CONTRIBUTIONS TO THE ECOLOGY OF SPITSBERGEN AND BEAR ISLAND

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(With Plates II–IV and seven Figures in the Text.)

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I. INTRODUCTION.

The account given below is the result of investigations carried out by us while members of the Oxford University Expedition to Spitsbergen during the summer of 1921. A fairly complete idea of the biology was obtained, as during the rest of the year nearly all the plants and animals remain dormant under thick snow, or have migrated southwards.

Owing to the varied requirements of the members of the Expedition, it was in many cases impossible to complete the work on the areas visited. In some cases a visit of a few hours only was possible. Ten days were spent on each of two areas—on Bear Island (June 13th–23rd) and on Prince Charles

1 “Results of the Oxford University Expedition to Spitsbergen, 1921.” No. 29.
Foreland, Spitsbergen (June 30th–July 10th)—while one of us stayed at the head of Klaas Billen Bay from July 19th to August 16th.

As the Rev. F. C. R. Jourdain is publishing in the future a manual on the birds of Spitsbergen, details of this group are only given in so far as they make clear the animal communities. The material collected was identified by various specialists, and we follow their nomenclature in most instances. We should like to express our thanks to them for identifying members of the following groups: PLANTS: Phanerogams and Pteridophytes, Mr. A. J. Wilmott; Mosses, Mr. H. N. Dixon; Liverworts, Dr. W. Watson; Lichens, Mr. R. Paulson; Marine Algae, Mr. A. Gepp; and Freshwater Algae, Mr. B. M. Griffiths. ANIMALS: Tunicata and Polyzoa, Mr. R. Kirkpatrick; Mollusca (and much other help), Mr. G. C. Robson; Spiders, Dr. A. R. Jackson; Land mites, Rev. J. E. Hull; Water mites, Mr. C. D. Soar; Diptera (Nematocera), Mr. F. W. Edwards; Diptera (Orthorrhapha, etc.), Mr. J. E. Collin; Hymenoptera (Sawflies), Mr. F. D. Morice; Parasitic Hymenoptera and Mallophaga, Rev. J. Waterston; Fleas, Mr. K. Jordan; Collembola, Dr. G. H. Carpenter and Miss K. C. Joyce Phillips; Mysidacea, Dr. W. M. Tattersall; help with Amphipoda, Dr. W. T. Calman; Leeches, Dr. H. A. Baylis; Polychaeta, Mons. P. Fauvel; Oligochaeta, Dr. J. Stephenson; Rotifera, Mr. D. Bryce; Hydroidea, Mr. K. Totten; and Protozoa and Bacteria, Mr. H. Sandon.

We also thank Mr. J. F. Manley for two water analyses and Mr. H. C. Mills for the chloride determinations. We are deeply indebted to Professor E. B. Poulton and to Professor F. W. Oliver for much help in getting the animal and plant collections determined, and in other ways. We should like to express our gratitude to the members of the Expedition, whose help is much appreciated. In particular we owe our thanks to the Rev. F. C. R. Jourdain (32), Dr. T. G. Longstaff, Messrs. J. S. Huxley, A. M. Carr-Saunders and J. Walton. We are indebted to Mr. J. Mathieson of the Scottish Spitsbergen Syndicate for permission to reproduce the map of Prince Charles Foreland, and to Messrs. A. M. Carr-Saunders and J. Walton for the use of various photographs.

Although a great many papers have been published on the Flora and Fauna of the region, yet few have dealt with the plant communities, and practically none with those of the animals. Of the latter we have found Olofsson’s papers (47, 48) a great help in connection with the freshwater communities. The first and almost the only important work on the plant communities is that of Nathorst (44) who divides the country into (1) Strand, (2) Bogs, (3) Slopes, and points out the main plants in each. Other writers have noticed prominent communities such as “slopes under bird cliffs,” etc., or have dealt with general life conditions in the Arctic.

The seasonal succession in the animals is not so marked as in temperate countries, and does not lead to many errors in collecting, the only exceptions being the Diptera and Hymenoptera. A short visit to a locality, if the ground is worked carefully, gives a true idea of most of the animal communities.
Owing to the labour of collecting animals typical areas were selected, and these were worked out in detail.

Detailed experimental work was only possible at Klaas Billen Bay, and the division into communities therefore rests usually on more easily obtained superficial evidence. The account is in no way to be considered an attempt at a final classification of communities in the region.

II. BEAR ISLAND.

INTRODUCTION.

We propose to deal with Bear Island first because it is much smaller, has fewer species of plants and animals, and is therefore simpler than Spitsbergen. Also, in some ways, it is transitional between Arctic Europe and Spitsbergen.

Bear Island lies 240 miles north of Scandinavia, on the western edge of the shallow submarine bank of the Barents Sea, while to the west is the deep Greenland Sea. The island (Fig. 1) consists of two distinct portions—a flat northern area of sedimentary rocks, and a southern mountainous part composed mostly of the faulted and metamorphosed layers of the Hecla-Hook system. Mount Misery (1800 feet) is the highest point on the island.

Although 120 miles south of Spitsbergen the climate of Bear Island is in many respects somewhat more severe. The mean temperature in February is \(-12.0^\circ\) C, while that of August is \(4.5^\circ\) C. The Gulf Stream drift here meets the cold polar current from eastern Spitsbergen, producing many fogs which give the island a bad reputation among seamen. This fogliness affects the plant life especially, since it reduces the amount of direct sunlight available. This is of much more importance in the Arctic than is the mean air temperature (68, etc.).

Another important factor affecting life is the frequency of storms in winter. The result of these is the complete removal of the snow from many places, and their exposure to the low temperatures then occurring. This is well seen in the extreme frost weathering visible in the mountainous part of the island. The sea does not usually freeze in winter, but at times there is much drifted ice from the north around the island and this adversely affects the climate.

We were only able to study the region south of the broken line on the map (Fig. 1). This area consists of very varied rocks—limestones, slates, sandstones, etc., but the vegetation, on the whole, seems to be the same on the different rocks. The following classification of communities was arrived at:

(a) Land Communities.

2. “Fjaeldmark” as defined by Warming (68).
3. Herb-mat (with “Skua hummocks”).
4. Moss Heath.
Owing to the labour of collecting animals typical areas were selected, and these were worked out in detail.

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4. Moss Heath.
FIG. 1. Map of Bear Island. Dotted lines are form-lines, not contours.

--- Boundary of area investigated.
5. Rock and Boulder Community.
   (a) Rock surfaces.
   (b) Crevices.


7. Wet Tundra.
   (a) Pond marginal community.
   (b) Stream marginal community.
   (c) Moss-bog.

(b) Freshwater Communities.

1. Still water.
   (a) Lakes.
   (b) Ponds.

2. Running water.

It must be remembered that all transitions occur between these groupings.

(a) Land Communities.


High, almost perpendicular cliffs, sometimes several hundred feet, occur all along the southern coast. They are inhabited by vast colonies of sea birds. There are three kinds of habitats which are not always clearly separable.

(a) Ledges on the sides of the cliffs. The following birds nest here in large numbers:

(The authority for each species is given when that species is mentioned for the first time. Frequency symbols are used throughout as follows: d., dominant; c.d., co-dominant; a., abundant; f., frequent; o., occasional; r., rare; l., local; + present, but frequency not determined.)

- Common Guillemot (Uria aalge aalge L.) a.
- Ringed Guillemot (U. alge var. ringvia Brünn.) a.
- Brünnich's Guillemot (U. lomvia lomvia L.) a.
- Mandt's Guillemot (U. grylle mandtii Mandt) o.
- Kittiwake (Rissa tridactyla tridactyla L.) a.
- Fulmar Petrel (Fulmarus glacialis glacialis L.) a.

The bird-louse Esthiopterus nigrolimbatus Gieb. occurred on the Fulmar. In a few places these birds were nesting on the cliffs of inland valleys. All these species feed at sea.

(b) In crevices of the rock the Little Auk (Plautus alle L.) and the Norwegian Puffin (Fratercula arctica arctica L.) occur in small numbers. The former also nests in the screes below. These two species feed also at sea.

(c) At the tops of the cliffs on the mainland, and on small skerries, one finds the Glaucous Gull (Larus hyperboreus Gunn.) and the Great Black-backed Gull (L. marinus L.). The former are abundant; of the latter only a few pairs were seen. The Glaucous Gull usually nests above the cliff-birds upon which it preys, eating the eggs and young of such birds as Guillemots. It will also devour anything in the nature of carrion or garbage. This gull is powerful enough to defend its nest against the Arctic Fox (Vulpes lagopus) which explains its choice of nesting place. The Fulmar also sometimes nests in the...
same places; this is probably due to the present scarcity of foxes. A few Northern Eider Ducks (*Somateria mollissima borealis* Brehm.) probably breed in this kind of place.

Kittiwakes use mosses chiefly for building their nests, but also algae, lichens, grasses, *Salix, Cerastium alpinum, Saxifraga oppositifolia*, etc. (62). The Glaucous Gull also uses moss. There is quite a varied fauna in these nests:

Collembola: Achorutes viaticus Tullb. 
Onychiurus armatus Tullb. var. arcticus Tullb. 
O. neglectus Schäf.

Tardigrades: Echiniscus testridi Doyère 
E. arctomys Ehrb. 
Macrobiotes hufelandi C. Schultze 
M. ornatus Richters

Diptera: Leria septentrionalis Collin

The Collembola were found by Wahlgren (65) in Glaucous Gull nests. The Tardigrades are some of the common moss species. The fly *Leria* was found both as pupae and adults in a Glaucous Gull’s nest, and has been found elsewhere on St Kilda only. This suggests that the fly may be associated with gulls. The warmth of the sitting birds would speed up the flies’ development.

Much bird dung is dropped on the cliffs, which enables the plants present to grow very luxuriantly. On the ledges around the nests are large plants of *Cochlearia officinalis* L. together with much grass (18). *Cochlearia* is indeed a well-known plant in such places, and has been recorded from nearly all arctic and sub-arctic countries. It also occurs in the British Isles at Great Orme’s Head, Abbotsbury, etc., where droppings accumulate. The plants observed on the cliffs near Mount Misery were 7 to 8 ins. in height and very bushy, while on the flat “fjaeldmark” above the cliff they were adpressed closely to the ground and about 1 inch in diameter.

2. “Fjaeldmark.”

Most of the region can be included under this heading. It consists of areas on which the vegetation is open. As a result of severe frost weathering in this district the ground is covered with rock detritus, mostly of small size, which varies in shape, etc., with the type of the parent rock.

The plants are almost all herbaceous, the only dwarf-shrubs being the three Dwarf Willows (*Salix polaris* Wahl., *S. herbacea* L. and *S. reticulata* L.). The first is the only one of these at all common. This “Herb fjaeldmark” passes over in favourable places into “Herb-” or “Grass-mat” and not into “Dwarf-shrub Heath” as in Greenland (28, 67). The plants are almost everywhere very small and stunted, being rarely over 2 or 3 ins. high. Many of them are cushion forms (e.g. *Papaver, Saxifraga caespitosa*), or else they form low creeping mats (*S. oppositifolia*).

The amount of animal life is very small, as is also the number of species. The local distribution of the invertebrates seems to depend a great deal on chance. The intense weathering must be constantly exposing fresh surfaces
and forming empty habitats, which are occupied by the first comers. As with the plants, one striking thing is the small size of the invertebrates, the largest being the sawfly *Amauronematus*, which is less than half-an-inch long. Another feature of the fauna is the complete absence of molluscs, butterflies or moths, beetles, ants, bees or wasps, etc.

The degree of plant covering, and with this the animals, varies considerably, there being all gradations from bare ground to the “herb-mat.” On the ridges of the hills, especially in the area of the Tetradium Limestone—the oldest stratum of the Hecla-Hook system—are large areas of rubble which are almost devoid of soil. The fragments are usually from one-half to 2 ins. in diameter forming a very unstable substratum similar to scree. Here life is very sparse. The only higher plants are isolated tufts of *Saxifraga oppositifolia* L. and *S. caespitosa* L., while here and there a few crustaceous lichens occur. The few animals living here are some flies sheltering under stones (e.g. *Lauterborina caracina* Zett., *Metriconemus urstnus* Holmg.), a mite (*Scutovertex lineatus* Thor.) congregated on the under sides of flat stones, and the spider *Coryphaeus holmgrenii* Thor.

On the slates and sandstones in similar places, probably owing to lower altitude, the vegetation is a little richer. Here, besides the Saxifrages, are to be found *Papaver nudicaule* L. var. *radicatum* Rottb., and *Salix polaris*. The substratum is more stable, with a little soil, and so there are numerous lichens, mainly crustaceous, on the small stones. The following were the commonest:

<table>
<thead>
<tr>
<th>Species</th>
<th>Additional Information</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acarospora sp.</td>
<td>Lecidea conflua Ach.</td>
</tr>
<tr>
<td>Alectoria bicolor Nyl.</td>
<td>L. pantherina Th. Fr.</td>
</tr>
<tr>
<td>A. nigricans Nyl.</td>
<td>Rhizocarpus geographicum DC. f.</td>
</tr>
<tr>
<td>G. proboscidea Ach.</td>
<td></td>
</tr>
</tbody>
</table>

This region has a rather less scanty fauna than the bare areas. The following were collected on the flat shaly top of a hill amongst the plants mentioned above:

<table>
<thead>
<tr>
<th>Taxonomy</th>
<th>Additional Information</th>
</tr>
</thead>
<tbody>
<tr>
<td>Collembola: Onychiurus armatus var. arcticus</td>
<td>Mites: Ctya brevirostris L.Koch</td>
</tr>
<tr>
<td>Diptera: Sciara sp.</td>
<td>Rhagidia gelda Thor.</td>
</tr>
<tr>
<td>Spiders: Coryphaeus holmgrenii</td>
<td>One or two other species</td>
</tr>
</tbody>
</table>

A large part of the area, which constitutes the typical “fjældmark” on Bear Island, has a richer vegetation than that already described, a number of phanerogams, mosses and lichens being common. In places *Salix polaris* forms quite large patches. There are practically no grasses on this area. The following is a general list of plants for the typical “fjældmark”:

<table>
<thead>
<tr>
<th>Phanerogams, etc.:</th>
<th>Additional Information</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arabis alpina L.</td>
<td>Salix herbacea</td>
</tr>
<tr>
<td>Cerastium alpinum L.</td>
<td>S. polaris</td>
</tr>
<tr>
<td>Cochlearia officinalis</td>
<td>S. reticulata</td>
</tr>
<tr>
<td>Draba alpina L.</td>
<td>Saxifraga caespitosa a.</td>
</tr>
<tr>
<td>D. hirta L. var. arctica Vahl</td>
<td>S. cernua L.</td>
</tr>
<tr>
<td>Equisetum variegatum Schl.</td>
<td>S. nivalis L.</td>
</tr>
<tr>
<td>Oxyria digyna Hill.</td>
<td>S. oppositifolia a.</td>
</tr>
<tr>
<td>Papaver nudicaule var. radicatum f.</td>
<td>Sedum rhodiola DC.</td>
</tr>
<tr>
<td>Ranunculus pygmaeus L.</td>
<td>l.</td>
</tr>
</tbody>
</table>
Bryophytes:

Bryum globosum Lindb.
B. pseudo-triquetrum Schw.
var. cavifolium Berggr.
*Cynodontium virens Hedw.
var. arcticum Berggr.
Dicranowisia crispa Hedw.
var. atrata Schimp.

Lichens:

Cladonia rangiferina Web.
*Cetraria islandica Ach.
C. aculeata Fr.

Of lower plants those with an asterisk are the most important.

Sedum and Cochlearia occur near the sea only. In slight hollows, especially where the general surface is rather exposed, a society of Salix polaris and Cetraria islandica is very common. The mosses and lichens are usually rather scattered. All the lichens mentioned above, together with a few others, occur on “fjældmark” (stony desert) in Iceland (20).

The following is a typical animal community from the “fjældmark”:

Collembola: Isotoma multisetis Carp. and Phillips
Diptera: Exechia frigida Boh.
Camptocladius longicosta Edw.
Hymenoptera: Pontania birulae Konow.
Spiders: Coryphaeus holmgrenii
Mites: Cyta brevirostris Suctovertex lineatus Sphaerozetes notatus Thor.
Oligochaeta: Enchytraeus albidus Henle.

Birds: Purple Sandpiper (Erolia maritima maritima Briinn.) nesting

The Arctic Fox, formerly common, has been almost exterminated by man, as in Spitsbergen. None was seen by us. In summer it feeds on birds and their eggs and young. In winter, in other countries it partly makes caches of lemmings, etc. (26), and partly goes out on to the sea-ice, where it eats mostly the leavings of bears, e.g. remains of seals, of which the bears often only eat the fat (59, 38), and their excreta (39). There does not seem to be enough food on land in Spitsbergen and Bear Island for making winter caches (e.g. no lemmings) and the foxes probably live then mostly on the sea-ice (cf. 41).

Thus the number of foxes depends not only upon the amount of direct destruction by man, but also indirectly on the number of bears killed. The Polar Bear still visits Bear Island in small numbers in winter, fifteen being shot in 1919–20 and three in 1920–21.

The Purple Sandpiper, the commonest “fjældmark” bird, will eat almost anything it can get, judging from its habits in Spitsbergen. The stomach of one bird contained Collembola and flies (June 15th). The following bird-lice occur on this species: Philopterus fusiformis Denny, Degeeriella zonaria Nitzsch and D. arctophilus Kell. and Chap.

The Collembola or Springtails appear to feed on decaying plants, and the mites, at any rate Scutovertex and Sphaerozetes, are vegetarian. Coryphaeus is known to eat Collembola in Jan Mayen (7), and probably feeds also on flies
and mites. It seems to make no web. The life histories of the flies are very little known. *Camptocladius longicosta* and the mite *Sphaerozetes* occur sometimes in flowers of *Saxifraga oppositifolia*. The sawfly *Pontania birulae* was seen walking about on *Salix polaris*, and probably lays eggs in it. The food of the adult is unknown. The Snow Bunting eats this sawfly.

The Enchytraid worms of the Arctic seem to replace ecologically the earthworms of lower latitudes, owing to their powers of withstanding freezing (see 60).

Other species occurring on the “fjeldmark” are:

**Collembola:**  
Achorutes viaticus  
*Isotoma viridis* Bourlet  
*Xenylla humicola* Fab.  
*Folsomia quadrioculata* Tab.  
Sminthurinus niger Labb., in fungi  
Tetracanthella pilosa Schoett. under moss

**Diptera:**  
*Camptocladius eltoni* Edw.  
*Diamesa hyperborea* H.  
*D. septima* Edw.  
*D. ursus* Kieff.  
Lauterborina caracina  
*Metriocnemus ursimus*  
Orthocladius conformis Holmg.  
*Sciara praecox* Mg.  
*Trichocera lutea* Becker

**Hymenoptera:**  
*Amauronematus villosus* Thoms.  
*Pristiphora frigida* Bohem.

**Mites:**  
*Bdella groenlandica* Trag.  
*Hypoaspis ovalis* L. Koch

**Birds:**  
Golden Plover (*Charadrius apricarius apricarius* L.) r. nesting  
Snow Bunting (*Plectrophenax nivalis nivalis* L.) feeding

The latter three Collembola are recorded by Wahlgren (65).

Of the Collembola *Onychiurus* is never present in exposed habitats, but lives under stones and among plants. *Isotoma viridis* seems able to stand air of a greater evaporating power than the other species; it often walks about on open ground. The closely allied *I. multisetis*, however, seems more often to inhabit plants. *Achorutes, Xenylla* and *Agrenia bidenticulata* Tullb. (another collembolan) occur typically on or near water. *Xenylla* was once found in flowers of the Purple Saxifrage. The two sawflies probably live on *Salix*.

### 3. Herb-mat (with Grass).

This is developed in sheltered places, and appears to be a climax to the “fjeldmark.” It seems to agree with the various herb-mats described from Greenland (50, 67), etc., but differs in having a good deal of grass, probably *Catabrosa algida* R.Br. The surface in these areas is comparatively stable owing to the closed vegetation binding the soil. On a sheltered rocky slope in the Tetradium Limestone region were:
Phanerogams:

- Catabrosa algida
- Cochlearia officinalis
- Cerastium alpinum
- Draba alpina
- Oxyria digyna
- Saxifraga caespitosa
- S. cernua
- S. oppositifolia

Lichen:

- Cladonia sylvatica Hoffm.

The flowering plants are the usual “fjaeldmark” species. *Saxifraga cernua* is much more luxuriant than in “fjaeldmark.” A few migrant Pink-footed Geese (*Anser brachyrhynchus* Baill.) were seen on the small areas of grassy land. Their dung consisted of remains of moss and grass. Brent Geese (*Branta bernicla bernicla* L.) also occur on migration. Neither species breeds here. Skuas and Purple Sandpipers nest.

“Skua Hummocks.” We have given this name to what is perhaps the most striking type of herb-mat occurring in the region. The Skua hummocks are small grassy patches scattered over the “fjaeldmark.” They are the result of constant manuring by the Arctic Skua (*Stercorarius parasiticus* L.), which nests on the tops of hillocks which are the first places to be clear of snow in spring. The male stands on neighbouring hummocks during the breeding season, watching for enemies, chiefly foxes, which the Skuas are able to drive off. Thus the hummocks become well manured by the birds. Middendorf (40) has described similar hummocks in Siberia.

There is a considerable layer of peaty soil (½ to 6 ins.) on these hummocks, and a varied flora of rather stunted individuals. The phanerogams are typical “fjaeldmark” species, *Saxifraga oppositifolia*, *S. caespitosa*, and *Catabrosa algida* being the most characteristic, while the presence of *Cochlearia* is significant. Wulff (70) gives a list of plants on these hummocks in Spitsbergen. The following cryptogams occur:

Bryophytes:

- Bryum pallescens Schl.
- B. pseudo-triquetrum
- Cynodontium viriphum
- Dicranum fuscescens Turn.
- D. congestum Huusot.
- D. spiculata
- Encalypta communis N. & Horsch.
- Hynum uncinatum
- Myurella julacea B. & S.
- Pseudoleskea testorum formas
- Rhacomitrium lanuginosum Brid.
- Tortula ruralis

Lichen:

- Alectoria ochroleuca Nyl.
- Biatorina reguligera Korb.
- Cetraria aculeata
- f. hispida Cromb.
- Cladonia furcata Schrad.
- var. spinosa Leight.
- C. rangiferina
- Leucora epiphyllum Ach.
- L. tartacea Ach.
- Sphaerophorus globosus Wain.

Algae:

- Nostoc sphaericum Vaucher.

(*among moss*)

*Hynum uncinatum* is the most prominent moss.
The invertebrate fauna is of the same type as on the “fjaeldmark.” The animals found were:

- **Collembola:** Isotoma multisetis
- **Diptera:** Diamesa ursus
- **Spiders:** Coryphaeus holmgrenii
- **Mites:** Bdella groenlandica
- **Oligochaeta:** +

The Skua lives by robbing other birds. It attacks sea-birds (Guillemots, Kittiwakes, etc.) causing them to disgorge their food, and also sucks the eggs both of the cliff-birds and of the Red-throated Diver (*Colymbus stellatus* Pontopp.) and Northern Eider. Thus the hummock communities depend for their existence ultimately on sea animals.

4. **Moss Heath.**

The community occurs in the centre of Bear Island west of Mount Misery, covering large areas, and also locally in other parts. It seems to be developed on dry, stony flats, and agrees generally with the various Moss Heath described for other arctic countries (9, 25). The famous “Grimmia Heath” of Iceland is of the same type (25). A certain amount of shelter from wind seems advantageous.

The dominant plant is *Rhacomitrium lanuginosum* as in other countries, but on Bear Island *Hypnum uncinitum* is relatively more important, and in slightly damper places, forms almost pure societies. *Salix polaris* is the only common phanerogam. A more complete list of plants is given below:

**Phanerogams, etc.:**
- *Equisetum variegatum* o.
- *Oxyria digyna* i.
- *Ranunculus pygmaeus* r.
- *Salix polaris* f.
- *Saxifraga cespitosa* o.
- *S. cernua* l.

**Lichens:**
- *Cladonia rangiformis* Hoffm. (f. among stones)

Species with an asterisk are characteristic of the society of *Hypnum uncinitum*.

The fauna of this area was not worked much, but it is rather poor. *Isotoma viridis* was found.

5. **Rock and Boulder Communities.**

In a great many places in Bear Island, owing to the intense weathering, there are large areas, often quite flat, which are covered by heaps of loose blocks, 6 inches to 10 feet in diameter. On Mount Misery the Spirifer Limestone weathers into large blocks which form ordinary sloping screes. There are also erratic boulders which often have many cracks and crevices, and may be
broken by frost into smaller fragments (27). Screes consisting of smaller particles are too unstable to support any life.

The production of the block plains and heaps may be due to the fact that by "solifluction" (2) the finer earth has flowed away leaving the large rocks behind. It is known that "solifluction" can occur on very gentle slopes, and such earth movements have been noticed on Bear Island.

The block community can be divided into two main divisions, which grade into one another in many places: (a) Community on rock surfaces (Lithophytes), (b) Community in rock crevices and between boulders (Chomophytes).

(a) The blocks support a rich lichen and moss flora on the parts protected by snow in winter. The lichens are usually crustaceous, but may be foliose or even fruticose in favourable spots. The following list includes the more important ones:

<table>
<thead>
<tr>
<th>Lichens</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gyrophora erosa</td>
</tr>
<tr>
<td>Lecanora galactina subsp. dispersa</td>
</tr>
</tbody>
</table>
| L. polytropa Schae.
| Leucidea goniophila Schae.
| L. pantherina    |
| Placodium crinum Ehrh. |
| P. elegans DC.    |
| P. rupestre Branth. & Rostr. |
| P. rupestre var. calvum AL.Sm. |
| Polyblastia interestrensis Loeinnr. |
| Rhizocarpon calcareum Th.Fr. |
| R. geographicum   |
| Thelidium pyrenophorum Massal. |

(b) The crevices between the boulders and depressions on them contain a much more varied vegetation. A succession to Moss Heath or "fjeldmark" takes place with the accumulation of humus in the crevices and on the surfaces. Two divisions of the crevice flora can be distinguished, viz.: (1) That at the mouths of crevices and on humus collected in depressions, and (2) the community inside the crevices.

(1) The flora is mainly cryptogamic. There are only a few phanerogams, such as Oxyria, Saxifraga oppositifolia, etc., as usually the humus is not deep enough. Most of the vegetation consists of bryophytes, although in places, e.g. on Mount Misery, there is a considerable admixture of lichens. The following plants occur:

<table>
<thead>
<tr>
<th>Bryophytes</th>
<th>Lichens</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brachythecium salebrosum</td>
<td>Ostraria hisacons Th.Fr.</td>
</tr>
<tr>
<td>B. &amp; S.</td>
<td>C. islandica var. tenuifolia Wain.</td>
</tr>
<tr>
<td>Dianium bonjeani de Not.</td>
<td>Cladonia bellidifolia Schae.</td>
</tr>
<tr>
<td>D. starkei</td>
<td>C. foliacea Willd.</td>
</tr>
<tr>
<td>Harpanthus scutatus Spruce</td>
<td>C. furcata</td>
</tr>
<tr>
<td>Hylocomium splendens</td>
<td>C. gracilis Willd.</td>
</tr>
<tr>
<td>Hypnum uncinatum</td>
<td></td>
</tr>
</tbody>
</table>

Jour. of Ecology XI
Bryophytes (cont.):
Hypnum vernicosum Lindb.
L. quinquedentata Cogn.
L. ventricosa Dum.
Polytrichum alpinum
Pullidium ciliare
Rhaacomitrium lanuginosum
Tortula ruralis
Webera cruda Schwgr.

Lichens (cont.):
Cladonia pyxidata Hoffm.
C. sylvatica
Lecanora tartaarea
Parmelia omphalodes Ach.
Peltigera canina
Sphaerophorus globosus
Stereocaulon paschale Fr.

The large number of lichens shows the dry nature of the substratum, but there is a definite admixture of wet-loving types among the mosses.

(2) Between the rocks there are often considerable cavities in which it is possible for a man to crouch. The inner parts of these holes are very dark, and indeed one reaches finally a region in which the light is insufficient for plant life. The sides of the blocks are usually wet with water trickling from above, and a hygrophilous type of vegetation is able to exist. In these crevices liverworts predominate, the more important being Blepharostoma trichophyllum Dum. and Lophozia longidens Macoun. The mosses Webera cruda and Swartzia montana Lindb. are also important.

Mosses:
Blindia acuta B. & S.
Dicranum molle Wils.
Hypnum sarmentosum Wahl.
H. stramineum Dicks.
H. uncinatum
Swartzia montana
Timnia austriaca
Webera cruda
W. nutans Hedw.

Liverworts:
Blepharostoma trichophyllum
Cephalozia bicuspidata Dum.
C. leucantha Spruce
C. serriflora Lindb.
Cephalozia byssacea Warnst.
Diprophyllum albicans Dum.
Lophozia alpestris Evans
L. longidens
L. porphyroleuca Schieff.
L. quintquedentata
L. ventricosa
Scaapania curta Dum.
S. irrigua Dum.

Blepharostoma and Diprophyllum occur in caves and clefts in Iceland (25).

The Snow Bunting nests in the crevices, but finds its food in many other places. It eats sawflies to a great extent. One cock when shot was found to be carrying half-a-dozen in its mouth (Amauronematus and other species). Amauronenomatus occurred in the stomach of one bird and Pontania in another with leaves of Sedum rhodiola. Swenander (62) found seeds of Cochlearia in the stomach of one bird.

The lower animals were not worked out.

6. MOSS-MAT.

This is similar to Cleve’s (9) moss-mat, but there are more phanerogams. It occurs in hollows where the snow melts slowly, or where snow-water trickles down continually from above. Mosses cover the soil, but they are not the very damp-loving species. The Hypnum uncinatum society described under “Moss Heath” is closely allied to this, but drier. The areas may dry up completely late on in the season, and this distinguishes moss-mat from wet tundra. Salix polaris is common in many places, while Ranunculus sulphureus Sol. is often
encountered. Other species not common in drier places are Saxifraga rivularis L. and Polygonum viviparum. There are also:

<table>
<thead>
<tr>
<th>Phanerogams, etc.</th>
<th>Bryophytes:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Draba alpina</td>
<td>Cynodontium virens</td>
</tr>
<tr>
<td>Equisetum variegatum</td>
<td>Hypnum uncinatum a.</td>
</tr>
<tr>
<td>Oxyria digyna</td>
<td>Timmia austriaca</td>
</tr>
<tr>
<td>Saxifraga caespitosa</td>
<td>S. nivalis Cladonia rangiferina</td>
</tr>
<tr>
<td>S. cernua</td>
<td>Lecidea vernalis Aech.</td>
</tr>
<tr>
<td>S. oppositifolia</td>
<td>Stereocaulon alpinum Laur.</td>
</tr>
</tbody>
</table>

The Kittiwakes were watched picking moss for their nests from moss-mat, and areas up to 1 ft. in diameter are torn up in that way. Swenander (62) states that the Kittiwakes use moss throughout the season for renovating their nests, and this must be of importance when one considers the vast number of birds concerned. The less common Glaucous Gulls also use this moss.

Similar vegetation occurs on the flat plateau at the top of Mount Misery, where on a damp mossy area were Brachythecium plicatum B. and S., Amblystegium serpens B. and S., and the lichens Solorina crocea Ach., and Pseoroma hypnorum S. F. Gray. A few Ptarmigan (Lagopus mutus Sund.) occur here and also one or two foxes. The Ptarmigan feeds on all kinds of plants, and, to a certain extent, on insects (39).

7. WET TUNDRA.

This consists of regions which are wet throughout the spring and summer. The largest stretches are in Ymers Valley between a number of ponds along the river. Mosses usually predominate while flowering plants are of little importance. Three divisions can be recognised:

(a) Pond Marginal Community—with still, fairly well-aerated water.
(b) Stream Marginal Community—with running well-aerated water.
(c) Moss Bog—with partially stagnant water.

(a) This type of wet tundra occurs around nearly all the ponds, except where there is a rocky bank. The vegetation forms a prominent mossy bank around the pond. Grasses and other phanerogams occur in places, but not frequently. The mosses were not worked very thoroughly, but probably include most of the bog species. The following list shows the type of vegetation:

| Aulacomnium turgidum Schwaegr. |
| Hypnum cordifolium Hedw. |
| Dicranoweisia crispula var. gracilis Berggr. |
| Hypnum brevifolium Lindb. |
| H. vernicosum |
| H. badium Hartm. |
| H. sarmentosum |

Berggren (5) records the last two species.

Under stones, on the margin of Ella Lake by an inflowing stream, the following animals occurred:

| Collembola: Achorutes viaticus |
| Isotoma multisetis |
| L. viridis |
| Smiththurides maimgreni Tulib. |
| Xenylla humicolae |

| Mites: Cyta brevirostris |

15—2
(b) This is present only locally, as owing to the erosion the stream sides are usually an unstable mass of rock fragments. Vegetation is practically inhibited in these latter places, but *Isotoma viridis* is often found there. In places there is a narrow band of moss by the streams. Berggren reports the following near Mount Misery and elsewhere:

- Bryum obtusifolium Lindb.
- B. turbinatum
- var. latifolium Schleich.
- Hyphnum ochraceum Wils.
- H. polygamum Schp.
- Paludella squarrosa Ehrh.
- Philonotis fontana Brid.
- Swartzia montana
- Wobera albicans Wahlb.
- var. glacialis Limpr.

On stones partly covered by the water occur *Hypnum polare* Öfvers and *H. flicinum* L.

(c) This is present in flat areas in valleys and consists mainly of mosses, a well-developed example occurring at Walrus Bay. The chief phanerogams are *Saxifraga rivularis*, *S. hirculus* L. and *Ranunculus sulphureus*. The first named is frequent in Walrus Bay bog, while the others are locally abundant in Ymers Valley. The following mosses occur in bogs on Bear Island:

- Cinclidium stygium Sw.
- Hypnum brevifolium
- H. fluitans L.
- H. intermedium Lindb.
- H. polygamum
- Meesia triquetra Angstr.
- Hypnum sarmentosum
- and var. fontinaloides Berggr.
- H. stellatum Schreb.
- H. vernicosum
- H. turgescens Schp.
- Hypnum fluitans L.
- H. stellatum Schreb.
- Hypnum intermedium Lindb.
- H. vernicosum
- H. polygamum
- H. turgescens Schp.
- Hypnum vasculosum L.
- Splachnum vasculosum L.

The following animals occur in Walrus Valley bog:

- Collembola: Achorutes viaticus
- Agrenia bidenticulata
- Diptera: Camptocladius eltoni
- C. oxonianus Edw.
- Metriocnemus ursinus

There are large numbers of old walrus bones lying here. The enormous numbers of walrus formerly occurring (e.g. a thousand were killed in seven hours in 1608 (12), while large herds still visited the island in 1825 (46)) must have been important in manuring the valleys. Under walrus skulls were a good many flies (*Metriocnemus* and *Exechia frigida*).

The micro-fauna was not worked out by us. Several Tardigrades occur of the genera *Echiniscus* and *Macrobiotes* (55).

(b) Freshwater Communities.


The ponds are all of an arctic type, and are not unfrozen for more than two to three months. It was too early in the season to do complete work. Almost all the ponds in the south of the island are rock basins, but most of them have a decided marginal moss vegetation.

(a) Ella Lake (June 17th and 19th). This is a large lake, whose greatest depth is 120 feet. The bottom consists of greyish brown loamy mud, but the shores are stony. The water is alkaline at the surface.
Some of our collections (algae and crustacea) were destroyed by accident. Lagerheim (35) recorded *Hormospora subtilissima* Lag., *Pediastrum boryanum* Menegh., and the diatom *Synedra filiformis* Grun. That and *Hormospora* formed the bulk of the plankton at his visit. The more common diatoms found by Cleve (10) and Lagerheim, were:

- *Campylodiscus hibernicus* Ehb.
- *Diatoma tenue* Ag. var. *elongata* Ag.
- *Navicula rotaena* Rabh.
- *Pinnularia curta* Cl.
- *Achnanthes microcephala* Grun.
- *Cocconeis placentula* Ehb. var. *euglypta* Ehb.

The last two were abundant on filamentous green algae.

Little is known of the fauna, but the following occur:

**Crustacea:** (Lilljeborg (37) June 1898, July 1899)
- *Chydorus sphaericus* Muller
- *Cyclops strenuus* Fischer
- *C. vicinus* Claus.

**Diptera:** *Chironomid larvae*

**Trichoptera:** *Apatania arctica* Boh. (larvae and 1 adult Ø)

**Hydrachnidae:** *Sperchon lineatus* S. Thor. (Ø, 5 nymphs) (57)

**Fish:** *Salmo umbra* var. *salvelinus-Insularis* Lønb.

The caddis-fly *Apatania* makes a case out of sand and mud. It and the water-mite *Sperchon* are abundant on the stones among algae, etc. The fish is a deep-water char, but nothing is known of its ecology. The fauna of Ella Lake forms an exception to the usual type in Spitsbergen and Bear Island, owing to the extent and depth of the lake.

(b) **Pond 1.** (June 13th and 15th) = Cleve (10) Habitat 13 and Lagerheim (35) “Pond near Russian Haven.”

In a rocky basin in the dolomite, 100 to 200 yards long. The water was unfrozen, and was very clear and alkaline. The depth is 7 metres, and the bottom is black mud (10). The shore is stony, and almost devoid of vegetation except algae and a little moss. The following occurred:

**Plants:**

**Chlorophyceae:**
- *Coelastrum microsporum* Naeg.
- *Gongrosira debaryana* Rab.
- *Pediastrum boryanum* var. *longicorne* Reinsch.
- *P. constrictum* Hassall.
- *P. integrum* Naeg.
- *P. muticum* Kuetz.
- *P. sturmi* Reinsch.
- Rhizoclonium sp.
- *Scenedesmus bijugatus* Breb.
- *S. obliquus* Kuetz.
- *S. quadricauda* Breb.

**Cyanophyceae:** *Oscillatoria tenuis* Ag.

**Diatoms:**
- *Amphora ovalis* Kuetz.
- *Diatoma elongatum* var. *tenue* VH.
- *Fragilaria mutabilis* Grun.
- *P. construens* Ehb.
- *Navicula peregrina* var. *polaris* Cl.
- *N. rhymocephala* Kuetz.

(Those with asterisks recorded by Lagerheim and Cleve.)
ANIMALS:
Rotifera: Polyarthra platyptera Ehrb.
Oligochaeta: Nais josinae Vejd.
Tardigrada: Macrobiotes macronyx Duj.
Diptera: Orthocladius conformis (adults on surface of water)
         Larvae.

Crustacea:
Plankton: Daphnia longispina Müller
         Cyclops strenuus
Littoral: Lepidurus arcticus Pallas
         Chydorus sphaericus
         Cyclops gigas Claus.

Pond 2. (June 17th.) A small pond in Ymers Valley fed by a large stream
flowing from the hills. These hills are occupied by sea-bird colonies, and so
the water is probably richly manured. It was alkaline. Cleve gives a long list
of diatoms (his Locality 10). *Cyclops gigas* occurs here.

Pond 3. A small pond in a rocky basin 100 or 200 feet above Ella Lake.
The crustacea showed that its fauna resembles Pond 1. There were no caddis-
flies or water-mites. The following algae occur:

Chlorophyceae: Pediastrum boryanum var. longicorne
         Rhizoclonium sp.
         Staurastrum bieneanum Raben.
Cyanophyceae: Tolypothrix distorta Kuettz. var. penicillata Lemm.

General Remarks.

The plankton includes *Daphnia longispina*, *Cyclops strenuus* and the
rotifer *Polyarthra platyptera*. *Cyclops vicinus* comes in Ella Lake. Other
crustacea recorded (37, 52) from this region are littoral and bottom-living
arctica* Sars., *Candona candida* Müller. Previous records confirm in a general
way the communities described here.

Large flocks of Kittiwakes were seen on the water bathing, probably partly
in order to get rid of marine parasites. Glaucous Gulls and Northern Eiders
also occur. The latter are known to breed by ponds in the north of the island.
The Long-tailed Duck (*Harelda glacialis* L.) and Common Scoter (*Oedemia
nigra nigra* L.) were observed in small numbers, and the former, at any rate,
breeds. Red-throated Divers are common, and nest by the water’s edge. They
evidently feed on the fish in Ella Lake since they eat *Salmo alpinus* in Green-
land (39). Purple Sandpipers also feed by the water. Certain Collembola are
said by Wahlgren (65) to occur on the surface of water, e.g. *Sminthurides
malgreni*, *Achorutes viaticus*, *Xenyilla humicola*.

2. RUNNING WATER (Streams).

The streams often have a large amount of filamentous green algae attached
to the stones. The following algae were found in various streams:

<table>
<thead>
<tr>
<th>Algae</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kentrosphaera sp.</td>
<td>Ulothrix subtilissima Rab.</td>
</tr>
<tr>
<td>Pediastrum boryanum var. longicorne</td>
<td>U. teneririma Kuettz.</td>
</tr>
<tr>
<td>P. integrum</td>
<td>U. sp. (allied to U. acutata)</td>
</tr>
<tr>
<td>Phormidium uncinatum Gomont.</td>
<td></td>
</tr>
</tbody>
</table>
Cleve records many diatoms (10). The more important ones are: *Achnanthes microcephala*, *Diatoma tenue* var. *elongata*, *Fragilaria arcus* Kuetz. and *Meridion circulare* Ag. The first is epiphytic on filamentous algae. *Ranunculus hyperboreus* Rottb. occurs in streams on Bear Island (1).

No animals were found among the algae. This is confirmed by observations (55) that none of the streams contains Tardigrades.

Miscellaneous.

The northern half of the island is different from the southern in that the Arctic Tern (*Sterna paradisea* Briinn) and Grey Phalarope (*Phalaropus fulicarius* Iredale) breed there.

The shores of Bear Island are mostly precipitous, and owing to the small rise and fall of the tide in the Arctic (not more than 4 or 5 feet) the inter-tidal zone is narrow and appears to be almost devoid of life.

An example of “red snow” collected turned out to consist of the remains of marine crustacea. Lamont (36) says that the “red snow” examined by him in Spitsbergen consisted of the droppings of Little Auks. Of course *Sphaerella nivalis* Som. does occur, but the cases given above show that it is not safe to judge by colour alone (see 42).

Food and Enemies (“Nitrogen Cycle”).

Food is extremely scarce in the Arctic, both on land and in fresh water, though it is plentiful in the sea. Most of the scavenging animals live on decaying plants, and are, therefore, practically equivalent to herbivores in the food cycle. There are no elaborate “chains” of species depending on animals which eat the dung or decaying bodies of other species. Such a “short-circuiting” of the nitrogen cycle (which exists in other countries, e.g. badgers eating beetles which prey on dung feeders in England) appears to be unimportant in Spitsbergen. Dead animals are very rarely found (46), and when they do occur are devoured by vertebrates (e.g. reindeer by Glaucous Gulls and dead whales by bears). Where animals like whales have the chance of decaying, they do so very slowly. The questions of nitrogen-fixing bacteria and of the effect of thunderstorms are left open, since there is no direct evidence either way for the Arctic regions, but thunderstorms at any rate are not at all frequent. Soils collected from Greenland (4) on examination showed several species of putrefactive organisms such as *Bacillus subtilis*, *B. vulgatus* and *Bacterium zopfi*. Nitrifying and denitrifying organisms were also discovered. Mr Sandon reports bacteria and protozoa from all the soils collected by us.

The diagram (Fig. 2) gives the food relations of the land and freshwater animals and plants in the southern part of Bear Island. Ella Lake is not included in this scheme, since it is an exceptional case. The direct evidence, where existing, for the truth of this diagram will be found at various places in this paper. Data from Spitsbergen animals of the same species are included,
and the diagram with some alterations would suffice for that country itself, but would be rather more complicated.

It will be seen that a large part of the food supply of animals and plants comes from the sea. The most striking case of this, the result of concentration in a small area, is the Bird Cliffs. The manuring of the Skua Hummocks is another example. The luxuriant vegetation in these places shows the effect of an exceptional supply of nitrogen. There are no Bird Cliffs in N.W. Greenland (51) owing to the permanently frozen sea, but plants occur although never luxuriantly. Here there can be no help from the sea and the presence of nitrogen-fixing bacteria seems necessary. However, there are also methods of loss of nitrogen from the land. One of these is the usual washing down of nitrates. Another is due to migratory birds. The Purple Sandpiper may be taken as an example. It feeds on Collembola, etc., which feed on dead plants, and the young sandpipers are reared on the same food. In the late summer both adult and young depart, and the nitrogenous material represented by the young is lost to the Arctic.

In fresh water we may note the almost total absence of carnivores. In temperate regions the Entomostraca form a “key-industry” whose function is the conversion of microscopic plant food into a form utilisable by larger animals (fish, insects, etc.). Here the Entomostraca have no enemies in the water itself (except in Ella Lake) though birds eat Lepidurus and probably the other animals. The rôles played by the various scavenging species are unknown, but there is sure to be some division of labour among them.
The parasitic cycles are not included in the diagram, since nothing is known of them. Parasites and carnivores are essentially the same in their food relations with other animals, and the differences are due to the relative sizes of the eater and the eaten. If the animal is below a certain size it may dwell in or on its food-host, if above that size it is free-living. The result of this is that the species in food-chains of parasites get smaller and smaller, while in food-chains of carnivores they get, on the whole, larger and larger (see Fig. 2).

III. SPITSBERGEN.

INTRODUCTION.

Unlike Bear Island, Spitsbergen is quite an extensive country, being 280 miles from North to South, and over 200 miles from East to West (see Map, Fig. 3). West Spitsbergen and Prince Charles Foreland only were visited by us. West Spitsbergen is cut into by many deep fjords, the chief one of these being Icelfjord, where most of our observations were made.

Spitsbergen is a mountainous country, there being very little flat ground or even lowland. Apart from raised beaches, etc., the mountains abut directly on to the sea. As might be expected from the latitude, glaciation is very severe and much of the interior of the country is covered by permanent néré and the glaciers arising therefrom, and is devoid of life. Since many of the glaciers reach the sea the narrow coastal strip is cut up into isolated parts, and dispersal is hindered.

The geology of the country is very varied, the rocks being of all types chemically, but as far as can be seen this has little effect on the life in Spitsbergen generally, although some plants seem to be restricted to certain soils, or at any rate grow better on them. In North Greenland according to Ostenfeld (51) the vegetation is richer on limestone than on other soils. The physical properties of the rocks seem more important in relation to denudation.

The climate of Spitsbergen is relatively mild for such a high latitude, owing to the Gulf Stream drift which approaches the west coast. The following table (Table I) is compiled from various records for different parts of Spitsbergen, but is in no sense complete. It includes records from 1872–1922.

<table>
<thead>
<tr>
<th>Month</th>
<th>Mean temperature °C.</th>
<th>Maximum °C.</th>
<th>Minimum °C.</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>-13.9</td>
<td>4.0</td>
<td>-32.4</td>
</tr>
<tr>
<td>February</td>
<td>-15.9</td>
<td>1.6</td>
<td>-38.2</td>
</tr>
<tr>
<td>March</td>
<td>-17.7</td>
<td>3.8</td>
<td>-40.0</td>
</tr>
<tr>
<td>April</td>
<td>-15.2</td>
<td>5.0</td>
<td>-32.6</td>
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<tr>
<td>May</td>
<td>-7.0</td>
<td>12.5</td>
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</tr>
<tr>
<td>June</td>
<td>1.2</td>
<td>16.0</td>
<td>-14.0</td>
</tr>
<tr>
<td>July</td>
<td>4.6</td>
<td>16.0</td>
<td>-6.1</td>
</tr>
<tr>
<td>August</td>
<td>2.6</td>
<td>9.0</td>
<td>-2.6</td>
</tr>
<tr>
<td>September</td>
<td>-2.5</td>
<td>8.3</td>
<td>-10.0</td>
</tr>
<tr>
<td>October</td>
<td>-8.4</td>
<td>0.0</td>
<td>-27.2</td>
</tr>
<tr>
<td>November</td>
<td>-10.6</td>
<td>4.2</td>
<td>-23.6</td>
</tr>
<tr>
<td>December</td>
<td>-12.7</td>
<td>5.6</td>
<td>-32.2</td>
</tr>
</tbody>
</table>
The parasitic cycles are not included in the diagram, since nothing is known of them. Parasites and carnivores are essentially the same in their food relations with other animals, and the differences are due to the relative sizes of the eater and the eaten. If the animal is below a certain size it may dwell in or on its food-host, if above that size it is free-living. The result of this is that the species in food-chains of parasites get smaller and smaller, while in food-chains of carnivores they get, on the whole, larger and larger (see Fig. 2).

III. SPITSBERGEN.

INTRODUCTION.

Unlike Bear Island, Spitsbergen is quite an extensive country, being 280 miles from North to South, and over 200 miles from East to West (see Map, Fig. 3). West Spitsbergen and Prince Charles Foreland only were visited by us. West Spitsbergen is cut into by many deep fjords, the chief one of these being Icefjord, where most of our observations were made.

Spitsbergen is a mountainous country, there being very little flat ground or even lowland. Apart from raised beaches, etc., the mountains abut directly on to the sea. As might be expected from the latitude, glaciation is very severe and much of the interior of the country is covered by permanent névé and the glaciers arising therefrom, and is devoid of life. Since many of the glaciers reach the sea the narrow coastal strip is cut up into isolated parts, and dispersal is hindered.

The geology of the country is very varied, the rocks being of all types chemically, but as far as can be seen this has little effect on the life in Spitsbergen generally, although some plants seem to be restricted to certain soils, or at any rate grow better on them. In North Greenland according to Ostenfeld (51) the vegetation is richer on limestone than on other soils. The physical properties of the rocks seem more important in relation to denudation.

The climate of Spitsbergen is relatively mild for such a high latitude, owing to the Gulf Stream drift which approaches the west coast. The following table (Table I) is compiled from various records for different parts of Spitsbergen, but is in no sense complete. It includes records from 1872–1922.

<table>
<thead>
<tr>
<th>Month</th>
<th>Mean temperature °C.</th>
<th>Maximum °C.</th>
<th>Minimum °C.</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>-13.9</td>
<td>4.0</td>
<td>-32.4</td>
</tr>
<tr>
<td>February</td>
<td>-15.9</td>
<td>1.6</td>
<td>-38.2</td>
</tr>
<tr>
<td>March</td>
<td>-17.7</td>
<td>3.8</td>
<td>-40.0</td>
</tr>
<tr>
<td>April</td>
<td>-15.2</td>
<td>5.0</td>
<td>-32.6</td>
</tr>
<tr>
<td>May</td>
<td>-7.0</td>
<td>12.5</td>
<td>-19.4</td>
</tr>
<tr>
<td>June</td>
<td>1.2</td>
<td>16.0</td>
<td>-14.0</td>
</tr>
<tr>
<td>July</td>
<td>4.6</td>
<td>16.0</td>
<td>-6.1</td>
</tr>
<tr>
<td>August</td>
<td>2.6</td>
<td>9.0</td>
<td>-2.6</td>
</tr>
<tr>
<td>September</td>
<td>-2.5</td>
<td>8.3</td>
<td>-19.0</td>
</tr>
<tr>
<td>October</td>
<td>-8.4</td>
<td>0.0</td>
<td>-27.2</td>
</tr>
<tr>
<td>November</td>
<td>-10.6</td>
<td>4.2</td>
<td>-23.6</td>
</tr>
<tr>
<td>December</td>
<td>-12.7</td>
<td>5.6</td>
<td>-32.2</td>
</tr>
</tbody>
</table>
The anomalies present here, such as the low maximum for October, are probably due to the few records available. A temperature of 19.5° C. in the shade was registered in the summer of 1922.

Temperature. During the winter the temperature is very low, but at that period the snow-covering protects the plants and invertebrates, and most of the birds have migrated. Apparently no month is free from frost over a series of years, but in reality July and August may be so in some years. The temperature in the sun is often quite high on clear days, especially in the interior of the fjords, temperatures of 27° and 28° C. having been recorded. Nathorst (45) has pointed out that the heads of the fjords enjoy a more continental climate than the coastal regions.

Precipitation. Recent records give 11.6 inches as the mean annual pre-
cipitation for Green Harbour. The west coast, e.g. Prince Charles Foreland, probably has rather more, the interior of the fjords less. In any case the total precipitation is very low. Most of this falls in the form of snow in autumn and spring, there being little snow or rain during the summer. In north-east Greenland, where the precipitation is comparable (6.0 inches per annum), two-thirds falls between October and March, and less than one-tenth falls as rain (38). The duration and amount of snow water in summer are of great importance in determining the plant communities. Owing to the prevalence of thick mists on the coastal areas much condensation takes place. Many lichens must depend largely upon these mists for their water supply.

**Humidity and Cloudiness.** The Relative Humidity is very high owing to the low temperatures, although the Absolute Humidity is probably rather small. Cloudy days are frequent in the summer especially around the coast, but once the temperature rises the actual small amount of water vapour is easily absorbed and a very clear atmosphere results. This is important in increasing the direct insolation which the ground receives. The distribution of such animals as Springtails (Collembola) is correlated with the humidity of the air.

**Wind.** Little is known of the direction and velocity of the wind in Spitsbergen. South-westerly winds occur at various times and help to raise the temperature. The direction of the wind depends on the orientation of the mountain ranges. The wind causes many storms throughout autumn and winter which tend to break up the ice, and thus to raise the temperature. This breaking up is also probably an important factor in dispersal (see Cassiope). On the plants, especially, wind is a very potent influence (66). Kihlman (33) has pointed out the drying-out effect of strong winds when the soil is at a low temperature, and probably “fjeldmark” is determined largely by wind effect.

**Denudation.** These and other factors produce a most intense weathering and erosion by frost, ice and water.

Of these the two first overlap as frost effect depends on the formation of ice and its splitting powers. By “ice” is meant more particularly the work of glaciers and of floating ice. Frost acts primarily as an agent in splitting off rock fragments, but it also produces other secondary effects. Even in the summer the soil is generally frozen below a depth of 18 inches. Högboöm (27) has shown that this frozen subsoil may act as a gliding plane down which the soil above, broken continuously by alternate freezing and thawing (“regelation”), gradually slides. If one also includes scree it seems that practically the whole surface where there is the slightest slope, is on the move. This is very destructive to plant life, and results in the almost total sterility of many areas.

The effect of water is either in river erosion, or in connection with snow-water which is very destructive during the spring. The latter works in conjunction with “regelation” in many places.
We will deal with the special regions which we visited in Spitsbergen. They will be found marked with dots on the general map (Fig. 3).

A. PRINCE CHARLES FORELAND. (North Eastern Region.)

The area dealt with is included in the map (Fig. 4). It consists essentially of three parts, a central core of mountains, an undulating lowland area next to it, and raised beaches of much later date on the coast. The first two parts consist of various rocks, quartzites, sandstones, conglomerates, etc., all poor in lime.

![Map of northern portion of Prince Charles Foreland](image-url)
The characteristic feature of the “Foreland” is the rawness and fogginess of its climate. This is due to frequent mists from the Greenland Sea. Clear days are much rarer than on the mainland, but temperature variations are probably not so great as in the fjords. This raw climate helps frost and other erosion, and the whole country shows the results of these.

The following subdivisions can be distinguished:

2. Maritime Communities.
   (a) Brackish Water.
   (b) Inter-tidal Zone.
   (c) Recent Shingle.
3. Raised Beach System.
4. Rocky Lowland.
   (a) With “polygon soils.”
   (b) Without “polygon soils.”
   (c) Moss-mat.
   (d) Fresh water.
   (e) Erratic Boulders and Rocks.
5. Upland Region.
   (a) Screes.
   (b) Stabilised Slopes.
   (c) Wet Ravines.


This community is dealt with here because although in some ways belonging to the upland region, yet its general characters depend on the sea. These cliffs are situated some little distance from the sea with intervening flat country.

The only colony of sea-birds in the area is that at Vogel Hoek. Here is a steep rock-wall of the usual type. The area may be divided into two parts: (a) the cliff face, and (b) the scree below.

(a) On the ledges there are large colonies of Brünnich’s Guillemot, Kittiwake, Fulmar Petrel, and usually above them their enemy the Glaucous Gull. In crevices the Spitsbergen Puffin (*Fratercula arctica naumanni* Norton) and the Little Auk nest. On the rock wall are large amounts of *Enteromorpha* sp. In this alga was found a rich fauna of rotifers, tardigrades, nematodes, protozoa and mites (*Scutovertex lineatus*). Plants could be seen on the ledges, probably *Cochlearia* which is present on the screes below.

(b) The Little Auk nests here while the Pink-footed Goose nests on the slopes around. The Arctic Fox and Glaucous Gull have been seen here (21) attacking young Guillemots as they left the nest.

There is a continuous mat of flowering plants on the scree. The absence of *Saxifraga oppositifolia* is interesting. It has long been recognised as one of the hardiest of Arctic and Alpine plants, growing under most severe conditions,
but always seems to be sensitive to competition, and is often absent in closed communities. Here occur:

**Phanerogams:**
- Alopecurus alpinus Sm.?
- Cochlearia officinalis
- Ranunculus pygmaeus
- R. sulphureus

**Mosses:**
- Aulacomnium palustre
- Hypnum uncinatum
- A. turgidum

*S. rivularis* and *R. pygmaeus* are very luxuriant. Comparison with later lists shows that the flora is poorer than that of similar habitats in Icefjord.

### 2. Maritme Communities.

**(a) Brackish Water.** This is represented by Richard Lagoon. It is a large tidal lagoon whose water is brackish at low tide. The lagoon is about \(3 \frac{1}{2}\) miles long and \(1\frac{1}{2}\) mile wide, and is separated from the sea by a bar of rough shingle, which is covered by storm tides only. The only entrance is a narrow channel through which the sea rushes in at the flow, and out at the ebb. A line of soundings (see Fig. 4) taken between high and low tides gave depths of from 4\(\frac{1}{2}\) to 6\(\frac{1}{2}\) feet, and the lagoon cannot be more than 3 feet deeper at high tide. The bottom is gravelly or sandy. Here occur masses of various algae. Dredging was carried out with Mr Huxley's help. The following occur:

<table>
<thead>
<tr>
<th>Algae:</th>
<th>Hydroidea:</th>
<th>Polyzoa (on algae and alive when taken):</th>
<th>Crustacea:</th>
<th>Mollusca:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chaetomorpha melagonium Kjellm.</td>
<td>Opercularella lacerta Johnston</td>
<td>Aleosidaedium gelatinosum Linn.</td>
<td>Gammaracanthus loricatus Sab.</td>
<td>Lioyma fluctuosa Gould</td>
</tr>
<tr>
<td>Cladophora arcta Kuetz.</td>
<td></td>
<td>Ophelia limacina Rathke</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Desmarestia aculeata Lamour.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dictyosiphon foeniculaceus Grev.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fucus serratus L. f. arctica J. G. Agardh</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Laminaria sp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phlocospora tortilla Strömf.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pyelaellia littoralis Kjellm.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhodomela lyopoiodioides Ag.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Algae:  
- Chaetomorpha melagonium Kjellm.
- Cladophora arcta Kuetz.
- Desmarestia aculeata Lamour.
- Dictyosiphon foeniculaceus Grev.
- Fucus serratus L. f. arctica J. G. Agardh
- Laminaria sp.
- Phlocospora tortilla Strömf.
- Pyelaellia littoralis Kjellm.
- Rhodomela lyopoiodioides Ag.

Hydroidea:  
- Opercularella lacerta Johnston

Polychaeta:  
- Capitella capitata Fab.
- Harmothoë imbricata Linn.
- Ophelia limacina Rathke

Polyzoa (on algae and alive when taken):  
- Aleosidaedium gelatinosum Linn.
- Gemellaëria loricata Linn.

Crustacea:  
- Gammaracanthus loricatus Sab.

Mollusca:  
- Lioyma fluctuosa Gould

The surface water tasted fairly fresh, but the lower layers in which the animals live (6 feet) may be more saline. Nearer the entrance, when the tide was flowing in, the surface chloride content ("salinity") was 15-77 grams per litre. Large numbers of Amphipoda occur in the shallow water on the inner side of the lagoon, where the chloride content at low tide (July 10th) was 6-34 grams per litre. Here are found *Gammaracanthus loricatus*, *Gammarus locusta* L. var. *zaddachi* Sexton and *Pseudalibrotus littoralis* Kröyer. Arctic Terns were seen fishing for these crustacea—some of the *Gammaracanthus* reached a length of 5-2 cm. Numbers of Ringed Seals (*Phoca hispida*) inhabit
the lagoon. They live to a great extent on crustacea, and other bottom animals.

The following birds were seen in small numbers:

<table>
<thead>
<tr>
<th>Northern Eider</th>
<th>Fulmar Petrel</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red-throated Diver</td>
<td>Mandt’s Guillemot</td>
</tr>
<tr>
<td>Arctic Tern</td>
<td>Glaucous Gull</td>
</tr>
<tr>
<td>Kittiwake</td>
<td></td>
</tr>
</tbody>
</table>

The divers use the lagoon for their sexual displays, but obtain their food from the sea, pointing to the probable absence of fish in the lagoon.

The flora is of the type usually occurring in the sub-littoral zone in the Faroes (6) and Iceland (31). Several of the species, e.g. Pylaiella and Phloeospora tortilis can grow in brackish water or where fresh water is discharged from streams (6). Chaetomorpha, Dictyosiphon and Pylaiella also occur in Iceland in very high pools which only rarely receive salt water, and often must be brackish, especially after rain (31).

The brackish character of the fauna is shown more by the absence of certain marine forms, than by the presence of any freshwater ones. Dead sea-urchins were seen on the bottom in one place, and plankton brought in by the tide (Copepods, etc.) was in a dying condition. The animals include several brackish forms. Gammarus locusta var. zaddachi is a form (probably environmental) of the typical G. locusta. This lives in a salinity of 2 to 6 grams per litre in Denmark, but also occurs occasionally in higher salinities there (61). The Lamellibranch Liocyma was slightly abnormal, which may have been due to its environment. The Gammaracanthus loricatus, however, showed no approach to the type of G. lacustris, the form (also probably environmental) occurring relict in fresh water in Northern Europe and in Spitsbergen (48). Richard Lagoon is of especial interest, since it is one of the largest of its type in Spitsbergen, and may ultimately be cut off from the sea by land elevation. It represents an intermediate stage in the process leading to the formation of relict lakes like those in Europe.

(b) Inter-tidal Zone. We have only a few notes on this region.

Along the unstable shingle shore both outside and inside Richard Lagoon there seems to be no rooted vegetation. Huge piles of Laminaria and Fucus are cast up by the tide. Collembola were found in large numbers: Achorutes viaticus, Agrenia bidenticulata, Archisotoma beselsi Packard, and Isotoma viridis. A. beselsi is confined to sea shores. Purple Sandpipers were seen feeding on these animals. A fly Fucomyia frigida Flm. occurs on the shore at Point Carmichael, and may breed in the seaweed cast up.

As the ice had not melted from the edge of most of the lagoon when we left, it was not possible to see if there are any salt marshes there. Mr Mathieson tells us that there are large areas of ice in this position which do not melt in ordinary years, but in the summer of 1922, which was exceptionally warm, these completely disappeared. The conditions seem, therefore, to be too unfavourable for the production of well-marked inter-tidal communities, although
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Glyceria vilfoidea Fr., which usually is common in salt marshes in Spitsbergen, is recorded from this district (53).

(c) Recent Shingle. This occurs only on the outside of Richard Lagoon. It is almost barren, except for a few Collembola, while Arctic Terns and Northern Eiders nest in small numbers.

3. The Raised Beach System.

The part studied stretches from Richard Lagoon almost to Point Carmichael (see Fig. 4). At its southern end it blends into the recent shingle, in the north into older rocks. Snow prevented observations inland. The Beach System is on an average about 30 feet above sea-level, and forms steep cliffs seawards. The system consists of parallel beaches, which meet the coast line at a small angle. The seaward beaches are higher so that most of the surface drainage is into the lagoon. The difference in height between "ridge" and "low" is never more than 10 feet and usually less. Most of the beach is composed of pebbles with diameters lying between 2 and 8 inches. In the cliff face, there is a sand layer from 2 to 15 feet in thickness. As the prevailing winds seem to be from the North East, this sand layer is continually being eroded and carried on to the shingle surface where the sand gradually accumulates. In the north very little sand has accumulated, especially on the landward beaches. The vegetation is very sparse, and consists only of very few stunted flowering plants and lichens. Gyrophora proboscidea, Rhizocarpon geographicum, and Lecidea confluens are the most important of the latter.

On the seaward beaches there is a little more sand, and as a result there is a richer, but still scattered, flora of higher plants and mosses. Saxifraga oppositifolia is the characteristic and most frequent species. Also:

Phanerogams:
- Cerastium alpinum f.
- Draba alpina o.
- D. subacutata Simmons o.
- Luzula confusa Lindeb. l.
- Oxyria digyna r.

Bryophytes:
- Dicranoweisia crispa Dicranum fusescens var. congestum

Lichens:
- Cetraria islandica

The Dicranoweisia occurs among the tufts of Purple Saxifrage. Many lichens occur on the pebbles. In addition to those mentioned above there are Buellia sorotia Th.Fr. and Parmelia alpica Th.Fr.

Among stones and plants were:
- Collembola: Isotoma viridis
- Diptera: Diamesa poultoni Edw. var. flavipila Edw.
- Scara tridentata Rubs.
- Mites: Bdella desipiens Thor.
- Spiders: Typhochrestus spetomagensis Thor.

A few insect larvae occur in the plants. The spider spins a few threads from flower to flower of Saxifraga oppositifolia, etc.
In damp hollows the flora is transitional to the *Luzula-Cetraria* community mentioned below. There is about 1 inch of humus, and the pebbles are small. *Luzula confusa* and *Cetraria islandica* occur here sparingly. The following also occur:

**Mosses:**
- *Cynodontium virens* f. *Rhacomitrium lanuginosum* o.
- *Dicranoweisia crispula* f. *Dicranum fuscescens var. congestum* o.

**Lichens:**
- *Cetraria nivalis* o. *Stereocaulon alpinum* l.a.
- *Microglaena sphinctrinoides* Nyl.

The micro-fauna of some *Rhacomitrium* was:

**Rotifers:**
- *Habrotrocha insignis* Bryce
- *Macrotrachelia plicata* var. *hirundinella* Murray
- *Mniobia russeola* Zelinka (with a parasite)
- *Pleuretra alpinum* Ehrb.

**Tardigrada, Nematoda, Rhizopoda:** r.

This is a typical dry moss. The rotifers, especially the larger ones, show greater powers of revival than the other animals (8).

As the sand accumulates, if not too rapidly, a characteristic community appears—the *Luzula-Cetraria* community. The three main plants in this are *Luzula confusa*, *Cetraria hiscens* Th.Fr. and *C. islandica*. There is usually 3 to 8 inches of sand, of which the top layer (\(\frac{1}{2}\) to 1 inch) is peaty. There also occur:

**Phanerogams:**
- *Cerastium alpinum* f. *S. oppositifolia* o.
- *Oxyria digyna* o. *Stellaria humifusa* a.

**Bryophytes:**
- *Hypnum uncinatum* var. *foeneum* Hagen.

**Lichens:**

The mosses occur in damper parts, and are more damp-loving types than the previous ones. Large masses of *Nostoc piscinale* Kuetz. occur in wet patches. The two crustaceous lichens mentioned above appear to be the first colonisers on bare ground. They are followed by fruticose forms such as *Cladonia fuscata*, *C. pyxidata*, and *C. cervicornis* Schaer.

No animals were found among the plants in the *Luzula-Cetraria* area. Many Collembola occur on the surface of melted snow-water in hollows.

Near the coast is a deep layer of sand, where *Luzula* and *Cetraria* are absent. There is much bare ground, *Saxifraga oppositifolia* being dominant, while *Silene acaulis* L. and *Draba subcapitata* are abundant. The mosses are similar to those on the almost bare shingle. The micro-fauna of the mosses is also similar, and the same may be said of the higher invertebrates. The flies *Campiocladius externus* Holmg. and *Fucomyia frigida* were seen on *Saxifraga*...
flowers. The community is therefore similar to that on almost bare shingle although the substratum is quite different.

When the sand accumulation increases, a distinct change takes place in the biota. In places a series of small dunes 3 to 6 inches in height is being formed. The only successful plant under these conditions is Saxifraga oppositifolia, which, by means of its creeping stems, keeps pace with the deposition of sand and binds it into solid hummocks. Other plants growing in the hollows are Oxyria, Saxifraga caespitosa, Silene, and Draba subcapitata. The Oxyria is very dwarfed and brilliant red in colour due to the production of anthocyanin. Both Silene and Draba form large compact tussocks here and there. Luzula and Cetraria are killed by the sand deposition. A grass, possibly Catabrosa algida, is abundant here, but was not in flower.

After a while the sand deposition is too rapid, the plants lose their hold, and "blow-outs" occur, 2 feet of sand being removed in some places. These probably originate at the denuded cliff-edge. The hummocks become undercut by the sand blast, and finally topple over. Silene, owing to its compact tussock form, is very resistant. In places re-colonisation by Saxifraga oppositifolia of such "blow-outs" was observed.

There was hardly any animal life in these areas.

Ponds. There are one or two small ponds on the beaches. Red-throated Divers nest near the edges. The algae consisted mainly of Desmids (species of Cosmarium, Stauroastrum and Euastrum), but some Cyanophyceae (Merismopedia glauca Naeg. and Lyngbya perelegans Lemm.) were also found. Diatoms, Flagellates and Ciliates were also recorded.

4. Rocky Lowland.

This area consists of a rolling tract of land between the lagoon and beaches and the mountains. The larger part of the area is differentiated by frost action into polygonal areas of varying nature and size.

(a) Areas with "polygonal soil." The type found is that called by Högbom (27) "Polygon Soil Type 1," and is produced from heterogeneous materials. It consists of polygon areas of which the centre is composed of fine silt while the edges are defined by lines of stones of various sizes. In addition to Högbom, Thoroddsen (63) and also other writers have dealt with the causes of their formation.

The nature of these polygons varies, depending apparently on the drainage (they are not formed where the drainage is good), and on the relative heterogeneity of the particles. In some places the rims are composed of small shale particles only, in others of stones up to 4 to 6 inches in diameter, and in others again blocks of 3 feet in diameter are present. The diameters of the polygons vary usually from 4 to 10 feet. The centre is usually much wetter than the rim owing to retention of water. Excavation showed that the ground-ice, which exists everywhere at a depth of about 18 inches, was so shaped that the
thaw-water could never drain away, and probably the interiors of the polygons never dry out in summer. The centres are almost always bare of plants (Plate III, fig. 1). The following were found in the centres of many types of polygons, but represent fairly uniform habitats.

**Phanerogams:**

- *Alopecurus alpinus* o.
- *Cerastium alpinum* o.
- *Draba alpina* r.
- *Luzula confusa* o.

**Bryophyte:**

- *Polytrichum alpinum* r.

**Algae:**

- *Nostoc piscinale* o

**Lichens:**

- *Cetraria hiscosa* l.f.
- *Solorina crocea* f.
- *C. islandica* l.f.

*Solorina crocea* is the most characteristic plant, and often is the only species here.

The edges of the polygons, on the other hand, often bear a luxuriant and varied flora. Colonisation of the edges was seen in all stages from the appearance of a few tufts of moss or small plant of *Saxifraga oppositifolia*, to a 2 to 6 inches high rampart of vegetation.

Apart from *Saxifraga* and *Salix polaris* the lower plants predominate on these rims. The following is a list compiled from many types of polygons, but there is considerable variation.

**Phanerogams:**

- *Alopecurus alpinus* l.
- *Saxifraga oppositifolia* o.-f.
- *Cerastium alpinum* o.-f.
- *Draba alpina* r.
- *S. cernua* r.-o.
- *Luzula confusa* o.
- *S. nivalis* o.
- *Oxyria digyna* l.
- *Phlox verna* r.
- *S. oppositifolia* f.-d.
- *Polytrichum alpinum* f.-a.
- *S. acutifolia* r.
- *Bryophytes:**

- *Aulacomnium palustre* r.
- *Hylocomium splendens* i.f.
- *A. turgidum* o.-a.
- *Hypnum exannulatum* Guenb. r.
- *C. nitens* Schimp. f.-c.d.
- *H. uncinatum* f.
- *Cynodontium virens* r.
- *Polytrichum alpinum* f.-a.
- *Diceranoweisia crisplata* r.
- *Ptilidium ciliare* r.
- *Dioranum bonjeangi* var. juniperifolium r.
- *Braithwa. o.-a.
- *Dicranum bonjeangi* r.
- *R. lanuginosum* f.-e.d.

**Lichens:**

- *Alectoria ochroleuca* o.
- *Lecanora rangiferina* f.
- *Buellia disciformis Mudd.* var. insignis AL. Gray. l.
- *Lecanora ephryon* o.
- *Cetraria hiscosa* o.-d.
- *L. tartarea* l.f.
- *C. nivalis* o.
- *Peligeria malacea Fr.* r.-o.
- *Cladonia bellicifolia* l.f.
- *Psoroma hypnorum* o.
- *O. pyxidata* o.
- *Sphaerophorus globosus* r.
- *Stereocaulon alpinum* o.-f.

*Nearly all the lichens are on the crests of the ramparts. *Rhacomitrium* and *Camptothecium* seldom occur together on the polygon edge. The mosses are not bog species; but dry ones are not very common either. At the crests the vegetation seems to dry up, and here occur the two species of *Lecanora*, often*
growing over the other plants. In Lapland a similar growth of *Lecanora tartarea* on dried-out mosses occurs, although on a much larger scale (33).

Animal life on these ramparts is either scarce or absent.

(b) Areas without "polygonal soil." These occur either where the slope allows drainage or else where the homogeneity of the particles prevents differentiation. The chief areas are those at the tops of the lower hills, that worked in most detail being one about 150 feet high named Silene Hill from the amount of *Silene acaulis* on its slopes. Most of the animal data are taken from here. In places the ground is rocky and covered with frost debris. Generally there is very little soil (e.g. Silene Hill) although in hollows it may collect. The community is really a "fjældmark" similar to that on Bear Island, but rather richer in species. The presence of *Dryas octopetala* and the abundance of *Salix polaris* in places mark a transition towards the "Dwarf-shrub Heath" of other countries. The complete list (including Silene Hill) is as follows:

**Phanerogams:**

- *Alopecurus alpinus*  
- *Alsine rubella*  
- *Cerastium alpinum*  
- *Draba alpina*  
- D. alpina var. oblongata RBr.  
- *D. subcapitata*  
- *Dryas octopetala* L.  
- *Luzula confusa*  
- *Oxystria digyna*  
- *Papaver nudicaule var. radicatum*  
- *Pedicularis hirsuta* L.  
- *Polygonum viviparum*  
- *Salix polaris*  
- *S. reticulata*  
- *Saxifraga caespitosa*  
- *S. nivalis*  
- *S. oppositifolia*  
- *Silene acaulis*  

**Bryophytes:**

- *Cynodontium virens*  
- *Dicranoweisia crisipula*  
- *Dicranum fusescens*  
- *Grimmia apocarpa*  
- *Gymnomitrium corallioides Nees.*  
- *Hylocomium splendens*  
- *Lycopodium annotinum*  

**Lichens:**

- *Alectoria ochroleuca*  
- *Ceraria vermicularis*  
- *Cetraria hispida*  
- *C. islandica*  
- *Cladonia rangiferina*  
- *C. sylvatica*  
- *Lecanora epibryon*  
- *L. tartarea*  
- *Peltigera malacea*  
- *Sphaerophorus globosus*  
- *Stereoconaulum alpinum*  

*Cetraria nivalis* is characteristic of places where the rock is near the surface. Generally speaking, the lower plants occupy a subordinate position.
On Aberdeen Machar there are more mosses and lichens. In this area a few Arctic Skuas and Purple Sandpipers nest. Seton Gordon (21) observed that the former nested on hummocks which were the only places at that time free from snow (see “Skua Hummocks” in the account of Bear Island). A few foxes also occur here.

In the Silene Hill region there are no Skuas. The following occur on Silene Hill:

- **Collembola:** Isotoma viridis r., Xenylla humicola r.
- **Diptera:** Camptocladius extremus o., Limnophora megastoma Bohem. o. On Silene flowers
- **Spiders:** Typhochrestus spetsbergensis f., B. decipiens f., Under stones and weathering rocks
- **Mites:** Bdella groenlandica f., Among plants
- **Diptera:** Camptocladius extremus o., Limnophora megastoma Bohem. o.
- **Spiders:** Typhochrestus spetsbergensis f., Among plants
- **Mites:** Bdella groenlandica f., Among plants
- **Diptera:** Camptocladius extremus o., Limnophora megastoma Bohem. o.
- **Spiders:** Typhochrestus spetsbergensis f., Among plants
- **Mites:** Bdella groenlandica f., Among plants

This differs from the fauna of the beaches in being richer, especially in mites. The two species of *Bdella* do not seem to live in the same kind of habitat. Numbers of young *B. decipiens* were found, each in a spherical spiny case, on the under side of stones, and in some cases were just emerging. All the oribatid mites (the last three given above) are vegetarian, and Mr Hull states that they prefer cryptogamic food. *Typhochrestus* lays 7 or 8 pale orange eggs, which are fastened to the under side of a stone in a cocoon of white threads. There are several records of mites, though not species found by us, “in the nest of *Typhochrestus spetsbergensis*” (34). But clearly most of the mites must be vegetarian, as there would not otherwise be enough food to support the number of spiders which occur. The food relations here are much the same as those shown in the diagram for Bear Island. Other animals were:

- **Collembola:** Achorutes viaticus
- **Diptera:** Diamesa poultoni Holmg.
- **Mites:** Hermannia reticulata Thor. Vegetarian

The two flies were flying about over almost completely snow-covered country in the first days of July.

(c) **Moss-mat.** Near Vogel Hoek there is a large flat mossy plain which may be included in this community, though it shows transitions to Moss Heath. The plants here are probably little affected by the sea-birds. There are practically no higher plants.

- **Bryophytes:** Cephalozia byssacea, Dicranum groenlandicum Brid. f., Lophozia alpestris a., D. scoparium Hedw. var. spadiceum Boul.
- **Moss:** Hypnum uncinatum a., Rhacomitrium lanuginosum o.
Wet moss areas probably occur, but were snow-covered.

(d) Freshwater Communities. There are a number of small ponds here and there along the courses of the streams. These were not worked for animals or plants since it was necessary not to disturb the Red-throated Divers nesting there, which were under observation. This species is limited in its choice of nesting site by the fact that it cannot walk properly on land, and the nest is hardly ever more than 10 feet from the water’s edge (21). The eggs were several times robbed by Skuas. There is never more than one pair of Divers on each pond.

The streams at this time were mostly rushing torrents of snow-water and devoid of life.

(e) Erratic Boulders and Rocks. Most of these support a flora either in cracks or on the surface of the stone. The crevice flora consists usually of species from the surrounding “fjeldmark.”

On the rock surfaces the flora consists mainly of lichens. A few mosses occur, but they are not important. The more common lichens, of all biological types, are the following:

- Alectoria nigricans
- Gyrophora probosicida
- Lecidea lapidea

The Xanthoria is particularly characteristic of large isolated boulders.

5. Upland Region.

The mountains here reach a height of about 1600 feet (see Fig. 4), with steep slopes, but there may be rather flat plateaux of limited extent. No “polygonal soils” were seen in the region.

(a) Screes. Ordinary screes occur in many places. The particles are usually rather large as the rock is a hard quartzite or gneiss. The screes are being fed continually from above, and thus plants are sparse or absent. The main species, as in all unstable and severe localities, is Saxifraga oppositifolia; Luzula confusa, Rhacomitrium canescens var. ericoides B. and S., and various crustaceous lichens are also present.

The animals of a scree in the mouth of Glen Mackenzie (300–400 ft) were:

- Collembola: Achorutes viaticus, Xenusylla humicola
- Spiders: Leptyphantes sobrius Thor.
- Mites: Bdella decipiens
- Birds: Snow Bunting, Nesting
In some *Rhacomitrium canescens* var. *ericoides* were a rotifer, *Macrotrachela plicata* var. *hirundinella*, and a few nematodes, tardigrades and protozoa. *Leptyphantes sobrius* is a fast runner and occurs almost only upon unstable mountain slopes in Spitsbergen, where *Typhochrestus* and other flat-lowland species are absent. It came on one hill here at 150 feet, and Mr Huxley found it together with *Isotoma viridis*, a fly and the Snow Bunting, on a stabilised slope on Lord Stairs' Heights at 1350 feet (see below).

(b) *Stabilised Slopes.* These are usually scree of fine particles, which have been stabilised by plants. Even now movement takes place as a result of "solifluction." A large area of soil, with the layer of vegetation on it, had slipped down recently in one place on Lord Stairs' Heights, and doubtless these landslips are not uncommon.

The slopes are usually covered by a close herbage which consists of dicotyledons on south aspects, and are identical with Nathorst's "sluttningar" (44). The luxuriance of the vegetation is doubtless due to the intense insolation received, as the slopes are nearly perpendicular to the sun's rays. This effect has been noticed in arctic countries by many writers. Kihlman (33) gives figures showing the extraordinary heating-up which the ground experiences, soon after the snow has melted, and with ground-ice near the surface. This is greatest according to him on the south side of small hummocks; how much more so must it be on steep slopes! Other factors are the good drainage of the soil and the early removal of the snow. These slopes, however, are very dry in late summer, but would never completely dry up owing to the melting of the ground ice. The following occur upon such slopes:

**Phanerogams:**

- *Cerastium alpinum* f.
- *Draba alpina* r.
- *D. wahlenbergii* Hartm.
- *Luzula confusa* f.
- *Papaver nudicaule* var. *radicatum* f.
- *Polygonum viviparum* f.
- *Saxifraga caespitosa* f.
- *S. cernua* o.
- *S. hieraciifolia* W. & K. o.
- *S. nivalis* r.—o.
- *S. oppositifolia* f.
- *Salix polaris* o.—f.
- *Silene acaulis* o.—f.

**Bryophytes:**

- *Hypnum uncinatum* r.

**Lichens:**

- *Cetraria hisascens* o.
- *Cladonia pyxidata* r.
- *C. nivalis* o.

A striking point is the lack of any dominant among the flowering plants, many of them being equally common.

On the north slope, which was then still partially snow-covered, there were many more mosses, and this agrees with other writers' observations. In some places a rather damper type of community occurs, including many mosses, the flowering plants being less important. In addition to some of those given above there were:

- *Alopecurus alpinus*
- *Cardamine bellidifolia*
- *Lycopodium selago* L. o.
- *Oxyria digyna* f.
- *Ranunculus sulphureus* l.a.
Nearly all of these denote a damper habitat. Lower plants include:

**Bryophytes:**
- Aulacomnium turgidum
- Dicranoweisia crispula
- Dicranum elongatum Schleich.
- D. fusescens var. congestum
- Hypnum revolutum Lindb.

**Lichens:**
- Alectoria ochroleuca
- Cladonia rangiferina
- Cetraria islandica
- Cladonia furcata
- Sphærophorus globosus

The moss flora is allied to that on the polygon rims. The lichens indicate a somewhat dryer habitat than the ravines.

The fauna of the stabilised slopes was not studied carefully.

(c) *Wet Ravines*. These are more of the nature of drainage hollows than clefts. The ground is sodden with water which trickles down among thick, foot-high moss hags, flowering plants being almost absent. A number of liverworts occur intertwined with the mosses. Curiously enough there are also quite a number of lichens, some in the wet parts, some on the summits of the hags. It is very probable that the whole region becomes much drier at a late period in the season. The following are the more important species:

**Phanerogams:**
- Oxyria digyna

**Bryophytes:**
- Aulacomnium palustre
- Dicranum elongatum
- Hypnum uncinatum
- Polytrichum juniperinum
- Aulacomnium turgidum
- Cephalozia bicuspidata
- Hypnum callichroum Brid.
- H. stramineum

**Lichens:**
- Cetraria hisaeens
- Pettigera aptica Wild.
- P. malacea

**GENERAL CONSIDERATIONS.**

The vegetation of the area is characterised by the great importance of cryptogams in many communities. In the Arctic, owing to the fog, the coastal areas are much less favourable for plant life than are the clearer, sunnier interiors of the fjords. The dwarf-shrub *Cassiope tetragona* Don. does not seem to occur on Prince Charles Foreland, and this is partly in agreement with conditions in North East Greenland. There *Cassiope* forms heaths inland only, while on the coasts it occurs scattered. It is also possible, that *Cassiope* has not yet been able to cross Foreland Sound, and as the west coast is often open in winter, due to violent storms, the seeds may not have been blown across owing to the absence of ice. See (28, 50).

Arctic animals work almost the whole 24 hours owing to the absence of darkness. Feilden (17) states, however, that there is a slight amount of rest
among the birds at midnight. The temperature is usually lower at night, and this must affect the activities of invertebrates. Johansen (29) states that bees in Greenland work all night, but that there are fewer at midnight. He says also that there are day-flying and night-flying moths, which is unusual for arctic animals. The absence of darkness accounts for the lack of night working animals (except the moths mentioned above), and thus the "relay system" of day and night forms which enables more animals to occupy any area in lower latitudes, is absent in the Arctic. This is one cause of the poorness in species of the fauna. Other causes in Spitsbergen are geographical isolation and severe conditions.

B. CAPE BOHEMAN REGION.

This district nowhere rises higher than 50 feet above sea level, and can be divided into two parts. The northern part consists of flat boggy country, where the underlying rock never appears at the surface. In the southern part, the soil is almost always very shallow, and there is a series of rock outcrops. The rocks are sandstones and slates deficient in lime, and dip at a slight angle, in places forming rock pavements. There are a number of ponds scattered over the whole area. Around the coast there are often cliffs, which are nowhere more than 30 feet high.

Dr G. J. van Oordt of Utrecht spent most of the summer in the vicinity. We are much indebted to him for information about the birds of the neighbourhood.

The following communities can be distinguished:

(a) Land Communities.
1. Inter-tidal Zone.
2. Maritime Communities.
3. "Fjaeldmark."
   (a) Dryas.
   (b) Other types.
5. Rock Communities.
   (a) Surface.
   (b) Crevices.
6. Streamside Communities.
7. Wet Tundra.
   (a) Moss-Salix Bog.
   (b) Pond and Stream Marginal Communities.

(b) Freshwater Communities.
1. Ponds.
   (a) Permanent.
   (b) Temporary.
2. Streams.
2,50 Contributions to Ecology of Spitsbergen and Bear Island

(a) Land Communities.

1. Inter-tidal Zone.

This may consist of shingle (not common) or of rocks. In the case of the shingle, owing to the instability, life is entirely lacking. On the rocks, especially near the Dutch coal mine, there is a rich algal vegetation. The following occur:

- **Algae:**
  - Fucus evanescens Ag.
  - Chaetopteris plumosa Kuetz.
  - Philospora tortilis

- **Hydrozoa:**
  - Gonothyraea loveni Allman

- **Mollusca:**
  - Littorina rudis var. groenlandica Uk.

- **Crustacea:**
  - Numerous amphipoda (Gammarus, etc.)

- **Birds:**
  - Purple Sandpiper Feeding
  - Grey Phalarope Feeding

2. Maritime Communities.

There is little special life on these areas. Mandt’s Guillemot and Arctic Tern nest in small numbers along the cliffs, and the latter together with geese and the Northern Eider are found on small rocky islands off the coast (see “Edinburgh Island”). The mite Bdella groenlandica lives among shaly rocks on the cliffs. In several places the usual “fjaeldmark” plant community changes in the vicinity of the sea. Stellarium humifusa is much commoner here, and is usually recorded from such places in arctic countries. Saxifraga flagellaris Willd. also occurs in this region, but Dryas is absent in many places.

3. “Fjaeldmark.”

(a) This community differs from that on Bear Island and Prince Charles Foreland in the abundance of Dryas octopetala, in many places this being dominant. However, it nowhere forms a complete plant covering, the soil being usually bare between the plant cushions. The ground is very gravelly with little soil. The community may be compared with Cleve’s (9) “Polster Heide” although there is only one other dwarf-shrub besides Dryas (Salix polaris). The Dryas plants form close cushions, as do most of the other plants. Saxifraga oppositifolia is the next commonest plant. The Dryas “fjaeldmark” occurs on dry exposed soils, and this distinguishes it from the other type described below.

The species are:

- **Phanerogams:**
  - Cerastium alpinum o.
  - Draba alpina with var. oblongata f.
  - D. wahlenbergii f.
  - Dryas octopetala a.
  - Luzula confusa o.
  - Oxyria digyna r.

- **Bryophytes:**
  - Hylonomium splendens f.

- **Lichens:**
  - Cetraria nivalis o.
  - Lecanora tartarea a.

In the open parts invertebrate animal life is almost absent.
(b) This is a more mixed type of "fjaeldmark" occurring on slightly damper slopes, where there is more real soil. *Dryas octopetala* is absent. The species are those usually growing in damper places than the plants in the last list. The plant covering is never continuous. The community grades into the streamside community below and into the *Dryas* community above. The following are present:

Phanerogams:

- *Luzula confusa*
- *Salix polaris* (abundant)
- *Saxifraga oppositifolia* o.—f.
- *S. caespitosa* o.
- *S. hieraciifolia* r.
- *Saxifraga nivalis* o.
- *Cerasitum alpinum* r.
- *Oxyria digyna* o.
- *Silene acaulis* r.
- *Stereoecaulon alpinum* l.f.

Lichens:

- *Cetraria islandica* l.a.
- *Stereocaulon alpinum* l.f.


Heath is known from most arctic countries and has been described by Warming (67), Cleve (9) and others. Generally the dwarf-shrubs forming the heath are of many species, as in Greenland. In the Cape Boheman region there is only one species, namely *Cassiope tetragona*. This grows to a height of a foot or so, and forms a thick carpet over the ground. The heath in the region is developed in sheltered localities. *Cassiope tetragona* forms large heaths in East Greenland (15, 24), but is there associated with *Empetrum, Cassiope hypnoides* and *Vaccinium uliginosum*. In East Greenland *Cassiope tetragona* only occurs where there is a complete snow-covering during the winter and spring (38), and its distribution at Cape Boheman can be easily explained on the same basis. With the *Cassiope*, but in very small numbers, are:

- *Papaver nudicaule* var. *radicatum* o.
- *Saxifraga oppositifolia* o.
- *Equisetum variegatum* r.
- *Dicranoweisia crispa* f.

The *Cassiope* heath is very dry and poor in animal life. In one area the mite *Sphaerozetes notatus* and a fly *Limnophora hyperborea* Bohem. were the only animals found after much search.

The birds of the dry-region communities are dealt with together. The following birds nest here:

- *Purple Sandpiper* f.
- *Grey Phalarope* f.
- *Arctic Skua* r.
- *Northern Eider* o.
- *King Eider* (*Somateria spectabilis* L.) o.

Pink-footed Geese and Brent Geese feed here and in other parts of the Cape Boheman region. The Skuas attack and eat young Eiders, and even Purple Sandpipers (64). The Grey Phalarope feeds both in fresh water and at sea. The stomach of one contained remains of flies, etc. One from Advent Bay (July, 1921) had over fifty, and another 205 large chironomid fly larvae in the stomach. One from the same place obtained by Mr Jourdain in 1922 contained...
fly larvae and moss, while two others had remains of marine crustacea including young \textit{Gammarus locusta}. The Purple Sandpiper feeds on land and on the shore at low tide. The stomachs of two birds from Cape Boheman had in them respectively four and six spiders, another three flies and some plant remains, and a fourth three tiny marine gastropods and remains of seaweed.

5. ROCK COMMUNITIES.

These are present on the rock outcrops. The majority of the outcrops consist of gently sloping rock pavements with a few shallow cracks and depressions. At the escarpments weathering has had a much greater effect, and the rock has been split into large fragments, many of which remain almost \textit{in situ}. A complicated series of parallel cracks is thus formed, many of them 4 to 6 feet deep. The communities fall naturally into two divisions: (a) Rock Surface Communities, and (b) Crevice Communities.

(a) The flora of the rock surfaces is very poor. There is none of the luxuriance of crustaceous and other lichens as on Bear Island and Prince Charles Foreland. This is doubtless bound up with the much drier climate at Cape Boheman.

(b) In the smaller cracks and in slight hollows on the pavement a little soil collects, and this can support stunted specimens of the "fjaeldmark" plants. However, in the deeper cracks a more special flora develops. The chief factor here is the small amount of light available. Since the cracks may be 6 feet deep, are usually under a foot wide and have vertical sides, it is patent that with the low altitude of the sun in these latitudes very little light can enter. This is shown by the higher plants, which are much drawn out and attenuated. The production of flowers also is much decreased. Plants of \textit{Oxyria} collected here were quite green, whereas those on the "fjaeldmark" outside were reddish with anthocyanin. Mosses are an important part of the vegetation, while as on Bear Island, there are several liverworts.

\begin{center}
\textbf{Phanerogams:}
\begin{tabular}{lll}
Cerastium alpinum & r. & Saxifraga cernua & f. \\
Oxysia digyna & o. & S. oppositifolia & o. \\
Ranunculus sulphureus & o. & Stellaria longipes Goldie & r. \\
\end{tabular}
\end{center}

\begin{center}
\textbf{Bryophytes:}
\begin{tabular}{lll}
Blepharostoma trichophyllum & f. & Lophozia ventricosa \\
Hylocomium splendens var. gracilis & c.d. & Polytrichum alpinum \\
Hypnum stellatum & f. & Pseudopleskea catenulata & f. \\
H. uncinatum & f. & Scapania curta \\
Lophozia longidens & & Thamnium australianum & c.d. \\
\end{tabular}
\end{center}

\textit{Saxifraga cernua} is the only higher plant which is at all normal here. It has been recorded from many countries in somewhat similar habitats.

Snow Buntings nest in the crevices, but were often seen feeding in boggy places. Stomachs of five birds from here each had about a dozen fly pupae in them, while one had also remains of adult flies.

Among plants outside the fallen blocks were:

\begin{center}
\begin{tabular}{lll}
Collembola: & \textit{Isotoma viridis} \\
Spider: & Immature \\
Oligochaete: & \textit{Mesenchytraeus} sp. \\
\end{tabular}
\end{center}
Between the block collections and the Cassiope heath is often much moss in which are many plants of *Ranunculus sulphureus*.

6. Streamside Communities.

There are many small streams, and some of them are probably running all through the season. Some, however, which drain temporary ponds, dry up in the late summer. The substratum is much damper than any described previously. In some places the banks may be flooded by large amounts of snow-water, but this is not general. Many phanerogams occur here, often forming the main vegetation. *Oxyria digyna* is the commonest plant, especially where the banks are steeper, and inundation rarer. Another characteristic plant is *Ranunculus nivalis* L. together with *R. sulphureus*. *Salix polaris* and *Luzula confusa* are also common. The community corresponds with that described by Cleve (9) in arctic Sweden. Along one stream two zones were visible. The one nearest the stream consisted of *Alopecurus alpinus*, that on slightly higher ground of *Poa alpina* L. and the two species of *Ranunculus*. Lundager (38) records an almost identical arrangement of zones in North-East Greenland. In addition the following are found:

<table>
<thead>
<tr>
<th>Phanerogams:</th>
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<tr>
<td>Alsine rubella</td>
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<tr>
<td>Ranunculus pygmaeus</td>
</tr>
<tr>
<td>Saxifraga cernua</td>
</tr>
<tr>
<td>Saxifraga hieraciifolia</td>
</tr>
<tr>
<td>Phanerogams:</td>
</tr>
</tbody>
</table>
| Alsine rubella | r.  
| Ranunculus pygmaeus | l.  
| Saxifraga cernua | l.f.  
| Saxifraga hieraciifolia | r.  

Bryophytes:

| Brachythecium salebrosum var. arcticum Berggr. | Polytrichum alpinum Juniperinum |
| Camptothecium nitens |  

7. Wet Tundra.

This occupies most of the northern half of the region; it also occurs around the ponds and in the valleys between the outcrops in the southern part. In nearly all cases it is formed of mosses together with *Salix polaris*. Two communities can be distinguished.

(a) Moss-Salix Bog (Plate II, fig. 1). The water is stagnant, and in many places forms pools. In the bog are numerous hummocks formed by the *Salix*, the spaces between its branches being filled with interwoven mosses. The following higher plants occur, mostly on the summits of the hummocks:

| Alopecurus alpinus | o.  
| Cardamine bellidifolia |  
| Draba alpina |  
| D. wahlenbergii | o.  
| Eriophorum scheuchzeri Hoppe. | o.  
| The *Alopecurus* and *Eriophorum* are scattered about between the hummocks, and form a region transitional to the damper type of "fjaeldmark."

A number of lichens also occur on the hummocks:

| Alelectoria ochroleuca | Cladonia rangiferina |
| Cerania vermicularis | Stereocaulon alpinum |
| Cetraria nivalis |  

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These show that the tops of the hummocks dry up in summer. There is a marked zonation of the mosses on the hummocks. The following shows the type of zonation, starting from above:

1. Camptothecium nitens  
   Hypnum uncinatum
2. Brachythecium salebrosum var. arcticum  
   Cynodontium virens and var. arcticum  
   Polytrichum alpinum
3. Paludella squarrosa and others
4. Hypnum cordifolium, in lowest pools  
   H. giganteum Schimp.  
   H. stramineum  
   Ranunculus hyperboreus

A certain number of liverworts occur among the mosses, especially on the Salix tussocks:

- Blepharostoma triphyllum
- Cephaloziella bifida Schiffn.
- and var. erosa
- Lophozia kunzeana Evans
- Lophozia quinquedentata f.
- and f. turgida Lindh. f.
- Odontoschisma sphagni Dum.
- and var. erosa- Odontoschisma sphagni Dum.
- Lophozia kunzeana Evans

These bogs agree very closely in moss constitution with the “Mýrar” in Iceland (25), and with those in East Greenland (14). The following is a general list of mosses for the Cape Boheman bogs:

- Aulacomnium palustre
- A. turgidum
- Brachythecium salebrosum var. arcticum
- Bryum obtusifolium
- Camptothecium nitens f.
- Cinclidium stygium
- Cynodontium virens and var. arcticum
- Dicranum fuscescens
- Hypnum brevifolium f.
- H. cordifolium
- H. intermedium
- Hypnum sarmentosum
- H. scorpioides L.
- H. stellatum
- H. stramineum f.
- H. revolvens Sw.
- Mnium affine var. integrifolium
- Orthothecium chryseum
- P. juniperinum
- Meesia triquetra
- Mnium affine var. integrifolium
- Paludella squarrosa
- Polytrichum alpinum
- P. juniperinum

The various species of Hypnum are most characteristic of the wetter parts.

(b) Pond and Stream Marginal Community. All the ponds and especially the permanent ones have a thick moss margin. The same is also true of some streams. In the latter case the moss community occurs in damper places than the phanerogamic one already described. Ranunculus nivalis and sulphureus, Oxyria digyna and Chrysosplenium alternifolium L. f. tetrandrum Lund. occur in these carpets. The latter was only once found, on the edge of a large permanent pond.

The moss flora is similar to that of the boggy areas. In addition Sphagnum fimbriatum Wils. var. concinnum Warnst. was found in a few places on the bank of the above-mentioned pond. The absence or relative rarity of Sphagnum in moss-bogs in Spitsbergen has been noted before (5, etc.). It is well-known that in bogs in the Arctic Sphagna are much less important than in temperate countries. Only in one place (Advent Bay) on Spitsbergen did we find any amount of Sphagnum, and even here it is rather local. In the valley between
Fig. 1. Cape Boheman. Wet Tundra of *Salix*, *Alopecurus*, etc., and mosses. A temporary pool with wet moss vegetation is in the middle distance.

Fig. 2. Klaas Billen Bay (Bruce City). In foreground on the right, unsilted beach with *Dryas*, etc.; on the left Pond VII with mossy margin. Behind this the Campbell Range.

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the two Longyear City mines moss-bogs occur in various places. In addition to the usual bog mosses given above, the following species of \textit{Sphagnum} occur:

\begin{itemize}
  \item \textit{Sphagnum acutifolium} var. subnitens Russ. & Warnst.
  \item \textit{S. subsecundum} var. contortum Schimp.
  \item \textit{S. squarrosum} var. semisquarrosum Warnst.
\end{itemize}

In agreement with the rarity of \textit{Sphagnum} there is very little peat produced in Spitsbergen. A small amount was seen at Cape Boheman, but none in other bogs. In most cases the mosses grow directly on the underlying soil. Nathorst (43) mentions the bog in Reindeer Valley near Cape Thordsen, where there is about 10 inches of peat. It is composed of \textit{Hypnum} spp. and the upper layers contain remains of \textit{Salix polaris}. It seems as though this was formed from a bog similar to those described above.

The zonation on the pond sides usually resembles that on the bog hummocks. The lowest layer, consisting of species of \textit{Hypnum} (e.g. \textit{H. scorpioides} and \textit{H. sarmentosum} var. \textit{fontinaloides}), was observed often completely submerged and possibly is always so.

There are often many Collembola on the surface of water in the bogs and at the edges of the ponds. Among these is \textit{Agrenia bidenticulata}. In mosses (including the \textit{Sphagnum} given and \textit{Cynodontium virens}, \textit{Hypnum brefvolium} and \textit{H. cordifolium}) from a pond margin were:

\begin{itemize}
  \item Rotifera: \textit{Adineta vaga} Davis
  \item \textit{Mniobia russeola}
  \item \textit{Rotifer soridius} Western
  \item also Tardigrades and Nematodes
\end{itemize}

There are a number of flies to be seen in the boggy region:

\begin{itemize}
  \item \textit{Orthocladius consobrinus}
  \item \textit{Chironomus lugubris} Zeit.
  \item \textit{Psectrocladius borealis} Kieff.
  \item \textit{Cricotopus basalis} Stalg.
  \item \textit{Metriocnemus urinus}
  \item \textit{Campocladus curvinervis var. polaris} K.
\end{itemize}

Phalaropes and Snow Buntings act as a big check on the aquatic flies.

Three species of birds nest here—Grey Phalarope (f.), King Eider (r.), and Long-tailed Duck (r.). The last two feed mainly at sea, but also on fresh water.

\textbf{(b) Freshwater Communities.}

\section{1. Ponds.}

These are scattered about, some in the hollows between the rock ridges, others in the flat boggy expanse in the north. The most striking feature at Cape Boheman is the large number of temporary pools which dry up before the end of the summer. Dr van Oordt kindly informs us that Pond 12 dried up completely before the end of the season. Many other ponds had much less water in them, and would certainly have dried up also. The biota confirms this idea. The frequency of these temporary ponds is due to the geological formation. The ground being rocky, hollows are formed which hold melted snow-water. Since the rock is close to the surface, there is not the underlying ground-ice which is found on shingle beaches as at Klaas Billen Bay, and thus the
ponds are not supplied with water by the gradual melting of this ice during the summer. Those small ponds at Klaas Billen Bay which one would expect to dry up, do not do so, and they contain the same fauna as the larger permanent ponds here. However, the water of small ponds is hotter in summer, and the animals are therefore able to complete their seasonal cycle in a shorter time (48). This makes the season virtually shorter in a large pond, and tends to equalise the conditions in small and large ones. About 20 ponds were examined at Cape Boheman, but typical examples only are given.

(a) Permanent Ponds. There are many large shallow (1–2 feet) ponds, usually with a definite bank of mosses, etc. These ponds contain a rich algal flora. Since the surrounding rock is siliceous and poor in lime, the algal flora is extraordinarily rich in Desmids mainly of the genera *Cosmarium*, *Staurastrum* and *Euastrium*. The large tuberculate *Cosmarium biretum* and *C. conspersum* are characteristic. The following occur typically in permanent pools and were not found in the temporary ones:

- **Chlorophyceae**: *Cosmarium biretum* Breb.
  - *C. conspersum* Ralfs. var. latum W. & G. S. West
  - *C. impressulum* Elfv.
  - *C. punctulatum* Breb. var. subpunctulatum Nordst.
  - *Euastrium* spp.

- **Cyanophyceae**: *Lyngbya perelegans*

A number of species occur which are also found in the temporary pools:

- **Chlorophyceae**: *Cosmarium crenatum* var. bifrenatum Nordst.
  - *C. holmense* var. integrum Lund.
  - *C. ochithodes* Nordst.
  - *C. protumidum* Nordst.
  - *C. quadratum* Ralfs.
  - *Staurastrum bieneanum*
  - *S. pachyrhynchum* Nordst.
  - *S. subbrebissonii* Schmidle var. hexagonum Sutwinski
  - *Pandorina morum* Bory.

- **Cyanophyceae**: *Chroococcus turgidus* Naeg.
  - *Oocystis solitaria* Witric
  - *Synechococcus aeruginosus* Naeg.

Pond 20 is a good example of this type. The bottom is sandy. The following subdivisions often mingle, especially the last two:

- **Crustacea**:
  - **Plankton**: *Daphnia pulex* De Geer
  - *Cyclops crassicaudis* Sars.
  - **Among moss, etc.**: *Chydorus sphaericus*
  - *Cyclops crassicaudis* Sars.
  - **On bottom mud**: *Lepidurus arcticus*
  - *Macrothrix hirsuticornis* Norman & Brady
  - *Eucypris arctica*
  - *Candona rectangulata* Alm.

All these animals are vegetarian and feed on diatoms and other algae, while the bottom-living forms are also scavengers. There is a rich fauna of rotifers, etc. Among the protozoa were large colonies of the green ciliate *Ophrydium*, upon which young *Lepidurus* were seen feeding. Chironomid fly larvae abundant.
Ponds 6, 7, 10, 19 are of the same type. The Copepod *Maraenbiotus brucei* occurs sometimes. The nature of the bottom has an important effect on the fauna. Pond 14 has a stony bottom and very little plant life, and contains only *Daphnia pulex* and *Chydorus sphaericus*. Close to it is Pond 15 which has a mud bottom, on which are *Lepidurus*, *Eucypris* and *Candona*. A rather different type of permanent pond is that which has a stream flowing through. Pond 1 is about 35 feet across and a foot deep. One edge has mosses, *Ranunculus hyperboreus*, *Eriophorum*, etc. Flies (*Cricotopus basalis* and others) are abundant near the water, and larvae and pupae in it. There is a stream flowing through, and therefore plankton crustacea are almost absent. On the bottom and edge are *Lepidurus arcticus*, *Chydorus sphaericus*, *Cyclops crassicaudis*, *Eucypris glacialis* Sars., also rhabdocoel flatworms, rotifers, etc. Pond 2 is also of this type.

(b) *Temporary Ponds* (Plate II, fig. 1). The algal flora of these ponds is very rich, and consists mainly of Desmids. Unlike the other type of pond these are characterised by the presence of *Staurastrum megalonotum* Nordst. and *S. oligoecanthum* Breb. which are absent in the permanent pools. The following species of algae are also typical of these temporary pools, and are absent in the permanent ones:

- **Chlorophyceae**: *Cosmarium arctoum* Nordst.
  - *C. bioculatum* Breb.
  - *C. cyclicum* Lund. var. *arcticum* Nordst.
  - *C. ochthodes var. amoebum* W. & G. S. West
  - *Euastrum* spp. (not the same ones as in the permanent ponds)
  - *Nephrocytium obtusum* West
  - *Staurastrum polymorphum* Breb.
  - *Eudorina elegans* Ehr.
  - *Gloeocystis infusionem* W. & G. S. West

- **Cyanophyceae**: *Aphanocapsa grevillei* Rabenh.
  - *Aphanothece microscopica* Naeg.

The fauna of these varies, and must depend to some extent on chance dispersal. They are not characterised by any peculiar crustacea, but by the absence of *Lepidurus*, *Daphnia* and *Macrothrix*, and usually of fly larvae. We should expect to find the richest fauna in those which have been formed by the encroachment of plants on a formerly larger pond. Ponds 3 and 4 appear to be of this type.

Pond 3. This is about 10 feet in diameter and a few inches deep. The vegetation at the edge consists of *Hypnum cordifolium* and a grass. Outside is a broad layer of *H. brevifolium* mixed with *H. cordifolium* and *H. stramineum*. On the outside of this again is a rather drier area. *H. cordifolium* is lacking here, but *Cynodonium virens* takes its place. The “fjældmark” lies beyond this. Of the crustacea *Acroperus harpae* Baird has not previously been found in Spitsbergen.

Pond 4. Here the pond has reached a further stage, being 5 feet wide and an inch or two deep. In this are found Rotifera: *Metopidia lepadella* Ehrb., and others; Protozoa: *Peridinium*; Nematodes; Tardigrades. The following
is a table (Table II) of all the temporary pools showing different stages in drying up:

**Table II.**

<table>
<thead>
<tr>
<th>Pond No.</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Clydorus sphaericus</td>
</tr>
<tr>
<td>17</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>Acroperus harpae</td>
</tr>
<tr>
<td></td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>Cyclops crassicaudis</td>
</tr>
<tr>
<td></td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>Maraenbiotus brucei</td>
</tr>
<tr>
<td></td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>Candona rectangulata</td>
</tr>
<tr>
<td></td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Eucypris glacialis</td>
</tr>
<tr>
<td></td>
<td>x</td>
</tr>
</tbody>
</table>

Ponds 11, 12, and 13 are close together in boggy land. Pond 11 resembles Pond 3 (*Hypnum cordifolium* in centre and *H. brevifolium* and a grass outside) and contains the rotifers *Metopidia lepadella* and *Euchlanis defllexa* Gosse. The other two ponds are larger and some of the bottom consists of bare mud. Larvae of Diptera are abundant in Pond 13 in floating masses of *Phormidium*. Ponds 18, 21, and 22 are of the Pond 3 type. In Pond 18 the rotifers *M. lepadella*, *Euchlanis dilatata* Ehrb., and *E. orophia* Gosse were found. Pond 17 is in a rocky pocket with water about a foot deep and has *E. dilatata* and *Monostyla sp*.

The usual aquatic birds occur, viz.: Grey Phalarope, Red-throated Diver, a few Long-tailed Ducks and King Eider. The young of the latter feed in freshwater ponds on crustaceae, plants, etc. (39, 64).

2. **Streams.**

These, generally speaking, are rather poor in life as far as could be ascertained. In some places there are filamentous green algae attached to submerged stones.

C. **KLAAS BILLEN BAY.** (Bruce City Region.)

This district lies at the head of Klass Billen Bay. The area consists of two parts, firstly, a very extensive raised beach, some of which is still more or less in its original condition, while the greater part has been silted over by streams, and secondly, the Campbell Range which rises abruptly from this beach to a height of 2500 feet.

The following communities can be distinguished:

(a) Land Communities.

1. Inter-tidal Zone.
2. Raised Beach.
   (a) Unsalted.
   (b) Silted.
3. Upland Region.

(b) Aquatic Communities.

1. Brackish.
2. Fresh-water.
   (a) Ponds.
   (b) Streams.
(a) **Land Communities.**

1. **INTER-TIDAL ZONE.**

The plant ecology of this region has been described by Walton (66). He has shown the transition from marine conditions through salt marsh to the unsilted beach on the one hand, and to the silted “moor” on the other.

The shingle shore outside the salt marsh area (see Plate III, fig. 2) is much exposed to the grinding action of floating ice broken off from the Nordenskjold Glacier. There is no plant life, but between the tide marks are the following animals:

- **Nemertinea:** Numbers of small specimens of some species
- **Collembola:** Archisotoma beselsi
- **Mites:** Bdella littoralis Linn.

On the drift line there is much seaweed, etc., deposited; in one place a dead seal had been cast up. The following live above the drift line on the shingle, but feed among the organic drift. The spiders feed on the other animals:

- **Collembola:** Onychiurus armatus var. arcticus
- **Spiders:** Erigone arctica White, E. tirolensis LK.
- **Mites:** Bdella littoralis scavenging, Another mite in dead seal
- **Oligochaeta:** Henlea sp., Lumbricillus aegialites Steph. va. in seaweed, L. necrophagus Steph. va. in dead seal

Purple Sandpipers feed along the shore. There is much dry driftwood on the beaches, but no animals were found in or under it. On the mud flats inside the boulders described later the mite *Bdella littoralis* is very common. A moss sample of *Bryum nitidulum* was taken from the salt marsh (Walton, p. 116, Zone II), and examined for the animals. This zone is not covered by ordinary tides, and consists of a close growing moss layer on black mud with much decaying humus. In the moss were:

- **Collembola:** Achorutes viaticus, Polasoma quadricristata
- **Diptera:** Larvae
- **Oligochaeta:** Enchytraeus crymodes Steph. a.

There were no rotifers. The worms were eating green moss leaves.

Counts of these enchytraeid worms were made in order to get some idea of their importance in the biology of the soil. The ground consisted of 1 cm. of moss and 7 cm. of black mud, the worms occurring in the moss only. In the first place examined, 14 sq. cm. of moss were taken. In this the worms averaged 2-3 worms per sq. cm. In another slightly drier place, an average of 1-75 worms per sq. cm. was obtained. The estimates are probably too low owing to the small size of the worms and the difficulty of counting them accurately. Enough data were obtained to show that these worms must play a not inconsiderable rôle in the soil where they occur.

17-2
2. RAISED BEACH.

(a) The unsilted part of this has been described by Walton with respect to the plants. Apparently this area is a type of open "fjaeldmark" which is on its way to heath. A heath of *Dryas* and *Salix polaris* seems to be the ordinary climax in this region, *Cassiope* heath only rarely being produced.

*Onychiurus armatus* var. *arcticus* occurs under shingle on the lower parts of the beach.

The larger ponds on the unsilted beach are surrounded by a marked marginal moss community (see Plate II, fig. 2). It is possible in Pond VII (= Walton VII) to distinguish zonation on the bank. The zones noted are as follows, the area outside being a typical sparse "fjaeldmark" community. Zone 1 is the highest, while part of Zone 3 is submerged:

<table>
<thead>
<tr>
<th>Phanerogams, etc.:</th>
<th>Nos.</th>
<th>1</th>
<th>2</th>
<th>3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cardamine pratensis</td>
<td>...</td>
<td>x</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Cassiope tetragona</td>
<td>...</td>
<td>-</td>
<td>-</td>
<td>1f</td>
</tr>
<tr>
<td>Dryas octopetala</td>
<td>...</td>
<td>-</td>
<td>-</td>
<td>1f</td>
</tr>
<tr>
<td>Equisetum variegatum</td>
<td>...</td>
<td>-</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Lůzula confusa</td>
<td>...</td>
<td>f.</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Pea sp.</td>
<td>...</td>
<td>-</td>
<td>x</td>
<td>-</td>
</tr>
<tr>
<td>Polygonum viviparum</td>
<td>...</td>
<td>x</td>
<td>f.</td>
<td>-</td>
</tr>
<tr>
<td>Salix polaris</td>
<td>...</td>
<td>-</td>
<td>1f</td>
<td>-</td>
</tr>
<tr>
<td>Saxifraga aizoides</td>
<td>...</td>
<td>x</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Bryophytes:

| Biopharostoma trichophyllum | ... | x | - | - |
| B. pseudotriquetrum | ... | - | f. | x |
| Camptothecium nitens | ... | - | a. | - |
| Cnidium stygium | ... | - | x | - |
| Equisetum brevifolium | ... | - | x | - |
| H. giganteum | ... | - | - | x* |
| H. polygamum | ... | - | x | - |
| H. revolvens | ... | x | - | - |
| H. stellatum | ... | x | x | - |
| H. vernicosum | ... | - | x | x* |
| Lophozia biorenata Dum. | ... | - | - | - |
| Orthothecium chryseum | ... | - | f. | - |
| S. montana | ... | x | f. | - |

Lichens:

| Cetraria nivalis | ... | x | - | - |
| Lecanora tartarea | ... | x | - | - |

Rotifers:

| Adineta barbata | ... | - | x | x |
| A. gracilis | ... | - | x | - |
| A. vaga | ... | - | - | x |
| Habrotrocha consticta | ... | - | x | - |
| H. sp. | ... | - | - | x |
| Macrotrachea ehrenbergii | ... | - | - | x |
| M. habita | ... | - | x | - |
| M. multispinosa | ... | - | x | - |
| Pond Rotifers—several spp. | ... | - | - | x |
| Nematoda | ... | - | x | x |
| Tardigrada | ... | - | - | x |
| Protozoa | ... | - | - | x |
| Oligochaeta: | ... | - | r. | |
| Enchytraeus crinodes | ... | - | x |
| Henlea helicotrophus | ... | - | x |
| Mesenchytraeus sp. | ... | - | x |

* Plants marked thus grow submerged. The Rotifers may not be constant, but those of *Adineta* probably show their normal distribution.
(b) Silted Region. This forms much the greater part of the area. The sub-stratum varies from dry stony areas on the ridges to damp boggy flats along the streams. On the seaward edge the beach merges into the salt marsh mentioned above, or else is terminated by a low cliff with a shingle beach below. Silt brought down by the streams in spring and early summer as a result of snow melting on the mountains is being deposited over the whole region. The large stream just next to the Nordenskjold Glacier has gradually worn away the raised beach, leaving a bare shingle flat. A large colony of Arctic Terns nests on the slightly higher parts.

(i) Wet Tundra. Owing to the frequent changes in the courses of the streams, bare areas of silt are constantly being produced. The first plants to appear in such habitats are *Eriophorum scheuchzeri* and *Dupontia fisheri* R.Br. In places *Juncus biglumis* L. also occurs. Silt is caught by these colonisers, and as the level rises a wet type of vegetation is produced.

<table>
<thead>
<tr>
<th>Phanerogams:</th>
<th>Bryophytes:</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Eriophorum angustifolium</em> Roth.</td>
<td><em>Hypnum scorpioides</em></td>
</tr>
<tr>
<td><em>f. triste</em> Th. Fr.</td>
<td></td>
</tr>
<tr>
<td><em>E. scheuchzeri</em></td>
<td><em>H. stellatum</em></td>
</tr>
<tr>
<td><em>Luzula confusa</em></td>
<td></td>
</tr>
<tr>
<td><em>Salix polaris</em></td>
<td></td>
</tr>
</tbody>
</table>

This grades off into the Dryas heath on drier soil.

The micro-fauna of moss (*H. stellatum*) from such a bog near the salt marsh was examined.

<table>
<thead>
<tr>
<th>Rotifera:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adineta barbata</td>
</tr>
<tr>
<td>A. vaga</td>
</tr>
<tr>
<td>Habrotrocha insignis</td>
</tr>
<tr>
<td><em>Macrotrachela aculeata</em> Milne</td>
</tr>
<tr>
<td><em>Pleurotra brycei</em> Weber</td>
</tr>
<tr>
<td><em>Enchytraeus sp.</em> a.</td>
</tr>
</tbody>
</table>

A worm count was also made here. There was an average of 3.25 worms per sq. cm. in an area of 20 sq. cm.

The small pools of these marshes and their flora have been described by Walton (p. 116). *Hypnum scorpioides* occurs typically, submerged in these pools. Samples were examined and showed a rich fauna of Rotifera, Nematoda, Tardigrada, and Protozoa (for Rotifers see Bryce (8) under “L 21”).

(ii) Heath. This consists of a more or less closed community of *Dryas octopetala*, on the ridges between the streams. In places the Dryas plants are orientated at right angles to the prevailing wind (66). The following species occur:

<table>
<thead>
<tr>
<th>Phanerogams:</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Braya purpurascens</em> R.Br.</td>
</tr>
<tr>
<td><em>Cassiope tetragona</em> (very locally)</td>
</tr>
<tr>
<td><em>Draba alpina</em></td>
</tr>
<tr>
<td><em>D. alpina var. oblongata</em></td>
</tr>
<tr>
<td><em>D. hirta var. arctica</em></td>
</tr>
<tr>
<td><em>Dryas octopetala</em> d.</td>
</tr>
<tr>
<td><em>Festuca brevifolia</em> R.Br.</td>
</tr>
<tr>
<td><em>Pedicularis hirsuta</em></td>
</tr>
<tr>
<td><em>Polygonum viviparum</em></td>
</tr>
<tr>
<td><em>Saxifraga aizoides</em></td>
</tr>
<tr>
<td><em>S. oppositifolia</em></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Bryophytes:</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Bryum globosum</em></td>
</tr>
<tr>
<td><em>and var. ruberrimum</em> Dixon</td>
</tr>
<tr>
<td><em>B. pendulum</em></td>
</tr>
</tbody>
</table>
A good deal of the area consists of "rute-marks" (see Plate III, fig. 1), which are polygonal areas in almost homogeneous soil (27) and thus differ from those already described on Prince Charles Foreland. As in the other type, the centre is bare of plants, while the cracks between adjacent areas are occupied by Dryas or Salix. Cetraria islandica often occurs with the latter.

(iii) Erratic Blocks. There are a number of these bearing a rich flora of mosses and lichens of the usual species, e.g. Xanthoria parietina, etc., and also the alga Prasiola crispa Menegh. This layer of vegetation forms a more favourable habitat for animals than the shingle. Here occur under the mosses, etc.:

Collembola:  Folsomia quadrioculata r.
Spiders:  Erigone arctica f.
Hilaire glacialis Thor. f.
Mites:  Bide la sp. r.
Rha gidia gelida f.
Oligochaeta:  Rare
Nematoda:  A large species.  Sporadic

Erigone was seen to eat the mite Rhagidia gelida. These boulders thus possess self-supporting communities of their own.

The fauna of both silted and unsilted beaches will be considered together. Most of the observations on the latter were made around Bruce City where there are a number of ponds. There is very little animal life except what comes from the water (flies). The presence of man during the last few years has driven away many of the birds.

Collembola:  Isotoma viridis
Diptera:  Chironomus riparius Mg.
          Metriocnemus ursinus
          M. brevinervis Holmg.
          Cricotopus basalis
          C. glacialis Edw. (on flowers of Dryas, Saxifraga oppositifolia, hirculus, aizoides)
          Orthocladius consobrinus
          O. decoratus Holmg.
          O. festivus Holmg.
          Psectrocladius borealis
          P. limbatus H.
          Campodeus pumilio Holmg.
          C. curvinervis var. polaris
          Aedes alpinus L.
          Exechia frigida
          Sciara praesox
          S. pallidiventris H.
          Limnophora hyperborea (on flowers of Dryas, Silene, and Saxifraga hirculus)
          L. megastoma (on Silene flowers)
          Scatophaga varipes Holmg. (on dung)
Hymenoptera:  Stenomacrus pedestris Holmg. (on Silene flowers, Aug. 2nd)
          Atractodes bicolor var. arcticus Holmg. (on flowers of Saxifraga hirculus, Aug. 4th)
          Ichneumones hyperboreus Holmg. (on flowers of Dryas and Saxifraga oppositifolia)
          (Pristiphora frigida)?
Spiders:  Typhochrestus spitsbergensis f.
          Hilaire glacialis r.
FIG. 1. Klaas Billen Bay. Area of silted raised beach showing "rute-marks." Between the large polygons are plants of *Salix polaris* and mosses.

FIG. 2. Klaas Billen Bay. Intertidal shingle beach with drift line. Note absence of plants; also the drifting ice, which is mainly responsible for the paucity of life.

SUMMERHAYES AND ELTON—ECOLOGY OF SPITSBERGEN AND BEAR ISLAND.
Mites: Bdella decipiens
B. pallipes L.Koch
Cyta brevirostris
Rhagidia gelida
Sphaerozetes notatus

Oligochaeta: Henlea brucei

Birds: Pink-footed Goose
Purple Sandpiper
Buffon’s Skua (Stercorarius longicaudus Vieill.)
Snow Bunting

Mammals: Dogs kept here in 1921

Reindeer must have roamed here formerly as shed antlers were found. There are very few collembola, mites and oligochaetes on account of the sparseness and dryness of the plants. Spiders are fairly abundant, especially near the ponds, and they must live largely upon the flies which breed there. One was seen to attack the fly Chironomus hyperboreus. Most of these flies seem to be aquatic (Chironomus, Orthocladius and Psectrocladius). Cricotopus basalis and glacialis were seen laying eggs in Pond VII on August 1st. The ichneumons Stenomacrus and Atractodes are probably parasitic on Diptera (69). It is clear by now that the Purple Sandpiper eats almost anything that it can get. The stomachs of two young birds had Lepidurus arcticus from the ponds in them (August 15th), and another hymenoptera. The birds are often infected with bird-lice:

Degeeriella actophilus
D. zonaria
Menopon lutescens Burm.
Philopterus fusiformis

The Sandpipers had mostly left Bruce City by August 1st.

Ichneutes hyperboreus is a braconid which probably parasitises the sawfly Pristiphora frigida (19). The latter was not seen here, but it may have been in the larval stage. Stenomacrus pedestris is recorded on flowers of Dryas, Saxifraga caespitosa and Cerastium alpinum in Spitsbergen (19).

It was surprising to find that a very dry moss (Grimmia commutata Huebn.) had a rich micro-fauna—13 species of rotifers (see Bryce (8) under “L 25”).

3. UPLAND REGION.

Several districts are included in the above term, but most of the information applies to the slopes of the Campbell Range. The greater part of this range is composed of sandstones and carbonaceous shales; there are also bands of Gypsum. This Gypsum may be 200 feet in thickness, but is generally much less. Across Adolf Bay is the De Geer Range, composed chiefly of Archaean gneiss and mica-slate. Almost all the surface of the Campbell Range is covered with scree, and as a result the vegetation is nowhere closed, being always a type of “fjaeldmark” (see Plate IV, figs. 1, 2). No flower slopes as in Prince Charles Foreland were noticed. This may be due to the northern aspect or to the greater dryness of this region. The slopes are also swept by winds from the snow-covered interior, and this increases the barrenness. Where the snow-
water drains along depressions a slightly damper type of vegetation than usual appears.

The following plants occur on the Campbell Range:

<table>
<thead>
<tr>
<th>Plant Name</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alsine rubella</td>
<td></td>
</tr>
<tr>
<td>Carex misandra R.Br.</td>
<td></td>
</tr>
<tr>
<td>*Cerastium alpinum</td>
<td></td>
</tr>
<tr>
<td>*C. caespitosum Malng.</td>
<td></td>
</tr>
<tr>
<td>Draba alpina</td>
<td></td>
</tr>
<tr>
<td>D. alpina var. oblongata</td>
<td></td>
</tr>
<tr>
<td>D. rupestris Wg.</td>
<td></td>
</tr>
<tr>
<td>D. subcapitata</td>
<td></td>
</tr>
<tr>
<td>D. wahlenbergii</td>
<td></td>
</tr>
<tr>
<td>*Dryas octopetala</td>
<td></td>
</tr>
<tr>
<td>*Eriophorum angustifolium f. triste</td>
<td></td>
</tr>
<tr>
<td>*Juncus biglumis</td>
<td></td>
</tr>
<tr>
<td>*Papaver nudicaule var. radicatum</td>
<td></td>
</tr>
<tr>
<td>*P. caespitosum Malmg.</td>
<td></td>
</tr>
<tr>
<td>Pedicularis hirants</td>
<td></td>
</tr>
<tr>
<td>Poa cenisia All.</td>
<td></td>
</tr>
<tr>
<td>*Poa cenisia</td>
<td></td>
</tr>
<tr>
<td>*Salix polaris</td>
<td></td>
</tr>
<tr>
<td>*Saxifraga aizoides</td>
<td></td>
</tr>
<tr>
<td>Saxifraga oppositifolia</td>
<td></td>
</tr>
<tr>
<td>*S. caespitosa</td>
<td></td>
</tr>
<tr>
<td>S. oppositifolia</td>
<td></td>
</tr>
</tbody>
</table>

Species marked with an asterisk occur on Gypsum screes at a height of 300-400 feet. Those marked thus occur at lower levels (up to 500 feet).

*Poa cenisia* is a common plant on limestone screes in the Alps (56). *Saxifraga oppositifolia* is the only plant occurring at 2000 feet in this area. In other parts of Spitsbergen *Papaver* and other species have been recorded at great heights. The following plants were found at 3000 feet (approx.) on Mount Terrier:

<table>
<thead>
<tr>
<th>Plant Name</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cerastium caespitosum</td>
<td></td>
</tr>
<tr>
<td>Draba alpina</td>
<td></td>
</tr>
<tr>
<td>Grimmia apocarpa</td>
<td></td>
</tr>
<tr>
<td>Papaver nudicaule var. radicatum</td>
<td></td>
</tr>
<tr>
<td>Saxifraga oppositifolia</td>
<td></td>
</tr>
</tbody>
</table>

and probably others occur. It is interesting to note that three of the above plants reach 2000 feet in Grinnell Land (23).

On the De Geer Range conditions are rather more favourable. This faces south so that in sheltered places a heath of *Cassiope tetragona* and *Dryas octopetala* is formed. Possibly the lack of lime here is of importance in determining the luxuriance of *Cassiope*.

The animals of the upland area were not worked out in detail. The spider *Typhochrestus* is confined to the flat shingle, and its place is taken by *Leptyphantes sobrium* at the point where scree slopes start. The limiting factor is clearly not the height, but the nature of the substratum. A few mites (*Bdella sp.*, *Cyta brevirostris*, etc.) occur in the screes. Snow Buntings nest in the boulder and scree regions. The exploring party brought back some Collembola from near the top of Mount Terrier (2800 ft)—*Achorutes viaticus*, *Agrenia bidenticulata*.

(b) Aquatic Communities.

The ponds and streams may be seen in the photo given by Walton (66, Plate VI, fig. 1). On the raised shingle beaches forming terraces of successive ages, there is a series of ponds, the lower being still tidal while the upper ones are freshwater. The latter contain relict brackish crustacea, and must once have been tidal. At a later date they were cut off from the sea as a result of the rising of the land which has been going on since the Glacial Epoch.

Figs. 5 and 6 show in a diagrammatic way the position of the Klaas Billen ponds. Nos. I–III are tidal, while IV–XI are freshwater. Walton gives a map showing the details of the tidal area, but he uses different numbers for the
FIG 1. Klaas Billen Bay. Scree on Campbell Range with plants of *Papaver medicaule* var. *radicatum* and *Saxifraga oppositifolia*.


**SUMMERHAYES AND ELTON—ECOLOGY OF SPITSBERGEN AND BEAR ISLAND.**
ponds. The diatoms of these pools show a transition from marine to freshwater conditions (66, p. 119).

We shall describe the aquatic communities in order of their natural succession, starting with marine and ending with freshwater.

![Diagram of Klaas Billen Ponds and Beach lines. Heights are accurate.](image1)

**Fig. 5.** Diagrammatic sketch of Klaas Billen Ponds and Beach lines. Heights are accurate.

![Diagram showing the relative positions of the ponds and the relation between successive elevations.](image2)

**Fig. 6.** This shows the relative positions of the ponds and the relation between successive elevations.

1. **Brackish Communities.**

   **The Boulders.** These really belong to the inter-tidal zone, but they are included here since the crustacea can be compared with those of the tidal ponds. They form a line lying at the outer edge of an alluvial fan of mud brought down by streams, and are completely uncovered at low tide. They are much battered by floating ice from the Nordenskjold Glacier, and act as a barrier preventing much ice from entering the ponds. The algae are described by Walton (p. 118).

   On the boulders (at low tide):

   - **Hydroida:** Gonothyraea loveni, Operculiarella lacerta
   - **Polyzoa:** On algae
   - **Crustacea:** Gammaracanthus loricatus, Gammarus locusta var. zaddachi, Pseudalibrotus litoralis, several species of copepods (*Dactylopusia*, *Harpacticus*, etc.) among hydroids and algae.
   - **Halacaridae:** On hydroids
   - **Birds:** Arctic Tern
A Tunicate, *Rhizomolgula globularis* Pallas, lives on the sandy mud around the boulders, just above low tide mark. A few Polychaete worms occur in the mud. The hydroids only grow on places protected from floating ice. The *Gammaracanthus* are of the usual marine type, and show no transition to the freshwater form *G. lacustris*. The *Gammarus*, however, are to some extent intermediate between *G. locusta* and the variety *zaddachi*. It has been shown in Denmark (61) that the structure depends on the salinity in which the animals are living. This is also true of those here, since those in Pond I are more like the extreme variety *zaddachi*, while those from these boulders and from Cape Scott are intermediate.

The fauna and flora of Ponds I–III are seen in Table III.

Table III. Fauna and Flora of the Tidal Ponds.

<table>
<thead>
<tr>
<th>Pond No.</th>
<th>I</th>
<th>II</th>
<th>III</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birds:</td>
<td>Arctic Tern</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Fish:</td>
<td>...</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Crustacea:</td>
<td>Mysis oualata Fab. var. relicta Lov.</td>
<td>young</td>
<td>...</td>
</tr>
<tr>
<td></td>
<td></td>
<td>adult</td>
<td>...</td>
</tr>
<tr>
<td>Schizopoda:</td>
<td>Gammarus locusta var. zaddachi</td>
<td>...</td>
<td>x</td>
</tr>
<tr>
<td>Amphipoda:</td>
<td>Pseudalibrotus litoralis</td>
<td>...</td>
<td>x</td>
</tr>
<tr>
<td>Copepoda:</td>
<td>Eurytemora raboti Richard</td>
<td>...</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>Tachidius spitzbergensis Olofsson</td>
<td>...</td>
<td>x</td>
</tr>
<tr>
<td>T. longicornis Olofsson</td>
<td>...</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Collembola:</td>
<td>Archisotoma beselisi</td>
<td>...</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>Arcturites viaticus</td>
<td>...</td>
<td>x</td>
</tr>
<tr>
<td>Hirudinea:</td>
<td>Pontobdella maricata</td>
<td>...</td>
<td>(x)</td>
</tr>
<tr>
<td>Rotifera:</td>
<td>Colurella colurus Ehrib.</td>
<td>...</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>Enecentrum? raptor Gosse</td>
<td>...</td>
<td>x</td>
</tr>
<tr>
<td>Tardigrada:</td>
<td>...</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Nematoda:</td>
<td>...</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Protozoa:</td>
<td>...</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Algae:</td>
<td>Chlorophyceae: Enteromorpha sp.</td>
<td>...</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>Ulotrix sp.</td>
<td>...</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>Zygnema sp.</td>
<td>...</td>
<td>x</td>
</tr>
<tr>
<td>Cyanophyceae:</td>
<td>Chroococcus turgidus</td>
<td>...</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>Gomphosphaeria aponica Kuetz.</td>
<td>...</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>Merismopedia glauca</td>
<td>...</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>Oscillatoria sp.</td>
<td>...</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>Rivularia sp.</td>
<td>...</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>Spirulina subsalsa Oersted</td>
<td>...</td>
<td>x</td>
</tr>
</tbody>
</table>

x normally present; -- definitely absent; (x) accidental or sporadic; ? probably present though not found.

Pond I (= Walton, Pool I). A shallow pond, not more than a foot or two deep at high tide. There are no plants except algae. The bottom is mostly sand and mud covered with a thin brown “felt” of organic matter, which contains many diatoms and blue-green algae. The leech was attached to the cephalothorax of an adult male *Mysis relicta* (August 10th). These, and a small fish about an inch long, were clearly brought in accidentally from the fjord. Tardigrades are noticeably absent. All the regular inhabitants seem to be scavengers or vegetarian.
V. S. Summerhayes and C. S. Elton

Pond II (= Walton, Pool III). Similar to the last, but smaller.
Pond III (= Walton, Pool IV). A small pond containing large numbers of *Eurytemora raboti* which live on the bottom, and feed on diatoms and other algae.

The Spring (S on Walton’s Map and on Fig. 5). This is fresh, but forms part of the water supply of the tidal ponds, and flows into Pond III. There are no crustacea. A collembolan *Sminthurides malmgreni* was seen on the surface. An oligochaete *Henlea heleotrophus* is abundant in submerged *Hypnum cordifolium*. Also rotifers, tardigrades, nematodes and protozoa.

**General Discussion.**

We propose to give some account of the conditions in these ponds, and of the limiting factors affecting the distribution of some of the animals.

The sea penetrates as far as Pond III at high tide. Complete water analyses were made in two cases by Mr Manley, and chloride determinations in the others by Mr Mills. Two series of samples were taken, one at high and the other at low tide.

**Table IV. Chloride content in gms. per litre.**

<table>
<thead>
<tr>
<th>Locality</th>
<th>Low tide</th>
<th>High tide</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Aug. 10th</td>
<td>Aug. 7th</td>
</tr>
<tr>
<td>Sea by Bruce City, Aug. 1st</td>
<td>18-26</td>
<td>—</td>
</tr>
<tr>
<td>&quot;    Aug. 3rd</td>
<td>17-57</td>
<td>—</td>
</tr>
<tr>
<td>Boulders</td>
<td>—</td>
<td>17-11</td>
</tr>
<tr>
<td>Pond I</td>
<td>—</td>
<td>1-91</td>
</tr>
<tr>
<td>&quot;    II</td>
<td>0-07</td>
<td>15-23</td>
</tr>
<tr>
<td>&quot;    III. Main pond</td>
<td>0-22</td>
<td>9-10</td>
</tr>
<tr>
<td>&quot;    III. Where stream enters</td>
<td>—</td>
<td>0-55</td>
</tr>
</tbody>
</table>

It will be seen that there is a gradient of chloride content from the sea to Pond III, both at high and low tide, though it is much more marked at high tide. The ponds are practically fresh at low tide, the time during which they remain so increasing as we pass from Pond I to Pond III. This, combined with the influence of the fresh water flowing in, causes the tides to have less effect in the inner than in the outer ponds. If Pond III were raised only a foot or two it would then be a relict freshwater pond like those higher up on the beaches. Table V gives the analyses, which show two opposite extreme cases. It will be seen that the total amount of salts in Pond III water at low tide is about 1/40th of that in Pond I water at high tide, and the osmotic pressures, etc., would differ accordingly. Also calcium carbonate is present in relatively greater proportion than the other salts in the fresher water of Pond III. Thus comparing the two samples, there is about 1/9th of the amount of calcium in one that there is in the other. But the amounts of other elements compared in the same way are far smaller, e.g. magnesium 1/50th, sodium 1/50th, chlorine 1/70th. This shows that the effect of tidal influence is not merely that of diluting or concentrating a given solution, but is much more complicated. The proportions of salts present may be altered, and such changes...
have great effects on aquatic animals. Therefore the chloride content is not in itself the main factor in the chemistry of the water, but is a rough indicator of other more important factors which are harder to determine directly. These are the amount of mixing of fresh and sea water (the chloride content is about half the total solids), the osmotic pressure, the proportions of different salts, etc.

**Table V. Pond I. High tide, inner side, August 7th.**

*Amounts given in gms. per litre.*

<table>
<thead>
<tr>
<th>Chemical</th>
<th>Amounts</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>CaO</td>
<td>0.754</td>
<td>= 1.346 CaCO₃ or 2.179 CaH₂(CO₃)₂</td>
</tr>
<tr>
<td>MgO</td>
<td>1.664</td>
<td>= 2.179 MgSO₄·2H₂O</td>
</tr>
<tr>
<td>Cl⁻</td>
<td>1.120</td>
<td>= 1.513 MgCl₂</td>
</tr>
<tr>
<td>SO₄²⁻</td>
<td>0.930</td>
<td>= 2.476 NaCl</td>
</tr>
</tbody>
</table>

**Total solids = 31.373**

(Direct determinations of Total Solids gave 31.00 and 31.05.)

Ammonium and Potassium salts absent.

**Pond III. Low Tide, August 10th. Amounts given in gms. per litre.**

<table>
<thead>
<tr>
<th>Chemical</th>
<th>Amounts</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>CaO</td>
<td>0.092</td>
<td>= 0.164 CaCO₃ or 0.266 CaH₂(CO₃)₂</td>
</tr>
<tr>
<td>MgO</td>
<td>0.049</td>
<td>= 0.191 MgSO₄·2H₂O</td>
</tr>
<tr>
<td>Cl⁻</td>
<td>0.225</td>
<td>= 0.371 MgCl₂</td>
</tr>
<tr>
<td>SO₄²⁻</td>
<td>0.079</td>
<td>= 0.078 Na₂SO₄</td>
</tr>
</tbody>
</table>

**Total Solids = 0.804**

(Direct determination of Total Solids gave 0.797.)

Ammonium and Potassium salts absent.

The Copepod *Eurytemora raboti* is most abundant in Pond III, and less so in Pond II, only adults occurring in the latter. Experiments were made to test its powers of survival in waters of different salinities, obtained by mixing fresh water with sea water. Pure sea water (chloride 18-26 and 17-57) killed the *Eurytemora* from Pond III in about 20 minutes, while controls in fresh water were quite healthy. In a salinity of 13-20 they died in about 1 hour 40 minutes, but in 8-82 they were unaffected after 3½ hours. These experiments show that it is limited in its distribution partly by salinity, and the results agree with its distribution in the ponds. (*Gammarus zaddachi* from Pond I would eat large numbers of *Eurytemora* in captivity. Table III shows that these two species hardly meet. This may be another limiting factor for *Eurytemora.*) It is clear that it is not only the degree of salinity which affects it, but also the time during which this salinity acts. These ponds lie very near high water mark, and are only flooded by the sea for an hour or two. The animals may be able to resist for a short time a high salinity which would kill them if it lasted much longer. This “time-salinity” factor may be one cause of the dwarfing which occurs among many marine animals living in tidal waters. Their metabolism is lowered during times of abnormal salinity, and thus less growth is possible in their lifetime.

*Mysis oculata* occurs in arctic and subarctic seas (we found it near the Anser Islands, at the mouth of Klaas Billen Bay). The form or variety known as *Mysis relicta* resembles a young *M. oculata*, but differs in some points, and
is sexually mature. It is, in fact, a *Mysis oculata* whose growth has been retarded. *M. relicta* has been found in freshwater lakes in the Baltic area, Ireland, N. America and Spitsbergen (48). In Spitsbergen *M. relicta* was found by Olofsson in three places: (1) in Sassen Bay (young ones washed into a lagoon at high tide and out again at low, and thus belonging really to the fjord fauna); (2) in these Klaas Billen ponds (young ones); (3) relict in a freshwater lake on Credner's Moraine at the head of Belsound (young ones, August 12th, 1910).

In Pond I young *Mysis relicta* occurs very abundantly. Only one or two adults were seen. This and the fact that one had a marine leech on it proves that these adults belong to the fjord fauna. These facts, combined with Olofsson's results from Sassen Bay, show that *Mysis oculata* undergoes a retardation of growth in the inner parts of long fjords in rather low salinity, and that under certain conditions it may become relict in fresh water. The process might occur by the cutting off of an arm of the sea which gradually became fresh. This may have occurred in the Baltic and in Belsound. Arctic conditions are especially favourable for such processes, on account of the land elevation associated with a retreating ice-sheet. The *Mysis relicta* found now in Europe, etc., were almost certainly left behind after the Glacial Epoch. A study of the ecology of *M. relicta* at Klaas Billen Bay showed some of the factors affecting its chances of becoming relict. Why has it not become relict in these freshwater ponds while *Eurytemora* has? Now the tidal ponds freeze solid in winter, and *Mysis* and *Gammarus*, which have no adaptation for surviving this, would all be killed. *Eurytemora*, however, has eggs which can stand freezing. Therefore *Mysis* and *Gammarus* must migrate into Pond I every year, only to be killed when winter sets in. The lake on Credner's Moraine, where *Mysis relicta* occurs, is over 9 metres deep, and waters over 2 metres deep are not frozen solid (48). How are we to explain the rarity of adult *Mysis* in Pond I since they might have been expected to migrate in from the fjord? The young ones are very abundant; Dr Tattersall describes them as being "all quite juvenile, none larger than 9 mm." (July 27th). Those obtained here on August 5th, 1910, by Olofsson were from 8.6 to 9.3 mm. long. Now Arctic Terns were often seen fishing in Pond I and sometimes in Pond II. They were also seen to hover over Pond III, but never to dive into it. Apparently they were not feeding upon *Mysis relicta*, the young of which are small, transparent and very agile, but on *Gammarus*, which hides in the mud and occasionally makes short journeys, during which it is quite conspicuous. The latter occur commonly in Pond I, and rarely in Pond II, which corresponds to the habits of the Terns. Examination of some Terns' stomachs from Pond I showed that they had been eating Amphipods, no trace of *Mysis* being found. Terns were seen feeding on Gammarids at Cape Boheman (64), and at Richard Lagoon. On the other hand, remains of adult *Mysis* were found in the stomach of a Tern which had been fishing by the Boulders. Thus the depredations of
Contributions to Ecology of Spitsbergen and Bear Island

Terns may prevent many adult *Mysis* from living in Pond I. Those seen were much more conspicuous than the young.

To sum up the probable manner of reliction of *Mysis oculata*: the first retardation of development takes place at the heads of long fjords or other places where the water is of a lower salinity than that of the open sea, though not necessarily in estuarine waters. The young of this fjord form (or of *M. oculata*?), if they get into estuarine waters, may survive the summer (partly on account of their small size and consequent immunity from Terns), but not the winter unless the water is deep enough to prevent the pond from freezing solid. If it is deep enough (over 2 metres) the *Mysis* will breed in the tidal waters, and will then be safe from the attack of Terns. It may ultimately become relict in fresh water.

Another problem is the absence of *Mysis* and *Gammarus* from the two inner ponds. A few *Mysis* were found in Pond III late in the season (August 14th), but before that none occurred. They are not limited by salinity since those in Pond I live most of the time in fresh water, and some *Mysis* and *Gammarus* were kept for over 12 hours in fresh water (chloride 0.027 gm. per litre) without being affected. *Mysis* and *Gammarus* have to recolonise these ponds every spring on account of the winter freezing, and the extent to which they can penetrate depends partly on their powers of dispersal. *Mysis relicta* was found to be positively rheotactic, but owing to its small size and weak powers of swimming against currents it only occurs for a certain distance up the stream connecting Ponds I and II, and seems unable to pass up the more rapid stretches. Since the *Mysis* live on the bottom, where they feed on algae, etc., their chance of being washed into Ponds II and III by tides is small, though it does occasionally happen.

*Gammarus zaddachi* probably finds most of its food in Pond I, where matter is brought in by the tide; Terns would act as a check on any pioneers entering Pond II. *Gammaracanthus loricatus* occurs in the relict lake on Credner’s Moraine and in Scandinavian lakes in its freshwater form *G. lacustris*, but was not found in these tidal ponds at all. It is rather remarkable that no chironomid flies inhabit the tidal ponds, since they are one of the few groups of insects which flourish in brackish conditions. They occur commonly in estuarine areas in temperate regions.

2. **Freshwater Communities.**

(a) *Ponds.* Figs. 5 and 6 show the relative positions and ages of the freshwater ponds on the raised beaches. They are all on shingle, the water being held in primarily by the ground-ice, also by the marginal vegetation. This ground-ice provides by its melting a continuous supply of water which is supplemented by drainage from higher ground. The result of this is the absence of temporary ponds of the Cape Boheman type. They differ also from the latter in having the relict Copepod *Eurytemora roboti.*
### Table VI. List of Crustacea occurring in the Freshwater Ponds.

<table>
<thead>
<tr>
<th>Pond No.</th>
<th>IV</th>
<th>VI</th>
<th>VII</th>
<th>VIII</th>
<th>IX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lepidurus arcticus</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td>Daphnia pulex</td>
<td>–</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td>Macrothrix hirsuticornis</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>0</td>
</tr>
<tr>
<td>Chydorus sphaericus</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td>Eurytemora raboti</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td>Cyclops crassicaudus</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>0</td>
</tr>
<tr>
<td>Maraenbiotus brucei</td>
<td>–</td>
<td>–</td>
<td>×</td>
<td>×</td>
<td>0</td>
</tr>
<tr>
<td>Candona rectangulata</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>0</td>
</tr>
<tr>
<td>Eucypris glacialis</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>0</td>
</tr>
</tbody>
</table>

0 = recorded by Olofsson (our collection lost).

Table VI shows the crustacea of these ponds. Olofsson gives the crustacea of some of the ponds, and these agree with our records. He also gives much information about the rotifers.

Pond IV (= Walton, V). One of several small pools in boggy land, and the newest of the series.

Pond V. Now dried up, but originally forming an intermediate link.

Pond VI (= Walton, VI and Olofsson, X). A large pond 300 yards long and 1–2½ feet deep. Bottom sandy-mud, moss bank, etc., on side. Its fauna is the same as that of Pond VII, which is described in detail below.

Pond VIII (= Olofsson, VIII). Two small ponds lying in boggy land connected by a narrow channel.

Ponds IX, X and XI (= Olofsson, VI and VII, not comparable individually). These are all at the same height, and appear to be remnants of a large lagoon, since the skeleton of a big whale was found lying near them. They are all of the same type—small ponds with sandy-mud bottom and plant-covered margins. These are the highest ponds in the series (about 40 feet above sea level), and are probably slightly higher than Pond VIII, though this is not certain. The latter may be of the same age.

Pond VII (= Walton, VII and ? Olofsson, IX) (Plate II, fig. 2). 140 yards long and 6 inches to 1 foot deep. It lies about 26 feet above sea level. The bottom is mostly shingle, with a few patches of mud, as a result of which *Lepidurus* is rather scarcer than in Pond VI. The following communities exist, but they mingle to a great extent:

**Plankton:**

- *Crustacea*: Daphnia pulex, Eurytemora raboti
- *Rotifera*: Polyarthra platyptera and other species
- *Protozoa*: A large colonial flagellate Uroglena sp. in masses. On this occurs a very large epizoic Vorticella

**In plants and in littoral region:**

- *Crustacea*: Chydorus sphaericus, Cyclops crassicaudus, Maraenbiotus brucei
- *Rotifera*: Monostyla cornuta Müller, M. lunaris Ehrb., Lepadella patella, *Mytilina ventralis* var. brevipina Ehrb., and others including many Bdelloids described under Zone 3 of the Pond Marginal Community
Diptera: Cricotopus basalis
C. glacialis (laying eggs on August 1st) and probably most
of the chironomids listed in Raised Beach
Oligochaeta: See Zone 3 of Pond Marginal Community
Protozoa, Nematoda, Tardigrada
On bottom:
Crustacea: Lepidurus, Macrothrix, Eucypris and Candona

Arctic Terns and Purple Sandpipers occur and occasionally other birds.

Fig. 7 gives the temperatures of the water during the end of July and
beginning of August. These were usually taken at 11 a.m., but on several
days they were taken at other times (July 25th at 1.30 p.m., July 28th at
5 p.m., Aug. 12th at 2.30 p.m.). These latter records show that the maximum
temperature is reached in the middle of the day. In this region it is usually
colder at night. It will be seen that the average daily range is about 3.5° C.,
the maximum temperature 14° C. and the minimum 4.3° C. These tempera-
tures are much lower than those of a temperate lowland pond of the same size.
They correspond to waters in the willow zone of Scandinavian Mountains, and
to those at about 2000 metres in the Rhaetic Alps (22). This low temperature
becomes a serious factor for animals like crustacea, which have to grow up
and breed during the short arctic season. According to Mr. R. F. Stobart,
this pond and Pond VI were just unfrozen in the middle on June 14th. Most
Spitsbergen waters freeze by the middle of September. This allows about
three months in the year for development, while during the other nine months
the ponds are frozen solid. The crustacea (Daphnia, Eurytemora, etc.) in the
smaller ponds (IV, VIII and X) were about a week ahead, in development,
of those in the large ones. This is probably due partly to differences in temperature. The flies can most likely winter in the water, at any rate in some stages. The eggs of Cricotopus glacialis a day or two old were frozen solid to \(-3.6^\circ\) C. for over half-an-hour, and subsequently developed into larvae. The worm Enchytraeus crymodes also was unharmed after being frozen to \(-2.5^\circ\) C. for 10 minutes. These are only rough experiments, and probably many animals can prepare themselves physiologically to resist freezing, if the process is more gradual.

The water is very clear, quite fresh and alkaline. The continuous daylight of the arctic summer enables photosynthesis by algae to continue all the time. This must cause the oxygen content of the water to be high and the CO₂ content low, which is probably one reason for the constant alkalinity of the water. All waters examined (on Bear Island and at Klaas Billen) had a \(p_H\) of 8.2–8.5. This is the same as that of many English lowland ponds in summer.

There is probably less light at night under water, since the sun is lower then; but it may be quite strong on a summer night is shown by the behaviour of Daphnia pulex in Pond VI. This species is very strongly positively phototropic, and could be seen on sunny days in a crowd on the side of the pond towards the sun. During the 24 hours this crowd made a complete circuit of the pond, following the sun.

Almost all the freshwater animals are vegetarian or scavengers. Lepidurus has been seen to eat Daphnia pulex in captivity, and Eucypris to attack old individuals of Lepidurus (30), but these occurrences are probably exceptional. The Eucypris and Candona here were found to feed mostly on diatoms, together with other algae. Lepidurus, except when moving, is hard to see, being coloured to match its surroundings, but during August small parties of Arctic Terns used to hover over Ponds VI and VII diving for Lepidurus. They then returned in the direction of the nesting colony—obviously carrying Lepidurus back to the young. Since this might go on for several hours, it will be seen that Terns act as a considerable check on Lepidurus, but at the same time may provide a means of dispersal by dropping their catch occasionally into other ponds on the way back to the nest. Purple Sandpipers’ gizzards contained remains of Lepidurus. Probably Phalaropes and other wading birds eat this species too.

Eurytemora raboti, really a brackish water animal, occurs in ponds on raised beaches in many parts of Spitsbergen. Olofsson has dealt in detail with this question, and there seems no doubt that it is in most places a true relict form. It may possibly have been distributed secondarily to some of the Klaas Billen ponds. Various animals might have done this accidentally. Reindeer formerly roamed over these beaches, while men have occupied Bruce City in the summer since 1919. Arctic Terns dive into the water when fishing for Lepidurus and they may carry things on their feathers. Phalaropes and other aquatic birds may also help in dispersal. The communities of crustacea are
so constant throughout Spitsbergen (except in temporary ponds) that it appears that they must have good means of dispersal. There is very little difference in the crustacea of this series of freshwater ponds according to age, except that in the newest (IV) *Daphnia* is absent.

Ponds of the shallow type such as at Klaas Billen and Cape Boheman are those most commonly found in Spitsbergen. There are, however, a certain number of deeper, cold lakes, whose fauna is different. *Cyclops strenuus* occurs in these, and also salmon (*Salmo alpinus*) in some places (e.g. in Lake Richard, in Red Bay, also at Cape Staratschin (11)).

(b) Streams. These occur naturally on the silted area since they are the agents producing the silting. They are very poor in life. The following algae were found in one stream:

- *Cosmarium botrytis* Menegh.
- *C. globosum* Bujhn.
- *Cylindrocystis brebissonii* Menegh.
- *Gonatozygon brebissonii* De Bary
- *Staurastrum alternans* Breb.

The filamentous *Gonatozygon* is the most important of these. Animal life is absent.

D. GIPS VALLEY.

This area, like Bruce City, is situated well inside Icefjord (see General Map, Fig. 3). It consists of a broad flat valley, whose floor is formed of a number of raised beaches, on either side of which is a high range of mountains. The Gips River runs along the valley. In the lower part are sandstones, etc., while Temple Range and the upper parts of the mountains generally consist of limestone which is hard, and forms nearly vertical precipices. Only the south part of the valley to the east of the river was studied. This area has a dry and somewhat continental climate with a very small annual precipitation.

We do not propose in this case to give a general classification of communities. We shall simply describe a few interesting ones.

1. RAISED BEACHES.

There are a number of parallel beaches running transversely across the valley bottom. The region can be divided into three zones.

(a) Seaward Beaches. These consist of loose shingle well above high tide level. Near the sea the stones, which are about 1 to 6 inches in diameter, and obviously sea-worn, are quite bare of plant life. On the crests of the second and third beaches there is a quite considerable flora of crustaceous and foliose lichens. The commonest of these is *Xanthoria parietina* which grows even on driftwood. Other lichens here are:

- *Buellia disciformis*
- *var. trifragmia* Boist.
- *Ephebe lanata* Wain.
- *Placodium elegans*
- *Placynthium nigrum* SF.Gray
- *Physcia lithotea* Nyl.
- *Rinodina demissa* Arn.
- *Thelidium pyrenophorum*

This is an entirely different flora from that of the raised beach at Prince Charles Foreland. The difference may be related to the different chemical constitution
of the substratum. In "lows" between these beaches a small amount of soil collects (1 inch in places), and here grow scattered plants of Saxifraga oppositifolia, S. caespitosa and Draba alpina. This passes into (b) as one proceeds inland.

(b) Stabilised Beaches. These beaches differ in being formed of more angular fragments, and in their great compactness due to settling down and the addition of silt. The crests support much the same type of vegetation as in the "lows" just described. In addition to the three species mentioned above, all of which are frequent, there are Draba hirta var. arctica, and Dryas octopetala. This community (a type of "fjaeldmark") resembles that at Klaas Billen Bay. Lichens are only subordinate. In the "lows" the vegetation consists of large tussocks of Dryas among which are a number of mosses.

Among the plants and under stones the following animals occur:

<table>
<thead>
<tr>
<th>Animal</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Collembola</td>
<td>Onychiurus armatus var. arcticus</td>
</tr>
<tr>
<td>Spiders</td>
<td>Typhochrestus spetsbergensis</td>
</tr>
<tr>
<td>Mites</td>
<td>Sphaerozetes notatus</td>
</tr>
<tr>
<td>Birds</td>
<td>Purple Sandpiper Nesting</td>
</tr>
<tr>
<td></td>
<td>Ringed Plover (Charadrius hiaticula hiaticula L.)</td>
</tr>
<tr>
<td></td>
<td>Arctic Tern Possibly nesting</td>
</tr>
<tr>
<td>Mammals</td>
<td>Arctic Fox (seen by Mr Tucker in 1922)</td>
</tr>
</tbody>
</table>

Pink-footed Geese also nest further up the valley. The Purple Sandpiper is always found within easy reach of the sea. This fauna differs in several respects from that on the raised beach at Prince Charles Foreland.

(c) Moss Bogs. Along the banks of the Gips River there are extensive moss-bogs, alternating with bare sandy areas. The moss community passes into the Dryas-moss community on slightly higher ground. Only a few flowering plants occur in these bogs. The chief mosses here are Brachythecium salebrosum var. arcticum and Orthothecium chryseum, but most of the usual bog mosses occur, and the list resembles that given for Cape Boheman. Camptothecium nitens does not appear to be so common as at Cape Boheman. A number of streams run into the river through the moss-bog. These have various algae, among them Zygnema sp., Oscillatoria limosa and O. amoena Gomont. The last two are present as "felts" on the muddy bottom.

2. SHELTERED VALLEY NEAR TEMPLE RANGE.

The slopes along Gips Valley support the usual "fjaeldmark" (Plate IV, fig. 2) described elsewhere (see especially Temple Bay). It is poor in species both of plants and animals.

In a valley cut out of the moraine and scree material just below Temple Range, a more luxuriant series of communities exists. Probably the south aspect and protection from winds, especially those from the snow-covered interior, are the master factors.

On the slopes of the valley are several definite zones. The highest, on a rather stony slope, consists of a rich type of "fjaeldmark"; in fact it could
almost be termed a “herb slope.” Salix polaris and Saxifraga oppositifolia are the chief species. The following also are found:

Phanerogams:
- Cerastium alpinum
- Draba alpina
- D. alpina var. oblongata
- D. hirta var. arctica
- Festuca rubra L. var. arenaria Oeb.
- Papaver nudicaule var. radicatum

Bryophytes:
- Hypnum uncinatum
- Thuidium abietinum

Lichens:
- Ceranía vermicularis
- var. taurica AL.Sm.
- Cetraria nivalis
- Lecanora epibryon

Below this there is a damper layer formed of large hummocks of Dryas with many mosses. The lowest zone is along the bottom of the valley, and here a stream runs through a thick moss carpet. The mosses are the usual bog species, e.g. Brachythecium salebrosum, Camptothecium nitens, Orthothecium chryseum, etc. The drainage prevents the establishment of a Hypnum bog as at Cape Boheman.

A number of boulders occur here, and these support a characteristic crevice community (see Bear Island) with Swartzia montana, Blepharostoma trichophyllum and others. Xanthoria parietina and Placodium elegans are common on the actual rock surfaces.

A rich fauna occurs in this valley:

Collembola: Isotoma viridis
- Onychiurus armatus var. arcticus

Diptera: Syrphus tarsatus var. Zett.
- Aceroptera grontata Zett.

Hymenoptera: Pristiphora frigida

Spiders: Immature

Mites: Bdella decipiens
- Sphaerozetes notatus

Birds: Snow Bunting Nesting
- Northern Eider r. Nesting

Mammals: Reindeer horns were found

A careful search on the ordinary “fjaedmark” gave the following poor collection of animals:

Spiders: Leptyphantes sobrius
- Immature of another species

Mites: Bdella decipiens
- Sphaerozetes notatus

Ptarmigan occur in small numbers further up the valley. The effect of favourable conditions is clearly seen from the above lists.

E. TEMPLE BAY (Sassendale).

This region lies on the south-east side of Temple Bay just north of Sassen-dale. It consists of the southern slopes and lower plateaux of the Colorado Range. Towards the valley the slopes are gentle, but there is a steep precipice
seawards. The main part of the region consists of limestones and dolomites; there are also sandstones, and a few thin layers of Gypsum. The region is thus predominantly calcareous. We shall only describe communities which are of especial interest, or illustrate types common in Spitsbergen.

1. **Bird Cliffs.**

This region can be divided into two parts: (a) the cliff, (b) the stabilised scree below.

(a) The cliff is almost vertical, and several hundred feet in height in some places. On ledges nest large numbers of the usual sea-birds, and there are a few geese nesting on the slopes just above. Around the nests, and on any ledges where soil collects, there is a very luxuriant phanerogamic vegetation. At the upper edge of the cliff *Cerastium alpinum* and *Saxifraga caespitosa* are the chief plants. On Green Mountain between Advent and Coles Bays, where there are similar cliffs, Mr Tucker saw large quantities of *Alopecurus alpinus* and *Cochlearia officinalis*; these are the characteristic plants of such places. *Saxifraga cernua* also grows very tall here. The *Alopecurus* grows extremely well, and forms almost continuous turf on the ledges. Lichens cover the rocks in an almost unbroken layer. Mosses occur on the cliff faces in such places, an interesting species in this connection being *Bryum argenteum* L. This is recorded from bird cliffs in N.W. Spitsbergen (5), from Iceland (25), and from East Greenland (14). It is considered to have been introduced by the sea-birds themselves.

(b) The manuring effect is most striking on the scree below where there is a continuous carpet of dicotyledons, grasses and mosses. This type of slope is described in Nathorst (44). At Temple Bay the following occur:

- *Cerastium alpinum* Polemonium humile Willd.
- *Chrysosplenium alternifolium* Ranunculus affinis R. Br.
- *Cochlearia officinalis* R. pygmaeus
- *Draba alpina* Salix polaris
- *D. alpina* var. *oblongata* Saxifraga caespitosa
- *D. hirta* var. *arctica* S. cernua
- *D. wahlenbergii* S. nivalis
- *Dupontia fisheri* S. oppositifolia
- *Glyceria angustata* Fr. Wahlbergella affinis Fr.
- *Luzula nivalis* Beurl. W. apetala Fr. f. arctica Th. Fr.
- *Poa pratensis* L.

This list is much longer than that given for Prince Charles Foreland. This is correlated with the much richer flora of the interiors of the large fjords. *Polemonium* is a characteristic plant in such localities, and sometimes forms continuous mats on the ground (3). Many of the plants grow much larger here than elsewhere (44). *Cerastium alpinum* sometimes dominates and forms pure growths over large areas. Hart (23) records several of the above species in Grinnell Land and elsewhere below bird cliffs. Where the snow-water traverses these slopes there are a number of mosses. They are bog species, but are much more luxuriant (5). Among those found in such places, the most
characteristic are Splachnum vasculosum, Webera schimperi O. Mull, W. ludwigii Spreng. var. subarctica Berggr., Hypnum uncinatum var. orthotheciodes Lindb. and Ceratodon purpureus Brid. Marchantia polymorpha is limited to this habitat. The third of these is considered by Berggren to be a variety due to the high organic content of the soil.

2. Raised Beaches.

A series of four of these occurs on the seaward slope just north of Sassendale. They are very narrow (less than 20 yards wide), but stretch for a considerable distance along the slope. The lowest is about 5 feet above sea-level, the highest 100 feet. There is a steep scree slope between adjacent beaches. The beaches can be divided into two parts longitudinally, the inner part having a much better developed plant community than the outer. This is due to the different lengths of duration of the snow-covering. Snow drifts would be formed in the angle between the beach and the scree above, whereas the outer part of the beach will have comparatively little snow.

On the lowest beach there is little vegetation except Saxifraga oppositifolia and a few mosses on the inner part.

The second beach, about 15 feet higher, has a more typical flora. On the outer region is a "fjaeldmark" community like that on the unsilted beach at Klaas Billen Bay (66) and Gips Valley. Dryas octopetala is the most abundant plant. On the inner part a heath of Dryas and Cassiope tetragona is developed. The following also occur here:

Draba alpina r. Pedicularis lanata
Luzula confusa f. Saxifraga oppositifolia r.
Papaver nudicaule var. radicatum f. Silene acaulis
Polygonum viviparum f. Wahlbergella affinis

At the angle of this beach is a block talus. Among the blocks occur Carex hepburnii Boott. (3), Cystopteris fragilis Bernh., Draba hirta var. arctica and Wahlbergella affinis.

The third terrace resembles the second, but there is no Cassiope; this appears again on the fourth. These beaches provide an example of the succession in time which occurs on raised beaches in Spitsbergen if the conditions are sufficiently favourable (compare with shingle beaches at Blakeney Point, Norfolk (54)). At Klaas Billen and Gips Valley such conditions are only rarely reached.

3. "Fjaeldmark."

The main part of the slopes and summit plateaux is occupied by a sparse "fjaeldmark." Dryas and Cassiope occur in places, and here the vegetation may be called "cushion-heath" ("Polster heide," Cleve (9)). The list below gives an idea of the type of community which occupies most of the drier, less favourable slopes in this part of Spitsbergen. Similar areas occur at Advent Bay and Green Harbour.
Phanerogams, etc.:

- Cassiope tetragona 1.f.
- Catabrosa alpina
- Dryas octopetala 1.a.
- Equisetum arvense
- Draba alpina var. alpestre Wg.
- Festuca brevifolia
- Luzula confusa o.
- Oxyria digyna r.
- Papaver nudicaule var. radicatum f.
- Pedicularis hirsuta
- P. lanata f. dasyantha
- Poa abbreviata R.Br.
- P. alpina
- Saxifraga caespitosa f.
- Saxifraga oppositifolia i.—1.a.
- S. oppositifolia
- Stereocaulon alpinum
- Wahlbergella affinis o.

Other rarer species also occur.

Lichens: Cetraria nivalis and probably others.

In many places the hardy Dryas is absent, scattered rounded cushions of Saxifraga oppositifolia and caespitosa only occurring (see Bear Island). The Cassiope occurs in slight hollows where snow collects. In some hollows on the slopes Salix polaris becomes dominant. With it are found Saxifraga nivalis, S. cernua, S. hieraciifolia, etc., also the moss Campylotheicum nitens and the lichen Stereocaulon alpinum. Where the earth is finer Saxifraga cernua is more frequent and the lichens Lecidea sanguineo-atra Ach. and Xanthoria parietina occur as thin circular crusts on the almost bare soil.

The animals of the “fjeldmark” were not examined carefully. The spider Leptyphantes sobrius occurs. At one time the neighbourhood was celebrated for the number of reindeer, which fed on the pastures in Sassendale. Their antlers are found scattered about the slopes. The reindeer is now found in Wijde Bay under similar conditions to those formerly present here. The moss Voitia hyperborea Grev. and Arn. is apparently limited to reindeer excrement (5) and its distribution depends on this animal. The Snow Bunting nests in crevices between rocks.

4. **STREAMSIDE COMMUNITIES.**

On the plateau the streams run in wide valleys, the whole of which have a damp type of vegetation. Alopecurus alpinus is the dominant plant. Papaver nudicaule var. radicatum also occurs in quantity, which is surprising since it is usually a plant of very dry habitats. Mosses occur here submerged, Philonotis fontana and var. alpicola Jur. and Hypnum giganteum being the commonest.

On the slopes is a thin marginal strip of mosses among which grow phanerogams. By one stream were:

**Phanerogams:**

- Cardamine bellidifolia
- Cochlearia officinalis
- Draba subacutata

**Bryophytes:**

- Bryum obtusifolium 1.f.
- B. rutulans Brid.
- Cinclidium stygium

- Saxifraga flagellaris
- S. hirsuta
- S. rivularis
- Hypnum sargentosum
- Mnium affinis var. integrifolium f.
- Orthothecium chryseum f.

These mosses are similar to those by streams in Iceland.
This is the second largest island of the group (see Fig. 3). The raw climate resulting from its proximity to the Greenland Sea is probably responsible for the poorness of the life there. The island, like others of its type, is characterised by the large number of sea-birds which nest there, chiefly the Northern Eider. It cannot be termed a true “Eider Holm” since man has interfered with the birds during the last few years. Eider Holms occur now only in remote unvisited regions such as Liefde Bay and Wijde Bay.

On the shingle there is no plant life except a few tiny plants of Cochlearia. The main part of the island consists of a flat area of moss-bog, out of which a few low grassy hummocks emerge. There are also a few shallow ponds in the main depressions.

On the hillocks besides the grass (not identified, but Catabrosa algida and Poa arctica R.Br. occur on the larger island) a few plants of Saxifraga caespitosa were found. This is the main nesting place of the Eider Ducks. The bogs are almost entirely occupied by mosses, the following being the commonest:

<table>
<thead>
<tr>
<th>Hypnum polygamum</th>
<th>Mnium affine var. integrifolium</th>
</tr>
</thead>
<tbody>
<tr>
<td>H. uncinatum</td>
<td>Splachnum vasculosum</td>
</tr>
</tbody>
</table>

H. polygamum has a well-known preference for maritime situations (49), whilst Splachnum depends on the large amount of dung dropped on the island.

The following birds occur on the island:

- Arctic Tern Nesting on shingle and on moss-bog
- Arctic Skua o.
- Northern Eider Nesting on shingle and on hillocks
- Brent Goose Feeding. Nesting on the other island
- Purple Sandpiper o. Feeding
- Dunlin (Erolia alpina alpina L.) o. Feeding
- Grey Phalarope Nesting among moss and shingle
- Red-throated Diver Nesting by ponds
- Snow Bunting Nesting among stones by shore

The Northern Eider, Brent Goose and Diver feed at sea. The waders feed on land, and in the ponds as well. Two species of Diptera (Metriocnemus ursinus and Cricotopus glacialis) occur, while the mite Scutovertex lineatus was found under small stones. On the surfaces of the ponds were very many Collembola. The main factor affecting the bird life of islands like the Edinburghs is the absence of foxes. The Brent Goose, Eider and Tern usually nest on islands for this reason. The Glaucous Gull and Arctic Skua are their chief enemies. In Arctic America the Eider and Geese are sometimes protected by the fierce attacks which the Terns make upon intruders in defence of their nests (58). This appears to be partly the case in Spitsbergen, a Skua often being seen pursued by a Tern. Skuas eat young Eiders and suck the eggs of various birds.
This island lies inside Foreland Sound, and enjoys a more favourable climate than the Edinburgh Islands. It is somewhat larger, but of the same type, and the same birds occur. In the centre is a rocky ridge which is nearly 75 feet above sea-level in places. No detailed animal notes were made. There are five main communities in the island:

1. Maritime Region.
2. "Fjaeldmark."
3. Rock Outcrops.
4. Wet Tundra.
5. Ponds.

1. Maritime Region.

This consists of cliffs and shingle, and is similar to that in the Edinburgh Islands. On the Anser Islands the Spitsbergen Puffin and Mandt's Guillemot nest in clefts in the cliffs, and they probably occur here. Terns nest in numbers on the shingle.

2. "Fjaeldmark."

This is not of such a stunted character as usually occurs owing to the dunging effect of the numerous birds. It occurs on the slopes between the bogs and the rocks. The ground is very dry, with more soil than usual. Saxifraga oppositifolia is the chief plant. So profusely was this blooming that from afar off it resembled somewhat a flowering heather-moor. The few other species are the usual "fjaeldmark" ones. A few Eider Ducks nest in this region.

3. Rock Outcrops.

This area is concentrated in the ridge, but small rocky areas occur at the tops of the cliffs and elsewhere. Here the richest vegetation occurs, due to the large number of Eiders which nest on the ledges of, or between, the rocks. The following plants occur:

**Phanerogams:**
- Alsine biflora Wg. r.
- Cardamine bellidifolia r.
- Cerastium alpinum f.
- Draba alpina f.
- D. alpina var. oblongata f.
- D. hirta var. arctica o.
- D. wahlenbergii o.
- Dryas octopetala l.d.
- Potentilla emarginata Persh. r.

**Lichens:**
- Alectoria nigricans

Other mosses and lichens also occur. On small isolated rock outcrops a moss-lichen vegetation occurs dominated by Rhacomitrium lanuginosum, Cetraria nivalis and Cladonia rangiferina. Here only a few Eider Ducks nest.
4. WET TUNDRA.

This consists of moss-bogs and pond marginal communities. The ponds occur as a ring near the edge of the island. The bogs are chiefly mossy, but there are a few phanerogams locally, Salix polaris and Saxifraga rivularis being the more important. The mosses are the usual bog species. Significant in connection with the extra nitrogen supply is the presence of Ceratodon purpureus and Tetraploidon wormskjoldii. The moss flora is similar to that at Cape Boheman. The Grey Phalarope and Red-throated Diver nest around the ponds.

5. PONDS.

The ponds are of the usual type, and are shallow. The animals were not examined. Large masses of Nostoc occur in places, while Hypnum cordifolium, H. giganteum and H. stramineum grow submerged.

H. ADVENT BAY.

This area was visited on several occasions, but only for short periods. There are a number of species, both of plants and animals, which are not recorded from other places, since Advent Bay and Coles Bay show more favourable conditions of life than do many other parts of Spitsbergen.

At Advent Bay the following were found on flowers of Dryas and Cerastium in the lateral valley behind Longyear City:

Diptera:
- Camptocladus pumilio
- Limnophora megastoma
- Psectrocladius borealis

The larvae of Syrphus feed on aphids, of which one species—Scaeva dryadis—is recorded from Advent Bay. No Hymenoptera were seen by us here, but several species have been recorded. An ichneumon Bassus arcticus is parasitic on the aphid. Pristiphora frigida occurs and is parasitised by Ichneutes hyperboreus. Several other ichneumons occur here.

The birds resemble those of Gips Valley except for the presence of the Barnacle Goose (Branta leucopsis), which nests on cliffs in the valley. A flea Ceratophyllum vagabundus was found abundantly in the down of Barnacle Goose nests. This also occurs in the nests of Pink-footed Geese. The bird-louse Trinoton anserinum Fab. was found on the Barnacle.

IV. SUMMARY AND CONCLUSIONS.

1. The plant and animal communities of part of Bear Island and of various districts in Spitsbergen are described.

2. A succession of plant communities can be traced, starting with “fjaeldmark” on unstable ground, such as screes, or on recently elevated land, as raised beaches, and terminating on stabilised ground with a heath vegetation of Cassiope tetragona, Dryas octopetala or Salix polaris. In most places this
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This area was visited on several occasions, but only for short periods. There are a number of species, both of plants and animals, which are not recorded from other places, since Advent Bay and Coles Bay show more favourable conditions of life than do many other parts of Spitsbergen.

At Advent Bay the following were found on flowers of *Dryas* and *Cerastium* in the lateral valley behind Longyear City:

Diptera:
- *Camptocladius pumilio*
- *Limnophora megastoma*
- *Psectrocladius borealis*
- *Rhaphomyia caudata* Zett.
- *Sciara* sp.
- *Syrphus tarsatus*

The larvae of *Syrphus* feed on aphids, of which one species—*Scaeva dryadis*—is recorded from Advent Bay. No Hymenoptera were seen by us here, but several species have been recorded. An ichneumon *Bassus arcticus* is parasitic on the aphid. *Pristiphora frigida* occurs and is parasitised by *Ichneutes hyperboreus*. Several other ichneumons occur here.

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climax is apparently never reached, owing to continued instability of the substratum, and "fjædmark" is retained.

3. When the drainage is bad, or where there is a constant supply of water, damper communities are established, and may be maintained indefinitely.

4. The comparative abundance of cryptogams, especially the Bryophyta, is a characteristic feature of the vegetation. The relative increase of the cryptogams in the communities in maritime regions such as Bear Island and Prince Charles Foreland as compared with districts at the heads of fjords can be seen from the lists, etc. This is probably due to the greater humidity of the air on the coasts.

5. The effect of abundant supply of nitrogen on the plants is pointed out and special communities depending on this extra supply are described. These communities agree to a great extent with those described from other arctic countries.

6. In both plants and animals the number of species is small. This is due to (a) severe conditions, (b) geographical isolation, (c) the absence of day and night as separate habitats so that fewer species of animals can live in the same area.

7. The animal species are not usually confined to any particular general (or "communal") habitat, plant association or plant species, but occur in or on more than one. Individuals may occur in more than one community at different times (e.g. birds, flies). Thus "communities" of animals exist only in the sense that each general habitat and each plant community has a fairly constant set of animal species associated with it, of which only a few are exclusive (i.e. confined to it).

8. As a result of this the best method of describing the animal communities appears to be by basing the account largely on the food relations. The method of Shelford and others, based on the "physiological response" of the animal to the habitat, although indispensable, is inadequate, since it only applies to a few species in each community (i.e. the exclusive ones), and these often are not very important in the life of the community.

9. The food cycle on Bear Island is sketched. The chief points are: (a) the addition of food by sea-birds and probably by nitrogen fixation by bacteria, (b) the loss of food by bird migration and washing down of soluble salts, (c) the importance of freshwater flies as food supply for land animals, (d) the "short-circuiting" of the "nitrogen cycle" owing to the activity of scavengers which feed on decaying animal matter is not of importance, (e) the scarcity of carnivores in the fresh water modifies the usual position of the Entomostraca as the "key-industry" of fresh water. These conclusions apply on the whole to Spitsbergen also.

10. In animals vertical differences in habitat are relatively unimportant or absent (except "exposed," "under stones and plants," and "subterranean"). The same may be said about the plants since there are no trees or shrubs, and very few dwarf-shrubs.
11. A series of brackish and freshwater ponds at Klaas Billen Bay is described. The conditions and succession of communities due to land elevation are dealt with. In particular, an account of the ecology of certain crustacea (Mysis relicta, Gammarus zaddachi, Eurytemora raboti) is given. A sketch of the probable manner in which Mysis relicta becomes relict in fresh water is given. The biota of freshwater ponds containing relict Eurytemora raboti is described and also temperature records from one pond.

12. The abundance of enchytraid worms in the soil in Spitsbergen is investigated and their importance indicated.

V. BIBLIOGRAPHY.


(33) Kihlman, A. O. *Pflanzenbiologische Studien aus Russisch Lappland.* Helsingfors, 1890.


(42) Nansen, F. *Farthest North,* 2. Ibid.


(48) Olofsson, O. “Studien über die Süßwasserfauna Spitzbergens.” Ibid.


(50) Porsild, M. P. “The Plant Life of Hare Island off the coast of West Greenland.” *Medd. om Grønland,* 47, 1911.

(51) Rasmussen, K. *Greenland by the Polar Sea.* London, 1921.


(56) Schröter, C. *Das Pflanzenleben der Alpen.* Zurich, 1908.


NOTICE OF PUBLICATION OF 
GENERAL BEARING

AN INTRODUCTION TO PLANT ECOLOGY


The spread of ecological interest in Britain suffers—and has suffered for a long time—from the absence of any text-book dealing with ecological methods, which might be placed in the hands of those unfamiliar with these methods. Such a book to be of real value requires to combine a certain felicity of expression with a rare discrimination as to subject matter. It needs to be compact in form, moderate in price and yet to cover adequately the variety of material and method which is included in the scope of plant ecology. It may safely be said that from all of these standpoints Mr Tansley’s book is an admirable one. While it is necessarily concerned largely with plant communities, plant ecology is viewed as “a means of approach to a large part of detailed botanical study” rather than as a name for a special branch of botany, and in this the author expresses the modern reaction from the purely laboratory (and academic?) aspects of plant life.

The book is divided into five parts, of which the first is introductory, while the second defines the units of vegetation and gives outlines of plant succession and of the main types of British vegetation. The third part deals with methods of studying and describing vegetation in the field, and this is followed by chapters on the habitat and the estimation of habitat conditions. The remaining part discusses the opportunities for ecological work in schools with suggestions as to profitable lines of attack. Useful appendices are added on the “life forms” of plants, methods of surveying and photographing vegetation, soil analysis (by Dr H. J. Page) and the determination of hydrogen-ion concentration. There is a classified list of books and papers suitable for further reference.

The book well fulfils the purpose for which it was written, as a “guide for beginners in field study of plant communities,” and it is difficult to make any suggestion which would improve it without greatly extending its scope. It will prove very useful to students and to those desirous of embarking on field or ecological work. At the same time it is interesting and suggestive, even to more experienced ecologists.

W. H. P.
Further Contributions to the Ecology of Spitsbergen

in another paper, in which will be found a general discussion of the means of dispersal of the various invertebrates (6); in the summer of 1924, vast swarms of hover flies (Syrphus ribesii) and spruce aphids (Dilachnus piceae) were blown from Northern Europe on to the ice-cap of North-East Land—a distance of over 800 miles. They were alive when they arrived, but perished later in a blizzard; in any case they could scarcely have survived very long. A similar swarm of aphids was encountered by Parry off the west of North-East Land in 1827 (24, p. 201). It is to be supposed that the other insects reached the archipelago by similar means, or by transport on birds. The result of the isolated position of Spitsbergen is that many groups of animals are absent, although these are found in Greenland under similar conditions of climate and vegetation. Examples are various butterflies, also bumble-bees and tipulid flies.

Furthermore, several mammals are absent, e.g. the Lemming, Arctic Hare, and Musk Ox. The absence of Lemmings is reflected in the almost complete absence of Snowy Owls, and the fact that there are no Ermine (which eat the Lemmings); nor are there any Arctic Wolves (which eat Hares). Since the wolves also attack deer, it is probable that their absence is due rather to dispersal difficulties than merely to absence of food. These questions, in so far as they affect the mammals, will be treated in a separate paper.

The fauna of Spitsbergen differs therefore from that of similar places in the same zones of climate and vegetation, in being rather more impoverished. We have already (Section VIII) traced the gradual increase in complication of the food-cycle as the climate improves, and have shown how the most highly developed animal communities in Spitsbergen foreshadow in a general way the very complicated communities of sub-arctic and temperate regions. At the present time we know very little about the animals of the sub-arctic zone (Empetrum, etc.) and it is to be hoped that future work in some place like South Greenland or Lapland will bridge the gap between our knowledge of the food-cycles of high arctic countries and those of our own regions.

X. SUMMARY.

1. In 1923 we published in this Journal an account (almost entirely descriptive) of the animal and plant communities of certain parts of Spitsbergen and Bear Island. Further investigations in Spitsbergen have enabled us to co-ordinate these and our later observations into a general scheme, which makes it possible to explain the general distribution of the plant and animal communities in terms of four master factors: climate (insolation and air-temperature), soil, manuring by sea-birds, and water-supply.

2. The climatic gradient produced by the meeting of the Polar ice-pack with the Gulf Stream, brings about a corresponding gradient in the types of vegetation. This gradient can be divided naturally into four zones, (1) Barren
Zone, (2) Dryas Zone, (3) Cassiope Zone, and (4) the Inner Fjord or Empetrum Zone.

3. This gradient in plant communities has also been traced in the communities of land-animals, and in the intertidal fauna. By combining all these lines of evidence, we have constructed a provisional map showing the main life-zones for the whole of the Spitsbergen archipelago.

4. These zones can be traced on a much broader scale right across Greenland and Arctic Canada, and in the mountains of northern Scandinavia; and they demonstrate the very high-arctic character of Spitsbergen communities.

5. The gradient outlined above is interfered with by bird-manuring, which produces distinctive (and usually grassy) communities even in the most barren parts of Spitsbergen. The effects of bird-manuring on animals and plants were studied intensively in several cases.

6. It is impossible in a short space to summarise any of the other points dealt with, and the reader may be referred to Sections VIII and IX, and to the map, since these are to some extent summaries of the rest of this paper.

XI. REFERENCES.

For a more complete list of works dealing with the flora and fauna of Spitsbergen, the reader is referred to our previous paper (29).


(2) Binney, F. G. With Seaplane and Sledge in the Arctic. London, 1925. (A shorter account may be found in the Geogr. Journ. 66, 9–40, 1924.)


(4) Bruce, W. S. Polar Exploration. London, 1911.


Further Contributions to the Ecology of Spitsbergen

(14) Holttum, R. E. “The Vegetation of West Greenland.” This Journal, 10, 1, 1922.

(15) Iversen, T. “Hopen (Hope Island), Svalbard.” Resultater av de Norske Statsundersøttede Spitsbergeneexpedisjoner, 1, No. 10, 1920.


(17) Kukenthal, W. Peternanni Mittel. 36 (1890).

(18) Longstaff, T. G. “Notes from Spitsbergen.” Ibis, July 1924, 480–495.


