MEDDELELSER OM GRØNLAND
UDGIVNE AF
KOMMISSIONEN FOR VIDENSKABELIGE UNDERSØGELSER I GRØNLAND
BD. 159 · NR. 12

BALANUS BALANOIDES (L.) (CIRRIPEDIA) LIFE CYCLE AND GROWTH IN GREENLAND

BY

G. HØPNER PETERSEN

WITH 67 FIGURES IN THE TEXT, 11 TABLES
AND 38 PLATES

KØBENHAVN
C. A. REITZELS FORLAG
BIANCO LUNOS BOGTRYKKERI A/S
1966

Denne afhandling er i forbindelse med de nedennævnte 2 tidligere offentliggjorte arbejder:

1. The distribution of *Balanus balanoides* (L.) and *Littorina saxatilis*, Olivi, var. *groenlandica*, Mencke, in Northern West Greenland.
2. The hydrography, primary production, bathymetry and "Tagsâq" of Disko Bugt, West Greenland.

af det matematisk-naturvidenskabelige fakultet ved Københavns universitet antaget til offentlig at forsvares for den filosofiske doktorgrad.

København, den 6. juni 1966.

J. K. Bøggild
h. a. dec.

CONTENTS

Abstract

A material of *Balanus balanoides*, regularly collected during the course of one season in different stations in Greenland, has established the seasonal-cycle and the life-cycle of the species. The hatching period, settling period and mating period indicate the sexual cycle. The pelagic stage is given as the period from maximum hatching to maximum settling. Fig. 33 shows a comparison between the sexual-cycle in the different localities. The dependence of this cycle on external factors is discussed and demonstrated, e. g., by curves on temperature and primary production. From the author's own observations and from the literature, it is shown that the cypris larvae prefer marine conditions at the northern limit and estuarine conditions at the southern limit. The influence of the West Greenland Current on the distribution taking place towards the north is shown by the settling periods and by the size distribution of the first winter ring.

The growth of the O.-gr. animals and adult animals is demonstrated by measurement and age determinations of the scutae. Figs. 45, 65 and 66 give comparisons between the different localities. Growth parameters, calculated preferably according to methods used for fish populations, are compared in Table 9. A comparison between the results obtained here and those of other scientists from the North Atlantic area are attempted in Table 10. However, the value of the comparison is reduced by the fact that no previous material has been treated in a similar manner. It is emphasized that the climatic differences inside Greenland are of importance—varying from the 11-month ice cover in Angmagssalik, to Sukkertoppen, which has no ice cover. The distribution of the species towards the north is discussed in the light of the results, and the possibilities are considered of forming a picture of the fluctuations in hydrographic and climatic conditions from the changes from year to year in the northern limit.

INTRODUCTION

This investigation started in August 1958 with a course held at the Arctic Station of the University of Copenhagen in Godhavn for teachers from the Education Department of Greenland. After the course the participants were dispersed to towns along the Greenland shores with the intention that they should gather material from the tidal-zone during the season 1959 from different localities (in their free time), in order to compare the sexual season and growth of rocky shore animals at localities situated long distances from each other. As the participants were given an adequate course in collecting technique, it was anticipated that the material would be of high and uniform quality.

Acknowledgements

The University of Copenhagen and the Danish State Science Foundation provided the economic and technical support necessary to accomplish the project. Sincere thanks are extended to the directory board of the Arctic Station of the University of Copenhagen in Godhavn, viz., Professor Dr. phil. R. Spärck, Professor Dr. phil. T. Böcher, Professor Dr. phil. M. Westergaard, and Dr. phil. M. Køie. Similarly, the author wishes to thank Dr. phil. H. Lemche, Zoological Museum Copenhagen, for his great help and understanding during the preparation of this paper, and Dr. phil. E. Ursin, Danmarks Fiskeri- og Havundersøgelser for valuable advice.

The participants in the collecting activities were:

In Sukkertoppen: John Jensen, Erik Lehm, Ellen Christensen.
In Godthåb: Ulrik Rosing.
In Arsuk: Henrik Heilmann, Bent Thillerup Rasmussen.
In Angmagssalik: John Jensen (in 1960).
In Umanak: stud. mag. Else Steenstrup (on a private trip to Umanak, 1962).

The author wishes to express warmest thanks to all these volounteer helpers for their careful and persistent work under cold and primitive conditions.

Information on the climatic conditions are obtained from the following institutions: "Magnetisk Observatorium, Godhavn", "Meteorologisk Institut", "Grønlands Ismeldetjeneste", "Grønlands Vejrmeldetjeneste", and "Grønlands Fiskeriundersøgelser". In addition, special maps were supplied from "Grønlands Tekniske Organisation". The author wishes to thank the personnel of these institutions for their cooperation during the study.

The material is deposited in the Zoologisk Museum, Copenhagen.

November 1964. G. Høpner Petersen

GEOGRAPHICAL SURVEY

As Greenland, for many people, means only a cold, homogeneous area, some general features of the localities mentioned in the text are given. There is a considerable gradient in the climate inside Greenland; a gradient comparable in order of magnitude to those found inside other climatic zones. It is not intended here to estimate the different climatic factors or their influence on the organisms. Likewise, no attempt will be made to enter into a delicate zoogeographical discussion (where viewpoint depends on definitions), but a few brief facts will be given:–

Fig. 1 shows the situation of the different localities, and also the town Holsteinsborg and the airport Søndre Strømfjord. It can be seen that the distance from the northernmost station Augpilagtoq to the southernmost station, Arsuk, corresponds to the distances Faroes-Cherbourg or Copenhagen-Nice. The distance from the westernmost station, Sukkertoppen, to the easternmost station, Angmagssalik, corresponds to the distances, Dublin-Haag or Bergen-Stockholm.

The distances alone are not sufficient to demonstrate the climatic differences, as three major ocean currents influence the Greenland shore. These currents are: the Baffin Land Current and East Greenland Current, both with polar water, and the West Greenland Current, with warm water, branching off from the Gulf Stream.

The shore, running approximately between Upernavik and Holsteinsborg, is influenced by the West Greenland Current during summer and by the Baffin Land Current during winter. The "Vestisen", the characteristic ice of the Baffin Land Current lies during winter close to the Greenland shore, as far south as Holsteinsborg. The shores of the Sukkertoppen and Godthåb districts are not normally influenced by polar water, but south of the Godthåb district to Kap Farvel there is a shift during the year in the East Greenland Current (this is characterized by the "Storis") and the warm West Greenland Current. Further details on the currents are given in Hachey (1961).

Sailing-conditions in the different areas also give a picture of the climate. Upernavik and Umanak are navigable for 5 months, Godhavn for 6 months, Sukkertoppen and Godthåb throughout the whole year, and Angmagssalik for 1 month. The degree of navigation at Arsuk is

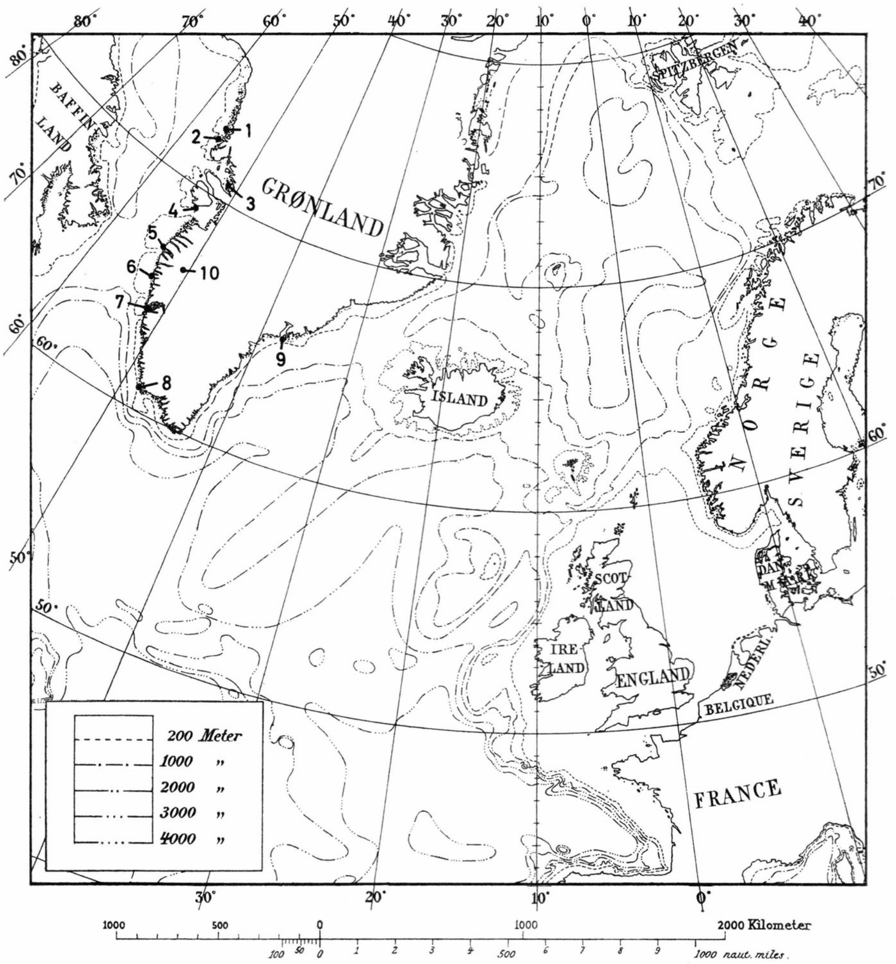


Fig. 1. Map of the area. 1: Upernavik and Augpilagtoq, 2: Prøven, 3: Umanak, 4: Godhavn, 5: Holsteinsborg, 6: Sukkertoppen, 7: Godthåb, 8: Arsuk, 9: Angmagssalik, 10: Søndre Strømfjord airport.

variable about 11 months, and depends on the extension of the East Greenland Current.

Some of the towns are situated in a system of fjords with widely spread archipelagos which contain huge amounts of local, stationary shore-water with special hydrographic conditions. Some stations are exposed to considerable amounts of melt-water or ice-bergs. It is difficult to obtain information of these local conditions or to judge their influence until further investigations have been made.

LOCALITIES

Description

Umanak.

According to the description given by Else Steenstrup (pers. comm.), the animals were not exposed to freshwater (apart from meltwater during the spring). The animals were protected against heavy surf. In Umanak there is normally sea-ice from the beginning of October to mid June, but during 1962, the sea-ice disappeared unusually early (about the beginning of May).

Godhavn.

The animals were collected on a small skerry situated at the south shore of the entrance to Godhavn Harbour. This skerry is further described in Petersen (1962 pp. 12–14 and 1964 pp. 20–21). The locality is not influenced by freshwater or heavy surf, and there are three natural terraces on the skerry – one at the upper limit of the barnacle zone, one a little below mid-water mark, and one at low-water mark. Samples were collected on each of these terraces, and the localities are designated H.W.M., M.W.M., and L.W.M. H.W.M. is not absolutely correct, as the barnacles do not reach high-water mark. The two lower terraces are approximately situated at mid-water and low-water mark respectively.

Sukkertoppen.

The following is an abstract of the descriptions given by Erik Lehm and John Nielsen. The locality is situated on a cape in "Kirkegårdsbugt", a bay protected against heavy surf. There is a small river at the head of the bay, but the animals are not greatly influenced by freshwater. The collections were carried out at mid-water mark.

Godthåb.

Ulrik Rosing's description (abbreviated) states that the locality is named "Kangitdlinguit" and is situated 2–3 km from the town. It faces Godthåbsfjord and is protected against freshwater, heavy surf and pollution. Collections were made in a small pool.

Arsuk.

Bent Rasmussen reports the following: – The locality is situated at the entrance to the Arsuk Fjord, south of the small summit "Pingo",

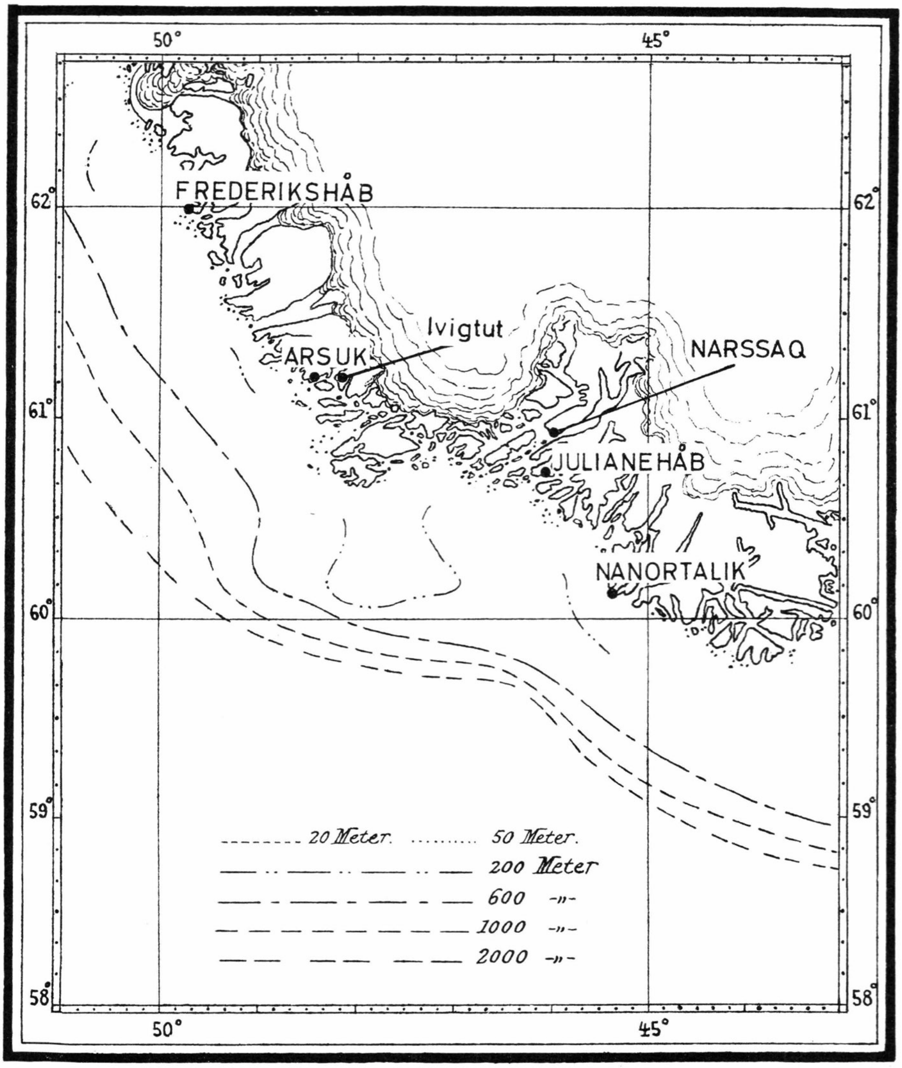


Fig. 2. Map of Julianehåb Bugt with Arsuk, the climate stations Ivigtut and Nanortalik, and the primary production station Narssaq.

and opposite a little island, "Qeqertasaugssuk". The area faces south, is protected against heavy surf, and there is no freshwater influx in the neighbourhood. It is free of ice throughout the year, even though during May-June "Storis" could be found in the outer part of "Arsuk Fjord" (see fig. 2).

Angmagssalik.

According to John Jensen, barnacles are not common in the area but are found on exposed shores.

Temperature observations

Figs. 3–8 gives the temperature-conditions for the different towns. In each figure air-temperature curves are drawn above and sea-surface temperature curves below if measurements are available. Between these curves the duration of the pelagic stage and the copulation period of *Balanus balanoides* is indicated (for compilation of these periods see page 32).

Daily maximum and minimum values are given for the air-temperature. This procedure is considered preferable to giving an average temperature curve as it was seen from field observations that the maximum and minimum temperatures had an important bearing on behaviour of the animals, especially periwinkles.

The Foehn or catabolic winds (Trans, 1955) appear on the curve in a series of violent temperature jumps, especially during the winter. It should be noted that these temperature jumps are not local phenomena, but appear simultaneously on all stations.

The sea-surface temperatures were not measured as regularly as air-temperatures, and different sources have been used to obtain the information necessary for drawing the curves.

No temperature observations were made at Arsuk. The author uses here the air-temperatures from Ivigtut, and the sea-surface temperatures from Nanortalik. Both stations are situated at some distance from Arsuk. Fig. 2 shows the situation of the towns. Ivigtut probably has a more continental character than Arsuk in climate, and Nannortalik is more influenced by the East Greenland Current. From the sea-surface temperature curve it can be easily seen when "Storis" lies off Nannortalik.

The difference in climate between all localities can be reviewed as follows.

The summer periods differ in length but not in maximal temperatures. The summer periods are oceanically influenced on all stations. The winter periods are oceanically influenced on the southern stations, and continentally influenced on the northern stations, where extremely low temperatures are encountered. These differences are linked to the sea-ice cover, as an ice covered sea gives a continentally influenced winter climate.

The maximal amplitude of the tide for some of the localities is as follows. Godhavn: about 2,5 m. Sukkertoppen and Godthåb about 5 m. Arsuk: about 3 m.

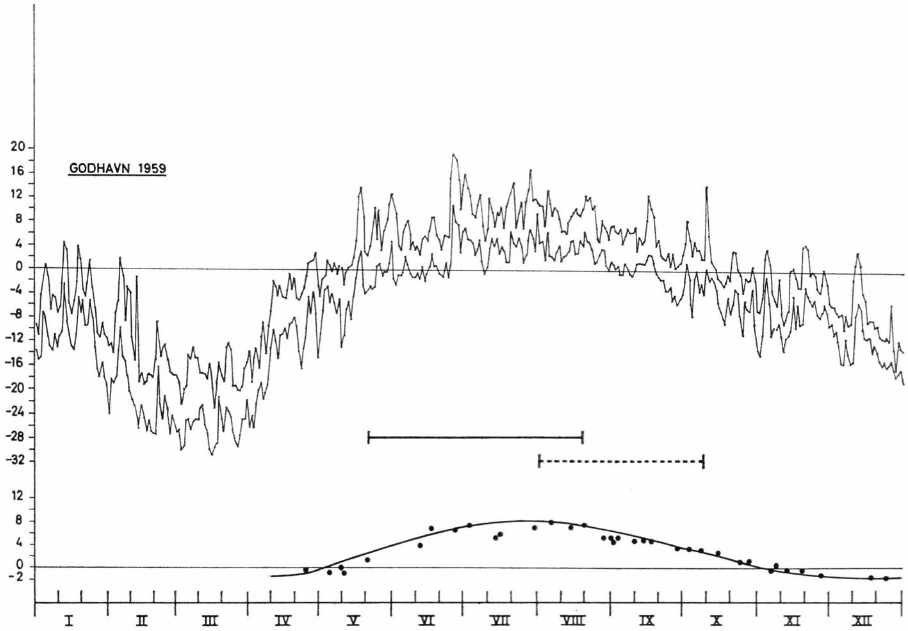


Fig. 3. The daily maximum- and minimum temperatures for the air (above) and the sea surface temperatures (below). Between these two curves are given the results from fig. 33, viz. the duration of the pelagic stage (unbroken line) and the copulation period (dotted line) of *B. balanoides*.

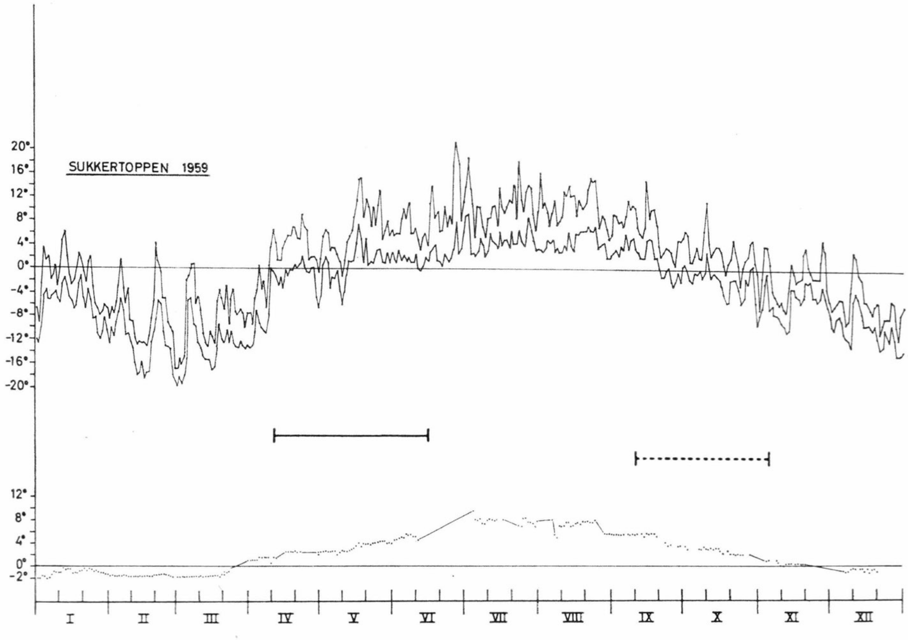


Fig. 4. Text see fig. 3.

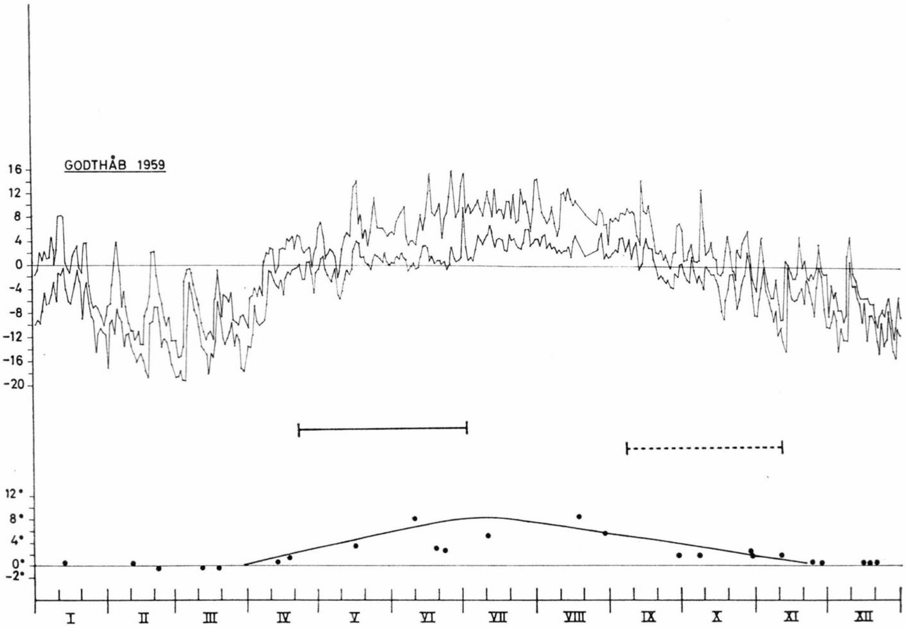


Fig. 5. Text see fig. 3.

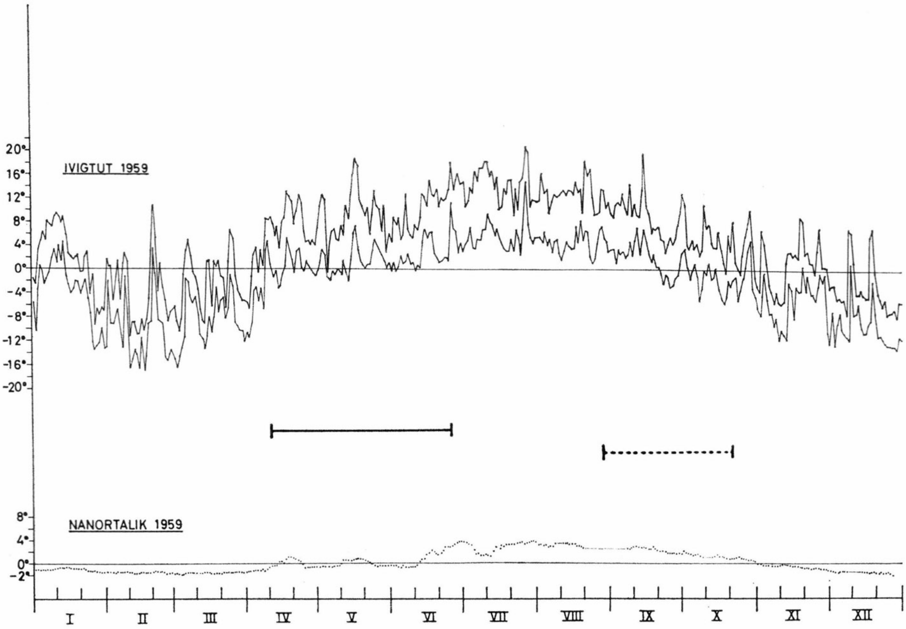


Fig. 6. Text see fig. 3.

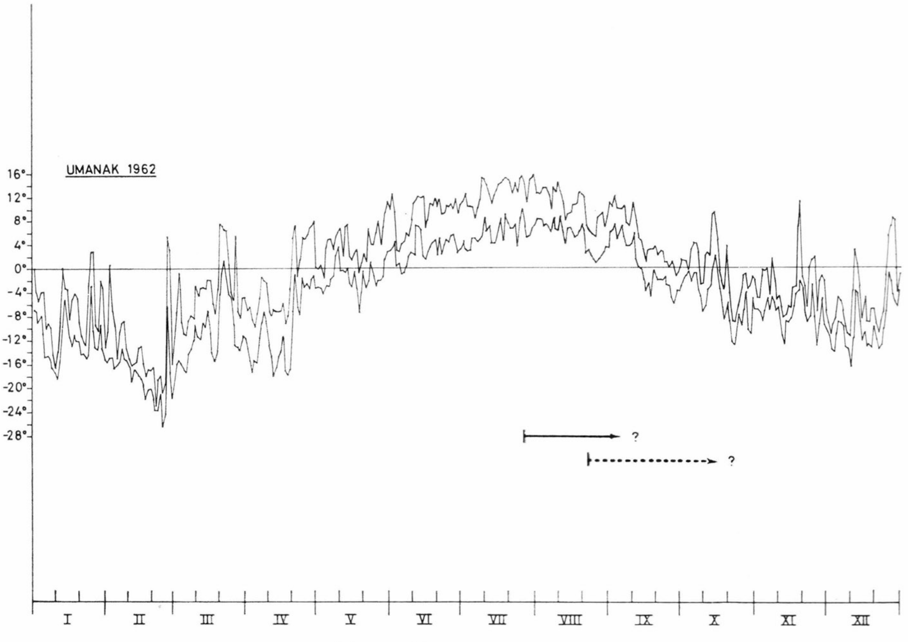


Fig. 7. Text see fig. 3.

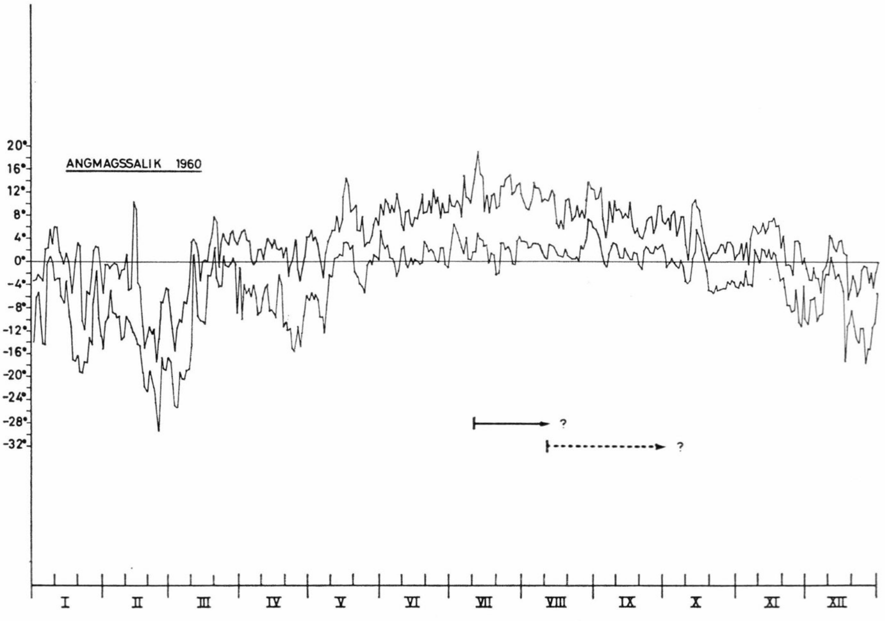


Fig. 8. Text see fig. 3.

"Heat sum"

Figs. 9 and 10 have been evolved to give an evaluation of the "heat-sum" the different populations "receive" during a season. The heat-sum is measured in "day degrees", and for the air temperatures the average of the daily maximum and minimum temperature is used as an average daily characteristic.

The "biological zero" is set at —1°C, as the animals show activity at temperatures below 0°C. Of course, it is questionable whether it is correct to multiply the number of days with the degree of centigrade, using —1°C as zero, but with the present scanty knowledge on these problems, this method might give the best estimate of the "heat-sum" for the different populations. Moreover, the temperature would hardly ever reach values high enough to be detrimental to the animals. The different populations might be differently adapted to the environment, but there is no reason to suppose that different genetic populations are present in the area. With regard to this problem see CRISP (1964).

The heat-sum is given for both the sea-surface and the air temperature. These two values follow each other closely, with the exception of Arsuk, where the values originate from Nanortalik and Ivigtut respectively.

Primary Production

The primary-production is used as a rough picture of the food-conditions. Information from Godthåb and Arsuk originates from STEEMAN NIELSEN (1958). The production-experiments at Godthåb were carried out in two places, viz., at the mouth and at the head of the Godthåbsfjord. The curve in fig. 11 is drawn by inspection, on the basis of both sets of measurements, and might give an idea of the food-conditions in the locality at Godthåb, which is located almost midway between the two production-stations. However, the possibility of great variations from year to year cannot be excluded.

For Arsuk the results from Narssaq are used, and this is of more doubtful value as Narssaq lies more than 100 km from Arsuk in the middle of a fjord-system, and is more influenced by the East Greenland Current and rivers. The primary production at Arsuk is probably higher, but as no better values than those from Narssaq are available, these will be used as being fairly representative for Arsuk.

No measurements of the primary production are at hand from Sukkertoppen, but the geographic, hydrographic and climatic conditions make it probable that the production off Godthåb corresponds to that off Sukkertoppen.

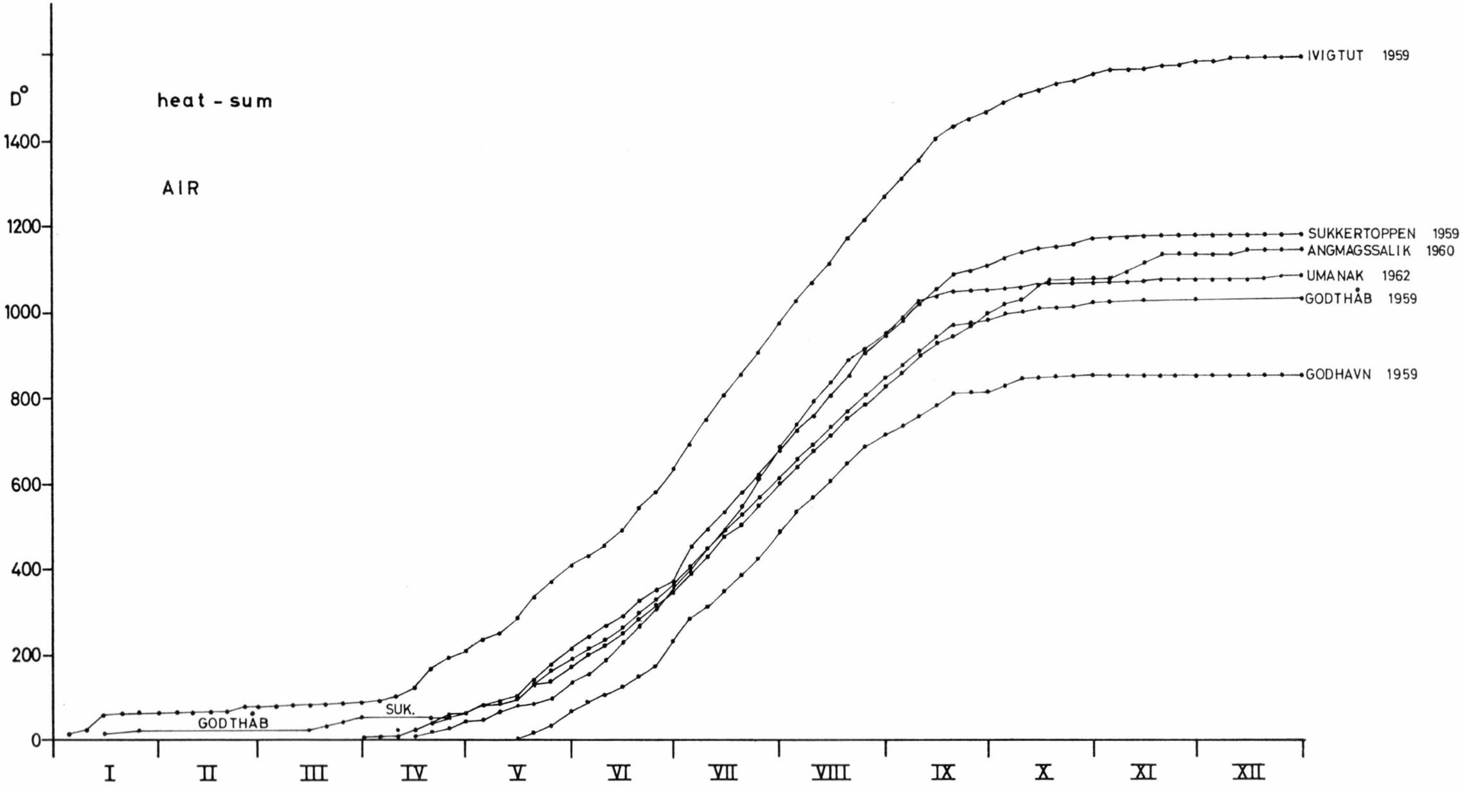


Fig. 9. Heat-sum for the air temperatures.

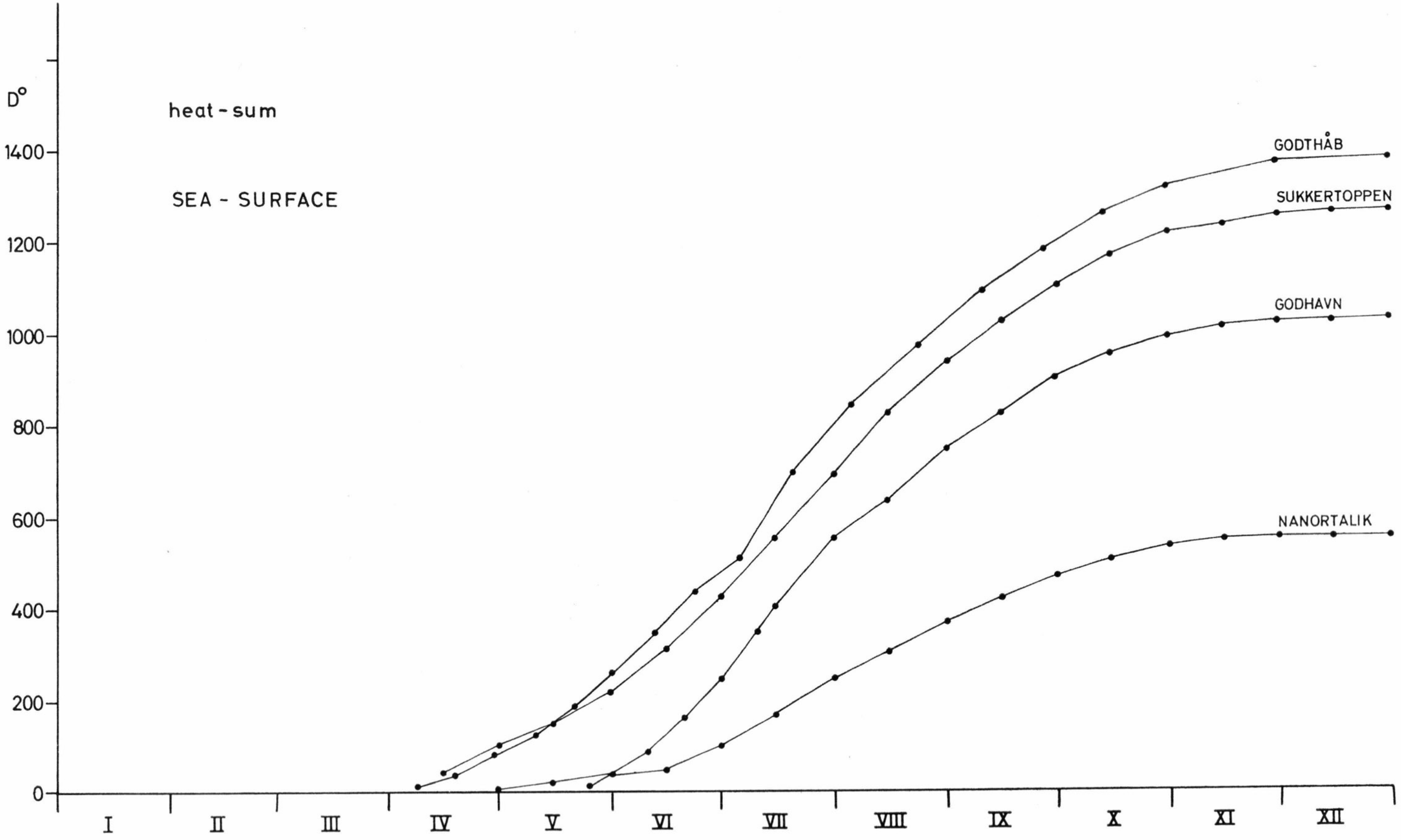


Fig. 10. Heat-sum for the sea-surface temperatures.

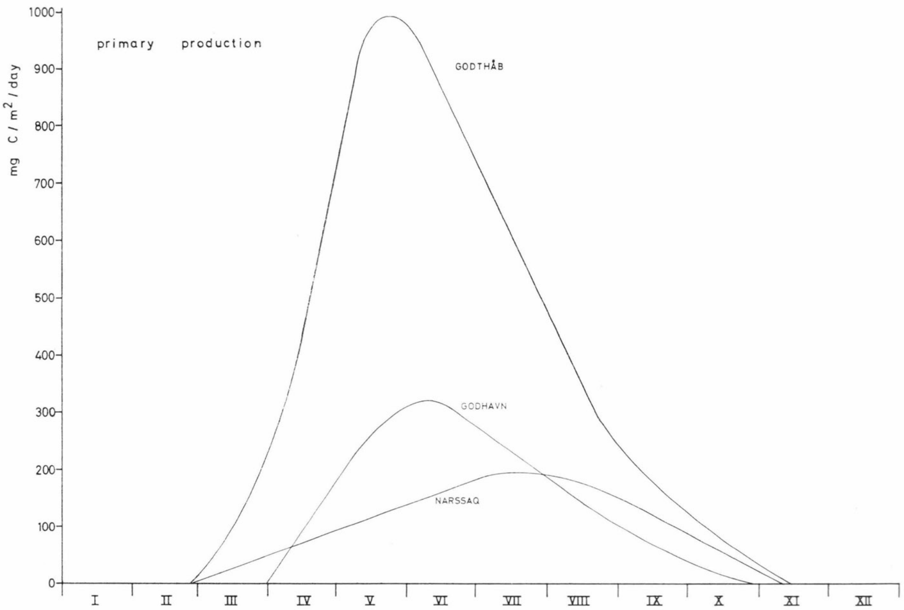


Fig. 11. Primary production for the stations in Greenland where experiments are carried out.

The measurements of the primary production at Godhavn are published in Petersen (1964).

We have no measurements from the Angmagssalik district or from the districts north of Godhavn, but it is probable that the production at Angmagssalik is less than at Narssaq, and that the production in the districts north of Godhavn is less than that at Godhavn.

METHODS

Field methods

According to instructions given to the volunteer helpers the animals were to be collected in an area without freshwater-influx, pollution or heavy surf. One of the conditions was that all the animals had to be found within a rather limited area situated in the middle of the barnacle-zone. They were collected by means of a knife and a forceps. The material was preserved in neutralised formaldehyde and sent to the Arktisk Station, Godhavn, where sorting was carried out. Naturally enough, the greater part of the material consists of *Balanus balanoides* and *Littorina saxatilis* var. *groenlandica*, but additionally, there is a rich material of isopods, worms and halacarids. There is also a smaller material of *Mytilus edulis*, *Acmœa testudinalis* and other less important animals from Greenland's tidal zone.

It was not possible to obtain any quantitative information from this material. Owing to the fact that the Greenland tidal-zone animals are very particular in their choice of habitation, quantitative collections are difficult to carry out. Moreover, for *B. balanoides* any quantitative information might be of dubious value, being only a measure of the fastidiousness of the cypris or of the size of the adult animals. In Godhavn, the author attempted quantitative collections by means of a small rope ladder placed on the cliffs at right angles to the low water line, and reaching up above high water line. Each square between the steps covered an area of 100 cm^2. This method had to be abandoned, as in order to obtain a reasonable figures of quantitative value, so many counts on so many shores and cliffs had to be undertaken that it was outside the scope of the present programme.

Laboratory methods

Size measurement

For the purposes of this paper a total of about 9,000 *B. balanoides* have been measured and determined as to gonad development and age. Moreover, a few samples from less important localities or dates have been investigated for cypris or nauplia.

The length of scutum is considered to be the best means of measuring the individual animal. The main reason for this is that the scutum is always present, whereas other measuring means, e. g. total-length, height, volume, weight, cannot be obtained from all the animals in a sample because animals can be somewhat damaged during actual collection.

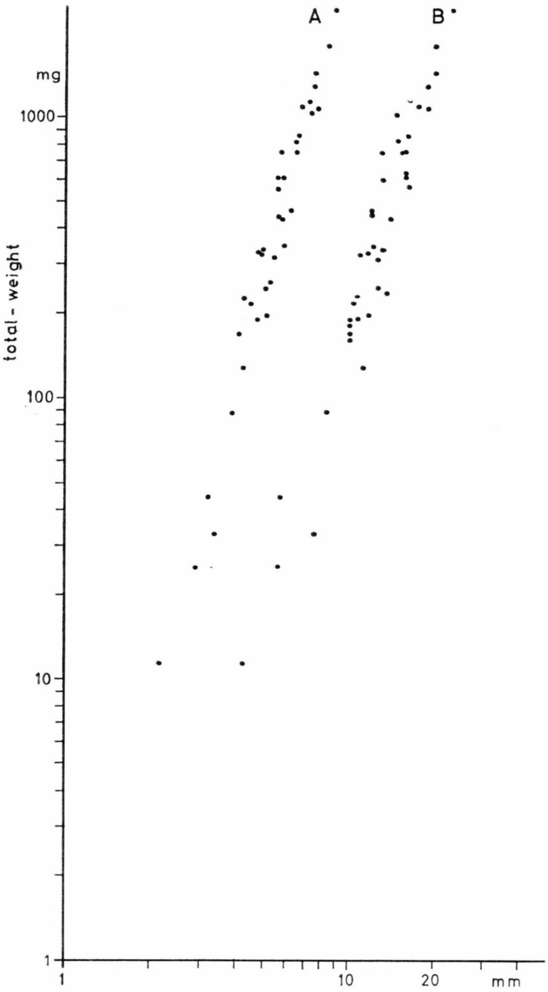


Fig. 12. Total weight related to scutum length (A) and total length of base (B).

Another reason for using the scutum length appears from fig. 12. For a series of undamaged, normally shaped, animals, individual measurements of total-length (carino-rostral-length), scutum-length, weight of shells and of soft-parts were made. The total-length was measured by a venier caliper. The scutum-length was measured by an eye-piece micrometre. Before being weighed, the shells and soft parts were separated and these parts treated separately. They were dried on filter-paper;

for the soft-parts the superfluous water only was dried away. The weight of the animals is calculated as the sum of the shell-weight and the weight of the soft parts.

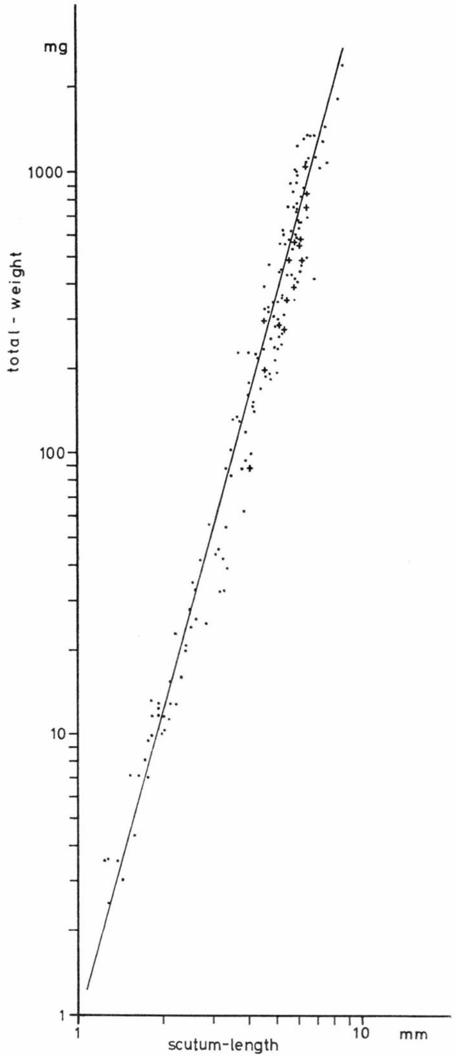


Fig. 13. Scutum length related to total weight. Dots: barnacles with a normal shape. Crosses: barnacles with an elongated shape.

Each animal is represented by two dots in fig. 12. The weight of each animal is given both per total-length of base and per scutum-length. It is immediately obvious from the figure that scutum-length is a better measure for the size of the animals than total-length.

For the majority of undamaged animals, scutum-length and weight were measured, but not the total-length. The result is shown in fig. 13,

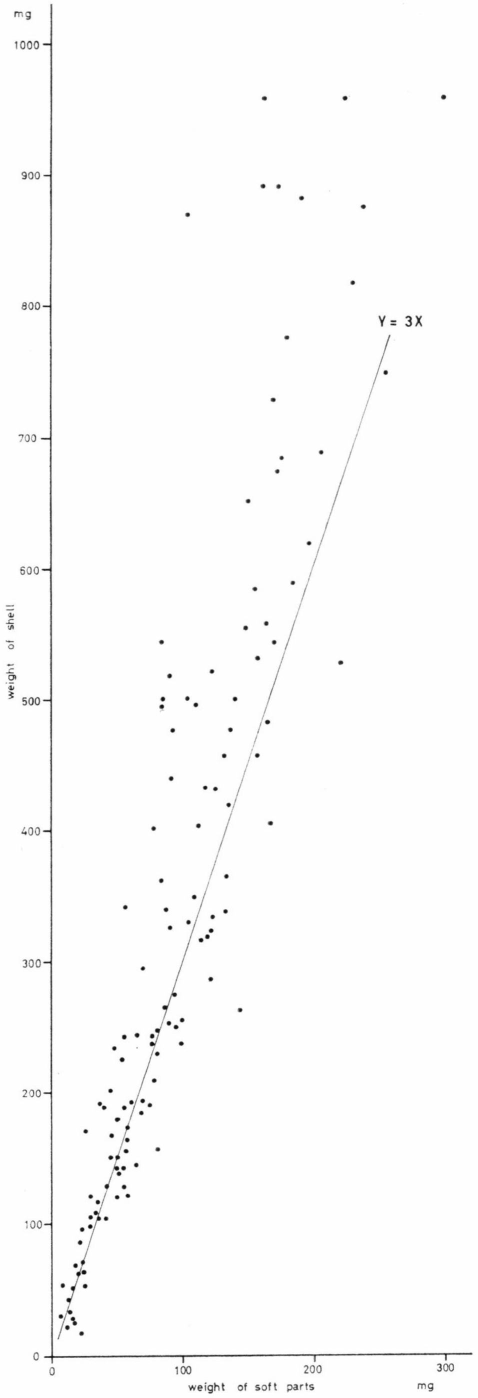


Fig. 14. Weight of shells related to weight of soft parts.

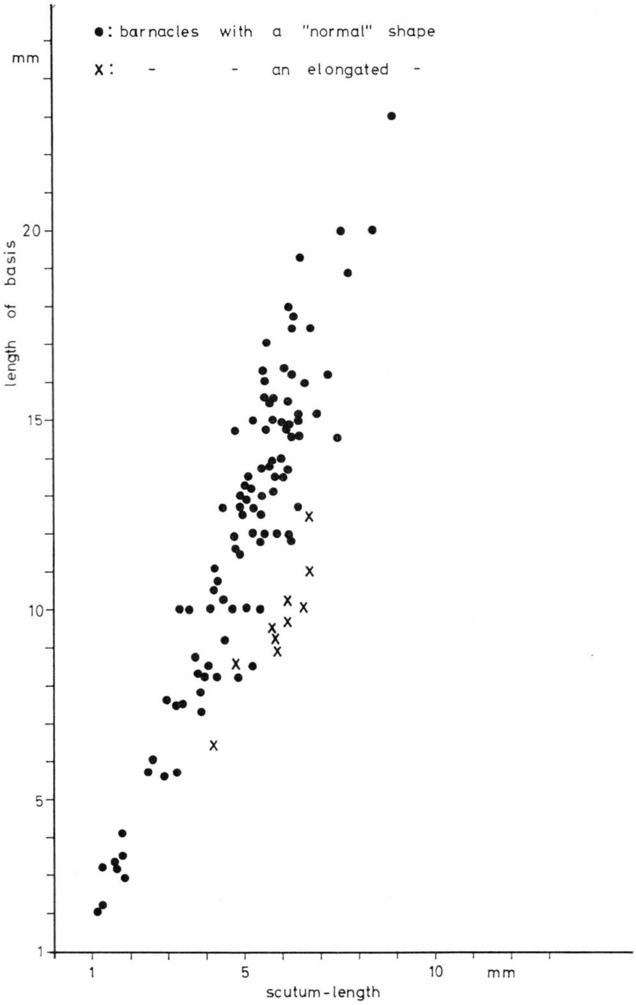


Fig. 15. Scutum length related to total length (carino rostral length) for the two types of barnacles.

where, in addition, the material is divided into normally shaped animals and extremely elongated animals. The regression-equation for normally shaped animals is: $\log W = 3{,}65 \cdot \log l - 0{,}08$. Isometric growth gives length the exponent 3. For practical purposes the exponent 3,65 will indicate an almost isometric growth.

The majority of the animals in all the samples were of normal shape, but as shown by fig. 13 scutum-length is also a good measure for the elongated animals. Of course it is to be expected that there should be a constant relation between the size of the soft parts and the size of scutum, as both are related to the size of the orifice between the wall-plates.

Moreover, the shells of the more elongated animals seem to be more delicately built, and the channels in the plates rarely filled with chalk.

The animals are heavier in the autumn, when the gonads are fully developed, than at any other time of the year (Barnes, Barnes & Finlayson 1963a). For present measurements, only animals with fully developed gonads are used; thus, the weight of the soft parts represents the maximum seasonal weight.

Fig. 14 gives the relation of shell-weight to weight of soft parts. An eye-fitted line shows that the shells weigh approximately three times as much as the soft parts. The shells also contain some organic matter. In order to give the proportion of chalk, water and organic matter, the following analyses were made. From some older animals shells and soft parts were kept apart. The shells were dried, weighed, treated with acid to remove the chalk and the organic matter, and then dried and weighed again. The soft parts were dried on filter-paper, weighed, and then dried by air, so that almost all the water inside the body evaporated. These rough experiments showed that an old *B. balanoides* with ripe gonads, consists, on an average, of 70 $^0/_0$ chalk, 24 $^0/_0$ water and 6 $^0/_0$ dry organic matter.

Scutum-length might be a good enough measure for the purpose of comparing different populations of *B. balanoides*, but for comparison with other species and for further considerations on metabolism and growth, other measures such as weight of soft parts or content of protein or nucleo-protein, should be employed (Barnes & Barnes 1959d).

The carino-rostral length has been the most commonly used measure for *B. balanoides* in previous papers e. g. (Runnström 1925, Hatton and Fisher-Piette 1932, Feyling-Hanssen 1953, several papers by Barnes, Crisp and co-authors). Moore (1934a) used the volume as a measure and in (1935a) abandoned scutum-length as a measure for *B. hameri*. Barnes, Barnes & Finlayson (1963a) used the weight of scutum. The relation of total length to scutum length is shown in fig. 15.

Age determinations

The shells show different types of growth-rings. The growth-rings on the scutae are usually easy to see, and in this way the age determined. Photo plate I shows various examples of scutae. When the shells were not too corroded, three types of growth-rings could be distinguished.

The winter-rings are as a rule very distinct, and as the growth-zone from the last winter to the collection date normally appears as a white, delicate shell, seasonal growth can be traced, and it can be seen that no false winter-rings are formed during the summer season. Moreover, as the scutum shows a rather isometric growth, the length of the winter-rings can be used as a measure for the size attained during the respective periods.

The moult-rings are rather distinct on the scutae and tergae, and on those parts of the other shells where the opercular plates are hinged.

The number of moult-rings between the winter-rings was noted when the latter were measured. This procedure ensured that the winter-rings were correctly treated, and that any subsequent doubts could be traced. The information obtained from the moult-rings is not fully utilised in this paper. It appeared that the number of moult-rings between two winter-rings on animals of the same size-group, was the same, irrespective of the magnitude of the growth. Thus, an animal with a slow growth has a rather large number of thin moult-rings, while an animal with a rapid growth has relatively few, but broad, moult-rings.

In the growth-zones between the moult-rings there are 8–12 smaller rings. These are difficult to see, and the reasons for the rhythms they indicate, unknown. A theory of their dependence on tidal-periods or day and night could not be verified by preliminary counts. As yet, no further studies have been made on these rings.

On uncorroded scutae the first $^1/_2$ mm of the shell is of a different structure. This part of the shell is thought to be the larval shell because of its size (the cypris is $^1/_2$ mm long) and position. The larval shell is characterized by a uniform, granular structure and a furrow running along the middle. Careful measurements of the larval shell might yield information on geographical variations in the size of the cypris; however, various test-samples show that such variations might not exist. As the larval shell is difficult to measure owing to its small size and the amount of corrosion, the question was abandoned.

Corrosion of scutae

The greatest difficulty when measuring and determining the age of scutae is the corrosion caused by algae burrowing in the shells. Only a small number of the animals were heavily attacked. Animals that could not be determined as to age were listed under the question mark (see plate 3–38), but it was usually possible to distinguish the growth-zone from the last winter-ring to the collection date. The degree of corrosion depends both on the animal's position at the respective localities and on the geographic situation of the localities. Thus, animals on an exposed shore are almost never corroded, while animals densely placed in fissures are heavily corroded. Moreover, it is the author's impression that *B. balanoides* on the cliffs at Bergen, Bangor, Plymouth and Roscoff, are more corroded than the Greenland animals.

Of course, the older animals are more corroded than the young ones. In some samples it appeared that the algae-attack occurred during a rather short period in the summer, and that the corrosion did not spread to the new shell which grew after the "attack-period". The corrosion affects only living shells, not dead ones. Schäfer's results (1938), support these observations. Parke and Moore (1935) made a study of the algae that attack shells in England.

Green halacarids were present in most samples; these were found in great numbers in the fissures between the barnacle-shells, and the present author presumes that they suck the algae out of the shells. According to descriptions in Motas (1961), these animals are tentatively determined to *Rhombognathus seahami* (Hodge).

The broken scutae

When making measurements the author frequently found scutae that had been broken and had afterwards grown together. Plate I shows examples of this condition. As it was not expected that broken scutae would be encountered when plans were being made for treating the material, several stations were worked up before the number of broken scutae in each sample was noted. This is given in percentage in the tables in plates 3–38.

In the beginning these broken scutae were considered to be the result of occasional accidents, but it soon became evident that this was not the sole explanation. Out of the 10 calcareous barnacle plates it was always only the scutae that were broken; usually only one, but both might be broken. Some of the scutae had been broken on two different occasions. It was evident that only a hard pointed object, piercing right down into the orifice, could make such damage. The only possibility is that birds e. g., the turnstone (*Arenaria interpres* (L.)), or the purple sandpiper (*Calidris maritima* (Brünnich)) or the ringed plover (*Charadrius hiaticula* L.), which are all common to the area (Salomonsen and Gitz-Johansen 1950), hack the barnacles out of the shells. It seems that some of the animals escape their fate; only the lid-plates are damaged and these later grow together again.

The present author has not made observations on birds in the tidal-zone, but Hørring (1926, p. 165) mentions that the turnstone hacks barnacles off the stones.

It can be considered fairly obvious that only a few of the barnacles exposed to this kind of attack will survive. With this in mind, it is remarkable that such a high percentage of the population, from 2–10 %, exhibit damage of this nature.

Moreover, these figures are only minimum estimations as some of the damage is not seen until measurements are made under the micro-scope. Some damaged animals will, therefore, not be listed, when only an undamaged scutum is used for measuring. The yearly mortality from bird predation cannot be estimated from these percentages, as the latter are the result of several years predation. However, bird predation must have an important bearing on the barnacle-population.

It appears that no false winter rings occur as a result of the damage.

Gonad-development

Gonad-development during the season was studied by classifying the gonads into five stages from "no gonads visible" to "gonads fully developed". In the figures and the plates these stages are reduced to three. Moreover, a character is given for the ovary and testes, when these are emptied. It is difficult to pluck the barnacles off the cliffs without damaging them; therefore, any information concerning the content of larvae is unreliable. The same could be said of the ovaries, but as the base is thick, and often has chalk precipitations during the period when the gonads develop, the ovary will remain attached to the animal. Taking everything into account, it was usually possible to determine the development of the ovary but, unfortunately, it was not found possible to give an exact determination of the hatching period.

The testes are easy to classify, but it appears that they are not so cleanly emptied during fertilization as the ovaries. It seems that the testes degenerate some time after copulation, at the time they are classified as being "empty". This explains why the testes "finish the season later" than the ovaries.

The penis is also easy to classify. Normally, the fully developed penis is shed by a moult after copulation, before the winter. In some of the spring samples from Umanak, animals with a long, slender penis were found; it was obvious that these had been used during fertilization in the preceeding autumn, but the animals had not managed to moult before winter.

The gonad-stages were erected during the preliminary stay in Greenland when the author had no access to the literature. Nevertheless, the stages correspond fairly well with those used in similar works, e. g., Crisp and Patel (1961).

RESULTS

Survey of the material

The tables on plates 2–38 show the material in partly treated form.

Firstly, for each sample is given the locality, date and the percentage of broken scutae. Next comes a diagram giving the complete material, arranged according to age and size. The next diagram gives the relative size-distribution for juvenile and adult animals respectively. Each of these groups is treated separately, so that each add up to 100 %.

The last three diagrams give the development for ovary, testes and penis, according to the size of the animal. It appears that the largest animals are the most developed. Great care has been taken to ensure that the size of the gonad has not influenced the evaluation of the gonad stage.

The survival of the first winter is of great importance in gonad development as the O.-gr. animals seldom have developed gonads and never fully developed gonads, even though these animals are as big as older animals that might be fertilized.

From the penis-diagram it appears that the largest animals are the first to slough off the penis in autumn, and in this case there is no possibility that the stage has been estimated wrongly.

It is possible from these tables to obtain an impression of the differences in gonad development in the different localities, but this is treated more thoroughly in the following chapters.

Fecundity

Fig. 16 shows the number of eggs according to the scutum-length. The egg-number is calculated from counts on a small part, i. e., one quarter or one tenth of the egg-masses. The normal-shaped animals tend to contain more eggs than the extremely elongated ones. This is in accordance with the observation that the normal-shaped animals have a space between the wall-plates (not conically shaped, as the external shape indicates), composed of a lower chamber from which a funnel-like tube leads to the opening. Within the chamber there is space for the egg-masses, and inside the tube there is space for the greater part of the body see also GUTMANN (1960). The elongated forms do not have a similar egg-chamber. The egg-number is linearly related to volume, as a plot against l^3 has shown (not figured here).

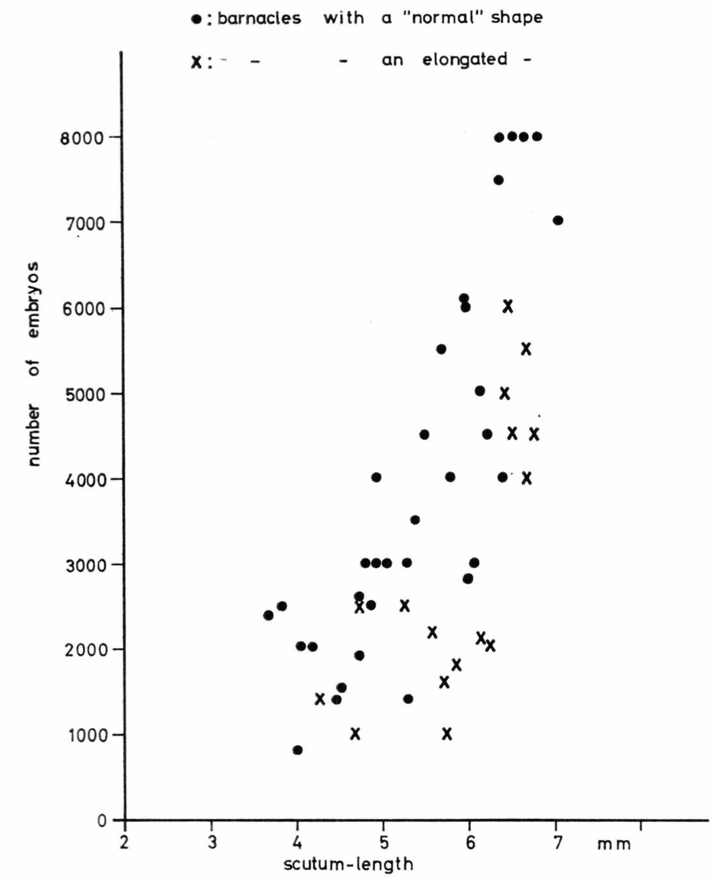


Fig. 16. Number of embryos in the animals related to size for the two types of barnacles.

Age-distribution

From the age-distribution it is possible to obtain a picture of samples taken from the same place. Figs. 17–24 give the age-distribution, with the O.-gr. animals omitted. Owing to the gregarious nature of these creatures, great differences in age-distribution in populations close to each other can be found. We know that the samples from Godhavn are taken within a small area, about 2 m² in each level, and moreover, the diagrams for Godhavn M.W.M. 1959 & 1960, plate 11–17, show that age-distribution can change radically from one year to the next. With this in mind the samples from the other towns seem also to be taken from a smaller area at the same level all through the season.

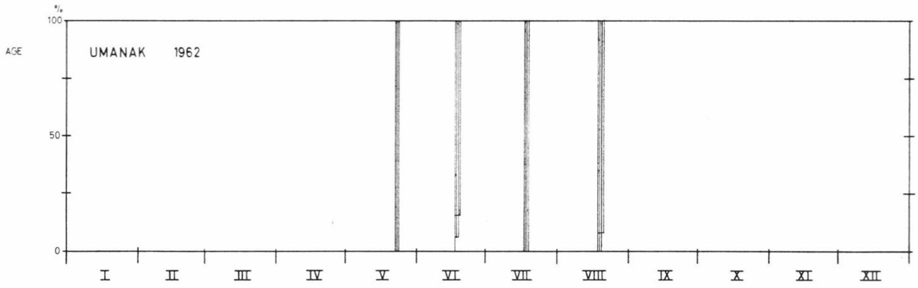


Fig. 17. Age distribution in the individual samples during the season. 0.-gr. animals omitted from the calculations.

One vertical line gives the percentage of I-gr.
two vertical lines give the percentage of II-gr.
three vertical lines give the percentage of III-gr.
four vertical lines give the percentage of IV-gr. and older.

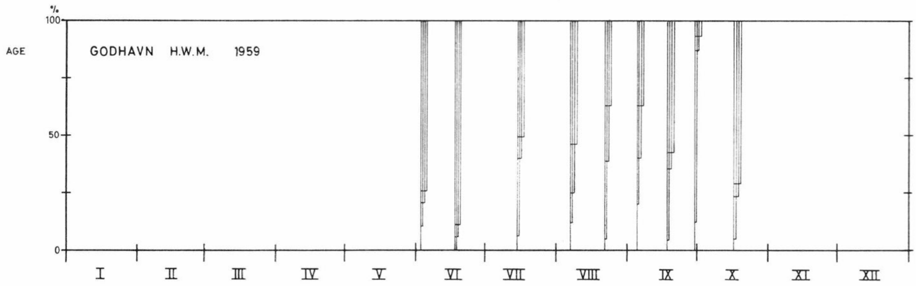


Fig. 18. Text see fig. 17.

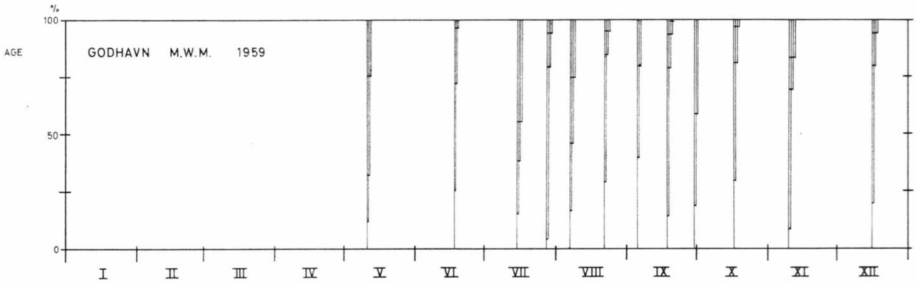


Fig. 19. Text see fig. 17.

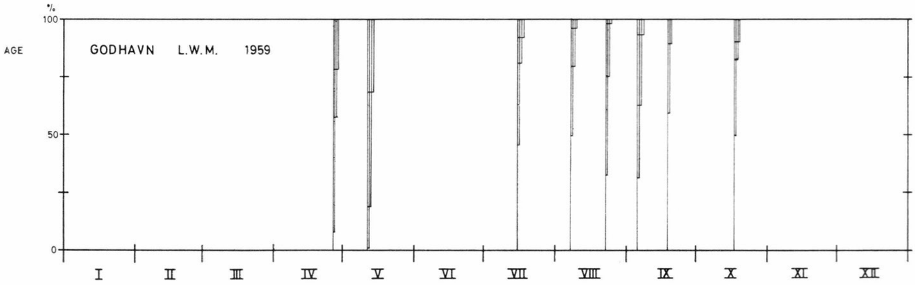


Fig. 20. Text see fig. 17.

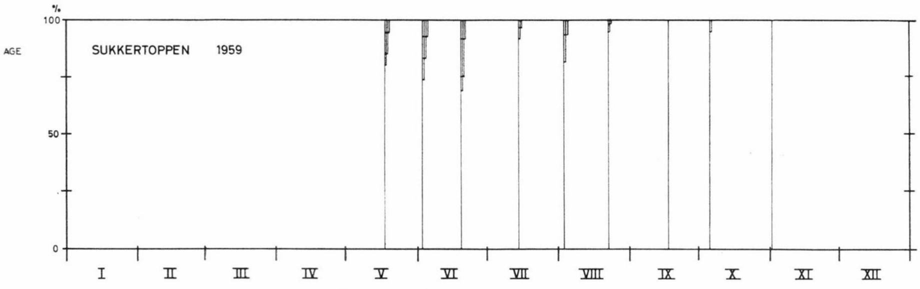


Fig. 21. Text see fig. 17.

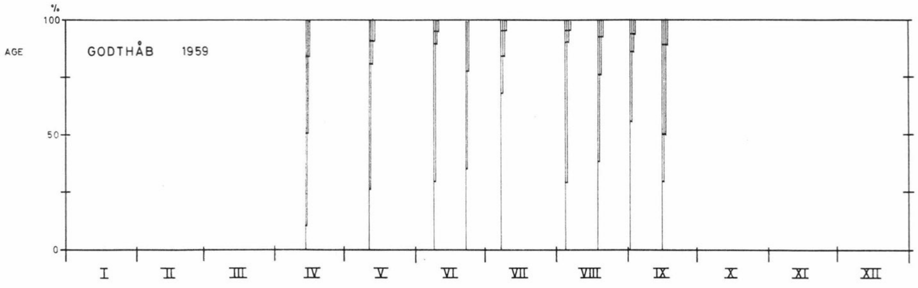


Fig. 22. Text see fig. 17.

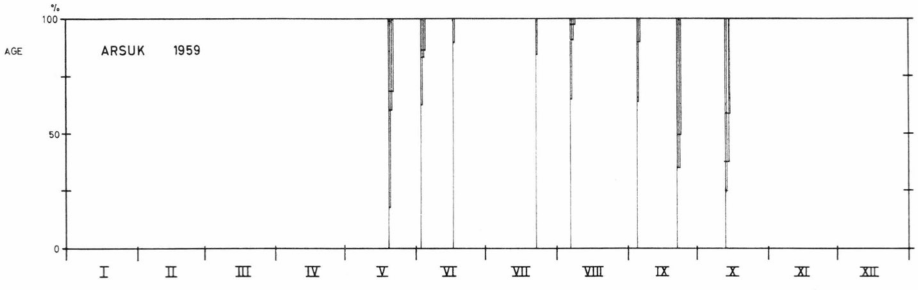


Fig. 23. Text see fig. 17.

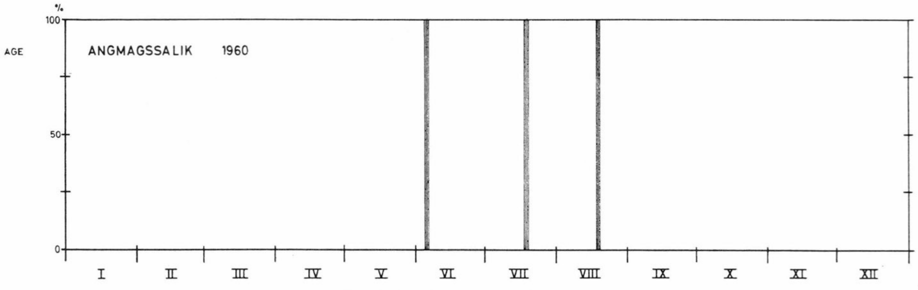


Fig. 24. Text see fig. 17.

The diagrams too show that the younger animals dominate the samples from the southern stations and at the lower levels.

The material cannot be used for calculation of mortality, as the recruitment varies so much from one year to another.

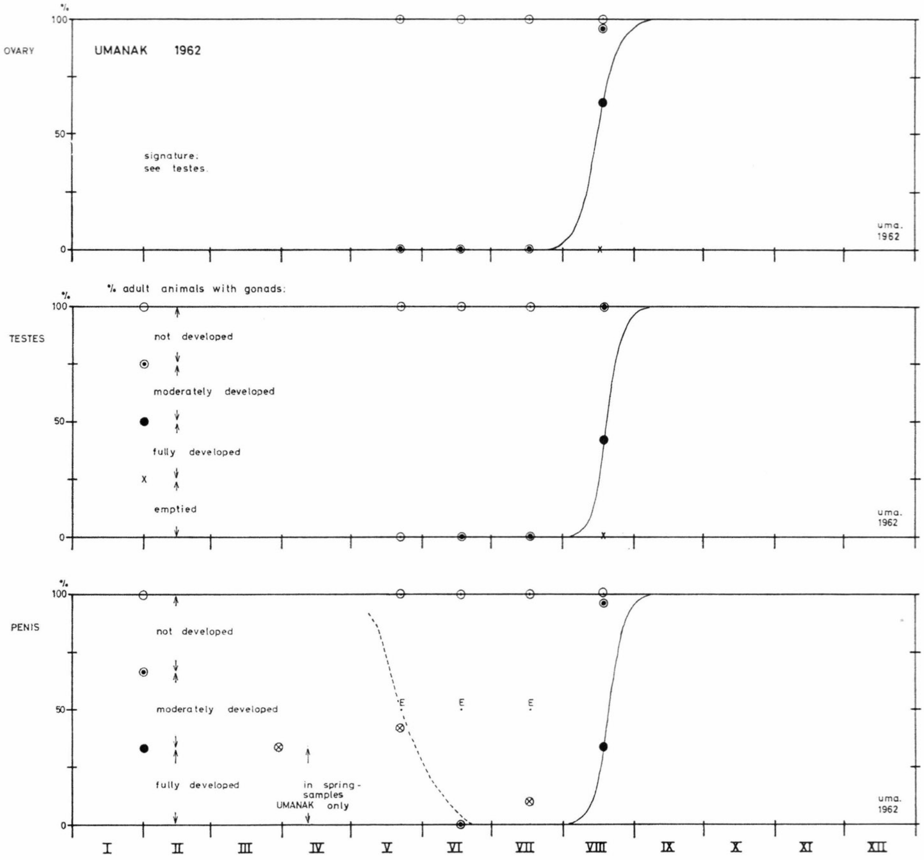


Fig. 25. Gonad development in Umanak 1962.

Figs. 25–32. The diagrams give the proportions of adult animals irrespective of size in the different stages of gonad development. Samples in which embryos fertilized in the preceding autumn are found (E), and samples in which cypris ready for attachment are found (C) are noted on the penis diagram. Estimated cumultative curves for the ripening of the gonads and the shedding of the penis are drawn.

Sexual cycle

The sequence of the sexual cycle in the calendar-year is indicated in figs. 3–8 and 33, by the larval period and the copulation period.

The duration of the larval period is estimated to be the period from the climax of hatching to the climax of settling. This method presupposes that the settling larvae originate from the local population without transport of larvae to or from the area. This supposition is not always correct, as will be shown on page 49.

An estimate of the sexual cycle is made first on the Godhavn material, which consists both of the direct observations in the field, and

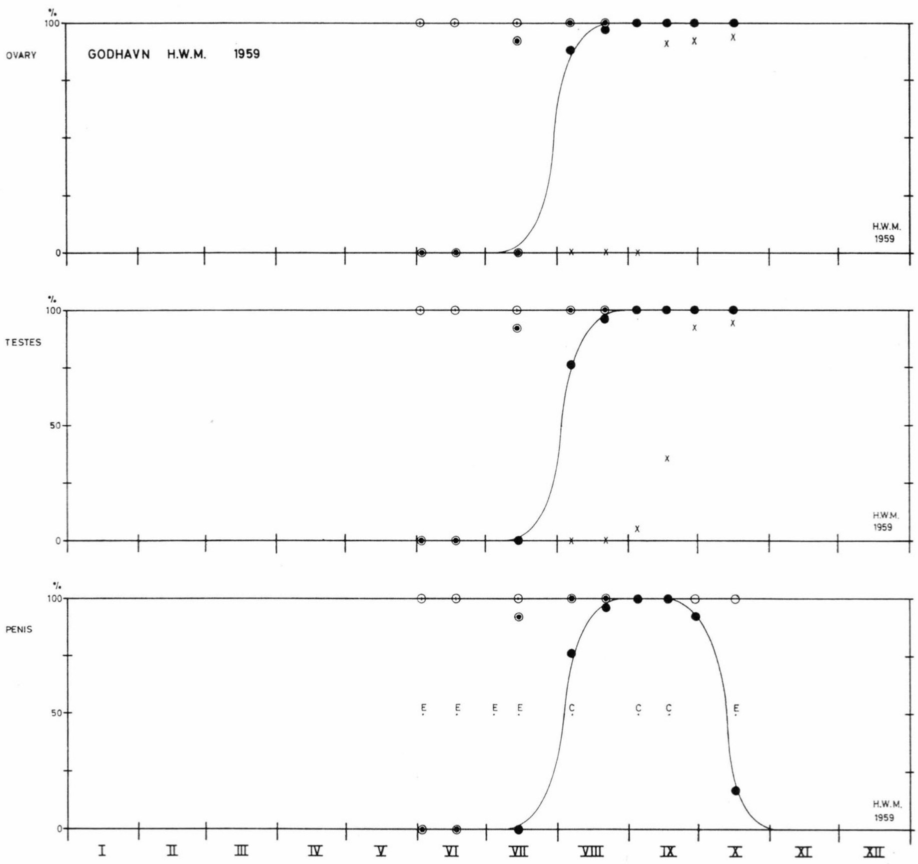


Fig. 26. Gonad development in Godhavn H.W.M. 1959. Explanation see fig. 25.

of the indirect results obtained from figs. 26–28. For the other localities, the indirect results in figs. 25 and 29–32 are the only basis for the estimate.

Hatching period

Direct observation material from Godhavn is best given in the form of the following extracts from the journal. For the localities mentioned see Petersen (1962).

25.2.1960: Investigation of the ice-foot at Udkiggen. The ice-foot stands in a perpendicular position. The lowest barnacles are not covered by the ice-foot. Both barnacles and mytilus were observed above sea-level. Collection impossible.

12.3.1960: On a skerry off Udkiggen some barnacles and mytilids were collected in a zone between the ice-foot and sea-level. The barnacles contained embryos.

12.4.1960: Skerry off Udkiggen. The animals in the lower part of the tidal-zone not covered by the ice-foot.

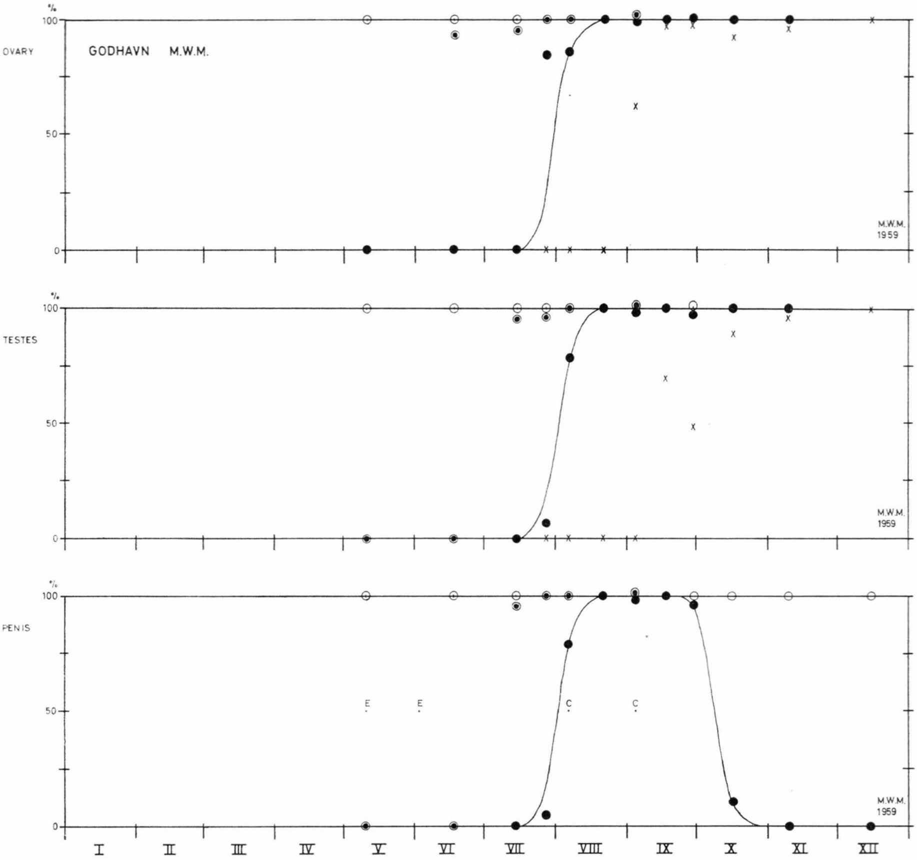


Fig. 27. Gonad development in Godhavn M.W.M. 1959. Explanation see fig. 25.

22.4.1959: Skerry at Udkiggen. The sea-ice disappeared from this cliff around 10.4. The ice-foot permitted collection only at low-water mark. The barnacles had naupliae.

23.4.1960: Skerry at Radionæsset. The sea-ice disappeared from the cliff around 15.4. Owing to the ice-foot only animals near L.W.M. were collected. The barnacles had naupliae.

25.4.1959: Skerry in the entrance to the harbour. The 2,5 m thick ice-foot was blown away with explosives. Animals collected from beneath the ice. The barnacles had naupliae.

6.5.1960: Skerry at Udkiggen. Most of the barnacles had liberated the embryos but some of the uppermost animals still had naupliae. The very uppermost animals were inaccessible owing to the ice-foot. Dried-up animals closed their lids when touched with the pincers.

8.5.1960. Skerry in Kirkegårdsbugt. Barnacles at L.W.M. had hatched.

10.5.1959: Skerry in the entrance to the harbour. Barnacles at L.W.M. hatched, while barnacles at M.W.M. still had naupliae. The ice-foot covered the uppermost barnacles.

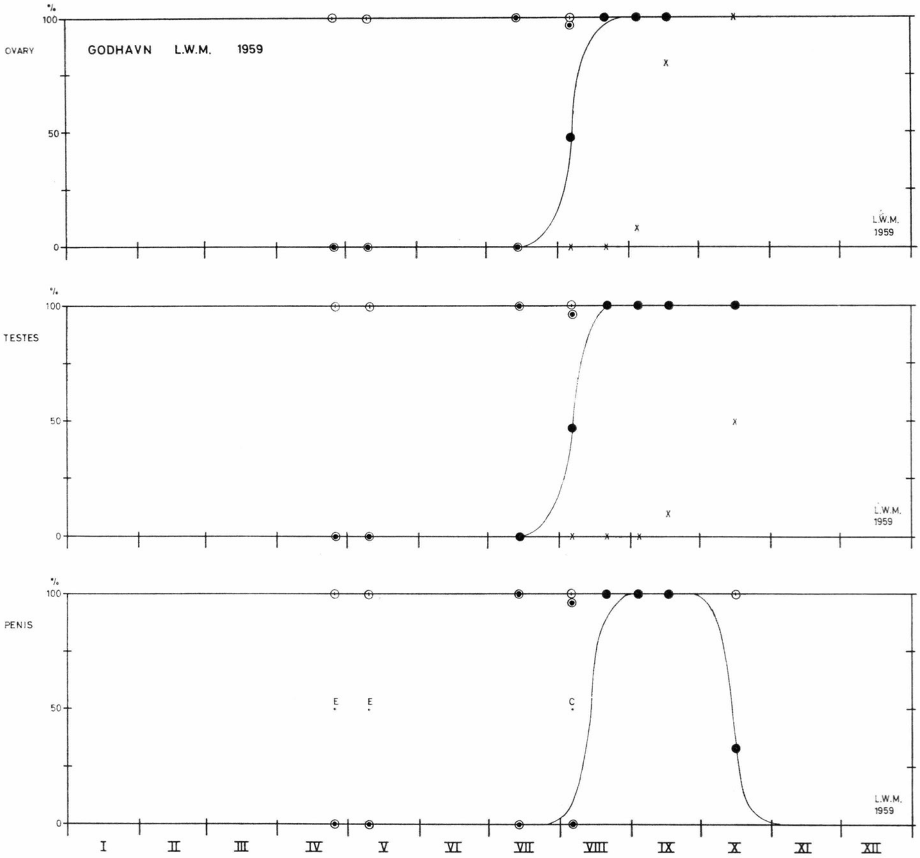


Fig. 28. Gonad development in Godhavn L.W.M. 1959. Explanation see fig. 25.

20.5.1959: The rocks beside Dog Food Rack. Animals from H.W.M. were collected after the ice foot had been exploded. Barnacles at H.W.M. had naupliae.

14.7.1959: Skerry in the Harbour Entrance, H.W.M. One barnacle of 173 still had naupliae, together with developing gonads. The ice-foot disappeared from this locality about one month earlier.

16.10.1959: Skerry in the Harbour Entrance, H.W.M. In one barnacle dark-brown egg-masses were found, with fully developed naupliae. Above these, was another pair of egg-masses with recently fertilised eggs of a light yellow colour, comparable to the egg-masses usually found in the sample.

These last two examples tend to show that some animals poorly placed in the tidal-zone can exhibit an abnormal sexual cycle, supposedly because various hatching-factors have not been present in sufficient amounts.

Information, from which the hatching-period is estimated for localities other than Godhavn, consists only on observing whether

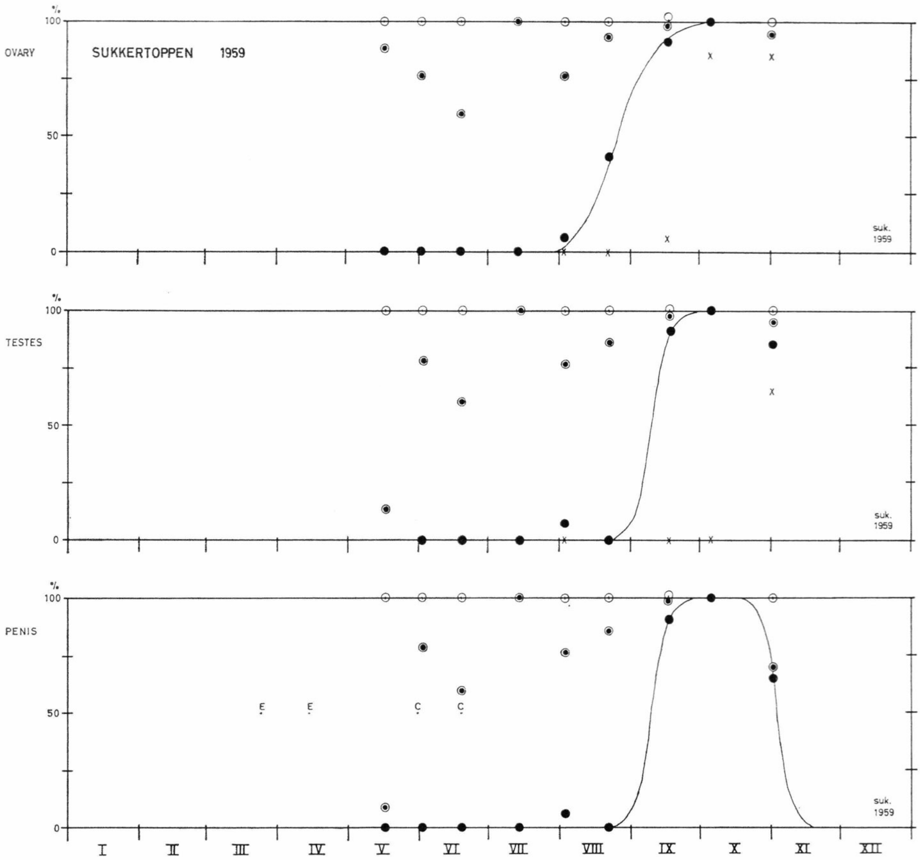


Fig. 29. Gonad development in Sukkertoppen 1959. Explanation see fig. 25.

naupliae are present in the glass-jar or not. A direct comparison between the condition of the samples from the different localities gives further information. Moreover, consideration has been given to the development of the gonads when estimating the hatching-period. In the case of Godhavn, approximately the same estimates of hatching-periods were obtained from both the direct and indirect observations.

Settling period

For Godhavn the settling-period is also estimated both from the direct and indirect observations. The following notes from the journal give the direct observations.

27.7.1959: Skerry in the Harbour Entrance. No pinheads.

29.7.1959: Egedesminde Harbour. Settling just started.

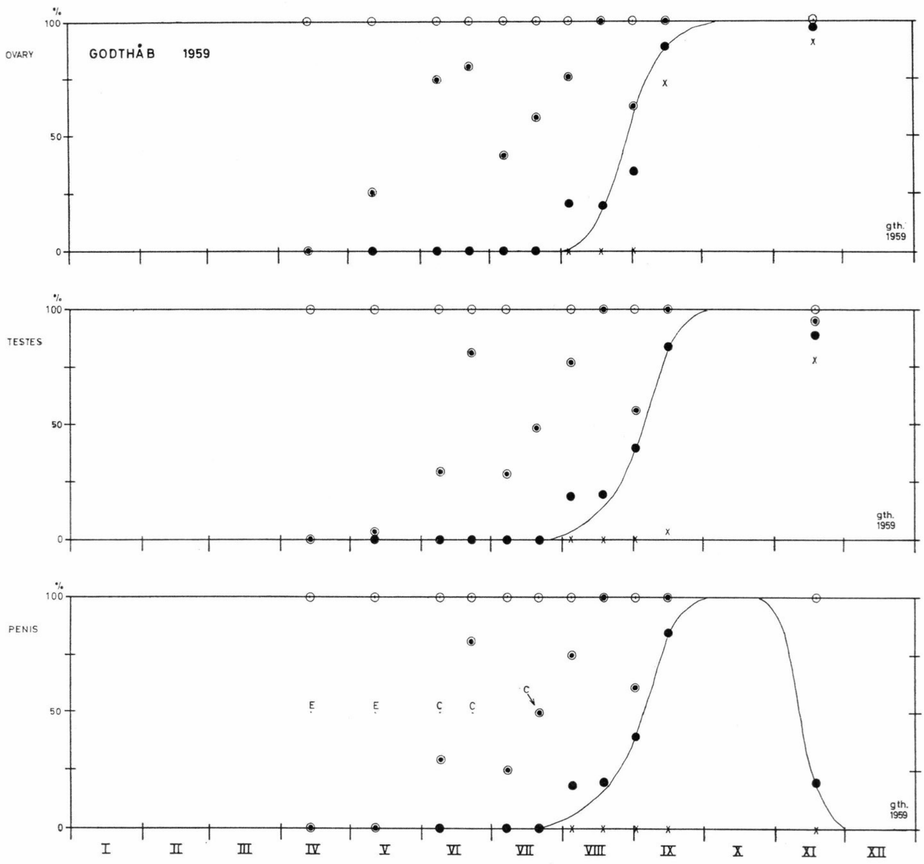


Fig. 30. Gonad development in Godthåb 1959. Explanation see fig. 25.

6.8.1959: Skerry in the Harbour Entrance. Many recently settled barnacles.

6.7.1960: Skerry in the Harbour Entrance. The settling started 3–4 days ago.

Note that settling started one month earlier in the year 1960 than in 1959.

Observations made in the inner part of Disko Bugt, in Atâ Sund (PETERSEN 1964, p. 33), showed that settling in 1960 started about 4 weeks later than at Godhavn. This can be explained either by the more arctic conditions in Atâ Sund or by an early settling at Godhavn of larvae originating from Sukkertoppen districts, see p. 49.

The indirect material comprises samples in which cyprids are found, see fig. 25–32. Moreover, the growth curves for the 0-gr. animals shown in fig. 39–45 are used for the estimate of the settling-period.

For the three levels from Godhavn it appears that settling starts later and finishes earlier at H.W.M. than at L.W.M.

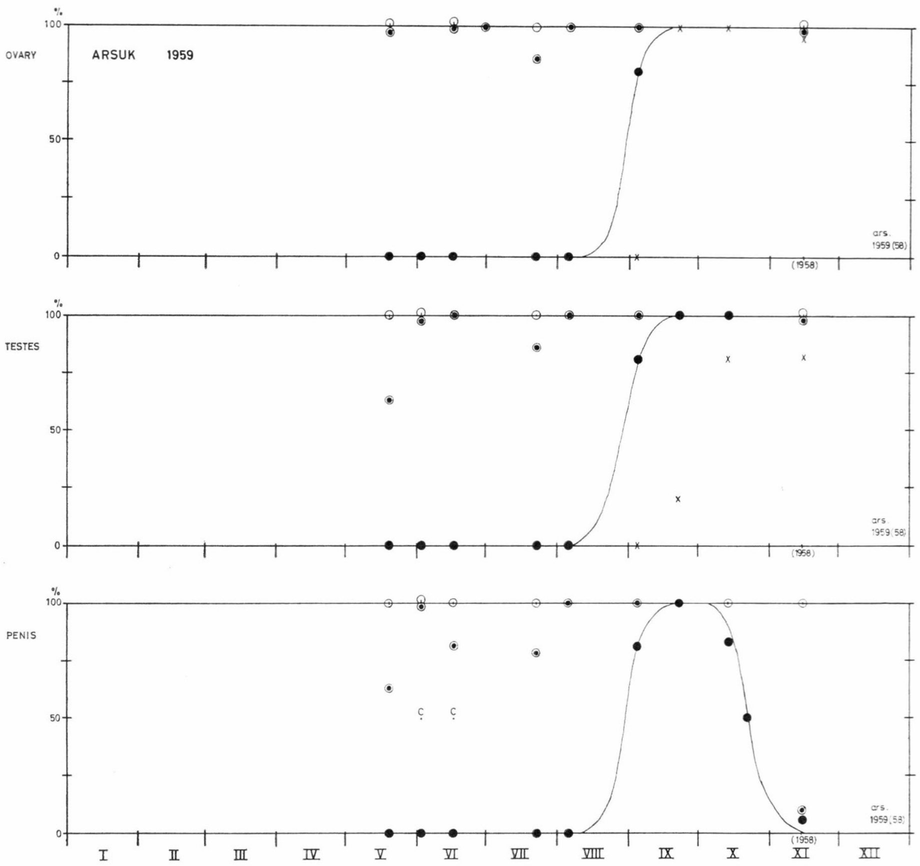


Fig. 31. Gonad development at Arsuk 1959. Explanation see fig. 25.

Material from Angmagssalik does not permit an estimate of the settling-period. Else Steenstrup reports that settling started in Umanak in 1962 in the middle of August. No settling had taken place in Umanak during the present author's visit from 11.8. to 14.8. in the year 1960, but in the samples from Upernavik and Augpilagtoq from 9.8.60, some 0.-gr. animals were found. Settling in the Umanak and Upernavik districts is, therefore, presumed to occur in August, viz., at the same time as in Disko Bugt. In the northern districts, settling may fail in some years.

Copulation period

The copulation-period is given as the period from the date when 50 $^0/_0$ of the population have a fully developed penis to the date when 50 $^0/_0$ have shed the skin with the fully developed penis. These dates can be determined with about 5 days standard deviation. For Umanak and

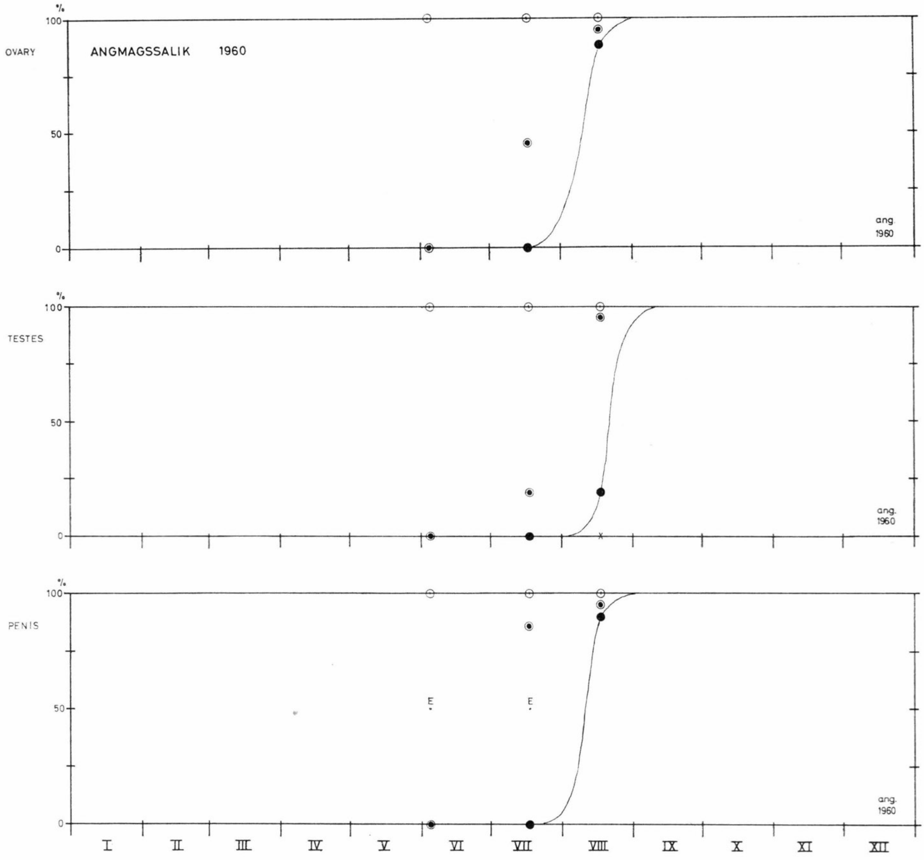


Fig. 32. Gonad development at Angmagssalik 1960. Explanation see fig. 25.

Angmagssalik the date of completion is doubtful. Too few samples are at hand, and some animals may not be able to shed the skin with great penis before the arrival of the winter-ice.

Duration of the embryonic development

The average length of this period can be estimated to be at most the period from the climax of copulation to the freeze-up in the ice-foot, as barnacles from beneath the ice have fully developed naupliae. It is not certain if the eggs reach the nauplius stage before the winter in the populations north of Godhavn. After the completion of the embryonic development there follows a diapause, interrupted by certain hatching-factors.

The technique used by Crisp (1959b) to study the development of embryos was noticed too late to be used in the present study.

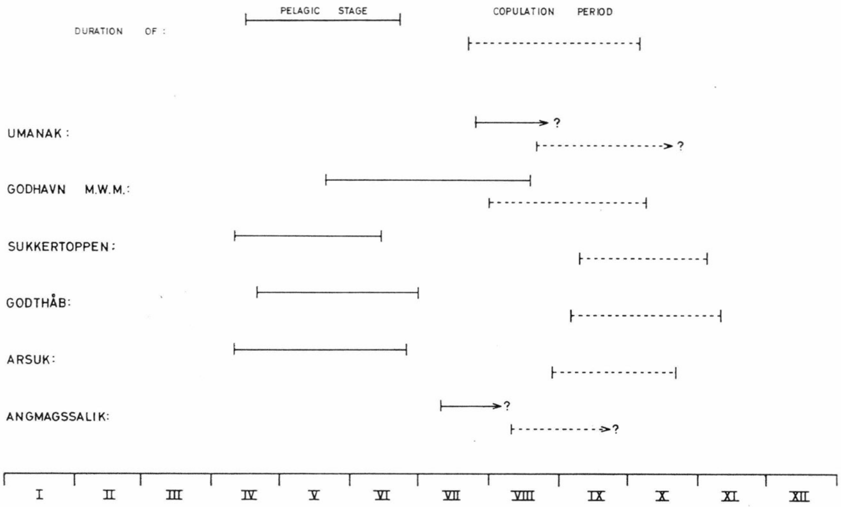


Fig. 33. Comparison between the sexual cycle at the different localities. The sexual cycle is indicated by the duration of the pelagic stage and the copulation period. See figs. 3–8 for relations to climate.

The embryonic development at Godhavn cannot last more than about 60 days. It was found to be about 70 days for the local population in Bangor (Crisp 1964).

In a sample from Umanak, 11.8.60, seven animals out of 80 contained egg-masses with naupliae and fully developed gonads. In the sample-jar from Prøven 10.8.60, there were several naupliae. The naupliae in these two samples originate from eggs fertilised in the preceding autumn. This instance is comparable to that mentioned from Godhavn H.W.M. 16.10.59, on page 35.

Factors acting on the sexual cycle

Hatching

Hatching cannot start before the animals are thawed out of the ice-foot. It is also necessary that the embryonic development is completed. In the northernmost districts part of the embryonic development might take place in the spring, but there is no evidence to support the theory that embryonic development cannot be completed in the northernmost population.

Even when these two first conditions are met, other factors are also necessary for hatching, (see Crisp 1956, 1959c, 1962a, Barnes 1957a). For the present material the following has been noted in relation to hatching factors: – Embryos are hatched in the spring only, even though they are already fully developed by autumn in all localities (except presumably, Umanak, Upernavik and Angmagssalik). Temperatures cannot play an important role for hatching, as the temperature is of almost the same magnitude and has the same variations in the autumn as in the spring. Similarly, amount of light and length of day cannot be of any importance, as a comparison between Sukkertoppen and Angmagssalik (both on the same latitude), will show.

The differences in hatching-time on the levels at Godhavn tend to show a correlation to time of water-coverage and to the date when the animals are thawed from the ice-foot, (note that the latter depends on the former factor). The L.W.M. animals hatch in the first week of May, while the H.W.M. animals hatch in June, or later; some may not hatch at all.

In Umanak, hatching occurred in July 1962, even though the animals, owing to an extraordinarily warm summer, were free of the ice-foot in May. The sea-ice also disappeared in May, indicating a spring-diatom increase during this month.

The hatching factors may be related to the spring diatom increase, as pointed out by BARNES (1962 a). The H.W.M.-population and the northern populations tend to show that the hatching factors act quantitatively and not qualitatively. Certain factors are needed in order to hatch the eggs; these influences can be summed up over a long period when they will be present to some degree, however slight.

The fate of animals forced to contain broods from two years is unknown.

Duration of larval stage

The duration of the larval stage was as follows in the different localities:

Godhavn	90 days
Sukkertoppen	65 days
Godthåb	72 days
Arsuk	76 days

This result agrees well with the geographic situation of the localities, Godhavn being the most arctic, Sukkertoppen the most boreal, and Arsuk, again, having more arctic conditions owing to the East Greenland Current.

As the larval-period occurs at different periods of the year in different places, the author made certain investigations as to whether the duration of the larval stage depends on the "heat-sum". It was presumed that the larvae are in the uppermost layers in all stages as they are photopositive during all the pelagic phases (THORSON 1964). If they spend part of the larval stages in only about 10 m depth, the heat-sum

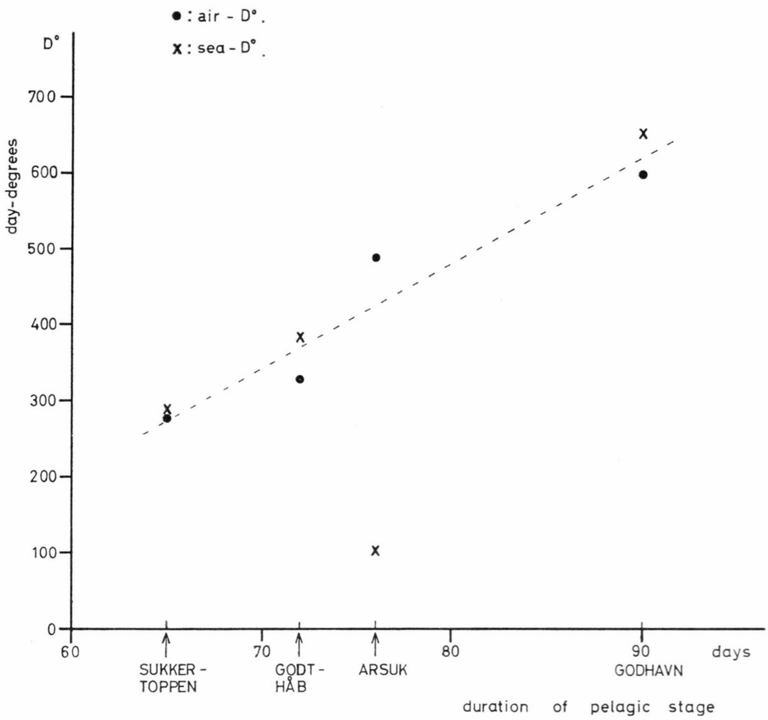


Fig. 34. The heat sum supplied during the pelagic stage related to the duration of the pelagic stage.

will be different, but for purposes of comparison the results are accurate enough. Moreover, only surface temperatures are available to the extent necessary. See p. 15 for calculations of the heat-sum.

Fig. 34 shows the remarkable result that the duration of the planktonic stages were positively correlated with the heat-sum. In this figure the heat-sum is calculated as to the number of day-degrees, D°, obtained from climax of hatching to climax of settling, for both air and sea temperatures. The Arsuk result consists of the Ivigtut and Nanortalik results, and with this in mind, the Arsuk results agree well with the others.

This result is not in accordance with other investigations on the growth-rate and temperatures (e. g. Larsen and Thomsen 1940, Nielsen and Evans 1960, Boëtius 1962, McLaren 1963, Ursin 1963a).

The author concludes that factors other than temperature were important for the growth-rate, see also Ursin (1963b).

Results on the investigations of the influence of primary production are shown in fig. 35. The sum of the primary production during the planktonic stage may be used as a rough measure of food-conditions

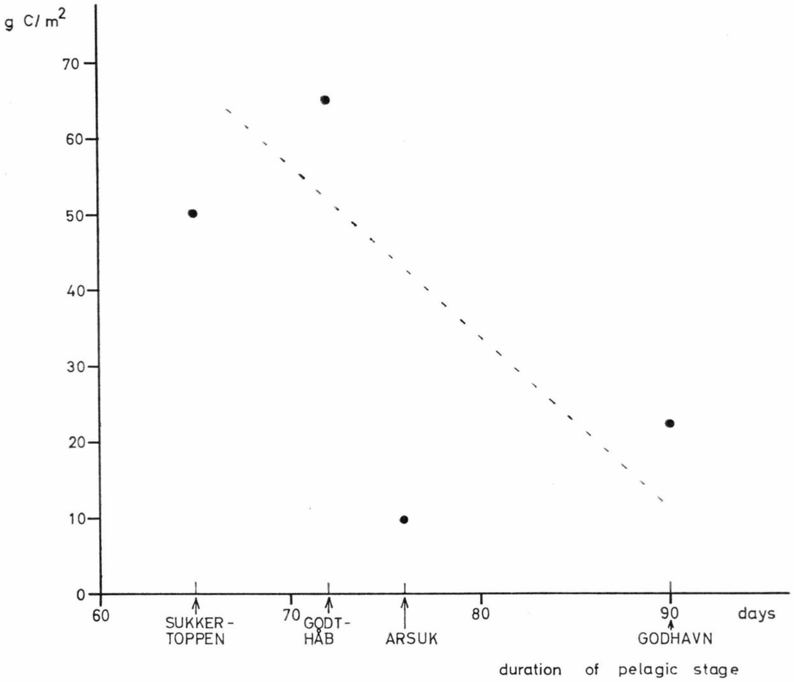


Fig. 35. The primary production supplied during the pelagic stage related to the duration of the pelagic stage.

for pelagic larvae. The relation obtained is reasonable enough, and we must conclude that food is more important for growth rate than temperature.

Settling

When the larval development is accomplished, settling starts, depending on a long row of biological and physical-chemical factors. Many attempts have been made to study these factors more closely, e. g., Knight-Jones (1953 a), Barnes (1956 a), Crisp (1961), Crisp and Meadows (1962).

In the present study the settling period is estimated from the presence of cypris in the samples, and the settling-factors are also considered when giving the results. First of all, the quality of sampling is presumed to be of high and uniform quality (the results show this to be so, in the opinion of the author).

In a previous work (Petersen 1962, p. 29) it was said that *B. balanoides* in Greenland is never found on shells of *Mytilus* and *Littorina*. The statement should be slightly amended, however, as the author has now found this to occur in a few samples from the most boreally marked localities, Sukkertoppen, Godthåb and Arsuk. However, this occurs only occasionally, with only one, two or three *B. balanoides* on a few shells, and never to the same degree of density found on shells from the English and French coasts. From Disko Bugt northwards, the author has never seen shells of *Mytilus* and *Littorina* with *B. balanoides*, either in the field or in the samples (see also SCHÄFER (1952) for a description of the comparable influence of brackish water).

Another geographic variation of settling behaviour is observed from the Greenland samples. In the samples from Disko Bugt northwards, it is extremely rare to find cypris of "pinheads" on the adult *B. balanoides*. In samples from the southern localities (except Angmagssalik), it is more common to find cypris and pinheads on the older animals, but it is still rare to find them on fast-growing O.-gr. and I.-gr. animals (see also PETERSEN (1962) for the variation in population types).

Observations from Godhavn indicate that cypris are more particular in the choice of habitat in the beginning of the settling period than at the end.

The difference in population type between the northern and the southern populations (where the northern animals prefer marine conditions and the southern avoid marine conditions), should be taken into consideration.

Observations mentioned indicate that a geographic variation which might bias the estimate of the settling-season, does exist. Fortunately, direct observations on settling are from the northern station, Godhavn, where it might be expected that the greatest faults occur, if the preserved material only is used as the basis of the results.

Maturation of the gonads

A necessary condition for gonad development is that the Greenland animals have passed the first winter. Sterile animals are rare, and obvious parasitism is never seen. The author has seen animals living under poor growth conditions with undeveloped gonads, but normally, poor food supply does not result in bad gonad development. Growth conditions may have some influence on the course of gonad development; this is seen from the difference between the three levels at Godhavn.

Light- and day-length do not have (as presumed by BARNES (1963b) and CRISP (1959a)), any obvious relation to gonad development; this is seen from the results from Sukkertoppen and Angmagssalik, both situated on approximately the same latitude.

Temperature conditions seem to be the most important factors for gonad development. The building-up of gonads seems to occur during the whole season, while copulation seems to be connected to drops in air-temperature, i. e., below the freezing-point of sea-water.

A mechanism that could be governed by external factors, inducing and syncronizing the internal rhythm, might have the following character:–

The animals' gonad development may be governed by two gonadotrope hormones that counterbalance each other. At a high metabolism, one of them dominates and the gonads are developing. At a lower metabolism the other dominates and copulation starts. Production of the hormones first starts after a period with very low metabolism (the first winter).

The production and the destruction depend on the metabolism, and the rate of the processes are different for the two hormones. The balance between the two hormones depends on the amount of hormones present. This could explain why a certain period of low temperature (and not sudden temperature shock), releases copulation. Whatever the low metabolism is due to, e. g., low temperature (the general factor), poor food-conditions (H.W.M.-animals), internal slow-down (big animals), the hormone that maturates the gonads dominates.

Crisp (1959a), Crisp and Clegg (1960) and Barnes (1963b), have given further evidence regarding the influence of the rate of metabolism on the sexual season.

Size distribution of 0.-gr. and 1st winter ring

This chapter deals with several observations and measurements which have an important bearing on the results in other chapters, but which cannot be treated separately.

Fig. 36 shows the size-distribution of the 1st winter ring measured on I, II, and III-gr. animals from the three levels from Godhavn. These distributions are bimodal or skew. The bimodality is most pronounced in the younger animals (perhaps an effect of Rosa Lee's phenomenon (Ricker 1958)). The size-distribution of the 1st winter ring should correspond with the size-distribution of the 0-.gr. animals collected immediately prior to the arrival of winter. Fig. 37 shows that this is not the case, as the 0.-gr. animals from 16-10-1959 have an approximately normal, and not bimodal distribution.

The author became aware of the heterogeneous quality of the material at an early stage of the measuring activity, as animals with an obviously large 1st winter ring were characterized by a rapid rate of growth during the 1st season and a fine, uncorroded shell. It was easy enough to measure the larval shell and count the number of moult-rings from the larval shell to the 1st winter ring. There is no liklihood that the second winter ring was erroneously counted as the first winter ring; moreover, this would not explain the bimodality.

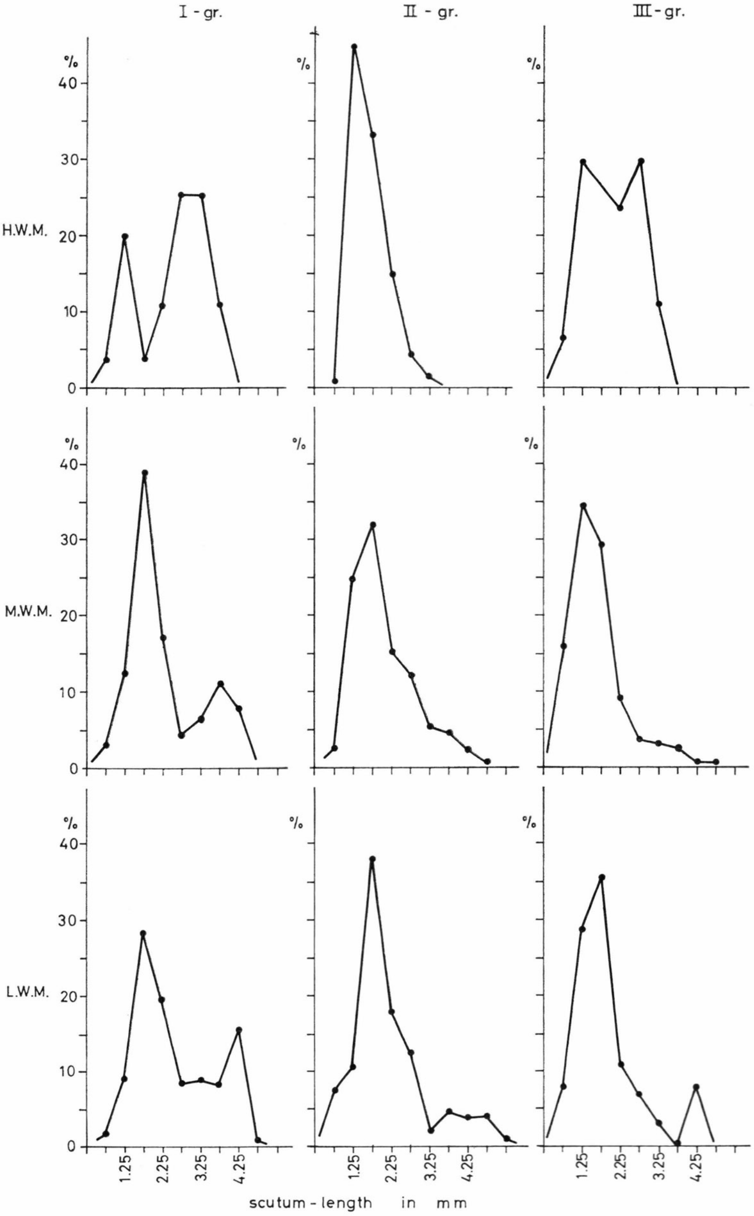


Fig. 36. Size-distribution of the 1st winter ring for age groups I, II, III, from the three levels at Godhavn 1959.

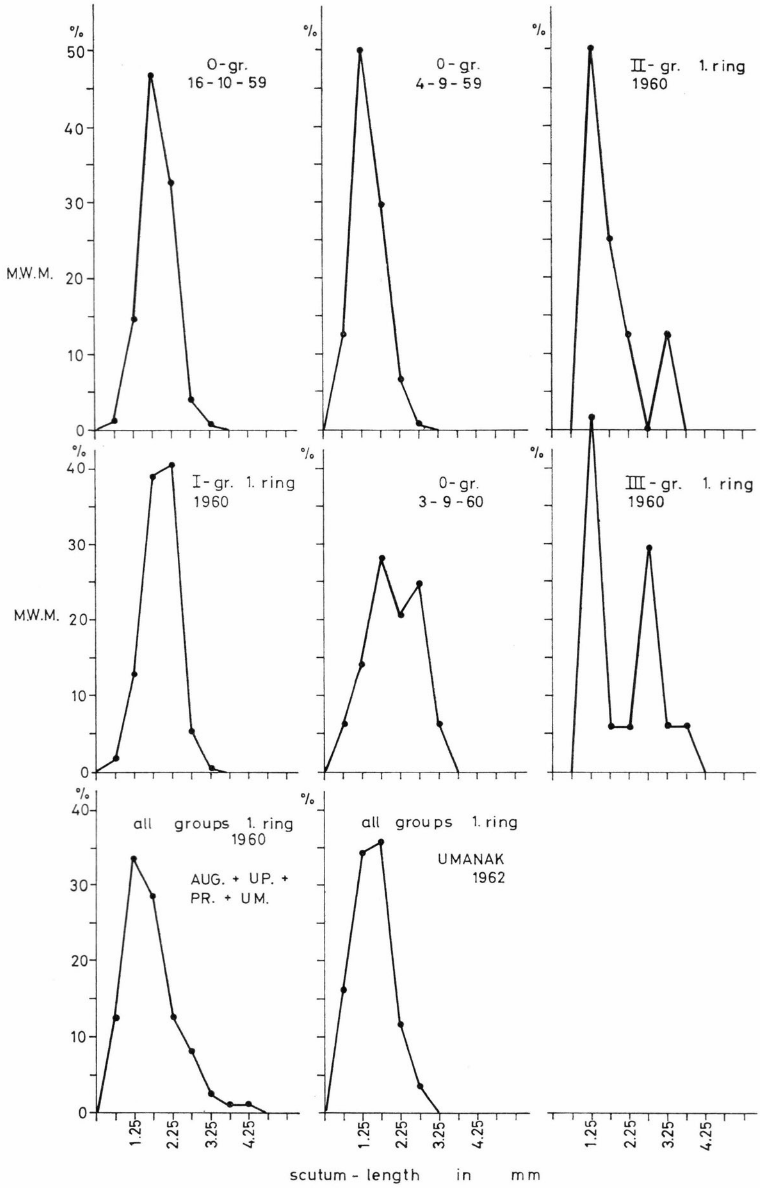


Fig. 37. Size distribution of total length of 0.-gr. compared to the size distribution of the 1st winter ring. The six upper diagrams are all from Godhavn M.W.M. Aug.: Augpilagtoq, Up.: Upernavik, Pr.: Prøven, Um.: Umanak.

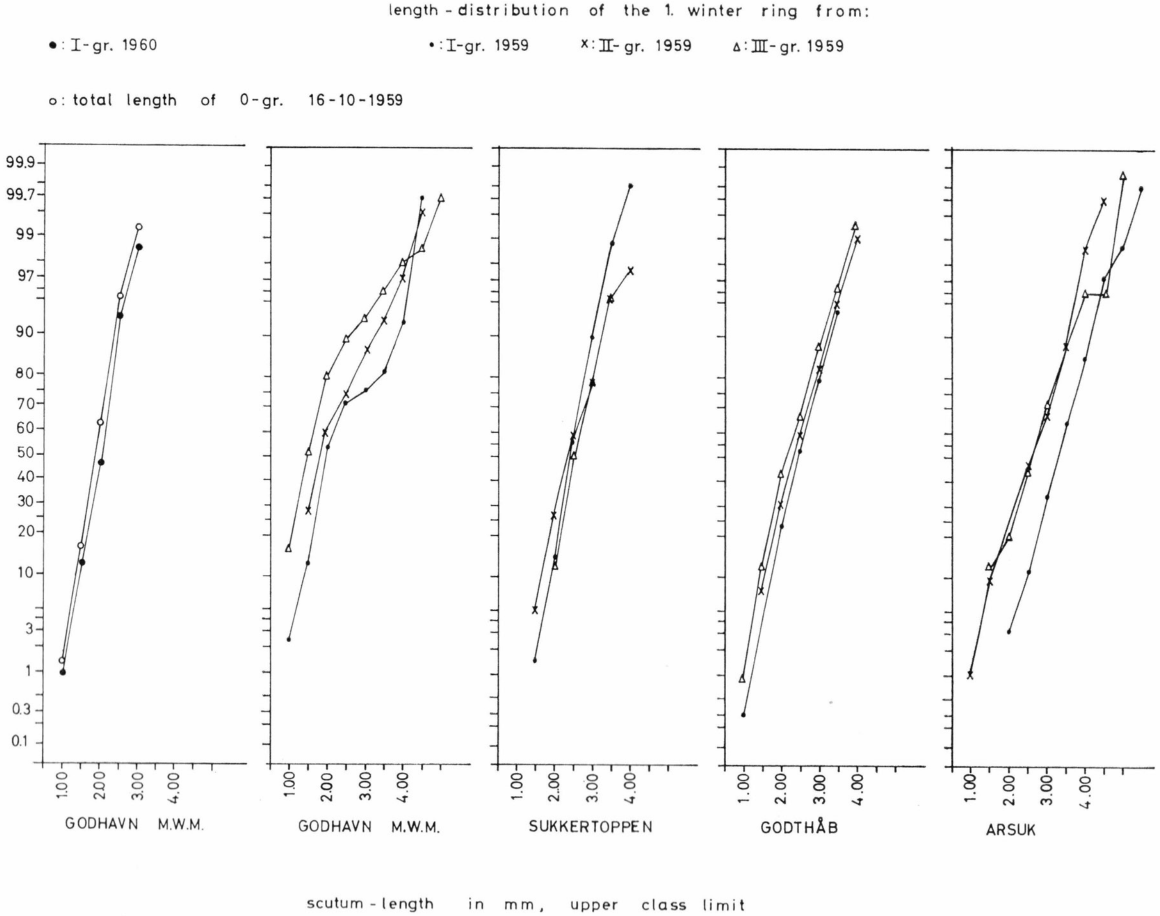


Fig. 38. Size distribution of the 1st winter ring and O.-gr. from different localities.

Unfortunately, the amount of material of 0.-gr. animals from the year 1958 is not sufficient to elucidate their size-distribution. Samples collected in 1960 show (fig. 37), that the 1st winter ring on this year's I.-gr. animals correspond well with the total-length of the 0.-gr. animals from 16-10-1959. Both distributions are monomodal, with roughly the same modus. A bimodal distribution of the 1st winter ring is found on the II and III gr. animals in the year 1960. The 0.-gr. animals from 1960 also show a tendency towards bimodality, and comparison between the samples from 4-9-1959 and 3-9-1960 clearly shows the difference between the two years. The difference between the two years was already noted during the collecting work, as settling started around 1st August in the year 1959, and around 1st July in the year 1960.

Fig. 38 shows a comparison between the distributions of the 1st winter ring from I, II and III gr. animals from the four main localities. To simplify this the material is drawn as sumfunctions on probit-paper. The function from Godhavn in this figure corresponds to the curves for M.W.M. in fig. 36 and 37. From fig. 38 it is seen that the material from Godhavn has a bimodal distribution, while the material from the other localities has an approximately normal distribution. In all localities there is a tendency for the 1st ring to be smaller the older the animal. This may be analogous to Lee's phenomenon, but the possibility of a difference in growth in the different seasons cannot be excluded.

The investigations indicate that settling had two maxima at Godhavn and one at the southern stations. The two maxima at Godhavn can be explained by a settling from two different larval populations; the first settlement is from a larval population which is carried northwards to Disko Bugt by the West Greenland Current, and the second settlement is from the local larval population.

If the explanation given above is correct there should be a discontinuity in hatching along the shore. This can be brought about by the extension of the Canadian Polar Current, which is characterized by the "Vestis". During winter, the "Vestis" lies close to the shore of Greenland as far south as Holsteinsborg. In spring the "Vestis" retreats and the warm West Greenland Current sweeps up along the shore to the Upernavik district. The extension of the "Vestis" might divide the shore into two parts, between which there is a sudden change in hatching conditions.

If the first larval population originates from Sukkertoppen district 400 km south of Godhavn and the pelagic stage is 65 days (the Sukkertoppen result), the transport speed is about 6 km per day (or about 3,2 nautical miles per day). In Kiilerich (1943) speeds of 17–40 nautical miles are given per 24 hours for stations off Southwest Greenland. According to these ciphers, it is feasible that a settlement of larvae from remote populations can be expected. Owing to the large amount of local shore water a settlement of larvae from the local population must also be expected. The monomodal distribution from the three southern stations is in accordance with the fact that hatching occurs almost simultaneously at these stations.

From the areas north of Godhavn only a few measurements of the 1st winter ring are at hand, as the animals are old and corroded. Nevertheless, the material shows a tendency towards bimodality, having two modes of the same magnitude as found at Godhavn. This strengthens the supposition that the populations in the northern districts are supported by larvae from the south and apparently both from the Disko Bugt area and from the districts south of Holsteinsborg. The possibility that local larvae survive the winter below the ice in the pelagic stage is not likely.

As the 0.-gr. in 1959 in Godhavn is not bimodal, it would greatly facilitate matters if measurements of 0.-gr. from previous years were at hand. This is not the case, but there is some information to indicate that the year 1959 was abnormal regarding plankton conditions. In this respect, it is mentioned several times in BERTELSEN and HANSEN (1960, 1961 and 1962), that the age-group 1959 of cod is very small.

Growth of 0.-gr. animals

The results of the measurements of 0.-gr. animals from plates 3–38 are plotted against the date on figs. 39–44 in a simplified manner; thus, for every sample the range is given, and for samples with an approximately normal distribution, the average and standard deviation for the single observations are given. An estimated modus is given for extremely skew distributions. Samples with cypris are marked with a dot.

When estimating the growth in this material it should be realized that even if samples from every locality are collected within a small area, these are not necessarily from the same population, as alterations in the composition of the 0.-gr. occur from one collection to the next. The following conditions are important with regard to alterations in the populations during the season.

1. Mortality: It is presumed that the mortality rate for the 0.-gr. is independent of size. As the large animals have spent the longest time on the cliffs they will have suffered the heaviest total mortality, and the earliest settlers in the late samples will be under-represented compared with the early samples. This presupposes a greater mortality for the settled stages than for the pelagic ones.

2. The progress of the settlement: The number of larvae settling every day has, presumably, a normal distribution with respect to time;

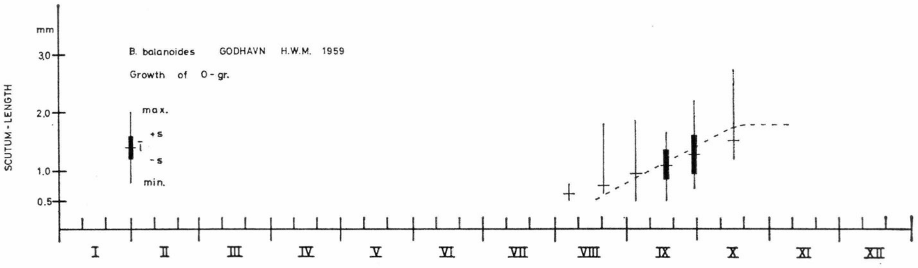


Fig. 39. Growth of 0.-gr. The thin vertical line gives the range in each sample. Samples with cypris, as the only representatives for the 0.-gr., are indicated by dots. Average and standard deviation are given for approximate normal distribution. An estimated modus is given for skew distribution.

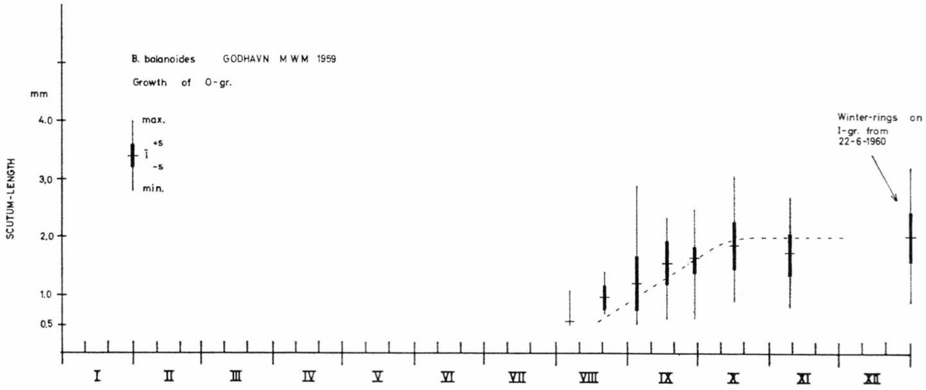


Fig. 40. Text see fig. 39.

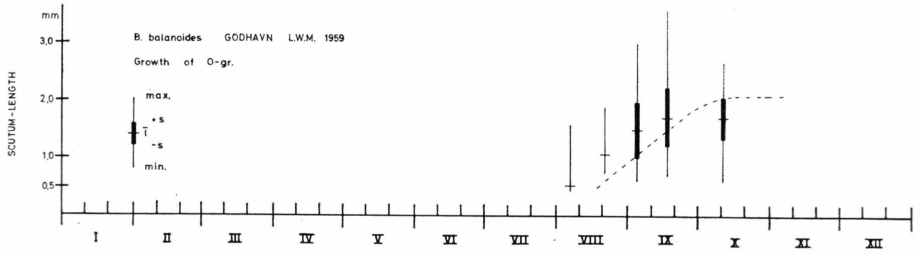


Fig. 41. Text see fig. 39.

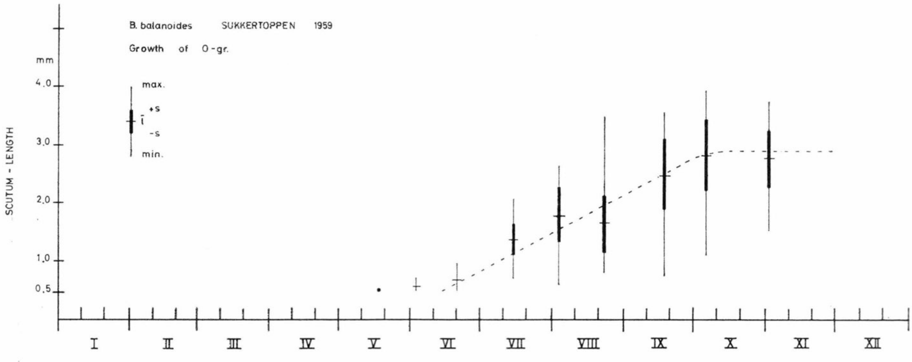


Fig. 42. Text see fig. 39.

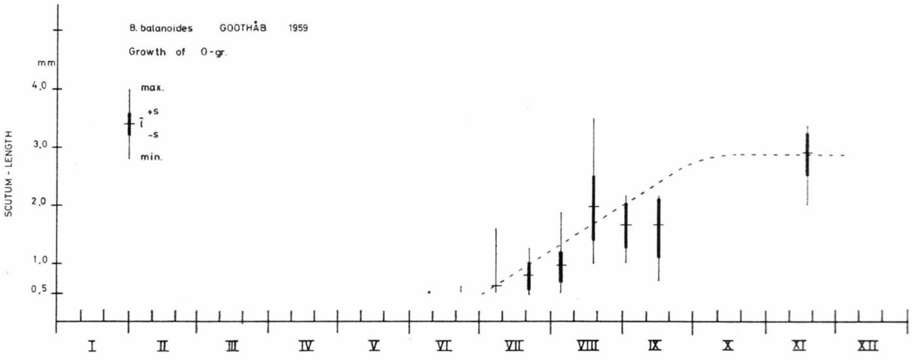


Fig. 43. Text see fig. 39.

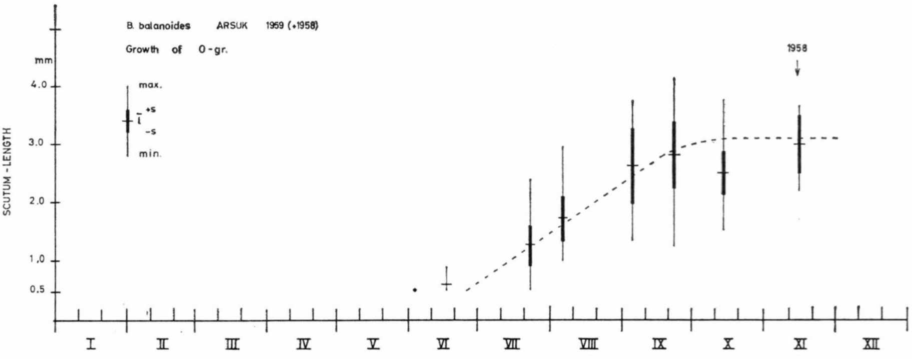


Fig. 44. Text see fig. 39.

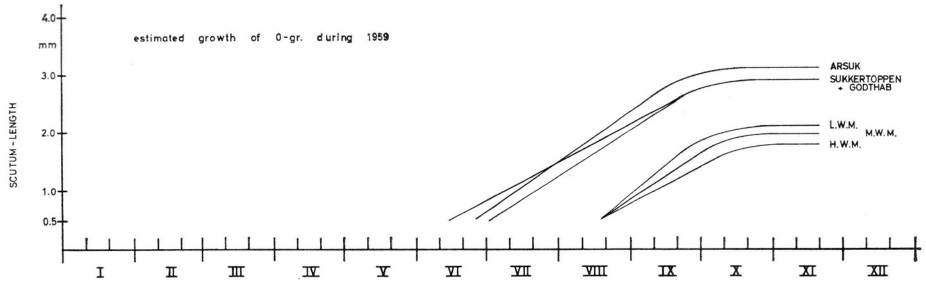


Fig. 45. Comparison between the growth curves obtained in figures 39–44.

thus, settling starts after a certain date, reaches a maximum, diminishes, and then stops again. Thus the early samples represent only the most advanced part of the larval population, while the late samples represent most of the year's brood.

3. The course of the growth: The metamorphosed larvae will rapidly gain in weight, and probably follow an exponential function. Thus, a growth-curve showing length as opposed to time will be approximately linear during the first part of the growth season. At a later date, the growth will be retarded, owing both to bad winter conditions and to alterations in the animals' growth process. It should be noted also that for the 0.-gr. size is a rough measure for age.

The following changes in size-distribution are to be expected during the season. Shortly after the start of settling the distribution will be skew, with a maximum among the smaller animals. As the smallest animals are probably under-represented owing to collecting errors, the skew distribution is more pronounced in the natural populations than in the samples. Shortly after the cessation of settling, the distribution might be skew, with a maximum among the larger animals owing to alterations following the growth-process; viz., the first animals to settle grow quickly, but they will spend more and more time in the larger length classes and accumulate in these classes. This might be counterbalanced by the mortality rate, which, in the course of time, tends to reduce the number of large (older) animals compared to the number of small (younger) animals.

When the growth curves are drawn, the modes or averages in the samples cannot be used alone, as possible alterations in the populations mentioned above must also be considered. This is shown in figs. 39–44, where stippled curves are used. These curves illustrate the growth of an animal at the maximum settlement, growing up under average conditions to an estimated average size by the end of the season. This average

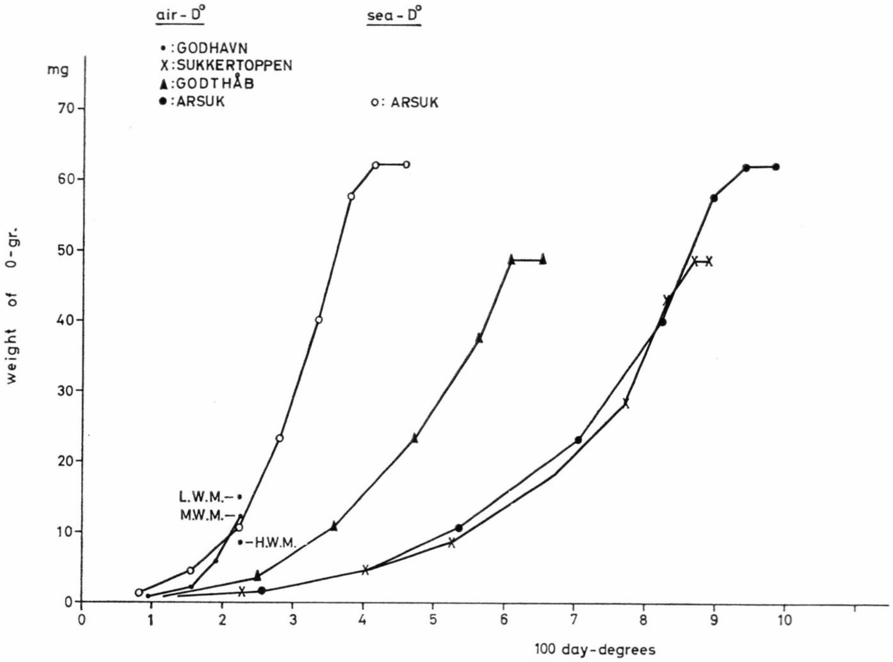


Fig. 46. The weight of the 0.-gr. animals related to the heat sum in the period after settling.

size is estimated both from the measurements of the 0.-gr. and from the measurements of the first winter ring. In fig. 45 all curves from all localities are compared.

In order to see how growth in weight depends on "heat-sum" and primary production, figs. 9, 10, 11, 13 and 45 should be studied. The result is seen in figs. 46 and 47, where the abcissa gives the "heat-sum" and the sum of the primary production, summed up and counted from the average settling-date. From these curves (figs. 46 and 47) it can be deducted that the growth of the 0.-gr. animals depends neither on temperature nor on primary production. Reasonably enough, it is the animal's individual capacity to catch and to utilize food which promotes growth-rate. From the three levels at Godhavn it is seen that growth is partly dependent on food supply, i. e., as measured by time spent under water. However, these differences are by no means as great as those between the other localities. If the animals are able to consume a certain amount of food, independent of temperature and food-density in the sea, merely the time spent in the water will be enough to influence growth. The independence of temperature and food-content in the sea may be understood by the way the animals procure their food. It was observed on several occasions that the animals utilize waves for the "collecting" of food. The animals merely let their "catching-net" passively follow the

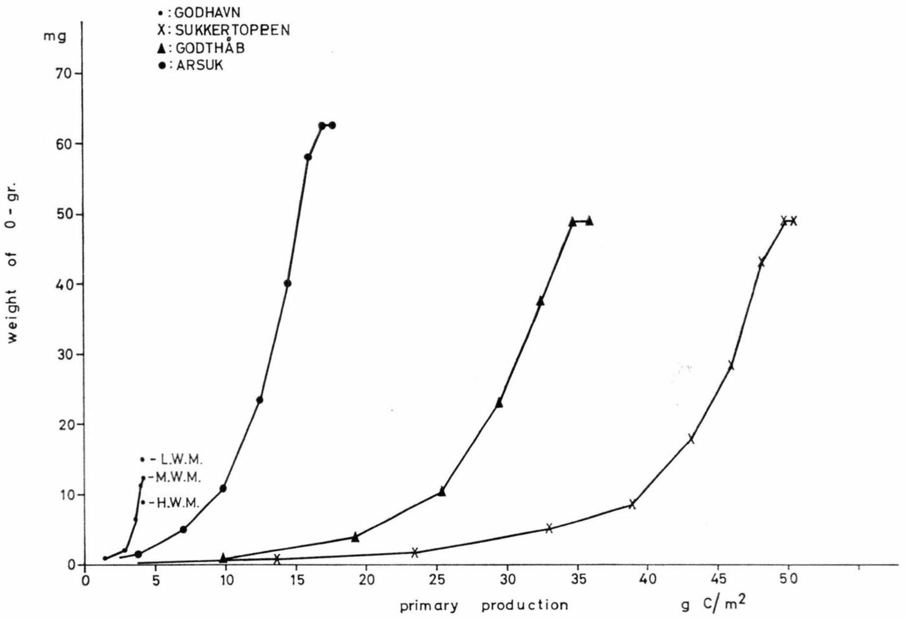


Fig. 47. The weight of the 0.-gr. animals related to the total primary production in the period after settling.

small currents produced by the waves (almost like a plankton-net). Active movements (Crisp and Southward 1961), seemed to be less important. In this way the animals might be able to procure sufficient food during a tide—even with low food-content and low temperature. Digestion of food may be dependent on temperature. However, if the animals also digest food during low tide (as suggested by the presence of a small air bubble between the opercular plates—probably to allow exchange of gases), digestion dependent on temperature may not influence growth, as long as the animals have enough time during low tide to digest food captured during high tide.

Growth of adult animals

The size of adult animals was measured by the length of the scutum at the end of each season. The length at the end of the season where sampling was carried out, was estimated from the lengths obtained during the season and from the winter rings of older animals.

Figs. 48–53 give the growth of I, II and III gr. from the 1959 samples. The material of the older age groups was too small to be treated in the same manner as the three younger age groups. The figures give the estimated size the animals were expected to obtain at the end of the season

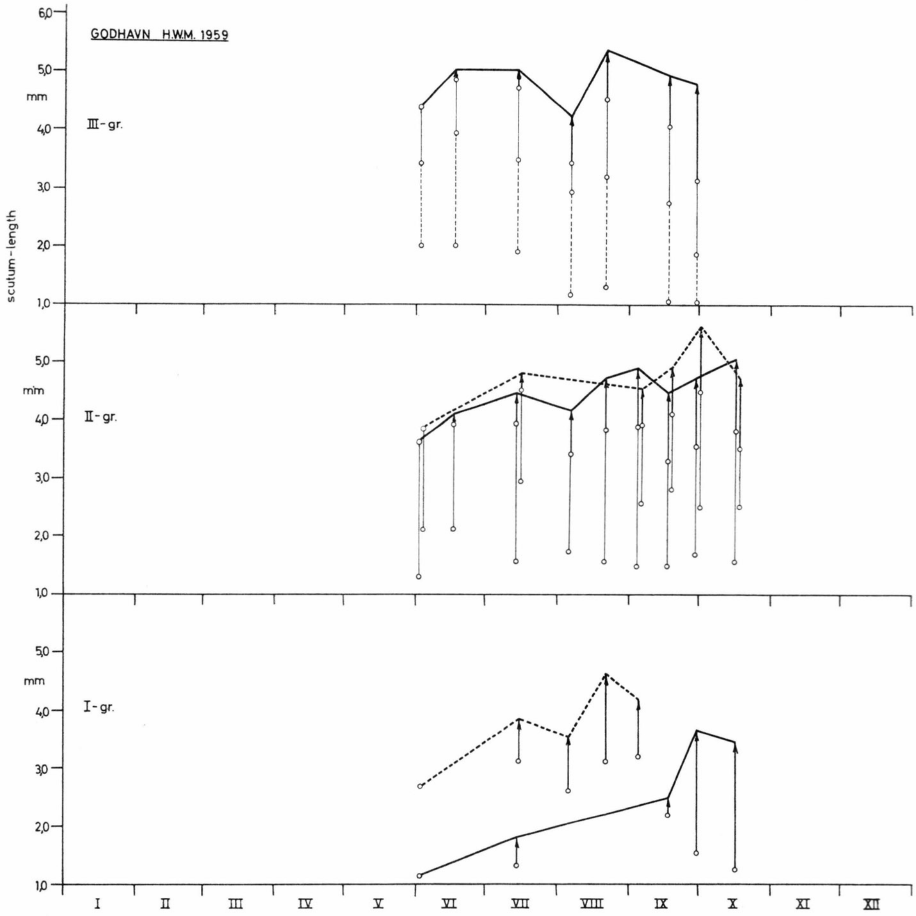


Fig. 48. The growth of age-groups I, II and III shown by results from the single samples during the season 1959. The circles give average length of the winter rings, and the arrows give average total length. The vertical stippled lines give the growth during the season 1957; the vertical, thin, unbroken lines give the growth during the season 1958, and the vertical, thick, unbroken lines give the growth in the period winter 1958/59 to the date of collection. For the Godhavn samples two growth curves are given for the season 1959. The unbroken curve shows the growth for the populations with a small 1st winter ring and the dotted curve shows the growth for the populations with a large 1st winter ring. Godhavn H.W.M.

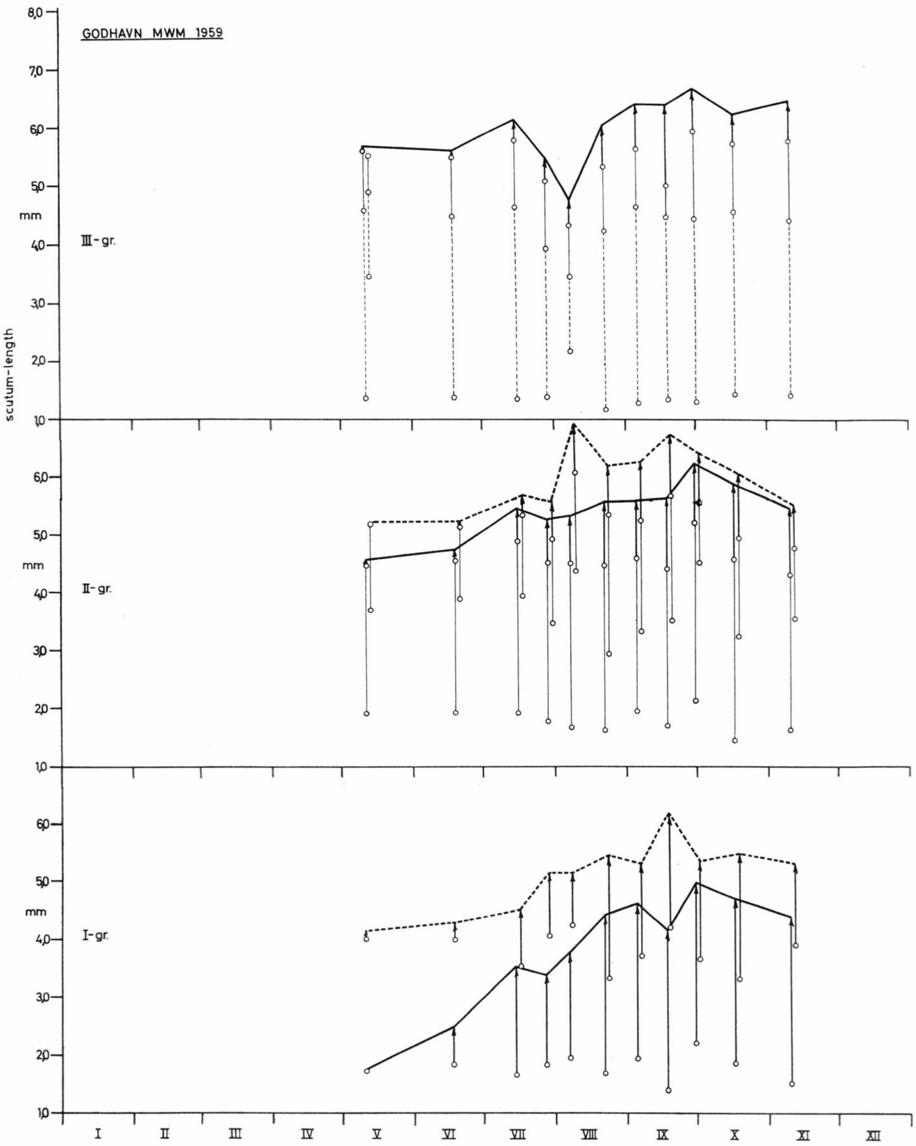


Fig. 49. Godhavn M.W.M. Text see fig. 48.

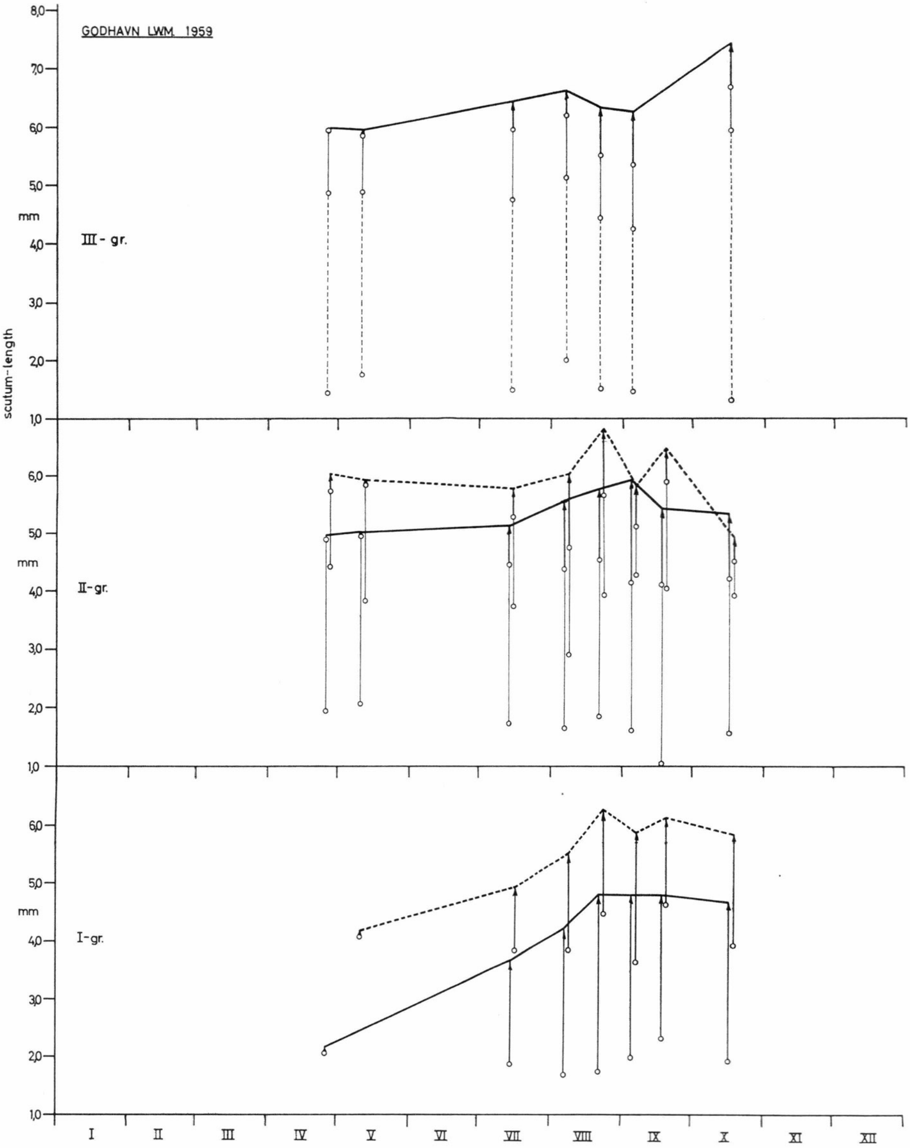


Fig. 50. Godhavn L.W.M. Text see fig. 48.

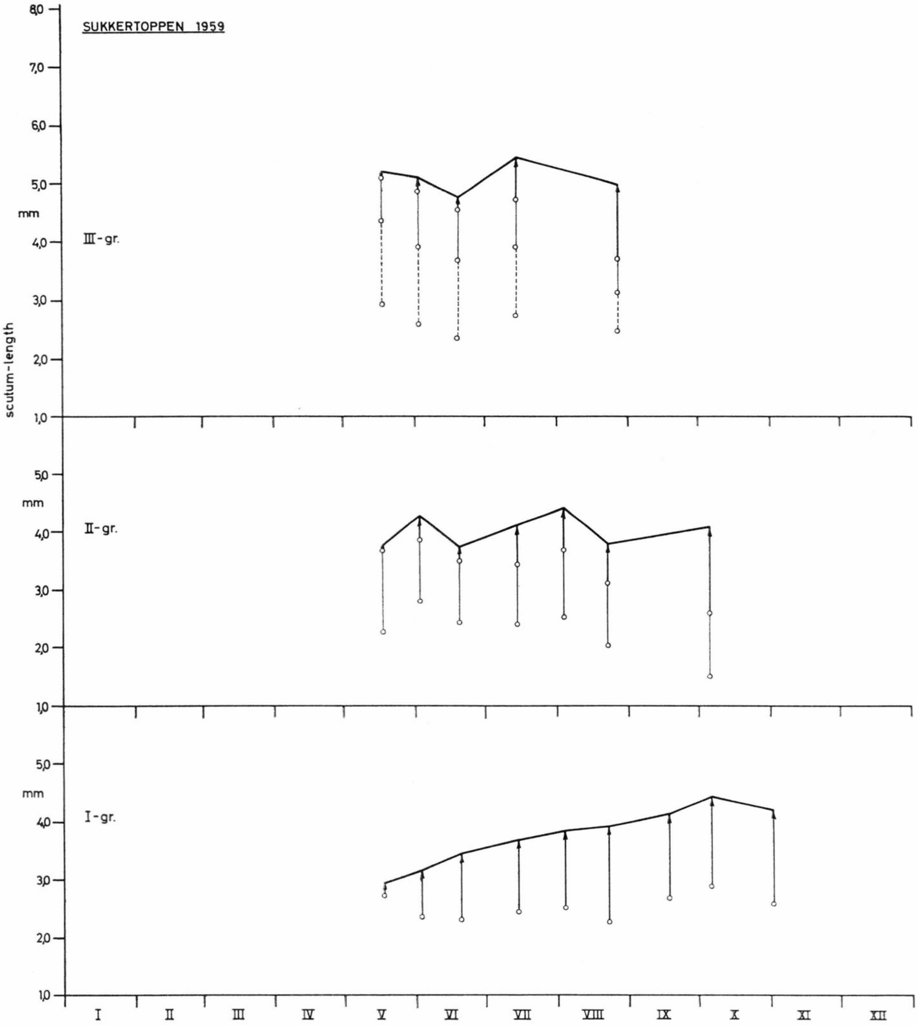


Fig. 51. Sukkertoppen. Text see fig. 48.

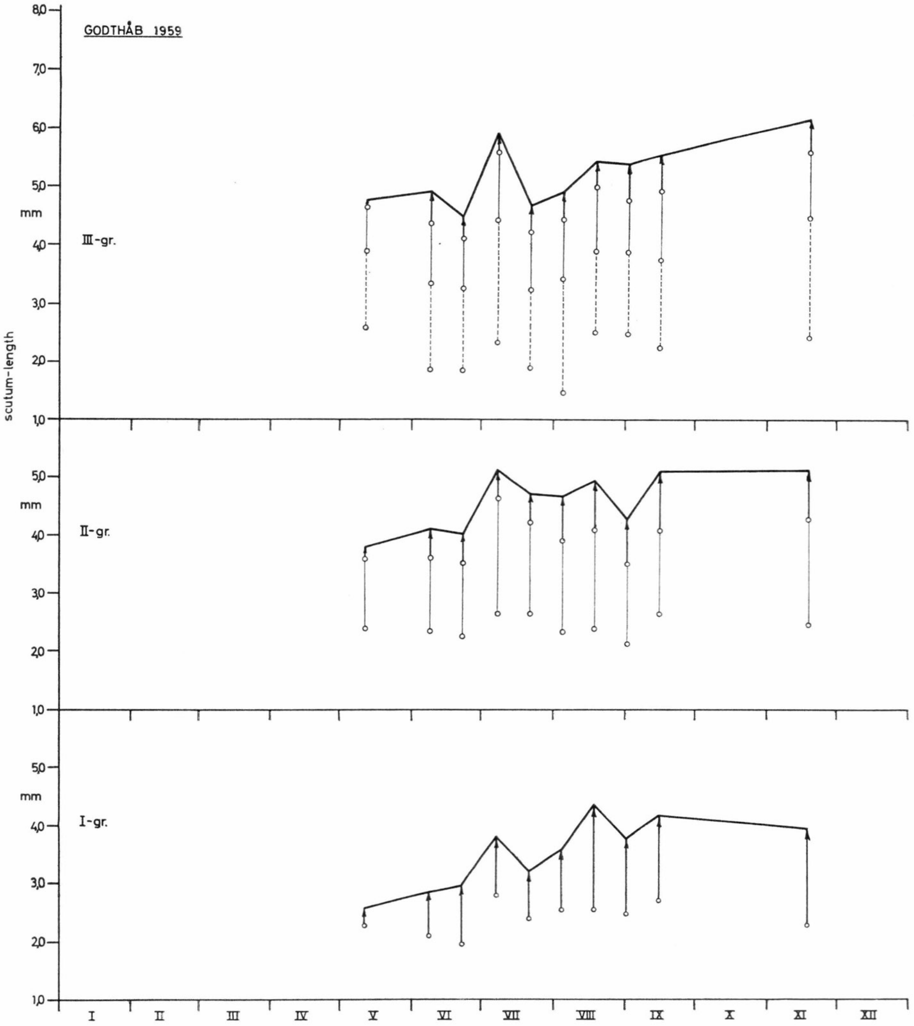


Fig. 52. Godthåb. Text see fig. 48.

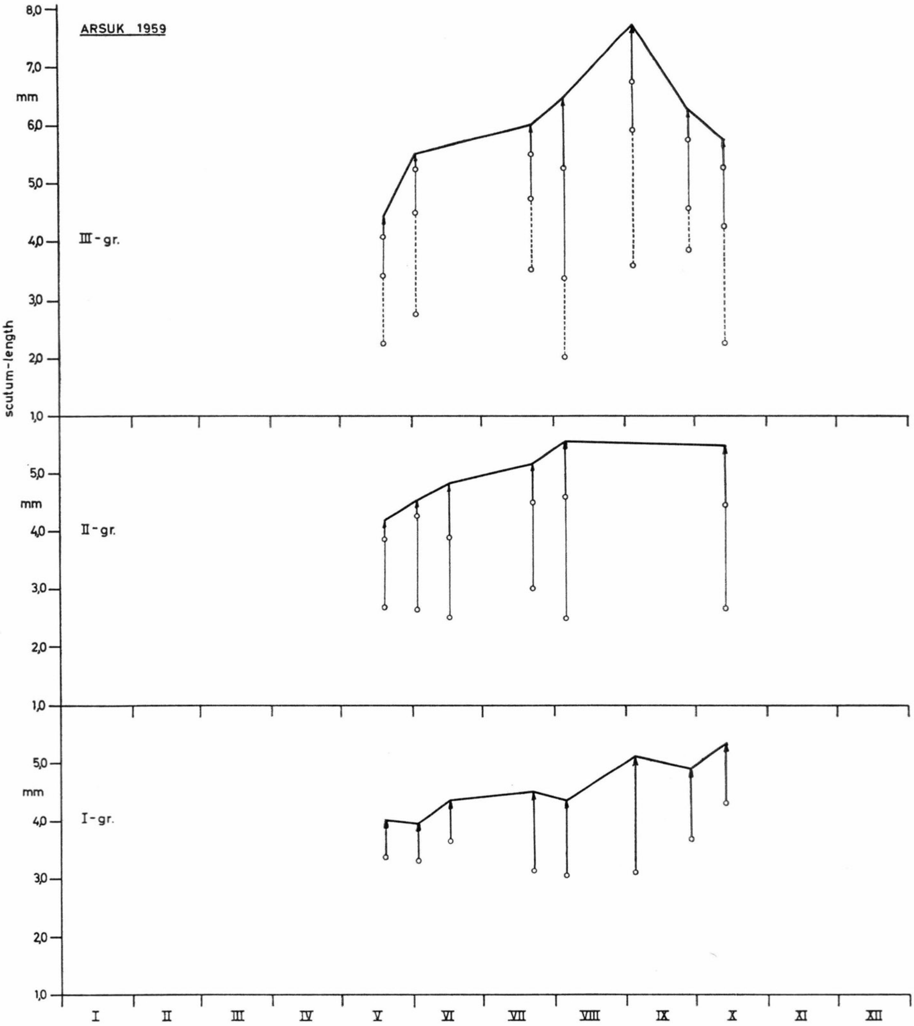


Fig. 53. Arsuk. Text see fig. 48.

1959, and also give the variation of the winter rings in the different samples.

Tables 1–8 give the averages of the winter rings for each age-group, and the length obtained by the end of the season. From these tables figs. 54–64 are drawn. It is seen that the older the animals are, the smaller the winter rings for the respective ages. This is in accordance with Rosa Lee's phenomenon (Ricker, 1958 p. 188). It should be noted that errors in the reading of the winter rings tend to give the opposite result, as the smallest winter rings on the old animals might be overlooked because of heavier corrosion. The actual (and only) growth curve for the populations cannot be obtained from figs. 54–64. This problem is further discussed in Ricker (1958, p. 189). For the present paper, however, it was decided to use a growth-curve of approximately the same form as that of the older animals, and the starting point of the curve for the first years is as indicated by the size of the younger animals.

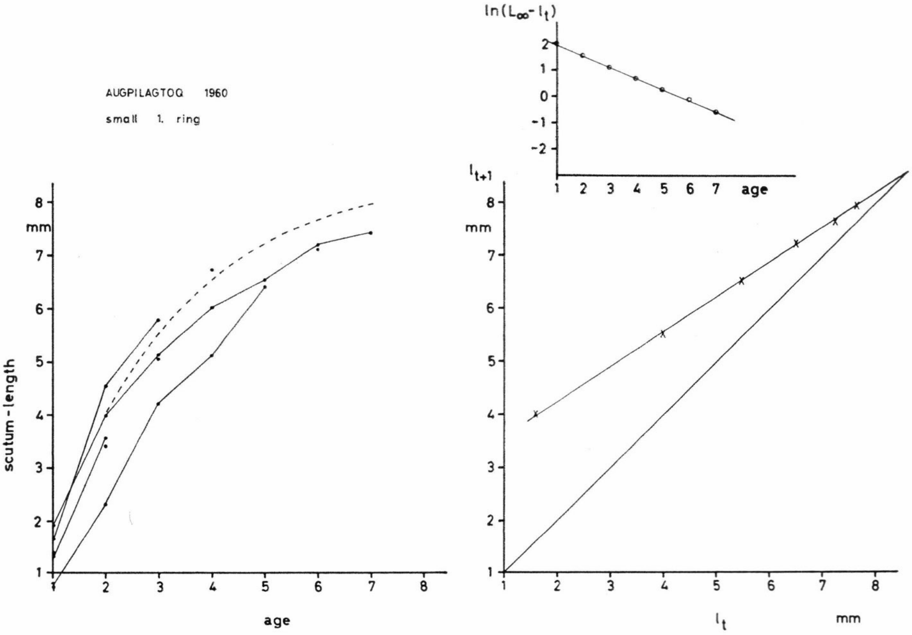


Fig. 54. Growth curves for the adult animals. In the length-at age diagram the unbroken line shows the growth of the individual age-groups as indicated by the winter rings, and the dotted line shows the estimated growth curve. Dots unconnected to a growth curve give the estimated length for the age groups at the end of season investigated.

In the Ford-Walford plot the lengths are taken from the estimated growth curve in the preceding diagram. Situated above the plot is the diagram for estimating K-value and t_0. Augpilagtoq, 1960, small 1st winter ring.

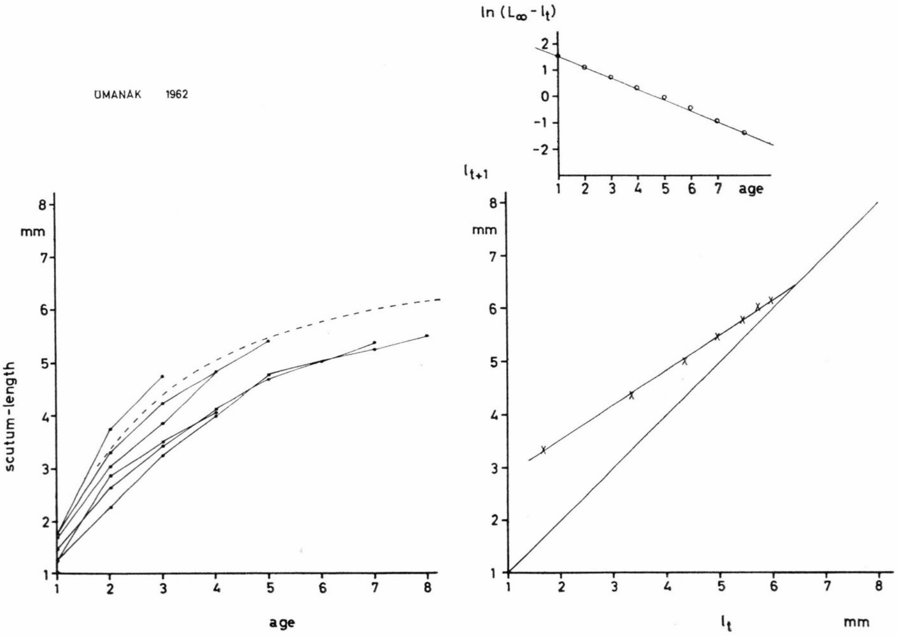


Fig. 55. Umanak 1962. Text see fig. 54.

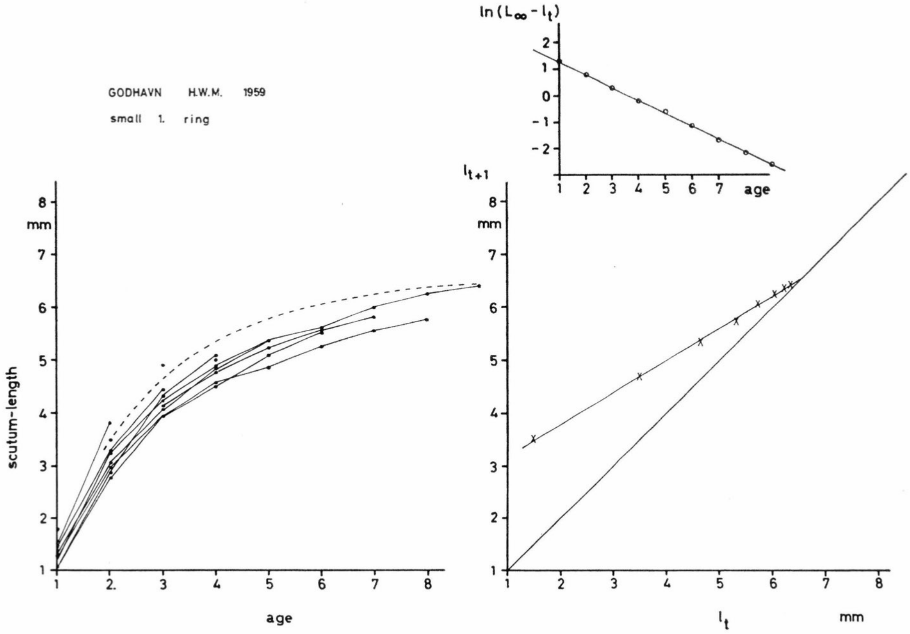


Fig. 56. Godhavn H.W.M. 1959, population with a small 1st winter ring. Text see fig. 54.

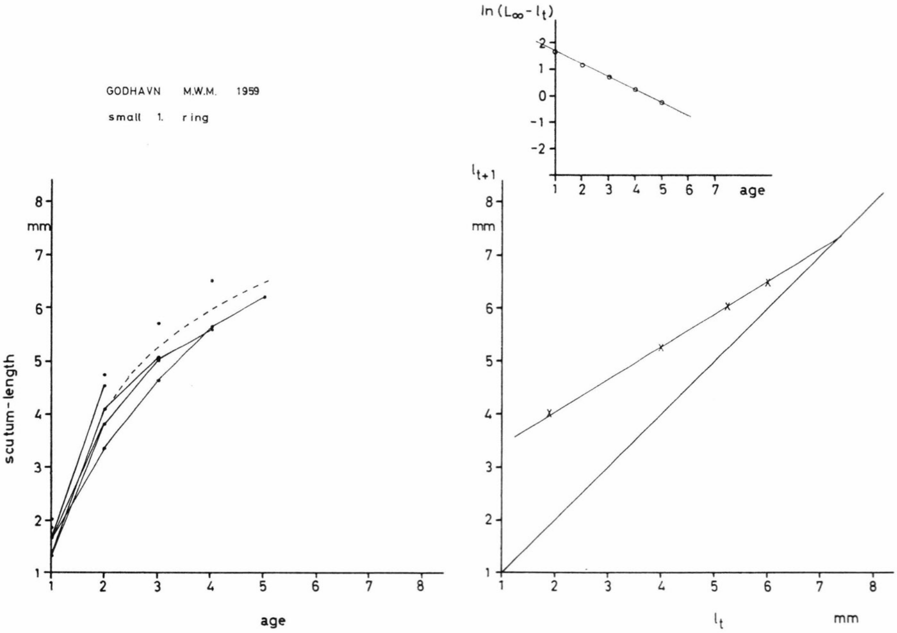


Fig. 57. Godhavn M.W.M. 1959, population with a small 1st winter ring. Text see fig. 54.

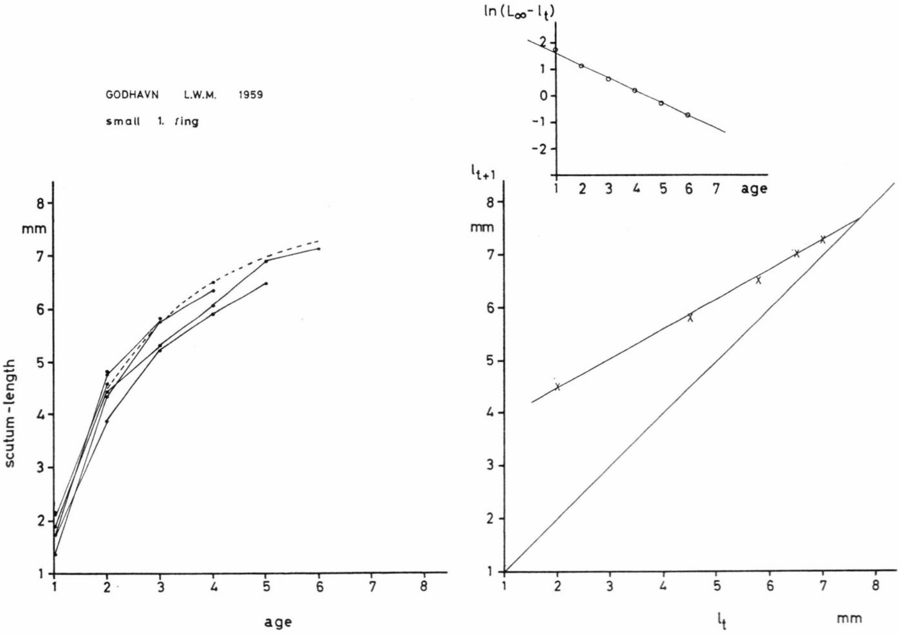


Fig. 58. Godhavn L.W.M. 1959, population with a small 1st winter ring. Text see fig. 54.

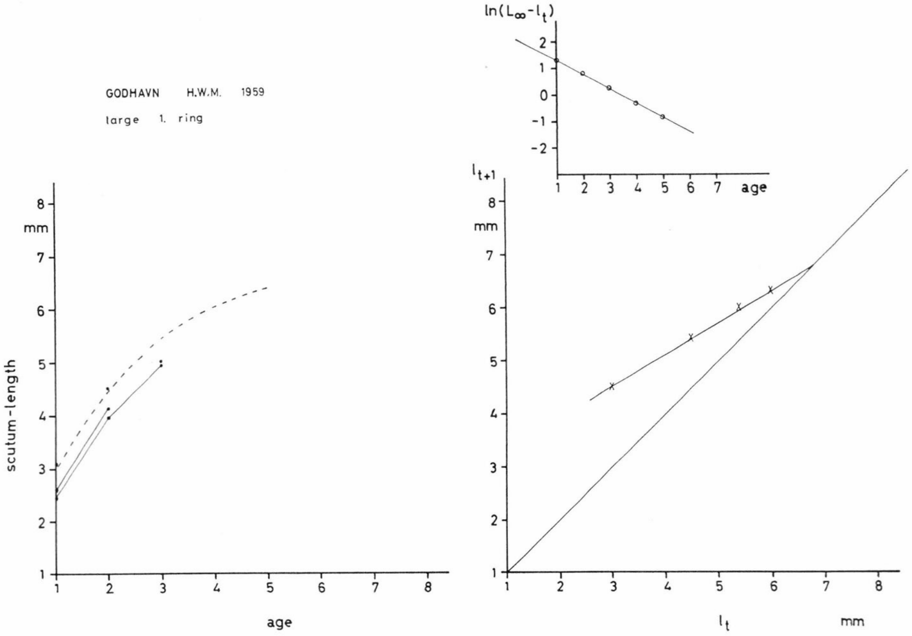


Fig. 59. Godhavn H.W.M. 1959, population with a large 1st winter ring. Text see fig. 54.

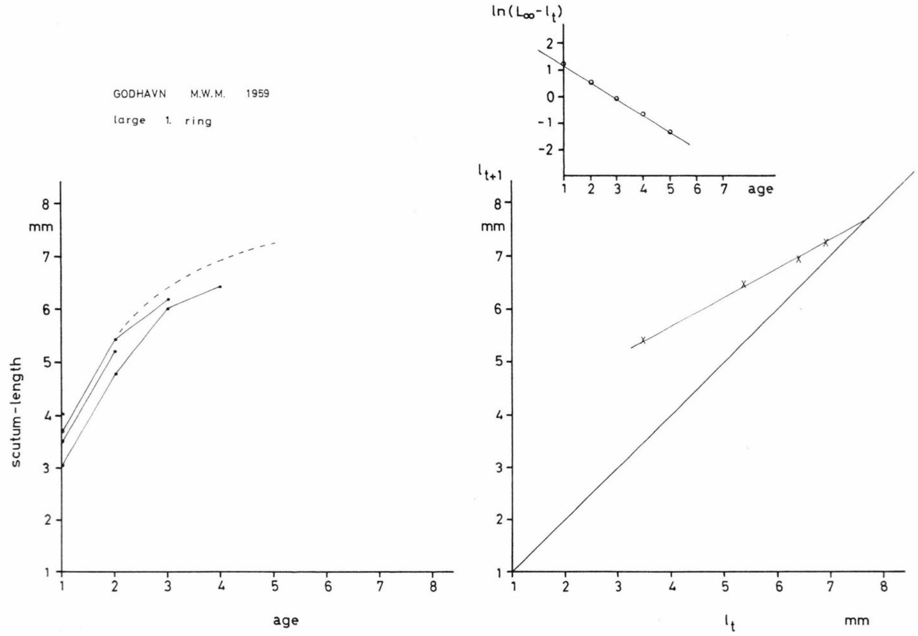


Fig. 60. Godhavn M.W.M. 1959, population with a large 1st winter ring. Text see fig. 54.

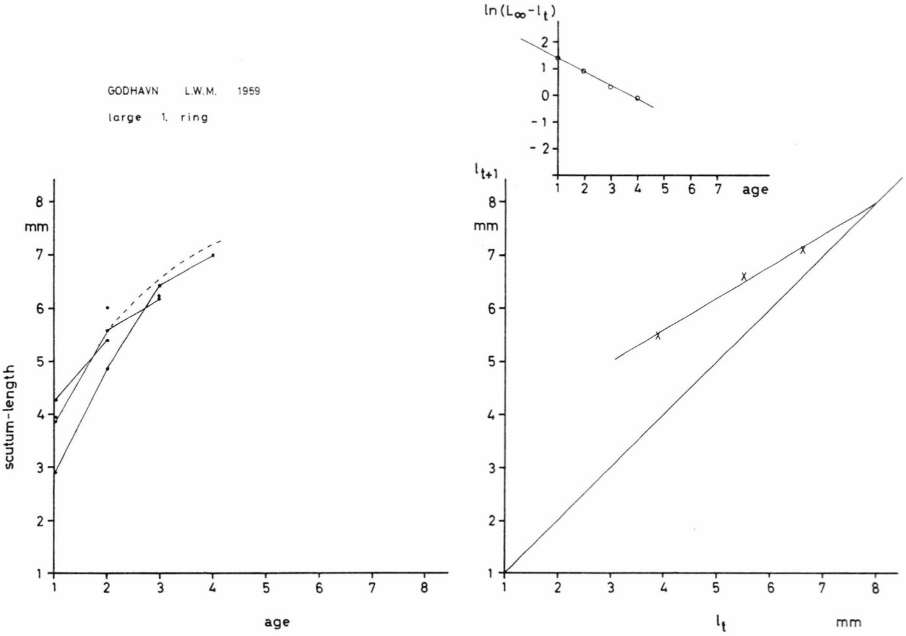


Fig. 61. Godhavn L.W.M. 1959, population with a large 1st winter ring. Text see fig. 54.

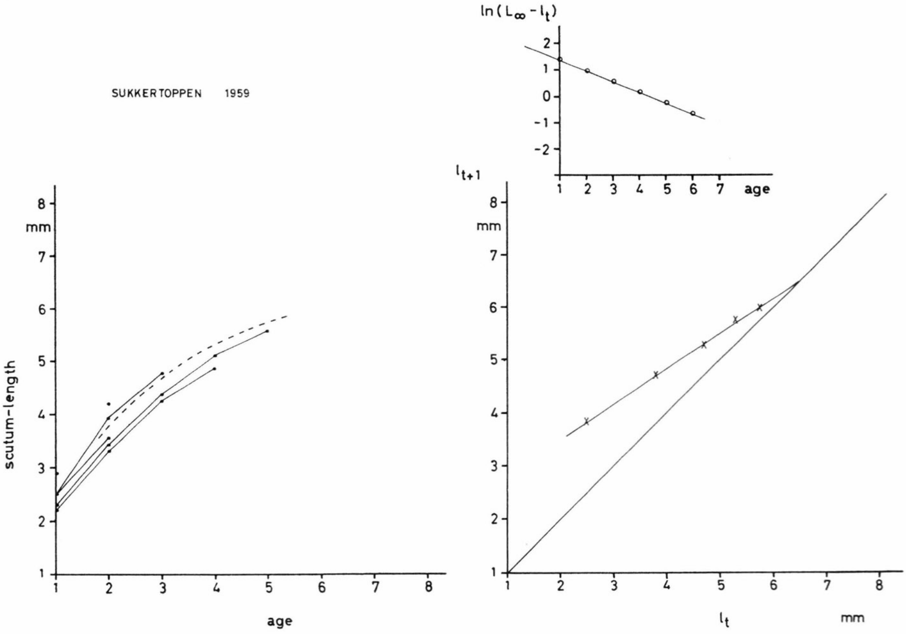


Fig. 62. Sukkertoppen 1959. Text see fig. 54.

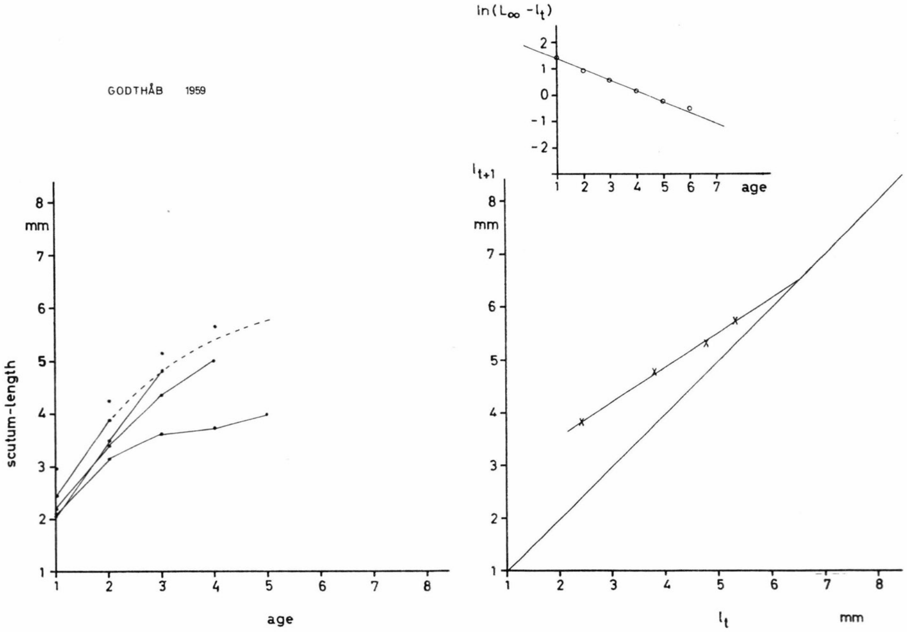


Fig. 63. Godthåb 1959. Text see fig. 54.

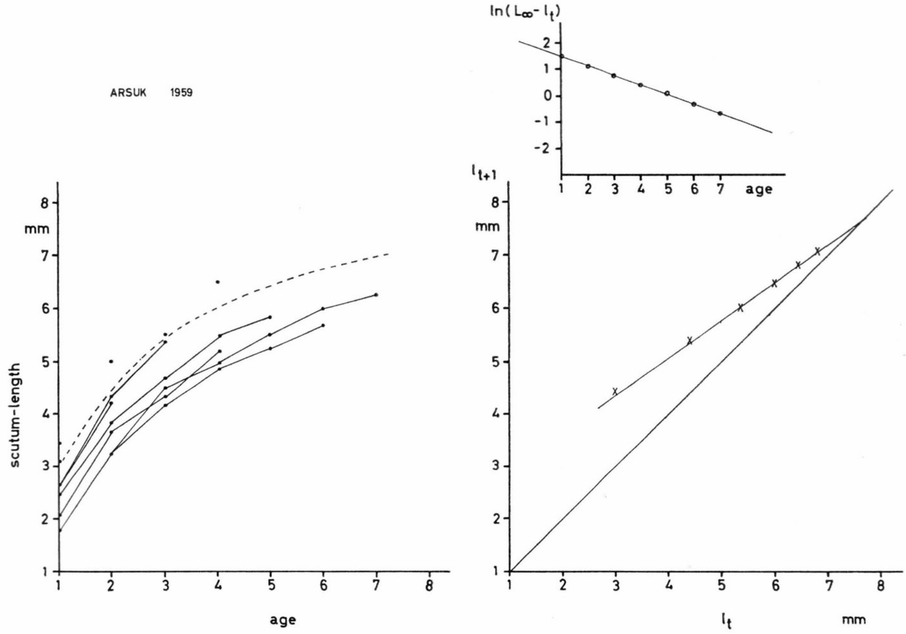


Fig. 64. Arsuk 1959. Text see fig. 54.

Of course, it is disputable whether the use of this curve is justified—especially when used for comparison between different populations. Among other things, growth-curves depend on an evident selective mortality rate in the larger animals. This can be due either to internal processes, which cause the organism to break down when a certain size is reached, or to external conditions such as bird-predation, which presumably strikes the larger animals. Both these conditions can, of course, vary from place to place and thus weaken comparison. However the quantity and quality of the present material does not permit further investigations of these problems.

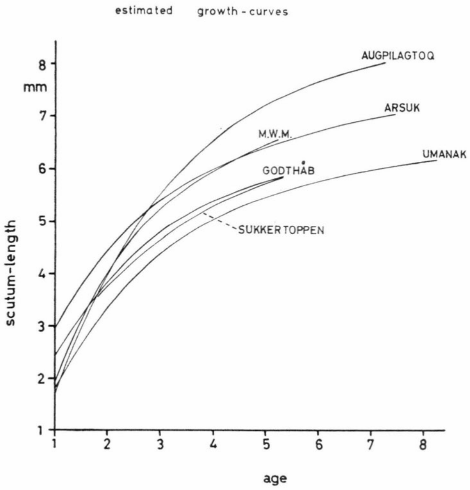


Fig. 65. Comparison between the growth curves from the individual localities. For Godhavn the curve from M.W.M. with small 1st winter ring is used.

Naturally enough, competition between the animals will also affect the growth-curve, but to judge from the animals' appearance, only very few of them have been taken from overcrowded areas.

The populations from Godhavn and further north seem to be composed of two populations, with each their own settling period (see p. 49). The material is divided into two groups with a small and a large 1st winter ring respectively. Grouping was made on the basis of the original measuring notes.

The growth-curves obtained seemed suitable for von Bertalanffy's method of growth-equation. This was prepared in accordance with methods described in Beverton and Holt (1957, pp. 282–285) and in Ricker (1958, pp. 185–199). Table 9 gives the results.

A comparison between the growth curves for the different populations is given in figs. 65 and 66.

Fig. 66 shows, that the rate of growth is better at the lower levels, and that the H.W.M. animals seem to live longer than the lower placed ones. The Godhavn results also give an idea of the variations in growth due to the different levels encountered at the individual stations. The results correspond to those obtained from the 0.-gr. growth.

Fig. 65 shows a comparison between the different stations. For Godhavn, the growth curve for the population from M.W.M. with small 1st winter ring is used. The results for the adult animals' growth are not so easy to interpret as the 0.-gr. results in fig. 45. Nevertheless, some explanations can be given for the individual localities.

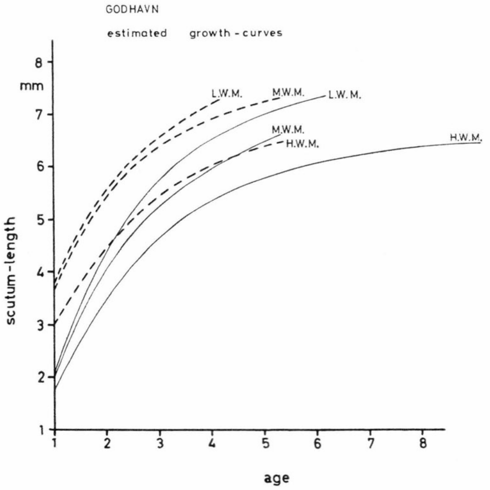


Fig. 66. Comparison between the growth of the populations on the different levels at Godhavn. Unbroken curves: populations with small 1st winter ring. Dotted curves: populations with large 1st winter ring.

It was expected that the growth at Umanak would be bad as the town is situated in the inner part of a great fjord system. There are several active glaciers in the area; the ice-cover is of long duration, and subsequently, the summer is short.

It is remarkable that growth at Godhavn is better than at Sukkertoppen and Godthåb. This feature does not correspond very well with the differences in climate and production or with the results from the 0.-gr. However, it should be remembered that the rate of growth for the 0.-gr. is as high at Godhavn as at Sukkertoppen and Godthåb. The differences might be explained by extreme micro-factors, e. g., competition from neighbour-organisms or the position on the cliffs, but these factors are presumably not valid in light of the fact that many samples, which must originate from a certain area, have been obtained. The better growth rate at Godhavn might be connected with the fact that the town is placed on an exposed shore, while both Sukkertoppen and Godthåb are situated in large archipelagos. It may be that the growth parameters vary according to the climate.

The growth at Sukkertoppen and Godthåb is of the same order of magnitude as that of the 0.-gr.-animals. The geographic and hydrographic conditions at the two towns are similar, and they lie only 150 km apart.

The growth rate at Arsuk proved to be very large and favoured by several factors, viz., the town is situated near the open sea, there is no ice-cover, and it is the southernmost station. On the other hand, the town is influenced by the East Greenland Current during the spring, and the sea-temperature is rather low. It is difficult to make any definite conclusions about conditions at Arsuk owing to poor information on the highly varying hydrography and climate.

The growth at Augpilagtoq falls outside the expected patterns. The animals were taken near the northern limit of the species in an area with about 8 months' ice-cover situated in the inner part of an archipelago, and close to the glacier "Upernaviks Isstrøm". The material is very small, as the animals are rare in the area. Animals collected were all found in crevices near L.W.M. (Petersen 1962, p. 23).

The animals from Angmagssalik could not be determined to age, but some measurements of the outer winter rings were obtained. These are set up in a Ford-Walford plot in fig. 67. This, of course, cannot be directly compared with the other plots, but it does show that the growth is fairly reasonable in this area (which is close to the northern limit of the species on the East Coast).

It would seem that the growth of the 0.-gr. animals depends mostly on the animals' own growth-capacity, and that the growth of the adult animals depends on local factors and not on global factors. Crisp (1960) gives further details on factors influencing the growth-rate.

The growth parameters given in table 9 might be related to some environmental factors.

The K-value, which is a symbol for catabolism, does not show the obvious trend found for several other animals (Taylor 1957, 1959, 1960, 1962). However, the temperature-variations are so large for tidal-zone animals in all localities that it is almost impossible to give a mean temperature at which growth could be compared.

L_∞, which is a symbol for the maximum size, seems to be positively correlated with food-conditions at the three levels from Godhavn. For the various geographical localities, this correlation is uncertain. L_∞ seems to be large at the arctically influenced localities such as Augpilagtoq, Angmagssalik and Arsuk, and low at the boreally influenced localities such as Sukkertoppen and Godthåb. The low L_∞ at Umanak, which has an arctic climate, might be explained by bad food conditions.

T_{max} is a symbol for longevity. This is when correlated to temperature negative viz., low temperature leads to longer life, a fact well known from many poikilotherms. For the three levels from Godhavn where the temperature can be considered constant, the differences in T_{max} may be correlated to food-conditions (poor food supply causing advanced age).

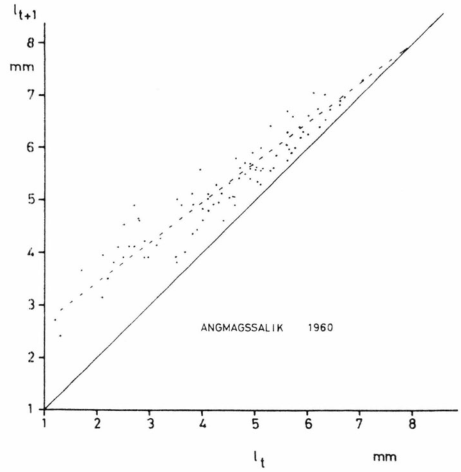


Fig. 67. Angmagssalik 1960. Ford-Walford plot of length of winter rings from individual animals.

In the considerations on L_∞ and T_{max} from the three levels at Godhavn, it should be noted that any danger from predatory birds might be more serious at H.W.M. than at L.W.M., because of the longer exposure to bird attack. Subsequently, one might expect small, young animals at H.W.M. and old, large animals at L.W.M. viz. the opposite of the results obtained. But of course if birds make only short attacks at low tide, no difference in predation at the different levels should exist. No predatory animals, marine or terrestial were observed to eat *B. balanoides.*

In this material there is no obvious connection between maximum size and maximum age, viz., L_∞ and T_{max}.

The age problem

In the present growth curves age is counted in seasons, a commonly used measure for age. However, it is evident that this measure is not particularly suitable for the different populations of *B. balanoides*, as some are frozen in the ice-foot for part of the year. Thus, during spring at Godhavn there is great difference in the dates for H.W.M. and L.W.M., when the animals are free of the ice. The earliest sample from H.W.M. originates from 20.5.1959 at the Dog Food Rack (Petersen 1962), when the ice-foot was blown away by explosives. The earliest sample from L.W.M. was taken 25.4.1959, when sampling was not hindered by ice (the animals in that sample had a green stomach-content). Thus, the L.W.M. animals have at least one months' lead on the H.W.M. animals in food uptake. In the autumn the season is also shorter for the H.W.M. animals than the L.W.M. animals.

The age of the animals ought rather to be measured according to the hours or days in which they have not been frozen, or in which they actually feed. Further considerations along these lines would lead to problems of metabolic age, and the growth and ageing processes; problems to which this paper is unable to make further contribution.

COMPARISON WITH SIMILAR INVESTIGATIONS

Table 10 makes a comparison with investigations which give a reasonable amount of information on the growth and life history of the *B. balanoides.* The last column gives the sources. The results from Great Britain, apart from those from Port Erin, are taken from sporadic information published in numerous papers by Barnes, Crisp, and their co-workers.

The columns dealing with the sexual cycle give only approximate periods for the peaks in the different stages of development.

The duration of the larval stage as calculated in this paper may seem prolonged compared with the results of other studies, but in some cases, the other results are estimated from the start of hatching to the start of settling, which may give the larval stage a shorter than average duration.

In Table 10 the length of the base (carino-rostral length), the commonly used size-measure, is used to compare growth. The Greenland results are converted by means of fig. 15. The size at the end of the first season, a measure found in many of the papers, is not a good measure for growth conditions during a season, as this depends on the period between settling and the 1st winter.

The information on climate is approximate only, and does not correspond to standard measurements or standard treatment.

The trend, as read from Table 10, is that the southern populations have the poorer growth. This might be explained in the following way. The food uptake depends on the animals' capacity of filtering, the water movement, and the duration of water cover, but not on the content of food in the sea. The rate of break down of the animals' tissue depends on the temperature; at high temperature the animals exhibit a great deal of activity (Southward 1957). However, raised activity may not result in a food-supply being any better than at cold periods with low activity, as the waves produce enough currents to secure surplus of food capture by passive filtering work. Thus, at high temperatures the animals use energy for useless filtering movements (or other processes involving high metabolism) and the growth will be slow. Another possibility is that the southern populations have a low L_∞, which they reach very quickly.

ZOOGEOGRAPHICAL REMARKS

One of the purposes of the present paper is to point out some causal factors in the distribution of *B. balanoides*. The results are generally in agreement with those of other investigations.

It was found that the northern limit is not determined by lethal values of temperature, salinity, ice-erosion or poor growth conditions. Even the northernmost populations are able to grow and to fertilize, but the summer season is too short for the accomplishment of the larval stage.

In the arctic, *B. balanoides* prefers exposed shores, which are avoided at its southern limit (Crisp and Fisher-Piette 1959, Fisher-Piette and Prenant 1956). Under marine conditions the species is essentially intertidal, but under estuarine conditions it is found in deeper waters (Bousfield 1954).

The northern limit of *B. balanoides* is taken as the limit between arctic and boreoarctic zones, see Hutchins (1947) and Barnes (1957b) for further discussions. As the occurrence of *B. balanoides* does not depend on short extreme climatic conditions, but on the length of the summer season and extension of northgoing currents, and as the animals at the northern limit live for 6–12 years, the occurrence depends on an average stage in the decline of climatic conditions, when going from south to north.

If the northern limit depends on the extension of the West Greenland Current, fluctuations in the current would be demonstrated by variations in the northern limit. The existence of a species in an area can be easily proven by finds, but evidence of non-existence is somewhat more difficult to prove. In this respect, three investigations (made prior to those mentioned in the present paper), are of interest.

Vanhöffen (1897 p. 210) found *B. balanoides* in "Sermitdlet" (Sermerdlît, (Geodætisk Institut, Grønland 1 : 250 000)) either in the year 1892 or in 1893 (1892 being the most likely). Sermerdlît fjord is situated between Umanak and Qarajaq Isfjord, but it is not an actual "isfjord", inasmuch as glaciers do not debouch into the fjord. Van-

HÖFFEN joined DRYGALSKI on many journeys in the Umanak district see DRYGALSKI (1897, pp. 15–19), and mentions the find of *B. balanoides* as being unique. Taking DRYGALSKI's description of the voyages together with VANHÖFFEN's description of the zoological result, one can state with some certainty that *B. balanoides* must have been very rare in the district in the years 1892 and 1893, and that it cannot have occurred in Umanak and Ikerasak, where it was found in 1960 (PETERSEN 1962, p. 20).

FRODA (1924) was not able to find *B. balanoides* in the summer of 1923 in the harbours, Upernavik, Prøven and Umanak. FRODA himself worked on the problem of the sinking or rising of Greenland, and determined the vertical distance from a fixed point inland to the upper edge of the barnacle populations, the "balanus stripe". As he had already made these measurements at Godhavn and at Egedesminde, it is quite probable that the species was absent in the northern districts, where he did not find it. The importance of the balanus stripes is further described in SAXOV (1958).

In 1936 the districts from Prøven northwards were investigated by VIBE and SALOMONSEN (MADSEN 1940). The expedition found one *B. balanoides* near Upernavik, and a few old animals were found in Prøven, lying up to 1 m above L.W.M.

In 1960 the present author studied the population-types in Upernavik and Umanak districts (PETERSEN 1962), and in 1962 ELSE STEENSTRUP found *B. balanoides* to be common in Umanak and at Agpat, some 30 km north of Umanak.

From the above-mentioned investigations it is concluded that *B. balanoides* was more common and extended further north in the Upernavik and Umanak districts in the years 1936, 1960 and 1962, than in the years 1892, 1893 and 1923.

CHR. VIBE [1]) was kind enough to provide the author with the monthly averages for air temperatures in Upernavik for the years required. He has, in addition, furnished valuable information on the problems of climatic alterations. If it is assumed that high air temperatures in the summer months indicate a northward extension of the West Greenland Current, and if the eight years before the year of investigation are considered the important years for the maintenance of the *B. balanoides* populations, it is possible to set up a table such as Table 11.

Evidence on the occurrence of the *B. balanoides* is in good accordance with information on the climate. Hence, it may be concluded that the northern limit of the species fluctuates according to the extension of the West Greenland Current, but more thorough studies on the northern populations are required in order to follow these fluctuations.

---

[1]) „Grønlands zoogeografiske Undersøgelser".

The human population in Greenland depends almost entirely on marine life, and therefore, humans like animals often suffer from changes in climatic conditions. In this respect, it is hoped that this study might contribute a better understanding of fishing and hunting conditions. *B. balanoides* can be said to represent small climatological "stations", in which the gonad development and the geographical distribution will give information comparable to sliding averages of several climatic factors, which are also important with regard to commercial marine animals.

SURVEY OF THE LITERATURE

The literature on the tidal-zone organisms is very large, including that for *Balanus balanoides*, one of the most important animals of the tidal zone in the North Atlantic. To reach a closer understanding of the tidal zone ecology, one should perhaps not concentrate as much interest upon one particular species as has been done here. However, to deviate even a little from the subject it would be necessary to give a list of literature twice as long as the present one.

The survey treats the phases in the life history of *B. balanoides* separately, a method with the drawback that many repetitions are necessary to give a complete list of papers dealing with each phase, as one phase depends on the preceding phase. However, many of the papers deal only with a limited part of the life history, thus making the used subdivision acceptable.

Systematic, anatomy

The placing of *B. balanoides* in the system was determined already in the 19th century on the basis of classic morphological investigations, see Darwin (1854), Gruvel (1905), Broch (1924) & (1927). The many populations varying greatly in shape hindered a good systematic description, but now all the different forms are regarded as responses on external factors, see Barnes & Powell (1950a), Schäfer (1952).

Darwin (1854, p. 270–271) describes monstrous animals with truncated cirri and penis. Feyling-Hanssen (1953) noted, that in *B. balanoides* from Spitsbergen the parietal tubes are not always secondarily filled out, and that the corrosion is not as severe as in animals from Norway. The shape of *B. balanoides* becomes more flat with increasing size according to the panel observations of Barnes & Powell (1953). Fast growing animals also flatten out (Connell 1961a). My experience confirms the above statements. However, this is not the case with the results of Barnes & Barnes (1962a) in which *B. balanoides* flattens according to how brackish the water is. As the basic material of these authors does not seem convincing, I have placed a questionmark behind the result despite Barnes and Barnes (1961a) refer to it as a stated fact.

Information collected here on the shape and the variation during growth seems enough to show that the carino-rostral length cannot be used as a measure of size without giving the relation to weight. In this respect it must be mentioned that the animals can twist their axis during growth, e.g. Stubbings (1956).

Chemical composition

Vinogradova (1953 p. 390) gives a few data on the chemical composition of the barnacles.

Barnes, Barnes & Finlayson (1963a) give a lot of data on the seasonal variations of the chemical composition. The size is given both as valve weight, dry and wet body-weight, shell base diameter and content of DNA.

The paper by Barnes & Barnes (1959d) has the title "Some parameters of growth in the common intertidal barnacle *Balanus balanoides* (L.)", but deals with the chemical composition. The paper gives relations between nitrogen content and body weight, weight of ovary, shell length, and volume.

Horizontal distribution

The distribution of *B. balanoides* in the North Atlantic is well known. The occurrence of the species in the Pacific Ocean is not commented upon here, as I do not have first hand knowledge of the populations in that area.

Among the more important papers describing the populations near the northern limit are: Vanhöffen (1897), Froda (1924), Madsen (1936, 1940), Bertelsen (1937), Stephensen (1938), Fisher (1943), Feyling-Hanssen (1953), Ellis (1955), Bousfield (1955a), Barnes (1957b), Ballantine (1961). To these should be added the many Russian papers dealing with the populations in the Barents Sea and White Sea, of which I have only an incomplete and often second-hand knowledge.

Descriptions of the southern limit are found in e.g. Fisher-Piette & Prenant (1956, 1957), Bishop *et al.* (1957), Crisp & Fisher-Piette (1959), Wells, Wells & Gray (1960).

The distribution toward the Baltic is described in e.g. Steffensen (1933), Poulsen (1935), Brattström (1958), Barnes & Barnes (1962a).

The peculiar shift in demand for increasing exposure going from south to north as was observed in Greenland (Petersen 1962) is further supported by the observations of Fisher (1943) and Ballantine (1961) who have both made journeys to Spain and Norway. Ballantine describes conditions thus: "Many species show a progressive change in their exposure tolerances from north to south"—"all the species behave in the same way, occupying increasingly sheltered shores towards the southern end of their range".

When *B. balanoides* is said to prefer exposed headlands both at Spitsbergen (Feyling-Hanssen 1953), in Greenland (Petersen 1962), and in Øresund (Brattström 1958), it is worth adding that in Spitsbergen the localities for *B. balanoides* are at the openings of the fjords and that the opening to the Baltic consists of Øresund and the Great Belt. We must underline the similarities in origin, bathymetri, hydrography and the marine life between the Baltic and the Norwegian and Greenlandic fjords. The Baltic is simply the southernmost and the biggest of such fjords. In Danish waters warmer than Øresund e.g. the Isefjord (Rasmussen, in press), *B. balanoides* can be found in sheltered localities.

Along the shores of Europe a shift in the exposure tolerance occurs. Southward & Crisp (1956) write that *B. balanoides* in the western part of the Channel, prefers estuarine areas, while *Chathamalus stellatus*, here near its northern limit, prefers exposed headlands. Crisp & Southward (1958) state: "In the western Bassin (of the Channel) *B. balanoides* thrives better and grows to a larger size in the estuaries and harbours than on the open coast. In the eastern part of the Channel it is dominant on the open coast, and in sheltered bays and harbours is replaced by *Elminius modestus*". This comment on growth is not in accordance with the general view that growth is better in an exposed site than in a sheltered site.

The southernmost populations in Europe are found only in the rias and harbours of Northern Spain and Northern Portugal. Alternatively, the southernmost populations on the American Atlantic coast are found on exposed wrecks immediately north of Cap Hatteras, (Wells, Wells & Gray 1960), who also note, that competition from other species is not involved in determining the southern limit. On the other hand, Barnes (1959b) writes: "at Sandy Hook, N.J. it is only common in the more protected situations". This sentence probably refers to *B. balanoides.*

The distribution of *B. balanoides* has been used for may zoogeographical considerations; for a survey see Madsen (1940) and Barnes (1957b). Hutchins (1947) brought the matter one step forward by making a scheme for the influence of temperature on the distribution of marine species. *B. balanoides* is used as an example of a species in which both the southern limit (close to the 8°C winterisotherm) and the northern limit (at the 4°C summerisotherm) depends on the possibilities of re-population and not on possibilities for survival. Hutchins discusses different possibilities for critical temperatures and trigger temperatures at different stages in the life history. The influence of the feeding season is also pointed out.

Many authors have commented upon the factors related to the distribution of *B. balanoides*, either simultaneous, consecutive or causal factors. Only some of the more important papers are mentioned here; others are mentioned later in this chapter.

Barnes (1957b) showed the relation between the maximal retreat of the "pack ice" in the autumn and the northern limit. Apart from a criticism on the vague conception "pack ice" such relations does not greatly expand our understanding of the ecology of *B. balanoides.* In Petersen (1962) evidence is given for the importance of the planktonic stage and the attachment stage for the northward distribution.

The southern limit has caused some trouble. Barnes (1958a) believes that the southern limit on the American eastcoast is not determined by the 8° winterisotherm as postulated by Hutchins (1947). Wells, Wells & Gray (1960) rejected Barnes' concept by finding *B. balanoides* several hundreds miles further south. Further arguments are found in Barnes (1961b). Barnes (1959a) gives a survey on important factors for the life history of *B. balanoides*, e.g.: spring diatom outburst, endogene processes, neurosecretory cells and a temperature block to maturation at temperatures above about 10°C.

As far as I know studies on the life-history of the southernmost populations are not being carried out, not even on the European coasts. Hence of great interest are the works of Southward and Crisp from the Channel, published in a number of papers. Southward & Crisp (1956) could not adequately explain the distribution of *Chathamalus stellatus* and *B. balanoides* by the action of the physical environment on either one of these two species, but they suggest a dynamic concept with the two competing species in a state of equilibrium. Minor changes in the physical environment cause the boundaries to alter. It is suggested that temperature may be the most important factor. In the papers of Southward (1957, 1958a) the direct influence of temperature on distribution is doubted, "Causal relationship between temperature and distribution must be sought in non-lethal terms" (Southward 1958a).

As the value of laboratory experiments may often be overestimated and the value of field observations underestimated (Schlieper 1962), the following quotation from Crisp & Southward (1958) is noteworthy: "It seems unlikely that experiments on the tolerances of animals to temperature extremes will be immediately relevant to understanding the effect of temperature in distribution". Of course, this statement is true for factors other than temperature.

Southward made an interesting survey on the distribution of the pelagic larvae of *B. balanoides* in the waters around the Scilly Isles and along Cornwall. No larvae were found off Scilly, where no adults are present (Crisp & Southward 1958). Before a conclusion on the influence of residual drift on distribution can be made control investigations are necessary at islands farther north, and in a relative position to a nearby continent similar to that of Scilly, e.g. some of the islands west and north of Scotland. At St. Kilda *B. balanoides* is common (Gould, Bagenal & Connell 1952). Plankton-investigations similar to those made in the Miramichi (Bousfield 1955b) should be made in a southern estuary, e.g., Rade de Brest or a port in the northwestern part of the Iberian Peninsula. In Miramichi *B. balanoides* is found at the marine positions, in the rias of Spain it is found in the estuarine positions. In Miramichi the distribution of the different species of barnacles could partly be explained by the reaction of the pelagic larvae to the hydrographic factors. It would be interesting to know the behaviour of the larvae in the rias of Spain.

We must suppose the larvae to possess a perception-choice system which enables them to find their permanent sites. The output of this system might be altered by e.g. temperature and salinity, thus explaining the difference in exposure of the sites going from south to north. Considered from a phylogenetic point of view the adults of *B. balanoides* have such special demands that the species cannot "afford" to let mere chance govern the settling of the larvae. Moreover, *B. balanoides* belong to a group, Cirrepedia, the members of which often have very peculiar biotopes.

Vertical distribution

B. balanoides occurs almost exclusively in the tidal zone in a belt from L.W.M. to a line between M.W.M. and H.W.M. The belt is usually very sharply defined and can be related to the tide. On exposed localities the animals occur both higher up and lower down the shore (Moore 1935c). Generally *B. balanoides* is considered to occur only above L.W.M. (Darwin 1854, Dons 1945, Ellis & Wilce 1962, Petersen 1962), but some authors report the animal from greater depths (Schäfer 1952, Bousfield 1954). Bousfield (1955a) give a find from 63 m depth. Poulsen (1935) doubts a find from 35 m depth in Kattegat published by Stephensen (1933); Poulsen only found *B. balanoides* in samples from depths of not more than a couple of meters, and never in the hundreds of samples from greater depths he investigated. Pyefinch (1948b) states: "Contrary to general experience these studies have shown, that this species can settle, metamorphose and grow on such surfaces, continually immersed, though settlement is probably less dense than on intertidal surfaces".

A chapter on the vertical distribution of *B. balanoides* populations should also deal with the zonation problems, but as these are a little out of the scope of the present paper, and as they are excellently treated in the papers of Southward (1958b) and Lewis (1961 and 1964) the reader is referred to these papers.

The causal factors behind the vertical distribution are very difficult to grasp. Some of the more relevant mentioned in literature, will be cited here.

Runnström (1925) noticed the influence of physical factors: "*Balanus balanoides* scheint eine bedeutend längere Austrochen zu vertragen als *Mytilus edulis*. Dies ist scheinbar einer der Faktoren, welche es bedingen, dass der Balanusgürtel in der Littoralregion höher hinaufreicht als der Mytilusgürtel". The lethal desiccation in Runnström's experiments greatly exceeded conditions experienced by the natural populations.

Feyling-Hanssen (1953) discusses the influence of the ice-foot on the *B. balanoides* populations. In Spitsbergen these populations never develop into the "white belt" found in Norwegian populations, as the animal occurs only in crevices. The species was not found below L.W.M. Feyling-Hanssen concludes, that the ice-foot protects the animals and that ice-foot and drifting ice do not hurt *B. balanoides*, see also Petersen (1962) for similar results.

Barnes & Powell (1953) noted, that *B. balanoides* is an intertidal species, but that total submersion does not prevent growth and development in experimental populations.

Bousfield (1955b) gives some valuable hints on the factors controlling distribution. He noted that interspecific competition for space or food does not limit the distribution, and that *B. balanoides* has no serious predator in the Miramichi. He suggests predation by starfish explains the rarity of *B. balanoides* below L.W.M. Moreover, he states: "The foregoing observations on the ecology of adult barnacles show that suitable conditions for all three species (*B. balanoides*, *improvisus* and *crenatus*) exist in the outer estuary and that differences in the distribution and abundance between the species must be the result of factors operating during the planktonic life history".

Bassindale (1958) writes that the adult pattern of distribution of the adult animals is determined mainly by the selection and choice shown by the larvae, and that this pattern is modified to only a slight extent by differential mortality.

Connell (1961b) gives some causes for zonation: "The upper limit of most intertidal animals are most probably determined by heat and/or desiccation, and not by competition and/or predation. The lower limit may be due to interspecific competition for space, predation or other biotic factors. Physical factors may act directly to determine this lower boundary". Similar arguments are given in Connell (1961a); Connell has given good reason for his view, but he does not report mass-death among *B. balanoides* settled above the sharp upper limit of the adults, nor does he report a gradual scarcity among animals settled below L.W.M. and downwards to greater depths. Such observations would seem necessary in order to support his view. Of two of the most important predators of the european *B. balanoides*, *Thais lapillus* and *Patella vulgata* (CONNELL 1961a), *Patella vulgata* does not occur in Greenland (THORSON 1941) and *Thais lapillus* is very rare, being present only in a small South Greenland fjord "Neritiksok" (MÖRCH 1857, Dr. POUL M. HANSEN, Greenland Fishery Investigations, personal communication). These intertidal predators were not found in my material. The subtidal predators on barnacles *Asterias rubens* and *Onchidoris fusca* are present in Greenland.

Development of embryos

The duration of embryo development is often taken as the time from fertilisation to hatching, but should be divided into the real development period from fertilisation to the fully developed nauplius, and a period of diapause broken by hatching.

The embryo-development has in particular been studied by CRISP and his co-authors. They have described different stages of the development and given their duration. From CRISP (1959b) it can be deduced that in Southern England the period from fertilisation to hatching is about 120 days, and the period of development to nauplius is about 96 days; thus the period of diapause is about 24 days. As CRISP's paper deals with field observations, raft-experiments and laboratory experiments, this extract must of course be taken with some reservation. PATEL & CRISP (1961) give the period from fertilisation to hatching as up to 150 days in temperate latitudes, a remarkable period compared with that of other species by being longer than the intermoult period. CRISP (1964) showed by transplantation experiments that East American *B. balanoides* fertilize $1^1/_2$ to 3 weeks earlier than the British ones and that their development was twice as fast as the British embryos; however, hatching occurred at the same time, in March, for both types. His conclusion on racial differences between East American and West European *B. balanoides* need the support of transplantation experiments inside the Western European populations, e.g. a comparison between animals from Northern Norway and Brittany using a standard technique.

BARNES & BARNES (1959a) deal with the development of *B. balanoides* eggs.

It is possible to give more or less precise estimates on the duration of the period from fertilisation to hatching from the many papers from different areas, and these are given in the following chapters.

Hatching

Within the whole area of distribution of the species hatching occurs once a year, viz. in the spring, but with the variation that spring occurs at different times in the different localities. In Western Europe hatching occurs in the months of February to April, the southernmost populations being the earliest. In Spitsbergen hatching occurs in June-August and may in some years fail (Feyling-Hanssen 1953). At Woods Hole January is the month for maximum hatching (Fish 1925). At St. Andrews it is in March-April and at Miramichi in April-May (Bousfield 1954).

A number of papers treat the factors that may induce the hatching and how this occurs.

Crisp (1956) showed that a heat-stable, nonspecific substance in aqueous body-extract promotes the breakdown of the sticky secretion into which the fertilised eggs lie as the eggmasses. The hatching was also dependent on food-uptake.

In Barnes (1957a, 1962a) and in Barnes & Barnes (1959e) the spring diatom outburst is related to hatching, and hatching substances are studied.

Crisp & Spencer (1958) investigated thoroughly the qualities of the hatching substance found in the tissue of the barnacles.

Crisp (1962a) found that the adults secrete the hatching factor when feeding actively in the spring, thus synchronising hatching with spring diatom outburst. East American *B. balanoides* transplanted to England fertilise earlier, develop embryos faster but withhold the release of nauplii until the march diatom outburst and hatch at the same time as the English ones. In Eastern America the diatom outburst occurs in mid-winter.

Many authors have observed that hatching occurs earlier at the higher levels (e.g. Moore 1935b).

Concerning the actual process of hatchings, Barnes (1955a) concludes, that the mechanical activity of the larvae bursts the egg capsule. Crisp & Costlow (1963) observed that the embryos swell about 30 % of their volume during the process of hatching.

Larval Life

The duration of the larval stage can be measured from serial samples either by studying the sessile population, viz. the progress of the hatching and the progress of the settlement, or by studying the planktonic stages, viz. the occurrence of the first naupliar stage and of the cypris stage.

According to FISH (1925) the duration of the larval stage at Woods Hole can be estimated at 55–60 days, in the months of January and March at surface temperatures from –1.5 to 3° C. At St. Andrews and Halifax the duration is 5–6 weeks, and at Miramichi 4–5 weeks (BOUSFIELD 1954).

PYEFINCH (1948b) found the duration to be about 4 weeks at Millport, with hatching in the beginning of March and settling in the beginning of April. By studying serial planktonic samples he also found the duration of the individual stages and discovered that several broods occurred during the season. BARNES (1956b) also gives the duration as 4 weeks at Millport, and BARNES (1953b) found several broods on the larval population. His conclusion on the adult populations being discontinually separated along the vertical seems difficult to accept, a continual gradient being more likely along that axis. The discontinuity may exist between different areas along the shore, viz. along the horizontal axis. The heterogenity of the larval population may be superimposed on larvae from a continually breeding adult population by currents varying in direction and speed, or by a breeding synchronized to the moon phases.

CRISP (1962b) gives the duration of the larval stage in Southwest Britain from February/March to April/May, in Northeast Britain from March/April to May/June and at Bear Island from February/March to perhaps May/June. In the Arktis the larvae are greater than in England.

Tables on the duration of the larval stage in different areas are found in BOUSFIELD (1955b) and in BARNES & BARNES (1958a). The last named authors claim that the estimate on the duration of the larval life is the same whether they use the first appearance or the peak values of the larval stages in the samples.

Little has been studied on the ecology of the planktonic stages compared with the immense amount of work on the settled or settling stages. BARNES (1953a) found that the larvae could endure a lowering in salinity to $15\,^0/_{00}$ without harm and gives further information on the tolerance of the larvae to low salinities. BOUSFIELD (1955b) and BOUSFIELD & LEIM (1959) give a discussion on the importance of the larval stage for the penetration of the species into an estuarium. MOYSE (1963) showed by laboratory experiments, that *B. balanoides* larvae could be reared successfully on diatoms, but not on flagellates. Tropical barnacle larvae gave the opposite result. This indicates the importance of food for the distribution of the species.

Settling

The cypris settle in March-April at St. Malo (HATTON & FISCHER-PIETTE 1932, HATTON 1938), in April-May in Britain (ELMHIRST 1923, Moore 1935b, c, Corlett 1948), in April at Bergen (Runnström 1925) and in the latter part of April on the Swedish westcoast (Blom & Nyholm 1961). At Spitsbergen settling occurs late in July and early in August, but it can fail (Feyling-Hanssen 1953). Along the West Atlantic coast settling occurs from middle of February to about first of April at Woods Hole (Fish 1925, Grave 1933), at St. Andrews and Miramichi from the middle of April to the first part of June (Bousfield 1954).

The cypris are not forced to settle at a random place when the pelagic development is completed. The active selection of site performed by the larvae is well described by Elmhirst (1923): "The cypris stage settle in April and May, particularly within neap tidal range. When settling shelter (of possibly moisture) is sought. The presence of freshwater seems to be avoided. Spat settles in rock pools especially at the edges but avoids apparently excellent sites which are continually submerged. Rockpool conditions are unsuitable and very few survive".

The description of Pyefinch (1948b) likewise agree with my observations from Greenland, he writes: "Settling is usually confined to cracks, crevises and other irregularities of the surface, though, if the supply of settling stages is maintained, this distinction later disappear".

The reactions of the cypris have been the subject of many studies. Light appears to be a major factor for the behaviour of many marine larvae (Thorson 1964). Runnström (1925) investigated the phototropism of the larvae. They were normally positive phototrope, but could change to negative, partly depending on temperature. He also noted the importance of adequate surfaces. Barnes, Crisp & Powell (1951) showed that the cypris settle with the front against the light, but the orientation to cracks, grooves etc. is more marked. Cypris prefer shaded positions to well-illuminated positions. As light orientation gives no advantage to the adults the authors explain it as a vestige of the light reactions in the pelagic stage. The "shading reaction" is supposed to be of little survival value for the species. In a continued study Barnes & Powell (1953) suggest that settlement is the result of two opposing factors, viz. gain from a thin waterfilm, when the tide crosses the panel, and due to desiccation exposure to air. These panel observation were not verified by observations on natural populations.

Crisp (1955) found by laboratory tests the current speeds by which the cypris settle. This has a very limited value for explaining zonation as current speed over the different surfaces in the tidal zone during the settling period varies so much that settling might occur everywhere, had current speed been the only factor. Crisp & Knight-Jones (1953) noted that cypris could release their hold and withdraw their attennules if exposed to air whilst crawling.

The texture of the surfaces is important for settling, as noted in many papers. Schäfer (1952) observed that the *B. balanoides* settle reluctantly on chalk, both limestone and shells of *Littorina* and *Mytilus*. In Petersen (1962) is described a similar case. Crisp & Barnes (1954) concluded from many experiments, that the cypris of *B. balanoides* is rugophilic and that they orientate their axis along that of the grove. Rugotropism is stronger than phototropism. Rugotropism is further treated in Barnes (1956a and 1956c).

The importance of a protein for gregariousness during settling was shown by Knight-Jones (1953a), and in Knight-Jones & Moyse (1961) further examples on both the gregarious response and the spacing-out response is given.

The very careful investigations of Crisp & Meadows (1962) lead to the result that arthropodin on a solid surface, and not in a solution, induces settling. Arthropodin of their own species being the most attractive.

Other factors not yet fully investigated are important for settling. Thus Crisp & Barnes (1954) noted: "The first larvae take the best sites, later larvae may undergo a lowering of treshold of the settling reaction". Additionally, Cornell (1961a) writes, that cessation of settlement was not due to an inadequate supply of larvae and that the rate of settlement would be proportional to the numbers already attached, if we suppose gregariousness to be the only settling factor.

Crisp (1961) showed experimentally that the later settlers tend to maintain a distance of about 2 mm from the earlier ones. The territorial separation is reduced but not eliminated as the population density rises. Though strongly attracted to pits cypris avoid pits containing previously settled individuals.

The anatomical alterations during metamorphosis from cypris to settled animal is described by Walley (1964), and the importance of phagocytotic cells for this process is demonstrated.

Density

Informations on the number of animals per surface unity are given in many papers or could be calculated from the data published. Informations on the size and age of the animals and on the quality of the shore seem necessary to make the informations on density useful, but as these are difficult to obtain from the literature simultaneously with the density, it has not been considered worth while to include information on density. Moreover, with problems like the settling behaviour and the hummock-formation in mind, mere information on density would be difficult to utilize at our present stage of knowledge.

Mortality

It is rather easy to study the mortality of a sessile animal like the adult *B. balanoides*, both by panel experiments or by observing natural populations, using techniques such as photographing, marking, mapping. Many different populations have been studied under different circumstances and during varying lengths of time, which taken together, make a comparison of data on mortality from different papers a doubtful task.

The causes of death might be easy to demonstrate, but are often unknown. Age, competition, predation, parasitism, starvation are biological factors that can cause death. Physical-chemical factors like extremes in the environment are mentioned in the passages on distribution, page 80–83. The more important predators recorded by several authors are *Thais lapillus*, *Patella vulgata* and *Asterias rubens*. Barnes & Powell (1954) observed *Onchidoris fusca* eat *B. balanoides* and *B. crenatus*. In Godhavn I saw *Onchidoris* eat *B. crenatus* but never *B. balanoides*, which lives above L.W.M. *Littorina* species have been recorded as predators on *B. balanoides* (e.g. Elmhirst 1923, Feyling-Hanssen 1953), but the observations are presumably a misinterpretation of the hiding reaction of the *Littorina* in empty barnacle shells.

The influence of the important predators are mentioned by e.g. Fischer-Piette (1935), Bousfield (1954), Connell (1961 a & b), Barnes & Barnes 1962 a). Predation by *Asterias* is considered important for determining the lower limit. *Thais*, preferring the larger animals, should have an effect on the age structure of the population. *Patella* seems to prefer the smaller barnacles.

Relation between mortality and density is studied in Hatton (1938).

In the southern populations of *B. balanoides* the parasite *Hemioniscus balani* is found, but not in the northern ones. The effect of this parasitism on mortality is not known.

Growth

The problem of growth has many aspects, including of course the size of the animals obtained during certain periods, the alterations in the course of time in shape, in metabolism, and in behaviour et cetera. All these conditions must be related to each other and to the surroundings. In this passage only the papers on the growth of the sessile animals will be treated, but as these papers are widely separated both in time, methods and place, they hardly provide a satisfying synthesis. The most important information on size and age of *B. balanoides* is given in Table 10. Some information on size and age was given by Darwin (1854).

Many methods have been used to measure size and age, and many methods have been used to demonstrate the growth results; the easiest of these might be the common growth curve, with length plotted against time. This is used in e.g. HATTON (1938), RUNNSTRÖM (1925), FEYLING-HANSSEN (1953).

The word growth rate is used in different ways. MOORE (1934 a) defines growth rate as the average percentage increase in volume per ten days. He found, with certain modifications, the best growth and the longest life span on the higher levels, while HATTON & FISCHER-PIETTE (1932) found these two features on the lower levels. BARNES & POWELL (1953) give the basal length at the end of the first 2 or 3 seasons for animals at different levels. They calculate "mean specific growth rate" as the increase in length per unit length per day ×100. The growth was better on panels than in natural populations, and better on submerged panels than on panels in the tidal zone. However, CRISP & PATEL (1960) state that it is beneficial for the barnacles to be out of water for about 8 hours each day.

CRISP (1960) uses both weight and rostro-carinal length as size measures. He speaks both of mean rate of growth and of growth-rate. Moreover he criticizes the "specific growth rate" used by BARNES & POWELL (1953). CRISP's considerations on the growth-curves is reminiscent of the more thorough considerations of BEVERTON & HOLT (1958). CRISP states that growth especially depends on food supply and he explains the sigmoid growth curve, common for many animals, by conditions specific for the barnacles.

CONNELL (1961 a) uses "mean specific growth rate" equal to increase in length per unit length per day ×100, and "absolute growth rate" equal to increase in length per day ×100 and compares these measurements from different areas. He suggests that *Thais*' selection of large sized barnacles may explain the conflict in the literature concerning the growth rate of *B. balanoides* at different shore levels.

From observations made on a short trip with short visits to many localities BARNES & BARNES (1962 a) attempt some data on growth in Swedish, Danish and German waters.

Factors influencing growth have been commented upon in BARNES (1952–53, 1959 c, 1961 a, 1963 a). DARWIN (1854) wrote of *B. balanoides* "when left uncovered by water they kept the orifice of their operculums a little open, with a buble of air within their sacs, so that the orifice was in fact closed by a thin septum of water, with air beneath. When disturbed, they closed their operculums with force and expelled the buble of air with a clicking noise". DARWIN also noticed, that *B. balanoides* was very sensitive to shadows. Observations on the airbuble by DARWIN (1854) is renewed by BARNES & BARNES (1957, 1958 b).

Beverton & Holt (1959) write: "Analysis of growth rates within populations of the same or closely related species living in different areas suggest that two factors account for most of the variation found: food and temperature. The asymptotic size is greatly modified by the supply of food available, but this does not affect the parameter K. Difference in environmental temperature, however, affect both K and L_∞; thus with an increase in water temperature K increases roughly proportionally with the logarithm of temperature and L_∞ decreases, but to a lesser extent".

Behaviour that may be important for the growth processes is studied in the case of the cirral beat by e.g. Southward (1955a, b), and by Crisp & Southward (1961), and in the case of the moulting cycle by Crisp & Patel (1960).

Some investigations on growth, metabolism, size and other factors are described in three papers by Barnes & Barnes (1959a, b, c). In Barnes, Barnes & Finlayson (1963a, b), measurements based on the respiration of animals dissected from their shells and ovary are published.

Gonad development and fertilisation

The time available for the gonads to reach maturity varies greatly within the distribution area of the species. It is common to give this period the duration from hatching to fertilization, which at the southern limit is approximately from February to December and at the northern limit approximately from June to August. The progress of the gonad development, which is important to know for estimating the factors synchronizing fertilisation, can be studied either by serial sampling during the season (e.g. Pyefinch 1948b) or by watching the gonads through a glass plate (e.g. Crisp & Patel 1961). The latter method has the drawback that *B. balanoides* avoids settling on glass surfaces.

The factors governing gonad development are not only global in character, but also local. The description of Moore (1935c) covers most of the collective findings: "At all the levels the ovaries develop and mature considerably earlier than the testes and are in fact well developed while the barnacle is still carrying in its mantle cavity the larvae of the previous brood". (Note: In Greenland animals with both naupliae and developed ovary are rare). Moore continues: "The barnacles from the highest level on the shore being the most advanced and shedding their genital products first". — — — "At Port Erin and Bradda the first year barnacles do not develop gonads on the shore above half tide level. Below this point maturation occurs in the first year, and development follows much the same course as it does in the second year at higher levels, except for being slightly slower in the earlier stages."

The close syncronization to the seasons peculiar to *B. balanoides* (PATEL & CRISP 1961) must depend primarily on external factors. CRISP (1959a) and CRISP & CLEGG (1960) mention that the following are important for the synchronization: the slowing down of metabolism, diminishing amount of light received, food supply and environmental factors acting over a long period. Temperature alone does not determine onset of fertilization.

BOUSFIELD (1954) notes that at St. Andrews, copulation starts in October when the daily air minimum drops to freezing point of water (about —2°C). BARNES (1963b) showed that a constant illumination inhibits breeding and that there is a critical temperature above which breeding will not take place.

CRISP (1957a) was able to accelerate the gonad development in the laboratory by keeping *B. balanoides* at low temperatures during summer.

Copulation has been observed by several authors. WALLEY (1965) describes the process of oviposition and the materials holding the eggs together. BARNES & BARNES (1956a) also give information on this subject.

DANSK RESUMÉ

På et kursus i naturhistorie for lærere ved det grønlandske skolevæsen afholdt i august 1958 på Arktisk Station, Godhavn, blev det besluttet at gennemføre en undersøgelse af de grønlandske tidevandszonedyrs økologi. De frivillige deltagere indsamlede med 2–3 ugers mellemrum, for så vidt forholdene tillod det, gennem en sæson på en begrænset lokalitet en prøve af alle dyr placeret ved midtvandsmærket i tidevandszonen. Alle prøverne sendtes til Arktisk Station til oparbejdelse. Den vigtigste af de fundne arter, *Balanus balanoides*, er behandlet i nærværende arbejde.

Der er givet en kort redegørelse for Grønlands geografiske placering særlig i forhold til de tre oceanstrømme: Østgrønlandsstrømmen, Vestgrønlandsstrømmen og den canadiske Polarstrøm, og disse strømmes betydning for de enkelte lokaliteter (se fig. 1). Udfra de enkelte deltageres originalbeskrivelser er lokaliteterne beskrevet, og de opfylder de på forhånd stillede betingelser, nemlig at de ikke måtte være udsat for ferskvand, forurening eller voldsom brænding i større stil.

Fra mange forskellige kilder er indsamlet oplysninger om havets overfladetemperaturer og luftens maximums- og minimumstemperaturer. De daglige værdier er så vidt muligt givet, idet feltobservationer tydede på, at extreme temperaturer havde betydning for dyrene, i hvert fald for littorinerne.

Der er tegnet en sumfunktion over "varmesummen" beregnet ud fra − 1°C som biologisk nulpunkt, en metode der må tages med forbehold og som må ses i sammenhæng med stofskifteprocesserne og aldersproblemet.

Det vises, at længden af scutum er det bedste størrelsesmål for *B. balanoides*. Ydermere kan scutum give gode oplysninger om væksten på grund af de veldefinerede vækstringe på de fleste scutae. De knækkede scutae er basis for en hypotese om, at fugle hakker balaner ud af skallerne, men at nogle overlever angrebet. Dette blev dog aldrig direkte iagttaget.

Studier over kønsorganerne samt forekomsten af nauplier og cypris i prøverne har resulteret i skøn over stadierne i den sexuelle cyclus. De vigtigste resultater er givet i fig. 33 samt på temperaturkurverne fig. 3–8, hvor sammenhængen mellem den årlige temperaturvariation og kønscyclus vises. Den årlige kønscyclus' afhængighed af andre faktorer, som forårsopblomstringen af diatomer, fødeforhold, daglængde og betydningen af kemiske externe og interne processer, diskuteres.

Den tid, larverne tilbringer pelagisk, synes helt uafhængig af temperaturforholdene, men afhænger formentlig af fødeforholdene.

Selv nær nordgrænsen synes voksne dyr at kunne gennemføre udvikling af gonader og befrugtning i den korte sæson, medens der ikke levnes tid til larveudviklingen. Ligeledes synes klækningsprocessen at blive hindret, formentlig på grund af manglende klækningsfaktorer.

Både feltobservationer og størrelsesfordelingen af 0.-gr. dyrene og af 1. vinterring (bimodal i Nordgrønland, monodal i Sydgrønland) affødte en hypotese om to bundfældninger i Nordgrønland, den første fra larver transporteret nord på med Vestgrønlandsstrømmen og den anden fra den lokale larvepopulation. En betydelig transport nordefter måtte ud fra publicerede hydrografiske observationer forventes. Udbredelsen af "Vestisen" (den canadiske Polarstrøm) om vinteren langs nordvestkysten og syd på til Holsteinsborg kan forklare en diskontinuitet i forholdene langs kysten om foråret.

Væksten af 0.-gr. dyrene demonstreres ud fra deres størrelsesfordeling i de periodiske prøver. Det understreges, at disse prøver ikke repræsenterer samme population af 0.-gr. dyr blot til forskellig tid, idet forholdet mellem de enkelte størrelsesgrupper af 0.-gr. dyr ændres ikke alene af hvert enkelt dyrs almindelige tilvækst i løbet af sæsonen, men også af ændringer i bundfældningens intensitet, af forskellig dødelighed og af ændringer i dyrenes vækstprocesser med stigende størrelse. Vækstkurverne i fig. 45 sammenligner væksten på de forskellige lokaliteter for et dyr, der tænkes bundfældet på tidspunktet for maximal bundfældning og med en vækst gennemsnitlig for den stedlige population. Disse vækstkurver har ingen rimelig relation hverken til temperaturforholdene, repræsenteret ved "varmesummen", eller til fødeforholdene, repræsenteret ved primærproduktionen. Det sluttes derfor, at væksten afhænger af dyrenes egen evne til at fange og fordøje føden, hvilket kan forklares at være uafhængig af temperaturforholdene og fødemængden inden for vide grænser.

Væksten af de ældre dyr kan måles både ud fra vinterringene og ud fra tilvæksten i løbet af den undersøgte sæson. Det viste sig, at jo ældre dyrene var, jo mindre var deres første vinterring, hvilket svarer til Rosa Lee's fænomen, velkendt fra fiskepopulationer. Dette kan her formentlig forklares ved en større dødelighed hos store og hurtigtvoksende dyr. En skønnet vækstkurve for længde-alder relationen er tegnet således, at den giver væksten for et dyr med en begyndelseslængde svarende til gennemsnittet for de yngre dyr og med en tilvækst svarende til den tilvækst, de ældre dyr har haft. Disse kurver er sammenlignet på fig. 65 og 66. Resultaterne for de forskellige niveauer ved Godhavn er let forståelige, idet de lavest siddende dyr i tidevandszonen vokser hurtigst. Men de ældste dyr findes på de højeste niveauer. Derimod er tendensen i resultaterne fra de forskellige geografiske lokaliteter mere uklar. Tilsyneladende er væksten størst ved de mest arktisk prægede lokaliteter. Væksten ved de to stationer: Augpilagtoq og Angmagssalik nær nordgrænserne på henholdsvis vest- og østkysten er ikke ringe. Vækstkurverne er bearbejdet efter metoder beskrevet i Beverton og Holt (1957) og Ricker (1958) med henblik på en senere sammenligning med andre arter. Resultaterne er givet i tabel 9. Det ses blandt andet, at på de mest arktisk prægede lokaliteter bliver dyrene både store og gamle, medens for dyr på samme lokalitet (Godhavn) findes de ældste på de højeste niveauer og de største på de laveste niveauer. Resultaterne forstyrres dog af den kendsgerning, at ved nordgrænsen (Augpilagtoq) fandtes arten kun ved lavvandsmærket.

Tabel 10 giver en sammenligning mellem de lokaliteter i det nordatlantiske område, hvorfra der foreligger en tilstrækkelig stor mængde oplysninger om *B. balanoides*. Tendensen i ændringerne af alderssammensætningen og vækstforhold, som kan udledes for lokaliteter uden for Grønland, svarer til de netop beskrevne for lokaliteterne inden for Grønland, naturligvis med mange modifikationer.

Ud fra de 5 undersøgelser over *B. balanoides*, som er foretaget i distrikterne nord for Disko Bugt, er det vist i tabel 11, hvorledes forekomsten af arten i disse distrikter svinger. Dette er sat i relation til temperaturforholdene i 8 år forud for de pågældende undersøgelser. Nordgrænsen for *B. balanoides* vil formentlig i kuldeperioder ligge ved Vaigat og i varmeperioder ved Upernaviks Isstrøm. Fortsatte studier over svingninger i artens nordgrænse vil formentlig kunne støtte undersøgelser over svingninger i klimaforholdene og Vestgrønlandsstrømmens udbredelse, forhold der er af stor betydning for den menneskelige population og de kommercielle fangstdyr i Vestgrønland.

En yderligere gennemgang af litteraturen om *B. balanoides* er givet i det sidste kapitel.

BIBLIOGRAPHY

Note: Not all papers listed are cited in the text.

Austin, A. P., D. J. Crisp and A. M. Patil, 1958: The chromosome numbers of certain barnacles in British waters. — Quart. Jl microsc. Sci., 99: 497–504.

Ballantine, W. J., 1961: A biologically-defined exposure scale for the comparative description of rocky shores. — Fld. Stud., I, nr. 3, 19 pp.

Barnes, H., 1949a: A statistical study of the variation in vertical plankton hauls, with special reference to the loss of the catch with divided hauls. — J. mar. biol. Ass. U.K., 28: 429–446.

— 1949b: On the volume measurement of water filtered by a plankton pump with an observation on the distribution of plankton animals. — J. mar. biol. Ass. U.K., 28: 651–662.

— 1950a: *Sagitta setosa* J. Müller in the Clyde. — Nature, Lond., 166: 447.

— 1950b: A note on the barnacle larvae of the Clyde sea area as sampled by the Hardy Continuous Plankton Recorder. — J. mar. biol. Ass. U.K., 29: 73–80.

— 1951a: A statistical study of the variability of catches obtained with two models of the Hardy Plankton Indicator. — Hull Bull. mar. Ecol. 2: 283–293.

— 1951b: Horizontal plankton hauls. — J. Cons. perm. int. Explor. Mer, 17: 133–139.

— 1952: The use of transformation in marine biological statistics. — J. Cons. perm. int. Explor. Mer, 18: 61–71.

— 1952–53: The effect of light on the growth rate of the two barnacles *Balanus balanoides* (L.) and *B. crenatus* Brug. under conditions of total submergence. — Oikos, 4: 104–111.

— 1953a: The effect of lowered salinity on some barnacle nauplii. — J. Anim. Ecol., 22: 328–330.

— 1953b: Size variations in the cyprids of some common barnacles. — J. mar. biol. Ass., 32: 297–304.

— 1953c: On the southern limits of the intertidal barnacle *Balanus balanoides.* — Ecology, 34: 429–430.

— 1953d: A note on cumulative frequency curves. — Memorie Ist. ital. Idrobiol., 7: 201–207.

— 1953e: An effect of parasitism on *Balanus balanus* (L.) da Costa. – Nature, Lond., 172: 128.

— 1953f: Considerazioni statistiche sulla distribuzione spaziale di alcuni organismi planctonici raccolti su un lungo percorso nel golfo della clyde. — Memorie Ist. ital. Idrobiol. 7: 109–127.

— 1953g: A simple and inexpensive closing net. — Memorie Ist. ital. Idrobiol., 7: 189–198.

— 1953h: Orientation and Aggregation in *Balanus balanus* (L.) da Costa. — J. Anim. Ecol., 22: 141–148.

Barnes, H., 1955a: The hatching process in some barnacles. — Oikos, 6: 114–123.

— 1955b: The growth rate of *Balanus balanoides* (L.). — Oikos, 6: 109–113.

— 1955c: Climatological and salinity data for Millport, Scotland. — Glasg. Nat., 17: 193–204.

— 1956a: Surface roughness and the settlement of *Balanus balanoides* (L.). — Arch. Soc. "Vanamo", 10: 164–168.

— 1956b: *Balanus balanoides* (L.) in the firth of Clyde. The development and annual variation of the larval population and the causative factors. — J. Anim. Ecol., 25: 72–84.

— 1956c: Further observations on rugophilic behaviour in *Balanus balanoides* (L.). — Vidensk. Meddr dansk naturh. Foren., 117: 341–348.

— 1956d: The growth rate of *Chthamalus stellatus* (Poli). — J. mar. biol. Ass. U.K., 35: 355–361.

— 1956e: Comparative marine biology conference in Roscoff. — Nature, Lond. 178: 404–405.

— 1956f: The biometry of the cirripede, *Chthamalus stellatus* (Poli). — Experientia, 12: 309–313.

— 1956g: Corrosion and shell composition in barnacles. — Nature, Lond. 177: 290.

— 1957a: Processes of restoration and synchronization in marine ecology. The spring diatom increase and the "spawning" of the common barnacle, *Balanus balanoides* (L.). — Année biol. 61: 67–85.

— 1957b: The northern limits of *Balanus balanoides* (L.). — Oikos, 8: 1–15.

— 1957c: Nutrients elements. — Treat. Mar. Ecol. & Paleoecol., 1, Geol. Soc. America, mem. 67: 297–344.

— 1958a: Regarding the southern limits of *Balanus balanoides* (L.). — Oikos, 9: 139–157.

— 1958b: The growth rate of *Verruca stroemia* (O. Müller). — J. mar. biol. Ass. U.K., 37: 427–433.

— 1959a: Temperature and the life-cycle of *Balanus balanoides*. — Marine Boring and Fouling Organism: 234–245, Seattle, University of Washington Press.

— 1959b: *Balanus-Chthamalus* relations on the North American Atlantic coast. — XV Int. Congr. Zool., sect. III: 293–294, London.

— 1959c: Stomach contents and micro feeding of some common cirripedes. — Can. J. Zool., 37: 231–236.

— 1959d: The world-wide distribution of intertidal barnacles, and interpretation in terms of physiology and ecology. — Int. Oceanogr. Congr., New York: 214–215.

— 1959e: Sea surface temperatures at Millport. — J. mar. biol. Ass. U.K., 38: 423–424.

— 1959f: *Balanus nubilus* Darwin. — Can. J. Zool., 37: 607–608.

— 1959g: Apparatus and methods of oceanography. — I., 341 pp., Georg Allen & Unwin, London.

— 1960: The behaviour and ecology of *Pollicipes polymerus*. — Rep. Challenger Soc., 3, (12).

— 1961a: Variation of the seasonal growth rate of *Balanus balanoides* with special reference to the presence of endogeneous factors. — Int. Rev. ges. Hydrobiol. Hydrogr., 46: 427–428.

— 1961b: *Balanus balanoides:* Recent observations on its southern limit. — Ecology, 42: 592–593.

— 1962a: Note on variations in the release of nauplii of *Balanus balanoides* with reference to the spring diatom outburst. — Crustaceana, 4: 118–122.

BARNES, H.. 1962b: The composition of the seminal plasma of *Balanus balanus*. — J. Exp. Biol., 39: 345–351.

— 1962c: The oxygen uptake and metabolism of *Balanus balanus* spermatosoa. — J. Exp. Biol., 39: 353–358.

— 1963a: So-called anecdysis in *Balanus balanoides* and the effect of breeding upon the calcareous shell of some common barnacles. — Limnol. Oceanogr., 7: 462–473.

— 1963b: Light, temperature and the breeding of *Balanus balanoides*. — J. mar. biol. Ass. U.K., 43: 717–727.

— 1965: Studies on the biochemistry of cirripede eggs. I. Changes on the general biochemical composition during development of *Balanus balanoides* and *B. balanus*. — J. mar. biol. Ass. U.K., 45: 321–339.

BARNES, H. and T. B. BAGENAL, 1951a: A statistical study of variability in catch obtained by short repeated hauls taken over an inshore ground. — J. mar. biol. Ass. U.K., 29: 649–660.

— 1951b: Observations of *Nephrops norvegicus* (L.) and on an epizoic population of *Balanus crenatus* BRUG. — J. mar. biol. Ass. U.K., 30: 369–380.

— 1952: The habits and habitat of *Aporrhais pes-pelecani* (L.). — Proc. Malac. Soc. London, 29: 101–105.

BARNES, H. and MARGARET BARNES, 1953: Biometry of the copepod *Calanus finmarchius* (GUNN.) in stages V and VI. — J. mar. biol. Ass. U.K., 32: 305.

— 1954: The general biology of *Balanus balanus* (L.) DA COSTA. — Oikos, 5: 63–76.

— 1956a: The formation of the egg-mass in *Balanus balanoides* (L.). — Arch. Soc. "Vanamo", 11: 11–16.

— 1956b: Contenuto di fosforo totale in Alecunni stadi di due comuni animali planctonici d'acqua dolce e suo rapporto con quello delle loro uova. — Memorie Ist. ital. Idrobiol., 9: 113–124.

— 1956c: The general biology of *Balanus glandula* DARWIN. — Pacif. Sci., 10: 415–422.

— 1957: Resistance to desiccation in intertidal barnacles. — Science, 126, nr. 2369: 358.

— 1958a: The rate of development of *Balanus balanoides* larvae. — Limnol. Oceanogr., 3: 29–32.

— 1958b: Note on the opening response of *Balanus balanoides* (L.) in relation to salinity and certain inorganic ions. — Veröff. Inst. Meeresforsch. Bremerh., V: 160–164.

— 1958c: Further observations on self-fertilization in *Chthamalus* sp. — Ecology, 39: 550.

— 1959a: The effect of temperature on the oxygen uptake and rate of development of the egg masses of two common cirripedes *Balanus balanoides* (L.) and *Pollicipes polymerus* J. B. SOWERBY. — Kieler Meeresforsch., 15: 242–251.

— 1959b: Studies on the metabolism of cirripedes. The relation between body weight, oxygen uptake, and species habitat. — Veröff. Inst. Meeresforsch. Bremerh. VI: 515–523.

— 1959c: A comparison of the annual growth patterns of *Balanus balanoides* (L.) with particular reference to the effect of food and temperature. — Oikos, 10: 1–18.

— 1959d: Some parameters of growth in the common intertidal barnacle *Balanus balanoides* (L.). — J. mar. biol. Ass. U.K., 38: 581–587.

— 1959e: Note on stimulation of cirripede nauplii. — Oikos, 10: 19–23.

Barnes, H. and Margaret Barnes, 1959f: The naupliar stages of *Balanus hesperius* Pilsbury. — Can. J. Zool., 37: 237–244.

— 1959g: The naupliar stages of *Balanus nubilis* Darwin. — Can. J. Zool., 37: 15–23.

— 1959h: Oscillatory respiration in *Balanus amphitrite* Darwin. — Experientia, 15: 438–441.

— 1960a: Recent spread and present distribution of the barnacle *Elminius modestus* Darvin in north-west Europe. — Proc. Zool. Soc. Lond., 135: 137–145.

— 1960b: *Elminius modestus* Darwin in south-west Scotland. — Nature Lond., 186: 989–990.

— 1961a: Salinity and the biometry of *Balanus improvisus.* — Commentat. Biol., 24: 1–7.

— 1961b: Recent spread and present distribution of the barnacle *Elminius modestus* Darwin in South-West Scotland. — Glasg. Nat., 18: 121–129.

— 1962a: The distribution and general ecology of *Balanus balanoides* together with some observations on *Balanus improvisus* in the waters around the coasts of Denmark, Southern Sweden and North-East Germany. — Lunds Univ. Årsskrift, N.F., Avd. 2, 58, nr. 8, 41 pp.

— 1962b: A note on *Balanus improvisus* in Finnish waters. — Commentat. Biol., 14: 1–11.

— 1962c: The growth rate of *Elminius modestus* (Crust, Cirripidia) in Scotland. — Int. Revue ges. Hydrobiol. Hydrogr., 47: 481–486.

— 1963: In vitro development of cirripede eggs. — Vidensk. Meddr. dansk naturh. Foren., 125: 93–100.

— 1964a: Repartition et ecologie generale des Cirripedes *Chthamalus depressus* (Poli) et *C. stellatus* (Poli) la long des côtes mediterranéennes d'Espagne et de France. — Bull. Inst. oceanogr. Monaco, 62, nr. 1299: 1–19.

— 1964b: Some relations between habitat, behaviour and metabolism on exposure to air of the high-level intertidal cirripede *Chthamalus depressus* (Poli). — Helgoländer wiss. Meeresunters., 10: 19–28.

— 1965: Egg size, nauplius size, and their variation with local, geographical, and specific factors in some common cirripedes. — J. Anim. Ecol., 34: 391–402.

Barnes, H. and J. D. Costlow, 1961: The larval stages of *Balanus balanus* (L.) da Costa. — J. mar. biol. Ass. U.K., 41: 59–68.

Barnes, H. and D. J. Crisp, 1956: Evidence of self-fertilization in certain species of barnacles. — J. mar. biol. Ass. U.K., 35: 631–639.

Barnes, H. and D. M. Finlayson, 1962: Presence of ascorbic acid in Cirripede semen. — Limnol. Oceanogr. 7: 1–98.

Barnes, H. and J. J. Gonor, 1958a: Neurosecretory cells in some Cirripedes. — Nature, Lond., 181: 194.

— 1958b: Neurosecretory cells in the Cirripede *Pollicipes polymerus* J. B. Sowerby. — J. mar. Res., 17: 81–102.

Barnes, H. and E. F. W. Goodley, 1958: A note on rainfall in the west of Scotland. — The Glasg. Nat., 18: 45–54.

— 1961: The general Hydrography of the Clyde sea area, Scotland. Part I: Description of the area, drift bottle and surface salinity data. — Bull. mar. Ecol. 5, nr. 43: 112–150.

Barnes, H. and G. R. Hassle, 1957: A statistical examination of the distribution of some species of Dinoflaggellates in the polluted inner Oslo Fjord. — Nytt Mag. f. Bot., 5: 113–124.

BARNES, H. and M. J. R. HEALY, 1965: Biometrical studies on some common cirripedes. I. *Balanus balanoides:* measurements of the scuta and terga of animals from a wide geographical range. — J. mar. biol. Ass. U.K., 45: 779–789.

BARNES, H. and S. M. MARSHALL, 1951: On the variability of replicicate plankton samples and some applications of "contagious" series to the statistical distribution of catches over restricted periods. — J. mar. biol. Ass. U.K., 30: 233–263.

BARNES, H. and H. T. POWELL, 1950a: The development, general morphology and subsequent elimination of barnacle populations, *Balanus crenatus* and *B. balanoides*, after a heavy initial settlement. — J. Anim. Ecol., 19: 175–179.

— 1950b: Some observations on the effect of fibrous glass surfaces upon the settlement of certain marine organisms. — J. mar. biol. Ass. U.K., 29: 299–302.

— 1951: The growth rate of juvenile *Asterias rubens* L. — J. mar. biol. Ass. U.K., 30: 381–385.

— 1953: The growth of *Balanus balanoides* (L.) and *B. crenatus* (BRUG.) under varying conditions of submersion. — J. mar. biol. Ass. U.K., 32: 107–128.

— 1954: *Onchidoris fusca* (MÜLLER), a predator of Barnacles. — J. Anim. Ecol., 23: 361–363.

BARNES, H. and E. S. REESE, 1958: Feeding in the pedunculate cirriped *Pollicipes polymerus* J. B. SOWERBY. — Proc. Zool. Soc. Lond., 132: 569–585.

— 1960: The behaviour of the stalked intertidal barnacle *Pollicipes polymerus* J. B. SOWERBY with special reference to its ecology and distribution. — J. Anim. Ecol. 29: 169–185.

BARNES, H. and F. A. STANBURY, 1948: The toxic action of copper and mercury salts both separately and when mixed on the harpacticid copepod, *Nitocra spinipes* (BOECK). — J. exp. Biol., 25: 270–275.

— 1951: A statistical study of plant distribution during the colonization and early development of vegetation of china clay residues. — J. Ecol., 39: 171–181.

BARNES, H., M. BARNES, and D. M. FINLAYSON, 1963a: The seasonal changes in body weight, biochemical composition and oxygen uptake of two common boreo-arctic Cirripedes, *Balanus balanoides* and *B. balanus.* — J. mar. biol. Ass. U.K., 43: 185–211.

— 1963b: The metabolism during starvation of *Balanus balanoides.* — J. mar. biol. Ass. U.K., 43: 213–224.

BARNES, H., D. J. CRISP, and H. T. POWELL, 1951: Observations on the orientation of some species of barnacles. — J. Anim. Ecol., 20: 227–241.

BARNES, H., D. M. FINLAYSON, and J. PIATOGORSKY, 1963: The effect of desiccation and anaerobic conditions on the behaviour, survival and general metabolism of three common cirripedes. — J. Anim. Ecol., 32: 233–252.

BARZANOVA, N. G., 1961: Some comparative data on the fauna of the rocky littorals of the Barents and the White Seas. — Trudy Inst. Okeanol., 46: 140–146.

BASSINDALE, R., 1936: The developmental stages of three English barnacles, *Balanus balanoides* (L.), *Chthamalus stellatus* (POLI) and *Verruca stroemia* (O. F. MÜLLER). — Proc. Zool. Soc. Lond. 1936, nr. 1: 57–74.

— 1958: The local barnacles. — Proc. Bristol Nat. Soc., 29: 381–392.

— 1964: British Barnacles. — The Linnean Society of London, Synopsis of the British Fauna, no. 14.

BEAUSHAMP, P. DE, 1925: Les variations de la faune et de la flore dans la zone intercotidale de la côte basque. — C. r. somm. Seanc. Soc. Biogeogr.: 103–105.

BERTELSEN, E., 1937: Contributions to the animal ecology of the fjords of Angmagssalik and Kangerdlugssuaq in East Greenland. — Meddr Grønland, 108, 3: 1–57.

Bertelsen, E. and Paul M. Hansen, 1960: Fiskeriundersøgelser i 1959 ved Danmark, Færøerne og Grønland. — Skr. Danm. Fisk.- og Havunders., nr. 20.

— 1961: Fiskeriundersøgelser i 1960 ved Danmark, Færøerne og Grønland. — Skr. Danm. Fisk.- og Havunders., nr. 21.

— 1962: Fiskeriundersøgelser i 1961 ved Danmark, Færøerne og Grønland. — Skr. Danm. Fisk.- og Havunders., nr. 22.

Beverton, J. H. and S. J. Holt, 1957: On the dynamics of exploited fish populations. — Fishery Investigations, ser. II, 19, 533 pp. Her Majesty's Stationary Office, London.

— 1959: A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. — Colloquia on Ageing, Ciba Foundation, 5: 142–177.

Bhatnager, K. M. and D. J. Crisp, 1965: The salinity tolerance of nauplius larvae of cirripedes. — J. Anim. Ecol., 34: 419–428.

Bishop, M. W. H., D. J. Crisp, E. Fischer-Piette and M. Prenant, 1957: Sur l'ecologie des Cirripedes de la côte atlantique française. — Bull. Inst. oceanogr. Monaco, 1099: 1–12.

Blom, Sven-Erik and Karl-Georg Nyholm, 1961: Settling times of *Balanus balanoides* (L.), *Balanus crenatus* Brug. and *Balanus improvisus* on the west coast of Sweden. — Zool. Bidr. Upps., 33: 149–155.

Boëtius, Inge, 1962: Temperature and growth in a population of *Mytilus edulis* (L.) from the northern harbour of Copenhagen (the Sound). — Meddr Danm. Fisk.- og Havunders. N.S., 3: 339–346.

Bousfield, E. L., 1954: The distribution and spawning seasons of barnacles on the Atlantic coast of Canada. — Bull. natn. Mus. Can., 132: 112–154.

— 1955a: The cirripede Crustacea of the Hudson strait region, Canadian Eastern Arctic. — J. Fish. Res. Bd. Can., 12, 762–767.

— 1955b: Ecological control of the occurrence of barnacles in the Miramichi Estuary. — Bull. natn. Mus. Can., 137, 69 pp.

— 1955c: Some physical features of the Miramichi Estuary. — J. Fish. Res. Bd. Can., 12: 342–361.

— 1956: Studies on the shore fauna of the St. Lawrence Estuary and Gaspe Coast. — Ann. Rep. Nat. Mus. Fiscal year 1953–65, Bull. nr. 136, Canada: 95–101.

Bousfield, E. L. and A. H. Leim, 1959: The fauna of Minas Basin and Minas Channel. — Bull. natn. Mus., Can., 166, Biol. Ser. nr. 61: 1–30.

Borsuk, W., 1929: Untersuchungen über den respiratorischen Gaswechsel bei *Balanus balanoides* in Luft-milieu. — Rab. murmansk. biol. Sta., 3.

Brattström, H., 1958: Cirripedia and Ascothoracia from the Sound and Southeastern Kattegat. — Undersökningar över Öresund, nr. 37, 25 pp.

Broch, Hjalmar, 1924: Cirripedia Thoracia von Norwegen und dem norwegischen Nordmeere. — K. norske Vidensk. Selsk. Skr. I. Mat.-nat. klasse 1924, nr. 17, 121 pp.

— 1927: Cirripedia. — Handbuch der Zoologie, 3, nr. 1: 503–552.

— 1933: Einige Probleme der biogeographischen Abgrenzung der arktische Region. - Mitt. zool. Mus. Berl., 19.

Claus, C., 1869: Die Cypris-aehnliche Larvae (Puppe) der Cirripedien und ihre Verwandlung in das festsitzende Thier. Ein Beitrag zur Morphologie der Rankenfuessler. — Naturwiss. Ges. Marburg., Suppl. Heft 5: 1–16.

Clegg, D. J., 1957: Some observations on pairing in *Balanus balanoides*. — The Challenger Soc., 3, nr. 9.

COLE, W. H., 1929: The relation between temperature and the pedal rythm of *Balanus.* — J. gen. Physiol. 12: 599–608.

— 1932: The sensitivity of the cirri and the variability of their movements in the barnacles *Balanus tintinnabulum* and *B. balanoides.* — J. exp. Zool., 63: 143–153.

COLE, W. H. and J. B. ALLISON, 1933: Stimulation by mineral and fatty acids in the barnacles. *Balanus balanoides.* — J. gen. Physiol., 16: 895–903.

CONNELL, J. H., 1961a: Effects of competition, predatation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides.* — Ecol. Monogr., 31: 61–104.

— 1961b: The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus.* — Ecology, 42: 710–723.

CORLETT, J., 1948: Rates of settlement and growth of the "pile"-fauna of the Mersey estuary. — Proc. Trans. Lpool biol. Soc., 56: 2–28.

CRISP, D. J., 1953: Selection of site and position by some marine larvae. — Brit. J. Anim. Behaviour, 1: 80–81.

— 1954: The breeding of *Balanus porcatus* (DA COSTA) in the Irish Sea. — J. mar. biol. Ass. U.K., 33: 569–590.

— 1955: The behaviour of barnacle cyprids in relation to water movement over a surface. — J. exp. Biol., 32: 569–590.

— 1956: A substance promoting hatching and liberation of young in Cirripedia. — Nature, Lond., 178: 263.

— 1957a Effect of low temperature on the breeding of marine animals. — Nature, Lond., 179: 1138–1139.

— 1957b: Liberation and hatching of barnacle nauplii. — The Challenger Soc., 3, nr. 9.

— 1959a: Factors influencing the time of breeding of *Balanus balanoides.* — Oikos, 10: 275–289.

— 1959b: The rate of development of *Balanus balanoides* (L.) embryos in vitro. — J. Anim. Ecol. 28: 119–132.

— 1959c: Breeding and exuviation in *Balanus balanoides.* — XV Int. Congr. Zool., sect. III: 298–300, London.

— 1960: Factors influencing growth-rate in *Balanus balanoides.* — J. Anim. Ecol., 29: 95–116.

— 1961: Territorial behaviour in barnacle settlement. — J. exp. Biol., 38: 429–446.

— 1962a: Release of larvae by barnacles in response to the available food supply. — Anim. Behav., 10: 3–4.

— 1962b: The planktonic stages of the Cirripedia *Balanus balanoides* (L.) and *Balanus balanus* (L.) from north temperate waters. — Crustaceana, 3: 209–221.

— 1964: Racial differences between north America and European forms of *Balanus balanoides.* — J. mar. biol. Ass. U.K., 44: 33–45.

CRISP, D. J. and H. BARNES, 1954: The orientation and distribution of barnacles at settlement with particular reference to surface contour. — J. Anim. Ecol., 23: 142–162.

CRISP, D. J. and D. J. CLEGG, 1960: The induction of the breeding conditions in *Balanus balanoides* (L.). — Oikos, 11: 265–275.

CRISP, D. J. and J. D. COSTLOW, 1963: The tolerance of developing Cirripede embryos to salinity and temperature. — Oikos, 14: 22–34.

CRISP, D. J. and E. FISCHER-PIETTE, 1959: Repartitation des Principales Espèces Intercotidales de la Côte Atlantique Française en 1954–1955. — Annls. Inst. oceanogr., Monaco, 36: 275–388.

Crisp, D. J. and E. W. Knight-Jones, 1953: The mechanism of aggregation in barnacle populations. A note on a recent contribution by Dr. H. Barnes. — J. Anim. Ecol. 22: 360–362.

Crisp, D. J. and P. S. Meadows, 1962: The chemical basic of gregariousness in Cirripedes. — Proc. R. Soc., Ser. B., 156: 500–520.

Crisp, D. J. and B. S. Patel, 1958: Relation between breeding and ecdysis in Cirripedes. — Nature, Lond., 181: 1078–1079.

— 1960: The moulting cycle in *Balanus balanoides* (L.). — Biol. Bull. mar. biol. Lab. Woods Hole, 118: 31–47.

— 1961: The interaction between breeding and growth rate in the barnacle *Elminius modestus* Darwin. — Limnol. Oceanogr., 6: 105–115.

Crisp, D. J. and A. J. Southward, 1953: Isolation on intertidal animals by sea barriers. — Nature, Lond., 172: 108.

— 1958: The distribution of intertidal organisms along the coasts of the English Channel. — J. mar. biol. Ass. U.K., 37: 157–208.

— 1961: Different types of cirral activity of barnacles. — Phil. Trans. R. Soc., Ser. B, 243: 271–308.

Crisp, D. J. and C. P. Spencer, 1958: The control of hatching process in barnacles. — Proc. R. Soc., Ser. B, 148: 278–299.

Darwin, C. R., 1854: A monograph of the sub-class Cirripedia. The Balanidae etc. — Ray Soc., London.

Davis, D. H. S., 1936: A reconnaissance of the fauna of Akpatok Island, Ungava Bay. — J. Anim. Ecol. 5: 319.

Dons, C., 1945: Vekstvariasjoner hos *Balanus balanoides.* Norges strandfauna 222III. — K. norske Vidensk. Selsk. Forh., XVIII, nr. 48, Trondhjem.

Drygalski, E., 1897: Grønland-expedition der Gesellschaft für Erdkunde zu Berlin, I. — Berlin 1897.

Ellis, D. V., 1955: Some observations on the shore fauna of Baffin Island. — Arctic, 8: 224–236.

Ellis, D. V. and R. T. Wilce, 1962: Arctic and subarctic examples of intertidal zonation. Arctic, 14: 224–235.

Elmhirst, R., 1923: Notes on the breeding and growth of marine animals in the Clyde sea area. Rep. Scott. mar. biol. Ass., 1922.

— 1932: Quantitative studies between tide marks. — The Glasg. Nat., X: 56–62.

Feyling-Hanssen, R. W., 1953: The barnacle *Balanus balanoides*, (Linné, 1766), in Spitsbergen. — Skr. norsk Polarinstitutt, 98, 64 pp.

Fischer, P.-H-, 1943: Observation sur les conditions de vie de *Balanus balanoides* dans quelques stations boréales et arctiques. — Bull. Lab. marit. Dinard, fasc. XXV: 65–72.

Fischer-Piette, E., 1934: Sur la repartition de la cirripède *Balanus balanoides* le long des côtes françaises et anglaises de la manche. — Assoc. France p. Avance de Sci., Chambery.

— 1935: Histoire d'une mouliere. — Bull. Biol., 69: 152–177.

Fischer-Piette, E. and M. Prenant, 1956: Distribution des cirripèdes intercotidaux d'Espagne septentrionale. — Bull. Cent. Etud. Rech. scient. Biarritz, 1956: 7–20.

— 1957: Quelques données ecologiques sur les cirripèdes du Portugal, de l'Espagne du sud et du nord du Maroc. — Bull. Cent. Etud. Rech. scient. Biarritz, 1: 361–368.

Fischer-Piette, E. and Juan Seoane-Camba, 1963: Examen ecologique de la Rio de Camariñas. — Bull. inst. oceanogr. Monaco, 61, nr. 1277, 38 pp.

Fish, C. J., 1925: Seasonal distribution of the plankton of the Woods Hole region. — Bull. Bur. Fish. Wash., 41: 91–179.

Froda, F., 1924: Some observations made in North-Greenland 1923. — Meddr Grønland, 59: 39–55.

Fuller, J., 1946: Season of attachment and growth of sedentary organisms at Lamoine Maine. — Ecology. 27: 150–158.

Gauld, D. T., T. B. Bagenal and J. H. Connell, 1952: The marine fauna and flora of St. Kilda 1952. — Scott. Nat., 65: 29–49.

Grave, B. H., 1933: Rate of growth, age at sexual maturity and duration of life of certain sessile organisms at Woods Hole, Massachusetts. — Biol. Bull. mar. biol. Lab. Woods Hole, 65: 375–386.

Gruvel, A., 1905: Monographie des Cirrhipedes ou Thecostraces. — Paris.

Gurjanowa, E., J. Sachs and P. Uschakow, 1930: Das Littoral des Kola-Fjords. — Trudy Leningr. Obshch. Estest., 60, nr. 2.

Gutmann, W. F., 1960: Funktionelle morphologie von *Balanus balanoides*. — Abh. senckenb. Naturforsch. Ges., 500: 1–43.

— 1962: Beobachtungen zum Formproblem der Seepocken-Schale. — Natur und Museum, 95: 193–200.

Hachey, H. B., 1961: Oceanography and Canadian atlantic waters. — Bull. Fish. Res. Bd. Can., 134, 120 pp.

Hatton, H., 1938: Essais de bionomie explicative sur quelques especes intercotidales d'algues et d'animaux. — Annls. inst. oceanogr. Monaco., 17: 241–348.

Hatton, H. and E. Fischer-Piette, 1932: Observations et experiences sur le peuplement des cotes rocheuses par les Cirripedes. — Bull. inst. oceanogr. Monaco., 592: 1–15.

Hutchins, L. W., 1947: The basis for temperature zonation in geographical distribution. — Ecol. Monogr., 17: 325–335.

Hørring, R., 1926: Fugle II. — Danm. Fauna, 30, København.

Klugh, A. B. and C. L. Newcombe, 1935: Light as an controlling factor in the growth of *Balanus balanoides*. — Can. J. Res., 13 (D.): 39–49.

Knight-jones, E. W., 1953a: Laboratory experiments on gregariousness during settling in *Balanus balanoides* and other barnacles. – J. exp. Biol., 30: 584–598.

— 1953b: Some further observations on gregariousness in marine larvae. — Br. J. Anim. Behav., I: 81–82.

Knight-Jones, E. W. and J. Moyse, 1961: Intraspecific competition in sedentary marine animals. — Symposia of the Society for Experimental Biology, nr. XV: 72–95.

Krüger, Paul, 1940: Cirripedia. — Bronns' Klassen und Ordnungen des Tierreiches, Teil III. – Leipzig.

Kiilerich, A., 1943: The hydrography of the West Greenland fishing banks. — Meddr Danm. Fisk.- og Havunders., ser. hydrografi III: 1–45.

Kuznetzov, W. W., and T. A. Matveeva, 1949: The influence of the density of the populations on certain biological processes in *Balanus balanoides* L. from eastern Murman. — Dokl. Akad. Nauk SSSR., 64, nr. 3: 413–415.

Larsen, Ellinor Bro and Mathias Thomsen, 1940: The influence of temperature on the development of some species of Diptera. — Vidensk. Meddr dansk naturh. Foren., 104: 1–75.

Le Cren, E. D. and M. W. Holdgate, 1962: The exploitation of natural animal populations. — British Ecological Society, symposium nr. 2, Blackwell, Oxford.

Lewis, J. R., 1961: The littoral zone on rocky shores – a biological or physical entity? – Oikos, 12: 280–301.

Levis, J. R., 1964: The ecology of rocky shores. — The English Universities Press Ltd., London.

McLaren, Ian, 1963: Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. — J. Fish. Res. Bd. Can., 20: 685–727.

Madsen, H., 1936: Investigations on the shore-fauna of East Greenland. — Meddr Grønland, 100, nr. 8: 1–79.

— 1940: A study of the littoral faua of Northwest Greenland. — Meddr Grønland, 124, nr. 3: 1–24.

Mohammad, M.-B. M., 1965: A new record for *Balanus balanoides*. — Limnol. Oceanogr., 6: 488.

Moore, H. B., 1933: Change of orientation of a barnacle after metamorphsis. — Nature, Lond., 132: 969–970.

— 1934a: The biology of *Balanus balanoides* I. Growth rate and its relation to size, season and tidal level. — J. mar. biol. Ass. U.K., 19: 851–868.

— 1934b: The rate of growth of *Balanus*. – Scott. Nat., 1934: 101–109.

— 1935a: The growth rate of *Balanus hameri* (Ascanius). — J. mar. biol. Ass. U.K., 20: 57–63.

— 1935b: The biology of *Balanus balanoides* III. The soft parts. – J. mar. biol. Ass. U.K., 20: 263–277.

— 1935c: The biology of *Balanus balanoides* IV. Relation to environmental factors. — J. mar. biol. Ass. U.K., 20: 279–307.

— 1935d: The biology of *Balanus balanoides* V. Distribution in the Plymouth area. — J. mar. biol. Ass. U.K., 20: 701–716.

Motas, C., 1961: Halacaridae. — Zoology Iceland, III, 55, 20 pp.

Moyse, J., 1963: A comparsion of the value of various flagellates and diatoms as food for barnacle larvae. — J. Cons. perm. int. Explor. Mer, 28: 175–187.

Mørch, O. A. L., 1857: Fortegnelse over Grønlands bløddyr. — Tillæg nr. 4, naturhistoriske tillæg til »Grønland geografisk og statistisk beskrevet« af H. Rink, København 1857.

Nielsen, E. T., and D. Gordon Evans, 1960: During of the pupal stage of *Aedes taeniorhynchus* with a discussion of the velocity of development as a function of temperature. — Oikos, 11: 200–222.

Patel, B. and D. J. Crisp, 1960: Rates of development of the embryos of several species of barnacles. — Physiol. Zool., 33: 104–117.

— 1961: Relation between the breeding and moulting cycles in cirripedes. — Crustaceana, 2: 89–107.

Parke, M. W. and H. B. Moore, 1935: The biology of *Balanus balanoides* II. Algal infection of the shell. — J. mar. biol. Ass. U.K., 20: 49–56.

Petersen, G. Høpner, 1962: The distribution of *Balanus balanoides* (L.) and *Littorina saxatilis*, Olivi var. *groenlandia*, Mencke in northern West Greenland. — Meddr Grønland, 159, nr. 9: 1–43.

— 1964: The Hydrography, Primary Production, Bathymetry and "Tagsaq" of Disko Bugt, West Greenland. — Meddr Grønland, 159, nr. 10: 1–45.

Poulsen, E. M., 1935: De danske Farvandes Rurer (Balanomorpha og Verracomorpha). — Vidensk. Meddr dansk naturh. Foren., 99: 5–27.

Pyefinch, K. A., 1948a: Methods of identification of the larvae of *Balanus balanoides* (L.), *B. crenatus* Brug. and *Verruca Stroemia* O. F. Müller. — J. mar. biol. Ass. U.K., 27: 451–463.

— 1948b: Notes on the biology of cirripedes. — J. mar. biol. Ass. U.K., 27: 464–503.

Rasmussen, E.: Isefjord marine fauna. — In press.

RICKER, W. E., 1958: Handbook of computations for biological statistics of fish populations. — Bull. Fish. Res. Bd. Can., 119, 300 pp.

RUNNSTRÖM, S., 1925: Zur Biologie und Entwicklung von *Balanus balanoides* (LINNÉ). — Bergens Mus. Aarbok 1924–1925, Naturvidensk. Række, nr. 5, 46 pp.

RUSANOVA, M. W., 1960: The biological differences between the White Sea and Barents Sea *Balanus balanoides* LINNÉ. — Dokl. Akad. Nauk. SSSR. Biol. Sci. Sect., 126, nr. 1–6: 568–571.

RZEPISHEVSKY, J. K., 1962: Conditions of the mass liberation of the nauplii of the common barnacle *Balanus balanoides* (L.) in the eastern Murman. — Int. Revue ges. Hydrobiol. Hydrogr., 47, nr. 3: 471–479.

SALOMONSEN, F. and GITZ-JOHANSEN, 1950: Grønlands fugle, the birds of Greenland. — Ejnar Munksgård, København.

SAVILOV, A. I., 1953: The growth and variation in growth of the White Sea invertebrates *Mytilus edulis*, *Mya arenaria* and *Balanus balanoides.* — Trudy Inst. Okeanol., 7: pp. 198–201, pp. 201–213 and pp. 252–258.

— 1957: Growth and its variability in the invertebrates of the White Sea: *Mytilus edulis*, *Mya arenaria* and *Balanus balanoides* II. *Balanus balanoides* in the White Sea. — Trudy Inst. Okeanol., 23: 216–236.

SAXOV, S., 1958: The uplift of western Greenland, a preliminary note. — Meddr dansk geol. Foren., 13: 518–523.

SCHLIEPER, C., 1962: Adäquate und inädaquate Methoden in der meeresbiologischen Forschung. — Kieler Meeresforsch., 18: 10–12.

SCHÄFER, W., 1938: Die geologische Bedeutung von Bohr-Organismen in tierischen Hart-Teilen, aufgezeigt an Balaniden Schill der Innenjade. — Senckenbergiana. 20: 304–313.

— 1952: Biologische Bedeutung der Ortswahl bei Balaniden-Larven. — Senckenbergiana, 33: 235–246.

SOKOLOVA, M. N., 1951: Influence of the conditions of the environment on the density of the colony and the shape of the shell in *Balanus balanoides.* — Dokl. Akad. Nauk. SSSR., N.S., 78: 1227–1230.

SOUTHWARD, A. J., 1955a: On the behaviour of barnacles I. The relation of cirral and other activities to temperature. — J. mar. biol. Ass. U.K., 34: 403–422.

— 1955b: On the behaviour of barnacles II. The influence of habitat and tide-level on cirral activity. — J. mar. biol. Ass., U.K., 34: 423–433.

— 1957: On the behaviour of barnacles III. Further observations on the influence of temperature and age on cirral activity. — J. mar. biol. Ass. U.K., 36: 323–334.

— 1958a: Note on the temperature tolerances of some intertidal animals in relation to environmental temperatures and geographical distribution. — J. mar. biol. Ass. U.K., 37: 49–66.

— 1958b: The zonations of plants and animals on rocky shores. — Biol. Rev., 33: 137–177.

— 1962: On the behaviour of barnacles IV. The influence of temperature on cirral activity and survival of some warm-water species. — J. mar. biol. Ass. U.K., 42: 163–177.

SOUTHWARD, A. J. and D. J. CRISP, 1954: Recent Changes in the distribution of the intertidal barnacles *Chthamalus stellatus* POLI and *Balanus balanoides* L. in the British Isles. — J. Anim. Ecol. 23: 163–177.

— 1956: Fluctuations in the distribution and abundance of intertidal barnacles. — J. mar. biol. Ass. U.K., 35: 211–229.

— 1963: Barnacles of European waters. — Catalogue of Main Marine Fouling Organisms, 1, Barnacles, O.E.C.D., Paris.

Southward, A. J. and D. J. Crisp, 1965: Activity rhythms of barnacles in relation to respiration and feeding. — J. mar. biol. Ass. U.K., 45: 161–185.

Steemann Nielsen, E., 1958: A survey of recent danish measurements of the organic productivity in the sea. — Rapp. P.-V. Reun. Cons. perm. int. Explor. Mer., 144: 92–95.

Stephensen, K., 1933: Havedderkopper (Pycnogonida) og Rankefødder (Cirripedia). — Danm. Fauna, 38, 158 pp.

— 1938: Cirripedia (incl. Rhizocephala). — Zoology Iceland, III, part 30–31, 11 pp.

Stephenson, T. A. and A. Stephenson, 1949: The universal features of zonation between tide-marks on rocky coasts. — J. Ecol., 38: 289–305.

Steven, D., 1938: The shore fauna of Amerdloq Fjord, West Greenland. — J. Anim. Ecol., 7: 53–70.

Stubbings, H. G., 1956: Orientation of Barnacles to light and water currents at the time of metamorphosis. — XIV Int. Congr. Zool., Copenhagen 1953.

Tarasov, N. J. and G. B. Zevina, 1957: Usonogie rake (Cirripedia Thoracica) Morei SSSR. — Fauna SSSR, No. 69, Tom. VI, vip. 1, Moskva & Leningrad, 267 pp.

Taylor, C., 1957: Cod growth and temperature. — J. Cons. perm. int. Explor. Mer., 23: 366–370.

— 1959: Temperature and growth of the razor clam. — J. Cons. perm. int. Explor. Mer., 23: 93–101.

— 1960: Temperature, growth and mortality—the Pacific cockle. — J. Cons. perm. int. Explor. Mer., 26: 117–124.

— 1962: Growth equations with metabolic parameters. — J. Cons. perm. int. Explor. Mer., 27: 270–286.

Thorson, G., 1941: Marine gastropoda prosobranchiata. — Zoology Iceland, IV, 60, 150 pp.

— 1964: Light as an ecological factor in the dispersal and settlement of larvae of marine bottom invertebrates. — Ophelia, 1: 167–208.

Trans, P., 1955: Report from the weather service. — Meddr Grønland, 127, 6, 40 pp.

Ursin, E., 1963 a: On the incorporation of temperature in the von Bertalanffy growth equation. — Meddr Danm. Fisk.- og Havunders. N.S., 4: 1–16.

— 1963 b: On the seasonal variation of growth rate and growth parameters in the Norway Pout (*Gadus esmarki*) in the Skagerrak. — Meddr Danm. Fisk.- og Havunders., N.S., 4: 17–29.

Walley, L. J., 1964: Histolysis and phagocytosis in the metamorphosis of *Balanus balanoides*. — Nature, Lond. 201, nr. 4916: 314–315.

— 1965: The development and function of the oviducal gland in *Balanus balanoides*. — J. mar. biol. Ass. U.K., 45: 115–128.

Vanhöffen, E., 1897: Die Fauna und Flora Grönlands. — Grønlandexpedition der Gesellschaft für Erdkunde zu Berlin 1891–1893, II: 1–383., Berlin 1897.

Wells, H. W., M. J. Wells and J. E. Gray, 1960: Of the southern limit of *Balanus balanoides* in the western Atlantic. — Ecology, 41: 578–580.

Vinogradova, A. P., 1953: The elementary chemical composition of marine organisms. — Sears Foundation for Marine Research, Memoir 2, 647 pp.

Manuscript completed July 1965.

TABLES

Table 1. *Augpilagtoq 9.8.1960. n = 35*

Animals with a small 1st winter ring

n	gr.	winter ring 1.	2.	3.	4.	5.	6.	7.
	0	(—)						
4	I	1.34	(3.40)					
15	II	1.24	3.55	(5.03)				
7	III	1.62	4.52	5.76	(6.82)			
0	IV	—	—	—	—			
1	V	0.80	2.30	4.20	5.10	6.40	(7.11)	
1	VI	1.90	3.99	5.11	6.02	6.51	7.20	(7.40)
28								
estimated length—age:		1.60	4.00	5.50	6.50	7.25	7.65	7.95

( ): estimated length obtained at the end of the season 1960.

Animals with large 1st winter ring

n	gr.	winter ring 1.	2.	3.	4.	
2	0	(2.50)				
1	I	2.70	(4.63)			
1	II	2.90	4.61	(5.42)		
1	III	3.75	7.01	8.20	(8.40)	
2	IV	2.85	5.10	6.50	7.60	(8.54)
7						

not used for growth computations.

Tables 1–8.

The tables give the average length of winter rings for each age-group, and the estimated length at the end of the season (in brackets).

The first column gives the number of animals in each age-group. The last row gives the length at the end of each season of the animal's life, estimated from the columns above. Animals on which age-determination or length of rings were uncertain are not included in these tables.

A Fortran-programme for IBM computers was written for the calculations of these tables with the kind help af "I/S Datacentralen af 1959", Copenhagen. This programme also gave the standard-deviations, but owing to problems with the bimodal composition of the northern populations, the present calculations are made with an ordinary desk calculation-machine.

Table 2. *Umanak 1962. n = 71*

n	gr.	winter ring							
		1.	2.	3.	4.	5.	6.	7.	8.
	0	—							
2	I	1.00							
0	II	—	—						
4	III	1.75	3.75	4.75					
14	IV	1.75	3.32	4.21	4.82				
21	V	1.72	3.05	3.85	4.82	5.37			
20	VI	1.49	2.65	3.43	4.10	4.68	5.00		
8	VII	1.25	2.88	3.50	4.06	4.69	5.00	5.38	
2	VIII	1.25	2.25	3.25	4.00	4.75	5.00	5.25	5.50
71									
estimated length—age:		1.70	3.35	4.35	5.00	5.45	6.00	6.15	

Table 3. *Godhavn H.W.M. 1959. n = 610*

Animals with a small 1st winter ring

n	gr.	winter ring								
		1.	2.	3.	4.	5.	6.	7.	8.	9.
	0	(1.80)								
16	I	1.31	(3.50)							
117	II	1.55	3.82	(4.90)						
57	III	1.48	3.30	4.41	(5.00)					
141	IV	1.18	2.88	4.29	5.09					
88	V	1.46	3.08	4.08	4.82	5.35				
87	VI	1.18	2.78	3.99	4.51	5.08	5.52			
22	VII	1.38	3.04	4.11	4.76	5.24	5.57	5.80		
15	VIII	1.35	2.98	3.95	4.52	4.88	5.25	5.55	5.75	
4	IX	1.25	3.25	4.25	4.88	5.38	5.63	6.00	6.25	6.38
547										
estimated length—age:		1.50	3.50	4.65	5.35	5.75	6.05	6.25	6.35	5.40

( ): estimated length obtained during the season 1959

Animals with large 1st winter ring

n	gr.	winter ring							
		1.	2.	3.	4.	5.	6.	7.	8.
37	I	3.06	(4.50)						
11	II	2.58	4.12	(5.00)					
15	III	2.42	3.95	4.88					
63									
estimated length—age:		3.00	4.50	5.40					

Table 4. *Godhavn M.W.M. 1959. n = 703*

Animals with a small 1st winter ring

n	gr.	winter ring 1.	2.	3.	4.	5.
	0	(2.00)				
111	I	1.81	(4.70)			
241	II	1.79	4.54	(5.70)		
170	III	1.49	4.56	5.65	(6.50)	
66	IV	1.61	3.81	5.02	5.59	
20	V	1.63	3.35	4.64	5.61	6.18
608						
estimated length—age:		1.90	4.00	5.25	6.00	6.50

( ): estimated length at the end of the season 1959

Animals with a large 1st winter ring

n	gr.	winter ring 1.	2.	3.	4.
34	I	3.66	(5.20)		
45	II	3.45	5.18	(6.00)	
13	III	3.63	5.43	6.16	
3	IV	3.03	4.75	6.00	6.40
95					
estimated length—age:		3.50	5.40	6.45	6.95

Table 5. *Godhavn L.W.M. 1959. n = 412*

Animals with a small 1st winter ring

n	gr.	winter ring 1.	2.	3.	4.	5.	6.
	0	(2.10)					
84	I	1.92	(4.80)				
110	II	1.81	4.59	(5.80)			
89	III	1.64	4.75	5.80	(6.50)		
34	IV	1.30	4.36	5.75	6.35		
12	V	1.69	3.89	5.21	5.94	6.50	
5	VI	2.09	4.43	5.31	6.08	6.92	7.20
335							
estimated length—age:		2.00	4.50	5.80	6.50	7.00	7.30

( ): estimated length obtained during the season 1959

Animals with a large winter ring

n	gr.	winter ring 1.	2.	3.	4.	5.
41	I	3.90	(6.00)			
22	II	4.24	5.37	(6.20)		
12	III	3.82	5.55	6.15		
2	IV	2.89	4.79	6.40	6.98	
77						
estimated length—age:		3.90	5.50	6.60	7.10	

Table 6. *Sukkertoppen 1959. n = 882*

n	gr.	winter ring				
		1.	2.	3.	4.	5.
	0	(2.90)				
768	I	2.47	(4.20)			
50	II	2.45	3.55			
52	III	2.48	3.92	4.78		
7	IV	2.19	3.30	4.25	4.86	
5	V	2.27	3.44	4.39	5.11	5.57
882						
estimated length—age:		2.50	3.80	4.70	5.30	5.75

Table 7. *Godthåb 1959. n = 746*

n	gr.	winter ring				
		1.	2.	3.	4.	5.
	0	(2.90)				
303	I	2.46	(4.20)			
319	II	2.41	3.83	(5.10)		
98	III	2.06	3.44	4.76	(5.60)	
24	IV	2.15	3.45	4.51	5.18	
2	V	2.05	3.10	3.58	3.67	3.99
746						
estimated length—age:		2.40	3.80	4.75	5.30	5.70

Table 8. *Arsuk 1959. n = 478*

n	gr.	winter ring						
		1.	2.	3.	4.	5.	6.	7.
	0	(3.10)						
314	I	3.42	(5.00)					
104	II	2.61	4.21	(5.50)				
25	III	2.61	4.35	5.36	(6.50)			
20	IV	2.03	3.65	4.34	5.23			
6	V	2.42	3.83	4.67	5.50	5.83		
7	VI	1.75	3.25	4.18	4.89	5.25	5.68	
2	VII	1.75	3.25	4.50	5.00	5.50	6.00	6.25
478								
estimated length—age:		3.00	4.40	5.35	6.00	6.45	6.80	7.05

Table 9. *The Growth-Parametres for the Individual Populations*

Locality	L ∞ mm	K	t_0	T_{max}
Augpilagtoq, small 1st ring	8.50	0.42	—1.05	6
Umanak	6.40	0.41	—1.15	8
Godhavn H.W.M. small 1st ring	6.50	0.50	—0.55	9
Godhavn M.W.M. small 1st ring	7.30	0.47	—0.50	5
Godhavn L.W.M. small 1st ring	7.80	0.47	—0.65	6
Godhavn H.W.M. large 1st ring	6.75	0.53	—1.15	5
Godhavn M.W.M. large 1st ring	7.60	0.61	—1.00	4
Godhavn L.W.M. large 1st ring	8.00	0.47	—1.25	4
Sukkertoppen	6.50	0.40	—1.15	5
Godthåb	6.50	0.41	—1.00	5
Arsuk	7.60	0.36	—1.40	7
Angmagssalik	7.90	?	?	10–12

Table 10. *Life history of B. balanoides*

Locality	Period of maximum			Fertile first summer?	Duration of larval stage days	Length at the end of the	
	Hatching	Settling	Fertilization			1st year	2nd year
Augpilagtoq				no		3.0	9.5
Umanak	June-July	August	Aug.-Sept.	no		3.3	7.9
H.W.M. small	June-July	Aug.-Sept.	September	no	90	2.8	8.3
M.W.M. —	May-June	Aug.-Sept.	September	no		3.9	9.5
L.W.M. —	May	Aug.-Sept.	September	no		4.2	10.8
H.W.M. great				no		7.0	10.8
M.W.M. —				no		8.3	13.5
L.W.M. —				no		9.2	13.7
Sukkertoppen	April	June	October	no	65	5.5	9.0
Godthåb	April-May	June	October	no	71	5.3	9.0
Arsuk	April	June	Sept.-Oct.	no	76	7.0	10.5
Angmagssalik.....	June-July		September	no			
Svalbard	June-August	July-Aug.	September?	no		2.5	
Norge		March-May				3.0–9.0	
Herdla...........	March	April	November	no	35–50	7.0	9.5
Millport upper....	March	April	Autumn	yes	21–35	9.0	18
Millport middle...	March	April	Autumn	yes		12.0	20
Millport lower	March	April	Autumn	yes		15.0	21.5
total submerged ..	March	April	Autumn	yes		17.5	26
Port Erin upper...	March	April-May	November	no	55	5.2	8.1
Port Erin middle..	March	April-May	November	no		5.3	7.6
Port Erin lower ...	March	April-May	November	yes		4.7	6.5
Liverpool		April-May		yes		5.9	
Menai Bridge.....	March-April		November	yes		12–17	
St. Malo upper....		March-April		yes		3.1–3.5	5.3–5.8
St. Malo middle...		March-April		yes		3.0–3.9	4.6–5.2
St. Malo lower		March-April		yes		3.3–4.5	4.4–5.8
Hudson Strait area		August					
Miramichi	April-May	May-June		no	28–35		
St. Andrews	March-May	May	October	no	35–42	6.3	11.0

at localities in the North Atlantic

Maximum		t°max	t°min	Duration of ice-cover	Remarks	Source
Length L_{max}	Age T_{max}					
23.0	6			7 months	natural population	present paper
16.8	8	15°	—27°	7 months	natural population	present paper
17.0	9				natural population	present paper
19.2	5				natural population	present paper
20.6	6	18°	—31°	6 months	natural population	present paper
18.0	5				natural population	present paper
20.0	4				natural population	present paper
21.5	4				natural population	present paper
17.0	5	22°	—20°	no ice	natural population	present paper
17.0	5	16°	—19°	no ice	natural population	present paper
20.0	7	19°	—16°	"Storis"	natural population	present paper
21.0	10–12	19°	—30°	"Storis"	natural population	present paper
16.1				4–8 months	natural population	Feyling-Hanssen, 1953
22				no ice	natural population	C. Dons 1945
14	3	15°	4°	no ice	natural population	S. Runnström 1925
		23°	2°	no ice	demi-natural population	Elmhirst 1923 Barnes & Powell 1953 Pyefinch 1948 Cornell 1961
16	5–6	14°	6°	no ice	natural population	H. Moore 1934 & 1935 b,c
14	2–3					
12	2–3					
24		16°	5°	no ice	demi-natural popul.	J. Corlett 1948
		15°	5°	no ice	demi-natural popul.	Crisp & co-workers
7?	3 2	17°	7°	no ice	natural population	Hatton 1938
				4–8 months	natural population	Bousfield 1955 a
	6	22°		4 months	natural population	Bousfield 1955 b
		15°	—30°	no ice	natural population	Bousfield 1954

Table 11.

Year of investigation	June		July		August		September		Occurrence of *Balanus balanoides*
	Av.	Max.	Av.	Max.	Av.	Max.	Av.	Max.	
1893............	*1.7*	3.1	*5.2*	7.9	*4.8*	7.3	*—0.1*	0.9	rare
1923............	*1.2*	2.5	*4.3*	6.4	*4.5*	5.6	*0.9*	2.1	rare
1936............	*3.2*	6.3	*6.5*	7.8	*6.6*	7.9	*2.7*	4.7	common
1960............	*2.6*	5.2	*5.7*	8.3	*5.4*	6.9	*1.3*	3.0	common
1962............	*2.7*	5.2	*6.0*	8.4	*5.9*	6.9	*1.1*	3.0	common

Occurrence of *B. balanoides* in Umanak district as observed by Vanhöffen (in 1893), Froda (in 1923), Vibe (in 1936), Petersen (in 1960) and Steenstrup (in 1962).
The averages in this table give the average of the monthly average for the 8 years before the year of the investigation, and the maxima give the maximum value of the monthly average for the 8 years; thus indicating the possibility that one very fine year will promote a barnacle population in the northern districts.

Færdig fra trykkeriet den 10. august 1966.

PLATES

Plate 1

Photographs of various scutae. L: larval shell, 1.W: 1st winter ring, 2.W: 2nd winter ring, T: total length.

Fig. A: II.-gr. animal with 6 moulting rings between 2.W and T.

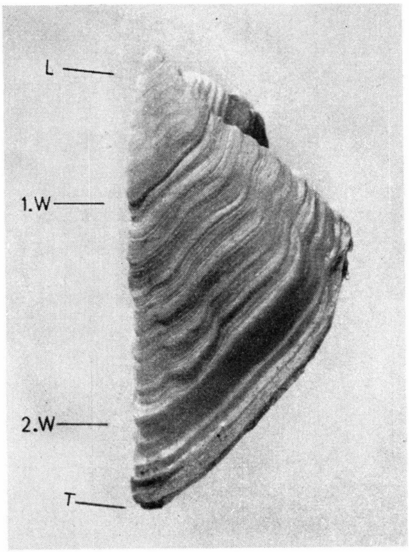
Fig. B: I.-gr. animal with 10 moulting rings between 1.W and T.

Fig. C: Enlargment of the shell in fig. B, to show the structure of the larval shell. Note that the rings between the moulting rings are visible.

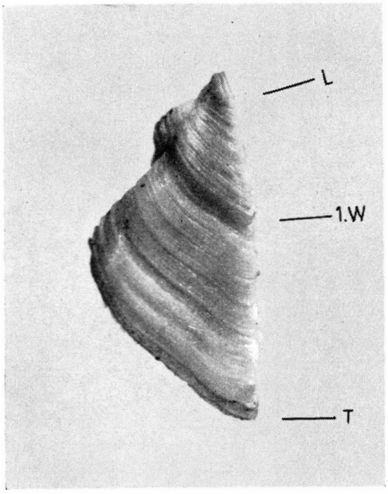
Fig. D: Scutum which was broken some time between the 1st winter ring and collection date and healed without noticeable influence on the growth.

Fig. E: Scutum which was broken during a winter period; the number of the winter ring cannot be read, as the first part of the shell is corroded.

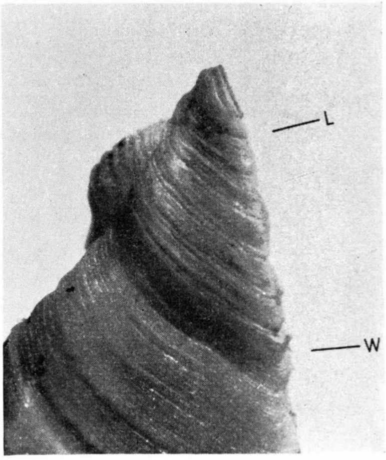
PLATE 1



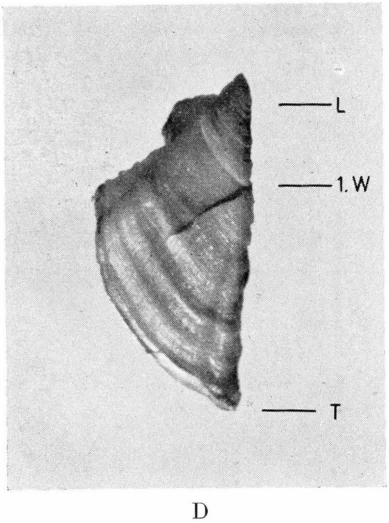
A



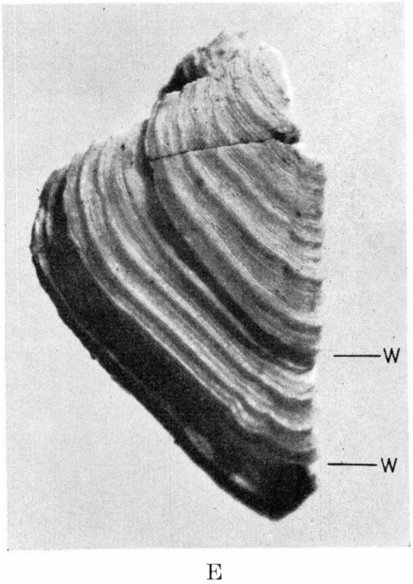
B



C



D



E

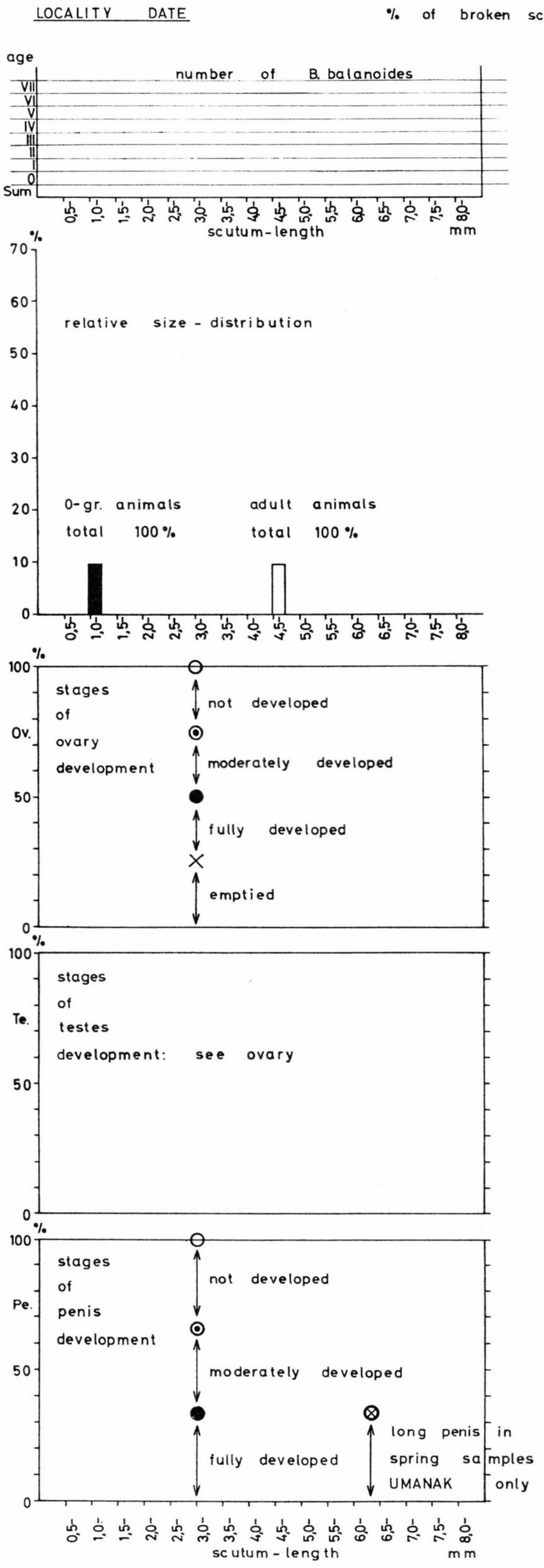
Plate 2

A scheme explaining plates 3–38.

1st diagram: The total material according to age and length.

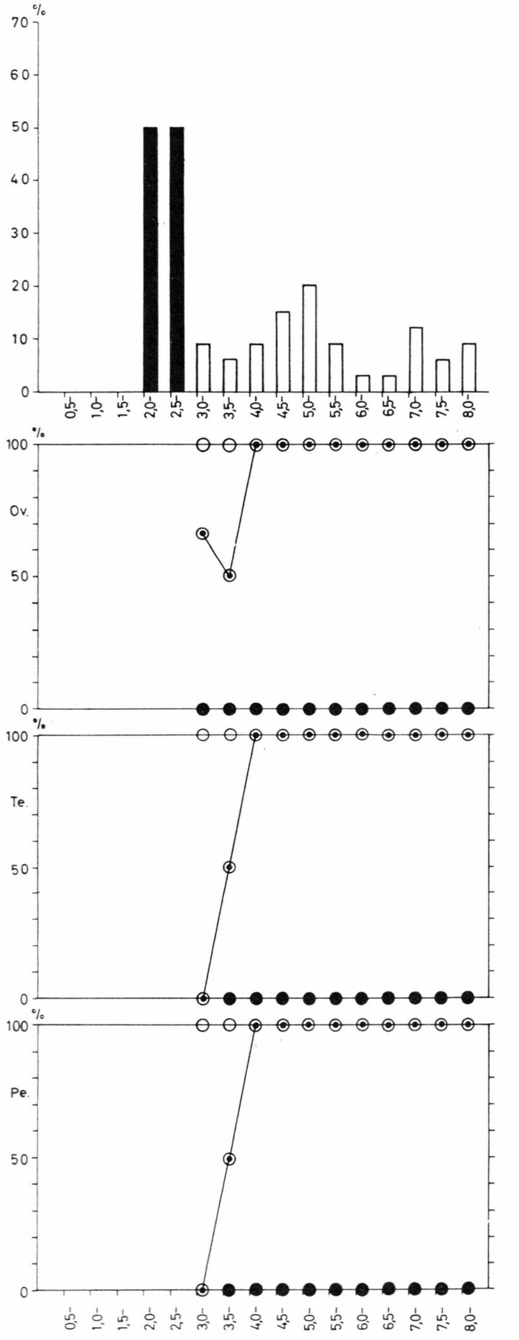
2nd diagram: Relative size-distribution and where 0.-gr. animals and adult animals are treated separately.

The three lower diagrams: Gonad development according to length. The stages used are indicated in the diagrams.


LOCALITY DATE
% of broken scutae
age
number of B. balanoides
VII
VI
V
IV
III
II
I
0
Sum
0,5- 1,0- 1,5- 2,0- 2,5- 3,0- 3,5- 4,0- 4,5- 5,0- 5,5- 6,0- 6,5- 7,0- 7,5- 8,0-
scutum-length
mm
%
70
60
50
40
30
20
10
0
relative size-distribution
0-gr. animals
total 100 %
adult animals
total 100 %
0,5- 1,0- 1,5- 2,0- 2,5- 3,0- 3,5- 4,0- 4,5- 5,0- 5,5- 6,0- 6,5- 7,0- 7,5- 8,0-
%
100
Ov.
50
0
stages
of
ovary
development
not developed
moderately developed
fully developed
emptied
%
100
Te.
50
0
stages
of
testes
development: see ovary
%
100
Pe.
50
0
stages
of
penis
development
not developed
moderately developed
fully developed
long penis in
spring samples
UMANAK only
0,5- 1,0- 1,5- 2,0- 2,5- 3,0- 3,5- 4,0- 4,5- 5,0- 5,5- 6,0- 6,5- 7,0- 7,5- 8,0-
scutum - length
mm

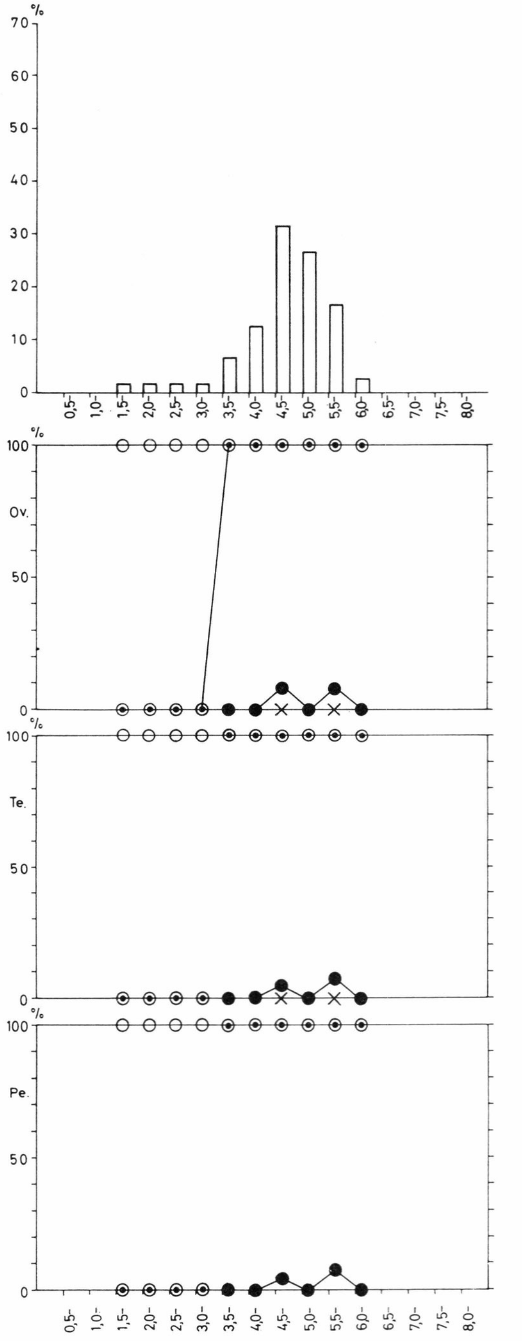
AUGPILAGTOQ 9-8-1960 0%

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI														1			1
V														1			1
IV																2	2
III											2	1		2	2	1	8
II							1	3	4	7	1		1				17
I						3	1		1								5
0				1	1												2
Sum				1	1	3	2	3	5	7	3	1	1	4	2	3	36



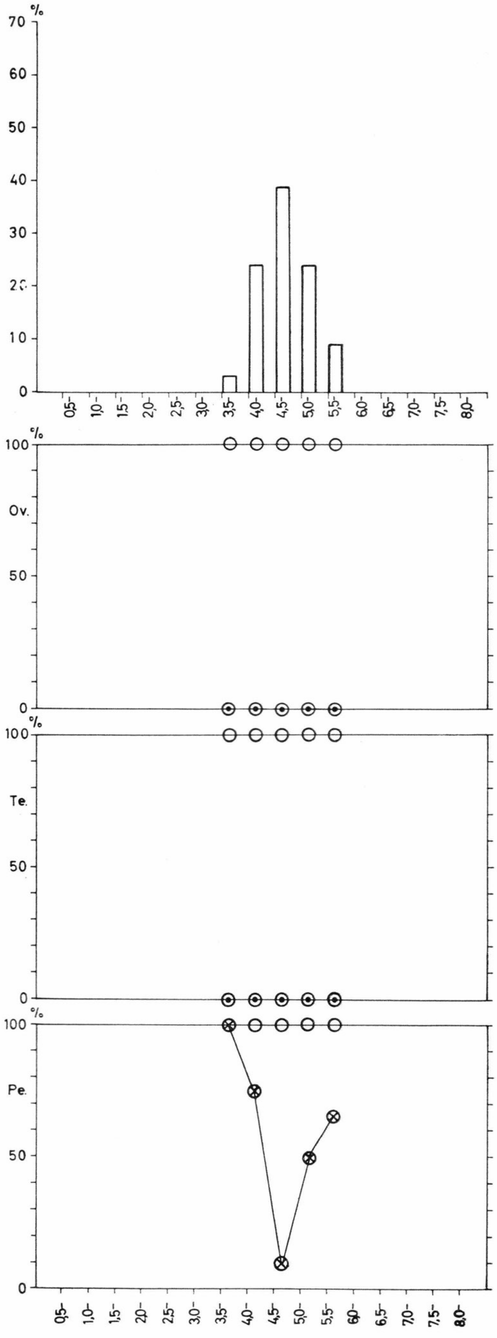
UMANAK 11-8-1960 1.3 %

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI							2	1	5	10	7	1					26
V										3							3
IV								3	5	4	4	1					17
III							3	6	6	1	2						18
II									9	3							12
I			1	1	1	1											4
0																	
Sum			1	1	1	1	5	10	25	21	13	2					80



UMANAK 22-5-1962

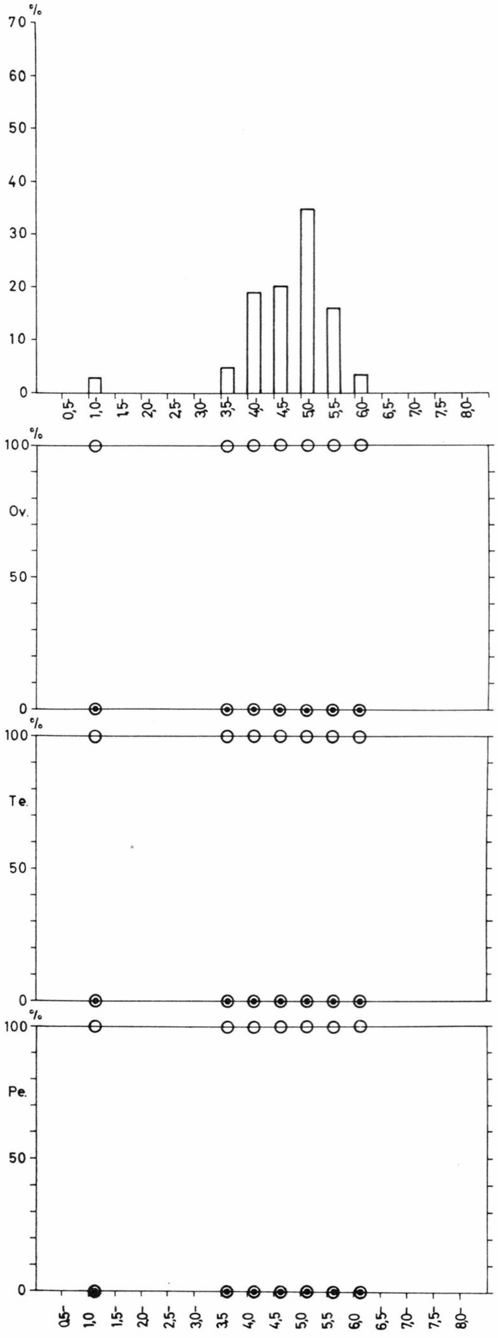
	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
?							1	4	9	4	1						19
VI									2	1	1						4
V								1	2	2	1						6
IV								3		1							4
III																	
II																	
I																	
0																	
Sum							1	8	13	8	3						33



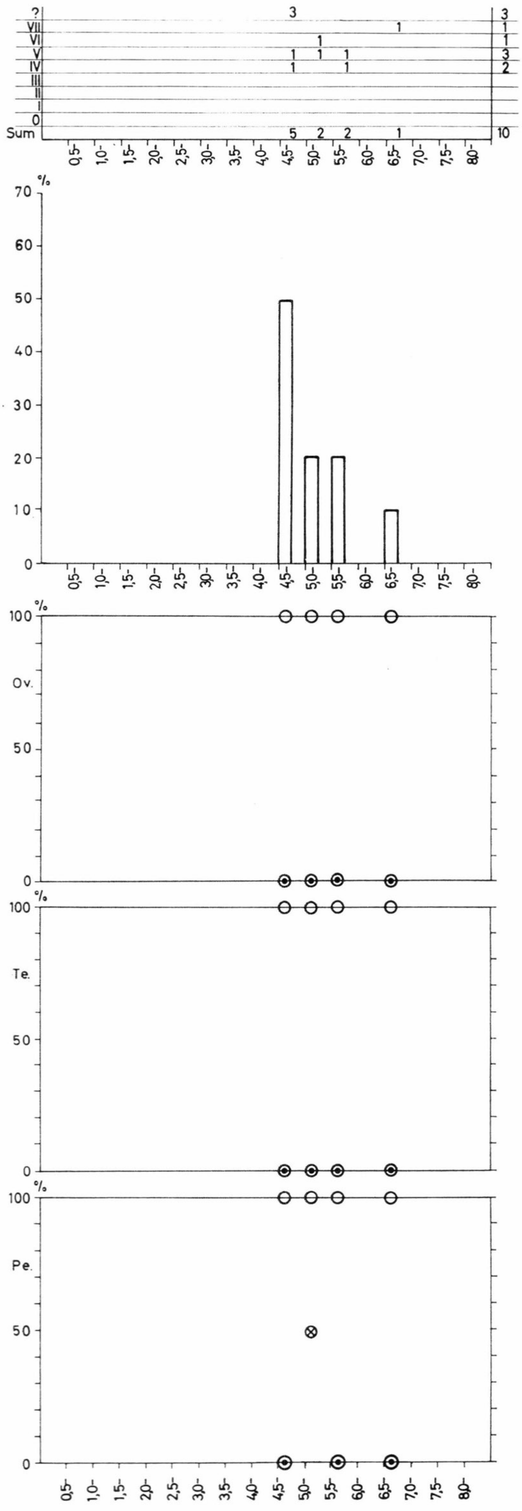
UMANAK 17-6-1962

1,5‰

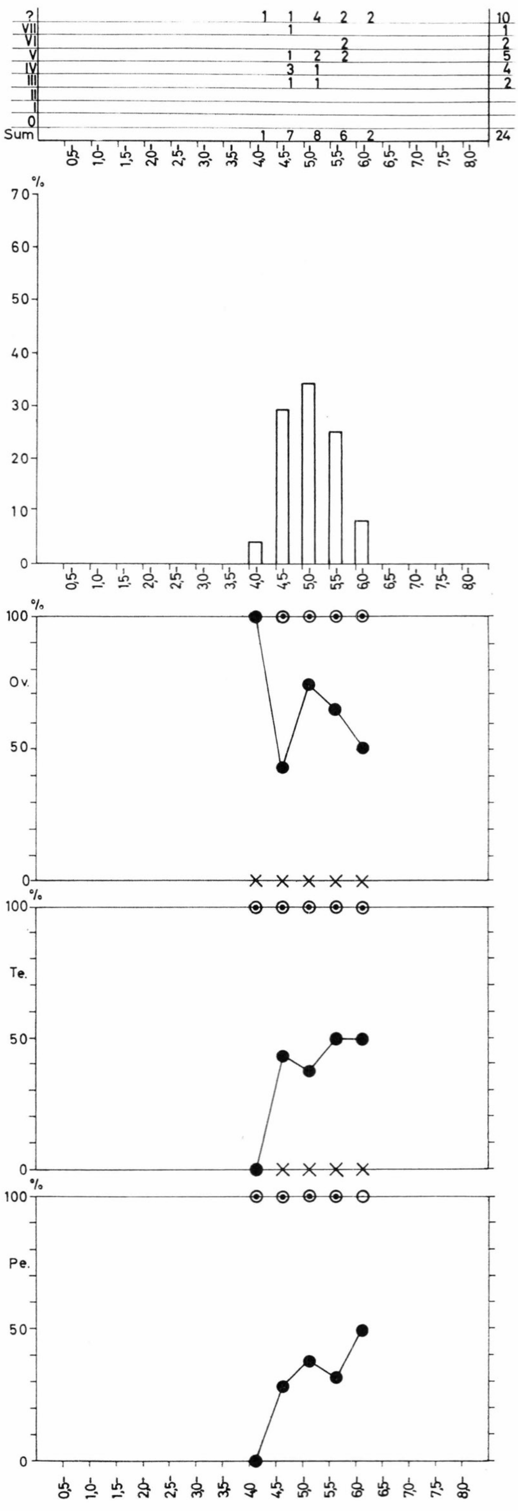
	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
?							1	6	5	4	2	1					19
VIII										1	1						2
VII										5	1						6
VI								4	1	8	3	1					17
V								1	3	2	3						9
IV							2		4	1							7
III								1		1							2
II																	
I		2															2
0																	
Sum		2					3	12	13	22	10	2					64



UMANAK 17-7-1962



UMANAK 18-8-1962

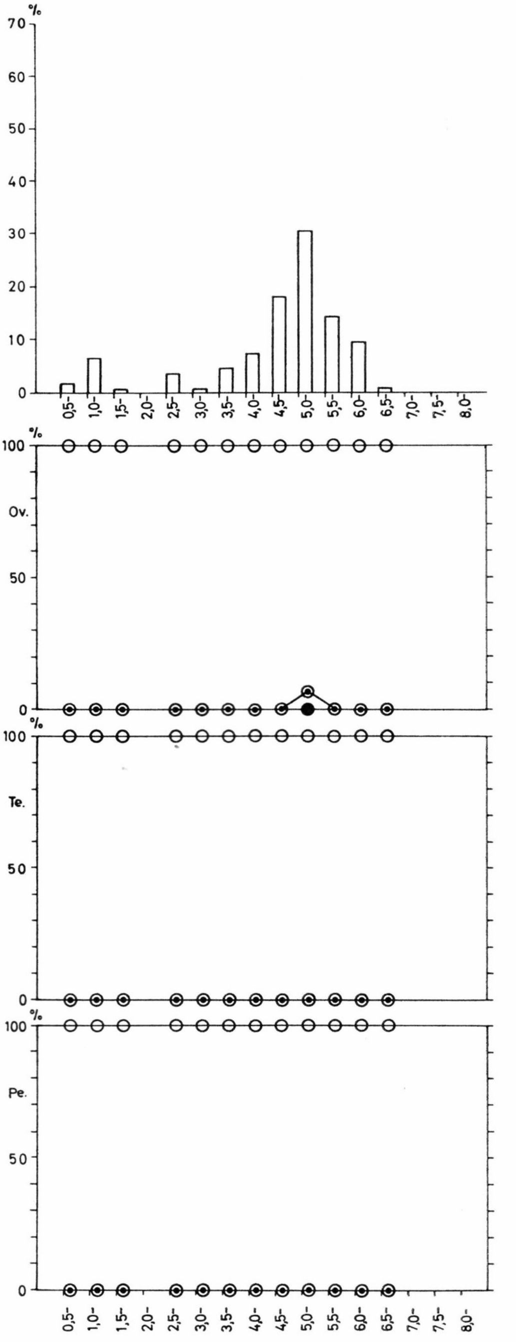


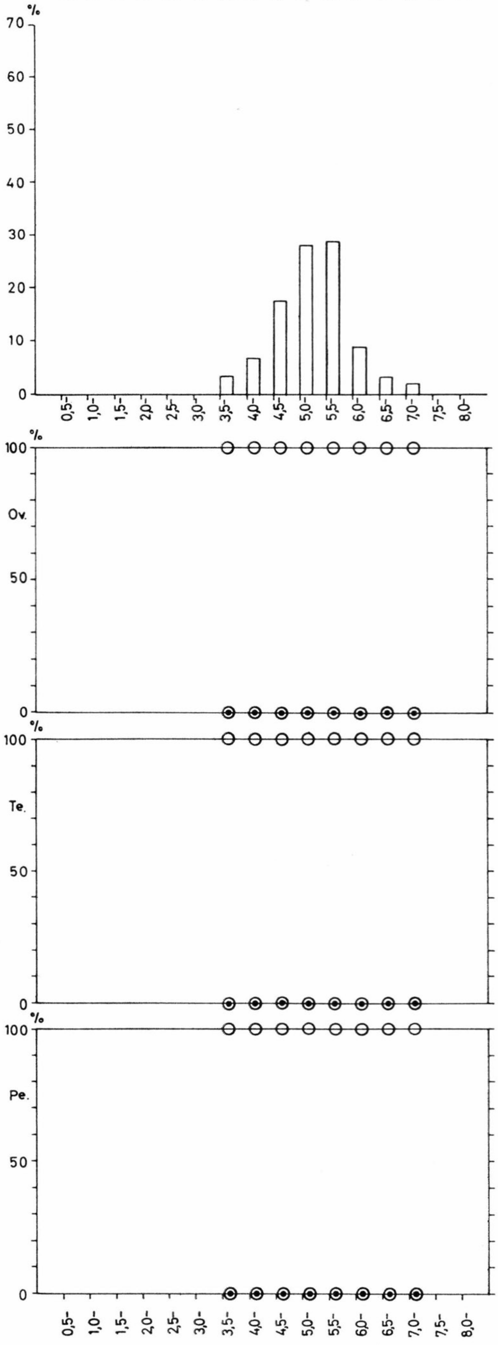
GODHAVN 2-6-1959 H.W.M. 5,7‰

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII												1					1
VI								1	2	6	7	5					21
V								1	3	4	3	4	1				16
IV								1	13	20	5						39
III					1			2	1	2							6
II					1	1	5	3									10
I	2	7	1		2												12
0																	
Sum	2	7	1		4	1	5	8	19	32	15	10	1				105

GODHAVN 17-6-1959 H.W.M. 3,3‰

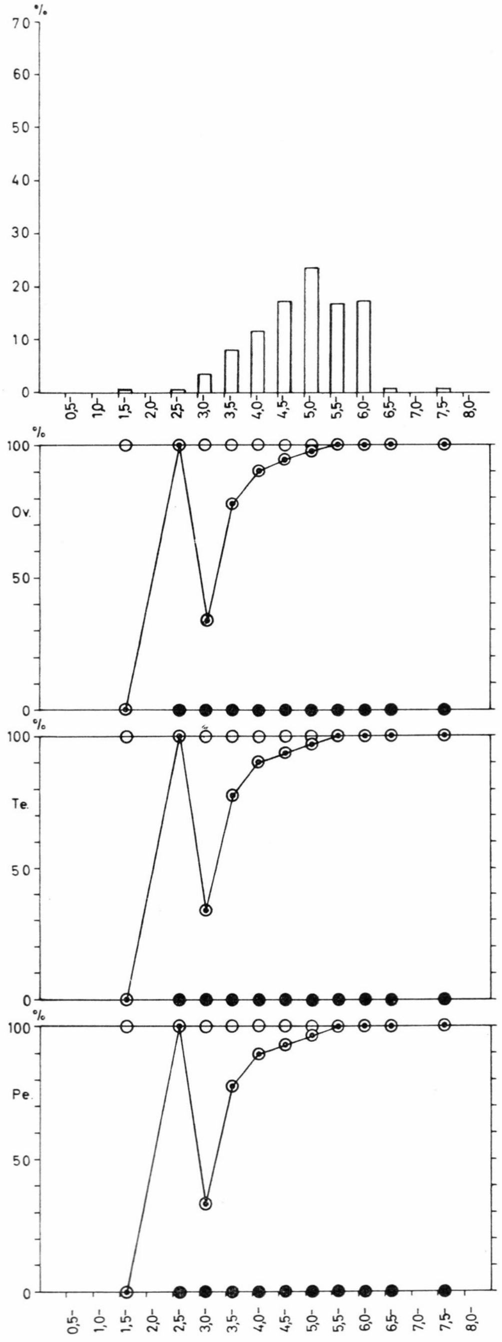
	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
IX										1		1	1	1			4
VIII									3	3	3	3	2	1			15
VII									2	2	6	3	1	1			15
VI								2	4	9	14	2	1				32
V							1	2	3	7	11	2					26
IV								2	9	14	7	2					34
III									3	4							7
II							4	4	1								9
I																	
0																	
Sum							5	10	25	40	41	13	5	3			142





GODHAVN 14-7-1959 H.W.M. 6,4 %

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
?													1				1
VII										1		3					4
VI									1	5	8	11					25
V									1	2	7	9			1		20
IV									5	12	11	7					35
III								3	3	9	2						17
II					1	1	10	15	19	12	1						59
I			1			5	3	2	1								12
0																	
Sum			1		1	6	13	20	30	41	29	30	1		1		173



GODHAVN 6-8-1959 H.W.M. 7,3%

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
?							1		2								3
VI								1	2			1					4
V								1	2	2	3	1					9
IV						1		1	4	3	4						13
III						2	1	3	2	4							12
II							2	4	1								7
I						3	4										7
0	8																8
Sum	8					6	8	10	13	9	7	2					63

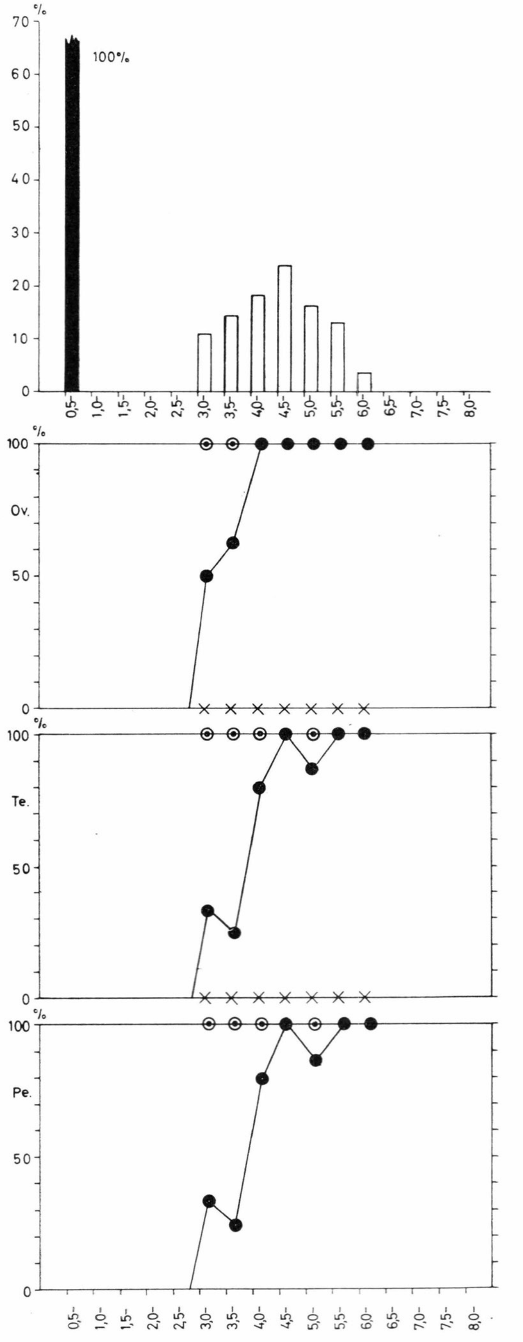
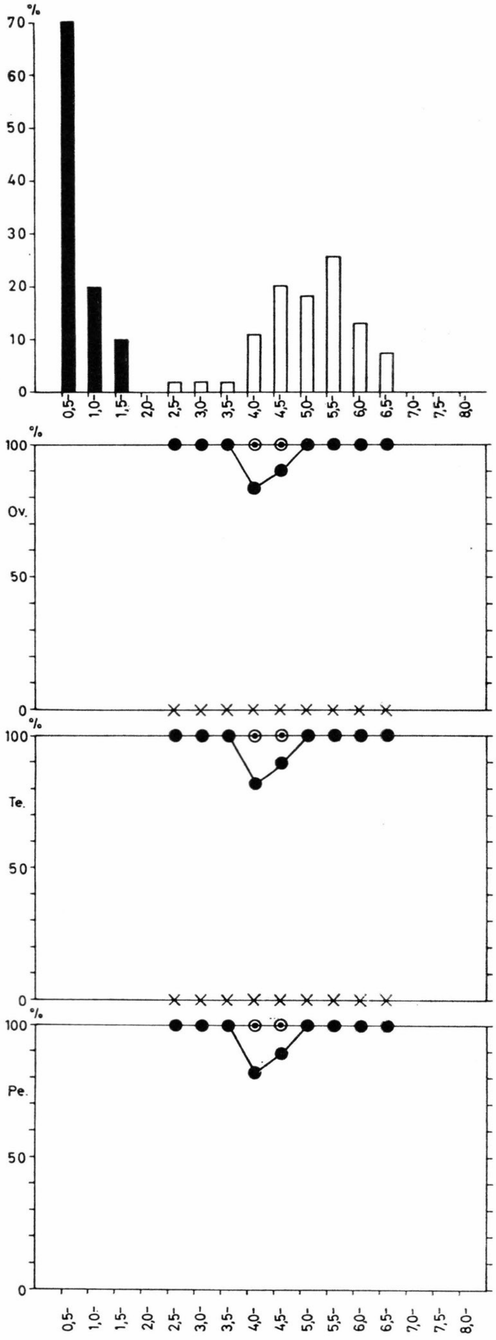


PLATE 8

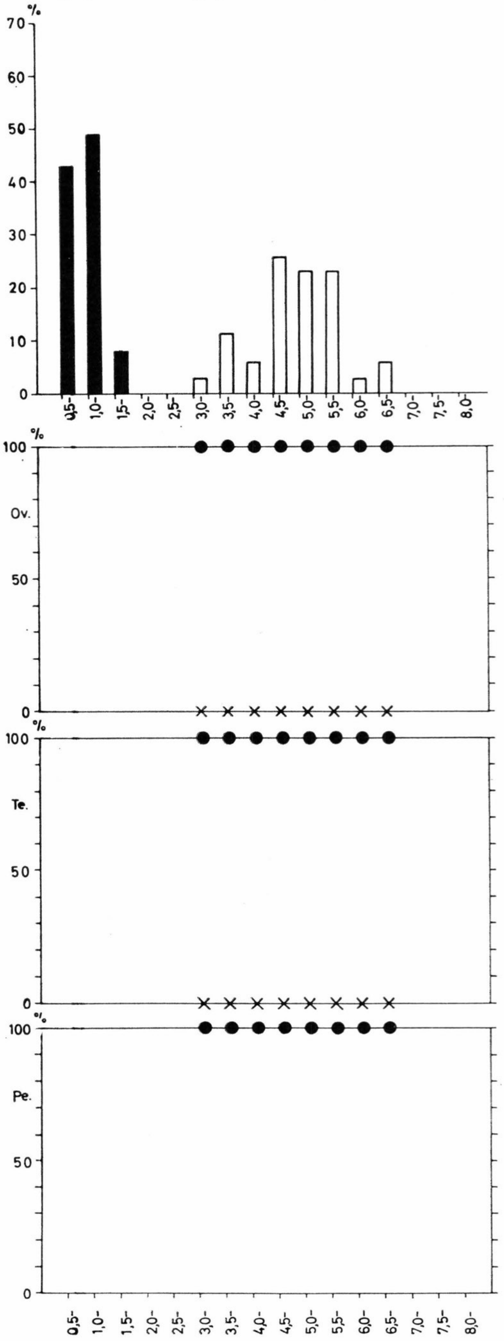
GODHAVN 21-8-1959 H.W.M. 5,4‰

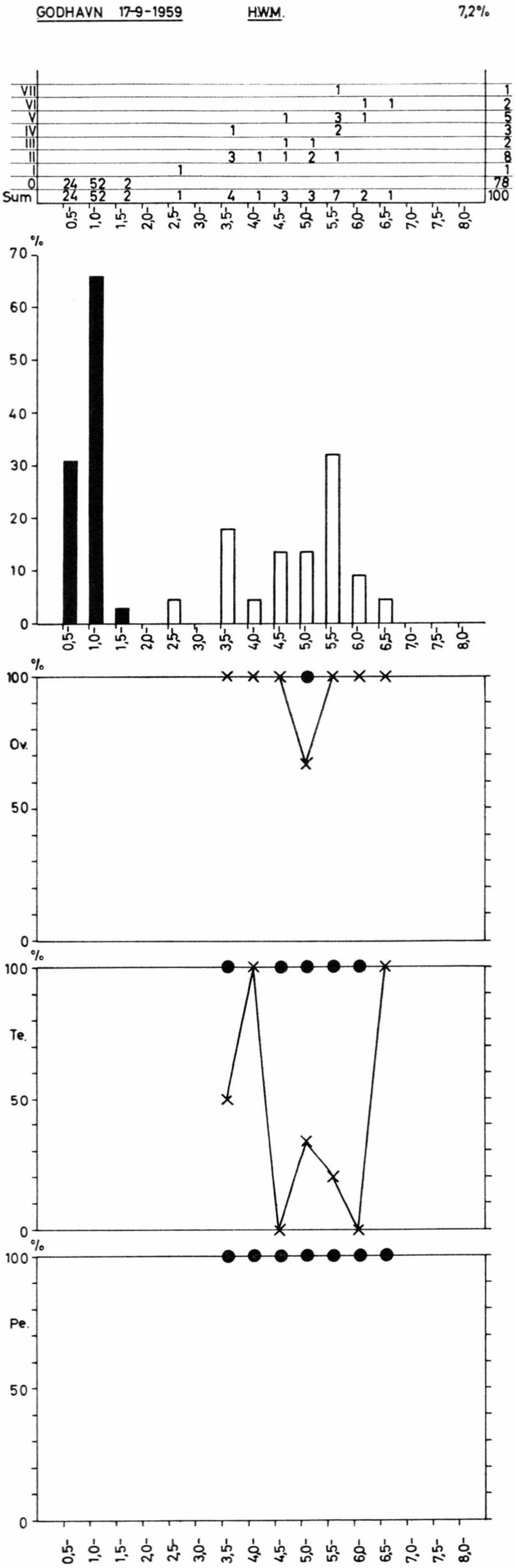
	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII													1				1
VI													1				1
V						1				1	2	2					6
IV										2	3	3	2				10
III								1	3	4	6	2					16
II								3	7	3	3						16
I					1		1	2	1								5
0	7	2	1														10
Sum	7	2	1		1	1	1	6	11	10	14	7	4				65



GODHAVN 4-9-1959 H.W.M. 2,9‰

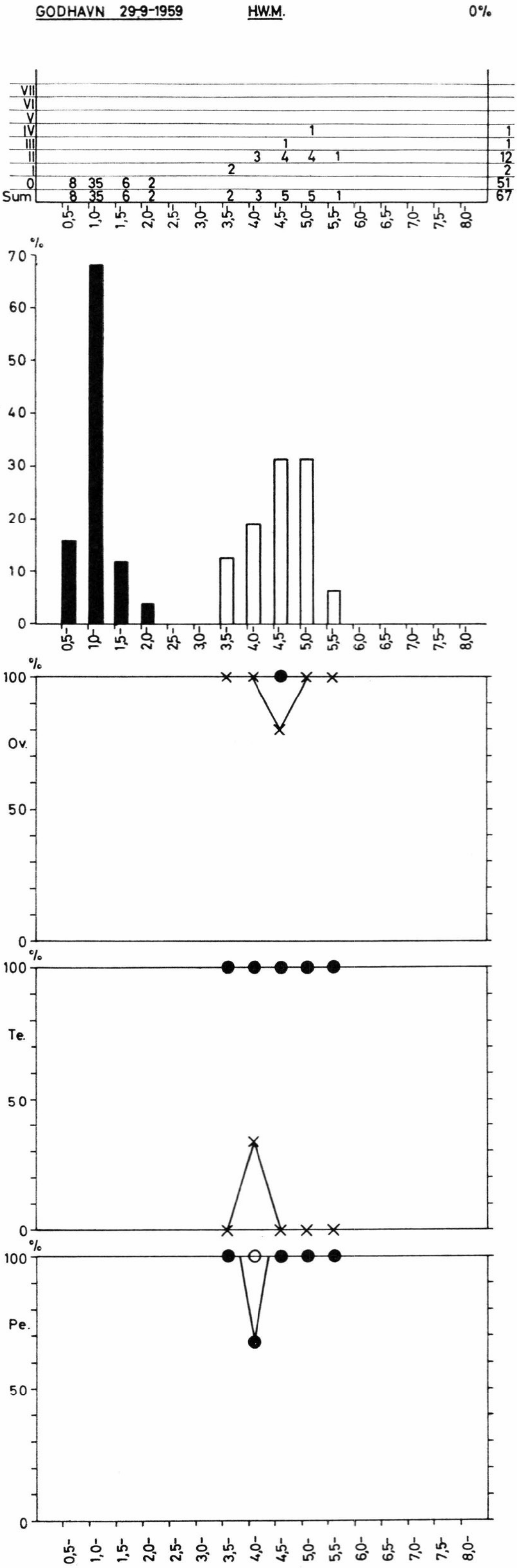
	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
?									1		3	1	1				6
V											1						1
IV										3	2		1				6
III									4	2	2						8
II							1	1	2	3							7
I						1	3	1	2								7
0	37	42	7														86
Sum	37	42	7			1	4	2	9	8	8	1	2				121





GODHAVN 17-9-1959 H.W.M. 7,2%

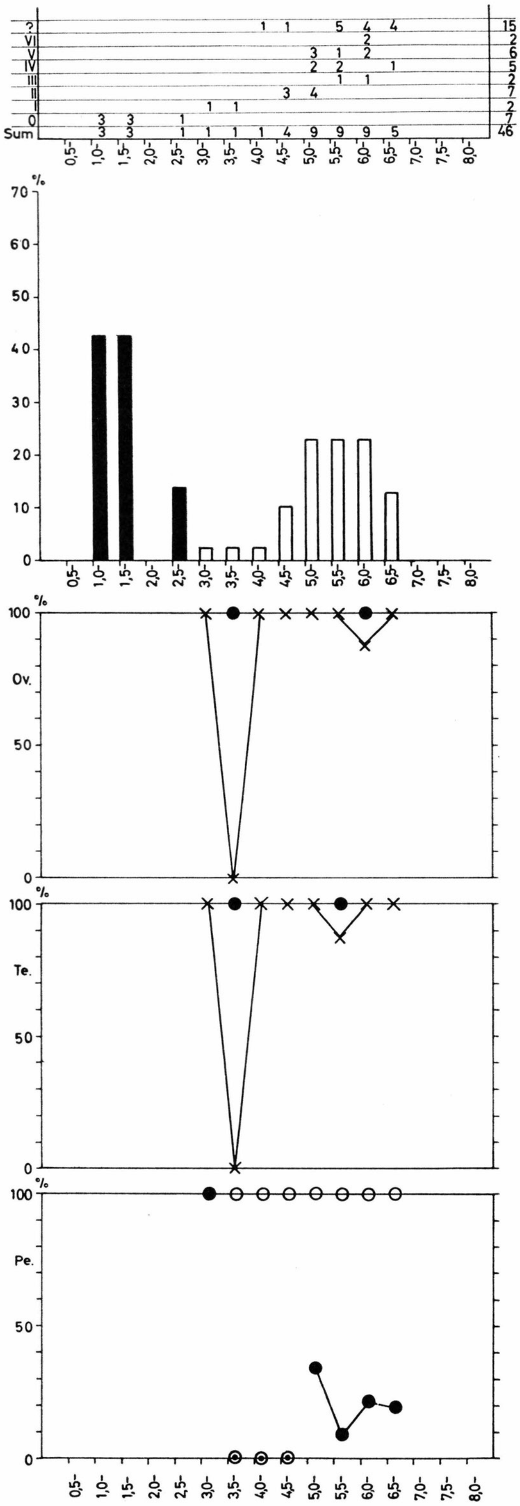
	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII											1						1
VI												1	1				2
V									1		3	1					5
IV							1				2						3
III									1	1							2
II							3	1	1	2	1						8
I					1												1
0	24	52	2														78
Sum	24	52	2		1		4	1	3	3	7	2	1				100



GODHAVN 29-9-1959 H.W.M. 0%

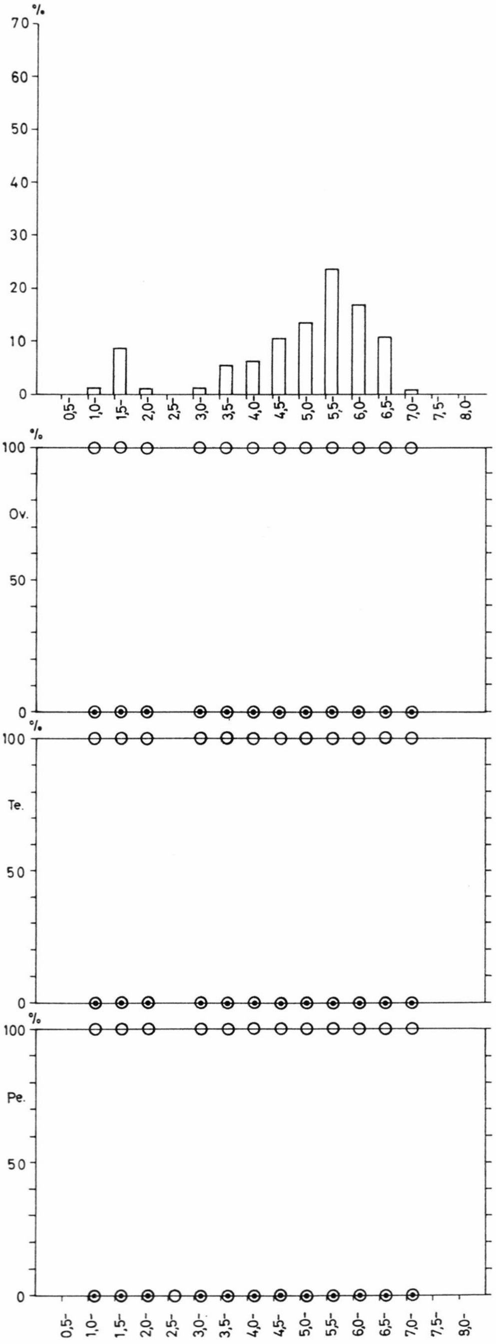
	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI																	
V																	
IV										1							1
III									1								1
II								3	4	4	1						12
I							2										2
0	8	35	6	2													51
Sum	8	35	6	2			2	3	5	5	1						67

GODHAVN 16-10-1959 H.W.M.



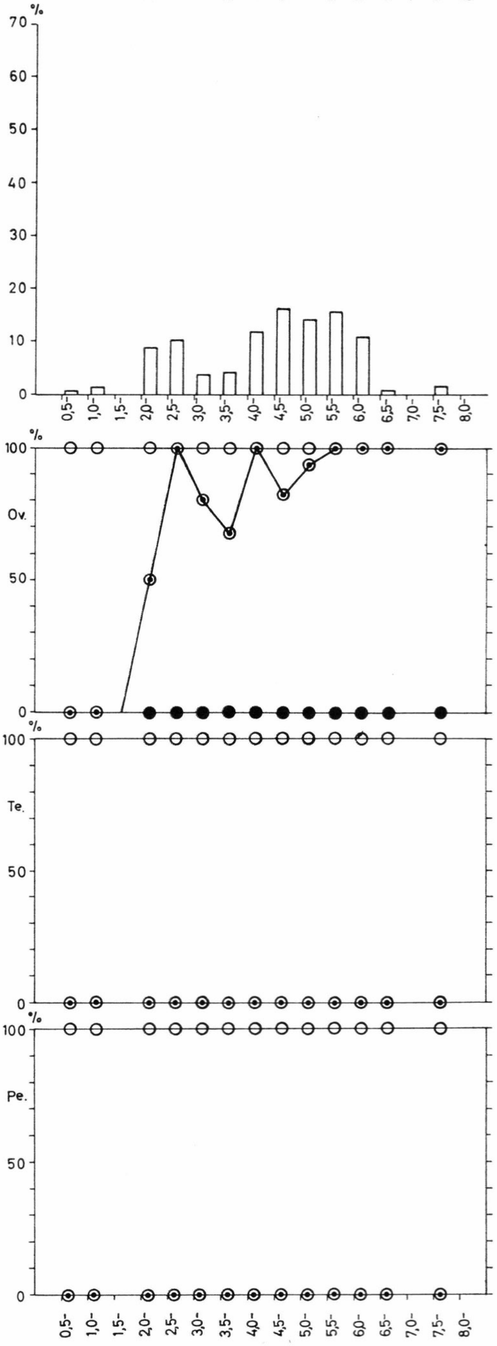
GODHAVN 10-5-1959 M.W.M.

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VIII																	
VI																	
V								1			3	2	2	1			9
IV						2	4		2	3	1	4	10				26
III							1		4	8	30	18	4				65
II							4	7	9	9	1	1					31
I		2	13	2				1									18
0																	
Sum		2	13	2		2	9	9	15	20	35	25	16	1			149

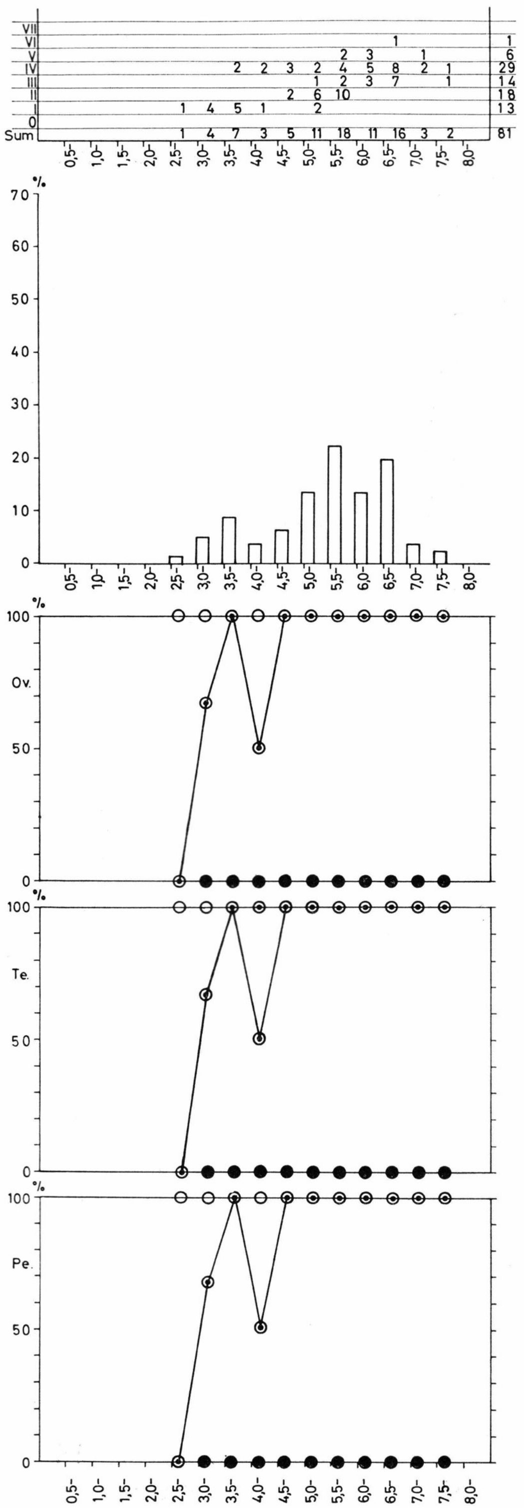


GODHAVN 17-6-1959 M.W.M.

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI																	
V																	
IV												4			1		5
III							2	2		1	15	11	1		1		33
II					3	1	2	12	21	18	6						63
I	1	2		12	11	4	2	3	1								36
0																	
Sum	1	2		12	14	5	6	17	22	19	21	15	1		2		137

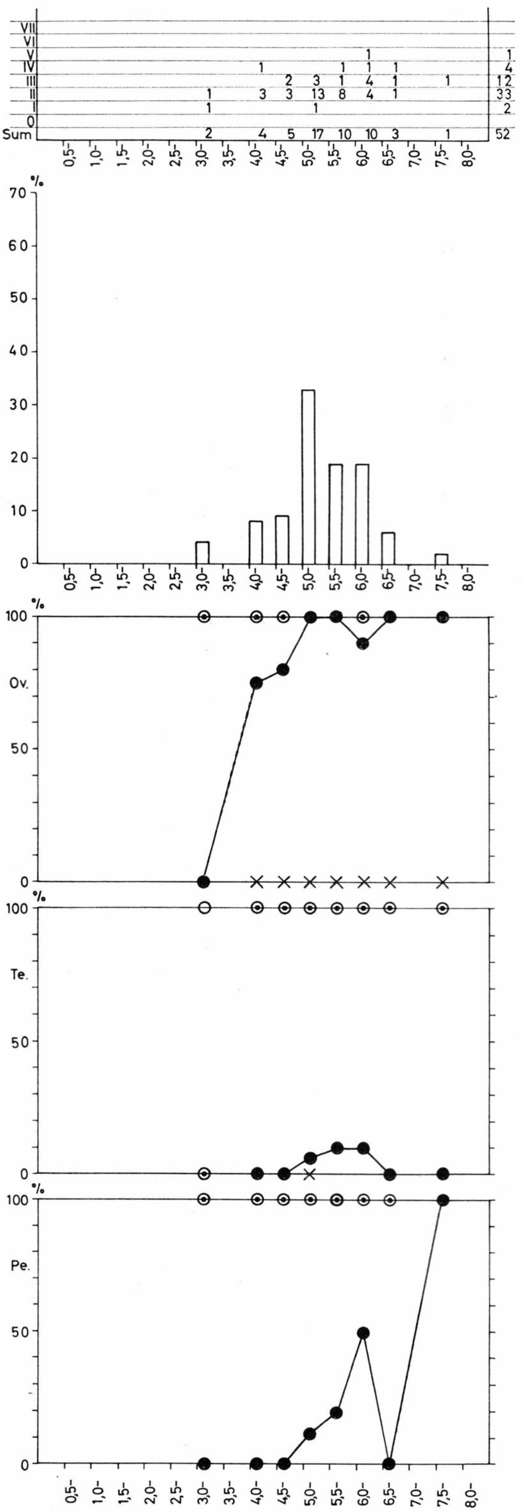


GODHAVN 14-7-1959 M.W.M.



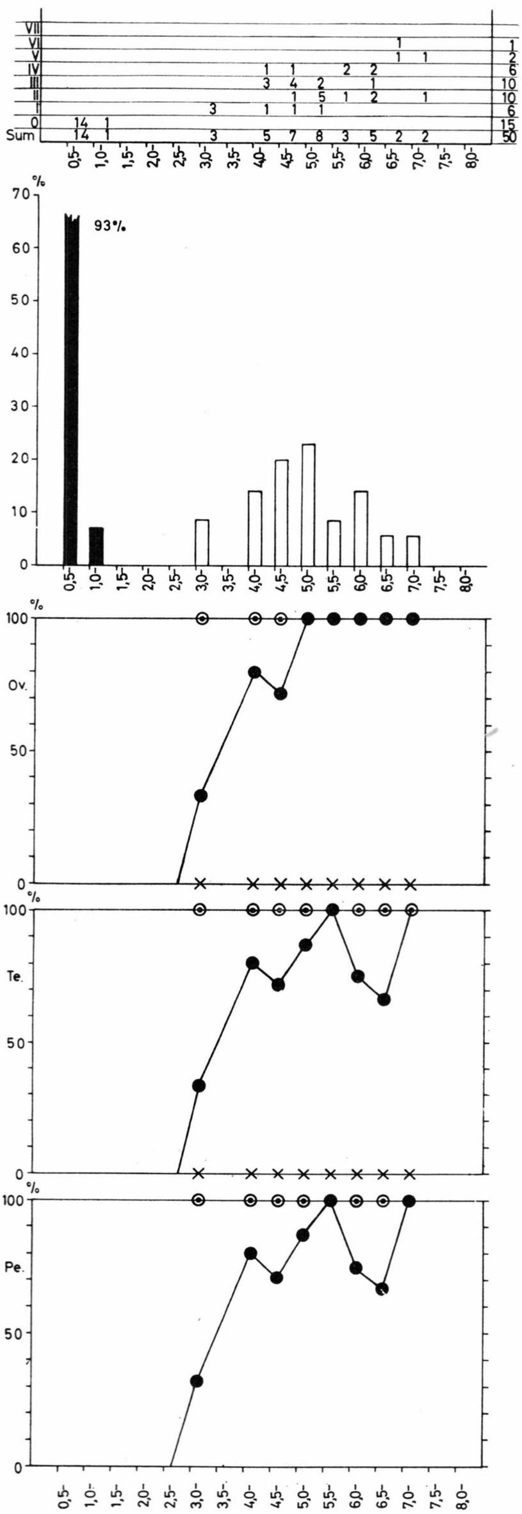
	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI													1				1
V											2	3		1			6
IV							2	2	3	2	4	5	8	2	1		29
III										1	2	3	7		1		14
II									2	6	10						18
I					1	4	5	1		2							13
0																	
Sum					1	4	7	3	5	11	18	11	16	3	2		81

GODHAVN 27-7-1959 M.W.M.

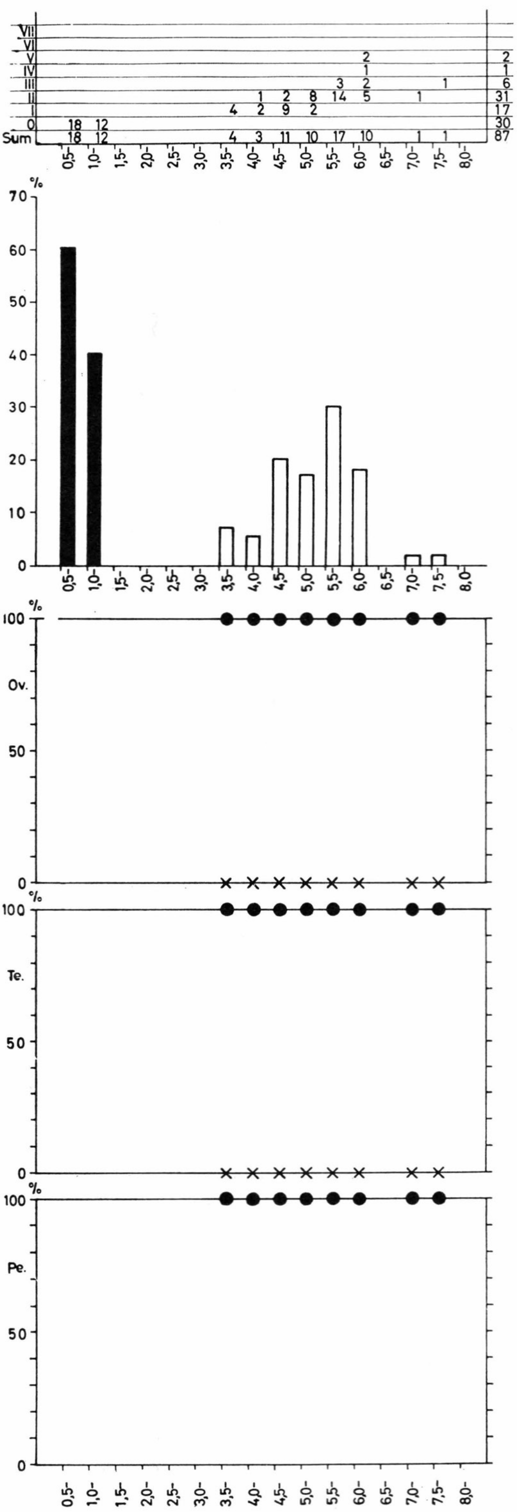


	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI																	
V												1					1
IV								1			1	1	1				4
III									2	3	1	4	1		1		12
II						1		3	3	13	8	4	1				33
I						1				1							2
0																	
Sum						2		4	5	17	10	10	3		1		52

GODHAVN 6-8-1959 M.W.M.

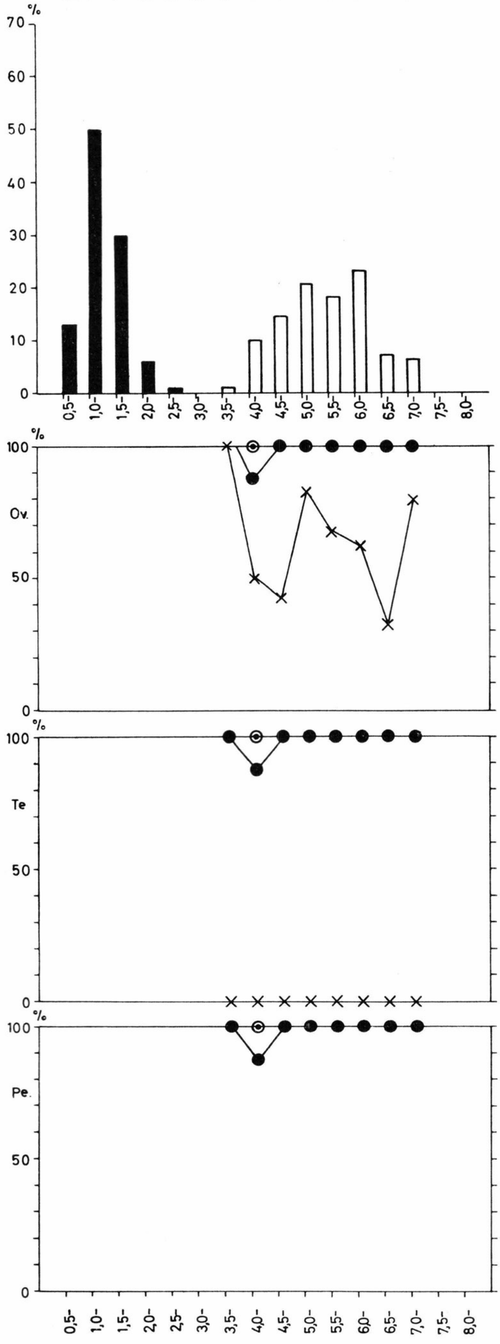


GODHAVN 21-8-1959 M.W.M. 5,3 %



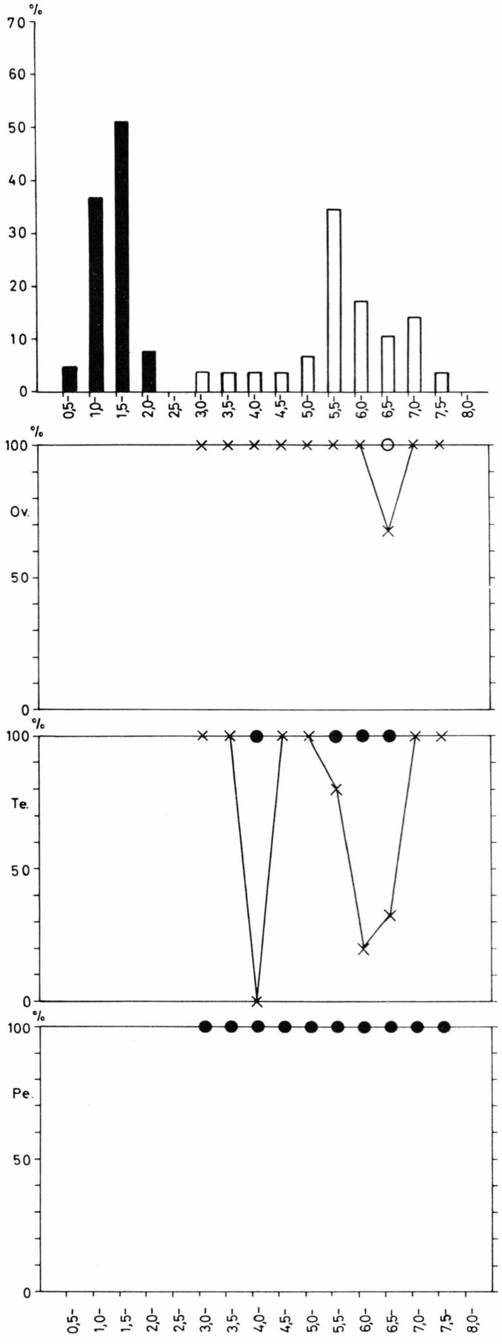
GODHAVN 4-9-1959 M.W.M. 6,2 %

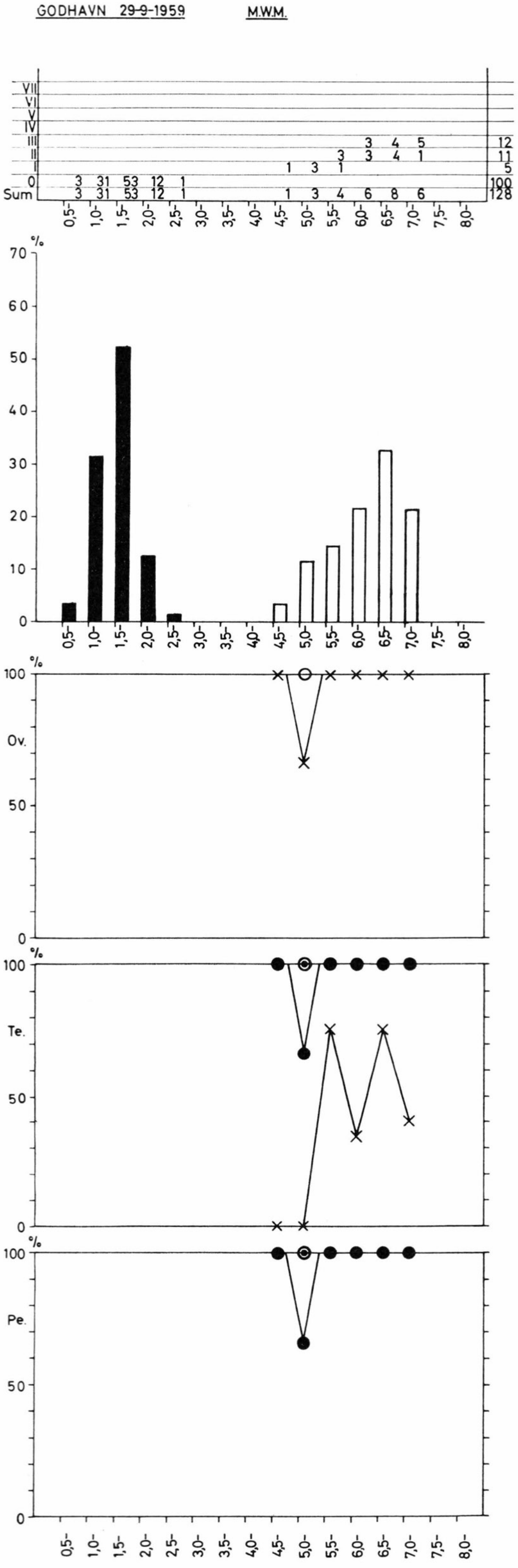
	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI																	
V																	
IV																	
III											2	8	2	5			17
II								2	3	6	9	10	3				33
I							1	6	9	11	4	1	1				33
0	15	59	35	8	1												118
Sum	15	59	35	8	1		1	8	12	17	15	19	6	5			201

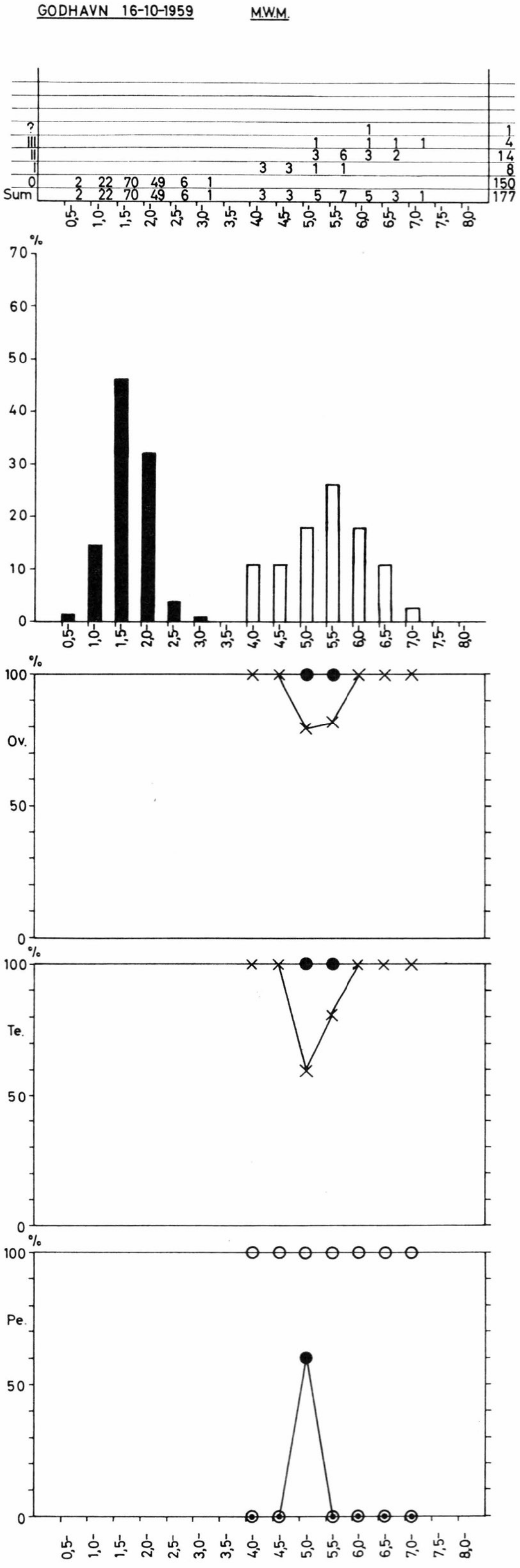


GODHAVN 17-9-1959 M.W.M.

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI																	
V														1			1
IV														1			1
III											2	3		1	1		7
II							1		1	1	8	1	3	1			16
I						1		1		1		1					4
0	6	49	69	10													134
Sum	6	49	69	10		1	1	1	1	2	10	5	3	4	1		163

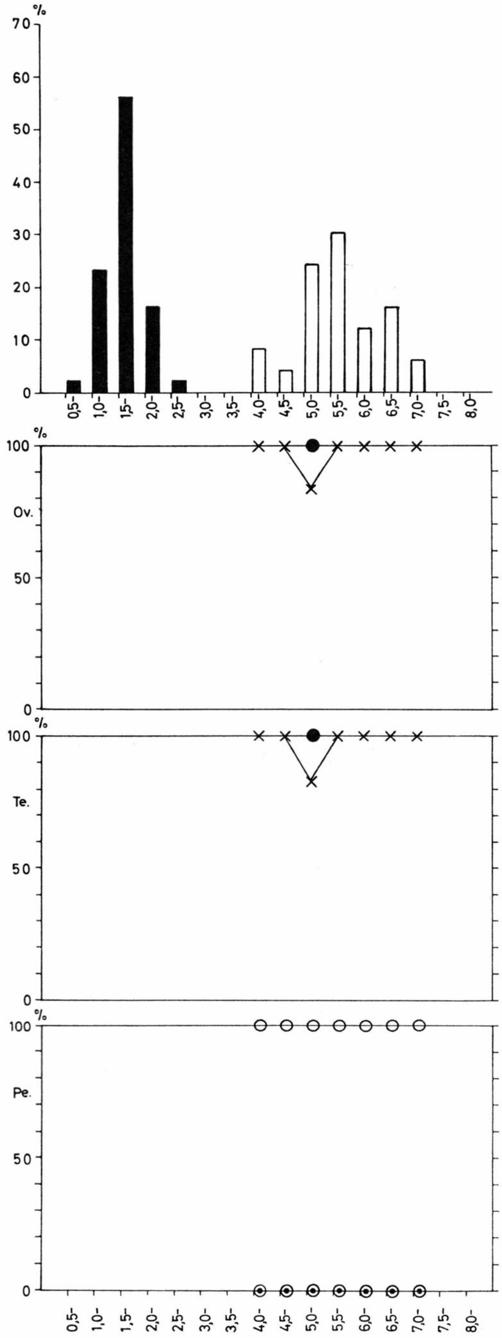



GODHAVN 29-9-1959
M.W.M.
VII
VI
V
IV
III 3 4 5 12
II 3 3 4 1 11
I 1 3 1 5
0 3 31 53 12 1 100
Sum 3 31 53 12 1 1 3 4 6 8 6 128
0,5- 1,0- 1,5- 2,0- 2,5- 3,0- 3,5- 4,0- 4,5- 5,0- 5,5- 6,0- 6,5- 7,0- 7,5- 8,0-
%
70
60
50
40
30
20
10
0
100
Ov.
50
0
100
Te.
50
0
100
Pe.
50
0


GODHAVN 16-10-1959
M.W.M.
? 1 1
III 1 1 1 1 4
II 3 6 3 2 14
I 3 3 1 1 8
0 2 22 70 49 6 1 150
Sum 2 22 70 49 6 1 3 3 5 7 5 3 1 177
0,5- 1,0- 1,5- 2,0- 2,5- 3,0- 3,5- 4,0- 4,5- 5,0- 5,5- 6,0- 6,5- 7,0- 7,5- 8,0-
%
70
60
50
40
30
20
10
0
100
Ov.
50
0
100
Te.
50
0
100
Pe.
50
0

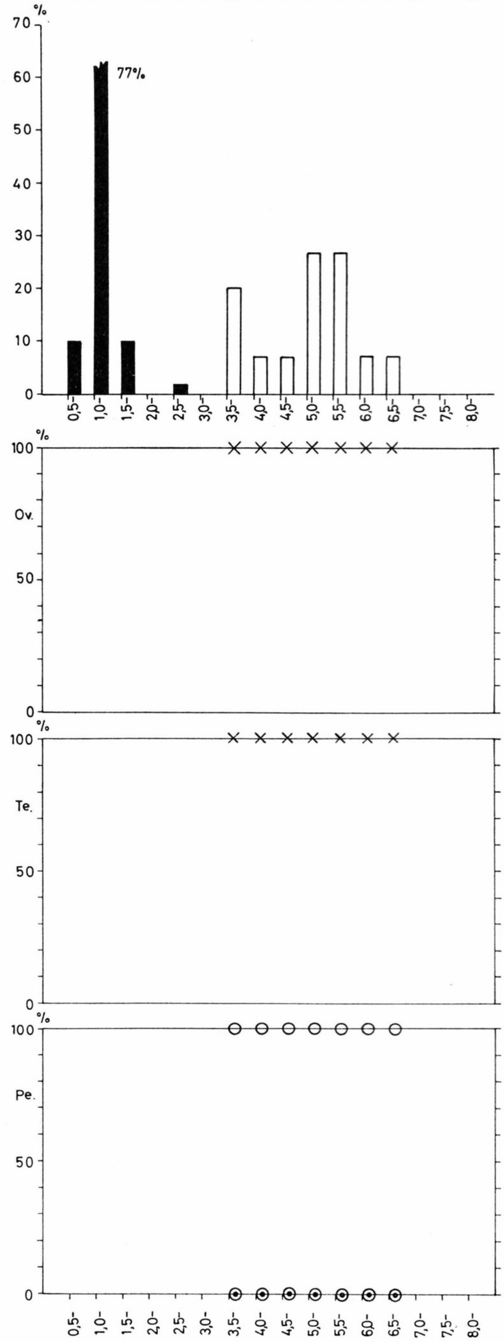
GODHAVN 9-11-1959 M.W.M.

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI										1				1			2
V													2				2
IV												1	2	1			4
III											1	1	4	1			7
II								2	1	10	14	4					31
I								2	1	1							4
0	4	48	115	33	4												204
Sum	4	48	115	33	4			4	2	12	15	6	8	3			254



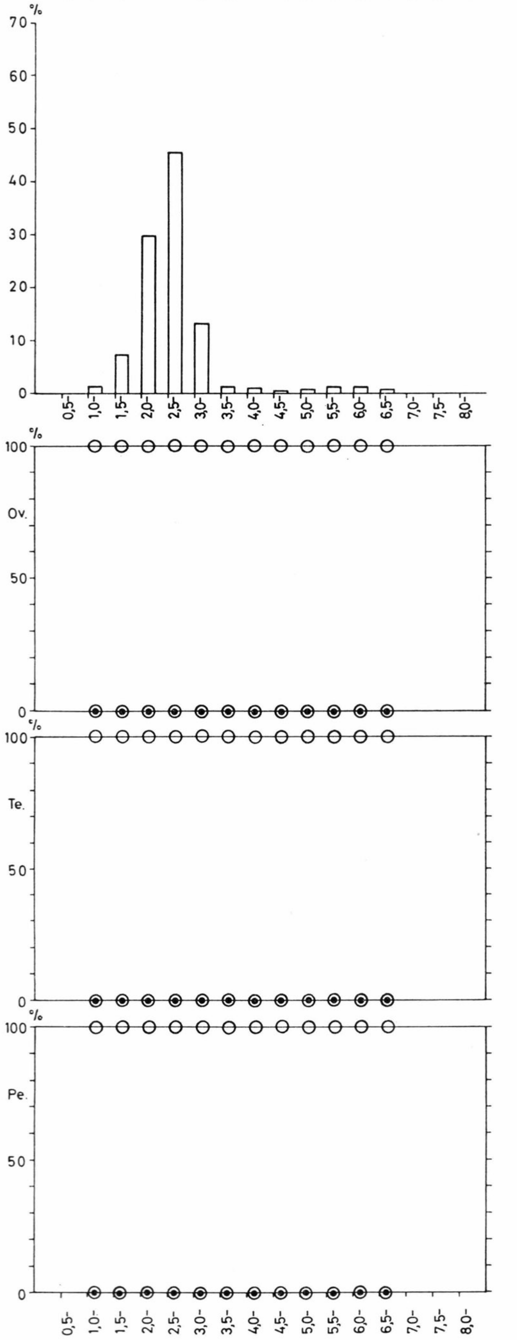
GODHAVN 15-12-1959 M.W.M. 6,7 %

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI																	
V													1				1
IV																	
III										1	1						2
II								1	1	3	3	1					9
I							3										3
0	5	36	5		1												47
Sum	5	36	5		1		3	1	1	4	4	1	1				62



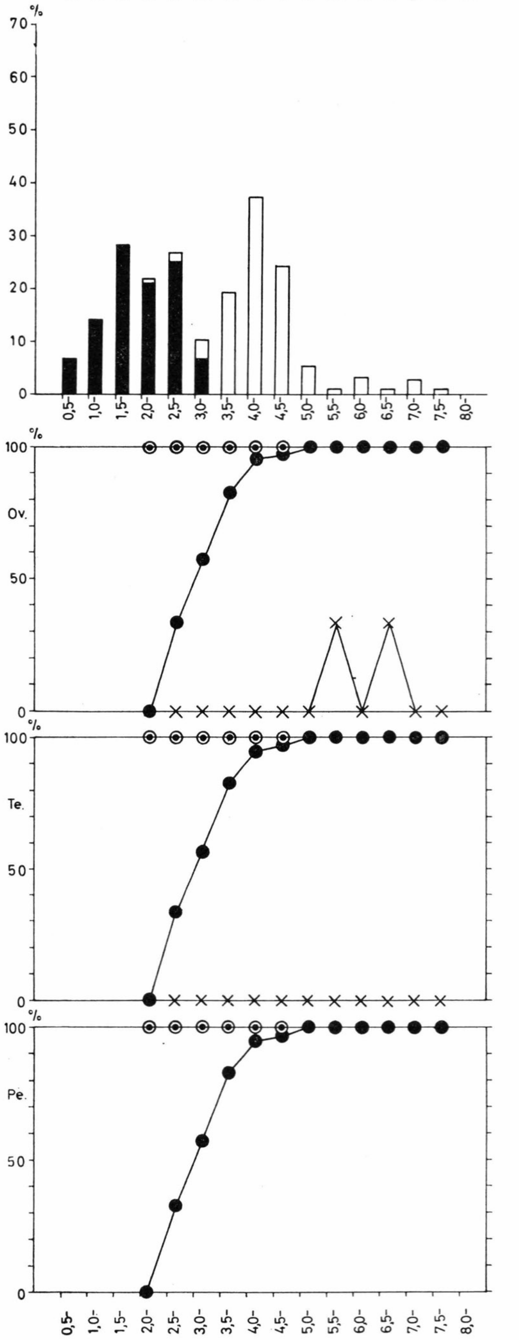
GODHAVN 22-6-1960   M.W.M.   1 %

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI																	
V																	
IV									1		2	3	2				8
III								2		2	2	2					8
II								1									1
I		4	31	129	194	56	4										418
0																	
Sum		4	31	129	194	56	4	3	1	2	4	5	2				435



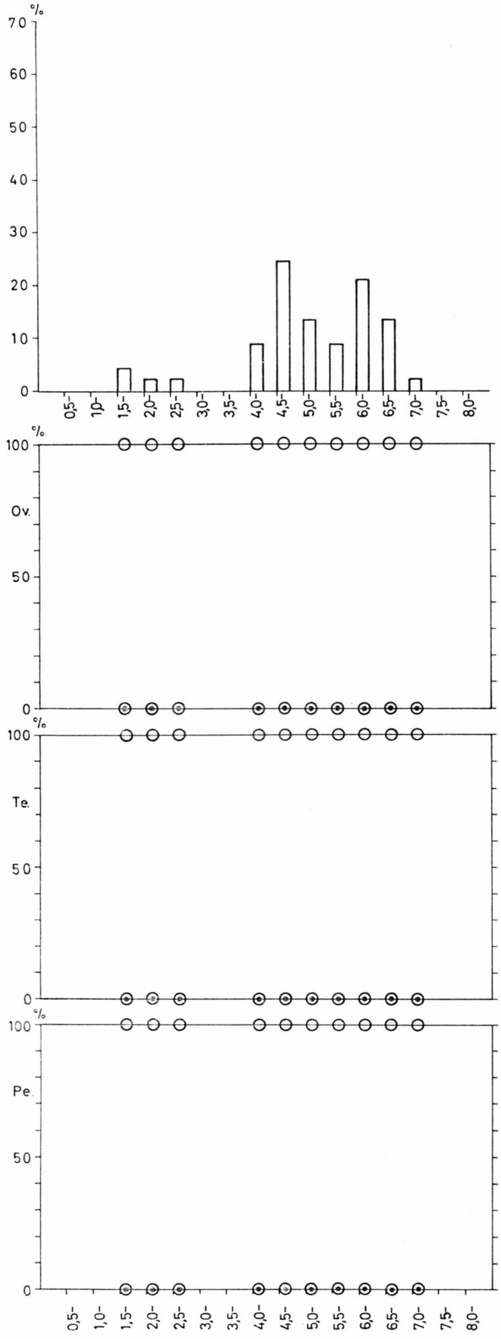
GODHAVN 3-9-1960   M.W.M.   3 %

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI																	
V																	
IV													1	3			4
III										1	1	4	1	1	1		9
II						1		1		1	2	1	1				7
I				1	3	6	33	65	43	7							158
0	6	14	27	20	24	6											97
Sum	6	14	27	21	27	13	33	66	43	9	3	5	3	4	1		275



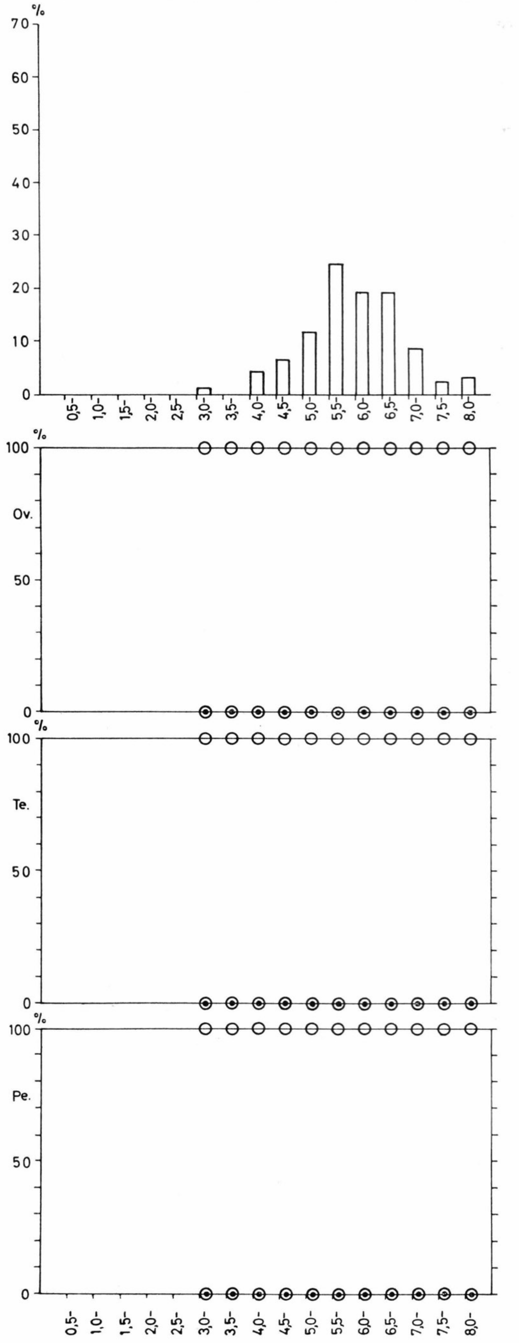
GODHAVN 25-4-1959 L.W.M.

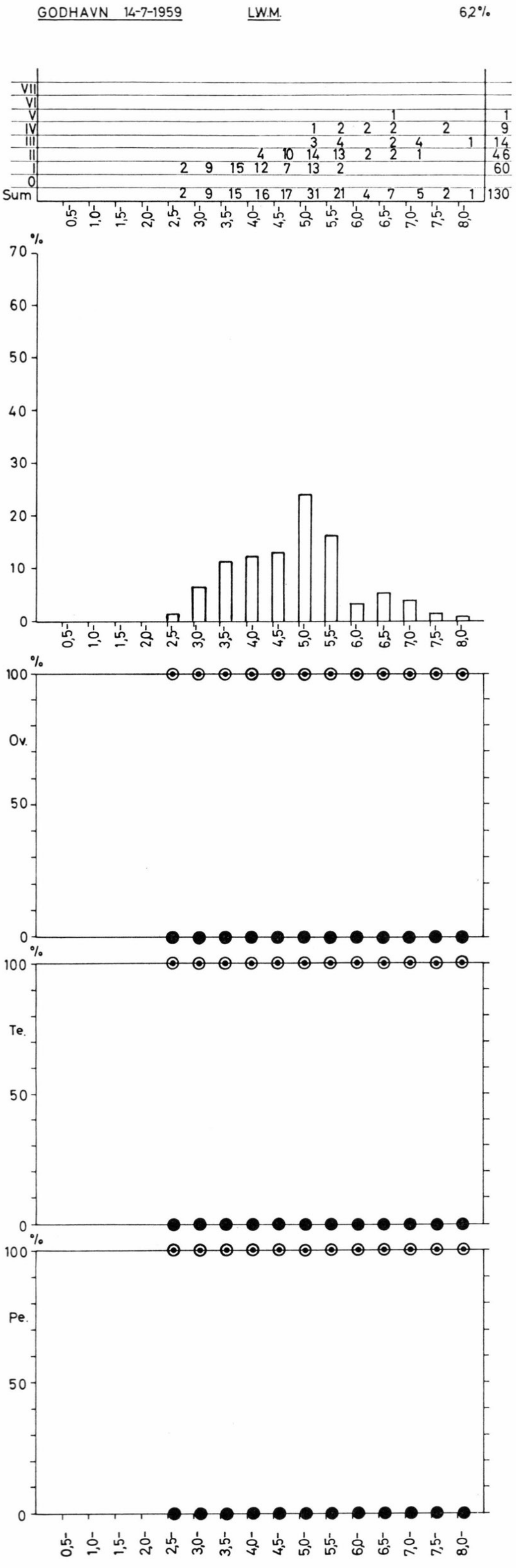
	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
?								2	1				1				4
IV										1		1	3	1			6
III										1		6	2				9
II								2	10	4	4	2					22
I			2	1	1												4
0																	
Sum			2	1	1			4	11	6	4	9	6	1			45

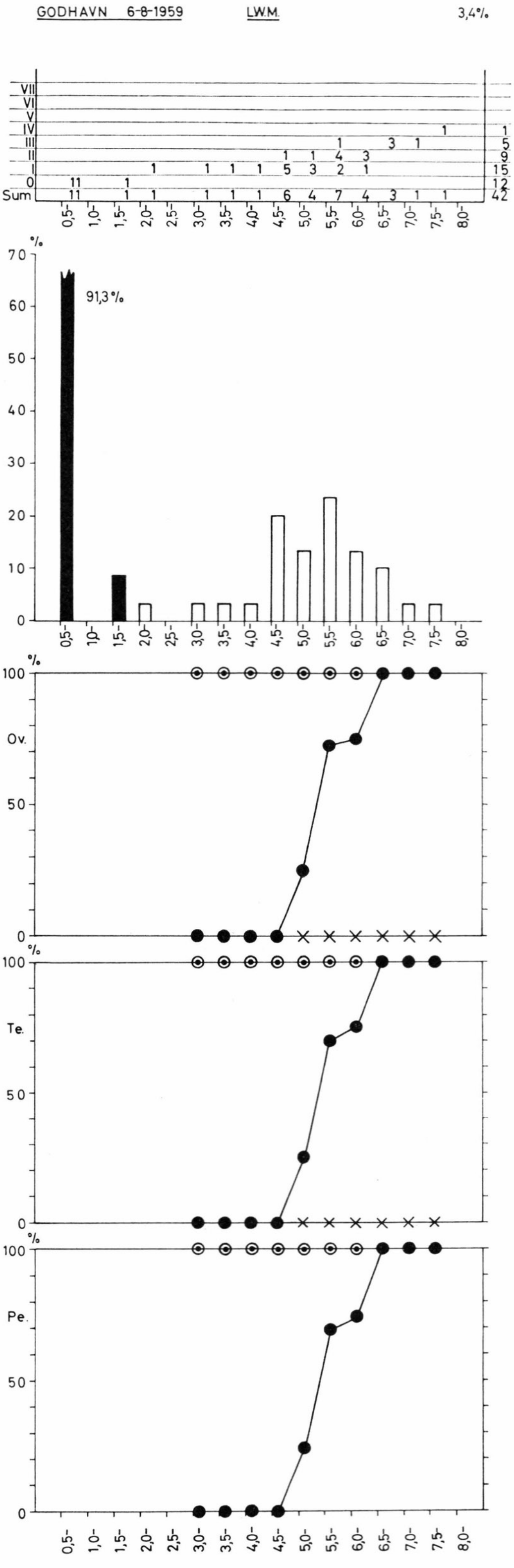


GODHAVN 10-5-1959 L.W.M. 5%

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI													2	2	1	1	6
V									1	1	2	1	1	2		2	10
IV											3	2	6	2	1		14
III								1	2	6	14	14	8	2			47
II						1		2	3	4	4	1	1				16
I								1									1
0																	
Sum						1		4	6	11	23	18	18	8	2	3	94

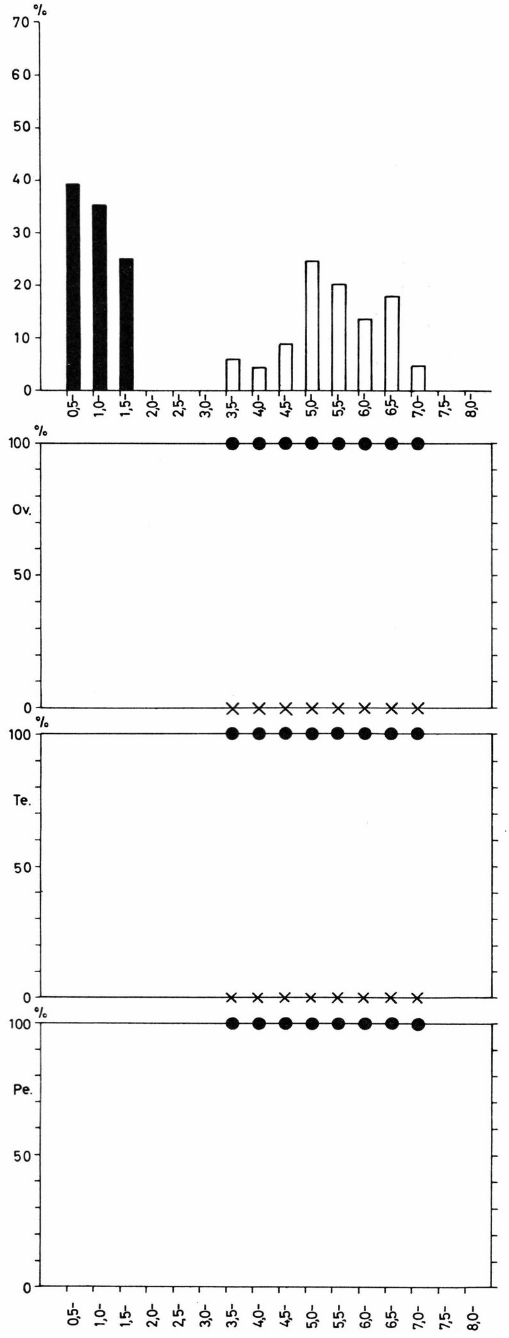



GODHAVN 14-7-1959
LW.M.
6,2%
VII
VI
V 1 1
IV 1 2 2 2 2 9
III 3 4 2 4 1 14
II 4 10 14 13 2 2 1 46
I 2 9 15 12 7 13 2 60
0
Sum 2 9 15 16 17 31 21 4 7 5 2 1 130
0,5- 1,0- 1,5- 2,0- 2,5- 3,0- 3,5- 4,0- 4,5- 5,0- 5,5- 6,0- 6,5- 7,0- 7,5- 8,0-
%
70
60
50
40
30
20
10
0
100
Ov.
50
0
Te.
Pe.


GODHAVN 6-8-1959
LW.M.
3,4%
VII
VI
V
IV 1 1
III 1 3 1 5
II 1 1 4 3 9
I 1 1 1 1 5 3 2 1 15
0 11 1 12
Sum 11 1 1 1 1 1 6 4 7 4 3 1 1 42
0,5- 1,0- 1,5- 2,0- 2,5- 3,0- 3,5- 4,0- 4,5- 5,0- 5,5- 6,0- 6,5- 7,0- 7,5- 8,0-
%
70
60
50
40
30
20
10
0
91,3%
100
Ov.
50
0
Te.
Pe.

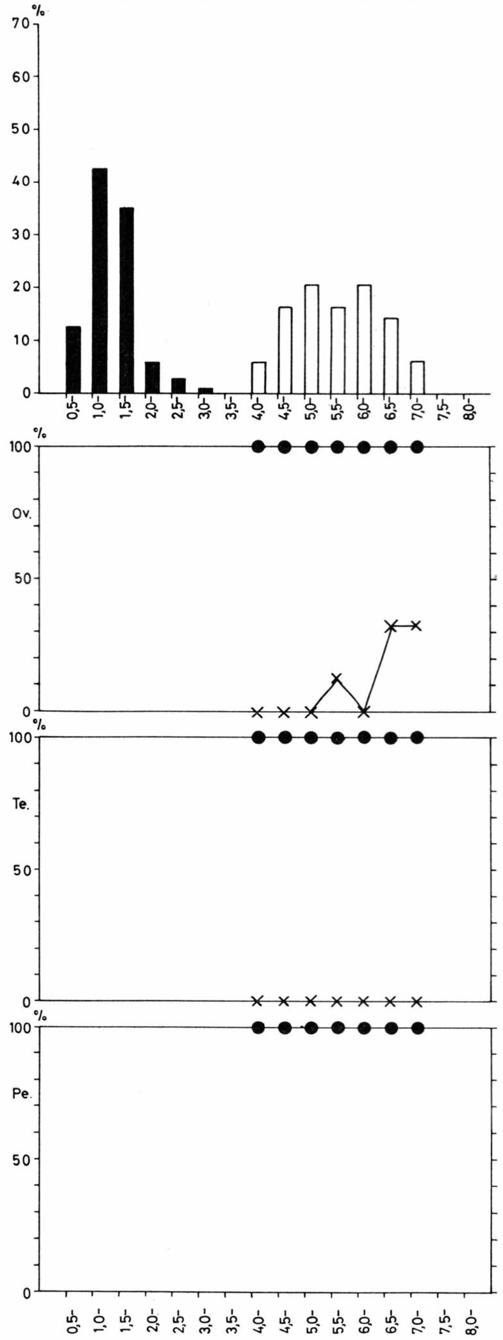
GODHAVN 21-8-1959 LW.M. 7‰

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI																	
V																	
IV													1				1
III											4	2	3	1			10
II							1		1	4	5	3	4	1			19
I							2	2	3	7		1					15
0	11	10	7														28
Sum	11	10	7				3	2	4	11	9	6	8	2			73



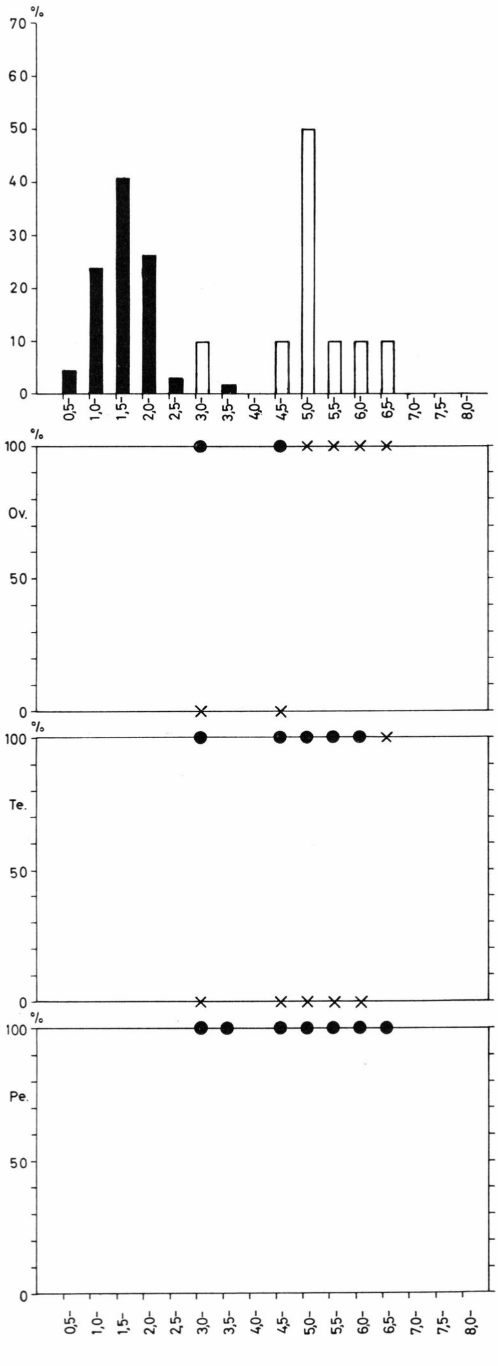
GODHAVN 4-9-1959 LW.M. 4,1‰

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI																	
V																	
IV											2			1			3
III										2	2	4	5	2			15
II									1	3	4	5	2				15
I								3	7	5		1					16
0	13	44	36	6	3	1											103
Sum	13	44	36	6	3	1		3	8	10	8	10	7	3			152



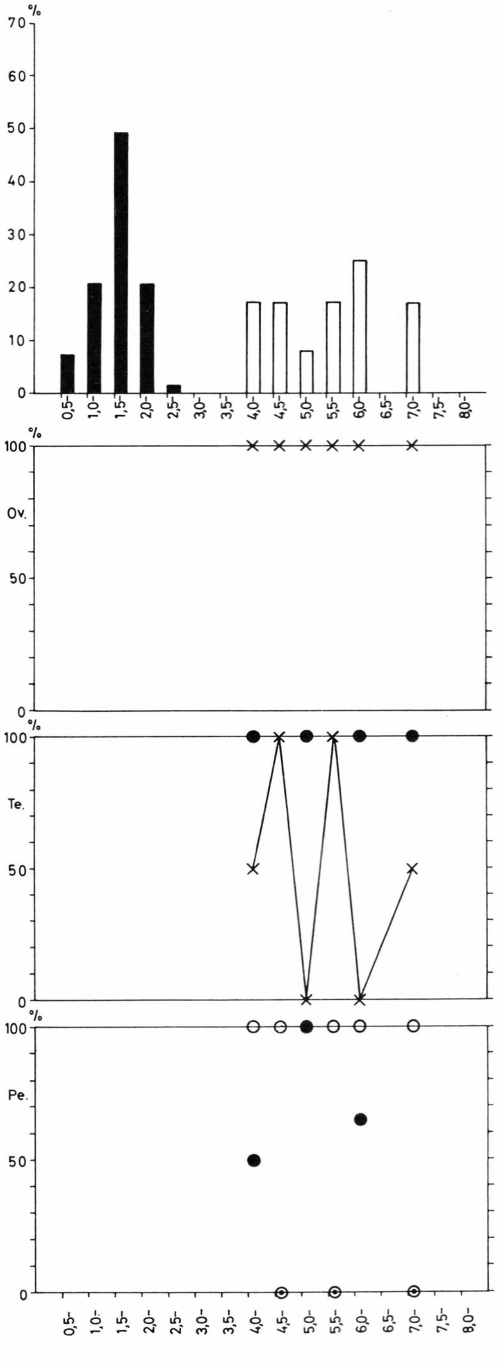
GODHAVN 17-9-1959 LWM. 0%

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI																	
V																	
IV																	
III																	
II										1			1				2
I						1			1	4	1	1					8
0	3	17	28	18	2		1										69
Sum	3	17	28	18	2	1	1		1	5	1	1	1				79



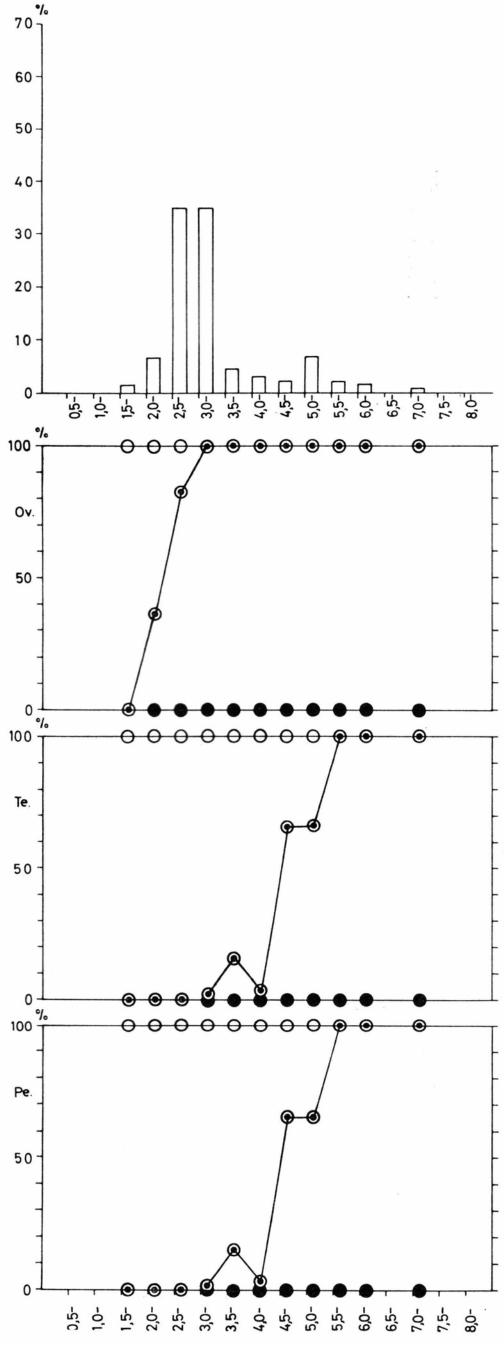
GODHAVN 16-10-1959 LWM. 16%

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI																	
V																	
IV														1			1
III														1			1
II								1	1		1	1					4
I								1	1	1	1	2					6
0	14	41	98	41	3												197
Sum	14	41	98	41	3			2	2	1	2	3		2			209



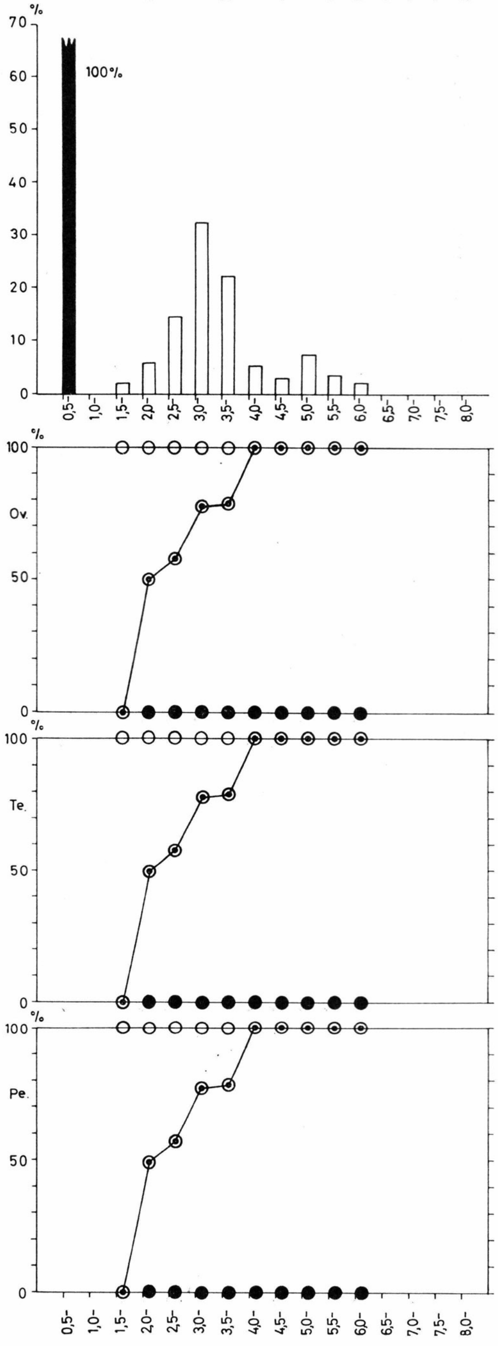
SUKKERTOPPEN 17-5-1959 0,8%

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI														1			1
V											2						2
IV										1							1
III								1	3	8	1	2					15
II				1			1	3									5
I			2	7	45	45	5										104
0																	
Sum			2	8	45	45	6	4	3	9	3	2		1			128



SUKKERTOPPEN 2-6-1959 4,6%

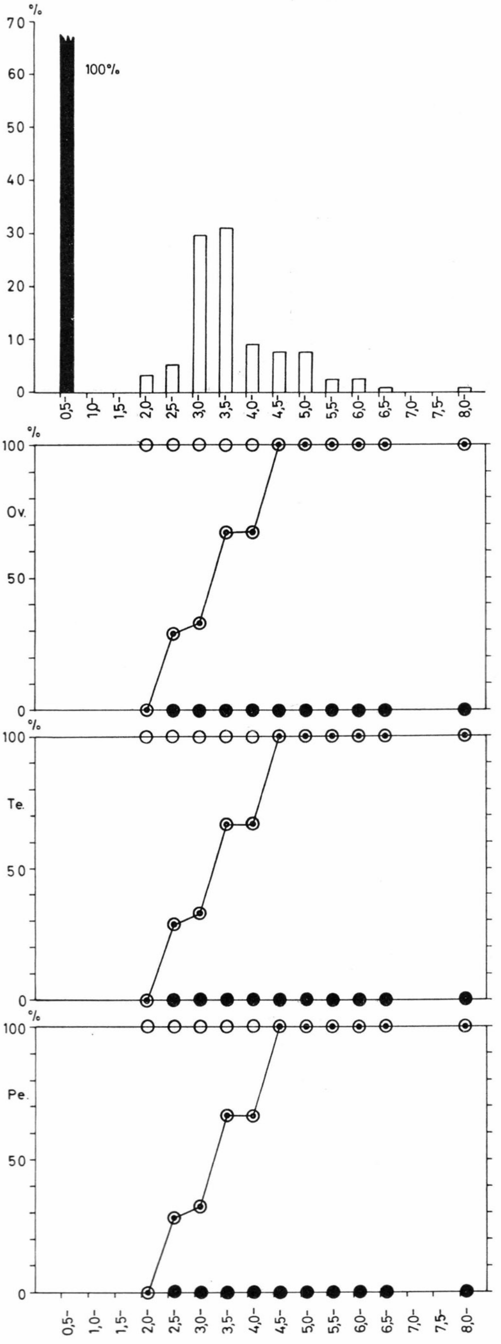
	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII												1					1
VI										1							1
V										2		1					3
IV									1			1					2
III								2	1	4	3						10
II				1		1	1	4	2	3							12
I			3	7	19	40	28	1									98
0	121																121
Sum	121		3	8	19	41	29	7	4	10	3	3					248



SUKKERTOPPEN 19-6-1959

0,76%

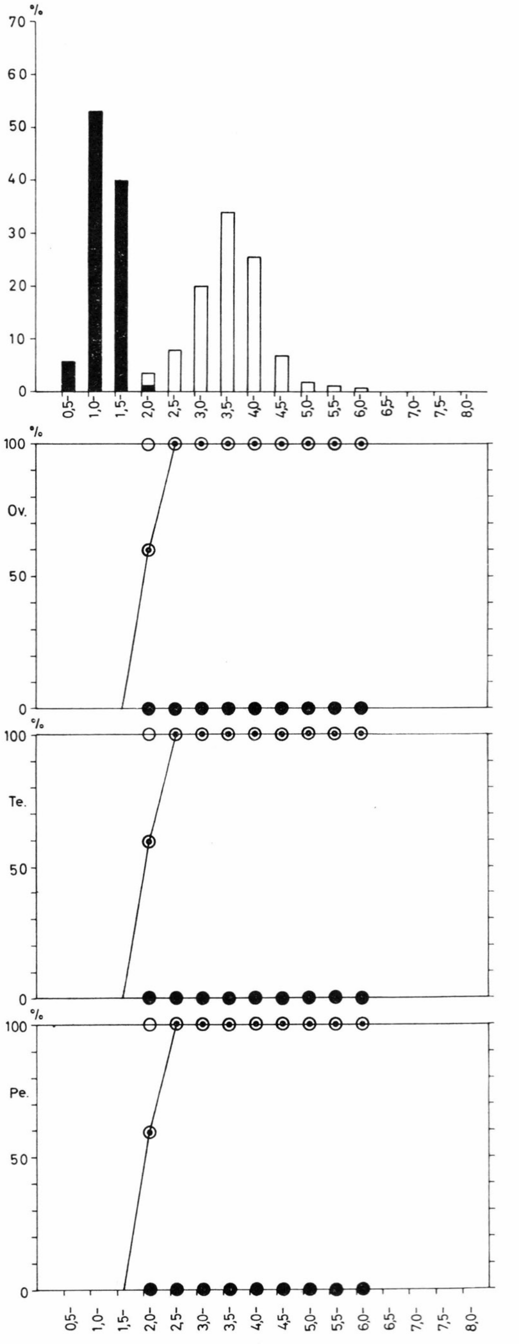
	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
?										2	1	3	1			1	8
IV									1								1
III							3	3	9	8	1						24
II						4	3	3									10
I				4	7	35	35	6			1						88
0	85																85
Sum	85			4	7	39	41	12	10	10	3	3	1			1	216



SUKKERTOPPEN 14-7-1959

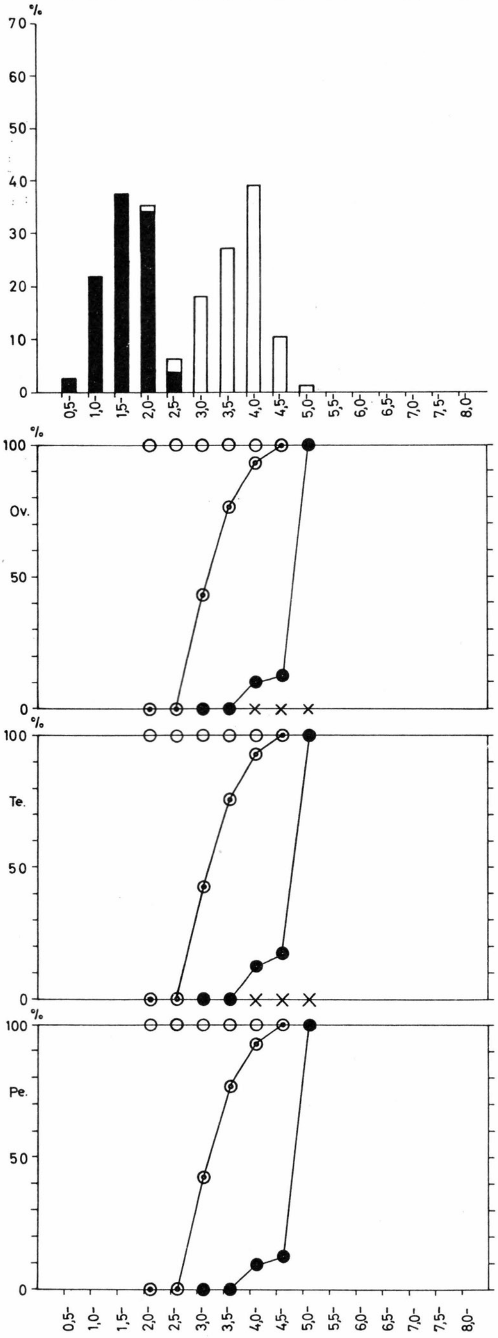
5,7%

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI																	
V																	
IV							1			2							3
III										1	2						3
II					1	1	1	1	1			1					6
I				3	14	38	64	48	12								179
0	9	85	63	2													159
Sum	9	85	63	5	15	39	66	49	13	3	2	1					350



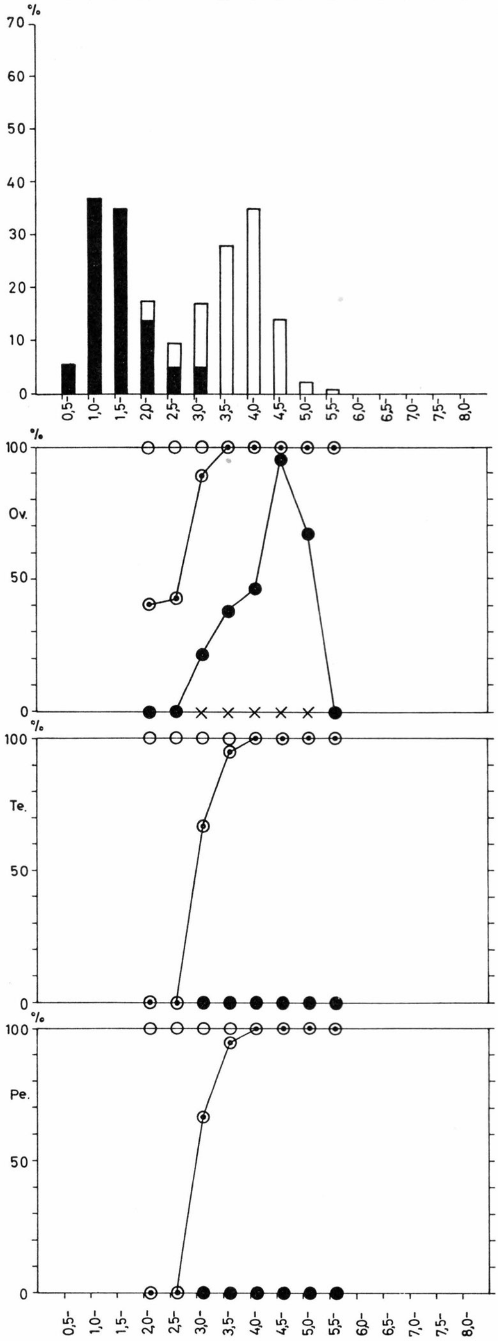
SUKKERTOPPEN 3-8-1959 0‰

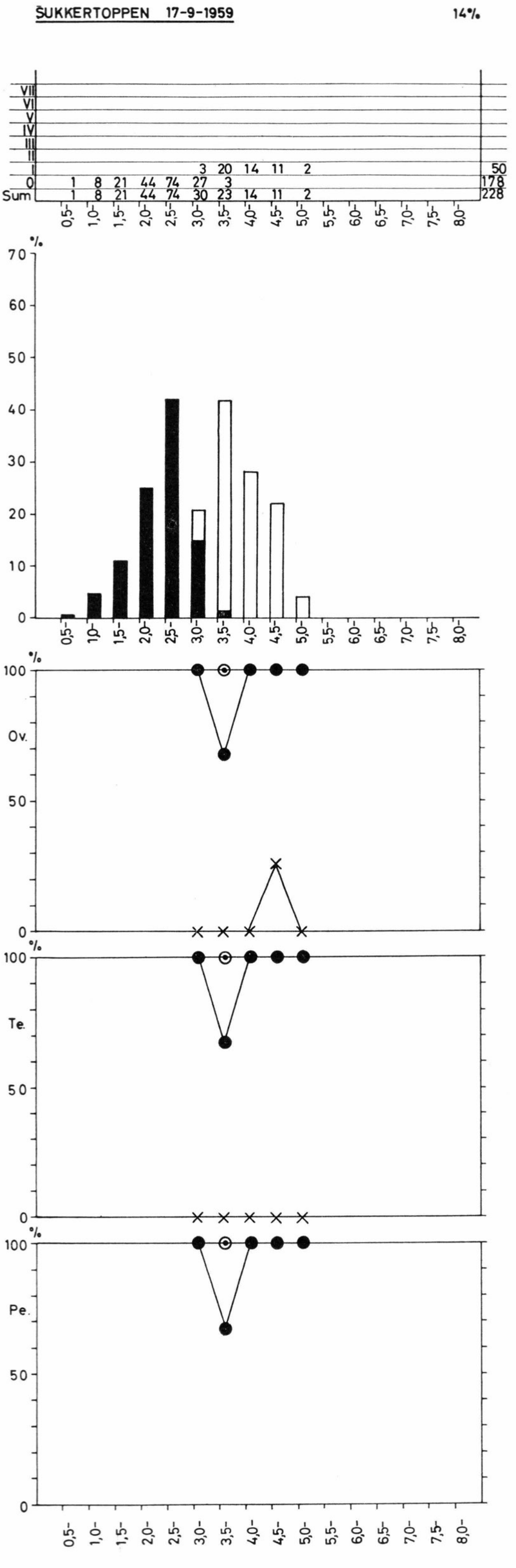
	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
?				1	1	3			1								6
II							2	2	4	1							9
I					1	11	19	28	3								62
0	7	63	106	96	10												282
Sum	7	63	106	97	12	14	21	30	8	1							359

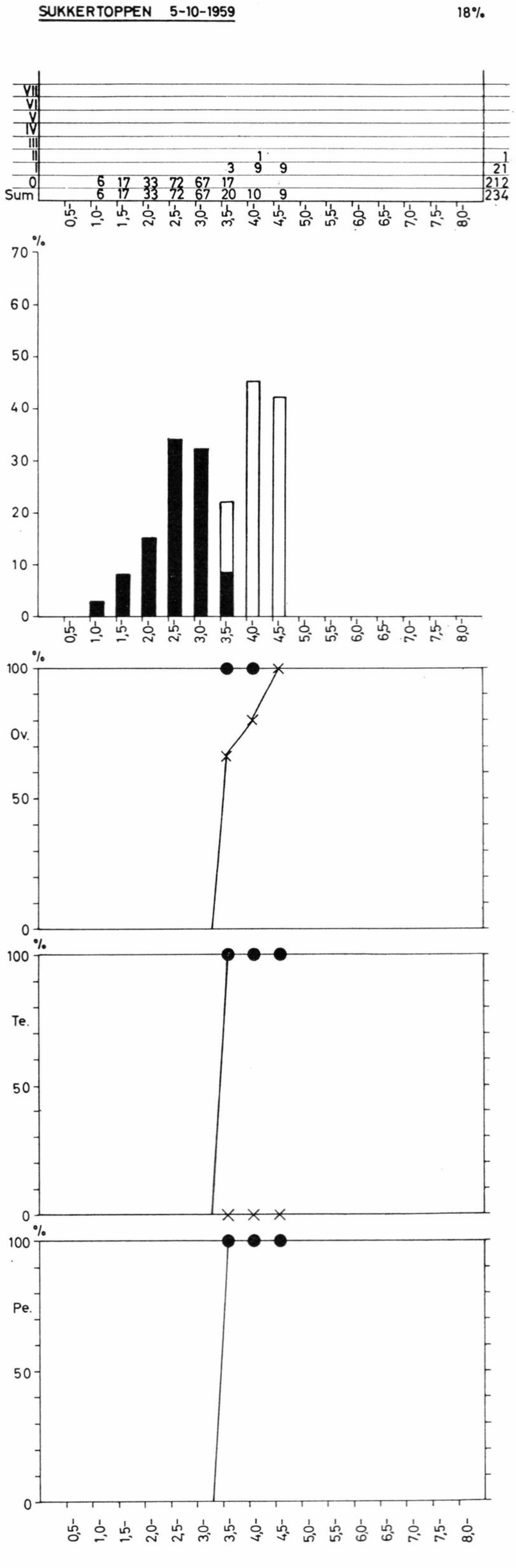


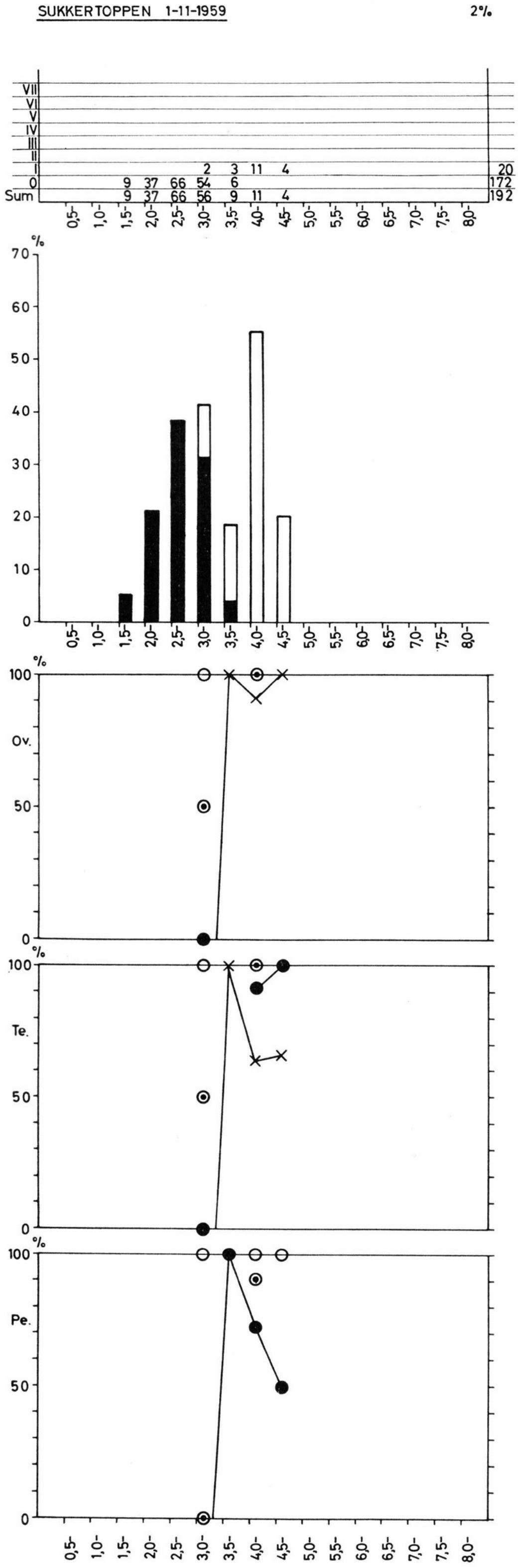
SUKKERTOPPEN 22-8-1959 0,7‰

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI																	
V																	
IV																	
III										1							1
II				1		2	1		2	1							7
I				4	10	16	41	53	18	1	1						144
0	6	40	38	15	5	5											109
Sum	6	40	38	20	15	23	42	53	20	3	1						261

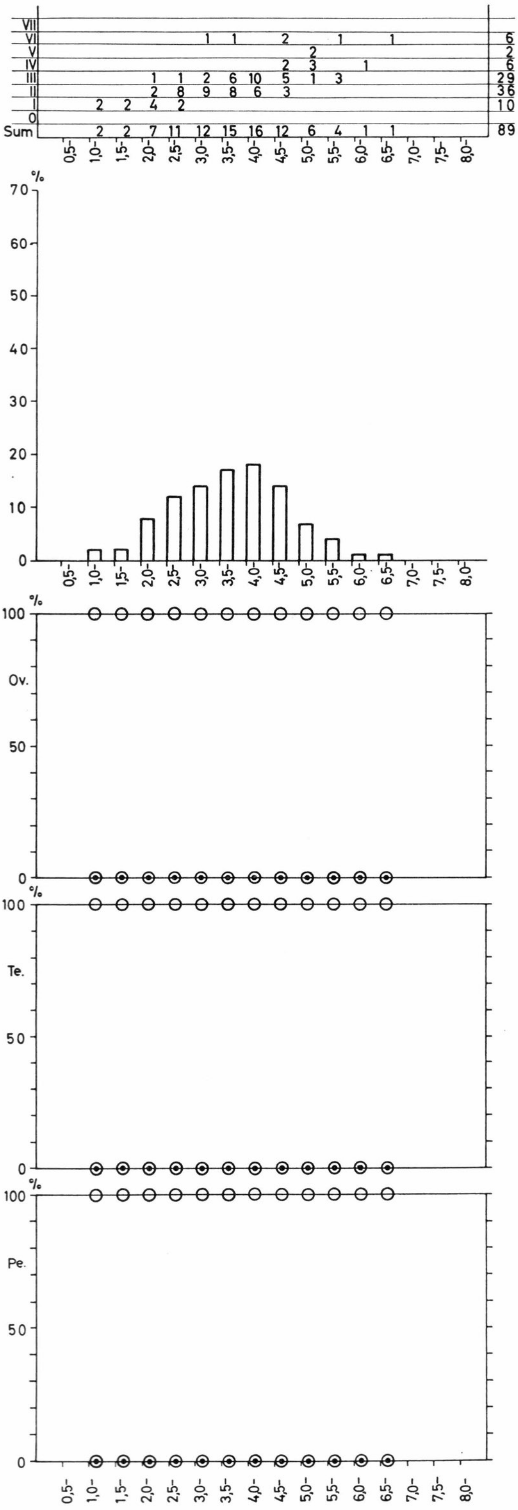



SUKKERTOPPEN 17-9-1959
14‰
VII
VI
V
IV
III
II
I 3 20 14 11 2 50
0 1 8 21 44 74 27 3 178
Sum 1 8 21 44 74 30 23 14 11 2 228
0,5- 1,0- 1,5- 2,0- 2,5- 3,0- 3,5- 4,0- 4,5- 5,0- 5,5- 6,0- 6,5- 7,0- 7,5- 8,0-
%
70
60
50
40
30
20
10
0
%
100
Ov.
50
0
%
100
Te.
50
0
%
100
Pe.
50
0

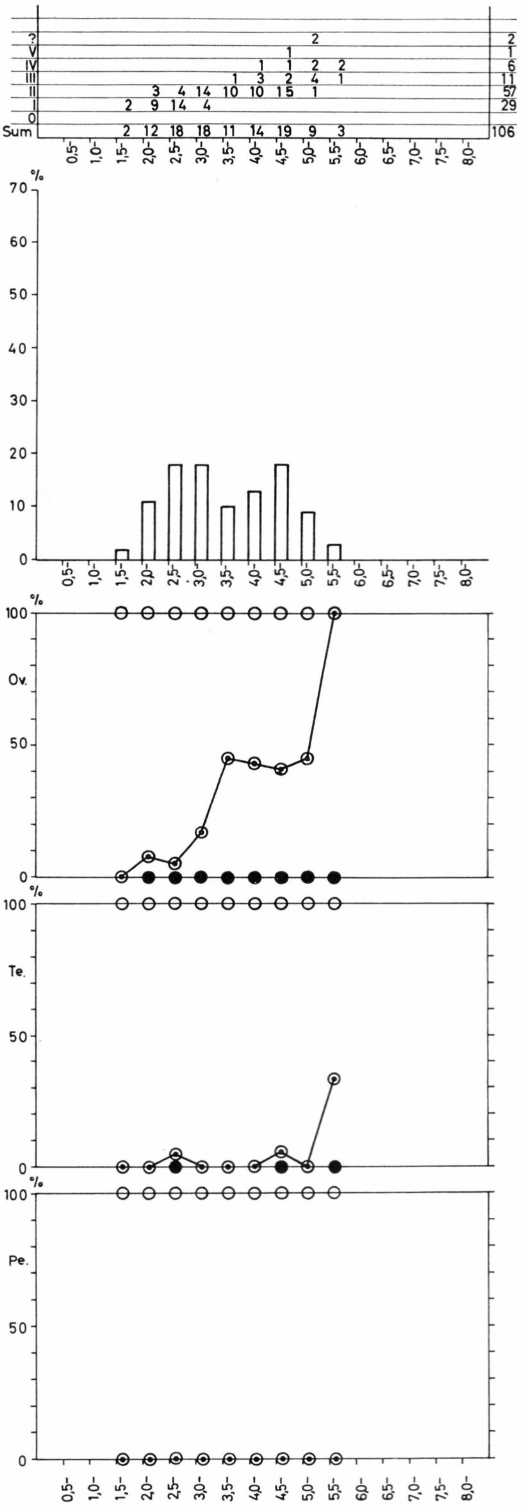

SUKKERTOPPEN 5-10-1959
18‰
VII
VI
V
IV
III
II 1 1
I 3 9 9 21
0 6 17 33 72 67 17 212
Sum 6 17 33 72 67 20 10 9 234
0,5- 1,0- 1,5- 2,0- 2,5- 3,0- 3,5- 4,0- 4,5- 5,0- 5,5- 6,0- 6,5- 7,0- 7,5- 8,0-
%
70
60
50
40
30
20
10
0
%
100
Ov.
50
0
%
100
Te.
50
0
%
100
Pe.
50
0


SUKKERTOPPEN 1-11-1959
2°/o
VII
VI
V
IV
III
II
I 2 3 11 4 20
0 9 37 66 54 6 172
Sum 9 37 66 56 9 11 4 192
0,5-
1,0-
1,5-
2,0-
2,5-
3,0-
3,5-
4,0-
4,5-
5,0-
5,5-
6,0-
6,5-
7,0-
7,5-
8,0-
°/o
70
60
50
40
30
20
10
0
100
Ov.
50
0
Te.
Pe.

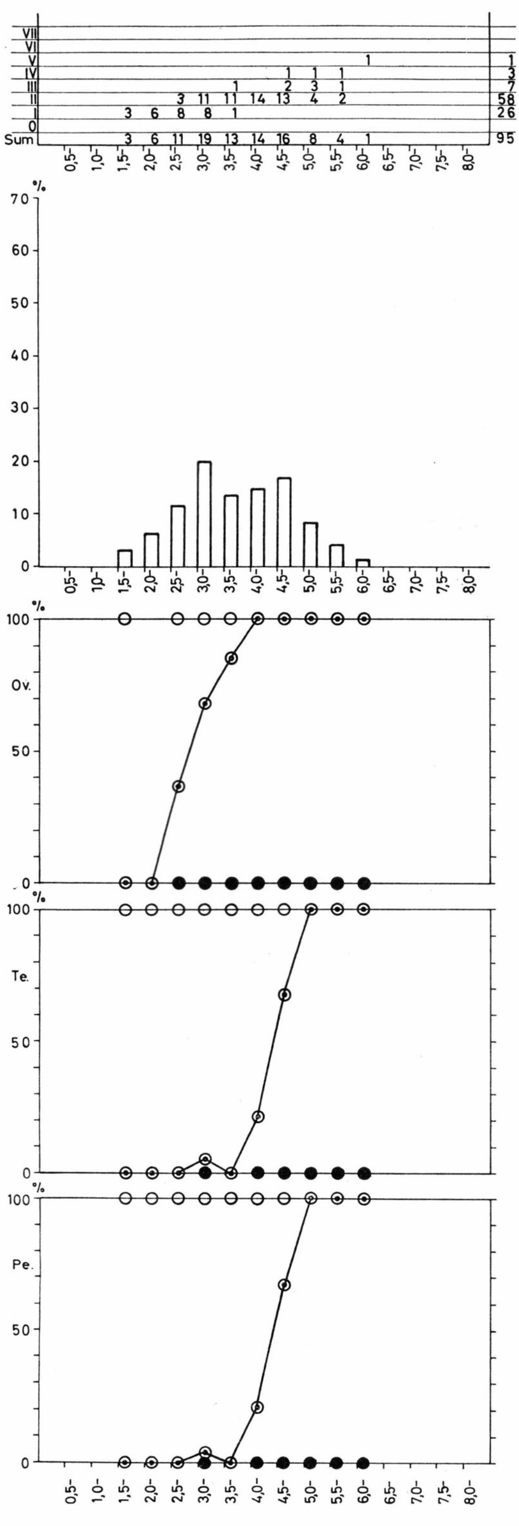
GODTHÅB 13-4-1959



GODTHÅB 11-5-1959

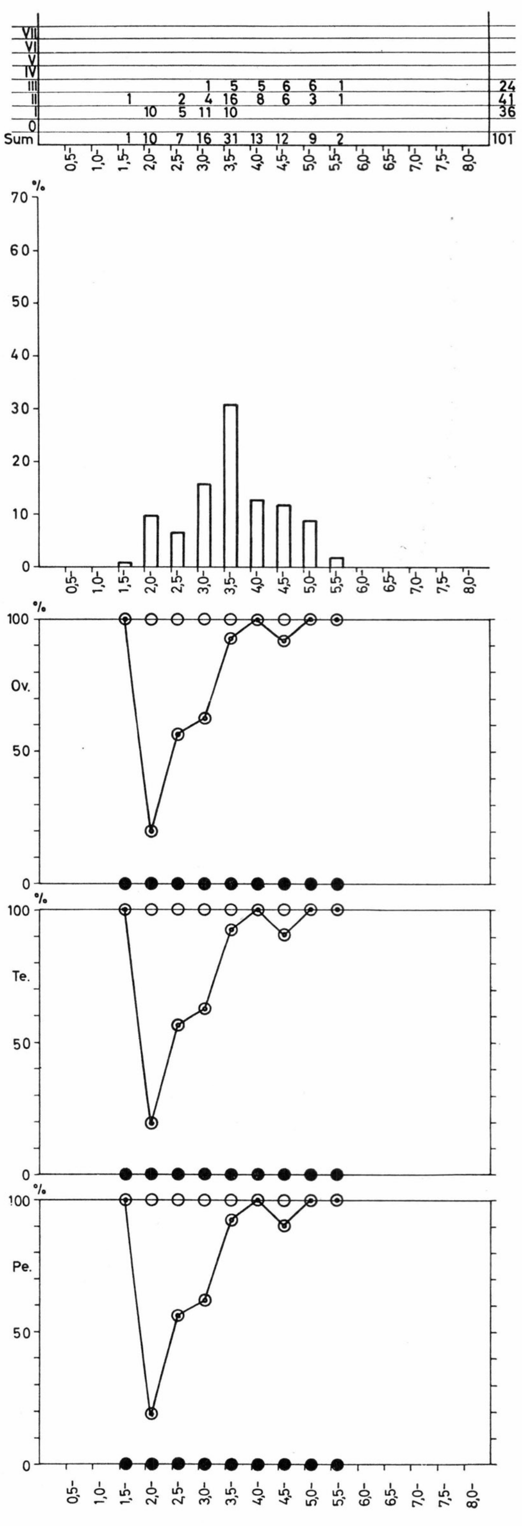


GODTHÅB 8-6-1959 4,4%



	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI																	
V												1					1
IV									1	1	1						3
III							1		2	3	1						7
II					3	11	11	14	13	4	2						58
I			3	6	8	8	1										26
0																	
Sum			3	6	11	19	13	14	16	8	4	1					95

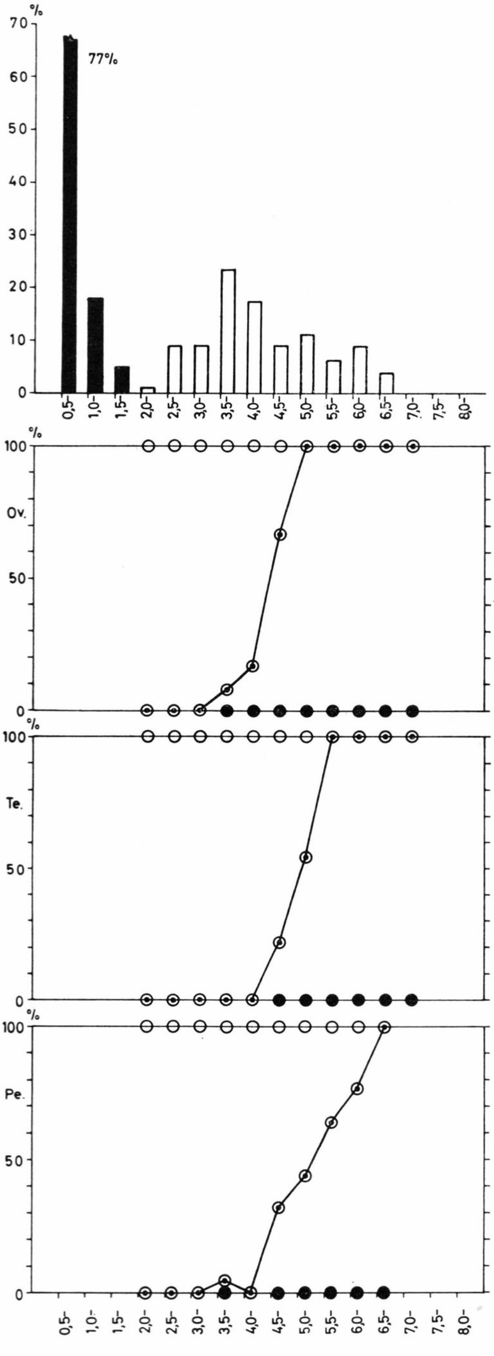
GODTHÅB 22-6-1959 2,4%



	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI																	
V																	
IV																	
III						1	5	5	6	6	1						24
II			1		2	4	16	8	6	3	1						41
I				10	5	11	10										36
0																	
Sum			1	10	7	16	31	13	12	9	2						101

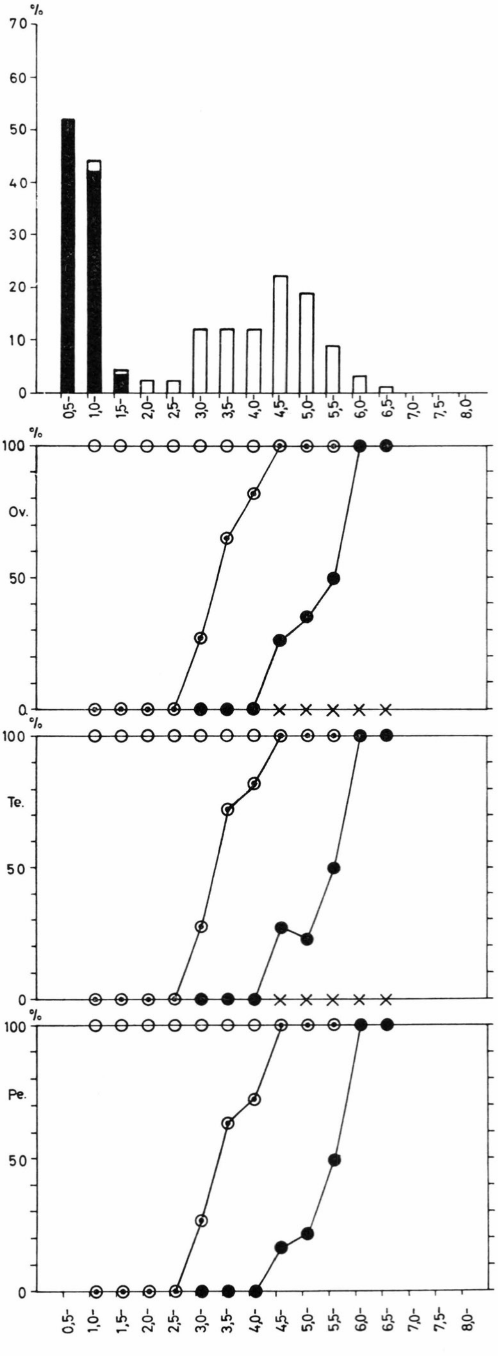
GODTHÅB 7-7-1959

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
?											1	1	1				3
IV												1					1
III										3	3	3	3				12
II						1		2	3	2	2	4					14
I				1	9	8	23	15	6	6							68
0	29	7	2														38
Sum	29	7	2	1	9	9	23	17	9	11	6	9	4				136



GODTHÅB 4-8-1959

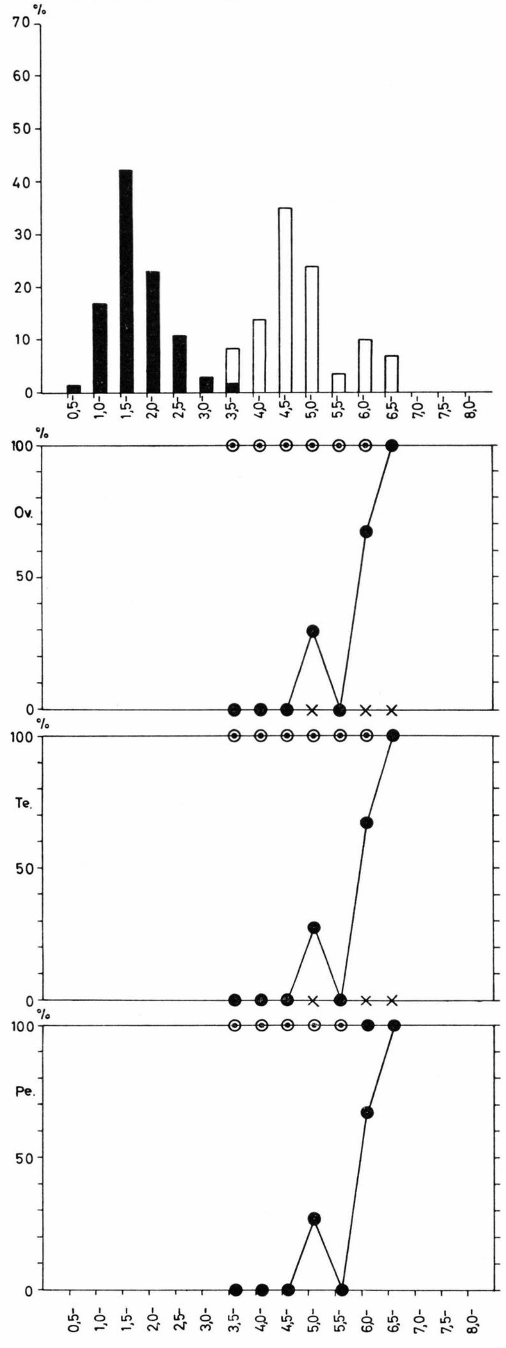
	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
?							1		1				1				3
III									2	2							4
II		1		1	1	6	2	6	14	14	8	3					56
I		1	1	1	1	5	8	5	4	1							27
0	14	11	1														26
Sum	14	13	2	2	2	11	11	11	21	17	8	3	1				116



GODTHÅB 18-8-1959

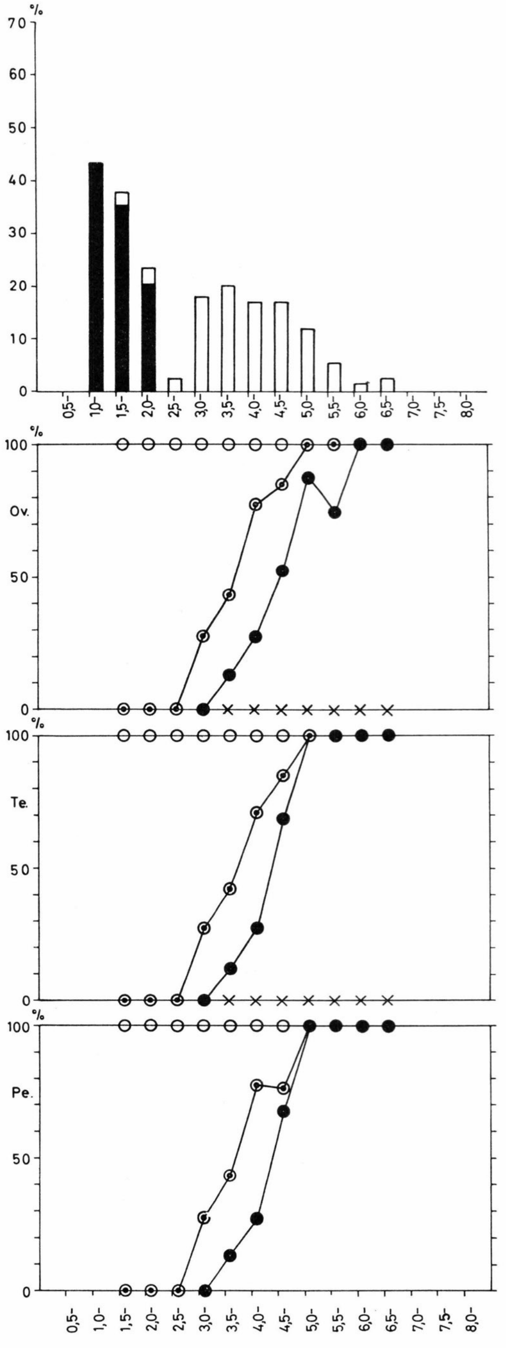
3,2‰

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI																	
V																	
IV												1	1				2
III									2			2	1				5
II									6	5							11
I							2	4	2	2	1						11
0	1	11	27	15	7	2	1										64
Sum	1	11	27	15	7	2	3	4	10	7	1	3	2				93



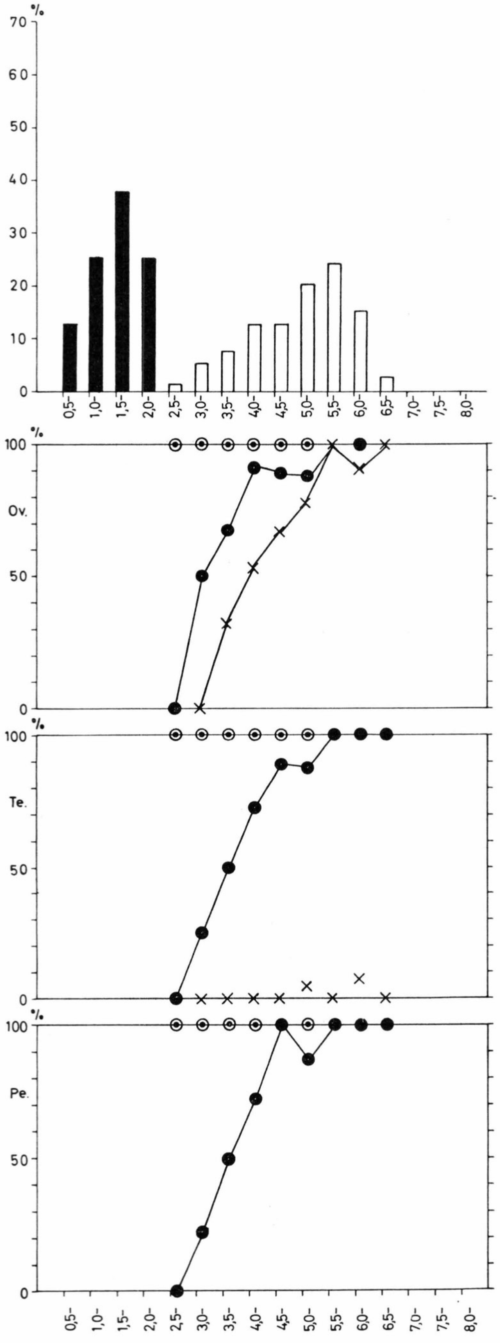
GODTHÅB 1-9-1959

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
?									1								1
IV											1		1				2
III							1			2	2	1	1				7
II				1	1	1	3	6	6	4	1						23
I			1	1	1	13	11	7	6	3							43
0		6	5	3													14
Sum		6	6	5	2	14	15	13	13	9	4	1	2				90



GODTHÅB 15-9-1959

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
?								1		2	5	2	1				11
IV									1		2	3					6
III							1	2	2	4	7	6	1				23
II							1	1	3	5	5	1					16
I					1	4	4	6	4	5							24
0	1	2	3	2													8
Sum	1	2	3	2	1	4	6	10	10	16	19	12	2				88



GODTHÅB 18-11-1959

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
?									1	3							4
III											1	1	1				3
II								5	5	8	5	3					26
I					1	2	9	11	3	1							27
0				3	7	8											18
Sum				3	8	10	9	16	9	12	6	4	1				78

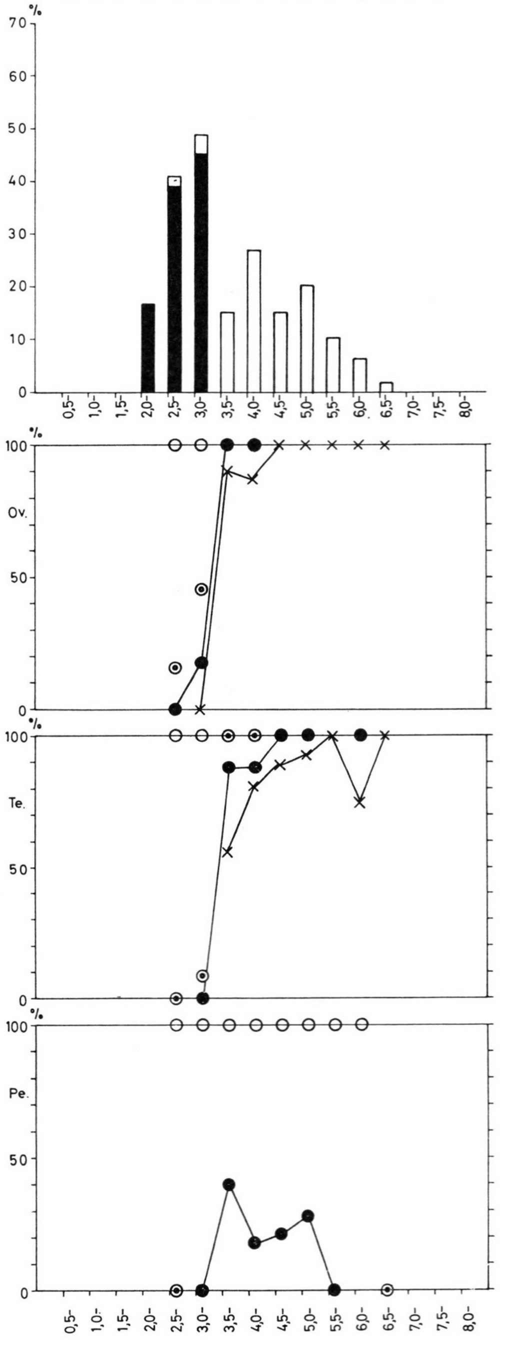
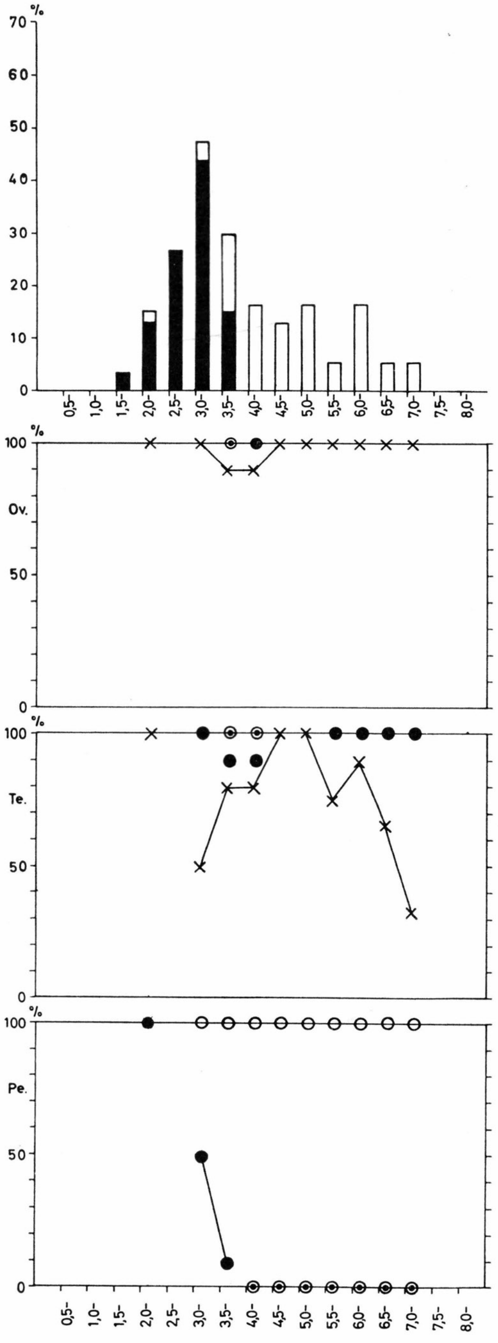


PLATE 32

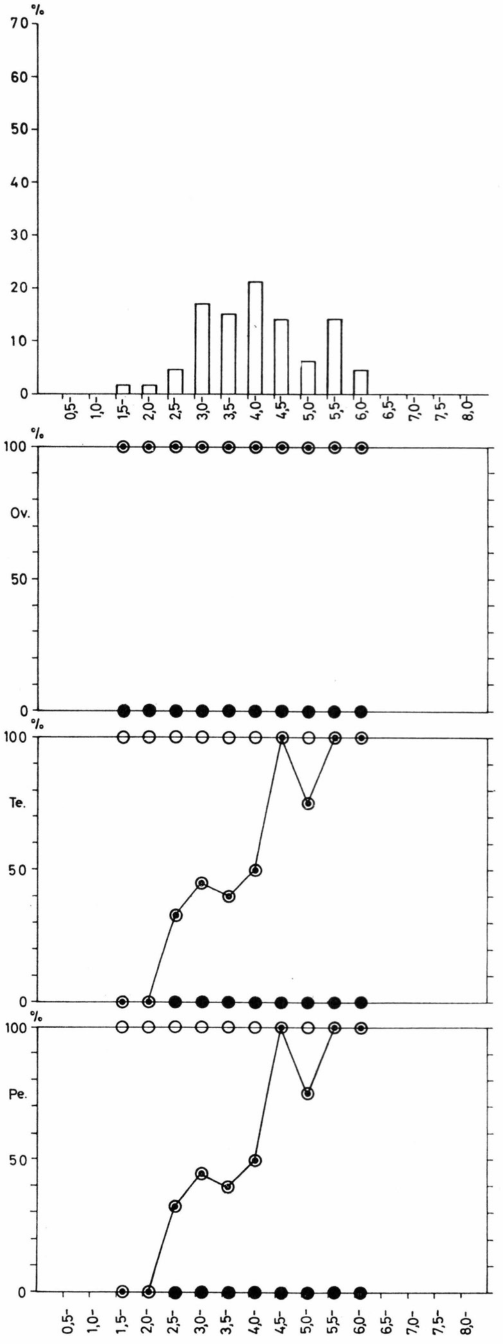
ARSUK 15-11-1958 10,8‰

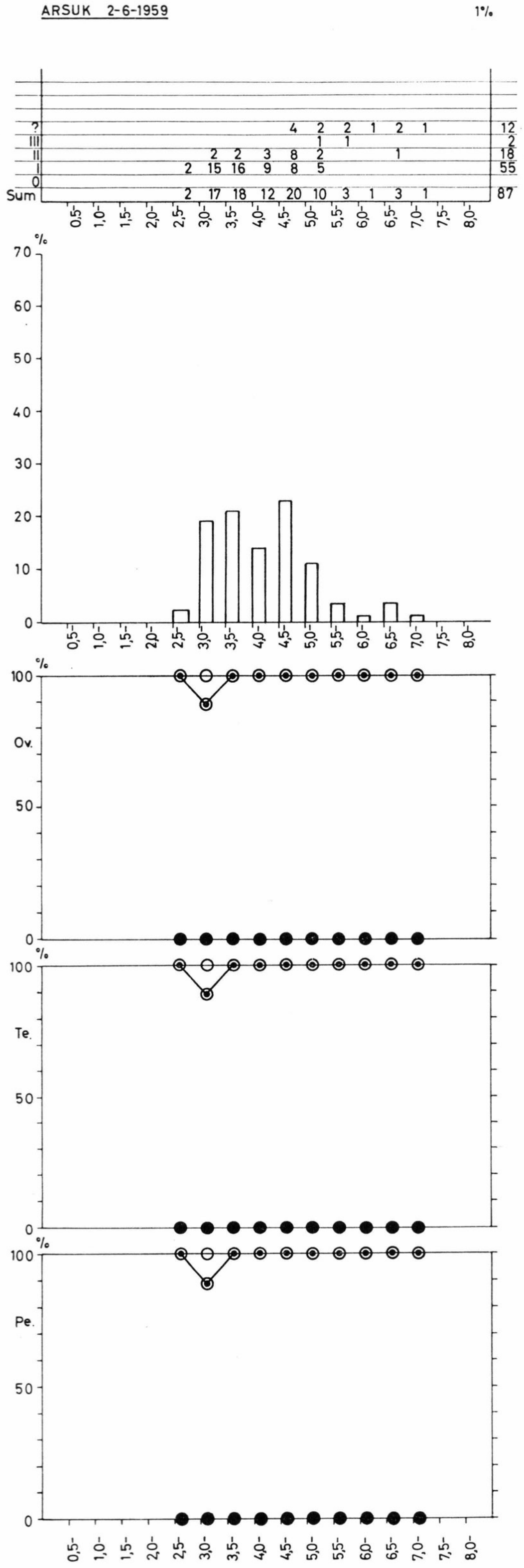
	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
?							1		2	1	1	4	1	1			11
IV												1					1
III							1				1	2	1	1			6
II						2	1	1		2		2	1	1			10
I				1			6	8	5	6	1						27
0			1	4	8	13	4										30
Sum			1	5	8	15	13	9	7	9	3	9	3	3			85



ARSUK 19-5-1959

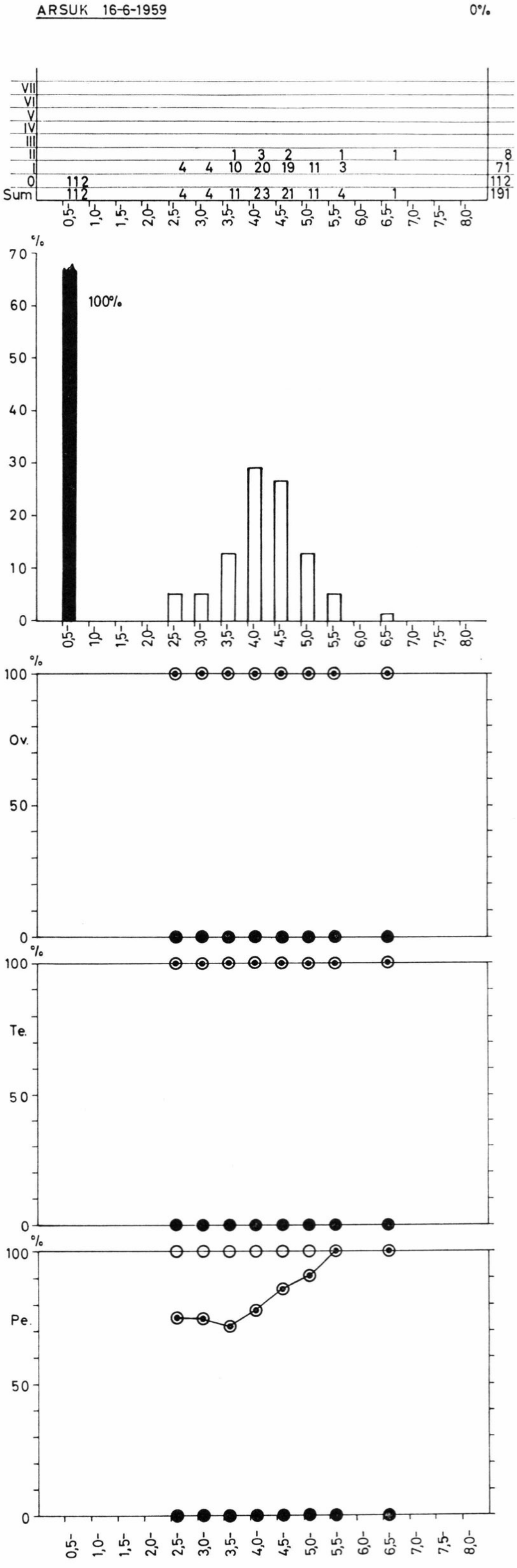
	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
?			1		2	1	2	6	3	1	4	3					23
III						1		1			1						3
II				1	1	8	3	4	4	3	4						28
I						1	5	3	2								11
0																	
Sum			1	1	3	11	10	14	9	4	9	3					65





ARSUK 2-6-1959 1%

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
?									4	2	2	1	2	1			12
III										1	1						2
II						2	2	3	8	2			1				18
I					2	15	16	9	8	5							55
0																	
Sum					2	17	18	12	20	10	3	1	3	1			87

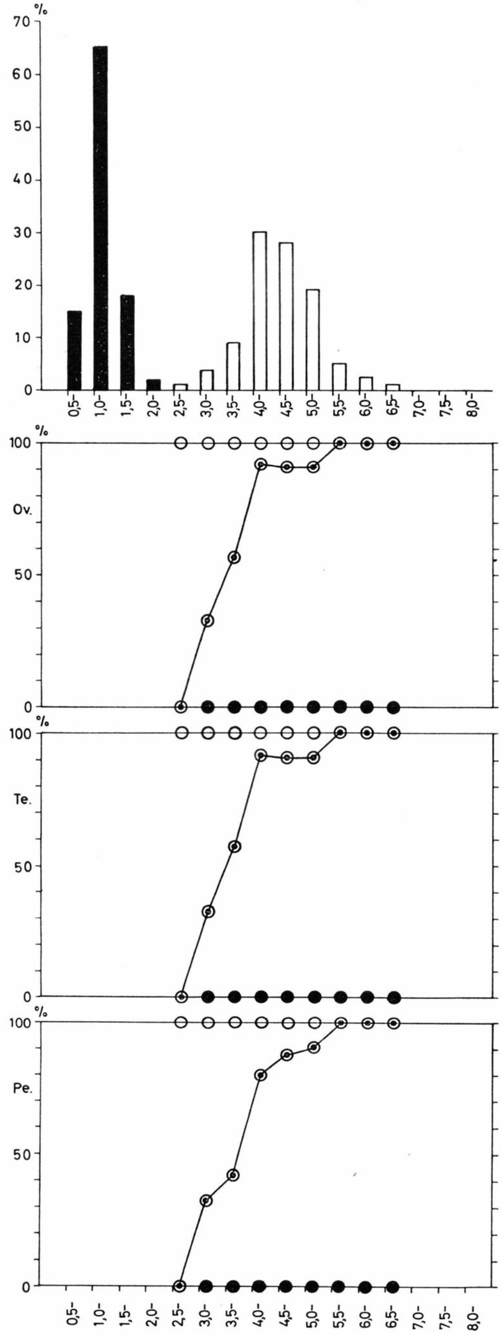


ARSUK 16-6-1959 0%

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI																	
V																	
IV																	
III																	
II							1	3	2		1		1				8
I					4	4	10	20	19	11	3						71
0	112																112
Sum	112				4	4	11	23	21	11	4		1				191

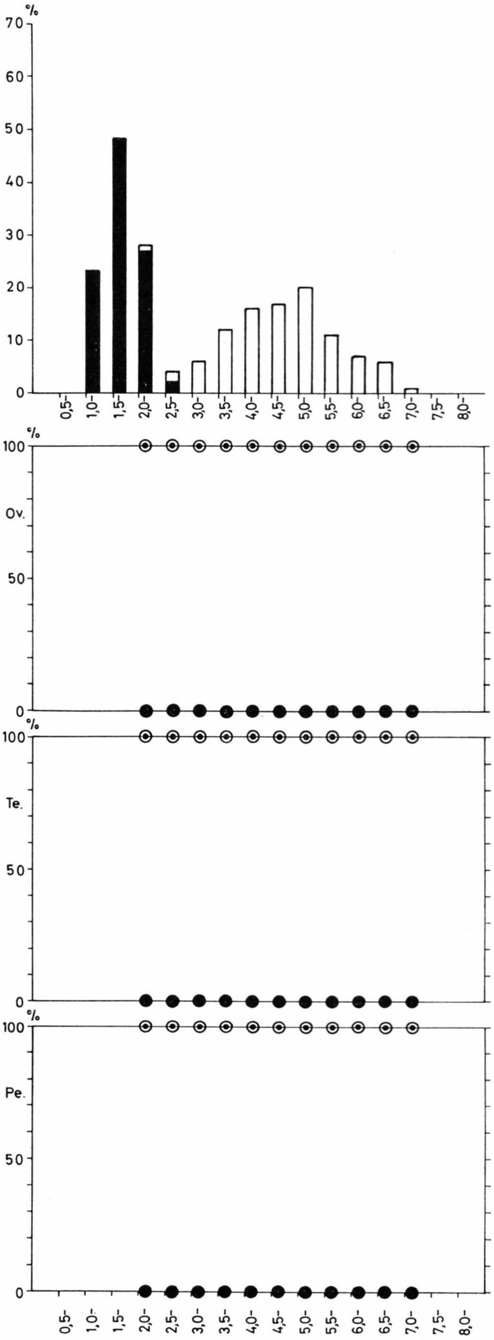
ARSUK 22-7-1959		2‰

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI																	
V																	
IV																	
III										1			1				2
II								2	2	3	2	1					10
I					1	3	7	22	20	11	2	1					67
0	34	148	41	3													226
Sum	34	148	41	3	1	3	7	24	22	15	4	2	1				305

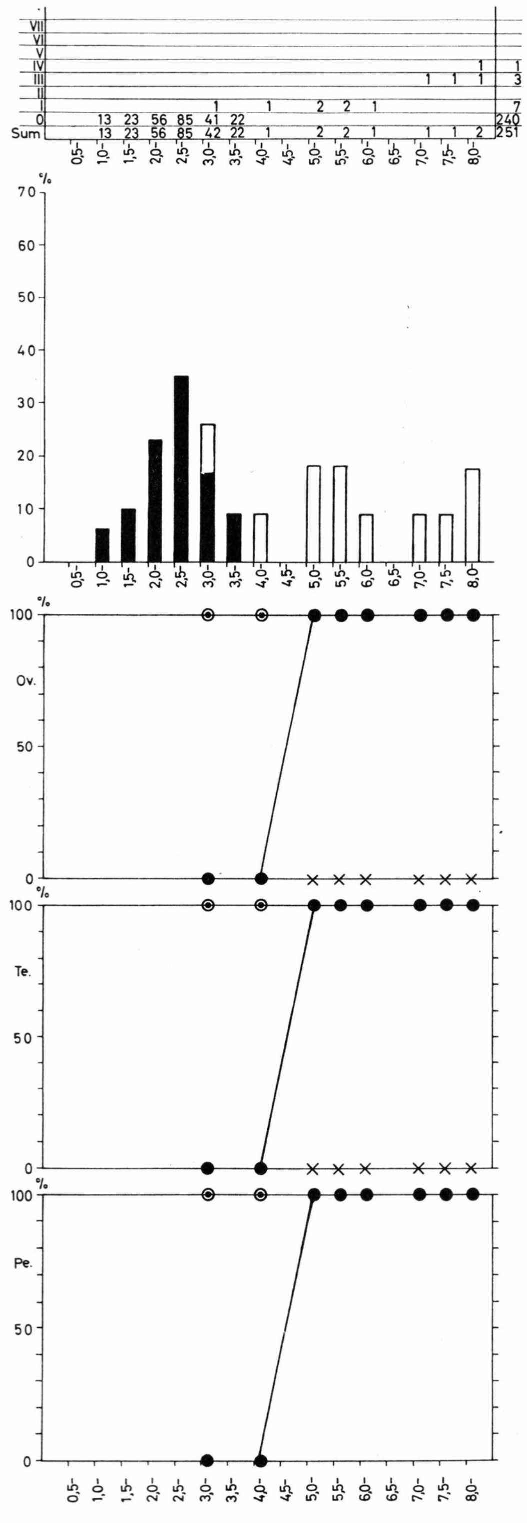


ARSUK 5-8-1959		2‰

	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
?										1							1
IV											1			1			2
III												2	2				4
II							1	1	3	4	7	4	2				22
I				1	2	5	9	12	11	12	1		1				54
0		28	56	32	2												118
Sum		28	56	33	4	5	10	13	14	17	9	6	5	1			201



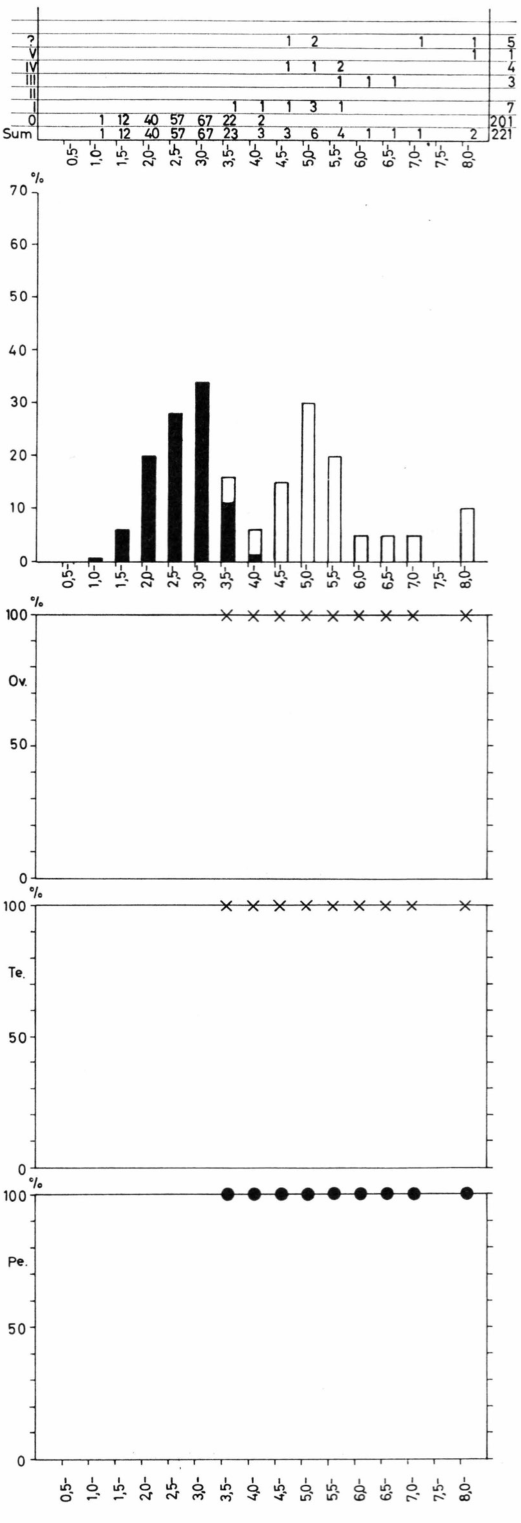
ARSUK 4-9-1959



	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
VII																	
VI																	
V																	
IV																1	1
III														1	1	1	3
II																	
I						1		1		2	2	1					7
0		13	23	56	85	41	22										240
Sum		13	23	56	85	42	22	1		2	2	1		1	1	2	251

ARSUK 22-9-1959

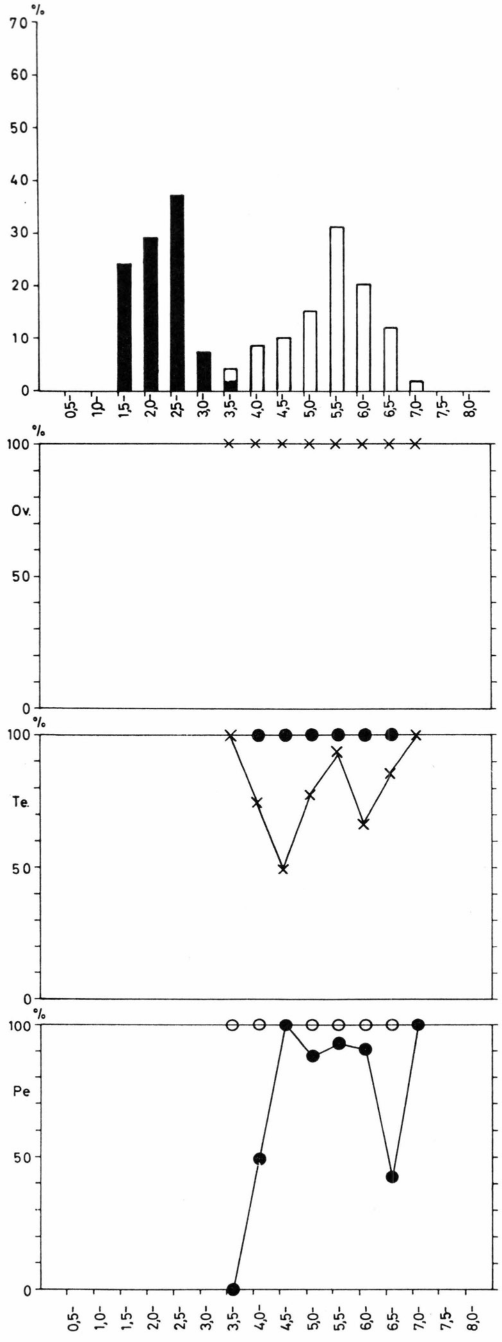
10%



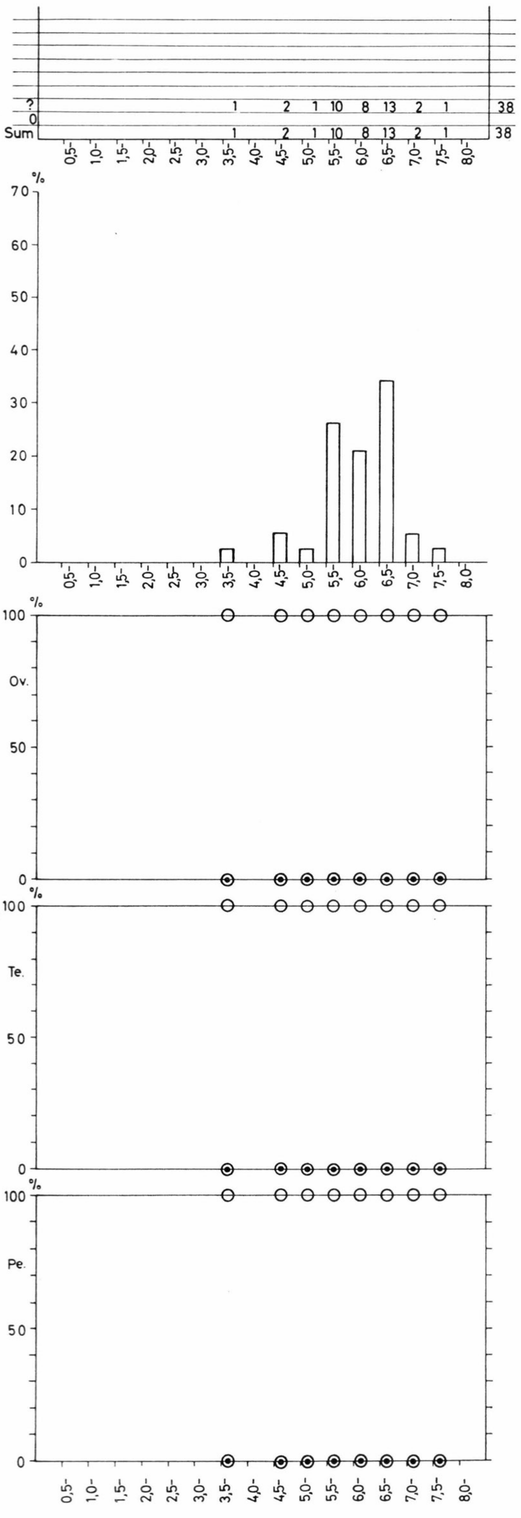
	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
?									1	2				1		1	5
V																1	1
IV									1	1	2						4
III											1	1	1				3
II																	
I							1	1	1	3	1						7
0		1	12	40	57	67	22	2									201
Sum		1	12	40	57	67	23	3	3	6	4	1	1	1		2	221

ARSUK 13-10-1959

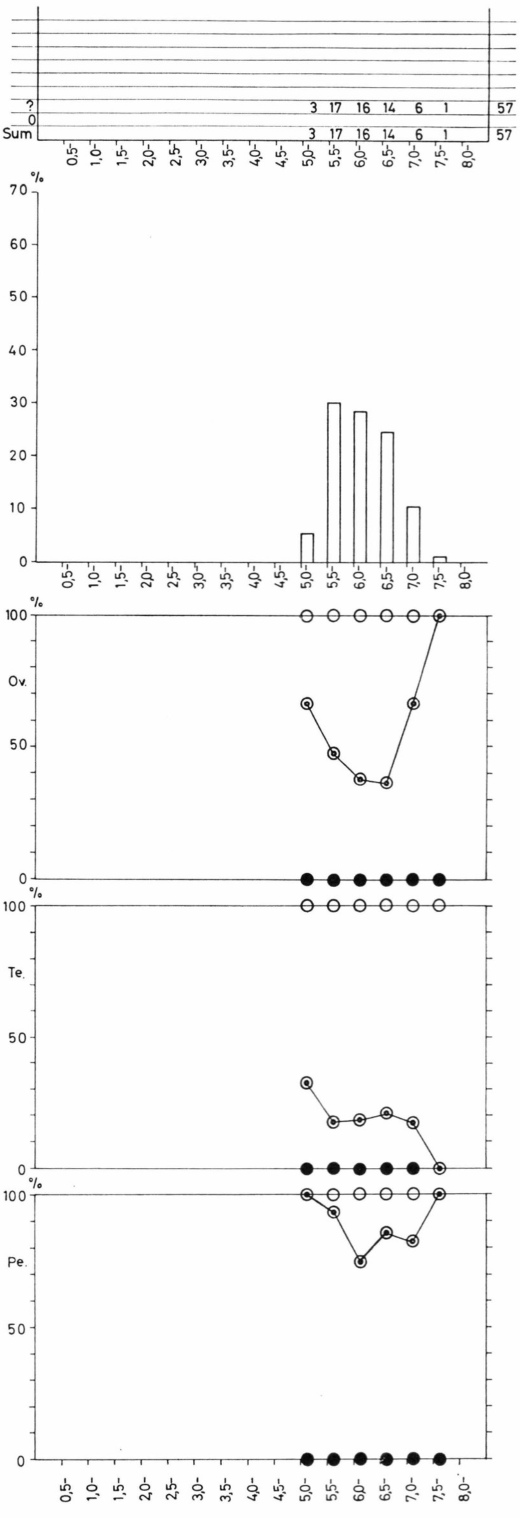
	0,5-	1,0-	1,5-	2,0-	2,5-	3,0-	3,5-	4,0-	4,5-	5,0-	5,5-	6,0-	6,5-	7,0-	7,5-	8,0-	
?								1			5	2	2	1			11
VII												1	1				2
VI											3	3	1				7
V								1		1	1	1	1				5
IV							1		2	5	1	2	1				12
III										1		1					2
II								1		1	2	1					5
I								2	4	1	6	1	1				15
0			20	24	30	6	2										82
Sum			20	24	30	6	3	5	6	9	18	12	7	1			141

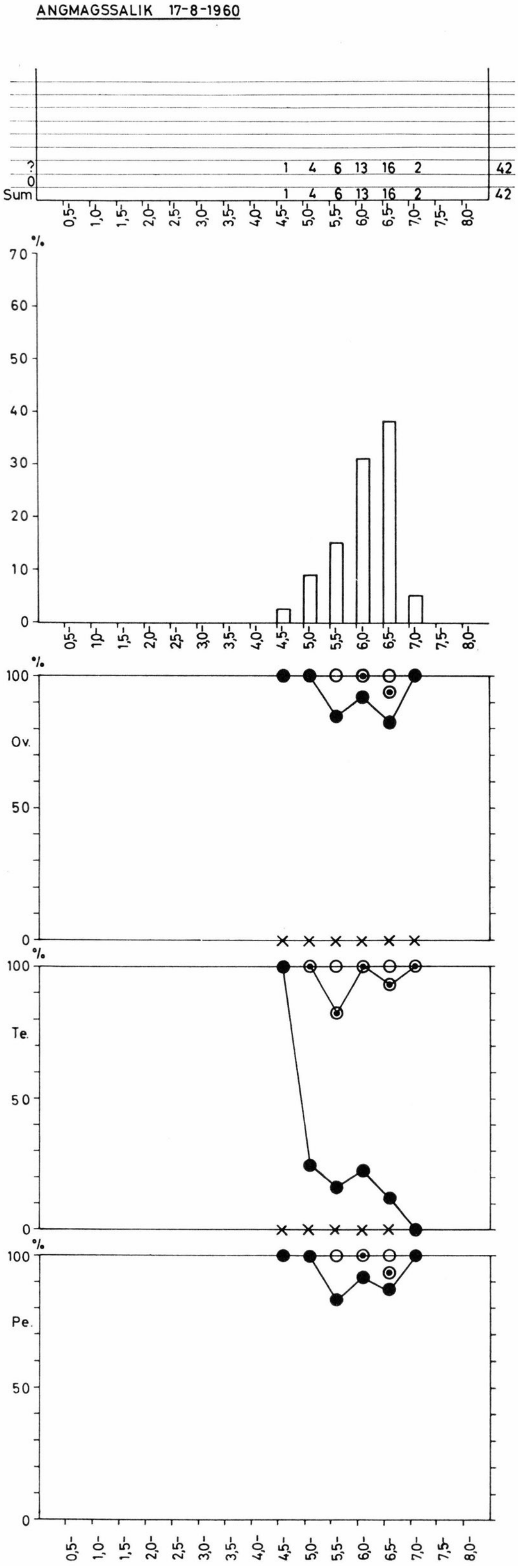


ANGMAGSSALIK 4-6-1960



ANGMAGSSALIK 17-7-1960




ANGMAGSSALIK 17-8-1960
?
0
Sum
1 4 6 13 16 2 42
1 4 6 13 16 2 42
0,5- 1,0- 1,5- 2,0- 2,5- 3,0- 3,5- 4,0- 4,5- 5,0- 5,5- 6,0- 6,5- 7,0- 7,5- 8,0-
%
70
60
50
40
30
20
10
0
%
100
Ov.
50
0
%
100
Te.
50
0
%
100
Pe.
50
0