Slatyer, R.O. *Plant-Water Relationships*. Experimental Botany International Monograph Series, Vol. 2. London, Academic Press, 1967.
Slavik, B. *Methods of Studying Plant Water Relations*. Ecological Studies **9**. Berlin, Springer-Verlag, 1974.
Smith, V.R. The effect of burrowing species of Procellariidae on the nutrient status of inland tussock grasslands on Marion Island. *J. S. Afr. Bot.*, **42**, 265-272, 1976a.
Smith, V.R. Standing crop and nutrient status of Marion Island (sub-Antarctic) vegetation. *J. S. Afr. Bot.*, **42**, 231-263, 1976b.
Smith, V.R. The chemical composition of Marion Island soils, plants and vegetation. *S. Afr. J. Antarct. Res.*, **7**, 28-39, 1977.
Smith, V.R. Animal-plant-soil nutrient relationships on Marion Island (sub-Antarctic). *Oecologia (Berl.)*, **32**, 239-253, 1978.
Turner, N.C. Stomatal behaviour and water status of maize, sorghum and tobacco under field conditions. II. At low soil water potential. *Plant. Physiol.*, **53**, 360-365, 1974.
Woolhouse, H.W. Light-gathering and carbon assimilation processes in photosynthesis; their adaptive modifications and significance for agriculture. *Endeavour, New Series*, **2** (1), 35-46, 1978.

The limnology of Marion Island: Southern Indian Ocean

J.U. Grobbelaar
Institute for Environmental Sciences,
University of the Orange Free State, Bloemfontein 9300.

The lentic waters of Marion Island are small shallow lakes, crater lakes, lava-lakelets and wallows, originating from ice-scouring, volcanic activity and biotic influences. Sedimentation and vegetation encroaching from the shore influence the morphology of the water bodies. The lotic water types are mere intermittent rivulets. The water bodies are homothermal and polymictic but in calm conditions energy absorption by the surface water layer and by the benthic algal felts and periphyton raises their temperatures. The waters are dystrophic, with low alkalinity. Nitrogen and phosphorus are detectable only in biotically fertilized waters. The ionic dominance resembles that of sea water. There is very little primary production in the unfertilized waters, and even in the biotically fertilized water bodies there are no fish and the food chain ends with zooplankton.

Introduction

Biological research has been undertaken on the sub-Antarctic island Marion since 1965 and observations on the limnology were made during the first (1965-1966), second (1971-72), third (1972-73) and fourth (1973-74) biological expeditions. Huntley (1971) reported on a few general features of some water bodies and streams, as well as on physical and chemical measurements. The work done during the second and third expeditions was presented by Grobbelaar (1974a) as a PhD thesis. The chemistry and primary production have been reported by Grobbelaar (1974b, 1975 and 1978a), factors affecting the algal growth by Grobbelaar (1978b) and observations on the zooplankton by Kok and Grobbelaar (1978).

The freshwater types

Lentic waters

It is misleading to use the term 'lake' for water bodies on Marion Island as no lake per definition (Odum, 1971) occurs on the island and all are mere ponds or pools restricted to areas of low relief close to the sea. This is due to the lack of suitable lake basins, steep island slope and porosity of the lava rocks. The term 'lake' is, however, used for convenience and indicates the larger water bodies.

Catchment areas of the water bodies are mainly restricted to their immediate surroundings and stream-fed ones are the exception. The water bodies are often clustered together in groups, e.g. Albatross, Skua, Swartkop Point and Kampkoppie Lakes.

The lentic waters have been classified into four types, i.e. (a) lakes, (b) crater lakes, (c) lava-lakelets, and (d) wallows. An additional distinction can be made between lakes which are: (a) situated on grey lava, (b) situated on black lava, (c) biotically influenced, and (d) not-biotically influenced.

Water bodies on the old grey lavas

There are a few lakes, of which the Albatross and Skua Lakes are the most notable (see Fig. 1). The old grey basalt was covered with glacial depositional landforms and the lake basins are formed in kettles or against moraines (K. Hall, personal communication). Most basins have a sandy-clayish bottom sediment and thicknesses of up to 2,5 m were measured.

A considerable degree of variation in form and size of these lakes is found and surface areas range between 100-32 600 m^2, with a mean of about 4 000 m^2. The lakes are all shallow, their maximum depth lying between 0,4 and 2,4 m, with a mean depth of approximately 1 m. None of the lakes has a profundal zone and the littoral zone extends over the entire basin. The basins are usually flat-bottomed with steep sides. Terrestrialization of the basins, mainly from the shores, can change the shapes, where the encroaching vegetation may, under extreme conditions, form a swinging mat or raft. The prevailing strong north-west winds produce waves which hinder terrestrialization and can lead to wave cutting. Three basic lake profile types thus result (see Fig. 2):

Type 1: Protected lakes where terrestrialization takes place along the whole circumference of the shore line.

Type 2: Exposed lakes with a north-westerly shore of peat and a south-easterly shore of rocks.

Type 3: Same as Type 2, except with a south-easterly shore of a sandy-scoria material.

The littoral and supra-littoral vegetation communities consist mainly of the mosses *Drepanocladus uncinatus*, *Blindia tenuifolia*, *Rhacomitrium lanuginosum*, and higher plants *Agrostis magellanica*, *Juncus scheuchzerioides*, *Limosella australis*, *Poa annua*, *Ranunculus biternatus*, *R. moseleyi* and *Uncinia dikei*, together with clumps of filamentous algae. Definite vegetation belts or zones are distinguishable with *Ranunculus biternatus*, *Juncus scheuchzerioides* and *Agrostis magellanica* occupying the zone at the water edge. *Poa annua* may also occupy this first zone, e.g. Albatross Lake 1 (Grobbelaar, 1974a).

Water bodies of the young black basaltic lava

The black lavas are extremely porous and a suitable basin must first be lined with peat and debris before it can hold water. A consequence of this is the relative scarcity of water bodies on the young lavas. Their appearance, exposure, littoral and supra-littoral development are much the same as that of lakes on the old grey lavas.

A. *Lakes*. The lakes are either isolated, e.g. Laekop Lake and Tweeling Lake, or grouped into areas, e.g. Kampkoppie and Swartkop Point Lakes. The vegetation surrounding a lake on the west coast is dependent upon the distance from the sea, because of the large amounts of sea-spray which are swept inland by the strong westerly winds, and lakes bordered by dense stands of the halophytic plants *Tillaea moschata* and *Cotula plumosa* are common, close to the sea.

B. *Crater lakes*. Approximately 130 volcanic cones scat-

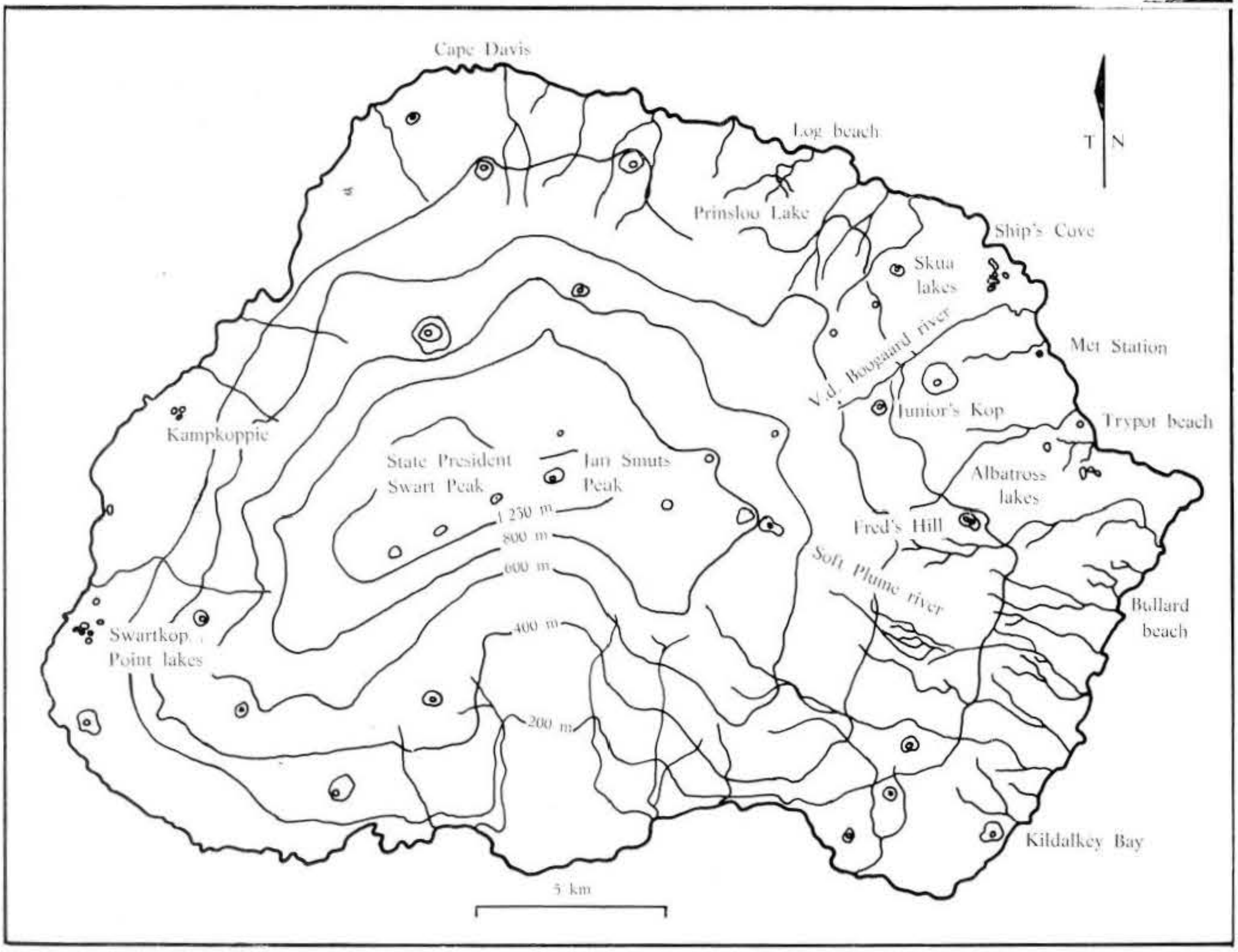


Fig. 1. Topographical map of Marion Island showing some of the lentic and lotic waters mentioned in the text.

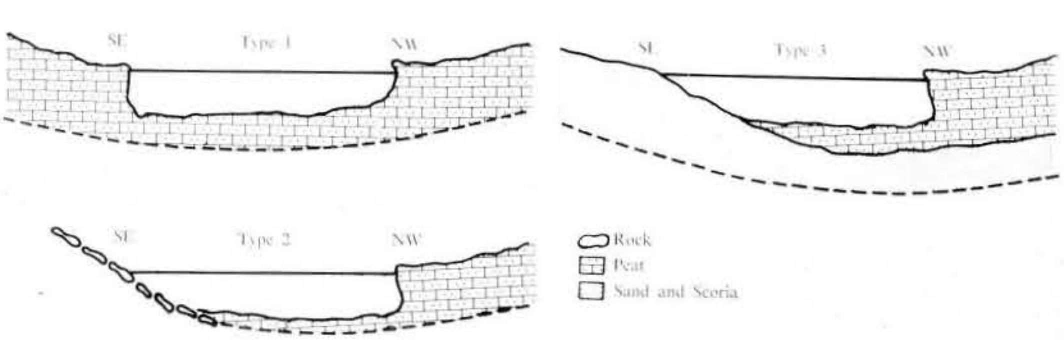


Fig. 2. Three shore profile types of the lentic waters.

tered over Marion Island mark the centres of eruption belonging to the second volcanic stage of the island's geological evolution. They are up to 200 m high with steep slopes consisting of coarse scoria. A few contain a central depression or bowl in which a lake is situated, e.g. Junior's Kop, Fred's Hill, Hendrik Fister Kop, etc. None of the craters on or around the central highland contain any lakes and those of the coastal plain are mostly restricted to the eastern side of the island.

Crater lakes are exposed to violent winds which sweep through the bowl, transforming the water into a foaming, churning mass with water spray being swept away by the winds. Relatively few plants are found in the bowl as the coarse scoria offers little support to any form of plant growth (E of Fig. 3).

Crater lakes are small and the surface areas range from 50-1 500 m². They are shallow, seldom exceeding 2 m in depth. A layer of peaty-sediment lines the basin and the bottom is usually covered with an algal felt.

C. *Lava-lakelets*. Numerous small water bodies are found in the black lava flows of the island. Huntley (1971) referred to them as 'tarns'. This term could be misleading as they are not found in the mountainous area of the island, but on the coastal plain below an altitude of 500 m above sea level.

The area of lava-lakelets is from 10 to 1 000 m². They are shallow, the deepest one measured being situated west of the meteorological station in study area 1 with a maximum depth of 1,9 m.

Terrestrialization of a lava-lakelet depends largely on exposure to the prevailing winds. They are, however, more protected than lakes and are usually flat-bottomed and their whole circumference is steep-sided. Large deposits of peat line the basins and surround the lakelets. The peat lining may collapse as a result of rock movement, and the catastrophic consequences of this could, in extreme cases, lead to the complete drainage of a lakelet.

Four lava-lakelet profiles are presented in Fig. 3 (A–D). Lakelet A is 500 m above sea level and has an area of 23 m² and a maximum depth of 70 cm. At this altitude the vegetation consists mainly of cushion plants (*Azorella selago*) and moss balls (*Ditrichum strictum*). There is a little peat in the basin.

Lava-lakelet B is exposed to wind and wave action. A peatless south-east shore is opposed to a peat-covered shoreline on the north-western side. Lava-lakelet C, the most frequent type, is protected and surrounded by an *Agrostis* mire. In these lakelets terrestrialization often results in the formation of a floating raft of encroaching vegetation. Lava-lakelet D is close to the sea in the spray zone. It is surrounded by a dense stand of the halophytes *Cotula plumosa* and *Tillaea moschata*.

D. *Wallows*. Large numbers of elephant seals (*Mirounga leonina*) use Marion Island for mating and moulting. These seals make depressions in the peat which fill with water and are called wallows.

Wallows are usually close to the landing sites of the seals. Landing sites are either sandy or boulder beaches, and as the animals do not move far on land, wallows are less than 600 m from the sea. There are wallow areas at Kildalkey Bay, Trypot Beach, Transvaal Cove, Ships Cove, Sea Elephant Bay and King Penguin Bay.

During the investigation several stages in the development of wallows were recognised (see Fig. 4). The first stage (A of Fig. 4) is caused when a seal occupies a specific spot for some time and the abandoned depression fills with water. There are numerous examples of this type on the island. Prolonged and multiple seal activity causes the enlargement and linking up of the depressions with the formation of ooze (B of Fig. 4), and results in wallows which differ greatly in size.

Wallow types other than C and D are mere stages of reclamation and terrestrialization and their development depends largely on the size of the wallow. Large wallows usually develop into water bodies where the water has a dark red-brown colour with dense stands of the alien grass *Poa annua* fringing the shores (C of Fig. 4). This type also represents the oldest stage where no trace of recent seal activity is found.

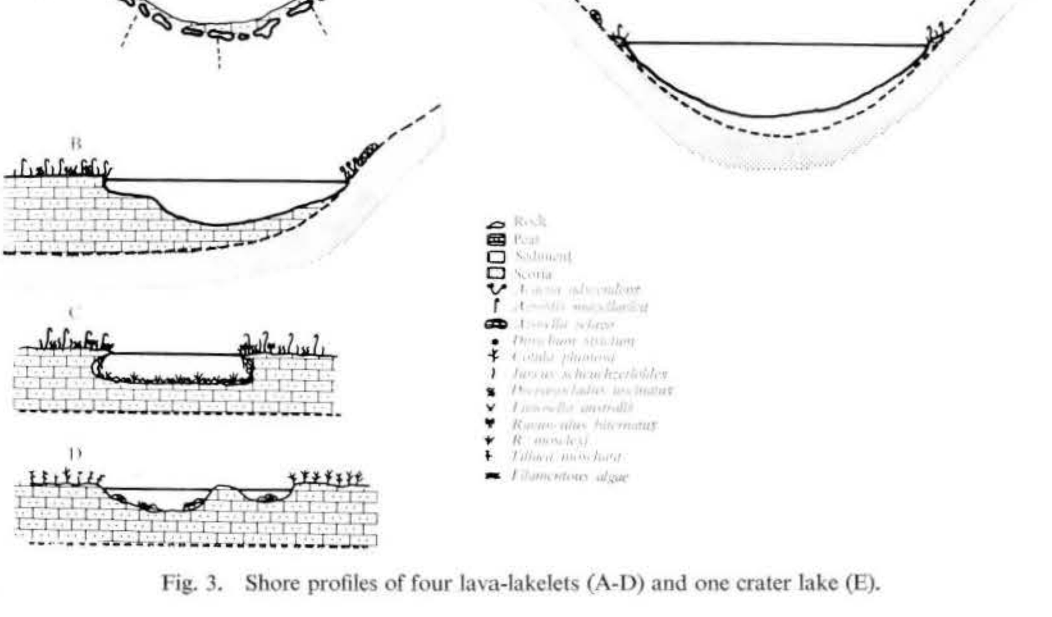
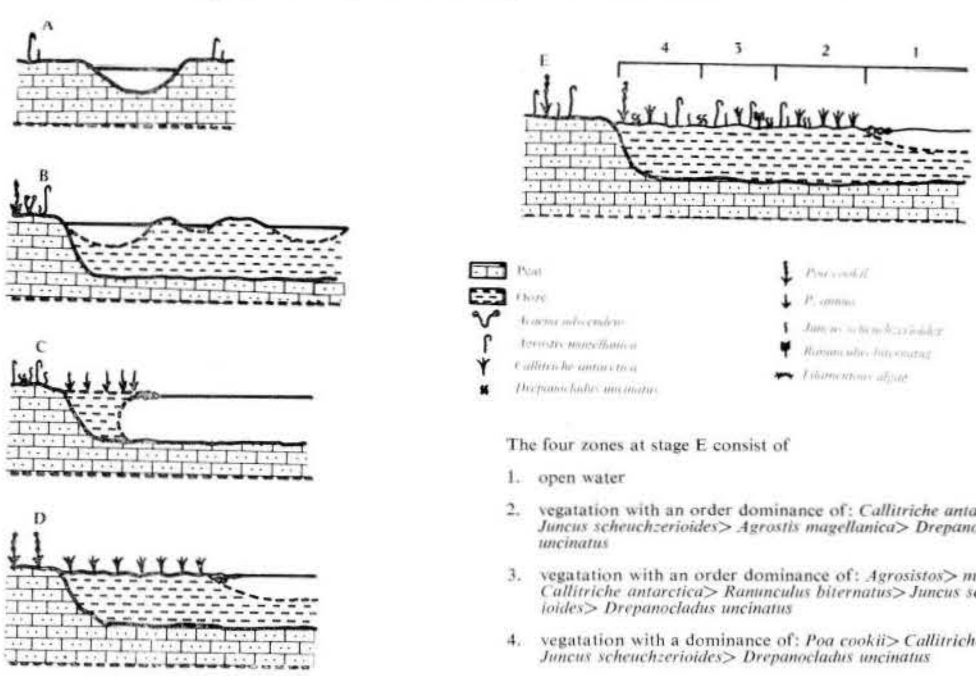


Fig. 3. Shore profiles of four lava-lakelets (A-D) and one crater lake (E).

Fig. 4. Five stages in the development and reclamation of wallows.



The four zones at stage E consist of

1. open water
2. vegatation with an order dominance of: *Callitriche antarctica*> *Juncus scheuchzerioides*> *Agrostis magellanica*> *Drepanocladus uncinatus*
3. vegatation with an order dominance of: *Agrosistos*> *magellanica* *Callitriche antarctica*> *Ranunculus biternatus*> *Juncus scheuchzeioides*> *Drepanocladus uncinatus*
4. vegatation with a dominance of: *Poa cookii*> *Callitriche antarctica* *Juncus scheuchzerioides*> *Drepanocladus uncinatus*

Smaller wallows with ooze are colonized by coprophyllous plants, the first and most conspicuous being an invasion of *Callitriche antarctica* (D of Fig. 4). *Poa cookii*, *P. annua*, *Agrostis magellanica*, *Juncus scheuchzerioides*, *Drepanocladus uncinatus* and *Ranunculus biternatus* follow as the wallow ages and a definite zonation of the vegetation can be seen (E of Fig. 4).

The small open water portion is usually colonized by a dense algal growth. Although no detailed algal survey was carried out, observations revealed that blue-greens dominated in young wallows, whereas greens were mostly present in old wallows. Only once was a green alga found to be dominant in a very young wallow and it was identified to be almost a pure mass of *Chlamydomonas* sp.

Biotically influenced lakes

Most of the lentic waters are occasionally enriched by birds, but this is usually insignificant and they cannot be considered to be truly biotically enriched. Only Gentoo and Prinsloo Lakes are noticeably enriched by elephant seals and king penguins (*Aptenodytes patagonica*) which come ashore annually to mate, breed and moult. The seasonal fluctuations in enrichment cause variations in algal populations and production, as well as in the physico-chemical characteristics of the contaminated water.

Gentoo Lake is also the only polluted lake on the island, as it is situated below the base camp with a dumping site for old diesel drums and hardware. Prinsloo Lake is the largest lake with an area of about 100 000 m². Water from both lakes is turbid because the bottom ooze is agitated by the animals.

Lotic waters

The lotic waters of Marion Island are mere rivulets or streams and no permanent, large or impassable waterway occurs. It is nevertheless fascinating to follow the larger water flows, with their numerous waterfalls, rapids, watertunnels, pools and rock gullies, through which crystal clear water cascades down to the sea.

Most of the rainwater, due to the porosity of the lavas, reaches the sea by underground drainage (Verwoerd, 1971) and most of the water flows are associated with lava of the old volcanics, which is finely-grained and forms an impermeable bottom layer. The old volcanics are found on the eastern side of the island, whereas young porous lava dominates the western side.

Fluvial erosion often results in valley cutting close to the sea, e.g. Van den Boogaard River, Soft Plume River and Watertunnel Stream. The banks consist mainly of peat and are usually steep-sided. The bottom can be rocky or peaty and is often covered with dense growths of filamentous algae. The fringing vegetation is mostly dominated by the alien grass *Poa annua*, often growing submerged together with filamentous algae. This forms a solid mass which is not easily eroded by flowing water.

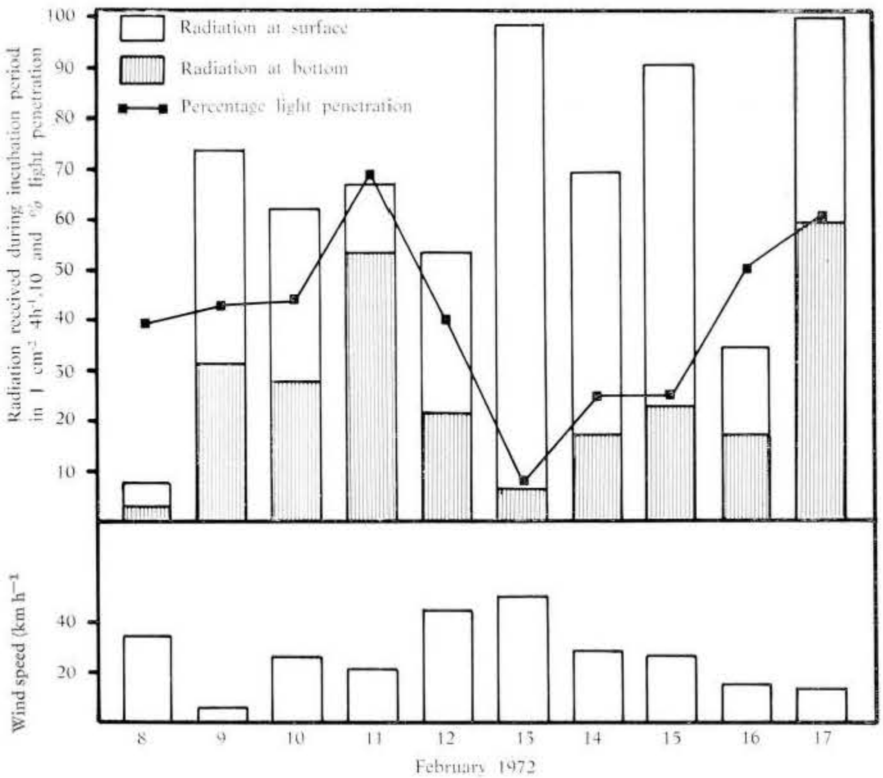
Man has influenced some of the niches on Marion Island. The introduction of trout to the Van den Boogaard River in the early 1960s by a member of the Public Works Department team is the only interference with the freshwater habitats of the island.

Physico-chemical properties of the freshwaters

Because of strong winds and shallowness all water bodies are polymictic. Surface heat build-up can, however, occur during calm sunny conditions and temperature differences of up to 6 °C were measured over the vertical profile. The absorption of radiant energy by the algae is of great importance in cold environments and temperature differences of up to 4,5 °C were measured between benthic algal felts and the overlying water (Grobbelaar, 1974a and 1975). As shown by Grobbelaar (1978b) this could increase the specific growth rate of a *Chlorella* sp. by almost 0,3 per day.

Although surface waters are generally clear, wind and wave action often resuspend bottom sediments, as shown in Fig. 5. Radiation received at the surface and bottom of Skua Lake 3 (Grobbelaar, 1974a) together with average daily wind speed are plotted for ten consecutive days. The bottom received 7-69 per cent of the surface radiation. Percentage penetration was negatively correlated ($r = 0,695$, significant at the 95 per

Fig. 5. Radiation received at the surface and bottom of Skua Lake 3.



cent confidence level) with wind speed. Animal activity also increased turbidity in Prinsloo and Gentoo Lakes. There the 1 per cent light intensity depths were between 50-75 cm and Secchi depths of as little as 3 cm were recorded in wallows. Humic acids colour most of the waters on the island and a colour range of 15-250 Hazen units was recorded (Grobbelaar, 1974a).

The water chemistry has been discussed in detail by Grobbelaar (1974a, 1975 and 1978a). The waters are generally acidic, have low alkalinities and vary widely in ionic content. The chemical composition is dominated by NaCl and an ionic dominance order of $Na > Mg > Ca > K : Cl > SO_4 > HCO_3$ prevailed, which is the same as for sea water. These ions are oceanic in origin, and enter the island's chemical cycles through the input mechanism of precipitation, either directly or as the washout component during wet fallout. The supply of these ions is affected by distance from the sea, wind direction, and amount of precipitation.

A minor component in the water chemistry is the leaching of Fe-containing humic acids which lower the pH, resulting in water with low alkalinities. The waters are generally deficient in N and P, which are detectable only in biotically enriched waters. Migratory birds and animals visit the island, causing considerable variations in contamination of the waters.

The high rainfall and small volumes of the water bodies ensure short retention times. Geochemical modification is minimal and consequently the oceanic dominated chemical composition is maintained with minor contributions and influences from biotic enrichment and leached humic compounds.

The chemical composition of the flowing waters differs little from the still waters, except for higher bicarbonate levels. This is attributed to greater geochemical modifications of the water because higher Ca^{2+} and HCO_3^- were measured in spring waters. Marked daily differences in conductivity alkalinity and Na+Cl content were found in the Van den Boogaard River (Fig. 6). A correlation coefficient of $r = -0{,}71$ (significant at the 99 per cent level) was calculated for conductivity and rainfall, showing the flushing nature of the streams. Alkalinity and Na+Cl were positively correlated with conductivity.

Biota of the freshwaters

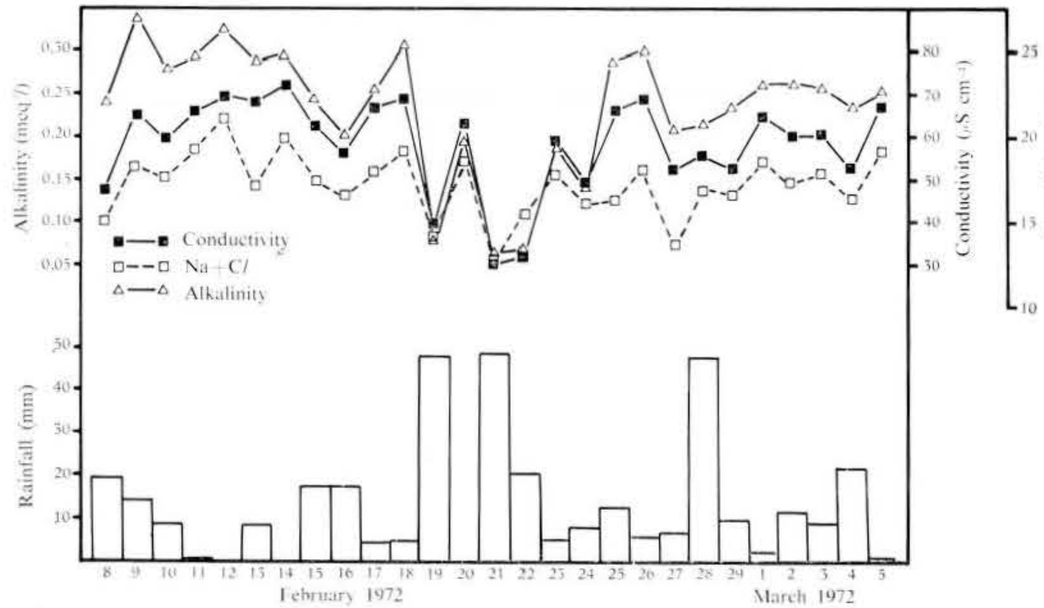
Although millions of birds and thousands of seals frequent the island there are few resident species of plants or animals. There is, furthermore, a general lack of endemic forms. This, together with the small species diversity, has been attributed to glaciation, the young geological age of the island and its westerly position in the Kerguelen Province, which would mean a migration route against the prevailing westerly winds and oceanic currents.

Primary production

In the pelagial zone in unfertilized water rates of primary production as low as 1,32 mgC m^{-2} day^{-1} were recorded and are amongst the lowest determined in the world (Grobbelaar, 1974a and b). Biotic enrichment stimulates primary production proportionate to the extent of fertilization. The highest rates of primary production, up to 6003,9 mgC m^{-2} day^{-1}, were measured in wallows, which represent extreme degrees of enrichment.

Primary production of the benthic algal felts was up to 42 times higher than that of the phytoplankton. Albatross Lake 1 (Grobbelaar, 1974a) is the only water body on the island with large stands of the macrophyte *Potamogeton*. Its production, with masses of epiphytic algae, was approximately 200 times that of the phytoplankton.

Fig. 6. Rainfall and alkalinity, conductivity and Na+Cl content of the Van den Boogaard River.



Growth conditions of algae in the freshwaters

Although there is a scarcity of planktonic algae on the island, benthic algal felts of Zygnemataceae are abundant. Determination of the maximum specific growth rates of *Chlorella* and *Scenedesmus* spp. isolated from the island, showed that the algae were not adapted for optimal growth at low temperatures (Grobbelaar, 1978b). The importance of absorbing radiant energy to achieve temperatures above that of the surroundings, as pointed out above, is evident.

In algal growth potential experiments, it was established that nitrogen and phosphorus were the nutrients limiting algal growth in most waters on the island (Grobbelaar, 1978b). Biotic enrichment is therefore of great importance. Not only were the rates of primary production higher in contaminated waters, but they sustained different algal populations. Blue-greens dominated the fertilized waters, whereas greens colonized the uncontaminated waters.

Estimates of the Autotrophic Indices (AI) showed that algae from unfertilized waters had low chlorophyll *a* contents, indicating poor physiological condition (Grobbelaar, 1978b). It was found that the AI values recorded in wallows agreed well with cultured algae.

Zooplankton and benthos

Although nine species of freshwater Entomostraca were recorded by Smith and Sayers (1971), Kok and Grobbelaar (1978) found that *Pseudoboeckella volucris* and *Daphniopsus studeri* dominated the zooplankton in the freshwaters. The largest numbers and biomass were found in fertilized waters in summer. A significant correlation was found between zooplankton biomass and phytoplankton primary production, indicating the importance of zooplankton as consumer.

Evidence of a zoobenthos was found in Albatross Lake 1 (Grobbelaar, 1974a) where small oligochaetes were found in the surface sediments. As there are no freshwater fish (except introduced trout) in the waters, zooplankton occupies the top of the food chain.

Acknowledgements

I am indebted to Professor E.M. van Zinderen Bakker, former head of the Department of Botany and director of the Institute for Environmental Sciences at the University of the O.F.S., for the opportunity to do this research and for valuable criticism. The South African Department of Transport provided financial and logistical support. Thanks are due to members of the Second and Third Biological Expeditions and 28th and 29th Relief Teams to Marion Island for help, and to Professor D.F. Toerien and Dr G.H. Wiltshire for valuable suggestions regarding the manuscript.

References

Grobbelaar, J.U. *A contribution to the limnology of the sub-Antarctic island Marion*. PhD thesis, U.O.F.S. 1974a.

Grobbelaar, J.U. Primary production in freshwater bodies of the sub-Antarctic island Marion. *S. Afr. J. Antarct. Res.*, **4**, 40-45, 1974b.

Grobbelaar, J.U. The lentic and lotic freshwater types of Marion Island (sub-Antarctic): a limnological study. *Verh. Internat. Verein. Limnol.*, **19**, 1442-1449, 1975.

Grobbelaar, J.U. Mechanisms controlling the composition of freshwaters on the sub-Antarctic island Marion. *Arch. Hydrobiol.*, **83**, 145-157, 1978a.

Grobbelaar, J.U. Factors limiting algal growth on the sub-Antarctic island Marion. *Verh. Internat. Verein. Limnol.*, **20**, 1159-1164, 1978b.

Huntley, B.J. Vegetation. In *Marion and Prince Edward Islands*, edited by E.M. van Zinderen Bakker Sr., J.M. Winterbottom & R.A. Dyer, 98-160. Cape Town, A.A. Balkema, 1971.

Kok, O.B. & Grobbelaar, J.U. Observations on the crustaceous zooplankton in some freshwater bodies of the sub-Antarctic island Marion. *Hydrobiologia*, **59**, 3-8, 1978.

Odum, E.P. *Fundamentals in Ecology*, 232-295. Philadelphia, Saunders, 1971.

Smith, W.A. & Sayers, R.L. Entomostraca. In *Marion and Prince Edward Islands*, edited by E.M. van Zinderen Bakker Sr., J.M. Winterbottom & R.A. Dyer, 361-372. Cape Town, A.A. Balkema, 1971.

Verwoerd, W.J. Geology. In *Marion and Prince Edward Islands*, edited by E.M. van Zinderen Bakker Sr., J.M. Winterbottom & R.A. Dyer, 40-62. Cape Town, A.A. Balkema, 1971.