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THE NATURAL HISTORY EXPEDITION TO
NORTHWEST GREENLAND 1936
LEADER: FINN SALOMONSEN

A STUDY OF THE LITTORAL FAUNA OF NORTHWEST GREENLAND

BY

HOLGER MADSEN

WITH 3 FIGURES IN THE TEXT

KØBENHAVN
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Introduction.

The main object of the "Natural History Expedition to Northwest Greenland 1936" was ornithological research, but, in addition, various ecological investigations were undertaken. The shallow water communities were described (VIBE 1939). The leader of the expedition Dr. F. SALOMONSEN investigated himself the littoral zone from Prøven northward on similar lines to those followed by me in East Greenland (HOLGER MADSEN 1936) emphasizing the importance of the surveyed area, notably for the question of zoogeographical limits. With great kindness he handed over to me the material collected and his diaries, and I wish to express my cordial thanks to Dr. SALOMONSEN. I am also much indebted to various members of the staff of the Zoological Museum, who kindly determined the animals, viz. Dr. phil. P. L. KRAMP (*Hydroidea*), Cand. mag. K. STEPHENSEN (*Crustacea*), Dr. phil. G. THORSON (*Mollusca*) and Mag. scient. E. WESENBERG-LUND (Worms).

Description of the Littoral (Tidal) Fauna of North West Greenland.

Littoral investigations were made in several localities from Prøven northward, the most detailed observations being from the harbours of Prøven and Upernavik, both natural bays.

It may be said at once that the statements made about the region in my previous paper (H. MADSEN 1936, p. 52) were confirmed in all essentials with a single exception, viz. *Balanus balanoides*, which according to verbal information from an official in Greenland, I mentioned from Upernavik (l. c. p. 54). At any rate it was not found north of Prøven (72°25′ N.) in 1936, and even there it was found only in a single place (cf. footnote p. 8).

The greatest attention has been directed to rocky habitats, partly because the zoogeographically important species occur here, partly because the sediment is very poor in species and more difficult to

investigate. Besides sediment only rarely occurs in the area surveyed. When present in the tidal zone it consists of very coarse sand. In this sand only *Ammodytes* sp. has been found in Prøvens harbour. In very shallow water (1 m) near Upernavik on clay bottom a single specimen of *Phascolosoma margaritaceum* was collected (June 25). *Arenicola marina* was observed nowhere, but the cause may be that no suitable bottom has been available. *Arenicola* is known along the West coast to Umanak.

During the preparation of my previous paper I felt the difficulty that the main features described for the littoral in East Greenland also extend to the upper part of the sublittoral on level bottoms, which present an almost bare zone (H. MADSEN 1936, p. 44). BERTELSEN 1937, p. 15 overcomes the difficulty in introducing the term "the euryhaline littoral fauna zone". This zone he divides in an upper, viz. the tidal zone, and a lower zone. The euryhaline littoral zone is evidently of common occurrence in arctic and many subarctic regions (H. MADSEN 1936, p. 62). For practical reasons, however, I confine myself to the tidal zone, especially as in North West Greenland no observations on the whole euryhaline zone are available. In all probability such a zone does occur also here.

The bay of Upernavik-harbour (72°47′ N.) was the first locality visited (June 6th) showing most interesting conditions. The harbour-bay itself is a fairly small basin, with a narrow entrance, with shelter in most places. The most completely investigated locality was a skerry situated in the southern part of the harbour. Although only 20 days had passed since the ice had broken up a comparatively rich littoral fauna was found. The temperature of the surface water ranged about 0.2° to 1° C.

On the most exposed part of the harbour, in the northern part (consequently with south exposure), only *Littorina saxatilis* var. *groenlandica* (the only *Littorina* found in the area, hereafter called simply *Littorina*) was present in the tidal zone in adult specimens, notably in crevices of the rock, together with some *Fucus*. *Littorina* at this early date had not yet appeared on the more sheltered skerry with north-west exposure. Here *Mytilus edulis* was present in comparatively large numbers in holes and crevices of the slightly sloping rocks in the lower part of the tidal zone and in the sublittoral zone, the specimens being fairly large. Some few large actinia were found on the mussels in the tidal zone. In the sublittoral zone, just below low water a rich fauna was found, notably in the dense *Fucus* vegetation. Of Molluscs *Buccinum groenlandicum*, *Margarita helicina*, eggs of an opistho-branchiate snail and *Modiolaria faba*, of Crustaceans *Gammarus locusta*, *Pontogeneia inermis*, *Calliopius laeviusculus*, *Ischyrocerus anguipes* and *Caprella septentrionalis*; further the hydroid *Laomedea longissima* and a great

number of copepods and large nematodes. In this connection the animals found (July 5th) on *Fucus* floating in the surface (Tasiusak, Nutarmiut, between Prøven and Upernavik) should be mentioned. These animals undoubtedly live in shallow water, and may also occur between tide marks, viz. the snails *Margarita helicina* and *Onoba aculeus*, the mussels *Cyamium minutum*, *Modiolaria discors* var. *laevigata* and *Modiolaria faba* and the Polychaete *Spirorbis spirillum*. All the species mentioned above are commonly met with along the whole west coast of Greenland.

The collection from July 2nd contained the isopod *Jaera marina*, turbellaria, various polychaetes (Hesionids, Sabellids, Serpulids) oligochaeta (both Enchytraeids and Tubificids) and nemertines (eggs) and halacarids. These latter, together with copepoda and nematodes occurred littorally (since they were found in the deposit from *Mytilus* collected in the tidal zone) and the more mobile crustaceans undoubtedly also occur there. The littoral occurrence (July 31st) of *Campanulina lacerata*, mostly a tidal form is of the greatest interest, having been recorded from Greenland only once before, viz. from Færingehavn (63°45′ N.) (Kramp 1932b, p. 29).

July 2nd *Littorina* occurred in great numbers on the skerry, where it was not found on June 12th, the temperature of the surface water now being 3.9°; on July 31st it was 4.5°, on August 22nd 4°.

From Upernavik also some few important observations on a rock pool were made. In a quite shallow rock pool, with a temperature on June 12th of 1.6° *Gammarus locusta* swarmed, with *Mytilus edulis* fixed to the bottom. On July 2nd the temperatures observed were 8.5° to 9.5°.

The harbour of Prøven (72°23′ N.) was visited twice, viz. July 10th and 17th. Both the sublittoral (Vibe 1939) and the littoral areas showed rather specific conditions. The harbour is a creek open to a narrow strait between two small islands (Fig. 1). There is always a strong current here. Therefore there is no continuous ice cover, and the ice is always thin. So in 1936 there was ice only for a few weeks in February, and it was so thin that one could not walk on it. The ice foot is only slightly developed. In this connection it is also remarkable that the surface temperature of the water was 6.9°, a temperature, so far as our observations go not reached in Upernavik.

The littoral life was much more abundant than in Upernavik, though for the most part the same forms were met with. Besides its usual habitat in crevices and inequalities *Littorina* occurred in great numbers and large specimens on the level flats about 0.5 m above ebb-tide level. But also quite young were more abundant than in Upernavik. At the same level *Mytilus* also occurred very abundantly, and with much spat. The small forms found in the deposit from the mussels were the same as enumerated above in Upernavik, the most remarkable

species being *Jaera marina* and *Campanulina lacerata*. Very conspicuous was the abundant occurrence at the same level of large *Acmaea testudinalis*. In the lower part of the littoral (about 10 cm above low water level) *Buccinum groenlandicum* and *Strongylocentrotus droebachiensis* were found, the latter often in a line along the edge of the water. They were also abundant in the upper sublittoral area together with actinia and *Asterias glacialis*. Very interesting was the only find in the surveyed region of *Balanus balanoides*, found in large but scattered specimens on a south exposed slope up to 1 m above ebb tide level.

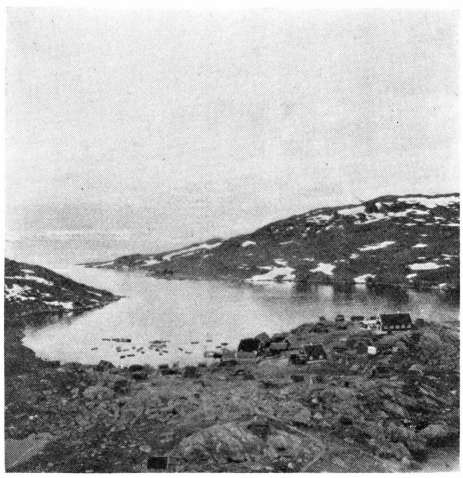

Fig. 1. The harbour of Prøven. *Balanus balanoides* was found on the cliffs round the pier.

Towards the end of July several points north of Upernavik were searched for littoral molluscs. The most northern point, where such were found is Tasiusak (73°22′ N.). Here *Littorina* occurred under similar conditions as in Upernavik. *Mytilus* was not found by SALOMONSEN, but it occurs here sublittorally, since specimens from this locality, collected by Mr. FRITS JOHANSEN August 16th, 1931, are in the collections of the Zoological Museum, together with *Modiolaria discors* var. *laevigata*. The place investigated lies at the head of a narrow little fjord, thus in a very sheltered position. Remarkably enough *Littorina* was searched for in vain in a more southern locality, viz. Kingigtuarsuk (73°15′ N.). This place is a very small island, lying isolated about 17 km out in Baffinbay, very exposed. The northern limit of littoral molluscs obviously runs about these degrees of latitude. A number of more northern places, comprising both sheltered and more exposed localities and isolated islands were searched in vain, viz. Kraulshavn (74°8′), Upernivíarsuk (74°15′), Kangerdluarsuk (74°20′), Devils Thumb (74°36′) and

Amdrups Ø (74°43′). The coast northward of this place up to Thule is inaccessible, owing to the enormous glaciers which flow out here, and the almost constant fog.

In Thule (76°23′) naturally no littoral molluscs are found and only a poor fauna occurs in the algal vegetation which has not been closely investigated. Quite similar conditions were found in other localities in the district, both south and north of the Thule colony. This applies to Savigssivik (76°0′), Carey Øer (77°37′) and Siorapaluk (77°48′) all types of habitat, shelter and exposure being represented.

The Greenlanders speak of a mussel, most likely *Mya truncata* which burrows in the clay in a bank north of the colony, about 1 m below ebb tide. And a Greenlander, who said he knew *Mytilus*, claimed that this mussel occurs sublittorally in a single locality. This does not seem quite improbable, since *Mytilus* also lives sublittorally near Novaja Zemlja in otherwise arctic regions, which indicates that the extreme branches of the Atlantic current reach as far as this.

Comparison with the Rest of Greenland.

The most remarkable feature of the littoral fauna of the southern area investigated is the obvious boreal stamp; especially in the occurrence of *Littorina*, *Mytilus edulis*, *Balanus balanoides*, *Jaera marina* and *Campanulina lacerata*, and also in finding a tubificid oligochaet. The boreal forms have their extreme limits somewhat north of Upernavik, about 74° N. The area shows much similarity to the conditions known in Ammagssalik on the East coast (H. Madsen 1936, p. 12, Bertelsen 1937, p. 21, Degerbøl 1937, p. 22). With the exception of *Campanulina* and the tubificid worm all the above mentioned forms have also been found here, but in addition the gastropode *Homalogyra atomus*. There is also evidence for the occurrence in the littoral zone of actual sublittoral molluscs, e.g. in N.W. Greenland *Margarita helicina* and *Buccinum groenlandicum*, viz. in E. Greenland *Onoba aculeus* (H. Madsen 1936, p. 12). Bertelsen 1937 found a further interesting evidence of the boreal stamp of the littoral area of Ammagssalik in the occurrence of *Arenicola marina*. As stated above it cannot at present be determined, whether this worm actually is missing in N.W. Greenland, since suitable sediment habitats have not been found. In E. Greenland the boundary between the real arctic and the subarctic (or boreo-arctic) regions, as defined by the present author (H. Madsen 1936, p. 65) lies very sharply, immediately north of Ammagssalik (about 66° N.), and is common to *Littorina*, *Mytilus* and *Balanus balanoides*. As shown above this is not the case in N.W. Greenland. Here the external factors evidently alter less suddenly than on the East coast, so allowing the individual species

to extend their range in different degrees. The limit, however, is also here pretty clearly defined, in my opinion an example of the usefulness of the zoogeographical delimitation of the littoral fauna according to the occurrence or non-occurrence of littoral molluscs. So e.g. the similarities of the tidal fauna in Upernavik and Prøven are evident, in spite of the non-occurrence of *Balanus balanoides*[1]). On the other hand Prøven has a more southern stamp also in the littoral occurrence of such forms as *Acmaea testudinalis* and *Strongylocentrotus*, even if the local favourable conditions due to the current and the resulting thin ice cover may contribute to the comparatively rich fauna.

VIBE 1939, p. 29, in his discussion of the boundaries has misunderstood some points. Thus he is of the opinion that *Pseudalibrotus littoralis*, characterising the littoral of the arctic and subarctic region, occurs only in the subarctic, since he himself found it only in Upernavik (the animals unfortunately not being collected), not in the more northern tracts. This undoubtedly is due to a mere chance, since it is well known in the northern tracts. Also his statement that *Buccinum groenlandicum* occurs only north of the boundary is incorrect, since this snail is commonly known along the whole West coast of Greenland.

In E. Greenland there is evidence for great differences also in the sublittoral south and north of the boundary (cf. notably BERTELSEN 1937). Also in N.W. Greenland differences can be traced, although they are not nearly so clear as in the littoral. The most striking feature is the occurrence of *Portlandia arctica*, which, both in E. and W. Greenland, was found only north of the boundary. Further the weight of animals per m^2 in Upernavik is greater than in Scoresby Sound on the E. coast and Thule on the W. coast (in corresponding shallow water animal communities), evidencing a productivity greater south than north of the boundary. But apart from the specific local conditions in Prøven the size of bottom samples does not reach that of Ammagssalik, thus emphasizing the aforementioned more sudden change of conditions on the E. than on the W. coast (BERTELSEN 1937, VIBE 1939).

I should like to stress some facts set out in my paper of 1936, since STEVEN 1938, the latest paper on arctic littoral fauna, does not consider these. STEVEN (p. 63) repeats the common view (e.g. set forth by ELTON and BADEN-POWELL 1931), that the temperature and salinity of the water etc. are decisive factors for the littoral fauna. But this

[1]) VIBE 1939, p. 29, it is true, mentions the find of a single specimen of *B. balanoides* from Upernavik; but this is evidently occasional. Unfortunately the specimen was not collected.—In this connection it seems necessary to deny the occurrence of *B. balanoides* at Port Foulke, north of Thule, quoted by STEVEN 1938, p. 67, after STEPHENSEN 1936. This quotation is based upon STIMPSON 1864. According to the present material it must be considered a wrong determination.

does not hold good for the question, whether a specific littoral fauna, consisting of molluscs or *Balanus balanoides*, in a given geographical region actually is able to develop. It seems to me a matter of fact that other causes here are decisive, causes which have some connection with the productivity of the sea, therefore also acting on the sublittoral. The evidence for that, for instance, the formation of ice cannot be a decisive factor, I see in the actual existence of a specific littoral fauna in Upernavik, which has at least as severe a climate as Scoresby Sound, where a littoral fauna is absent. The formation of ice is wholly dependent on the climate. That also the formation of fjord water of low salinity cannot play a decisive role is seen in the relatively well developed littoral fauna in the Ammagssalik district, where the fjord water attains a greater development than in the more northern regions where it is absent (cf. BERTELSEN 1937, p. 14).

The connection with the productivity of the sea seems probable in consideration of the above mentioned quantitative conditions in the animal communities and also the distinct sublittoral boundary. The clearest boundary, viz. that north of Ammagssalik, is evidently also somehow dependent on the Irminger current here washing the coast, partly intermingling with the polar current (see i.a. HELLAND-HANSEN, p. 72, in THOR IVERSEN 1936). On the N.W. coast it is more difficult to connect the boundary with particular currents. But at any rate a comparatively warm current partly dependent on the tidal movement runs northward along the coast (NIELSEN 1928, pp. 225—226). But its further course is not known.

Local precipitation at least cannot be responsible according to the above mentioned climatic differences, and the same applies to the height of the tides, which does not differ essentially on either side of the limit.

STEVEN in his aforementioned paper gives a description of the shore fauna of the Amerdloq fjord in the Holsteinsborg district, about 67° N.

The area is especially interesting through its position between the only areas hitherto investigated, viz. the Frederikshaab and Umanaq districts (cf. H. MADSEN 1936, p. 52 ff.). STEVEN arranges his description on similar lines, but partly with other names than those used by the present author. What I called the rock facies he calls rock shore. He does not add essential new features to this habitat. He adds some few species, which were not previously found on the Greenland littoral, and this is also the case in other habitats. On the other hand, he did not find many of the species mentioned in the literature, partly owing to the relatively northern position, partly on account of the local conditions. In the sediment facies he found the sand (and gravel) beach

to be very poor in species (*Turbellaria* not being systematically searched for). The most remarkable feature was the absence of burrowing worms and mussels. But according to the description it seems possible that the cause of this may be the coarseness of the sand. This seems to be confirmed by the find of *Arenicola marina* in the *Mytilus* beds.

The *Mytilus* beds, which more properly should be called clay shore, in conformity with the other names, was the richest, both in species and individuals, partly burrowing forms as *Arenicola marina*, and other polychaetes, especially *Eteone longa*, well known in this habitat, and partly epifaunal animals, notably snails, e.g. *Skeneopsis planorbis*, *Acmaea testudinalis* and *Onoba aculeus*.

The most interesting details were found in the habitat which I called clay and sand flats off the river mouths, by STEVEN called by the better name stream mouth. Here he only found the amphipod *Pseudalibrotus littoralis*. This species is well known from the whole W. coast of Greenland, but without record of the habitat. In 1936 I wrote (p. 55): "No doubt *Pseudalibrotus littoralis*—may be found here (*i.e.* in stream mouths). In Kola fjord, the shore fauna of which is very similar to that of W. Greenland, *Pseudalibrotus* is especially associated with river mouths. As shown below, it is able to thrive in practically fresh water, at any rate in E. Greenland. Further it seems probable that in W. Greenland, with its abundance of species, it is more easily ousted from other localities than in E. Greenland". This is in good accordance with its habits in the Ammagssalik district a further argument for the subarctic character of this region (BERTELSEN 1937, p. 21). The great similarities with conditions in Kola fjord is also highly stressed with the frequent occurrence of the polychaete *Pygospio elegans*, which be it said, seems to be new to Greenland.

In all habitats the special littoral organisms are found although not in the same number, as can be seen of some counts made by STEVEN. Unfortunately he did not weigh the animals, and it is also regrettable that he did not count the *Arenicola*, which could be done very easily by counting the excrement piles. I have computed the weight per m^2 for the animals, he has counted, viz. *Mytilus edulis*, *Littorina saxatilis* var. *groenlandica* and *Balanus balanoides*. For *Mytilus* I used the very low mean figures obtained by THAMDRUP 1935, for *Littorina* I weighed 100 specimens from Upernavik, for *Balanus* 50 specimens from Egedesminde, both species in the collections of The Copenhagen Zoological Museum. Notably in the clay shore, where *Mytilus* occurs in regular beds, very large figures were found, of *Mytilus* alone over 1300, about 5000 g, so approaching conditions in the *Mytilus* beds in the mud flats on the W. coast of Jutland (Danmark), investigated by THAMDRUP, and naturally enough, far exceeding those hitherto found in Greenland

(cf. VIBE 1939). The number and weight of the other epifaunal animals counted were quite inconsiderable. The most numerous, *Littorina* with about 60, weight 99 g. On the rock shore the special littoral animals, *Littorina* and *Balanus* are particular frequent, as might be expected in their most natural habitat. But even here the numbers are small, compared with those given by MOORE 1935 in England. His smallest figures from the upper and lower part of the *Balanus* belts are 400—500, in the central part 3500 (his highest are about 30,000), all animals of 2 years and older. Similar figures are given by HATTON 1938 in France. In W. Greenland, they are about 300, with a weight of about 50 g. *Littorina* occurs in a number of about 100 per m^2. With the 5 *Mytilus* the entire weight is about 100 g, a comparatively small figure. But the *Mytilus* evidently on the place of sampling has been seldom. Somewhat higher figures were obtained on stones in river mouths, with 55 *Mytilus*, weight 210 g, while *Littorina* (about 30) and *Balanus* (about 11) were much more infrequent; the entire weight was about 215 g. Is this really a result of better conditions of nutrition in the stream mouth, or has it quite casual causes in the counting technique?

Remarks on the Delimitation of the Arctic Region in the Littoral Zone.

As previously mentioned (H. MADSEN 1936, p. 64 f.) I have given a revised definition of the arctic regions in the littoral, first established by GURJANOVA, SACHS and USCHAKOV (1925). I proposed for the present to confine them to two regions, an arctic and a subarctic (or boreo-arctic) region. The arctic region seemed to be delimited most easily by the non-occurrence of littoral molluscs, and possibly *Balanus balanoides*. This can be more plainly expressed by saying that the arctic region is characterized by the absence of a specific littoral fauna (littoral naturally in the sense of tidal) of the larger animals. So oligochaete worms occur as specific littoral animals also in the arctic. The most important organisms in this connection are *Littorina saxatilis* var. *groenlandica*, and *Balanus balanoides*, since they are nowhere known to occur sublittorally without also being found between tide marks as in the case of *Mytilus*, e.g. in the northernmost N.W. Greenland and in Novaja Zemlja. As shown above *Littorina* is most significant when the limit is not very distinct (as on the E. coast of Greenland). It has also been shown that the limit of the arctic to some extent coincide in the littoral and sublittoral zone.

This also is in favour of the delimitation of the subarctic region which I made using the simultaneous occurrence of *Pseudalibrotus littoralis*, *Mysis oculata* and specific littoral fauna. These boundaries in

broad features coincide with those commonly acknowledged for the sublittoral e.g. in Iceland, Northern Norway, and in the Bering strait. (For references see i.a. BROCH 1937, DONS 1934—37, EKMAN 1935, SCHENCK and KEEN 1936, SPÄRCK 1937, THORSON 1936, p. 122). It seems reasonable in our present state of knowledge not to attach too much importance to the boundaries, as STEVEN 1938 does, when, regarding my statement he writes: "Thus for the distinction to have any significance it is necessary to show that the southern limits of *Mysis oculata* and *Pseudalibrotus* more or less coincide throughout the world and the same of the northern limits of *Balanus balanoides* and the molluscs to which MADSEN referred". Further, in his summary (p. 69) he states: "The usefulness of delimiting a subarctic area in the littoral, as recommended by MADSEN (1936) is discussed. It is concluded that in view of the wide distribution of the majority of the species concerned, such a zoogeographical division is without value, unless it can be restated in physiological (climatic) terms".

In the first place this criticism seems to me to apply to all the accepted zoogeographical delimitations. Secondly it should be remembered that the subarctic region is a pronounced transition area. Thirdly I should like to draw attention to the evident, although not exactly known, connection with sea currents (strongly emphazised by DERJUGIN 1928 among others).

Great differences within the subarctic region are foreshadowing the possibilities for a subdivision in the future. In this respect I draw attention to the bare zone occurring not only in the arctic but also in many subarctic regions such as E. Greenland, Spitzbergen, and Waigatsch south of Novaja Zemlja (see above p. 4 and STRELNIKOV 1929b).

Since my survey in 1936 I have found in the literature fresh information concerning the delimitation of the littoral zone; on p. 68 I drew the eastern boundary of the subarctic region in Northern Russia at Tscheschskaja Guba according to BROTZKY and ZENKEWITSCH's (1932) statement that *Balanus balanoides* occurs here, "or possibly a little farther east, since GURJANOVA 1932, p. 182, mentions *B. balanoides* from the Kara Sea, but without indicating the locality". Later BROCH 1936 examined BROTZKY and ZENKEWITSCH's specimens and they all proved to be *Balanus crenatus*. He comes to the conclusion that "*Balanus balanoides*—probably has its easternmost border towards the Arctic somewhere along the Murman coast." Nevertheless the observations of STRELNIKOV 1929a extend the eastern boundary of the subarctic littoral to the Varnek Bay on the south coast of Vaigatsch, since from here he records *Littorina saxatilis*. He also mentions *Balanus balanoides*. Though according to the above it seems reasonable to consider this statement with a certain scepticism, it must be admitted that TARASOV

(1937, p. 53) examining littoral material collected later comes to the same conclusion as STRELNIKOV. The latter author and TARASOV (*l. c.*) maintain that naupliae of *B. balanoides* at times can penetrate into the southern part of the Kara Sea, viz. the Baidarata Bay and here begin the development of the early fixed stages. If it really is *B. balanoides*, such a short lived growth is not improbable, since a constant current runs through the Yugorsky Shar (MAXIMOV 1938). However, a definite decision can only be made in the future. At any rate the greater part of the littoral of the Kara Sea is purely arctic as shown by STRELNIKOV's papers, and confirmed by BIRULAS investigations (1937), since he (p. 703) stresses the fact that a special littoral fauna is absent from the Kara Bay. The same is the case in the Matotschkin Shar and all along the West coast of Novaja Zemlja (GURJANOVA, SACHS and USCHAKOV 1925). But sublittorally *Mytilus edulis* is found along the southern half of the West coast of Novaja Zemlja and in the Matotschkin and the Yugor Shar. (GRIEG 1924, STRELNIKOV 1929a, MESSJATZEW 1931).

My supposition that Jan Mayen belongs to the arctic region (p. 67) seems strengthened by the paper of PARAT and DEVILLERS 1936, who found the sublittoral fauna in complete accord with that of E. Greenland.

On the American East coast DAVIS 1936 extends our knowledge of the regions so much that we can say that so far north as 60°20′ N., *i.e.* at Akpatok Island in Ungava Bay on the North coast of Labrador, we are in the subarctic region, since *Littorina saxatilis* occurs. Curiously enough *Balanus balanoides* does not seem to have been found. The supralittoral zone shows great similarities with that of E. Greenland through the occurrence of the specific littoral species *Hypogastrura viatica*, *Archisotoma besselsi*, *Molgus littoralis* and *Fucellia ariciiformis*. Even the only spider found, *Erigone tirolensis* I have found also in East Greenland. PILSBRY 1916 mentions Nain on the East coast of Labrador (about 56° N.) as the northernmost known locality of *Bal. balanoides*. TARASOV 1937 gives Cumberland Sound on Baffinland (about 66° N.) as the northernmost locality, but without giving any authority for this statement.

As mentioned above the paper by SCHENCK and KEEN supports the limit for the subarctic region drawn by me on the East coast of the Bering Strait. The conditions on the West coast have been incompletely investigated. But according to the conditions in the sublittoral (BROCH 1936b, 1937, EKMAN 1935, p. 243, GURJANOVA 1936), one should expect that the subarctic region there extends farther south, since in the sublittoral this is evidently the case, comprising Kamtsjatka and the Okotsk Sea. AURIVILIUS 1887, p. 325, stated that *Littorina saxatilis* var. *groenlandica* occurs on Bering Island. So long, however, as the interrelations between *Littorina saxatilis* and *L. sitchana*, also mentioned

from Bering Island (GURJANOVA 1935) are not quite clear (DALL 1921), nothing definite can be concluded. The papers dealing with the littoral of the east coast of Kamtsjatka (POPOV 1935) and the Commandora Islands (GURJANOVA *l. c.*) show a comparatively rich littoral fauna —especially rich in the Commandora Islands—with a distinct boreal stamp, without any evidence of arctic influence. Round the Commandora Islands the sea only seldom freezes, and even in the spring the salinity of the water seldom goes below 32 $^0/_{00}$. On rocky shores the very rich fauna (p. 69) consists of bryozoans, sponges, actinians, ascidians, various polychaetes, chitons, gastropods, a large number of crustaceans, among them several species of *Pagurus*. Of special interest are *Mytilus edulis*, *Littorina sitchana* and *Semibalanus cariosus*, the latter seemingly here taking the place of *Balanus balanoides*. The algal flora is also rich. On the sandy shores are several burrowing mussels (species of *Spisula*, *Siliqua* and *Tellina*). In contradistinction to the conditions on Kamtsjatka the fauna consists of a number of warm water species also living in the Aleutians and California. The fauna in every respect is richer than on the Murman coast (see GURJANOVA, SACHS and USCHAKOV 1930). Also the supralittoral, with a well developed *Orchestia*-community with a rich fauna also of isopods, pseudoscorpions spiders, millipedes, mites, and machilids and the shore flora (p. 511) is equally or better developed than in boreal regions in Europe (cf. H. MADSEN 1936, p. 69).

Notes on the Biology of *Balanus balanoides* and *Mytilus edulis*.

STEVEN 1938, p. 64, writes upon *Balanus*: "The question is whether individuals survive the winter frozen in the ice foot, or whether the whole zone is colonized afresh each summer. There appears to be no direct observation on this point, or on the resistance of *Balanus* to freezing, but certain features noticed during the collecting period (July) gives reason to believe that the latter is the case. In the first place all the individuals were small, those on the more exposed places especially so, and there was a great deal of spat, freshly settled. That growth during the short summer period is extremely rapid is shown by the enormous quantities of shed limbs, which floated on the edge of each flood tide. On the other hand occasional specimens occurred in exceptionally sheltered situations, ..., which were a good deal larger than the average. These may well be survivors from the year before.——It is therefore suggested that as a whole the zone occupied by the ice foot is recolonized each spring by the brood of those individuals which survive round about low water springs and those few occupy especially sheltered positions", (italicized by me).

In the first place, the limbs shed by no means prove a rapid growth, but only that casting of the skin occurred at the time of observation. It seems also improbable that an animal with a boreal distribution should grow exceedingly rapidly just in the northern part of its area of distribution. Even the contemporaneous occurrence of small individuals and of spat so early in the season as July proves that the small individuals are from the year before. Unfortunately STEVEN does not give the size of any of the animals, but only states that they are smaller than British specimens. With the purpose of clearing the subject I have measured the lengths of some specimens from the Godthaab expedition, collected in Egedesminde August 10th, 1928, (systematically worked up by STEPHENSEN 1936, now in the collections of the Zoological Museum in Copenhagen), resulting in the curve of fig. 2. The animals in the two first peaks were not mature, as were the rest of them. It may be doubted how many peaks are represented in the latter part of the curve. But a comparison of the material collected by SALOMONSEN, July 10th, 1936, showed that it seems reasonable to make allowance for two, the more so as the material collected by BERTELSEN (1937, p. 17) June 21st, 1935, is distributed about the same figures as that of SALOMONSEN, viz. 2 specimens 12 mm, 1 specimen each on 13, 14 and 18 mm. Probably of the peaks in the curve the first represents spat settled in the same year, the next the one year group or probably also the two year group, since in boreal regions the growth in the third year is very inconsiderable according to the curves of HATTON 1938. As in boreal regions they probably first become mature in the second year, I should think that STEVEN's above mentioned small individuals really contain 2 size groups. The fourth peak represents the individuals in more favourable places, possibly representing several years, this no doubt being the case with the isolated specimens of 23 and 24 mm. MOORE 1934 for the boreal region showed that *Balanus* in the upper part of the littoral zone can attain an age of at least 5 years. It is interesting to note that VANHÖFFEN (p. 210) notes a size of 23 mm for individuals found in the Umanak district.

Balanus balanoides in the southern part of W. Greenland must be supposed to spawn early in the summer and to be sexually ripe in August, since in this month the penis is well developed, whereas this is not the case in July and September, judging from the somewhat sparse material in the Zoological Museum, since none contained nauplii during these months. On the other hand, the specimens from Prøven, of July 10th, 1936, contained nauplii, indicating the very reasonable possibility that the species here in its northernmost locality spats somewhat later.

After all the odds are that *Balanus balanoides* in these regions can

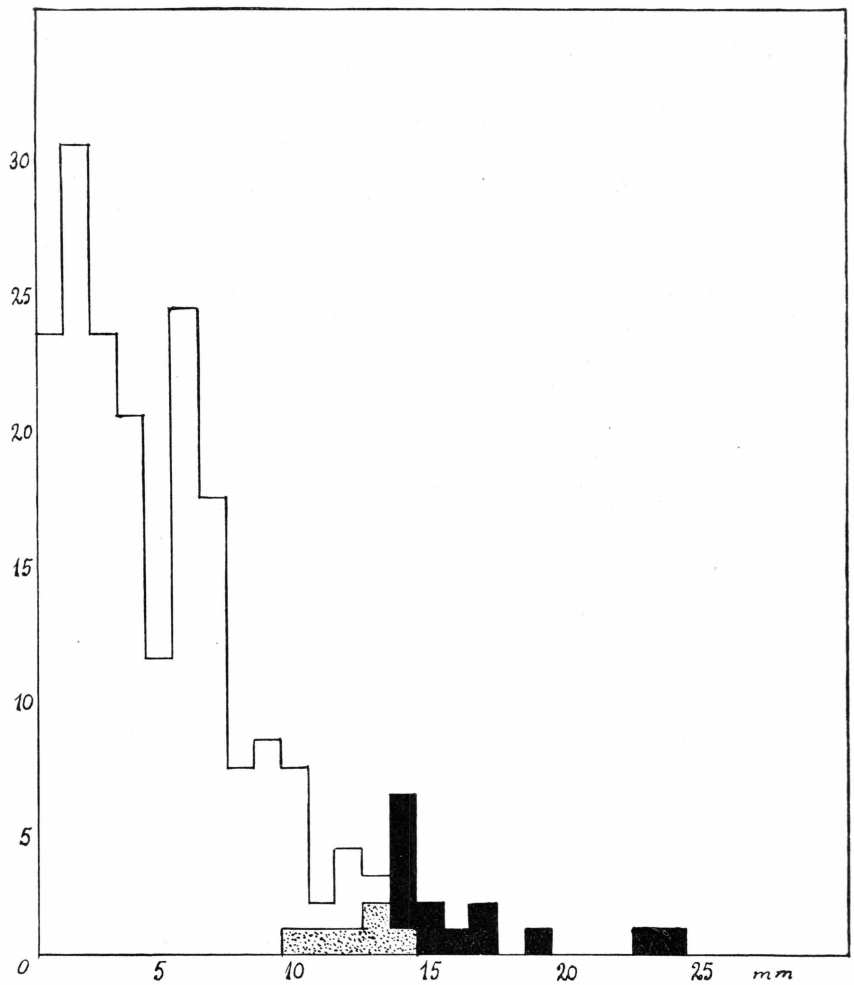

Fig. 2. Size curves of *Balanus balanoides*. White area shows specimens from Egedesminde. Black areas specimens from Prøven. Overlapping areas are dotted. For further explanation see the text.

endure being frozen in the ice during the winter, which they cannot in boreal regions (cf. H. MADSEN 1936, p. 51). But it must be admitted that the solution would be best obtained through protracted observations on the spot[1]).

This to some extent is also true of the problems concerning *Mytilus*. It has, however, been possible to answer some of the questions formulated by me (*l. c.* p. 51). AD. S. JENSEN 1905, p. 325, states that in Ammagssalik the natives take *Mytilus* through holes and cracks in

[1]) Concerning the quantitative occurrence of *Balanus* in the Amerdloq fjord, see p. 11.

the ice in the spring. I supposed (1936, *l. c.*) that these mussels were dead because they had been frozen in the ice. To this BERTELSEN 1937, p. 16, rightly replies that it probably was through tidal cracks that the Greenlanders caught their mussels. He made some observations in the locality "Strømstedet", where the mussels were found in a very shallow sound, only half a meter below low-water, under such conditions that they could not get away. According to the observations on the resistance of *Mytilus* to cold, also cited by me (*l. c.*) he concludes that the tidal currents must be able to prevent the sound from freezing. This may be so. But the conditions under which *Mytilus* was found in Upernavik (p. 5) prove that *Mytilus* in these northern regions can survive being frozen. Quite decisive in this respect is in my opinion the find of *Mytilus* on the quite shallow rock pool. At the same time they do not all come unhurt through the winter, since many dead animals were found, also in the littoral zone proper. If the supposition of the mortality of the mussels in the tidal zone, which I set forth, does not prove to be correct, my supposition that the size attained by the mussels might be taken as an expression of the growth of one year also falls to the ground. A glance at the curve in fig. 3 evidently shows that the mussel lives several years in the littoral, which could already have been derived from the fact that the species attains a length of 84 mm at Ammagssalik (AD. S. JENSEN 1905), thus exceeding the largest specimens found on the N.W. coast by 12 mm. The growth of *Mytilus* can vary much according to its surroundings, and even supposing the most rapid yearly growth known, about 25 mm (FIELD 1922, p. 200) the largest specimens must be several years old, and *Mytilus* in these regions probably does not enjoy ideal conditions. A fairly common average is about 10—15 mm (FIELD *l. c.*). The first peak in the curve evidently represents the spat from the same year, the average growth up to that time being 8 mm. Even if supposing that this average is continued there must be mussels of an age of at any rate seven years, and probably even older. Perhaps the 17—18 concentric furrows, which AD. S. JENSEN 1905 counted on a specimen of 84 mm, really represent years? The youngest specimen found in Upernavik evidently must be at least one year old. This fact, I suppose, can only be explained by presuming that *Mytilus* does not spawn every year, at any rate in Upernavik.

The eggs (already developed in individuals in their first year) presented a distinct nucleus, but even in the specimens collected at the latest date (August 22nd) the eggs did not lie loose and so apparently would not be shed in the near future. This can be connected in the most interesting manner with a great maximum of mussel larvae setting in October (and already falling during November) in the Umanak district (VANHÖFFEN 1897, p. 288). Almost the only mussel with pelagic larvae

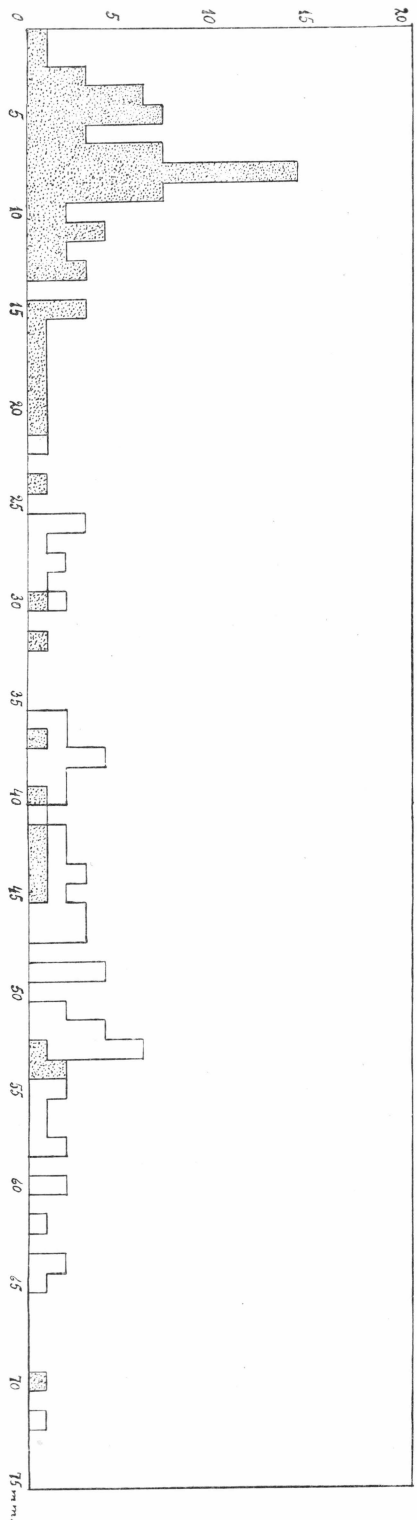

Fig. 3. Size curves of specimens of *Mytilus edulis* from Prøven (dotted) and Upernavik (white).

which is of importance in this region is *Mytilus* (cf. THORSON 1936). If this is correct, there is agreement with the results obtained by RUNNSTRÖM in 1927 and 1929. In the Mediterranean the spawning time extends over 5—6 months (January—February to the middle of June), on the Norwegian coast (Bergen) 4 months (March to June), here hardly 2 months (October to November).

In the Mediterranean *Mytilus edulis* in the form *galloprovincialis* has 8° as its lower temperature limit for normal development; in Norway (Herdla) the corresponding limit is 4°. In N.W. Greenland the development is completed at a temperature at or somewhat (about 0.2°) below zero. (STADE 1897, p. 555). RUNNSTRÖM 1936, p. 33 f., is inclined to see a racial basis for these differences, although no experimental evidence has been given, but he draws the attention to various papers which seem to support this view.

All these questions can only be definitely decided through plankton studies and breeding experiments in Greenland. But the above may give some preliminary information.

Concerning the quantitative occurrence of *Mytilus edulis* in Amerdloq fjord see p. 11.

Corrections and Additional Remarks to my Paper 1936.

I have described the oligochaetes which are common almost everywhere in the littoral, as *Enchytraeus albidus* and *Lumbricillus lineatus*. Later Dr. L. CERNOSVITOV had the kindness to look at my preparations, and it turned out that all the specimens, although they varied considerably, could be identified as one species: *Lumbricillus* (*Pachydrilus*) *lineatus* (O. F. Müll.).

STEVEN 1938, p. 64, in discussing the possible vertical movements of the littoral fauna writes: "*Littorina* and the oligochaetes are capable of arriving there by independent movement after the ice has melted, though the latter may possibly survive the winter buried deep in the sand." In this connection it seems convenient to mention some direct observations. According to STEPHENSON *Lumbricillus crymodes* (1922, p. 1133) and *L. aegialites* (1925, p. 1302) both found on the shore in Spitzbergen (cf. H. MADSEN 1936, p. 62) are able to survive being frozen hard (1925, p. 1320). He supposes that oligochaeta hibernate as eggs, the adult animals dying off in the winter. This does not hold good of *Lumbricillus lineatus* in E. Greenland, since immediately after the snow had melted, I found individuals sexually mature and of considerable size. Also the fact that at the end of August, the frost already setting in, animals were found with feebly developed sexual organs, together with evidently quite young animals, showing that the animals hibernate,

although it cannot be denied that the eggs also hibernate. At any rate the animals do not wander.

For comparison with marine communities (see *e.g.* VIBE 1939, p. 34—35) I computed the number and weight per m^2 of the oligochaeta in the littoral meadows in Spitzbergen and E. Greenland (H. MADSEN 1936, p. 62). The figures were about 20,000, 20 g and about 12,000, 12 g respectively, thus not coming nearly up to the figures for the marine communities.

The amphipod common everywhere in the littoral, named by me *Gammarus wilkitzki?* (H. MADSEN 1936, p. 11, footnote), turned out to be *Gammarus locusta* (L.) *setosus* Dementieva (STEPHENSEN 1940, p. 321).

The following collembola were erroneously determined:

Hypogastrura longispina, p. 19, should be *H. armata* HAMMER 1938, p. 6.
Xenylla mucronata, p. 30, should be *X. humicola* HAMMER 1938, p. 10.

The new find of *Ågrenia bidenticulata* near the shore in northernmost E. Greenland (HAMMER 1938, p. 26) is very interesting, considering that the species occurs under similar conditions in Spitzbergen (cf. H. MADSEN 1936, p. 61). Another interesting new find, viz. of *Micralymma marinum* in the southern part of E. Greenland was recorded by HENRIKSEN in 1939 (p. 43).

LONGSTAFF 1932, shortly mentions a non-typical upper beach and the occurrence of *Zostera* near Kugssuk and TRAPNELL 1933 the littoral flora. They are given as supplements to my literature list 1936. Together with the last in the present paper, the list of ecological literature concerning the shore in arctic regions is regarded as almost complete.

Finally attention should be given to the coming volumes of the "Zoology of East Greenland".

Summary.

1) The littoral fauna of the two southernmost places investigated, viz. Prøven (72°25′ N.) and Upernavik (72°47′ N.) had an obvious boreal stamp, notably through the occurrence of *Littorina saxatilis* var. *groenlandica*, *Mytilus edulis*, *Jaera marina* and *Campanulina lacerata*. Prøven showed peculiar conditions notably through the frequent occurrence of sublittoral organisms such as *Acmaea testudinalis* and *Strongylocentrotus droebachiensis*. Here only *Balanus balanoides* was found. On the northernmost point, where a specific littoral fauna (of larger animals such as molluscs) was found, viz. Tasiusak (73°22′ N.), *Mytilus* was sublittoral. From 74° northward in 9 different localities inclusive the Thule colony (76°23′ N.) no specific littoral fauna was found.

2) New facts support the conclusion of my paper of 1936 that other causes than the specific littoral factors as ice, fresh water etc.

are decisive for the question whether a specific littoral fauna in a given geographical region actually is able to develop. This conclusion is drawn from the fact that in Scoresby Sound a littoral fauna is absent, in Upernavik it is present, both places having the same type of climate, and the specific littoral factors being determined through the climate. The greater weight of animals in the bottom samples south of the boundaries both on the E. and N.W. coast of Greenland and the coincidence of sublittoral and littoral boundaries indicate that they depend upon causes which have some connection with the productivity in the sea. The boundaries almost everywhere can be connected with the sea currents.

3) The boundary between the arctic and subarctic region (as defined by the present author 1936) in the littoral zone in N.W. Greenland lies about 73.5° N. The new information from the literature concerning the delimitation of the littoral zone in the arctic regions has been referred to. The literature given in my previous and present papers makes the list of ecological literature concerning the littoral fauna in arctic regions practically complete.

4) A most important new feature of the biology of *Balanus balanoides* and *Mytilus edulis* is brought out, viz. that they are found in W. Greenland to be able to survive being frozen in the ice; the littoral zone is therefore not recolonized each year as Steven (1938) supposes. It has been shown to be probable that *Balanus* spawns early in the summer and *Mytilus* in October.

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