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STUDIES ON THE TERRESTRIAL PROTOZOA

OF THE MARITIME ANTARCTIC

HUMPHREY G. SMITH

Doctor of Philosophy

Department of Forestry and Natural Resources
University of Edinburgh

1973

With Compliments

and thanks for loan

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PREFACE

This thesis is submitted to the University of Edinburgh in accordance with regulations prescribed for the degree of Ph.D.

The work reported here was undertaken while I was under contract to the British Antarctic Survey to carry out research on the terrestrial protozoa of British Antarctic Territory - the land south of 60°S and bounded by longitudes 20°W and 80°W.

Work in the Antarctic was carried out chiefly from the base on Signy Island, South Orkney Islands, which comprises a biological research laboratory and a meteorological station. During the southern summer 1968-69, I made a survey of the terrestrial protozoan fauna of Signy Island; the survey was subsequently extended to other islands in the South Orkney group and to other island groups.

From November 1969 to April 1971 I undertook intensive studies upon the population ecology of selected protozoan species in contrasting terrestrial habitats on Signy Island.

I returned to the U.K. in June 1971 and since then was resident at Edinburgh University doing laboratory work in the Department of Forestry and Natural Resources upon stored material brought from the Antarctic in a refrigerated condition. This work included analysis of samples obtained by the Combined Services Expedition to Elephant Island, South Shetland Islands, 1970-71. Subsequently I have performed experiments using single species cultures of selected protozoa.

It is intended that the material of Chapter II will be incorporated in a monograph upon the terrestrial protozoa of the maritime Antarctic, sub-Antarctic and cool-temperate south Atlantic, to be submitted for publication as a British Antarctic Survey Scientific Report. The material of Chapters III and IV has been accepted for publication as papers in the British Antarctic Survey Bulletin and these are now in press. It is intended that the material of Chapter V will be submitted as a paper for publication in the British Antarctic Survey Bulletin.

The raw data and field notes on which this thesis is based are at present in my possession. During or before July 1974 they will be deposited in the library of the British Antarctic Survey (Zoological Section), Monks Wood Experimental Station, Abbots Ripton, Huntingdon.

I declare that this thesis is my own work and has not been submitted for any degree other than that of Ph.D in the University of Edinburgh.

Humphrey G. Smith

April 1973

CONTENTS

Methods

Discussion

ABSTRACT

The maritime Antarctic region comprises the islands of the Scotia Ridge and the islands and west coastal lands of the Antarctic Peninsula. This region has an oceanic climate with at least one month each summer when the mean temperature exceeds 0^{o}C. Land mammals are absent and flowering plants rare, but bryophytes and lichens cover large areas and the soils contain a diverse microflora and invertebrate fauna.

Between 1968 and 1971 a survey was made of the protozoa occurring in terrestrial habitats on maritime Antarctic islands. Habitats investigated included clay of glacier moraines, volcanic ash, moss peats, grass soil and guano of penguin colonies and elephant seal wallows. Samples from 68 sites were analysed for protozoa by culturing and direct examination. 96 species of protozoa were observed (27 Mastigophora, 32 Rhizopoda, and 37 Ciliata). The results suggested that the remoteness of Antarctica is not a geographical barrier to the dispersal of protozoa, but that the composition of the fauna is determined by local ecological conditions. Mastigophora were the most ubiquitous group, naked amoebae were rare, testate amoebae showed a clear preference for acid vegetated habitats and ciliates occurred in vegetated habitats and in mineral and guano habitats which were species-rich.

The numbers of the testate amoeba _Corythion dubium_ Taranek in three horizons of moss turf peat were determined on 16 occasions over 15 months together with observations on the physical properties and microclimate of the peat and on the climatic environment of the site. No consistent differences between the three horizons in numbers of _C. dubium_ were detected. Seasonal fluctuations in population size followed the annual cycle of temperature, a spring bloom occurring with the thawing of the

peat during October and November; numbers remained relatively high until the onset of freezing conditions at the end of March when the population once again declined. It appeared that the mid-summer population was limited by moisture - either directly or as a result of low moisture restricting the microflora.

Observations on the protozoan fauna of the guano of chinstrap penguin colonies led to the formation of a hypothesis describing the influence of the penguin population upon the guano fauna through their effect upon physical and chemical properties of the guano. In one colony, the numbers of three guano-specific species of protozoa (Tetramitus rostratus Perty, Philaster sp., and Vorticella microstoma Ehrenberg) in an experimental area from which penguins were artificially excluded, and in a control area, were determined on 16 occasions over 15 months, together with observations on guano properties. Seasonal variation and differences between the experimental and control areas were examined in an attempt to distinguish between the influence of climate and that of the penguin population upon the protozoa in the guano. The guano in the experimental area had a lower pH than that in the control area and became overgrown by the alga Prasiola crispa. No significant changes in the protozoan fauna of the exclosed guano had been observed by the end of the third summer since the erection of the exclosure.

No species of the ciliate genus Colpoda was observed during these studies - a surprising result because Colpoda spp have been frequently recorded from soils in temperate and Arctic regions. Previous work suggested that resting cycts of Colpoda could certainly survive maritime Antarctic winters. It was therefore suggested that it was Antarctic summers which were too cool and short for Colpoda spp to maintain active multiplication phases long enough to establish themselves in terrestrial habitats, and that it was because those Arctic lands which support a terrestrial fauna have longer warmer summers that Colpoda has been detected there. This hypothesis was supported by experiments with single-species cultures in which Colpoda cucullus showed poorer ability to survive at 0° and 4°C than three species of protozoa which do occur in the maritime Antarctic, and by comparative meteorological data which showed that Arctic localities from which Colpoda has been recorded have warmer summers than do maritime Antarctic islands from which it has not, even though they may have colder winters.

Taking together the data in all the studies, it was concluded that vegetation, marine animals and possibly geology influence the distribution of terrestrial protozoan species in the maritime Antarctic; while temperature and sometimes moisture influence their numbers.

CHAPTER I

THE MARITIME ANTARCTIC

INTRODUCTION AND DEFINITIONS

The Antarctic zone of the Earth may be defined as the continent of Antarctica together with the seas and islands south of the Antarctic Convergence - the circumpolar line at which the cold surface waters of the Southern Ocean sink below the warmer waters of the southern Atlantic, Indian and Pacific Oceans (Fig. 1). This line (Mackintosh, 1946) varies between 48° and 62° S.

Within the Antarctic zone there is considerable diversity in the geographical and climatic conditions. Subdivision of the zone into regions is necessarily arbitrary as conditions are continuously variable; however geographical discontinuities and the correlated vegetational differences of many of the areas involved makes classification convenient. The classification of Holdgate (1964) is adopted here:

Sub-Antarctic region

Monthly mean temperatures are greater than 0°C for at least 6 months each year, but never greater than +8°C and never lower than -2°C. There are no trees; vascular plants are abundant in lowland areas, bryophytes and lichens in highland.

Examples: South Georgia, Macquarie Island (Fig. 2 and Fig. 1)

Maritime Antarctic region

Monthly mean temperatures are usually sub-zero, but exceed 0°C for at least one month each summer, are never greater than +4°C and never lower than -20°C. Some of the precipitation in summer falls as rain. Bryophyte vegetation covers large areas of the lowlands; two angiosperm species - *Deschampsia antarctica* and *Colobanthus quitensis* occur infrequently.

Examples: Islands of the Scotia Ridge, Palmer Archipelago and the west coast of the Antarctic Peninsula (Fig. 2).

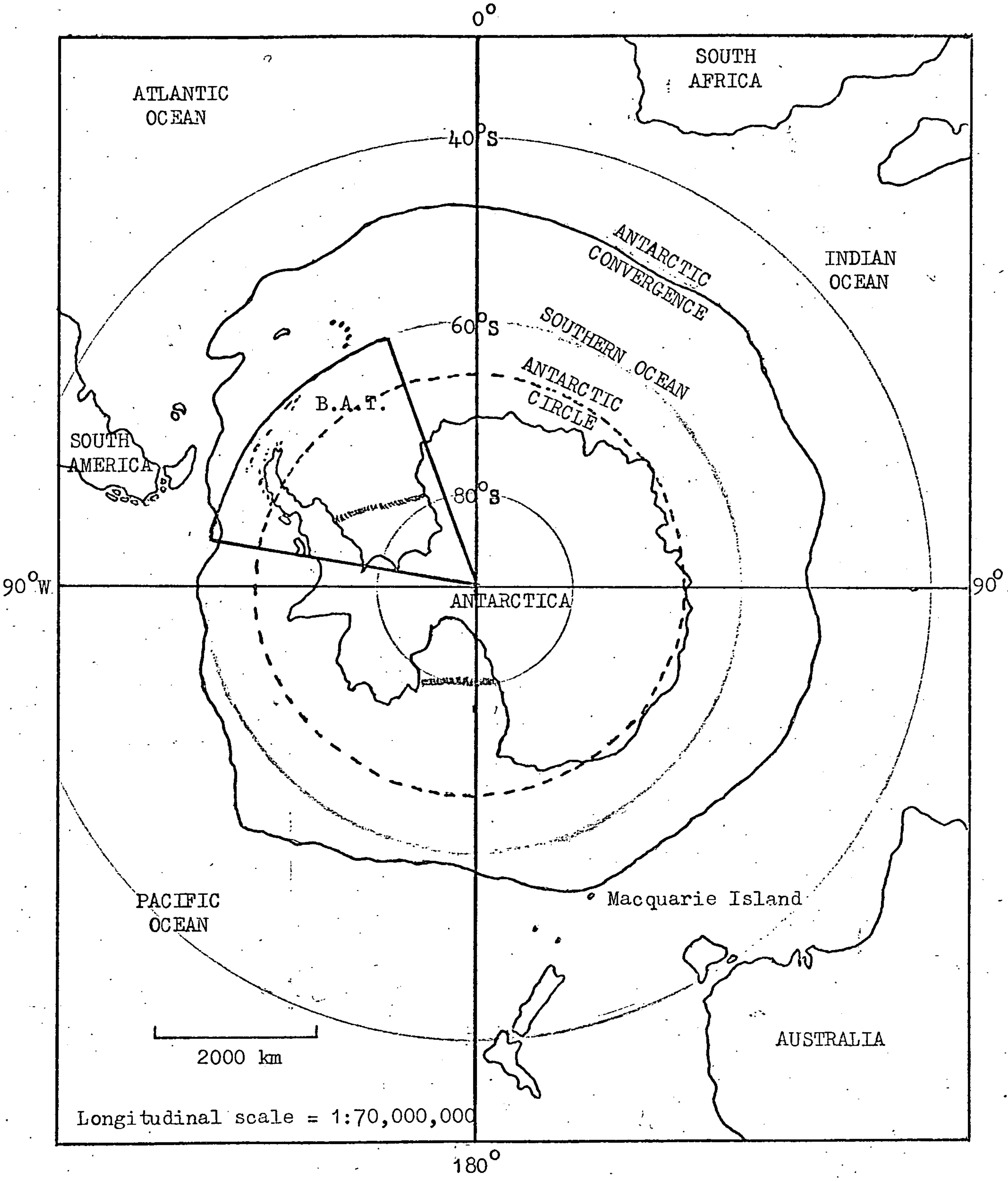


Fig. 1: Sketch map showing Antarctica in relation to the southern continents (after Deacon, 1964)

B.A.T. = BRITISH ANTARCTIC TERRITORY

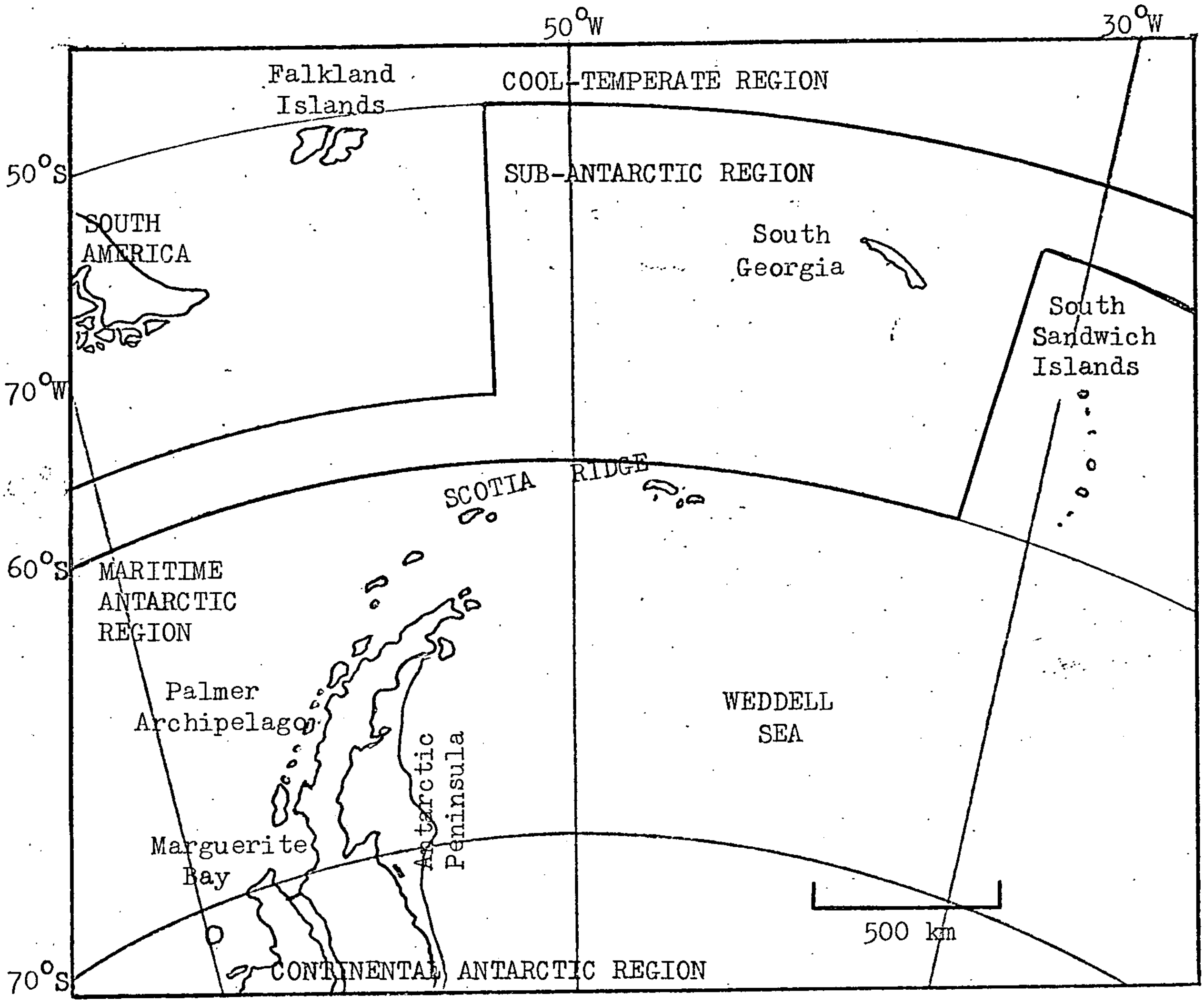


Fig. 2: Sketch map of the Antarctic Peninsula - Scotia Ridge sector of Antarctica, showing division into regions (after Longton, 1967) Longitudinal scale = 1:20,000,000

Continental Antarctic region

Monthly mean temperatures never exceed 0°C; they are frequently below -20°C in winter. Vegetation is absent or very sparse - occasional mosses and lichens on isolated snow-free rocky outcrops.

The studies reported in this thesis were made on material obtained from the following island groups within the maritime Antarctic region:

South Orkney Islands	60° 40° S; 45° 40' W.
South Shetland Islands	61° to 63° S; 55° to 60° W.
Argentine Islands	65° 15' S; 64° 17' W.
Islands in Marguerite Bay	67° to 68° S; 67° to 69° W.

GEOLOGY AND TOPOGRAPHY

Geomorphologically these islands are a continuation of the Andean cordillera. The Antarctic Peninsula forms the Antarctandean Ridge (Harrington, 1965) which is linked to South America by the Scotia Ridge from which rise South Georgia and the South Sandwhich, South Orkney and South Shetland Islands. The geology of the Antarctic Peninsula and associated islands is dominated by igneous rocks of the Andean Granite-Gabbro Intrusive Suite (Harrington, 1965); the South Orkney and eastern South Shetland Islands are dominated by a petrographically distinct sequence of quartz-mica-schists (Thomson, 1968).

All the islands, except the smallest islets are mountainous with highly indented coastlines. High ground is extensively covered with snow and ice which extend to the coast as glaciers. The cover of permanent snow is interrupted by rocky peninsulas and cliffs around the coast, and by nunataks inland, which are snow free for at least two months each summer. Plates 1 and 2, taken from Signy Island when looking towards Coronation Island in the South Orkneys, show characteristic scenery in summer and winter. In some areas there are extensive

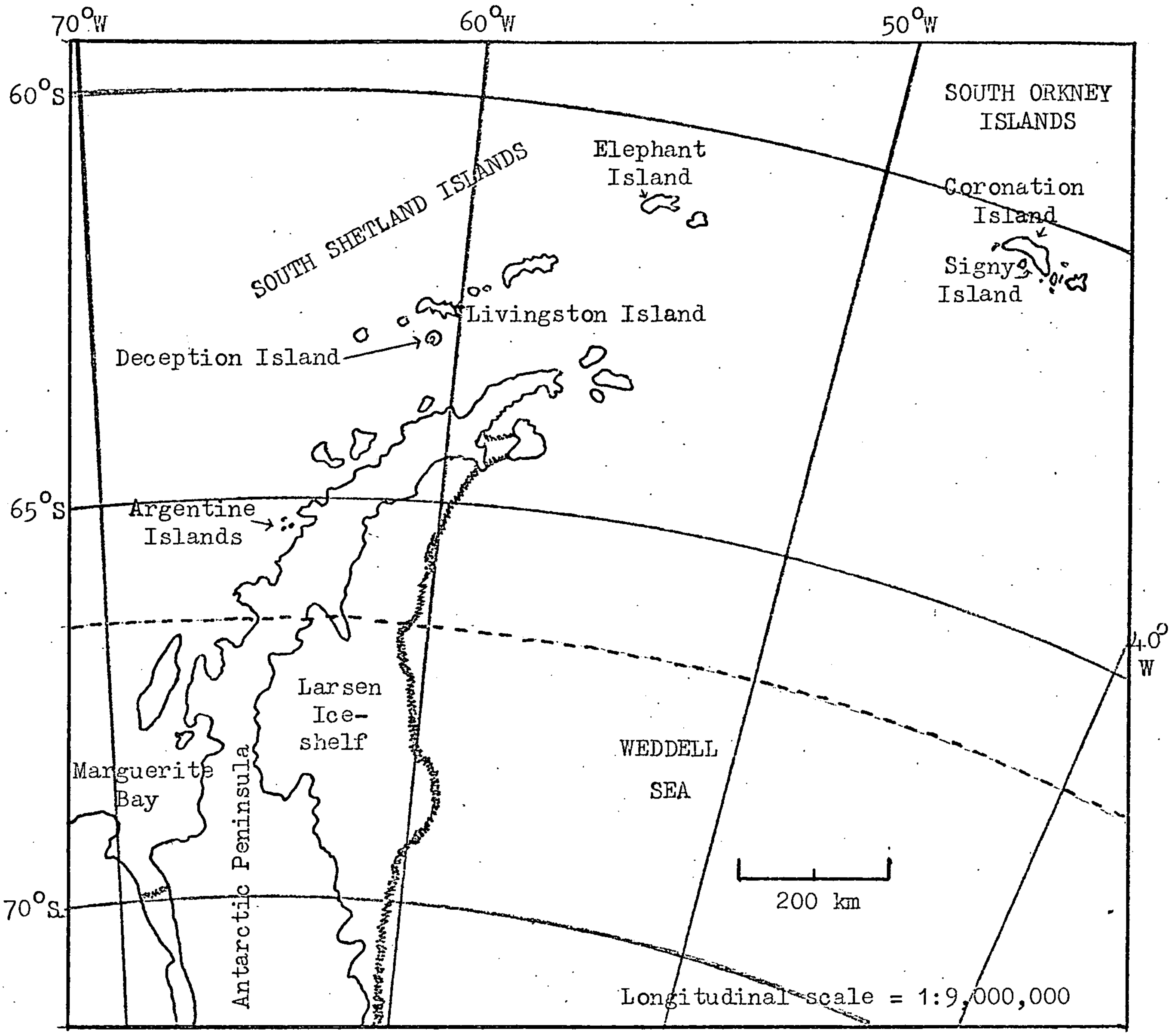


Fig. 3: Sketch map of the Antarctic Peninsula and island groups in the maritime Antarctic (after D.O.S., 1964, 10,000/1/04/489/SPC)

Plate I. Summer scenery in the South Orkney Islands: Coronation Island viewed from Signy Island, January 1969

Plate 2. Winter scenery in the South Orkney Islands: Coronation Island viewed from Signy Island, August 1970

coastal lowlands with inland valleys bounded by scree slopes which are also clear of snow in summer. Plate 3 shows an area of this kind on the east coast of Signy Island.

CLIMATE

Islands in the maritime Antarctic experience an oceanic climate regime, dominated by the prevailing westerly airflow and with relatively small annual variations in temperature compared with the continent. At least one month each summer has a mean air temperature greater than 0^{o}C., while summer ground temperatures may rise to $+15^{o}$C. or more (Longton and Holdgate, 1967). The seas are usually ice-free in summer, but are blocked some years by heavy pack-ice. Ice-bergs are always present. Most precipitation throughout the year is in the form of snow; there is some rain in summer. The coldest months of the year are June to September when monthly means around -10^{o}C. are usual. Sea-ice is often present between May and October, but it may be broken up by gales.

A summary of meteorological observations in the region are shown in Table 1. These are abstracted from Pepper (1954), the Annual Meteorological Tables published by the British Antarctic Meteorological Service (1951-1963) and Tables of Temperature, Relative Humidity and Precipitation for the World, Part II, published by H.M.S.O. (Met. O.61.7b). The figures for Signy Island are supplemented from base records and the author's original observations. The figures for Elephant Island are obtained from the observations made by the Combined Services' Expedition there, 1970-71 (R.M.G. O'Brien, personal communication).

HABITATS OF THE TERRESTRIAL FAUNA

Ground which is free of snow in summer is potentially available for colonisation by living organisms. Exposed surfaces vary considerably and include bare rock faces, scree slopes, glacial clays, open and closed

Plate 3. Topography of Signy Island: Snow-free hills and valleys on the east coast, January 1971

TABLE 1: SUMMARY OF DATA FROM METEOROLOGICAL STATIONS ON ISLANDS OF THE SCOTIA RIDGE AND OFF THE WEST COAST OF THE ANTARCTIC PENINSULA

	SIGNY ISLAND	ELEPHANT ISLAND	DECEPTION ISLAND	ARGENTINE ISLANDS	MARGUERITE BAY
Period of observations	1948-1970	Dec. 1970-March 1971	1951-1964	1951-1964	1946-1949
TEMPERATURE (°C):					
Monthly mean (January)	+0.8	-0.2	+1.6	+0.5	+0.7
Monthly mean (July)	-9.9	...	-9.4	-13.8	-16.4
Overall mean	-3.6	...	-3.2	-5.4	-7.6
Extremes					
Mean highest summer maximum	+8.6	...	+7.8	+6.3	+6.7
Mean lowest winter minimum	-29.7	...	-19.7	-30.3	-37.5
Overall highest summer maximum	+13.9	+15.0	+11.1	+11.7	+7.8
Overall lowest winter minimum	-34.4	...	-27.8	-43.3	-39.4
WIND SPEED (knots): Mean	14.3	10.9	13.4	7.7	8.3
PREVAILING WIND DIRECTIONS:	W/NW, SE	W	ENE, W	N/NE, S	E/SE
SUNSHINE (hours): Mean per day	1.5	...	1.7	2.1	...
OVERCAST DAYS (frequency):	71%	(mean cloud cover = 7 oktas)	67%	65%	52%

stands of vegetation, and areas habitually occupied by marine birds or mammals. A classification of vegetation types in the maritime Antarctic was proposed by Longton (1967); this was subsequently elaborated by Gimingham and Smith (1970). Following a survey of soils on Signy Island in 1962 (Holdgate _et al._, 1967), a classification of soil types was proposed by Allen and Heal (1970). Consideration of the data in these publications together with the author's original observations led to the construction of a classification of terrestrial habitats in the maritime Antarctic was a framework for the studies on protozoa described in Chapter II. This classification is presented below with photographic illustrations taken from Signy Island.

NON-VEGETATED HABITATS

These are areas which are potentially available for colonisation by plant life; they are without vegetation either because they have been released from permanent snow cover for too short a time, or because the substrate is too unstable - owing to continual weathering and erosion or as a result of agitation by marine birds or mammals.

1. _Glacier moraines and mineral debris_ (Plate 4)

Raw mineral material occurs as glacier moraines or as debris from weathered outcrops of rock. Particle sizes vary from coarse gravel to fine clay. The material is frequently base-rich and, where the parent material is quartz-mica-schist or marble (as on Signy Island and Elephant Island), it has a pH of 6.5 - 7.0. It has a very low organic content (loss on ignition = 2% or less), but it does contain a sparse microflora and protozoan fauna.

2. _Volcanic ash_

Most of the rock types in the maritime Antarctic are pre-cambian metamorphics or early Tertiary intrusives. However recent volcanic ash occurs on Deception Island, South Shetland Islands (Fig. 3), where there have been three pyroclastic eruptions since 1967 (Baker _et al._, 1969, 1971). The pyroclastic materials vary

Plate 4. Lateral moraine of the Orwell Glacier, Signy Island, January 1969

from large bombs, through cinders, to fine ash and dust, and consist largely of dark scoriaceous glass. Deposited ash, although it has a barely detectable organic content (loss on ignition = 0.04% or less) has become colonised by some microorganisms where it has stabilised. It has a pH of c. 6.5. In areas influenced by fumaroles some colonisation of the ash by a moss species of the Funariaceae family has occurred (Collins, 1969), providing a habitat for a more diverse, but still very sparse, microfauna.

3. Penguin Guano (Plate 5)

Three penguin species of the genus Pygoscelis - P. antarctica (chinstrap), P. adeliae (Adelie) and P. papua (gentoo) - breed in the maritime Antarctic in numbers large enough to produce extensive deposits of guano in their breeding colonies. The guano is a brown reducing mud, alkaline (pH = 6.5-8.2), containing nitrogen phosphorus and potassium in high concentrations. The trampling and nest building activities of the penguins result in the guano becoming mixed with underlying mineral material. It has a loss on ignition of 30-45% and is inhabited by a restricted microflora and fauna of protozoa and nematodes. Detailed studies upon this habitat are reported in Chapter IV.

Similar accumulations of guano are found around the nesting colonies of blue-eyed shags (Phalacrocorax atriceps).

4. Elephant Seal Wallow Grounds (Plate 6)

Elephant seals (Mirounga leonina) moult ashore in "wallow grounds", wherein compacted hair, excrement and faeces form a black reducing mud with physical and chemical properties similar to those of penguin guano - the concentration of ammonium-nitrogen being particularly high. Its fauna is very similar to that of

Plate 5. Breeding colony of chinstrap penguins on Signy Island, December 1969

Plate 6. Elephant seal wallows on Signy Island, January 1969

penguin guano.

VEGETATED HABITATS

These are areas where vegetation in macroscopic quantities has become established, providing habitats for a diverse terrestrial fauna. Two formations can be readily identified: one in which only algae and bryophytes occur; the other has grasses and herbs. The major vegetation sub-formations which occupy extensive areas are listed below.

A. ANTARCTIC CRYPTOGAM FORMATION - Four sub-formations

1. Thallose alga (Plate 7)

Those penguin guano deposits and elephant seal wallow grounds which are not physically agitated, and other nutrient-rich areas subject to heavy contamination by sea-birds, become colonised by the green alga *Prasiola crispa* which forms extensive thallose mats (up to 70% cover over several hundred sq m). The material under *Prasiola* has a pH of 5.5 - 6.0 - lower than that of uncolonised penguin guano. It has a higher organic content (loss on ignition = 50-65%) and contains a richer fauna. The influence of *Prasiola* colonisation upon the protozoan fauna and upon the physical and chemical properties of penguin guano is discussed in detail in Chapter IV.

2. Moss cushions (Plate 8)

The mosses *Andreaea sp.* and *Grimmia sp.* grow directly upon glacier moraines, scree slopes and bare rock faces in the form of small cushions or mats. They accumulate little organic matter beneath them (loss on ignition = c. 7%) and the basic nature of the substrate is not greatly altered (pH = 6.0-7.0). The cushions do however provide a habitat for a diverse fauna including protozoa, nematodes and arthropods.

Plate 7. Thallose mat of alga Prasiola crispa which has colonised an area which was apparently once an elephant seal wallows, Signy Island, January 1969

Plate 8. Moss cushions Andreaea sp. colonising a glacial moraine, Signy Island, January 1969

3. Moss turf peat (Plate 9)

Polytrichum alpestre and Chorisodontium aciphyllum are tall turf-forming mosses. Stands of these species consist of densely packed, erect, sparingly branched shoots and may cover considerable areas - several thousand sq. m. Moss shoot remains overlie compact fibrous peat which builds up into peat banks (exceptionally up to 3 m. deep) with little compression. The fibres do not degenerate into the amorphous peats common in temperate blanket bogs. The peat is acid (pH 3.0-4.5), almost entirely organic (loss on ignition = 93-98%) and usually moist (moisture = 300 - 800% dry weight). It is a habitat for a diverse fauna of protozoa (particularly testacida), nematodes, rotifers, tardigrades and arthropods. The ecology of testacida in moss turf peat on Signy Island is discussed in detail in Chapter III.

4. Moss carpet peat (Plate 10)

The pleurocarpous mosses Brachythecium sp., Calliergon sp. and Drepanocladus uncinatus form spongy carpets, usually in wetter and less stable areas than the turf-forming species, which overlie a layer of peat a few cm. thick. Carpets may be formed of any one, two or all three species, and like the turf-forming species may cover considerable areas. Carpet peat is less acid than turf peat, having a pH of 4.0-5.5 and may contain some mineral matter (loss on ignition = 50-90%). It is frequently very wet (moisture = 500-1000% or more). It contains the same faunal group as turf peat.

B. ANTARCTIC PHANEROGAM FORMATION

Grass soil (Plate 11)

The grass Deschampsia antarctica, often in association with the

Plate 9. Moss turf Polytrichum-Chorisodontium, Signy Island, January 1969

Plate IO. Moss carpet <u>Drepanocladus uncinatus</u>, Signy Island, February I97I

Plate 11. Profile of the soil under grass Deschampsia antarctica, Signy Island, January 1969. The white marker is 15 cm long.

small cushion-forming herb Colobanthus crassifolius, grows in small patches (usually less than 10 m across) on sheltered north-facing slopes. The sites are usually flushed and enriched by sea-birds. A dark loam-like soil is developed below the grass swards, which has a much greater degree of microbial activity and greater mineral nutrient availability than the moss peats. Its structure is similar to that of temperate brown earths, with an intimate mixture of mineral and organic material. The amount of organic matter is variable (loss on ignition = 20-75%) and the soil is fairly acid (pH = 4.5-5.5.) It contains the same faunal groups as the moss peats but usually in greater numbers.

It is apparent that, despite severe climatic conditions, a considerable diversity of terrestrial habitats exists in the maritime Antarctic, supporting a diverse fauna. An abundance of life is favoured by a supply of mineral nutrients from the base-rich parent rocks, from sea spray carried inland and from the activities of breeding sea-birds. Further direct radiant heating of the ground produces microclimates more favourable to living organisms than the ambient temperatures suggest. The temperature regime of a moss turf peat on Signy Island is discussed in detail in Chapter III.

The maritime Antarctic has an abundant microflora of bacteria, algae, yeasts and fungi and a fauna of protozoa, rotifers, tardigrades, nematodes, collembola and acari (Tilbrook, 1967). Enchytraeid oligochaetes are present but rare (Holdgate et al., 1967). Lumbricid oligochaetes and myriapods - the animals chiefly responsible for soil mixing in temperate regions - are absent and mature soils are not developed.

CHAPTER II

SURVEY OF THE PROTOZOAN FAUNA

REVIEW OF LITERATURE

Protozoa belonging to four groups are commonly found in soils and other terrestrial habitats (Sandon, 1927, for example):

Mastigophora

Rhizopoda: Amoebida

Rhizopoda: Testacida.

Ciliata.

Since 1911 species in each of these groups have been reported from some part of the Antarctic, but none is specific to the Antarctic. The records to date, which are summarized in Table 2, are incomplete as descriptions of the total protozoan fauna; frequently samples were examined for Testacida only, and not all the possible habitats in any one locality were investigated. The most comprehensive list of species is that of Sudzuki (1964); however many of his identifications were uncertain and much of his list must be regarded as doubtful. Few publications give estimates of numbers of protozoa or attempt to relate the distribution of species to environmental conditions. However the records are ample evidence that the Antarctic is far from devoid of protozoa and, as pointed out by Penard (1913) and Heal (1965), the species diversity of Testacida in the richest habitats in the maritime Antarctic localities is only slightly less than in northern temperate mosses and moorland soils.

Quantitative data on protozoa were given by Heal (1965) who reported a count of $40 \pm 7 \times 10^3$ testacida per g dry weight, or $890 \pm 150 \times 10^6$ per m^2, in the 0-8 cm horizon of grass soil on Signy Island, South Orkney Islands; these figures do not differ significantly from those obtained for temperate samples. A surprising result was Heal's

TABLE 2: SUMMARY OF PUBLISHED RECORDS OF TERRESTRIAL PROTOZOA IN THE ANTARCTIC

LOCATION	Latitude	Longitude	HABITAT	PROTOZOAN TAXON	NUMBER OF SPECIES RECORDED	AUTHORITY
** Ross Island	77°33' S	166°09' E	Lake moss	Mastigophora	3	Murray (1910)
				Rhizopoda	3	
				Ciliata	9	
** Ross Island	77°33' S	166°09' E	Moss, moraine, sediment	Testacida	13	Penard (1911)
* South Shetland Islands, Antarctic Peninsula	62°-70° S	57°-76°W	Moss and sediment	Testacida	21	Penard (1913)
* Elephant Island	61°10' S	55°14' W	Moraine	Mastigophora	5	Sandon and Cutler (1924)
				Rhizopoda	3	
** Terre Adelie	67° S	141° E	Moss	Testacida	1	Decloitre (1960)
** Terre Adelie	67° S	141° E	*Prasiola*	Testacida	7	Decloitre (1964)
** Langhovde	69°13' S	39°45' W	Moss water	Mastigophora	9 (all uncertain)	Sudzuki (1964)
				Rhizopoda	35 (9 uncertain)	
				Ciliata	24 (17 uncertain)	
* Signy Island, South Orkney Islands	60°43' S	45°36' W	Grass soil	Testacida	18	Heal (1965)
			Mosses	Testacida	7	
			Marble debris	Testacida	4	
** Ross Island	77°33' S	166°09' E	Soil and meltwater	Mastigophora	3	Dillon (1967), Dillon *et al*, (1968)
				Rhizopoda	6	
				Ciliata	16	

* Maritime Antarctic region
** Continental Antarctic region

observation that a single species of testate Corythion dubium Taranek constituted 72% of all testates observed in his samples of grass soil; single species dominance being a feature not recorded in temperate soil.

THE PRESENT STUDY

The aim of the present study was to make, as far as practicable, a comprehensive survey of the protozoan fauna of Signy Island; the survey to be extended to the rest of the South Orkney Islands and other island groups in the maritime Antarctic as opportunity permitted.

To sample the total snow-free ground on even a small island like Signy (7.2 x 5.0 km), and subsequently analyse for protozoa, was quite impossible. In order, therefore, to achieve as comprehensive a survey as possible in the time available, it was decided to concentrate effort on 13 sites widely distributed through the Island. These covered the complete range of terrestrial habitats listed in Chapter I (except volcanic ash), and a series of samples was obtained which, it was hoped, were representative of the whole of the island. Samples taken from these sites were analysed for protozoa in the laboratory at the Base, Factory Cove, Signy Island, in order to obtain species lists for the sites. It was hoped that the results would show some pattern whereby species distribution could be related to habitat factors.

Samples from islands other than Signy Island were collected as opportunities arose. Frequently it was impossible for the author to take samples himself; in these cases instructions were lodged with the Captains of the British Antarctic Survey ships, and personnel on board were requested to collect samples when practicable. Inevitably these collections were less comprehensive than those made on Signy Island, but were sufficient to demonstrate the variety of habitats and species composition of the protozoan faunas throughout the maritime Antarctic.

FIELD METHODS

From each of 13 sites selected for study, material was taken from to 0-5 cm horizon, there being six randomly selected sub-sampling points at each site. Moss peats and grass soil were sampled using a steel corer (2.5 cm diameter) with a toothed cutting edge. Other materials like penguin guano and moraine clays were sampled with a trowel. Extracted material was carried for laboratory examination in sealed polythene containers. Precautions were taken to avoid contamination of samples during extraction and transport.

The following sampling instructions were provided for Survey personnel:

"On any island where it is possible to make collections, select (as available and convenient) a site of each of the following types:

1. Moss turf peat (Polytrichum-Chorisodontium)
2. Moss carpet peat (Brachythecium-Calliergon-Drepanocladus)
3. Grass
4. Clay of glacier moraines
5. Guano of penguin colonies

"Sample material from six random points within each site. Take material from the 0-5 cm layer. Label each sample with date and precise location.

"A sterile trowel for sampling is provided. Take samples from virgin untrodden ground and clean the trowel as thoroughly as possible between taking one sample and the next (this is to avoid contamination of one sample with material properly belonging to the one before). A rinse in boiling water when possible is a good idea.

"Store collected samples between 0^{o} and 4^{o}C, completely sealed in polythene bags. Outside deck temperatures are suitable while the ship is south of Port Stanley."

As an introduction, personnel requested to do collecting were shown examples on Signy Island of what was meant by "moss turf" and "moss carpet".

In addition to the 13 samples taken on Signy Island, the author was able to collect a further 16 samples from other islands in the South Orkney group, while other collectors obtained 39 samples from the South Shetland Islands, Argentine Islands and islands in Marguerite Bay.

LABORATORY METHODS: A. ANALYSIS OF SAMPLES FOR PROTOZOA

Information on the protozoan fauna of each set of six sub-samples was obtained by two laboratory procedures: culture methods (Singh, 1955) for flagellates, naked amoebae and ciliates; direct examination (Couteaux, 1967) for testate amoebae.

1. Cultures

Sterile petri dishes were used with 15 ml soil extract agar poured into each. The soil extract was prepared by soaking 250 g grass soil in 1 l cold tap water and immediately steaming for 2 hours. After cooling the supernatant was filtered and the filtrate gelled with 3% agar after adding 0.5% NaCl. Soil extract instead of nutrient agar was used so that the growth of bacteria, possibly toxic to protozoa, was not unduly favoured, while the growth of protozoa was encouraged (Stout, 1965). Aerobacter aerogenes (NCIB strain 418) was supplied as food for the protozoa because it is known to be an organism on which many protozoa thrive (Singh, 1946 and 1955). Aerobacter was cultured separately on a rich nutrient agar -

Beef extract	10 g	NaCl	5 g
Bacteriological peptone	6 g	Agar	15 g
Yeast extract	2 g	Distilled water	1 l -

and incubated at 25°C. After 3 days the bacterial culture was harvested with a glass spatula and spread over the surface of the soil extract agar. 2 g of each field sample were immediately inoculated onto the agar, moistened with sterile 0.5% NaCl and incubated at 12°C - a suitable temperature for both mesophilic and psychrophilic organisms (R.A. Herbert, personal communication). The petri-dish cultures (Plate 12) were examined for protozoa species after being incubated for 1,3,7,15 and 30 days; a final examination was made between the 50th and 60th days. Cultures were examined by placing drops (about 0.05 ml) of liquid from the plates upon glass slides and observing under the microscope by transmitted light and by phase contrast. Observations were normally made on fresh material. To aid recognition, the movement of motile cells was slowed down either physically, by adding a drop of 2% methyl cellulose, or chemically by adding a drop of 0.1% $NiSO_4$. In addition preparations were stained with Noland's stain/fixative (Noland, 1928) to make cilia and flagella more conspicuous. Species observed were identified morphologically and a species list was built up for each field site.

2. Direct examination

A small sub-sample of field material, about 0.25 g, was placed in Bouin's fixative for 24 hours. The fixative was removed by centrifugation (5 minutes at 1,500 rpm). The residue was then rinsed, suspended in distilled water and made up to 250 ml, so diluting the original material by a factor of 1000. After being stirred for two hours, 20 ml aliquots of the suspension were passed through 0.45 grade membrane filters. The filter bearing the previously suspended material

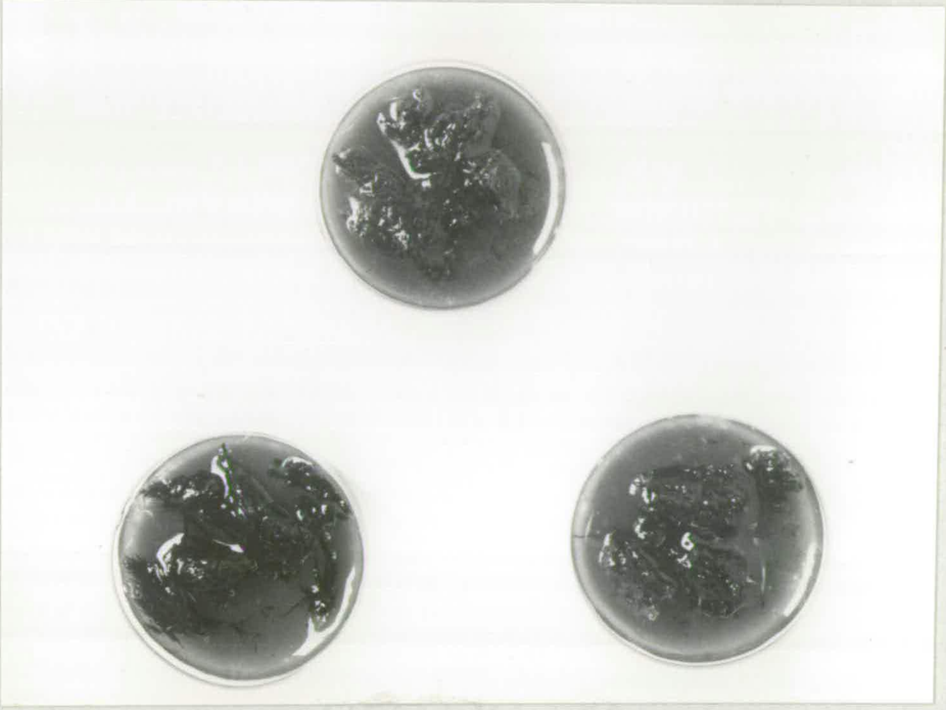


Plate I2. Petri-dish cultures with an inoculum of moss turf peat on a base of soil extract agar was air-dried at room temperature. Sections of the filter were placed on slides, cleared in xylene and mounted in Canada balsam. 6 replicate slides were made for each site. This treatment destroyed cytoplasmic structures, but the siliceous or chitinous tests of testate amoeba remained intact, so allowing microscopic identification.

LABORATORY METHODS B. MEASUREMENTS OF PHYSICAL AND CHEMICAL PROPERTIES OF SAMPLES

1. The pH of each field sample was measured as soon as possible after collection (with minimum wetting with distilled water where necessary) using a glass electrode and a pH meter.

2. Loss on ignition (per cent dry weight) - a crude estimate of organic content - was assessed by ashing oven-dry material in a muffle furnace at 450 - 500°C. Samples collected early in the survey were ignited to constant weight; later a period of 10 hours was adopted as the standard time.

3. Because the distribution of mosses on Signy Island is influenced to some extent by the nature of the bedrock (Allen, et al., 1967), it seemed possible that geology might be an ecologically relevant factor for the terrestrial fauna. Attempts were therefore made to ascertain the geology of the areas from the samples in the present survey were taken, either from the published literature or by personal communication with field geologists.

IDENTIFICATION OF PROTOZOA - POLICY ON TAXONOMY

The survey of protozoa described here was an essential preliminary to subsequent intensive ecological studies. While it was hoped that the survey would provide worthwhile biogeographical and distributional data

Amoebida

The naked amoebae which occur in terrestrial habitats are small species (usually less than 50μm) and are very difficult to identify. The taxonomic literature on this group is extremely confused. The life histories of many species are unknown; protozoa belonging to other groups sometimes possess an amoeboid stage; individual amoebae can show considerable changes in morphology from minute to minute. The manuals by Sandon (1927) and Kudo (1966) were found to be inadequate for the identification of this group. It was decided to employ the taxonomic scheme of Schaeffer (1926) which is based on the larger free-living amoebae. The advantage of this scheme is that it uses morphological patterns of the amoebae as they appear in 'normal' existence. Shaeffer did not provide for the identification of small amoebae, such as occur in terrestrial habitats, but studies by Bovee (1953), using phase contrast microscopy, showed that the scheme could be used for small species also. Using this scheme, the amoebae observed could be identified to genus level, though very few to species. The book by Jahn and Jahn (1949) was occasionally consulted.

Testacida

Testate amoebae are probably the best described group of protozoa in the published literature, because the species-specific features of their tests are more easily recognisable than the cytoplasmic features which characterise non-testate groups. The manuals by Sandon (1927), Kudo (1966) and Deflandre (1959) were used extensively for identification. Where more detail was required reference was made to monographs on particular genera (Deflandre, 1928 and 1937; Chardez, 1969) and to published species lists where descriptions of the species are given (Hoogenraad and Groot, 1948; Oye, 1956). The Penard Slide Collection at the British Museum

(Natural History) was consulted, and was a considerable aid to the identification of species.

Ciliata

Ciliates are usually large enough (30-120µm) for morphological features to be distinguished relatively easily. However they are difficult to observe because of the high motility of most ciliate species; killing them with a fixative often distorts cytoplasmic features so as to make them unrecogniseable; also there is frequently considerable individual variation within species. Cautious use of physical or chemical "slowing-down" agents usually enabled sufficient detail of ciliary arrangements to be observed to identify ciliates to genus level but in many instances it was not possible to identify species. Sandon (1927) was of limited value for identifying ciliates; Kudo (1966) and the large monograph by Kahl (1935) were used extensively. The illustrated key by Curds (1969) was useful for some species. The genus Vorticella was speciated following Noland and Finley (1931).

SITES INVESTIGATED

The 68 samples from which samples were analysed were distributed as follows:

South Orkney Islands (Figs. 4 and 5)	29 sites
Elephant Island (Fig. 6)	23 sites
Livingston Island (Fig. 7)	1 site
Deception Island (Fig. 8)	5 sites
Argentine Islands (Fig. 9)	4 sites
Islands in Marguerite Bay (Fig. 10)	6 sites

These sites with details of collection dates, ground cover, geology and sample properties are listed in Tables 3, 4 and 5.

TABLE 3: LIST OF SITES SAMPLED IN THE SOUTH ORKNEY ISLANDS

CODE	LOCATION OF SITE	DATE OF COLLECTION OF SAMPLES	NATURE OF SAMPLES	pH OF SAMPLES	% L.O.I. OF SAMPLES	GEOLOGY OF AREA IN WHICH SITE LOCATED
SO-MIN-1	Signy Island, Moraine of Orwell Glacier	7. 1.69	Moraine clay	6.8±0.4	c. 1.0	Q.M.S. (1)
SO-MIN-2	Signy Island, Marble Knolls	17. 2.69	Marble debris	6.9±0.2	c. 2.0	Marble (1)
SO-PG-1	Signy Island, North Point	11.12.68	Chinstrap penguin guano	7.4±0.2	39±5	Q.M.S. (1)
SO-PG-2	Signy Island, Spindrift Rocks	26. 3.71	Adelie penguin guano	7.6±0.3	48±5	Q.M.S. (1)
SO-PG-3	Signy Island, North Point	4. 4.71	Gentoo penguin guano	6.7±0.2	30±3	Q.M.S. (1)
SO-ShG-1	Signy Island, Shagnast Islet	1. 2.70	Shag guano	c. 8.2	-	Q.M.S. (1)
SO-ESW-1	Signy Island, Gourlay Peninsula	17. 1.69	Elephant seal wallows	7.0±0.2	c. 70	Q.M.S. (1)
SO-PRAS-1	Signy Island, Gourlay Peninsula	17. 1.69	*Prasiola*	5.6±0.7	c. 25	Q.M.S. (1)
SO-PRAS-2	Fredriksen Island	29. 3.70	*Prasiola*	5.7±0.4	57±8	Greywacke (Tilley, 1935)
SO-MCu-1	Signy Island, Moraine of Orwell Glacier	7. 1.69	Moss cushion *Andreaea*	6.4±0.2	c. 2.0	Q.M.S. (1)
SO-MCu-2	Signy Island, Marble Knolls	17. 2.69	Moss cushion *Grimmia*	6.8±0.3	c. 8.0	Marble (1)
SO-MTP-1	Signy Island, Rethval Point	11. 1.70	Moss turf peat	3.6±0.3	97±1	Q.M.S. (1)
SO-MCP-1	Coronation Island, Mansfield Point	9. 2.71	Moss carpet peat	5.5±0.2	78±4	Q.M.S. (2)
SO-MCP-2	Coronation Island, Meier Point	9. 2.71	Moss carpet peat	5.5±0.2	83±6	Q.M.S. (2)
SO-MCP-3	Gosling Island	9. 2.71	Moss carpet peat	5.1±0.3	84±2	Q.M.S. (2)
SO-MCP-4	Coronation Island, Return Point	10. 2.71	Moss carpet peat	4.5±0.3	56±6	Q.M.S. (2)
SO-MCP-5	Monroe Island	10. 2.71	Moss carpet peat	4.9±0.2	86±6	Q.M.S. (West, 1968)
SO-MCP-6	Matthews Island	11. 2.71	Moss carpet peat	5.1±0.4	81±18	Conglomerate (Thomson, 1971)
SO-MCP-7	Christoffersen Island	11. 2.71	Moss carpet peat	4.3±0.2	81±9	Conglomerate (Thomson, in press)
SO-MCP-8	Michelsen Island	11. 2.71	Moss carpet peat	4.0±0.5	72±7	Conglomerate (Thomson, in press)
SO-MCP-9	Laurie Island, Davis Point	12. 2.71	Moss carpet peat	4.5±0.2	87±2	Greywacke-Shale (3)
SO-MCP-10	Laurie Island, Valavielle Point	13. 2.71	Moss carpet peat	4.6±0.4	90±1	Greywacke-Shale (3)
SO-MCP-11	Laurie Island, Cape Geddes	13. 2.71	Moss carpet peat	4.4±0.3	87±2	Greywacke-Shale (3)
SO-MCP-12	Saddle Island, east end	14. 2.71	Moss carpet peat	6.0±0.4	85±4	Greywacke-Shale (3)
SO-MCP-13	Laurie Island, Cape Dundas	15. 2.71	Moss carpet peat	5.2±0.2	87±4	Greywacke-Shale (3)
SO-MCP-14	Coronation Island, Olivine Point	16. 2.71	Moss carpet peat	4.4±0.2	54±6	Q.M.S. (2)
SO-MCP-15	Fredriksen Island	29. 3.70	Moss carpet peat	4.5±0.1	84±4	Greywacke (Tilley, 1935)
SO-MCP-16	Signy Island, Clowes Moor	16. 3.71	Moss carpet peat	4.6±0.1	93±4	Q.M.S. (1)
SO-GS-1	Signy Island, below Observation Bluff	27. 1.69	Grass soil	4.6±0.2	77±6	Q.M.S. (1)

Abbreviations:
% L.O.I. Loss on ignition, per cent dry weight
Q.M.S. Quartz-mica-schist

Figures for pH and % L.O.I. are means ± 95% confidence limits

Geological authorities:
(1) Matthews and Maling (1967)
(2) Matthews (Personal communication)
(3) Dalziel (1971)

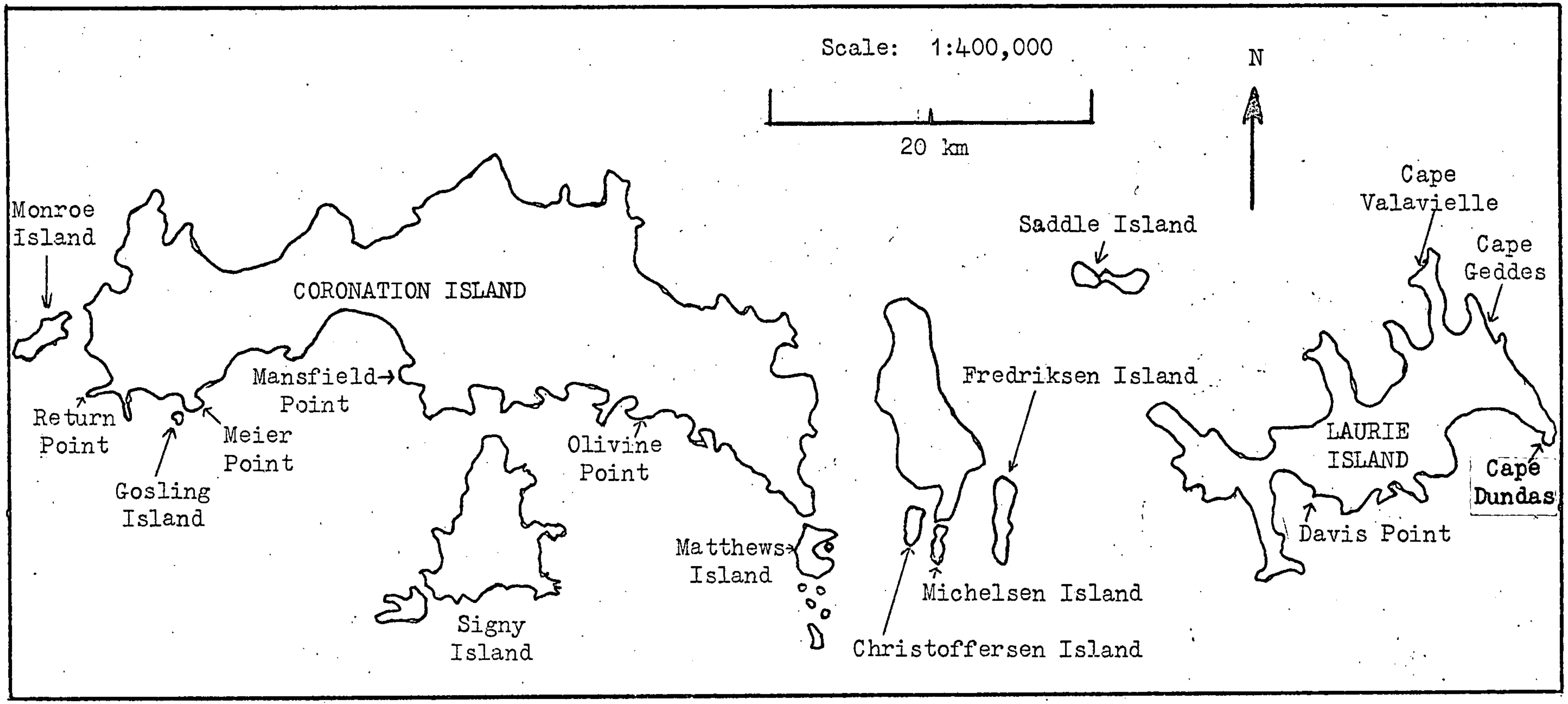


Fig. 4: Sketch map of the South Orkney Islands (after Admiralty Chart 1775)

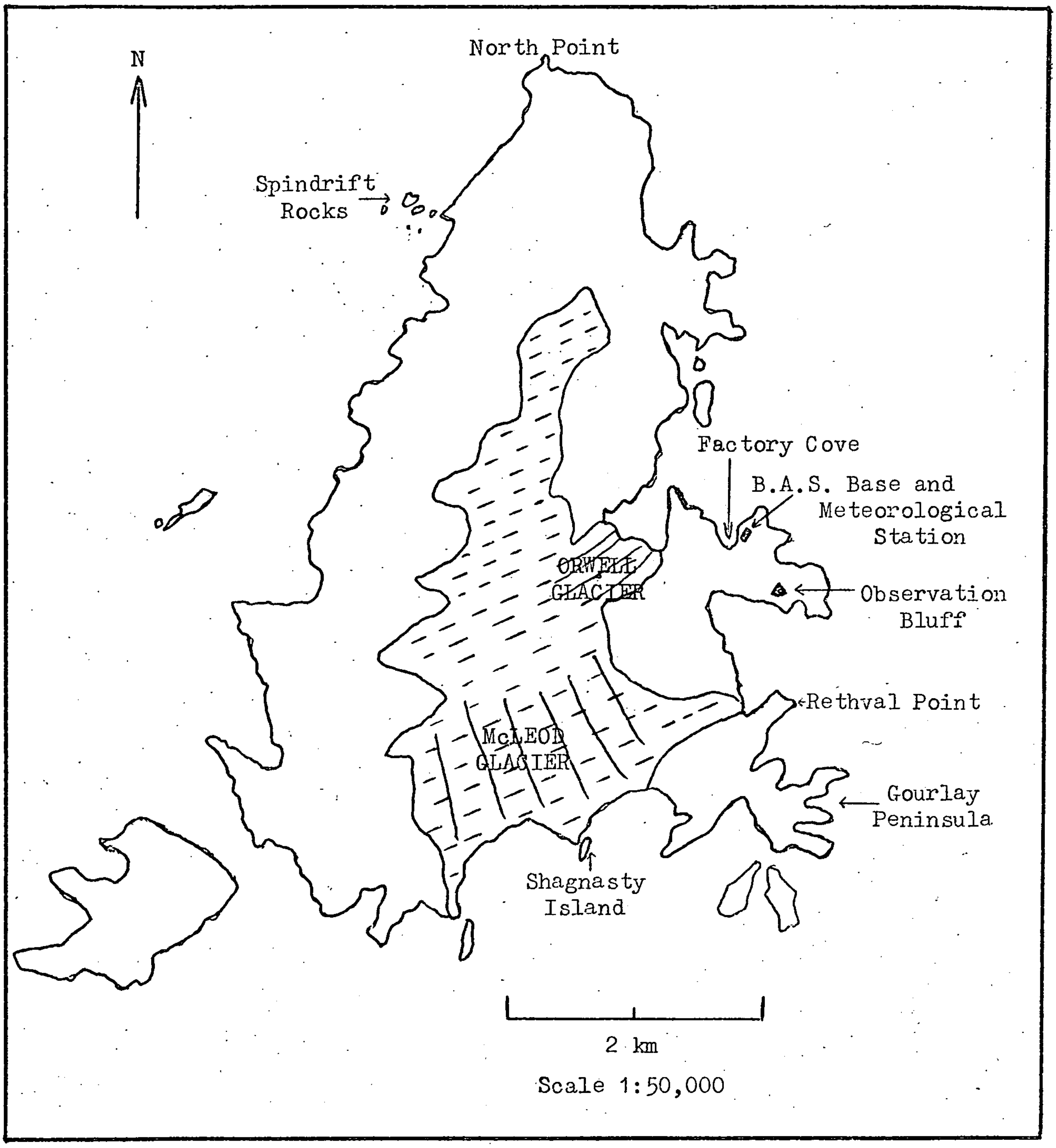


Fig. 5: Sketch map of Signy Island, South Orkney Islands (after D.O.S., map DCS (misc) 81d). The main areas of the ice-cap are indicated by stipple

B.A.S. = British Antarctic Survey

TABLE 4: LIST OF SITES SAMPLED ON ELEPHANT ISLAND, SOUTH SHETLAND ISLANDS

CODE	LOCATION OF SITE	DATE OF COLLECTION OF SAMPLES	NATURE OF SAMPLES	pH OF SAMPLES	% L.O.I. OF SAMPLES	GEOLOGY OF AREA IN WHICH SITE LOCATED	
E-MIN-1	Moraine of Endurance Glacier (chinstrap penguin moulting site)	13.3.71	Moraine clay	8.0±0.1	4.1±1.6	Q.M.S.	(4)
E-MIN-2	Moraine below Mount Elder	16.3.71	Moraine clay	7.1±0.1	1.5±0.2	Q.M.S.	(4)
E-MIN-3	Moraine below Mount Elder	16.3.71	Moraine clay	7.5±0.2	0.9±0.3	Q.M.S.	(4)
E-MIN-4	Moraine of Endurance Glacier	16.3.71	Moraine clay	7.0+0.6	1.6±0.6	Q.M.S.	(4)
E-MIN-5	Moraine of Endurance Glacier	16.3.71	Moraine clay	7.3±0.3	1.2±0.3	Q.M.S.	(4)
E-PG-1	Chinstrap penguin colony, south of Base Camp	13.3.71	Chinstrap penguin guano	6.8±0.1	49±2	Q.M.S.	(4)
E-PG-2	Chinstrap penguin colony near Base Camp	13.3.71	Chinstrap penguin guano	8.1±0.1	21±5	Q.M.S.	(4)
E-PG-3	Chinstrap penguin colony, south side of Endurance Glacier	13.3.71	Chinstrap penguin guano	8.2±0.1	23±2	Q.M.S.	(4)
E-PG-4	Chinstrap penguin colony, south of Base Camp	16.3.71	Chinstrap penguin guano	7.1±0.1	53±4	Q.M.S.	(4)
E-PG-5	Chinstrap penguin colony, south side of Endurance Glacier	16.3.71	Chinstrap penguin guano	8.2±0.1	39±2	Q.M.S.	(4)
E-MTP-1	"Chinstrap Camp"	25.2.71	Moss turf peat	4.5±0.3	58±11	Phyllite	(4)
E-MTP-2	South of Base Camp	18.3.71	Moss turf peat	5.9±0.2	47±8	Q.M.S.	(4)
E-MTP-3	South of Base Camp	18.3.71	Moss turf peat	5.4±0.1	42±5	Q.M.S.	(4)
E-MTP-4	Bluff above Base Camp	23.3.71	Moss turf peat	5.6±0.1	62±4	Q.M.S.	(4)
E-MCP-1	"Chinstrap Camp"	25.2.71	Moss carpet peat	5.0±0.2	68±4	Phyllite	(4)
E-MCP-2	Point Belsham	4.3.71	Moss carpet peat	4.9±0.1	36±5	Phyllite	(4)
E-MCP-3	South of Endurance Glacier	13.3.71	Moss carpet peat	3.9±0.1	40±5	Q.M.S	(4)
E-MCP-4	Stinker Point	21.1.71	Moss carpet peat	4.7±0.3	6±1	Q.M.S.	(4)
E-MCP-5	Bluff above Base Camp	23.3.71	Moss carpet peat	4.7±0.1	44±13	Q.M.S.	(4)
E-GS-1	South of Endurance Glacier	13.3.71	Grass soil	4.4±0.4	7±1	Q.M.S.	(4)
E-GS-2	South of Base Camp	18.3.71	Grass soil	4.8±0.2	30±8	Q.M.S.	(4)
E-GS-3	South of Base Camp	18.3.71	Grass soil	4.6±0.2	30±4	Q.M.S.	(4)
E-GS-4	Stinker Point	21.3.71	Grass soil	4.7±0.1	28±5	Q.M.S.	(4)

Abbreviations:		
	% L.O.I.	Loss on ignition per cent dry weight
	Q.M.S.	Quartz-mica-schist

Geological authority

(4): Roxburgh (1971)

Figures for pH and % L.O.I. are means ± 95% confidence limits

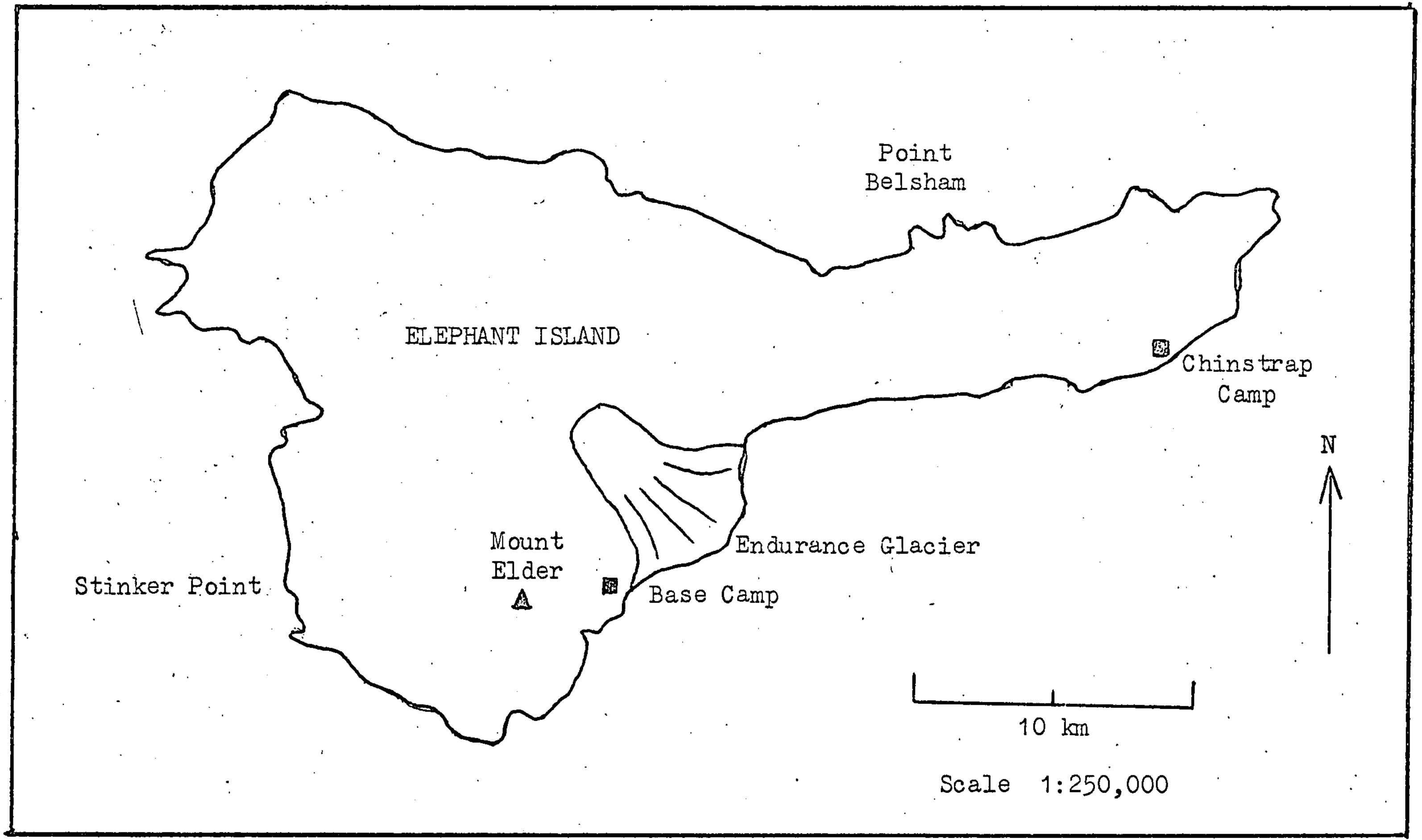


Fig. 6: Sketch map of Elephant Island, South Shetland Islands (after D.O.S. sheet W61 54, provisional issue, 1971)

TABLE 5: LIST OF SITES SAMPLED ON LIVINGSTON ISLAND, DECEPTION ISLAND, ARGENTINE ISLANDS AND ISLANDS IN MARGUERITE BAY

CODE	LOCATION OF SITE	DATE OF COLLECTION OF SAMPLES	NATURE OF SAMPLES	pH OF SAMPLES	% L.O.I. OF SAMPLES	GEOLOGY OF AREA IN WHICH SITE LOCATED
LIV-MCP-1	Livingston Island, Cape Sherrif	19. 2.71	Moss carpet peat	4.7±0.1	12±4	Basalt and sandstone (Hobbs, 1968)
D-VA-1	Deception Island, new island in Telefon Bay, northeast end	11.12.69	Volcanic ash, two years old	6.8±0.1	0.3±0.1	D.S.G. (5)
D-VA-2	Deception Island, new island in Telefon Bay, southwest end	11.12.69	Volcanic ash, two years old	6.5±0.2	0.3±0.1	D.S.G. (5)
D-VA-3	Deception Island, land centre of 1967 eruption	11.12.69	Volcanic ash, two years old, with moss (Collins, 1969)	5.5±0.5	2.1±0.5	D.S.G. (5)
D-VA-4	Deception Island, Cathedral Craggs	27.11.69	Volcanic ash, ten months old	6.3±0.2	0.04±0.01	D.S.G. (5)
D-VA-5	Deception Island, Collins Point	11.12.69	Volcanic ash, ten months old	c. 6.4	0.15±0.06	D.S.G. (5)
A-MTP-1	Argentine Islands, Galindez Island	21. 1.70	Moss turf peat	3.7±0.1	99±1	Porphyritic andesite (6)
A-MTP-2	Argentine Islands, Galindez Island	21. 1.70	Moss turf peat	4.0±0.2	98±1	Porphyritic andesite (6)
A-MCP-1	Argentine Islands, Galindez Island	21. 1.70	Moss carpet peat	4.3±0.1	94±1	Porphyritic andesite (6)
A-MCP-2	Argentine Islands, Galindez Island	21. 1.70	Moss carpet peat	3.9±0.1	88±2	Porphyritic andesite (6)
MB-MIN-1	Marguerite Bay, Pourquoi Pas Island	21. 2.70	Moraine clay	4.9±0.2	0.8±0.1	Diorite (7)
MB-PG-1	Marguerite Bay, Cone Island	23. 2.70	Adelie penguin guano	8.2±0.1	36±2	Andesite (Dewar, 1970)
MB-MTP-1	Marguerite Bay, Pouquoi Pas Island	21. 2.70	Moss turf peat	4.6±0.1	51±15	Diorite (7)
MB-MCP-1	Marguerite Bay, Pourquoi Pas Island	21. 2.70	Moss carpet peat	4.7±0.2	50±6	Diorite (7)
MB-MCP-2	Marguerite Bay, Avian Island	9. 2.70	Moss carpet peat	5.0±0.5	90±2	Quartz-feldspar tuff (Skinner, personal communication)
MB-MCP-3	Marguerite Bay, Cone Island	23. 2.70	Moss carpet peat	4.4±0.2	89±4	Andesite (Dewar, 1970)

Abbreviations:
% L.O.I. Loss on ignition, per cent dry weight
D.S.G. Dark scoriaceous glass

Figures for pH and % L.O.I. are means ± 95% confidence limits

Geological authorities:

(5): Baker, Davies and Roobol (1969)

(6): Elliot (1964)

(7): T.G. Davies (personal communication)

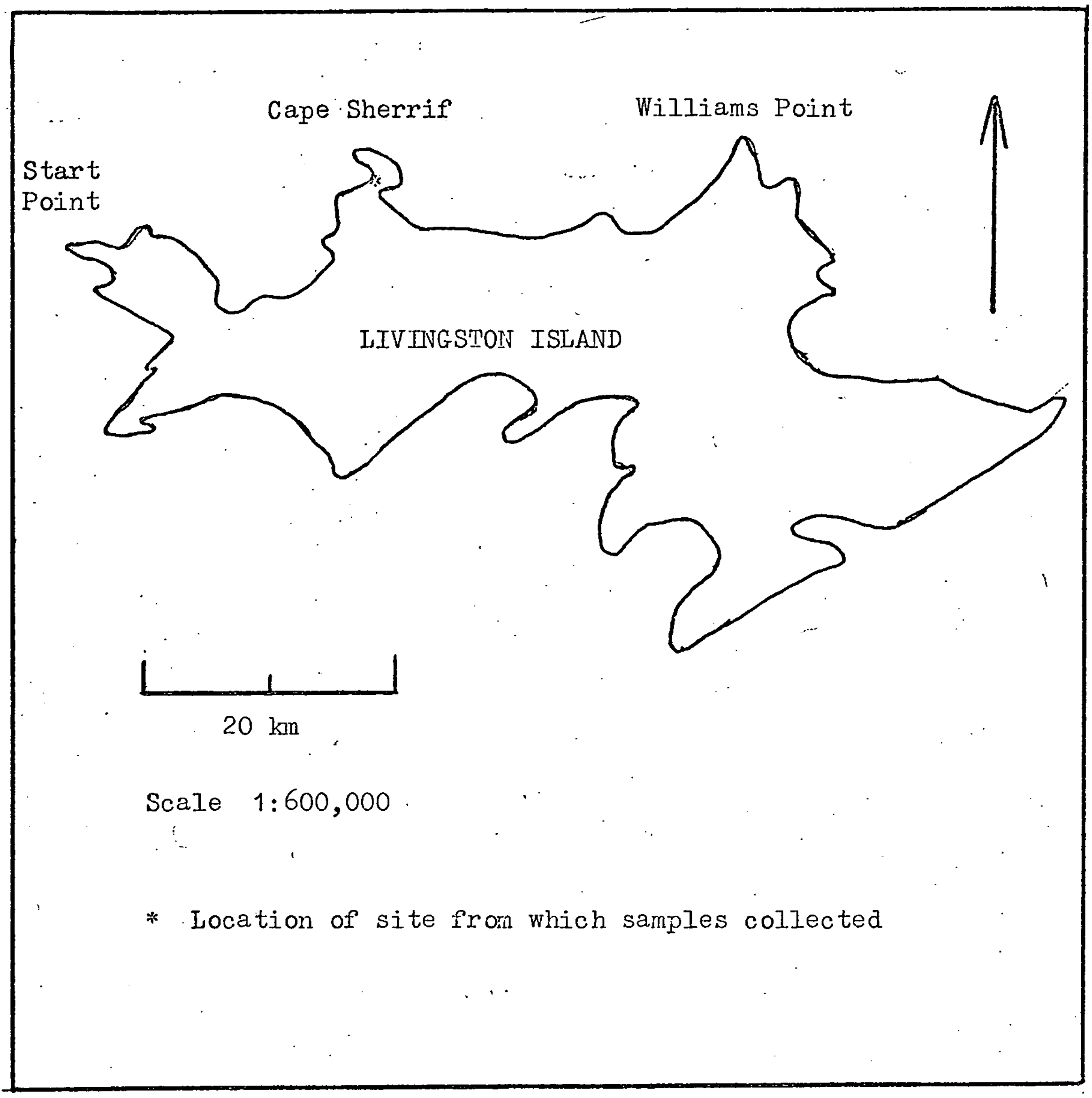


Fig. 7: Sketch map of Livingston Island, South Shetland Islands (after Hobbs, 1968)

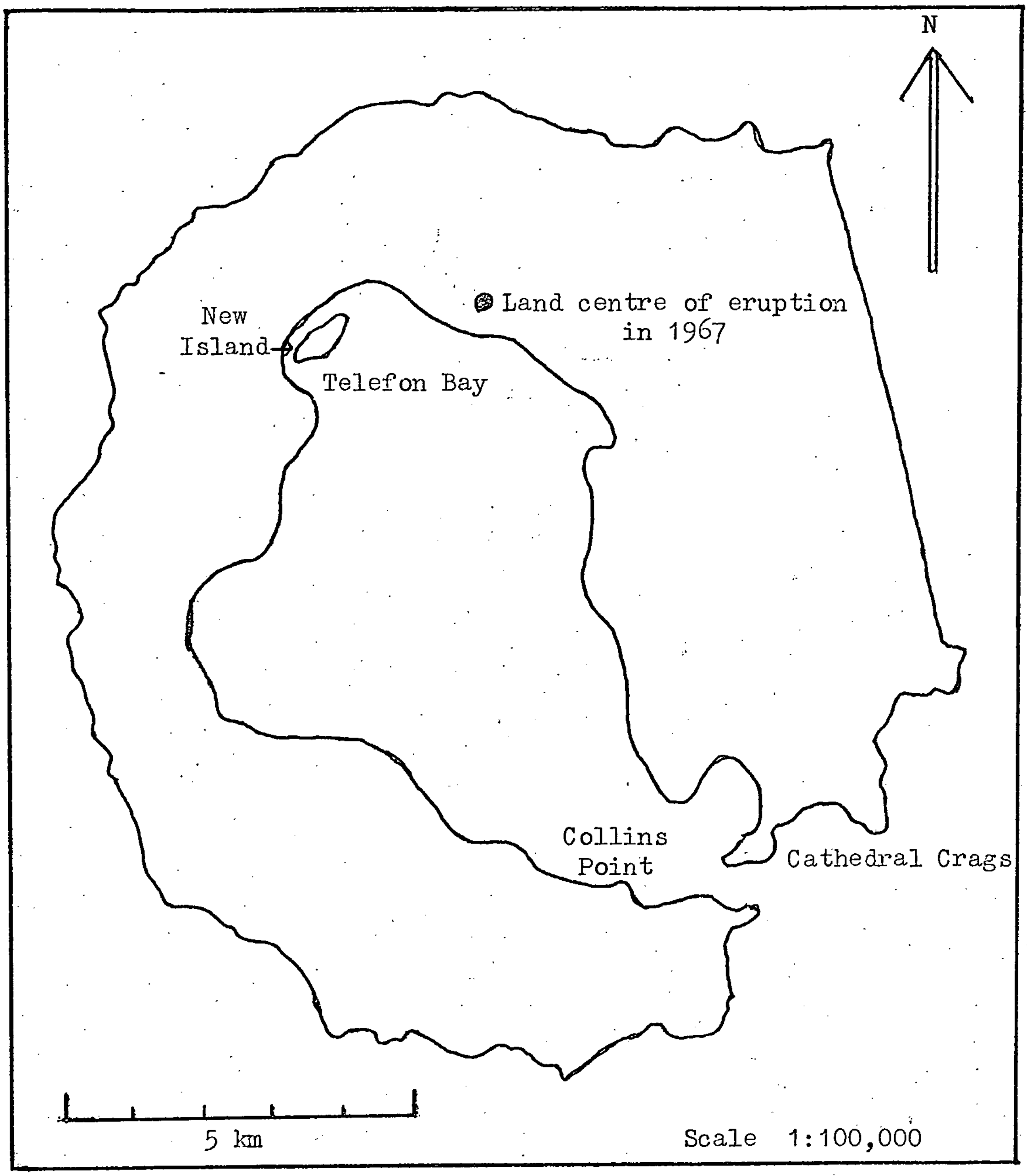


Fig. 8: Sketch map of Deception Island, South Shetland Islands, during 1968 (after Collins, 1969)

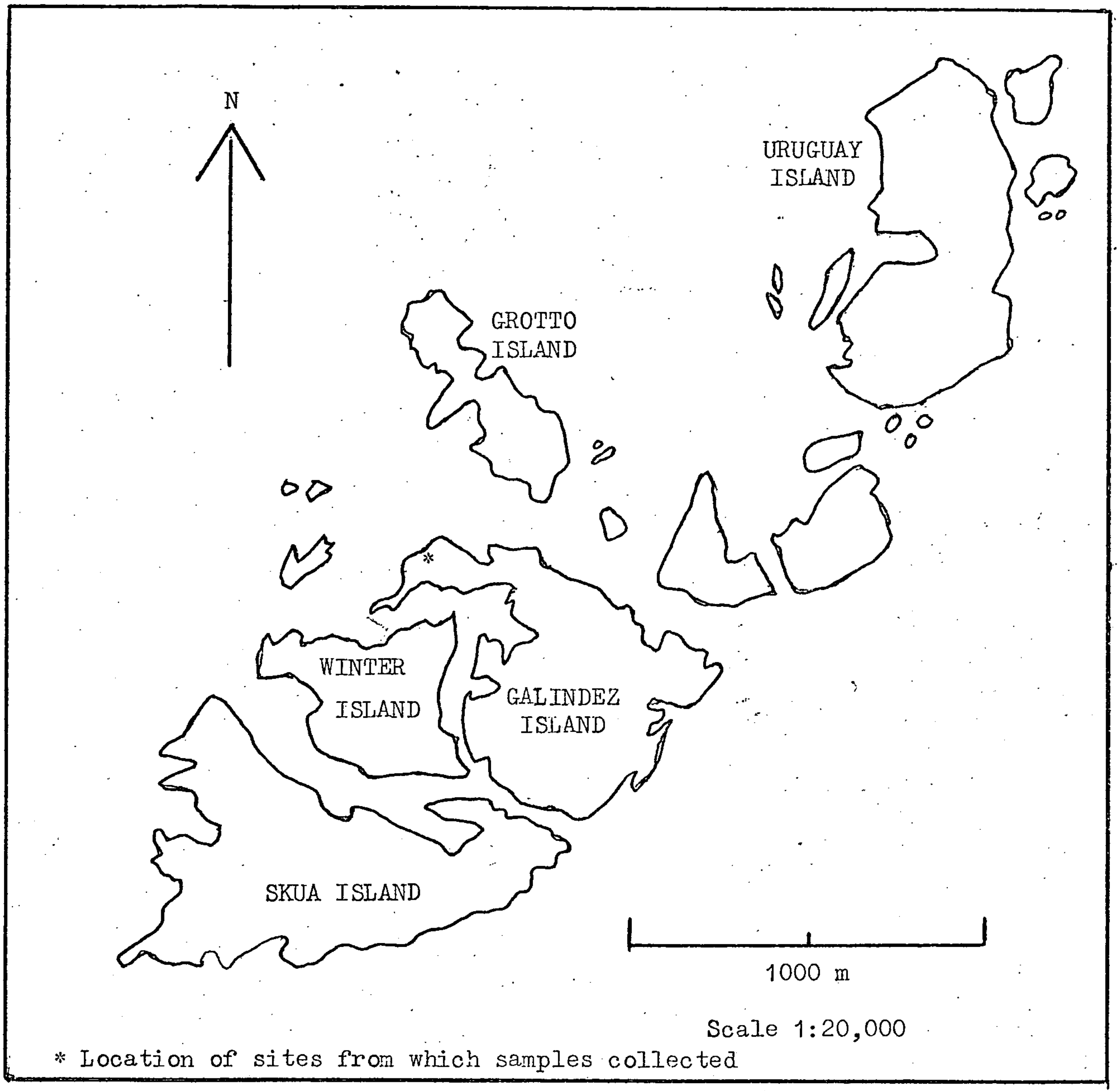


Fig. 9: Sketch map of Argentine Islands (after Elliot, 1964)

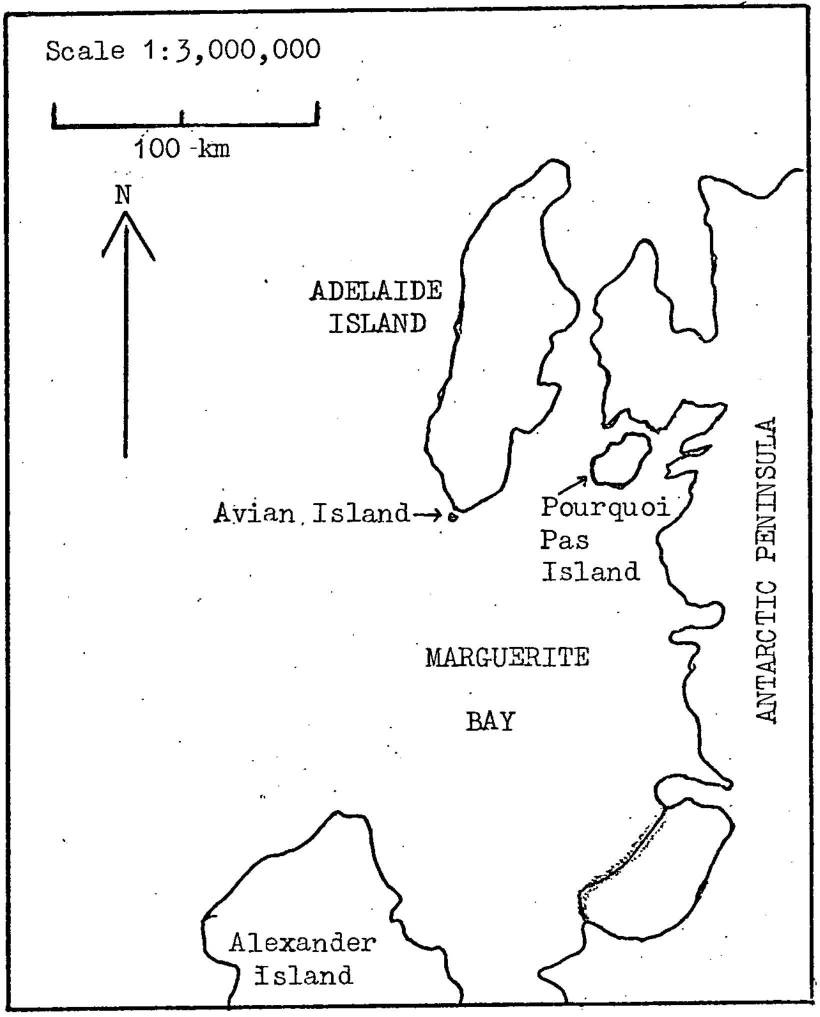


Fig. 10: Sketch map of Marguerite Bay, west coast of the Antarctic Peninsula (after D.O.S. 813, series 3203, 1963)

Cone Island is a small islet off the southern tip of Adelaide Island

COMPOSITION OF THE FAUNA

From observations made, 96 species of protozoa were recorded:

Mastigophora		27 species
Rhizopoda:	Amoebida	8 species
Rhizopoda:	Testacida	24 species
Ciliata		37 species

MASTIGOPHORA

PHYTOMASTIGIA

CHRYSOMONADIDA	*Cephalothamnium cyclopum* Stein
	Oikomonas mutabilis Kent
	Oikomonas termo Ehrenberg
	Polypseudopodius bacterioides Pusch
PHYTOMONADIDA	*Chlamydomonas sp.* Ehrenberg
EUGLENOIDIDA	*Petalomonas angusta* (Klebs) Lemmerman
	Petalomonas mediocanellata Stein
	Polytoma uvella Ehrenberg

ZOOMASTIGIA

PROTOMONADIDA	*Allantion tachyploon* Sandon
	Bodo caudatus Dujardin
	Bodo celer Klebs
	Bodo saltans Ehrenberg
	Bodo terricolus Martin
	Cercobodo agilis Martin
	Cercobodo vibrans Sandon
	Cercomonas crassicauda Alexeieff
	Cercomonas longicauda Stein
	Heteromita lens Muller
	Heteromita obovata Lemmerman
	Heteromita globosa Stein

	Phalansterium solitarium Sandon
	Pleuromonas jaculans Perty
	Sainouron mikroteron Sandon
	Spongomonas uvella Stein
POLYMASTIGIDA	*Spironema multiciliata* Klebs
	Tetramitus pyriformis Klebs
	Tetramitus rostratus Perty
RHIZOPODA	
AMOEBIDA	*Astramoeba radiosa* Ehrenberg
	Flabellula mira Schaeffer
	Hyalodiscus sp. Hertwig and Lesser
	Mayorella sp. Schaeffer
	Metachaos sp. Schaeffer
	Naegleria gruberi (Schardinger) Wilson
	Thecamoeba verrucosa Ehrenberg
	Valkampfia sp. Chatton and Lalung-Bonnaire
TESTACIDA	*Arcella vulgaris* Ehrenberg
	Assulina muscora Greef
	Clypeolina sp. Penard
	Corythion dubium Taranek
	Difflugia constricta Ehrenberg
	Difflugia lucida Penard
	Difflugia penardi Wailes
	Difflugiella sp. Cash
	Diplophrys archeri Barker
	Euglypha ciliata (Ehrenberg) Leidy
	Euglypha laevis (Ehrenberg) Perty
	Euglypha rotunda Wailes and Penard
	Euglypha strigosa (Ehrenberg) Leidy

	Heleopera sp. Leidy
	Hyalosphenia elegans Leidy
	Hyalosphenia minuta Cash
	Lecythium hyalinum (Ehrenberg) Hertwig & Lesser
	Nebela minor Penard
	Nebela wailesi Deflandre
	Parmulina cyathus Penard
	Phryganella acropodia (Hertwig and Lesser) Hopkinson
	Pseudodifflugia gracilis Schlumberger
	Trinema enchelys (Ehrenberg) Leidy
	Trinema lineare Penard
CILIATA	
HOLOTRICHA	
GYMNOSTOMATIDA	*Chillodonella* sp. Strand
	Choenia sp. Quennerstedt
	Chilophrya sp. Kahl
	Dileptus sp. Dujardin
	Enchelys sp. Hill
	Holophrya sp. Ehrenberg
	Lagynophrya sp. Kahl
	Litonotus sp. Wresniowski
	Loxophyllum sp. Dujardin
	Nassula elegans Ehrenberg
	Spathidium sp. Dujardin
	Urotricha agilis Stokes
SUCTORIDA	*Hallezia* sp. Sand
	Podophrya sp. Ehrenberg
TRICHOSTOMATIDA	*Leptopharynx sphagnetorum* (Levander) Mermod

	Microthorax simulans (Kahl) Engelmann
HYMENOSTOMATIDA	*Cryptochilium nigricans* (Muller) Maupas
	Cyclidium glaucoma Muller
	Dichilium cuneiforme Schewiakoff
	Glaucoma pyriformis Ehrenberg
	Philaster sp. Fabre-Domergue
PERITRICHIDA	*Vorticella microstoma* Ehrenberg
	Vorticella striata Dujardin var *octava* Stokes
SPIROTRICHA	
HETEROTRICHIDA	*Blepharisma* sp. Perty
OLIGOTRICHIDA	*Halteria grandinella* Muller
HYPOTRICHIDA	*Euplotes* sp. Ehrenberg
	Gonostomum affine Stein
	Holosticha sp. Wresniowski
	Hypotrichidium sp. Ilowaisky
	Keronopsis sp. Penard
	Onychodromus sp. Stein
	Oxytricha fallax Stein
	Oxytricha pellionella (Muller) Ehrenberg
	Oxytricha setigera Stokes
	Pleurotricha lanceolata (Ehrenberg) Stein
	Uroleptus sp. Ehrenberg
	Urostrogylum contortum Kahl

All these genra and species of protozoa have been recorded in temperate regions of the Earth. The species occurring in the maritime Antarctic are therefore not endemic to the region; instead they are types with an ability to tolerate diverse conditions including those of the

Antarctic. Interestingly the ciliate species Colpoda steini, usually considered to be the commonest of terrestrial protozoa (Sandon, 1927; Stout and Heal, 1967) and the best adapted to soil habitat conditions (Stout, 1955), was absent. A possible explanation of the absence of Colpoda spp. is given in Chapter V. A considerable number of protozoa species are present, however, suggesting that the remoteness of Antarctica is no geographical barrier to the dispersal of protozoa (presumably as wind-borne cysts), but that the composition of the fauna of any one site is determined principally by local ecological conditions.

The species diversity of the fauna of each site is shown in Tables 6, 7, 8 and 9 where the numbers of species of flagellates, rhizopods, ciliates and total protozoa identified in samples from each site are recorded. The full list of records for each species in each site is given in Appendix I.

ASSOCIATION ANALYSIS

The results of the survey of the protozoan fauna, given in full in Appendix I, constitute a presence/absence matrix of 96 species in 68 sites. In this raw form it was difficult to draw conclusions about the distribution of the protozoan fauna in relation to habitat type from so large a quantity of data. Consequently the data were subject to direct and inverse association analyses in order to make the results more compact and more comprehensible. These involved grouping sites together on the basis of their tending to have similar faunas, and grouping species together on the basis of their tending to occur or be absent together in sites.

In direct analysis the sites were divided dichotomously into groups on a hierarchical system. At each stage the sites were divided dichotomously into those with and those without the "best" species.

TABLE 6: NUMBERS OF SPECIES OF MASTIGOPHORA OBSERVED IN SAMPLES FROM EACH SITE

Site code	No. of species
SO-MIN-1	3
SO-MIN-2	8
SO-PG-1	4
SO-PG-2	0
SO-PG-3	2
SO-ShG-1	2
SO-ESW-1	3
SO-PRAS-1	5
SO-PRAS-2	5
SO-MCu-1	3
SO-MCu-2	4
SO-MTP-1	14
SO-MCP-1	3
SO-MCP-2	3
SO-MCP-3	3
SO-MCP-4	4
SO-MCP-5	1
SO-MCP-6	2
SO-MCP-7	3
SO-MCP-8	3
SO-MCP-9	3
SO-MCP-10	5
SO-MCP-11	7
SO-MCP-12	3
SO-MCP-13	4
SO-MCP-14	4
SO-MCP-15	4
SO-MCP-16	10
SO-GS-1	8
E-MIN-1	3
E-MIN-2	3
E-MIN-3	2
E-MIN-4	3
E-MIN-5	3
E-PG-1	3
E-PG-2	3
E-PG-3	4
E-PG-4	4
E-PG-5	4
E-MTP-1	2
E-MTP-2	4
E-MTP-3	3
E-MTP-4	3
E-MCP-1	6
E-MCP-2	4
E-MCP-3	3
E-MCP-4	5
E-MCP-5	3
E-GS-1	4
E-GS-2	2
E-GS-3	3
E-GS-4	3
LIV-MCP-1	3
D-VA-1	0
D-VA-2	0
D-VA-3	3
D-VA-4	0
D-VA-5	2
A-MTP-1	3
A-MTP-2	3
A-MCP-1	2
A-MCP-2	1
MB-MIN-1	4
MB-PG-1	1
MB-MTP-1	3
MB-MCP-1	6
MB-MCP-2	3
MB-MCP-3	2

TABLE 7: NUMBERS OF SPECIES OF RHIZOPODA OBSERVED IN SAMPLES FROM EACH SITE

Site code	No. of species	Site code	No. of species	Site code	No. of species
SO-MIN-1	0	SO-MCP-13	6	E-GS-1	3
SO-MIN-2	1	SO-MCP-14	6	E-GS-2	4
SO-PG-1	1	SO-MCP-15	2	E-GS-3	7
SO-PG-2	0	SO-MCP-16	10	E-GS-4	2
SO-PG-3	0	SO-GS-1	12	LIV-MCP-1	3
SO-ShG-1	0	E-MIN-1	0	D-VA-1	0
SO-ESW-1	0	E-MIN-2	0	D-VA-2	0
SO-PRAS-1	3	E-MIN-3	0	D-VA-3	0
SO-PRAS-2	2	E-MIN-4	0	D-VA-4	0
SO-MCu-1	1	E-MIN-5	0	D-VA-5	0
SO-MCu-2	4	E-PG-1	0	A-MTP-1	3
SO-MTP-1	14	E-PG-2	0	A-MTP-2	7
SO-MCP-1	5	E-PG-3	0	A-MCP-1	4
SO-MCP-2	4	E-PG-4	0	A-MCP-2	4
SO-MCP-3	6	E-PG-5	0	MB-MIN-1	0
SO-MCP-4	1	E-MTP-1	2	MB-PG-1	0
SO-MCP-5	4	E-MTP-2	6	MB-MTP-1	5
SO-MCP-6	1	E-MTP-3	2	MB-MCP-1	2
SO-MCP-7	5	E-MTP-4	4	MB-MCP-2	4
SO-MCP-8	4	E-MCP-1	2	MB-MCP-3	2
SO-MCP-9	4	E-MCP-2	3		
SO-MCP-10	2	E-MCP-3	5		
SO-MCP-11	1	E-MCP-4	3		
SO-MCP-12	2	E-MCP-5	3		

TABLE 8: NUMBERS OF SPECIES OF CILIATA OBSERVED IN SAMPLES FROM EACH SITE

Site code	No. of species	Site code	No. of species	Site code	No. of species
SO-MIN-1	4	SO-MCP-13	3	E-GS-1	6
SO-MIN-2	13	SO-MCP-14	4	E-GS-2	5
SO-PG-1	4	SO-MCP-15	6	E-GS-3	5
SO-PG-2	0	SO-MCP-16	10	E-GS-4	5
SO-PG-3	5	SO-GS-1	15	LIV-MCP-1	8
SO-ShG-1	0	E-MIN-1	3	D-VA-1	0
SO-ESW-1	5	E-MIN-2	0	D-VA-2	0
SO-PRAS-1	11	E-MIN-3	0	D-VA-3	4
SO-PRAS-2	5	E-MIN-4	0	D-VA-4	0
SO-MCu-1	11	E-MIN-5	0	D-VA-5	0
SO-MCu-2	11	E-PG-1	0	A-MTP-1	1
SO-MTP-1	11	E-PG-2	1	A-MTP-2	2
SO-MCP-1	6	E-PG-3	0	A-MCP-1	0
SO-MCP-2	5	E-PG-4	0	A-MCP-2	3
SO-MCP-3	0	E-PG-5	0	MB-MIN-1	0
SO-MCP-4	5	E-MTP-1	2	MB-PG-1	0
SO-MCP-5	4	E-MTP-2	3	MB-MTP-1	2
SO-MCP-6	0	E-MTP-3	3	MB-MCP-1	3
SO-MCP-7	7	E-MTP-4	2	MB-MCP-2	6
SO-MCP-8	1	E-MCP-1	2	MB-MCP-3	3
SO-MCP-9	6	E-MCP-2	6		
SO-MCP-10	3	E-MCP-3	7		
SO-MCP-11	1	E-MCP-4	4		
SO-MCP-12	3	E-MCP-5	2		

TABLE 9: TOTAL NUMBERS OF SPECIES OF PROTOZOA OBSERVED IN SAMPLES FROM EACH SITE

Site code	No. of species	Site code	No. of species	Site code	No. of species
SO-MIN-1	7	SO-MCP-13	13	E-GS-1	13
SO-MIN-2	22	SO-MCP-14	14	E-GS-2	11
SO-PG-1	9	SO-MCP-15	12	E-GS-3	15
SO-PG-2	0	SO-MCP-16	30	E-GS-4	10
SO-PG-3	7	SO-GS-1	35	LIV-MCP-1	15
SO-ShG-1	2	E-MIN-1	6	D-VA-1	0
SO-ESW-1	8	E-MIN-2	3	D-VA-2	0
SO-PRAS-1	19	E-MIN-3	2	D-VA-3	7
SO-PRAS-2	12	E-MIN-4	3	D-VA-4	0
SO-MCu-1	15	E-MIN-5	3	D-VA-5	2
SO-MCu-2	19	E-PG-1	3	A-MTP-1	7
SO-MTP-1	39	E-PG-2	4	A-MTP-2	12
SO-MCP-1	14	E-PG-3	4	A-MCP-1	6
SO-MCP-2	12	E-PG-4	4	A-MCP-2	8
SO-MCP-3	9	E-PG-5	4	MB-MIN-1	4
SO-MCP-4	10	E-MTP-1	6	MB-PG-1	1
SO-MCP-5	9	E-MTP-2	13	MB-MTP-1	10
SO-MCP-6	3	E-MTP-3	8	MB-MCP-1	11
SO-MCP-7	15	E-MTP-4	9	MB-MCP-2	13
SO-MCP-8	8	E-MCP-1	10	MB-MCP-3	7
SO-MCP-9	13	E-MCP-2	15		
SO-MCP-10	10	E-MCP-3	13		
SO-MCP-11	9	E-MCP-4	12		
SO-MCP-12	8	E-MCP-5	8		

The "best" species was the one carrying the 'maximum total χ^2,' calculated by the method of Williams and Lambert (1959). The working of this technique may be explained by giving three selected examples of the results:

(i) In the first stage of direct analysis the "best" species was Halteria grandinella, a small ciliate species, which out of the 68 sites investigated occurred in only two exceptionally species rich sites (one grass and one moss turf), which were thus divided from the other 66 sites.

(ii) In the 9th stage, the "best" species was a testate amoeba, Corythion dubium, a frequent and abundant species in moss peats and grass soils, to which it is specific. It occurred in 15 of the 53 sites being analysed at this stage which were thus divided from the other 38 sites.

(iii) In the 10th stage, the "best" species was the ciliate Philaster sp. which is specific to animal guano habitats. Of the 38 sites being analysed at this stage, it occurred in 5 sites, all of these being heavily enriched by penguins or elephant seals, which were thus divided from the other 33 sites.

The analysis ran to 19 stages and the results were plotted as a dendrogram. (Fig. 11).

In inverse analysis the species were divided into groups, at each stage by the "best" site, using the same method. Again three selected examples may be used to explain this operation:

(i) At the first stage of the inverse analysis, the "best" site was one of penguin guano (E-PG-1) which contained, out of 96 species of protozoa, only three: Oikomonas termo, Bodo saltans and Tetramitus rostratus. T. rostratus was specific to animal guano sites; the other

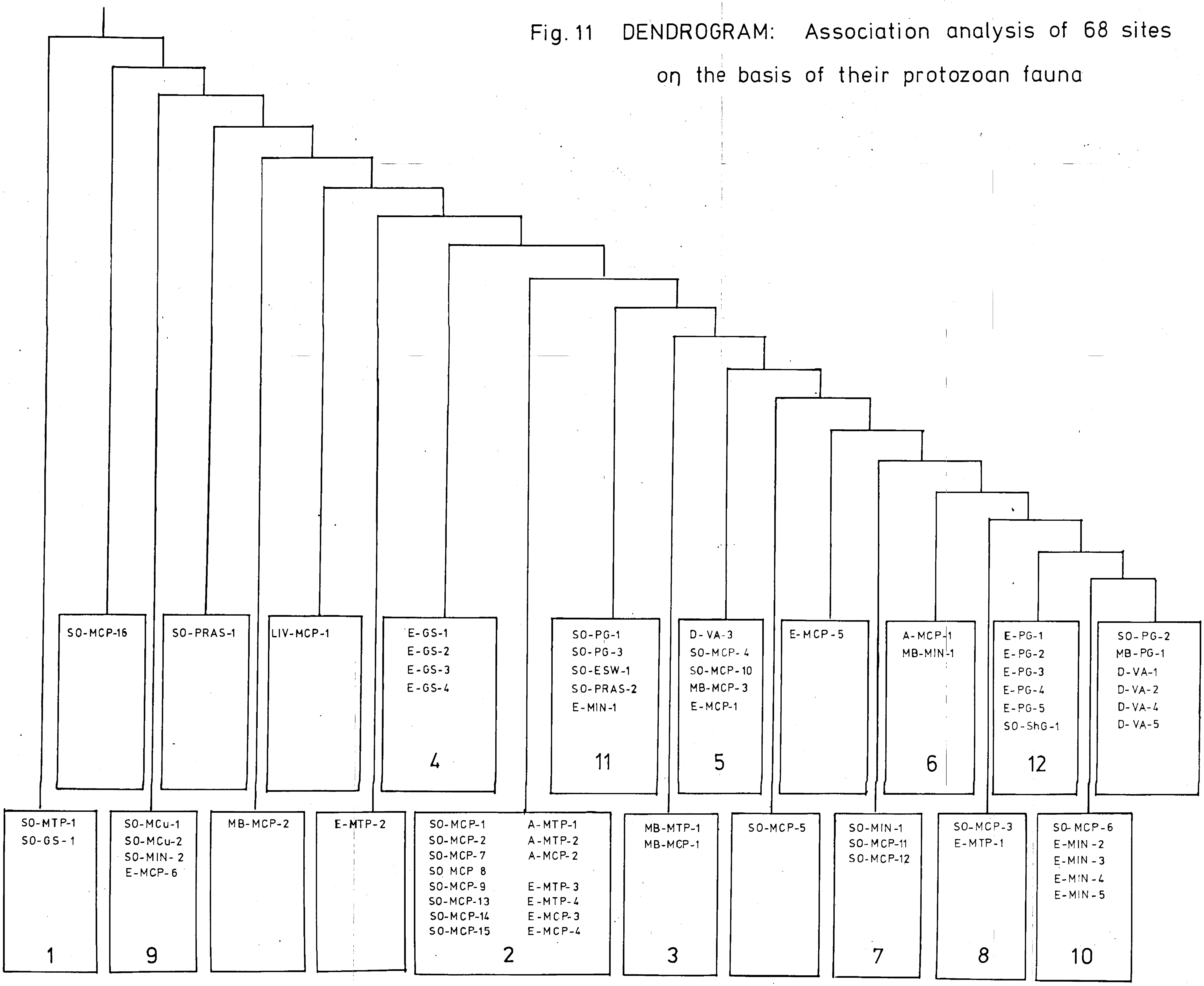


Fig. 11 DENDROGRAM: Association analysis of 68 sites on the basis of their protozoan fauna

two species occurred also in some moss peats. These three species were divided from the other 93 species which did not occur in this site.

(ii) At the 5th stage, the "best" site was one of moss carpet peat (SO-MCP-1) which contained, out of 81 species still being analysed at this stage, four ciliate species: Cyclidium glaucoma and three species of Oxytricha, a group specific to moss peat habitats, which were thus divided from the other 77 species.

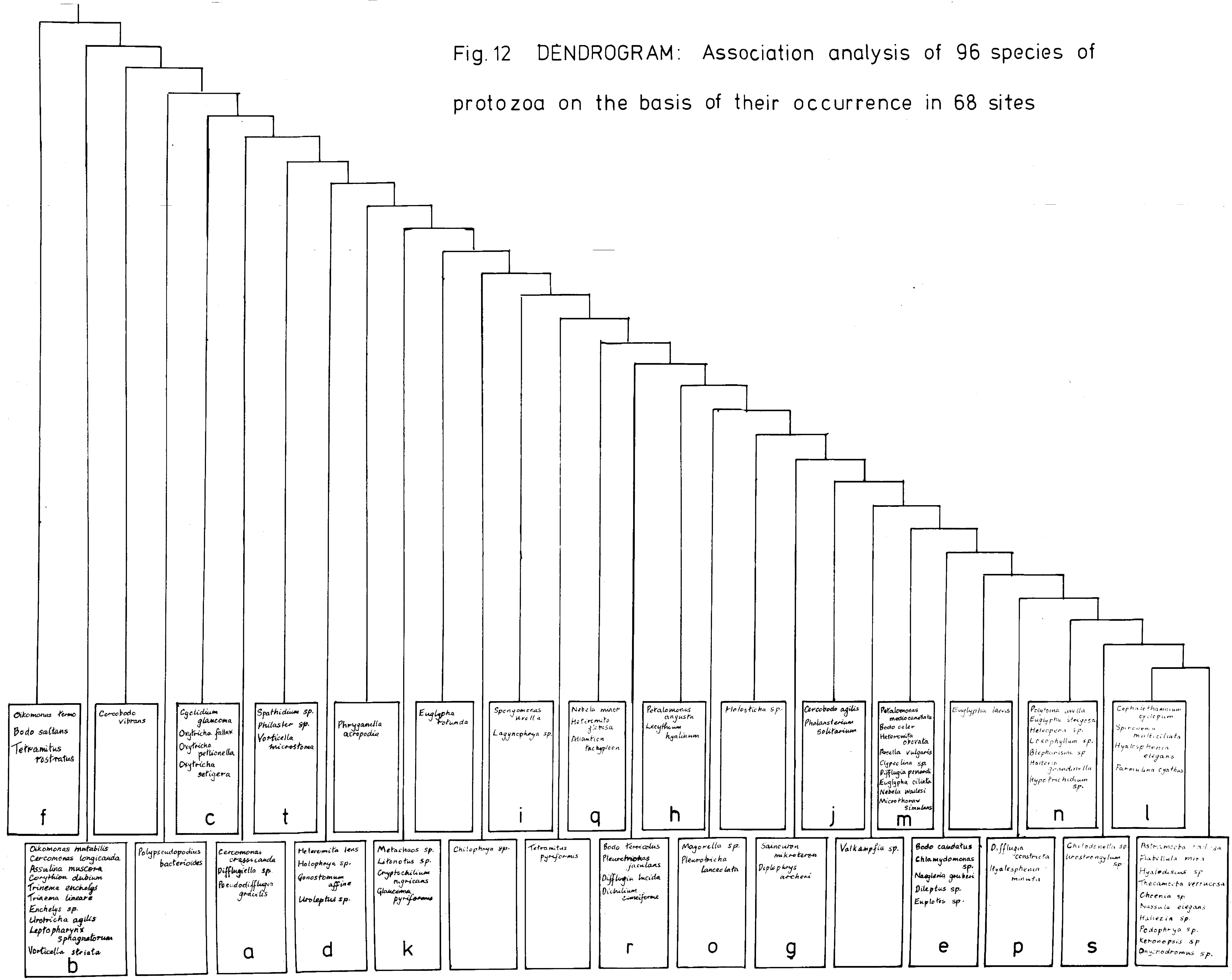
(iii) At the 7th stage, the "best" site was a glacier moraine, occupied by a colony of moulting chinstrap penguins (E-MIN-1). It contained, out of 74 species still being analysed at this stage, three ciliate species: Spathidium sp., Philaster sp. and Vorticella microstoma, a group specific to animal guano habitats, which were thus divided from the other 71 species.

The inverse analysis ran to 29 stages and the results were plotted as a dendrogram (Fig. 12).

Both dendrograms (Figs. 11 and 12) show "chaining" throughout and some of the 'groups' contain only one site or species. This indicates the existence of considerable heterogeneity in the composition of the faunas of the different sites. This is possibly an artefact of the survey policy which was deliberately designed to include samples from as wide a range of habitats as possible. Despite the heterogeneity, it proved possible to combine the results of the direct and inverse analyses into a matrix showing the tendency of certain groups of species to occur in certain groups of sites, using the following procedure:

Each group of sites in the direct analysis containing two or more sites was assigned a number, and each group of species in the inverse analysis containing two or more species was assigned a letter (Figs. 11

Fig. 12 DENDROGRAM: Association analysis of 96 species of protozoa on the basis of their occurrence in 68 sites



and 12). Each group containing only one site or species was then allocated to the numbered or lettered group which it most nearly resembled. Those which showed no tendency to resemble any group were designated as 'unclassifiable residuals' and were not considered further. The species list of each site was then inspected in order to determine which groups of species tended to occur in it. Where half or more of the species in X (where X is a lettered group of species) were found to occur in half or more of the sites in N (where N is a numbered group of sites), then X was said to 'tend to occur' in N. A presence/absence matrix of 20 groups of species in 12 groups of sites was then drawn up. By inspection the 20 groups of species were aggregated into 6 'communities' and the 12 groups of sites into 6 'habitat classes'. This matrix with aggregations into communities and habitat classes is shown in Fig. 13.

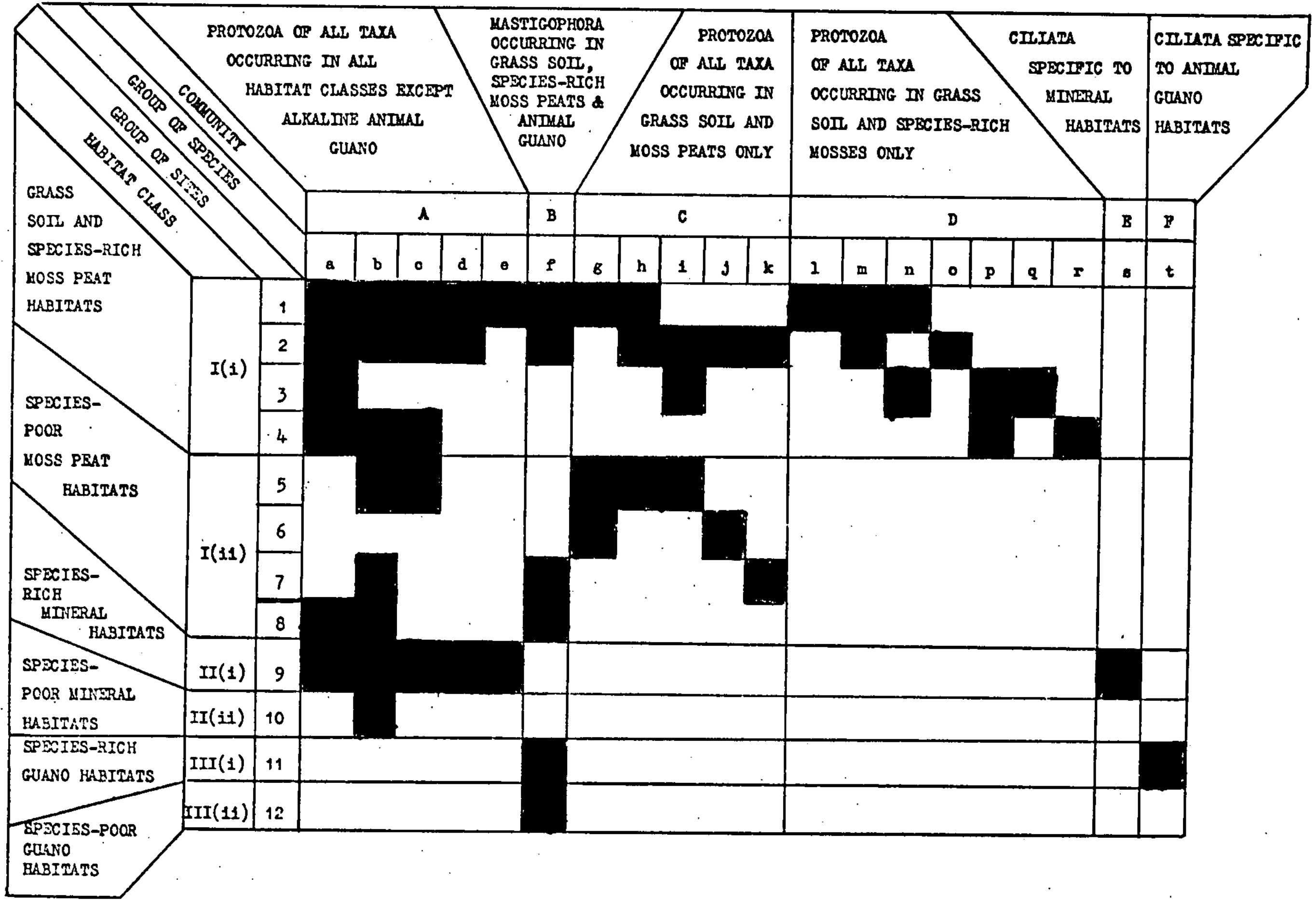
Examination of the properties of the sites in each habitat class showed that the sites, on the basis of their protozoan faunas, had been grouped (by association analysis followed by aggregation) into three fairly discrete types:

1. Acid moss peat or grass soil habitats with high organic content (Classes I(i) and I(ii)).
2. Near-neutral mineral habitats with low organic content (Classes II (i) and II(ii)).
3. Alkaline animal guano habitats with intermediate organic content (Classes III(i) and III(ii)).

Each of these three types was divided into relatively species-rich and species-poor, thus giving 6 habitat classes.

Examination of the species lists of the sites in each habitat class showed that there were considerable differences between the habitat classes in the relative proportions of the different taxonomic

Fig. 13: Distribution of the terrestrial protozoan fauna in relation to habitat: Presence/absence matrix of 20 groups of species in 12 groups of sites with aggregation into 6 communities and 6 habitat classes



HABITAT CLASS	GROUP OF SITES		PROTOZOA OF ALL TAXA OCCURRING IN ALL HABITAT CLASSES EXCEPT ALKALINE ANIMAL GUANO					MASTIGOPHORA OCCURRING IN GRASS SOIL, SPECIES-RICH MOSS PEATS & ANIMAL GUANO	PROTOZOA OF ALL TAXA OCCURRING IN GRASS SOIL AND MOSS PEATS ONLY					PROTOZOA OF ALL TAXA OCCURRING IN GRASS SOIL AND SPECIES-RICH MOSSES ONLY							CILIATA SPECIFIC TO MINERAL HABITATS	CILIATA SPECIFIC TO ANIMAL GUANO HABITATS
COMMUNITY			A					B	C					D							E	F
GROUP OF SPECIES			a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q	r	s	t
GRASS SOIL AND SPECIES-RICH MOSS PEAT HABITATS	I(i)	1	■	■	■	■	■	■	■	■				■	■	■						
		2	■	■	■	■		■		■	■	■	■		■		■					
SPECIES-POOR MOSS PEAT HABITATS		3	■								■					■		■	■			
		4	■	■	■													■		■		
	I(ii)	5		■	■				■	■	■											
		6							■			■										
SPECIES-RICH MINERAL HABITATS		7		■				■					■									
		8	■	■				■														
SPECIES-POOR MINERAL HABITATS	II(i)	9	■	■	■	■	■														■	
	II(ii)	10		■																		
SPECIES-RICH GUANO HABITATS	III(i)	11						■														■
SPECIES-POOR GUANO HABITATS	III(ii)	12						■														

groups constituting the protozoan fauna (Fig. 14). Mastigophora were the most ubiquitous group as they constituted a substantial proportion of the protozoan fauna in all habitat classes and almost the total fauna in those mineral and animal guano habitats which were species-poor. Testacida showed a clear preference for the acid vegetated habitats and were rare or absent in the others. Ciliata also occurred frequently in vegetated habitats; they also constituted the most prominent faunal group in mineral and animal guano habitats which were species-rich, but were absent or very rare in those which were species-poor. Naked amoebae were absent or rare and their few occurrences showed no detectable pattern in relation to habitat type.

There was no detectable pattern in the distribution of the protozoan fauna in relation to the geology of the areas in which the sites were located.

The habitat classes with site properties and the species composition of each community are listed below:

CLASS I(i)

Moss peat and grass soil habitats; acid with high organic content; relatively species rich; testacida a substantial proportion of the fauna.

pH 3.6-5.9, mean 4.7 Loss on ignition 13-97% mean 63%

Number of protozoa species observed per site: 8-39, mean 14

Mean composition of the protozoan fauna:

Mastigophora	29% (11-57%)	Amoebida	2% (0-15%)
Testacida	35% (18-58%)	Ciliata	37% (13-57%).

CLASS I(ii)

Moss peat habitats; less acid and slightly lower organic content than Class I(i); relatively species-poor; testacida a smaller proportion of the fauna; mastigophora a greater proportion.

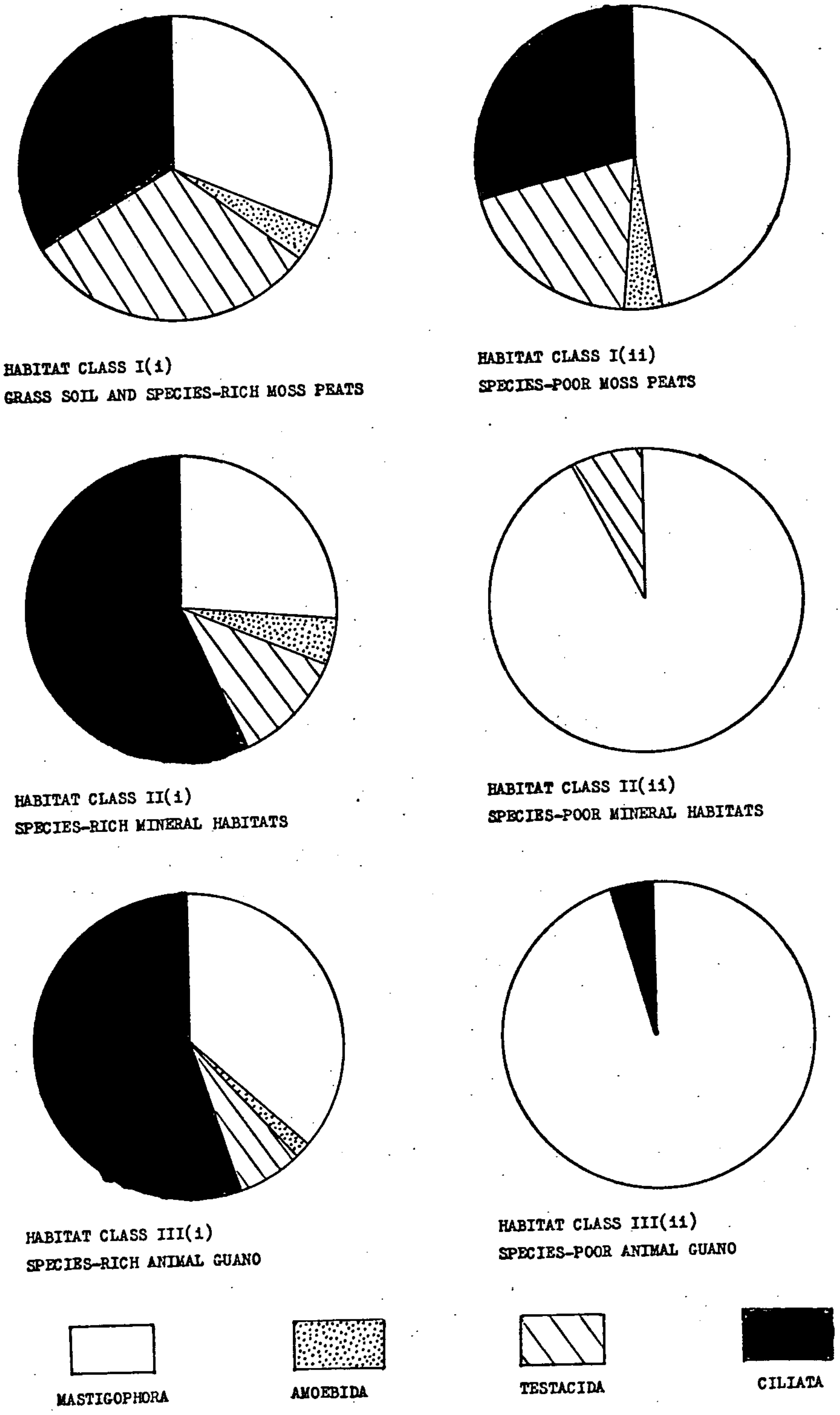
pH 4.4-6.8, mean 5.0 Loss on ignition 1-94%, mean 60%

Number of protozoa species observed per site: 4-10, mean 8

Mean composition of the fauna:

Mastigophora	48% (29-100%)	Amoebida	3% (0-15%)
Testacida	20% (0- 55%)	Ciliata	28% (0-57%)

Fig. 14: Comparison of the mean composition of the protozoan fauna, by taxonomic groups, in each habitat class



HABITAT CLASS I(i)
GRASS SOIL AND SPECIES-RICH MOSS PEATS

HABITAT CLASS I(ii)
SPECIES-POOR MOSS PEATS

HABITAT CLASS II(i)
SPECIES-RICH MINERAL HABITATS

HABITAT CLASS II(ii)
SPECIES-POOR MINERAL HABITATS

HABITAT CLASS III(i)
SPECIES-RICH ANIMAL GUANO

HABITAT CLASS III(ii)
SPECIES-POOR ANIMAL GUANO

CLASS II(i)

Mineral habitats; slightly acid with low organic content; relatively species-rich; fauna predominantly ciliata and mastigophora, testacida a small proportion only; vegetation absent or lichen and moss cushion.

pH 4.9-6.9 mean 6.3 Loss on ignition 2-36%, mean 12%

Number of protozoan species observed per site: 13-22, mean 17

Mean composition of the fauna:

Mastigophora	27% (20-36%)	Amoebida	5% (0-8%)
Testacida	12% (05-21%)	Ciliata	59% (46-73%).

CLASS II(ii)

Mineral habitats; slightly acid or alkaline with low organic content; relatively species-poor; fauna almost entirely mastigophora, testacida absent or rare, ciliata absent, vegetation absent or sparse moss.

pH 5.1-7.5, mean 6.8 Loss on ignition 1-18%, mean 17%

Number of protozoan species observed per site; 2-3, mean 2.8

Mean composition of the fauna:

Mastigophora	93% (67-100%)	Amoebida	0%
Testacida	7% (00-33%)	Ciliata	0%.

CLASS III(i)

Animal guano habitats; slightly acid or alkaline with intermediate organic content; relatively species-rich; fauna predominantly mastigophora and ciliata, testacida absent or rare; vegetation sparse or Prasiola only.

pH 5.6-8.0, mean 6.7 Loss on ignition 4-70%, mean 38%

Number of protozoan species observed per site: 3-19, mean 10

Mean composition of the protozoan fauna:

Mastigophora	35% (26-45%)	Amoebida	2% (0-11%)
Testacida	4% (00-16%)	Ciliata	55% (44-71%)

CLASS III(ii)

Animal guano habitats; alkaline with intermediate organic content; relatively species-poor; fauna almost entirely mastigophora, testacida absent, ciliata absent or rare; vegetation absent.

pH 6.8-8.2, mean 7.8 Loss on ignition 21-53%, mean 37%

Number of protozoan species observed per site; 2-4, mean 3.5

Mean compositon of the protozoan fauna:

Mastigophora	96% (75-100%)	Amoebida	0%
Testacida	0%	Ciliata	4% (0-25%)

COMMUNITY A contains species from all taxa and tends to occur in all types of habitat except the most alkaline animal guano.

Oikomonas mutabilis
Chlamydomonas sp.
Bodo caudatus
Cercobodo vibrans
Cercomonas crassicauda
Cercomonas longicauda
Heteromita lens

Naegleria gruberi
Assulina muscora
Corythion dubium
Difflugiella sp.
Phryganella acropodia
Pseudodifflugia gracilis
Trinema enchelys
Trinema lineare

Dileptus sp.
Enchelys sp.
Holophrya sp.
Urotricha agilis
Leptopharnyx sphagnetorum
Vorticella striata
Cyclidium glaucoma
Euplotes sp.
Gonostomum affine
Oxytricha fallax
Oxytricha pellionella
Oxytricha setigera
Uroleptus sp.

COMMUNTIY B contains a small group of common flagellate species and tends to occur in guano, species-rich moss peats and grass soil.

Oikomonas termo
Bodo saltans
Tetramitus rostratus

COMMUNITY C contains species from all taxa and tends to occur in moss peats and grass soil.

Polypseudopodius bacterioides
Petalomonas angusta
Cercobodo agilis
Phalansterium solitarium
Sainouron mikroteron
Spongomonas uvella
Metachaos sp.
Diplophrys archeri
Euglypha rotunda
Lecythium hyalinum
Lagynophrya sp.
Litonotus sp.
Glaucoma pyriformis
Cryptochilium nigricans

COMMUNITY D contains species from all taxa and tends to occur in species-poor moss peats only.

Cephalothamnium cyclopum
Petalomonas mediocanellata
Polytoma uvella
Allantion tachyploon
Bodo celer
Bodo terricolus
Heteromita globosa
Heteromita obovata
Pleuromonas jaculans
Spironema multiciliata
Mayorella sp.
Arcella vulgaris
Clypeolina sp.
Difflugia constricta
Difflugia lucida
Difflugia penardi
Euglypha ciliata
Euglypha laevis
Euglypha strigosa
Heleopera sp.
Hyalosphenia elegans
Hyalosphenia minuta
Nebela minor
Nebela wailesi
Parmulina cyathus
Loxophyllum sp.
Microthorax simulans
Dichilium cuneiforme
Blepharisma sp.
Halteria grandinella
Hypotrichidium sp.
Pleurotricha lanceolata

COMMUNITY E contains a small group of ciliate species and tends to occur in mineral habitats only.

- *Chilodonella* sp.
- *Chilophrya* sp.
- *Urostrongylum contortum*

COMMUNITY F contains a small group of ciliate species and tends to occur in animal guano habitats only.

- *Spathidium* sp.
- *Philaster* sp.
- *Vorticella microstoma*

RESIDUALS

Rare species which show no detectable pattern of distribution in this survey

- *Tetramitus pyriformis*
- *Astramoeba radiosa*
- *Flabellula mira*
- *Hyalodiscus* sp.
- *Thecamoeba verrucosa*
- *Valkampfia* sp.
- *Choenia* sp.
- *Nassula elegans*
- *Hallezia* sp.
- *Podophrya* sp.
- *Holosticha* sp.
- *Keronopsis* sp.
- *Onychodromus* sp.

CHAPTER III

POPULATION ECOLOGY OF *Corythion dubium* TARANEK (RHIZOPODA: TESTACIDA) IN MOSS TURF PEAT

INTRODUCTION

Corythion dubium Taranek is a commonly occurring species of testate amoeba in northern temperate moorland soils; it is described by Heal (1961, 1964) as a eurytope species of acid fens and bogs. Heal (1965) also observed that it was the most abundant testate species in samples from Signy Island, taken during a soil survey (Holdgate et al, 1967). My results (Chapter II) confirmed and extended those of Heal, C. dubium being widespread in moss peats and grass soils but entirely absent from animal guano.

A study of this species, to describe its seasonal fluctuations in numbers and to determine how these are influenced by environmental factors, in a moss turf peat on Signy Island, was made from January 1970 to the end of March 1971.

FIELD SITE

The site chosen for the study was located on the north-west face of a knoll 500 m south-west of Rethval Point (Chapter II, Fig. 4). It was subject to the general oceanic climate of Signy Island: a relatively small temperature range, frequent precipitation and overcast skies; it was particularly influenced by the prevailing westerly and north-westerly winds which blow onto the slope across the McLeod Glacier, but was sheltered from cold south-easterly winds. The site consisted of two stands of moss in an area of more or less continuous bryophyte vegetation interrupted by small rock outcrops and deposits of drift and scree, most of which were lichen covered, lying between the 40 m and 60 m contours and having an average slope of 1 : 3.9 (Fig. 15).

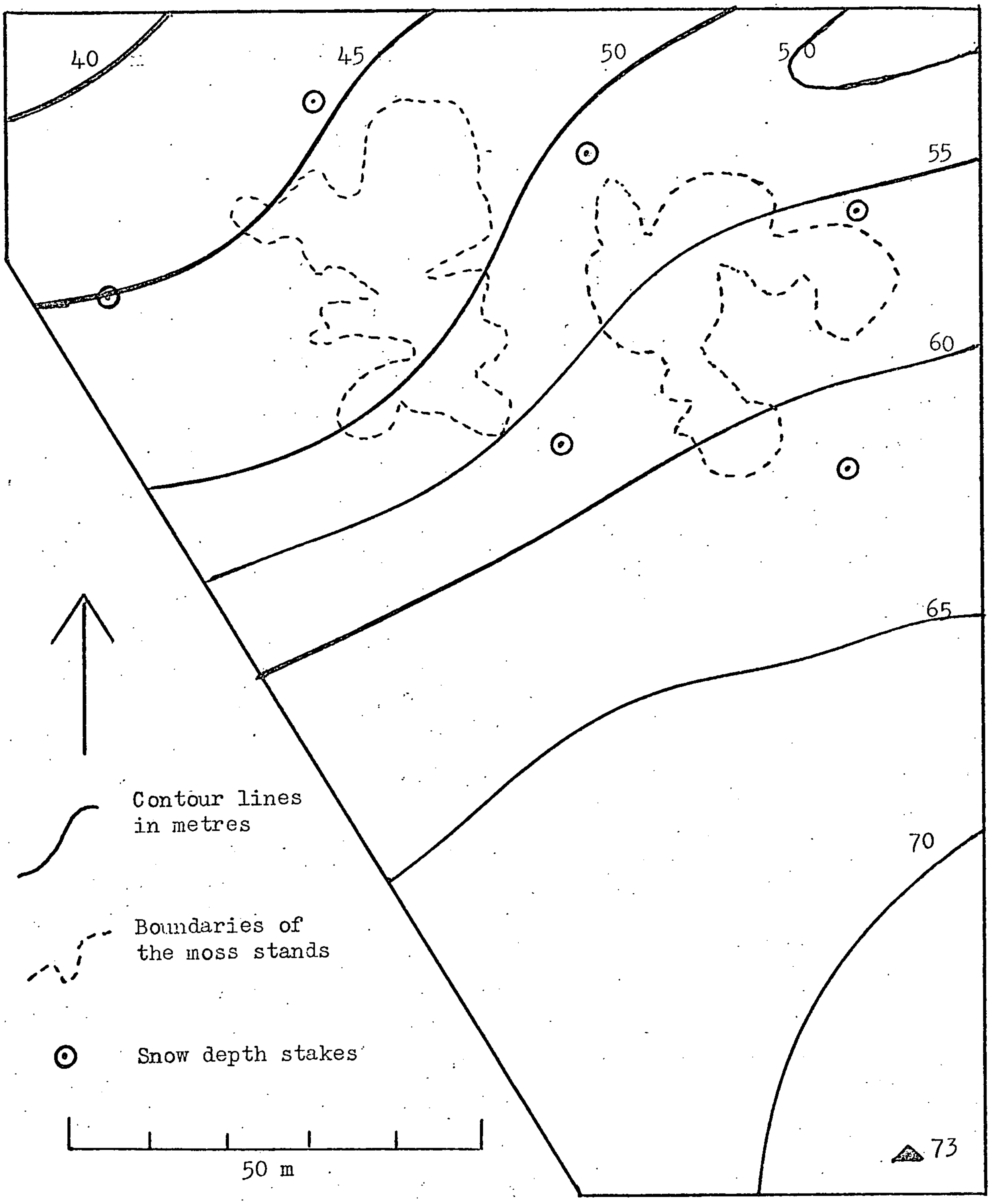


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Fig. 15: Sketch map of field site near Rethval Point, Signy Island, used in studying the ecology of the testate amoeba Corythion dubium, showing positions of stands of Polytrichum-Chorisodontium moss (after original survey, N.J. Collins, O.H.S. Darling, H.G. Smith and V.W. Spaull, January 1970)

Plate I3. Field site used for the study on the population ecology of <u>Corythion dubium</u> in moss turf peat. The site is viewed from 200 m away looking south-east, January I97I

Plate I4. Part of the field site used for the study on the population ecology of Corythion dubium in moss turf peat - the eastern moss stand. The white box houses the continuously recording thermograph.

Plate 13 is a view of the site from 200 m away, looking south-east.

Plate 14 is a close view of the eastern moss stand.

The moss was predominantly the Polytrichum alpestre - Chorisodontium aciphyllum association of the moss turf sub-formation (Longton, 1967). An acid peat had built up below the moss. The mid-summer depth of unfrozen peat, in January 1970, was 21 ± 1 cm (minimum 13 cm, maximum 32 cm). Properties of the 0-9 cm horizon of peat at this time are shown below:

Peat horizon	Peat properties ± 95% confidence limits		
	pH	Moisture % dry weight	Loss on ignition % dry weight
0-3 cm	4.1 ± 0.3	365 ± 57	89 ± 5
3-6 cm	3.8 ± 0.3	450 ± 83	97 ± 1
6-9 cm	3.7 ± 0.4	531 ± 52	95 ± 4

In the association analysis of the data collected in the survey of the protozoan fuana (Chapter II), this site was allocated to habitat class I(i). It was particularly species-rich: 39 species were observed in samples from this site (14 flagellate, 14 rhizopod and 11 ciliate species).

METHODS

LABORATORY DETERMINATIONS UPON CORES OF PEAT

On 16 occasions, at approximately monthly intervals, a random sample of six cores of peat was taken from the site using a steel corer 2.5 cm in diameter. They were cut into 3 cm horizons with a sharp knife and each fresh core was weighed. For each of three horizons, 0-3 cm, 3-6 cm and 6-9 cm, the following measurements were made:

1. Total numbers of testacida
2. Numbers of Corythion dubium
3. Mean pH
4. Mean moisture, per cent dry weight
5. Mean loss on ignition, per cent dry weight.

Populations of testacida were determined by Couteaux' (1967) direct examination technique. For each 3 cm horizon, the peat from six cores was mixed and a single sub-sample of 250 mg was treated with Bouin's fixative for 48 hours, after which the fixative was removed by centrifugation (5 minutes at 1500 rpm). Subsequently the residue was rinsed, suspended in distilled water and made up volumetrically to 250 ml (a 1/1000 w/v dilution). After stirring for two hours, 20 ml aliquots of the suspension were filtered under pressure through grade 0.45 membrane filters, so that each filter carried about 20 mg of peat (Plate 15). The filters were air dried and portions of each filter, one tenth its total area - bearing about 2 mg peat material - were cleared in xylene and mounted on slides in Canada balsam (Plate 16). To avoid any bias which might arise from the peat material being unevenly distributed from the circumference to the centre of the filter, the selected portions were taken along a radius of the filter. The slides were examined microscopically and counts made of C. dubium and of total testacida. Entire tests, presumed to have contained live amoebae at the time the cores were taken, were counted. It proved impossible to differentiate encysted from active individuals, and this was not attempted. Empty tests of dead individuals were usually too fragmented to be recognised reliably so no count was made of these. Since each filter bore

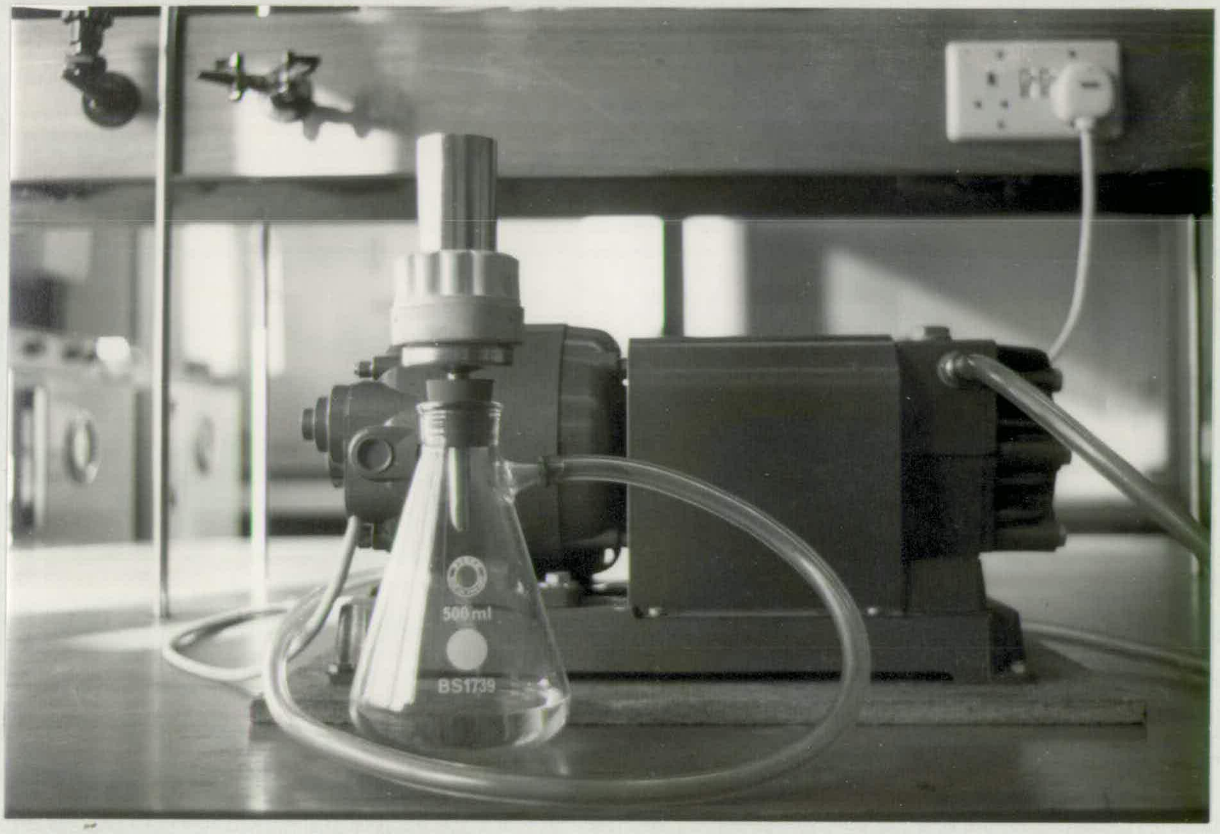


Plate I5. Filtration apparatus used in the preparation of slides of moss turf peat for the enumeration of testacida by Couteaux' (I967) method

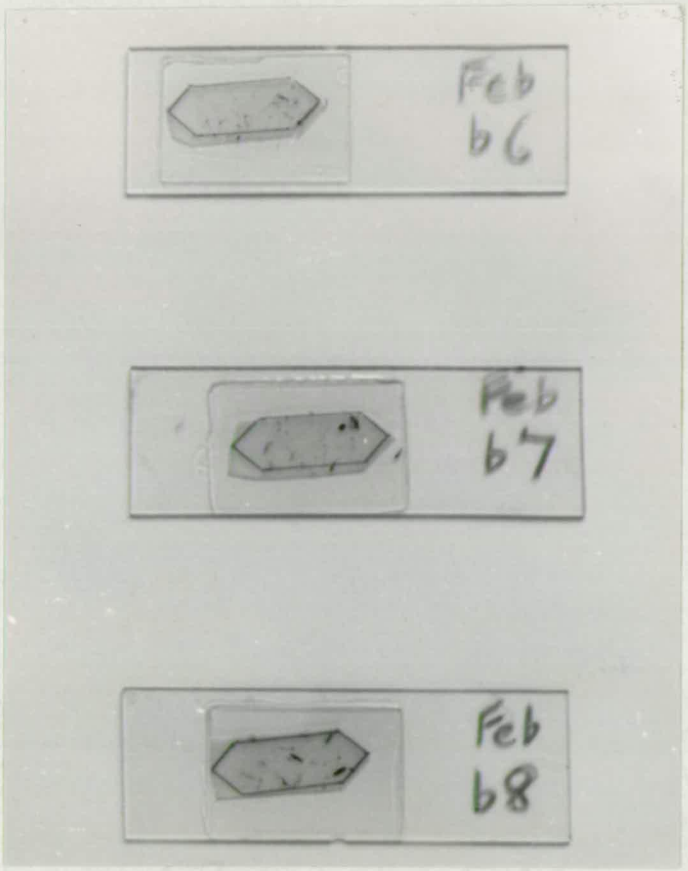


Plate I6. Slides of moss turf peat prepared for the enumeration of testacida by Couteaux' (I967) method on average 2 mg of peat, an estimate of numbers per g was obtained by multiplying the count per slide by 500. Numbers per g fresh weight in a 3 cm horizon were converted to numbers per cm^2 by a factor equal to three times the density of the core. Ten replicate counts were made allowing an estimate of experimental variance to be obtained. Because the peat from cores randomly distributed through the site was pooled, the results obtained by this method did not give any estimate of site variance.

Measurements of pH were made with a glass electrode and a pH meter immediately upon arrival at the laboratory after the cores had been taken. Moisture was determined by oven-drying at 100°C for 48 hours, and loss on ignition by ashing in a muffle furnace at 450-500°C for 10 hours.

METEOROLOGICAL OBSERVATIONS AT THE SITE

During the winter months (May to October 1970) the following spot observations were made at weekly intervals:

Snow depths
Air temperature at 1.5 m
Moss surface temperature.

Early in November 1970 a thermograph station was established on the site, at an altitude of 48 m. It gave a continuous record of temperatures at 76 mm above the moss surface from November until the end of March 1971. During these summer months the following spot observations were made three times weekly between the hours of 0900 and 1600:

Air temperature at 1.5 m
Air temperature at 76 mm
Moss surface temperature

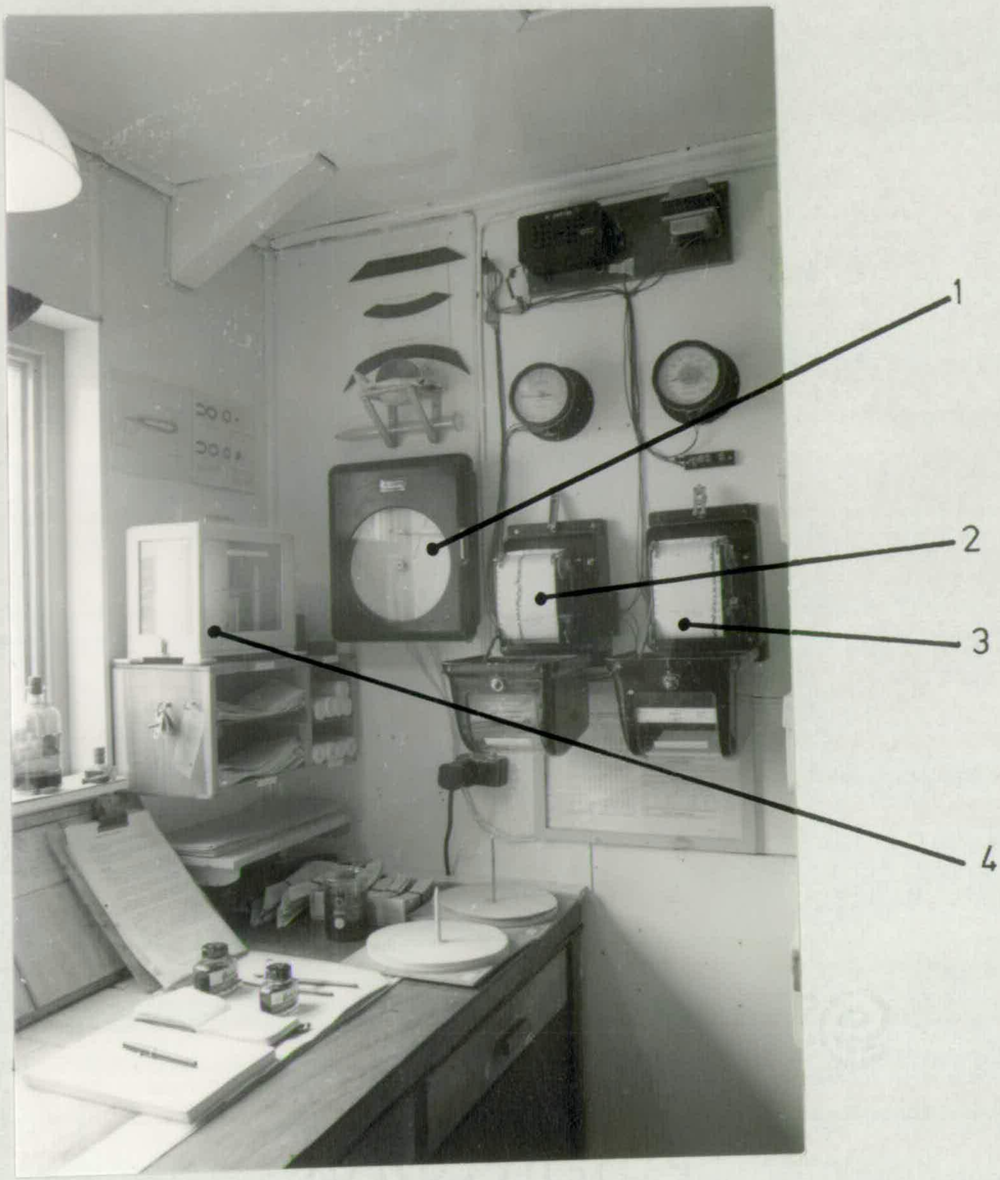


Plate I7. The meteorological office, Signy Island Base, showing the autographic recorders:

I. Mercury-in-steel thermograph

2. Wind direction recorder

3. Wind speed recorder

4. Barograph

Fig. 16:

Fluctuations in the numbers of C. dubium in three 3 - cm horizons of moss turf peat during the period January 1970 to March 1971

Figures plotted are means ± 95% confidence limits

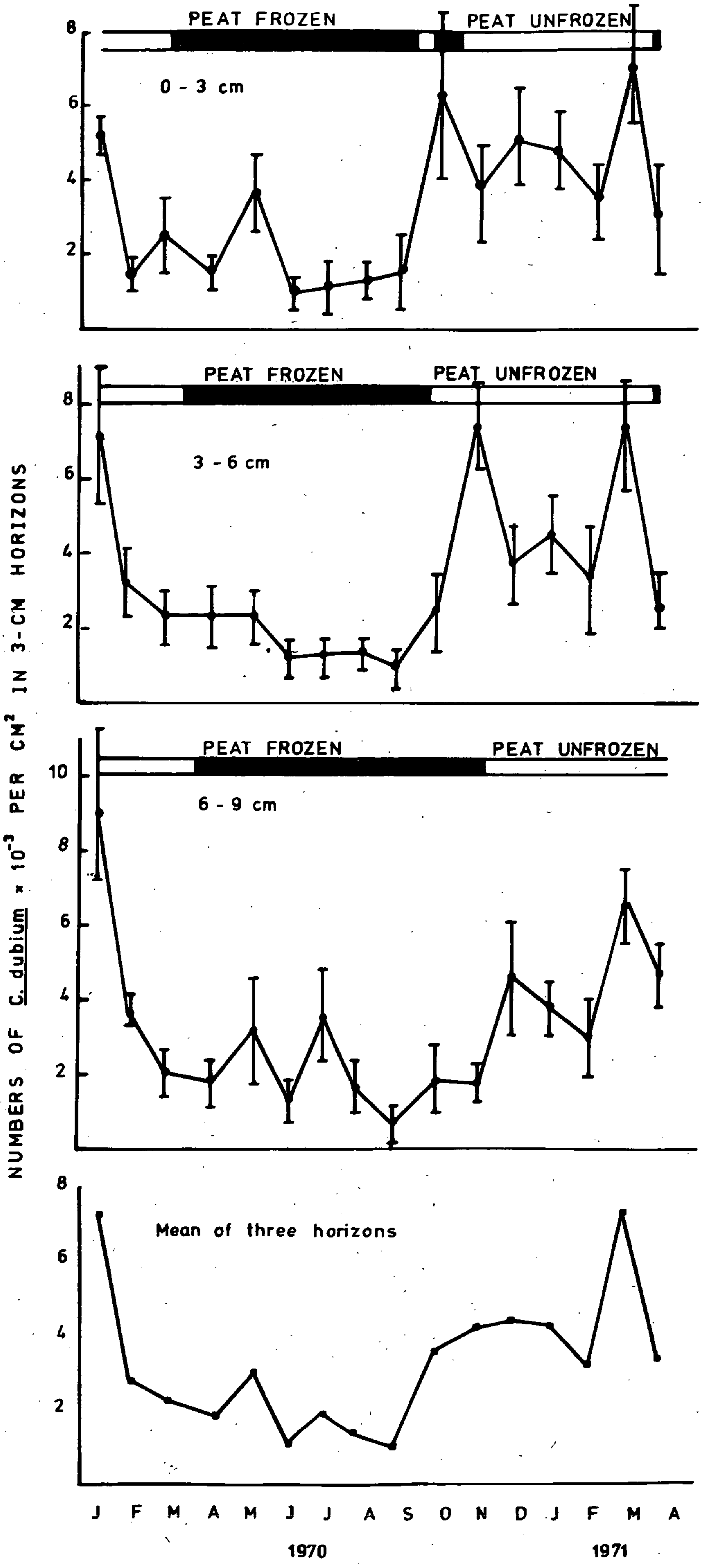


TABLE 10: MEAN NUMBERS OF <u>C. dubium</u> IN THREE HORIZONS OF MOSS TURF PEAT ± 95 % CONFIDENCE LIMITS

DATE	0 – 3 cm HORIZON		3 – 6 cm HORIZON		6 – 9 cm HORIZON	
	Numbers/cm^2	% Total testacida	Numbers/cm^2	% Total testacida	Numbers/cm^2	% Total testacida
16. 1.70	5,240± 520	46± 5	7,220±1,860	49± 5	9,250±2,010	45± 6
8. 2.70	1,390± 560	36±12	3,140± 910	36±12	3,700± 360	40± 4
6. 3.70	2,460±1,100	35± 8	2,280± 660	43±11	1,980± 580	41± 8
11. 4.70	1,460± 410	29± 8	2,350± 830	42± 9	1,680± 570	49± 8
15. 5.70	3,650± 960	49±12	2,300± 720	44±10	3,120±1,450	37±12
12. 6.70	930± 460	39±27	1,030± 390	32±12	1,190± 500	32±14
8. 7.70	1,110± 730	43±22	1,160± 500	45±25	3,470±1,210	54±10
5. 8.70	1,300± 480	44± 9	1,300± 440	40±13	1,600± 750	44±13
4. 9.70	1,550±1,050	44±21	900± 530	40±23	620± 520	42±24
6.10.70	6,460±1,960	51± 9	2,410±1,090	44± 9	1,760± 910	49±16
9.11.70	3,610±1,280	36±12	7,380±1,120	61± 5	1,650± 470	42± 8
5.12.70	5,050±1,300	53± 8	3,600±1,070	45± 8	4,520±1,560	50±10
5. 1.71	4,740±1,150	40± 4	4,370± 970	46± 4	3,690± 740	35± 3
6. 2.71	3,350± 970	42± 8	3,330±1,380	38± 7	2,850±1,010	38± 9
4. 3.71	7,060±1,520	47± 6	8,420±1,850	45± 6	6,460± 960	37± 5
29. 3.71	2,900±1,470	46±14	2,660± 770	44± 8	4,650± 800	44± 5

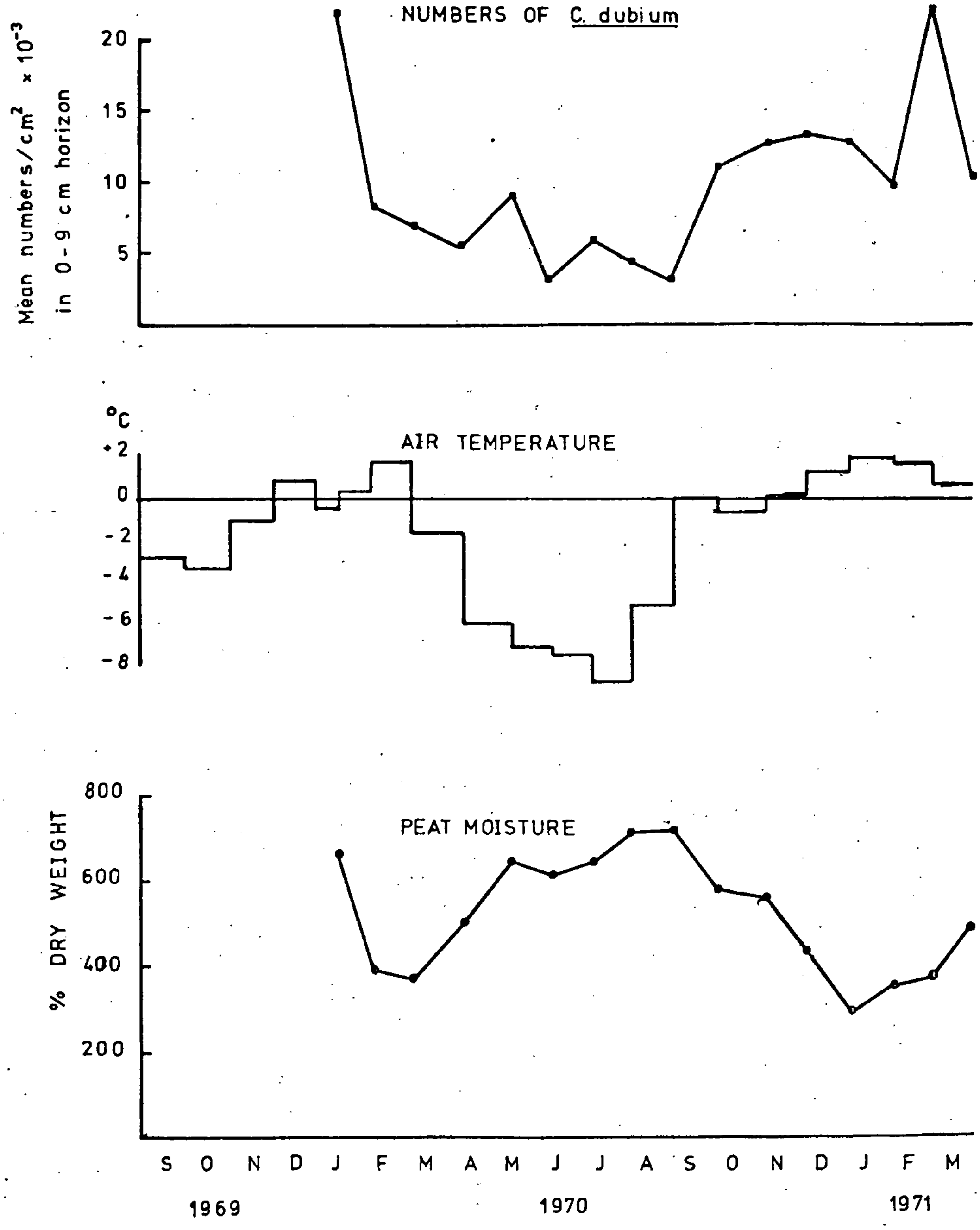


Fig. 17: Fluctuations in mean numbers of C. dubium in the 0-9 cm horizon of moss turf peat, monthly mean air temperatures and peat moisture

The pH of the peat however was fairly constant, being always between 3.5 and 4.5 in all three horizons. The loss on ignition of the peat was similarly constant being always between 94 and 97% (Appendix II).

The microclimate temperature regime of the site is plotted in Fig. 18. Temperatures are plotted as mean values for the periods between sampling occasions (of approximately one month). The values for 24 hours are exact means calculated from continuous thermograph records. The values for 0900-1600 are estimated means calculated from the thrice weekly thermometer readings; these are plotted with standard errors attached. Comparison of 77 temperature readings of the air at 1.5 m. at the site with the mercury-in-steel thermograph record of screen temperatures at Factory Cove revelaed a mean difference between them of only 0.1°C which does not deviate significantly from zero (t-test: $0.4 < p < 0.5$). Mean temperatures for month-periods calculated from the Factory Cove thermograph record are therefore considered to be accurate for the site ± 0.1°C. The mean temperatures for the air at 76 mm. (24 hour values) are calculated from the continuous bimetallic thermograph record in site. The trace recorded showed a clear diurnal cycle of temperature with peaks at mid-day. Typical examples of thermograph traces are shown in Fig. 19. The thermograph was subject to errors owing to heating of the screening box in sunlight; the trace was therefore corrected by the thermometer readings.

Other factors of the physical environment, for the same periods, are plotted in Fig. 20. The values for mean wind speed (index of convectional cooling) and for mean sunshine per day (index of incident radiation) refer to Factory Cove and are only an approximate guide to conditions at the site. Values of mean snow cover refer to the site; owing to extremely uneven cover of the moss stands by snow, the variance about these means is high, and they have standard errors of about ± 3 cms.

Fig. 18:

Temperature regime of moss turf. Plots are mean, temperatures for periods between sampling occasions, from June 1970 to March 1971, for the air at 1.5 m, and 76 mm, the moss surface and peat at depths of -15 mm and -45 mm.

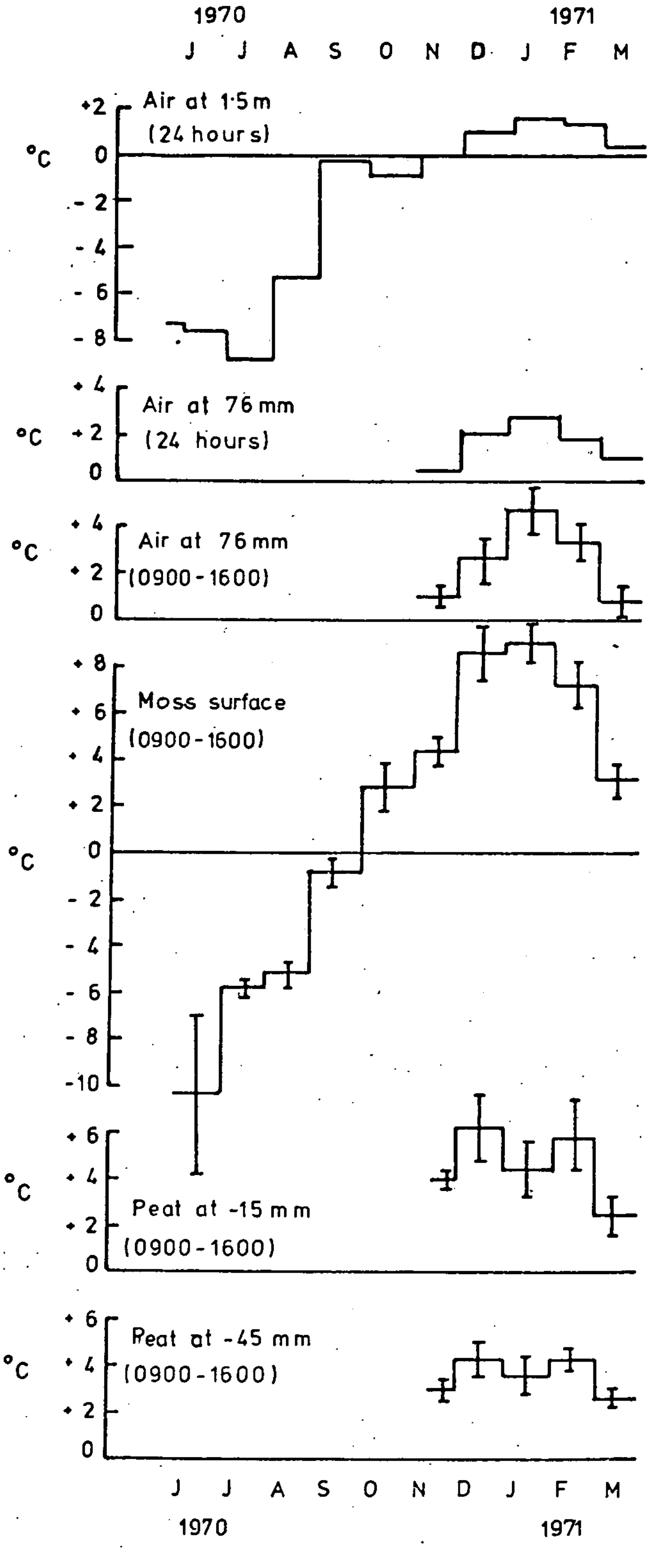
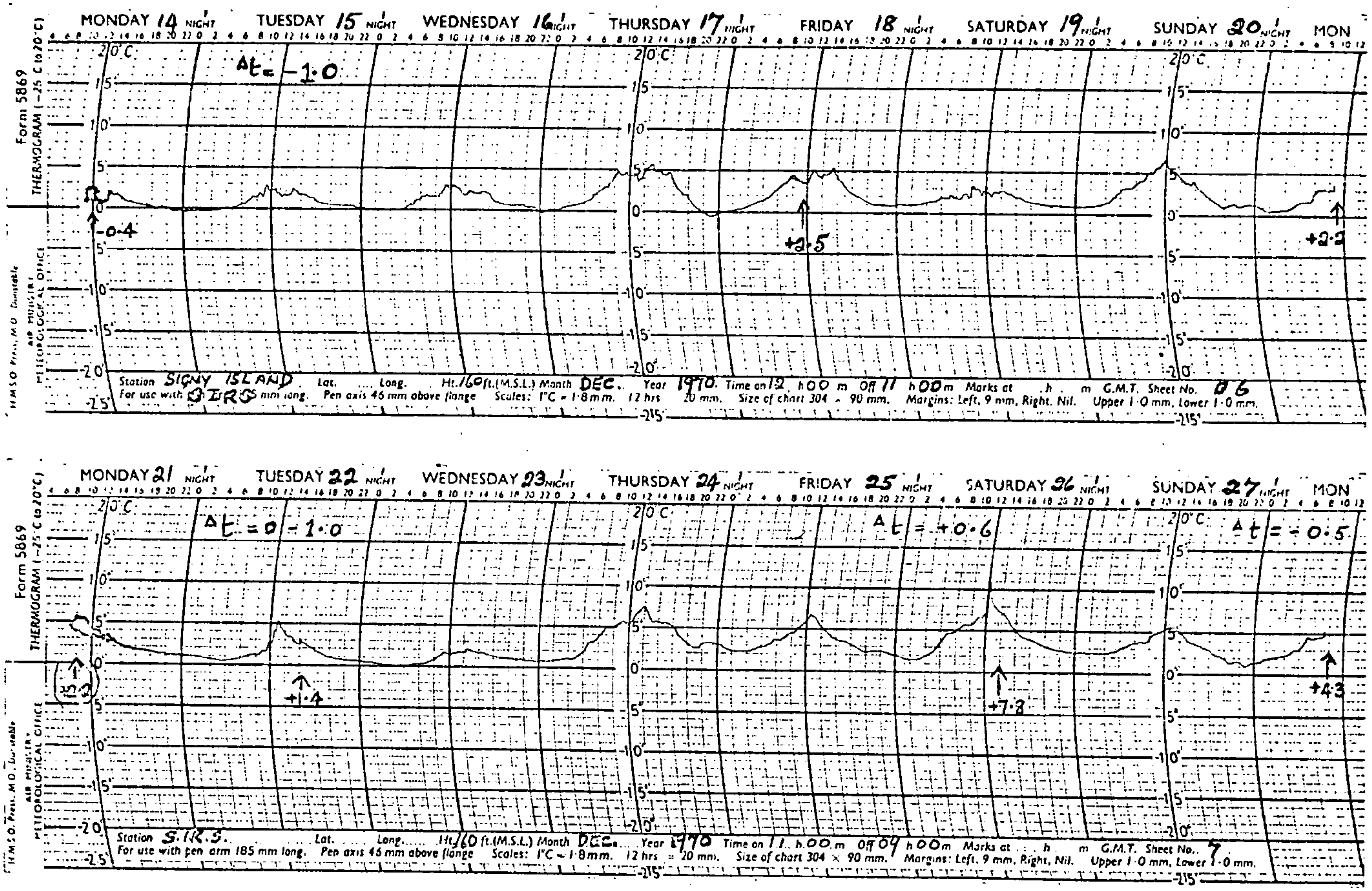


Fig. 19: Examples of the thermograph traces made by the thermograph recording temperatures at 76 mm above the moss surface



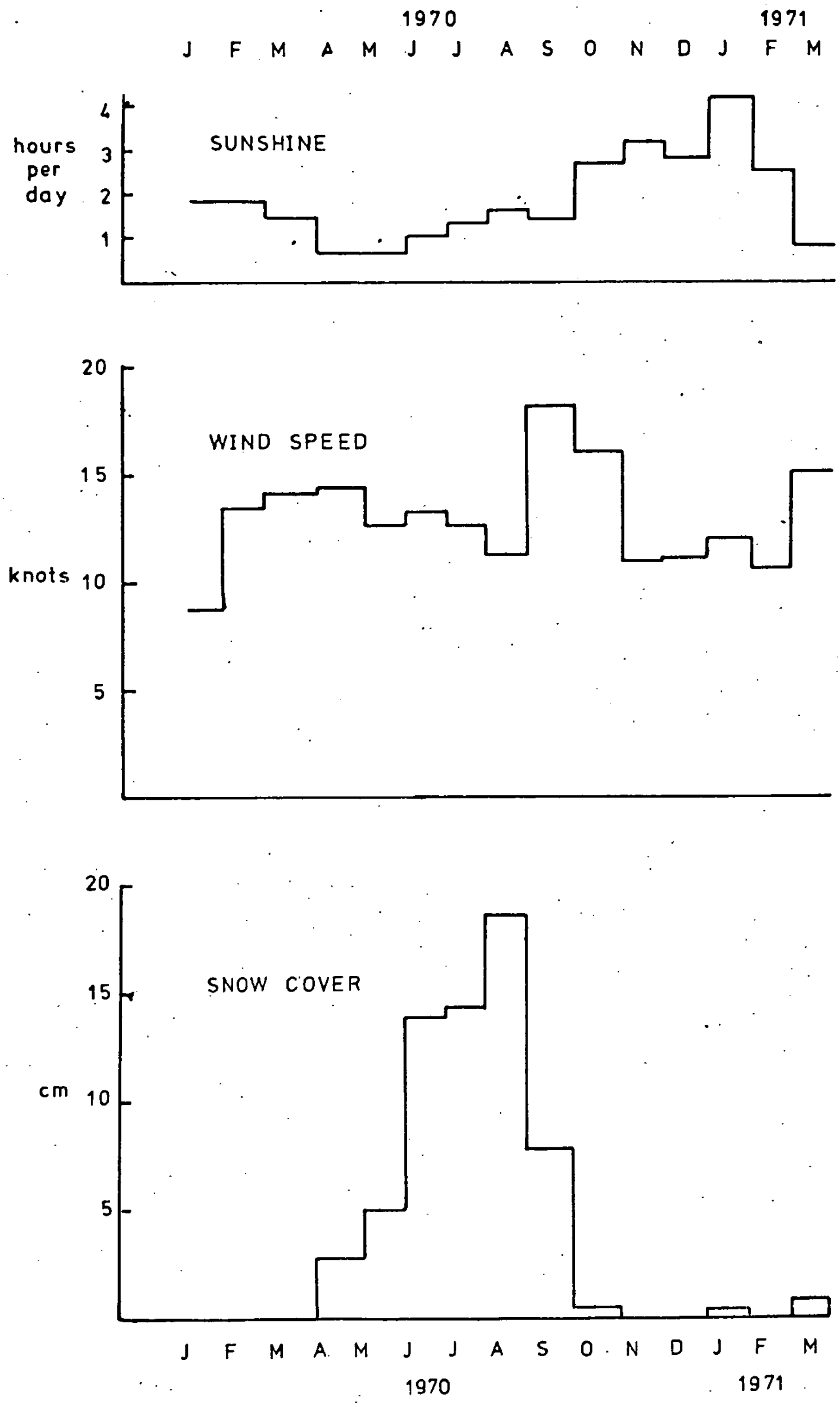


Fig. 20: Climatic environment of the moss turf site: Sunshine, wind-speed and snow cover. Plots are means for the periods between sampling occasions.

This means that the deep snow cover during the months July to early September 1970 is significantly greater than that before June and after September; otherwise the mean values for consecutive months are not significantly different. The data are therefore more useful in a qualitative sense - denoting the presence or absence of snow.

DISCUSSION

VERTICAL DISTRIBUTION OF C. dubium

No consistent differences in the numbers of C. dubium between the three horizons were apparent (Fig. 16). There was no evidence either of the sharp drop in numbers below the 0-3 cm horizon shown by metazoan species in similar habitats (Tilbrook, 1967), or of the increase in numbers with depth shown by bacteria (Baker, 1970).

SEASONAL VARIATION IN NUMBERS OF C. dubium

The data for the 15-month period of study (Fig. 16) show that there was a considerable difference in the numbers of C. dubium between winter and summer. In each horizon a dramatic increase in numbers occurred with the thawing of the peat during September to November 1970; this was possibly causally related to peaks in the numbers of yeasts and bacteria which have been observed following a thaw in a similar moss turf peat (Baker, 1969). Increases in extractable phosphate, ammonium and sodium ions have also been shown to occur in peat on Signy Island at this time of year (Northover and Allen, 1967). This "spring bloom" in the population of C. dubium occurred progressively later at increasing depths of peat as the thaw extended downwards (Fig. 16). The thawing occurred while the air temperatures were still sub-zero (Fig. 17); presumably the necessary heat came from absorbed radiant energy. After increasing during October to December, the numbers of C. dubium remained relatively high until the onset of freezing conditions at the end of March, when numbers again decreased.

Air temperatures at 1.5 m (Fig. 17) show that the summer of 1970-71 was considerably milder than that of 1969-70, the period September 1970 to March 1971 being consistently warmer by an average of 1.6°C than the same period the previous year. Given this difference between the years, it is possible that the high numbers of C. dubium in January 1970 represented a single mid-summer bloom in a cold short summer (though the absence of population data for 1969 means that this cannot be proved), while the long mild summer of 1970-71 allowed both an early spring bloom and a late autumnal bloom (Fig. 16).

SHORT-TERM VARIATION IN NUMBERS OF C. dubium

Whilst the numbers of C. dubium follow the annual cycles of temperature (directly) and peat moisture (inversely) on a seasonal scale (Fig. 17), there are no simple correlations between numbers and environmental factors on a month to month basis. The data therefore require more sophisticated scrutiny. The data plotted in Fig. 16 refer to the standing crop population of C. dubium at points in time; for an understanding of this species' ecology, its rates of activity over periods of time are more useful. To aid interpretation the data have been converted using the logistic equation:

$$\underline{r} = \frac{\log_e N_t / N_o}{T}$$

where N_o = Number of C. dubium on a sampling occasion (at time 0)

N_t = Number of C. dubium on the next sampling occasion (at time t)

T = Time in days between consecutive sampling occasions (time t − time 0).

r is the geometric rate of population growth or mortality; it constitutes an index of the net activity of the population (positive or negative) over the period of time T.

To obtain a measure of the activity of the C. dubium population relative to the total testate fauna, the following equation has been used:

$$\underline{d\%N} = \left(\frac{N_t}{A_t} \times 100\right) - \left(\frac{N_o}{A_o} \times 100\right)$$

where A_o = Number of all testacida at time 0

A_t = Number of all testacida at time t.

A positive value of d%N indicates that the C. dubium population has grown more rapidly (or died off less rapidly) than the rest of the testate fauna; a negative value indicates the reverse. The parameters r and d%N for each of the three peat horizons are plotted in histogram form in Figs. 21, 22 and 23.

The plots of r for all horizons show the burst of spring activity in September, October or November 1970, further activity in February-March 1971, and the high mortality at the onset of winter in late March. An apparent anomaly is the high positive value for r in the 6-9 cm horizon in the middle of winter (Fig. 23). This is possibly a result of sampling error - when numbers are low as they are in winter, a small increase in absolute numbers, due to random error, will appear as a relatively large geometric increase.

An interesting feature of the plots (Figs. 21, 22 and 23) is the correlation of r with d%N which is significant for the 0-3 cm and 3-6 cm

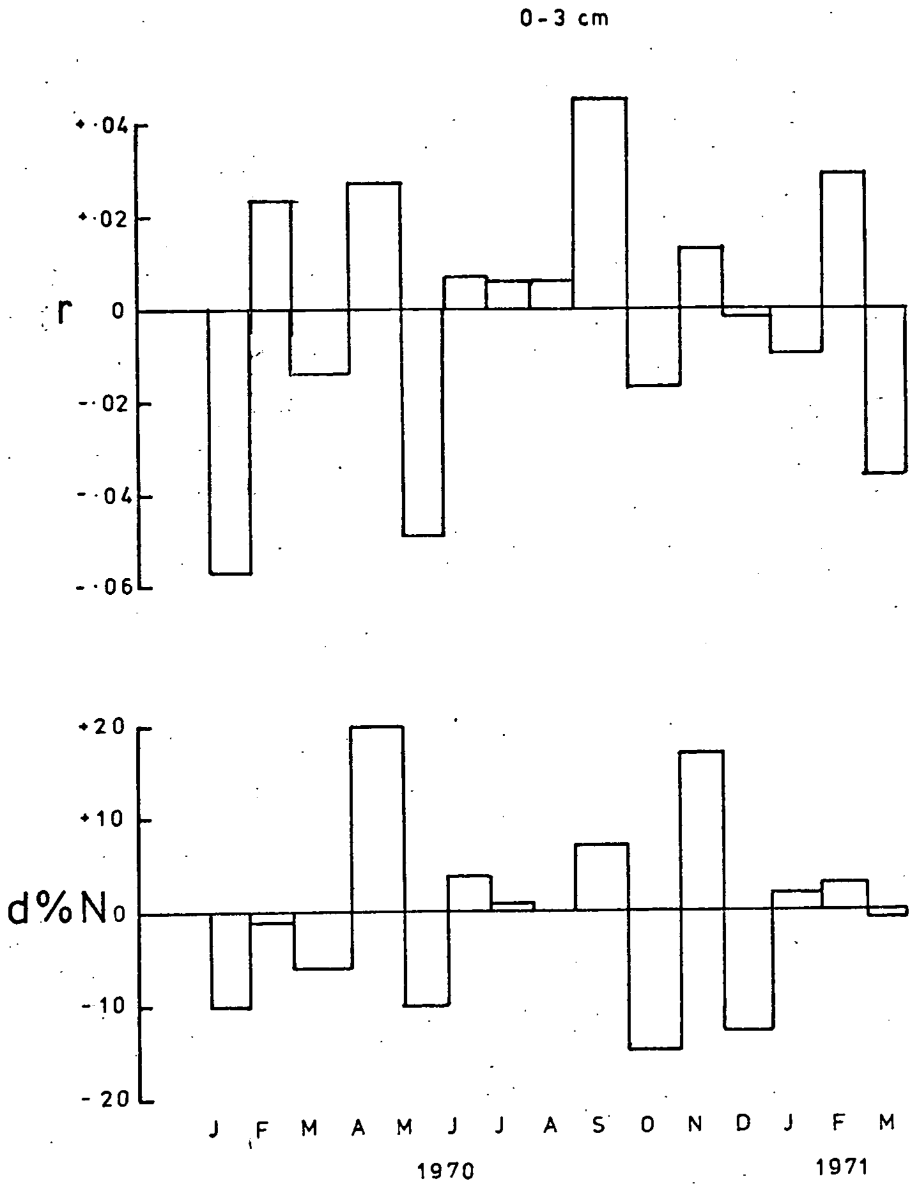


Fig. 21: <u>r</u> Geometrical rate of population growth or mortality of <u>C. dubium</u>

<u>d%N</u> Arithmetic change in numbers of <u>C. dubium</u> as % total testacida

0-3 cm horizon of moss turf peat

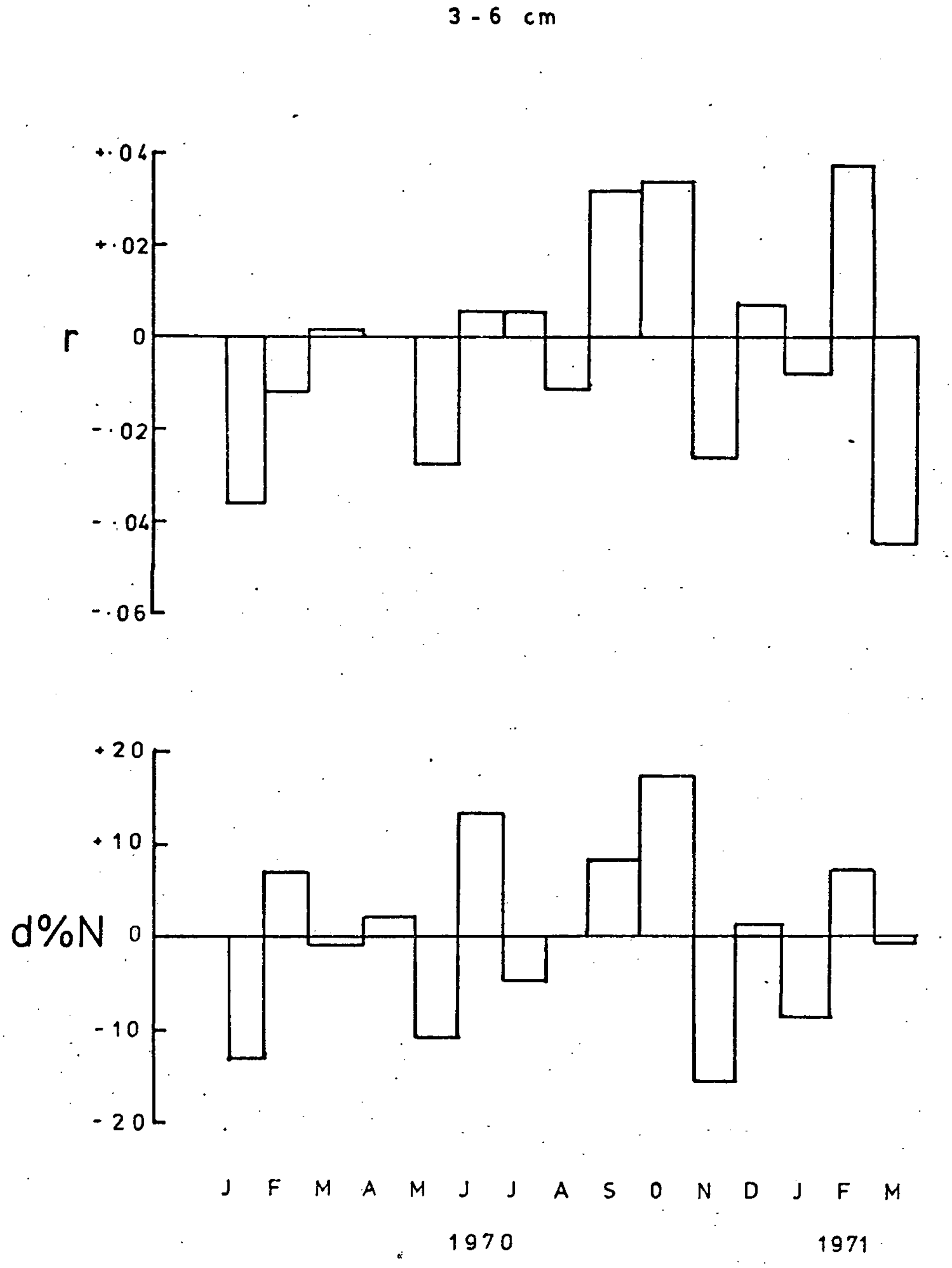


Fig. 22: r Geometric rate of population growth or mortality of C. dubium

d%N Arithmetic change in numbers of C. dubium as % total testacida

3-6 cm horizon of moss turf peat

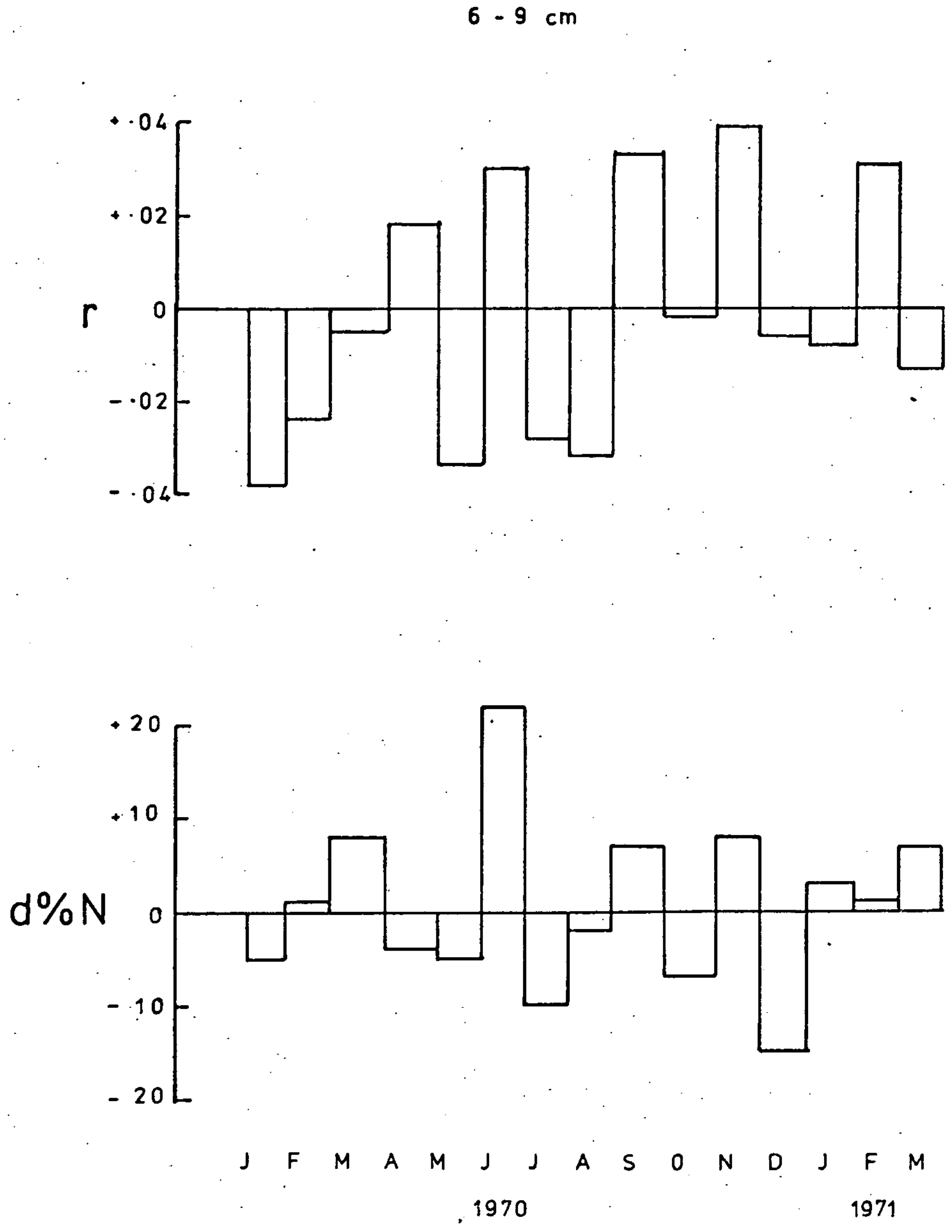


Fig. 23: r Geometric rate of population growth or mortality of C. dubium

d%N Arithmetic change in numbers of C. dubium as % total testacida

6-9 cm horizon of moss turf peat

horizons: Spearman's rank correlation coefficient:

0-3 cm $\rho = 0.81$ $P < 0.001$
3-6 cm $\rho = 0.70$ $P < 0.01$
6-9 cm $\rho = 0.35$ $P < 0.2$

If all species of testate in the peat showed simultaneous growth and mortality, *d%N* would be independent of *r*. That this is not so indicates that the growth and mortality of the *C. dubium* population was in some degree asynchronous with the rest of the testate fauna - when *C. dubium* increased, other species did not behave similarly. It is possible that *C. dubium* responds more rapidly to changes in environmental conditions than other species and so has come to occupy a dominant position in the fauna.

Figs. 18 and 20 show that, during the summer 1970-71, the warmest period and also the period of maximum sunshine was 5th January to 6th February, yet during this period there was net mortality of the *C. dubium* population in all horizons (Figs. 21, 22 and 23). However this was also the period of minimum peat moisture (Fig. 17). Previous observations on a similar moss turf peat by Baker (1969) indicated that lack of moisture in mid-summer may cause the numbers of bacteria to decline, and these were supported by experimental evidence which suggested that low moisture content depressed the repiration rate of the total peat community. It is therefore possible that, at this time of year, the *C. dubium* population was limited by moisture - either directly or as a result of limited moisture restricting the peat microflora. Further the mean temperature of the peat, between 0900 and 1600 (the time of maximum heating by radiation), was lower during this mid-summer period than during the periods immediately before and after (Fig. 18), despite maximum air temperature and maximum incident radiation (Figs. 18 and 20). This is an anomaly for which the data available are insufficient to account completely; however the following hypothesis provides a possible explanation:

During the summer daytime the moss absorbs solar radiation resulting in surface temperatures considerably greater than those of the ambient air (+ 17.5°C was recorded on 26 December 1970). The peat below is heated by conduction from the surface at a rate which depends upon the thermal diffusivity of the peat.

$$D = \frac{K}{d.s}$$

where D = Thermal diffusivity

K = Thermal conductivity

d = Density

s = Specific heat.

As the peat becomes drier water is removed from interstitial spaces and is replaced by air. This process will affect all three properties of the peat mentioned above, but will reduce conductivity more than density or specific heat since the conductivity of water is approximately 30 times that of air and (assuming there is no heat transfer by convection or percolation within the peat) the boundary layer resistance to the flow of heat from peat particle to air space is approximately 150 times that to the flow from peat particle to water space (Patten, 1909). The low moisture content of the peat in January 1971 will thus reduce the thermal diffusivity of the peat and so impede conduction of heat from the moss surface. Evidence in support of this is the fact that the mean temperature gradient below the moss surface, during the hours of maximum incident radiation (0900-1600) was at a maximum during this period:

Period	Temperature gradient from surface to 45 mm depth (°C per cm) ± standard error
5.12.70 - 5. 1.71	- 0.98 ± 0.15
5. 1.71 - 6. 2.71	- 1.42 ± 0.24
6. 2.71 - 4. 3.71	- 0.59 ± 0.14
4. 3.71 - 29. 3.71	- 0.36 ± 0.11

The slightly greater wind speed during January 1971 (Fig. 20) will also cause an increase in evaporation rate and consequently have a greater cooling effect on the moss surface. It is possible that the combination of these two effects could have resulted in the observed lower temperatures of the moss peat.

CHAPTER IV

ECOLOGY OF PROTOZOA IN CHINSTRAP PENGUIN GUANO

INTRODUCTION

On the coast of Signy Island there are several large areas occupied from late October to late April each year by colonies of breeding, and later moulting, chinstrap penguins - Pygoscelis antarctica (Chapter I, plate 5). Chicks are present during January and February. Penguins are completely absent in winter. Full details of the annual cycle of the chinstrap penguin on Signy Island are described by Conroy et al. (in press). The penguins deposit on the ground acid excreta (pH c. 5.9) and moulted feathers which, as a result of physical agitation by the penguins' feet and nest-building activities, become intimately mixed with previously deposited material and mineral material derived from the substratum. They decompose into guano described by Holdgate et al. (1967) as a black, alkaline, reducing mud containing high concentrations of extractable potassium, phosphorus and nitrogen.

While making the survey of terrestrial protozoa of the maritime Antarctic (Chapter II), it was found that the guano of chinstrap penguin colonies was inhabited by a small group of protozoan species, some of which occurred only in penguin colonies or other areas heavily contaminated by marine birds and mammals. In the association analysis these habitats were allocated to habitat classes III(i) and III(ii). Three species specific to such areas were:

Tetramitus rostratus Perty (Mastigophora: Polymastigida)
Philaster sp. Fabre-Domergue (Ciliata: Hymenostomatida)
Vorticella microstoma Ehrenberg (Ciliata: Peritrichida).

T. rostratus is known as a 'coprozoic' or 'coprophilic' species (Bunting, 1926; Brent, 1954); V. microstoma is very common in activated sludge particularly when the effluent is of inferior quality (Curds, 1969) and is an excellent indicator of 'polysaprobic' conditions (Kolkwitz and Marsson, 1909). Specimens of Philaster could not be identified to species level; they resembled Philaster (= Philasterides) armata Kahl, but were much smaller.

Penguin guano then, is a habitat for a group of protozoa adapted to alkaline (pH = 6.5-8.0), eutrophic, mobile conditions, with low organic content (loss on ignition = 30-45%), where the major habitat-determining factor is the biotic influence of penguins. It contrasts markedly with the acid (pH = 3.0-4.5), oligotrophic, stable conditions of moss peats with high organic contents (loss on ignition = 80-98%), where the major habitat-determining influence is vegetation. Testacida, which are abundant in moss peat (Chapter III), are entirely absent from penguin guano.

Areas on Signy Island which apparently were once penguin colonies or elephant seal wallows, but from which animals had been absent for an unknown number of years, were observed to be overgrown by Prasiola crispa Meneghini - a green alga described by Prescott (1954) as typical of arcto-alpine habitats and common on soil rich in nitrogen. One such area contained the three guano-specific species of protozoa listed above, and also some of the species belonging to 'Community A' (Chapter II, Association analysis) which tends to occur in mineral habitats and acid grass soils and moss peats:

Phryganella acropodia (Hertwig and Lesser) Hopkinson (Rhizopoda: Testacida)

Oxytricha fallax Stein (Ciliata: Hypotrichida)

Uroleptus sp. Ehrenberg (Ciliata: Hypotrichida).

Material from this Prasiola-covered area had a pH of 5.6 and a loss on ignition of 50-60%, characteristics intermediate between those of alkaline guano and acid moss peat.

A parallel phenomenon was observed in the nematode fauna by V. W. Spaull (personal communication): Caenorhabditis sp. (Osche) Dougherty was with rare exceptions the only nematode observed in chinstrap penguin guano, and it did not occur outside areas contaminated by animals. Areas which had become overgrown by Prasiola also contained Panagrolaimus sp. Fuchs, a species commonly occurring in animal-enriched habitats.

In view of their distinct habitat preferences, the three guano-specific species of protozoa already mentioned were selected as useful species for an intensive ecological study.

MODEL

In order to provide a conceptual framework for the study, a hypothetical model was constructed showing the relationships of ecological factors affecting the protozoan fauna. In the model the protozoa and the components of their environment were considered to form a web of dependent and independent variables (Fig. 24), the direction of causality linking two variables being indicated by an arrow. The model did not aim to represent the total environment of the protozoa - for instance the abundance in guano of bacterial food was not considered. It attempted to describe specifically the biotic influence of penguins upon the protozoan fauna through their effect upon some readily measureable properties of the guano: pH, moisture (per cent dry weight) and loss on ignition (per cent dry weight). It was considered that the significant effects of penguins were the supply of nutrients through the deposition of penguin litter (excreta and moult feathers), which supports the guano fauna and microflora, and physical agitation of the guano (trampling and

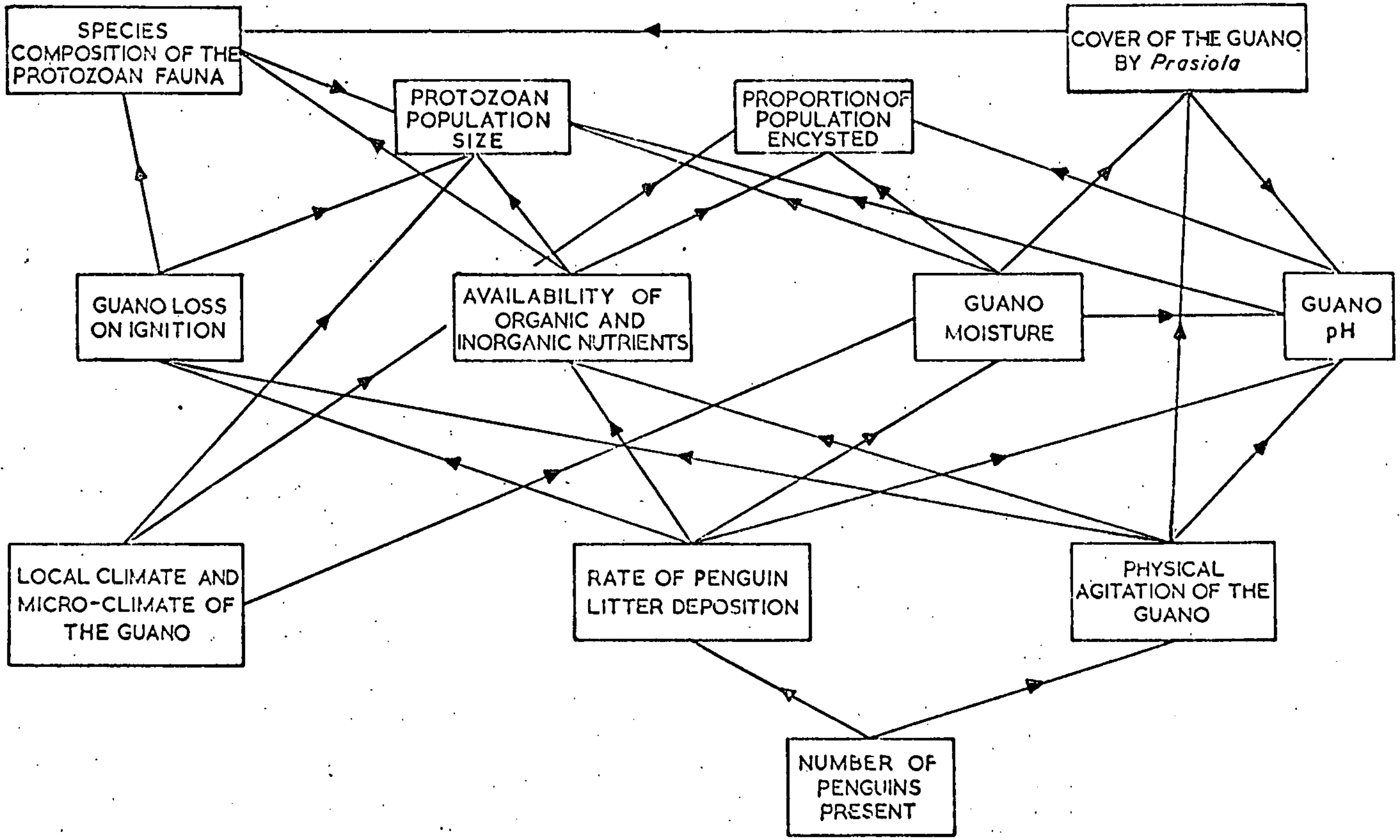


Fig. 24: Hypothetical model of the ecological relationships of protozoa inhabiting chinstrap penguin guano

nest building), which prevents the growth of vegetation. It was then predicted that, if penguins cease to occupy an area where guano had accumulated, the effects of their removal would be: a drop in guano pH, overgrowth of the guano by Prasiola crispa, increase in organic content (higher loss on ignition) and colonisation of the guano by more acid-tolerant protozoa. It was not known at what speed these changes would occur. Studies upon an Adelie penguin colony on Inexpressible Island (Campbell and Claridge, 1966) indicated that the abandonment of nesting sites by penguins resulted in chemical decomposition of the colony "soil" and leaching of carbon, nitrogen and phosphorus from the site, but they gave no indication of the time-scale of these processes.

There would be a lag between the attainment of suitable conditions for other protozoan species and the colonosation by them of the guano. However, since there is presumably a continual influx of wind-blown cysts of protozoa from other habitats in the vicinity, it was assumed that, despite a lag, once suitable conditions for the development of these species existed in the guano, their presence would be detectable the same season.

PENGUIN EXCLOSURE EXPERIMENT

To test the hypothesis a study of the guano-specific species of protozoa (Tetramitus rostratus, Philaster sp. and Vorticella microstoma) was carried out between December 1969 and April 1971, at a site within a chinstrap penguin colony at North Point, Signy Island (Fig. 25), consisting of an experimental area, from which penguin had been artifically excluded since September 1968, and an adjacent control area. On sixteen occasions at approximately monthly intervals the following measurements were made on a sample of guano, consisting of material from the 0-5 cm horizon, taken from six points at random, both within the exclosure and from the control area:

1. Total numbers each of T. rostratus, Philaster sp. and V. microstoma
2. Numbers of each of these species in an encysted state
3. Guano pH
4. Moisture (per cent dry weight) of guano
5. Loss on ignition (per cent dry weight) of guano.

The depths of snow and ice, if any, covering the site were measured on each sampling occasion. During the summer months the numbers of penguins occupying the control site were counted. Both adults and chicks were counted, and the adults classified as breeding (nesting, incubating or brooding), moulting or post-moulting. While the colony was snow-free during the second summer (November 1970 to March 1971), fortnightly measurements were made of the per cent area of guano in the exclosure colonised by macroscopic thalli of Prasiola, and of the rate of production of litter (excreta and feathers) per penguin per day in the control area.

No assessment was made of the local climate of the site, or of the microclimate of the guano. Throughout the period of the study, meteorological observations were made at the British Antarctic Survey base at Factory Cove, Signy Island, 4.3 km distant.

THE EXPERIMENTAL SITE

The site selected for study was an area of flat ground in the middle of the Chinstrap penguin colony at North Point (Fig. 25). The exclosure had been erected, and an unfenced control area staked out immediately adjacent to it, by V. W. Spaull in September 1968, before the arrival of the first penguins of the 1968-69 season. The colony was still under snow at this time and no preliminary tests were made for homogeneity of the guano in the exclosure and the control area. The exclosure had an area of 68 m^2, its size being limited by the availability of fencing materials, and the control an area of 198 m^2; it was hoped that these areas would be large enough to include sufficient within site variation to minimize variation between the exclosure and the control area. They had apparently the same local climate and drainage, and had snow cover of even depth in winter.

A view of the exclosure in November 1970 (early in the penguin breeding season) is shown in Plate 18.

The exclosure was a fence 80 cm high of chicken wire supported by wooden stakes held in stone-filled oil drums, and reinforced at the corners with guy-ropes. It was kept repaired as necessary. The fence was observed to have been breached by 30 moulting penguins on 25th February 1970; they were removed. Moulting penguins do not normally appear on the colonies in great numbers till after the beginning of March (Conroy _et al_, in press), so the breach must have occurred only a few days before it was observed. The influence of the intruders was therefore considered to have been minimal.

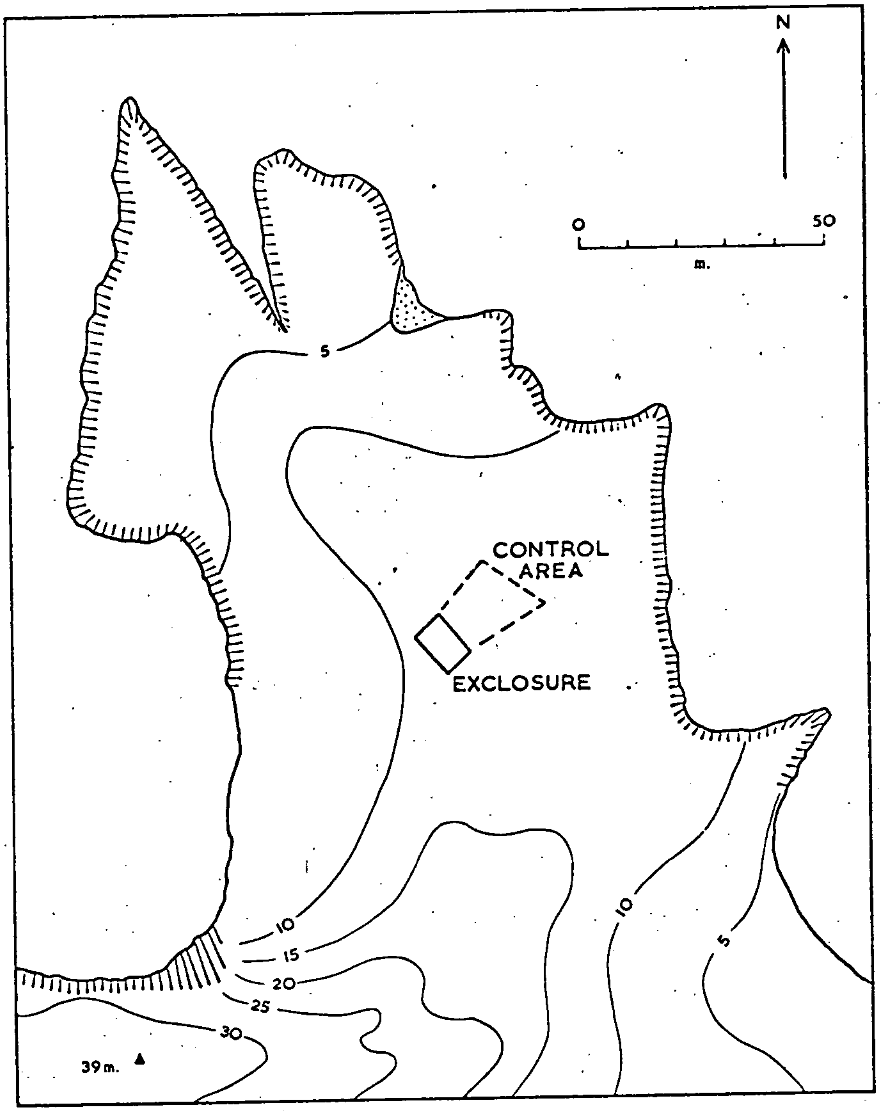


Fig. 25: Sketch map of the chinstrap penguin colony at North Point, Signy Island, showing the position of the experimental site

Contour lines are in metres.

Plate I8. Penguin exclosure in the chinstrap penguin colony at North Point, Signy Island, November I970

FIELD METHODS

Guano was sampled with a trowel in summer and with an ice-axe in winter. Samples were transported for laboratory examination in polythene containers.

Prasiola cover was measured by the point-quadrat method (Goodall, 1952). The quadrat frame was a one-metre length of wood bearing five 15 cm nails at random intervals. The nail points were sharpened to 100 μm diameter. 400 points throughout the area within the exclosure were examined by this method and scored as positive or negative for Prasiola.

The rates of litter deposition per penguin per day were obtained from pairs of penguins placed in a cage, lined with a polythene sheet, for 96 hours. The sheet was weighed at the beginning and end of the 96-hour period to determine the fresh weight of litter deposited; samples of the material were taken for dry weight determinations.

LABORATORY METHODS AND CALCULATION PROCEDURES

Protozoa in the guano samples were enumerated by a modification of Singh's (1955) dilution-culture method. A suspension of 5 g fresh guano in 20 ml 0.5% sterile saline was used to prepare a series of doubling dilutions of guano: 1/5, 1/10, 1/20, 1/40 and 1/80. Cultures were established by inoculating 0.10 ml of each dilution into polypropylene rings (eight replicates at each level) on a soil extract agar base with Aerobacter aerogenes (NCIB 418) as food organism (Plate 19). Cultures were kept moist with 0.5% saline, incubated at 12°C for 14 days, then inspected for the development of protozoa. Each of the three species was scored as present or absent in each ring culture. Note was also taken of any hitherto unobserved species appearing in cultures of guano from the exclosure. A replicate enumeration procedure was performed on each sample using guano which had been treated with 2% HCl for 12 hours, the aim being to kill active cells, but to leave cycts unaffected. Numbers of protozoa per g of guano fresh weight were calculated from their frequency in the ring cultures by Fisher's method (Fisher and Yates, 1963):

$$Q_i = \frac{\text{Antilog}\,(\frac{X_i}{n} \cdot \log a - K)}{d \cdot v}$$

where Q_i = Number of species 'i' per g of guano fresh weight

X_i = Frequency of species 'i' in ring cultures irrespective of dilution level

n = Number of replicates at each level

a = Serial dilution factor

d = Dilution at highest level

v = Volume of inoculum in ml

K is obtained from Fisher and Yates (1963) Table VIII_2

95% confidence limits were attached to $\frac{X_i}{n}$ using as the mean value of its variance $\frac{1}{n} \cdot \frac{\log 2}{\log a}$. Separate upper and lower limits for each value of Q_i could then be calculated.

The pH of each sample was determined electrometrically; moisture by oven-drying at 100°C for 48 hours; loss on ignition by ashing in a muffle furnace at 450-500°C for 10 hours.

The quantity of penguin litter (excreta and feathers) deposited on the control area was calculated as:

$$T = \frac{n(b).f(b) + n(m).f(m) + n(p\text{-}m).f(p\text{-}m) + ch.f(ch)}{A}$$

where T = Quantity of litter deposited per m^2 per day

n(b) = Number of breeding adults present on the site

n(m) = Number of moulting adults present on the site

n(p-m) = Number of post-moulting adults present on the site

ch = Number of chicks present on the site

f(b) = Quantity of litter deposited per breeding adult per day

f(m) = Quantity of litter deposited per moulting adult per day

f(p-m) = Quantity of litter deposited per post-moulting adult per day

f(ch) = Quantity of litter deposited per chick per day

A = Area on control site in m^2.

Because there seems to be virtually no diurnal rhythm in the behaviour of breeding chinstrap penguins (Conroy *et al*, in press), counts of penguins present on the control area made at any time of day were considered to be representative of the 24 hours.

The per cent cover of the guano in the exclosure by *Prasiola* was calculated from the point quadrat results:

$$\frac{\text{Number of points positive for } \underline{\text{Prasiola}}}{\text{Number of points examined}} \times 100\%$$

From data given by Goodall (1952, Table 1), it was estimated that, since the nails of the point-quadrat were sharpened to 100 μm diameter, the error owing to the finite size of the 'point' would be about 1 or 2%. Significant changes in cover, increases or decreases, with time were assessed from χ^2 values calculated from 2 x 2 contingency tables.

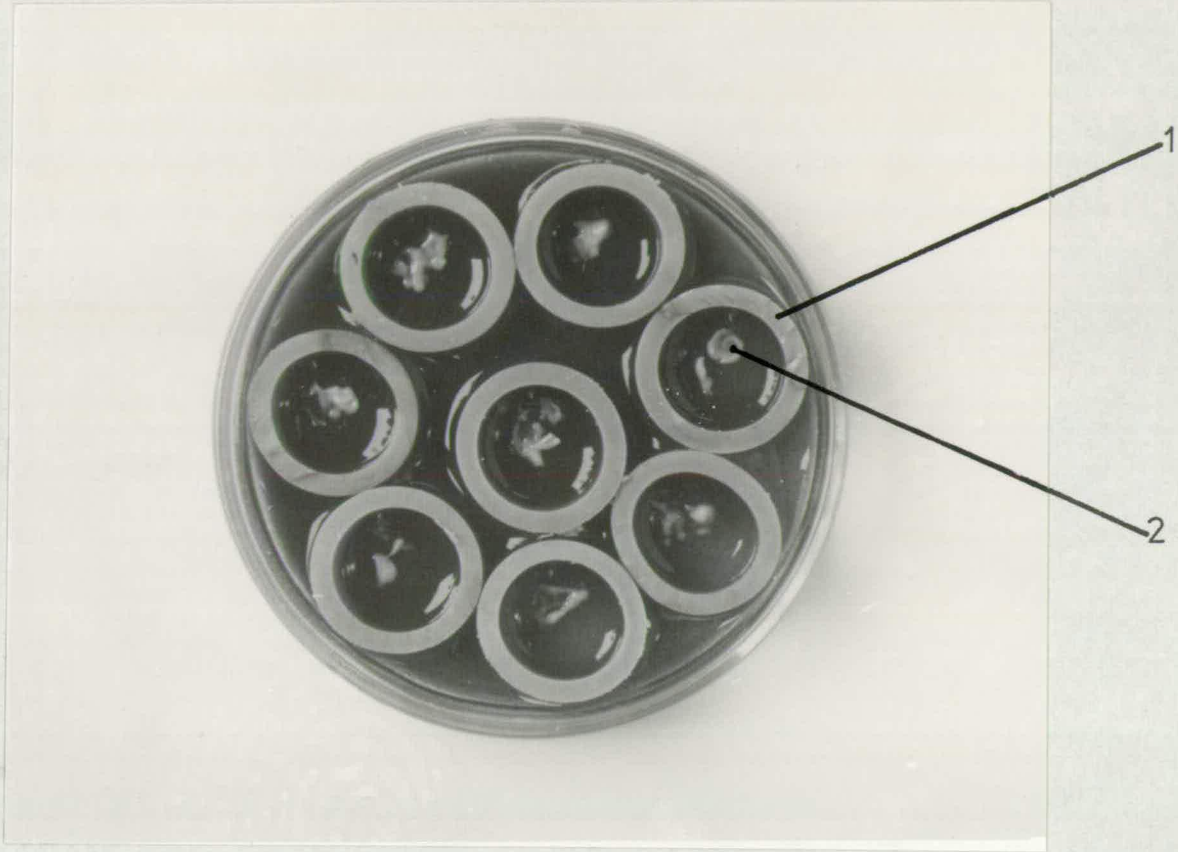


Plate I9. Culture plate used in the enumeration of protozoa by Singh's (I955) method.

I. Polypropylene rings embedded in soil extract agar base

2. <u>Aerobacter aerogenes</u> supplied as food source for protozoa

RESULTS

Numbers of the three protozoa species per g fresh weight of guano are plotted in Figs. 26, 27 and 28. The populations of Tetramitus were very much smaller than those of the ciliate species; their winter minima were almost undetectably low, while their summer peaks were always less than 100 per g (Fig. 26). Philaster was at all times the largest population, its numbers exceeding 100 per g on nearly every sampling occasion and a peak in the second summer reaching almost 1000 per g (Fig. 27), while the numbers of Vorticella dropped below 50 per g in winter and were never greater than 400 per g in summer (Fig. 28). Owing to the large estimation errors inherent in the dilution-culture method of enumeration, no significance can be attached to the month to month variation in mean numbers during the winter. Significant results are the summer peaks in the numbers of all three species, and that the total populations over-winter in an encysted state. There appear to be no consistent differences between the exclosure and control area in numbers of protozoa. No evidence was obtained of the guano in the exclosure becoming colonised by different species.

In order to elucidate the relationship between seasonal changes in the protozoan populations and those in the physical environment, the index I_j was calculated for both the exclosure and control area on each sampling occasion:

$$I_j = \frac{\sum_{1}^{3} \frac{(Q_{ij} - \bar{Q}_i)}{\bar{Q}_i}}{3}$$

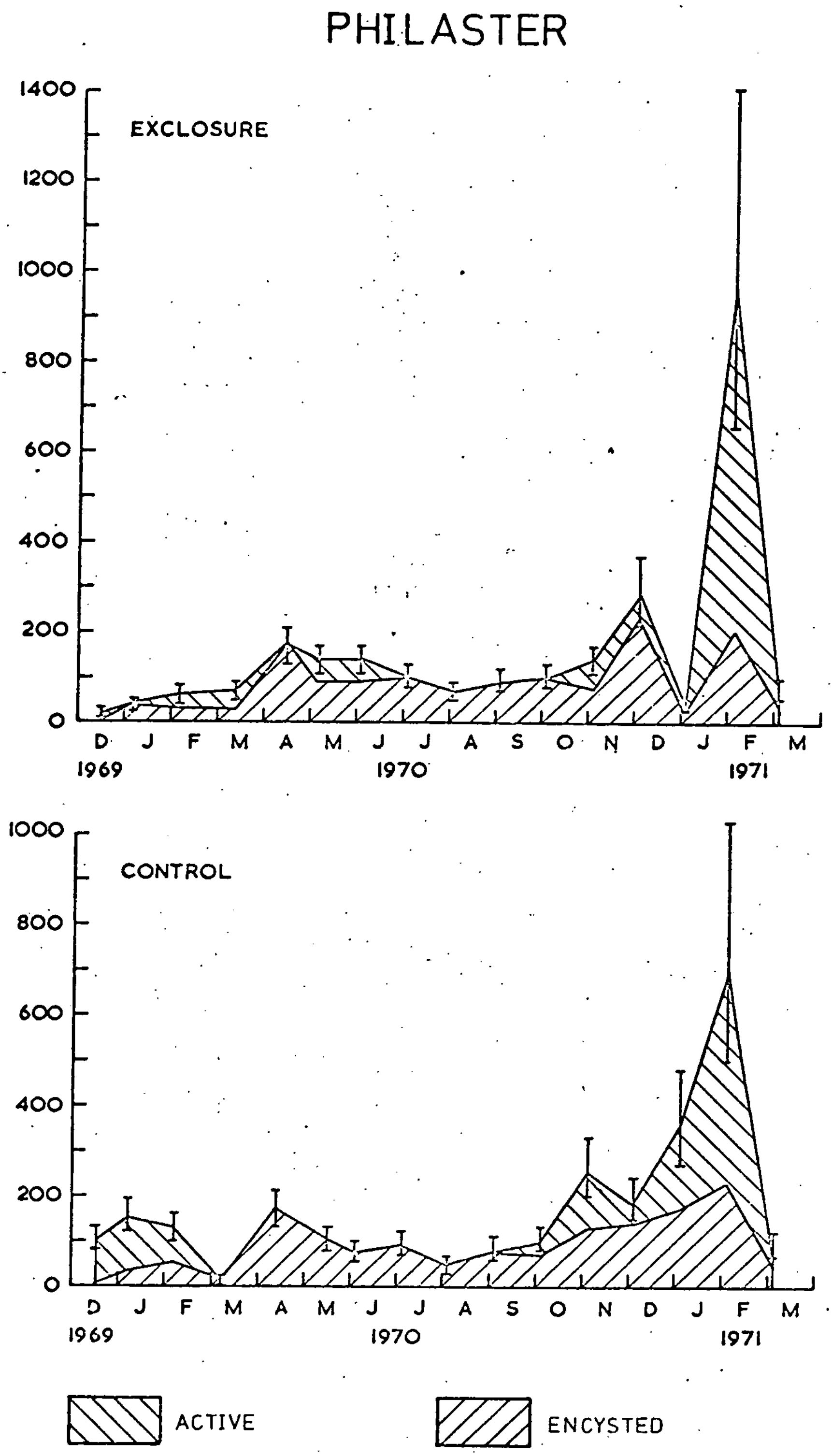


Fig. 27: Fluctuations in mean numbers of Philaster sp. per g guano (fresh weight) ± 95% confidence limits, from December 1969 to March 1971

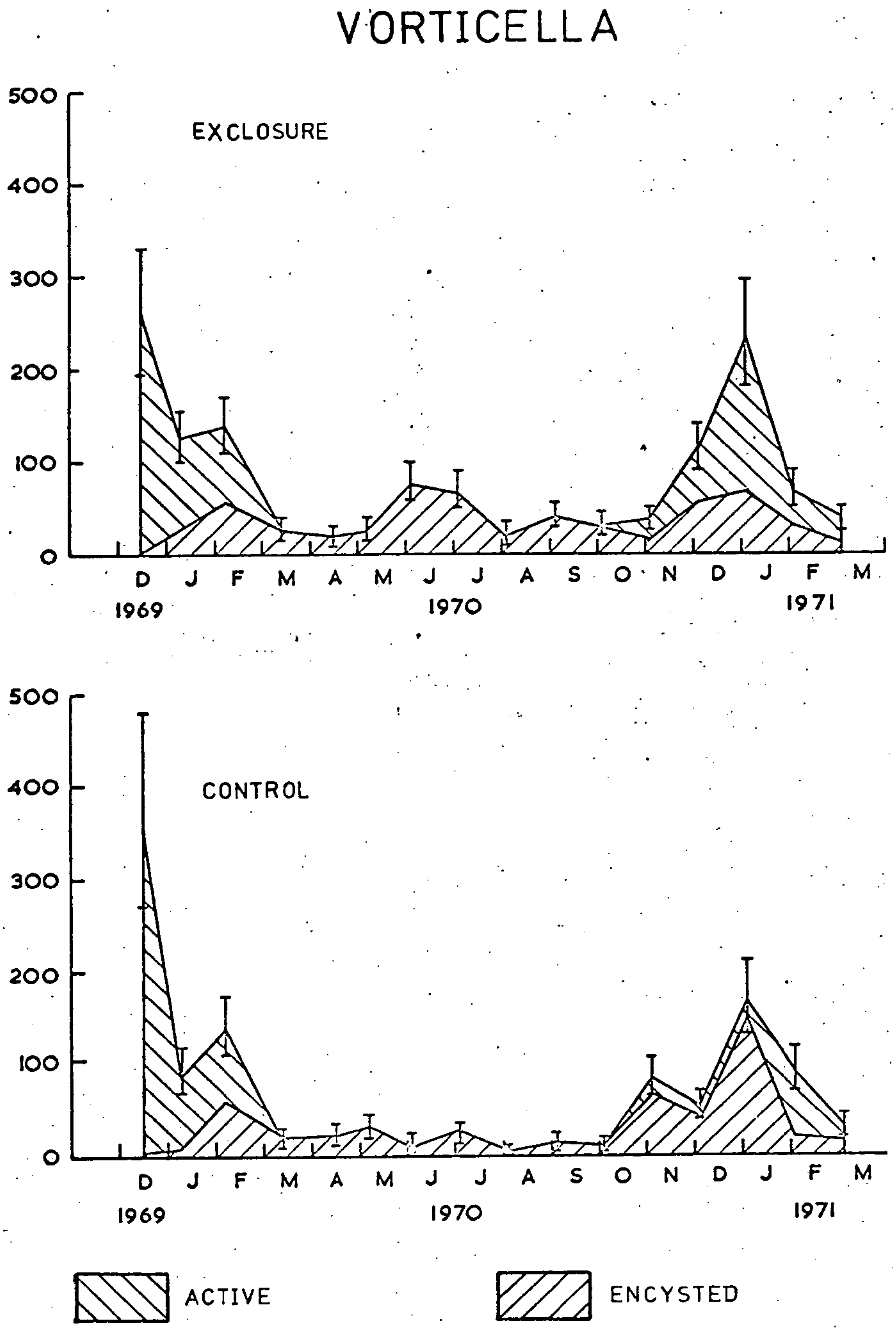


Fig. 28: Fluctuations in mean numbers of <u>Vorticella microstoma</u> per g guano (fresh weight) ± 95% confidence limits, from December 1969 to March 1971

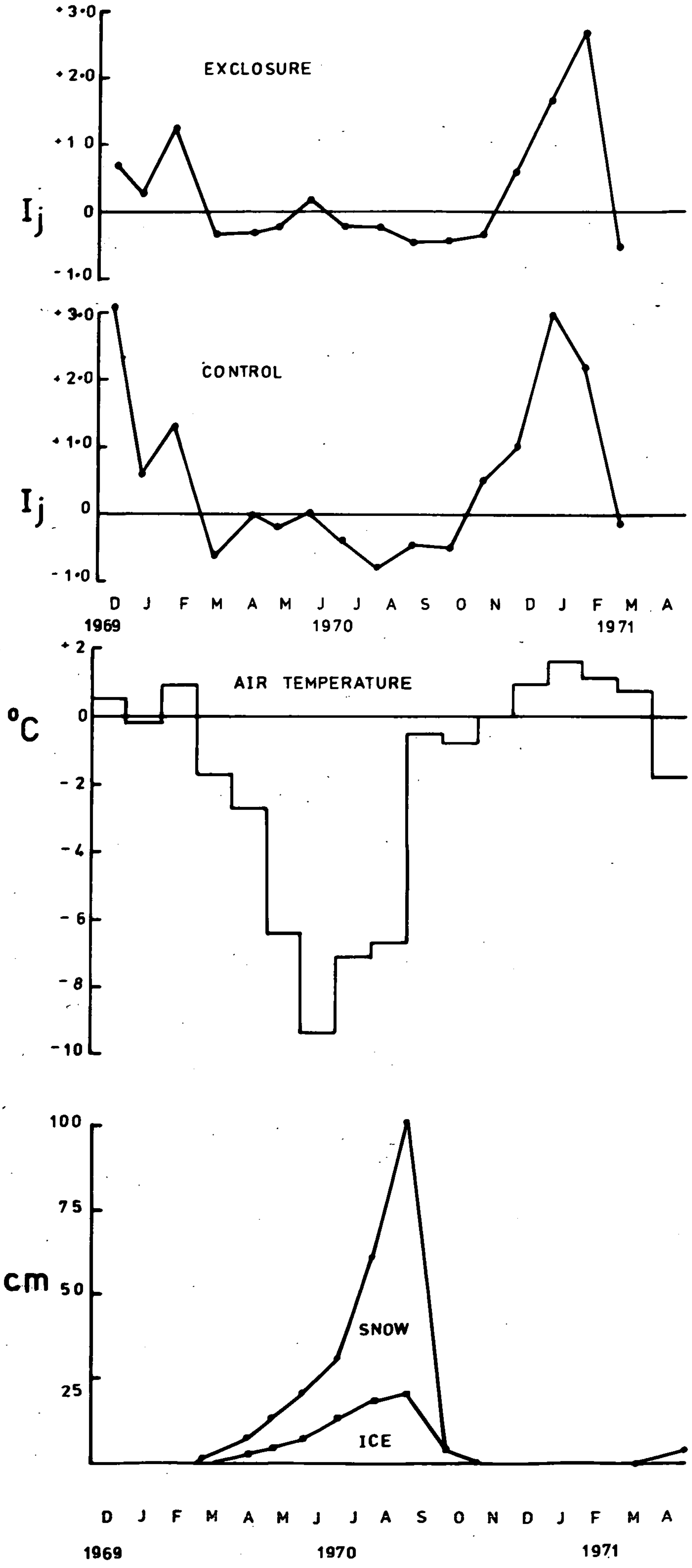


Fig. 29: Fluctuations in I_j (an index of the condition of the three protozoan populations combined), monthly mean air temperatures and snow cover on the experimental site, from December 1969 to March 1971

where Q_{ij} is the number of species 'i' per g fresh weight of guano on sampling occasion 'j'

$\overline{Q}_i$ is the mean number of species 'i' per g fresh weight of guano for the calendar year 1970.

I_j is an index of the condition, on a sampling occasion, of all three protozoan populations combined, with equal weight given to each of the three populations. Its values for the study period are plotted in Fig. 29 together with the depths of snow and ice at the site and the monthly mean air temperatures recorded in the Stevenson screen at the meteorological station, Factory Cove. I_j shows a similar seasonal pattern for both the exclosure and control area, with peaks in summer and low values in winter. From being snow-free in mid-summer 1969-70, the site experienced a build-up of snow and ice through the autumn and winter until the thaw in September when the snow rapidly disappeared. The site was snow-free from early November 1970 until late March 1971.

The pH, moisture (% dry weight) and loss on ignition (% dry weight) of the guano, together with the differences between the exclosure and control for each of these properties, are plotted in Figs. 30, 31 and 32. There was considerable variation in all three properties during the period of study, but the only one showing a consistent difference between the exclosure and control was pH, which was always lower (by an average of 1.0 pH points) in the exclosure than in the control.

The rates of litter deposition per penguin per day, determined from caged penguins, were:

$f(b) = 5.67 \pm 0.44$ g

$f(m) = 24.14 \pm 0.64$ g

$f(p\text{-}m) = 14.79$ g

$f(ch) = 10.64 \pm 2.31$ g

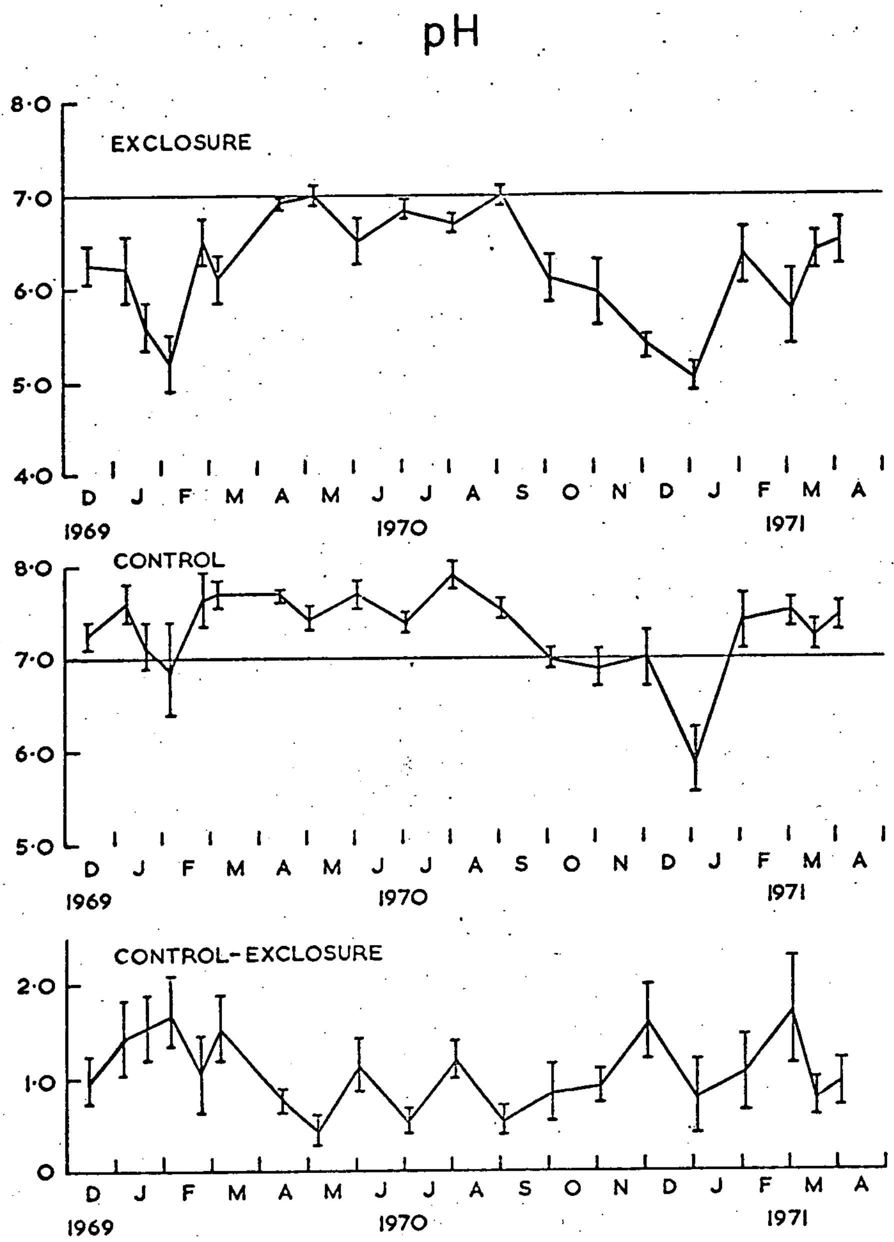


Fig. 30: Fluctuations in the mean pH of guano ± 95% confidence limits, from December 1969 to April 1971

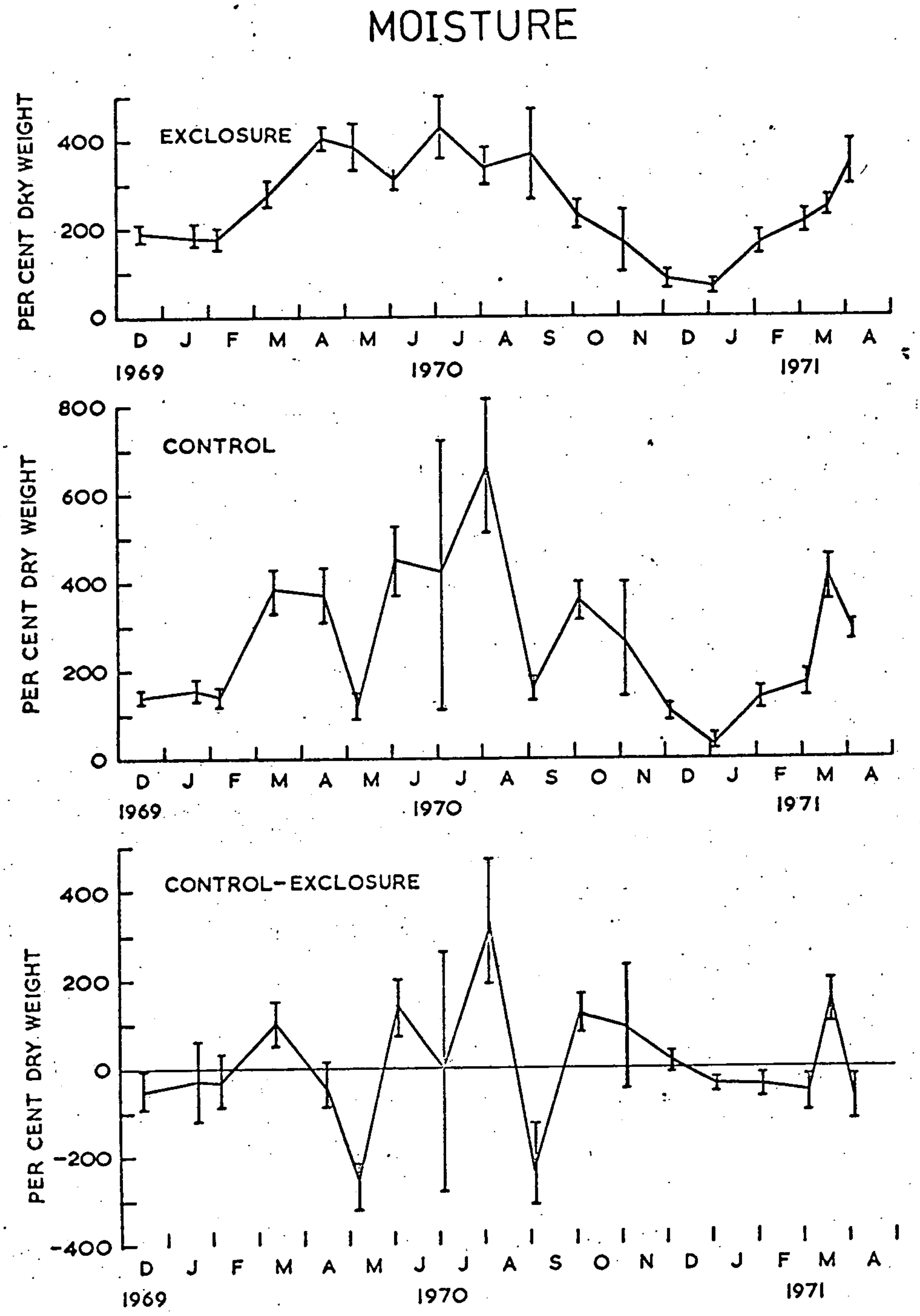


Fig. 31: Fluctuations in the mean moisture of guano (per cent dry weight) ± 95% confidence limits, from December 1969 to April 1971

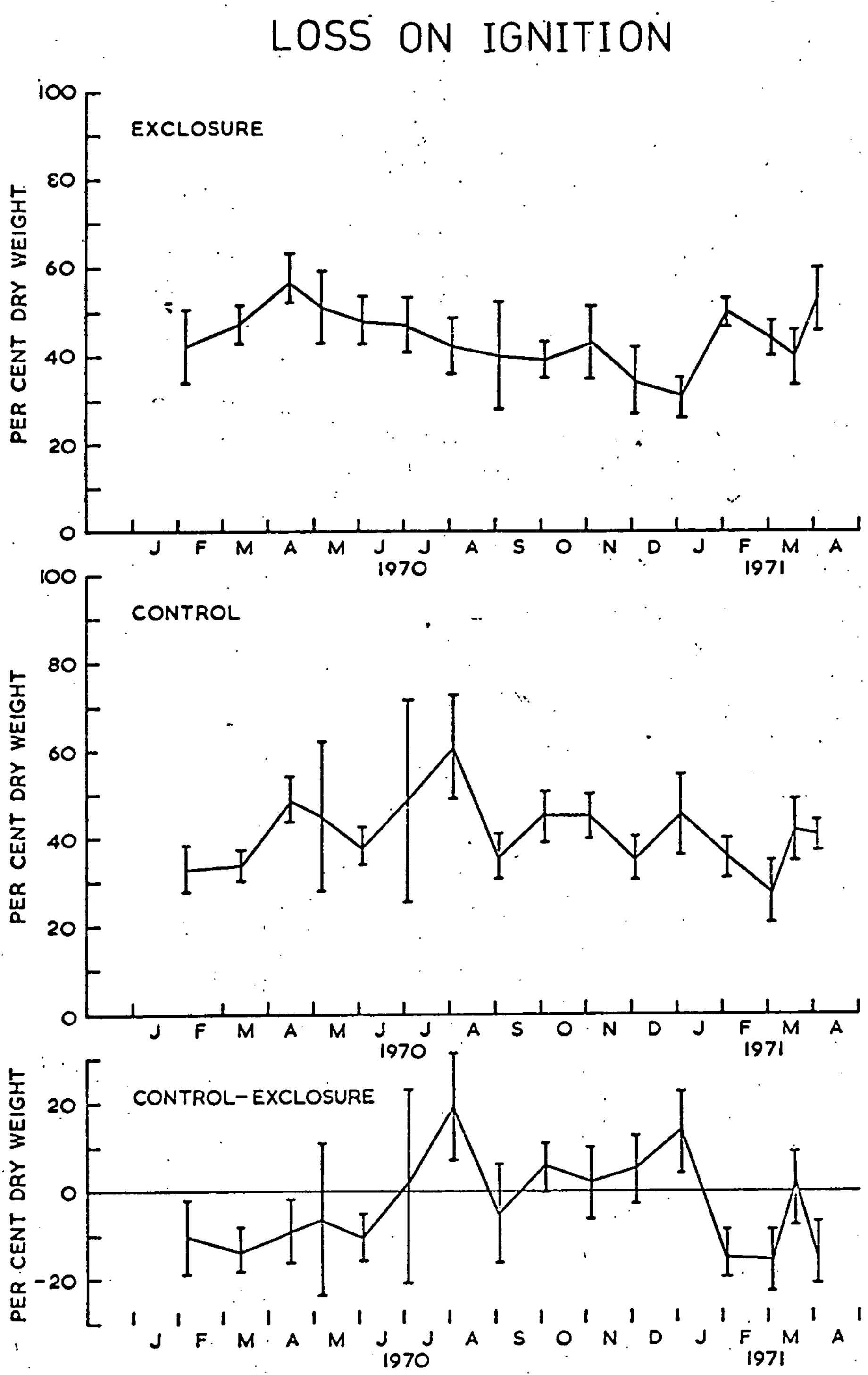


Fig. 32: Fluctuations in the mean loss on ignition of guano (per cent dry weight) ± 95% confidence limits, from February 1970 to April 1971

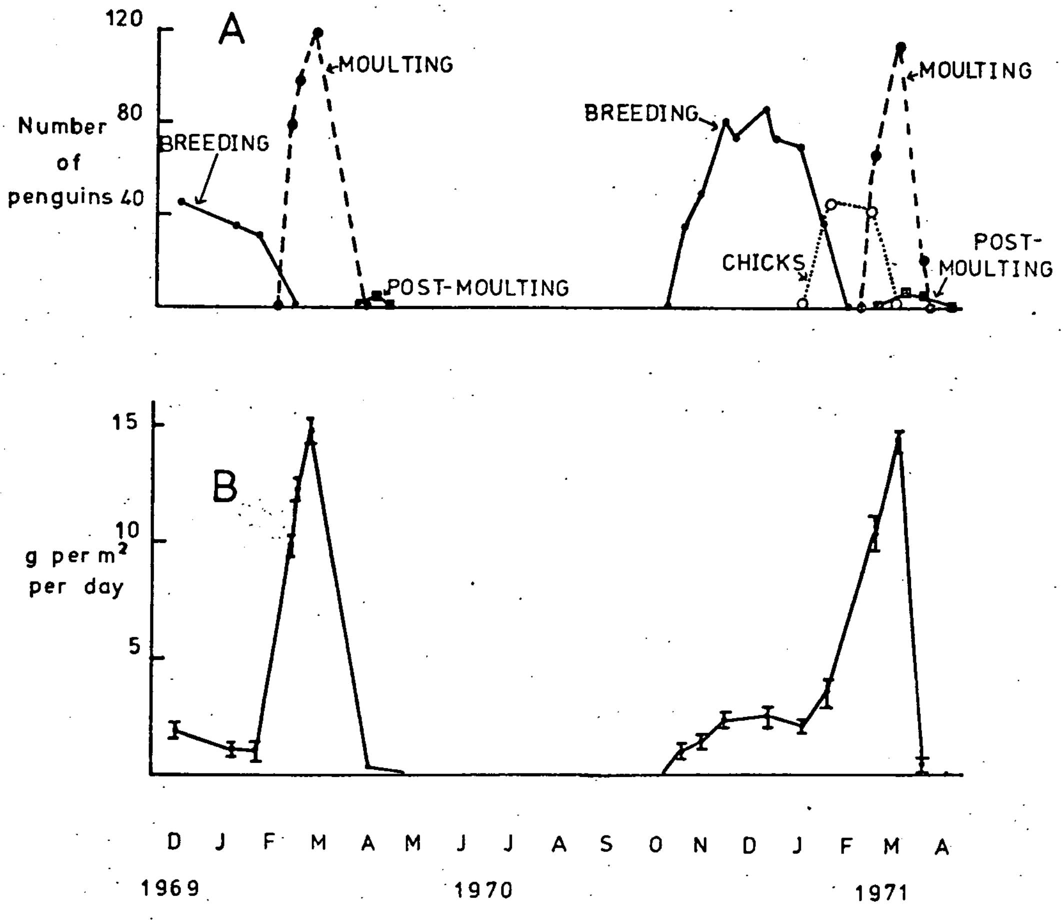


Fig. 33: A. Fluctuations in the numbers of penguins occupying the control site

B. Fluctuations in the rate of litter deposition by penguins on the control site

Significance of changes in cover:

*** P<0.001

** P<0.01

N.S. P>0.05

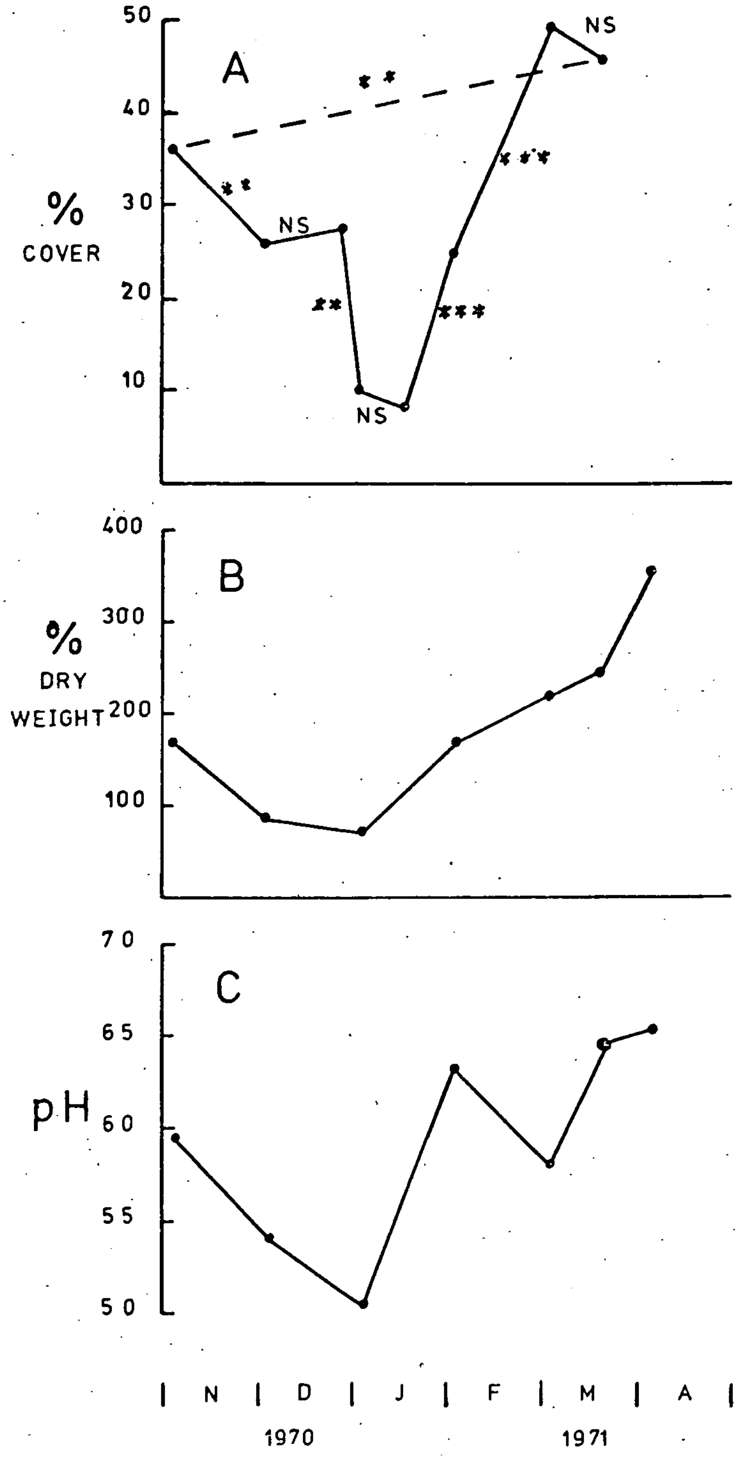


Fig. 34: Fluctuations in properties of guano in the exclosure from November 1970 to April 1971

A. Colonisation by Prasiola (% cover)

B. Moisture (% dry weight)

C. pH

The figures are means with 95% confidence limits, calculated from replicate measurements made on caged penguins. There were no replicate estimates of f(p-m), but as the number of post-moulting penguin was always very low (Fig. 33:A) any inaccuracy in the value of f(p-m) had a negligible effect. Moulting penguins showed a higher rate of litter deposition, and were present on the control area in greater numbers than penguins at other stages of the breeding cycle. They are therefore responsible for the greater part of the litter deposited on the control area, as shown by the coincidence of peaks in the numbers of moulting penguins (Fig. 33:A) with peaks in the rate of litter deposition per m^2 per day (Fig. 33:B) in March 1970 and March 1971. These peaks do not coincide with peaks in the numbers of protozoa which occur earlier in the summer (Figs. 26, 27 and 28).

No macroscopic thalli of Prasiola were ever observed in the control area but the guano in the exclosure was observed in both summers to be extensively colonised. The first quantitative measurement of Prasiola cover in November 1970 showed that the guano in the exclosure had 36% cover by macroscopic thalli (Fig. 34:A). During dry weather in December 1970 and January 1971 when guano moisture was extremely low (Fig. 34:B), there was considerable die-back of Prasiola; the thalli became dry and lost green pigment. They recovered rapidly with the return of moist conditions in February (Fig. 34:B). Between November and mid-March there was a small but significant net increase in cover of 10%.

DISCUSSION

The results suggest that variation in the quantities measured in this study can be attributed to three causes:

1. The influence of physical factors - particularly the annual cycle of ambient temperatures
2. The instantaneous influence of the presence or absence of penguins
3. The long-term influence of the presence or absence of penguins.

Clearly seasonal climate was responsible for the summer peaks in the numbers of all three protozoa species (Figs. 26, 27, 28 and 29). It is interesting to note that there were high numbers in early January 1971 (and a large proportion of these active) when the guano was extremely dry (Fig. 31). This contrasts with observations upon the testacida population in moss turf peat (Chapter III, Fig. 16) which showed a decline in numbers during this period.

The instantaneous influence of penguins is indicated by the figures for loss on ignition of the guano which showed no consistent difference between the exclosure and control, but did show a seasonal difference (Fig. 32). Whilst litter was being deposited (Fig. 33:B) it had the effect of maintaining a higher concentration of mineral matter in the guano so that the guano in control area had a lower loss on ignition than that in the exclosure during the summer. It is also possible that photosynthetic production by Prasiola was contributing organic matter to the guano in the exclosure. These influences did not operate in winter, and the guano in the control area had a higher loss on ignition than that in the exclosure.

The long-term influence of penguins is indicated by the consistent differences in pH and Prasiola cover of the guano between the exclosure and the control area (Fig. 30). Within season variation in Prasiola cover of the guano in the exclosure is positively correlated with guano moisture (Fig. 34): rank correlation $\varrho = 0.84$, $P < 0.01$. This suggests that it was necessary for the physical agitation of guano by the penguins to be stopped for macroscopic thalli of Prasiola to grow, but that the extent to which it could maintain cover depended upon an adequate supply of moisture. However, during January 1971 the guano in the exclosure, though very dry compared with its state the rest of the year, was significantly more moist than the guano of the control area (Fig. 31). It is possible that this was a feedback effect of the Prasiola cover upon the guano: the cover conserving moisture in the guano by reducing evaporation from the surface.

Seasonal variations in guano pH in both the exclosure and the control area are also positively correlated with moisture.

Rank correlations: Exclosure $\varrho = 0.89$, $P < 0.001$
Control $\varrho = 0.46$, $P < 0.05$

However, the differences in pH between the exclosure and control are not correlated with differences in moisture (rank correlation $\varrho = 0.19$, $P < 0.5$). It seems likely therefore that the consistently lower pH in the guano in the exclosure was caused by the absence of the penguins.

The results did not provide any evidence that the protozoan fauna of the guano in the exclosure had responded to changed conditions. No different species were observed and the numbers of the guano-specific species were rarely significantly different from those in the control.

A study of the nematode fauna of the guano in the exclosure and control area from 1968 to 1970 gave similar results (Spaull, personal communication). Apart from a few isolated specimens of Panagrolaimus, Caenorhabditis was the only nematode observed in the guano over the period of two years.

CONCLUSION

The predictions made by the original hypothesis regarding a decrease in guano pH and overgrowth of the guano by Prasiola in the absence of penguins have been fulfilled. It appears however that changes in the physical and chemical properties of the guano must proceed further before changes are observed in the protozoan fauna of the guano.

CHAPTER V

THE TEMPERATURE RELATIONS AND BI-POLAR BIOGEOGRAPHY OF THE CILIATE GENUS *Colpoda*

INTRODUCTION

Colpoda Ehrenberg is the most abundant and most widespread of soil ciliate genera. Colpoda cucullus Muller and Colpoda steini Maupas were recorded by Sandon (1927) from 103 soils in the tropics, northern and southern temperate zones and the Arctic. They have also been recorded from many parts of the world by other investigators (e.g. Dixon, 1939; Horvath, 1949; Gellert, 1955; Stout, 1963; Nickolyuk, 1963; Chardez, 1967; Bamforth, 1969). A survey of ciliates and testates in North America by Bamforth (1971) indicated that, in most of the soils and litters investigated (which extended from Alaska to sub-tropical Louisianna), more than half the ciliate population belonged to these species. Less frequently recorded than these two species but still common in soils are Colpoda maupasi Enriques (Sandon, 1927; Horvath, 1949; Nickolyuk, 1963; Chardez, 1967) and Colpoda inflata Stokes (Horvath, 1949; Gellert, 1955; Chardez, 1967; Stout, 1970).

Studies by Stout (1955) suggested that Colpoda spp have exceptionally good adaptation to soil habitats: small size, capacity to multiply rapidly under favourable conditions and ability to encyst rapidly in response to adverse conditions and excyst rapidly and continue growth and multiplication when favourable conditions return. The cysts can withstand extreme temperatures (Taylor and Strickland, 1936); they can remain viable for years (Goodey, 1915; Dawson and Mitchell, 1929).

Before the present studies on Antarctic protozoa were begun, it was confidently anticipated (in view of the observations reviewed above) that, if any ciliates at all were to be found in terrestrial habitats in the Antarctic, then Colpoda spp would be prominent members of the fauna. In the event, 37 species of ciliates were recorded from the maritime Antarctic, but none of the genus Colpoda (Chapter II). Nor have any other investigators (with one exception) observed Colpoda in the Antarctic. The exception was Sudzuki (1964) who recorded "Colpoda sp" from moss water at Langhovde (69°13'S; 39°45'E). However, many of his identifications are uncertain and this record must be regarded as doubtful.

The remarkable absence of Colpoda was all the more surprising because C.steini was observed in peat samples from the cool-temperate Falkland Islands, and both C. cucullus and C. steini in peat samples from sub-Antarctic South Georgia (unpublished observations, 1969-71).

The absence of a species from a particular locality may be attributable either to restrictions imposed by geographical barriers, or to the unsuitability of the local environment. As far as species of Colpoda are concerned, geographical barriers do not seem to be the cause: the maritime Antarctic islands are certainly remote, but this has not prevented their acquiring a fauna of many species of protozoa and other taxa; also C. cucullus and C. steini are present in the soils of Tristan da Cunha and St. Helena (Sandon and Cutler, 1924) which are islands equally remote. It seems likely, therefore, that some environmental factors are responsible for the absence of Colpoda from the Antarctic - low temperatures being the most obvious possibility. It may be objected that Colpoda spp have been recorded from several Arctic localities where mean temperatures are as low as, or lower than, those in the maritime Antarctic. However, there is also evidence from laboratory studies that Colpoda may be particularly sensitive to low temperatures: in the course of experiments using C. steini, Darbyshire (1972) was unable to detect any Colpoda cells in a culture which had been incubated at +5°C for one month, although they grew and multiplied in identical cultures incubated at 15° and 20°C.

HYPOTHESIS

From observations on the temperature relations and longevity of Colpoda (Dawson and Mitchell, 1929; Stout, 1955), it appears that resting cysts of Colpoda could certainly survive maritime Antarctic winters. However, since any terrestrial organisms which survive polar winters do so under an insulating layer of snow, it is the summer and not the winter temperatures that are of critical importance. It is,therefore, suggested that it is the Antarctic summer which is too cool and short for Colpoda spp to maintain active multiplication phases sufficient to establish themselves in terrestrial habitats, and that it is because Arctic lands which support a terrestrial fauna have longer warmer summers that Colpoda has been detected there.

This hypothesis may be examined in two ways:

(1) Compare the ability of Colpoda with that of other protozoan genera, which do occur in the maritime Antarctic, to survive and grow in single-species laboratory cultures incubated at low temperatures.

(2) Compare the climatic temperature regimes of the Arctic localities where Colpoda has been recorded with those of the maritime Antarctic islands where it has not. Ideally, ground and soil temperatures (those actually experienced by the protozoa) should be used, but because they are mostly unavailable, screen temperatures have been employed. However, areas with higher air temperatures than others will tend to have higher soil temperatures also, so air temperatures can be used for comparative purposes.

(1) CULTURE EXPERIMENTS

MATERIALS AND METHODS

A series of culture experiments was performed in order to compare the temperature relations of <u>Colpoda cucullus</u> (CCAP 1615/2) with those of three other species (one flagellate, <u>Bodo saltans</u> CCAP 1907/2; one rhizopod, <u>Euglypha rotunda</u> CCAP 1520/1; and one ciliate, <u>Philaster</u> sp. original isolation) which had been observed to occur in the maritime Antarctic (Chapter II).

<u>Colpoda</u> was cultured on lettuce infusion. 1.5 g dried lettuce were soaked in 1 litre distilled water and boiled for two hours. After cooling, the infusion was filtered and its pH adjusted to 6.8-7.0 with $CaCO_3$. Test-tube cultures were prepared with 5 ml of medium per tube. The tubes were autoclaved, inoculated with <u>Aerobacter aerogenes</u> (NC1B 418) when cool and incubated at 20°C. Protozoa were inoculated after 24 hours.

<u>Bodo</u> and <u>Euglypha</u> were cultured on <u>Erdschreiber</u> medium. Stock solution was prepared by boiling 500 g sterilized soil with 1 litre of tap water for two hours and, after settling, pipetting off the supernatant. The liquid was then centrifuged and the supernatant diluted: 50 ml stock made up to 1 litre with tap water. This 5% solution was pasteurised for two hours at 80°C. To every 20 ml of solution used, 0.05 ml of 4% $NaNO_3$ + 0.6% Na_2HPO_4 solution was added.

For <u>Bodo</u> test-tube cultures were prepared: 5 ml aliquots of pasteurised erdschreiber were poured aseptically into autoclaved test-tubes and a wheat grain, surface sterilised in boiling water, placed in each tube.

For <u>Euglypha</u> plate cultures were prepared using 36 mm petri-dishes; the bottom was covered with a thin layer of 1.5% agar and a surface sterilised wheat grain inserted just before the agar set; 5 ml aliquots of erdschreiber were poured aseptically onto the agar dishes when cool.

Immediately after preparation the tubes or plates of media were inoculated with *Bodo* or *Euglypha*.

Philaster was cultured on liver infusion medium prepared from:

Liver infusion (Oxoid L25)	20 g
Bacteriological peptone	10 g
NaCl	5 g
Distilled water	1 litre

and used without filtration. Test-tube cultures were prepared with 5 ml of medium per tube. The tubes were autoclaved, inoculated with *Aerobacter* when cool and incubated at 20°C. Protozoa were inoculated after 24 hours.

Protozoa were inoculated into media at room temperature (18°-20°C) and cultures subsequently transferred to incubators at experimental temperatures. The temperatures of cultures to be incubated at 12°C or less were decreased gradually (at a rate of -2°C per hour); similarly that were increased gradually to room temperature at the end of the experimental period of incubation.

Test-tube cultures were stoppered with cotton-wool bungs which effectively prevented losses by evaporation. To keep the atmosphere around plate cultures humid, they were placed inside larger petri-dishes together with a small open dish of distilled water.

Stock cultures of *Colpoda*, *Bodo* and *Euglypha* were grown at room temperature. *Philaster* did not grow successfully at room temperature; stock cultures were grown at 12°C.

The densities of protozoa in cultures were determined by counting the numbers of cells in samples of culture fluid of known volume.

Colpoda, *Bodo* and *Philaster* were motile cells at densities of the order of 10^4 per ml or more. To kill the cells 0.01 ml of Noland's stain-fixative (Noland, 1928) was added to a 0.05 ml sample of culture fluid. A count of the cells was then made with a haemocytometer.

Euglypha was more difficult to count as the cells in culture formed into clumps. Cells adhering to the agar base were first scraped clear with a micro-spatula so that they were suspended in the culture fluid. The fluid was pipetted into a Jorgensen bottle and shaken for 5 minutes to break up the clumps and disperse the individual cells. Because the cells were at densities of 10^2 or 10^3 per ml (too low for haemocytometer counting) a sample of culture fluid, volume 0.05 ml, was taken with a calibrated pasteur pipette and the total number of cells in it counted. As the cells were virtually non-motile, it was not necessary to kill them before counting.

Nine replicate counts were made on each culture so that a mean figure with 95% confidence limits could be obtained.

EXPERIMENTAL

Experimental cultures of each species were incubated at 7 temperatures:

0°, 4°, 10°, 12°, 15°, 18° and 25°C.

(The 10° and 18° cultures of Philaster were omitted.) Each culture of 5 ml was inoculated with 0.05 ml of a growing stock culture of known density, so that the initial density of the experimental culture could be calculated. Three replicate cultures were established at each temperature. After 14 days' incubation, the densities of the cultures at each temperature was measured. (Euglypha, being a testate rhizopod and growing more slowly than the other species, was incubated for 25 days.) When no cells could be detected, or only cysts were observed, incubation of the culture was continued at room temperature (12° for Philaster) and a sample of the culture inoculated into fresh media. After a further 14 days these were inspected for the growth of protozoa, a positive result indicating that the original culture contained viable cells at the end of its experimental incubation period.

RESULTS

The initial and final densities of cultures of each species are shown in Table 11. In the 0°C culture of Colpoda and the 25°C culture of Philaster no cells could be detected at the end of incubation, and no evidence of cells having survived was obtained from further incubation or from inoculation of samples into fresh media. In the 0°, 4° and 15°C cultures of Philaster, cysts were detected in numbers too low for a count to be made. Further incubation at 12°C showed these cysts to be viable. The survival of each species at each temperature at the end of incubation is summarised in Table 12.

In order to make a graphical comparison of the performances in culture of the different species, the ratio final density : initial density was plotted against incubation temperature. Graphs for Colpoda, Bodo and Euglypha are shown in Fig. 35. There was insufficient numerical data on Philaster for a graph to be plotted. The parts of the graph below the line $\frac{\text{Final density}}{\text{Initial density}} = 1$ indicate the relative ability of the different species to survive at low temperatures. The parts of the graph above this line indicate their relative growth performances at more favourable temperatures. Bodo showed faster growth and better survival than Colpoda at all temperatures; Euglypha showed slower growth than Colpoda above about 4°C, but considerably better survival below this temperature. In all three species, increased temperatures resulted in increased growth rates, though these appeared to be levelling out at about 25°C.

TABLE 11: INITIAL AND FINAL DENSITIES OF FOUR SPECIES OF PROTOZOA IN EXPERIMENTAL CULTURES INCUBATED AT A RANGE OF TEMPERATURES

SPECIES	INCUBATION TIME (days)	INITIAL DENSITY (cells/ml)	FINAL DENSITY (cells/ml) AFTER INCUBATION AT (°C):						
			0	4	10	12	15	18	25
Colpoda	14	$6.8 \pm 1.6 \times 10^3$	None detected	$2.9 \pm 1.1 \times 10^3$	$38 \pm 19 \times 10^3$	$48 \pm 17 \times 10^3$	$95 \pm 36 \times 10^3$	$340 \pm 87 \times 10^3$	$426 \pm 82 \times 10^3$
Bodo	14	$0.9 \pm 0.1 \times 10^4$	$0.3 \pm 0.1 \times 10^4$	$3.6 \pm 0.7 \times 10^4$	$31 \pm 3 \times 10^4$	$45 \pm 15 \times 10^4$	$50 \pm 15 \times 10^4$	$66 \pm 10 \times 10^4$	$109 \pm 19 \times 10^4$
Euglypha	25	$1.4 \pm 0.2 \times 10^2$	$0.3 \pm 0.1 \times 10^2$	$0.6 \pm 0.2 \times 10^2$	$0.8 \pm 0.2 \times 10^2$	$1.0 \pm 0.3 \times 10^2$	$7.3 \pm 1.6 \times 10^2$	$24 \pm 2 \times 10^2$	$69 \pm 5 \times 10^2$
Philaster	14	$0.8 \pm 0.1 \times 10^3$	Cysts present	Cysts present	....	$419 \pm 61 \times 10^3$	Cysts present	....	None detected

TABLE 12: THE INFLUENCE OF INCUBATION TEMPERATURE ON THE PRESENCE OF VIABLE CELLS IN EXPERIMENTAL CULTURES OF FOUR SPECIES OF PROTOZOA

SPECIES	INCUBATION TIME (days)	VIABLE CELLS PRESENT IN CULTURE AFTER INCUBATION AT (°C):						
		0	4	10	12	15	18	25
<u>Colpoda</u>	14	–	+	+	+	+	+	+
<u>Bodo</u>	14	+	+	+	+	+	+	+
<u>Euglypha</u>	25	+	+	+	+	+	+	+
<u>Philaster</u>	14	+	+	...	+	+	...	–

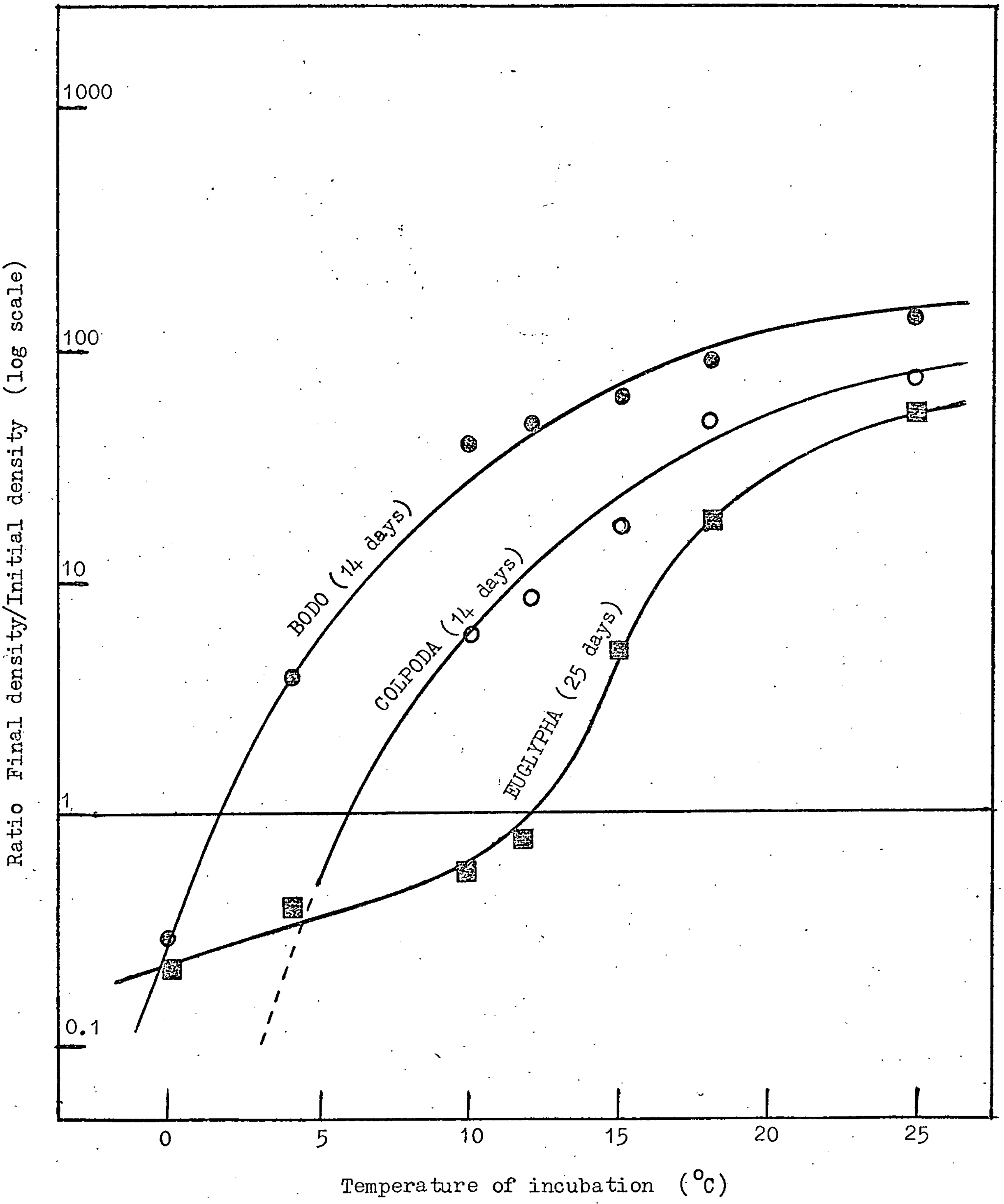


Fig. 35: Influence of incubation temperature on the growth and survival of three species of protozoa in single-species culture

DISCUSSION

The results show that viable cells of the three species recorded from the maritime Antarctic could be recovered from cultures which had been incubated at 0°C for 14 days (25 days for *Euglypha*), but that none was recovered from *Colpoda* cultures at the same temperature. Laboratory cultured organisms are in a highly artificial environment, so this data should not be considered as giving a precise indication of the ability of these protozoan species to survive or grow at various temperatures in their natural habitats. They do, however, allow inter-specific comparisons to be made, and the results show that *Colpoda* has less ability to tolerate low temperatures than the other three species. This result is consistent with the original hypothesis.

The fact that *Euglypha* grows less rapidly than *Colpoda* above 4°C (Fig. 35) might be thought to indicate that its numbers should, therefore, increase less rapidly than those of *Colpoda* during the Antarctic summer, and so the fact that it does occur in the maritime Antarctic in numbers sufficient to be detected requires further explanation. Data on the diurnal cycle of temperatures in moss peat on Signy Island (Longton and Holdgate, 1967) indicate that the temperatures of terrestrial habitats in the maritime Antarctic may oscillate very frequently above and below 4°C during the summer - perhaps once every 24 hours. If this is so, then the balance between growth and mortality under such environmental conditions might result in a net gain in the numbers of *Euglypha* but a net loss in the numbers of *Colpoda*, so that *Colpoda* would never become established in the fauna.

The results for *Philaster* are incomplete. It was found impossible to grow stock cultures of *Philaster* at room temperature and viable cells could not be recovered from the experimental culture incubated at 25°C, though they could be recovered from cultures at 0° and 4°C. This suggests that Philaster might be an obligate psychrophile but further investigation would be required to prove this.

(2) BI-POLAR BIOGEOGRAPHY

DATA COLLECTION

After a search of the literature, a list of sites in Spitsbergen, Greenland and Northwest Territory, Canada, from which one or more species of Colpoda had been recorded, was prepared together with a list of meteorological stations, each being the nearest one to the site of the Colpoda record for which temperature records were available. The following data were abstracted from the published meteorological records of each station:

1. Annual mean temperature
2. Monthly mean temperature (warmest month)
3. Monthly mean temperature (coldest month)
4. Mean temperature of the four warmest months.

Data for one cool-temperate site, the Faroe Islands, from which Colpoda had been recorded, was added to the list.

For comparison, a list of three maritime Antarctic areas, which had been examined for protozoan fauna (Chapter II) but had failed to reveal the presence of Colpoda, together with the same meteorological parameters, was prepared in a similar way. In this list, data for one sub-Antarctic site (South Georgia) and one southern cool-temperate site (Falkland Islands), from both of which Colpoda had been recorded, were included also.

The lists are shown in Table 13.

TABLE 13 RECORDS OF GENUS COLPODA AND TEMPERATURE IN POLAR AND COOL-TEMPERATE REGIONS

SITE	POSITION	HABITAT	SPECIES OF COLPODA RECORDED	AUTHORITY	METEOROLOGICAL STATION	POSITION	AIR TEMPERATURES ANNUAL MEAN °C	MONTHLY MEAN OF WARMEST MONTH °C	MONTHLY MEAN OF COLDEST MONTH °C	MEAN OF FOUR WARMEST MONTHS °C	PERIOD OF OBSERVATIONS	SOURCE OF DATA
NORTHERN HEMISPHERE												
Faroe Islands, Nolsoy	62°00'N; 6°40'W	Peat	C. cucullus, C. steinii	Original observation 1967	Thorshavn	62°01'N; 6°44'W	+7.1	+11.1	+3.9	+10.3	1931-60	(1)
Canada, Northwest Territory												
Fort Resolution	61°10'N; 114°00'W	Coarse soil with humus	C.steinii	Sandon, 1927	Fort Smith	60°00'N; 111°52'W	-3.2	+16.2	-25.4	+12.8	1931-60	(1)
Mission Providence	61°22'N; 117°59'W	Soil deficient in humus	C. steinii	Sandon, 1927								
Spitsbergen												
Prince Charles Foreland	78°30'N; 11°00'E	Black peat	C. cucullus	Sandon, 1924	Isfjord Radio	78°04'N; 13°38'E	-3.8	+5.0	-11.9	+3.3	1951-60	(1)
West Greenland												
Disko Island	69°30'N; 53°35'W	Soil	C. cucullus, C. maupassi C. steinii	Sandon, 1927	Jacobshavn	69°13'N; 51°02'W	-3.8	+7.9	-14.3	+5.8	1921-50	(2)
East Greenland,												
Angmagssalik	65°40'N; 37°40'W	Peat	C. steinii	Dixon, 1939	**Angmagssalik**	65°37'N; 37°34'W	-0.5	+7.3	-7.5	+6.0	1931-60	(1)
East Greenland, Scoresby Land												
Schaffhaverden	72°14'N; 25°30'W	Flushed soil, no vegetation	C. cucullus	Stout, 1970	**Scoresbysund**	70°25'N; 21°58'W	-7.3	+3.0	-16.5	+1.9	1948-60	(1) (2)
Kap Petersens	72°25'N; 24°30'W	Outwash sands	C. inflata	Stout, 1970	**Myggbukta**	73°29'N; 21°34'W	-9.7	+4.0	-20.4	+2.0	1932-39 and 1947-50	(2)
"Base Camp"	72°20'N; 24°15'W	Lichens and algae	C. steinii	Stout, 1970								
Mestersvig	72°14'N; 23°55'W	Salix soil	C. cucullus, C. inflata C. steinii	Stout, 1970								
SOUTHERN HEMISPHERE												
Falkland Islands,												
Stanley Common	51°42'S; 57°48'W	Heath peat (Empetrum rubrum)	C. steinii	Original observation, 1971	Stanley	51°42'S; 57°52'W	+5.5	+9.0	+2.2	+8.4	1951-60	(1)
South Georgia												
Hestesletten	54°17'S; 36°30'W	Tussock grass peat (Poa flabellata)	C. cucullus, C. steinii	Original observation 1969	Grytviken	54°16'S; 36°30'W	+2.0	+5.3	-1.5	+4.5	1951-60	(1)
South Orkney Islands 29 sites	60°36' to 60°45'S; 44°26' to 46°07'W	Moraines, mineral debris, moss peats, grass soil, animal guano.	NEGATIVE	Chapter II	Signy Island	60°43'S; 45°36'W	-3.6	+0.9	-9.9	+0.4	1948-70	(3)
					Orcadas	60°44'S; 44°39'W	-4.2	+0.4	-10.2	0.0	1931-60	(1)
Elephant Island 23 sites	61°04' to 61°14'S; 54°40' to 55°24'W	Moraines, moss peats, grass soil, penguin guano	NEGATIVE	Chapter II	Elephant Island	61°12'S; 55°09'W	....	-0.1	....	-0.5	December 1970 - January 1971	(4)
Argentine Islands 4 sites	65°15'S; 64°16'W	Moss peats	NEGATIVE	Chapter II	Argentine Islands	65°15'S; 64°16'W	-5.4	-0.1	-12.8	-0.6	1951-60	(1)

SOURCES:

(1) Climatic Normals for Climat and Climat Ship Stations for the period 1931-1960 WMO/OMM No.117 TP.52 (1971)

(2) Clayton (1934); Clayton and Clayton (1947); Conover (1959)

(3) Base records of British Antarctic Survey Base H (Signy Island)

(4) Observations of the Combined Services Expedition to Elephant Island, 1970-71, (R.M.G. O'Brien, personal communication)

DISCUSSION

Table 13 shows that the mean mid-summer temperatures for the Arctic areas from which Colpoda has been recorded, are in the range +3° to +16°C, whereas those for the maritime Antarctic areas are below +1°C, in spite of some of the Arctic areas being at much higher latitudes. The annual mean temperatures of these Arctic areas are mostly similar to those of the maritime Antarctic, though Angmagssalik, Greenland, is milder throughout the year, and in summer is even milder than sub-Antarctic South Georgia. Scoresby Land, Greenland, the coldest of the Arctic areas investigated, has an annual mean temperature 3° to 6°C lower than that of the maritime Antarctic, but still has a summer about 2°C warmer.

Fort Smith, situated in the middle of the continental land mass of Canada, has the greatest annual temperature range: its coldest month being 12°C colder than that in the maritime Antarctic; while its warmest month is about 15°C warmer. Its summer is even warmer than those of the cool-temperate islands in both hemispheres: Faroe Islands and Falkland Islands.

The data in Table 13 are fully consistent with the hypothesis that, despite having colder winters, Arctic areas have summers warm enough to permit Colpoda to be present in detectable numbers, while the maritime Antarctic summers are too cold for this to happen. The data suggest that the climatic temperature threshold for conditions to be suitable for Colpoda to become established is a mean for the four warmest months of between +0.4° and +1.9°C.

CHAPTER VI

CONCLUSIONS ABOUT THE DISTRIBUTION AND ABUNDANCE OF TERRESTRIAL PROTOZOA IN THE MARITIME ANTARCTIC

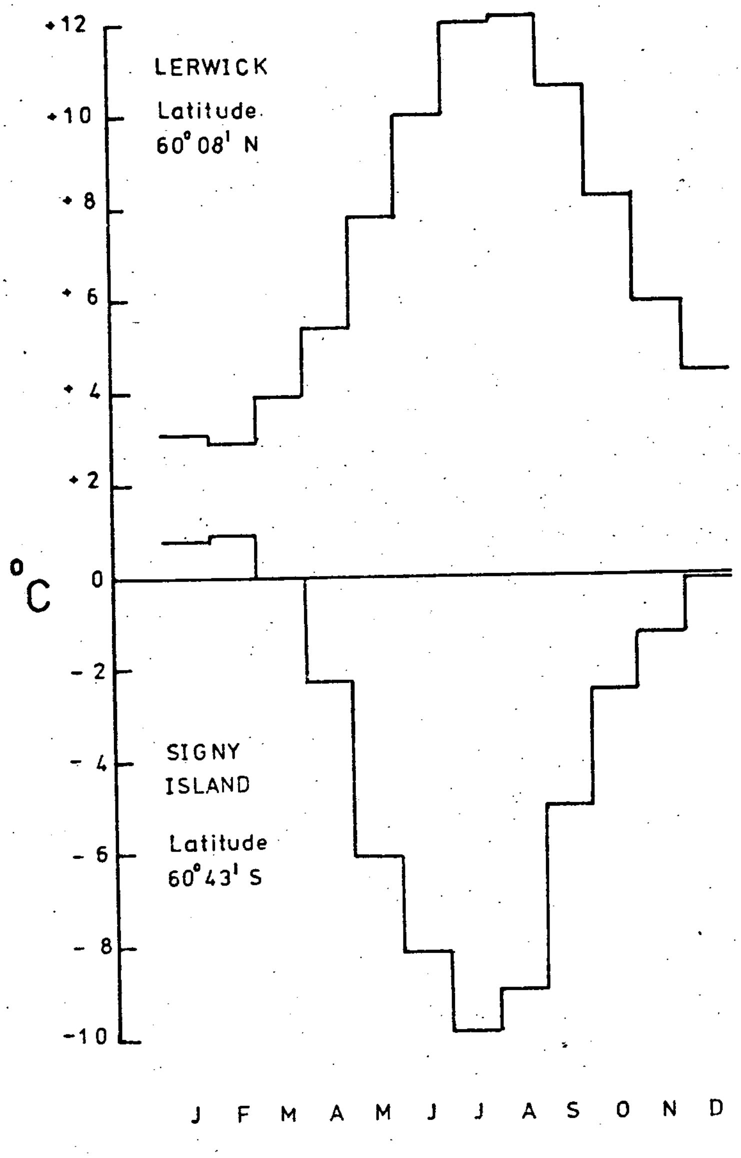
Superficial observations of maritime Antarctic islands suggests that, while the seas contain an abundance of life of many kinds, the land is almost lifeless, a few stunted mosses and lichens eking out a precarious existence on cold windswept rocks. However, detailed research during the last 10 years has revealed a very different picture. While land mammals are absent and flowering plants rare, bryophytes and lichens cover extensive areas (Longton, 1967) and the soils contain a diverse microflora (Heal et al,1967) and invertebrate fauna (Heal, 1965; Tilbrook, 1967; Spaull, in press). The results of the present survey of the protozoan fauna (Chapter II) confirm and extend previous observations, the species diversity of the protozoan fauna in the maritime Antarctic being only slightly less than that in temperate regions.

Taking together the data presented in Chapters I to V, it is now possible to come to some conclusions about how the environment of the maritime Antarctic influences the distribution and abundance of the terrestrial protozoa found there. Five environmental factors are considered here: temperature, moisture, geology, vegetation and marine animals.

TEMPERATURE

Compared with temperate lands, the most distinctive features of the Antarctic environment are low temperatures (Fig. 36). There is evidence (Chapter V) that they are the cause of the apparent absence from the maritime Antarctic of Colpoda, the most common of all ciliate genera found in soils. Otherwise temperature appears to have suprisingly little determinant influence on the distribution of species. This is probably because the temperatures actually experienced by the protozoa are, for much of the time, less extreme than the meteorological

Fig. 36: Comparison of monthly mean temperatures in two island groups: Lerwick, Shetland Islands (northern temperate zone) and Signy Island, South Orkney Islands (maritime Antarctic region)



Sources of the data: <u>Lerwick</u> - Climatological normals for climat and climat ship stations for the period 1931-60 (WMO No.117; TP 52, 1971); <u>Signy Island</u> - Signy Island Base meteorological records, 1947-70 data (Chapter I, Table 1) suggest. Microclimate measurements (Fig. 18) show that during one summer, between the hours 0900 and 1600, the top few centimetres of a moss peat on Signy Island experienced mean temperatures greater than + 2°C for at least four months.

By contrast, seasonal temperatures appear to be an influence of dominating importance upon the population sizes of protozoan species (Chapters III and IV). In the two habitats studies intensively, the seasonal fluctuations in population sizes followed the annual cycle of temperatures (Figs. 17, 26, 27, 28 and 29), numbers in summer being on average about ten times those in winter. Protozoa in laboratory cultures showed, as might be expected, strong positive correlations between growth rates and incubation temperatures (Fig. 35).

MOISTURE

There is no evidence that moisture influences the distribution of species. It was not possible during the survey (Chapter II) to distinguish between habitats on the basis of moisture because it varies considerably with time within habitats of all kinds. Considering the great seasonal variability of moisture observed in both moss peat and penguin guano (Figs. 17 and 31), it may be assumed that the terrestrial protozoa in the Antarctic are, as in other parts of the world, those species which can tolerate wide fluctuations in moisture.

Given suitable temperatures, the numbers of testate amoebae in moss peat do seem to be strongly influenced by moisture (Chapter III) and experience mortality when the peat is dry; but no correlation is apparent between moisture and the numbers of flagellates and ciliates inhabiting penguin guano (Chapter IV).

GEOLOGY

As stated in Chapter II, there seems to be no detectable pattern in the distribution of protozoan species in relation to geology. However, two unvegetated mineral habitats on Signy Island, where the material was derived from quartz-mica-schist or marble, and had pH's of 6.8 and 6.9, contained 7 and 21 protozoan species (Chapter II); whereas a similar habitat on South Georgia (which has a milder climate, Chapter V, Table 13), where the material was derived from quartzose and tuffaceous greywackes, and had a pH of 5.2, contained only 3 protozoan species (Smith, unpublished observations). Therefore it is possible that the base-richness of much of the rock in the maritime Antarctic is in part responsible for the richness of the fauna.

VEGETATION

The organic matter which accumulates under stands of moss and grass provides habitats for many acidophilic species of flagellates, rhizopods and ciliates - an influence particularly clear for testate amoebae which are almost entirely absent from non-vegetated habitats. Out of the 96 species observed in the survey (Chapter II) 48 occurred only in acid vegetated habitats. Vegetation is therefore an extremely important influence upon the distribution of protozoan species. The data are not sufficient to establish whether or not differences in types of vegetation affect the sizes of the population of protozoa associated with them.

MARINE ANIMALS

The alkaline guano deposits of marine birds and mammals provide suitable conditions for a small group of flagellate and ciliate species specific to saprobic habitats. The activities of marine animals are therefore an extremely important factor determining the distribution of these species and, further, seem to have a lasting effect: In the intensive study of protozoa in chinstrap penguin guano (Chapter IV), penguins were artificially excluded from an area of their colony, so preventing any further deposition of litter. The guano already in this area continued to be a habitat for guano-specific species of protozoa, without becoming colonised by other species, for at least three years.

In conclusion, the results suggest that vegetation, marine animals and possibly geology influence the distribution of terrestrial protozoa species in the maritime Antarctic; while temperature and sometimes moisture influence their numbers.

ACKNOWLEDGEMENTS

I wish to acknowledge with grateful thanks:

Prof. F. T. Last, for allowing me to work in the Department of Forestry and Natural Resources and for his valuable comments on the manuscript.

Dr. D. R. Gifford, my supervisor, for his advice and encouragement at all times.

R. J. Cook, O. H. S. Darling, A. Feenan, A. H. Gilmour, P. Hardy, J. J. Light, E. L. Twelves and V. W. Spaull for extremely valuable assistance with field work on Signy Island.

T. G. Davies, S. P. Finigan, R. Townley-Malyon and Lt. E. C. Walshaw for collecting samples for me in the Antarctic.

Mrs. K. M. G. Adam, Dr. J. F. Darbyshire and Dr. O. W. Heal for information on the literature and advice on protozoological techniques.

Dr. C. R. Curds and Dr. C. Ogden for access to the Penard Slide Collection (British Museum) and for supplying cultures of testate amoebae.

Dr. D. H. Matthews, A. Skinner and Mrs. J. W. Thomson for geological advice.

N. J. Collins and Dr. R. I. Lewis Smith for botanical advice.

Dr. J. F. Darbyshire, Dr. R. M. Laws, D. W. S. Limbert, P. J. Tilbrook and V. W. Spaull for reading sections of the manuscript and for their valuable comments.

Miss V. Greenshields for excellent library services.

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APPENDIX I

APPENDIX I

Appendix to Chapter II

Complete lists of protozoan species observed in samples from 68 sites in the maritime Antarctic

SOUTH ORKNEY ISLANDS

Table 1: Mastigophora

Table 2: Rhizopoda

Table 3: Ciliata

ELEPHANT ISLAND

Table 4: Mastigophora

Table 5: Rhizopoda

Table 6: Ciliata

LIVINGSTON ISLAND, DECEPTION ISLAND, ARGENTINE ISLANDS AND ISLANDS IN MARGUERITE BAY

Table 7: Mastigophora

Table 8: Rhizopoda

Table 9: Ciliata

KEY TO SITE CODES

LOCALITIES

SO	South Orkney Islands
E	Elephant Island
LIV	Livingston Island
D	Deception Island
A	Argentine Islands
MB	Islands in Marguerite Bay

HABITATS

MIN	Mineral debris and moraine clay
VA	Volcanic ash
PG	Penguin guano
ShG	Shag guano
ESW	Elephant seal wallows
PRAS	Prasiola
MCu	Moss cushion
MTP	Moss turf peat
MCP	Moss carpet peat
GS	Grass soil

APPENDIX I - TABLE 1: SOUTH ORKNEY ISLANDS - MASTIGOPHORA

	SO-MIN-1	SO-MIN-2	SO-PG-1	SO-PG-2	SO-PG-3	SO-ShG-1	SO-ESW-1	SO-PRAS-1	SO-PRAS-2	SO-MCu-1	SO-MCu-2	SO-MTP-1	SO-MCP-1	SO-MCP-2	SO-MCP-3	SO-MCP-4	SO-MCP-5	SO-MCP-6	SO-MCP-7	SO-MCP-8	SO-MCP-9	SO-MCP-10	SO-MCP-11	SO-MCP-12	SO-MCP-13	SO-MCP-14	SO-MCP-15	SO-MCP-16	SO-GS-1
Cephalothamnium cyclopum	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Oikomonas mutabilis	+	+	+	−	−	−	−	+	−	−	+	+	+	−	−	+	−	−	−	−	−	+	+	+	+	+	−	+	+
Oikomonas termo	+	+	+	−	+	−	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Polypseudopodius bacterioides	−	−	−	−	−	−	−	−	+	−	−	+	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	+	−
Chlamydomonas sp.	−	+	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Petalomonas angusta	−	−	−	−	−	−	−	−	+	−	−	+	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−
Petalomonas mediocanellata	−	+	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+
Polytoma uvella	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+
Allantion tachyploon	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Bodo celer	−	−	−	−	−	−	−	+	+	−	−	+	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	+	−
Bodo caudatus	−	+	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Bodo saltans	−	+	+	−	+	+	+	−	−	−	−	+	−	+	+	−	−	−	−	+	−	−	+	−	+	+	−	−	+
Cercobodo vibrans	−	−	−	−	−	−	−	−	−	+	−	+	−	−	−	−	−	−	+	−	+	+	+	−	−	−	−	+	−
Cercomonas crassicauda	−	−	−	−	−	−	−	−	+	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	+
Cercomonas longicauda	−	+	−	−	−	−	−	−	−	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	+
Heteromita globosa	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−
Heteromita lens	+	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−
Heteromita obovata	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−
Spongomonas uvella	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	+	−
Spironema multiciliata	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Tetramitus rostratus	−	−	+	−	−	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−

APPENDIX I - TABLE 2: SOUTH ORKNEY ISLANDS - RHIZOPODA

	SO-MIN-1	SO-MIN-2	SO-PG-1	SO-PG-2	SO-PG-3	SO-ShG-1	SO-ESW-1	SO-PRAS-1	SO-PRAS-2	SO-MCu-1	SO-MCu-2	SO-MTP-1	SO-MCP-1	SO-MCP-2	SO-MCP-3	SO-MCP-4	SO-MCP-5	SO-MCP-6	SO-MCP-7	SO-MCP-8	SO-MCP-9	SO-MCP-10	SO-MCP-11	SO-MCP-12	SO-MCP-13	SO-MCP-14	SO-MCP-15	SO-MCP-16	SO-GS-1
Hyalodiscus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
Mayorella sp.	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Metachaos sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Naegleria gruberi	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Valkampfia sp.	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	-	-
Arcella vulgaris	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Assulina muscora	-	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	+	+	+	-	-	-	-	-	+	-	+	+
Clypeolina sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
Corythion dubium	-	-	-	-	-	-	-	-	-	-	-	+	+	+	-	-	-	-	+	+	+	-	-	-	+	+	+	+	+
Difflugia penardi	-	-	-	-	-	-	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
Difflugiella sp.	-	-	-	-	-	-	-	-	-	-	+	+	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	+
Diplophrys archeri	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Euglypha ciliata	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euglypha rotunda	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	+
Euglypha strigosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+
Heleopera sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
Hyalosphenia elegans	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lecythium hyalinum	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Nebela wailesi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
Parmulina cyathus	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phryganella acropodia	-	-	-	-	-	-	-	+	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
Pseudodifflugia gracilis	-	-	-	-	-	-	-	+	-	-	+	+	+	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	+
Trinema enchelys	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	+
Trinema lineare	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	+	-

APPENDIX I - TABLE 3: SOUTH ORKNEY ISLANDS - CILIATA

	SO-MIN-1	SO-MIN-2	SO-PG-1	SO-PG-2	SO-PG-3	SO-ShG-1	SO-ESW-1	SO-PRAS-1	SO-PRAS-2	SO-MCu-1	SO-MCu-2	SO-MTP-1	SO-MCP-1	SO-MCP-2	SO-MCP-3	SO-MCP-4	SO-MCP-5	SO-MCP-6	SO-MCP-7	SO-MCP-8	SO-MCP-9	SO-MCP-10	SO-MCP-11	SO-MCP-12	SO-MCP-13	SO-MCP-14	SO-MCP-15	SO-MCP-16	SO-GS-1
Chillodonella sp.	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chilophrya sp.	+	+	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dileptus sp.	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Enchelys sp.	-	+	-	-	+	-	+	-	-	-	+	+	-	+	-	+	-	-	-	-	-	+	-	-	-	+	+	+	+
Holophrya sp.	-	-	-	-	-	-	-	+	-	-	+	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-	+
Lagynophrya sp.	-	-	-	-	-	-	-	-	-	-	-	+	+	-	+	+	-	-	-	-	-	-	-	-	-	-	-	+	+
Litonotus sp.	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Loxophyllum sp.	-	-	-	-	-	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Nassula elegans	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Spathidium sp.	-	+	+	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Urotricha agilis	+	+	-	-	-	-	-	-	-	+	+	+	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	+	+
Podophrya sp.	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leptopharynx sphagnetorum	-	+	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+
Microthorax simulans	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
Cryptochilium nigricans	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-	+	-	-	+	+	+	-	-	-
Cyclidium glaucoma	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	+	+	+	-	-	-	-	-	-	+	-
Glaucoma pyriformis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-
Philaster sp.	-	-	+	-	+	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vorticella microstoma	-	-	+	-	+	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vorticella striata var octava	-	+	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Blepharisma sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Halteria grandinella	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Gonostomum affine	-	+	-	-	-	-	-	+	+	+	+	+	-	-	-	-	-	-	+	-	+	-	-	-	-	-	+	-	+
Holosticha sp.	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Hypotrichidium sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Oxytricha fallax	-	+	-	-	-	-	-	+	+	-	-	-	+	+	-	+	+	-	+	-	+	+	+	-	-	-	-	+	-
Oxytricha pellionella	+	-	-	-	-	-	-	+	-	+	+	+	+	+	-	+	-	-	+	-	-	-	-	-	-	-	-	+	+
Oxytricha setigera	-	+	-	-	-	-	-	+	-	+	-	-	-	+	-	+	+	-	-	-	-	-	-	-	-	-	-	+	+
Pleurotricha lanceolata	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	+	-	-
Uroleptus sp.	+	+	-	-	-	-	-	+	+	+	+	+	-	-	-	-	-	-	-	-	+	-	-	-	+	+	+	-	+
Urostrongylum contortum	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euplotes sp.	-	+	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+

APPENDIX I - TABLE 4: ELEPHANT ISLAND - MASTIGOPHORA

	E-MIN-1	E-MIN-2	E-MIN-3	E-MIN-4	E-MIN-5	E-PG-1	E-PG-2	E-PG-3	E-PG-4	E-PG-5	E-MTP-1	E-MTP-2	E-MTP-3	E-MTP-4	E-MCP-1	E-MCP-2	E-MCP-3	E-MCP-4	E-MCP-5	E-GS-1	E-GS-2	E-GS-3	E-GS-4
Oikomonas mutabilis	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	+	−	−	−	−
Oikomonas termo	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Polypseudopodius bacterioides	−	−	−	+	−	−	−	−	−	+	−	−	−	−	−	+	−	+	−	−	−	−	+
Petalomonas angusta	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−
Petalomonas mediocanellata	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−
Allantion tachyploon	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Bodo saltans	+	−	−	−	−	+	+	+	+	+	−	−	−	−	−	−	+	−	−	−	−	−	−
Bodo terricolus	−	−	−	−	−	−	−	+	−	−	−	−	+	−	−	−	−	−	−	+	−	−	−
Cercobodo agilis	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−
Cercobodo vibrans	−	+	+	−	−	−	−	−	−	−	−	−	−	−	+	+	+	−	−	+	−	+	+
Cercomonas crassicauda	−	−	−	−	−	−	−	−	−	−	−	+	−	+	−	−	−	−	+	−	+	−	−
Cercomonas longicauda	−	+	−	+	+	−	−	−	−	−	+	+	+	+	−	−	−	+	−	−	−	+	−
Phalansterium solitarium	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−
Pleuromonas jaculans	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	+	−	−	−
Spongomonas uvella	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−
Tetramitus pyriformis	−	−	−	−	+	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−
Tetramitus rostratus	+	−	−	−	−	+	+	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−

APPENDIX I - TABLE 5: ELEPHANT ISLAND - RHIZOPODA

	E-MIN-1	E-MIN-2	E-MIN-3	E-MIN-4	E-MIN-5	E-PG-1	E-PG-2	E-PG-3	E-PG-4	E-PG-5	E-MTP-1	E-MTP-2	E-MTP-3	E-MTP-4	E-MCP-1	E-MCP-2	E-MCP-3	E-MCP-4	E-MCP-5	E-GS-1	E-GS-2	E-GS-3	E-GS-4
Astramoeba radiosa	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−
Flabellula mira	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−
Thecamoeba verrucosa	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−
Metachaos sp.	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−
Assulina muscora	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	−	+	+	−
Corythion dubium	−	−	−	−	−	−	−	−	−	−	−	−	+	+	−	−	+	+	−	−	−	+	−
Difflugia constricta	−	−	−	−	−	−	−	−	−	−	−	+	+	+	−	−	+	−	−	−	−	+	−
Difflugia lucida	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	+	−	−	−	+	−	−	+
Difflugiella sp	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Euglypha rotunda	−	−	−	−	−	−	−	−	−	−	+	−	−	+	−	−	−	−	−	−	−	−	−
Heleopera sp.	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	+	−	−
Hyalosphenia minuta	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−
Lecythium hyalinum	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	+	−	−	−	−	−
Phryganella acropodia	−	−	−	−	−	−	−	−	−	−	−	+	−	−	+	−	−	−	+	+	+	+	−
Pseudodifflugia gracilis	−	−	−	−	−	−	−	−	−	−	−	+	−	+	−	+	−	−	−	+	+	+	+
Trinema enchelys	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−
Trinema lineare	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−

APPENDIX I - TABLE 6: ELEPHANT ISLAND - CILIATA

	E-MIN-1	E-MIN-2	E-MIN-3	E-MIN-4	E-MIN-5	E-PG-1	E-PG-2	E-PG-3	E-PG-4	E-PG-5	E-MTP-1	E-MTP-2	E-MTP-3	E-MTP-4	E-MCP-1	E-MCP-2	E-MCP-3	E-MCP-4	E-MCP-5	E-GS-1	E-GS-2	E-GS-3	E-GS-4
Choenia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Dileptus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Enchelys sp.	-	-	-	-	-	-	-	-	-	-	-	+	+	-	+	-	+	-	-	+	+	+	+
Holophrya sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-
Spathidium sp.	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
Urotricha agilis	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	-	+	+	+	+	-	+	+
Leptopharynx sphagnetorum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	+	+	-	+	+
Microthorax simulans	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Cyclidium glaucoma	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	-	+	-	-
Dichilium cuneiforme	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+
Philaster sp.	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oxytricha fallax	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	+	-	-	+
Oxytricha pellionella	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	+	+	-	-
Oxytricha setigera	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	+	-	-	-	-	-
Pleuritricha lanceolata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
Uroleptus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
Euplotes sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Vorticella microstoma	+	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

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TABLE 7: LIVINGSTON ISLAND, DECEPTION ISLAND, ARGENTINE ISLANDS AND ISLANDS IN MARGUERITE BAY - MASTIGOPHORA

	LIV-MCP-1	D-VA-1	D-VA-2	D-VA-3	D-VA-4	D-VA-5	A-MTP-1	A-MTP-2	A-MCP-1	A-MCP-2	MB-MIN-1	MB-PG-1	MB-MTP-1	MB-MCP-1	MB-MCP-2	MB-MCP-3
Oikomonas mutabilis	−	−	−	−	−	−	−	−	−	−	−	−	+	+	−	−
Oikomonas termo	+	−	−	+	−	−	+	−	+	−	−	−	−	−	+	+
Polypseudopodius bacterioides	−	−	−	+	−	−	+	+	−	+	+	−	+	+	−	−
Allantion tachyploon	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−
Bodo saltans	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Cercobodo agilis	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−
Cercobodo vibrans	−	−	−	+	−	+	−	−	−	−	−	−	−	+	−	−
Cercomonas crassicauda	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−
Cercomonas longicauda	+	−	−	−	−	−	+	+	−	−	−	−	−	−	−	−
Heteromita globosa	−	−	−	−	−	−	−	−	+	−	+	−	+	+	−	−
Phalansterium solitarium	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−
Sainouron mikroteron	−	−	−	−	−	+	−	−	−	−	−	−	−	−	+	+
Spongomonas uvella	−	−	−	−	−	−	−	+	−	−	+	−	+	−	−	−
Tetramitus pyriformis	−	−	−	−	−	−	−	−	−	−	−	+	−	−	+	−

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TABLE 8: LIVINGSTON ISLAND, DECEPTION ISLAND, ARGENTINE ISLANDS AND ISLANDS IN MARGUERITE BAY - RHIZOPODA

	LIV-MCP-1	D-VA-1	D-VA-2	D-VA-3	D-VA-4	D-VA-5	A-MTP-1	A-MTP-2	A-MCP-1	A-MCP-2	MB-MIN-1	MB-PG-1	MB-MTP-1	MB-MCP-1	MB-MCP-2	MB-MCP-3
Mayorella sp.	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−
Arcella vulgaris	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−
Assulina muscora	−	−	−	−	−	−	+	+	−	−	−	−	−	−	−	−
Corythion dubium	+	−	−	−	−	−	+	+	−	+	−	−	−	−	+	−
Difflugia constricta	+	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−
Difflugiella sp.	−	−	−	−	−	−	−	−	−	−	−	−	+	+	−	−
Diplophrys archeri	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	+
Euglypha laevis	−	−	−	−	−	−	+	+	−	−	−	−	−	−	−	−
Euglypha rotunda	−	−	−	−	−	−	−	+	+	+	−	−	−	−	−	−
Euglypha strigosa	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−
Lecythium hyalinum	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	+
Nebela minor	−	−	−	−	−	−	−	−	−	−	−	−	+	+	−	−
Phryganella acropodia	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−
Pseudodifflugia gracilis	−	−	−	−	−	−	−	−	−	+	−	−	+	−	+	−
Trinema enchelys	+	−	−	−	−	−	−	+	+	−	−	−	−	−	−	−
Trinema lineare	−	−	−	−	−	−	−	−	+	+	−	−	−	−	+	−

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TABLE 9: LIVINGSTON ISLAND, DECEPTION ISLAND, ARGENTINE ISLANDS AND ISLANDS IN MARGUERITE BAY - CILIATA

	LIV-MCP-1	D-VA-1	D-VA-2	D-VA-3	D-VA-4	D-VA-5	A-MTP-1	A-MTP-2	A-MCP-1	A-MCP-2	MB-MIN-1	MB-PG-1	MB-MTP-1	MB-MCP-1	MB-MCP-2	MB-MCP-3
Chilophrya sp.	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−
Dileptus sp.	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Enchelys sp.	−	−	−	+	−	−	+	−	−	−	−	−	+	+	+	+
Lagynophrya sp.	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−
Spathidium sp.	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−
Urotricha agilis	−	−	−	−	−	−	−	+	−	−	−	−	−	+	−	−
Hallezia sp.	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−
Leptopharynx sphagnetorum	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Cryptochilium nigricans	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Vorticella microstoma	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−
Gonostomum affine	−	−	−	−	−	−	−	−	−	+	−	−	+	−	−	+
Holosticha sp.	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−
Keronopsis sp.	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Onychodromus sp.	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Oxytricha fallax	+	−	−	−	−	−	+	+	−	+	−	−	−	+	+	−
Oxytricha pellionella	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−
Oxytricha setigera	+	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−
Uroleptus sp.	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−

APPENDIX II

APPENDIX II

Appendix to Chapter III

pH, moisture and loss on ignition of cores of peat taken from three horizons of moss turf on sixteen occasions between January 1970 and March 1971

Table 1: Horizon 0-3 cm
Table 2: Horizon 3-6 cm
Table 3: Horizon 6-9 cm

Figures are means ± 95 % confidence limits

TABLE 1: HORIZON 0-3 cm

DATE	pH	MOISTURE (% dry weight)	LOSS ON IGNITION (% dry weight)
16. 1.70	4.1±0.3	566± 76	...
9. 2.70	4.3±0.4	300± 64	...
6. 3.70	4.3±0.2	343± 59	97.8±1.0
11. 4.70	4.3±0.1	465± 60	96.9±0.7
15. 5.70	4.2±0.2	542± 78	97.3±0.4
12. 6.70	4.6±0.1	653± 82	95.7±0.7
8. 7.70	4.2±0.1	596± 49	97.4±0.6
5. 8.70	4.3±0.2	671± 95	96.8±0.9
4. 9.70	4.1±0.2	677± 86	96.2±1.1
6.10.70	3.9±0.3	463± 28	96.2±0.6
9.11.70	3.9±0.2	474± 75	96.6±0.8
5.12.70	3.7±0.1	384± 36	96.7±1.5
5. 1.71	3.5±0.3	215± 20	96.0±0.7
6. 2.71	3.5±0.2	311± 99	97.0±1.3
4. 3.71	3.6±0.2	320± 69	97.0±0.4
29. 3.71	3.9±0.1	420± 36	96.9±0.4

TABLE 2: HORIZON 3-6 cm

DATE	pH	MOISTURE (% dry weight)	LOSS ON IGNITION (% dry weight)
16. 1.70	3.8±0.3	715±192	...
9. 2.70	4.3±0.2	449± 82	...
6. 3.70	4.1±0.3	393± 85	98.3±0.9
11. 4.70	4.2±0.1	556± 65	97.0±0.8
15. 5.70	4.0±0.1	693± 67	96.5±0.5
12. 6.70	4.2±0.2	596± 57	95.8±1.5
8. 7.70	4.1±0.1	673±121	96.2±0.9
5. 8.70	4.5±0.3	698±124	97.0±0.6
4. 9.70	3.9±0.2	719±132	94.3±4.9
6.10.70	3.9±0.3	482± 27	96.5±0.7
9.11.70	4.0±0.1	543± 70	94.7±1.6
5.12.70	3.7±0.2	449± 16	96.0±1.7
5. 1.71	3.8±0.2	311± 37	93.7±1.6
6. 2.71	3.6±0.9	371± 65	96.1±0.5
4. 3.71	3.8±0.2	410± 48	95.9±0.9
29. 3.71	3.6±0.2	564± 73	96.7±1.1

TABLE 3: HORIZON 6-9 cm

DATE	pH	MOISTURE (% dry weight)	LOSS ON IGNITION (% dry weight)
16. 1.70	3.7±0.3	699±138	...
9. 2.70	4.3±0.2	428± 71	...
6. 3.70	4.2±0.2	380± 66	98.3±0.9
11. 4.70	4.0±0.1	488± 42	97.0±0.8
15. 5.70	4.4±0.1	691± 32	96.5±0.5
12. 6.70	4.3±0.3	591± 17	95.8±1.5
8. 7.70	4.0±0.3	661± 19	96.2±0.9
5. 8.70	4.3±0.2	758±121	97.0±0.6
4. 9.70	4.0±0.2	751±219	94.3±4.9
6.10.70	3.8±0.3	785± 75	96.5±0.7
9.11.70	3.9±0.1	650± 48	94.7±1.6
5.12.70	3.8±0.1	491± 47	96.0±1.7
5. 1.71	3.9±0.2	333± 28	93.7±1.6
6. 2.71	3.6±0.2	364± 36	96.1±0.5
4. 3.71	3.6±0.1	383± 30	95.9±0.9
29. 3.71	3.8±0.2	493± 28	96.7±1.1