DiSALVO, L.H. & DANIELS, G.W. 1975. Observations on estuarine microfauling using the scanning electron microscope. *Microbiol Ecol.* 2: 234-240.

GREMMEN, N.J.M. 1981. The vegetation of the sub-Antarctic islands Marion and Prince Edward. *Geobotany* 3: 149 pp.

HEAL, O.W., BAILEY, A.D. & LATTER, P.M. 1967. Bacteria, fungi and protozoa in Signy Island soils compared with those from a temperate moorland. *Phil. Trans. Roy. Soc. Ser. B.* 252: 191-197.

HOLDING, A.J., COLLINS, V.G., FRENCH, D.D., D'SYLVA, B.T. & BAKER, J.H. 1974. Relationship between viable bacterial counts and site characteristics in tundra. In: Soil organisms and decomposition in tundra: eds A.J. Holding, O.W. Heal, S.F. Maclean Jr. & P.W. Flanagan. Tundra Biome Steering Committee, Stockholm, pp 49-64.

HUNTLEY, B.J. 1971. Vegetation. In: Marion and Prince Edward Islands; report on the South African biological and geological expedition 1965-1966, eds E.M. van Zinderen Bakker (Sr.) J.M. Winterbottom & R.A. Dyer. A.A. Balkema, Cape Town. pp 98-100.

JANNASCH, H.W. 1958. Studies on planktonic bacteria by means of a direct membrane filter method. *J. Gen. Microbiol.* 18: 609-620

JENKIN, J.F. 1975. Macquarie Island, sub-Antarctic. *Ecol. Bull.* 20: 375-397.

LINDEBOOM, H.J. 1979. Chemical and microbiological aspects of the nitrogen cycle on Marion Island (sub-Antarctic). Ph.D. thesis, University of Gröningen. 138 pp.

MARSHALL, K.C. 1978. The effects of surfaces on microbial activity. In: Water Pollution Microbiology, Vol. 2, ed R. Mitchell. John Wiley and Sons, New York. pp 51-70.

SMITH, R.I.L. & STEPHENSON, C. 1975. Preliminary growth studies on *Festuca contracta* T. Kirk and *Deschampsia antarctica* Desv. on South Georgia. *Br. Antarct. Surv. Bull.* 41/42: 59-75.

SMITH, V.R. 1977. The chemical composition of Marion Island soils, plants, and vegetation. *S. Afr. J. Antarct. Res.* 7: 28-39.

SMITH, V.R. 1978. Soil chemistry of Marion Island (sub-Antarctic). *S. Afr. J. Sci.* 74: 174-175.

SMITH, V.R. 1979. Evaluation of a resin-bag procedure for determining plant available P in organic, volcanic soils. *Plant and Soil* 53: 245-249.

STOUT, J.D. 1961. A bacterial survey of some New Zealand forest lands, grasslands and peats. *N.Z. J. Agric. Res.* 4: 1-30.

THAUER, R.K., JUNGERMANN, K.J. & DECKER, K. 1977. Energy conservation in chemotrophic anaerobia bacteria. *Bact. Rev.* 41: 100-180.

VALERA, C.L. & ALEXANDER, M. 1961. Nutrition and physiology of denitrifying bacteria. *Plant and Soil* 15:268-280.

Animals as agents of erosion at sub-Antarctic Marion Island

K.J. Hall

Geography Department
University of Natal, Pietermaritzburg 3200

A.J. Williams

Percy FitzPatrick Institute of African Ornithology,
University of Cape Town, Rondebosch 7700

Birds and seals act as agents of erosion on the coastal lowlands of sub-Antarctic Marion Island. Erosion primarily occurs where birds congregate at high densities to breed and is accentuated by the soft-foliage vegetation, easily eroded peaty substrate and wet climate. Different groups of birds - flying surface breeders, flying subterranean breeders and flightless penguins - each have particular erosive effects. Penguins cause most erosion and even affect bedrock. Bird activity causes slumping on steep slopes. The erosive effect of seals is minor.

Voëls en robbe dien as bewerkers van erosie op die kustelike laaglaande van sub-Antarktiese Marion-eiland. Erosie kom hoofsaaklik voor waar voëls in hoë digtheid vergader om te broei en word beklemtoon deur sagte loof plantegroei, die maklik verweerbare turfagtige substraat en die nat klimaat. Verskillende groepe van voëls - vlieënd wat op die oppervlakte broei, vlieënd wat onderaards broei en vluglose pikkewyne, het elk 'n spesifieke erosie effek. Pikkewyne veroorsaak die meeste erosie en selfs rotsbeddings word geaffekteer. Die bedrywighede van voëls veroorsaak ineenstortings teen steil hoogtes. Die erosie effek van robbe is van minder belang.

Introduction

Nowhere is the proportion of sea to land greater than in the southern hemisphere between latitudes 40° and 60°S. This vast productive oceanic region supports large populations of seabirds and seals, all of which must return to land to breed and many also to moult. This results in large, seasonal concentrations of animals on the sub-Antarctic islands. The animals affect the islands in two ways: by transferring minerals and energy from the sea to the land (Burger *et al.* 1978, Siegfried *et al.* 1978, Williams *et al.* 1978) and by vegetation destruction and consequent erosion of the substrate. The role of birds and seals as agents of erosion at Marion Island (46°54'S, 37°45'E) is the subject of this paper.

Environmental Situation

Marion Island (area 290 km²) is the exposed section of a submarine shield volcano (Verwoerd 1971). The island is composed of two basalt lava suites; an older, massive and glaciated grey suite, and a young scoriaceous, blocky and unglaciated black suite. During the last (approximately)

276 000 years the island has been glaciated on three occasions (Hall 1978, 1979a, in press) and the coastal lowlands include areas of glacial debris (Hall 1979a, 1981) and raised beaches (Hall 1977).

Precipitation on Marion Island averages 2 600 mm per year and occurs on 25 days in each month, mainly in the form of rain (Schulze 1971). Due to the extensive cloud cover (average 6 oktas) the radiation received at the ground is very limited, only 20 to 33 per cent of that possible (Schulze 1971) and thus evaporation is relatively low. During the infrequent dry periods the strong westerly winds may cause desiccation of the surface few millimetres of soil and peat. The heavy precipitation, coupled with low evaporation rates, results in continually saturated ground with frequent overland flow. The strong winds which accompany the rain (mean 32 km per hour with gusts up to 198 km per hour, Schulze 1971) may result in further physical damage to surface vegetation and peat, together with the transport of material up to granule size. According to palynological investigations (Schalke & Van Zinderen Bakker 1971) the climate has been very similar to the present since about 11 000 BP.

Marion Island has a typical sub-Antarctic flora with a paucity of species (Huntley 1971, Alexandrova 1980). Many of the plants are soft-foliaged and so are easily damaged by trampling (Gillham 1961). Much of the coastal lowlands, except where covered by the more recent black lava flows, or to a lesser extent, directly exposed to the prevailing westerly winds, has a peat cover which is up to four metres in thickness

Erosion by Seabirds

Twenty-six species of seabirds breed at Marion Island (Williams *et al.* 1979). These birds can be regarded as forming three groups: (1) surface-breeding species which can fly, (2) burrowing or hole-breeding species which can fly, and (3) flightless, surface-breeding penguins. Each of these groups exerts a different effect in terms of the type and amount of erosion caused.

(i) The flying, surface-breeding species

These are generally dispersed over the ground surface and thus, other than plucking vegetation for nest material, they have little erosive effect (Lindsay 1971). An exception occurs where concentrations of albatrosses (*Diomeda* and *Phoebetria* spp.) breed on steep, vegetated slopes. The combination of vegetation removal for nest material and the loading, particularly the impact when landing, of the birds on saturated high angle (35-60°) slopes frequently causes localised slumping. The material on the cliff faces is often beyond the angle of repose and is only maintained by the binding action of the vegetation. Hence, with the removal of some of this binding matter and the shock of landing this may cause the shear strength of the material to be overcome and thus slumping takes place (Taylor 1948). Occurrences of this were observed on the cliffs at Macaroni Bay where units of vegetation and soil in the region of 0,4 x 0,3 x 0,1 m were seen to be removed.

(ii) The flying, subterranean-breeding species

The numbers of burrowing petrels and prions at Marion Island are unknown, but have been estimated at many hundreds of thousands to millions (Van Zinderen Bakker Jnr. 1971, Williams *et al.* 1979). Investigations of petrel and prion burrows by Van Zinderen Bakker Jnr. (1971) show that excavation is extensive and may involve removal of up to 1 m³ of peaty soil from each burrow. The excavated material is transported away from the burrow by a combination of surface run-off and aeolian action during wet and dry periods respectively. Unfortunately no accurate calculations can be attempted as the total number of birds is unknown and burrow size varies. However a rough estimate of the magnitude of erosion can be seen if each burrow is assumed to necessitate the removal of about 0,2 m³ of material and a range of bird numbers from 600 000 to 1 000 000 is used. This would suggest the quantity of material removed, to date, to be in the order of 120 000 m³ to 200 000 m³.

In addition to the direct removal of material, burrowing has an effect on slope stability. Extensive removal of material, coupled with the frequent saturation of the substrate, causes slumping where slope angles are relatively steep (16° to 35°) due to the decreased shear strength of the soil.

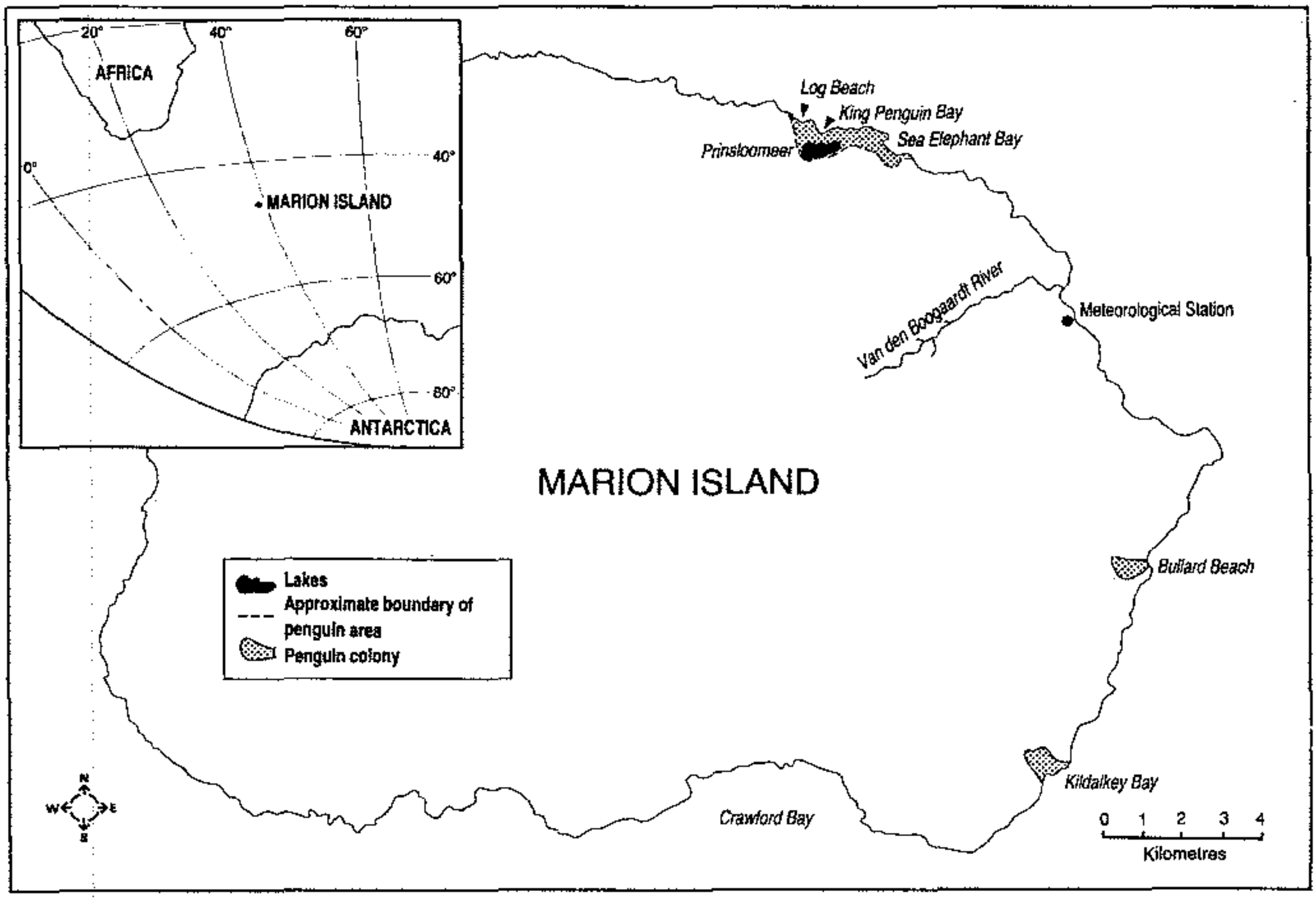
(iii) The flightless, surface-breeding penguins

Their large numbers (the combined Marion Island penguin population is about 3,4 million individuals), high breeding densities (Fig. 2) and relatively high individual body mass makes them the most potent animal agent of erosion at Marion Island. The number of journeys each individual penguin makes annually between the sea and its breeding locality is dependent upon its breeding status and success. Birds which successfully rear chicks must, in order to feed the chicks, make many more journeys between the sea and the colony than those whose breeding attempt is unsuccessful. It is this movement of these birds, to and fro between their nests and the sea, which is the effective agent of erosion.

Each species of penguin has a habitat preference (Van Zinderen Bakker Jnr. 1971, Williams 1978, Hall 1979b). Erosion is most pronounced in colonies of king (*Aptenodytes patagonicus*) and macaroni (*Eudyptes chrysolophus*) penguins, both of which prefer flat or gently sloping terrain where they can breed at high densities (2,3 and 4,5 pairs per m² respectively). In colonies of these species, vegetation is entirely destroyed by trampling and manuring. The destruction of vegetation diminished progressively away from the colonies (Fig. 3), and Huntley (1971) estimated that 95 per cent of the vegetation is affected at 5 m from the edge of the colony, 50 per cent at 25 m, and only at 55 m is no effect discernable. Once the surface mat of vegetation has been destroyed the soft, wet peaty subsoil is "clawed" by the penguins and removed either on their feet or by surface run-off. At the two largest colonies, Kildalkey Bay and Bullard Beach (Fig. 1), a peat cover of up to 4 m thickness has been removed from areas of 110 000 and 82 000 m² respectively. Assuming an average peat thickness of 1,5 m over these areas, the total volume of peat removed from these two localities amounts to 2 900 m³. King penguin erosion is also extensive in the Sea Elephant Bay to Log Beach area (Fig. 1) with severe erosion over an area of 630 000 m², while adjacent areas become increasingly affected as the population of penguins increases (pers obs).

Erosion is particularly concentrated along the main routeways between penguin breeding colonies and the sea. For example, at Bullard Beach 200 000 pairs of macaroni penguins must pass from a narrow landing beach up a steep valley about 30 m wide, in order to reach their breeding colony. Their passage has not only removed all vegetation and soil, but also grooved the massive grey lava bedrock and polished it to a mirror-smooth finish (Fig 4). The grooves, up to 150 mm long, 10 mm deep and 6 mm wide, occur where birds not successful in their jump from one level to another higher up slither back down, raking the rock surface with

Fig. 1 The locations and approximate areas of the major penguin colonies mentioned in the text.



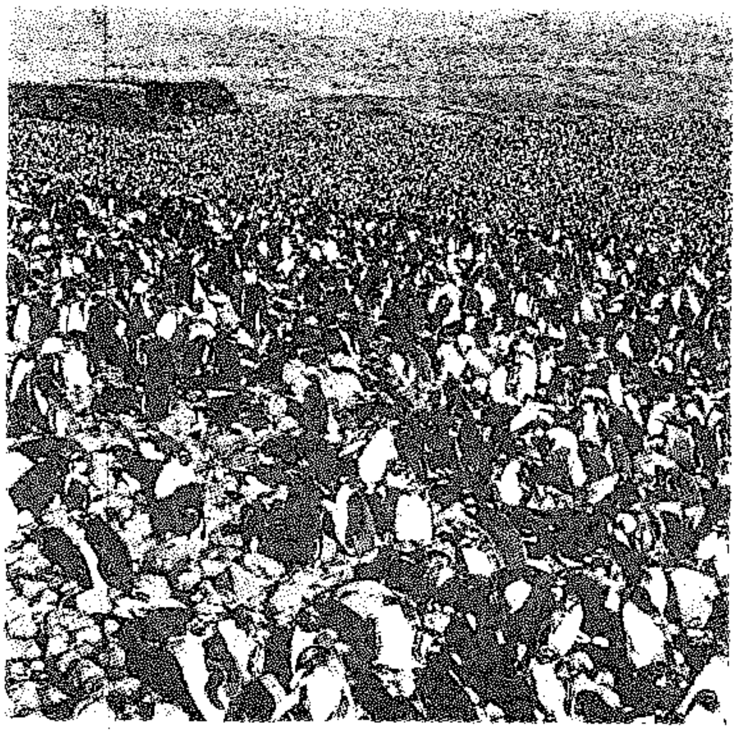


Fig. 2 Part of the macaroni penguin colony at Kildalkey Bay. Note the birds are resting on bedrock having eroded the peat cover (peat cliff in upper left corner is 4 m high).

Fig. 4 Grooving and polishing of a massive basalt along a macaroni penguin routeway at Bullard Beach.

their claws. This effect can also be observed at all the older macaroni penguin colonies on the island.

Rockhopper penguins (*Eudyptes chrysocome*) prefer broken ground, particularly the rugged black lava areas along the the coast. Where colonies spread onto vegetated ground, the effect is the same as at the king and macaroni penguin colonies. Grooving of bedrock by rockhopper penguins has been observed at Gough Island (Broekhuysen 1948) and at the Falkland Islands (Murphy 1936) but not at Marion Island. The absence of grooving by this species at Marion Island is probably a function of rock structure. The black Marion basalts are vesicular, with a clinkery or blocky structure. The friable nature of these lavas forestalls groove formation but does facilitate fracturing. The amount of erosion resulting from this form of destruction is impossible to assess, but freshly exposed rock surfaces have been observed.

Gentoo penguins (*Pygoscelis papua*) are the least numerous of the penguins at Marion Island but make the largest number of overland journeys per individual, because of their habit of returning to the colony each evening throughout the extended breeding season. Gentoo penguins prefer to breed on vegetated areas some distance from the sea but, unlike the other three penguin species at Marion Island, often change the location of breeding colonies not only from year to year but sometimes between the laying of initial and replacement clutches. Gentoo nesting density is also lower than that of the other penguins. Their low nest density coupled with the habit of changing colony location reduces the erosive effects of this species. Gentoo penguins do, however, wear deep tracks through the vegetation and peat surrounding their main landing beaches, and these tracks may form local drainage lines.

Erosion by seals

Elephant seals (*Mirounga leonina*) are only able to haul ashore on stony or sandy beaches (Condy 1977). During the mating season they remain in these areas, but during their annual moult they move inland for distances of up to several hundred metres. Elephant seals do not feed during their three to six week moult and so their body mass upon arrival is enhanced by the large fat reserves necessary to maintain them during the period of fasting ashore (Carrick *et al.* 1962). At the start of the moult, females may weigh about 900 kg and adult males up to 3 600 kg (King 1964).

The population at Marion Island is currently about 4 500 individuals (Condy 1977) but was larger in the past (Rand 1955). As seals move inland to moult, generally in the same localities used year after year, their great bulk flattens and damages the vegetation. The depressions they create in the moulting areas often act as drainage lines which concentrate run-off and initiate small-scale fluvial erosion and transport. Within the moulting area they create hollows which, through time, become deepened into wallows. Typical wallows are elongate with rounded ends and an outward bulge in the middle. Measurement of 12 such wallows indicated an average of 3,07 m^3 of material displaced per unit. This displacement may, in part, be explained by compaction although the effect of dilatancy on the granular mass is, as yet, unknown and may inhibit the amount of compaction which is intuitively thought to take place.

Wallows become full of water with a mixture of sediment and manure in suspension when in use. As a seal enters or moves within a wallow it displaces this mixture, and overland flow, especially during the rainy periods, removes sediment from the wallow site downwards towards the coast.

In areas where many moulting seals congregate, a number of wallows may coalesce to form a "compound wallow", which can vary from a combination of two to many tens of single wallows (Fig. 5). Two compound wallows measured indicated a volume of material displaced of 768 m^3 and 129 m^3. Because the seals moult only in certain months of the year, and may not use the same area for moulting in consecutive years, vegetation in moulting areas is not completely destroyed. Vegetation in the wallows themselves, whilst razed

Fig. 3 The severely eroded peat at the edge of the Kildalkey Bay colony.

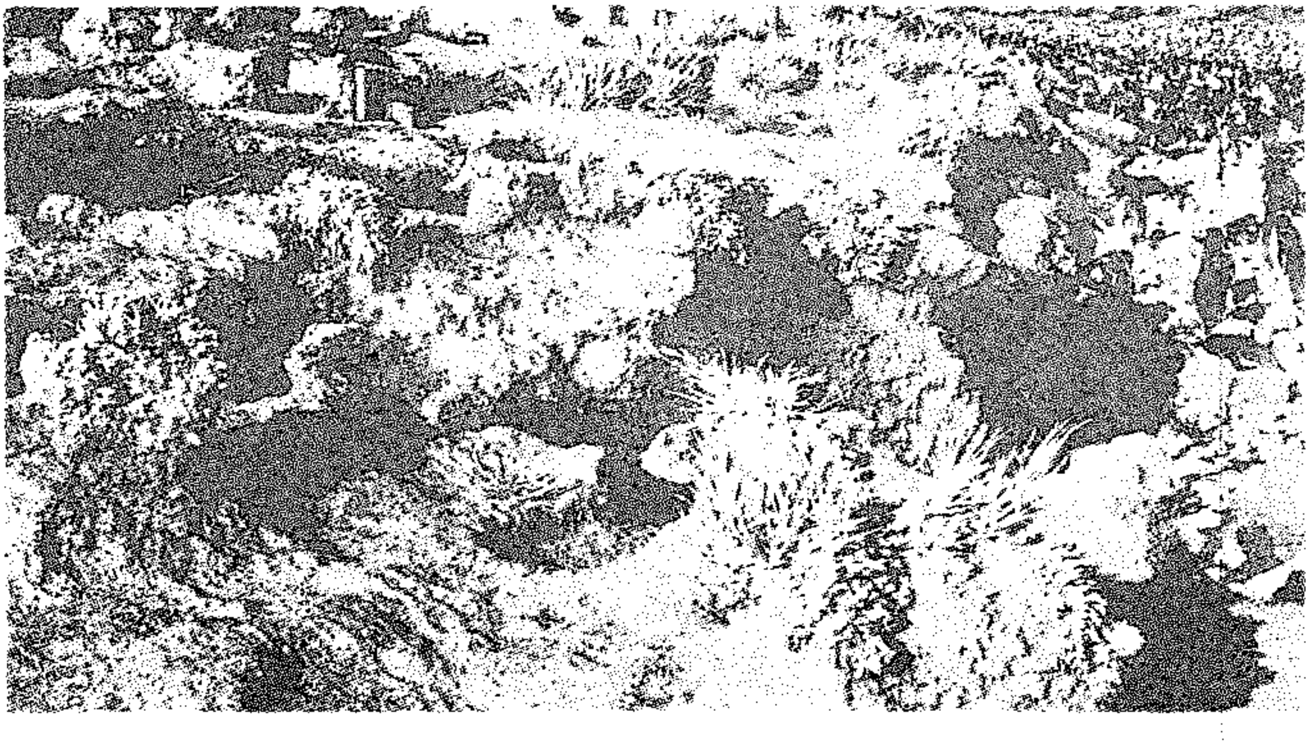


Fig. 5 A compound seal wallow surrounded by coalescing single wallows (near Trypot Beach). Note the damaged status of the vegetation within the general area of wallows and total destruction within the actual wallows.

during seal occupancy, rapidly regrows once the seals have left (Condy pers comm). However, a distinctive topography is developed in which extensive wallow systems are interspersed with vegetated ridges and humps (see Condy 1977; Plate 4).

Two species of fur seals (*Arctocephalus tropicalis* and *A. gazella*) are found at Marion Island. Both are confined to the west and northwest of the island where they breed on boulder and bedrock beaches. They make only limited excursions into vegetated areas and so have little erosive effect, although distinctly "flattened" vegetation has been observed (Condy pers comm).

The time element

Prior to about 17 000 BP the localities where the major present-day penguin and seal colonies are found would have been beneath an extensive ice cover (Hall 1978). However, during the glacial phase world sea level was in the region of 140 m lower than at present (John 1979) and so breeding could have taken place on the low-lying areas beyond the glacier cover. During the main glacier retreat stage, after approximately 14 000 BP, penguins and seals could have colonised the glacial outwash areas and so have begun to move inland as, at the same time, sea levels began to rise due to melting of the world's ice cover. However, on Marion Island (Hall 1982), as elsewhere (Dietrich 1980, Mörner 1978), extensive tectonic movements are considered to have occurred immediately upon the retreat of the ice. The location of Marion Island within a potentially active volcanic area resulted in the tectonics initiating volcanism (Hall 1982). Thus, as animals moved to higher elevations this would have been initially to areas of grey lava or glacial deposits as movement onto the black lava flows could only have taken place once they had cooled sufficiently.

There is some evidence to show (Lindeboom pers comm) that ammonia released from penguin guano is volatised and, where blown onto land adjacent to the colonies, stimulates vegetation growth and hence peat production. Penguins are thus associated with the production of peat which they may later erode. C^{14} dates from some thick peats at Kildalkey Bay (Lindeboom pers comm) yielded a basal date of c. 14 000 BP and only a short distance above a date of 7 000 BP. This indicates that the area was certainly ice-free by 14 000 BP. The possibility then arises that the slow growth of peat between 14 000 and 7 000 BP was due to the lack of nutrients introduced by the fauna (penguins in this instance) and that rapid growth after that date results from an increase in the penguin numbers and hence introduced nutrients. Other factors will obviously complicate this simplistic appraisal but, nevertheless, it does fit the present state of knowledge.

Other erosion agents at Marion Island

Subjectively it appears that the erosion by animals exceeds that of any other agent currently active on the island although, in the absence of any quantitative data, this is a tenuous statement. However, certainly glacial activity can be considered as negligible, since there is only a small area of permanent snow and ice and comparison of photographs taken 11 years apart indicates no sign of ice movement. Rock breakdown by freeze-thaw activity, whilst undoubtedly active in the past, is at present limited except in the higher parts of the island. Within the coastal lowlands the incidence of freeze-thaw cycles is low (Hall 1979c) and the few daily cycles monitored are of small amplitude. The porous nature of much of the bedrock inhibits runoff and stream activity so that, despite the heavy precipitation, there are very few permanent streams on the island. There is little observational evidence to suggest that these streams are currently causing extensive erosion, especially as the main part of their courses occur in the flat coastal lowlands rather than in the steep inland areas. After periods of heavy rain overland flow occurs but, except where aided by another agent (e.g. animals), does not cause any discernable erosion.

Animal erosion elsewhere in the sub-Antarctic

The erosive role of animals at other sub-Antarctic islands has been commented on by a number of workers. Holdgate (1964) notes that many areas on Signy Island are "... influenced to some extent by seabirds", particularly the tunnelling prions and that other areas are "... markedly affected by wallowing seals". Holdgate *et al.* (1968) found that seals caused extensive trampling and dunging on the beach at Bouvetøya such that it "... was almost completely bare ...". In the South Shetlands, Lindsay (1971) notes the effects of large penguin and seal aggregations and how nitrogen enrichment resulting from the proximity to animal concentrations causes "... maximum vegetative growth ...".

On Elephant Island (South Orkney Islands), Allison and Smith (1973) found that the effects of animals were of only local significance but that "... where there were colonies of birds their effects on the vegetation was considerable". Severe erosion at the periphery of a growing chinstrap penguin (*Pygoscelis antarctica*) colony was also observed. In the South Sandwich Islands Holdgate (1963) found that the barrenness of platforms at 15 to 30 m above the sea "... was probably accentuated by the presence of abundant penguins". Smith and Corner (1973) observed burrows in a peat bank in the Argentine Islands caused by Wilson's storm petrels (*Oceanites oceanicus*) but considered that "... they did not appear to be a cause of serious erosion". Conversely, Wace (1961) found that the major cause of peat instability on Gough Island is "... the disruption caused by the burrowing activities of the millions of ground-nesting sea birds ...". On Kerguelen Island (Hall pers obs) observed that in some areas, particularly valley trains at sea level, burrowing by prions caused localised subsidence over much of the surface.

In one of the few direct investigations on the role of sub-Antarctic animals in modifying flora, Gillham (1961) notes that on Macquarie Island the main cause of damage was trampling and that this was related to animal numbers. Run-off was considered (Gillham 1961) to exploit the initial surface damage, whilst the wet nature of the ground was thought to minimise the amount of wind erosion despite the strong westerlies. At a large royal penguin (*E. chrysolophus schlegeli*) colony, 1,52 m of erosion in peat was measured along a tract to the sea. Finally, Ealey (1954) reconstructed the colonisation sequence, following glacial recession, for Heard Island. The postulated sequence, with consideration for local variations in species and topography, is very similar to that suggested here for Marion Island.

Acknowledgements

This work constitutes part of a programme of multidisciplinary studies undertaken on Marion Island by the Institute for Environmental Studies, University of the O.F.S., and the Percy FitzPatrick Institute of African Ornithology, University of Cape Town. Financial and logistical support was provided by the Department of Transport on the advice of the South African Committee for Antarctic Research. Professors E. M. van Zinderen Bakker and W. R. Siegfried offered constructive comments on the paper and various members of both Institutes provided useful discussion. Suggestions by P. R. Condy and two anonymous referees effected several beneficial changes in content and style.

References

ALEXANDROVA, V.D. 1980. The Arctic and Antarctic: their division into geobotanical areas. Cambridge, Cambridge University Press.

ALLISON, J.S. & SMITH, R.I.L. 1978. The vegetation of Elephant Island, South Shetland Islands. *Brit. Ant. Surv. Bull.* 33: 185-212.

BURGER, A.E., LINDEBOOM, H.J. & WILLIAMS, A.J. 1978. Mineral and energy contributions of guano of selected species of birds to the Marion Island terrestrial ecosystem. *S. Afr. J. Antarct. Res.* 8: 59-70.

BROEKHUYSEN, G.J. 1948. Observations on the Great Shearwater in the breeding season. *British Birds* 41: 338-341.

CARRICK, R., CSORDAS, S.E., INGHAM, S.E. & KEITH, K. 1962. Studies on the southern elephant seal *Mirounga leonina*, III. The annual cycle in relation to age and sex. *CSIRO. Wildl. Res.* 7: 119-160.

CONDY, P.R. 1977. The ecology of the southern elephant seal *Mirounga leonina* (Linnaeus, 1758), at Marion Island. D.Sc. thesis, University of Pretoria.

DIETRICH, R. 1980. Vertikale Erdkrustenbewegungen und Potentialanderungen bei wechselnden Eis-Auflasten. *Geodatische und geophysikalische Veroffentlichungen* ser. 1 (7): 47-51.

EALEY, E.H.M. 1954. Ecological notes on the birds of Heard Island. *Emu* 54: 91-112.

GILLHAM, M.E. 1961. Modification of sub-Antarctic flora on Macquarie Island by sea birds and sea elephants. *Proc. R. Soc. Victoria* 74: 1-12.

HALL, K.J. 1977. Some observations on the former sea levels of Marion Island. *S. Afr. J. Antarct. Res.* 7: 19-22.

HALL, K.J. 1978. Quaternary geology of Marion Island. Ph.D. thesis, University of the Orange Free State, Bloemfontein.

HALL, K.J. 1979a. Late glacial ice cover and palaeotemperatures on sub-Antarctic Marion Island. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 29: 243-259.

HALL, K.J. 1979b. Population pressure in the Roaring Forties. *The Geographical Magazine*, July, 707-710.

HALL, K.J. 1979c. Sorted stripes orientated by wind action: some observations from sub-Antarctic Marion Island. *Earth Surface Processes* 4: 281-289.

HALL, K.J. 1980. Push moraines on Marion Island. *S. Afr. J. Sci.* 76: 421-424

HALL, K.J. 1982. Rapid deglaciation as an initiator of volcanic activity: an hypothesis. *Earth Surface Processes and Landforms*, 7; 45-51.

HALL, K.J. In press. A reconstruction of the Quaternary ice cover on Marion Island. *Proceedings of 4th International Symposium on Antarctic Earth Sciences, Adelaide*, in press.

HOLDGATE, M.W. 1963. Observations in the South Sandwich Islands, 1962. *Polar Record* 11: 394-405.

HOLDGATE, M.W. 1964. Terrestrial ecology in the maritime Antarctic. In: Biologie Antarctique, eds R. Carrick, M.W. Holdgate and J. Prévost. Paris, Herman.

HOLDGATE, M.W., TILLBROOK, P.J. & VAUGHAN, R.W. 1968. The biology of Bouvetøya. *Brit. Ant. Surv. Bull.* 15:1-7.

HUNTLEY, B.J. 1971. Vegetation. In: Marion and Prince Edward Islands, eds E.M. van Zinderen Bakker Snr., J.M. Winterbottom & R.A. Dyer. Cape Town, Balkema, pp. 98-160.

JOHN, B.S. 1979. The Winters of the World. Devon, David and Charles.

KING, J.E. 1964. Seals of the World. London, British Museum (Natural History).

LINDSAY, D.C. 1971. Vegetation of the South Shetland Islands. *Brit. Ant. Surv. Bull.* 25: 59-84.

MORNER, N-A. 1978. Faulting, fracturing, and seismicity as functions of glacio-isostasy in Fennoscandia. *Geology* 6: 41-45.

MURPHY, R.C. 1936. Oceanic birds of South America. New York, American Museum of Natural History.

RAND, R.W. 1954. Marion Island – home of South Africa's elephant seal. *African Wildlife* 9: 7-9.

SCHALKE, H.J.W.G. & VAN ZINDEREN BAKKER, E.M. Snr 1971. History of the vegetation. In: Marion and Prince Edward Islands, eds E.M. van Zinderen Bakker Snr., J.M. Winterbottom & R.A. Dyer. Cape Town, Balkema, pp. 29-27.

SCHULZE, B.R. 1971. The climate of Marion Island. In: Marion and Prince Edward Islands, eds E.M. van Zinderen Bakker Snr., J.M. Winterbottom & R.A. Dyer. Cape Town, Balkema, pp. 16-31.

SIEGFRIED, W.R., WILLIAMS, A.J., BURGER, A.E. & BERRUTI, A. 1978. Mineral and energy contributions of eggs of selected species of seabirds to the Marion Island terrestrial ecosystem. *S. Afr. J. Antarct. Res.* 8: 75-86.

SMITH, R.I.L. & CORNER, R.W.M. 1973. Vegetation of the Arthur Harbour – Argentine Islands region of the Antarctic Peninsula. *Brit. Ant. Surv. Bull.* 33: 89-122.

TAYLOR, D.W. 1948. Fundamentals of Soil Mechanics. New York, John Wiley.

VAN ZINDEREN BAKKER, E.M. Jnr. 1971. Comparative avian ecology. In Marion and Prince Edward Islands, eds E.M. van Zinderen Bakker Snr., J.M. Winterbottom & R.A. Dyer, Cape Town, Balkema, pp. 161-172.

VERWOERD, W.J. 1971. Geology. In: Marion and Prince Edward Islands, eds E.M. van Zinderen Bakker, Snr., J.M. Winterbottom & R.A. Dyer, Cape Town, Balkema, pp. 40-62.

WACE, N.M. 1978. Geology and the distribution of Macaroni Penguin colonies at Marion Island. *Polar Record* 19: 279-281.

WILLIAMS, A.J. 1978. Geology and the distribution of Macaroni Penguin colonies at Marion Island. *Polar Record* 19: 279-281.

WILLIAMS, A.J., BURGER, A.E. & BERRUTI, A. 1978. Mineral and energy contributions of carcasses of selected species of seabirds to the Marion Island terrestrial ecosystem. *S. Afr. J. Antarct Res.* 8: 53-58.

WILLIAMS, A.J., SIEGFRIED, W.R., BURGER, A.E. & BERRUTI, A. 1978. The Prince Edward Islands: a sanctuary for seabirds in the southern oceans. *Biol. Conserv.* 15: 59-71.

Bryophyte-cyanobacteria associations on sub-Antarctic Marion Island: are they important in nitrogen fixation?

V.R. Smith

Institute for Environmental Sciences,
University of the O.F.S., Bloemfontein 9301.

P.J. Ashton

National Institute for Water Research,
Council for Scientific and Industrial Research, Pretoria 0002.

Five Marion Island bryophyte species containing epiphytic cyanobacteria showed acetylene reduction in the laboratory at ca. 20 °C. Only Ditrichum strictum *exhibited reduction* in situ *at low (around zero) temperatures. This species occurs as a spherical cushion or ball on cold, windswept, rocky plateaux and contains a band of cyanobacteria a few millimetres below the surface of the cushion. The absence of acetylene reduction* in situ *for mire bryophyte species containing epiphytic cyanobacteria is ascribed to low temperatures during the incubation and it is thought that during the warm summer months fixation by bryophyte-cyanobacteria associations may significantly contribute towards the nitrogen status of mire habitats.*

Vyf van Marioneiland se briofietspesies met epifitiese siaanbakterieë het in die laboratorium by ongeveer 20 °C asetileenreduksie getoon. Slegs Ditrichum strictum *het* in situ-*reduksie by lae temperatuur (ongeveer nul grade) getoon. Hierdie spesie kom as sferiese kussings of balle op die koue, winderige, rotsagtige plato's voor en die siaanbakterieë kom as 'n band enkele millimeters onderkant die kussing se oppervlak voor. Die feit dat asetileenreduksie nie* in situ *by moerasbriofiete aangetoon kon word nie, word aan die lae temperatuur toegeskryf wat tydens die eksperimente geheers het. Daar word egter vermoed dat stikstoffiksering in die warm somermaande 'n belangrike bron van stikstofverbindings vir die moerasagtige gebiede moet uitmaak.*

Introduction

Moss-cyanobacteria associations have been found to be significant agents of nitrogen fixation in sub-Arctic bogs, Fennoscandia tundra and Arctic tundra (Granhall & Selander 1973, Granhall & Basilier 1973, Granhall & Lid-Torsvik 1975, Alexander, Billington & Schell 1978). This has also been noted for alpine tundra and humid, cool-temperate oceanic island ecosystems (Porter & Grable 1969, Alexander *et al.* 1978, Englund 1976, 1978).

Bryophytes are an important component of the vegetation of sub-Antarctic islands (Taylor 1955, Greene 1964, Hébrard 1970, Huntley 1971) and are often closely associated with cyanobacteria which occur epiphytically on (occasionally endophytically in) the leaves. To date, however, no assessment of the possible role of these associations in nitrogen fixation has been made for a sub-Antarctic site. Croome (1973) found