Ecological studies at South Georgia

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Introduction

Matthews (1931) describes the early voyages to South Georgia. The first landings and the first accurate accounts of the island and its biological resources resulted from Cook's discovery in 1775, for three naturalists, the two Forsters and Sparrman, were on board the *Resolution*. Modern scientific investigations began with the German International Polar Year Expedition of 1882–83 and were continued by other expeditions travelling to the Antarctic. From 1925 to 1931 the British *Discovery* Investigations operated a marine biological station at King Edward Point in West Cumberland Bay, mainly directed towards research on whales and their food organisms, but also reporting on birds and seals (Hardy, 1967).

Cook had commented on the large numbers of seals and penguins and this was followed by intensive exploitation during the nineteenth century (Roberts, 1958). The Antarctic whaling industry began at South Georgia with the establishment of the Grytviken station in 1905, and several other stations were built between then and 1920; the last closed in 1964 following the decline of the whale stocks. An elephant sealing industry flourished and provides an example of rational management under government control from 1910 to 1964 (Laws, 1953a, 1960; Bonner, 1958).

Following the termination of these industries for economic reasons, the administrative settlement on King Edward Point (57°17′S, 36°30′W) was taken over by the British Antarctic Survey (BAS) in 1969 and multidisciplinary research has since been conducted there. The name of the station reverted to Grytviken in 1977, after the nearby disused whaling station. It is from Grytviken that much of the research described in this paper was carried out. Another smaller station was set up on Bird Island (54°00′S, 38°03′W) for a United States project on albatross biology, carried out between 1958 and 1964 (Tickell, 1968). It was subsequently taken over by BAS and is the site of intensive continuing studies on fur seals and seabirds. In addition a number of field huts have been installed around South Georgia to facilitate scientific field studies.

The environment

South Georgia is the largest island of the Scotia Ridge, about 160 km long and varying from 5 to 40 km in width, its axis from northwest to southeast. It is situated some 2 000 km east of Tierra del Fuego in the South Atlantic Ocean at latitude 54–55°S, longitude 36–38°W. Work by BAS geologists has suggested that an active island arc was situated southwest of South Georgia during the Cretaceous. Systematic large-scale geological mapping of the island was completed in 1977. The BAS work has shown that the island may be divided into five major strato-tectonic units, together with a prominent mylonite zone. These are the Cumberland Bay formation of marginal basin sediments occupying most of the island, of turbidite facies and poorly fossiliferous; the Sandebugten formation, also sedimentary but geochemically distinct from the Cumberland Bay formation; the Annenkov Island formation, a sedimentary island arc assemblage with igneous plutons and sills; the Larsen Harbour formation in the southwest, consisting largely of pillow lava and stratiform breccia; and the adjacent Drygalski Fjord Complex of plutonic rocks (British Antarctic Survey, 1977a, 1977b, 1978).

The island has an alpine topography, the mountains reaching almost 3 000 m in Mount Paget, and about 60 per cent of the island is covered by permanent ice, which reaches the sea in many large glaciers at the head of fjords. The island lies south of the Antarctic Convergence and the surrounding cold water mass results in an oceanic climate which is cool with prevailing westerly winds, high precipitation (1 200–2 000 mm per annum) and frequent summer snowfalls. Although temperatures are low, the annual range is small (annual mean 1,8°C, warmest monthly mean 5,3°C, coldest monthly mean –1,5°C). Temperatures within vegetation during the summer are often much higher than the ambient temperature, reaching as much as 40°C in the *Festuca* grassland litter layer. Near surface temperatures of moss banks rarely fall below 0°C in summer, or under snow cover during most of the winter. There is deep snow cover for six months or more during the year at sea level (Smith & Walton, 1975).

Pack ice occasionally reaches the southern end of South Georgia in winter and although sheltered coves may freeze over there is no formation of fast ice. Between 1972 and 1974 the inshore temperature at 10–15 m depth in King Edward Cove varied from 3,4°C in summer to –0,3°C in winter.

The floristic history is quite well covered. Five pollen analyses from South Georgia were reported by Barrow (1976, 1977 and 1978); these diagrams are the first to be constructed for the island. They indicate that conditions ameliorated by about 10 000 years B.P. and peat began to accumulate; the oldest radiocarbon date is 9 500 years B.P. Many elements of the present vascular flora were flourishing then, having possibly survived the last glacial (about 20 000–10 000 years B.P.), in low altitude refugia. Post-glacial conditions did not prevent South Georgian plants from flowering, and there appear to have been no major changes in the flora since about 9 500 years B.P. The distribution of peat deposits is suggestive of post-glacial sea level changes which may have altered the quantity of coastal tussock grass, *Poa flabellata*, pollen deposited in the peat. *Nothofagus* pollen is found in all the cores and pollen blown from South America may amount to 3 per cent of the native South Georgia pollen.

Moraine systems show a series of glacier oscillations since the last glacial period, indicating long-term climatic fluctuations. The glaciers have been retreating since the 1880s, but a temporary re-advance between 1925 and 1935 interrupted the general trend. Detailed studies of heat and ice balances from the Hodges Glacier, near Grytviken, should

help to establish the causes of past glacier fluctuations, including the temporary re-advance, by reference to the more than 70-year meteorological record at Grytviken (British Antarctic Survey, 1978). These data show that there has been a 33 per cent increase in summer rainfall at South Georgia since 1905 (British Antarctic Survey, 1977a). The 10-year running means of annual temperature reached a peak in the 1950s and are now decreasing slightly.

A reasonable summary of the range of South Georgia soils within the International Biological Programme study area near Grytviken, including chemical data, has been published by Smith and Walton (1975).

The organic soils consist of peat deposits, from bog communities, tussock grass, turf forming mosses, and dwarf shrubs. Meadow tundra soils occur below eutrophic moss-dominated communities. Brown soils occur beneath dry grassland. Mineral soils range from fine clays, silts and sands to coarse gravels, pebbles and boulders. There is no permafrost, but current surface microtopographical phenomena (earth mounds and ridges), which are probably relics of an era when permafrost existed, have been described.

Terrestrial studies

Plant taxonomy and biogeography

South Georgia would appear to be far ahead of all the other sub-Antarctic islands in the production of floras for the various plant groups, largely due to the efforts of Greene and his co-workers. The approximate total number of plant species on South Georgia is 374, classified as follows: grasses 5; rushes 3; sedges 1; dwarf shrubs 2; forbs 6; pteridophytes 7; mosses 120; liverworts 80; lichens 150; but only 48 achieve dominance (Smith & Walton, 1975).

South Georgia is still the only island in the Antarctic regions to have a published phanerogam flora. Greene (1964) has published a systematic account of the vascular flora, which includes an historical survey of botanical exploration there. His check list comprises 51 species, of which 24 were regarded as native to South Georgia, 5 as naturalized aliens and the remaining 22 were classified as transient aliens. The distribution of native and naturalized species was plotted using a grid with 5-km squares as sample areas. Species classed as transient aliens were demonstrated to be dependent on artificial habitats around the whaling stations. Greene (1969) published additional distributional records; Walton and Smith (1973) and Greene and Walton (1975) increased the list of aliens to 54 and added two native species.

Morphological and cyto-taxonomic variation have been considered in relation to the biogeography of selected species, particularly the two South Georgian species of *Acaena* and their hybrid (Moore & Walton, 1970; Walton & Greene, 1971).

Greene and his co-workers are over halfway towards producing a synoptic flora of South Georgia mosses (Bell & Greene, 1975; Greene *et al.* 1974; Matteri, 1977; Newton, 1977). Grolle (1972) and Hassel de Menendez (1977) have published on the hepatics and the latter is near to producing a hepatics flora; the latest revision has increased the number of species known from the island from 24 to over 80.

A lichen flora for South Georgia now covers all the macrolichens and some of the microlichens (Lindsay, 1971, 1973b, 1974a, 1974b, 1976). The fungi are very under-worked (Dennis, 1968), but BAS has in hand some routine identifications to supplement the earlier list. Recently, two myxomycetous fungi have been reported from South Georgia, the first time from Antarctic regions. This considerably extends the known geographical range of the group (Ing & Smith, in press).

Biogeographically, the Antarctic and sub-Antarctic are being included in a variety of distribution hypotheses. In many cases cryptogamic taxa are being used and this is misleading because most of them are in need of generic review.

BAS has studied freshwater ecology primarily at Signy Island, South Orkneys, with more extensive surveys over a wide range of latitude in the maritime Antarctic and Alexander Island. Studies are planned for South Georgia and will extend the latitudinal series. In a preliminary survey of lakes and rivers of the Cumberland Bay area of South Georgia, Dartnall and Heywood (in press) found 16 rotifer species, 11 arthropod species and single species representing Protozoa, Platyhelminthes, Gastrotricha, Nematoda, Tardigrada and Annelida. This is similar to the better-known Signy Island fauna and they discuss the zoogeography of the Scotia arc. Light and Heywood (1973) have drawn attention to the occurrence of a dense growth of several mosses to a depth of 30 m in some lakes.

Vegetation survey and phytosociology

This work began in 1969 and continues intermittently. It will eventually produce a phytosociological survey and continuum analysis of the vegetation, and chemical and edaphic analysis of soils in relation to the distribution, composition and development of the plant communities. All the major community types are represented in the IBP study area in East Cumberland Bay (see below), but the extensive stands of closed vegetation are not typical of the island as a whole; this area has been ice-free for longer than other parts of the island and has a more favourable climate. Smith and Walton (1975) have described these communities and they need only be summarized here. They include: dry *Festuca contracta* grassland, *Deschampsia antarctica* grass-and, *Rostkovia magellanica* bog, *Tortula robusta-Juncus scheuchzerioides* bog, *Acaena magellanica* heath and *Poa flabellata* tussock grassland. Up to about 75 m above sea level there is an apparent gradation of vegetation types.

The tussock grassland is the climax vegetation type and most widespread community. It occurs in coastal areas, most densely at sea level, but is found up to 225 m. It is particularly luxuriant where seals and birds provide nitrogen enrichment. On wet level ground amongst tussock grass or on raised beaches, *Deschampsia antarctica* forms local swards of meadow. The *Rostkovia* bog is found on wet valley floors, at lake margins and in rock basins. The *Tortula-Juncus* bog is found on wet eutrophic seepage slopes which undergo some flushing. The *Acaena* and *Tortula* predominate where drainage improves and *Acaena* forms dense pure stands on dry stony slopes. In fairly sheltered situations extensive close swards of *Festuca* occur, becoming mixed with *Acaena*, and various bryophytes and lichens on drier, more exposed slopes. Above 100 m for the most part, all dry windswept mineral soils receiving little or no winter snow cover have an open fell-field vegetation dominated by short mosses, crustose lichens and malformed fruticose lichens, with scattered grasses and dwarf shrubs.

Smith and Walton (1975) also describe the most common types of succession, vegetation gradients usually being related to moisture changes in the substratum; in some areas frost heaving influences the pattern.

Infrared aerial photographs have been taken from helicopters flown by H.M.S. *Endurance*, to allow us to map communities more accurately than from conventional black-and-white photographs. In a typical aerial photograph taken in Cumberland East Bay, the false colour enhances the distinctions between vegetation types. A pink tussock fringe is conspicuous along the shore, *Acaena magellanica* shows up as dark red on the slopes behind, white tufts on the ridges are tussock grass again, nutrient-poor compared with the pinker clumps on the sea shore. *Festuca* grassland is indicated by extensive grey areas, with dark red in the stream beds due to the bright green *Juncus*.

Autecological and ecosystem studies

A bi-polar botanical project was undertaken on South Georgia as part of the IBP Tundra Biome Programme; comparisons were made with field sites at Disko Island, West Greenland (69°15′N, 53°30′W). The fieldwork was carried out between 1967 and 1971 and resulted in the collection of a large amount of primary production data, now nearly all published (Callaghan, Smith & Walton, 1976; Smith & Walton, 1975). This project, conceived by M.C. Lewis and S.W. Greene, was part of a world-wide study of growth and potential yield in alien test species (phytometers) such as oats, barley and radish, grown in standard edaphic conditions (fertilized vermiculite) in different local sites of varying microclimatic severity, or in different local soils at one site. It provides a comparison with the development of the same species at other IBP sites. Experiments with fertilizers were carried out to assess nutrient limitations in certain soils. The bi-polar project also involved preliminary productivity and eco-physiological studies of native species, both at the individual plant level and at the community or ecosystem level. These led to the development of separate projects (on *Poa flabellata* grassland, *Festuca contracta* grassland, *Acaena* species, and *Rostkovia magellanica* bog ecosystem), and also to the setting up of special study sites and the monitoring of microclimate there.

We now have standing crop and estimated annual production figures for most of the important communities and species on the island. The productivity of dominant communities on South Georgia proved to be very high compared with other tundra communities, and the rates and components of production showed great similarities to alpine areas (Smith & Stephenson, 1975; Walton *et al.* 1975). Table I summarizes mid-season standing crop and net annual production for three dominant communities. Production by individual species of mosses such as *Pohlia wahlenbergia* (Clarke *et al.* 1971), dwarf shrubs such as *Acaena magellanica* (Walton, 1973, 1976) and grasses such as *Phleum alpinum* (Callaghan, 1973) was high on both islands compared with other tundra locations. Smith and Walton (1975) also discuss production processes in quantitative terms.

Regular sampling and analysis of 14 species of vascular plants, 2 pteridophytes and 5 mosses for total Na, K, Mg, P and N showed that plants from soils near bird and seal colonies had much higher levels of P and N than those from unoccupied areas (Walton & Smith, 1980). Seasonal trends were similar to those shown by previous work on temperate species, but absolute values were higher. Living leaves of *Acaena magellanica* had N concentrations up to 5,5 per cent of dry weight. Rates of recycling differed, as shown by comparison of the percentage of elements in the dead material of two communities. *Festuca contracta* grassland had 41 per cent of the elements in dead material at mid-season, increasing to 53 per cent at the end of summer. Calorific values for 18 common and widespread South Georgian plants have been published by Smith and Walton (1973).

The general conclusions of the bi-polar project on adaptive strategies were that 'The Arctic climate has selected species capable of short periods of fast growth and opportunistic reproduction or rapid reproductive development. Alternatively, the South Georgian climate has favoured species with slow but consistent rates of reproduction and growth. The higher incidence of sexual reproduction on South Georgia has allowed considerable genotypic differentiation, although some species with wide ecological tolerances show instead a high degree of plasticity' (Callaghan *et al.* 1976).

Callaghan (1977), in discussing adaptive strategies of South Georgian graminoid species, also points out that the major constraints imposed by the environment are the low temperature, restricting growth, and the short growing seasons, which limit flowering development, and that any strategy that makes growth possible in these conditions, or facilitates or bypasses flowering, will be of adaptive significance. He gives examples from *Phleum alpinum*, *Rostkovia magellanica*, *Uncinia smithii* and *Juncus scheuchzerioides*. The most important adaptations are the protracted life cycles and flowering phases. Vast vegetative clones reflect the development of highly organised systems adapted to conserve energy.

A series of autecological studies have investigated life cycles, fixation and movement of energy sources, dry matter accumulation and partition, patterns of reproduction — floral and vegetative, population dynamics, productivity, and inter-population variation. Species studied include *Phleum alpinum*, *Poa flabellata*, *Festuca contracta*, *Acaena* spp. and *Rostkovia magellanica*. The perennial rush, *Rostkovia magellanica*, can adapt its rhizomatous growth form to different conditions. Each year no more than two or three leaves are produced and they remain attached to the tiller for some years after death. This facilitates studies of the chemical changes involved in leaf growth, senescence and decomposition. Experimental studies of the decomposition of leaf material of known age were made, using litter bags introduced below the moss understorey; these provide standardized comparisons of decomposition across seasons and sites (Lawson, unpublished).

Younger leaves showed high initial weight loss in summer

Table 1

Mid-season standing crop and net annual production for three predominant community types (g m^{-2}). (Extracted from Smith & Walton, 1975).

	Acaena magellanica dwarf shrub community	*Festuca contracta* grassland community	*Poa flabellata* grassland community
Standing crop			
above ground	2 037	2 675	12 785
below ground	7 536	1 642	5 000
Total	9 573	4 317	17 785
Net production			
above ground	1 105	490	5 025
below ground	*c.*500	*c.*350	1 000
Total	1 605	840	6 025

(around 40 per cent); they lost little weight over winter, and in the following summer decomposition had more or less stopped in a dry site but restarted in a wet site. Large differences in chemical composition of leaf age fractions at the two sites persist for more than 2 years. The cotton strip method (Walton & Allsopp, 1977), which depends on changes in tensile strength caused by varied decomposition rates, provides another standardized comparison of decomposition rates and these again are found to be markedly higher at the wet site than at the drier site.

Another investigation dealt with the ecology, primary production and biochemistry of *Poa flabellata* (Gunn, 1976). The carbohydrate strategy is unusual compared with most tundra plants as it does not store starch in its root and rhizome system, but in its shoots and leaves. The exceptionally high levels of fructose are translocated to younger foliage in January and February as the mature leaves age. The young leaves act as the major food reserve during winter and this perennial plant may survive by continual production of new tillers for well over 50 years.

At high latitudes, plants must adapt to make best use of the short summer, and the reproductive cycle usually takes two seasons, flower buds only partly developing in the first season and overwintering. Although South Georgia and the other sub-Antarctic islands lie in relatively low latitudes, they have unexpectedly rigorous climates because of their proximity to the Antarctic Convergence, whilst their remoteness has resulted in impoverished floras. The South Georgia flora grows at low altitude and latitude, but the cold and short growing season has led to various floristic adaptations. Walton (unpublished) has given flowering periods for most of the native vascular flora and discusses reproductive adaptations and specializations.

The vascular flora of South Georgia shows several adaptations to cold summer climates, notably preformation of flowers, cleistogamy, self-compatibility and self-fertilization, predominantly anemophilous flowers (related to the limited insect fauna). Walton (unpublished) has investigated these and other adaptations.

Poa flabellata and *Festuca contracta* show only partial development of their flowers in the summer prior to flowering, the buds of tussock growing above the snow in late winter; the only two Antarctic flowering plants, *Deschampsia antarctica* and *Colobanthus quitensis*, also show flower preformation in the South Orkneys, but it is not known whether this is necessary at South Georgia.

In the Arctic and many alpine floras most plants flower synchronously. Asynchrony of flowering is a feature of the South Georgian flora, in some cases probably associated with flower preformation and overwintering. *Callitriche antarctica* and *Galium antarcticum* flower continuously during most of the summer, as do the naturalized aliens *Taraxacum officinale* and *Cerastium fontanum*. The successful *Poa annua* begins flowering in late winter beneath the snow from buds that may have overwintered, and continues flowering throughout the summer. *Acaena magellanica* often flowers in two phases, the main one a few weeks after snow melt and a second later in mid-summer. Other species such as *Uncinia meridensis*, *Ranunculus biternatus* and *Phleum alpinum* show more synchrony, flowering in November-December and ripening fruit from late January (Walton, unpublished).

Four South Georgia ecosystems are now being studied in a series of intensive study sites established in 1976 in the vicinity of the Grytviken station and representative of *Acaena magellanica* dwarf-shrub sward, *Festuca contracta* grassland, *Tortula robusta–Rostkovia magellanica* soligenous peat bog and *Polytrichum alpestre* ombrogenous peat bog (British Antarctic Survey, 1977b, 1978). Research is being concentrated into all aspects of the selected ecosystems. Eventually, it is hoped to make integrated total ecosystem analyses and to produce a model of production and energy flow through each system.

Initially, three research programmes were started at the study sites: a detailed investigation of bacterial and fungal decomposition of cellulose, involving analysis of replicate cores from each site at monthly intervals, using Gilson respirometry; a study of terrestrial arthropods, extracted from monthly sample cores of *Festuca* grassland and *Polytrichum–Choristodontium* moss turf; and to provide environmental data, the automatic recording of microclimate (British Antarctic Survey, 1977b).

Microbial activity in the moderately organic loamy soil beneath a closed stand of *Acaena* is exceptionally high (16,3–21,3 $\mu l\ O_2\ cm^{-2}h^{-1}$ in the top 9 cm) even during winter. The soligenous peat bog shows fairly high activity (6,0–8,3 $\mu l\ O_2\ cm^{-2}h^{-1}$) but the ombrogenous peat bog has fairly low activity (1,9–4,9 $\mu l\ O_2\ cm^{-2}h^{-1}$), as does the grassland site (2,7–5,1 $\mu l\ O_2\ cm^{-2}\ h^{-1}$).

At the *Polytrichum* and *Festuca* sites, total populations of both fungi and bacteria are being monitored throughout the year. Densities are much higher at the *Polytrichum* site than the *Festuca* site (up to $5\,400 \times 10^4$ and $125 \times 10^4\ g^{-1}$ fresh soil or peat, respectively) and numbers decline rapidly with depth. No cellulolytic bacteria have been detected, but low numbers of cellulolytic fungi are present, especially in the top 3 cm of the profiles (up to $8 \times 10^4\ g^{-1}$ fresh weight in both sites) (British Antarctic Survey, 1978).

Compared with the botanical studies, little work has yet been carried out on the invertebrate fauna. High gradient heat extraction, pitfall traps, wind nets and adhesive traps are being used to sample surface and aerial faunas. Recently published taxonomic studies for South Georgia include: Protozoa (Smith, 1978), Collembola (Wise, 1970), Acari (Strandtmann, 1970; Wallace, 1970), Coleoptera (Gressitt, 1970; Watt, 1970) and Diptera (Brundin, 1970). Estimates of total arthropod numbers in the study sites range from 56 250 (winter) to 229 540 (summer) individuals per square metre in a *Polytrichum* moss bank, and from 91 245 (winter) to 207 180 (summer) individuals per square metre in *Festuca* grassland.

Description of the South Georgia rotifer fauna is near completion (Dartnall, pers. comm.). Most specimens are designated to cosmopolitan species, although they tend to differ slightly from type descriptions; several new species and new forms have been discovered. The diversity of terrestrial protozoa is only slightly less than in temperate moorland soils; Smith (1978) has described two types of habitat on South Georgia, each with virtually discrete fauna. Animal guano, alkaline with moderate organic content, has a restricted fauna of coprozoic, polysaprobic species (averaging 6), not found outside areas enriched by birds and seals. Vegetated habitats, acid with high organic content, show greater species diversity (up to 20) and angiosperm vegetation has a more diverse fauna than bryophyte dominated communities.

Preliminary investigations were undertaken of the characteristics of plant level and soil microclimate in relation to different plant communities, energy transfer in ecosystems

and the growth and production of ecologically important plant species on South Georgia (Walton, unpublished). This work has shown that the climate experienced at and within plant level is often vastly different from that measured in a standard Stevenson screen. BAS automatic data-logging stations are now functioning over *Festuca* grassland and over a *Polytrichum* stand. Coverage will be extended to the *Acaena* and tussock grass stands in the future. At the grass site, temperature is monitored at 50 cm above ground level, 5 cm within a *Festuca* tuft, 2 cm within the litter layer, and at 5, 10 and 20 cm depth in the soil; a radiometer, albedometer, and anemometer are placed at 100, 150 and 200 cm above the surface, respectively. Three soil flux plates are placed 5 cm deep in the soil. At the moss site, temperature is recorded at 50 and 1 cm above the moss apices, and at 0,5, 5, 10 and 20 cm below the apices, while a rain gauge, solarimeter and anemometer are positioned at 0, 100 and 200 cm above the ground, respectively. Snow depth is recorded at eight positions within each of the four sites. These are vertical profiles and, to extend the data across the study sites, we are trying to establish the horizontal heterogeneity of selected types of microsites using a chemical integration technique (sucrose inversion) to obtain monthly mean temperatures.

Reindeer and vegetation

On three occasions between 1911 and 1925, small numbers of reindeer were introduced to South Georgia by the Norwegian whalers. Other introductions to islands in the Arctic were followed by rapid population increases and then crashes as the populations outstripped their winter food supply. Three introductions were made at South Georgia and two of these, in geographically isolated areas in the vicinity of Cumberland Bay, were successful, but the subsequent history has been different from the pattern of the Northern Hemisphere introductions (Leader Williams, 1978a).

Adaptation to the new habitat was rapid and two years after their arrival they had reversed their breeding season to conform with the seasons, producing calves in November, the austral spring. The ten animals introduced to the Barff Peninsula in 1911 increased by about 40 per cent annually until 1920; and by 1958 numbered about 3 000, representing an average rate of increase over nearly half a century of 14 per cent annually. The reindeer were protected by legislation but permits were issued for reindeer hunting by whalers and others. Between the 1930s and 1950s, up to 100 animals were taken annually from the Barff herd. Subsequently, far fewer animals were taken. The herd began to decrease from the mid-1950s and in the early 1960s, part of it spread across or in front of a restricting glacier to form a new herd at Royal Bay. By 1972 the Barff herd numbered 1 300 and the Royal Bay herd 600 animals. There is no evidence that the Royal Bay herd has declined in numbers.

The other herd — the Busen herd — was introduced near whaling stations and its increase was restricted by poaching during the 1940s. In the 1950s, protection became effective and it began to increase, numbering 800 by 1972 but subsequently decreasing (Leader Williams, 1978a).

Two genetically different stocks of reindeer now form three herds in contrasting stages of population growth and decline, and comparisons are being made with the introductions to northern islands and to Îles Kerguelen. There is no indication that a rapid population crash, such as that on St Matthew Island, Bering Sea, will occur in the near future.

Leader Williams (1978b, and unpublished) is undertaking an investigation of the population ecology of the South Georgia reindeer. He has studied population dynamics and natural mortality by combining field observations and counts with post-mortem examination of collected and naturally dying animals. Tooth eruption patterns and annual incremental layers in the incisor teeth are used to age the reindeer. Females were found to live for up to 12 years, males for only 7 years; there is a strong bias towards females in the sex ratios of adults. Annual mortality in the female is about 33 per cent in the Barff herd and about 22 per cent in the Royal Bay herd.

In most females conceptions occur at 1½ years and the first calf is born at 2 years. The pregnancy rate in all three herds is very high (over 90 per cent). Mortality of young calves is substantial in each herd and is highest in the Barff herd; further calf mortality occurs in their first winter after weaning and varies according to the severity of the weather. The differential mortality between the sexes does not begin until the second winter. The number of females recruited to the breeding herd thus depends on the levels of calf mortality from year to year. Most males die in early winter after intense rut activity, but most females die in late winter when food availability becomes limiting. The apparent paradox of males dying before food becomes short still remains to be explained.

The coastal tussock grass, *Poa flabellata*, is the major winter forage and is highly nutritious (see above); it is also the only grass which is not completely covered by snow in winter. The influence of reindeer grazing on the vegetation is being studied and long-term exclosure experiments have been established in various plant communities (Lindsay, 1973a; Kightley & Smith, 1976). At sites where tussock grass is most accessible degradation occurs and, even after reindeer exclusion, heavy damage is irreversible. Extensive tussock destruction is now evident in all three reindeer ranges; its appearance on the Barff Peninsula dates from the 1950s peak in numbers and subsequent decline of reindeer. This progressive decrease in the available winter forage will result in progressively higher mortality of calves and adult females.

In summer, more forage is available on low-lying ground when the snow melts, but most macrolichen species (especially *Cladonia*), and *Acaena magellanica* have been severely grazed, and moss banks trampled. The exclusion experiments show that *Acaena* and moss can recover fairly rapidly, but the slow-growing lichens need a much longer period. However, the nutritive condition of the herd is good enough to maintain the high reproductive rates and early maturity.

Intensive studies on various aspects of reindeer biology are in progress, including seasonal changes in diet, nutrition and reindeer condition; rates of growth; causes of mortality (including an unusually high incidence of lumpy jaw associated with actinomycosis); the reproductive cycle; and the antler cycle (Leader Williams, unpublished); as well as the long-term vegetation studies already mentioned.

Rats and mice

Brown rats, *Rattus norvegicus*, have been found in South Georgia since the beginning of the 19th century, having been accidentally introduced by sealers. A field study was undertaken at Grytviken and Dartmouth Point (Pye, unpublished). They depend on tussock grass, *Poa flabellata*, as a major food resource and for shelter; specimens collected throughout the year show that breeding is seasonal with a lengthy winter anoestrus. In addition to tussock, the rats eat sub-

stantial amounts of animal food, including chicks of burrowing petrels, perimylopial beetles and carrion, and they also feed at low tide on marine invertebrates such as the bivalve mollusc *Gaimardia*. Cytogenetic studies have been carried out to ascertain whether genetic changes have occurred since the original introductions, but the results were negative.

A population of house mice, *Mus musculus*, was found at Queen Maud Bay in 1975/76 (Bonner & Leader Williams, 1977). Like the rats, they have probably been isolated since the early years of the 19th century, and they also live in tussock grass. There are a number of discrete territorial groups, each occupying 2 to 6 individual tussocks, with burrow systems. Tussock seeds appear to be a major part of the diet, together with small arthropods. A large series of mice was collected in 1978 and all were of the dark-bellied agouti phenotype. Mice occur on other sub-Antarctic islands, but mice in this population probably represent the most environmentally stressed mice in the world. They are big animals with much brown fat, in response to their cold environment. They offer an opportunity to study the response of a well-known, widely distributed species to an environment especially rigorous for a small mammal. Berry *et al.* (1979) have investigated natural selection in this population.

Marine biology

Pollution studies

A whaling station was operating at Grytviken from 1904 to 1964 and considerable quantities of organic matter and fuel oil entered the bay. Platt (1978) has estimated that the organic waste reaching the sea each season was about 15 000-25 000 tons up to 1930, falling to about 1 800 tons in 1959/60. Not all would have reached the sea bed, but even if only one per cent did and was spread evenly over the area of the cove it would represent 18-250 g organic matter m^{-2} yr^{-1}, greatly enriching the bottom sediments and producing some eutrophication and oxygen deficiency. No estimate has been made of fuels and other pollution, but in places there are still thick tarry deposits along the shore, and much metal, glass and other scrap litters the floor of the cove.

A sediment experiment has been run for several years to establish the rate of accumulation on the floor of King Edward Cove and to estimate the net input of organic material from pelagic to benthic systems. The annual accumulation appears to be 0,3 cm, similar to results from Northern Hemisphere studies. Variations are mainly associated with winds, rainfall, and land run-off following the spring melt. Sediment levels laid down during whaling activity showed evidence of hydrocarbon enrichment in summer, suggesting that, despite its intermittent nature, the extra organic input could not be dealt with by the ecosystem. Information on the pathways of organic material through the entire ecosystem is given by the quantitative and qualitative distribution of the hydrocarbons and lipids (Platt, unpublished).

Analyses for petroleum oil components, primarily n-alkanes, were made on samples of sediment, fish, benthos and a land plant mixture from the floor of the cove (Mackie *et al.* 1978). No trace of fuel oil from previous spills or leaking storage tanks could be found in any of the samples examined, although possible evidence of such wastes was found in the deepest sediment layers in the centre of the cove.

Platt (1978) established six sampling stations on the floor of the cove on a transect seawards from the former whaling station, along the 11 m depth line; a seventh site was located at 4–6 m depth on the north side of the cove. Samples for determination of biomass data were taken by suction sampler, grab and bottom corer. The biomass ranged from 34–279 g m^{-2} wet weight (Platt, in press). Platt (1978) found no sign of a residual gradient along the transect out from the original source of pollution. He compared data from other polar and temperate localities, similar in terms of substrate type and depth, and concluded that there was 'little evidence to suggest the biomass of the cove is now unusual.' The macrobenthic community had evidently recovered to a state indiscernible from the natural within eight years after pollution ceased. He suggested that there was no reason to suppose that these low-temperature ecosystems were markedly less able to recover from severe pollution effects than more temperate equivalents.

Inshore studies

Knox (1970) and White (1977), among others, have discussed ecological adaptations of Antarctic marine poikilotherms. The Antarctic Continent is centred on the southern geographical pole surrounded by the Southern Ocean, with an open circulation with the other world oceans. As a consequence, the ecosystem is characterized by the physical environment's exhibiting a progressive reduction in seasonal variation towards the pole, whereas the features associated with solar radiation, such as primary production and sea-ice development, become more extreme on approaching higher latitudes.

Many of the features typical of the high polar environment, such as low stable temperatures, a short burst of primary production, deep continental shelf and the regular development of seasonal ice, are less marked in the sub-Antarctic. Glacial influences are much reduced, sea temperature variations are greater, production takes place over a longer period, and a longer period of isostatic recovery means that the shelves are less deep.

Throughout the Antarctic and sub-Antarctic regions, below the immediate influence of seasonal ice, benthic biomass is high. This has tended to lead to the assumption that production is similarly high; however, the benthic communities are largely composed of longevious species, many of which attain large size. Slow growth is the normal characteristic of the benthic fauna. The high biomass, especially of sessile filter-feeding groups such as sponges, ascidians, annelids and molluscs, continues into deep water on the continental shelf. This is thought to be due to the wide range of niches offered by the glacially deposited sediments. Hard substrates are not normally available at depth at lower latitudes because they are usually covered by silt from terrigenous sources.

The distribution of the Antarctic and sub-Antarctic benthos demonstrates the influence of the west-wind drift, as they show closest affinities with the nearest neighbour to the east. However, although the benthic communities have obvious east-to-west relationships, they are more characterized by marked independence since very high levels of species endemism are exhibited by both the Antarctic and sub-Antarctic benthic communities. Much of this trend is attributable to the extreme geographical isolation of the high latitude land masses, and also because a large proportion of the benthic invertebrates has adopted a breeding strategy which has reduced dependence on a planktonic feeding larval stage. This reduces dispersal capacity and leads to genetic isolation and, consequently, a high level of species endemism.

Perhaps the most obvious feature which distinguishes sub-Antarctic benthic communities from those in the Antarctic is the presence of the coastal fringe of giant kelp,

Macrocystis and *Durvillea*, which would be unable to resist the persistent ice-scour characteristic of the Antarctic benthic environment.

The marine biological research of BAS has been concentrated at Signy Island, South Orkneys, since 1961 and it was only in the early 1970s that similar work began at South Georgia. Year-round research has been undertaken there with the aim of integrating autecological and physiological studies, quantifying the more important components of the near-shore ecosystem and comparing the results with those from similar habitats and biological groups in different geographical regions. Monitoring of the environment by means of regular measurements at standard oceanographical stations is undertaken. A central theme of the autecological studies, both at South Georgia and Signy Island, concerns ecological and physiological adaptation to a cold, seasonally oscillating environment. Studies have been completed or are in progress on a number of benthic invertebrates, including densities, population structure and dynamics, reproduction, feeding studies and behaviour. Species, chosen for their intrinsic interest or apparent importance in the ecosystem, include the opisthobranch mollusc, *Philine gibba* (Seager, 1978), the brittle star *Ophionotus hexactis* (Morison, unpublished), *Chorismus antarcticus* and *Notocrangon antarcticus* (Maxwell, 1977). Studies have also been carried out on oxygen consumption and growth of the limpet, *Nacella concinna* (Ralph & Maxwell, 1977a), and the lamellibranchs, *Gaimardia trapesina* (Ralph & Maxwell, 1977b), *Adamussium colbecki* and *Laternula elliptica* (Ralph & Maxwell, 1977c). These, and other studies, show that reproductive strategies are closely adapted to exploit the seasonal burst of production during the brief summer bloom. The physiological experiments demonstrate that the phenomenon of elevated metabolic rates, which was supposed to be typical of cold-adapted aquatic organisms, does not have as wide a distribution as formerly believed. Everson (1977a) has brought the available information together and discusses some of its implications.

The lipid biochemistry of benthic invertebrates has been studied. A variety of benthic invertebrates from the sub-Antarctic show a generally low lipid content (0,6–2,1 per cent fresh weight), dominated by phospholipid and containing only traces of wax ester. Detailed studies were carried out on the prawn, *Chorismus antarcticus*, particularly in relation to late summer spawning, egg brooding over winter and hatching of pelagic larvae the following spring (Maxwell, 1977; Clarke, 1977a, b, c, d). The eggs are large and lipid-rich. The lipid contents and compositions are broadly similar to temperate water benthos, but planktonic invertebrates often have very high lipid contents dominated by wax esters. This appears to be caused by the patterns of feeding imposed by the strongly seasonal cycle of Antarctic primary production. Zooplankton feed actively in summer and survive on the stores of wax ester then laid down during the winter.

Various physiological, histochemical, biochemical and ultrastructural studies have been carried out on South Georgian fish, including the white-blooded Channichthyid or 'ice fish' *Champsocephalus gunneri* (Johnston & Walesby, 1977; Johnston *et al.* 1977).

With the development of an offshore biological programme at South Georgia, the intention is to run down the field effort devoted to benthic species. However, in addition to the studies summarized above, extensive collections of fish and invertebrates are available from benthic surveys, using beam trawls, various grabs and other methods from the RRS *John Biscoe*, both at the South Orkneys and South Georgia in the early 1970s.

Offshore Biological Programme

In 1978 an Offshore Biological Programme (OBP) was initiated by BAS, using the RRS *John Biscoe*. It will develop as a contribution to the international BIOMASS programme (El-Sayed, 1977), and is a response to the need to know more about the biology of krill, *Euphausia superba*, which has such a key position in the Southern Ocean (Everson, 1976, 1977b; Laws, 1977a, b). The OBP concentrates on the biology of krill, its environment and its principal predators. The field operations will be based on South Georgia and the Scotia Sea and will involve land-based studies of ecology, behaviour, physiology and biochemistry of invertebrates and fish from Grytviken; studies of birds and seals on Bird Island; and an annual series of offshore cruises, staggered over a number of years, to give replicate coverage of all seasons of the year. During the offshore cruises, studies of primary production, zooplankton, fish, squid, birds and seals will be undertaken, as well as the physical and chemical oceanography necessary to understand the biology. The results of the first season are described in the Annual Report (British Antarctic Survey, 1978). A new departure in such studies was the use of drifting icebergs as integrators of surface water flow, the position of sampling stations in each cruise being relative to the iceberg.

Seabird studies

Work on seabirds is carried out mainly on Bird Island, and is concerned with food and feeding ecology linked to work on population ecology and basic biology, of albatrosses, petrels and penguins. Factors promoting ecological separation are investigated by comparative studies of 'species pairs'. This work is still largely unpublished, but fuller accounts can be found in the BAS Annual Reports.

Albatrosses

Work, begun in 1975, centres on the similar black-browed, *Diomedea melanophrys* and grey-headed, *D. chrysostoma* albatrosses, the former having an annual breeding cycle, the latter biennial (Prince, in press). Their diet was investigated by collecting several hundred regurgitated samples from adults about to feed chicks. Analysis by weight showed that the black-browed albatross takes mainly krill, with smaller amounts of fish and squid, while the grey-headed albatross takes mainly squid, some fish, small amounts of krill and a small but significant quantity of lampreys, *Geotria australis*. Analyses for fat, protein and calcium content and calorimetry were made. Feed sizes and frequency of feeding were determined throughout the season to establish the amount of food given to chicks between hatching and fledging; weight losses between feeds were recorded. Experiments involving the transfer of eggs between species, and measurements of the growth of the foster chicks provide further insight. Grey-headed chicks with black-headed parents grew in wing length and weight, better than with their natural parents. Black-browed chicks under grey-headed parents maintained wing growth, but weight gain was drastically reduced.

There is a 25-day difference in fledging period and a 14-day difference in attendance at the colony before laying, producing a 40-day difference in breeding season duration. Grey-headed albatrosses which fledge chicks do not breed the following year, although unsuccessful ones do. Consideration of calorific values of the prey, dietary composition, feed

size, feeding frequency and assimilation efficiency account for much of the 25-day difference in fledging period.

The major difference in breeding frequency is compensated for by differences in breeding adult survival rather than by reproductive success. Five age classes, ringed as chicks between 1959 and 1964 by Tickell (1968), were monitored. Mean annual mortality of adult black-browed albatrosses is about 10 per cent; much greater than for grey-headed albatrosses (6 per cent). This work continues (Prince, in press).

In addition to the above studies on mollymauks, recovery of ringed wandering albatrosses, *D. exulans*, which was begun by Tickell (1968), has been resumed as a continuation of a long-term study of survival, recruitment and breeding success. In recent seasons all chicks have been ringed and almost all breeding individuals are checked. Seven and a half per cent of the breeding population was of known age (13, 14 and 15 years old) in 1977. Each year further generations of known-age birds return to the breeding grounds for the first time and more data accumulate. In 1976, 860 chicks survived from the previous season, representing a winter survival of 87 per cent.

Petrels

Similar research on the breeding biology, food and feeding ecology of four species of small petrels (forming two 'species pairs') began in 1972. The paired species are the sub-Antarctic diving petrel, *Pelecanoides urinatrix exsul*, and South Georgia diving petrel, *P. georgicus* (Payne & Prince, 1979); blue petrel, *Halobaena caerulea* and dove prion, *Pachyptila desolata* (Prince, 1980). Within both pairs there is no overlap in the period of chick feeding, sub-Antarctic diving petrels and blue petrels breeding earlier than the other member of each pair. Other adaptive differences in breeding biology, feeding methods and foraging areas were discovered. The crustacean diets reveal the prey available to or selected by the petrels, and differences in their feeding ecology. *P.georgicus* takes largely krill, *P.u. exsul* chiefly copepods; the difference seems to be due to selection because copepods are important in the diet of the dove prion, which breeds at the same time as the krill-eating *P. georgicus*. The identified food of blue petrel comprises 91 per cent crustacea, by weight, 8 per cent fish and 1 per cent squid. Dove prions take crustacea almost exclusively (97 per cent). Of the crustacea taken, blue petrels consume 86 per cent euphausids, the remaining 14 per cent being mysids, decapods, amphipods and copepods. Dove prions take 59 per cent euphausids and 37 per cent copepods. Within several prey species, the blue petrel takes larger individuals than the dove prion, and blue petrels appear to feed further from the breeding colony.

A similar study has begun on the giant petrel 'species pair' of *Macronectus giganteus* and *M. halli*, which breed on Bird Island.

The stomach oil produced by many procellariiformes is an important aspect of their breeding ecology and analyses of samples from six species have been reported. These indicated that the oil was derived from food often containing wax esters from zooplankton. Such stomach samples could be used to monitor offshore pollution, and no substantial offshore pollution by petroleum hydrocarbons was indicated in these samples (Clarke & Prince, 1976).

Penguins

Two penguin species are being studied on Bird Island, the gentoo, *Pygoscelis papua*, and the macaroni, *Eudyptes chrysolophus*. They are ecologically important because of their abundance (the macaroni in vast numbers) and, consequently, large potential impact on the surrounding ecosystem. Their general biology has been documented and broadly confirms other studies, although several features reflect the rich offshore food resources.

Gentoo penguins lay two eggs and successfully hatch 70 per cent of them; nearly 90 per cent of chicks reach independence. Elsewhere, chicks are rarely raised from both eggs of the clutch. In macaroni penguins the mean duration of the period when up to 5 kg of fat is deposited, in preparation for the moulting fast, is 12 days as against about 25 days in the very closely related royal, *E. schlegelii*, and rockhopper, *E. crestatus*, penguins on Macquarie Island. Changes in weight of gentoo and macaroni penguins have been followed throughout the season and energy demands of moult assessed (Croxall, unpublished).

There are marked differences in food and feeding ecology. Each gentoo penguin parent feeds both chicks every day, mainly on mature krill (*c*.55 mm length); one macaroni parent feeds the single chick each day with immature krill (*c*. 20 mm). The slow rate of digestion of krill permits estimation of the minimum number of krill caught during feeding trips of known duration (Croxall & Prince, unpublished).

A census of macaroni penguin breeding numbers at South Georgia has begun; the greatest concentration occurs on Willis Islands just to the west of Bird Island. Smith and Tallowin (1980) have made an assessment of changes in numbers of king penguins, *Aptenodytes patagonica*, at 32 colonies. The maximum population is estimated at 57 000 birds, including immatures, which suggests a substantial population increase during the past 50 years.

Seals

Four species of seal occur regularly at South Georgia, the Antarctic fur seal, *Arctocephalus gazella*, the Southern elephant seal, *Mirounga leonina*, the Weddell seal, *Leptonychotes weddelli*, and the leopard seal, *Hydrurga leptonyx*. The first two species have been studied intensively by BAS biologists. Both were reduced to low levels as a result of commercial sealing in the 19th century and both showed a remarkable recovery under protection.

Fur seals

Initially, the fur seal recovered more slowly and in the 1930s there were possibly fewer than 100 animals in the South Georgia population; only 12 pups were counted on Bird Island in 1936. Under complete protection, the population increased rapidly and the first accurate count in 1957 revealed a population of 5 350, which increased to 10 200 in 1962 (Bonner, 1968). From 1972 a long-term programme of research has been undertaken, the increase has been monitored by counts of pup production and the expansion of the breeding range on Bird Island and on the main island of South Georgia has been mapped. The population increased by 16,8 per cent annually from 1958 to 1972 and 14,5 per cent from 1972 to 1975 (Payne, 1977). This is a faster rate of increase than has been recorded for any other pinniped and is thought to be due to increased krill availability, related to the decline of the baleen whales. The method of estimating population size is described by Payne (1978). The 1975 estimate of pup production was 90 000, indicating a total

population in March 1976 of 369 000, with a biomass of 14 500 tonnes and annual food consumption of 353 000 tonnes (Payne, 1979). In the breeding season this is largely krill, but fish and squid are taken at other times. The age structure and recruitment to the female herd were determined from tooth growth-rings (Payne, 1978) and ovarian and uterus examination. Annual survival of adult cows (89,8 per cent) and of first year animals (64,5 per cent) was calculated, making allowance for the known population increase (Payne, 1977).

Growth was determined from measurements of length, body weight, flipper lengths, neck and axillary girths, and blubber thickness from 556 collected specimens of known age. Data on absolute and relative size of various organs were summarized. Pup growth in the 110-115 day suckling period averages 98 g d^{-1} and 84 g d^{-1} for males and females respectively, the most rapid rate for any fur seal (Payne, 1979). Detailed observations of the duration and frequency of the cows' feeding trips to sea were made. Material has been collected for study of the reproductive cycle.

Between 1971 and 1973, 16 000 pups were tagged on Bird Island and counts are made of the frequency of tagged animals amongst the breeding cows in other areas; 80 000 observations were made in 1975/76 and 1976/77. These confirmed census results which showed main island colonies — derived from Bird Island — sustaining a very high rate of increase, but the rate halving at Bird Island. The possible relationship between density of breeding fur seals and pup mortality on the beaches is being studied at high density sites (established and stable population) and low density sites (colonising and increasing population) over a number of years. Population monitoring and tag recovery operations continue.

A study of the territorial behaviour of bull fur seals has provided quantitative information on duration of territory ownership and changes in territory size (McCann, unpublished). Territories were up to 60 m^2 at the start of the season, but were decreased to 18 m^2 by the time all bulls arrived; mean tenure for bulls with harems was 34 days, for unsuccessful bulls only 13 days. Harem bulls lose nearly 50 per cent of body weight during the season (Payne, 1979) and a number of older bulls (10+ years) are found dead on the beaches after the breeding season.

Elephant seal

The elephant seal population initially built up more rapidly than the fur seal. A sealing industry began in 1910 under government control and lasted until 1964, as a subsidiary of the whaling industry. In the 1940s and 1950s, about 6 000 adult bulls were taken annually (Laws, 1953a). Studies were made by Laws (1960) at Signy Island, South Orkney Islands and at South Georgia. These reported on growth, reproduction, population dynamics and reproductive and social behaviour. Changes due to sealing were described, including a population decline, changes in harem size, cow:bull ratios, and timing of the season. New regulations were introduced in 1952 to retrieve the situation, including catch quotas by areas, related to the estimated stocks, a minimum size limit and monitoring of the age composition of the catch from tooth rings. These were very successful; the average age of the catch, the oil production per seal, and the catch per unit effort increased; the length of the catching season decreased (Laws, 1960, 1979). At the same time it was shown that growth rates were higher and ages at maturity were lower than those obtaining in the Macquarie Island population.

Field studies on population structure and social behaviour were begun in 1974 by McCann. The work was carried out in one of the study areas where Laws worked in 1951 and has provided data for comparison with the situation 26 years ago when the adult bulls were being exploited. Judged by such criteria as mean age of first breeding of cows, cow:bull ratios, harem size and maximum number of cows controlled by a single bull, the breeding organization of the study population has changed significantly since 1951 (or since 1964 when exploitation ceased) and now closely resembles that at Macquarie Island.

A number of seals were collected for ageing from tooth growth-rings (Laws, 1953b) and determination of female reproductive history. Although South Georgia bulls are the same size as those at Macquarie Island, they are on average some 4 years younger (10-11 as against 14-15 years). In 1951 all South Georgia cows examined had pupped by 3 years of age, but only 30 per cent of the recent sample had done so, a further 50 per cent breeding first at 4 years. These differences are probably related to the stopping of exploitation, with implications for intraspecific competition between the sexes, and to changes in number and age structure of the bull population, producing effects on social organization. Behavioural studies addressed the relationship between social behaviour and harem structure with particular attention to cow–cow, cow–pup interactions and activity budgets, and their influence on reproductive success. Bull dominance hierarchies were studied and the number of copulations achieved by bulls of different status was monitored. These data are currently being analysed by McCann.

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Origin and general ecology of the Marion Island ecosystem

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Introduction

The Marion and Prince Edward islands are situated in an ideal position for geological and biological research. Lying halfway between the continents of Africa and Antarctica, their oceanographic and climatic settings have moulded these islands into typical examples of the sub-Antarctic region. The surrounding ocean with its abundance of life and the stormy, wet and cool climate have made of these two small islands, with their millions of birds and thousands of seals, a rare, untouched and extremely interesting paradise which should be preserved for posterity.

Marion Island was annexed by the South African Government in 1948 and from that year onward continuous meteorological observations have been made on the island. The interesting bird and seal fauna immediately attracted attention and some studies of basic value have been published by Rand (1954, 1955) and La Grange (1962).