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# THE DISTRIBUTION OF *BALANUS BALANOIDES* (L.) AND *LITTORINA SAXATILIS*, OLIVI, VAR. *GROENLANDICA*, MENCKE IN NORTHERN WEST GREENLAND

## WITH REMARKS ON SOME CAUSATIVE FACTORS

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WITH 18 FIGURES IN THE TEXT AND 2 PLATES

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# INTRODUCTION

Investigations on the fauna of the tidal zone on the rocks at Godhavn were started in the autumn of 1958. These rocks were studied regularly during the period from the autumn of 1958 to the autumn of 1960. Furthermore, there was a possibility, especially in the summer of 1960, of extending the investigations to other parts of the Disko Bugt and to localities in the districts of Umanak and Upernavik.

The investigations were exclusively based on observations in nature and collections among naturally occurring populations.

In the present paper the various localities will first be described, then each species will be discussed in detail, and finally the species and their ecological requirements will be compared.

I am greatly indebted to the Board of Directors of the Arctic Station of the University of Copenhagen, viz. Professors M. Westergaard, R. Spärck and T. W. Böcher and Dr. M. Köie, for assistance in many ways during my stay in Greenland. Special thanks are due to Professor R. Spärck for help and laboratory facilities at the Zoological Laboratory Copenhagen.

Finally, I want offer my best thanks to Mr. August Godbersen for never ceasing interest and valuable help during his stay at the Arctic Station.

## POPULATION TYPES OF *BALANUS BALANOIDES*

In order to facilitate the description of the distribution of *Balanus balanoides* the populations of the species will be grouped in the following four types:

(1) The barnacles are found as a dense white zone on horizontal as well as vertical rock surfaces.

(2) The barnacles are found close-set, but not on horizontal surfaces, only on vertical surfaces and in crevices.

(3) The barnacles are found only in crevices.

(4) The barnacles are found only in crevices with a horizontal main direction, or under overhanging rocks. It seems that the barnacles demand "a roof over their heads".

It will be reasonable to ask whether this grouping in population types has real contents. In the field, where the various localities are divided by stretches of sand, inaccessible stretches of coast, or the distance that can be made good between two low tides, possible transitional stages between the types mentioned perhaps may be overlooked. There are, however, a number of localities in which 2 or 3 of the population types are found in well-defined zones above each other. But I have not seen all the four types in the same locality.

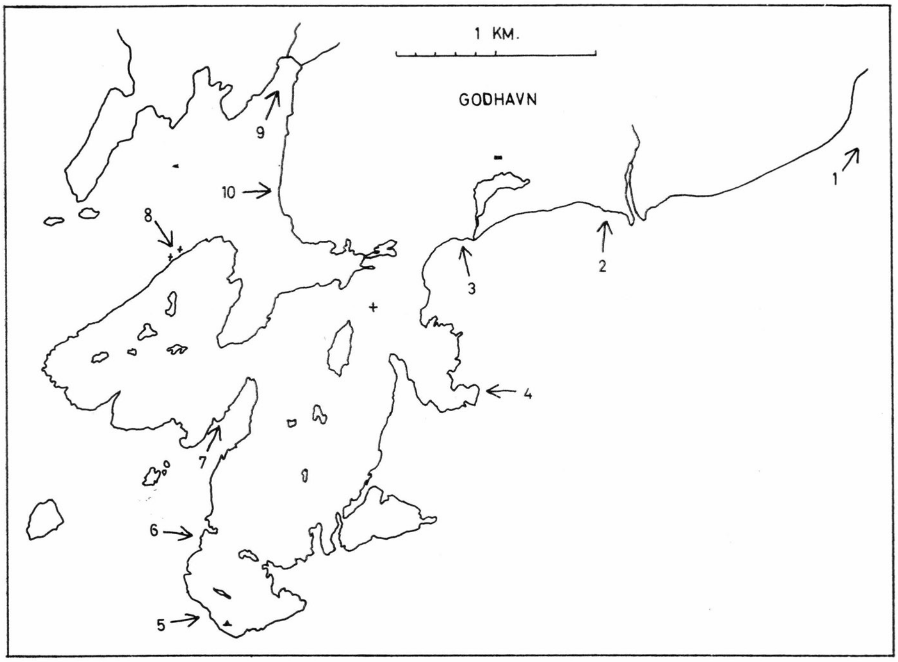



Fig. 1. Localities at Godhavn. 1. Kuánit. 2. The Rocks at the Refuse Dump. 3. The Rocks beside the Dog Food Rack. 4. Radionæsset. 5. Udkiggen. 6. The Skerry at the Landing-Stage for Dories. 7. Kirkegårdsbugt. 8. The Skerry in the Harbour Entrance. 9. Lyngmarksbugten. 10. The Rocks off the Oil Tank.

# DESCRIPTION OF LOCALITIES

## Godhavn.

The settlement of Godhavn itself surrounds a bay which constitutes one of the best harbours of Greenland, situated on gneissic rocks which form a modestly developed archipelago round Godhavn. Immediately east of the settlement there are breccial and volcanic rocks. There is also the mouth of the "Rødeelv". The water from the Rødeelv is from the spring thaw in late May to August-September coloured red by the weathering products of the volcanic rocks, and this freshwater surface layer can be seen far into the sea. As easterly winds are prevalent, this red layer as a rule stretches from the mouth of the river to Radionæsset and covers the whole bay. The thickness of this fresh or brackish layer of course varies highly according to wind and current and season; but it hardly ever exceeds a thickness of 20–30 cm closest to the mouth of the river. Off Radionæsset it has flattened considerably and is hardly more than a few centimetres thick.

On the rocky coasts near Godhavn some localities were selected for description in some detail. Their situations appear from fig. 1.

*1. Kuánit.*

In this locality the rocks exclusively consist of black volcanic rocks. In the places exposed to waves the barnacles are found in a dense white zone (Type 1). In indentations of the coast there are often influxes of freshwater from so-called hot springs, which are only a few degrees (centigrade), but still above the mean temperature of the place, as they do not freeze up in winter. Near the outlets of these brooks, which as a rule are waterfalls from the very steep rock down on to the beach or direct into the sea, there are no barnacles; at some distance from the waterfalls they are found as described under Type 4. This locality has not, however, been examined so thoroughly as the others, as the tidal zone there is difficult of access, from the landward side because of the very rugged rocks and from the seaward side because of the exposed situation of the place and the frequent surf. I have, however, made an observation there which I have been unable to make elsewhere. On a short stretch there was a pebbly foreshore where there was no influx of fresh water. On the rocks which the pebbles could beat against, there were no barnacles. On rocks immediately beside this place, where, however, there were no pebbles, there was rather an abundant population of barnacles (occurrence Type 3). The boundary between the two areas was very sharply defined. The phenomenon cannot be explained from the assumption that the pebbles destroy the barnacles, for there was a considerable depositing of larvae on the latter rock, but none on the rock worn by pebbles. Some of the phenomenon can be explained by the affinity of the larvae to older individuals, but in other places the larvae at that time, viz. on July 22, could very well settle without particular attachment to older animals. I had an impression that the larvae could perceive that "this rock is dangerous". I have not had any possibility of investigating this problem in more detail, as in all the other localities with pebbles visited by me there were influxes of fresh water.

*2. The Rocks at the Refuse Dump.*

These consist of breccia and are situated immediately west of the mouth of the Rødeelv and thus are greatly exposed to fresh water. On the rocks closest to the river there were no barnacles at all. Only on the parts turned away from the river it is possible to find barnacles, but only in pits and crevices, thus a Type 4 occurrence. The population gives a pronounced impression of being "cowed". The rocks are covered by a layer of slimy algae, but there are no *Littorina* individuals at all. I tried to transfer periwinkles from the rocks beside the dog-food rack to this place, but they disappeared and thus have been unable to survive conditions on this rock.

*3. The Rocks Beside the Dog Food Rack* (see figs. 11 and 12).

These consist of gneissic rock and are situated immediately west of the mouth of the lagoon. On all these rocks there is rather an abundant population of *B. balanoides*, which most frequently occurs on vertical surfaces and in crevices, types of occurrence 2 and 3. There are many *Littorina* individuals and no slimy layer of green algae. *Fucus* occurs closely attached to crevices immediately above the L.W.M. This locality was originally intended to be the main locality, from which also animals were to have been collected in winter. As this rock is highly exposed to surf and ice pack, it was, however, impossible to remove the icefoot and the ice pack so that we could get down to the animals, even if we used explosive to blast the ice. Furthermore, the fauna is also somewhat affected by the fresh water of the Rødeelv. The fresh water from the lagoon hardly means anything in this connexion. For long periods in summer time the mouth of the lagoon can be closed by sand washed up by heavy surf, and as all the time some water flows into the lagoon, this must disappear by evaporation and oozing through "Sorte Sand". On these rocks I have seen barnacles buried in sand thrown up by heavy surf. This observation does not agree very well with the assumption mentioned above that the larvae can perceive whether the rock is dangerous. But these rocks are not worn by the drift of material and are full of the small sharp-edged pits in which the cypris larvae prefer to settle, whereas the rocks worn by pebbles at Kuánit are completely smooth and without small sharp-edged pits.

*4. Radionæsset.*

This headland is much exposed to surf as well as ice pressure. Investigations into the influence of the sea ice and the icefoot on the intertidal fauna have been concentrated there in order to see the maximum action. Barnacles are very rarely found on horizontal or oblique surfaces there. The occurrence is a pronounced Type 2 in the zone between L.W.M. and M.W.M., and a pronounced Type 3 around M.W.M. The first impression obtained by this type of occurrence (3) is that it must be due to ice pressure against the rocks, so that the animals are scraped away from exposed places. But a closer examination shows that the ice pressure cannot mean anything. In the first place, there are so many small creeks and indentations in the coast where pressure of the ice can never occur, but where this type of occurrence still is prevalent so that horizontal surfaces do not carry barnacles even though they are actually protected better than many vertical surfaces. Secondly, a pressure of ice that can scrape barnacles off a rock, ought also to be able to scrape *Mytilus*, *Littorina* individuals, and *Fucus* out of the crevices in which they have settled and most of which would not yield any protection in cases of ice pressure against the rock. Thirdly, I have many times tried to see such pressure of ice when there was an easterly gale. As examples I shall mention two occasions on which there were good possibilities of ice pressure.

Radionæsset was inspected on Jan. 1, 1960. During the two preceding days there had been a Foehn-like easterly gale which brought the temperature from about $-20°$ C. to about $+^1/_2°$ C. The icefoot was good and firm, and there was nothing to indicate that the ice floes could scrape the rock itself. The sea ice was broken up in front of the icefoot or in ice pack farther from the coast.

On April 4, 1960, a sample of the animals was taken on the skerries near Radionæsset. The temperature was about $-10°$ C., and there was an onshore wind from the northeast, force 5. In spite of a fairly high onshore wind I did not see any pressure of the ice. There were many floes, but they were apparently pressed against each other so that there was pressure against the land on very few points. See fig. 18.

Another argument can be adduced here against the view that the occurrence of the animals in the tidal zone is determined by ice erosion, viz. that if this were so, it also ought to manifest itself below the L.W.M., as the sea ice in this area attains to a thickness of 60–80 cm and many floes are still thicker because they have been formed by one floe being pushed under the other. I have seen such floes of a thickness of 3–4 metres. I have never, however, seen the least trace to be interpreted as ice erosion below the L.W.M.

5. *Udkiggen.*

On the rock which is named "Udkiggen" there is an old conning-tower constructed by whalers from jawbones of whales. Off this rock there is so strong a current that there is rarely any passable sea ice there. As a rule the place is avoided, as there is often ice cut up by the current there. At a short distance from the coast there are two skerries. This rock and the two skerries together with Radionæsset belong to the most exposed stretches of this coast. In the tidal zone immediately below Udkiggen there is a dense population of barnacles. From immediately above the L.W.M. to immediately below the M.W.M. the occurrence is of a characteristic Type 2 and about the M.W.M. Type 3. In this locality it has been possible to study the icefoot in detail. In most places there is a transitional zone from the icefoot to the sea ice consisting of a folding system of ice floes placed edgeways. But off Udkiggen this transitional zone is often missing, and there is an opportunity to see the development of the icefoot even during the severest winter. On figs. 2–3 and Plate IIb, it is seen how the icefoot reaches down into the middle of the barnacle

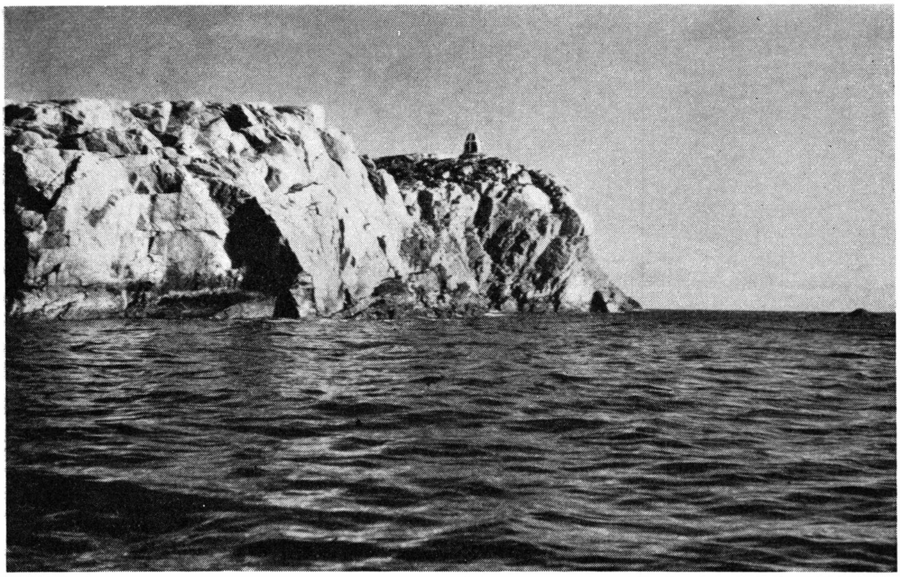


Fig. 2. Udkiggen. On the left a dense population of barnacles. A close-up of this part is shown in the coloured Plate Ib. September 19, 1960.

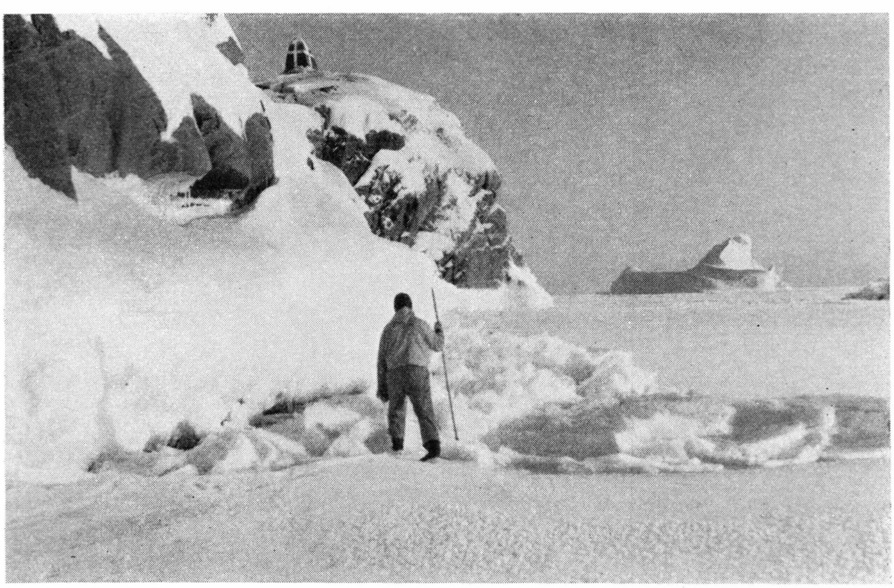


Fig. 3. Udkiggen. The lower part of the tidal zone is not protected by the icefoot. In this zone both *Balanus balanoides* and *Mytilus edulis*, which survives cooling to about $-35°$ C., were observed. March 12, 1960.

zone Type 2, but so that the barnacles settled lowest are bared and exposed to temperatures down to −35° C. I have not observed any connexion between the lower boundary of the icefoot, which is situated between the M.W.M. and the L.W.M., and the zonation in the tidal zone. It was not possible to collect animals from this place because of a transitional zone consisting of ice floes too small to carry a man. On the other hand it was possible to get to the two skerries, as there were there sufficiently large floes between the firm sea ice and the tidal zone. But nothing was found there which might be interpreted as ice erosion of the rock.

*6. The Skerry at the Landing-Stage for Dories.*

Immediately north of Udkiggen there is a valley in which in winter there is a sledge track from Godhavn to the sealing and fishing grounds west of Udkiggen. Immediately before this track passes on to the sea ice some dories are carried into safety on the icefoot which is very well-developed there. In front of this icefoot there are some skerries which are one of the places where the tidal zone is first made accessible for collection of animals in spring. Fig. 17 shows the development of the icefoot on these skerries.

*7. Kirkegaardsbugten.*

This locality is to be briefly mentioned because I have seen the icefoot being broken off for a short stretch there. Otherwise the icefoot is rarely seen to have been broken off. The strange thing is, however, that on the rock on to which the icefoot had been frozen, there were a few barnacles, but none in the contact surface of the icefoot, which shows that the barnacles are settled more firmly on the rock than in the icefoot.

*8. The Skerry in the Harbour Entrance.*

This skerry is situated close to the shore on the southern side of the entrance to the harbour of Godhavn.

In this locality, which was selected because it was easily accessible throughout the year, protected, but without receiving any influx of fresh water, collections were made regularly from April 25, 1959, when with explosive we blasted off some of the icefoot in order to collect animals that had been frozen up from the beginning of the winter. The last sample was taken on September 3, 1960.

This skerry, like all other groups of rocks in the neighbourhood, is very irregularly shaped. The most important topographical features are to be mentioned. There are two high parts, one of them nearly reaching the H.W.M., the other a little above the M.W.M. The highest part is provided with a mooring post. There are some faults, so that it was possible to select terraces, one at the L.W.M., a second in the middle of the zone of the barnacles, and a third at the upper boundary of the barnacles. From these three terraces both barnacles, periwinkles, and other organisms have been collected for the purpose of following the development and growth of the animals. On the second high part several observations have been made for the elucidation of the biology of the animals.

On May 9, 1960, it was for the first time that year possible to get down to the tidal zone because of the ice. The ice margin was close to the skerry, and there was an icefoot more than 2 m thick on the greater part of the skerry. To my surprise I found many crushed barnacle shells and

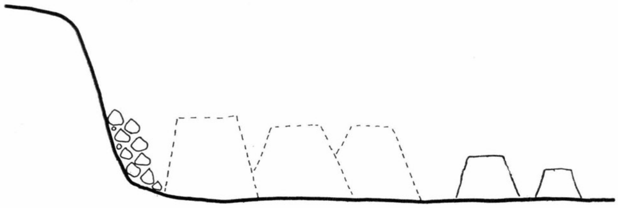


Fig. 4. Schematic presentation of Terrace A shown in Plate IIa. In the inmost part of the incision some periwinkles clustered together are seen, next the acorn barnacles detached by breaking due to freezing are indicated by a dotted line, and in the outermost part some smaller, still attached barnacles are seen.

large "cakes" of adult live barnacles. As I had gradually got the impression that neither the icefoot nor the sea ice was of importance to the fauna in the tidal zone, of course I investigated this phenomenon more closely. It appeared that I could find the places where the barnacles had been broken off. It was peculiar that the "cakes" of adult barnacles apparently had not been injured, the basal membrane was intact, and the animals were still attached to each other in crusts of ten to twenty specimens. They had been removed from the rock much more nicely than was possible with knife and pincers, and still they were splashing in the water line 10–20 cm below the place where they had been settled. They had been attached to both horizontal and vertical surfaces in some incisions in the rock. A few of these incisions were much exposed to a possible ice erosion, but the greatest parts, where recently detached barnacles had been settled, were markedly sheltered from the ice. Fig. 4 and Plate IIa show conditions there. In the inmost part of the incision, against the vertical surface, *Littorina* individuals sat in clusters, next followed the rock surface from which the barnacles had been torn, and farthest away from the vertical surface, thus most "exposed", there was a dense population of Group 0 barnacles which were not injured in any way. The detached barnacles thus cannot have been scraped off by any kind of ice pressure. The only explanation must be that breaking due to freezing had detached the larger barnacles, which were settled in "cakes" from the rock, and that this breaking could not effect the smaller or isolated animals. The correctness of this explanation is corroborated by an observation made on June 24, 1960, when I noticed that certain old barnacles in "cakes" were sitting in a dent above the rock and that they could easily be picked off by the fingers in great "flakes", which is otherwise very difficult with normally attached barnacles. These flakes contained both live animals and empty shells. The live animals showed great growth on the underside of the shells, apparently in order to obtain good contact with the rock again. But these animals, which obviously had been detached from the rock by breaking due to freezing, had not been exposed to actions that could remove them from the place.

On several surfaces on the skerry a population of barnacles is almost completely missing, and they are exposed in such a way that this fact would immediately be explained by the assumption that the barnacles have been pressed off by the pressure of the ice on the rock. That this explanation is not tenable appears from the fact that there may very well be a dense *Littorina* population and a growth of algae which at any rate still more easily than barnacles can be removed from the rock, and by the fact that other surfaces which are even more exposed still have a dense population of barnacles.

The best and most observations of the habits of life of the periwinkles and their relation to the cover with green algae also originate from this skerry (Plate I a and b).

*9. Lyngmarksbugt.*

A small river which is water-bearing throughout the year debouches into the head of Lyngmarksbugten. On the rocks closest to the river the barnacles occur as a pronounced Type 4, viz. only in horizontal crevices or under overhanging rocks. On rocks farther out in the bay the barnacles occur in the way that has been described as Type 2. It is, however, the rocks in the innermost bay, thus closest to the river, which are best protected from ice erosion. Conditions in this bay are excellent for illustration of the assumption that the different occurrences of the barnacle populations should be related to influxes of fresh water and not to ice erosion. Furthermore, it can be seen here that the contents of particles in suspension in the fresh water are not of any importance for the barnacles either, as the river at the head of Lyngmarksbugt is hardly polluted by ooze at any time of the year. This may be compared with conditions in the Disko Fjord, which will be mentioned below and where there are well-developed populations of barnacles in spite of the presence of considerable amounts of materials in suspension in the water.

*10. The Rocks off the Oil Tank.*

This locality has been used for making collections when it was not possible to cross to the skerry in the harbour entrance. It is characteristic by having many flat stones which are wedged together so that they do not roll. On these stones there are barnacles which are easy to get hold of for aquarium experiments.

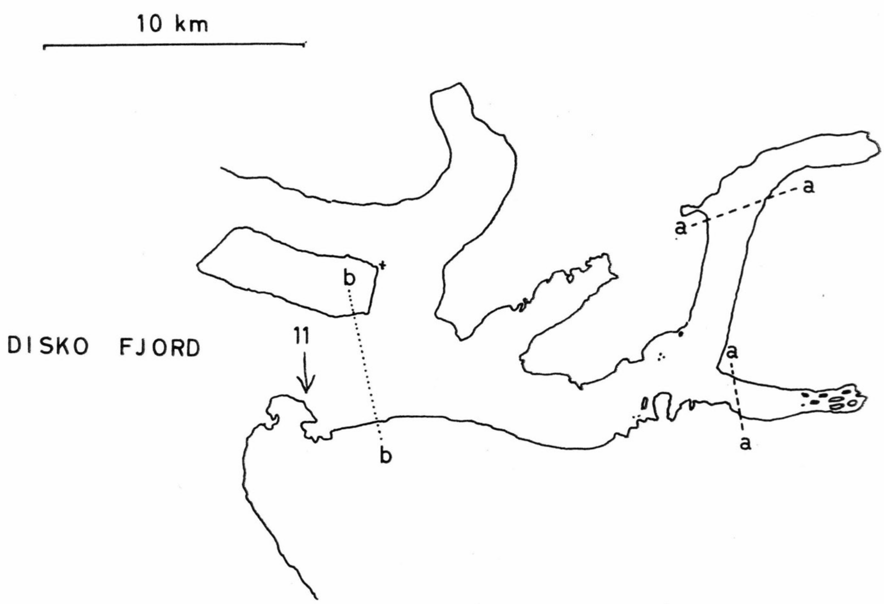



Fig. 5. The Disko Fjord. The lines a–a indicate the limits of distribution of *Balanus balanoides* and *Littorina saxatilis* towards the mouths of rivers. The line b–b indicates an approximate limit of highly ooze-bearing surface water in the month of July. 11. Nipisat.

## The Disko Fjord.

*11. Nipisat.*

On the rocks at Nipisat there is a dense population of barnacles Type 2. The rocks are highly exposed and the place is mentioned because we had an opportunity to observe ice-drift against the rocks there. On May 21, 1960, we had entered the small harbour at the Loran station at Nipisat. While we stayed there, the ice in the Disko Fjord began to break up and came drifting in a fringe along the south coast of the fiord. We had to go by dinghy through this current of pancake ice to the anchored motor boat. Many of these floes hit the coast, but as it was possible for us to get through with the dinghy by jumping on to the floes and dragging the dinghy through the cracks, I very much doubt that any ice floe should be able to push a barnacle off the rocks, more especially as sea ice is very soft and therefore will not easily exert pressure direct on the barnacles, but will slide off.

*12. The Disko Fjord.*

The map fig. 5 shows the distribution of the marine fauna in the Disko Fjord. This fiord receives many and considerable influxes of fresh water, which carry much material in suspension into the fiord. The fiord water is very opaque and turbid as far as Sioraq, of course highly varying according to the season. The most important in this connexion is the fact that there is no relation between the material in suspension and the distribution of barnacles and periwinkles (Feyling-Hansen (1953)). Near the influxes of fresh water the barnacles are found only in the horizontal pits and under overhanging rocks (Type 4). Their uppermost limit in the tidal zone has been pressed down to the L.W.M., and near the mouths of the rivers there are no barnacles.

## Egedesminde to Augpilagtoq.

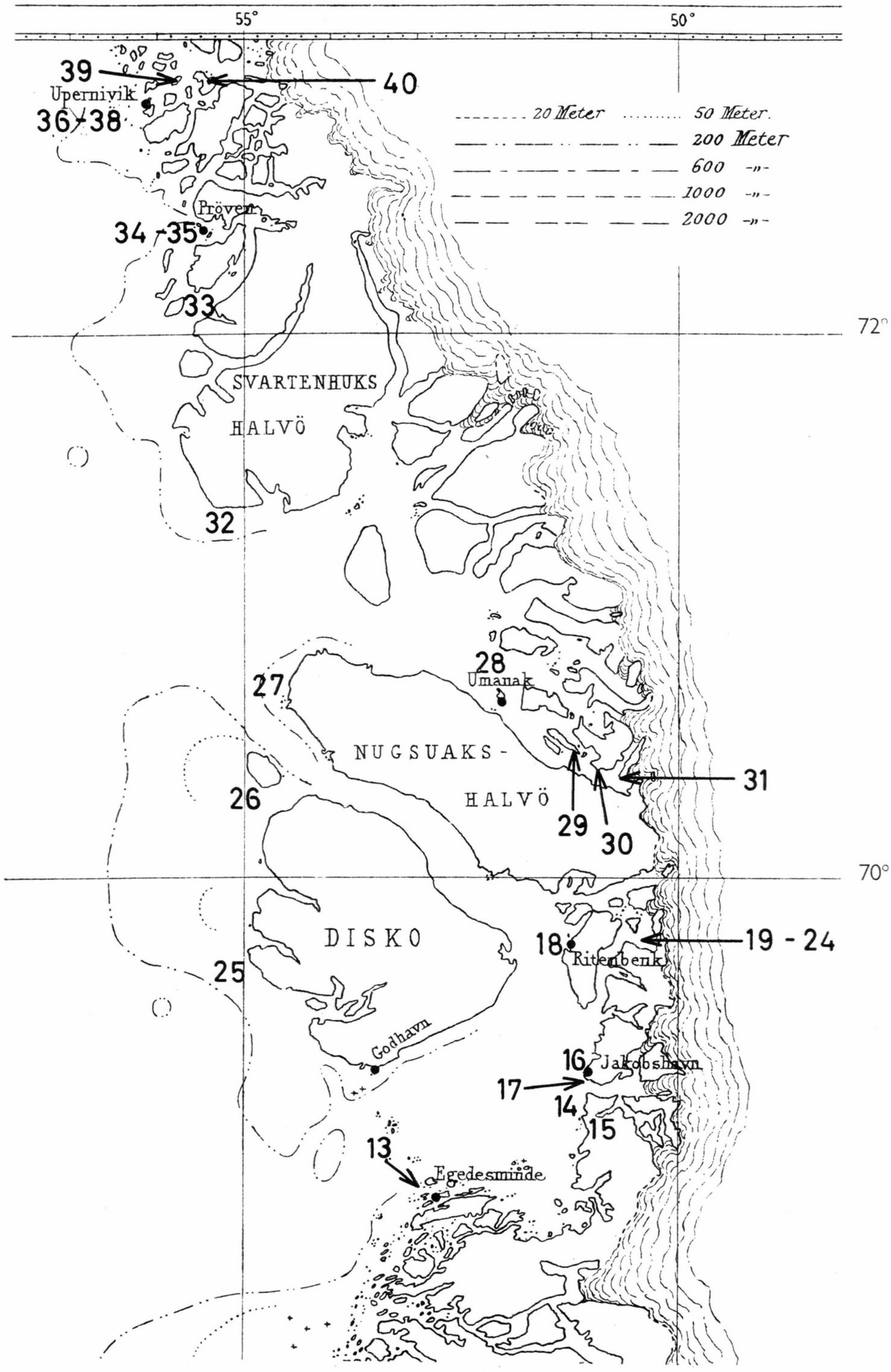
*13. Egedesminde.*

Egedesminde is situated on an island in the middle of a large archipelago, where in the tidal zone as well as in deeper water there is a large uncultivated field of research within marine biology. The locality is mentioned here because I saw there the best developed barnacle population in Disko Bugt. E.g. on "Fiskeøen" there was a very dense cover of barnacles on all types of surfaces, vertical as well as horizontal, in a zone from the L.W.M. to above the M.W.M. Above this pronounced Type 1 occurrence the barnacles were found to pass rather high up towards the H.W.M. in crevices, a Type 3 occurrence.

*14. Claushavn.*

On the rocks at Claushavn, which is situated immediately south of the large Jakobshavns Isfjord, there was a well-developed marine tidal fauna. There was a Type 2 occurrence of barnacles.

Fig. 6. Localities from Egedesminde to Augpilagtoq which were visited only once. 13. Egedesminde. 14. Claushavn. 15. Tasiussaq. 16. Jakobshavn. 17. Jakobshavns Isfjord. 18. Ritenbenk. 19. Atâ. 20. Atâ Sund—Eqip sermia. 21. Qingârssuaq. 22. Qeqertánguaq—Qingmilivik. 23. Qerrukasik. 24. Alángoq. 25. Nordre Laksebugt. 26. Hareøen. 27. Bjørnefælden. 28. Umanak. 29. Ikerasak. 30. Akuliaruserssuaq (Drygalski's Peninsula). 31. Nûgârssuk. 32. Svartenhuk. 33. Søndre Upernavik. 34. Prøven. 35. Sandøen. 36. Upernavik. 37. Skerry off the Harbour of Upernavik. 38. Sound between the Upernavik Island and the Island Northeast of it. 39. Ikermiut. 40. Augpilagtoq.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Godhavn
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Jakobshavn
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Egedesminde

Fig. 6.

*15. Tasiussaq.*

This is a tributary fiord of Jakobshavns Isfjord and thus is only connected with the sea water of Disko Bugt through the ice fiord. It is possible to go by land from Claushavn to Tasiussaq, where a well-developed marine tidal fauna with *Balanus balanoides* and *Littorina saxatilis* was found.

*16. Jakobshavn.*

On the rocks between Jakobshavns Isfjord and Jakobshavn the barnacle population was pressed down towards the L.W.M. and only as a Type 4 occurrence. The *Littorina* occurrences were also sporadic, only, but in return the rocks were covered by a slimy layer of green algae. These facts are undoubtedly due to influence of the melt water from the Jakobshavns Isfjord, which tends to flow northwards, not southwards towards Claushavn, presumably because of sea currents and Coriolis' force.

*17. Jakobshavns Isfjord.*

The marine tidal fauna forces its way along the north coast to Sermermiut, but is very poorly developed. Immediately beyond Sermermiut there is a headland and the rocks on this headland gives an impression of being exposed to a considerable ice erosion, as they are completely devoid of organisms.

*18. Ritenbenk.*

On the west side of Arveprinsens Ejland at the relinquished settlement of Ritenbenk there were well-developed populations of barnacles and periwinkles. The barnacles occurred in a Type 2 population with a Type 3 population above it.

*19. Atâ.*

At Atâ on the east side of Arveprinsens Ejland the barnacles were pronouncedly attached to crevices, a Type 3 population.

*20. Atâ Sund – Eqip sermia.*

On the rocks below Paul Emile Victor's expedition house there was a dense slimy cover of green algae. There were no periwinkles to consume the green algae. The barnacles were found in the form of a Type 4 population, closely attached to pits and similar places that seem to protect the barnacles from ice erosion. But there is nothing to indicate that there should be any greater ice erosion there than on an open coast in Disko Bugt. If there were any ice erosion, the green algae would not have any possibility of growing as they did.

On very short visits to the localities at the head of Atâ Sund mentioned below, it was found that conditions there were just as described, viz. no periwinkles, a dense cover of green algae, and a barnacle population Type 4. These localities are indicated on the map Grønland 1:250000, 69 v. 2 Jacobshavn, Geodætisk Institut, København.

*21. Quingârssuaq.*

*22. Quertanguaq*, an island where eiders nest, and *Quingmilivik.*

*23. Qerrukasik.*

*24. Alángoq.*

On account of rising tide we sailed direct from Qerrukasik to Alángoq in order quickly to find an approximate limit to the distribution of periwinkles. At Alángoq there were many periwinkles, no layer of algae, and a barnacle population Type 2. I did not see the exact limit of the periwinkles, but it is presumably closer to Qerrukasik than to Alángoq.

*25. Nordre Laksebugt.*

There were many periwinkles and barnacles there, but it was evident that the barnacles near their limit of distribution towards the mouth of the river thinned out and were found as a Type 4 population before they disappeared completely. In this place there were some vesicular rocks, and in almost every hole there was a *Littorina*, which closely fitted the size of the hole. It should be noted that the ice formation does not increase towards the influx of fresh water, as the rivers in the autumn freeze up inland and most of them are not water-bearing in winter.

*26. Hareøen.*

This locality was visited on May 23, 1960. It was only possible to go ashore on the south coast as from Hareøen to Nûgssuaq there was a close pack ice. There were no organisms in the tidal zone there, neither on firm rock nor on loose stones. The south coast consists of a marine foreland built of very large stones; both these as well as the individual firm rocks were much worn, which suggested that there was a violent drift of material.

On a small island where sea-gulls nest, east of Hareøen, there were some barnacles.

*27. Bjørnefælden.*

On the headland at Bjørnefælden north of the relinquished trading station Nûgssuaq there was on the inner side a well-developed Type 2 population of barnacles and many periwinkles, while on the exposed north side of the headland there were few periwinkles, a slimy cover with green algae, and a Type 4 population of barnacles. The locality was not studied in detail, but the possibility of ice erosion on this coast could not be excluded.

*28. Umanak.*

On the wharf and the rocks at the power station and the hospital there were a cover of slimy green algae, few periwinkles, no *Fucus*, and hardly any barnacles. The few barnacles that were there were settled under overhanging rocks in a Type 4 population. The place was visited on August 11 and 12, 1960. There was no influx of fresh water, but it was evident that the localities mentioned were exposed to melt water during the spring thaw and in the early summer. It should be noted that the summer of 1960 was very fine and dry in these districts. On rocks and skerries in the harbour and at the entrance to the harbour, thus at a longer distance from the temporary influxes of melt water, there were abundant populations of periwinkles and no green algae; barnacles and *Fucus* were attached to crevices, i.e. the barnacles occurred in a Type 3 population.

*29. Ikerasak.*

Conditions at Ikerasak resembled those just described from Umanak. At the head of the bay continuing as a depression inland past the houses of the trading station, there is a cover of green algae and no periwinkles, no barnacles, nor *Fucus* on a short stretch, where the melt water has the greatest influence, while the cover of green algae disappears and periwinkles, barnacles, and *Fucus* are found at the mouth of the bay on exposed rocks. It should be mentioned that pollution is of no importance in this connexion near towns in Northern Greenland.

*30. Akuliaruserssuaq (Drygalski's Peninsula).*

In this about 300 m high, almost vertical mountain side there was an indentation with a stone slide. It was quite dry at our visit there on August 13, 1960, but must carry some melt water in the early summer. At the bottom of the indentation for a stretch of about 5 m there were a slimy cover of green algae, no periwinkles, no barnacles, nor *Fucus*. But next to this place, only some 3 m from the bottom of the indentation, *Fucus*, periwinkles, and barnacles began to make their appearance, all, however, poorly developed. Especially, there were few barnacles all in a pronounced Type 4 population. But the whole coast in this fiord is influenced by the melt water from the Qarajaq glacier and other glacial streams.

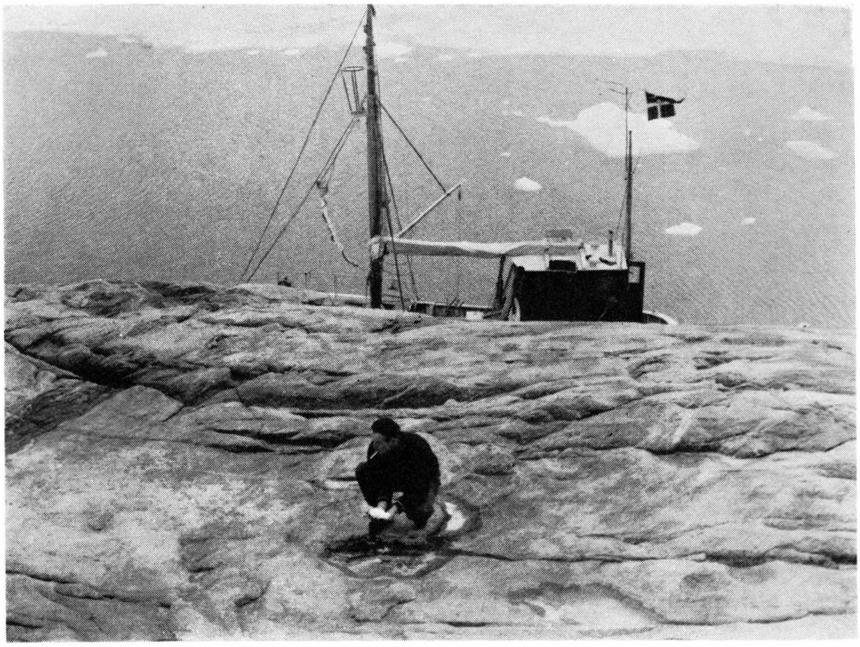

Fig. 7. Nûgârssuk. In puddles about 15 m above sea level there were salt deposits originating from bores, which, when the glacier calves, wash salt water far up over the rocks. Both here and at other glaciers there were bottom animals, e.g. large specimens of *Mya truncata*, which had been flung far above the high water mark. August 13, 1960.

*31. Nûgârssuk.*

There were neither periwinkles, barnacles, nor *Fucus* there. There were green algae in crevices and rockpools. See fig. 7.

*32. Svartenhuk.*

A breach with a stone slide in the 600 m high steep rock wall was inspected. There were neither periwinkles nor barnacles, but only vegetation. The observation was made under unfavourable circumstances, as the water had risen above the M.W.M. and the locality is rather inaccessible.

*33. Søndre Upernavik.*

On the pier there were both periwinkles and barnacles, the latter in a Type 4 population.

*34. Prøven.*

Conditions at Prøven (fig. 8) reminded of those in the harbour of Umanak, as off a dried up sudden thaw stream there was a green slimy cover of algae on the rocks, whereas there were no periwinkles and very

Fig. 8. The harbour of Prøven. The dark-coloured stones are covered by a slimy layer of algae, but there are no winkles. The boundary between the area with layers of algae and the area with periwinkles was found immediately right of the area shown in the picture. On the stone in the foreground there is a population of barnacles on the side turned towards the sea, towards the sudden thaw brook there are none. This phenomenon for that matter can be observed in many places in deltas, etc. August 10, 1960.

few barnacles, which all had settled under overhanging surfaces. But at only a short distance from there, there were abundant populations of periwinkles and barnacles. There were no green algae, but *Fucus* and barnacles were found in crevices (Type 3 population) and barnacles even here and there on vertical surfaces (Type 2 population). The boundary between areas with green algae, but no periwinkles, and the neighbouring areas with periwinkles, but no green algae, was very well-defined. In one place it was found across a large stone.

*35. Sandøen.*

On the exterior side of Sandøen, in close proximity of Prøven, there were few barnacles and periwinkles in very poorly developed populations. The locality could not be eroded by ice, but was hardly exposed to sudden thaw streams.

*36. Upernavik.*

In the harbour of Upernavik there was a very rich population of periwinkles, but no barnacles at all, even though the locality seems

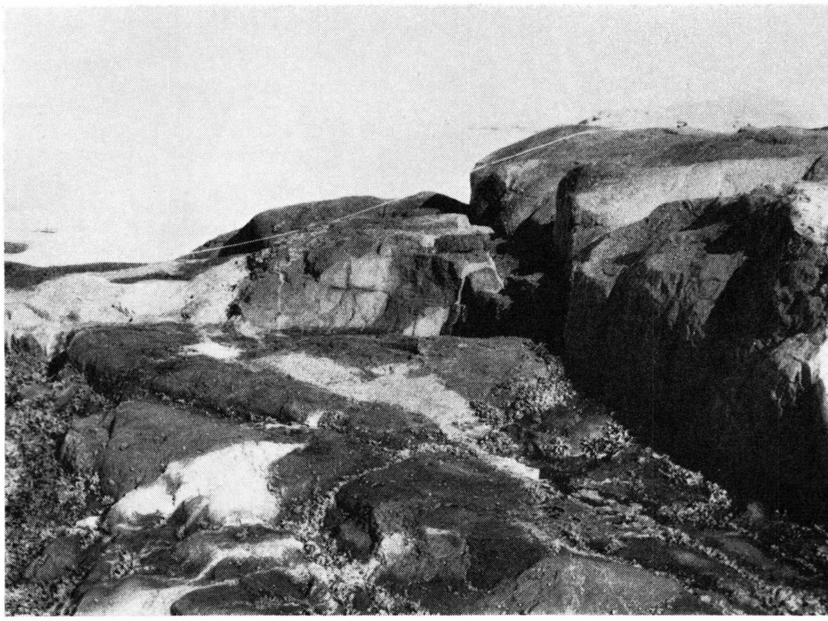

Fig. 9. Skerry in the harbour of Upernavik. The picture shows a well-developed population of periwinkles and a fair growth of *Fucus*, but there were no barnacles. August 9, 1960.

very suitable for a barnacle population. There was *Fucus*, but no green algae. See fig. 9.

*37. Skerry off the Harbour of Upernavik.*

On this skerry there were neither periwinkles nor barnacles, neither on the exposed nor on the protected side of the skerry.

*38. Sound between the Upernavik Island and the Island Northeast of it.*

In this very narrow sound, where there was a vigorous current, four barnacles were found after energetic search. They were all settled in very much "protected" recesses near the L.W.M. There was a rich population of periwinkles.

*39. Ikermiut.*

No barnacles, only periwinkles.

*40. Augpilagtoq.*

Near the L.W.M., well hidden in some crevices, there were a few barnacles in a Type 4 position. There were many periwinkles. This was the northernmost locality examined, situated immediately south of Upernaviks Isstrøm. Unfortunately we had no opportunity to go north of this glacier.

## FACTORS ACTING ON THE DISTRIBUTION

### *Balanus balanoides* (L.).

*1. Factors Inhibiting Distribution at the Adult Stage.*

It is remarkable that the populations of *Balanus balanoides* close to the limits of distribution, both towards influxes of freshwater and towards the north, occur in a Type 4 position, thus well hidden in caves and crevices. This fact makes it very tempting to advance the theory that the barnacles are scraped off the rocks by the sea ice or destroyed by the icefoot. Above, arguments have several times been put forward against this view, even though it is undeniable that the phenomenon will occur (WILCE (1959)); but as there is no connexion between the distribution of the barnacles and the occurrence of the sea ice, ice erosion of the rocks cannot be used as an explanation concerning conditions of distribution. The barnacles are found north of Upernavik and there are well-developed sea ice and an icefoot as far as south of Holsteinsborg. No exact information about the distribution of sea ice and icefoot is available, but in the towns south of Holsteinsborg the keeping of sledge dogs is prohibited, as the freezing up is never sufficient for profitable use of dog sledges.

As a further argument against the theory of ice erosion of the rocks, it may be stated that in such an area as Disko Bugt, where there are sea ice and an icefoot for six or seven months, the best developed populations of barnacles are found in the places with marine exposure, while the poorest populations (Type 4) are found on protected rocks in creeks with influx of fresh water. On large boulders off outlets of freshwater the side with marine exposure may have a dense population, while the side protected from ice-drift, which is facing the river, does not carry one barnacle. In the Upernavik district even a temporary influx due to the spring thaw is sufficient to give rise to the above-mentioned differences in the populations.

Nor can the tidal movement of the sea ice give rise to ice erosion of the rocks, and there is no connexion between the limits of the icefoot and the zonation in the tidal zone. Under the low-water mark there are never any traces of a possible ice erosion, even though the sea ice may become 3–4 m thick when floes are pushed under each other.

I have myself only seen ice-eroded rocks in ice fjords, but they were eroded by glacier ice, not by sea ice.

Thus an adult *Balanus balanoides* seems to be unassailable. It has no enemies of any importance in this area. It must be a misinterpretation when it is maintained that periwinkles can consume barnacles FEYLING-HANSEN (1953). The periwinkles only hide in empty barnacle shells. Fresh water, ooze, and drying-up do not seem to influence the adult barnacles. Breaking due to freezing is of subordinate importance. I have, however, observed one case of large-scale death. On May 20, 1959, when we blasted the icefoot from the rock with explosive in order to get barnacles that had been frozen up since November, we found that the lower barnacles, which were not covered by the icefoot, were dead. They were not closed, but swollen and blistered, and they gave out a considerable stench of rotten animals. There was no demonstrable cause of this large-scale death.

It has not been possible to find any factor that by affecting the sessile barnacles will explain the limits of distribution of this species. There is, however, a possibility that the growing season at the northern limit is too short for the animals to spawn a sufficient number of larvae at a sufficiently early time to secure the survival of the population. This, however, leads to the next problem.

*2. Factors Inhibiting Distribution at the Plankton Stage.*

The effect of these factors should be that there are too small contents of larvae in the water masses for rocks near the northern limit to be populated, as none of these factors will be relevant to the limit of distribution as regards influx of fresh water in the Disko Bugt area, since the water masses here must always have sufficient contents of plankton larvae. As an argument it may be stated that rocks only 50–100 m from freshwater outlets will carry a rich population of barnacles. Moreover the larvae are very tolerant to low salinities BARNES (1953).

On the other hand, certain features about the populations near the northern limit and near the limits towards the glaciers perhaps are to be explained from too low contents of larvae in the water masses. Near these limits the barnacles, as mentioned above, only occur as Type 4 populations, viz. under overhanging rocks and in deep crevices, but one may search for a long time even in such places before finding a few isolated animals. This should probably be explained from the fact that too few larvae get into contact with the rocks for all suitable localities to be populated. Near the northern limit it is also probable that the number of plankton larvae is small, as the local population of barnacles presumably, because of too short a growing season and perhaps too small a production of plankton in general, will have difficulty in producing a sufficient number of larvae, and even if this happens, they will be spawned so late in the season, probably in the month of July, and the season will be so short and poor, that the larvae cannot grow into the attachment stage before the winter sets in. There is a possibility that the populations especially are maintained by larvae conveyed by a branch of the West Greenland current, which just reaches as far as Upernavik.

As to the populations in ice fiords the same views may be advanced. In this case, however, larvae are hardly conveyed from elsewhere, but on the contrary larvae of the local population perhaps are carried away from the area by the outgoing surface current.

*3. Factors Inhibiting Distribution at the Attachment Stage.*

It must be taken for granted that what first of all determines the distribution of *Balanus balanoides*, both the total geographical distribution and the occurrence within the area of distribution, is factors acting on the larvae at the time when they are to attach themselves to the rock. It is evident from observations made in nature that the larvae actively seek out and select the localities where they may be found during the rest of their lifetime and where, indeed, the adults are found. The problem therefore consists in encircling factors inducing or inhibiting the attachment of the larvae on the basis of observations in the field.

The first conspicuous point is that *B. balanoides* always occurs in localities above the L.W.M. Even on a raft moored only a few metres from rocks with a dense *B. balanoides* population, this species was never found, but only *B. crenatus*. The raft of course never rose above the L.W.M. This observation might induce one to the assumption that the larvae required a drying-up of the locality, but this is not so. In rock-pools found in the barnacle zone and never drying up, there is often a dense population of barnacles.

The classification of types of locality made at the description of the populations of *Balanus balanoides* presumably is based on actual fact, the larvae seeking out these localities. Near influxes of fresh water the larvae only settle under overhanging surfaces (Type 4) and only near the L.W.M. In localities with less influence from fresh water the larvae settle in crevices up to about the M.W.M. The commonest locality in the Disko Bugt area is vertical surfaces on exposed coasts, while horizontal surfaces are usually avoided, the larvae preferring the crevices which are always found on these rocks. In the Egedesminde archipelago the larvae settle in dense crowds on vertical as well as horizontal surfaces between the L.W.M. and the M.W.M., while above the M.W.M. they prefer crevices.

The fact that the populations of larvae follow the same features as the adult populations also shows that it is not the winter factors that influence the distribution of the barnacles.

It is very conspicuous that the larvae are attracted by animals already attached, i.e. as a rule adult animals, as attached "pinheads" apparently rarely afford any attraction for young larvae. Especially in the beginning of the attachment period it is of great importance for the larvae to settle near adults. On the other hand, it is hardly possible to find an adult without it having one or more "pinheads" settled as planets in the immediate proximity. Dense cakes of barnacles attract many larvae, there are especially many "pinheads" on surfaces seeping with water from a dense population of barnacles, i. e. that more larvae settle immediately below than immediately above the adult barnacles. Isolated barnacles do not attract so many larvae. The parts of rocks from which cakes of barnacles have been broken in the spring, are very early and very densely repopulated (fig. 4 and Plate IIa).

In this connexion attention should be called to the fact that indeed the larvae are attracted by the adults, but this attraction cannot exceed a certain limit. Thus "pinheads" are astonishingly rarely found on the shells of adults, and one also rarely finds cakes of O-group animals. The larvae only settle so densely that they grow into cake during their second summer. Thus "pinheads" are not found clustered together in the same way as e.g. recently settled *Mytilus* larvae.

The fact that the adults attract the larvae at the attachment stage, is not sufficient to explain that populations of larvae prefer the same types of locality as those in which the adults occur. Later in the season the larvae are not nearly as closely attached to the adult populations and may settle on surfaces where there are no adults near. But e.g. on rocks near an influx of fresh water we shall still only find larvae attached under overhanging surfaces and never on vertical or horizontal open surfaces.

The observations collected suggest that microhydrographical factors can be perceived by the larvae and induce them to attachment. It seems as if the film of water covering the rock is to be of a certain high salinity, or the layer of salt crystals of a certain thickness, to make the larvae settle. I have not had any apparatus to be used for measuring salinities of so small quantities of water. But if, for the sake of argument, we imagine conditions when the tide is falling, we shall see the water seeping down over the rocks and because of drying-up becoming more and more saline. The salinity will be highest in the area between L.W.M. and M.W.M., exactly where the population of acorn barnacles is densest. Rocks from which no parts rise above the M.W.M., carry small populations of barnacles, while rocks from which parts rise high above the

H.W.M., at the same level will carry abundant populations of barnacles, which may stretch right down to the low water of spring tide. On rocks near influxes of fresh water the quantity of salt required will only be obtained under overhanging surfaces (the salt water perhaps cleaves to the rock while the fresh water drains off).

In the summer season the water film will also rise to a higher temperature than the surface water of the sea, but in the Godhavn area it seems especially to be the salinity that is the limiting factor. In the Upernavik district, where the barnacles occur in a Type 4 position, even though they are not under the influence of fresh water, there is a possibility that a higher salinity will compensate for a lower temperature, while in the Egedesminde archipelago conditions presumably are to the effect that a higher temperature will compensate for a lower salinity, and that therefore the characteristic Type 1 population has developed there.

I have tried to test the theory of the importance of the water film by examining various rock-pools in the tidal zone, as rock-pools which drain off a large area without being too deep so that the possibility of a high salinity is present, as a rule generally will carry a population of barnacles, while rock-pools in which conditions of a high salinity are not present, do not contain barnacles.

An examination on August 24, 1960, on Radionæsset yielded the following result:

| | | |
|---|---|---|
| Rock-pool with many barnacles ..... | 32.72‰ | Too small for measurement of temperature |
| Rock-pool almost without barnacles.. | 31.93‰ | 9.7° C. |
| Surface of the sea .................. | 31.51‰ | 9.7° C. |

An examination on September 3, 1960, on the skerry in the harbour yielded the following result:

| | | |
|---|---|---|
| Rock-pool near the upper limit of barnacles; some barnacles ........... | 36.31‰ | 15.3° C. |
| Rock-pool full of green algae, very few barnacles........................ | 32.45‰ | 15.4° C. |
| Rock-pool with many barnacles, large draining area.................... | 32.44‰ | 11.0° C. |
| Surface of the sea ................. | 32.31‰ | 8.0° C. |
| Temperature of the air............. | | 13.0° C. |

These results are too sporadic to form a basis of further conclusions, but they show the tendency, viz. that the sea water left on the rocks at low tide, of course changes salinity and temperature, and does so in a highly varying way according to circumstances. It was intended on the return to Denmark, when better laboratory facilities were available, to study the water film experimentally.

If the theory of the importance of the water film for the attachment of the larvae will hold water, it will require another assumption, viz. that the larvae are also induced by the rising tide to settle.

This assumption, however, is supported by the positive observations that the number of newly settled larvae and the number of shed skins floating on the surface of the water, are largest about the spring tides, which shows that the life cycle of the barnacles also is connected with the phases of the moon. Furthermore, in spite of taking great pains, I never succeeded in seeing free-swimming cypris larvae in rock-pools, even if these were densely set with larvae, settled a few hours ago. These rock-pools have never been studied at rising tide. When the present investigations were made, I was not aware of a possible relation to the tidal rhythm. It would have been easy experimentally to study these conditions in more detail.

It was evident from the observations that the larvae always settle in small pits of the same order of magnitude as themselves. Wherever these "pinheads" were studied, in crevices, in deep rock-pools, on exposed surfaces, they were always "put" into a tiny cave, so that it was very difficult even with fine pincers to pick them out without injuring them. It did not appear that any particular advantage was connected with this "rugophily". Perhaps this tendency to settle in small pits is contributory to the fact that the larvae are not found on shores with pebbles and worn rocks and that they do not settle too close to each other on the rocks.

The "rugophily" of the cypris larvae has been studied in detail by BARNES (1955). Attention should be called to the work by SMITH & NEWELL (1955), in which it is mentioned that *Elminius modestus* Darw. settles on shells of *Littorina littorea* L. By way of comparison it would be inconceivable that *Balanus balanoides* should settle on shells of periwinkles, which just do not offer good conditions for satisfying the demands of the larvae for small pits.[1]

Originally it was tried to explain the predilection of the barnacles for crevices in the area between L.W.M. and M.W.M. by the fact that periwinkles highly cleaned the rock surfaces there from their cover of

[1] After having finished this paper, I made an expedition to study the conditions in the tidal zone along the south coast of the "Channel". Along this stretch it is very common to find *Balanus balanoides* on *Littorina littorea*, *Patella vulgata*, and *Mytilus edulis*. *Balanus balanoides* will in Greenland never and in Denmark very seldom be found on other shell-bearing animals. The value of this observation with regard to the geographical distribution will be further dealt with in a later paper.

green algae. This explanation, however, proved to be insufficient, but the possibility that the fact mentioned can play a part in certain situations cannot be denied.

No connexion between the colour of the rock surfaces and the populations of barnacles has been observed. In the area there are rocks of many colours, from quite pale quartz stones to quite black basalt rocks. Nor has any connexion been observed between illumination and the populations of barnacles, apart from the fact that barnacles in the shade are often tall and slim, while in light they mostly are flat and broad.

## *Littorina saxatilis.*

In the area from Disko Bugt to Upernaviks Isstrøm this species practically exclusively occurs in the tidal zone. There are possibilities of finding isolated individuals in bottom samples from shallow, water, but so far only dead shells of the species have been found, which thus during its whole life is a characteristic tidal zone organism.

The species is interesting by the fact that it makes migrations determined by seasons. In summer the animals are dispersed over the rocks from L.W.M. to H.W.M. In the autumn, the beginning of September, when the first night frost sets in, the animals begin to gather in dense clusters in crevices and cavities, e.g. empty barnacle shells, in the zone from halfway between L.W.M. and M.W.M. to about M.W.M. (see fig. 10). During the autumn the green algae get a chance of settling on the rocks above and below this zone. The periwinkles like the other tidal organisms winter in part frozen up, in the icefoot. The lowest ones can be exposed to very low temperatures at low tide. This occurence of the periwinkles clearly shows that the tidal zone is not exposed to any appreciable ice erosion, as the periwinkles would not obtain any protection in the crevices in which they occur, in cases of only slight ice erosion.

Obviously the periwinkles at a certain low air-temperature actively seek out places where a high salinity, from a microhydrographical point of view, might be expected. The larger the periwinkles, the lower the air temperature which drives them to the winter places of refuge. This reaction causes that the periwinkles winter in the barnacle zone in places corresponding to the description of the places where a Type 3 population of barnacles may be found.

In the spring, the end of May, when the air temperatures in the middle of the day rise to about 10–15° C., the periwinkles begin to leave their winter quarters. The largest and the medium sized ones are first on the go, while the smallest ones are much attached to the crevices, and even in the warmest period the small ones are mainly found in the crevices.

The periwinkles which emigrate, divide into two groups, one eats its way through the layer of green algae above the winter zone up towards the H.W.M. (Plate I b), while the other eats its way through the lower green algae down towards the L.W.M. (Plate I a). This last-named layer of green algae as a rule is the most vigorous one and thus perhaps

Fig. 10. Close-up of crevices full of *Littorina saxatilis.* September 9, 1960.

contributes to the fact that the largest periwinkles are found near the L.W.M. On rocks and skerries from which no parts rise to about the M.W.M., up into the winter zone of the periwinkles, the green algae get an opportunity to develop, and in such localities the green algae in summer are found at a higher level than in places where the periwinkles have only a short stretch to crawl in order to eat the algae right down to the L.W.M. I have never seen periwinkles go down under the L.W.M. In certain places one may see two generations of green algae, e.g. on the skerry in the entrance to the harbour, where a low group of rocks connects two higher groups, both with periwinkles. Halfway between these high groups of rocks there was a rather tall, dense growth of green algae. Around these, which must have been saved from the grazing by the periwinkles during the preceding summer because of the long distance from their winter quarters, there was a growth of smaller green algae, around which, again, there was a black border of periwinkles which were eating their way towards the middle of this layer. The two growths of green algae were distinctly separated.

In many places the rocks are full of crevices, and in the spring, when the periwinkles get out of the crevices and begin eating the green algae on the surfaces, there will often be interesting patterns in which the crevices, which are often at right angles to each other, form a midline in a bare streak of rock, after which follows a black border of periwinkles, and finally the layer of green algae situated halfway between two crevices. This phenomenon was observed most distinctly on the rocks at Godthåb in the summer of 1958, but, for that matter, can be seen everywhere in the tidal zone in the month of June, perhaps in July as well.

As mentioned in the description of localities, the periwinkles will not stand fresh water. Near influxes of fresh water the green algae therefore will be able to grow up. Often a transitory influx of melt water apparently will be sufficient to suppress the population of periwinkles, so that the rocks are covered with a slimy layer of green algae. It has not, of course, been possible to take exact measurements of these conditions of salinity, which would have to be extended over a long stretch of coast and over a long period in order to yield any result, but I got an immediate impression that the farther north one went, the less fresh water was necessary to suppress the population of periwinkles.

Apparently it was especially the very small stages that were most sensitive to fresh water, which agrees with the fact that these were most closely attached to the crevices.

Unfortunately I had no opportunity to go north of the northernmost limit of the periwinkles. It is, however, remarkable that even immediately below Upernaviks Isstrøm there were dense populations of these periwinkles, while *Balanus balanoides* was very rare. These two species thus have not the same limits of distribution towards the north.

## Other Organisms.

As a further argument that certain ecological conditions preferred by certain marine organisms arise in crevices and pits in the tidal zone, two photographs of places where algae take refuge are shown here (figs. 11 and 12).

*Mytilus* also occurs in the tidal zone immediately above the L.W.M., but always distinctly attached to crevices.

Fig. 11. The rocks at the dog-food rack, which are under some influence of fresh water. The algae also prefer crevices, here on a horizontal surface. August 6, 1960.

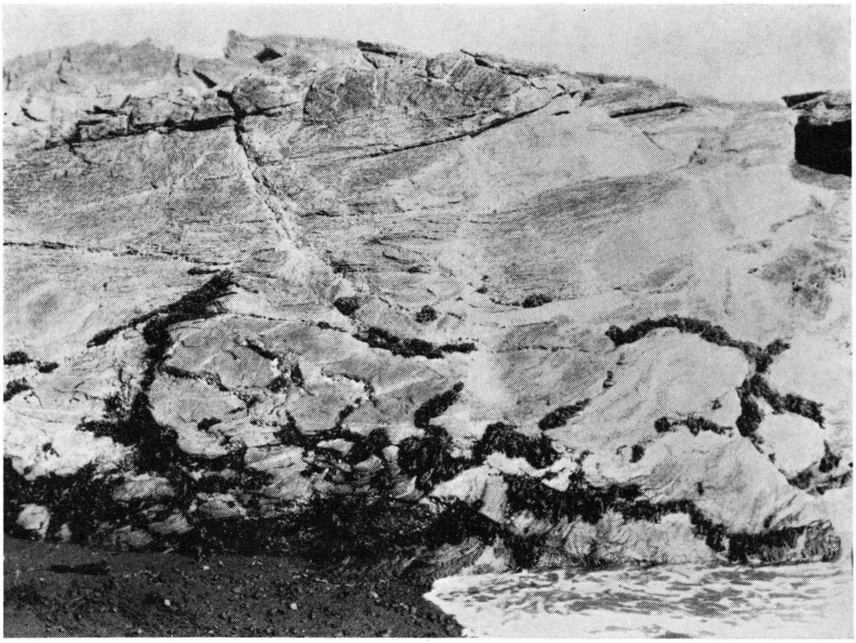

Fig. 12. Vertical surface from the rocks at the dog-food rack. *Fucus* prefers crevices. It is inconceivable that an ice erosion which might scrape the organisms off the surface, should not be able to free these crevices of animals and plants too. August 6, 1960.

# ZOOGEOGRAPHICAL REMARKS

The zoogeographical importance of the littoral fauna has been discussed by BARNES (1957) and MADSEN (1940). The most important species in that respect are *Littorina saxatilis* and *Balanus balanoides.*

According to MADSEN (1940) *L. saxatilis* was in 1936 found farthest north at Tasiussaq, but not at Kingigtuarssuk farther south. This agrees with my observations, viz. that in certain places in this archipelago there are dense populations of periwinkles, but in other places there are none. The northern limit of *L. saxatilis* is presumably first of all determined by factors of the ecology of distribution. The species, which is viviparous without any pelagic stage, will have difficulties in invading new areas. The species would probably be able to survive still farther north, but it cannot go there. Nothing is known about the way in which it spreads apart from its crawling on the rocks. The following observation may perhaps give some information: In order to see when the periwinkles sought out the crevices in relation to the tide I tried to observe the animals through a water telescope, but the shadow cast by the telescope caused the periwinkles to let go their hold on the rock and allowed themselves to roll in the surf like pebbles. This reaction perhaps may give the species a possibility of some pelagic spreading. Perhaps it is spread by man.

In 1936 *Balanus balanoides* was not found farther north than Prøven and at that time, only a few large specimens (MADSEN (1940)). In August 1960 I found dense populations at Prøven. This fact, as compared with my observations that in August there were no newly settled larvae farther north than Umanak, confirms the supposition that the northernmost populations of *Balanus balanoides* are maintained by larvae conveyed from the south. The northern limit of populations of barnacles which can give birth to a new adult population is presumably at Prøven.

The northern limit at Angmagssalik, East Greenland, is presumably determined by the fact that the surface water as a consequence of the layer of melt water and the East Greenland current is fresher and colder than at the corresponding latitude on the west coast, and that therefore the microhydrographical conditions required in the crevices in the tidal zone are only obtained so much farther south than on the west coast. Because of the southward current it will also, of course, be more difficult for the two species to force their way northwards on the east coast than on the west coast.

It appears from a comparison of the distribution and occurrence of the two species that both of them have quite definite requirements according to which their distribution and occurrence coalesce through large stretches, while their biological and ecological conditions are otherwise widely different.

*Balanus balanoides* has only during a short period in the summer season to find localities in which the microhydrographical conditions, presumably especially salinity, can induce the cypris larva to attach itself to the rock. It has a possibility of spreading far and wide and can be found far into fiords and close to influxes of fresh water. In return it is dependent on the season being sufficiently long for the adults to obtain and be induced to spawning and for the larvae then to grow up and always succeed in finding satisfactory localities.

*Littorina saxatilis* var. *groenlandica* can be completely knocked out even by rather a shortlived influence of fresh water. It has no plankton stage, but in return it can more easily maintain a dense population even close to the northern limit, as it can feed, as soon as conditions allow this, and deliver larvae, which stay in the same locality.

The taxonomic problem should be noted, as e.g. in Danish waters *Littorina saxatilis* will very well stand brackish water. In its demands for salinity *Littorina saxatilis* Olivi var. *groenlandica* Mencke is more closely related to *L. littorea* than to *L. saxatilis* in Danish waters.

If the effective northern limit of a species is taken to mean the northern limit of areas in which populations of the species can sustain life, it may be postulated that *Littorina saxatilis* has not reached its effective northern limit. The northernmost specimens of *Balanus balanoides* on the other hand, are found north of the effective northern limit of this species.

# DEVELOPMENT OF THE ICEFOOT

The formation of the icefoot begins as soon as the air temperature falls below $-1.7°$ C. At each low tide the rocks are covered by a sheet of ice and the spray freezes on to the rocks above the H.W.M. The icefoot in exposed places, e.g. Radionæsset, can thus reach 6–8 m above

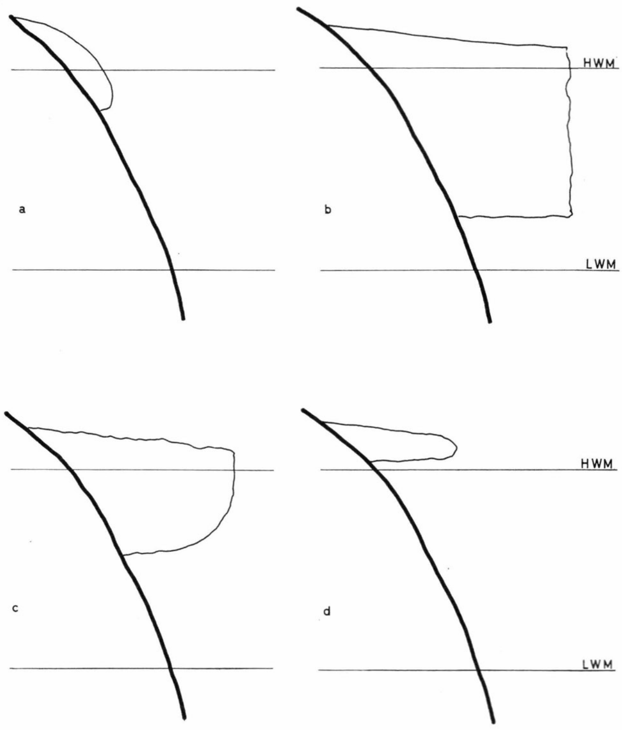


Fig. 13. Development of the icefoot on a rocky coast. (a) Embryonic stage. Growing in the months of October–December at each high tide and from ice from spindrift. (b) Maximum stage. The months of February–March. The tidal movement of the sea ice by erosion of the outermost vertical surface prevents further increase. The icefoot grows upwards because of depositing of snow, but not downwards, as the ice gradually isolates more and more against the cold. Perhaps the icefoot in high arctic areas can grow down under the low water mark. (c) Stage of melting. In April–May, already before the sea ice has disappeared, the sea water makes the icefoot melt. (d) The last rests of the icefoot, which may project as eaves until the beginning of the month of July.

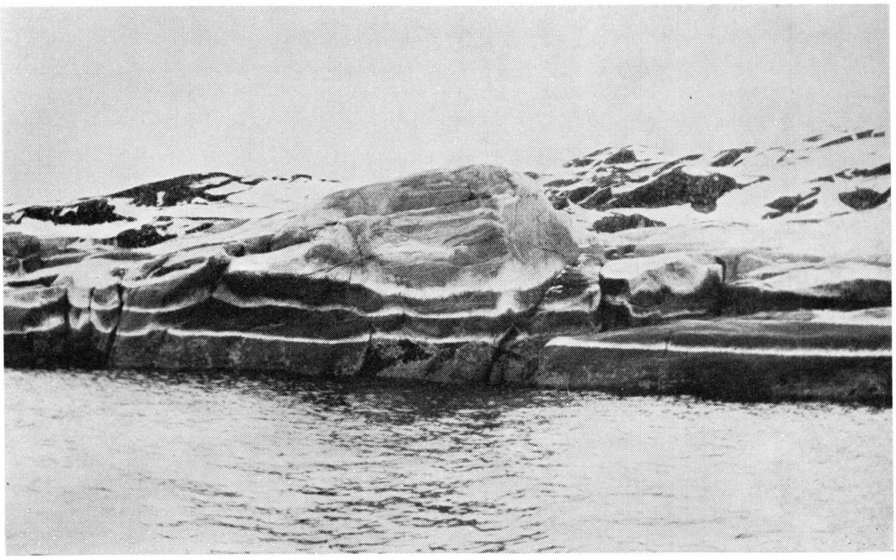

Fig. 14. Embryonic stage of the icefoot. Streaks of sea ice deposited at different levels dependent on the tide in relation to minima of cold. November 9, 1959.

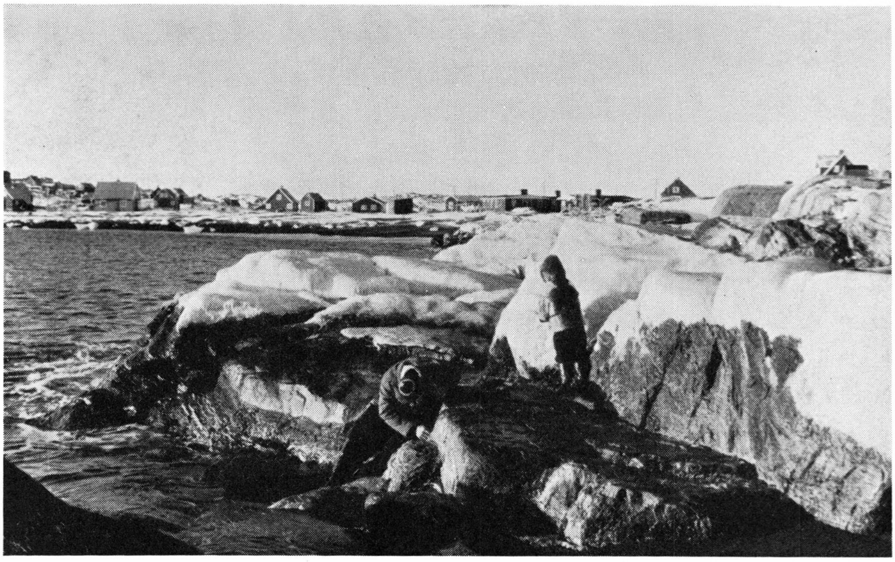

Fig. 15. The icefoot sits like a firm ice armour round the high water mark. Barnacles around M.W.M. are collected. October 23, 1958.

the H.W.M. To begin with these sheets of ice will constantly thaw at high tide, but in November the formation of the icefoot begins in earnest. The formation of ice during that period mainly takes place about and above the H.W.M., but gradually the icefoot grows downwards

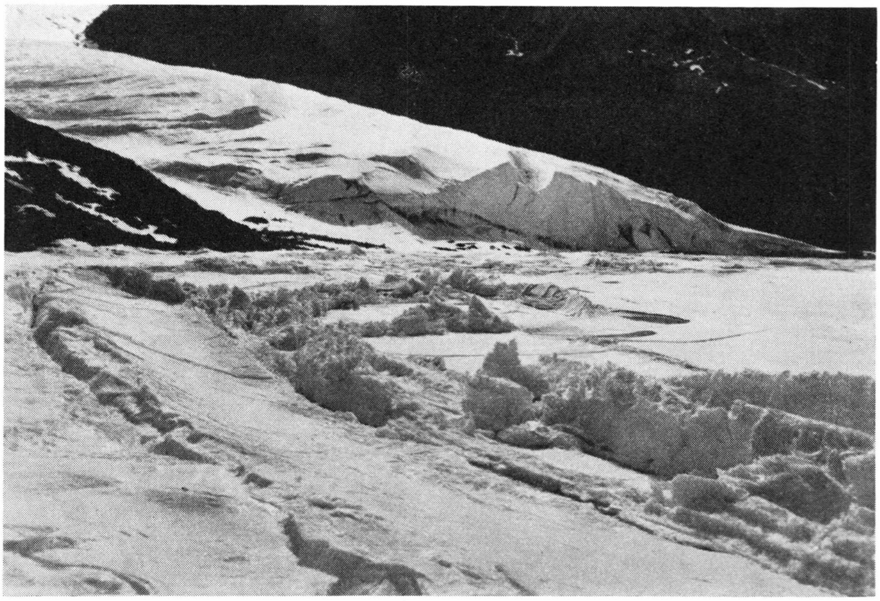

Fig. 16. The transitional zone between the icefoot (on the left) and the sea ice. Phot. Hans Valeur.

towards the L.W.M. In protected places the icefoot, when fully developed, lies like a boxlike fringe of ice frozen on to the rocks. The upper side is above the H.W.M., as snow is conveyed to the place, but lies as a fairly horizontal surface, which can be used as a road when the sea ice is not good. The under side is also a horizontal surface, which projects at right angles from the rock between L.W.M. and M.W.M. The boundary surface towards the sea is kept vertical by the sea ice scoring the icefoot up and down in time with the tide. Normally there is a folding-system of ice floes from the icefoot to the sea ice, which "springs" the tidal movements of the sea ice against the icefoot (fig. 16). At rising tide the sea water forces its way up into the clefts in this folding-system. After snowfall the new ice in these clefts is preferred for sledge tracks. When walking among these ice floes one constantly hears a creaking sound from the movements. Only in a few places and in the spring, when the sea ice is gone, is it possible to observe the icefoot directly. On certain skerries the icefoot can reach such a development that it breaks off and tears frozen-up organisms with it, e.g. *Fucus*, *Mytilus*, and periwinkles. This phenomenon is of very rare occurrence.

The icefoot reaches its maximum development at Godhavn in the month of March. In April, already before the sea ice has disappeared, it begins to melt away from below, a process which further gathers

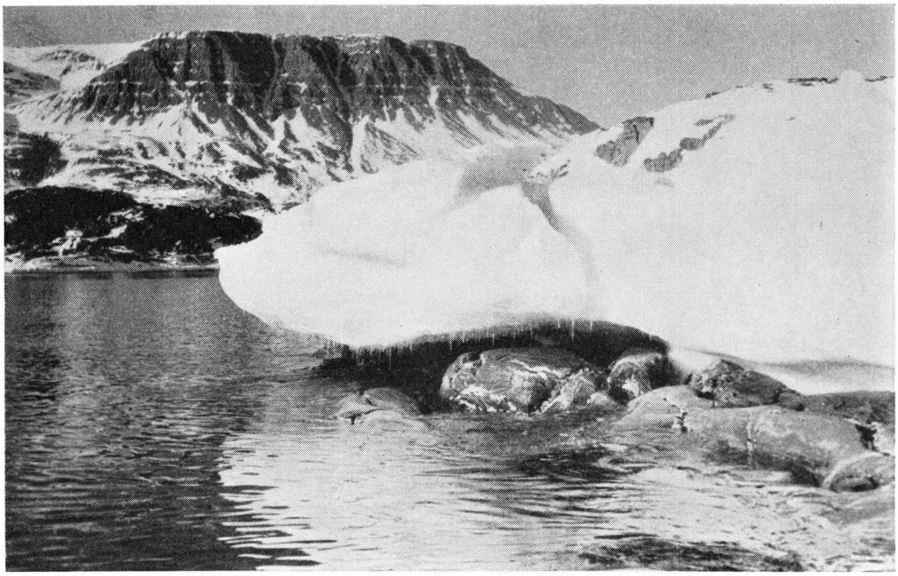

Fig. 17. The skerry at the landing-stage for dories. The icefoot at that time is greatly undermined; this process continues until the icefoot stands as eaves projecting from the H.W.M. The melting-away to this stage takes place very fast, while it may take long until the last rest of the icefoot has disappeared. April 22, 1959. The sea ice disappeared from there about April 10, 1959.

Fig. 18. The icefoot immediately after the sea ice has disappeared. Radionæsset. April 28, 1960.

momentum in May when the sea ice has disappeared. It is, however, the sea water which makes the icefoot melt away, not the higher air temperatures. The icefoot therefore remains like eaves at H.W.M. until far into June; indeed, I have seen these eaves in clefts in rocks even in July. There is of course a great difference between the various times when the sea ice disappears from the various rocky coasts. At Godhavn the sea ice disappears from the exposed stretches as early as April 1, while e. g. the ice in the harbour must be blasted with explosive in the middle of May in order to make room for the first ship of the year. In protected bays the sea ice may remain until the middle of June. There are, however, great variations from year to year, as rough weather conditions make the sea ice disappear earlier.

# SUMMARY

First, a description is given of the distribution of the two species in the area, and a number of localities are described with special reference to the ecological factors that may be supposed to play a part in an arctic tidal zone. The development of the icefoot is illustrated with photographs and it is argued that neither the icefoot, the sea ice, nor ooze in the melt water is of importance for the distribution of the species.

It is shown that the crucial point in the life of the *Balanus balanoides* is the time when the larvae are to select a suitable locality in which to settle, and that the distribution of the species is determined by conditions operating at this time. It is assumed that the salinity in the water film or the layer of salt crystals which covers the rocks at falling tide is the most important factor, while the conditions of temperature are subordinate, though in the way that a high temperature can compensate for a low salinity and vice versa. The larvae are attracted by populations of adults and by small pits. The populations of adults are divided into four types which are related to the salinity of the water film when the rocks are drying up.

*Littorina saxatilis* has a winter refuge in crevices in the tidal zone about M.W.M. The specimens of *L. saxitilis* make migrations determined by the season. They prove to be very sensitive to fresh water, the more so the lower the temperature is.

The limits of distribution of the two species do not coalesce. It is true that they are both dependent on partly the same special factors in the tidal zone, which in this arctic area especially appear in crevices, but these factors are active at different times in the lives of the animals, and the species, for that matter are so different in their biology that the same limits of distribution might not be expected for the two species.

The growth of green algae in the tidal zone proves to be dependent on the populations of periwinkles.

The "ecology of crevices" proves to be of importance also to other organisms of the tidal zone, e.g. *Fucus* and *Mytilus*.

# LITERATURE


BARNES, H. 1953. The effect of lowered salinity on some barnacle nauplii. J. Anim. Ecol., 22, 328–330.

— 1955. Further observations on rugophilic behaviour in Balanus balanoides (L.). Vid. Medd. Dansk. Naturhist. For., 117, 341–348.

— 1957. The Northern Limits of Balanus balanoides (L.). Oikos, 8, 1–15.

BENTHAM, R. 1937. The Ice-foot. Appendix III in Shackleton: Arctic Journeys, The Story of the Oxford University Ellesmere Land Expedition 1934/35, London.

BOUSFIELD, E. L. 1955. Ecological control of the occurrence of barnacles in the Miramichi Estuary. Nat. Mus. of Canada, Bull. 137, Biol. ser. 46.

BROCH, H. 1924. Cirripedia Thoracia von Norwegen und dem norwegischen Nordmeere. Videnskabsselskabet Skrifter. I., Mat.-nat. Klasse 1924, no. 17., 121 pp.

CRISP, D. J. 1955. The behaviour of barnacle cyprids in relation to water movement over a surface. J. Exp. Biol. 32, 569–590.

CRISP, D. J. & SOUTHWARD, A. J. 1953. Isolation of Intertidal Animals by Sea Barriers. Nature, 172, p. 208.

DANIEL, A. 1957. Influence of Stage of Tide on the Attachment of Barnacle Cyprids. J. Bombay Nat. Hist. Soc., 54, p. 866–868.

FEYLING-HANSSEN, R. W. 1953. The Barnacle Balanus balanoides in Spitsbergen. Norsk Polarinstitutt, Skrifter nr. 98.

GREGG, J. H. 1945. Background Illumination as a Factor in the Attachment of Barnacle Cyprids. Biol. Bull. Woods Hole, 88, 44–49.

KITCHING, J. A. 1935. An Introduction to the Ecology of Intertidal Rock Surfaces on the Coast of Argyll. Trans. Roy. Soc. Edinb. 58, 351–374.

KNIGHT-JONES, E. W. 1953. Laboratory Experiments on Gregariousness during Settling in Balanus balanoides and Other Barnacles. J. Exp. Biol., 30, 584–598.

KOCH, L. 1928. Contributions to the Glaciology of North Greenland. Medd. om Grønland. 65, p. 181–464.

MADSEN, H. 1940. A Study of the Littoral Fauna of North Greenland. Medd. om Grønland, 124, no. 3, 24 pp.

MOORE, H. B. 1935. The Biology of Balanus balanoides, IV. J. Mar. Biol. Ass. U. K., 20, 279–307.

SMITH, F. G. W. 1948. Surface Illumination and Barnacle Attachment. Biol. Bull. Woods Hole, 94, 33–39.

SMITH, J. E. & G. E. NEWELL. 1955. The Dynamics of the Zonation of the Common Periwinkle Littorina littorea (L.) on a Stony Beach. J. Anim. Ecol., 24, 35–56.

THORSON, G. 1933. Investigations on Shallow Water Animal Communities in the Franz Joseph Fjord (East Greenland) and Adjacent Waters. Medd. om Grønland, 100, No. 2. 70 pp.

VIBE, C. 1950. The Marine Mammals and the Marine Fauna in the Thule District (Northwest Greenland) with Observations on Ice Conditions in 1939–41. Medd. om Grønland, 150, No. 6.

WILCE, ROBERT T. 1959. The Marine Algae of the Labrador Peninsulae and Northwest New Foundland (Ecology and Distribution). Nat. Mus. Canada, Bull. 158, Biol. Ser. No. 56, 107 pp.



Færdig fra trykkeriet den 22. juni 1962.

# PLATES

## Plate I.

a. The *Littorina* front on its way down towards the L.W.M. through the layer of green algae which is much more vigorous than the layer near H.W.M. June 24, 1960.

b. The periwinkles have started their feeding migration from their winter refuge in the barnacle zone through the layer of green algae towards the H.W.M. The pincers are 10 cm long. June 7, 1960.

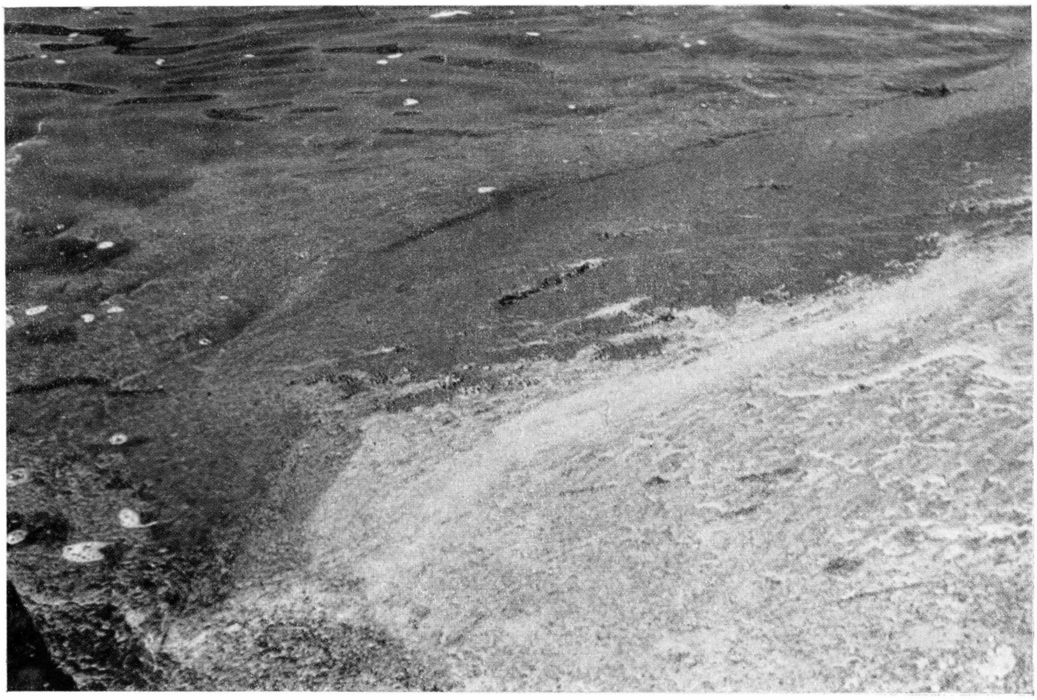

Fig. I a.

Fig. I b.

## Plate II.

a. On Terrace A the dense group of large barnacles has been broken off by the frost to the right of the pincers and the glass. See schematic presentation in fig. 4. On Terrace B the cakes of barnacles were loosened by the frost, but remained in place. May 10, 1960.

b. Close-up of the acorn barnacles on the rock under Udkiggen (figs. 2 and 3). Closest to the L.W.M. there is a Type 2 population and above that there is a Type 3, the barnacles of which are attached to crevices. September 19, 1960.

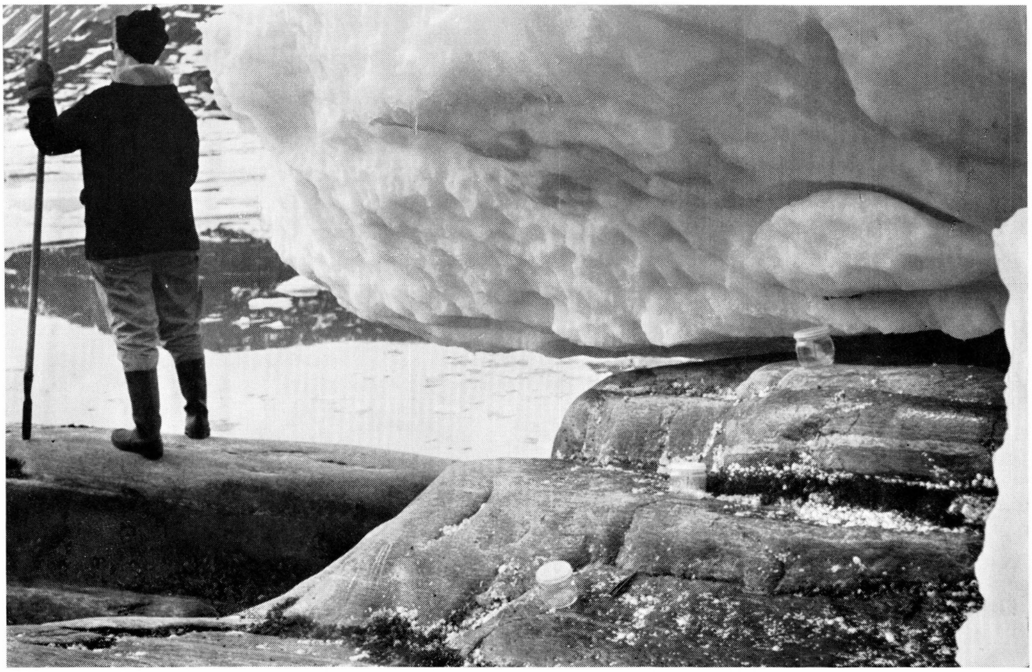


Fig. II a.

Fig. II b.