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INVESTIGATIONS ON THE SHORE FAUNA
OF EAST GREENLAND WITH A SURVEY OF
THE SHORES OF OTHER ARCTIC REGIONS

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WITH 17 FIGURES IN THE TEXT

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PREFACE

On an expedition the fauna of the seashore is as a rule not much noticed, at any rate a complete survey of it is rarely taken. While the boreal and subarctic shore faunas have been comparatively well investigated, the available information of the arctic shore fauna is but sparse and mainly occurs as scattered notes in the literature, notably the systematic-zoogeographical literature.

On the arctic shore life-conditions are very severe, and for this reason alone a special interest attaches to the study of its fauna, despite, or possibly because of, its paucity of forms.

That it has been possible to carry through this work, is principally due to the helpfulness and courtesy shown me from a number of persons, whom I here tender my most cordial thanks. First, my thanks are due to the leader of the expedition, Dr. LAUGE KOCH, and to Professor AD. S. JENSEN, who enabled me to join the expedition, and who with never-failing patience and interest facilitated my work in every respect. Professor C. M. STEENBERG willingly placed his laboratory at my disposal. Dr. R. SPÄRCK, cand. mag. K. STEPHENSEN, and mag. sc. G. THORSON never tired of assisting me in difficult questions of literature, supplying me with information of different kinds, and have handed over to me various unpublished material. For the determination of the different species I am indebted to cand. mag. J. BRÆNDEGAARD (*Arachnida*), mag. sc. MARIE JØRGENSEN (*Acarina* and *Collembola*), Dr. R. SPÄRCK (*Diptera*), Professor O. STEINBÖCK (*Turbellaria*), cand. mag. K. STEPHENSEN (*Amphipoda*), mag. sc. H. THAMDRUP (*Molgus*), mag. sc. S. TUXEN (*Collembola*, *Micralymma*), and cand. mag. H. USSING (*Copepoda*).

Dr. M. DEGERBØL, Dr. K. L. HENRIKSEN, Dr. P. KRAMP, mag. sc. PFAFF, cand. mag. THOMSEN, and mag. sc. ELISE WESENBERG-LUND have supplied information about several special questions. The Geodetic Institute, Copenhagen, has kindly allowed me to reproduce some air-photos. Cand. mag. P. GELTING and mag. sc. SØREN LUND kindly supplied me with various botanical particulars. Finally Mr. FRIIS has translated the Russian literature for me.

I. INTRODUCTION

The investigations treated in this paper were made in the following localities:

- St. 1. Eskimonæs, Clavering Island, latitude $74^{\circ}05'$ N., near the Danish main station.
 - a) West Harbour (fig. 12, p. 36).
 - b) East Harbour (fig. 16, p. 40).
- St. 2. Cape Stosch, latitude c. $74^{\circ}04'$ N.
- St. 3. Nordfjord, Strindberg Land, near the Danish expedition house, latitude c. $73^{\circ}47'$ N. (see fig. 2, p. 15).
- St. 4. Dusén Fjord, Ymer Island, about 7 km from the head of the fjord, northern bank, latitude c. $73^{\circ}19'$ N. (see fig. 1, p. 6).
- St. 5. Solitærbugt, Ella Island, near the Danish main station, latitude c. $72^{\circ}54'$ N. (see fig. 5, p. 21).
- St. 6. Hurry Inlet, eastern bank opposite the Fame Islands, latitude c. $70^{\circ}49'$ N. (see fig. 7, p. 27).
- St. 7. Charcot Harbour, Milne Land, southern bank, latitude c. $70^{\circ}48'$ N. (see fig. 4, p. 17).
- St. 8. Danmark Island, northeastern end, latitude c. $70^{\circ}30'$ N. (see fig. 3, p. 16).
- St. 9. The bay west of Rödeö, Gaaseland, latitude c. $70^{\circ}29'$ N.

As will appear from the above list, the area treated in the present paper extends from latitude $74^{\circ}05'$ to $70^{\circ}29'$ N., but the essential points of the general conclusions may, for reasons to be discussed later (pp. 10, 12, and 43), be extended northward at any rate to c. $76^{\circ}47'$ N. lat. and southward to about 66° — 67° N. lat. This part of the East Greenland coast is of a highly varying character, comprising some of the largest fjord systems of the world. But although the shore here exhibits different and changing life conditions, its fauna and flora are very poor and uniform, even though they are well characterised.

The causes of the poor development of the littoral biocenoses



Fig. 1. Air-photograph of the head of Dusén Fjord (with station 4). It can be distinctly seen that sediment shores are only found near river mouths. In the background Franz Joseph Fjord. (Reproduced by permission of the Geodetic Institute, Copenhagen).

are partly ecological, partly zoogeographical. Some of these factors will be explained below.

In the tidal zone collections were made by means of a water racket; I stirred up the sea bottom and passed the racket through the muddy water (in principle the same method as is employed in MORTENSEN's detritus collector. The latter was used in a single locality, St. 4). In this way notably Crustaceans were collected. *Turbellaria* were collected by washing sand in a flat cup; in this way the animals were easily spotted and secured by means of a pipette. By washing sand and washed up algæ, *Oligochaeta*, *Collembola*, etc., were secured. Imagines of *Diptera* were collected by means of the air racket.

The *Oligochaeta* collected were preserved either in trichlorous acetum acid, which seems to have been effective (the finer histological details were not observed), or in formol. Next, the animals passed through absolute alcohol to creosote, in which they were excellently cleared, to be mounted finally in canada balsam as total preparations. The *Turbellaria* also were treated with trichlorous acetum acid, which in this case (according to Professor STEINBÖCK) was not very satisfactory. This liquid has previously been successfully used on *Turbellaria* (pelagic) (HOFKER).

II. DEFINITION OF THE TERM SHORE

By the shore is meant by most biologists that part of the land which is directly influenced by the sea, especially by its salinity. The shore falls into two main divisions, the littoral and the supralittoral region.

The littoral area is the zone which periodically, more or less regularly, is flooded by the sea and again laid bare. In seas with tide-water the low-water mark and the high-water mark during spring-tide form the boundary lines, while in seas with no tide the more irregular changes of level caused by the wind delimit the area. In its strictest sense this delimitation applies only to rock facies in absolutely sheltered localities (i. e. sheltered against the wind). If the coast is less sheltered, the boundaries shift upwards or downwards, especially on sediment facies. The littoral area will shift upwards partly on account of the waves, partly (on shores of sediment facies) on account of the capillary effect. Thus the upper boundary of the littoral region should be drawn where the substratum is permanently moistened by sea-water at the highest level of the sea. Downwards the shifting extends to the point to which the waves recede at the lowest water-level. Accordingly the boundary will occur at different levels for the epi-, hypo-, and endobioses (for these terms, see GISLÉN 1929—30 II, pp. 75 et seq.). It will also vary somewhat according to the season, etc.; a long period of calm weather on an unsheltered shore, for instance, may force it downwards.

As will be seen, this division presents rather sharp limits. A further subdivision of the littoral region, however, will be more difficult, since it will necessitate a distinction between shores with tide-water and shores with no tide-water, even though there may be some few points of contact.

A subdivision of the tidal shore has especially been made by the Frenchmen VAILLANT, PRUVOT, etc.; this subdivision has lately been employed by the Russians GURJANOWA, SACHS and USCHAKOW (1925) and in a number of later works.

The second main division of the shore, the supralittoral area, occurs, as indicated by the name, above the littoral, and its boundary landwards coincides with the appearance of the land vegetation. Frequently this boundary is not very well marked off.

Sometimes the supralittoral and the first horizon are comprised under the name upper beach.

The above account agrees in all essentials with that given by GISLÉN (1929—30, II, pp. 46 et seq.). In the same paper he gives an excellent historical account of the delimitation and conceptions of the littoral set forth by the various authors.

III. THE SHORE FAUNA OF EAST GREENLAND

A. Rock facies.

Only scattered observations were made of the life on rock facies, even though I noted certain characteristic features. The information about the algal vegetation is due to SØREN LUND, who in 1933 collected algæ within the district in question (the material is not yet worked up), and to the available literature about the algal flora of East Greenland (JONSSON 1911, ROSENVINGE 1910 and 1933).

As regards the supralittoral zone it can only be stated that it is covered with *Verrucaria*-like lichens, and that the mite *Molgus littoralis* (L.) occurs here.

It is impossible, on the basis of the available investigations, to distinguish between the various horizons; hence in the following I shall chiefly give a characterisation of the tidal zone as a whole.

In the upper part of the tidal zone the dominant algæ are *Calothrix scopulorum* (WEB. et MOHR), *Pylaiella littoralis* KJELLM., and *Rhodochorton rothii* (TURT.). In the lower part of the tidal zone *Fucus inflatus* L. occurred. It is the only *Fucus* species that has been observed in the district from Danmarkshavn to Kangerdlugssuak (68°30' N. lat.), while south of this point *Fucus vesiculosus* L. occurs in the tidal zone, in a belt above *Fucus inflatus*. These two species are the only *Fucacea* that were found in the littoral zone.

In addition to these two dominating algæ, various other algæ occur in greater or smaller numbers in the tidal zone of the district in question.

As will be seen, a fairly rich littoral flora has developed, in contrast to that of the north coast of Asia mentioned by KJELLMAN (1883).

If now we turn to animal life, we shall find it strikingly poor, especially on vertical cliffs. The algal vegetation is very short, only a few centimetres high, and tomentose. Dominant here are both *Enchytræus albidus* HENLE and *Lumbricillus lineatus* (O. F. MÜLLER). Further the Oribatide *Ameronothrus lineatus* (THORELL) var. *nigrofemoratus* TRÄGÅRDH. The latter, it is true, was only found in a single specimen (at Eskimo-

næs, St. 1b, in company with the two above-mentioned species); but it was found on vertical cliffs without afflux from suitable localities (littoral meadows) in such a way that its presence was hardly accidental. Moreover, it has been found in corresponding localities both on Spitsbergen (THORELL 1872 [according to SIG THOR 1930, p. 5]) and on the shores of Ireland (HALBERT 1915 and 1920). No other species were observed by me, doubtless on account of my few observations. In all probability the *Harpacticoidae* *Zaus spinatus* GOODSIR, *Tisbe furcata* (BAIRD), and *Laophonte strömi* (BAIRD) will be found in company with the above-mentioned species. I found these species in the tidal zone of the sedimentary shore, but in the remaining part of their area of distribution they are mostly associated with the algal vegetation, and therefore it seems justifiable to mention them here. The same applies to *Monoecelis fucsa* ØRSTED, which in other parts of its area have mostly been taken as epibiotic on stones and rocks among *Mytilus* and *Balanus*, etc.

With the tidal zone on rock facies, finally, is associated *Gammarus wilkitzki* (BIRULA)?¹⁾

In addition to the forms mentioned above, a number of the more mobile sublittoral forms of Amphipoda may on rare occasions be met with more casually, for instance *Paroediceros lynceus* M. SARS, *Atylus carinatus* I. C. FABR., and *Gammaracanthus loricatus* (SABINE), especially the latter. This has some connection with the fact that like *Gammarus wilkitzki*? it is particularly adapted to endure fresh water. On the west coast of Greenland it was once taken at a river mouth. This species has also formed the variety *lacustris* G. O. SARS (*syn. relictus* G. O. SARS), which occurs in the large Scandinavian and Russian lakes. Something similar applies to *Mysis oculata* (O. FABR.); this species is found in the tidal zone and is the ancestral form of a relict species occurring in fresh water, viz. *Mysis relicta* (LOVÉN), which in addition to the places inhabited by *G. l. var. lacustris* is also found in northern Germany, America, and Spitsbergen.

In this connection it will further seem natural to mention three species of *Harpacticoida*. I did not find them myself, but they have previously been recorded from East Greenland (STEPHENSEN 1913,

¹⁾ According to K. STEPHENSEN, the *Gammarus* species found in the material is probably *wilkitzki* (BIRULA) (GURJANOWA 1930), which is otherwise known from the Bering Sea. From this locality two other *Gammarus* species are described, though very deficiently, viz. *G. locusta* var. *sovinski* GURJANOWA and *G. setosus* (DEMENTIEVA, Transas, State Oceanogr. Inst., Vol. 1 Nos. 2—3, pp. 65—82. Moscow 1931). Accordingly no certain identification of the species can be made until further information or material is at hand. Finally it may be mentioned that probably all the specimens of "*Gammarus locusta*" from Greenland will turn out to belong to the same form as that found by me. Random samples, taken by STEPHENSEN, seem to support this conjecture.

pp. 327, 328, 333); they are *Laophonte curticauda* BOECK, *Harpacticus chelifera* O. F. MÜLL., and *Harpacticus gracilis* CLAUS. The latter, it is true, has not been found near land, but all three species occur as littoral forms elsewhere, though they may also be met with in somewhat deeper water.

Various *Polychaeta* may occasionally be found.

On further investigation it will no doubt be possible to make a more detailed division of the algal vegetation on the basis of the external factors, more especially the degree of shelter (against waves and ice) prevailing in a certain locality, but also the distribution in the various horizons. However, certain broad features are conspicuous even now. In no place, I suppose, will littoral algæ be absent on account of the action of the waves, which, as already mentioned, will hardly be sufficiently strong anywhere to prevent their occurrence. Consequently the littoral fauna will not be absent either, since it is associated with the dense covering of algæ. The observations at St. 1b mentioned above (p. 10) were made on rocks which, considering the East Greenland conditions, might be subjected to rather a heavy surf. The ice, however, may scour away the algæ from the rock surfaces and thus destroy the littoral fauna, too, whereas in the rock crevices both will survive.

A comparison with the littoral of the remaining part of Greenland.

In future investigations some more species of *Oligochaeta*, *Copepoda*, etc. may possibly be found within the tidal zone (no doubt *Nematoda* and *Halacarida* also), but this will not cause essential changes in the picture of the littoral fauna, which is especially distinguished by the lack of a number of forms characteristic of the littoral in other, notably more southerly, latitudes. The forms of particular interest in this connection are *Mytilus edulis* L., *Littorina saxatilis* (OLIVI) var. *groenlandica* MENCKE, *Homalogyra atomus* (PHILIPPI), *Balanus balanoides* (L.), and *Jaera marina* (O. FABR.), since they are known with certainty to occur on the east coast of Greenland as far as, but not north of, about 66°—67° N. lat. The same applies to *Ascophyllum nodosum* (L.) and *Rhodymenia palmata* (L.) (ROSENVINGE 1933). In addition there are some forms that have been found in Greenland, but so far not on the east coast (no doubt partly owing to lack of investigations), viz. all the littoral *Hydroida*, of which five species are recorded from Greenland, partly molluscs such as *Littorina palliata* SAY, *Purpura lapillus* (L.), and *Skeneopsis planorbis* (O. FABRICIUS), and various Nemertines. Finally, there are some animals which in addition to the west coast and the southern part of the east coast, also inhabit our district, but never the tidal zone. An example is *Onoba striata* MONTAGU,

which has been collected in the tidal zone near Ammagssalik, as also on the west coast¹⁾.

Similar observations have been made regarding a number of animal forms occurring in other facies (see p. 43).

This problem of limits will be treated in greater detail below, after the description of the other forms occurring in the littoral region.

B. Sediment facies.

This facies falls into several groups according to the fineness of the material, and in boreal regions with a rich littoral life distinct differences can be observed in the distribution of the organisms on gravel, sand, sandy clay, clay, etc. The area investigated, however, does not present such great possibilities of variation. The facies forms are just as numerous as in other places, for instance in Kola Fjord, but they are inhabited by a much smaller number of organisms, even though there are some differences in their distribution.

On account of the conditions within the area investigated it will be most convenient to treat the material under three main groups, viz. 1) the tidal zone proper, 2) the upper beach, and 3) lagoons and littoral meadows. The tidal zone proper comprises the two lowermost littoral horizons, while the upper horizon, especially the bank of sea-weed, belongs to the upper beach, which, as stated above, denotes the uppermost littoral horizon and the supralittoral area, here limited to the sand and gravel shore. Most of the lagoons and portions of the littoral meadows occur in the littoral area, while some of the littoral meadows are supralittoral and influenced by fresh water. The same applies to some lagoons.

Over wide stretches of the area investigated sediment facies occur only in association with river estuaries, often such as dry up in the summer. This is beautifully illustrated in fig. 1. Similar conditions are encountered in most places within the Franz Joseph Fjord area, for instance in all the localities investigated as well as in many places only observed from the ship. This view is supported by the information supplied by the botanist THORV. SØRENSEN, who investigated several localities here without finding a single example of a well developed littoral meadow. In the district round Clavering Island, but especially in certain parts of Scoresby Sound, there are several exceptions from the rule. This structure of the shore has possibly some connection with the sparse occurrence of the diluvial formations especially in the Franz Joseph Fjord district.

The shore as a whole has originated by a cooperation of sea and fresh

¹⁾ Found by me on *Fucus* in the Arctic Herbarium of the Botanical Museum in Copenhagen. (Collected at Ammagssalik).

water, the tidal zone and the upper beach being the work of the sea (though the fresh water has supplied the material), while the substrata of the lagoons and the littoral meadows are mainly fresh-water deposits, bounded to seaward by the marine deposits.

1. The Tidal Zone Proper.

This zone can be subdivided into three zones, 1) the ordinary gravel and sand shore, 2) the clay shore, and 3) the clay and sand flats formed off river estuaries (see fig. 2, p. 15). They are all characterised by a very poor animal life, as is on the whole the case with the littoral life. Plants are practically absent, only the coarse gravel at the river mouths may harbour a poorly developed epiflora of small green algæ (*Enteromorpha*?)

a) Gravel and sand strand.

The most conspicuous animals living here are the Amphipoda *Gammarus wilkitzki*? and *Pseudalibrotus littoralis* (KRÖYER). The former is present almost everywhere in the littoral area; as mentioned above it occurs on rock facies also, and is a frequent inhabitant of the lagoons influenced by salt water, etc. This is connected with the fact that *Gammarus* is rather independent of the substratum. It does not burrow at all, at most it seeks cover below a stone or accumulated algæ. *Pseudalibrotus*, however, is the typical burrowing form. Personally I found it in sand and clay only, and only in the Scoresby Sound district, but it is doubtless distributed throughout the area, since it has been found near Danmarkshavn, partly in the littoral area, partly in very shallow water on the same kind of bottom (STEPHENSEN 1912). The reason why I failed to find it in the Franz Joseph Fjord and the Clavering Island districts may be that it does not invade the littoral area till late in the year; I did not collect it myself till after the middle of August. The specimens from Danmarkshavn were all secured at the end of that month. But the chief reason may have been that the bottom was unsuitable in the particular localities. The fact that I did not find it at Danmark Island, St. 8, despite a zealous search, also speaks in favour of this supposition. In this place the bottom was gravelly, stony, with but scattered patches of sand, while the other localities had a purely sandy or (St. 7) clayey bottom.

In company with these animals there are other animals which lead a more unnoticed life and require one's full attention to be discovered, viz. small crustaceans, *Harpacticoida*, as well as various worms.

Three species of *Harpacticoida* were met with, two of which have been mentioned above (p. 11), viz. *Zaus spinatus*, *Tisbe furcata*, and *Harpacticus uniremis* KRÖYER. They were only found in some few localities, it is true, but there was neither time nor opportunity to collect *Copepoda* in other places. However, they are all forms which are mostly

found in the littoral area or in very shallow water, even though they are recorded as pelagic, too. According to USSING, *Tisbe furcata* has even been collected as pelagic in East Greenland. Thus none of the species are exclusively littoral, they are also sublittoral forms, though the two *Amphipoda* have their main distribution in the littoral region. The worms, partly *Oligochaeta* (of which only *Enchytræus albidus* was found), partly *Turbellaria*, are more especially littoral animals. The *Oligochaeta*



HOLGER MADSEN photo.

Fig. 2. Nordfjord, St. 3, August 7, 1933. In the foreground the tidal zone and the upper beach. Note the sandy patches in the tidal zone in which *Notokaryoplana arctica* lived. In the middle of the picture the large sand flats extend in front of the river. — In the background Waltershausen Glacier.

are small and rather few in number. No doubt they have their main distribution in the areas to be treated later.

Thus only the *Turbellaria* remain as wholly littoral animals in the zone in question. They comprise two species, *Notokaryoplana arctica* nov. gen. & sp. STEINBÖCK and *Monocelis fusca* ÖRSTED. I only looked for these animals in the Franz Joseph Fjord and the Scoresby Sound districts, where, on the other hand, they were present in most localities. They both occurred on sand, no matter whether it formed patches in the gravel or built up the whole shore. Despite a careful search *Notokaryoplana* was found in two localities only. *Monocelis* was not found in three localities, namely stations 3, 7, and 8, all of which were much influenced by fresh water. Station 3 (see fig. 2) and station 7 are situated

very near the termini of large glaciers and at river mouths, which cause the surface water to be practically fresh; in the small bay, station 8, there was a considerable afflux of fresh water, partly from a small river, partly from a snow-patch (see fig. 3). *Notokaryoplana*, however, was found at St. 3 only and a single specimen at St. 4.

The animals mentioned above represent those that are fairly regularly met with on this type of shore. Quite exceptionally, as mentioned



HOLGER MADSEN photo.

Fig. 3. Northeastern end of Danmark Island, St. 8. August 23, 1933. In the foreground a perennial snow-patch, forming at its foot the lagoons described as type 8 (p. 35). The littoral meadow to the left, at the edge of a lagoon, is situated on the outskirts of the range of influence of the snow-patch. The upper beach, which like the tidal zone is very stony, extends as a light-coloured stripe across the picture.

A river debouches in the small bay at the back.

under the treatment of the rock facies, some of the more mobile sublittoral animals may be found here.

A somewhat richer animal life is harboured on the second subdivision, the clay shore.

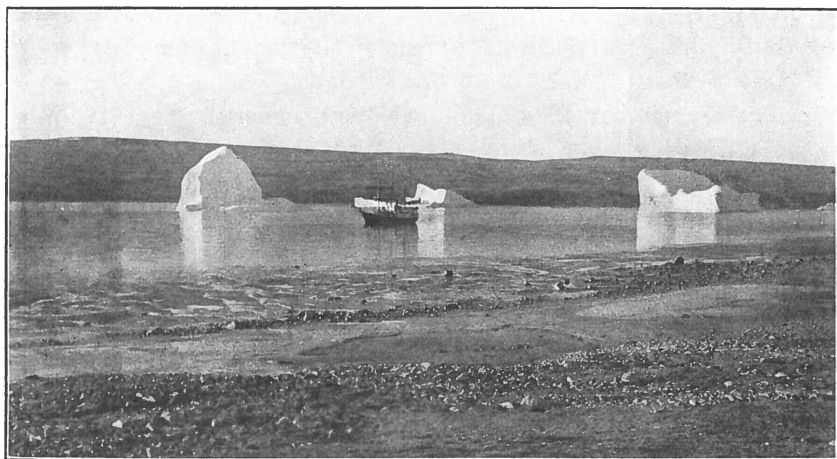
b) The clay shore.

I only observed this type of shore in one place, namely St. 7 (fig. 4). It is situated in a small cove, Charcot Harbour, in Milne Land. Streams of melt-water from a glacier which does not descend to the sea debouch at the head of this cove. These streams stir up the water and make it less

saline. Their influence can be traced right down to the bottom, which is covered everywhere by a *Portlandia arctica* community (THORSON 1934, p. 43, pl. IV).

The tidal zone in this place has a peculiar appearance. The slope is inconsiderable, so that at low-water a very broad belt is exposed, which is covered with a layer, about 20 cm thick, of viscous, greasy clay. This clay is so fine that it cannot be retained in a racket which catches *Copepoda*, *Nematoda*, etc. The upper part of the tidal zone contains a sandy belt, in which, as mentioned above, no *Turbellaria* were found.

Several animals were found in the clayey tidal belt. These were the species usually met with, *Gammarus wilkitzki*? and *Pseudalibrotus*



HOLGER MADSEN photo.

Fig. 4. Charcot Harbour, St. 7, August 24, 1933. The clayey tidal zone. In the foreground the lagoon mentioned as type 7 (p. 33). In the fjord, the "Godthaab".

littoralis, and in addition *Mysis oculata* (O. FABR.). The latter, however, is no strictly littoral form, though it is frequently found in this zone; it also extends to the sublittoral zone and may be found as pelagic. Of special interest is the occurrence of the Harpacticoid *Bradya typica* BOECK, a form that is associated with a clayey bottom, but which mostly occurs in somewhat deeper water, 20—60 m (SARS V, 1911, p. 46). Of Crustaceans some Ostracodes not closely identified were found. Various species of worms were present in large numbers, thus *Nematoda* (not more precisely identified), small individuals of *Enchytræus albidus*, and *Dinophilus (gigas WELDON?)*. Of special interest is the presence of two species of *Turbellaria*, *Protomacrostomum groenlandicum* nov. gen. & sp. STEINBÖCK and *Proschizorhynchus* sp. The latter is of great interest, since it belongs to a family, the *Schizorhynchidae*, whose species are all associated with sand and mostly occur in the tidal zone.

Finally some infusoria were found, which were not further identified.

A much poorer animal life is encountered on the clay and sand flats formed off the river mouths and in direct association with the latter.

c) Clay and sand flats at river mouths.

These flats may often occupy considerable areas, but are in some cases difficult to distinguish from certain forms of lagoons (see p. 28). Observations were made especially at three stations, Sts. 1, 3, and 5. The flats were most strongly developed at St. 3 (see fig. 2). They are exposed at low tide, when the water of the rivers will move through grooves in the flats, which are chiefly made up of gravel and sand. At high-water they are flooded by comparatively saline water, which, however, is largely mixed with the fresh water from the rivers. Accordingly the salinity varies greatly. Here, of course, the usual *Gammarus wilkitzki*? as also *Enchytræus albidus* were observed.

At St. 1a similar flats had developed, consisting chiefly of sand but covered with a layer of clay about 2 cm thick. It harboured a richer fauna, which in its composition showed association with the fauna of the lagoons, including various *Diptera* larvæ, a fly larva, in all probability *Fucellia ariciformis* HOLMGR. and Chironomid larvæ, *Smittia* sp., probably *extrema* (HOLMGR.), and *Orthocladus* sp. In the same current holes in the clay, with washed down detritus (of land plants), in which the above-mentioned animals were found, there further occurred *Lumbricillus lineatus*, *Enchytræus albidus*, and *Nematoda*. Finally, *Infusoria* and *Flagellates* should be mentioned.

It was strange to find here small fish larvæ, *Cottus* sp., about 1½ cm long, since I investigated these flats at a time (June 25, 1933) when the ice had not yet broken up. Off the river mouth only was there a little open water, which, however, was completely fresh, so that none of the animals had yet been in contact with the salt water. When the flats were exposed at low-water, various *Podura* jumped about here, and such might also be encountered on the surface of the water both above the flats and in the lagoons. However, these forms will be discussed in a subsequent chapter, since they should rather be referred to the fauna of the storm-shelf and the littoral meadows.

The reason why so comparatively rich an animal life was found at St. 1a is probably, as in the lagoons, the comparatively calm conditions prevailing there, as evidenced by the deposition of clay. The accumulation of detritus which may serve as food is probably also of importance. However, this deposition, too, is due to the calm weather conditions.

I was not the only being who was aware of the rich animal life on these flats, as I learned from numerous tracks in the clay and disturbances of the detrital accumulations. These were due to the small waders,

in the first place the ringed plover, *Charadrius hiaticula hiaticula* (L.) (according to B. LØPPENTHIN), and, especially in June, the sanderling *Crocetia alba* (PALL.), the turnstone *Arenaria interpres* (L.), and the dunlin *Calidris alpina arctica* (SCHIØL.). As is well known, none of these species is especially associated with the shore in East Greenland, more particularly none of them breed there; only the ringed plover is regularly met with on the shore, besides in many other localities, revelling in the large quantities of *Oligochaeta* that live in the aggregations of blue algæ in the lagoons. Other birds of common occurrence are the big glaucous gulls, *Larus hyperboreus* GUNN, which leave deep footprints in the lagoons in which the small *Cottus quadricornis* bustle about, further the barnacle goose (*Branta leucopsis* [BECHST.]), the pink-footed goose (*Anser brachyrhynchus* BAILL), which often, in addition to other grassy places, grazes off the closed *Puccinellia* littoral meadows. It is these animals that keep the vegetation quite low. (Nomenclature after LØPPENTHIN 1932).

2) The Upper Beach.

As mentioned above, the upper beach forms a combination of the uppermost littoral horizon and the supralittoral zone (in contradistinction to the littoral meadows and the lagoons).

a) The first littoral horizon. The uppermost littoral belt is mostly represented by a washed up bank of seaweed. In some cases this bank is entirely buried under gravel, and if so, the animal life has remained in the bank. If for some cause or other no algæ have been washed on to the shore, the characteristic animal life is almost entirely absent. This for instance was the case at St. 3, probably because here the sublittoral zone was greatly influenced by the proximity of the huge Waltershausen Glacier and the river draining it. Algæ were almost totally absent in the sublittoral zone in this place.

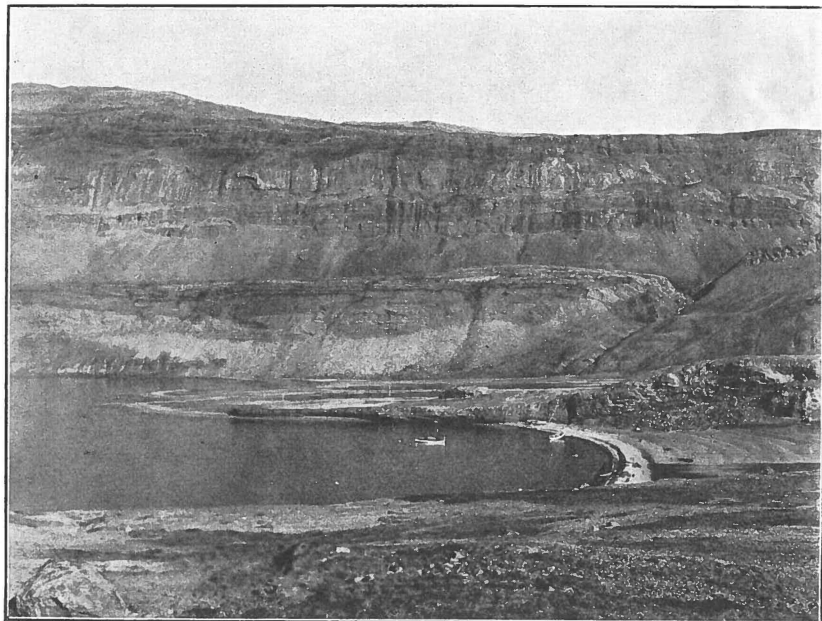
In a single locality, St. 1a, the first littoral horizon was represented by some clay flats inhabited by a rather rich animal life, especially *Collembola*, but in the composition of its fauna it showed close association with the fauna of the lagoons and the littoral meadows. As stated above, at the time of their investigation these areas had not yet been in contact with the sea water (the surface water of the sea being completely fresh). The animal most numerously represented was *Pseudisotoma sensibilis* (TULLB.). *Folsomia quadrioculata* (TULLB.) and *Hypogastrura viatica* (TULLB.) also were present in great quantities. Less numerous were *Hypogastrura longispina* (TULLB.) and *Trichoribates trimaculatus* (C. L. KOCH). No doubt it was a mere chance that I did not secure any *Archisotoma besselsi* (PACK.), since it was very common in all the other shore

localities investigated. Of the forms mentioned, only *Hypogastrura viatica* and *Archisotoma besselsi* can be considered shore forms. It is rather interesting that *Folsomia quadrioculata* and *Pseudisotoma* are animals characteristic of the banks of lakes, while *Hypogastrura longispina* is of common occurrence there. *Trichoribates*, however, is characteristic of the bogs, while it is rare on the banks of lakes (cf. MARIE JØRGENSEN 1934₁). There is no reason to assume that these animals have been washed out quite casually, for if so, I should have come across *Onychiurus sibiricus* (TULLB.) in one of my localities, since it is the commonest and most abundant animal in all the localities whose faunas have been studied by MARIE JØRGENSEN (1934₁). It is also of great interest that the two littoral forms mentioned above were not found in one of the same numerous samples apart from those collected by myself.

In this connection mention should be made of a peculiar locality observed at St. 2. Behind Cape Stosch, which consists of an aggregation of rocks, some extensive sand flats are found, which are probably flooded at spring-tide. White, shiny patches, due to precipitated salt, were visible from a great distance. These sand flats were very barren, with only occasional tufts of vegetation, chiefly *Salix arctica* PALL., *Dryas octopetala* L., and *Armeria vulgaris* WILLD. var. *sibirica* (TURCZ), but no trace of animals could be seen. I did not examine this locality very carefully for *Collembola*, but these as well as some *Oribatidae* would probably have been found in the plant tufts; but neither flies nor *Molgus* were observed, and no littoral meadows had developed. However, P. GELTING informs me that littoral meadows occur near Cape Stosch, but if so, this must be farther south. I investigated an area of a few kilometres of the shore east of the cape and the above-mentioned flats behind it. These extensive, salt-covered deserts had resulted from a union of a number of delta cones formed by some small rivers descending from the mountains behind the cape. Most of these rivers had dried up at the time of their investigation (July). The great paucity of life is presumably due to the fact that the whole area is ploughed up during the breaking up of the frost, which sets in very suddenly. HARTZ (1895, p. 153) mentions similar flats from the mouth of Schuchert River, which debouches in Nordøst Bay situated in Nordvest Fjord in the Scoresby Sound district.

Most frequently the uppermost littoral horizon occurs in the form of a more or less distinct bank of washed up seaweed. A single record of the zoological conditions of this zone in East Greenland is available in the literature, where *Enchytræus* sp., small black *Podura*, and small brown red-legged mites (young *Molgus*?) from the washed up algæ (Hekla Havn, Danmark Island, July 1892) are mentioned by HARTZ (1895, p. 262).

The most conspicuous animals are the *Oligochaeta*, principally *Enchytræus albidus*, which here attains its largest size, and in some localities I also noticed *Lumbricillus lineatus*. In company with these there occurred numerous *Podura*, first of all *Archisotoma besselsi* and *Hypogastrura viatica*, in a single locality (St. 5, see fig. 5) also *Sminthurinus concolor* (MEINERT). The latter is rather a ubiquitous form. In the same place were further found some *Parasitidae* (*Gamasidae*), unfortunately not identified. Some small, black spiders were seen crawling about



HOLGER MADSEN photo.

Fig. 5. Ella Island, Solitærbugt, St. 5, July 28, 1933. In the middle, beach with washed up algæ. Inside this a lagoon. In the background, river mouths with lagoons of different types (loc. 1, 2, and 3 situated in the eastern part). Looking approximately east.

pursuing the *Collembola*. The Araneida proved to be *Micryphantes nigripes* SIMON, which was the most frequent, and *Erigone arctica* WHITE. The former is a sand and gravel form, so its occurrence here is no mere chance. *Erigone arctica* is more hygrophilous.

Ameronothus lineatus var. *nigrofemoratus* may be supposed to occur here. But with my collecting methods I could not expect to find it. It is recorded from similar localities in Spitsbergen (SUMMERHAYES and ELTON).

Molpus littoralis also hunts in company with the spiders just mentioned; however, like the *Diptera* mentioned below, it also extends its domain to the supralittoral shore.

b) The supralittoral shore.

Botanically the supralittoral shore is very poorly equipped, as is the rule for sandy and especially gravelly shores. The most frequent plant, and the only specific shore plant, is *Honckenya peploides* (L.) ЕНДН., which was of common occurrence throughout the area, possibly somewhat more frequent at the outer coast than in the fjords. It may, however, be met with in the interior of the fjords also, since I observed it *i. a.* at St. 9, Gaaseland, the bay opposite Røde Ø (whence it is also recorded by HARTZ [1895, p. 143]), the interior of the Scoresby Sound fjord complex. In addition various other plants are frequently met with, nearly all of which are more or less coprophilous, and accordingly are especially found in regions abounding in birds, or near the old Eskimo house ruins. Very frequently the crowd of shore plants is recruited from coprophilous species in addition to specific species. This is probably due to the comparatively high content of salts (though of different kinds) found in these localities. Finally, in association with these, there occur some plants which must be considered to be sand plants. To this group belong such forms as for instance *Draba cinerea* ADAMS and *Armeria vulgaris* var. *sibirica*. Of more or less coprophilous species may be mentioned *Sedum roseum* (L.), which I observed in several localities as far towards the interior as St. 9, *Potentilla pulchella* R., BR., *Arnica alpina* (L.), *Matricaria inodora* L. var. *grandiflora* (HOOK) (decidedly coprophilous), and *Poa hartzi* (GDRG.) emend. TH. SØRENSEN (see GELTING 1934, p. 209), which may also appear as a dune plant.

In addition to what has been stated above, it is a common feature of all the above-mentioned plants that they are mostly associated with, or at any rate can endure, very dry soil.

Finally it may be briefly mentioned that within our area of East Greenland dunes may occur, partly in connection with the shore, partly independently of the latter. Personally, however, I observed none. The most detailed mention of these is made by HARTZ and KRUSE 1911 (p. 384 et seq.), who especially describe the locality Klitdalen (70°53' N. lat.).

The characteristic animal of the supralittoral shore is *Molgus littoralis*, which was found in great abundance in all the localities investigated. However, it is not absolutely associated with this zone, but may also be met with in the other zones of the shore (and even farther towards the interior of the country, independently of the shore), though it is less dominant there (see also TRÄGÅRD 1917).

About the middle of June (St. 1a and b) large numbers of *Molgus* egg capsules may be found below nearly every flat stone in this zone, and towards the end of the month these places teem with quite small red mites. Adult animals were not observed at this time, whereas later

in the season no young were to be found. Accordingly it must be assumed that *Molgus* winters in the egg state only.

In the same places, but also on the flotsam and following the receding water, swarms of flies were observed in favourable weather, viz. *Fucellia ariciformis* HOLMGR., whose larvæ occur on clay flats near river mouths and in lagoons. At any rate, I did not find them in other places. Thus it is a true shore form. However, this does not apply to the other flies found by me.

In this connection it may be mentioned that *Fucellia pictipennis* BECKER, which is known from Heklahavn and Danmarkshavn in East Greenland, has previously been found within the area investigated, though not by me, and *Scatophaga litorea* FALL. also is recorded (Røde Ø) (see HENRIKSEN and LUNDBECK 1918). Nothing at all is known of the biology of *Fucellia pictipennis*, so we do not even know whether or not it is a shore form. However, since this applies to most *Fucellia* species, I include it here. *Scatophaga litorea* is mostly, though not exclusively, a shore form. Nothing is stated about its mode of occurrence in East Greenland.

In the area treated here three species of *Chironomidae* also may be met with which have proved to be true shore forms, their larvæ being associated with lagoons and littoral meadows, and, as mentioned above, with littoral clay flats formed near river mouths. These are *Smittia (extrema)* [HOLMGR.]¹⁾, *Orthocladius decoratus* (HOLMGR), and *O. groenlandensis* GOETGHEBUER. It should be noted that the material contains two types of larvæ, no doubt representing these two species.

In two places, Sts. 2 and 5, I found *Ichneumonida* on the supra-littoral shore. It is no doubt by mere chance that they have been taken on the shore. Another *Ichneumonida*, *Phygadeuon cylindraceus* RUTHE was never met with by me, but it occurs as a shore form both in West Greenland and Iceland (parasitic on *Fucellia* chrysales), though not specifically. This, however, seems rather to be the case in Europe, where KROGERUS (1932, p. 127) regards it as a littoral, tychocenus form. In East Greenland it is recorded from Heklahavn, hatched from fly pupae; unfortunately, however, it is not known from which. No doubt it also occurs as a parasite on the *Fucellia* species within the area in question (HENRIKSEN and LUNDBECK 1917, p. 525).

Finally mention should be made of *Micralymma brevilingue* SCHIØDTE. In West Greenland this species has mostly been taken from the tidal zone in company with the larva, but it seems to be of common occurrence in nearly all kinds of damp localities. It has previously been found

¹⁾ Three species of *Smittia* are known from East Greenland (J. GOETGHEBUER 1933). Of these *Smittia extrema* HOLGR. has been found repeatedly on the shore, hence it may be concluded that the larvæ found belong to this species.

at Heklahavn, and is characterised as common, but nothing is stated about the kind of locality in which it grew. In a lagoon at St. 3 I found two specimens of a *Micralymma* sp., larvæ probably of *brevilingue*, but despite the most zealous search, also on Danmark Island, whence it is recorded as common, I failed to find it in any other place. Hence it may be inferred that it is no characteristic form on the shore. It may occasionally occur, but at any rate it is extremely rare.

It is an interesting fact that the above description applies to both sandy and gravelly shores. There are no forms which are characteristic of the supralittoral sand strand alone, not even where it is very well developed, as for instance at Sts. 1a and b (see fig. 16) and at St. 6. As is well known, in several more southerly regions it harbours a very characteristic and comparatively rich fauna.

3. Lagoons and Littoral Meadows.

a) Botanical conditions.

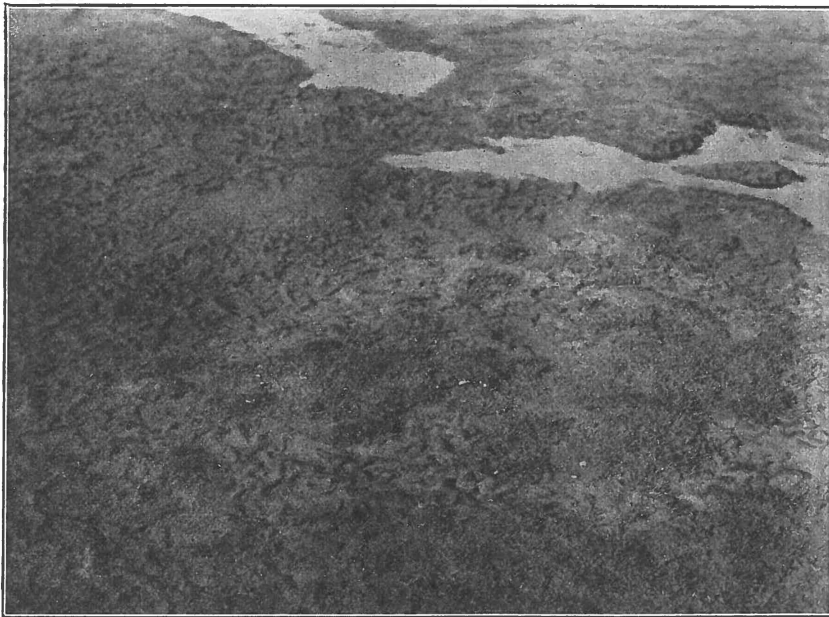
This part of the shore exhibits a rich vegetation of lower plants, especially *Cyanophyceae*, *Chlorophyceae*, and diatoms, while the higher plant life is somewhat poorer in species though to a less extent in individuals. Still it is very characteristic. The lower plants of Christian X. Land have never been subjected to a systematic investigation. Altogether there is only one systematic work from which information about the algal flora of the lagoons and the littoral meadows of Greenland can be obtained, viz. that of ROSENVINGE (1893). A few records of *Cyanophyceae* and *Chlorophyceae* are given by HARTZ (1895, pp. 125 and 150) and JONSSON (1911).

No investigations are available on the diatoms, which occur in great abundance. All these plants may form regular surface films, which may even become folded during their growth (see fig. 6).

The above-mentioned plants are chiefly associated with the littoral region, or are at any rate most numerous there. Of the lower plants of the supralittoral the mosses (*Musci*) are especially dominant, and in the patches that are highly affected by fresh-water *Hepaticae* (at St. 1b *Anthelia* sp.) predominate. HARTZ (1895, pp. 125 and 263) and HARTZ & KRUSE (1911, p. 416) mention various mosses and liverworts from littoral meadows more or less affected by fresh-water, from Jameson Land and Fleming Inlet (Liverpool Land) respectively.

The most important higher plants are *Stellaria humifusa* ROTTB., *Puccinellia phryganodes* (TRIN) SCHRIEBN. & MERR., and *Carex ursina* DEW., all of which are specifically associated with the shore. Of halophilous plants there further occur *Carex subspathacea* WORMSKJ. and *Carex lachenali* SCHKUR var. *glareosa* (WAHLB.) GELTING (see GELTING 1934, p. 162).

All of these, in particular the three first-mentioned, form dense growths in many places. As in the supralittoral zone, a couple of genuine coprophilous plants often occur in the littoral meadows, viz. *Cochlearia officinalis* var. *groenlandica* and *Puccinellia angustata* (R. BR.). Round the lagoons showing fresh-water influence there sometimes occur the following forms, which are on the whole associated with damp places:



HOLGER MADSEN photo.

Fig. 6. West Harbour, Eskimonæs, St. 1a, June 25, 1933. *Puccinellia phryganodes* littoral meadow with folded covering of blue-green algæ, and lagoon.

Dechampsia arctica (TRIN.) var. *pumila* (LEDEB.), *Dupontia fischeri* R. BR. and *Phippsia algida* (SOLAND).

Of the three specific species, *Carex ursina* has not hitherto been found north of Cape Giesecke on Wollaston Foreland (lat. 74°30' N.) (GELTING 1934, p. 177); no doubt, however, it may be found farther north, where owing to the few investigations it may easily have been overlooked. On Spitsbergen it occurs up to the extreme northern point (SCHOLANDER 1934, p. 62).

Puccinellia phryganodes, *Stellaria humifusa*, and *Carex subspathacea* have been found northward to Danmarkshavn. The same applies to several of the less exclusive shore plants mentioned in p. 22 (OSTENFELD and LUNDAGER 1910).

The distribution in associations is closely dependent on external factors especially low and high tide, the pure *Puccinellia phryganodes* association being decidedly littoral, mostly immersed at normal high-

water, and rather sharply delimited from the *Carex ursina* association (see fig. 7), which is associated with the first horizon and the supra-littoral zone.

The other species mentioned are distributed according to the degree of flooding and the influence of fresh-water.

The difference in climate between the inner and the outer parts of the fjords is also of importance for the distribution (see further GELTING 1934).

In this connection it should be mentioned that although HARTZ (1895, p. 143) expressly states that he did not collect *Stellaria humifusa* in the interior of the fjords, thus for instance not from Røde Ø, I collected it in a locality just west of this place, viz. St. 9.

Often the littoral meadows cover extensive areas, sometimes consisting of the *Puccinellia* association alone (as in St. 1a). This is the case in several localities in the district round Clavering Island.

As mentioned above, nothing of the kind has been observed within the Franz Joseph Fjord district, whereas several localities are known from the Scoresby Sound district, as stated by HARTZ (1895) and HARTZ and KRUSE (1911). Personally I observed well developed littoral meadows at Sts. 6 and 7.

In places *Carex ursina*, in particular, forms much tufted meadows (see fig. 8) of exactly the same character as the littoral meadows of our country with similar "loer", irregularly shaped water holes. I found this type to be most distinctly developed at St. 7. In the pure *Puccinellia* meadow in this place there further occurred some peculiar bare, clayey patches on a level not very much below that of the surroundings (see fig. 9). I do not know the cause of the formation of these flats. HARTZ and KRUSE found "loer" in Mudderbugt and at Point Constable, like those found at St. 7.

As will appear from the succeeding pages, the distribution of the animals is in very slight degree conditioned by the vegetation of higher plants, whereas the vegetation of the lower plants plays a more important part, together with the other external factors, which also determine the distribution of the plants, though in another respect.

b) Zoological conditions.

Table showing the distribution of animals in the lagoons and littoral meadows of the various localities.

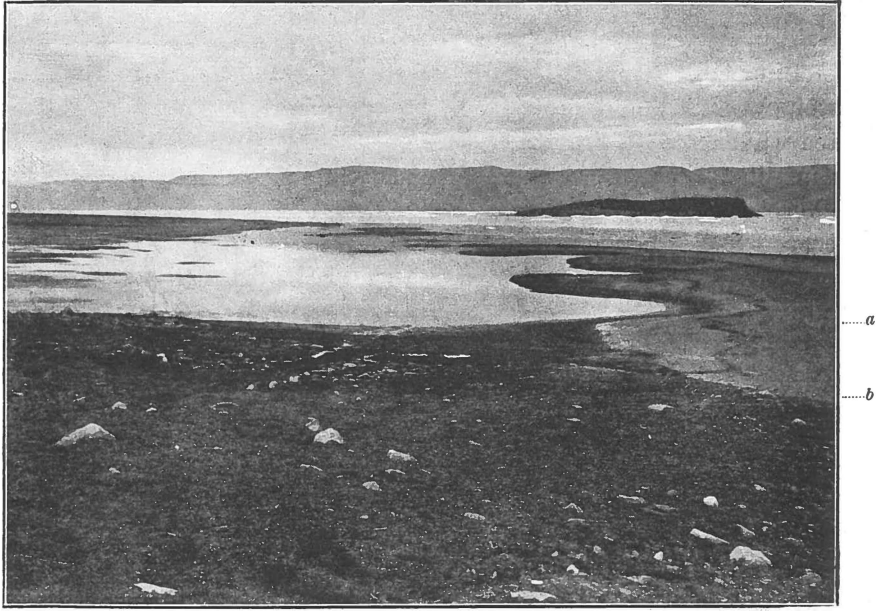
Explanation of the table.

The meaning of column-group 1 (see the bottom of the table) is obvious. In column-group 2 I have gathered the factors which in my opinion may especially be supposed to condition the distribution of

Stations	date	number of samples of 25 sq. cm (b = Berlese sample) — = not quantitative	external factors				slightly mobile animals										mobile animals					
			Fe S-layer at the bottom × absent ÷	constant influence of fresh water f. rarely flooded ×	facies s = sand, l = clay	vegetation ¹⁾	quantitative samples				qualitative samples						qualitative samples					
							Chironomidae-larvae Smittia and (or) Orthocladius	Oligochaeta a = Ench. alb. b = Lumbricillus lineatus	Ameronothrus lineatus var. nigrofemoratus	Larvae and pupae of Limnophora (malaisei?)	Nematoda	Tardigrada	Trichoribates trimaculatus	Tectocephus velatus	Rotatoria	Archisotoma besselsi	Hypogastrura viatica.	Folsomia sexoculata	Onychiurus affinis var. groenlandica	Sminthurides malmgreni	Folsomia quadrioculata	Xenylla mucronata
St. 1a.....	23—6	4(b)	×	÷	s	p	(+)	$\begin{Bmatrix} a \\ c \end{Bmatrix}$	0	0	(cc)	(0)	0	0	(c)	0	0	0	0	0	0	0
St. 1b.....	9—7	4(b)	÷	f	s	u	31	$\begin{Bmatrix} a \\ c \end{Bmatrix}$	85	0	(cc)	(0)	2	0	(c)	0	0	0	12	14	0	0
loc. 1.....	26—6	4(b)	÷	f	s	(u)	23	(0)	0	0	(cc)	(0)	12	50	(0)	2	1	0	20	138	10	0
St. 3.....	7—8	2	÷	$\begin{pmatrix} \cdot \\ \cdot \end{pmatrix}$	sl	h	0	0	0	0	0	0	0	0	0	+	—	—	—	—	—	—
		2	×	$\begin{pmatrix} \cdot \\ \cdot \end{pmatrix}$	sl	h	0	0	0	0	0	0	0	0	0							
		2	×	$\begin{pmatrix} \cdot \\ \cdot \end{pmatrix}$	sl	h	86	0	0	0	0	0	0	0	0							
St. 4.....	9—8	3	÷	÷	l	h	0	0	0	0	cc	0	0	0	0	+	—	—	—	—	—	—
		3	÷	÷	l	i	0	0	0	0	0	0	0	0	0							
		4(b) ²⁾	×	÷	l	p	0	$\begin{Bmatrix} a \\ b \\ c \end{Bmatrix}$	0	0	(cc)	—	0	0	—	0	0	0	0	0	0	0
St. 5																						
loc. 1.....	4—8	2	÷	÷		i	0	$\begin{Bmatrix} a \\ b \\ 34 \end{Bmatrix}$	0	0	cc	0	0	0	0							
		3	÷	÷	l	i	0	$\begin{Bmatrix} a \\ b \\ 43 \end{Bmatrix}$	0	0	cc	0	0	0	0							
loc. 2.....		2	÷	f	l	(i)	0	$\begin{Bmatrix} a \\ 100 \end{Bmatrix}$	0	0	cc	0	0	0	0							
		2	÷	f	l	(i)	0	$\begin{Bmatrix} a \\ 82 \end{Bmatrix}$	0	0	cc	0	0	0	0	+	—	—	—	—	—	—
loc. 3.....		2	×	f	l	i	0	0	80	0	c	+	0	0	0							
		2	÷	f	l	i	0	$\begin{Bmatrix} a \\ 74 \end{Bmatrix}$	0	0	+	0	0	0	0							
		2	÷	f	l	h	0	0	0	0	+	0	0	0	0							
	3—8	—	×	÷	l	h	0	$\begin{Bmatrix} a \\ c \end{Bmatrix}$	+	0	cc	+	0	0	0							
	29—7	—	÷	÷	l	i	0	$\begin{Bmatrix} a \\ c \end{Bmatrix}$	0	0	—	+	0	0	0							
St. 6.....	16—8	1	×	f	s	p	4	$\begin{Bmatrix} a \\ b \\ 152 \end{Bmatrix}$	ca. 1000	0	cc	0	0	0	0							
		1	×	f	s	p	0	$\begin{Bmatrix} a \\ b \\ 96 \end{Bmatrix}$	2060	0	cc	0	0	0	0							
		4	×	$\begin{pmatrix} \cdot \\ \cdot \end{pmatrix}$	sl	h	0	$\begin{Bmatrix} a \\ b \\ 180 \end{Bmatrix}$	0	0	cc	0	0	0	0	+	cc	—	—	—	—	—
		4	×	$\begin{pmatrix} \cdot \\ \cdot \end{pmatrix}$	sl	h	0	$\begin{Bmatrix} a \\ b \\ 165 \end{Bmatrix}$	0	0	cc	0	0	0	0							
	15—8	—	×	$\begin{pmatrix} \cdot \\ \cdot \end{pmatrix}$	sl	h	0	$\begin{Bmatrix} a \\ b \\ c \end{Bmatrix}$	+	0	cc	—	0	0	—							
		—	×	f	s	u	0	$\begin{Bmatrix} a \\ b \\ c \end{Bmatrix}$	cc	0	cc	+	0	0	0							
St. 7.....	24—8	3	?	(f)	sl	h	233	$\begin{Bmatrix} a \\ 7 \end{Bmatrix}$	71	16	cc	0	0	0	0	+	+	—	—	—	—	—
		4(b) ²⁾	÷	(f)	s	u	0	$\begin{Bmatrix} a \\ + \end{Bmatrix}$	15	0	(cc)	0	0	0	0	(+)	(cc)	0	0	0	(+)	0
		—	×	(f)	l	i	0	0	0	0	c	0	0	0	+	—	—	—	—	—	—	—
		—	÷	(f)	s	u	0	0	0	0	c	0	0	0	0	—	—	—	—	—	—	—
St. 8.....	23—8	2	÷	f	s	u	0	$\begin{Bmatrix} a \\ b \\ 106 \end{Bmatrix}$	650	0	cc	0	0	0	0	—	—	—	—	—	—	—
St. 9.....	22—8	2	÷	×	s	u	0	0	0	0	0	0	0	0	0	—	—	—	—	—	—	—
		2	÷	×	s	u	4	0	0	0	0	0	0	0	0	—	—	—	—	—	—	—
		4(b) ²⁾	÷	×	s	u	0	$\begin{Bmatrix} a \\ + \end{Bmatrix}$	2	0	0	0	0	0	7	0	0	0	37	0	0	3
1			2				3				4				5							

¹⁾ i = no blue-green algal film; h = blue-green algal film only; u = *Carex ursina* or *Pucc. phryg.* meadow with mosses; p = *Puccinellia* meadow with blue-green algal film.

²⁾ Living sample brought home and subsequently treated.



HOLGER MADSEN photo.

Fig. 7. Hurry Inlet, St. 6, August 15, 1933. In the foreground a *Carex ursina* meadow, mossy, tufted. At *b* the sharp boundary towards the *Puccinellia phryganodes* littoral meadow is seen, at *a* the transition to the bluish-green algal carpet of the lagoon. Fresh-water is seen to ooze through the littoral meadow. In the *Puccinellia* meadow *Ameronothrus* occurred in great abundance, up to 2060 individuals per 100 sq. cm.

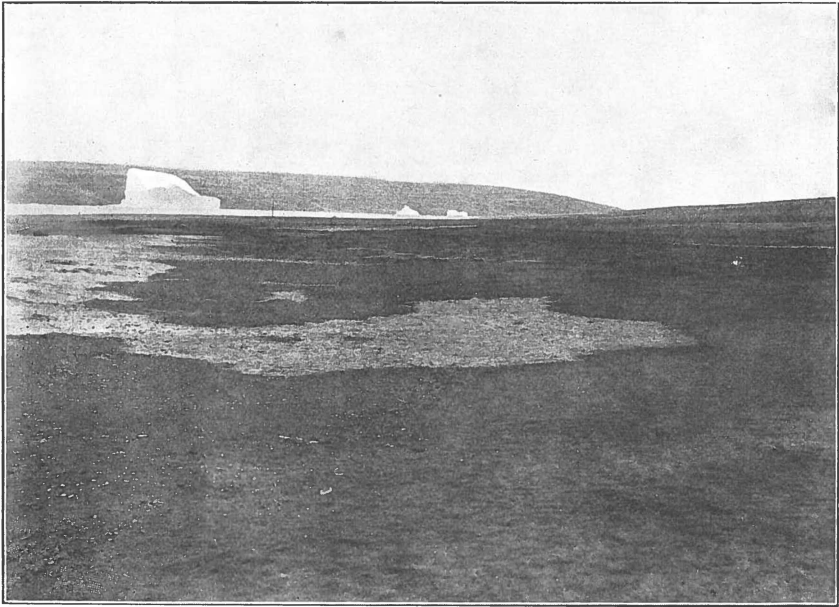
The island in the fjord is the southernmost of the Fame Islands.



HOLGER MADSEN photo.

Fig. 8. Charcot Harbour, St. 7, August 26, 1933. *Carex ursina* meadow. Close view of tufts.

the animals. A parenthesis indicates that the influence of the particular factor was but slight or obscure. In column-group 3 the animals are listed which could be investigated quantitatively. A parenthesis indicates (as in column-groups 4 and 5) that the animal could not be recognised on account of the character of the sample (Berlese sample), but was observed in a different way. In group 4 the less mobile animals are listed, which are either rare or not counted. The indications +, c, and cc (also used in group 5) indicate, respectively, that the species is present,



HOLGER MADSEN photo.

Fig. 9. Charcot Harbour, St. 7, August 26, 1933. Littoral meadows. In the background tufts. In the foreground the patches without vegetation mentioned in the text.

frequent, or abundant, while a — indicates that the sample is of such a nature that the particular animal, even though it may have been present, could not very well be found in it. Column-group 5 gives the more mobile animals, the *Collembola*, which have only occasionally been collected quantitatively. Generally there is only one indication for a station as a whole.

It is impossible to draw a sharp boundary between the clay and sand flats off the river mouths and some of the lagoons formed in the same places. These lagoons are open towards the sea. On the whole they show the same external conditions, a gravelly and sandy bottom with a sparse vegetation of lower plants (no higher plants), absolutely

no formation of film, which is otherwise so frequently met with in lagoons and no formation of ferrous sulphide (FeS). Accordingly the animal life is broadly the same. At St. 5 (see fig. 5, p. 21), where these lagoons were especially well developed, a few *Copepoda*, *Laophonte strömi* (BAIRD) and *Tachidius* sp. (*longicornis* OLOFSS.), were also found; both belonged to the *Harpacticoidea*.

Laophonte strömi as well as the *Tachidius* species known from Arctic regions are brackish-water forms.

If one wades through such a lagoon, small fishes are constantly slipping round one's legs. They proved to be young (from the same year) of *Cottus quadricornis* L. It is interesting to observe this phenomenon in the Arctic which is so commonly met with in boreal waters, e. g. in the shallow water at the west coast of Jutland, that the young fishes prefer quite shallow water.

These small fishes must be exceedingly resistant to fluctuations in the salinity of the water; I found them repeatedly in practically fresh water (cf. p. 18).

It was also peculiar to observe the small *Cottus* in some lagoons that form a transition from the above-mentioned to the most typical lagoons, which often occur in close association with littoral meadows.

The transitional lagoons also communicate with the fjord, but exhibit a more or less dense covering of *Cyanophyceae*, etc. Often a thick layer of FeS clay or sand will form beneath, but this seemed to have no influence on the fishes or on *Gammarus wilkitzki*?, although the black layer might occur directly below the surface film.

Typical transitional lagoons were especially found at St. 4. As shown in fig. 7, they pass evenly into the commonest lagoon form, i. e. that which is sheltered from the sea by a sand-bank.

The only records of the animal life of the East Greenland littoral meadows that I have found in the literature are some brief notes, partly by HARTZ (1895, p. 125), who records *Nematoda* from the filmy sheet of green algæ and blue-green algæ on a littoral meadow at Cape Stewart, partly by HARTZ and KRUSE (1911, p. 340), who from a littoral meadow of a similar character to that described below from St. 1b, loc. 1 (i. e. marked by fresh-water influence) mention "quantities of small worms". It appears from the following description that they refer to *Enchytræus albidus* and (or) *Lumbricillus lineatus*. In the same place (as well as a few other places in the two papers) they mention that the littoral meadows are grazed off by geese (see above, p. 19).

Quantitatively, as regards weight, the main stock of the lower animal life of lagoons and littoral meadows is formed by *Oligochaeta*, *Enchytræus albidus* and *Lumbricillus lineatus*, the former being the most frequent. They are present in fairly large numbers, up to about 180 individuals

per 100 sq. cm. Almost certain inhabitants also are *Nematoda*, which occur in great numbers (not closely identified). Associated with these is a fauna of *Diptera* larvæ, *Collembola*, *Arachnida*, *Tardigrada*, and *Rotatoria*, the individual elements of which are distributed differently according to the variations of the individual external factors. The most conspicuous of the *Diptera* larvæ are those of the *Chironomidae*, *Smittia* (*extrema*?), *Orthocladius decoratus*, and *O. groenlandensis*, all of the terrestrial type. As will appear from the table, they may occur in considerable numbers (about 230 per 100 sq. cm), generally, however, in much smaller numbers. Less frequent are the larvæ of *Fucellia ariciformis*. In a single locality (St. 7) the most conspicuous animal was a small fly, *Limnophora* (*malaisei* RINGDAHL?), which flew in small jerks and moved rapidly over the surface of the lagoons. Its larvæ, and especially its pupæ, were very numerous (16 living larvæ and pupæ, about 48 empty chrysalis exuviae in 100 sq. cm) in lagoons with a bluish-green algal film in company with several typical strand forms.

Among the latter the *Oligochaeta* were sparse, while the *Arthropoda* were dominant. The locality showed marks of fresh-water influence. Association with the shore does not seem to have been known previously for any Greenland *Limnophora*. (KROGERUS [1932, pp. 119 and 174] describes *Limnophora balthica* RUDG. as a littoral halophilous form in Finland. This species was also met with, especially near salt lagoons).

Three species of *Collembola* are of special interest, viz. *Archisotoma besselsi*, *Hypogastrura viatica*, and *Folsomia sexoculata* (TULLB.). As stated above (p. 20), *Archisotoma* is exclusively, and *Hypogastrura* largely associated with the shore. This tendency is less pronounced in *Folsomia* (only found in St. 9), which is designated by LINNANIEMI as a distinctly hygrophilous shore form, but which according to the statements of later authors may be met with in many other damp localities. It was not found in any other of the samples examined by MARIE JØRGENSEN (1934₁), but has previously been found in East Greenland (Hvalrosø). In regions much influenced by fresh-water the following forms were further found: *Folsomia quadrioculata*, *Sminthurides malmgreni*, and *Onychiurus affinis* var. *groenlandica*, and in a single locality (St. 9) *Xenylla mucronata* AXELS, which is new to Greenland.

The *Arachnidae* are represented by several species, spiders and mites. Not quite casual is the occurrence of *Micryphantes nigripes* on the dried-up parts of the edges of lagoons. This species is on the whole associated with sandy and gravelly places. Three species were only observed in the very luxuriant littoral meadow at St. 7 (see fig. 9), but here they occurred in great abundance, viz. *Coryphaeolana holmgreni* THORELL, *Erigone tirolensis* L. KOCH, and *Erigone whymperei* COMBR. However, none of these species are strictly associated with the shore,

even though their occurrence was not quite casual; no doubt they constantly live there, which is evidenced by the presence of numerous egg-webs. *Erigone tirolensis* is also recorded from the shores of Spitsbergen (shingle bank) (SUMMERHAYES and ELTON 1923, p. 259). Here, too, the most frequent *Acarina* are *Molgus littoralis* and *Ameronothrus lineatus* var. *nigrofemoratus*.

The presence of *Tardigrada* (unfortunately not determined) on the shore is rather interesting; they have not previously been observed in Greenland, but are recorded from Spitsbergen.

I observed *Rotatoria* in a few places only, but no doubt they will prove to be very common.

An important part of the fauna of the littoral meadows and the lagoons is formed by the Protozoans, which are especially abundant in the thick film of blue-green algæ, which often covers the bottom. Thus in St. 1a there was quite a bustle of *Flagellata* (*Chlamydomonadidae* and *Euglenoidea*, at any rate three species) and many species of *Infusoria*. In St. 1b (both localities) the influence of the fresh water, which sets its mark on the plant life and the Metazoan life as well, was also evidenced in the Protozoan fauna by the presence of *Thekamoebae*. Further, large numbers of *Flagellata* and *Infusoria* occurred here (many *Vorticellid* swimmers, *Pleuronematidae*, *Stentor*, various *Hypotricha*, etc.).

If we consider the distribution of the animals in relation to the external factors, as shown in the table, we shall see that the *Oligochaeta* and the *Nematoda* are fairly independent of the factors enumerated, since they are present almost everywhere in sufficiently moist places. It is in agreement herewith that they are only sparsely represented in the samples from Sts. 7 and 9, which were rather dry and situated in the uppermost horizon of the littoral. Remarkable was the absence of *Oligochaeta* in St. 3.

Curiously enough, the formation of ferrous sulphide at the bottom has no reducing effect on the plant and animal life, not even where the FeS-layer occurs immediately below the surface. The reason is probably that the animal life is restricted to the uppermost layer, only a few millimetres thick, where the ferrous sulphide is oxydised.

The bottom, whether sand or clay, does not seem to be of importance either, nor is the type of vegetation or the lack of vegetation (i. e. if the vegetation is not dense enough to form a film) apparently of any importance.

A certain correlation, however, exists between the nature of the bottom and the formation of the film, which chiefly consists of *Cyano-phyceae* and *Chlorophyceae*, but also of immense numbers of diatoms. It proves that in most places where the bottom is made up of sand a film will form, either in association with a *Puccinellia* meadow or a

Carex ursina meadow. When the bottom is made up of clay, there is mostly but a slightly developed or no film.

When the film is distinctly developed, it is much incrustated with fine grains of clay.

The factors that have the greatest delimiting effect are the degree of fresh-water influence and the degree of submersion at high-tide. A slight degree of fresh-water influence or of inundation at spring-tide (uppermost littoral horizon) is essential for a strong development of *Ameronothrus lineatus* var. *nigrofemoratus*, and the same seems to be the case with the *Tardigrada*, which, wherever found, always occurred in company with *Ameronothrus*. OLOFSSON (1917—18, pp. 286 and 288), and SUMMERHAYES and ELTON (1923, p. 266), who made investigations on Spitsbergen, also show that the halophilous *Tardigrada* are dependent on a certain supply of fresh-water. If the fresh-water influence is especially strong, various other forms will occur too, which show greater association with fresh water or are of a more ubiquitous character. If the influence of fresh-water is predominant, *Ameronothrus* disappears or is very sparsely represented (St. 1b, about 4 per 100 sq. cm).

The factors that determine the distribution of the Chironomide larvæ are more difficult to investigate. In most cases the localities are clearly influenced by fresh-water. Exceptions are, however, Sts. 1a and 3. At the time St. 1a was investigated, it was only influenced by fresh water, the ice having not yet disappeared, while later in the year the whole locality is regularly flooded by sea-water. It is remarkable, however, that the larvæ were more numerous in a lagoon which was traversed by a small brook. The locality in St. 3 was a lagoon with salt water, but the presence of dead *Cyclops strenuus* as well as detritus of land plants indicated frequent influence of fresh water. It is rather interesting that of the three samples taken one contained detritus of land plants, and it was in this sample that the Chironomide larvæ were found (*Smittia [extrema?]*).

On the basis of what has been stated above we may distinguish between several animal communities (or rather subdivisions of the large Oligochaet-Nematode community), viz.

1) A community associated with lagoons influenced by sea-water (i. e. flooded daily at high tide) and littoral meadows. Dominant animals: *Oligochaeta* (*Enchytræus albidus* and *Lumbricillus lineatus*). Common animals are also Nematodes and Protozoans. In quantitative samples from this community the number of individuals of *Oligochaeta* per 100 sq. cm (average of seven samples) was 61.

2) Communities associated with lagoons influenced by fresh water and littoral meadows flooded at spring-tide. Dominating animals:

Oligochaeta (*Enchytræus albidus* and *Lumbricillus lineatus*) and *Ameronothrus lineatus* var. *nigrofemoratus*. Other common animals were Chironomide larvæ, Nematodes, Tardigrades, and Protozoans. Number of *Oligochaeta* per 100 sq. cm (average of 8 samples) 76 (or a little higher than the preceding community). Number of *Ameronothrus* per 100 sq. cm (average of 8 samples) about 475.

3) Communities associated with *Carex ursina* littoral meadows, mossy and with lagoons with algal films, influenced by sea-water only at spring-tide, and strongly influenced by the afflux of fresh water. Only occurring at St. 7 (see fig. 9). Dominant animals: Chironomide larvæ and *Ameronothrus*. *Oligochaeta* present in small numbers. Accompanying animals: *Limnophora (malaisei)*, Nematodes, and Protozoans. Number of Chironomide larvæ per 100 sq. cm (average of two samples) about 115. Number of *Ameronothrus* per 100 sq. cm (average of two samples) about 43.

4) Communities associated with stony *Carex ursina* vegetation with a film of blue-green algæ. Fairly dry. Only flooded at spring-tide. Slightly influenced by fresh water. Only observed at St. 9 (see fig. 10). Dominating animal: *Folsomia sexoculata*. Number per 100 sq. cm (one sample) 37. Accompanying animals: *Oligochaeta*, *Tectocephus velatus*, *Xenylla mucronata* and *Ameronothrus*.

5) Communities associated with littoral meadows essentially influenced by fresh water. Dominating are forms that are mostly associated with bogs or the banks of lakes. The influence of sea-water is evidenced by the presence of *Oligochaeta* and *Ameronothrus* which may be almost absent in extreme cases.

In all these subdivisions the two shore forms *Archisotoma besselsi* and *Hypogastrura viatica* are also frequent (the number cannot be stated, as this would require several more Berlese samples on the spot). Occasionally other *Collembola* may be found, especially the ubiquitous forms.

In this connection mention should be made of some forms of special lagoons which cannot be grouped in the above classification.

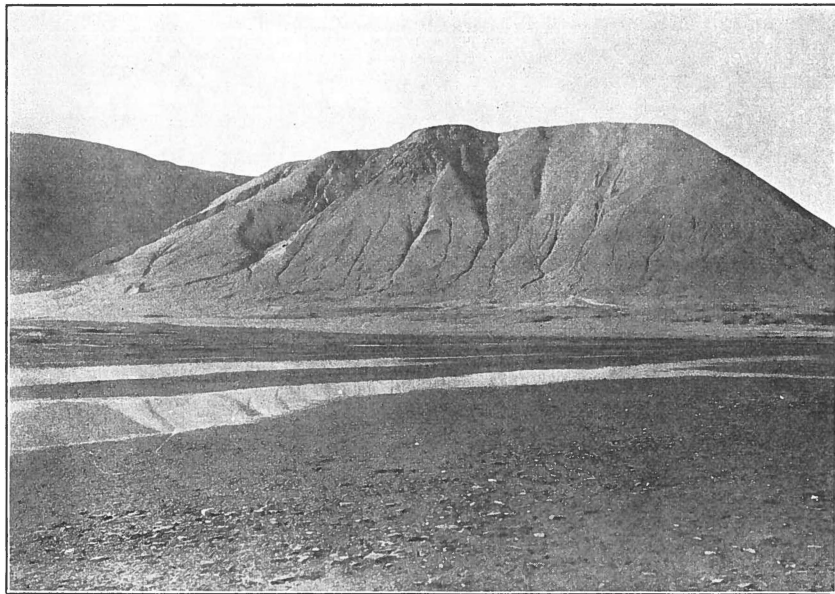
6) Lagoons with a special kind of bottom film. Sand-grains dominate. At first sight *Cyanophyceae* were only recognisable by removing the uppermost sand layer in flakes. The animal life at the bottom was extremely poor, neither *Oligochaeta* nor *Nematoda* being found. Only in places where detritus of land plants had accumulated was *Smittia* found in large numbers. It was in this lagoon that the larvæ of *Micralymma (brevilingue?)* (see p. 24) occurred in company with the common plankton *Copepoda* as for instance *Calanus finmarchicus*, etc., and dead specimens of *Cyclops strenuus*. Lagoons of this type were only observed at St. 3 (see fig. 11).

7) At St. 7 (see fig. 4, p. 17) a peculiar lagoon was found in close



HOLGER MADSEN photo.

Fig. 10. The bay west of Rødeø, St. 9, August 22, 1933. Stony *Carex ursina* meadow.
Only locality for *Folsomia sexoculata* and *Xenylla mucronata*.



HOLGER MADSEN photo.

Fig. 11. Nordfjord, St. 3, August 7, 1933. Lagoons with sea-water. Only locality
for the larvæ of *Micralymma (brevilingue)*.

association with the fjord, but it was so deep that it did not become dry at ebb-tide. The bottom was made up of a very thick layer of fat clay. There was no well defined bottom film, but the bottom was covered with a yellowish layer of diatoms. Despite a zealous search only Nematodes and *Rotatoria* were found.

8) Lagoon occurring in association with summering snow-patches, but situated so as to become flooded by the sea at spring-tide. No vegetation of higher plants at the edges of the lagoon (see fig. 3, p. 16). It was teeming with *Daphnia*, *Ostracoda*, fresh-water *Copepoda*, and Chironomid larvæ, partly *Chironomus* sp. and partly *Orthocladius*, the only perceptible result of the influence of the sea on the fauna. This lagoon-form is not considered in the table.

An interesting transitional form between this type and that defined under point 5) is described by HARTZ and KRUUSE (1901, p. 340). This lagoon, too, was teeming with *Daphnia* and Chironomid larvæ as also *Lepidurus arcticus*. None of these animals have been closely identified, but the effect of the sea is evidenced here by the presence of the three usual plants of littoral meadows, *Puccinellia phryganodes*, *Carex ursina*, and *Stellaria humifusa*. In addition a similar vegetation to that of St. 1b was found.

I am fully aware that the groups enumerated above are not very well defined, but it seems to me that a general view of the conditions is best obtained in this way.

The first-mentioned type was found in several localities, Sts. 1a, 4, 5 (see fig. 5, p. 21), and 6 (fig. 7, p. 27).

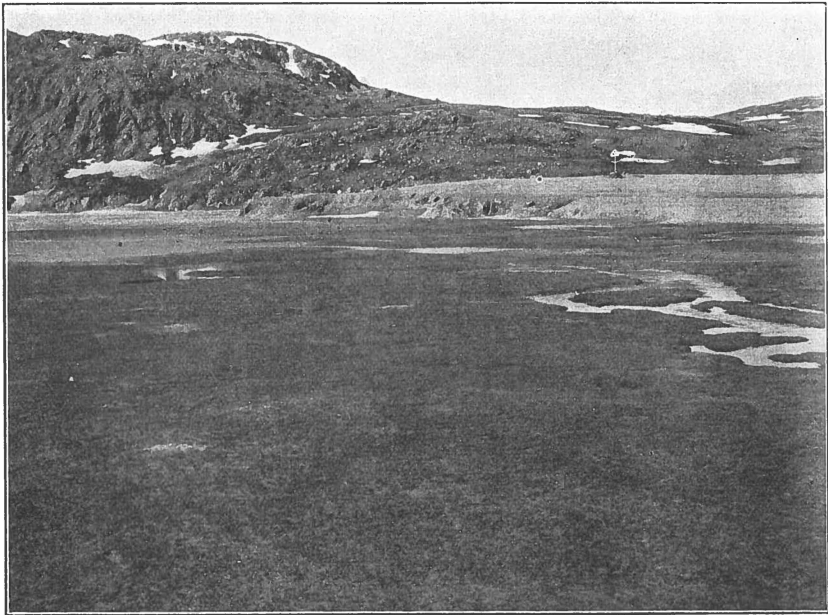
c) Structure and special conditions.

Since, as far as I know, no description of the structure of the bottom of lagoons and littoral meadows in Arctic regions has so far been given, I shall describe below these formations as they appeared at St. 1. For a number of particulars, more especially botanical ones, I am indebted to P. GELTING.

Behind the broad bank of sand or the supralittoral strand at St. 1a there extended some vast flats, which were covered with a blue-green algal film and in most places a dense growth of *Puccinellia phryganodes* (see figs. 12 and 13A). A black, reeky, ferro-sulphurous layer of sand extended everywhere. On June 25, 1933, a random sample gave the result shown in fig. 14. However, the ferro-sulphurous layer varied considerably in thickness, ranging from 2 to 30 cm, that is, right down to the icy substratum. Especially in the lagoons this layer would be directly subjacent to the blue-green algal film. In places where the black layer was not too thick, it was underlain by sand of the normal colour, or

slightly darker. At a temperature of the air of 9° the temperature of the ground-water was 4° and the temperature of the lagoon 12° (sunshine). The water, the groundwater as well as the water of the lagoon and the fjord water beyond, was perfectly fresh (according to areometric determinations $0.0^{\circ}/_{00}$). On June 11, 1933, the locality was partially free of snow, but covered by about 20 cm of running water, derived from the melting of the snow. On June 16, 1933, only scattered snow-patches occurred, and the littoral meadow was free from water.

The second type was observed in St. 5 (fig. 5, p. 21), St. 6 (fig. 7, p. 27) and St. 8 (fig. 3, p. 16). For types 3 and 4, see above.



HOLGER MADSEN photo.

Fig. 12. West Harbour, Eskimonæs, St. 1a, June 25, 1933. Littoral meadow with *Puccinellia phryganodes*.

Type 5 was only represented in St. 1b (figs. 13B and 16). The meadows in question are situated inside a broad shingle bank, and their only regular connection with the sea is by way of a channel in its eastern part, formed, at any rate partially, by the brook that empties into the littoral meadow. In August, 1931, and in July, 1932, the brook had nearly dried up, so that hardly any lagoons occurred. In the autumn of 1931 it was filled with water at spring-tide. However, this did not take place in 1932, or at any rate to a very slight extent only, probably because the channel had been barred by sand. But in 1933, when I stayed at the locality til July 20, there was a strong formation of lagoons, though of fresh water, due to the great snow-fall in the winter.

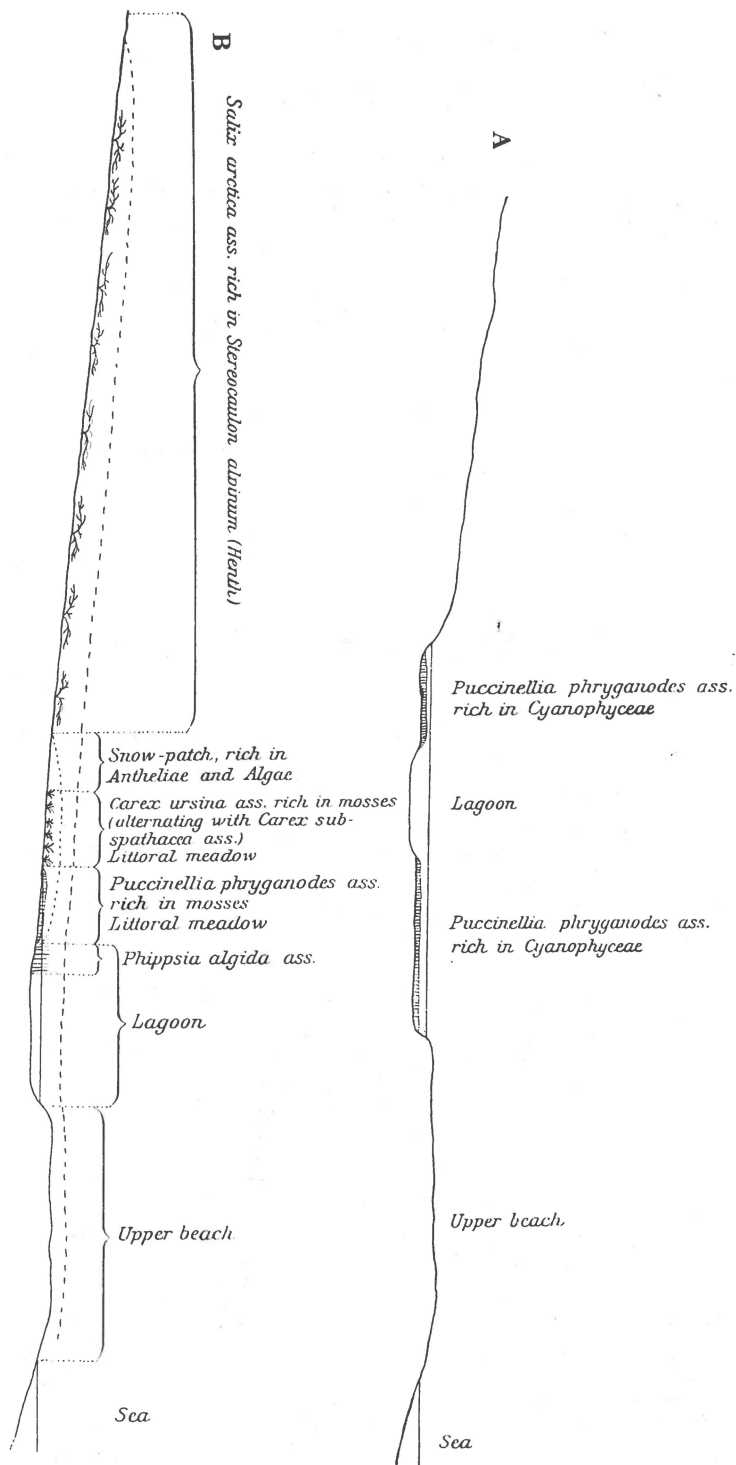


Fig. 13. (Prepared in cooperation with P. GELTING). A. Diagrammatic section through the shore in St. 1a. B. Diagrammatic section through the shore in St. 1b, locality 1. - - - - - Snow-cover in winter. Snow-cover in the first week of June, 1932. The snow entirely disappeared on July 7, 1932 (June 23, 1933). In A the level of the sea marks the daily level of flow-tide, while in B it indicates the level at spring-tide.

Hence this year the locality was not affected by the sea, though this may have been the case later in the year. At the time of the investigation (July 9) the water was entirely fresh (groundwater, lagoon water, and the water at the edge of the sea) as a result of the melting of snow and ice.

Investigations were made in two localities. The easternmost locality, loc. 4, was situated nearest the channel, and was separated from the

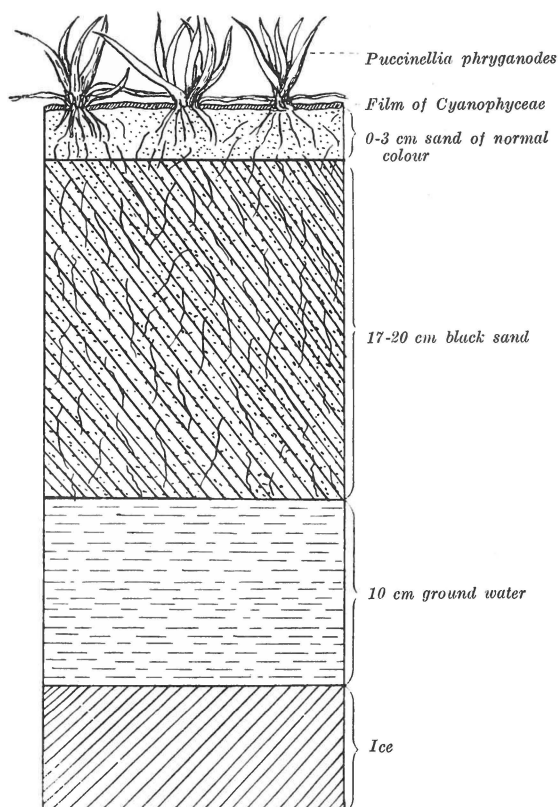


Fig. 14. Diagrammatic section through a *Puccinellia littoral* meadow in St. 1a, on June 25, 1933.

remaining part of the lagoon. It was a *Dupontia fischeri* association, with a dense growth of mosses and liver mosses at the bottom. No formation of ferrous sulphide. Accordingly the vegetation of the locality is but slightly influenced by sea-water.

That an influence of sea-water may take place is evidenced by the remains of washed up algæ. It has been observed once during a violent gale that the lagoons were filled by the waves washing across the crest of the bank. However, this very rarely happens, and did not happen during my stay in the region.

The influence of sea-water on the animal life was evidenced by the presence of *Hypogastrura viatica*, more especially *Archisotoma besselsi* and *Orthocladus* larvæ. The dominant forms, however, were *Trichoribates trimaculatus* and *Tectocephus velatus*, characteristic bog forms, while *Sminthurides malmgreni* and *Folsomia quadrioculata* are especially

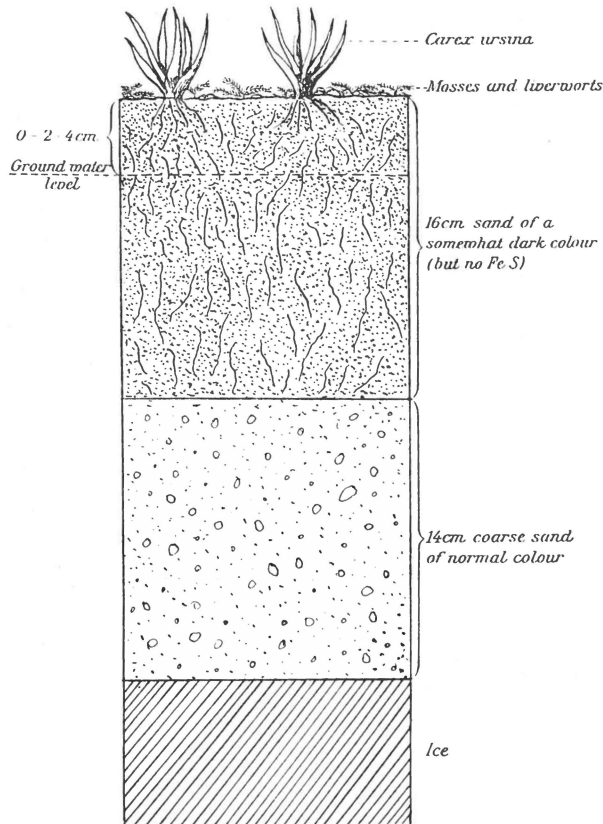


Fig. 15. Eskimonæs, East Harbour, St. 1b, loc. 1. Diagrammatic section through a *Carex ursina* littoral meadow.

associated with the banks of lakes. *Onychiurus affinis* var. *groenlandica* is more probably a bog form.

The westernmost locality, loc. 1, is shown in the section in fig. 13B. Botanically it shows a peculiar mixture of halophilous vegetation and snowpatch and fresh-water vegetation. Nearest the shore there is a belt of *Phippsia algida* with floating leaves, in the spring in running water. Inside this belt is a *Puccinellia phryganodes* littoral meadow. On July 20, 1933, it was still covered by the lagoon, while in 1931, as mentioned above, it was only covered at spring-tide. Beyond this again there followed a *Carex ursina* meadow with mosses, and finally



Fig. 16. East Harbour, Eskimonæs, St. 1b. Air photo.
(Reproduced by permission of the Geoditic Institute, Copenhagen).

a snow-patch vegetation. The samples are derived from the uppermost part of the *Carex ursina* meadow, where liver mosses made their appearance beside the mosses. Thus the meadow is more affected by the sea than locality 4. This is also evidenced in the fauna, which exhibits a considerable number of *Ameronothrus*, further *Smittia*, *Orthocladius*, and large numbers of *Oligochaeta*, but still there occur non-halophilous animals, as for instance *Trichoribates*, *Onychiurus affinis* var. *groenlandicus*, and *Sminthurides malmgreni*.

The structure of the bottom appears in all essentials from fig. 15. No indication of ferrous sulphide was observed here. The icy substratum occurred at a depth of about 30—40 cm. As late as June 18, 1933, about 40—50 cm of snow still lingered in localities 1 and 4. On June 23, 1933, loc. 1 was free of snow, but as stated above, large portions of it were submerged by the lagoon. On June 24, 1933, loc. 4 was free from snow. This locality, too, was partially submerged.

d) Ferrous sulphide and sulphur bacteria.

The formation of ferrous sulphide is apparently only mentioned a couple of times in the literature about Greenland. Thus C. KRUSE (1898, p. 358) (Vegetationen i Egedesminde Skærgaard. Medd. om Grønland. XIV, pp. 348—399) records it from Egedesminde, and HARTZ and KRUSE (1911, p. 402) write as follows (Point Constable, in Hurry Inlet): "Upon the bottom of the holes" — in the salt marsh — "lay red ochre films, below these black mud of at least 20 cm thickness." Neither HARTZ (1890), PORSILD (1902), nor BARTHEL (1927) mention the formation of ferrous sulphide.

Ferrous sulphide is often found in association with a *Puccinellia* vegetation. A single time, in St. 6, a thin layer of ferrous sulphide was observed beneath a *Carex ursina* littoral meadow with mosses. It is mostly found beneath a blue-green algal film, but such a film is not invariably associated with the formation of ferrous sulphide, and the latter may also take place quite independently of a continuous vegetation, whether of blue-green algæ or of higher plants. This was observed at St. 4, in a lagoon that was open towards the fjord, and also in the clayey tidal zone of St. 7. Nor does the nature of the bottom, whether of sand or clay, play a decisive role, even though the phenomenon is frequent on clayey bottom. Not rarely the formation of ferrous sulphide takes place in patches.

Whence the material for the ferrous sulphide is derived, it is difficult to decide. In some cases it is probably derived from a *Puccinellia* vegetation which has been buried by sand, but this explanation is not universally valid, as will appear from the above. Algal aggregations seem to be out of the question; I repeatedly observed considerable

accumulations of algæ, but not the slightest indication of ferrous sulphide was observed. Possibly it is fine deposition of detritus which by decomposition supplies the necessary sulphates, possibly the sulphates are derived from the seawater (cf. WARMING 1904, p. 42).

In this connection it is interesting to note that despite a careful search, I failed to find red sulphur bacteria. Colourless sulphur bacteria may probably be found. However, as far as I know, no investigations on this question are available from Greenland. The only work on Greenland bacteria which I have been able to find, is by CHR. BARTHEL (1927), who made a number of investigations of samples of soil, i. a. also some few shore samples, one even from a (mixed) *Puccinellia phryganodes* vegetation (p. 33), but no sulphate-reducing bacteria nor any purple sulphur bacteria are recorded from it. His general conclusion, however, is, that all the bacteria of common occurrence in Greenland are equivalent to those met with in Europe.

(WARMING (1904, p. 42) found *Microspira æstuarii*, which at any rate at the shores of Holland causes a formation of ferrous sulphide).

Hence it is peculiar that purple sulphur bacteria seem to be absent from Greenland. Neither HARTZ (1896), HARTZ and KRUUSE (1911), KRUUSE (1898), nor PORSILD (1902) mention them, and there is no particular reason to assume that these authors have overlooked such a conspicuous phenomenon as the occurrence of red sulphur bacteria. They must all have visited the places in which these bacteria were likely to be found, since they give a detailed description of the vegetation of the littoral meadows and the lagoons.

e) The geological importance of the plant and animal life.

As will appear from the above, and as I wish to point out again, the conditions of lagoons and littoral meadows are greatly variable. A factor which also plays a considerable part, is the power of the water originating from the melting of the snow in the spring. *Puccinellia phryganodes* may possibly in places serve to safeguard the soil (cf. PORSILD 1902, p. 194), but this effect will often be destroyed by the torrents of melt-water which plough up the ground or cover the existing vegetation with sand. The greatest destructions will be brought about in regions in which the mountains descend rather abruptly towards the shore. The protective effect of *Puccinellia phryganodes* is most pronounced in regions with mainly diluvial formations or with but slightly sloping territory.

At St. 7 the protection of the land afforded by *Puccinellia* seems to have been of some importance. The presence of "loer" points in the same direction. The animal life, however, has no geologic effect; this is chiefly conditioned by wind and current and the discharges of fresh-water streams (see p. 13).

4) A comparison with the littoral and the supralittoral of the remaining part of Greenland.

In the tidal zone of the shore with sediment facies a number of forms are absent which are common in the remaining part of Greenland, especially in the southerly regions. The east coast of Greenland is too little known to be included in the comparison, but on the west coast there occur a number of species which are either absent from our area or descend to, and are restricted to, the sublittoral.

As regards the animal life on the upper beach and in lagoons and littoral meadows no general account for the remaining part of Greenland is available; thus the area of the east coast south of Scoresby Sound is very poorly investigated, while some scattered information on the west coast can be gathered from the literature. The main result is that the fauna is very poor compared for instance with that of Iceland. However, on the west coast we find a greater variety of forms than on the east coast. Most conspicuous is the occurrence of *Micralymma marinum* (STROEM) and several flies.

As regards the shore vegetation a limit can be drawn for some few species. At Ammagssalik *Potentilla anserina* L. var. *groenlandica* SER, and *Puccinellia retroflexa* (CURT) subsp. *borealis* HOLMB. belong to the vegetation of the littoral meadow, while *Carex ursina* has disappeared, not having been found south of Turner Sound (69°35' N. lat.) on Blossville Coast. Along the greater part of this coast southward to Ammagssalik conditions are very unfavourable for the formation of sediment shores, and very few shore plants have been found here (BØCHER 1931₁). In the littoral meadows *Carex ursina* has apparently been replaced by *Carex lachenali* var. *glareosa*. Farther south, from about 64°30' N. lat., *Elymus arenarius* L. and *Lathyrus maritimus* (L.) also are common shore plants.

These species, however, are not strictly associated with the shore, but possibly rather with manured soil. This also applies to their occurrence on the west coast of Greenland.

Throughout Greenland the shore flora has on the whole a very uniform character. The main stock of the associations is mostly constituted by *Puccinellia phryganodes*, and *Stellaria humifusa*, in addition to the forms mentioned from our area, such as *Carex lachenali* var. *glareosa* and *Carex subspathacea*, etc. *Carex ursina* seems to have a southern limit on the west coast, too, somewhat south of Egedesminde (PORSILD 1926, p. 52). In addition there occur on the west coast some forms especially associated with littoral meadows, for instance *Puccinellia retroflexa* subsp. *borealis* (whose northern limit is near Egedesminde), *Plantago maritima* L., *Plantago borealis* LANGE, etc., while from sandy

shores besides *Honckenya peploides* there occur *Elymus arenarius* (northern limit in about 70°30' N. lat.) and *Mertensia maritima* (L.), and on the southern part of the west coast *Lathyrus maritimus* and *Haloscias scoticum* (L.).

It is characteristic of most of these species that they grow in numerous places in addition to the shore, especially in localities manured in different ways, by the activities of man or by birds. In the remaining part of their area of distribution the species are chiefly associated with the shore. This phenomenon, which is common to nearly all organisms, is very characteristic in Greenland, and is presumably in the first place due to competition. (See further ROSENVINGE 1898, p. 234, KRUISE 1912, pp. 279—280, PORSILD 1926, WARMING 1928, p. 316, BØCHER 1933₁, and 1933₂, p. 105, and DEVOLD and SCHOLANDER 1933, p. 155).

On the whole the shore within our area of East Greenland is distinguished by a special, though very poor, fauna and flora. The absence of a number of forms which are otherwise generally found in the littoral is very conspicuous. On account of the lack of competition due to the paucity of species the organisms present extend over nearly every kind of shore, so that the biocenoses are difficult to keep distinct.

The paucity of species, notably sessile species, characterising the littoral zone is traceable into the sublittoral to about 3 m depth, as already pointed out by THORSON (1933, p. 16). He regards the ice-foot, and especially the fresh-water formed during the breaking up of the frost (its influence is traceable as far out as about 5 m depth [THORSON loc. cit.]) as the chief causes of this. According to my own observations I agree with him on all essential points.

However, conditions are not quite as simple as described.

In other places the influence of the ice-foot and the fresh water may be considerable, and still a littoral fauna will develop. The fact that the time in which the said factors are inactive, or, in other words, that the period most favourable for the development of a littoral fauna, is very short, will especially conduce to its destruction.

Finally, as mentioned below, there are various reasons for not regarding the special littoral factors as delimiting factors, but seeking such elsewhere, among the factors which also act upon the sublittoral.

C. External Factors.

Turning now to the external factors, which exert their greatest influence in the littoral zone proper, we shall see that the most important are 1) the temperature (of both the sea and the air) and salinity, 2) the ice, and 3) the tide-water.

1) Temperature and Salinity.

As is well known, the so-called East Greenland Polar Current moves southward along the east coast of Greenland; it carries water of a negative temperature and a salinity of over 30 per mille. Below the Polar Current there occurs a layer with positive temperature (in the fjords, however, conditions are somewhat different), consisting of water derived from the Gulf Stream.

No direct effect of the Gulf Stream can be observed in the littoral. Very possibly, however, the branch of the Irminger Current exerts a certain influence on the climate and consequently indirectly on the littoral. The Polar Current is only some few hundred kilometres broad, and outside this the Gulf Stream extends as a surface current all the way southward to Cape Farewell.

Within the area investigated the so-called fjord water is formed in the summer; it is a surface layer of a thickness of a few metres and with positive temperatures and a salinity below 30 per mille. The thickness of this fjord water layer may vary considerably from year to year, being greatest in the interior of the fjords and smallest near the open sea. It may be about 25 m thick, but no doubt this thickness is rarely attained; the year in which it was observed (1932, Franz Joseph Fjord) was exceptionally favourable.

The peculiar conditions of the fjord water are due to a mixture of fresh water from the land, by which the surface water increases in temperature and decreases in salinity.

Further a heating of the water takes place by insolation. When the temperature is at its highest, it ranges about 7—8°, locally, however, a temperature of 10.7° has been observed, and in the littoral zone it may be still higher (thus in a lagoon at Nordfjord a temperature of 17.2° was measured, and this is hardly the maximum temperature in that kind of localities). The salinity generally ranges about 22—27 per mille, if local conditions (river debouchures) do not interfere. The period in which temperature and salinity are as outlined above is very short, never, or at any rate very rarely, one month. Under favourable conditions the high salinity may prevail for more than one and a half months.

During the breaking up of the frost the fjord water is practically fresh (as stated by THORSON 1933), partly on account of the melting of the snow, partly on account of the melting of the ice, the fjord ice generally melting away almost completely in the fjords (this, for instance, was the case at St. 1 both in 1932 and 1933). This effect of the fresh water on the tidal zone lasts for about one month, mostly longer.

In particularly unfavourable years the ice will not break up till the beginning of August, and sometimes the formation of new ice may

begin at the end of the same month. This gives an idea of the extremely unfavourable life conditions offered by the littoral.

As will be seen, as regards temperature and salinity the factors of the littoral life are directly dependent on the climate. The same applies to conditions on the west coast of Greenland.

Off Upernivik (which region is of the greatest interest, because littoral molluscs still occur here), as at the east coast, there occurs a surface layer with negative temperatures throughout the greater part of the year. Only in the summer will the uppermost layer of this cold water be heated, which here, in contrast to the east coast, has originated by cooling in the winter. Subjacent to this layer, at a depth of about 100 m, the Atlantic water with a positive temperature occurs (NIELSEN 1928).

The account given above is further based on the following works: BRÅRUD and RUD 1932, SPÄRCK 1933, THORSON 1933, and USSING 1934.

2) The Ice.

In the area of East Greenland treated in this paper the ice must have a considerable influence on the littoral life. The ice attains a thickness of about 2 m, and remains very long, at any rate in the fjords. Generally it does not break up till the beginning of July, sometimes still later, even as late as the beginning of August. The formation of new ice begins by the middle or end of September, at times earlier. In the interior of the fjords the ice melts almost entirely before breaking up. At the outer coast, however, it may break up during storms in the winter months, but here the ice-foot remains, so that the effect on the littoral is nearly the same; and no doubt the ice will disappear almost simultaneously with the ice in the fjords, where the ice-foot, resting on a dark substratum and hence much affected by the heat of the sun, will melt soon after the breaking up of the ice.

The time at which the ice disappears within the various parts of the area varies somewhat, but generally only some few days.

To sum up, the littoral is affected by the ice throughout the greater part of the year, since it is only free from ice for about one and a half or two months. These conditions are aggravated in many places, in that pack-ice drifts into the fjords, and scrapes the rocks more or less bare of vegetation, which will only remain in the crevices.

As regards the persistence of the ice-foot in other Arctic regions, very sparse information is available. In fact, its persistence is a point of the greatest interest, since it is the ice-foot that exerts the greatest influence on the life conditions of the organisms of the littoral, more than the land-fast ice itself. However, so much is true that in places

where the ice breaks up on account of currents and wind the ice-foot remains longer than the latter, while it must be assumed to melt at about the same time as the fjord ice.

At Ammagssalik the fjord ice will usually form about the middle or the end of November, but it breaks up at the end of May or the beginning of June. Mostly the outer coast is entirely free from ice in September and October. Accordingly the ice-conditions at Ammagssalik are much more favourable than in the area treated here.

On the whole the climatic conditions seem to be of decisive importance to the ice-foot (ROSENVINGE 1899, p. 150 et seq., SPEER-SCHNEIDER). The whole question stands in great need of a close investigation.

3) The Tide-Water.

Along the coast of Greenland there is a rather gradual decrease of the amplitude of the tidal-water from south to north, though it naturally varies considerably according to local conditions. In the district investigated it is about 1 m (see also *Zweite deutsche Nordpolarfahrt 1869—70*. Kapt. KOLDEWEY, Bd. 2, p. 664, 1874, and TROLLE, 1913, *Medd. om Grønland*. XLI). At Ammagssalik the height of the mean tide is about 1.5 m. The tidal amplitude has evidently no great influence upon the shore life, since it differs greatly in the various arctic regions (Rep. Canad. Arctic Exp. 1913—18, vol. X, part c; HARRIS 1911, GURIANOWA, SACHS, and USCHAKOW 1925₂).

4) Climate.

As shown above, it seems to be the climate which determines the majority of the factors exerting their influence on the littoral. Let us consider now the climatological conditions as they appear from the tables below, which have been compiled on the basis of the works of HELGE PETERSEN 1928, BIRKELAND and SCHOU 1932, and BØCHER 1933₁, and on information concerning Upernivik and Ammagssalik supplied by the Meteorological Institute of Copenhagen (Mr. H. J. HANSEN).

Not all the records are of equal value, thus for instance the observations from Danmarkshavn, Myggebugt, and Scoresby Sound were made through a short series of years only and accordingly are not fully comparable with the rest of the records.

As expressions of the climate the mean precipitation of the year, the mean temperature of the year, and the mean temperature of the months, which in Greenland may be positive or nearly positive, are given, and in addition a table of the mean precipitation of the month.

Table I.

East Greenland	Mean preci- pitation of year in mm	Mean temperature in C°.							
		Year	Apr.	May	June	July	Aug.	Sept.	Oct.
Danmarkshavn.....	146	..	—19.5	—7.3	1.1	4.4	2.2	—4.0	—14.4
Myggebugt.....	80	—10.5	—16.4	—7.0	0.4	3.7	3.0	—2.5	— 9.7
Scoresby Sound.....	317	— 8.2	—12.9	—4.6	1.8	4.1	3.2	—0.7	— 6.9
Ammagssalik.....	891	— 1.9	— 4.5	0.8	4.9	6.6	5.8	3.0	— 1.3
West Greenland									
Upernivik.....	235	— 8.5	—14.1	—3.9	1.7	4.9	4.9	0.8	— 4.0
Godthaab.....	668	— 2.0	— 3.9	0.7	4.5	6.6	6.3	3.2	— 0.9
Ivigut.....	1167	— 0.6	— 0.5	4.5	8.0	9.7	8.4	4.9	1.0

Table II.

Monthly mean precipitation in mm	Jan.	Febr.	March	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Myggebugt.....	5	11	5	4	1.2	6	12	11	1	5	11	6
Scoresby Sound.....	45	43	14	38	7.0	25	14	11	27	28	26	39
Ammagssalik.....	83	51	62	61	61.0	53	49	60	94	144	84	70
Upernivik.....	11	12	17	15	15.0	13	24	29	27	28	27	14

It will appear from the tables that the mean temperature of Upernivik is about the same as in Scoresby Sound and somewhat above that of Myggebugt. The precipitation is less than at Scoresby Sound, considerably higher than at Myggebugt, but less than one-third of the precipitation at Ammagssalik (which, if we disregard Ivigut, is the locality in Greenland that has the greatest precipitation). For comparison may serve that the precipitation on Iceland ranges about the same values. At Myggebugt, Scoresby Sound, and Upernivik most of the precipitation comes down in the form of snow, and accordingly large quantities of fresh water will form during the melting period, which will affect the littoral. The temperature conditions in the two areas on the east and west coasts are much alike.

D. Discussion of the zoogeographical limits on the east coast of Greenland.

It is well known that littoral molluscs occur northward to Upernivik, while on the east coast they extend but slightly north of Ammagssalik, where the climate must in all essentials be like that of the colony itself, that is to say, milder than at Upernivik. Hence it may be concluded that it is not due to any of the special littoral factors that the littoral molluscs, *Balanus balanoides*, etc., have their northern limit in this place. The delimiting factor (or factors) must be sought in the sublittoral.

This view is supported by the fact that a climatic limit seems to run some distance north of 66—67° N. lat., namely in about 68°43'—68°48' N. lat.

This much is true that on this part of the coast there is a distinct floristic and faunistic limit on the land, both to the north and south.

According to information supplied by Dr. DEGERBØL, the southern limits of the Arctic hare as well as the collared lemming occur within this stretch of the coast. A number of butterflies also have their southern limits here, viz. *Colias hecla* LEFEB., *Eupithecia gelidata* MOSCHL., *Bothys tarvalis* MOSCHL., *Pempelia fusca* HUS., and *Plutella semileda* ZETT.; while for instance the snail *Vitrina angelicae* (BECK), and the beetles *Bembidion grapei*, GYLL., *Byrrhus fasciatus*, FORST, and *Otiorhynchus arcticus* (O. FABR.) have their northern limits in this area.

The observations of BØCHER (1933₁, pp. 38 et seq.) also seem to confirm the conjecture as to a climatic limit.

As regards the fauna of the sea, the main limit occurs immediately north of Ammagssalik, at any rate at Kangerdlugssuak, as shown by THORSON (1934₂).

According to SPÄRCK (1933) and THORSON (1933, and 1934₁, and 1934₂) the production of organic matter throughout the area investigated (including Kangerdlugssuak) is inconsiderable. THORSON adds that the few bottom samples from Ammagssalik exhibit a much larger number of animals per square metre than any of the samples from more northerly districts.

The causes of the limit, which evidently occurs somewhere between Kangerdlugssuak and Ammagssalik, and as far as the littoral molluscs are concerned runs at about 66—67° N. lat., are not quite clear. However, there must be some connection with the branch of the Irminger Current that passes from Iceland to the east of Greenland and moves southward along this coast.

It seems natural to seek the causes in improved food conditions, even though these are not the sole causes. It might be assumed that the encounter of the two water masses, the Polar Current and the Irminger Current, gives rise to an increased production of plankton (as is always the case when a cold and a warm current meet (cf. AD. JENSEN 1928, p. 45).

As has been shown above, it is the same factors that delimit the littoral molluscs and the sublittoral southern molluscs; and since the littoral molluscs occur at Upernivik, which has a smaller precipitation than Scoresby Sound, where they are not represented, it may be inferred that it cannot be the increased precipitation at Ammagssalik alone that is responsible for the more favourable food conditions, all the more so since the precipitation is only of special importance in

the fjords, but that we must for the time being be satisfied with the above explanation.

The height of the tidal wave on either side of the limit differs so little that it can exert no influence on the littoral which may result in a difference of the faunas north and south of the limit.

The occurrence of *Fucus vesiculus* at Kangerdlugssuak (ROSENVINGE 1933) might possibly indicate that the climatic factors exert a more direct influence on the littoral algæ. It cannot be denied that the species may occur farther north, even though no specimen has been found.

The absence of an animal form from a particular area may be due to two causes (apart from insufficient investigations). Either the animal cannot survive in that particular place on account of unfavourable external factors, or it has not yet spread to that place.

In our area, at any rate, there are various indications that the species are unable to sustain life there. This especially applies to *Mytilus edulis*, which has lived here in very late geological (postglacial) time; this is evidenced by numerous finds of fossils only a few metres above the level of the present shore (cf. NOE-NYGAARD 1932). Thus the conditions must have been more favourable at that time.

As regards the two other important littoral species, *Littorina saxatilis* var. *groenlandica* and *Balanus balanoides*, it seems most probable that they too are unable to live farther north on the east coast. Both species occur on Spitsbergen, where *Mytilus*, as stated above, is absent. They would seem to have fairly good conditions for spreading with the Irminger Current. None of them has been found as fossils in East Greenland (cf. NOE-NYGAARD 1932).

In fact, a biological investigation of the animals in the boundary zone is required, for it would seem that the animals may change their physiological properties within very wide limits, so that we have to be very cautious in drawing inferences from physiological and biological investigations in other regions. An important evidence of this appears to me to be the formation of relicts.

From Greenland no direct observations concerning the wintering of the above-mentioned littoral species are at hand, whereas some are available from Europe partly by AURIVILIUS (1895), partly by BLEGVAD (1929) and GURJANOVA, SACHS, and USCHAKOV (1930).

It appears from these works that the more mobile species, that is to say the snails, in particular, spend the winter in the sublittoral. That similar conditions exist in East Greenland is indicated by the finds of *Littorina saxatilis* var. *groenlandica* (manuscript by AD. S. JENSEN, Østgrønlandsexp. 1891—92; 1900). The greatest depths at which they were taken are 3—5 fathoms and 6—30 fathoms, on October 22 and May 28 respectively, or immediately before the winter sets in, and at the end of

the winter. No information is available regarding migrations of *Mytilus* on account of the frost (although it is well known that *Mytilus* may move). Only AURIVILIUS (1895) mentions that it burrows somewhat on sandy bottom. Both AURIVILIUS and BLEGVAD (l. c.) record the death of large numbers of *Mytilus* in severe winters, while it may endure short periods of frost (cf. for instance GURJANOVA, SACHS, and USCHAKOV, l. c., p. 36). As to East Greenland, it is stated to be taken in the spring through holes and cracks in the ice (and it forms an important supplement to the food of the natives). Unfortunately, however, nothing is stated as to whether the mussels were taken alive, but it seems reasonable to assume that this was not the case; very probably they have been frozen up in the ice, since they could be taken by the hands at the above-mentioned time (AD. S. JENSEN 1905, p. 324).

According to the above it would seem that the tidal zone is inhabited every summer by sublittoral recruits, so that the size attained by the mussels in the tidal zone may be taken as an expression of the growth of one year (or one summer). However, an investigation of the age and rate of growth of the mussels is required before a final judgment can be made.

Balanus balanoides has no possibility of passing into the sublittoral zone, but it is decidedly and exclusively associated with the tidal zone, so that there is hardly any doubt that it is frozen up in the ice-foot in the winter. But is *Balanus balanoides* on the east coast (and on the west coast) of Greenland annual or biennial? In boreal regions it is mostly biennial, while it is hardly ever annual (cf. RUNNSTRÖM 1925). Are the young better suited to endure frost than the adults? The adults cannot withstand a protracted period of frost (AURIVILIUS l. c.), but at any rate 48 hours (G., S., and U. 1930, p. 36).

AURIVILIUS (l. c.) points out that at a time when the effect of the ice sets in (on the Swedish coast, January and February), the nauplia lie free in the pallial cavities, so that even if the mother animal is scraped off the rocks and perishes, it means no catastrophe to the species. The young, the Cypris larvæ, attach themselves in the spring, often they even swarm in nearly fresh water. But what about conditions when an icefoot is formed?

As will be seen, a number of questions must be solved before we can proceed to a discussion of the details.

IV. THE SHORE FAUNA OF WEST GREENLAND

In the following I shall give an account of the shore fauna of West Greenland on the basis of the particulars found in the available literature. It will deal especially with the southern part of the west coast, since most of the biological data (supplied by O. FABRICIUS in *Fauna groenlandica* 1780) concern the Frederikshaab district, though the available information from more northerly regions will be considered, too. The survey will be worked out according to the same plan as the description of the area investigated by me. The treatment of the identification of species will follow the lines of the *Conspectus Faunae Groenlandicae* given in *Meddelelser om Grønland*, the special papers of which are found in the list of literature.

Rock Facies.

The littoral flora has previously been described, especially by ROSENVINGE (1899, pp. 189—208) and LUND (1933). From these papers it should only be mentioned that the most conspicuous species of the tidal zone are *Fucus vesiculosus* and *Ascophyllum nodosum*. The latter is known northward to Umanak, where it is probably rare, *Fucus vesiculosus* is known northward to Upernivik (72°45' N. lat.), but not found farther north and seems for instance to be absent at Thule.

The littoral fauna is very rich, comprising both sessile and more migratory forms. It will be described in its richest development. There may be great differences locally, for instance at the mouth of glacier rivers, etc. The greater or smaller distance from the outer coast and the degree of shelter will prove to be of very great importance (cf. GURJANOVA, SACHS, and USCHAKOV 1930, p. 185).

Among the sessile forms *Mytilus edulis* and *Balanus balanoides* are especially prominent. These two forms occur in the littoral northward to Upernivik. At Umanak the littoral fauna is still fairly rich.

VANHÖFFEN (1897, pp. 178, 180, 187, 203, and 210) gives some scattered information about conditions in the tidal zone within the Umanak

district. From this description it appears that in the interior of the fjords, in the vicinity of glaciers, the littoral fauna, is very poor, both *Mytilus* and *Balanus balanoides* being absent. Various crustaceans, as for instance *Caprella septentrionalis* and *C. microtuberculata*, occur in the tidal zone; the former is recorded by FABRICIUS, and thus has a wide distribution in the tidal zone. *Gammarellus pinguis*, "*Gammarus locusta*"¹⁾, and *Mysis oculata* are represented. In places where the fresh-water influence is not too marked, *Balanus balanoides* and *Mytilus*, as already stated, are encountered, further *Modiolaria discors* var. *laevigata*, and of other molluscs *Littorina saxatilis* var. *groenlandica*, *Dendronotus frondosus*, and *Onchidorus bilamellata*. All these species are also recorded by FABRICIUS from the tidal zone, where they are thus widely distributed. However, the two latter are regarded by FABRICIUS as rather rare in the littoral. VANHÖFFEN states nothing about Hydroids, etc.

Of other sessile molluscs from the tidal zone FABRICIUS mentions *Saxicava arctica*. How far it extends to the north in the tidal zone is unknown.

Five species of *Hydroidea* occur, none of which have been encountered north of Egedesminde, but no doubt they may also be found in the tidal zone farther north in future. The commonest form must be considered to be *Dynamena pumila*, which is of common occurrence all the way to Egedesminde, where *Laomedea loveni* has been found too. The other species, *Coryne loveni*, *Campanulina lacerata*, and *Laomedea flexuosa*, have only been found in more limited areas, but will no doubt prove to have a wider distribution (KRAMP 1932). FABRICIUS mentions several littoral hydroids, which, however, have not been identified.

Of other sessile animals may be mentioned *Acthelmis intestinalis* (which is recorded as far as Godhavn [from the tidal zone?]), *Urticina felina crassicornis*, *Flustrella hispida*, and *Ascidia prunum*. The other littoral Bryozoans and Ascidians mentioned by FABRICIUS could not be identified.

The migratory forms too are present in immense numbers. The most important *Turbellaria* are *Provortex balticus*, *Astrotorhynchus bifidus*, *Promesostoma marmoratum marmoratum*, *Promesostoma lenticulatum*, *Monocelis fusca*, and *Monocelis lineata*. They have also been found in rock pools with the exception of *Promesostoma lenticulatum* and *Monocelis fusca*. From rock pools alone *Plagiostomum girardi* is recorded.

Here only such *Turbellaria* are included for which the nature of the bottom is given. For these and a number of other forms found in the tidal zone, see STEINBÖCK (1932).

¹⁾ See footnote p. 11.

From rock facies FABRICIUS further mentions (according to REMANE *Fauna arctica* 6, p. 114, Jena 1933) *Dinophilus vorticoides*?, the ubiquitous Polychaete *Harmothoe imbricata*, *Autolytus prismaticus* (ascends only to the third horizon), and three species of *Spirorbis*, viz. *verruca*, *cancellatus*, and notably *violaceus*. LEVINSEN records *Ophyotrocha puerilis* from Egedesminde.

The only Oligochaete found in rock facies is *Lumbricillus minutus*.

Of the Crustaceans *Jaera marina* is of special interest; however, like the majority of the animals inhabiting the tidal zone, it also occurs in deeper water in Greenland. It is known to occur northward to 72° N. lat.

In addition "*Gammarus locusta*" and several of the previously mentioned crustaceans are met with throughout. FABRICIUS further mentions *Spironothocaris groenlandica* (ascends to the third horizon only), and *Hyas araneus*.

Pantopoda also occur in the tidal zone. FABRICIUS mentions four species: *Pycnogonum littorale*, *Phoxichilidium femoratum*, *Pseudopallene spinipes*, and *Nymphon grossipes*.

Strongylocentrotus droebakiensis may, though more exceptionally, venture into the littoral. In company with this species, but more frequently, *Cucumaria frondosa* occurs.

Among the mobile animals, too, the molluscs dominate, partly the purely littoral forms, as for instance *Littorina saxatilis* var. *groenlandica*, *Littorina palliata*, *Purpura lapillus*, *Homalogyra atomus*, *Skeneopsis planorbis*, *Onoba striata*, and *Acmaea testudinalis*, partly forms more frequently associated with the sublittoral, viz. *Margarita helicina*, *M. groenlandica*, *M. cinerea*, *Sipho islandicus*, *Neptunea despecta*, *Buccinum groenlandicum*, and *B. glaciale*. Further the three Nudibranchs recorded by FABRICIUS deserve mention, viz. *Coryphella salmonacea*, *Dendronotus frondosus*, and *Onchidorus bilamellata*. Of these both *Littorina saxatilis* and *Acmaea testudinalis* occur northward to Upernivik, no doubt in the tidal zone. Mr. Vinterberg, for a number of years governor of the colony there, has informed me that he often observed snails in the tidal zone in company with *Balanus balanoides* and *Mytilus edulis*.

Of special interest is the occurrence of *Micralymma marinum* in rock facies in the area of the coast that is affected more or less directly by the Gulf Stream. (Cf. HENRIKSEN and LUNDBECK 1917, p. 497, LINDROTH 1931, pp. 206 and 498).

Sediment Facies.

The tidal zone proper.

(Gravel and) sand strand.

Gravelly shores are no doubt mostly poor in animal life, harbouring especially small worms, *Oligochaeta* and *Turbellaria*, in a considerable number of species (see STEINBÖCK and REISINGER 1930—31, p. 21),

the most important of which are *Promonotus longirostris*, *Otoplana borealis*, and *Paramacrostomum tricladoides*.

On sandy shores we find *Acthelmis intestinalis*, various *Turbellaria*, notably *Otoplana borealis* and *Jensenia angulata*, also *Monocelis fusca* (STEINBÖCK 1932), the Nematodes *Oncholaimus steineri* and *O. onchouris* (DITLEVSEN 1928), the Nemerteans *Amphiporus angulatus angulatus* (extends to the third horizon), *Prostoma candidum*, and *Lineus ruber* (both extending into the second horizon) (E. WESENBERG-LUND 1925).

In addition a number of *Polychaeta* occur, more or less buried in the soil. Throughout the sediment facies (as on rock facies) *Harmothoe imbricata* is found. Below stones *Cirratulus cirratus* and *Naidonereis quadricuspida* are found, and buried in the soil *Eteone longa*, *Nephtys coeca*, *Glycera capitata*, *Syllis cornuta*?, and especially *Arenicola marina* (known throughout the west coast as far as Umanak [in the tidal zone?]). In company with these there occur, buried in the sand, *Mya truncata*. Beneath stones and crawling freely on the sand *Gammarellus homari*, *Clitellio arenarius*, *Purpura lapillus*, *Skeneopsis planorbis*, and *Coryphella salmonacea* are met with. Finally, *Micralymma marinum* and *brevilingue* may be encountered.

Clay shore.

Several of the animals of the sand shore occur on the clay shore in addition to some special forms. Buried in the clay we find: *Eteone longa*, *Spio filiformis*, *Arenicola marina* (extraordinarily big specimens), *Priapulius caudatus*, *Chiridota laevis* (E. WESENBERG-LUND 1930, p. 7), *Tellina baltica* (occurring northward to Umanak), and *Mya truncata*. On the surface: *Clitellio arenarius*, *Coryphella salmonacea*, *Mytilus edulis*.

Clay and sand flats off river mouths.

In contrast to the investigated area of East Greenland, a comparatively rich animal life thrives on clay and sand flats off river mouths in West Greenland, at any rate to the south.

Eteone occurs especially off river mouths, but otherwise mostly crustaceans are encountered. FABRICIUS mentions "*Gammarus locusta*", *Hoplonyx cicada*, and *Nebalia bipes*. Further the Halacarid *Rhombognathus notops*; and in rare cases *Colymbetes dolabratus* was found by FABRICIUS.

No doubt *Pseudalibrotus littoralis*, which is known from the whole west coast, may be found here. In Kola Fjord, whose shore fauna is very similar to that of West Greenland, *Pseudalibrotus* is especially associated with river mouths. As shown below, it is able to thrive in practically fresh water, at any rate in East Greenland. Further it seems probable that in West Greenland with its abundance of species it is more easily ousted from other localities than in East Greenland.

The Upper Beach.

The animal life of the upper beach is but slightly richer than in East Greenland. Below the washed up seaweed we find *Enchytræus albidus*, *Lumbricillus lineatus* (as in East Greenland), and in addition *Lumbricillus profugus*. The *Collembola* are represented by *Onychiurus armatus*, *Isotoma viridis*, and especially *Archisotoma besselsi*, but other species may be found, for instance *Hypogastrura viatica*. Further, the larvæ of the flies mentioned below are encountered here. The bright red-coloured *Molgus littoralis* moves about everywhere. *Phygadeuon cylindraceus* occurs as a parasite on the fly larvæ. Hovering above the shore and in some degree following the receding water *Fucellia fucorum*, *Fucellia intermedia*, *Fucellia ariciformis* (absent from the south, while the others only extend northward to Umanak), and *Scatophaga littorea*, more occasionally *Scatophaga squalida* and *Scatella stagnalis* may be found. *Smittia extrema* (only found to the north) must also be associated with the shore. Finally, beneath the seaweed a number of small beetles, chiefly *Micralymma brevilingue*, occur.

Lagoons and Littoral Meadows.

Hardly any observations of these kinds of shore are available from the west coast of Greenland. LUNDBECK (1893, Medd. om Grønland, Bd. 7, p. 107) records *Deltocephalus lividellus* and, below stones, *Micralymma brevilingue*, apparently from a supralittoral meadow. Further a single Nematode, *Mononchus spectabilis*, is known. However, no doubt the same fauna as observed by me on the east coast is in the main represented here, viz. chiefly *Oligochaeta* and *Nematoda* and, if affected by fresh water, mites, partly *Ameronothrus lineatus*¹⁾, partly *Hermannia scabra*, *Collembola*, Chironomid larvæ (in the north at any rate *Smittia extrema*) and larvæ of shore flies. Where the influence of the fresh water is more prominent, a haloxene fauna with all transitional forms will make its appearance.

¹⁾ Both the main form and the variety are previously recorded, though as subfossils, from Igaliko, West Greenland by GRAVERSEN (1931, p. 11), who distinguished between the two forms on the basis of the dorsal sculpture only, and even found all transitions represented among them. My specimens, too, varied considerably in dorsal sculpture, but still all belonged to *var. nigrofemoratus*, characterised by their feet having only one claw (distinguished from the species *bilineatus* (MICHAEL) by the presence of pseudostigmal organs) (TRÄGÅRDH 1905, p. 21). In GRAVERSEN'S specimens the legs are lacking. As their mode of living must have been the same (according to information supplied by Professor K. JESSEN, the locality was a subfossil littoral meadow), there are various reasons for assuming that *Ameronothrus lineatus var. nigrofemoratus* occurs in West Greenland. In company with *Ameronothrus* GRAVERSEN (1931, pp. 6 and 10) found *Hermannia scabra* (L. KOCH), which, however, has also been found in other localities in West Greenland (MARIE JØRGENSEN 1934, p. 42).

In the lagoons "*Gammarus locusta*" may no doubt be encountered.

The particulars given above represent the main facts recorded about the littoral of Western Greenland. A number of important littoral forms have their northern limits north of Upernivik. This applies to *Fucus vesiculosus*, *Mytilus edulis*, *Littorina saxatilis* var. *groenlandica*, *Acmaea testudinalis*, and *Balanus balanoides*. (STIMPSON's record [1864] of the species from Port Foulke [78°20' N. lat.] must be considered with the greatest scepticism and cannot be accepted until new finds are available).

At Thule the littoral fauna must thus in all essentials be of the same character as in the area of East Greenland investigated by me. However, north of Upernivik the available investigations are so sparse that no detailed information can be deduced from them. An investigation of the shore along the whole of the west coast and the southern part of the east coast is particularly desirable, more especially of the transitional areas.

As we pass northward along the west coast, an increasing number of the animals that are found in the littoral to the south, pass into the sublittoral. At present, however, it is impossible to follow the details of this process. But on the whole it agrees well with the conditions treated by GURJANOWA, SACHS, and USCHAKOW (1930, p. 105). According to these authors, the littoral forms occurring on the north coast of Russia also show a tendency to settle in the sublittoral, which tendency is the more pronounced the more Arctic the climate is.

In both places the littoral animals are on the whole less closely associated with the littoral biotopes than in more southerly regions; for instance *Jaera marina* extends to deeper water at West Greenland than elsewhere.

This shows a peculiar parallelism with conditions in the Baltic. Here, for instance, *Mytilus edulis*, *Cardium edule* L., *Macoma balthica*, and *Mya arenaria* L. occur in much deeper water than in other places (JENSEN and SPÄRCK 1934). The same applies to *Clitellio arenarius* (UDE 1933, p. 50).

This parallelism is very probably due to some extent to competition (cf. JENSEN and SPÄRCK 1934, p. 129).

It is difficult to give a definite answer to the question why a number of insects, for instance *Hydrophilidae* and *Staphylinidae*, which are very characteristic of the upper beach in many other places, e. g. on Iceland (cf. LINDROTH 1931, p. 411), are absent. However, since life conditions, at any rate in the south of Greenland, must be assumed to be very similar to those of Iceland (the climatic conditions, for instance, present great points of resemblance), the reason probably is that the species in question have been unable to spread to Greenland.

V. COMPARISON OF THE SHORE FAUNA IN ARCTIC REGIONS OUTSIDE GREENLAND

Special shore investigations from Arctic regions outside Greenland are but sparsely available, such investigations, though not very detailed, having only been made on Spitsbergen and Novaya Zemlya (SUMMERHAYES and ELTON 1923 pp. 238, 250, 259 and 265; 1928, p. 248 et seq.; GURJANOVA, SACHS, and USCHAKOV 1925₂). However, certain general results and interesting details may still be mentioned, partly on the basis of the above-mentioned works, partly by a combination of the results of the general systematic and zoogeographic papers. The following works have been of the greatest importance: GURJANOVA 1932, ODHNER 1915, ÖKLAND 1928, POPPIUS 1910, Rep. Canad. Arct. Exp. 1913—18, STEPHENSEN 1923 and 1933, STEPHENSON 1925, STUXBERG 1882, SIGTHOR 1930.

Several of the species, for instance *Ameronothrus lineatus* and some of the Oligochaeta (*Enchytræus albidus* and *Lumbricillus aegialites* on Spitsbergen), seem to be present throughout the littoral irrespectively of facies, though always associated with fairly abundant organic substances. Something similar applies for instance to *Molgus littoralis* and *Archisotoma besselsi* in the supralittoral. However, the fauna also shows some difference according to facies; thus the upper beach harbours a fairly rich fauna of land arthropoda notably *Collembola*, flies, and spiders, to some extent different species in the different regions. On the whole conditions are thus very like those of East Greenland, though in more southerly parts with an admixture of more southerly littoral forms. Some details will be given below.

Rock facies.

The fauna of the littoral is very poor everywhere, the essential constituents being at any rate on Spitsbergen, as in East Greenland,

Oribatidae and *Oligochaeta*, but in addition there occur, at any rate in the southern parts of the Arctic region, various of the boreal littoral animals. Thus on Spitsbergen *Balanus balanoides* is found to the south (BERUL 1906, quoted from GURJANOVA, SACHS, and USCHAKOV 1925₂, BROCH 1924, p. 86, Cap Brun), *Littorina saxatilis* var. *groenlandica* in Icefjord (to a depth of 45 m, living and abundant), and also some Hydroids and Bryozoans. It is remarkable that *Mytilus edulis* is not found there, though it is known from post-glacial deposits. In this connection it may be mentioned that *Skeneopsis planorbis* has not been found either¹). The southern character is strongly emphasised by the presence of *Micralymma marinum* at the southern point of Spitsbergen (LINDROTH 1931, pp. 498 and 579). Since this species occurs on Bear Island also, it may be supposed that the shore fauna is of a similar type to that of southern Spitsbergen, even though littoral molluscs are not recorded from the island (the southern character of its fauna is also emphasised by the finding of boreal *Oligochaeta*, *Lumbricillus fossarum* and *Enchytraeoides ebudensis* (UDE 1933, pp. 45—46)).

On the southwest coast of Novaya Zemlya *Mytilus edulis* and *Acmaea testudinalis* are to be found (GRIEG 1924, pp. 5 and 13, see also AD. S. JENSEN 1912, p. 47), while *Balanus balanoides* has been searched for in vain on Matotschkin Schar. Very possibly *Mytilus edulis* and *Acmaea testudinalis* do not occur in the tidal zone on the west coast of Novaya Zemlya. Thus in the Baltic *Mytilus edulis* may descend to much greater depths, and the available specimens are not derived from the tidal zone. However, it cannot be inferred from this fact that they do not occur in the tidal zone also. Wherever it was found in Greenland, it occurred in the tidal zone as well as in the uppermost zone of the sublittoral. The remaining part of Novaya Zemlya, northern Spitsbergen, Jan Mayen²), the north coast of Sibiria, and the northernmost parts of North America with the exception of the north coast of the North American continent, where *Mytilus edulis* and *Littorina saxatilis* var. *groenlandica* are present, seem to agree in all essentials with the northern part of East Greenland. Finally it may be mentioned that "*Gammarus locusta*"³) is recorded from Spitsbergen and Arctic America, *Gammarus locusta* var. *sovinski* from Novaya Zemlya, and *Gammarus wilkitzki* from Franz Josef Land and the north coast of Sibiria.

¹) Although it is recorded in the literature right up to recent years on account of an erroneous quotation of JEFFREYS.

²) BECHER (1886, p. 76) records *Littorina palliata*. Since this find is quite isolated and rather improbable, a closer investigation should be awaited.

³) See footnote p. 11.

Sediment facies.

In the tidal zone proper conditions seem to be very like those of East Greenland everywhere. *Turbellaria*, it is true, have not yet been found (*Nemertina* is recorded from Spitsbergen), but may no doubt be discovered if suitable collecting methods are employed. In the south of Spitsbergen the southern character of the fauna is evidenced by the occurrence of *Rhizomolgula globulus*. With a similar mode of living to that of *Pseudolibrotus littoralis* (which on the east coast of Novaya Zemlya and the Siberian coast is replaced by *Pseudolibrotus birulai*) *Mesidothea entomon* occurs on Novaya Zemlya and along the north coast of Siberia and Arctic America (GURJANOVA 1930, p. 239; BIRNSTEIN 1933; BOONE 1920, p. 20). In Arctic America also *Mesidothea sabinei* (BOONE l. c.). *Harpacticoidea* may probably also be found everywhere, thus *Harpacticus uniremis* and *Tisbe furcata* are recorded from Arctic America (WILLEY 1920, pp. 32 and 34); the same forms occur in East Greenland.

The upper beach, particularly the bank of washed up sea-weed and the undersides of the stones, harbours a comparatively rich animal life. As in East Greenland mites and *Oligochaeta* predominate, in part different species, and in addition *Collembola*, flies, and spiders. *Molgus littoralis* is evidently circumpolar (though curiously enough it is not mentioned from Franz Josef Land). Widely distributed also is *Bdella decipiens*, which is found on Spitsbergen, along the north coast of Siberia, and in Arctic America (Bernard Harbour) (TRÄGÅRDH 1902, BANKS 1911).

In northern Spitsbergen the two above-mentioned species of mites, like *Molgus* in East Greenland, are not strictly associated with the shore (as in boreal regions), but also occur farther inland, a fact which has doubtless some connection with the lack of competition from other species. Similar interesting observations may no doubt be made on Jan Mayen. From this island, which is very poor in species, *Lumbricillus profugus* (CERNOSVITOV 1935) and *Ameronothrus lineatus* (TRÄGÅRD 1904) are recorded from mosses; these species are elsewhere associated with the shore, and no doubt they also live on the shores of Jan Mayen. In the drift line *Ameronothrus* is found in Spitsbergen (undoubtedly overlooked in such localities in East Greenland) and Arctic America (Bernard Harbour, BANKS 1911, both the main species and the variety).

Enchytræus albidus has been found in many localities (Spitsbergen Bear Island, Novaya Zemlya) and may no doubt be found in most places. Peculiarly enough *Lumbricillus lineatus* has not been found on Spitsbergen (which has been fairly well searched for *Oligochaeta*) but is replaced by *Lumbricillus aegialites*. *Lumbricillus lineatus*, however, is recorded from Bernard Harbour (SMITH and WELCH 1919, p. 15). Along the coast of Siberia only *Henlea ventriculosa* and on the New Siberian Island *Mesenchytraeus kincaidi* have been found (UDE 1933).

As regards the Collembola, detailed information is only at hand from Spitsbergen. Here the same forms dominate as in East Greenland. *Agrenia bidenticulata* also is of regular occurrence. Something similar no doubt applies to Jan Mayen, *Archisotoma besselsi* having at any rate been found there.

Arctic America and East Greenland have the fauna of shore flies in common, *Fucellia ariciformis* and *Fucellia pictipennis* occurring in both places (MALLOCH 1919, p. 25), while *Fucomyia frigida* (which according to LINDROTH 1931 also includes *Fucomyia parvula*, mentioned by SUMMERHAYES and ELTON) is common to Spitsbergen and Novaya Zemlya. No shore flies are known from Siberia. From Jan Mayen, Spitsbergen, West Greenland, and boreal areas on either side of the Atlantic *Fucellia fucorum* is recorded (HENRIKSEN and LUNDBECK 1917).

As in East Greenland *Erigone tirolensis* occurs on Spitsbergen, and in addition *Typochrestus spitsbergensis* (spider) is found, which also occurs as a shore form in Arctic America. From the latter locality another shore spider, too, is recorded, viz. *Microneta maritima* (EMERTON 1919). It is of special interest that *Erigone palaeartica*, which was formerly confused with *Erigone arctica* (BRÆNDEGAARD 1934, p. 48), occurs as a shore form on Spitsbergen, as in boreal regions, while the real *Erigone arctica*, as mentioned above, appears as a shore animal in East Greenland. The occurrence of beetles at the shore (as in West Greenland) is only known from northern Siberia, where *Microlymma dicksoni* has evidently exactly the same mode of living as *Micralymma brevilingue* in Greenland. The presence of *Atheta prope frigida* on Spitsbergen is probably quite casual (only found once). It is an interesting fact that on the north coast of Russia the eastern limit of a number of decidedly littoral beetles occurs near the boundary between the subarctic and the arctic littoral faunas (see below), *Micralymma marinum* and *Omalium laeviusculum* extending as far as the Kola Peninsula, while *Dichirotrichus pubescens* and *Agonum archangelicum* occur as far as the Kanin Peninsula.

About the animal life of lagoons and littoral meadows rather exhaustive information is available from Spitsbergen, notably through the papers of SUMMERHAYES and ELTON, and OLOFSSON. The lagoons are of a somewhat different character from those investigated by me in East Greenland. Some of them are of a considerable size and, what is of special importance, fairly deep. It is these large lagoons that give rise to the well-known relict lakes on Spitsbergen. SUMMERHAYES and ELTON (1923, p. 238) describe such a lagoon (Prince Charles Foreland) about 3 m deep. It contained a great number of purely marine organisms, for instance *Hydroida*, Bryozoans, various *Polychaeta*, and even a mussel (*Liocyma fluctuosa*) in addition to the euryhaline crustaceans, *Mysis*

oculata (often the variety *relicta*), and brackish-water *Copepoda*, e.g. *Eurythemora raboti*, *Tachidius spitzbergensis*, and *T. longicornis* (more occasionally other *Copepoda* [see OLOFSSON 1917—18, p. 286]). The animal life of these larger or smaller lagoons and to some extent of the littoral meadows is similar to that of East Greenland. However, the *Oligochaeta* are chiefly represented by other species, viz. *Enchytræus crymodes*, *E. eltoni*, *E. muscicola*, *E. aporus*, which are largely associated with the areas of the littoral meadows showing fresh-water influence, and in addition the forms living in the shingle bank besides the ubiquitous species *Enchytræus liefdeensis*.

The number of individuals of *Enchytræus crymodes* in a sample of moss was found to be 230 individuals per 100 sq. cm, while another moss sample from a drier locality contained 175 individuals per 100 sq. cm. These figures are much higher than the mean figure for East Greenland (about 75 individuals per sq. cm), though some samples containing about 180 individuals per sq. cm were taken (p. 32).

In the lagoons and littoral meadows the larvæ of *Smittia extrema* and *Orthocladius decoratus* may no doubt be met with in several places. Curiously enough, however, SUMMERHAYES and ELTON (1923, p. 270) expressly state that in some particularly well investigated lagoons, the bottom of which were covered with blue-green algal films, they failed to find Chironomide larvæ. It is further remarkable that they do not record *Oligochaeta* from the same lagoons. This may be a mere accident, but it seems more probable to me that they have been working with rackets, since both the *Oligochaeta* and the Chironomide larvæ may be expected to live in the blue-green algal film (*Smittia* and *Orthocladius* larvæ belong to the terrestrial type) and may easily have escaped the racket. The Collembola fauna is mainly of the same type as that of East Greenland, supplemented by *Agrenia bidenticulata*. Noteworthy is the occurrence of *Folsomia sexoculata*. Curiously enough *Ameronothrus lineatus* has not been found in the littoral meadows. There can be no doubt, however, that this is due to unsuitable collecting methods. It is probably from similar localities that *Svalbardia paludicola* (SIG. THOR 1930, p. 76) has been found "an feuchten Lokalitäten, am Meere".

SCHOLANDER (1934) gives an account of the shore vegetation, especially from the north of Spitsbergen, from which it appears that the three dominant species are the same as in East Greenland, and that they all extend to the extreme northern point. The vegetation of the littoral meadows has also been investigated by WALTON (1922).

As stated in p. 44, the sediment facies of East Greenland exhibits an almost lifeless zone from low-water mark to a depth of about 3 m. A similar zone is found on Spitsbergen, at any rate in Icefjord, but it only extends to a depth of 2 m. This appears partly from the description

of the above-mentioned lagoon about 3 m deep, partly from the conditions under which molluscs were found in Icefjord (ODHNER 1915). In certain parts of Spitsbergen the zone may no doubt extend to greater depths.

The small extent of this zone devoid of animal life is in good agreement with the southern character of the shore fauna, as compared with the investigated area of East Greenland. On Matotschkin Schar (Novaya Zemlya) the sediment facies also includes such a zone to a depth of c. 4 m (GURJANOVA, SACHS and USCHAKOV 1925₂).

VI. ERECTION OF ZOOGEOGRAPHICAL REGIONS

In the following an attempt will be made to explain, on the basis of the information given above, the zoogeographical regions into which the strictly littoral zone may be divided (the supralittoral will only be discussed more incidentally).

The only attempt so far made to subdivide the Arctic littoral, has been made by GURJANOVA, SACHS, and USCHAKOV (1925₂). They treat especially the North Russian seas, but also discuss the littoral of Novaya Zemlya, Spitsbergen, Siberia, etc.

These authors distinguish between what they term three littoral provinces, 1) the high-arctic, which is stated to be distinguished by a completely dead littoral zone, 2) the arctic, with traces of a littoral fauna and flora, and 3) the sub-arctic province, especially represented by the littoral of Kola Fjord, which they have treated in great detail in a series of works.

The subarctic province is distinguished by a rich littoral fauna, comprising in the first place a number of littoral molluscs, hydroids, *Balanus balanoides*, etc. The western boundary of this zone is not discussed at all, but they simply state: "The western boundary of the sub-arctic province is entirely unknown to us". To the east they draw the boundary almost at the mouth of the White Sea, the White Sea proper being included in the region.

As will be seen from the above-mentioned definition by GURJANOVA, SACHS, and USCHAKOV, their delimitation of the various regions is very vague.

STUXBERG (1882, p. 731) states that he failed to find any animals in the littoral, but later GURJANOVA found both *Gammarus wilkitzki* and *Pseudalibrotus birulai* on the north coast of Siberia. Why should not, then, *Gammarus wilkitzki*, which was observed by me in completely fresh water in tidal cracks, extend into the littoral? The algal vegetation has not at any rate disappeared everywhere (KJELLMANN 1882, p. 223).

Thus the "high-arctic" province is very poorly delimited. Even the

height of the tidal wave, which they state to be inconsiderable in this province, affords an unsuitable basis for a delimitation, more especially since several of the heights measured attain those of their Arctic province.

The delimitation of the "arctic" province is hardly better. In this province is included the western end of Matotschkin Schar, which is especially distinguished by its richer algal vegetation, and Spitsbergen, because *Balanus balanoides* occurs there.

In my opinion a more natural division may be obtained by operating for the time being with two regions only, viz. an arctic and a subarctic (or boreo-arctic) region.

The boundary of the arctic region should be drawn where the littoral molluscs and *Balanus balanoides* disappear. This division seems to me to be clearer and more natural, as it is an expression of specially arctic conditions.

The southern boundary of the subarctic region should in my opinion most naturally be drawn at the southern limits of two specially Arctic littoral animals, *Mysis oculata* and *Pseudalibrotus littoralis*. As shown above, these animals are of great importance in the Arctic littoral region.

It seems to me that there is all the more reason to adopt the latter delimitation, since other changes also take place at that limit.

Of special interest is the main occurrence within the same areas (i. e. the subarctic region as defined above) of *Littorina palliata* and notably *Littorina saxatilis* var. *groenlandica*, since wherever *Littorina saxatilis* is represented within the limits given above it is by the variety *groenlandica*.

However, the region does not present any very sharp boundary lines, since the various forms may in various ways spread beyond their limits as defined above, the different species reacting differently to the external factors. Nor does the subarctic region exhibit its full stock of animals to its extreme limits. Accordingly, when in future more detailed investigations become available, there may be a possibility of subdividing the large regions as an expression of the varying life conditions within the various parts of the regions.

Indications of such differences appear even from the particulars now available. I shall confine myself to giving a few examples.

GURJANOVA, SACHS, and USCHAKOV (1925₁) separate the littoral of the White Sea as a special sub-province, characterised by its heavier ice-cover and a stronger influence of fresh-water. Especially remarkable is the absence of *Purpura lapillus*, which, however, seems to be a local phenomenon since in the interior of Kola Fjord the littoral fauna exhibits almost the same character (for the same reasons).

A comparison between the subarctic provinces of northern Europe and northern Iceland shows that on Iceland conditions are more severe than in northern Europe. Thus on the littoral of northern Iceland a number of species are lacking which extend far into the European subarctic region, for instance *Idothea balthica* (PALLAS) (HANSEN 1916, p. 187) and *Purpura lapillus* (BARÐARSON 1920, p. 100). Some other species are met with in both places, but within the European subarctic region in the tidal zone only, while on Iceland they chiefly pass into the sublittoral, viz. *Cyamium minutum*, and *Buccinum undatum* (BARÐARSON 1920, pp. 63 and 102; SARS 1878, pp. 65 and 254). These species occur in the tidal zone on the west coast of Iceland. From these examples it also appears that the littoral conditions in the southern part of West Greenland are milder than at the north coast of Iceland (cf. above p. 54).

At the west coast of Norway the boundary line that has been drawn for the littoral is further confirmed by other species; thus the limit is not passed by *Patella vulgata* L. (SARS 1878, p. 118). (This species does not occur on Iceland), and *Littorina palliata* and *Littorina saxatilis* var. *groenlandica* keep within the limit (SARS l. c. p. 165); nor do *Pantopoda* occur in the littoral of the subarctic zone of Norway (DONS 1932), whereas, as stated above, they have been found in the littoral of South Greenland.

The severe conditions for life on Iceland are revealed by the fact that *Littorina palliata* and *Littorina saxatilis* var. *groenlandica* spread beyond the limits of the subarctic littoral province. However, *Littorina palliata* is doubtless commonest on the north coast, while (according to BARÐARSON) all the Icelandic forms of *Littorina saxatilis* belong to var. *groenlandica*. On the other hand, *Littorina obtusata* L. is most commonly met with on the south coast of Iceland (BARÐARSON 1920, pp. 89—90).

The presence of a subarctic province here is no doubt due to some extent to the branch of the East Greenland Polar Current that moves along the north coast of Iceland, while on the other hand the Irminger Current running along the west coast contributes to the boreal character of this coast. However, the causes of these phenomena have not yet been fully elucidated, no doubt they are very complicated.

The littoral of southern Spitsbergen also occupies an exceptional position within the subarctic province. However, special investigations are required before a more detailed subdivision can be made.

Below I shall briefly define the extension of the arctic and subarctic regions. The results are shown in the map fig. 17.

In Greenland both the arctic and the subarctic regions are represented, as appears from the account of the shore fauna of Greenland given above. On the east coast the limit occurs in about 66—67° N. lat.,

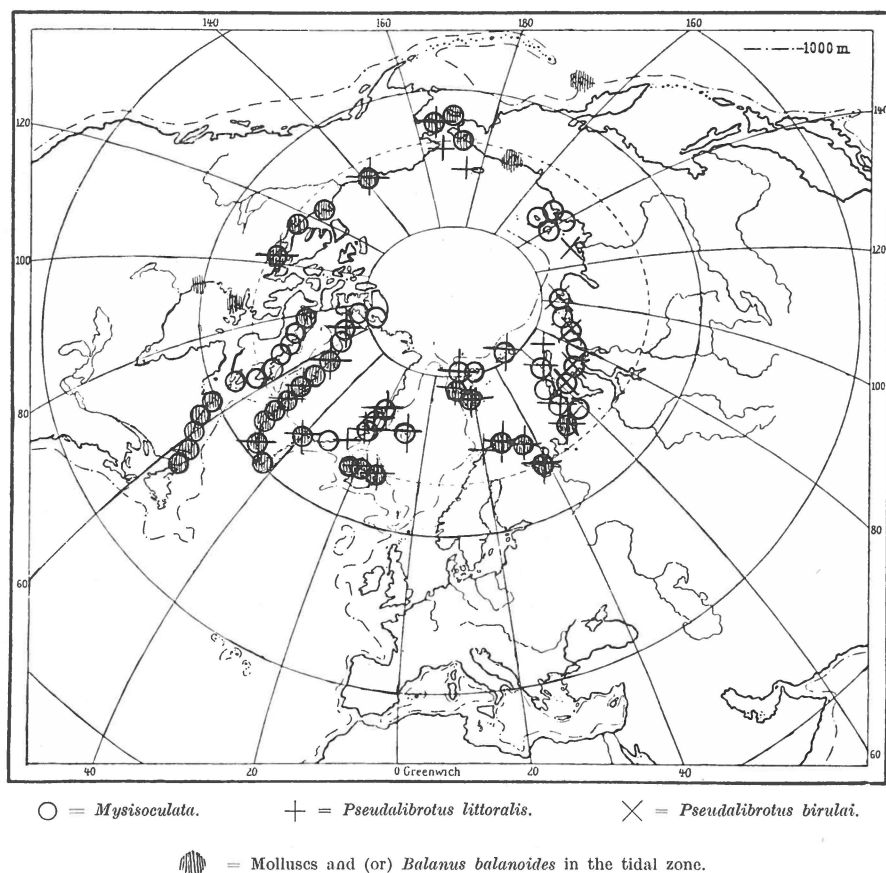


Fig. 17. Map showing the extension of the arctic and subarctic littoral regions, the arctic distinguished by the lack of littoral molluscs, etc., the subarctic delimited by the distribution of *Mysis oculata* and *Pseudalibrotus littoralis*.

The map is based on the following maps: STEPHENSEN 1923, chart. 11, p. 57, GURJANOVA 1932, map p. 166, and STEPHENSEN 1933 II fig. 5, p. 13, and on particulars given in the text.

The littoral of Jan Mayen should probably be regarded as arctic. (The occurrence of *Littorina palliata* at any rate needs confirmation).

the arctic province occurring north of and the subarctic province south of the limit. Where the limit should be drawn on the west coast, is unknown, but it is a fact that Upernivik is situated in the subarctic region, whereas in all probability the Thule district and the coasts north and east of this district belong to the arctic province.

As regards the littoral of Iceland, the north coast must be referred to the subarctic region, while the remainder of the country belongs to the boreal province.

The south and west coasts of Spitsbergen must be regarded as

the farthest outposts of the subarctic region, while the remainder of the country probably belongs to the arctic province. As regards the littoral of Bear Island nothing definite can be stated; if littoral molluscs occur here (which they probably do), it must be referred to the subarctic province.

Franz Josef Land is undoubtedly arctic.

The greater part of Novaya Zemlya also belongs to the arctic province. However, the southwestern part of the country is in need of a closer investigation before the question can be definitely settled (see above p. 59).

On the basis of the information supplied by Sars (1878) and STEPHENSON (1923 and 1933) the western limit of the subarctic littoral region should be drawn near the Lofoten, while the eastern boundary must be drawn at Tscheschskaja Guba (or possibly a little farther east, since GURIANOVA 1932, p. 182 mentions *Balanus balanoides* from the Kara Sea [but without indicating the locality]). The arctic province extends from this point to the vicinity of Cape Schelagskoj (170°17' E. long.), east of which the subarctic region extends at any rate to the west side of Bering Strait, possibly somewhat farther south, due to the cold current that moves southward along the coast of Kamtchatka, *Littorina saxatilis* var. *groenlandica* (according to AURIVILIUS 1887, p. 325) being found on Bering Island. *Pseudalibrotus littoralis* is known from Wrangel Island to Bering Strait, while *Mysis oculata* extends at any rate to Lorenz Island.

The southern boundary of the subarctic region of America is on the east side of Bering Strait (according to SHELFORD [1930] a well developed *Balanus balanoides*-*Littorina* community extends thus far). *Mysis oculata* is recorded as far as Collinson Point slightly west of the mouth of Mackenzie River, while *Pseudalibrotus littoralis* has been found as far as Bering Strait (SCHMITT 1919, SHOEMAKER 1920, and GURJANOVA 1932, p. 166, map). *Littorina saxatilis* var. *groenlandica* has not been collected west of Bernard Harbour, while *Mytilus* is known even beyond Bering Strait (DALL 1919).

Turning eastward, probably the whole coast of the American continent including Hudson Bay as far as Cape Charles at the southeastern corner of Labrador, should probably be referred to the subarctic province¹).

¹) The same applies to the east coast of Baffin Land northward to Lancaster Sound, since *Mytilus edulis* has been found at Ponds Inlet (in two localities), though it is not recorded from the intermediate regions. It should be noted that this record is based on the finding of washed up, but undoubtedly fresh, shells found in the material of the 5th Thule Expedition. Thus more detailed investigations are required before these regions can be definitely grouped.

Mysis oculata has its southern limit at Cape Charles (nothing is known about *Pseudalibrotus* in these tracts). PACKARD (1865) records some particulars about certain littoral species in this area; *Dynamena pumila* has been collected in the tidal zone at Belle Isle (i. e. in the boundary area). Of special interest is his record of *Littorina palliata*. *Mytilus edulis* is stated to be abundant. *Balanus balanoides* is mentioned. *Littorina saxatilis* is also common, but no varieties, if such are present, are mentioned. "*Gammarus locusta*" and *Mysis oculata* are of common occurrence. *Ischnochiton albus* and *Acmaea testudinalis* "occurred just below low-water mark". The same applies to the species of *Margarita* enumerated.

The remaining part of Arctic America is so poorly investigated that it is impossible to obtain an idea of conditions there.

Judging from its algal flora, Ellesmere Land should be referred to the arctic province. The algal flora as a whole is fairly poor, and the species so characteristic of the subarctic littoral of Greenland, viz. *Fucus vesiculosus* and *Ascophyllum nodosum*, have at any rate not been met with there (ROSENVINGE 1926, SØREN LUND 1933). However, this reference is quite hypothetical, an investigation of the fauna being much needed.

In this connection it may be mentioned that neither the Canadian Arctic Expedition nor the Second Norwegian Expedition in the "Fram" brought home any littoral hydroids, the latter also no littoral molluscs from America (GRIEG 1909).

It is impossible to enter into a detailed discussion of cause and effect in connection with the regions erected. However, there are some few conspicuous features in Greenland and the area round the Barentz Sea. Here an amelioration of the external factors can be observed when warm currents pass by, while a deterioration is produced by cold sea-currents.

The farthest subarctic outpost on Spitsbergen has decidedly some connection with the branch of the Gulf Stream that extends to these quarters. The same applies to East Greenland. In the north of Iceland the cold current produces the subarctic province, while the Gulf Stream along the coasts of Norway and Finmark clears a way for the subarctic province in a northern area.

In America the Labrador current causes an extension of the subarctic province to southern latitudes.

As regards the animals of the upper beach the limits will follow different courses, corresponding more closely to the climatic limits; a few characteristic features may be enumerated.

Exclusively littoral insects (apart from *Collembola*) do not spread to the arctic littoral region, while the subarctic region is everywhere distinguished by its lack of the *Orchestia* community so characteristic

of many boreal areas (though not present in all boreal regions, thus it is absent from the northern boreal Norway [according to our division] and from the whole of Iceland). It is therefore interesting that *Ligia oceanica* (L.), which in Norway chiefly follows the *Orchestia* community (though it extends somewhat farther north), has been found on Vestmann Islands (HANSEN 1916; STEPHENSEN 1929, table 2, p. 32).

As regards the *Orchestia* community, see MORTENSEN (1922) and DAVENPORT (1903). As regards especially boreal shore faunas, see FLATTELEY and WALTON (1922); the latter paper as also GISLEN (1929—30 II, pp. 1—46) contribute comprehensive lists of references concerning the shore fauna and the shore ecology. GISLEN gives a historic survey of marine ecology.

As pointed out by BROCH (1933), a zoogeographic delimitation based on the different depths is necessary, and it is such a delimitation which I have attempted to give above. I have tried to comply with the claim, in my opinion justified, that a limit "einigermassen ausgesprochene doppelseitige Bedeutung hat". Thus we cannot expect a full agreement with the regional divisions of other deep regions, but as shown by BROCH (l. c.), the sea-currents exert a considerable influence on the littoral regions as well as on the other divisions, not only on account of the temperature conditions (Cf. especially BROCH l. c. p. 11), so that no limits can be drawn in close connection with certain isotherms.

BROCH (l. c., p. 18) shows various limits on a map, but they agree only approximately with those outlined by me. However, as pointed out above, a closer fixation of the limits will require more detailed and special investigations, and these may possibly increase the agreement. Very likely an investigation of the conditions prevailing on the west coast of Greenland will throw light on these problems. The possibility of a subdivision is foreshadowed by the available facts, but definite rules for such a division must depend on the results of future investigations.

SUMMARY

1) A survey is given of the shore fauna of East Greenland north of c. 66°—67° N. lat., based on my own investigations in Christian X.'s Land. The littoral fauna (strictly in the tidal zone) is especially characterised by the absence of littoral molluscs and *Balanidea*, notably *Mytilus edulis*, *Littorina saxatilis* var. *groenlandica*, and *Balanus balanoides*, all of which occur south of the above-mentioned limit. The *Oligochaeta* *Enchytræus albidus* and *Lumbricillus lineatus* as also the mite *Ameronothrus lineatus* var. *nigrofemoratus* are distributed nearly throughout the littoral independently of facies, being associated with the occurrence of abundant organic substances. Further *Gammarus wilkitzki*?¹⁾ and *Mysis oculata* are present everywhere. Similarly the mite *Molgus littoralis* was found in the supralittoral, and on sediment facies the *Collembola* *Hypogastrura viatica* and *Archisotoma besselsi*. In the tidal zone proper *Turbellaria*, notably *Monocelis fusca* and *Harpacticoidea*. On sand and clay the Amphipode *Pseudalibrotus littoralis*. On the upper beach, besides the ubiquitous shore forms, flies, especially *Fucellia ariciformis*, *Chironomides*, *Smittia (extrema?)*²⁾, *Orthocladius decoratus*, and *O. groenlandensis*, and various *Araneida*. In lagoons and littoral meadows an Enchytraeid-Nematode community occurs, which with fresh water influence includes *Arthropoda*, chiefly *Ameronothrus* and larvae of the above-mentioned Chironomides.

Rock facies exhibit a comparatively well developed littoral flora, which, however, lacks *Ascophyllum nodosum* and, north of Kangerdlugsuak, *Fucus vesiculosus*. Some other botanical phenomena are also treated on the basis of the available literature. A survey of the bird life is given in p. 19.

The plant life is of but slight, and the animal life of no importance geologically.

2) It has been ascertained that the absence of littoral molluscs and *Balanus balanoides* is not due to a special littoral factor, but

¹⁾ See footnote p. 11.

²⁾ See footnote p. 23.

to a factor that also affects the sublittoral, presumably poor food conditions. Near the northern limit of the littoral molluscs these conditions are improved on account of the meeting of the Irminger Current and the East Greenland Polar Current.

3) An account is given of the shore fauna of West Greenland on the basis of the available literature, chiefly the biological investigations by OTTO FABRICIUS (in *Fauna groenlandica* 1780). The southern part, in particular, has a rich littoral fauna including many littoral molluscs, *Balanus balanoides*, Hydroids; the sediment facies exhibits molluscs and *Arenicola marina*, that is to say, great similarity to the littoral faunas of Iceland and the Kola Fjord (GURJANOVA, SACHS, and USCHAKOV). It must be assumed that the lack of a number of insects, such as *Hydrophilidae* and several *Staphylinidae*, which are very characteristic of the upper beach in boreal regions, for instance on Iceland, is due to ecological causes of dispersal.

4) A similar survey is given of other Arctic regions. They agree in broad features with East Greenland; only the most southerly parts (for instance southern Spitsbergen, possibly southwestern Novaya Zemlya, and the north coast of the American continent) show an admixture of boreal littoral forms. Spitsbergen alone has been fairly well investigated.

5) On the basis of the information thus procured, a zoogeographical division of the littoral of the northern seas has been made. This appears from the map in fig. 17, p. 67.

6) It has turned out that many species (both plants and animals) of the Arctic are not so strictly associated with the shore as in boreal tracts. This is due to some extent to a less keen competition between the smaller number of species present (examples in pp. 22, 44, 57 and 60).

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