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Animal Plankton of the Norwegian Coast Waters and the open Sea

I

Production of *Calanus finmarchicus* (Gunner) and *Calanus hyperboreus* (Krøyer) in the Lofoten Area

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Introduction.

This memoir is the first part of an investigation carried out for the purpose of studying the more general laws of horisontal distribution and the production capacity of different areas of the sea as regards plankton animals. My first intention was to study *Calanus hyperboreus* from its whole distribution area and I have in this work used different materials collected by several expeditions. So far I have from these investigations only published a very short preliminary report (Sømme 1929). During the work the necessity of a comparison with the chief lines of distribution also of other species e. g. *Calanus finmarchicus* and certain *Euphausidae* became evident. Hjort and Ruud (1929 pp. 65—68) has kindly made use of some of my observations and charts made on the distribution of *Euphausidae*.

The present paper is chiefly based upon the excellent materials collected by mr. Oscar Sund during his cruises to the Lofoten area. I am greatly indepted to mr. Sund for entrusting me with these materials and for collecting after my suggestions material especially ment to throw light upon certain questions.

After serious reconsiderations I have in the present paper not only given a detailed description of the features from my investigations from the Lofoten area (special part), but I also found it convenient to introduce the problems of the open sea and their possible solution suggested by the literature and my own material (general part).[1] In a future part of my work, the investigation of *Calanus hyperboreus*, which have for some time been under preparation, the problems of the open sea and the arctic regions will be discussed in more details.

Concerning the general laws of vertical distribution of planktonic animals many open questions are in my opinion still left. More investigations of experimental character, more investigations on the optics of the sea, and more exact quantitative methods are absolutely necessary. These problems have therefore as far as possible been kept out of my discussions.

During one year of my work I have been engaged to The Norwegian Fishery Board. Further grants have been made by »Fiskeribedriftens forskningsfond«, the »Nansen fond« and »Colletts legat« for which I want to express my aknowledgements.

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[1] Earlier printed in American Naturalist. Vol. LXVII. 1933.

GENERAL PART.

Damas's Circulation Hypothesis.

I.

Through the many plankton investigations carried out during the last 50 years we know that every planktonic species, animal or plant, has its own characteristic geographical distribution. Only few of the papers published on this subject attempt, however, to discuss the reason for this phenomenon. A very interesting exception in this respect forms a paper by Damas (1905), where Damas not only raises the problem of the specific distribution of plankton organisms, but also suggest a method for its possible solution. Damas's questions we may form in the following way:

Why are the species of plankton animals in their distribution limited to distinct areas of the sea? Why is it that these animals, which we know may be carried far away with the currents, are not within a short time evenly distributed from pole to pole?

Damas's investigations included 3 important species from the southern Norwegian Sea, *Calanus finmarchicus* (Gunner), *Calanus hyperboreus* Krøyer and *Pseudocalanus elongatus* Boeck. His treatment of the *Calanus finmarchicus* most clearly demonstrates his method. For this species Damas succeeded in determinating 11 moulting stages (later investigations has proved the existence of 12 stages). The occurrence of eggs, as well as each of the moulting stages or groups of such, and also the adult animals were now by Damas mapped out separately. These charts Damas now compared with charts showing the differences in external conditions of the area investigated, hoping by this method to find an interrelationship between distribution and environment.

Damas's charts of the distribution of eggs, males and females of the species mentioned (Fig. 2 a) proved the existence of a large and distinct spawning area during May—June 1904, a spawning area which was found to be situated within the surface isothermes for 2° and 6° C. The main spawning was even found to occur between the narrow limits of 4° and 6°. The larval stages from this spawning area, had on the other hand, a far wider distribution than the eggs. They followed the current northwards and eastwards through the Norwegian Sea.

In order to give a feasible explanation of the phenomenon just discribed Damas put forward his circulation hypothesis, a hypothesis which he also tried to extend to other species and other areas. The foundation for this hypothesis was the discovery by Helland-Hansen and Nansen of the great cyclonic system of the waters of the southern part of the Norwegian Sea, which, however, in 1905 had not yet been published. Damas assumed that the whole life cycle of the species in this area depended upon this cyclonic system. Spawning could apparently only take place within the limits of temperature which he had found inside the spawning area. The new generation derived from the spawning was first carried with the current away from the spawning area, and later with the cyclonic current back again to the same area and to the same physical conditions where spawning could once more take place and another generation could then start its drift. The necessary time for each drift along the course of the cyclonic system and each generation would, according to Damas, have to be one year.

II.

From a biological and hydrographical point of view grave doubts may be raised against Damas's famous circulation hypothesis. Our present knowledge of the temperatures at which the spawning of *Calanus finmarchicus* takes place thus forms a conclusive objection. If we compare the different temperatures of the areas from which this widespread species has regularly been recorded a considerable variation in spawning temperatures are found. The papers by Farran (1927) and Russel (1928) clearly show that the spawning at the English coast takes place at a temperature of about 10° or more. The frequent occurence of the species during the whole year in more southern waters proves that the upper limits of spawning are not herewith reached. In the Lofoten area, at the Norwegian coast, from where I shall below give some results from my own investigations, I have actually found spawning females and eggs of the earliest cleavage stages in waters of a temperature down to 1°, 22. The frequent occurrence of the species in waters where even lower temperatures are predominating suggest still lower limits. Certainly, it is thus very improbable that in the southern Norwegian Sea — among holoplanktonic species — we should find a local race preadapted to spawn in the narrow temperature interval of 4°—6°.

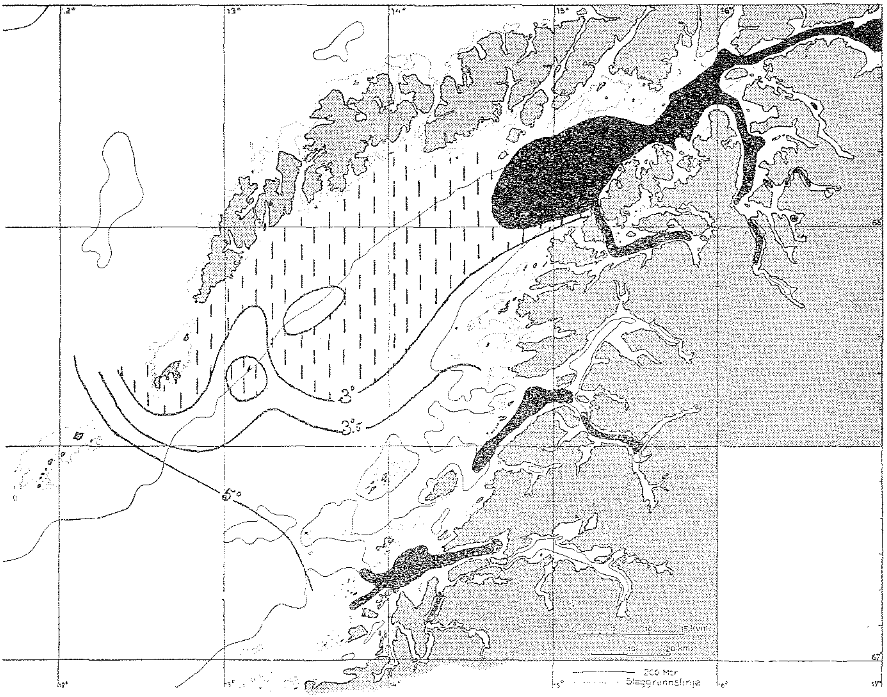

Fig. 1. The Lofoten area with the surface temperatures for March to April 1922. The darkened areas show the centers where rich hauls have been made during winter time for both species investigated, and to which the spawning of *Calanus hyperboreus* is limitted. The area shaded is the cold area into which most numbers of *Calanus hyperboreus*, females and larval stages, are carried after spawning time, and where the main spawning of *Calanus finmarchicus* takes place.

Spawning of Calanus finmarchicus and Calanus hyperboreus in the Lofoten area.

An extensive material collected by The Norwegian Fishery Board in the Lofoten area together with materials collected by Nordgård from the same area 1899 and 1900 has given me an opportunity for investigating the spawning areas of the two species Calanus finmarchicus and *Calanus hyperboreus* according to the methods of Damas.

Damas gives in his paper only very few details as to his methods for determinating the younger stages. The first task of my work has therefore been to give a more complete description of the younger stages and to work out a method for the determination of the quantities of each stage present in the sample. A morphological difference was in the two closely related species only found in the structure of the eggs, while in the early larval stages (6 nauplius and 3 first copepodid stages) no such difference could be found. By measuring the Carapace, however, a decided difference in size was found, and by this means a separation of the species and a quantitative determination can be effected.

By using this method I have succeeded in mapping out the spawning areas for the two species during their spawning time, March—April. (Fig. 1).

Spawning *Calanus finmarchicus* and their eggs were found in every locality investigated, but the numbers of female and eggs show a great deal of variation within different parts of the area. A cross section on the 9. of April 1922 (Fig. 39) where the numbers of females and eggs of this species have been recorded graphically with the temperatures of the water, show a marked increase in the numbers in the northwestern part of the section, where the surface temperature is less than 3°. This characteristic feature has been found in all cases investigated. The table thus gives the average numbers of eggs and females in March—April plotted against intervals of surface temperatures. From waters of a surface temperature below 3°.5 the number of individuals are strikingly predominant. Apparently we have here a characteristic spawning area very much like the spawning area described by Damas. The proportion between eggs and females show, however, no marked difference in different parts of the entire area investigated. The predominant spawning in the northern area of cold waters is thus simply due to the great excess in numbers of spawning females found there; the fewer specimens spawning freely outside this part of the area clearly shows that no limiting factor exist for the spawning process itself.

Surface temperature.	Vertical hauls. Nansen closing net.			Surface hauls.	
	n =	Eggs	♀♀	n =	♀♀
1°.5 — 3°.5	39	5 972	98	20	8 400
3°.5 — 5°	19	490	2.8	—	—
More than 5°	9	560	5.9	—	—
More than 3°.5	—	—	—	28	98

Average numbers of eggs and females of *Calanus finmarchicus* march—april 1922, plotted against surface temperatures. n = number of hauls.

For *Calanus hyperboreus* the spawning area was found to be strongly limited to the inner parts of the area, mostly inside the surface isotherm of 2° (Fig. 1 and 32 a). In this species the many samples examined from the years 1922, 1923, 1924 and 1929 clearly reveals that no spawning takes place outside this part of the area; the species in question is here not found outside the inner area before the first days of April, and the samples are then found to consist of females which already have spawned (recognized by their wide oviducts) and later larval stages.

An interesting fact in the biology of this species is a scarce stock ot actually spawning females with their newly spawned eggs, which was found inside the spawning area in hauls from below 100 or 200 meters more than a month after the spawning in the upper layers had been finished. The temperature during this spawning was from 6°.5—7°. In cultures I have moreover succeded in observing the mature females spawning in temperatures from —1°.5—7°.5. If the temperature represented the limiting factor for the spawning of this species, spawning would according to these observations take place not only in the whole area investigated by me, but also in most parts of the Norwegian Sea and in wide areas in the north Atlantic. About the same conclusions would be reached regarding the salinities at which spawning has been observed.

What then is the reason for the peculiar arrangement of the two species during the spawning time?

The stations from December 1928 (Fig. 27) shows the large numbers which at this time of the year are accomodated in great depths. *Calanus hyperboreus* is only found in hauls which are representing waters deeper than 300 meters, *Calanus finmarchicus* is most frequent in the deepest hauls, but is also meet with in considerable numbers in waters up to 200 meters. This type of vertical distribution, which has always been found in materials from December, January and the two first weeks of February lead to an interesting conclusion. The absence of *Calanus hyperboreus* in the outer parts of Norwegian coast waters before the 15. of March (found by Nordgård (1899), Ruud (1929), from my materials and others) are quite simply explained by the fact that those great depths, which are a matter of necessity to the species at this time of the year, do not exist in these parts of the ocean. In *Calanus finmarchicus* the materials give the same picture, only not so marked as in the preceeding species. A few specimens have during winter been caught outside the deep areas by Nordgård, Ruud and by myself, but the numbers caught are always less than 1 % of the numbers from the rich hauls in the deeper water masses.

This winter situation is in both species interrupted by an active vertical migration of the animals in spring.

Figure 28 shows the type of vertical distribution in *Calanus finmarchicus* before and after the migration. The intermediate stages — catches from the period of actual migration — are fairly well demonstrated in Nordgårds materials and partly in my own materials (Fig. 29, 30, 32 and 33). In this way it has been possible to determinate the time at which the migrations take place. In the case of *Calanus finmarchicus* migrations is finished before the 15. of March, in *Calanus hyperboreus* not before the 15. of April, the difference in time between the two species thus being about 1 month.

In the deep water where the water masses are but comparatively slowly renewed the animals are well protected against the stronger effects of current. As soon, however, as they by vertical migration reach the surface layers, they arrive in water masses which on account of the flow of freshwater are forced away from the coast. The total numbers of induviduals caught in the hauls from bottom to surface at a station thus always show a marked decrease during and after the vertical migration in those places where great numbers were found to be stationary during the winter. In the southern part of the Lofoten area, where the coastal current carrying water of comparatively high temperature and high salinities runs into the area, nearly all specimens from the winter time are washed away shortly after the migration. At one station here (Økssund) I obtained on the 10. December 1928 4085 specimens of *Calanus finmarchicus* before the migration. Nordgård obtained 1443 on the 17. of February 1899 during the period of migration and only 186 on the 29. of March 1899 after the migration. In April 1922 several catches from this same locality has shown me none or only single specimens. In the fjord of the northeastern part of the area, where the currents are of more local character, more specimens are left after the migration. On an average I have found that about 19/20 of the winter stock are carried away, only 1/20 are left behind in the original area.

Simultaneously with the decrease in numbers inside the areas where the species are found during winter, an increase has been found in certain areas outside, especially in the northern part, caused by the transport with the currents from the inner parts.

The average numbers found in different months of winter and spring thus gives us the means of defining the areas from which the species disappear after the migration and to which areas they are carried away.

Another factor which is of great interest for the definition of the extent of the spawning areas has been found in the study of the breeding season of the species. The females of *Calanus hyperboreus* have their oviduct filled with eggs, and the copulation takes place in January and the first week of February.

During the 3 last weeks of February they are only found with unripe eggs in the later stages of growth. The males die off and disappear from the plankton before the vertical migration. During migration the composition of the stock was in 1929 found to consist of 57 % females and 43 % belonging to the two last larval stages. The spawning takes place during or immediately after the vertical migration and males, or females with eggs, have — in spite of the exess of larval stages — never been found after the migration.

Thus in *Calanus hyperboreus* but one factor appears to determinate the extention of the spawning area, namely the distribution of the species during winter time.

In *Calanus finmarchicus* this is different. On an average this species — as already mentioned — undertakes the vertical migration a month earlier than the preceeding species, while the appearance of eggs, in the oviducts of the females and in the samples collected, shows that it spawns more than a month later. Two factors are accordingly found determinating the spawning area of this species, namely the winter area of distribution and more than two months exposure to the scattering effect of the surface currents before spawning season.

The phenomenon that the spawning areas are found limited to certain isothermes and isohalines thus appears to obtain a quite natural explanation. The limiting isothermes and isohalines are merely these characteristic limits of different currents, well known to oceanographers, in this case the limits of cold coastal water carrying the species away from the inner areas.

The chief features of the seasonal distribution and the production of individuals of the two species investigated, are, as will be seen, due to a combined biological — hydrographical mechanism. Many important questions are however, left to future investigations. The winter stock in the deep waters is thus certainly due to an invasion of specimens who have sunk to great deepths in summer and authumn, but the materials are so far quite insufficiant for further studies of this phenomenon. As regards the biological part of the mechanism still more questions are left, questions which will demand more extensive experimental studies than the very few hitherto carried out. What are — for instance — the factors determining the maturity of the animals? It is an interesting point that, in the arctic species investigated, males and females with eggs in the oviducts are only found in deep water and at the darkest period of the year. In the widespread boreal species, *Calanus finmar-*

chicus, mature individuals have only been observed after the specimens have for some time been exposed to the stronger light intensities of the surface layers. Possibly light measurements carried out simultaneously with the collectings will give a more complete understanding of these features?

Helland-Hansens and Nansens hypothesis.

Neither in Damas's paper nor in the Bulletin Trimestriell (May—June 1904), where the figures of frequencies of the species in Damas's materials are published, have I been able to find any foundation for Damas's opinion that the spawning of the animals is limited to certain isothermes. Both papers mentioned quite simply show the same phenomenon as just described from the Lofoten area, certain limited areas with high frequencies of certain planctonic species.

It would at present have been very difficult to find any relation between the distribution of Damas's 3 species and the environment, had it not been that Helland-Hansen and Nansen (1909 pp. 312—316), when they published their discovery of the cyclonic system in the southern Norwegian Sea, had also made the problems raised by Damas object of a short discussion:

»When he wrote his interesting paper, Damas did not know in details the result of our investigations as regards the movements of the water in the southern Norwegian Sea; he only knew our discovery of the great cyclonic system. He could not therefore give a detailed explanation of the distribution observed. We think that our circulation gives a quite naturel explanation. According to Gran's (1902) and Damas's investigations it seems as if there are different species of plankton organisms e. g. *Calanidæ,* that are quite characteristic for certain areas in open sea; within these areas they abound, while they are comparatively rare outside them. We may assume that they are in a way stationary there. We can only explain this fact by assuming that the water masses of those areas also more or less stationary, and are renewed comparatively slowly. We have found in the southern Norwegian Sea especially three different areas where there is probably a very slow renewal of the water-masses, and where a great part of the water probably remains for a long time, exposed to circulatory movements in various directions.«

After having given an account of these areas (which will be seen in the figur 2 a and b), the two authors continue:

»If we now look at Damas's chart (Fig. 2 a) it is striking how exactly his areas of three kinds of *Calanidæ* coincide with the four areas

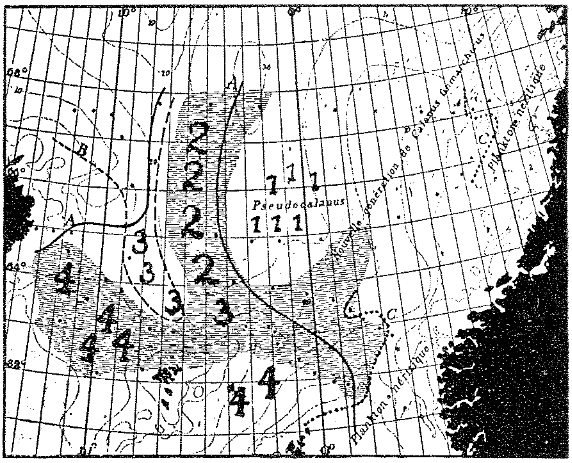

Fig. 2 a.

Distribution of *Calanidae* in the southern Norwegian Sea according to Damas. The lines mark the boundaries of regions where the different species abound: A, adults of *Calanus finmarchicus;* B, *Calanus hyperboreus;* C, Neritic plankton. The broken hatching indicates the distribution of larvae of *Calanus finmarchicus* (reconstructed from Damas, 1905, Pl. I).

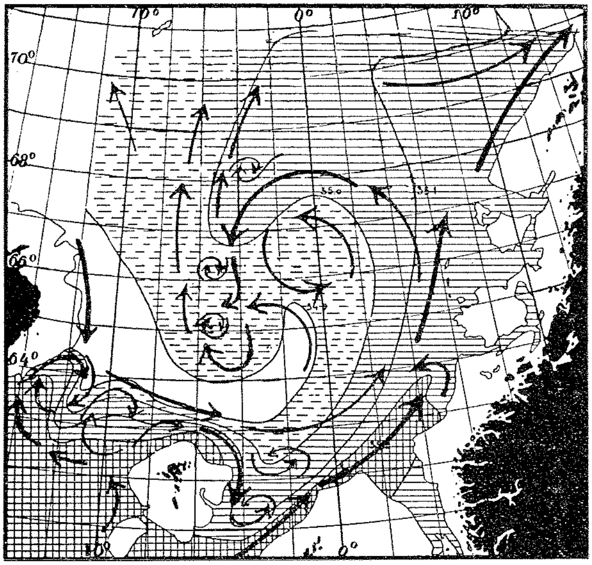

Fig. 2 b.

Direction of currents in upper 300 meters and distribution of salinity at 300 meters in the southern Norwegian Sea (Helland-Hansen and Nansen, 1909).

just described. Pseudocalanus is stationary in the central water chiefly of Atlantic origin, in our central area 1 of the cyclonic system. *Calanus hyperboreus* is stationary in the axis of cold and heavy Arctic water described as our area 3. Damas's boundaryline (Fig. 2 a) of the area coincides almost exactly with the equilines mentioned above. *Calanus finmarchicus* is evidently stationary in the mixed waters of Arctic and Atlantic origin, in our areas 2 and 4.«

In their paper Helland-Hansen and Nansen have not mentioned any reason why they have compared Damas's chart of the distribution of the species, which Damas regards as surface species, with the chart of the movements of the water masses at upper 300 meters. As we have seen above from Lofoten it is only during winter that the species are stationary, and then they are stationary in depths of 300 meters or more, where the water is comparatively slowly renewed. In spring and early summer they are exposed to the swift surface currents and carried far away from their original area. The temperature, and still more light conditions are however somewhat different in Lofoten and the southern Norwegian Sea. The behavior of the species in the two places therefore are not directly comparable, had it not been that materials from the southern Norwegian coast (Nordgård and Jørgensen 1905. Ruud 1929 and my materials from Oslofjord and Møre), where the conditions are not much different, had already shown the same main features as in Lofoten. No doubt, Helland-Hansen and Nansen were right in choosing just a depth of 300 meters for comparing the biological and hydrographical conditions. Damas's chart shows the species some time after the vertical migration, accordingly they have already been exposed to the effect of the swifter surface currents. The narrower areas where they have previously been stationary accordingly have to be found in places which the surface current have already passed. It is striking how we, by regarding Helland-Hansens and Nansens stationary areas as winter areas for the species in question, especially as regards the best studied species *Calanus finmarchicus,* can recognize the main features from Lofoten. The species has been carried away just in the direction of the surface currents. In the Shetland—Færoe ridge, through which the strongest current runs, the species is nearly completely washed away, corresponding to what we have seen from where the current runs into the Lofoten area. Under certain circumstances we may in details follow the effect of the surface current upon the extension of the spawning area. The manifoldness and complexity of these results — each of them reached independently — have now become so great as to make it extremely improbable that this agreement between hydrographical and biological data is fortuitous. No doubt, we have here arrived at a more natural and more well founded explanation of these phenomena than assumed by Damas in his circulation hypothesis.

General discussion,

I.

Most authors discussing the factors limiting the geographical distribution of animals have regarded temperature as a factor of dominant influence. This matter has recently been the object of a brief account by Brown (1929) in The American Naturalist, and it should not therefore be necessary to go further into this question here; only a few additional remarks will have to be made.

Regarding marine and limnetic plankton animals and bottom animals with pelagic larvae many other ecological factors than temperature, especially the light, have according to the many papers on this subject an important influence upon physiological processes of animals, and certainly therefore ought to have been given a wider space in discussions dealing with the geographical distribution.

Of great importance for the understanding of the effect of temperature on the distribution are the suggestions made by Hofsten (1915) as regards marine bottom animals, recently strongly supported by the experiments carried out by Runnstrøm (1925, 1927 and 1930). The chief line in the theory of Hofsten is that the temperature limits for the younger stages and the reproduction process are much narrower than the temperature limits at which it is possible for older specimens to live. Runnstrøm has found that the cleavage process of the eggs and the gastrulation can only take place within a limited part of the temperature scale. At temperatures outside this interval these processes show pathological features.

The temperature interval which Runnstrøm found for the normal development of different species could like the temperature reactions described by Brown be arranged in certain groups characterised by lower or higher limits. These groups where found to correspond to the different distributional types, arctic boreal (—1°—11°), boreal (4°—16°) and mediterran boreal (8°—23°).

Usually Runnstrøm, for the same species, found the same reactions to temperatures at different localities (Norwegian coast, Mediterranean), Brown having arrived at the same conclusions by comparing his own observations from United States to those of Weismann from Germany. In other cases Runnstrøm found a discontinous splittering (e. g. *Mytilus edulis*) of the species, followed by difference in spawning time and horisontal distribution, very much like the difference mentioned by Brown between »clone 984« and the normal *Daphnia pulex.* Accordingly we can not always regard the morphologically determinated species as being physiological units in the geography of animals.

II.

In an ocean without any convection current, but with the other ecological factors unchanged, we should surely find the planktonic species arranged in circumpolar belts closely following the limits of temperature and light conditions.

What are now the effect of convection currents?

The Gulf Stream, from which much of the waters of the Norwegian Sea originates, has in the Mexican Gulf and neighbouring areas in the upper 100 meters a temperature of between 22°—28°. When entering the Norwegian Sea its temperatures is usually about 9°. Chiefly according to the space of time after its entrance in this area it will further get temperatures between 9° and —2°. Altogether the Gulf Stream thus includes more of the temperature scale than found by Runnstrøm for the normal development of animals from three different regions. In addition to the change in temperature also other ecological factors like light conditions, light reactions of the animals and nutritive substances are changed.

The pelagic life of the Gulf Stream is in its origin tropical. The many papers on the distribution of the different species in the Atlantic shows us that it is but very few of the Atlantic species that really, together with the water masses, enter the Norwegian Sea and succeed in reproducing there (Hjort and Ruud 1929 pp. 86). The copepod *Rhincalanus nasutus* represents for instance a typical Atlantic species; its limits of distribution into the Norwegian Sea was determined by international investigations 1902—08 (Farran 1910), only in years with extraordinary strong supply of warm water (Sømme 1929) some few specimens are brought further north.

It here appears to be a typical phenomenon due to changes in the environment along a convection current which is demonstrated, a phenomenon certainly well known to marine biologists. It might possibly be due to mortality along the current, but as we do not know how much may be due to sinking of organisms, deficiency should be preferred as a more adequate name.

The salinities along the Gulf Stream do not show a great deal of variation. This is, however, the case for other convection currents, for instance the current system of the Baltic and the eastern part of the North Sea. According to Ekman (1913), the copepod *Limnocalanus grimaldii,* (de Guerne) appears to be stationary in the northern and eastern bay of the Baltic where the waters are almost fresh. The species was here (l. c. pp. 496) found to be present in 97 % of the hauls made. In other parts of the Baltic it was found in 83.3, 71.4, 16.6 and 9.1 % of the hauls, the percentage of occurrence decreasing with an increase of salinity and the distance from the areas where the species was found to be stationary. Ekman's materials thus demonstrate different stages in deficiency of the species in the convection current running out of the area. Of great interest is further the statement made by Oberg (1906 pp. 63) regarding the oceanic specimen *Paracalanus parvus* Claus. The copepodid and the three later nauplius stages of this species were frequently found in the western part of the Baltic, while the three earliest stages were always missing. Apparently the species do not succeed in breeding in the waters of low salinity.

While the water masses of a convection current thus appears to be characterized by an increasing deficiency of certain species, the more stillstanding water masses of the ocean will contain the species preadapted to the area, species which can live and reproduce there.

Calanus finmarchicus, this important and characteristic species of the northern seas, is according to Farran (1920) along the English coast but very scarce outside the isohaline of 35.5 %. Surely this scarce stock, however, is stationary in the Northeastern Atlantic (Nordgård and Lysholm 1915 and others), the water of the Gulf Stream therefore having already in this place obtained an admixture of this species. An increasing admixture takes place during and after the entrance of the water into the Norwegian Sea, partly from the areas to the west of the curren (Damas 1905) and partly from the coastal centres and more stillstanding water masses on the eastern side. According to Ruud (1929), however, the species is poorly represented in the axis of the current off the southern Norwegian coast. Areas rich in this species are, in the Norwegian Sea, only found along the edge of the continental slope, in the coastwaters, and in widely extended areas on the western side. Some of these are the areas described by Damas, others are found further to the north (Nordgård 1902, Gran 1902, Damas and Koefoed 1907, With 1915 and others). The surface waters of some of these localities here mentioned may sometimes be coloured red from the abundance of this species.

For the arctic species, *Calanus hyperboreus*, I have recently got a similar picture by examining the very representative samples from the danish »Godthåb«-expedition 1928 from the Davis-Strait and Baffins Bay. The water masses entering this extensive arctic area along the Greenland coast are exceedingly poor as regards this species. In the northwestern Baffins Bay, however, where more stillstanding waters are found, generally covered with heavy ice, and therefore not previously entered by expeditions, large numbers were discovered. The numbers caught here are on average 10 000 times as high as in the poorer parts of the area. The current running out of this rich area, following the western side, also showed great numbers, the catches usually being of similar size order.

Regarding *Calanus hyperboreus* the very interesting investigations by Biegelow (1926) from Gulf of Marine also seem to me be in striking accordance with these observations. It seems to be in the more stillstanding water masses of the western part of the Gulf that this species is stationary during the winter. The current entering the area from the eastern side carries this species into the area during late summer and autumn.

No doubt, in these 4 areas, the Norwegian Sea, Baffins Bay, the Lofoten area and the Gulf of Main, as regards the species mentioned, we meet with a factor in the production of animal plankton hitherto only mentioned by Helland-Hansen and Nansen, namely the age of the water masses in their biological area. The exact valuation of this new factor must be reserved for future investigations planned and carried out for this purpose. A more intensive study of the distribution also in the winter is for instance wanted. Certainly the possible relation between the current system and the production from different areas may be fairly well demonstrated in species like *Calanus finmarchicus* and *Calanus hyperboreus* where reproduction takes place comparatively slowly. *Calanus finmarchicus* having 2, possibly under certain circumstances 3 spawning periods a year, *Calanus hyperboreus* having but one very short breeding season and a number of eggs seldom exceeding 400 in each female. It will take many years for these species, in areas where they are scarce, to establish numbers like those which are actually found within the rich areas. Large numbers of these species therefore can thus not be produced in a short time unless there is a great stationary stock during the winter before reproduction takes place.

If other species of planctonic organisms will follow the same rule cannot be discussed at present. Judging from the many papers on the distribution of holoplanktonic species, however, and from the instances here treated, it seems to me that the two oceanographers Helland-Hansen and Nansen, whose work in many directions has been of fundamental importance to our present knowledge of the physics of the sea, in their short chapter on the biological consequenses of their discoveries, which has been practically burried for 20 years, has also pointed out main lines for a future biological research of the oceans.

SPECIAL PART I.

Systematics, differentiation of species by measurement, quantative determination of biological groups.

Material.

The materials used in these investigations were chiefly collected by Mr. Oscar Sund during his cruises along the coasts of Lofoten and north Norway in 1922, 1923, 1924, 1928 and 1929. In addition, by the courtesy of Professor Dr. August Brinkmann, curator of the zoological section of the Bergen Museum, I obtained the loan of specimens from the »Belgica's« cruise in 1905.

Professor Johan Hjort kindly placed at my disposal specimens collected on the M/C »Morild« in the years 1926 and 1927 from Romsdals Fjord. The late mr. O. Nordgård, Trondheim, placed at my disposal sorted specimens of *Calanus hyperboreus* from the Lofoten district, 1899 and 1900.

Fixation.

The material from the »Corona« 1922 was fixed in Fleming's fluid according to Gran's method for phytoplankton (Gran 1912). The other materials were fixed in formalin.

Nets.

Vertical hauls from the »Corona« 1922 were collected in silk nets No. 14 and diameter 42 cms. Vertical hauls were made in 1928 and 1929 with standard nets of silk 0 and 8. (See Hjort and Ruud, 1927). This net will in subsequent accounts be called net 8/72. In addition, during the collections in 1929 there were employed nets with a diameter of 42 cms and silk 25, referred to as net 25/42.

Nomenclature.

Regarding the nomenclature used for the species see With (1915).

Identification of the adult specimens.

Regarding the synonyms and identification of the adult specimens and the latest stages of development reference is made to the following papers: Giesbrecht (1893), Mrazek (1902), Sars (1903), van Breemen (1908) and With (1915). By means of the characters given in these works a certain identification of the 3 last stages of the two species is possible.

Identification of the various biological groups and of the larval stages of the two species.

In the following chapters a description will be found of the larval stages and of the various biological groups whose distribution has been studied. Chapter I contains a description of the morphological characters. Chapter II contains a description of the method of measurement employed for the identification of the larval stages and its results, and also statements as to how the various samples were analysed and how the various groups were determined quantitatively in the samples.

Graphical Figures.

Throughout this work, where there are found graphical figures of the relative quantities of the two species, these are given in numbers per 100 meters. Each unit of area thus corresponds to a number of individuals determined for each figure.

CHAPTER I.

Life history of *Calanus finmarchicus* and *Calanus hyperboreus.*

Earlier description of larval stages of marine copepods.

Krøyer (1845) was the first to identify the larval stages of marine copepods. He was thus able to give drawings of 6 nauplius stages and several copepodid stages of *Calanus hyperboreus.* Claus (1866) in a work on the copepods of the Mediterranean was also able to identify and figure a number of larval stages. He gives the identification of the species, however, as doubtful. The first certain and complete description of the life history of a marine copepod is found in a very interesting work by Grobben (1881). He succeeded in describing the eggs of *Calanus finmarchicus* and the main features of its further development to the copepodid stages. Grobben, however, did not intend to give a description of the systematic characters of all the larval stages in such a way that they could be used for separating, from larval stages of other marine copepods. The first study of the occurrence and distribution of the larval stages is to be found in Gran (1902). He succeeded in separating the various copepodid stages by measurement. He was able to ascertain that, including adults, there are 6 stages of copepodids of *Calanus finmarchicus.* Damas (1905) gives further information regarding the young stages of *Calanus finmarchicus.* From Grobben's descriptions he was able to identify their eggs in samples of plankton and to map out their distribution. He also gave a description of 5 nauplius stages and gave a scheme by which from the morphological characters it is possible to identify the 6 copepodid stages of the same species. He also mentions that he found eggs and larval stages of *Calanus hyperboreus* in samples collected near Franz Josefs Land. But neither in the case of *Calanus finmarchicus* nor *Calanus hyperboreus* does he give an adequate description for the certain identification of the larval stages to species. In a detailed work on the life history of a number of copepods from Kiel Bay Oberg (1906) gave an excellent foundation for the further study of the systematics of the young stages. In the species which he investigated he generally found 6 nauplius stages and 6 copepodid stages. (His statement that Damas found 8 nauplius stages of *Calanus finmarchicus* must be based upon a misunderstanding of a purely linguistic character). He also found that the larval stages of the various species are very much alike, and that it is difficult to separate them on the basis of their morphological characters without the most careful study of morphological details. In a work on the northern part of the Norwegian Sea Damas and Koefoed (1907) give further information regarding the distribution of the larval stages of *Calanus finmarchicus* and *Calanus hyperboreus,* but even this work does not give detailed descriptions or drawings of these stages. Kraefft (1910) studied the distribution of the larval stages of a number of marine copepods from the North Sea and the Baltic, and gives a number of supplemental remarks to the work by Oberg mentioned above.

With (1915) studied the distribution of the copepodid stages of *Calanus finmarchicus* and *Calanus hyperboreus.* He gives several details and draws the copepodid stages of *Calanus finmarchicus.* His drawings are, however, as regards various details, very schematic and differ as to arming and number of segments greatly from what I have found in the same species.

Lebour (1916) described the development of *Calanus finmarchicus* in 5 nauplius stages and 6 copepod stages. The material for the investigation consisted of specimens experimentally reared by Mr. L. R. Crawshay at the laboratory in Plymouth. In this material one of the stages given by Grobben (1881) was lacking viz. the 6th nauplius stage. On the basis of Grobben's investigations and the existing material, Lebour has succeeded in ascertaining that all together there are 6 nauplius stages of *Calanus finmarchicus*. In this case the species therefore shows agreement with those investigated by Oberg.

As regards details I have found many and in some cases great discrepancies from Lebour's drawings and descriptions of the larval stages of *Calanus finmarchicus*. Thus in Plate I Lebour draws the first two nauplius stages of *Calanus finmarchicus* as quite oval, egg-shaped. In all the cases which I have investigated I have found a well marked hind end protruding from the body, without, however any segmentation. (See fig.s 8, 9 & 10). Figures 4 & 5 on Plate I show that the carapace ventrally covers the body and the innermost part of the limbs. As far as I am aware nothing similar has been found in any other copepod nauplius, and it has not been found in any of the specimens examined by me. Also in the descriptions of the copepodids I have found great discrepancies from the specimens examined by me. Thus Lebour draws and describes the segmentation of the antennula in the second copepodid stage as having 12 segments, in the third stage as having 16 and the fourth stage 23 segments. In all the cases I have examined I have found 17, 22 and 25 segments respectively.

Thus the deviations which I have found from Lebour's drawings and descriptions are many and in some cases considerable. This has been an important factor to induce me in these investigations to choose to put forward my observations of the morphology of the young stages in all its details, both as regards *Calanus finmarchicus* and *Calanus hyperboreus*.

Determination of larval stages of *Calanus finmarchicus* and *Calanus hyperboreus*.

In determining the larval stages of the two species *Calanus finmarchicus* and *Calanus hyperboreus*, the following method has been employed: 1) Observation of the morphological characters which show to which stage of development the specimen belongs. In addition, as regards nauplii, the characters given by Lebour (1916) are used together with a comparison with the descriptions of *Pseudoclanus* and

Paracalanus given by Oberg (1906). As regards copepodids Damas scheme is used. (Damas 1905 P. 8 and Størmer 1929 P. 5). 2) Observation of the morphological characters which show that the specimen is a larval stage of the family *Calanus*. 3) Measurement of the specimen according to a special method which permits a determination of the individual to species.

Thus for the identification of species there were employed both morphological characters and measurements. In the following account it has been decided to give the observations of the morphological characters first. Proof that the specimens really belong to the stated species will thus not be forthcoming until the chapter on the special method of measurement and its results.

As stated above, Oberg's work on the life history of plankton copepods from Kiel Bay is characterized by its particularly comprehensive and complete account of the species examined. In view of future investigations and surveys of the life history of *Calanoidea* it is important that the original description is as homogeneous as possible. I have therefore in my account chosen to follow Oberg's method as closely as possible, so much the more so because in the course of my investigations I found Oberg's method of description clear and concise and well adapted to a comparison of the various species.

In my tables and figures, however, I have as far as possible discarded the terms nauplius, metanauplius and copepodit stages, and instead I have indicated all the stages of development by the Roman figures I to XII (the adult stage). This was mainly done because of the geographical part of the present work. It naturally involves a considerable simplification both of text tables and figures, in that each stage can be represented by a number. At the same time it has not been found difficult to keep this method of denomination apart from that used in other works, and I venture to suggest that my method of naming the stages should be generally used in copepod literature.

In investigating the morphological characters I have not, like Oberg (1906), used total preparations. Each specimen examined has been dissected, and each limb prepared as by degrees the drawing proceeded. Regarding the method of colouring employed see the chapter on the technique of the method of measurement.

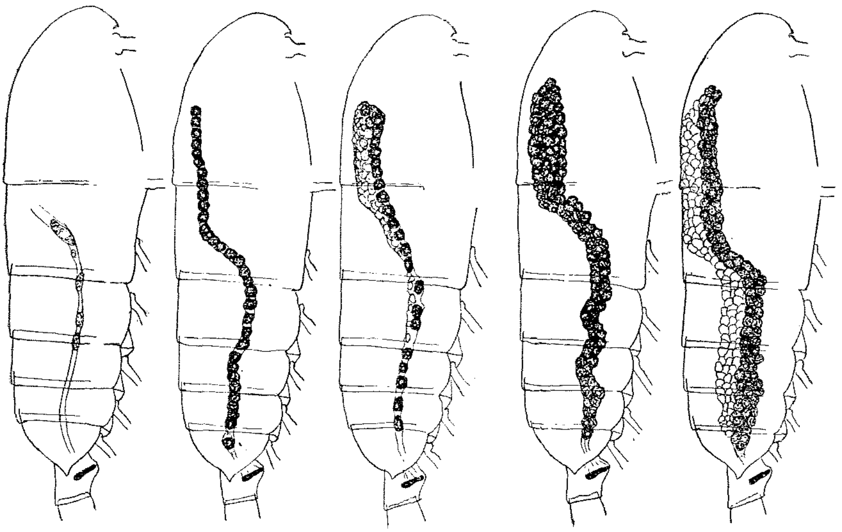

Fig 3. Sideway view of females of *Calanus hyperboreus* with their oviducts filled with eggs. (Specimens from "Johan Hjort" $^{18}/_{2}$ 1924, st. 31.)

Development of the eggs in the oviducts in ***Calanus hyperboreus.***

On the »Johan Hjort« cruise in the Spring of 1924, on the 18th of February (Station 31, 400 m. w. — about 130 meters from surface), a horizontal haul was taken in the inner part of Vest Fjord (Ofot Fjord). The preserved part of the sample contained 1 specimen of *Calanus hyperboreus,* stage XI, one male and 38 females, the majority having the oviducts filled with eggs.

The single ovary (fig. 4, fig. 6 ov.) in *Calanus hyperboreus* is situated dorsally in the posterior part of carapace, from when the paired oviducts originate. 2 blind sacs proceed anteriorly in carapace. The oviducts run posteriorly laterally and more ventrally. (Fig. 3, Fig. 4). Thus in its main features the structure is found to be the same as that in *Calanus finmarchicus*, with the one exception viz. that in the latter species the oviducts proceed farther forward. (See Sars 1903, Pl. I).

In the material fixed in formalin the eggs appear to be nearly transparent at the beginning of the growth period, and have then a large yellowish nucleus. After the growth period they have obtained a certain maximum size and are then in the fixed specimens (formalin) dark with large lighter coloured nuclei. (See Fig. 5). These eggs are fully grown and unripe. The number of eggs varies greatly. (See Fig. 3).

In some specimens there were 65, in others 180 and in certain cases they even exceeded 400.

During my investigations in the Oslo Fjord at Drøbak I had an opportunity of observing living specimens with eggs in their oviducts. The eggs were found to be colourless before they are fully developed and to show a marked orange colour after they are developed.

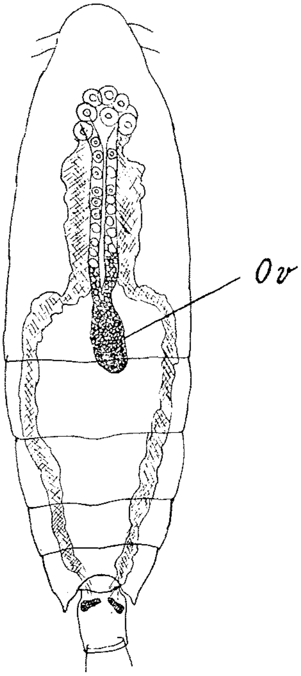

Fig. 4. Dorsal view of female of *Calanus hyperboreus* with eggs. (Specimen from "Johan Hjort" 1924, st. 31.)

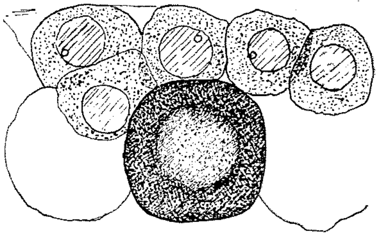

Fig. 5. Unripe eggs inside the oviduct of a female of *Calanus hyperboreus* during and after the growth period.

Spent Females of ***Calanus hyperboreus.***

In the course of a number of experiments with *Calanus hyperboreus* with eggs in the oviducts from the Oslo Fjord at Drøbak in the Spring of 1929, I succeeded in observing a number of details of spawning. (See page 79). I also succeeded in obtaining specimens of *Calanus hyperboreus* which had finished spawning. On comparing the spent females with virgin females from hawls earlier in the year before the eggs had begun to ripen, it was possible to find characters whereby the virgin and the spent females can be distinguished. When the large quantities of eggs have left the oviducts the latter shrink somewhat, but they always remain wider than in the virgin females. With 50 times enlargement one at once sees in spent females the swollen oviducts and may trace their course. (See Fig. 6). If the animal is viewed from the dorsal side it is easy to trace the cul de sacs which run forwards. In virgin females on the other hand the oviducts are very difficult to discern without special preparation. From the dorsal side it is possible to trace the cul de sacs which proceed forwards a short distance in front of the ovary. In stage XI, where as a rule the oviducts do not contain eggs or have contained eggs, one always has a good opportunity of studying the appearance of the virgin oviduct. In the virgin female the oviduct always has the same appearance as in stage XI.

With some practice one can by this method with certainty identify spent females.

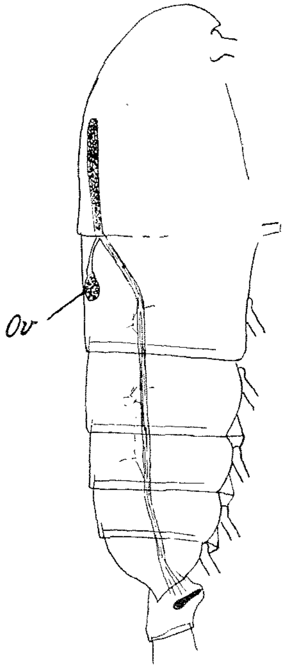

Fig. 6. Spent female of *Calanus hyperboreus*.
(Specimen from culture jar.)

Eggs of *Calanus finmarchicus.*

The eggs of *Calanus finmarchicus* were described by Grobben (1881) from cultivated specimens. He gives (page 4) the following description whereby they can readily be identified in samples of plankton. »Das Ei wird von einer Hülle umgeben, welche an der Aussenfläche in zarte, unregelmässig verlaufende und verzweigte Leisten erhoben ist. Die Leisten hängen jedoch nicht zusammen, sondern sind unterbrochen und verlaufen sich an ihren Enden allmählig. Von der Oberfläche besehen, findet man daher am Ei eine grosse Anzahl sich verlaufenden Linien, die Kanten der genannten Leisten; im optischen Schnitt kleine Spitzchen, so dass das Ei in dieser Ansicht wie mit Stacheln besetzt erscheint.«

Grobben gives the size as 0.17 mm diameter. The eggs of *Calanus finmarchicus* examined by me have always been smaller. In specimens fixed with formalin the diameter was usually 0.16. In a very few cases the diameter was 0.15. From Station 79 25/0 meters, on April 4th 1929 18 eggs were measured. In 17 cases the diameter was 0.16 and in 1 case 0.15 mm. From Station 18, 1922, 100/50 meters, Flemming fixed material, the diameter in 14 instances was 0.15 and in 12 instances 0.16 mm. In the counting chamber the diameter was always measured as a control of my determinations. It was found in the great majority of cases to be 0.16 and in a few cases 0.15 mm. Other size groups than these two, I have never observed.

The eggs of *Calanus finmarchicus* are probably colourless. In the oviducts of living females with ripe eggs they are colourless, and also in preserved material both before and after spawning. This is not the case with the eggs of *Calanus hyperboreus* where the colour is visible both in living females and in specimens preserved in formalin before and after laying.

Eggs of *Calanus hyperboreus.*

Damas (1905) and Damas and Koefoed (1907) mention the finding of eggs of *Calanus hyperboreus.* The authors do not give any description.

On February 10th 1929, I collected at Drøbak in the Oslo Fjord a sample of adult females of *Calanus hyperboreus.* The animals were kept in a culture jar where the eggs were laid.

The eggs of *Calanus hyperboreus* like the eggs of *Calanus finmarchicus* are surrounded by a thin membrane. This membrane, unlike that found in the other species, is smooth. (Fig. 7).

Tab. 1. Measurements of eggs of *Calanus hyperboreus* preserved in formalin from Lofoten 1929 and eggs laid in cultures, alive, or preserved in alcohol.

Hundreth millimeter	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	n =	
Longest diameter ..			1	1	2	4	1	5	7	6	12	17	9	2			67	Preserved in Formalin
Shortest diameter ..	1	1	2	5	2	4	12	18	11	9	1	1						
Longest diameter ..			1	1	2	2	1	5	5	3	2	4				1	27	Alive eggs
Shortest diameter ..		1		3	1	4	5	2	3	5	1				1			
Longest diameter ..				1	2	5	4	4	1								17	Preserved in Alcohol
Shortest diameter ..			2	1	7	2	3	2										

Tab. 2. Variation, standard deviation, aritmetric mean, its standard error and coeficient of variation for measurements of eggs of *Calanus hyperboreus* given in Tab. 1.

	Var.	σ =	M ± 3m	v=	
Longest diameter ..	21—32	2·51	28·33 ± 0·92	8·90	Preserved in Formalin
Shortest diameter ..	19—30	2·47	25·85 ± 0·91	9·57	
Longest diameter ..	21—34	2·52	27·04 ± 1·45	9·30	Alive eggs
Shortest diameter ..	20—29	2·66	25·56 ± 1·54	10·40	
Longest diameter ..	22—27	1·28	24·65 ± 0·93	5·20	Preserved in Alcohol
Shortest diameter ..	21—26	1·46	23·52 ± 1·03	6·20	

Tab. 3. Proportion between longest and shortest diameter for measurements of eggs of *Calanus hyperboreus* given in Tab. 1.

⁰/₀ =	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Preserved in Formalin	1	2	3			10	8	4	8	4	4	8	2		1	8			1
Alive eggs										1	1	5		1	9	6			3
Preserved in Alcohol .						1					2			1	12				2

When laid, the eggs are often in groups of 2—6. This has also been the case with eggs of the species in samples from the Lofoten area. In culture this grouping lasts for some hours and then the eggs fall away from each other.

Unlike the eggs of *Calanus finmarchicus* the eggs in the oviducts of living females or in the oviducts of females freshly preserved in formalin are markedly orange coloured. They also retain this colour after spawning has taken place[1]).

Unlike the eggs of *Calanus finmarchicus* they show a marked variation in diameter. There is a variation both in different diameters in the same egg, and in the diameters of different eggs. As this variation appears to be the best mark of identification for eggs of this species I will in the following give the measurements made of 1) living eggs from culture, 2) eggs fixed in alcohol from culture, 3) eggs fixed in formalin from Lofoten 1929.

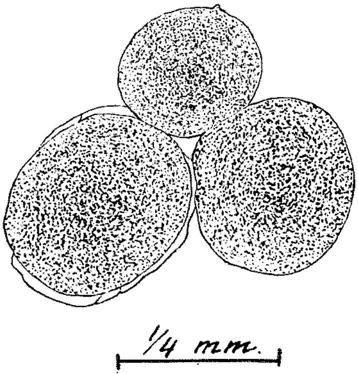

Fig. 7. Three laid eggs of *Calanus hyperboreus* in a group. (Specimen from "Johan Hjort" 1929, st. 79, 300—150 meter.)

Table 1 shows the measurements of eggs of *Calanus hyperboreus*. In Tables 2 and 3 are given the sizes calculated from these. It will appear from the tables that there is a close agreement between the eggs taken from culture jars and the eggs found in samples from Lofoten in 1929. In addition to the agreement in the appearance of the eggs, and the circumstance that the eggs came from samples in which there were spawning females it must be regarded as proved beyond doubt that the eggs from the samples have been correctly identified.

One pecularity of the eggs of *Calanus hyperboreus* is that they do not sink to the bottom of the samples, but float in the fixation liquid. It is thereby easy to prove whether they are present even though it may be in small numbers.

Stages I to VII of *Calanus hyperboreus.*

Stages I to VII will be found described in Table 4. This table was prepared according to a scheme used by Oberg (1906) for *Pseudocalanus* and *Paracalanus.*

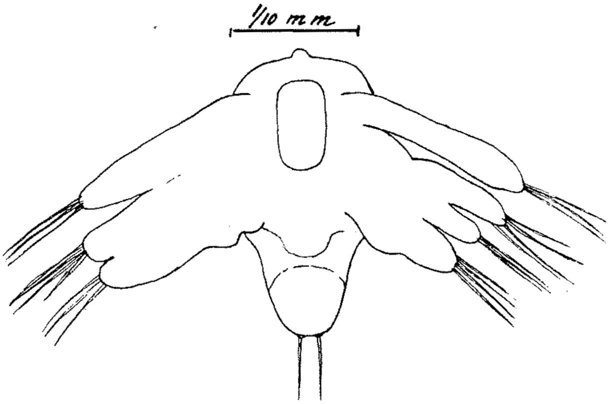

Fig. 8. Stage II of *Calanus hyperboreus* from the counting chamber showing the characteristic enormous limbs of the two first stages of both *Calanus* species.

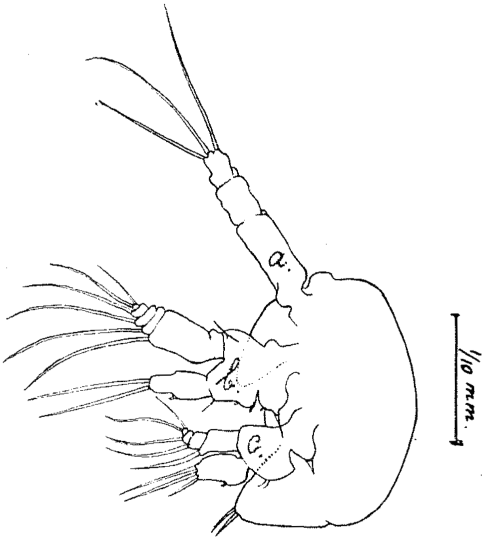

Fig. 9. Stage I of *Calanus hyperboreus* with the limbs turned to the distal portion in order to have the armature visible.

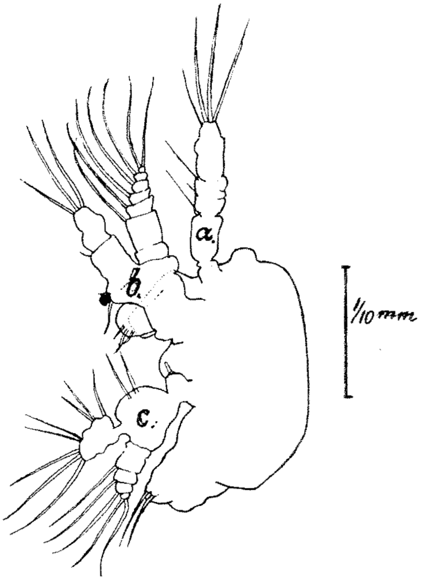

Fig. 10. Stage II of *Calanus hyperboreus*.

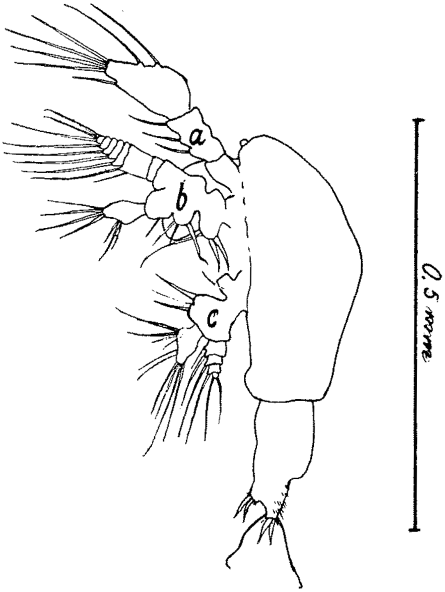

Fig. 11. Stage III of *Calanus hyperboreus.*

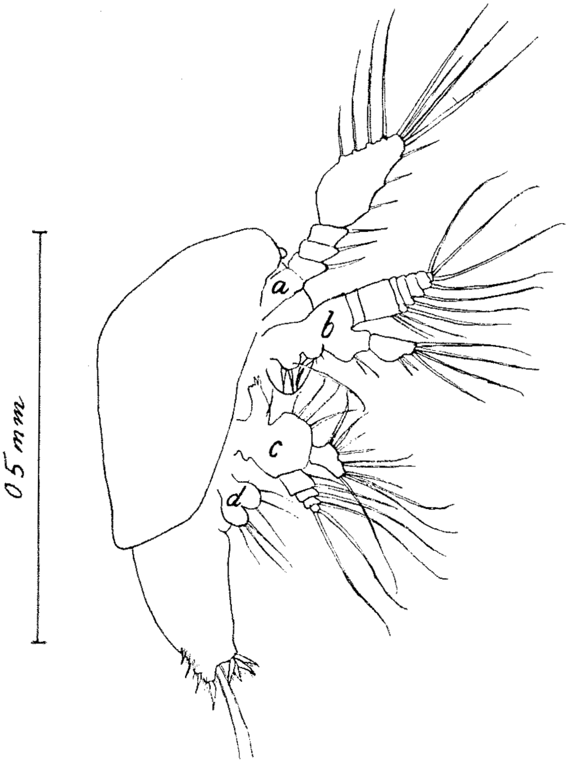

Fig. 12. Stage IV of *Calanus hyperboreus.*

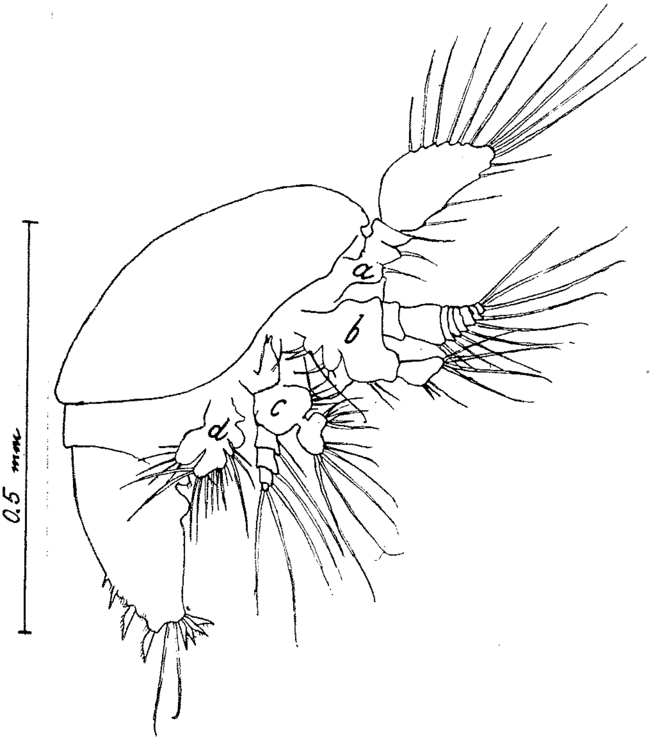

Fig. 13. Stage V of *Calanus hyperboreus.*

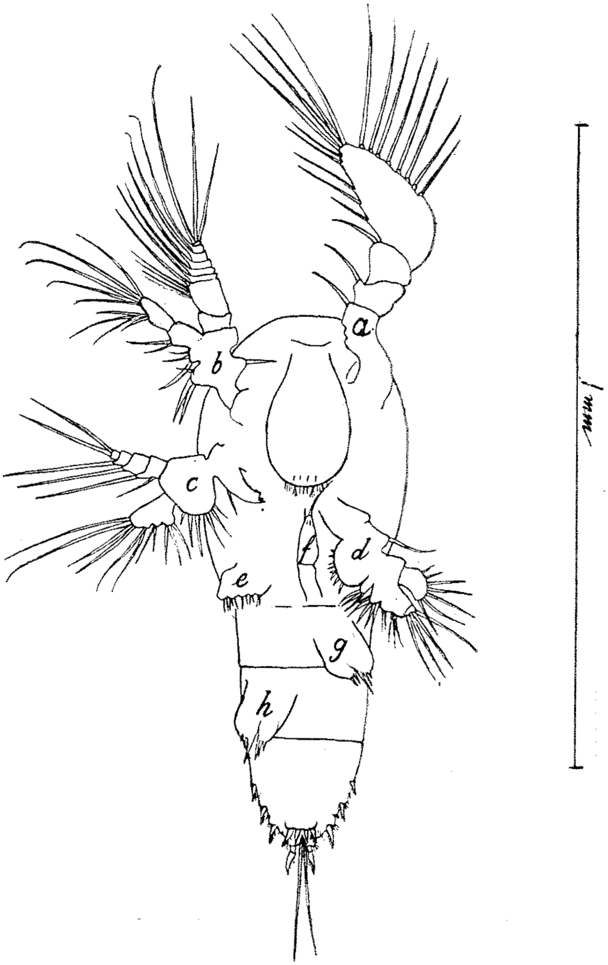

Fig. 14. Stage VI of *Calanus hyperboreus*.

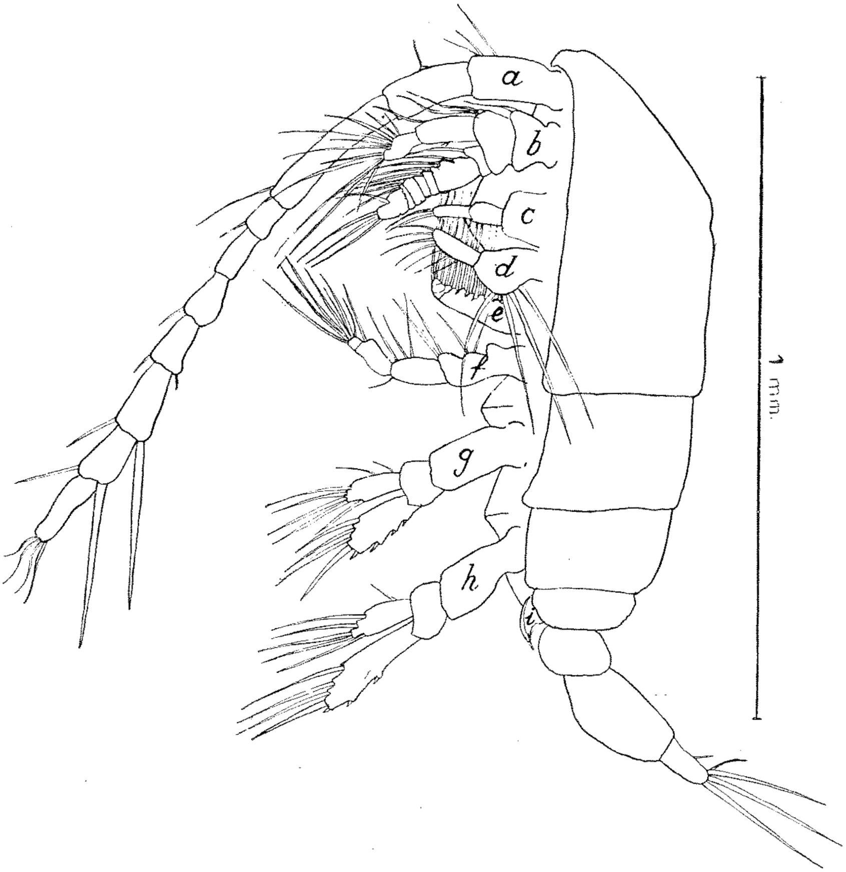

Fig. 15. Stage VII (copepodid stage I) of *Calanus hyperboreus.*

Tab. 4. *Calanus hyperboreus* Kröyer and *Calanus*

	Stage	Nauplius Stage I	Nauplius Stage II	Nauplius Stage III
Body.	General Appearance	Short and oval, hind end somewhat protruding from the body	Short and oval, hind end more well protruding from the body	Front of body oval, hind end cylindrical segmentally devided from body
	Number of Segments	3 (4?)	4	5 (?)
	Number of Segments in front of body	3	3	4 (?)
	Number of Segments in hind end	0 (?)	1	1
	Appendage at the free Segment		No Appendage (Hind end of body)	Same as II
	Armature of the hind end (Furca)	2 thin feelers	2 long thin feelers	2 end hooks 2 long thin feelers 2 ventral hooks
Antennule (a)	Number of sections	3	3	3
	I. Section (“Whirl”)	Cylindrical No bristle	Short cylindrical No bristle	Same as II
	II. Section (‘Shaft”)	No bristle (?)	With 3 conspicuous prominences	
	III. Section “Leaf” Number of bristles Ventral	No bristle	No bristle	1
	III. Section “Leaf” Number of bristles Dorsal	No bristle	No bristle	2
	III. Section “Leaf” Number of bristles The end	3	4	4
Antenna (b)	Coxopodite	Lobe with 1 long and 1 short bristle	Lobe with 3 bristles	Great lobe with 1 very
	Basipodite	2 prominences with 2 and 1 bristle. 1 bristle at outer margin.	2 prominences with 2 and 1 bristle	First prominence with 1 eating and 2 small bristles second prominence 1 bristle
	Endopodite	Prominence with 1 bristle, 2 terminal bristles	Prominence with 1 (?) bristle, 3 bristles at the end	Prominence with 3 bristles, 4 bristles at the end
	Exopodite	6 (?) jointed, 6 bristles	7 jointed, 7 bristles	7 jointed, 9 bristles

Continued next page.

finmarchicus (Gunner) Scheme after Oberg (1906).

Nauplius Stage IV	Nauplius Stage V	Nauplius Stage VI	Stage VII = Copepodid Stage I
Body more elongated than in *Pseudocalanus* (See Oberg 1906 Taf. I and my fig. 7, 8 and 9). Hind end bent dorso ventrally			Shape mainly as the adult animals
6	7	10	11
5	5	Same as adults 6	6 Shape and appendages mainly as the adult animals
1	2	4	5
Same as II	Maxilliped	1 ST Swimming Foot	1 ST Swimming Foot
2 end hooks 2 long thin feelers 4 ventral hooks 3 pairs of lateral hooks	Same as IV	Same as IV	3 pairs of long bristles 1 pair of short bristles 1 pair of very short bristles
3	3	3	Mainly as by the adult animals with the 2 long sensory bristles which is characteristic for *Calanus*, 4 (?) bristles at the end joint. 10 jointed and 17 bristles
Same as II	Same as II	Same as II	
each with 1 bristle. No well marked segmentation			
3	4	5	
4	6	8	
4	4	4	
long bristle and 2 conspicuous eating hooks		Same as III, the eating hooks however rudimentary in *C. hyperboreus* more than in *C. finmarchicus*	Lobe disappeared, 1 bristle left
Same as IV, but 2 bristles at the second prominence	Same as IV	Same as IV, but 1 bristle at outer margin	With 2 bristles
Same as III	Same as III	Prominence with 4 bristles 5 terminal bristles	First segment 1 bristle and 2 thorns, terminal segment 11 bristles
7 jointed, 10 bristles	8 jointed, 10 bristles	8 jointed, 12—13 bristles	7 jointed, 1 ST Segment 1 bristle, 2 ND 3, 3 RD 1, 4 TH 1, 5 TH 2, 6 TH 1 and 4 terminal bristles

Tab. 4. *Calanus hyperboreus* Kröyer and *Calanus*

Mandible (c)	Coxopodite	Lobe with 1 thorn	Lobe with 1 thorn	1 Process with 1 small bristle
	Basipodite	Great lobe with 2 small bristles	Great lobe with 2 bristles	3 bristles
	Endopodite	One prominence with bristle, 2 long and 1 short bristle at the end	2 prominences, I 3 bristles, II 2 bristles, 3 bristles at the end	3 prominences, I 4 bristles, II 2 bristles, 4 bristles at the end
	Exopodite	4 jointed, 5 bristles	4 jointed, 5 bristles	4 jointed, 6 bristles
Maxillule (d)	Coxopodite			Lobes beginning to show
	Basipodite			
	Endopodite			
	Exopodite			
Maxilla (e)	General Appearance			
Maxilliped (f)	General Appearance			
1st Swimming Foot (g)	General Appearance			
	Endopodite			
	Exopodite			
2nd Swimming Foot (h)	General Appearance			
	Endopodite			
	Exopodite			

finmarchicus (Gunner) Scheme after Oberg (1906) (continued).

Process elongated, toothed and 1 small bristle	Same as IV	Same as IV, somewhat rudimentary	Process conspicuous, toothed
4 bristles	5 bristles	6 bristle	Elongated, 4 weak bristles
Same as III	2 (3?) prominences, I (?) 5 bristles, II 2 bristles and 4 bristles at the end	3 prominences with 3, 2 and 2 bristles. Eating bristle in *C. hyperboreus* strongly reduced, 4 bristles at the end	2 jointed. First segment 4 bristles, terminal segment 6 bristles.
Same as III	Same as III	Same as III	5 jointed, 6 bristles
Hardly visible	Lobe visible, but without armature	Lobe with 8 short bristlee, one long bristle at outer margin	Large lobe (gnathobase) with 10 spiky bristles
	2 lobes (?), 3 bristles	2 lobes (?), 3 bristles	*Lobus externus* I 4 long bristles. *L. e.* II 1 bristle. *L. internus* I and II 2 bristles each.
With 4 bristles	3 prominences with 7 bristles, 4 bristles at the end	First prominence 3, second 2 and third 2 bristles, 4 bristles at the end	2 jointed, 3 prominences at first segment. Bristles same as VI
With 3 bristles	One segment with 5 bristle on the dorsal margin	Same as V, 7 bristles	Same as VI
Lobes beginning to show	Lobes with hairs	Developed with 11 bristle-like hooks	Mainly as by the adult animals 21 or 22 very long bristles
	Lobes beginning to show	Well developed, with hairs and 1 long and 1 short bristle	Mainly as by the adult animals Protopodite with first segment hardly visible and no bristle, second segment with 2 prominences (each 2 bristles). First segment of endopodite with 4 bristles, second 1 and 7 at end segment. (See fig. 15 and Borradaile (1926 p. 211)
		Bilobed structure with hooks	Mainly as by the adult animals, only 2 segments
		3 hooks	7 bristles
		2 hooks	4 thorns outside a terminal blade and 3 bristles inside
		Same as 1ST Swimming Foot	Same as 1ST Swimming Foot
		3 hooks	6 bristles
		3 hooks	3 thorns outside, a terminal blade and 3 bristles

Metamorphosis of different limbs in *Calanus hyperboreus*.
Stages VII—XII.

Antennule (Fig. 15 a, Fig. 16 a, b and c) in stage VII 10 jointed, in stage VIII 17 jointed and in stage IX 22 jointed. In stage X 25 jointed as in adult animals.

Antenna (Fig. 15 b) in stage VII mainly as in adult animals. By the further metamorphosis the number of bristles on endopodite is enlarged.

Mandible (Fig. 15 c, 17 a) in stage VII mainly as in adult animals. By further metamorphosis the number of bristles at the terminal segment are enlarged.

Maxillule (Fig. 17 b, 18 b) in stage VII mainly as in adult animals, the number of bristles are, however, in later stages greatly enlarged. In stage XI the following bristles have been found: *Coxo-*

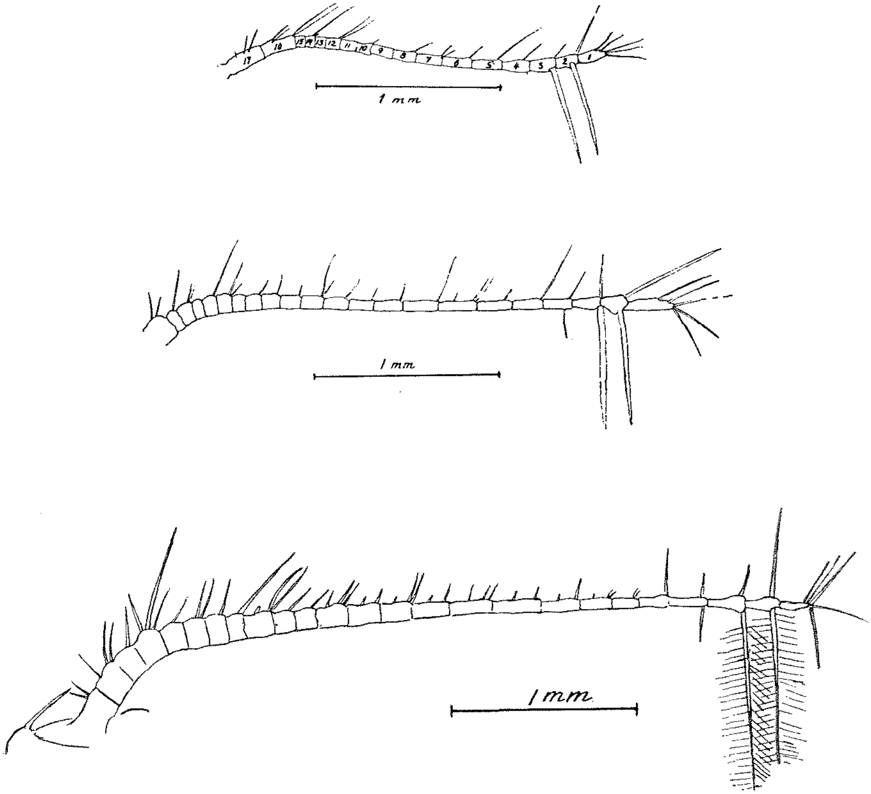

Fig. 16 a, b and c. Antennule of *Calanus hyperboreus* stage VIII, IX and X.

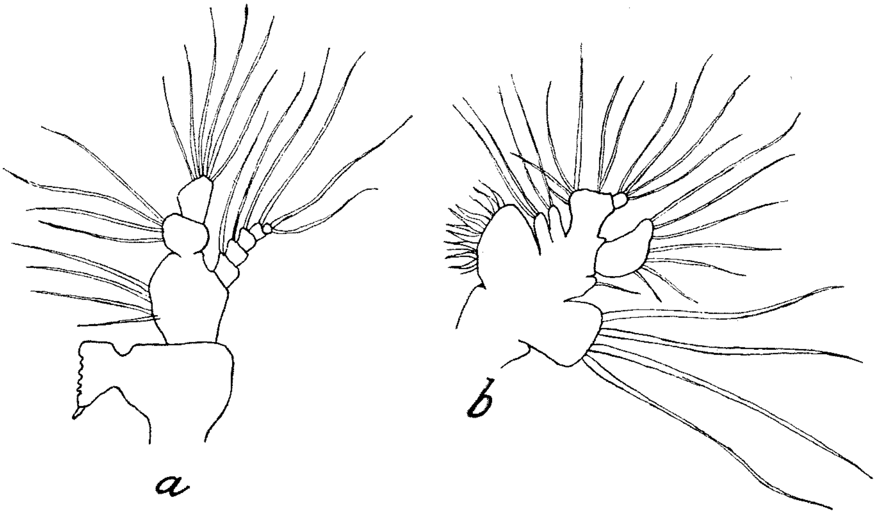

Fig. 17 a and b. a mandible and b maxillule of *Calanus hyperboreus* stage VII

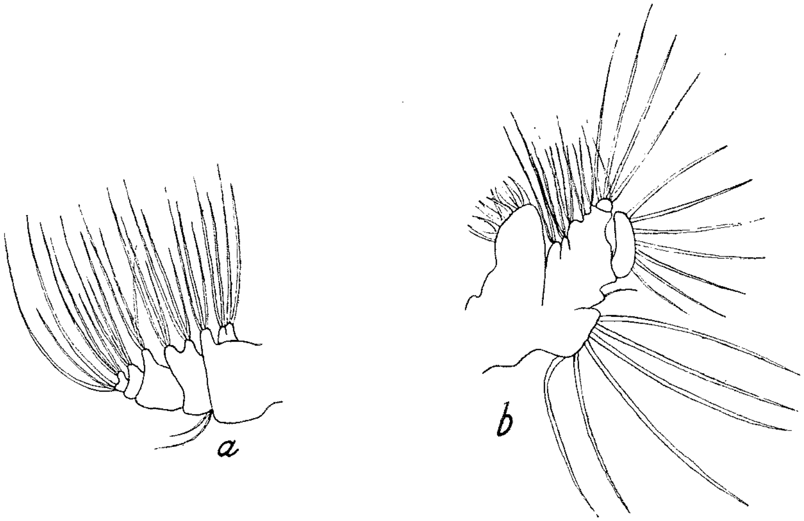

Fig. 18 a and b. *a* maxilla and *b* maxillule of *Calanus hyperboreus* stage VIII.

podite: gnathobase with 12 spiky bristles, *Basipodite:* proepipodite with 9 long bristles, 2nd and 3rd exite each with 4 bristles and metepipodite with 1 bristle, *Endopodite:* 1st segment 2 prominences with 4 and 3 bristles, 2nd segment with 10 bristles. Except for the 1st and 2nd exite, this is the same numbers as found by Borradaile (1926 p. 209, pl. IX) in adult animals, but somewhat different from Sars (1903).

Maxilla (Fig. 18 a) in stage VII mainly as in adult animals, in stage VIII the number of bristles like that in adult animals.

Maxilliped (Fig. 15 f) in stage VII mainly as in adult animals. By further metamorphosis the number of joints and bristles in the endopodite are enlarged. Sars (1903 Pl. II) has drawn the endopodite as 5 jointed, but already in stage XI I have found 6 well marked segments.

The swimming feet are always first visible as 2 thorny lobes (Fig. 14 g and h, Fig. 15 i). After the first moulting they appear as a »biramous« limb with coxopodite, basipodite, endopodite and exopodite. After the next moulting the exopodite and the endopodite are always 2 jointed, and they remain 2 jointed, the 1st and 2nd swimming feet through 3 moultings, the 3rd swimming feet through 2 and the 4th through 1 moulting until stage XI is reached. They are then all simultaneously 3 jointed. The exopodite and endopodite of the 5th swimming foot, which are first visible in stage IX, is in stage XI 2 jointed, and are thus not fully develloped before the adult stage.

Note on descriptions of *Calanus hyperboreus* male.

Nordgård (1899) has given the first description of *Calanus hyperboreus* male. He describes the last pedigerous segment with a rounded tip as in *Calanus finmarchicus* (Nordgård 1899 p. 21). Sars (1903 p. 12 and Pl. V) describes and draws the last pedigerous segment as similar in male and female. In the materials left from Sars at the zoological museum in Oslo I have found one by Sars determined male, but in this specimen the acute angle at the tip of the last pedigerous segment is failing. In my materials I have found more than a hundred specimens of *Calanus hyperboreus* male, including Nordgård's specimens, which all agree with Nordgård's description. The determination of my specimens I should think is beyond any doubt as they have been found together with females with eggs and females with spermatophores affixed to the genital segment. Also the measurements of carapace are in agreement with this, the carapace being somewhat smaller in the male, but very different from carapace in *Calanus finmarchicus.*

Variations in morphological charackters?

For investigation of morphological characters in *Calanus hyperboreus* I have always used more than 10 specimens, in a few cases of *Calanus finmarchicus* I have used a smaller number. If variations in the morphological characters were more common, they would in a quite natural way have explained the big differences which I have found between the different authors and between the earlier publications and my own observations. In no case have I, however, been able to find any variations. The number of segments and the armature of the different limbs seems to me to be very constant. In the antennule, however, the armature is sometimes very difficult to determine in formaline and alcoholpreserved specimens, and the possibility of variations can for this feature not be excluded. The number of joints in the antennule once in my material proved to have an abnormal segmentation, segment number 17 (reckoned from the end of the limb) being in one specimen of *Calanus hyperboreus* divided into 2 well marked segments. Cases like that is certainly, however, very rare.

Determination of stages.

Stage I, Nauplius. Fig. 9.

Stage I and II are easily recognized from later stages by the hind end, which is not segmentated from the body, and by its 2 hind feelers which represent their whole armature. Stage I may be separated from stage II by means of the very short terminal segment of its antennule (Fig. 9 and 10). The 2 bristles at the endopodites of the antenna and the mandible are also frequently visible, and are also shorter than the corresponding 3 bristles X in stage II.

Stage II, Nauplius. Fig. 8 and 10.

Hind end more markedly protruding from body, and hind feelers longer. Terminal segment of antennule longer and well marked from the »whirl«, carrying 4 terminal bristles. The 3 thin bristles at the »whirl« can often be seen without any preparation of the limb. The 3 very long bristles of the endopodites of antenna and mandible are usually visible.

— — —

The two stages are usually not to be separated in the counting chambers, they are therefore not separated in the greater part of my tables.

— — —

Tab. 5. Scheme of armature of swimming feet of *Calanus hyperboreus* and *Calanus finmarchicus*.

	Stage	VII					VIII					IX					X					XI				
Swimming Foot		Outer margin bristles	Terminal bristles	Inside margin bristles	Terminal thorns	Outer margin thorns	Outer margin bristles	Terminal bristles	Inside margin bristles	Terminal thorns	Outer margin thorns	Outer margin bristles	Terminal bristles	Inside margin bristles	Terminal thorns	Outer margin thorns	Outer margin bristles	Terminal bristles	Inside margin bristles	Terminal thorns	Outer margin thorns	Outer margin bristles	Terminal bristles	Inside margin bristles	Terminal thorns	Outer margin thorns
1st	Coxopodite								1					1					1					1		
	Basipodite													1					1					1		
	Endopodite 1			4	2	1			1					1					1					1		
	—„— 2								4	2	1			5	2	1			5	2	1			2		
	—„— 3																							3	2	1
	Exopodite 1	3	1	3	1		1					1		1			1		1			1		1		
	—„— 2						2	1	4	1		2	1	3	1		2	1	4	1		1		1		
	—„— 3																					1	1	4	1	
2nd	Coxopodite								1					1					1					1		
	Basipodite						1					1					1					1				
	Endopodite 1			3	2	1			1					1					1					1		
	—„— 2								3	2	2			4	2	2			5	2	2	1		2		
	—„— 3																							4	2	2
	Exopodite 1	2	1	3	1		2					2		1			2		1			2		1		
	—„— 2						1	2	4	1		2	2	5	1		2	2	5	1		2		1		
	—„— 3																					1	2	5	1	
3rd	Coxipodite	Bilobes present												1					1					1		
	Basipodite						1					1					1					1				
	Endopodite 1								3	2	1			1					1			1		1		
	—„— 2													3	2	2			4	2	2	1		2		
	—„— 3																							4	2	2
	Exopodite 1						2	2	3	1		2					2					2		1		
	—„— 2											1	2	4	1		2	2	5	1		2		1		
	—„— 3																					1	2	5	1	
4th	Coxopodite						Bilobes present												1					1		
	Basipodite																1					1				
	Endopodite 1													3	2	1			1			1		1		
	—„— 2																		3	2	2	1		2		
	—„— 3																							3	2	2
	Exopodite 1											2	2	3	1		2					2		1		
	—„— 2																2	2	5	1		2		1		
	—„— 3																					1	2	5	1	
5th	Coxopodite											Bilobes present														
	Basipodite																					1				
	Endopodite																		3	2	1	1		1		
	—„—																							3	2	2
	—„—																									
	Exopodite																2	2	3	1		2				
	—„—																					2	2	5	1	
	—„—																									

Stage III, Nauplius. Fig. 11.

Hind end segmentally divided from body. Easily recognized by the 2 bristles at the outer margin of the terminal segment of the antennule or by the 2 ventral hooks on furca.

Stage IV, Nauplius. Fig. 12.

Usually well recognized by the unsegmentated and short hind end of body. The outer margin of the terminal segment of the antennule with 4 bristles, which are often visible. Sometimes the maxillule is visible as an early biramous limb.

Stage V, Nauplius. Fig. 13.

The two segments of hind end of body easily seen behind the dorsal margin of carapace (Fig. 13). The outer margin of the terminal segment of the antennule with 6 bristles.

Stage VI, Nauplius. Fig. 15.

Hind end of body divided in 4 well marked segments 8 bristles at the outer margin of the terminal segment of the antennule. Usually this stage is easily recognized.

Stage VII, Copepodid stage I. Fig. 15.

Seen dorsoventrally the 3 long bristles present at the caudal furca are easily seen. Laterally viewed the 3 long and thick bristles are easily detected and very characteristic. Shape of the antennule and of the dorsal margin of carapace also very characteristic.

Stage VIII, Copepodid stage II.

Carapace as in stage VII, but somewhat more rounded.

Stages VII — XI, Copepodid stages I — V.

Are all easily determinated after the scheme of Damas (1905 p. 8) by the number of segments of furca and number of developed swimming feet. (Se also Störmer 1929 p. 5).

The Life History of ***Calanus finmarchicus***.

An investigation of a considerable number of specimens of all stages of *Calanus finmarchicus* shows that the larval stages of this species agree in all details with *Calanus hyperboreus*. All the figures and tables here given of the morphological characters can thus at once be employed for the identification of the larval stages of both species. The only morphological character which exhibits any difference is the bristles of the limbs which are shorter in proportion to the length of the limbs in *Calanus hyperboreus* than in *Calanus finmarchicus.* In addition the reduction of the bristles on the coxopodite of the 2 antenna and the endopodite of the mandible in Stage VI is more marked in *Calanus hyperboreus* than in *Calanus finmarchicus.* Neither of these characters, however, is of any importance in the separation of the larval stages of the two species. The difference is far too insignificant, and neither of these characters are readily accessible for investigation.

Separation of the larval stages of the 2 *Calanus* species from the young stages of *Pseudocalanus* and *Paracalanus*.

As will be seen from a comparison of Oberg's plan of the life history of *Pseudocalanus* and *Paracalanus* (Oberg 1906 pages 48 and 49), and my plan of the life history of the 2 *Calanus* species, even here readily accessible and distinct characters for the differentiation of all the stages are not easily found. Stage I of the 2 *Calanus* species, however, is easily separated from Stage I of *Pseudocalanus* by the bristles at the hind part of the body. *Pseudocalanus* has two thorn-like bristles, whilst the *Calanus* species have thin feelers. It is not known what the position is as regards *Paracalanus* since Oberg did not find the early stages of this species.

In Stage VI the 2 *Calanus* species have 8 bristles on the outer margin of the terminal segment of the antennule, whilst *Pseudocalanus* and *Paracalanus* have 6 bristles. The characters here dealt with are easily recognisable and should be capable of utilisation even in the counting chamber.

A number of other characters are less distinct. A comparison with Oberg's figures of the said species with my own of *Calanus hyperboreus* will show that the early stages of *Calanus* are more slender in form than the corresponding stages of *Pseudocalanus* and *Paracalanus.* The dorsal side of the terminal segment of the antennule as compared with the forms examined by Oberg is more curved in the two *Calanus* species, which also have a broader terminal segment.

The copepodid stages of the two *Calanus* species are easily separated from all those described by Oberg by the two long censory bristles, one on the antepenultimate and one on the penultimate segment of the antennule, which are such well-known characters of the adult *Calanus.*

The safest and best method of separating the nauplius stages of *Paracalanus* from the nauplius stages of *Pseudocalanus* and also the nauplius stages of these species from the nauplius stages of the two *Calanus* species is, however, by measurement. Measurement of the species described by Oberg show that they are much smaller than the corresponding stages of *Calanus*.

Separation of the nauplius stages of the two species of *Calanus* from the undescribed nauplius stages in samples of plankton.

In samples of plankton from the Norwegian coast, especially in the spring, the nauplius stages of the two species of *Calanus* will occur together with a number of other copepod nauplii which have as yet not been described. The early stages of *Calanus* will then in the counting chamber be easily mistaken for the later stages of other species which have far smaller larval stages. *(Microsetella, Oithona, Acartia* etc.). The later stages of *Calanus* will always be easily separated from these forms on account of their size. The later stages of *Calanus* frequently occur together with other large copepods, the nauplii of which have not been described, for instance *Metridia* and *Euchaeta.* Even though these species do not occur in large numbers in the upper layers of water, it is quite possible that their larval stages occur with the larval stages of species of *Calanus.* The first nauplius stage of *Euchaeta* I found by hatching them in culture. They are egg-shaped and noticeable by three extremely small pairs of limbs which are situated at the front of the body. The nauplius stages of *Metridia* and later stages of *Euchaeta* have not been definately identified in the material dealt with by me. There always occur, however, in larger or smaller numbers, nauplius stages together with the nauplius stages of *Calanus* species, which in several respects differ from the *Calanus* species. The differences are evident. (See Fig. 24 e), but in order to discover them the greatest accuracy with regard to morphological details must be observed in the examination of each sample.

It is always easy to determine the eggs of *Calanus hyperboreus* in the samples of plankton. The eggs of *Calanus finmarchicus,* however, may be mistaken for eggs of other forms. Amongst these other copepods may come into consideration, but it is also conceivable that the eggs of amphipods may be mistaken for eggs of *Calanus finmarchicus.* By using a slight magnification during the determination of these eggs, they may even be mistaken for globular algæ *(Halosphaera).* But in the determination of the eggs, just as in the determination of the larval stages, it will always be possible by using great accuracy to decide the doubtful cases which are met with in the samples.

CHAPTER II.

Measurements and method for counting.

As previously mentioned, the larval stages of *Calanus finmarchicus* and *Calanus hyperboreus* are not distinguishable by plain morphological characters. It is quite possible, however, that they might be distinguished by the difference in size, which at least as regards the last three stages of development is very striking. It will also be seen from my measurements of eggs of the two species that even at such an early stage of life a difference in size is easily discernable.

It will be found, however, from the existing literature that identification is not so easy. Thus With (1915) says: »This species *(Calanus hyperboreus)* is in the three last stages easily distinguished from *Calanus finmarchicus*. But the distinction in the earlier stages, in which the difference is only found in the size etc., may as pointed out by Damas and Koefoed be very difficult if not impossible, especially in the Polar Sea, where *Calanus finmarchicus* attains a size of 5 mms or more.« Størmer (1929, Fig. 10 P. 28) also tried measurements and writes. »We see from Fig. 10 that the two species cannot be definitely distinguished by their size.«

Ruud (1929) takes another point of view (P. 7). »I have not experienced any difficulty in separating the smaller stages of *Calanus hyperboreus* and *finmarchicus* from each other because the difference in size in the Møre district is too striking.« As will appear from my tables there is no difference of importance in this respect between Møre and Lofoten. In neither case did I succeed in separating all the young stages of the two species without special methods of measurement differing from those employed by Damas and Koefoed (1907), With (1915) and Størmer (1929). Even after finishing this work it is not possible for me to see the difference in size of all the larval stages of the two species. The subjective estimate which I have used before making a determination of the contents of a sample as to which of the larval stages are present has often proved to be correct, but often to be erroneous and misleading. I therefore consider it desirable to warn against a determination of the larval stages of these species exclusively by a subjective estimate, without checking this estimate by means of frequently repeated certain methods.

Attempts were made by With (1915) and Størmer (1929) to determine the larval stages of the two species by measuring the total lengths of the nauplii or the length of the cephalothorax of the copepodids.

It is known from anthropometry that the various parts of the skeleton of a mammal, when measuring a large number of individuals, show a difference in variation. Thus the periferal parts of a skeleton show a more marked variation than the central parts. Similar conditions have also been found in the investigation of races of herring.

In my attempt to find better methods of determining the larval stages of the two species *Calanus hyperboreus* and *Calanus finmarchicus,* it was therefore natural to take several measurements from different parts of the body, and to examine whether there could be found dimensions which varied less than those used by With and Størmer and which could thus form the basis of a more certain distinction of the larval stages by aid of measurements.

Technique of the Measurement Method.

For the first measurements there were employed samples from the »Belgica« 1905 station 47 20/0 meters where Damas and Koefoed (1907) reported nauplii of *Calanus hyperboreus* in large quantities.

A large number of nauplii of *Calanus* were sorted out. They were stained with Bismark brown (vesuvin) about 1 % in 30 % of alcohol. They were then slowly transferred to increasing concentrations of glycerine in alcohol and placed upon an object glass where the last part of the alcohol (about 50 %) was evaporated. The nauplii were then turned in order to get a sideway view. (The antennulae and often also the other limbs must then in many cases be carefully bent in towards the body by the aid of needles). In the course of this work care must be taken so that the body is not squaezed and loses its natural bend. (A photograph of a preparation will be found in Fig. 24).

The specimens were then measured both as to length of body and of carapace. (See Fig. 19 a). As cover glasses were not used, it was also examined whether variations in the amount of glycerine around the animals with changes in refraction could alter the result. It was stated that such changes could not be found. In measuring the closest possible sorting was employed. Specimens with the least indication of irregular contours which might mean disturbances during preservation or preparation were not measured. Specimens in which the anterior and posterior parts of the body or the carapace were not adjusted near the same position of the micrometer screw were also not measured. These precautions proved to be absolutely necessary. Without a close sorting of the specimens, one at once gets represented length groups, both larger and smaller than the average, which can be avoided. Neither can there be any doubt that these length groups are artificially produced.

A similar method was employed in the case of copepodids. (Fig. 19 b). Here the use of glycerine preparations and staining are advantageous, in any case as regards the first stages. As regards the last 4 stages staining and glycerine are unnecessary. As a rule it is sufficient to transfer them to 70 % of alcohol. Then at least during the first time until the osmotic tension in and outside the chitin is equalized one gets very finely distended specimens.

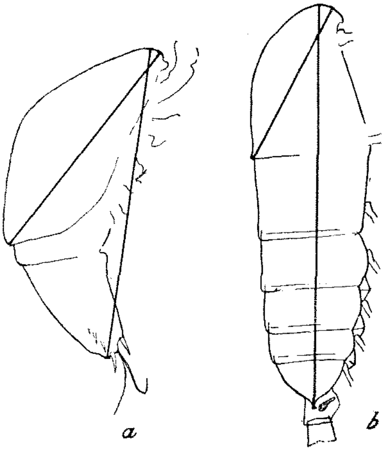

Fig. 19. Method of measuring nauplius and copepodid stages.

All transfers from alcohol to glycerine must be made slowly. The method employed, e. g. for nematodes, viz. transfer to 5 % of glycerine and then evaporation in a thermostat, in order to remove the alcohol, will in the case of nauplii lead to marked shrinkage. It is recommended to allow them to remain for 1 hour in about 70 % of alcohol to which glycerine is gradually added.

A minimum of shrinkage will, however, always prevail. In any case I am inclined to attribute small variations which in measuring specimens from a series of samples from Lofoten 1929 appeared simultaneously and uniformly in both species to this phenomenon. This was most evident in the copepodids when from one and the same sample were measured, both specimens which had been treated with glycerine and those which had not. The following table gives examples of the degrees of these small variations which are probably due to deficient technical methods. The group of specimens marked »Stained I« contains specimens from several groups. The groups marked »Stained II« and »Unstained« are from the same sample, Station 135 25/0 meters. It will be seen that in one case the variations even exceed the standard error of the arithmetical mean.

Var.	M ± 3m	σ = ±	V =	n =	
45—50	47,33±0,84	1,29	2,72	21	Stained I
47—51	49,29±0,67	1,03	2,10	21	Stained II
48—53	50,93±0,74	1,34	2,64	30	Unstained
45—53	49,40±0,69	1,96	3,97	72	Total

Var. gives the greatest and least values observed in a hundred parts of a millimeter. *M.* is the arithmetical mean, *m.* the standard error of the arithmetical mean, σ the standard deviation and v the coefficient of variation. In samples where nauplii and early stages of copepodids occur together with large quantities of plant plankton the outsorted specimens must first be claimed. They are suddenly transferred from 70 $^0/_0$ of alcohol to water. The powerful currents which then occur around them will free the bodies and limbs from the plant plankton which otherwise renders the morphological characters less visible. All measurements have been raised to the nearest figure to the right of the scale. Thus if 47 is given as the measurement, this means, that the length of the animal was equal to or less than 47, but distinctly greater than 46. In all cases of doubt the measurements have been increased.

Results of the measurements from the “Belgica” 1905, St. 47.

The results of the measurements of the total lengths of the nauplii and the length of the cephalothorax1) of the copepodids are shown in Table 6. The specimens referred to have for the last three stages in this table from their morphological characters been assigned to *Calanus hyperboreus*. The measurements for *Calanus finmarchicus* in these stages are shown in Table 7. Table 8 gives a survey of the actual range,

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1) According to Claus (1863), Oberg (1906) and Kraefft (1910) the three first stages of copepodids (VII—IX) have a urosome of one segment. The anterior segment of almost the same diameter thus belongs to the cephalothorax but is not included in the measurements given by me for the cephalothorax.

Tab. 6. Variables and frequencies by measuring the total length of nauplii and cephalothorax of copepodid stages of 273 specimens of *Calanus hyperboreus* from "Belgica" 1905, St. 47, 20/0 meter.

A hundreth of a millimeter.

Stage	Number measured	40	1	2	3	4	5	6	7	8	9	50	1	2	3	4	5	6	7	8	9	60	1	2	3	4	5	6	7	8	9	70	1	2	3	4	5	6	7	8	9	80
IV	11	1	0	2	0	0	0	1	0	1	3	2	0	0	0	0	1																									
V	57											3	0	2	2	4	3	8	12	4	7	7	2	2	0	0	0	0	0	1												
VI	38																					1	1	2	3	0	1	0	1	3	2	5	1	5	4	2	1	2	1	2	1	1

A hundreth of a millimeter.

Stage	Number measured	81	2	3	4	5	6	7	8	9	90	1	2	3	4	5	6	7	8	9	100	1	2	3	4	5	6	7	8	9	110	1	2	3	4	5	6	7	8	9
VII	55					2	1	2	2	1	3	2	5	6	7	8	3	5	2	0	2	0	2	1	0	0	0	0	0	0	0	0	0	1						
VIII	0																																							

A tenth of a millimeter

Stage	Number measured	24	5	6	7	8	9	30	1	2	3	4	5	6	7	8	9	40	1	2	3	4	5	6	7	8	9	50	1	2	3	4	5	6	7	8	9	60	1	2	3	4
IX	28	4	8	7	8	4																																				
X	30								1	1	1	0	0	6	7	6	3	4	1																							
XI	54																						1	0	2	2	0	4	4	7	9	10	10	1	1	1	2					

A tenth of a millimeter.

Stage	Number measured	60	2	4	6	8	70	2	4	6	8
XII	40		1	5	12	10	7	3	1	1	

Tab. 7. Measurements of cephalothorax of 139 specimens of *Calanus finmarchicus* from "Belgica" 1905, St. 47 20/0 meter.

Stage	Numbers measured	A tenth of a millimeter.																							
		19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
X	4	2	2																						
XI	103		1	0	4	5	10	11	9	21	14	11	6	3	0	0	1	6	0	1					
XII ♀	32										1	3	4	3	4	1	0	2	2	0	0	2	1	6	1

Tab. 8. Variation (var.), standard deviation (σ), arithmetic mean (M), its standard error (3 m) and coeficient of variation by measurements of total length of nauplii and length of cephalothorax of copepodid stages from "Belgica", St. 47 20/0 meter. Ch = *Calanus hyperboreus*, Cf = *Calanus finmarchicus*.

Stage and species		n =	Var.	M ± 3 m	σ = ±	v =
IV	Ch	11	40— 55	47·27 ± 3·8	4·21	8·91
V	Ch	55	50— 68	57·05 ± 1·29	3·20	5·62
VI	Ch	39	60— 80	60·18 ± 2·50	4·58	6·50
VII	Ch	54	85 – 103	93·82 ± 1·16	4·07	4·35
IX	Ch	31	240—280	260·00 ± 6·90	1·29	4·99
X	Ch	30	310 – 410	372·00 ± 12·18	2·25	6·05
XI	Cf	103	200—370	271·65 ± 9·4	3·21	11·90
	Ch	54	450—600	528·70 ± 11·20	2·74	5·20
XII	Cf	30	280—420	345·70 ± 25·9	4·72	13·7
	Ch	40	620—760	677·50 ± 13·70	2·90	4·29

arithmetical mean, standard deviation, three times the standard error of arithmetical mean and the coefficient of variation calculated on the basis of the class frequencies found in Tables 6 and 7.

The results of measuring the Carapace of specimens from the same sample are shown in Table 14 A. (This table gives a survey of the variants found and of the frequency of all the individuals in stages III—XII upon which these investigations are based). A survey of these

Tab. 9. Measurements of carapace from "Belgica" St. 47. (See also Tab. 8).

Stage and species	n =	Var.	M ± 3 m	σ = ±	v =
III Ch	2	29 - 30	29·50		
IV Ch	31	35— 38	36·94 ± 0·47	0·87	2·35
V Ch	138	42— 45	43·59 ± 0·24	0·92	2·12
VI Ch	86	48— 52	50·24 ± 0·40	1·24	2·45
VII Ch	65	57— 64	60·28 ± 0·58	1·59	2·58
VIII Ch	22	70— 85	77·50 ± 2·68	4·19	5·25
IX Ch	29	110—130	120·17 ± 2·79	5·00	4·12
X Cf	5	100—100	100·00 —	—	—
Ch	31	150—180	169·36 ± 3·86	7·16	4·22
XI Cf	98	100—180	123·77 ± 4·43	14·62	11·50
Ch	49	210—250	229·92 ± 4·68	10·87	4·76
XII Cf	27	120 - 200	157·04 ± 7·71	13·20	14·80
Ch	37	260—310	287·30 ± 5·60	11·30	3·95

measurements of the carapace and of the dimensions calculated from them will be found in Table 9.

It will already be seen from Tables 6 and 8 that the measurements found for the total length of the cephalothorax show a marked variation. Thus the various stages cannot be determined by measurements alone. The morphological characters must be utilised.

Table 9 shows as a main result that the stages according to this method of measurement can be determined without reference to the morphological characters. In addition we see in the earlier stages that the coefficient of variation is decidedly more favourable in measurements of the carapace than in measurements of the total length.

In the tables the measurements found have already been referred to the two species. This determination will be discussed when measurements from other places are given.

Measurements of ***Calanus hyperboreus*** and ***Calanus finmarchicus*** from Romsdal Fjord St. I. 108 20/0 1927 (Ruud 1929).

The sample was selected and kindly placed at my disposal by mr. Ruud, who thought that possibly there were present nauplii of *Calanus hyperboreus*. The results of this measuring have already been recorded by Ruud (1929) and are strengthened by his report on the stationary stock of *Calanus hyperboreus* in Romsdal Fjord and on its breeding conditions.

The sample contained adult specimens and copepodids of the three last and easily determinable stages of *Calanus finmarchicus* and *Calanus hyperboreus*.

The variants found by measurements are given in Table 14 B. A

Tab. 10. Measurements of carapace from "Morild" 1927 St. F, 108, 20/0 meter. (See also Tab. 8).

Stage and species		n =	Var.	M ± 3 m	σ = ±	v =
III	Cf	5	25— 26	25·60 —	—	—
	Ch	4	30— 31	30·50 —	—	—
IV	Cf	42	29— 32	30·81 ± 0·38	0·82	2·67
	Ch	13	35— 38	36·38 ± 0·83	1·00	2·75
V	Cf	70	34— 38	35·90 ± 0·31	0·86	3·27
	Ch	17	40— 45	42·35 ± 0·63	0·87	2·06
VI	Cf	98	38— 43	40·67 ± 0·32	1·07	2·63
	Ch	48	47— 52	48·83 ± 0·51	1·26	2·59
VII	Cf	21	44— 49	46·57 ± 0·76	1·14	2·44
	Ch	20	56— 61	58·90 ± 0·87	1·30	2·21
VIII	Cf	30	57— 62	59·50 ± 0·66	1·18	2·02
	Ch	23	80— 90	82·83 ± 1·80	2·88	3·51
IX	Cf	32	75— 85	78·59 ± 1·58	2·86	3·64
	Ch	14	110—120	114·54 ± 2·86	2·96	2·59
X	Cf	30	90—105	97·25 ± 1·86	3·48	3·58
	Ch	14	150—160	152·21 ± 3·27	4·10	2·69
XI	Cf	6	110—130	120·00 ± 1·00	8·12	6·75
	Ch	1	200—200	200·00 —	—	—
XII	Cf	37	110—150	127·80 ± 4·55	9·25	7·25
	Ch	6	210–240	225·00 ± 12·40	10·40	4·49

survey of variation, arithmetic mean, standard deviation, 3 times the arithmetic mean and the coefficients of variation will be found given in Table 10.

Neither in this sample nor in the sample from the »Belgica«, 1905, were earlier stages than III, present.

Measurements of *Calanus hyperboreus* and *Calanus finmarchicus* from Lofoten, Spring 1922 and 1929.

From the »Corona's« cruise 1922 and the »Johan Hjort« cruise 1929 there exist a number of samples in which there are eggs, nauplii

Tab. 11. Variables and frequencies by measurements of total lengths of *Calanus hyperboreus* and *Calanus finmarchicus* stage I and II from "Corona" 1922 and "Johan Hjort" 1923 and 1929.

Stage	Specimens from:	A hundreth of a millimeter.														
		16	17	18	19	20	21	22	23	24	25	26	27	28	26	n=
I	"Johan Hjort" 1923 St. 69, 71 og 72	1	2	1	1	2	1									8
II				1	2	2	4	5	0	1						15
I & II	"Corona" 1922		4	9	13	19	7	3								55
	"J H" 1929 ..			3	10	18	15	11	5	2	1	1	3	4	2	75

Tab. 12. Measurements of carapace from "Corona" 1922.
(See also Tab. 8).

Stage and species		n =	Var.	M ± 3 m	σ = ±	v =
III	Cf	56	22—27	25·36 ± 0·47	1·18	4·67
	Ch	8	30—34	31·38 ± 1·29	1·22	3·88
IV	Cf	93	27—34	31·85 ± 0·39	1·25	3·92
	Ch	29	35—39	37·24 ± 0·54	0·97	2·60
V	Cf	73	34—40	37·45 ± 0·43	1·22	3·25
	Ch	7	42—45	43·43 ± 1·02	0·90	2·09
VI	Cf	38	40—45	42·76 ± 0·62	1·27	2·96
	Ch	20	48 - 54	51·07 ± 1·18	1·75	3·40
VII	Cf	45	45—52	48·47 ± 0·74	1·65	3·42
	Ch	50	57—65	61·12 ± 0·72	1·81	2·96
VIII	Cf	15	60—68	63·40 ± 1·38	1·78	2·80
	Ch	12	85—95	91·25 ± 1·96	2·17	2·49

Tab. 13. Measurements of total length of stages I and II and carapace of later stages from "Johan Hjort" 1929. (See also Tab. 8).

Stage and species.		n =	Var.	M ± 3m	σ = ±	v =
I & II	Cf	64	18— 24	20·69 ± 0·53	1·41	7·05
	Ch	11	25— 29	27·46 ± 1·02	1·16	4·25
III	Cf	64	21— 26	23·44 ± 0·42	1·11	4·75
	Ch	66	28— 33	29·88 ± 0·40	1·07	3·58
IV	Cf	31	28— 32	30·32 ± 0·62	1·15	3·80
	Ch	66	34— 37	35·28 ± 0·33	0·89	2·50
V	Cf	33	34— 37	35·45 ± 0·39	0·75	2·10
	Ch	107	38— 44	41·16 ± 0·42	1·45	3·53
VI	Cf	34	37— 44	40·88 ± 0·74	1·43	3·50
	Ch	78	46— 53	49·56 ± 0·49	1·43	2·90
VII	Cf	73	45— 53	49·40 ± 0·69	1·96	3·97
	Ch	129	56— 64	60·07 ± 0·49	1·86	3·11
VIII	Cf	38	61— 67	63·84 ± 0·71	1·46	2·29
	Ch	27	70— 90	83·30 ± 2·72	2·57	3·07
IX	Cf	66	80— 90	83·94 ± 0·99	2·68	3·18
	Ch	19	110—125	117·90 ± 0·74	4·70	4·00
X	Cf	56	100—115	107·86 ± 1·58	3·95	4·66
	Ch	24	150—170	158·33 ± 3·85	6·27	3·96

and copepodids of *Calanus*. In Chapter V there will be found a further account of the distribution of these various groups within the area during the period investigated. The measurements of eggs have already been discussed in Chapter I. From a number of these samples measurements have also been made of nauplii and copepodids. A survey of the measurements found is given in Tables 11, 12, 13 and 14. Table 11 gives the variables and frequency of the two stages I and II.

Tab. 14. Variables and frequencies found by measuring carapace of 2719 specimens of *Calanus hyperboreus* and *Calanus finmarchicus* in the stages III—XII. The following samples have been used: A "Belgica" 1905 St 47, B "Morild" St. F, 108 1927, C "Corona" 1922 (several samples) and D "Johan Hjort" 1929 (several samples). The variables are given in 1) a hundreth of a millimeter, 2) 5 hundreths of a millimeter, 3) a tenth of a millimeter. In a few cases individuals measured in a tenth of a millimeter have been marked in the columns for 5 hundreths of a millimeter. This is indicated by a —.

Stage		n =	A. hundreth of a millimeter.																																	
			21	2	3	4	5	6	7	8	9	30	1	2	3	4	5	6	7	8	9	40	1	2	3	4	5	6	7	8	9	50	1	2	3	4
III	A	2									1	1																								
	B	9					2	3				2	2																							
	C	64		1	2	9	17	18	9			2	3	2	0	1																				
	D	130	2	10	23	19	7	3		7	16	26	13	3	1																					
IV	A	31															1	6	18	6																
	B	55									2	13	18	9			4	4	3	2																
	C	122							1	1	2	5	22	35	21	6	3	8	12	5	1															
	D	99								2	6	8	10	5		14	29	17	6																	
V	A	138																						18	42	53	23									
	B	87														4	17	32	16	1		1	4	5	3	3	1									
	C	80														1	3	11	21	24	10	3		1	3	2	1									
	D	140														3	14	14	2	3	9	21	24	27	18	5										
VI	A	86																													7	14	23	24	18	
	B	146																		1	12	32	16	1						7	14	14	7	5	1	
	C	58																				1	6	9	10	9	3			2	2	3	3	6	2	2
	D	112																	1	1	2	9	10	7	3	1			1	6	11	17	23	14	5	1

Stage		n =	A hundreth of a millimeter																															
			44	5	6	7	8	9	50	1	2	3	4	5	6	7	8	9	60	1	2	3	4	5	6	7	8	9	70	75	80	85	90	95
VII	A	65														1	9	10	18	13	8	4	2											
	B	41	1	2	7	7	3	1							1	1	6	6	3	3														
	C	95		3	2	7	10	10	9	3	1					1	2	7	10	9	8	8	4	1										
	D	202		1	5	8	11	10	16	11	7	4			4	8	15	23	26	17	25	9	2											
VIII	A	22																											2	10	7	3		
	B	53														2	4	7	12	4	1										11	11	1	
	C	27																	1	1	1	6	3	2	0	0	1						9	3
	D	65																		3	3	9	12	6	3	2			1	2	14	16	4	

Stage		n =	A hundreth of a millimeter												A tenth of a millimeter																	
			75	80	85	90	95	100	105	110	115	120	125	130	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
IX	A	29								2	16	12	7	2																		
	B	51	14	21	2					3	9	2																				
	C	8			4	2					2																					
	D	85		18	44	4				1	8	9	1																			
X	A	31						5								1	6	18	6													
	B	34				2	14	13	1							11	3															
	D	80						4	18	32	2					7	14	3														
XI	A	147					—	2	—	25	—	33	—	27	4	1	3	2	1			6	11	17	11	4						
	B	7								2	2	2									1											
	D	71																	1	20	30	18	2									
XII ♀	A	37									—	1	—	3	9	2	1	2	5	3	1						1	4	11	10	10	1
	B	43							—	1	—	14	—	15	6	1						1	2	2	1							
	D	166									1	0	5	14	20	11	3	1					5	33	46	27						

Results of the measurements made and the determination of species by measurement.

In Tables 6—14 an account is given of 3284 measurements of the 12 different stages of development of *Calanus finmarchicus* and *Calanus hyperboreus.* The material for stages I and II is 153 individuals and for the 3 last stages determinable according to morphological characters, X, XI and XII the material is also not richly represented. For the other stages III—IX the material must certainly be characterised as adequate.

It will be seen for the waters investigated and the periods of investigation that by measuring carapace of the two *Calanus* species for each stage it is possible to show 2 distinct groups of individuals. In each stage we find a group of individuals which is noticeable by the high figure for the length of carapace, and another group which is noticeable by the low figure for the length of carapace. We obtain the best survey of these conditions in the comprehensive table (No. 14). In this table we find in 28 cases the two groups completely separated by their length. In 2 cases (Stage IV C and Stage V D) we find a markedly two-topped curve without interval between the two parts.

A preliminary consideration renders it probable that the larval stages of the largest group represent larval stages of the largest species *Calanus hyperboreus* and that the larval stages of the smaller group represent larval stages of the smaller species *Calanus finmarchicus.*

The specimens from the »Belgica« 1905 came from an area where this expedition (Damas & Koefoed 1907) found males, females with eggs in the oviducts of *Calanus hyperboreus,* and a number of larval stages of *Calanus.* Damas and Koefoed referred the eggs and the larval stages to *Calanus hyperboreus,* which of course is very probable, since at the same time there were not found any signs, that a spawning of *Calanus finmarchicus* had taken place, while certain signs were found showing that spawning of *Calanus hyperboreus* took place during the period of collecting. In Fig. 20 will be found a graphical representation of the variants and frequency by measurements of carapace of larval stages from those waters. It will be seen how each of the morphologically determined stages shows an even curve for the length found. The last three stages were determined morphologically as *Calanus hyperboreus* and the figure clearly shows how by the addition of the measurements found for the larval stages we obtain a fine series of curves with a regular increase in length for each moul-

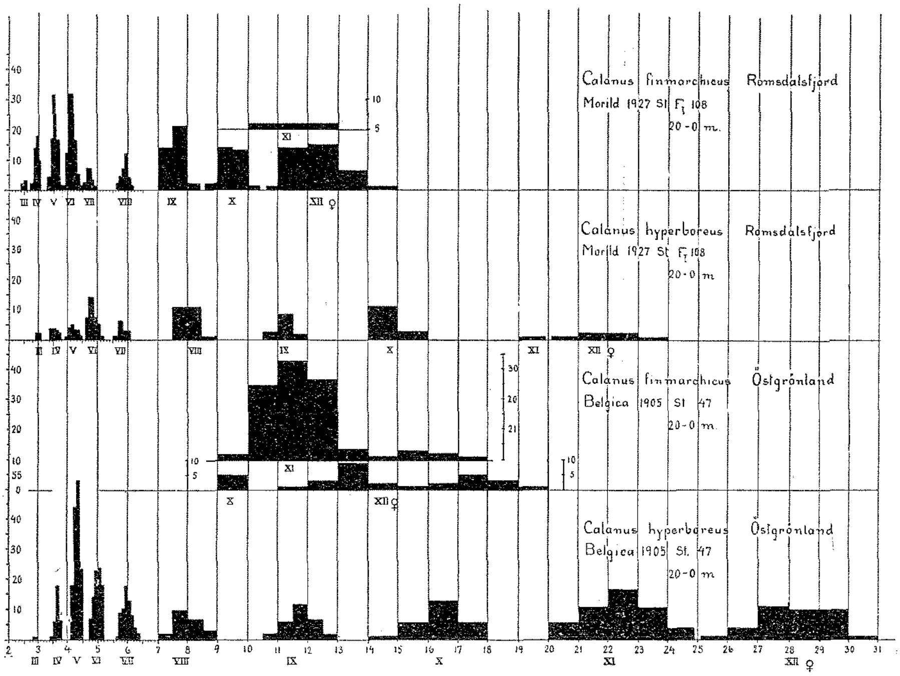

Fig. 20. Graphical representation of the variables and frequencies found by measurement of larval stages of *Calanus finmarchicus* and *Calanus hyperboreus* from "Belgica" 1905, st. 47, and "Morild" 1927, st. F. 108. The measurements are made in tenths of a millimeter. The observations are given in table 14.

ting.[1]) The addition of the measurements found for the larval stages to those for the 3 determined stages of *Calanus finmarchicus* cannot be made as will appear from Fig. 20. Stage X of *Calanus finmarchicus* is of course far smaller than Stage X, of the larval stages measured here.

In Fig. 18 there is also given a graphic representation of variables and frequency of the specimens measured from Romsdal Fjord ex the »Morild« 1927. Specimens of the larger group are here attached to specimens of determinable stages of *Calanus hyperboreus*. Individuals of the smaller group belong to determinable stages of *Calanus finmarchicus*. We see that the larval stages of the group of larger specimens agree very well with the measurements found from the »Belgica« 1905. At the same time a series of curves is also formed showing a regular increase in length for each moulting. In a corresponding manner we have for the smaller group curves with a regular increase in length for

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[1]) Regarding the regular increase in length at change of shell in crustaceans reference is made to Brooks (1886) and Skogsberg (1920). No analysis of this regularity has been made of the material here submitted.

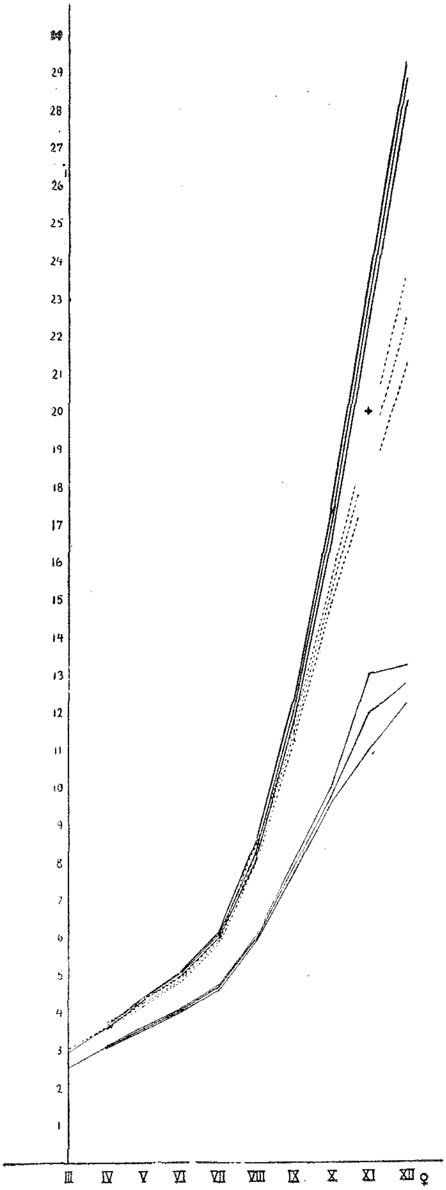

Fig. 21. Graphical representation of the increase in length of carapace of *Calanus hyperboreus* and *Calanus finmarchicus* from "Belgica" 1905, st. 47, and "Morild" 1927, st. F, 108. The drawn graph represent *Calanus hyperboreus* from East Greenland, the dotted graph *Calanus hyperboreus* from Møre. The abscissa shows the stage determined morphologically, the ordinate the length in tenths of a millimeter. The middle line in each graph gives the arithmetric mean (Tab. 9 and 10 m), the one each side the standard error (3 m). There was only one specimen of stage XI in the samples from Møre. The length of this specimen is indicated by +.

each moulting which can readily be connected with the curves for the determinable stages of *Calanus finmarchicus.* Any other arrangement of the measurements found in regular series, is not possible.

Fig. 21 shows the mean values and their standard error in the measurements of larval stages of the two *Calanus* species from the »Belgica« 1905 and the »Morild« 1927. We see how the graphs for the groups of the largest individuals in the earlier stages completely coincide as far as concerns East Greenland and the Romsdal Fjord. In Stage IX and in the further stages we find a difference which lies outside the standard error, increasing outwards towards the adult stage. The graph for the group of smaller individuals forms a growth curve which in main features reminds one of the growth curve for the larger individuals, and which has its direct continuation in the graph for the determinable stages of *Calanus finmarchicus.* It appears perhaps most clearly from Fig. 19 how impossible it is to classify the measurements found and the dimensions calculated therefrom in any other system where, with each moulting, there takes place an increase in length.

The graphical representations in Figs 20 and 21 also show two other phenomena which will here be referred to briefly.

Calanus finmarchicus shows in the later stages a marked variation in length from Møre and to an even greater degree from East Greenland. The great variation of this species in Arctic waters has been investigated and described by Størmer (1929 p. 6—10).

The specimens of *Calanus hyperboreus* measured in this last copepodid stages from East Greenland show a much greater length than corresponding specimens from the Romsdal Fjord. This feature will be the subject of a subsequent publication. (See also Sømme, 1929 a).

Both phenomena here mentioned are a result of the dominating influence of temperature upon the increase in length at each moulting, but the congruenty which one finds in the lengths of earlier stages in Tables 8—14 show that the two phenomena does not make themselves noticeable until later stages, and that the differences increase towards the adult stage. In the earlier stages there is no distinct difference noticeable. These phenomena will in consequence not be of any importance for the question of the determination of the earlier stages of the species by measurement.

Combined, the measurements from East Greenland and Romsdal Fjord, strongly indicates that it has been possible to identify the two groups of individuals in each stage to each of the two species *Calanus finmarchicus* and *Calanus hyperboreus.* An analysis of the geographical distribution of spawning and the breading season, however, will afford a still better basis for a complete decision of the question. The investigation at Lofoten which will be reported in the last chapter of the present work show that from the occurrence of females with eggs in the oviducts, males, and in the case of *Calanus hyperboreus* also spent females, we can obtain a definite picture of the spawning of the two species, and its arrangement in space and time. It will be seen that the spawning of *Calanus hyperboreus* is practically finished at the moment when a considerable spawning of *Calanus finmarchicus* takes place. It will also be seen that the spawning of *Calanus hyperboreus* is restricted to the inner part of the fjord, whilst spawning of *Calanus finmarchicus* to a great extent also extends over the banks in the outer parts of the fjord. As will be seen from Tables 17—22 and Figures 32 and 33 individuals of the greater length groups prevail during the period when *Calanus hyperboreus* has finished spawning whilst spawning of the other species has not yet commenced. Their greatest occurrence is shown to be in the inner part of the fjord where *Calanus hyperboreus* spawns. Later on, when spawning of *Calanus finmarchicus* begins, individuals of the smaller length for each stage appear successively in the samples, and individuals of the larger groups are superseded more and more, as by degrees the smaller group predominates in numbers. These facts permit the conclusion that it must be regarded as adequately proved that by measurements of the carapace of the earlier stages of the two *Calanus* species we can determine them as belonging either to *Calanus hyperboreus* or to *Calanus finmarchicus*.

The reasons why measurements of carapace are better suited for determination of species than measurements of the total length or of cephalothorax.

Table 6 shows that by measuring total length of nauplii and cephalothorax one obtains a very large variation, so that different morphological determined stages have common length groups. Table 14 shows that this does not apply to measurements of carapace. A comparison of the coefficients of variation given in Table 9 and Table 10 shows that the earlier stages, by the first mentioned method of measurements, are characterized by high coefficients of variation, and by the latter method low coefficients of variation. No complete analysis of the causes of this phenomenon was made. We would only point out here some of the factors that certainly play a part in this connection.

In investigating the nauplii of the two *Calanus* species it is soon noticeable that the body of the various individuals is often more or less bent. It is thus evident that in measuring the anterior part where there are no joints, it is possible to avoid the variations which are directly due to the curve of the body.

Brinkmann (1926) has made some very interesting histological investigations of the posterior part of the body of individuals of *Paguridae*, which had been more or less well fed. He proved a considerable difference according to the distension of the posterior part of the body. It is very probable that similar conditions contribute towards increasing the variation of copepod nauplii when measuring the total length.

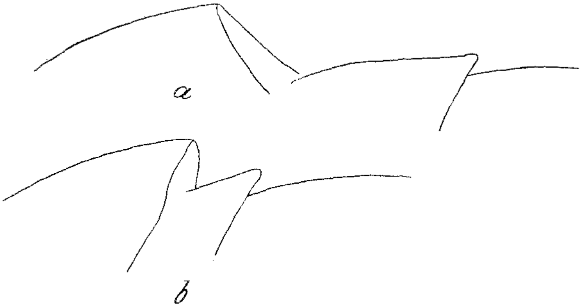

Fig. 22. The hind part of carapace with the following segments of two specimens of *Calanus hyperboreus* stage V.

Fig. 22 represents the hind part of the carapace of two nauplii of *Calanus hyperboreus* stage V with the two following segments (Individuals from the »Belgica« 1905). Both specimens has the same length of carapace (0.44 mm). As will be seen, specimen *a* is more greatly distended than specimen *b*. If we measure to the hind part of the first free segment, the two specimens show a difference in length of 0.05 mm. This gives an increase in the degree of variation for the two observations of 11.4 %. If a phenomenon like the one drawn in Fig. 22 shows alterations in the individual which can take place during a certain stage, it will also give an increased variation for the population when measuring the total length. The stated individual difference in nauplii has frequently been observed and shows all stages of transition.

Oberg (1906) shows that there is a growth of the hind part of the body in the earlier stages of *Pseudocalanus*. Observation of the hind part of the body of stage III of nauplius shows as a clear and distinct phenomenon that there may be a great difference from individual to individual in the appearance and form of the hind part of the body. It may be relatively short and thick, or it may be more or less elongated and thin. This applies to both species of *Calanus*. It must therefore also be assumed that we have here the possibility of a factor which would contribute towards the degree of variation for a population when measuring the total length.

Fig. 23 represents the hind part of 2 specimens of *Calanus hyperboreus* stage X from the »Corona« 1922, St. 47 o.m. Both specimens had the same length of carapace but it will be seen that the length of the hind part of cephalothorax and abdomen in one specimen is considerably shortened. The body of the shorter specimen was less distended and at the same time more flexible and soft than in normal individuals. Similar cases have been observed several times, and may be more or less marked. The phenomenon, however, must be regarded as rare in a stage as late as X. It is very probable that such individuals are those which a short time before fixation underwent moulting. We have also here possibly a factor which in the copepodit stages will occasion variations in length characteristic of the individual in question, but not characteristic of the length groups of a population.

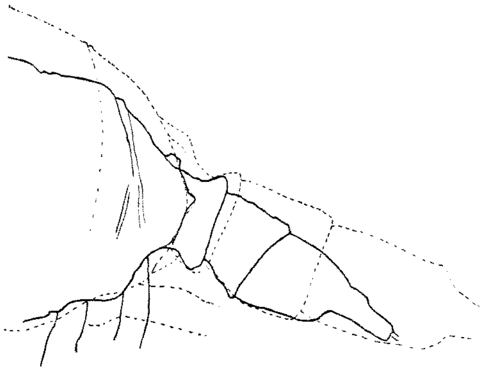

Fig. 23. The hind part of the body of two specimens of *Calanus hyperboreus* stage X from "Corona" 1922.

If we ask the general question as to which measurements in crustaceans, where the part between the segments consists of thin and not firmly united parts of skin (Euphausides, e. g. have of course the various segments connected by distinctly permanent joints), give the most favourable and lowest coefficient of variation, we must reply that in measurements of the size of the body in *Calanus* species it is decidedly most advantageous to measure parts in which there are no segments.

Quantitative Determinations of all Biological Groups of the Two Species in the Samples.

It was shown in Chapter I how by exact examination it is possible to identify the larval stages of the two species of *Calanus* and to determine to what stage they belong. The results of the measurements made show that when the stage has been determined the species of the individual can be determined by measurement of carapace.

In order to get exact determination of genus and an exact determination of stage, the individuals should be sorted out and stained in accordance with the method given on Page 51. If the measurements shall be sufficiently accurate for a separation of the two species, it is necessary, as already described, for the individual to lie in a favourable position so that the front and hind parts of carapace are at the same time sharply adjusted by the micrometer screw.

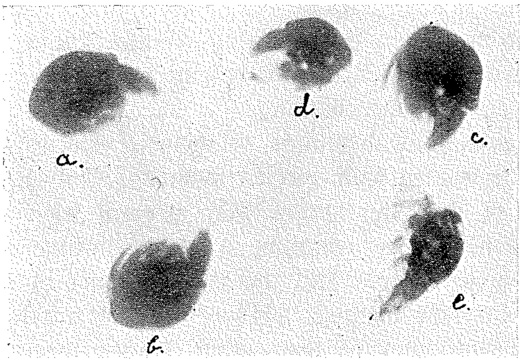

Fig. 24. Photograph of a preparation from "Corona" 1922. *a*, *b* and *c* are of *Calanus hyperboreus* stage IV, *d* of *Calanus finmarchicus* stage IV, *e* an unknown nauplius.

I have not succeeded in finding any other way of identifying the species with certainty. Quantitative determination thus usually requires sorting, and in any case special preparation of a considerable number of specimens. Fig. 24 shows a photograph of such a preparation. *a*, *b* and *c* are nauplii of *Calanus hyperboreus* stage IV and *d* is a nauplius of *Calanus finmarchicus* stage IV. The difference in size in this case where all are of the same stage will be evident without measurement, but it will not give certainty, ~~and~~ even after great practice I have been mistaken when using a subjective estimate for individuals of different species but of the same stage laying side by side. As a rule we have many different stages side by side, and then, even though the preparation may be good, every such determination will be vague and uncertain. Fig. 24 *e* shows an undescribed nauplius which when prepared is clearly characterised by the great distance between the various brushes on furca. As will be seen, the limbs are also smaller than those in the corresponding stages of *Calanus.* In addition they show characteristic differences from *Calanus* nauplii. None of these characters, however, are easily seen in the counting chamber.

With the knowledge now at our disposal we can only arrive at a certain identification of the larval stages of the two species by preparations and measurements. Thereby one obtains the relative proportion of the individuals in the samples. The total number can be determined collectively by counting in the counting chamber, and if necessary by correction for nauplii which do not belong to *Calanus* and which are erroneously included in the counting.

The various biological groups of the two species are so different that they must be treated with specific methods. Only in samples where large numbers of the later stages were present have the quantity of these been determined by counting a representative sample and by weighing the whole sample and the counted part in accordance with Hjort's and Ruud's method. (Hjort and Ruud 1927). For the *quantitative determination of the earlier stages* there were employed two counting chambers, one of 1 ccm and the other of 5 ccm. The 1 ccm chamber will as a rule give reliable values for eggs and nauplii, the 5 ccm counting chamber was partly used for counting nauplii when the smaller one does not give a sufficient number, but mainly for the quantitative determination of copepodids. Representation samples for the counting chambers were taken with graduated pipettes after vigorous shaking of the samples. Counting of the whole area of the counting chamber was always made.

In sorting out individuals for measurement one must remember that it is of importance to obtain a quantitative sorting of the part of the sample which is to be examined. Individuals counted in the counting chambers were preferably used. They have often been supplemented by sortings from flat dish where all individuals of the two species are sorted out in a prescribed area.

The following scheme is found practical for the analysis of the various samples:

1. The sample is inspected in order to see whether there are eggs of *Calanus hyperboreus* present, floating in the liquid above the precipitate.
2. The sample is poured into a dish where the number of *Calanus hyperboreus* and *Calanus finmarchicus*, adults and stages XI and X is determined by total counting.

3. The liquid volume of the sample is measured, decanted or diluted to the nearest 100 or 50 ccms. The sample is poured back and shaken. 1 ccm is then taken out for counting under the counting chamber.

4. The number of eggs of *Calanus finmarchicus* counted and each egg checked by high power magnification and measurement.

5. The number of *Calanus* nauplii I and II is counted and measurement made direct.

6. The number of nauplii of *Calanus* III—VI is counted.

7. The number of copepodids of *Calanus* is counted. We first count the total number and then the number of each stage.

8. A sample of 5 ccms is taken out for counting in a larger counting chamber if the first sample does not give a representative selection of one or several groups.

9. Samples of the nauplii stages III—VI and the first copepodid stages are taken for staining and measurement. The relative composition of the two species and of stages is determined.

10. The total number of both species of all stages in the sample is determined.

The following two examples are given for a further illustration of this method of analysis:

Example 1.

Station 79 25/0 meters, net 8/72, 4/4 1929.

1. Eggs not present.

2. *Calanus hyperboreus:* 17 females, 16 stage XI, *Calanus finmarchicus:* 39 females 4 XI. Generative organs: *Calanus hyperboreus:* Spent females, *Calanus finmarchicus:* A number of females with eggs in different stages of growth.

3. Volume of the sample 50 ccms. 1 ccm taken.

4. 18 eggs of *Calanus finmarchicus.*

5. Stages I and II not present. (Subsequent sorting from the sample showed that these stages of both species were present in minute quantities).

6. 147 nauplii of stages III—VI.

7. Copepodids not present.

8. Unnecessary.

9. *Calanus finmarchicus:* Stage III 2 specimens, IV 3, VI 1. *Calanus hyperboreus:* Stage III 4, IV 33, V 66, VI 2.

10. Estimated total number per 100 meters:

Calanus finmarchicus: 156 females, eggs 3600, III 530, IV 795 and VI 265, total 5190.

Calanus hyperboreus: 68 females, III 1030, IV 8750, V 17 500, VI 530, total 27 810.

Number determined: *Calanus finmarchicus* 24, *Calanus hyperboreus* 105. (Total sum and number determined are only given for the new generation).

Example 2.

Station 135, 25/0 meters, net 8/72, 29/4 1929.

1. Eggs not present.
2. *Calanus finmarchicus* 1 male and 1 female.
3. Volume of sample 50 ccms, 1 ccm taken.
4. 23 eggs of *Calanus finmarchicus.*
5. 4 nauplii of stages I and II.
6. 136 nauplii of stages III—VI.
7. Total 109 copepodids 51 stage VII, 23 VIII, 23 IX, 10 X and 2 XI.
8. Unnecessary.
9. *Calanus finmarchicus:* Stage III 4 specimens, IV 12, V 14, VI 29, VII 32, VIII 37, IX 65, X 55.[1]) *Calanus hyperboreus:* V 1 specimen, VI 2, VII 2 (IX observed in a non-representative sample).
10. Total estimated number per 100 meters:

Calanus finmarchicus: Eggs: 23 × 50 × 4 = 4600, I and II : 800, III 1760, IV 5280, V 6160, VI 12 760, VII 9600, VIII 4600, IX 4600, X 2000, XI 400, total 38 160.

Calanus hyperboreus: V 440, VI 880, VII 600, IX 10, total 1930.

Number determined: *Calanus finmarchicus* 272, *Calanus hyperboreus* 7.

Checking the methods employed.

By analysing the same sample several times the methods were repeatedly checked. In no single case where many individuals were present in the samples has the difference exceeded 10 %. The error of the methods is therefore negligible in proportion to the differences which are taken into account in the geographical part of this work.

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[1]) In the case of the last three stages unusually many were here measured.

SPECIAL PART II.

Biology and Distribution of *Calanus finmarchicus* and *Calanus hyperboreus* in Norwegian Coast Waters.

CHAPTER III.

Some Observations on the Biology *Calanus hyperboreus* from different Parts of the Norwegian Coast.

As mentioned previously, I have in addition to the investigations from Lofoten reported in the present work, undertaken investigations of *Calanus hyperboreus* of a more special nature. Some of the results of these investigations are finished and are of interest for an understanding of the distribution of the species in the Lofoten area. A short account will therefore be given of these results.

Remarks on the Distribution of Larval and Adult Stages and the Longevity of Males and Females.

Ruud (1929 p. 50) found in 1927, 11/8 a considerable number of females of *Calanus hyperboreus* in the Romsdal Fjord. In a sample taken at the same place on 21/6 no females were found, only later copepodid stages. On this basis Ruud naturally raises the question whether the development of individuals from the spawning of the same spring had not as early as 11/8 developed so far that the females would spawn in the same autumn.

From the cruise of the »Johan Hjort« along the coast of North Norway, 1923, I had the opportunity of examining a large number of samples from the months June and July, in some cases these samples were from the coastal banks, in others from the fjords. These samples show that the composition of the stages of *Calanus hyperboreus* at that time of the year is subject to great variations. Thus females are often present in large numbers, in other cases they are lacking, whilst the copepodit stages X and XI are well represented. The same appears from the samples which I had an opportunity of collecting in the Oslo Fjord at Drøbak in the months of July and August, 1926 and 1928. These materials thus when combined show that the composition of stages in the summer months along the coast of Norway is subject to very great and apparently chance variations. It is therefore very probable that the phenomenon described by Ruud on the basis of very few samples is solely due to these variations.

It appears from my investigations both from the Lofoten area and from other parts of the coast that the best sign of a coming or existing spawning of *Calanus hyperboreus* is the presence of females with eggs in the oviducts. On the one hand there are a number of samples containing females with eggs from the months of January and February, in a few cases also March and April. (In the Lofoten area in the years 1899 and 1900, Nordgårds material), 1924 and 1929 (the author's material), from the Oslo Fjord 1929, (the author's material). From January and February females with eggs have occurred in all the representative samples which have been available. On the other hand there are a number of samples from spring, summer and autumn which in all cases lack females with eggs in the oviducts. Altogether the existing materials for the determination of the occurrence of females with eggs in the oviducts prove that spawning of *Calanus hyperboreus* along the coast of Norway normally only occurs in the months of February and March for the bulk of the stock, in addition to which there is a delayed spawning of about 1 % of the stock in the depths of the fjord in April. (See p. 116).

This conclusion is further confirmed by the following circumstances:

Males are very commonly found in January and February, exceptionally in December, March and at the latest April 4th, otherwise not at all.

Earlier larval stages than X of the species are only found in March and April.

On measurement, the species shows no typical seasonal dimorphism like that found by Ruud (1929) in the case of *Calanus finmarchicus*, Adler and Jespersen (1920) in the case of several species off the Danish coast, and also by a series of investigations of fresh-water cladoceri, in all cases in species with several spawning periods a year.

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Since *Calanus hyperboreus* has such a short period of spawning per year, the next questions that arise are the following:

1. How is the new generation developed from spawning and when do the individuals attain the stage of adult males and females?

2. How long do males of the old generation live and how long do females live after spawning?

In the consideration of these two questions it is of the greatest importance as regards females to have a method which can decide direct whether the individual in question has spawned or not.

In order to examine whether an easily accessible method existed, I started with females with unripe eggs in the oviducts collected in the Oslo Fjord at Drøbak 10/2, 1929. About 70 females from one catch (see Table 15), were transported to the laboratory in Oslo and in the course of the next 3 weeks or so they spawned.

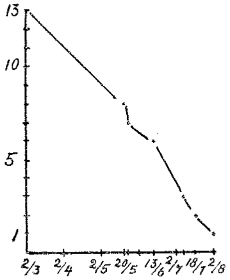

Fig. 25. Mortality among 13 spent females of *Calanus hyperboreus* in a culture jar 1929.

In females which had undoubtedly spawned no easily recognisable changes were found either in the ovary or the genital segment. The oviducts on the other hand shortly after spawning proved to be very much swollen by alimentary cells and connective tissue, which to some extent receded at first, but the oviduct still remained very thick. (See description on P. 28 og and Fig. 6).

An investigation of the longievity of females after spawning in water with about 26 ‰ salinity and temperature 0° and practically speaking completely dark is shown in Fig. 25. The last individual in a culture with these conditions lived until the 2/8. It then died accidentally.

An investigation was then made in the existing material as to which periods of the year this group of females with swollen oviducts occur along the Norwegian coast. It appeared that all the females which were caught in the Lofoten area in March—April, 1922 and 1929 belonged to this group, and likewise the females which were caught in the summer months June and July, some from the Oslo Fjord at Drøbak

1926 and 1928, and others from the coast of North Norway, 1923. With great generosity Ruud placed his samples from 11/8, 1927 from the Romsdal Fjord at my disposal, and it was found that the females in the samples had swollen oviducts.

The next step was to investigate the females which were collected just before the period when the development of eggs begins, as to whether they also had swollen oviducts. The available materials was that of the females mentioned in Tables 15 and 16, and also a number of females from Nordgårds material, January 1899, from the Lofoten district. In this material females with swollen oviducts were lacking.

Before the period of spawning we find virginial females with oviducts which in the last copepodid stage are only visible a very thin string. After the period of spawning we find females which have spawned with slightly visible, swollen oviducts. The first group was at Drøbak first observed on 4/11 1929 (see Table 15) in one specimen, and a considerable number on 19/1 and 10/2 1930. Along the North and West Coast 253 specimens were caught in the days 7/12—15/12, but in very small quantities in proportion to the large number of larval stages caught at the same time. (Se Table 16). Some specimens were also found in Nordgård's material.

The material therefore permits of the following conclusions:

The new generation from spring spawning thus develop females as early as in November, but not in considerable numbers until after the middle of December. After spawning the females continue to live in any case until 11/8 and they form a very common group in summer plankton. In November and December females which have spawned are not found.

The reason for the great variation in the distribution of the stages in the summer months in Norwegian coastal waters may possibly be found in the following conditions. As shown during the following discuscion of the conditions in the Lofoten area there occurs just after spawning a partial separation of the old and the new generations because they are differently vertical distributed. In hauls from the summer months we may therefore find: 1) Practically only individuals of the old generation, 2) exclusively individuals of the new generation, 3) a mixture of the old and new generations. In case 1 we find large numbers of females which have spawned e. g. Ruud's sample from 11/8, in case 2 no females e. g. Ruud's sample from 21/6, and in case 3 varying numbers of females which have spawned as in my samples from North Norway 1923 and Drøbak 1926 and 1929.

With the exception of single specimens, 4/4 1929 (Table 17), males are not found after the period of spawning, and they are never found amongst the individuals which take part in or have taken part in the yearly vertical migration. In the Oslo Fjord at Drøbak they were first caught 19/1 1929, and in material from other parts of the coast in 9 specimens, 15/12 1928 in the Romsdal Fjord (see Table 15). Large numbers of males were caught by Nordgård 9/2 1899 in Ofoten Fjord and 6/2 of the same year in Tranødypet (see p. 90), and by the present author 19/1 and 10/2, 1929 at Drøbak. The lack of them in material collected later on shows a short longevity. Towards the end of the time when females with eggs in the oviducts are found, that is to say just before spawning, they are already found to be present in very small numbers. Thus in a sample from the Ofoten Fjord 18/2 1924 (see p. 27). Table 15 shows 19/1 275 males per 100 females, exactly like Farran (1927) who found males in excess in *Calanus finmarchicus* in January off the Irish Coast. 10/2 on the other hand shows in Table 16 only 7.8 males per 100 females.

Tab. 15. Numbers of *Calanus hyperboreus* in standardhauls near Drøbak with net 8/72 along the bottom at 200—225 meters July 17. 1928 to February 2. 1929.

Station	Date	Correction for duration of haul	Stages				Total number
			X	IX	XII ♀	XII ♂	
D 98	17/7	1		6			6
D 99	25/7	1	1	17			18
D 100	4/11	2/3	24	51	1		76
D 102	19/1	2	12	44	16	40	112
D 103	10/2	1	267	93	291	22	673

The total material of the occurrence of males shows that they only exceptionally occur outside the period 15/12—15/2, but within that period even a short time with a surplus over the number of females. Their normal length of life can thus not exceed 2 months. and if during the period 15/12 and 15/2 there is a steady formation and death of males, the length of life of each individual is only a fraction of two months.

I have only in one case succeeded in keeping a male in culture. From Table 15 it will be seen that of 22 males caught 10/2 1929, 21 were dead or dying already when the samples were sorted out whilst all the females (291) were very lively. One male, however, was comparatively active; it was sorted out and placed under —1.5° and in darkness for some hours whereby it was evidently quickened. It survived transport by motor-car to the laboratory in Oslo and lived there for 13 days under 0° and in darkness.

Some Remarks on Stage Distribution in Arctic Regions.

A number of writers, inter alia Giesbrecht (1893), Mrazec (1902), With (1915) and Sars (1900, 1925 etc.), do not report the discovery of *Calanus hyperboreus* male in Arctic regions. Certain other writers state that they have found a few specimens. Personally I have had an opportunity of examining a large quantity of material from Arctic regions, e. g. that from the »Belgica« 1905, the material which is kept in the Zoological Museum in Oslo (including the »Fram« 1893—96) and in Copenhagen (including the »Ingolf« and Krøyer's East Greenland Expedition) and the Danish »Godthaab« expedition 1928 to Davis Strait and Baffin's Bay with samples from May 24th to October 10th. The distribution of stages in the Arctic Regions will be further discussed in a coming publication, but two or three main results may perhaps be of interest here.

Females which have spawned comprise the bulk of the individuals caught in the summer months in the Arctic regions. A lack of females with normal eggs in the oviducts (pathological pictures are not rare) during the time when the samples were collected shows that normally, spawning does not take place in the summer months. The stage composition of the new generation shows that most often spawning must have taken place very early in the year, buth with a considerable difference in time in regions situated far to the north and more to the south, and also in regions covered with ice and those not covered with ice. (Compare Damas and Koefoed 1907). Males are extremely rare. From the »Godthaab Expedition« 1928, where the material was very abundant (during my examination there were sorted out and measured 4926 specimens, the total number of individuals examined considerable exceeding ten times that number), there was only found 1 male, in spite of the considerable time used for the collection and the very varying regions from which it came.

Samples from the Polar Sea show a considerable difference from these of other Arctic regions. Material collected between March and

August shows in all cases the presence of numerous females with eggs in the oviducts, but never males. It is also striking that in no case were the eggs in the later periods of growth.

Observations of the Spawning of *Calanus hyperboreus* in Culture Jars.

A number of observations made in 1929 of spawning animals will be of interest for the investigations of the Lofoten area and are therefore included here. At the same time I feel bound to draw attention to the following: 1) At the time when the experiments were made my experiences regarding the biology of the species had not a very solid foundation. The experiments therefore are of a more occasional nature, and are not specially designed to give an answer to questions which have arisen during the ecological investigations. 2) In the winter of 1928/1929 the species was very numerous in South Norway, but since then it has practically been lacking and therefore I have not been in a position to repeat the experiments on a larger scale.

The experiments must therefore not be assigned a greater value than that which they may have for further and more thorough studies of the questions raised.

The approximately 70 living females ready to spawn which have already been discussed, from the Oslo Fjord at Drøbak, 10/2 1929, were during the time they were not subjected to observation kept at a temperature of 0° in complete darkness. Unfortunately it was unavoidable that to a certain extent the animals were exposed to light while the sample were hauled up, sorted, transported and so on. It was found, however, that the animals during the treatment to which they were subjected were not greatly influenced by milieu factors stimulating spawning, because not until the 14/2 was any spawning observed in the main culture jar, and after that date only a few eggs were observed floating in the culture without any of the females showing a marked decrease in the number of eggs in the oviducts. In the course of experiments with spawning at various temperatures, spawning was observed at —1°.5 and +7°.5 C and also at a number of intervening temperatures. No experiments were made at temperatures higher or lower than the limits here given.

When a female had laid a considerable number of eggs in a culture jar and it was not at once isolated from them, the number of eggs floating in the culture diminished very rapidly. Even if this was not observed directly, it must be assumed that a female eats her own new-laid eggs. We cannot therefore in the case of this species determine the total number of eggs of a female by counting the eggs which are laid when it is spent. (There is even a question whether we can venture to regard Grobben's (1881) determination of the number of eggs in *Calanus finmarchicus* according to this method as reliable). The number of eggs which are laid in a prescribed period cannot be used for determining the rate with which spawning takes place.

As will appear from the observations in the Lofoten area and from Drøbak a large number of females of the over-wintered stock arrive at full spawning capacity without traceable spawning taking place a very long time before the vertical migration and period of spawning. On the other hand it is striking to find in the Lofoten area how the actual period of spawning is very short (see p. 117). In these circumstances it is quite conceivable that environment is of very great importance for the rate with which spawning takes place. Are the environment factors to which the animals are exposed before the period of spawning so unfavourable that the animals only spawn very slowly or do not spawn at all, in spite of the fact that fertilisation has taken place and the eggs have passed through the period of growth? Are the factors to which the animals are exposed during the period of spawning very favourable so that they spawn their eggs in the course of a very short time?

In this connection it is of interest that all the 70 females or so which were used during the experiments could be brought to spawn. Certain females with all the eggs fully grown were able to spawn all the eggs on one side, and keep the eggs on the other for a longer or shorter period. As a rule, however, spawning proceeded equally on both sides. Sometimes females which spawned with great rapidity kept one or two eggs left in one or in both oviducts, and for days they could not be brought to finish their spawning. Specially interesting were a few individuals who had both fully grown eggs and eggs in the period of growth in their oviducts. It appeared that they could be made to spawn their fully grown eggs, but they retained those eggs which were still in the period of growth.

These observations seem to allow the conclusion that females which have over-wintered are quite ready to spawn before the vertical migration even though spawning does not take place.

There is, however, another question which is more difficult to solve from the existing observations, viz. what factors are favourable and what are unfavourable for spawning. As far as my experiences are concerned there is a striking difference between the vitality of the animals in various environments. After a stay for some time in darkness the animals are dull and sluggish, they do not for instance react if we knock on the glass with a hard object. After staying for some time in a subdued light their liveliness increases. They swim actively around in the culture jars and strongly react against all disturbances such as knocking at the glass wall or stirring the culture. In the cases where spawning was observed it was always in lively individuals.

It is very difficult, however, to measure the quantities of eggs laid by the animals in a certain period. As already mentioned, counting of the eggs can not be used. The best method appears to be an examination of the oviducts of each individual before and after the experiment, but even here we are debarred from obtaining reliable values, since of course it is quite conceivable that any disturbance of the animals will influence the result. At the same time we can always easily decide whether a certain individual has practically speaking all its eggs left, whether it has spawned opportinuately ⅓, ½ or ⅔ of its quantity of eggs. These observations may then be supplemented by direct observations of the number of eggs laid during the experiment before the female in question has had an opportunity of eating them.

Some details of the experiments will be given: 13/2 a culture which had remained for 48 hours at 0° C in darkness was exposed to subdued day light. The individuals had not spawned before the experiment. After the culture had been exposed from 13 to 14 o'clock several individuals started spawning. At 14 o'clock the temperature had risen to 5°. Spawning continued until the experiment was stopped at 16 o'clock, the temperature still being 5°. None of the individuals had laid a large number of eggs, the speed of spawning was comparatially low.

14/2 more experiments was carried out.

A culture jar containing 3 individuals was at 0° during 5 hours exposed to subdued daylight as during the experiment the previous day. After about one hours exposure the individuals had started spawning, and as the experiment was stopped, one female showed a decided decrease in number of eggs, the two other animals had spawned from ⅓—½ of their number of eggs. The rate of spawning was comparatively low.

Another culture jar containing 3 females was at 0° exposed to the light from a hundred units electric bulb at a distance of 1 meter for 2 hours. One female had then spawned noticeable quantities and the two others had spawned the whole quantity of eggs present in their oviducts. The rate of spawning during this experiment was in consequence very high.

A culture jar containing 3 females was during half an hour placed under the same conditions as in the previous experiment and the spawning began freely in two of them. Then the culture was exposed to sunlight outside the laboratory and temperatures from 0°—1°.5 during two hours. The spawning was under these conditions immediately interrupted. When brought back again to the previous conditions two of the females successively again started spawning but at the beginning at very low rate. After 22 hours the two females had spawned the majority of their eggs. One female had not spawned noticeable quantities and was not before some days afterwards brought to spawn at high rates.

By experiments repeated later on individuals which had been kept under 0° and in darkness for a considerable time, were exposed to 0° and various degrees of light, strong electric light, subdued electric light and subdued daylight. In some cases these individuals had spawned some of their eggs before and in other cases the females used had never spawned. After the 14/2 there was constantly observed spawning in the main culture from which the individuals were obtained, but always at a very low rate. In all cases where the individuals were exposed to light the rapidity was greatly increased. There were repeatedly observed individuals which spawned all their eggs in the course of a few hours.

Although these experiments were very deficient in several respects, they give strong indications in the same direction as the observations from the Lofoten area (see p. 115), viz. that the rate of spawning varies in different environments and that definite conditions of light can stimulate the rate of spawning.

It will appear from the above that spawning can take place at great rate at 0°. An experiment to see whether also the temperature had any influence was commenced on 14/2. A culture containing 10 individuals was placed in the most favourable light conditions known, viz. the above-mentioned 100 units electric bulb, and they were surrounded by a cloak of running tap water. Unfortunately it was found that in these circumstances the temperature varied somewhat, viz. from 5° to 7°.5. Spawning took place during the whole time of the experiment but at a low rate. On 2/3 the experiment was stopped. One individuals was then dead, 6 had partially spawned and 3 showed no signs of having spawned.

If we compare this experiment with that at 0° and under the same conditions of light on the 14/2, it will be seen that at a low temperature 2/3 of the exposed individuals spawned completely in the course of 2 hours, whilst the experiment at a high temperature did not show any case of complete spawning, only 2/3 of the individuals having partly spawned after an exposure of 386 hours. The experiment gives strongly indicate that a low temperature also represent a factor which stimulates the rate of spawning.

Relative numbers in standard hauls from the Oslo Fjord at Drøbak.

In the summers of 1926, 1928 and 1929 I took a number of hauls with nets 8/72 at Drøbak along the bottom at a depth of from 200—225 meters. A number of hauls from that time were quite negative. The largest catch was made on 18/7, 1926, 64 individuals in a haul of one hour. In the summer of 1928 the greatest catch was 18 individuals and in the summer of 1929 only 2 individuals. Both Sars (1903) and Hjort and Ruud (1929) state that this species is very common at Drøbak at great depths in winter. A similarly numerous occurrence was also found by the present writer in the winter of 1928/29. In Table 15 the various catches in the period from 17/7 to 10/2 are adjusted to the same standard because the hauls were not all taken with trawls of equal duration. The total catch is also shown in figure 26. The material shows an enormous increase in the number of individuals through the autumn and winter. In·may account of the conditions at Lofoten I raise the question whether in the autumn and winter there is not a concentration of the animals in the deep waters of our fjords. The material from Drøbak 1928/29 appears to confirm this assumption, and renders it highly desirable that more investigations should be made in connection with this phenomenon.

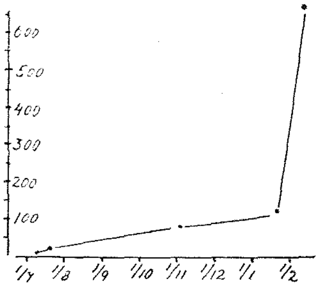

Fig. 26. Total numbers of *Calanus hyperboreus* caught in standard hauls near Drøbak July 17. 1928 to February 2. 1929. (Se also tab. 15.)

CHAPTER IV.

Investigations in the Lofoten Area and the Winter Conditions in *Calanus finmarchicus* and *Calanus hyperboreus.*

Topographical Description of the Area Investigated.

Nordgård (1900) and Nordgård and Jørgensen (1905) differentiate between two hydrographically different types of Norwegian fjords. In certain fjords Nordgård found during winter time a great variation in hydrographical conditions at various depths. He found during spring and winter a cold surface stratum of low salinity and warmer water of higher salinity at the bottom. In other fjords he found uniform hydrographical conditions at all depths (Lyngenfjord, Kvænangen). Nordgård shows that it is the topographical conditions which are here of great importance. In certain fjords the warm water from the Gulf Stream enters and forms a warm stratum in the depths. Gårder (1916) shows that in the fjords at Bergen belonging to this type in April and June an exchange of water takes place down to a depth of 300 meters. In other fjords where the topographical conditions prevent such an influx of water, the deeper layers of water are colder and of a lower salinity. Nordgård (1900) shows that the vertical distribution of *Calanus finmarchicus* is different during the winter in these two different types of fjords. Where a warm bottom water is present the species is mainly found here, and where the conditions are more homogeneous at all depths the species show a numerous occurrence right up to the surface.

The Lofoten area and the other areas from which the material in this investigation originate, all belong to the type where the warm water is able to penetrate to the deeper layers.

A longitudinal section through the Vest Fjord (see Fig. 32) shows that in the outer part there are far smaller depths than in the inner part. In the outermost part between Støt and Røst the depth never exceeds 300 meters. If we follow the fjord inwards we find that the depth in its middle, deepest part only increases very slowly in the outer half of the fjord. About halfway in towards the inner end of the fjord, at Høla, the depth as an exception exceeds 400 meters. Inside Høla on the other hand we frequently meet with greater depths than 400 meters. Here soundings have been made down to 630 meters.. The innermost part of the fjord mainly consists of two large branches, the Ofot Fjord and the Tys Fjord. Both of these fjords show great depths. Thus in the Ofot Fjord 553 meters and in the Tys Fjord 897 meters have been measured. In its main features the Vest Fjord therefore can be characterised as an ordinary Norwegian threshold fjord, with a depth of threshold in the outer part of a little less than 300 meters, and an extensive, branched basin in the inner part, a deep basin whose waters are separated from the deep waters of the Norwegian Sea and form an independent area of depth.

In many other respects, however, the fjord presents other natural conditions which are not usual in Norwegian fjords. Both in length and in breadth the extent of the fjord is so great that we are on the borders of what may be called a fjord and what may be called a sea. In addition the limits towards the north are not those of a continuous fjord side, but consist of a number of large and small islands. Towards the south the fjord is limited by a markedly indented coast with a number of deep fjord arms, and outside this coast a system of smaller islands and skerries with at some places great intervening depths (down to 627 meters).

In the area investigated we must be aware that the limits towards the north and south partly consist of islands and skerries, and we must therefore take into consideration a greater exchange of water than in an ordinary Norwegian fjord.

Hydrography of the area investigated.

The hydrography of the Lofoten area has been submitted to investigations for many years. As regard earlier investigations I would refer to Nordgård and Jørgensen (1905) and Helland-Hansen and Nansen (1909). Simultaneously with the collection of material for the presents work there have also been made hydrographical investigations. The main features of the hydrography of the area will appear from figures 32, 33, 38, 39 and 40.

As mentioned by Sund (1924, p. 470), there is in the Lofoten area during spring a pronounced correlation between temperature and salinity. It will therefore be suficient for a short survey of hydrographical conditions, to set forth the main features of the distribution of temperature. Sund (1926) mentions 3 distinct strata of water in the area. There is a bottom water with practically speaking constant temperatures, 6°.8—7°.1 and salinity 34.5 ‰—35.0 ‰ in 1926. Its extent upwards varies a good deal. In general it extends up to a depth of 150—200 meters. Above this lies a stratum of »bank water« which varies greatly in thickness. This is characterised by temperatures of between 4°.5—6°.5 and a salinity of 33.5 ‰—34.5 ‰ in 1926. The upper layer consists of »coast water« (Mosby, 1923). It is characterised by temperatures in the winter months lower than 4°.5, and salinity 32.0 ‰—33.5 ‰ in 1926. The thickness of this layer of water varies greatly. It is usually thickest in the inner part of the fjord (up to 100 meters). In the outer part of the fjord it is often thicker on the northern side of the fjord. (See Fig. 39 and 40, and also Mosby (1923), Sund (1924 and 1926).

In addition to temperatures and salinity the 3 various strata of water are characterised by a difference in movements and changes in the physical conditions. Moreover they are of different origins.

The situation of the different strata of water along the mid line of the Ofot Fjord and the Vest Fjord in 1929 during the period of the investigations is shown in Figs 32 *c* and 33 *c*. As seen the main features of the hydrographical conditions are the same at the first and second time of investigation. The chief change is a fall in temperature in the upper strata of the innermost part of the fjord. Some of the water masses have a temperature lower than 1°.5, at one station even at a depth of more than 20 meters. The horisontal distribution of temperature during the investigations in 1922 will appear from Fig. 38. It will be seen that there is a characteristic difference between the northern and the southern sides of the fjord. The northern side is characterised by a surface temperature lower than 3°. The southern side of the fjord, and the area which lies between the numerous islands and skerries, are characterised by temperatures higher than 3°. The low temperatures in the northern part of the fjord extend right out to Værøy, probably also beyond it. The Røst group of islands lies in far higher temperatures. It falls outside the isotherm for 5°. Further information regarding the various strate of water will appear from figures 32, 33, 39 and 40.

Mosby (1923 Figs 1—7) shows that in 1923 the isotherms has a course similar to that of 1922.

Currents in the Area investigated.

From 1922 to 1930 the hydrography of the Lofoten area has been the subject of exhaustive investigations. The material is being examined by Oscar Sund but no complete account so far exist as regards the material and the conclusions which may be drawn regarding the currents. Sund, however, has given me some information and has kindly read this part of my manuscript. In the area investigated there were found both tidal currents, wind currents and convection currents on account of the outflow of fresh water from the land.

The tidal currents in the area investigated may be of great rapidity especially in the outer part. Thus the sound between Værøy and the outermost Lofoten islands on account of the strong tidal currents is very dangerous for small vessels.

Both on account of the tidal currents and the wind currents we must take into account that the masses of water, especially in the outer part of the area, may change very rapidly. As an instance reference may be made to Fig. 38 where it will be seen that the isotherms in the area just inside Værøy have a markedly curved course, and that the water masses are irregularly distributed. Thus stations 61 and 62, 10/4 (Fig. 41, Table 25) represent far higher temperatures than those found at the adjacent stations 16, 24/3 and 35, 1/4. We thus have an influx of warm water to that part of the area. There also appeared (see P. 152) at Stations 61 and 62 corresponding changes in the composition of the plankton.

As is well known, there runs along the west coast of Norway a northwardgoing coast current, the waters of which to some extent also (Mosby 1930) cause great exchanges of water in the middle strata far into the fjords. It is an old experience from the Lofoetn area, as is also confirmed by the hydrographical investigations, that a convection current proceeds along the eastern side of the fjord and out along the northern side. This current will be augmented by a more local surface current from the inner parts of the area out towards the banks.

Dividing of the investigated area into sections.

In this account there will be employed the following division of the investigated area:

1) The inner area. This comprises that part of the fjord which lies inside Høla and thus comprises the inner and deep part of the fjord and its branches. It is also characterised by the cold and only slightly salt upper layers during the time of the investigations.

2) The northern area. This is bounded by the Lofoten-islands to the north. To the south and west it is bordered by the isotherms for 3° at the surface, 1922. To the east it extends up to and includes the waters at Høla. It is also characterised by water masses belonging to the cold outgoing convection current along the north side of the fjord.

3) The southern area. This area is bounded on the north by the isotherm for 3° at the surface, 1922. It thus comprises the southern part of the fjord and the skerries south and east of them. It is also characterised by relatively high temperatures in the upper layers of water.

4) The outer area. This is bounded to the east by the isotherm for 5° at the surface, 1922. It thus comprises the sections of the coastal banks nearest to the West Fjord. It is also characterised by high temperatures in the upper layers of water, temperatures which generally lie above these in the southern section.

The various sections and their limits will be found in Fig. 38.

The vertical distribution of *Calanus finmarchicus* and *Calanus hyperboreus* during winter.

From a number of investigations from Scandinavian waters we know that in the months of February, March or April, the time varies, a numerous occurrence of the two species here investigated takes place in the upper layers of water. As the occurrence of the organismes even at first is so numerous it indicates that a vertical migration of the entire stock of the species has been completed in a very short space of time. The time before this appearance in the upper layers sometime during the months of spring will here be called the winter conditions. It will

Tab. 16. Numbers and stage distribution of *Calanus hyperboreus* and *Calanus finmarchicus* from nets 72/8 december 1928. The situation of the stations is seen in fig. 31. Station 374 is from the Romsdalsfjord.

Station	Date	Depth	*Calanus hyperboreus*					*Calanus finmarchicus*			
			♀	♂	Numbers along 100 meter of the haul	XI	X	♀	Numbers along 100 meter of the haul	XI	X
357	7/12	400/200	51	—	769	917	570	—	1030	1830	229
		200/100	—	—	20	15	5	—	19	16	3
		100/0	—	—	1	1	—	—	8	6	2
364	10/12	300/100	3	—	69	102	32	—	1062	1890	234
		100/0	—	—	1	1	—	—	11	9	2
367	10/12	550/300	117	—	1606	3510	413	—	1420	3120	195
		300/100	—	—	17	29	4	—	380	665	95
		100/0	—	—	2	1	1	—	10	7	3
368	12/12	375/150	69	—	931	1380	180	—	1140	1600	400
374	12/12	400/200	13	9	49	63	12	—	1310	2300	320
		200/100	—	—	3	1	2	5	360	266	89
		100/0	—	—	—	—	—	—	13	10	3

thus be a conception with well defined limits in one direction as to the rise of the organisms. There is, however, small chances that the reverse process, descent, can so easily be limited and generalised.

From »Johan Hjort«s cruise in December 1928 a number of samples exist from several places on the Norwegian coast between 68°.30 and 62°.30 N. One station is from Vågsfjord just north of the Lofoten-area (357, 1′ N of Engenes Lighthouse, Dyrøy), one station from Skråven in the West Fjord in the Lofoten area (304), 2 from the southern section (367 and 368) and 1 from the Romsdal Fjord (374). All the stations have a homogeneous topographical situation in closed, deep fjords or between skerries.

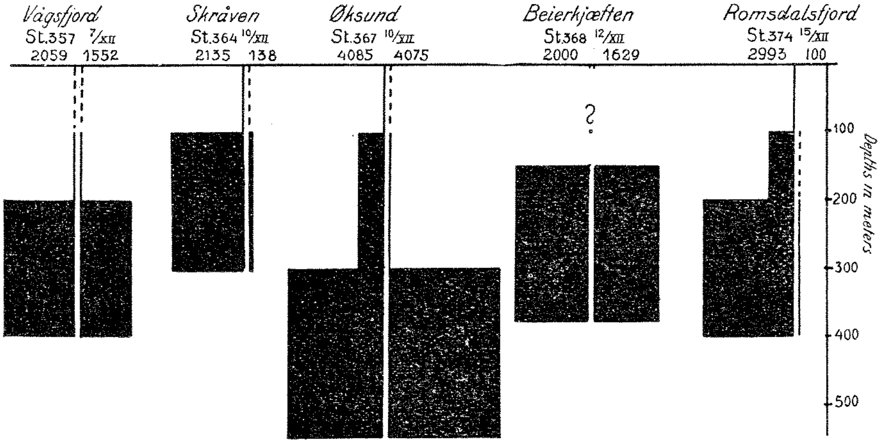

Fig. 27. Vertical distribution of *Calanus finmarchicus* (to the left) and *Calanus hyperboreus* (to the right) December 1928). (Se also table 16.)

The vertical distribution of the two species at that time will appear from Table 16 and Fig. 27. It will be seen from the table and the figure mentioned the two species in December show a very homogeneous distribution in relation to deepths of the hauls. The largest numbers are always found in the deepest hauls. It will also be seen that a distinct difference exist between the two species. *Calanus hyperboreus* is frequent only in those hauls which go down to more than 300 meters. *Calanus finmarchicus,* in the other hand, is also frequent in hauls which reach below 200 meters. The most frequent occurrence of the two species decidedly was at station 367 in a haul from 550 to 300 meters. Mainly because of this deep haul it will be seen that the total catch at this station (or catch per surface unit) is about twice the size of the other stations.

Nordgård's materials (Nordgård and Jørgensen 1905) also present an excellent material for the determination of the vertical distribution during the winter condition in Jannuary and February 1899. As will be seen from Nordgård's tables (l. c., PP. 25—36) the material gives splendid support to the results shown by the much smaller material here presented. Thus Nordgård says (p. 41), »It will be seen from these observations that in winter a really considerable number of this important plankton form may be found in the basins of the fjords.« We must therefore entirely agree with this statement regarding *Calanus finmarchicus.* On one point there is however a disagreement between Nordgård's account and that here presented. Nordgård, on the basis of stations taken after the first week of February, maintains that there are only a few individuals present at greater depths than 300 meters. In a later chapter where these conditions are subjected to a closer examination, we shall see that these stations of Nordgård do not belong to the winter condition. His material is derived precisely from the short period when the species is on the point of migrating to the surface. Nordgård's material must to a great extend be referred to the time when the winter condition is past, and thereby forms the very important connecting link which is almost lacking in all the material here presented. It affords an excellent opportunity of studying the vertical migration of *Calanus finmarchicus* and the time when this occurs. Reference is here made to Figs 29 and 30 prepared after Nordgård's material. Before 7/2 this material shows that *Calanus finmarchicus* is numerous at great depths. Before 17/2 they show that *Calanus hyperboreus* (which migrates upwards later) is numerous at great depths.

We may sum up Nordgård's observations and my own concerning the two species as showing that they spend the winter at great depths. *Calanus finmarchicus* extends below 200 meters with a rising concentration down to at least below 300 meters. *Calanus hyperboreus* in the winter condition has its vertical distribution at an even greater depth than *Calanus finmarchicus.*

The horisontal distribution in winter.

The direct result of the vertical distribution in winter is that the horisontal distribution is very limited. As mentioned on Page it is only in the inner half of the fjord and in the southern area that extensive depths of more than 300 meters is found at all. Large numbers of wintering animals of both species can therefore only be expected to be found in this inner part. One side of this question has already been well elucidated. The enormous numbers in these regions are a certain and frequently demonstrated phenomenon. Another side of the question is whether the two species are lacking in the shallow outer parts of the area.

It must here be pointed out that our knowledge concerning this is still deficient. In the first place it is impossible with the existing material to decide at what time during the winter the two species attain their maximum average distance from the surface. In order to decide this question a material collected continuously throughout the winter months at the same place is required.

Further it is a near problem to map out the horisontal distribution of the animals at the time when they have their greatest distance from the surface over a large area and endeavour to elucidate the question as to how far there is a relationship between the total catch from the bottom and upwards (or the catch per surface unit), and depth of bottom. It has already been mentioned in Chapter III how hauls in the Oslo Fjord at Drøbak give a catch of *Calanus hyperboreus* in large numbers by using a sledge which keeps the net at a distance of one or two meters from the bottom. The depth of the bottom where hauls were taken was 225—200 meters. If we compare this with the two figures 29 and 30 *a* and *b* one sees that. Nordgård's material also indicates a stronger concentration of the animals near the bottom in places where the depth is less than the maximum depth of distribution. We have here a possibility that must be taken into account in planning more thorough special investigations.

The only available material for the study of the horisontal distribution of the two species in winter is that given in Nordgård's tables (Nordgård and Jørgensen, 1905) pages 25 and 27. It will be seen from these that for the period 13/1—18/1 1899 there are 17 hauls from the northern area. The hauls are representative of all the depths occurring. In 4 deep hauls *Calanus finmarchicus* is indicated by c. (In order to form an idea of the dimensions of this sign reference is made to Fig. 29 *a* and *b* where the upper hauls are also indicated by c and which only contain about 1/10 of what was caught in the hauls marked cc). Two hauls of middle depth are indicated by r +, 9 hauls the majority of which were at a small depth are indicated by r and the species was not present in 2 hauls. From 31/1—1/2 Nordgård has 4 hauls in the northern area of which the catch in 3 is designated by + and in one by r.

Unfortunately there are a number of hauls from the days 13/2—15/2, 1924 which were lost by fire. It appears distinctly, however, from Sund's and my own journal from the collections made that year, that none of them contained *Calanus finmarchicus* with the exception of a very few specimens. *Calanus hyperboreus* did not occur.

Even if these problems cannot yet be regarded as sufficiently elucidated we have here a distinct contrast between the occurrence in the winter in the northern area and the occurrence in the winter in the inner and southern area. In the inner area and in the deep parts of the southern area there have been found in all investigations very considerable numbers of the two species at great depths. In the northern area, where these depths are lacking, a numerous occurrence of wintering animals has never been demonstrated.

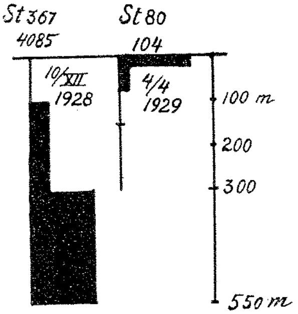

Fig. 28. Different types of vertical distribution of *Calanus finmarchicus* in the Lofoten area in December and April. The total numbers caught are in each case found beneath the number of the station.

The annual vertical migration of the two species.

As already mentioned the winter condition is interrupted by an annual vertical migration of the two species. The vertical distribution after 15/3 1929 and 1922 will appear from Figs. 32, 33, 39 and 40, and Tables 17—23. The vertical migration is thus confirmed by an extremely large amount of material. A characteristic instance of vertical distribution before and after the vertical migration of *Calanus finmarchicus* will be found in Fig. 28. It shows the vertical distribution at two quite adjacent stations, viz. 10/12 1928 and 4/4 1929.

It will be of considerable interest to investigate what the material available from the area in question can show regarding the time of vertical migration for each of the two species.

We should observe at once that at the commencement of the investigations in 1929 (15/3), *Calanus finmarchicus* has completed its vertical migration (see Fig. 32 *a*). On 4/4 1929 there are two stations from the inner part of the fjord (see 32 *a*) which show that *Calanus hyperboreus* at that time was on the point of completing its vertical migration. Investigations at the same stations 20/4—22/4 show that this species had completed its vertical migration so that practically speaking the whole stock was distributed between 75 meters and the surface.

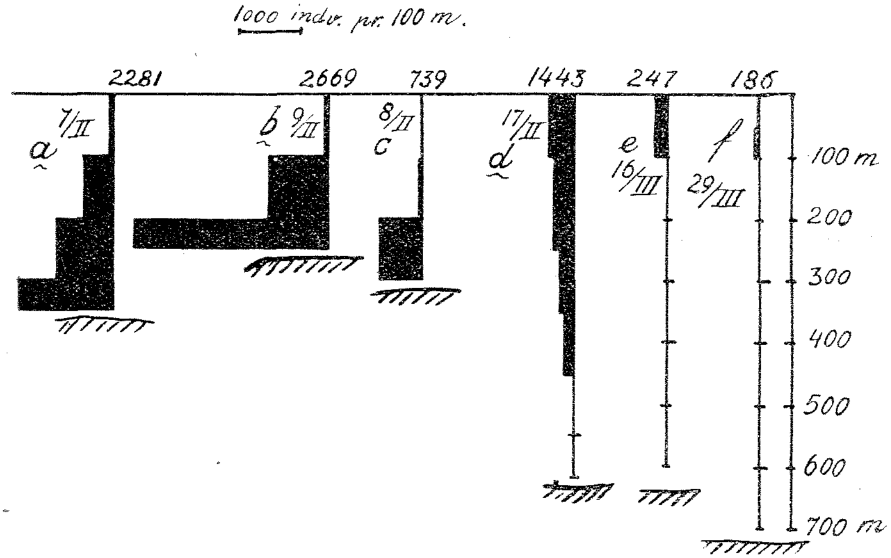

Fig. 29. Vertical distribution of *Calanus finmarchicus* in the inner area 7. February —29. March 1899 after Nordgårds tables (Nordgård and Jørgensen 1905 pp. 41—42). The total numbers caught are given for each station. None of the hauls were negative.

Calanus finmarchicus must thus migrate upwards before 15/3. We have drawn Fig. 29 according to Nordgård's tables (P. 41—42). In the first place we see here that the stations 7/2—9/2 are characteristic of the winter condition. Station 17/2 on the other hand shows a quite different picture. The occurrence is already greatest in the upper 100 meters, but there are still individuals left in the deep water. On 16/3 the occurrence in the upper 100 meters completely dominates as at station 103, 15/3, 1929. On 29/3 we have almost the same distribution as on 16/3. We thus find here a striking agreement between Nordgård's material from 1899 and that from 1929. There can be no doubt that the picture 17/2 as already mentioned on P. 90 cannot be used in a consideration of the distribution in the winter condition. It can only be regarded as a stage in the annual vertical migration.

At the same time in Fig. 29 we have figures giving the total catch per station. Station 8/2 forms an exception, in that it belongs to a branch of the Ofot Fjord and can thus not be representative of the main fjord. The two stations from the winter condition (7/2 and 9/2) show little depth, and are thus not directly comparable with the last 3 stations with their great depths. Nevertheless it will be seen how the total catch at the stations shows a considerable and regular decrease as by degrees the vertical migration proceeds. The vertical migration is accompanied by considerable changes in concentration, a circumstance which will be the object of further study in a subsequent chapter.

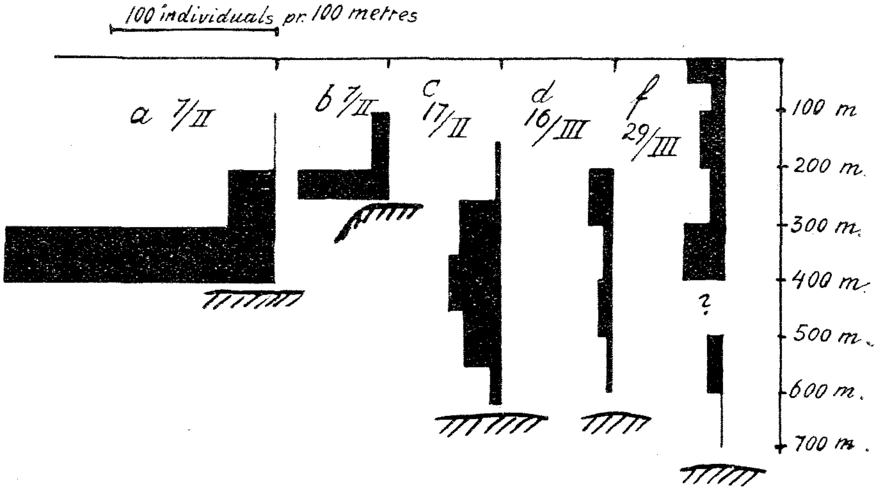

Fig. 30. Vertical distribution of *Calanus hyperboreus* in the inner area 7. February —29. March 1899 after Nordgårds tables (Nordgård and Jørgensen 1905 p. 42). One haul were the figures are lacking is marked? otherwise where no figures the haul was negative.

Calanus hyperboreus on 4/4 1929 had not completed its vertical migration (see Fig. 32 a). Nordgård's material is also for this species very suitable for studies of the time when vertical migration begins and its progress during the first period. It will be seen from Fig. 30 that as late as 16/3 no signs of vertical migration can be proved. On the other hand, on 29/3 we have a picture which fully corresponds to the picture 17/2 of *Calanus finmarchicus*, a considerable occurrence also in the upper layers of water, a diminished occurrence in the deeper layers. For this species too we have a surprising agreement for the two years 1899 and 1929, an agreement which allows us to follow directly the migration during the period, without paying regard to the year in which the collection was made. Because the material as regards depths is not very homogeneous it does not however permit of an exact study of changes in concentration during the vertical migrations. As compared with the foregoing species the material was collected too early for great changes to have taken place. This question will be further discussed in a subsequent chapter.

Finally, mention should be made of two factors which may cause a complication in the quantitative studies of these vertical migrations.

In the first place vertical migration will be accompanied by a change in the total catch at the stations. Individuals in the upper layers of water will drift away more or less completely as by degrees they migrate upwards. It is thus not possible to calculate directly the number of individuals which migrate upwards. We must assume that the catch in upper hauls is considerably less than the total number of individuals which have migrated up. The diminution in concentration at greater depths will on the contrary be easier to determine, and offers a favourable task for the further study of these conditions.

Periodic daily migrations of *Calanus finmarchicus* have been shown by a number of authors. (Esterley 1912, Russel 1928 and others). Determinations of these migrations in the Lofoten area during the time here dealt with have not been made, but the material submitted shows that the extent of migration is small.[1]). With (1915) asserted on the basis of 109 surface hauls from Kröyer's East Greenland Expedition that *Calanus hyperboreus* does not make periodical daily migrations, a result, however, which needs further confirmation by investigations at all times of the year and in different localities.

Stage Distribution in the Winter Condition.

The investigations of *Calanus hyperboreus* from the Oslo Fjord at Drøbak which are described in chapter III, show that during the autumn months there takes place a considerable migration of individuals to that locality from outside whilst the individuals which are to be found at Drøbak throughout the summer mainly consist of females which have spawned, survivors from spawning in the previous spring, the immigrants of the later autumn months consist of larval stages. The stage distribution and the changes made by immigration of the distribution of stages will appear from Table 15. It will be seen that the first virginal female was caught 4/11, and that by degrees this group

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[1]) Such determinations of daily vertical migrations has been carried out December 1931 an January 1932 near Tromsø and they show that the species in question do not undertake extensive daily vertical migrations during winter time.

is subjected to a great increase both as regards the total number and the percentage of the stock. The larval stages X and XI are, however, always numerous in the samples.

Table 16 shows the distribution of stages during the period 7/12—15/12, 1928 along a great part of the Norwegian coast. In the case of *Calanus hyperboreus* we notice a striking agreement with the results from Drøbak. The larval stages X and especially XI predominate in the samples. A number of females are present, and an examination of their oviducts shows that they are all virginal. All the samples in Table 16 belong to a period when the transition to females has commenced but is by no means completed. None of the females in Table 16 had eggs in the oviducts. It was not possible to find stages earlier than X in the samples. Males of *Calanus hyperboreus,* which at Drøbak were not found before 19/1, are only present in one instance and that at the last and most southerly station (374). This is the earliest occurrence of males which has ever been noticed on the Norwegian coast.

The interpretation of the entire picture of the distribution of stages of *Calanus hyperboreus* in Table 16 must be that the survivors after the spawning in 1928 (then 1 year old) has disappeared and a new generation from the 1928 spawning are predominant. The occurrence of females and males in small numbers is the first sign that we are approaching the time for the new generation 1929.

The young stages of *Calanus finmarchicus* also remain to a great extent throughout the winter. Thus Table 16 shows Stages X and XI and also a number of females. Males or stages earlier than X could not be found. As shown by a number of authors (Aurivillius (1928), Nordgård (1901), Farran (1927), Russel (1928) and Ruud (1929), this species has more than one spawning period a year. It is therefore likely that the larval stages of this species present in the samples are younger of age than the larval stages of *Calanus hyperboreus.*

Distribution of Stages before and during the Vertical Migration.

The most complete material for the period immediately before and during vertical migration of the two species will be found in Nordgård's paper. It gives, however, no detailed information regarding the distribution of stages, a feature which will be illustrated by material from 1922 and 1929. On the other hand we find a number of interesting details regarding the occurrence of the mature animals. Nordgård in two cases observed females of *Calanus finmarchicus* with firmly attached spermatophores. In addition he gives information regarding the occurrence of *Calanus hyperboreus,* males and females with eggs in the oviducts. Moreover he also in this species discovered females with spermatophores.

Nordgård has with great kindness placed at my disposal selected samples from his investigations. As, however, these problems will form the subject of a subsequent publication, they will only be briefly mentioned here. One sample 9/2, 1899 from Ofoten Fjord consisted of 24 males, 7 females with eggs in the oviducts, 1 female without eggs and also individuals of stages XI and X. The females with eggs showed these to be in various stages of growth. None of the females had spermatophores affixed to the genital segment. One very interesting case was an individual of Stage XI which had started development of eggs. I found similar conditions in individuals of this stage in the Oslo Fjord at Drøbak 19/1 1929. (See Chap. III). This circumstance is of considerable interest because it has otherwise never been observed in larval stages, in spite of the enormous numbers which have been examined. It indicates that the development of eggs is a process independent of moulting, probably also connected with certain definite physical conditions. Earlier in the year the larval stages and also the already fully developed females showed no signs of a development of eggs. A sample from 6/2 1899 from Tranøydypet contained 3 males, and 5 females all with eggs in their oviducts. In 4 cases the oviducts were filled with eggs at very early stage of development. Three of these females had spermatophores fixed to their genital segment. I have made the same observation from Drøbak in the Oslo Fjord, viz. that it is only in females with eggs at a very early stage of development that we find affixed spermatophores. As is known sperms in these crustaceans are transferred (see Giesbrecht 1921) from the spermatophore to a spermathecum in the genital segment, where they are kept until the eggs are laid and fertilised.

As mentioned on Page 77, it must be assumed that the longievity of the males is but very short. As will appear from Table 15 they have their maximum occurrence prior to the numerous occurrence of females. They also occurs earlier than the appearance of the great masses of females with eggs in the oviducts. In Nordgård's sample from 9/2 they formed quite a predominating group. It will be seen from Table 15 that they also predominated over females at Drøbak. I have never discovered similar conditions in the case of *Calanus finmarchicus.* I have never found such a high percentage of males as e. g. that given by Ruud (1929 P. 29). Farran (1927 P. 137) on the other hand found off the Irish Coast in Jannuary similar conditions for *Calanus finmarchicus* as those observed for *Calanus hyperboreus,* i. e. a number of males which quite predominated over the number of females.

On Page 27 mention is made of sample from »Johan Hjort« 1924 with one male and 38 females, only one of which had no eggs in the oviducts. 18/2. On 10/2 there were caught at Drøbak 291 females practically all of which had eggs in the oviducts. In addition we have Nordgård's numerous figures from the same period. As will be seen from the material of 1929, the phenomenon has practically speaking disappeared entirely at the beginning of April. Only a few of the individuals remaining in the deep water have any eggs left, but these few individuals is of no importance in relation to the whole stock. One mention by Nordgård of a female with eggs 2/4 1900 in a haul 330—0 meters from Skjærstads Fjord (southern area) presumably belongs to the same group, viz. females with eggs which have remained in the deep water. From these reports we should be able to conclude that the main spawning of the species takes place in February and March. It probably takes place after 15/2 and (see p. 74) is practically speaking finished 15/3. The time of spawning of this species thus coincides entirely with the time of the annual vertical migration. As will be seen later, these assumptions regarding the time of spawning and its dependence upon vertical migration are largely supported by the occurrence of the larval stages, the occurrence of females which have spawned and other conditions in the material from 1929.

As will be seen, the ripening of the genital organs of *Calanus finmarchicus* occurs much later than the vertical migration. As already mentioned, the vertical migration of this species takes place earlier than that of *Calanus hyperboreus,* whilst the ripening of the genital organs in the bulk of the stock takes place much later. Nordgård states that he saw two females with spermatophores, one on 7/2 1899 and another on 17/2 1899. These two instances, however, form such a small part of Nordgård's entire catch (see e. g. Fig. 29) that there is no reason to assume that the conditions in 1899 were essentially different from those in 1922, 1924 and 1929.

The spawning period of both species thus takes place after the winter condition. For the coming investigations when young stages earlier than X are present in the samples, we shall divide the stock into two main groups: the old generation and the new generation.

Causes of the vertical migration.

No doubt, the vertical migration both in *Calanus finmarchicus* and *Calanus hyperboreus* is an activ migration by the animals. The animals move directly from the deeper strata of high temperature and high salinity towards the surface strata of low temperature and low salinity. Vertical convection currents as proposed by Nordgård (Nordgård and Jørgensen 1905) cannot take place in a scale that would be necessary to explain the altered vertical distribution of the animals. The controlling factor, or factors, for the migration must be sought for in altered environmental conditions.

A complete discussion as to our present knowledges of the factors controlling the vertical distribution of pelagic animals cannot be given here. The problem has been made object to many discussions in the present literature. Only a few papers will be mentioned here.

Davenport (1897) divides the reactions of pelagic animals in two main groups. Phototaxy means that an animal moves in the direction of the light rays, posetively or negatively. Photopathy means that the animal moves towards the lighter spot, always positively. Under natural conditions photopathy thus always appears to be a movement in opposite direction of the sinking rate of the animals.

Ditlevsen (1906) shows that photophaty can be demonstrated experimentally in several organisms with pelagic habits. His material comprises pelagic freshwater crustacean (cladocera and copepods) and marine pelagic species, holoplanktonic animals and pelagic larvae. All these he proved to be photopathical. Control experiments simoultaneously showed that the species used were not phototaxical, but that they went to the lighter part of the aquarium independently of the direction of the rays.

Schulz (1927) has extensively and very carefully studied the different reactions towards light exhibited by lower crustacean. In a series of experiments he shows the different physiological effect of different intensities of light. The light intensities has for instance an effect upon number of offspring, increase in length between each moulting, pigmentation, building and destruction of fats, and number of movements. His statements thus includes factors which is very probably of importance both for photopathy and sinking rate of pelagic animals. Partly by means of different light intensities, partly by operations Schulz succeeded in proving that the much discussed »Augen — Antenne Reflex« has no physiological basis. The physiological effect of light he found can be measured by means of the heart rate, number of pulsations of the heart pr. minute. A direct irradiation of the eyes gave no effect, while direct treatement of the heart or the abdomen had an immediate effect. In a series of aquarium experiments Schulz confirmed the phenomenons of photopathy found by Ditlevsen. Curiously enough he calls them phototaxy and seems not to be aware of the fact that these phenomenons are quite different from the reactions which for instance he himself has found with regard to ultraviolett light. Ultra-violett rays, according to Schulz, produces a total change in the movements of the animals. They turn their heads down and flee towards deeper water. Schulz thus showed phototaxy towards ultra-violett rays in pelagic animals.

Borowski (1927) found that the reactions of daphnids towards light depends also upon the chemical conditions of the surrounding water, and upon the composition of the light rays. A solution of different poisons, especially acids and among them CO_2 proved to cause a change in the heart rate and thereby a change in the photopathical reaction.

Mac. Arthur and Baillie (1927) shows that the heart rate in *Daphnia magna* is different in male and female. The heart rate depends upon the temperature. Mac. Arthur and Baillie gives very few details, but they are probably right in assuming that the heart rate is an important factor for every vital function.

Harvey (1929) examined the heart frequencies and the reactions towards light in *Calanus finmarchicus*. He found that the heart rate depends upon temperature and the quality of light. Strong light causes a decrease of the heart rate, an effect strong enough to be lethal in cases of long exposure. Direct sunrays (which in his case passed through thick glass-walls) had the strongest effect. Blue rays act strongly, while read and green rays have much lesser effect. Harveys work seems to me to be of very great importance for understanding the effect of light on pelagic animals, both regarding the daily vertical migrations and the annual vertical migrations. His experiments has prooved that the animals may use several days before they have become adapted to new environmental conditions. Thereby he shows that the many experiments of only a few minutes duration hardly can be applied to animals under natural conditions.

This short summary of some facts regarding the reactions towards light and temperature present in lower pelagic crustacean certainly is of importance for understanding the causes underlying the phenomenon of the yearly vertical migrations of the two species *Calanus finmarchicus* and *Calanus hyperboreus*. Many factors will have to be taken under consideration, and in details our knowledge both regarding the reaction and the sinking rate of the species is however as yet very deficient.

We must be content with the result that the yearly vertical migration of the two species seems to be a photopathical phenomenon. The animals moves towards the stronger light in early spring and the stimulant for this movement increase as they approach the surface layers. Possibly this explains why the vertical migration is completed in such a short time both by adult individuals and larvae?

In any case, it must be taken for granted that the light intensity represent the only factor which can be subject to considerable changes, practically speaking at the same date every year, at the end of the winter condition. In this connection it is of interest to recall the fact that *Calanus finmarchicus* spend the winter months in lesser depths, and start its vertical migration at an earlier date than *Calanus hyperboreus*. At present it is only from the Lofoten area that the vertical migration is known in details. As will be shown later on, spawning starts earlier at Møre than in Lofoten in both species. Whether this applies also to the vertical migration is a question not yet settled.

CHAPTER V.

Cessation of the Winter Condition and the Period of Spawning in *Calanus finmarchicus* and *Calanus hyperboreus*.

The material from »Johan Hjort's« cruise in the Spring of 1929 was collected according to a principle differing from that of the previous collections. A general investigation on the basis of material from 1922, 1923 and 1924 gave in the case of *Calanus hyperboreus* the remarkable result that there occurred both individuals of the old and of the new generation. Neverthless spawning of the species could not be found, although the material from 1924 was collected both before and after spawning time. In other words it was clear that the material before 1929 was not representative of the spawning area and thus of course could give no information regarding the situation of the spawning area and the time of spawning. In addition these materials were not representative for all depths occurring in the area. In the case of *Calanus finmarchicus*, however, the materials were more representative. Thus the material from 1922 proved quite suitable for studies of the spawning conditions of this species, but even here it was found, before the material from the autumn of 1928 and spring of 1929 was available, that we lacked very important links in the chain that was necessary in order to obtain a full elucidation of the questions raised.

The plan for the collections in 1929 was in brief as follows: — The collection of zooplankton was to be concentrated over a longitudinal section from the inner end of Ofot Fjord to the outermost parts of the West-fjord. If possible this section was to be investigated 3 times, before the commencement of the flowering of the plankton and the vertical migrations, during the vertical migration and last of all at the end of April before the conclusion of the cruise. The collections should as far as possible be standardised so that there would be available comparable tables and figures for the various periods. Of course such material cannot be as schematic as might be desired. The weather conditions give rise to obstacles, and in addition the investigation of zooplankton was a minor object of the cruise. Thus the main spawning of *Calanus hyperboreus* is unfortunately again not represented. A vertical mapping of the spawning of this species is thus impossible. But on the other hand the group of females which have spawned and also the new generation is so fully represented, and so sharply defined as to its distribution, that it is not a difficult matter to map the spawning of this species in its main features as regards its horisontal extent.

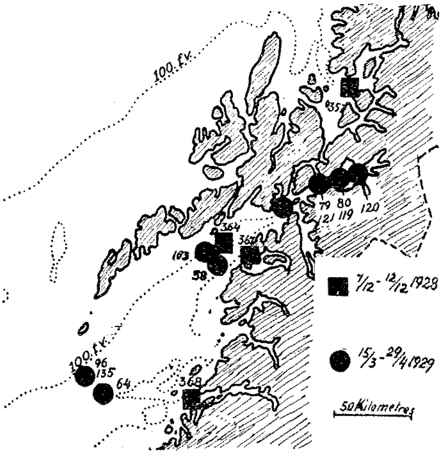


Fig. 31. Map showing the situation of the stations in the autumn 1928 and spring 1929.

The bulk of the material was collected in nets of 72 diameter and silk 0 and 8 (net 72/8). At some stations investigations were also made with nets of diameter 45 cms and silk 25 (net 45/25).

The distribution and composition of stages of the old generation will appear from Tables 17 and 18. That of the new generation will appear from Tables 19—22.

On the basis of these tables there have been constructed the two figures 32 and 33, *a* and *b*. Figures 32 and 33 *c* show the course of the isotherms during the period of the investigations. The observations can be summarised as follows: —

Tab. 17. Numbers and stage distribution of *Calanus hyperboreus* and *Calanus finmarchicus* of the old generation in samples from nets 72/8 from spring 1929. The situation of the stations is shown in fig. 31. The number of individuals of the new generation at the latest stations is given in brackets.

			Calanus hyperboreus					*Calanus finmarchicus*					
Station	Date	Depth	♀	Number of females along 100 meters of houl	♂	XI	X	♀	Number of females along 100 meters of houl	♂	XI	X	Total
58	15/3	100/0	—	—	—	—	—	345	345	139	104	35	623
64	19/3	150/75	—	—	—	—	—	7	10		3		10
		75/25	—	—	—	—	—	6		—	—	—	6
79	4/4	300/150	212	142	1	141	5	8	5		4	3	15
		150/75	18	24	—	8	1	—	—	—	—	—	—
		75/25	39	78	—	27		12	24	1	—	—	13
		25/0	17	68	—	16		39	156	—	4	—	43
80	4/4	300/150	1000	666	—	700	21	1	—	2	—	—	3
		150/75	39	29	—	50	3	6	4	—	—	—	6
		75/25	150	300	—	144	—	9	18	3	3	—	15
		25/0	112	448	—	91	—	65	260	3	12	—	80
96	12/4	250/150	3	6	—	—	—	5	10	—	—	—	5
		150/0	6	4	—	1	—	96	67	1	9	—	106
		75/0	1	1	—	2	1	91	120	2	16	—	109
103	13/4	250/150	39	39	—	28	—	4	4	—	—	—	4
		75/0	27	36	—	44	—	316	420	4	45	6	371
119	20/4	500/300	5	3	—	7	—	1	—	—	—	—	1
		300/150	16	11	—	3	—	2	—	—	—	—	2
		150/0	144	96	—	40	—	36	24	—	2	—	38
121	22/4	300/150	29	19	—	17	2	2	2	—	1	—	3
		150/75	1	1	—	—	—	2	2	—	—	—	2
		75/0	223	300	—	154	—	56	74	—	4	—	60
135	29/4	150/75	29	40	—	24	(6)	30	40	13	13	—	56
		75/25	20	40		5	(24)	48	96	24	—	(1065)	72
		25/0	—	—	—	—	—	1	4	1	(400)	(2000)	2

Tab. 18 see pag. 106.

Tab. 19. Numbers and stage distribution of *Calanus finmarchicus* of new generation from nets 72/8 spring 1929. The situation of the stations is shown in fig. 31. The numbers given in brackets are the total numbers of both species investigated. x means that the stage has been observed in small numbers which have not been counted.

St.	Date	Depths	Eggs	I & II	III	IV	V	VI	VII	VIII	IX	X	Total	Number determinated
58	15/3	100/0	—	—	—	—	—	—	—	—	—	—	—	—
64	19/3	150/75	—	—	x	x	—	—	—	—	—	—	—	4
		75/25	—	—	50	—	50	—	—	—	—	—	100	2
79	4/4	300/150	—	—	x	—	x	—	—	—	—	—	(80)	2
		150/75	160	—	—	—	—	—	—	—	—	—	160	7
		75/25	360	—	—	x	—	—	—	—	—	—	(440)	21
		25/0	3600	x	530	795	—	265	—	—	—	—	5190	24
80	4/4	300/150	265	—	—	—	—	—	—	—	—	—	(345)	2
		150/75	—	—	—	—	—	—	—	—	—	—	(133)	—
		75/25	—	—	—	—	—	—	—	—	—	—	(80)	—
		25/0	4800	x	820	224	74	—	—	—	—	—	5918	29
96	12/4	250/150	420	—	x	x	x	—	x	—	—	—	730	48
		150/0	2340	165	x	x	x	x	600	33	33	—	(8806)	94
		75/0	5850	458	4650	3070	1050	1050	457	262	65	—	16912	138
103	13/4	250/150	80	—	—	—	—	—	—	—	—	—	(120)	4
		75/0	13900	1940	1730	653	1940	213	310	—	—	—	20686	238
119	20/4	500/300	—	—	—	—	—	—	—	—	—	—	—	—
		300/150	—	—	—	—	—	—	—	—	—	—	(67)	—
		150/0												
121	22/4	300/150	—	—	—	—	—	—	—	—	—	—	(134)	—
		150/75	—	—	—	—	—	—	—	—	—	—	—	—
		75/0	1440	160	845	153	230	192	115	—	—	—	3135	69
135	29/4	150/75	—	—	—	—	—	—	—	—	—	—	(275)	—
		75/25	1600	120	360	240	360	960	192	244	644	1005	5481	77
		25/0	4600	800	1760	5280	6160	12760	9600	4600	4600	2000	13160	272

Tab. 20. Numbers and stage distribution of *Calanus hyperboreus* of new generation from nets 72/8 spring 1929. (See also Tab. 19).

25

St.	Date	Depths	Eggs	I & II	III	IV	V	VI	VII	VIII	IX	X	Total	Number determinated
58	15/3	100/0	—	—	2350	—	—	—	—	—	—	—	2350	29
64	19/3	150/75	—	—	—	—	—	—	—	—	—	—	—	—
		75/25	—	—	50	—	—	—	50	—	—	—	100	8
79	4/4	300/150	x	x	x	—	x	—	—	—	—	—	(80)	29
		150/75	—	—	—	—	—	—	—	—	—	—	—	—
		75/25	—	—	x	x	x	—	—	—	—	—	(440)	4
		25/0	—	x	1030	8750	17500	530	—	—	—		27810	105
80	4/4	300/150	x	x	x	x	x	—	—	—	—	—	(80)	23
		150/75	x	x	—	—	—	—	—	—	—	—	(133)	7
		75/25	—	—	x	x	x	—	—	—	—	—	(80)	8
		25/0	—	—	1700	1340	1110	—			—	—	4150	56
96	12/4	250/150	—	—	—	—	—	—	—	—	—	—	—	—
		150/0	—	—	—	—	—	—			—	—	—	—
		75/0	—	—	—	—	—	—	67	67			134	4
103	13/4	250/150	—	—	—	—	—	—	—	x	—	—	(40)	2
		75/0	—	—	—	—	427	2130	1620	75			4252	101
119	20/4	500/300	x	x	x	—	—	—	—	—	—	—	—	13
		300/150	x		—	—	—	100	—	—	—	—	100	8
		150/0	—	—	—	—	50	800	100	—	—	—	950	19
121	22/4	300/150	x	x	x	67	67	—	—	—	—	—	134	17
		150/75	—	—	—	—	—	—	—	—	—	—	—	—
		75/0			153	191	305	267	1220	805	—	—	2941	71
135	29/4	150/75	—	—	—	—	—	—	—	—	—	—	(275)	—
		75/25	—	—	—	120	360	240	96	122	38	24	900	53
		25/0	—	—	—	—	440	880	600	—	x	—	1920	7

Tab. 18. Numbers and stage distribution of *Calanus finmarchicus* and *Calanus hyperboreus* of old generation in samples from nets 42/25 spring 1929. The situation of the stations is shown in fig. 31.

			Calanus hyperboreus				*Calanus finmarchicus*				
Station nr.	Date	Depths	♀	Number of females along 100 meters of the haul	XI	X	♀	Number of females along 100 meters of the haul	XI	X	Total
119	20/4	150/75	4	18	3	—	3	14	1	—	4
		75/25	3	21	2	—	—	—	1	—	—
		25/0	62	855	35	—	49	670	6	2	57
120	20/4	75/0	20	92	—	—	28	128	4	2	34
121	22/4	75/25	69	469	27	—	10	69	3	1	14
		25/0	49	672	18	1	18	248	5	1	24

Tab. 21. Numbers and stage distribution of *Calanus finmarchicus* of new generation in samples from nets 42/25 1929. (See also Tab. 19).

St.	Date	Depths	Eggs	I & II	III	IV	V	VI	VII	VIII	IX	Total	Number determinated
119	20/4	150/75	920	345	50	25	—	—	—	—	—	1335	14
—	—	75/25	1930	1240	—	—	—	25	—	—	—	3195	17
—	—	25/0	21100	4800	1500	1200	—	900	—	—	—	29500	51
120	20/4	75/0	3200	2300	173	—	231	462	173	—	—	6539	29
121	22/4	75/25	4930	550	4370	225	225	225	—	—	—	10525	39
—	—	25/0	9380	2140	5900	1390	2080	2830	695	—	—	25415	83

Tab. 22. Numbers and stage distribution of *Calanus hyperboreus* of new generation in samples from nets 42/25 spring 1929. (See also Tab. 19).

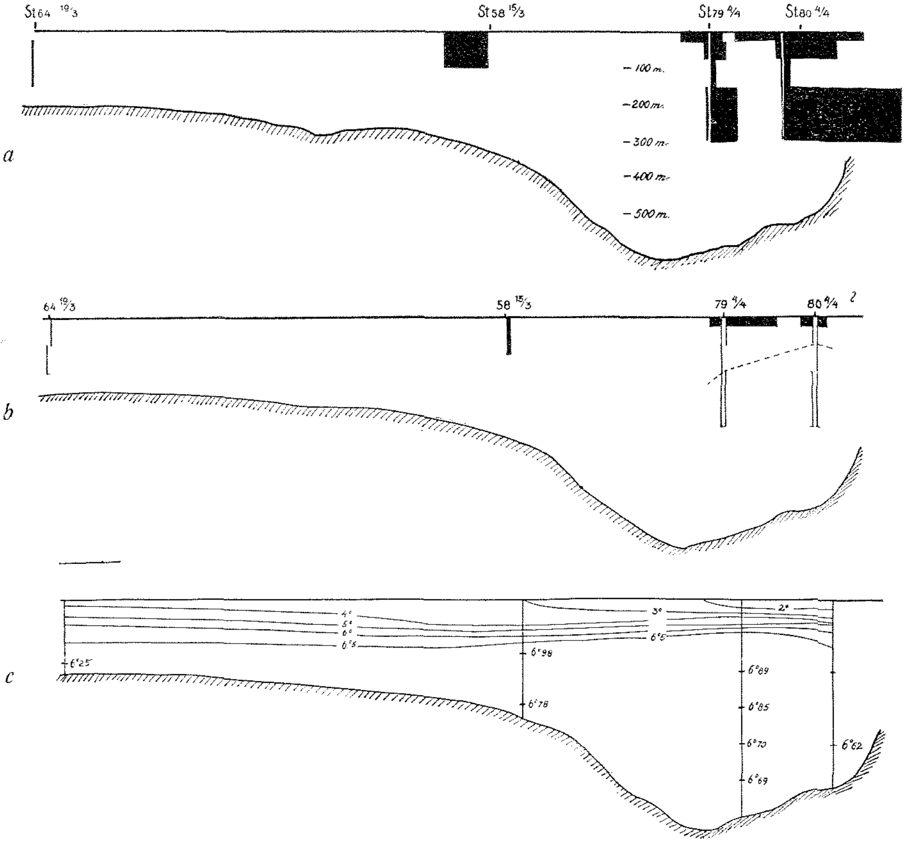
St.	Date	Depths	I & II	III	IV	V	VI	VII	VIII	Total	Number determinated
119	20/4	150/75	x	—	—	x	75	25	—	100	6
—	—	75/25	—	—	—	277	—	32	—	309	18
—	—	25/0	—	—	—	300	11500	8100	1000	20900	54
120	20/4	75/0	x	—	173	403	633	1670	179	3058	53
121	22/4	75/25	--	—	—	276	1380	2480	—	4136	30
—	—	25/0	—	x	415	1240	2900	4240	830	9625	43

Tab. 23. Numbers and stage distribution of *Calanus hyperboreus* of new generation from nets 42/25 spring 1929. (See also Tab. 19).

Station	Date	Depth	III	IV	V	VI	VII	VIII	IX	X	XI	Total	Number determinated
4	18/3	50/5	22	207	38	—	—	—	—	—	—	267	35
44	4/4	70/50	575	—	290	290	850	—	—	—	—	2005	28
		50/10	—	115	—	228	695	115	—	—	—	1153	12
		10/0	—	—	—	—	—	—	—	—	—	0	0
68	11/4	75/50	680	—	—	1700	2130	332	263	—	—	5110	36
		50/10	—	1660	415	415	250	—	125	—	—	2865	11
		10/0	—	—	—	—	—	—	—	—	—	0	0
76	24/4	50/10	210	—	—	105	18	—	—	43	8	384	24

Vertical distribution of the old generation of *Calanus hyperboreus* 1928 and 1929.

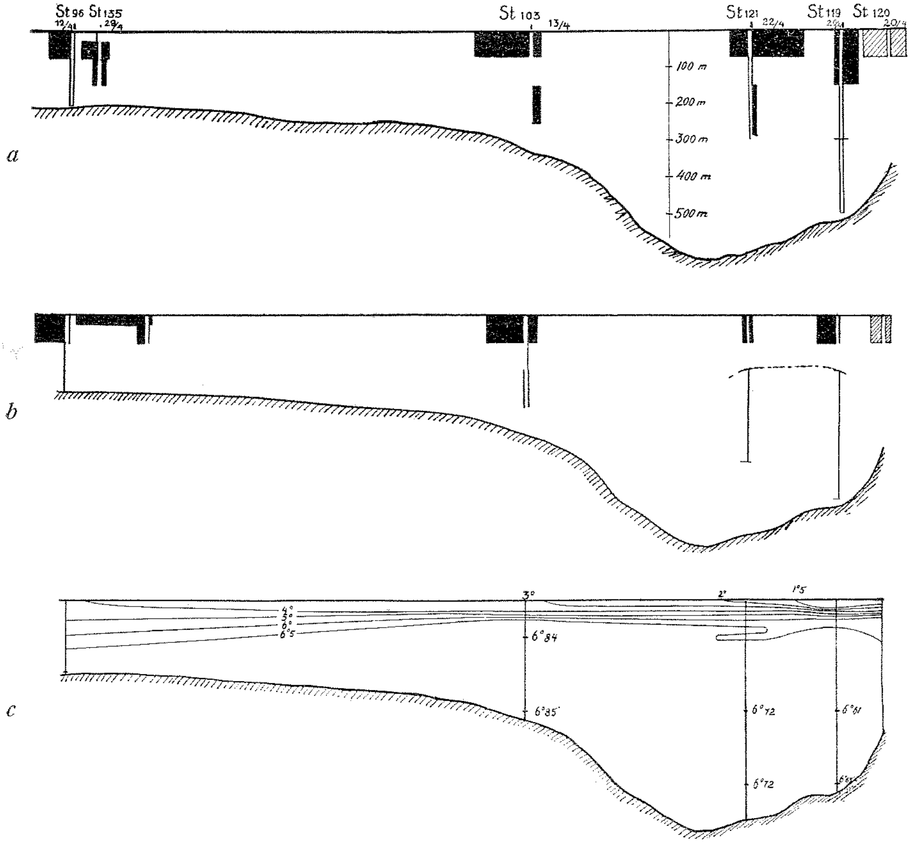
The old generation of *Calanus hyperboreus* in the inner area of the 2 stations 79 and 80, 4/4 1929, are found both in the deep layers of water, 300—150 and the overlying layers. The picture thus obtained entirely corresponds to that shown by Nordgård's material from 1899. Thus figure 29 *d* shows *Calanus finmarchicus* 7/2 1899 in the



Figs. 32 *a*, *b* and *c*. Longitudinal section of the West Fjord 15. March—4. April 1929. *Calanus finmarchicus* is marked on each station to the left, *Calanus hyperboreus* to the right. *a* number of females per 100 meters, *b* numbers of larval stages per 100 meters, the hatched line gives the upper limit of occuring of egg of *Calanus hyperboreus*, *c* shows the distribution of temperatures. Station 80 has in *a* been moved somewhat to the left because of the space. The situation of the stations will appear from figure 31, further reference is also made to table 16. All hauls were made with nets 72/8.

course of upward migration. Figure 30 *f* shows *Calanus hyperboreus* 29/3 1899 in the course of upward migration.

When the two stations 79 and 80, 1929, in the inner area 20/4—22/4 were investigated a second time (stations 121 and 119) we could form a good idea of a complete vertical migration. The best conception of the vertical distribution at that time is formed from Table 18, the hauls 45/25 being more specified than those which form the basis of Figure 33 *a*. It will be seen from Table 18 that the most numerous occurrence of the species is in the water between the depth of 25 meters and the



Figs. 33 *a*, *b* and *c*. Longitudinal section of the West Fjord 12. April—29. April 1929. *Calanus finmarchicus* is marked on the station to the left, *Calanus hyperboreus* to the right. *a* indicates number of females per 100 meters, *b* indicates number of larval stages per 100 meters, the hatched line gives the upper limit of occuring of egg of *Calanus hyperboreus*, *c* shows the distribution of temperature. The station 135 has been moved somewhat to the right because of space. The situation of the stations will appear from fig. 31. The shaded haul was taken with net 45/25 and have been adjusted to diameter of 72 cms. The other hauls were made with nets 72/8. Reference is also made to table 17.

surface. In one case (Station 121), however, there are also considerable numbers in the layers between 75 and 25 meters. At that time the species can be characterised as an entirely surface form in the inner part of the fjord. It shows a distribution entirely corresponding to the characteristic distribution of *Calanus finmarchicus* as shown in Fig. 28.

Fig. 33 *a* shows that the old generation of *Calanus hyperboreus* at the second investigation of the area in the inner part of the fjord (Stations 96, 103 and 135) is more deeply distributed. A clearer picture of this is given, however, by the material from 1922 where the outer parts of the fjord are more fully represented. In 18 hauls between 10 meters and the surface 9 individuals of the old generation of *Calanus hyperboreus* were caught. (On an average 0,5 per haul). In 28 hauls 50/10 meters there were 7 specimens, an average of 0,25 per haul. In 10 hauls 75/50 meters there were 21 specimens, an average of 2,1 per haul. In 15 hauls 100/50 meters there were 18 specimens, an average of 1,2 per haul. In 2 hauls 150/100 there were 15 specimens, an average of 7,5 per haul. The observations extend over the period 19/3—24/4 and chiefly comprise individuals which have drifted out to the northern area after vertical migration. (See Fig. 41). The material from 1929 and 1922 when combined shows that the old generation after vertical migration is more deeply distributed in the outer parts of the fjord than in the inner parts. It seems highly probable that the specimens sinks into the deep water again shortly after the vertical migrations on account of the higher temperature at the surface layers in the areas into which they have been transported.

Changes in Concentration of the Old Generation of *Calanus hyperboreus*, 1929.

Figure 28 shows the characteristic change in concentration of a species which takes place immediately after the annual vertical migration. We shall see how the species when it has its distribution in the great depths gives a very high total catch in hauls from the bottom and upwards. It we compare the material from the autumn 1928 with that from the spring of 1929, we find this phenomenon everywhere and in all cases the same order of dimensions. Figure 29 gives us an opportunity of following the various phases, even though the last phases are represented by stations where the bottom depth is great and where we should therefore expect large total catches.

A comparison between Figs 32 and 32 a at once shows us that in the total catch of the old generation of *Calanus hyperboreus* there has taken place a similar change in concentration. If we include the other stages, we obtain (according to Table 17) the following figures for the two stations. (79—121 and 80—119): At the first investigation 4/4 collected from the bottom upwards, 2972 individuals. At the second investigation 20/4—22/4, 641 individuals.

The high figures of the first time investigation are not confirmed at the adjacent stations or by other hauls. The low figures at the second time investigation, on the other hand, are confirmed by the hauls 45/25 at station 120 a little farther in the fjord (see Fig. 33 a) and hauls at the same stations (see Table 18).

As the difference in the catch here is of very considerable dimensions and as it is a phenomenon which has always appeared where we have material showing changes in concentration after vertical migration, we should be able to state the following: — The stock of the old generation of *Calanus hyperboreus* in the inner area has diminished during the course of 16—18 days to one fifth. Four-fifths of the stock have been carried away by currents in the upper layers of water, and must be sought for in other areas.

Horisontal distribution of the old generation of *Calanus hyperboreus,* Spring of 1929.

It has already been mentioned on pages 112—113 that *Calanus hyperboreus* was lacking in Nordgård's representative material from the northern area in Jannuary and the first half of February 1899. The species was also lacking during the investigations at the same place in Jannuary and February, 1924, and likewise in a section taken from Røst in a north-westerly direction out to the edge. The first catch of the species in vertical hauls was at the close of the investigations on 11/4 at Station 172, the same place as Station 58 in 1929, where in a haul 75/20 meters there were caught 36 females which had spawned and 31 of Stage XI. (A very numerous occurrence). We can with certainty conclude that the species was lacking in the northern area before the vertical migration.

It will be seen from Figure 32 *a* that before the completion of the vertical migration the species is only present in the inner area. At Station 58 15/3 the old generation was entirely lacking (whilst the young stages of the species and the old generation of *Calanus finmarchicus* were numerously represented). Thus we can assert that at the beginning of the investigations in 1929 the old generation of *Calanus hyperboreus* was only found in the inner part of the area investigated over the deep parts of the fjord and was here very numerous.

It will be seen from Fig. 33 *a* that in the outer part of the fjord the species was present at the second investigation of the longitudinal section. There can be no doubt that we have here a part of the stock which has drifted away from the winter quarters after the vertical migration. We will not here take into consideration the question whether these individuals in the outer part of the area came from that part of the inner area which is here investigated or from more southern winter quarters.

Vertical Distribution of the New Generation of *Calanus hyperboreus,* 1929.

Figures 32 and 33 (see also Table 18) for the last investigations 1929, show that the vertical distribution of the new generation of *Calanus hyperboreus* is quite different to that of the old generation. Whilst the latter was distributed in greatest numbers in hauls below 150 meters in the first time investigations of the inner area, the new generation was practically speaking only found between 25 meters and the surface. At one station one sees that the new generation can also be numerous in hauls between 75 and 25 meters, but only in less than half the numbers of those found above 25 meters. We cannot decide from the existing material whether this is due to special conditions at spawning. As already mentioned, spawning is only sparingly represented in the material. Nor do we know whether the spawning stock has great vertical daily migrations during the period when it disappears from the deep water and gets its chief occurrence in the surface layers. In Chapter III it is stated that external conditions may have a stimulating effect upon the rate of spawning, and we are fully justified in raising the question whether the main spawning only takes place in the coldest surface layers, and whether it is also dependent upon the changes in light during day and night. We must of course also reckon with the possibilities of the early larval stages being themselves able to change their place of abode during the first time of their existence.

Changes in Concentration of the New Generation of *Calanus hyperboreus* in the Spring of 1929.

In investigating the changes in concentration in the old generation we can of course assume that we are dealing with a constant stock. Under reference to the coming chapter on the distribution of stages and the occurrence of spawning we may here mention beforehand that also as regards the new generation we are dealing with a constant group. That part of the spawning which remained at the commencement of the investigations is of such a negligible size that it can be entirely ignored.

During the very short time in consideration here also the mortality can be ignored.

The two groups, the old and the new generation of *Calanus hyperboreus* thus both offer a specially favourable opportunity for studying the changes in concentration and the drifting of the organisms with the ocean currents. As will be seen later on, *Calanus finmarchicus* is in no way so favourable for that kind of study. In addition *Calanus hyperboreus* offer particularly favourable circumstances because the old and the new generation each has a different vertical distribution. In other words we can decide whether the question regarding changes in concentration is dependent upon the depth of distribution.

At the first investigation in the inner area 4/4, 1929 there was a total catch at the two stations 79 and 80 of 31 960 individuals of the new generation of *Calanus hyperboreus.* At the second investigation 20/4—22/4 there were 3125 individuals in the same hauls from the bottom upwards. In this last investigation the numbers were also checked by hauls 45/25.

We thus have here a change in concentration on a far larger scale than that for the old generation. Only onetenth of the stock remains. Nine-tenths of the stock have drifted away and must be sought for in other parts of the area of distribution.

In many respects Station 58 15/3, 1929 is remarkable. The catch of the old generation of *Calanus finmarchicus* is almost twice the size of those in the other hauls of the same year. The numerous larval stages of *Calanus* present were found, however, to belong to *Calanus hyperboreus,* a species which in the stage of the old generation was lacking in the sample. (See Table 17). This however is simply explained by the data already submitted. The station lies outside the winter quarter of *Calanus hyperboreus* and was taken at a time when this species had by no means completed its vertical migration. The drifting with the upper layers of water outwards is still of minimum dimensions. The larval stages on the other hand, which always remain in the upper layers, are in drift outwards. *Calanus finmarchicus* which completes its vertical migration more than one month before the other species and whose vertical distribution after migration practically speaking coincides with that which we found for *Calanus hyperboreus* in the new generation, shows a mass occurrence. May we not simply use the new generation of *Calanus hyperboreus* as an indicator of the origin and drift of the old generation of *Calanus finmarchicus?*

Just one more remark before we leave the discussion of these questions of the distribution of *Calanus hyperboreus*. It will appear from Fig. 33 a that in the second investigation of the outer part of the fjord we found large numbers of *Calanus hyperboreus* of the new generation. These are not, like individuals of the old generation which are carried there simultaneously more deeply distributed here than in the inner area.

Distribution of Stages of the Old Generation of *Calanus hyperboreus* Spring 1929.

In the coming chapter on the rapidity of development of the new generation of *Calanus hyperboreus* all the observations of that group will be given. It will appear from Table 20 and Fig. 34 that at the beginning of the investigations 15/3 no later stages than III were caught. On 4/4 there were not caught later stages than VI. Stage X was not observed until 29/4. We shall also see from Table 23 and Fig. 35 that the conditions in 1922 were very nearly the same. It will be seen from Table 15 that the winter stock at Drøbak as late as 10/2 1929 consisted of a very considerable group of stages X and XI. In the essential points this agree with the material from the autumn of 1928. It is therefore beyond doubt that all the stages X and XI which we find at the beginning of the investigations 1929 and 1922 and 11/4 1924 are to be referred to the old generation.

The distribution of stages in the spring of 1929 will appear from Table 17. With net 72/8 there were totally caught 63 individuals of Stage X, 1308 of Stage XI, 1 male and 1788 females.

The male caught is the latest occurring male which has ever been caught off our coast. The material was thus with this exception collected after the occurrence of males.

The oviducts in the females captured were carefully examined. 1768 females could be referred to the group females which had spawned. 20 females had still many or a few eggs left in the oviducts.

In the chapter om changes in concentration of the new generation of *Calanus hyperboreus* we have already mentioned that the main spawning were already finished at the first investigation of the inner area. This contention is further confirmed by the numbers given. As will be seen, only 1 % of the females have not completely spawned. In addition in most of the females which still had eggs there only comprised a very few of the total numbers. It thus amounts to merely some few per thousand of the new generation which can still be reckoned with as a possibility, and changes of this dimension will not play any part in the changes in concentration observed.

There are however other sides of these phenomena which will be of interest in the consideration of the conditions of propagation of this species.

At Station 79 there were caught in one haul, 300/150 meters, 212 females of which one had 4 eggs left in the oviducts and 1 had 38 eggs. The remainder of the females had spawned all their eggs and the females in the hauls higher up had also spawned all their eggs. At Station 80 in one haul 300/150 1000 females were caught. Among these 1 had probably the whole number of eggs left, 1 had 60 eggs and 10 had a few eggs left. The other females were completely spent. In 1 haul 75/25 meters at the same station 1 female was caught with 1 egg left. Otherwise all the females in the upper layers of water had finished spawning. At Station 96 in a haul 200/150 meters there were caught 3 females of which 1 had two or three eggs in the oviducts on each side. At Station 103 there were caught 39 females of which 1 had several eggs left. At Station 119 5 females were caught in a haul 500/300 meters. 1 had spawned, 1 had all the eggs left, 1 had many eggs irregularly distributed in the ovary in a manner which has never been observed before, 1 female had eggs in period of growth left in the anterior part of the oviduct, 1 female had undeveloped eggs during the growth period and a few fullgrown as a remainder in the whole oviduct. In a haul 300/150 meters at the same station there were caught 16 females of which 1 had 54 eggs left. Otherwise all the females caught during the investigations given in Tables 17 and 18 had spawned.

The question here presents itself, whether at that time there still took place a ripening of the sex organs, so that the group of females with eggs in the oviducts was still in formation, or whether we have before us a number of the stock with which spawning has not had the same course as with the main stock.

18 of the 20 females with eggs in the oviducts had fully developed eggs only. 1 had only eggs in the growth period in the front part of the oviducts and not, as has always been the case in individuals observed in the act of developing eggs, throughout the whole oviducts. 1 individual had undeveloped eggs in the whole oviduct in addition to two eggs left after spawning, exactly the same picture as that observed in spawning individuals in culture (see p. 80). The most important factor, however, in considering the questions raised is that none of the females observed with eggs showed early stages of growth, eggs which had recently entered the oviduct from the ovary. In addition we must take into consideration the fact that only one male was present in the material.

We thus arrive at the conclusion that development of animals ready to spawn no longer took place in the stock investigated in spite of the existing excess of young stages.

The next question is whether spawning actually took place. In practically all cases the pictures shown by the investigations were exactly the same as those observed in spawning animals in culture. A more certain elucidation of the question is, however, given by the fact that the new generation was different in these deep hauls where females with eggs were found from that of the hauls from higher layers of water where females with eggs were not found. As will appear from Table 20 it is just in the majority of these deep hauls that there were also found eggs of the species, and the two stages I and II which were lacking in the higher layers of water as early as 15/3.

We thus arrive at the result that after the main spawning of *Calanus hyperboreus* were finished in 1929, there took place in the deep water amongst animals which had not finished their vertical migration a delayed spawning during the whole time of the investigations.

We have here before us the remarkable fact that the various parts of the stock spawn at different rates. That part of the stock which migrates upwards spawns at high rates, and the minor part which does not migrate upwards with the others spawns very slowly. Many reflections will occur in considering such a phenomenon. Some of these will be mentioned here, even though they may be of a hypothetical nature, because they will be of importance for further problems.

The preliminary investigations which are mentioned on Page 79 also appear to show that differences in environment influence the rate of spawning. Even though the experiments hitherto conducted are deficient, the differences in dimensions observed are such that they exclude chance. In addition we know from a number of works on lower crustaceans how great is the influence of light and temperature upon all the physiological processes investigated (Schultz 1927, Harvey 1929, Brown 1929 and many others). The results of the experiments mentioned was that low temperature and certain conditions of light stimulate the rate of spawning. Both in the direction of temperature and of light the animals which migrate upwards will enter an environment where both of these factors are changed, and will have the most favourable conditions for rapid spawning.

One factor, however, which is extremely obscure, is that during the time of the vertical migration there takes place a selection of the individuals into two groups, one which migrates upwards and one which remains in deep water. A new and open question involuntary presents itself. Is the winter stock quite homogeneous in genetic respect? Are there present variations in the physiological reactions of the individuals which are due to the fact that from a genetic point of view they are heterogeneous? By culture experiments Banta (1925) and Brown (1929) discovered in daphnii a recessive mutation which was demonstrated by a difference in reaction with respect to temperature.

Another consideration seems me to be of interest for further investigations of these problems. In the many above mentioned samples from the winter conditions where females with fullgrown unripe eggs in their oviducts were frequently found, the striking phenomenon was always found, that no spawning had taken place. No visible quantity of eggs had left the oviducts, and no eggs or young stages could simoultaneously be found in the samples. In the above (p. 79) mentioned experiments with living specimens from such a sample, it was found that a majority of the individuals even in the course of the next few days could be brought into a lively and quickly finished spawning. It is of course not conceivable that all these samples containing females ready to spawn from the various areas and various times taken with exactly two days' interval should represent individuals just at the time when spawning was about to commence. It is far more reasonable to suppose that they come from an environment where the conditions are not favourable for the occurrence of spawning.

Taking all things into consideration, there are many factors which point in the same direction. We must assume that the occurrence and progress of spawning is directly dependent upon vertical migration, even though we are still unable with certainty to indicate the factors which directly decide this question.

From the above investigations of the organs of generation of the female it must be regarded as certain that the formation of females ready to spawn no longer takes place as in the months of Jannuary and February. This is a remarkable result at a time when the winter stock consist of a large percentage of stages X and XI. At the conclusion of the spawning period in 1929 this group of the stock amounted to about 43 $^0/_0$ and the females which had spawned to about 57 $^0/_0$. If we reckon that the sex proportion is normal (equal number of males and females), there are about 27 $^0/_0$ of the winter stock which do not attain maturity.

The present material does not permit of a decision as to whether these 27 % of the stock later on attains maturity. The facts given in Chapter III show, however, that we can conclude that they do not attain maturity in the following 10 months. In the later spring months, in the summer months and in the autumn months, in spite of a large amount of material, there have never been found males, females with eggs in the oviducts or early larval stages.

The fact that sex maturity is so sharply defined as to time, and can only be demonstrated towards the cessation of the winter condition, appears to indicate strongly that the process of ripening is dependent upon definite physical conditions. The fact that the period of ripening has such a sudden conclusion in spite of the existing larval stages, indicates that the physical conditions upon which it depends off our coast are only present for a short time. These conditions will undoubtly be of the greatest importance for the complete understanding of the causes of the geographical distribution of the species and comparative investigations from year to year and in other waters will be of considerable interest.

Distribution of Stages of the New Generation of *Calanus hyperboreus* during the Spring Cruises, 1922 & 1929.

The distribution of the old generation at the beginning of the investigations in 1929 showed that only a few per thousand of the total spawning were not completed. The few per thousand which remained were localised at great depths. Studies of the distribution of the stages of the new generation will serve to increase the certainty of these conclusions and to give supplementary information.

It will appear from Table 20 that the three groups, eggs and Stages I & II were never present in the representative samples for the counting chambers of the material from 1929. They were only found by careful sorting of larger parts of the samples, and could not be determined quantitatively by the methods employed. In other words they are so scarce that they play no part in the quantitative picture of the new generation and its development.

It will appear from Table 20 that eggs and stages I and II show a vertical distribution which quite correspond to the vertical distribution of the females of the old generation which have not yet spawned. In one case only (Station 79, 25/0 meters) has one individual been observed outside the very deep waters, and then in a sample where the countings showed nearly 228 000 individuals of the other stages.

The representative samples and their content of the new generation of *Calanus hyperboreus* thus afford a rare opportunity of studying spawning and the further course of development. We shall see later on how *Calanus finmarchicus* on account of the very long spawning period, which had not culminated at the conclusion of the present investigations, does not permit of studies of the entire development of the new generation.

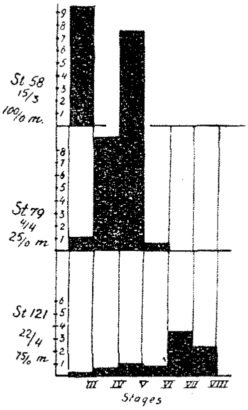
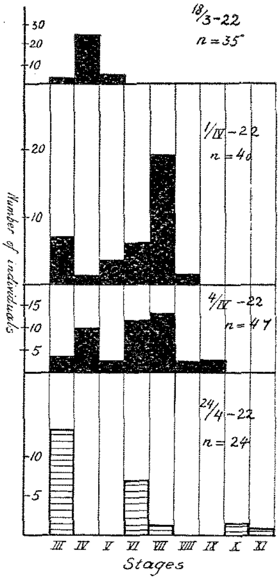


Fig. 34. Graph showing the changes in stage distribution in *Calanus hyperboreus*, new generation, during spring 1929. (See also table 20.)



Fig, 35. Graph showing the changes in stage distribution of *Calanus hyperboreus* new generation, during spring 1922. The last observation is from the outer area where the stock probably is of a more southern origin and is therefore shaded.

The distribution of stages for 1929 will be found in Tables 20 & 22. Fig. 34 gives a graphic representation of its changes during the period of the investigations.

It will be seen that at the commencement of the investigations (15/3) there were only present individuals of Stage III of the new generation of *Calanus hyperboreus*. It is true that not more than 29 specimens were measured, but the sample was very well investigated outside the representative sample. Other stages were not found.

The investigations of 1929 thus took place after the main spawning of *Calanus hyperboreus* had finished. We can only determine how long before 15/3 it finished by a knowledge of the interval between the development of the fertilised eggs and the first moulting. The distribution of stages in 1922 will be included here before the other data concerning the entire material is given. The distribution of stages will appear from Table 23, where it will be seen that only a very small number of individuals from this material were measured. The reason is that in the material there was always a predominance of *Calanus finmarchicus* of the new generation, so that in order to obtain a large number of *Calanus hyperboreus* it was necessary to make an almost overwhelming number of measurements. The main features of the changes in the distribution of stages, however, will appear clearly from the existing material. They are represented graphically in Fig. 35.

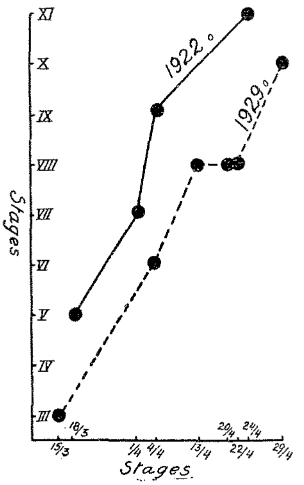


Fig. 36. Graph showing the first appearance of the different stages of *Calanus hyperboreus* of the new generation 1922 and 1929. (See also table 24.)

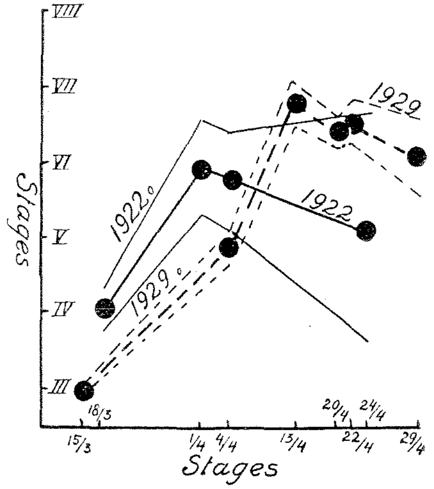


Fig. 37. Graph showing the mean of the stages (table 24) of *Calanus hyperboreus* 1922 and 1929.

There is a close agreement between the material from 1929 and that from 1922. We shall see that the sample 18/3 1922 shows a development which is more advanced than that on 15/3 1929. But there is one common feature, i. e. that there are not many stages present.

There first arises the question whether from the material of the new generation we can conclude that there was some difference in the spawning times in 1929 and 1922.

It will be seen from Tables 20, 22 and 23 that the first time a stage of *Calanus hyperboreus* is observed in the samples many individuals

Tab. 24. Changes in stage distribution of the new generation of *Calanus hyperboreus* after the breading season 1922 and 1929. Var. gives the earliest and latest stage observed, M ± 3m has been calculated by regarding the stages as variables. σ = standard deviation, v = coeficient of variation and n = numbers investigated. The dates given in brackets are from the outer part of the fjord where the specimens probably are of more southern origin. (See also Tab. 20, 22 and 23).

Year	Date	Var.	M ± 3m	σ = ±	V =	n =
1922	18/3	III — V	4·06 ± 0·24	0·48	11·8	35
	1/4	III — VII	5·98 ± 0·69	1·47	21·6	40
	4/4	III — IX	5·79 ± 0·69	1·57	26·2	47
	(24/4)	III — XI	5·10 ± 1·54	2·52	49·5	24
1929	15/3	III	3·00 ± 0·00	0·00	0·0	29
	4/4	III — VI	4·90 ± 0·18	0·52	11·8	161
	13/4	V — VIII	6·58 ± 0·31	1·04	15·8	101
	20/4	IV — VIII	6·38 ± 0·21	0·80	12·5	126
	22/4	III — VIII	6·49 ± 0i29	1·17	18·0	144
	(29/4)	IV — X	6·02 ± 0·55	1·40	23·2	61

can be observed. There have not been observed single instances of individuals of advanced development unconnected with the entire stock. Fig. 36 graphically shows the first occurrence of each stage in the samples. We obtain regular curves without markedly chance deviations. One must thus definitely conclude that the spawning in 1922 began one or two weeks earlier than in 1929.

For the further analysis of the distribution of stages the number of the stage is regarded as a variant and the number of each stage found as a frequency. A general survey of the values thus found is given in Table 24.

Fig. 37 shows how the mean values appear for the two years. We shall also see that the mean value for 1929 lies lower for the first period than for 1922, which also indicates an earlier spawning in its entirety for that year than for 1929.

There is one remarkable feature which is common to the material from 1922 and 1929. Under the assumption of a regular time of development for each individual stage and for each individual of the stock we must at the end of the spawning time find the same number of stages during the whole time of the investigations. Both in 1922 and in 1929 from 1 to 3 stages were present in the samples during the first period of the investigations. When these are further developed there will constantly occur later stages in the samples, and in a corresponding manner the earlier ones should be expected to disappear. This however is not the case. It is true that we can follow the occurrence of the new stages (Fig. 36) but the earlier stages do not disappear. Stage III was the earliest stage found in the surface layers in 1929 and 1922. In both of these years it was present in large numbers as late as 22/4—24/4. Thus the assumption, of an equally long time between each moulting and a regular rate of development for each individual, does not hold good.

It will be seen from the figures and tables produced that there is no stage between III and X which is distinguished by being specially numerous in the samples. Thus none of these stages can be of particular duration. The case is different with Stage III. It occur during the whole time of the investigations, in spite of the fact that the influx of earlier stages can only amount to a few per thousand of the entire stock. For *Calanus finmarchicus* reared artificially Lebour (1916 P. 3) states: »Nauplius Stage III is much the commonest stage and occurred all the time the material was being examined. The animal probably stays some time in this stage«. It is highly probable that the present material goes to show that the same is the case with *Calanus hyperboreus*

The other possibility that the various individuals may have different rates of development is also highly probable. A number of works on fresh-water copepods and Daphnids indicate a great variability in rate of development and longievity. (See Brehm 1927 P. 475). Thus Ekmann (1900) shows in the case of *Diaptomus laciniatus* that the time from the occurrence of the first nauplius until it becomes a egg-laying female is in North Sweden only 2 months, in Central Europe 10—11 months. Brown (1927) shows how temperature with cladocera may cause great differences in the time between moultings, and in genetic respect he also shows that the various individuals may be heterogeneous.

Individuals in the area investigated are exposed to differences in a number of factors of environment, e. g. nourishment, temperature, salinity and light. It may perhaps be of interest in this connection to mention that the material from 1922 shows in general greater variation in the distribution of stages than the material from 1929. The individuals from 1922 are from the northern area and the individuals from 1929 mainly from the inner area. The northern area has throughout higher temperatures and salinity than the inner area in these water layers where the young stages are distributed. The greatest variation both in 1922 and in 1929 is found, besides at the latest date, also at the outer stations where the temperature and salinity were highest.

Specially noticeable is the course of the mean value of the development of the larval stages. Whatover the course of the brief period of spawning we should naturally expect to find the steepest rise in mean value between the two stages VI and VII. The exact opposite of this is, however, show by Fig. 37. But of course a number of other factors may here interfin. If the various stages are differently distributed vertically (and the material appears to show that this is not the case to any appreciable degree during the daytime), they may be subjected to a difference in changes in concentration. Moreover it is not certain that the net catches represent the various stages homogeneously as they are distributed in the living stock.

If we consider the distribution of stages in the winter condition it clearly appears that a difference must exist in the rate of development of the various individuals. The spring material shows that certain individuals even 2 months after spawning have developed into stage XI. Other individuals have during the winter condition not advanced farther than Stage X, and even at the next spawning period and later, when over 12 months have elapsed after the development of eggs, a number of individuals have not developed farther than Stage X. The material does not allow us to decide yet whether this is the phenomenon which can be traced already a short time after spawning, but it is a problem for future investigations which will be of great importance for the complete understanding of the causes of the geographical distribution of the species.

From a purely methodical view this part of the investigation affords a very important result. The presence of early larval stages only, Stage III and onwards, offers no certain means of determinating the distribution and time of the spawning. The numerous individuals of Stage III present at Station 76 4/4 1922, thus tell us little of the actual spawning. They are from 75—150 kilometers distant from the nearest spawning area from which they might have come. 1½—2 months have elapsed since spawning and the temperatures is 2°—3° higher in the surface layers than at the place where spawning was found to take place. In order to map the spawning there is of course required far more thorough investigations of the entire stock and of the distribution of the various biological groups.

At the early date, when the investigations began, the picture was quite a different one. The later stages were then lacking and only the earlier ones were present. At that time we have the closest agreement between the observations of the distribution of the old generation and of the new. At the commencement of the investigations we find both groups with the same restricted distribution. Together the two groups fully justify the conclusions regarding the occurrence of spawning and the horisontal position of the spawning area.

Causes of the Extent of the Spawning Area as regards *Calanus hyperboreus.*

The data produced in the foregoing section will be sufficient for a determination of the causes of the limitations found in the spawning area of *Calanus hyperboreus*. It is true as mentioned above that we lack a knowledge of the time in the winter condition, when the species is at its greatest distance from the surface, and we only know approximately how great that distance is. Moreover we lack analyses of its quantative extent in relation to the bottom depth during the time just before vertical migration, and we also lack to a considerable extent a knowledge of the movements of the masses of water in the strata where the species is to be found before, during and after vertical migration. Mosby (1930) shows from the fjords near Bergen 3 different strata of currents, the surface current, the intermediate current and the deepest current, each characterised by differences in the physical conditions of the masses of water and the direction and rate of the currents. We cannot here decide whether these results from the fjords near Bergen can be transferred to the fjords here investigated, but if the conditions are somewhat homogeneous they may to a minor degree exercise an influence upon the distribution of spawning.

If we compare the distribution of the species in the inner area with that in the northern area, we shall find in the winter condition large numbers of the animals at great depths in the inner area. In the northern area there are lacking both great depths and animals. The winter condition is interrupted by an active vertical migration in which all groups of the winter stock, whether adult or not, take part. During and after this vertical migration the new generation appear, and the mature females finish their spawning. During the first period after spawning both the new and the old generation of the species are closely restricted to the inner area and above great depths. Thereupon occurs a great change in concentration in the inner area. The animals are scattered by the strong currents and may then be found even in the outer parts of the fjord.

In other words, we have here a predominating factor in determination of the position of the spawning area. As the species winter at such great depths and are ready to spawn before they migrate upwards, the purely topographical conditions are decisive for the situation of the spawning area. It is only in connection with the occurrence of such great depths that a winter stock will be present.

The other factors which might be thought important for determining for the spawning area can be put out of consideration. It is the occurrence of the spawning animals which is limited. If it were the physical conditions which cause a limitation in spawning we should find outside the spawning area individuals which had not reached maturity or which had not spawned. Such animals have never been found, and are also lacking in the material in question. It is true that we find a large percentage of individuals which do not reach maturity, but they occur in the spawning area itself and are scattered just after spawning. In addition we find a group of individuals (about 1 % of the stock) which show a delayed spawning, probably on account of the unfavourable conditions of environment, but these individuals are only found vertically separated from the bulk of the stock. Horisontal they keep within the limits of the spawning area.

As regards the question as to the growth of the larvae it is not impossible that we may find the conditions very different in the various parts of the area investigated. As mentioned above, it is probable that even in the present material there is a difference in the rate of development. On the other hand we find individuals which as regards rate of development are favourable situated in all parts of the area. It is quite possible that these conditions may mean much for the size and distribution of the winter stock, but they cannot be of importance as regards the limits of the area of spawning.

The Spawning of *Calanus hyperboreus* in Relation to Temperature and Salinity.

As already mentioned, the material in question is not representative of the bulk of the spawning of *Calanus hyperboreus*. It is therefore not possible to state the limits of temperature and salinity under which spawning generally takes place in the Lofoten area. The delayed spawning in very deep water takes place at temperatures of 6°.5 to 7° and a salinity of between 34.50 and 35 ‰. If the greater part of the spawning takes place in the upper layers of water, the temperatures can not be lower than about 1°.5 and the salinity not much below 33 ‰.

As mentioned above, even before the delayed spawning was observed there had taken place a selection within the stock into one part which migrates upwards and another part which remains in deep water. We are therefore not allowed to conclude that the part which migrates upwards is capable of spawning under the same conditions as that part which remains behind. On the other hand the experiments mentioned on P. 79 with individuals from the Oslo Fjord show that normal individuals from that area can spawn at temperatures as high as 7°.5.

With the observations hitherto submitted the main data regarding distribution etc. with respect to *Calanus hyperboreus* have been dealt with finally. A few observations which remain, especially on the basis of the material from 1922, will be mentioned when discussing the conditions in the southern areas, P. 149. In the following the conditions in which spawning of *Calanus finmarchicus* takes place and the reasons for the special spawning area of this species will be discussed.

Vertical Distribution of the Old Generation of ***Calanus finmarchicus,*** March April 1922 and 1929.

Mention has already been made on P. 93 of the circumstance that *Calanus finmarchicus* completes its annual vertical migration earlier than *Calanus hyperboreus.* The investigations in 1929 coincide with the time when *Calanus hyperboreus* completes its vertical migration, whilst it has already been completed by *Calanus finmarchicus.*

The 1929 material is the most complete as regards the great depths in the time after the annual vertical migration of *Calanus finmarchicus.* The 1922 material has only two hauls which are representative of greater depths than 100 meters and these hauls lie in areas where large numbers of the species are never present.

It will be seen from Tables 18 and 19 that large numbers of *Calanus finmarchicus* of the old generation are only present at one station (Station 135) in hauls which are representative of depths greater than 75 meters. The greatest numbers are found in hauls between 25 meters and the surface in cases where such very specified hauls have been taken.

We can summarise these observations as follows: The greatest number of *Calanus finmarchicus* in the latter half of March and in April are found in the strata of water above 75 meters.

The question as to how the species of the old generation is distributed between 75 meters and the surface can hardly be settled on the basis of the existing material. Here the question of the daily vertical migration also arises, and the material is not very usefull for an analysis of this problem. It is true that the material has been collected at various times, both during the day and in the morning and evening, but it was not collected at one place.

The various localities are not very homogeneous as regards the occurrence of the animals, and in large parts of the area the currents vary greatly.

One factor, however, appears to indicate that the daily vertical migrations are not as great as e. g. at San Diego (Easterley 1912) and at Plymouth (Russel 1928). There have never been found large numbers of the species below 75 meters even in the middle of the day. if we calculate the number of animals per 100 meters (See Fig. 32 *a*, 33 *a*, 39 and 40) we see that the material from 1929 shows that the greatest density of animals is found in the upper 25 meters and the material from 1922, where there are many hauls from between 10 meters and the surface, very frequently shows the same phenomenon for the upper 10 meters (Tab. 25). This applies to a great extent to hauls taken in the middle of the day or in the afternoon.

Horisontal Distribution of the Old Generation of *Calanus finmarchicus*, 1922 and 1929.

It appears from Table 18 (and Fig. 32 a) that the old generation of *Calanus finmarchicus* during the first investigation of the area in 1929 had not the same strictly limited horisontal distribution in the inner area as *Calanus hyperboreus*. We also find the species at the outer stations of the fjord. At the second investigation the number had increased in the hauls at the outermost stations. At the same time it will be seen that the number at the middle stations (58 and 103) is higher than that at the outermost station. The reason for this can better be studied in the material from 1922.

Fig. 38 shows the hydrographical conditions during the investigations in 1922. The situation of the stations will appear from Fig. 41. The temperatures observed are partly given in Table 25 where at the same time we find the number of females and eggs of *Calanus finmarchicus* in vertical hauls with nets of 42 cms diameter and silk 14. For reasons which will be further discussed in the section on the distribution of stages of the old generation we have decided to describe its horisontal distribution on the basis of observations of the number of females.

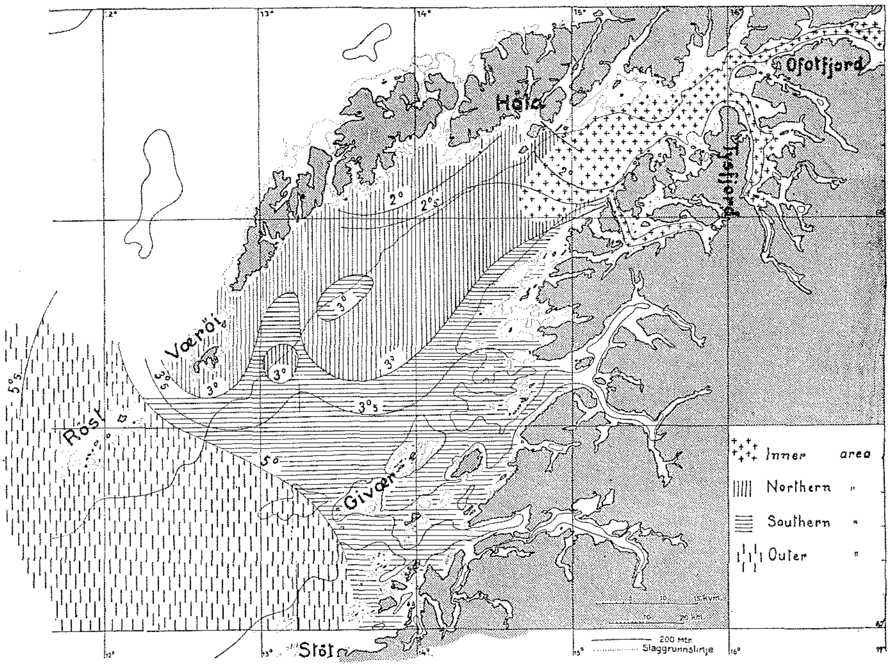


Fig. 38. Map of surface isotherms in the area investigated during March-April 1922. The map also shows the various parts of the area mentioned on page 87.

Fig. 39 represents the number of females of *Calanus finmarchicus* in the section across the outer part of the fjord. The two stations 54 and 56 lie in the southern area and show only a small occurrence of females of *Calanus finmarchicus*. Station 57 in the northern area, however, shows an abundance of females. Without taking up a standpoint with regard to whether this material is reliable or not, we can sum up the results so that the occurrence in the northern area is quite predominant, about 14 times as high as in the southern area.

Figure 40 shows a longitudinal section from the outer part of the fjord in towards the eastern limits of the northern area. It should here be observed, (See the figures for the total catch), that the scale of this figure is much smaller than that of the foregoing one. We first see that the large catch from Station 57 was also made at Station 33 which has almost the same situation and the same physical conditions. Station 35 (which lies at a considerable distance from land) shows a smaller occurrence. The number then increases greatly inwards towards Høla. The abundance here is confirmed at several stations (See Table 25), inter alia Station 43, which for reasons of space is not included in the figure and which shows the highest catch (461 females).

Continued pag. 132.

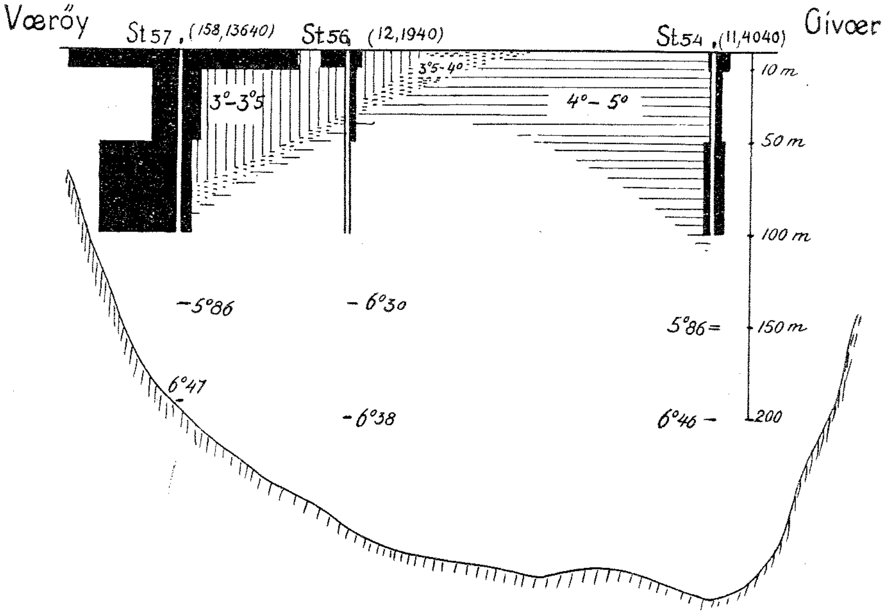


Fig. 39. Cross section from the outer part of the Lofoten area on the 9. April 1922 with temperatures together with numbers of females (to the left) and eggs (to the right) of *Calanus finmarchicus* calculated as numbers in hauls of 100 meters. Total numbers are given beneath the number of the station. (See also table 25.)

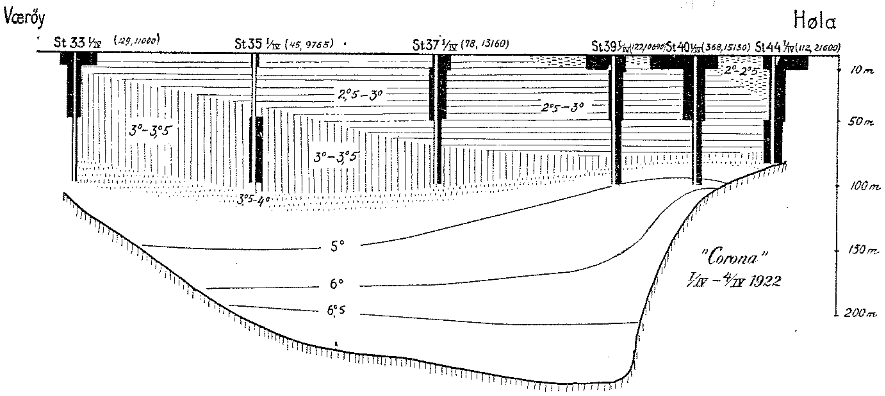


Fig. 40. Longitudinal section along the Lofoten isles from Verøy to Høla 1. April —4. April 1922 with temperatures together with the numbers of females (to the left) and eggs (to the right) of *Calanus finmarchicus* calculated as numbers in hauls of 100 meters. (See also fig. 39 and table 25.)

Tab. 25. Number of eggs and females of *Calanus finmarchicus* in vertical hauls from the "Corona" 1922. The temperatures at each station are given in the following manner: At 10/0 meters the temperature is given for 0 meters, at 50/10 for 10 meters, at 75/50 for 50 meters and at 100/50 for 100 meters. In the cases where 50 or more females were caught the proportion between eggs and females is given in the column i =. The station numbers in the northern area are shown by open type, and likewise all catches of more than 25 females and 5 000 eggs. The situation of the stations is shown in fig. 44.

St. Date	**4** 18/III				**6** 20/III				**7** 20/III				**8** 20/III			
Depths	Temp	♀	Eggs	i=	Temp	♀	Eggs	i=	Temp	♀	Eggs	i =	Temp	♀	Eggs	i=
10/0	2·3				2·1				2·4				2·5			
50/10	2·2	**64**	1080	17	2·3	**44**	815		2·3	**195**	1280	6	2·4	**280**	4500	16
75/50	4·0				4·3	12	495		2·9	23	805		2·9	2	1320	
100/50									6·4				6·4			
Sum						**56**	1310	23		**218**	2085	10		**282**	**5820**	21

St. Date	**13** 24/III			**15** 24/III				**18** 24/III			23 26/III			28 29/III		
Depths	Temp	♀	Eggs	Temp	♀	Eggs	i=	Temp	♀	Eggs	Temp	♀	Eggs	Temp	♀	Eggs
10/0	2·8			3·0				3·0			4·0			3·8	1	585
50/10	2·7	**41**	875	4·0	**94**	4260	55	3·3	18	4500	3·8	0	150	3·9	1	600
75/50	4·9			5·3				3·7			4·1	0	45	4·4		
100/50				6·7	0	1000		4·4			4·2			4·4		
Sum					**94**	**5260**	56					0	195		2	1185

St. Date	**30** 29/III				**32** 29/III			**33** 1/IV				**35** 1/IV		
Depths	Temp	♀	Eggs	i =	Temp	♀	Eggs	Temp	♀	Eggs	i =	Temp	♀	Eggs
10/0	3·3	**35**	2025		2·8			3·0	**50**	3850	77	2·9	3	480
50/10	3·5	22	1840			**31**	840	3·0	**75**	4550	61	3·0	3	1085
75/50	4·9				4·3			3·4				3·0		
100/50	5·0				5·7			3·7	4	2600		3·3	**39**	**8200**
Sum		57	3865	68					**129**	11000	85		**45**	**9765**

St. Date	**37** 1/IV				**39** 1/IV				40 1/IV				**43** 4/IV			
Depths	Temp	♀	Eggs	i =	Temp	♀	Eggs	i =	Temp	♀	Eggs	i =	Temp	♀	Eggs	i =
10/0	2·5	2	1960		2·4	**108**	1700	9	2·4	**170**	3010	18	2·4	**367**	**8950**	25
50/10		**73**	**7600**	105	2·6	**44**	**6300**		2·6	**152**	**7320**	48	2·5			
75/50					2·6				2·6				2·6			
100/50		3	3600		5·5	20	2640		6·1	46	4800		6·3	**94**	1960	21
Sum		**78**	**13160**	168		**172**	**10640**	62		**368**	**15130**	41		**461**	**10919**	24

St. Date	**44** 4/IV				46 4/IV			47 4/IV			54 9/IV			**57** 9/IV			
Depths	Temp	♀	Eggs	i =	Temp	♀	Eggs	Temp	♀	Eggs	Temp	♀	Eggs	Temp	♀	Eggs	i =
10/0	2·4	**30**	**6500**		3·4	1	85	2·9	0	86	4·6	1	640	3·1	**30**	**6070**	
50/10	2·4	**28**	**9400**		3·5	5	475	2·9	0	0	4·8	1	1250	3·4	**29**	3720	
75/50	2·5	**54**	**5700**	105	6·4			6·1			4·9			3·3			
100/50					6·7	1	132	6·8	1	15	5·0	9	2150	5·1	**99**	3850	39
Sum		**112**	**21600**	193		7	692		1	100		11	4040		**158**	**13640**	86

St Date	61 10/IV			**68** 22/IV			70 22/IV			73 22/IV			74 22/IV		
Depths	Temp	♀	Eggs	Temp	♀	Eggs	Temp	♀	Eggs	Temp	♀	Eggs	Temp	♀	Eggs
10/0	3·5			2·3	10	1560	2·4	1	510	5·7			5·2	4	320
50/10	3·7	5	770	2·6	2	3600	2·3			4·9	8	760	4·7	3	510
75/50	6·5			2·6	8	720	5·3			5·3			5·3		
100/50	6·4	0	7	6·7			6·7	0	525	5·5	8	480	5·6	15	126
Sum		5	777		20	**5880**		1	1035		16	1240		22	956

St. Date	75 22/IV			76 24/IV			80 27/IV		
Depths	Temp	♀	Eggs	Temp	♀	Eggs	Temp	♀	Eggs
10/0	5·2	15	1100	5·2	0	170	5·2		
50/10	4·7			4·9	5	880	5·1	1	0
75/50	5·9			5·1	13	675	4·9	7	1300
100/50	5·5			5·5			5·2		
Sum					18	1725		8	1300

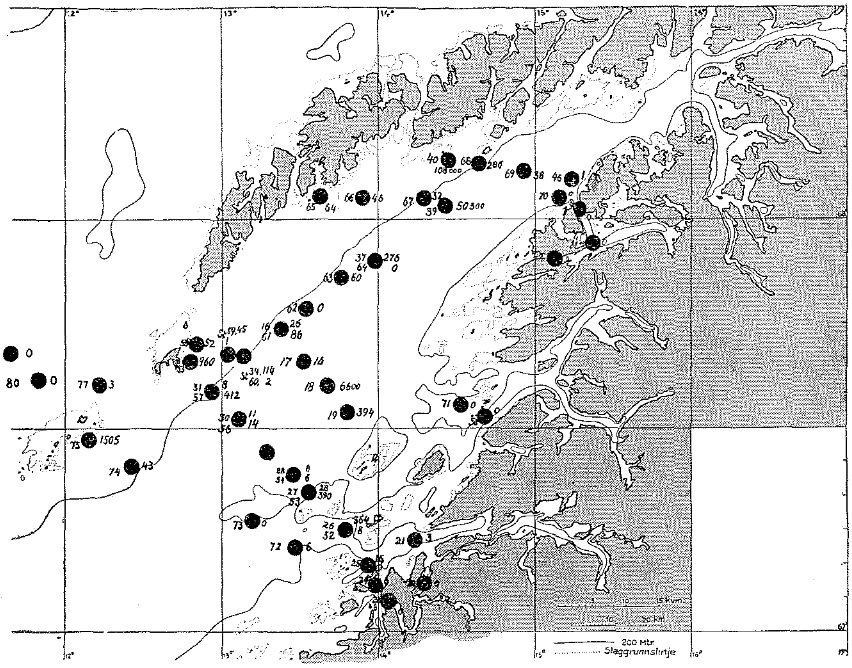


Fig. 41. Map showing the station numbers (to the left) and the numbers of females *Calanus finmarchicus* (to the right) from surface hauls March—April 1922.

These two figures show in broad outline the highest catch to coincide with the lowest temperatures present. The next question is whether this result holds good for a larger material.

Table 25 shows the distribution in the vertical hauls from 1922. The stations in the northern area, the number of females above 25 and the number of eggs above 5.000 are printed in heavy type. We can thereby comparatively quickly obtain a general view as to how the rich catches on the whole are situated in the northern area and how very frequent they are. Numerically the catch in the vertical hauls in the various areas is: —

Northern area, 39 hauls, 2404 females, average 98 females per haul.

Southern area, 19 hauls, 53 females, average 2.8 females per haul.

Outer area, 9 hauls, 53 females, average 7 females per haul.

The occurrence in the northern area according to 67 vertical hauls is thus 14—35 times as great in the northern areas in the southern and outer areas.

From the cruise of 1922 we have 48 hauls with 1 meter egg net at the surface. The distribution of the catch in the area will appear from Fig. 41. It is possible that these hauls, especially if there are considerable daily migrations, are not as characteristic as the vertical hauls. Thus the catches at Station 18, 39 and 40, are the three largest, made in the late afternoon, which, however, is the case with a number of hauls which were not abundant. From the numerical point of view the catches are distributed over the various areas as follows: —

Northern area, 20 hauls gave 168 496 females, average 8425 females per haul.

Southern and Outer Area, 28 hauls gave 2600 females, average 98 females per haul.

Thus the occurrence in horisontal hauls is about 100 times as large in the northern area as in the outer and southern area.

It has been mentioned that the old generation of *Calanus hyperboreus* 1929 was more deeply distributed in the outer part of the fjord than in the inner part. Figs. 32 and 33 a show that the same can be the case also as regards the old generation of *Calanus finmarchicus.*

The material from 1929 shows little regarding the distribution within the various areas. Reference has already been made to the abundant catches made at the middle stations in the fjord, (58 and 103) which fully correspond to those made in 1922. The material confirms that when we search from the outer part of the fjord inwards we find an increase in the catch. Further information on this point is also furnished, inside the investigations of 1922, in the inner area, (Stations 79, 80, 119, 120 and 121) this increase does not continue. The catch, however, is still far greater than that made, e. g. in 1922, in the southern area.

The horisontal mapping here made of the distribution of the females of *Calanus finmarchicus* thus shows a predominant occurrence in the inner and the northern areas. We shall also see later on that the same applies to the new generation. The phenomenon here found is thus entirely the same as that found by Damas (1905) (see Fig. 2 a, P. 15) in the southern part of the Norwegian Sea. There is the same distribution according to certain isotherms as that found by Damas, but the limiting isotherms of this area are, for the same species, different from those found by Damas in the Norwegian Sea.

The Vertical Distribution of the New Generation of *Calanus finmarchicus* in 1922 and 1929.

The vertical distribution of the new generation of *Calanus finmarchicus* in 1922 will appear from Tables 26 and 25 (comprise eggs only) and Figs. 39 and 40 (comprise eggs only). The vertical distribution in 1929 will appear from Table 19 and 20 and also Figs 32 and 33 *b*.

It will appear from the material for 1929 that the new generation of the species is practically speaking entirely confined to the layers of water above 75 meters. Where the hauls are sufficiently specified, we find in addition an extremely numerous occurrence in the layers of water between 25 meters and the surface. The 1922 material shows that also the layers of water above 10 meters have quite a predominant occurrence of the larval stages. These conditions apply both to the eggs and to the later stages right up to the last copepodit stage (XI).

We thus find here exactly the same conditions as met with in *Calanus hyperboreus*. The new generation is more strongly concentrated near the surface than the old generation. The phenomenon, however, is not so strongly pronounced as in *Calanus hyperboreus*. The new generation of *Calanus finmarchicus* is, it is true, equally strongly confined to the surface layers, but the old generation of *Calanus hyperboreus* is more deeply distributed than the old generation of *Calanus finmarchicus*.

Horisontal Distribution of the New Generation of *Calanus finmarchicus* 1922 and 1929.

The 1929 material shows a close agreement in the distribution of the old and the new generation of *Calanus finmarchicus*. The conditions will appear from Tables 17, 18, 19 and 21 and figures 32 and 33 *a* and *b*. However, the 1922 material is more suitable for studies of this phenomenon, not only because more hauls were made in that year but also because those hauls show greater differences in the occurrence of the species.

For reasons which will be explained later (se P. 142) we can regard the eggs as representative of the occurrence of the new generation of *Calanus finmarchius*. On P. 133 mention is made of the occurrence of females of this species in the area investigated. We have the following figures for eggs from the same hauls:

The northern area, 39 hauls 137 000 eggs, average 5972 eggs per haul.

Southern area, 19 hauls 9264 eggs, average 489 eggs per haul.

Outer area, 9 hauls 5081 eggs, average 565 eggs per haul. We thus have here a predominating occurrence of the new generation in the northern area, quite analogous to that found as regards females. The two sections, Figs 39 and 40, show how these eggs follow exactly the same laws of distribution as the females. We find an increase towards the north side of the fjord, and an increase from the outer part of the fjord towards the inner area.

The 1929 material as far as it goes shows the same phenomenon (see Tables 19 and 21) and also shows large catches in the inner area, catches however, which are not as great as those made in the middle part of the fjord.

Obviously it would seem natural from the present material to study the proportion between the old and the new generation. The material is, however, as regards time not very homogeneous, so that it is not suitable for comparative studies of the horisontal distribution of the new generation in proportion to the old, beyond what has already been done. On the other hand the proportion between eggs and females is very important for studies of the details of spawning.

Distribution of Stages of the Old Generation of *Calanus finmarchicus* in 1922 and 1929.

Table 16 shows that the winter stock in the middle of December 1928 consisted almost entirely of the two last young stages, X and XI. Thus Station 364 10/12 in the middle part of Vest Fjord the stock consisted of 89 % of Stage XI and 11 % of X. It was only at the most southerly and last station 374 in the Romsdal Fjord that females were found in the samples. This is the station where also *Calanus hyperboreus* exhibited a more advanced development, and it is in an area where by comparison with Ruud's material (Ruud 1929) it will be seen that the spawning period is far earlier than in the Lofoten area.

The situation 15/3, 1929, in the Lofoten area gives a quite different picture, a far more advanced development towards the spawning period. Table 17 shows the distribution of Stages at that time. The stock then consisted of 55,4 % females, 22,4 % males, 16,6 % Stage XI and 5,6 % Stage X. Table 19 shows that no young stages earlier than X were present. A very large number of the females had eggs in their oviducts, but the eggs in all cases observed were at a very early stage of development. In other words the sample shows a time when spawning had not commenced but which at the same time gives evidence of an approaching spawning.

The further distribution of stages during the time comprised by the investigations will appear from Tables 17 and 18. It will be seen that throughout that time the larval stages XI and X were found. As late as 22/4 the development of the new generation had not advanced beyond Stage IX, so that we can assume that individuals of Stage X still belong to the old generation.

On April 4th at Station 80 we find the following distribution per cent of the stock: 76,0 % females, 6,2 % males and 18,8 % of Stage XI. At that time most of the females had eggs in their oviducts, but in addition to the earlier stages we also find fully developed eggs and we get the same picture of spawning females as that mentioned in the case of *Calanus hyperboreus.*

29/4 (Station 135) was the last date investigated. It is possible that the distribution of stages is somewhat different in the outer part of the fjord where that station was taken, but this will not cause any essential change in the whole picture. The distribution per cent was at that time: 61 % females, 29 % males and 10 % of Stage XI. At that station there were observed females with spermatophores (this is a surprisingly rare phenomenon, and is therefore certainly not a reliable means of estimating the beginning of spawning) and females with eggs at all stages of development.

Throughout the time comprised by the investigations in 1929 we can thus conclude that ripening of females ready to spawn constantly took place. At the end of the investigations this process was by no means completed.

It would require too much space to give all details observed concerning the distribution of stages of the old generation in 1922. During the course of the investigations it exhibited very nearly the same picture as in 1929. Thus on 20/3 we find at Station 7, 293 individuals of the old generation showing the following distribution per cent: 75 % females, 3 % males and 22 % of Stage XI. On 1/4 at Station 40 we find 389 individuals with the following distribution: 95 % females, 1 % males and 4 % of Stage XI. Males occurred in small numbers right up to the end of the investigations 24/4. At that time the new generation was so far advanced that the number of larval stages belonging to the old generation could not be determined.

As will be seen from the figures given, the larval stages are fewer in the old generation in 1922 than in 1929. Another remarkable result which to some extent will appear from the tables is that the distribution of stages is not always homogeneous at the various depths. This is perhaps best illustrated by the conditions at Station 40 in 1922. The distribution per cent in vertical hauls has already been mentioned. In the horisontal surface haul where the catch was 108 000 individuals it was not possible in spite of a very careful examination to find any stage except females.

The catch from vertical hauls in 1922 was fixed in Flemming's fluid, and studies of eggs in the oviducts could therefore not be made. In surface hauls throughout the whole period of the investigations there were found females with eggs at all stages of the period of growth.

We can thus conclude from the distribution of stages and the development of eggs that in the period comprised by the investigations in 1922 animals ready to spawn were always present.

The Distribution of Stages of the New Generation of *Calanus finmarchicus* 1922 and 1929.

The distribution of stages in 1922 will appear from Table 26 and Fig. 42. That in 1929 will appear from Tables 19 and 21 and Fig. 43.

It will be seen from Table 19 that at the beginning of the investigations at Station 58, where as already mentioned there was a large occurrence of individuals of the old generation almost ready to spawn, no eggs or larval stages were present. Spawning had not yet commenced here. The other early samples both those from 1929 and from 1922 are characterized by the presence of eggs, some times in considerable quantities, and by small quantities of early stages. The later samples constantly show a rich invasion of eggs and a successively rapid further development, so that as early as 24/4 we find individuals of Stage XI and the same stage on 29/4 1929.

On account of the steady increase of eggs the new generation of *Calanus finmarchicus* will not constitute such a constant group of plankton as the new generation of *Calanus hyperboreus*. Without an exact knowlegde of the invasion of eggs we cannot therefore study the rate of development of the various individuals, but as was done in the case of *Calanus hyperboreus* we can study the earliest occurrence of the various stages.

It will be seen from Tables 19 and 21 that also in the case of *Calanus finmarchicus* this first occurrence of a stage is not a chance conception. Separate individuals differing from the entire stock were never observed. On the contrary, the stage at its first occurrence is regularly connected with the foregoing stages.

Tab. 26. Numbers and stage distribution of *Calanus finmarchicus* of new generation, spring 1922. (See also Tab. 19).

St.	Date	Depth	Eggs	I & II	III	IV	V	VI	VII	VIII	IX	X	XI	Total	Number determinated
4	18/3	50/5	2400	750	85	16	—	—	—	—	—	—	—	3251	144
44	4/4	70/50	28500	10300	6600	3170	575	575	595	—	—	—	—	50315	274
		50/10	23500	13500	790	1120	910	1010	232	—	—	—	—	41062	406
		10/0	65000	23500	3500	4700	2800	1600	1070	410	—	—	—	102580	350
68	11/4	75/50	2800	4100	1700	680	680	—	—	—	—	—	—	9960	60
		50/10	8300	12200	—	5400	6700	2500	440	58	—	—	—	35598	203
		10/0	20000	17100	1860	7900	9300	4200	470	—	—	—	—	60830	115
76	24/4	50/10	1690	2450	840	1990	1250	210	185	220	110	93	78	8116	103

An irregularity will at once be noticed in Tables 19 and 21, where the material for the new generation is arranged in point of time. Thus on 15/3 no spawning has commenced. On 19/3 the development has reached Stage V. On 12/4 Stage IX was observed, 20/4—22/4 (Table 21) there are no stages later than VII. This irregularity in the distribution of stages is found throughout the material.

If we arrange the material according to areas we obtain another aspect. Fig. 44 shows the first occurrence of the various stages in the inner half of the fjord as compared with the first occurrence at the 3 outer stations. We notice a characteristic and general difference at the two localities. *The first occurrence of the various stages lies about 2 weeks later in the inner half of the fjord.*

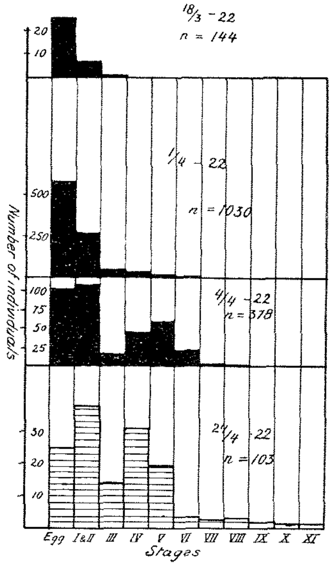


Fig. 42. Graph showing the changes of stage distribution of the new generation of *Calanus finmarchicus* during the investigations in 1922. The distance between the base lines of the graphs indicates the time between the stations selected. The last observation is from the outer area where the stock probably is of a more southern origin, and the curve is therefore shaded. (See also table 26.)

Two possibilities are conceivable to explain this phenomenon. It may be due to a difference in the rate of development of the individuals in the inner and the outer parts, or it is possible that it is due to a difference in the time of spawning in the inner and the outer parts. Moreover it may be due to both factors in combination.

If it was entirely due to a difference in the rate of development within the area it must be assumed that spawning commenced in the days between 15/3 and 19/3. For on 15/3 we found a number of animals almost ready to spawn in the inner part of the fjord, but no larval stages. On 19/3 we find in the outer part a development which has advanced as far as Stage V. If we also take into consideration the circumstance that as late as 4/4, in the inner area we only find a very few individuals which have developed as far as Stages V and VI, it must be evident that we are confronted with a difference in spawning time between the inner and the outer parts of the fjord. In the outer area spawning, must have commenced several days before 19/3. In the inner area it can not have begun till after 15/3. Assuming that the individuals in the samples 19/3 in the outer area are practically speaking equally developed as the individuals in the samples 4/4 in the inner area, we have a difference in spawning time which very closely corresponds to the difference in time of the first occurrences of the various stages throughout the time of the investigations.

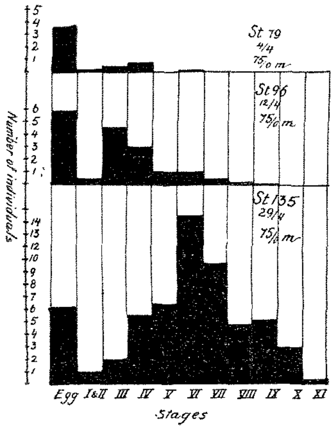


Fig. 43. Graph showing the changes of stage distribution of the new generation of *Calanus finmarchicus* during the investigations in 1929. (See also fig. 42 and table 19.)

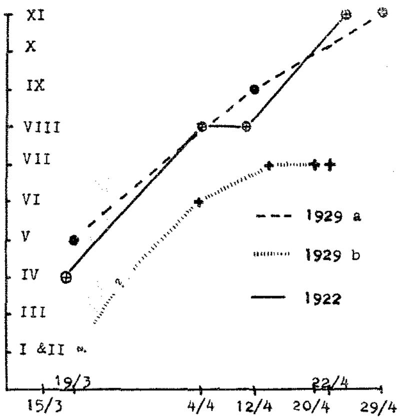


Fig. 44. Graph showing the first appearance of each stage of the new generation of *Calanus finmarchicus* during 1922 and 1929, during 1929 from the inner part of the fjord (b) and from the outer part of the fjord (a). The part of the graph for 1929 *b*, which is marked with ? only denotes that the graph cuts the base line somewhere after the date 15. March. (See also tables 19, 21 and 26.)

We can thus conclude from Fig. 44 that there is a difference in spawning time for *Calanus finmarchicus* for the inner and the outer halves of the fjord.

On Fig. 44 there is also marked the first occurrence of the various stages in 1922, when material only comprises the outer part of the fjord. Considering the errors which such a curve must necessarily show, (for with close observations one must obtain a Stair-case shaped curve) the curves for the outer area in 1922 and 1929 coincide surprisingly well throughout their course.

We can thus conclude that the time for the commencement of spawning in the outer part of the fjord, in the years 1922 and 1929 cannot have varied greatly.

Speaking generally, the observations of the distribution of stages of the new generation completely confirm the observations of the distribution of stages of the old generation. Spawning of *Calanus finmarchicus* took place in 1922 and in 1929 throughout the time comprised by the investigations. Only from the inner part of the fjord one sample was collected before the commencement of spawning in that part of the area.

Spawning of *Calanus finmarchicus*, 1922 and 1929.

We have already in the foregoing pages described a number of features regarding the spawning of *Calanus finmarchicus*. Thus we have found that the species is distributed over the whole of the area investigated, but that there is a considerable difference in its quantity in the different parts of the area. By studying the distribution of stages of the old generation it has been shown that spawning takes place throughout the time comprised by the investigations. Studies of the distribution of stages of the new generation confirm this result, and also show that there may be a difference in the time for the occurrence of spawning in the various parts of the area investigated.

The question now remaining, and one which is of great importance for the general part of this work, is whether spawning takes place on the same scale in the various parts of the area. We have already shown both for the new and the old generation that there is a numerically predominating occurrence in the northern area. This occurrence can be limited to the isotherm for 3°.5 1922. It is the same phenomenon which Damas (1905) found in the southern part of the Norwegian

Sea and which he interpreted to mean that it was the temperature which was decisive for the limitation of spawning. It is of course quite as conceivable that we are here only confronted with a difference in the occurrence of spawning animals, and that the production per number of individuals of the old generation is equal within the area.

As already mentioned previously, it would be natural to examine whether the proportion between the old and the new generation is different within the area. An investigation of this kind, however, would be difficult to carry out. The new generation forms a plankton group which throughout the time of the investigation is subject to a great increase. The material is so heterogeneous as regards time that by studying the proportion between the old and the new generation in its entirety we are obviously unable to arrive at exact and comparable values.

The case is different if we select the eggs as characteristic of the new generation, but even then we must not make too great demands upon the exactitude of the investigation. There are many unknown factors which must be of importance, and which quite conceivably may be different in the various parts of the area. Thus as regards *Calanus hyperboreus* we have already seen that considerable differences may exist in the rate of spawning of the various individuals, and that this rate of spawning influenced by factors of environment. It is of course highly probable that environment may also have a strong influence upon the time it takes for development of the eggs into free nauplius. Other factors, e. g. vertical migrations and dispersion by currents are also likely to influence the proportion between females and eggs. There are many links in the chain which must left out, but on the other hand if the isotherms form border lines for the spawning, the differences would have to be of such dimensions that they would at once be visible in the material.

There are many things which speak in favour of the proportion between females and eggs being an important aid to the further study of spawning, its course in time and its relation to the various parts of the area in which the species is found. I therefore venture to introduce a special term of designating this dimension, which will here be called the intensity of spawning.

The first condition for comparative studies of the intensity of spawning is that the material should be collected in nets of such a fine mesh that the eggs cannot slip through the meshes. For studies of this ratio there will here only be employed that part of the material which was collected in silk No. 14 (1922) and 25 (1929). Nets 8/72 as a rule allow the eggs to slip through.

It has already been mentioned that in March 15th, 1929 spawning had not commenced in the inner part of the fjord. Thus at that time we can regard the intensity of spawning = 0, even through there are no hauls with fine silk nets. (There were only 6 hauls with fine meshed nets in 1929). Figure 45 shows how the intensity of spawning appears in 1929 based upon this material. We shall see that at the conclusion of the investigations the intensity was very high.

Already Figs 39 and 40 for 1922 already show that there is a certain proportion between the occurrence of females and eggs in the material. A better material for the study of the intensity of spawning is found in Table 25, where all the observations are collected. It will appear from this table that the intensity of spawning is a variable quantity. It varies greatly from one haul to another, and we only find it somewhat constant where a large catch of females is made. For that reason it is here only used where the catch of females is large. For studies of changes in intensity of spawning in time and its magnitude in the various parts of the area investigated only the average of all the observations can of course give relatively reliable values.

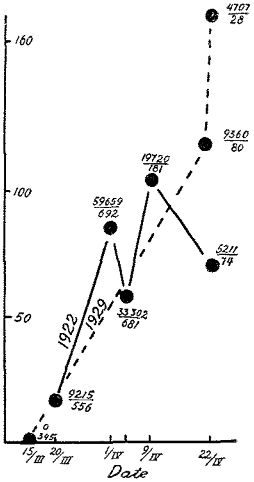


Fig. 45. Proportion between the number of females of *Calanus finmarchicus* and number of eggs during the investigations 1922 and 1929. The actual numbers are given beside each observation.

It will be seen from Fig. 45 that the intensity of spawning for 1922 shows the same features as that for 1929 we find that it is very low at the beginning of the investigations and high at their conclusion. The figure shows that there cannot be a very great difference between the commencement of spawning in 1922 and in 1929, the same result which has already been found by studying the distribution of stages of the new generation.

In 1922 the intensity of spawning in the various parts of the area was as follows:

Northern area (39 hauls) — 57.
Southern area (19 hauls) — 170.
Outer area (9 hauls) — 81.

Although the variations in the intensity of spawning appear to be so great, it is quite conceivable that the high intensity of spawning in the southern area is simply due to chance, and that the material is not sufficiently homogeneous in point of time. The entire material shows, that with our present methods we have no basis to conclude that spawning is confined to certain isotherms. An equally active if not more active spawning takes place outside the area where the main production of the species takes place.

The restriction of spawning to certain isotherms is first and foremost due to a heterogeneous occurrence of spawning animals in the area investigated.

On the basis of the present material we can state that the duration of spawning for *Calanus finmarchicus* is a minimum of 1½ months. We do not know, however, whether females of this species like those of *Calanus hyperboreus* only spawn once. Neither do we know what time it takes for the egg to develop into a free nauplius. Grobben (1881) states that it takes 24 hours, but makes no claim to this figure being reliable. In spite of our lack of knowledge of these conditions, it must even at this stage be allowed to point out that the values for the intensity of spawning closely approach the figures for number of eggs in the oviducts in the females of *Calanus finmarchicus*. Closer investigation of these conditions should tell us something regarding this question which is of such important for the methodics of plankton investigation. Are all groups of zooplankton caught homogeneously in the nets, or does there take place for unknown reasons a selection of the various groups?

Spawning in relation to Temperature and Salinity.

Spawning at the lowest temperature and salinity observed in the area was recorded at Station 119 on 20/4, 1929 with a haul 25/0 meters. The temperature was 1°.18—1°.58 C. and the salinity 32,65 ‰ — 32,73 ‰. The sample contained numerous females of *Calanus finmarchicus* with eggs in the oviducts, eggs at different cleavage stages and both early and later larval stages. The haul was very rich and lively spawning must have taken place in these water masses.

Spawning in the upper layers of water was observed in 1922 at temperatures up to 5° (Stations 75 and 76) and salinity up to 34,80 ‰. In 1929 spawning was observed in the upper 75 meters at 4°.03—5°.46 and salinity 33,75 ‰—34,42 ‰ more over in a number of deeper hauls were found females with eggs and eggs in different cleavage stages, and also both early and later larval stages. As regards *Calanus hyperboreus* of which eggs and the two first larval stages were never found in the surface layers, there can be no doubt that spawning really took place in deep water. The case is different with *Calanus finmarchicus*. Here one must always take into consideration that a small quantity from the surface hauls may remain in the nets, and get mixed with the catch in deep hauls. Such individuals which are not removed after the net has been cleaned will, however, be more or less dried or squeezed, so that they may at once be recognised in the samples. It is highly probable that the females and eggs observed in these cases came from spawning in deep water, with temperatures up to 7° and salinity up to 35,00 ‰.

Causes of the Spawning Area of *Calanus finmarchicus.*

If we take into consideration the possibility of certain minor modifications (See P. 124) the extent of the winter area of *Calanus hyperboreus* is quite decisive for the situation of the spawning locality. Spawning takes place during or immediately after the annual vertical migration of the species, and spawning takes place before the great changes in concentration after the vertical migration exercises its effects.

The spawning localities of the two species here investigated, *Calanus hyperboreus* and *Calanus finmarchicus*, differ greatly. The spawning of *Calanus hyperboreus* is very sharply restricted to the inner parts of the fjord. If we use the surface isotherms as a border line, it falls both in 1922 and in 1929 within the isotherms of 2° and 3°. Spawning of *Calanus finmarchicus* extends over a much wider area. In the first case it is not so sharply defined. Horisontally, spawning has been found everywhere in the area investigated, and it is also probable that spawning has taken place wherever the area was investigated vertically. But quantitatively there is an enormous difference between the various parts of the area. Thus the northern part differs from the southern and outer parts in that its production of the new generation is about 20 times as great.

What then are the causes of this condition of spawning of *Calanus finmarchicus?* Wherein lie these differences between the two species investigated?

There is no essential difference between the distribution of the two species in the winter stock. Both species have their greatest distribution at such great depths that large quantities of them can only occur in the inner part of the fjord during the winter period. *Calanus hyperboreus,* however, is somewhat more deeply distributed than *Calanus finmarchicus.* Both the material from 1928 and that of Nordgård from 1899 show that in December, Jannuary and February there must exist a middle strata between 150 and 300 meters where *Calanus hyperboreus* is no longer to be found, but where *Calanus finmarchicus* is still found in quantities of almost the same dimensions as deeper down. Nordgård, quite in accordance with this, (P. 91) finds small quantities of *Calanus finmarchicus* in the outer part of the fjord before the cessation of the winter condition, whilst *Calanus hyperboreus* is quite lacking. There must thus be a simple and clear connection between this phenomenon and the fact that we do not find spawning sharply confined to certain isotherms. There are always small quantities of the species to be found outside the isotherms which circumscribe the great quantities of spawning animals.

Towards the cessation of the winter condition we find, on the other hand, that the two species differ in more essential features of the greatest importance for the situation of the spawning area. The great annual vertical migration takes place earlier for *Calanus finmarchicus* than for *Calanus hyperboreus.* The ripening of the organs of sex takes place much later for *Calanus finmarchicus* than for *Calanus hyperboreus.*

The great changes in concentration which we found in the case of *Calanus hyperboreus* to be in direct connection with the vertical migration, and which we also found for the new generation of that species, are not found for *Calanus finmarchicus* in the material from the spring of 1922 and 1929. The quantitative picture is quite homogeneous both for the old and the new generation during the time of these investigations. If on the other hand we compare the material from December 1928 with that from March—April 1929 we shall see that characteristic great changes in concentration in connection with vertical migration must have taken place. We find a thorough change in the dimensions of the catch at the various stations. The catch in December must be divided by 20—40 in order that we can arrive at the same dimensions as the catch in March—April. Figure 28, which was drawn on the basis of Nordgård's tables is not an ideal demonstration of the course of the changes in concentration in *Calanus finmarchicus* of the old generation. The bottom depths at the stations investigated are not sufficiently homogeneous for that, but the table shows the time of the occurrence of the change in concentration, and as far as can be judged it shows full accordance with the dimensions found during the investigations in 1928—1929.

Dispersion of the winter stock of the old generation of *Calanus finmarchicus* over the banks commenced much earlier than in the case of *Calanus hyperboreus.*

In the 1928 material there is a considerable difference in the distribution of stages in *Calanus hyperboreus* and *Calanus finmarchicus.* In the former, an occurrence of females has begun and at the most southerly station also an occurrence of males. In the latter, it was only at the most southerly station that a few females occurred. In other words we find a far more advanced development in *Calanus hyperboreus* than in *Calanus finmarchicus.*

In the spring material the difference is still more plainly demonstrated. At the beginning of the investigations practically speaking all the specimens of *Calanus hyperboreus* caught had spawned. At that time *Calanus finmarchicus* showed only a few females which had commenced to develop eggs in the oviducts. It is during the period of these investigations that the great masses of eggs are transferred to the oviducts and undergo their period of growth.

The winter stock of *Calanus finmarchicus* does not mature its eggs until long after the vertical migration has taken place and the dispersion by the surface currents has begun.

It is thus the difference in time between the vertical migration and spawning which forms a determinative factor in the extent of the spawning area of *Calanus finmarchicus.* It is this factor which causes the area which has the high production of the species to extend so much farther out from the fjord, and to get so much wider than the corresponding area for *Calanus hyperboreus.*

The question which remains is how the spawning area can be restricted to definite isotherms.

The water which forms the upper layers in the inner part of the Norwegian fjords is characterised by a low salinity throughout the year. The temperatures are characterised by great yearly fluctuations and have, in the area investigated, the lowest values precisely in February—April. At that time when the two species here investigated have their spawning periods, *Calanus hyperboreus* its sole annual one, and *Calanus finmarchicus* its first annual one, the coastal water here under consideration will be characterised by far lower temperatures than those of the other categories which are represented.

In its extent towards the Norwegian Sea this coastal water will exhibit great seasonal variations. In the autumn it will have greatly receded. In the spring and early summer it will have its maximum extent. The transition from one of these states to the other will be characterised by great horisontal displacements of water, convection currents which proceed from the inner areas to the outer ones.

When the two species under discussion have completed their annual vertical migrations, they are in the surface coast water with low temperatures and salinity. As the bulk of them follow the strong convection currents of those waters, they must of necessity constantly be found inside the boundary lines which separate the various waters.

It is thus for purely mechanical reasons that we can localise the spawning localities of the two species to definite boundaries. The same border lines will be those of a number of factors of environment, temperature, salinity and for a certain period also high quantities of the local plant plankton (Ruud, Føyn, 1929). The circumstance that we find for *Calanus finmarchicus* the most important life processes, sexual ripening, spawning and the growth of the spawn also, in the few individuals which are to be found outside the border lines, shows that the differences in environment are of far smaller dimensions than those which are decisive for the production of the species.

Winter Stock and Changes in Concentration in the Southern Area.

In the foregoing chapters we have endeavoured to find the general features of the distribution of the two species investigated, before, during and after the annual vertical migration. In this account mention has chiefly been made of the conditions in a winter habitat. In the discussion of the topography of the area investigated it was stated that even in the southern area there are to be found local parts of various sizes where the depth is so great that we find a considerable stock spending the winter there. Nevertheless, in discussing the horisontal distribution of the two species it is shown that after the vertical migrations there are practically no individuals in the southern area. The entire area after the many tests made must be characterised as extremely poor in the occurrence of the two species. In this respect the conditions differ greatly from those of the other area with great depths, the inner area.

The question naturally arises as to the nature of this difference Do they not exist the great masses of animals which the occurrence of great depths would lead us to expect? Or, is there any essential difference between the conditions of currents in the southern and the inner area so that the changes in concentration after the vertical migrations are of other dimensions?

Material is available from the autumn of 1928, from two stations in the southern area (Stations 367 and 368) which shows catches in great depths of quite the same dimensions as those at the other stations. Nordgård investigated 2 stations in the southern area, 1899, before *Calanus finmarchicus* had completed its vertical migration and before *Calanus hyperboreus* had begun to migrate upwards. One station (See Figs 29 d and 30 c) is the same as 367, 1928, and also shows for 1899 very large catches before the changes in concentration had had any effect. Nordgård's other station (Sagfjord 18/2, 1899) where the depth does not essentially exceed 300 meters shows that *Calanus hyperboreus* was present between 200 and 300 meters and *Calanus finmarchicus* numerous from 300 meters to 50 meters. (See Nordgård and Jørgensen 1905 P. 29—30).

We can summarise the above-mentioned observations by stating that also in the southern area, from which we have samples of the winter stock, there were found large numbers of wintering *Calanus finmarchicus* and *Calanus hyperboreus.* 3 samples from Sørfjord 5/12, 1929 show very large catches of the two species in the most southerly part of the southern area.

Thus the small catches of the two species after vertical migration in the southern area cannot be due to lack of a wintering stock. The possibility which remains is that the changes in concentration on account of the conditions of currents in the area must be of dimensions differing from those in the inner area.

The existing material for the study of this phenomenon is not very homogeneous. It suffers greatly from the disadvantage that in no case material exist before and after the vertical migrations of the same year, but on the other hand it is extremely unlikely that the variations from year to year can be as enormous as those which we find if we arrange the various stations in the southern area according to season, irrespective of the year in which the collection was made.

If we investigate the changes in concentration at the station most frequently examined (Økssund Station 1 and 47, 1922, Station 367 1928) as regards *Calanus finmarchicus* we obtain the following values (Stated as the relation between the total catch and the area of the opening of the net):

10/12 1928 1.000 individuals.
17/2 1899 1.600 individuals.
4/4 1922 7 individuals.

In support of the last low figure we can refer to the surface hauls in 1922 from the station in question and the adjacent stations (See Fig. 41 Stations 1, 46, 48, 49 and 70) with a total catch of one individual, and the meagre vertical hauls from the adjacent station 46 (See Table 25).

If we review the above-mentioned hauls from the winter condition and the previously mentioned halus from the southern area 1922 we find everywhere differences of the above-mentioned dimensions, and we find that these apply to both species investigated.

There are a number of circumstances which indicate that the currents must be very different in the southern and in the inner areas. It has already been mentioned that the current in the whole area investigated (See P. 107) goes in along the southern (eastern) side of the fjord and out along the northern (Western) side. The parts of the southern area investigated (See Fig. 41) consist of small fjords and of comparatively open skerries which do not offer resistance to the ingoing convection current. The fact that a great exchange of water from without (or from the south) must take place is also shown by the high temperature and salinity in the area.

These hydrographical conditions are in marked contrast to the conditions in the well protected inner area, where during the investigations we found low temperatures and salinity. The data submitted thus indicates that the changes in concentration in the southern area are of quite different dimensions to those in the inner area. On account of the greater exchange of water, practically speaking all the wintering stock is removed by the coastal current immediately after vertical migration.

It is more probable that the small quantities of the two species which were found in the southern area were carried there from farther south, than that they are survivals of the wintered stock.

Origin of the Individuals in the Northern Area.

It will appear from the present investigations that it is much easier to carry out studies of the quantities of a species which disappears from an area than to determine whence the individuals come which are transferred to another area. It has thus been possible from the existing material to form an idea of the large masses of individuals which disappear from the inner and the southern area immediately after the vertical migrations. It is at present, largely because very few hydrographical data have yet been published, very difficult to form an idea as to the origin of the great masses which are carried into the northern area after the vertical migrations. It is certain that the bulk of them come from the wintering places in the inner and southern areas. But it cannot yet be determined to what extent individuals are supplied from localities south of the area investigated. Neither do we know in what quantities the two species already during the period of the investigations may be carried by the outgoing coastal current further northwards and westwards, away from the area comprised by the investigations. It is possible that even with the existing material we can approximately estimate the number of wintering animals and compare them with the calculations of the total number in the northern area, but it would be natural to postpone investigations of that kind until subsequent material has thrown more light over the details of these questions.

Origin of the Individuals in the Outer Area.

Neither have the investigations given many data for a consideration of the origin of the individuals in the outer area. Judging from the high temperature and salinity in the outer area very likely its water belongs to the north-going coastal current, and is less stationary than the water in the northern area.

As will appear from the following comparison between Ruud's investigations from Møre (Ruud 1929) and the material here submitted, spawning of the two species takes place earlier off the southern part of our west coast. It is therefore of considerable interest for determining the origin of the individuals in the outer area that it was found that the individuals at the outermost stations in 1929 were more advanced in their development and belonged to an earlier spawning than the individuals in the inner part of the fjord.

Comparison between the Distribution of the two species of *Copepods* and *Euphausidae* in the Area Investigated.

The present material has simultaneously with investigations of the two species of *Calanus* been examined with regard to other elements of zooplankton, including euphausidae. Hjort and Ruud (1929) have kindly published some of my data regarding the biology and distribution of euphausidae in the area (See Hjort and Ruud 1929, Pp 65—68 and Figs 41, 42 and 43). It will be seen from Fig. 41 (Hjort and Ruud 1929) that *Thysanoessa inermis* (et *neglecta)* Krøyer were absolute predominant in the 1922 material. The old generation of that species consisted of males, and females with eggs and spermatophores. In a number of females with eggs it was also observed that spawning had partly commenced. The new generation, which thus in this case may be referred to this species, consisted chiefly of eggs, nauplii and metanauplii.

As regards distribution, we find one feature common to euphausidae and the 2 species of copepods. For euphausidae also the area may have a predominant occurrence of the old generation (See Hjort and Ruud Fig. 41) and a predominant occurrence of the new generation. (See Hjort and Ruud Fig. 43). This spawning area can further be restricted as regards *Thysanoessa inermis* to certain isotherms.. It lies between the isotherms for 3° and 5° C.

There is one feature which differs in *Thysanoessa inermis* and in the 2 *Calanus* species. Their distribution is in separate parts of the area investigated. *Thysanoessa inermis* and its eggs are almost totally lacking in the northern area where the two species of *Calanus* predominate. This difference in distribution can be traced in the slightest details. Thus it has already been mentioned that on 10/4 1922 an innovation of warm water could be traced that part of the northern area which lies directly east of Værøy. It will be seen from Fig. 41 in the present work that the catch at Stations 60, 61, 62, 63 and 64, those stations which showed high temperatures and salinity, was low in respect of the two *Calanus species*. Two stations were negative, and the other three had a total catch of 148 *Calanus finmarchicus*, females. The catch per surface haul had decreased from 140, at the first observation, to 30. At the same time the catch of euphausidae eggs had increased. (See Hjort and Ruud 1929 Fig. 43), at Station 60 from 900 to 1100, at Station 61 from 250 to 2000 and at Station 64 from 0 to 250.

Very interesting are further the large figures for the catch of euphausidae eggs at Stations 46, 47 and 70 near Økssund, where as just mentioned *Calanus finmarchicus* must have been removed by an invasion of water from the south. There too the temperatures were far higher than at the adjacent stations on the northern side of the fjord.

The results of the investigations of euphausidae from 1928 and 1929 have not been published, but the material shows two very interesting features which will only briefly be mentioned here. The material from the autumn of 1928 shows that the euphausidae during the winter condition at the coast of North Norway are not, like the copepods, accommodated at great depths. They are frequently found in hauls between 100 meters and the surface. The 1929 material shows that the occurrence of euphausidae and their eggs in the inner area is very meagre. Altogether the material shows that the characteristic difference in the spawning area can be traced already in and with the difference in the vertical distribution during the winter condition. The causes of the characteristic spawning area must be sought in conditions quite different to those which we have found in the case of the two species of *Calanus.*¹)

Comparison between the two species of *Calanus* at Møre and at Lofoten.

It will appear from Table 16 that the development of both species of *Calanus* at Station 374 in Romsdal Fjord, 15/12 1929 was far more advanced than at the stations some days earlier and 5—6 degrees farther north. In the case of *Calanus hyperboreus* this is the only station from the winter condition of that year where an occurrence of males had commenced. Likewise the number of females is relatively higher than at the stations farther north. As regards *Calanus finmarhicus* this was the only station where the occurrence of females had commenced.

Ruud (1929) gives us an opportunity of comparing the conditions at Møre in 1926 and in 1927 and the conditions at Lofoten in 1922 and in 1929.

From Ruud's Table 9 (Ruud 1929 P. 33)²) it will be seen that the development of the new generation in the Romsdal Fjord 22/3 1927 had at least reached a frequent occurrence of Stage X, whilst it will be seen from Fig. 44 of his work that the same stage cannot have occurred in the Lofoten area, 1922 and 1929, until about 20/4 in the outer part of the Vest Fjord. In its inner part the development 22/4 1929 had not advanced beyond Stage VII. It will be seen from Ruud's

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¹) Investigations December 1931 and January 1932 has prooved the existence of very large numbers of Euphausidae, predominating *Thyssanoessa inermis* in certain fjords in the Tromsø area during winter conditions. The specimens undertake at this time of the year extensive daily vertical migrations, during the few hours of day they have been found between 200 and 100 meters and from 8 o'clock in the evening to to 8 o'clock in the morning they are mainly found between 100 meters and surface.

²) See also Tab. 8 in the present work where the same sample was investigated.

Table 23 that the development of the new generation of *Calanus hyperboreus* 22/3 had gone as far as Stage X, a stage (See Fig. 36) which in the Lofoten area 1929 did not appear until one month later, and in 1922 from 14 days to three weeks later.

The spawning time for the two species of *Calanus* thus commenced in the Romsdal Fjord 1926 and 1927 somewhat earlier than in the Lofoten district 1922 and 1929. In addition the development in December 1928 was farther advanced at Møre than in the Lofoten area.

Ruud's Tables 7 and 8 further show that the occurrence of copepodits of *Calanus finmarchicus* in 1926 and 1927 also over the banks off Møre commenced far earlier than in the Lofoten area, 1922 and 1929.

Ruud described the spawning period for *Calanus hyperboreus* in the Romsdal Fjord in the following manner: — (P. 50). »From this we may conclude that Spawning began in February and was probably still going on at the end of March«. Assuming that the rate of development is the same in the Lofoten area and in the Romsdal Fjord, we may conclude from the first appearance of the stages mentioned, that Spawning 1927 in the Romsdal Fjord must have commenced at the beginning of February, possibly as early as in January. The sample from the Romsdal Fjord in which the distribution of stages also of nauplii of *Calanus hyperboreus* was analysed (See Table 8 in the present work and Ruud (1929) P. 33) did not contain earlier stages than III. This stage, as we have seen from the Lofoten area, may occur even 1½ months after spawning from that part of the stock which has finished the vertical migration. There is therefore so far no reason to conclude that there is a more prolonged spawning period in the Romsdal Fjord than in the Lofoten area. Ruud too makes no mention of having found delayed spawning in deep waters which could explain his account of the protracted spawning period.

Ruud states that *Calanus finmarchicus* over the banks off the coast of Møre »has a source of its own from which it is replenished by immigrants from the coastal current farther to the south, and not from the water on the other side of the Atlantic Ocean Current«. (Hjort and Ruud 1929, P. 99). The conditions off Møre are therefore exactly the same as those over the banks investigated in the Lofoten area. It is natural to assume that the stock off Møre is renewed from the wintering localities in the fjords or the inner coastal waters in the same manner as in the Lofoten area. This is also indicated by the occurrence of *Calanus hyperboreus* over the banks which Ruud (Ruud 1929, Table 22) records from the hauls made in March—May 1926 and 1927.

An analysis of these samples also with a view to the earliest stages of *Calanus hyperboreus* will undoubtedly further elucidate the question of the origin of the great masses of *Calanus finmarchicus*.

Comparison between the Gulf of Maine and the Lofoten Area.

Biegelow (1926) gives a summary of many years' investigations of the Gulf of Maine. The work has already aroused much attention amongst European scientists because the plankton species in the Gulf of Maine are practically the same as those of the North European waters, and the faunistic conditions are mostly the same as those on the east side of the Atlantic.

Biegelow gives very few data regarding the breeding conditions in the Gulf of Maine of the two species here dealt with. He refers to investigations of that kind as an important task for future investigators. Most interesting is a comparison of his statistics of the seasonal distribution and regional distribution of the two species.

Of very great interest are the great changes in the quantities of *Calanus finmarchicus* at the various stations which Biegelow records from the months of March and April. Thus he mentions a change in concentration at a station between 12/3 and 15/4 from 103.000 to about 600 (P. 201). This indicates changes in concentration similar to those found in the southern area off Lofoten and far higher than those found in the inner area.

In some cases Biegelow states that *Calanus finmarchicus* is often restricted in its occurrence to certain isotherms as was also found in the Lofoten area. Thus for the summer of 1916 (P. 210) he states that south of New York it was limited both vertically and horisontally to water and temperature between 4° and 7°, whilst in other circumstances he was able to show that the species can live at temperatures as high as 24°. (P. 209).

The seasonal occurrence of *Calanus hyperboreus* coincides very closely with that found in the Lofoten area. In some cases Biegelow's material has permitted a far better mapping of the horisontal distribution during the different months of the year than the material from the Lofoten area. Thus in February and May he finds the species distributed over the whole of the area investigated as is the case in the Lofoten area during the time after the vertical migration. As early as in the summer months and later on through the winter months he finds the species restricted to the inner part of the area. (See Fig. 68).

Certain features of the distribution of this species appear to be very different in the Gulf of Maine from those off the coast of Norway.

Thus the material from »Johan Hjort«s cruise in the summer of 1923 shows that *Calanus hyperboreus* in the summer (June—July)was still found scattered over the outer coastal banks (See P. 73—74). In the inner parts of the fjords we mainly find remaining individuals from the spawning of the old generation. The material from the Oslo Fjord at Drøbak shows how an invasion of the new generation to the wintering places occurs in the autumn and winter months. Biegelow's material indicates that the the new generation from spawning in the Gulf of Maine is scattered over the entire area in the same manner as in the Lofoten area, but that they already very early are removed from the outer part of the area.

Biegelow (Fig. 69) shows an invasion into the Gulf of Maine from the localities lying to the north. Probable this invasion plays a very important part for the existence of the species in the Gulf og Maine, and that the conditions are thus essentially different from those in Scandinavian waters where such an invasion on a large scale cannot take place.

Nordgård (1918) and Sars (1925) show how this species occurs in the Atlantic as far south as 30 degrees N., and we must agree with Nordgård's view that this sporadic occurrence is due to cold convection currents. Is it not conceivable that the stock in the Gulf of St. Lawrence (Willey 1919) and the Gulf of Maine, even if breeding takes place at both of these places, is not a stationary stock like that in our fjords, but consists of individuals which by these convection currents have been transported from Arctic waters and on account of local conditions are more or less delayed in their further drift southwards and eastwards.

Summary.

1) The general part of the present work contains a discussion of the general laws controlling the geographical distribution and the production within a certain marine area of zooplanctonic species, illustrated by investigations of *Calanus finmarchicus* and *Calanus hyperboreus*.
2) Chapter I contains a morphological description of biological groups, eggs and larval stages of *Calanus hyperboreus* and *Calanus finmarchicus*.
3) Chapter II shows how the larval stages of the two species cannot be distinguished by measurements of the total length. By measuring the carapace it has been possible to find a method for separating the larval stages and of determining them quantitatively in the samples.
4) Chapter III deals with the biology of *Calanus hyperboreus* on the basis of experimental studies and analyses of samples from the coast of Norway from the various seasons of the year.
5) Chapters IV and V deal with investigations of the two species from the Lofoten area.
6) The two species spend the winter in the Lofoten area at great depths. *Calanus hyperboreus* in the winter condition is so deeply distributed that its horisontal extent is restricted only to the inner areas where the great depths occur. *Calanus finmarchicus,* which is somewhat less deeply distributed, is not so sharply restricted to the inner parts as the foregoing species, some few percents of the stock are also found outside the area where the greater depths occur.
7) The winter condition is for both species interrupted by an annual vertical migration. This is as regards *Calanus finmarchicus* completed about the middle of March and as regards *Calanus hyperboreus* about the middle of April.
8) During the completion of and after the vertical migration there takes place a change in concentration in those parts of the area in which a winter stock existed. This change in concentration is due to the circumstance that the individuals after reaching the higher layers of water are carried away by strong convection currents from the winter localities out over the coastal banks.

9) The changes in concentration are of various dimensions in the different parts of the area investigated. In well protected parts some of the stock remains, but in winter localities among the skerries, where there is no protection, the stock is completely carried away by the convection currents.

10) *Calanus hyperboreus* has a very restricted spawning area which may be limited to the surface isotherms for 2°—3° C.

11) This restriction to isotherms does only apply vertically. Within the prescribed area spawning takes place in layers of water with a temperature up to 7° C., the highest temperature observed in the area during spawning. Experimentally, spawning has been observed at temperatures between —1°.5 to 7°.5 C.

12) The development of eggs takes place as regards. *Calanus hyperboreus* before the annual vertical migration.

13) Spawning takes place at different rates in the upper water layers and in deep water. Experiments appear to show that both certain conditions of light and low temperatures have a stimulating effect upon the rate of spawning. Spawning is therefore probably dependent upon the annual vertical migration.

14) The extent of the spawning area as regards this species is mainly dependent upon one factor, viz. the extent of the winter area of distribution.

15) The spawning area of *Calanus finmarchicus* is not so sharply defined as that of *Calanus hyperboreus.* This is connected with the circumstance that the horisontal distribution of the species in the winter condition is not as restricted as that of *Calanus hyperboreus.*

16) About 19/20 of the stock of *Calanus finmarchicus* spawn inside the surface isotherms for 3°.5 C., but spawning takes place both horisontally and probably also vertically at all the temperatures represented in the area during the investigations. Spawning takes place with almost the same intensity everywhere where females ready to spawn are present.

17) In *Calanus finmarchicus* the development of eggs takes place after the completion of the annual vertical migration. The period of spawning is much more protracted than that of *Calanus hyperboreus.*

18) The circumstance that 19/20 of the stock spawn within definite isotherms and isohalines is due to the determination of the spawning area by two factors, 1) The horisontal distribution during winter. 2) the dispersion of the winter stock by surface currents during the time between the annual vertical migration and the development of the fullgrown eggs.

19) It is possible that the development of the new generation of *Calanus hyperboreus* into the later stages can only take place at low temperatures, a circumstance which will be of great importance in future investigations of the geographical distribution of the species and of the production of the species in various parts of the ocean.

20) Damas (1905) was able to localise a spawning area for *Calanus finmarchicus* in the southern part of the Norwegian Sea. It is most probable that the phenomenon shown by Damas is due to a numerical difference in the occurrence of spawning animals as in the Lofoten area. Helland-Hansen and Nansen (1909) show that the 3 species *Calanus hyperboreus, Calanus finmarchicus* and *Pseudocalanus elongatus* are stationary in more stationary water exposed to movements in various directions and for each species of different origin. *Calanus hyperboreus* in water of pure Arctic origin, *Calanus finmarchicus* in water consisting of a mixture of Arctic and Atlantic water, and *Pseudocalanus* in water of pure Atlantic origin. From the investigations in the Lofoten area we may conclude that the species are only stationary during the winter condition. It seems to be extremely probable that we from the investigations now carried out can establish the following rules for the geographical distribution and the production of marine pelagic animals:

21) When a species is stationary in an area of the sea, also the water of this area will have to be comparatively stationary.

22) When a species occur in waters where convection currents are prevailing a deficiency (p. 18) due to changes in ecological factors will be found.

23) The age of the water masses in their biological area is a factor of dominant influence in the production of marine pelagic animals of different areas of the northern seas.

Literature.

1920 Adler, G. & Jespersen, P.: Variations saisonniéres chez quelques copépodes planctoniques marins. Med. fra Komm. for Havundersøkelser. Serie plankton Bd. II København.

1898 Aurivillius, C. W. S.: Die Planktonfauna des Skageraks, Kgl. svenska Vetensk. Akademiens Handlingar, Bd. XXX nr. 3.

1925 Banta, A. M.: A Thelytokous Race of Cladocera in which Pseudosexual Reproduction occurs, Zeitschr. f. Ind. Abst. u. Vererb. Bd. 40, 28.

1926 Biegelow, H. B.: Plankton of the Offshore Waters of the Gulf of Maine. Departm. of Comm. Bureau of Fish. Document No. 968, Washington.

1922 Biegelow, H. B.: Exploration of the Coastal Waters off the northeastern United States in 1916 by the U. S. Fisheries schooner Grampus. Bull. Mus. of Comp. Zool. at Harvard College Vol. LXV No. 5. Cambridge.

1927 Borowski, V.: Über das Verhalten von Daphnia pulex in verschieden farbigen Licht. (In Russian) Zoologischer Bericht 1928 no. 1343.

1926 Borradaile, L. A.: Notes upon crustacean Limbs. Annales and Magazine of Natural History. Ser 9 Vol. XVII.

1908 Breemen, P. J.: van. Copepoden. Nordisches Plankton.

1927 Brehm, V.: Copepoden. Handbuch der Zoologie.

1926 Brinkmann, A.: Untersuchungen an »enthäusten« Paguriden. Bergen Mus. Årb. Natv. rekke 1924—25, No. 6.

1927 Broch, Hj.: Untersuchungen über die Marine Bodenfauna bei Lindesnes im Juni 1926: Avhandl. Norske Videnskapsakademi i Oslo, Matem. Natv. Kl. No. 5.

1886 Brooks, W. K.: Report on the Stomatopoda etc. »Challenger« Zool. Vol XVI part II. London.

1927 Brown, L. A.: On the Nature of the Equation for Growth Processes. Jorn. Gen. Physi. Bd. II. 1927—28.

1927 Brown, L. A.: Temperature Characteristics for Duration of an instar. Ibidem Bd. 10 1927.

1929 Brown, L. A.: The Natural History of Cladocerans in Relation to Temperature. I, II & III. American Natur. Vol. LXIII.

1927 Brown, L. A. and Crozier, W. J.: The Rate of Killing of Cladocerans at Higher Temperatures. Journ. Gen. Phys. Bd. 11.

1863 Claus, C.: Die freilebenden Copepoden. Leipzig.

1866 Claus, C.: Copepodenfauna von Nizza. Marburg und Leipzig.

1888 Chun, C.: Die pelagische Tierwelt in grösseren Meerestiefen und ihre Beziehung zu der Oberflachen-Fauna. Bibliotheca zoologica, Heft I.

1905 Damas, D.: Notes Biologiques sur les capépodes de la mer Norvégienne. Publ. de Circonstance No. 22.

1909 Damas, D.: Plankton. Report on Norw. Fish. and Marin. Invest. Vol. II part I. Bergen.

1907 Damas, D. et Koefoed, E.: Le plankton de la mer du Grønland. Croisière Ocean. Belgica 1905. Bruxelles.

1897 Davenport: Experimental Morphology. New York.

1915 Derjugin, K. M.: The fauna of the Kolafjord. (Russian) Petrograd.

1906 Ditelvsen, Hj.: Forsøg over Nogle Planktondyrs forhold overfor lys. Kgl. Danske Vid. Forhandl. No. 2.

1900 Ekmann, S.: Phyllophoden und Copepoden der schwedischen Hochgebirge. Zool. Jahrbücher, Abt. System. Bd. 18.

1914 Ekmann, S.: Studien über die marinen Relikte der Nordeuropäischen Binnengewässer III. Internat. Revue d. ges. Hydr. und Hydr. Bd. VI Heft 6.

1911 Esterley, O. C.: Diurnal Migrations of *Calanus finmarchicus* in the San Diego Region during 1909. Ibidem Bd. IV.

1912 Esterley, O. C.: The Occurrence and vertical Distribution of the Copepoda of the San Diego Region. Univers. of California Publ. Zool. Vol. 8 No. 6.

1919 Esterley, O. C.: Reactions of various plankton animals with reference to their diurnal migrations. Ibidem Vol. 19 No. 1.

1910 Farran, G. P.: Copepoda. Bull. trimesteriel Part I—II.

1920 Farran, G. P.: On the local and seasonal distribution of the pelagic copepoda of the South-west coast of Ireland. Publ. Circ. No. 73.

1927 Farran, G. P.: The reproduction of *Calanus finmarchicus* off the South Coast of Ireland. Journal du Conseil. Vol. II No. 2.

1916 Gårder, T.: De vestlandske fjorders hydrografi. Bergen Mus. Årb. 1915—16.

1893 Giesbrecht. W.: Systematik und Faunistik der Pelagischen Copepoden des Golfes von Neapel und der angrenzenden Meeresabschnitte. Berlin.

1898 Giesbrecht, W. und Schmeil: Copepoda I Gymnoplea. Das Tierreich.

1921 Giesbrecht, W.: Arthropoda II in Lang: Handbuch d. Morphologie. Jena.

1900 Gran, H. H.: Hydrographic-Biological Studies of the Northern Ocean and the Coast for Nordland. Report Norw. Fish. and Marin Invest. Vol I No. 5.

1902 Gran, H. H.: Das Plankton des norwegischen Nordmeeres. Ibidem Vol. II Part II No. 5.

1912 *a.* Gran, H. H.: Preservation of Samples and Quantitative Determination of the Plancton. Publ. de Circ. No. 62.

1912 *b.* Gran, H. H.: Pelagic Plant Life (I Murray and Hjort 1912).

1881 Grobben, C.: Die Entwicklungsgeschichte von *Cetochilus septemtrionalis* Goodsir. Arb. aus d. Zool inst. Wien.

1929 Harvey, J. M.: The action of light on *Calanus finmarchicus* (Gunner) as determinated by its effect on the hart rate. Contr. to Canadian Biol. and Fish. N. S. Vol. V no. 4.

1909 Helland-Hansen, B. and Nansen, F.: The Norvegian Sea. Report on the Norv. Fish. and Marin. Vol. II Part I.

1899 Hjort, J. and Gran, H. H.: Currents and Pelagic Life etc. Report on Norv. Fish. and Marin 1895—97. Bergen Museum.

1900 Hjort, J. and Gran, H. H.: Hydrographic Biol. Invest on the Skagerak and the Kristiania-fjord. Report on Norv. Fish. and Marin Vol. I.

1927 Hjort J, and Ruud J. T.: A Method for the analysis and Comparision of Plancton Samples. Journ. d. Conseil Vol. II.

1929 Hjort, J. and Ruud, J. T.: Whaling and Fisching in the North Atlantic. Conseil Perm. Internat.

1915 Hofsten, N.: Die Echinodermen des Eisfjords. Kgl. Svenska Vet.-Akad. Handlingar Bd. 54.

1910 Jensen, Johansen and Levinsen: De danske farvandes plankton i årene 1898—1901. Kgl. Danske Vid. Skr. 6 rekke XII No. 3.

1842-45 Krøyer, H.: Voyages en Scandinavie en Laponic aux Spitzberg et aux Férøe 1842–45.

1910 Kraefft, F.: Über das Plankton im Ost und Nordsee uud den Verbindungsgebieten mit besonderer Berücksichtigung der Copepoden. Wiss. Meeresunt Abt. Kiel Bd. XI.

1916 Lebour, M.: Stages in the Life-history of *Calanus finmarchicus* (Gunnerus) experimentally reared by Mr. L. R. Crawshay in Plymouth Laboratory. Journ. Marin Biol. Ass. Vol. XI No. 1.

1912 Lysholm, B.: Trondhjemsfjordens planktoncopepoder. Kgl. Norske Videnskapsselskaps Skr. No. 7.

1921 Lysholm, B. and Nordgård, O.: Copepoda collected on the cruize of the M/S Armauer Hansen in the north Atlantic 1913. Bergens Mus. Årb. 1918—19 Natv. No. 2.

1927 MacArthur, J. W. and Baillie, W. H. T.: Relations between Metabolisum, Longevity, and Sex in *Daphnia magna* as expressed at different temperatures. Anatomical Rec. 37.

1924 Mosby, O.: Temperaturen i sjøen under Lofotfisket. Årsberetning for Norges Fiskerier Hefte 2 1923.

1930 Mosby, O.: De Vestlandske fjordes hydrografi III. Bergen Mus. Årb. Nat. rekke No. 1.

1902 Mràzek, A.: Arktische Copepoden. Fauna Arctica. Bd. II Jena.

1912 Murray and Hjort: Depths of the Ocean. London.

1929 Nikitine, B.: Les Migrations Vertikales Saisonniéres des Organismes Planctoniques dans la mer Noire. Bull. de L'inst. Ocean. Monaco No. 540.

1899 *a.* Nordgård, O.: Contribution to the Study of hydrography and Biology on the Coast of Norway. Report on the Norv. Fish. and Marin 1895—97. Bergen Museum.

1899 *b.* Nordgård, O.: Undersøkelser i fjordene ved Bergen 1897—1898. Bergen Mus. Årb. 1898.

1900 Nordgård, O.: Some hydrographical Results from an expedition to the north of Norway. During the Winter of 1899. Ibidem 1899.

1901 Nordgård, O.: Undersøkelser i fjordene ved Bergen 1899. Ibidem 1900.

1902 Nordgård, O.: Hydrography of the North Ocean. Ibidem 1901.

1911 Nordgård, O.: Faunistiske og biologiske iagttagelser ved den biologiske station i Bergen. Kgl. Norske Vidensk. Skrifter No. 6.

1918 Nordgård, O.: Planktonorganismene, spesielt Copepodene som indikasjon for havets strømme. Forh. Ved de Skand. Naturf. 16. Møte, Kristiania.

1905 Nordgård, O. and Jørgensen, E.: Hydrographical and Biological Investigations in the Norwegian fjords. Bergen Mus. Skrifter.

1906 Oberg, M.: Die Metamorphose der Planctoncopepoden der Kieler Bucht. Wiss. Meeresu. Abt. Kiel Neue Folge Bd. 9.

1906 Paulsen, O.: Studies on the biology of *Calanus finmarchicus* in the Waters round Iceland. Med. Komm. for Havundersøgelse Serie Plankton. Bd. 1 No. 4.

1924-25 Rose, M.: Les Copépodes pelagiques de la mer de Monaco. Bull. de L'Inst. Ocean. Monaco. No. 439, 447, 448. 449, 459, 460.

1925 Rose, M.: Contribution a L'Etude de la Biologie du Plancton. Arch. de Zool. Expér. et Gènerale Tome 64.

1925 Runnstrøm, S.: Temperatur og utbredning etc. Naturen. Bergen.

1927 Runnstrøm, S.: Über die Thermopathie der Fortpflanzung und Entwicklung mariner Tiere in Beziehung zu ihrer geographischen Verbreitung. Bergen Mus. Årb. No. 2.

1929 Runnstrøm, S.: Weitere Studien über die Temperaturanpassung der Fortpflanzung und Entwicklung mariner Tiere. Ibidem No. 10.

1929 Ruud, J. T.: On the Biology of Copepods off Møre 1925—27. Conseil Perm. Internat.

1929 Ruud—Frøyn, B.: Investigation of the Phytoplankton at Lofoten, Mars—April 1922—27. Vid. Akadem. Skr. Nat. No. 10.

1828 Russel, F. S.: The vertical distribution of marin macroplankton VII *Calanus finmarchicus*. Journ. Mar. Biol. Ass. 152.

1900 Sars, G. O.: Crustacea. The Norwegian North Polar Expedition 1893—96, Vol. I. Christiania.

1903 Sars, G. O.: An account of the Chrustacea of Norway etc. Bergens Mus. Bergen.

1925 Sars, G. O.: Copepodes particulierement bathypelagiques provenant des Champagnes Scientifiques du Prins Albert I er de Monaco. Impremiere de Monaco.

1927 Schulz, H.: Über die Bedeutung des Lichtes im Leben niederer Krebse (nach versuchen an Daphnien). Zeitsch. Vergl. Physiol. Bd. 7 No. 3.

1920 Skogsberg, T.: Studies on marine Ostracods I Zool. Beitr. aus Upsala Suppl. bd. I.

1929 Størmer, L.: Copepods from the Michael Sars Expedition 1924. Conseil Perm. Internat.

1924 Sund, O.: Temperaturen i sjøen. Årsbetetning Norske fiskerier 1924 hefte 2.

1926 Sund, O.: Undersøkelser i Vestfjorden 1926. Ibidem 1926 H. 2.

1927 Sømme, J. D.: Faunistische und Quantitative Studien über Polychaeten aus dem Lenefjord und dem Grønsfjord. Zool. Anzeiger Bd. LXXIV heft 5—6.

1929 *a*. Sømme, J. D. Lengdevariasjoner hos *Calanus hyperboreus*. Report of the 18. Scandinav. Naturalist Congress in Copenhagen. 1929.

1929 *b*. Sømme, J. D.: Note on the northern limit of the distribution of *Rhincalanus nasutus* Giesbr. Journ. du Conseil Vol. 4 No. 3.

1876-79 Weismann, A.: Beiträge zur Naturgeschichte der Daphnoiden. Leipzig.

1919 Willey, A.: Report on the Copepoda etc. Gulf of St. Lawrence. Canad. Fish. Exped. 1914—15. Ottawa.

1915 With, C.: Copepoda I Calanoidea Amphascandria. The Dan. Ingolf Expd. Vol. III. Copenhagen.