Notes on the Flora, Vertebrate Fauna and Biological Significance of Beaufort Island, Ross Sea, Antarctica.

By Rodney D. Seppelt¹, T.G.A.Green² and M Skotnicki³

Abstract: Beaufort Island, Ross Sea, Antarctica, is a Specially Protected Area originally designated on account of, and still supporting, a small winter sea ice breeding colony of Emperor penguins, a large summer breeding colony of Adélie penguins, and several colonies of Skuas. A substantial area of moss, approximately 2.5 ha and probably the largest continuous patch of moss in the McMurdo region, has now been discovered and found to be almost entirely composed of Bryum subrotundifolium Jaeg. (= B. argenteum Hedw.). No lichens were found although many parts of the island are impassible due to steep cliffs. This contrasts strongly with the much more complex vegetation at Botany Bay, Granite Harbour, which is at an almost identical latitude (around 77 °S) but where seven mosses, one hepatic and over thirty species of lichens have been reported. Genetic analysis of Beaufort Island moss populations using RAPD procedures revealed a mixture of genotypes which could be divided into two groups that are related to populations at Cape Bird and Cape Royds on Ross Island and to coastal populations of the Dry Valleys. This suggests at least two introductions of moss to the island followed by considerable mixing, both processes probably being accomplished by the large skua population. Continued specially reserved status is warranted, as much for the vegetation as for the bird

Zusammenfassung: Beaufort Island, Ross Sea, Antarktis, ist als antarktisches Schutzgebiet (Special Protected Area) ausgewiesen, da sich hier Brutkolonien von Kaiserpinguinen und Adélie-Pinguinen sowie mehrere Brutkolonien der antarktischen Raubmöwe befinden. Auf Beaufort Island wurde nun eine ca. 2.5 ha große zusammenhängend von Moosen bewachsene Fläche entdeckt. Die $Moosgesells chaft besteht fast vollständig aus \textit{Bryum subrotundifolium} \ Jaeg. \ (=$ B.argenteum Hedw.) und bildet den flächenmäßig wohl größten zusammenhängenden Moosbestand in der McMurdo-Region. Es konnten keine Flechtenarten nachgewiesen werden, allerdings waren die steilen Kliffgebiete für diese Untersuchung unzugänglich. Die Vegetation auf Beaufort Island steht im Gegensatz zu der komplexen Vegetation, die in Botany Bay, Granite Harbour, auf demselben Breitengrad (77 °S) zu finden ist. Hier konnten im Gegensatz zu Beaufort Island sieben Moosarten, ein Lebermoos und mehr als 30 Flechtenarten nachgewiesen werden. Eine genetische Analyse der Moosgesellschaften von Beaufort Island mit RAPD-Protokollen ergab eine Mischung von Genotypen, die, aufgeteilt in zwei Gruppen, Verbindung zu den Populationen von Cape Bird und Cape Royds auf Ross Island und zu küstennahen Populationen der Dry Valleys aufweisen. Unsere Ergebnisse weisen darauf hin, daß Beaufort Island von zwei verschiedenen Moospopulationen besiedelt worden ist, die sich in der Folge stark durchmischt haben. Besiedelung und Durchmischung sind wahrscheinlich durch die großen Raubmöwenbestände gefördert worden. Der spezielle Schutzstatus für Beaufort Island sollte aufgrund der Besonderheiten der Vegetation und der bestehenden Kolonien aufrecht erhalten werden.

INTRODUCTION

Beaufort Island (76° 57' S, 166° 55' E) is a small, mostly ice and snow covered island in the Ross Sea, approximately 5 km in

length, 2.5 km in width, and reaching a highest point (Paton Peak) at 771 m (Fig. 1). The island was discovered and named in 1841 by Capt. James Clark Ross in honour of Capt. Francis Beaufort, RN, Hydrographer to the Admiralty. Moderately sloping ice fields cover most of the western side of the island while the eastern side is bounded by steep, rugged cliffs. The rocks of the island are probably Tertiary and Quaternary McMurdo volcanics, consisting of olivine-basalt, trachyte and kenyte lava flows and pyroclasitc rocks (WARREN 1969). The soils of the very few ice-free areas have not been studied.

The island was originally designated as a Specially Protected Area in 1966 on the grounds that it "contains substantial and varied avifauna, that it is one of the most important breeding grounds in the region, and that it should be protected to preserve the natural ecological system as a reference area." As an isolated island with difficult access there have apparently been few recorded visits. Recent studies have shown that the avifauna is not as diverse as originally thought. A large colony of Adélie penguins (Pygoscelis adeliae) estimated at 37,700 breeding pairs in 1991 (Woehler & Croxall 1996), occupies a low, raised, 1.0 km long beach terrace, Cadwalader Beach, at the south west end of the island. A small breeding colony of Emperor penguins (Aptenodytes forsteri) is located on annual sea ice at the northern end. No published recent counts are available but a count of 179 chicks was made in 1983 (Woehler 1993). Breeding colonies of South polar skua (Catharacta maccormicki) are associated with both penguin colonies. No other birds are known to breed on the island although occasional Southern fulmar (Fulmarus glacialoides) and Snow petrel (Pagodroma nivea) are seen. There is a strong westerly setting current of up to 1.5 m s⁻¹ between Beaufort Island and Cape Bird, to the south, which ensures early break up of the sea ice each spring and by mid-November a polynia up to 20 km across develops to the west of Beaufort Island and Cape Bird (Stonehouse 1966).

VEGETATION

A visit was made to the northern beach area on 18-19 January 1997 to survey vegetation reported to be present (Colin Harris, ICAIR, pers. comm.), to provide baseline data for the Management Plan for the island which was then being reviewed, and to collect samples for genetic analysis. Of particular significance was an area at the north end of the island which is situated on a raised platform or bench, approximately 500 m in length and up

¹ Australian Antarctic Division, Channel Highway, Kingston 7050, Tasmania, Australia

² Biological Sciences, University of Waikato, Hamilton, New Zealand

³ Photobioenergetics Unit, Research School of Biological Sciences, Institute of Advanced Studies, Australian National University, P.O. Box 475, Canberra, ACT 2601, Australia Manuscript received 2 July 1998; accepted 5 November 1998

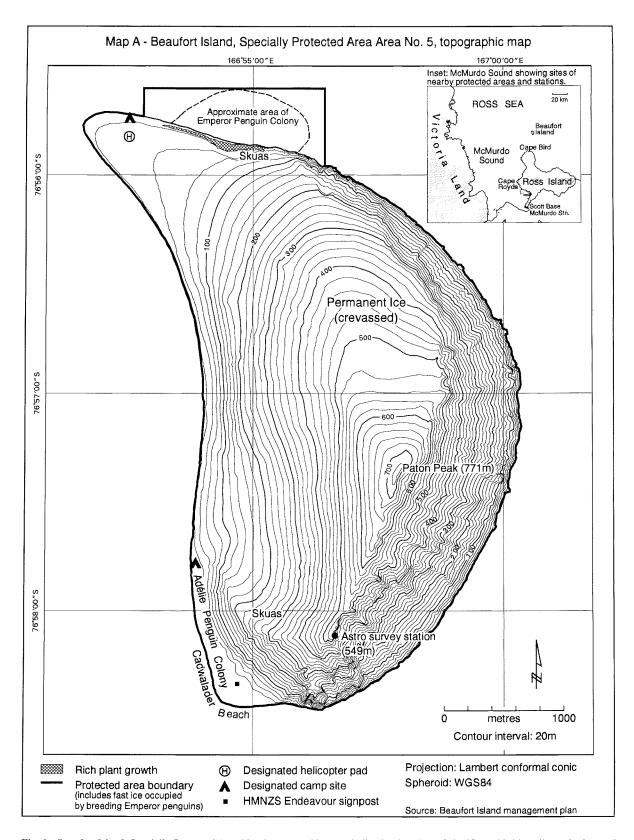


Fig. 1: Beaufort Island, Specially Protected Area No. 5, topographic map, indicating location of significant bird breeding colonies, and area of vegetation near northern end. Image prepared using GIS by M. Lythe, International Centre for Antarctic information and Research, New Zealand, from digital orthophotography data originally commissioned by the NZ Ministry of Foreign Affairs and Trade for management plan maps for SPA-5, Beaufort Island.

Abb. 1: Beaufort Island, Specially Protected Area No. 5, topografische Karte mit den wichtigsten Vogel-Brutkolonien und der Moosvegetation an der Nordseite. Abbildung erstellt mit Hilfe von GIS von M. Lythe, International Centre for Antarctic Information and Research, Neuseeland, aus digitalen orthofotografischen Daten zur Verfügung gestellt von NZ Ministry of Foreign Affairs and Trade für den Managementplan von SPA-5, Beaufort Island.

to 100 m in width, at approximately 15-20 m a.s.l. bounded by a curved ablating ice cliff about 30-40 m high to the south and steep till slopes or cliffs to the north. The cross slope trend of the bench is 2-5° to the north but becoming steeper, up to 15°, at its eastern end. The bench dips at about 5° to the west-northwest for most of its length but rises sharply, at around 15-20°, at its eastern end. The bench surface in high summer is very wet, owing to the level of melt derived from surface snow and ablation of the ice cliff. Algae are abundant, with Prasiola crispa (Lightf.) Meneghini, unicellular chlorophytes and xanthophytes, including representatives of Botrydiopsis, Pseudococcomyxa, and oscillatorialeans and other cyanobacteria. The algal flora, although not specifically collected, appears similar to that of other localities in the Ross Sea region (P.A.Broady, pers. comm). There is a significant nutrient input from skuas. The gently undulating bench supports a large breeding colony of around 50 pairs of skuas nesting on slightly elevated ground, particularly at the broader, eastern end of the bench where the nests are within a large area of moss-covered ground, approximately 2.5 ha in extent.

An extensive survey was made of the bench and nearby areas. The moss turf was very well developed, 1-2 cm thick and generally convoluted into an intricate hummock-hollow pattern, and formed extensive, continuous stands especially at the eastern end of the bench (Fig. 2). The larger moss patches and all other smaller occurrences were found to be virtually a monospecific moss turf of *Bryum subrotundifolium* Jaeg. (= *B. argenteum* Hedw. see below). Only one other moss species, a small tuft (around 10 cm²) of *Hennediella (Pottia) heimii* (Hedw.) Zander, was found in this extensive *Bryum* covered area. No lichens were found either growing on the moss or on surrounding rock

surfaces. Moss samples have been lodged with the Australian Antarctic Division Herbarium (ADT) and duplicates will be lodged in the herbarium at Landcare Research, Lincoln, New Zealand (CHR) and the national Museum of New Zealand, Wellington (WELT).

The vegetation contrasts strongly with that present at other localities at about the same latitude in the Ross Sea region. At Botany Bay, Granite Harbour, which is at an almost identical latitude of 77 °S, seven species of moss have been reported, one liverwort (Cephaloziella exiliflora (Tayl.) Steph.) and over thirty lichens (Seppelt & Green 1998). At Kar Plateau (77 °S, 600 m altitude) there are 5 mosses and 22 lichens (SEPPELT et al. 1995a, b). At the Canada Glacier flush (77° 37' S in the much drier Taylor Valley) there are three mosses and around 6 lichen species (Schwarz et al. 1992, Seppelt et al. 1992). B. subrotundifolium is present at both localities where it occupies wet sites (Schwarz et al. 1992). Three explanations seem possible for the almost monospecific moss turf: the extreme wetness, high salt levels from the nearby sea or the probably very high nutrient status. Although the area is extremely wet and B. subrotundifolium is characteristic of very wet sites at the other localities, this does not seem to be the likely explanation. At Botany Bay Ceratodon purpureus (Hedw.) Brid. excludes B. subrotundifolium from the central part of water flows and would certainly be expected to do the same on Beaufort Island. Salt effects cannot be excluded but are unlikely because of the high water flows. It is interesting to note that a similar moss monoculture (as B. argenteum) has been reported from Cape Hallett (72° 19' S, 170° 16' E) (Rudolph 1973) where the water flow originates from a large penguin colony. It thus seems that nutrient enrichment could be the explanation but this needs further studies to

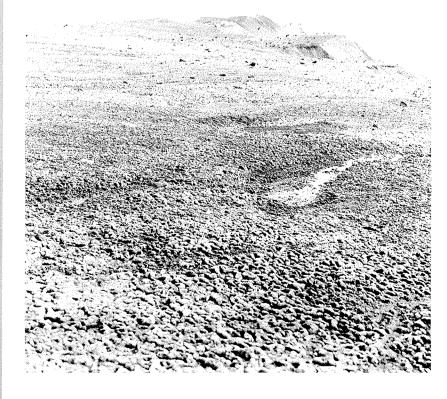


Fig. 2: Beaufort Island. Dense stand of hummocked *Bryum sub-rotundifolium* with associated algae and breeding Skuas.

Abb. 2: Beaufort Island. Dichter Stand von *Bryum subrotundi-folium* mit vergesellschafteten Algen sowie brütenden Raubmöwen.

be confirmed. The absence of lichens is also unexpected but three reasons, acting together, seem to explain the situation. The high water flow over the moss would exclude lichens from growing on the moss directly, as found at the Canada Glacier flush (Schwarz et al. 1992) and the wetter areas of Botany Bay. High salt levels from the surrounding seas could prevent lichen growth as proposed for other areas on Ross Island (Broady 1989) and the highly eroded nature of the volcanic rock would also not help.

Bryum subrotundifolium has been referred to as Bryum argenteum in recent revisionary studies (SEPPELT & KANDA 1986), other studies of the Victoria Land flora (Schwarz et al. 1992, Seppelt et al. 1995) and various molecular genetic studies (ADAM et al. 1997, SELKIRK et al. 1998). However, unlike B. argenteum elsewhere, the Antarctic plants are a yellowishgreen to light green and the cells of the upper part of the leaf contain chloroplasts whereas, even when grown in deep shade, the upper part of the leaves of B. argenteum remains hyaline. The antarctic plants, unlike B. argenteum from temperate latitudes, can also adapt rapidly to incident light environment, becoming quite green within a day or so of being shaded from direct sunlight but still capable of reverting to the yellow-white sun form when returned to high irradiances (MASEYK 1997). The taxonomic relationship of the Antarctic material with Australian populations of B. subrotundifolium, has yet to be fully evaluated.

Genetic relationships between *B. subrotundifolium* samples collected throughout the bench area on Beaufort Island were investigated using RAPD techniques according to Skotnicki et al. (1998a). DNA was extracted from single shoots, amplified with primers (OP-A13, OP-A17, OP-C4. OP-C13 or OP-P16, Operon Technologies), electrophoresed through 1.5 % agarose gels, stained with ethidium bromide and photographed under UV light. Up to 74 RAPD bands were scored as present or absent on gels with PCR reactions being done in duplicate or triplicate to confirm reproducibility. The RAPDistance program (ARMSTRONG et al. 1995) was used to compare pairwise the patterns of DNA fragments obtained in order to obtain a distance matrix. From the distance matrix a neighbour-joining tree was calculated (Armstrong et al. 1995). The resulting tree is shown in Fig. 3a, together with a diagram (Fig. 3b) of where the specimens were collected. A considerable amount of genetic variability existed in the population with no two samples being identical. However, most of the genetic differences occurred between clumps rather than between the sampled melt channel lines since the branch lengths for individual samples are longer than those joining clusters of samples. There is some evidence of clustering along channels but this is far from complete and not so strong as found for B. subrotundifolium populations (as B. argenteum) in the Garwood Valley (78° 02' S, 164° 10' E) (SELKIRK et al. 1998).

The Beaufort Island samples were also compared with isolates of *B. subrotundifolium* from several nearby locations: Cape Bird (77° 10' S, 166° 41 E), Cape Royds (77° 33' S, 166° 09' E) and Cape Crozier (77° 31' S, 169° 24' E) on Ross Island, Cape

Chocolate (77° 56' S, 164° 35' E), Marble Point (77° 26' S, 163° 50' E), Garwood Valley, Miers Valley (78° 06' S, 164° 00' E), Lake Fryxell (77° 37' S, 163° 11' E) and Canada Glacier in the Dry Valleys, and Granite Harbour. The Beaufort Island samples grouped into two main clusters: one group was most closely related to populations at Cape Bird and Cape Royds whilst the other samples clustered with some from Marble Point and Cape Chocolate, and less closely with Granite Harbour. This suggests

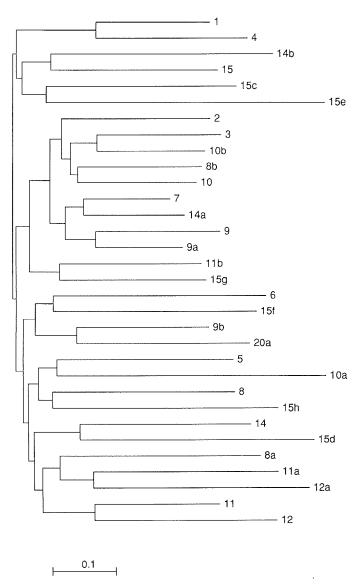


Fig. 3a: Neighbour-joined tree of relatedness for *B. subrotundifolium* samples from Beaufort Island. Samples are numbered according to location along the bench and within drainage channel as shown in the diagram below the dendrogram. A total of 63 RAPD bands for the numbered samples, prepared as described by Skotnicki et al. (1998a), were analysed using the Jacard algorithm of the RAPDistance package; five other algorithms from the RAPDistance pakkage gave similar dendrograms.

Abb. 3a: Dendrogramm der Verwandschaftsbeziehungen von Proben von *B. subrotundifolium* von Beaufort Island. Die Numerierung der Proben folgt der Abfolge der Probenstellen auf der Strandterrasse und den Abflußkanälen (siehe Diagramm). Insgesamt wurden 63 RAPD Banden für die numerierten Proben mit Hilfe des Jacard Algorhythmus (RAPDistance package) analysiert. Fünf andere Algorhythmen (RAPDistance package) ergaben ähnliche Dendrogramme. Die Probenaufbereitung folgte Skotnicki et al. (1998a).

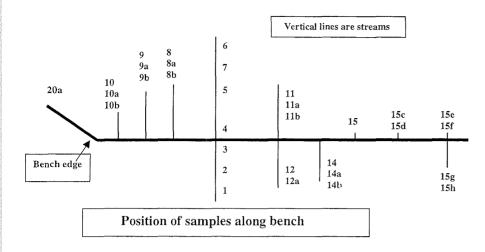


Fig. 3b: Relative location of moss samples, from east (left) to west (right) and from the raised terrace (upper) to the beach (lower).

Abb. 3b: Relative Lage der Moosproben, von ost (links) nach west (rechts) und von der erhöhten Terrasse (obere) zum Strand (tiefere).

more than one colonization event has occurred and further support comes from the pattern where samples from the ends of the bench at Beaufort Island clustered with the mainland coastal samples, whereas samples from the central bench clustered with the Ross Island samples. The generally high variability within the bench and the evidence of a double colonization suggests that skuas are the likely vectors.

Several samples of coloured snow were collected and examined and found to contain representatives of *Chloromonas* and *Klebsormidium* in green snow, with *Chloromonas* and *Chlamydomonas* cf. *nivalis* (Bauer) Wille from brownish-red snow.

SUBFOSSIL PENGUIN REMAINS

A remnant boulder beach lies below the till deposits which form the present slopes between the boulder beach and the vegetated bench. It sits on a laminar fractured basalt and is overtopped, at about 4 m a.s.l., by a stratified zone of feathers, bones and organic debris interspersed with rounded cobbles, gravels and sand (Fig. 4). The age of these penguin deposits is unknown and is worthy of careful investigation. No determination of the penguin species, Adélie or Emperor, has been made for these remains. Some of the bone and bill pieces found part way up the seaward till face are identifiable as Emperor penguin remains



Fig. 4: Beaufort Island. Stratified subfossil penguin remains overlying an elevated remnant boulder beach, northern coast of the island. Feather, bone and shell deposits indicated by arrows.

Abb. 4: Beaufort Island. Stratifizierte subfossile Überreste einer Pinguinkolonie auf einer Strandterrasse, Nordseite der Insel. Die Pfeile weisen auf Federn, Knochen und Muschelschalen bin

but it was not possible to determine if these were subfossil or relatively recent and carried to their present position by skuas from the nearby Emperor penguin colony located on annual sea ice. The laminar deposits could represent a former terrestrial Emperor penguin colony. At the present time two terrestrial colonies are known in Antarctica: at Taylor Glacier (67°27'S, 60°52'E), Mac.Robertson Land, and on the Dion Islands (67°52'S, 68°43'W), near Adelaide Island in the Maritime Antarctic. It is possible that the remains may also represent a former Adélie penguin colony which has now relocated to the beach terrace at the south western tip of the island. A study by palaeontologists, to analyse the composition of these deposits and to determine their age, is planned for the near future.

SKUAS

The northern beach and the elevated bench were estimated to support around 50-60 breeding pairs of skuas, as well as attendant non-breeders and failed breeders. On 18 January, while surveying the bench terrace, 40 chicks were counted, ranging in age from a few days to almost fully fledged, and one unhatched egg in a nest scoop was noted. Nest scoops were scattered throughout the bench area where there were exposed gravels. There were three sets of chick pairs present on the bench, and one pair located on the north western end of the sandy beach. Cursory examination of boluses indicated that the diet of the skuas was primarily penguin species and fish. The expanse of open water around the island in mid summer, together with the large Adélie penguin colony about 4 km distant, provides an abundance of food for the birds. One banded skua, from a beach nesting pair, was noted. It bore a red plastic ring over a metal numbered ring but the bird was not caught and the number not observed. Skuas have been ringed over many years in the McMurdo Sound area and it is likely that the bird was ringed at Cape Bird (77° 10' S, 166° 41′ E), the northern extremity of Ross Island (Gary D.Miller, University of New Mexico, pers. comm.). However, the date of ringing and individual identity of the bird could not be determined without close examination of the numbered ring.

OTHER BIRDS

Emperor penguins breed on sea ice during the winter months. At the time of our visit there was no physical evidence of the colony and there were no sightings of any birds.

Not surprisingly, occasional Adélie penguins come ashore on the northern beach. Most penguin activity seemed to be confined to swimming past, either in an easterly or a westerly direction, presumably in transit between the major colony at the south western corner of the island and feeding grounds.

A solitary Snow petrel was sighted flying around the northern end of the island on both the 19th and 20th January and a single Southern fulmar on 18 January. There is no evidence of these birds nesting on the eastern or southern cliffs of the island.

WEDDELL SEALS

The northern beach is used as a haul out site by Weddell seals (*Leptonychotes weddellii*). During the two days spent on the island 3-5 seals were noted each day. One adult male animal was tagged (Red 459, id No. 6419) as a pup in 1984 at Turtle Rock (77° 44' S, 166° 46' E), a small island west of Hut Point Peninsula, Ross Island. After tagging the animal was next seen off Cape Barne (77° 35' S, 166° 14' E), between Cape Royds and Cape Evans on the west side of Ross Island. Additional sightings were in 1988 off the Erebus Glacier Tongue (77° 42' S, 166° 40' E), in 1992 and 1993 at Turtle Rock, and in November 1996 off Tent Island (77° 41°S, 166° 23' E), south of Cape Evans, (Tom Gelatt, University of Minnesota, pers. comm.).

CONCLUDING REMARKS

Beaufort Island has several features of exceptional biological significance that fully support its classification as an SPA. The original grounds for reserve designation, based on birds, still exist but are less compelling than originally thought. However, the presence of the exceptionally large moss area adds a new dimension to the need for protection. The additional fact that the moss area is almost monospecific, being almost entirely B. subrotundifolium, makes the island totally different from other sites on Ross Island or the nearby continent. In fact the most closely comparable site is at Cape Hallett suggesting that nutritional enrichment by the skuas is important. Skuas are also implicated in transporting the mosses to Beaufort Island and in producing a highly mixed population. There is evidence that colonization has occurred from distant sites on the continent as well as from Ross Island. The lack of lichens is also of considerable interest and requires further detailed investigation. The sub-fossil penguin deposits are also impressive and need to be both properly described and dated. There is no question that Beaufort Island is deserving of specially reserved status. However, it is our contention that while originally established to protect the fauna, the extensive area of moss-covered ground has, at least, equal significance in the context of the biology of the Ross Sea area.

ACKNOWLEDGMENTS

Antarctica New Zealand and the University of Waikato Antarctic Research Program for the opportunity to work in Antarctica. The US Coast Guard for logistic support. Tom Gelatt (University of Minnesota, USA) and Gary Miller (University of New Mexico) for providing information on the tagged Weddell seal and Skua, respectively. Rysiek Ochyra, Krakow, Poland, for comments on the identity of *Bryum*. Paul Broady (University of Canterbury) for comments on the non-marine algal samples. Burkhard Schroeter (University of Kiel, Germany) for the German translations.

The image map was prepared using GIS by M. Lythe, International Centre for Antarctic Information and Research, New Zealand.

References

- Adam, K.D., Selkirk, P.M., Walsh, S.M. & Connett, M.B. (1997): Genetic variation and patterns of colonisation in the moss Bryum argenteum in East Antarctica. In: D.W.H. WALTON, B. BATTAGLIA, & J. VALENCIA (eds.), Antarctic Communities, 33-38, Cambridge University Press, Cambridge.
- Armstrong, J., Gibbs, A., Peakall, R. & Weiller, G. (1995): The RAPDistance package. http://www.life.anu.edu.au/molecular/software/rapd.html.
- Broady, P.A. (1989): Broadscale patterns in the distribution of aquatic and terrestrial vegetation ar three ice-free regions on Ross Island, Antarctica. – Hydrobiologia 172: 77-95.
- Schwarz, A.-M.J., Green, T.G.A., & Seppelt, R.D. (1992): Terrestrial vegetation at Canada Glacier, southern Victoria Land, Antarctica. Polar Biology 12: 397-404.
- Selkirk, P.M., Skotnicki, M.L., Ninham, J.A., Connett, M.B. & Armstrong, J. (1998): Genetic variation and dispersal of Bryum argenteum and Henediella heimii populations in the Garwood Valley, Southern Victoria Land; Antarctica. – Antarctic Science (In press).
- Seppelt, R.D. & Green, T.G.A. (1998): A bryophyte flora for Southern Victoria Land, Antarctica. New Zealand J. Botany 36 (4): 615-632.
- Seppelt, R.D., Green, T.G.A., & Schroeter, B. (1995a): Lichens and mosses from the Kar Plateau, southern Victoria Land, Antarctica. – New Zealand J. Botany 33: 203-220.

- Seppelt, R.D., Green, T.G.A., & Schroeter, B. (1995b): Additions and corrections to the lichen flora of the Kar Plateau, southern Victoria Land, Antarctica. New Zealand J. Botany 34: 329-331.
- Seppelt, R.D. & Kanda, H. (1986): Morphological variation and taxonomic interpretation in the moss genus Bryum in Antarctica. Memoirs National Inst. Polar Res., Ser. E. 37: 27-42.
- Skotnicki, M.L., Selkirk, P.M. & Beard, C. (1998a): RAPD profiling of genetic diversity in antarctic populations of the moss Ceratodon purpureus. – Polar Biology 19: 172-176.
- Skotnicki, M.L., Ninham, J.A. & Selkirk, P.M. (1998b): High levels of RAPD diversity in the moss Bryum argenteum in Australia, New Zealand and Antarctica. The Bryologist 101(3): 412-421.
- Stonehouse, B. (1966): Emperor penguin colony at Beaufort Island, Ross Sea, Antarctica. Nature 210: 925-926.
- Warren, G. (1969): Geology of the Terra Nova-McMurdo Sound area, Victoria land. – In: V.C. BUSHNELL, & C. CRADDOCK (eds.), Geologic maps of Antarctica, Amer. Geogr. Soc., Antarctic Map Folio Series, Folio 12, Plate XIII.
- Woehler, E.J. (1993): The distribution and abundance of antarctic and subantarctic penguins. SCAR, Cambridge, England. pp. iv + 76.
- Woehler, E.J. & Croxall, J.P. (1996): The status and trends of Antarctic and Subantarctic seabirds. SC-CAMLR-XV/BG/29, p. 46.