ourselves with some caution. Large and easily mobile species, in particular, will show some tendency to be collected in too small a number, since they escape the net. This is no doubt the reason why the *Euphauciidae* are represented by a single specimen only, a *Calyptopis* stage, collected at Eskimonæs. For *Euphausiidae* are collected in no small number by ring-trawl in many places in the fjords. It is also remarkable that only quite young specimens of *Themisto* have been collected.

Certain species disappear almost completely when collected. This, for instance, is the case with the *Ctenophores*. Thus in 1933 I observed in Scoresby Sound that the uppermost water layer was teeming with a species of *Pleurobrachia* part of the summer, but merely unrecognisable jelly lumps were secured in the plankton nets. As a rule remnants of the cilia bands are preserved; but we can form no opinion as to the number of individuals.

Survey of the species found.

(The survey comprises merely purely pelagic species, while bottom animals and planktonic larvæ of bottom animals have been omitted).

Medusae.

Aglantha digitalis (O. FR. MÜLLER). Not rare.

Copepoda.

Calanus finmarchicus (GUNNERUS). Very common at both stations throughout the year.

Calanus hyperboreus. KRØYER. Common in July and August, totally absent from November to May.

Pseudocalanus minutus. KRØYER. Very frequent at all seasons.

Microcalanus pygmaeus. G. O. SARS. Fairly common except in the summer months.

Bradyetes brevis. FARRAN. The type specimen of this species, an adult female animal, was collected at Ella Island on October 30th, 1932 (see FARRAN, 1936).

Pareuchaeta sp. Copepodid stages of this genus were rather frequently found in the winter samples. It has proved impossible to determine their species. Probably they represent *P. glacialis* or *P. norvegicia*, or perhaps both.

Metridia longa. LUBBOCK. Fairly common, though almost absent from May to and including July.

Oithona similis. CLAUS. Very frequent at all seasons of the year.

Oncaea borealis. G. O. SARS. Rather common, especially in the summer.

Microsetella norvegica. BOECK. Some few specimens were collected at all seasons of the year.

Euphausiidae.

A single specimen of an *Euphausid* larva, a *Calyptopis* stage, was collected at Eskimonæs.

Mysidae.

According to the counts of H. MADSEN two specimens of a *Mysis* species were collected at Eskimonæs on August 16th, 1932. They were not found again in the samples.

Amphipoda.

Themisto libellula. MONDT. Not common.

Themisto abyssorum. BOECK. Quite small specimens of this species were collected at all seasons.

Isopoda.

Occasional young stages of *Epicardia* (*Microniscus*) were collected at all seasons.

Mollusca.

Limacina helecina PHIPPS. Common, though almost exclusively small specimens.

Clione limacina PHIPPS. Occasional larvæ were collected at Ella Island on May 11th, 1932.

Chaetognatha.

Sagitta elegans VERRIL. Rather common.

Eukrohnia hamata MÖBIUS. Some few specimens were observed at Ella Island.

Copelata.

Fritillaria borealis LOHM. Rather common.

Oikopleura labradoriensis LOHM. Rather common.

Possibly other species of *Oikopleura* are found, too. Owing to the poor state of preservation, however, it has been possible to identify this species only.

As will appear from the above, these samples testify to a fauna very poor in species. Some few species, which actually occur in these waters, may not have been collected because they have fled before the net. Others are absent because they chiefly or exclusively occur at depths of more than 50 m. This applies for instance to *Heterorhabdus norvegicus*, the *Conchoecia* species, and others which occur in these waters. But even if these species are included, the pelagic fauna is very poor in species.

However, this fact is an advantage rather than an obstacle to biological study, for it makes it easier to trace the development of the individual species and the part it plays in the household of Nature. Another factor of a similar effect is that the production of phytoplankton which forms the basis of the nourishment of the species, takes place during 2—3 months only. The food conditions of the animals are more easily overlooked. We may say that the life conditions in Arctic regions present an almost schematic picture as compared with conditions in boreal seas, where the whole is less clear. A study of the Arctic animals and animal communities will probably give us a better understanding of the corresponding, but more intricate, conditions in warmer seas.

Survey of the hydrographical conditions.

In the months January—May, 1932, water samples were regularly taken and temperature observations made in the uppermost 50 m near Ella Island. The temperature and salinity of these samples will be seen from Table 1. From this it appears that in that period (January 16—May 23) very small alterations took place in the hydrographical conditions. At a depth of 50 m the salinity increased gradually from 32.0 to 33.1 per mille, while at the same time the temperature fell from —1.50°

to —1.69° C. At the surface the salinity increased from 27.3 to 30.77 per mille, and the temperature fell from —1.46° to —1.59°. In the whole water mass the changes in salinity amount to 1—3 per mille and the temperature fluctuations to 0.1°—0,3°. From the month of June no samples are available, as the thaw rendered the collection of samples difficult. The further development of the hydrographical conditions must be assumed to be as follows: Immediately below the ice a layer of nearly fresh water will form, at most some metres thick, and of a temperature of about 0° C. Deeper down the rise of temperature will hardly be felt at the beginning of the summer. It is not till the solid ice breaks and drifts away or melts that the temperature at the surface rises above 0° C, and at the same time the water layer which is influenced by the fresh and warm water of the surface, the fjord water layer, will increase in thickness. Conditions in these fjords in July—August have been described by Spärck (1933). It appears from his description that the fjord water layer with positive temperatures and a salinity of less than 30 per mille had in August attained a thickness of 10—15 m in most places. Below this layer occurs the Polar Current water with temperatures ranging about — 1.5° C. and a salinity of 30—35 per mille. Outside the fjords the Polar Current water is underlain by water with positive temperatures (0—1.6° C). This water layer is debarred from the interior of the fjords by thresholds of varying depths. Where the depth of the threshold is not less than 200 m, the warm water may sometimes make its way into the deeper basins inside the thresholds. At Ella Island, for instance in the summer of 1932, water with positive temperatures was found from a depth of about 250 m down to the bottom. At Eskimonæs, however, where the depth of the threshold at the mouth of Godthaab Gulf is about 120 m, the warm bottom layer was lacking. When present, it is only about 0° C. in most places and nowhere above 1.6°. The salinity of this layer ranges from 34.5 to 35 per mille.

From the period September to December no observations are available. In September—October the water will freeze up, and the fjord water layer is cooled both from above and below. Probably convection currents will arise in the uppermost water layers, which currents contribute to obliterate the fjord water layer, which is absent in the winter.

The Phytoplankton.

The conditions of the phytoplankton have been described by Thorson (1936). Here only such questions will be dealt with as are of special interest for the food conditions of the zooplankton.

Throughout the winter the amount of phytoplankton is extremely slight, and no production takes place. At the beginning of June a strong diatom maximum suddenly sets in. In July—August the amount of diatoms is small, but not quite inconsiderable. In September the quantity has decreased markedly, but as late as October occasional diatoms are found in the samples. From November to May the quantity is negligible.

THE ANNUAL NUMERCIAL VARIATION OF THE SPECIES

In the investigation of the numerical variation of the species during the year the following procedure was adopted: In the plankton hauls from Ella Island, designated above as "fine gauze, rapid hauls 50—0 m", a total count of all the individuals was made. The samples were emptied into a glass bowl, whose bottom was divided into squares with a length of the side a little smaller than the field of vision of the binocular microscope used in the enlargement normally employed, each field being counted apart. In some few cases, in which the number of some species or other was extraordinarily great, that species was counted in a smaller number of fields, and the total number was computed. That this type of hauls was preferred as a basis for comparisons is due in part to the fact that generally they gave the richest yield, especially of smaller individuals, as for instance nauplii; but it is also because the samples collected in the autumn of 1932 by the Greenlander BENJAMIN SAMUELSEN at the request of G. THORSON, were taken in this way. Thus this type of hauls is the only one of which a complete annual cycle is available from Ella Island. The material from Eskimonæs could not be treated on the same principle, since samples collected on the same day, but by different methods, were mostly mixed owing to a lack of glasses. Hence a comparison of the absolute numbers from the two stations can only be made with the greatest caution. The results of the counts are found below.

It will appear from the tables that the numbers of individuals of the different species are subject to great variations. These variations must chiefly be due to three causes; 1) The varying efficiency of the plankton net. This defect is partially eliminated by taking ten hauls each time under as uniform conditions as possible; their average will then supply fairly comparable figures. However, there will still be an error, because the perforations of the net will be filled if the quantity of phytoplankton is great, with the result that the net will catch less efficiently. 2) The number of individuals of a species in a given place is not equally great at all seasons of the year. Species with a certain

breeding season will often immediately after that period exhibit a very great increase in their number of individuals. Likewise the currents, especially in the surface layers, may carry individuals to and fro. 3) The vertical distribution of the species may vary at different seasons. If the main number of individuals is at times found in water layers below the depths at which the samples are taken, the species will apparently be rarer at the place, or it may even disappear entirely.

Which of these causes has exerted its influence in the individual case must be determined to some extent by what is otherwise known about the biology of the particular species, and it will therefore be natural to treat the most important species separately.

Calanus finmarchicus.

This species dominates, in bulk if not always in number, in the uppermost 50 m of the fjords of East Greenland. It is not lacking in a single plankton haul, but it varies in number from about 10 specimens per haul, for instance in December, to several hundreds in July—August.

A study of the conditions at Ella Island will show that the number of individuals in January and February is very small. At the end of March the number begins to increase; however, this increase is not due to reproduction, since the youngest stage of this species, collected in February and March, is the third copepodid stage. In the course of April and June the number is constantly increasing, growing, in July, to more than ten times that of January. At the end of July and August a further increase will take place owing to the reproduction. But in September the number begins to decrease, and from October the species is present in quite small numbers.

This variation is no doubt connected with the feature in the biology of the species, pointed out by GRAN (1902) and PAULSEN (1906), that in the autumn it leaves the surface layers to spend the winter at greater depths, whence it ascends in the spring some time before the reproduction begins. That there is actually an ascent of a large part of the stock may be seen from the ratio between the number of individuals taken in hauls from 25—0 m and that from 50—0 m. On February 25th, 1932, this was 0.38 (9:24), on March 27th, 0.05 (3:67), on April 26th, 0.52 (29:50), and on June 2nd, 0.86. When the stock is evenly distributed over the uppermost 50 m, this figure should be 0.5. Thus it will be seen that the uppermost 25 m from being the most sparsely inhabited water layers during the winter will be the most densely inhabited in the spring. That the figure is greater on February 25th than on March 27th is no doubt due to a continuation throughout the winter of the passive descent which commenced in the autumn, so that the uppermost 25 m have become almost destitute of this species at the time the ascent begins.

As regards Norway this problem has been thoroughly studied by SØMME (1934). Of other causes that may contribute to the variation it seems natural to think of the influence of the currents. However, at Ella Island the current is inconsiderable, being only of importance during the melting time of June to some time into July. The currents therefore can play only a subordinate part in this connection.

In East Greenland, however, conditions deviate distinctly from those of Northern Europe. For while at the Lofoten very few specimens

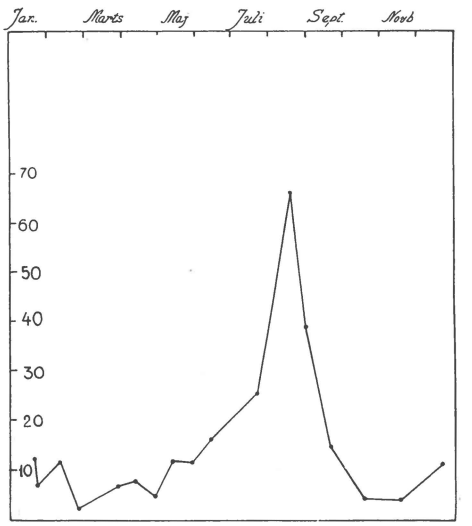

Fig. 2. Numerical variation of *Calanus finmarchicus* at Ella Island. Ordinates indicate specimens per haul. Vertical haul 50—0 m.

are secured in the upper water layers in the winter, in East Greenland a not quite inconsiderable number will always be found even in hauls from 25 to 0 m. This may be due to several causes. Thus the lower temperature of the water (at East Greenland about —1.5° below the ice as against 4—5° at the Lofoten) will cause a greater viscosity of the water, which obstructs a passive descent; and moreover low temperatures, according to experiments made by ROSE (1925), seem to have the effect on the "niveau de flottation" of the copepods that they become evenly distributed in the water column. Finally the highly sheltered situation of Ella Island far into the Franz Joseph Fjord complex may possibly prevent the upper water layers and their stock of animals from being easily carried away by the currents. The latter point is no doubt of importance if a comparison is made with the conditions prevailing at Iceland. Here PAULSEN (l. c.) found large quantities of this species at certain times and in certain places, while a few months before and after the species was absent from the same place. Here the currents

no doubt exert their influence. However, at Eskimonæs, situated near the outer coast, the species was present in the uppermost 50 m all the winter, though in small numbers.

The cause of these vertical migrations has not been fully elucidated; but there can be no doubt that the light plays an exceedingly great part. It seems natural to compare the vertical migrations with the vertical daily migrations which this and other species perform in temperate seas. The latter migrations have especially been investigated by RUSSELL (1924—34), and it has been ascertained that they are dependent in the first instance on the light. That the ascent in the spring is not a consequence of the incidence of the time of reproduction will appear from the fact, as ascertained by SØMME (1934) at the Lofoten, that all stages found at that time take part in the ascent.

This is the case in East Greenland, too. Here hydrographical conditions can hardly be of importance either; for precisely in the period when the ascent begins (March-April) they are extremely stable. As will appear from the table showing the hydrographical conditions at Ella Island, the ice is so good an isolator against heating that as late as the beginning of June, shortly before the ice melts, no change is traceable even in the upper water layers either as regards temperature or salinity.

The phytoplankton production does not commence until shortly before the ice disappears, that is to say in June, so it cannot be the greater supply of food, either, which gives rise to the ascent. Of factors which change considerably during that period, the light only seems to remain.

A great amount of the light is, of course, reflected and absorbed by the ice, but still an appreciable amount must pass through it, at any rate at the end of the ice period, when the snow has melted and the ice becomes transparent. This would appear from the fact that the samples collected on June 17th and 18th, 1933, through the ice at Eskimonæs were thick with diatoms, which accordingly must obtain sufficient light through the ice for their assimilation.

All details of how the light causes these migrations have not been fully agreed upon, but a great number of investigations and observations are available which seem to supply some explanation. ROSE (1925) distinguishes between three effects of the light on plankton organisms, viz. 1) a shock effect at sudden changes in intensity; it may be disregarded in this connection; 2) "phototropism", which is positive at low light intensities (the animal will move towards the light), is nil at a value characteristic of the species, stage, and time, and negative at higher intensities (the animal moves away from the light); 3) a photokinesis, a direct effect of the light on the activety of the animals, which is considerably greater in the light than in the dark.

The latter effect agrees with an observation by SØMME (1934). He says that *Calanus hyperboreus*, when kept in the dark for some time, will be almost motionless and remain at the bottom of the jar, while illumination will after a short time bring about an increased activity (and, as regards adult female animals, the spawning). MARSHALL, NICHOLLS & ORR (1935) have shown that the metabolism of *Calanus finmarchicus* is up to 100 per cent. higher in the light than in the dark. However, they noted this increase without any increase of the activity. This is possibly due to a varying sensitiveness at different seasons of the year. For in the same paper it is pointed out that at times *Calanus finmarchicus* will swim at the very surface, while at other times it will be killed by the same light intensities.

SPOONER (1933) has shown in some careful experiments that the reaction will always take place in the direction of the light rays. I shall not here enter further into the literature on light reactions, which have recently been discussed i. a. by ROSE (1925) and SØMME (1934). SØMME also arrived at the result that the annual ascent of *Calanus finmarchicus* and *C. hyperboreus* must be due to the light.

The following mechanism might be supposed for the vertical annual migrations: In the autumn, when the sunlight decreases and finally disappears entirely, the movements of the animals will be slow and sluggish owing to the decreasing photokinesis, and the animals will sink passively down to greater depths. That the migration does not take place actively, seems evident from the fact that a fairly considerable percentage of all stages of the stock remains in the upper 50 m all the winter, and for that part of the winter whence samples from 25—0 m are at hand, it will be seen that here, too, the species is fairly well represented throughout the winter. In the spring the increasing light causes a photokinesis, an increased activity, which in connection with a positive phototaxis will make the animals ascend into the upper water layers. It may no doubt be assumed that their sentitiveness to light has changed in the course of the winter, since the light intensities found under the ice in the spring are no doubt lower than those prevailing in September—October when the animals sink down to greater depths. Unfortunately observations on light intensities in Arctic waters all the year round are lacking, as well as investigations of the varying sensitiveness to light of the species under the light conditions prevailing there, so future investigations must decide what the quantitative relations are. The question as to the greater or slighter influence of light on the various stages cannot, unfortunately, be elucidated on the basis of the available material, samples having been taken from 50—0 m and 25—0 m only; in these types of hauls the stages are present in almost

the same proportion. For a closer study of this problem hauls with closing nets at different depths would be required.

An interesting difference between the interior parts of the fjords and the outer coast was revealed in the plankton hauls taken by means of a stramin net in the summers of 1932 and 1933 from the expedition ship the *Godthaab* in Franz Joseph Fjord and Scoresby Sound respectively. These plankton hauls have been examined by Dr. P. JESPERSEN (1938). It appears from his description that the majority of copepod species (*Calanus finmarchicus*, *C. hyperboreus*, *Pseudocalanus minutus Microcalanus pygmaeus*, and *Metridia longa*) are most abundant in the interior of the fjords, but occur sparsely in the Polar Current. An exception forms *Microsetella norvegica*, as to which conditions are reverse. As an example may merely be mentioned three stramin hauls taken in Scoresby Sound in the summer of 1933 under the same conditions (200 m. W., hauls during a quarter of an hour), viz. St. 1 at the mouth of the fjord on June 28th: 4000 *Calanus* sp; St. 333 between Cape Stevenson and Cape Leslie, August 24th (farther towards the interior of the fjord): 16,000 *Calanus* sp.; St. 243, Northwest Fjord off the North Bay, July 24th, in the longest fjord branch: 25,000 *Calanus* sp. It is true that there is a long space of time between the hauls at these stations, but it will be seen from the dates that at any rate the difference is not exclusively due to an increase of the number in the course of the summer. This peculiar fact, that the species increases in the number of individuals towards the interior of the fjords, is presumably due to its spending the winter in the deep fjords with the stagnant water, as at the Lofoten, while the individuals found at the outer coast in the water, mostly only about 200 m deep, above the Greenland shelf are carried southward by the East Greenland Polar Current. This current moves at an average rate of up to $^1/_4$ mile in the hour, and contains only a small number of *Calanus finmarchicus*.

As pointed out by LEBOUR (1919), ESTERLY (1916), and others, this species lives principally on diatoms and other microorganisms. As, now, the species increases rapidly in number towards the interior of the fjords, a comparatively greater quantity of phytoplankton will be devoured by it. However, the phytoplankton constitutes, in addition, a more or less direct food basis for the bottom animals, and accordingly the quantity left for them in the inner fjords will be smaller, provided the phytoplankton production is the same everywhere. Judging from the plankton samples I have inspected I am inclined to think that the volumes are greatest at the outer coast, though I am unable to accompany my statement with figures. How large are the volumes of phytoplankton consumed by the plankton copepods, is very difficult to decide at present, but it is hardly inconsiderable quantities.

This is no doubt one of the chief causes of the peculiar fact that the quantity of bottom animals decreases towards the interior of the fjords at the same time as the quantity of zooplankton increases. (SPÄRCK, 1933, THORSON, 1933).

Calanus hyperboreus.

This species shows a similar annual variation in number to that shown by *C. finmarchicus*, but to an even greater extent.

In the winter it is totally absent from the uppermost 50 m. In nearly 400 plankton hauls taken in the winter in East Greenland I have only observed three individuals of this species. In May it begins to appear in the plankton, and in the summer months July and August it constitutes a very considerable part of the plankton. If all the copepodid stages are included, it may even at times surpass *Calanus finmarchicus* in the number of individuals.

In September the number suddenly decreases considerably. However, as late as October (Ella Island, 1931) some few individuals in Stage III were taken, but after that time it was entirely absent all winter.

As regards this species, too, it must be assumed that the annual vertical migration is caused by the light. But since it leaves the uppermost 50 m completely in the winter, it seems natural to assume that the species spends the winter in deeper water than does *Calanus finmarchicus*. This agrees entirely with SØMME's observations on the two species at the coasts of Norway. If one accepts the hypothesis as to the light as the cause of migration towards the surface in the spring, it must be assumed that individuals of this species run a considerable risk of descending to such great depths during the wintering that the light in the spring and summer does not reach them in a sufficient degree to affect them. As is well known, the intensity of the light decreases rapidly with the increasing depth of the water. In the Atlantic, for instance, the intensity of the light may in places be reduced to between 1/100 and 1/1000 at a depth of 10 m, as compared with the intensity at the surface (CLARKE & OSTER, 1934). Since, now, the hydrographic conditions must be supposed to be exceedingly stable all the year round at great depths, the animals cannot in this way, either, receive any stimulus to ascend. As pointed out by SØMME, the ascent takes place without connection with the reproduction functions, and takes place simultaneously for all stages. Thus there is no positive reason, either, to assume that the incidence of sexual maturity should cause any ascent.

The consequence of this, it seems to me, would be that the animals that have descended deepest in the course of the winter, will remain down there if the depth is sufficiently great, while the others will ascend to

the surface. Hence in the summer we may expect a division of the stock into two layers, viz. one relatively near the surface and, separated from this by an interval with few or no animals, a layer at great depths. To decide whether this is correct, plankton hauls with a closing net at different depths are required. Unfortunately not very many hauls seem to have been taken in this way in Arctic waters. DAMAS and KOEFOED (1907), however, record some suitable samples taken near the east coast of Greenland. Three stations only (Sts. 17, 22, and 48) have samples from 1000 m or more. They show the following quantitative distribution at the different depths:

St. 17	St. 22	St. 48
	20— 0 m cc	10— 0 m cc
1800—1200 m c	38— 60 m +	50— 20 m +
	125— 70 m +	100— 60 m +
	300—125 m c	400—200 m cc
	1300—800 m c	1000—800 m c

All the other stations show a maximum between 0 and 200 m, whence the quantity decreases downwards with a single exception (St. 14), at which the quantity remains constant down to about 550 m. This seems to speak in favour of the hypothesis set forth above; but for a definite decision a larger material would be required.

If my hypothesis is correct, it may perhaps contribute to an understanding of the phenomenon that in plankton hauls from great ocean depths individuals of species belonging to the upper water layers are often found.

Part of these have probably lost their power of orientation by light and consequently the connection with the water layers to which they belong.

DAMAS and KOEFOED state that *Calanus hyperboreus* is not found multiplying above oceanic depths, but only in shallower water, as for instance above the Greenland shelf, and that the young from this place spread over the Arctic Ocean and sink downwards in the autumn. At greater depths the species may be met with far down into the Atlantic (see e. g. LYSHOLM and NORDGAARD (1919)), but it never multiplies here although the temperature and salinity do not differ essentially from the conditions under which the species multiply at the coasts of Norway. For as shown by SØMME, it requires light in order to spawn, and there is a great probability that all these individuals have descended to such great depths that they have lost their light orientation and therefore never ascend again except by chance with an ascending current.

At present it may thus be said that it is essential to the survival

of this species not only at the Norwegian coast, but also at the coast of Greenland and possibly everywhere, that fjords, bays, os similar waters of suitable depth are found, in which the animals can spend the winter without being carried away by currents, but not deeper than that the light in the spring may make them ascend again. The large quantities found in the sea between Greenland and Norway at depths of about 1000 m or more should thus be without importance for the survival of the species.

Something similar is probably the case with *Calanus finmarchicus*, However, as it does not sink to great depths in the winter, the fjords are hardly of such vital importance to this species.

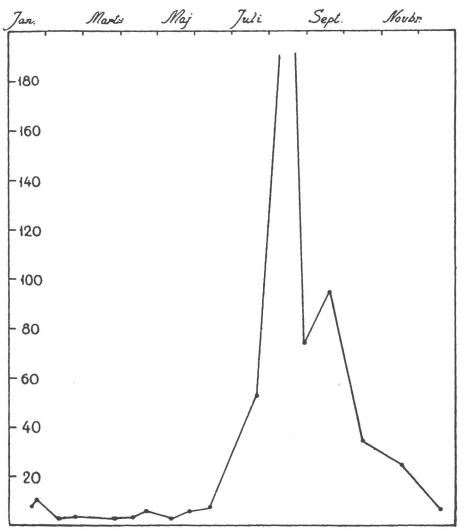

Fig. 3. Numerical variation of *Pseudocalanus minutus* at Ella Island. Vertical haul 50—0 m. Ordinates = specimens per haul.

Pseudocalanus minutus.

In the winter a small yet not quite inconsiderable stock of this species is present. In April—May it seems to increase in number, and in June the increase is very conspicuous without any reproduction having taken place. In July—August the number of individuals increases with explosion-like rapidity; however, now it is chiefly owing to the reproduction, as appears from the fact that the increase is found in the first two copepodid stages which had entirely disappeared in the course of the winter.

At the end of August the number decreases again, and in the course of September and October it decreases considerably, so that in December the species exhibits quite low values. A comparison of Ella Island and

Eskimonæs will show that the summer maximum is smaller in the latter place, no doubt because Eskimonæs is somewhat influenced by the Polar Current, for which reason part of the animal stock is carried away. As will be seen, this species has a similar annual variation to that of *Calanus finmarchicus*.

Microcalanus pygmaeus. (+ *pusillus*).

The annual variation in the number of this species is of quite a different type from that of the three preceding species. In the winter

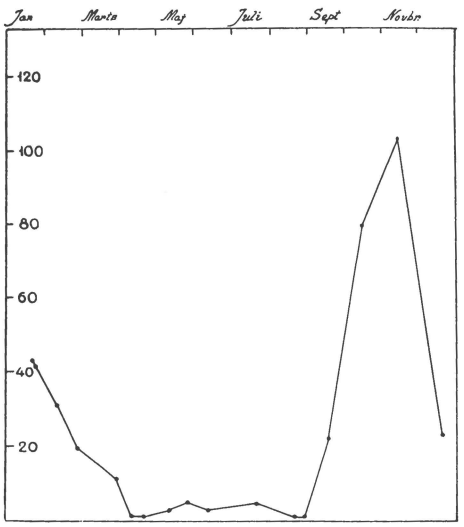

Fig. 4. Numerical variation of *Microcalanus pygmaeus* at Ella Island. Vertical haul 50—0 m. Ordinates = number of specimens per ten hauls.

months this species constitutes numerically no small part of the plankton. But in the course of the spring the number decreases rapidly, and from June to October it is almost absent from the uppermost 50 m. However, at the same time we know from hauls made with the Hensen net that the species is common at depths of 100—200 m throughout the summer. This species, too, then evidently performs annual vertical migrations, shunning the upper water layers in the summer, while in the winter it is found in these also. The cause of this is probably a phototaxis, which is negative as regards the values which the light shows in the summer in approximately the uppermost 100 m. Hydrographic alterations as the cause of migrations may almost be disregarded, since the hydrographic conditions in the uppermost 50 m, as shown by Table 1, change extremely little in the very period in which the species gradually leaves the upper water layers. Previous investigators (WITH, 1915, JESPERSEN, 1923, STØRMER, 1929), whose materials are

derived from the summer time, accordingly regard the species as an inhabitant of depths exceeding 50 m.

Metridia longa.

This species behaves in a similar way to the preceding one. In the winter it plays a considerable part and is one of the commonest species. At times it even surpasses *Calanus finmarchicus* in frequency.

In April, however, it decreased considerably in number, and from May 11th it had almost totally disappeared. But precisely on May 15th

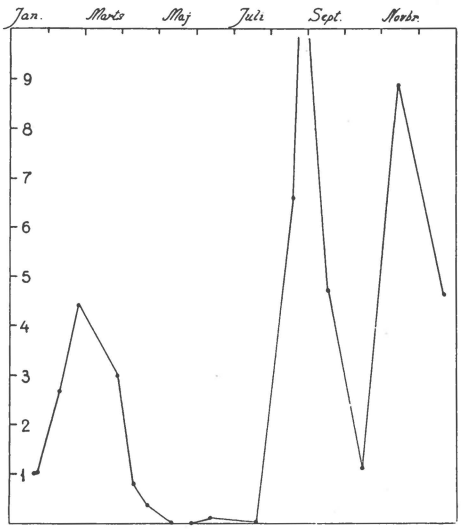

Fig. 5. Numerical variation of *Metridia longa*, Ella Island. Vertical hauls 50—0 m. Ordinates indicate number of specimens per haul.

THORSON took a series of hauls (ten) from 155—0 m, and no less than twelve specimens were found in the samples. In the August samples it suddenly became exceedingly common. This strong increase was not observed at Eskimonæs (Table 3); it was found at Ella Island because the August samples from that place were collected in the night. At this season the species makes diurnal migrations (se below). The considerable number present in September is common to both stations, and is due to an annual vertical migration of a similar type to that of *Microcalanus pygmaeus*. But then the complication occurs, to which we shall return under the reproduction, that the whole old stock dies in September—October after the spawning. Neither eggs nor nauplii have been observed, and hence it is probable that they occur in deeper water. But in November the copepodid stages ascend to the upper 50 m, causing the second maximum. It would seem that a secondary minimum occurred in December—January. However, it was not observered at Eski-

monæs, so it is possibly merely an atypic fluctuation. As will be noted, this species differs from the preceding one by appearing in the upper 50 m much earlier than that species, viz. in August as against *Microcalanus pygmaeus* in October, whereas they disappear from the upper water layers almost simultaneously, *Metridia longa* most likely first. If there were an adaptation to a certain intensity of light, it might be assumed that the species which was the first to disappear, that is to say, is the most sentitive to the light, would be the last to reappear, and that these two dates were nearly symmetrical to the date when the intensity of light in the water is greatest. (Regard should, of course, be taken to the ice-cover and the opacity of the water, and the dates cannot, therefore, be expected to lie symmetrically to the summer solstice). However, as regards *Metridia* a peculiar factor will exert its influence. For, as mentioned above, this species makes distinct diurnal migrations in the late summer as soon as there is a marked difference between night and day, i. e. at the end of July and especially in August.

I noticed this phenomenon for the first time in August, 1933, in Scoresby Sound. The splendid bluish-white phosphorescence of the sea seen at East Greenland at this season of the year proved to be brought about essentially by *Metridia longa*. The surface of the water was teeming with this species, while plankton hauls taken in the surface layers in the day only quite exceptionally yielded occasional specimens. Unfortunately the hour was not noted for most of the hauls from Ella Island and Eskimonæs. But we happen to know with certainty that the samples from August 28th, 1932, were taken in the night, and precisely these plankton hauls were exceptionally rich in *Metridia longa*. Thus the species remains during daytime at fairly great depths, and this has made previous investigators believe that the species lives entirely at greater depths. However, as has been shown, this is not the case. Only during the lightest time of the year does *Metridia longa* shun the surface of the water. It should be mentioned that STØRMER (1929) assumed that *Metridia longa* makes diurnal migrations like its near relative *Metridia lucens*.

Thus as regards diurnal migrations *Metridia longa* differs from *Microcalanus pygmaeus*, which probably owing to its small size cannot undertake long diurnal migrations, and therefore, even in August—September, when the intensity of the light might suit it in the upper water layers, must remain at greater depths.

Pareuchaeta sp.

Copepodid stages of this genus occur regularly in the samples taken during the winter. But they were not found in the summer samples. It is difficult to see which species (one or several) are represented in

such young stages, but probably they belong to *P. norvegica* or *P. glacialis*. It is possible that here, too, an annual migration from deeper water to more superficial layers takes place in the winter. However, the material is too small to allow us to say anything definite about this point. By means of larger nets than those here employed representatives of the genus may also be secured occasionally in the summer from the surface layers. Hence it is very possible, too, that these large species avoid the nets, and can do so more easily when it is light, when

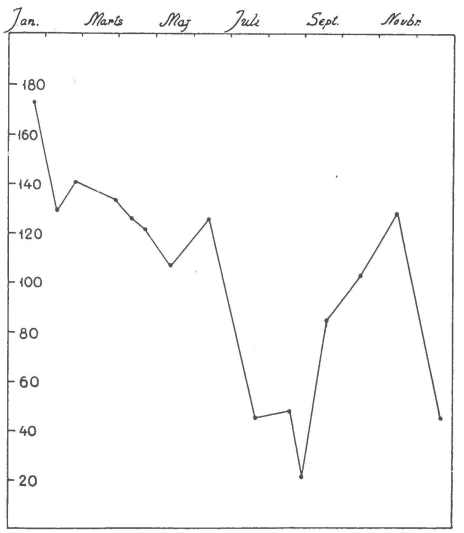

Fig. 6. Numerical variation of *Oithona similis* at Ella Island. Vertical haul 50—0 m. Ordinates = number of specimens per haul.

they may possibly discern the nets. Fully grown-up specimens of the genus have neither been taken in the annual series from Ella Island or from Eskimonæs. However, one point might indicate that the light sensitivity and the consequent annual migrations play a part here, too. For *P. norvegica* must be assumed to perform diurnal migrations near Iceland. PAULSEN (1909) writes as follows: "It (*P.* n.) appears frequently at or near the surface of the sea, especially in the night, but is then generally not full-grown or fry". This can hardly be accounted for otherwise than by assuming that at any rate the younger stages make diurnal migrations. These migrations must be regarded as being essentially caused by variations in the intensity of the light, and it is therefore natural to assume that the light summer in Greenland, when the sun does not set, to some extent acts as a long day, while conversely the dark time acts as a night.

Oithona similis.

This species does not exhibit any especially marked annual variation in number. It appears, however, from fig. 6 that it is comparatively sparse near Ella Island in the months of July and August, while throughout the remainder of the year it is exceedingly common. The table showing the conditions at Eskimonæs does not show this equally distinctly, there being fairly great atypic fluctuations. However, here, too, the largest figures are derived from the winter half of the year.

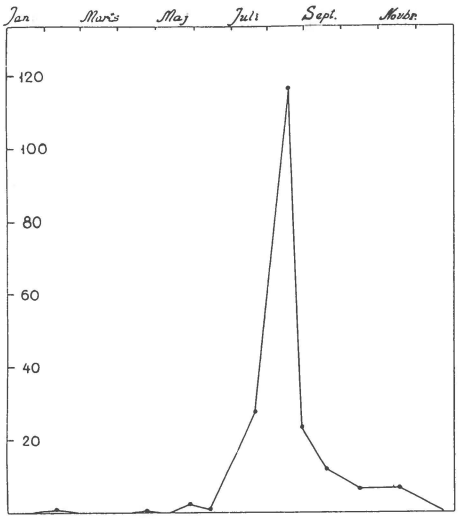

Fig. 7. Numerical variation of *Oncaea borealis*. Vertical haul 50—0 m. Ordinates = number of specimens per haul.

It is evident that this species does not belong to the group which has a summer maximum. However, the species differs from the two preceding ones in that it is hardly the light reaction which causes the decrease in number in the summer. For *Oithona similis* shows no sign of decrease in number in June, when the intensity of the light is high enough to expel completely the other two species from the upper water layers. As will be mentioned below under the reproduction, the nauplii of this species disappear in July and August also, though many females carry eggs in June. It is a rule in most copepode species that the young stages, and especially the nauplii, live nearer the surface than the adult. It is therefore not very probable that almost the whole stock, both adults and nauplii, should descend to greater depths than 50 m in July and August. Their disappearance should rather be connected with the particularly great frequency of the two large *Calanus* species in the same months. It is true that these species live chiefly on diatoms, but their manner of securing their food by filtering the water brings about

that smaller crustaceans also will be included (cf. LEBOUR, 1919—22). Thus the maximum of the species will not occur till the autumn at the same time as the two *Calanus* species become fewer in number.

Oncaea borealis.

This species exhibits a very beautiful annual variation both at Ella Island and at Eskimonæs. In the winter the number is small; in June and July the number increases, and in August it is numerically one of the most important species in the plankton. Even as late as September and October it is prominent, but after that time it is present in a very small number.

The increase in number which takes place in the course of July seems, however, to be chiefly due to the reproduction, the addition consisting almost exclusively of quite young stages. The material hardly warrants inferences as to whether there is also a variation due to horizontal migrations.

Microsetella norvegica.

The species is of rather sparse occurrence all the year round. The material from Ella Island seems to show slight indications of an annual variation, the species being distinctly rarer in the summer than in the winter. The material from Eskimonæs is too sparse to either confirm or invalidate such an assumption. Quantitatively, however, the species is not of any importance at any time of the year.

Other crustaceans do not occur so regularly that we may speak about an annual variation. As regards the copepode nauplii, reference is made to the chapter on reproduction. The other invertebrates do not present many features of interest; a few species should, however, be mentioned, viz.

Limacina helicina.

A considerable number of quite small individuals of this species are met with in the first months of the year. They grow in the course of the spring, but at the same time decrease in number. During the remaining part of the year the number is very low.

Copelata.

Of this animal group *Oikopleura labradoriensis* and *Fritillaria borealis* are of rather frequent occurrence. As regards these species, which behave much the same, there is a fairly conspicuous difference between Ella Island and Eskimonæs. In the former place the rather sparse material seems to show a minimum in the summer and a maximum in the winter. At Eskimonæs, however, both species show a great

maximum in August. (It should be pointed out that the August samples from Ella Island and Eskimonæs were collected in the same year). Altogether *Appendicularia* are much commoner at Eskimonæs than at Ella Island. This fact may perhaps be taken to indicate that the forms belong to the open sea, but are carried by the currents into the fjords, and accordingly in a particular degree to Eskimonæs, which is situated nearest the coast.

Sagitta elegans.

This species shows a variation in number which is chiefly due to the reproduction. In the winter the number is small; but from the end of April (Ella Island) and the beginning of May the number will increase, since a considerable number of quite young individuals will appear, and the old ones disappear in the course of the early summer. At the same time as the young ones grow, the number decreases somewhat, and in the course of August—September the species again reaches the rather low number of exclusively adult individuals found in the winter.

Aglantha digitalis.

This species occurs too sparsely to allow of any definite statement about it. It should, however, be pointed out that it is present in all the autumn samples from Ella Island, while from January to August it is only found in one of every fifty plankton hauls.

REPRODUCTION AND DEVELOPMENT

Calanus finmarchicus.

In studying this species one is faced with the difficulty that the nauplius stages and the first copepodid stages are not immediately distinguishable from the corresponding stages of the related *Calanus hyperboreus*. SØMME (1934) has shown that by accurate measurements of a large number of individuals it is possible to divide each stage into two groups, the large individuals being *C. hyperboreus*, while the small ones are *C. finmarchicus*. However, a definite line of distinction cannot be drawn between the sizes of the two species, as it varies from place to place.

However, to determine this line for each stage in each sample is a highly time-consuming work; and since, as far as is known, the nauplius development is completed in a fairly short time (cf. LEBOUR (1916)), it has only been found necessary to measure the copepodid stages. The measurements were made by means of a measuring ocular and a binocular microscope. The scale of the measuring ocular was divided into 50 graduations. The distance between two division lines in the two magnifications used was 0.078 mm and 0.0257 mm respectively. By using a binocular microscope a theoretical error is introduced, the optic axis not being at right angles to the object in all positions. By control measurements in an object micrometer it is seen, however, that the error was not recognisable in the magnifications used. The binocular microscope was preferred because the manipulation when adjusting the animals was easier with the upright picture in the binocular microscope. As a measure of the size was used the length of the cephalothorax. The measurements were made in such a way that all individuals whose cephalothorax-length lay between two division lines were measured to the highest graduation. In comparing these measurements with those of others it should be borne in mind that two views prevail as regards the number of segments in the cephalothorax and tail of *Calanus* in the first two stages. According to CLAUS (1863) and OBERG (1906) Stage I has four thoracic segments and one

abdominal segment, Stage II five thoracic segments and one abdominal segment. According to LEBOUR (1916) and others both stages exhibit one thoracic segment less and one more abdominal segment. In the present paper the first-mentioned view is adopted.

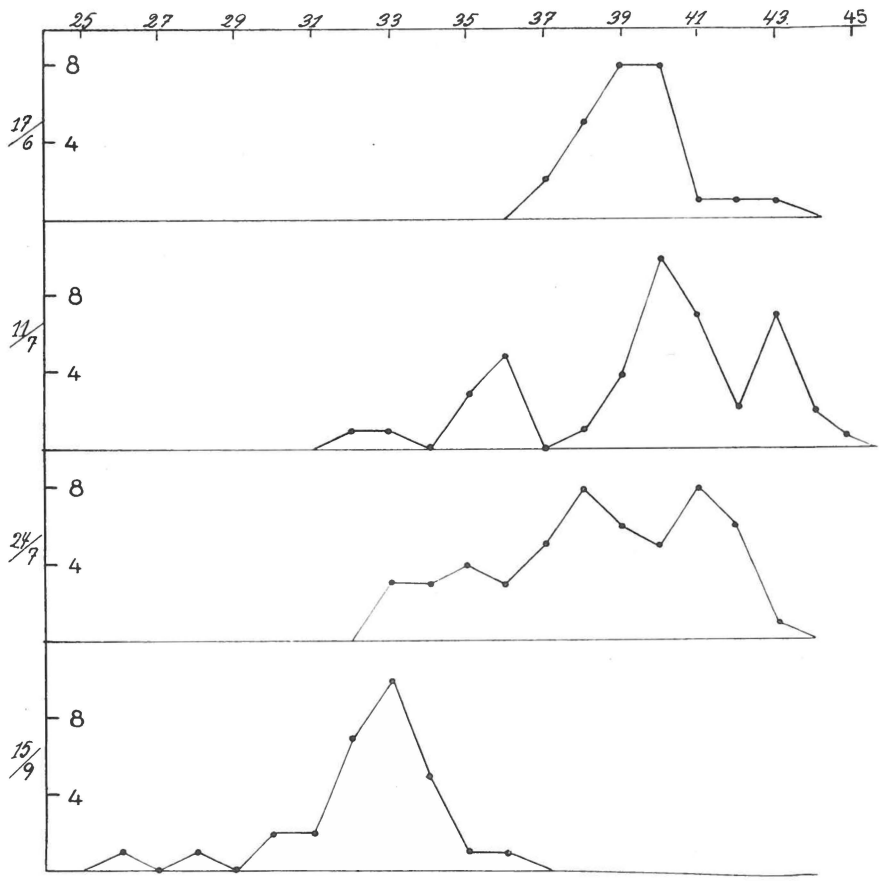

Fig. 8. Variation in length of cephalothorax in Stage I of the *Calanus*-species. Coordinates = number of specimens; micrometer divisions = 0.0257 mm.

The accuracy of measurement used makes it difficult to distinguish the species in the first copepodid stage. It will be natural, however, to draw the line of distinction for the species between 36 and 37 measurement units (M. = 0.0257 mm). In support of this fig. 8 shows the variation in size for *Calanus* sp. in its first stage, at Eskimonæs, in the summer of 1933. As late as June 17th *Calanus hyperboreus* alone had reached the first copepodid stage, and all individuals were more than 36 M. On July 11th a group of smaller animals made its appearance; it is natural, then, to refer these smaller individuals to *C. finmarchicus*. On July 24th the two groups were apparently mixed. Finally, on September

15th only the group of small individuals under 37 M was found. At this time all the individuals of *C. hyperboreus* had passed the first copepodid stage, while many individuals of *C. finmarchicus* were still at that stage, as the breeding time of this species lasts for the greater part of the summer. Accordingly it seems justifiable to draw the line of distinction between the species between 36 and 37 M, and in this way the numbers found in the tables have been arrived at. There is no difficulty in distinguishing the later stages by means of measurements, and in the fourth and later stages there is further a distinct morphological difference.

In Stage II and later stages the species are usually distinguishable from each other, *C. hyperboreus* being more transparent than *C. finmarchicus*, at any rate when preserved in alcohol. The life cycle of *C. finmarchicus* is very clearly displayed from the relative frequency of the different stages. From October 7th, 1931, some plankton hauls are at hand from 30—0 m which contained i. a. *C. finmarchicus*. They showed the distribution of the stages represented in fig. 9. Stage V is dominant, but a considerable stock of younger stages is found, too. From the lack of females it may be concluded that the reproduction for this year had been completed. In January the development may be seen to have advanced during the past time. The first two copepodid stages are entirely lacking, nor are any more nauplii of this genus to be found. A considerable number of individuals have reached the full-grown stage; it will especially be noted that the males constitute a greater part of the stock than is usually the case in the summer. What is of special interest, however, is that several of the females carry spermatophores. Thus as regards a large number of individuals mating takes place at this early time of the year. On February 10th conditions had changed somewhat, the females now forming the largest group. Males still occurred, but in smaller numbers. Some females carried spermatophores. On March 27th the females entirely dominated. The samples from April 10th show the same, though there seems to be an increase of the third and fourth copepodid stages, and this increase continues in the samples from April 26th, when Stage V, too, increases in number. From now on Stages III, IV, and V constantly increase in relative and absolute number in May and June, but no traces of the earlier stages appear. On July 20th Stage V dominated again, and on July 31st Stages III and IV had entirely disappeared, while Stage V constituted the largest group. But now the new generation appeared in the form of the first two copepodid stages. On August 18th the pioneers of the new generation had reached Stages III and IV. Whether some had reached StageV, it is impossible to say. In September the maximum formed by Stage III of the new generation was higher than that formed by Stage

V, which in all probability consists of individuals of both the new and the old generation.

In October the old generation, characterised by the adult females, has evidently disappeared. From October to December the development seems to have almost stopped. The maximum remains at Stage III, the great majority of which evidently do not moult during this period. If we compare October, 1932, with October, 1933, we shall see that the development as a whole was considerably more advanced in 1931 at the same time. Thus the stage of development reached at the end of the summer varies somewhat from year to year.

The plankton series from Eskimonæs show similar conditions to those of the Ella Island series; on August 13th, 1932, the new generation showed a maximum in Stage III; of the old generation, however, there was no trace. On September 15th the maximum had reached Stage IV, and on December 11th, Stage V; many sexually mature females now occurred. In January males appeared and were rather common in the first months of the year. From April to May a great increase in number of Stages III and IV took place. At the beginning of July Stage V dominated, and at the end of July (24th) Stages I and II of the new generation occurred.

Accordingly the observations of both annual cycles show the following result: In January a considerable number of animals are sexually mature (Stage IV), and many of them mate. However, neither eggs nor nauplii of this species occur in the plankton until June—July, and thus a large number of female animals are presumably impregnated half a year before spawning. During the first months of the year the ovaries are entirely undeveloped, so that from this fact, too, it may be concluded that the impregnation of the females and the spawning must be separated by no small interval of time.

In the course of February—March an ever increasing number of individuals at Stage V develop into females and males, so that Stage V almost disappears. But in April—May the ascent from greater depths sets in, and the individuals that ascend belong predominantly to Stages III and IV. In the course of June and July they pass into Stage V and subsequently into the sexually mature stage.

In July or at the end of June egg-laying presumably begins; for at the end of July and the beginning of August Stages I and II of the new generation appear. The period of spawning for this species must be fairly long, for even as late as September nauplii belonging to this species occur, and from the middle of July to and including September eggs of *Calanus finmarchicus* are rather frequently seen. Judging from the position of the maximum of the first copepodid stages the main spawning seems to occur at the end of July.

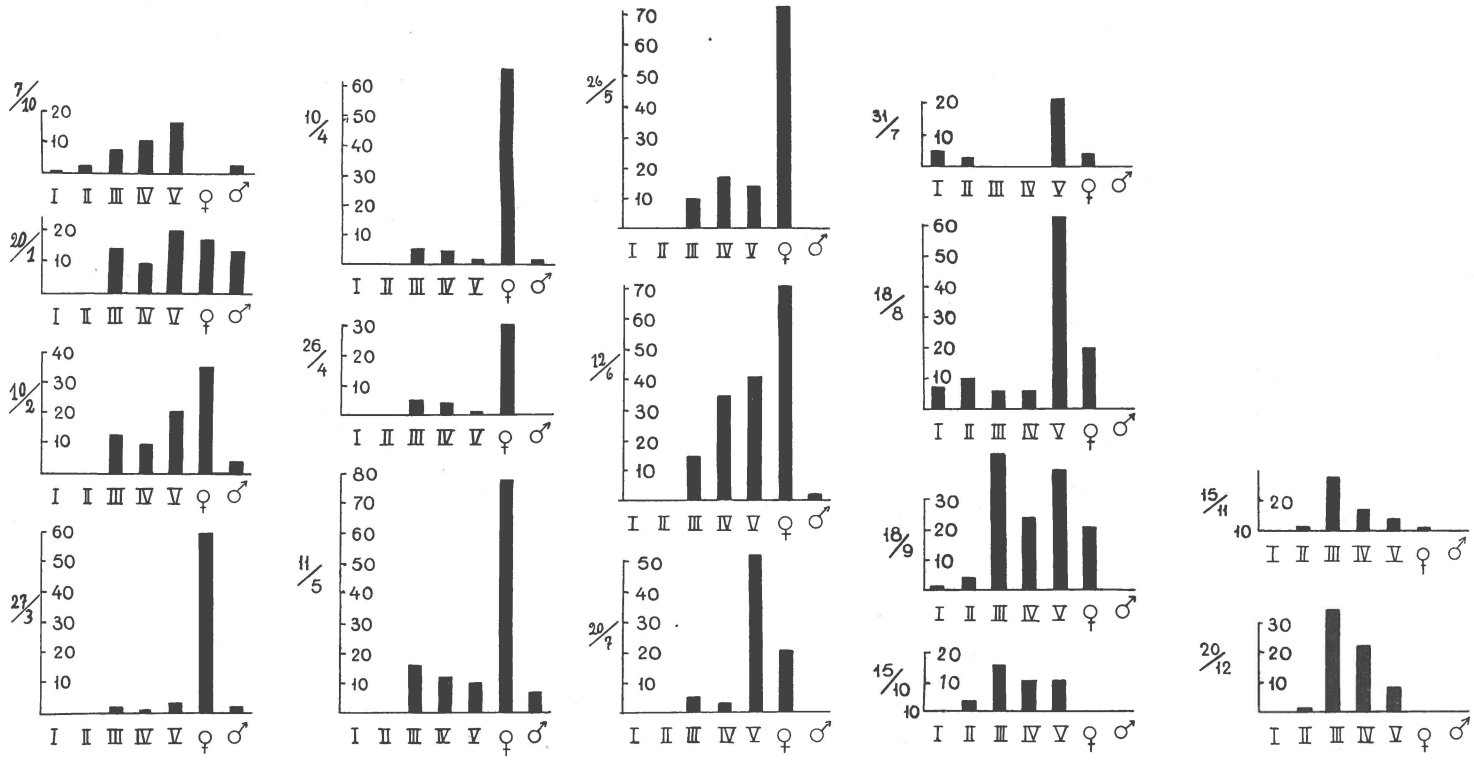

Fig. 9. Diagram showing the representation of the various stages of *Calanus finmarchicus* per ten hauls, July and August per one haul. Ella Island.

Gradually the new generation grows, and in September it is the only one, or almost the only one, present. In the period July to October the moultings evidently occur in fairly rapid succession, for the numerical maximum constantly advances to older stages. After that time, however, the moulting takes place more slowly, and many of the individuals which in October—November have reached Stage III, do not, apparently, develop further until next spring, when the moulting sets in again in May—June. That moulting takes place more slowly in the winter than in the summer, agrees with GRAN's assumption (GRAN, 1902); but he assumes that the animals will attain a larger size if a long interval of time occurs between the moultings. This is not the case, as will be shown below.

As regards the life duration of *Calanus finmarchicus*, the phenomena here discussed seem to indicate that the life cycle of the species is annual in the fjords of East Greenland. Most investigators seem to agree that the species is mostly annual in more northerly waters.

GRAN (1902), however, is of opinion that *C. finmarchicus* in the northern part of the Norwegian Sea completes its development in the course of two years. STØRMER (1929) writes as follows (about the waters west of Greenland), "The annual life cycle is the normal for *Cal. fin.*, but the present material from the "Michael Sars" expedition to Greenland 1924 suggests that external circumstances, such as transportation by currents, may prolong (and perhaps also shorten) the annual life cycle."

Although the complete proof that the species may live two years or even more is lacking, it is rather probable that it may be so. For as mentioned in the preceding chapter (under *Cal. hyperboreus*), several individuals of *C. hyperboreus* and *C. finmarchicus* probably descend so far into the depths in the course of the winter that the light in spring fails to reach them and to give rise to the annual migration; and it is probable, then, that these individuals may live long here without spawning, and possibly later be conveyed to the upper water layers by ascending currents. A proof of the probability that this and other northern species may live for long periods at great depths is furnished by the fact, pointed out by DAHL (1894) (cf. further NORDGAARD (1916)) that these species, *Calanus finmarchicus*, *C. hyperboreus*, *Pareuchaeta norwegica*, and others, have been collected at depths of several thousand metres in the Sargasso Sea. They must have been conveyed there by deep-sea currents, whose velocity is mostly slight. As the species do not multiply in the depths (at any rate not the *Calanus*-species), there is a possibility of arriving at a minimum figure for the age of these animals in the time it takes for the current to move to the said places of the Sargasso Sea from the nearest place where the species breed. However, such a computation is no doubt hardly practicable as yet.

Calanus hyperboreus.

As this species is absent from the uppermost 50 m all the winter, its development during this period cannot be directly investigated. At the end of August, shortly before the species disappears into the depths, the greater number of individuals are at the copepodid Stage III, few are at a more advanced stage of development, and hardly any more have not reached the former stage. Thus the individuals of the new generation strictly keep pace with one another in development. In September a number of individuals reach Stage IV. As late as October some few individuals at Stage III have been observed. After that time the species is not seen until next spring, when in May—June it ascends to the upper water layers. The stock then consists of female animals in Stages V and IV. Accordingly the development has only advanced through two moultings in the course of eight months.

The nauplii of this species appeared at Ella Island on May 26th, at Eskimonæs on June 1st of the following year. Eggs corresponding to SØMME's description (1934) were, however, not found in any of the samples. The spawning proper possibly takes place farther towards the interior of the fjords or possibly above deeper water than found at the two stations. On July 20th the majority of individuals collected at Ella Island belonged to Stage II, while on August 18th the maximum had advanced to Stage III.

At Eskimonæs the corresponding maximum for Stage I was observed on July 11th, for Stage II on July 24th, and for Stage III on August 13th.

Thus it would seem that the great majority spawn some time at the end of May; it is remarkable how the individuals of the new generation keep pace in development. Judging from this it must be assumed that all six nauplius stages are passed in about one month. The first copepodid stage lasts for about two weeks, Stage II about three weeks. As regards some individuals Stage III lasts for a similar period, as they pass into Stage IV in August—September, while the majority probably remain at this stage even longer, since, as mentioned above, eight months elapse before they reach Stages IV, V and ♀; it must even be assumed that the greater number of the individuals which had arrived at maturity in the spring, had reached Stage IV already in the preceding autumn.

In both the years from which the samples are derived, the main spawning seems to have taken place at the end of May and the beginning of June. However, SØMME (1934) has investigated this species in a plankton haul taken by the *Belgica* on August 8th, 1905, off the east coast of Greenland in latitude 76°47′ N., longitude 15°21′ W. (St. 47). At this time nauplii occurred, though only the last three stages, and the

copepodid Stage I of the new generation. However, judging from SØMME's tables no individuals seem as yet to have been in the copepodid Stage II. Comparing this with the results from Ella Island and Eskimonæs, where the copepodid Stage II showed a maximum at the end of July, one receives the impression that the development must have been much delayed in 1905, even though the somewhat more northerly

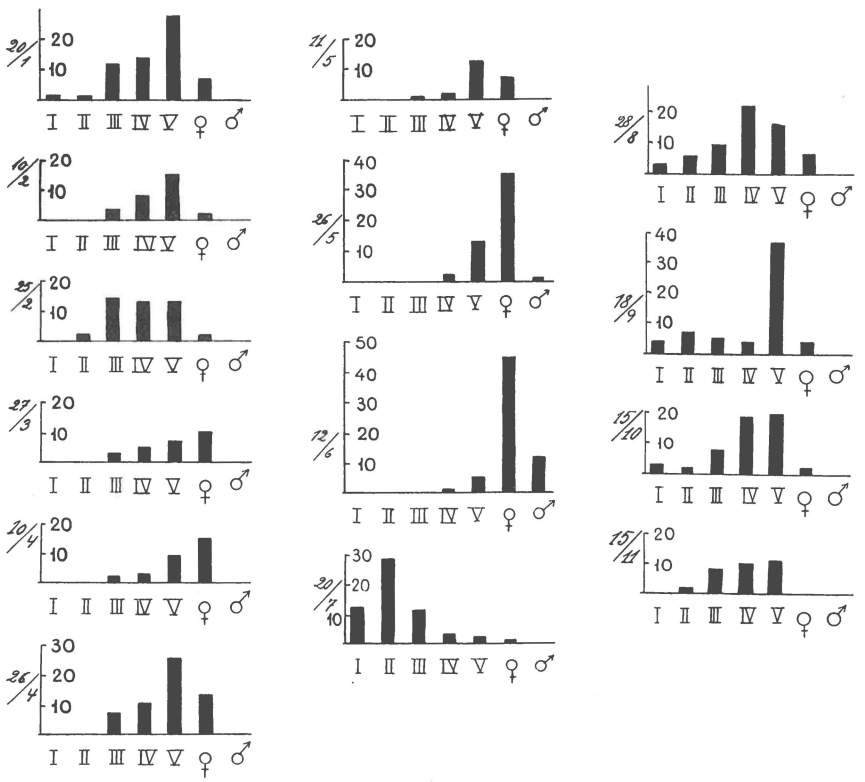

Fig. 10. Diagram showing the representation of the various stages of *Pseudocalanus minutus* per ten hauls, July and August per one haul. Ella Island.

position of the *Belgica* station might perhaps account for part of the difference. Fluctuations of the climatic and hydrographic conditions may also be supposed to exert their influence. It is a fact that the temperature of the water of the East Greenland fjords has been higher in recent years than about the beginning of the century (see e. g. THORSON and USSING, 1934).

Pseudocalanus minutus.

In accordance with the view first set forth by WITH (1915) and later adopted by JESPERSEN (1923) and STØRMER (1929), all the individuals of the genus *Pseudocalanus* from the waters round Greenland are referred to *P. minutus*. This question will be treated in a succeeding

section of the present paper under the variations in the size of the copepods.

On January 20—22th, 1932, a distinct maximum for the copepodid Stage V was found at Ella Island. The first two stages were very sparsely represented. Male animals were apparently entirely absent. Quite similar conditions prevailed in February, only that the first two stages

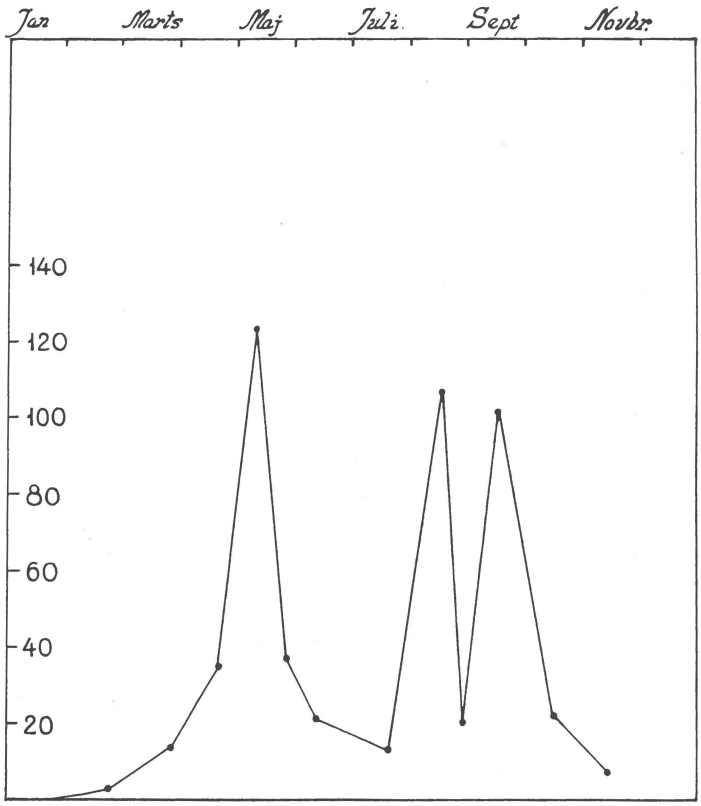

Fig. 11. Number of Calanide nauplii. Ella Island.

had now entirely disappeared. In the course of March and April the females increased in relative importance at the same time as Stages III and IV decreased in number. On May 26th State III had disappeared entirely, and males occurred. On June 12th Stage V was rapidly declining, and large numbers of males occurred in company with the females. Nauplii of *P. minutus* were present in considerable numbers. Fig. 11 shows the number of Calanide nauplii all the year round at Ella Island. The May sample was composed almost exclusively of *Pseudocalanus* plus some few individuals of *Calanus hyperboreus*. The large numbers later in the summer, however, consisted chiefly of *Calanus finmarchicus*. It is peculiar that nauplii of *Pseudocalanus minutus* occurred

as early as March, however, without apparently reaching the copepodid Stage I.

On July 20th the new generation dominated entirely; of the old generation possibly only some females were left. On August 28th the numerical maximum had advanced to Stage IV, and in September to Stage V. Whether the females that occur at this time belong to the new or the old generation, it is difficult to say; but it is quite possible that for a smaller part of this species there are two generations a year.

Nauplii of the species still occur, though sparsely, as late as November. As a whole, however, the development stops almost entirely in October—November. As late as December the majority does not seem to have passed beyond Stage V.

The material from Eskimonæs so to speak follows the scheme from Ella Island in all particulars. Males were, however, observed from the end of April, and many females with ovisacs occurred on June 1.

According to these observations the life cycle of the species is as follows. The majority of individuals arrive at maturity in the course of the winter and spring. Mating probably takes place in April—June. The main spawning takes place in May—June, after which the development of the larvæ proceeds rapidly, so that some individuals possibly arrive at maturity and reproduce in the same summer. However, the majority starts wintering at the copepodid Stages III—V. During the wintering the moultings take place at long intervals. Thus apart from a few individuals, or especially favourable years, this species has an annual life-cycle, too, in the fjords of East Greenland.

From individuals of this species, in contrast to the *Calanus*-species, it is possible to make out even in the last two copepodid stages, whether the individual will develop into a male or a female, since those developing into males have suggestions of the fifth pair of legs, which is normally lacking in such individuals as develop into females (see WITH (1915)).

Pseudocalanus minutus, distribution of ♂♂ and ♀♀ in Stages IV and V.

	IV		V	
	♂	♀	♂	♀
Eskimonæs $^{11}/_{12}$ 1932	15	16	7	6
Eskimonæs $^{15}/_{9}$ 1932	8	7	5	6

It is a well-known fact that adult males of many calanids are much rarer than females. This, for instance, is the case with the *Calanus*-species and *Pseudocalanus*. However, on counting Stages IV and V of

P. minutus it proves that the two sexes are practically equally numerous. Remembering that in June the males are almost just as common as the females, we must conclude that the two sexes are originally equally numerous, but that the life-time of the adult males is much shorter than that of the females. Probably they die shortly after the mating (or matings?). It seems natural to assume that the same is the case in the species in which it cannot be directly ascertained.

Microcalanus pygmaeus.

The investigation of the development and breeding habits of this species is attended with considerable difficulty. In the first place, as stated in the preceding section, the species was almost totally absent from the uppermost 50 m all the summer, and samples were not collected from the expedition ship s. s. *Godthaab*, from the depths at which it lives during that period, by means of nets with such small meshes that its exceedingly small nauplii and first copepodid stages could be expected to be secured. Secondly, the small size of the species necessitates the use of a rather high magnification in order to determine the stage with certainty; and finally the material of the species is not particularly large. Yet it supplies some information of interest. It will be seen that the females of the preceding species increase in number towards the time of the main spawning, which is quite natural. It is natural, too, to suppose that the same is the case with this species.

If we compute how many per cent. of the total number of individuals of the species the adult females constitute each month (nauplii not included), we shall arrive at the following values (Ella Island)

	Sept.	Oct.	Nov.	Jan. (20th)	Febr. (10th)	Febr. (25th)	March (27th)
Females, %	0	14	10	53	48.5	60	45
Total number	18	59	73	18	31	20	11

The percentage of females is accordingly much higher in the months after the New Year than before.

An accurate determination of the copepodid stages in four samples from Eskimonæs showed the following result:

	I	II	III	IV	V	♀
October			5	3	2	2
November			1	1	5	4
February					1	1
April		2			3	8

Although the figures for Eskimonæs are in themselves too small to warrant any inferences, they have been included because they agree excellently with those for Ella Island. Besides, it will be seen from the figures for April 12th that while Stages III and IV, which were especially prominent in October, have disappeared, Stage II is now present. That these individuals of Stage II should originate from the preceding year does not seem very probable considering the usually short duration of this stage in *Calanus* and *Pseudocalanus*. They should, therefore, more probably be interpreted as the result of a spawning in January—March. A further indication in this direction is the presence of some very small nauplii, presumably belonging to this species, in the samples from Ella Island from February 10th and April 10th. The nauplii of *M. p.* have not been described, but OBERG (1905) has described the nauplii of *Calanus finmarchicus*, *Pseudocalanus minutus*, and *Paracalanus parvus* from the Kiel Bay. All these are of a certain type which differs distinctly from most other known copepodid nauplii, while they resemble each other very much. The above-mentioned small nauplii from Ella Island belong precisely to this type, but are too small to belong to *Pseudocalanus*, the smallest of the forms that may come into question.

The only small copepod in these waters which is closely related to the forms mentioned above is precisely *Microcalanus pygmaeus;* it must therefore be taken for granted that it belongs to this species.

It is a question, however, whether it is the main spawning that takes place at this early date. As stated above, *Pseudocalanus minutus*, too, had early spawning to some extent, since nauplii of this species occurred even in March; but apparently they failed to develop, as no early copepodid stages were found till after the main spawning in June. Possibly *M. pygmaeus*, too, has a spawning in the early summer. The fact that such a small number of individuals have reached the sexually mature stage in the autumn would seem to point in the same direction.

However, this of the part biology of the species escapes observation, as it lives in deeper water all the summer.

Only one observation of the occurrence of the males is at hand, only one adult male having been collected at Ella Island (Oct. 30, 1932).

Metridia longa.

The January samples from Ella Island are very poor in this species, so it is difficult to say anything about the distribution of the various stages at that time. The samples from February 10th contain Stages II—V incl., represented by a maximum number of Stage III. On February 25th some few females occurred in addition to these stages. In the samples from February 25th and March 27th the maximum is seen to have advanced to the copepodid Stage IV. In April the material

is too sparse, since, as stated above, the majority of the individuals have migrated to deeper water, probably owing to the increasing intensity of light.

On May 11th the species was entirely absent; but from May 15th a series of vertical hauls from 155—0 m is available, in which a number of individuals of *Metridia longa*, represented by Stages IV, V, and ♀

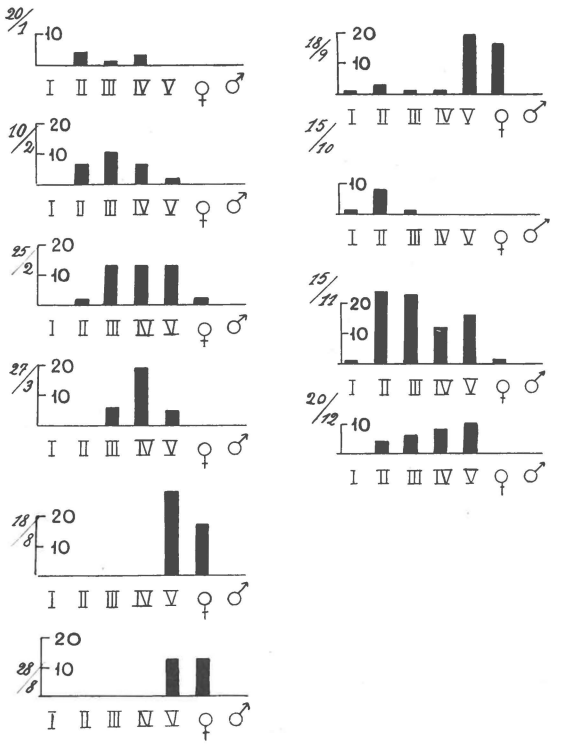

Fig. 12. Diagram showing the representation of various stages of *Metridia longa* per ten hauls, August per one haul. Ella Island.

and with a maximum of Stage V, were found. From this date till the end of July the species was only taken singly.

On August 18th Stages V and ♀ exclusively were found, and the same was the case on August 28th. On these two dates all the females contained large and apparently quite ripe eggs — an indication that the spawning was soon to take place. It is peculiar that no males were found in these hauls. In all probability they live at greater depths (cf. Bogorov, 1932), similarly as the males of *Calanus finmarchicus* according to Paulsen (1906) remain at greater depths in the summer than the females.

In addition to Stages V and ♀ of the old generation there occur in September the first traces of the new generation, since the copepodid

Stages I, II, and III occur after having been totally absent for several months; Stage I is not even found in the samples from January—February.

In October the old generation has entirely disappeared. It seems most probable that all the old individuals die in the autumn. At any rate they are seen no more.

In the course of November and December the early stages become rarer, while the later stages increase in number. Whether the figure for December gives a correct picture of the conditions at this time, is perhaps doubtful, the material being rather small. If the picture is correct, it would indicate that the development that year was considerably more advanced at that date than at the same time the preceding year, since in 1931 Stage III dominated as late as February.

The samples from Eskimonæs show in all essentials a repetition of the conditions prevailing at Ella Island. However, as early as August 30th, a Stage I of this species was found. On the other hand, females are rare in the August samples from Eskimonæs — a difference from conditions at Ella Island which is no doubt due to the diurnal migrations of the species, the samples from Eskimonæs (August 26th) having been collected by day, while the samples from Ella Island (August 28th) were collected in the night. For this reason the maturity of the ovaries in August could not be checked in material from Eskimonæs. But in the numerous specimens of the species collected by the *Godthaab* in Scoresby Sound in 1933, I observed that all the females in the hauls taken on August 23th and 24th contained mature eggs. The life cycle of the species, then, is as follows: In the course of the winter, the spring, and the first months of the summer, the majority of individuals arrive at maturity, but no noteworthy spawning takes place till August. In this month the species undertake marked diurnal migrations, and produce a splendid phosphorescense on the surface of the sea.

Eggs and nauplii that might be supposed to belong to this species have not been observed. Possibly, therefore, it passes these stages at greater depths than 50 m. However, in September the first copepodid stages appear in the upper water layers, and in the course of the autumn the development proceeds, so that the first two stages are rare as early as November.

Oithona similis.

The characteristic egg-masses of this species have been found in the plankton in all months of the year, and egg-bearing females may likewise be found at all seasons, though not always in equally great numbers. Thus the number of the egg-bearing females increases greatly

in June, almost simultaneously with the spring maximum of the phytoplankton. However, this increased production of eggs does not result in an increased number of individuals. On the contrary the curve of the nauplii of the species shows a decrease at that season, and in the summer months July and August the number of individuals of the species is comparatively low, as stated above. Thus on August 13th, 1932, at Eskimonæs it was only 12 per cent. of all the copepods, as against about 80 per cent. in the months of January and February,

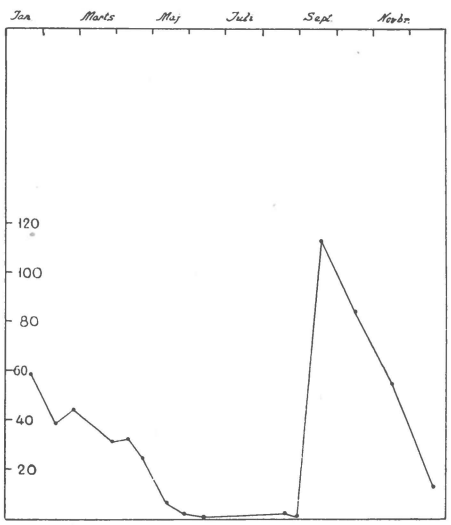

Fig. 13. Variation in the number of nauplii of *Oithona similis*. Ella Island.

and these figures may also be taken as a fairly good expression of the conditions at Ella Island. The individuals occurring in the summer are generally adult or older copepodid stages. The younger copepodid stages constitute only a small minority, and the nauplii have almost entirely disappeared.

In September there is again a considerable number of females with eggs, and at the same time the number of nauplii and younger copepodid stages increases rapidly. In October and November the production of nauplii is still considerable, but decreases somewhat in December.

According to the above, the species reproduces at all seasons, which is in good agreement with the statement by GRAN (1902, p. 66), who says: "von den kleineren Formen wie *Oithona similis*, *Oncaea conifera*" (synonym for *borealis*) "und *Microsetella atlantica* habe ich den Eindruck bekommen, dass sie ihre Entwicklung in sehr kurzer Zeit durchmachen können, da ich sie von Norwegens Küsten zu verschiedenen Jahreszeiten geschlechtsreif gesehen habe."

But the most productive spawning is probably that which takes place in September and October. It is interesting that the spawning which takes place in June, when the phytoplankton production is at its highest and when, accordingly, the food conditions for the nauplii would seem to be the best, does not result in an increased number of individuals.

Hydrographic conditions can hardly be very important either; for the species, which has a very wide geographic distribution, multiplies excellently at higher temperatures and lower salinities than found at East Greenland in the uppermost 50 m in the summer.

There is hardly a direct food competition with the other plankton organisms, as the plankton samples from the greater part of the period mentioned are quite turbid with diatoms, which serve as food for this species. But it is no doubt of importance that the two *Calanus*-species in addition to phytoplankton also consume nauplii and other small animals.

A large proportion of the brood of *Oithona similis* is probably eaten by the large copepods, and the species therefore rather decreases in number until September. At that time, however, *Calanus hyperboreus* disappears from the uppermost 50 m, and *C. finmarchicus* becomes much less frequent. The result is a considerable rise in the number of *Oithona similis*, whose young now obtain a greater possibility of reaching the adult stage without being devoured.

Throughout the winter the species is very prominent in the upper water layers, while a great number of the large species live at greater depths.

Oncaea borealis.

The nauplii of this species have not been described, and as no females with eggs have been found in the material, it is impossible to decide with certainty at which season or seasons reproduction takes place.

Males and females in copulation have been collected at all seasons and this would seem to indicate that spawning may take place at any time of the year.

However, this is no infallible argument. It has previously been shown that the copulation of *Calanus finmarchicus* takes place to a great extent in the winter, while the spawning takes place almost exclusively in the summer. From SØMME's investigations (1934) it is known that *Calanus hyperboreus* behaves similarly in the Norwegian fjords.

As regards the mere facts, a very small stock of this species is found in the uppermost 50 m from January to May. Nearly all the individuals collected during this period are full-grown.

At the end of May, however, a considerable number of quite young

copepodids occur. In June and July the early stages are still numerous and at the same time the older stages, too, increase in number. In August it is one of the commonest species, being surpassed by *Pseudocalanus minutus* and *Calanus finmarchicus* only. In the autumn, when the species, as stated above, decreases in number, chiefly full-grown individuals are met with. The production of young at this season, if there is any, must accordingly be inconsiderable.

According to these observations, *Oncaea borealis* should be annual at East Greenland, probably with its main spawning in April—May.

It is not impossible, however, that several generations may occur in the course of the summer. This point cannot be decided on the basis of the available material.

Limacina helicina.

As stated above, the adult individuals are of rather sparse occurrence all the year round. But in the first months of the year a very considerable number of quite small individuals suddenly appear. The changes that take place from the New Year to the summer appear very beautifully from a comparison of hauls made with fine gauze and such made with coarse gauze. The subjoined table gives the total number of individuals in ten hauls. The hauls were taken with fine and coarse plankton gauze respectively (No. 12 and No. 3), but otherwise uniformly (50—0 m, rapid haul).

	$^{20}/_{1}$	$^{10}/_{2}$	$^{25\text{-}27}/_{2}$	$^{11}/_{3}$	$^{27}/_{3}$	$^{10}/_{4}$	$^{26}/_{4}$	$^{11}/_{5}$	$^{30}/_{5}$	$^{12\text{-}14}/_{6}$
Fine	484	867	425 (1 ad.)	292	390	437	180	111	121	57
Coarse...	3	4 (ad.)	3	2 (ad.)	0	6 (+ 10 ad.)	2 (ad.)	1	2	40

It will be seen that the number of young individuals decreases from January to June. They were almost only collected by the fine net until June 12th, when suddenly the great majority had attained the size corresponding to the size of the meshes of the coarse net.

It seems natural to couple this sudden growth with the better food, since, as is well-known, the phytoplankton maximum sets in at the beginning of June. According to LOHMANN (1911) *Limacina* feeds chiefly on nannoplankton.

The spawning presumably takes place in December—January, the quite small individuals not having been collected earlier than January.

Fritillaria borealis.

The eggs and earliest stages of this species were not observed; they are probably too small to be collected by means of zooplankton

gauze. However, very early stages, resembling the adult in all essentials, suddenly appeared at Ella Island on June 26th, and were present in considerable quantities throughout the month of July. But these small individuals were not observed at other seasons of the year, so the main spawning probably takes place in June.

Oikopleura labradoriensis.

The first early stages of the genus *Oikopleura* are derived from June 2nd. They should no doubt be referred to this species, the only species of the genus observed with certainty in the available material. The material is in a rather poor state of preservation, which rendered the identification very difficult.

Judging from the comparatively great number of quite young individuals from June, it must be assumed that the spawning takes place in May.

Sagitta elegans.

The eggs of this species, which are easily recognisable, rather like big fish-eggs, occurred at Ella Island for the first time on February 25th. From March to June they were constantly found in the plankton, but they disappeared in the course of June. At the end of April (27th) the first emerged young were seen, and they gradually constituted an ever increasing percentage of the species. The old generation apparently disappears in the course of the summer.

Eggs of this species were not observed from July to February. Thus the species seems to produce only one generation annually in East Greenland. It is peculiar that at West Greenland the species, according to KRAMP (1918), seems chiefly to spawn in the autumn.

Considering the reproduction of all the plankton forms together, it will be seen that as far as could be gathered from the material, they are all of them annual, mostly with a single marked period of main spawning. As regards the majority, this period occurs in the summer. Only *Limacina*, *Sagitta*, and possibly *Microcalanus* form exceptions from this rule. The main spawning of the majority of forms occurs in May—June, so that the development of the larvæ takes place while the production of phytoplankton is at its highest. This applies to the *Calanus* species, *Pseudocalanus minutus*, probably *Oncaea borealis*, *Fritillaria borealis*, *Oikopleura labradoriensis*. As to *Calanus finmarchicus* MARSHALL, NICHOLLS & ORR (1934) have shown that only when a spawning takes place in connection with a phytoplankton maximum, will the young develop into adult individuals; otherwise the nauplii will die. The short production period for phytoplankton in the fjords of Northeast Greenland is no doubt one of the reasons why the phytoplankton feeders,

e. g. the greater number of copepods, appendicularians, and *Limacina* produce only one generation annually. Another important factor is no doubt the low temperature, which impedes the development. It is probably owing to the temperature that a form like *Sagitta*, which feeds on copepods, is an annual here, while according to RUSSELL (1932—33) it occurs at Plymouth in several generations in the course of the summer. It is peculiar that a phytoplankton feeder like *Limacina helicina* apparently breeds in the middle of the winter. But, as stated above, the young remain small till June, when the growth suddenly quickens along with the increased supply of food.

REMARKS ON THE FOOD OF THE COPEPODS

According to our present knowledge, the phytoplankton constitutes the basis of the nutrition of the zooplankton. The food conditions for the plankton animals in Arctic regions must therefore be of especial interest. During the eight months of the year, from October to May, the phytoplankton production in the fjords of Northeast Greenland is very nearly nil, and the quantity of phytoplankton in this period is very slight, even though a few peridineans and diatoms are found in the plankton samples during the whole period. THORSON (1936) has briefly described the phytoplankton conditions. I shall merely state that the production is greatest in June, but even in September noticeable quantities of diatoms occur. Thus it may be stated at the outset that the possibilities for the phytoplankton feeders of securing food in the winter are the poorest possible. It must be of some interest, however, to study this problem directly on the fixed material, and the copepods seem to be best suited for the purpose. As a whole the other animal groups do not occur in sufficient quantities to form the basis of an investigation that would give a reliable result.

Sagitta elegans and *Aglantha digitalis* are known with certainty to be carnivorous animals, which feed on copepods (see LEBOUR, 1919—22), and their nutrition will therefore depend on the quantity and nutritive condition of the animals on which they feed.

Of the copepods, *Calanus hyperboreus*, *Calanus finmarchicus*, and *Metridia longa* are especially well suited for an investigation owing to their relatively great size.

Among the large copepods occurring in the fjords of East Greenland there are further two species of the genus, *Pareuchaeta* and *Heterorhabdus norwegicus*. However, these species are carnivorous animals which live on other copepods. *Pareuchaeta norvegica* is able to consume copepods of the size of *Calanus finmarchicus*, and accordingly these species only depend indirectly on the phytoplankton. In the months June to September, that is to say, the period in which the production of phytoplankton takes place, the intestinal canal of the majority of

diatom-feeding copepods at all stages from nauplii to adult females may be seen to be more or less filled with the food elements consumed; in addition the plankton samples contain considerable quantities of "faecal pellets" of the large copepods (*Calanus finm.* and *hyp.* and *Metridia longa*).

In the stomachs of these forms the "food pellets" may often be seen to be arranged in a fine spiral, the space being too short for them to lie in a straight line.

The samples from the period October to May, however, will not contain a single individual whose contents of the intestinal canal will be visible from the outside, and no "faecal pellets" are found in the samples. This shows, what might be expected, that the consumption of food is much greater in the period of phytoplankton production than at other times.

LEBOUR (1919—22) has shown, however, that certain copepods, i. a. *Calanus finmarchicus*, in addition to phytoplankton (predominantly diatoms) consume smaller animals, e. g. nauplii and small copepods. As regards *Metridia longa* I made the same observation, since I repeatedly found fragments of crustacean limbs in its stomach contents. Thus there is a possibility that the large copepods are carnivorous in the winter. As stated above, no stomach contents are observable from without. For the sake of greater certainty twenty specimens of *Calanus finmarchicus* V and ♀ from December, January, and February were opened, and the intestinal canal was taken out and examined in glycerine. In no case were remains of animals or any determinable organic remains found. Three specimens of *Metridia longa* from Eskimonæs, collected in February 1933, have been examined in the same way, but with no result. The examination is impeded by the intestinal canal being much shrunken in the winter, at any rate in the fixed material, so that it is often attended with great difficulty to find it, while it is nearly always easily secured in the summer material. Naturally the material examined is too small to warrant the inference that these species never consume other animals in the winter; but we are allowed to assume that this is not the rule.

After CLARKE & GELLIS (1935) and others have set forth the theory that bacteria might constitute an essential part of the food of the copepods, it is necessary to discuss briefly the possibility of this as a food in the winter.

Actually this is a question of the greatest interest for an understanding of the circulation of matter in the sea.

As is well known, the copepods constitute an important food element for a very large number of the animals of the sea. Actually they are probably the most important link in the chain of transformation from

the phytoplankton to the macroscopic animals. The bacteria on which the copepods feed must necessarily live on the organic substances found in solution or suspension in the water. According to KROGH (1934) the dissolved organic matter in the sea is present in a quantity amounting to at least three hundred times that of living organisms

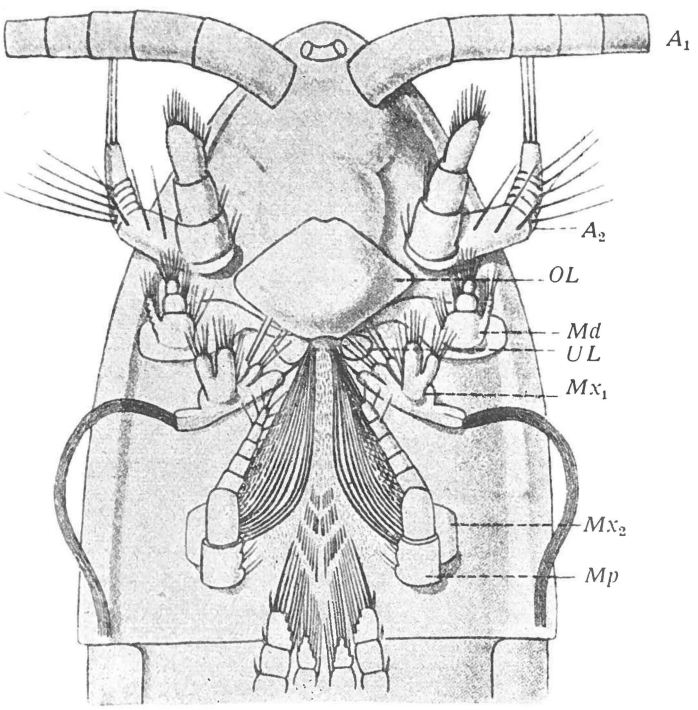

Fig. 14. Ventral view of anterior part of cephalothorax of a copepod (*Diaptomus* sp.) A_1 = 1st antenna; A_2 = 2nd antenna; Md = mandible; Mx_1 = 1st maxilla; Mx_2 = 2nd maxilla; Mp = maxilliped. — After O. STORCH.

found at a given time; if this matter through bacteria and copepods may be included in the circulation of the food elements, an investigation of the phenomenon would be of great importance.

These bacteria are hardly directly demonstrable in the intestinal canal of the copepods; but we may come still closer to the problem by asking: Are these copepods able to catch and consume bacteria? In order to secure the bacteria the copepods must filter the water and retain the food elements. According to ESTERLY (1916) the absorption of food in the phytoplankton-eating copepods takes place in the following way (see fig. 14). The setaceous 2nd antenna, mandible, and 1st maxilla are forced strongly backwards, thus producing a water stream running backwards at either side. However, the 2nd pair of maxillae are not moved during this process. They are covered with a row of

parallel setae which together form an oblique filter; these two filters together form a kind of fish-trap. When, now, the 2nd antenna, the mandible, and the 1st maxilla strike backwards, a low pressure will form in the front median line, towards which the water will stream from behind, through the filter formed by the 2nd maxilla. Particles which cannot pass the filter are kept back and gradually form a "pill", which is finally conveyed to the mouth by the first maxilla, and thence, by means of a peristaltic movement, to the stomach.

Thus, if an organism is to be caught by this apparatus, it is essential that its largest diameter should be greater than the square distance between the barbs of the setae of the 2nd maxilla.

With high magnification these barbs may be counted along a suitable part of a seta, which is measured by means of an ocular micrometer, and in this way the distance between the barbs may be computed. This distance proved to vary considerably in the same individual. In the following only the smallest distance measured for the species and stage in question is stated. In adult females (Dusén Fjord, Aug. 12th, 1932, 50—0 m) the following values were found: *Calanus finmarchicus* 5.7 μ, *Calanus hyperboreus* 4.7 μ, *Pseudocalanus minutus* 1.6 μ, and *Metridia longa* 8.2 μ. The measurements of the copepodid Stage V showed the following values: *Calanus finmarchicus* 3.8 μ, *Calanus hyperboreus* 3.3 μ, and *Pseudocalanus minutus* 1.5 μ. Finally some *Calanus finmarchicus* at Stage III measured 3.2 μ. The size of the bacteria generally ranges between $^1/_4$ μ and 1 μ in diameter; in rare cases it may be 2 μ.

Thus it would seem obvious that the older stages, at any rate, of the species mentioned are unable to keep back bacteria with their filters even if bacteria are present in sufficient quantities to be of importance as food for the animals.

As to the smaller species, *Microcalanus pusillus* and *Oithona similis*, no measurements are available; but it applies to them as well as to the nauplii of the larger species that contents in the intestinal canals are only seen in animals collected in the summer.

Thus the result of this investigation is that the species of copepods mentioned do not take in a noteworthy amount of food during the dark time; during this time they must live on their stored nourishment. Towards the end of the summer the copepods contain large amounts of oil, while in May their content of oil is much smaller.

Since in the winter no crustacean-remains are found in *Calanus finmarchicus* and *Metridia longa*, whereas such are found among the phytoplankton-remains in the summer, it seems natural to assume that these species do not look for their prey, but that it is quite by chance that the animals come into their filter together with the diatoms.

In the early summer, when the water contains fine sand from the rivers, sand-grains are found in the "faecal pellets" of *Calanus finmarchicus*, which indicates that the two species mentioned do not make a qualitative selection of their food. In this respect they differ from the actual carnivorous copepods, e. g. *Euchaeta*, *Heterorhabdus*, *Candacia*, etc., which mostly entirely lack filters (see the figures in SARS, 1900), and consequently must actively look for their prey.

VARIATIONS IN THE SIZE OF THE COPEPODS

Calanus finmarchicus.

It has long been known that this species varies greatly in size from place to place as well as from season to season in the same place, so far, however, no complete explanation of the phenomenon has been given. JESPERSEN (1934) has recently discussed the fairly copious literature on the subject. Hence only such works will be cited below as are of importance for the interpretation of the results.

STØRMER (1929) has shown that Stage V and the females of *Calanus finmarchicus* from West Greenland constitute two marked size groups, whereas a distinct division into two groups of Stage IV is impossible. He further says: "The large specimen exhibited a morphological approximation to *Calanus hyperboreus*. The posterior thoracic segment was not so evenly rounded as in the ordinary *Cal. fin.*, but had no distinct spines". He believes, however, that it is only a biological variation within the same species. JESPERSEN (1934) arrived at the same result on the basis of the material collected on the *Godthaab* Expedition 1928. He writes as follows: "The most minute investigation of the different characters has failed to reveal differences beyond that of size and the relative dimensions incident to it."

As the fifth pair of legs of the male often exhibit valuable systemtical characters in the copepods, a very careful examination of this pair of legs in males from both the large and the small group has been made; but here, too, there was not so great a difference that different races, to say nothing of species, could be distinguished. It should be pointed out at once that the measurements of the present material, too, show that we are concerned with a variation within the same species.

As previously stated, the species is of common occurrence in the material from Ella Island all the year round, and it has therefore been possible to measure the size of all stages found at any time. The measures dealt with below are the length of the cephalothorax from the front to the posterior edge of the last thoracic segment. In agreement with CLAUS (1863) and OBERG (1906) it is assumed here that only one caudal

segment is found in Stages I and II. The technique of measurement is mentioned under the reproduction p. 31. In the following account all copepodid stages (with the exception of Stage I) as well as females and males will be treated in regard to their variation in size. That Stage I is not included is due to the difficulties in distinguishing it from the corresponding stage of *Calanus hyperboreus*.

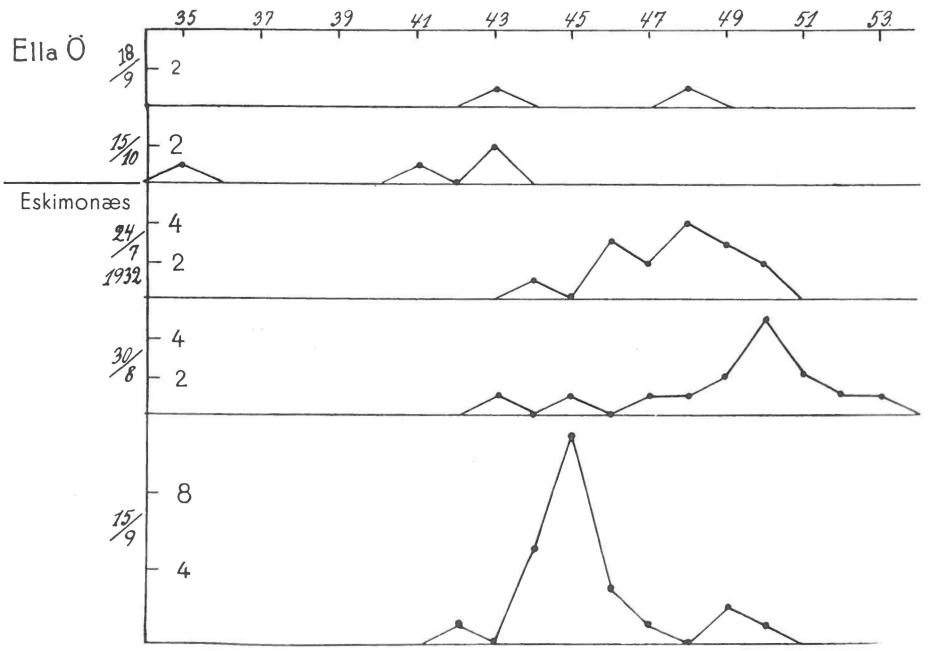

Fig. 15. Variation in length of cephalothorax in Stage II of *Calanus finmarchicus*. Ordinates = number of specimens; micrometer divisions = 0,0257 mm.

Copepodid Stage II. As has been shown above, this stage is absent all the winter and spring, and does not appear till the end of July. The measured material from Ella Island is too sparse to allow of inferences. The measurements of the material from Eskimonæs show that the average size decreases gradually as the summer and autumn proceed.

Copepodid Stage III. In contrast to the two preceding stages, Stage III is present nearly all the year. Only in July and the beginning of August it is rare.

The rather few measurements from Ella Island show that the size of this stage measured with the unit chosen (0.078 mm) remains fairly constant all the year round. The material is too small to allow of a further discussion of the variation.

The material from Eskimonæs, however, shows a decrease in size, measureable though not great, from August 30th to December 11th,

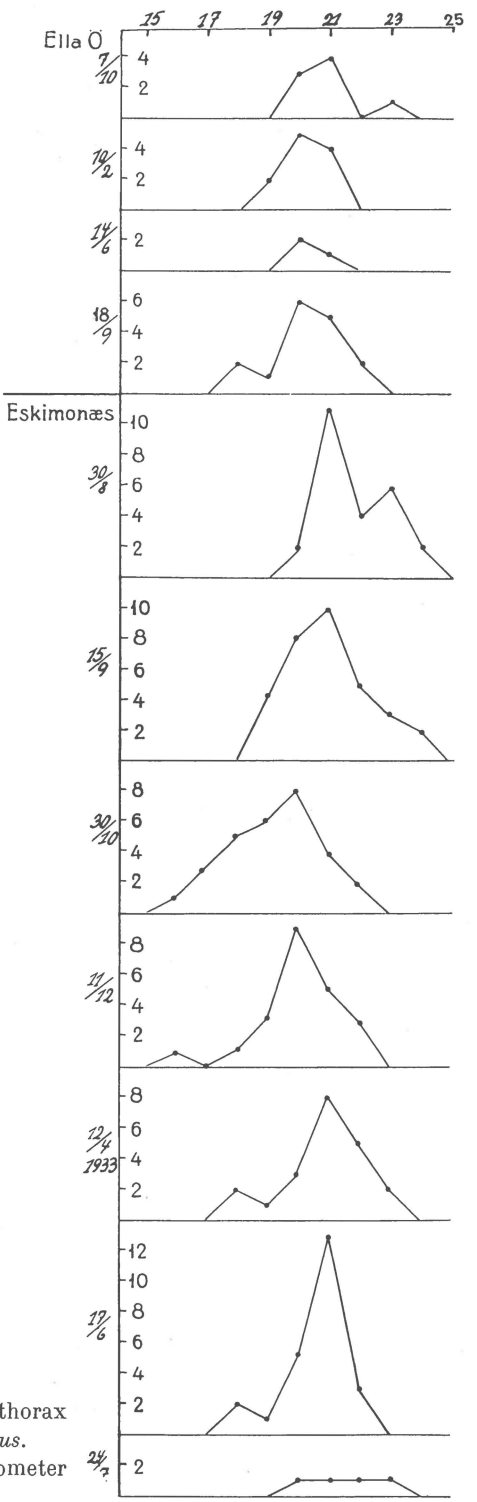

Fig. 16. Variation in length of cephalothorax in Stage III of *Calanus finmarchicus*. Ordinates = number of specimens; micrometer divisions = 0.078 mm.

that is to say, a shifting in the same direction as that assumed for Stage II, viz. a decrease in size in the course of the autumn. In the spring the size would seem to remain unaltered from April 12th to June 17th. This is very natural since, as previously shown, no individuals of earlier stages than Stage III occur in the period from January to July. Thus a change of the mean size cannot take place by the addition of new individuals through moulting, but possibly only if certain size groups of Stage III moult and pass into Stage IV before the others. Whether this takes place, it is impossible to decide on the basis of the available material; but there seems to be no marked tendency in that direction.

Copepodid Stage IV. The material from Ella Island shows in February a strong spreading of the measured individuals within the groups measured, the very sparse material shows no maxima. On June 14th a similar spreading was found, but there is a decided maximum about 24 M (= units of measurement); a smaller one is indicated at 28 M. In the summer months this stage is but sparsely represented, but in September it is common again, and the maximum now occurs at 27 M. The very small number of individuals measured from October and December possibly suggests that it is still this size group that dominates. The same is shown by the measurements of the material from October, 1931.

From the Eskimonæs material a much larger number has been measured. As this annual cycle was commenced in August, it will be natural here, too, to consider this month first. On August 30th the stock consisted exclusively of rather large individuals. The size curve has its maximum at 33 M. As early as September 15th the maximum had decreased to 29—30 M, and in the course of the following months constantly lower size groups will be represented, while at the same time the large individuals become comparatively rarer. However, on December 11th there was still a marked maximum at 29 M.

In the course of the winter the large individuals become constantly rarer, and the small ones commoner, and on June 17th the same great spreading with a maximum among the small individuals is seen, which was found at Ella Island.

However, on July 11th the picture has totally changed. The maximum has again moved to 31 M, and the small individuals have entirely disappeared. This can only be accounted for by assuming that nearly all the individuals found in June have moulted and passed into Stage V, while the large individuals in June have originated from the hibernating specimens of Stage III. As shown above, they cannot belong to the new generation, since at this date it has not yet reached Stage I.

Thus the material from both stations shows that Stage IV decreases

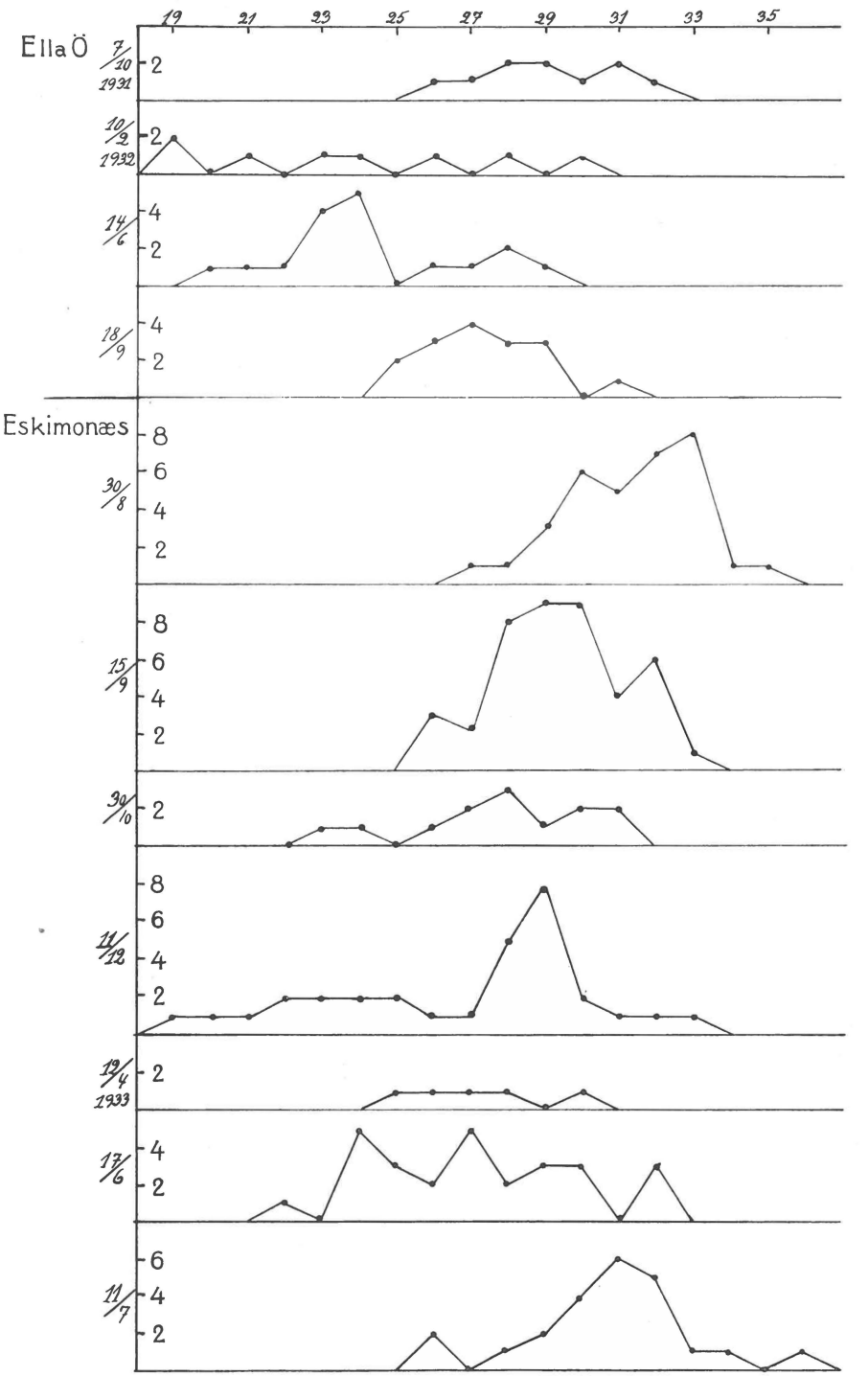

Fig. 17. Variation in length of cephalothorax in Stage IV of *Calanus finm.* Ordinates = number of specimens; micrometer division = 0.078 mm.

in size in the course of the late summer and winter, to increase again in July before the old generation entirely vanishes. Thus the summer individuals are generally larger than the winter individuals no matter to which generation they belong. It will be noted that a fairly large number of the small winter specimens of Stage IV are smaller than the average of Stage III. Thus it would seem that the moulting in the winter takes place without any noteworthy increase of size.

Copepodid Stage V. The cephalothorax measurements of the Ella Island material of this stage from February 10th reveal exclusively small individuals grouped about 30—31 M. In the course of the months March to May the mean size evidently further decreased; for on June 14th the peak of the size curve was found at 28 M. However, on July 31st a considerable stock of larger individuals had appeared in addition to the small ones; the larger individuals belonged to size classes which were not found in the plankton in the preceding six months. On August 28th only large individuals were found. In September the small individuals became prominent again; but judging from the very few individuals from December, some few big individuals were found even at that date. From the autumn of 1931 samples are at hand collected on October 7th at Ella Island, i. e. the autumn before the great plankton series was commenced in January. In these autumn samples the maximum occurs at 38 M. As shown above, this and the other high size groups have disappeared in February, and we must therefore assume that the animals have moulted and passed into the sexually mature stage, while the February stock of Stage V must have originated from Stage IV of the autumn and winter.

Of the Eskimonæs material only some few individuals from August 31st, September 9th, and October 30th have been measured. The few measurements suggest, however, that large individuals are common in August and that in addition a number of small ones begin to appear in the following months. From December 11th 83 individuals of Stage V were measured. A very considerable maximum was found at 30 M, about which nearly all the individuals are grouped, while the high size classes around 40 M and above are only represented by some few individuals. On April 4th, only small individuals were found, and this was still the case on June 17th.

But in July (11th and 24th) a large group of large individuals of 40 M or more occur in addition to the group of small individuals which alone occurred all the winter.

According to the material at hand, copepodid Stage V shows the following variations in size in the course of the year: In July and August both large and small individuals occur, more or less distinctly distributed in two large size groups. In August the large individuals

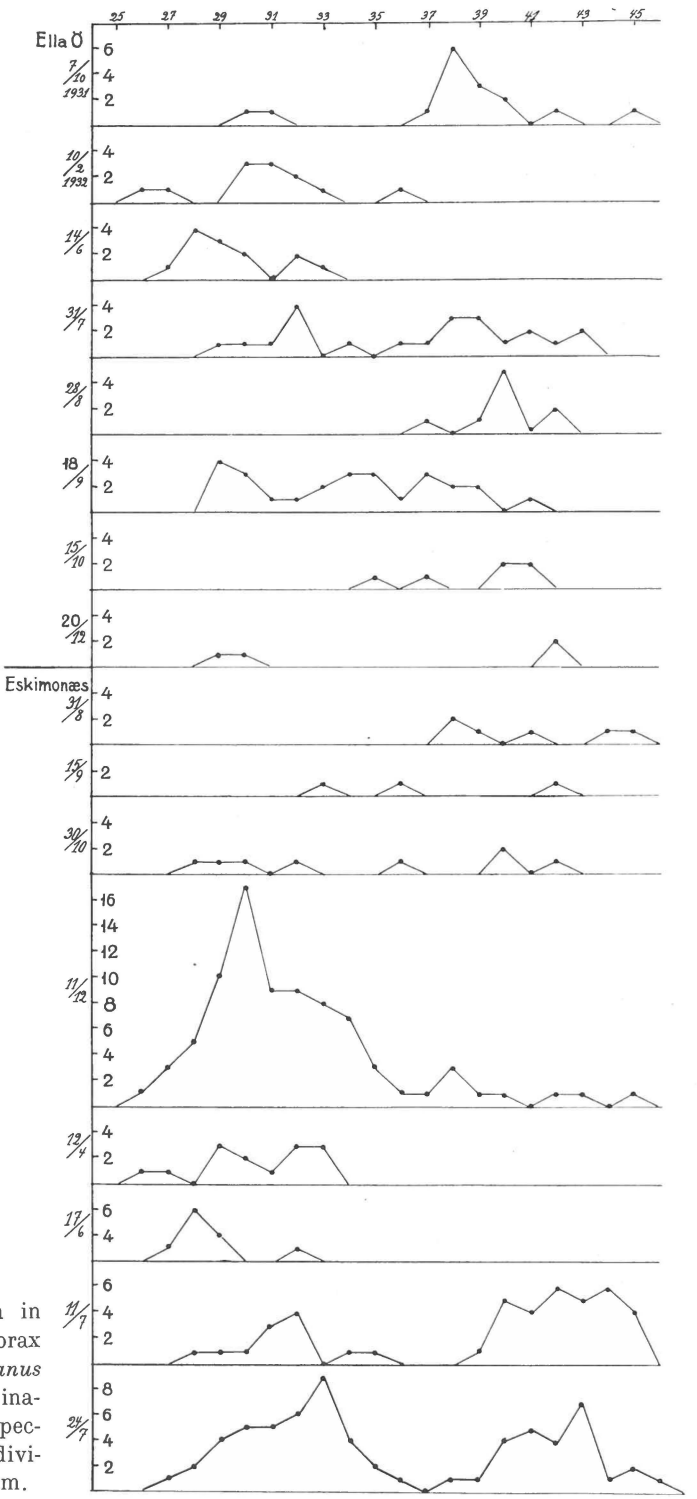

Fig. 18. Variation in length of cephalothorax in Stage V of *Calanus finmarchicus*. Ordinates = number of specimens; microm. divisions = 0.078 mm.

seem to dominate. In the course of the autumn the small individuals increase in number, and after the New Year the small individuals only occur for half a year until July.

The adult females.

In the Ella Island material from February 10th nearly all the individuals are "large", of a size about a maximum of 45 M. The small individuals are very few in number. On April 26th the small individuals had increased relatively in number, while the main part was still constituted by the large ones, grouped around 45 M. On June 14th small and large individuals were almost equally numerous. Judging from the small number of measurements from July, August, and September the large individuals dominate again in the summer time. After September females have only been collected in quite few specimens, the great majority having evidently died at this time.

In order to supplement the sparse summer material measured from Ella Island, a series of measurements of animals collected by means of a Nansen-net (50—0 m) in the Dusén Fjord nearby on August 12th, 1932, has been included. It shows a distribution corresponding to that which might be expected from the few measurements from Ella Island with mainly large individuals grouped around 45 M.

In the Eskimonæs material adult males are entirely absent from the samples from August 30th and September 15th. On October 30th a single female of 40 M was found. The samples from December 11th and April 12th are still too poor in females to show anything about the proportion between small and large individuals. The samples from July indicate that small and large individuals are almost equally frequent at this season.

If the series of measurements from Ella Island is used as a basis, the different seasons show the following variations in size: In the months after the New Year there occur at first exclusively large females; later on, in the course of April, May, and June, small individuals become just as common; but in August the large ones dominate again.

This variation in size will be understandable if we compare it with the variation of Stage V. In October, 1931, large individuals of Stage V were highly dominant, as shown by fig. 18. From October to January—February they thus arrive at sexual maturity and form the stock of large individuals occurring in the following months. Later on, in January and February, as will appear from fig. 18, only small individuals of Stage V were found, which in the course of the succeeding months moulted and turned into the stock of females which is just as frequent as the large ones in June. However, in July—August Stage V increases in size again, and correspondingly the large females dominate in August.

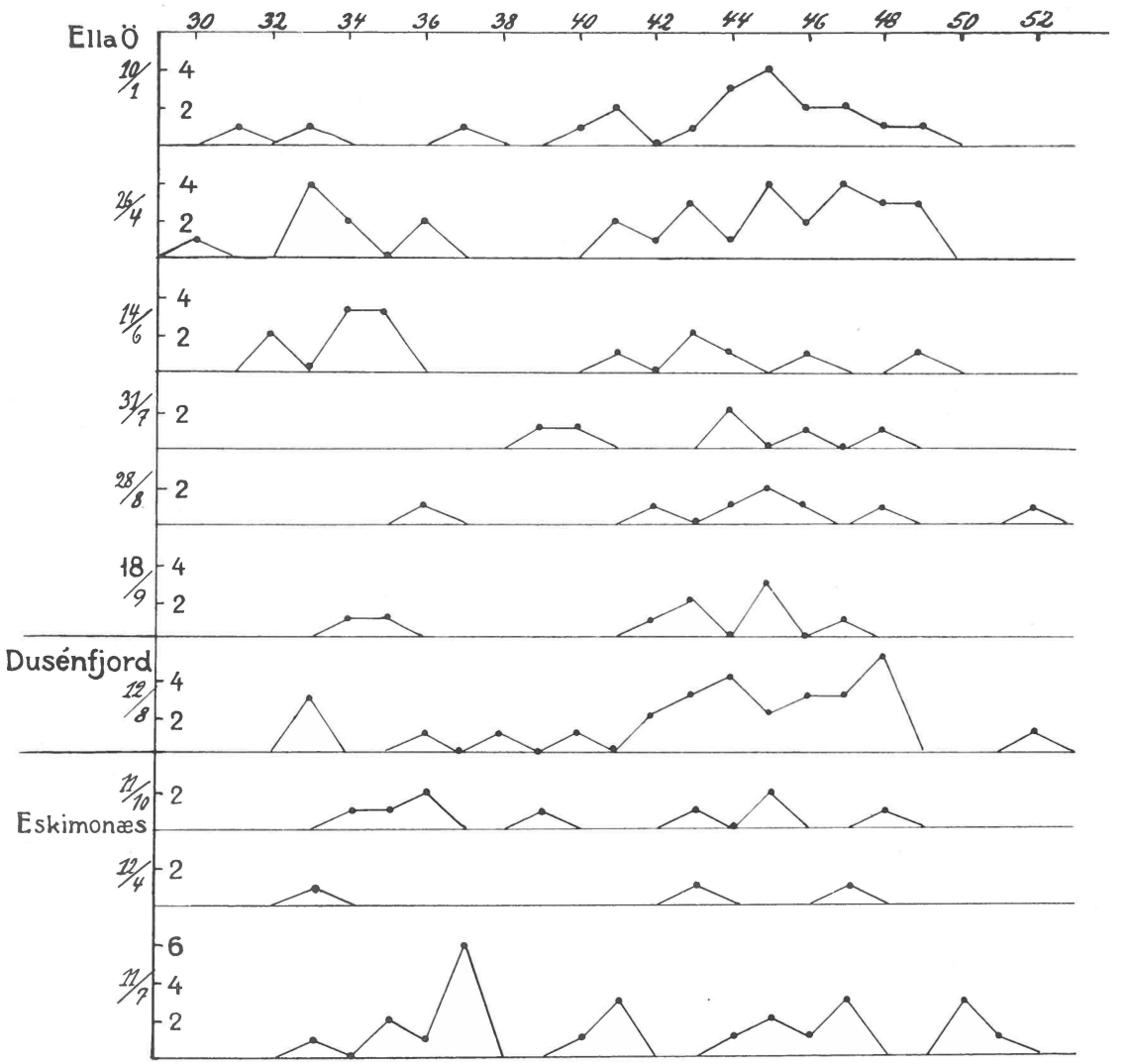

Fig. 19. Variation in length of cephalothorax in adult females of *Calanus finmarchicus*. Ordinates = number of specimens; micrometer divisions = 0,078 mm.

Thus there is a possibility that a number of the large females found in August may have arrived at maturity in January, having accordingly remained at this stage for eight months. Probably, however, the greater number of them develop in the course of the summer from Stage V. Whether they die immediately after the spawning, or they subsist for a long time, it has been impossible to decide.

The males are much rarer than the females, and it is therefore impossible to construct curves showing the variation in size on the basis of the sparse material. There seems to be a tendency for the individuals

from October—February to be large, while those from the early summer are smaller.

The rare occurrence of the males is no doubt due to their shorter lifetime in the sexually mature stage, corresponding with the reduced mouth parts, which are hardly suited for the intake of food. Moreover, according to PAULSEN (1906), the males generally live at greater depths than the females, and consequently are not found, or found in small numbers only, in the available hauls from 50—0 m.

The result of the investigation of the variation in size of the various stages is as follows: Stages I, II, and III are subject to slight variations only; there is, however, an indication that the largest individuals of Stage III are found in August—September.

Stage IV attains its greatest size in July—August, and the individuals are still fairly large in September. Thus they are large in the summer, no matter whether they belong to the old generation (July) or the new one (August—September), but they soon decrease in size in the course of the autumn, and remain rather small right till June.

Stage V exhibits two size groups in the summer, the smaller individuals of which must have developed from the small individuals of Stage IV of the spring and winter, while the large ones have developed from the large individuals of Stage IV occurring in July—August.

In the course of the autumn Stage V decreases in size, and about the New Year all the individuals are small; this state prevails during the remaining part of the winter and spring, until big individuals appear in July.

The females, finally, show a maximum in size about the New Year, after which more and more small ones appear until June, when the small and the large ones are about equally numerous. In July—August the large females increase in number again.

These peculiar variations may be accounted for if it is assumed that the size of an individual after a moulting, under the conditions prevailing here, is determined 1) by its size before moulting, and 2) by its state of nutrition before moulting. The first assumption hardly needs any further statement of grounds. Under conditions otherwise equal large individuals of a certain stage will, of course, develop into large individuals of the next stage. The conjecture as to the importance of the food, on the other hand, perhaps requires a more detailed discussion. As mentioned under the nutrition, these animals only consume a noteworthy amount of food during the period in which the phytoplankton is present in appreciable quantities, viz. from June to September. The occurrence of the copepodid Stages I and II is practically entirely limited to this period, and consequently they must all be assumed to be well fed. Correspondingly, the variation in size is slight within these stages.

In the course of October the last individuals of Stage II have developed into Stage III; according to the conjectures set forth above the size of this last stage should depend on the size and state of nutrition of the preceding stages. Since this stage (II) consists of individuals of about the same size and generally uniformly fed, Stage III, too, will be subject to but slight variations in spite of the fact that the stage to a great extent spends the winter practically without any intake of food. The size is determined once for all by the moulting, and later unfavourable conditions cannot alter it materially.

In Stage IV the following conditions are found: the individuals developing in the autumn from such individuals of Stage II as have been comparatively well fed in August, will be large, whereas those which develop later in the year, when Stage II has been poorly fed for some time, will be small. All the winter and spring exclusively small individuals will occur, till the individuals of Stage III, which have survived the winter, are again well fed in June when the phytoplankton maximum sets in. This causes an increase in the size of Stage IV in July.

As to Stage V, chiefly large individuals, corresponding to the well fed individuals of Stage IV from August, occur in the late summer and the beginning of the autumn. However, these large individuals of Stage V disappear gradually in the course of the autumn, as they pass into the sexually mature stage, and in December—January almost exclusively small individuals occur, corresponding to the poorly fed ones of Stage IV from the autumn months.

Not till July do large individuals of Stage V appear again, corresponding to the good feeding of the two preceding stages in June, when the phytoplankton production is at its highest. At the same time there occur, in July and August, a small number of small individuals of this stage. It is most natural to assume that they are "winter individuals" which have not yet developed into sexually mature individuals.

In an estimation of the variation of the females it should be borne in mind that the individuals that become sexually mature and mated in the period December—February do not spawn till July. Hence the stock of relatively large individuals during these winter months, developed from the large Stage V of the autumn, will be found side by side with the small females which in the course of February—June develop from the small Stage V of the winter. And, indeed, the relative number of the small females increases in the course of this period. After the preceding stages have been well fed in June—July, and Stage V has consequently increased in size, a surplus of big females will be found again in July—August.

It will be seen that the available facts are readily explained by the above-mentioned assumptions. It remains, then, to investigate whether there are other possibilities of explanation.

Here the influence of the temperature should principally be considered. ADLER and JESPERSEN (1920) have shown for the Danish waters that the variation in size of the copepods may be explained by the fact that low temperatures will result in larger individuals than high temperatures. Furthermore it is a well-known fact that the average size of *Calanus finmarchicus* increases towards the north (cf. JESPERSEN, 1934, p. 36), that is to say, it is largest where the water is coldest. However, we may soon convince ourselves that this mode of explanation does not hold good for East Greenland. For precisely in the winter when the lowest temperatures prevail, the growth, as shown above, is slightest. One should not here be misled by the considerable stock of large females which occur at Ella Island in the winter; for they only develop till January, as long as any of the well-fed individuals of Stage V from the late summer still occur. When they have moulted, no more large Stage V or females will appear until the food conditions have become favourable again. In the summer, while the temperature is highest, large individuals of all stages are found in which the variation in size has been ascertained. The objection might of course be raised that only the uppermost 50 m have been investigated. It might then be supposed that the large individuals of Stage V, which, as stated above, are absent from January to June, during this period descend to greater depths; but this does not explain the fact that large individuals of Stages IV, V, and VI dominate in the upper water layers in the summer.

It may accordingly be regarded as proved that temperature fluctuations are of subordinate importance for the variations in size of *Calanus finmarchicus* in East Greenland.

A third explanation of the two size groups of *Cal. finm.* has been given by STØRMER (1929): "Summing up the results, then, we should, in the Greenland waters, have at least 2 groups of *Cal. finm.* One of large specimens spawned in Greenland waters during the previous summer, and another of small specimens spawned farther south the same spring and carried northward with the current". In East Greenland, however, an addition of small individuals carried there from the south by the current, is impossible, owing to the East Greenland Polar Current, which moves southward in a broad belt off the coast. Even though such a supply conveyed by the current may be of some importance at the west coast of Greenland, it must be assumed that the phenomenon is due to the same main cause on both sides of Greenland.

STØRMER, however, arrived at his hypothesis through correct reasonings. If the temperature conditions caused the variation, it was

to be expected that there would be an even transition between the groups, as the temperature changes gradually from one season to the other. That nevertheless distinct size groups exist for Stages V and VI, must be due to a special cause, which he found in the supply by the current. If it is assumed, however, that the cause is to be found in the food conditions, the formation of size groups will be easily understood. For the phytoplankton maximum in June sets in very suddenly, so that the food conditions in the course of some few days change from the poorest possible to the optimal. The individuals which moult before that time, must necessarily be much more poorly fed than those moulting only one week later, and it is doubtless this advantage in the state of nutrition which conditions the two maxima of the size curve in the summer.

That Stage IV does not show two distinct maxima is no doubt due to the shorter duration of this stage than of the two succeeding stages, and consequently not very many individuals remain at this stage from winter conditions to summer conditions. As has been previously shown, the annual variation of Stage IV is exceedingly conspicuous.

The next question that presents itself is whether the variation in size of *Calanus finmarchicus* shows any dependence on the food in other places than at Greenland. However, here one is confronted with the difficulty that the majority of investigators have not studied this phenomenon. There is, however, one exception, in that MARSHALL, NICHOLLS and ORR (1934) record a thorough investigation of size conditions and diatom maxima in the area of the Clyde Sea. They arrive at the result that a spawning of *Cal. finm.* only results in adult individuals if the development of the nauplii takes place during a phytoplankton maximum. On the other hand, they correlate the variation in size with the temperature fluctuations. Considering their curves, however, one will be in doubt as to a single point. The first spawning takes place in February—March. This new generation was full-grown in April and yielded the largest individuals measured in the course of the year. The greatest diatom maximum of the year occurred during the development of this generation. The development of the second generation occurred in May—June at a somewhat smaller diatom maximum, and the development of the third generation at an even smaller maximum. It might be supposed, then, that the decreasing size in the course of the summer is due, at any rate partially, to a constantly poorer food supply during the growth of the different generations. This assumption is supported by the fact that the first individuals developed of each generation are generally the largest, which corresponds to their having benefited from a greater part of the diatom maximum during which the particular generation developed. The authors mention this possibility (p. 807):

"The size maxima depend mainly on the broods, but it is possible that a rich food supply may also have a direct effect on the size". When, however, the average size shows a small, but distinct increase from September to March, the cause of this is no doubt to be found in the temperature, which during this period falls from about 11° to 6° (at a depth of 30 m). A corresponding increase does not seem to take place in East Greenland; but it should be borne in mind that here the temperature fluctuations at a depth of 30 m do not exceed 2° during the year. How much of the size variation in the Clyde Sea area is due to temperature conditions, and how much to food conditions, it is rather difficult to investigate, since the two factors tending to increase the size, low temperature and a good supply of food, as a rule act in the same direction here. However, in East Greenland it seems beyond doubt that the size variations are predominantly due to alterations in the food. On the other hand, it is undoubtedly owing to the lower temperature in the Greenland waters that *Cal. finm.* as a whole is larger here than in the North Sea.

The Variation in size of *Pseudocalanus minutus.*

This species shows a considerable variation in size, even so great that several species, otherwise indistinguiable morphologically, have been erected chiefly on the basis of their size. Thus SARS (1903) erected three species, viz. *P. major*, *P. elongatus*, and *P. gracilis.*

His view has later been opposed, i. a. by WITH (1915), who was of opinion that there is only one species, *P. minutus.*

However, no large series of measurements of this species in Arctic waters are recorded in the literature. A similar analysis of the variations in size of *P. m.* to that made for *Calanus finmarchicus*, is therefore made here. As was the case with that species, the measurements taken are the length of the cephalothorax from the forehead to the posterior margin of the last thoracic segment. One unit of measurement (M.) = 0.0257 mm.

Copepodid Stage I. Ella Island. This stage, present only from July to October, shows a very slight variation in size. It would seem, however, that the largest individuals occur in the early summer (cf. July 11th, Ella Island). Of the material from Eskimonæs only two individuals from July 15th have been measured, of 16 and 17 M respectively.

Copepodid Stage II. This stage, also, shows a slight variation. Possibly there is a tendency here, too, for the largest individuals to occur in the first part of the summer. As previously mentioned, this stage occurs in about the same period as Stage I. Quite naturally,

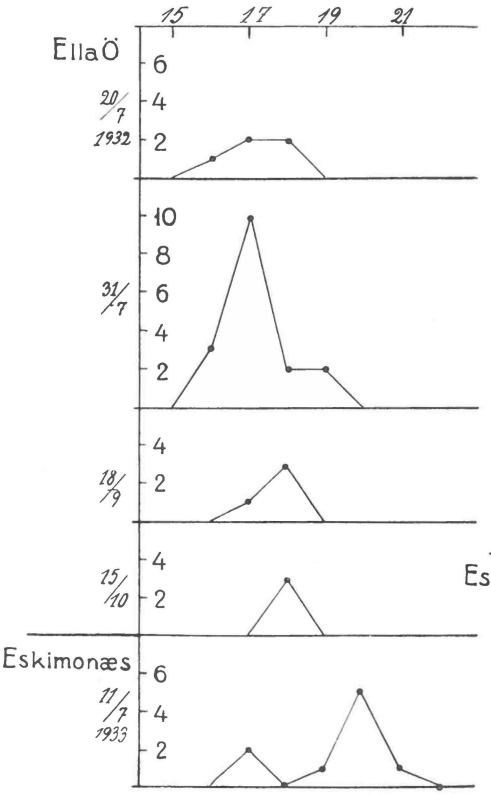

Fig. 20. Variation in length of cephalothorax in Stage I of *Pseudocalanus minutus*. Eskimonæs 1933. Ordinates = number of specimens per haul; micrometer divisions = 0.0257 mm.

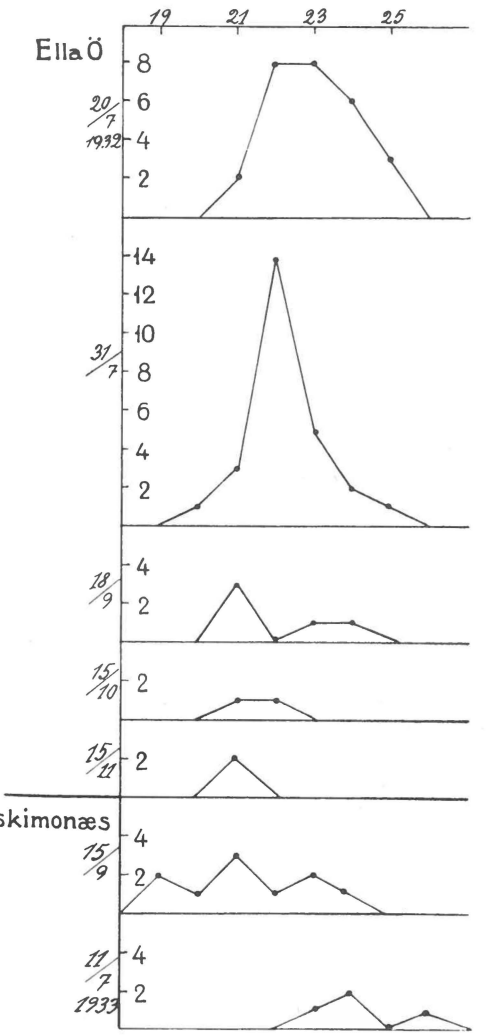

Fig. 21. Variation in length of cephalothorax in Stage II of *Pseudocalunus minutus*. Ordinates = number of specimens per haul; micrometer divisions = 0.0257 mm.

however, it is present till later in the autumn, but then in very small numbers only.

Copepodid Stage III. The material from Ella Island shows that from January to May rather small individuals of a size of 25 M, at most, occur. From June no measurements are available, because Stage III is absent in this month. The whole of the old generation of Stage II have by now passed into later stages.

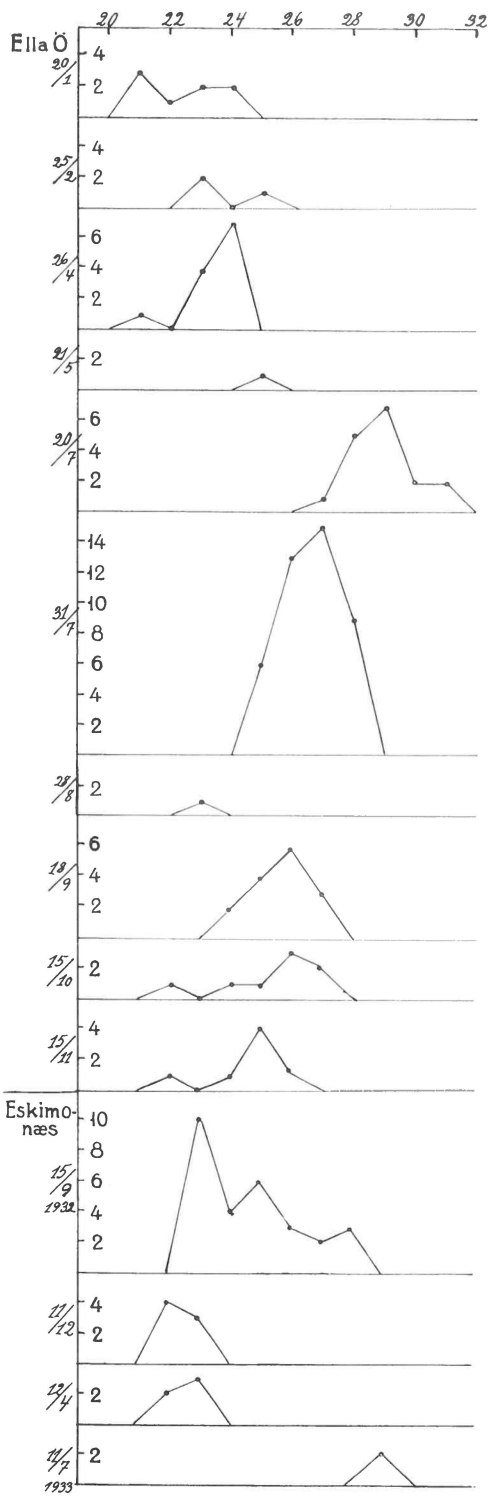

Fig. 22. Variation in length of cephalothorax in Stage III of *Pseudocalanus minutus*. Ordinates = number of specimens per haul; micrometer divisions = 0.0257 mm.

In July the first Stages III of the new generation appear. From July 11th only two individuals of 29 M were measured, but from July 20th a greater number was measured, and it will be seen that all the individuals exceed the range of variation of this stage during the winter. However, as early as July 31st the average size had decreased somewhat, and the two highest size classes, 30 and 31 M, were not represented, whereas groups 26 and 27 M, not previously represented, numbered a multitude of individuals. This decline continued throughout the summer. In September the maximum lies at 26 M, and in November it has decreased to 25 M. However, the size is constantly above the size of the preceding winter, when none of the individuals measured exceeded 25 M.

From Eskimonæs measurements are at hand from September 15th, December 11th, and April 12th. It will be seen, that here, too, many individuals exceeding 25 M in size are present as late as September, while later, in December and April, they have disappeared.

Thus Stage III of *Pseudocalanus minutus*, in contrast to the corresponding stages of *Calanus finmarchicus*, shows a very marked annual variation in size, since from a maximum at the beginning of July its size decreases, to attain, about the New Year, its lowest value, which is retained till the appearance of the new generation in July.

Copepodid Stage IV. Ella Island. Small individuals are present from January to and including April. The maximum of the size curve lies at 28 M. This stage is almost completely absent in May and June, but on July 20th the new generation begins to come into prominence, and now consists of big individuals of 30 M or more. On July 31st a slight decrease may be assumed, corresponding to that which seems to take place in the preceding three stages during the same period. However, the material is hardly sufficient to settle this question definitely. The August material of this stage is very sparse; but the curve for September shows that the peak has moved down to 31 units of measurement. In the course of October and November the size decreases further, to attain finally the same values as prevailed the preceding winter.

Eskimonæs. On September 15th the maximum lies at 30 M. In the rather poor samples from December 11th and April 12th small individuals of less than 30 M dominate, on June 17th a great number of measurements showed small individuals to be dominating, while individuals exceeding 30 M were extremely scarce.

Thus Stage IV attains its size maximum in July; after that time it decreases gradually in size, to reach its lowest value in the winter, which value prevails till the old generation has vanished.

Copepodid Stage V. Ella Island. In January and February both small and large individuals of this stage are present. We cannot, as in

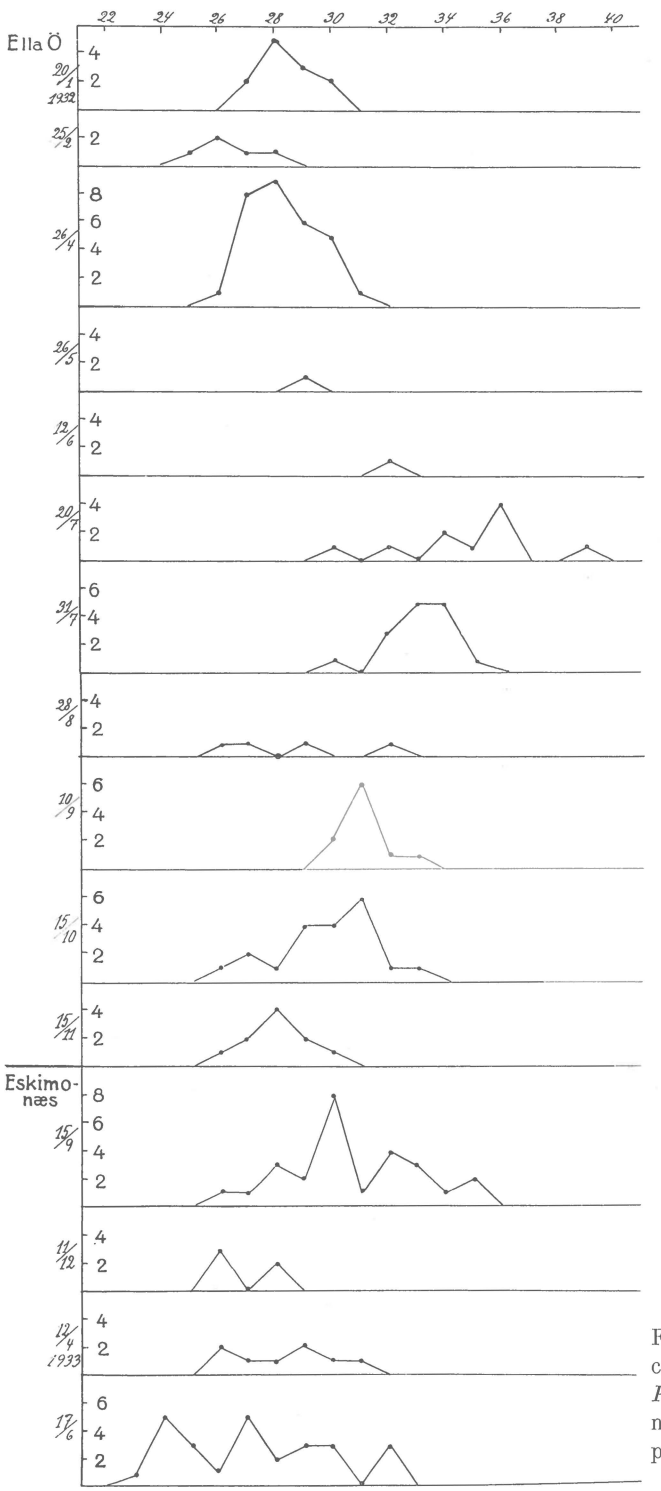

Fig. 23. Variation in length of cephalothorax in Stage IV of *Pseudocalanus minutus*. Ordinates = number of specimens per haul; micrometer divisions = 0.0257 mm.

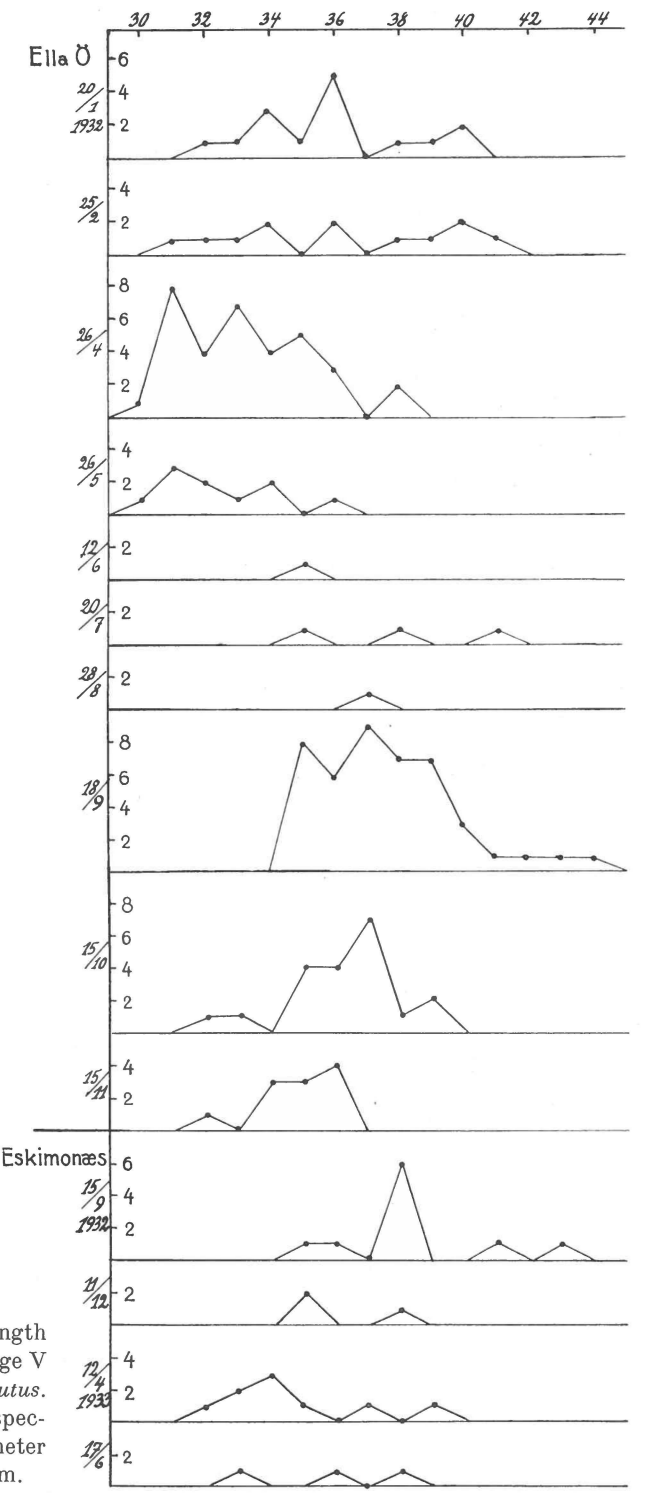

Fig. 24. Variation in length of cephalothorax in Stage V of *Pseudocalanus minutus*. Ordinates = number of specimens per haul; micrometer divisions = 0.0257 mm.

Calanus finmarchicus, distinguish two distinct size groups. On April 26th the average size had decreased, the great majority of individuals being less than 35 units of measurement. The same was the case on May 26th. In June Stage V had almost entirely disappeared, all individuals having passed into the sexually mature stage.

Until September Stage V was present in a very few specimens; but in September the new generation had grown up, and a considerable number had reached Stage V. In this month exclusively large individuals occurred, none measuring less than 35 units. In October conditions are somewhat similar; however, the highest size groups are no more represented, whereas some few individuals of less than 35 M have appeared. In November this state of affairs became even more distinct, an additional number of the highest size groups having disappeared.

Eskimonæs. The number of individuals of this stage measured from Eskimonæs is but small. It will be seen, however, that individuals exceeding 35 M are predominant in September, while such of less than 35 M dominate in March.

Thus Stage V attains its maximum size in September, after which time the size decreases gradually, to reach its minimum in the spring months April and May.

The adult females. Ella Island. The variation within this stage is not distinctly associated with the seasons. Still there seems to be an indication of an increasing size from January to June. Females are fairly common in the period April to June only. The few individuals that have been collected at other periods afford no clues for further conjecture.

Eskimonæs. The individuals from April seem generally to be larger than those from June; but the material is too small to allow of any inferences.

On the whole it may thus be said that this stage does not show any time-conditioned variation in size within the comparatively short period (three months) in which it is of common occurrence.

The adult males. Only four adult males were measured, all from June 12th, 1932, Ella Island. The result of the measurements was: one individual of the size of 33 M, three of 35 M, and one of 38 M.

The result of the investigation of the variation in size of *Pseudocalanus minutus*, then, is as follows:

Stages I and II show an inconsiderable size maximum at the beginning of July, after which time the size decreases slightly until the stages disappear in the course of the autumn. Stages III and IV show

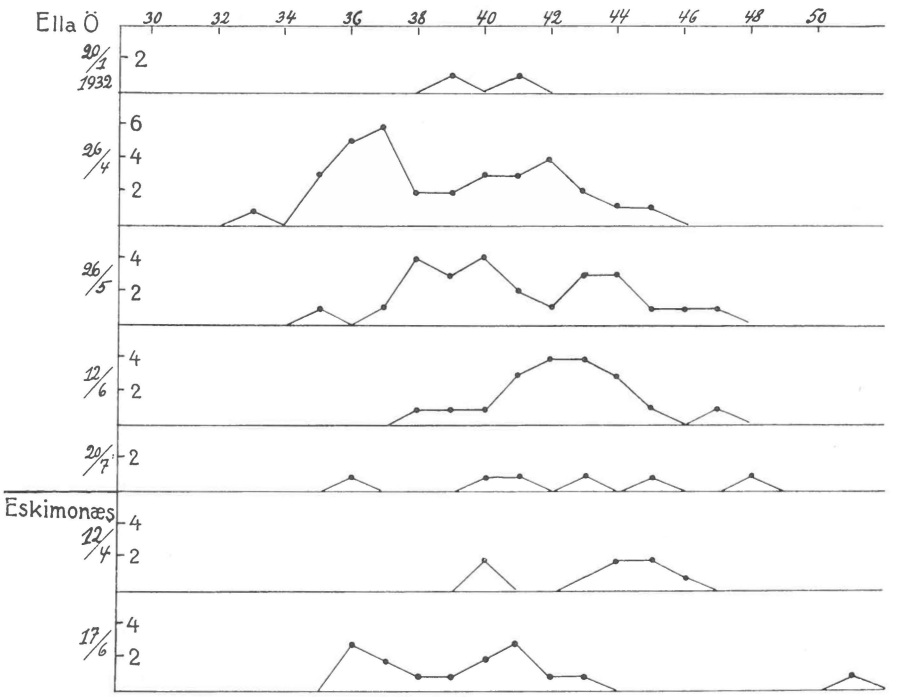

Fig. 25. Variation in length of cephalothorax in adult females of *Pseudocalanus minutus*. Ordinates = number of specimens per haul; micrometer divisions = 0.0257 mm.

a distinct size maximum at the beginning of July, subsequently the size decreases, to attain, about the New Year, its lowest value, which is retained until the old generation has disappeared in June. Stage V has its size maximum in September; then the size gradually decreases, to attain its lowest value in April and May, until the stage disappears entirely in June—July. The females, finally, show no distinct variation in size in the three months, April—June, in which the stage is common.

These phenomena will be easily understood by means of the same assumptions as were considered satisfactory in the treatment of the variations in size of *Calanus finmarchicus*, viz. that the size of an individual after moulting in these waters is determined 1) by its size before moulting, and 2) by its state of nutrition before moulting.

This will appear from the following facts: As shown under the reproduction, the spawning of this species begins earlier than that of *Calanus finmarchicus*, viz. at the end of May and the beginning of June, precisely in the period in which the large production of diatoms sets in. The food conditions of the nauplii will therefore be exceedingly favourable, and the individuals which reach the first two copepodid stages in June will therefore be comparatively large. For that reason, again, the individuals which reach Stages III and IV at the beginning of July

will be especially large. In the course of July the quantity of phytoplankton will decrease considerably, which is reflected in a slight decrease in the size of the first two stages. As early as the end of July this effect is also traceable in Stages III and IV, which, however, are still of a fairly large size. In September the majority of large individuals from the early summer reach Stage V, which attains its size maximum at the same time as the younger stages decrease somewhat in size. However, by now the production of phytoplankton ceases. The food becomes poorer, and the decrease in size is evident in all stages except in the adult individuals, which have not yet appeared. After the New Year Stage III no longer decreases in size; this is no doubt due to the fact that no more individuals of the preceding stages which may pass into Stage III are left. That the decrease in size of Stage IV, too, nearly ceases at this time is doubtless due to the longer intervals between the moultings in the winter, as was the case in *Calanus finmarchicus*. In the course of April—May the greater number of the individuals pass into the sexually mature stage, which before that time was almost entirely absent. As in April—May the phytoplankton production is practically nil, there is no special cause of variation within this period; and it proves, indeed, that such a variation fails to appear. On the other hand, the size shows a great divergence corresponding to the varying food conditions to which the various individuals have been subjected during the preceding summer. Unlike the conditions manifested in the case of *Calanus finmarchicus*, practically no copepodid stages of the old generation manage to survive the phytoplankton maximum of the spring, and accordingly the size maximum for Stage V and the adult individuals, which appears in the summer in *Calanus finmarchicus*, does not occur in *Pseudocalanus*. Thus it will be seen that the same factor, the food, may cause quite a different variation in size in two closely related species, according as the main spawning sets in a month sooner or later.

As regards other possibilities of explaining the variation in size, the reader is referred to the discussion under *Calanus finmarchicus*. It should merely be pointed out once more that the temperature conditions alone cannot furnish a satisfactory explanation. For the size maxima of the different stages set in in the course of the summer, while the minima occur in the winter, or quite the opposite of what would have been the case if the variations were caused by temperature fluctuations.

Yet another feature deserves mention. The gradual change in size from month to month, and the markedly one-peaked variation curve, especially for the younger stages, seem hardly compatible with the assumption of the existence of several species of this genus in East

Greenland. At any rate, one of the species must be entirely dominant. As stated above, WITH (1915), too, arrived at the result that the genus is represented by one species only in the northern waters.

The Variation in size of *Microcalanus pygmaeus.*

The material of this species is much smaller than that of the two preceding species. Notably, as stated above, the species is almost completely absent from the uppermost 50 m during the summer months. For this reason it has been impossible to follow the variation. Only adult females have been measured in a fairly considerable number;

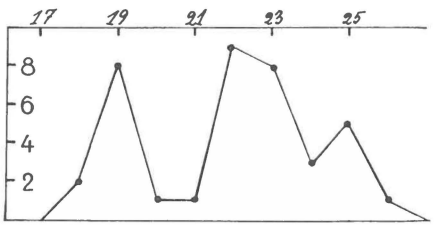

Fig. 26. Variation in length of cephalothorax in adult females of *Microcalanus pygmaeus*. Ordinates = number of specimens per haul; micrometer division = 0.0257 mm.

but even of these the number for the individual months is insufficient to show anything reliable.

If, however, a curve is plotted of all the individuals measured, there seem to be two distinct size groups, one about 19 M and one about 24 M (1 M = 0.0257 mm). Hence it is natural to assume that a variation takes place in this species similar to that of *Calanus finmarchicus*. However, the question needs closer investigation.

Metridia longa.

As mentioned under the reproduction, this species has its main period of spawning in August, and the development of the new generation takes place in the course of the winter. The whole stock keeps pace fairly closely as regards stages, so that it is impossible to collect the same stage at intervals of for instance half a year. Stage V, however, forms an exception, as it would seem that nearly the whole stock is collected in the course of the autumn and winter at this stage, to pass into the sexually mature state in the course of the spring and the summer. A very few measurements of this stage have been made of the material from Ella Island from February 25th and August 28th:

	23 M	24 M	25 M	26 M	(M = 0.078 mm)
February 25th	1	2	6	1	
August 28th		2	4	1	

However few, these measurements show the greatest conceivable agreement between the two dates.

As already stated, females are present in some few months only. Fig. 27 shows a curve of the variation in size of all individuals measured from Ella Island and Eskimonæs, supplemented by a number of measurements from a plankton haul in Scoresby Sound, St. 299, 1933. The curve is markedly one-peaked, and seems to indicate decidedly that no noteworthy annual variation takes place in this species.

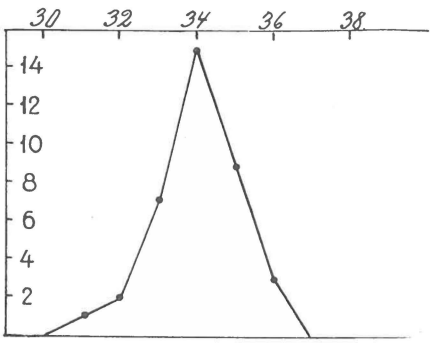

Fig. 27. Variation in length of cephalothorax in adult females of *Metridia longa*. Ordinates = number of specimens per haul; micrometer divisions = 0.078 mm.

The reason why no annual variation in size takes place in *Metridia longa* as in the preceding species is possibly as follows: The spawning of this species is apparently limited to a very short period in the late summer, and when in October the young reach the first copepodid stages, the amount of phytoplankton has already grown very small. The further development now takes place under equally good, or equally poor, food conditions for all individuals in the course of the winter, and when in June the vernal phytoplankton maximum sets in, all individuals have reached Stages V or VI. While different food might act upon several, possibly all, stages of *Calanus finmarchicus* and *Pseudocalanus minutus*, in *Metridia longa* it has the opportunity of acting upon one stage at most, viz. V—VI.

THE INFLUENCE OF THE EXTERNAL FACTORS ON THE PLANKTON ANIMALS

On the basis of the account given above an attempt will be made to explain in broad features the influence of the external factors on the biology of the zooplankton in the fjords of East Greenland.

Temperature.

As repeatedly mentioned, the temperature fiuctuations in the deeper water layers are exceedingly small and hardly of any biological importance. In the fjord-water layer, however, the temperature may rise noticeably in the summer, up to about 10° C, in the uppermost 5—28 m, while in the winter the temperature of the same water layers is about — 1.5° C. This high temperature in the uppermost water layers is probably of fairly great importance for the development of a number of young stages, especially of the copepod nauplii. From the material treated here it will be seen that hauls from 25—0 m in the summer contain practically the same number of nauplii as hauls from 50—0 m, which means that nearly all nauplii are found in the uppermost 25 m. Other investigators have arrived at the same result; probably the nauplii are even chiefly concentrated in the uppermost 5—10 m (cf. DAMAS & KOEFOED, 1909). Since, now, the rate of development is a function of the temperature, according to KROGH (1914) a linear function in several species, a rise in temperature of 10°—12° may cause a fairly noticeable increase in the rate of development. How great this increase will be, it is difficult to say. A species like *Calanus finmarchicus* has one annual generation at the Lofoten (SØMME, 1934), at Møre in southern Norway two (NORDGAARD, 1905, RUUD, 1929), and at Plymouth three (MARSHALL, NICHOLLS & ORR, 1934). It is, of course, impossible on this basis to calculate the gradient of the curve showing the rate of development, since other factors, notably the food, exert their influence. Still these factors would seem to indicate that the larvæ of many forms would have difficulty in completing their development during the relatively short time in which the production of phytoplankton is going

on, i. e. while the food conditions are favourable, if the temperature did not rise precisely in the water layers in which the production is most vigorous, and where the larvæ themselves live. Many young larvæ, e. g. copepod nauplii, do not endure starvation very long. Thus as previously mentioned, MARSHALL, NICHOLLS & ORR (1935) have shown that only if the development of the nauplii coincides with a diatom maximum, will they continue their development. A reduction of their larval life, for instance of merely a week, may accordingly be of vital importance to the animals. The copepodid stages, especially from Stage III and upwards, however, seem to be capable of sustaining starvation for nearly seven months. Thus it would seem that when the copepods have reached Stage III and more advanced stages, they are less liable to die from starvation.

If the warm fjord water is of such great importance for the development of certain species, the fjords will, for this reason alone, be of vital importance to these species, since the water layer with positive temperatures outside the fjords is extremely thin, a couple of metres at most, and never attains such high temperatures as are met with in the fjords.

Salinity.

Just like the temperature fluctuations, the fluctuations in salinity are chiefly limited to the uppermost 10 m, where the thaw-water, notably in the early summer, causes a decrease. This may be so great that it may be inimical to the plankton organisms if they do not escape downwards. Such an inimical effect, however, will probably be limited to about the uppermost 5 m, in which the salinity may decrease to less than 20 per mille.

As regards *Calanus finmarchicus* experimental investigations of the effects of a reduced salinity are available. Thus MARSHALL, NICHOLLS & ORR (1935) found that the metabolism remained unaltered down to about 17 per mille, after which it decreased abruptly and the animals died. Furthermore, it is a fact that e. g. *Oithona similis*, *Calanus finmarchicus*, and *Pseudocalanus minutus* thrive excellently in Danish waters at a salinity as low as about 20 per mille. Thus it must be assumed as to these species that a reduction of the salinity to 20 per mille will not have any injurious effect.

Accordingly very little is known about the importance of fluctuations in the total salinity. Even less known, however, is the importance of special salts or ions. As regards the phytoplankton it is well known that especially nitrates and phosphates may occur in such small quantities that they will act as limiting factors to the growth. That small quantities of salts may be of importance for animals, too, is likewise

a fact. As regards marine animals especially, it is known that the presence of minimal quantitites of copper decides whether oyster larvæ will become fixed and develop further (PRYTHERCH, 1931). Whether the absence of special salts is of any importance for the normal biology of the zooplankton, it is probably impossible to say at present. Often an especially great biological importance is attached to the hydrogen ion and it is most frequently treated separately. Owing to the strong buffer effect of the salts, especially the carbonates, however, the fluctuations in the pH values in the sea are small.

From Ella Island a number of measurements are available, all ranging about a pH value of 8.04. It is therefore hardly probable that fluctuations in the hydrogen ion concentration here is of any importance for the biology of the plankton animals.

Dissolved organic substances.

As was first pointed out by PÜTTER (1909), the sea-water contains considerable quantities of dissolved organic matter. According to KROGH (1934) the quantity in different places and at different depths remains fairly constant about 2.35 mg organic C per l. According to KROGH (1931) it seems indisputable that this organic matter, possibly with a very few exceptions (bacteria, spongia), is of no importance as food for organisms. Nor do the results of the present investigation indicate that such substances are utilised as food. The fact that for instance *Calanus finmarchicus* and *Pseudocalanus minutus* almost cease to grow during the period in which the phytoplankton production ceases, while the amount of dissolved organic matter must be assumed to be practically the same, can only be interpreted to mean that the dissolved organic substances cannot constitute an important foodstuff for these animals.

However, because the dissolved organic substances do not serve as food for the plankton organisms, they need not be without any importance for the zooplankton.

STEEMANN NIELSEN (1934) is of the opinion that an accumulation of certain metabolic products in neritic water results in an increased size of the body and sometimes an elongation of the horns of the *Ceratium*-species.

One of the reasons why in many species of bottom animals all individuals spawn practically at the same time over large areas, is probably that those spawning first give off certain substances to the water which causes the spawning of other mature individuals.

However, so far there is no basis for assumptions in these directions as regards the zooplankton. (The hormone-like substances which are given off to and absorbed from the water, producing certain reac-

tions, pass without any sharp limits into substances which only affect the sense organs (smell or taste senses). As a rule such substances are not, probably, regarded as outer factors, but are actually analogous to light as an outer factor, since light most frequently merely or chiefly affects the sense of sight).

Suspended inorganic substances.

Quantitative determinations of the transparency and content of suspended matter all the year round have not been undertaken here. However, G. THORSON informs me that the transparency at Ella Island is high in the winter, suddenly becoming very slight in the spring when the streams of thaw-water carry suspended clay particles into the fjords. Throughout the summer the transparency is slight, especially in the inner parts of the fjords, as was also observed by me in 1933.

This inorganic detritus is hardly of any direct importance for the copepods. Indirectly, however, it affects their food conditions by reducing the intensity of light in the water and accordingly the phytoplankton production.

To another group of animals, viz. the appendicularians, these suspended particles may be assumed to be disastrous. For it must be assumed that the fine filtering apparatus in their houses will be blocked up so that the intake of food will be rendered entirely or partially impossible. LOHMANN (1911) says about these animals (p. 4): "Die Copelaten... werden auf der hohen See in keiner Nezfange vermisst; in Küstengebiete kann unter den schädigenden Einfluss des Brachwassers, vielleicht auch die Temperatur und das in Wasser suspendierten Detritus eine Reduktion auf eine oder zwei Arten und eine Beschränkung auf bestimmte Jahreszeit eintreten". With the exception of the surface layer proper the water of the fjords does not present essential deviations from that of the open sea as regards temperature and salinity. The cause of the scarcity of these animals, especially at Ella Island, may naturally be found in the opacity of the water. The appendicularians are commoner at Eskimonæs, probably because this station is situated nearer to the open sea than Ella Island; it must be assumed that the stock of appendicularians in the fjords is recruited from the Polar Current.

Whether the inorganic detritus exerts an injurious influence on other phytoplankton feeders must be left undecided. Besides by appendicularians and copepods, this type of feeder is chiefly represented by *Limacina* and larvæ of mussels, polychaetes, and echinoderms. The surprisingly small number of adult *Limacina* that were collected might tempt one to assume that the life conditions for this species are poor;

however, the material at hand does not furnish sufficient information about the cause of this question.

Movements of the water.

Nothing is known about vertical currents in the fjords. Judging from the hydrographic investigations made in the summer (SPÄRCK, 1933, USSING, 1934), the stability is very great, especially in the upper water layers, the specific gravity of the water increasing considerably downwards right down to the warm bottom layer.

Horizontal currents play a considerable part. 1) The Polar Current is especially of importance along the outer coast, on which it sets its mark by its more oceanic plankton. It further seems to influence the larger bays such as Gael Hamkes Bay (at Eskimonæs), either directly or in connection with 2) tidal currents. At any rate H. MADSEN informs me that the current near Eskimonæs was often so strong that the plankton net was forced into an oblique position when being hauled in. At Ella Island both kinds of currents are less marked. It is possibly a consequence of these conditions that appendicularians are commoner at Eskimonæs than at Ella Island. 3) Thaw-water currents, i. e. the system of currents produced by the melted ice and snow in the spring. Roughly speaking there is an outward movement in the surface layers, while probably a slight reaction current moves inward along the bottom. These currents in connection with the tidal currents play a very important role, especially in the biology of the copepods. As previously stated, the great majority of the species *Calanus finmarchicus*, *C. hyperboreus*, and *Pseudocalanus minutus* ascend to the upper water layers in the spring, and considerable quantities of these will accordingly be carried out of the fjords and into the Polar Current. This applies to the nauplii to an even greater degree than to the adult animals. Since, now, the fjords receive supplies of river-water throughout their whole length, the amount of water streaming outwards will increase towards the mouths of the fjords and the chance of being carried away will increase outwards. In agreement with this it will be seen that the number of *Calanus finmarchicus* and *C. hyperboreus* is highest in the interior of the fjords and decreases outwards.

Similar conditions no doubt apply to other species also, adult or larvæ, which live in the upper water layers; but the material does not warrant definite conclusions as to this phenomenon.

These conditions, viz. the Polar Current poor in species along the outer coast and the outward moving thaw-water current, cause the inner parts of the fjords to be almost entirely cut off from any supply of species which are not indigenous to the area. Thus it may be stated

with a fair degree of certainty that species that are of tolerably common occurrence, breed in the fjords.

Amount of food.

As regards food the plankton animals may be divided into two main groups, viz. zooplankton feeders and phytoplankton feeders.

To the former belong decapods, *Euphasiacea*, amphipods; of copepods *Parcuchaeta* and *Heterorhabdus*; *Chaetognates*, *Clione*, *Medusæ*, and *Ctenophores*.

Of these *Clione* is said to feed chiefly on *Limacina*. However, it is of no importance in the area (altogether only two larvæ have been collected). The remaining zooplankton feeders live chiefly on copepods, and accordingly the frequency of the latter is decisive for the nutrition of the zooplankton feeders.

The phytoplankton feeders, or principally phytoplankton feeders, are the appendicularians, *Limacina helicina* and the greater number of copepods (the *Calanus* species, *Pseudocalanus*, *Microcalanus*, *Metridia*, *Oithona*, and *Microsetella*), possibly the ostracods, and most bottom animal larvæ. To all these forms it applies that during a great part of the year, at any rate from November to May inclusive, they are practically debarred from the intake of food, the phytoplankton production being nil and the amount present very small. As regards the bottom animal larvæ the problem is possibly somewhat facilitated by the fact that, when the production ceases, they have already reached the bottom stage (cf. THORSEN, 1936). As to the euplanktonic animals, however, the difficulty must be overcome by their using part of their substance to cover the strictly necessary metabolism. No determinations of the metabolism of plankton animals from Greenland are recorded in the literature, but in other places, e. g. at Plymouth, the metabolism especially of *Calanus finmarchicus* has been carefully investigated (MARSHALL, NICHOLLS, and ORR, 1935).

Starting from these determinations we may make the following calculations: 1000 *Calanus finmarchicus* at Stage V consume 0.13 cc O_2 per hour at the temperature prevailing below the ice in Greenland waters in the winter, viz. from 0 to —1.5° C. If the period during which no intake of food takes place is calculated to be short, seven months = 5040 hours, we shall have an oxygen consumption of 0.66 cc per animal. If 1 cc O_2 is taken in, about 1 mg proteins, 0.5 mg fat, or 1.2 mg carbohydrates may be broken down. If it is assumed that these animals chiefly consume fat, this means that an individual at Stage V in the course of one winter will consume 0.33 mg fat. This might seem a rather small amount, but as Stage V within the Plymouth area has a maximum content of 0.13 mg fat and 0.09 mg protein (A. P. ORR, 1934), it will

be seen that the animal would break down about twice its organic substance in the course of the winter. The value applied for the metabolism must accordingly be more than halved. But that does not suffice. In the course of the winter the great majority of Stage V pass into the sexually mature stage, that is to say, they undergo a moulting and a consequent, though inconsiderable, loss of substance. Finally, the females generally show a higher metabolism than Stage V. According to MARSHALL, NICHOLLS and ORR (1935), 1000 females would, at a temperature of 0 to —1.5° C., assimilate about 0.28 cc O_2 in an hour, or more than twice the assimilation of Stage V. If these facts are taken into consideration, we shall find that the intake of oxygen during the starvation period must be less than one-fourth of the values found in short experiments, when the animals have not previously been starving. No doubt the same applies to these animals as is known from certain other invertebrates, viz. that they have no standard metabolism, but gradually reduce their metabolism during the period of starvation (TETENS NIELSEN, 1935).

As regards one species only, *Calanus finmarchicus*, a calculation could be made; but it no doubt applies to all phytoplankton feeders that their metabolism is much reduced during the winter. With this in view it will be easily understood that in *Calanus finmarchicus* and *Pseudocalanus minutus* moulting takes place at long intervals during the starvation period, and that the longitudinal growth during these moultings is inconsiderable.

As regards which organisms within the phytoplankton are consumed it is known that the appendicularians especially catch centrifuge plankton (LOHMANN, 1911), whereas the copepods probably especially consume diatoms (LEBOUR, 1919—21, MARSHALL, 1923, and others). Judging from the measurements made here, the filter of the copepods is not able to retain nannoplankton at all.

Light.

Indirectly light is of great importance for the zooplankton, in so far as it is required for the assimilation of the phytoplankton organisms, which are the more or less direct source of nutrition for the zooplankton. This question will not be discussed in detail here.

Directly, however, light is of great biological importance for these animals. Thus light is to many forms the factor (or one of the factors) by which they find their bearings in relation to the surface of the water. At the coasts of Europe and America this question has been investigated by RUSSELL (1924—34), CLARKE, etc., and the importance of light for the so-called diurnal migrations has thus been ascertained.

In the material treated here it has been possible to investigate the annual migrations performed by a number of forms, induced by the annual change from dark time to light time in Arctic regions. Only a number of copepods have been represented in sufficient number to allow of definite conclusions; but in all probability the same reaction types may be found within other groups of plankton animals.

One reaction type is represented by the *Calanus*-species and *Pseudocalanus minutus*. These forms are abundantly represented in the upper water layers in the summer. In the autumn, when the light decreases and finally disappears entirely, they leave the upper water layers more or less completely (cf. SØMME, 1934) and sink downwards. In the spring they ascend again to the upper water layers under the influence of the increasing light.

To the other reaction type belong *Microcalanus*, *Metridia longa*, and probably the *Pareuchaeta*-species. These forms are entirely or partially lacking in the upper water layers in the summer, while they are present in these layers during the dark time.

As regards *Metridia longa* it has further turned out that in August it makes diurnal migrations, so that it is much more frequent in the upper water layers by night than by day.

However, no absolutely positive phototaxis can be ascribed to the first type, and no negative phototaxis to the second type. Adult specimens of the *Calanus*-species avoid the surface layers proper; they are accordingly negatively phototactical to the light intensities prevailing there. Reversely, *Metridia* and *Microcalanus* are in the summer most frequent at a depth of about 200 m, where, accordingly, they are not negatively phototactical. Animals of both groups are thus positively phototactical to weak light intenties, negatively so to stronger light. The essential difference between the two groups is not to be found in a positive or a negative phototaxis at a higher or lower light intensity, but depends on whether they are able to remain in the upper layers or to ascend higher up in the water when the light intensity is quite inconsiderable or nil, that is to say whether or not the influence, called by ROSE (1929) the photokinetic effect of light, is necessary.

If the copepods of the *Calanus*-type are not exposed to light during a fairly long period, their movements will probably be slack and they will sink downwards (cf. SØMME, 1934). It has been discussed above that this condition involves a considerable danger to the animals, for in oceanic depths they may sink so deep that the light will fail to reach them again and give rise to the activity required for an ascent. Since the amount of phytoplankton is minimal at great depths, the food conditions for these animals are exceedingly poor; in all probability

they are under the necessity of living on their own substance until they die from starvation or are devoured by other animals.

The *Metridia*-type, however, does not need this photokinetic effect of light; the forms belonging to this type are present in the upper water layers during the whole of the dark time, and must accordingly ascend from deeper layers in the autumn, to leave these layers when the light of the spring begins to exert its influence.

As previously stated, we cannot ascribe any great importance to any other taxis than phototaxis in regard to the vertical migrations of the *Calanus*-group. The assumption of a negative geotaxis (cf. CLARKE & GELLIS, 1935) seems to be incompatible with the observations made on the reactions of these animals. SPOONER (1933) has shown that copepods during a light reaction follow the direction of the light rays, no matter whether the light intensity increases or decreases in that direction, or whether it is vertical or horizontal. The animals used in his experiments probably all of them belong to the *Calanus*-type. As regards the *Metridia*-group the question as to a negative geotaxis is of considerable interest. If we assume that such a negative geotaxis exists, we must expect a concentration of the whole stock of these animals in the upper water layers during the dark time. The question now arises: Is the number of individuals caught in hauls from 50—0 m during the dark time an expression of the whole stock, or is an essential part of the stock to be found in deeper water layers? A direct answer to the question cannot be given, hauls from greater depths not being available. However, if as regards *Metridia longa* the average number of individuals per haul in the winter months, 3.8 per haul from November to and including February, is compared with hauls from an August night (August 28th) 23.6 per haul, when the greater part of the stock owing to the diurnal migrations is found in the uppermost 50 m, one receives the definite impression that only a small part of the stock is found in the upper water layers in the winter. Distributed over a water column of the thickness of 640 m the August quantity would exhibit a similar density to that found in the winter. Thus quantitatively we may very well suppose a fairly even distribution of this species through all depths in the winter. In the spring the animals from the upper water layers must be supposed to be forced downwards by a negative phototaxis to a certain depth, where the light intensity is "optimal", while conversely the animals from greater depths, as far down as the light will penetrate, must be assumed to move upwards to the layer with an optimal intensity of light.

The final result of these considerations must be that as regards *Metridia longa* we need not assume a negative geotaxis, and that such

an assumption would merely render the interpretation of the results more difficult.

All plankton copepods are probably referable to one of the two reaction types mentioned. This must in part remain a postulate. Here only a single feature should be mentioned, which speaks in favour of such a division. If we consider the stock of copepods at greater oceanic depths of the Atlantic, we shall arrive at the following result. A large number of forms are collected at highly varying depths, but never in about the uppermost 200 m. Among these are many carnivorous forms which feed on other copepods, e. g. *Megacalanus princeps*, *Geatanus*, *Valdiviella*, etc. Such forms, which never make their way into the upper water layers, must no doubt belong to the *Metridia*-type. But in addition to the actual deep-sea forms, forms such as *Eucalanus elongatus*, *Rhincalanus nasutus*, and *Calanus finmarchicus* are most frequently met with. These forms are pronounced phytoplankton feeders; when found at depths at which hardly any phytoplankton occurs, the cause is in all probability that they have, quite by chance, descended so far down that the light cannot lead them back to the upper water layers. They will then be sluggish of motion and will continue to sink. But hardly many of them will reach the bottom; for on their downward course they will encounter merely carnivorous animals, the carnivorous copepods mentioned above as well as decapods, *Medusæ*, *Chaetognaths*, fishes, etc., to which the sluggish surface forms will fall an easy prey. These forms doubtless belong to the *Calanus*-type.

SURVEY OF THE BIOLOGY OF THE COMMONEST SPECIES

Calanus finmarchicus.

This species is exceedingly common in the fjords of East Greenland and throughout the greater part of the year it is the dominating species in the upper water layers, at any rate in a quantitative respect.

All through the winter the number per sample is rather low in the uppermost 50 m, since the majority of wintering individuals sink to greater depths during the dark time. In the autumn the stock consists of the copepodid Stages III, IV, and V. In January a considerable number grow sexually mature. The number of males is considerable, and the large number of females with affixed spermatophores testify that many individuals mate at this season. An examination of the ovaries shows, however, that the eggs are quite undeveloped, and they continue to be so until May—June. The main spawning does not take place till July, so apparently six months may elapse between the mating and the spawning. The ratio between the stages is but slightly altered in the course of the winter, which shows that moultings take place at long intervals only. It is further characteristic that the growth during the moultings is slight in the winter. The cause of this is supposed to be the poor food, since the animals do not, apparently, take in food from October to and including May. In May—June there is a fair increase in the number of individuals, as the animals migrate upwards from the great depths, in all probability under the influence of a positive phototaxis. All the stages occurring at this time, viz. Stages III, IV, and V, as also sexually mature individuals, take part in this ascent. At the beginning of July the main spawning takes place, but lasts for rather a long time, and even as late as October occasional nauplii of this species may be seen. This long period of spawning is no doubt due to the fact that a very large number of individuals have passed the winter at Stage III. When in May—June they ascend from the greater depths, they must thus pass through Stages IV and V before becoming sexually mature. However, in the summer this development is rapidly

completed, and the increase in size during the moultings in June—July is fairly large, which has probably some connection with the more abundant supply of food due to the diatom maximum which usually sets in about the middle of June. In the course of July—September the new generation develops up to Stages III and IV. The nauplii seem chiefly to remain in the fjord water layer, where the temperature is positive. This must necessarily increase the rate of development, and it is perhaps doubtful whether at a negative temperature the nauplii would be able to pass through the six nauplius stages during the rather short period in which the production of diatoms supplies sufficient food for them. — In September the number of individuals decreases, especially the adults. The latter probably die, the females when the eggs have been laid, and the males after mating.

The majority of individuals at the younger stages sink downwards to pass the winter at greater depths. In the waters in question the species is annual; however, it seems not improbable that some few individuals which have not completed their development to sexual maturity when the species partially leaves the upper water layers in the autumn, live for another winter, being thus between one and a half and two years when they spawn.

Calanus hyperboreus.

In its biology this species greatly resembles the preceding one. In the winter it is practically entirely absent from the uppermost 50 m, as it spends the whole of the dark time at greater depths, whereas a fairly large number of *Calanus finmarchicus* remain in this water layer. It would be tempting to connect this circumstance with the greater size of *C. hyperboreus* and its consequent smaller surface in relation to its weight, which should cause a more rapid sinking under otherwise uniform conditions. Even if this point is no doubt of importance, it does not comprise the whole truth. *C. hyperboreus* passes through the winter chiefly in Stages IV and V and perhaps the sexually mature stage; for *C. finmarchicus* Stage III is also of great importance in this respect. It proves by measurement that Stage IV of *C. hyperboreus* is of about the same size as Stage V of *C. finmarchicus*, and accordingly should sink with about the same rapidity. Nevertheless Stage V of *C. finmarchicus* is fairly abundant in the upper water layers in the winter, whereas no Stages IV of *C. hyperboreus* are present. This proves that other circumstances, too, are involved, probably we are here concerned with a different reaction to light. In May the species migrate to the upper water layers, most likely under the influence of the increasing light. At approximately the same time the spawning must take place; for at the end of May nauplii of the species may be seen in the

plankton. This has no doubt some connection with the phenomenon observed by SØMME (1934), that the females do not spawn till the light exerts its influence. In contrasts to the preceding species the period of spawning is short, which is also manifested by the fact that nearly all individuals of the new generation may be found to be in the same stage of development at the same time during the whole summer. This means that nearly all the individuals live under practically the same life conditions during their development; which, again, explains the absence of a temporal variation in this species. All the summer nauplii and copepodids of the species are very prominent in the upper water layers, where they may at times surpass *F. finmarchicus* in number. The nauplii, like those of the preceding species, seem chiefly to be limited to the fjord water layer, where the temperature renders a more rapid development possible, and where the food conditions must be assumed to be most favourable, the phytoplankton assimilation taking place here. It should no doubt be regarded as an adaptation to the specially Arctic life conditions that the species spawns immediately before the phytoplankton production sets in, so that the new generation may derive the full benefit from the short period of phytoplankton production.

In September there is a great decline in numbers; the females probably die and the younger stages gradually sink to greater depths.

Pseudocalanus minutus.

In the summer this species is the commonest of all copepods. From the end of August, however, it decreases in number, and in the winter it plays an inconsiderable role in the upper water layers. To this, as to the two preceding species, it applies that a great part of the stock sinks to greater depths in the winter, though a number of individuals are present in the upper layers during the whole winter. It passes the winter in Stages II, III, IV, and V; however, Stage II will have disappeared in March, and in the course of the winter several individuals reach the sexually mature stage. The increase in size during the moultings is small in the winter, corresponding to the poor food. In May—June there is an increase in the number of individuals, because many migrate upwards from greater depths, probably a phototactic reaction. But the spawning must have commenced at an even earlier date; for in March occasional nauplii of this species are met with, and in May the number is considerable. At the same time almost the whole stock reaches the sexually mature stage, and at the beginning of June many males occur. The latter have only a short life-time as full-grown, in contrast to the females; for while males and females are equally

frequent in the last two copepodid stages, the females are highly preponderating as adults.

While the nauplii which appeared in March—April did not seem to develop further, as no copepodid individuals at Stage I occurred, the development proceeds rapidly in June—July. This has doubtless some connection with the scarcity of food in March—April. In June the diatom maximum sets in, and consequently there is an abundant supply of food. For the same reason the increase in size during the moultings is larger after the beginning of the phytoplankton production. Later in the summer the increase becomes smaller again, probably partially owing to the decrease of the quantity of diatoms. Possibly it is of some importance also that the fjord water layer, in which the youngest stages live, become heated in the course of the summer. At the end of July the old generation has greatly decreased; the females probably die shortly after the spawning. The new generation develops rather rapidly; possibly some few individuals reach the sexually mature stage in the same summer so that quite exceptionally there may be two annual generations.

Microcalanus pygmaeus.

In the summer this species is of little importance in the uppermost 50 m, as it avoids the light and therefore remains at greater depths. In September—October it is of common occurrence in the upper water layers, where it is among the commonest species all the winter. When in May the light intensity increases sufficiently, it will be forced into the depths again by a negative phototaxis. Much indicates that the spawning takes place in the spring, but since the species is absent from the water layers here investigated during the whole summer, it is impossible to fix definitely the period of spawning. For the same reason it is difficult to decide whether there is a temporal variation. As two size groups are found among the females, a similar variation to that of *Calanus finmarchicus* may perhaps be assumed.

Metridia longa.

To this as to the preceding species it applies that it remains at depths greater than 50 m during most of the light time. When in August the nights begin to grow dark, it makes diurnal migrations, being present in the upper water layers in the night but absent during daytime. These diurnal migrations are apparently made by Stage V and females only, whereas the males probably remain at greater depths both day and night.

The eggs are probably laid in August—September; at that time all females are filled with mature eggs. In October the old generation

has disappeared, probably all of them have died; but at the same time the first copepodid stages of the new generation will appear. The species is frequent in the upper water layers all winter. The development proceeds gradually, and when the species leaves the upper water layers, the greater number of individuals have reached Stages IV and V.

No temperal variation can be demonstrated in this species, which is probably to some extent due to the short period of spawning and the fairly uniform life conditions for all individuals during the development.

Oithona similis.

All the year round this species is among the commonest forms. In the upper water layers, however, the number is somewhat reduced in the summer. This is not because the species as a whole migrates to greater depths in the summer; it is no doubt a case of an absolute reduction in number, which has possibly some connection with the fact that such small forms are consumed by the *Calanus*-species together with the phytoplankton, the *Calanus*-species being much commoner in the upper water layers in the summer than in the winter. The spawning may apparently take place at all seasons, egg-sac-bearing females having been observed all the year round. But the spawning which is of importance for the subsistence of the species takes place in September—October after the majority of the *Calanus*-species have left the upper water layers but while there is still some food present.

Oncaea borealis.

In the summer this species is extremely common, while in the winter it is present in rather a small number. The strong increase in number in the early summer is due in the first instance to a vertical migration of the stock. The cause is chiefly a very lively reproduction at this season. The mating takes place at all seasons, but apparently it is only the spring-spawning in May—June which results in an increase of the number of individuals.

Limacina helicina.

Adult individuals of this species are not common at any time of the year; evidently it is no fjord form. The spawning probably takes place about the New Year; for from January quite small young specimens are found in the samples. They remain quite small till the production of phytoplankton sets in, after which they grow rapidly at the same time as they decrease in number. Probably they are carried out of the fjords by the surface current.

Sagitta elegans.

Sagitta elegans may be collected all the year round, though never in such great numbers as the copepod species mentioned above. As it is a carnivorous form which lives on copepods, it is quite understandable that it occurs in essentially smaller numbers. The spawning begins at the end of February, when the eggs are first observed in the plankton. Even as late as the end of May its eggs may be met with; but after that time only the young that have just emerged are seen. There seems to be only one annual generation.

SUMMARY

The present work has chiefly been based on two annual cycles of plankton hauls taken at Ella Island and Eskimonæs in 1931—32 and 1932—33 respectively. The plankton hauls are vertical hauls from 50—0 m or 25—0 m. From the survey of the species found it will appear (see the list p. 11) that the fauna living here is very poor in species. It should, however, be noted that at greater depths in the fjords a number of species are found which were not collected in the upper water layers whence the samples here treated are derived.

The survey of the hydrographical conditions is in part based on the literature on the hydrography of the fjords in the summer. Here it should merely be pointed out that positive temperatures and a reduced salinity even in the summer are only to be found in a surface layer about 10—15 m thick, viz. the fjord water layer; below this layer occurs the Polar Current layer with negative temperatures. Below the Polar Current water, at a depth of 250—300 m, the temperatures may rise a little above zero. Further, G. THORSON's hydrographical observations during the winter are published here. From these it appears that the fjord water layer is absent in the winter. From the New Year to May the hydrographic variations in the uppermost 50 m are extremely small, and the temperature constantly negative. Phytoplankton in appreciable quantities is only found from June to and including September. The maximum production occurs in June.

The Numerical Variation of the Species in the Course of the Year.

Calanus finmarchicus. The species is exceedingly frequent in the uppermost 50 m in the summer (June—September), while during the remainder of the year it is less frequent, though it is never entirely absent. This variation is essentially due to two causes, 1) the reproduction, which is treated in the succeeding chapter, and 2) the ascent

of large parts of the stock from greater depths in the spring and their sinking down to lower levels in the autumn. The ascent in the spring and early summer takes place before the season of reproduction, so that the two factors are not directly dependent on one another. It is rendered probable that variations in the intensity of light is the decisive external factor for these annual migrations of the stock. In the spring a positive phototaxis is active. The passive sinking in the autumn is possibly due to the lack of the "photokinetic effect" of the light. A change in the sensitiveness of the light-percipient organs presumably takes place in the course of the summer.

Calanus hyperboreus. The species is frequent in the upper water layers from June to September, while during the remainder of the year it is almost totally absent from the uppermost 50 m. The ascent about June 1st coincides with the incidence of the reproduction. In this species, too, the existence of a positive phototaxis must be assumed, which in the spring carries the animals to the upper water layers, while the lacking photokinesis causes the animals to sink deeper in the winter. If the water in which the animals live is sufficiently deep, it may be assumed that the animals will sink so deep that the light is too weak to stimulate them to ascend next spring. This no doubt applies to many other forms in other waters.

Pseudocalanus minutus. The numerical variation of this species entirely resembles that of *Calanus finmarchicus*, and will not, therefore, be described in detail here.

Microcalanus pygmaeus. It is characteristic of this species that it is more abundant in the upper water layers in the winter than in the summer. Here, too, variations in the light intensity must be assumed to be decisive for the depths in which the animals live; but this species is negatively phototactically adapted to the light intensities found in the uppermost 50 m in the summer.

Metridia longa. Like the preceding species, this species is commoner in the upper water layers in the winter than in the summer, and the phenomenon may be explained in the same way. In August the species makes diurnal migrations, with the result that it is much commoner in the upper water layers by night than by day.

Pareuchaeta sp. The sparse material indicated that of this genus, too, one or two species are more frequent in the upper water layers in the winter than in the summer.

Oitona similis is frequent all the year round, the smallest number being present in July—August. However, this is not because the species

moves to greater depths in the summer; its decrease in number seems to be real and is here coupled with the circumstance that this small copepod, and more especially its nauplii, is very liable to be consumed by the large *Calanus*-species.

Oncaea borealis is much commoner in the summer than in the winter. However, this seems to be mainly due to an excessive reproduction in the spring. The other species are not particularly frequent, and do not exhibit features of any great interest in this connection.

Reproduction and Development.

Calanus finmarchicus. The main spawning takes place at the beginning of July; however, spawning takes place all the summer, nauplii of this species appearing even as late as September.

The moultings follow upon each other in rapid succession till October, while in the six winter months the development seems to proceed very slowly. The winter is spent in Stages III, IV, and V; however, no small number of individuals become sexually mature about the New Year, and many females carry spermatophores, a sign that mating takes place at this season. On the other hand the ovaries are entirely undeveloped and remain so until the spawning season is getting near. The species is annual in these waters; but in exceptional cases it may be assumed to live for one and a half to two years.

Calanus hyperboreus. The spawning takes place about the end of May. The period of spawning is short, and the greater number of the generation keep abreast in their development. When in September the species leaves the upper water layers, the majority has reached Stage III. At the time of ascent in May—June the stock consists of Stages IV, V, and adult females. The species is annual.

Pseudocalanus minutus. The greater number of individuals become sexually mature in the course of the winter and spring. The mating seems to take place from April to June. The main spawning takes place in May—June. The species spends the winter in the copepodid Stages III—V. It is annual here, but under favourable conditions some few individuals may perhaps spawn in the same summer in which they were born.

It is shown that although adult males are far rarer than adult females during the greater part of the year, the two sexes are equally frequent in the two last copepodid stages. This means that the adult males live relatively much shorter than the females.

Microcalanus pygmaeus. It is difficult to fix the spawning time. It must occur in the first half of the year.

Metridia longa. The spawning takes place in August—September. In the course of the autumn and winter a new generation is developed, while the old one probably dies out immediately after the spawning.

At the beginning of the summer most individuals have reached Stage V. The species is annual.

Oithona similis. The spawning seems to take place at all seasons of the year, egg-bearing females being encountered all the year round. They are particularly frequent in June simultaneously with the diatom maximum; but this spawning does not result in an increase of the number of individuals (cf. the numerical variation in *Oithona similis*).

In September many egg-bearing females may again be met with, and now an immense increase of the number of nauplii and copepodids takes place. From December the number of nauplii is small again.

Probably the species has mostly only one generation a year; however, several generations may no doubt develop under favourable conditions.

Oncaea borealis. Males and females in copulation may be encountered all the year round. The main spawning is probably in April—May.

Limacina helecina. The main spawning probably takes place in December—January, but the young remain quite small until June, when the growth suddenly quickens at the same time as the phytoplankton production sets in.

Fritillaria borealis. The main spawning seems to occur in June.

Oikopleura labradoriensis. The main spawning probably takes place in May. Both these species seem to be annual.

Sagitta elegans. Eggs of this species may be found from the end of February to June.

Accordingly most species are annual in the fjords of East Greenland. This is probably due to two causes, 1) the low temperature, which impedes the development; and 2) the short period of the phytoplankton production. The breeding time of the greater number of species occurs precisely at a time when their young may draw benefit from the favourable food conditions of the early summer.

Remarks on the Nutrition of the Copepods.

From June to September, i. e. the period in which phytoplankton production takes place, the intestinal canal of the *Calanus*-species, *Pseudocalanus minutus*, *Microcalanus pygmaeus*, and *Metridia longa*, is filled with food elements, while during the remaining part of the year the canal is empty. Accordingly these animals take in very little or no food for about eight months. Measurements of the filter apparatus of a number of species showed that these species were unable to retain bacteria or other organisms of a diameter of less than 1 μ.

Variation in the Size of the Copepods.

Calanus finmarchicus. The variation in size of copepodid Stages II, III, IV, and V and the sexually mature stage has been studied all the year round, and it is shown that the two size groups which as regards the last stages have been observed in other Arctic waters, too, are not races, but are due to ecological variations within the same species. This variation cannot be the result of temperature variations. But it is easily accounted for if we assume that the size of a given stage after moulting under the conditions prevailing there is determined by 1) its size prior to moulting and 2) its state of nutrition before moulting.

The conditions under which a given individual is found are not decisive for its size, but are concurrent factors in determining the size which it is to attain in its next stage.

The cause of the two size groups is the large difference in the food conditions in summer and in winter.

Pseudocalanus minutus. The great size variation in this species may be explained in the same way as the variation in *Calanus finmarchicus.*

Microcalanus pygmaeus. The rather sparse material might indicate similar conditions as in the preceding species. The two species, *M. pygmaeus* and *M. pusillus*, which in the main differ in size only, no doubt belong to the same species.

Metridia longa. The species shows no seasonal variation in size. This has some connection with the fact that the breeding season is short and the whole stock keep abreast in their development, the life conditions for the great majority of individuals being uniform. In *Calanus finmarchicus* and *Pseudocalanus minutus*, however, the breeding

time comprises the whole summer, and the new generation accordingly grows up under very diverse conditions.

The Influence of the External Factors on the Plankton Animals.

Temperature. Temperature fluctuations of importance are only found in the uppermost 25 m. The positive temperature of the surface layers in the summer is probably of importance for the development of the larvæ of the planktonic animals which might perhaps not otherwise complete their development during the period in which the food conditions are good.

Salinity. In the uppermost 5 m the salinity may in the summer fall below 20 per mille, which may cause the death of many species.

Dissolved organic substances seem to be of no importance in respect to nutrition.

Suspended inorganic matter. The water of the fjords, notably during the melting of the ice, contains fairly large quantities of suspended terrigenous material in contrast to the open sea outside the fjords. This must be assumed to be an essential reason why *Appendicularia* and possibly *Limacina*, too, apparently thrive so poorly in the fjords.

Water movements. Thaw-water currents and tidal currents will show a tendency to carry animals, e. g. copepods, from the fjords, relatively richer in animals, to the Polar Current poor in animals. This tendency will be greatest near the outer coast, and consequently the interior parts of the fjords as a whole will be richest in copepods. Species which thrive best in the open sea, e. g. *Appendicularia*, are, however, most frequent near the outer coast.

Amount of food. A brief survey is given of the foods on which the various species live, according to the available literature. It is pointed out that the phytoplankton feeders must starve for about eight months. A computation shows that with the metabolic values found for *Calanus finmarchicus* at Plymouth this species would consume its own substance several times in the course of the winter. When the animals starve for a long period, the metabolism must be much lower.

Light. Light is the most essential of the factors which give the animals their bearings in relation to the surface. Among the copepods there seem to exist two types of reaction towards the light, the *Calanus*-

type and the *Metridia*-type. Both types may show both positive and negative phototaxis. The difference is that animals of the *Calanus*-type lose their activity and sink to greater depths when exposed to darkness for a long time, while the *Metridia*-type does not need the photokinetic action of the light. These reaction types may be found again in the copepods in other waters. It seems difficult to make the assumption of a negative geotaxis accord with the available facts.

Table 1. Temperature and Salinity at Ella Island

Date	$^{16\text{-}17}/_{1}$		$^{3}/_{2}$		$^{18}/_{2}$		$^{6}/_{3}$	
	° C.	‰	° C.	‰	° C.	‰	° C.	‰
m								
0	—1.46	27.3	—1.45	29.16	—1.59	30.10	—1.50	30.0
5	—1.50	29.5	—1.50	30.19	—1.60	30.2	—1.52	30.08
10	—1.51	29,9	—1.35	30.73	—1.33	30.74	—1.51	31.2
15	—1.44	30.0	—1.30	30.97	—1.38	31.45	—1.54	31.8
20	—1.33	30.8	—1.36	31.20	—1.41	31.67	—1.56	31.82
25	—1.31	30.95	—1.52	31.58	—1.45	31.76	—1.59	31.92
30	—1.26	31.3	—1.55	31.69	—1.48	31.89	—1.57	32.10
35	—1.24	31.4	—1.59	31.8	—1.57	—	—1.55	32.33
40	—1.31	31.7	—1.63	31.91	—1.59	—	—1.52	32.4
45	—1.51	31.9	—1.63	31.9	—1.63	32.37	—1.58	32.59
50	—1.50	32.0	—1.63	32.18	—1.63	32.50	—1.59	32.70

Table 2. Showing the number of specimens of the different species

Date	$^{20}/_{1}$	$^{22}/_{1}$	$^{10}/_{2}$	$^{25}/_{2}$	$^{27}/_{3}$	$^{10}/_{4}$	$^{21}/_{4}$
Calanus finmarchicus	12.5	7.0	11.9	2.4	6.8	7.7	4.8
Calanus hyperboreus	0	0	0	0	0	0	0
Pseudocalanus minutus	7.5	10.2	2.8	3.4	2.4	3.0	5.3
Microcalanus pygmaeus	4.3	4.2	3.1	2.0	1.1	0.2	0.2
Metridia longa	1.0	1.0	2.7	4.4	3.0	0.8	0.4
Oithona similis	173	—	128	140	133	125	121
Oncaea borealis	0	0	0.1	0	0	0	0.2
Microsetella norvegica	1.8	1.3	0.2	1.6	1.3	1.9	0.3
Pareuchaeta sp.	0.5	0.3	0	0.1	0	0.2	0
Nauplii "large"	0	0	1	3	14	26	34.3
Nauplii "small"	59.5	—	38.8	44.3	31.8	32.7	25.5
Themisto sp.				0.6	1.3		
Lamellibranch larvæ	0.2	—	0.3	0.1	0.1	0	0
Limacina helicina	48.4	—	46.7	41.5	39.0	43.7	17.2
Oikopleura	1.4	—	3.7	4.3	1.9	2.3	1.0
Fritillaria borealis							
Aglantha digitalis			1				
Eggs	0.9		2.1			4.4	0.8
Sagitta elegans	1.5	—	0.7	0	0.3	0	0.7

in the period January 16th—May 20th 1932.

$^{20}/_{3}$		$^{3}/_{4}$		$^{17}/_{4}$		$^{4}/_{5}$		$^{23}/_{5}$	
° C.	$^{0}/_{00}$	° C.	$^{0}/_{00}$	° C.	$^{0}/_{00}$	° C.	$^{0}/_{00}$	° C.	° C.
— 1.54	29.12	— 1.59	31.29	— 1.59	31.02	— 1.62	30.82	— 1.59	30.77
— 1.40	—	— 1.30	31.29	— 1.45	30.61	— 1.35	31.22	— 1.44	31.63
— 1.40	31.22	— 1.48	31.80	— 1.54	31.92	— 1.35	31.90	— 1.51	32.01
— 1.53	31.92	— 1.51	32.00	— 1.48	32.16	— 1.50	32.22	— 1.56	32.20
— 1.57	32.16	— 1.59	32.31	— 1.58	32.49	— 1.55	32.52	— 1.62	32.52
— 1.59	32.26	— 1.60	32.60	— 1.60	32.66	— 1.56	32.69	— 1.65	32.72
— 1.59	32.35	— 1.65	32.73	— 1.63	32.79	— 1.62	32.88	— 1.69	33.08
— 1.59	32.45	— 1.67	32.79	— 1.64	32.85	— 1.65	33.04	— 1.70	32.92
— 1.60	32.59	— 1.67	32.84	— 1.63	32.97	— 1.66	33.08	— 1.69	33.04
— 1.59	32.66	— 1.67	32.94	— 1.65	33.01	— 1.66	33.14	— 1.70	33.08
— 1.59	32.83	— 1.67	32.99	— 1.65	33.08	— 1.66	33.12	— 1.69	33.1

collected per haul at Ella Island (vertical haul 50—0 m, fine gauze).

$^{11}/_{5}$	$^{26}/_{5}$	$^{12}/_{6}$	$^{20}/_{7}$	$^{18}/_{8}$	$^{28}/_{8}$	$^{18}/_{9}$	$^{15}/_{10}$	$^{15}/_{11}$	$^{20}/_{12}$
11.6	11.5	16.3	26.0	66.8	3.9	14.7	4.2	3.9	11.4
0.1	0.1	1.3	3.0	20.9	4.4	0.3	0.1	0.1	0
2.4	5.2	6.7	5.2	353.6	7.3	94.9	33.8	24.9	5.2
0.3	0.5	0.3	0.5	0.1	0.1	2.3	8.0	10.4	2.3
0	0	0.1	0	6.6	23.6	4.7	1.1	8.9	4.6
106	—	125	44	47.1	19.3	83.5	101.5	126.9	40.4
0	2.1	1.0	27	116.1	22.8	11.6	6.6	7.0	0.4
0.7	0.3	—	0	0.1	0	0.5	1.7	1.4	0.6
0	0	0	0	0	0	0	0	0	0
123.1	36.9	20.5	12	107.1	19.6	102.5	22.2	6.1	0
6.4	1.4	0.7	0	2.7	0.4	113.6	84.4	55.9	12.2
				1.9		0.1			
14.1	25.9	41.5	4.0	21.9	38.2	14.9	3.1	0.9	0
11.1	12.1	5.7	2.5	0.6	0.3	2.4	5.4	1.9	1.4
0.3	1	1	0	0	0	0.1	0.7	1.5	1.0
			juv. juv.			2.9	3.0	3.9	0.6
				0.4	0	1.1	1.0	0.6	0
9.4	35.4	515,4	—	14.8	3.1	5.4	1.9	1.0	0.6
0.6	0.9	0.8	1.0	1.3	1.3	1.1	0.3	0.8	0.6

Table 3. Showing the number of Copepods per haul (50—0 m) collected at Eskimonæs. 1932—33.

Date	$^{13}/_{8}$	$^{15}/_{9}$	$^{30}/_{10}$	$^{10}/_{11}$	$^{12}/_{12}$	$^{12}/_{1}$	$^{2}/_{2}$	$^{18}/_{2}$	$^{29}/_{3}$	$^{13}/_{4}$	$^{30}/_{4}$	$^{19}/_{5}$	$^{1}/_{6}$	$^{11}/_{7}$
Calanus finmarchicus	124	95	5	31	37	37	37	10	18	17	17	31	18	55
Calanus hyperboreus	50								1			+		181
Pseudocalanus minutus	88	62	67	109	32	11	9	10	13	39	23	23	13	23
Microcalanus	+		3	42	7	15	9	18	6	12	12	25	18	4
Metridia longa		4		5	7	9	5	3	1	1			+	
Oithona similis	88	175	54	349	155	140	380	195	62	69	65	72	92	121
Oncaea borealis	9	29	5			2	9	15	6	6	2	7	7	16
Microsetella	6				2									
Pareuchaeta							+			2				
Nauplii	99.5	143.5	98.3	6.7	4		0.2	5	32.8	116.6	145	315	384	680

Table 4. Showing the number of specimens of the different species collected per haul at Eskimonæs (vertical haul 50—0 m, fine gauze).

Species	Date																
	$^{16}/_{8}32$	$^{30}/_{8}32$	$^{15}/_{9}32$	$^{3}/_{11}32$	$^{19}/_{11}32$	$^{12}/_{12}32$	$^{12}/_{1}33$	$^{2}/_{2}33$	$^{18}/_{2}33$	$^{9}/_{3}33$	$^{29}/_{3}33$	$^{13}/_{4}33$	$^{30}/_{4}33$	$^{19}/_{5}33$	$^{2}/_{6}33$	$^{19}/_{6}33$	$^{12}/_{7}33$
Amphiphoda	1	0	0	0,3	0	0	0,2	0,5	0	0	4	3,5	0,4	0	0	1	0,5
Isopoda	0	0	0	0	0	0	0	0	0,4	0	0,2	0	0,2	0,5	0,2	0	0
Copepoda	313,5	105,5	364	339	471,5	351	216	477	250	155	101	143	119	165	148.6	116	402,5
Nauplii	99,5	149,5	98,3	6,7	4	0	0.2	5	32,8	50,5	116	145	315	384	411	480,5	179,5
Oikopleura / *Fritillaria borealis*	34,5	5,5 / 31,5	8 / 11	2,3 / 1	5 / 3,5	7 / 1	4,8 / 0,6	7,5 / 0	9 / 0,2	3,5 / 0,5	2,8 / 0	5 / 0	2,8 / 0	2,5 / 1	0,8 / 0	4 / 17	1 / 3,5
Ophiopluteus	19,5	2,5	6	1,3	1	1	0,6	3	0,2	0	0,2	0,5	0	0	0,2	0	47
Echinopluteus	3	0,5	0	0	0	0	0	0	0	0	0	0	0	0	0,2	12	8
Limacina helicina	13	4	4	1,3	0	1	0	0	0,2	0	0	0	0	1	0,2	0	2
Lamellibranch-larvæ	131,5	12,5	18	9	3	2,5	0,2	0	0,2	0	0	0	0	0	0	0	12,5
Sagitta	6,5	2	2,3	1,3	2	0	0,4	0,5	0,4	0	0,4	0	0,2	10 [1])	13 [1])	4,5 [1])	16,5 [1])
Polychaete-larvæ	16,5	3,5	1,7	0,3	0,5	1	0,2	0	0	0	0	0	0,2	0	0	7,5	0
Hydromedusae	3,5	0	0,3	0,7	0,5	0	0,8	0	0	0,5	0,2	0,5	0	0	0,4	0	0
Ctenophora	0	0	2	0,7	0,5	1	0	0	1	0,5	0,8	1,5	0,2	0	0	0	0
Radiolaria	133,7	3.5	4	0,3	0	0	0	0	0	0	1	0	0	1	0	0	55,5
Tintinnidae	10	2	1,7	0,3	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceratium	5	0,5	5,3	1,7	0	3,5	3.8	0	5,4	0	1,2	1,5	1,8	5,5	3,2	0	12
Eggs	31	3,5	1,7	1	0	1	1,6	11,5	55,4	53	24,2	30,5	27,6	10	18,6	728	126

[1]) juv.

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