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TREÅRSEXPEDITIONEN TIL CHRISTIAN DEN X'S LAND 1931-34

UNDER LEDELSE AF LAUGE KOCH

THE LARVAL DEVELOPMENT, GROWTH,
AND METABOLISM OF ARCTIC MARINE
BOTTOM INVERTEBRATES

COMPARED WITH THOSE OF OTHER SEAS

BY

GUNNAR THORSON

WITH 32 FIGURES IN THE TEXT

KØBENHAVN

C. A. REITZELS FORLAG

BIANCO LUNOS BOGTRYKKERI A/S

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PREFACE

The Danish Three-Year Expedition to East Greenland in 1931—34, which, under the leadership of Dr. LAUGE KOCH, was to make a thorough scientific investigation of the regions between Scoresby Sound and Danmarkshavn on the north-east coast of Greenland, had for its object among other things a detailed investigation of the topography, hydrography, and animal life of the large fjord systems — an object which was to be attained not only through faunistic and zoogeographic investigations, but in which the main stress was to be laid on biologic-ecological results.

As a member of this expedition the author had the opportunity of wintering, from August 1931 to August 1932, on Ellæ in the Franz Joseph Fjord district, investigating exclusively marine-biological problems, which, among other things, rendered it possible to make a series of investigations of the animal life of the fjords through all the months of the year, and to operate fairly extensively with living material. Several of these investigations were continued the following year (August 1932 to August 1933) from Eskimonæs on Claveringø by mag. sc. HOLGER MADSEN, so that the risk of generalising purely local variations or drawing too many conclusions on the basis of a single year's observations would thereby be considerably minimised. Moreover in the summer of 1932 a thorough investigation of the whole Franz Joseph Fjord complex was made from the expedition ship, s.s. "Godthaab", under the leadership of Dr. R. SPÄRCK, and in 1933 the author was able to make a similar investigation of Scoresby Sound from the "Godthaab".

The material secured during these investigations was brought back to the Zoological Museum of the University of Copenhagen, where the preparation was subsequently continued. As a result of this work a series of papers have already been published (SPÄRCK 1933, H. MADSEN 1936, THORSON 1933, 1934a, 1934b, 1935a, and 1935b), and the present paper, too, is to be regarded as part of this examination and description of the material.

A work like the present, which deals with so many different animal groups, cannot, of course, be carried through without the author receiving help from many quarters.

Professor zoologiæ AD. S. JENSEN secured to me the unique opportunity of wintering in Northeast Greenland under conditions which rendered it possible to do zoological work all the year round, and Dr. R. SPÄRCK has been of great assistance to me both during my stays in East Greenland and during the working up of the material in Copenhagen. I beg both these gentlemen to accept my most cordial thanks.

Further, my colleagues at the Zoological Museum of the University have assisted me in the determination of difficult animals; thus cand. mag. K. STEPHENSEN (*Crustacea*), mag. sc. Mrs. E. WESENBERG-LUND (*Polychaeta*), and Mr. S. HEDING (*Echinodermata*). Dr. TH. MORTENSEN, Dr. P. L. KRAMP, and Professor C. WESENBERG-LUND helped me in questions concerning literature and have also otherwise shown great interest in my work. Stud. mag. E. BERTHELTSEN determined a large part of the crustacean material, stud. med. Miss BERTHA JENSEN dissected out the large gonad material which forms the basis of the investigations on spawning, Miss E. GLEERUP translated the present paper into English and Mr. H. RØHLING plotted the numerous curves. Further, mag. sc. HOLGER MADSEN, who continued the investigations at Eskimonæs, placed material at my disposal, cand. mag. H. USSING undertook the examination and description of the plankton animals and also supplied me with observations on larvæ of bottom animals found among these, which I had not observed myself. The two latter gentlemen have further been my zoological collaborators in Northeast Greenland. The Greenlander BENJAMIN SAMUELSEN, Godhavn, collected monthly plankton samples at Ellaø in the autumn of 1932. To all these I here wish to express my grateful acknowledgements.

Finally, my special thanks are due to the leader of the Three-Year Expedition, Dr. LAUGE KOCH, who by the excellent planning of the winterings and by placing the expedition ship the s.s. "Godthaab" at the disposal of the marine-biological investigations in the summers of 1932 and 1933 created such rich possibilities for carrying out the biological work, and who also during the subsequent working up of the material has assisted me in every way.

INTRODUCTION

As part of the results of the marine-biological investigations in Northeast Greenland in recent years (topography, hydrography, and the animal-communities of the sea-bottom) have now been worked up and published, it is possible to survey the bottom fauna in its main features.

The object of the present work, then, is to attempt, on the basis of the material collected from Northeast Greenland, to point out important biological features common to the invertebrate species that compose the bottom fauna of the arctic seas, and, if such common features can be ascertained, to compare them with biological features common to the bottom animals within other areas of the sea-bottom.

Of the more important biological functions of the marine invertebrates reproduction and nourishment seemed to me to be well suited to serve as a basis for such an investigation of common features. As regards reproduction this choice proved very happy, it being possible to take a survey of its main features. However, as regards the nutritive problem the case is somewhat different, the physiology of nutrition in the marine invertebrates being still so little known that a real survey must for the present be regarded as impossible. In this paper, therefore, only some few aspects of the question of nourishment have been indirectly elucidated through a survey of the growth and the consumption of oxygen.

During the work with these matters it has been a great impediment that after the return from Northeast Greenland in 1933 the investigation has been entirely dependent on the observations and material collected up to that time, supplementary investigations in the localities where collections were made not being possible. Thus a number of observations which might perhaps have been established with certainty by renewed investigations on the spot were reduced to mere hypotheses and conjectures. If these observations have nevertheless been included here, it is in the hope that marine biologists will in future direct their attention towards them and subject them to a thorough investigation.

The area of the sea whose bottom fauna is to be treated in the present paper comprises partly the outer coast of Northeast Greenland from Kangerdlugssuak ($68^{\circ}10'$ N. lat., $32^{\circ}00'$ W. long.) in the south to Danmarkshavn ($76^{\circ}50'$ N. lat., $19^{\circ}00'$ W. long.) in the north, partly the immense fjords which open out along this stretch of the coast. While in this work the designation "Northeast Greenland" includes the coast and fjords as a whole, the term "the Northeast Greenland fjords" will be used in the description of phenomena ascertained in the fjords alone. As by far the greater part of the material collected is derived from "the Northeast Greenland fjords", these will be described in somewhat greater detail here.

The Scoresby Sound and the Franz Joseph Fjord districts are the largest and the second largest fjords of the world, respectively. From the outer coast their many ramifications extend 250 to 300 km into the country, where their interiors are bounded by huge perpendicular mountain walls and terminate directly in the glaciers of the inland ice. During eight and a half to nine months of the year the surfaces of the fjords are covered by a layer of ice 1 m to 2 m thick, which only disappears during the actual summer months (July, August, and September). These facts alone will render it obvious that marine-biological work in these regions is very difficult, and when it is further added that the ships of the expedition in order to be able to push into the fjords at all often have to pass an ice barrier along the outer coast 100—200 km in width, it is not to be wondered at that the animal life of the fjords has hitherto been very little known. It is true that earlier expeditions have brought home animal material from these tracts, so that it has been possible to obtain a quite provisional faunistic survey of the fjords, but investigations have never before been made from purely biologic-ecological points of view, the special relations between the stock of bottom animals and the particular conditions of the fjords having so far been entirely unknown.

However, through the investigations made in Northeast Greenland during the last few years we have succeeded in obtaining in broad features a general view of the topography, the hydrography and the animal communities of these fjords, and as the subjects to be discussed in the present paper are based entirely on the view gained during the last few years, it seems reasonable here to give a summary of the conditions especially characteristic of Scoresby Sound and Franz Joseph Fjord.

1) Topography (cf. SPÄRCK 1933 and THORSON 1934a). In those parts of the Franz Joseph and Scoresby Sound fjords that are situated nearest to the open sea the rocks are chiefly sediments, which form not particularly high, often fairly rounded mountains. In the interior

of the fjords conditions are quite different. Here the crystalline rocks make their appearance — at a sharp boundary nearly in the middle of the fjord areas — and these rocks are now predominant throughout the interior of the fjord areas. Where the crystalline rocks begin, the landscape immediately changes its character. Perpendicular mountain walls, about 1500 to 2000 m high, with jagged, often ice-clad peaks bound the fjords; at the heads of the ramifications of the fjords the inland ice sends out its glaciers, and here, especially in summer, the large production of huge icebergs, which lend their special character to these inner fjords, takes place.

The bathymetrical conditions of the fjords correspond entirely to the configuration of the surrounding territory. Thus at a rather small depth (about 200 m) a "shelf" extends along the outer coast. The shelf is cut across by grooves, through which the Greenland Sea communicates with the outer fjord basins, which attain a depth of 400 to 600 m. In the inner fjords the depths — corresponding to the much higher mountain walls — are much greater, ranging in the Franz Joseph Fjord district from 600 to 900 m, while in Scoresby Sound they may be even about 1450 m (Northwest Fjord) — the greatest depth of any fjord known so far. While in the Franz Joseph Fjord area the various basins are often separated by shallow-watered thresholds (at a depth of less than 200 m), and the whole fjord area thus consists of typical threshold fjords (e. g. Dusén Fjord, Geolog Fjord, and Franz Joseph Fjord itself), the thresholds in Scoresby Sound are but few in number and occur at a depth of at least 400 m. In Scoresby Sound a threshold is absent, among other places at the mouth of the fjord, and the outer basin of Scoresby Sound, 150 km long, seems throughout the greater part of its depth to communicate directly with the open sea, and moreover Scoresby Sound opens into the sea with a much wider mouth than Franz Joseph Fjord.

2) Hydrography (cf. SPÄRCK 1933, THORSON and USSING 1934a). In Scoresby Sound and Franz Joseph Fjord a surface layer with positive temperatures of a thickness of 10—25 m is formed in the summer. At the surface proper the temperature may rise to about 12° C and even to a depth of 10 m temperatures of 5°—6° have been measured (average temperature, however, 2.5° C). This surface layer has an average salinity of about 30 per mille. Immediately below the surface layer and down to a depth of 300—400 m there is a layer of water with negative temperatures (0° to —1.70° C, salinity 32.30—34.80 per mille), the so-called "Polar Current water", and below this another layer with positive temperatures (0° to 1.70° C and a fairly constant salinity of 34.60 to 34.95 per mille). At the beginning of October the positive surface layer disappears and soon assumes the same temperature as the subjacent

layer of Polar Current water, and at the same time the surface of the fjord is covered by a layer of ice, which towards springtime may be more than 2 m thick. Not till the end of June or the beginning of July, when this layer of ice breaks up or melts, will a positive surface layer form again and remain for 3—4 months. During the melting of the ice this surface layer may for a short period (about two weeks) be extremely fresh (thus at a depth of 3 m at Ellaø the salinity was 3—4 permille).

It seems indispensable for the occurrence of positive bottom water in the deep East Greenland fjords that the threshold of the fjord, if any, should lie below the surface of the bottom water layer with positive temperatures (i. e. deeper than 300—400 m). As stated above, several of the thresholds in Franz Joseph Fjord occurred at a depth of 200 m only, and fjords of this type, therefore, in addition to the positive surface layer, contain only Polar Current water (e. g. Dusén Fjord and Geolog Fjord). In Scoresby Sound, however, no thresholds occur at depths less than 400 m, which naturally has the effect that the positive bottom water layer occurs even in the innermost fjord ramifications. This also results in a difference in the movements of the water within the two fjord areas, the movement being somewhat stronger in Scoresby Sound than in Franz Joseph Fjord, where it seems to be extremely slight. The latter conjecture is supported i. a. by the fact that the deeper water layers of the inner fjords are known to be very poor in oxygen and consequently can hardly be supposed to be renewed very often. A zoological phenomenon that might perhaps be supposed to indicate the same is, that sedentary animals like hydroids and bryozoans are very rare in the inner fjords, and that actinians are normally only found adhering to living snails (*Sipho*, *Buccinum*), and their nourishment therefore is less dependent on the movements of the water. In the outer district of Scoresby Sound the communication with the sea is so open and the movements of the water so considerable that extensive areas with a sandy bottom are found, a phenomenon which according to the available literature does not seem to be common in the Arctic.

Finally it should be noted that in summer — especially in the month of August — the transparency of the water in the inner fjords is very slight, i. a. on account of the mud carried down by the large water-streams and the glaciers of the inland ice, which may make the surface of the water quite milky. This opacity of the water is of great ecological importance, since it prevents the light from penetrating through the water and thereby reduces the intensity of the assimilation of the phytoplankton even within the already very limited summer time (cf. pp. 83—95).

3) The animal communities of the fjord bottom (cf. SPÄRCK 1933 and 1935, THORSON 1933 and 1934a).

I. The animal communities of the level sea bottom. By means of $\frac{1}{10}$ and $\frac{1}{5}$ sq.m. PETERSEN bottom samplers a large number of quantitative bottom samples were taken in the Franz Joseph Fjord and Scoresby Sound in the years 1931, 1932, and 1933. The details of these investigations with tables and plates showing the distribution of the bottom animals were published in the above-mentioned works. Here merely a brief summary of the animal communities and their distribution as a basis for the subsequent investigations will be given.

The *Macoma-calcaria*-community. The type animal is the lamellibranch *Macoma calcaria*, which is always frequent in the samples. This community occurs everywhere on the soft bottom along the coasts of the Northeast Greenland fjords from 4 m out to 45 m depth. As this community may vary considerably in its composition in the different localities, some of the more frequent variations will be described in greater detail.

The *Astarte-borealis*-zone. In addition to *Macoma calcaria* there occur here as typical accompanying animals the lamellibranch *Astarte borealis* and the worms *Priapulus caudatus*, *Nereis zonata*, and *Harmothoe imbricata*, while ophiurans are entirely absent. In Franz Joseph Fjord the polychaete *Pectinaria granulata* is extremely characteristic of this zone, while it is wholly absent from Scoresby Sound. The *Astarte-borealis*-zone is the shallow-water zone of the *Macoma-calcaria*-community, which zone both in Franz Joseph Fjord and in Scoresby Sound has its main distribution at depths ranging between 4 m and 15 m, and thus in summer attains fairly high water temperatures (up to 5° to 6° C).

The lower *Ophiecten*-zone. In addition to *Macoma calcaria* the ophiuran *Ophiecten sericeum* and the crustaceans *Philomedes globosus* and *Diastylis* sp. are characteristic of this zone, and in Franz Joseph Fjord further *Pectinaria granulata*. In Franz Joseph Fjord this zone is found throughout the fjord area at depths of from 14 m to 25 m, and thus lives even in the water layers which have positive temperatures in the summer (though only slightly above 0° C). In Scoresby Sound this zone is not distinguishable from:

The deeper *Ophiecten*-zone. *Macoma* is still the type animal. *Ophiecten sericeum* is a frequent accompanying animal, and in addition the lamellibranchs *Pecten groenlandicus*, *Portlandia lenticulata*, *Nesera obesa*, and *Macoma moësta* are of common occurrence, though none of them can be said to be especially frequent. In Franz Joseph Fjord, too, *Pectinaria granulata* is absent from this zone, while the zone proper is distinct at all depths from 25 m to 45 m, and thus is characteristic by living constantly at negative temperatures. In Scoresby Sound the zone is completely fused with the preceding one to a common *Ophiecten*-zone, which is found in the same localities and at the same depths as the two *Ophiecten*-zones in Franz Joseph Fjord.

The *Halcampoides*-zone. *Macoma* is a type animal, but in regard to weight it ranks second to the accompanying animal, the actinia *Halcampoides purpurea*, which may occur in a number of over 100 individuals per sq.m. and of a weight of about 280 gr. Of other typical accompanying animals may be mentioned *Ophiecten sericeum* and the lamellibranch *Axinus flexuosus*. This zone is only known from Hurry Inlet in Scoresby Sound, where it was found at depths of about 30 m. Thus it seems to live under constantly negative temperatures, but to all appearance (judging e. g. by the large number of sedentary actiniae and the considerable weight, about 370 g per sq.m), this zone will only develop under particularly favourable food conditions.

The *Macoma-calcaria*-community is unquestionably the shallow water community most widely distributed within the Northeast Greenland fjords, where it extends along the coasts out to about 45—50 m depth. Its weights also are fairly considerable, for the four above-mentioned zones about 110 g, about 80 g, about 100 g, and about 380 g per sq.m respectively.

The *Macoma-calcaria*-community is further widely distributed in the other arctic seas, whence it is known i. a. from Storfjord at Spitsbergen (the *Ophiecten*-zone, cf. BROTZKY 1930), from the Spitsbergen Bank (IDELSON 1931), from the waters round the Kánin Peninsula (ZENKEWITSCH 1931), from the Barents Sea (the *Astarte-borealis* and *Ophiecten*-zones), and from the White Sea (ZENKEWITSCH 1927), as also from northern Norway (SOOT-RYEN 1924), (cf. also SPÄRCK 1935). From the Faroes and Iceland, too, this community is known (SPÄRCK 1929), and it also occurs as a relict in the Baltic and the southern part of the Great Belt (C. G. JOH. PETERSEN 1913, THORSON 1933, p. 50).

For the succeeding investigation of the reproduction and nourishment of the animals of the sea bottom this even distribution of the *Macoma*-community throughout the Arctic means that a large proportion of the results gained may be generalised for other arctic seas also, which necessarily gives the investigation a wider range.

The *Venus-fluctuosa*-community. The type animal is the lamellibranch *Venus fluctuosa*. Frequent accompanying animals are the lamellibranchs *Thracia truncata*, *Pandora glacialis*, and *Astarte borealis*. Thus only lamellibranchs are of quantitative importance within this community. The community is known from the shallow-watered coast stretches at the mouth of Scoresby Sound (Cape Hope), where a strong movement of the water has sorted the suspended material, so that a "pure" sandy bottom is found. The community is known here from depths of 9 m to 20 m, and as the surface temperature at the mouth of Scoresby Sound is generally lower than in the inner fjords (cf. THORSON and USSING 1934a), it means that the community lives at constantly

negative temperatures. The weights (about 370 g per sq.m) are very considerable, presumably on account of the rich supply of nourishment furnished by the strong movement of the water.

The *Venus*-community is not known from any other arctic localities, but will probably prove to be present wherever a suitable sandy bottom is found.

The *Portlandia-arctica*-community. The only type animal is the lamellibranch *Portlandia arctica*, and hardly any accompanying animals occur. In its typical form the community is found off river mouths and in front of the large glaciers in Franz Joseph Fjord and Scoresby Sound, in the loose, light-grey mud deposited by the melt-water. It occurs at depths ranging from 10 to 60 m. On account of the melt-water of the rivers the temperature in the localities of the community will probably not rise above 0° C even in the summer. The weights are inconsiderable (about 40 g per sq.m). The community is so far known from the Northeast Greenland fjords only, and its distribution can hardly be compared with that of the other Northeast Greenland animal communities, but must be regarded as more local.

The *Astarte-crenata*-community. Type animals are the lamellibranchs *Astarte crenata* and *Arca glacialis*. Typical accompanying animal is the lamellibranch *Axinus flexuosus*. The community is very poor in species, and occurs at all depths from 40 m to at least 550 m. However, in the area of Franz Joseph Fjord the community seems to occur chiefly in the Polar Current layer (only down to 300—400 m depth), and to be replaced in deeper water by the succeeding community. In Scoresby Sound it is found (in Northwest Fjord) at far greater depths, and is especially in the outer completely mixed with the *Foraminifera*-community. On account of the poor food conditions in the fjords it must even be considered ecologically as a "deep water community", and in agreement herewith the weights are inconsiderable, but vary greatly (3 to 40 g per sq.m). In contrast to the communities previously mentioned, the *Astarte-crenata*-community is characteristic in that the lamellibranchs form less than 50 per cent. of the total weight, the polychaetes and ophiurans constituting the remainder.

The *Astarte-crenata*-community is abundantly distributed in the Northeast Greenland fjords and is also known from a number of other localities in the Arctic, for instance from Storfjord at Spitsbergen (BROTZKY 1930), from the Spitsbergen Bank (IDELSON 1931), from the Barents Sea (according to written information from Mrs. V. A. BROTZKY), and from the fjords of northern Norway (SOOT-RYEN 1924). In contrast to the *Macoma-calcaria*-community, which also had a wide distribution, the *Astarte-crenata*-community is not known from Iceland and the Faroes, the possibility exists, however, that the community does occur there,

though if so, in much deeper water, whence no bottom-samples have hitherto been available. The wide distribution of this community in the Arctic renders it probable — as for the *Macoma*-community — that several of the biological results arrived at through the subsequent investigation may be generalised for larger areas of the arctic seas (cf. pp. 122—127).

The *Foraminifera*-community. The type animals are various *Foraminifera* (*Rhabdamina cornuta*, *Miliolina bucculenta*), and as accompanying animals may be mentioned *Axinus flexuosus*, *Axinopsis orbiculata*, and the polychaete *Asychis biceps*. Known from all depths between 50 m and 780 m from Franz Joseph Fjord, however, generally only from depths over 200 m, while in Scoresby Sound the community is mixed with the *Astarte-crenata*-community in the outer districts, and in the middle basin (Hall Fjord) it is the sole community present at all depths over 40 m. Ecologically it must, like the *Astarte-crenata*-community, be regarded as a “deep water community”, and its weights are small and varying (3 to 138 g per sq.m), but on an average about 30—40 g per sq.m, or somewhat higher than the weights of the preceding community.

As mentioned above, the community is widely distributed in the Scoresby Sound and Franz Joseph Fjord. It is unknown from other arctic seas, where, however, it no doubt lives, and it must be presumed to be identical with the *Foraminifera*-community described by STEPHEN 1923 (from the deep portions of the northern Atlantic).

II. The epifauna.

A. The epifauna of the level sea bottom.

The *Saxicava-arctica*-community. The type animal is the lamellibranch *Saxicava arctica*. Various polychaetes are accompanying animals. Sometimes found in huge lumps adhering to stones and other inequalities of the sea bottom. Occurs at all depths from about 8 m to about 40 m, that is to say, at both positive and negative summer temperatures. This community is the arctic equivalent of the *Mytilus* and *Modiola* epifaunas of the boreal seas, and it seems to be far more frequent in the Franz Joseph Fjord area than in Scoresby Sound. It must be presumed to be widely distributed in the Arctic.

In deeper water (100 m and more) an *Ascidia*-epifauna and a *Gorgonocephalus*-epifauna are further met with, whose geographical and quantitative distribution are too little known to allow of a more detailed discussion.

B. The epifauna of the vegetation.

The *Margarita-groenlandica*-community. The type animals are the snail *Margarita groenlandica* and the lamellibranch *Modiolaria discors* (var. *laevigata*). Typical accompanying animals are the echinoderms *Stephanasterias albula*, *Ophiura robusta*, and *Strongylocentrotus droebakiensis*. This very productive zone, which corresponds entirely to the *Zostera*-

epifauna of the boreal seas, is of common occurrence from a depth of some 4—5 m to about 25—30 m, associated with growths of *Desmarestia* and *Fucus*. Thus nearly throughout its zone of occurrence positive summer temperatures prevail, and it is widely distributed in the arctic seas.

In deeper water (about 25—40 m) there occurs a red algal epifauna with *Acmaea rubella*, *Antedon* sp., and *Pecten islandicus* as type animals.

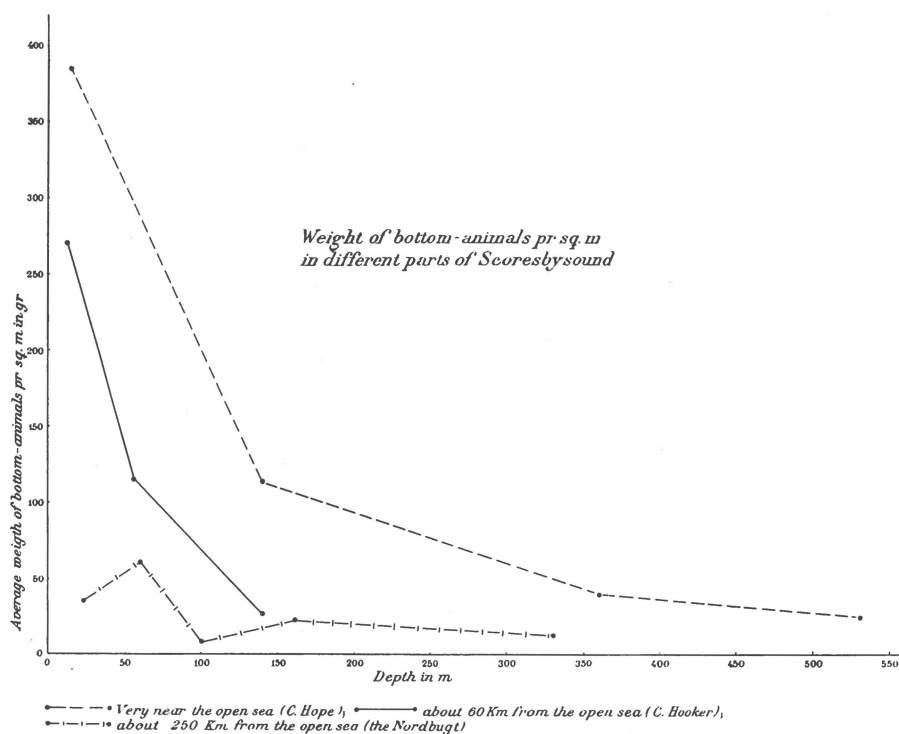


Fig. 1. Curves showing weight of bottom animals per sq.m. in gr. in different localities within the Scoresby Sound.

However, this zone seems in East Greenland, as well as in other parts of the Arctic, to be of small quantitative importance.

Most of the animal communities summarised here have been discussed in a recently published paper (SPÄRCK 1935) and considered in relation to the animal communities of other seas.

From the weights of the various animal communities given above it is strikingly evident that the shallow-water communities (the *Macoma*- and *Venus*-communities) present the highest weights, while the animal weight for the "deep water communities" is very low. This is further illustrated by fig. 1, which also shows the astonishing decrease of the weights with increasing distance from the open sea. That

this must have some relation to the food conditions and the factors on which they depend (water movement, illumination, salinity, oxygen content, etc.), must, I suppose, be taken for granted at the outset.

For the succeeding investigation the animals of the *Macoma-calcaria*- and the *Astarte-crenata*-communities as well as the animals of the two shallow-water epifaunas (the *Saxicava-arctica*- and the *Margarita-groenlandica*-communities) have especially been used. All these communities are known to be extensively distributed in the arctic seas, so that part of the results gained must be assumed to be valid for large portions of the bottom fauna of the arctic seas. As moreover these four communities show four widely different ecological types, viz. a shallow water community, including zones with positive and zones with negative summer temperatures, a "deep water community", which lives under very unfavourable food conditions, a level bottom epifauna, and finally a fauna associated with the vegetation and hence free from the competition at the sea bottom, it should be possible through these animal stocks to obtain a general view of important biological functions of the animals of the sea bottom within these fjord areas and, in part, to generalise these results for other areas of the arctic seas.

REPRODUCTION

The object of the first of these investigations of the bottom animals of the Northeast Greenland fjords was to study their reproduction. The material must at the outset be regarded as suitable for such an investigation. Thus a whole-year plankton investigation from the Solitærbugt, Ellæ, for the year 1932 was of great importance. For each month of the period January—July 50 monthly vertical hauls from 50 m depth (bottom) to the surface of a certain locality of the bay were available, and from the period August—December 10 monthly hauls were taken in the same place and in the same manner. During the winter these samples were taken in a shed built on the ice for this purpose. Through a hole in the ice floor, and by a special heating of the shed the plankton samples were placed in glass tubes without freezing, so that a counting of the contents could take place on living material. During the first half of 1932, from which so many plankton hauls are at hand, hauls were taken by means of plankton gauze of different density from different depths; but first of all it was arranged that in each month all the year round 10—20 vertical hauls should be taken through the same water column, with the same plankton net (gauze No. 12), and with the same velocity of the hauls, so that the averages of these sample series throughout the year are directly comparable and thus provide a reliable annual cycle both for plankton animals and — what is of special interest for the present investigation — for pelagic bottom animal larvae. Further, for the period from August, 1932, to July, 1933, an exactly corresponding series from Eskimonæs on Claveringsø (74°20' N. lat.) is at hand, collected by mag. sc. HOLGER MADSEN; here, however, the monthly number of samples is smaller than that from Ellæ.

In addition to these very valuable plankton series, which will also be worked up later as regards the plankton animals proper, a very large material, preserved in alcohol, is at hand from the wintering on Ellæ 1931—32, consisting of bottom animals from the months of May to October. In the summers of 1932 and 1933 this material was further

supplemented by numerous collections from the Scoresby Sound and Franz Joseph Fjord areas, and a control material was likewise collected at Ellaø in August, 1933. To these must be added a large number of observations on living material made during the long stays in East Greenland, and special investigations on the reproduction of particularly difficult groups. As regards the prosobranchs, whose larvæ were entirely absent from all the plankton samples, it was necessary to collect egg-capsules and egg-masses of as large a number of species as possible in order to elucidate the mode of development. This necessitated a special investigation, whose results assumed such proportions that a separate treatise was necessary (cf. THORSON 1935a), as the numerous details would fall outside the scope of the present work.

For quite practical reasons it has further proved necessary to restrict the investigations of the reproduction to the groups of bottom animals which are quantitatively predominant in these regions. Hence the various systematical groups have not been given an equally detailed treatment; on the contrary, ecologically important groups of animals have been dealt with at greater length than the groups which are less dominant within the areas in question. Thus the *Echinodermata* are only treated in a fairly small section, which has even given comparatively few fresh data, while the highly dominant groups such as the *Gastropoda* and the *Lamellibranchiata* have both of them been subjected to a special, detailed examination, etc.

In the treatment of the problem of reproduction for each group an accurate account is given of the material employed and the way in which it has been treated.

A. Echinodermata.

In the monthly plankton investigations at Ellaø in the year 1932 the echinoderm larvæ played but a subordinate part, qualitatively as well as quantitatively. Thus only two different types of larvæ could be demonstrated with certainty in the plankton, viz. the larvæ of *Strongylocentrotus droebakiensis* and *Ophiecten sericeum*, of which the latter larva had not previously been described. At Ellaø the *Ophiecten* larva was easily identifiable, partly on account of its great frequency, which corresponded entirely to the great dominance of *Ophiecten sericeum* in the place, partly through a comparison of the egg-size and time of spawning of the mother animals with the time of occurrence of the larva in the plankton (cf. THORSON 1934b). In the summer of 1933 it was further possible to identify the larva of the common epifauna-ophiuran *Ophiura robusta*; its characteristic larva as well as *Ophiura robusta* itself occurred in large numbers at Cape Hope (Scoresby Sound). The latter form is only known from its occurrence in the plankton during the short

summer, while the larvæ of the two other forms are distributed as follows in the plankton in the different months of the year:

*Ophiecten sericeum*¹⁾.

	Jan.	Febr.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Ellæ	7	4	15	5	0	0	6	4	1	0	1	0
Eskimonæs	10	10	5	5	0	0	470	195	75	?	10	10

Strongylocentrotus droebakiensis.

	Jan.	Febr.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Ellæ	0	0	0	0	0	0	Larvæ found	0	0	0	0	0
Eskimonæs	0	0	0	0	0	65	8	1	0	?	0	0

These two tables show that the larvæ of *Ophiecten sericeum* are far more frequent in the plankton than those of *Strongylocentrotus*, and while the latter were only found in the plankton in June, July, and August, the *Ophiecten* larvæ seem to have two annual maxima in the plankton, a summer maximum in July, August, and September, and a winter maximum in January and February. In agreement herewith the investigations of the spawning period of *Ophiecten* at Ellæ showed a summer spawning and a late autumn spawning (November, December) (THORSON 1934a). This is a remarkable fact, as the larvæ of *Ophiecten* are the only larvæ of bottom animals normally occurring in the plankton at Ellæ and Eskimonæs in January and February. A large number of the larvæ found during these winter months had started the metamorphosis into the youngest bottom stage. As the length of the larval stage is fairly considerable, it is quite possible that the last part of the larval stage is passed without feeding. This isolated occurrence of *Ophiecten* larvæ in the winter plankton may possibly be due to the fact that only such individuals of *Ophiecten* which are exposed to positive temperatures in the shallow water, spawn during the summer, while the *Ophiecten* individuals which live in somewhat deeper water and consequently at constantly negative temperatures spawn later in the year.

Our only knowledge about the time of spawning and the occurrence of larvæ of *Ophiura robusta* is that young larvæ were common in the plankton at Cape Hope, Scoresby Sound, on July 13, 1933, and that fully developed larvæ of this species were found in the plankton off the colony of Scoresby Sound on August 14, 1933. At Ellæ and Eskimonæs no larvæ of this species were found.

Thus, despite the large material of plankton samples from Ellæ

¹⁾ The figures indicate the amount of larvæ per 10 samples.

and Eskimonæs and the supplementary summer samples from other parts of the fjord complexes, only three pelagic echinoderm larvæ are known from the Northeast Greenland fjord plankton, viz. *Strongylocentrotus droebakiensis*, *Ophiecten sericeum*, and *Ophiura robusta* (cf. THORSON 1934b). As all these three species are extremely common as bottom animals in the fjords, it is quite conceivable that some of the rarer species also have pelagic larvæ, but that these have been overlooked. Hence it seems reasonable to ascertain the size of the eggs and the time of spawning in as large a number of the echinoderms of the area as possible in order to obtain a general view of their reproduction. The size of the egg in particular is of interest, since LUDWIG (1904, p. 684) and TH. MORTENSEN (1920) and others have shown as regards a great number of echinoderms that big eggs rich in yolk as a rule develop into bottom forms without any pelagic stage or with a much shorter larval development.

From Northeast Greenland in all 40 species of echinoderms are known from the literature and through the supplementary investigations of recent years, viz. 3 *Crinoidea*, 18 *Asteroidea*, 10 *Ophiuroidea*, 2 *Echinoidea*, and 7 *Holothurioidea* (cf. MORTENSEN 1903, 1910, 1913, HEDING 1935). As regards the mode of reproduction however, most of them are almost unknown.

By means of the available literature on the reproduction of the echinoderms the following types of reproduction and development can be erected:

- 1) Reproduction by small eggs with a small content of yolk, shed directly into the sea. Long pelagic larval stage.
- 2) Reproduction by eggs with a large content of yolk, shed directly into the sea. Much reduced larval stage or direct development.
- 3) Reproduction by means of large eggs with abundant yolk, which develop protected by or attached to the mother animal. Direct development with no pelagic larval stage.
- 4) Reproduction by viviparity. The big eggs rich in yolk develop without pelagic stages in the reproductive organs of the mother animal. When only the yolk mass of the egg itself is used for this development, it does not differ essentially from type 3).
- 5) Asexual reproduction by division.

In order to obtain some clue to the mode of development of the Northeast Greenland forms it will, as stated above, be reasonable to investigate the size of the mature eggs in as large a number of species as possible. MORTENSEN (1910, 1924, and 1927) has already observed such large-sized eggs in four of the echinoderms occurring within the area that he thinks it justifiable to assume that these forms lack a pelagic larval

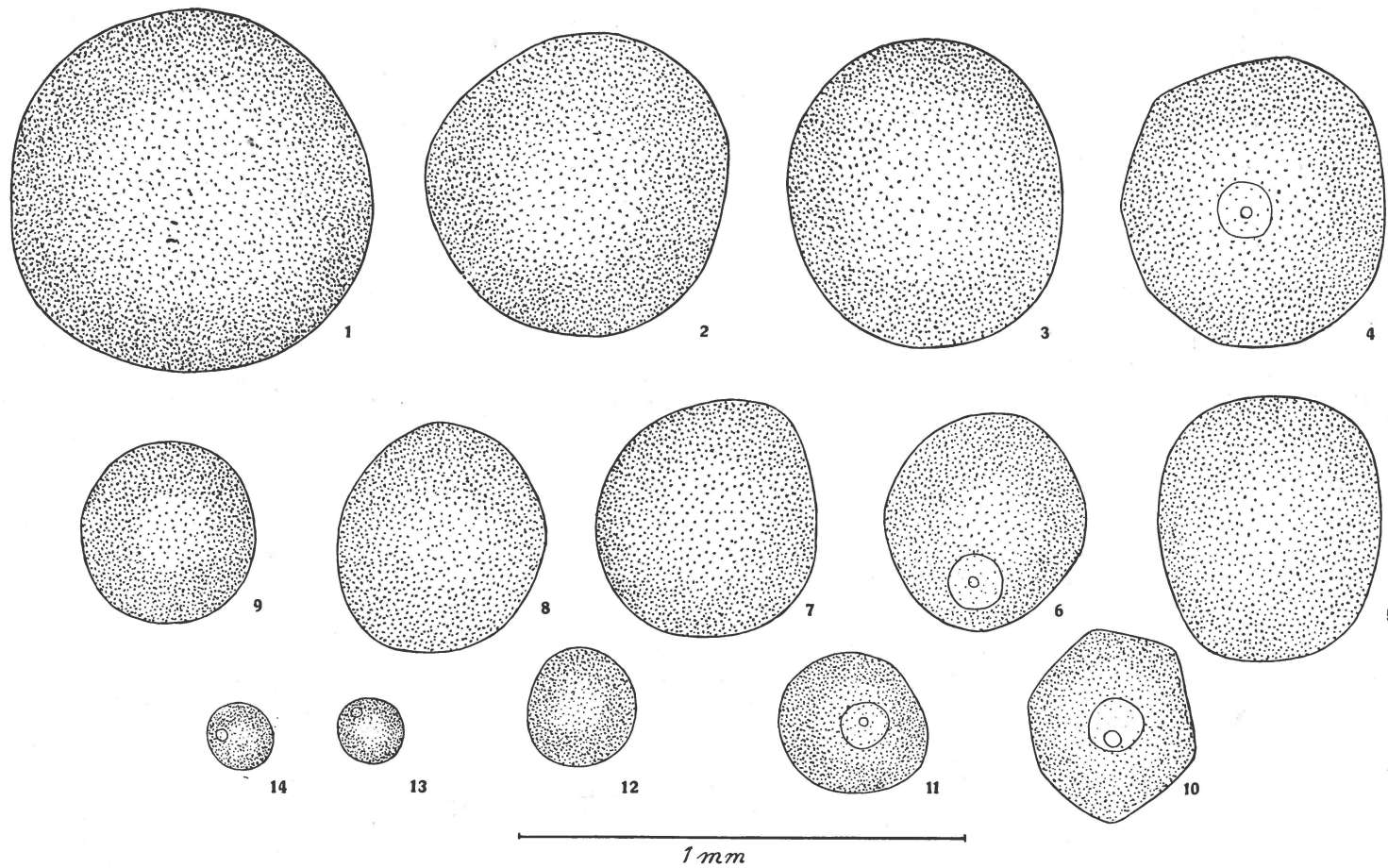


Fig. 2. Volume of nutrient matter in eggs of different echinoderms from the Northeast Greenland fjords. The two smallest eggs belong to the only two forms figured which are known with certainty to have pelagic larvæ.

1. *Ophiacantha bidentata* (0,8 mm.), 2. *Asterias linki* (0,68 mm.), 3. *Ctenodiscus crispatus* (0,60—0,70 mm.), 4. *Pontaster tenuispinus* (0,60—0,65 mm.), 5. *Hymenaster pellucidus* (0,50—0,60 mm.), 6. *Ophiopleura borealis* (0,55—0,58 mm.), 7. *Foraniomorpha tumida* (0,50—0,52 mm.), 8. *Ophioscolex glacialis* (0,46—0,51 mm.), 9. *Ophiopus arcticus* (0,40 mm. after MORTENSEN), 10. *Bathylaster vexillifer* (immature egg, 3,8—4,5 mm.), 11. *Pourtalesia jeffreysi* (3,8—3,6 mm.), 12. *Elpidia glacialis* (immature egg, 2,5—2,8 mm.), 13. *Ophiura robusta* (0,17 mm.), 14. *Ophiocten sericeum* (0,17 mm.).

stage. This applies to *Pontaster tenuispinus*, *Ctenodiscus crispatus*, *Ophiopus arcticus*, and *Ophiacantha bidentata*. The examination was continued on the recently collected large material, and in eight additional species the present author found eggs of a similar considerable size, viz. in *Elpidia glacialis* (not yet mature egg 2.3 mm in diameter), *Bathybiaster vexillifer* (4.0 mm in diameter), *Poraniomorpha tumida* (5.0 mm in diameter), *Hymenaster pellucidus* (5.5 mm in diameter), *Asterias lincki* (6.8 mm in diameter), *Ophiopleura borealis* (4.5 mm in diameter), *Ophioscolex glacialis* (4.5 mm in diameter), and *Pourtalesia jeffreysi* (3.2 mm in diameter).

Fig. 2 shows the size of the eggs of those echinoderms within the area whose egg-diameters are known. For comparison the eggs of two forms occurring in the Arctic are inserted, which are known to have pelagic larvæ, viz. *Ophiecten sericeum* and *Ophiura robusta*; the eggs of these two species prove to be of quite another and much smaller order of magnitude than the eggs of the other forms of the area. As regards *Hymenaster pellucidus*, the above-mentioned large eggs are known definitely to develop without pelagic larvæ, the species having protection of the young and the young being visible through the thin dorsal skin of the mother animal (MORTENSEN 1927). Furthermore, the literature records several forms with protection of the young or direct development. This form of reproduction has been ascertained in *Pteraster militaris* (DANIELSEN and KOREN 1856), *Henricia sanguinolenta*, *Asterias mülleri* (M. SARS 1844)¹), *Heliometra glacialis*, *Hathrometra proluxa* (MORTENSEN 1910), and *Solaster papposus* (according to MORTENSEN 1927, p. 114).

In the starfish *Stephanasterias albula*, however, the mode of reproduction was entirely unknown, although this form is of common occurrence throughout the fjord area on *Fucus* growths in shallow water. With this frequent occurrence in mind it was remarkable that all the plankton samples examined from all times of the year never contained one single *Bipinnaria* larva. Hence it was natural to assume that the species reproduces by large eggs and direct development. To examine the egg-size 32 adult individuals of the species were therefore opened, i. e. the 32 largest individuals found in the fjord area in the period May to September. Great was my astonishment when sexual organs were only found in one of the 32 individuals, namely in the largest individual, in the shape of an undeveloped testicle, while in the remaining 31 individuals sexual organs were entirely lacking. Since moreover this species always show traces of selfdivision, having arms of two markedly different sizes, and since, as mentioned above, sexual organs are lacking, it is very probable that in the Northeast Greenland fjords the species normally

¹) Here in the form *groenlandica*, which is possibly a distinct species (cf. LIEBERKIND 1921).

multiplies by division, i. e. by asexual reproduction. This is further supported by the fact that the smallest individuals found of this species (greatest length of arms 2 mm) already showed distinct traces of division. Finally there is a possibility that the species may have sexual reproduction in the winter months, whence no collections of bottom animals are available. However, this is very improbable, the species being a distinct shallow water form, which in the summer is exposed to considerable positive temperatures and thus precisely in the summer time must be assumed to possess particularly favourable conditions for spawning. As larvæ of starfishes have never been collected from the plankton, the species must thus, in case it spawns in the winter, have large eggs; and that sexual organs with large mature eggs, though lacking entirely in the summer, should be able to develop in the course of such a short time, does not agree very well with conditions in the other animal forms of the area. However, since, despite all, the largest individual of the species found contained one undeveloped testicle, this indicates that the species — either at a rather high age or in particularly favourable years — may reproduce sexually also, but it is hardly to be doubted that the commonest method of reproduction of the species in East Greenland is asexual, i. e. by division.

By combining our knowledge of the methods of reproduction in the Northeast Greenland echinoderms gained from the literature and the reproductive data of these arrived at through the most recent years, the following general view of the reproduction of the Northeast Greenland echinoderms may be given: Of the 40 species of echinoderms of the area the method of reproduction is known entirely or in part in 24 species (60 per cent.), which may be grouped as follows:

- 1) Small eggs, pelagic larvæ, 5 species (*Ophiocten sericeum*, *Ophiura robusta*, *Ophiura sarsi*?, *Strongylocentrotus droebakiensis*, and *Cucumaria frondosa*)¹⁾.
- 2) Big eggs rich in yolk, shed directly into the sea. Much reduced larval stage or direct development. 12 species (*Pontaster tenuispinus*, *Bathylaster vexillifer*, *Ctenodiscus crispatus*, *Poraniomorpha tumida*, *Asterias linki*, *Solaster papposus*, *Ophiopleura borealis*, *Ophiopus arcticus*, *Ophiacantha bidentata*, *Ophioscolex glacialis*, *Elpidia glacialis*, and *Pourtalèsia jeffreysi*.
- 3) Big eggs, rich in yolk. Protection of the young. Direct development. 6 species (*Pteraster militaris*, *Henricia sanguinolenta*, *Hymenaster pel-*

¹⁾ *Ophiura sarsi*, which is not particularly common within the area, is supposed to have pelagic larvæ (presumably *Ophiopluteus compressus* (MORTENSEN 1924)), *Cucumaria frondosa* (only known from the outer coast) has barrel-shaped red larvæ (MORTENSEN 1927), but in their pelagic stage they do not take any nourishment from the surrounding water masses.

lucidus, *Asterias groenlandica*, *Heliometra glacialis*, and *Hathrometra proluxa*).

- 4) Big eggs rich in yolk, developed in the sexual organs. Viviparous. No species.
- 5) Asexual reproduction by division. One species (*Stephanasterias albula*).

It will be seen that of the 24 species examined, 19 species (i. e. 79 per cent. of the forms examined or about 48 per cent. of all the forms known from Northeast Greenland) have direct development with no pelagic larval stage. These 79 per cent. include all the investigated forms with a "purely" arctic distribution, since 13 of the 19 species live almost exclusively in the Arctic, while 6 are arctic-boreal or have an even more southerly distribution¹). All the five forms with pelagic larvæ have an arctic-boreal or still wider distribution.

Since it is chiefly the same forms of echinoderms that occur throughout the arctic area, the results of this investigation can in all essentials be generalised for the whole Arctic. In support of this, reference may further be made to a paper on the plankton in the Eisfjord in Spitsbergen (HJ. BROCH 1908). Of echinoderm larvæ only two different ophiurid larvæ occurred in the summer plankton at Spitsbergen (*Ophioplutei*). I have had the opportunity to see the larval slides from this material, and was able to ascertain that they were the larvæ of *Ophiecten sericeum* and *Ophiura robusta*, or precisely the same two ophiurid larvæ that were found in the Northeast Greenland plankton, viz. larvæ of arctic-boreal forms.

In addition to the echinoderms known from East Greenland some few other forms with direct development, known from the Arctic, will be mentioned here for the sake of completeness. *Cucumaria glacialis* (Spitsbergen, Novaya Zemlya, the Kara Sea) has protection of the young, the eggs are 1 mm in diameter, *Ophiotjalfa vivipara* (Davis Strait) is viviparous (MORTENSEN 1913, p. 37), *Ceramaster granularis* (arctic-boreal distribution, i. a. Spitsbergen and Southeast Greenland) has big eggs with direct development (MORTENSEN 1927, p. 82), *Hippasteria phrygiana* (arctic-boreal distribution, i. a. Southeast Greenland) has big eggs and direct development (MORTENSEN 1927, p. 88).

¹) By the Arctic I mean here the area (Northeast Greenland, Spitsbergen, the Barents Sea, etc.) where the arctic animal communities (the *Macomacalcaria*-community, the *Venus-fluctuosa*-community, the *Arca-Astarte-crenata*-community, the *Saxicava-arctica*-community, etc.) predominate or are the only communities represented, while by boreal seas I mean seas (from the Faroes in the north to the Channel in the south, where boreal animal communities (the *Macomabaltica*-community, the *Syndosmya-alba*-community, the *Modiola-modiolus*-community, and the *Tellina-tenius*-community) are entirely or essentially dominant. The seas surrounding Iceland should accordingly be regarded as arctic-boreal transitional zones (cf. SPÄRCK 1935 and 1936).

Fig. 3 shows the relation between forms with a direct development and a pelagic development in the fauna of echinoderms at Northeast Greenland, Iceland, the Faroes, and Denmark. From the four areas mentioned the species whose development is known number 23, 25, 33, and 44 species respectively, in my opinion a sufficiently large number to allow of such a comparison. The graphs show distinctly that even at Iceland conditions are quite different from those at Northeast Greenland and in fact approach rather closely to the purely boreal reproductive proportions of the echinoderm fauna found at the Faroes and in the Danish waters.

Very little is known about the length of the spawning time

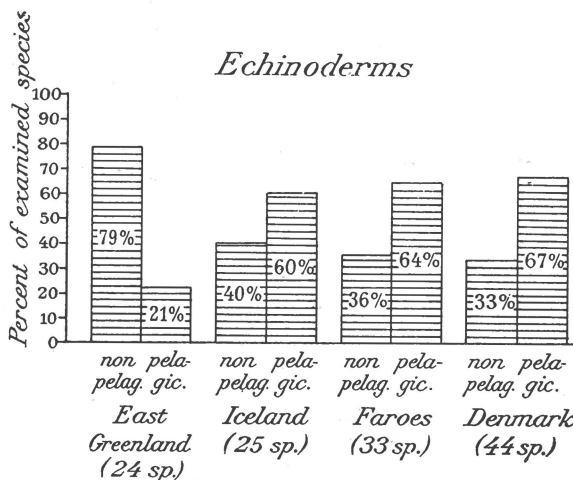


Fig. 3. Graph showing the percentage distribution of the æchinoderms as regards modes of reproduction in Northeast Greenland, at Iceland, at the Faroes, and in the Danish waters. The number of species whose development is known constitutes in Northeast Greenland 62%, at Iceland 60%, at the Faroes 75% and in Danish waters 69% of the whole Echinoderm-fauna in the locality.

in the Northeast Greenland forms. By far the greater number of the forms examined contained big, nearly mature eggs in the summer (more especially from July to September), but the few forms that were carefully examined as to spawning times, viz. *Ophiacantha bidentata* (MORTENSEN 1910, p. 274), and *Ctenodiscus crispatus* (v. HOFSTEN 1915, p. 20), show that their eggs are spawned during a very long period. However, as regards *Ctenodiscus* it can be stated that the spawning does not take place with the same intensity all the year round, since by measurements of the stock in a locality it is possible to distinguish distinct "age groups" (HOFSTEN l. c.). Such a long time of spawning — i. e. less interdependency of reproduction and summer time than in forms with small eggs and pelagic larvæ — seems to be a normal phenomenon in all forms with big eggs and direct development within other groups of invertebrates also.

Hermaphroditism as a normal occurrence is not known from any of the Northeast Greenland echinoderms. In *Ophiecten sericeum* only two hermaphrodites were found in the very large material investigated (749 individuals) (cf. THORSON 1934, p. 14), and this species thus has decidedly separate sexes. The investigations of the other species are based on much smaller series, but no trace of hermaphroditism was found in them.

As regards viviparous ophiurans it has been ascertained (MORTENSEN 1920 and 1936) that these forms are almost always hermaphrodites, and it might therefore be anticipated that similar conditions would be found in the arctic species with their big eggs. However, it may be very difficult to decide whether or not a species is hermaphroditic, since the change from one sex into the other may take place through a long period during which it is difficult to ascertain the sex, so that only observations of the animal through several years may reveal its hermaphroditic character.

Summarising the data arrived at concerning the reproduction of the Northeast Greenland echinoderms, the result may be briefly given as follows: all the *Echinodermata* with an arctic distribution so far examined showed reproduction by big eggs and have probably a direct development or possibly a reduced larval stage. Only a small part of the species (about 21 per cent.) have small eggs and pelagic larvæ, and such forms had in all cases an arctic-boreal distribution. However, several arctic-boreal forms also had large eggs and a non-pelagic development.

B. Polychaeta.

As in the case of the *Echinodermata*, it will be reasonable for the *Polychaeta* also to consider first the distribution of the larvæ throughout the year in the considerable material of plankton from Ellæ and Eskimonæs. The subjacent table gives such a view of the polychaete larvæ found in the plankton, the figures in the table showing the total amount of polychaete larvæ in ten samples. The figures in parentheses indicate the number for each date of fully comparable samples on which the amounts in each individual case are based.

As appears from the table, the plankton hauls are altogether extremely poor in polychaete larvæ at nearly all times of the year. This may mean either that the polychaetes living within the area spawn at a uniform rate throughout the year, but only some few species at a time. In that way the number of eggs for the individual month would be so low that they would leave no quantitative traces in the plankton in the form of larvæ. Or it may mean that the larvæ occurring in the plankton belong to a very few species, while all the other species reproduce themselves by direct development without pelagic larvæ.

A careful examination of the plankton larvæ found showed them to be the larvæ of a very few forms only (cf. figs. 4 and 5). The only

Ellaø			Eskimonæs		
Date	Number of larvæ per 10 samples		Date	Number of larvæ per 10 samples	
	50—0 m	25—0 m		50—0 m	25—0 m
18-25/1 1932	0 (20) ¹⁾	0 (20)	12/1 1933	2 (5)	..
10/2 1932	1 (10)	..	2/2 1933	2 (4)	0 (2)
26/2 1932	0 (20)	0 (20)	18/2 1933	0 (5)	..
11/3 1932	1 (10)	..	9/3 1933	2 (4)	3 (2)
28/3 1932	0 (20)	0 (20)	29/3 1933	0 (5)	..
10/4 1932	1 (10)	..	13/4 1933	0 (4)	0 (2)
26/4 1932	0 (20)	0 (20)	30/4 1933	0 (5)	..
11/5 1932	1 (10)	..	19/5 1933	0 (4)	0 (2)
26/5 1932	0 (20)	0 (20)	..	..	..
12/6 1932	2 (10)	..	2/6 1933	0 (5)	..
26/6 1932	3 (10)	0 (10)	18/6 1933	80 (4)	20 (2)
26/7 1932	10 (9)	..	12/7 1933	0 (2)	..
18/8 1932	2 (10)	..	16/8 1932	160 (2)	..
28/8 1932	1 (9)	..	30/8 1932	30 (4)	0 (2)
18/9 1932	0 (10)	..	15/9 1932	17 (3)	..
15/10 1932	4 (9)	..	..	..	..
15/11 1932	5 (9)	..	3/11 1932	2 (5)	0 (2)
20/12 1932	0 (9)	..	18/11 1932	5 (2)	..
..	..	..	12/12 1932	7 (4)	..

really large maximum of polychaete larvæ found in the plankton hauls (Eskimonæs, August 16, 1932, 50—0 m, hand net, 165 polychaete larvæ per ten samples) proved to consist exclusively of the larvæ of a single species, whose larval development was traceable in all stages (fig. 4). In the plankton from Ellaø only two different types of larvæ were of regular occurrence (fig. 5), and from Ellaø, even from all the months of the year, not a single specimen of an unsegmented pelagic polychaete larva is known (*Mitraria* or similar forms). The least seg-

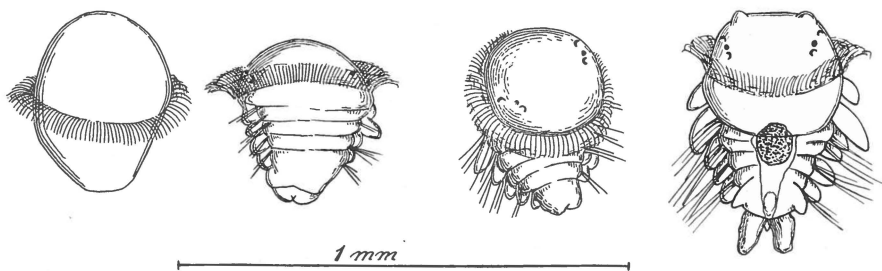


Fig. 4. Polychaete larvæ from plankton taken at Eskimonæs. Four stages of development of the same species. The youngest stage is a typical *Trocophora* larva. Sample taken on August 16, 1932.

¹⁾ The figures in parantheses indicate the real number of samples taken on the different dates.

mented polychaete larvæ found in the plankton from Ellæ already had a front segment and three following segments (fig. 5F). The above-mentioned larval type from Eskimonæs (fig. 4), however, had unsegmented larvæ in the youngest stages found.

It will now be natural to investigate the quantitative distribution of the polychaetes on the sea bottom, especially in the bay at Ellæ

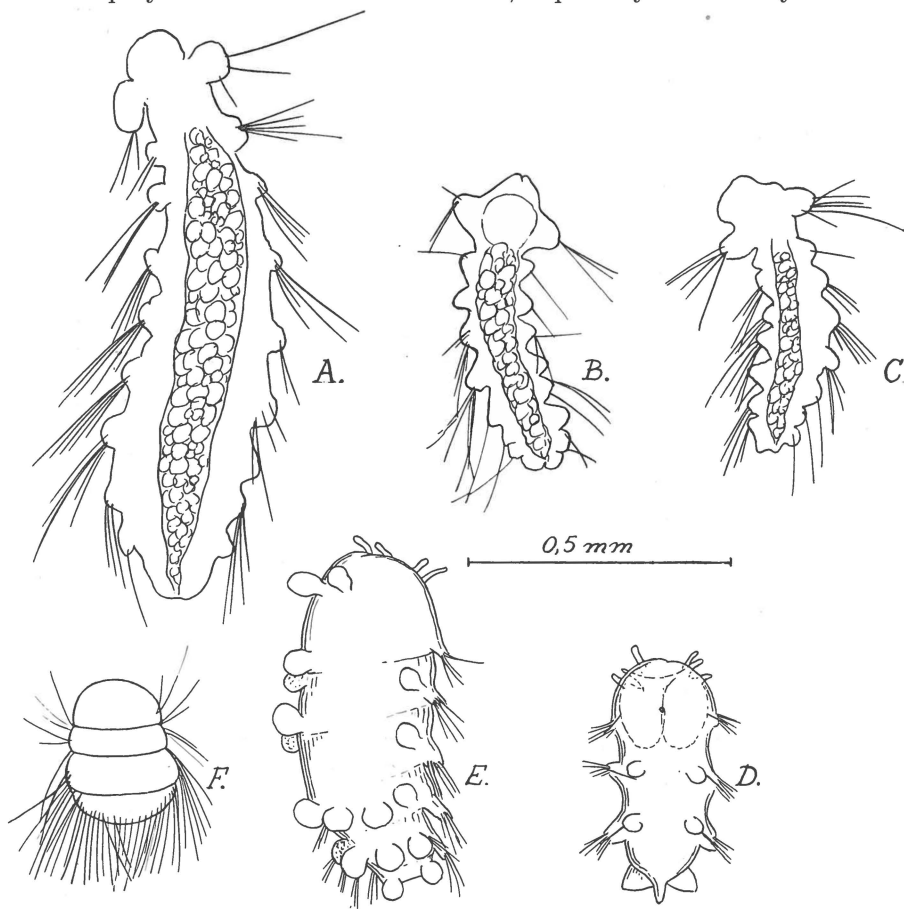


Fig. 5. Polychaete larvæ from plankton at Ellæ, summer 1932.

A, B, and C, larvæ of the same species. — D and E presumably different stages of development of another form. — F, the youngest polychaete larva found in the plankton at Ellæ.

where most of the plankton hauls were made. In the shallow water at Ellæ the following polychaetes abound: *Pectinaria granulata* (3—25 m, about 16 species per sq.m), *Terebellides strømi* (3—45 m, about 8 sp. per sq.m), *Aricia cuvieri* (3—45 m, about 4—12 sp. per sq.m), *Nereis zonata* (3—14 m, about 8 sp. per sq.m, soft bottom, more numerous in the shallow water vegetation), and *Harmothoë imbricata* (3—14 m,

about 8 sp. per sq.m, soft bottom, and in large numbers in the shallow water vegetation). Further the following species are frequently found, though in much smaller quantities: *Flabelligera affinis*, *Ammotrypane aulogaster*, *Brada villosa*, and — in deeper water — *Onuphis conchylega* (cf. THORSON 1933, Table I, IV, and XI).

Of these forms *Terebellides strømi* is known to develop in more southern seas without pelagic larvæ, the young individuals passing directly into the uppermost bottom layer (LESCHKE 1903, p. 128), and precisely the same applies to the genus *Aricia* (*Scoloplos*), whose larva when escaping from the common egg-mass is very like the adult (LESCHKE 1903, p. 126; GRAVIER 1923, p. 175). These two forms may thus be left out of consideration in the investigation of the origin of the pelagic larvæ. Of the forms which are especially dominant at Ellaø there remain, then, *Pectinaria granulata*, *Nereis zonata*, and *Harmothoë imbricata* — three forms, of which a considerable material preserved in alcohol has been brought home from Ellaø. By means of investigations of the time of spawning and of the size of the eggs, and by comparisons with related larval forms mentioned in the literature it must be possible to decide to what extent the larval stages of these forms were traceable in the plankton.

First the spawning was investigated. For this purpose a fairly large material preserved in alcohol, of ♀♀ of these three forms, collected at Ellaø at various dates during the period May to September was used.

The spawning of *Pectinaria granulata* showed the following facts: May 24 to June 8, 1932. Depth 3—8 m, length of tube 16—30 mm, 30 ♀♀ and two ♂♂ were investigated with the following result: quite young eggs (0), semi-mature, closely coherent eggs (3), loose eggs almost ready to be spawned (17), eggs in the stage of spawning (9), the ovary almost empty with some few big eggs (3). Spawning commenced, but most ♀♀ have not yet spawned.

June 25 to July 5, 1932. Depth 8—18 m. Length of tube 15—36 mm, 23 ♀♀ and 1 ♂ were investigated with the following result: quite young eggs (0), semi-mature, closely coherent eggs (0), loose eggs nearly ready to be spawned (15), eggs in the spawning stage (9), the ovary almost empty with some few big eggs (0). (Size of individuals as in the preceding sample, the depth, however, slightly greater). Spawning commenced, but most ♀♀ have not yet spawned. Condition precisely as that of the preceding series of samples.

August 3 to 5, 1933. 4—16 m depth. Length of tube 20—50 mm. 63 ♀♀ investigated: quite young eggs (6), semi-mature, closely coherent eggs (0), loose eggs nearly ready to be spawned (2), eggs in the spawning stage (3), ovary nearly empty with some few big eggs (53). As the

individuals are on an average much larger than those of the preceding series, no direct comparison can be made. Of the six ♀♀ with a length of tube ranging from 20 to 36 mm, corresponding to the preceding series, one showed quite young eggs, one eggs in the spawning stage, and four nearly empty ovaries with some few big eggs, and thus conditions correspond to those observed in larger individuals. Conclusion: in *Pectinaria granulata* the spawning seems in all essentials to be completed at the beginning of August. The circumstance that this series of samples is derived from 1933 and the two preceding ones from 1932 would seem to be of subordinate importance according to former experience, as the breaking up of the frost, heating of the water, etc., varied within about ten days, at the most, during the three years in which the observations were made (1931, 1932, and 1933), and also observations of the time of spawning in lamellibranchs, plankton, etc., showed nearly the same conditions at the same times of the different years.

September 15—19, 1931. 5—18 m depth. Length of tube 17—36 mm. Of 30 individuals investigated four were identifiable as ♂♂, while no individuals with recognisable eggs were found. Result: as no recognisable ♀♀ were found, the spawning must be assumed to be quite finished in the month of September.

The data arrived at here concerning the spawning of *Pectinaria granulata* may be summarised as follows: Spawning seems to take place at a uniform rate from the end of May to the end of July. The spawning is finally completed at the beginning of August. As no eggs were ascertained in the September individuals, spawning equally distributed throughout the year is excluded. In ♀♀ maturity seems to be reached when the tube has a length of 20 mm, in ♂♂ at 16—17 mm.

The spawning of *Harmothoë imbricata* showed the following facts: May 24 to June 8, 1932. 3—8 m depth. Length of body 19—24 mm. Of 113 individuals 63 recognisable as ♀♀. The latter may be classed as follows: quite young eggs (1), semi-mature, closely coherent eggs (15), loose eggs almost ready to be spawned (34), eggs in the spawning stage (7), ovaries almost empty with some few big eggs (6). Result: Spawning commenced, but most ♀♀ have not yet spawned. Corresponds precisely to the observations made in *Pectinaria granulata* at the same date.

August 3—8, 1933. 3—16 m depth. Length of body 20—40 mm. Of 28 individuals only 8 were recognisable as ♀♀, all of which had quite young eggs. Result: Judging from the rather small material the spawning seems already to be finished, since no individuals with big eggs were observed.

September 15, 1931. 5—5 m depth. Length of body 18—30 m. Of seven individuals examined none could be determined as to sex, the gonads being entirely reduced. As the samples from May 24 to June 8

have shown that individuals of a body length of 20 mm are sexually mature, it seems justifiable to assume that the seven September individuals have finished their spawning.

Thus the data concerning the spawning of *Harmothoe imbricata* arrived at here show a fairly close agreement with *Pectinaria granulata*. A uniform spawning takes place at the end of May and in the month of June, but is completed before the beginning of August.

The available material of *Nereis zonata* is somewhat smaller than that of the two preceding species, but still show the course of the spawning sufficiently well. An August series of *Nereis zonata* (Aug. 3—5, 1933, Ellasø, 4—16 m depth, length of animal 40—115 mm, 7 ♂♂, 16 ♀♀, 8 ??) showed the following features: no visible eggs (8 sp.), quite young eggs (3 sp.), semi-mature, closely coherent eggs (0 sp.), almost mature eggs (5 sp.), eggs in the spawning stage (4 sp.), the ovaries of the mother animals almost empty (4 sp.), that is, a period of spawning continuing till somewhat later in the summer than in *Pectinaria* and *Harmothoe*. A considerable number of individuals with a body length of less than 80 mm had undeveloped sexual organs, which fully explains that a series of this species (Ellasø, July 5, 1932, 10—15 m, 36 sp., length of body 20—70 mm) did not show the least sign of maturity even though this date actually falls at the maximum spawning of the species.

It will be seen that in the above-mentioned three forms of *Polychaeta* — all of which are extremely common in Northeast Greenland — the spawning is intense in early summer (May—June) and presumably is completed in July or the beginning of August, in *Nereis zonata* probably at the end of August. It should, however, be noted that in all three species spawning was repeatedly observed in living material at Ellasø in May and June 1932.

Within the period of spawning of these common shallow-water species the plankton tables from Ellasø only show an increase in the number of polychaete larvæ from 0 per sample (May 26, 1932) to about 1 larva per sample (July 26, 1932), while the corresponding increase in the number of e. g. the lamellibranch larvæ ranges from about 10 larvæ per sample in May to about 125 larvæ per sample in July (cf. p. 47). Thus the rise in the number of polychaete larvæ per sample at Ellasø in June is so slight that it can be stated with almost absolute certainty that animals of such common occurrence in the Northeast Greenland fjords as *Harmothoe imbricata*, *Nereis zonata*, and *Pectinaria granulata* cannot have pelagic larval stages. Since, however, all these three genera are known to have species in boreal seas whose larvæ pass through a pelagic larval stage, a closer examination of these phenomena would seem to be called for.

Harmothoe imbricata, which is distributed from the Mediterranean

to the Arctic, where it is circumpolar, is known to have pelagic larvæ (LESCHKE 1903, p. 130) in boreal seas (e. g. in the Baltic near Kiel), which larvæ cannot be distinguished with certainty from those of *Lepidonotus squamatus*. The larva of the latter species is figured by LESCHKE (l. c.), and it can be definitely stated that in the plankton series from Ellaø throughout the whole year not a single larva is found which presents even the slightest similarity to that pictured by LESCHKE. Thus *Harmothoe imbricata* must have a direct development in Northeast Greenland, while in boreal seas it has normally pelagic larvæ. This assumption is supported by the fact that in Misaki in Japan *Harmothoe*

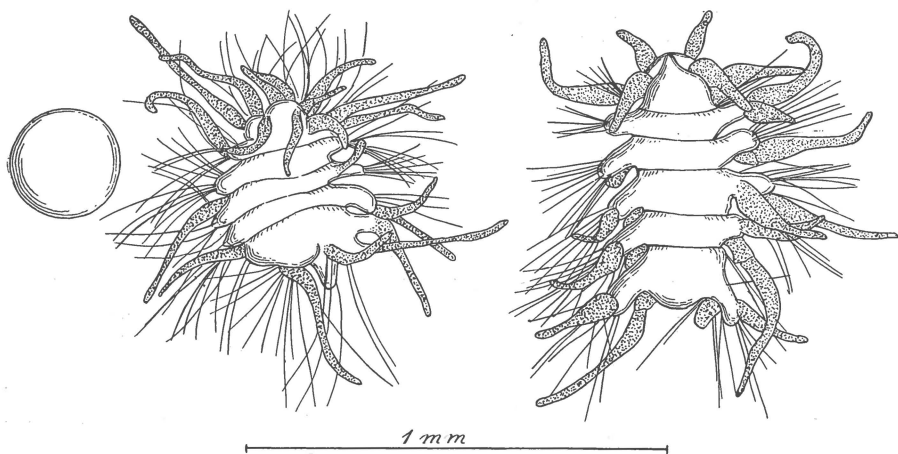


Fig. 6. Young polychaetes in the bottom stage. Presumably young *Harmothoe imbricata*. To the left, a mature egg of the same species. Bottom stages taken in May, 1932. at a depth of 50—155 m.

imbricata has been found with eggs and big larvæ respectively under the elytra, and in Japan these larvæ are known not to leave the mother animal till a fairly advanced *Trocophora* stage (GRAVIER 1923, p. 177). In the living East Greenland individuals of this species the eggs were also found under the elytra, and the same phenomenon was also observable in part of the material brought home preserved in alcohol. Now there is a possibility that the species in boreal seas uses both this and the pelagic method of reproduction, but although the species in boreal waters is often observed and examined on account of its great frequency, it has never been found here with eggs below the elytra. Thus there can hardly be any doubt that this species reproduces itself by different methods under different ecological conditions.

Since accordingly *Harmothoe imbricata* must be supposed to have a direct development with no pelagic stage in Northeast Greenland, it seems probable that in the time about the period of spawning of the species

the quite young animals may be found in the uppermost bottom layer. This seems, indeed, to be the case. In the bottom material from Ellaø, from 50 and 155 m depth, May 1932, a couple of quite young polynoids were found, which were less developed (i. e. with neither elytra nor eyes) but otherwise agreed entirely with LESCHKE's pelagic polynoid larvæ from the Kiel Bay (cf. fig. 6). There is therefore a great probability that we are here concerned with the larvæ of *Harmothoë imbricata*, which thus in Northeast Greenland are not pelagic at this stage of development. The very slight difference in size of the mature egg of *Harm. imbricata* and that of the smallest of these larvæ provides further evidence that no protracted pelagic stage can occur.

Nereis zonata is mainly distributed in the Arctic¹), and so far its mode of reproduction is entirely unknown. It is known, however, that in the time of reproduction the species may be epitoque (according to verbal information by HJ. DITLEVSEN). However, this is not the normal method of reproduction of the species in the Northeast Greenland fjords. In May—June, 1932, when numerous spawning individuals were observed in an aquarium at Ellaø, neither ♂♂ nor ♀♀ were epitoque. As moreover the author in the months May, June, and July, 1932 (i. e. during the spawning period of the species), worked daily in the inner fjords round Ellaø and Cape Hedlund at all hours of the day and night without ever observing epitoque individuals, there is a strong probability that the species may spawn in these places without becoming epitoque. Great, therefore, was my astonishment when in the summer of 1933 at Amdrup Harbour in Scoresby Sound (near the open sea) I had an opportunity of observing two epitoque free-swimming individuals of this species (both ♂♂). The crew of the ship reported that during the night they had seen numerous individuals of the species swimming about the ship near the surface of the water. Hence there can hardly be any doubt that the species reproduces itself in two different ways in Northeast Greenland. From the area of Kangerdlugssuak also (Uttental Sound, August 22, 1933, 50 m wire, depth 50 m, coiled trawl, E. BERTHELSEN leg.) two epitoque individuals are at hand, one of which is an ♂, while the other had already discharged its sexual products.

At Ellaø no larvæ were found in the plankton which bore even the slightest resemblance to the well-known types of *Nereis* larvæ, so at the outset it was extremely probable that the species here had a direct development. But how, then, were conditions at the outer coast, where epitoque individuals had been found? From the literature one example is known which seems to agree closely with the peculiarities observed in *Nereis zonata*. Thus WISTINGHAUSEN (1891) ascertained that

¹) Some few records are, however, at hand from the Channel and the Mediterranean.

Nereis dumerili at Naples reproduces itself by two methods; by far the greater number of individuals spawn without being epitoque, and if so, the eggs develop directly without a pelagic larval stage, whereas other individuals of the same spawning become epitoque (*Heteronereis*) and have pelagic eggs and larvæ.

It seems quite natural to combine these phenomena with the data ascertained for the Northeast Greenland *Nereis zonata*, and the possibility is then near at hand that the individuals that spawn without being epitoqueis have an unpelagic larval development, while the epitoque individuals will presumably prove to have pelagic larvæ. In this connection it should be noted that pelagic larvæ are known to be more frequent near the open sea, whence the epitoque individuals are known so far, than in the inner fjords, so that the above-mentioned possibility seems probable for that reason also (cf. the larval tables for Ellæs and Eskimonæs).

The main impression obtained from these considerations is the considerable lability in the method of reproduction of this genus, which must enable it to subsist under extremely varying ecological conditions. As a further confirmation of this it may be mentioned that according to METSCHNIKOFF's investigations (1871) both *Nereis dumerili* and *Nereis pelagica* (the latter normally with a pelagic larval stage) may occur as hermaphroditic as well as viviparous individuals.

There remains, then, *Pectinaria granulata*. LESCHKE (1903, p. 127) mentions a larva from the Kiel Bay which to all appearance belongs to *Pectinaria belgica*, and SØMME (1927, p. 84) describes the oldest larval stages of *Pectinaria auricoma* and *P. koreni*. The latter older stages are provided already in their pelagic life with the tube characteristic of the genus *Pectinaria*, while the young larva described by LESCHKE has a typical *Trocophora* stage. From the Northeast Greenland plankton no larvæ are at hand which bear any resemblance to these well-known forms. This is all the more peculiar, since *P. granulata* in contrast to *Nereis zonata* and *Harmothoe imbricata* have very small eggs (0.07 mm in diameter; *Harm. imbricata* 0.25 mm in diameter; *Nereis zonata* 0.22 mm in diameter; *Onuphis conchylega* 0.18 mm in diameter), a common characteristic of forms with pelagic larvæ. However, *Terebellides strømi* has just as small eggs (0.072 mm), which are laid in slimy lumps and developed without a pelagic stage (LESCHKE 1903, p. 128), and a similar mode of reproduction may therefore be assumed for *P. granulata*. There is also another possibility, namely, development by means of nurse eggs, in cases where the eggs are laid in a capsule and only some of the eggs are developed, securing nourishment by devouring the rest of the eggs. Such a procedure is known from *Spio filiformis* (MESNIL & CAULLERY 1917, p. 646), which develops in the autumn

without any pelagic stage by means of nurse eggs, while in the spring it develops without the aid of nurse eggs and with pelagic larvæ.

Thus the mode of reproduction in *Pectinaria granulata* can only be guessed at. The only thing that can be stated with some degree of certainty is that the species in Northeast Greenland develops without pelagic larvæ.

Other species living in the fjords of Northeast Greenland and whose methods of reproduction are known, are the above-mentioned *Spio filicornis* (cf. p. 34), which is very frequent, among other places in the very shallow-watered areas with sandy bottom at the mouth of Scoresby Sound; *Syllis incisa*, which is viviparous, and whose embryos develop in the posterior part of the body (LEVINSEN 1882, vol. 1, p. 246); *Pomatocerus triqueter* (found at Danmarkshavn), which is viviparous, and whose big eggs (0.44 mm in diameter) are developed in the posterior part of the body (GRAVIER 1923, p. 218); *Spirorbis verruca*, whose reproduction is unknown, whereas the other species of the genus are hermaphroditic and viviparous (LESCHKE 1903); and *Mikroserpula inflata*, which has a reduced larval stage (DONS 1933). Finally, *Nephtys ciliata*, *Capitella capitata*, and *Onuphis conchylega* are known to have pelagic larvæ in boreal seas, while their reproduction in arctic seas has not been investigated. As regards *Onuphis conchylega*, a direct development in the Arctic may very well be conceived, since the mature eggs (in Scoresby Sound 0.18 mm in diameter) very nearly attain the size of the eggs of *Nereis zonata* (at Ellæ 0.22 mm in diameter).

Thus it has not been possible to determine with certainty the species of polychaete larvæ found in the plankton. It can only be stated that the larvæ found originate from a very few species, and that even these forms showed a distinct tendency to a shorter pelagic larval stage, all the polychaete larvæ found in the plankton at Ellæ having an advanced organisation, a considerable size, and a complete lack of the pelagic *Trocophora* stage, which even at Eskimonæs was ascertained in one single species only,

In the summer of 1933 a further sign of this non-pelagic development in by far the greater number of the polychaetes of the area was ascertained. While thus plankton hauls in the month of August at Ellæ only yielded the usual quite few polychaete larvæ, in a haul made by means of a MORTENSEN detritus collector (MORTENSEN 1925, p. 445) through the uppermost bottom layer in the same locality a large number of quite young — in part unsegmented and absolutely indeterminable — polychaete larvæ were found, which moved briskly through the detritus layer in the Petri-dishes in which they were placed. Similar experiences were made during an investigation in shallow water in the areas of sandy bottom in Scoresby Sound.

Of the three shallow-water forms investigated in Northeast Greenland *Harmothoe imbricata* proved to be normally hermaphroditic, and in *Pectinaria granulata*, which is normally unisexual, a number of hermaphroditic individuals were also found. In *Nereis zonata*, however, hermaphroditism was not ascertained.

Our present knowledge of the reproduction of the Northeast Greenland *Polychaeta* may be briefly summarised as follows: 73 polychaete species in all are known from Northeast Greenland (DITLEVSEN 1911, E. WESENBERG-LUND 1934, and the results of the collections made during the last few years). Of these 73 species, the mode of reproduction is known altogether or in part in only 13 species (about 18 per cent.), seven of which, belonging to the genera *Syllis*, *Pomatocerus*, *Spirorbis*, *Spio*, *Terebellides*, *Scoloplos*, and *Aricia*, normally have a non-pelagic development, while three species, viz. *Nereis zonata*, *Pectinaria granulata*, and *Harmothoe imbricata*, are in all probability able to reproduce themselves without any pelagic larval stage, and accordingly ten of the above-mentioned 13 species must be assumed to be able to reproduce themselves in this way. Zoogeographically these ten species are distributed as follows: Arctic distribution, three species (*Pectinaria granulata*, *Spirorbis verruca*, *Syllis incisa*), arctic-boreal distribution, two species (*Aricia cuvieri* and *Spio filicornis*), and a wider distribution, five species (*Scoloplos armiger*, *Harmothoe imbricata*, *Nereis zonata*, *Terebellides strømi*, and *Pomatocerus triqueter*).

Further, three species (*Capitella capitata*, *Onuphis conchylega*, both of a wide distribution, and *Nephtys ciliata*, which has a arctic-boreal distribution) are known to pass through a pelagic larval stage in more southerly seas, but it is not known whether they develop in the same way in Northeast Greenland (cf. the above remarks on *Onuphis*).

The small number of polychaete larvæ found in the Northeast Greenland plankton, which moreover only belong to a very few species, renders it probable that several other polychaetes in Northeast Greenland reproduce without any pelagic larval stage.

In 70 of the 73 species of polychaetes occurring in Northeast Greenland the distribution is sufficiently known to allow of a regional characterisation, and zoogeographically they are distributed as follows:

1) Arctic distribution.....	20 species	28.60 per cent.
2) Mainly arctic and sparse boreal distribution.....	11 —	15.70 —
3) Arctic-boreal or still wider distribution	39 —	55.70 —

The fact that the number of arctic-boreal or more widely distributed species even in Northeast Greenland is higher (55.70 per cent.) than the

number of forms with an arctic or mainly arctic distribution (44.30 per cent.) may possibly be partially accounted for by the lability in their mode of reproduction characteristic of the polychaetes. Such a lability in the few species investigated having been ascertained with certainty in *Spio filicornis* and *Harmothoë imbricata* and with a great degree of probability in *Nereis zonata*, it is to be expected that similar labile modes of reproduction are found in a considerable additional number of Northeast Greenland forms not yet examined.

C. Gastropoda.

In the monthly plankton hauls made near Ellaø throughout the year 1932 larvæ of the pteropods *Clione limacina* and *Limacina helicina* were found, whereas all the samples were absolutely free from larvæ of prosobranchs and other opisthobranchs. It was therefore natural to investigate more closely the reproduction of these groups, and since the opisthobranchs occurred in small numbers and with no quantitative importance, the investigation was especially concentrated on the prosobranchs. During the wintering at Ellaø 1931—32 and on the summer trips with the "Godthaab" in 1932 and 1933 a considerable material of gastropod egg-clusters was collected, which after the return of the expedition was subjected to a special study (cf. THORSON 1935a). The technique was rather simple, the distribution of the species in the fjords being highly different within the individual genus, some species occurring only on sandy bottom, others on clay bottom, some at the outer coast, others in the inner fjords, etc. By applying the principle of elimination it was therefore as a rule possible to find localities in which only one species of a particular genus occurred, to which the egg-capsules of that genus found in that place probably belonged. The decisive proof of the identity of species was then obtained through a comparison of the shape and shell structure of the embryonal shells with the apex of the adults. In this way it was possible to identify the egg-capsules and the embryos of 27 Northeast Greenland prosobranchs, in twenty of which the mode of reproduction was entirely unknown. It turned out that in all the 27 species the embryos pass directly from the egg-capsules into the free-swimming bottom stage without any pelagic larval life (THORSON 1935a). From the literature the mode of reproduction in three species of Northeast Greenland prosobranchs is known, viz. *Sipho propinquus*, *Sipho turritus*, and *Onchidiopsis glacialis* (FRIELE 1882, BERGH 1886), and the process of reproduction is thus known for altogether 30 Northeast Greenland prosobranchs.

Reproduction without a pelagic larval stage may take place in different ways in the Northeast Greenland forms. A summary of the

different methods of reproduction and of the East Greenland species in which they were found will be given below.

- 1) Eggs with a small amount of yolk and with primitive pelagic larval stages. This method of reproduction is unknown from Northeast Greenland.
- 2) Eggs with a small amount of yolk, laid in larger or smaller coherent masses. Only a few of the eggs in each mass develop, and use the undeveloped eggs (nurse eggs) for food. This stage is succeeded either by a much shorter pelagic stage or by a direct transition to the free-living bottom stage.

This method of reproduction is known for 15 Northeast Greenland species (*Sipho curtus*, *S. islandicus*, *S. lachesis*, *S. krøyeri*, *S. propinquus*, *S. turritus*, *Neptuna despecta*, *Jumala ossiana*, *Volutopsis norvegica*, *Buccinum hydrophanum*, *B. belcheri*, *B. groenlandicum*, *B. ovum*, *B. sericatum*, and *Onchidiopsis glacialis*).

- 3) Eggs with a large amount of yolk, which develop directly into the free-living bottom stage or possibly have a very short pelagic larval stage.

This mode of reproduction is known in 12 of the forms occurring within the area (*Bela simplex*, *B. exarata*, *B. pyramidalis*, *B. bicarinata*, *B. nobilis*, *Raphitoma amoena*, *Pyrene rosacea*, *Trichotropis borealis*, *Tr. conica*, *Margarita cinera*, *Marg. helicina*, and *Velutina undata*).

- 4) Eggs with a considerable amount of yolk, which is further surrounded by white, which is devoured by the embryo. Direct development with no pelagic larval stage. This mode of development has not previously been known in prosobranchs, and will be discussed in detail below.

This method of reproduction was observed in three species only (*Natica groenlandica*, *N. affinis*, and *Natica islandica*).

- 5) Eggs developed inside the body of the mother animal, presumably in the ovary. (In the case considered here it was impossible to decide whether the development took place in the ovary or in the pallial cavity. Accordingly it is either a case of protection of the young or of viviparity.)

Known from one Northeast Greenland species only (*Acmaea rubella*).

It will be seen that among these forms several genera are represented which also have species in more southern seas, and it will now be of interest to compare the methods of reproduction of such southern species with the data found here for their arctic relations. The most interesting in this connection is probably the genus *Natica*. The mode of reproduction in *Natica pulchella* (HERTLING 1932) is known from

boreal seas, where it reproduces itself by means of small eggs and primitive pelagic larvæ; and also that of *Natica catena* (ANKEL 1930), which has nurse eggs and consequently large embryos. In the summer of 1935 the author had an opportunity of investigating the egg-masses of this species at Frederikshavn (the Kattegat), and here observed that the embryos of *N. catena* on leaving the egg-mass pass directly to the seabottom without any pelagic stage¹). From the Adriatic Sea ODHNER (1914) has further described a pelagic *Veliger* larva of *Natica* sp., which, however, was already able to crawl about by means of its foot. The fact that pelagic larvæ are found in several species within this group in boreal seas but are totally absent in the Arctic, agrees well with our knowledge of other animal groups; but it is peculiar that the genus may arrive in two quite different ways — either by means of nurse eggs (*Natica catena*) or by a combination of yolk and white (cf. the Northeast Greenland *Natica* species) — at the same result, namely a direct development. As regards *Natica catena* the problem might perhaps be unravelled by observations of its reproduction in a series of localities with as different an ecology as possible. For it is well known that other forms with nurse eggs (e. g. *Sipho*, cf. THORSON 1935a, pp. 7—16) have a greatly varying embryonal period according to the number of nurse eggs per embryo (see also below), and as it has been suggested i. a. for *Buccinum* that the failing ability of the nurse eggs to develop is due to impregnation by “sterile” (“atypische”) spermatozoa (HYMAN 1901, PORTMANN 1926 and 1927); it is possible that under other conditions such species would develop far more eggs, and if so, the larvæ, on account of the smaller amount of nourishment per embryo, must leave the egg-capsule at a more primitive stage, in which case they may probably have a pelagic development. In *Natica*, however, atypic spermatozoa have not yet been ascertained, and thus the nurse eggs here are perhaps of a different character (ANKEL 1930). In Northeast Greenland such a pelagic development seems absolutely impossible, judging from the methods of reproduction of all the prosobranchs living there; here we find the mode of reproduction perfectly suitable for a direct embryonal development, viz. yolk combined with white, by which it is made possible for the embryos not to leave the egg-mass until they are 1½ mm broad, two-whorled bottom stage forms.

In a number of other genera, too, boreal and southern species with a pelagic development and arctic species with a direct development are known. In the *Lamellariidae* this phenomenon is particularly striking, the boreal species *Velutina laevigata* and *Lamellaria perspicua* having a

¹) In a paper just out (March 1936) MARIE LEBOUR states that she has found pelagic larvæ of this species at Plymouth.

pelagic larval form, "*Echinospira*", which is especially suitable for a protracted plankton life, while the arctic *Velutina undata* has a direct development without any trace of a pelagic stage (cf. M. LEBOUR 1935, p. 170, and THORSON 1935a, p. 65). Within the genus *Bela*, *Bela turricola* is known to have pelagic plankton larvæ in boreal seas (VESTERGAARD 1935), while the five Northeast Greenland species of *Bela* all have a direct development. The *Trochus* species of the boreal seas also have pelagic larvæ (ROBERT 1902, LEBOUR 1933), while the arctic subgenus of this group, *Margarita*, has a direct development. Finally, the genus *Acmaea* is normally egg-laying and has pelagic larvæ, while the arctic *Acmaea rubella* is viviparous (see, however, below).

Among the species with direct development hitherto known from the literature, none is known with bigger eggs than *Fulgur carica* (CONKLIN 1907), which has a southerly distribution and whose egg-diameter is 1.7 mm. Among the Northeast Greenland species this size is probably exceeded by *Natica groenlandica*, whose egg-diameter is 2.25. The eggs of the remaining Northeast Greenland prosobranchs, however, are much smaller, the eggs of the genus *Bela* in the Arctic being about 0.8 mm in diameter.

The above-mentioned great variation in the method of reproduction in species of the same genus shows that too great importance has hitherto been attached to the systematic position of the individual gastropod species in the theoretical indication of its larval form. Thus the *Lamellariidae* are generally regarded as characteristic on account of their "*Echinospira*" larvæ (i. e. larvæ that are especially well adapted for a pelagic stage). The genus *Natica* was known to have pelagic larvæ; now, however, four forms with direct development are known; *Acmaea* belongs to a group with pelagic larvæ, the arctic species, however, is viviparous. All this, and especially the peculiar varying methods of reproduction within the genus *Natica*, warn us to be very cautious in drawing conclusions from the systematic position of the species to its ecological type of larval development. It would seem that genera distributed over an extensive area may often show a greater variation from species to species in their methods of reproduction than species belonging to different genera but living in the same localities (i. e. under the same ecological conditions).

While in boreal seas the genus *Natica* showed examples of reproduction by means of nurse eggs, but in the Arctic had quite a different mode of reproduction, the genera which normally reproduce themselves by means of nurse eggs (*Buccinum*, *Neptunea*, *Sipho*, *Jumala*, *Volutopsis*) seem both qualitatively and quantitatively to have their optimum occurrence in the Arctic. This appears very plainly from the subjoined table, which gives the specific number of forms reproducing by means of nurse eggs, for Northeast Greenland, Iceland, the Faroes, and Denmark.

- 1) Northeast Greenland, in all 18 species¹⁾ (*Buccinum* 6 sp., *Sipho* 8 sp., *Volutopsis norvegica*, *Neptunea despecta*, *Jumala ossiana*, and *Onchi-diopsis glacialis*).
- 2) Iceland, in all 16 species (*Buccinum* 5 sp., *Sipho* 8 sp., further *Volutopsis norvegica*, *Neptunea despecta*, and *Chrysodomus turtoni*).
- 3) The Faroes, in all 6 species (*Buccinum* 1 sp., *Sipho* 4 sp., further *Neptunea despecta*).
- 4) Denmark, in all 5 species (*Buccinum* 1 sp., *Sipho* 2 sp., further *Neptunea antiqua* and *Natica catena*).

The Northeast Greenland *Natica* species excepted, these nurse egg forms have no doubt gone furthest in respect of direct development. Here *Jumala ossiana* with its embryo 20 mm high, having $4\frac{1}{2}$ whorls (cf. THORSON 1935a, fig. 16), should especially be mentioned. As mentioned above, the examination of the material brought home of these *Buccinidae* showed that the amount of nourishment present for each embryo is of decisive importance for the size of the embryo on leaving the egg-capsule. Capsules with the same quantity of nurse eggs always had larger embryos if only one individual per capsule was found than if the capsule contained several embryos. Thus according to the number of nurse eggs per embryo in *Sipho islandicus* the embryos ready to emerge may vary from $3\frac{1}{2}$ whorls and a shell-height of 8.5 mm to $1\frac{1}{2}$ —2 whorls and a shell-height of 3.5 mm. This shows that embryos feeding on nurse eggs do not escape at a definite stage, but are directly dependent on the number of nurse eggs, or, in other words, that the number of embryonic whorls is a direct indicator of the conditions of nourishment under which the embryo lived in the egg-capsule (cf. THORSON 1935a, pp. 10—16). This warns us to be very cautious in using the apex as an especially reliable systematic character. For if it is possible — and much speaks in favour of this assumption — that a species in different places of its area of distribution is able to feed its embryos in different ways, so that the larval period is not always the same, the apex will first of all be affected and accordingly be a very uncertain systematic character.

The sole method of reproduction prevailing within the prosobranchs of Northeast Greenland, namely the direct development, opens up a very interesting perspective if we compare it with conditions at Iceland, the Faroes, and Denmark, as done above with those forms alone that reproduce themselves by means of nurse eggs. As regards the latter forms the sharp line of demarcation between a large and a small number of species occurred between the seas around Iceland on the one hand and those around the Faroes on the other. If, however, we compare the methods

¹⁾ Herein are included all the species with nurse eggs found along the coast of Northeast Greenland.

of reproduction within the whole fauna of prosobranchs in the four localities mentioned, the transition from the high percentage of directly developing forms in Northeast Greenland to the percentage of species with pelagic development in the Danish waters appears to be quite even (cf. fig. 7). The percentage comparison seems to show a very close relation between the locality and the method of reproduction.

Of the Northeast Greenland forms whose reproduction has been investigated, one species, *Natica groenlandica*, even occurs in

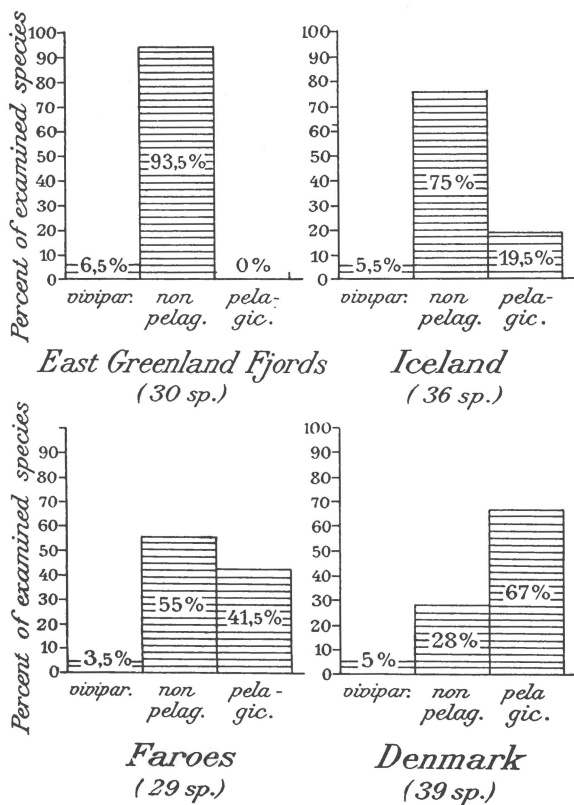


Fig. 7. Graphs showing the percentages of the modes of reproduction of the prosobranchs in Northeast Greenland, at Iceland, at the Faroes, and in the Danish waters. The number of species, whose development is known, constitutes in Northeast Greenland 59%, at Iceland 38%, at the Faroes 36% and in Danish waters 44% of the whole Prosobranch-fauna in the locality.

Danish waters, that is, in boreal seas. It will be interesting to investigate whether here the species reproduces itself in a different way from that prevalent in the Northeast Greenland fjords. A couple of egg-masses of this species from the Sound was therefore examined, and it proved that the size of the eggs and the mode of development was exactly the same as in Northeast Greenland. This shows

that the peculiar method of reproduction of this species is not a purely phenotypic property induced by the local conditions, but a property characteristic of the species.

It will now be of interest to investigate whether the methods of reproduction of the prosobranchs in Northeast Greenland agree with those of other arctic seas. Particularly interesting in this respect is the Karajak Icefjord near Umanak in West Greenland, the only locality in arctic seas in addition to the fjords of Northeast Greenland in which plankton samples have been taken in nearly all months of the year (cf. VANHÖFFEN 1897). While this plankton contained large quantities of lamellibranch larvæ and pteropod larvæ, prosobranch larvæ seem to be entirely absent in all the months of the year — that is, similar conditions to those of the Northeast Greenland fjords. However, VANHÖFFEN does not call attention to this phenomenon, which appears so distinctly from his plankton lists, and consequently gives no explanation of it either (cf. also p. 124, where the results from Karajak are discussed in detail).

From the Eisfjord at Spitsbergen a large number of plankton samples are at hand from July and August (Broch 1910, p. 37). In this material shells of four different pelagic gastropod larvæ were found which did not agree with any known forms and which cannot even be referred to any genus or family. Thus this plankton indicates quite different conditions from those shown by the Northeast Greenland fjord plankton; the explanation is near at hand, since the Spitsbergen waters are known to harbour a number of arctic-boreal or even more widely distributed forms of gastropods (e. g. *Turritella reticulata*, *Machaeroplax varicosa*, *Trophon clathratus*, and *Aeolidia papillosa*), which are not found at Northeast Greenland. It is very probable that the gastropod larvæ found belong to the species mentioned here, whose methods of reproduction are otherwise quite unknown.

However, even from Northeast Greenland a single example of a pelagic gastropod larva is known. In the innermost broad of Dusén Fjord some plankton hauls were taken on August 12, 1933, which contained several larvæ, in which the shape of the shell resembled the larval stages of tectibranchiate snails. The gastropod fauna on the spot was carefully investigated, and it proved later that all the prosobranchs found there were forms whose direct development could be ascertained by means of material brought home. Then only the opisthobranchs remained; of these the arctic-boreal *Cylichna alba* was unquestionably the most dominating form in the place, and hence it is highly probable that it is the larvæ of this form that were found in the plankton. However, even these larvæ represented a much advanced *Veliger* stage, and probably have but an extremely short larval life.

The large material of egg-masses from the fjords of Northeast Greenland i. a. supplied a fairly good idea of the time and length of the period

Species \ Month	May	June	July	Aug.	Sept.	Oct.	Nov.
* <i>Sipho curtus</i>			—————	—————	—————		
<i>Sipho islandicus</i>	— — — —	— — — —	—————	—————	—————	— — — —	— — — —
* <i>Sipho lachesis</i>			—————	—————			
* <i>Sipho krøyeri</i>			—————	—————			
* <i>Jumala ossiana</i>	—————	—————					
<i>Volutopsis norvegica</i>				—————	—————		
* <i>Buccinum hydrophanum</i> ..	—————	—————	—————	—————	—————	—————	
* <i>Buccinum belcheri</i>	— — — —	— — — —	—————	—————			
<i>Buccinum groenlandicum</i> ¹⁾		— — — —	— — — —	— — — —	—————	—————	—————
* <i>Buccinum sericatum</i>		—————	—————	—————			
* <i>Buccinum ovum</i>		— — — —	— — — —	— — — —			
* <i>Bela simplex</i>	— — — —	— — — —					
* <i>Bela exarata</i>	— — — —	— — — —					
<i>Bela bicarinata</i>				—————	—————	— — — —	— — — —
<i>Bela pyramidalis</i>			—————	—————	—————		
* <i>Bela nobilis</i>			—————	—————			
<i>Trichotropis borealis</i>		— — — —	— — — —				
* <i>Trichotropis conica</i>				—————	—————	— — — —	— — — —
<i>Natica groenlandica</i>	— — — —	— — — —	—————	—————	—————		
<i>Natica clausa</i>			—————	—————	— — — —		
<i>Natica islandica</i>		—————	—————	—————			
<i>Margarita cinerea</i>			— — — —	— — — —			
<i>Margarita helicina</i> ?		— — — —	— — — —	— — — —			
* <i>Acmaea rubella</i>			?	—————	—————	—————	?

¹⁾ This species lives only at the southeast coast of Greenland and is only included here for comparison with other *Buccinidae*.

of spawning and development in several of the prosobranchs occurring within the area. This is shown by the table p. 44. A heavy line indicates that the material at hand is sufficient to allow of a fairly accurate determination, while the thin lines indicate that the material is defective and does not give an exhaustive picture of the conditions. If an egg-capsule at the earliest date of the year whence samples are available, contained large embryos, this is a sign that the spawning had commenced some time before, and this is indicated by a stipled line preceding the continuous line. If, however, an egg-capsule at the latest date of the year whence samples are at hand, still contained undeveloped or slightly cleaved eggs, it can be inferred that the development will not be completed till some time afterwards, and this is indicated by a stipled line after the continuous line¹).

Thus the time intervals given in this table for each species comprise the length of the period of spawning plus the length of the time of development, that is, the time interval between the earliest date of the year at which an egg-capsule with undeveloped eggs of the particular species was found and the date at which the last embryos have left the last laid egg-capsules.

In spite of the longer and shorter periods of spawning in the various prosobranchs of the area in question, all these forms seem to have relatively short periods of spawning as compared with those of more southern forms. Thus the *Littorina* species are known to spawn all the year round; LEBOUR (1934, p. 529) states that larvæ of *Rissoa parva* can be found in the plankton during ten months of the year, etc. At Northeast Greenland the developmental stages of all the egg-capsules found seem to show that the maximum of reproduction occurs within the ice-free summer time, and that the development is as a rule completed within that period. This could be ascertained with certainty in several species (*Sipho curtus*, *Buccinum belcheri*, *Bela pyramidalis*, *Natica groenlandica*, and *Margarita helicina*), and the table indicates that nearly all the forms follow this rule. As all the species mentioned in the table with the exception of *Sipho lachesis*, *Volutopsis norvegica*, and *Bela nobilis* have their main distribution at depths of less than 25 m, their period of spawning thus coincides with the period of the year in which the temperature of the water at that depth is positive (cf. pp. 9 and 80). Further it seems as if the arctic species of a genus as regards reproduction differ fairly much from species of the same genus which are distributed outside the Arctic also; both *Bela simplex* and *Bela exarata* spawn in the early summer, and since the embryos of both these species were almost of the same size in nearly all the egg-capsules at the same

¹) The forms marked with an asterisk are almost exclusively distributed in arctic seas.

dates, the spawning process proper must be presumed to take place within a very limited period, whereas *Bela bicarinata* and *Bela pyramidalis* spawn later in the summer and — judging from the size of the embryos — over a longer space of time. Something similar is known for the genus *Sipho*, *S. curtus* spawning within a fairly limited period and completing both spawning and embryonic development in little over three months, while *S. islandicus* has a longer period of spawning and accordingly a considerably longer combined period of spawning and development. However, the specimens at hand are too few to show whether or not this rule is universally valid.

As usual in the prosobranchs, by far the greater number of the species of this group, too, are unisexual in arctic seas. Of hermaphrodites only the following forms are known, viz. *Onchidiopsis glacialis*, *Marsenina micromphala*, *Velutina laevigata*, *Velutina undata*, and finally the viviparous *Acmaea rubella*. Further, hermaphroditism was found, as normally, in the opisthobranchs, which, as mentioned above, are not very numerous.

Thus hermaphroditism plays a rather subordinate role for this animal group in arctic seas, and the percentage of hermaphrodites as compared with unisexual forms seems not to be much greater here than in more southern seas.

A survey of the methods of reproduction in the Northeast Greenland prosobranchs show the following facts: Of the 51 prosobranchs found at Northeast Greenland, 25 species have an almost exclusively arctic distribution, 17 species are mainly distributed in the Arctic but may also occur in the northern parts of the boreal seas, 4 species are arctic-boreal, and 5 species have a still wider distribution (the Mediterranean, etc.). The 30 species of prosobranchs whose reproduction is known, and which all had a direct non-pelagic larval development, may be grouped as follows in respect of distribution: exclusively arctic distribution, 17 species; mainly arctic and slight boreal distribution, 10 species; arctic-boreal distribution, 1 species; and still wider distribution, 3 species. It will be seen that within the forms investigated as well as within all the prosobranch species of Northeast Greenland there is a great dominance of forms whose distribution comprises exclusively or essentially the Arctic. This corresponds closely to the observations made concerning the echinoderms, but is in contrast to those of the polychaetes (p. 36), the fauna of which in Northeast Greenland is largely made up of widely distributed forms.

Of the invertebrate groups investigated in Northeast Greenland the prosobranchs is moreover the group within which the non-pelagic larval development is most pronounced, since hitherto not a single case of pelagic larval development has been ascertained. The above-mentioned investigation of *Natica groenlandica* indicates (cf. p. 42) that this non-

pelagic method of reproduction is characteristic of the species under other ecological conditions also, and very probably the same applies to the mode of reproduction in the remainder of the Northeast Greenland species. Here, too, the prosobranchs of Northeast Greenland must therefore be assumed to contrast with the polychaetes, since in the latter there seems to be a great lability in the methods of reproduction in the individual species.

D. Lamellibranchiata.

In the fjords of Northeast Greenland the lamellibranchs are represented by a fairly considerable number of species, and while the majority of the prosobranchs were decidedly arctic, the lamellibranchs include a somewhat greater percentage of widely distributed forms. In the prosobranchs pelagic larval stages were not observed at all in Northeast Greenland, whereas the series of plankton hauls from all the months of the year show that pelagic lamellibranch larvæ occur through a fairly long period and in the actual summer time (May to August) even in a very considerable number. Thus in the month of July an average

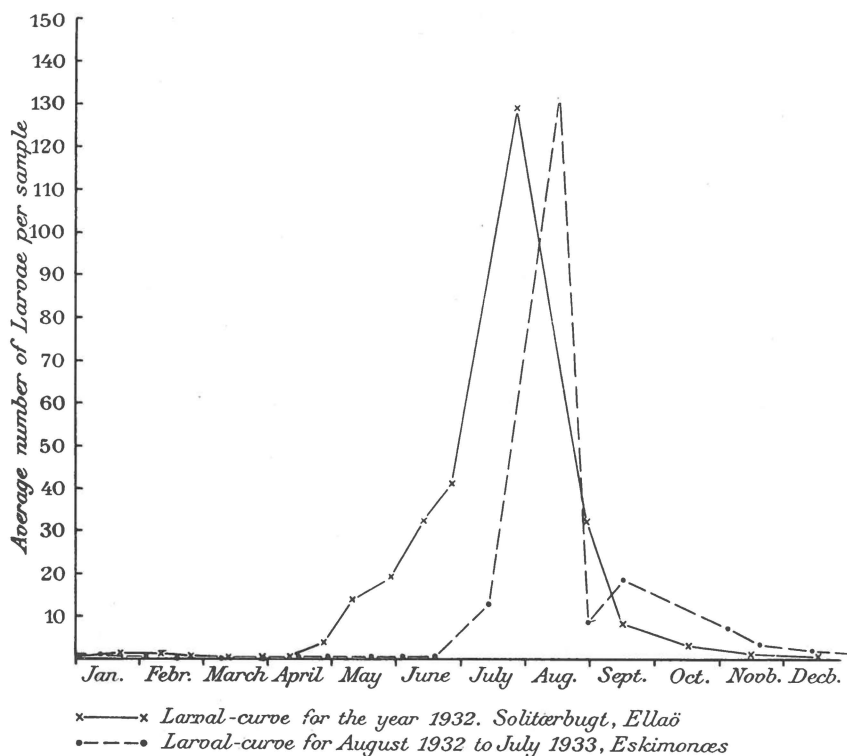


Fig. 8. Curves showing the number of lamellibranch larvæ in the plankton in all the months of the year at Ellasø and Eskimonæs, Northeast Greenland.

of 125 individuals for each sample taken with hand net (vertical haul, 50—0 m, Ellaø) was found (cfr. Fig. 8).

Hence we are certain that some of the lamellibranch species found in the Northeast Greenland fjords have pelagic larval stages, and the question then arises whether such a pelagic stage is the rule in all the arctic lamellibranchs, or whether the lamellibranch larvæ in the arctic plankton are derived from a small number of species. If the latter is the case, a new problem presents itself, namely the determination of the species of the pelagic larvæ in order to decide whether they belong to purely arctic or to more widely distributed forms. Such an identification is, however, extremely difficult and is normally only possible through observations of living material, either directly by the hatching of eggs whose species is known, or by cultivation of pelagic larvæ. In this way it is attempted to attain such an advanced stage of development that an identification of their species is possible.

The rather limited time during which work in Northeast Greenland was possible did not allow of such detailed investigations on the spot. It was therefore decided tentatively to work out a method by which it would be possible by means of the collected material of plankton samples and bottom animals alone, which was preserved in alcohol, to answer the immediate questions bearing on reproduction and biology. This led to a slow and troublesome procedure, which, however, was rather rich in results. By this method the material preserved in alcohol was treated in such a way that the biological results could be largely utilised; however, the methods used became of special importance with respect to the plankton series at hand from all the months of the year. The working plan was briefly as follows:

- 1) An investigation of the period of spawning in all lamellibranchs of frequent occurrence within the area, in order to make out the relation between the period of spawning and the time when the lamellibranch larvæ appear in the plankton.
- 2) An investigation of the size of the egg in all frequent lamellibranchs within the area. From the size of the egg an attempt was made to calculate the minimum size of the pelagic larva, and by comparing this minimum size with the larvæ occurring in the plankton, still with a view to the time of spawning of the various species, an identification of the larvæ should be rendered probable.
- 3) Parallel to these investigations observations were made concerning other aspects of the question of reproduction (e. g. late or early maturity in the different species, hermaphroditism, etc.), which might be supposed to render the species especially well suited for competition in the arctic seas.

1) The periods of spawning. As already mentioned, only few and scattered observations have been made on living lamellibranchs in Northeast Greenland, also regarding times of spawning, and the final elucidation of these questions must therefore be based entirely on the considerable material, preserved in alcohol, of adult lamellibranchs. This material was collected in the period May to September¹⁾ — that is, the same months in which lamellibranch larvæ dominated in the plankton — and consequently the spawning time, at any rate for those species which had pelagic larvæ, must fall within the said interval. The following procedure was employed in the investigation: When the spawning time of a species was to be investigated, a number of adult individuals were selected from a series of dates distributed at suitable intervals over the months May to September (a particularly large material was at hand from the months July, August, and September). The length of the shell of the individual specimens was measured and taken down, and subsequently part of the gonad was dissected out and — after checking under a monocular microscope — in stained or unstained state placed in a simple glycerine slide and set aside for later investigation. When the material had become sufficiently comprehensive, 30 to 40 ♀♀ from each date were used for such gonad preparations. When a species had been treated in this way from all the suitable dates whence sufficient material was available, all the gonad slides were superficially examined under a monocular microscope, and three random, but typical and easily recognisable “egg-size stages” were selected from among the ovaries and drawn carefully at the same magnification. In selecting these three “egg-size stages”, stage 1 was always selected from among ovaries with the least developed eggs, stage 3 among ovaries with large eggs, and stage 2 from among ovaries with eggs of an intermediate size between stages 1 and 3. Using these three stages as bases, all the ovary preparations were then examined again, and each preparation designated according to the size of the eggs with a figure corresponding to the “egg-size stage”, for instance egg-size 1, 1—2, 2, 2—3, 3, and 3—1. By subsequently counting the percentage of ♀♀ falling upon the different “egg-size stages” at each of the particular dates used, a fairly reliable idea of the size of the ♀♀ eggs at the particular date was obtained, and thereby a reliable control of the date of the

¹⁾ It should be noted that the samples from the different months are derived from different years; the May, June, and July samples from 1932, the August samples from 1933, and the September samples from 1931. However, experience has shown that the ecological conditions in the summer change very regularly (changes of temperature within a limit of about ten days, etc.); this is also supported by the available observations from Ellæ made in the same month of different years.

beginning of the spawning. If thus a series from the month of July shows a maximum of eggs of size 2—3 (i. e. eggs nearly ready to be spawned) and the corresponding series from August for the same species shows a maximum of egg-size 1 (quite young eggs), we are certain that the species has spawned in the intervening period.

By this method the egg-sizes in all the lamellibranch species of fairly frequent occurrence within the fjord districts were investigated. In all about 4000 slides of gonads of the Northeast Greenland lamellibranchs are at hand; by means of which it was possible to demonstrate the spawning times for most of the lamellibranchs of the area. The table in p. 51 shows some of the results of this investigation as expressed through the percentages of individuals with big, loose eggs and individuals with recently emptied ovaries respectively of each species from different dates throughout the summer. It will be seen from the figure that there is a considerable difference between the spawning times of the different species.

Of specially characteristic features it may be pointed out that *Pecten groenlandicus*, of such common occurrence in Northeast Greenland, does not spawn at all within the period whence the material preserved in alcohol is derived (i. e. June to the end of September). Within this period the maximum number of the eggs contained in the ovaries of this species has moved from egg-size 1 (small, undeveloped eggs) to egg-size 2 (semimature, closely coherent eggs), and thus it is impossible to decide when the spawning sets in. The egg-size stages for the four *Astarte* species show that all the Northeast Greenland species of this genus (*A. borealis*, *A. banksi*, *A. elliptica*, and *A. crenata*) follow the same rule and spawn very late in the autumn. Independently of these egg-size stages for *Astarte*, which are distinctly indicative of that fact, I observed, in October 1931, loose eggs in the pallial cavity of individuals of all four species. The investigations of the maturity further show that these *Astarte* species throughout the summer have big, loose eggs in their ovaries, but nevertheless do not spawn till late in the autumn. These periods of spawning found for the genus *Astarte* and for *Pecten groenlan-*

Table (p. 51) showing the spawning of some species of lamellibranchs at Ellæ (adult individuals). The columns marked A give the number of individuals with big, loose eggs ready to be spawned, expressed as a percentage of the total number of individuals examined of that species from the particular date. The columns marked B give the number of individuals with empty ovaries which showed traces of having recently completed their spawning, expressed in the same way as in the columns marked A. The figures in parentheses indicate the whole number of individuals of the species examined from the particular date.

Dates	June		July		August		September	
	1—15	15—30	1—15	15—31	1—15	15—31	1—15	15—30
Summer-spawning species								
<i>Saxicava arctica</i>	{ A (21) 47	..	..	..	(36) 19	..	..	(10) 10
	{ B 14	..	..	..	28	..	..	70
<i>Mya truncata</i>	{ A (14) 27	..	..	..	..	..	(9) 10	..
	{ B 0	..	..	..	..	..	44	..
<i>Cardium ciliatum</i>	{ A ..	..	(25) 48	..	(23) 34	..	..	(35) 9
	{ B ..	..	4	..	18	..	..	12
<i>Macoma calcaria</i>	{ A ..	..	(22) 4	..	(18) 5	..	(13) 0	..
	{ B ..	..	0	..	17	..	0	..
<i>Modiolaria laevigata</i>	{ A (17) 24	..	(17) 19	..	(49) 30	..	..	..
	{ B 0	..	0	..	17	..	..	..
<i>Axinus flexuosus</i>	{ A ..	..	..	..	..	..	(17) 42	..
	{ B ..	..	..	..	..	..	53	..
<i>Arca glacialis</i>	{ A ..	..	(24) 25	..	(18) 38	..	..	(26) 34
	{ B ..	..	0	..	34	..	..	28
Winter-spawning species								
<i>Astarte elliptica</i>	{ A ..	..	(33) 4	..	(32) 22	..	..	(36) 42
	{ B ..	..	0	..	4	..	..	6
<i>Astarte borealis</i>	{ A (20) 5	..	..	..	(40) 8	..	..	..
	{ B 0	..	..	..	0	..	..	..
<i>Astarte banksi</i>	{ A ..	..	(30) 0	..	(31) 4	..	..	(11) 10
	{ B ..	..	0	..	0	..	..	0
<i>Astarte crenata</i>	{ A ..	..	(30) 0	..	..	..	..	(27) 22
	{ B ..	..	0	..	..	..	..	0
<i>Pecten groenlandicus</i>	{ A ..	(23) 4	..	..	..	..	..	(24) 0
	{ B ..	8	..	..	..	..	..	0

dicus are especially noteworthy in that they occur in the months for which the plankton samples from the same locality (Ellasø) show an almost total lack of lamellibranch larvæ, despite the fact that all the forms mentioned are exceedingly common at Ellasø, and their larvæ must thus be presumed to play a dominating role in the plankton, provided these larvæ are pelagic at all. At Ellasø *Astarte borealis* thus occurs at a depth of 3—14 m in a number of about 80—90 individuals per sq.m., *Astarte elliptica* at 3—50 m depth in a number of 12—28 individuals per sq. m., *Astarte banksi* at 3—50 m depth in a number of 8—24 individuals per sq. m., and finally *Pecten groenlandicus* at a depth of 25—45 m in a number of 4 individuals per sq.m. It being thus a fact that these frequent species spawn at a time when the lamellibranch larvæ are absent from the plankton, the consequence must necessarily be that either these forms have a very short larval stage (e. g. some few hours only, and moreover are presumably spawned by night, as is usual in the molluscs (cf. PELSENEER 1926, pp. 3—4)), or that a pelagic larval stage is lacking.

Axinus flexuosus spawns at a somewhat earlier time than the *Astarte* species (viz. in August—September). At Ellasø the species occurs at all depths in a number of 7—30 individuals per sq.m., and hence in this form, too, the pelagic stage seems to be very short or entirely absent. At a somewhat earlier time than the forms mentioned so far — viz. August — the spawning of *Portlandia arctica*, and *Nucula tenuis*¹⁾, i. e. the taxodonts investigated, takes place (the end of July and the beginning of August), somewhat earlier still, at the end of July (or the beginning of August) the species *Cardium ciliatum*, *Macoma calcaria*, and *Arca glacialis* were found to spawn (cf. the table). Finally, as early as (May) June and the beginning of July, *Mya truncata* and *Saxicava arctica* spawned, and this spawning was also observed in living individuals in aquaria on Ellasø in May and June, 1932.

If, now, we compare all the times of spawning observed at Ellasø with the curve for the lamellibranch larvæ in the plankton in the same locality, we shall find that the curve showing the frequency of the lamellibranch larvæ has its maximum in the plankton about the middle of July. Compared with the times of spawning of the various lamellibranchs this means that only *Saxicava arctica* and *Mya truncata* spawn immediately before and at the time when the large maximum of lamellibranch larvæ occurs in the plankton. Even in the forms spawning at a somewhat later date (*Cardium ciliatum*, *Macoma calcaria*, and *Arca glacialis*) conditions seem to be different, the number of lamellibranch larvæ in the plankton decreasing rapidly at that time (August) when these forms spawn, and as regards all the forms that spawn later

¹⁾ The investigation of these two species was based on material from Hurry Inlet, Franz Joseph Fjord, and Dusén Fjord.

in the year, i. e. the taxodonts, and *Axinus* and more especially, *Astarte*, and *Pecten groenlandicus*, the larval stage seems to be much shorter or to be absent altogether. The same applies to *Modiolaria discors* and *Modiolaria nigra* — two lamellibranchs extremely common within the area. Thus *Modiolaria discors* var. *laevigata* spawns throughout the period from the beginning of June to the end of August, and both species lack pelagic larval stages (cf. THORSON 1935 a).

2) Egg-sizes. As stated above, the amount of nourishment contained in the individual egg normally bears a direct relation to the size and development of the embryo. This proved to be the case both in echinoderms and prosobranchs, and it is therefore natural to investigate this relation in the lamellibranchs, too. As mentioned above, it was possible on the summer trips to Northeast Greenland to clear up the modes of reproduction in the two arctic *Modiolaria* species, *M. discors* var. *laevigata* and *M. nigra* (cf. THORSON 1935 b). These two species lay their eggs in characteristic egg-strings, in which the eggs develop into embryos of such a size that a pelagic stage cannot possibly exist (larval stages of this size are not known at all from the plankton of Northeast Greenland). Thus two species were found here with a direct development and with no pelagic stage. It would be interesting, then, to compare the egg-size in these two forms with that of other arctic and boreal species, belonging partly to the same or related genera, partly to genera of quite a different type. *Modiolaria nigra* was found to have the largest eggs (0.40—0.50 mm in diameter), but the eggs of *M. laevigata* also were of a considerable size (0.25—0.30 mm in diameter)¹⁾. For comparison may serve that the egg of the boreo-lusitanous species *Modiolaria marmorata* (LOVÉN 1879, pl. 10) has a diameter of only 0.06 mm and a subsequent pelagic larva, and among other *Mytilidae* the egg of *Mytilus edulis* has a diameter of 0.07 mm and has also pelagic larvæ. Thus the two *Mytilidae* occurring in arctic seas have big eggs and direct development, in contrast to the known species of the same group which only occur farther south. It would be natural now to investigate the egg-size of the four *Astarte* species and of *Pecten groenlandicus*, which, as stated above, all spawn at a time when the number of larvæ in the plankton is minimal. In fact, it turned out that all the four *Astarte* species have eggs with an amount of nourishment of a diameter of 0.15—0.20 mm, that is, very big eggs. It should be noted here that the largest lamellibranch egg known to develop into a pelagic larval stage, has an egg-diameter of 0.15 mm (*Yoldia limatula*, cf. DREW 1888), while eggs with a larger diameter in all the cases investigated were found to have a direct non-pelagic development (cf. *Modiolarca trapezina* (BISPINGHOF 1915), *Nucula*

¹⁾ The diameters given here only apply to the size of the egg proper, while the size of the mucous membrane is disregarded.

delphinodonta (DREW 1901), *Modiolaria nigra*, and *M. laevigata* (THORSON 1935a). The pelagic larva of *Yoldia limatula* mentioned above has moreover only a larval stage of a duration of 95 hours at the normal temperature in the place where these observations were made, i. e. a very short larval stage¹). From this comparison alone it will be evident that the Northeast Greenland species of *Astarte* must have an exceedingly short pelagic larval life, or, probably, a direct development with no pelagic larva, which thus agrees excellently with the data found for the period of spawning. It will be necessary to add here that the species of *Astarte* in an adult state belong to the same category of magnitude as *Yoldia limatula*, a fact which must also be taken into consideration, as conditions in the *Modiolaria* species suggest that the size of the species has some relation to the egg-size.

It will now be appropriate to investigate the egg-size in all the lamellibranch species of common occurrence in Northeast Greenland. In connection with this investigation all the available literature on the subject was studied, with the principal object to secure any data about species with a more southerly distribution belonging to the same genera as occurred in Northeast Greenland. Fig. 9 shows the result of these comparisons; in all the cases investigated the boreal species were found to have much smaller egg-sizes than the corresponding arctic forms. A number of particularly typical examples will be given below, namely such cases in which both arctic and more southerly representatives of the same or very closely related genera were investigated.

Arctic (A) or arctic-boreal (AB) distribution	Boreal (B) or more southern (S) distribution
<i>Modiolaria nigra</i> (AB) (0.40—0.50 mm)	<i>M. marmorata</i> B og S (0.06 mm)
<i>Modiolaria laevigata</i> (AB) (0.25—0.30 mm)	
<i>Macoma calcaria</i> (AB) (0.17 mm)	<i>Macoma baltica</i> (B) (0.08—0.06 mm)
<i>Venus fluctuosa</i> (A) (0.32—0.24 mm)	<i>V. mercenaria</i> (S) (0.08 mm)
	<i>V. ovata</i> (BS) (ca. 0.05 mm)
<i>Cardium ciliatum</i> (A) (0.12 mm)	<i>Card. exiguum</i> (BS) (0.064 mm)
<i>Pecten groenlandicus</i> (A- and abyssal) (0.14 mm)	<i>P. maximus</i> (S) (0.05 mm)
	<i>P. irradians</i> (S) (0.062 mm)
	<i>P. opercularis</i> (BS) (0.068 mm)
<i>Portlandia arctica</i> (A) (0.14 mm)	<i>Yoldia sapotilla</i> (S) (0.05—0.04 mm)
<i>Portlandia lenticula</i> (A) (0.12 mm)	
<i>Nucula tenuis</i> (AB) (0.13—0.14 mm)	<i>Nucula proxima</i> (S) (0.09 mm)
<i>Arca glacialis</i> (A- and abyssal) (0.17 mm)	<i>Arca noae</i> (S) (0.07—0.05 mm)

¹) For comparison may serve that *Cummingia tellinoides*, *Mytilus edulis*, and *Mya truncata* (at a temperature of about 20° C) take three weeks (GRAVE 1927, NELSON 1928) and *Ostrea virginica* normally 13—17 days (at a temperature of 20°—24° C) for the pelagic larval development.

If, now, we compare the sizes of the eggs of the Northeast Greenland forms with each other, it turns out that the above-mentioned species *Modiolaria nigra* and *M. laevigata* have the largest eggs. On a level with the latter are the eggs of *Venus fluctuosa* (0.32—0.25 mm), which species in all probability has no pelagic development. In the next class of magnitude, i. e. eggs whose amount of nutritive matter has a diameter ranging from 0.15 to 0.20 mm, belong the four *Astarte* species, *Macoma calcaria*, and *Axinus flexuosus* (which despite its small size — maximum length in Northeast Greenland 6 mm — has very large eggs, cf. fig. 9). Thus the eggs of all the forms mentioned here exceed the egg-size which according to the literature develops into pelagic larvæ (limit 0.15 mm egg-size for *Yoldia limatula*).

In contrast to these there are a number of Northeast Greenland forms in which the nutritive matter of the egg varies from 0.12 to 0.14 mm in diameter, viz. *Leda pernula*, *Nucula tenuis*, *Portlandia arctica*, *Portlandia lenticula* (that is, the majority of taxodonts), and further, *Cardium ciliatum*, *Pandora glacialis*, and *Lyonsia arenosa*. Despite their comparatively large eggs, all these forms come within the order of magnitude in which a pelagic larval stage — even though short — may be assumed to occur. However, in this connection it should be noted that even among eggs of a diameter of only 0.10 mm — i. e. decidedly smaller than those occurring here — examples of a development without pelagic larvæ are known (e. g. *Phaseolicama magellanica*, cf. IGEL 1908, p. 24), and accordingly the larval stage in the Northeast Greenland forms of this egg-size, too, must be presumed to be extremely short or lacking altogether. The above-mentioned period of spawning of the lamellibranchs in the Northeast Greenland waters points in the same direction. Of the forms of common occurrence in Northeast Greenland there remain, then, only two whose egg-size belongs to quite another class, and whose egg-diameter (0.07—0.08 mm) is so small that they correspond entirely to the egg-sizes from which the pelagic larval stages of the boreal and southern seas develop, viz. *Mya truncata* and *Saxicava arctica*, i. e. precisely the two species which according to the egg-size scale spawn at a time when the large masses of larvæ appear in the plankton. *Saxicava* has no more southerly species with which its egg-size can be compared, but if we compare the egg-size in the boreal *Mya arenaria* and the arctic-boreal *Mya truncata*, we shall find that the diameter of the eggs are exactly the same in both species, from which it may naturally be inferred that *Mya truncata*, in agreement with the data known for *Mya arenaria*, must be assumed to have pelagic larvæ (cf. STAFFORD 1912).

As stated above, it must be considered as certain, according to the available investigations, that *Saxicava arctica* and *Mya truncata* — the two species with the smallest eggs — spawn earlier in the summer than

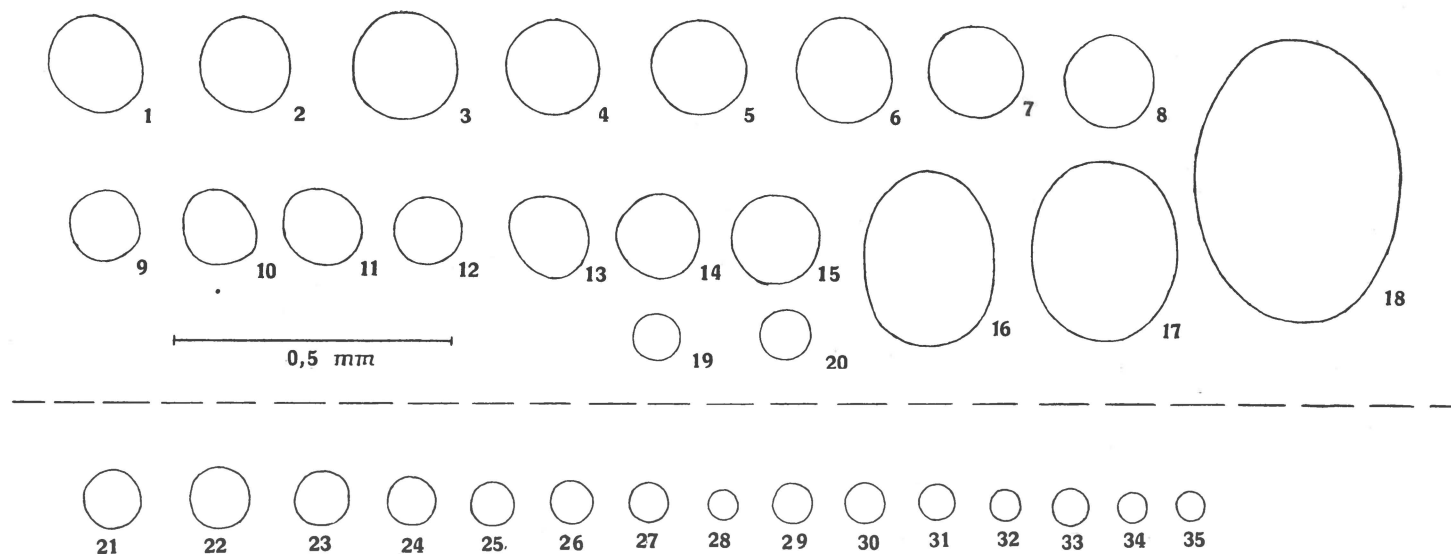


Fig. 9. Egg-sizes of arctic lamellibranchs (above the broken line) compared with egg-sizes of boreal and more southerly lamellibranchs.

Mucous membranes, if any, surrounding the eggs disregarded, only the nutritive contents of the eggs being compared.

1. *Macoma calcaria*, 2. *Astarte elliptica*, 3. *Astarte crenata*, 4. *Astarte borealis*, 5. *Astarte banksi*, 6. *Axinus flexuosus*, 7. *Arca glacialis*, 8. *Pandora glacialis*, 9. *Cardium ciliatum*, 10. *Leda pernula*, 11. *Nucula tenuis*, 12. *Portlandia lenticula*, 13. *Portlandia arctica*, 14. *Lyonsia arenosa*, 15. *Pecten groenlandicus*, 16. *Modiolaria discors*, 17. *Venus fluctuosa*, 18. *Modiolaria nigra*, 19. *Mya truncata*, 20. *Saxicava arctica*, 21. *Ostrea edulis*, 22. *Ostrea denselamellosa*, 23. *Nucula proxima*, 24. *Mya arenaria*, 25. *Mytilus edulis*, 26. *Pecten opercularis*, 27. *Pecten irradians*, 28. *Pecten maximus*, 29. *Cardium exiguum*, 30. *Macoma baltica*, 31. *Arca noae*, 32. *Yoldia sapotilla*, 33. *Ostrea gigas*, 34. *Ostrea virginica* and 35. *Ostrea angulata*.

any of the other forms, and in the broad features there seems to exist a certain relation between the egg-size and the period of spawning, the species with the large eggs spawning later in the summer than the species with smaller eggs. However, several distinct exceptions from this rule are known.

The question how the spawning process proper takes place in the species with large eggs must as yet remain unanswered. In addition to the above-mentioned example of the eggs being laid in egg-strings attached to the vegetation (*M. discors*) or to the byssus of the animal itself (*M. nigra*), adhesive eggs or egg-masses are only known in a minority of lamellibranchs, namely in *Loripes lacteus* (PELSENEER 1926), *Cyamium minutum* (JEFFREYS 1864, Bd. 2), *Nucula delphinodonta* (DREW 1901), and *Cardium exiguum* (LOVÉN 1879). The spawning of the latter is characteristic in that the eggs are attached singly to the bottom by means of a peculiar double mucous membrane (LOVÉN 1879, pl. 11). However, precisely the same type of mucous membrane is found in the eggs of *Macoma calcaria* and the four arctic species of *Astarte*, and accordingly it is highly probable that these eggs at the spawning are attached to a substratum in a similar way.

The question now arises whether widely distributed lamellibranch species have eggs of the same size throughout their area of occurrence, or whether the egg-size within the same species varies somehow with the ecological conditions under which the species lives. During the mention of the prosobranchs (cf. p. 42) one case was recorded in which such a control investigation could be made. It was ascertained that the arctic species *Natica groenlandica*, which occurs as a relict in the Danish waters, has exactly the same mode of development and egg-size in the Sound as in Northeast Greenland, and precisely the same applies to those lamellibranchs for which a control examination has been carried through. Thus the peculiar egg-strings laid by *Modiolaria discors* are known not only from the Arctic, but also from the Kiel Bay (western Baltic) (MEYER and MÖBIUS 1872, p. 79) and from the Kattegat, where, as in the Arctic, it has been found with large embryos (cf. THORSON 1935b). A similar control examination has been made of Danish material of *Astarte borealis* and *Astarte elliptica*, which also proved to have exactly the same egg-size in boreal seas and in Northeast Greenland. As regards these controlled forms it is therefore probable that the large egg-size and the associated direct development without pelagic stages is characteristic of the species (cf. also p. 79).

3) The relation between egg-size and larval stage. Let us now compare the egg-size observed in the different Northeast Greenland lamellibranch species with the size of the larvæ occurring in the plankton at different times of the summer. However, in order to obtain reliable

results of such a comparison it is necessary to know the size of the larva which develops from an egg of a known size. During the cleaving of the egg some amount of energy will be lost, but at the same time the lumina formed through the gastrulation, etc., will increase the surface of the animal. In the fairly copious literature available on the subject a number of examples of lamellibranch eggs are recorded whose development has been traced from the earliest gastrulation stages to the free-swimming larval stage, before the larva has taken any nourishment, i. e. the stage it has reached solely on the nourishment contained in the egg proper. It should be noted that at this youngest free-swimming stage all lamellibranch larvæ resemble each other so greatly as regards the shape of their shell that the error which might arise by using the length of the

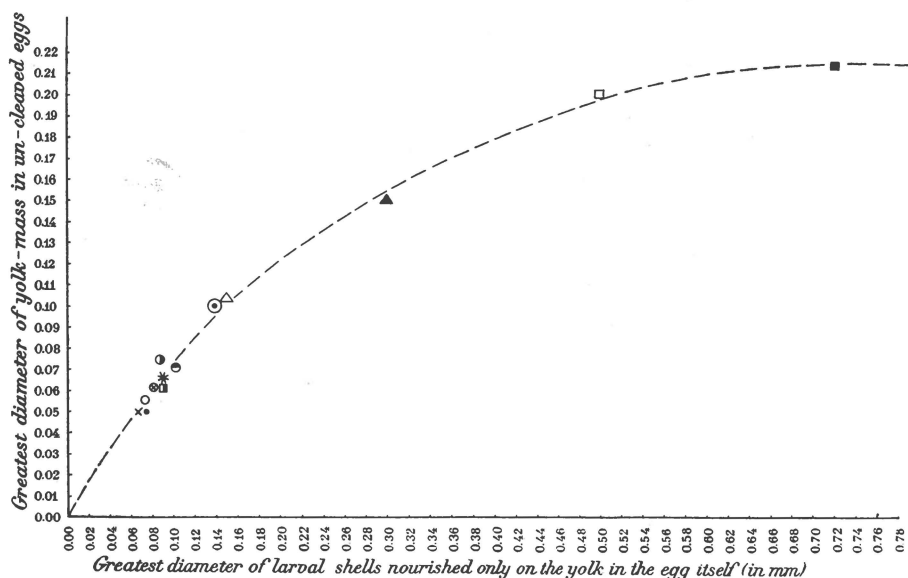


Fig. 10. Curve showing the relation between the volume of nutritive matter of the egg (indicated by the diameter of this matter) and the largest shell length of the lamellibranch larva developed from this mass (i. e. the shell length of the larva developed exclusively on the nutritive matter present in the egg).

- *Ostrea virginica* (AMEMIYA 1926).
- *Modiolarca trapezina* (BISPINGHOF 1915).
- *Nucula delphinodonta* (DREW 1901).
- ⊙ *Pecten irradians* (GUTSELL 1930).
- * *Cardium exiguum* (LOVÉN 1879).
- *Mya arenaria* (BATTLE 1832, STAFFORD 1912).
- × *Ostrea angulata* (AMEMIYA 1926).
- ▲ *Yoldia limatula* (DREW 1899).
- *Ostrea gigas* (FUJITA 1929).
- △ *Ostrea denselamellosa* (SENÔ 1929).
- ▣ *Cumingia tellinoides* (GRAVE 1927).
- *Mytilus edulis* (BATTLE l. c., STAFFORD l. c.).
- ⊙ *Ostrea edulis* (SPÄRCK, verbal information).

shell as a comparative basis for the indication of the size from one species to another is quite minimal. The curve (fig. 10) is based on thirteen observations recorded in the literature on this part of the development in different lamellibranchs. This curve shows that in all the cases examined the length of the shell in the pelagic larva just developed is always larger than the diameter of the uncleaved egg of the same lamellibranch species, and that this size of the shell of the larva is in direct relation to the size of the egg. As regards small eggs, this relation in size seems to be quite uniform, while in somewhat larger eggs it is more labile. It is noteworthy, however, that in eggs containing a large amount of nutritive matter there is an immense difference in size between the diameter of the egg and the length of the shell of the young larva. Thus the diameter of the egg of *Yoldia limatula* is 0.15 mm, while the length of the shell of the newly developed larva is 0.30 mm; *Modiolarca trapezina* has an egg diameter of 0.20 mm and a shell length of 0.50 mm in the newly developed individual. In *Nucula delphinodonta* the egg diameter is 0.215 mm and the length of the shell of the youngest individual 0.71 mm.

This relation is of fairly great importance for the identification of the lamellibranch larvæ found in the Northeast Greenland plankton, and may probably in all waters be used as a factor of identification as regards these problems. Let us imagine a lamellibranch larva with a shell length of for instance 0.15 mm, which may at the outset be supposed to be derived from one of the two lamellibranch species living in that locality. If an investigation shows that one species possesses eggs ready to be spawned of a diameter of 0.08 mm, and the other eggs ready to be spawned with a diameter of 0.15 mm, the larva with a shell length of 0.15 mm, according to the curve in fig. 10, cannot be derived from the egg with a diameter of 0.15 mm, an egg of that diameter corresponding to a larval shell length of at least 0.22—0.24 mm. If it is only a question of these two species, the larva must therefore represent an older stage of the species whose egg-diameter is 0.08 mm.

At Ellaø a typical example of the case sketched out above was observed. The plankton material for June, i. e. the month in which *Saxicava arctica* and *Mya truncata* were the only spawning species, contained a large number of lamellibranch larvæ whose shell length ranged from 0.10 and 0.15 mm with a maximum at 0.13 mm. According to the curve this shell length corresponds to eggs with an amount of nutritive matter 0.07 to 0.10 mm in diameter, or such a small egg-size that in Northeast Greenland it was only observed in the two above-mentioned forms, *Mya truncata* and *Saxicava arctica*; and consequently all the lamellibranch larvæ existing in July must be derived from one or both of these two species. However, all the lamellibranch larvæ found were of an appearance which is extremely characteristic of lamellibranch

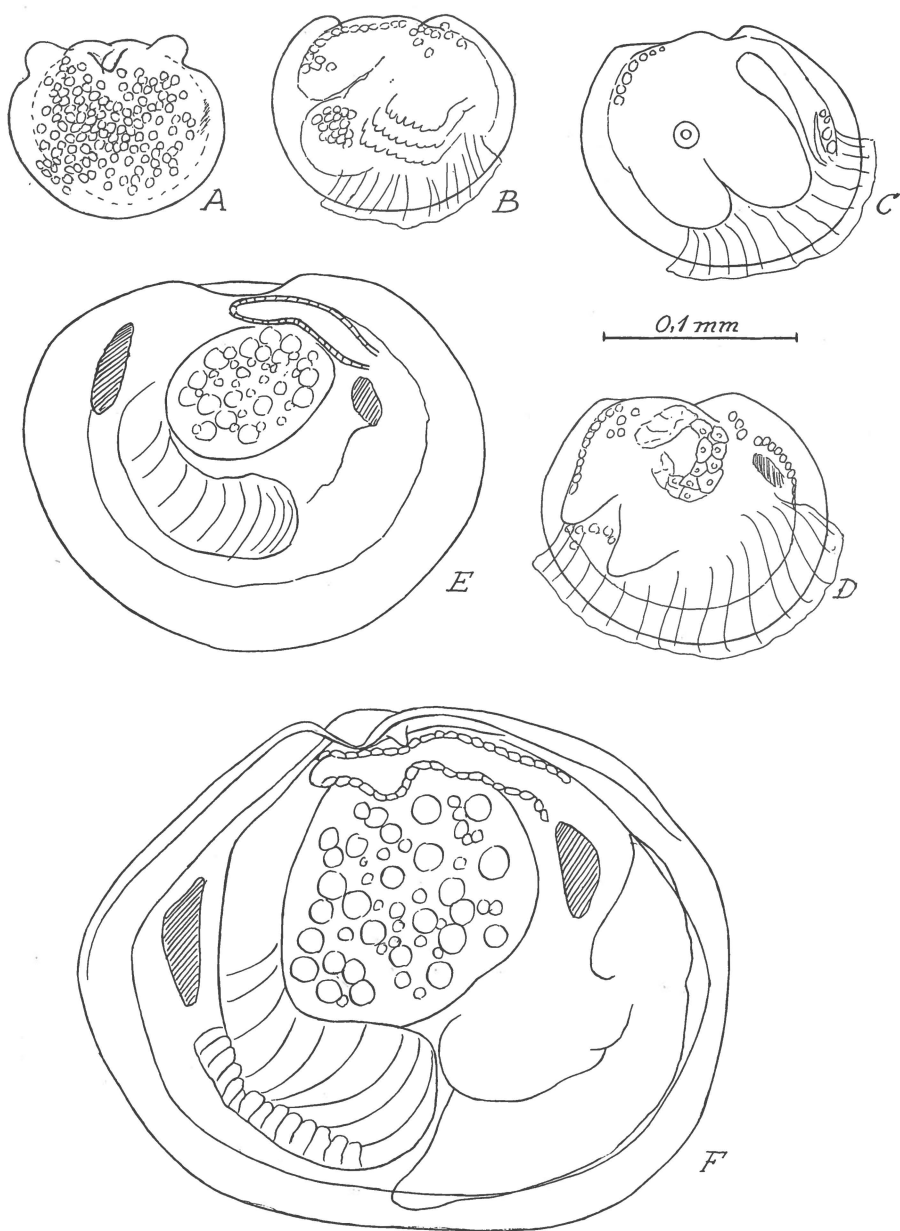


Fig. 11. Lamellibranch larvæ from Ellas plankton, all of them probably various stages of development of *Saxicava arctica*. It is remarkable that all the larger stages (E, F) constantly showed a distinct development of their organs, and thus must be later larval stages and consequently cannot be supposed to be derived from large eggs, but rather to be later stages originating from small eggs. A, B, C, and D taken on June 14, 1932, while E and F were taken on August 28, 1932.

larvæ at this stage, and apparently all belonged to the same species (cf. fig. 11). It was therefore natural to refer them to *Saxicava arctica*, which, quantitatively, plays a prominent part from the coast right out to about 100 m depth, while *Mya truncata* is far less numerous and lives at smaller depths. Moreover the well described larvæ of the boreal *Mya arenaria* — a form closely related to *Mya truncata* — differ exceedingly in appearance from the larvæ of common occurrence in the Northeast Greenland plankton in July (STAFFORD 1912), and a careful study of these plankton samples from July showed a very few larvæ of an appearance corresponding to those known of *Mya arenaria*¹).

Thus conditions are now clear as regards July; however, despite the great fall in the number of the lamellibranch larvæ in August, there are also a considerable number of larvæ in the plankton at the beginning of this month, and moreover on an average much larger larvæ than in July. The variation in the length of the shell of the lamellibranch larvæ in August thus ranged from 0.15 to 0.39 mm, with a maximum at 0.25 mm. However, as stated above, the period of spawning in the taxodonts as well as in *Macoma calcaria* and *Cardium ciliatum* falls in the end of July or the beginning of August, and the question now arises whether some of the large August-larvæ originate from these species. According to the curve shown in fig. 10 this is quite conceivable, since the egg-size of the species spawning in August agrees well with the shell length of the pelagic August larvæ. In order to clear up this question a long series of lamellibranch larvæ from various dates throughout the summer, in all stages from the smallest to the largest individuals, were drawn, and apart from the very few *Mya* larvæ found, they all showed the same, peculiar, appearance deviating rather much from that of other lamellibranch larvæ (cf. fig. 11), and the mutual resemblance between the individuals was so distinctly traceable throughout the developmental series that there is every indication that the August larvæ are merely later stages of the larvæ of *Saxicava arctica* and do not originate from the lamellibranch species spawning in August. Since, as mentioned above, all lamellibranch larvæ in these younger stages resemble each other very much, no definite proof can be obtained; however, comparisons with the lamellibranch larvæ known from the literature have shown that compared with them the Northeast Greenland larvæ are very characteristic and at the same time so greatly alike in appearance that the conjecture set forth above is in all probability correct.

¹) Investigations in Danish waters (Limfjord) have further shown that a large production of young of *Mya truncata* often only takes place at intervals of several years (cf. BOYSEN-JENSEN 1919), and hence it is not impossible that the spawning of this species may be of different intensity in the different years.

4. Hermaphroditism. While in the prosobranchs (p. 46) the hermaphrodite percentage was not higher in arctic than in boreal seas, hermaphroditism has been ascertained in a large number of lamellibranch forms. While the majority of lamellibranchs are unisexual, it is generally known that the hitherto investigated representatives of the much specialised lamellibranch genera *Thracia*, *Lyonsia*, *Lyonsiella*, *Pandora*, and *Cuspidaria* (-*Nexra*) are normally hermaphrodites, moreover with a complete separation of the male and the female gonads in the same individual (PELSENEER 1890, 1891, 1894, and 1903). Of the forms of these genera living in Northeast Greenland, only *Lyonsiella abyssicola* had been investigated and found to be a hermaphrodite (PELSENEER); however, in the material brought home from Northeast Greenland hermaphroditism with distinct male and female gonads was found to be the rule also in *Thracia truncata*, *Pandora glacialis*, and *Lyonsia arenosa*. Thus the mode of reproduction of the arctic species agrees entirely with that previously observed in these genera.

In all other known hermaphroditic lamellibranchs the hermaphroditism is of quite a different character, ova and sperma being here formed in different, not particularly sharply separated sections of the same gonad. This also applied to the repeatedly mentioned Northeast Greenland *Mytilidae*, *Modiolaria laevigata* and *Modiolaria nigra* (THORSON 1935b), both of which were distinctly protandric hermaphrodites. In *M. laevigata*, for instance, all one year old animals function as ♂♂ and also pass into their second year as ♂♂. However, in this second year of their life the eggs begin to develop, in which way the species pass into the hermaphroditic stage, and finally, at the end of the third year, are "purely" female. The examples mentioned here represent the first examples of hermaphroditism ascertained in *Mytilidae*, and while thus both *Modiolaria marmorata* (LOVÉN 1879) and *Mytilus edulis* are known to be unisexual — the latter, however, with a considerable percentage of hermaphrodites — it is noteworthy that precisely the two species living in the Arctic behave differently from other forms of the genus, though in the same manner on this point.

Within other lamellibranch species, too, there seem to be many hermaphrodites among the arctic forms. This applies for instance to the genus *Cardium*. While the majority of boreal *Cardium* species investigated (*Card. edule*, *Card. fasciatum*, etc. ORTON 1924) are normally unisexual¹⁾, an investigation of the Northeast Greenland *Cardium* species showed that *Cardium ciliatum* as well as *Cardium groenlandicum* were distinctly protandric hermaphrodites, and in the older specimens of these species

¹⁾ As is well known, *Cardium norvegicum* and *Cardium oblongum* are hermaphrodites (PELSENEER 1924).

ova as well as sperma were found to be developed simultaneously in the same gonad.

These are briefly the cases in which it was possible to demonstrate hermaphroditism in the forms occurring within the area in question. However, there is much to indicate that some more Northeast Greenland lamellibranchs are hermaphrodites, but this cannot be efficiently controlled, the change from one sex into the other being separated by a period in which it is difficult to recognise the sex, or else it takes place very suddenly, so that both sexual products are found at the same time in the gonad for a very short time only. Only under quite special conditions will it be possible to recognise hermaphroditism here, and generally observations of living material kept for years in an aquarium will be required if these phenomena are to be cleared up. Here a case will be mentioned in which hermaphroditism might normally occur in the species, but it could not be ascertained with certainty on the material available.

Locality	<i>Arca glacialis</i> . Date	Depth	Number of individuals examined ¹⁾	Number ♂♂
Ellasø	July 5, 1932	90 m	42	7
Ellasø	Aug. 3—5, 1933	30 m	37	0
Ellasø	Sept. 27, 1931	52 m	45	1
Cape Hedlund	July 11, 1932	c. 50 m	39	5

The large hermaphrodite percentage in July both at Ellasø and at Cape Hedlund makes it probable that a change of sex takes place at this time of the year and is completed in August. In spite of the comparatively low hermaphrodite percentage found here, the species may thus very well be a normal hermaphrodite.

Hermaphroditic individuals have been found in other genera, too. Thus a small number of hermaphrodites were regularly found in each series of *Pecten groenlandicus* examined, which moreover belongs to a genus comprising many hermaphroditic species. Within the genus *Astarte* also hermaphrodites have been found, though rarely, but the peculiar distribution of the sexes within this genus in the Northeast Greenland series investigated (series from one depth, i. e. at one temperature, contained a large majority of ♂♂, at another depth with another temperature, but at the same time of the year, mostly ♀♀, etc.) indicate that here, too, a change of sex takes place after an intermediate resting period, the species thus being hermaphrodites although both sexual products are rarely found simultaneously in the gonad. However, this is merely a conjecture and requires closer investigation.

¹⁾ All the individuals examined were adults and of about the same size.

Finally it should be mentioned that hermaphroditic individuals of *Axinus flexuosus* were also found, and that not a single hermaphrodite was found in the very large material of *Saxicava arctica* examined.

The reproduction of the Northeast Greenland lamellibranchs may be summarised as follows. The geographic distribution of the 37 lamellibranch species known from this district is as follows: Arctic distribution (14 species or 38 per cent.); mainly arctic, slightly boreal distribution (9 species — 24 per cent.); arctic-boreal distribution (3 species — 8 per cent.); wide distribution, but outside the Arctic only at great depths (5 species — 14 per cent.); and widely distributed species (6 species — 16 per cent.). The egg-size was investigated in 20 of these species, and the period of spawning in most of them. Of these 20 species, 18 had eggs of such a size that the pelagic larval development must be assumed to be very short or absent altogether. The distribution of the 18 species was as follows. Arctic distribution (5 species — 28 per cent.); mainly arctic and slightly boreal distribution (5 species — 28 per cent.); arctic-boreal distribution (3 species — 16.5 per cent.); widely distributed species but outside the Arctic in deeper water (2 species — 11 per cent.); wide distribution (3 species — 16.5 per cent.) — a percentage distribution corresponding fairly closely to that of the whole fauna of Northeast Greenland lamellibranchs. Within this group, too, all the species investigated with a mainly arctic distribution were found to have large eggs and probably a non-pelagic development. Only two of the 20 species investigated, viz. *Saxicava arctica* and *Mya truncata*, had small eggs and a prolonged pelagic larval stage. They are both widely distributed species, also outside the Arctic, and the large maximum of lamellibranch larvæ observed in the plankton from July is made up of the larvæ of these two species only.

The egg-size of the lamellibranchs has a direct relation to the size of the newly developed larva, and in the lamellibranchs the non-pelagic larval development is effected exclusively through an accumulation of yolk in the eggs, which makes an active absorption of nourishment for the larvæ at the youngest stages superfluous. Of the lamellibranch species with large eggs found in Northeast Greenland a considerable number are hermaphrodites.

E. Crustacea.

The two whole-year investigations of the plankton at Ellæs and Eskimonæs showed it to be very rich in *Nauplia* as well as *Metanauplia* of pelagic *Copepoda*, whereas it contained not a single *Zoëa* larva or other earlier larval stages referable with certainty to the bottom crustaceans. Hence it might be anticipated that such bottom crustaceans which normally have pelagic larvæ, are either absent from the Northeast Greenland fjords or reproduce in a manner unusual to the group in question.

The modes of reproduction known so far in the larger groups of marine bottom crustaceans may be broadly outlined as follows:

- Ostracoda.* — In marine bottom forms as a rule no metamorphosis and consequently no pelagic stage. Four species of this group are known from Northeast Greenland¹).
- Cirripedia.* — Free-swimming pelagic larval stage of a characteristic appearance, which through another pelagic *Cypris* stage passes into the fixed bottom stage. One species of this group known from Northeast Greenland.
- Mysidacea.* — The big eggs develop in the brood-pouch into young, which do not leave it until the metamorphosis has been completed. Fourteen species of this group are known from Northeast Greenland.
- Cumacea.* — The big eggs develop in the brood-pouch into young, which, on emerging, resemble the adults in all essentials. Accordingly no pelagic stage is found. Six species of this group known from Northeast Greenland.
- Isopoda.* — The big eggs develop in the brood-pouch into young, which, on emerging, resemble the adult in all essentials. Pelagic stage lacking. Six species of this group known from Northeast Greenland.
- Amphipoda.* — The big eggs develop in the brood-pouch, and the young leave it as fully developed individuals. From Northeast Greenland 75 species of this group are known.
- Decapoda.*
- Natantia.* — Eggs adherent to the caudal feet of the mother animal. At the *Zoëa* stage the young as a rule pass into a fairly protracted pelagic life, whence they pass (mostly through the *Mysis* stage) into the final shrimp stage. Thirteen species of this group known from Northeast Greenland.
- Reptantia.* — Eggs adherent to the caudal feet of the mother animal. At the *Zoëa* stage the young usually commence their pelagic life and pass (as a rule without any *Mysis* stage) into the shrimp (*Megalops*) stage and hence into the bottom stage. No species of this group known from Northeast Greenland.

If we compare the number of forms within the individual groups, a strong predominance of forms belonging to groups without pelagic larval development will be found (in all 105 forms), while only 14 forms

¹) For the preparation of the crustacean fauna list for Northeast Greenland the papers of H. I. HANSEN (1895 and 1900) and K. STEPHENSEN (1912, 1917, and 1933) have been used.

belong to groups which normally have a pelagic larval stage (*Balanidae*, 1 species; *Decapoda natantia*, 13 species). *Decapoda reptantia* was not found at all within the area, which was all the more remarkable since this group is usually richer in species in boreal seas than *Decapoda natantia*. Thus in the inner Danish waters including Skagerak and Bohuslän 26 species of *Decapoda natantia*, but 38 species of *Decapoda reptantia* were found, which shows a typical difference between the composition of the decapod faunas in boreal and in arctic seas. According to the experience already gained from an investigation of the other invertebrate groups, it can be stated that the 105 forms which in Northeast Greenland develop without pelagic larval stages, correspond excellently in their mode of reproduction to the other groups found in the Northeast Greenland waters, and do not, therefore, call for a detailed discussion.

However, in the fourteen forms belonging to groups whose larval development in other seas is mainly pelagic, the methods of reproduction should be more closely investigated. Of the greatest importance in this connection is the group *Decapoda natantia*, including thirteen of the above-mentioned fourteen forms, viz. *Sclerocrangon ferox*, *Sclerocrangon boreas*, *Nectocrangon lar*, *Spirontocharis gaimardi*, *Spir. spinus*, *Spir. turgida*, *Spir. polaris*, *Spir. groenlandica*, *Sabinea septemcarinata*, *Bythocaris payeri*, *Bythocaris leucopsis*, *Bythocaris simplicirostris*, and *Hymenodora glacialis*. It will be seen that very few genera only are represented, and of these the three *Bythocaris* species and *Hymenodora* are decidedly deep-sea forms, of which but a sparse material is at hand. The genus *Bythocaris* is further known to have "a development without any metamorphosis" (cf. G. O. SARS 1912, p. 12).

A much larger material is available of *Crangoninae* and of the genus *Spirontocharis*, and a thorough investigation of them is therefore possible. The material was found to contain specimens of all the Northeast Greenland species (eight) belonging to these groups with eggs on the caudal feet. As regards reproduction these species showed the following features:

<i>Sclerocrangon ferox</i> :	8 individuals taken at four stations in August and September, one of these with eggs (Aug. 25, 1932, at 250 m). Egg-diameter $5 \times 4 \text{ mm}^1$.
<i>Sclerocrangon boreas</i> :	43 individuals taken at 29 stations in June to October, five of them with eggs (June 22—Aug. 5, at 4—40 m). Egg-diameter 2.8 mm.
<i>Nectocrangon lar</i> :	24 individuals taken at 22 stations in June—September, one of which with eggs (July 18,

¹) Egg-diameter here denotes the diameter of the egg proper, the mucous membrane not included.

	1932, at 15—18 m). Egg-diameter 1.5×1.9 mm.
<i>Spirontocharis gaimardi</i> <i>forma typica</i> :	255 individuals taken at 84 stations in June—September, 31 of them with eggs (June 10—Sept. 26, at 19—95 m). Egg-diameter 0.8×1.1 mm.
<i>forma gibba</i> :	129 individuals taken at 51 stations in June—September. No individuals with eggs. Must all be assumed to be the ♂♂ corresponding to <i>forma typica</i> ¹).
<i>Spirontocharis spinus</i> :	143 individuals taken at 59 stations in June—September, 22 of them with eggs (June 22—Sept. 26, at 10—56 m). Egg-diameter 0.8×1.1 mm.
<i>Spirontocharis turgida</i> :	283 individuals taken at 45 stations in May—October, 72 individuals with eggs (May 24—Oct. 10, at 3—24 m). Egg-diameter 0.8×1.1 mm.
<i>Spirontocharis polaris</i> :	80 individuals taken at 40 stations in May to September, 4 individuals with eggs (June 10—Sept. 15, at 10—35 m). Egg-diameter 1.4×2.1 mm.
<i>Spirontocharis groenlandica</i> :	5 individuals taken at four stations in July—August, 2 individuals with eggs (July 4—Aug. 5, at 15—38 m). Egg-diameter 1.5×2.1 mm.

As the egg-size may vary considerably in relation to the size of the adult species, it is necessary to point out that *Sclerocrangon ferox* and *Sclerocrangon boreas* belong to the same order of magnitude, while *Nectocrangon lar* is much smaller. Further, *Spirontocharis polaris* and *Spir. groenlandica* are of the same order of magnitude, while *Spir. spinus*, *Spir. gaimardi*, and *Spir. turgida* are of equal size, but smaller than the preceding forms. Fig. 12 shows the eggs of the five arctic *Spirontocharis* species, as compared with the egg of a decidedly boreal *Spirontocharis* species, *Spir. cranchi*, of about the same order of magnitude as *Spir. turgida*. It is obvious that the eggs of the arctic species are much larger than the eggs of the boreal representative of the genus. Still more conspicuous is the difference between the arctic and the boreal forms of *Crangoninae* (cf. fig. 13). While thus the mother animals of the arctic *Nectocrangon lar* and the boreal *Crangon vulgaris* belong to the same

¹) KRØYER (1842) described *forma gibba* exclusively on the basis of ♂♂.

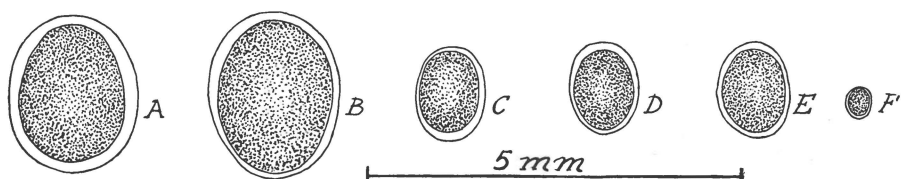


Fig. 12. A—E. Eggs of arctic *Spirontocharis* species. A. *Spir. polaris* (Ellaø, June 10, 1932). B. *Spir. groenlandica* (Hurry Inlet, July 4, 1933). C. *Spir. gaimardi* (Ellaø, Sept. 20, 1931). D. *Spir. turgida* (Ellaø, Aug. 6, 1932). E. *Spir. spinus* (Ellaø, June 22, 1932). F. ripe egg of the boreal *Spir. cranchi* from Danish waters (undated).

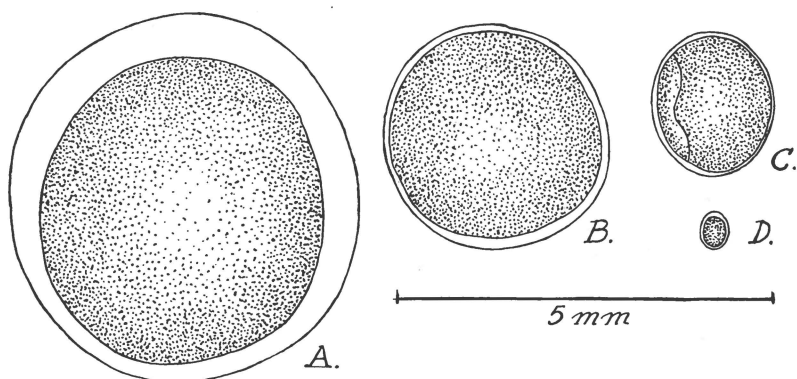


Fig. 13. A—C. Eggs of arctic *Crangoninae*. A. *Sclerocrangon ferox* (Ellaø, 250 m, Aug. 25, 1932). B. *Sclerocr. boreas* (Ellaø, 4—16 m, Aug. 5, 1933). C. *Nectocrangon lar* (Cape Hedlund, 18 m, July 18, 1932). D. Egg of the boreal *Crangon vulgaris* (Nymindegab, Denmark, June 10, 1905).

order of magnitude, their egg-sizes are entirely different (fig. 13), whereas the two species of *Sclerocrangon* have eggs of a very large size.

The only form among the *Decapoda natantia* mentioned here that is common to boreal as well as to arctic seas is *Spirontocharis gaimardi*, which thus affords us an opportunity for investigating whether the egg-size of this species is constant under different ecological conditions. Fig. 14 A shows the uncleaved egg of *Spir. gaimardi* collected from the caudal feet of an individual from Northeast Greenland, fig. 14 B shows

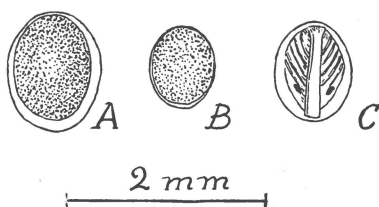


Fig. 14. Eggs of *Spirontocharis gaimardi*. A. from Ellaø, undeveloped egg (Sept. 20, 1931), B. from Denmark, undeveloped egg (undated), C. from Denmark, with big embryo (undated).

the corresponding uncleaved egg from the caudal feet of a Danish individual, and fig. 14 C, finally, another egg of this species collected from a Danish individual, but at a fairly advanced stage of development. Even at this late stage of development the eggs of the boreal individuals are smaller than the eggs of the same species from the seas of Northeast Greenland. In fact we are here confronted with a similar phenomenon to that pointed out by BOAS (1890, p. 794) for the shrimp *Palaeomonetes varians*, whose eggs in brackish water at the coasts of northern Europe have a diameter of 0.75 mm, while in fresh water lakes in southern Europe the same species has an egg-size of 1.5—1.75 mm in diameter. This phenomenon will be discussed in greater detail on p. 139.

It being thus established that big eggs are dominant within the decapods of the Arctic, it will be appropriate to find out from the literature, if possible, whether the arctic species of *Spirontocharis* and *Crangon* lack pelagic development, or whether it exists, but is very short. As to *Sclerocrangon ferox* the enormous egg-size as well as the larval development are known. STEPHENSEN (1935, p. 50) gives the following facts about these phenomena on the basis of statements by WOLLEBÆK and WILLIAMSON: "The eggs are of a considerable size: 3.5 mm in length (deep-sea species!), the larval development much abbreviated." As regards *Sclerocrangon boreas* he states that "the eggs are very large (2 mm in length) and probably the larval development is much abbreviated or not-existent" (STEPHENSEN 1935, p. 50, after SARS and WILLIAMSON)¹. In *Nectocrangon lar* the egg-size was not known before, whereas a larval stage — almost at the shrimp stage, with distinctly developed telson — described by STEPHENSEN (1916, p. 244) is assumed to belong to this species.

On the arctic representatives of the genus *Spirontocharis* STEPHENSEN writes (1935, p. 51) that "... several of the northern-arctic species have much abbreviated larval developments", which thus agrees excellently with the egg-sizes found in Northeast Greenland. From West Greenland six different *Spirontocharis* larvæ are described (STEPHENSEN 1916 and 1935), and since six frequent *Spirontocharis* species are known from the same stretch of the coast — among which are the five Northeast Greenland forms — STEPHENSEN draws the natural inference that the six larvæ belong to the six above-mentioned species. As regards two of the Northeast Greenland species, viz. *Spir. polaris* and *Spir. turgida*, the identity of the larvæ has been definitely established (cf. STEPHENSEN 1935, p. 52). It applies to all the larvæ of arctic *Spirontocharis* species found that the youngest known pelagic larvæ as regards development occupy an intermediate stage between the *Mysis* and the shrimp stage,

¹) Only the egg-size of this form is known, not the developmental stages of the larva.

and accordingly must be assumed to have a very short pelagic stage. Whether they absorb nourishment during this short stage, is not known. A further fact pointing towards a very short pelagic stage in these forms is that the ring-trawl of the "Godthaab" Expedition, in spite of its normally large content of crustacean larvæ, secured only a very small number of *Spirontocharis* larvæ per sample, generally only 1, 2, 3, or 4 individuals per haul, while a large number of hauls from various times in the course of the summer were entirely devoid of *Spirontocharis* larvæ (JESPERSEN 1933, STEPHENSEN 1935).

As to 11 of the 13 forms of *Decapoda natantia* occurring in Northeast Greenland and belonging to the genera *Sclerocrangon*, *Nectocrangon*, *Spirontocharis*, and *Bythocaris* it has been ascertained that they possess big eggs either with direct development or with a reduced pelagic larval stage of very short duration, while the boreal and more southerly representatives of the same genera and other related forms living in boreal and more southerly seas have small eggs with a normal pelagic larval development. In the arctic-boreal *Spirontocharis gaimardi* the egg-size was smaller in boreal than in arctic seas.

There only remains, then, an investigation of *Balanus balanus* (= *Balanus porcatus*), the only one of the Northeast Greenland bottom crustaceans besides the decapods which belongs to a group whose larval development is normally pelagic. That the characteristic *Balanus-Nauplia* were not found in the plankton series from Ellaø is of no importance in this connection, since the *Balanidae* — no doubt on account of insufficient food conditions — are entirely absent from the inner fjords. A comparison with the plankton series from Eskimonæs shows that here the *Balanus* larvæ occur as *Nauplia* in the plankton in the samples taken on June 17 and on July 11, with their maximum occurrence at the latter date. Along the outer coast and in Scoresby Sound *Balanus balanus* is fairly common at depths ranging from 20 to 40 m. On examining the material of this species brought home from the period July to September, in all 15 adult individuals, it was found that not a single specimen contained even fairly mature eggs or larvæ. Thus the first of the adult individuals examined from July, had presumably already shed their eggs, and the spawning seems on the whole to be very distinct in this species and, judging from the Eskimonæs material, would seem to take place at the beginning of the ice-free summer period (compare the times at which lamellibranch larvæ occur in the plankton). It may be mentioned that a closely related species, *Balanus balanoides*, is known to reproduce itself late in the autumn (October—November) in Norway (cf. RUNNSTRÖM 1925).

No information concerning the reproduction of *Balanus balanus* is found in the literature, whereas the reproduction of the closely related

forms *B. improvisus* (VAN BREEMEN 1934) and *B. balanoides* (RUNNSTRÖM 1925) is well known. Of particular interest in this connection is RUNNSTRÖM's (l. c.) observation that the larvæ of *B. balanoides* under special — not precisely known — conditions do not leave the pallial cavity of the mother animal until they are at the *Cypris* stage, while under normal conditions they move about already as *Nauplia*. Hence it is natural to assume that a similar lability may exist in the method of reproduction of *B. balanus* in Northeast Greenland, so that in years particularly unfavourable to the development of plankton the species may develop in that way. However, nothing definite can be stated about this point at the present time.

It will be evident from the above that 105 forms of the Northeast Greenland bottom crustaceans — the copepodes excepted — are known to belong to groups which normally have a non-pelagic larval development, and as regards the fourteen species belonging to groups having as a rule a pelagic larval development it has been proved that at least eleven of these have very large eggs and direct development or a much abbreviated larval stage. Of these eleven species, nine (82 per cent.) occur almost exclusively in arctic seas, one (9 per cent.) (*Spirontocharis spinus*) has a mainly arctic though also to some extent a boreal distribution, and one species (9 per cent.) (*Spirontocharis gaimardi*) is arctic-boreal; however, according to STEPHENSEN (1910, p. 104) the arctic form must be considered a special race. Hence the examined species of *Decapoda natantia* with big eggs are predominantly species with a typical arctic distribution.

Thus 116 of the bottom crustaceans of the area are known to have a non-pelagic development, while only one species, *Balanus balanus*, is known to pass through a full pelagic development. Accordingly the bottom crustaceans as regards their reproduction in the Arctic follow the same rule as the other invertebrate groups investigated; here, too, the only exception from the rule is a form with arctic-boreal distribution.

F. Other Invertebrate Groups.

In addition to the large groups of marine invertebrates treated in the preceding pages, the available material of which is so considerable that a detailed investigation was possible, there are some smaller groups of invertebrates in which the mode of reproduction could not be ascertained to the same extent from the individuals brought home. However, the available literature regarding some of these groups supplies valuable information about the reproduction, and some of these data will be briefly summarised below.

In all 15 species of *Actinia* are known from Northeast Greenland (CARLGREN 1928), 12 of which were found near the outer coast or in the fjord areas proper. The mode of reproduction is only known in three of these species, in which three species viviparity or protection of the young was observed, viz. *Bunodactis* (*Tealiopsis*) *stella* (VERRILL 1922, p. 110, pl. XX), *Urticina* (*Tealia*) *crassicornis* (VERRILL l. c. p. 105, CARLGREN 1928), and *Actinostola spitzbergensis* (CARLGREN 1928). From other arctic regions an additional number of species with protection of the young are known, belonging to the genera *Rhodactinia*, *Cribrina*, *Actinostola*, *Epiactis*, *Epigonactis*, *Pseudophellia*, and *Leiodealia* (CARLGREN 1928). CARLGREN (l. c.) was aware of the peculiar mode of reproduction in the arctic *Actinia*, and adds a number of similar examples from the antarctic species of the genera *Condylactis* and *Marsupifer*, but he expressly emphasises that the antarctic forms with protection of the young belong to other genera than such forms in the Arctic. On the phenomenon CARLGREN (l. c.) states as follows: "... während in südlichen Gegenden die Embryonen nur selten über ein Stadium mit zwölf Tentakeln in dem Körperinnern bleiben, ehe sie von der Mutter ausgeworfen werden, erreichen die in den Muttertieren sich entwickelnden Jungen der Genera *Urticina* und *Actinostola* aus arktischen Gegenden eine beträchtliche Grösse, ehe sie ihren Schutzort verlassen".

As a rule the reproduction of the viviparous forms within an area will always be described first, since this mode of development can be directly studied on the material brought home in alcohol by the various expeditions. Hence it is still uncertain whether or not the remaining Northeast Greenland *Actinia* have pelagic larval stages. In the plankton samples from Ellaø and Eskimonæs *Actinia* larvæ have not been found at any time of the year, and it should further be noted that the genera which are known with certainty to have pelagic larvæ (e. g. *Metridium*, *Sagartia*, *Actinia*, *Anemonia*, and *Callactis*) have never been found in arctic seas. Thus in this group, too, much would seem to indicate that the arctic forms normally reproduce without pelagic larvæ.

Of other small invertebrate groups the *Pycnogonidae* among others play an important part in the Arctic. They are known on account of their peculiar mode of reproduction and protection of the young, in that eggs and young, often of very different ages and in great numbers, are attached to the legs of the male individuals. Thus normally this group reproduces without pelagic larvæ, and must therefore, according to the available data, seem to be well suited for life in the arctic seas. In the Northeast Greenland fauna, which is rather poor in species, the *Pycnogonidae* are represented by 15 species while from the inner Danish waters including Skagerak and Bohuslän which are far richer in species, only 17 species of *Pycnogonidae* are known. This means that the *Pycnogonidae*

are the only group of marine bottom arthropodes which in Northeast Greenland are represented by (almost) just as large a number of species as in boreal seas.

It will be seen that the non-pelagic mode of development seems to predominate within these smaller groups of invertebrates too, and must therefore be assumed to be the most suitable mode of reproduction in the Arctic. It may therefore be anticipated that on a close investigation all the other small marine invertebrate groups will show similar conditions.

G. Summary and Discussion of the Methods of Reproduction.

The results of the investigations recorded in the above of the methods of reproduction in the bottom invertebrates of Northeast Greenland may be briefly summarised as follows:

- 1) Reproduction by small eggs poor in nutritive substances. Embryos develop through a pelagic larval stage. In boreal and more southerly seas this is the commonest mode of reproduction in marine bottom invertebrates, whereas it is rare in the Arctic and only known from species distributed also outside the Arctic of the following groups:

Echinodermata: Only in *Strongylocentrotus droebakiensis*, *Ophiura robusta*, *Ophiocten sericeum*, *Cucumaria frondosa* (and *Ophiura sarsi*?).

Polychaeta: In the plankton from Eskimonæs several *Trocophora* larvæ were found, all belonging to the same species. Apart from this species, the youngest pelagic polychaete larvæ found at Ellæ as well as at Eskimonæs had a front segment plus three further segments.

Gastropoda: No *Prosobranchia* are known to reproduce themselves in this way in the Arctic. From Dusén Fjord a very well developed pelagic larval stage of an opisthobranch (probably *Cylichna alba*) is known.

Lamellibranchiata: Only in *Saxicava arctica* and *Mya truncata*.

Crustacea: Only in *Balanus balanus* (= *B. porcatus*). (*Copepoda* not examined).

- 2) Reproduction by large eggs with a great amount of yolk. Embryos developing without, or with a much abbreviated, larval stage. In the Arctic by far the commonest mode of reproduction in widely distributed, arctic-boreal as well as in arctic species. In the Arctic this type of reproduction is known from the following groups:

Echinodermata:

Asteroidea: In the genera *Pontaster*, *Ctenodiscus*, *Hippasteria*, *Bathybiaster*, *Poraniomorpha*, *Hymenaster*, *Asterias*, *Henricia*, and *Pteraster*.

Ophiuroidea: In the genera *Ophiacantha*, *Ophiopus*, *Ophiopleura*, and *Ophioscolex*.

Echinoidea: In the genus *Pourtalesia*.

Holothurioidea: In the genus *Elpidia*.

Crinoidea: In the genera *Heliometra* and *Hathrometra*.

Polychaeta: In the genera *Syllis*, *Spirorbis*, *Pomatocerus*, *Nereis*, and *Harmothoë*. Probably in several additional species e. g. belonging to the genera *Onuphis*, *Flabelligera*, *Ammotrypane*, *Brada*, etc.

Gastropoda: In the genera *Bela*, *Raphitoma*, *Pyrene*, *Trichotropis*, *Margarita*, *Velutina*, and *Acmaea*.

Lamellibranchiata: In the genera *Arca*, *Leda*, *Portlandia*, *Astarte*, *Macoma*, *Venus*, *Axinus*, *Modiolaria*, *Cardium*, *Pecten*, *Lyonsia*, and *Pandora*.

Crustacea: In *Mysidacea*, *Cumacea*, *Amphipoda*, *Isopoda*; among the *Decapoda*, in the genera *Sclerocrangon*, *Nectocrangon*, *Spirontocharis*, and *Bythocaris*.

- 3) Reproduction by large eggs with a small content of yolk but abundant amounts of white. Embryos developing directly without a pelagic larval stage. This method of reproduction in the Arctic is known from the following species only:

Gastropoda: In *Natica groenlandica*, *Natica affinis*, and *Natica islandica*.

- 4) Reproduction by means of small eggs poor in nutritive substances, a minority of which develop. The embryos feed on the other — undeveloped — eggs in the same egg-room (nurse eggs). This mode of reproduction not known from the *Echinodermata*, *Lamellibranchiata*, and *Crustacea*, but from:

Polychaeta: In *Spio filicornis*, which in boreal and more southern seas may also have a pelagic larval development.

Gastropoda: In the genera *Buccinum*, *Sipho*, *Neptunea*, *Jumala*, *Volutopsis*, and *Onchidiopsis*.

- 5) Asexual reproduction: In the Asterid *Stephanasterias albula* of common occurrence in the Arctic, which here normally reproduces by division.

The large groups of marine invertebrates dealt with here, viz. *Echinodermata*, *Polychaeta*, *Lamellibranchiata*, *Gastropoda*, and *Crustacea*, all show a characteristic feature in the mode of reproduction of their

Northeast Greenland forms, in that these forms have predominantly large eggs. In most of them (i. e. in ca. 95 per cent. of the forms within the groups investigated in which the mode of reproduction is known) the embryonic development takes place either through a much abbreviated pelagic larval stage or with no such stage and in the forms solely distributed in the Arctic a pelagic larval development was not ascertained in any single case.

It goes without saying that these peculiar modes of reproduction, found moreover in such a large number of different invertebrate groups, have not remained unobserved by the numerous explorers who have in the course of years had an opportunity to work on arctic material.

Thus it has been stated above (1902) that CARLGREN ascertained protection of the young in arctic (and antarctic) *Actinia*, that LUDWIG (1904) and later MORTENSEN (1920, 1936) found direct development, protection of the young, or viviparity in a considerable number of arctic — and especially antarctic — *Echinodermata*, all of which had large eggs, and that GRAVIER (1923) has pointed out the non-pelagic development and often even protection of the young in a number of arctic — and especially antarctic — *Polychaeta*. The phenomenon has also been observed in the *Crustacea*; i. a. the large predominance of *Amphipoda* and *Isopoda* in arctic seas has been mentioned in connection with their protection of the young. As regards the genus *Scalpellum* it is known (AURIVILLIUS 1894) that in warmer seas it develops by free-swimming *Nauplia*, while in colder seas it begins its pelagic life as a *Cypris* larva. Entirely similar modes of development are known from *Balanus balanoides* (RUNNSTRÖM 1925), which in Norway under special conditions, not more closely known, begins its larval life at the *Cypris* stage, while normally it begins its pelagic life already at the *Nauplia* stage.

GIARD (1904, p. 621) called attention to the feature common to some invertebrate groups that they have species with large eggs in arctic (and antarctic) seas, and on the basis of a comparison of these phenomena in the *Echinodermata* (l. c. p. 621) he states that in a delimited group the forms with an abbreviated metamorphosis grow more frequent the nearer they approach the poles. GIARD here calls attention to CARLGREN's investigations of the *Actinia*, and mentions part of the above-mentioned literature dealing with crustaceans. However, at present the evidence is rather sparse though sufficient to give rise to the problem.

HESSE (1924, p. 170) in his "Tiergeographie" goes rather fully into this subject and points out, in addition to the literature already referred to, that protection of the young in *Nemertinae* is only known from antarctic seas (according to JOUBIN 1914), that *Artemia salina* in certain localities lays eggs in the summer while in the winter it is viviparous (according to ARTOM 1905), and that the only known ctenophore with

protection of the young, viz. *Tjalfiella tristoma*, is arctic (according to MORTENSEN 1912).

It will be seen that in several invertebrate groups this non-pelagic mode of reproduction in "cold-water forms" has long been known, and HESSE discussed the problem from the conviction that eggs rich in yolk are characteristic of invertebrates in "colder seas". He says as follows: "Wie dem auch sei, so lässt sich, . . . , annehmen, dass Dotterreichtum und Brutpflege auf unmittelbarer Einwirkung von niederer Temperatur entstehen" (l. c. p. 171).

However, as late as when HESSE wrote this paper, the modes of reproduction, as shown above, were nearly unknown for three of the main marine groups of arctic invertebrates, viz. *Polychaeta*, *Gastropoda*, and *Lamellibranchiata*, and it was not till the present investigation of the reproduction of these groups in Northeast Greenland was carried through that it was ascertained what a dominating role the non-pelagic development plays for all the examined invertebrate groups in the Arctic. By means of the large material now available for such a comparison, it is of course possible to a far greater extent than previously to demonstrate the relations between ecological conditions and the modes of reproduction of the bottom invertebrates living in the Arctic, especially since the variations in a series of ecological factors in Northeast Greenland were investigated throughout the same years and in the same localities whence our material of bottom animals and plankton is derived.

A point that has been of special importance for the elucidation of the question of reproduction in the Arctic is the identification of the bottom animal larvæ that actually occur in a pelagic stage in the arctic plankton. It will be easily understood that it is of considerable interest to find out the features common to such pelagic larvæ, and to examine whether these species behave alike on a number of essential biological points, and differently from the other animal forms of the Arctic. With respect to this question it has been ascertained among other things 1) that these pelagic larvæ originate from a very small number of species, 2) that the species in all the cases examined were forms with a more or less wide distribution also outside the Arctic, 3) that these larvæ have a quantitative maximum in the plankton at the time when the food conditions must be assumed to be optimal, and 4) that these few species with pelagic larvæ in spite of their mode of reproduction, so rare in the Arctic, belong to the animals quantitatively most frequent in the area investigated and probably also throughout the arctic seas (*Saxicava*, *Ophiocten*, *Ophiura*, etc.).

However, if we disregard the small percentage of species (4 to 5 per

cent.)¹⁾ which in Northeast Greenland also pass through a pelagic larval development and exhibit the corresponding small egg-sizes, there remain a large number of species (about 95 per cent.) which reproduce themselves in four widely different ways, viz. reproduction by means of big eggs with a considerable amount of yolk (173 species — 86 per cent.), reproduction by means of big eggs with a considerable amount of white (3 species — 1.5 per cent.), reproduction by means of small eggs, several of which serve as nurse eggs for some few eggs that develop into young individuals (15 species — 7.5 per cent.), and finally asexual reproduction (1 species — 0.5 per cent.). Of these four methods, reproduction by means of big eggs with a large amount of yolk is thus by far the commonest, but also the method by “nurse eggs” is widely represented among the molluscs of Northeast Greenland.

Reproduction by means of eggs with a large amount of white is very rare everywhere among the bottom invertebrates, whereas the three other methods of reproduction are somewhat more frequent in warmer seas also. Thus nurse eggs are known in the boreal *Natica catena* and in some tropical *Murex* and *Fasciolaria* species, eggs with large amounts of yolk occur for instance in the southern prosobranch *Fulgur carica*, and in the echinoderm *Asterina gibbosa* in the Mediterranean; and asexual reproduction for instance in the Mediterranean in the echinoderms *Ophiactis virens* and *Carcinasterias virens* (according to KÄHLER 1924)²⁾. However, as will be gathered from these random examples, it is not the fact that these methods of reproduction are found in the Arctic which deserves interest, but it is peculiar that so large a percentage of the arctic bottom invertebrates reproduce themselves by these methods.

While HESSE (l. c.) and earlier authors only discuss the fact that “eggs rich in yolk” and accordingly with direct development are more frequently met with in the Arctic than in southern seas, the present investigation has shown that the forms with nurse eggs also increase considerably in number from southern towards arctic seas (cf. p. 41). Thus we find here two widely different methods of reproduction, both with predominance in the Arctic, which have only the feature in common that the larval development is non-pelagic. There seems therefore to be a possibility that it may be an advantage to the species in Northeast Greenland to reproduce themselves without a pelagic larval stage. However, a fact that apparently speaks against this is that the few bottom invertebrates which reproduce by pelagic larvæ in Northeast

¹⁾ The percentages are here calculated on the basis of all the echinoderms, polychaetes, prosobranchs, lamellibranchs, and crustaceans occurring in Northeast Greenland whose modes of reproduction are known, in all 200 species.

²⁾ These two forms probably also reproduce by the sexual method.

Greenland, are precisely those species which quantitatively are the commonest within the area.

To solve these problems the modes and possibilities of reproduction of the species in Northeast Greenland will be more closely analysed. Thus it will be of interest to find out whether the methods of reproduction observed in Northeast Greenland should be regarded as phenotypic results induced by conditions, or as properties characteristic of the species throughout their area of distribution.

As to the lamellibranchs *Astarte elliptica*, *Astarte banksi*, *Astarte borealis*, *Modiolaria nigra*, *Modiolaria discors*, and *Axinus flexuosus*, and the snail *Natica groenlandica* it is known that the same considerable egg-size which is found in Northeast Greenland occurs in boreal waters, and that here, too, the consequent non-pelagic development is the usual method of reproduction. The considerable egg-size and the consequent non-pelagic development thus seems to be the genotypically determined mode of reproduction characteristic of these species.

The elucidation of these questions is attended with much greater difficulties if a species reproduces by a different method in the Arctic than in boreal and more southerly seas. As an example hereof may be mentioned the polychaete *Harmothoë imbricata*, which in boreal seas has pelagic larvæ while in Northeast Greenland it has protection of the young and direct development (cf. p. 32). As regards forms with this method of reproduction it is at present impossible to decide whether there exists a genotypically determined arctic form (i. e. a special geographic race) or whether we are here concerned merely with a quite phenotypical variable form of reproduction influenced by the ecology of the place. Only experiments with transplantation of arctic material of such species to boreal seas or conversely may definitely settle this question.

This type of reproduction is also found in the arctic-boreal shrimp *Spirontocharis gaimardi* (cf. p. 68), which in the Arctic reproduces by much bigger eggs than in the boreal seas. There is, however, some reason to assume that a certain egg-size is, after all, characteristic of the species within extensive contiguous areas, since the arctic and the boreal form of the species must on this point be assumed to be genotypically different. For from arctic seas a peculiar form of this species is known, *Spirontocharis gaimardi forma gibba*, which in contrast to the arctic-boreal *Spirontocharis gaimardi forma typica* is entirely absent from boreal seas. In the large Northeast Greenland material comprising 129 individuals of *Spir. gaim. f. gibba* taken in all the months from June to September not a single individual was found with eggs, while *Spir. gaim. f. typica* from the same period and the same localities was found in large numbers with eggs on the caudal feet. As *S. gaim. forma gibba* is erected by KRØYER

(1842) exclusively on the basis of ♂♂, it can hardly be doubted that *S. gaim. forma typica* in Arctic seas only represents the ♀♀ corresponding to the ♂♂ hitherto designated *S. gaim. forma gibba*. This special ♂-type of the species known from the arctic seas only strongly suggests that the *Spir. gaimardi* living in arctic seas is a special "geographical race" which only deviates from the boreal form by its larger, more robust appearance, its characteristic ♂-form, and the bigger eggs of the ♀♀. STEPHENSEN (1910, p. 104) mentions the possibility that the arctic *Spir. gaim.* is actually a special race, bigger than the more southerly form and with a short toothed process on the back of the third pleon segment.

In connection with the latter types of reproduction (*Harmothoe imbricata* and *Spirontocharis gaimardi*) may be mentioned a third type found especially among the polychaetes. Here we are concerned with species which are able to reproduce themselves in different ways in the same locality. Such a reproduction, then, may take place either by the species reproducing differently at the different seasons of the year (e. g. *Spio filicornis*), or by the species at a certain time of the year, i. e. within the same spawning period, reproducing in different ways (e. g. *Nereis zonata* and, in the Mediterranean, *Nereis dumerili*). It is evident that as regards modes of reproduction such forms agree well with those predominating in the arctic seas, since in the cases known one of the modes of reproduction of the species is always non-pelagic, while the other — pelagic — form of reproduction and development might possibly be employed also in the Arctic under especially favourable conditions or in especially favourable localities, all this naturally provided that the biology of the species is in other respects adapted to the life in arctic seas. (Thus *Nereis zonata* may not only reproduce itself in an "epitoke" manner in Northeast Greenland, but may also spawn during the bottom stage, and is known in the latter case to have a non-pelagic larval development). However, it is still unknown whether the two modes of reproduction of these species are to be found in the same individual, and it is therefore impossible to decide whether the mode of reproduction of these forms in the Arctic is invariable and constant, or whether it may undergo purely phenotypic changes due to local ecological conditions.

It will be seen that while it has not been possible in any case to prove that the big egg-size in species in arctic seas is a mere phenotypic result due to local conditions, there is every probability that the big eggs and the subsequent non-pelagic development in the gastropods as well as the lamellibranchs and the shrimps is a method of reproduction characteristic of the species throughout their area of distribution.

H. The Spawning Temperatures of the Northeast Greenland Bottom Invertebrates.

It will be evident from the preceding description of the individual invertebrate groups that by far the greater number of the forms examined spawn in the summer, i. e. at a time when the fjord ice has melted and the sea ice becomes more scattered and the upper water layers have positive temperatures. Hence it will be of interest to investigate to what extent the spawning of these bottom invertebrates may be affected by this rise of temperature in the water.

For this purpose it will be necessary to mention here certain hydrographical features at somewhat greater length than has been done in the general view given in pp. 9—10. From the summer months of 1932 and 1933 a considerable number of temperature measurements in the upper water layers are available from the Franz Joseph Fjord (R. SPÄRCK 1933, p. 38) and Scoresby Sound (USSING 1934, pp. 11—12) respectively. In the Franz Joseph Fjord the surface temperature (August 1932) as a rule ranged between 5° and 8° C, in some few places it was even 9° C, and at Cape Hedlund (July 1932) a surface temperature of 12° C was measured. Even at a depth of 5 m the temperature in August is much lower (on an average 4.5° C) and at a depth of 10 m on an average 2.5° C, some of the water samples here showing a negative temperature (cf. SPÄRCK l. c.). The greatest depth at which positive temperatures have been registered in the surface water of Franz Joseph Fjord in August is about 20—25 m (at a depth of 20 m the temperature fluctuated between 0.01° C and —0.85° C). In Scoresby Sound the surface temperature seems to be somewhat lower. Thus in July, 1933, the surface temperatures at the mouth of Scoresby Sound were negative (July 11, 1933, —0.18° C to —1.66° C), though in the inner ramifications of this fjord the temperature may rise to 6°—8° C. At a depth of 10 m the samples from both July and August had very low temperatures (July —1.16° to 0.57° C, August 0.97° to 3.15° C), and from depths of 25 m no examples of positive temperatures are known from Scoresby Sound.

This shows that only bottom invertebrates living at depths less than 25 m will be exposed to annual temperature fluctuations, and only such species (and within them such individuals) as live at depths less than 10 m will experience temperatures essentially higher than 2.5° C¹). As moreover none of the marine invertebrates of Northeast Greenland treated here remain constantly at depths of less than 4—5 m (cf. THORSON 1933, p. 17), it is a very small area of the sea bottom in these regions whose animals are exposed to temperatures higher than 2.5° C even in summer.

¹) It should be borne in mind that all species at depths of more than 300—400 m live at constantly positive temperatures (0° to 1.70° C) (cf. pp. 9—10). Confer however Dusenfjord and Geologfjord p. 10.

But how does the distribution as to depth of the bottom invertebrates correspond to these temperatures? By means of the available literature supplemented by the most recent collections from Northeast Greenland it is possible to establish in broad features the distribution as to depth of the bottom invertebrates in these seas. In cases where deficient information was at hand, the material has further been supplemented by indications of depth for the same species in other arctic waters, since in cases which it has been possible to control, these indications agreed closely with the distribution as to depths of the species in Northeast Greenland. In the calculations account has only been taken of the smallest depth at which a species is normally found, since, if this depth is less than 20—25 m, at any rate some of the individuals of this species have been given an opportunity of spawning at the higher summer temperatures.

The following distribution as to depth was observed:

Echinodermata. 39 species known from Northeast Greenland.

18 species	(46 %)	lived at depths of more than 25 m
15 —	(38.5 %)	— - — from 10 to 25 m
6 —	(15.5 %)	— - — from 4 to 10 m

Polychaeta. 73 species known from Northeast Greenland.

36 species	(49.5 %)	lived at depths of more than 25 m
10 —	(13.5 %)	— - — from 10 to 25 m
27 —	(37 %)	— - — — 4 - 10 m

Prosobranchiata. 51 species known from Northeast Greenland. The distribution as to depth of three of these species is too little known to be considered here.

17 species	(35.5 %)	lived at depths of more than 25 m
16 —	(33 %)	— - — from 10 to 25 m
15 —	(31.5 %)	— - — — 4 - 10 m

Lamellibranchiata. 37 species known from Northeast Greenland, the distribution as to depth of one of these species is too little known to be used here.

9 species	(25 %)	lived at depths of more than 25 m
12 —	(33 %)	— - — from 10 to 25 m
15 —	(42 %)	— - — — 4 - 10 m

Crustacea. Computed upon the groups *Decapoda natantia* (13 species, one of which unemployable), *Mysidacea* (14 species), *Cumacea* (6 species), *Amphipoda* (75 species, one of which unemployable), and *Isopoda* (6 species).

50 species	(44.5 %)	lived at depths of more than 25 m
31 —	(27.75 %)	— - — from 10 to 25 m
31 —	(27.75 %)	— - — — 4 - 10 m

The total distribution as to depth of the 308 Northeast Greenland species of these invertebrate groups is as follows:

130 species (42.5 %)	lived at depths of more than 25 m
84 — (27.5 %)	— - — from 10 to 25 m
94 — (30 %)	— - — — 4 - 10 m

or, in other words, 42.5 per cent. of the total number of species live all the year round at a constant temperature, namely in from 25 m to 300—400 m at a constantly negative temperature (0° to -1.70° C) and at still greater depths at a constantly positive temperature (0° to 1.70° C) that is, at all depths of more than 25 m, within a temperature interval of 3.5° C, equally distributed round zero. 27.5 per cent. of the species which live from October to June under constantly negative temperatures, are exposed in the summer to temperatures ranging from 0° C (25 m) to 2.5° C (10 m), while finally 30 per cent. of the species are exposed in the summer to temperatures ranging from 2.5° C (10 m) to 4.5 — 5° C (4 m). As the spawning as a rule takes place in the summer, in most species it thus coincides with the above-mentioned summer temperatures. Among the forms living at depths between 4 m and 10 m there are, however, a number of exceptions. Thus among the lamelli-branches *Saxicava arctica* and *Mya truncata* are known to commence spawning in May, i. e. at a time when the bottom temperature at this depth is still negative, and the same applies to the polychaetes *Nereis zonata*, *Harmothoe imbricata*, and *Pectinaria granulata*. The three *Astarte* species (*A. borealis*, *A. banksi*, and *A. elliptica*), which also live at this depth, spawn so late in the autumn that the bottom temperature at this time has again become negative. Accordingly these eight species spawn at negative temperatures, even though they live at a depth at which the temperature is positive in the summer, and the spawning process proper in these species is thus at any rate not directly affected by a rise of temperature. Consequently the number of species spawning at a summer temperature of from 2.5 to 4.5 — 5° C is reduced from 94 to 85, or 27.5 per cent. of the total number of species living in the Northeast Greenland fjords.

Of the 308 species treated here, 223 species or 72.5 per cent. spawn at temperatures lower than 2.5° C, and of the remaining 85 species several individuals spawn at temperatures ranging from 2.5° to 4.5 — 5° C, while by far the greater number of individuals belonging to these species, too, are distributed at depths of more than 10 m, and consequently spawn at lower temperatures than those mentioned above.

Altogether the spawning in Northeast Greenland even in the summer takes place at very low temperatures, and quantitatively the number of individuals which in the summer are exposed to higher temperatures

than 2.5° C, play a much smaller part than appears from the computations set out above, since the area of sea bottom lying within the said depth interval of from 4 m to 10 m, on account of the steepness of the coasts, has a very small areal extent. This zone with summer temperatures higher than 2.5° coincides in all essentials with the *Astarte-borealis*-zone of the *Macoma-calcaria*-community (cf. p. 11).

Spawning at very low temperatures is thus a feature common to the bottom invertebrates of Northeast Greenland, and this already accounts for the fact that a large number of boreal and more southerly species are absent from Northeast Greenland, since the water never attains the temperatures required for these animals to ripen their sexual products and to spawn.

I. The pelagic larval development and the ecological conditions of Northeast Greenland.

The investigation of the spawning temperatures of the bottom invertebrates of Northeast Greenland has already explained why a considerable number of the boreal and more southerly species do not occur in Northeast Greenland, and since the majority of these species are known to have pelagic larvæ, this fact is presumably one of the causes of the small number of pelagic larvæ found in Northeast Greenland. The question now arises why the forms that are actually able to reproduce themselves in Northeast Greenland have predominantly a non-pelagic larval development. As mentioned above, the non-pelagic larval development in these regions is chiefly based on big eggs with a large amount of yolk, and it is then conceivable, and perhaps even probable, that a direct relation exists between reproduction at low temperatures and big eggs, as also presumed by HESSE (l. c.). However, this still remains a conjecture, since no proofs or explanations of the phenomenon are available and the physiology of these animals is still so slightly known that an actual analysis of this relation can hardly be made at the present time.

While thus this connection between the reproduction at lower temperatures and big eggs rich in nutritive matter still remains an unproved as well as an unchallenged possibility, it seems natural to investigate what chances there are for the bottom animal larvæ which actually are pelagic in Northeast Greenland to pass through the pelagic stage, and what are the possibilities, if any, for a pelagic larval development in the Northeast Greenland seas.

While the *Nauplia* of the plankton copepodes and the larvæ of pteropods and of *Sagitta* may be found in the plankton at many different seasons of the year or during a considerable continuous period of the year, the larvæ of the bottom animals, on the other hand, almost exclusively dominate within the actual, very short, summer time. At Ellø

the amount of eggs in the plankton on the 25th of May, 1932, was about 10 eggs per sample, but on the 12th of June the same year the number of eggs had increased to about 600 eggs per sample (vertical haul with hand net from the bottom to the surface, 50—0 m, average of 10 hauls). Shortly after this increase in the number of eggs follows the great increase in the number of lamellibranch larvæ (cf. p. 47) represented by an almost equally abrupt curve, which suggests that part of the above-mentioned number of eggs have developed into lamellibranch larvæ, and altogether the great maximum of other pelagic bottom animal larvæ, too, occurs in June and July¹).

It will therefore be appropriate to investigate the changes in the ecological conditions (hydrography, climate, etc.) of the fjord area in this period from May to June in order to find out, if possible, the cause of the great larval maximum.

From our present knowledge of the nutrition and growth biology of the pelagic larvæ of the bottom animals it will be natural in relation to this sudden maximum of bottom animal larvæ in the Northeast Greenland plankton in June and July to expect also a corresponding increased production of phytoplankton — the food of the pelagic larvæ of the bottom animals. When one has been able all the year round to observe the conditions prevailing in the fjords of Northeast Greenland, it will be clear — from a number of observations which will be discussed in greater detail below — that at this time all the possibilities are present for a sudden rise in the production of phytoplankton. This conjecture was decisively confirmed by a number of plankton hauls secured at these times. As late as May 25 the plankton samples were quite clear and colourless and contained but a slight amount of phytoplankton, while the plankton hauls from June 12 were turbid with large quantities of phytoplankton, which gave the net a deep greenish hue. Since counts on the spot of these plankton hauls were only taken of the zooplankton, and since the phytoplankton was not treated with all desirable care in the conservation, it is impossible to supply exact figures for the phytoplankton organisms at the two dates mentioned above — a fact which is now highly to be deplored. However, the increase in the amount of phytoplankton during the period from May 25 to June 12 was so enormous that the mere observation under a binocular microscope of the samples collected excludes any possibility of mistake.

The same seems to be the case at Eskimonæs, where a number of phytoplankton samples were collected by HOLGER MADSEN. DR. E. STEEMANN NIELSEN has kindly supplied me with the following information concerning these samples:

¹) See, however, *Ophiocten sericeum*.

August 30, 1932. Rich phytoplankton (especially the diatomeans *Chaetoceros furcellatus*, *C. contortus*, and *C. decipiens*).

September 15, 1932. Some phytoplankton (*Chaetoceros furcellatus*).

October 30, 1932. Very few diatomeans (*Chaetoceros decipiens*).

November 19, 1932, to May 18, 1933. "Practically no phytoplankton present".

June 1, 1933. Phytoplankton production commencing. Small quantities of the diatomean *Nitschia frigida* (probably developed on the under side of the melting ice).

June 17, 1933. Much phytoplankton present (especially the diatomeans *Fragilaria oceanica* and *Nitschia seriata*).

July 11, 1933. Extremely small quantities of phytoplankton (*Fragilaria oceanica*, *Nitschia seriata*).

From this STEEMANN NIELSEN draws the following inferences:

The normal phytoplankton maximum does not commence till June and does not exceed one month. At that time the nutrient salts will be consumed, and under normal conditions the phytoplankton production of the summer will accordingly be completed. The samples from August 30, 1932, must be due to a deeper-lying water layer rich in nutrient matter having risen to the surface, which has resulted in a second maximum; this, however, must be assumed to be an exception and not to occur every year.

Thus it is a direct observation that at the beginning of June there was a considerable increase in the production of phytoplankton in the Northeast Greenland fjords, and in the following pages an attempt will be made to find out what factors cause this increase, or, in other words, what factors create that basis of nutrition which is necessary for the pelagic larvæ to complete their development.

1. The Temperature of the Water and the Phytoplankton Production.

Throughout the period from the middle of October to the end of June or the beginning of July the surface of the fjords of Northeast Greenland are covered by a continuous layer of ice, which in the spring attains a thickness of about 2 m. Throughout this period the temperature of the water is therefore negative from the surface down to a depth of about 400 m (SPÄRCK 1933, USSING 1934), where the cold Polar Current water is separated from the Gulf Stream water with positive temperatures by a spring layer. The Gulf Stream water occurs at all depths of more than 400 m. It is not till the last ice on the fjord surface has drifted away or melted (as a rule by the end of June) that the temperature of the surface water begins to rise, and the temperature of the water

becomes positive down to a depth of about 20—25 m (cf. pp. 9—10). The above-mentioned plankton hauls from June 12, 1932, which contained such large quantities of phytoplankton (and larvæ of bottom animals), were all secured through a hole in the ice before it had melted, and a series of water samples proved that the temperature throughout the height of the water column passed by the haul (50—0 m) was negative. It was on the basis of these observations that it could be definitely stated in the preceding section (pp. 82) that the bottom invertebrates living in shallow water and spawning at this time of the year (*Saxicava*, *Mya*, *Pectinaria*, *Harmothoe*, etc.) spawn at negative temperatures.

It might therefore be anticipated that judging from the available temperature measurements, the phytoplankton production, which starts at exactly the same time, must take place at negative temperatures. However, Dr. SPÄRCK kindly pointed out to me that this could not be taken for granted on the basis of the available material. The above-mentioned measurements of the water temperature, which on June 12 showed negative temperatures throughout the water column, were made at intervals of 5 m from the surface of the water down to the bottom at 50 m. Thus the temperature is known from the surface (negative), from a depth of 5 m (negative), etc., whereas the temperature of the intermediate water column is unknown. However, experience from the Norwegian oyster polls shows that a surface layer of brackish water may by insolation act as a lense and produce higher temperatures at a depth of 0.5—2 m in the sea-water layer below this brackish water layer (cf. GAARDER and SPÄRCK 1932, p. 44), and it is quite conceivable that in June the ice of the Northeast Greenland fjords may act as a lense in a similar way to the brackish water layers above the oyster polls, so that a rise of the temperature at a depth of 1—2 m may be a concurrent cause of the phytoplankton production.

2. The Melting of the Ice and the Phytoplankton Production.

While at the end of June the ice still covers the fjords, its consistency is not by far the same as earlier in the year. As early as the beginning of May the temperature of the air is positive in the day, and at the end of May the melting of the sea-ice is in rapid progress. From being a greyish-green, intransparent mass whose surface is covered with a thick layer of snow, the sea-ice at the end of May turns clear as glass, transparent, and much thinner. At the same time a layer of almost fresh water will form immediately below the ice (even at a depth of 3 m below the low-water mark a salinity of only 3—4 per mille was observed at Ellø at the end of May (cf. THORSON 1933, p. 17)). In May the melting on the land, too, is in active progress, and the rivers carry considerable quantities

of fresh water into the fjords. This fresh water is pressed down below the still unbroken ice on the surface of the fjords, and on account of the resulting pressure may penetrate still deeper into the water layers than might be expected considering the slight specific gravity of the fresh water (cf. THORSON 1933, pp. 63—65). This will presumably bring about an increased movement of the water, which, however, can hardly be assumed to be of any great importance for the increased production in the fjords¹). The temperature of the melt-water must necessarily be higher than that of the fjord water, and it also seems reasonable to assume that the vast quantities of fresh water and the large amounts of salts conveyed into them by the rivers may exert some influence on the phytoplankton production and accordingly on the occurrence of the pelagic larvæ of bottom animals. USSATSCHEW (1935, p. 91) explains the presence of the large quantities of phytoplankton in the surface layer of the Barents Sea in the summer by the sudden precipitation of phosphates and nitrates due to the melting of the ice, referring to hydrographic investigations by WIESE and LAKTIONOW (1931, only Russian titles), who ascertained an increase of the numerator of the fraction $\frac{\text{alkali}}{S^{\text{‰}}}$ within the area at the time when extensive melting of the ice takes place.

3. The Light Intensity and the Phytoplankton Production.

The wintering station on Ellas in the Franz Joseph Fjord, where the largest number of plankton samples was taken, is situated in about 73° N. lat., which corresponds to a "dark time" and consequently a "period of midnight sun", each of a duration of about three months. At Ellas the midnight sun appeared on May 9, at which time the sea-ice still forms a nearly 2 m thick intransparent layer on the surface of the fjord. Moreover, the angles of incidence of the light-rays in these latitudes are very oblique, so that only an extremely small part of the light is able to penetrate through the ice layer into the subjacent water masses. However, even this slight amount of light is only partially utilised, the absorption of the light-rays in the water having no relation to the depth of the water to which they penetrate, but to the distance through the water covered by the rays.

Towards the end of May or the beginning of June the ice, as stated above, grows thinner and turns clear as glass, and at the same time the light increases, and its angle of incidence becomes decreasingly oblique. The author himself had an opportunity to ascertain the astounding difference in the intensity of the light from May to the middle of June, which

¹) There is, more probably, some reason to assume that the fresh-water layer by gathering directly below the ice will further contribute to a stabilisation of the water masses and prevent the movement of the water.

was due also to the considerable transparency of the water at this time (in June the plankton nets at Ellaø were visible down to much greater depths than at any other time of the year). In the inner fjords another factor, too, plays an important role for the light intensity in the water, viz. the opacity of the upper water layers. SPÄRCK (1933, p. 35) states that the transparency in the inner fjord ramifications is 0.5—1 m, while at the mouths of the fjords and in the East Greenland current proper it is 13—16 m. This intransparency, which is due to the large amounts of mud transported into the fjords by the rivers and the glaciers from the inland ice, is not nearly of the same importance at Ellaø as in the inner fjord ramifications. However, while the water in June is still clear and transparent, an increasing intransparency is noticeable towards the end of the summer when the large rivers are full of water and the melting of the glaciers is at its height, and in the inner ramifications of the fjords the intransparency is doubtless a factor of very great importance, which must necessarily reduce the light intensity in the water to a considerable extent.

The light intensity at Ellaø was not controlled by photometric methods, but in spite hereof it will appear from the preceding description of these phenomena with fairly great certainty that the light intensity must be one of the main causes of the sudden increase of the quantity of phytoplankton in June which forms a basis for the existence of a pelagic larval stage.

4. The Water Movement and the Phytoplankton Production.

From January to August, at regular fortnightly intervals, measurements of temperature and salinity were made at Ellaø through a water column reaching from the surface of the water to the bottom at a depth of 50 m. These measurements were carried out at every 5 m from the surface to the bottom, and throughout the period from January to June showed a perfectly regular increase of the salinity and a decrease of the temperature from the surface towards the bottom. This regularity of the salinity and temperature down through the water masses is also a distinct proof of the exceedingly slight vertical movement of the water throughout this period. The above-mentioned addition of fresh water (p. 86) is hardly a factor of great importance for the movement of the water, and there is thus every reason to believe that the vertical water movement is quite minimal even in the summer months. This slight movement of the water is of essential importance for the plankton, since it acts as a limiting factor in the phytoplankton production. On account of the slight penetration of the light into the water layers, the phytoplankton production at the favourable season of the year also — dependent as it is on assimilation — must take place in the uppermost

water layers, but is at the same time limited by the quantities of salts (nitrates and phosphates) present in these water layers, since the amount of these salts, precisely on account of the inconsiderable vertical movement, is but slightly renovated from the subjacent water layers. As the larvæ of the bottom animals and a large number of other plankton animals depend on this amount of phytoplankton for food, their occurrence and growth must also be limited to these upper water layers. This, indeed, proves to be the case. At several stations in the fjords a number of vertical hauls were taken in the summers of 1932 and 1933 from different depths to the surface (50—0 m, 100—0 m, 150—0 m, 200—0 m, etc.). It turned out that the samples from 50 m and from 200 m to the surface contained almost the same quantity of plankton, and exactly the same was the case with the hauls from all the intermediate depths to the surface. Thus it can be definitely stated that in the early summer, when the largest phytoplankton production takes place, the great majority of plankton animals are found in the uppermost water layers, and that the production as regards the phytoplankton feeders must have a direct correlation to the available amount of phytoplankton and consequently to the factors regulating it.

Of the four factors treated here the temperature of the water is thus of but slight importance to fluctuations in the quantity of phytoplankton and consequently to the amount of pelagic bottom animal larvæ. The melting of the ice seems to be of a certain importance, the extent of which, however, is unknown, whereas the intensity of the light is the principal factor, which determines the sudden increase of the phytoplankton production in the fjords of Northeast Greenland, while the movement of the water is a very essential factor for the regulation of the phytoplankton production. The fact that the fjord ice (or the sea ice) as late as May may essentially impede the penetration of the light rays into the water, so that the light cannot till the end of May influence the production, must thus be considered the main cause of the sudden maximum of phytoplankton found in June. The rapid decrease of this maximum is due to the slight movement of the water and its increasing intransparency; already at the beginning of August the quantity of phytoplankton is decreasing rapidly, and at the end of August it is in the main consumed. In agreement herewith the number of bottom animal larvæ decrease rapidly in the plankton, having almost entirely disappeared at the end of August (cf. the curve for the lamellibranch larvæ p. 47). This decrease of the number of larvæ seems, at any rate as regards the lamellibranchs, to take place simultaneously at Eskimonæs (74°20' N. lat.) and at Ellæ (about 73° N. lat.), although the large rise in the number of lamelli-

branch larvæ at Eskimonæs occurs about one month later than at Ellæs. However, since the samples from these two localities are derived from two different years, a comparison of these features is perhaps of doubtful value.

BRAARUD (1935, pp. 55—65) gives an analysis of some plankton hauls from the Franz Joseph Fjord and the district round Claveringø, taken in the period from July 16 to August 19, 1930. He states that the influence of the fjord ice on the production of plankton was distinctly traceable, and compare conditions here with those of the East Greenland Polar current, which he describes (l. c., p. 44), showing that the phytoplankton production in the Polar current is of short duration and rather sparse.

The features of the phytoplankton production described so far apply in all essentials to the Northeast Greenland fjords only, but since the present work also treats the bottom invertebrates and their reproduction at the outer coast of Northeast Greenland, it will be of interest to obtain a general view of the modes of reproduction along that coast, too. OSTENFELD and PAULSEN (1909—11) have demonstrated that the plankton at Danmarkshavn (76° to 77° N. lat.) was an arctic coast plankton with a very short period of production. BRAARUD arrived at quite similar results in his investigations of the pack-ice northeast of Angmagssalik (1935, p. 44), where he ascertained that the plankton production sets in as soon as the ice became more scattered, but at the same low temperature as before this scattering, and the direct cause of the increasing phytoplankton production must consequently be the increasing amount of light in the water¹). He mentions that the phytoplankton production is sparse, which he ascribes to the ice-masses, which prevent the light from penetrating into the water. Finally STEEMANN NIELSEN (1935, pp. 57—58) has treated the plankton of this area, and records a series of observations from the East Greenland current (also in the Angmagssalik area). STEEMANN NIELSEN demonstrates that here the production is not in active progress till June (precisely as in the Northeast Greenland fjords), since at this time the ice becomes scattered, and the water layer originating from the melting of the ice stabilises the water masses and prevents vertical movements of any importance. The latter phenomenon, which at the beginning of the period of production tends to further the production, since strong vertical movements will remove the phytoplankton organisms from the uppermost, illuminated, water masses and thereby prevent assimilation, at the same time involves the drawback that all the salts contained in the surface layer will be consumed already in July, and as a consequence hereof the plankton content in the late summer is extremely poor.

¹) It seems probable that the phenomenon mentioned on p. 86 and pointed out by USSATSCHEW plays a part here.

It will appear from the different observations recorded above that conditions in the East Greenland current proper are very like those observed in the Northeast Greenland fjords. In the East Greenland current, too, the ice is an important factor in preventing production. The slight vertical movement of the water, which is a nearly constant feature of the Northeast Greenland fjords, is also characteristic of the East Greenland current during the period of production, on account of the stabilising capacity of the melt-water layer, and here, too, prevents a fresh supply of salts of the surface layer; in both areas the light is the most important factor for furthering the production, etc. It is true that in the fjords the summer temperature is somewhat higher than in the East Greenland current, but as mentioned above, the temperature seems to be of subordinate importance for the phytoplankton production. Since, moreover, the surface layer is intransparent in the interior of the fjords, it may be anticipated that the phytoplankton production will be even slighter here than in the East Greenland current.

If now we compare these data on the period of production of the phytoplankton with observations on the occurrence of the pelagic larvæ of bottom animals in the plankton at Ellaø, we shall find at Ellaø a maximum of pelagic larvæ from the beginning of June to the middle of August, while the number of these larvæ in the plankton outside these two months is quite minimal; and as shown above, the phytoplankton production sets in simultaneously with this larval maximum. Very probably the phytoplankton production ceases at the end of July or the beginning of August, partly on account of lack of phosphates or nitrates, partly on account of the increasing opacity of the water. According to STEEMANN NIELSEN (1935, pp. 57—58) the period of production of the phytoplankton in the East Greenland current, in which the conditions for production are the same or rather somewhat more favourable than at Ellaø, lasts a little over one month only, and hence it would seem probable that the period of production of the phytoplankton at Ellaø, which in the present work is stated to be nearly two months, is too amply estimated. However, no plankton hauls are available from Ellaø from the period July 26 to August 18, so it can only be stated that the samples from August 18 were poor in phytoplankton. Hence there is a probability that the consumption of phytoplankton by the pelagic larvæ of bottom animals and the other plankton animals already at the beginning of August exceeds the production of phytoplankton.

After outlining the main features of the phytoplankton production in Northeast Greenland and viewing it in relation to the occurrence of the pelagic larvæ of bottom animals, it will be possible to form a judgment of the conditions for completing the pelagic larval life in these waters. Considering for instance the lamellibranch *Saxicava arctica*, which has

pelagic larvæ and moreover is exceedingly frequent in all the arctic seas, we find the following features. The spawning sets in as early as the end of May or the beginning of June, that is, simultaneously with the rise in the phytoplankton production, but as late as August 3—5 a considerable number of individuals may be observed to spawn. Thus the eggs first spawned have two months at the most within which to complete their pelagic larval development, and the eggs spawned at later dates have a still shorter time, the eggs spawned in July, which must be assumed to constitute a considerable proportion of the aggregate egg production, one month at the most. Several horizontal surface hauls from June showed that the pelagic larvæ were not frequent in the uppermost water layers, being only numerous at a depth of about 10 m or deeper, and accordingly they complete their larval development at temperatures of 2.5° C at most, often at even lower temperatures. Thus the larva of *Saxicava* must be assumed to complete its pelagic development¹⁾ at a temperature of 2.5° C or a lower temperature in the course of about one month, or possibly a still shorter time. The same applies to the larvæ of *Mya truncata* and other pelagic bottom animal larvæ in Northeast Greenland. The bottom animal larvæ found in the plankton in Northeast Greenland must consequently have a very rapid larval growth, and since there is some relation between the larval metabolism and the temperature, *Saxicava* and similar forms probably have a very high larval metabolism in order to complete the pelagic larval development in such a comparatively short time at the above-mentioned low temperature. This will appear from some few comparisons. SPÄRCK (1924, p. 44) states that the temperature seems to exert some influence on the growth and development of the larva of *Ostrea edulis* even while in the pallial cavity of the mother animal, and accordingly this period is the longer the lower the temperature, and the larvæ consequently develop more slowly. He further states that according to information supplied by other authors the pelagic larval development in Italy for the same species is 14 days at a temperature of 17° C and 17—18 days at a temperature of 16° C. NELSON (1928) mentions that the larvæ of *Ostrea edulis* at temperatures of 20° C swim freely about for a very few days only. Similar conditions have been ascertained in *Ostrea virginica* (NELSON l. c.), whose pelagic larval life at a temperature of 23—24° C lasts for 13 days and at 20° C for 17 days. As for *Mytilus edulis* and *Mya arenaria*, which both have eggs and pelagic larvæ of exactly the same size as *Saxicava arctica* and *Mya truncata*, the pelagic larval stage according to NELSON (l. c.) lasts for about three weeks at a temperature of about 20° C, and several other examples might be mentioned. Hence it is very probable that such forms at the

¹⁾ During this pelagic larval development the larva absorbs food from the surrounding water masses and increases in size.

temperatures at which the pelagic larval development takes place in Northeast Greenland, may not be able to complete their larval development as quickly as is necessitated by the short period of phytoplankton production, and that only forms with a very rapid larval growth and in consequence probably a very high larval metabolism will be able to complete their pelagic larval development in Northeast Greenland.

Another factor, too, may be of some importance for the completion of the pelagic larval life in Northeast Greenland, namely competition. As the period of production of the phytoplankton is so short, it is only during the one or two months in which this production is going on that the bottom animal larvæ can complete a pelagic development¹⁾. If, however, a similar high percentage of forms with a pelagic larval development was found among the Northeast Greenland bottom invertebrates as among those of boreal and more southern seas, the larvæ of all these species must occur in the plankton at the same time within the one or two summer months in which the phytoplankton production takes place; the consumption and the consequent food competition would thereby become very great, and considerable quantities of bottom animal larvæ would perish. In such a competition those larval forms will naturally come off best which are able to utilise most economically the available food conditions, and whose larval growth at the particular temperature can take place at a sufficiently rapid rate to be completed within the short period of phytoplankton production.

According to the above, the conditions for the completion of the pelagic larval life in Northeast Greenland may be summarised as follows. (both for the outer coast and for the fjords):

1) On account of the small intensity of light due to the ice-cover and, in the fjords, the opacity of the water, the phytoplankton production must be limited to a very short period — at Ellæ two months at most, in the East Greenland current a little over one month — and during this period it takes place in the uppermost water layers only, where the production is further governed by the rather limited quantities of phosphates and nitrates, the lack of which again is due to the slight vertical movements of the water.

2) The rather short production time for phytoplankton in connection with the rather limited intensity of production even within this time affords good food conditions for only a comparatively small number of pelagic larvæ of bottom animals. If all the bottom invertebrates had a pelagic larval development in these regions, the food competition among the larvæ would therefore be very keen.

3) Among the pelagic larvæ of bottom animals only such forms will

¹⁾ Cf., however, *Ophiocten sericeum* p. 19.

be able to hold their own in the competition whose time of occurrence in the plankton coincides with the production period of the phytoplankton, and whose pelagic larval development during growth and feeding at temperatures under 2.5°C can be completed at the latest shortly after the conclusion of the phytoplankton production (i. e. in one month at most); in other words, forms whose larval growth is very rapid and whose larval metabolism is probably very high.

When it is further added that all the species, in order to be able to reproduce themselves in Northeast Greenland, must be able to ripen their sexual products and to spawn at temperatures under 4.5°C , most frequently under 2.5°C , this shows distinctly that the conditions for reproduction in Northeast Greenland and in large areas of the remaining parts of the Arctic must be very special and differ from conditions in more southerly seas (cfr. fig. 3 and fig. 7).

However, if a species of bottom animals is actually able to fulfil the demands made in Northeast Greenland for reproduction by a pelagic larval stage, the species will by this mode of reproduction be still better suited for the life in the high-arctic seas than the forms with non-pelagic larval development, which are so numerous in these regions. On account of its small egg-size it will be able to commence the process of reproduction at a much younger stage than the species whose eggs require a large amount of nutritive substances, and in the spawning time will probably be satisfied with a smaller amount of nourishment than the Northeast Greenland forms with large eggs (cf. pp. 116). It will, moreover, on account of its much better conditions of dispersal, belong to the most widely distributed and quantitatively dominating species in the Arctic.

It is a point of great interest in this connection that all the species with pelagic larval stages examined in Northeast Greenland have a wide distribution outside the Arctic also, while the Northeast Greenland species with a direct larval development are often purely arctic forms, or, if more widely distributed, very often deep-sea forms¹⁾. Hence it is quite possible that the Northeast Greenland species with a pelagic larval development should be regarded as the few offshoots of a more southerly shallow-water fauna which have been able to meet the requirements of this mode of reproduction in the Arctic.

¹⁾ In Northeast Greenland a number of widely distributed shallow-water species with a non-pelagic development are also found.

GROWTH

The main features of the method of reproduction, spawning time, and larval development having now been cleared up for a large number of Northeast Greenland bottom invertebrates, it will be of interest to investigate the growth of these forms.

For this purpose an investigation as to age groups was made for a large number of individuals of Northeast Greenland bottom invertebrates by the aid of C. G. JOH. PETERSEN'S measuring method. Chiefly such animals were examined (*Lamellibranchiata*, *Pectinaria*, *Strongylocentrotus*, etc.) whose shells or tubes supplied a basis for a quick and certain measurement, which in the cases mentioned here was executed by means of a calliper and with an accuracy of 1 mm, each measurement being increased to the next whole millimetre.

In order that such a measurement of the age groups of bottom invertebrates may give a scientifically serviceable result, the material used must, however, fulfil certain conditions. Thus the spawning time of the individual species must only extend over a comparatively short period of the year, so that in respect of time all the larvæ obtain a fairly contemporaneous start. The individuals must be sufficiently uniformly distributed over an area with the same ecological conditions, so that the whole fauna will have a fairly uniform growth, etc.

Hence it is only in few cases that a measurement of the age groups of bottom invertebrates will supply a directly applicable result. This also held good for the Northeast Greenland investigations, since these have supplied useful curves in but a small number of cases, although very large materials were measured. For such forms as for instance *Strongylocentrotus droebakiensis*, *Ophiocten sericeum*, *Cardium ciliatum*, *Macoma calcaria*, *Pectinaria granulata*, etc. — that is, a large number of animals very frequent within the area, as to which most measurements were based on 300—500 individuals from each date — the result was entirely negative, as no distinguishable age groups at all were arrived at.

However, some few useful results were, despite all, arrived at by the investigation, and these are in all cases based on measurements of the lamellibranchs occurring within the area. But even within these it is only the least distinguishable age group — that is, the animals hardly one year old (the 0-group) — which could be distinguished, since all the succeeding age groups do not appear distinctly from the measurements. These lamellibranchs of the 0-group are of fairly great interest, since they afford an opportunity for a comparison of the growth in the first

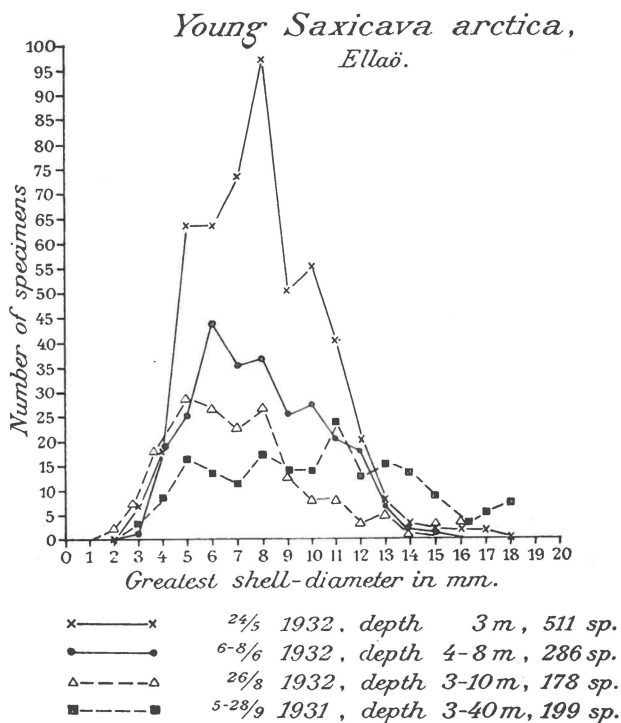


Fig. 15. Growth of young *Saxicava arctica*. Ellø.

year of life of forms partly with a pelagic larval development and partly with a direct larval development by large eggs rich in yolk. For such a comparison the conditions prevailing in Northeast Greenland present the further advantage that it can be stated with great certainty — for the pelagic forms even with full certainty — that the Northeast Greenland lamellibranchs spawn only once a year. As will appear from the following section, nearly all the Northeast Greenland shallow-water lamellibranchs (i. e. lamellibranchs living at depths of less than 25 m) at the temperatures at which they live in these regions have almost the same consumption of oxygen per unit of weight (with the exception of *Modiolaria discors*), and accordingly their metabolism and consequently

their rate of growth must be assumed to be essentially the same. This means that for species of the same category of size, all other factors being equal, one year's growth should be an expression of the conditions of nutrition of the species through its whole first year of life, thus also the larval stage, whether the larvæ were pelagic or subsisted on the amount of nourishment contained in the egg.

Especially well suited for such comparisons are a number of age groups based on material derived from Ellæ 1931 and secured by means of a grab, by which method one is certain that all the individuals,

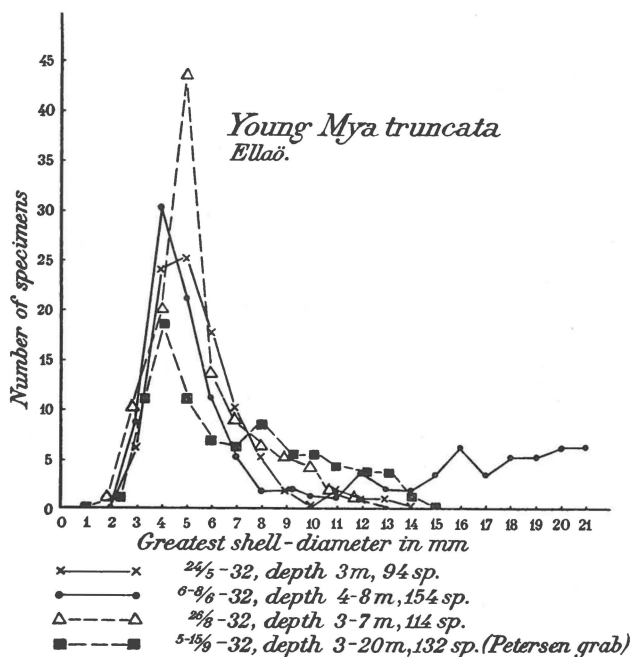
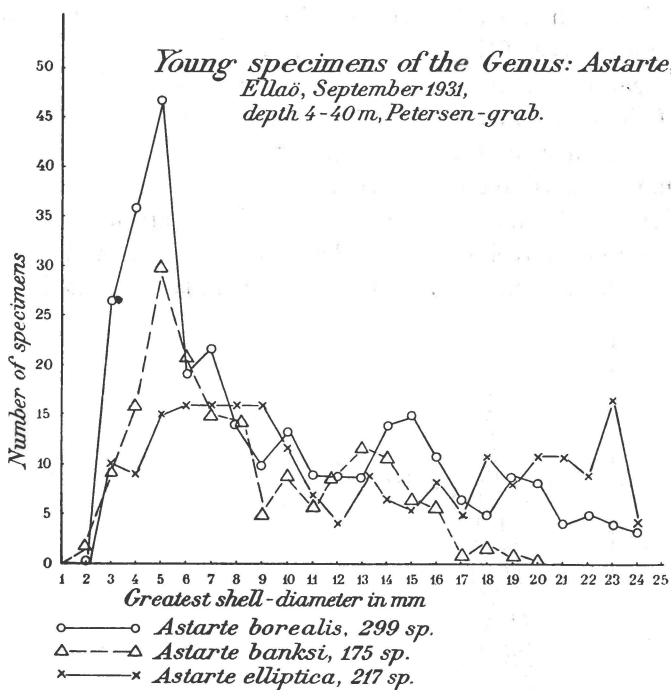
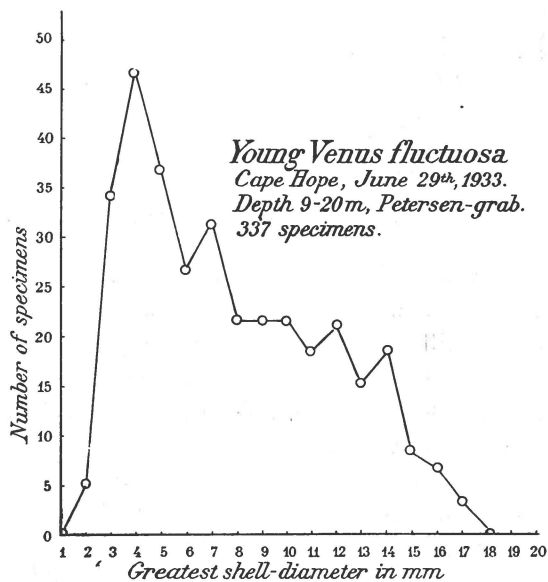


Fig. 16. Growth of young *Mya truncata* at Ellæ.

even the smallest, are included in the measurements. Figs. 15, 16, and 17 show the distribution as to size of the lamellibranchs of the 0-group in September 1931¹⁾. It will be seen that the 0-group of *Astarte borealis* and *Astarte banksi* (reproduction by direct development and big eggs) varies in shell length from 3—6 mm and 4—7 mm respectively, while the corresponding groups of *Mya truncata* and *Saxicava arctica* (actually 1-groups) (reproduction by pelagic larvæ) at the same time show a shell length of 4—5 mm and 5—8 mm respectively. As mentioned above, it must here be taken into consideration that both *Mya* and *Saxicava*

¹⁾ For the *Astarte* species, which spawn in October or later in the year, the designation 0-group is justified here, while *Saxicava* and *Mya*, which spawn in June—July, come under the 1-group.

Fig. 17. Growth of young individuals of the genus *Astarte*, September, Ellao.Fig. 18. Growth of young *Venus fluctuosa*. Cape Hope.

spawn in June and July (cf. p. 52), while the *Astarte* species do not spawn till October, so that in September the youngest recognisable groups of *Mya* and *Saxicava* are three months older than the 0-group of the *Astarte* species. The curves represented in figs. 15 and 16 show, however, that the increase of growth for *Mya* and *Saxicava* within this time is extremely slight. Moreover, it must be taken into consideration that *Mya* and *Saxicava* have a more elongated shell and consequently will show a comparatively larger shell length than for instance the *Astarte* species. Even when all these factors are taken into consideration, it will be seen that the variation in size of the 0-group within the examined forms with a pelagic development does not deviate in any perceptible degree from that of the examined 0-group animals with a non-pelagic larval development. *Saxicava*, which has pelagic larvæ, and whose young consume more oxygen than those of the other species (cf. p. 119), in the first year of its life grows somewhat larger than the *Astarte* species with a non-pelagic development, while *Mya truncata*, which has a pelagic development, is of the same size or rather a little smaller than the *Astarte* species. It is interesting to note, as appears from the curve in fig. 17, that *Astarte banksi*, whose final size is much smaller than that of *Astarte borealis*, in the first year of its life grows just as rapidly or even more rapidly than the latter. The reason is probably that *Astarte banksi*, though a much smaller species, lay eggs which are of the same size and with the same content of nutritive substances as *Astarte borealis*, so that they will start under the same conditions.

The above-mentioned comparison of the growth of species having a pelagic and such as have a direct larval development may be further controlled by considering the curves for the 0-groups of *Mya*, *Saxicava*, and *Venus fluctuosa* for June (figs. 15, 16, and 18). While *Mya* and *Saxicava* have a pelagic larval development, *Venus fluctuosa* has extremely big eggs with an immense amount of yolk (figs. 9 Nr. 17, p. 56). The variation in size within the 0-group was for *Mya truncata* 3—6 mm, *Saxicava arctica* 5—7 mm, and *Venus fluctuosa* 3—6 mm, which means that the rate of growth of these three species in the first year of their life is essentially the same in spite of the highly differing modes of development. It is true that the comparison of growth is based on material of *Venus* from Cape Hope and *Mya* and *Saxicava* from Ellæs, but the considerations set forth in the preceding chapters have shown that the food conditions near the outer coast (Cape Hope) agree in all essentials with those in the inner fjords (Ellæs), or, when deviating, are probably more favourable at the outer coast, and a comparison cannot therefore give rise to errors of any importance. Thus in regard to growth and nutrition the embryos of the big eggs rich in yolk do not seem to have a much better "start" than the lamellibranch larvæ originating

from small eggs which are actually able to complete their pelagic development in the Northeast Greenland plankton in the course of the summer.

As will appear from the distribution as to size of *Mya* and *Saxicava* (figs. 15 and 16) the curves for August and September are by no means richer in individuals of the smallest sizes than the curves for May and June. Hence it may be stated with certainty that the larvæ of these two forms, even when spawned in May or June, do not attain such a size as can be ascertained by the methods employed and consequently cannot be indicated in the curves for September of the same year.

Only one of all the species of lamellibranchs for which the 0-group

Growth of Pecten groenlandicus.
Ellæø, September 1931, 719 sp.

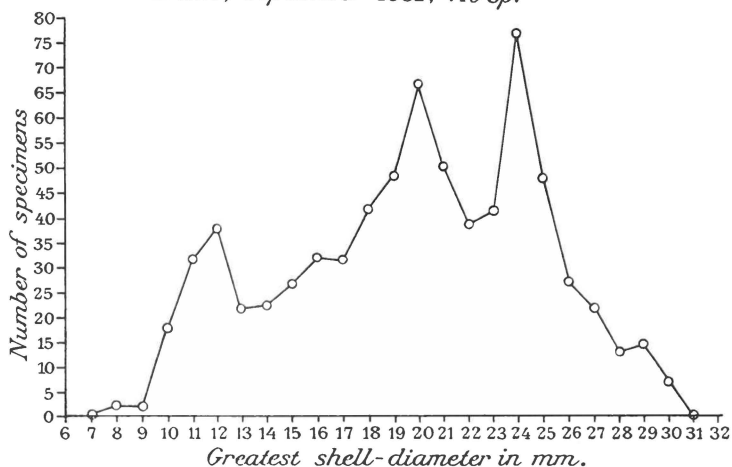


Fig. 19. Growth of *Pecten groenlandicus*. Ellæø. September 1931.

could be segregated by means of measurements, showed entirely deviating conditions of growth, namely *Modiolaria discors*. Fig. 20 shows the 0-group of this species measured on a material (470 individuals) from Hurry Inlet, Scoresby Sound, July 1933. The individuals which at this time were one year at most, already showed a shell width of 6—11 mm. This corresponds well with the fact that this species has a much greater consumption of oxygen than any other lamellibranch examined from the Arctic (p. 117).

If now we consider the growth of this species at Ellæø, it proves difficult to separate the 0-group (fig. 21). This is probably partly due to the fact that the material available for measurements is much smaller than that from Hurry Inlet, partly because the species is decidedly an "epifauna" animal, so that the various individuals do not live under the same ecological conditions. However, the growth curves from Ellæø give another, fairly interesting, result, since the curve from the beginning

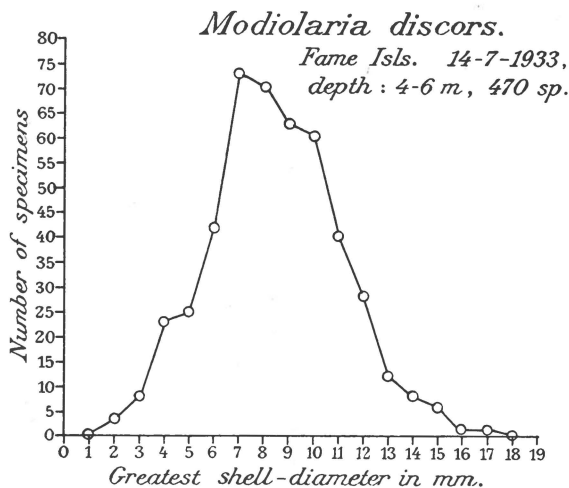


Fig. 20. Growth of young *Modiolaria discors*. Hurry Inlet. July 1933.

of June for the smallest individuals shows a shell length of 4 mm, while the curve from the beginning of July shows a shell length of 2 and 3 mm for the smallest individuals, and finally the curve for the end of August shows 10 individuals of 2 mm and 30 individuals of 3 mm shell length (cf. fig. 21). Thus it can be stated with certainty that a large number of young individuals have been added in the course of the summer. As the species is known to spawn throughout the summer from the beginning of June (THORSON 1935b, p. 302), it may be taken for granted that it is the young from the same year which even in late summer appear in the bottom stage, and which at this time, i. e. three months, at most, after being laid, have attained a shell length of at least 2—3 mm.

In one single of the forms occurring within the area it was possible

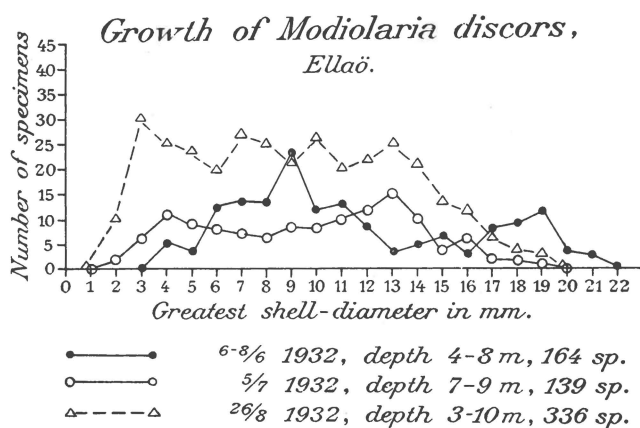


Fig. 21. Growth of young *Modiolaria discors*. Ellaö.

to distinguish three distinct age groups, viz. in *Pecten groenlandicus*, which on account of its flat shells thin as paper increases considerably in shell size with a comparatively slight increase of the organic weight. The 719 individuals measured of this species (Ellaø, September 1931) showed a 0-group of 11—13 mm shell length, an 1-group of 20—21 mm, and a 2-group of 23—25 mm (fig. 19). That the 0-group as regards the number of individuals is so much below the 1- and 2-groups, is largely due to the fact that several of these young individuals were crushed during collection on account of their thin shells, and consequently could not be measured. As the spawning time for *Pecten groenlandicus* (p. 50), despite investigations on maturity, is not yet known, it is impossible to say how many months old the so-called 0-group of the species is.

It applies, however, to all the examined 0- and 1-groups of Northeast Greenland lamellibranchs that growth in their first year is inconsiderable, and since the individuals live under precisely the same conditions in the subsequent years, at the same time as the oxygen consumption of the somewhat older individuals decreases (cf. p. 107—121), it must be assumed that a similar slow growth as takes place in their first year of life, will be the rule throughout the lifetime of the individual. In the few cases in which "annual rings" were ascertained with some degree of certainty in the lamellibranch shells (i. e. particularly distinct growth-rings, of which the first ring at the beginning of the spawning time corresponds to the size of the 0-group), they show that the growth and consequently the lifetime of the animal extends over several years. Even in *Modiolaria discors* (see above), which grows particularly rapidly as compared with other arctic lamellibranchs, the annual rings showed with fairly great certainty that the growth, or life, of the species extends over at least three years, frequently even four years. In *Pecten groenlandicus*, which is also a species with a rather rapid growth, at least three distinct age classes were found, of which the one comprising the largest individuals must be assumed to include representatives of several years. This is what is known about the growth rate and life duration in the forms with rapid growth. In the slow-growing forms it has never been possible to distinguish the number of years represented besides the 0- and 1-groups, but there is hardly any doubt that the largest individuals found of these species are many years old. Some examples speaking in favour of the correctness of this assumption will be enumerated below.

Astarte borealis, when one year old, has a shell length of 3—6 mm (cf. the curve in fig. 17). The oldest Northeast Greenland individuals generally attain a shell length of 30—36 mm, and a large number of living individuals of a shell length of 40—46 mm are known.

Mya truncata, when one year old, has a shell length of 3—6 mm (cf. fig. 16, June). Older individuals normally attain a shell length of

32—37 mm, but much larger individuals (up to 43—46 mm) are known.

Saxicava arctica, when one year old (cf. fig. 15, June), has a shell length of 5—7 mm. Older individuals normally attain a shell length of 33—37 mm, and individuals of up to 48 mm may occur.

Of *Modiolaria discors* individuals of a shell length of over 30 mm are often found; individuals of 13—16 mm seem to be three years old (THORSON 1935, p. 303).

Macoma calcaria, whose 0-group (hardly one year old) is not exactly known, but at Ellæ seems to have a maximum at a shell length of 4—7 mm, often occurs in the fjords with a shell length of 29—32 mm, and specimens of up to 44 mm are known.

These are some random examples. There is, however, every reason to assume that the remaining lamellibranchs of the area will show a similar slow growth and a long life. As mentioned above (cf. also p. 112), all the examined Northeast Greenland shallow-water lamellibranchs with the exception of *Modiolaria discors* at the temperature at which they generally occur (about 0° C) have about the same consumption of oxygen and their growth must therefore be assumed to be fairly alike. This also applies to the forms living in deeper water, with the exception to some extent of *Pecten groenlandicus*.

How, then, do these results from the Northeast Greenland fjords agree with the growth in the boreal and more southerly seas? It will be natural to consider first the growth of arctic-boreal species partly in Northeast Greenland and partly in boreal seas to find out whether the growth of the particular species is alike in both places. However, we lack sufficient material for such a comparison. The available literature seems to contain only one record that may be used in this connection. BOYSEN-JENSEN (1919, p. 13) states that *Mya truncata* in Denmark (the Limfjord) may become at least eight years old, a fact which indicates that the growth of the species in boreal seas corresponds rather closely to conditions in Northeast Greenland. A further indication hereof is that the closely related boreal species, *Mya arenaria*, in unheated basins in the Limfjord even at an age of three months showed a shell length of 15 mm (SPÄRCK 1929, p. 279), while *Mya truncata* in Northeast Greenland at an age of one year has a shell length of 3—6 mm only. Since in the Limfjord, too, *Mya truncata* grows slowly, this means that the boreal *Mya arenaria* in boreal seas grows far more rapidly than the arctic-boreal *Mya truncata*. Similar conditions seem to prevail in other genera also. The arctic-boreal mytilide *Modiolaria discors* at an age of one year has a shell length of 6—11 mm in Northeast Greenland, while the southern-boreal *Modiolaria marmorata*, which is much smaller (shell length of adult individuals 15 mm), in the unheated basins of the Limfjord in the course of two summer

months grew from larva to a shell length of 5 mm (BOYSEN-JENSEN 1919, p. 33). In the same basins another mytilide, *Mytilus edulis*, within the same period grew from larva to a shell length of 30 mm (BOYSEN-JENSEN l. c.).

However, this does not imply that all boreal and more southern species have a more rapid growth than the arctic-boreal and arctic forms. In several cases a fairly slow growth and a long lifetime is known in purely boreal forms also. *Macoma baltica* in the Limfjord attains an age of 3—4 years (BOYSEN-JENSEN l. c. p. 27), *Cardium edule* at the coast of Scotland will normally attain an age of 3—4 years (ORTON 1926, p. 257), *Corbula gibba* is known to have a very slow growth in the Limfjord (BOYSEN-JENSEN l. c. p. 17), etc. However, what brings about the great difference in the rate of growth between the Northeast Greenland fjords and the boreal or more southerly seas is that the latter harbour a considerable number of really rapidly growing (i. e. early sexually mature) species with a relatively short lifetime — forms that are entirely absent from the arctic seas. From the above-mentioned investigations in Denmark (Limfjord) such a series of examples of rapid growth is known. Thus the two southern-boreal species of lamellibranchs, *Abra* (*Syndosmya*) *alba* and *Abra* (*S.*) *nitida*, are normally only annual in the Limfjord (BLEGVAD 1928, p. 37) and as to *Abra alba* the 0-group is known in the spring — i. e. after half a year's life — to have a shell length of 7—9 mm (BOYSEN-JENSEN 1919, plate p. 45). From the same water a number of biennial species are also known, thus among the lamellibranchs *Cultellus pellucidus* and *Cardium fasciatum* (BLEGVAD l. c. p. 37). The former is known at an age of one year to have a shell length of 13—17 mm, at an age of two years 23—28 mm (MORTENSEN 1897, p. 321). In the Limfjord it is mainly these and similar forms with a rapid growth that condition the very considerable annual production of this fjord.

If now we consider the available results from Northeast Greenland there is no reason to assume that any of the Northeast Greenland lamellibranchs has a similar rapid growth to that of the above-mentioned boreal and southern forms, or that they are able to reproduce themselves in the first year of their life. In all cases in which the growth could be controlled it was exceedingly slow except in one species, *Modiolaria discors*, which had a much more rapid growth and at the same time, alone of all the lamellibranchs examined, showed a much greater consumption of oxygen (cf. p. 117). However, even in this species the growth is slow as compared with the rapidly-growing southern and boreal forms.

In agreement with this slow growth of the Northeast Greenland bottom invertebrates, maturity is not attained until the animal is several years old. The long series of egg-size investigations discussed in an earlier chapter of the present paper (cf. pp. 53—57) afforded an opportu-

ity to me to investigate also a large number of 0- and 1-group individuals belonging to different species, but in none of them did I succeed in ascertaining sexual maturity. From these investigations it must be assumed that the 2-group (i. e. animals in the third summer of their life) of the Northeast Greenland lamellibranchs will normally be the group in which the sexual organs first reach maturity. Of interest in this connection are ORTON's investigations (1920, p. 363), in which he shows by means of a great number of examples that "size and age at maturity are directly dependent upon temperature". At the low temperatures at which the animals spawn in Northeast Greenland (cf. pp. 80—83) a late maturity should accordingly be expected.

According to the above, the result of the comparison as regards the lamellibranchs is that the fauna of the Northeast Greenland fjords consists of slowly growing, multiannual and late-mature forms, while the boreal and more southern seas in addition to those just mentioned harbour a large number of rapidly growing and early mature forms with a short life. As regards the early maturity, reference is made to ORTON's investigations (1924, p. 244), where individuals not over eight months old of *Abra alba* and *Cardium fasciatum* — two of the most rapidly-growing forms of the Limfjord — were capable of reproduction and after artificial fertilisation produced perfectly normal larvæ. Furthermore, there is a possibility that while the rapidly-growing boreal forms (*Abra*, *Mactra*, *Cultellus*, etc.) have an intensive spawning period every or every other year, it may be conceived that *Mya truncata* in Northeast Greenland has spawning periods, or at any rate a greater deposition of young, at intervals of several years. Thus 1907 was "spatfall year" for this species in the Limfjord (Denmark), and the next great "spatfall year" did not occur till 1915 (BOYSEN-JENSEN 1919, p. 13). If a similar rare spatfall is found in a number of Northeast Greenland species, this rare advent of fresh young will further reduce the production. As all the weights per sq. m. of bottom in Northeast Greenland are much smaller than those of boreal seas, and as the lamellibranchs dominate quantitatively in the majority of Northeast Greenland bottom samples (SPÄRCK 1933, THORSON 1933), it can be stated with fairly great probability that the annual production in the Northeast Greenland seas is extremely small. It being precisely the rapidly growing and early mature species which in boreal seas constitute that part of the production which is designated "first class fish food" (BLEGVAD 1928), it is understandable among other things why bottom fish play such an inconsiderable part in the Northeast Greenland fjords. — As regards the remaining marine invertebrate groups the investigations of growth in Northeast Greenland have yielded no scientifically useful results. However, since these forms live at exactly the same tem-

peratures and under the same food conditions as the lamellibranchs, it may be anticipated that they will show essentially the same conditions of growth as the latter.

It must therefore be assumed that the bottom invertebrates in the Northeast Greenland seas will on the whole have a slow growth, a long life, and a late maturity, which means that the production must be extremely small. However, the considerations set forth here merely quite provisionally suggest certain lines of inquiry, and it is highly desirable that similar investigations should be made on the growth of a number of other invertebrate groups.

CONSUMPTION OF OXYGEN

In the preceding chapter a survey has been taken of the growth of the Northeast Greenland bottom invertebrates, more especially the lamellibranchs. An attempt will now be made, by investigating their consumption of oxygen, to find out the main features of their requirements in the Northeast Greenland waters.

About 600 experiments on the oxygen consumption of the bottom invertebrates are available from the Northeast Greenland fjords. As in the investigations of the growth, here, too, the lamellibranchs have especially been used for the experiments. The experiments were made after the WINKLER method (BJERRUM 1904, KROGH 1914), and in the subjoined computations and curves the consumption is expressed in cubic centimetres of oxygen per kilogram of living weight without the shells per experimental hour. Several series of experiments have been used for each species in order to investigate the metabolic processes in young as well as in half-grown individuals, and in adult individuals both during the spawning time and outside it. In order the better to form a judgment of the particular reaction of the individual species, the experiments were not only made at the temperatures at which the species normally occur in Northeast Greenland, but also at a series of other temperature intervals ranging about 8°, 16°, and 24° C. respectively. In this way material was secured for a future comparison with the consumption of oxygen in boreal and more southerly seas at the same temperatures at which they normally occur. About three-fifths of the available experiments were made in the autumn (October and November) of 1931, while the remaining two-fifths were made in the spring (May—June) of 1932. By using material from these two seasons of the year material for comparison has been obtained for a number of species in spawning and out of spawning, and the influence of the season on the consumption of oxygen has been controlled.

Whenever possible, six experiments were made for each series at each temperature. The glass jar used was selected with a view to the

number and size of the individuals, and at each temperature normally two one-hour experiments, three two-hour experiments, and one four-hour experiment were made. While the one- and two-hour experiments as a rule gave quite identical results at the same temperature, this was not always the case with the four-hour experiments, in which the oxygen consumption per hour for a number of species was always less than the consumption per hour in the one- and two-hour experiments. The water used contained at the beginning of all the experiments from 7 to $8\frac{1}{2}$ c.c. oxygen per liter, in the great majority of cases about 8 c.c. Species as for instance *Astarte borealis*, *Astarte elliptica*, *Mya truncata*, and *Arca glacialis* showed a reduced oxygen consumption already in the four-hour experiments, in which one-sixth or one-fifth of the oxygen content of the water was consumed (thus at the end of the experiments the water contained from 5.6 to 7 c.c. oxygen per liter), while *Macoma calcaria* and *Saxicava arctica* showed not the slightest sign of a reduced oxygen consumption even in the four-hour experiments, in which one-third or half of the oxygen content of the water was used (at the end of the experiment the water thus contained from 3 to 5.5 c.c. oxygen). Hence there seems to be a possibility that *Astarte*, *Mya*, and *Arca* respond to a small decrease in the oxygen content of the water by reducing their oxygen consumption, while *Macoma* and *Saxicava* seem to be less sensitive to fluctuations in the oxygen content. As the results of all the four-hour experiments for *Astarte elliptica*, *Astarte borealis*, *Mya truncata*, and *Arca glacialis* were much below the uniform results of the five one- and two-hour experiments for each series at each temperature, the four-hour experiments for these species were disregarded in the computation of the average result of the experiments, whereas for *Macoma* and *Saxicava*, for which the four-hour experiments showed exactly the same results as the one- and two-hour experiments, the average was computed on the basis of the results of all the experiments. Thus for the species which showed a decrease of the oxygen consumption in the four-hour experiments, none of the experiments in which the oxygen content at the end of the experiment was smaller than six-sevenths of the oxygen content at the start of the experiments (i. e. never less than 6—7 c.c. per liter) were used in the computations.

For several species the oxygen consumption increased evenly at rising temperatures, while for other species a rise of temperature of merely 0° to 8° caused great variation in the results of the individual experiments. As regards most of the Northeast Greenland lamellibranchs the temperature at which they normally occur is -1° to 0° C. This applies to all species living at depth of more than 25 m, where the temperature all the year round remains constant down to a depth of about

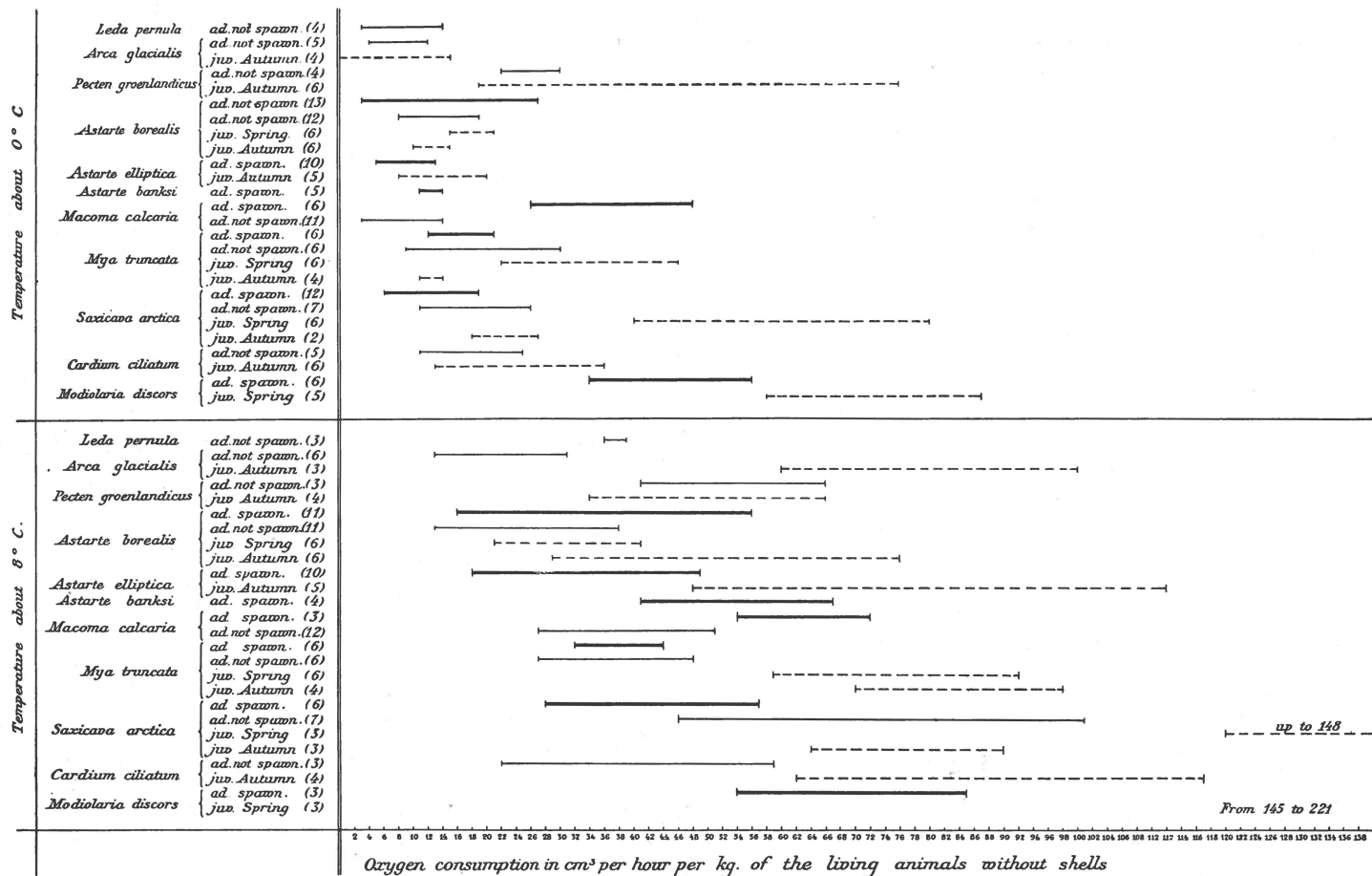


Fig. 22.

400 m. From the positive water layer at still greater depths (temperature 0° to about 1° C.) only quite few lamellibranchs are known, viz. *Arca glacialis*, *Arca pectunculoides*, *Astarte crenata*, *Axinus flexuosus*, and *Axinopsis orbiculata*. The oxygen consumption is known in only one of these species, viz. *Arca glacialis*. For species living at smaller depths than 25 m, -1° to 4.5° C. is the "temperature of normal occurrence", since at Ellø temperatures below 0° C. remain constant up to the surface from the middle of October to the middle or end of June. During the short ice-free summer time (about $3\frac{1}{2}$ months), however, the temperature of the water may (especially in June—August) rise to 2.5° C. at a depth at 10 m, and to 4.5° C. at a depth of 5 m (cf. pp. 80—83). All the lamellibranchs living within this depth interval will accordingly experience a temperature fluctuation, which will influence the oxygen consumption of the species. Hence it will be of interest to compare the oxygen consumption of the various species at the "normal temperature of occurrence" in the winter (-1° to 0° C.) and at higher temperatures, so that the oxygen consumption is known at all temperatures to which the animals are subjected in the Northeast Greenland fjords. Fig. 22 shows such a comparison. While the curves in the other figures illustrating the oxygen consumption at each temperature show only the mean consumption for each series of experiments, fig. 22 shows also the greatest and the smallest results for all the individual experiments at the different temperatures, and if sufficient material is available, it shows the oxygen consumption of adult individuals in spawning, adult individuals outside the spawning time, and the young, in the spring as well as in the autumn.

1) The oxygen consumption of the adult individuals outside the spawning time (cf. fig. 22, thin, continuous lines). At 0° C. the oxygen consumption seems to be almost the same in a large number of the species examined. This applies to *Leda pernula*, *Arca glacialis*, *Astarte borealis*, *Macoma calcaria*, *Mya truncata*, *Saxicava arctica*, and *Cardium ciliatum*; however, in *Astarte*, *Mya*, *Saxicava*, and *Cardium* the oxygen consumption seems to be somewhat higher than in the other forms. The question now arises whether this apparent difference in the oxygen consumption is not due solely to the influence of the experimental errors on the result. At the low temperatures employed here the oxygen consumption is so inconsiderable that a small error in the titration may easily cause a considerable percentage variation in the result. If, for instance, we consider the range of variation of the oxygen consumption for *Macoma*, *Astarte*, and *Mya* at 0° C. (fig. 22) outside the spawning time, an average of the individual experiments seems to show that at this temperature *Mya* has twice, and *Astarte borealis* one and a half times as large an oxygen consumption as *Macoma*.

But if we consider the corresponding experiments at 8° C., it proves that the oxygen consumption is exactly the same in *Mya* and *Macoma*,

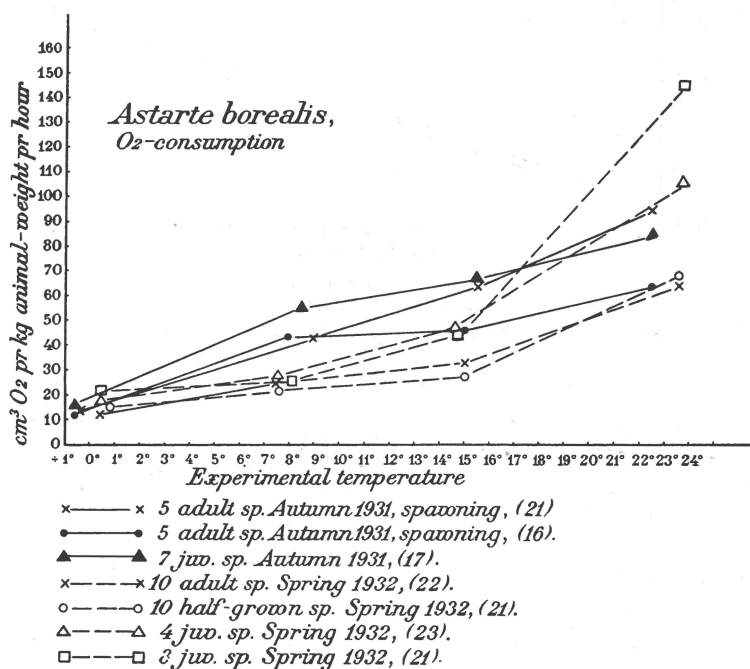


Fig. 23. Oxygen consumption of *Astarte borealis*.¹⁾

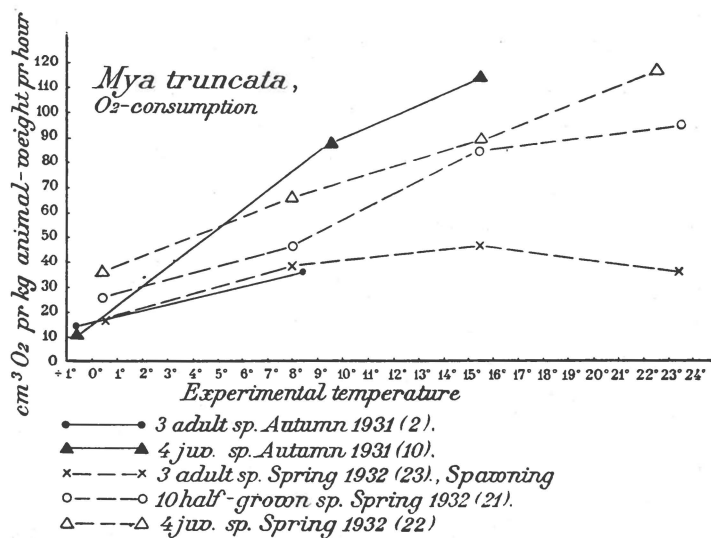


Fig. 24. Oxygen consumption of *Mya truncata*.

¹⁾ The figures in parentheses indicate the number of samples on which the particular curve is based.

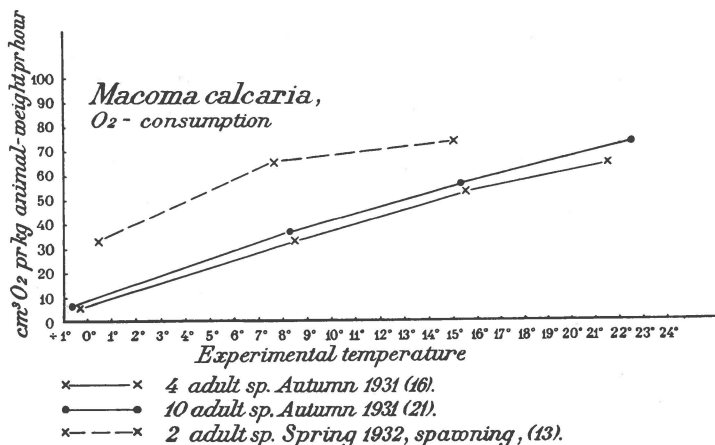


Fig. 25. Oxygen consumption of *Macoma calcaria*.

while for *Astarte borealis* it is a little lower. This might indicate that the deviations from one species to the other found at 0° C, are due merely to experimental errors or individual variations for the different series, so that the oxygen consumption of the above-mentioned species at this temperature is essentially the same. At 8° C. also the oxygen consumption, at any rate for *Astarte borealis*, *Macoma calcaria*, *Mya truncata*, and *Cardium* — all common shallow-water species — seems to be essentially the same, and moreover the oxygen curves for all these species run almost parallel and very close to each other at all temperatures from 0° to 24° C. (cf. figs. 23, 24, 25, 26, 27).

A remarkable form is *Pecten groenlandicus*, whose oxygen consumption both at 0° and 8° C. is considerably higher than that of the forms mentioned so far (cf. figs. 22, 28). It is probably the only lamellibranch which in the Northeast Greenland fjords constantly occurs at temperatures below 0° C. It lives only at depths of more than 25 m, and rarely at depths exceeding 50—60 m, and accordingly does not reach the bottom water with positive temperatures at depths exceeding 400 m, where for instance *Arca glacialis* is fairly common¹). A physiological expression hereof is supplied by the experiments shown in fig. 28. While the experiments at —1° C. give fairly constant results, the experiments at 0° and 1.5° show a considerable increase of the oxygen consumption, and in no case did the individuals survive experiments at higher temperatures than 8° C. Thus but a small rise of the temperature implies such a highly increased oxygen consumption for this species, and in consequence hereof such an increase in the demand for food, that the requirements of the animal at temperatures over —1° to 0° C. cannot presumably

¹) Outside Northeast Greenland, however, *P. groenlandicus* occurs in the deep seas at considerably higher temperatures than those mentioned here.

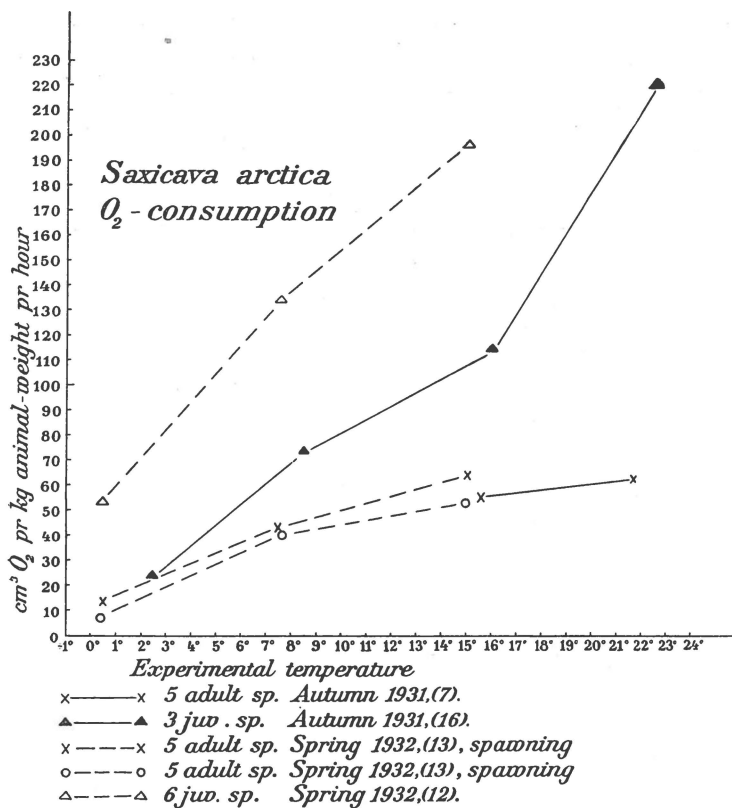


Fig. 26. Oxygen consumption of *Saxicava arctica*.

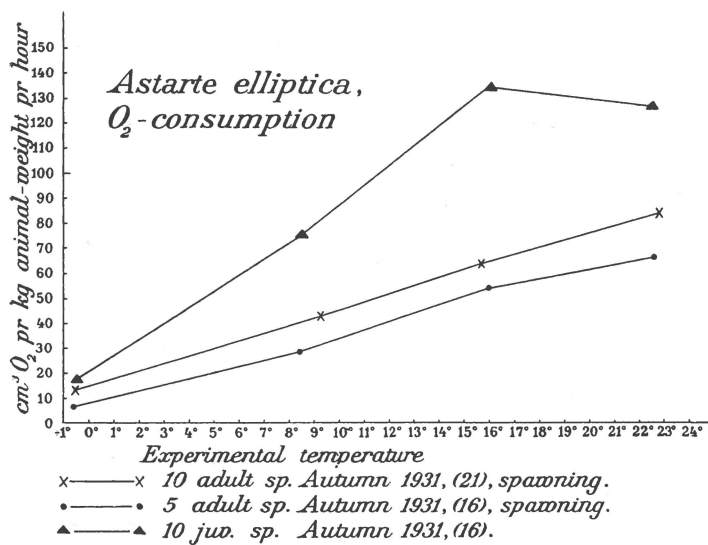


Fig. 27. Oxygen consumption of *Astarte elliptica*.

be satisfied under the conditions of nutrition prevailing in Northeast Greenland. Even at the temperature at which the species "normally" occurs, the oxygen consumption and consequently the food requirements are so great that it must be assumed to be unable to live under the unfavourable food conditions prevailing in the deeper parts of the fjords, even though the water temperatures in these localities fall within the temperatures at which the species "normally" occurs. In the Northeast Greenland fjords such a species will necessarily have its optimum occurrence in as shallow water as possible (greatest amount of nourish-

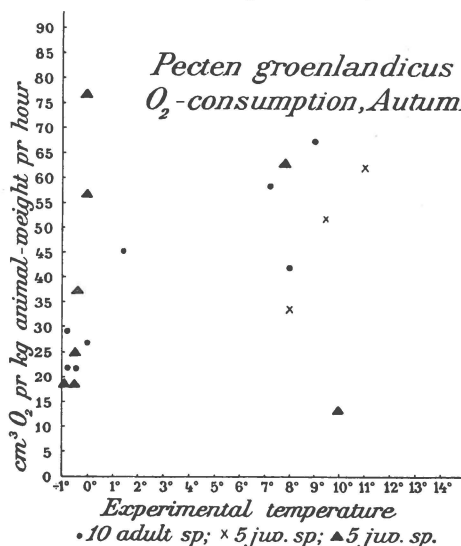


Fig. 28. Oxygen consumption of *Pecten groenlandicus*.

ment), but at the same time at the lowest possible temperature (smallest oxygen consumption, i. e. a reduced food requirement) and therefore have its main distribution at the smallest depths (25—50 m) at which a constant low temperature prevails.

Arca glacialis, which likewise lives only outside the shallow water zone that is heated in the summer (it rarely occurs at depths of less than 45—50 m), is of frequent occurrence in the deep-sea zone with a positive temperature, that is to say, at depths exceeding 400 m. Its oxygen consumption both at 0° and at 8° C. is much lower and more stable than that found for *Pecten groenlandicus* (figs. 22 and 29), and gives fairly constant results in the individual experiments. By heating, the oxygen consumption of the species increases steadily and slowly (cf. fig. 29), and it will easily survive experiments at 24° C. Thus the species is well equipped to hold its own under the poor food conditions prevalent at the depths of the fjords, but on account of its oxygen consumption increasing steadily and slowly, will be able to sustain

life in the coastal zone, provided the competition for food is not too keen. At Kangerdlugssuak (East Greenland), where the arctic shallow-water community, the *Macoma-calcaria*-community, is absent, *Arca glacialis* occurs at smaller depths (10—14 m) than in the other Northeast Greenland waters (45—50 m) (according to information by E. BERTELSEN).

2) The oxygen consumption of the adult individuals during the spawning time (cf. fig. 22, heavy continuous lines). While most of the species outside the spawning time have a fairly constant oxygen consumption at low temperatures, the case is somewhat different for the species during spawning. A number of intervals between the highest and the lowest experimental result for spawning species at 0° and 8° C. are given in fig. 22. Of special interest is a comparison of the oxygen consumption and its variation in the same species during and out of the spawning time. Such a comparison can be made for four of the species examined, viz. *Astarte borealis*, *Macoma calcaria*, *Mya truncata*, and *Saxicava arctica*. In *Astarte borealis* the spawning individuals show a greater difference in the results of the experiments (at 0° C.) and also a somewhat greater oxygen consumption (especially at 8° C.) than individuals outside the spawning time, and this appears even more distinctly in *Macoma calcaria*, whose oxygen consumption during the spawning time is much higher than after that time (both at 0°, 8°, and

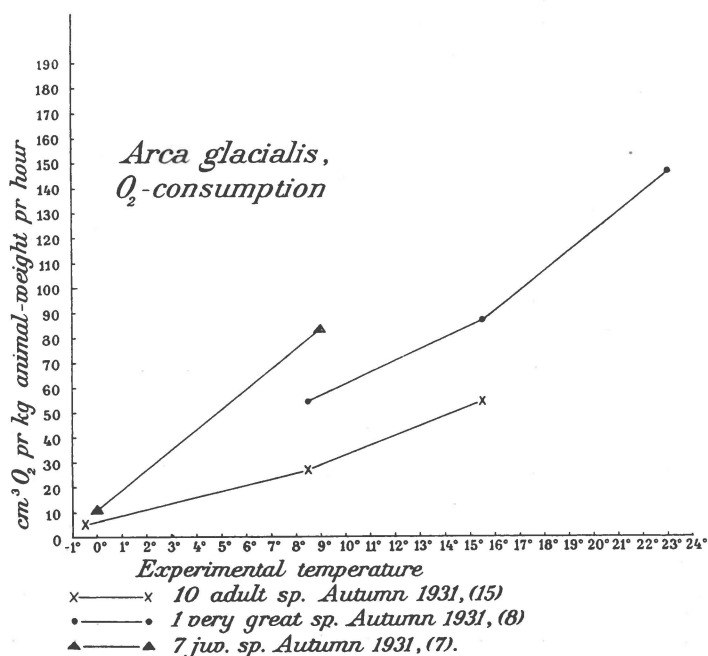


Fig. 29. Oxygen consumption of *Arca glacialis*.

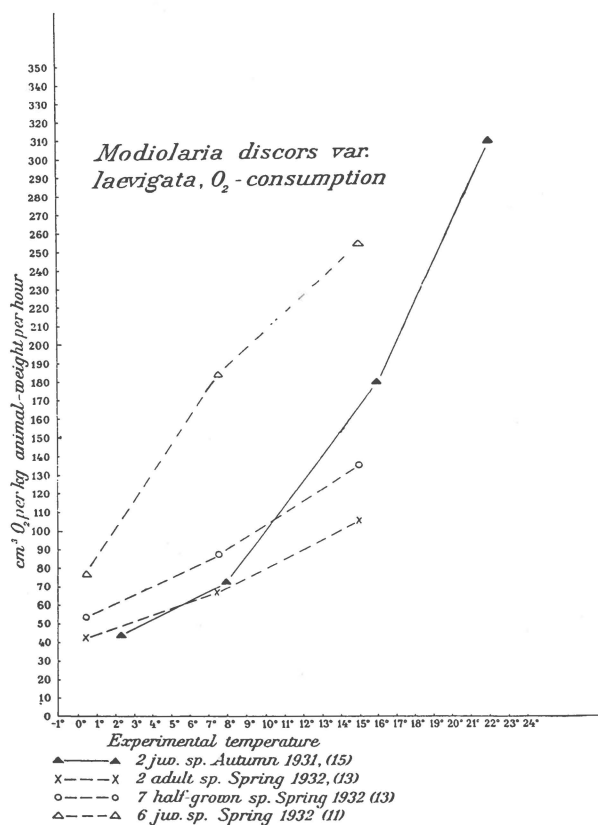


Fig. 30. Oxygen consumption of *Modiolaria discors* var. *laevigata*.

16° C. cf. also fig. 25)). The individuals of *Macoma calcaria* not in process of spawning (though adult) had very reduced gonads, and not even in simple glycerine slides was it possible to recognise the sex, whereas the individuals examined in the spring had well developed gonads with big eggs and movable sperma. Thus it would seem that the oxygen consumption of *Macoma* and *Astarte* in the spawning time increases more than that of *Saxicava* and *Mya*, and there is a possibility that this has some connection with the different methods of reproduction of these forms, *Mya* and *Saxicava* by small eggs and pelagic larvæ, *Astarte* and *Macoma* by big eggs and a non-pelagic larval development. If so, it might be anticipated that the ♀♀ of *Astarte* and *Macoma* would show a higher metabolism during the spawning time than the ♂♂; however, since each of the series of experiments employed here comprises ♂♂ and ♀♀ in the same experiment, it is impossible to draw any conclusions concerning this point from the available results. As the four species employed in the experiments all live in Danish waters, the experiments

will be continued; in order to verify the above supposition experiments with single individuals, both male and female, will be made of species with big and small eggs both during and after the spawning time.

Of the species examined during their spawning time *Modiolaria discors* var. *laevigata* showed by far the greatest oxygen consumption, and in the young of this species in the Northeast Greenland fjords the oxygen consumption was so high that by this alone the species distinguishes itself from the other examined lamellibranchs occurring within the area. A definite explanation of this oxygen consumption can hardly be given at the present time, since investigations of the corresponding level-bottom species *Modiolaria nigra*, which is also frequent in the Northeast Greenland fjords, are lacking. A comparison of the oxygen consumption in these two forms will probably settle whether this high oxygen consumption is characteristic of the genus or whether it has some relation to the mode of living of the species. A series of investigations in Danish waters planned, but not yet made, will probably show this. The most probable explanation will presumably be that *Modiolaria discors*, on account of its special mode of living, has a particularly high oxygen consumption. As the only lamellibranch species occurring in Northeast Greenland it is a typical epifauna animal, associated with and attached to the vegetation (*Desmarestia*, *Fucus*, and *Laminaria*); it is raised above the level of the sea-bottom, and in consequence has far better food conditions than the actual bottom animals, so that its great food requirement precisely in the places in which it occurs has a special chance of being satisfied¹). The results of the above-mentioned experiments on forms with big eggs during their spawning time show, however, that another explanation, too, is quite possible. For *Modiolaria nigra* and *Modiolaria discors* are the two lamellibranchs within the area which have the largest eggs (cf. THORSON 1935), and since the experiments were made at a time when the species were spawning, an increased oxygen consumption might be expected at the outset. The fact that the oxygen consumption of the young is even higher than that of the spawning individuals, does not invalidate this explanation, as will be shown below.

3) The oxygen consumption of the young individuals (cf. fig. 22, stippled lines). The fluctuation in the range of variation of the oxygen consumption and the increase of the oxygen consumption proper which was characteristic of lamellibranchs in the spawning time in contrast to the consumption of immature lamellibranchs, appears still more distinctly from the experiments on young individuals. In all the species examined the oxygen consumption was higher

¹) It is known that *Mytilidae* in other seas, too, have a fairly considerable oxygen consumption, e. g. *Mytilus edulis* (cf. BRUCE 1926).

in the young than in the adult individuals even when the latter were in the spawning stage. However, this difference in the oxygen consumption of the young and the old individuals is not equally pronounced in all the species examined. In *Pecten groenlandicus*, which on the whole shows such a peculiar oxygen consumption, the young are still more sensitive to a slight temperature fluctuation than the adult individuals, and even at temperatures between -1° and 0° C. have a range of variation like that of no other species examined, with the highest oxygen consumption at about 0° C. (cf. fig. 28). Among the forms investigated the highest oxygen consumption in the young is found in *Modiolaria discors*, whose oxygen consumption curves for both adult and young, as previously mentioned, are much higher than that of the other forms examined within the area (cf. fig. 30), but the young

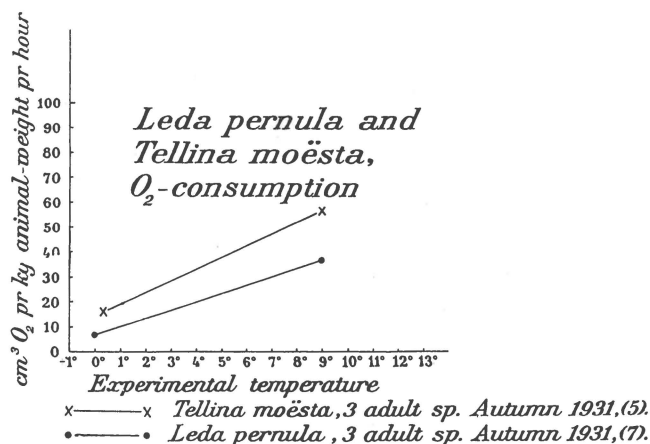


Fig. 31. Oxygen consumption of *Leda pernula* and *Tellina moësta*.

of *Saxicava arctica* also show a considerable oxygen consumption, especially in the spring (Fig. 26).

As regards *Mya truncata*, *Saxicava arctica*, and *Astarte borealis*, series of experiments on the oxygen consumption of the young are available both for spring and autumn. The individuals of *Mya truncata* used in the experiments from these two seasons were of exactly the same size (shell-length 11—15 mm), so that the results of the experiments for these two seasons could be directly compared. The same was the case with *Saxicava arctica* (shell-length 12—15 mm). At 0° C. both these species show a much greater oxygen consumption in the spring samples than in the autumn samples, and it will be of interest to examine whether this increase of the oxygen consumption has a direct connection with the season of the year or is due to other causes. However, no such connection with the season seems to exist. This seems to appear from the

results for *Astarte borealis*, which in no way shows the same tendency as the two other species. At 0° C. *Astarte borealis* has about the same oxygen consumption in the spring and in the autumn, although the young from the autumn (shell-length 15—18 mm) are older than the young from the spring (11—13 mm shell-length), and consequently might be expected to have a smaller oxygen consumption than the latter. At 8° C. the oxygen consumption of these larger autumnal young animals is even considerably higher than in the vernal young of the same species (cf. fig. 22). While thus these conditions show no correlation to any season of the year, they seem, on the other hand, to agree perfectly with the spawning time of the adult individuals; though this cannot be finally proved on the basis of the material available for the experiments, it must be considered probable that the increasing metabolism of the young at the very time at which the adult individuals of the same species spawn, should be regarded as the first results of a sexual rhythm in these, still far from mature, individuals (cf. further figs. 23, 24, and 26).

The experiments on the oxygen consumption in the lamellibranch young in Northeast Greenland have further shown that as a rule it is not only higher than that of the adult individuals of the same species, but that the curve showing the oxygen consumption rises more steeply at higher temperatures for the young animals than the corresponding curves for the adult individuals — in other words that the young are far more sensitive to and respond more intensely to temperature changes. This appears distinctly i. a. from the curves for *Saxicava arctica* (fig. 26), *Astarte borealis* (fig. 23), *Astarte elliptica* (fig. 27), *Arca glacialis* (fig. 29), *Mya truncata* (fig. 24), and especially distinctly for *Modiolaria discors* (fig. 30).

As the mean temperature in the summer is 4.5° C. at a depth of 4 m — a depth at which a number of the forms here investigated normally occur (*Astarte borealis*, *Astarte banksi*, *Macoma calcaria*, *Mya truncata*, *Saxicava arctica*, and *Modiolaria discors*), it is thus at this season of the year a fairly considerable requirement for food which these forms must have satisfied. The experiments would seem to show that this is especially the case in forms with big eggs which spawn within this period and at this depth, viz. *Modiolaria discors* and *Macoma calcaria*, and to a still higher extent for the young of all the shallow water species, of which the young of *Saxicava* and *Modiolaria discors* exhibit a considerable requirement for food. As mentioned above (pp. 83—93), the production of food in the Northeast Greenland fjords in June, before the ice-cover of the fjords has melted, increases very considerably, so that rather large amounts of nourishment are present when the ice melts away, and the water temperature and consequently the food demand of the shallow water lamellibranchs begin to increase. In the late summer,

when the quantity of nutritive substances in the water decreases rapidly, the surface temperature also falls gradually, so that the food production and the food requirements of the shallow water lamellibranchs throughout this whole period, in which the fluctuations in the demand for food are so considerable, may after all keep abreast.

In addition to these investigations of the oxygen consumption of the lamellibranchs, investigations were also made of the polychaete *Pectinaria granulata*. The results of the experiments with this species were very constant, and showed that this common sedentary level-bottom polychaete behaved in the same way as the shallow-water lamellibranchs among which it lives; at 0° C., for instance, it showed

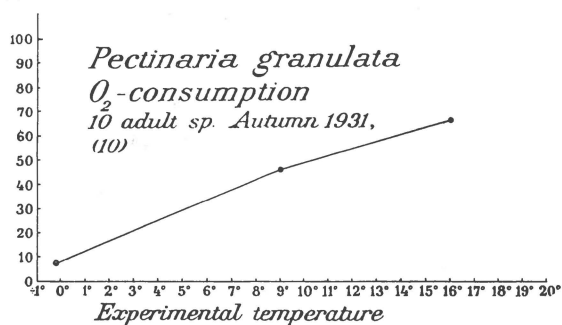


Fig. 32. Oxygen consumption of *Pectinaria granulata*.

an oxygen consumption corresponding entirely to that of *Saxicava*, *Macoma*, and *Astarte borealis* (cf. fig. 32).

A comparison between the above-mentioned results of the experiments on the oxygen consumption of the arctic lamellibranchs with the oxygen consumption of more southerly species as known from the literature (BRUCE 1926, SPÄRCK 1936, and THAMDRUP 1935) shows the following facts: The systematical groups which in the Mediterranean and in boreal waters have a high oxygen consumption (e. g. *Pectinidae* and *Mytilidae*) show a high oxygen consumption in their arctic species, too (*Pecten groenlandicus* and *Modiolaria discors*). The groups which in the southern seas show a low oxygen consumption (e. g. *Astartidae* and *Tellinidae*) have a comparatively low oxygen consumption in the arctic forms examined. Thus both as regards the Arctic and the southern seas there seems to be a fairly close correlation between the oxygen consumption and the mode of living, so that epifauna forms like *Pecten* and *Modiolaria* and to some extent also *Arca* and *Saxicava* have a comparatively high oxygen consumption, especially at higher temperatures, whereas digging species and level-bottom forms like *Macoma*, *Astarte*, and *Mya* have a somewhat lower oxygen consumption and especially a slower increase at higher temperatures. As might be anticipated, the arctic bottom fauna

does not seem to differ in this respect from the faunas of more southern seas. If, however, we compare the arctic species with more southerly species of the same or related genera or the same species in more southerly and arctic seas in regard to oxygen consumption, we shall observe the very conspicuous difference that the oxygen consumption of the arctic species is essentially higher at the same temperature than that of the more southerly species. Thus at 5° C. *Pecten flexuosus* (the Mediterranean) has an oxygen consumption of about 10 c.c. per kg per hour, *Pecten varius* (also distributed in boreal seas) about 25 c.c. per kg per hour, *Pecten groenlandicus* (Northeast Greenland) about 45 c.c. per kg per hour; *Cardium edule* (the Mediterranean) has about 10 c.c. per kg per hour, and *Cardium ciliatum* (East Greenland) about 20 c.c. per kg per hour, also at 5° C. Similarly, *Mya arenaria* has a lower oxygen consumption in Danish waters than *Mya truncata* in Northeast Greenland at the same temperature, and the same applies to *Macoma baltica* in Denmark as compared with *Macoma calcaria* in Northeast Greenland. Hence it would seem that species with a northerly distribution have a higher metabolism than southerly distributed species of the same genus at the same temperature, a hypothesis previously conjecturally set forth by SPÄRCK (1926, p. 282).

THE BOTTOM FAUNA AND ITS RELATION TO THE ECOLOGY OF NORTHEAST GREENLAND COMPARED WITH OTHER ARCTIC SEA AREAS, WITH A SUMMARY OF THE COMMON BIOLOGICAL FEATURES

In the present investigation of the larval development, growth, and metabolism of the Northeast Greenland bottom invertebrates the following characteristic common biological features have been ascertained:

A. The bottom invertebrates of Northeast Greenland are able to ripen their sexual products and to spawn at temperatures below 4.5°C. , and about 70 per cent. of the species at temperatures below 2.5°C.

B. About 95 per cent. of the bottom invertebrates of Northeast Greenland complete their larval development without a pelagic larval stage. In the great majority of these forms the reproduction takes place by large eggs rich in yolk; in gastropods, however, reproduction by means of nurse eggs is also frequently met with. Other methods of reproduction do not affect the percentage. Among the bottom invertebrates with a non-pelagic development are all the species examined which are only distributed in arctic seas, further a number of more widely distributed deep-sea forms and a smaller number of widely distributed shallow water forms.

C. Of the forms with large eggs rich in yolk, this egg-size seems in lamellibranchs, gastropods, and crustaceans to be a characteristic property of the species throughout its area of distribution. As regards the polychaetes it is known that some species may have a non-pelagic mode of development in Northeast Greenland and a pelagic method of reproduction in more southerly seas.

D. The small number of bottom invertebrates (about 5 per cent.) which in Northeast Greenland reproduce themselves by small eggs and pelagic larvæ, were in all the cases investigated forms which were also distributed outside the Arctic. In Northeast Greenland and in the other arctic seas they belong to the quantitatively dominant forms.

E. The larvæ of these bottom invertebrates must complete their

pelagic development within a period of about one month at a temperature of less than 2.5°C ., from which it appears that the larvæ must have a very rapid growth and possibly a very high rate of metabolism.

F. The lamellibranchs of Northeast Greenland have as a whole a very slow growth, a long lifetime, and a late maturity (in the third summer at the earliest) — a phenomenon which can be directly correlated with the low temperature at which the animals live.

G. The bottom invertebrates of Northeast Greenland which were examined have a fairly high oxygen consumption as compared with more southerly forms at the same temperature, but at the temperature at which they live they have a smaller oxygen consumption than the more southerly form at the temperature at which they live. The oxygen consumption of by far the majority of species at the temperature at which they occur in the Arctic seems to be of about the same order of magnitude, provided their mode of living is the same. The experiments seem to show that some species have a higher oxygen consumption in their period of spawning than at other times, while in other species this is not the case.

These common features were all ascertained on material derived from the fjords and the outer coast of Northeast Greenland. However, even within this area there were great differences in the composition of the fauna and the ecological conditions, and since moreover most of the material used is derived from the Solitærbugt near Ellæ in Franz Joseph Fjord, it will be interesting to investigate how far the composition of the fauna there should be regarded as a local phenomenon and to what extent it agrees with the faunas of other arctic seas. A survey of the bottom fauna, the plankton larvæ, and the climate for some other arctic seas may perhaps throw some light on these problems.

The conditions in **Northwest Greenland** will be considered first. Literature: MORTENSEN 1913, DITLEVSEN 1914, POSSELT 1898, STEPHENSEN 1913, VANHÖFFEN 1897 and others.

The bottom fauna. No quantitative samples available. The fauna comprises a much greater number of southern species than in the same latitude in Northeast Greenland. Thus, for instance, *Mytilus edulis*, *Littorina littorea*, *Pagurus pubescens*, *Ophiopholis aculeata* and a number of other southern forms which in East Greenland have their northern limit near Angmagssalik ($66^{\circ}67'$ N. lat.) or even farther south, occur on the west coast at Umanak (70° — 71° N. lat.) or north thereof (e. g. at Upernivik or even in Melville Bay). It is not till we come to the region north of Upernivik and in the Thule District that, according to the above-mentioned authors and judging from recent material acquired by the Zoological Museum, the composition of the fauna seems to agree in all essentials with that of Northeast Greenland.

Plankton. Karajak Icefjord (70° N. lat.) is the only locality in the Arctic besides the Northeast Greenland fjords whence plankton hauls have been taken fairly regularly throughout most months of the year (cf. VANHÖFFEN 1897), and a special interest therefore attaches to a comparison between the results arrived at in Karajak and in Northeast Greenland. However, the plankton hauls from the different months are not quantitatively comparable; the nets employed and the depths at which the vertical hauls were taken have varied greatly at different times. Qualitatively, however, VANHÖFFEN's results are of great importance. Prosobranch larvæ are entirely lacking in all samples, as in Northeast Greenland; ophiurid larvæ occur, and, as in Northeast Greenland too, in large numbers in the autumnal samples, whereas polychaete larvæ are especially common in May—June and seem to play a much greater role than in Northeast Greenland. *Balanus* larvæ are frequent in the period August to October. Thus this plankton differs from that of Northeast Greenland in various respects. This will be especially obvious by comparing the times of occurrence of the lamellibranch larvæ in the two areas. While at Ellæ the lamellibranch larvæ disappeared entirely from the plankton at the end of August, a large maximum of lamellibranch larvæ is found in the Karajak Fjord in October. Even though the hauls from the Karajak Fjord from the various months are not quantitatively comparable, it is unquestionable that the lamellibranch larvæ are extremely common here in the October plankton. Thus there is here an essential difference from Northeast Greenland, which agrees well with the distribution of the southern forms on the west coast. Hence it is probable that the late maximum of lamellibranch larvæ is due solely to the larvæ of *Mytilus edulis*.

Climate. The hydrographic and climatic conditions off the west coast of Greenland are much milder than along the east coast. While at Northeast Greenland the Polar Current appears as a surface current along the coast, only the southernmost part of the southwestern coast of Greenland is washed by the Polar Current (the East Greenland Current), while an undercurrent of warm Atlantic water is traceable far towards the north (I. N. NIELSEN 1928, p. 225). Moreover, the west coast is ice-free throughout the summer to a much wider extent than the east coast.

Thus it can be stated that Northwest Greenland is a faunistic transitional area, the southernmost part of which still harbours many southern species (with pelagic larval stages), while the fauna north of Upernivik and at Thule corresponds fairly well to that of Northeast Greenland.

Turning now to conditions at the southern part of Spitsbergen

we shall find them to be as follows. Literature: VON HOFSTEN 1915, HÄGG 1904—05, ODHNER 1915, BROCH 1910, IDELSON 1931, and BROTZKY 1931.

The bottom fauna. A number of quantitative investigations made by Russians in the Storfjord and on the Spitsbergen Bank have shown that the level-bottom fauna is very like that of Northeast Greenland, both the *Macoma-calcaria*-community and the *Arca-Astarte-crenata*-community being distinctly recognisable (cf. pp. 11—14). Of the epifauna animals, however, a number of more widely distributed species are known from Spitsbergen (*Ophiopholis aculeata*, *Psolus phantapus*, *Machaeroplax varicosa*, *Turritella reticulata*, *Trophon clathratus*, *Aeolidia papillosa*, etc.) which are not recorded from Northeast Greenland.

Plankton. (BROCH 1910). An investigation of the summer plankton of the Icefjord showed that it contained among other things four different pelagic gastropod larvæ of forms which have never been taken at Northeast Greenland, and which must consequently be assumed to originate from the more southerly species living at South Spitsbergen, since nearly all the forms living at South Spitsbergen, with an arctic distribution only, are known to have a non-pelagic larval development (shown by investigations in Northeast Greenland). The ophiurid larvæ occurring in the plankton from Spitsbergen which the author has had the opportunity of examining (1934) were all exclusively larvæ of *Ophiocten sericeum* and *Ophiura robusta*, the same two larval forms which occurred in the Northeast Greenland plankton, whereas larvæ of *Ophiopholis* have not been found at Spitsbergen, although they are known to be pelagic. Hence it may be stated that the number of bottom animals with pelagic larvæ is larger at South Spitsbergen than in Northeast Greenland, which is in accord with the greater number of southern species occurring at South Spitsbergen.

Climate. Despite its more northerly position South Spitsbergen has a climate of a more southern character than Northeast Greenland, since a branch of the Gulf Stream extends as a surface current to the southern part of this area, where it dives down below the Polar Current. The consequence is that a mixing of the water masses takes place here, which again causes a stronger movement of the water, so that South Spitsbergen obtains a much longer ice-free period than Northeast Greenland. The experience gained through many years' investigations has shown that where the ice-cover of the Polar water is dispersed, and the latter is mixed with Atlantic water, a very considerable phytoplankton production (and in connection therewith a zooplankton production) sets in (cf. NANSEN 1902, GRAN 1902, BRAARUD 1935), and this accounts for the greater number of pelagic larvæ of bottom animals found at South Spitzbergen.

As regards the southern part of Spitsbergen it may thus be stated that it has a fauna of a somewhat more southern character and corresponding to this a larger number of species with pelagic larvæ than Northeast Greenland. The climate, too, is more southerly than that of Northeast Greenland and thus corresponds to the biological conditions observed.

The conditions round **North and Northeast Spitsbergen and round Franz Joseph Land** (78° — 82° N. lat.) are quite different. Literature: GORBUNOW 1932, HÄGG 1904—05, KNIPOWITSCH 1901—02 and others. No quantitative investigations are available, but judging from the available faunistic literature, the composition of the bottom fauna is in all essentials like that of Northeast Greenland, since southern forms and accordingly a large number of pelagic larvæ are lacking.

Plankton. No observations on bottom animal larvæ in the plankton are known to me. BRAARUD (1935, pp. 66—67), however, gives a characterisation of the phytoplankton found in the sea between Northeast Spitsbergen and Franz Joseph Land, stating that the phytoplankton production here corresponds entirely to that of the Northeast Greenland fjords and the East Greenland Current.

Climate. The climate, judging for instance from the temperature, the ice-cover, dispersal of the latter in the summer, etc., seems to agree rather closely with the climate off the outer coast of Northeast Greenland.

North and Northeast Spitsbergen and Franz Joseph Land seem to have a bottom fauna which agrees rather closely with that of Northeast Greenland. The same apparently applies to the phytoplankton production and the climate.

The Barents Sea, the White Sea, and the sea round the Kánin Peninsula. Literature: ZENKEWITSCH 1927 and 1931, BROTZKY 1930, COLLIN, 1886, KNIPOVITSCH 1896, GORBUNOW 1933. Quantitative investigations made by Russians have revealed a bottom fauna which corresponds in all essentials to that of Northeast Greenland. The *Macoma-calcaria*-community as well as the *Arca-Astarte-crenata*-community here appear in easily recognisable forms, but the fauna includes some southern forms with a pelagic larval development which are unknown from Northeast Greenland (e. g. *Hyas araneus*, *Eupagurus pubescens*, *Cyprina islandica*, *Macoma baltica* (White Sea), and a number of the above-mentioned southern forms known from South Spitsbergen).

Plankton. Nothing is known to me about the bottom animal larvæ in the plankton from these areas.

Climate. The White Sea as well as the Barents Sea are known to have higher summer temperatures than Northeast Greenland, and in the

Barents Sea there is a more considerable and protracted cattering of the ice-cover than along the outer coast of Northeast Greenland.

Accordingly the Barents Sea, the White Sea, and the sea round the Kánin Peninsula seem with regard to the bottom fauna to show essential points of agreement with that of Northeast Greenland, though they include a far greater number of southern forms with pelagic larvæ than the latter. The climate also and the resulting ecological conditions seem to be considerably more favourable than in Northeast Greenland.

The above comparison with some few other arctic seas would seem to show the following facts. At the northernmost part of Northwest Greenland and at North and Northeast Spitsbergen and Franz Joseph Land a bottom fauna was found which in its composition agrees rather closely with the bottom fauna of Northeast Greenland, while the faunas of the other areas treated here — South Spitsbergen, the Barents Sea, the White Sea, the sea round the Kánin Peninsula and the southern part of Northwest Greenland — agreed on many points with the bottom fauna of Northeast Greenland, but include a larger or smaller element of southern species with pelagic larvæ which are absent from the fauna of Northeast Greenland. The ecological conditions of these seas seems also to agree with this, the temperature being lower, the ice-cover thicker and the phytoplankton production consequently smaller in the areas whose bottom faunas agree with that of Northeast Greenland than in areas in which southern species with pelagic larvæ occur in greater numbers.

A bottom fauna corresponding in regard to reproduction to that of Northeast Greenland must therefore be assumed to occur in such areas of the Arctic in which the ecological conditions correspond to those of Northeast Greenland, North and Northeast Spitsbergen, Franz Joseph Land, and the northern part of Northwest Greenland, and it is probable that a bottom fauna with similar conditions of reproduction and a similar composition to those of the above-mentioned areas may be found throughout the Polar Sea proper, i. e. north of Greenland, north of Spitsbergen and Franz Joseph Land, in the Siberian Arctic Sea, at the north and northeast coasts of Canada, etc., and that the common biological features ascertained for the Northeast Greenland bottom fauna will prove to be characteristic of the bottom faunas of these seas too.

A COMPARISON BETWEEN THE BOTTOM ANIMALS OF THE ARCTIC AND THOSE OF OTHER SEAS

The demonstration of these important biological features common to the bottom invertebrates of the Arctic seas has answered in all essentials the questions which it was the object of this paper to elucidate. It will now be interesting to find out whether there exist other seas the faunas of which exhibit similar biological features.

As regards the growth and oxygen consumption of the bottom invertebrates a comparison has already been made for areas in which such phenomena are known (cf. pp. 103—06 and 119—20), and the more detailed comparison will therefore in the main be limited to the methods of reproduction and larval development characteristic of the various faunas. It has been shown (figs. 3 and 7) that the pelagic larval development among the bottom invertebrates increases from the Arctic towards the boreal seas and presumably still farther south. An example hereof, selected at random, may be given. Of the 82 echinoderm species which according to KÆHLER (1921) are known from the French coast of the Mediterranean the methods of reproduction are recorded in the literature for 32 species (i. e. about 40 per cent. of the total number), which may be grouped as follows: pelagic larvæ (25 species or 78 per cent.), direct development with or without protection of the young (5 species or 16 per cent.), and asexual reproduction (2 species or 6 per cent.) — percentages corresponding entirely to what might be expected according to figs. 3 and 7. The large number of pelagic larvæ also of other groups of bottom animals known from the coasts of the warmer seas (cf. MURRAY 1895) suggest that pelagic larval development predominates there, too.

However, in some areas outside the Arctic, too, a non-pelagic larval development is the rule. It will be appropriate to compare the ecological conditions in these areas and in the Arctic, to find out whether it is the same factors which decide whether the larval development is pelagic or non-pelagic within the various areas. The areas in which the marine faunas have in the main a non-pelagic larval development are 1) the deep oceans, 2) the antarctic seas, and 3) areas with brackish water (and fresh water).

A. Methods of Reproduction in the Deep Seas.

Through the numerous studies of deep-sea invertebrates it has long been established as a universally valid rule that the deep-sea invertebrates have large eggs and presumably a non-pelagic larval development. In the summary of the results of the Challenger Expedition, MURRAY (1895, p. 1459) writes after mentioning "the almost total absence of pelagic larvae belonging to benthonic organisms" that "the same appears to be true of the animals living about and deeper than the mud-line in all parts of the world"¹). In more modern works also this rule is regarded as valid. G. O. SARS (1912, p. 3) writes as follows on the decapod genera *Cryptocheles* and *Bythocaris*: "Both genera agree in so far that the young do not pass through the usual metamorphosis, but leave the comparatively large ova with all the appendages present. A similar suppression of the larval metamorphosis has also been stated, as is well known, in some deep-water species of the genus *Spirontocharis* sp. BATE (*S. polaris* SAB.), in which likewise the ova, born by the female, are of unusually large size." BALSS (1927, p. 951) writes as follows: "Bei manchen (nicht allen!) Formen der Tiefsee sowie des Kalt- und Süsswassers verringert sich die Zahl derselben²), zum Beispiel auf etwa 200 bei *Potamobius* oder nur 20 bei bathypelagischen Garnelen; doch wächst dann die Grösse und der Dotterreichtum des einzelnen Eis. So trägt das Weibchen von *Parapasiphaë sulcatifrons* SMITH nur 15 bis 19 Eier, jedoch von je 4,2 mm Durchmesser". HESSE (1924, p. 169) gives a typical example of this in the egg-size in species of the genus *Scalpellum* at different depths, and shows that the eggs of the deep-water species are much bigger than those of the shallow-water species. Dr. MORTENSEN, who has thoroughly studied these phenomena as regards the echinoderms, has informed me that with a single exception, the deep-sea echinoderms must, according to the experience gained so far, be assumed to have a non-pelagic larval development, and the same seems to be the case with the other invertebrate groups.

It is quite natural that the deep-sea species must have a non-pelagic larval development. As the phytoplankton production, on account of the processes of assimilation, can only take place in the uppermost water layers, the larvæ of the deep-sea species, if they are actually to pass through a pelagic larval development, must move through a water column often 2000—4000 m high or even more from the bottom to the food-producing surface layer, to cover the same distance after having completed their pelagic development, and sink to the bottom. It is

¹) The "mud-line" is normally found at depths about 1000 m.

²) I. e. the eggs.

obvious that under these circumstances the conditions for completing the pelagic larval development are extremely unfavourable; a great number of the larvæ will be destroyed on the way, and if the vertical water movement is slight, it will probably be quite impossible for eggs and larvæ to get from the bottom to the food-producing surface layer. As already stated, it is therefore the opinion of biologists that the deep-sea animals complete their reproduction without any pelagic larval stage.

The conditions for a pelagic larval development in the bottom invertebrates of the deep sea seem accordingly to be even more difficult than in the arctic seas, since the difficulties as regards the deep-sea fauna are of such a nature that they almost exclude the possibility of a pelagic larval development. As is well known, the food conditions in the deep sea are very unfavourable, which is a simple consequence of the great distance of the deep-water fauna from the food-producing surface layer, so that the fauna at this point also lives under food conditions similar to, or rather even poorer than those of the arctic seas. The temperature of the deep sea (cf. MURRAY and HJORT 1912, p. 16, Table 3) in all oceans is on an average about 4°C at a depth of 1000 m, about 3°C at a depth of 1500 m, about 2.25°C at a depth of 2000 m, and about 1.75°C at a depth of 4000 m. This means that the temperature interval corresponds entirely to that found in the Solitærbugt at Ellæø, Northeast Greenland (cf. pp. 80—83). Thus it applies both to the Northeast Greenland bottom fauna as a whole and to the deep-water faunas of the oceans that the species must be able to ripen their sexual products and to spawn at temperatures under $4\text{--}4.25^{\circ}\text{C}$, and most forms at temperatures under $2.5\text{--}2.25^{\circ}\text{C}$.

A comparison between the life conditions of the bottom fauna of the deep sea and the arctic bottom fauna gives briefly the following result:

- 1) Both faunas live under conditions which render it extremely difficult for them to complete their pelagic larval stage.
- 2) The food conditions are unfavourable for both faunas.
- 3) The temperatures of the deep sea and the Arctic vary within about the same limits so that both faunas must be able to ripen their sexual products and to spawn at the same low temperatures.

Thus the deep-sea fauna and the arctic fauna as regards the common biological features treated here and the analysed ecological factors seem to live under almost identical ecological conditions; in both cases these conditions largely obstructed the completion of a pelagic larval life.

B. Reproduction in the Antarctic.

As already stated in the present paper, the non-pelagic larval development seems to be the rule in the Antarctic. By "Antarctic" I here mean only the Atlantic sector of the areas which in the publications of the Discovery-Expedition are designated the antarctic and the sub-antarctic zone (cf. the map in HART 1934, p. 5, fig. 1). The boundary of the Antarctic zone runs north of South Georgia, the South Orkney Islands, and the South Shetland Islands, but south of the Falkland Islands and Cape Horn, while the boundary of the sub-antarctic zone runs north of Tristan da Cunha and north of the Falkland Islands. Thus the area termed Antarctic here is situated between about 38° and about 67° S. lat., i. e. much nearer the equator than the corresponding areas of the Arctic. It is necessary in this discussion to include the sub-antarctic zone also, since a number of the cases of non-pelagic larval development to be mentioned are known from this zone.

A number of examples of the dominance of the non-pelagic larval development in the Antarctic will first be given. WYVILLE THOMSON (1876, p. 56) mentions that pelagic bottom animal larvæ are rarely found in the Antarctic seas. ÖSTERGREEN (1912, p. 329) states that echinoderm larvæ are almost entirely absent from the Antarctic. MACKINTOSH (1934), who treated the macroplankton collected by the Discovery Expedition from the Atlantic sector of the Antarctic, in his lists of the species constituting the macroplankton (l. c. pp. 72—77) mentioned the holothurioid *Auricularia antarctica* as the only bottom animal larva found. The investigations of the reproduction of the Antarctic bottom animals agree entirely with this. MORTENSEN (1910) among the 45 echinides known from the Antarctic found protection of the young in 14 species (31 per cent.). LUDWIG (1904) found protection of the young in 9 ophiurans¹⁾, 11 asterides, and 6 holothurioids in the Antarctic. MORTENSEN (1936) in the material of the Discovery Expedition further found 25 antarctic ophiurid species, which are viviparous or have protection of the young; which thus applies to in all 31 species or about 50 per cent. of the ophiurans occurring within the area; MORTENSEN states (l. c.) that the highest percentage of viviparous ophiurans recorded from any other sea (New Zealand) is about 15 per cent. This phenomenon is known from other animal groups also. Thus the only five Antarctic lamellibranchs whose reproduction is known have protection of the young (species belonging to the genera *Modiolarca*, *Phaseolicama*, *Limopsis*, *Lasaea*, and *Pseudokellya*, cf. PELSENEER 1903 and MORTENSEN 1910 b). In 1923 GRAVIER treats the reproduction of the polychaetes and mentions a large number of forms with protection of the young precisely from the Antarctic,

¹⁾ As to three of these the statement has proved to be incorrect.

stating that protection of the young is especially frequent here (found in the genera *Polynoë*, *Cirratulus*, *Eteone*, *Flabelligera*, *Polydora*, *Potamilla*, etc.). An additional number of examples have been recorded.

The great majority of these species are derived from the Antarctic zone (South Georgia, South Shetland, etc.), but from the Falkland Islands in the sub-antarctic zone also a considerable number of viviparous forms and forms with protection of the young are known.

Thus the high percentage of forms with protection of the young and viviparous forms in the Antarctic has long been known, and the first biologists who began to work with these problems took it for granted that the non-pelagic larval development was typical of the Antarctic alone in contrast to the arctic seas. CARL GREEN's investigations (1902) and GIARD's work (1904), however, told strongly against this view, but as late as 1912 ÖSTERGREEN attempted to explain the antarctic methods of reproduction by contrasting them with the methods of reproduction prevailing in the Arctic.

ÖSTERGREEN (l. c.) supplies a number of the above-mentioned examples of protection of the young and viviparity in the Antarctic, and points out as the essential feature of this observation, not the protection of the young or the viviparity, but the fact that pelagic larvæ are absent. He demonstrates that the problem in the Antarctic does not only apply to forms living in the deep sea, but also to a large number of forms belonging to the coastal fauna (several forms live at depths of less than 100 m), a phenomenon which is fully confirmed by MORTENSEN's recent investigations of the ophiurans (1936). On the basis of this view and with the lack of pelagic bottom animal larvæ as a main starting point ÖSTERGREEN gives the following explanation: The coastal areas investigated in the Antarctic are of small extension, as only a small number of island groups are found which consist of small islands at great distances apart. The coasts descend almost perpendicularly into the surrounding deep sea. Movements in the water, in particular strong currents, are considerable. If the bottom invertebrates of the coastal zone reproduced themselves by pelagic larvæ, the species would run the risk of the larvæ being carried away by the current from the coastal area to areas where they cannot live as bottom stages. As the groups of islands are so scattered, the stock of such a species cannot be recruited from the other groups of islands, and the species will therefore die out. Thus ÖSTERGREEN's explanation only applies to coastal forms, and, as shown in the preceding chapter (p. 128), an explanation has already been given as regards the deep-sea forms. As a contrast to the conditions at the Antarctic coasts ÖSTERGREEN mentions those of the Arctic Ocean, a shallow-watered sea with long, continuous coast stretches, where the species can be recruited from other parts of the shore if the larvæ perish in some places. Consequently

ÖSTERGREEN is of the opinion that pelagic larvæ are absent from the Antarctic, but are frequent in the Arctic (despite CARLGREN's and GIARD's investigations). The investigations made in Northeast Greenland, from which it appeared that only about 5 per cent. of the bottom animal fauna has pelagic larvæ, shows distinctly that ÖSTERGREEN has started from a wrong basis, and the problem must therefore still be considered as unsolved.

Mention will now first be made of the zooplankton of the Antarctic, as it is generally a direct indicator of the production of the area. MACKINTOSH (1934, p. 157) has made investigations within the Atlantic sector of the Antarctic from 52°—68° S. lat., and arrives at the following results: the quantity of the plankton varies greatly in different places and at different times. Round the South Orkneys and the South Shetlands as also in the eastern part of the Bellinghausen Sea the plankton is always present in small quantities. In the other areas the amount of plankton is very variable, but generally very rich except in the winter. HART (1934) in his great work on the phytoplankton production of the South-West-Atlantic and the Bellinghausen Sea treats these questions in detail. He states (p. 190): "The commencement of the spring increase off South Georgia in November corresponds exactly with VANHÖFFEN's (1897, pp. 264—282) observation that the main diatom increase in Karajak-Fjord, North Greenland, some fifteen degrees further from the Equator, occurred in May". HART is of opinion that the reason why the production does not commence till November, is that the ice and the strong currents earlier in the year act as limiting factors to the production. He states that the production only proceeds above a depth of some 35 m, and that the surface temperature during the period of production (summer) ranges from -1.0°C to 3.5°C in the Antarctic zone and from 5.5°C (in the southern part) to 14°C (in the northern part) in the subantarctic zone, of which, however, only the southernmost part is of interest to us. HART (p. 190) draws the following conclusion from his investigations: In the southern part of the Antarctic the phytoplankton production is moderately rich and uniform, while in the northern part it is sometimes extremely rich and much more variable. He explains this by the fact that at all seasons of the year, even while the greatest production takes place, the water contains a considerable surplus of phosphates and nitrates, which allow of an unlimited production as long as the illumination is sufficiently favourable.

These are the conditions at the surface of the Antarctic deep sea. But this production, which, as stated above, only takes place in the uppermost 35 m, is of but little benefit to the fauna living at the bottom of the deep sea, and which on account of the long distance to the source of nourishment cannot have a pelagic larval development. On the other

hand, it might be anticipated that this great production would allow of a pelagic larval development within the Antarctic coastal fauna. As mentioned above, this is not the case, and hence it will be of interest to investigate more closely the phytoplankton production in the coastal water. Such an investigation is recorded in HART's work (l. c. pp. 215—216), in which a summary is given of the phytoplankton production in the coastal water at South Georgia from November to March, i. e. the whole Antarctic summer time. It is a point of interest that it is precisely from the same areas of South Georgia that an essential part of the viviparous bottom invertebrates and those having protection of the young are known. The investigations were made in a certain bay by taking weekly samples in the form of vertical hauls from 25 to 0 m and from 50 to 0 m; the temperature of the water column fluctuated between 0° and 2° C during the months in which observations were made. By a peculiar coincidence the depth of the plankton-hauls and the temperature of the water column agree closely with our observations at Ellaø and Eskimonæs in Northeast Greenland, and thus allow of a direct comparison. HART (l. c. p. 203, fig. 81) gives a diagram of the phytoplankton production throughout the summer in this bay in relation to a number of the more important ecological factors, and it appears distinctly from this diagram that the phytoplankton production does not begin till November and is finished by the middle of January. However, it is not one continuous period of production from November to the middle of January, it comprises various maxima between which the quantity of phytoplankton in the bay is reduced to some few organisms or has totally disappeared. The longest continuous period of production lasted from November 12 to December 2, the next from December 18 to December 31, or three and two weeks respectively. HART also describes the phytoplankton production in this coastal area as "very scanty", and comparing it with the conditions prevailing at Northeast Greenland, we shall find that the duration of the period of production is nearly the same at South Georgia and at the coast of Northeast Greenland. Thus as regards the pelagic larval development the bottom invertebrates of the coastal area of South Georgia are faced by the same difficulties — hard to overcome — as in Northeast Greenland. At a temperature ranging between 0° and 2° C they must complete the pelagic larval development in the course of two or three weeks, which implies an exceedingly rapid larval growth and presumably a very high larval metabolism (cf. p. 93).

As the main cause of the scanty production HART mentions the rapid movements of the surface layers caused by strong winds and the opacity of the water due to inorganic material in suspension brought down by land drainage. And on the basis of several samples he states

that "the reasons to which the poverty of the inshore phytoplankton is attributed probably hold good all round the island" (cf. l. c. p. 216).

No investigations are recorded on the inshore plankton of the other groups of islands, but the factors (rapid water movements and opacity) which HART takes to be the main causes of the scanty production may possibly also play a part in the other inshore areas in the Antarctic as well as the sub-antarctic zone (South Shetland, the South Orkneys, and the Falkland Islands). If a similar scanty production takes place at these groups of islands to that found at South Georgia — and much speaks in favour hereof — it appears to me that attention is here called to an important hindrance to the completion of a pelagic larval stage in the Antarctic, since the inshore fauna cannot use this mode of development on account of the scanty phytoplankton production in the coastal waters, and the remaining part of the fauna, the deep-sea forms, is prevented from a pelagic larval development on account of their great distance from the productive surface layer.

As regards South Georgia, whence so many viviparous forms and forms with protection of the young are known, it may thus be shown that the ecological conditions render a pelagic larval development difficult, after the analogy of the results found for the Arctic and the deep sea, and it is therefore probable that this explanation may be generalised for the remaining Antarctic coastal area. However, the investigations of the ecological conditions in the Antarctic seem only to explain why the pelagic larval stage is lacking, but not why the non-pelagic development predominantly takes place by protection of the young and by viviparity, and not, as in the Arctic, by big eggs rich in yolk and shed directly into the sea. At present it is hardly possible to give an explanation of this phenomenon. It is, however, probable that history plays a part here, in that the fauna of the Antarctic seas may have had a much longer space of time to undergo a development away from the pelagic larval stage than the fauna of the Arctic seas, corresponding to the much higher age of the Antarctic sea area.

A comparison between the life conditions of the Antarctic inshore fauna and those of the deep-sea fauna and the arctic inshore fauna will briefly give the following result:

1) All the three bottom faunas mentioned here live under conditions which render it extremely difficult to complete a pelagic larval stage.

2) The food conditions are unfavourable in the deep sea as well as in the Arctic, and the same applies to the only Antarctic inshore sea (South Georgia) in which the production of food has been investigated.

3) In all three areas the temperature fluctuates within about the same limits, and the three faunas must therefore ripen their sexual products and spawn at the same low temperatures.

C. Reproduction in Brackish and Fresh Water.

A similar change of reproduction to that found at the transition from southern to arctic or antarctic seas and from the inshore regions to the deep sea is found in marine forms at the transition to brackish and fresh water. This is shown by several examples. For the marine prosobranch genus *Littorina* we find that the viviparous *Littorina rudis* extends into much more brackish water than *Littorina littorea* and *Littorina obtusata*, which have pelagic larvæ and big eggs shed directly into the sea with a non-pelagic development respectively. According to new investigations on the genus *Hydrobia*, the marine form *H. ulvae* has pelagic larvæ, while there exists a brackish water form (*H. stagnalis*) whose big eggs are shed directly into the sea and develop without a pelagic larval stage; and finally *H. jenkinsi*, which sometimes lives in entirely fresh water, is viviparous. Of the prosobranch genera which live almost exclusively in fresh water, the genus *Paludina* is viviparous, the genus *Bythinia* lays big eggs without pelagic larvæ, etc. Corresponding features are known for other invertebrate groups. The shrimp *Palaemonetes varians* has much bigger eggs in fresh water than in sea-water (BOAS 1890), the crayfish (*Potamobius astacus*), in contrast to most other decapods, has an abbreviated larval development, the typical brackish water polychaete *Alkmaria rominji* (E. WESENBERG-LUND 1935) is viviparous, etc. An additional number of examples are given by HESSE (1924, p. 36).

As shown above, the corresponding methods of reproduction in the Arctic, the Antarctic, and the deep sea seem to depend on the amount of food present and the duration of the phytoplankton production all in relation to the temperature. However, this must be regarded as impossible in the fresh waters, which are much richer in nutritive matter. BOAS (l. c.), who discusses the modes of reproduction in fresh water, cannot supply an explanation, and concludes by saying that "so far the case in question exhibits nothing new; it only shows us a result of the well known law — otherwise quite unknown in its causes — that life in fresh water predisposes to a dispensation with or an abbreviation of the metamorphosis¹⁾." However, subsequently a number of different explanations of these conditions have been given.

When thus it is known that the eggs of the plaice (*Pleuronectes platessa*) according to whether the salinity is 19.45, 17.3, or 15.68 per mille, increase in diameter from 1.876 and 1.901 mm respectively to 1.953 mm, (HESSE 1924, p. 36), it will be reasonable to assume that this slight increase of size in fresher water is exclusively due to osmosis. However, for the really big eggs rich in nutritive matter osmosis cannot

¹⁾ Translated from the Danish.

account for this phenomenon. For if the egg-size in fresh water were due to osmosis, it might be anticipated that the new-born young developed from these eggs would be hatched at the same stage of development as the corresponding marine forms, since the nutritive content of the egg must in that case be the same in both forms. In *Palaemonetes*, the newly hatched young of the fresh-water form, it is true, is bigger and more clumsy than the larva of the marine form, but at the same time it has reached a more advanced stage than the latter (Boas 1890, p. 794), which does not agree with the supposition that this should be due to osmosis. Something similar applies to the remaining fresh water animals, in which the larval stages not only attain a larger size, but in which the free-swimming larval stage is lacking, i. e. the whole metamorphosis is abbreviated or lacking. This development directly into the bottom stage cannot be conceived to take place by means of a similar small amount of nutritive matter to that which in marine forms suffices only for the development of a small pelagic larva. To ascribe this to osmosis, must therefore doubtless be said to be too facile an explanation.

SOLLAS (1884) set forth another explanation of these phenomena, viz. that the immigration of species with pelagic larvæ into fresh water is simply prevented by the outward current in rivers and rivulets, which will constantly carry the pelagic larvæ back to the sea. However, this explanation is not exhaustive either, because, as shown above, a similar tendency in the variation of the egg-size is traceable even at the transition from sea-water to brackish sea-shore areas, where no such outward current can segregate the pelagic larvæ.

Finally WESENBERG-LUND (1909, p. 424) gives quite a different explanation, which is now the generally accepted explanation among hydrobiologists. WESENBERG-LUND states (l. c.) that the extremely sparse occurrence of pelagic eggs and larvæ in fresh water must be explained partly through the much smaller power to buoy up of fresh water than of sea water, partly because this power changes regularly in the course of the year, so that the larvæ which may remain swimming in sea water, will inevitably sink to the bottom in fresh water. This is further supported by the same author's description of the eggs and larvæ which can actually live in a pelagic state in fresh water, and which are equipped with apparatus especially suited for keeping them afloat in the water quite different from those found in pelagic eggs and larvæ in sea water. Moreover, WESENBERG-LUND points out that the pelagic larval stage actually found in various bottom forms in fresh water (e. g. bryozoans) cannot be compared with the larval stages of the marine forms, since the fresh water forms have already in the egg completed the larval stages which in the marine forms are free-swimming and

pelagic. Thus the pelagic stages in the fresh-water forms are new-formations especially adapted to swim in fresh water.

However, it appears to me that the problem is not, after all, fully exhausted through these explanations, and that one or more additional factors must exert their influence, factors, whose importance and function cannot be clearly recognised at the present time. According to both the last-mentioned explanations (SOLLAS 1884 and WESENBERG-LUND 1909) it is only the pelagic larval development proper which seems to be incompatible with conditions in fresh water. The question then arises why genera which even in brackish water have big, non-pelagic developing eggs (cf. the above-mentioned *Hydrobia*-forms), are only represented in fresh water by viviparous forms (*Hydrobia jenkinsi*), for which reason *Littorina obtusata*, which has big, non-pelagic developing eggs shed directly into the sea, does not extend so far into brackish water as the viviparous *Littorina rudis*, etc. — similar problems to those mentioned for the Antarctic bottom animals (cf. p. 135). As regards the above-mentioned phenomena of *Hydrobia* and *Littorina* the questions must still remain open.

However, it appears distinctly from the available investigations and literature, that the factors which have caused the non-pelagic development in fresh water must be explained by agents quite different from those exerting their influence in the three sea areas in which a similar mode of reproduction prevails, and cannot therefore be included in considerations as to the causes of the biological features common to the arctic bottom fauna.

THE COMPOSITION AND ORIGIN OF THE ARCTIC SHALLOW WATER FAUNA

The comparisons made in the preceding chapter showed that essentially the same methods of reproduction are found for the bottom invertebrates of the arctic seas, the deep seas, and the antarctic seas, at any rate in those areas of them which have been carefully investigated. Moreover, it would seem to appear from these comparisons that the ecological factors in all three areas impede the completion of the pelagic larval stage, partly on account of the low temperatures, partly, in the Arctic and in the Antarctic, on account of the scanty phytoplankton production, and in the deep seas on account of the considerable distance of the fauna from the food-producing surface layer. The poor food conditions are characteristic of the deep seas throughout their extent, while for the shallow-water zones they are only characteristic of some few areas, among which are the arctic as well as the antarctic seas. As regards the deep-sea fauna it further seems that even during warmer post-glacial periods, if such have existed, it had a non-pelagic larval development, since a rise of temperature cannot possibly be of any importance, nor can it change the fact that the deep-sea fauna has lived at a considerable distance from the food-producing surface layer. As regards the coast fauna, however, it is indubitable that such post-glacial heat periods will, through a rise of temperature as well as through their great importance for the phytoplankton production, exert a considerable influence on the composition of the fauna — according to whether or not the production and the rise of temperature permit a pelagic larval development. Only in places where the temperature is low, and the phytoplankton production in the coastal waters is inconsiderable, does the non-pelagic larval development seem to dominate among the bottom invertebrates. Through investigations made in Northeast Greenland it is known that the coastal fauna of these regions in warmer post-glacial periods has numbered species with a pelagic larval development which are now absent from these parts (NATHORST 1901, AD. JENSEN 1905, NOE-NY-

GAARD 1933). Thus *Mytilus edulis*, which now only occurs at Angmagssalik, is frequently found in raised beaches from post-glacial time. Similar conditions may be ascertained for other arctic regions. At Franz Joseph Land NANSEN (1899) collected *Mytilus edulis* on an old shore-line; from Spitsbergen *Mytilus edulis*, *Cyprina islandica*, and *Littorina littorea* are known from fossil shell beds (LOVÉN 1870); from the Kara Sea area fossil individuals of *Macoma baltica*, *Cyprina islandica*, and *Zirphaea crispata* are recorded (AD. JENSEN 1905), and from Disko Bay, West Greenland, post-glacial deposits containing *Zirphaea crispata* and *Anomia ephippium* are known (AD. JENSEN and HARDER 1910) — all forms with small eggs and the majority with pelagic larvæ. When subsequently the climate grew colder again, these forms disappeared, and only a small number of forms with a pelagic development remained, forms with a rapid larval growth and presumably a very high larval metabolism.

Thus it can be stated with certainty that a number of species with a pelagic larval development which are distributed in more southerly (i. a. boreal) seas, have during a post-glacial warm period lived in arctic seas, whence they have now disappeared. When such a faunal element disappears from a sea, it is probable that hitherto excluded forms may obtain an opportunity of holding their own in the competition, their former competitors in the struggle for food having disappeared. As an example of this it may be mentioned that distinctly boreal shallow-water forms (e. g. *Macoma baltica* and *Cardium edule*) occur in the Baltic at greater depths than in the other boreal seas, a phenomenon which is generally considered to be due to the total absence of their enemies (the echinoderms). E. BERTELSEN has kindly informed me that at Kangerdlugssuak, East Greenland, the *Arca-Astarte-crenata*-community (cf. p. 13) occurs in much shallower water (found in dredge-hauls of 10—14 m and 20—25 m) than in other East Greenland sea areas (*Arca glacialis* is only common here at depths exceeding 45—50 m), while the arctic shallow-water community capable of competing with it (the *Macoma-calcaria*-community) is entirely absent at Kangerdlugssuak. Both these examples show a shifting as to depth which must be assumed to be a result of the lack of the usual equilibrium between the competitors in these areas. In the Baltic we find a shifting from smaller to greater depths, at Kangerdlugssuak the reverse is the case.

If now we consider the arctic fauna with the fact in mind that a number of forms with pelagic larvæ have lived in this area during a warmer post-glacial period, and have later disappeared simultaneously with a decrease of the temperature, it will seem probable, bearing in mind the above-mentioned displacements as to depth, that the deep-sea fauna has had an opportunity of spreading in arctic coastal areas, because the last remains of the actual coastal fauna have disappeared.

Accordingly part of the arctic coastal fauna should consist of species which in their other areas of distribution live in deeper water. This, in fact, is the case. FISCHER (1883, p. 1498) mentions ten species of different molluscs which were only known from arctic coastal areas, but which have now been found in the tropical part of the Atlantic at great depths (usually at depths exceeding 2000 m). In addition some examples of a similar distribution of species belonging to the Northeast Greenland fauna will be mentioned. *Arca glacialis* occurs in the Mediterranean out to depths of 2500 m. *Pecten groenlandicus* is known outside the Arctic from depths exceeding 1000 m. *Modiolaria discors* and *Natica groenlandica* have been found outside the Arctic at depths of 3250 m and 2350 m respectively (COOKE 1895). *Ophiacantha bidentata* is known from the Azores, where the species occurs at depths of 4450 m (KÆHLER 1924). As moreover the deep-sea fauna must be supposed to have had a non-pelagic larval development during warmer post-glacial periods too, its species must thus have had good opportunities of immigrating into the arctic coastal areas and of reproducing themselves there precisely at the time when the shallow-water forms better suited for competition were ousted from these regions, i. a. because of obstacles to their reproduction (spawning-temperature or pelagic larval development); and considering the above-mentioned deep-sea occurrences of arctic shallow water forms it seems reasonable to assume that part of the present arctic shallow water fauna has been recruited from profound ocean depths. This explanation, which was already set forth by MURRAY (1896) and used by him i. a. as an explanation of the bipolarity problem, has been strongly attacked by BERG (1933, p. 459), who considered it erroneous. BERG bases his criticism i. a. on the fact that the forms for which the bipolarity has been ascertained, are largely littoral forms ("jedenfalls streng genommen keine Tiefseeformen,"), but at the same time admits (l. c. p. 471) that "für echte Tiefseeformen, die an Tiefen von mehr als 1000 m gefunden sind, stellt die Verbreitung aus einer Hemisphäre in die andere keine Schwierigkeiten dar...". Since it is a fact that a large number of arctic shallow water forms (among which are several species recorded as bipolar) have been found at ocean depths far exceeding 1000 m and thus despite all correspond to BERG's "echte Tiefseeformen", since it can further be shown that the methods of reproduction of the deep-sea fauna and the arctic coastal fauna entirely agree (non-pelagic larval development), and since to all appearance the arctic fauna in its present composition must be assumed to have been formed much later than the deep-sea fauna, it seems to me that MURRAY's suppositions are far less unwarranted than assumed by BERG. It is true that it is but a small number of the shallow water species of the Arctic which have hitherto been found at great depths outside the Arctic, but since the deep-sea fauna has so far

only been very deficiently investigated, there is a possibility that an additional large number of arctic shallow-water forms will be found there, and the fairly large number of examples already known must, at any rate, be taken into consideration in judging of these conditions.

However, the arctic bottom invertebrates living in shallow water seem to include an actual arctic faunal element, viz. a number of species which are only known from shallow water and only from arctic seas, and a number of species characteristic of the shallow water zone in boreal as well as in arctic seas.

The arctic shallow water fauna seems to consist of the following components:

- 1) Some few shallow-water forms with a pelagic larval development, distributed also outside the Arctic (e. g. *Saxicava arctica*, *Mya truncata*, *Strongylocentrotus droebakiensis*, *Ophiura robusta*, and *Balanus balanus*).
- 2) A number of shallow-water forms with a non-pelagic larval development, distributed outside the Arctic also (e. g. *Modiolaria nigra*, *Scoloplos armiger*, *Terebellides strömi*, *Gammarus locusta*).
- 3) A number of forms with a non-pelagic larval development, living in shallow water in the Arctic, distributed outside the Arctic at great depths (e. g. *Arca glacialis*, *Pecten groenlandicus*, *Ophiacantha bidentata*, *Troschelia bernicensis*, species of the genus *Sipho* etc.).
- 4) A number of forms with a non-pelagic larval development, known exclusively from arctic seas (e. g. *Tectura rubella*, *Velutina zonata*, *Venus fluctuosa*, *Pandora glacialis*, *Thracia truncata*, *Portlandia arctica*, *Eupyrghus scaber*, and a number of *Spirontocharis* species).

Thus the arctic shallow-water fauna comprises species which occur in the deep seas, species which occur in boreal shallow-water zones, and finally a purely arctic faunal element, within which some species belong to genera living in the deep seas (*Thracia*, *Pandora*, *Portlandia*), while others belong to genera which are known from more southerly shallow water areas (*Tectura*, *Velutina*, *Venus*, *Spirontocharis*), and this purely arctic faunal element therefore seems to have various origins.

The demonstration of a number of animals common to the arctic shallow-water zone and the deep seas has, as stated above, been associated with the problem of bipolarity. MURRAY (1896) followed this train of thought, and PELSENEER (1903) as late as in the publications of the Belgica Expedition expressed the view that a number of the molluscs occurring in the Arctic and in the Antarctic are cosmopolitan deep-sea species which in the arctic and antarctic regions have ascended into the littoral regions, and mentions in contrast to them a number of typically "unipolar Benthos species" which are never met with in deep water.

BERG (1933) in his survey of bipolarity holds that the latter is largely due to migration towards the south of the northern fauna along the west coasts of the continents during the Glacial Period, and that this migration has mainly taken place at the surface or at rather small depths, where the temperature during the Glacial Period even in the tropics has been sufficiently low for such a migration to take place. He bases this supposition i. a. on the record from Senegal of Quaternary fossiliferous deposits containing a "boreal marine fauna (*Cardium edule*, *Bittium reticulatum*, *Hydrobia ulvae*, *Tapes aureus*, *Rissoa parva*, etc.). All these forms, which have a pelagic larval development, are, however, even at the present time characteristic of much warmer seas than most of the bipolar forms of invertebrates, and a previous boreal fauna of the said character in the tropics seems to me not to be a sufficient proof of a possible shallow water migration of arctic forms, which may lead to a bipolar distribution.

The investigations made in Northeast Greenland may perhaps supply some information which in future should be taken into consideration in researches on the bipolarity problem. With the exception of the correlation of temperature and distribution, the biology of the individual species has only to a slight degree been included in the investigations of the bipolarity problem. It seems to me to be of no little importance that almost the whole arctic shallow-water fauna, in migrations towards the south, are not to the same extent as for instance the boreal shallow-water fauna, associated with the shallow-water zones, but on account of their non-pelagic larval development have good conditions for, and on account of high metabolism even greater benefit from a migration through the deep seas than through the shallow water areas along the coasts — a migration which moreover need not be limited to the Glacial Period, but might presumably take place at the present day.

That a migration has taken place along the coasts, too, as supposed by BERG (l. c.) to be by far the most frequent procedure, is indicated by the bipolarity of *Saxicava arctica*, since this species has pelagic larvæ and consequently cannot be supposed to have spread by migration in the deep-sea areas proper. Indeed, *Saxicava arctica* is also known at the present day from the shallow-water areas of the temperate seas, and thus is no arctic species proper.

These are only a few examples. The problem of bipolarity will not be discussed at length in the present paper. Probably, however, the working methods used in the Arctic, — viz. an analysis of the method of reproduction, growth, and oxygen consumption of the individual bottom species, and other important biological functions succeeded by a demonstration of important biological features common to the whole fauna, which again should be correlated with locality and dis-

tribution, — may be employed with advantage in the elucidation of this and similar problems.

According to the above, there is hardly any doubt that the bottom faunas of the Arctic, the deep oceans, and the Antarctic are related, and as stated above, a number of forms whose nearest relatives live in the deep-sea areas, are met with in the Arctic and the Antarctic. The comparison made in the preceding chapter of the bottom faunas of the Arctic, the Antarctic, and the deep-sea areas has proved that all three faunas as regards their methods of reproduction behave alike, having mainly a non-pelagic larval development. Similarly there is every reason to believe that the other biological features found to be common to the Arctic (e. g. oxygen consumption and growth) will also apply to the bottom faunas of the deep seas and the Antarctic.

Another feature common to the arctic and the antarctic seas and the deep oceans is the low temperature — in all three areas less than 4°C — and there is hardly any doubt that this low temperature is the main cause of the characteristic composition and the common biological features of these bottom faunas. The fact alone that the low temperature is known to exclude a large number of the bottom animals of the temperate and warmer seas (a number of species with a pelagic development), which require a higher temperature in order to spawn, seems to confirm this supposition. In addition to such an exclusion of species which demand a higher temperature for spawning, the temperature in the Arctic and the Antarctic in connection with the poor food conditions, which are apparently also common to the three areas, may render the pelagic larval development impossible or difficult, and this is presumably of no slight importance to the composition of the fauna. However, in this respect also, at any rate in the Arctic, the temperature is the main factor, since here, too, it is the indirect cause of the poor food conditions.

As will appear from the above, there seems to be a great probability that the characteristic composition of the bottom faunas of the Arctic, the Antarctic, and the deep seas and the biological features common to them can be explained by the influence of a great number of different ecological conditions, all of which are either caused by or act through the same main factors, viz. the low temperature alone, or through this low temperature in connection with the poor food conditions.

SUMMARY

The investigations recorded in the preceding pages are based on observations and collections made by the author as a member of the Danish Three-Year Expedition to East Greenland 1931—34. Of special importance is a series of plankton investigations from two different localities from all the months of the year, a considerable number of dredgings and quantitative bottom samples, part of which were preserved in alcohol and studied in Copenhagen after the expedition was brought to an end, and finally 600 experiments on the oxygen consumption of the bottom invertebrates made during the wintering in East Greenland.

After a brief survey of the topography, hydrography, and animal communities of the fjords (cf. pp. 9—16), the reproduction and larval development of the bottom invertebrates are discussed. The following results were arrived at: Of the Northeast Greenland forms investigated (in all about 200 species) within the groups *Echinodermata*, *Polychaeta*, *Gastropoda*, *Lamellibranchiata*, and *Crustacea*, about 95 per cent. were found to reproduce themselves without a pelagic larval stage, and for a number of these bottom invertebrates (*Gastropoda*, *Lamellibranchiata*, and shrimps) there is a great probability that the egg-size and consequently the pelagic larval development is a geno-typically determined character of the species throughout its area of distribution, while in no case was the egg-size ascertained to be a phenotypic phenomenon due to local conditions. As regards the remaining c. 5 per cent. of the forms, which have a pelagic larval development in Northeast Greenland, the following common features were ascertained: 1) All the forms which develop by this method are more or less widely distributed outside the Arctic also; 2) the pelagic larvæ have their quantitative maximum in the plankton at the time when the food conditions must be presumed to be optimal; and 3) the pelagic larval development, which is otherwise so rare in the Arctic, was observed in a number of forms which dominate quantitatively in the arctic seas.

It is shown that about 70 per cent. of the bottom invertebrates in

Northeast Greenland spawn at temperatures below 2.5° C, the remainder at temperatures below 4.5° C, although the majority of the species spawn in the summer.

The conditions for the nutrition of the pelagic bottom animal larvæ, the phytoplankton production, are discussed. These conditions are viewed in relation to the available plankton samples, and it is found that the phytoplankton production in the fjords lasts nearly two months and at the outer coast nearly one month. Thus at a temperature of 2.5° C the pelagic bottom animal larvæ hatched in July have hardly one month in which to complete their larval development, and a comparison with more southerly seas shows that the larval growth must be very rapid and the larval metabolism presumably very high.

Growth. Definite results were found only for the *Lamellibranchiata*. Differences in the growth of the first year in forms with a pelagic and a non-pelagic larval development respectively were not ascertained. The lamellibranch *Modiolaria discors* grows more rapidly than the other species examined. All the lamellibranchs examined in Northeast Greenland showed a slow growth, late sexual maturity, and a long life. As in the fjords the lamellibranchs are the bottom animals which dominate quantitatively, the bottom production is altogether slight.

Oxygen consumption. Lamellibranchs were principally employed in the experiments. Both autumnal and vernal experiments were made with adult individuals within and outside the spawning time and with young individuals. In by far the majority of the Northeast Greenland species the oxygen consumption seems to be of nearly the same order of magnitude at the same temperature, provided the mode of living is the same. Some species seem to have a higher oxygen consumption during the spawning time than outside this period, while in other species this was not the case. It was attempted to ascertain the relations between the distribution as to depth and the oxygen consumption for *Pecten groenlandicus* and *Modiolaria discors*. It is shown that the bottom invertebrates investigated in Northeast Greenland have a fairly high oxygen consumption as compared with more southerly forms at the same temperature, while at the temperature at which they live they have a smaller oxygen consumption than the more southerly species at their normal temperature of occurrence.

The common biological features found are recorded on pp. 122—123. A comparison of the Northeast Greenland bottom fauna with that of other arctic seas renders it probable that the bottom fauna found in Northeast Greenland in a fairly constant composition may be found over wide areas of the arctic seas, for which the common biological features found may therefore presumably be generalised.

A comparison between the fauna of the Arctic and that

of other seas shows that outside the Arctic a bottom fauna with a similar reproductive biology (non-pelagic larval development) is known from the deep seas, the Antarctic, and brackish and fresh water. The conditions within each of these areas are analysed in detail, and a suggestion is made as to the causes of the methods of reproduction of the bottom faunas. It is shown that the Arctic, the Antarctic, and the deep-seas have low temperatures and probably unfavourable food conditions, whereas quite different conditions prevail in fresh water. Thus the non-pelagic development of fresh water seems to be due to entirely different factors from those of the three sea areas mentioned.

The composition and origin of the arctic shore fauna is discussed. It is shown that the bottom fauna has species in common with the deep seas and the boreal shallow-water fauna, and that it includes a purely arctic shallow water faunal element, which again seems to originate partly from deep-sea species, partly from boreal shallow-water species. The agreement between the arctic fauna and the deep-sea fauna is discussed, and it is shown that the common biological features may probably be employed for the elucidation of the bipolarity problems.

On the basis of the comparison made between the Arctic, the Antarctic, and the deep seas it is concluded that the non-pelagic larval development and probably also the characteristic conditions of growth and the oxygen consumption within all three areas may be explained through the influence of a great number of ecological factors, each of which is either caused by or acts through the same main factors, viz. the low temperature alone or through this low temperature in connection with the poor food conditions.

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