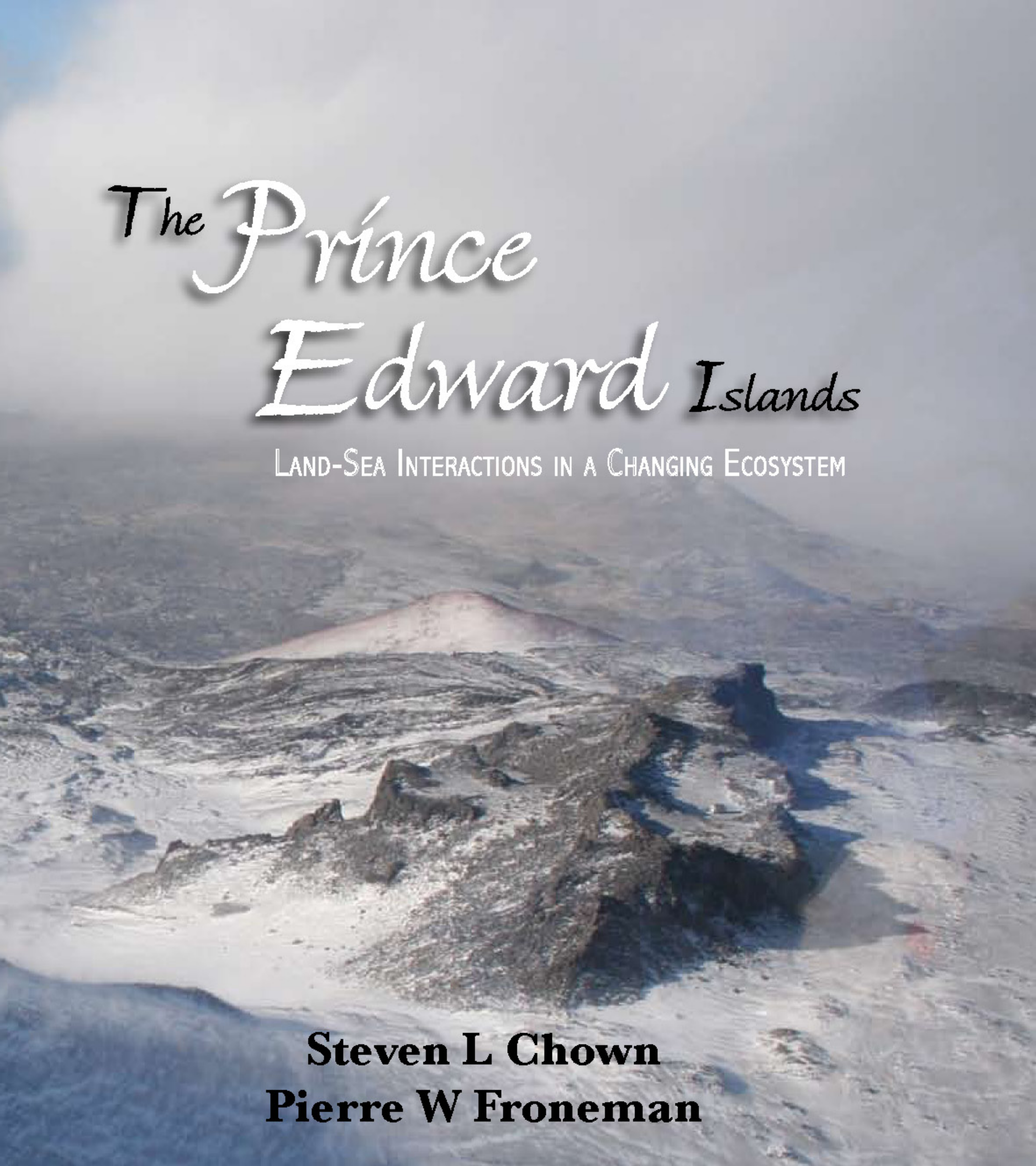
The Prince Edward Islands

LAND-SEA INTERACTIONS IN A CHANGING ECOSYSTEM



Steven L Chown
Pierre W Froneman

THE PRINCE EDWARD ISLANDS

LAND-SEA INTERACTIONS IN A CHANGING ECOSYSTEM

EDITED BY

STEVEN L CHOWN
STELLENBOSCH UNIVERSITY

PIERRE WILLIAM FRONEMAN
RHODES UNIVERSITY

SUN PRESS

The Prince Edward Islands
Land-Sea Interactions in a Changing Ecosystem

Published by SUN PReSS, an imprint of AFRICAN SUN MeDIA (Pty) Ltd.,
Stellenbosch 7600

www.africansunmedia.co.za

www.sun-e-shop.co.za

First edition 2008

ISBN 978-1-920109-85-1
ISBN 978-1-928357-06-3 (e-book)

Set in 11 Baskerville

Cover design and typographic setting by Liezel Meintjes

SUN PReSS is an imprint of AFRICAN SUN MeDIA (Pty) Ltd. Academic, professional and reference works are published under this imprint in print and electronic format. This publication may be ordered directly from www.sun-e-shop.co.za

CONTENTS

Appendices

FOREWORD

> *In conclusion, it appears to me that nothing can be more improving to a young naturalist than a journey in distant countries ... the effect ought to be to teach him good-humoured patience, freedom from selfishness, the habit of acting for himself, and of making the best of every occurrence.* Charles Darwin, The Voyage of the Beagle.[1]

Darwin was a 22 year old Cambridge graduate when he left England on 27th December 1831 to spend the next five years circumnavigating the globe and describing its geology, biology and history as no other scientist had done before or since. His exhortation to young scientists to leave the comforts of their home countries to discover the wonders of nature in distant lands has been followed to this day, exemplified by the continuing stream of young South Africans heading south to the Prince Edward Islands to work in this naturalist's paradise as they learn the method and excitement of field research.

It was my good fortune, in late December 1964, to sail from Cape Town aboard the MV *RSA*, South Africa's first ice-strengthened research vessel, as the youngest member of the Biological-Geological Expedition to Marion and Prince Edward Islands. Arriving at Transvaal Cove on the morning of 4th January 1965, we awakened to the sight of Marion Island, described somewhat romantically, but accurately, by Marsh[2] –

> *She rose, a jade jewel, out of the sea. Her lush green coat was fringed with the black lace of the cliffs and her heights draped in scintillating snow.*

The atmosphere was more palpable than the view. As we stumbled ashore off an inflatable raft, we were greeted by a cacophony of Rockhopper and Gentoo penguins, the sharp, breath-catching pall of ammonia rising from their rookery, and the icy bite of wind and spray off the surf. *Poa cookii* tussocks, *Cotula plumosa* swards and a scattering of the small succulents, *Crassula moschata* and *Montia fontana* on rough black basalts, introduced the strange and intriguing ecosystems that awaited us.

The expedition was the brain-child of Professor E.M. van Zinderen Bakker, pioneer of palynology and palaeoecology in South Africa. The prevailing understanding of Africa's Pleistocene climates was based almost completely on northern hemisphere models, and van Zinderen Bakker had been building up evidence from across Africa to test existing hypotheses, particularly in relation to past climate and vegetation patterns. Marion Island, with the deep peats of its lowlands, offered an ideal opportunity to collect cores for palynological analysis.

The expedition, fitted out and funded by CSIR on a total grant of R30 000 over two years, was perceived to be a once-off opportunity for scientists to visit and describe the geology, biology and history of these remote sub-Antarctic islands. The small team thus tackled their tasks with energy and excitement, covering as wide a diversity of features and collecting or describing every taxon, rock type and landform in all possible detail, in the belief that no further scientific visit would be financed for many years. Records of altitudinal zonation of plants, the distribution and abundance of invasive species, the size and structure of bird and seal populations, photographs of the ice plateau and the routine weather recordings at the Meteorological station were collected for descriptive rather than monitoring purposes. Little

---

[1] Selsam, M.E. Ed. 1959. *The Voyage of the Beagle*. The World's Work, Surrey, U.K.

[2] Marsh, J.H. 1948. *No Pathway Here*. Howard Timmins, Cape Town.

did we realize at the time that these observations would, four decades later, provide some of the most important evidence on global change processes in the southern hemisphere.

Contrary to our limited expectations of future funding for research on the islands, the 1965/66 expedition was followed by an ever increasing diversity and richness of scientific endeavour. In the four decades since those modest, early beginnings, South African scientists, with a significant contribution from colleagues around the globe, have developed a body of knowledge on the Prince Edward Islands and their oceanic environments that is unequalled elsewhere in the sub-Antarctic.

The scientific results synthesized in this volume, in their depth and breadth, and in the multiple scales in space and time integrated across terrestrial and oceanic systems, present a unique contribution to the understanding of earth/ocean/atmosphere systems. This volume joins a recent and growing tradition of syntheses on South African ecosystems – on fynbos,[3] on savanna,[4] on karoo,[5] and on the dynamics of large mammal populations in the extensive Kruger National Park.[6]

This volume illustrates so well the application of the scientific method – of developing hypotheses, building evidence for and against these, challenging, testing and perhaps rejecting current thinking, and providing convincing alternative explanations to what might have been the accepted understanding. The diversity of research, from the composition and eco-physiology of invertebrate populations in a single *Azorella* cushion, to the dynamics of southern ocean systems and their marine/terrestrial interactions, demonstrates how far the research programme has advanced since the descriptive accounts of the 1965/66 expedition.

What is not immediately evident from a reading of this volume is the impact that the islands' research programme has had on South African science – not only through its published papers, but through the young people who spent their formative years on the islands. The Prince Edward Islands' legacy is carried by the many dozens of professionals that experienced the exhilarating challenges, both physical and intellectual, and discovered the islands and themselves on these remote, windswept and unforgiving specks of land in the endless oceans of the southern hemisphere.

The South African government's commitment of very substantial funds for the establishment of a new, state-of- the-art research facility on Marion Island, and to the declaration of an extensive Marine Protected Area surrounding the islands, and the provision of a comprehensive conservation management regime for the biota and ecosystems on the islands, provides considerable optimism for the future of these unusually special islands and their oceanic surrounds. As the world enters an uncertain future of global change at multiple scales, this volume provides a unique benchmark against which to monitor and guide adaptation to the greatest challenge humanity has ever faced.

Brian J Huntley
Plant Ecologist, Marion Island Expedition, 1965/66
Chief Executive, South African National Biodiversity Institute, 1990/2006

---

[3] Cowling, R.M. Ed. 1992. *The Ecology of Fynbos: Nutrients, Fire and Diversity*. Oxford University Press, Cape Town.

[4] Scholes, R.J. & Walker, B.H. 1993. *An African Savanna: Synthesis of the Nylsvley Study*. Cambridge University Press, Cambridge.

[5] Dean, W.R. & Milton, S.J. Eds. 1999. *The Karoo: Ecological Patterns and Processes*. Cambridge University Press, Cambridge.

[6] Du Toit, J.T., Rogers, K.H. & Biggs, H.C. Eds. 2003. *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Island Press, Washington D.C.

PREFACE

In 1978, South Africa's new research and supply vessel, the *SA Agulhas*, set out on her maiden voyage, to Marion Island. For the past 28 years the '*Agulhas*' has plied the Southern Ocean, and for what often feels like substantial parts of that time we have been among the ship's researchers. As many of the *Agulhas*' passengers will appreciate, our blessings on the vessel have been mixed. We have seen the ship operating in poor and excellent conditions, both at sea and administratively. And we have entrusted our lives and the fates of our research programmes to her officers and crew, and to those managing her activities through the South African National Antarctic Programme, respectively. Notwithstanding our occasional doubts about the seaworthiness of both, that trust has been rewarded.

The South African National Antarctic Programme has produced a substantial and profound body of work on the marine and terrestrial systems of the Prince Edward Islands as part of a well-supported programme of science throughout the broader Antarctic and Southern Ocean region. For the past 20 years we have had the good fortune to be part of that work and to interact with many of the researchers whom have produced it. Although some of that interaction has taken place in university halls, conference venues and government offices, the most memorable parts of it have taken place on the *Agulhas*. These interactions have varied from formal 'ship workshops', through data discussions in the library, arguments over innumerable cups of tea, idle conversations during bird and whale watching on deck, barely remembered, though innovative solutions to all Southern Ocean science problems, developed well past midnight in the ship's bar, to productive 'end-of-cruise' discussions. Participants have come and gone from the conversations with an informality and a generosity that remains a perpetual surprise and delight: probably one of the primary reasons the Antarctic programme continues to attract some of the best of our students.

It would be unwise for us to disclose during which of our ship-based activities we decided to undertake the task of bringing together the authors of this book. Nonetheless, as that particular voyage wore on, our regular conversations, and discussions with fellow passengers made it clear that this idea was not one to be consigned to the resting place of previous innovative solutions. The book, edited by E.M. Van Zinderen Bakker Sr., J.M. Winterbottom and R.A. Dyer and produced on the basis of the research undertaken during the first scientific expedition in 1965-1966, was certainly still the Prince Edward Islands book 'to have', but much had happened since its publication in 1971. By the return to Cape Town our minds were made up: a book summarizing what is known about the marine and terrestrial systems of the Prince Edward Islands and interactions between them would fill a substantial need. Few island systems have been so well researched, and fewer still in the Antarctic region.

Fortunately, our enthusiasm was highly contagious, and we had no trouble signing up as authors many of the researchers that have made and continue to make substantial contributions to knowledge of the islands and their surrounding waters. In 2004 we held a small workshop in Stellenbosch to determine what form the book might take and what knowledge was available. When that meeting was effectively 'gate-crashed' by a team responsible for developing the Marine Protected Area (MPA) for the Prince Edward Islands, following the Minister of Environmental Affairs and Tourism's statement that a large MPA would be established in the area, we knew that our decision to produce a book about land-sea interactions at the Prince Edward Islands was timely and would be welcomed by a larger community than we had anticipated.

Perhaps reflecting its birth on the *Agulhas*, this project has encountered its fair share of rough weather. Nonetheless, it has given us great pleasure, and, judging by the comments of authors and referees alike, has given others satisfaction too. Much of our enjoyment has come from working with enthusiastic authors and reviewers, and a helpful publisher. In consequence, we would like to thank the authors for attempting valiantly to stick to our deadlines, for cursing only a little when we altered the scope of their involvement, and for agreeing to contribute in the first place. We would also like to thank the reviewers: Igor Belkin, Jim Bockheim, Jaco Boshoff, Peter Convey, Sarah Davies, Mark Gibbons, Sebastien Jacquemet, Ron Lewis Smith, Jeronimo Lopez, Melodie McGeoch, Norm McKenzie, Ian Meiklejohn, Christopher McQuaid, Evgeny Pakhomov, Renzo Perissinotto, Stefanie Plon, Antonio Quesada, John Turner, Philippe Vernon and David Walton provided comments on one or more of the chapters. Josephine de Mink and Anel Garthwaite looked after copy editing and organizational matters in their usual indefatigable ways. Justa Niemand, Liezel Meintjes and the publishing staff at Sun Media were uniformly helpful and patient with our repeated queries. The project was supported by the United States Agency for International Development/Department of Environmental Affairs and Tourism/ Stellenbosch University Capacity Building Programme for Climate Change Research, the National Research Foundation, the DST-NRF Centre of Excellence for Invasion Biology, and by Stellenbosch and Rhodes Universities.

Much of the research in the region has been done in collaboration with students. We are grateful to them for their humour, ideals, patience, hard work, and inspiration. Work at the islands has been supported for many years by the Department of Environmental Affairs and Tourism, by the Master, Officers and Crew of the *SA Agulhas* (latterly through Smit Marine), by the National Department of Public Works, and by the South African National Defence Force and latterly the Canadian Helicopter Corporation. Research is now supported through direct grants by the National Department of Science and Technology, via the National Research Foundation. Candice Levieux is the unsung hero in this new funding regime.

Research in the Antarctic and Southern Ocean regions necessarily means prolonged absences from home. We are grateful to our families for bravely waving us goodbye and, remarkably, for accepting us so happily on our return, knowing that in often less than a few months brave faces would be needed again.

This book is dedicated to the scientists who have preceded and inspired us, and to the memories of Joseph Daniels, J.G. Bold, and an unknown crew member of the *R.S. Africana II*, all of whom lost their lives in support of the South African scientific presence at the Prince Edward Islands.

Grahamstown
September 2006

CONTRIBUTOR AFFILIATIONS

Isabelle J. Ansorge
Department of Oceanography,
University of Cape Town,
South Africa

Marthán N. Bester
Department of Zoology and Entomology,
University of Pretoria, South Africa

Jan C. Boelhouwers
Department of Earth Sciences,
Uppsala University, Sweden

Steven L. Chown
Centre for Invasion Biology,
Stellenbosch University,
South Africa

John Cooper
Avian Demography Unit,
University of Cape Town,
South Africa

Marienne S. de Villiers
Avian Demography Unit,
University of Cape Town,
South Africa

P. William Froneman
Department of Zoology and Entomology,
Rhodes University,
South Africa

Niek J. M. Gremmen
Data Analyse Ekologie,
The Netherlands

David W. Hedding
Department of Geography,
Geoinformatics and Meteorology,
University of Pretoria, South Africa

Stephen D. Holness
Department of Geography,
Geoinformatics and Meteorology,
University of Pretoria, South Africa

Elizabeth A. Hugo
Department of Conservation Ecology
and Entomology, Stellenbosch University,
South Africa

Johann R. E. Lutjeharms
Department of Oceanography,
University of Cape Town,
South Africa

DAVID J. MARSHALL
Department of Biology,
Universiti Brunei Darussalam,
Brunei

MELODIE A. MCGEOCH
Department of Conservation Ecology
and Entomology, Centre for Invasion
Biology, Stellenbosch University,
South Africa

CHRISTOPHER D. MCQUAID
Department of Zoology and Entomology,
Rhodes University,
South Africa

K. IAN MEIKLEJOHN
Department of Geography,
Geoinformatics and Meteorology,
University of Pretoria, South Africa

MAWETHU J. NYAKATYA
Department of Conservation Ecology
and Entomology, Stellenbosch University,
South Africa

RYSZARD OCHYRA
Wladyslaw Szafer Institute of Botany,
Polish Academy of Sciences

DAG O. ØVSTEDAL
Botanical Institute,
Norway

PETER C. LE ROUX
Department of Conservation Ecology
and Entomology, Stellenbosch University,
South Africa

EVGENY A. PAKHOMOV
Department of Earth and Ocean Sciences,
University of British Columbia,
Canada and University of Forth Hare,
South Africa

PETER G. RYAN
Percy Fitzpatrick Institute for African
Ornithology, University of Cape Town,
South Africa

VALDON R. SMITH
Department of Botany and Zoology,
Stellenbosch University,
South Africa

BART VAN DE VIJVER
National Botanical Garden of Belgium,
Belgium

CHAPTER 1

THE PRINCE EDWARD ISLANDS IN A GLOBAL CONTEXT

STEVEN L. CHOWN AND P. WILLIAM FRONEMAN

The history of the planet is one of change. Continental positions have moved, sea-levels have advanced and retreated, mountains have been formed and eroded, climates have varied from warm to cool and back again, and life has responded to and sometimes driven these processes, with species and higher taxa waxing and waning for the last several billion years (Stanley 1989; Behrensmeyer *et al.* 1992). More recently, humans have come to influence these changes. Our recent history has been one of significant effects on the abiotic environment, including elevation of atmospheric greenhouse gas concentrations, depletion of stratospheric ozone, and alterations to the global climate (Watson 2002; Domack *et al.* 2005). In turn, changing climates have had and continue to have profound effects on biodiversity, ranging from population and species loss (Pounds *et al.* 2006) to alterations in species distributions, changes in phenology, and shifts in ecological regimes (Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003).

Humans have also had profound direct effects on landscapes, populations and species. Habitat destruction and transformation have been responsible for considerable biodiversity loss, with co-extinctions exacerbating the scale of the problem (e.g. Beier *et al.* 2002; Brooks *et al.* 2002; Koh *et al.* 2004; Dunn 2005; Millennium Ecosystem Assessment 2005). Likewise, direct and indirect

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 1-16

utilization has meant that many species are critically endangered (Baum *et al.* 2003; Brashares *et al.* 2004; Pauly *et al.* 2005). As a consequence of human activities such as trade and shipping, the movement of species from their indigenous ranges to areas where they have previously not occurred, is also having significant effects on global biodiversity (Mack *et al.* 2000; Bax *et al.* 2001; Grosholz 2002; Blackburn *et al.* 2004; Drake & Lodge 2004; Richardson & Van Wilgen 2004; Cassey *et al.* 2005). The interactive effects of invaders can lead to wholesale ecosystems changes, termed invasional meltdown (O'Dowd *et al.* 2003; Sanders *et al.* 2003; Grosholz 2005), and the extent and pace of invasion globally (e.g. Gaston *et al.* 2003) has led many to suggest that the next period in the earth's history might be one of substantial biotic homogenization (McKinney & Lockwood 1999; Olden *et al.* 2004).

In many instances, the effects of habitat destruction and alteration, climate change, and biological invasions are likely to be interactive. For example, nutrient loading and disturbance often promote biological invasions, increasing the chances for the progress of non-indigenous species from establishment to full invasion (e.g. Dukes & Mooney 1999; Huston 2004). Habitat availability and fragmentation also substantially alter the extent and nature of the response of species to changing climates (Hill *et al.* 1999, 2006). At least in some instances, changing climates might favour introduced over indigenous species as a consequence of substantial differences in the life history and physiological traits of the two sets of organisms (Stachowicz *et al.* 2002; Walther *et al.* 2002; Daehler 2003; Chown *et al.* 2007). In consequence, an understanding of human impacts on the environment must not only involve investigations of direct effects of major processes, such as climate change and habitat transformation, but also their interactive effects (Dukes & Mooney 1999). Indeed, in describing the effects of interactions between global change (of all kinds) and biological invasions, Mooney and Hobbs (2000) have noted that such interactions are becoming an ever more important feature of the world, substantially affecting our capacity to retain biodiversity and the services we derive from it.

1.1 Environmental change in the Antarctic region

Antarctica, its surrounding islands, and the Southern Ocean have changed in concert with global changes, and geological and oceanographic evolution in the region has precipitated large-scale alterations of the global climate (see summaries in Crame 1997; Clarke 2003; Peck *et al.* 2006; Chown & Convey 2007). However, in many ways the region has long been considered comparatively isolated from the rest of the planet. The Southern Ocean is recognized as a particularly well-defined marine ecosystem, especially given that the Antarctic Circumpolar Current has been in evidence for c. 25 million years, endemism of many marine groups is substantial (Longhurst 1998; Clarke & Johnston 2003; Clarke *et al.* 2005), and in several terrestrial taxa endemism is significant too (Chown & Convey 2007). Likewise, and despite their varied histories (LeMasurier & Thompson 1990; Hall 2002), many of the Southern

Ocean islands are well removed from major landmasses, and show substantial endemism in a range of groups (Gressitt 1970; Chown *et al.* 1998; Greve *et al.* 2005). In terms of direct human influence, the first landing on Antarctica took place only in 1821. Many of the Southern Ocean islands have had similarly short human histories (Headland 1989; Chown *et al.* 2005), and permanent human settlements in the region have remained rare.

This perception of isolation is nonetheless deceptive. Climatic teleconnections between the Antarctic and elsewhere are well-established (Bender *et al.* 1994; Carleton 2003), and many regions, such as the Antarctic Peninsula and several sub-Antarctic islands, are showing evidence of pronounced climate change in step with global events. For example, temperatures have increased by several degrees over the past half century at some sites along the Antarctic Peninsula (King & Harangozo 1998), and rain is falling there for the first time in recorded history. In the sub-Antarctic, temperature increases over similar periods have been lower, but still substantial, whilst precipitation has declined by as much as 600 mm per annum (Bergstrom & Chown 1999). Likewise, despite the late arrival of humans in the region, their impacts on vertebrate populations escalated rapidly, leading to widespread declines in several species (many of which have now recovered) and likely irreversible regime shifts (Laws 1984; Weimerskirch *et al.* 2003). Whilst resource depletion has shifted away from seals, whales and seabirds, fish continue to bear the brunt of exploitation (Brandão *et al.* 2002). More recently, scientific research and its logistic support in the Antarctic, and tourism to a more limited number of sites have increased dramatically (Naveen *et al.* 2001; Frenot *et al.* 2005). In consequence, a wide range of species has been introduced from elsewhere, often having significant impacts on local populations and ecosystem functioning (Frenot *et al.* 2005). Moreover, interactions between climate change and alien species are expected to exacerbate the impacts of these species, and to facilitate additional human-mediated colonization events and invasions (Kennedy 1995; Bergstrom & Chown 1999; Chown & Convey 2007).

Therefore, the Antarctic and Southern Ocean regions are in many ways a microcosm of the situation found elsewhere on the planet. Significant changes in many systems have taken place rapidly (Bergstrom & Chown 1999; Weimerskirch *et al.* 2003; Barnes *et al.* 2006), and major concerns about the conservation of the region and its biodiversity have been raised (e.g. Dingwall 1987, 1995). Nonetheless, the region also differs from others in ways that offer advantages for understanding interactive effects of major environmental changes, their conservation implications, and the ways in which they might be addressed. For example, in terrestrial systems the direct impacts of humans (e.g. habitat destruction as a consequence of agriculture) are less pronounced in the Antarctic than elsewhere, and, because the region is more isolated than many others, immigration can be reasonably well documented and the source of propagules identified (e.g. Crafford & Chown 1987; Marshall & Chalmers 1997; Greenslade *et al.* 1999; Muñoz *et al.* 2004). Thus, the effects on biodiversity of rapidly changing climates and biological invasions can be readily comprehended because of the absence of many factors that confound investigations elsewhere (Bergstrom & Chown 1999; Chown *et al.* 2005). Moreover, it has long been appreciated in the region that an understanding of the ecology of coastal, offshore and island ecosystems, and comprehension and prediction of the effects of environmental change on these systems, cannot be achieved without considering interactions between the marine and terrestrial environments (see Smith 1977; Smith & Steenkamp 1990; Pakhomov & Chown 2003). In consequence, research that has been done in the region not only provides a useful perspective on Antarctic biodiversity and ecosystem functioning (Knox 1994; Peck *et al.* 2006), but also provides broader insights into the patterns in and processes underlying biodiversity more generally, and how this diversity will respond to environmental change (Chown *et al.* 2000; Clarke 2003). In this regard, the Prince Edward Islands are a model system.

1.2 The Prince Edward Islands

Marion Island and Prince Edward Island form the Prince Edward Islands. Together with a small number of other islands and archipelagos, such as South Georgia, Bouvetøya, Crozet, Kerguelen, Heard, Auckland and Campbell, they represent the only land in the vast Southern Ocean, which occupies half of the area between 30° and 60° South (as opposed to the 7% of area that ocean occupies in the same northern latitudes) (Chown *et al.* 2004). The nearest landfall to both of the islands is Île aux Cochons of the French Crozet Island Group, which lies 950 km to the east. The two islands lie close to each other, with the more southerly and larger island, Marion (46° 54´S, 37° 45´E), separated from the smaller Prince Edward Island (46° 38´S, 37° 57´E) by 19 km.

The islands are young in geological terms. The oldest recorded date for lavas on Marion Island is 450 000 years, and it seems likely that the islands are less than one million years old (McDougall *et al.* 2001). Local climates and the extent of glaciation have varied substantially since the islands became sub aerial (McDougall *et al.* 2001; Hall 2002), in keeping with global climatic fluctuations (Augustin *et al.* 2004). It seems likely that Marion Island was subjected to at least five, though possibly more, glaciations during the Quaternary, whereas there is no evidence for glaciation on Prince Edward Island. The glacial cycles on Marion Island had a major effect on the vegetation. Glacial maxima generally caused the local extirpation of vascular plants, with the possible exception of species such as the cushion-forming *Azorella selago* (Scott 1985). During the more recent interglacials the vegetation resembled that currently found on the island, although in some cases it included species, such as the brassica *Cardamine*, that are not present in the modern flora (Scott & Hall 1983). The glacial cycles are also thought to have had a substantial influence on the invertebrate fauna, reflected in low habitat specificity and species richness in the vegetated biotope, but much higher richness and greater habitat specificity in the epilithic biotope (rock faces, fellfield, polar desert) (Chown 1989, 1990; Barendse *et al.* 2002). This pattern seems to be repeated across most of the sub-Antarctic islands and in Antarctica (Chown 1994; Chown & Klok 2001; Marshall & Convey 2004).

More recent changes have included historical decimation of seal populations (Cooper & Headland 1991) and modern over-exploitation of marine resources (specifically the Patagonian toothfish, *Dissostichus eleginoides*) (Brandão *et al.* 2002). The latter has had substantial indirect impacts on several seabird species as a consequence of long-line fishing-associated mortality (Nel & Nel 1999; Nel *et al.* 2000). Climates have also been changing rapidly at the islands. Sea surface temperatures and Stevenson Screen temperatures have increased by more than 1°C over the past 50 years, and on land mean annual precipitation has declined by ≈ 600 mm (Smith 2002; Mélice *et al.* 2003; le Roux & McGeoch 2007). These changes in climate have had or seem set to have major impacts on assemblage structure and ecosystem functioning in both marine and terrestrial environments (Smith & Steenkamp 1990; Chown & Smith 1993; Smith 2002; Pakhomov & Chown 2003).

Many of the impacts of climate change are being mediated through interactions between indigenous and invasive species (Chown & Smith 1993; Frenot *et al.* 2005). Since the discovery of the islands and their exploitation by sealers, but particularly since their annexation by South Africa in 1947 and the establishment of a scientific station, a steady stream of non-indigenous species has colonized the island (Watkins & Cooper 1986; Cooper & Condy 1988; Chown *et al.* 2002). Some of them have become highly invasive, and have caused local extinctions and/or major changes to the local ecosystem. Amongst the most damaging invaders have been feral cats (now extirpated) (Bester *et al.* 2002), house mice (Crafford 1990; Chown & Smith 1993), the grass *Agrostis stolonifera*, and the forb *Sagina procumbens* (Gremmen *et al.* 1998; Gremmen & Smith 1999). Some evidence now exists that house mice are starting to attack procellariiform chicks (including those of albatrosses), as is the case on Gough Island (Jones *et al.* 2003; Cuthbert & Hilton 2004). What the effects are of other alien species, such as aphids, mosses and isopods (Crafford *et al.* 1986; Slabber & Chown 2002) is not known, nor is the extent of marine invasions. Hull fouling is known to be a significant concern elsewhere in the region (Lewis *et al.* 2003, 2006), and recent studies have recorded both hull fouling and invasive alien species in the sea chests of the research and supply vessel, the *SA Agulhas* (Lee & Chown 2007).

Thus, just like other areas in the region, the Prince Edward Islands have been subject to considerable past geological and climatological variability, are experiencing rapid modern changes owing to climate change and biological invasions, and have been at the receiving end of historical resource exploitation and continue to experience it today. However, unlike many other areas, a considerable body of scientific research has been undertaken to understand these changes and how they have affected interactions between marine and terrestrial systems of the islands, and to determine and demonstrate, what lessons they hold for other areas of the planet.

1.3 Research at the Prince Edward Islands

1.3.1 Early terrestrial work

Although the Prince Edward Islands were probably discovered in the mid 1600s, it was not until the early 1800s that the first landing was effected. By the early 1900s most of the fur seals and elephant seals on the two islands had been exterminated (Cooper & Headland 1991). The early history of the islands was thus one of considerable exploitation, as was the case for most other Southern Ocean islands (Headland 1989; Downes 2002). Although a variety of scientific expeditions visited the Prince Edward Islands from the late 1800s onwards (Cooper & Headland 1991), it was only in 1965/66 that the first formal geological and biological research was conducted. This resulted in a substantial volume providing comprehensive baseline information on the climatology, geology, glacial and vegetation histories, and biodiversity of the islands (Van Zinderen Bakker *et al.* 1971). It also set the stage for a large and comprehensive terrestrial research programme.

In essence, the programme addressed four major sets of goals from the early 1970s through to the end of the century, and can therefore be divided into four phases, named by Smith (1991): the reconnaissance, whole island systems, national priorities, and climate change phases. The reconnaissance phase was just that, focussing largely, but not exclusively, on cataloguing the biota. In the next phase, the emphasis switched to understanding the whole island ecosystem, a goal that was influenced to a large degree by the contemporaneous International Biological Programme's Biome Project. This work also involved detailed investigations of nutrient inputs by vertebrates to the terrestrial environment, so forming the first investigations of land-sea interactions. The whole systems approach continued to dominate in the national priorities phase, but by then research also came to include a variety of topics that did not directly address the whole systems model, but were concerned with national significance or especially suited to the opportunities provided by the island system and its biota. Investigations of the impacts of alien species, especially feral cats and house mice had already been established as important avenues of conservation research (Bester & Skinner 1991; Smith 1991). The late 1980s and early 1990s saw a switch in emphasis to studies of the impacts of climate change on the islands. Shortly thereafter a change in administration of research of the islands led to a focus on conservation and monitoring issues identified by the Prince Edward Islands Management Plan (Anonymous 1996), precipitated largely by the declaration of the islands as Special Nature Reserves in 1995. Whilst some other work took place, the emphasis of terrestrial studies was largely on conservation-related science.

Much of this research was essentially land-based, even though large projects were concerned with marine vertebrate predators and their diets. What these predators were doing at sea was more poorly known, mostly as a consequence of an early, negligible oceanographic capacity, and a later oceanographic focus on other significant questions and regions of the Southern Ocean (Lutjeharms 1991). Although much work was done on the nearshore and intertidal zones (see de Villiers 1976; Beckley & Branch 1992), only a single programme (the Marion Offshore Ecosystem Study) focussed on deeper waters.

1.3.2 Marine investigations

The study of the marine environment in the vicinity of the Prince Edward Islands can be traced to the late nineteen century when the *HMS Challenger* briefly visited the islands in 1873. Nearly a hundred years later (1976), the first comprehensive investigation of the biology of the marine environment was undertaken when the *MS Marion Dufresne* visited the islands (Grindley & Lane 1979; Pakhomov & Froneman 1999a; McQuaid & Froneman 2004). This study provided the first scientific information on plankton community structure and distribution within the vicinity of the Prince Edward Islands (Grindley & Lane 1979).

The systematic study of the link between the marine and terrestrial environment only began in the late 1980s. The Marion Offshore Ecosystem Study (MOES) addressed the problem of how the Prince Edward Islands, located within the relatively unproductive Polar Frontal Zone waters (PFZ), could seasonally sustain enormous numbers of top predators including seals, penguins and flying seabirds. The initial target of investigation was the existence of an island mass effect at the archipelago, a phenomenon of greatly enhanced primary production in a low productivity part of the ocean, and how, or whether this production fed through to the top predators (Boden 1983; Allanson *et al.* 1985; Pakhomov & Froneman 1999a). The programme was unique in that it placed equal emphasis on the availability of food and the importance of its physical supply to consumers. By the end of the programme an understanding of trophic relationships between autochthonous or allochthonous food sources and the top predators was developed as what became known as the "life support system" of the islands (Pakhomov & Froneman 1999a; Pakhomov & Chown 2003; McQuaid & Froneman 2004).

The subsequent research programmes conducted in the 1990s and early 21st century, the Marion Islands Offshore Variability Study (MIOS), the Marion Offshore Variability Study (MOVES) and Dynamics of Eddies Impact on Marion's Ecosystem (DEIMEC), modified or refined the concept of the "life support system of the islands" (Pakhomov & Froneman 1999b; Pakhomov & Chown 2003; McQuaid & Froneman 2004). These investigations have focused on the upstream region (west) of the islands. The main finding thereof was that plankton distribution and species composition was closely linked to mesoscale variability in the oceanographic environment, including meanders in fronts that delimit the Polar Frontal Zone and the presence of both warm and cold core features. More significantly, these studies highlighted the importance of the interaction of the Antarctic Circumpolar Current (ACC) with prominent topographic features, and its effects on zooplankton community composition and the delivery of food to pelagic predators on the islands (Pakhomov & Froneman 1999a; Pakhomov & Chown 2003; McQuaid & Froneman 2004).

1.3.3 Recent developments

Over the last decade, research at the islands has focussed mostly on the terrestrial system, although considerable advances were made in understanding marine processes around the islands. Unfortunately, the marine research has been restricted to the autumn months, and investigations of seabirds and seals have been land-based, with limited work on at-sea distributions. Despite proposals for detailed work on understanding the marine system and the resource base it provides, especially during the months when the majority of seabirds and seals reproduce, such work was much delayed (Cooper & Ryan 2001), or scaled-down (Nel *et al.* 2001), and has only recently become the focus of attention. Therefore, whilst understanding of the terrestrial system and its inhabitants is becoming ever more sophisticated, insights into the surrounding marine systems and the ways in which they influence terrestrial processes has lagged behind. One of the major consequences of the limited marine work is that the development of a major Marine Protected Area for the islands has had to be based largely on surrogate environmental information, rather than spatially comprehensive biological data (Lombard *et al.* 2007).

In the mid 2000s, another administrative change saw the research component of the South African National Antarctic Programme transferred from the Department of Environmental Affairs and Tourism to the relatively new Department of Science and Technology, with management thereof being undertaken by the National Research Foundation. A new science policy for the region (the Antarctic Research Strategy for South Africa) was articulated, with major themes including, *inter alia*, climatic variability and the responses of biodiversity to earth system variability. Since then, research has largely been required to address these goals and those of various international polar programmes, such as the International Polar Year. At the Prince Edward Islands, several new projects have started to build on the past work, including joint marine and terrestrial work on seabirds and seals and their foraging areas, investigations of microbial diversity using molecular techniques, and studies of the interactions between biodiversity and geomorphological processes.

1.4 This book

The period from the mid 1960s to the present has been an exceptionally productive one scientifically (Hänel & Chown 1999). Substantial knowledge of the geology and biodiversity of the islands now exists, much is known about how the marine and terrestrial systems of the islands function, and comprehension of the nature of the interactions between the marine and terrestrial systems is well advanced. However, not since the landmark volume by Van Zinderen Bakker *et al.* (1971) has a review and synthesis of scientific knowledge of the islands and their biodiversity been presented. This book does just that in the context of the contribution this research has made to our understanding of environmental change in a system dominated by land-sea interactions.

1.5 References

Allanson, B.R., Boden, B.P., Paker, L. & Duncombe Rae, C. 1985. A contribution to the oceanology of the Prince Edward Islands. In: Siegfied, W.R., Condy, P.R. & Laws, R.M. (Eds.). *Antarctic Nutrient Cycles and Food Webs*. Springer, Berlin, pp 38-45.

Anonymous 1996. *Prince Edward Islands Management Plan*. Department of Environmental Affairs and Tourism, Pretoria.

Augustin, L., Barbante, C., Barnes, P.R.F., Barbola, J.M., Bigler, M., Castellano, E., *et al.* 2004. Eight glacial cycles from an Antarctic ice core. *Nature* **429**, 623-628.

Barendse, J., Mercer, R.D., Marshall, D.J. & Chown, S.L. 2002. Habitat specificity of mites on sub-Antarctic Marion Island. *Environmental Entomology* **31**, 612-625.

Barnes, D.K.A., Hodgson, D.A., Convey, P., Allen, C.S. & Clarke, A. 2006. Incursion and excursion of Antarctic biota: past, present and future. *Global Ecology and Biogeography* **15**, 121-142.

Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J. & Doherty, P.A. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. *Science* **299**, 389-392.

Bax, N., Carlton, J.T., Mathews-Amos, A., Haedrich, R.L., Howarth, F.G., Purcell, J.E., *et al.* 2001. The control of biological invasions in the world's oceans. *Conservation Biology* **15**, 1234-1246.

Beckley, L.E. & Branch, G.M. 1992. A quantitative scuba-diving survey of the sublittoral macrobenthos at subantarctic Marion Island. *Polar Biology* **11**, 553-563.

Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H.-D. & Wing, S.L. 1992. *Terrestrial Ecosystems Through Time. Evolutionary Paleoecology of Terrestrial Plants and Animals*. University of Chicago Press, Chicago.

Beier, P., Van Drielen, M. & Kankam, B.O. 2002. Avifaunal collapse in West African forest fragments. *Conservation Biology* **16**, 1097-1111.

Bender, M., Sowers, T., Dickson, M.-L., Orchardo, J., Grootes, P., Mayewski, P.A. *et al.* 1994. Climate correlations between Greenland and Antarctica during the past 100,000 years. *Nature* **372**, 663-666.

Bergstrom, D. & Chown, S.L. 1999. Life at the front: history, ecology and change on Southern Ocean islands. *Trends in Ecology and Evolution* **14**, 472-477.

Bester, M.N., Bloomer, J.P., Van Aarde, R.J., Erasmus, B.H., Van Rensburg, P.J.J., Skinner, J.D., *et al.* 2002. A review of the successful eradication of feral cats from sub-Antarctic Marion Island, Southern Indian Ocean. *South African Journal of Wildlife Research* **32**, 65-73.

Bester, M.N. & Skinner, J.D. 1991. South African research on Antarctic seals. *South African Journal of Antarctic Research* **21**, 165-166.

Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L. & Gaston, K.J. 2004. Avian extinction and mammalian introductions on oceanic islands. *Science* **305**, 1955-1958.

Boden, B.P. 1983. Observations of the island mass effect in the Prince Edward archipelago. *Polar Biology* **5**, 81-93.

Brandão, A., Watkins, B.P., Butterworth, D.S. & Miller, D.G.M. 2002. A first attempt at an assessment of the Patagonian Toothfish (*Dissostichus eleginoides*) resource in the Prince Edward Islands EEZ. *CCAMLR Science* **9**, 11-32.

Brashares, J.S., Arcese, P., Sam, M.K., Coppolillo, P.B., Sinclair, A.R.E. & Balmford, A. 2004. Bushmeat hunting, wildlife declines, and fish supply in West Africa. *Science* **306**, 1180-1183.

Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Rylands, A.B., Konstant, W.R., *et al.* 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* **16**, 909-923.

Carleton, A.M. 2003. Atmospheric teleconnections involving the Southern Ocean. *Journal of Geophysical Research Oceans* **108**, Art. No. 8080.

Cassey, P., Blackburn, T.M., Duncan, R.P. & Chown, S.L. 2005. Concerning invasive species: Reply to Brown and Sax. *Austral Ecology* **30**, 475-480.

Chown, S.L. 1989. Habitat use and diet as biogeographic indicators for subantarctic Ectemnorhinini (Coleoptera: Curculionidae). *Antarctic Science* **1**, 23-30.

Chown, S.L. 1990. Possible effects of Quaternary climatic change on the composition of insect communities of the South Indian Ocean Province Islands. *South African Journal of Science* **86**, 386-391.

Chown, S.L. 1994. Historical ecology of sub-Antarctic weevils (Coleoptera: Curculionidae): patterns and processes on isolated islands. *Journal of Natural History* **28**, 411-433.

Chown, S.L. & Convey, P. 2007. Spatial and temporal variability across life's hierarchies in the terrestrial Antarctic. *Philosophical Transactions of the Royal Society of London B* **362**, 2307-2331.

Chown, S.L., Gaston, K.J. & Gremmen, N.J.M. 2000. Including the Antarctic: Insights for ecologists everywhere. In: Davison, W., Howard-Williams, C. & Broady, P.A. (Eds.). *Antarctic Ecosystems: Models for Wider Ecological Understanding*. New Zealand Natural Sciences, Christchurch, pp. 1-15.

Chown, S.L., Gremmen, N.J.M. & Gaston, K.J. 1998. Ecological biogeography of southern ocean islands: Species-area relationships, human impacts, and conservation. *American Naturalist* **152**, 562-575.

Chown, S.L., Hull, B. & Gaston, K.J. 2005. Human impacts, energy availability, and invasion across Southern Ocean Islands. *Global Ecology and Biogeography* **14**, 521-528.

Chown, S.L. & Klok, C.J. 2001. Habitat use, diet and body size of Heard Island weevils. *Polar Biology* **24**, 706-712.

Chown, S.L., McGeoch, M.A. & Marshall, D.J. 2002. Diversity and conservation of invertebrates on the sub-Antarctic Prince Edward Islands. *African Entomology* **10**, 67-82.

Chown, S.L., Sinclair, B.J., Leinaas, H.P. & Gaston, K.J. 2004. Hemispheric asymmetries in biodiversity – a serious matter for ecology. *PLoS Biology* **2**, e406, 1701-1707.

Chown, S.L., Slabber, S., McGeoch, M.A., Janion, C. & Leinaas, H.P. 2007. Phenotypic plasticity mediates climate change responses among invasive and indigenous arthropods. *Proceedings of the Royal Society of London B* **274**, 2531-2537.

Chown, S.L. & Smith, V.R. 1993. Climate change and the short-term impact of feral house mice at the sub-Antarctic Prince Edward Islands. *Oecologia* **96**, 508-516.

Clarke, A. 2003. Evolution, adaptation and diversity: global ecology in an Antarctic context. In: Huiskes, A.H.L., Gieskes, W.W.C., Rozema, J., Schorno, R.M.L., Van der Vies, S.S. & Wolff, W.J. (Ed.). *Antarctic Biology in a Global Context*. Backhuys Publishers, Leiden, pp.3-17.

Clarke, A., Barnes, D.K.A. & Hodgson, D.A. 2005. How isolated is Antarctica? *Trends in Ecology and Evolution* **20**, 1-3.

Clarke, A. & Johnston, N.M. 2003. Antarctic marine benthic diversity. *Oceanography and Marine Biology Annual Review* **41**, 47-114.

Cooper, J. & Condy, P.R. 1988. Environmental conservation at the sub-Antarctic Prince Edward Islands: a review and recommendations. *Environmental Conservation* **15**, 317-326.

Cooper, J. & Headland, R.K. 1991. A history of South African involvement in Antarctica and at the Prince Edward Islands. *South African Journal of Antarctic Research* **21**, 77-91.

Cooper, J. & Ryan, P.G. 2001. The agreement on the conservation of albatrosses and petrels: implications for research and monitoring at the Prince Edward Islands. *South African Journal of Science* **97**, 78-79.

Crafford, J.E. 1990. The role of feral house mice in ecosystem functioning on Marion Island. In: Kerry, K.R. & Hempel, G. (Eds.). *Antarctic Ecosystems. Ecological Change and Conservation*. Springer, Berlin, pp. 359-364.

Crafford, J.E. & Chown, S.L. 1987. *Plutella xylostella* on Marion Island. *Journal of the Entomological Society of Southern Africa* **50**, 257-260.

Crafford, J.E., Scholtz, C.H. & Chown, S.L. 1986. The insects of sub-Antarctic Marion and Prince Edward Islands; with a bibliography of entomology of the Kerguelen Biogeographical Province. *South African Journal of Antarctic Research* **16**, 42-84.

Crame, J.A. 1997. An evolutionary framework for the polar regions. *Journal of Biogeography* **24**, 1-9.

Cuthbert, R. & Hilton, G. 2004. Introduced house mice *Mus musculus*: a significant predator of threatened and endemic birds on Gough Island, South Atlantic Ocean? *Biological Conservation* **117**, 483-489.

Daehler, C.C. 2003. Performance comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. *Annual Review of Ecology, Evolution and Systematics* **34**, 183-211.

de Villiers, A.F. 1976. Littoral ecology of Marion and Prince Edward Islands (Southern Ocean). *South African Journal of Antarctic Research* **suppl. 1**, 1-40.

Dingwall, P.R. 1987. *Conserving the Natural Heritage of the Antarctic Realm*. IUCN, Gland.

Dingwall, P.R. 1995. *Progress in Conservation of the Subantarctic Islands.* IUCN, Gland.

Domack, E., Duran, D., Leventer, A., Ishman, S., Doane, S., McCallum, S., *et al.* 2005. Stability of the Larsen B ice shelf on the Antarctic Peninsula during the Holocene epoch. *Nature* **436**, 681-685.

Downes, M. 2002. First visitors to Heard Island. *Anare Research Notes* **104**, 1-70.

Drake, J.M. & Lodge, D.M. 2004. Global hot spots of biological invasions: evaluating options for ballast-water management. *Proceedings of the Royal Society of London B* **271**, 575-580.

Dukes, J.S. & Mooney, H.A. 1999. Does global change increase the success of biological invaders? *Trends in Ecology and Evolution* **14**, 135-139.

Dunn, R.R. 2005. Modern insect extinctions, the neglected majority. *Conservation Biology* **19**, 1030-1036.

Frenot, Y., Chown, S.L., Whinam, J., Selkirk, P.M., Convey, P., Skotnici, M., *et al.* 2005. Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews* **80**, 45-72.

Gaston, K.J., Jones, A.G., Hänel, C. & Chown, S.L. 2003. Rates of species introduction to a remote oceanic island. *Proceedings of the Royal Society of London B* **270**, 1091-1098.

Greenslade, P., Farrow, R.A. & Smith, J.M.B. 1999. Long distance migration of insects to a subantarctic island. *Journal of Biogeography* **26**, 1161-1167.

Gremmen, N.J.M., Chown, S.L. & Marshall, D.J. 1998. Impact of the introduced grass *Agrostis stolonifera* on vegetation and soil fauna communities at Marion Island, sub-Antarctic. *Biological Conservation* **85**, 223-231.

Gremmen, N.J.M. & Smith, V.R. 1999. New records of alien vascular plants from Marion and Prince Edward Islands, sub-Antarctic. *Polar Biology* **21**, 401-409.

Gressitt, J.L. 1970. Subantarctic Entomology and Biogeography. *Pacific Insects Monograph* **23**, 295-374.

Greve, M., Gremmen, N.J.M., Gaston, K.J. & Chown, S.L. 2005. Nestedness of South Ocean island biotas: ecological perspectives on a biogeographical conundrum. *Journal of Biogeography* **32**, 155-168.

Grindley, J.R. & Lane, S.B. 1979. Zooplankton around Marion and the Prince Edward Islands. *Comité National Française des Recherches Antarctiques* **44**, 111-125.

Grosholz, E. 2002. Ecological and evolutionary consequences of coastal invasions. *Trends in Ecology and Evolution* **17**, 22-27.

Grosholz, E.D. 2005. Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. *Proceedings of the National Academy of Sciences of the USA* **102**, 1088-1091.

Hall, K. 2002. Review of Present and Quaternary periglacial processes and landforms of the maritime and sub-Antarctic region. *South African Journal of Science* **98**, 71-81.

Hänel, C. & Chown, S.L. 1999. Fifty years at Marion and Prince Edward Islands: A bibliography of scientific and popular literature. *South African Journal of Science* **95**, 87-112.

Headland, R.K. 1989. *Chronological List of Antarctic Expeditions and Related Historical Events*. Cambridge University Press, Cambridge.

Hill, J.K., Hughes, C.L., Dytham, C. & Searle, J.B. 2006. Genetic diversity in butterflies: interactive effects of habitat fragmentation and climate-driven range expansion. *Biology Letters* **2**, 152-154.

Hill, J.K., Thomas, C.D. & Huntley, B. 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proceedings of the Royal Society of London B* **266**, 1197-1206.

Huston, M.A. 2004. Management strategies for plant invasions: manipulating productivity, disturbance, and competition. *Diversity and Distributions* **10**, 167-178.

Jones, A.G., Chown, S.L., Ryan, P.G., Gremmen, N.J.M. & Gaston, K.J. 2003. A review of conservation threats on Gough Island: a case study for terrestrial conservation in the Southern Oceans. *Biological Conservation* **113**, 75-87.

Kennedy, A.D. 1995. Antarctic terrestrial ecosystem response to global environmental change. *Annual Review of Ecology and Systematics* **26**, 683-704.

King, J.C. & Harangozo, S.A. 1998. Climate change in the western Antarctic Peninsula since 1945: observations and possible causes, *Annals of Glaciology* **27**, 571-575.

Knox, G.A. 1994. *The Biology of the Southern Ocean*. Cambridge University Press, Cambridge.

Koh, L.P., Dunn, R.R., Sodhi, N.S., Colwell, R.K., Proctor, H.C. & Smith, V.S. 2004. Species coextinctions and the biodiversity crisis. *Science* **305**, 1632-1634.

Laws, R.M. (Ed.). 1984. *Antarctic Ecology Volumes 1 and 2*. Academic Press, London.

Lee, J.E. & Chown, S.L. 2007. *Mytilus* on the move: transport of an invasive bivalve to the Antarctic. *Marine Ecology Progress Series* **339**, 307-310.

LeMasurier, W.E. & Thomson, J.W. 1990. *Volcanoes of the Antarctic Plate and Southern Oceans*. American Geophysical Union, Washington.

le Roux, P.C. & McGeoch, M.A. 2007. Changes in climatic extremes, variability and signatures on sub-Antarctic Marion Island. Climatic Change, in press. doi: 10.1007/s10584-007-9259-y

Lewis, P.N., Bergstrom, D.M. & Whinam, J. 2006. Barging in: a temperate marine community travels to the subantarctic. *Biological Invasions* **8**, 787-795.

Lewis, P.N., Hewitt, C.L., Riddle, M. & McMinn, A. 2003. Marine introductions in the Southern Ocean: an unrecognised hazard to biodiversity. *Marine Pollution Bulletin* **46**, 213-223.

Lombard, A.T., Reyers, B., Schonegevel, L.Y., Cooper, J., Smith-Adao, L.B., Nel, D.C. *et al.* 2007. Conserving pattern and process in the Southern Ocean: designing a marine protected area for the Prince Edward Islands. *Antarctic Science* **19**, 39-54.

Longhurst, A. 1998. *Ecological Geography of the Sea*. Academic Press, London.

Lutjeharms, J.R.E. 1991. A history of recent South African marine research in the Southern Ocean. *South African Journal of Antarctic Research* **21**, 159-164.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* **10**, 689-710.

Marshall, D.J. & Convey, P. 2004. Latitudinal variation in habitat specificity of ameronothroid mites (Oribatida). *Experimental and Applied Acarology* **34**, 21-35.

Marshall, W.A. & Chalmers, M.O. 1997. Airborne dispersal of Antarctic terrestrial algae and cyanobacteria. *Ecography* **20**, 585-594.

McDougall, I., Verwoerd, W. & Chevallier, L. 2001. K-Ar geochronology of Marion Island, Southern Ocean. *Geological Magazine* **138**, 1-17.

McKinney, M.L. & Lockwood, J. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* **14**, 450-453.

McQuaid, C.D. & Froneman, P.W. 2004. Rhodes Southern Ocean Group: scientific findings from seventeen years of biological oceanography in the South African National Antarctic Programme. *South African Journal of Science* **100**, 571-577.

Mélice, J.-L., Lutjeharms, J.R.E., Rouault, M. & Ansorge, I.J. 2003. Sea-surface temperatures at the sub-Antarctic islands Marion and Gough during the past 50 years. *South African Journal of Science* **99**, 363-366.

Millennium Ecosystem Assessment. 2005. *Ecosystems and Human Well-being: Biodiversity Synthesis*. World Resources Institute, Washington D.C.

Mooney, H.A. & Hobbs, R.J. (Eds.). 2000. *Invasive Species in a Changing World*. Island Press, Washington D.C.

Muñoz, J., Felicísimo, A.M., Cabezas, F., Burgaz, A.R. & Martínez, I. 2004. Wind as a long-distance dispersal vehicle in the Southern Hemisphere. *Science* **304**, 1144-1147.

Naveen, R., Forrest, S.C., Dagit, R.G., Blight, L.K., Trivelpiece, W.Z. & Trivelpiece, S.G. 2001. Zodiac landings by tourist ships in the Antarctic Peninsula region, 1989-99. *Polar Record* **37**, 121-132.

Nel, D.C., Lutjeharms, J.R.E., Pakhomov, E.A., Ansorge, I.J., Ryan, P.G. & Klages, N.T.W. 2001. Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche chrysostoma* in the southern Indian ocean. *Marine Ecology Progress Series* **217**, 15-26.

Nel, D.C. & Nel, J.L. 1999. Marine debris and fishing gear associated with seabirds at sub-Antarctic Marion Island, 1996/97 and 1997/98: in relation to longline fishing activity. *CCAMLR Science* **6**, 85-96.

Nel, D.C., Nel, J.L., Ryan, P.G., Klages, N.T.W., Wilson, R.P. & Robertson, G. 2000. Foraging ecology of grey-headed mollyhawks at Marion Island, southern Indian Ocean, in relation to longline fishing activity. *Biological Conservation* **96**, 219-231.

O'Dowd, D.J., Green, P.T. & Lake, P.S. 2003. Invasional 'meltdown' on an oceanic island. *Ecology Letters* **6**, 812-817.

Olden, J.D., Poff, N.L., Douglas, M.R., Douglas, M.E. & Fausch, K.D. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution* **19**, 18-24.

Pakhomov, E.A. & Chown, S.L. 2003. The Prince Edward Islands: Southern Ocean Oasis. *Ocean Yearbook* **17**, 348-379.

Pakhomov, E.A. & Froneman, P.W. 1999a. The Prince Edward Islands pelagic ecosystem: a review of achievements 1976-1990. *Journal of Marine Systems* **18**, 297-310.

Pakhomov, E.A. & Froneman, P.W. 1999b. Macroplankton/micronekton dynamics in the vicinity of the Prince Edward Islands (Southern Ocean): new concept for the biomass build up for higher trophic levels. *Marine Biology* **134**, 501-515.

Parmesan, C. & Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37-42.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. 2005. Fishing down marine food webs. *Science* **279**, 860-863.

Peck, L., Convey, P. & Barnes, D.K.A. 2006. Environmental constraints on life histories in Antarctic ecosystems: tempos, timings and predictability. *Biological Reviews* **81**, 75-109.

Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., *et al.* 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439**, 161-167.

Richardson, D.M. & Van Wilgen, B.W. 2004. Invasive alien plants in South Africa: how well do we understand the ecological impacts? *South African Journal of Science* **100**, 45-52.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. 2003. Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57-60.

Sanders, N.J., Gotelli, N.J., Heller, N.E. & Gordon, D.M. 2003. Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences of the USA* **100**, 2474-2477.

Scott, L. 1985. Palynological indications of the Quaternary vegetation history of Marion Island (sub-Antarctic). *Journal of Biogeography* **12**, 413-431.

Scott, L. & Hall, K.J. 1983. Palynological evidence for interglacial vegetation cover on Marion Island, subantarctic. *Paleogeography, Paleoclimatology, Paleoecology* **41**, 35-43.

Slabber, S. & Chown, S.L. 2002. The first record of a terrestrial crustacean, *Porcellio scaber* (Isopoda, Porcellionidae), from sub-Antarctic Marion Island. *Polar Biology* **25**, 855-858.

Smith, V.R. 1977. A qualitative description of energy flow and nutrient cycling in the Marion Island terrestrial ecosystem. *Polar Record* **18**, 361-370.

Smith, V.R. 1991. Terrestrial biological research at the Prince Edward Islands. *South African Journal of Antarctic Research* **21**, 118-123.

Smith, V.R. 2002. Climate change in the sub-Antarctic: An illustration from Marion Island. *Climatic Change* **52**, 345-357.

Smith, V.R. & Steenkamp, M. 1990. Climatic change and its ecological implications at a subantarctic island. *Oecologia* **85**, 14-24.

Stachowicz, J.J., Terwin, J.R., Whitlatch, R.B. & Osman, R.W. 2002. Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. *Proceedings of the National Academy of Sciences of the USA* **99**, 15497-15500.

Stanley, S.M. 1989. *Earth and Life Through Time*. W.H. Freeman, New York.

Van Zinderen Bakker, E.M., Winterbottom, J.M. & Dyer, R.A. (Eds.). 1971. *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965-1966*. A.A. Balkema, Cape Town.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., *et al.* 2002. Ecological responses to recent climate change. *Nature* **416**, 389-395.

Watkins, B.P. & Cooper, J. 1986. Introduction, present status and control of alien species at the Prince Edward Islands, sub-Antarctic. *South African Journal of Antarctic Research* **16**, 86-94.

Watson, R.T. 2002. *Climate Change 2001: Synthesis Report*. Cambridge University Press, Cambridge.

Weimerskirch, H., Inchausti, P., Guinet, C. & Barbraud, C. 2003. Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. *Antarctic Science* **15**, 249-256.

CHAPTER 2

OCEANOGRAPHIC SETTING OF THE PRINCE EDWARD ISLANDS

JOHANN R.E. LUTJEHARMS AND ISABELLE J. ANSORGE

The Prince Edward Islands are the most southerly part of South Africa's official territory. They consist of Marion Island and Prince Edward Island, two volcanic outcrops approximately 500 000 years old, but still active. Marion Island covers an area of 270 km^2; whereas Prince Edward Island – 19 km to the north-east – is only about 45 km^2. The nearest landfall is Crozet Island, 950 km to the east, whereas contiguous South Africa lies over 2 000 km to the north-west. The islands were annexed by the South African government in 1947 for strategic reasons (Crawford 1982, 1999), but they are important for a number of other reasons as well. These have a lot to do with their oceanographic setting.

First, the islands are important because they are a haven for a large number of breeding birds and marine mammals. Some of these are critically dependent on the ambient oceanic conditions during their stay on the islands. It has for instance been demonstrated (Nel *et al.* 2001) that at least one bird species, the Grey-headed Albatross *Thalassarche chrystomota*, feeds preferably on specific mesoscale circulation features found nearly exclusively in the general vicinity of the Prince Edward Islands. Other birds, such as penguins, are unable to range so far afield and are dependent to a greater degree on the conditions

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 17-38

in the immediate environment of the islands (e.g. McQuaid & Froneman 2004). There are therefore two aspect of the oceanic setting of the Prince Edward Islands that are of importance for the ecosystem of the islands: first, the biological productivity of the wider surrounding ocean and, second, the productivity close to the islands.

The wider ocean environment of the Prince Edward Islands is low in primary productivity, as expressed by the density of chlorophyll-*a*. The greatest exception to this oligotrophy is a zone of higher chlorophyll-*a* equatorward of the islands, largely coincident with the Agulhas Front and the Subtropical Convergence (Comiso *et al.* 1993). The physico-chemical nature of these fronts is discussed in greater detail in following sections. The chlorophyll-*a* concentrations are highest at the Subtropical Convergence, but have been shown (Weeks & Shillington 1996) to vary considerably from year to year. This variation is most pronounced in the zone where the primary productivity is highest. Farther to the south, in the sub-Antarctic zone in which the Prince Edward Islands lie, the primary productivity is much lower. Here the inter-annual variations are also much smaller. Using satellite remote sensing as well as numerical models, it has furthermore been shown (Machu & Garçon 2001; Llido *et al.* 2004) that the chlorophyll-*a* concentrations at the Agulhas Front-Subtropical Convergence exhibit a distinct seasonal variation. Values are high during the period that includes spring, summer and autumn. A distinct minimum is however seen in winter. On even shorter time scales, it has now been demonstrated (Llido *et al.* 2005) that the enhanced primary productivity at the Subtropical Convergence takes place as distinct bloom events with limited spatial and temporal scales. This process has considerable consequences for scavenging birds that cannot rely on high concentrations of phytoplankton – or primary productivity – at the fronts in the same location at all times. This unexpected variability has been observed on numerous crossings of the fronts (e.g. Lutjeharms *et al.* 1986).

On one of the first South African research cruises between South Africa and Antarctica during which biological activity was measured in the upper ocean layers (Allanson *et al.* 1981), distinct peaks in chlorophyll-*a* values were observed close to the Subtropical Convergence and the Antarctic Polar Front. However, subsequent cruises in the same (Laubscher *et al.* 1993) as well as in other parts of the Southern Ocean south of Africa (Lutjeharms *et al.* 1985) have shown that on occasion high values of chlorophyll-*a* may be found at these fronts, but at other times there is no evidence of such enhancement at all. These results adumbrated the abovementioned work and results by Llido *et al.* (2005) on the intermittency of blooms at the fronts. They demonstrated unequivocally that the physical processes occurring at these fronts are of considerable importance to the ecosystems not only of the fronts themselves (e.g. Barange *et al.* 1998), but also for birds feeding far from the Prince Edward Islands and thus the ecosystem of the islands. In fact, correlations between high densities of marine birds and frontal systems in this general ocean region have been documented extensively (e.g. Abrams 1983; Abrams & Lutjeharms 1986; Pakhomov & McQuaid 1996; Chown & Gaston 1999). As is to be expected from the subsequent knowledge on the intermittency of bloom events at the fronts, the increased presence of birds at Southern Ocean fronts is also sporadic. Thus, the ocean fronts and their dynamics in this part of the Southern Ocean are a key component in understanding the ecosystems of the islands. The physics of the fronts are therefore dealt with in detail in a subsequent section of this chapter.

If the Prince Edward Islands are therefore important as a bird habitat because of their larger oceanic setting, i.e. their location within striking distance of oceanic fronts with high levels of biological production, how about the effect on birds that are not able to fly such great distances? What is the oceanic situation closer to the islands that may possibly have a positive effect on the feeding opportunities of such birds with a limited feeding range?

A local process that may potentially be of considerable benefit to certain species birds on the islands might be the so called "island mass effect" (Doty & Oguri 1956). This effect can be due to runoff of nutrients from the island, the increased stratification of the water column near islands due to substantial runoff of fresh – and therefore less dense – water and the retention of water in the vicinity of islands long enough to allow a plankton bloom to occur. Such an enhancement of marine productivity has been recorded at other islands in the Southern Ocean (e.g. Perissinotto *et al.* 1992). If such blooms were to be found at the Prince Edward Islands, it would have substantial consequences for subsequent investigations concerning the oceanic setting of the islands.

One of the first to suggest an island mass effect for the Prince Edward Island was Boden (1988), but his conclusions were based on observations quite close to the islands only, preventing an appropriate comparison with the surrounding ocean regions. Subsequent observations (e.g. Perissinotto & Duncombe Rae 1990) have suggested that the mechanism responsible for enhanced primary productivity here was an anti-cyclonic eddy that was frequently to be found on the shallow bathymetric saddle between the islands. This eddy, by retaining runoff water high in nutrients in this region and by enhancing the vertical stratification of the water column (Duncombe Rae 1989; Perissinotto *et al.* 1990) could indeed lead to a pronounced island mass effect and explain the high plankton densities found on these cruises. It was, however, not observed during all cruises to the islands, nor was the perceived island mass effect persistent. In fact, the phytoplankton bloom between the islands was soon recognised as being highly intermittent (Pakhomov *et al.* 2000).

During subsequent cruises in which the surrounding ocean regions were explored to a much greater distance from the islands, the biological-physical interactions and pelagic productivity were shown to be considerably more complex (Perissinotto *et al.* 2000). The distributions of terrigenous urea and ammonia circumscribe the immediate island mass effect and it has been demonstrated that these nutrients do not as a rule extend more than 80 km from the islands. The influence of eddies in the wake of the islands was perceived to have a considerably greater influence on the pelagic productivity and the plankton distribution of the immediate region (Froneman *et al.* 1999) than the island itself. This placed the whole concept of an important island mass effect in jeopardy.

Furthermore, investigations on the type of marine organisms to be found in the plankton of waters surrounding the islands, showed some unexpected results. Boden & Parker (1986) have shown that organisms not only of the expected sub-Antarctic types were to be found here, but that subtropical, Antarctic and even tropical species were also encountered. On certain cruises zooplankton species from Antarctic water were in fact dominant (Grindley & Lane 1979). Froneman *et al.* (1999) have demonstrated that the contrasting plankton species found in this way are excellent indicators of the origin of the water masses in which they are caught.

These observational results have thus demonstrated that the local effect of the islands may not be the most important from an ecological perspective, but that the larger oceanic setting is overriding. The complex interactions between the biology and the physics of the ocean environment has indicated the importance of a better understanding of this larger oceanic setting of the islands and this has developed through a number of stages (Ansorge & Lutjeharms 2000).

2.1 Conceptual developments

On some of the first supply cruises to the islands (Table 2.1) observations of the sea surface temperature were undertaken and the geographic location of the Subtropical Convergence relative to the islands described for the first time (e.g. Lloyd 1973). During the first dedicated cruises to the islands (Grindley 1978) the distribution of organisms and the physical readings undertaken suggested that a coastal upwelling cell existed on the eastern side of the islands, considered to be the lee due to the eastward moving waters in the Antarctic Circumpolar Current.

With the onset of the first programme of dedicated research cruises to the islands, the MOES (Marion Offshore Ecological Study, Table 2.1), this presumed upwelling was not found, but instead the seemingly enhanced primary productivity between the islands lead to the concept of a Taylor column retaining water masses on the saddle between the islands (Perissinotto & Duncombe Rae 1990). The second cruise of this research programme, the MOES II (Marion Offshore Ecosystem Studies; Van Ballegooyen *et al.* 1989) extended the area being investigated enormously (e.g. Ansorge & Lutjeharms 2002). The physical environment of the islands that was thus established suggested quite strongly that a train of eddies, alternating between cyclonic and anti-cyclonic, lay in the wake of the islands. This very suggestive portrayal led to the concept of a Von Karman vortex street being the main oceanic setting of the islands (e.g. Allanson *et al.* 1985). The hydrographic results obtained during the subsequent cruise (MIOS II, Marion Island Oceanographic Study, Table 2.1), covering a somewhat larger area around the islands, put the cat amongst the pigeons. No vortex street was to be seen on this occasion, but instead a disparate collection of mesoscale eddies in no clearly defined order (Pakhomov *et al.* 1998).

Table 2.1 Research cruises to the Prince Edward Islands during which physical observations were made by the institution shown.

Period	Vessel	Cruise	Institute
1873	H.M.S. Challenger		
1929 - 1931	Discovery		
1933 - 1935	Discovery		
1950 - 1951	Discovery II		
Feb 1957	Ob		
Apr-May 1958	Vema		
Jun 1962	Africana II	263, IIOE	DSF
Apr 1963	Africana II	273	DSF
Jan-Mar 1974	Conrad	Conrad 17	LDGO
Sep-Oct 1978	SA Agulhas	3, Marion	NRIO, CSIR
Apr-May 1979	SA Agulhas	6, Marion/Gough	NRIO, CSIR
May-Jun 1979	SA Agulhas	7, Marion relief	
Sep 1979	SA Agulhas	9, Marion	
May-Jun 1980	SA Agulhas	14, Marion relief	NRIO, CSIR
Sep 1980	SA Agulhas	15, Marion	UCT
Feb-Mar 1981	SA Agulhas	18, FIBEX	NRIO, CSIR
Apr-May 1981	SA Agulhas	19, Marion relief	UCT
Aug-Sep 1982	SA Agulhas	25, Marion	DoT
Sep 1982	F.R.V. Africana	Marion	SFRI
Nov-Dec 1983	SA Agulhas	33, Marion relief	RU
Mar-May 1984	SA Agulhas	35, SIBEX	RU
Sep 1984	SA Agulhas	36/37, Marion	NRIO, CSIR
Apr-May 1985	SA Agulhas	40, Marion	RU
Aug-Sep 1985	SA Agulhas	Marion	NRIO, CSIR
Apr-May 1986	SA Agulhas	Marion relief	NRIO, CSIR
Apr-May 1987	SA Agulhas	49, MOES I	UCT
Dec 1986-Jan 1987	R.R.S. Discovery	Discovery, 164	IOS, NERC
Apr-May 1989	SA Agulhas	57, MOES II	NRIO, CSIR
Apr-May 1991	SA Agulhas	SAAMES I	UCT

Period	Vessel	Cruise	Institute
Apr-May 1992	SA Agulhas	Marion relief	RU
Mar-May 1993	R.R.S. Discovery	Discovery, 201	IOS, NERC
Jun-Jul 1993	SA Agulhas	SAAMES III	UCT
Jan-Feb 1995	R.R.S. Discovery	Discovery 213	ISO, NERC
Apr-May 1997	SA Agulhas	84, MIOS II	UCT
Apr-May 1998	SA Agulhas	87, MIOS III	UCT
Apr-May 1999	SA Agulhas	98, MIOS IV	UCT
Apr-May 2000	SA Agulhas	MIOS V	RU
Apr-May 2002	SA Agulhas	103, DEIMEC I	UCT
Mar-Apr 2003	SA Agulhas	108, DEIMEC II	UCT
Apr-May 2004	SA Agulhas	115, DEIMEC III	UCT
Apr-May 2005	SA Agulhas	123, DEIMEC IV	UCT

BIOMASS:	Biological Investigations of Marine Antarctic Systems and Stocks
CSIR:	Council for Scientific and Industrial Research
DEIMEC:	Dynamics of Eddy Impacts on Marion's Ecosystem
DoT:	Department of Transport
DSF:	Division of Sea Fisheries
FIBEX:	First International BIOMASS Experiment
IIOE:	International Indian Ocean Expedition
IOS:	Institute of Oceanographic Sciences
LDGO:	Lamont-Doherty Geological Observatory
MIOS:	Marion Island Oceanographic Study
MOES:	Marion Offshore Ecological Study
NERC:	Natural Environment Research Council
NRIO:	National Research Institute of Oceanology
RU:	Rhodes University
SAAMES:	South African Antarctic Marine Ecosystem Study
SFRI:	Sea Fisheries Research Institute
SIBEX:	Second International BIOMASS Experiment
UCT:	University of Cape Town

This conundrum was subsequently resolved by the use of the then new product of measurements of sea surface height from satellite altimetry. Ansorge and Lutjeharms (2003) have effectively demonstrated that the range of eddies found in the vicinity of the Prince Edward Islands is not generated by the flow past the islands themselves, but that all come from the south-west, more particularly from the Andrew Bain fracture zone in the South-West Indian Ridge. Here the Antarctic Circumpolar Current is constrained to move through a narrow gap, where it speeds up and as a result generates considerable mesoscale turbulence. This makes the oceanographic setting of the Prince Edward Islands most unusual and this is described in more detail in sections that follow.

2.2 Climate change

It is clear from the above that the Prince Edward Islands are important from a marine ecosystem point of view. A further, but crucial, point on the importance of the islands has to do with climate and climate change. The islands lie in a part of the globe where very few accurate atmospheric and ocean variables are measured on a regular basis. This makes the records of such variables observed at Marion Island, which extend over a period of 50 years, enormously valuable and nearly unique (Mélice *et al.* 2003). It has also been shown (Sumner *et al.* 2004) that recent climate change at the Prince Edward Islands has become evident in the melting of perennial snow and ice. Smith and Steenkamp (1990) have explored the implications of such climate change on the ecology of the islands, whereas Rouault *et al.* (2005) have analysed the climate change at the islands since 1960 and postulated the responsible mechanisms. Such climatic changes may have a dramatic effect on the breeding success of a number of bird species on the islands (e.g. Cooper & Lutjeharms 1992). The detail of these processes of climatic change is discussed in le Roux (2007). Suffice here to point out the importance of the islands as a bellwether for climate change in the sub-Antarctic.

2.3 General current environment of the Prince Edward Islands

As discussed below, the oceanographic setting of the Prince Edward Islands is in many ways unique. Its general setting however, is similar to other islands of their kind in the Southern Ocean. The Prince Edward Islands lie in the sub-Antarctic Zone of the Southern Ocean, between the Subtropical Convergence to the north and the Antarctic Polar Front to the south. Although a surface map shows their isolated location, a chart of the bottom topography (Plate 2.1) demonstrates how they fit into the general bathymetric background.

The major feature in this part of the ocean is a mid-ocean ridge, the South-West Indian Ridge, that extends from the south-west to the north-east and lies to the immediate west of the islands. As in the case of all mid-ocean ridges it is criss-crossed by fracture zones (Plate 2.1). A particularly well-developed one in this region is the Andrew Bain fracture zone that can be seen as a relatively shallow part of the ridge at about 50° S, 30° E. As will be seen below, it plays a crucial part in the ocean currents of the region. The Prince Edward Islands lie directly east of the South-West Indian Ridge on a distinct and independent pinnacle that rises from about 5 000 m depth. This is particularly clear to the south, whereas to the north it is somewhat complicated by other seamounts that do not break the sea surface (Plate 2.1). To the north-east lies an extensive shallow feature, the Crozet Plateau. A large part of this zonal rise is shallower than 2 000 m. The Crozet Islands lie on its easternmost extremity. It is clear that these ridges and rises will form important restrictions to the flow of the dominant current in the region, the Antarctic Circumpolar Current.

The Antarctic Circumpolar Current, generally flowing zonally in an eastward direction, is the main background current affecting the general environment of the Prince Edward Islands. It lies between the Subtropical Convergence to the north and the East Wind Drift, a westward setting current at the continental shelf of Antarctica (e.g. Ledenev 1964; Tchernia & Jeannin 1980), to the south. Although generally zonal in this region, the flow does exhibit small meridional excursions (e.g. Harris & Stavropoulos 1978). Furthermore, the bottom topography has a substantial effect on the current trajectory at certain locations. This is the case east of the Crozet Islands (Park *et al.* 1993) and particularly in the general vicinity of the Prince Edward Islands. Pollard & Read (2001) have shown that a major part of the flow is forced equatorward at the South-West Indian Ridge and that another large part is constrained to move through the Andrew Bain fracture zone. This is also evident from studying the geostrophic flow based on all existing hydrographic data (Park *et al.* 2001).

In general, the geostrophic volume transport of the Antarctic Circumpolar Current in the Southern Ocean is concentrated at the embedded frontal systems, to whit, the Subtropical Convergence, the sub-Antarctic Front and the Antarctic Polar Front (Hoffman 1985). This is also the case in the general vicinity of the Prince Edward Islands. Park *et al.* (2001) have calculated a zonal geostrophic speed of 0.9 m s^{-1} at the Subtropical Convergence, about 0.2 m s^{-1}at the sub-Antarctic Front and about 0.6 m s^{-1} at the Antarctic Polar Front. The latter may not be representative since it was obtained in the Andrew Bain fracture zone where the current moves more rapidly. In the ocean regions between these high velocity jets the speed of the Antarctic Circumpolar Current lies between 5-10 cm s^{-1} (Park *et al.* 1993). In the vicinity of the Prince Edward Islands about 20 Sv (Sv = 10^6 m^3 s^{-1}) is transported by the stronger currents at the Subtropical Convergence (Pollard & Read 2001), with an attendant 60 Sv in the Agulhas Return Current; about 40 Sv is to be found at the Antarctic Polar Front. It is estimated that a total of 100 Sv moves through the Andrew Bain fracture zone.

To recapitulate, the Subtropical Convergence lies equatorward of the Prince Edward Islands, at about 42° S on average, and is reinforced by the juxtaposition of the Agulhas Return Current. This current carries the remnants of the Agulhas Current proper eastward (Stramma 1992; Sparrow *et al.* 1995) but gets steadily weaker along its path (Park *et al.* 1993; Stramma & Lutjeharms 1997). By about 70° E it has completely petered out (Lutjeharms & Ansorge 2001), but by 40° E, i.e. equatorward of the Prince Edward Islands, the Agulhas Return Current is still fairly strong. Here it carries at least 60 Sv and creates a number of eddies of different dimensions (Pollard & Read 2001). This process is important, since it is in the regions where the Agulhas Return Current is still strong and the flow is still turbulent and as a result the primary productivity is highest. This may attract certain marine animals.

Of some importance to the movement of immotile organisms in the Southern Ocean is the water movement not of the bulk of the ocean described above, but in the upper few centimetres. This has been studied over a period of three years using plastic drift cards (Lutjeharms *et al.* 1988). Average drift rates at the latitude of the Prince Edward Islands were about 16 cm s^{-1}; those of drifters drogued at 50 m were about 15% higher.

2.4 General hydrographic environment of the Prince Edward Islands

The most important hydrographic variables that constitute the environment of the Prince Edward Islands are the salinities, temperatures and nutrients. These also define the locations of the fronts to be found in the region. The geographic distribution of ocean temperatures at a depth of 200 m for the South-East Atlantic and for the South-West Indian sectors of the Southern Ocean, based on all existing observations, is given in Fig. 2.1. It is immediately evident that the distributions of the isotherms have a general zonal nature, but that there are substantial deviations from such a strict zonal tendency. The 10°C isotherm has been selected because it lies at the poleward extremity of the Subtropical Convergence zone, the 6°C corresponds with the location of the sub-Antarctic Front and the 2°C isotherm with the Antarctic Polar Front (Table 2.2). South of Africa the Subtropical Convergence lies farther poleward due to the influence of the termination of the Agulhas Current, but its location steadily decreases in latitude on moving eastward so that at the longitude of the Prince Edward Islands it lies at less than 39°S. By contrast the sub-Antarctic Front (~ 6°C) extends quite zonally until it reaches the South-West Indian Ridge at about 35° E after which it swings strongly equatorward (Belkin & Gordon 1996). The Antarctic Polar Front at 2°C moves through the South-West Indian Ridge at 50° S after which it seems to exhibit more meridional meanders than upstream in the Atlantic sector. This greater tendency to meander is also evident in the results of a similar analysis by Belkin and Gordon (1996). From a direct point of view for the Prince Edward Islands is the fact that these islands lie close to the sub-Antarctic Front at an average temperature of about 6°C. How does this vary temporally?

The seasonal changes in the sea surface temperature as measured at Marion Island are given in Fig. 2.2a. These are based on a record of 50 years (Mélice *et al.* 2003). These observations show the expected seasonal cycle, the temperature having a summer maximum of 6.5 (± 0.9)°C in February and a minimum of 4.3 (± 0.8)°C in the month of September, after the austral winter. This seasonal cycle is not invariant, but varies from year to year as the standard deviations in Fig. 2.2a suggest.

Furthermore, some secular changes have been noted (Mélice *et al.* 2003, 2005). These climatic changes are discussed in le Roux (2008). Suffice here to point out that the sea surface temperatures at Marion Island exhibit a cycle with an amplitude of about 1°C and a wavelength of about a decade, suggesting the influence of the Antarctic Circumpolar Wave. A long-term increase in temperature of 1.4°C over a period of 50 years has also been observed (Fig. 2.2b). These changes in sea surface temperatures may be due to heating of the surface layers of the ocean in this region, or may be due to meridional shifts in the frontal systems.

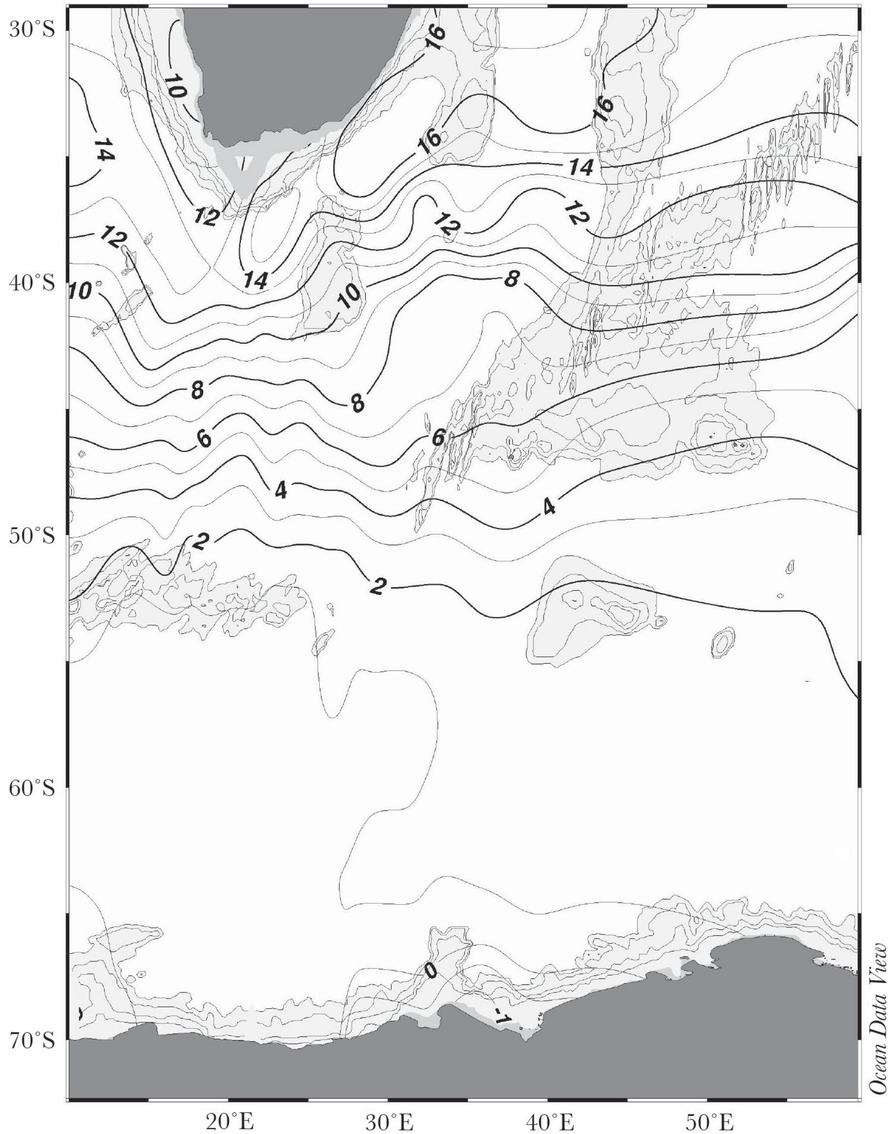


Figure 2.1 Average ocean temperatures at 200 m depth in the general vicinity of the Prince Edward Islands. The isotherms have been selected to coincide with the subsurface expressions of the Subtropical Convergence (10°C), the sub-Antarctic Front (6°C) and the Antarctic Polar Front (2°C). The bathymetry is given in 1 000 m intervals with parts shallower than 3 500 m shaded. Data represent hydrographic measurements which have been made over the past 30 years.

Table 2.2 Thermal characteristics of the surface expression of frontal systems south of Africa (after Lutjeharms & Valentine 1984).

Latitudinal position					Temperature (°C)				
	From	To	Middle	Width (km)	From	To	Middle	Range	Gradient (°C km^{-1})
Agulhas Front	39°09’	40°01’	39°37’	96.3	21.0	15.7	18.4	5.4	0.102
Subtropical Convergence	40°35’	42°36’	41°40’	225.1	17.9	10.6	14.2	7.3	0.047
Sub-Antarctic Front	45°15’	47°25’	46°23’	241.4	9.0	5.1	7.0	3.9	0.018
Antarctic Polar Front	49°39’	50°47’	50°18’	126.0	1.4	2.5	3.4	1.8	0.018

2.5 Frontal systems in the vicinity of the Prince Edward Islands

A large number of hydrographic sections have been carried out in the vicinity of the Prince Edward Islands so that the location and character of the neighbouring ocean fronts are relatively well known (Jacobs & Georgi 1977; Lutjeharms 1990; Belkin & Gordon 1996; Moore *et al.* 1999).

As mentioned above, the most intense front here is the Subtropical Convergence, sometimes enhanced by the Agulhas Front – part of the Agulhas Return Current – sometimes distinctly separate (e.g. Lutjeharms & Valentine 1984; Belkin & Gordon 1996). As intimated by the isotherms in Fig. 2.1, this system of fronts lies roughly at 40°S but can be quite complex, consisting at times of a number of fronts and sub-fronts (Lutjeharms 1985). Much of this complexity may be due to the formation of a range of eddies of different sizes and circulation direction at the fronts (e.g. Lutjeharms & Valentine 1988a, b). This turbulent tendency is evident at this front as far east as 70°E and seems to be important for creating a specific biological habitat at this front. Eddies, both cyclonic and anti-cyclonic, would have the tendency to eventually move back to the fronts from which they were generated, to be re-absorbed and to strengthen this front. This has in fact been observed in other, comparable, parts of the Subtropical Convergence (Boebel *et al.* 2003). This process of eddy shedding from fronts has also been observed at the other fronts in the region. Detail of this is given in the section on the eddy behaviour in the vicinity of the Prince Edward Islands. So what are the hydrographic characteristics of the Subtropical Convergence?

The basic thermal nature of the front is given in Table 2.2. It should be recognised that these values are averages obtained for a wider extent of the Southern Ocean south of Africa (Fig. 2.1) and therefore not for the fronts near the Prince Edward Islands only. Furthermore, the variations in these values are quite large. So, for instance, the mean thermal gradient across the Agulhas Front is 0.102°C km^{-1}, but the standard deviation based on 24 crossings is 0.106°C km^{-1}. A very strong gradient of 0.2°C km^{-1} is therefore not uncommon (Lutjeharms & Valentine 1984). As mentioned, this front may on many occasions be found in conjunction with the Subtropical Convergence, making the resultant front one of the most intense to be found in the world ocean. The temperature gradient across the Subtropical Convergence on its own is much weaker than across the Agulhas Front by itself, but remains quite formidable for an ocean front (Table 2.2). By contrast the sub-Antarctic Front and the Antarctic Polar Front are much weaker. The nature of these fronts with depth is shown in Plate 2.2.

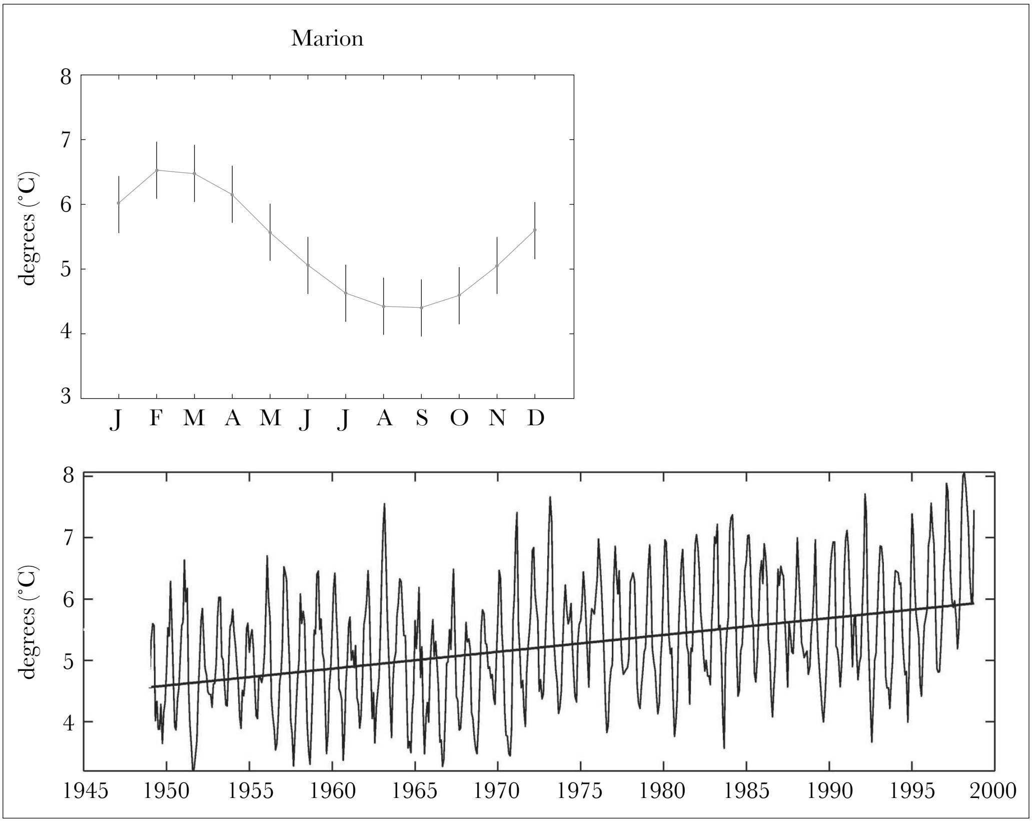


Figure 2.2 Trends in the sea surface temperatures as measured on a daily basis at Marion Island since the 1950s. The upper panel shows the average seasonal cycle of temperature with the standard deviations observed over this period for each calendar month (after Mélice *et al.* 2003). The lower panel shows the actual monthly averages of sea surface temperature for this period with a linear trend superimposed. The latter indicates a general rise of 1.4°C (after Mélice *et al.* 2003).

The Subtropical Convergence north of the Prince Edward Islands was on this occasion very sharply defined (Plate 2.2a) to a depth of at least 750 m with a 2°C meridional gradient up to a depth of 700 m (not shown). The surface expression on this occasion was not very intense, but consisted of a step-like structure that has also been observed elsewhere (Lutjeharms *et al.* 1993) during austral summer. This relatively simple frontal structure is unusual (Lutjeharms 1990). The more typical complexity of the frontal systems is shown clearly. Here the Subtropical Convergence was found at about 39° 30'S, but a secondary front can be seen in the figure at about 43° S. It has a reasonably strong surface expression and its surface temperatures lie on the lower end of what could be expected (Table 2.2). A third front can be identified just south of 44° S. This might have been the sub-Antarctic Front, but its location is unusually far north and its temperatures too high. The sub-Antarctic Front defines the northern border of the Antarctic Polar Front Zone. Its origin and forcing is not well understood. Perhaps the weak front at ~ 48° S would be a better candidate for the sub-Antarctic Front. This imposed subjectivity illustrates the complexity of the system. The Antarctic Polar Front is more easily defined. It is the farthest equatorward extent of 2°C water at a depth of 200 m. At times this subsurface expression agrees well with a small surface gradient of about 0.018°C at a middle temperature of 3.4°C. This is the case in the vertical temperature section shown in Plate 2.2b where it was observed at 49° 15'S while a secondary front lay at 53° 45'S.

The locations of the different fronts near the Prince Edward Islands, based on measurements made on research cruises between 1978 and 1986 (Table 2.1), is shown in Fig. 2.3. It is quite apparent that the latitude of the fronts show substantial meridional shifts (Nagata *et al.* 1988; Lutjeharms 1990). The Antarctic Polar Front does not exhibit such extensive movements as the other two fronts, but this may in this case be an artefact of only a small number of crossings of the Antarctic Polar Front to the south of the islands. This front actually lies quite close to the islands to the south, whereas the meridional range of the sub-Antarctic Front includes the islands (Lutjeharms 1985; Holliday & Read 1998). The presence of the front at the islands has in fact been observed a number of times (e.g. Duncombe Rae 1989) and even short-term shifts documented (e.g. Lutjeharms *et al.* 2002) fairly extensively. No clear short-term or inter-annual movement patterns have to date been established. This intermittency of the sub-Antarctic Front passing between Marion and Prince Edward islands has given rise to the hypothesis that a trapped eddy may be formed in between the islands when the front and its associated currents – with higher speeds – are not present, but that this eddy may be swept away when the front returns (Perrisinotto *et al.* 2000). The continuation of these fronts farther east in the vicinity of Crozet Island has been amply described by Belkin & Gordon (1996) and by Park *et al.* (1991, 1993) as well as by Park & Gambèroni (1995, 1997). To some degree these described fronts in the vicinity of the Prince Edward Islands also indicate the borders of specific water masses. These are shown in Plate 2.3.

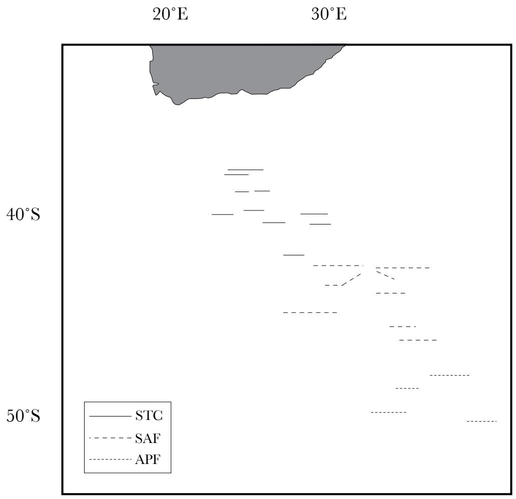


Figure 2.3 Geographic locations of the main ocean fronts in the general surrounding of the Prince Edward Islands. The fronts are: the Subtropical Convergence (solid line); the sub-Antarctic Front (broken line) and the Antarctic Polar Front (dotted line). Details of the characteristics of the surface expressions of these fronts are given in Table 2.2. These locations are based on data collected at closely spaced oceanographic stations during the period 1978 to 1986 (Table 2.1).

2.6 Water masses in the vicinity of the Prince Edward Islands

The characteristic temperature/salinity relationships of the waters in the vicinity of the Prince Edward Islands are little different from those found at the same latitude at other locations in the Southern Ocean. In Plate 2.3a they have been colour distinguished according to their location (Plate 2.3b) between different fronts along a meridional line extending across the islands.

The blue curve shows the water masses north of the Subtropical Convergence. Clearly there is much warmer water with surface temperatures of 20°C. The very surface water is slightly less saline, indicating Subtropical Surface Water. The slight subsurface salinity maximum at slightly lower temperatures denotes Subtropical Surface Water and the salinity minimum at 5°C represents Antarctic Intermediate Water. This is the more saline Indian Ocean variety of Antarctic Intermediate Water with a salinity of about 34-35 whereas the Atlantic variety has a salinity of only 34.2 (Read & Pollard 1993). This eastward increase in the salinity of Antarctic Intermediate Water is due to mixing with more saline waters along its route. According to Fine (1993) the Antarctic Intermediate Waters at the Prince Edward Islands come directly from the west.

The rectilinear curve between the two extremes of Subtropical Surface Water and Antarctic Intermediate Water is the Central Water. The salinity maximum at about 34.8 represents Circumpolar Deep Water and below that is found

Antarctic Bottom Water. The next two stations (yellow and red traces in Plate 2.3a), in the sub-Antarctic, no longer exhibit the presence of Subtropical Surface Water, as one would expect. Their surface salinities are below 34.3, denoting sub-Antarctic Surface Water. This is the water mass that forms the low salinity Antarctic Intermediate Water once it has moved equatorward and been subducted beneath the lighter Subtropical Surface Waters at the Subtropical Convergence. At depth the Circumpolar Deep Waters are slightly colder to the south than in the curves for the water masses to the north. Last, the water to the south of the Antarctic Polar Front (green trace in Plate 2.3a) is consistently colder than 2.5°C and relatively fresh due to the melting of pack ice. The highest salinity values are found for the Circumpolar Deep Water in the Antarctic zone.

These temperature/salinity characteristics define the different water masses and indicate their origins. In the direct vicinity of the Prince Edward Islands it is only the two middle curves representing the sub-Antarctic waters that are of greatest importance since this is the band in which the islands are situated. However, it has been noted that water and organisms with Antarctic characteristics and even with Subtropical characteristics are intermittently found near the islands, carried there by eddies (Boden & Parker 1986; Froneman *et al.* 1999). This is discussed at greater length in the section below. For the ecosystem of the islands as well as for its weather and climate it is only the very upper layers of the ocean that are of importance. Nonetheless, it is known that marine mammals from the Prince Edward Islands, such as elephant seals, dive to depths of 1 000 m, so deeper water masses may conceivably be of importance to such animals. The temporal variability in water characteristics at these depths would be minute however.

2.7 Eddy behaviour in the vicinity of the Prince Edward Islands

As stated previously in this chapter the general oceanic environment of the Prince Edward Islands is in most respects, very similar to that of other islands in the sub-Antarctic. This aspect has now been dealt with. It was also stated that in certain respects the Prince Edward Islands are in a unique location and environment. This is amply illustrated in Plate 2.4.

Throughout the Southern Ocean there are regions of high mesoscale variability in a background of generally low variability. These regions of high variability were first identified from statistical analyses of historic hydrographic data (Lutjeharms & Baker 1980), but subsequently with much greater detail using the trajectories of drifters (Daniault & Ménard 1985) and from satellite altimetry (e.g. Colton & Chase 1983). Increased current variability may be caused by ring shedding (e.g. Gouretski & Danilov 1994) or by the meandering of fronts. A few regions of extreme variability stand out in this ocean as a whole. These regions are where the Subtropical Convergence is intensified by other currents such as at the Falkland-Brazil Current confluence and where the Agulhas Return Current flows along this front, e.g. equatorward of the

Prince Edward Islands. South of these regions, in the Southern Ocean proper, the variability is enhanced at the cores of the Antarctic Circumpolar Current and where this current interacts with shallower bottom topography such as mid-ocean ridges (e.g. Park & Saint-Guily 1992). It can be shown from theory that the Antarctic Circumpolar Current is very sensitive to changes in the bottom topography and to bottom currents (e.g. Craneguy & Park 1999). Such a case of the current interacting with the bottom topography is illustrated in Plate 2.4. Whereas the general ocean environment here is relatively quiescent as measured by sea surface height variability (representing variability in ocean currents), the region at 50°S, 30°E has very high values of variability. From there a band of higher variability than the surroundings extends north-eastward in the direction of the Prince Edward Islands. This geographic configuration of the variability is most unusual for the Southern Ocean. It varies slightly intra-annually and inter-annually, but the key elements remain invariant. This particular region of high variability has a significant impact on the islands' environment and potentially on the ecology of the islands (e.g. Nel *et al.* 2001). What would bring about such an unusual circulation?

Ever wider observational grids of hydrographic stations around the Prince Edward Islands (Table 2.1) have shown unequivocally that the region is characterised by the presence of an ever-changing population of eddies (Plate 2.5a) of different sizes and contrary circulation directions (Ansorge & Lutjeharms 2000). These eddies have been shown to extend to depths of more than 1 000 m and many have remnant Antarctic characteristics (Plate 2.5b). Even more important, it has been demonstrated that the intensity of these eddies is in all observed cases strongly correlated with changes in sea surface height as observed by satellite altimetry (Ansorge & Lutjeharms 2000). This means that sea surface height anomalies in the region can be assumed to represent eddies and can be followed in time and their life history studied. Such investigations have produced some seminal results.

It has been shown (Ansorge & Lutjeharms 2003) that the origin of these eddies is with few exceptions the Andrew Bain fracture zone. This is apparent if the bathymetry of Plate 2.1 and the variability shown in Plate 2.4 are compared. The most extreme variability in sea surface height is found at the location where the Antarctic Circumpolar Current is constrained to move through the South-West Indian Ridge. From there eddies move into the Enderby Basin, downstream of the ridge, but with tracks that are predominantly in a north-easterly direction (Plate 2.6). In the case shown in this figure, the eddy moved from the ridge where it had been spawned and eventually passed the islands. It became indistinguishable soon after, suggesting that it had been totally eroded. It is clear from the distribution of variability shown in Plate 2.4 that little remains of the mesoscale turbulence east of 40°E. This implies that the eddies start their life at the ridge, but decay by mixing with the ambient waters before they reach this longitude (Ansorge & Lutjeharms 2005). These eddies may carry Antarctic biota along with their water masses and cause a substantial negative heat transfer in an equatorward direction (Ansorge *et al.* 2006). What do these eddies look like hydrographically?

As may be expected they have a range of features. Some are warm, anti-cyclonic eddies; others are cold and rotate cyclonically. To a large degree this shows their origin. A well-studied example of a cold eddy is shown in Plate 2.5. A horizontal cut through the eddy at a depth of 200 m (Plate 2.5a) gives its dimensions and demonstrates the contrast between the temperature of its waters and that of the surrounding waters. The core of the eddy had temperatures of less than 1°C whereas the surrounding water was warmer than 3°C. The eddy was not entirely circular, but had a mean diameter of about 220 km. This, and satellite altimetry, shows unambiguously that its waters had their origin south of the Antarctic Polar Front. This is also evident from a vertical hydrographic section through the eddy (Plate 2.5b).

The observed temperatures to a depth of 920 m demonstrate the sharp distinction of waters in the eddy and those outside it. This was when the eddy was still fairly young and had not undergone much mixing with its environment. The temperature minimum at roughly 240 m depth is Antarctic Winter Water still intact so shortly after the eddy had formed. The eddy was first observed in satellite altimetry in October 2004 and by August 2005 has sufficiently dissipated that it was no longer observable as a distinct sea surface height anomaly. This lifetime of less than a year is typical for this type of eddy. Its speed of translation in a north-easterly direction (Plate 2.6) was 2 km day^{-1}. When observed hydrographically (Plate 2.5) its peripheral speeds were up to 1.4 m s^{-1}, extremely high for such features in the Southern Ocean. So what are the implications of this unusual eddy street for the Prince Edward Islands?

2.8 Conclusions

Due to the eddies that continually traverse the islands, the direct environment of the islands is much more variable in current speeds, current directions and water types than would normally be expected. This is also reflected in a much higher variety of ocean habitats that come about in the region, evident in the patchy nature of chlorophyll distribution in the vicinity of the islands (Froneman *et al.* 1999). Furthermore, these eddies carry with them organisms from their region of origin so that the surrounding waters of the Prince Edward Islands have a much more diverse spectrum of biota than one would normally expect from an island in the sub-Antarctic. Moreover, these and other eddies create unusual habitats of their own, particularly at their borders. This has become evident from the feeding behaviour of some birds (Nel *et al.* 2001). The further study of this mechanism and its implications is being planned.

2.9 Acknowledgements

The knowledge of the oceanic environment of the Prince Edward Islands, summarised here, would not have existed without funding and logistics supplied by the South African National Antarctic Programme. The support from numerous masters of the research and supply vessel *SA Agulhas* and the ever-changing complement of officers and sailors made the investigations possible. We thank in particular the Southern Ocean Group of Rhodes University, under the able leadership of first Professor Brian Allanson and then Professor Christopher McQuaid, for congenial collaboration and support through a number of projects over a period of no less than 25 years.

2.10 References

Abrams, R.W. 1983. Distribution of seabirds in the African sector of FIBEX. *South African Journal of Antarctic Research* **13**, 24-28.

Abrams, R.W. & Lutjeharms, J.R.E. 1986. Relationship between seabirds and meso-scale hydrographic features in the Agulhas Current retroflection region. In *Acta XIX Congressus Internationalis Ornithologici*. Ottawa, Canada, 22-29. VI. 1986, Vol. 1, pp. 991-996.

Allanson, B.R., Boden, B.P., Parker, L.D. & Duncombe Rae, C.M. 1985. A contribution to the oceanology of the Prince Edward Islands. In: Siegfried, W.R., Condy, P.R. & Laws, R.M. (Eds.). *Antarctic Nutrient Cycles and Food Webs*. Springer, Berlin, pp. 30-45.

Allanson, B.R., Hart, R.C. & Lutjeharms, J.R.E. 1981. Observations on the nutrients, chlorophyll and primary production of the Southern Ocean south of Africa. *South African Journal of Antarctic Research* **10/11**, 3-13.

Ansorge, I.J. & Lutjeharms, J.R.E. 2000. Twenty-five years of physical oceanographic research at the Prince Edward Islands. *South African Journal of Science* **96**, 557-565.

Ansorge, I.J. & Lutjeharms, J.R.E. 2002. The hydrography and dynamics of the ocean environment of the Prince Edward Islands (Southern Ocean). *Journal of Marine Systems* **37**, 107-127.

Ansorge, I.J. & Lutjeharms, J.R.E. 2003. Eddies originating from the South-West Indian Ridge. *Journal of Marine Systems* **39**, 1-18.

Ansorge, I.J. & Lutjeharms, J.R.E. 2005. Direct observations of eddy turbulence at a ridge in the Southern Ocean. *Geophysical Research Letters* **32**, L14603, doi: 10.1029/2005GL0225 88.

Ansorge, I.J., Lutjeharms, J.R.E., Swart, N.C. & Durgadoo, J.V. 2006. Observational evidence for a cross frontal heat pump in the Southern Ocean. *Geophysical Research Letters* **33**,19601, doi: 1029/2006GL026174.

Barange, M., Pakhomov, E.A., Perissinotto, R., Froneman, P.W., Verheye, H.M., Taunton-Clark, J., *et al.* 1998. Pelagic community structure of the Subtropical Convergence region south of Africa and in the mid-Atlantic Ocean. *Deep-Sea Research I* **45**, 1663-1687.

Belkin, I.M. & Gordon, A.L. 1996. Southern Ocean fronts from the Greenwich meridian to Tasmania. *Journal of Geophysical Research* **101**, 3675-3696.

Boden, B.P. 1988. Observations of an island mass effect in the Prince Edward Archipelago. *Polar Biology* **9**, 1-8.

Boden, B.P. & Parker, L.D. 1986. The plankton of the Prince Edward Islands. *Polar Biology* **5**, 81-93.

Boebel, O., Rossby, T., Lutjeharms, J.R.E., Zenk, W. & Baron, A. 2003. Path and variability of the Agulhas Return Current. *Deep-Sea Research II* **50**, 35-56.

Chown, S.L. & Gaston, K.J. 1999. Patterns in procellariiform diversity as a test of species-energy theory in marine systems. *Evolutionary Ecology Research* **1**, 365-373.

Colton, M.T. & Chase, R.R.P. 1983. Interaction of the Antarctic Circumpolar Current with bottom topography: an investigation using satellite altimetry. *Journal of Geophysical Research* **88**, 1825-1843.

Comiso, J.C., McClain, C.R., Sullivan, C.W., Ryan, J.P. & Leonard, C.L. 1993. Coastal Zone Color Scanner pigment concentrations in the Southern Ocean and relationships to geophysical surface features. *Journal of Geophysical Research* **98**, 2419-2451.

Cooper, J. & Lutjeharms, J.R.E. 1992. Correlations between seabird breeding success and meteorological conditions at Marion and Gough Islands. *South African Journal of Science* **88**, 173-175.

Craneguy, P. & Park, Y.-H. 1999. Contrôle topographique de courant circumpolaire antarctique dans l'océan Indien sud. *Comte Rendu Académie des Sciences, Sciences de la terre et de planètes* **328**, 583-589.

Crawford, A. 1982. *Tristan da Cunha and the Roaring Forties*. Charles Skilton, Edinburgh.

Crawford, A. 1999. *Penguins, Potatoes and Postage Stamps*. Anthony Nelson, London.

Daniault, N. & Ménard, Y. 1985. Eddy kinetic energy distribution in the Southern Ocean from altimetry and FGGE drifting buoys. *Journal of Geophysical Research* **90**, 11877-11889.

Doty, M.S. & Oguri, M. 1956. The island mass effect. *Journal du Conseil* **22**, 4-17.

Duncombe Rae, C.M. 1989. Physical and chemical marine environment of the Prince Edward Islands (Southern Ocean) during April/May 1987. *South African Journal of Marine Science* **8**, 301-311.

Fine, R.A. 1993. Circulation of Antarctic Intermediate Water in the South Indian Ocean. *Deep-Sea Research I* **40**, 2021-2042.

Froneman, P.W., Ansorge, I.J., Pakhomov, E.A. & Lutjeharms, J.R.E. 1999. Plankton community structure in the physical environment surrounding the Prince Edward Islands (Southern Ocean). *Polar Biology* **22**, 145-155.

Gouretski, V.V. & Danilov, A.I. 1994. Characteristics of warm rings in the African sector of the Antarctic Circumpolar Current. *Deep-Sea Research I* **41**, 1131-1157.

Grindley, J.R. 1978. Marine ecosystems of Marion Island. *South African Journal of Antarctic Research* **8**, 38-42.

Grindley, J.R. & Lane, S.B. 1979. Zooplankton around Marion and Prince Edward Islands. *Campagne MD.08/Benthos – Premiers résultats, C. N. F. R. A., Publication 44*, pp. 111-125.

Harris, T.F.W. & Stavropoulos, C.C. 1978. Satellite-tracked drifters between Africa and Antarctica. *Bulletin of the American Meteorological Society* **59**, 51-59.

Hofmann, E.E. 1985. The large-scale horizontal structure of the Antarctic Circumpolar Current from FGGE drifters. *Journal of Geophysical Research* **90**, 7087-7097.

Holliday, N.P. & Read, J.F. 1998. Surface oceanic fronts between Africa and Antarctica. *Deep-Sea Research I* **45**, 217-238.

Jacobs, S.S. & Georgi, D.T. 1977. Observations on the Southwest Indian/ Antarctic Ocean. In: Angel, M. (Ed.). *A Voyage of Discovery*. George Deacon 70th Anniversary volume, Pergamon, Oxford, pp. 43-84, supplement to *Deep-Sea Research* **24**.

Laubscher, R.K., Perissinotto, R. & McQuaid, C.D. 1993. Phytoplankton production and biomass at frontal zones in the Atlantic sector of the Southern Ocean. *Polar Biology* **13**, 471-481.

Ledenev, V.G. 1964. Direction of surface currents in the West Wind Drift zone. *Information Bulletin, Soviet Antarctic Expedition 1955-8* **49**, 198-200.

le Roux, P.C. 2008. Climate and climate change. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 39-64.

Llido, J., Garçon, V., Lutjeharms, J.R.E. & Sudre, J. 2005. Event-scale blooms drive enhanced primary productivity at the Subtropical Convergence. *Geophysical Research Letters* **32**, L5611, doi: 10.1029/2005GL022880.

Llido, J., Machu, E., Sudre, J., Dadou, I. & Garçon, V. 2004. Variability of the biological front south of Africa from SeaWiFS and a coupled physical-biological model. *Journal of Marine Research* **62**, 595-609.

Lloyd, I.H. 1973. Sub-tropical convergence zone along 40ºS: July 1973. *News Letter, (South African) Weather Bureau* **297**, 244-245.

Lutjeharms, J.R.E. & Baker, D.J. 1980. A statistical analysis of the meso-scale dynamics of the Southern Ocean. *Deep-Sea Research* **27**, 145-159.

Lutjeharms, J.R.E. & Valentine, H.R. 1984. Southern Ocean thermal fronts south of Africa. *Deep-Sea Research* **31**, 1461-1476.

Lutjeharms, J.R.E. 1985. Location of frontal systems between Africa and Antarctica: some preliminary results. *Deep-Sea Research* **32**, 1499-1509.

Lutjeharms, J.R.E. 1990. Temperatuurstruktuur van die oseaanbolaag tussen Kaapstad en Marion-eiland. *South African Journal of Antarctic Research* **20**, 21-32.

Lutjeharms, J.R.E., Allanson, B.R. & Parker, L. 1986. Frontal zones, chlorophyll and primary production patterns in the surface waters of the Southern Ocean south of Cape Town. In: Nihoul, J.C.J. (Ed.). *Marine Interfaces Ecohydrodynamics*. Proceedings of the 17th International Liège Colloquium, Elsevier Oceanography Series, Amsterdam, pp. 105-117.

Lutjeharms, J.R.E. & Ansorge, I.J. 2001. The Agulhas Return Current. *Journal of Marine Systems* **30**, 115-138.

Lutjeharms, J.R.E., Jamaloodien, S. & Ansorge, I.J. 2002. The temporal displacement of ocean fronts south-east of Africa. *South African Journal of Science* **98**, 304-306.

Lutjeharms, J.R.E., Shannon, L.V. & Beekman, L.J. 1988. On the sea surface drift of the Southern Ocean. *Journal of Marine Research* **46**, 267-279.

Lutjeharms, J.R.E. & Valentine, H.R. 1988a. Eddies at the Sub-Tropical Convergence south of Africa. *Journal of Physical Oceanography* **18**, 761-774.

Lutjeharms, J.R.E. & Valentine, H.R. 1988b. On mesoscale ocean eddies at the Agulhas Plateau. *South African Journal of Science* **84**, 194-200.

Lutjeharms, J.R.E., Valentine, H.R. & Van Ballegooyen, R.C. 1993. The Subtropical Convergence in the South Atlantic Ocean. *South African Journal of Science* **89**, 552-559.

Lutjeharms, J.R.E., Walters, N.M. & Allanson, B.R. 1985. Oceanic frontal systems and biological enhancement. In: Siegfried, W.R., Condy, P.R. & Laws, R.M. (Eds.). *Antarctic Nutrient Cycles and Food Webs*. Springer, Berlin, pp. 11-21.

Machu, E. & Garçon, V. 2001. Phytoplankton seasonal distribution from SeaWiFs data in the Agulhas Current system. *Journal of Marine Research* **59**, 795-812.

McQuaid, C.D. & Froneman, P.W. 2004. The Southern Ocean Group at Rhodes University: seventeen years of biological oceanography in the Southern Ocean reviewed. *South African Journal of Science* **100**, 571-577.

Mélice, J.-L., Lutjeharms, J.R.E., Goosse, H., Fichefet, T. & Reason, C.J.C. 2005. Evidence for the Antarctic circumpolar wave in the sub-Antarctic during the past 50 years. *Geophysical Research Letters* **32**, L14614, doi: 10.1029/2005GRL233 61.

Mélice, J.-L., Lutjeharms, J.R.E., Rouault, M. & Ansorge, I.J. 2003. Sea-surface temperatures at the sub-Antarctic islands Marion and Gough during the past 50 years. *South African Journal of Science* **99**, 363-366.

Moore, J.K., Abbot, M.R. & Richman, J.G. 1999. Location and dynamics of the Antarctic Circumpolar Front from satellite sea surface temperature data. *Journal of Geophysical Research* **104**, 3059-3073.

Nagata, Y., Michida, Y. & Unimura, Y. 1988. Variation of positions and structures of the oceanic fronts in the Indian Ocean sector of the Southern Ocean in the period from 1965-1987. In: Sarhage, D. (Ed.). *Antarctic Ocean and Resources Variability*. Springer, Berlin, pp. 92-98.

Nel, D.C., Lutjeharms, J.R.E., Pakhomov, E.A., Ansorge, I.J., Ryan, P.G. & Klages, N.T.W. 2001. Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche chrystomota* in the southern Indian Ocean. *Marine Ecology Progress Series* **217**, 15-26.

Pakhomov, E.A., Froneman, P.W. & Ansorge, I. 1998. Prince Edward Islands' offshore oceanographic study: report of research cruise April-May 1997. *South African Journal of Science* **94**, 153-156.

Pakhomov, E.A., Froneman, P.W., Ansorge, I.J. & Lutjeharms, J.R.E. 2000. Temporal variability in the physico-biological environment of the Prince Edward Islands (Southern Ocean). *Journal of Marine Systems* **26**, 75-95.

Pakhomov, E.A. & McQuaid, C.D. 1996. Distribution of surface zooplankton and seabirds across the Southern Ocean. *Polar Biology* **16**, 271-286.

Park, Y.-H., Charriaud, E., Craneguy, P. & Kartavtseff, A. 2001. Fronts, transport, and Weddell Gyre at 30°E between Africa and Antarctica. *Journal of Geophysical Research* **106**, 2857-2879.

Park, Y.-H. & Gambèroni, L. 1995. Large-scale circulation and its variability in the south Indian Ocean from TOPEX/POSEIDON altimetry. *Journal of Geophysical Research* **100**, 24911-24929.

Park, Y.-H. & Gambèroni, L. 1997. Cross-frontal exchanges of Antarctic Intermediate Water and Antarctic Bottom Water in the Crozet Basin. *Deep-Sea Research I* **44**, 963-986.

Park, Y.-H., Gambèroni, L. & Charriaud, E. 1991. Frontal structure and transport of the Antarctic Circumpolar Current in the south Indian Ocean sector, 40–80°E. *Marine Chemistry* **35**, 45-62.

Park, Y.-H., Gambèroni, L. & Charriaud, E. 1993. Frontal structure, water masses, and circulation in the Crozet Basin. *Journal of Geophysical Research* **98**, 12361-12385.

Park, Y.-H. & Saint-Guily, B. 1992. Sea level variability in the Crozet-Kerguelen-Amsterdam area from bottom pressure and Geosat altimetry, In: Woodworth, P.L. (Ed.). *Sea Level Changes: Determination and Effects*, Geophysical Monograph Series 69, AGU, Washington D.C., pp. 117-131.

Perissinotto, R. & Duncombe Rae, C.M. 1990. Occurrence of anti-cyclonic eddies on the Prince Edward Plateau (Southern Ocean): effects on phytoplankton biomass and production. *Deep-Sea Research* **37**, 777-793.

Perissinotto, R., Duncombe Rae, C.M., Boden, B.P. & Allanson, B.R. 1990. Vertical stability as a controlling factor of the marine phytoplankton production at the Prince Edward Archipelago (Southern Ocean). *Marine Ecology Progress Series* **60**, 205-209.

Perissinotto, R., Laubscher, R.K. & McQuaid, C.D. 1992. Marine productivity enhancement around Bouvet and the South Sandwich Islands (Southern Ocean). *Marine Ecology Progress Series* **88**, 41-53.

Perissinotto, R., Lutjeharms, J.R.E. & Van Ballegooyen, R.C. 2000. Biological-physical interactions and pelagic productivity at the Prince Edward Islands, Southern Ocean. *Journal of Marine Systems* **24**, 327-341.

Pollard, R.T. & Read, J.F. 2001. Circulation pathways and transports of the Southern Ocean in the vicinity of the Southwest Indian Ridge. *Journal of Geophysical Research* **106**, 2881-2898.

Read, J.F. & Pollard, R.T. 1993. Structure and transport of the Antarctic Circumpolar Current and Agulhas Return Current at 40°E. *Journal of Geophysical Research* **98**, 12281-12295.

Rouault, M., Mélice, J.-L., Reason, C. & Lutjeharms, J. 2005. Climate variability at Marion Island, Southern Ocean, since 1960. *Journal of Geophysical Research* **110**, CO5007, doi:10.1029/2004JC00 2492.

Smith, V.R. & Steenkamp, M. 1990. Climatic change and its ecological implications at a subantarctic island. *Oecologia* **85**, 14-24.

Sparrow, M.D., Heywood, K.J., Brown, J. & Stevens, D.P. 1995. Current structure of the South Indian Ocean. *Journal of Geophysical Research* **102**, 5513-5530.

Stramma, L. 1992. The South Indian Ocean Current. *Journal of Physical Oceanography* **22**, 421-430.

Stramma, L. & Lutjeharms, J.R.E. 1997. The flow field of the subtropical gyre of the South Indian Ocean. *Journal of Geophysical Research* **102**, 5513-5530.

Sumner, P.D., Meiklejohn, K.I,. Boelhouwers, J.C. & Hedding, D.W. 2004. Climate change melts Marion Island's snow and ice. *South African Journal of Science* **100**, 395-398.

Tchernia, P. & Jeannin, P.F. 1980. Observations on the Antarctic East Wind Drift using tabular icebergs tracked by satellite *Nimbus F* (1975-1977). *Deep-Sea Research* **27**, 467-474.

Van Ballegooyen, R.C., Perissinotto, R., Ismail, A., Boden, B.R., Lucas, M., Allanson, B.R., *et al.* 1989. Data report of the second cruise of the Marion Offshore Ecological Study (MOES-II). *CSIR Report* **EMA-D 8910**, 16 pp. + figures + tables.

Weeks, S.J & Shillington, F.A. 1996. Phytoplankton pigment distribution and frontal structure in the subtropical convergence region south of Africa. *Deep-Sea Research I* **43**, 739-768.

CHAPTER 3

CLIMATE AND CLIMATE CHANGE

PETER C. LE ROUX

The climate of the sub-Antarctic islands, along with their geographic isolation and biotic influences, makes them unique (French & Smith 1985; Smith & French 1988). The highly oceanic nature of this climate, coupled with the strong influence of passing frontal systems creates an unusual climate where freezing temperatures can occur during any month, gale force winds blow most weeks and daily temperature maxima can occur during the middle of the night. The sub-Antarctic climate is even more interesting, however, because of the climate change currently being experienced in the region. Relative to the region's buffered thermal regime, the rapid warming in the sub-Antarctic represents an exceptional change (e.g. the rise in temperature over the last 50 years is roughly equivalent to 50% of the daily temperature range; Smith & Steenkamp 1990).

Due to its duration and the scarcity of similar datasets from the sub-Antarctic, the continuous weather record available from Marion Island since the 1950s provides a valuable and unique dataset. Marion Island's meteorological station was originally established to improve weather forecasting capabilities for South Africa, but has also helped to characterize the climate of the mid-latitudes of the Southern Ocean, and to describe recent climate change in the region.

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 39-64

3.1 The hyper-oceanic climate

Marion Island has one of the most oceanic climates in the world, termed hyper-oceanic by Van Zinderen Bakker (1978) and Smith & Steenkamp (1990). As on other sub-Antarctic islands, the Southern Ocean moderates daily and annual temperature fluctuations due to its high thermal inertia (Schulze 1971; Bonan 2002). In consequence, Marion Island has low daily (mean difference between maximum and minimum temperatures < 2°C in winter; < 3°C in summer) and seasonal (mean difference between mean winter and summer temperatures is 4.1°C) thermal variability (Fig. 3.1; Schulze 1971; Smith & Steenkamp 1990). Indeed, the oceanic climate of the Southern Hemisphere sub-polar terrestrial habitats distinguishes them from their Northern Hemisphere equivalents, which have continental climates with pronounced seasonality (French & Smith 1985). The dominant effect of the Southern Ocean on Marion Island's temperatures is evident from the tight correlation between sea surface temperature and air temperature (linear correlation coefficient for mean monthly temperatures = 0.54; Smith & Steenkamp 1990), with the island's mean annual air temperature differing little from mean sea surface temperatures (Schulze 1971; Smith & Steenkamp 1990; see also Mélice *et al.* 2003). Similarly, the island's narrow mean daily temperature range of only 1.9°C corresponds with the low amplitude of the daily temperature cycle in the surrounding open ocean (Schulze 1971). Another result of the ocean's thermal inertia is that the island's temperature regime lags behind solar radiation inputs, with the warmest temperatures being recorded in January, February and March, despite maximum solar radiation being received in December (Fig. 3.1a; Schulze 1971; see also Huntley 1970). Similarly, on average, daily temperature maxima are recorded just after midday, although can occur at nearly any time of the day due to the influence of frontal systems (Fig. 3.1b; Schulze 1971). A consequence of Marion Island's low mean annual temperature and buffered thermal variability is that sub-zero temperatures can be experienced during any month of the year, with temperatures regularly crossing the 0°C threshold (Schulze 1971; see also Boelhouwers *et al.* 2003). No meteorological records exist for Prince Edward Island, but its climate is assumed to be similar to that of Marion Island, although with slightly lower diurnal temperature variation due to its smaller size (Schulze 1971), as well as a weaker Föhn effect and less orographic cloud due to its lower maximum altitude (see below).

The close association between Marion Island's air and sea surface temperatures not only buffers temperature variation, but is possibly also responsible for some of the medium-term variation in the island's temperatures. This is likely since the passage of warm and cold oceanic eddies probably affects air temperatures on the island (warm or cold circulation anomalies take 1-2 months to drift past the island; see Mélice *et al.* 2003). Over a longer time scale, changes in the latitudinal position of the sub-Antarctic front (as well as other ocean fronts in the vicinity) could affect the island's temperature, because waters passing the island will be warmer when the front is located to the south of the island than when the front is north thereof (Ansorge & Lutjeharms 2000; Pakhomov & Chown 2003). The Antarctic Circumpolar Wave (ACW) could also influence inter-decadal variation in sea surface temperatures around Marion Island (Mélice *et al.* 2005), although it is not yet possible to confidently attribute long-term variation in sea surface temperatures to the ACW due to the relatively short duration (e.g. satellite data) and sparse nature (e.g. meteorological stations

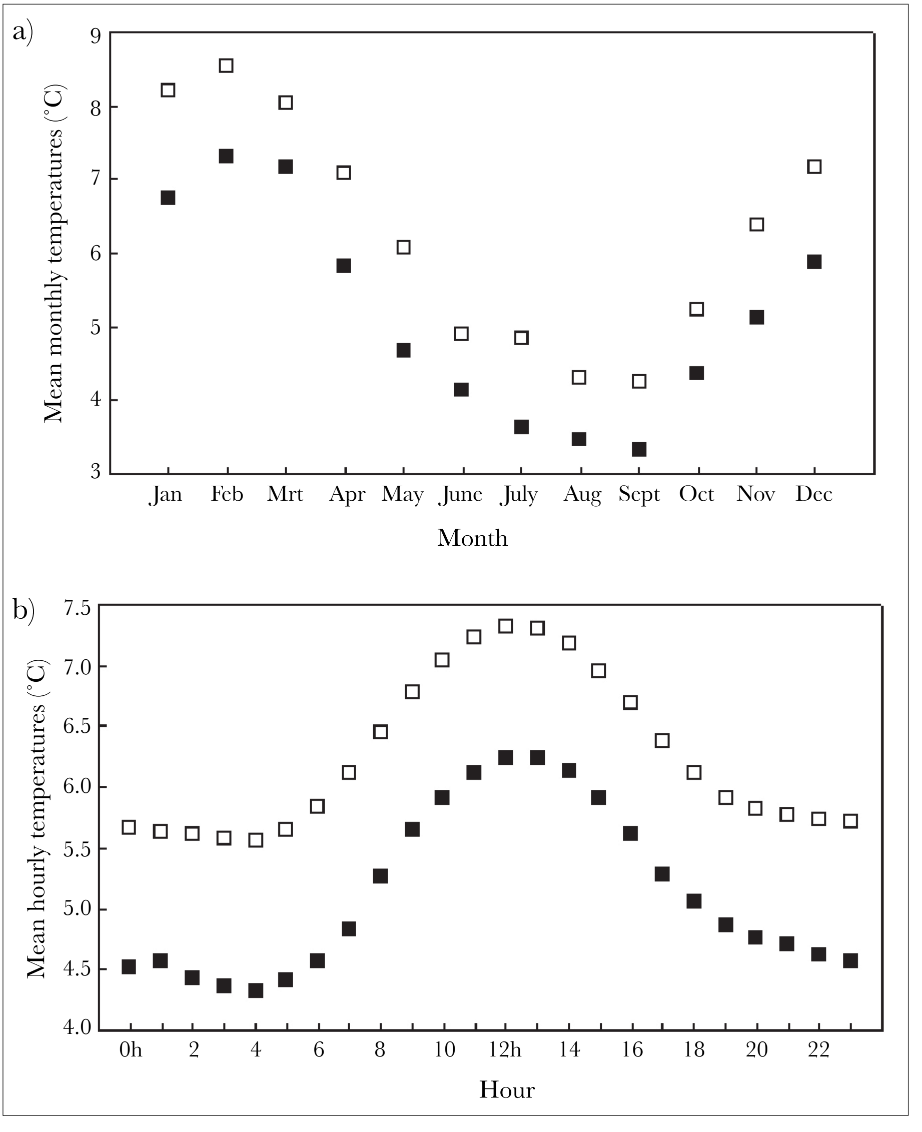


Figure 3.1 Temporal variation in air temperature (within Stevenson screen) on Marion Island. a) mean monthly temperatures, b) mean hourly temperatures. Filled symbols represent data from 1951-1961, empty symbols 1993-2003. Standard error bars excluded for clarity; for a) S.E. ranged between 0.026-0.032; for b) between 0.041-0.047.

in the sub-Antarctic and around Antarctica) of appropriate data (see Venegas 2003). The ACW is an eastward-moving circumpolar bimodal anomaly in sea surface temperature, air pressure and sea ice extent (White & Peterson 1996). However, the ACW was only clearly evident during the late 1980s and early 1990s (Venegas 2003; for Marion Island see Mélice *et al.* 2005), and even then had a weaker influence on sea surface temperatures in the Indian Ocean (including around Marion Island) than in the southern Pacific and Atlantic Oceans (Mélice *et al.* 2005).

Marion Island's climate is also distinguished by high precipitation and humidity, strong winds, and near complete cloud cover on most days – characteristics also exhibited by the other sub-Antarctic islands (French & Smith 1985; Bergstrom & Chown 1999). Marion Island receives precipitation as rainfall, snow, hail and mists, with some form of precipitation falling on most days and total annual precipitation averaging 1 975 mm in the 1990s. Rainfall is the dominant form of precipitation at lower altitudes (Schulze 1971), with rainfall events of ≤ 5 mm and > 5 mm occurring on roughly 45% and 35% of days, respectively (le Roux & McGeoch 2008). Graupel (a form of soft hail) and snow are common on the island, with the latter being far more common in winter months than in summer (Schulze 1971). Mists are possibly also an important form of precipitation, because they can lead to considerable condensation on some landforms and vegetation, especially when accompanied by strong winds (see e.g. Smith 1972). Precipitation is approximately evenly distributed throughout the year, although two minima can be distinguished; February-March and October-November, with the latter receiving the least precipitation (Rouault *et al.* 2005; see Fig. 3.2a). Weak diurnal variation in precipitation exists on Marion Island, with a higher probability of precipitation around sunrise and sunset, but only in the summer months (Schulze 1971). Marion Island's high precipitation is matched by near complete cloud cover (on average ≥ 75% of sky covered by cloud). The persistent cloud results in the island only receiving 20% (winter) – 30% (summer) of the possible solar radiation (Schulze 1971; Smith & Steenkamp 1990). A significant proportion of the cloud observed on the eastern side of Marion Island could be of orographic origin with both low stratus and lenticularis clouds being commonly observed (Schulze 1971; see also Thost & Allison 2005 for similar observations from Heard Island). Diurnal variation in cloud cover is not pronounced, with cloudier mornings in summer, but clearer mornings during winter months (Schulze 1971).

Relative humidity is high on the island (averaging 80%), although short periods (usually < 5 hours) of low (< 50%, even dropping below 20%) humidity can occur due to Föhn winds (Schulze 1971; Smith & Steenkamp 1990). This occurs on the leeward side of the island as air moves over the central plateau. As the air moves up the windward mountain slope, it cools at the saturated adiabatic lapse rate (on average 0.43°C per 100 m elevation on Marion Island; Schulze 1971) and loses moisture (because its moisture-holding capacity declines with a decline in temperature). When the desiccated air then descends the leeward slope of the mountain, its temperature increases rapidly at the dry adiabatic lapse rate (0.98°C per 100 m). Therefore, due to the differential rates of cooling and warming on the windward and leeward slopes (due to a change in the air's moisture content), the winds on the leeward side of the island can be much warmer and drier than the winds initially experienced on the windward slope (Schulze 1971; Bonan 2002). A Föhn wind can rapidly (within 30 minutes) raise air temperatures by 10°C and lower relative humidity by more than 20% (Schulze 1971). Föhn winds are also important on other sub-Antarctic Islands (Fabricius 1957): e.g. Macquarie (Tweedie 2000), Heard (Thost & Allison 2005) and Kerguelen Islands (Frenot *et al.* 1998; Frenot *et al.* 2001). On the latter island, these winds are thought to be responsible for the large (> 2 000 mm vs 800 mm) precipitation difference between the eastern and the western sides of the island (Frenot *et al.* 1998).

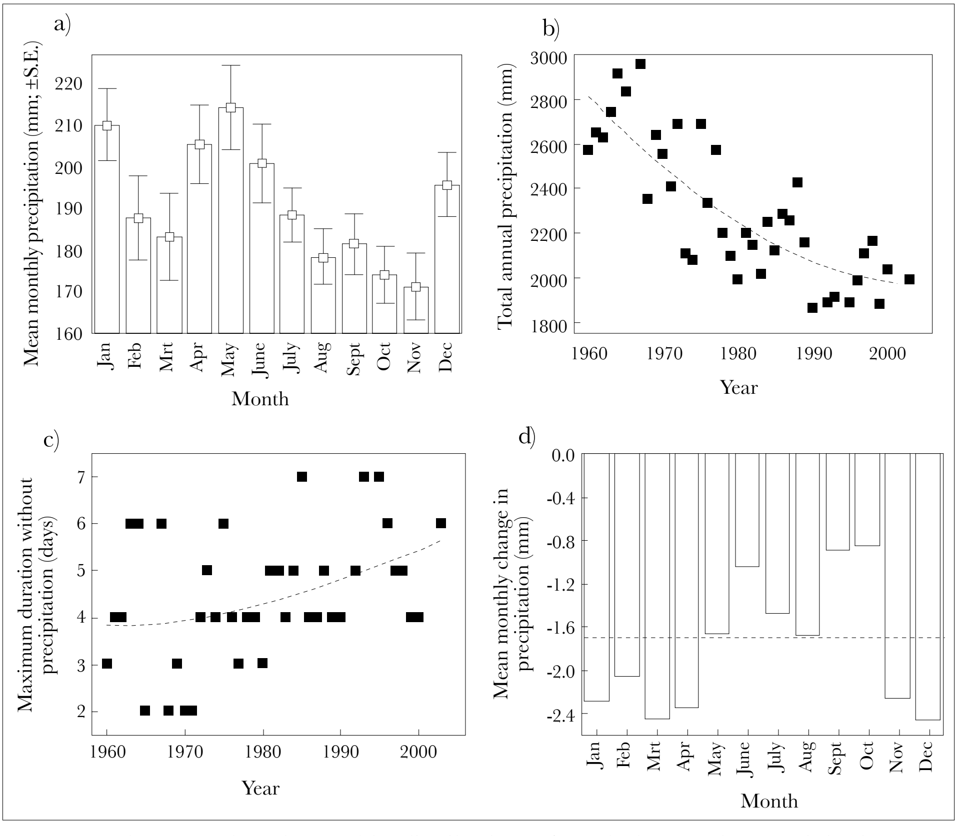


Figure 3.2 The annual and monthly distribution of, and changes in, precipitation on Marion Island, between 1960 and 2003. a) the mean monthly distribution of precipitation, b) the total annual precipitation, c) the duration of the maximum period without precipitation, d) the mean monthly change in precipitation. A negative exponentially-weighted curve (dashed line) has been fitted to the data in graphs b) and c). In d) the mean rate of change in precipitation is not significantly different from zero only in May, June, September and October. b) and c) with kind permission from Springer Science and Business Media (after minor modifications) from le Roux & McGeoch (2008).

Marion Island has a windy climate, in accordance with its position in the "roaring forties", experiencing gale force winds (> 15 m sec^{-1}) on more than 100 days per year (Schulze 1971). Extended periods (> 12 hours) of continuous gales are not uncommon and calm periods are comparatively rare (< 10% of observations, Schulze 1971). Late summer winds are generally weaker (with disproportionately few gale strength winds) and have a stronger northerly component (Schulze 1971; Rouault *et al.* 2005). Diurnal variation in wind speed is much clearer, with faster wind speeds during the day than at night (Blake 1996), particularly in summer (Schulze 1971). The dominant wind direction recorded at the meteorological station is from the west, as expected from the island's location in a belt of strong, large-scale westerly atmospheric circulation, with north-westerlies being the strongest (averaging > 10 m sec^{-1}) and most common winds (60% of observations; Schulze 1971; see also Rouault *et al.* 2005). Winds from south-west are a little weaker (7 m sec^{-1}) and the second most frequent (20% of observations; Schulze 1971). By contrast, winds with an easterly component are rare (< 10%) and relatively weak (mean speeds of 3-6 m sec^{-1}; Schulze 1971). These winds differ not only in frequency of occurrence and speed, but also in temperature and moisture content, with winds with a northerly component being warmest (coming from the warmer sub-tropical zone) and carrying the most moisture (Schulze 1971; Hugo *et al.* 2004). By contrast, southerly winds comprise cold and dry Antarctic air (Schulze 1971; Smith & Steenkamp 1990). Therefore, the climate of Marion Island is oceanic and, on average, cold, cloudy, wet and windy. However, an understanding of the circulation patterns around the island is required to recognize the factors responsible for short-term variation in weather, as well as longer-term changes in climate.

3.2 Atmospheric circulation and the frontal nature of the weather

In the Northern Hemisphere, the longitudinally-orientated continents provide a physical barrier to atmospheric and oceanic circulation. However, in the Southern Ocean strong eastward-flowing atmospheric and oceanic circumpolar circulation occurs due to the lack of such land masses at mid- and high latitudes of the Southern Hemisphere (Bonan 2002; Hall & Visbeck 2002). The fastest winds in this eastward circulation occur within the southern polar jet stream, which is a relatively narrow air current near the troposphere-stratosphere boundary which dominates mid-latitude circulation (Bonan 2002; Hall & Visbeck 2002). The modal latitudinal position of the jet stream varies with time, and is related to the meridional (north-south) pressure and temperature gradients between the ocean-dominated mid-latitudes and the polar continental latitudes (Hartmann *et al.* 2000; Hall & Visbeck 2002; although changes in mean ocean temperature could also play a role; Kushner *et al.* 2001). Even small changes in the latitudinal position of the southern polar jet stream have implications for large areas of the Southern Hemisphere, due to its effects on atmospheric and oceanic circulation (Fyfe & Saenko 2005). For example, a southward shift in the modal position of the jet stream strengthens westerly winds at high Southern Hemisphere latitudes, but weakens those in the mid-latitudes (25-45° S; Hall & Visbeck 2002; Gillett & Thompson 2003; Rouault *et al.* 2005) with implications for air and ocean temperatures and currents (Hall & Visbeck 2002).

Variation in the meridional pressure gradient, and therefore in the latitudinal position of the southern polar jet stream, is dominated by two processes: the Semi-Annual Oscillation (SAO) and the Southern Annular Mode (SAM). Both describe changes in the atmospheric mass (i.e. pressure anomalies) between mid- and high Southern Hemisphere latitudes, and have a similar spatial structure (Ainley *et al.* 2005; Rouault *et al.* 2005). The SAM and SAO can be considered distinct but related measures of the same phenomenon (i.e. the latitudinal gradient in pressure and temperature), with the SAO describing the magnitude of intra-annual variation and the SAM measuring interannual variation in the strength of the same gradient (Ainley *et al.* 2005; CLIVAR 2005; Raphael & Holland 2006).

The SAO measures the magnitude of the half-yearly cycle in air pressure, temperature and westerly winds at mid- and high latitudes of the Southern Hemisphere. This biannual cycle is driven by an out of phase relationship between the annual temperature cycles between the ocean-dominated mid-latitudes and the ice-dominated high latitudes (due to differences in heat storage, and therefore differential rates of spring warming and autumnal cooling, between Antarctica and the surrounding oceans; Van Loon 1967; Van den Broeke 1998). As a result a twice-yearly peak in the latitudinal temperature and pressure gradients exist (i.e. temperature and air pressure at mid-latitudes exceed the temperature and air pressure at high latitudes by greater than average amounts during spring and autumn), causing a poleward shift of both the jet stream and the circumpolar trough (a belt of low pressure and strong westerly winds encircling the globe at high southern latitudes) (Van Loon 1967). It is the strength of these temperature and pressure gradients that the SAO measures, with a common index being the difference between the zonally averaged (i.e. across all longitudes) 500-hPa temperatures at 50° and 65° S (Van Loon 1967; Meehl *et al.* 1998). A weaker SAO therefore indicates a shallower latitudinal pressure and temperature gradient, and suggests less month-to-month variability in the latitudinal position of the jet stream than a stronger SAO (Meehl *et al.* 1998).

The SAM (also known as the Antarctic Annular Oscillation, AAO) appears to determine the largest proportion of the long-term climate variability in the Southern Hemisphere south of 20° S (Thompson & Wallace 2000; Thompson & Solomon 2002). It measures the non-seasonal change in the atmospheric pressure between high and mid-latitudes of the Southern Hemisphere, and describes changes in the extent of the polar vortex (the large cyclonic system driving westerly circulation around the pole) and the associated changes in the strength of the westerly winds (Thompson & Wallace 2000; Hall & Visbeck 2002). A positive phase of the SAM is associated with a steeper latitudinal pressure gradient (e.g. measured between 40° and 60° S; Raphael & Holland 2006), and therefore with the southward movement of the jet stream, stronger high latitude circumpolar circulation and faster westerly winds around continental Antarctica (i.e. stronger polar vortex), but weaker westerly circulation at mid-latitudes (Hall & Visbeck 2002; Thompson & Solomon 2002). In recent times, anthropogenic ozone depletion (cooling the troposphere over continental Antarctica) and increased greenhouse gas concentrations (raising tropospheric temperatures globally) have altered the strength and the seasonality of the latitudinal temperature and pressure gradient, affecting the strength of the SAM (Marshall *et al.* 2004). Changes in the SAM have been particularly evident during spring and summer months due to ozone loss being concentrated in spring (Hartmann *et al.* 2000; Marshall *et al.* 2004).

The presence of Rossby waves introduces additional variation to the position of the jet stream. Rossby waves (also known as long, planetary or westerly waves) are large-scale wave perturbations (wave lengths exceeding 2 000 km) in the westerly winds in the middle and upper troposphere, which can be observed as a meandering of the jet stream (Lutgens & Tarbuck 1995; Tyson & Preston-Whyte 2000; O'Hare *et al.* 2005). These waves cause regular distortions in the speed and direction of the air flow, with the degree of distortion varying through time (O'Hare *et al.* 2005). When the westerly air flow is smooth (i.e. westerly winds have a high zonal index, indicating that the air flow is predominantly zonal [west to east]), wind speeds are high and weather systems are rapidly transported eastwards. However, as the amplitude of the Rossby wave increases, westerly flow becomes slower and more distorted (i.e. a low zonal index state, indicating that meridional air flow [north-south] is increasing). Thus variation in the southern polar jet stream comprises both variability in its modal latitudinal position (affected by the latitudinal pressure and temperature gradients; measured by the SAO and the SAM) and variability in the distortion of its flow (due to Rossby waves).

Both the latitudinal position and the distortion of the jet stream are important for the weather of the mid-latitudes because the southern polar jet stream is a major source of both cyclones and anticyclones (transient atmospheric eddies) (Hall & Visbeck 2002). The magnitude of Rossby waves within the jet stream influences the development of eddies, with eddy formation being most likely during low zonal index state flow (i.e. when the wave distortions are large and unstable enough that large cells of air can become detached from the jet stream) (O'Hare *et al.* 2005). During these periods of disrupted air flow, cyclones tend to form ahead of areas of low air pressure (troughs in the Rossby waves, i.e. zones of surface convergence of winds; Tyson & Preston-Whyte 2000; O'Hare *et al.* 2005). In particular, the cyclones and anticyclones passing near Marion Island originate from the south Atlantic Ocean between 30° and 40° S (Schulze 1971), one of the two foci for extra-tropical cyclogenesis in the Southern Hemisphere (Simmonds & Keay 2000a). Both of these types of atmospheric circulation anomalies alter the prevailing westerly airflow, drawing warmer sub-tropical and/or cooler sub-Antarctic air masses over Marion Island (Smith & Steenkamp 1990; Smith 2002).

By locally altering wind patterns, transient cyclones can dominate short-term weather variation on Marion Island if they pass close to the island. Cyclones (also known as depressions or low pressure systems) are characterized by clockwise circulation and the upward movement of the air column, and are therefore associated with cloudy weather. After their formation, cyclones move to the south-east, usually passing over, or to the west of Marion Island (Fig. 3.3). As a cyclone approaches the island, its associated clockwise winds draw warm sub-tropical air over the island, leading to a warm pre-cyclonic period (Smith & Steenkamp 1990). The pre-cyclonic phase is also marked by an increased probability of precipitation and high cloud cover (since as the air moves upwards in the cyclone it cools and saturates, leading to cloud formation) as well as a strengthening of north-westerly winds. Once past Marion Island, a cyclone forces cooler, dry Antarctic air over the island, causing cold and clear conditions with weak south-westerly winds. The path followed by each cyclone, relative to Marion Island, determines the relative duration of pre- and post-cyclonic conditions (Fig. 3.3), and therefore the effect the cyclone will have on the island's weather. A cyclone passing far south of the island has a longer but less intense pre-cyclonic period, followed by a shorter post-cyclonic period (Smith & Steenkamp 1990; Smith 2002). In addition, when cyclone tracks are displaced southwards, the island is also affected more strongly by the distant, near-permanent South Indian Ocean anticyclone, which forces warmer winds with a more northerly component over Marion Island (Rouault *et al.* 2005). By contrast, when cyclones pass over the island, more intense pre- and post-cyclonic conditions are experienced, with a roughly equal duration of each. As a result, with the passing of each cyclone (roughly 100 per year; Smith 2002), Marion Island experiences a recurrent switch from wet, warm pre-cyclonic days to cold, clear, dry post-cyclonic days, with the duration in each state determined by the cyclone's path (storm track) (Smith & Steenkamp 1990).

By contrast with cyclones, anticyclones move eastward after formation, usually passing far north of Marion Island (Schulze 1971). They are high pressure systems (i.e. predominantly downward movement of air), surrounded by anti-clockwise rotating winds. As a result, anticyclones are associated with clear weather (colder higher altitude air becomes relatively drier as it warms when moving to lower altitudes). The effect of these transient anticyclones on the island's weather is weak, except when storm tracks have shifted far southwards, bringing the cores of the anticyclones closer to Marion Island (Schulze 1971). By contrast, the near-permanent South Indian Ocean anticyclone, despite being centred far to the north-east of Marion Island, can have strong effect on the island's climate during periods of weak or infrequent cyclones (Rouault *et al.* 2005; see also Fig. 3.3). Thus, both cyclones and anticyclones have considerable effects on Marion Island's climate, depending on the proximity of storm tracks to the island.

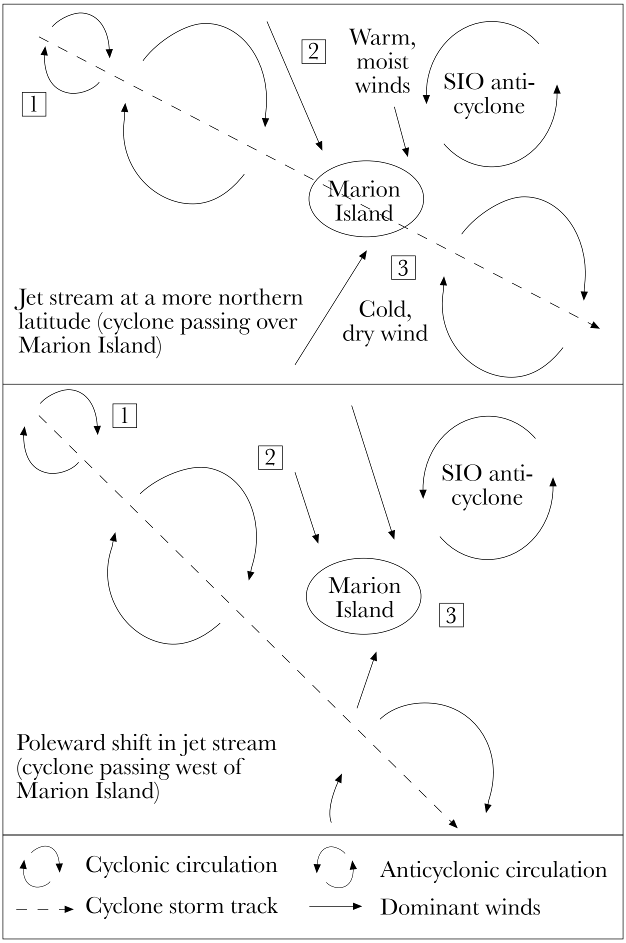


Figure 3.3 A comparison of the wind patterns generated by different cyclone storm tracks. The numbers indicate the eastward progression of the cyclones. The length of the straight arrows indicate the relative changes in wind strength between the two panels. SIO anticyclone – South Indian Ocean anticyclone.

Top: a more northerly storm track (i.e. during winter) causes an approximately equal duration of pre- (2) and post-cyclonic conditions (3). Strong north-westerly (2) and south-westerly (3) winds are experienced. Bottom: a poleward shift in storm tracks causes longer but less intense pre-cyclonic conditions (2). The duration of post-cyclonic conditions is shorter (3). The SIO anticyclone has a stronger influence, increasing the northerly component of winds, bringing warm, moist sub-tropical air over the island. If a cyclone passes north of the island, the opposite pattern would occur, with the duration of post-cyclonic conditions exceeding that of the pre-cyclonic conditions.

The position of the southern polar jet stream strongly determines the position of storm tracks (Kushner *et al.* 2001; Hall & Visbeck 2002). Therefore, a southward shift of the jet stream leads to a poleward shift in storm tracks, altering the relative effects of the passing cyclones and anticyclones on Marion Island's weather (Rouault *et al.* 2005). This effect is evident in the seasonal variation in storm tracks past Marion Island (storm tracks pass further south in summer months, following the poleward shift of the mean pressure distribution; Schulze 1971). The correlation between storm track position and jet stream latitude is also known over larger temporal and spatial scales in the Southern Hemisphere (Kushner *et al.* 2001). Marion Island, along with Heard Island, lies close to the mean cyclone storm track, and therefore their climates probably have a stronger frontal nature than some of the other sub-Antarctic islands (e.g. Macquarie Island lies in a zone of cyclone deterioration, while Bouvet and the Crozet Islands are located relatively far from the passage of most storm tracks; see Simmonds & Keay 2000a). Thus, despite broad similarity in climate across the sub-Antarctic, the proximity of each island to storm tracks does cause some differences in their climates. While the latitude at which these eddies are formed is determined by the latitudinal position of the jet stream, the subsequent movement of an eddy is also strongly affected by the Rossby waves propagating along the jet stream (Lutgens & Tarbuck 1995; O'Hare *et al.* 2005). As a result, both the latitudinal position of the jet stream and the amplitude of Rossby waves within the jet stream are important for the formation and subsequent movement of transient eddies.

Therefore, the passage (and number) of passing atmospheric eddies and the position and state of the jet stream strongly affect Marion Island's climate, with the short-term alternation between warm-wet and cold-clear weather being determined by the passage of individual frontal systems. Longer-term climate is affected by the broader-scale circulation patterns that determine the position of the southern polar jet stream and the number, intensity and mean position of the frontal systems that the jet stream spawns.

3.3 Spatial variation in climate on Marion Island

> On numerous occasions I found it necessary to cover the final fifty metres to the summit of a volcano on hands and knees for fear of being blown off, while on my return to the meteorological station have found that only a gentle breeze had been recorded. (Huntley 1970)

Spatial variation in Marion Island's climate is widely recognized (e.g. Schulze 1971; Chown & Avenant 1992; Blake 1996), but is as yet still not completely understood (a problem not unique to Marion Island; see e.g. Thost & Allison 2005). Data from the island's meteorological station describes the climate inside a Stevenson screen located near the coast on the eastern side of the island (Schulze 1971). However, since weather conditions vary with topography, aspect, altitude and recording height (Bonan 2002; see also e.g. Beggs *et al.* 2004), considerable variation in climate occurs across the island.

The nature of climatic differences between the different sides of the island have long been speculated about (e.g. Schulze 1971; le Roux 2004; Rouault *et al.* 2005), but little comparable meteorological data exist with which to test these ideas. Due to the prevalence of westerly winds, it has been hypothesized that climate differs most between the eastern (predominantly leeward) and western (windward) sectors of the island. The western sector has been suggested to have stronger and less variable winds, higher humidity and rainfall, and less variable temperatures (Rouault *et al.* 2005; see also Gremmen 1981). Additionally, the west should rarely experience Föhn winds (which are not uncommon on the east), and could have a different pattern of cloud cover (Schulze 1971; see also Thost & Allison 2005 for Heard Island). The only available data suggest that, indeed, temperatures are less variable on the western side of the island relative to those on the east, with warmer temperatures during winter and cooler temperatures during summer (temperatures in *Azorella selago* cushions on both sides of the island; Nyakatya & McGeoch 2008; see Fig. 10.7a in McGeoch *et al.* 2008). Observations from other sub-Antarctic islands suggest that climate can, in some situations and for some climate parameters, differ greatly between eastern and western sectors. For example, annual precipitation differs more than four-fold between the eastern and western parts of Kerguelen Island (due to a pronounced Föhn effect; Frenot *et al.* 1998). On Heard Island, large differences in climate are observed between the eastern and western sectors, with the eastern slopes experiencing faster and more variable winds (due to the formation of Von Karman vortices in the lee of the island; Beggs *et al.* 2004), and lower cloud cover and precipitation (Hughes 1987). By contrast, temperature does not differ between the eastern and the western sides of Macquarie and Kerguelen Islands (Frenot *et al.* 1998; Davies & Melbourne 1999; wind speed also does not differ between the eastern and western sectors on Macquarie Island; Davies & Melbourne 1999). Thus on Marion Island significant topographically-generated differences in climate are likely between the eastern and western sides of the island, although these require more extensive documentation.

Altitudinal variation in climate on Marion Island has also been poorly explored (see Fig. 10.6 in McGeoch *et al.* 2008 for some observed and hypothesized altitudinal gradients). Mean altitudinal lapse rates of 4.5°C per 1 000 m in winter and 4.0°C in summer have been calculated from radiosonde data collected on the island (Schulze 1971), with surface data showing slightly higher rates (Boelhouwers *et al.* 2008). Research by Blake (1996) confirmed that higher altitudes are both cooler and windier, with higher cloud cover and a greater daily temperature range than lower elevations. In agreement with Blake's (1996) speculation, the decline in temperature appears to be mainly due to daily minimum temperatures dropping with increasing altitude, while daily thermal maxima are independent of elevation (soil temperatures: Slabber & Chown 2004; see also Boelhouwers *et al.* 2003 for air and soil temperatures). This difference in the behaviour of the thermal minima and maxima explains the wider temperature range at higher elevations (also observed on Heard Island; Allison & Keage 1986; but not observed for within-*Azorella selago* cushion temperatures on Marion Island across an altitudinal range of +400 m; Nyakatya & McGeoch 2008). Interestingly, this pattern can sometimes be reversed during winter at high altitudes, where snow cover strongly buffers temperatures, causing a very narrow daily temperature range (Blake 1996, but see also Boelhouwers *et al.* 2008). Increasing wind speed with altitude is another consistent trend observed among the sub-Antarctic islands (Blake 1996; Davies & Melbourne 1999; Beggs *et al.* 2004). Altitudinal trends for precipitation on Marion Island are less clear than for other weather parameters and suggested that maximum precipitation occurs at mid-altitudes, although this could be an artifact of topographical differences between observation sites (Blake 1996). On Macquarie Island, precipitation varies independently of altitude, but relative humidity and rates of evapotranspiration both increase with elevation (Tweedie 2000). Therefore, on that island, the rate of moisture loss (via evaporation from the soil surface and transpiration by plants) is fastest at high altitudes, possibly due to higher wind speeds, despite the air moisture increasing with elevation. Wind direction also differs between altitudes on Marion Island, although this is probably due to topographical differences between sites (Blake 1996; see also Chown & Avenant 1992). These results, therefore, indicate that distant locations on the island can experience rather different weather, but again that more comprehensive climate recording and modelling is needed for the island.

Even sites separated by smaller distances can have distinctly different weather conditions. Indeed, at these finer-scales, microclimate and the climate recorded within a Stevenson screen (“macroclimate”) can be decoupled, with microclimatic conditions varying nearly independently of macroclimate. As a result, steep temperature, moisture and wind gradients can be observed over very short distances. For example, temperatures within *A. selago* cushions and *Poa cookii* tillers can be 1-4°C warmer than those recorded inside a nearby Stevenson screen (Chown & Crafford 1992; see also Fig. 10.2 in McGeoch *et al.* 2008). Similarly, the thermal environment within mouse burrows in *Blechnum penna-marina* and *A. selago* is buffered relative to ambient air temperature (Avenant & Smith 2003). Due to the highly oceanic nature of Marion Island’s climate, these variations in microclimate are important determinants of community properties (since macroclimate differs relatively little between sites; Smith & French 1988). For example, despite little above-ground vegetation on higher altitude scoria cones, within the shelter created by the blocky substrate a “hypolithic” community of mosses, liverworts and invertebrates survives (Van Zinderen Bakker 1978).

The difference between macro- and microclimate varies between microhabitats, with the degree of shelter from the wind and the amount of solar insolation received being the most important determinants of microclimate (Chown & Crafford 1992). Indeed, microclimate temperature is most decoupled from macroclimate where a habitat is sheltered from the wind, with the difference exaggerated on clear, cloudless days (Van Zinderen Bakker 1978; Smith 1992). Slope aspect also affects microclimate, with north-facing slopes warming more than south-facing slopes (Huntley 1971). Similarly, the northern aspects of *A. selago* cushions may be warmer than their southern portions, with wind direction also affecting the microclimate in different sectors of a single cushion (Hugo *et al.* 2004; McGeoch *et al.* 2008). Thus the climate on Marion Island shows considerable spatial variation, across both large and small scales.

3.4 Contemporary changes in climate

Over the last half century Marion Island has experienced rapid changes in climate, with warming taking place at more than twice the mean global rate. The island may thus be a true sentinel for future changes in climate (Bergstrom & Chown 1999). Relative to the island's diurnal and seasonal climate variability, these changes are considerable (Smith & Steenkamp 1990), and have already had measurable impacts on the physical (lower peat moisture levels; Chown & Smith 1993; reduction in the size of the ice cap, and the disappearance of a permanent snow line; Sumner *et al.* 2004) and biotic features (higher *Uncinia compacta* cover; Chown & Smith 1993; changes in productivity; Pakhomov *et al.* 2004; see also le Roux & McGeoch 2008) of the Prince Edward Islands. In addition, if current climate trends continue, further ecological changes are predicted (e.g. increased house mouse abundance, with negative effects on nutrient cycling and the abundance of macro-invertebrates and Lesser Sheathbills; Smith & Steenkamp 1990; Chown & Smith 1993; Huyser *et al.* 2000; increased stem senescence in *A. selago*; le Roux *et al.* 2005; changes in the structure of the micro-invertebrate community associated with *A. selago*; McGeoch *et al.* 2006; Chown *et al.* 2007).

The air and sea (surface and sub-surface) temperatures at mid-latitudes of the Southern Ocean have warmed significantly between the 1950s and 2000s, although at a spatially and temporally variable rate. The most pronounced changes in sea temperatures have occurred within the Antarctic Circumpolar Current, with sub-surface sea temperatures rising by 0.17°C between the 1950s and 1980s (Gille 2002). Around Marion Island greater warming occurred with sea surface temperatures increasing by 1.4°C between 1949 and 1999 (Mélice *et al.* 2003). Matching the increased sea temperatures, air temperature on Marion Island increased by 1.2°C over the same period (Fig. 3.4a; Smith 2002; le Roux & McGeoch 2008). This high rate of warming is relatively consistent among the sub-Antarctic islands (Frenot *et al.* 1997; Tweedie & Bergstrom 2000; Weimerskirch *et al.* 2003; Thost & Allison 2005), and is comparable to the warming experienced on the Antarctic peninsula over the same period (Vaughan *et al.* 2003), suggesting a regional change in climate, rather than, for example, a change in distant ocean processes (Reason & Lutjeharms 2000). On Marion Island, daily maximum and minimum temperatures have risen at a similar rate to mean temperatures, resulting in a roughly constant daily temperature range (le Roux & McGeoch 2008). This is an unusual pattern because globally, thermal minima are increasing faster than maxima, leading to a narrowing of the daily temperature range (IPCC 2001). Annual maxima and minima on Marion Island have also risen, with the five warmest years on record in the last decade (1996-2000; le Roux & McGeoch 2008; see also Smith 2002). In addition, Marion Island's thermal regime has become less variable over this period (despite daily temperature ranges not decreasing), with decreased day-to-day variability in temperatures (Fig. 3.4b; le Roux & McGeoch 2008). Ocean temperatures have risen significantly in all months, with minimum warming in the mid-winter months (June and July; Rouault *et al.* 2005). By contrast, there has been a clear seasonal pattern to increasing air temperatures, with the greatest warming in the late summer months (Fig. 3.4c; Smith 2002; Rouault *et al.* 2005).

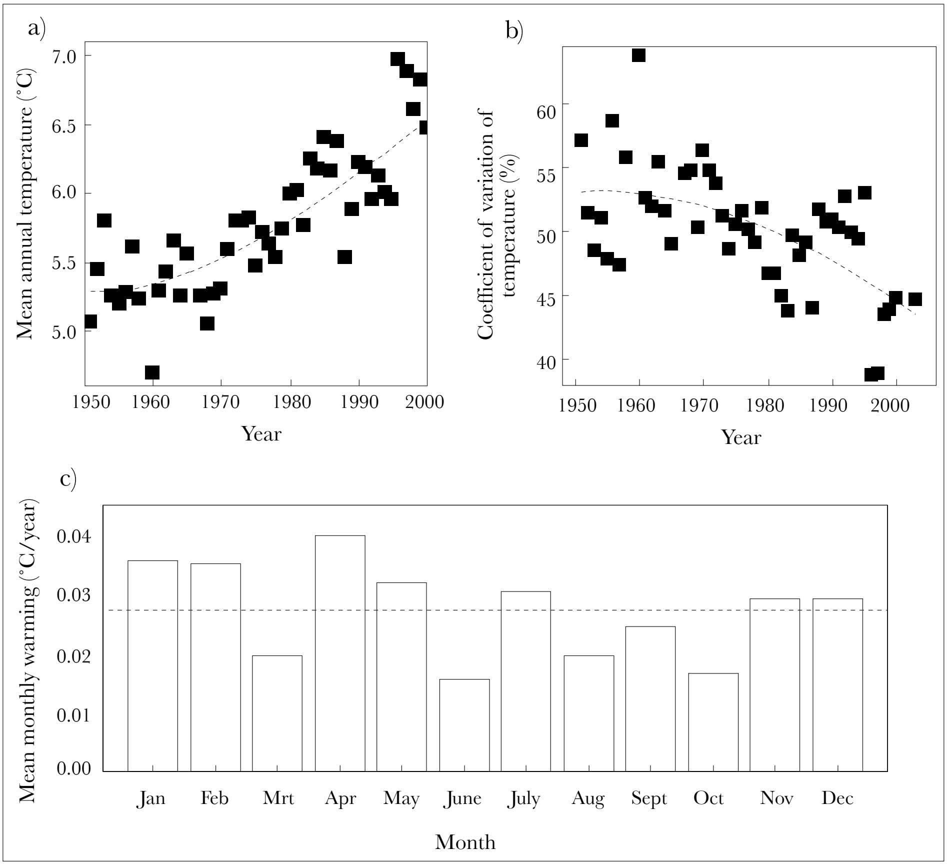


Figure 3.4 Changes in temperature on Marion Island, between 1951 and 2003. a) mean annual temperature, b) annual coefficient of variation for 08h00 temperatures, c) mean warming rate split by month (the warming trend was significant in all months, except June). A negative exponentially-weighted curve (dashed line) has been fitted to the data in a) and b). The dotted line in c) represents the mean monthly rate of warming. a) and b) with kind permission from Springer Science and Business Media (after minor modifications) from le Roux & McGeoch (2008).

Over the same period Marion Island's precipitation has decreased significantly (Fig. 3.2b), in contrast with other sub-Antarctic islands (e.g. no trend on Kerguelen Island; Frenot *et al.* 1997; increased precipitation since the 1970s on Macquarie Island; Kirkpatrick & Scott 2002). The decline in precipitation is a result of both fewer and smaller precipitation events (le Roux & McGeoch 2008). The mean and maximum duration between precipitation events have also increased (Fig. 3.2c; le Roux & McGeoch 2008; see also Rouault *et al.* 2005). These changes therefore represent a considerable shift in the island's precipitation patterns (i.e. the timing, frequency and size of events). The reduction in precipitation has been most pronounced between November and April (Fig. 3.2d), although the increase in the number of days without precipitation has been more uniform throughout the year (increases of up to six days per month; Rouault *et al.* 2005; see also Smith 2002; le Roux & McGeoch 2008). Mean cloud cover has decreased over the last 50 years, although it peaked in the 1970s before declining to current levels (Fig. 3.5a). These changes in precipitation and cloud cover, in unison with the warmer temperatures, appear to have driven the loss of Marion Island's permanent snowline, which in the 1960s occurred down to 500-850 m a.s.l. (Huntley 1970; Sumner *et al.* 2004). These trends are also thought to be responsible for the melting of much of Marion Island's ice plateau (Sumner *et al.* 2004), as well as similar changes in the ice caps and glaciers on Heard and Kerguelen Islands (Allison & Keage 1986; Frenot *et al.* 1993; Budd 2000).

Analyses of wind data suggest that wind patterns on Marion Island have also changed, with an increasing northerly component. Since the 1960s, mean wind direction has shifted northward during late summer and autumn, with

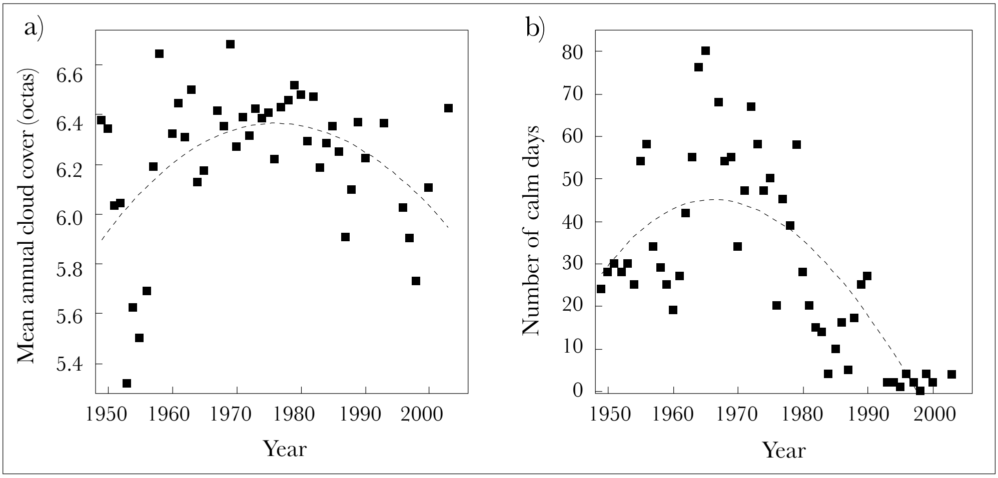


Figure 3.5 Changes in cloud cover and wind speed on Marion Island, between 1949 and 2003. a) mean cloud cover (08h00 observations), b) number of wind still measurements (08h00 observations). A negative exponentially-weighted curve (dashed line) has been fitted to the data in both graphs. With kind permission from Springer Science and Business Media (after minor modifications) from le Roux & McGeoch (2008).

shifts in some months exceeding 20° (based on NCEP reanalysis climate data; Rouault *et al.* 2005). Wind speeds on Marion Island increased during the 1970s, but decreased again after peaking in the mid-1980s (le Roux & McGeoch 2008). However, comparing wind speed between 1960-70 and 1980-2000 still shows higher meridional wind speed in the latter period (but no difference for zonal (east-west) winds; Rouault *et al.* 2005). Thus, over the last 50 years, northerly winds have become stronger and more frequent, while westerly winds have become less common (although not weaker). Despite the peak in wind speed in the 1980s, variability in wind speed declined throughout the period, possibly due to the considerable drop in the number of calm periods (Fig. 3.5b). Therefore, the recent changes in Marion Island's wind patterns differ between parameters, with peak wind speed in the 1980s, maximum calm days in the 1960s, declining wind variability since the 1950s, and different trends for meridional and zonal winds. These trends partly agree with the hemisphere-wide trends for faster westerly winds around 60° S, and increasing northerly components to winds around 40° S (Kushner *et al.* 2001; Hall & Visbeck 2002).

Overall, these changes have lead to non-linear changes in Marion Island's climate system as a whole. Over the last five decades, Marion Island's climate has become consistently warmer (with lower thermal variability) and drier (with increased variability in precipitation), with winds which are more frequent (fewer calm days) and less variable (Fig. 3.6; le Roux & McGeoch 2008). These climate trends have occurred roughly concurrently, with approximately linear trends over time, and comprise a trend complex (i.e. a group of climate parameters with corresponding trends over time; Huth & Pokorná 2005). However, over the same period, changes in wind speed have been distinctly non-linear, and represent a second trend complex. Therefore, climate change on Marion Island is not a simple process of all variables responding at the same rate to the same forcing, but rather an example of where trends in climate parameters are decoupled (e.g. roughly linear changes in temperature, precipitation and wind direction, but non-linear (parabolic) trends in wind speed). This is especially pronounced since wind variables usually form a single trend complex, with concurrent changes in wind speed and direction usually observed (Huth & Pokorná 2005).

3.5 Mechanisms driving sub-Antarctic climate change

The coincident increases in temperature across the sub-Antarctic since the 1960s suggest that shifts in large-scale circulation patterns are responsible for recent changes in climate. Specifically, changes in regional atmospheric circulation appear to be responsible for the changes in Marion Island's climate (Reason & Lutjeharms 2000). In particular, the increased influence of the South Indian Ocean anticyclone on air and ocean currents in the mid-southern latitudes around Marion Island seems to be the most important recent change to regional circulation (Rouault *et al.* 2005). While the strength and position of the South Indian Ocean anticyclone has not changed over this period, its influence on the climate of Marion Island has increased during recent years due to the weaker influence of transient cyclones closer to the island (e.g. see Fig. 3.3). Thus, due to the weakening effect of transient cyclones in recent years, the South Indian Ocean anticyclone has increased the advection of warmer tropical water into the mid-latitudes of the sub-Antarctic by strengthening the Agulhas current (Reason & Lutjeharms 2000; Rouault *et al.* 2005). This could be responsible for the apparent southward shift of the sub-Antarctic front, resulting in warmer oceanic waters in the vicinity of Marion Island (Pakhomov & Chown 2003; see also Hall & Visbeck 2002).

The weakening of the effect of passing cyclones on Marion Island's climate appears to be due to a reduction in the number of sub-Antarctic cyclones as well as a poleward shift in mean cyclone storm track position. Between 1970 and 1997, the number of cyclones in the sub-Antarctic declined by 10% (Fyfe 2003), probably as a result of the warming of the Southern Hemisphere (Simmonds & Keay 2000b). Changes in the position of cyclone storm tracks

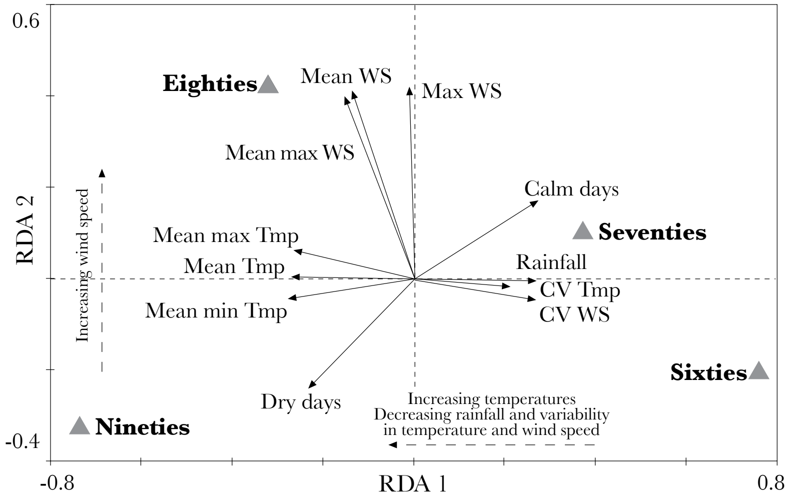


Figure 3.6 Ordination (Redundancy analysis) of annual climate (excluding 1950s due to lack of precipitation data for that period; axes explain 33.2 + 8.6% of annual variability) showing the centroid for each decade (triangles; i.e. the average climate for each decade) and fitted climate variables (arrows). The distance between centroids approximates the dissimilarity in climate between decades. Climate arrows pointing in the direction of a particular centroid indicate that the specified climate parameter had the highest mean value during that decade, with arrow length equal to the relative contribution of that climate variable to the ordination subspace definition. Dashed arrows indicate hypothesized gradients across the ordination space. CV – coefficient of variation, Dry days – number of days without precipitation, Max – maximum, Min – minimum, Tmp – temperature, WS – wind speed. With kind permission from Springer Science and Business Media (after minor modifications) from le Roux & McGeoch (2008).

have also had an effect on the current climate trends. Indeed, a pronounced southward shift in storm tracks is thought to have accompanied the poleward shift of the southern polar jet stream in recent years (indicated by increasingly positive values of the SAM; Kushner *et al.* 2001; Rouault *et al.* 2005). This suggests that anthropogenically-driven stratospheric ozone depletion (cooling the Antarctic) and increased greenhouse gas concentrations, causing steeper latitudinal temperature and pressure gradients (i.e. increasing the SAM and shifting the jet stream polewards), are at least partly responsible for changes in the storm track positions (Thompson & Solomon 2002; Marshall *et al.* 2004; Shindell & Schmidt 2004), and therefore for increasing the influence of the South Indian Ocean anticyclone on Marion Island's climate (Rouault *et al.* 2005).

The recent positive trend in the strength of the SAM also indicates the possibility of the weakening of Rossby waves in the southern polar jet stream. Indeed, since the 1980s a negative relationship has been observed in the Northern Hemisphere between the strength of Rossby waves and the magnitude of the Northern Annual Mode (the Northern Hemisphere equivalent of the SAM; Hartmann *et al.* 2000). Furthermore, the stronger high latitude winds associated with the positive phase of the SAM (and the stronger polar vortex) could cause Rossby waves to be deflected to lower latitudes (Hartmann *et al.* 2000; Hu & Tung 2003; see also results of Simmonds & Keay 2000b). This suggests that the conditions driving a stronger SAM are also probably influencing the amplitude and position of Rossby waves in the jet stream, with possible consequences for the formation and subsequent movement of cyclones and anticyclones.

The southward shift of the jet stream could also be influencing sea surface temperatures directly. The weaker and warmer sub-Antarctic winds (associated with the positive phase of the SAM) reduce evaporative heat loss from mid-latitudes in the Southern Ocean, causing a rise in ocean surface temperatures (Hall & Visbeck 2002; Rouault *et al.* 2005). Interestingly, over the same period the SAO has weakened considerably, as a result of uneven warming throughout the year at both mid- and high southern latitudes (Meehl *et al.* 1998; Simmonds & Jones 1998). This suggests that intra-annual variability in jet stream position and cyclone activity has decreased since the 1970s (Meehl *et al.* 1998). Indeed, both the increasing strength of the SAM and the decreasing magnitude of the SAO are strongly correlated with the climate trends on Marion Island (Rouault *et al.* 2005), although the mechanism by which a weakening SAO could have caused the long-term trends observed in the island's climate is still unclear. Thus, changes in the frequency, intensity and passage of cyclones in the sub-Antarctic, driven by stratospheric ozone loss and global warming, appear chiefly responsible for the observed changes in climate on Marion Island (Smith & Steenkamp 1990; Rouault *et al.* 2005).

Similar to the SAM, another interannual, large-scale circulation pattern, the *El Niño* Southern Oscillation (ENSO), has also increased in intensity and frequency over the same period (IPCC 2001). ENSO affects both tropical and Antarctic regions (e.g. South Pacific Ocean, and the Ross, Amundsen and

Bellingshausen seas west of the Antarctic Peninsula; Turner 2004; Rouault *et al.* 2005), but appears to have little influence on Marion Island's climate (see le Roux & McGeoch 2008). Interestingly, though, it has been speculated that unusual bird breeding success levels in 1997/98 (including the highest success rates on record for Marion Island for the Northern and Southern Giant Petrels, but low success rates for the Gentoo Penguin and Crozet Shag) could be related to a particularly strong *El Niño* that year (Crawford *et al.* 2003, see also Cooper & Lutjeharms 1992). If bird breeding on Marion Island in 1997/98 was really affected by *El Niño*, this suggests that while *El Niño* has little effect on the climate experienced on Marion Island, it may have a strong influence in areas which are important for the species' prey (especially since there was a sharp distinction in performance between near-shore and distant-feeders; Crawford *et al.* 2003).

3.6 Future climate trends

Coarse-scale climate models suggest further warming across the globe for at least the next 200 years (Meehl *et al.* 2005). The southern Indian Ocean is predicted to warm by a further 1-3°C by 2070-2100, suggesting that air temperatures on Marion Island are likely to increase by a similar magnitude (IPCC 2001). Indeed, this figure fits with the current rate of warming on the island, but is considerably larger than estimates for Macquarie Island (+ 0.1°C per decade between 1998 and 2030, based on ARIMA analyses; Tweedie & Bergstrom 2000). Fewer predictions have been made regarding changes in precipitation, with the current consensus being that changes in precipitation will be spatially variable (IPCC 2001), in agreement with the dissimilarity of current precipitation trends across the sub-Antarctic islands. However, if current climate trends continue on Marion Island, moisture availability could decline due to lower precipitation and/or higher temperatures driving faster evaporation.

Continued increases in greenhouse gas concentrations are predicted to not only cause warmer temperatures, but also further southward shifts in the southern polar jet stream (i.e. more positive SAM values) and of the northern boundary of the Antarctic Circumpolar Current (Kushner *et al.* 2001; Fyfe & Saenko 2005). This suggests stronger atmospheric and oceanic circulation near the Antarctic continent, but weaker circulation in the sub-Antarctic (Hall & Visbeck 2002; Gillett & Thompson 2003). As a result, warming may be matched by slower winds (with a stronger northerly component) on Marion Island. Furthermore, the number of cyclones in the sub-Antarctic is predicted to decline by a further 30% by 2100, in response to the warming of the Southern Hemisphere (Fyfe 2003). As a result, the climate of Marion Island can be expected to be more strongly affected by the South Indian Ocean anticyclone in the future, suggesting warmer temperatures and weaker winds on the island.

These scenarios, however, focus only on the effects of increased greenhouse gas concentrations, ignoring the important effects of the ozone layer on atmospheric dynamics. In the mid-1990s, the rate of stratospheric ozone loss levelled off, marking the start of the recovery of the layer (Yang *et al.* 2005). This could have a variety of effects on Marion Island's climate, because higher concentrations of stratospheric ozone will intercept more ultra-violet radiation, leading to a warming of the upper, and then lower, atmosphere above Antarctica. The concurrent replenishment of the ozone layer and the continued increase in greenhouse gas concentration are predicted to act antagonistically on circulation (i.e. having little effect on wind patterns; Shindell & Schmidt 2004), but to have a synergistic effect on raising temperatures (Hartmann *et al.* 2000; Shindell & Schmidt 2004). Warming of the Antarctic will also weaken the latitudinal temperature gradient between the tropics and the polar regions, probably causing a northwards shift in the position of the jet stream, with the SAM returning to a more neutral phase. As a result, cyclone storm tracks could pass closer to Marion Island again, with associated changes in temperature, precipitation, cloud and wind patterns on the island. Thus, while the rate of warming at high latitudes in the Southern Hemisphere is likely to increase, associated changes in the position of storm tracks could result in Marion Island actually becoming cooler and wetter again, with strengthened westerly and weakened northerly winds. Thus, Marion Island's climate could conceivably shift to either being cooler, wetter and windier (i.e. more strongly affected by passing cyclones) or, as supported by current trends, to warmer and drier conditions (no change or decreasing effects of cyclones). The outcome is likely to depend on the balance of relative effects of warming temperatures, declining cyclone abundance, and changing storm tracks. Either way, the climate of Marion Island is likely to continue to change rapidly over the next century, remaining an important indicator of climate in the Southern Ocean, and highlighting the importance of continued quality weather monitoring on the island. Finally, if we are to understand the consequences of such change to the island itself, far more detailed and comprehensive meteorological readings are needed at both fine and island-wide scales because of the island's topographic complexity.

3.7 Acknowledgements

The South African Weather Service and its personnel are thanked for collecting and providing weather recordings from Marion Island. M.A. McGeoch, M.J. Nyakatya, V.R. Smith and S.L. Chown are thanked for advice and discussion.

3.8 References

Ainley, D.G., Clarke, E.D., Arrigo, K., Fraser, W.R., Kato, A., Barton, K.J., *et al.* 2005. Decadal-scale changes in the climate and biota of the Pacific sector of the Southern Ocean, 1950s to the 1990s. *Antarctic Science* **17**, 171-182.

Allison, I.F. & Keage, P.L. 1986. Recent changes in the glaciers of Heard Island. *Polar Record* **23**, 255-271.

Ansorge, I.J. & Lutjeharms, J.R.E. 2000. Twenty-five years of physical oceanographic research at the Prince Edward Islands. *South African Journal of Science* **96**, 557-565.

Avenant, N.L. & Smith, V.R. 2003. The microenvironment of house mice on Marion Island (sub-Antarctic). *Polar Biology* **26**, 129-141.

Beggs, P.J., Selkirk, P.M. & Kingdom, D.L. 2004. Identification of Von Karman vortices in the surface winds of Heard Island. *Boundary-layer Meteorology* **113**, 287-297.

Bergstrom, D.M. & Chown, S.L. 1999. Life at the front: history, ecology and change on Southern Ocean islands. *Trends in Ecology & Evolution* **14**, 472-477.

Blake, B.J. 1996. *Microclimate and prediction of photosynthesis at Marion Island*. M.Sc. Thesis, University of the Orange Free State, South Africa.

Boelhouwers, J., Holness, S. & Sumner, P. 2003. The maritime sub-Antarctic: a distinct periglacial environment. *Geomorphology* **52**, 39-55.

Boelhouwers, J., Meiklejohn, I., Holness, S. & Hedding, D. 2008. Geology, geomorphology and climate change. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 65-96.

Bonan, G. 2002. *Ecological Climatology*. Cambridge University Press, Cambridge.

Budd, G.M. 2000. Changes in Heard Island glaciers, King Penguins and Fur Seals since 1947. *Papers and Proceedings of the Royal Society of Tasmania* **133**, 47-60.

Chown, S.L. & Avenant, N.L. 1992. Status of *Plutella xylostella* at Marion Island six years after its colonization. *South African Journal of Antarctic Research* **22**, 37-40.

Chown, S.L. & Crafford, J.E. 1992. Microhabitat temperatures at Marion Island (46°54' S 37°45' E). *South African Journal of Antarctic Research* **22**, 51-58.

Chown, S.L., Slabber, S., McGeoch, M.A., Janion, C. & Leinaas, H.P. 2007. Phenotypic plasticity mediates climate change responses among invasive and indigenous arthropods. *Proceedings of the Royal Society of London B* **274**, 2531-2537

Chown, S.L. & Smith, V.R. 1993. Climate change and the short-term impact of feral house mice at the sub-Antarctic Prince Edward Islands. *Oecologia* **96**, 508-516.

Cooper, J. & Lutjeharms, J.R.E. 1992. Correlations between seabird breeding success and meteorological conditions at Marion and Gough Islands. *South African Journal of Science* **88**, 173-175.

CLIVAR 2005. Reports of the Modes of Southern Hemisphere Climate Variability Workshop (27-28th June 2005) and the Third Session of the Clivar/CliC/SCAR Southern Ocean Region Panel Meeting (29-30th June 2005). CLIVAR Publication Series No. 98, International CLIVAR Project Office, Southampton.

Crawford, R.J.M., Rae, C.M.D., Nel, D.C. & Cooper, J. 2003. Unusual breeding by seabirds at Marion Island during 1997/98. *African Journal of Marine Science* **25**, 453-462.

Davies, K.F. & Melbourne, B.A. 1999. Statistical models of invertebrate distribution on Macquarie Island: a tool to assess climate change and local human impacts. *Polar Biology* **21**, 240-250.

Fabricius, A.F. 1957. Climate of the sub-Antarctic islands. In: Van Rooy, M.P. (Ed.). *Meteorology of the Antarctic*. Weather Bureau, Pretoria, pp. 111-135.

French, D.D. & Smith, V.R. 1985. A comparison between northern and southern hemisphere tundra and related ecosystems. *Polar Biology* **5**, 5-21.

Frenot, Y., Gloaguen, J.-C., Cannavacciuolo, M. & Bellido, A. 1998. Primary succession on glacier forelands in the sub-Antarctic Kerguelen Islands. *Journal of Vegetation Science* **9**, 75-84.

Frenot, Y., Gloaguen, J.-C., Masse, L. & Lebouvier, M. 2001. Human activities, ecosystem disturbance and plant invasions in subantarctic Crozet, Kerguelen and Amsterdam Islands. *Biological Conservation* **101**, 33-50.

Frenot, Y., Gloaguen, J.-C., Picot, G., Bougère, J. & Benjamin, D. 1993. *Azorella selago* Hook. used to estimate glacier fluctuations and climatic history in the Kerguelen Islands over the last two centuries. *Oecologia* **95**, 140-144.

Frenot, Y., Gloaguen, J.-C. & Tréhen, P. 1997. Climate change in Kerguelen Islands and colonization of recently deglaciated areas by *Poa kerguelensis* and *P. annua.* In: Battaglia, B., Valencia, J. & Walton, D. (Eds.). *Antarctic Communities: Species, Structure and Survival.* Cambridge University Press, Cambridge, pp. 358-366.

Fyfe, J.C. 2003. Extratropical southern hemisphere cyclones: Harbingers of climate change? *Journal of Climate* **16**, 2802-2805.

Fyfe, J.C. & Saenko, O.A. 2005. Human-induced change in the Antarctic Circumpolar Current. *Journal of Climate* **18**, 3068-3073.

Gille, S.T. 2002. Warming of the Southern Ocean since the 1950s. *Science* **295**, 1275-1277.

Gillett, N.P. & Thompson, D.W.J. 2003. Simulation of recent Southern Hemisphere climate change. *Science* **302**, 273-275.

Gremmen, N.J.M. 1981. *The Vegetation of the Sub-Antarctic Islands, Marion and Prince Edward.* Junk, The Hague.

Hall, A. & Visbeck, M. 2002. Synchronous variability in the Southern Hemisphere atmosphere, sea ice, and ocean resulting from the Annular Mode. *Journal of Climate* **15**, 3043-3057.

Hartmann, D.L., Wallace, J.M., Limpasuvan, V., Thompson, D.W.J. & Holton, J.R. 2000. Can ozone depletion and global warming interact to produce rapid climate change? *Proceedings of the National Academy of Sciences of the USA* **97**, 1412-1417.

Hu, Y.Y. & Tung, K.K. 2003. Possible ozone-induced long-term changes in planetary wave activity in late winter. *Journal of Climate* **16**, 3027-3038.

Hughes, J.M.R. 1987. The distribution and composition of vascular plant communities on Heard Island. *Polar Biology* **7**, 153-162.

Hugo, E.A., McGeoch, M.A., Marshall, D.J. & Chown, S.L. 2004. Fine scale variation in microarthropod communities inhabiting the keystone species *Azorella selago* on Marion Island. *Polar Biology* **27**, 466-473.

Huntley, B.J. 1970. Altitudinal distribution and phenology of Marion Island vascular plants. *Tydskrif vir Natuurwetenskap* **10**, 255-262.

Huntley, B.J. 1971. Vegetation. In: Van Zinderen Bakker, E.M., Sr, Winterbottom, J.M. & Dyer, R.A. (Eds.). *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expeditions 1965-1966.* A.A. Balkema, Cape Town, pp. 98-160.

Huth, R. & Pokorná, L. 2005. Simultaneous analysis of climatic trends in multiple variables: an example of application of multivariate statistical methods. *International Journal of Climatology* **25**, 469-484.

Huyser, O., Ryan, P.G. & Cooper, J. 2000. Changes in population size, habitat use and breeding biology of Lesser Sheathbills (*Chionis minor*) at Marion Island: impacts of cats, mice and climate change? *Biological Conservation* **92**, 299-310.

IPCC 2001. *Intergovernmental Panel on Climate Change Working Group I, Climate Change 2001: The Scientific Basis*. Cambridge University Press, Cambridge.

Kirkpatrick, J.B. & Scott, J.J. 2002. Change in undisturbed vegetation on the coastal slopes of Subantarctic Macquarie Island, 1980-1995. *Arctic, Antarctic, and Alpine Research* **34**, 300-307.

Kushner, P.J., Held, I.M. & Delworth, T.L. 2001. Southern Hemisphere atmospheric circulation response to global warming. *Journal of Climate* **14**, 2238-2249.

le Roux, P.C. 2004. Azorella selago *(Apiaceae) as a model for examining climate change effects in the sub-Antarctic*. M.Sc. Thesis, University of Stellenbosch, South Africa.

le Roux, P.C. & McGeoch, M.A. 2008. Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. *Climatic Change* **86**, 309-329

le Roux, P.C., McGeoch, M.A., Nyakatya, M.J. & Chown, S.L. 2005. Effects of simulated climate change on a keystone plant species in the sub-Antarctic. *Global Change Biology* **11**, 1628-1639.

Lutgens, F.K. & Tarbuck, E.J. 1995. *The Atmosphere: An Introduction to Meteorology*, 6th edition. Prentice-Hall, Englewood Cliffs.

Marshall, G.J., Stott, P.A., Turner, J., Connolley, W.M., King, J.C. & Lachlan-Cope, T.A. 2004. Causes of exceptional atmospheric circulation changes in the Southern Hemisphere. *Geophysical Research Letters* **31**, Article number L14205.

McGeoch, M.A., le Roux, P.C., Hugo, E.A. & Chown, S.L. 2006. Species and community responses to short-term climate manipulation: Microarthropods in the sub-Antarctic. *Austral Ecology* **31**, 719–731.

McGeoch, M.A., le Roux, P.C., Hugo, E.A. & Nyakatya, M.J. 2008. Spatial variation in the terrestrial biotic system. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 245-276.

Meehl, G.A., Hurrell, J.W. & Van Loon, H. 1998. A modulation of the mechanism of the semiannual oscillation in the Southern Hemisphere. *Tellus Series A – Dynamic Meteorology and Oceanography* **50**, 442-450.

Meehl, G.A., Washington, W.M., Collins, W.D., Arblaster, J.M., Hu, A., Buja, L.E., *et al.* 2005. How much more global warming and sea level rise? *Science* **307**, 1769-1772.

Mélice, J.-L., Lutjeharms, J.R.E., Goosse, H., Fichefet, T. & Reason, C.J.C. 2005. Evidence for the Antarctic circumpolar wave in the sub-Antarctic during the past 50 years. *Geophysical Research Letters* **32**, Article number L14614.

Mélice, J.-L., Lutjeharms, J.R.E., Rouault, M. & Ansorge, I.J. 2003. Sea-surface temperatures at the sub-Antarctic islands Marion and Gough during the past 50 years. *South African Journal of Science* **99**, 363-366.

Nyakatya, M.J. & McGeoch, M.A. 2008. Temperature variation across Marion Islands associated with a keystone plant species [*Azorella selago* Hook. (Apiaceae)]. *Polar Biology* **31**, 139-151.

O'Hare, G., Sweeney, J. & Wilby, R. 2005. *Weather, Climate, and Climate Change: Human Perspectives*. Pearson Education, Harlow.

Pakhomov, E.A. & Chown, S.L. 2003. The Prince Edward Islands: Southern Ocean oasis. *Ocean Yearbook* **17**, 348-379.

Pakhomov, E.A., McClelland, J.W., Bernard, K., Kaehler, S. & Montoya, J.P. 2004. Spatial and temporal shifts in stable isotope values of the bottom-dwelling shrimp *Nauticaris marionis* at the sub-Antarctic archipelago. *Marine Biology* **144**, 317-325.

Raphael, M.N. & Holland, M.M. 2006. Twentieth century simulation of the southern hemisphere climate in coupled models. Part 1: Large scale circulation variability. *Climate Dynamics* **26**, 217-228.

Reason, C.J.C. & Lutjeharms, J.R.E. 2000. Modelling multidecadal variability in the South Indian Ocean region: local forcing or a near-global mode? *South African Journal of Science* **96**, 127-135.

Rouault, M., Mélice, J.-L., Reason, C.J.C. & Lutjeharms, J.R.E. 2005. Climate variability at Marion Island, Southern Ocean, since 1960. *Journal of Geophysical Research-Oceans* **110**, Article number C05007.

Schulze, B.R. 1971. The climate of Marion Island. In: Van Zinderen Bakker, E.M., Sr, Winterbottom, J.M. & Dyer, R.A. (Eds.). *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expeditions 1965-1966*. A.A. Balkema, Cape Town, pp. 16-31.

Shindell, D.T. & Schmidt, G.A. 2004. Southern Hemisphere climate response to ozone changes and greenhouse gas increases. *Geophysical Research Letters* **31**, Article number L18209.

Simmonds, I. & Jones, D.A. 1998. The mean structure and temporal variability of the semiannual oscillation in the southern extratropics. I*nternational Journal of Climatology* **18**, 473-504.

Simmonds, I. & Keay, K. 2000a. Mean Southern Hemisphere extratropical cyclone behavior in the 40-year NCEP-NCAR reanalysis. *Journal of Climate* **13**, 873-885.

Simmonds, I. & Keay, K. 2000b. Variability of Southern Hemisphere extratropical cyclone behavior, 1958-97. *Journal of Climate* **13**, 550-561.

Slabber, S. & Chown, S.L. 2004. Thermal tolerance and cold hardiness strategy of the sub-Antarctic psocid *Antarctopsocus jeanneli* Badonnel. *Polar Biology* **28**, 56-61.

Smith, A.P. 1972. Notes on wind-related growth patterns of paramo plants in Venezuela. *Biotropica* **4**, 10-16.

Smith, V.R. 1992. Surface air temperatures at Marion Island, sub-Antarctic. *South African Journal of Science* **88**, 575-578.

Smith, V.R. 2002. Climate change in the sub-Antarctic: an illustration from Marion Island. *Climatic Change* **52**, 345-357.

Smith, V.R. & French, D.D. 1988. Patterns of variation in the climates, soils and vegetation of some sub-Antarctic and Antarctic islands. *South African Journal of Botany* **54**, 35-46.

Smith, V.R. & Steenkamp, M. 1990. Climate change and its ecological implications at a sub-Antarctic island. *Oecologia* **85**, 14-24.

Sumner, P.D., Meiklejohn, K.I., Boelhouwers, J.C. & Hedding, D.W. 2004. Climate change melts Marion Island's snow and ice. *South African Journal of Science* **100**, 395-398.

Thompson, D.W.J. & Solomon, S. 2002. Interpretation of recent Southern Hemisphere climate change. *Science* **296**, 895-899.

Thompson, D.W.J. & Wallace, J.M. 2000. Annular modes in the extratropical circulation. Part I: Month-to-month variability. *Journal of Climate* **13**, 1000-1016.

Thost, D. & Allison, I. 2005. The climate of Heard Island. In: Green, K. & Woehler, E.J. (Eds.). *Heard Island: Southern Ocean Sentinel.* Surrey Beatty & Sons, Sydney, pp. 62-68.

Turner, J. 2004. The El Niño-Southern Oscillation and Antarctica. *International Journal of Climatology* **24**, 1-31.

Tweedie, C.E. 2000. *Climate change and the autecology of six plant species along an altitudinal gradient on sub-Antarctic Macquarie Island.* Ph.D. Thesis, University of Queensland, Australia.

Tweedie, C.E. & Bergstrom, D. 2000. A climate change scenario for surface air temperature at Subantarctic Macquarie Island. In: Davison, W., Howard-Williams, C. & Broady, P. (Eds.). *Antarctic Ecosystems: Models for Wider Ecological Understanding.* New Zealand Natural Sciences, Christchurch, pp. 272-281.

Tyson, P.D. & Preston-Whyte, R.A. 2000. *The Weather and Climate of Southern Africa, 1st ed.* Oxford University Press, Oxford.

Van den Broeke, M.R. 1998. The semi-annual oscillation and Antarctic climate. Part 1: Influence on near surface temperatures (1957-79). *Antarctic Science* **10**, 175-183.

Van Loon, H. 1967. The half-yearly oscillations in the middle and high southern latitudes and the coreless winter. *Journal of the Atmospheric Sciences* **24**, 472-486.

Van Zinderen Bakker, E.M., Sr. 1978. Origin and general ecology of the Marion Island ecosystem. *South African Journal of Antarctic Research* **8**, 13-21.

Vaughan, D.G., Marshall, G.J., Connolley, W.M., Parkinson, C., Mulvaney, R., Hodgson, D.A., *et al.* 2003. Recent rapid regional climate warming on the Antarctic Peninsula. *Climatic Change* **60**, 243-274.

Venegas, S.A. 2003. The Antarctic Circumpolar Wave: a combination of two signals? *Journal of Climate* **16**, 2509-2525.

Weimerskirch, H., Inchausti, P., Guinet, C. & Barbraud, C. 2003. Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. *Antarctic Science* **15**, 249-256.

White, W.B. & Peterson, R.G. 1996. An Antarctic circumpolar wave in surface pressure, wind, temperature and sea-ice extent. *Nature* **380**, 699-702.

Yang, E.S., Cunnold, D.M., Newchurch, M.J. & Salawitch, R.J. 2005. Change in ozone trends at southern high latitudes. *Geophysical Research Letters* **32**, Article number L12812.

CHAPTER 4

GEOLOGY, GEOMORPHOLOGY AND CLIMATE CHANGE

JAN C. BOELHOUWERS, K. IAN MEIKLEJOHN,
STEPHEN D. HOLNESS AND DAVID W. HEDDING

Reports from the early expeditions to the Marion and Prince Edward Islands provided the first physiographic and geological description of the islands (Van Zinderen Bakker *et al.* 1971; Van Zinderen Bakker 1973). The island group provides a small terrestrial environment (293 km^2 for Marion Island and 46 km^2 for Prince Edward Island) within the Southern Hemisphere mid-latitudes and much initial attention was focused on the terrestrial record of Quaternary environmental change (Schalke & Van Zinderen Bakker 1971; Hall 1978; Scott 1985). Associated geomorphological studies were exploratory and descriptive in nature, as typifies much of the geomorphological research in the sub-Antarctic (Hall 2002). Similarly, following the initial geological descriptions by Verwoerd (1971) geological studies have been sporadic on various aspects of Marion Island.

Over the past decade several studies have established a new focus on the geomorphological dynamics of Marion Island, its record of Late Quaternary environmental change and geological evolution. Here, we synthesize these recent findings and re-evaluate their implications in terms of the geological and geomorphological dynamics of the island, and the sensitivity and responses of the terrestrial ecosystem to climate change.

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 65-96

4.1 Geological evolution

Marion and Prince Edward Islands are young islands that represent the peaks of Hawaiian type shield volcanoes associated with a mantle plume (McDougall *et al.* 2001). The islands are located in an intraplate fracture zone at the edge of the African tectonic plate, approximately 300 km south of the South West Indian Ridge (Mahoney *et al.* 1992; McDougall *et al.* 2001).

On both islands, older Pleistocene grey basaltic lavas, with distinct western and eastern episodes, are covered by Holocene black basaltic lava and scoria (Verwoerd 1971; Hall 1978) (Fig. 4.1). The three commonly recognised types of black lavas, pahaoehoe, aa and block lava all occur on the Prince Edward Islands (Verwoerd 1971). Surface topography, particularly of Marion Island, is visually dominated by the youngest black lavas and is said to be sectioned by radial faults along which recent eruptive centres are found in the form of scoria cones (Verwoerd 1971; Hall 1978; Verwoerd *et al.* 1981). Two volcanic centres for Marion Island are proposed (Verwoerd 1971; McDougall *et al.* 2001) (Fig. 4.1). However, three-dimensional visualisation of satellite imagery suggests that the situation may be more complex (Meiklejohn, unpublished data).

Early research indicated that Marion Island consisted of two geological units (McDougall 1971; Verwoerd 1971; Hall 1978; Verwoerd *et al.* 1981). The first suggested unit ages between 276 ka and 100 ka before present (BP) and comprises alkaline basalt lava flows with interbedded pyroclastics from two volcanic periods, as well as intercalated glacial tills, at the beginning and end of

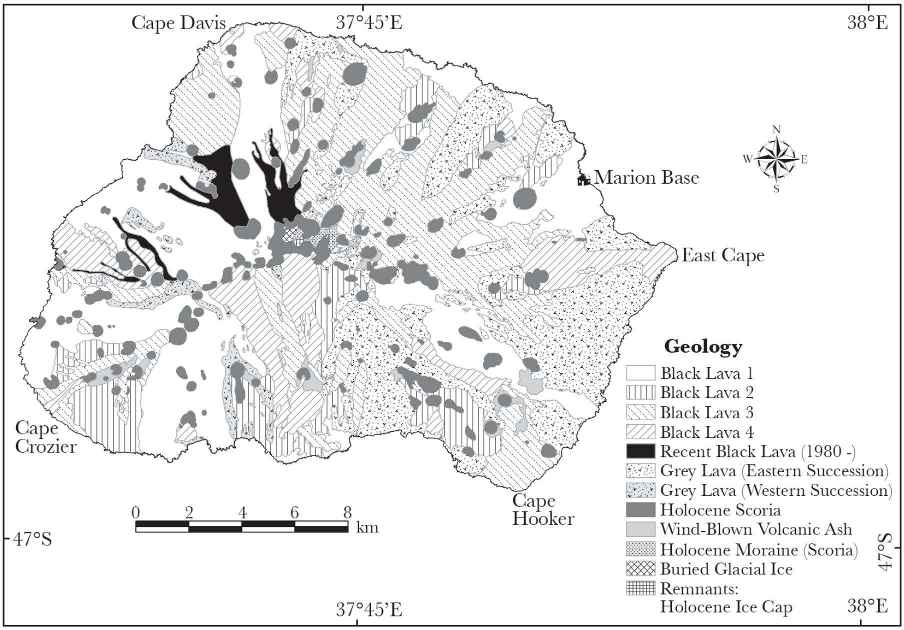


Figure 4.1 Simplified geology of Marion Island (Modified after Verwoerd 1971; Chevallier 1986; Chevallier *et al.* 1992; McDougal *et al.* 2001).

each period. The second unit comprises black lava, over 130 scoria cones and a tuff cone on Marion Island, and at least 15 scoria cones and three tuff cones on Prince Edward Island; these were originally dated between 15 ka BP and 400 ka BP (McDougall 1971). However, the oldest recorded dates for lavas on Marion Island have now been extended to *c.* 450 ka BP and indications are that the islands are less than one million years old (McDougall *et al.* 2001). McDougall *et al.* (2001) used K-Ar (potassium-argon) dating to improve the geochronological resolution and suggest more episodic volcanic activity than previously suggested, identifying eight volcanic episodes (Fig. 4.2). Recent eruptions (Verwoerd *et al.* 1981; Meiklejohn & Hedding 2005) are clear indications that volcanic activity still continues. Current investigations following the recent melting of the permanent snow on Marion Island, together with Global Position Systems and aerial photography, have facilitated the updating of the original geological map (see Vewoerd 1971). This map is presented as Figure 4.1 (Hedding 2006).

Volcanism on Marion Island is suggested to have been initiated by isostatic adjustment, following deglaciation at the end of the Last Glacial Maximum (Hall 1982, 2004). This led to the contention that rapid deglaciation at the end of the Last Glacial Maximum resulted in thrust faulting of the areas that were overlaid by the thickest ice (Hall 1982). Two large topographically dominant landforms are suggested to have arisen as a result of the faulting, namely Long Ridge and the Feldmark Plateau, which are proposed as horst structures, while Santa Rosa Valley is thought to be a graben. Chevalier (1986), however, suggested that Santa Rosa Valley and other Graben-type landforms are the result of landslides that result from volcanic activity. Marion and Prince Edward Island volcanics result from regional crustal control that provides the lava from the mantle and localised edifice tectonics on the cone itself (Chevalier 1986). The possibility also exists that many of the valley landforms and scarps on Marion Island are the result of volcanic eruptions (I. Meiklejohn, unpublished data). Santa Rosa Valley and the Basalt Curtain area are not dissimilar in form to the landscape that resulted from eruptions at Mt St Helens and Montague Island (see Wunderman *et al.* 2004). There is a clear need to resolve the nature and age of the grey lava plateaus at Feldmark and Long Ridge to clarify the Quaternary glacial and periglacial history of these high lying surfaces and their role as possible refuge areas during Late Quaternary glacials.

4.2 The glacial record

Glacial reconstruction for the entire sub-Antarctic region is speculative and lacks the rigour required for accurate interpretation of former glacial conditions (Hall 2004). An evaluation of glacial extents is extremely difficult as most sub-Antarctic islands were almost entirely covered by ice during the Last Glacial Maximum and glacial margins and associated sedimentary evidence extended beyond coastal margins (Hall 2004). Of the Prince Edward Islands, only Marion Island has evidence for a glacial history and the earliest interpretations of the Quaternary glacial history are reliant on few dates and

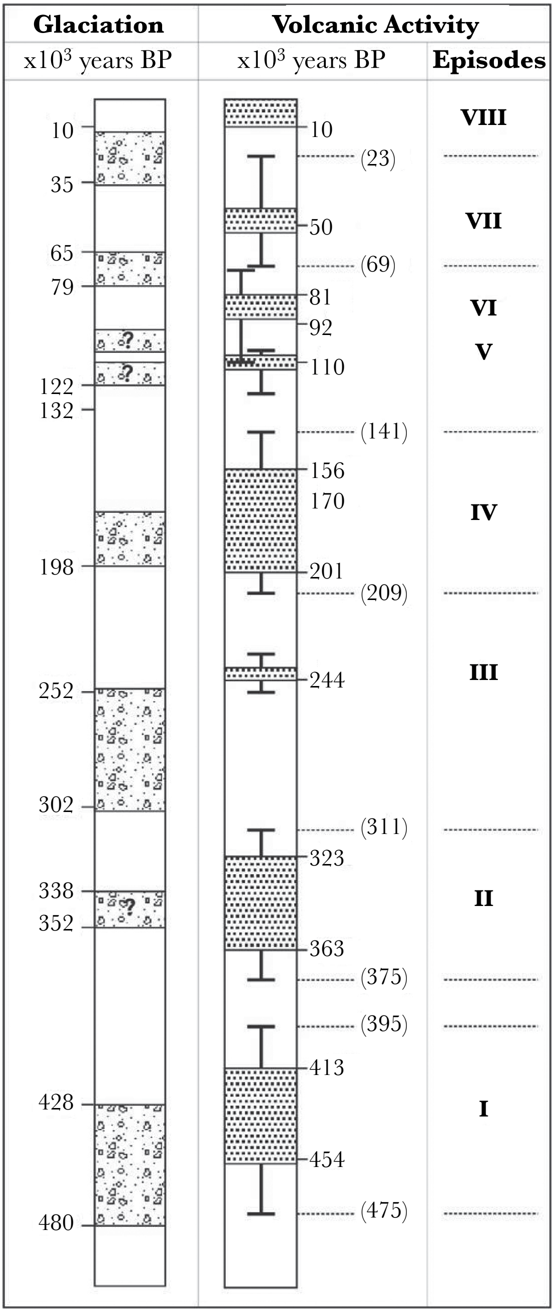


Figure 4.2 Glacial and volcanic chronology from Marion Island (After McDougall *et al.* 2001).

suggested three glacial episodes that were named “Oldest”, “Penultimate” and “Würm” (McDougall 1971; Hall 1978, 1982). Recent K-Ar dating of volcanic lavas has allowed improved chronological resolution of intercalated glacial tills and it is possible that Marion Island was subjected to at least five (and possibly eight) glaciations during the Quaternary (McDougall *et al.* 2001) (Fig. 4.2). The glacial periods dated on Marion are, within the available time resolution, contemporaneous with Northern Hemisphere Mountain Glaciation events (McDougall *et al.* 2001).

Deposits from the earliest glacial periods on Marion Island are covered by subsequent lava flows and are only visible in exposures along coastal cliffs, large vertical exposures, and incised stream courses (Hall 1977, 1978, 1980). Glacio-depositional and glacio-erosional features resulting from the more recent glacial episodes (79 ka –11 ka BP) represent the most prominent glacial evidence on Marion Island and are most evident on the eastern side of the island (Hall 1980; McDougall *et al.* 2001). Landforms such as moraines, striations and sculptured bedrock are described by Hall (1977, 1978, 1980), and are part of a sequence resulting from periods of major ice advance within the Late Pleistocene (Hall 1980) (Fig 4.3). While some debate has existed over the interpretation of sediments as being glacial in origin on Marion Island (Kent & Gribnitz 1983; Gribnitz *et al.* 1986), Hall’s (1981a) interpretation is now generally accepted as being correct (McDougall *et al.* 2001).

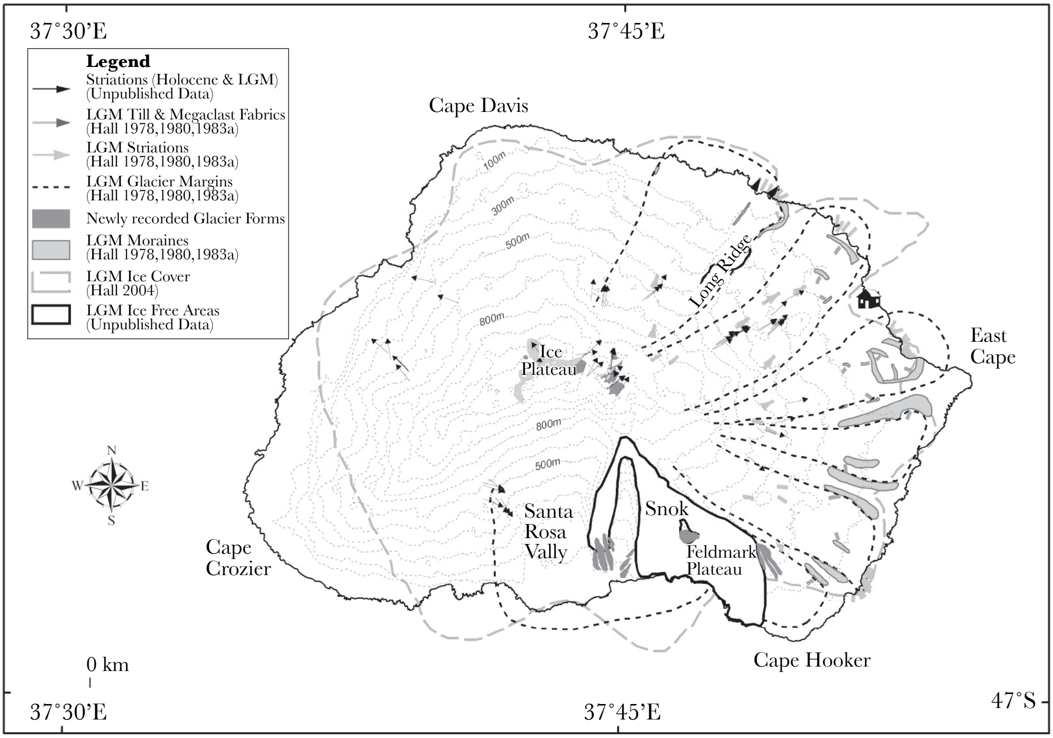


Figure 4.3 Glacial margins, striae, and moraines as identified by Hall (1977, 1978, 1980, 1983a, 2004) and a cirque near Snok.

The mean annual air temperatures on Marion Island for the Last Glacial Maximum were constructed by estimating the altitudinal range of the palaeo-snowlines from their relationship with the position and altitude of the lateral moraines (Hall 1978, 1980). It was suggested that the mean annual air temperatures on Marion Island fell by 2-4°C and that the glaciation of the island resulted from an increase in the amount of precipitation falling as snow (Hall 1982). The location and direction of several former glaciers on the eastern side of Marion Island were proposed from striations on grey lava and from fabric analyses, while the boundaries of the glaciers are indicated by moraines (Hall 1978, 1980) (Fig. 4.3). It is suggested that almost the entire Marion Island was covered by ice during the Last Glacial Maximum (Hall 2004) (Fig 4.3). However, the extent of the glaciation off-shore is unclear.

Rapid deglaciation of Marion Island at the end of the Last Glacial Maximum was proposed as the trigger for the latest volcanic events and movement along scarps, particularly Long Ridge and the Santa Rosa Valley (Hall 1978, 1982, 2004). McDougall *et al.* (2001), however, disputed the vertical displacement along fault scarps resulting from deglaciation, and as argued below, there is evidence, particularly on Long Ridge, that faulting has not taken place.

Recent research (e.g. Nel 2001; Nel *et al.* 2003, unpublished data) largely confirmed the spatial extent of palaeo-glaciers suggested by Hall (1978) in the eastern sector (south of Long Ridge to the northern extent of the Feldmark Plateau). Glacial moraines, glacially polished and striated bedrock surfaces identified by Hall (1978, 1980, 1983a, 1990a), have been verified, while previously unrecorded glacial evidence has been documented, particularly in the interior of Marion Island (Hedding 2006).

Apart from the link between rapid deglaciation and massive faulting, the spatial extent of glaciers, particularly on Long Ridge and the Feldmark Plateau, contradict Hall's (1978, 1980, 1982) findings. Moraines, clearly from Late Quaternary glacial events, that exist on the edges of Long Ridge are stable and would have been considerably altered if faulting had occurred, show no evidence of alteration. Similarly, landforms on the edges of Skua Ridge and the Feldmark Plateau show no evidence of faulting. Furthermore, the topography of Feldmark Plateau and Long Ridge, and other similar grey lava areas would have channelled ice-flow away from higher relief areas. Current research (unpublished data) identifies four locations where Hall's (1978, 1980, 1982, 2004) findings on the glacial extent during the Last Glacial Maximum can be reviewed.

First, despite the apparent suitable location of the Feldmark Plateau, specific evidence for the glaciation is sparse. Moraines on the lower northern and southern extents are related to glacial activity in the adjacent low-lying areas, while localised niche glacial activity has been proposed for a basin on the slopes of Snok (550 m), where a well-developed end moraine has been identified (Boelhouwers *et al.* 2001). The cirque at Snok consists of a basin in grey lava on the lee-side of the Feldmark plateau between 550 and 600 m a.s.l. (Figs 4.3-4.4), while a terminal moraine exists at 750 m distance from the backwall. A Holocene scoria cone occupies the central floor and post-dates the moraine. A distinct relict protalus rampart in the vicinity of the backwall indicates a subsequent and more restricted phase of snow accumulation.

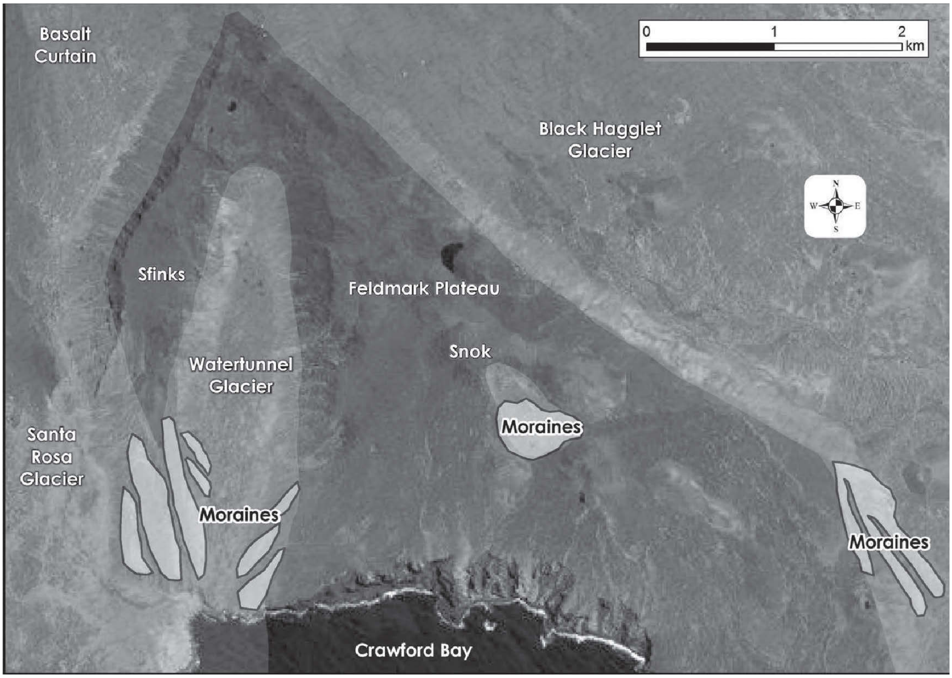


Figure 4.4 Glacial deposits and landforms of the Feldmark and Watertunnel area associated with the last glaciation.

The Feldmark Plateau area is unique with respect to periglacial landforms. Nowhere else on the grey lava areas on Marion Island are there features of comparable size (Holness 2001a; Nel 2001). Holness (2001a) identified extensive blockstreams, stone-banked terraces with risers of up to 3 m in height and stone-banked lobes up to 4 m in height. Stone-banked lobes associated with bedrock outcrops have riser heights of approximately 6 m (Nel 2001). Holness (2001a) argued that the large features on Feldmark Plateau were formed while much of the rest of the island was glaciated. However, it may be, as suggested later in this chapter, that the size of the observed periglacial features is related to location (*i.e.* on the colder southern slopes of the island) and to the availability of material (Boelhouwers *et al.* 2001). Nevertheless, it is likely that by channelling ice flow around the high relief of the Feldmark Plateau, the topographic configuration resulted in the area either remaining ice-free through much of the Last Glacial Maximum, or alternatively the area was deglaciated before other areas.

Second, evidence from Long Ridge suggests that while the area was glaciated during the Last Glacial Maximum, parts remained free of ice, and that the moraines to the north were incorrectly interpreted by Hall (1978, 1983a). The existence of autochtonous blocky deposits (Sumner & Meiklejohn 2004) associated with a dyke can be used to mitigate against the area being covered by ice (Fig. 4.5). Given the length of time required for development of the blocky deposits (Sumner & Meiklejohn 2004) and that glaciation would have altered their appearance, it is argued that they have developed under continuous ice-free conditions over a long period. However, if the argument presented above is incorrect and the area was glaciated, the inherent stresses associated with deglaciation and dilatation, as well as moisture and temperature regimes, would have been favourable for classic frost to occur, wedging along stress-released bedrock fractures, thereby resulting in the blockfield development.

Third, reinvestigation of the Watertunnel Valley has led to the identification of small, previously undocumented lateral moraines (Fig. 4.4) that are thought to indicate the retreating frontal zone of a glacier. While the origin of the Watertunnel Valley cannot necessarily be ascribed to glaciation, it clearly has all the characteristics of a glacial valley.

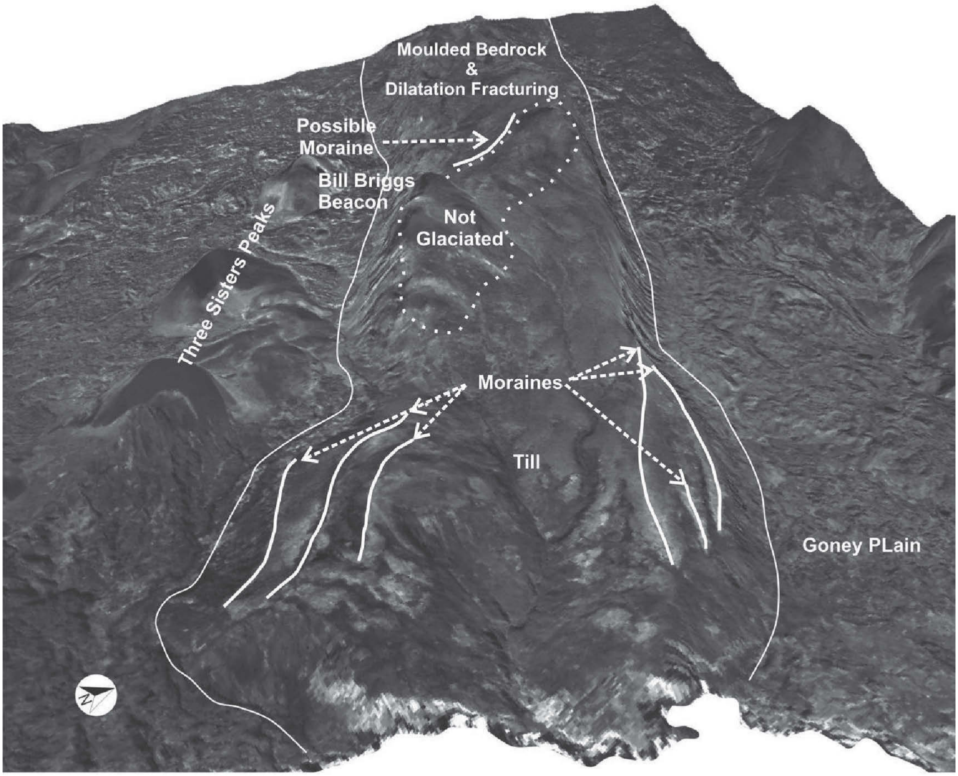


Figure 4.5 Glacial deposits and landforms of the Long Ridge area associated with the last glaciation.

Fourth, until approximately the year 2000, the interior of Marion Island had a permanent snowline and snow covered evidence for glaciation (Sumner *et al.* 2004). Climatic amelioration of Marion Island has resulted in the loss of permanent snow cover and the rapid reduction in the size of the Ice Plateau (Sumner *et al.* 2004) and it is now possible to identify glacial evidence that has previously not been documented. Almost without exception, grey lavas in the high altitude areas of the Island's interior (above 800 m) show clear evidence of glaciation in the form of striae, moulded bedrock (including textbook examples of *rouche moutonnée* forms), moraines, striated clasts and dilatation shattering (Fig. 4.6). While it is assumed that much of the glacial evidence is from the Last Glacial Maximum, Holocene glaciation has occurred from a small icecap, called the "Ice Plateau", and on the slopes of the highest peaks of the island. The extent of Holocene ice cover is currently being investigated, and moraines, striations and three cirques have been identified. However, given that the highest peaks have erupted since the Last Glacial Maximum it is difficult to ascertain the full extent of Holocene glaciation.

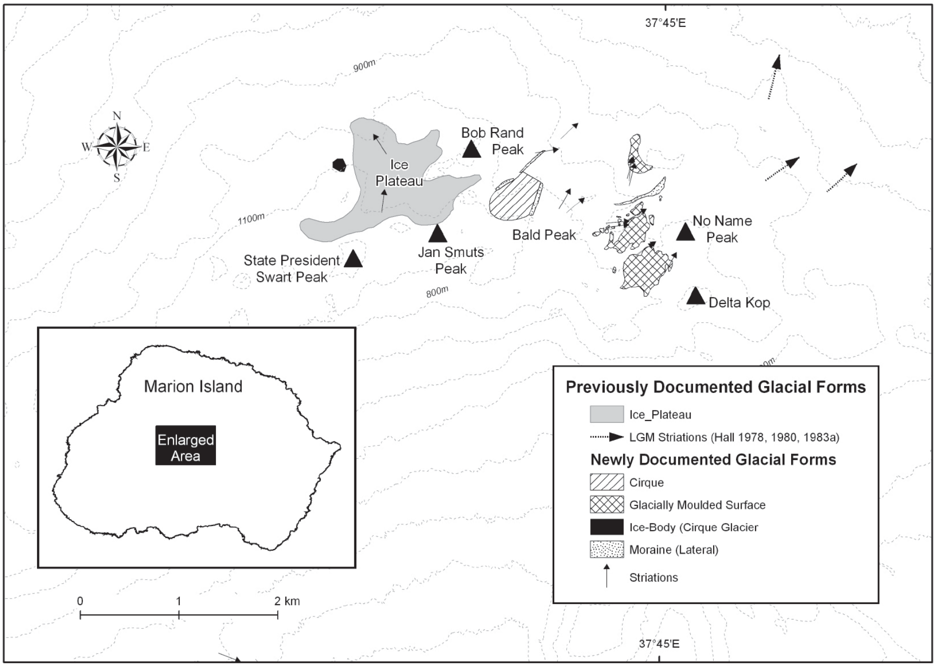


Figure 4.6 Newly recorded glacial evidence from the interior of Marion Island.

The full glacial history on Marion Island remains a conundrum, but with improved spatial resolution of landforms, analyses are beginning to produce a more realistic picture of the island's geomorphology. Further dating by K-Ar and cosmogenic isotopes, and identification and analyses of geomorphic phenomena on Marion Island will not only improve the chronological resolution of landscape development, but will enable more accurate interpretations.

4.3 Geomorphology

The broad landscape features of Marion Island reflect its volcanic origin and have been described in Van Zinderen Bakker *et al.* (1971). The last glacial cycle has interacted with this structural setting to erode the grey lava surfaces that existed at the time, leading to both glacially polished and striated surfaces, as well as till covers and moraines. Post glacial black lavas vary in age from ten thousand to younger than ten years. The younger lava surfaces have bare, blocky surfaces, while vegetation succession along the coast has led to extensive wetlands and mires. The young terrestrial landscape is highly dynamic as reflected by active coastal cliff erosion, weathering of lava surfaces and basalt outcrops and slope processes on grey lava derived till, debris slopes and scoria cones. Despite the maritime setting, fluvial processes are restricted due to high rates of sub-surface drainage.

Important interactions between animal activity and erosion processes at the coast have been highlighted (Hall & Williams 1981) and are briefly discussed in this chapter, but have, to date, not received the attention they deserve. An additional consideration for future geomorphic research is that high wind velocities throughout the year potentially have a large impact in areas where vegetation is limited or absent, and which were formerly covered by snow, as is the case for much of the interior of the islands. The result is the exposure of material that is susceptible to transport by wind. Aeolian (wind related) processes are, therefore, likely to play a larger geomorphic role in future and will potentially impact on the colonisation of vegetation.

4.3.1 Weathering

The primary rock structural setting is dominated by the individual lava flow composition, its boundary planes and the columnar cooling joints within the basalt. The blocky surface zone present in the Holocene black lava flows results in a higher porosity and water absorption capacity than grey lava, which in contrast has a higher micro-porosity (Table 4.1). Additional zones of weakness are created by the island scale radial faulting patterns and the post-glacial stress release in the grey lava bedrock. This is visible as surface-parallel fracture patterns with increasing density to the surface that have supplied the platy clasts in the basal till on grey lava surfaces and associated moraines. Stress release upon deglaciation has resulted in blocky disintegration facilitating *in situ* blockfield development (Sumner & Meiklejohn 2004) and scree build-up along fault scarps, as described by Nel *et al.* (2003).

Sumner (2004) presented a first estimation of current weathering rates by mass loss analysis of small clasts. Black and grey lava samples of 100-380 g showed mass loss rates of 0.41-0.72%.a^{-1} (i.e. per year) and 0.02-0.10%.a^{-1}, respectively. The grey lava mass loss rates increase consistently with altitude, a trend not observed for the black lava, and are compatible with those reported for quartz-mica schist and marble at Signy Island (Hall 1990b; Hall & Walton

1992). Sumner (2004) pointed out that, assuming constant weathering rates, small black lava clasts will completely weather in *c*. 200 years, compared to *c*. 1 000 years for grey lava clasts. By contrast, observations along glacially polished grey lava surfaces suggest surface weathering in the order of a few mm since deglaciation, with striations still visible. Differences in mass to surface area ratio between small clasts and bedrock surfaces may explain some of this discrepancy.

Table 4.1 Rock physical properties of grey and black lava clasts (from Sumner 2004).

Rock type		**Porosity (%)**	**Micro-porosity (%)**	**Water absorption (%)**	**Saturation coefficient**
Grey lava	mean	6.04	91.84	3.63	0.61
(n=10)	std. dev.	0.92	3.49	0.64	0.10
Black lava	mean	17.86	61.67	7.65	0.47
(n=10)	std. dev.	6.89	8.32	0.34	0.13

Weathering mechanisms in the sub-Antarctic have been poorly studied. Boelhouwers *et al.* (2003) presented detailed rock moisture and temperature data for Marion Island and suggest conditions to be favourable for frost action at 1 000 m a.s.l. No studies of chemical weathering have been published, despite its suggested importance in the mass loss study by Sumner (2004) and in soil development and nutrient balance studies.

4.3.2 Present-day periglacial landforms, processes and environment

Periglacial geomorphological studies in the sub-Antarctic have mostly focused on landform descriptions with process interpretations based on Northern Hemisphere comparisons (Hall 2002). Recent process studies from Marion Island have provided first insights into the distinct environment-process-landform relationships of the contemporary sub-Antarctic periglacial environment, its permafrost distribution and responses to climate change. As on Macquarie Island, vegetation – geomorphological process relationships are striking in the landscape, but have only received limited attention to date.

4.3.2.1 Periglacial landforms

All till or moraine covered land surfaces and most scoria slopes display evidence of periglacial activity; observed as small forms of patterned ground and solifluction, which occur at all altitudes. Large solifluction terraces and lobes, blockstreams and blockfields and large-scale patterned ground are relict features at all altitudes and are discussed in the context of Holocene climate change.

The patterned ground of Marion Island has been described in detail (Hall 1979, 1983b; Holness & Boelhouwers 1998; Holness 2001b; Boelhouwers *et al.* 2003). The homogeneous material composition of the Marion Island till and scoria slopes results in the strikingly uniform morphology of active patterned ground. This has been used as a basis for dimensional scaling analysis using altitude as a climate proxy from mild coastal conditions to severe-diurnal and seasonal frost environments at the summit (Holness 2003a). Strong positive correlations exist between various circle dimensions and altitude, as well as between the dimensional parameters (Table 4.2). A similar dimensional scaling with altitude for active sorted stripes has been described by Hall (1983c) for Kerguelen and by Boelhouwers *et al.* (2003) for Marion Island.

A conspicuous characteristic of some sorted stripes on Marion Island is their preferential orientation parallel to the dominant wind direction (Hall 1979). Similar observations are noted for Kerguelen (Hall 1983c) and Macquarie (Löffler 1983). Holness (2001b) noted that, although sorted stripes are oriented down the maximum local slope gradient, sorted stripes occur preferentially on windward slopes and to some extent on low-angled leeward slopes. On near-horizontal surfaces sorted stripes are aligned with the wind and seldom occur on slopes with cross winds. Holness (2001b) ascribed these spatial patterns to wind-induced surface cooling effects associated with needle ice growth. In addition, surface desiccation would lead to ice crystallisation beneath the dry surface layer, enhancing the geomorphic effectiveness of the frost heave. These observations suggest that wind may play an important role in enhancing diurnal frost effectiveness and its spatial distribution in the sub-Antarctic.

Solifluction landforms have been reported for all sub-Antarctic islands (Hall 2002; Boelhouwers *et al.* 2003). On Marion Island, stone- and vegetation-banked lobes, sheets and terraces occur at all but the highest altitudes (Hall 1979, 1983b, 1983c). Vegetation-banked solifluction terraces are typically bordered by *Azorella selago* (Holness & Boelhouwers 1998; Holness 2003b). At Long Ridge, riser heights of stone- and turf-banked terraces increase with altitude from *c.* 0.3 m to between 0.5 and 1.2 m, over an altitude range from 200 to 550 m a.s.l. Only the smallest forms are considered active under present-day climate conditions, but larger forms may show secondary, surficial movement on their tread surfaces (Holness & Boelhouwers 1998).

Stone- and vegetation-banked lobes, sheets and terraces on scoria cones show a distinct internal stratification (Holness 2001b; Boelhouwers *et al.* 2003). Individual units are comprised of vertically sorted layers that vary in thickness between 5 and 13 cm, but build landforms with riser heights of 0.25 to 1 m (stone-banked sheets) or 0.5 to 1.5 m (max. 3.5 m) in the case of turf-banked forms (Boelhouwers *et al.* 2003). These landforms build actively by diurnal frost creep under present-day conditions and closely resemble the features described by Francou (1988, 1989, 1990) and Bertran *et al.* (1997). These observations illustrate that solifluction landform dimensions may not reflect the severity of the ground frost climate. Rather, here they should be viewed as complex forms

Table 4.2 Correlation coefficients between patterned ground morphometry and environmental parameters. Correlations are significant at $p < 0.05$ (based on Holness 2001a, 2003a).

Sorted circles (n = 121 sets of 10 circles)						
	Altitude	**Slope angle**	**Depth of sorting**	**Height of fine centre above border**	**Distance between fine centres**	**Size of fine centres**
Slope angle	-0.35					
Depth of sorting	0.95	-0.36				
Height of fine centre above border	0.93	-0.40	0.89			
Distance between fine centres	0.95	-0.37	0.95	0.92		
Size of fine centres	0.95	-0.41	0.95	0.94	0.95	
Width of coarse borders	0.36	-0.05	0.38	0.31	0.52	0.23

Sorted stripes (n = 150 sets of 10 pairs of stripes)						
	Altitude	**Slope angle**	**Depth of lateral sorting**	**Depth of vertical sorting**	**Fine stripe width (FSW)**	**Coarse stripe width (CSW)**
Slope angle	-0.02					
Depth of lateral sorting	0.92	0.13				
Depth of vertical sorting	0.89	0.14	0.93			
Fine stripe width	0.93	0.05	0.95	0.89		
Coarse stripe width	0.80	0.09	0.88	0.85	0.93	
Difference between CSW & FSW	-0.91	0.02	-0.83	-0.76	-0.88	-0.64

developed under high sediment fluxes during diurnal frost conditions. The spatial patterns of sediment removal, transport and deposition associated with these forms have not been studied. However, there appears to be a dynamic interactive environment between vegetation, slope processes and landforms leading to the growth and senescence of these features.

4.3.2.2 Periglacial processes

Field observations on Marion Island give overwhelming evidence for the occurrence of needle-ice and ice lens formation under diurnal frost cycles. First observed by Van Zinderen Bakker (1973) and Hall (1979), Holness (2001b) described extensive and frequent needle ice growth in all grey lava areas without vegetation or snow cover. Ice lens formation occurs to a depth of 150 mm at 350 m a.s.l. and 270 mm at 700 m a.s.l.

Sediment heave and downslope movement in the grey lava and scoria areas have been measured by traditional techniques (painted stone lines, wooden dowels, vertical marker columns) from sea level to c. 1 000 m a.s.l. on the east side of the island (Holness 2001b, 2004; Boelhouwers *et al.* 2003). Movement profiles are typically concave upward in the upper 5-7 cm and demonstrate the dominance of surficial creep by needle-ice (e.g. Mackay & Mathews 1974; Pérez 1993; Harris & Davies 2000; Matsuoka 2005). A solifluction component exists in the profiles above 300 m a.s.l. as shown by a convex shaped deformation in the lower profile sections. This reaches down to 20 cm at 1 000 m a.s.l. In some places shearing at 6-8 cm is observed at the zone that differentiates the faster, surficial, needle-ice dominated creep from the solifluction zone beneath. Rates and depths of wooden dowel heave highlight the effective differential frost heave associated with needle ice and indicate ice lens formation above 300 m a.s.l. (Holness 2004). Holness (2001a) demonstrated re-growth of sorted stripes on a scoria cone at 550 m a.s.l. within one winter season.

Sediment movement rates of markers on till and scoria slopes compare well with those of other sub-Antarctic islands, are on par with alpine diurnal frost environments and are among the highest in any periglacial environment (Table 4.3). Fine-textured soils show significantly higher movement rates than coarse materials (Holness 2001a, 2004). Holness (2001a, 2004) used multivariate analysis to identify factors controlling movement rates in both the scoria and till materials. Slope angle, altitude and percentage fines were identified as significant controls ($p = 0.05$) for the scoria and till, explaining 65% and 49% of the movement variability, respectively (Holness 2004). Better correlations with these three environmental parameters can be found by separating the sites by surface texture in the till, explaining 72%, 62% and 38% of the variability in fine, stony and blocky sites respectively.

Table 4.3 Average sediment movement rates on grey lava, till and scoria slopes (from Holness 2001a).

Grey lava and till slopes

Altitude (m a.s.l.)		Slope angle	% <63ym of the fraction <2mm	Average movement rates (mm/year)			
				Combined	Fine	Stony	Blocky
75	Avg	3.9	12.6	21.8	57.6	20.4	0.9
	S.D.	3.0	3.1	13.7	22.1	13.4	1.9
150	Avg	5.4	19.2	10.7	29.0	11.7	4.2
	S.D.	2.1	8.3	4.8	5.5	6.0	7.4
200	Avg	3.6	9.1	42.7	84.0	27.8	5.9
	S.D.	3.0	2.5	24.5	32.9	13.3	9.2
300	Avg	6.8	15.0	50.1	157.0	53.4	0.0
	S.D.	3.1	5.8	46.4	58.0	25.3	0.1
550	Avg	8.1	11.3	90.5	302.7	95.1	32.3
	S.D.	5.1	4.0	62.0	215.3	55.9	39.9
750	Avg	13.4	25.4	276.8	464.1	170.4	45.8
	S.D.	8.6	7.9	319.2	494.6	168.2	59.7
1000	Avg	8.0	3.6	109.7	257.1	115.7	40.1
	S.D.	4.3	1.7	49.5	28.0	49.3	27.0
All sites	Avg	7.1	13.3	81.5	180.7	65.5	17.4
	S.D.	5.2	7.9	135.8	239.4	80.2	33.2

Scoria slopes

Altitude (m a.s.l.)		Slope angle	% <63ym of the fraction <2mm	Average movement rates (mm/year)			
				Combined	Fine	Stony	Blocky
150	Avg	8	17	36		36	
	S.D.	3	5	9		9	
200	Avg	17	12	143	406	142	26
	S.D.	7	6	156	262	134	23
550	Avg	16	17	600	757	384	
	S.D.	6	11	406	392	286	
750	Avg	8	4	124		124	
	S.D.	5	1	96		96	
750	Avg	14	4	80	125	49	
	S.D.	1	0	61	42	22	
All sites	Avg	15	12	216	532	161	26
	S.D.	7	8	281	382	179	23

4.3.2.3 The periglacial environment

At the island scale, material distribution poses the most obvious control on the spatial distribution of soil frost processes and landforms. Frost susceptibility has been defined by Holness (2001a), using Meentemeyer & Zippin's (1981) threshold value of 7.9% as the minimum percentages of fines (fraction < 63 μm) for saturated soils to develop segregation ice. Precipitation recorded on average 26 days per month at the meteorological station suggests that high soil moisture conditions prevail throughout the year on the island. At lower altitudes this is further enhanced by rapid snowmelt during the winter months. Based on monthly gravimetric sampling at 13 sites, Holness (2001a) concluded that in grey lava areas moisture and soil texture provide no constraint for segregation ice growth except during occasional dry spells. Scoria materials show a stronger spatial heterogeneity in fines and moisture content, leading to a higher potential spatial variability in soil frost process activity and associated landforms. Finally, all black lava areas were found to be non-frost susceptible and contain insufficient moisture for needle ice growth.

The maritime, mid-latitudinal setting of Marion Island results in low annual and diurnal temperature ranges. Mean annual ground surface temperatures range from +5.5 to +1.4°C, from sea level to 1 000 m a.s.l., respectively (Boelhouwers *et al.* 2003). The near-surface air temperature lapse rate is 0.5°C/100 m, which is marginally higher than the 0.45°C/100 m summer, and 0.4°C/100 m winter lapse rates measured in the free atmosphere (Schulze 1971). The island's thermal regime results in a soil frost climate dominated by diurnal frost cycles. Table 4.4 describes the increased frequency of soil frost cycles, freeze days and frost depth penetration with altitude as measured at four ground temperature logging sites. At 200 m a.s.l. soil frost is restricted to the May-September period, but occurs throughout the year at higher altitudes.

Despite the dominant diurnal frost environment, Boelhouwers (2003) reported the existence of permafrost at altitudes above 1 000 m a.s.l. Permafrost conditions occur in valley bottoms and on insolation-protected south and east facing ice-cemented slopes of scoria cones, which maintain slope angles of 46°, well in excess of the angle of repose of 36° at low altitudes. In addition, cryotic ground conditions are associated with snow and ice bodies in the summit region. Most of the existing permafrost is rapidly degrading, or has already disappeared, under current climate warming.

Slope aspect may also influence the local radiation budget and resulting thermal regime. Recent measurements of soil surface temperature around a coastal volcanic cone indicate that the role of aspect is strongly dependent on cloud cover and air circulation conditions (J. Boelhouwers, unpublished data). Overcast conditions associated with westerly circulation result in minimal ground temperature contrasts with slope aspect. By contrast, clear sky conditions under southerly air circulation result in strongly contrasting day-time differences in magnitude and timing of temperature change. Differences by aspect in nocturnal radiative heat loss are also enhanced under clear sky conditions with shaded slopes more readily reaching ground frost conditions. Thus, while the generally high cloud cover conditions minimize the role of slope aspect on ground frost frequency, climate change impact studies must consider the impact of change in cloud cover. Smith (2002) described a *c.* 200 hour, or *c.* 16%, increase in sunshine hours over the period 1951 to 1999. This trend is likely to enhance thermal contrasts by slope aspect and may partially offset warming trends through enhanced nocturnal cooling and, thus, maintain a high soil frost potential. This may in turn enhance spatial variability in soil movement rates by frost creep and solifluction.

Table 4.4 Soil frost frequency, intensity, duration for different altitudes (from Boelhouwers *et al.* 2003).

	+10 cm	**-1 cm**	**-5 cm**	**-10 cm**	**-20 cm**	**-40 cm**	**-80 cm**
Long Ridge North (200 m a.s.l.) June 1998 – April 2000							
Mean Annual Temp. (°C)	4.8	5.5	5.5	5.5	5.7	5.7	
Freezing index	-9.5	-3.5	0	0	0	0	
Freeze/thaw days (n/a)	87	62.5	1	0	0	0	
Freeze days (n/a)	3.5	4	0	0	0	0	
Days (n/a) with temps:							
0°C to > -2°C	71.5	61.5	1	0	0	0	
-2°C to > -4°C	22.5	10.5	0	0	0	0	
≤ -4°C	3	0	0	0	0	0	
Katedraalkrans Nek (750 m a.s.l.) May 1997 – October 1998							
Mean Annual Temp. (°C)	1.5	2.5	2.2	2.3	2.3	1.9	
Freezing index	-194.6	-99.6	-73.3	-31.1	-25.2	-36.9	
Freeze/thaw days (n/a)	189.5	180.5	126	29	19.5	14.5	
Freeze days (n/a)	98.5	114	126	106.5	97	103	
Days (n/a) with temps:							
0°C to > -2°C	131.5	204.5	245.5	135.5	116.5	117.5	
-2°C to > -4°C	101	75.5	6.5	0	0	0	
≤ -4°C	55.5	14.5	0	0	0	0	
Delta extension (1000 m a.s.l.) April 1999 – April 2000							
Mean Annual Temp. (°C)	0.8	1.4	1.8	1.2	1.7	2.0	2.0
Freezing index	-372.9	-215.4	-86.0	-96.4	-7.6	0	0
Freeze/thaw days (n/a)	221	212	121	68	27	0	0
Freeze days (n/a)	59	43	42	126	110	0	0
Days (n/a) with temps:							
0°C to > -2°C	80	115	116	181	137	0	0
-2°C to > -4°C	92	75	40	13	0	0	0
≤ -4°C	108	65	7	0	0	0	0

The role of snow on the ground thermal regime is generally considered to be one of insulation that limits ground frost cycles beneath the snow cover (e.g. Chambers 1966; Thorn 1979; Matsuoka 1996). Temperature profiles at Katedraalkrans describe near-isothermal conditions beneath snow, the lack of frost cycles and the reduction in soil frost intensity, at the soil surface. However, in contrast to regions with high seasonal and diurnal temperature ranges (Benedict 1976), snow cover has a distinct cooling effect on the underlying soils. The snow cooling effect extends the soil freeze from 10 cm to 40 cm depth and maintains a low intensity freeze until snow melt (Holness 2001a, 2003b). This explains the higher number of freeze days at the snow-rich site of Katedraalkrans Nek, compared to the snow-free, higher elevation, site of Delta extension (Table 4.4). Similar results from South Georgia (Smith 1960; Heilbronn & Walton 1984) suggest that this is a regional phenomenon. On Marion Island, above 750 m a.s.l. snow cover is present for much of the winter period, but is spatially discontinuous due to rapid wind re-distribution. This results in spatially heterogeneous ground frost conditions, favouring soil frost processes at wind exposed sites. Snow accumulation at preferential sites above 1 000 m a.s.l. survives over the summer period, thus further limiting periglacial process activity. The sites create local cryotic ground conditions, especially where additional insulation results from sediment deposition on snow bodies by wind or mass movements.

The new insights from the soil frost process studies highlight that although fundamental mechanisms are the same, the uniform material and moisture conditions much simplify the spatial patterns of movement dynamics on the island. The distinct combination of environmental conditions results in a periglacial process regime that is distinct from other periglacial landscapes and highly active. Slope angle, the altitudinal gradient of the soil frost regime (frost cycle frequency and depth), percentage fines, slope aspect, wind and vegetation interactions emerge as important environmental variables in understanding the spatial pattern and intensity of sediment movement rates. Some of these driving factors are sensitive to ongoing climate change. The emerging empirical database provides a basis for the spatial modelling of the landscape-scale terrestrial geomorphic dynamics of Marion Island to improve quantitative understanding of its responses to climate change and ecosystem interactions.

4.3.3 Other slope processes

In addition to the slow mass wasting processes induced by soil frost conditions, a range of rapid mass wasting landforms exists on the island. At present no full inventory of rapid mass wasting forms has been undertaken, but is most likely to have its largest concentration along the escarpment zone that separates the west island coastal platform from the interior slope. To date, observations have mostly focused on the eastern sector of the island as summarized by Nel *et al.* (2003). The authors described the occurrence of translational and rotational slides and debris flows on peat slopes at altitudes below 400 m a.s.l. and at slope angles from 17° to 55°. Translational slides are noted to be shallow (< 1 m) with the plane of failure either within the peat or at the bedrock contact. Rotational slides in peat are noted for drier parts of the island. Debris flows in the peat are channel-confined and appear triggered by disintegration of material released by peat slides. These observations on the peat slopes of Marion Island closely resemble those described for Macquarie Island (Campbell 1981; Selkirk 1998; Selkirk-Bell 2000). Similar to Macquarie Island, gradual peat accumulation is thought to increase shear stress over time, with failure being triggered by heavy rainfall events (Selkirk-Bell 2000; Nel *et al.* 2003).

Screes flank most scarps that border grey lava areas. Their surface material is largely stable as indicated by extensive lichen cover, but some rockfall activity is still ongoing (Nel *et al.* 2003). Small debris flows are described for a scoria cone by Boelhouwers *et al.* (2000). These are associated with low permeability surfaces where frost-heaved surface material becomes saturated, triggering the debris flow. Landforms are rapidly obliterated during subsequent frost heave events. Holness (2004) considered these flow events to be highly restricted spatially due to the general high permeability of the scoria slope surfaces.

No sediment budgets studies have been undertaken on Marion Island and especially the understanding of non-periglacial slope dynamics is still far from complete. There is no consensus as to the dominance of periglacial slope processes in the sub-Antarctic. However, on Marion Island slope materials have now been demonstrated to be highly mobile by diurnal frost creep and solifluction and to be more important than surface runoff. The volcanic materials with their high permeability are likely to reduce the effects of slope wash, which have been argued to be important on Macquarie Island (Taylor 1955a, 1955b; Selkirk 1998; Selkirk-Bell 2000). Rapid mass wasting is likely to be important both in terms of sediment fluxes and as a landscape disturbance factor in specific zones. To date no research has focused on these dynamics in any depth.

4.3.4 Zoogeomorphology

Although it is clear that periglacial (and previously glacial processes) are the major agents of geomorphic change in the interior and higher altitude areas of Marion Island, in the coastal areas the erosion, transport and deposition of sediment by wild animals may play a dominant role in shaping sections of the landscape.

Although a range of bird and marine mammal species is present on Marion Island, only nine species appear to play a significant role in shaping the landscape (Table 4.5). Each of these species has specific geomorphic impacts, and these impacts vary spatially according to their specific habitat usage pattern and behaviour. Further, through impacting populations of these species, humans have altered the geomorphic effectiveness of these agents and have altered the landscape.

Table 4.5 Key zoogeomorphic agents on Marion Island.

	Geomorphic action	Spatial extent	Populations	Anthropogenic influences
Surface nesting, flightless colonial seabirds				
King Penguins	Complete removal of peat and other unconsolidated material within large breeding colony boundaries. Extensive breeding areas of up to 50 ha at Sea Elephant Bay to Log Beach.	High density colonies on flat or gently sloping terrain adjacent to the coast. Impacts concentrated in a few large colonies.	165 000 to 380 000 breeding pairs (based on various estimates and dates)	
Macaroni Penguins	Complete removal of peat and other unconsolidated material within colony boundaries. Erosion of gullies and grooving of bedrock along paths to interior colonies. Observations of peat erosion to depth 1.4 m up to 5 m over an area of 10 ha at Kildalkey Bay suggest a total of 285 000 m^3 removed.	High density colonies on flat or gently sloping terrain adjacent to the coast, with some colonies on steeper rocky slopes or further inland where coastal sites not available. Impacts concentrated in a few large colonies in peat areas.	356 000 to 434 000 breeding pairs	
Rockhopper Penguins	Impacts limited by habitat preferences, but some limited striation of rock and removal of peat and unconsolidated sediment where colonies extend beyond un-vegetated lava areas.	Rugged black lava areas along the coast. Less concentrated colonies than the other two species.	67 000 to 173 000 breeding pairs	

Table 4.5 Continued

	Geomorphic action	Spatial extent	Populations	Anthropogenic influences
Burrowing seabirds				
Salvins Prions	Excavation of burrows at average densities of up to 88-115 burrows/ha in favoured habitats. Burrow volumes average 0.05 m^3 implying 5.8 m^3/ha excavated in favoured habitats. Total moved for Marion Island 4 610 m^3 to 46 104 m^3.	Vegetated hummocky black lava areas especially favouring closed fernbrake and *Acaena* herbfield, also using *Poa* tussock grassland	100s of 1 000 breeding pairs.	Feral cats were rapidly exterminating burrowing petrel populations (455 000 /a) in the 1970s and 1980s. There has been a rapid recovery of populations since cats were eliminated.
Blue Petrels	Excavation of burrows at average densities of up to 105-189 burrows/hectare in favoured habitats. Burrow volumes average 0.05 m^3 imply approximately 9.5 m^3/ha excavated in favoured habitats. Produces characteristic hummocky terrain in dense colonies. Total moved for Marion Island 461 m^3 to 4 610 m^3.	Vegetated flatter areas especially favouring *Cotula* herbfield, also using *Poa* tussock grassland	10s of 1 000 breeding pairs.	
Greatwinged Petrels	Excavation of burrows at average densities of 11-46 burrows/hectare in favoured habitats. Burrow volumes average 0.12 m^3 imply approximately 5.5 m^3/ha excavated in favoured habitats. Total moved for Marion Island 1 222 m^3 to 12 220 m^3.	Vegetated hummocky areas especially favouring *Poa* tussock grassland, as well as closed fernbrake and to a lesser extent *Cotula* herbfield.	10s of 1 000 breeding pairs.	

Table 4.5 Continued

	Geomorphic action	Spatial extent	Populations	Anthropogenic influences
Burrowing seabirds				
Whitechinned Petrels	Excavation of burrows at average densities of up to 15-31 burrows/hectare in favoured habitats. Burrow volumes average 0.4 m^3 imply approximately 12.4 m^3/ha excavated in favoured habitats. Nest structure includes a characteristic flooded entrance. Nests often associated with local slope collapse. Total moved for Marion Island 3 956 m^3 to 39 563 m^3.	Vegetated hummocky areas especially favouring *Poa* tussock grassland and *Acaena* herbfield.	10s of 1 000 breeding pairs	
Seals				
Sub-Antarctic Fur Seals	Localized trampling and disruption of vegetation occurs where breeding colonies extend onto vegetated areas.	Impacted areas include *Poa* tussock grassland and *Cotula* herbfield adjacent to landing beaches.	48 658	Exploitation started in 1803; within 7 years fur seals were economically extinct. Populations (along with the less common Antarctic Fur Seal) now rapidly expanding.
Elephant Seals	The great bulk of these animals flattens and compacts vegetation and peat bogs creating local hollows that coalesce and deepen to form composite wallows. Local drainage is disrupted, and a distinctive topography of vegetated ridges with intervening wallows results.	Moulting areas usually in *Poa* tussock grassland and *Cotula* herbfield adjacent to sandy or stony beaches where landing is possible.	2 009	Mostly exploited from 1810 to 1860 by which time elephant seals were economically extinct. Initial population recovery trends appear to be reversing.

Burrow volumes and impact observations from Holness unpublished data, burrow densities and habitat preferences from Schramm (1986), petrel populations from Cooper & Brown (1990), penguin populations from Crawford *et al.* (2003), seal populations and exploitation from Hänel & Chown (1998).

From a geomorphological point of view the nine keystone species can be divided into three broad groups, namely surface nesting flightless colonial seabirds, burrowing seabirds, and seals (Table 4.5). Surface nesting colonial seabirds result in significant, but localized, erosion. Macaroni and King penguins have the greatest geomorphic effect due to their numbers, concentrated breeding habit, breeding habitat preferences and individual mass, and are capable of rapidly eroding surfaces down to bedrock. Although their impacts are amongst the most spectacular examples of zoogeomorphic activity, they are spatially restricted to a handful of large colonies in close proximity to suitable landing beaches. Rockhopper penguins have a far more limited effect as they favour rocky areas and do not breed in the concentrated coastal colonies.

Nest excavation activity by burrowing seabirds (petrels and prions) moves a significant amount of material and creates a distinctive topography in vegetated lowland areas of Marion Island. Each species has specific breeding habitat preferences in terms of topography and vegetation, and hence impacts vary spatially. Furthermore, burrow size and characteristics for each species differ, and hence the geomorphic impacts differ. Table 4.5 provides estimates of the amount of material moved, based on burrow volumes and published species densities.

The activities of sub-Antarctic fur seals result in a distinctive hummock topography. Seal activity results in the compaction of peat surfaces, as well as vegetation destruction in the immediate vicinity of landing beaches. In addition, fur seal activity results in modification of pond and stream morphology in coastal areas. In vegetated areas near stony or sandy beaches suitable for landing, elephant seals exert a significant, but localized, effect on the landscape through the creation of wallows. The great bulk of these animals flattens and compacts vegetation and peat bogs, creating local hollows which combine and deepen to form composite depressions. Local drainage is disrupted, and a distinctive topography of vegetated ridges with intervening depressions results.

Animal populations, and hence their geomorphic impacts, have experienced significant changes due to direct and indirect human intervention during the past 200 years. Commercial exploitation in the 1800s drove populations of fur and elephant seals to economic extinction. Although their original populations are unknown, relict elephant seal wallows across suitable areas of the island attest to a dramatic reduction in geomorphic impact caused by the human-induced population crash. Fur seal populations are now recovering rapidly (and their impact is increasing), while initial recovery trends in elephant seal populations appear to be stabilizing. Indirectly, human actions have impacted on landscapes via alien fauna introductions. Feral cats were rapidly exterminating burrowing petrel populations (455 000 per year) in the 1970s and 1980s (Cooper & Brown 1990). However, there has been an apparent recovery of populations since cats were eliminated, with a consequent increase in zoogeomorphic activity.

4.4 The record of Holocene climate change

To date, much of the geomorphological research on Marion Island has focused on the terrestrial glacial and periglacial record as a proxy for Late Quaternary climate change. Paleoecological proxies from the coastal peat deposits have provided additional insights.

The glacial record of Holocene environmental change is fragmented with poor temporal constraints. Hall (1978) suggested a rapid deglaciation, now established to have started at 17-18 ka BP (Bianchi & Gersonde 2004), but does not further consider Holocene glacial activity. Evidence for possible early Holocene glacial activity exists in the form of cirque basins at Snok and at the summit. The summit basins carried remnants of permanent ice bodies when first observed in 1954 and 1961, but have undergone rapid degradation over the past four decades (Sumner *et al.* 2004). A terminal moraine has been identified in one of the basins, with a small active nival rampart on its lee-side margin. However, the Marion Island cirques have not produced the much more detailed record of glacial advance and retreat such as reported for other sub-Antarctic Islands (e.g. Frenot *et al.* 1997).

Depending on the extent of glaciation of the Feldmark plateau, the development of the glacial cirque at Snok and the valley glacier at Watertunnel are temporally constrained by the island-wide last glaciation, which started its termination at *c.* 18 ka BP and the obtaining of Holocene temperatures following the Younger Dryas at *c.* 11 ka BP (Bianchi & Gersonde 2004). Summit glacial basins are likely to have persisted throughout most of the Holocene with the possible exception of the Holocene optimum (10-8 ka BP), but geomorphological evidence is likely to have been disturbed by Holocene volcanic activity. The present moraines at the summit and the nival rampart at Snok are best placed as indicative of Little Ice Age cooling with present day nival activity still maintaining ramparts at preferential snow accumulation sites. Current warming is also likely to increasingly marginalize these processes at the higher altitudes in the Island's interior.

In the interior of Marion Island, thermal erosion and subsidence of areas underlain by buried glacial ice has been recorded (Hedding 2006). The result is the manifestation of thermokarst-like features such as thaw slumps on scoria slopes and the creation of a unique undulating or "kettle" topography. These meltout features and processes represent distinct landscape-process responses to climate change which is unique in the southern African context.

The summer snow line has risen from 600-850 m a.s.l. in 1954 and 1961, to 950 m a.s.l. in 1971 and is currently above summit level (1 200 m a.s.l.) (Sumner *et al.* 2004). The existence of a high altitude permanent snow cover in the late Holocene is also suggested by the absence of the large-scale relict periglacial landforms that occur at altitudes below 800 m a.s.l. (Hall 1981b, 1983b; Holness & Boelhouwers 1998; Holness 2003b). This suggests that the stone-banked landforms above 800 m a.s.l. formed upon snowline retreat over the past decades. Relict periglacial landforms are present in all Last Glacial deposits associated with grey lava areas and coastal moraines and take the form of stone-banked lobes and terraces, vegetation-banked terraces, blockfields and blockstreams. The dominance of stone-banked forms and vertically sorted blockstream surfaces in till indicate frost heave and creep-dominated movement with solifluction-dominated unsorted terraces restricted to sites with impervious substrates or upslope moisture sources. The similar morphometry and depth of vertical sorting in relict coastal forms and recent forms above 800 m a.s.l. (0.2-0.7 m) suggests formation under conditions similar or somewhat more severe than recorded at present at 1 000 m a.s.l. (mean annual ground surface temperature of +1.2°C). This indicates a temperature decrease of approximately 4-5.5°C from the present (Holness 2003b). Based on the closely corresponding summer sea surface temperature (Bianchi & Gersonde 2004) and Dome C deuterium records (Jouzel *et al.* 2001), this places the main phase of Holocene periglacial activity to the period immediately following deglaciation, terminating at around 11 ka BP when temperatures stabilized, enforced by the Holocene optimum. This interpretation is supported by the single-phase development of the landforms (Holness 2003b) and the steeper periglacial gradient in the relict record at Long Ridge (Holness & Boelhouwers 1998). It also implies the Marion Island plateau surfaces (e.g. Long Ridge, Feldmark Plateau) to have been at least seasonally snow free upon deglaciation.

Holness (2003b) interpreted the absence of gelifluction-dominated landforms as an argument against the existence of early Holocene permafrost. However, the occurrence of differential frost heave and resulting sorting does not preclude gelifluction. Rather, given the temperature scenario estimated for the coastal landforms and the morphometrical data in Holness (2003b), permafrost is likely to have occurred in a temporally restricted and spatially narrow altitudinal zone between *c.* 400 m a.s.l. and the permanent snow and ice bodies that stabilized above *c.* 800 m a.s.l.

Paleoecological studies on the coastal peat deposits on the east side of the island have provided additional proxies of Holocene environmental change. Schalke & Van Zinderen Bakker (1971) and Van Zinderen Bakker (1973) interpreted pollen spectra to indicate the transition of a low-altitude fjeldmark vegetation to the present dense grasses and phanerogram dominated vegetation during the amelioration period between deglaciation and the early Holocene. They note no marked vegetation or climate changes in the younger sections and obtain an oldest date of 9 500 BP, with an extrapolated age, assuming constant deposition, at the base of the core of 16 ka BP (Schalke & Van Zinderen Bakker 1971). Scott (1985) extended the pollen analysis from new peat cores, while Yeloff *et al.* (2007) provide a multi-proxy environmental reconstruction from a new core using pollen/non-pollen microfossil and macrofossil analyses, diatom, peat humification and tephra analyses. Both studies identify a vegetation succession in a landscape depression from barren fjeldmark to increasing *Azorella selago* abundance during initial peatland initiation. Ponds in the depressions are dominated by *Ranunculus biternatus* and *Montia fontana*. This is overgrown to develop a *Agrostis magellanica* and *Acaena magellanica* peatland. While the earliest example of this succession is recorded in the Macaroni Bay record to at least 10 ka BP, Scott (1985) and Yeloff *et al.* (2007) demonstrated this succession to have been initiated at different times during the Holocene at different locations. Based on the presence of tephra layers (Scott 1985; Yeloff *et al.*, 2007) and association with peat slides, Scott (1985) suggested that disturbances created by volcanic activity and geomorphic activity can have a long-term impact on vegetation succession. The spatial extent of the tephra layers is unknown, limiting assessment of the scale of impact of these volcanic events on Holocene vegetation development. As such, the paleoecological record appears to largely indicate local successional changes with no direct evidence for Holocene changes in temperature or precipitation. Yeloff *et al.* (2007) do, however, suggest a Little Ice Age signal at *c.*630 cal BP associated with increased mire wetness, followed by drier conditions from 170 cal BP to present.

4.5 Discussion and conclusions

Research on Marion Island's volcanic tectonic setting and evolution has not yet been able to conclusively explain the topography of the older grey lava surfaces. Glacial geomorphological evidence indicates sufficiently thick ice to cover most grey lava surfaces with the possible exception of the elevated topographies of the Feldmark Plateau and a portion of Long Ridge. Arguments by Chevalier (1986), supported by recent remote sensing visualisations, suggest that the elevated position of such grey lava surfaces, already existed in pre-Holocene times. Furthermore, the qualitatively older appearance of surface materials and the existence of the largest periglacial landforms on the island suggest an ice free environment. Glacial moraines at Watertunnel and a cirque at Snok, in the Feldmark area, are, thus, likely to have resulted from Late Glacial or early Holocene stages of ice cover.

None of the arguments supporting glaciation, or the absence thereof, are unequivocal. The nature of the Feldmark regolith has not been investigated or dated and the presence of landforms there, that are used to suggest an absence of ice-cover, may simply be a manifestation of a post-glacial Holocene weathering and mass wasting regime resulting from island-wide aspect differences. Globally, there are many problems associated with linking the morphometry of periglacial slow mass wasting forms with the severity of ground climate. While Matsuoka (2001) established a basic correlation between riser height and depth of movement, the maximum depth of movement recorded in solifluction lobes did not exceed 60 cm. Riser heights in excess of 3 m on Marion Island are, thus, likely the result of complex forms built from abundant local material supply (Boelhouwers *et al.* 2001), a local topography that allows deceleration (Matsuoka 2001), and abundant moisture supply (Holness 2003b).

The Holocene record of periglacial landforms and its relation to Late Quaternary environmental change presents further conundrums. While a rich record of relict periglacial landforms has been described, chronological uncertainties limit a more detailed interpretation of the island's climate history. There is a clear need to establish a better geochronology of volcanic and geomorphological features to unravel the sequence of events that has resulted in the present-day physical landscape. Additional K-Ar dating and the application of cosmogenic exposure techniques provide new possibilities to answer these long-standing questions. New research documenting glacial geomorphological landforms (Hedding 2006; I. Meiklejohn, unpublished data) highlights the need for mapping to establish clearer spatial correlations of available proxies, using a combined approach of modern remote sensing and GPS-based field mapping.

The application of traditional empirical methods in slope process studies on Marion Island has highlighted the distinctiveness of maritime, mid-latitudinal periglacial environments (Holness 2001a; Boelhouwers *et al.* 2003). These relate to the dominance of diurnal soil frost processes and resulting high soil surface movement rates, the importance of wind and the stratified solifluction landforms. The uniform material properties within till and scoria, abundant moisture, and high cloud cover, result in strong correlations between patterned ground morphometry, process rates and environmental parameters. Periglacial soil creep on sub-Antarctic islands has clear interactions with vegetation dynamics (e.g. Selkirk 1998; Holness 2001a). This is particularly evident in the form of the slope-scale patterns of vegetation and micro-topography, e.g. turf-banked steps and crescent-shaped *A. selago* cushions (Holness 2001a; Boelhouwers *et al.* 2003). The nature of the interaction between sediment movement and vegetation dynamics however remains unclear.

An understanding is emerging regarding the responses of the sub-Antarctic periglacial environment to climate change. Degradation of landforms is clearly evident at the higher altitudes of Marion Island and is associated with the contemporary disappearance of the glacial ice bodies and permanent snow (Boelhouwers 2003; Sumner *et al.* 2004). The responses to current warming are likely to be non-linear and spatially differentiated. While warming results in a decrease in frost cycle frequency, reduced snow cover may enhance summit altitude frost cycles (Holness 2001a, 2003b). Reduced precipitation may offset the sustained latent heat effects due to abundant soil water at high altitude (Boelhouwers 2003) and enhance freeze-thaw efficacy. On the other hand, while moisture is not presently a constraint, it may become so in specific topographic settings. Reduced cloud cover, as reported by Smith (2002), may enhance evaporation and leads to a greater differentiation of the radiation balance by slope aspect, both at the slope and island scale (J. Boelhouwers, unpublished data). These considerations may indicate an increased spatial variability or patchiness in the occurrence and rates of soil movement processes. This is likely to impact the vegetation dynamics on the island. Given the existing empirical database, spatial modelling of the periglacial dynamics at an island scale now provides the most rational way to develop a quantitative understanding of the slope dynamics and its sensitivity and responses to changes in climate variables.

Areas of importance that have not received adequate attention are the soil development and succession in response to Holocene volcanic activity, the interaction between animals and landscape dynamics and terrestrial sediment and nutrient budgets. Each of these identifies important elements and interrelations between the abiotic and biotic components of the island's ecosystem. Their interface between earth scientific and biological disciplines may explain their historical absence from the research agenda, but, equally, highlights their importance in terms of developing an integrated understanding of the islands' terrestrial and off-shore geo-ecological system.

4.6 References

Benedict, J.B. 1976. Frost creep and gelifluction features: a review. *Quaternary Research* **6**, 55-76.

Bertran, P., Hétu, B., Texier, J-P. & Van Steijn, H. 1997. Fabric characteristics of subaerial slope deposits. *Sedimentology* **44**, 1-16.

Bianchi, C. & Gersonde, R. 2004. Climate evolution at the last deglaciation: the role of the Southern Ocean. *Earth and Planetary Science Letters* **228**, 407-424.

Boelhouwers, J.C. 2003. Sensitivity and responses to climate change in the Subantarctic periglacial environment. In: Phillips, M., Springman, S-M. & Arenson, L.U. (Eds.). *Permafrost, Proceedings of the 8th International Conference on Permafrost.* Zürich, Switzerland, pp. 67-71.

Boelhouwers, J.C., Holness, S. & Sumner, P. 2000. Geomorphology of debris flows at Junior's Kop, Marion Island. *Earth Surface Processes and Landforms* **25**, 341-352.

Boelhouwers, J.C., Holness, S. & Sumner, P. 2003. The maritime Subantarctic: a distinct periglacial environment. *Geomorphology* **52**, 39-55.

Boelhouwers, J.C., Holness, S.D., Sumner, P.D. & Nel, W. 2001. Cryogenic *Landforms and Processes on Marion Island.* Final Report submitted to the South African Committee for Antarctic Research (SACAR), April 1996-March 2001.

Campbell, I.B. 1981. Soil pattern of Campbell Island. *New Zealand Journal of Science* **24**, 111-135.

Chambers, M.J.G. 1966. Investigations of patterned ground at Signy Island, South Orkney Islands: II temperature regimes in the active layer. *British Antarctic Survey Bulletin* **10**, 71-83.

Chevallier, L. 1986. Tectonics of Marion and Prince Edward Volcanoes (Indian Ocean): result of regional control and edifice dynamics. *Tectonophysics* **124**, 155-175.

Chevallier, L., Verwoerd, W.J., Bova, P., Stettler, E., du Plessis, A., du Plessis, J.G., *et al.* 1992. Volcanological features and preliminary geophysical investigations on Marion Island. *South African Journal of Antarctic Research* **22**, 15-35.

Cooper, J. & Brown, C.R. 1990. Ornithological research at the sub-Antarctic Prince Edward Islands: a review of achievements. *South African Journal of Antarctic Research* **20**, 40-57.

Crawford, R.J.M., Cooper, J., Dyer, B.M., Greyling, M.D., Klages, N.T.W., Ryan, P.G., *et al.* 2003. Populations of surface-nesting seabirds at Marion Island, 1994/95-2002/03. *African Journal of Marine Science* **25**, 427-440.

Francou, B. 1988. Eboulis stratifies dans les Hautes Andes Centrales du Perou. *Zeitschrift für Geomorphologie* **31**, 47-76.

Francou, B. 1989. Stratogenesis in slope waste deposits submitted to freeze – thaw action : a new conception. *Bulletin de l'Association Française pour l' etude du Quaternaire* **4**, 185-199.

Francou, B. 1990. Stratification mechanisms in slope deposits in high subequatorial Mountains. *Permafrost and Periglacial Processes* **1**, 249-263.

Frenot, Y., Gloaguen, J.C., Van de Vijver, B. & Beyens, J. 1997. Dating of some peat sediments and glacier fluctuations in the Kerguelen Islands. *Committée Récherche l'Académie Scientifique Paris (Life Sciences)* **320**, 567-573.

Gribnitz, K.H., Kent, L.E. & Dixon, R.D. 1986. Volcanic ash, ash soils and the inferred Quaternary climate of sub-Antarctic Marion Island. *South African Journal of Science* **82**, 629-635.

Hall, K. 1977. Evidence for Quaternary glaciation of Marion Island (sub-Antarctic) and some implications. In: Van Zinderen Bakker, E.M. (Ed.). *Antarctic Glacial History and World Palaeoenvironment*. Proceedings of a symposium held on 17th August 1977, during the 10th INQUA Congress, Birmingham, UK, pp.137-147.

Hall, K. 1978. *Quaternary Glacial Geology of Marion Island*. Ph.D. Thesis, University of the Orange Free State, South Africa.

Hall, K. 1979. Sorted stripes orientated by wind direction: some observations from sub-Antarctic Marion Island. *Earth Surface Processes and Landforms* **4**, 281-289.

Hall, K. 1980. Late glacial ice cover and palaeotemperatures on sub-Antarctic Marion Island. *Palaeogeography, Palaeoclimatology, Palaeoecology* **29**, 243-259.

Hall, K. 1981a. Quantitative analysis of till lithology on Marion Island. *South African Journal of Science* **77**, 86-90.

Hall, K. 1981b. Observations on the stone-banked lobes of Marion Island. *South African Journal of Science* **77**, 424.

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

Hall, K. 1983a. A reconstruction of the Quaternary ice cover on Marion Island. In: Oliver, R.L., James, P.R. & Jago, J.B. (Eds.). *Antarctic Earth Science*. Australian Academy of Science, Canberra, pp. 461-464.

Hall, K. 1983b. Observations of some periglacial features and their palaeoenvironmental implications on sub-Antarctic islands Marion and Kerguelen. *South African Journal of Antarctic Research* **13**, 35-40.

Hall, K. 1983c. Sorted stripes on sub-Antarctic Kerguelen Island. *Earth Surface Processes and Landforms* **8**, 115-124.

Hall, K. 1990a. Quaternary Glaciations in the Southern Ocean: Sector 0° Long. - 180° Long. *Quaternary Science Reviews* **9**, 217-228.

Hall, K. 1990b. Mechanical weathering rates on Signy Island, maritime Antarctic. *Permafrost and Periglacial Processes* **1**, 61-67.

Hall, K. 2002. Review of present and Quaternary periglacial processes and landforms of the maritime and sub-Antarctic region. *South African Journal of Science* **98**, 71-81.

Hall, K. 2004. Quaternary glaciation of the sub-Antarctic Islands. In: Ehlers J. & Gibbard P.I. (Eds.). *Quaternary Glaciations – Extent and Chronology, Part III*. Elsevier, Amsterdam, pp. 339-345.

Hall, K. & Walton, D.W.H. 1992. Rock weathering, soil development and colonisation under a changing climate. *Philosophical Transactions of the Royal Society of London B* **338**, 269-277.

Hall, K. & Williams, A.J. 1981. Animals as agents of erosion at sub-Antarctic Marion Island. *South African Journal of Antarctic Research* **10/11**, 18-24.

Hänel C. & Chown, S.L. 1998. *An Introductory Guide to the Marion and Prince Edward Island Special Nature Reserves*. Department of Environmental Affairs and Tourism, Pretoria.

Harris, C. & Davies, M.C.R. 2000. Gelifluction: observations from large-scale laboratorium simulations. *Arctic, Antarctic and Alpine Research* **32**, 202-207.

Hedding, D.W. 2006. *Geomorphology and geomorphological responses to climate change in the interior of sub-Antarctic Marion Island*. M.Sc. Thesis, University of Pretoria, South Africa.

Heilbronn, T.D. & Walton, D.W.H. 1984. The morphology of some periglacial features on South Georgia and their relationship to local environment. *British Antarctic Survey Bulletin* **64**, 21-36.

Holness, S.D. 2001a. *Periglacial slope processes, landforms and environment at Marion island, Maritime Subantarctic*. Ph.D. Thesis, University of the Western Cape, South Africa.

Holness, S.D. 2001b. The orientation of sorted stripes in the maritime Subantarctic, Marion Island. *Earth Surface Processes and Landforms* **26**, 77-89.

Holness, S.D. 2003a. Sorted circles in the maritime Subantarctic, Marion Island. *Earth Surface Processes and Landforms* **28**, 337-347.

Holness, S.D. 2003b. The periglacial record of Holocene environmental change of Subantarctic Marion Island. *Permafrost and Periglacial Processes* **14**, 69-74.

Holness, S.D. 2004. Sediment movement rates and processes on cinder cones in the maritime Subantarctic (Marion Island). *Earth Surface Processes and Landforms* **29**, 91-103.

Holness, S.D. & Boelhouwers, J. 1998. Periglacial indicators for Holocene climate change at Long Ridge, Marion Island, maritime sub-Antarctic. *South African Journal of Science* **94**, 399-403.

Jouzel, J., Masson, V., Cattani, O., Falourd, S., Stievenard, M., Stenni, B., *et al.* 2001. A new 27ky high resolution East Antarctic climate record. *Geophysical Research Letters* **28**, 3199-3202.

Kent, L.E. & Gribnitz, K.-H. 1983. Problematic Quaternary succession on Marion Island: volcanogenic or glacigenic? *South African Journal of Antarctic Research* **13**, 15-23.

Löffler, E. 1983. Macquarie island: a wind molded natural landscape in the Subantarctic. *Polarforschung* **53**, 59-74.

Mackay, J.R. & Mathews, W.H. 1974. Movement of sorted stripes, the Cinder Cone, Garibaldi Park, B.C., Canada. *Arctic and Alpine Research* **6**, 347-359.

Mahoney, J., le Roex, A.P., Peng, Z., Fisher, R.L. & Natland, J.H. 1992. Southwestern limits of Indian Ocean ridge mantle and the origin of low 206Pb/204Pb mid-ocean ridge basalt: Isotope systematics of the central Southwest Indian Ridge (17°-50°E). *Journal of Geophysical Research* **97**, 19771-19790.

Matsuoka, N. 1996. Soil moisture variability in relation to diurnal frost heaving on Japanese high mountain slopes. *Permafrost and Periglacial Processes* **7**, 139-151.

Matsuoka, N. 2001. Solifluction rates, processes and landforms: a global review. *Earth-Science Reviews* **55**, 107-134.

Matsuoka, N. 2005. Temporal and spatial variations in periglacial soil movements on alpine crest slopes. *Earth Surface Processes and Landforms* **30**, 41-58.

McDougall, I. 1971. Geochronology. In: Van Zinderen Bakker, E.M., Winterbottom, J.M. & Dyer, R.A. (Eds.). *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965-1966*. A.A. Balkema, Cape Town, pp. 72-77.

McDougall, I., Verwoerd, W. & Chevalier, L. 2001. K-Ar geochronology of Marion Island, Southern Ocean. *Geological Magazine* **138**, 1-17.

Meentemeyer, V. & Zippin, J. 1981. Soil moisture and texture controls of selected paramenters of needle ice growth. *Earth Surface Processes and Landforms* **6**, 113-125.

Meiklejohn, K.I. & Hedding, D.W. 2005. Marion Island. In: Wunderman, R., Venzke, E. & Mayberry, G. (Eds.). *Bulletin of the Global Volcanism Network* **30**, 16.

Nel, W. 2001. *A spatial inventory of glacial, periglacial and rapid mass movement forms on part of Marion Island: Implications for Quaternary environmental change*. M.Sc. Dissertation, University of Pretoria, South Africa.

Nel, W., Holness, S. & Meiklejohn, K.I. 2003. Observations on rapid mass movement and screes on sub-Antarctic Marion Island. *South African Journal of Science* **99**, 177-181.

Pérez, F.L. 1993. Talus movement in the high equatorial Andes: a synthesis of ten years of data. *Permafrost and Periglacial Processes* **4**, 199-215.

Schalke, H.J.W.G. & Van Zinderen Bakker, E.M. 1971. History of the vegetation. In: Van Zinderen Bakker, E.M., Winterbottom, J.M. & Dyer, R.A. (Eds.). *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965-1966*. A.A. Balkema, Cape Town, pp. 89-97.

Schramm, M. 1986. Burrow densities and nest site preferences of petrels (Procellariidae) at the Prince Edward Islands. *Polar Biology* **6**, 63-70.

Schulze, B.R. 1971. The climate of Marion Island. In: Van Zinderen Bakker, E.M., Winterbottom, J.M. & Dyer, R.A. (Eds.). *Marion and Prince Edward Islands: Report on the South African Biological and Geological Expedition 1965-1966*. A.A. Balkema, Cape Town, pp. 16-31.

Scott, L. 1985. Palynological indications of the Quaternary vegetation history of Marion Island (sub-Antarctic). *Journal of Biogeography* **12**, 413-431.

Selkirk, J.M. 1998. Active vegetation-banked terraces on Macquarie Island. *Zeitschrift für Geomorphologie* **42**, 483-496.

Selkirk-Bell, J.M. 2000. *Geomorphic processes and environmental change on Subantarctic Macquarie Island*. Ph.D. Thesis, Macquarie University, Australia.

Smith, J. 1960. Cryoturbation data from South Georgia. *Biuletyn Peryglacjalny* **8**, 72-76.

Smith, V.R. 2002. Climate change in the sub-Antarctic: an illustration from Marion Island. *Climate Change* **52**, 345-357.

Sumner, P.D. 2004. Rock weathering rates on Subantarctic Marion Island. *Arctic, Antarctic and Alpine Research* **36**, 123-127.

Sumner, P.D. & Meiklejohn, K.I. 2004. On the development of autochthonous blockfields in the grey basalts of Subantarctic Marion Island. *Polar Geography* **28**, 20-32.

Sumner, P., Meiklejohn, I., Boelhouwers, J. & Hedding, D. 2004: Climate change melts Marion's snow and ice. *South African Journal of Science* **100**, 395-398.

Taylor, B.W. 1955a. Terrace formation on Macquarie Island. *Journal of Ecology* **43**, 133-137.

Taylor, B.W. 1955b. The flora, vegetation and soils of Macquarie Island. *Australian National Antarctic Research Expedition Reports* **B11**, 84-192.

Thorn, C.E. 1979. Bedrock freeze-thaw weathering regime in an alpine environment, Colorado Front Range. *Earth Surface Processes and Landforms* **4**, 211-228.

Van Zinderen Bakker, E.M. 1973. The second South African biological expedition to Marion Island, 1971-1972. *South African Journal of Antarctic Research* **3**, 60-63.

Van Zinderen Bakker, E.M., Winterbottom, J.M. & Dyer, R.A. (Eds.) 1971. *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965-1966*. A.A. Balkema, Cape Town.

Verwoerd, W.J. 1971. Geology. In: Van Zinderen Bakker, E.M., Winterbottom, J.M. & Dyer, R.A. (Eds.). *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965-1966*. A.A. Balkema, Cape Town, pp. 40-53.

Verwoerd, W.J., Russell, S. & Berruti, A. 1981. 1980 volcanic eruption reported on Marion Island. *Earth and Planetary Science Letters* **54**, 397-422.

Wunderman, R., Venzke, E. & Mayberry, G. (Eds.) 2004. *Bulletin of the Global Volcanism Network* **29**(9), Smithsonian National Museum of Natural History, Washington DC.

Yeloff, D., Mauquoy, D., Barber, K., Way, S., Van Geel, B. & Turney, C.S.M. 2007. Volcanic ash deposition and long-term vegetation change on Subantarctic Marion Island. *Arctic, Antarctic and Alpine Research* **39**, 500-511.

CHAPTER 5

BIOLOGY IN THE OCEANOGRAPHIC ENVIRONMENT

CHRISTOPHER D. MCQUAID AND P. WILLIAM FRONEMAN

The earliest recorded study of the marine environment around the Prince Edward Islands was preliminary oceanographic work in the late nineteenth century done when HMS Challenger briefly visited the islands in 1873. However, it was only in 1976, that the French vessel, the *MS Marion Dufresene* undertook the first comprehensive investigation of the biology of the marine environment (Pakhomov & Froneman 1999a). Another ten years lapsed before a focussed programme began the systematic study of the marine biology of the islands and the links between physical oceanography, life in the water column, and the air breathing, land-based top predators breeding on the islands. During the late 1980s, the Marion Offshore Ecosystem Study (MOES) addressed the problem of how a tiny archipelago of two small islands could sustain the enormous populations of pinnipeds and birds that aggregate there during summer and autumn (Pakhomov & Froneman 1999a; McQuaid & Froneman 2004). The initial target of investigation was the existence of an island mass effect at the archipelago, a phenomenon of greatly enhanced primary production in a low productivity part of the ocean, and how, or whether this production fed into the top predators. The programme was unusual in laying equal emphasis on the availability of food and the importance of its physical supply to consumers. By the end of the programme an understanding of trophic relationships between autochthonous or allochthonous food sources and the top predators was developed as what became known as the "life support system" of the

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 97-120

islands (Pakhomov & Froneman 1999a; Pakhomov & Chown 2003; McQuaid & Froneman 2004). Over the past decade, two further research programmes have modified and refined this concept, expanding the physical scale of study to concentrate more explicitly on the offshore environment, particularly towards the west or upstream of the islands (McQuaid & Froneman 2004). The results of these investigations have clearly demonstrated the close link between the physical environment and the distribution and species composition of the plankton assemblages within the Polar Frontal Zone in the region of the islands. More significantly, they have demonstrated the importance of both horizontal and vertical hydrodynamics as the ultimate determinants of the carrying capacity of the islands, and the intimate relationships among sea floor topography, large-scales current systems and the biology of the islands, with ramifying effects from phytoplankton primary production to nutrient exchange between land and sea. Throughout the 15 years of study of the islands' marine ecosystem, there has been a major logistic constraint on the research. Research is primarily based on the research vessel, *SA Agulhas* during re-supply cruises to the island weather station. As a result there has been limited ship's-time for research. More critically, cruises have been confined to late summer/autumn so that there is little understanding of seasonal variation in functioning of the ecosystem. This puts an important caveat on the findings: in such a high latitude region, seasonality is likely to be profoundly significant.

The physical oceanography of the region is described elsewhere (Lutjeharms & Ansorge 2008), but two broad aspects are important. The islands lie within the Polar Frontal Zone; that is north of the Antarctic Polar Front and south of the sub-Antarctic Front. The islands also lie in the path of the Antarctic Circumpolar Current, giving them a west-east or upstream-downstream axis.

5.1 Phytoplankton studies

The open waters of the Polar Frontal Zone (PFZ) of the Southern Ocean are not particularly poor in nutrients, but they are subject to almost continuous deep mixing due to wind stress. In fact, Perissinotto *et al.* (1990a) calculated that water column stability accounts for the majority of the total variance in primary production in the region of the islands. As a result, phytoplankton biomass and production is generally low and normally dominated by small-celled picophytoplankton (< 2.0 μm) (Fig. 5.1). These microalgae are able to tolerate both the poor light environment caused by a deep mixed layer, and the comparatively low macronutrient availability, (Perissinotto *et al.* 1990a; Laubscher *et al.* 1993; Balarin 2000). This allows them to dominate the overall phytoplankton community, and at times they form over 90% of total integrated biomass and production (Fig. 5.1).

Exceptions to this scenario occur in terms of both chlorophyll density and phytoplankton size structure at the two major frontal systems in the region, the sub-Antarctic Front (SAF) to the north and the Antarctic Polar Front (APF) to the south of the islands (Fig. 5.1). An exception also occurs in the shallow shelf waters between Marion and Prince Edward Islands, which demonstrate the so-called "island mass effect" of markedly enhanced primary production close to oceanic islands (Fig. 5.2; Table 5.1) (Allanson *et al.* 1985; Boden 1988; Perissinotto *et al.* 1990a, b). In all three cases, total phytoplankton biomass and phytoplankton production are two to three times higher than in the open waters of the PFZ. Equally significant is that different size classes dominate the phytoplankton community within these areas of elevated biomass. In these areas the most important size classes are not the picophytoplankton, but the nano- (2.0-20.0 µm) and microphytoplankton (> 20.0 µm) (Fig. 5.1) (Froneman & Pakhomov 1998a; Pakhomov & Froneman 1999a).

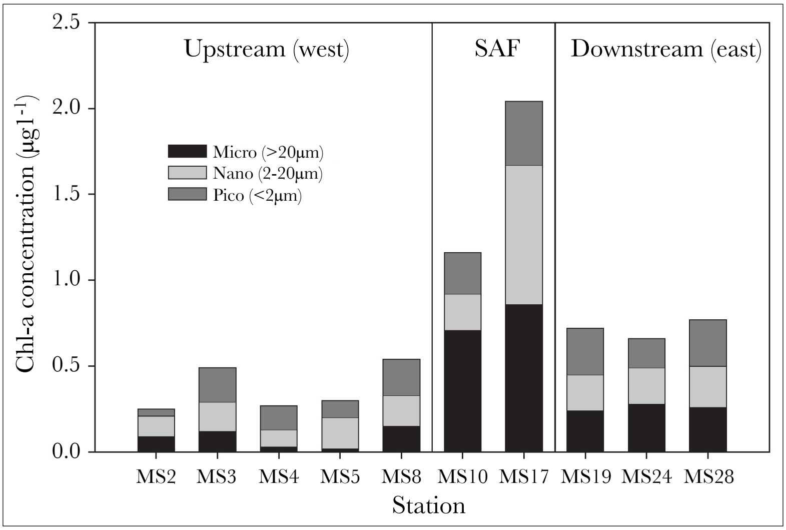


Figure 5.1 Size fractionated chlorophyll-a concentrations at selected stations occupied in the open waters of the Polar Frontal zone upstream and downstream of the Prince Edward islands in the vicinity of the sub-Antarctic Front (SAF) during April/May 1996 (modified from Froneman & Pakhomov 1998a).

In the absence of data for most months of the year, it is not possible to assess whether there are strong seasonal patterns in total chlorophyll-a concentration and primary production in the region of the islands (see Pakhomov & Froneman (1999a) and references therein). However, studies in the PFZ in the Atlantic sector of the Southern Ocean during summer have recorded values two to three times higher than in the vicinity of the island during winter, suggesting that seasonality is likely to be marked (Laubscher *et al.* 1993; Froneman *et al.* 1995, 2001).

Using data collected during three cruises in the waters between and in the immediate vicinity of the Prince Edward Islands, Perissinotto *et al.* (1990a) showed that elevated phytoplankton biomass and productivity in the shallow shelf waters between the islands could be attributed to the vertical structure of the water column and increased availability of macronutrients. The more pronounced vertical structure of the water column between the islands was attributed to high levels of freshwater run-off from the islands being retained over the shelf by anti-cyclonic eddies of the Taylor Cone type (Perissinotto *et al.* 1990a). In addition there was increased availability of macronutrients (mainly ammonia and urea) in these waters, derived from guano run-off from the islands, with this high nutrient water also being entrained by the anti-cyclonic eddies (Perissinotto & Duncombe Rae 1990). This combination of elevated water column stability and macronutrient availability in the inter-island region generated phytoplankton blooms dominated by chain forming diatom species of the genera *Chaetoceros* (mainly *Chaetoceros radicans*) and *Fragilariopsis*. During these blooms, the total chlorophyll-a concentration may exceed 1.5 mg chl-a m^{-3} (Allanson *et al.* 1985; Pakhomov & Froneman 1999a; Pakhomov & Chown 2003).

Table 5.1 Estimates of total phytoplankton biomass and production during the various cruises conducted in the open waters of the Polar Frontal Zone of the Southern Ocean and in the immediate waters surrounding the Prince Edward Islands. SAF = sub-Antarctic Front; ND = no data.

Source	Period	Region	Phytoplankton Biomass (mg chl-a m^{-3})	Phytoplankton Production (mg C m^{-2} d^{-1})
El-Sayed *et al.* (1979)	March, 1976	Inter-island region	0.09-1.88	211
Miller *et al.* (1984)	September 1982	Inter-island region	0.01-0.5	ND
Allanson *et al.* (1985)	May, 1983	Inter-island region	0.10 –2.30	84-2100
Allanson *et al.* (1985)	November, 1983	Inter-island region	0.06-0.87	ND
Van Ballegooyen *et al.* (1989)	May 1987	Inter-island region	0.05-0.45	47-312
Perissinotto & Duncombe Rae (1990)	April, 1985	Inter-island region	0.1-2.8	70-3000
Balarin (2000)	April, 1998	Inter-island region	0.2-0.8	119-353
		Open water	< 0.2	94-442
Pakhomov *et al.* (2000b)	April, 1989	Open waters	< 0.1	ND
		Inter-island region /SAF	0.31-0.45	ND
Froneman & Balarin (1998)	April 1997	Open waters	0.29 –0.52	ND
Bernard & Froneman (2005)	April/May 2003	Open waters	0.15-0.28	ND

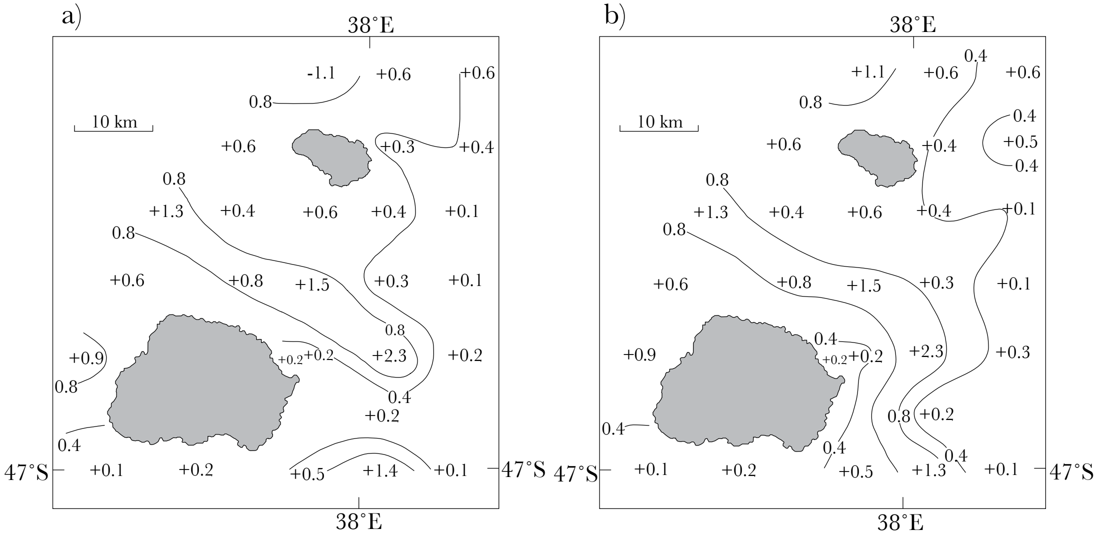


Figure 5.2 Spatial distribution of total chlorophyll-a concentrations at surface (A) and 50 m (B) depths in the vicinity of the Prince Edward Islands in May 1983. Units are mg chl-a m^{-3}. (Modified from Allanson *et al.* 1985).

The occurrence of Taylor Cone type eddies in the shelf waters is thought to be linked to the proximity of the SAF to the islands. The Antarctic Circumpolar Current (ACC) shows highest flow rates near the fronts that delimit it (Pakhomov *et al.* 2000a; Ansorge & Lutjeharms 2002) and under conditions when the SAF lies far to the north of the islands, current speeds past the islands are comparatively low (Ansorge & Lutjeharms 2002). This results in a weak interaction between the ACC and the archipelago and this in turn allows the domination of frictional over advective forces. As a consequence, eddies are trapped between the two islands. On the other hand when the SAF lies farther south (i.e. closer to the islands), advective forces prevail and the islands act as a through-flow system (Perissinotto & Duncombe Rae 1990; Pakhomov *et al.* 2000b). Eddies are absent from the inter-island region under flow through conditions.

Although it is clear that large-scale oceanographic processes are responsible for generating periodic phytoplankton blooms in the shelf waters, recent work suggests that phytoplankton growth may also be enhanced on much smaller scales through the localised effects of kelp beds. The local kelp, *Macrocystis laevis*, forms extensive beds in shallow waters close to shore and in relatively deep water (60 m) over the Natal Bank. (Attwood *et al.* 1991; Perissinotto & McQuaid, 1992a). This species grows to nearly 30 m in length and forms a dense surface canopy that visibly subdues the effects of swells. The canopy also retains freshwater run-off from the islands. An extensive survey conducted near Marion Island demonstrated that retention of freshwater by kelp beds promotes local water column stability (Pakhomov *et al.* 2002). Thus, physical retention of freshwater in and close to kelp beds could potentially promote the growth of phytoplankton in a manner similar to that proposed for the anti-cyclonic eddies, but on very much smaller scales.

5.2 Zooplankton studies

Only a single survey has investigated the community composition and distribution of the protozooplankton (< 200 μm) in the waters surrounding the Prince Edward Islands (Froneman & Balarin 1998). This study indicated that the densities of protozooplankton ranged between 5 x 10^3 and 7 x 10^3 ind. l^{-1} and were numerically dominated by nanoflagellates (< 20 μm), dinoflagellates and ciliates. The values, measured during autumn, are in the range recorded in the PFZ in other sectors of the Southern Ocean during both summer and winter (Froneman & Perissinotto 1996a, b), suggesting that there is little seasonality in the densities or the broad taxonomic composition of the protozooplankton within the PFZ. Comparison of offshore and inshore waters of the islands gives no evidence of clear spatial patterns in the community structure and distribution of the protozooplankton, nor are there obvious temporal patterns on scales of days (Froneman & Balarin 1998).

When we consider the larger zooplankton (> 200 μm), it is clear that there is no endemism among the holoplankton of the PFZ (Boden & Parker 1986; Pakhomov & Froneman 1999a) and that the zone effectively acts as an ecotone. There is often extreme spatial variability in species composition of the zooplankton, which can largely be ascribed to the periodic intrusion of tongues of Subtropical surface waters from the north, and of Antarctic surface waters from the south (Pakhomov & Froneman 1999a; Hunt *et al.* 2001; Bernard & Froneman 2002, 2003). Far field generated eddies or frontal meanders from both the Subtropical Convergence (STC) and the APF, which penetrate into the PFZ, may further contribute to the variability in the zooplankton community (Ansorge *et al.* 1999; Froneman *et al.* 1999). Because the oceanographic environment is spatially so variable, the zooplankton community within the PFZ contains animals with quite different biogeographic affinities. For example, the crustaceans include species that are sub-Antarctic, Subtropical and Antarctic in origin (Ansorge *et al.* 1999; Pakhomov *et al.* 2000a; Hunt *et al.* 2001; Bernard & Froneman 2002, 2003).

The macrozooplankton may contribute substantially (up to 45%), to the total zooplankton biomass (Pakhomov & Froneman 1999b), but generally both numbers and biomass of the zooplankton community in the region are dominated by mesozooplankton (200-2 000 μm) (Perissinotto & Boden 1989; Hunt *et al.* 2001; Bernard & Froneman 2002, 2003). For example, a study by Hunt *et al.* (2001) showed that copepods comprised 52-88% of all zooplankton counted during six surveys carried out over the period 1996 to 1999. Among the mesozooplankton, the pteropod *Limacina retroversa* and small copepods (200-500 μm) of the genera *Oithona*, *Calanus* and *Metridia* are especially abundant, forming 47-71% of total numbers (Bernard & Froneman 2002). Despite this, mesozooplankton biomass is dominated by the larger (1 000-2 000 μm) size classes, which form an average of 66% (SD = ± 10.2%) of total biomass (Bernard & Froneman 2002). The most well represented species within these larger mesozooplankton size classes are chaetognaths (*Eukrohnia hamata* and *Sagitta gazellae*), amphipods (*Themisto gaudichaudi*) and euphausiids (*Thysanoessa* spp.).

By far the most important groups (by numbers and biomass) in the macrozooplankton are euphausiids (*Euphausia vallentini* and *Nematoscelis megalopes*), chaetognaths (*Sagitta gazellae* and *S. maximum*) and tunicates (mainly *Salpa thompsoni*) (Pakhomov & Froneman 1999b; Pakhomov *et al.* 2000a; Gurney *et al.* 2002). The contribution of these main groups demonstrates a high degree of spatial and temporal variability with no clear patterns (Pakhomov & Froneman 1999b). Average abundance and biomass of the macrozooplankton within the upper 300 m of the water column is generally low, < 20 ind. 1 000 m^{-3} and < 300 mg dwt 1 000 m^{-3} respectively (Pakhomov & Froneman 1999b; Pakhomov *et al.* 2000b; Gurney *et al.* 2002). There are no seasonal data on the macrozooplankton, but the presence of up to 5 million breeding pairs of top predators on the islands during summer (Williams *et al.* 1979), the majority of which are directly dependant on the surrounding oceans for their food, suggests that there is a strong seasonal pattern in macrozooplankton availability. Certainly estimates of total macrozooplankton abundance and biomass for the PFZ and indeed in the vicinity of the Prince Edward Islands during winter are nearly an order of magnitude lower than the values recorded in the PFZ in other sectors of the Southern Ocean in summer (Pakhomov *et al.* 2000b).

Patterns in the spatial distribution of zooplankton abundance and biomass in the PFZ and near the Prince Edward Islands are well documented (see reviews of Pakhomov & Froneman 1999a; McQuaid & Froneman 2004). Shifts in the zooplankton community structure within the PFZ are strongly coupled to the periodic intrusion of water masses into the region. Generally, each water mass intruding into the PFZ contains a unique zooplankton community (Fig. 5.3). In the absence of obvious oceanographic features, the open waters of the PFZ exhibit a high degree of spatial variability in zooplankton abundance and biomass with no clear patterns (Fig. 5.4) (Froneman & Balarin 1998; Hunt *et al.* 2001; Bernard & Froneman 2002, 2003). There is however, some evidence to suggest that the lowest zooplankton abundances and biomass values in the PFZ are associated with the warmer sub-Antarctic surface waters (Hunt *et al.* 2001), while the colder Antarctic surface waters that periodically penetrate into the PFZ are usually characterised by elevated zooplankton abundance and biomass values (Hunt *et al.* 2001).

Although there are no clear patterns on such smaller scales, on larger scales, the zooplankton shows similar spatial patterns to the phytoplankton. The main frontal systems to the north and south of the islands are usually characterised by a zooplankton community with high abundances and biomass (Pakhomov & Froneman 1999a; Bernard & Froneman 2003). Just as higher chlorophyll levels at the fronts are due to the presence of large microphytoplankton cells, so elevated zooplankton biomass at the fronts is linked to an increase in the contribution of the larger macrozooplankton, particularly euphausiids, tunicates and chaetognaths to the total zooplankton abundance and biomass (Pakhomov & Froneman 1999b).

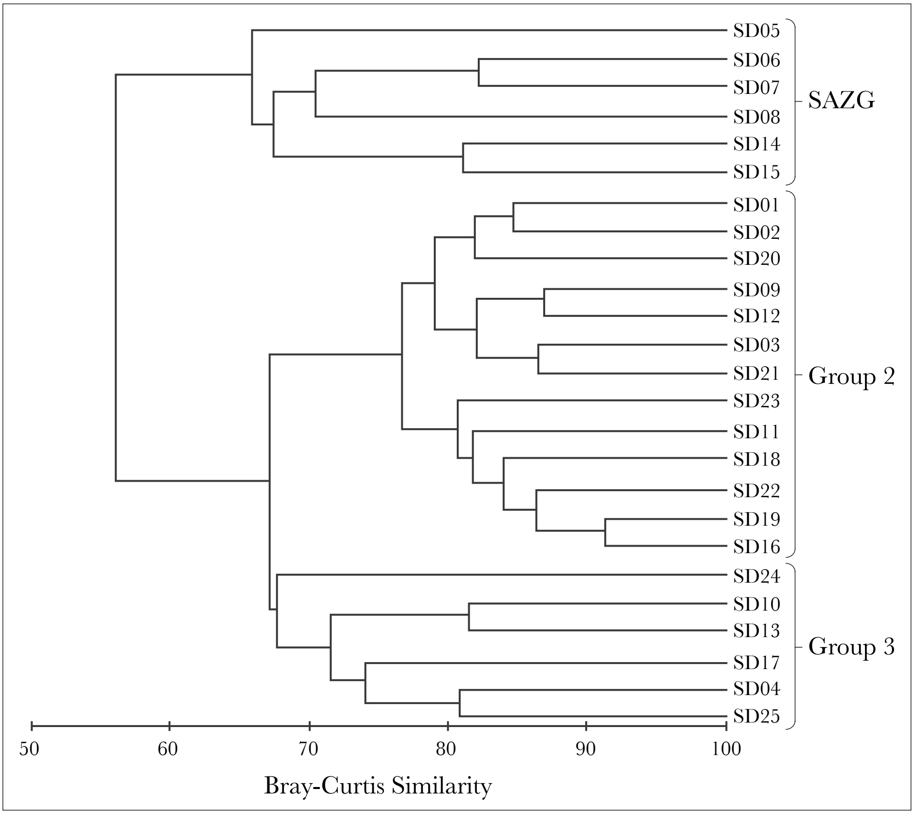


Figure 5.3 Dendrogram showing the classification of mesozooplankton abundance data collected during the first Marion Offshore Ecosystem Variability Study (MOEVS I), April 2001 (PRIMER Computer Package). SAZG – sub-Antarctic Zone Group (after Bernard & Froneman 2002).

Another spatial pattern that is emerging reflects the interaction of the ACC with the South-West Indian Ridge to the west of the islands. This interaction generates both warm and cold core features that subsequently drift in an easterly direction towards the islands (Ansorge & Lutjeharms 2003; Ansorge *et al.* 2004). A biological survey conducted within a warm core feature generated in this way indicated that such features can be characterised by stocks of both macrozooplankton (mainly euphausiids and amphipods) and micronekton that are higher than in the surrounding waters (Pakhomov *et al.* 2003). This is because the features are spawned from the frontal systems, which are characterised by elevated zooplankton biomass (Pakhomov & Froneman 1999b; Bernard & Froneman 2003). This characteristically high biomass of macrozooplankton and nekton biomass makes it likely that these features, especially their edges, represent important foraging grounds for some of the top predators found at the islands, such as the Grey-headed Albatross, *Thalassarche chrysostoma* (Nel *et al.* 2001). More recently, a similar pattern has been shown for Frigatebirds in the Mozambique Channel (Weimerskirch *et al.* 2004).

While the zooplankton and phytoplankton show similar increases at the fronts, they show contrasting patterns close to the islands. Diatom blooms often occur in the inter-island region, but in the immediate vicinity of the islands, total zooplankton biomass is generally lowest in the shallow shelf water between the two islands. This is especially true during the daytime (Perissinotto & McQuaid 1992b; Pakhomov & Froneman 1999a, b). The observed pattern was thought to reflect the predation impact of the large number of top predators feeding on zooplankton trapped by the shallow bottom topography of the shallow shelf waters and so unable to avoid predation by sinking to depth (Perissinotto & McQuaid 1992b). The zooplankton in the shelf water would subsequently be replenished during the night when the majority of the top predators were inactive. This process was termed the "*replenishing hypothesis*" (Perissinotto & McQuaid 1992b), and preliminary calculations showed that approximately 3 200 tons of zooplankton and 310 tons of myctophid fish could be advected over the island shelf every 24 hours (Perissinotto & McQuaid 1992b). This mass of zooplankton would be sufficient to sustain the zooplanktivorous top predators on the two islands (Perissinotto & McQuaid 1992b). The advection of zooplankton to the islands by the easterly flowing ACC and the periodic development of dense phytoplankton blooms between the two islands generated by the anti-cyclonic eddies trapped on the shallow shelf waters was subsequently termed the "*life support system*" of the Prince Edward Islands (Pakhomov & Froneman 1999a; Pakhomov & Chown 2003; McQuaid & Froneman 2004).

A more recent survey employing both trawling and acoustic surveys (Fig. 5.4) suggested that the low zooplankton biomass observed on the shallow island shelf could be ascribed to the interaction between the physical environment and behavioural patterns of the macrozooplankton rather than the predation impact of the top predators on the islands (Pakhomov & Froneman 1999b). Because the islands act as an obstacle to flow of the ACC, it is suggested that flow acceleration will cause the bulk of the water containing the zooplankton to flow around, rather than between the two islands (Pakhomov & Froneman 1999b). Also, many of the larger zooplankton are found below the depth at which water would be transported onto the shallow island shelf. As a result, the macrozooplankton would drift around the islands forming a belt of high concentration in close proximity to the island shelf (Fig. 5.5). The elevated macrozooplankton stocks associated with the outer edges of the island shelf would be likely to form important foraging grounds for many of the top predators found on the islands.

Finally, on a very small scale, a distinctive zooplankton community is associated with the kelp beds (Pakhomov *et al.* 2002). Combined with the suggestion that water column stability within kelp beds may enhance phytoplankton production, this suggests that not only the benthos of the kelp beds is unique, but the pelagic communities of kelp beds may also be quite different from those of the open waters of even the inshore region.

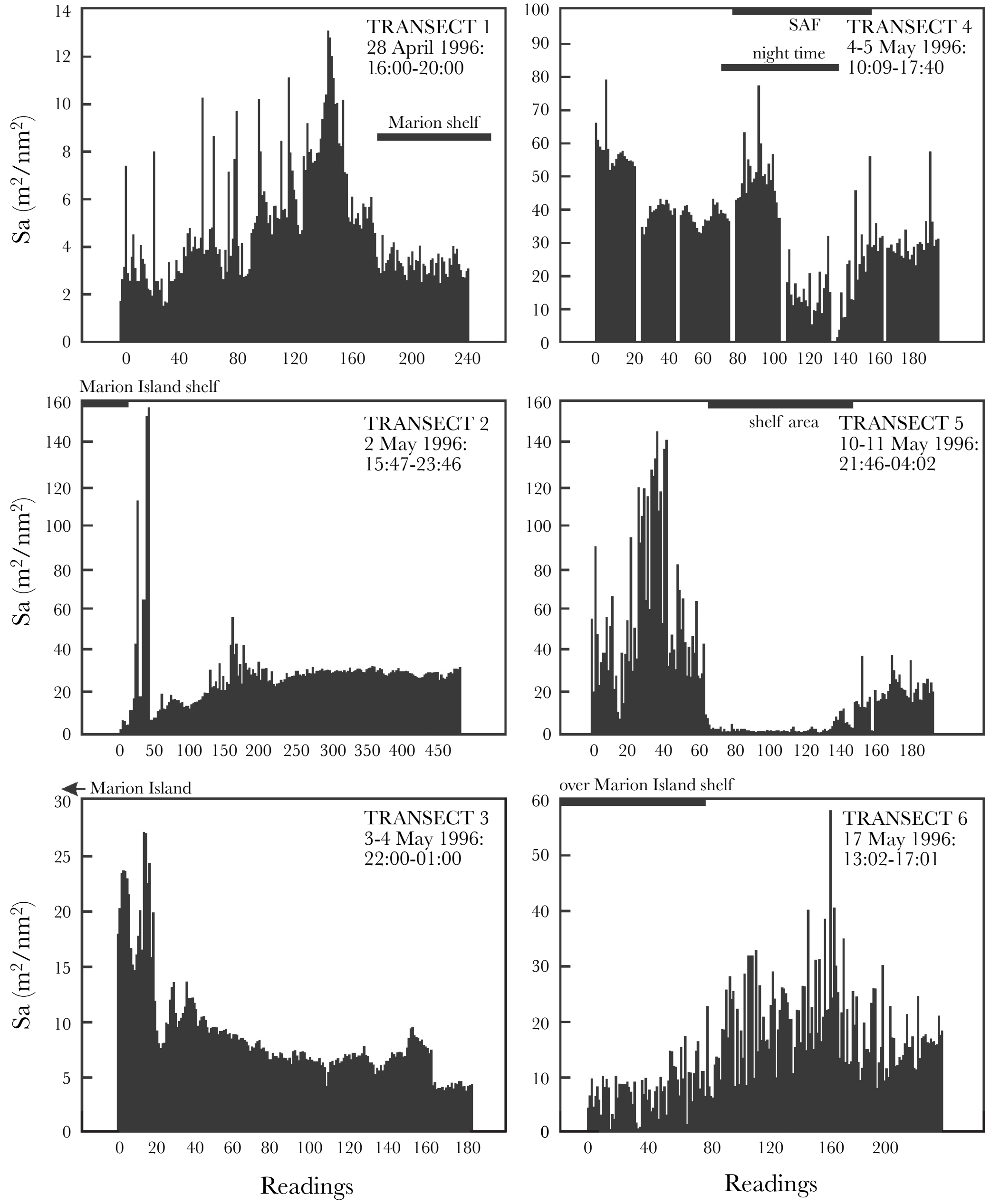


Figure 5.4 Acoustic surveys in the vicinity of the islands highlighting the spatial variability in the macrozooplankton biomass in the offshore waters and in the waters between and adjacent to the Prince Edward Islands; SAF = sub-Antarctic Front (after Pakhomov & Froneman 2000).

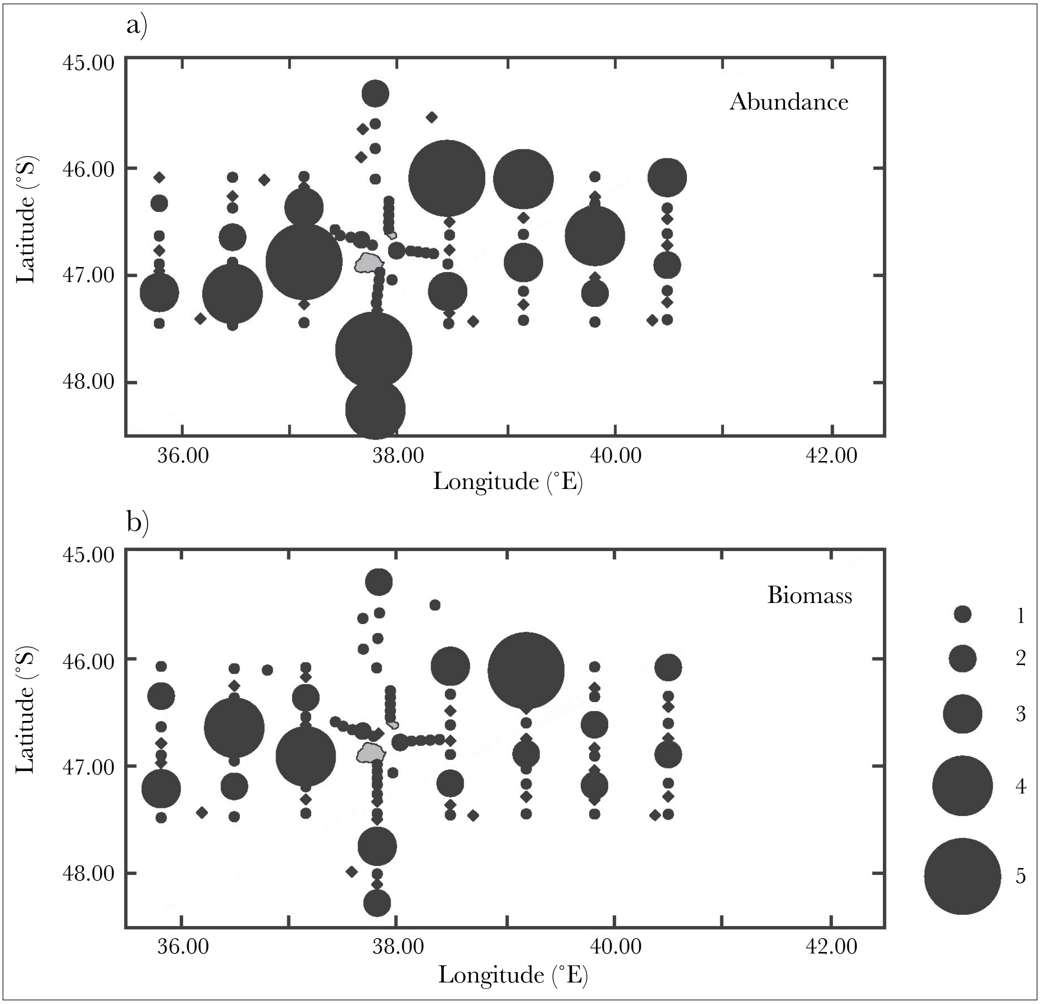


Figure 5.5 Spatial variability in total mesozooplankton abundance and biomass during the MOES cruise conducted in 1989. Abundance: 1: < 10; 2: 10-49; 3: 50-99; 4: 100-200; 5: > 200 individuals m^{-3}. Biomass: 1: < 1; 2: 1-5; 3: 5-10; 4: 10-20; 5: > 20 mg dwt m^{-3} (after Pakhomov *et al.* 2002).

Short-term variability in the zooplankton community structure and biomass in the shallow shelf region of the Prince Edward Islands has been investigated by Pakhomov *et al.* (2000a). Results of these studies indicate that shifts in the zooplankton community within the region were strongly coupled with pronounced water pulses that occurred within the trench located between the two islands. In accord with previous studies (Pakhomov & Froneman 1999b), the biomass of macrozooplankton in the offshore region was three to eight fold higher than that recorded within the waters of the shallow island shelf region (Pakhomov *et al.* 2000c).

Thus we see high spatial variability in the zooplankton, partly because the PFZ is functionally an ecotone, and partly because of permanent (frontal systems, island shelf region) and temporary (upstream eddies) features of the area. In addition to this spatial variability, a key feature of the larger zooplankton in particular is the extreme inter-annual variability in biomass and species composition of the major taxonomic groups (Grindley & Lane 1979; Boden & Parker 1986; Perissinotto & Boden 1989; Hunt *et al.* 2001; Bernard & Froneman 2002, 2003, 2005). Estimates of total zooplankton abundance and biomass in the open waters of the PFZ and close to the islands demonstrate a high degree of inter-annual variability and range from < 10 to 4 500 ind. m^{-3} and between < 0.01 and 150 mg Dwt. m^{-3}, respectively (Table 5.2; Fig. 5.5). While there is no doubt that there is enormous real inter-annual variability, some of the differences in estimates of zooplankton abundance and biomass may be ascribed to the differences in sampling methodology (both the gear employed and depth of sampling) during the different surveys (Pakhomov & Froneman 1999a). It is also likely that the contribution of the larger macrozooplankton (> 2 cm) to total zooplankton abundance and biomass was underestimated as the majority of surveys used sampling gear (Bongo or WP-2 nets) that would have under-sampled the larger components of the zooplankton because of net avoidance.

One species deserves special consideration as a key component of the zooplankton community of the entire ecosystem, the caridean shrimp *Nauticaris marionis*. *Nauticaris marionis* is restricted to the shallow shelf waters within the inter-island region (Perissinotto & McQuaid 1990; Pakhomov *et al.* 1999; Vumazonke *et al.* 2003) with maximum abundances typically occurring at depths of 50 to 100 m (Branch *et al.* 1993). Although no quantitative surveys on the abundance and distribution of the shrimp have been undertaken around the islands, preliminary data from dredge and photographic surveys suggest that the shrimp ranks only after bryozoans in terms of total shelf benthic biomass (Perissinotto & McQuaid 1990). Further evidence of its numerical abundance in the shallow shelf waters can be derived from gut content analyses of a number of top predators that feed relatively close inshore, with foraging ranges of < 300 km. *Nauticaris marionis* forms a substantial component in the diets of a variety of penguins including the King, Macaroni and Gentoo Penguins (Adams & Klages 1987, 1989), flying seabirds (e.g. Crozet Shag) (Espitalier-Noel *et al.* 1988) and demersal fish (Pakhomov & Froneman 1999a).

The life history and population dynamics of the shrimp have recently been investigated in the waters surrounding the Prince Edward Islands (Vumazonke 2004). These studies indicate that the shrimp is a partially protandric hermaphrodite with peak reproduction in late summer/early autumn (March-May). It was previously assumed that the extensive kelp beds in the shallow shelf waters provided a refuge for the planktonic larvae of the shrimp. However, a survey conducted within the kelp beds showed that larvae of *N. marionis* were rare and as a consequence, the kelp beds could be ruled out as a primary habitat for its larvae (Pakhomov *et al.* 2002). The mechanism by which larvae of the shrimp are retained in the vicinity of the islands, rather than being swept downstream, remains unknown (Pakhomov *et al.* 2002).

Table 5.2 Estimates of the total zooplankton abundance and biomass during the various surveys conducted to the region of the Prince Edward Islands over the period 1976 to 2004.

Source	Season	Abundances (ind. m^{-3})	Biomass (mg dwt. m^{-3})	Net type
Grindley & Lane (1979)	March, 1976	400-4850	8.7-28.4	WP-2
Grindley & Lane (1979)	November, 1976	1575-1854	14.6-34.9	WP-2
Boden & Parker (1986)	May, 1983	22-594	13.0-53.0	N70V
Perissinotto (1992)	April, 1985	150-229	17.4-30..0	Bongo
Perissinotto (1992)	April, 1989	130-191	32.3-56.8	Bongo
Froneman *et al.* (1998a)	April, 1996	23-184	0.76 –8.39	Bongo
Froneman *et al* (1998b)	April/May, 1997	5- 263	0.55-15.7	Bongo
Ansorge *et al.* (1999)	April, 1989	10-312	2.47-62.70	Bongo
Bernard & Froneman (2002)	April/May, 2001	49-1512	0.7-25.0	Bongo
Bernard & Froneman (2003)	April, 2002	78-1034	9.8-27.9	Bongo

5.3 Nekton studies

Nekton tends to be scarce around the islands, with generally low values of abundance and biomass in both offshore and inter-island waters of the Prince Edward Islands (Gon & Klages 1988). Typical values are < 1.5 ind. 1 000 m^{-3} and < 0.1 g dwt. 1 000 m^{-3} (Pakhomov *et al.* 2001; McQuaid & Froneman 2004), though these may be underestimates, as they include data from surveys that employed Bongo nets for sampling, when net avoidance was undoubtedly a problem.

Although there are no significant differences in total nekton abundance or biomass between the open waters of the PFZ and the inter-island shelf waters, there is a distinct spatial pattern in the composition of the nekton community (Pakhomov *et al.* 2001). Adult mesopelagic fish predominate in the open waters of the PFZ, but are virtually absent within the inter-island region, where only their larvae occur (Pakhomov *et al.* 2001). This pattern is believed to reflect the behavioural responses of individual fish and the consequences of their vertical migration patterns, rather than the removal of adults by top predators foraging from the islands (Pakhomov *et al.* 2001; McQuaid & Froneman 2004). Within the shelf waters, numbers and biomass of the nekton are dominated by demersal fish species. The situation is quite different in the vicinity of the SAF and the APF, where demersal fish show low numbers and biomass (> 2 ind. 1 000 m^{-3} and > 0.5 mg dwt. 1 000 m^{-3}), but densities of mesopelagic fish are elevated (Pakhomov & Froneman 1999b).

5.4 Biological interactions

Studies of the biological interactions among the biota of the system have focussed on trophic relationships (Perissinotto *et al.* 1990a; Froneman *et al.* 2002; Gurney *et al.* 2002; Bernard & Froneman 2002, 2003). These studies have spanned a wide range of spatial and size scales, particularly addressing the role of grazing in controlling phytoplankton populations and of predation in regulating prey populations. An important trend is the tendency for grazing efficiency, food chain length, the efficiency of energy transfer and the dominant patterns of energy flow to be set according to which size classes of phytoplankton predominate. Thus absolute levels of primary production may ultimately determine zooplankton biomass, but which groups of zooplankton predominate depends largely on the size composition of the phytoplankton. The size structure of the phytoplankton in turn mainly depends on conditions of mixed layer depth and nutrient availability. This dependence highlights the intimate connection between oceanographic conditions and the biology of this ecosystem, but there are other ways in which physical conditions, particularly hydrodynamics, influence biological interactions. One is the concentration of macrozooplankton around the perimeter of the island plateau because of flow patterns around the obstacle formed by the islands themselves. This has implications for biological interactions over the shallow shelf waters and for where the land-based predators are likely to find profitable foraging grounds. A second example is the generation of anti-cyclonic eddies formed upstream of the islands by the interaction of the ACC and the South-west Indian Ridge. These offer high concentrations of zooplankton around their margins, which make them potentially good foraging sites for birds. A third is the existence of different zooplankton communities within and outside the kelp beds, partly due to the changes in water movement characteristics imposed by the dampening effects of kelp fronds.

Turning to the importance of phytoplankton size structure, we have already seen that picophytoplankton dominate in the open waters of the PFZ, with larger cells forming the bulk of primary producer standing stocks at the fronts and close to the islands (Fig. 5.1). As a result there are two broad scenarios in which the primary consumers of phytoplankton differ and different groups form the bulk of consumer biomass. The open waters of the PFZ are characterised by small organisms such as picophytoplankton, protozooplankton and copepods, while the fronts and the waters in the vicinity of the islands are similar in supporting additional components of large organisms such as microphytoplankton, macrozooplankton and mesopelagic fish.

The situation is not always so simple as the zooplankton appear to track phytoplankton biomass under some conditions, but not others. For example the biomass of both groups is higher at the fronts than in open waters of the PFZ, but this does not hold near the islands where the phytoplankton form occasional blooms of very high biomass, but zooplankton biomass over the shelf is relatively low. The broad correlation of producer and consumer biomass is not unexpected, but there are competing hypotheses to account for the breakdown of this correlation at the islands: predation by the land-based predators and advection around the perimeter of the island plateau (see above).

Estimates of the protozooplankton grazing impact on phytoplankton in the waters surrounding the islands range between 1 and 8% of the daily standing stock and between 9 and 71% of potential primary production (Froneman & Balarin 1998). A distinct spatial pattern in the grazing activities of protozooplankton was evident, with the lowest rates being recorded upstream of the islands, where picophytoplankton predominate, and the highest downstream, where large phytoplankton cells are more abundant (Froneman & Balarin 1998). Thus the pattern in protozooplankton grazing pressure reflects the difference in size structure of the phytoplankton community, which in turn reflects the physical environment. The estimates of grazing impact of the protozooplankton for the region are in the range reported for other aquatic environments where small picophytoplankton cells dominate total chlorophyll-a concentration (Froneman & Perissinotto 1996a, b; Froneman *et al.* 1997).

The feeding ecology of the numerically dominant meso- and macrozooplankton within the region of the islands and in the open waters of the PFZ during austral autumn and winter has received considerable attention over the past two decades (see for example Perissinotto & Boden 1989; Perissinotto 1992; Gurney *et al.* 2002; Bernard & Froneman 2003; Froneman & Bernard 2004). Unfortunately data for the other seasons are lacking, so that it is not possible to gauge the strength of seasonality in grazing impact of the zooplankton that undoubtedly exists within the region.

In the open waters of the PFZ the grazing impact of the mesozooplankton is highly variable, but generally their effect on the phytoplankton is only moderate, accounting for < 25% of the integrated chlorophyll-a biomass or < 50% of the daily-integrated phytoplankton production (Perissinotto 1992; Bernard & Froneman 2002, 2003). The relatively weak effect of zooplankton grazing is attributable to the size composition of the phytoplankton, which is dominated by picophytoplankton cells that are too small to be grazed efficiently (Fortier *et al.* 1994). Paradoxically, during periods when phytoplankton blooms occur in the vicinity of the islands, mesozooplankton grazing impact is even lower. The daily impact of the zooplankton under these conditions accounts for < 10% (range 5-10%) of the chlorophyll-a standing stock and < 20% (range 9-17%) of the daily phytoplankton production (Perissinotto 1992). This is unexpected as these blooms are formed by diatoms, however, the predominant species are large chain forming species (e.g. *Chaetoceros* spp.), which are too large for the mesozooplankton to feed on (Perissinotto 1992). As a result, the bulk of bloom production appears to be exported to the benthic community of the inter-island shelf (Perissinotto 1992; Pakhomov & Froneman 1999a).

There have been limited studies of macrozooplankton grazing, but they appear to take an even smaller proportion of integrated chlorophyll-a biomass and production, usually < 5% (Gurney *et al.* 2002). This is due partly to the small size of phytoplankton cells in the PFZ, and partly to the low abundances of the macrozooplankton throughout the region (see above).

In response to the unfavourable size composition of the phytoplankton, the zooplankton consume alternative carbon sources to meet their daily carbon requirements. A response of the zooplankton the unfavourable phytoplankton size composition within the PFZ is a broadening of diet to include alternative carbon sources in order to meet their daily carbon requirements. These include protozooplankton and metazoans, and, closer to the islands, detritus derived from the extensive kelp beds that surround them (Kaehler *et al.* 2000; Gurney *et al.* 2001; Froneman & Bernard 2004; Kaehler *et al.* 2006). Although much of the focus has been on grazing interactions between zooplankton and phytoplankton, it is important to recognise that communities in the vicinity of the island do not rely exclusively on allochthonous carbon imported as oceanic phytoplankton carried to the islands by the Antarctic Circumpolar Current. Food web analyses based on the analysis of stable isotopes indicate that the contribution of kelp detritus is considerable, particularly in the case of the near shore benthic and kelp associated communities (Kaehler *et al.* 2000). Similarly, autochthonous inter-island diatom blooms influenced the isotope signature of the benthos of the island plateau (Kaehler *et al.* 2000). Given the probability of extreme seasonality in patterns of primary production within the region, it is likely that the zooplankton show high temporal variability in diet, but there are no data available to test this.

One of the key features of the zooplankton community within the PFZ is the high contribution of the carnivorous zooplankton to total zooplankton standing stock (Froneman & Pakhomov 1998b; Froneman *et al.* 1998b, 2002; Gurney *et al.* 2002). In fact, the carnivorous zooplankton can contribute up to 20% of the total zooplankton biomass (Froneman & Pakhomov 1998b; Froneman *et al.* 1998b, 2000a). The carnivorous zooplankton may play an important role in structuring the local zooplankton community and may also increase the localised efficiency of the biological pump (Froneman *et al.* 2002).

Key groups among the zooplankton predators are chaetognaths, amphipods and medusae (Froneman & Pakhomov 1998b; Froneman *et al.* 1998b, 2000b, 2002). Gut content analyses indicate that in the waters surrounding the islands, most of these are opportunistic predators, feeding on the most abundant mesozooplankton prey, which are mainly copepods (Froneman & Pakhomov 1998b; Froneman *et al.* 1998b, 2002). The daily predation impact of the carnivorous zooplankton ranges between < 1 and 45% of the mesozooplankton standing stock with values of 20% being not uncommon (Froneman & Pakhomov 1998b; Froneman *et al.* 2002). The high variability in the effects of these predators in the region is linked to the extreme variability in their abundance and biomass, which in turn reflects the extreme variability of the oceanographic environment. Predator behaviour is also important as swarming behaviour (e.g. among amphipods) can enormously enhance the variability driven by the physical environment of the PFZ (Froneman *et al.* 2002).

Lastly, one of the key biological interactions at the islands involves the swimming shrimp, *N. marionis*. Gut content analyses and feeding experiments indicate that *N. marionis* is an opportunistic predator feeding on a variety of prey including detritus, benthic organisms and plankton (Pakhomov *et al.* 1999; Vumazonke *et al.* 2003). Preliminary evidence suggests that there are distinct differences in the composition of the diet of males and females, with the diet of females comprising a greater proportion of plankton compared to the males (Vumazonke *et al.* 2003). Localised diatom blooms are poorly grazed, with much of their biomass sedimenting out and fuelling the benthic suspension feeders. *Nauticaris marionis* in turn feeds on both benthic species and detritus (Perissinotto & McQuaid 1990). Because it forms a substantial component of the diets of seabirds feeding close to the islands, *N. marionis* appears to be a key species, indirectly routing autochthonous diatom production to the land-based predators. *Nauticaris marionis* is thus important in coupling the pelagic and benthic components and also the marine and terrestrial components of the Prince Edward Island ecosystem (Pakhomov *et al.* 1999; Vumazonke *et al.* 2003).

It is clear that there are especially intimate links between the physics and the biology of this ecosystem, with the consequences of physical effects ramifying to the very top of the food chain. This implies that long-term shifts in the oceanographic environment will have extremely powerful, if indirect, effects on the top predators.

5.5 Impact of global climate change on biology of the oceanographic environment

Although evidence of the impact of global climate change on the terrestrial ecosystem of the Prince Edward Islands is now relatively well documented (Smith & Steenkamp 1990; Smith 1992, 2002; Chown & Smith 1993; le Roux & McGeoch 2008), the impact of global climate change on the marine ecosystem of the Prince Edward Islands has only recently received attention. Global climate change in the Southern Ocean is likely to be associated with shifts in the position and intensity of the major frontal systems and changes in oceanic circulation patterns within the region of the islands. There are clear signs of change associated with warming effects. In each case these changes seem ultimately to be driven by a southward shift in the average latitude at which the sub-Antarctic Front is found (see also le Roux 2008). Perhaps the strongest evidence of long-term changes in the ecosystem associated with climate change, concerns long-term changes in the average meridional position of the SAF and changes in seabird populations. Data collected over 16 years suggested that, since the 1970s, the SAF has shown an erratic, but discernible shift to the south (Hunt *et al.* 2001). While there is enormous inter-annual (and shorter-term) variability in the position of the front, it is generally recorded 1 degree of latitude farther south at present than in the 1970s.

The most direct effect of a meridional shift in the position of the SAF concerns the species composition of the zooplankton. An examination of the zooplankton community structure in the region of the islands over the past two decades indicates that the contribution of Antarctic species to total zooplankton species richness has decreased by some 20% (Pakhomov *et al.* 2001), while at the same time, the contribution of subtropical species has increased from 6% to 26% (Pakhomov *et al.* 2001) (Fig. 5.6). This shift in species composition of the zooplankton is likely to be associated with an increase in the frequency of intrusions of warmer waters into the PFZ resulting from southward migration of the SAF (Pakhomov *et al.* 2001). In addition to changes in the zooplankton species composition, Hunt *et al.* (2001) suggested that the more frequent intrusion of sub-Antarctic surface waters into the PFZ will coincide with a decrease in the total zooplankton biomass in the vicinity of the islands as sub-Antarctic surface waters are generally characterised by low productivity (Hunt *et al.* 2001; Bernard & Froneman 2003).

Less direct than the effects of long-term changes on species composition, but perhaps more significant, are changes in hydrodynamics around the islands. Because flow speeds are relatively high at the SAF, a shift in the position of the front implies changes in the balance between advective and frictional forces where the ACC interacts with bottom topography around the islands. Essentially, we anticipate that, if the front becomes closer to the islands and advective forces become more powerful, then retention of water over the island plateau will become less frequent, while through-flow conditions become more frequent. This should result in less frequent diatom blooms over the plateau, so that sources of primary production near the islands change, while the feeding grounds of the front itself shift farther south, decreasing foraging distances for land-based predators on the islands.

Support for both predictions is strong. Considering first a change in the types of food available to consumers, a stable isotope study of the swimming prawn *N. marionis*, indicated that the δ^{13}C values of the shrimp had undergone a significant decrease over the period 1984 to 2000 (Pakhomov *et al.* 2004). The decrease in δ^{13}C signature suggests a shift in the primary carbon sources utilised by the shrimp. The most likely driving force for the shift in the diet of the shrimp is a reduction in overall marine productivity in the region of the islands, mediated by a reduction in the frequency of occurrence of diatom blooms within the inter-island region (Pakhomov *et al.* 2004). This is linked to predictions on higher-order consumer populations. The absence of phytoplankton blooms within the inter-island region is likely to coincide with a decrease in the biomass of *N. marionis*. We have no data on the population dynamics of *N. marionis*, but there is strong evidence from long-term changes in bird populations that the indirect effects of a meridional shift in the position of the SAF have ramifications to the top of the food chain. The period over which the SAF has shifted south has seen medium- to long-term increases in populations of offshore feeding birds such as Grey-headed Albatrosses and Northern Giant Petrels, that are likely to feed at the front, and a simultaneous decrease in inshore feeders such as Rockhopper Penguins (Pakhomov & Chown 2003; see also Ryan & Bester 2008). Interestingly, species with mixed diets, like the Macaroni Penguin, have showed less of a decline over the corresponding period.

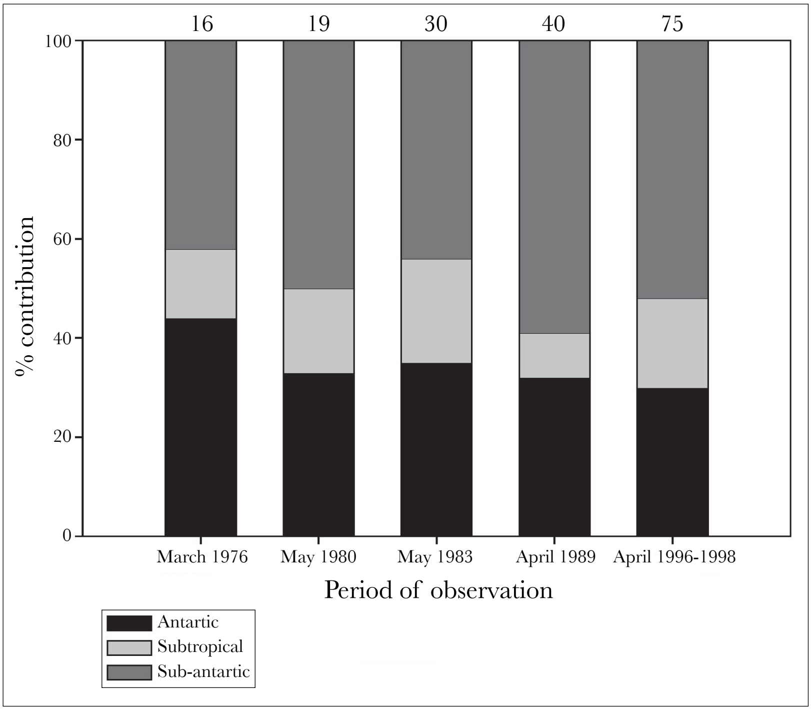


Figure 5.6 Long term changes in the contribution of Antarctic, sub-Antarctic and subtropical species to total zooplankton in the vicinity of the Prince Edward Islands. Values at the top of the bars indicate the number of species positively identified (after Pakhomov *et al.* 2001).

The observed changes in zooplankton community structure, isotopic signature of *N. marionis* and the dynamics of bird populations all suggest that global climate change has already influenced the biology of the region in quite profound ways. There is always an argument for further study of an ecosystem. However, in this case, it is clear that the entire system is in a state of perhaps dramatic flux and if we are to be able to differentiate between natural background variability in the system and long-term trends driven by extrinsic forces such as climate change, then long-term research on the biology of the marine ecosystem of the Prince Edward Islands is critical.

5.6 Acknowledgements

We would like to thank the National Research Foundation (NRF), Department of Environmental Affairs (DEAT), USAID and the Centre for Invasion Biology for providing funds and facilities for the book. Finally, we would like

to thank the officers and crew of the research vessel *SA Agulhas*, our colleagues from the University of Cape Town and the postgraduate students from the Department of Zoology and Entomology, Rhodes University for contributing to the successful completion of numerous surveys to the Prince Edward Islands over the past two decades.

5.7 References

Adams, N.J. & Klages, N.T. 1987. Seasonal variation in the diet of the King Penguin (*Aptenodytes patagonicus*) at the sub-antarctic Marion Island. *Journal of Zoology* **212**, 313-334.

Adams, N.J. & Klages, N.T. 1989. Seasonal variation in the diet of Gentoo penguins (*Pygoscelis papua*) at the sub-antarctic Marion Island. *Waterbirds* **12**, 30-36.

Allanson, B.R., Boden, B.P., Paker, L. & Duncombe Rae, C. 1985. A contribution to the oceanology of the Prince Edward Islands. In: Siegfied, W.R., Condy, P.R. & Laws, R.M. (Eds.). *Antarctic Nutrient Cycles and Food Webs*. Springer, Berlin, pp. 38-45.

Ansorge, I.J., Froneman, P.W., Lutjeharms, J.R.E., Bernard, K.S., Bernard, A., Lange, L., *et al.* 2004. An interdisciplinary cruise dedicated to understanding eddies upstream of the Prince Edward Islands. *South African Journal of Science* **100**, 319-323.

Ansorge, I., Froneman, P.W., Pakhomov, E.A., Lutjeharms, J.R.E., Van Ballegooyen, R. & Perissinotto, R. 1999. Physical-biological coupling in the waters surrounding the Prince Edward Islands (Southern Ocean). *Polar Biology* **21**, 135-145.

Ansorge, I.J. & Lutjeharms, J.R.E. 2002. The hydrography and dynamics of the ocean environment of the Prince Edward Islands (Southern Ocean). *Journal of Marine Systems* **37**, 107-127.

Ansorge, I.J. & Lutjeharms, J.R.E. 2003. Eddies originating at the South-west Indian ridge. *Journal of Marine Systems* **39**, 1-18.

Attwood, C., Lucas, M.I., Probyn, T.A., McQuaid, C.D. & Fielding, P.J. 1991. The contribution of the kelp *Macrocystis laevis* to primary production in the Prince Edward seas. *Polar Biology* **11**, 129-133.

Balarin, M.G. 2000. *Size fractionated phytoplankton biomass and primary production in the Southern Ocean*. M.Sc. Thesis, Rhodes University, South Africa.

Bernard, K. & Froneman, P.W. 2002. Mesozooplankton community structure in the Southern Ocean upstream of the Prince Edward Islands. *Polar Biology* **25**, 597-604.

Bernard, K. & Froneman, P.W. 2003. Mesozooplankton community structure and grazing impact in the Polar Frontal Zone during austral autumn 2002. *Polar Biology* **26**, 268-275.

Bernard, K.S. & Froneman, P.W. 2005. Trophodynamics of selected mesozooplankton in the Polar Frontal Zone, Southern Ocean, during austral autumn 2004. *Polar Biology* **28**, 594-606.

Branch, G.M., Attwood, C.G., Gianakouris, D. & Branch, M.L. 1993. Patterns in the benthic communities on the shelf of the sub-Antarctic Prince Edward Islands. *Polar Biology* **13**, 23-34.

Boden, B.P. 1988. Observations of the island mass effect in the Prince Edward archipelago. *Polar Biology* **9**, 61-68.

Boden, B.P. & Parker, L.D. 1986. The plankton of the Prince Edward Islands. *Polar Biology* **5**, 81-93.

Chown, S.L. & Smith, V.R. 1993. Climate change and short term impact on feral house mice at the sub-Antarctic Prince Edward Islands. *Oecologia* **96**, 508-516.

El-Sayed, S.Z., Bennon, P., David, P., Grindley, J.R. & Murail, J-F. 1979. Some aspects of the biology of the water column studies during the 'Marion-Durfresne' cruise 08. *Comité National Française des Recherches Antarctiques* **44**, 127-134.

Espitalier-Noel, G., Adams, N.J. & Klages, N.T. 1988. Diet of the Imperial *Cormorant Phalacrocorax* atriceps at sub-Antarctic Marion Island. *Emu* **88**, 43-46.

Fortier, L., Le Fevre, J. & Legendre, L. 1994. Export of biogenic carbon to fish and the deep ocean: the role of large planktonic microphages. *Journal of Plankton Research* **16**, 809-839.

Froneman, P.W., Ansorge, I., Pakhomov, E.A. & Lutjeharms, J.R.E. 1999. Plankton communities and the physical environment in the waters surrounding the Prince Edward Islands in late austral summer 1997. *Polar Biology* **22**, 145-155.

Froneman, P.W. & Balarin, M.S. 1998. Structure and grazing impact of the protozooplankton community in the waters surrounding the sub-antarctic Prince Edward Islands. *Polar Biology* **20**, 198-205.

Froneman, P.W. & Bernard, K.S. 2004. Trophic cascading in the Polar Frontal Zone of the Southern Ocean in austral autumn 2002. *Polar Biology* **27**, 112-118.

Froneman, P.W., Laubscher, R.K. & McQuaid, C.D. 2001. Size fractionated primary production in the south Atlantic and Atlantic sectors of the Southern Ocean. *Journal of Plankton Research* **23**, 611-622.

Froneman, P.W. & Pakhomov, E.A. 1998a. Biogeographic study of the planktonic communities of the Prince Edward Islands. *Journal of Plankton Research* **20**, 653-669.

Froneman, P.W. & Pakhomov, E.A. 1998b. Trophic importance of the chaetognaths *Eukrohnia hamata* and *Sagitta gazellae* in the pelagic subsystem of the Prince Edward Islands in late austral summer 1996. *Polar Biology* **19**, 242-249.

Froneman, P.W., Pakhomov, E.A., Gurney, L.J. & Hunt, B.P. 2002. Predation impact of carnivorous zooplankton in the vicinity of the Prince Edward Island archipelago in austral autumn 1998. *Deep-Sea Research II* **49**, 3243-3254.

Froneman, P.W., Pakhomov, E.A. & Meaton, V. 1998a. Surface distribution of microphytoplankton of the southwest Indian Ocean along a repeat transect between Cape Town and the Prince Edward Islands. *South African Journal of Science* **94**, 124-128.

Froneman, P.W., Pakhomov, E.A., Perissinotto, R. & Laubscher, R.K. 1997. Dynamics of the plankton communities during seasonal ice melt in the Lazarev Sea in austral summer 1994-1995. *Marine Ecology Progress Series* **149**, 201-214.

Froneman, P.W., Pakhomov, E.A., Perissinotto, R. & Meaton, V. 1998b. Community structure and predation impact of two chaetognath species, *Sagitta gazellae* and *Eukrohnia hamata* in the vicinity of the Prince Edward Archipelago (Southern Ocean). *Marine Biology* **131**, 95-101.

Froneman, P.W., Pakhomov, E.A., Perissinotto, R. & McQuaid, C.D. 2000a. Zooplankton structure and grazing in the Atlantic sector of the Southern Ocean in late austral summer 1993. Part 2. Biochemical zonation. *Deep-Sea Research I* **47**, 1687-1702.

Froneman, P.W., Pakhomov, E.A. & Treasure, A. 2000b. Trophic importance of the hyperiid amphipod, *Themisto gaudichaudi*, in the Prince Edward Archipelago (Southern Ocean) ecosystem. *Polar Biology* **23**, 429-436.

Froneman, P.W. & Perissinotto, R. 1996a. Structure and grazing of the microzooplankton communities of the Subtropical Convergence and a warm-core eddy in the Atlantic sector of the Southern Ocean. *Marine Ecology Progress Series* **135**, 237-245.

Froneman, P.W. & Perissinotto, R. 1996b. Microzooplankton grazing and protozooplankton community structure in the South Atlantic and in the Atlantic sector of the Southern Ocean. *Deep-Sea Research* **43**, 703-721.

Froneman, P.W., Perissinotto, R., McQuaid, C.D. & Laubscher, R.K. 1995. Summer distribution of netphytoplankton in the Atlantic sector of the Southern Ocean. *Polar Biology* **15**, 77-84.

Gon, O. & Klages, N.T.W. 1988. The marine fish fauna of the sub-Antarctic Prince Edward islands. *South African Journal of Antarctic Research* **18**, 32-54.

Grindley, J.R. & Lane, S.B. 1979. Zooplankton around Marion and the Prince Edward Islands. *Comité National Française des Recherches Antarctiques* **44**, 111-125.

Gurney, L.J., Froneman, P.W., Pakhomov, E.A. & McQuaid, C.D. 2001. Trophic positions of three euphausiid species from the Prince Edward islands (Southern Ocean): implications for the pelagic food web structure. *Marine Ecology Progress Series* **217**, 167-174.

Gurney, L.J., Froneman, P.W., Pakhomov, E.A. & McQuaid, C.D. 2002. Diel feeding patterns and daily ration estimates of three sub-antarctic euphausiids in the vicinity of the Prince Edward Islands (Southern Ocean). *Deep-Sea Research II* **49**, 3207-3227.

Hunt, B.P.V., Pakhomov, E.A. & McQuaid, C.D. 2001. Short term variation and long term changes in the oceanographic environment and zooplankton community in the vicinity of a sub-Antarctic archipelago. *Marine Biology* **138**, 369-381.

Kaehler, S., Pakhomov, E.A., Kalin, R.M. & Davis, S. 2006. Trophic importance of kelp-derived suspended particulate matter in a through-flow sub-Antarctic system. *Marine Ecology Progress Series* **316**, 17-22.

Kaehler, S., Pakhomov, E.A. & McQuaid, C.D. 2000. Trophic structure of the marine food web at the Prince Edwards Islands (Southern Ocean) determined by 13C and 15N analysis. *Marine Ecology Progress Series* **208**, 13-20.

Laubscher, R.K., Perissinotto, R. & McQuaid, C.D. 1993. Phytoplankton production and biomass at frontal zones in the Atlantic sector of the Southern Ocean. *Polar Biology* **13**, 471-481.

le Roux, P.C. 2008. Climate and climate change. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 39-64.

le Roux, P.C. & McGeoch, M.A. 2008. Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. *Climatic Change* **86**, 309-329.

Lutjeharms, J.R.E. & Ansorge, I.J. 2008. Oceanographic setting of the Prince Edward Islands. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 17-38.

McQuaid, C.D. & Froneman, P.W. 2004. Rhodes southern Ocean Group: scientific findings from seventeen years of biological oceanography in the South African National Antarctic Programme. *South African Journal of Science* **100**, 571-577.

Miller, D.G.M., Boden, B.P. & Parker, L. (1984). Hydrology and bio-oceanography of the Prince Edward Islands. *South African Journal of Antarctic Research* **14**, 29-32.

Nel, D.C., Lutjeharms, J.R.E., Pakhomov, E.A., Ansorge, I.J., Ryan, P.G. & Klages, N.T.W. 2001. Exploitation of mesoscale oceanographic features by the grey headed albatross *Thalassarche chrystomata* in the southern Indian Ocean. *Marine Ecology Progress Series* **217**, 15-26.

Pakhomov, E.A., Ansorge, I.J. & Froneman, P.W. 2000b. Variability in the inter-island environment of the Prince Edward Islands (Southern Ocean). *Polar Biology* **23**, 593-603.

Pakhomov, E.A., Ansorge, I.J., Kaehler, S., Vumazonke, L.U., Gulekana, K., Bushula, T., *et al*. 2003. Studying the impact of ocean eddies on the ecosystem of the Prince Edward Islands: DEIMEC ll: research in action *South African Journal of Science* **6**, 187-190.

Pakhomov, E.A. & Chown, S.L. 2003. The Prince Edward Islands: Southern Ocean Oasis. *Ocean Yearbook* **17**, 348-379.

Pakhomov, E.A. & Froneman, P.W. 1999a. The Prince Edward Islands pelagic ecosystem: a review of achievements 1976-1990. *Journal of Marine Systems* **18**, 297-310.

Pakhomov, E.A. & Froneman, P.W. 1999b. Macroplankton/micronekton dynamics in the vicinity of the Prince Edward Islands (Southern Ocean): new concept for the biomass build up for higher trophic levels. *Marine Biology* **134**, 501-515.

Pakhomov, E.A. & Froneman, P.W. 2000. Composition and spatial variability of macroplankton and micronekton within the Antarctic Polar Frontal Zone of the Indian Ocean during austral autumn 1997. *Polar Biology* **23**, 410-419.

Pakhomov, E.A., Froneman, P.W., Ansorge, I.J. & Lutjeharms, J.R.E. 2000a. Temporal variability in the physico-biological environment of the Prince Edward Islands (Southern Ocean). *Journal of Marine Systems* **26**, 75-95.

Pakhomov, E.A., Froneman, P.W., Kuun, P.J. & Balarin, M. 1999. Feeding dynamics and respiration of the bottom-dwelling caridean shrimp *Nauticaris marionis* Bate, 1888 (Crustacea: Decapoda) in the vicinity of Marion Island (Southern Ocean). *Polar Biology* **21**, 112-121.

Pakhomov, E.A., Froneman, P.W. & McQuaid, C.D. 2001. The Prince Edward Islands life support system and variability of living resources in the Southern Ocean. Final report submitted to South African Committee on Antarctic Research.

Pakhomov, E.A., Kaehler, S. & McQuaid, C.D. 2002. Zooplankton community structure in the kelp beds of the Sub-Antarctic Prince Edward Archipelago: are they a refuge for larval stages. *Polar Biology* **25**, 778-788.

Pakhomov, E.A., McClelland, J.W., Bernard, K.S., Kaehler, S. & Montoya, J.P. 2004. Spatial and temporal shifts in the stable isotope values of the bottom dwelling shrimp, *Nauticaris marionis* at the sub-Antarctic archipelago. *Marine Biology* **144**, 317-325.

Pakhomov, E.A., Perissinotto, R., McQuaid, C.D. & Froneman, P.W. 2000c. Zooplankton structure and grazing in the Atlantic sector of the Southern Ocean in the last austral summer 1993. Park 1. Ecological zonation. *Deep-Sea Research I* **47**, 1663-1686.

Perissinotto, R. 1992. Mesozooplankton size-selectivity and grazing impact on the phytoplankton community off the Prince Edward Archipelago (Southern Ocean). *Marine Ecology Progress Series* **70**, 243-258.

Perissinotto, R., Allanson, B.R. & Boden, B.P. 1990b. Trophic relations within the seas of the Prince Edward Archipelago, Southern Ocean. *Trophic relationships in the Marine Environment*. 296-314.

Perissinotto, R. & Boden B.P. 1989. Zooplankton-phytoplankton relationships at the Prince Edward Island during April/May 1985 and 1986. *South African Journal of Antarctic research* **19**, 26-30.

Perissinotto, R. & Duncombe Rae, C.M. 1990. Occurrence of anticyclonic eddies on the Prince Edward Plateau (Southern Ocean): effects on phytoplankton biomass and production. *Deep-Sea Research I* **37**, 777-793.

Perissinotto, R., Duncombe Rae, C.M., Boden, B.P. & Allanson, B.R. 1990a. Vertical stability as a controlling factor of the marine phytoplankton production at the Prince Edward Archipelago (Southern Ocean). *Marine Ecology Progress Series* **60**, 205-209.

Perissinotto, R. & McQuaid, C.D. 1990. Role of the sub-Antarctic shrimp, *Nauticaris marionis* in coupling benthic and pelagic food webs. *Marine Ecology Progress Series* **64**, 81-87.

Perissinotto, R. & McQuaid, C.D. 1992a. Deep occurence of the giant kelp *Macrocystis laevis* in the Southern Ocean. *Marine Ecology Progress Series* **81**, 89-95.

Perissinotto, R. & McQuaid, C.D. 1992b. Land-based predator impact on vertically migrating zooplankton and micronekton advected to a Southern Ocean archipelago. *Marine Ecology Progress Series* **80**, 15-27.

Ryan, P.G. & Bester, M.N. 2008. Pelagic predators. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 121-164.

Smith, V.R. 1991. Climate change and its ecological consequences at Marion and Prince Edward Islands. S*outh African Journal of Antarctic Research* **21**, 223-224.

Smith, V.R. 1992. Surface air temperatures at Marion Island, sub-Antarctic. *South African Journal of Science* **88**, 575-578.

Smith, V.R. 2002. Climate change in the sub-Antarctic: an illustration from Marion Island. *Climatic Change* **52**, 345-357.

Smith, V.R. & Steenkamp, M. 1990. Climatic change and its ecological implications at a sub-antarctic island. *Oecologia* **85**, 14-24.

Van Ballegooyen, R.C., Perissinotto, R., Ismail, A., Boden, B.R., Lucas, M., Allanson, B.R., *et al.* 1989. Data report of the second cruise of the Marion Offshore Ecological study (MOES). CSIR report EMA-D 8910.

Vumazonke, L.U. 2004. *Growth, feeding and sex change in the sequential protandric shrimp* Nauticaris marionis *at the Prince Edward Islands*. M.Sc. Thesis, Rhodes University, South Africa.

Vumazonke, L.U., Pakhomov, E.A., Froneman, P.W. & McQuaid, C.D. 2003. Diet and daily ration of male and female *Nauticaris marionis* at the Prince Edward Archipelago. *Polar Biology* **26**, 420-422.

Williams, A.J., Siegfried, W.R., Burger, A.I. & Berutti, A. 1979. The Prince Edward islands: a sanctuary for seabirds in the Southern Ocean. *Biological Conservation* **15**, 59-71.

Weimerskirch, H., Le Corre, M., Jaquemet, S., Potier, M. & Marsac, F. 2004. Foraging strategy of a top predator in tropical waters: great frigatebirds in the Mozambique Channel. *Marine Ecology Progress Series* **275**, 297-308.

CHAPTER 6

PELAGIC PREDATORS

PETER G. RYAN AND MARTHÁN N. BESTER

Given the general paucity of land-masses in the Southern Ocean, sub-Antarctic islands are characterised by vast populations of marine organisms that require terrestrial breeding and moulting sites – seabirds and seals. The islands are important for the conservation of these species, because when seabirds and seals breed and, in some species, moult, they are forced to aggregate in high densities at relatively few sites where they are vulnerable to disturbance, habitat modification and especially the threat of introduced predators and pathogens. At the same time, the vast numbers of breeding seabirds and seals influence terrestrial ecosystems and the near-shore marine environment around the islands by importing substantial amounts of nutrients and energy from more distant pelagic waters. This subject is covered in more detail by Smith & Froneman (2008), but penguins alone are estimated to import more than 30 000 tons of guano, feathers, carcasses and eggs to Marion Island each year (Burger *et al.* 1978; Siegfried *et al.* 1978; Williams & Berruti 1978). Seabirds and seals also influence the islands' terrestrial ecosystems through trampling, erosion and transport of propagules (Cooper & Brown 1990). Other pelagic predators, such as cetaceans, are not constrained to visit land to reproduce, yet also may aggregate in the waters around the islands because of locally enhanced production caused by oceanographic features around the island (McQuaid & Froneman 2008) and nutrient inputs from the land-based predators, or in the

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 121-164

case of large predators, simply be attracted by concentrations of their seal and seabird prey. This chapter briefly introduces the pelagic predators occurring at the Prince Edward Islands, reports their spatial and temporal distribution both at sea and on the islands, and considers how their populations respond to environmental variability in the surrounding oceanic environment and to human impacts, both at sea and on land.

6.1 The abundance, distribution and phenology of pelagic predators ashore

6.1.1 Pinnipeds

Three species of seals breed at the Prince Edward Islands: Southern Elephant Seal *Mirounga leonina* (Phocidae), and sub-Antarctic *Arctocephalus tropicalis* and Antarctic Fur Seals *A. gazella* (Otariidae). All three species were exploited historically, resulting in severe population decreases within a few years in the early 1800s (Cooper & Headland 1991), with hunting continuing sporadically until 1931 (Kerley 1987). Populations of fur seals possibly have recovered to pre-exploitation levels (Bester *et al.* 2003; Hofmeyr *et al.* 2006). Annual pup production of Elephant Seals at the islands is *c.* 560 (Table 6.1), which suggests an overall population of *c.* 1 800 individuals older than pups (Pistorius *et al.* 2004; Bester & Hofmeyr 2005). The pup production is only 0.26% of the world total (SCAR EGS 2004). Fur seal pup counts at Marion Island were *c.*16 000 sub-Antarctic Fur Seals and 760 Antarctic Fur Seals in 2003/04 (Hofmeyr *et al.* 2006). Together with Prince Edward Island (Bester *et al.* 2003), this suggests a total population of *c.*150 000 sub-Antarctic Fur Seals and 5 600 Antarctic Fur Seals (Hofmeyr *et al.* 2006; Table 6.1), 33% and 0.2% of the world populations, respectively (SCAR EGS 2004). The biomass of seals breeding at the islands is approximately 7 500 tons, with some 2 500 tons of Elephant Seals and 5 000 tons of fur seals. Marion Island supports the majority of seals (58% of biomass overall), mainly due to the greater numbers of Elephant Seals (72% of the population; Table 6.1).

Seals cause significant erosion and trampling of coastal habitats (Hall & Williams 1981) and import nutrients and energy to terrestrial ecosystems through faeces, placentas, corpses (mainly pups) and moult skin and hair (Panagis 1984). Elephant Seals mainly visit sheltered beaches along the eastern coast of both Marion and Prince Edward Islands (Condy 1978a; Bester & Hofmeyr 2005), and have their peak impact during spring and summer (Panagis 1984). Much of the material from breeding Elephant Seals is likely washed out to sea, but during moult it is largely retained, because of the formation of characteristic hummocky and boggy areas at traditional moult sites (Hall & Williams 1981). Fur seals are more agile than Elephant Seals, able to land at more exposed beaches and to venture further inland. On Marion Island, sub-Antarctic Fur Seals preferentially visit beaches composed of large jumbled boulders, exposed to the prevailing westerlies (Condy 1978b), possibly for thermoregulatory reasons (Bester 1982; Bester & Roussouw 1994), whereas on Prince Edward

Island breeding sites occur primarily in the eastern part of the island (Bester *et al.* 2003), possibly because of the paucity and extremely exposed nature of west-facing beaches (Condy 1978b; Kerley 1983a). Antarctic Fur Seals on both islands prefer flat pebble beaches with adjacent open vegetated areas on sheltered coasts (Condy 1978b; Kerley 1984; Bester *et al.* 2003). Breeding aggregations of the two fur seal species are almost entirely allopatric (Bester *et al.* 2003; Hofmeyr *et al.* 2006). Adult and subadult male Antarctic fur seals kill King Penguins *Aptenodytes patagonicus* and, to a lesser extent, Macaroni Penguins *Eudyptes chrysolophus*, mainly during August to October at Goodhope Bay, Marion Island (Hofmeyr & Bester 1993; Mammal Research Institute, unpublished data). It is possible that the decline in the small King Penguin colony at Goodhope Bay (Van Heezik *et al.* 1995; Crawford *et al.* 2003a) is due to seal predation.

Table 6.1 Body mass and approximate numbers of seals breeding annually at the Prince Edward Islands. Adapted from Payne (1979), Laws (1993), Bester & Van Jaarsveld (1994), McCafferty *et al.* (1998), Pistorius *et al.* (1999b), Kirkman *et al.* (2002), Bester *et al.* (2003), McMahon *et al.* (2003), Bester & Hofmeyr (2005), Hofmeyr *et al.* (2006) and M.N. Bester unpublished data.

Species		**Mean mass (kg)**	**Marion Island**	**Prince Edward**
Southern Elephant Seal *Mirounga leonina*	Total population		1 764 [a]	540 [b]
	Adult males	3 000-4 000		
	Adult females	400-900		
	Pups (at weaning)	120.6	434 [a]	130 [b]
Sub-Antarctic Fur Seal *Arctocephalus tropicalis*	Total population		77 000 [c]	72 000 [d]
	Adult males	88.3		
	Adult females	34.1		
	Immature males	26.4		
	Immature females	12.8		
	Pups (300 d mean age)		16 045 [c]	15 000 [d]
	males	13.4-15.7		
	females	11.4-15.1		
Antarctic Fur Seal *Arctocephalus gazella*	Total population		3 600 [c]	2 000 [d]
	Adult males	125.2		
	Adult females	37.9		
	Immature males	37.8		
	Immature females	16.0		
	Pups (110 d mean age)		759 [c]	400 [d]
	males	11.1-14.5		
	females	10.2-12.2		

[a] 1999 breeding season [b] 2004 breeding season [c] 2003/04 breeding season [d] 2001/02 breeding season

Southern Elephant Seals come to land to breed, moult and winter. The duration and timing of the different haul-outs depend on an animal's age, sex and social status, with a high degree of synchronization and consistent timing across years (Condy 1979; Kirkman *et al.* 2001, 2003, 2004). The breeding season begins with bulls hauling out in mid-August to establish territories, and pregnant cows follow early in September, aggregating in harems (Condy 1979). Harems reach their maximum size in mid-October, with peak numbers of pups about one week later (Condy 1979; Wilkinson 1992). After parturition and three weeks of lactation, mated females leave. The moult haul-out is obligatory to all seals except pups of the year, which commence moulting while still suckling. Timing of moult depends on age and sex, with yearlings of both sexes hauling out first from mid-November, remaining until late January. Subadults of both sexes and adult females moult from mid-December to mid-March, and adult males from late December to mid-April (Condy 1979). The third and least understood haul-out is the resting or winter haul-out (Hofmeyr 2000; Kirkman *et al.* 2001). It involves mostly juveniles of both sexes, with occasional appearances by mainly adult males (Kirkman *et al.* 2001).

Both fur seals have similar annual cycles, differing mainly in the duration of lactation, which lasts four months in Antarctic Fur Seals and 10 months in sub-Antarctic Fur Seals (Kerley 1985). After giving birth primarily in December (median birthdates of 6 December and 17 December for Antarctic and sub-Antarctic Fur Seals, respectively; Kerley 1985), they care for the single pup by alternating foraging trips at sea where they feed, and visits ashore where they suckle their pup (Bester & Bartlett 1990). There is a second peak in numbers ashore during April, probably related to moulting (Kerley 1983a).

6.1.2 Penguins

Four species of penguins (Spheniscidae) breed at the Prince Edward Islands: King, Gentoo *Pygoscelis papua*, Macaroni and Southern Rockhopper *Eudyptes chrysocome filholi*. At least King Penguins were exploited historically, but they have not been hunted since the 1930s (Cooper & Headland 1991), and the numbers taken were such that current populations probably show little if any impact of past exploitation (Crawford *et al.* 2003a). Current populations are summarised in Table 6.2. The islands support some 13% of King Penguins worldwide, 4% of Macaroni Penguins and only 0.5% of Gentoo Penguins (Woehler 1993; Williams 1995; Crawford & Cooper 2003). The population of Southern Rockhopper Penguins is about 5% of the world population (and 17% of the eastern race *filholi*), but this is affected by the rapid decreases observed at many colonies, including Marion Island (Crawford *et al.* 2003b; BirdLife International 2004a). Penguins dominate the avian biomass at the islands, comprising some 97% of the biomass of breeding adults at Marion Island (9 200 tons) and 60% of the biomass at Prince Edward Island (750 tons). Their combined biomass exceeds that of seals breeding at the islands. Penguins also contribute most of the material imported to Marion Island by seabirds, although much of it is deposited close to the coast on soil-free areas, where large amounts are washed into the sea and is thus more significant to enriching near-shore waters (Cooper & Brown 1990; Perissinotto & Duncombe Rae 1990).

Table 6.2 Body mass and approximate numbers of adult seabirds breeding annually at the Prince Edward Islands. Adapted from Cooper & Brown (1990), Marchant & Higgins (1990), Crawford *et al.* (2003a, b, c), Ryan *et al.* (2003a).

Species	Mass (kg)	Marion	P. Edward
King Penguin *Aptenodytes patagonicus*	12.0	440 000	6 000
Gentoo Penguin *Pygoscelis papua*	6.0	1 800	1 200
Macaroni Penguin *Eudyptes chrysolophus*	4.6	720 000	30 000
Rockhopper Penguin *Eudyptes chrysocome*	2.7	134 000	90 000
Wandering Albatross *Diomedea exulans*	9.0	3 600	3 700
Grey-headed Albatross *Thalassarche chrysostoma*	3.7	15 800	6 000
Yellow-nosed Albatross *Thalassarche carteri*	2.6	0	15 000
Light-mantled Sooty Albatross *Phoebetria palpebrata*	2.8	400	300
Dark-mantled Sooty Albatross *Phoebetria fusca*	2.5	2 400	2 000
Southern Giant Petrel *Macronectes giganteus*	4.5	3 500	2 000
Northern Giant Petrel *Macronectes halli*	4.0	700	600
Fairy Prion *Pachyptila turtur*	0.14	2 000	2 000
Salvin's Prion *Pachyptila salvini*	0.17	200 000	500 000
Blue Petrel *Halobaena caerulea*	0.20	100 000	200 000
Great-winged Petrel *Pterodroma macroptera*	0.59	20 000	20 000
Soft-plumaged Petrel *Pterodroma mollis*	0.31	10 000	20 000
Kerguelen Petrel *Lugensa brevirostris*	0.35	20 000	20 000
Grey Petrel *Procellaria cinerea*	1.0	2 000	10 000
White-chinned Petrel *Procellaria aequinoctialis*	1.3	20 000	10 000
Grey-backed Storm Petrel *Garrodia nereis*	0.03	?	2 000
Black-bellied Storm Petrel *Fregetta tropica*	0.05	?	10 000
South Georgian Diving Petrel *Pelecanoides georgicus*	0.11	1 000	10 000
Common Diving Petrel *Pelecanoides urinatrix*	0.15	?	20 000
Crozet Shag *Phalacrocorax melanogenis*	2.2	540	100
Sub-Antarctic Skua *Catharacta antarctica*	1.6	1 200	500
Kelp Gull *Larus dominicanus*	1.0	200	60
Antarctic Tern *Sterna vittata*	0.14	50	10
Kerguelen Tern *Sterna virgata*	0.12	100	10

In addition to importing nutrients and energy, penguins are significant local agents of erosion. Macaroni and King Penguins breed in dense colonies, which typically kill all vegetation and erode peat to bedrock (Hall & Williams 1981). However, both species are spatially limited, with King Penguins breeding in up to 15 colonies on Marion Island and three on Prince Edward Island, all at sheltered sites with gently-shelving landing beaches (Hall & Williams 1981; Van Heezik *et al.* 1995; Ryan *et al.* 2003a). Macaroni Penguins are less constrained by a need for sheltered landing sites, breeding in more than 50 colonies at Marion Island and seven at Prince Edward Island, but some 80% breed at two sites on the east coast of Marion Island, at Bullard and Kildalkey (Crawford *et al.* 2003c; Ryan *et al.* 2003a), where they have removed some 3 x 10^5 m^3 of peat (Hall & Williams 1981). By comparison, more agile Rockhopper Penguins occur around the coasts of both islands, breeding along all but the most sheer of cliffs (Crawford *et al.* 2003b; Ryan *et al.* 2003a). They also penetrate further inland, at least locally, but do not venture as far from the coast as the small numbers of Gentoo Penguins breeding at both islands (Adams & Wilson 1987; Crawford *et al.* 2003d; Ryan *et al.* 2003a).

Apart from King Penguins, which lay a single egg, all species lay two eggs, but only Gentoo Penguins very occasionally raise two chicks (Williams 1995). In terms of phenology, King Penguins have a complex breeding system, laying eggs from mid-November to March (Williams 1995). Chicks must grow rapidly and store sufficient body reserves by June in order to survive 3-4 months with little or no food (Van Heezik *et al.* 1993). Only chicks from eggs laid early in the summer (hatching before 7 February) typically survive to fledge the following summer (Van Heezik *et al.* 1993). However, this forces successful breeders to lay eggs late the following summer, almost invariably causing their breeding attempts to fail, and many birds elect to skip breeding in successive years (Van Heezik *et al.* 1994). Macaroni and Rockhopper Penguins both breed in summer. Macaroni Penguins occupy colonies slightly earlier (from early October), fledging chicks around the end of February (Crawford *et al.* 2003c), whereas Rockhoppers return to the island in mid-late October, fledge chicks in March (Cooper & Brown 1990). Gentoo Penguins are inshore feeders that remain at the islands year round and have a protracted breeding season. Egg laying takes place from June-November, with chicks present as late as February (Cooper & Brown 1990). They differ from other penguins at the islands, in that they may lay replacement clutches if a breeding attempt fails (Williams 1980).

Penguins are unusual among seabirds at the Prince Edward Islands in also having to return to land to moult. They replace all their feathers in a simultaneous moult lasting 15-30 days, during which time they remain ashore, fasting (Brown 1986; Williams 1995). This is energetically expensive, and requires pre-moult fattening and post-moult recovery periods lasting several weeks. Adult King Penguins moult in summer, from October-February (Van Heezik *et al.* 1995), with early birds having failed in their breeding attempt the previous year (Weimerskirch *et al.* 1992). Adult Macaroni and Rockhopper penguins return to the island to moult a few weeks after they finish raising their chicks; Macaroni Penguins moulting in March-April, and Rockhopper Penguins in April-May (Cooper & Brown 1990). Adult Gentoo Penguins also moult after breeding, mainly during December-February (Williams 1995). Immature penguins also have to return to land to moult on a roughly annual basis, usually returning earlier than adults because they are not constrained to moult after breeding (Williams 1995).

6.1.3 Albatrosses

Five species of albatrosses (Diomedeidae) breed at the Prince Edward Islands: Wandering Albatross *Diomedea exulans*, Grey-headed Albatross *Thalassarche chrysostoma*, and Light-mantled *Phoebetria palpebrata* and Dark-mantled *Phoebetria fusca* Sooty Albatrosses breed at both islands, whereas Indian Yellow-nosed Albatrosses *Thalassarche carteri* only breed at Prince Edward Island. Annual breeding populations are summarised in Table 6.2, but with the exception of Yellow-nosed Albatrosses, most pairs breed only every second year if they successfully raise a chick (Brooke 2004), and thus the actual breeding population is up to 80% larger than the numbers given in Table 6.2. The islands support some 44% of all Wandering Albatrosses, 10% of Grey-headed Albatrosses and 21% of Indian Yellow-nosed Albatrosses (Tickell 2000; Crawford & Cooper 2003). Numbers of sooty albatrosses are poorly known globally, but the islands support perhaps 10% of Dark-mantled and 2% of Light-mantled Sooty Albatrosses (Tickell 2000; Crawford & Cooper 2003). Annual breeding biomass is *c.*100 tons on each of Marion and Prince Edward Islands.

All species lay a single egg, which is not replaced if the breeding attempt fails (Warham 1990). Wandering Albatrosses breed in loose colonies on level coastal plains and are scattered around the islands, reaching peak densities in Albatross Valley on the north-east coast of Prince Edward Island (*c.* 22 nests.ha^{-1}); average density in colonies at Marion Island is *c.* 5 nests.ha^{-1} (Underhill *et al.* 2003). Their nests are large mounds of vegetation and peat, plucked from the area immediately surrounding each, creating a localised source of disturbance and nutrient input. The other four albatrosses all breed on cliffs, with sooty albatrosses scattered singly or in small colonies around the islands and Grey-headed Albatrosses and Yellow-nosed Albatrosses in large, dense colonies. Grey-headed Albatrosses breed on cliffs along the south coast of Marion Island and in a mixed colony with Yellow-nose Albatrosses on the north-east coast of Prince Edward Island. The nests of all four cliff-nesting species are tall cones of muddy-peat, built by the birds, also creating point sources of disturbance and nutrient input. The dense, cliff-side colonies of *Thalassarche* albatrosses also promote local slump erosion (Hall & Williams 1981).

The four smaller albatrosses all breed in summer, returning to colonies from August to late September and fledging chicks from March (Yellow-nosed Albatross) to May (sooty albatrosses). The larger Wandering Albatross lays in mid-summer, eggs hatch in March, and chicks fledge from December-February

(Cooper & Brown 1990; Marchant & Higgins 1990). All species have delayed onset of maturity, first breeding at 10-12 years old on average (Nel *et al.* 2003; Brooke 2004), with onset of breeding linked to acquisition of high body mass (Weimerskirch 1992).

6.1.4 Petrels

At least 14 species of petrels (Procellariidae) breed at the Prince Edward Islands, and with the exception of the two species of giant petrels *Macronectes* spp., all breed in burrows, commuting mainly at night to reduce the risk of predation by sub-Antarctic Skuas *Catharacta antarctica* (Lariidae). As a result, their populations are much less well known than are those of the surface-nesting species. The population estimates presented in Table 6.2 are conservative, and the proportions of global populations breeding at the islands are not known, other than for the two species of giant petrels (Northern *Macronectes halli* 5% and Southern *Macronectes giganteus* 9%; Crawford & Cooper 2003). The islands are important sites for Salvin's Prions *Pachyptila salvini*, which breed in vast numbers and are confined to sub-Antarctic islands in the Indian Ocean sector of the Southern Ocean. Populations of many burrow-nesting species at Marion Island were severely depressed by predation by feral cats *Felis catus* (Van Aarde 1980), now removed from the island (Bester *et al.* 2002), leading to the local extinction of some species (Cooper & Brown 1990). The total breeding biomass is *c.* 300 tons, with probably slightly more on smaller Prince Edward Island than on Marion Island.

All species lay a single egg, which is not replaced if the breeding attempt fails (Warham 1990). Giant petrel nests are low mounds of vegetation, similar to those of Wandering Albatrosses, with Northern Giant Petrels breeding singly or in loose groups against sheltering rocks, whereas Southern Giant Petrels breed colonially in more open areas (Cooper *et al.* 2001). Both are important for transporting material further inland from coastal seal and penguin colonies (Hunter 1985). The burrow-nesting species breed singly, in loose colonies or, in the case of Blue Petrels *Halobaena caerulea*, in dense colonies. Their burrowing activity removes up to 1 m^3 of peat and lithosol per nest, with an average of around 0.2 m^3 (Hall & Williams 1981; Boelhouwers *et al.* 2008). Given a population of at least 500 000 pairs, they are highly significant agents of erosion (Hall & Williams 1981). Most breeding occurs on the coastal plain and lower slopes of the islands (Hunter 1990), but extends to the highest parts of Prince Edward Island (Ryan *et al.* 2003a). Because of their wide spatial range and deposition of guano and other material underground, they are extremely important sources of nutrients for terrestrial vegetation (Cooper & Brown 1990; Smith & Froneman 2008).

Most species breed in summer, but Great-winged *Pterodroma macroptera* and Grey *Procellaria cinerea* Petrels breed in winter, laying eggs in May and fledging chicks in September-October (Cooper & Brown 1990). Like albatrosses, most species spend the non-breeding season at sea, but Blue Petrels return to the islands in April-May to clean out burrows and apparently re-establish pair bonds (Cooper & Brown 1990).

6.1.5 Other seabirds

Five other seabird species breed at the Prince Edward Islands: Crozet Shags *Phalacrocorax melanogenis* (Phalacrocoracidae), and sub-Antarctic Skuas, Kelp Gulls *Larus dominicanus*, and Antarctic *Sterna vittata* and Kerguelen *Sterna virgata* Terns (Laridae). All feed on the island or in coastal waters, and are thus not strictly pelagic predators. They occur in relatively small numbers (Table 6.2), with a total biomass at both islands of *c.* 4.5 tons. However, the islands are important as one of only two archipelagos where Crozet Shags breed (33% of world population), and one of only three where Kerguelen Terns breed (3% of world population; Crawford & Cooper 2003). All are surface nesters that breed in summer (Cooper & Brown 1990), although some Crozet Shags at Prince Edward Island occasionally nest in winter (Ryan & Hunter 1985). As mainly coastal foragers, they lay larger clutches than pelagic-feeding species, usually 2 (1-3) eggs. Crozet Shags breed on cliffs and offshore rocks (Crawford *et al.* 2003e; Ryan *et al.* 2003a). Sub-Antarctic Skuas breed throughout Prince Edward Island (Ryan *et al.* 2003a) and occur widely on the coastal plain at Marion Island, with aggregations around large penguin colonies. They are important in transporting penguin material away from the immediate coastal zone (Hunter 1995), and the islands support 11% of the world population (Crawford & Cooper 2003). Kelp Gulls and terns breed at scattered localities along the coast and inland, mainly along the more sheltered eastern coasts (Crawford *et al.* 2003a; Ryan *et al.* 2003a).

Apart from seabirds, there is only one breeding bird at the Prince Edward Islands, the Lesser or Black-faced Sheathbill *Chionis minor* (Chionidae), represented by an endemic subspecies *C. m. marionensis*. We mention it here because it derives a substantial portion of its food directly or indirectly from the sea. It breeds in summer, when it obtains most of its food from breeding seabirds, either scavenging or stealing food (Burger 1981). Sheathbills are well known for knocking over chicks as parents regurgitate food into their mouths, causing the food to be spilled and thus made available to the sheathbills (Marchant & Higgins 1993). In winter some scavenge in King Penguin colonies, but others forage along the coast or hunt for insects inland (Burger 1982; Huyser *et al.* 2000). The Lesser Sheathbill is confined to sub-Antarctic islands in the southern Indian Ocean. The Prince Edward Island population is some 1 400 pairs, around 20% of the world total (Marchant & Higgins 1993). There is some evidence that numbers have decreased at Marion Island, possibly due to competition with introduced House Mice *Mus musculus* for invertebrate prey in winter (Huyser *et al.* 2000).

6.2 Diets and foraging methods of pelagic predators

Virtually all studies of the diets of pelagic predators have taken place on animals at the breeding islands (Table 6.3). Analysis of regurgitated pellets and scats overestimates the contributions of prey with hard, indigestible remains such as squid beaks and otoliths (Cooper & Brown 1990). Development of non-destructive stomach flushing techniques for seabirds (Wilson 1984; Ryan & Jackson 1986) revolutionised diet studies, although rapidly-digested, soft-bodied prey, such as tunicates, salps and jellyfish, probably are overlooked in most species (Duffy & Jackson 1986). However, information is largely confined to the chick-rearing period. Seals are more problematic, because they do not bring food back to the islands to feed their young, but scat analysis provides some information for fur seals. As a result, knowledge of predator diets ranges from fairly well known for some breeding seabirds to poorly known for elephant seals and non-breeding seabirds (Table 6.3). Stable isotope analyses provide a way to infer diet and feeding areas at other times of the year (e.g. Cherel *et al.* 2005; Bearhop *et al.* 2006; Hilton *et al.* 2006), and can also indicate where moult takes place in birds (Cherel *et al.* 2000), but there have been no studies conducted to date at the Prince Edward Islands.

Selectivity of predator diets are in part determined by their foraging methods. Southern Ocean seabirds use a diversity of foraging methods (Harper *et al.* 1985), with the major factors affecting diet being body size (which determines the size range of prey; Ridoux 1994) and diving ability (which to a large extent determines the extent to which species can afford to be selective in their diet). Diving ability is, in turn, traded off against cost of flight, due to the buoyancy costs of having large wings (Kuroda 1954; Wilson *et al.* 1992). In general, pursuit divers tend to be more selective predators, whereas species confined to feeding at the surface are generalist scavengers (Ryan 1987a; Ridoux 1994). Knowledge of foraging behaviour of pelagic predators has been revolutionised over the last two decades due to the development of miniature data loggers that can be attached to the animals (Boyd 1997; Wilson *et al.* 2002).

6.2.1 Pinnipeds

Seals are accomplished divers. Adult Southern Elephant Seals dive to depths of up to 1 500 m, with adult females primarily diving to 300-400 m at night and 500-600 m during the day (Jonker & Bester 1994). They spend virtually no time foraging at or near the surface, and those from Marion Island were not recorded to perform benthic dives (Jonker & Bester 1998). Their diet at the Prince Edward Islands is virtually unknown, with only the squid *Kondakovia longimana* found in one stomach (M.N. Bester, unpublished data). Elsewhere, Southern Elephant Seals prey upon a range of fish and squid species (Laws 1956), with composition differing between sites, season and sex (Slip 1995; Daneri *et al.* 2000; Daneri & Carlini 2002; Van den Hoff *et al.* 2003).

Table 6.3 Diets of pelagic predators breeding at the Prince Edward Islands (% contribution by mass or approximate importance denoted by +, ++ and +++). Data from the Prince Edward Islands except for species marked *, where data are from adjacent sub-Antarctic islands.

Species	Crustacea	Squid	Fish	Other^1	Source
Southern Elephant Seal*	0	55	45	0	Green & Burton 1993
Sub-Antarctic Fur Seal	0	1	99	0	Makhado 2002
Antarctic Fur Seal	<1	4	96	+	Makhado 2002
King Penguin	<1	14	86	0	Adams & Klages 1987
Gentoo Penguin	40	1	59	0	La Cock *et al.* 1984; Adams & Klages 1989
Macaroni Penguin	79	3	18	<1	Brown *et al.* 1990; Crawford *et al.* 2003c
Rockhopper Penguin	91	2	7	0	Brown & Klages 1987; Brown *et al.* 1990
Wandering Albatross	<1	59	36	5	Cooper *et al.* 1992a
Grey-headed Albatross	3	33	58	6	Hunter & Klages 1989; Nel *et al.* 2000
Yellow-nosed Albatross*	4	38	58	<1	Ridoux 1994; Cherel & Klages 1998
Light-mantled Sooty Albatross	4	34	46	16	Cooper & Klages 1995
Dark-mantled Sooty Albatross	<1	42	33	25	Cooper & Klages 1995
Southern Giant Petrel (male)	<1	2	2	96	Hunter & Brooke 1992
(female)	<1	9	6	85	Hunter & Brooke 1992
Northern Giant Petrel (male)	<1	4	1	95	Hunter & Brooke 1992
(female)	<1	35	17	48	Hunter & Brooke 1992
Fairy Prion*	95	5	<1	<1	Ridoux 1994
Salvin's Prion	66	9	22	3	Gartshore *et al.* 1988a; Ridoux 1994
Blue Petrel	59	16	21	4	Steele & Klages 1986

Table 6.3 Continued.

Species	Crustacea	Squid	Fish	Other[1]	Source
Great-winged Petrel	6	90	4	0	Schramm 1986
Soft-plumaged Petrel	10	89	1	0	Schramm 1986
Kerguelen Petrel	24	70	6	0	Schramm 1986
Grey Petrel*	<1	71	28	1	Ridoux 1994
White-chinned Petrel	24	17	57	2	Cooper *et al.* 1992b
Grey-backed Storm Petrel	100	0	0	<1	Klages *et al.* 1995; Ridoux 1994
Black-bellied Storm Petrel*	55	10	35	<1	Ridoux 1994
South Georgian Diving Petrel*	99	<1	1	0	Ridoux 1994; Bocher *et al.* 2000
Common Diving Petrel*	100	<1	0	<1	Ridoux 1994; Bocher *et al.* 2000
Crozet Shag	18	6	72	4	Blankley 1981; Espitalier-Noel *et al.* 1988
Sub-Antarctic Skua	<1	<1	<1	99	Adams 1982, Hunter 1990
Kelp Gull*	–	–	+	+++	Blankley 1981
Antarctic Tern*	++	–	++	++	Marchant & Higgins 1990
Kerguelen Tern*	++	–	++	++	Marchant & Higgins 1990

[1] mainly remains of seabirds and marine mammal carrion for larger species; diverse array of marine species for smaller birds

Fur seals typically make shallower dives than Elephant Seals, although this has not been studied at the Prince Edward Islands. At Macquarie Island, females of both species dive mainly at night, making short dives (40-50 sec) to 10-20 m (maximum 100 m) (Goldsworthy 1999; Robinson *et al.* 2002). Fur seal scats collected at Marion Island suggest that both species feed predominantly on myctophid fish, primarily *Electrona carlsbergi*, *Electrona subaspera*, *Gymnoscopelis fraseri*, *Gymnoscopelis piabilis*, *Krefftichthys andersoni*, *Metelectrona antarctica* and *Protomyctophum choriodon* (Klages & Bester 1998; Makhado 2002). Other fish and squid comprise a minor portion of the diet, with Antarctic Fur Seals occasionally taking some crustaceans (Table 6.3). The diets of both species vary seasonally, taking mainly *E. carlsbergi*, *E. subaspera*, *G. fraseri* and *M. antarctica* in winter, and *G. piabilis*, *P. choriodon* and *Protomyctophum tennisoni* in summer (Klages & Bester 1998; Makhado 2002).

6.2.2 Penguins

Penguins are flightless pursuit divers (Harper *et al.* 1985). Diets of all four species breeding at the Prince Edward Islands have been well studied (Table 6.3; Ridoux 1994). There is little overlap between the diets of the three penguin genera (Adams & Brown 1989). King Penguins provisioning chicks feed mainly on myctophid fish (*E. carlsbergi*, *K. anderssoni* and *Protomyctophum* spp.) and small squid (juvenile *K. longimana*), with little seasonal variation in diet (Adams & Klages 1987). At the Crozet Islands, they regularly dive to 300 m (Pütz *et al.* 1998; Charrassin *et al.* 1999), diving deeper and more often when feeding chicks than when incubating (Charrassin *et al.* 1999). Gentoo Penguins take mainly fish (chiefly juvenile *Notothenia squamifrons*, with lesser amounts of myctophids and *Channichthys rhinoceratus*) and crustaceans (*Euphausia vallentini* all year, and *Nauticaris marionis* mainly in winter) (Adams & Klages 1989). They usually dive to less than 40 m at Marion Island (Adams & Brown 1983), but regularly dive to > 100 m, occasionally > 200 m at the Crozet Islands (Bost *et al.* 1994). Both Macaroni and Rockhopper Penguins feed their chicks mainly on small crustaceans, *E. vallentini* and *Thyssanoessa vicina*, with small amounts of fish and squid, especially in Macaroni Penguins (Brown & Klages 1987; Crawford *et al.* 2003c). Macaroni Penguins mostly dive to 10-80 m, rarely to 160 m (Green *et al.* 1998), whereas Rockhopper Penguins mostly dive less than 40 m, rarely to 70 m (Wilson *et al.* 1997; Tremblay & Cherel 2000). Inter-annual variation in diet has been best studied in Macaroni Penguins, where there are considerable differences in the proportion of fish taken (Crawford *et al.* 2003c). Based on population estimates and diet samples collected in the 1980s, the penguin community at the Prince Edward Islands was estimated to consume 880 000 tons of food annually (Adams *et al.* 1993).

6.2.3 Albatrosses

Albatrosses mainly forage by surface seizing (Harper *et al.* 1985). Diets of all species breeding at the Prince Edward Islands have been fairly well studied, except the Yellow-nosed Albatross (Table 6.3). Wandering Albatrosses are primarily scavengers, confined to the upper metre of the water column (Prince *et al.* 1994) and feeding on a wide diversity of squid (chiefly Histoteuthidae, Cranchiidae and Onychoteuthidae) and fish (Cooper *et al.* 1992a). Most prey is presumably moribund and dead animals scavenged by day (Cooper *et al.* 1993), caught at a rate of 2-4 kg.d^{-1} (Weimerskirch *et al.* 1994a). The diet of Wandering Albatrosses switched to include large amounts of offal and non-target fish species caught in the Patagonian Toothfish *Dissostichus eleginoides* fishery in 1997, when the fishery started operating around the Prince Edward Islands (Nel *et al.* 2002a).

Grey-headed Albatrosses are more proficient divers, reaching depths of up to 6 m (Prince *et al.* 1994), but also take a wide range of mainly squid and fish prey, with slightly more crustaceans than Wandering Albatrosses (Hunter & Klages 1989; Nel *et al.* 2000). Although large numbers were killed initially by the toothfish fishery, when some setting took place during the day and birds plunge-dived for bait (Nel *et al.* 2002b), they seldom scavenged from the fishery (Nel *et al.* 2000). Sooty albatrosses are the best divers among albatrosses, attaining depths of up to 12 m (Prince *et al.* 1994). They eat mainly squid, with the same species predominating as those eaten by the other albatrosses (Cooper & Brown 1990; Cooper & Klages 1995). Light-mantled Sooty Albatrosses take slightly more fish, and both species frequently scavenge dead seabirds and other carrion (Cooper & Klages 1995).

6.2.4 Petrels

Most petrels breeding at the Prince Edward Islands feed by surface seizing or filtering (Harper *et al.* 1985), but some species are proficient divers, with White-chinned Petrels *Procellaria aequinoctialis* capable of diving up to 12 m (Huin 1994) and diving petrels *Pelecanoides* spp. to 50-60 m (Prince & Jones 1992; Chastel 1994). Diet is varied, but the importance of crustaceans generally increases with decreasing body size (Table 6.3). The vast populations of Salvin's Prions and Blue Petrels feed mainly on euphausids (*E. vallentini*) and amphipods (chiefly *Themisto gaudichaudii*), with smaller amounts of fish (chiefly myctophids) (Steele & Klages 1986; Gartshore *et al.* 1988a). Small crustaceans are equally important for storm petrels and diving petrels (Ridoux 1994). Dietary segregation among the two very similar species of diving petrels is achieved by almost complete spatial segregation at sea during the breeding season (Bocher *et al.* 2000). Among medium-sized petrels, squids dominate the diet of *Pterodroma* petrels (Schramm 1983), whereas fish and squid are important in the diets of White-chinned, Grey and Kerguelen Petrels *Lugensa brevirostris* (Schramm 1983; Cooper *et al.* 1992b; Ridoux 1994). Giant petrels are unusual among pelagic seabirds in having marked sexual dimorphism. The larger males mainly forage on the islands, scavenging from seal and penguin colonies, but also killing penguins and smaller petrels (Hunter & Brooke 1992). Their larger size is an adaptation to compete successfully at carcasses (Hunter

1983). The smaller females, by comparison, feed mainly at sea, taking more squid and fish (Hunter & Brooke 1992).

6.2.5 Other seabirds

Crozet Shags are pursuit divers (Cooper 1985), feeding chiefly on benthic fish and the decapod crustacean *N. marionis* (Blankley 1981; Espitalier-Noel *et al.* 1988). Sub-Antarctic Skuas are aggressive predators and scavengers, mainly associated with large penguin colonies on Marion Island (Hunter 1988), but they kill large numbers of adult burrowing petrels, especially on Prince Edward Island (Adams 1982; Ryan *et al.* 2003a). The gulls and terns are mainly inshore feeders, also obtaining some food from terrestrial sources (Blankley 1981; Ryan 1987b; Ridoux 1994).

6.3 Distribution of pelagic predators at sea

Where seals and seabirds forage depends on their travelling speed and breeding status. During the breeding season, when animals have eggs or dependent young ashore, they are constrained to forage within commuting distance of the islands. This distance varies as a function of travelling speed, and with stage of breeding. For example, seabirds typically travel much further during incubation, when they may leave the island for up to 10-20 days at a time, than when provisioning a small chick. As chicks grow, and feeding intervals increase, birds can once again travel further from the islands. By comparison, immature animals and adults who have completed their reproductive activities ashore are free to wander widely, in some cases migrating to distant non-breeding areas, or even circumnavigating the Southern Ocean (Croxall *et al.* 2005). In general, more is known about the movements of breeding animals, because they return to the islands regularly and thus can be tracked with various logging devices (which require recovery of devices) or transmitters (where deployment on breeders gives a good chance of device recovery) (Boyd 1997; Wilson *et al.* 2002). However, we know a little about the movements of non-breeding animals from tag recoveries (Gartshore *et al.* 1988b), one-time deployment of transmitters (BirdLife International 2004b) and from recently-developed long-term loggers (Croxall *et al.* 2005). Observations at sea also provide information on the general foraging range of different species, but for wide-ranging, highly mobile taxa like many seabirds it is not possible to differentiate birds from different colonies, or breeding adults from non-breeders, nor, for most species, can one distinguish adults from immatures.

6.3.1 Pinnipeds

Southern Elephant Seals range widely in the south-west Indian Ocean. During the two month post-breeding period, 13 adult females remained within 1 500 km of Marion Island both to the north and the south of the island, spending most time in areas at the outer edge of their feeding range, largely within inter-frontal zones south of the Antarctic Polar Front (APF), and between the Subtropical Convergence (STC) and the sub-Antarctic Front (SAF). Four adult males, only one definitely born on Marion Island, behaved similarly during the post-breeding period (Malherbe 1998). Three post-moulting adult females ranged further afield, some 2 000-3 100 km distant to the APF and south to the Antarctic continental shelf, within the outer edge of the pack-ice (Jonker & Bester 1998). Eleven post-moult adult males (not necessarily born at Marion Island) travelled widely between 40-55°S and 3-70°E (Bester *et al.* 2005). Twenty satellite-tracked immatures born on Marion Island spent most of their time upstream of the island during winter 2004 (Bester *et al.* 2005).

Movements of fur seals are little known. Lactating females of both species spend about 6 days at sea on average during foraging trips in mid-summer (Bester & Bartlett 1990; Kirkman *et al.* 2002, 2003) and sub-Antarctic Fur Seals on average 25 days in winter (Kirkman *et al.* 2002). Of five lactating females tracked from the east coast of Marion Island, both species moved east along the 2 000-3 000 m shelf break, with sub-Antarctic Fur Seals ranging to 1 000 km from the island (Osbourne *et al.* 2002), similar to the maximum range recorded at Amsterdam Island (Georges *et al.* 2000). At Macquarie Island, where females of both species spend on average 3.4 days during foraging trips at sea in summer, foraging activity was concentrated at two sites, within 30 km and at 60 km north of the island (Robinson *et al.* 2002).

6.3.2 Penguins

Like seals, penguins are difficult to observe at sea, unless sea conditions are calm (Enticott 1986). Consequently, knowledge of foraging ranges of penguins around the Prince Edward Islands is mainly limited to maximum commuting distances, based on estimates of swimming speed and trip durations (Adams *et al.* 1993). When birds are provisioning chicks in summer, there is limited spatial overlap between species, with King Penguins feeding within 300-500 km of the islands (Adams 1987), Macaroni Penguins within 60-300 km (Brown 1987), Rockhopper Penguins within 5-150 km (Brown 1987), and Gentoo Penguins within 40 km (Adams & Wilson 1987). Differences result mainly from differences in foraging trip durations and, to a lesser extent, the proportion of time at sea spent travelling, because all four species travel at 7-9 km.h^{-1} (Adams 1987; Adams & Wilson 1987; Brown 1987). Birds provisioning large chicks spend more time travelling than do birds with small chicks (Adams 1987; Brown 1987). Diets of Rockhopper and Macaroni Penguins change significantly during the breeding season, probably reflecting changes in their foraging ranges (Brown *et al.* 1990).

Actual foraging areas of penguins from the Prince Edward Islands are poorly known, but it is likely that the major pelagic predators, King and Macaroni Penguins, do not disperse randomly around the islands. Tracking of King Penguins breeding at other sub-Antarctic islands show that birds forage mainly at frontal zones (Charrassin & Bost 2001; Pütz 2002). At the Crozet Islands, immediately to the east of the Prince Edward Islands, King Penguins forage south of 45° S year round, travelling 500-750 km to the Antarctic Polar Front in summer and up to 1 800 km during winter, south of the front into Antarctic waters, including into pack ice at 62° S (Charrassin & Bost 2001). A similar situation probably occurs at the Prince Edward Islands, where observations of birds at sea are all from south of the islands, despite a bias in observer effort towards waters north of the islands (Enticott 1986).

Much less is known about the ranges of non-breeding penguins. Gentoo Penguins remain around the islands year round, often coming ashore at night even when not breeding (Williams 1995). They have not been sighted at sea far from the islands, although two birds seen near 45°S, 0°E as well as vagrant records at Gough Island (40°S, 10°W) and South Africa indicate some potential for long-distance movements (Enticott 1986). Macaroni and Rockhopper Penguins probably remain fairly close to the breeding islands during the short pre-moult fattening period. One Macaroni Penguin satellite-tracked from Marion Island foraged up to 700 km south of the island (Osbourne *et al.* 2002). After moulting, they are absent from the islands for around five months in winter, when virtually nothing is known about their movements. No Macaroni Penguins have been observed at sea away from the islands, but two groups of Rockhopper Penguins were seen 750 km west-north-west of the islands in September, approximately one month before birds return to the islands to breed (Enticott 1986).

6.3.3 Albatrosses

Albatrosses are large enough to carry miniature data loggers and satellite transmitters, resulting in a large body of information on their movements (BirdLife International 2004b). Breeding adults range widely during incubation and on some trips provisioning large chicks, when they can remain away from their colonies for 10-20 days at a time, but are more constrained to the vicinity of the colony when feeding small chicks (Nel *et al.* 2000, 2002a). During the large-chick stage, many albatrosses and petrels alternate short and long foraging trips, primarily gathering food for the chick on the former, when adults lose body mass, and provisioning both themselves and their chicks on the latter (Weimerskirch *et al.* 1994b).

Wandering Albatrosses breeding at Marion Island range widely between 35-55°S and 0-52°E, from Bouvet to the Crozet Islands and north to the African continental shelf (Nel *et al.* 2002a). Males typically forage further south than females (Nel *et al.* 2002a). During foraging trips, adults spend 60% of the time sitting, mostly at night (Weimerskirch *et al.* 2002). They use extremely efficient dynamic soaring to travel at an average speed of 54 km.h^{-1} and regularly exceed 85 km.h^{-1} (Weimerskirch *et al.* 2002). Heart rate in flight is similar to that of birds resting at sea and only 1.4 times resting heart rate on land (Weimerskirch *et al.* 2000). Landing and taking off (twice resting rate) are the most costly activities (Weimerskirch *et al.* 2000), with energy expenditure on foraging trips largely a function of the number of landings (Shaffer *et al.* 2003).

Flight costs increase as flight direction heads into the wind, so birds structure foraging trips to exploit prevailing wind direction, making large anti-clockwise loops when heading north from colonies and clockwise loops when heading south (Weimerskirch *et al.* 2000). Movements are most constrained during the early chick-rearing period, when they typically remain within 400 km of the colony (Nel *et al.* 2002a). After breeding, adults (and probably recently-fledged juveniles (Prince *et al.* 1998)) mainly travel east to the central Indian Ocean or waters off Australia (Nel *et al.* 2002a). During their sabbatical year between successful breeding attempts, most birds remain within the South Atlantic and South Indian Oceans between 20°W and 120°E, but some circumnavigate the Southern Ocean (P.G. Ryan, unpublished data).

Grey-headed Albatrosses breeding at Marion Island range even more widely during incubation than Wandering Albatrosses, foraging between 40-55°S and 8-83°E, moving up to 4 000 km from the island and travelling up to 18 000 km on one trip (Nel *et al.* 2000). During this period, foraging is centred on eddies in the Subtropical Convergence across the entire range and more locally at the sub-Antarctic and Antarctic Polar Fronts (Nel *et al.* 2001). They are more constrained during chick rearing, when trips are shorter, mainly < 1 500 km south-west of Marion Island (47-57°S) (Nel *et al.* 2000) and foraging is concentrated at both warm and cold eddies in the sub-Antarctic Front formed by the South-West Indian Ridge (Nel *et al.* 2001). During their sabbatical year between successful breeding attempts, most birds circumnavigate the Southern Ocean, heading eastwards with the prevailing westerly winds, but some remain within the South Atlantic and South Indian Oceans (P.G. Ryan, unpublished data). At least one of these resident birds was a male that attempted to breed during its sabbatical year (P.G. Ryan, unpublished data). Recently fledged juveniles probably also disperse eastwards; one juvenile from Marion Island was recovered in New Zealand within three months of fledging (Gartshore *et al.* 1988b).

Little is known about movements of Yellow-nosed Albatrosses breeding at Prince Edward Island, but observations at sea suggest they mainly forage in warmer waters north of the Subtropical Convergence. Adults feeding chicks at Amsterdam Island (37.8°S, 77.5°E) undertake long flights to forage in tropical oceanic waters north (Weimerskirch 1998). Movements of sooty albatrosses breeding at the Prince Edward Islands also have been little studied, although observations at sea and differences in diet indicate that Dark-mantled birds forage mainly north of the islands, whereas Light-mantled birds forage further south (Cooper & Klages 1995). One adult Light-mantled Sooty Albatross breeding at Marion Island ranged 45-60°S, travelling more than 2 500 km to southwest of Bouvet Island on two of four foraging trips (Osbourne *et al.* 2002). Elsewhere, Light-mantled Sooty Albatrosses from Macquarie Island forage mostly west of the island 48-66°S during incubation, travelling up to 2 200 km from the island (Weimerskirch & Robertson 1994), and Dark-mantled Sooty Albatrosses range further from their colony during incubation (average 600 km) than when rearing chicks (Weimerskirch 1998).

6.3.4 Petrels

Foraging movements of breeding giant petrels and White-chinned Petrels have been tracked from other colonies, but not from the Prince Edward Islands. Giant petrels satellite-tracked from South Georgia and Patagonia show marked sexual differences in foraging ranges, with females spending more time at sea and travelling further from their colonies than males (Quintana & Dell'Arciprete 2002; BirdLife International 2004b). Northern Giant Petrels from South Georgia tend to forage further north than do Southerns, and males remain closer to colonies than do male Southerns (González-Solís *et al.* 2000). Outside the breeding season, giant petrels disperse widely in the Southern Ocean and adjacent continental waters. Ringed Southern and Northern Giant Petrel chicks from Marion Island have been recovered east of the islands, in Australia, New Zealand, Chile and at Macquarie Island, mainly within one year of fledging (Gartshore *et al.* 1988b). In addition, adult Northern Giant Petrels breeding at Marion Island have been sighted at Bouvet Island (Keith *et al.* 2002) and recovered along the coast of South Africa (Gartshore *et al.* 1988b), with birds ringed at seal colonies in central Namibia recaptured breeding on Marion Island (Gartshore *et al.* 1988b).

Breeding White-chinned Petrels travel even further than albatrosses because they fly both by night and day, travelling from the Crozet Islands to forage in southern African and Antarctic waters during incubation (Weimerskirch *et al.* 1999). During chick rearing they remain closer to their colonies, feeding along the shelf edge around the islands and in Antarctic waters south of the islands (Catard *et al.* 2000). Virtually all White-chinned Petrels leave the waters around the Prince Edward Islands in winter (May-August), probably moving north to forage around the African continental shelf (Rand 1963).

Most other petrels are too small to allow deployment of tracking or logging devices using current technologies, resulting in less detailed knowledge of their movements. Much of what we know comes from direct observations at sea, which gives only a crude idea of the total ranges of each species. Some species remain in the Southern Ocean year round, rarely venturing north of the Subtropical Convergence (e.g. Salvin's and Fairy Prions *Pachyptila turtur*, Blue, Kerguelen and Grey Petrels, Grey-backed Storm Petrels *Garrodia nereis*, and diving petrels), whereas others move north into temperate and tropical waters when not breeding (e.g. Great-wing Petrel and Black-bellied Storm Petrel *Fregetta tropica*). These differences are normally quite consistent, but in winter 1984 large numbers of Blue and Kerguelen Petrels irrupted north of the Subtropical Convergence throughout the Southern Ocean, suggesting that a large-scale perturbation occurred in the normal foraging areas of these species (Ryan *et al.* 1989). Range at sea also can be inferred from differences in diet. At Kerguelen, diving petrels are spatially segregated during the breeding season, with Common Diving Petrels *Pelecanoides urinatrix* feeding in inshore waters and South Georgian Diving Petrels *Pelecanoides georgicus* in pelagic waters (Bocher *et al.* 2000). This difference breaks down in winter, when both species feed on the same prey (Bocher *et al.* 2000).

6.3.5 Other seabirds

Crozet Shags, Kelp Gulls and Kerguelen Terns remain at the Prince Edward Islands year round, foraging in coastal waters and, in the case of the gull and tern, in adjacent terrestrial habitats. By comparison, most sub-Antarctic Skuas and Antarctic Terns leave the islands in winter, moving north to temperate waters and, in the case of the skuas, some reach tropical waters, occasionally crossing the equator (Hockey *et al.* 2005).

6.4 Movements between islands

Individuals of two of the three seal species, marked at Marion Island, have been re-sighted elsewhere (Bester 1989), including the coast of South Africa (sub-Antarctic Fur Seal) and the Crozet Islands (Southern Elephant Seal). In addition, Elephant Seals marked at the Crozet Islands have hauled out to moult and breed at Marion Island (Mammal Research Institute, unpublished data). Elephant seals from Marion Island have been sighted on Prince Edward Island, where some may breed (Bester & Hofmeyr 2005). However, in general, Elephant Seals show high levels of site fidelity, with some 50% of breeding females and 65% of breeding males hauling out within 5 km of their natal site at Marion Island (Hofmeyr 2000). Fur seals probably also exhibit some degree of site fidelity, with re-sightings of tagged females with pups at the same site over a number of years (Mammal Research Institute, unpublished data).

Most seabirds also show extremely high site fidelity, returning not only to their natal island to breed, but to the same colony on that island (Warham 1990). However, there is some movement between islands, both between Marion and Prince Edward Island (Ryan *et al.* 2003a) and more distant sub-Antarctic islands including the Crozet archipelago, 960 km farther east (Gartshore *et al.* 1988b; Cooper & Weimerskirch 2003) and Bouvet Island, 2 000 km west-south-west (Keith *et al.* 2002). Most of these movements are made by young birds who subsequently return to their natal islands to breed, but at least some involve emigration (Cooper & Weimerskirch 2003; Ryan *et al.* 2003a).

The main importance of such movements, other than maintaining genetic continuity between island populations in the case of effective dispersal, is the potential for seabirds to transport seeds and other propagules. Several widespread plants in the sub-Antarctic are adapted for long-distance dispersal by birds; e.g. *Acaena* spp. and *Uncinia* spp. have hooked seeds adapted for attaching to bird feathers. Alien plants also probably are dispersed by birds, including movement from Marion to Prince Edward Island (Ryan *et al.* 2003b). Seeds also may be transported in the gizzards of some seabirds. Petrels often contain hard-shelled seeds in their gizzards, and can store them there for months (Ryan & Jackson 1987). They probably inadvertently eat the seeds at sea, mistaking them for food, in the same way they ingest large numbers of plastic particles (Ryan 1987a). The seeds may be released at the breeding islands if the carrier is killed (e.g. by a skua), and the seeds regurgitated together with the petrel's bones and feathers. Such a mechanism probably accounts for the peculiar distribution of the Island Tree *Phylica arborea* at islands in the south Atlantic and Indian Oceans.

6.5 Recent population changes

Populations of pelagic predators breeding on Marion Island have been monitored since the 1970s, with regular counts since the 1980s. Trends in seal populations are best monitored through pup counts, but this has been complemented by a comprehensive long-term mark-recapture programme for Southern Elephant Seals at Marion Island (Pistorius *et al.* 1999a, 2002, 2004; McMahon *et al.* 2003). Pup production of Elephant Seals is determined by annual marking at weaning of almost all pups born on Marion Island, and weekly checks of harems to assess pre-weaning mortality. Determining fur seal pup production is more difficult due to their greater range and numbers, coupled with the rough topography of many breeding sites and the inclination of pups to hide. Complete counts have only been conducted in a few years (Rand 1956; Condy 1978b; Kerley 1983a; Wilkinson & Bester 1990; Hofmeyr *et al.* 1997, 2006). Counts of pups are conducted in February, when all pups have been born, but are still limited to land. Populations at Prince Edward Island are less well known, although recent expeditions have allowed further assessments of fur seal (Bester *et al.* 2003) and Elephant Seal numbers (Bester & Hofmeyr 2005).

For seabirds, population monitoring involves annual counts of selected colonies (or subsets thereof) for surface-nesting species, with complete island counts at least every five years (e.g. Nel *et al.* 2002c; Crawford *et al.* 2003a, 2003b, 2003c, 2003d). Demographic parameters are estimated from individually-marked birds in several study colonies that have been followed since the early 1980s (Nel *et al.* 2002c). Burrow-nesting species are much harder to census accurately, so for these species there is very little information on trends. Unlike seals, all seabirds are monogamous, requiring bi-parental care to breed successfully (Warham 1990; Williams 1995). They also have fixed nest sites, at least during the egg stage, making censuses easier to conduct. The main problem with using counts of birds at breeding colonies as an index of population trends is that not all adults may elect to breed each year. However, without closely-monitoring colonies of individually-marked birds it is very difficult to estimate what proportion of pairs attempts to breed. In general, given the high adult survival rates of most seabirds, marked short-term fluctuations in breeding numbers are mainly due to changes in the proportion of adults breeding in successive years, whereas consistent long-term changes may reflect changes in the underlying population size.

6.5.1 Pinnipeds

The Prince Edward Island population of Southern Elephant Seals forms part of the Kerguelen stock, including Kerguelen, the Crozets and Heard Island

(Hoelzel *et al.* 1993; Slade 1997), which has decreased across its range since the 1950s (Hindell & Burton 1987; Guinet *et al.* 1992; Bester & Wilkinson 1994). At Marion Island, pup numbers decreased 37.5% from 1986 to 1997, at an average rate of 4.3% per year from 1986-91 (Pistorius *et al.* 1999a). Pup numbers appeared to stabilise after 1994 (Pistorius *et al.* 2004). Compensatory responses to the decreasing population size included an earlier onset of reproduction, increased fecundity and faster pup growth (Pistorius *et al.* 2001; McMahon *et al.* 2003). However, mean pup weaning masses were significantly higher (120.6 kg) in the recent period of stable population size (McMahon *et al.* 2003) than when the population was decreasing (114.1 kg) (Burton *et al.* 1997). Density dependence in fecundity could not be demonstrated, suggesting an extrinsic form of control (Bradshaw *et al.* 2002). Similar stabilization in populations has occurred at Kerguelen (Guinet *et al.* 1999). There appears to have been a major alteration of food availability in the southern Indian Ocean, probably linked to environmental change, in the mid 1990s (McMahon *et al.* 2003, 2005). Food availability may drive Elephant Seal demography through its impact on adult survival (particularly of females; Pistorius *et al.* 1999a, 1999b, 2004; Pistorius & Bester 2002) and/or juvenile survival and recruitment into the breeding population (Hindell 1991; McMahon *et al.* 2003).

Commercial sealing in the 18th and early 19th centuries severely impacted fur seal populations in the Southern Ocean, resulting in local extinctions at some sites. The Prince Edward Islands supported one of only three remnant populations of sub-Antarctic Fur Seals (Bester 1987; Kerley 1987), and probably were the main source area for re-colonization of the Crozets and Macquarie Island (Wynen *et al.* 2000). The historical status of Antarctic Fur Seals at the Prince Edward Islands is unclear, due to confusion between the two species (King 1959). However, genetic evidence indicates the Prince Edward Island population is part of a western stock, centred on South Georgia and Bouvet, rather than the eastern stock at Kerguelen and Macquarie Island (Wynen *et al.* 2000). Fur seal populations increased rapidly after the cessation of sealing, with c. 10% per year growth at Marion Island between 1951 and the late 1980s (Wilkinson & Bester 1990). Subsequently, growth has slowed to 5.2% per year for sub-Antarctic Fur Seals (1994/95 to 2003/04; Hofmeyr *et al.* 2006), whereas Antarctic Fur Seal numbers have grown at grown at 14.8% per year over the past 21 years (Hofmeyr *et al.* 2006). The demographic changes underpinning the slower population growth rate in sub-Antarctic Fur Seals are unknown. Some insights on prey availability can be gained from the rate of pup provisioning and growth rate, with body mass at weaning important for future survival (Georges & Guinet 2000). Generally, poor foraging conditions result in longer foraging trips by fur seal mothers, and slower pup growth (Boyd *et al.* 1997; McCafferty *et al.* 1998; Kirkman *et al.* 2003; Lea *et al.* 2006). Foraging trip durations by lactating females of both species were shorter in 1987 (Bester & Bartlett 1990) than in 1998-2000, but 1987 may simply have been a favourable year (Kirkman *et al.* 2002, 2003). No changes in pup growth rates were found at Marion Island during 1993-2000, nor was there any evidence that growth was affected by *El Niño* Southern Oscillation (ENSO) events (Kirkman *et al.* 2002).

6.5.2 Penguins

The King Penguin is the only penguin species that has apparently not decreased in numbers at the Prince Edward Islands over the last two decades (Crawford *et al.* 2003a). The number of colonies has increased over the last 50 years, probably linked to recovery from past exploitation, but there has been little consistent trend in the breeding population over the last 20 years (Crawford *et al.* 2003a). Its ability to maintain a high population while other penguins have been decreasing may relate to its distinctive diet and/or to its greater foraging range, which presumably enables it to adapt more readily to local changes in prey distribution. However, numbers of chicks surviving to the end of winter each year were correlated at the two largest colonies on Marion Island (Kildalkey and King Penguin Bay) during 1987-2002 (Crawford *et al.* 2003a), suggesting consistent inter-annual variation in breeding conditions, presumably linked to differences in prey availability. Winter survival of King Penguin chicks was exceptionally high in 1997, a year with a large ENSO event (Crawford *et al.* 2003f).

Gentoo Penguins are listed as Near-threatened globally (BirdLife International 2004a), and their numbers have decreased by *c.* 40% at Marion Island over the last 10 years (Crawford *et al.* 2003d). Most of the decrease took place between 1995 and 2000, with little decrease since 2001 (Crawford *et al.* 2003d). It is uncertain whether there has been a corresponding decrease at Prince Edward Island, because there hasn't been a spring census there since 1984 (Adams & Wilson 1987), but a mid-summer count suggests they may have decreased, with the colony at Boggel disappearing (Ryan *et al.* 2003a). Human disturbance may have contributed to the decrease close to the base on Marion Island, where at least two colonies have disappeared since the base was built in 1948 (Crawford 1952; Crawford *et al.* 2003d), but changes in food availability are thought to be responsible for the island-wide decrease (Crawford *et al.* 2003a, 2003d). Breeding success was exceptionally low in 1997, a year with a large ENSO event, when birds also started breeding later than usual (Crawford *et al.* 2003f).

Macaroni and Rockhopper Penguins are both listed as globally Vulnerable due to consistent population decreases at several colonies throughout the Southern Ocean (BirdLife International 2004a). The population of Macaroni Penguins has decreased by 10-15% over 15 years at Marion Island (Crawford *et al.* 2003c) and by closer to 50% at Prince Edward Island (Ryan *et al.* 2003a). At Marion Island, there have been steady decreases at several well-studied small colonies, and although the total occupied area at the two large colonies has remained constant, the density of nests has decreased consistently at both Bullard and Kildalkey (Crawford *et al.* 2003c). Breeding success has increased over the last decade, but appears to have been too low to maintain a stable population (Crawford *et al.* 2003c). The decrease in the population of Rockhopper Penguins has been even more marked at Marion Island, falling by *c*. 40% in 14 years (Crawford *et al.* 2003b). Most of the decrease occurred in the late 1990s, with the breeding population decreasing by an average of 12% per year from 1994/95 to 2001/02 (Crawford *et al.* 2003b). The population at Prince Edward Island has apparently remained stable over the last two decades (Ryan *et al.* 2003a), although the accuracy of the previous estimate from Prince Edward Island is unknown. The increasing fur seal population may account for some of the decrease in Macaroni Penguins at Prince Edward Island (Ryan *et al.* 2003a), but changes in food availability are thought to be mainly responsible for the reductions in both *Eudyptes* penguins (Crawford *et al.* 2003b, 2003c; Hilton *et al.* 2006). This is supported, at least for Rockhopper Penguins, by the low fledging mass of chicks relative to other colonies (Crawford *et al.* 2003b).

6.5.3 Albatrosses

All five albatrosses are listed as Threatened or Near-threatened, primarily due to accidental mortality in long-line fisheries (BirdLife International 2004a). Birds are caught while trying to snatch baits during longline setting, dragged under and drowned (Brothers 1991). Numbers of Wandering Albatrosses at Marion Island decreased between the 1970s and early 1980s, presumably due to mortality on pelagic long-lines targeting tuna, but have since increased through the late 1980s and 1990s (Nel *et al.* 2002c, 2003), stabilising since 2000 (Crawford *et al.* 2003a). Adult survival is correlated with Japanese long-line fishing effort in the southern Indian Ocean, with females having a lower survival rate because they forage further north than males, overlapping more with tuna fishing effort (Nel *et al.* 2003). The excess of males in the breeding population reduces population fecundity (Mills & Ryan 2005), and may lead to social disruption (Ryan 2002). Wandering Albatrosses have benefited from the long-line fishery for Patagonian Toothfish that commenced at the Prince Edward Islands in 1997, because very few birds have been killed (Nel & Nel 1999; Nel *et al.* 2002b), and supplemental food obtained by scavenging from this fishery has increased adult survival and halted the long-term decrease in breeding success (Nel *et al.* 2003). Wandering Albatross demography also is influenced by broad-scale environmental factors, with the proportion of first-time breeders correlated with ENSO indices (Nel *et al.* 2003) and peak numbers of pairs breeding during the 1997/98 ENSO year (Crawford *et al.* 2003f). Past population trends at Marion Island can be predicted using a simple model incorporating observed estimates for survival, breeding success and the proportion of different age classes breeding (including the proportion of first-time breeders) (Nel *et al.* 2003). Population trends and annual estimates of adult survival are correlated with those of the population studied on Possession Island in the Crozets, and the closely-related Amsterdam Albatross *Diomedea amsterdamensis*, but not South Georgia, suggesting Wandering Albatross demography is driven by factors operating at an ocean basin scale (Nel *et al.* 2002c, 2003).

Grey-headed Albatross numbers at Marion Island have remained roughly constant over the last decade (Nel *et al.* 2002c; Crawford *et al.* 2003a), despite an estimated 1 000-2 500 birds killed during the first four years of the Patagonian Toothfish fishery in the Prince Edward Islands' Exclusive Economic Zone (EEZ) in late 1990s (Nel *et al.* 2002b). Virtually all birds killed were breeding adults, with a strong male bias (Ryan & Boix-Hinzen 1999; Nel *et al.* 2002b), probably leading to an excess of females in the population. Their foraging range overlaps with tuna fisheries in the southern Indian Ocean (Nel *et al.* 2000), with mainly immature birds killed on tuna long-lines off Australia (Gales 1998) and South Africa (P.G. Ryan, unpublished data). Less is known about the population dynamics of Yellow-nosed Albatrosses, because they only breed on Prince Edward Island. A recent mid-summer survey suggests that their numbers also have remained fairly constant over the last two decades (Ryan *et al.* 2003a). This contrasts with their status on Amsterdam Island, where the population has fallen by 50% from 1980-2000 and is decreasing by 3.6% per year (Weimerskirch & Jouventin 1998; Weimerskirch 2004). However, the decrease at this colony is now thought to be largely due to avian cholera *Pasturella multicida* and another bacterial disease (*Erysipelothrix rhusiopathidae*), probably introduced with poultry kept at the island's base (Weimerskirch 2004). Yellow-nosed Albatrosses are killed in long-line fisheries for tuna (Gales 1998; Ryan *et al.* 2002) and toothfish, with an estimated 500-1 200 killed in the first four years of toothfish fishing at the Prince Edward Islands (Nel *et al.* 2002b). Like Grey-headed Albatrosses, most birds killed were adult males (Nel *et al.* 2002b). Mortality of both species in the sanctioned fishery virtually ceased once a ban on day-time setting was enforced (Nel *et al.* 2002b).

Numbers of sooty albatrosses are less easy to monitor, because they breed at low densities on inaccessible cliffs, and are less visible than other albatrosses. However, count data suggest that populations of both species have decreased consistently over the last 10-20 years at Marion Island (Crawford *et al.* 2003a). Decreases have been most marked among Dark-mantled Sooty Albatrosses, which appear to have almost halved in numbers between the late 1990s and early 2000s (Crawford *et al.* 2003a). There was no evidence for a decrease in numbers at Prince Edward Island during the summer survey in 2001, but the accuracy of estimates made in the 1970s and 1980s are unknown (Ryan *et al.* 2003a). Similar decreases have been reported for Light-mantled Sooty albatrosses at the Crozets over the last 20 years (Weimerskirch & Jouventin 1998). The main threat appears to be long-line mortality (Gales 1998, BirdLife International 2004a), although diseases may be a problem for Dark-mantled Sooty Albatrosses at Amsterdam Island (Weimerskirch 2004).

6.5.4 Petrels

Both giant petrels are listed as Threatened or Near-threatened, primarily due to accidental mortality in long-line fisheries, although disturbance at breeding colonies is a significant problem for Southern Giant Petrels (BirdLife International 2004a). Counts of breeding Northern Giant Petrels at the Prince Edward Islands have increased, probably linked to increases in numbers of fur seals (Nel *et al.* 2002c). By comparison, the population of Southern Giant Petrels breeding at Marion Island almost halved from the 1980s and early 1990s to late 1990s and 2000s (Nel *et al.* 2002c; Crawford *et al.* 2003a), but the population at Prince Edward Island is stable or increasing (Ryan *et al.* 2003a). The difference between the two island populations may be a function of high levels of disturbance on Marion Island, especially during the cat eradication programme, although the sharp decrease at Marion occurred several years after cat operations ceased (Nel *et al.* 2002c). Emigration of chicks ringed on Marion Island in the late 1980s to breed on Prince Edward Island is consistent with this hypothesis (Ryan *et al.* 2003a), but because no chicks have been banded on Prince Edward Island we have no way of telling if similar movement is occurring in the opposite direction. An estimated 200-400 birds were killed during the first four years of toothfish fishing at the Prince Edward Islands (Nel *et al.* 2002b), and they are also killed on other long-line fisheries (Ryan *et al.* 2002). Small numbers are also killed by ingesting fisheries wastes or becoming entangled in discarded fishing gear (Nel & Nel 1999).

Numbers of burrowing petrels are much harder to monitor accurately, and there are few data on population trends at the Prince Edward Islands. White-chinned Petrels are listed as Vulnerable (BirdLife International 2004a), with populations at Bird Island, South Georgia, having decreased by *c.* 28% over 17 years (Berrow *et al.* 2000). Occupied burrows in a study colony at Marion Island also decreased in the late 1990s (Nel *et al.* 2002c). Decreases at South Georgia have resulted partly from habitat loss due to increases in numbers of Antarctic Fur Seals, but probably are mainly due to long-line mortality (Berrow *et al.* 2000). It is the species most frequently killed on long-lines in most Southern Ocean fisheries, with an estimated 6 000-14 000 birds killed in the first four years of toothfish fishing at the Prince Edward Islands (Nel *et al.* 2002b), and large numbers killed in other regional fisheries (Barnes *et al.* 1997; Ryan *et al.* 2002). The impact of mortality in the toothfish fishery is exacerbated by most birds killed being adult males (Ryan & Boix-Hinzen 1999). It also was impacted by introduced cats at Marion Island, with breeding success greater in cat-free areas (Van Rensburg & Bester 1988). Breeding success in 1996-2000, after the removal of cats, was almost twice that prior to their removal (P.G. Ryan, unpublished data).

Grey Petrels are listed as Near-threatened due to long-line mortality and significant predation by introduced predators at breeding islands (BirdLife International 2004a). Relatively few were killed on toothfish longlines around the Prince Edward Islands (Nel *et al.* 2002b), but as a winter breeder it was one of the species hardest hit by cat predation on Marion Island (Van Rensburg & Bester 1988; Newton & Fugler 1989). Great-winged Petrels also breed in winter, and their breeding success increased from 0-20% to 60-64% following the removal of cats (Cooper *et al.* 1995). Breeding success of other, summer breeding petrels also increased in cat-free areas or after the removal of cats (Van Rensburg & Bester 1988; Cooper *et al.* 1995). However, there are no accurate data to monitor the recovery of burrowing petrel populations at

Marion Island following the eradication of cats. It would be very interesting to know whether immigration is occurring, although it seems likely given the rapid recolonisation of other former petrel colonies following the removal of predators (e.g. Harper 1983).

6.5.5 Other seabirds

Although not listed as globally threatened (BirdLife International 2004a), perhaps the most endangered seabird at the Prince Edward Islands is the Crozet Shag, a localised endemic confined to the Prince Edward and Crozet Islands. Numbers of breeding pairs have decreased at Marion Island by at least 50% since the 1980s, and by 12% annually between 1994/95 and 2002/03, excluding the anomalous 1997/98 season, when some 25% of adults didn't attempt to breed (Crawford *et al.* 2003e). There has been a corresponding decrease at Prince Edward Island (Ryan *et al.* 2003a). Reasons for this decrease are unclear, but probably relate to a reduction in food availability (Crawford *et al.* 2003e). Their decrease mirrors that in the other inshore-feeding pursuit diver, the Gentoo Penguin (Crawford *et al.* 2003d).

Numbers of sub-Antarctic Skuas appear to have decreased at Marion Island over the last 15 years, possibly linked to a reduction in penguin populations (Crawford *et al.* 2003a), although small numbers were killed by toothfish longlines (Nel *et al.* 2002b) and by traps set for cats (Bester *et al.* 2002). At Prince Edward Island, skuas rely much more heavily on burrowing petrels as a source of food, and the count in 2001 was much higher than any previous estimate, but this was probably due to better coverage in 2001 (Ryan *et al.* 2003a). Kelp Gulls may also have decreased at Marion Island (Crawford *et al.* 2003a), but reliability of counts is low. Kerguelen Terns are confined to the Kerguelen Arc islands and are listed as Near-threatened globally (BirdLife International 2004a). Their numbers apparently have decreased at Prince Edward Island over the last 20 years, corresponding with an increase at Marion Island following the removal of cats (Ryan *et al.* 2003a).

6.6 Summary of human impacts on pelagic predators

Although the Prince Edward Islands remain largely untransformed, wilderness areas, human actions have had some significant impacts, both directly and indirectly, on the region's pelagic predators. Historically, there was commercial exploitation of seals and seabirds (mainly King Penguins) for their skins (fur seals) and oil, mainly during the 19th and early 20th centuries (Cooper & Headland 1991). This led to dramatic decreases in all seal populations (Richards 1992). Some whaling also took place in the island's waters (Cooper & Avery 1986). Shore-based gangs of sealers doubtless also exploited a wide range of the larger seabirds for food, and introduced a variety of organisms alien to the islands, including House Mice *Mus musculus* to Marion Island (Watkins & Cooper 1986). Commercial exploitation on land ceased in the 1930s, although small numbers of live animals were removed up to the 1970s for supplying zoos. There was little commercial fishing activity close to the islands until 1997, when a largely illegal fishery for Patagonian Toothfish developed, resulting in the formation of a sanctioned fishery within the islands' EEZ (Nel *et al.* 2002b). This fishery initially killed large numbers of albatrosses and large petrels, but implementation of mitigation measures, coupled with complete observer coverage of the sanctioned fishery, reduced this to acceptable levels (Nel *et al.* 2002b). More damaging have been long-line fisheries operating in more distant waters, notably the extensive fishery for tunas *Thunnus* spp. throughout the Southern Ocean, which has caused significant decreases in many albatross and petrel populations (Brothers 1991; Nel *et al.* 2002c, 2003; Ryan *et al.* 2002).

Recent human impacts ashore have largely been through disturbance and introduced predators. The establishment of a weather station on Marion Island in 1948, staffed year-round by contract personnel, resulted in localised disturbance to breeding seabirds and seals. Species vary in their tolerance of human disturbance, with species such as Gentoo Penguins (Crawford *et al.* 2003d) and Southern Giant Petrels (Nel *et al.* 2002c) being especially prone to disturbance during the breeding season. However, even relatively 'tolerant' species such as Wandering Albatrosses are affected by human disturbance (de Villiers *et al.* 2005). The most severe impacts have resulted from introductions of alien species to the islands. In terms of pelagic predators, the introduction of domestic cats to control mice around the base in 1949 (Watkins & Cooper 1986), has had the most destructive impact, reducing populations and even causing local extinctions of several seabirds (Van Aarde 1980; Cooper & Brown 1990). Cats have now been removed from the islands (Bester *et al.* 2002), but there is concern about the possible impacts of mice, which are proving to be significant predators of seabird chicks at other islands (Cuthbert & Hilton 2004).

6.7 Predicting the effects of climate change

Little is known about the likely effects climate change will have on the populations of pelagic predators. There is some evidence that climate change has altered the breeding phenology of two penguin species at the Prince Edward Islands. The first Macaroni Penguin chicks apparently hatched *c.* 2 weeks earlier in the late 1990s (Crawford *et al.* 2003c) than in 1951 (Rand 1954). Occupation of colonies and laying dates of Gentoo Penguins were up to one month earlier in 2001 than during 1994-1998, but this is subject to considerable variation (Williams 1980; Crawford *et al.* 2003d), and there does not appear to be a longer-term trend compared with observations from 1948 (Crawford 1952) or 1951 (Rand 1954). There is no evidence of earlier breeding among Rockhopper Penguins (Rand 1954; Crawford *et al.* 2003b).

Probably the most significant impact will be if there are changes in oceanographic circulation around the islands, resulting in changes in food availability for different predator populations. Strong ENSO events appear to benefit some species and disadvantage others (Crawford *et al.* 2003f; Lea *et* *al.* 2006), and may be responsible for occasional irruptions outside of normal ranges, with concomitant high mortality (Ryan *et al.* 1989). Among Wandering Albatrosses, the proportion of first-time breeders is correlated with ENSO events, suggesting they provide good foraging conditions for birds considering breeding for the first time (Nel *et al.* 2003). Similarly, among Grey-headed Albatrosses, there is a strong correlation between breeding success and the Southern Oscillation Index (Fig. 6.1).

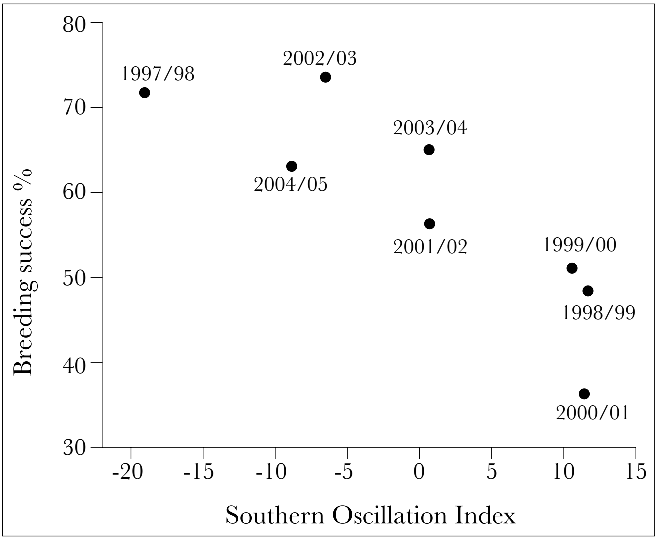


Figure 6.1 The relationship between breeding success of Grey-headed Albatrosses at Marion Island and the Southern Oscillation Index in the summer breeding season (average of monthly values from November-March).

Other population trends appear to be largely independent of short-term climatic fluctuations. There has been a consistent decrease in populations of inshore, pursuit-diving species (Gentoo and Rockhopper Penguins, Crozet Shag) over the last decade, apparently linked to changes in environmental conditions. Macaroni Penguins, as intermediate-distance feeders have been impacted to a lesser degree. By comparison, wide-ranging species such as King Penguins, albatrosses and some petrels may have benefited from environmental changes linked to increased variability in circulation patterns.

6.8 Other pelagic predators

Little is known about the abundance and distribution of pelagic predators that are not constrained to come ashore to breed in the waters around the Prince Edward Islands. Killer Whales *Orcinus orca* (Delphinidae) are seasonally common, predominantly in near-shore waters (Condy *et al.* 1978; Keith *et al.* 2001), with 25-30 hunting around Marion Island during their peak presence in early December 2000 (Pistorius *et al.* 2002). Elephant Seal pups remain in near shore waters during play and local post-weaning dispersion and are prone to predation (Guinet *et al.* 1992). They also target female Elephant Seals and penguins as they enter and exit the sea (Keith *et al.* 2001; Pistorius *et al.* 2002). Killer Whales, Long-finned Pilot Whales *Globicephala melas* (Delphinidae) and Sperm Whales *Physeter macrocephalus* (Physeteridae) often take toothfish off longlines during hauling (Ashford *et al.* 1996; B.P. Watkins, personal communication). Less is known about the presence of other cetaceans, but sightings and strandings confirm the presence of Strap-toothed Beaked Whales *Mesoplodon layardii* (Ziphiidae), Dusky Dolphin *Lagenorhynchus obscurus*, Hourglass Dolphin *Lagenorhynchus cruciger* and Southern Right Whale Dolphin *Lissodelphis peronii* (Delphinidae), Southern Right Whales *Balaena Australis* (Balaenidae), and Humpback *Megaptera novaeangliae* and Blue Whales *Balaenoptera musculus* (Balaenopteridae) in the waters around the Prince Edward Islands (La Grange 1962; Condy & Burger 1975; Watkins 2000; B.M. Dyer & M. Meyer, personal communication). Leopard Seals *Hydrurga leptonyx* (Phocidae) are infrequent visitors, occasionally hauling out in late winter and early spring, but are probably seasonally resident in offshore waters (Bester *et al.* 2006), taking penguins and possibly seals (Bester & Roux 1986; Borsa 1990; Walker *et al.* 1998).

Even less is known about predatory fish around the islands. The Patagonian Toothfish (Nototheniidae) is a predatory species, mainly taking other fish, although smaller fish take more crustaceans (Gon & Heemstra 1990). They in turn are prey for Sperm Whales. The largest predatory fish found off the islands is the Greenland Shark *Somniosus microcephalus* (Squalidae), a deep-water species that attains lengths of up to 4.5 m (Gon & Heemstra 1990). Small numbers have been caught on long-lines set for toothfish in waters 200-500 m deep. They are opportunistic feeders, taking a wide range of prey, including fish, crustaceans and carrion (Gon & Heemstra 1990).

Several seabirds are regular non-breeding visitors to the waters of the Prince Edward Island, including Black-browed Albatrosses *Thalassarche melanophrys* (Diomedeidae), Pintado Petrels *Daption capense*, Southern Fulmars *Fulmarus glacialoides*, Antarctic Prions *Pachyptila desolata*, White-headed Petrels *Pterodroma lessonii*, Little *Puffinus assimilis* and Sooty Shearwaters *Puffinus griseus* (Procellariidae), and Wilson's Storm Petrels *Oceanites oceanicus* (Hydrobatidae) (Appendix XI). Some of these species occasionally come ashore, and may even breed in small numbers on Prince Edward Island. Several other seabirds and seal species are vagrants to the island's waters, including one record of Cape Fur Seal *Arctocephalus pusillus pusillus* (Otariidae) and one Weddell Seal *Leptonychotes weddellii* (Phocidae) ashore at Marion Island (Kerley 1983b; Skinner & Smithers 1990).

6.9 Acknowledgements

We thank our many colleagues, students and field assistants who have collected data on seabirds and seals at the Prince Edward Islands over the last 25 years.

Special thanks go to John Cooper and Rob Crawford, for leading much of the research on seabirds, and Greg Hofmeyr for his endeavours in the field and inputs to this chapter.

6.10 References

Adams, N.J. 1982. Subantarctic Skua prey remains as an aid for rapidly assessing the status of burrowing petrels at Prince Edward Island. *Cormorant* **10**, 97-102.

Adams, N.J. 1987. Foraging range of King Penguins (*Aptenodytes patagonicus*) during summer at Marion Island. *Journal of Zoology, London* **212**, 475-482.

Adams, N.J. & Brown, C.R. 1983. Diving depths of the Gentoo Penguin (*Pygoscelis papua*). *Condor* **85**, 503-504.

Adams, N.J. & Brown, C.R. 1989. Dietary differentiation and trophic relationships in the sub-Antarctic penguin community at Marion Island. *Marine Ecology Progress Series* **57**, 249-258.

Adams, N.J. & Klages, N.T.W. 1987. Seasonal variation in the diet of the King Penguin (*Aptenodytes patagonicus*) at sub-Antarctic Marion Island. *Journal of Zoology, London* **212**, 303-324.

Adams, N.J. & Klages, N.T. 1989. Temporal variation in the diet of the Gentoo Penguin *Pygoscelis papua* at sub-Antarctic Marion Island. *Colonial Waterbirds* **12**, 30-36.

Adams, N.J., Moloney, C.L. & Navarro, R. 1993. Estimated food consumption by penguins at the Prince Edward Islands. *Antarctic Science* **5**, 245-252.

Adams, N.J. & Wilson, M.-P. 1987. Foraging parameters of Gentoo Penguins *Pygoscelis papua* at Marion Island. *Polar Biology* **7**, 51-56.

Ashford, J.R., Rubilar, P.S. & Martin, A.R. 1996. Interactions between cetaceans and longline fishery operations around South Georgia. *Marine Mammal Science* **12**, 452-457.

Barnes, K.N., Ryan, P.G. & Boix-Hinzen, C. 1997. The impact of the hake *Merluccius* spp. longline fishery off South Africa on procellariiform seabirds. *Biological Conservation* **82**, 227-234.

Bearhop, S., Phillips, R.A., McGill, R., Cherel, Y., Dawson, D. & Croxall, J.P. 2006. Stable isotopes indicate sex-specific foraging and long-term individual foraging specialisation in diving seabirds. *Marine Ecology Progress Series* **311**, 157-164.

Berrow, S.D., Croxall, J.P. & Grant, S.D. 2000. Status of White-chinned Petrels *Procellaria aequinoctialis* Linnaeus 1758, at Bird Island, South Georgia. *Antarctic Science* **12**, 399-405.

Bester, M.N. 1982. Distribution, habitat selection and colony types of the Amsterdam Island Fur Seal *Arctocephalus tropicalis* at Gough Island. *Journal of Zoology, London* **196**, 217-231.

Bester, M.N. 1987. The Subantarctic Fur Seal *Arctocephalus tropicalis* at Gough Island (Tristan da Cunha Group). In: Proceedings of the Fur Seal Workshop, Cambridge, April 1984. *NOAA Technical Report NMFS* **51**, 57-60.

Bester, M.N. 1989. Movements of Southern Elephant Seals and Subantarctic Fur Seals in relation to Marion Island. *Marine Mammal Science* **5**, 257-265.

Bester, M.N. & Bartlett, P.A. 1990. Attendance behaviour of Antarctic and Subantarctic Fur Seal females at Marion Island. *Antarctic Science* **2**, 309-312.

Bester, M.N., Bloomer, J.P., Van Aarde, R.J., Erasmus, B.H., Van Rensburg, P.J.J., Skinner, J.D., *et al.* 2002. A review of the successful eradication of Feral Cats from sub-Antarctic Marion Island, southern Indian Ocean. *South African Journal of Wildlife Research* **32**, 65-73.

Bester, M., Bornemann, H., Burton, H., Pistorius, P., Plötz, J., Ramdohr, S., *et al.* 2005. Southern Elephant Seals at sea: the Marion Island connection. Abstract. "32nd Conference of the Zoological Society of Southern Africa", 12-15 July 2005, Rhodes University, Grahamstown.

Bester, M.N. & Hofmeyr, G.J.G. 2005. Numbers of Elephant Seals at Prince Edward Island, Southern Ocean. *South African Journal of Wildlife Research* **35**, 85-88.

Bester, M.N., Hofmeyr, G.J.G., Kirkman, S.P., Chauke, L.F., De Bruyn, P.J.N., Ferreira, S.M., *et al.* 2006. The Leopard Seal at Marion Island, vagrant or seasonal transient? *South Afrian Journal of Wildlife Research* **36**, 195-198.

Bester, M.N. & Roussouw, G.J. 1994. Time budgets and activity patterns of Subantarctic Fur Seals at Gough Island. *South African Journal of Zoology* **29**, 168-174.

Bester, M.N. & Roux, J-P. 1986. Summer presence of Leopard Seals *Hydrurga leptonyx* at the Courbet Peninsula, Iles Kerguelen. *South African Journal of Antarctic Research* **16**, 29-32.

Bester, M.N., Ryan, P.G. & Dyer, B.M. 2003. Population numbers of Fur Seals at Prince Edward Island, Southern Ocean. *African Journal of Marine Science* **25**, 549-554.

Bester, M.N. & Van Jaarsveld, A.S. 1994. Sex-specific and latitudinal variance in postnatal growth of the Subantarctic Fur Seal (*Arctocephalus tropicalis*). *Canadian Journal of Zoology* **72**, 1126-1133.

Bester, M.N. & Wilkinson, I.S. 1994. Population ecology of Southern Elephant Seals *Mirounga leonina* at Marion Island. In: Le Boeuf, B.J. & Laws, R.M. (Eds.). *Elephant Seals; Population Ecology, Behavior, and Physiology*. University of California Press, pp. 85-97.

BirdLife International. 2004a. *Tracking Ocean Wanderers: The Global Distribution of Albatrosses and Petrels. Results from the Global Procellariiform Tracking Workshop, 1-5 September, 2003, Gordon's Bay, South Africa*. BirdLife International, Cambridge.

BirdLife International. 2004b. *Threatened Birds of the World* (CD Rom). BirdLife International, Cambridge.

Blankley, W.O. 1981. Marine food of Kelp Gulls, Lesser Sheathbills and Imperial Cormorants at Marion Island (Subantarctic). *Cormorant* **9**, 77-84.

Bocher, P., Cherel, Y. & Hobson, K.A. 2000. Complete trophic segregation between South Georgian and Common Diving Petrels during breeding at Iles Kerguelen. *Marine Ecology Progress Series* **208**, 249-264.

Boelhouwers, I., Meiklejohn, I., Holness, S. & Hedding, D. 2008. Geology, geomorphology and climate change. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem.* African Sun Media, Stellenbosch, pp. 65-96.

Borsa, P. 1990. Seasonal occurrence of the Leopard Seal (*Hydrurga leptonyx*) in the Kerguelen Islands. *Canadian Journal of Zoology* **68**, 405-408.

Bost, C.-A., Laage, J. & Pütz, K. 1994. Maximal diving depth and diving patterns of the Gentoo Penguin *Pygoscelis papua* at the Crozet islands. *Marine Ornithology* **22**, 237-244.

Boyd, I.L. 1997. Electronic marine mammals. *Trends in Ecology and Evolution* **12**, 327-328.

Boyd, I.L., McCafferty, D.J. & Walker, T.R. 1997. Variation in foraging effort by lactating Antarctic Fur Seals: response to simulated increased foraging costs. *Behavioural Ecology and Sociobiology* **40**, 135-144.

Bradshaw, C.J.A., McMahon, C.R., Hindell, M.A., Bester, M.N. & Pistorius, P.A. 2002. Do Southern Elephant Seals show density dependence in fecundity? *Polar Biology* **25**, 650-655.

Brothers, N. 1991. Albatross mortality and associated bait loss in the Japanese long-line fishery in the Southern Ocean. *Biological Conservation* **55**, 255-268.

Brooke, M. 2004. *Albatrosses and Petrels across the World*. Oxford University Press, Oxford.

Brown, C.R. 1986. Feather growth, mass loss and duration of moult in Macaroni and Rockhopper Penguins. *Ostrich* **57**, 180-184.

Brown, C.R. 1987. Travelling speed and foraging range of Macaroni and Rockhopper Penguins at Marion Island. *Journal of Field Ornithology* **58**, 118-125.

Brown, C.R. & Klages, N.T. 1987. Seasonal and annual variation in diets of Macaroni and Rockhopper Penguins at sub-Antarctic Marion Island. *Journal of Zoology, London* **212**, 7-28.

Brown, C.R., Klages, N.T. & Adams, N.J. 1990. Short and medium-term variation in the diets of penguins at Marion Island. *South African Journal of Antarctic Research* **20**, 13-20.

Burger, A.E. 1981. Food and foraging behaviour of Lesser Sheathbills at Marion Island. *Ardea* **69**, 167-180.

Burger, A.E. 1982. Foraging behaviour of Lesser Sheathbills *Chionis minor* exploiting invertebrates at a sub-Antarctic island. *Oecologia* **52**, 236-245.

Burger, A.E., Lindeboom, H.J. & Williams, A.J. 1978. The mineral and energy contributions of guano of selected species of birds to the Marion Island terrestrial ecosystem. *South African Journal of Antarctic Research* **8**, 59-70.

Burton, H.R., Arnbom, T., Boyd, I.L., Bester, M., Vergani, D. & Wilkinson, I. 1997. Significant differences in weaning mass of Southern Elephant Seals from five sub-Antarctic islands in relation to population declines. In: Battaglia, B., Valencia, J. & Walton, D.W.H. (Eds.). *Antarctic Communities: Species, Structure and Survival.* Springer, Berlin, pp. 335-338.

Catard, A., Weimerskirch, H. & Cherel, Y. 2000. Exploitation of distant Antarctic waters and close shelf-break waters by White-chinned Petrels rearing chicks. *Marine Ecology Progress Series* **194**, 249-261.

Charrassin, J.-B. & Bost, C.-A. 2001. Utilisation of the oceanic habitat by King Penguins over the annual cycle. *Marine Ecology Progress Series* **221**, 285-297.

Charrassin, J.-B., Bost, C.-A., Pütz, K., Lage, J., Dahier, T. & le Maho, Y. 1999. Changes in depth utilization in relation to the breeding stage: a case study with the King Penguin *Aptenodytes patagonicus*. *Marine Ornithology* **27**, 43-47.

Chastel, O. 1994. Maximum diving depths of Common Diving Petrels *Pelecanoides urinatrix* at Kerguelen Island. *Polar Biology* **14**, 211-213.

Cherel, Y., Hobson, K.A. & Weimerskirch, H. 2000. Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. *Oecologia* **122**, 155-162.

Cherel, Y., Hobson, K.A. & Weimerskirch, H. 2005. Using stable isotopes to study resource acquisition and allocation in procellariiform seabirds. *Oecologia* **145**, 533-540.

Cherel, Y. & Klages, N.T.W. 1998. A review of the food of albatrosses. In: Robertson, G. & Gales, R. (Eds.). *Albatross Biology and Conservation*. Surrey Beatty & Sons, Chipping Norton, pp. 113-136.

Condy, P.R. 1978a. The distribution and abundance of Southern Elephant Seals *Mirounga leonina* (Linn.) on the Prince Edward Islands. *South African Journal of Antarctic Research* **8**, 42-48.

Condy, P.R. 1978b. The distribution, abundance and annual cycle of Fur Seals *Arctocephalus* spp. on the Prince Edward Islands. *South African Journal of Wildlife Research* **8**, 159-168.

Condy, P.R. 1979. Annual cycle of the Southern Elephant Seal *Mirounga leonina* (Linn.), at Marion Island. *South African Journal of Zoology* **14**, 95-102.

Condy, P.R. & Burger, A. 1975. Southern Right Whale at Marion Island. *South African Journal of Science* **71**, 349.

Condy, P.R., Van Aarde, R.J. & Bester, M.N. 1978. The seasonal occurrence and behaviour of killer whales *Orcinus orca* at Marion Island. *Journal of Zoology, London* **184**, 449-464.

Cooper, J. 1985. Foraging behaviour of non-breeding Imperial Cormorants at the Prince Edward Islands. *Ostrich* **56**, 96-100.

Cooper, J. & Avery, G. (Eds.). 1986. Historical sites at the Prince Edward Islands. *South African National Scientific Programmes Report* **128**, 1-77.

Cooper, J., Brooke, M.de L., Burger, A.E., Crawford, R.J.M., Hunter, S. & Williams, A.J. 2001. Aspects of the breeding biology of the Northern Giant Petrel (*Macronectes halli*) and the Southern Giant Petrel (*Macronectes giganteus*) at sub-Antarctic Marion Island. *International Journal of Ornithology* **4**, 53-68.

Cooper, J. & Brown, C.R. 1990. Ornithological research at the sub-Antarctic Prince Edward Islands: a review of achievements. *South African Journal of Antarctic Research* **20**, 40-57.

Cooper, J., Fourie, A. & Klages, N.T.W. 1992b. The diet of the Whitechinned Petrel *Procellaria aequinoctialis* at sub-Antarctic Marion Island. *Marine Ornithology* **20**, 17-24.

Cooper, J. & Headland, R.K. 1991. A history of South African involvement in Antarctica and at the Prince Edward Islands. *South African Journal of Antarctic Research* **21**, 77-91.

Cooper, J., Henley, S.R. & Klages, N.T.W. 1992a. The diet of the Wandering Albatross *Diomedea exulans* at Subantarctic Marion Island. *Polar Biology* **12**, 477-484.

Cooper, J. & Klages, N.T.W. 1995. The diets and dietary segregation of sooty albatrosses (*Phoebetria* spp.) at Subantarctic Marion Island. *Antarctic Science* **7**, 15-23.

Cooper, J., Marais, A.v.N., Bloomer, J.P. & Bester, M.N. 1995. A success story: breeding of burrowing petrels (Procellariidae) before and after the eradication of Feral Cats *Felis catus* at subantarctic Marion Island. *Marine Ornithology* **23**, 33-37.

Cooper, J. & Weimerskirch, H. 2003. Exchange of the Wandering Albatross *Diomedea exulans* between the Prince Edward and Crozet Islands: implications for conservation. *African Journal of Marine Science* **25**, 519-523.

Cooper, J., Wilson, R.P. & Adams, N.J. 1993. Timing of foraging by the Wandering Albatross *Diomedea exulans*. *Proceedings of the NIPR Symposium on Polar Biology* **6**, 55-61.

Crawford, A.B. 1952. The birds of Marion Island, South Indian Ocean. *Emu* **52**, 73-85.

Crawford, R.J.M. & Cooper, J. 2003. Conserving surface nesting seabirds at the Prince Edward Islands: the roles of research, monitoring and legislation. *African Journal of Marine Science* **25**, 415-426.

Crawford, R.J.M., Cooper, J., du Toit, M., Greyling, M.D., Hanise, B., Holness, C.L., *et al.* 2003d. Population and breeding of the Gentoo Penguin *Pygoscelis papua* at Marion Island, 1994/95-2002/03. *African Journal of Marine Science* **25**, 463-474.

Crawford, R.J.M., Cooper, J. & Dyer, B.M. 2003c. Population of the Macaroni Penguin *Eudyptes chrysolophus* at Marion Island, 1994/95-2002/03, with information on breeding and diet. *African Journal of Marine Science* **25**, 475-486.

Crawford, R.J.M., Cooper, J., Dyer, B.M., Greyling, M.D., Klages, N.T.W., Nel, D.C., *et al.* 2003b. Decrease in numbers of the Eastern Rockhopper Penguin *Eudyptes chrysocome filholi* at Marion Island, 1994/95-2002/03. *African Journal of Marine Science* **25**, 487-498.

Crawford, R.J.M., Cooper, J., Dyer, B.M., Greyling, M.D., Klages, N.T.W., Ryan, P.G., *et al.* 2003a. Populations of surface nesting seabirds at Marion Island, 1994/95-2002/03. *African Journal of Marine Science* **25**, 427-440.

Crawford, R.J.M., Cooper, J., Dyer, B.M., Wolfaardt, A.C., Tshingana, D., Spencer, K., *et al.* 2003e. Population, breeding, diet and conservation of the Crozet Shag *Phalacrocorax [atriceps] melanogenis* at Marion Island, 1994/95-2002/03. *African Journal of Marine Science* **25**, 537-547.

Crawford, R.J.M., Duncombe Rae, C.M., Nel, D.C. & Cooper, J. 2003f. Unusual breeding by seabirds at Marion Island during 1997/98. *African Journal of Marine Science* **25**, 453-461.

Croxall, J.P., Silk, J.R.D., Phillips, R.A., Afanasyev, V. & Briggs, D.R. 2005. Global circumnavigations: tracking year-round ranges of nonbreeding albatrosses. *Science* **307**, 249-250.

Cuthbert, R.J. & Hilton, G.M. 2004. Introduced House Mice *Mus musculus*: a significant predator of endangered and endemic birds on Gough Island, South Atlantic Ocean? *Biological Conservation* **117**, 483-489.

Daneri, G.A. & Carlini, A.R. 2002. Fish prey of Southern Elephant Seals, *Mirounga leonina*, at King George Island. *Polar Biology* **25**, 739-743.

Daneri, G.A., Carlini, A.R. & Rodhouse, P. 2000. Cephalopod diet of the Southern Elephant Seal, *Mirounga leonina*, at King George Island, South Shetland Islands. *Antarctic Science* **12**, 16-19.

de Villiers, M.S., Cooper, J. & Ryan, P.G. 2005. Individual variability of behavioural responses by Wandering Albatrosses (*Diomedea exulans*) to human disturbance. *Polar Biology* **28**, 255-260.

Duffy, D.C. & Jackson, S. 1986. Diet studies of seabirds: a review of methods. *Colonial Waterbirds* **9**, 1-17.

Enticott, J.W. 1986. Distribution of penguins at sea in the southeastern Atlantic and southwestern Indian Oceans. *Cormorant* **13**, 118-142.

Espitalier-Noel, G., Adams, N.J. & Klages, N.T. 1988. Diet of the Imperial Cormorant *Phalacrocorax atriceps* at sub-Antarctic Marion Island. *Emu* **88**, 43-46.

Gales, R. 1998. Albatross populations: status and threats. In: Robertson, G. & Gales, R. (Eds.). *Albatross Biology and Conservation*. Surrey Beatty & Sons, Chipping Norton, pp. 20-45.

Gartshore, N.A., Cooper, J. & Hunter, S. 1988b. Bird ringing at Marion and Prince Edwards Islands, 1982-1987; with an analysis of movements since 1951. *South African Journal of Antarctic Research* **18**, 23-29.

Gartshore, N.A., Steele, W.K. & Klages, N.T. 1988a. Summer diet of the Salvin's Prion at sub-Antarctic Marion Island. *South African Journal of Zoology* **23**, 309-313.

Georges, J-Y. & Guinet, C. 2000. Maternal care in the Subantarctic Fur Seals on Amsterdam Island. *Ecology* **8**, 295-308.

Georges, J-Y., Tremblay, Y. & Guinet, C. 2000. Seasonal diving behaviour in lactating Subantarctic Fur Seals on Amsterdam Island. *Polar Biology* **23**, 59-69.

Goldsworthy, S.D. 1999. Maternal attendance behaviour of sympatrically breeding Antarctic and Subantarctic Fur Seals, *Arctocephalus* spp., at Macquarie Island. *Polar Biology* **21**, 316-325.

Gon, O. & Heemstra, P.C. 1990. *Fishes of the Southern Ocean*. J.L.B. Smith Institute of Ichthyology, Grahamstown.

González-Solís, J., Croxall, J.P. & Wood, A.G. 2000. Foraging partitioning between giant petrels *Macronectes* spp. and its relationship with breeding population changes at Bird Island, South Georgia. *Marine Ecology Progress Series* **204**, 279-288.

Green, K. & Burton, H.R. 1993. Comparison of the stomach contents of the Southern Elephant Seal, *Mirounga leonina*, at Macquarie and Heard islands. *Marine Mammal Science* **9**, 110-122.

Green, K., Williams, R. & Green, M.G. 1998. Foraging ecology and diving behaviour of Macaroni Penguins *Eudyptes chrysolophus* at Heard Island. *Marine Ornithology* **26**, 27-34.

Guinet, C., Jouventin, P. & Weimerskirch, H. 1992. Population changes and movements of Southern Elephant Seals on Crozet and Kerguelen archipelagos in the last decades. *Polar Biology* **12**, 349-356.

Guinet, C., Jouventin, P. & Weimerskirch, H. 1999. Recent population change of the Southern Elephant Seals at Iles Crozet and Iles Kerguelen: the end of the decrease? *Antarctic Science* **11**, 193-197.

Hall, K.J. & Williams, A.J. 1981. Animals as agents of erosion at sub-Antarctic Marion Island. *South African Journal of Antarctic Research* **10/11**, 18-24.

Harper, P.C. 1983. Biology of the Buller's Shearwaters (*Puffinus bulleri*) at the Poor Knights Islands, New Zealand. *Notornis* **30**, 299-318.

Harper, P.C., Croxall, J.P. & Cooper, J. 1985. A guide to foraging methods used by marine birds in Antarctic and Subantarctic seas. *Biomass Handbook* **24**, 1-22.

Hilton, G.M., Thompson, D.R., Sagar, P.M., Cuthbert, R.J., Cherel, Y. & Bury, S.J. 2006. A stable isotopic investigation into the causes of decline in a sub-Antarctic predator, the Rockhopper Penguin *Eudyptes chrysocome*. *Global Change Biology* **12**, 611-625.

Hindell, M.A. (1991) Some life-history parameters of a declining population of Southern Elephant Seals, *Mirounga leonina*. *Journal of Animal Ecology* **60**, 119-134.

Hindell, M.A. & Burton, H.R. (1987) Past and present status of the Southern Elephant Seal (*Mirounga leonina*) at Macquarie Island. *Journal of Zoology, London* **213**, 365-380.

Hockey, P.A.R., Dean, W.R.J. & Ryan, P.G. (Eds.) 2005. *Roberts' Birds of Southern Africa*, 7th ed. John Voelcker Bird Book Fund, Cape Town.

Hoelzel, A.R., Halley, J., O'Brien, S.J., Campagna, C., Arnbom, T.R., Le Boeuf, B.J., *et al.* 1993. Elephant Seal genetic variation and the use of simulation models to investigate historical bottlenecks. *Journal of Heredity* **84**, 443-449.

Hofmeyr, G.J.G. 2000. *Dispersal and dispersion of southern elephant seals at Marion Island. M.Sc. dissertation*. University of Pretoria, South Africa.

Hofmeyr, G.J.G. & Bester, M.N. 1993. Predation on King Penguins by Antarctic Fur Seals. *South African Journal of Antarctic Research* **23**, 71-74.

Hofmeyr, G.J.G., Bester, M.N. & Jonker, F.C. 1997. Changes in population sizes and distribution of fur seals at Marion Island. *Polar Biology* **17**, 150-158.

Hofmeyr, G.J.G., Bester, M.N., Makhado, A.B. & Pistorius, P.A. 2006. Population changes in Subantarctic and Antarctic Fur Seals at Marion Island. *South African Journal of Wildlife Research* **36**, 55-68.

Huin, N. 1994. Diving depths of White-chinned Petrels. *Condor* **96**, 1111-1113.

Hunter, S. 1983. The food and feeding ecology of the giant petrels *Macronectes halli* and *M. giganteus* at South Georgia. *Journal of Zoology, London* **200**, 521-538.

Hunter, S. 1985. The role of giant petrels in the Southern Ocean ecosystem. In: Siegfried, W.R., Condy, P.R. & Laws, R.M. (Eds.). *Antarctic Nutrient Cycles and Food Webs*. Springer, Berlin, pp. 534-542.

Hunter, S. 1988. The feeding ecology of avian predator-scavengers at Marion Island. In: Tasker, M.L. (Ed.). *Seabird Food and Feeding Ecology. Proceedings of the 3rd International Conference of the Seabird Group*. African Seabird Group, Cape Town, pp. 28-29.

Hunter, S. 1990. The impact of introduced cats on the predator-prey interactions of a sub-Antarctic avian community. In: Kerry, K.R. & Hempel, G. (Eds.). *Antarctic Ecosystems: Ecological Change and Conservation*. Springer, Berlin, pp. 365-371.

Hunter, S. 1991. The impact of avian predator-scavengers on King Penguin *Aptenodytes patagonicus* chicks at Marion Island. *Ibis* **133**, 343-350.

Hunter, S. & Brooke, M. de L. 1992. The diet of giant petrels *Macronectes* spp. at Marion Island, southern Indian Ocean. *Colonial Waterbirds* **15**, 56-65.

Hunter, S. & Klages, N.T. 1989. The diet of Grey-headed Albatrosses *Diomedea chrysostoma* at the Prince Edward Islands. *South African Journal of Antarctic Research* **19**, 30-33.

Huyser, O.A.W., Ryan, P.G. & Cooper, J. 2000. Changes in population size, habitat use and breeding biology of Lesser Sheathbills at Marion Island: impacts of cats, mice and climate change? *Biological Conservation* **92**, 299-310.

Jonker, F.C. & Bester, M.N. 1994. The diving behaviour of Southern Elephant Seal, *Mirounga leonina*, cows from Marion Island. *South African Journal of Antarctic Research* **24**, 75-93.

Jonker, F.C. & Bester, M.N. 1998. Seasonal movements and foraging areas of adult southern female Elephant Seals, *Mirounga leonina*, from Marion Island. *Antarctic Science* **10**, 21-30.

Keith, M., Bester, M.N., Bartlett, P.A. & Baker, D. 2001. Killer Whales (*Orcinus orca*) at Marion Island, Southern Ocean. *African Zoology* **36**, 163-175.

Keith, D.G., Harck, B.I.B., Ryan, P.G. & Mehlum, F. 2002. Post-breeding dispersal of Northern Giant Petrels *Macronectes halli* from Marion to Bouvet Islands. *Marine Ornithology* **30**, 31.

Kerley, G.I.H. 1983a. Relative population sizes and trends, and hybridisation of fur seals *Arctocephalus tropicalis* and *A. gazella* at Prince Edward Islands, Southern Ocean. *South African Journal of Zoology* **18**, 388-392.

Kerley, G.I.H. 1983b. Record for the Cape Fur Seal *Arctocephalus pusillus pusillus* from sub-Antarctic Marion Island. *South African Journal of Zoology* **18**, 139-140.

Kerley, G.I.H. 1984. *The relationship between two species of fur seals* Arctocephalus tropicalis *(Gray) and* A. gazella *(Peters) on Marion Island*. M.Sc. Dissertation, University of Pretoria, South Africa.

Kerley, G.I.H. 1985. Pup growth in the fur seals *Arctocephalus tropicalis* and *A. gazella* on Marion Island. *Journal of Zoology, London* **205**, 315-324.

Kerley, G.I.H. 1987. *Arctocephalus tropicalis* on the Prince Edward Islands. In: Croxall, J.P. & Gentry, R.L. (Eds.). *Status, Biology, and Ecology of Fur Seals*. NOAA Technical Publication Report NMFS 51, 61-64.

King, J. 1959. The northern and southern populations of *Arctocephalus gazella*. *Mammalia* **23**, 19-40.

Kirkman, S.P., Bester, M.N., Hofmeyr, G.J.G., Jonker, F.C., Pistorius, P.A., Owen, R., *et al.* 2004. Variation in the timing of the breeding haulout of female Southern Elephant Seals at Marion Island. *Australian Journal of Zoology* **52**, 379-388.

Kirkman, S.P., Bester, M.N., Hofmeyr, G.J.G., Pistorius, P.A. & Makhado, A.B. 2002. Pup growth and maternal attendance patterns in Subantarctic Fur Seals. *African Zoology* **37**, 13-19.

Kirkman, S.P., Bester, M.N., Makhado, A.B. & Pistorius, P.A. 2003. Female attendance patterns of Antarctic Fur Seals at Marion Island. *African Zoology* **38**, 402-405.

Kirkman, S.P., Bester, M.N., Pistorius, P.A., Hofmeyr, G.J.G., Owen, R. & Mecenero, S. 2001. Participation in the winter haulout by Southern Elephant Seals, *Mirounga leonina*. *Antarctic Science* **13**, 380-384.

Klages, N.T.W. & Bester, M.N. 1998. The fish prey of Fur Seals *Arctocephalus* spp. at subantarctic Marion Island. *Marine Biology* **131**, 559-566.

Klages, N.T.W., Nel, D.C. & Cooper, J. 1995. Stomach contents of a Greybacked Storm Petrel from Subantarctic Marion Island. *Marine Ornithology* **23**, 163-164.

Kuroda, N. 1954. *On the Classification and Phylogeny of the Order Tubinares, particularly the Shearwaters* (Puffinus). Author, Tokyo.

La Cock, G.D., Hecht, T. & Klages, N.T. 1984. The winter diet of Gentoo Penguins at Marion Island. *Ostrich* **55**, 188-191.

La Grange, J.J. 1962. Notes on the birds and mammals on Marion Island and Antarctica (S.A.N.A.E.) *Journal of the South African Biological Society* **3**, 27-84.

Laws, R.M. 1956. The Elephant Seal (*Mirounga leonina* Linn.). II. General, social and reproductive behaviour. *Falkland Islands Dependencies Survey Scientific Reports* **13**, 1-88.

Laws, R.M. 1993. Identification of species. In: Laws R.M. (Ed.). *Antarctic Seals: Research Methods and Techniques*. Cambridge University Press, Cambridge, England, pp. 1-28.

Lea, M.A., Guinet, C., Cherel, Y., Duhamel, G., Dubroca, L., Pruvost, P., *et al.* 2006. Impacts of climatic anomalies on provisioning strategies of a Southern Ocean predator. *Marine Ecology Progress Series* **310**, 77-94.

Makhado, A.B. 2002. *The diet of fur seals (*Arctocephalus tropicalis *and* A. gazella*) at Marion Island*. M.Sc. Dissertation, University of Pretoria, South Africa.

Malherbe, J. 1998. *The diving behaviour of Southern Elephant Seal,* Mirounga leonina*, bulls*. M.Sc. Dissertation, University of Pretoria, South Africa.

Marchant, S. & Higgins, P.J. (Eds.) 1990. *Handbook of Australian, New Zealand & Antarctic Birds, Vol. 1: Ratites to Ducks*. Oxford University Press, Melbourne.

Marchant, S. & Higgins, P.J. (Eds.). 1993. *Handbook of Australian, New Zealand & Antarctic Birds, Vol. 2: Raptors to Lapwings*. Oxford University Press, Melbourne.

McCafferty, D.J., Boyd, I.L., Walker, T.R. & Taylor, R.I. 1998. Foraging responses of Antarctic Fur Seals to changes in the marine environment. *Marine Ecology Progress Series* **166**, 285-299.

McMahon, C.R., Bester, M.N., Burton, H.R., Hindell, M.A. & Bradshaw, C.J.A. 2005. Population status, trends and a re-examination of the hypotheses explaining the recent declines of the southern elephant seal *Mirounga leonina*. *Mammal Review* **35**, 82-100.

McMahon, C.R., Burton, H.R. & Bester, M.N. 2003. A demographic comparison of two Southern Elephant Seal populations. *Journal of Animal Ecology* **72**, 61-74.

McQuaid, C.D. & Fronemann, P.W. 2008. Biology in the oceanographic environment. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 97-120.

Mills, M.S.L. & Ryan, P.G. 2005. Modelling impacts of long-line fishing: what are the effects of pair-bond disruption and sex-biased mortality on albatross fecundity? *Animal Conservation* **8**, 359-367.

Nel, D.C., Lutjeharms J.R.E., Pakhomov, E.A., Ansorge, I.J., Ryan, P.G. & Klages, N.T.W. 2001. Exploitation of mesoscale oceanographic features by Grey-headed Albatrosses *Thalassarche chrysostoma* in the southern Indian Ocean. *Marine Ecology Progress Series* **217**, 15-26.

Nel, D.C. & Nel, J.L. 1999. Marine debris and fishing gear associated with seabirds at sub-Antarctic Marion Island, 1996/97 and 1997/98 in relation to longline fishing activity. *CCAMLR Science* **6**, 85-96.

Nel, D.C., Nel, J.L., Ryan, P.G., Klages, N.T.W., Wilson, R.P. & Robertson, G. 2000. The foraging ecology of Grey-headed Mollymawks at Marion Island, southern Indian Ocean, in relation to known longline fishing activity. *Biological Conservation* **96**, 219-231.

Nel, D.C., Ryan, P.G., Crawford, R.J.M., Cooper, J. & Huyser, O.A.W. 2002c. Population trends of albatrosses and petrels breeding at sub-Antarctic Marion Island. *Polar Biology* **25**, 81-89.

Nel, D.C., Ryan, P.G., Nel, J.L., Klages, N.T.W., Wilson, R.P., Robertson, G., *et al.* 2002a. Foraging interactions between Wandering Albatrosses *Diomedea exulans* breeding on Marion Island and long-line fisheries in the southern Indian Ocean. *Ibis* **144**, E141-E154.

Nel, D.C., Ryan, P.G. & Watkins, B.P. 2002b. Seabird mortality in the Patagonian toothfish longline fishery around the Prince Edward Islands, 1996-2000. *Antarctic Science* **14**, 151-161.

Nel, D.C., Taylor, F., Ryan, P.G. & Cooper, J. 2003. Population dynamics of Wandering Albatrosses *Diomedea exulans* at sub-Antarctic Marion Island: long-line fishing and environmental influences. *African Journal of Marine Science* **25**, 503-517.

Newton, I.P. & Fugler, S.R. 1989. Notes on the winter-breeding Greatwinged Petrel *Pterodroma macroptera* and Grey Petrel *Procellaria cinerea* at Marion Island. *Cormorant* **17**, 27-34.

Osbourne, R.F., Naidoo, A.D. & Verheye, H.M. (Eds.) 2002. *Research Highlights 2001-2002*. Marine & Coastal Management, Cape Town.

Panagis, K. 1984. *The influence of Southern elephant Seals* Mirounga leonina *(Linnaeus) on the coastal terrestrial ecology of Marion Island*. M.Sc. Thesis, University of Pretoria, South Africa.

Payne, M.R. 1979. Growth in the Antarctic Fur Seal *Arctocephalus gazella*. *Journal of Zoology, London* **187**, 1-20.

Perissinotto, R. & Duncombe Rae, C.M. 1990. Occurrence of anti-cyclonic eddies on the Prince Edward Plateau (Southern Ocean): effects on phytoplankton biomass and production. *Deep-Sea Research* **37**, 777-793.

Pistorius, P.A. & Bester, M.N. 2002. Juvenile survival and population regulation in Southern Elephant Seals at Marion Island. *African Zoology* **37**, 35-41.

Pistorius, P.A., Bester, M.N. & Kirkman, S.P. 1999a. Dynamic age-distributions in a declining population of Southern Elephant Seals. *Antarctic Science* **11**, 446-451.

Pistorius, P.A., Bester, M.N. & Kirkman, S.P. 1999b. Survivorship of a declining population of Southern Elephant Seals, *Mirounga leonina*, in relation to age, sex and cohort. *Oecologia* **121**, 201-211.

Pistorius, P.A., Bester, M.N., Kirkman, S.P. & Taylor, F.E. 2001. Pup mortality in Southern Elephant Seals at Marion Island. *Polar Biology* **24**, 828-831.

Pistorius, P.A., Bester, M.N., Lewis, M.N., Taylor, F.E., Campagna, C. & Kirkman, S.P. 2004. Adult female survival, population trend, and the implications of early primiparity in a capital breeder, the Southern Elephant Seal (*Mirounga leonina*). *Journal of Zoology, London* **263**, 107-119.

Pistorius, P.A., Taylor, F.E., Louw, C., Hanise, B., Bester, M.N., de Wet, C., *et al.* 2002. Distribution, movement, and estimated population size of Killer Whales (*Orcinus orca*) at Marion Island, December 2000. *South African Journal of Wildlife Research* **32**, 86-92.

Prince, P.A., Croxall, J.P., Trathan, P.N. & Wood, A.G. 1998. The pelagic distribution of South Georgia albatrosses and their relationships with fisheries. In: Robertson, G. & Gales, R. (Eds.). *Albatross Biology and Conservation*. Surrey Beatty & Sons, Chipping Norton, pp. 137-167.

Prince, P.A., Huin, N. & Weimerskirch, H. 1994. Diving depths of albatrosses. *Antarctic Science* **6**, 353-354.

Prince, P.A. & Jones, M. 1992. Maximum dive depths attained by South Georgian Diving Petrel *Pelecanoides georgicus* at Bird Island, South Georgia. *Antarctic Science* **4**, 433-434.

Pütz, K. 2002. Spatial and temporal variability in the foraging areas of breeding King Penguins. *Condor* **104**, 528-538.

Pütz, K., Wilson, R.P., Charrassin, J.-B., Raclot, T., Lage, J., le Maho, Y., *et al.* 1998. Foraging strategy of King Penguins (*Aptenodytes patagonicus*) during summer at the Crozet Islands. *Ecology* **79**, 905-1921.

Quintana, F. & Dell'Arciprete, O.P. 2002. Foraging grounds of Southern Giant Petrels (*Macronectes giganteus*) on the Patagonian Shelf. *Polar Biology* **25**, 159-161.

Rand, R.W. 1954. Notes on the birds of Marion Island. *Ibis* **96**, 173-206.

Rand, R.W. 1956. Notes on the Marion Island fur seal. *Proceedings of the Royal Society of London* **126**, 65-82.

Rand, R.W. 1963. Seabirds in the southern Indian Ocean. *Ostrich* **34**, 121-128.

Richards, R. 1992. The commercial exploitation of sea mammals at Iles Crozet and the Prince Edward Islands before 1850. *Polar Monographs* **1**, 1-19.

Ridoux, V. 1994. The diets and dietary segregation of seabirds at the Subantarctic Crozet Islands. *Marine Ornithology* **22**, 1-192.

Robinson, S.A., Goldsworthy, S.G., Van den Hoff, J. & Hindell, M.A. 2002. The foraging ecology of two sympatric fur seal species, *Arctocephalus gazella* and *Arctocephalus tropicalis*, at Macquarie Island during the austral summer. *Marine and Freshwater Research* **53**, 1071-1082.

Ryan, P.G. 1987a. The incidence and characteristics of plastic particles ingested by seabirds. *Marine Environmental Research* **23**, 175-206.

Ryan, P.G. 1987b. The distribution, population size and foraging behaviour of Kerguelen Terns at the Prince Edward Islands. *South African Journal of Antarctic Research* **17**, 163-166.

Ryan, P.G. 2002. More than an island fling? Attempted rapes by Wandering Albatrosses. *Africa Birds & Birding* **7**, 15.

Ryan, P.G., Avery, G., Rose, B., Ross, G.J.B., Sinclair, J.C. & Vernon, C.J. 1989. The Southern Ocean seabird irruption to South African waters during winter 1984. *Cormorant* **17**, 41-55.

Ryan, P.G. & Boix-Hinzen, C. 1999. Consistent male-biased seabird mortality in the Patagonian Toothfish long-line fishery. *Auk* **116**, 851-854.

Ryan, P.G., Cooper, J., Dyer, B.M., Underhill, L.G., Crawford, R.J.M. & Bester, M.N. 2003a. Counts of surface-nesting seabirds breeding at sub-Antarctic Prince Edward Island, summer 2001/02. *African Journal of Marine Science* **25**, 441-451.

Ryan, P.G. & Hunter, S. 1985. Early breeding of Imperial Cormorants at Prince Edward Island. *Cormorant* **13**, 31-34.

Ryan, P.G. & Jackson, S. 1986. Stomach pumping: is killing seabirds necessary? *Auk* **103**, 427-428.

Ryan, P.G. & Jackson, S. 1987. The lifespan of ingested plastic particles in seabirds and their effect on digestive efficiency. *Marine Pollution Bulletin* **18**, 217-219.

Ryan, P.G., Keith, D.G. & Kroese, M. 2002. Seabird bycatch by tuna longline fisheries off southern Africa. *South African Journal of Marine Science* **24**, 103-110.

Ryan, P.G., Smith, V.R. & Gremmen, N.J.M. 2003b. The distribution and spread of alien vascular plants on Prince Edward Island. *African Journal of Marine Science* **25**, 555-561.

SCAR EGS 2004. Scientific Committee for Antarctic Research – Expert Group on Seals Report: http:/www.fagmed.uit.no/info/imb/aab/Scar/pdf/statusofstocs.pdf

Schramm, M. 1983. The breeding biologies of the petrels *Pterodroma macroptera, P. brevirostris* and *P. mollis* at Marion Island. *Emu* **83**, 75-81.

Schramm, M. 1986. The diet of chicks of Greatwinged, Kerguelen and Softplumaged Petrels at the Prince Edward Islands. *Ostrich* **57**, 9-15.

Shaffer, S.A., Costa, D.P. & Weimerskirch, H. 2003. Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. *Functional Ecology* **17**, 66-74.

Siegfried, W.R., Williams, A.J., Burger, A.E. & Berruti, A. 1978. Mineral and energy contributions of eggs of selected species of birds to the Marion Island terrestrial ecosystem. *South African Journal of Antarctic Research* **8**, 75-87.

Skinner, J.D. & Smithers, R.H.N. 1990. *The Mammals of the Southern African Subregion*. University of Pretoria, Pretoria.

Slade, R.W. 1997. Genetic studies of the Southern Elephant Seal, *Mirounga leonina*. In: Hindell, M. & Kemper, C. (Eds.). *Marine Mammal Research in the Southern Hemisphere. Vol. 1: Status, Ecology and Medicine*. Surrey Beatty and Sons, Chipping Norton, pp. 11-29.

Slip, D.J. 1995. The diet of Southern Elephant Seals (*Mirounga leonina*) at Heard Island. *Canadian Journal of Zoology*, **73**, 1519-1528.

Smith, V.R & Froneman, P.W. 2008. Nutrient dynamics in the vicinity of the Prince Edward Islands. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 165-179.

Steele, W.K. & Klages, N.T. 1986. Diet of the Blue Petrel at sub-Antarctic Marion Island. *South African Journal of Zoology* **21**, 253-256.

Tickell, W.L.N. 2000. *Albatrosses*. Pica Press, Sussex.

Tremblay, Y. & Cherel, Y. 2000. Benthic and pelagic dives: a new foraging behaviour in Rockhopper Penguins. *Marine Ecology Progress Series* **204**, 257-267.

Underhill, L.G., Petersen, S.L. & Cooper, J. 2003. Nest densities of the Wandering Albatross *Diomedea exulans* at the Prince Edward Islands, estimated using GPS. *African Journal of Marine Science* **25**, 529-535.

Van Aarde, R.J. 1980. The diet and feeding behaviour of feral cats, *Felis catus* at Marion Island. *South African Journal of Wildlife Research* **10**, 123-128.

Van den Hoff, J., Burton, H. & Davies, R. 2003. Diet of male Southern Elephant Seals (*Mirounga leonina* L.) hauled out at Vincennes Bay, East Antarctica. *Polar Biology* **26**, 27-31.

Van Heezik, Y.M., Seddon, P.J. & Cooper, J. 1995. Effects of inter-annual and inter-colony variability on counts of King Penguin colonies on Marion Island. In: Dann, P., Norman, I. & Reilly, P. (Eds.). *The Penguins: Ecology and Management*. Surrey Beatty & Sons, Chipping Norton, pp. 96-110.

Van Heezik, Y.M., Seddon, P.J., Cooper, J. & Plös, A.L. 1994. Interrelationships between breeding frequency, timing and outcome in King Penguins *Aptenodytes patagonicus*: are King Penguins biennial breeders? *Ibis* **136**, 279-284.

Van Heezik, Y.M., Seddon, P.J., du Plessis, C.J. & Adams, N.J. 1993. Differential growth of King Penguin chicks in relation to date of hatching. *Colonial Waterbirds* **16**, 71-76.

Van Rensburg, P.J.J. & Bester, M.N. 1988. The effect of cat *Felis catus* predation on three Procellariidae species on Marion Island. *South African Journal of Zoology* **23**, 301-305.

Walker, T.R., Boyd, I.L., McCafferty, D.J., Huin, N., Taylor, R.I. & Reid, K. 1998. Seasonal occurrence and diet of Leopard Seals (*Hydrurga leptonyx*) at Bird Island, South Georgia. *Antarctic Science* **10**, 75-81.

Warham, J. 1990. *The Petrels, their Ecology and Breeding Systems*. Academic Press, London.

Watkins, B.P. 2000. Killer Whale group attacks Sperm Whales. *African Environment and Wildlife* **8**, 16-17.

Watkins, B.P. & Cooper, J. 1986. Introduction, present status and control of alien species at the Prince Edward Islands, sub-Antarctic. *South African Journal of Antarctic Research* **16**, 86-94.

Weimerskirch, H. 1992. Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction and survival in the Wandering Albatross. *Oikos* **64**, 464-473.

Weimerskirch, H. 1998. Foraging strategies of Indian Ocean albatrosses and their relationships with fisheries. In: Robertson, G. & Gales, R. (Eds.). *Albatross Biology and Conservation*. Surrey Beatty & Sons, Chipping Norton, pp. 168-179.

Weimerskirch, H. 2004. Diseases threaten Southern Ocean albatrosses. *Polar Biology* **27**, 374-379.

Weimerskirch, H., Bonadonna, F., Bailleul, F., Mabille, G., Dell'Omo, G. & Lipp. H.-P. 2002. GPS tracking of foraging albatrosses. *Science* **295**, 1259.

Weimerskirch, H., Catard, A., Prince, P.A., Cherel, Y. & Croxall, J.P. 1999. Foraging White-chinned Petrels *Procellaria aequinoctialis*: at risk from the tropics to Antarctica. *Biological Conservation* **87**, 273-275.

Weimerskirch, H., Chastel, O., Ackermann, L., Chaurand, T., Cuenot-Chaillet, F., Hindermeyer, X., *et al.* 1994b. Alternate long and short foraging trips in pelagic-seabird parents. *Animal Behaviour* **47**, 472-476.

Weimerskirch, H., Doncaster, C.P. & Cuenot-Chaillet, F. 1994a. Pelagic seabirds and the marine environment: foraging patterns of Wandering Albatrosses in relation to prey availability and distribution. *Proceedings of the Royal Society of London B* **255**, 91-97.

Weimerskirch, H., Guionnet, T., Martin, J., Shaffer, S.A. & Costa, D.P. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proceedings of the Royal Society of London B* **267**, 1869-1874.

Weimerskirch, H. & Jouventin, P. 1998. Changes in population size and demographic parameters of six albatross species breeding in the French sub-Antarctic islands. In: Robertson, G. & Gales, R. (Eds.). *Albatross Biology and Conservation*. Surrey Beatty & Sons, Chipping Norton, pp. 84-91.

Weimerskirch, H. & Robertson, G. 1994. Satellite tracking of Light-mantled Sooty Albatross. *Polar Biology* **14**, 123-126.

Weimerskirch, H., Stahl, J.-C. & Jouventin, P. 1992. The breeding biology and population dynamics of King Penguins *Aptenodytes patagonicus* on the Crozet Islands. *Ibis* **134**, 107-117.

Wilkinson, I.S. 1992. *Factors affecting reproductive success of Southern Elephant Seals,* Mirounga leonina, *at Marion Island*. Ph.D. Thesis, University of Pretoria, South Africa.

Wilkinson, I.S. & Bester, M.N. 1990. Continued population increase in fur seals, *Arctocephalus tropicalis* and *A. gazella*, at the Prince Edward Islands. *South African Journal of Antarctic Research* **20**, 58-63.

Williams, A.J. 1980. Aspects of the breeding biology of Gentoo Penguins, *Pygoscelis papua*. *Gerfaut* **70**, 283-295.

Williams, A.J. & Berruti, A. 1978. Mineral and energy contributions of feathers moulted by penguins, gulls and cormorants to the Marion Island terrestrial ecosystem. *South African Journal of Antarctic Research* **8**, 71-74.

Williams, T.D. 1995. *The Penguins Spheniscidae*. Oxford University Press, Oxford.

Wilson, R.P. 1984. An improved stomach pump for penguins and other seabirds. *Journal of Field Ornithology* **55**, 109-112.

Wilson, R.P., Bost, C.-A., Pütz, K., Charrassin, J.-B., Culik, B.M. & Adelung, D. 1997. Southern Rockhopper Penguin *Eudyptes chrysocome chrysocome* foraging at Possession Island. *Polar Biology* **17**, 323-329.

Wilson, R.P., Grémillet, D., Syder, J., Kierspel, M.A.M., Garthe, S., Weimerskirch, H., *et al.* 2002. Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Marine Ecology Progress Series* **228**, 241-261.

Wilson, R.P., Hustler, K., Ryan, P.G., Burger, A.E. & Nöldeke, E.C. 1992. Diving birds in cold water: do Archimedes and Boyle determine energetic costs? *American Naturalist* **140**, 179-200.

Woehler, E.J. 1993. *The Distribution and Abundance of Antarctic and sub-Antarctic penguins*. SCAR, Cambridge.

Wynen, L.P., Goldsworthy, S.D., Guinet, C., Bester, M.N., Boyd, I.L., Gjertz, I., *et al.* 2000. Post-sealing genetic variation and population structure of two species of fur seal (*Arctocephalus gazella* and *A. tropicalis*). *Molecular Ecology* **9**, 299-314.

CHAPTER 7

NUTRIENT DYNAMICS IN THE VICINITY OF THE PRINCE EDWARD ISLANDS

VALDON R. SMITH AND P. WILLIAM FRONEMAN

Nutrient concentrations in the open waters of the Polar Frontal Zone (PFZ) are highly variable, reflecting the region's complex oceanographic regime. Surface concentrations of nitrate, silicate and phosphate range from 9.5 to 97.5, from 0.2 to 16.5 and from < 0.1 to 16.6 mmol m^{-3}, respectively (Allanson *et al.* 1985; Duncombe Rae 1989; Ismail 1990; Balarin 2000). Changes in nutrient concentrations coincide with the intrusion of Antarctic surface water from the south and sub-Antarctic surface water from the north (Ansorge *et al.* 1999; Froneman *et al.* 1999). Mesoscale features such as far field eddies or the eddies generated by the interaction between the Antarctic Circumpolar Current (ACC) and the South-West Indian Ridge further contribute to the heterogeneity in nutrient concentrations within the surface waters of the PFZ (Ansorge & Lutjeharms 2002, 2003; Ansorge *et al.* 2004).

Terrestrial nutrient dynamics on the Prince Edward Islands are strongly affected by the marine environment, through nutrients in aerosols blown in from the sea and brought in by seabirds and seals. In turn, the islands significantly influence nutrient composition of the surrounding ocean. Here we describe the dynamics of these land-sea nutrient interactions and provide a scenario of how the present warming being experienced by the islands and surrounding ocean (le Roux 2008) might influence these dynamics.

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 165-179

7.1 Oceanic inputs of nutrients to the Marion Island terrestrial system

7.1.1 Rainwater input

The ocean overwhelmingly dominates the chemical composition of rainwater at the island, so that the rainwater is simply a very dilute solution of seawater, with the same ionic concentration order ($Cl^{-}>Na^{+}>SO_4^{2-}>Mg^{2+}>Ca^{2+}\approx K^{+}$) as seawater and an Oceanic Origin Number of 103% (seawater has an O.O.N. of 100%; Grobbelaar 1978). Total ionic concentration ($Cl^{-} + Na^{+} + SO_4^{2-} + Mg^{2+} + Ca^{2+} + K^{+}$) in the rainwater decreases from 400 to 700 mg l^{-1} about 15 m from the shore to 100 to 200 mg l^{-1} 800 m from the shore and does not decline appreciably further inland (Grobbelaar 1974, 1978).

Appreciable concentrations of NH_4-N (up to 0.3 mg l^{-1}) and NO_3-N (up to 0.1 mg l^{-1}) occurred in 88 rainwater samples collected over a one year period about 450 m inland on the eastern part of the island; the NH_4-N probably originated as ammonia volatilised from penguin colonies on the coast and the NO_3-N as aerosols of seawater (Smith 1987). No PO_4-P has ever been detected in the island's rainwater, which is surprising since appreciable levels of PO_4-P (up to 0.03 mg l^{-1}) are found in the surrounding ocean. In total, about 0.21 g N m^{-2} y^{-1} is deposited through precipitation 450 m inland on the eastern part of the island (Smith 1987), a small fraction of the amount contained in the soil or taken up annually by the vegetation (Smith 2008), but probably sufficient to compensate for losses of N from the area through leaching and wind removal of plant litter (Smith 1988). Estimated deposition rates for other nutrients at the same locality were 10.4 g Na m^{-2} y^{-1}, 1.2 g Mg m^{-2} y^{-1}, 0.4 g K m^{-2} y^{-1}, 0.4 g Ca m^{-2} y^{-1}, 16.4 g Cl m^{-2} y^{-1} and 2.1 g S m^{-2} y^{-1}. In total, 31 g m^{-2} y^{-1} of these elements were added to the site through rainwater, which agrees well with the input of 35 g m^{-2} y^{-1} at the nearby meteorological station (computed from data in Grobbelaar 1974).

7.1.2 Bird and seal input

Table 7.1 provides an estimate of the amounts of nutrients brought in through the guano of surface nesting birds in the mid 1970s and in 2002/03 and the excreta of Elephant Seals in 1980/81. Table 7.2 gives the amounts of nutrient input as moulted feathers and Elephant Seal fur. Elephant seal inputs are from Panagis (1984). The 1970 values for the avian inputs are from a reanalysis of guano nutrient inputs given by Burger *et al.* (1978) and of feather nutrient input by Williams & Berruti (1978), the reanalysis being based on more accurate census data for the period (Cooper & Brown 1990; Huyser *et al.* 2000; Crawford *et al.* 2003), a refinement of feather production at moult for the two most abundant species (Brown 1985) and a more comprehensive data base on guano nutrient composition (unpublished data; Smith 1976; Lindeboom 1979). The 2002/03 estimates of nutrient input through guano and feathers are based on bird census data in Crawford *et al.* (2003), assuming that the proportion of non-breeders to breeders, the amounts of guano and feathers produced per bird, the number of days spent ashore and the nutrient composition of the guano and feathers were the same in 2002/03 as in 1974/75.

Burrowing bird species have been shown to markedly enhance the nutrient status of plants and soils at the island (Smith 1976), but hitherto a lack of information on the population sizes of burrowing birds made it impossible to estimate the quantity of nutrients they bring to the island. Ryan and Bester (2008) give body masses and population sizes of the various burrowing species. These were used to estimate the amounts of nutrients input by each species, from feather mass and feather nutrient concentration data in Williams (1978), and published (Fugler 1985) and unpublished nutrient composition data for the guano of burrowing species. Daily guano production of adult burrowers was estimated from body mass using the body mass:guano production relationship for the smaller surface nesters (Lesser Sheathbill, Kelp Gull, sub-Antarctic Skua and Crozet Shag). It was assumed that the adults of all of the burrowing species spend 150 days at the island. Guano production of the chicks of burrowing species was obtained from Fugler (1985).

In total, the 2002/03 population of seabirds brought in 4 279 tons of guano per year to the island (Table 7.1), containing 640 t N, 106 t P and 222 t Ca, amounts that represented a substantial proportion of the annual uptake of nutrients by the island's vegetation (c.37% of N, 67% of P and 31% of Ca uptake). However, most guano is produced in a very narrow shore-zone strip; King Penguins, Macaroni Penguins and Rockhopper Penguins account for 76% of all guano, most of which is deposited on bare ground and washes down to the sea or (or in the case of N) is volatilised. This has a considerable local effect since the surrounding vegetation around colonies has a much enhanced nutrient status (Smith 1978), forming what Lindeboom (1984) termed an "ammonia shadow" around the island's penguin colonies. However, on a whole island basis, it is not known to what extent the nutrients deposited in penguin colonies affect the vegetation inland. There has been one study of the fate of guano N in the penguin colony, at Kildalkey Bay on the island's south east coast (Lindeboom 1979, 1984). There, in the mid 1970s 350 000 Macaroni Penguins and 150 000 King Penguins daily produced 2 900 kg of guano containing 600 kg N, about 80% as uric acid and the rest as proteins, NH_4-N and NO_3-N. Uric acid N and protein N are rapidly transformed to NH_4-N ammonia, but about 24 kg is washed down to the sea in small streams that flow through the colony. About 11 kg of the NH_4-N is nitrified (and then probably denitrified) and about 10 kg is washed to the sea. Most (about 430 kg N) volatilises, about 370 kg of which is blown out to sea and about 60 kg blown inland. An unknown amount of the latter is deposited inland through rain and dry deposition. About 16 kg N day^{-1} is deposited directly on the vegetation near the colony, mainly by non-breeding King Penguins. This, with the ammonia blown inland (and assuming all that ammonia is deposited somewhere on the island), means that only about 12% of the penguin guano N produced at Kildalkey Bay influences the island's soils and vegetation. A similar situation

Table 7.1 Annual input of nutrients (kg per annum) in excreta of seabirds and seals.

Species	1974/75				2002/03			
	Guano production (tons y^{-1})	N	P	Ca	Guano production (tons y^{-1})	N	P	Ca
King Penguin	2 182	23 666	61 320	136 169	2 210	239 700	62 108	137 919
Gentoo Penguin	46	5 531	1 541	2 640	27	3 315	924	1 582
Macaroni Penguin	1 145	225 644	27 031	34 591	930	183 151	21 941	28 077
Rockhopper Penguin	179	35 641	4 227	5 409	129	25 598	3 036	3 885
Sub-Antarctic Skua	14	1 716	147	559	6	745	64	243
Lesser Sheathbill	22	1 645	279	940	17	1 332	226	761
Crozet Shag	12	866	55	1 870	6	439	28	949
Kelp Gull	6.1	446	29	963	0.8	56	4	120
Wandering Albatross	5.3	810	58	25	4.6	696	50	21
Grey-headed Albatross	2.1	319	23	10	2.1	317	23	10
Sooty Albatross	0.9	129	9	3.9	0.3	45	3	1.4
Light-mantled Sooty Albatross	0.08	12.2	0.9	0.4	0.05	7.7	0.5	0.2
Northern Giant Petrel	0.13	26.7	1.2	1.1	0.08	16.6	0.7	0.7
Southern Giant Petrel	0.92	188	8	8	0.56	114	5	5

Table 7.1 Continued.

Species	1974/75				2002/03			
	Guano production (tons y^{-1})	N	P	Ca	Guano production (tons y^{-1})	N	P	Ca
Fairy Prion					4	877	78	220
Salvin's Prion					456	91 214	8 152	22 851
Blue Petrel					234	43 535	4 876	14 395
Great-winged Petrel					64	11 537	730	1 620
Grey Petrel					8	1 889	113	258
Soft-plumaged Petrel					26	5 411	462	2 370
Kerguelen Petrel					54	10 856	970	2 720
White-chinned Petrel					96	18 983	2 471	3 943
South Georgian Diving Petrel					2	426	38	107
Shore	3 519	498 939	92 643	178 042	3 275	448 934	87 116	170 830
Inland	95	10 694	2 087	5 149	59	6 600	1 296	2 743
Burrows	-	-	-	-	945	184 728	17 891	48 483
Total birds					4 279	640 262	106 303	222 056
Elephant Seal excreta (1980/81)		6 683.0	387.3	57.5				

probably occurs at the island's other large penguin colonies, since the prevailing wind is westerly and all of them are on the island's north, south and east coasts.

In contrast to the large inputs of nutrients in the shore-zone, much smaller amounts are brought in by surface nesting birds inland. However, the nutrients deposited inland very markedly influence the stature, vitality and nutrient status of the vegetation surrounding the nests (Smith 1978). For instance, the yearly deposition of guano N around a single occupied Wandering Albatross nest is about 720 g N, all of which is rapidly transformed to NH_4-N and NO_3-N (Lindeboom 1979) and, since low soil pH prevents volatilisation of ammonia, is available for uptake by the vegetation. In addition to the local effect around the nest, down-slope leaching of nutrients improves soil fertility of a large area away from the nest. A similar situation applies for other inland surface nesting species, such as the Grey-headed Albatross, Giant Petrel, Kelp Gull, Skua and Light-mantled Sooty Albatross.

Moulted feathers represent another important avian input of nutrients to the island, in 2002/03 bringing in 54 t N, 214 kg P and 670 kg Ca (Table 7.2). Again, penguins on the shore zone account for most (88% to 98%) of the feather input of nutrients and it is not known how much of the nutrients become incorporated into the soils and vegetation.

With the exception of the King Penguin and Grey-headed Albatross, populations of the surface nesting species have declined since the mid 1970s (Crawford *et al.* 2003), for reasons suggested by Ryan and Bester (2008). The biggest decrease in absolute numbers has been for Macaroni Penguins (83 000 breeding pairs) and Rockhopper Penguins (26 000 pairs), but relative to population size the largest declines (40% to 88%) have been for Gentoo Penguins, Crozet Shags, Skuas, Sooty Albatrosses and Kelp Gulls. These declines have lead to a significant lowering of the annual input of nutrients to the island via guano or feathers, and the most marked effect has been inland. For instance, between the mid 1970s and 2002 the input of N, P and Ca through guano of the surface nesters declined by 4% to 10% in the shore zone and by 38% to 47% inland. N, P and Ca input through moulted feathers declined by 15% to 18% in the shore zone and by 22% to 24% inland. These changes refer to nutrient inputs by the surface nesters only. It is not known exactly how the populations of burrowing species have changed during the period, but it is likely that such changes have been notable, with marked effects on nutrient dynamics (Gremmen & Smith 2008).

Elephant seals excreta represent an annual input of 6 683 kg N, 387 kg P and 57 kg Ca to the island (Table 7.1). Moulted Elephant Seal fur represents an input of 699 kg N, 5 kg P and 4 kg Ca (Table 7.2). In total, Elephant Seal excreta and fur inputs of N and P are about two orders of magnitudes less than the inputs via bird excreta or feathers. Elephant Seals input three orders of magnitude less Ca than do birds. The input of nutrients to the island by sub-Antarctic Fur Seals and Antarctic Fur Seals, which together have a

Table 7.2 Annual input of nutrients (kg per annum) through moulted feathers and fur by seabirds and seals.

Species	1974/75				2002/03			
	Feather production	N	P	Ca	Feather production	N	P	Ca
King Penguin	154 380	13 365	52	119	156 363	13 536	53	120
Gentoo Penguin	1 095	108	0.13	1.6	656	65	0.08	1.0
Macaroni Penguin	398 045	42 997	151	458	323 086	34 900	123	372
Rockhopper Penguin	71 406	5 872	17	220	51 286	4 217	12	158
Sub-Antarctic Skua	269	31	0.07	0.4	117	14	0.03	0.2
Lesser Sheathbill	232	24	0.12	0.6	188	19	0.09	0.5
Crozet Shag	131	13.4	0.1	0.4	67	7	0.03	0.2
Kelp Gull	79	9.2	0.02	0.1	10	1	0.00	0.01
Wandering Albatross	878	101.9	0.23	1.1	756	88	0.20	1.0
Grey-headed Albatross	1 685	195	0.44	2.2	1 675	194	0.43	2.2
Sooty Albatross	549	63.7	0.14	0.7	193	22	0.05	0.3
Light-mantled Sooty Albatross	57	6.6	0.01	0.07	36	4	0.01	0.05
Northern Giant Petrel	110	13	0.03	0.14	68	8	0.02	0.09
Southern Giant Petrel	1 076	125	0.3	1.4	655	76	0.2	0.9

Table 7.2 Continued.

Species	1974/75				2002/03			
	Feather production	N	P	Ca	Feather production	N	P	Ca
Fairy Prion					15	2	0.04	0.02
Salvin's Prion					2 460	299	6.2	2.1
Blue Petrel					1 570	161	8.3	6.7
Great-winged Petrel					904	97	1.4	1.0
Soft-plumaged Petrel					209	30	0.5	0. 7
Kerguelen Petrel					584	53	1.9	0.9
Grey Petrel					156	22	3.5	0.1
White-chinned Petrel					1 644	176	2.5	1.9
South Georgian Diving Petrel					7	1	0.02	0.06
Shore	624 511	62 310	221.1	797.6	530 994	52 683	188	650
Inland	5482	613	1.3	8.3	4 160	468	1	6
Burrows	-	-	-	-	7 549	841	24	14
Total birds					542 703	53 992	213	670
Elephant seal fur (1980/81)		699.2	5.4	3.9				

population size nearly two orders of magnitude higher than that of elephant seals, is presently unknown. However, given the large numbers of Fur seals it is likely that their contribution to the nutrient dynamics of the island's terrestrial ecosystem will be substantial.

Nutrients brought in by seabirds and seals influence terrestrial ecosystem function at the island beyond the direct effect of vegetation production through enhanced soil nutrient concentrations. Various studies (discussed by Smith 2008) have shown that seabird and seal manuring, by providing readily oxidisable organic substrates and inorganic nutrients, is the principal determinant (even more so than temperature or moisture content) of other components of ecosystem energetics and nutrient cycling on the island, especially at the decomposition level. These include the size and activity of soil microorganism populations, soil heterotrophic activity, soil respiration and cellulose decomposition, and the numbers and diversity of microbivores.

7.2 Terrestrial/pelagic coupling

Macronutrient concentrations in the ocean in the immediate vicinity of the islands are largely determined by the interaction between the oceanographic environment and the activity of seabirds and seals (Lindeboom 1984; Allanson *et al.* 1985; Duncombe Rae 1989; Ismail 1990; Balarin 2000). In the shallow shelf waters between the two islands, concentrations of macronutrients, particularly reduced nitrogen (ammonia and urea) and phosphate are elevated compared to the open waters of the PFZ (Fig. 7.1) (Pakhomov & Froneman 1999; Pakhomov & Chown 2003). These elevated nutrient concentrations are largely derived from the guano of sea going animals, dung, urine and animal remains which are carried off the islands to the shelf waters via freshwater runoff (Allanson *et al.* 1985; Duncombe Rae 1989). Indeed, good correlations are found between the concentrations of the nutrients between the two islands and water column stability generated by freshwater runoff from the islands (Allanson *et al.* 1985; Duncombe Rae 1989). Maximum concentrations of phosphate derived from the mineralization of feathers are recorded from April to May in the shallow shelf waters of the islands whereas the peak in guano production occurs from December to February (Pakhomov & Froneman 1999). Temporal variation in the main sources of reduced nitrogen and phosphate culminates in a highly variable N:P ratio in the shallow shelf waters of the islands, which may range from 6.5:1 to 38:1 (Pakhomov & Froneman 1999). The elevated concentrations of nutrients derived from the land are not restricted to the immediate vicinity of the island. Elevated concentrations of ammonia and urea have been detected up to 80 km offshore (Pakhomov & Froneman 1999). Perissinotto *et al.* (1990a) attribute this to the advection of shelf waters downstream of the islands.

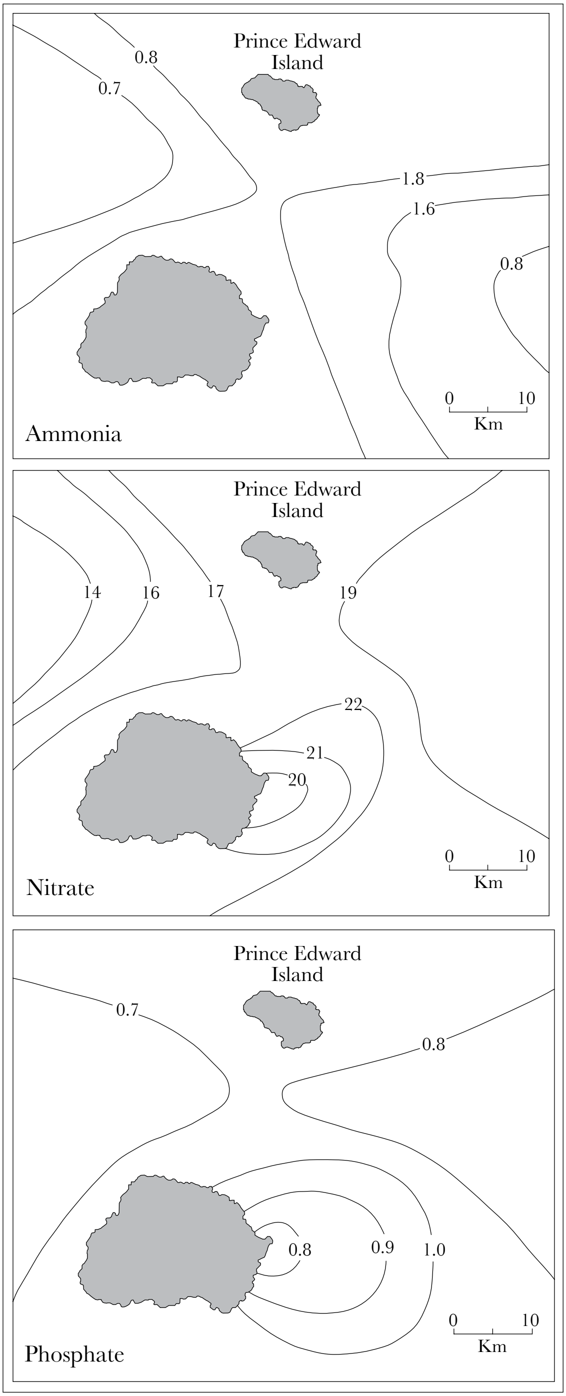


Figure 7.1 Surface concentrations (μmol l^{-1}) of selected nutrients in the vicinity of the Prince Edward Islands during austral autumn 1998. Data are from Balarin (2000).

Although activities of the seals and seabirds on the islands contribute to the nutrient levels in the waters surrounding the islands, oceanic phenomena are largely responsible for the build up of nutrient concentrations in the shallow shelf waters. The Antarctic Circumpolar Current (ACC) shows highest flow rates near the fronts that delimit it (Pakhomov *et al.* 2000a; Ansorge & Lutjeharms 2002) and under conditions when the SAF lies far to the north of the islands, current speeds past the islands are comparatively low (Ansorge & Lutjeharms 2002). This results in a weak interaction between the ACC and the archipelago and this in turn allows the retention of waters on the inter-island shelf (Pakhomov & Chown 2003). By contrast, when the SAF lies in close proximity to the islands, advection forces prevail and a flow through-flow system is established between the islands (Perissinotto & Duncombe Rae 1990; Pakhomov *et al.* 2000b). The retention of waters over the shallow island shelf when eddies are trapped between the islands contributes to the build-up of nutrient concentrations derived from the freshwater runoff from the islands within the inter-island region (Allanson *et al.* 1985). These elevated nutrient concentrations coupled with the increased water column stability derived from the freshwater runoff from the islands generates periodic phytoplankton blooms between the two islands; a phenomenon known as the, "island mass effect" (Allanson *et al.* 1985; Boden 1985; Pakhomov & Froneman 1999; Perissinotto *et al.* 1990a, ; Pakhomov & Chown 2003; McQuaid & Froneman 2004). Conversely, when the flow through prevails, concentrations of nutrients in the shelf waters are in the range of the open waters of the PFZ, due to a strong dilution effect (Balarin 2000).

Although large-scale hydrodynamic processes are largely responsible for determining nutrient concentrations in the waters between the islands, recent work suggests that smaller scale processes may also contribute to the build up of nutrient concentrations in the vicinity of the archipelago. The kelp *Macrocystis laevis* forms extensive beds in shallow waters close to shore and in relatively deep water (60 m) over the Natal Bank. It grows to nearly 30 m and forms a dense surface canopy that visibly subdues swell and retains freshwater run-off from the islands (Pakhomov *et al.* 2002). If this freshwater is nutrient-rich there will be a build up of nutrient concentrations in and around the kelp beds. The biological consequences of this process are as yet not known.

7.3 Impact of global climate change on nutrient dynamics of the Prince Edward Islands ecosystem

Although evidence of climate change (especially warming) in the sub-Antarctic is now well documented (Adamson *et al.* 1988; Jacka & Budd 1998; Smith 2002; Mélice *et al.* 2003) and some of the consequences on the terrestrial ecosystem of the Prince Edward Islands have been described (Smith & Steenkamp 1990; Chown & Smith 1993; Smith 2002), the effect of global climate change on the nutrient dynamics of the ocean around the Prince Edward Islands has received little attention.

The strongest evidence of change in the marine ecosystem is the southward shift, since the 1970s, in the average meridian position of the SAF (Hunt *et al.* 2001). While there is considerable inter-annual (and shorter-term) variability in the position of the front, it is currently *c.*1 degree farther south than in the 1970s. The shift in the position of the front can be linked to large-scale changes in atmospheric circulation patterns resulting from global climate change. Alterations in the ocean circulation patterns will in all probability be associated with changes in food availability and the foraging behaviour of the top predators, particularly flying seabirds on the two islands (Pakhomov & Chown 2003; Ryan & Bester 2008). These factors combined may result in changes in the populations of top predators on the islands, with subsequent decrease in the input of nutrients by these organisms. Clearly any decrease in the populations of the top predators on the islands coupled with the expected decrease in rainfall resulting from global climate change will alter the delivery of nutrients from the terrestrial to the marine environment.

7.4 References

Adamson, D.A., Whetton, P. & Selkirk, P.M. 1988. An analysis of air temperature records for Macquarie Island: Decadal warming, ENSO cooling and Southern Hemisphere circulation patterns. *Papers and Proceedings of the Royal Society of Tasmania* **122**, 107-112.

Allanson, B.R., Boden, B.P., Paker, L. & Duncombe Rae, C. 1985. A contribution to the oceanology of the Prince Edward Islands. In: Siegfied, W.R., Condy, P.R. & Laws, R.M. (Eds.). *Antarctic Nutrient Cycles and Food Webs*. Springer, Berlin, pp. 38-45.

Ansorge, I.J., Froneman, P.W., Lutjeharms, J.R.E., Bernard, K.S., Bernard, A., Lange, L., *et al.* 2004. An interdisciplinary cruise dedicated to understanding eddies upstream of the Prince Edward Islands. *South African Journal of Science* **100**, 319-323.

Ansorge, I., Froneman, P.W., Pakhomov, E.A., Lutjeharms, J.R.E., Van Ballegooyen, R. & Perissinotto, R. 1999. Physical-biological coupling in the waters surrounding the Prince Edward Islands (Southern Ocean) *Polar Biology* **21**, 135-145.

Ansorge, I.J. & Lutjeharms, J.R.E. 2002. The hydrography and dynamics of the ocean environment of the Prince Edward Islands (Southern Ocean). *Journal of Marine Systems* **37**, 107-127.

Ansorge, I.J. & Lutjeharms, J.R.E. 2003. Eddies originating at the South-west Indian ridge. *Journal of Marine Systems* **39**, 1-18.

Balarin, M.G. 2000. *Size fractionated phytoplankton biomass and primary production in the Southern Ocean*. M.Sc. Thesis, Rhodes University, South Africa.

Boden, B.P. 1985. Observations of the island mass effect in the Prince Edward archipelago. *Polar Biology* **5**, 81-93.

Brown, C.R. 1985. Energetic cost of moult in Macaroni penguins (*Eudyptes crysolophus*) and Rockhopper penguins (*E. chrysocome*). *Journal of Comparative Physiology B* **155**, 515-520.

Burger, A.E., Lindeboom, H.J. & Williams, A.J. 1978. The mineral and energy contributions of guano of selected species of birds to the Marion Island terrestrial ecosystem. *South African Journal of Antarctic Research* **8**, 59-70.

Chown, S.L. & Smith, V.R. 1993. Climate change and the short-term impact of feral house mice at the Sub-Antarctic Prince Edward Islands. *Oecologia* **96**, 508-516.

Cooper, J.C. & Brown, C.R. 1990. Ornithological research at the sub-Antarctic Prince Edward Islands: a review of achievements. *South African Journal of Antarctic Research* **20**, 40-57.

Crawford, R.J.M., Cooper, J., Dyer, B.M., Greyling, M.D., Klages, N.T.W., Ryan, P.G., *et al.* 2003. Populations of surface nesting seabirds at Marion Island, 1994/95-2002/03. *African Journal of Marine Science* **25**, 427-440.

Duncombe Rae, C.M. 1989. Data report of the first cruise of the Marion Off-shore Ecological study (MOES-1). *South African National Science Progress Report* **159**, 384 pp.

Froneman, P.W., Ansorge, I., Pakhomov, E.A. & Lutjeharms, J.R.E. 1999. Plankton communities and the physical environment in the waters surrounding the Prince Edward Islands in late austral summer 1997. *Polar Biology* **22**, 145-155.

Fugler, S.R. 1985. Chemical composition of guano of burrowing petrel chicks (Procellariidae) at Marion Island. In: Siegfied, W.R., Condy, P.R. & Laws, R.M. (Eds.). *Antarctic Nutrient Cycles and Food Webs*. Springer, Berlin, pp. 169-172.

Gremmen, N.J.M. & Smith, V.R. 2008. Terrestrial vegetation dynamics. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 215-244.

Grobbelaar, J.U. 1974. *A contribution to the limnology of the sub-Antarctic island Marion*. D.Sc. Thesis, University of the Free State, South Africa.

Grobbelaar, J.U. 1978. Mechanisms controlling the composition of freshwaters on the sub-Antarctic island Marion. *Archiv für Hydrobiologie* **83**, 145-157.

Hunt, B.P.V., Pakhomov, E.A. & McQuaid, C.D. 2001. Short-term variation and long-term changes in the oceanographic environment and zooplankton community in the vicinity of a sub-Antarctic archipelago. *Marine Biology* **138**, 369-381.

Huyser, O., Ryan, P.G. & Cooper, J. 2000. Changes in population size, habitat use and breeding biology of Lesser Sheathbills at Marion Island: Impact of cats, mice and climate change? *Biological Conservation* **92**, 299-310.

Ismail, H.E. 1990. Surface nutrients in the vicinity of the Prince Edward Islands during April/May 1989. *South African Journal of Antarctic Research* **2**, 33-36.

Jacka, T.H. & Budd, W.F. 1998. Detection of temperature and sea ice extent changes in the Antarctic and the Southern Ocean. *Annals of Glaciology* **27**, 553-559.

le Roux, P.C. 2008. Climate and climate change. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 39-64.

Lindeboom, H.J. 1979. *Chemical and microbial aspects of the nitrogen cycle of the nitrogen cycle on Marion Island*. Ph.D. Thesis, Groningen University, Holland.

Lindeboom, H.J. 1984. The nitrogen pathway in a penguin rookery. *Ecology* **65**, 269-27.

McQuaid, C.D. & Froneman, P.W. 2004. Rhodes southern Ocean Group: scientific findings from seventeen years of biological oceanography in the South African National Antarctic Programme. *South African Journal of Science* **100**, 571-577.

Mélice, J-L., Lutjeharms, J.R.E., Rouault, M. & Ansorge, I.J. 2003. Sea-surface temperatures at the sub-Antarctic islands Marion and Gough during the past 50 years. *South African Journal of Science* **99**, 363-366.

Pakhomov, E.A., Ansorge, I.J. & Froneman, P.W. 2000a. Variability in the inter-island environment of the Prince Edward Islands (Southern Ocean). *Polar Biology* **23**, 593-603.

Pakhomov, E.A., Ansorge, I.J., Kaehler, S., Vumazonke, L.U., Gulekana, K., Bushula, T., *et al.* 2003. Studying the impact of ocean eddies on the ecosystem of the Prince Edward Islands: DEIMEC II: research in action. *South African Journal of Science* **6**, 187-190.

Pakhomov, E.A. & Chown, S.L. 2003. The Prince Edward Islands: Southern Ocean Oasis. *Ocean Yearbook* **17**, 348-379.

Pakhomov, E.A. & Froneman, P.W. 1999. The Prince Edward Islands pelagic ecosystem: a review of achievements 1976-1990. *Journal of Marine Systems* **18**, 297-310.

Pakhomov, E.A., Froneman, P.W., Ansorge, I.J. & Lutjeharms, J.R.E. 2000b. Temporal variability in the physico-biological environment of the Prince Edward Islands (Southern Ocean). *Journal of Marine Systems* **26**, 75-95.

Pakhomov, E.A., Kaehler, S. & McQuaid, C.D. 2002. Zooplankton community structure in the kelp beds of the Sub-Antarctic Prince Edward Archipelago: are they a refuge for larval stages? *Polar Biology* **25**, 778-788.

Panagis, K. 1984. *The influence of Southern elephant Seals* Mirounga leonina *(Linnaeus) on the coastal terrestrial ecology of Marion Island*. M.Sc. Thesis, University of Pretoria, South Africa.

Perissinotto, R., Allanson, B.R. & Boden, B.P. 1990a. Trophic relations within the island seas of the Prince Edward Archipelago, Southern Ocean. In: Barnes, M. & Gibson, R.N. (Eds.). *Trophic Relationships in the Marine Environment*. Aberdeen University Press, Aberdeen, pp. 296–314.

Perissinotto, R. & Duncombe Rae, C.M. 1990. Occurrence of anticyclonic eddies on the Prince Edward Plateau (Southern Ocean): effects on phyto-plankton biomass and production. *Deep-Sea Research I* **37**, 777-793.

Perissinotto, R., Duncombe Rae, C.M., Boden, B.P. & Allanson, B.R. 1990b. Vertical stability as a controlling factor of the marine phytoplankton production at the Prince Edward Archipelago (Southern Ocean). *Marine Ecology Progress Series* **60**, 205-209.

Ryan, P.G. & Bester, M.N. 2008. Pelagic predators. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 121-164.

Smith, V.R. 1976. The effect of burrowing species of Procellariidae on the nutrient status of inland tussock grasslands on Marion Island. *South African Journal of Botany* **42**, 265-272.

Smith, V.R. 1978. Animal-plant-soil nutrient relationships on Marion Island (sub-Antarctic). *Oecologia* **32**, 239-253.

Smith, V.R. 1987. Chemical composition of precipitation at Marion Island (sub-Antarctic). *Atmospheric Environment* **21**, 1159-1165.

Smith, V.R. 1988. Production and nutrient dynamics of plant communities on a sub-Antarctic Island. 5. Nutrient budgets and turnover times for mire-grasslands, fjaeldmark and fernbrakes. *Polar Biology* **8**, 255-269.

Smith, V.R. 2002. Climatic change in the Sub-Antarctic: an illustration from Marion Island. *Climatic Change* **52**, 345-357.

Smith, V.R. 2008. Terrestrial and freshwater primary production and nutrient cycling. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 181-214.

Smith, V.R. & Steenkamp, M. 1990. Climatic change and its ecological implications at a sub-Antarctic Island. *Oecologia* **85**, 14-24.

Williams, A.J. 1978. Mineral and energy contributions of petrels (Procellariiformes) killed by cats, to the Marion Island terrestrial ecosystem. *South African Journal of Antarctic Research* **8**, 49-53.

Williams, A.J. & Berruti, A. 1978. Mineral and energy contributions of feathers moulted by penguins, gulls and cormorants to the Marion Island terrestrial ecosystem. *South African Journal of Antarctic Research* **8**, 71-74.

CHAPTER 8

TERRESTRIAL AND FRESHWATER PRIMARY PRODUCTION AND NUTRIENT CYCLING

VALDON R. SMITH

The first biological/geological research expedition to Marion Island in 1965/66 concentrated on the taxonomy of the island's biota and on the physiognomy and floristics of its vegetation (Van Zinderen Bakker *et al.* 1971). The next four expeditions (1971 to 1976) were mostly devoted to quantifying energy flow and nutrient pathways in the island ecosystem, particularly how the transfer of nutrients from the ocean to the island via saltspray, seabirds and seals influences the nutrient composition of freshwaters, soils and plants (Van Zinderen Bakker 1978). In the late 1970s and early 1980s, research at the island was heavily influenced by the systems approach of the International Biological Programme's Biome Project (Rosswall & Heal 1975), which at the time dominated ecological science efforts and had as it's chief objective "to measure net primary production of the main types of terrestrial ecosystems" and "to define the relationships between production and the main factors influencing it" (Heal 1981). Primary production and nutrient cycling of the most common plant communities on the island were investigated.

Subsequent research has focussed on factors that determine rates of the component processes of energy and nutrient flow in the island's ecosystem, such as photosynthesis, decomposition and nutrient interactions between

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 181-214

plants, soils, micro organisms and soil invertebrates. This chapter describes production and nutrient cycling in the island's vegetation and the factors that influence both. Since most of the energy and nutrients incorporated in the vegetation go through a decomposition rather than a grazing chain, the factors that influence rates of decomposition and nutrient mineralization are discussed, including threats to these processes posed by an invasive alien organism. Finally, an account is given of the primary production and nutrient composition of the island's freshwaters.

8.1 Terrestrial communities

8.1.1 Vegetation standing crop and primary production

Production and nutrient cycling studies have been carried out in eight plant communities:

- A fellfield (dominated by the cushion plant *Azorella selago*).
- Two fernbrakes (an open type with *A. selago*, the fern *Blechnum penna-marina* and the grass *Agrostis magellanica*, and a closed type dominated by *B. penna-marina*).
- A drainage line on a slope (dominated by the dicot herb *Acaena magellanica*, *B. penna-marina* and the moss *Brachythecium rutabulum*).
- Two tussock (*Poa cookii*) grass communities; one a dense cover of *P. cookii*, *Acaena magellanica*, *B. penna-marina* and *B. rutabulum* on a slope occupied by burrowing birds and the other a narrow strip of *P. cookii* with an understory of *A. selago* cushions (some of which occurred over subterranean prion nests) on the crest of a slope.
- Two mire communities (dominated by the graminoids *Agrostis magellanica*, *Uncinia compacta* and *Juncus scheuchzerioides* and several bryophytes).

Together, these communities are representative of about 90% of the island's low altitude vegetation and are described in more detail by Gremmen & Smith (2008). Harvested quadrats were used to estimate standing crop and primary production. At each community, all the above- and belowground plant material in 0.1 m^2 or 0.25 m^2 quadrats was collected at approximately fortnightly intervals throughout the growing season and sorted into species, organ and, for the aboveground material, according to whether it was alive or dead. The plant material was dried at 105°C, weighed and chemically analysed. The dry masses were converted to biomass (the mass of living material per m^2) or necromass (the mass of dead material per m^2). Here, the maximum (biomass plus necromass) value found over the sampling period is reported as the standing crop of the particular community. Peak-trough analyses of the biomass and necromass dynamics (on a per-species basis) over the sampling period were carried out to estimate primary production for each community. The production values were corrected for decomposition using rates of disappearance of plant litter contained in nylon mesh bags. Nutrient concentrations in the biomass and necromass were converted to standing stocks, (g nutrient in the vegetation per m^2). Peak-trough analyses of the standing stock dynamics of a particular nutrient over the season yielded estimates of uptake of that nutrient at the particular community. Details of the harvest sampling procedures and computations of standing crop, primary production and nutrient uptake and losses are given by Smith (1987a, b).

8.1.1.1 Standing crop

Despite the low stature of their vegetation (there are no trees or even shrubs on the island, the tallest plants being the tussock grass), all the communities contain substantial amounts of plant matter. Vegetation standing crop (dry mass of living plus dead plant material) is 2 519 to 2 696 g m^{-2} in fellfield and mires, 4 406 to 5 269 g m^{-2} in fernbrakes and the drainage line, and 5 566 to 7 494 g m^{-2} in the tussock grass communities (Table 8.1). Substantial proportions (33% to 82%) of the standing crop occur belowground. Of the aboveground standing crop, much (32% to 82%) is dead plant material; this might also be true for the belowground standing crop but it was not possible to reliably distinguish living from dead roots.

Table 8.1 Vegetation standing crop, standing stocks and pool sizes of nutrients. All values are g m^{-2}. The contribution of bryophytes to the aboveground standing crop or nutrient standing stock is indicated in brackets. From Smith (1987b, 1988a, b) and unpublished data.

Community	Standing crop	Nutrient standing stock			
		N	P	K	Ca
	Tussock grassland				
In vegetation:					
Aboveground live	1 245 (340)	21.90 (6.59)	2.36 (0.71)	13.53 (2.96)	3.32 (1.16)
Aboveground dead	1 375	18.16	1.72	3.07	5.88
Aboveground total	2 620	40.06	4.08	16.60	9.20
Belowground	2 947	35.32	4.27	18.39	5.64
Total above- & belowground	5 566	75.37	8.35	34.99	14.84
In soil:					
Available pool		1.17	3.49	101.82	90.01
Organic pool		981.25	78.50	23.55	341.47
Total soil pool		982.42	81.99	125.37	431.48
Total pool (veg. plus soil):		1 057.79	90.34	160.36	446.32
Proportion of total pool in veg.		7%	9%	22%	3%

Table 8.1 Continued.

Community	Standing crop	Nutrient standing stock			
		N	P	K	Ca
Drainage line					
In vegetation:					
Aboveground live	1 170 (358)	15.95 (5.20)	1.81 (0.78)	7.60 (2.61)	5.80 (2.42)
Aboveground dead	549	8.70	0.83	1.50	5.69
Aboveground total	1 719	24.65	2.64	9.10	11.49
Belowground	2 687	22.51	2.95	11.97	4.38
Total above- & belowground	4 406	47.16	5.59	21.07	15.87
In soil:					
Available pool		0.33	0.67	12.98	65.67
Organic pool		722.00	41.80	30.40	570.00
Total soil pool		722.33	42.47	43.38	635.67
Total pool (veg. plus soil):		769.49	48.06	64.45	651.54
Proportion of total pool in veg.		6%	11%	32%	2%
Slope crest					
In vegetation:					
Aboveground live	1 121	16.77	2.03	13.23	2.23
Aboveground dead	3 504	35.10	3.27	4.80	16.35
Aboveground total	4 625	51.87	5.30	18.02	18.58
Belowground	2 868	34.09	3.81	15.04	6.91
Total above- & belowground	7 494	85.96	9.11	33.06	25.49
In soil:					
Available pool		0.47	1.03	21.78	7.61
Organic pool		856.75	30.17	37.25	525.22
Total soil pool		857.22	31.20	59.03	532.83
Total pool (veg. plus soil):		943.18	40.31	92.09	558.32
Proportion of total pool in veg.		9%	23%	36%	5%
Closed fernbrake					
In vegetation:					
Aboveground live	592	9.29	1.49	10.22	2.62
Aboveground dead	1 487	20.08	1.18	1.59	11.49
Aboveground total	2 079	29.37	2.67	11.81	14.11
Belowground	3 190	34.62	5.39	19.25	10.08
Total above- & belowground	5 269	63.99	8.06	31.06	24.19
In soil:					
Available pool		0.20	0.89	5.92	42.85
Organic pool		793.28	78.42	14.42	310.50
Total soil pool		793.48	79.31	20.34	353.35
Total pool (veg. plus soil):		857.47	87.37	51.40	377.54
Proportion of total pool in veg.		8%	9%	60%	6%

Table 8.1 Continued.

Community	Standing crop	Nutrient standing stock			
		N	P	K	Ca
	Open fernbrake				
In vegetation:					
Aboveground live	580	7.55	0.81	6.67	3.11
Aboveground dead	1 839	17.68	0.83	0.61	15.65
Aboveground total	2 419	25.23	1.64	7.28	18.76
Belowground	2 036	20.03	2.08	13.23	7.99
Total above- & belowground	4 455	45.26	3.72	20.51	26.75
In soil:					
Available pool		0.15	0.64	3.25	75.33
Organic pool		679.58	59.62	27.32	285.16
Total soil pool		679.73	60.26	30.57	360.49
Total pool (veg. plus soil):		724.99	63.98	51.08	387.24
Proportion of total pool in veg.		6%	6%	40%	7%
	Fellfield				
In vegetation:					
Aboveground live	330 (15)	3.86 (0.10)	0.43 (0.01)	4.17 (0.02)	1.95 (0.03)
Aboveground dead	1 483	12.81	0.57	0.13	14.42
Aboveground total	1 813	16.67	1.00	4.30	16.37
Belowground	883	8.38	0.59	6.32	4.85
Total above- & belowground	2 696	25.05	1.59	10.62	21.22
In soil:					
Available pool		<0.01	0.10	1.32	66.97
Organic pool		237.10	42.83	16.17	551.75
Total soil pool		237.10	42.93	17.49	618.72
Total pool (veg. plus soil):		262.15	44.52	28.11	639.94
Proportion of total pool in veg.		10%	4%	38%	3%
	Mire 1				
In vegetation:					
Aboveground live	173 (34)	2.25 (0.46)	0.22 (0.03)	2.03 (0.11)	0.23 (0.09)
Aboveground dead	282	2.22	0.15	0.35	0.39
Aboveground total	455	4.47	0.37	2.38	0.62
Belowground	2 064	30.58	2.05	2.57	2.60
Total above- & belowground	2 519	35.05	2.42	4.95	3.22
In soil:					
Available pool		0.69	0.67	5.11	26.66
Organic pool		386.85	18.54	10.40	37.59
Total soil pool		387.54	19.21	15.51	64.25
Total pool (veg. plus soil):		422.59	21.63	20.46	67.47
Proportion of total pool in veg.		8%	11%	24%	5%

Table 8.1 Continued.

Community	Standing crop	Nutrient standing stock			
		N	P	K	Ca
Mire 2					
In vegetation:					
Aboveground live	457 (279)	4.04 (2.22)	0.26 (0.11)	5.37 (3.33)	1.16 (1.00)
Aboveground dead	332	2.49	0.15	0.12	0.40
Aboveground total	789	6.53	0.41	5.49	1.56
Belowground	1 759	11.73	0.95	6.46	0.97
Total above- & belowground	2 548	18.26	1.36	11.95	2.53
In soil:					
Available pool		0.26	0.84	6.81	14.09
Organic pool		326.31	18.03	10.33	56.77
Total soil pool		326.57	18.87	17.14	70.86
Total pool (veg. plus soil):		344.83	20.23	29.09	73.39
Proportion of total pool in veg.		5%	7%	41%	3%

High vegetation standing crops have also been reported for other sub-Antarctic islands. On South Georgia, *Festuca contracta*-dominated mires and meadows (which are physiognomically similar to the Marion Island mires) have standing crops of 3 930 to 4 317 g m^{-2} (Greene *et al.* 1973; Lewis Smith & Stephenson 1975), and an *Acaena magellanica* herbfield (very similar to the Marion Island drainage line community) a standing crop of 9 578 g m^{-2} (Lewis Smith & Walton 1975). On Macquarie Island, a *Pleurophyllum hookeri-Stilbocarpa polaris* herbfield 235 m above sea level had a total standing crop of 2 727 g m^{-2}; a similar community at lower altitude had 2 343 g plant material m^{-2} aboveground alone (Jenkin 1975). Like at Marion Island, however, it is the tussock grass-dominated communities that possess the highest standing crops – 8 411 g m^{-2} for *Poa foliosa* tussock at Macquarie (Jenkin 1975) and 17 785 g m^{-2} for *Poa flabellata* tussock at South Georgia (Lewis Smith & Walton 1975).

Sub-Antarctic island vegetation has most often been described as "tundra" since it shows strong physiognomic similarities to Northern Hemisphere tundra vegetation (low-growing, dominated by cryptogams, cushion plants, small shrubs, herbs and graminoids, mostly occurring on wet organic soils or peats). Aboveground standing crops of the Marion Island plant communities (455 to 4 625 g m^{-2}) are mostly higher than values reported for physiognomically-similar vegetation types in Northern Hemisphere tundra (< 100 to 2 500 g m^{-2}), but belowground standing crops at the island are in the range of tundra values. Bryophytes are an important component in many of the island's communities and actually contribute more to the standing crop than is suggested in Table 8.1. The table shows standing crops at the time of peak aboveground mass of living plant material (late March/early April, i.e. late summer/

autumn). This corresponds to the time of maximum vascular plant live mass but not maximum bryomass, which is in winter and spring. Peak bryomasses are 451 g m^{-2} in the tussock grassland, 482 g m^{-2} in the drainage line and 245 g m^{-2} at mire 1, considerably higher than the values in Table 8.1. However, even these peak values are in the lower part of the range (40 to 1 682 g m^{-2}) of bryomasses found in Northern Hemisphere tundras.

8.1.1.2 Primary production

Annual net primary production (ANP) of all the island's communities is high – from 685 g m^{-2} y^{-1} at fellfield to 2 178 g m^{-2} y^{-1} at one of the mires, and belowground production contributes between 41 and 68% to the ANP (Table 8.2). High ANP values have also been reported from other sub-Antarctic islands; 1 014 g m^{-2} y^{-1} for a herbfield on Macquarie Island (Jenkin 1975) and 842 g m^{-2} y^{-1} and 1 605 g m^{-2} y^{-1} for a *F. contracta* meadow and *Acaena magellanica* herbfield, respectively, on South Georgia (Clarke *et al.* 1971; Lewis Smith & Walton 1975). Very much higher ANPs have been reported for *Poa* tussock grasslands on these two islands – 5 581 g m^{-2} y^{-1} at Macquarie and 6 025 g m-2 y-1 at South Georgia (Jenkin 1975; Lewis Smith & Walton 1975). It is thus somewhat surprising that the two tussock communities on Marion Island (1 982, 1 936 g m^{-2} y $^{-1}$) were not the most productive of the Marion Island communities.

Excepting for the fellfield, total ANPs of the island communities are higher than those (7 to 885 g m^{-2} y^{-1}) reported for the 52 Northern Hemisphere sites investigated as part of the IBP Tundra Biome Study (Wielgolaski *et al.* 1981). Bryophyte ANPs at the island (172 to 307 g m^{-2} y^{-1}) are in the upper part of the range shown by Northern Hemisphere tundra; e.g. 9 to 350 g m^{-2} y^{-1} at Arctic and sub-Arctic mires and sedge-moss meadows and 5 to 210 g m^{-2} y^{-1} at shrub, dwarf shrub and sedge-heath communities. Even compared with temperate plant communities, ANPs of the island's plant communities are high; for instance, total ANPs at mire 1 (2 178 g m^{-2} y^{-1}), tussock grassland (1 982 g m^{-2} y^{-1}) and slope crest community (1 936 g m-2 y-1) are greater than the maximum (1 425 g m-2 y-1) found for temperate North America grasslands by the IBP Grassland Biome Study (Sims & Singh 1978). They are very much in the upper part of the range reported for temperate wetlands and marshes – vegetation types considered to be particularly productive; e.g. 918 to 1 741 for sedge wetlands (Bernard & Gorham 1978), 1 539 g m^{-2} y^{-1} for bog marshes (Reader 1978) and 2 187 g m^{-2} y^{-1} for a freshwater tidal wetland (Whigham *et al.* 1978).

Table 8.2 Annual net primary production (ANP) and cycling of nutrients at the plant communities. All values are g m^{-2} y^{-1}. The contribution of bryophytes to the aboveground production is given in brackets. The percentage contribution of belowground to the total ANP is shown in italics. From Smith (1987a, b, c; 1988a, b) and unpublished data.

Community	ANP	N	P	K	Ca
Tussock grassland					
Aboveground	949 (172)				
Belowground	1 033 *52%*				
Total	1 982				
Uptake into aboveground		18.93 (3.34)	2.38 (0.36)	10.36 (1.50)	4.91 (0.60)
Backtranslocated		3.38	0.82	6.55	0
Lost in litterfall		15.55	1.56	3.81	4.91
Uptake into belowground		11.80	1.50	6.34	1.55
Total net uptake for ANP		27.35	3.06	10.15	6.46
Drainage line					
Aboveground	891 (274)				
Belowground	612 *41%*				
Total	1 503				
Uptake into aboveground		17.11 (3.98)	1.94 (0.60)	8.78 (2.00)	8.89 (1.86)
Backtranslocated		2.98	0.41	5.01	0
Lost in litterfall		14.13	1.53	3.77	8.89
Uptake into belowground		4.77	0.73	2.95	1.22
Total net uptake for ANP		18.90	2.26	6.72	10.11
Slope crest					
Aboveground	809				
Belowground	1 127 *58%*				
Total	1 936				
Uptake into aboveground		12.48	1.66	9.55	3.64
Backtranslocated		3.86	0.88	8.33	0
Lost in litterfall		8.62	0.78	1.22	3.64
Uptake into belowground		12.14	1.34	6.12	3.05
Total net uptake for ANP		20.76	2.12	7.34	6.69
Closed fernbrake					
Aboveground	728				
Belowground	1 230 *63%*				
Total	1 958				
Uptake into aboveground		12.05	1.33	8.06	5.71
Backtranslocated		1.64	0.62	6.89	0
Lost in litterfall		10.41	0.71	1.17	5.71
Uptake into belowground		13.94	2.47	8.68	4.01
Total net uptake for ANP		24.35	3.18	9.85	9.72

Table 8.2 Continued.

Community	ANP	N	P	K	Ca
Open fernbrake					
Aboveground	502				
Belowground	1 076 *68%*				
Total	1 578				
Uptake into aboveground		6.34	0.61	6.34	3.99
Backtranslocated		0.70	0.30	5.82	0
Lost in litterfall		5.64	0.31	0.52	3.99
Uptake into belowground		11.08	1.25	7.70	4.57
Total net uptake for ANP		16.72	1.56	8.22	8.56
Fellfield					
Aboveground	266 (4)				
Belowground	419 *61%*				
Total	685				
Uptake into aboveground		3.54 (0.03)	0.32 (0.004)	3.26 (0.005)	2.14 (0.008)
Backtranslocated		1.04	0.22	3.13	0
Lost in litterfall		2.50	0.10	0.13	2.14
Uptake into belowground		4.04	0.36	3.40	2.24
Total net uptake for ANP		6.54	0.46	3.53	4.38
Mire 1					
Aboveground	883 (307)				
Belowground	1 295 *59%*				
Total	2 178				
Uptake into aboveground		8.97 (3.41)	0.72 (0.15)	4.41 (1.47)	1.85 (0.89)
Backtranslocated		0.69	0.22	2.09	0.03
Lost in litterfall		8.28	0.50	2.32	1.82
Uptake into belowground		16.55	1.29	3.00	2.10
Total net uptake for ANP		24.83	1.79	5.32	3.92
Mire 2					
Aboveground	570 (253)				
Belowground	547 *49%*				
Total	1 117				
Uptake into aboveground		6.17 (1.75)	0.56 (0.13)	5.78 (3.85)	1.35 (0.98)
Backtranslocated		1.06	0.31	1.76	0
Lost in litterfall		5.11	0.25	4.02	1.35
Uptake into belowground		4.38	0.31	2.29	0.35
Total net uptake for ANP		9.49	0.56	6.31	1.70

8.1.1.3 Growth season duration, primary productivity and production efficiency

The island's hyperoceanic climate results in small seasonal and diurnal variations in temperature and in rain falling throughout the year (le Roux 2008). On temperature and moisture considerations, the growing season for the vegetation is potentially long. From the harvest quadrat data and phenological observations (Huntley 1970, 1972), the growing season for vascular plants at low altitudes (< 300 m) is mid-August to mid-June, or about 10 months. Bryophytes carry out most of their growth during the same period but there is some bryomass production even in midwinter (Smith 1987a). Long growing seasons have also been suggested for other sub-Antarctic islands (Wielgolaski *et al.* 1981). By contrast, the Northern Hemisphere tundra communities mentioned in the comparisons above have much shorter growing seasons, from a few weeks at high Arctic sites to about 6 months for sub-Arctic and alpine tundras. It is the long growing season that allows such high annual primary productions at sub-Antarctic islands, rather than any intrinsic capability of the vegetation to grow fast. In fact, production rates (termed here *productivity*, and considering only the aboveground ANP) are between 0.9 g m^{-2} day^{-1} for fellfield and 3.1 g m^{-2} day^{-1} for tussock grassland, lower than aboveground productivities of most sub-Arctic shrub- or dwarf shrub-dominated tundras (3 to 10 g m^{-2} day^{-1}; Wielgolaski *et al.* 1981) where the growing season is thermally more favourable for plant growth. They are more similar to the productivities (2.2 to 3.3 g m^{-2} day^{-1}; Wielgolaski *et al.* 1981) of sedge-moss and grass-herb communities at higher latitude Arctic regions, which also have cool summers.

The low productivities are also related to low radiation levels at the island. The oceanic climate results in incessant cloudiness and the daily radiation receipt in the growing season is only about 50% of that at the top of the atmosphere. This is lower than at polar and sub-polar regions of the Northern Hemisphere. Production efficiencies of the island's plant communities, based on the radiation receipt for the seasons when the production studies were carried out (mean, 409 x 10^{4} kJ m^{-2}) and the energy contents of the plants (Smith 1987c), and considering both above- and belowground components, are between 0.7% (fellfield) and 2.1% (mire 1), similar to values (0.7% to 2.4%) for sub-Arctic and Arctic tundras (Wielgolaski *et al.* 1981). This shows that although the island vegetation grows more slowly during the growing season, it uses the incident radiation as effectively as do the Northern Hemisphere tundras.

Various regression models relating primary production to temperature, precipitation or evapotranspiration have been proposed (Whittaker 1970; Lieth 1972, 1974; Lieth & Box 1972; Lauenroth 1979; Walter 1979). They all predict higher ANPs at Marion Island than what are actually found. For instance, Lieth's model (Lieth 1974), which is reasonably successful across a range of other vegetations, from tundra to tropical, predicts an aboveground ANP of 990 g m^{-2} y^{-1} based on temperature and 1 968 g m^{-2} y^{-1} based on precipitation. Both predictions are higher than any of the measured values (266 to 949 g m^{-2} y^{-1}, Table 8.2), suggesting that, in addition to temperature and precipitation, other factors are important in determining primary production at the island. The role of light has been mentioned above. Wind is another factor that has long been considered an important, even dominant, factor for the vegetation of sub-Antarctic islands (Skottsberg 1912; Taylor 1955; Löffler 1983). The almost incessant high wind is a strong determinant of vegetation structure at Marion Island (Huntley 1971; Gremmen 1981) and it probably also influences vegetation function through its chill-factor effect and by depressing stomatal conductance. A similar suggestion was made by French & Smith (1985), based on multivariate ordination comparisons of microclimatic, edaphic and vegetation parameters from sub-Antarctic, Northern Hemisphere tundra and oceanic moorland ecosystems. In the ordinations based on climate only, sub-Antarctic plant communities linked with Northern Hemisphere tundra communities at a higher latitude than their own. Including vegetation and soil parameters in the ordinations increases the latitudinal shift, so that the vegetation and its variation at sub-Antarctic islands is more typical of the most climatically-extreme high-latitude Arctic sites than of sub-Arctic tundras or oceanic moorlands. French & Smith (1985) concluded that abiotic factors other than those included in the ordination analyses must be having a marked effect on the vegetation of sub-Antarctic islands and suggested that the most important one is wind. Smith and Steenkamp (2001; see also Gremmen & Smith 2008) showed that the most widespread vegetation type on Marion Island, that of mid-to-high altitude regions exposed to exceptionally strong winds, is structurally (an extremely sparse vegetation made up only of mosses and lichens on a barren unstable surface caused by active periglacial activity) and functionally (ecosystem processes controlled by abiotic rather than biotic factors) typical of high Arctic polar deserts, the most climatically-extreme type of tundra.

8.1.2 Nutrient cycling

8.1.2.1 Nutrient pool sizes

Nutrient pool sizes in the communities are given in Table 8.1. The total N pool (N in the vegetation and the soil) is low in fellfield (262 g N m^{-2}) due to shallow soils with low N concentrations. N and P pools in the mires (345 to 423 g N m^{-2}, 20 to 22 g P m^{-2}) are lower than at the slope communities (725 to 1 058 g N m^{-2}, 40 to 90 g P m^{-2}). This is due to lower peat bulk densities at the mires rather than lower gravimetric N or P concentrations, which are actually similar to those of the slope communities. Ca pools are largest in the communities dominated by dicotyledonous plants or on mineral soils (e.g. the drainage line and fellfield with > 600 g Ca m^{-2}) and lowest in communities dominated by graminoids and bryophytes and on peats (e.g. the mires with *c.*70 g Ca m^{-2}).

The pattern of K pool size across the communities is less clear and does not follow a simple differentiation between slope/mire or dicot/graminoid-bryophyte vegetation. K pool size is closely related ($r^2 = 0.71$, $P < 0.001$) to the amount of aboveground living plant material (especially living leaves), which contains much higher concentrations of K than does dead or belowground plant material. It also correlates strongly with soil K concentration ($r^2 = 0.94$; $P < 0.001$). Hence, tussock grassland, with a large proportion of living leaf material and enriched in soil K by burrowing birds (Smith 1976), has the largest K pool (160 g K m^{-2}) of all the communities. For all the communities, 22 to 60% of the total K pool is contained in the vegetation. Only 3 to 11% of the total pools of N, P or Ca occur in the vegetation, except for P at the slope crest community, where the vegetation contains 23% of the total P pool.

Total N pools at the island (262 to 1 058 g N m^{-2}) are similar to those found for other sub-Antarctic and Maritime Antarctic plant communities (426 to 1 164 g N m^{-2}), Northern Hemisphere tundras (330 to 1 014 g N m^{-2}) and oceanic moorlands, bogs and montane grasslands (309 to 1 075 g N m^{-2}; all these non-Marion Island values are from collations of nutrient pool size information by Smith 1987b, 1988a). P pools at the island (20 to 90 g m^{-2}) are lower than for most Northern Hemisphere tundras (42 to 461 g P m^{-2}) and are more similar to those (9 to 85 g P m^{-2}) for oceanic bogs, heaths and grasslands. As is the case at Marion Island, soils at these oceanic sites are highly organic peats with low total P concentrations. K pools of the island's communities (20 to 160 g K m^{-2}) are in the lower part of the range of values (16 to 474 g K m^{-2}) reported for Northern Hemisphere tundras and similar to those (17 to 160 g K m^{-2}) for oceanic bogs, heaths and grasslands. The strong distinction in Ca pool size between graminoid/bryophyte-dominated vegetation and dicot-dominated vegetation is also shown in Northern Hemisphere tundra. Within the two types, Ca pools at the island are smaller than in the Northern Hemisphere communities. The two mires possessed 67 to 73 g Ca m^{-2}, compared with 134 to 750 g Ca m^{-2} for tundra sedge meadows and tundra grasslands, and the fellfield and slope communities have Ca pools of 378 to 652 g Ca m^{-2}, compared with 537 to 1 219 g Ca m^{-2} for shrub and heath tundras. In summary, the island communities have total N pools that are similar to, but total P, K and Ca pools that are lower than, their counterparts in Northern Hemisphere tundra.

Despite the fact that most of the total nutrient pool occurs in the soil, rather than the plants, the island vegetation actually supports larger N, P and K standing stocks (quantity of nutrients contained in plant material; Table 8.1) than most Northern Hemisphere tundras, especially if only the aboveground vegetation is considered. This reflects the higher vegetation standing crops on the island and the fact that the island's climate allows for greater aboveground plant growth than in Northern Hemisphere tundra, which is more climatically-extreme and where a greater proportion of nutrient standing stocks are maintained in belowground plant parts. In contrast to the larger N, P and K, standing stocks, Ca standing stocks at the island are lower than in most tundra vegetations.

8.1.2.2 Nutrient uptake, nutrient turnover times and nutrient costs of the ANP

The high ANP means that the vegetation takes up substantial amounts of nutrients; 7 to 27 g N m^{-2} y^{-1}, 0.5 to 3 g P m^{-2} y^{-1}, 5 to 10 g K m^{-2} y^{-1} and 2 to 10 g Ca m^{-2} y^{-1} (Table 8.2). In some instances the quantity taken up annually is greater than the standing stock of the particular nutrient in the vegetation (Table 8.1), suggesting fast circulation rates. Nutrient turnover times in the vegetation (Table 8.3) are, in fact, short (1.4 to 4.1 years for N, 1.4 to 4.3 y for P, 0.9 to 4.5 y for K and 0.8 to 4.8 y for Ca), in the lower part of the range reported for Northern Hemisphere tundra vegetation (1.1 to 17.5 y for N, 1.0 to 14.0 y for P, 0.9 to 15.0 y for K and 1.5 to 17.0 y for Ca; Dowding *et al.* 1981; Van Cleve & Alexander 1981). However, despite the large amounts of nutrients taken up in the ANP, and the fast circulation rates through the vegetation, only a small fraction (1 to 8%) of the total pools of N, P or Ca circulates annually through the vegetation (Table 8.3). A larger proportion (6 to 26%) of the total K pool circulates through the vegetation.

Nutrient costs (the amounts of nutrient required to produce one g of plant material) are given in Table 8.3. For particular nutrients, the difference in cost between communities is mostly related to differences in the type of plant material (species, organ) that form the predominant component of the ANP. Hence, the amount of Ca taken up per g ANP is low for the mires (1.5 to 1.8 mg Ca g^{-1}), where monocotyledon plants and bryophytes (with a low Ca requirement) contribute solely to the ANP, and high for the fellfield, fernbrakes and drainage line (5.0 to 6.7 mg Ca g^{-1}), where dicotyledon plants and *B. penna-marina* (with a substantial requirement for Ca) predominate in the ANP. Intermediate Ca costs are shown by the tussock grassland and slope crest communities, where monocotyledon and dicotyledon plants both contribute to the ANP. *Blechnum penna-marina* fronds also have a high growth requirement for K and contribute a substantial proportion of the ANP at the tussock grassland, fellfield and fernbrakes, accounting for the high K cost of the ANP at these communities. ANP at mire 2 also carries a high K cost, and, interestingly, there is a different relationship between the N and K costs of the two mire communities. N cost is greater at mire 1 than at mire 2, whereas the opposite is true for K cost. This is because the bryophyte layer at mire 1 comprises mainly *Jamesoniella colorata* and *Racomitrium lanuginosum* which, like most of the other bryophytes on the island, accumulate more N than K. Mire 2 is dominated by two bryophytes (*Blepharidophyllum densifolium* and *Clasmatocolea humilis*) that are unusual in that they accumulate more K than N (Smith 1987d).

There is no information on the costs of individual nutrients to the ANP of Northern Hemisphere tundra, but Swift *et al.* (1979) reported the *total nutrient costs* (i.e. the sum of the costs of N, P, K, Ca, Mg Na, Si, Fe and Mn) of the aboveground ANP for 18 vegetation types, ranging from tundra to tropical forest. Total nutrient costs for the island's communities (17 to 40 mg nutrients g^{-1} aboveground ANP; Table 8.3) are very much in the lower part of the range (18 to 135 mg g^{-1}) for the vegetations considered by Swift *et al.* (1979). Boreal

Table 8.3 Nutrient cycling parameters for the communities. From Smith (1987b, 1988a, b) and unpublished data.

Community	N	P	K	Ca	N	P	K	Ca
	Turnover time in vegetation (years)				Percentage of total nutrient pool that circulates through the vegetation annually (%)			
Tussock grassland	2.8	2.7	3.4	2.3	3	3	6	1
Drainage line	2.5	2.5	3.1	1.6	3	5	10	2
Slope crest	4.1	4.3	4.5	3.8	2	5	8	1
Closed fernbrake	2.6	2.5	3.2	2.5	3	4	19	3
Open fernbrake	2.7	2.4	2.5	3.1	2	2	16	2
Fellfield	3.8	3.5	3.0	4.8	3	1	13	1
Mire 1	1.4	1.4	0.9	0.8	6	8	26	6
Mire 2	1.9	2.4	1.9	1.5	3	3	22	2

Community	N	P	K	Ca	Total nutrients
	Nutrient "cost" of the above- and belowground ANP (mg nutrient taken up per g ANP)				Total nutrient cost of the aboveground ANP only (mg g^{-1})
Tussock grassland	13.8	1.5	5.1	3.3	34.0
Drainage line	12.6	1.5	4.5	6.7	40.1
Slope crest	10.7	1.1	3.8	3.5	21.9
Closed fernbrake	12.4	1.6	5.0	5.0	33.1
Open fernbrake	10.6	1.0	5.2	5.4	27.9
Fellfield	9.5	0.7	5.1	6.4	23.9
Mire 1	11.4	0.8	2.4	1.8	17.4
Mire 2	8.5	0.5	5.6	1.5	22.1

Community	N	P	K	Ca	N	P	K	Ca
	Percentage of amount taken up aboveground by vascular vegetation that is backtranslocated (%)				Replenishment of available nutrient pool needed to meet the vegetation's requirements (times per year)			
Tussock grassland	22	40	74	0	23	0.9	0.1	0.1
Drainage line	23	31	74	0	57	3.4	0.5	0.2
Slope crest	31	53	87	0	44	2.1	0.3	0.9
Closed fernbrake	14	47	85	0	122	3.6	1.7	0.2
Open fernbrake	11	49	92	0	111	2.4	2.5	0.1
Fellfield	30	71	96	0	2 179	4.6	2.7	0.1
Mire 1	12	39	71	3	36	2.7	1.0	0.1
Mire 2	24	71	92	0	36	0.7	0.9	0.1

forests are generally regarded as being extremely efficient at maintaining appreciable primary production levels under severe nutrient limitation and the lowest nutrient costs (18 to 25 mg nutrients g^{-1}) given by Swift *et al.* (1979) were, in fact, for three boreal forests. The island's fellfield (24 mg nutrients g^{-1}) and mires (17 and 22 mg g^{-1}) are as efficient in maintaining their productivity at a low unit nutrient uptake.

This efficiency is achieved mainly by having plant tissue with low nutrient concentrations (N, P and Ca concentrations in the mire graminoid plants and bryophytes are considerably lower than in tundra graminoids and bryophytes; Smith 1987b), rather than by conserving nutrients through efficient backtranslocation of nutrients from senescing tissue into perennial organs. This is apparent from the short turnover times of all the nutrients in the vegetation, but also from estimates of the amounts of nutrients taken up into the aboveground vascular vegetation that are retranslocated to storage organs (mainly leaf sheaths, stem bases, rhizomes and roots) before senescence (Table 8.3). Only 12 to 31% of the N taken up into the aboveground vascular vegetation is retranslocated, the rest is lost in the litterfall. For P, less than half of the amount taken up is retranslocated, except for the fellfield and one of the mires, where 71% of the P is retranslocated. In tundra vegetation commonly more than 50%, and up to 90%, of the aboveground N and P is retranslocated before senescence (Berendse & Jonasson 1992). Between 71 and 96% of K taken up by the island vegetation is retranslocated. This is in the upper part of the range for tundra plants but might be an overestimate due to possible leaching of K from senescing tissue. Almost all the Ca taken up into the aboveground vascular vegetation is lost in the litterfall.

8.1.2.3 Plant-available nutrient pools and their replenishment rates

The communities considered in this chapter possess low soil levels of plant-available forms of P, and exceptionally low levels of plant-available N. Pools of available N (NH_4-N + NO_2-N + NO_3-N) were between < 0.01 and 1.2 g N m^{-2} (Table 8.1), corresponding to volumetric soil concentrations of between 0.004 and 4.68 μg N cm^{-3}. Even the most ultra-oligotrophic sub-Arctic and Arctic tundra mire peats possess much higher concentrations of inorganic N (17 to 43 μg N cm^{-3}; Gersper *et al.* 1980; Rosswall & Granhall 1980). Similarly, available P pools in the island's communities (0.1 to 3.5 g P m^{-2}; Table 8.1) equate to volumetric concentrations of 0.4 to 14 μg P cm^{-3}, in the lower part of the range for tundra soils (0.1 to 101.4 μg P cm^{-3}; Brown & Veum 1974; Everett *et al.* 1981). There is a close correlation between N and P concentrations in plant litter and the amounts of available N and P in the soils (Figs 8.1a, b). Likewise, N and P concentrations in the bryomass (which in some communities form the main input into the decomposer system, but for which dead shoots cannot be distinguished from live ones) are also positively related to available N and P levels (Figs 8.1c, d). The significance of the positive relationship between plant litter or bryomass N and P concentrations and soil levels of available N and P will become apparent later.

The available N pool needs to be replenished from 23 to 2 179 times per year to meet the vegetation's annual requirement for N (Table 8.3). The P pool needs to be replenished 0.7 to 4.6 times per year. The available Ca pool at all the communities is larger than the vegetation's annual requirement and needs to be replenished only every 1.1 to 10 years. Available K pools need to be replenished 1.7 to 2.7 times per year at the fernbrakes and fellfield (where *B. penna-marina* fronds take up substantial amounts of K), but K pools at the other communities are at least as large as the annual requirement.

8.1.2.4 Nutrient inputs

The fact that the available N pools need to be turned over much more rapidly (from four hours at fellfield to 16 days at the tussock grassland) than the pools of available P, K or Ca (80 days to 10 years) suggests that N might be the element most likely to limit primary production. Only the tussock grassland (possibly also the slope crest community) is directly influenced through manuring of birds (Smith 1976), but ammonia from penguin rookeries in the nearby shore zone reaches the communities via precipitation and dry deposition. However, as a source for replenishing the N pool, this is insignificant, bringing in only 0.21 g N m^{-2} y^{-1} (Smith 1987e), or 1 to 3% of the annual requirement for N by the vegetations of the various communities. Precipitation also supplies only 4 to 11% of the K, and 4 to 22% of the Ca, needed for plant growth. No P occurs in the precipitation. None of the island's plants form associations with N-fixing rhizobia, but nitrogen is fixed by heterotrophic soil bacteria (Smith 1985) and cyanobacteria (the latter in algal mats on the soil surface and as epiphytes on mosses; Smith 1984). For five of the eight communities considered here the amounts of N fixed heterotrophically- and autotrophically were determined. In total, a maximum of 0.1 g N m^{-2} y^{-1} is added to the communities by N fixation (Smith 1988b), a negligible amount compared with the needs of the vegetation.

By contrast with the very small pools of plant-available (inorganic) N, the island's soils contain appreciable reserves of organic N (237-981 g N m^{-2}; Table 8.1). This is also true of the other nutrients (e.g. 18-79 g P m^{-2} and 10-39 g K m^{-2}) and is because the low level of herbivory leads to most of the plant material produced in the ANP becoming incorporated into the soil. Decomposition, with its concomitant mineralization of nutrients from organic matter, is the chief process by which the available nutrient pools in the soil are replenished. However, the same oceanicity of climate (no warm periods and high, recurrent precipitation) leads to cold, waterlogged, acid, leached soils, all of which are expected to restrict soil microbial activity. It has been shown that decomposition, with the concomitant release of nutrients, is the main bottleneck in nutrient cycling and primary production for most of the island's plant communities (Smith 1988b; Smith & Steenkamp 1992a). Consequently, much research has focussed on understanding decomposition of plant litter and soil organic matter at the island.

8.1.3 Decomposition and nutrient mineralization

8.1.3.1 Decomposition and soil heterotrophic activity

Vascular plant leaf litter enclosed in mesh bags shows a 33 to 59% mass loss over the first year (excepting for *B. penna-marina* fronds which lose only 13% of mass, possibly because they contain high concentrations of polyphenols; unpublished data). This is higher than mostly found from litter bag studies at Arctic (10 to 20%; Widden 1977) or sub-Arctic (4 to 42%; Rosswall *et al.* 1975) tundras and is more similar to loss rates of litters in warm oceanic bogs, mires and moorlands (16 to 57%; Heal *et al.* 1981).

The most intensive and extensive study of decomposition at the island has been an assessment of soil decomposition potential using the so-called "cotton strip" technique (Harrison *et al.* 1988) which is based on the tensile strength loss (TSL) of standardised cotton strips buried in soil. There are strong correlations between TSL and other measures of decomposition, such as plant litter mass loss (Heal *et al.* 1974) and nutrient mineralization (French 1988). The cotton strip technique has been shown to be useful for comparing soil decomposition potentials between different communities and even ecosystems, especially in cold temperate and sub-polar regions (Heal *et al.* 1981; Walton 1988; Wynn-Williams 1988). TSL rates of the island's non-manured soils are at the upper extreme of the range found for tundra, largely due to the relatively greater warmth of the island's soils (Smith *et al.* 1993). Soil nutrient status is the most important determinant of TSL, so that the island's manured soils have TSL rates up to an order of magnitude greater than those in tundra.

Soil respiration rate (as measured by the efflux of CO_2) in the unmanured communities considered in this chapter ranges from 0.9 μmol CO_2 g^{-1} h^{-1} (fellfield, to 6.3 μmol CO_2 g^{-1} h^{-1} (mire) (Smith 2003), very similar to those reported for arctic and sub-arctic tundra soils (0.2 to 6.0 μmol CO_2 g^{-1} h^{-1}; Nadelhoffer *et al.* 1991; Vanhala *et al.* 1996; Vance & Chapin 2001). However, these comparisons are based on respiration rates at 10°C. For most of the year tundra soils are much colder, mostly frozen, and soil activity will be low. By contrast, soil temperature under closed vegetation on the island is much more stable throughout the year (Blake 1997) and freezing does not occur. Like TSL, soil respiration is also very markedly enhanced by animal manuring, due to inorganic nutrient enrichment (Smith 2003) as well as an enhanced input of labile organic C substrate in the form of excreta (Smith 2005). Mean respiration rate of tussock grassland soils is 9.4 μmol CO2 g^{-1} h^{-1} at 10°C; soils more heavily influenced by birds or seals have up to three times higher rates.

The importance of seabirds and seals has also been shown for other decomposition-related soil characteristics. For instance, 48% of the variation in plate-count numbers of soil aerobic bacteria is explained by differences in soil inorganic N content, related to the manuring influence of seabirds or seals (Smith & Steyn 1982). Direct (epifluorescence microscopy) counts of soil bacteria are also significantly positively related to soil N and P levels (French & Smith 1986). From information on bacterial cell numbers, types (shapes and sizes) and total volumes, French & Smith (1986) predicted the growth and metabolic activities of soil bacteria in relation to site conditions. Grobler *et al.* (1987) subsequently showed that bacterial metabolic activity (^{14}C-glucose kinetics and dehydrogenase activity) varied across communities in the manner predicted: manured soils have higher bacterial activity than unmanured soils, but within these two groups there is a clear effect of altitude (taken to indicate climatic severity). The pattern of TSL across the plant communities is also entirely consistent with the soil heterotrophic activity data of Grobler *et al.* (1987).

8.1.3.2 Nutrient mineralization and the role of soil fauna

Detailed investigations of nutrient mineralization rates have only been carried out at one of the communities (mire 1) and only N has been considered. From changes in peat inorganic N concentrations and concomitant uptake rates by the mire vegetation, it has been calculated that mineralization rates are 178 mg N m^{-2} d^{-1} in summer and 55 mg N m^{-2} d^{-1} in winter (Smith & Steenkamp 1992a). In mid-summer, when the vegetation is growing most actively, the rate of uptake by the vegetation is 336 mg N m^{-2} d^{-1}, equivalent to a mineralisation of 0.1% of the organic reserve of N per day. Laboratory and field measurements, by several techniques, of N mineralization in the mire peat all yield values that are too low to account for these estimated rates of N release, or for the requirements of the vegetation. For instance, at the maximum measured mineralisation rate (48 mg N m^{-2} d^{-1}; Smith & Steenkamp 1992a), uptake by the vegetation in summer would have led to depletion of the available N pool in about seven days.

These mineralization results are limited by the usual ambiguities associated with simplistic N transformation studies that consider small soil samples and where the fate of some of the inorganic forms of N are uncertain (e.g. it is not known how important denitrification is at the island). However, their main shortcoming is that they reflected N release by microbial organisms on their own, ignoring the effect of soil fauna. The island's soils contain large numbers of meso- and macrofauna (e.g., nematodes, springtails, mites, earthworms and insect larvae (Burger 1978; Gabriel *et al.* 2001; Barendse *et al.* 2002), most of which are detritivores and/or microbivores, and which account for a substantial proportion of energy flow at the island. For instance, Crafford (1990a) estimated that the larvae of one moth species alone consumes about 150 g plant litter m^{-2} y^{-1} and also processes large quantities of peat.

Soil fauna stimulate decomposition rate by comminuting the decomposing substrate, by chemically altering it so that it is more amenable to microbial action, and by enlarging the suite of microorganisms acting on it (Anderson *et al.* 1981). Microcosm studies have confirmed that this is true for the island's soil fauna (Smith & Steenkamp 1992b, 1993). The release of inorganic nutrients from decomposing plant litter and peat in the microcosms, with or without macroinvertebrates, is shown in Table 8.4. Moth larvae (*Pringleophaga marioni*) and earthworms (*Microscolex kerguelarum*) significantly enhance mineralization rates of N, P and K from litter. The effect is even more marked with peat, where N release is up to 30 times faster in the presence of moth larvae, earthworms or weevil larvae. No inorganic P release can be detected in microcosms containing only peat but there is substantial release when moth larvae or earthworms were present.

Table 8.4 Release rates of nutrients from plant litter or peat in microcosms (μg nutrient g^{-1} litter or peat d^{-1}, ± standard error). "Control" indicates microcosms without macroinvertebrates. Otherwise the microcosms contained either two moth larvae, two earthworms or five weevil larvae. Four plant (species) litters were tested with moth larvae and three with earthworms. Asterisks indicate that the difference between the animal and control microcosms is significant at ***$P = 0.001$ or **$P = 0.01$. From Steenkamp (1991).

Plant litters	**N**	**P**	**K**	**Ca**
Control	0.7 ± 0.06	0.3 ± 0.05	2.8 ± 0.27	1.3 ± 0.22
Moth larva	3.8 ± 0.68***	1.1 ± 0.19***	5.0 ± 0.12***	2.2 ± 0.20***
Control	0.7 ± 0.04	0.4 ± 0.04	3.3 ± 0.17	0.9 ± 0.13
Earthworm	1.8 ± 0.17***	0.7 ± 0.10**	4.0 ± 0.25**	0.9 ± 0.12
Peat	**N**	**P**	**K**	**Ca**
Control	1.5 ± 0.26	0	0.8 ± 0.09	2.2 ± 0.03
Moth larva	42.1 ± 2.45***	8.4 ± 0.69***	7.4 ± 0.99***	2.5 ± 0.16
Earthworm	29.9 ± 1.50***	8.0 ± 0.79***	2.0 ± 0.05***	2.3 ± 0.33
Weevil larva	10.2 ± 1.07**	0	2.4 ± 0.18***	1.4 ± 0.06***

Smith & Steenkamp (1992c) used the microcosm results in a model to estimate rates of N cycling at mire 1. The model considered macroinvertebrate densities, peat:macroinvertebrate mass ratios, microorganism biomasses, N pool sizes of the soil microorganisms and of the macroinvertebrates, temporal changes in soil inorganic N concentration and rates of N uptake by the vegetation. Of specific interest here is the contribution of macroinvertebrates to N mineralization. Earthworms cause the release in the mire peat of 265 mg N m^{-2} d^{-1}, moth larvae 67 mg N m^{-2} d^{-1}, weevil larvae 8 mg N m^{-2} d^{-1}, snails 0.7 mg N m^{-2} d^{-1} and slugs 4.3 mg N m^{-2} d^{-1}. To this combined total of 345 mg N m^{-2} d^{-1}, due to the macroinvertebrates, must be added the 48 mg N m^{-2} d^{-1} caused by microbes alone. This gives a total mineralization rate of 393 mg N m^{-2} d^{-1}, sufficient to account for the maximum daily requirement for N by the vegetation plus the observed concomitant changes in peat inorganic N in midsummer (336 mg N m^{-2} d^{-1}). A mineralization of 393 mg N m^{-2} d^{-1} means that soil macroinvertebrates and microorganisms together release an amount of N equivalent to that contained in their combined biomasses (1.2 g N m^{-2}) at mire 1 in three days. This indicates a very short turnover time of N in the two components (more correctly, it is a "pseudo-residence time"; Frissel 1981) and clearly shows that although soil macroinvertebrates and soil microflora constitute only a small fraction of the total N pool (0.3% at mire 1), their interaction is a crucial determinant of N mobilization.

The contribution of soil fauna to the release of nutrients besides N has not been quantified since no field studies have been carried out to parameterise the model. A simple extrapolation of the enhancements of P, K and Ca release from peat in microcosms (Table 8.4), using invertebrate densities at mire 1 given by Smith & Steenkamp (1992c), suggests a mineralization of 5.5 g P y^{-1} through the combined action of moth larvae, earthworms and weevil larvae, or about three times the annual requirement of the mire vegetation (1.8 g m^{-2} y^{-1}; Table 8.2). For K, the three invertebrate species cause a release of about 1.5 g m^{-2} y^{-1}, which is only a third of the vegetation's requirement. However, as shown in Table 8.3 there is substantial recirculation of K within the vegetation and the mean pool size of plant-available K in the soil is equal to the annual requirement. None of the three invertebrate species significantly stimulate release rate of Ca from peat over that caused by microorganisms alone. In fact, weevil larvae cause a net immobilization of Ca (Table 8.4). Microbially-mediated Ca mineralization is probably fast enough to replenish the available Ca pool, which at mire 1 is about 10 times larger than the amount taken up annually by the vegetation.

8.1.3.3 Impact of invasive biota on nutrient cycling

Factors detrimental to the soil macroinvertebrate populations will impact on nutrient cycling and hence on vegetation production at the island. One such factor that has been identified is the introduced House Mouse (*Mus musculus*) which has become feral on the island (Matthewson *et al.* 1994). Smith *et al.* (2002) investigated the diet of mice at three sites near the communities at which production and nutrient cycling studies were carried out. They showed that, on average over the year, moth larvae and adults, weevil larvae and adults and earthworms together contribute between 51% and 81% to the volume of stomach contents of the mice. Mice daily consume between 45 and 184 g (dry mass) ha^{-1} of those invertebrates; daily consumption of moth larvae alone is between 30 and 107 g ha^{-1}. These values agree with those from earlier studies. For instance, Rowe-Rowe *et al.* (1989) estimated that mice consume 108 g macroinvertebrates ha^{-1} d^{-1} on the island's coastal plain as a whole, 65 g ha^{-1} d^{-1} being moth larvae (Crafford 1990a). The species-specific consumption rates found by Smith *et al.* (2002) and Crafford (1990a) imply that mice annually remove between a third and six times the instantaneous biomass of the macroinvertebrate prey species in the particular study areas. This must severely impact on the macroinvertebrates, especially since most have long life cycles (e.g. the moth larvae take 2-10 years to mature; Crafford 1990b; see also Barendse & Chown 2000), and confirms conclusions from other studies that mice are cardinal determinants of macroinvertebrate population dynamics on the island (Crafford & Scholtz 1987; Chown 1990;

Chown & Smith 1993). It offers an explanation for the decline in densities of the preferred macroinvertebrate prey (moth larvae, weevil larva and adults, and spiders; Hänel 1999).

In the context of this chapter, predation by mice on terrestrial macroinvertebrates causes decreased rates of nutrient mineralization, quantitatively and qualitatively affecting vegetation production. A lowered nutrient availability will not only lower primary production, but the plant material which is produced will have a lower nutrient concentration (Fig. 8.1), resulting in a lower quality litter that will decompose even more slowly. Ultimately, this will change the balance between peat accumulation and decay, which is the most important factor governing vegetation succession at the island (Smith *et al.* 2001). This, along with the more direct effects of mice on the vegetation (e.g. granivory; Chown & Smith 1993), is a striking example of how insidious the effects of an alien invasive species may be on ecosystem structure and function at an oceanic island, especially when the invader is in a functional group or groups (in this instance, terrestrial herbivore and insectivore) poorly represented or absent at the island.

The limacid European slug *Deroceras panormitanum* was inadvertently introduced to the island in the mid- to late 1960s (Smith 1992). Since then it has spread throughout the low altitude regions of the island and in some habitats occurs in greater numbers than any indigenous macroinvertebrate. Slugs do not appear to be preyed on regularly by mice since their remains are seldom found in mouse stomach contents and captured starved mice refuse offered slugs (Smith *et al.* 2002). Like the indigenous macroinvertebrates, slugs markedly stimulate rates of nutrient release from plant litter (Smith & Steenkamp 1992b). However, they cause inorganic nutrient release rates that, relative to rates of carbon release, are different to those caused by indigenous invertebrates. This leads to different carbon:nutrient ratios in the decomposing substrate, ultimately affecting peat nutrient quality and hence primary production (Smith 2007) and suggesting that slugs cannot simply replace indigenous macroinvertebrates as nutrient recyclers without consequences for ecosystem structure and functioning on the island.

8.1.3.4 Climate change and nutrient cycling

The island's climate has changed significantly over the past 40 years, having become warmer and drier (Smith 2002; le Roux 2008). A warmer, drier climate will directly influence ecological functioning at the island through its effect on changed rates of primary production, decomposition and nutrient cycling. Climate change will also have other, less direct effects, as discussed by Smith & Steenkamp (1990), Gremmen & Smith (2008) and Smith & Froneman (2008). For instance, altered atmospheric and oceanic circulation patterns underlie the climatic changes at the island (Rouault *et al.* 2005) and this might affect the trophic dynamics of the seal and seabird populations, by moving their feeding grounds, or making it harder/easier for them to reach the feeding grounds.

This will result in a changed rate of transfer of nutrients from the ocean to the island, an important determinant of ecosystem function at the island. However, probably the most important effect of a warming climate is that it increases the ease with which invasive alien organisms can become established on the island (Bergstrom & Chown 1999). Like the example of the House Mouse, this can have far-reaching implications for ecological functioning at the island.

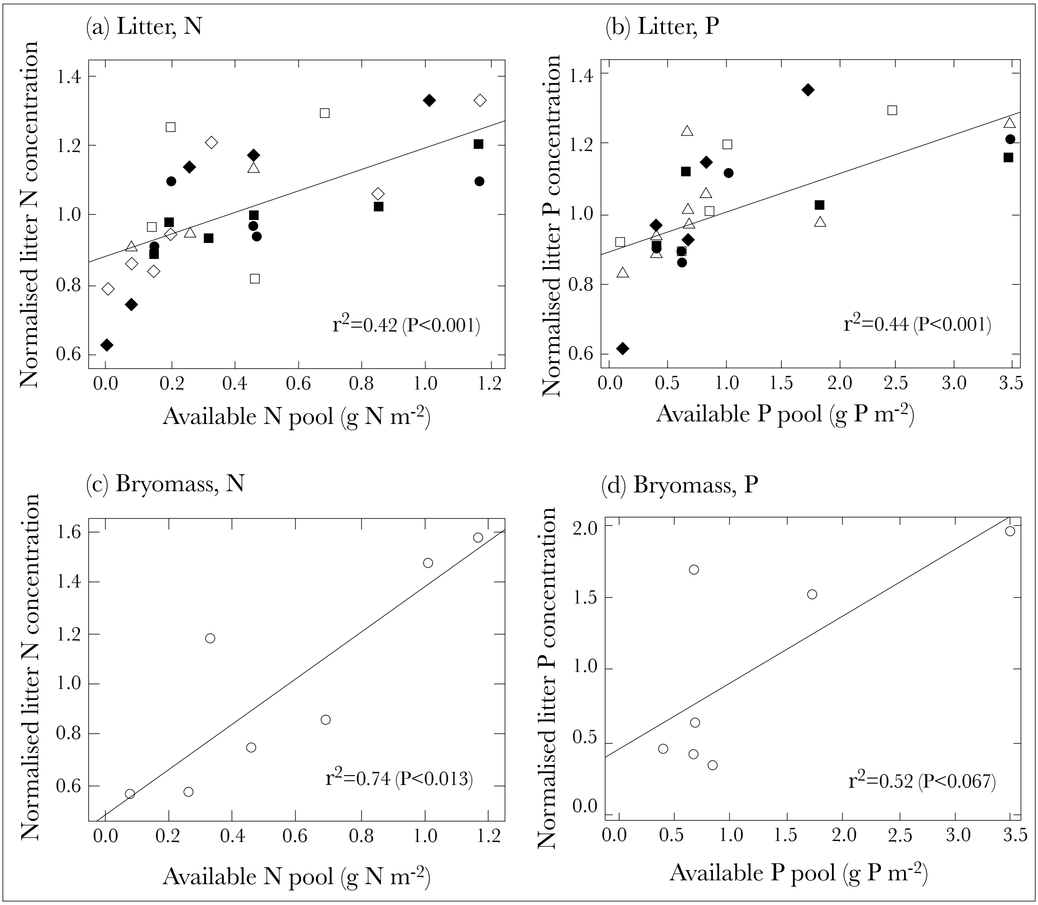


Figure 8.1 Relationship between N or P concentrations in plant litter or in bryomass and size of the available N or P soil pools. Each symbol represents the litter of a particular vascular plant species from three or more communities having different nutrient pool sizes. Within species, the concentrations were normalized by dividing by the mean concentration for that species. Based on data in Smith (1987b, d, e, 1988a, b) and unpublished data.

8.2 Freshwater communities

8.2.1 The freshwater bodies

The island's freshwater bodies are lakes, lava-lakelets, crater lakes, wallows and streams (Grobbelaar 1978a). The term "lake" is a misnomer – none of the waterbodies are large enough, or deep enough, to be considered a lake in the usual sense. Rather, it designates a small number of larger ponds (over 1 000 m^2) on the island; the largest about 10 ha, the second largest about 3 ha and the rest < 1 ha. Since they mostly occur on flat, raised grey lava flows, they are exposed to the wind so strong wave action limits terrestrialization of the shore. Where terrestrialization does occur, this is generally on the northwest (windward) side, the rest of the shore being occupied by rocks or fine scoria. The bottoms consist of scoria or peat and are unvegetated or only sparsely vegetated by vascular species, all but two of which are much more common and abundant in the terrestrial habitats. Lake fringes not subjected to wave action are occupied by filamentous algae, mosses and vascular plants. Only two lakes possess a large submerged macrophyte (*Potamogeton nodosus*), which is very abundant throughout those lakes. None of the lakes are more than 2.5 m deep and most are shallower than 1.5 m. Lakes are less common on black lava flows, which are much more "blocky" and porous. However, because they are more protected, they are more terrestrialised than lakes on grey lava and their bottoms and sides commonly covered by epipelic algae, which often form a benthic felt-like layer.

In addition to this distinction between grey lava lakes and black lava lakes, the island's larger freshwater bodies are also classed according to whether they are, or are not, influenced by seal and seabird manuring; hence a subcategory "biotically-influenced lake" has been recognized (Grobbelaar 1978a).

Lava lakelets occur only on black lava and are the most common water body on the island. They are small (< 1 000 m^2 – most are only a few m^2 or tens of m^2) and mostly < 1 m deep. Several vascular plant species and mosses, often covered with filamentous algae, occur in them. Their bottoms and sides consist of peat and almost always support an epipelic algal layer.

Crater lakes occur in the craters of some of the island's numerous scoria cones. They are small (50 to 1 500 m^2), mostly shallow (< 2 m) and incessantly subjected to very strong winds, which results in strong wave action that moves the loose scoria that makes up their bottom and sides. Plants thus rarely root in crater lakes, but in some of them a peaty sediment does accumulate on the bottom and this contains epipelic algae.

In the coastal region, moulting elephant seals churn up the peat, forming depressions in which they wallow. Occupied wallows have no rooted vegetation, but their edges may have a cyanobacterial slime. When the wallows are abandoned, coprophilous vascular plants encroach from the sides and may eventually cover the wallow. In many instances the wallows fill with water that is highly nutrient-enriched by the seals and also by penguins and petrels which usually occur in the same area. The wallows take on the nature of small, highly eutrophic ponds. These water-filled wallows persist for many years and are common in shore regions.

In view of the high rainfall, there are surprisingly few streams on the island – most water flows underground. Those that do occur, are narrow (1 to 4 m wide), rarely > 1 m deep even in spate, and few flow persistently. The bottom is mainly rocky (small stones to large boulders), but it may be a layer of pebble-sized scoria. Where erosion is not severe, filamentous algae and mosses occur on the rocks. Where streams flow through peat areas there is generally a thick mat of fringing vegetation that extends over the stream.

Because they are shallow, and their waters regularly mixed by wind, all the island's water bodies are polymictic and thermal stratification is rare, although on sunny, calm days the bottom sediments absorb radiation and can become substantially warmer (4.5°C) than the overlying water (Grobbelaar 1975).

8.2.2 Nutrient composition

The chemical composition of the island's freshwaters is given in Table 8.5. They can be simply but accurately described as very dilute dilutions of seawater. The ionic composition order of the major ions is $Cl^- > Na^+ > SO_4^{2-} > Mg^{2+} > Ca^{2+} > K^+ > HCO_3^-$, identical to that in seawater. The same is true of rainwater at the island (Grobbelaar 1978b; Smith 1987e). This does not imply that the island's freshwater bodies are saline. In contrast, apart from some wallows, lava lakelets and west coast lakes that are close to the shore and heavily subjected to saltspray, they are very "fresh". Because of the dominance of Cl^- over HCO_3^- and the influence of the acidic peats and igneous rocks through which they percolate, they are also extremely soft. In the absence of limestone or any other calcareous rock, the waters are not enriched in Ca or HCO_3^- so they have a low alkalinity and buffering capacity. The island's freshwaters rarely contain detectable levels of N and P, unless they are influenced by seabirds or seals.

PCA ordination of the chemistry data for 257 waterbody and 71 precipitation samples listed in the appendix of Grobbelaar (1974a) has shown that freshwater chemical composition at the island is characterised by two components. The major component comprises Na, Mg, Ca, K, Cl, SO_4 and conductivity. It accounts for 49% of the total variance in the data and represents the oceanic influence on freshwater chemical composition. The other component comprises NH_4-N, NO_3-N and PO_4-P, accounts for 27% of the total variance, and shows the influence of animal manuring. Grobbelaar (1975, 1978a), also from PCA, found a third component (Fe, pH and alkalinity) and argued that this represented the influence of inflowing humic-rich groundwater, on the basis that humic acids would lower pH and alkalinity and increase Fe concentration. However, Fe, pH and alkalinity are significantly positively

Table 8.5 Chemical composition and primary productivity of the freshwater bodies on Marion Island. Mean values are given, with the range in brackets. Chemical concentrations are in mg l^{-1}, except where indicated otherwise. Primary productivity was measured as net ^{14}C uptake and expressed as mg C m^{-2} d^{-1}. Brackets in column headings indicate the number of water samples used for chemical analysis. Water chemistry from Grobbelaar (1978b) and primary productivity from Grobbelaar (1974b). Where a value of zero is given it means the concentration of the nutrient was below the limit of detection by the particular method used for the analysis.

Water chemistry	Lakes (130)	Lava lakelets (31)	Crater lakes (12)	Streams (26)	Biotic Lakes (12)	Wallows (45)
pH	6.0 (5.2-7.3)	5.8 (5.2-6.8)	6.1 (5.8-7.0)	6.6 (6.1-7.3)	5.3 (4.5-6.7)	5.9 (4.5-8.3)
Conductivity (µS cm-1)	139 (40-3180)	52 (30-107)	63 (36-196)	63 (40-160)	138 (74-257)	228 (58-1630)
Alkalinity (µequiv. l-1)	24 (0-220)	20 (0-178)	14 (0-54)	117 (37-210)	42 (0-193)	460 (0-3370)
Na	19.7 (5.6-420)	7.2 (4.4-16.2)	10.0 (5.1-43.5)	9.2 (5.6-33.0)	16.1 (9.0-27.2)	38.4 (7.0-312.0)
K	0.8 (0.1-17.5)	0.4 (0.1-1.4)	0.4 (0.1-1.7)	0.5 (0.1-1.5)	1.5 (0.6-2.5)	3.4 (0.1-16.3)
Ca	0.9 (0.2-12.0)	0.5 (0.2-3.6)	0.5 (0.3-1.3)	0.6 (0.3-1.5)	0.8 (0.3-1.1)	1.8 (0.2-11.0)
Mg	2.6 (0.8-50.3)	1.0 (0.5-2.6)	1.3 (0.7-5.1)	1.4 (0.5-5.2)	2.2 (1.5-3.2)	5.4 (0.7-35.0)
Fe	0.1 (0-1.2)	0.02 (0-0.3)	0	0.01 (0-0.1)	0.9 (0-7.0)	1.3 (0-11.3)
Cl	46 (7-1100)	17 (10-62)	21 (12-82)	17 (10-72)	32 (15-59)	142 (25-930)
SO4	4.5 (0-106.0)	0.3 (0-4.0)	1.6 (0-16.5)	1.9 (0-17.5)	3.8 (0-11.3)	7.3 (0-67.2)
NO3-N	0.04 (0-0.6)	0.02 (0-0.5)	0	0	9.4 (4.5-14.8)	3.7 (0-21.4)
NH4-N	0.01 (0-0.5)	0	0	0	2.9 (1.0-9.5)	8.8 (0-55.2)
PO4-P	0(0-0.04)	0	0	0	0.4 (0-2.1)	0.2 (0-4.3)
Primary productivity	**Lakes (130)**	**Lava lakelets (31)**	**Crater lakes (12)**	**Streams (26)**	**Biotic Lakes (12)**	**Wallows (45)**
Phytoplankton	19 (1-102)	32 (20-41)	-	-	270 (46-793)	4985 (3494-6004)
Benthic algae	258 (91-556)	44 (17-61)	-	-	-	-
Macrophytes and epiphytic algae	833 (446-1270)	-	-	-	-	-

intercorrelated and occurred on the same side of the principal component, so it is difficult to accept Grobbelaar's interpretation. This is not to deny that groundwater influences the chemical composition of the island's freshwaters (many of which are coloured by humic acids), simply that the degree and nature of the influence cannot be established from the available data.

8.2.3 Primary production

Phytoplankton productivities in the non-biotically influenced lakes (1 to 102 mg C m^{-2} d^{-1}) and lava lakelets (20 to 41 mg C m^{-2} d^{-1}; Table 8.5) are low and typical of cold, oligotrophic waters of shallow lakes in temperate and sub-polar areas. For instance, similar phytoplankton productivities (3 to 85 mg C m^{-2} d^{-1}) are found in Northern Hemisphere tundra ponds (Kalff 1970; Alexander *et al.* 1980). Benthic (epipelic) algal productivity in the island's lakes (mean, 258 mg C m^{-2} d^{-1}) and lava lakelets (44 mg C m^{-2} d^{-1}) are also similar to those in tundra ponds (53 to 131 mg C m^{-2} d^{-1}; calculated from total season production values and growing season duration given in Alexander *et al.* 1980). Mostly, benthic production far outweighs phytoplankton production. Highest production of all the components of the island's non-manured freshwater bodies was for *P. nodosus* and the epiphytic filametous algae that occur on it; between 446 and 1 270 mg C m^{-2} d^{-1}, considerably more than the maximum reported for submerged macrophytes in tundra ponds (250 mg C m^{-2} d^{-1}; Alexander *et al.* 1980).

Phytoplankton productivity in biotic lakes (46 to 793 mg C m^{-2} d^{-1}) and wallows (3 500 to 6 000 mg C m^{-2} d^{-1}) is high, in keeping with their high N and P status. Enrichment studies (Grobbelaar 1978c) showed that it is the combination of N and P that stimulates algal production at the island; neither element has any effect if added alone. No other macro- or micronutrients, alone or in combination, enhanced algal production.

In the absence of aquatic insects, decapod crustaceans, fish or amphibians, the top of the trophic chain in the island's freshwaters is occupied by zooplankton. Nine species have been recorded, but by far the most abundant ones are the calanoid copepod *Boeckella vallentini* (previously *Pseudoboeckella volucris*, see Pugh *et al.* 2002) and the water flea *Daphniopsis studeri* (Kok & Grobbelaar 1978). A detailed investigation of primary and secondary production in the pelagic zone of a lava lakelet (Grobbelaar *et al.* 1987) revealed that grazing by these two zooplankton species, together with their respiration and phytoplankton photosynthesis, dominated carbon flow, with only a small contribution by bacteria. Phytoplankton fixed, on average, 24.3 mg C m^{-2} d^{-1}. Of this, 15.3 mg C was grazed by zooplankton, which also grazed 2.7 mg bacterial C and respired 24.1 mg C. The heavy rates of zooplankton grazing, coupled with low phytoplankton and bacteria biomasses, result in fast C turnover in the lava lakelet. The basic structure and rates of C flow in the lava lakelet's pelagic zone are thus essentially similar to those in a typical tundra pond (Hobbie 1980). The contribution of the benthic system to C flow has not been measured.

8.3 The trophic dynamics disparity between the island's terrestrial and aquatic systems – how real is it?

The presence of an active herbivore level results in the island's freshwater bodies having a very different trophic dynamic to that of the terrestrial ecosystem. In the freshwaters most of the carbon (and hence energy and nutrients) go through a grazing chain rather than a detritus chain, whereas the opposite is true for the terrestrial system. However, this distinction, held since the early days of ecological research at the island (Smith 1977; Kok & Grobbelaar 1978) might not be that definite. Certainly, a grazing chain dominates in the pelagic zone of the freshwater bodies, but nothing is known about the fate of the very substantial inputs of energy and nutrients by benthic algae, or by submerged macrophytes and their algal epiphytes. It is possible that a detritus chain predominates in the benthic mats. Similarly, in terrestrial communities the grazing chain might be more important than currently thought, since there might be appreciable levels of meso- and/or microherbivory. Our current concept of terrestrial ecosystem functioning at the island is almost entirely based on information on large organisms; animals the size of insect larvae and upward, plants as large as mosses and upwards. Recent studies of the larvae of small insects such as the midge *Limnophyes minimus* (Hänel & Chown 1998), and of springtails and mites (Chown *et al.*, unpublished data), are making it increasingly clear that smaller organisms are cardinal to the spatial and temporal dynamics of the island's terrestrial communities. Likely, they also play an important role in the functional dynamics of the communities.

8.4 References

Alexander, V., Stanley, D.W., Daley, R.J. & McRoy, C.P. 1980. Primary producers. In: Hobbie J.E (Ed.). *Limnology of Tundra Ponds, Barrow Alaska*. Dowden, Hutchinson & Ross, Stroudsberg. US/*IBP Synthesis Series* **13**, 179-250.

Anderson, R.V., Coleman, D.C. & Cole, C.V. 1981. Effects of saprotrophic grazing on net mineralization. In: Clark, F.E. & Rosswall, T. (Eds.). *Terrestrial Nitrogen Cycles. Ecological Bulletins (Stockholm)* **33**, 201-216.

Barendse, J. & Chown, S.L. 2000. The biology of *Bothrometopus elongatus* (Coleoptera, Curculionidae) in a mid-altitude fellfield on sub-Antarctic Marion Island. *Polar Biology* **23**, 346-351.

Barendse, J., Mercer, R.D., Marshall, D.J. & Chown, S.L. 2002. Habitat specificity of mites on sub-Antarctic Marion Island. *Environmental Entomology* **31**, 612-625.

Berendse, F. & Jonasson, S. 1992. Nutrient use and nutrient cycling in northern ecosystems. In: Chapin, F.S. III., Jefferies, R.L., Reynolds, J.F., Shaver, G.R. & Svoboda, J. (Eds.). *Arctic Ecosystems in a Changing Climate: An Ecological Perspective*. Academic Press, San Diego, pp. 337-356.

Bergstrom, D.M. & Chown, S.L. 1999. Life at the front: history, ecology and change on Southern Ocean islands. *Trends in Ecology and Evolution* **14**, 472-477.

Bernard, J.M & Gorham, E. 1978. Life history aspects of primary production in sedge wetlands. In: Good, R.E., Whigham, D.F. & Simpson, R. (Eds.). *Freshwater Wetlands. Ecological Processes and Management Potential*. Academic Press, New York, pp. 39-51.

Blake, B.J. 1997. *Microclimate and prediction of photosynthesis at Marion Island*. M.Sc. Thesis, University of the Free State, South Africa.

Brown, J. & Veum, A.K. 1974. Soil propeties of the International Tundra Biome sites. In: Holding, A.J., MacLean, S.F. & Flanagan, P.W. (Eds.). *Soil Organisms and Decomposition in Tundra*. Tundra Biome Steering Committee, Stockholm, pp.27-48.

Burger, A.E. 1978. Terrestrial invertebrates: a food source for birds at Marion Island. *South African Journal of Antarctic Research* **8**, 87-99.

Chown, S.L. 1990. Speciation in the sub-Antarctic weevil genus *Dusmoecetes* Jeannel (Coleoptera: Curculionidae). *Systematic Entomology* **15**, 283-296.

Chown, S.L. & Smith, V.R. 1993. Climate change and the short-term impact of feral house mice at the sub-Antarctic Prince Edward Islands. *Oecologia* **96**, 508-516.

Clarke, G.C.S., Greene, S.W. & Greene, D.M. 1971. Productivity of bryophytes in polar regions. *Annals of Botany* **35**, 99-108.

Crafford, J.E. 1990a. The role of feral house mice in ecosystem functioning on Marion Island. In: Kerry, K.R. & Hempel, G. (Eds.). *Antarctic Ecosystems: Ecological Change and Conservation*. Springer, Berlin, pp. 359-364.

Crafford, J.E. 1990b. *Patterns of energy flow in populations of the dominant insect consumers on Marion Island*. Ph.D. Thesis, University of Pretoria, South Africa.

Crafford, J.E. & Scholtz, C.H. 1987. Quantitative differences between the insect faunas of sub-Antarctic Marion and Prince Edward Islands: A result of human intervention? *Biological Conservation* **40**, 255-262.

Dowding, P., Chapin, F.S. III., Wielgolaski, F.E. & Kilfeather, P. 1981. Nutrients in tundra ecosystems. In: Bliss, L.C., Heal, O.W. & Moore, J.J. (Eds.). *Tundra Ecosystems: A Comparative Analysis*. Cambridge University Press, Cambridge, pp. 647-683.

Everett, K.R., Vassiljevskaya, V.D., Brown, J. & Walker, B.D. 1981. Tundra and analogous soils. In: Bliss, L.C., Heal, O.W. & Moore, J.J. (Eds.). *Tundra Ecosystems: A Comparative Analysis*. Cambridge University Press, Cambridge, pp. 139-179.

French, D.D. 1988. Patterns of decomposition assessed by the use of litter bags and cotton strip assay on fertilized and unfertilized heather moor in Scotland. In: Harrison, A.F., Latter, P.M. & Walton, D.W.H. (Eds.). *Cotton Strip Assay: An Index of Decomposition in Soils*. ITE Symposium 24. Institute of Terrestrial Ecology, Grange-over-Sands, pp. 100-108.

French, D.D. & Smith, V.R. 1985. A comparison between Northern and Southern Hemisphere tundras and related ecosystems. *Polar Biology* **5**, 5-21.

French, D.D. & Smith, V.R. 1986. Bacterial populations in soils of a sub-Antarctic Island. *Polar Biology* **6**, 75-82.

Frissel, M.J. 1981. The definition of residence times in ecological models In: Clark, F.E. & Rosswall, T. (Eds.). *Terrestrial Nitrogen Cycles. Processes, Ecosystem Strategies and Management Impacts. Ecological Bulletins (Stockholm)* **33**, 117-122.

Gabriel, A.G.A., Chown, S.L., Barendse, J., Marshall, D.J., Mercer, R.D., Pugh, P.J.A., *et al.* 2001. Biological invasions on Southern Ocean islands: the Collembola of Marion Island as a test of generalities. *Ecography* **24**, 421-430.

Gersper, P.L., Alexander, V., Barkley, S.A., Barsdate, R.J. & Flint, P.S. 1980. The soils and their nutrients. In: Brown, J., Miller, P.C., Tieszen, L.L. & Bunnel, F.L. (Eds.). *An Arctic Ecosystem. The Coastal Tundra at Barrow, Alaska*. Dowden, Hutchinson & Ross, Stroudsberg. *US/IBP Synthesis Series* **12**, 219-254.

Greene, D.M., Walton, D.W.H. & Callaghan, T.V. 1973. Standing crop in a *Festuca* grassland on South Georgia. In: Bliss, L.C. & Wielgolaski, F.E. (Eds.). *Primary Production and Production Processes, Tundra Biome*. Tundra Biome Steering Committee, Stockholm, pp.191-194.

Gremmen, N.J.M. 1981. *The Vegetation of the Subantarctic Islands Marion and Prince Edward*. Dr W. Junk, The Hague.

Gremmen, N.J.M. & Smith, V.R. 2008. Terrestrial vegetation and dynamics. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 215-244.

Grobbelaar, J.U. 1974a. *A contribution to the limnology of the sub-Antarctic island Marion*. D.Sc. Thesis, University of the Free State, South Africa.

Grobbelaar, J.U. 1974b. Primary production in freshwater bodies of the sub-Antarctic island Marion. *South African Journal of Antarctic Research* **4**, 40-45.

Grobbelaar, J.U. 1975. The lentic and lotic freshwater types of Marion Island (sub-Antarctic): a limnological study. *Verhandlungen Internationale Vereinigung für Limnologie* **19**, 1442-1449.

Grobbelaar, J.U. 1978a. The limnology of Marion Island: Southern Indian Ocean. *South African Journal of Antarctic Research* **8**, 113-118.

Grobbelaar, J.U. 1978b. Mechanisms controlling the composition of freshwaters on the sub-Antarctic island Marion. *Archiv für Hydrobiologie* **83**, 145-157.

Grobbelaar, J.U. 1978c. Factors limiting algal growth on the sub-Antarctic island Marion. *Verhandlungen Internationale Vereinigung für Limnologie* **20**, 1159-1164.

Grobbelaar, J.U., Jarvis, A.C., Robarts, R.D., Sephton, L.M., Steenkamp, M. & Cawood, M.E. 1987. A diel study of carbon flow in the pelagic zone of a small lava lakelet on Marion Island (sub-Antarctic). *Polar Biology* **7**, 115-124.

Grobler, D.C., Toerien D.F. & Smith, V.R. 1987. Bacterial activity in soils of a sub-Antarctic Island. *Soil Biology & Biochemistry* **19**, 485-490.

Hänel, C. 1999. *The distribution and abundance of macro-invertebrates in the major vegetation communities of Marion Island and the impact of alien species*. M.Sc. Thesis, University of Pretoria, South Africa.

Hänel, C. & Chown, S.L. 1998. The impact of a small, alien invertebrate on a sub-Antarctic terrestrial ecosystem: *Limnophyes minimus* (Diptera, Chironomidae) at Marion Island. *Polar Biology* **20**, 99-106.

Harrison, A.F., Latter, P.M. & Walton, D.W.H. 1988. *Cotton Strip Assay: An Index of Decomposition in Soils*. ITE Symposium 24. Institute of Terrestrial Ecology, Grange-Over-Sands.

Heal, O.W. 1981. Introduction. In: Bliss, L.C., Heal, O.W. & Moore, J.J. (Eds.). *Tundra Ecosystems: A Comparative Analysis*. Cambridge University Press, Cambridge, pp. xxvii-xxxvii.

Heal, O.W., Flanagan, P.W., French, D.D. & MacLean, S.F. 1981. Decomposition and accumulation of organic matter. In: Bliss, L.C., Heal, O.W. & Moore, J.J. (Eds.). *Tundra Ecosystems: A Comparative Analysis*. Cambridge University Press, Cambridge, pp. 587-633.

Heal, O.W., Howson, G., French, D.D. & Jeffers, J.N.R. 1974. Decomposition of cotton strips in tundra. In: Holding, A.J., MacLean, S.F. & Flanagan, P.W. (Eds.). *Soil Organisms and Decomposition in Tundra*. Tundra Biome Steering Committee, Stockholm, pp. 341-362.

Hobbie, J.E. 1980. Major findings. In: Hobbie J.E. (Ed.). *Limnology of Tundra Ponds, Barrow Alaska*. Dowden, Hutchinson & Ross, Stroudsberg. *US/IBP Synthesis Series* **13**, 1-18.

Huntley, B.J. 1970. Altitudinal distribution and phenology of Marion Island vascular plants. *Tydskrif vir Natuurwetenskappe* **10**, 255-262.

Huntley, B.J. 1971. Vegetation. In: Van Zinderen Bakker, E.M., Winterbottom, J.M. & Dyer, R.A. (Eds.). *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965-1966*. A.A. Balkema, Cape Town, pp. 98-160.

Huntley, B.J. 1972. Notes on the ecology of *Azorella selago* Hook. f. *South African Journal of Botany* **38**, 103-113.

Jenkin, J.F. 1975. Macquarie Island, Subantarctic. In: Rosswall, T. & Heal, O.W. (Eds.). *Structure and Function of Tundra Ecosystems. Ecological Bulletins (Stockholm)* **20**, 375-397.

Kalff, J. 1970. Arctic lake ecosystems. In: Holdgate, M.W. (Ed.). *Antarctic Ecology* Vol. 2. Academic Press, London, pp. 651-663.

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

Lauenroth, W.K. 1979. Grassland primary production: North American grasslands in perspective. In: French, N.R. (Ed.). *Perspectives in Grassland Ecology. Ecological Studies* **32**, 3-24. Springer, New York.

le Roux, P.C. 2008. Climate and climate change. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 39-64.

Lewis Smith, R.I. & Stephenson, C. 1975. Preliminary growth studies on *Festuca contracta* T. Kir and *Deschampsia antarctica* Desv. on South Georgia. *British Antarctic Survey Bulletin* **41/42**, 59-75.

Lewis Smith, R.I. & Walton, D.W.H., 1975. South Georgia, Subantarctic. In: Rosswall, T. & Heal, O.W. (Eds.). *Structure and Function of Tundra Ecosystems. Ecological Bulletins (Stockholm)* **20**, 399-423.

Lieth, H. 1972. Über die Primärproduktion der Pflanzendecke der Erde. *Angewandte Botanik* **46**, 1-37.

Lieth, H. 1974. Modelontwikkeling voor de primaire produktie Van de Aarde. *Vakblad Biologie* **19**, 312-315.

Lieth, H. & Box, E. 1972. Evapotranspiration and primary productivity: C.W. Thornthwaite memorial model. *Publications in Climatology* **25**, 37-46.

Löffler, E. 1983. Macquarie Island- eine vom Windgeprägte Naturlandschaft in der Sub-Antarktis. *Polarforschung* **53**, 59-74.

Matthewson, D.C., Van Aarde, R.J. & Skinner J.D. 1994. Population biology of house mice (*Mus musculus*) on sub-Antarctic Marion Island. *South African Journal of Zoology* **29**, 99-106.

Nadelhoffer, K.J., Giblin, A.E., Shaver, G.R. & Laundre, J.A. 1991. Effects of temperature and substrate quality on element mineralization in six arctic soils. *Ecology* **72**, 242-253.

Pugh, P.J.A., Dartnall, H.J.G. & McInnes, S.J. 2002. The non-marine Crustacea of Antarctica and the islands of the Southern Ocean: biodiversity and biogeography. *Journal of Natural History* **36**, 1047-1103.

Reader, R.J. 1978. Primary production in northern bog marshes. In: Good, R.E., Whigham, D.F. & Simpson R.L. (Eds.). *Freshwater Wetlands. Ecological Processes and Management Potential*. Academic Press, New York, pp. 53-62.

Rosswall, T. & Granhall, U. 1980. Nitrogen cycling in a subarctic ombrotrophic mire. In: Sonesson, M. (Ed.). *Ecology of a Subarctic Mire. Ecological Bulletins (Stockholm)* **30**, 209-234.

Rosswall, T. & Heal, O.W. 1975. The IBP tundra biome – an introduction. In: Rosswall, T. & Heal, O.W. (Eds.). *Structure and Function of Tundra Ecosystems. Ecological Bulletins (Stockholm)* **20**, 7-16.

Rosswall, T., Veum, A.K. & Kärenlampi, L. 1975. Plant litter decomposition at Fennoscandian tundra sites. In: Wielgolaski, F.E. (Ed.). *Fennoscandian Tundra Ecosystems, Part 1. Plants and Microorganisms. Ecological Studies* **16**, 268-278. Springer, Berlin.

Rouault, M., Mélice, J-L., Reason, C.J.C. & Lutjeharms, R.E. 2005. Climate variability at Marion Island, Southern Ocean, since 1960. *Journal of Geophysical Research* **110**, C05007, doi:10.1029/2004JC002492.

Rowe-Rowe, D.T., Green, B. & Crafford, J.E. 1989. Estimated impact of feral house mice on sub-Antarctic invertebrates at Marion Island. *Polar Biology* **9**, 457-460.

Sims, P.L. & Singh, J.S. 1978. The structure and function of ten western North American grasslands. 3. Net primary production, turnover and efficiencies of energy capture and water use. *Journal of Ecology* **66**, 573-597.

Skottsberg, C. 1912. The vegetation of South Georgia. *Wissenschafteliche Ergebnisse der Südpolar-Expedition 1901-1903* **4 (12)**, 1-36.

Smith, V.R. 1976. The effect of burrowing species of Procellariidae on the nutrient status of inland tussock grasslands on Marion Island. *South African Journal of Botany* **42**, 265-272.

Smith, V.R. 1977. A qualitative description of energy flow and nutrient cycling in the Marion Island terrestrial ecosystem. *Polar Record* **18**, 361-370.

Smith, V.R. 1984. Effects of abiotic factors on acetylene reduction by cyanobacteria epiphytic on moss at a sub-Antarctic island. *Applied and Environmental Microbiology* **48**, 594-600.

Smith V.R. 1985. Heterotrophic acetylene reduction in soils at Marion Island. In: Siegfried, W.R., Condy, P.R. & Laws, R.M. (Eds.). *Antarctic Nutrient Cycles and Food Webs*. Springer, Berlin, pp. 186-191.

Smith, V.R. 1987a. Production and nutrient dynamics of plant communities on a sub-Antarctic Island. 1. Standing crop and primary production of mire-grasslands. *Polar Biology* **7**, 57-75.

Smith, V.R. 1987b. Production and nutrient dynamics of plant communities on a sub-Antarctic Island. 3. Standing stocks, uptake and loss of nutrients in mire-grasslands. *Polar Biology* **8**, 135-133.

Smith, V.R. 1987c. Production and nutrient dynamics of plant communities on a sub-Antarctic Island. 2. Standing crop and primary production of fjaeldmark and fernbrakes. *Polar Biology* **7**, 125-144.

Smith, V.R. 1987d. Seasonal changes in plant and soil chemical composition at Marion Island (sub-Antarctic): I – Mire grasslands. *South African Journal of Antarctic Research* **17**, 117-132.

Smith, V.R. 1987e. Chemical composition of precipitation at Marion Island (sub-Antarctic). *Atmospheric Environment* **21**, 1159-1165.

Smith, V.R. 1988a. Production and nutrient dynamics of plant communities on a sub-Antarctic Island. 4. Standing stocks, uptake and loss of nutrients in fjaeldmark and fernbrakes. *Polar Biology* **8**, 191-211.

Smith, V.R. 1988b. Production and nutrient dynamics of plant communities on a sub-Antarctic Island. 5. Nutrient budgets and turnover times for mire-grasslands, fjaeldmark and fernbrakes. *Polar Biology* **8**, 255-269.

Smith, V.R. 1992. Terrestrial slug recorded from sub-Antarctic Marion Island. *Journal of Molluscan Studies* **58**, 80-81.

Smith, V.R. 2002. Climate change in the sub-Antarctic: an illustration from Marion Island. *Climatic Change* **52**, 345-357.

Smith, V.R. 2003. Soil respiration and its determinants on a sub-Antrctic Island. *Soil Biology & Biochemistry* **35**, 77-91.

Smith, V.R. 2005. Moisture, carbon and inorganic nutrient controls of soil respiration at a sub-Antarctic island. *Soil Biology & Biochemistry* **37**, 81-91.

Smith, V.R. 2007. Introduced slugs and indigenous caterpillars as facilitators of carbon and nutrient mineralisation on a sub-Antarctic island. *Soil Biology and Biochemistry* **39**, 709-713.

Smith, V.R., Avenant, N.L. & Chown, S.L. 2002. The diet and impact of house mice on a sub-Antarctic island. *Polar Biology* **25**, 703-715.

Smith, V.R. & Froneman, P.W. 2008. Nutrient dynamics in the vicinity of the Prince Edward Islands. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 165-179.

Smith, V.R. & Steenkamp, M. 1990. Climatic change and its ecological implications at a sub-Antarctic Island. *Oecologia* **85**, 14-24.

Smith, V.R. & Steenkamp, M. 1992a. Soil nitrogen transformations on a sub-Antarctic island. *Antarctic Science* **4**, 41-50.

Smith, V.R. & Steenkamp, M. 1992b. Macroinvertebrates and litter nutrient release on a sub-Antarctic island. *South African Journal of Botany* **58**, 105-116.

Smith, V.R. & Steenkamp, M. 1992c. Soil macrofauna and nitrogen on a sub-Antarctic island. *Oecologia* **92**, 201-206.

Smith, V.R. & Steenkamp, M. 1993. Macroinvertebrates and peat nutrient mineralization on a sub-Antarctic island. *South African Journal of Botany* **59**, 106-108.

Smith, V.R. & Steenkamp, M. 2001. Classification of the terrestrial habitats on sub-Antarctic Marion Island based on vegetation and soil chemistry. *Journal of Vegetation Science* **12**, 181-198.

Smith, V.R., Steenkamp, M. & French, D.D. 1993. Soil decomposition potential in relation to environmental factors on Marion Island (sub-Antarctic). *Soil Biology & Biochemistry* **25**, 1619-1633.

Smith, V.R., Steenkamp, M. & Gremmen, N.J.M. 2001. Terrestrial habitats on sub-Antarctic Marion Island: their vegetation, edaphic attributes, distribution and response to climate change. *South African Journal of Botany* **67**, 641-654.

Smith, V.R. & Steyn, M.G. 1982. Soil microbial counts in relation to site characteristics at a sub-Antarctic Island. *Microbial Ecology* **8**, 253-266.

Steenkamp, M. 1991. *Decomposition and nutrient mineralization studies on sub-Antarctic Marion Island*. Ph.D. Thesis, University of the Free State, South Africa.

Swift, M.J., Heal, O.W. & Anderson, J.M. 1979. *Decomposition in Terrestrial Ecosystems. Studies in Ecology* **5**. Blackwell Scientific Publications, Oxford.

Taylor, B.W. 1955. The flora, vegetation and soils of Macquarie Island. *A.N.A.R.E. Reports Series B* **2**, 192 pp.

Van Cleve, K. & Alexander, V. 1981. Nitrogen cycling in tundra and boreal ecosystems. In: Clark, F.E & Rosswall, T. (Eds.). *Terrestrial Nitrogen Cycles. Processes, Ecosystem Strategies and Management Impacts. Ecological Bulletins* **33**, 375-404.

Van Zinderen Bakker, E.M. 1978. Origin and general ecology of the Marion Island ecosystem. *South African Journal of Antarctic Research* **8**, 13-21.

Van Zinderen Bakker, E.M., Winterbottom, J.M. & Dyer, R.A. (Eds.) 1971. *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965-1966*. A.A. Balkema, Cape Town, 427 pp.

Vance, E.D. & Chapin, F.S. III. 2001. Substrate limitations to microbial activity in taiga forest floors. *Soil Biology & Biochemistry* **33**, 173-188.

Vanhala, P., Fritze, H. & Neuvonen, S. 1996. Prolonged simulated acid rain treatment in the subarctic: Effect on the soil respiration rate and microbial biomass. *Biology and Fertility of Soils* **23**, 7-14.

Walter, H. 1979. *Vegetation of the Earth and Ecological Systems of the Geo-biosphere*. Springer, New York.

Walton, D.W.H. 1988. Problems and advantages of using the cotton strip assay in polar and tundra sites. In: Harrison, A.F., Latter, P.M. & Walton, D.W.H. (Eds.). *Cotton Strip Assay: An Index of Decomposition in Soils*. ITE Symposium 24. Institute of Terrestrial Ecology, Grange-over-Sands, pp. 43-45.

Whigham, D.F., McCormick, J., Good, R.E. & Simpson R.L. 1978. Biomass and primary production in freshwater tidal wetlands of the Middle Antlantic coast. In: Good, R.E., Whigham, D.F. & Simpson, R.L. (Eds.). *Freshwater Wetlands. Ecological Processes and Management Potential*. Academic Press, New York, pp. 3-20.

Whittaker, R.H. 1970. *Communities and Ecosystems*. The Macmillan Co., New York.

Widden, P. 1977. Microbiology and decomposition on Truelove Lowland. In: Bliss, L.C. (Ed.). *Truelove Lowland, Devon Island, Canada: A High Arctic Ecosystem*. University of Alberta Press, Edmonton, pp. 505-530.

Wielgolaski, F.E., Bliss, L.C., Svoboda, J. & Doyle, G. 1981. Primary production of tundra. In: Bliss, L.C., Heal, O.W. & Moore, J.J. (Eds.). *Tundra Ecosystems: A Comparative Analysis*. Cambridge University Press, Cambridge, pp. 187-225.

Wynn-Williams, D.D. 1988. Cotton strip decomposition in relation to environmental factors in the Maritime Antarctic. In: Harrison, A.F., Latter, P.M. & Walton, D.W.H. (Eds.). *Cotton Strip Assay: An Index of Decomposition in Soils*. ITE Symposium 24. Institute of Terrestrial Ecology, Grange-over-Sands, pp. 126-133.

CHAPTER 9

TERRESTRIAL VEGETATION AND DYNAMICS

NIEK J.M. GREMMEN AND VALDON R. SMITH

From offshore the Prince Edward Islands appear bleak and barren with monotonous vegetation, mainly due to the absence of trees or shrubs. Closer inspection, of the low altitude regions at least, reveals dense and often complex vegetation consisting of a variety of plant communities distributed along gradients of moisture, exposure and soil nutrient status. Vascular plants determine the physiognomy of the vegetation at low altitudes, but in almost all the communities there is a diversity and abundance of bryophytes. At higher altitudes cryptogams become dominant. Above 600 m only one vascular species occurs and the vegetation is sparse and consists mainly of mosses and lichens.

The impoverished flora and harsh climate of the islands result in a close coupling of plant community structure with abiotic and biotic factors. Soil moisture and exposure to wind (the latter through its direct effect on the plants through chilling, drying, mechanical injury, as well as its indirect effects through changing the micro- and mesoclimate) are the most important of these, so that the pattern of variation in species composition and vegetation structure between plant communities is dominated by a conspicuous gradient from dry-exposed to wet-sheltered conditions (Smith & Steenkamp 2001). Related to this gradient is a change in soil type, from organic peats at sheltered sites to mineral soils at exposed ones. At any point along the wet/sheltered/organic to dry/exposed/mineral gradient the type of vegetation that develops depends

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 215-244

on the intensity to which the site is influenced by wind-blown saltspray and manuring and trampling by seals and seabirds. This interaction of abiotic and biotic gradients gives rise to a complex mosaic of habitats and plant communities. Other factors are also important. For instance, soil hydrology strongly influences community composition, so that ombrotrophic (rainwater-influenced) mires have a very different species composition to minerotrophic (groundwater-influenced) mires, and drainage lines in slopes support a very different vegetation to that of the slopes (Gremmen 1981). Differences in geological substratum also add to the complexity of the vegetation cover.

In this chapter we describe the flora of the two islands and give an overview of the ecology and distribution of the vegetation types on Marion Island. We present the main patterns of vegetation succession and how the vegetation has changed due to changes in the population sizes of seals and seabirds and the impact of human activities, including the introduction of alien plant species.

9.1 The Flora

Only 23 indigenous vascular plant species occur on Marion Island and 21 on Prince Edward Island (Appendix IV). The bryophyte and lichen floras are much more diverse: 90 mosses and 44 liverworts have been recorded on Marion Island and 63 mosses and 29 liverworts on Prince Edward Island (Appendices II & III). For both islands together, 118 lichen species have been recorded (Appendix V). About 5% of the island's indigenous plant species appear to be restricted to the Prince Edward Islands, while about 20% are endemic to the Southern Indian Ocean Province islands (the Prince Edward Islands, Heard and Macdonald Islands, Îles Kerguelen, Îles Crozet). This is a preliminary estimate of the flora's endemism, because the bryophyte and lichen floras of many of the sub-Antarctic islands have been insufficiently studied and many taxonomic problems need to be resolved. Biogeographical relationships of the islands' biota are discussed by Chown *et al.* (2008).

Eighteen "alien" (introduced by humans) vascular species have been recorded on Marion Island and three on Prince Edward Island (Table 9.1). Six of these have disappeared again or have been eradicated. There are another three vascular species on Marion Island whose status is unclear and which do not occur on any other sub-Antarctic island. *Juncus* cf. *effusus* occurs at three widely separated sites in the north-eastern coastal plain. The other two species with unknown status (*Luzula* cf. *multiflora* and an unidentified thorny shrub) were discovered only recently, at sites far away from the meteorological station, the most likely place for the introduction of plants by humans.

Table 9.1 Status and distribution of the introduced vascular plants at the Prince Edward Islands. (WS) means the species was introduced at the weather station after 1948. (SS) means it was introduced by sealers or shipwrecked parties, at a site or sites other than the weather station and probably in the 1800s. From Gremmen (1975, 1982), Gremmen & Smith (1999) and Ryan *et al.* (2003).

Species	Distribution and locality of introduction
Transient aliens	
Avena sativa	Meteorological station (WS)
Holcus lanatus	Meteorological station (WS)
Hypochoeris radicata	Meteorological station (WS)
Plantago lanceolata	Meteorological station (WS)
Naturalised aliens with a restricted distribution	
Agropyron repens	One large patch at Ship's Cove, c. 250 m^2; eradication in progress (SS)
Alopecurus geniculatus	One small (< 1 m^2 patch) at Mixed Pickle Cove (SS)
Festuca rubra	One patch at Ship's Cove, a group of patches 1500 m inland (SS)
Rumex acetosella	4 sites; meteorological station, Skua Ridge, Sealer's Cave, and Goney Plain (SS)
Naturalised aliens with a widespread distribution	
Agrostis castellana	At meteorological station, Albatross Lakes and Trypot Beach (WS)
Agrostis stolonifera	Widespread on Marion Island (WS)
Cerastium fontanum	Widespread on Marion Island; on western part of Prince Edward Island (SS)
Poa annua	Widespread on Marion and Prince Edward Islands (SS)
Poa pratensis	Between Ship's Cove and Stony Ridge (WS)
Sagina procumbens	Widespread on both islands (WS)
Stellaria media	Widespread on Marion Island (SS)
Unclassified aliens	
Agrostis gigantea	At meteorological station in 1994 about 4 m^2, increased to about 200 m^2 in 1996. Eradicated by 2006 (WS)
Senecio sp.	At meteorological station in 1988; all plants removed (WS)
Sonchus sp.	At meteorological station in 1983, 1984, 1998; all plants removed each time (WS)
Status unknown	
Juncus cf. effusus	Three patches: near Trypot Beach, east of Ship's Cove, Goney Plain
Luzula cf. multiflora	Several large and many small patches in a c.1 ha area north of Sealer's Cave
Unidentified shrub	One patch (plant?) discovered between Arthur's Hill and Kildalkey Bay in 2004.

Seven of the alien vascular species on Marion Island were introduced at sites of sealers' camps or shipwreck sites (Gremmen 1975, 1981) and three of those were widespread on the island when the vegetation was first surveyed in 1965/66 (Huntley 1971). Since the establishment of the weather station at Transvaal Cove in 1948, 14 new introductions have been observed there, some being re-introductions of species that had been eradicated previously (Gremmen & Smith 1999). Some of the introduced species have not spread far from the station but others have dispersed widely, at rates of up to 400 m per year. Two have crossed the 22 km of ocean between Marion and Prince Edward Island, apparently without human assistance (Bergstrom & Smith 1990; Ryan *et al.* 2003). The influence of alien vascular species on the vegetation is discussed later.

Despite the preventative measures that have been put in place (De Villiers & Cooper 2008) new species continue to be recorded at or near the station. Since 1990 there have been four successful introductions, i.e. that resulted in the species becoming established (Gremmen & Smith 1999). In all four cases the plants were eradicated.

Only two moss species are suspected as being human-introduced, mainly because of their highly disjunct global distribution (Ochyra *et al.* 2003). *Thuidium delicatulum* occurs only in a small area near the meteorological station, and nowhere else in the sub-Antarctic, or in Africa, southern South America and Oceania. *Leptodontium gemmascens* is a European species that is not found anywhere between Europe and the island. It is consistently sterile and is dispersed over short distances by gemmae, which are too large to be good candidates for long-distance transoceanic dispersal (Ochyra *et al.* 2003).

9.2 Vegetation, plant communities and habitats

Huntley (1971) classified the islands' vegetation on floristic composition and autecological characteristics of the dominant species and recognized 13 plant communities (which he called "noda"). He grouped these into five complexes, based on the most important factor controlling their distribution (salt-spray, manuring and trampling, exposure, and drainage). Gremmen (1981) used floristic data in a phytosociological approach to classify the island's vegetation into 41 communities and then combined the floristic data with environmental information (soil depth, moisture content, pH, loss-on-ignition, depth of groundwater, severity of manuring and trampling by animals and of salt spray) to group the plant communities in six community complexes. Smith & Steenkamp (2001) applied ordination and clustering methods to vegetation and soil chemistry information to compile a classification of Marion Island's terrestrial habitats. They grouped the habitats into six habitat complexes and added one more complex in order to accommodate polar desert, the most widespread of the island's vegetation types.

In the recently produced map of the vegetation of South Africa, two biomes were recognized on the islands, the sub-Antarctic Tundra Biome and the

Polar Desert Biome (Smith & Mucina 2006). The vegetation mapping units defined for sub-Antarctic Tundra Biome were Coastal Vegetation, Biotic Herbfield and Grassland, Mire, Drainage Line & Spring Vegetation, Fernbrake Vegetation, Fellfield Vegetation and Cinder Cone Vegetation. The Polar Desert Biome comprises only one vegetation unit, sub-Antarctic Polar Desert. The distributions, important taxa, geology, soils, hydrology, climate and landscape patterns of these units are described by Smith & Mucina (2006). However, the units are too broad to allow a detailed account of the ecology, distribution and successional pattern of the islands' vegetation types. To achieve this, we hybridised the ecological classification of Huntley (1971), the floristic classification of Gremmen (1981) and the habitat classification of Smith & Steenkamp (2001). Since edaphic and ecological criteria, and not only floristics, were important in defining the categories in the hybridised classification, we prefer to term the categories "habitats" rather than plant communities or vegetation types. Table 9.2 lists the habitats and the total areas they occupy on Marion Island and provides some information on the chemical composition their soils. Fig. 9.1 shows the positions of the habitats on two ordination axes from a Canonical Correspondence Analysis that defined the habitats. Interpretations of the edaphic gradients represented by the axes are given, as are the directions of the main ecological forcing variables that determine vegetation succession on the islands. Table 9.3 gives the areas occupied by the various habitat complexes at different altitudes.

9.2.1 Mire Complex

Oligotrophic mires form a conspicuous and extensive component of the islands' lowland areas (Plate 9.1, 9.2). The habitats in the Mire Complex have vegetations that are physiognomically almost identical (dominated by bryophytes) and they have similar soil characteristics (highly organic, wet peats that may be deep and are mostly very nutrient-poor). One or more of three graminoid species (*Agrostis magellanica, Uncimia compacta* and *Juncus scheuchzerioides*) generally form a canopy over the bryophyte layer. High moisture content is the principal soil characteristic of mire habitats but the nature of the soil water (ombrotrophic, directly from rain or minerotrophic, from surrounding slopes) is cardinally important to what type of mire develops. Also, subtle differences in soil moisture content, watertable depth, and the degree to which watertable depth fluctuates, result in marked differences in plant species composition. These changes may occur over short distances (meters) to produce areas with a fine-scale spatial mosaic of mire communities that may extend over many thousands of square meters. Gremmen (1981) distinguished 18 mire communities. We have grouped them into four habitats, following Smith & Steenkamp (2001); Wet mires, Mesic mires, Dry mires and Mire drainage lines. Together, these mire habitats occupy about 22 km^2 of the total island area, but are almost wholly restricted to the area where closed vegetation can occur (below 300 m a.s.l., Table 9.3). Biotic mires and Saline mires, which Smith & Steenkamp (2001) grouped in the Mire Complex, are here considered as part of the Biotic and the Saltspray Complexes, respectively.

Table 9.2 Terrestrial habitats of the Prince Edward Islands. Area is the total area occupied by the particular habitat on Marion Island, from measurements made in the 1990s. Area and soil chemistry values extracted from Smith *et al.* (2001). Habitat abbreviations in the first column are used in Fig. 9.1. Soil chemistry concentrations (min.-max.) are on an oven-dry mass basis. Exch. = exchangeable form of the particular cation.

Habitat		Area (ha)	pH	Moisture (%)	Organic C (%)	Organic N (%)	Total P (mg g^{-1})	Inorganic N (µg g^{-1})	Inorganic P (µg g^{-1})	Exch. Ca (% CEC)	Exch. Mg (% CEC)	Exch. K (% CEC)	Exch. Na (% CEC)
Mire Complex													
M.d.	Dry Mire	792	4.5-5.3	506-1332	7-37	0.5-2.6	0.9-2.2	0-6	4-105	2-18	5-13	0-1.6	1-2
M.m.	Mesic Mire	570	4.2-5.3	725-1667	34-48	1.8-2.7	0.6-2.0	0-18	7-1.3	4-10	5-13	0.7-3.0	1-5
M.w.	Wet Mire	597	4.3-5.5	1124-2263	31-41	1.0-2.5	0.8-2.0	1-59	12-198	0-23	4-15	0.1-1.1	1-3
M.dl.	Mire Drainage Line	246	5.5-6.2	433-1399	8-25	0.5-1.6	0.8-2.1	0-17	0-16	4-13	3-8	0-0.7	0.7-1
Slope Complex													
Sl.ofb.	Open Fernbrake	429	4.5-5.0	238-870	13-32	0.9-2.6	0.5-2.4	0-15	4-44	0-13	2-14	0.2-1.2	0.5-5
Sl.cfb	Closed Fernbrake	1765	4.0-5.2	484-735	17-44	1.2-2.5	0.7-3.9	0-3	4-100	1-21	2-40	0.1-7.0	0.2-5
Sl.mfb.	Mesic Fernbrake	111	5.0-5.4	610-812	23-25	1.6-2.0	1.5-1.9	6-9	4-11	1-9	4-9	0.5-0.7	0.2-1
Sl.dsfb.	Dwarf Shrub Fernbrake	113	4.4-4.6	545-782	21-28	1.8-2.3	2.0-2.9	0-0.3	1-16	6-13	3-7	0.2-0.3	0.3-1
Sl.d&s.	Slope Drainage Line & Streambank	119	4.5-6.5	495-1002	5-43	0.3-2.5	0.7-2.8	3-13	6-23	4-27	6-32	0-2.0	1-4
Sl.s&f.	Spring and Flush	8	6.0-6.4	1049-1407	13-20	1.4-2.0	2.2-3.1	10-14	12-16	9-15	6-10	0.2-0.5	1-3

Table 9.2 Continued.

Habitat		Area (ha)	pH	Moisture (%)	Organic C (%)	Organic N (%)	Total P (mg g^{-1})	Inorganic N (µg g^{-1})	Inorganic P (µg g^{-1})	Exch. Ca (% CEC)	Exch. Mg (% CEC)	Exch. K (% CEC)	Exch. Na (% CEC)
Fellfield Complex													
F.x.	Xeric Fellfield	7963	5.5-6.2	46-371	2-14	0.1-1.0	0.9-1.6	0-4	0-18	3-49	1-10	0-0.3	0.4-5
F.m.	Mesic Fellfield	5749	4.9-5.9	217-453	6-25	0.5-1.0	0.4-1.9	0-1	0-25	3-18	2-9	0.1-2.0	0.1-4
Polar Desert													
	Polar Desert	10876	-	-	-	-	-	-	-	-	-	-	
Coastal Saltspray Complex													
C.h.	Coastal Herbfield	57	4.8-7.1	121-770	8-36	0.5-2.5	0.9-1.7	2-34	13-180	14-38	18-37	0.3-2.0	14-35
C.f.	Coastal Fellfield	36	4.5-6.2	162-1107	9-44	0.7-3.1	0.5-1.2	2-2	23-100	11-17	16-50	0.2-0.6	8-46
C.sm.	Saline Mire	14	4.4-5.2	1225-2247	39-54	1.8-2.4	0.7-1.3	39-45	98-131	4-18	16-58	0.5-1.7	6-17
	Coastal Rock Habitat	?	-	-	-	-	-	-	-	-	-	-	-

Table 9.2 Continued.

Habitat		Area (ha)	pH	Moisture (%)	Organic C (%)	Organic N (%)	Total P (mg g^{-1})	Inorganic N (µg g^{-1})	Inorganic P (µg g^{-1})	Exch. Ca (% CEC)	Exch. Mg (% CEC)	Exch. K (% CEC)	Exch. Na (% CEC)
Biotic Complex													
B.ptg.	Pedestalled Tussock Grassland	13											
	(a) Pedestals		4.2-4.3	437-548	36-34	3.4-4.0	1.6-2.5	22-43	154-291	5-14	2-5	0-0.2	1-4
	(b) Mud between pedestals		4.5-4.9	295-849	13-30	1.1-3.2	1.3-1.9	12-92	70-257	10-24	8-22	0-0.1	2-4
B.ctg.	Coastal Tussock Grassland	75	3.8-4.7	429-610	32-40	2.4-4.7	1.2-2.9	2-18	33-997	6-13	1-4	0-0.1	0.5-3
B.itg	Inland Tussock Grassland	12?	3.8-4.9	355-960	19-32	1.5-3.7	0.9-4.6	8-61	11-347	0-14	1-13	0.1-1.0	1-5
B.*Cot*h.	*Cotula* Herbfield	221	4.0-5.9	181-887	10-45	0.7-4.1	0.8-4.7	9-57	33-822	0-38	5-24	0.1-1.7	1-13
B.mud	Biotic Mud	27	3.7-5.6	520-1441	34-43	4.0-12.1	1.1-1.7	29-109	41-234	7-10	4-15	0-0.1	1-4
B.l.	Biotic Lawn	66	4.6-7.7	155-1194	12-37	1.2-4.1	0.1-2.1	15-27	40-1350	5-21	6-11	0-0.7	1-3
B.mire	Biotic Mire	41	4.7-5.6	1066-2015	38-42	2.2-3.4	1.3-2.2	8-48	159-281	0-9	8-14	0.2-1.5	2-4

Table 9.3 Percentages of the areas occupied by the various habitat complexes in four altitudinal zones on Marion Island.

Complex	0-100 m	100-300 m	300-500 m	>500 m
Mire	30	5	<0.1	0
Slope	26	11	<0.5	0
Fellfield	33	75	68	15
Polar Desert	1	8	32	85
Saltspray	2	0	0	0
Biotic	7	<0.1	<0.1	0
Total area:	**61 km^2**	**81 km^2**	**60 km^2**	**98 km^2**

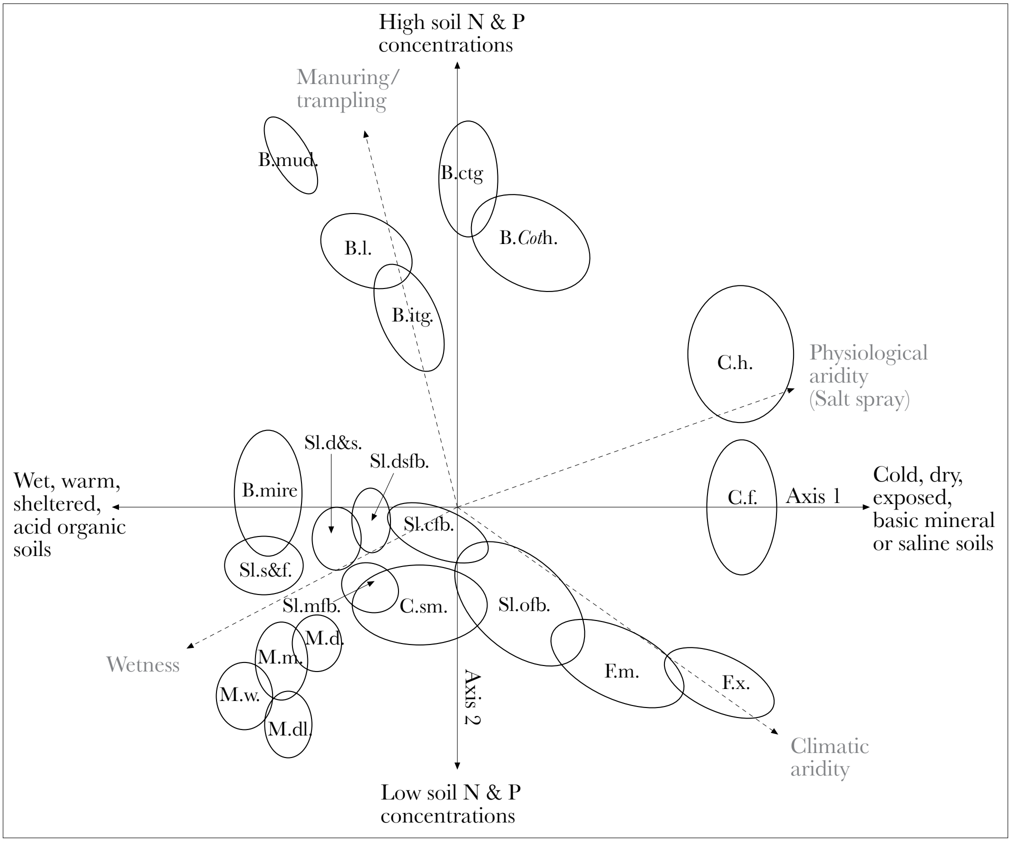


Figure 9.1 Distribution of the terrestrial habitats of Marion Island along the first two axes of the ordination of soil and botanical variables that defined the habitats. Interpretations of the gradients in soil conditions represented by the axes are provided at the ends of the axes. The direction of the main ecological forcing variables that drive ecological succession on the island is shown by the dashed arrows. Modified from Smith & Steenkamp (2001).

The Wet Mire Habitat occurs on very wet peat soils. *Agrostis magellanica*, *J. scheuchzerioides* and *Ranunculus biternatus* are the dominant (and often the only) vascular species. There is usually a well-developed bryophyte stratum, dominated by *Sanionia uncinata*, *Distichophyllum fasciculatum*, *Blepharidophyllum densifolium* and/or *Clasmatocolea humilis*. The wet mire habitat comprises a range of plant communities, from pioneer communities dominated by graminoids and dense mats of bryophytes around ponds, lava-lakelets and lakes, through bryophyte-dominated, very wet depressions where the watertable is at or just below the surface for much of the time, to a high cover of both graminoids and bryophytes on deep consolidated peats where the watertable can be up to 20 cm below the surface but where capillarity ensures that the surface layer remains saturated.

Mesic Mire Habitat has lower soil moisture content than wet mire. The dominant bryophyte is usually *Jamesoniella colorata*, but wet mire species such as *B. densifolium* are often important. *Agrostis magellanica* and *J. scheuchzerioides* are the dominant vascular species.

Dry Mire Habitat occurs on relatively dry peats. *Jamesoniella colorata*, *Racomitrium lanuginosum* and *Ptychomnion densifolium* (= *P. ringianum*, see Appendix III) are usually the dominant bryophytes, and *Agrostis magellanica* and *U. compacta* the dominant vascular plants. Dry mire is the only mire habitat in which *Blechnum penna-marina* and the cushion plant *Azorella selago* may be significant components of the vegetation. Dry mire represents a transition between mire and fernbrake (specifically the Mesic Fernbrake Habitat), but also contains some sites that have floristic (presence of cushion dicots and pteridophytes) and soil chemistry (relatively low organic C, high total Ca and Mg contents) affinities with the Mesic Fellfield Habitat.

The mire habitats dealt with above are ombrotrophic so lateral water flow from surrounding areas does not affect the surface layers in which the vegetation is rooted. Where there are water tracks draining water from higher parts of the mire, or there is subsurface flow of water into the mire from an adjacent slope, the Mire Drainage Line habitat occurs, mostly in a narrow ribbon but sometimes over an extensive area (Plate 9.2). Mire drainage line peats are less acidic and possess higher Ca and Mg concentrations than peats of the other mire habitats. A number of bryophytes (e.g. *Breutelia integrifolia*, *Bryum laevigatum*, *Riccardia* spp. and, on more mineral soils, *Cryptochila grandiflora*) are restricted to, and dominant in mire drainage lines. Mire drainage lines become the predominant mire type with increasing altitude; between 0 to 100 m altitude they account for 7%, between 100 and 300 m for 16% and above 300 m for 80% of all the of mire vegetation in these zones. However, this does not mean that drainage line mires are a common habitat above 300 m; in total they occupy only about 5 ha.

Mire complex habitats all occupy that part of the ordination space in Fig. 9.1 where wetness and shelter (the two are partly confounded since protection from wind reduces desiccation, but shelter also implies greater warmth) are the important ecological factors, and where manuring by seabirds or seals does not occur. This is consistent with the distribution of mires on the islands – restricted to wet, oligotrophic peats in sheltered, low-altitude areas away from the heaviest influence of saltspray.

9.2.2 Slope Complex

Most slopes at low and middle altitudes are covered by dense vegetation dominated by *B. penna-marina* and/or *Acaena magellanica*. Soils are well drained and, while still very organic, have a greater mineral content than mire soils, except for the surface layer which usually consists only of organic matter. The impact of animals or saltspray is negligible at all Slope Complex habitats. The main edaphic factors which distinguish the different slope habitats are related to water, especially soil moisture content and whether the hydrological regime is ombrotrophic or minerotrophic. Together, slope habitats occupy about 18% of the area where closed vegetation can develop (< 300 m altitude), about 25 km^2 in total. Above 300 m they are rare, occupying only about 20 ha.

Open Fernbrake occurs on shallow, mineral soils of dry slopes and on flat areas. The vegetation is open and has a scrubby appearance. *Blechnum penna-marina* shares dominance with other vascular species, mainly *A. selago*, *Agrostis magellanica* (usually growing epiphytically on *A. selago* cushions) and *Acaena magellanica*. Lichens and cushion-forming mosses occur, unlike at the other slope complex habitats. With regards to vegetation and soil development, Open Fernbrake represents a stage in the ecological succession from Mesic Fellfield to Closed Fernbrake, as is clear from its position in Fig. 9.1 and from comparisons of the rates of ecological functional processes (primary production, nutrient cycling, decomposition and soil respiration) between fellfield, Open Fernbrake and Closed Fernbrake (Smith 1987a, 1988a, b, 2003; Smith *et al.* 1993).

Closed Fernbrake is the most conspicuous and widespread slope habitat on the island and is the climax vegetation on inland slopes that are not directly influenced by seabirds or seals (Plate 9.3). It occurs on relatively dry, well-drained soils covered by a dense carpet of the fern *B. penna-marina*. Only 5-10 species (vascular plants and bryophytes) are found per 9 m^2 in Closed Fernbrake.

Mesic Fernbrake is found on damper slopes that are generally less steep than those occupied by Closed Fernbrake. It is also common on flat areas. The vegetation is still a carpet of *B. penna-marina*, but species diversity (up to 25 species per 9 m^2 plot) is higher than at Closed Fernbrake. Graminoids such as *U. compacta*, *Agrostis magellanica* and *Poa cookii* occur, as do ombrotrophic mire bryophytes (e.g. *S. uncinata*, *Lepidozia laevifolia*, *B. densifolium*), although never abundantly. Ecologically, Mesic Fernbrake represents a transition between closed fernbrakes and dry mire.

The Dwarf Shrub Fernbrake Habitat occurs in sheltered depressions on slopes otherwise dominated by Closed or Mesic Fernbrake. As well as *B. penna-marina*, it is dominated by *Acaena magellanica* which although actually a suffruticose herb, is the only woody plant on the island and fulfils the same ecological role as deciduous dwarf shrubs in more temperate vegetations and shrub tundras of the Northern Hemisphere. The most common mosses are *Brachythecium rutabulum* and *S. uncinata*. Dwarf Shrub Fernbrake is intermediate between the Mesic Fernbrake Habitat and the Slope Drainage Line and Streambank Habitat described next.

The Slope Drainage Line and Streambank Habitat occurs on slopes where percolation of water down the soil profile is impeded (for example by an impermeable rock layer on grey lava slopes or a hard plinthic layer on some black lava slopes) so that there is substantial subsurface lateral movement of water. Stream banks form essentially the same habitat, where groundwater from the surrounding area drains into the stream. Such areas are minerotrophic, rather than an oligotrophic, and support a closed cover of *Acaena magellanica*, often with a lush understory of bryophytes (mainly species of *Brachythecium* but *S. uncinata* may also be abundant). Sometimes whole slopes (especially on grey lava) are occupied by the Drainage Line Habitat.

At the foot of steep slopes, water wells up locally as springs and flushes. Sometimes the same happens in sites away from the slopes, e.g. at the source of some tributaries of the Van den Boogaard River. In these very minerotrophic Spring and Flush Habitats, bryophyte mats dominated by *Brachythecium subplicatum*, *Philonotis* spp. and *Drepanocladus aduncus* occur. Vascular plants (*Acaena magellanica*, *Montia fontana* and sometimes *P. cookii* are the most common) are usually of minor importance.

Slope habitats are not that well separated from mire habitats along the wet/organic – dry/mineral and the low soil fertility – high soil fertility gradients represented by the axes in Fig. 9.1. However, the two types occupy distinctly different regions of an ordination space formed by Axis 1 and an axis representing a gradient from ill-drained amorphous peats to well-drained mineral soils with clear horizon development (data not shown – see Fig. 3 in Smith & Steenkamp 2001).

9.2.3 Fellfield Complex

Cushions of *A. selago* are the characteristic aspect of fellfield vegetation (Plates 9.4, 9.5). Fellfield soils are mineral and often contain a large proportion of scoria or lava rocks. During heavy rains some fellfield areas can become very wet, even locally inundated, but during dry periods the soils become quite dry. Cushion-forming mosses (*Andreaea acuminata*, *Andreaea acutifolia*, *Bucklandiella* spp. *Ditrichum* spp., *Bartramia patens*, *Grimmia kerguelensis*) and crustose lichens (*Coccotrema stellata*, *Fuscidea asbolodes*, *Lecanora disjungenda*, *Lecidea lygomma*, *Lecidea medusula*, *Lithographa* spp., *Ramonia sub-Antarctica*, *Stephanocyclos henssenianus*) are common. Species richness in fellfield communities can be high, (15-25 species of vascular plants and bryophytes per 25 m^2), related to the wide range of microhabitats in the fellfield habitat. Bare soil, the tops, sides and bottoms of rocks, the edges of *Azorella* cushions and spaces in the cushions between the stems all offer different microhabitats and support different assemblages of species. Most fellfield in lowland areas (< 300 m a.s.l.) belongs to the Mesic Fellfield Habitat, which may have a substantial (up to 50%) plant cover. Xeric Fellfield Habitat is also found at low altitudes, but is the dominant fellfield at higher altitudes. Xeric Fellfield rarely has more than 10% plant cover. Fellfield vegetation covers about 137 km^2, or 47%, of the total area of Marion Island, and is the dominant vegetation type between 100 and 300 m a.s.l., occupying 72% of that altitudinal zone. The two fellfield habitats occupy the cold/dry, infertile mineral soil extremes of the gradients represented in Fig. 9.1, well separated from all other habitats except Open Fernbrake.

9.2.4 Polar Desert

Polar Desert is the characteristic, almost only, habitat of the mid to high altitude regions of the islands. The vegetation consists of very open communities of bryophytes and lichens, with total plant cover rarely exceeding 1% (Plate 9.6). Few vascular plants extend above 600 m altitude (Huntley 1970) and only one, *A. selago*, occurs in Polar Desert. Common bryophytes are *Ditrichum strictum*, *A. acutifolia*, *A. regularis*, *B. patens*, *Bucklandiella orthotrichacea*, *Guembellia kidderi*, *Hymenoloma antarcticum*, *Notoligotrichum australe* and *Philonotis scabrifolia*. Most of these form balls or cushions. On some scoriae slopes bryophytes grow under the scoria surface, protected from the drying and chilling effects of wind. At sheltered, moist localities (e.g. depressions where snow-melt accumulates) a more luxuriant bryophyte vegetation occurs, dominated by *Dicranella gremmenii* and *C. grandiflora*.

Vegetation ecologists have avoided using the term polar desert when describing a vegetation type on sub-Antarctic islands, all of which are at mid-latitudes and receive substantial rainfall. Huntley (1971) referred to the vegetation of what we call polar desert as *Ditrichum-Bartramia* montane desert and included it with *A. selago* fellfield in a Wind Desert Complex. Corresponding vegetation formations on other sub-Antarctic islands have been considered to be fellfield (Taylor 1955; Hughes 1987; Bergstrom 1998) or included with fellfield in a Fellfield Formation (Lewis Smith 1993). However, fellfield (*Fjaeldmark*, *Felsenfluren* or *Felsentundra*) was originally used to describe vegetation in which vascular plants, especially cushion-forming ones, are dominant. This is certainly not the case for the Marion Island Polar Desert Habitat, which contains only one vascular species, and then only at lower altitudes. Rather, on the basis of its environmental and botanical characteristics (a barren unstable surface caused by frequent freeze-thaw cycles and frost heaving, and an extremely sparse vegetation dominated by mosses and lichens), the habitat conforms well with the definitions of high Arctic polar deserts given by Aleksandrova (1970) and Bliss (1981). With its single vascular species, it is even more polar desert-like than many high Arctic polar deserts. For instance the uplands of Devon, Bathurst, Cornwallis and Ellesmere islands (all > 75° N and considered to be true polar deserts) possess 4-12 vascular plant species (Bliss 1981). Hence, the Polar Desert Habitat on the island resembles the most extreme northern hemisphere polar deserts; those dominated by mosses and lichens and which have been termed "polar barrens" (Benninghof 1974) or simply "barrens" (Longton 1998), to distinguish them from fellfield where vascular plants are more important. Polar Desert occupies about 109 km^2 of Marion Island. Polar Desert and fellfield thus occupy 246 km^2, or 85% of the island's total surface, so the two can be considered to be the archetypical vegetation types for the island.

9.2.5 Coastal Saltspray Complex

This complex is restricted to the islands' coastal zone at sites subjected to saltspray and inundation by waves. On the eastern and southern coasts it occurs within 50 m of the shore, but on the northern and western coasts, which are more exposed to the prevailing sea and wind, it is found up to 300 m inland. The complex occupies about 1 km^2 of Marion Island. Coastal Herbfield (Plate 9.7) is dominated by the halophyte *Crassula moschata*, a small reddish chamaephyte with succulent leaves, which occurs on fibrous, black or dark-brown peats with high sodium and magnesium contents. *Cotula plumosa* is often co-dominant (in some cases dominant) and forms short, compact rosettes. Few other vascular species occur, and bryophytes are important only in very wet areas where the effect of saltspray is diluted by incoming freshwater.

On rocky exposed locations with skeletal soils in the saltspray zone an open Coastal Fellfield occurs, dominated by *C. moschata* and the cushion-forming dicot *A. selago*. *Colobanthus kerguelensis* and *P. cookii* may also occur. Rocks closer to the shore and subject to very intense saltspray form a distinctive Coastal Rock Habitat where lichens such as *Amandinia subplicata*, *Arthothelium evanescens*, *Mastodia tesselata* and several species of *Verrucaria* and *Caloplaca* form distinct zonations from the intertidal to several meters above sea level (De Villiers 1976). These lichen zonations are best developed on grey lava coastal rocks and are fragmentary on black lava. On exposed coasts, *Mastodia* and *Caloplaca*-communities may be found up to 50 m a.s.l. Characteristic mosses on coastal rocks are *Eriopus apiculatus* and *Muelleriella crassifolia*.

On very wet peat soils along the inland margins of Coastal herbfield are Saline Mires, dominated by the hepatic *Clasmatocolea vermicularis*. *Crassula moschata*, *Agrostis magellanica* and *R. biternatus* also occur here, but never abundantly. Coastal herbfield and Coastal fellfield are well separated from all other habitats in the ordination space occupied by the habitats (Fig. 9.1). Saline mire is closer to habitats of the mire complex, which is why Smith & Steenkamp (2001) included it in the Mire Complex.

9.2.6 Biotic Complex

The impact of seabirds or seals on vegetation and soil ranges from moderate enrichment of nutrient status on inland slopes inhabited by burrowing prions or petrels, to complete eutrophication of the soil and complete destruction of the plant cover, as in penguin rookeries, Elephant Seal wallows and some areas occupied by Fur Seals. Following terminology commonly used in the island's ecological literature (e.g. Huntley 1971; Gremmen 1981; Smith & Steenkamp 2001) the term *biotic* is used here to indicate sites, vegetation or habitats that are influenced by seals and seabirds. About 4.5 km^2 of Marion Island is occupied by such habitats, which predominantly occur on the coastal lowlands. Some biotic habitats are found at higher elevations around albatross nests and on slopes colonized by burrowing bird species, but in total they occupy only about 3 ha of the area above 100 m altitude.

Characteristic vascular species in biotic vegetation are the tussock grass *P. cookii*, *Callitriche antarctica*, *M. fontana* and *C. plumosa*. Unlike in the Saltspray Complex, the *Cotula* plants occur as large (up to 30 cm tall) lax rosettes. *Poa annua* and/or *Agrostis stolonifera* dominate in one habitat of the complex. Other than in the biotic mire habitat (see below) bryophytes are not an important component of biotic vegetation, although *B. rutabulum*, *Marchantia berteroana*, *Schizymenium campylocarpum*, and *L. gemmascens* occur.

In heavily trampled areas around penguin rookeries and seal wallows Pedestalled Tussock Grassland occurs, consisting of *P. cookii* tussocks on peat pedestals up to 1 m high, formed by peat erosion between the tussocks. Heavy trampling prevents the development of vegetation between the *Poa* pedestals, except for *C. antarctica* and, less frequently, *P. annua*. Bryophytes are rare, except for *M. berteroana* which is sometimes found on the sides and eroded crests of the pedestals.

On flatter areas where erosion due to the activities of seals and penguins is less intense, or on shore-zone slopes occupied by burrowing petrels, a Coastal Tussock Grassland occurs (Plate 9.8). Here, *P. cookii* forms smaller tussocks that are not, or are only slightly, pedestalled. *Callitriche antarctica*, *M. fontana* and *C. plumosa* are common under the grass canopy but are rarely abundant. Bryophytes such as *C. vermicularis*, *L. gemmascens*, and *B. rutabulum* occur, but are also not abundant. Where burrowing birds colonise inland slopes, Inland Tussock Grassland occurs. Trampling is less intensive than in the other two tussock grassland habitats and the grass is never pedestalled. Burrow densities are generally lower than in Coastal Tussock Grassland and, other than both having a dense canopy of *P. cookii*, the two habitats carry distinctly different vegetations. Inland Tussock Grassland has a greater vascular plant diversity, with *Acaena magellanica*, *M. fontana*, *B. penna-marina* and *A. stolonifera*. Bryophytes are common and often abundant; *B. rutabulum* is the most usual one, but *Lophocolea randii*, *S. campylocarpum* and *L. gemmascens* frequently occur. Although most common on slopes, small stands of Inland Tussock Grassland also occur on level areas surrounding wandering albatross and giant petrel nests. Inland Tussock Grasslands have become scarce on Marion Island over the last 20 years, for reasons suggested later in this chapter. This is why a question mark occurs in Table 9.2 against the estimate (made in the mid 1990s) of the total area occupied by this habitat.

The *Cotula* Herbfield habitat occupies the greatest total area of all the coastal habitats on the islands, occurring as large expanses up to a kilometer inland and also as smaller stands between tussock grasslands. The intensity of animal influence seems to be less here than in the tussock grassland habitats, but this might be true only with respect to trampling, rather than manuring. The characteristic (and often only) species is *C. plumosa*. *Poa cookii* is sometimes co-dominant, but few other vascular plants occur. Bryophytes are rare, except for *M. berteroana* and *C. vermicularis*. The soils have high Na and K concentrations and very high levels of N and P.

Where heavy trampling churns up wet organic soils (seal wallows and the edges of penguin rookeries are typical examples), a eutrophic Biotic Mud habitat occurs (Plate 9.8). It is dominated by *C. antarctica* and/or *M. fontana*, but few other species are able to withstand the high level of disturbance and intense nutrient enrichment. There are no bryophytes. On more mineral soils, or where the substrate is fibrous peat rather than mud, heavy trampling (especially by seals) results in compaction of the soil and a Biotic Lawn habitat is found (Plate 9.8). The vegetation consists of a very dense lawn of the introduced grasses *P. annua* and/or *A. stolonifera*. Soils of this habitat are extremely nutrient-enriched.

Where very wet peats are influenced by animals to a lesser extent than is the case for the two previous habitats, Biotic Mire occurs, dominated by the hepatic *C. vermicularis*. *Agrostis magellanica*, *M. fontana* and *R. biternatus* are the most common vascular species, but are rarely important. The Biotic Mire community does not tolerate trampling and most nutrients come from surrounding, animal-inhabited slopes, rather than through direct deposition of excreta. Even so, concentrations of soil nutrients in this habitat are appreciably higher than in any of the other mire habitats.

In Fig. 9.1 the biotic habitats are clearly separated from all other habitats on the soil fertility axis, with the exception of Biotic Mire which occurs between the main biotic group and non-biotically influenced mires.

9.2.7 Aquatic communities

The islands' freshwater bodies (lakes, lava-lakelets, crater lakes, wallows and streams) are described by Smith (2008). Macrophytic aquatic vegetation is poorly developed and generally originates from the terrestrialization of the water body. Plants (especially *Agrostis magellanica*, *A. stolonifera*, *J. scheuchzerioides*, *R. biternatus*) encroach into the water body from the shore. *Limosella australis* and *Ranunculus moseleyi* grow on the bottom of shallow lakes and ponds, but are quite rare. *Potamogeton nodosus* occurs in two of the Albatross Lakes on Marion

Island, forming dense stands in 50-100 cm deep water. The species does not reproduce sexually and is not found in any other of the island's water bodies, or on Prince Edward Island. *Drepanocladus aduncus*, *Drepanocladus polycarpos*, and *S. uncinata* are the most common submerged mosses in ponds. In rivers, aquatic vegetation is limited to mosses (*Schistidium falcatum*, *Schistidium rivulare*, *Orthotheciella varia*, *Blindia magellanica*, *Bucklandiella didyma*) attached to rocks and mats of *A. stolonifera*.

9.3 Vegetation dynamics

9.3.1 Autogenic succession

The earliest colonizers of lava flows are generally mosses. On the 7 ha lava flow that resulted from the 1980 volcanic eruption near Kaalkoppie (Verwoerd *et al.* 1981), a careful search in 1981 yielded only a few stems of a single species of moss (*Bryum* sp.). By 1994, sheltered localities on the flow supported a lush growth of bryophytes and lichens, with *R. lanuginosum* as the most common moss, and *Stereocaulon cymosum* as the most common lichen. Total vegetation cover in a series of 1 m^2 sample plots ranged from < 1% to 95% and the plots contained up to three species, with 10 species being recorded in a 1 ha area on the flow. By 1998, 14 species were found in the same area, including 4 vascular species; *B. penna-marina*, *Agrostis magellanica*, *P. annua* and *Cerastium fontanum*. In 1998 there were three to four species, on average, per 1 m^2 plot, but one plot contained nine species. By 2003, 23 years after the eruption, most of the lava flow was covered by vegetation, often dense and mainly comprised of bryophytes. The rapid colonisation and subsequent succession to an almost complete vegetation cover of the Kaalkoppie lava flow is probably due to the fact that the flow is at less than 100 m altitude. Succession at higher altitudes is probably much slower, and instigated by cushion- and ball-forming forming mosses and *A. selago*, rather than fast-growing species such as *R. lanuginosum* and *Bryum* species, which are restricted to lower altitudes and are relatively dependent on continuously moist conditions.

The pattern of vegetation succession on Marion Island is depicted in Fig. 4 of Smith (1987b). Scoria or solid lava are generally colonised first by *A. selago*, the cushions of which are crucial to further vegetation succession since they accumulate organic matter which is added to fine volcanic ash to form a loamy-textured soil in which other plant species can establish and add further organic matter. A similar type of soil formation has been described for glacier forelands on Kerguelen Island (Frenot *et al.* 1998). Other plant species root in living or dead *A. selago* cushions and add to the accumulation of organic debris, which eventually fills the crevices and porous structure of the lava or scoria and impedes drainage, ultimately leading to peat formation. If the rate of water acquisition by the area is greater than the rate of drainage, bryophyte-dominated mire develops. Peat accumulation may raise the mire surface above the watertable, resulting in a dry mire dominated by graminoids and bryophytes. Further peat accumulation may make the surface even drier, and fernbrake vegetation then develops. However, closed fernbrake on flat, level areas is rare. Dry mire communities dominated by *B. penna-marina*, *R. lanuginosum* and *U. compacta* generally represent the culmination of the wet-dry succession on level surfaces.

Where drainage from the fellfield area is unimpeded, the cushion plants develop a stable peat for fernbrake elements to develop. At first these elements may arise epiphytically on, or in the shelter of, the cushions, but eventually extend across the peat to form an open fernbrake that is often succeeded by a closed carpet of *B. penna-marina*. This sequence from fellfield to fernbrake occurs predominantly on slopes. On flat plateaus, impeded drainage (caused by peat blocking the drainage channels) diverts the fellfield-fernbrake succession to the one toward mire vegetation.

At rocky coastal sites subjected to salt-spray, *A. selago* and *M. crassifolia* first occur, followed by *C. moschata*. Peat accumulation in these areas results in the coastal herbfield vegetation dominated by *C. moschata* and sometimes also *C. plumosa*. Impeded drainage in such areas diverts the succession to a saline mire dominated by *C. vermicularis*.

Strong lateral flow of water (for instance, in drainage lines, water tracks, flushes and springs) may modify the vegetation at any level of succession, leading to a group of plant communities characterized, on slopes and stream banks, by a dominance of *Acaena magellanica* in the herb layer, and *B. subplicatum* or *B. rutabulum* in the bryophyte layer. In mires, drainage lines are dominated by *B. integrifolia* and *B. laevigatum*.

Seabird and/or seal activity may have a marked influence at any stage of succession. Other than Salvin's Prions (*Pachyptila salvini*), animals seldom establish nests or otherwise exploit fellfield areas, preferring mires and well-vegetated slopes (Schramm 1986). In the coastal zone, a *C. plumosa-P. cookii* dominated vegetation, or a *P. cookii* tussock grassland, develops at sites influenced by animals, except at very wet sites where communities of coprophilous, trampling-tolerant species (mainly *C. antarctica*, *M. fontana* and *P. annua*) occur. Where fernbrake communities are colonized by burrowing birds, tussock grassland dominated by *P. cookii*, *Acaena magellanica*, *B. penna-marina* and *B. rutabulum* develops (Smith 1976a).

9.3.2 Vegetation and climate change

The climate of the entire sub-Antarctic region is currently undergoing marked change (Jacka & Budd 1998). Marion Island (and presumably also Prince Edward Island) has become significantly warmer and drier over the past 35 years (Smith 2002; Sumner *et al.* 2004). Table 9.4 shows how the islands' terrestrial habitats might respond to changes in temperature and moisture. The suggested responses of the habitats to the various perturbations are based on an analysis of the positions of the habitats on the axes of the ordinations on which the habitat classification was based (Fig. 9.1) and a prediction of how a particular habitat would move on the axes in response to a particular perturbation or combination of perturbations. The predictions were also based on soil chemistry information, a re-appraisal of botanical and environmental data for 510 sites studied by Gremmen (1981) and a consideration of soil and air temperature data in Huntley (1971), Smith (1987a, c), Chown & Crafford (1992), Smith *et al.* (1993) and Blake (1996). Some predictions are simply subjective, based on an appreciation of how vegetation pattern on the island, and on colder sub-Antarctic islands such as Heard Island and South Georgia, is related to environmental forcing variables.

Climate change might also affect the vegetation in less direct ways. For instance, changing atmospheric and oceanic circulation patterns that underlie the changing climate at the islands (Smith & Steenkamp 1990; le Roux 2008) could influence the seabird and seal populations by moving their feeding grounds or, in the case of the birds, changing the positions and frequencies of the atmospheric frontal systems they use to reach the feeding grounds (Ryan & Bester 2008). Such alterations in the trophic dynamics of the islands' seal and seabird populations might result in a change in the amounts of nutrients transferred from the ocean to the terrestrial ecosystem, an important determinant of both the structure and function of the islands' vegetation (Smith & Froneman 2008; Smith 2008). Similarly, easterly winds are becoming more common (and also stronger; le Roux 2008) and this might increase the extent of salt-spray dominated habitats on the eastern side of the islands. Table 9.4 suggests how the habitats might respond to a change in levels of manuring and saltspray.

9.3.3 Changes in population sizes of indigenous animals

Large changes have occurred in the numbers of burrowing prions and petrels at Marion Island, and in the size of Fur Seal populations on both Marion and Prince Edward Islands. Both groups of animals have a major impact on the islands' vegetation, specifically on the tussock grasslands.

Tussock grassland is the climax vegetation of slopes occupied by petrels and prions, and results from the nutrients deposited by the birds (Smith 1976a). The populations of all the burrowing species on Marion Island were severely affected by predation by Domestic Cats, which were introduced in 1949 and quickly became feral (Skinner *et al.* 1978). The cat population increased to about 2 000 by 1975, when they killed an estimated 450 000 birds per year (Bester & Skinner 1991). Transects on the north-eastern lowlands of Marion Island (between the Van den Boogaard River and Fred's Hill, and between 100 m and 2 500 m from the shore) showed that tussock grassland occupied c.1% of the area in 1971/72 (Smith 1976b, 1977). This had decreased to 0.1% by 1991 (Smith *et al.* 2001) and by 2005 no inland tussock grasslands occurred in the area. Mostly, the inland tussock grasslands have been replaced by closed fernbrake or dwarf-shrub fernbrake. Hence, although the cats were eradicated in 1991 (Bester *et al.* 2000) and the petrel and prion populations appear to be recovering (Cooper *et al.* 1995), this has not yet reversed the decline of the tussock grasslands.

Table 9.4 Suggested response of habitats to environmental change. The number shows the habitat that replaces the one in the first column should the environment change in the way specified by the column heading. – indicates that no change is expected. L and H indicate what may happen to a habitat in the lower and higher parts, respectively, of its altitudinal range. More/less biotic indicates a greater/lesser intensity of seabird or seal manuring and more/less salt indicates an increase/decrease in the intensity of salt spray deposition. From Smith *et al.* (2001).

Habitat		Warmer & Dryer	Warmer & Wetter	Colder & Dryer	Colder & Wetter	More Biotic	Less Biotic	More Salt	Less Salt
1.1	Coastal Herbfield	1.2	6.6	1.2	6.6	5.1	-	-	3.1, 3.2, 3.3, 6.1, 6.2
1.2	Coastal Fellfield	-	1.1	-	1.1	4.1, 5.1	-	-	2.2
2.1	Xeric Fellfield	-	2.2	7.1	-	-, 4.2	-	1.2	-
2.2	Mesic Fellfield	2.1	3.1	2.1	-	5.1, 4.2	-	1.2	-
3.1	Open Fernbrake	2.2	3.2	2.2	(L;3.2, 6.1) (H; 2.2)	4.2	-	1.2	-
3.2	Closed Fernbrake	3.1	3.3	3.1	3.3	4.2	-	1.1	-
3.3	Mesic Fernbrake	3.2	6.1	3.2	3.4, 6.1	4.2	-	1.1?	-
3.4	Dwarf Shrub Fernbrake	3.2	3.5	3.2	3.5	4.2	-	1.1?	-
3.5	Slope Drainage Line and Streambank	3.4?	-, 3.6?	?	-, 3.6?	4.2	-	1.1,	-
3.6	Spring and Flush	3.3, 3.4, 3.5	-	3.5	-	5.2?	-	6.6	-
4.1	Coastal Tussock Grassland	-	-	-	-	-, 4.3	5.1	-	4.2
4.2	Inland Tussock Grassland	-	-	-	-	-	3.2, 3.1	4.1	-
4.3	Pedestalled Tussock Grassland	-	-	-	-	-	4.1, 5.1	-, 5.1	-

Table 9.4 Continued.

	Habitat	Warmer & Dryer	Warmer & Wetter	Colder & Dryer	Colder & Wetter	More Biotic	Less Biotic	More Salt	Less Salt
5.1	Cotula Herbfield	-, 4.1	-, 6.5	-, 1.2?, 4.1	-, 6.5	4.1, 5.2, 5.3	1.1, 3.2	-, 1.1?	-, 3.2
5.2	Biotic Mud	5.1, 5.3	-	5.1, 5.3	-	-	5.1, 6.5	-	-
5.3	Biotic Lawn	-	5.2, 6.5	-	5.2, 6.5	-	5.1, 3.5	-	-
6.1	Dry Mire	3.3	6.2	3.1	6.2	4.2	-	1.1	-
6.2	Mesic Mire	6.1	6.3	6.1	6.3	4.2, 6.5	-	1.1, 6.6	-
6.3	Wet Mire	6.2	-	6.2	-	6.5	-	6.6	-
6.4	Mire Drainage Line	-, 6.3	-	-, 6.3	-	6.5	-	6.6	-
6.5	Biotic Mire	5.1	-	5.1	-	5.2	6.6, 6.2, 6.3	-, 6.6	-
6.6	Saline Mire	1.1	-	1.1	-	6.5	-	-	6.1 to 6.4
7.1	Polar Desert	2.1	2.1	-	(L; 2.1), (H; -)	-?	-	-	-

Fur seals have increased on Marion Island from less than a thousand in the early 1950s (Rand 1956) to 7 000 in 1975 (Condy 1978) and *c.* 50 000 in 1995 (Hofmeyr & Bester 1997). Fur Seal numbers have also increased on Prince Edward Island (Ryan & Bester 2008). The area occupied by these animals on the islands has increased immensely and, as on Bird Island, South Georgia (Bonner 1985), this has lead to widespread destruction of tussock grassland. This is especially conspicuous on the west coast of Marion Island and all the coastal areas of Prince Edward Island. Fur seals have not yet significantly encroached inland on the east coast of Marion Island and are not responsible for the disappearance of tussock grasslands in the area considered above.

9.3.4 Impact of changing human activities

With the deployment of field huts on Marion Island the amount of fieldwork increased markedly and a network of tracks has developed. The effect of trampling in and around the tracks depends on habitat type and the nature of the soil. On dry soils, trampling results in soil compaction, but the tracks remain quite narrow and disturbance is slight. In contrast, wet soils and peat are churned up and become difficult or impossible to traverse. The tracks become wider as people skirt around their edges. Most trampled areas have less plant species than the surrounding undisturbed habitats, but there are exceptions. For instance, trampling in closed fernbrake opens up the dense *Blechnum* mat and increases species richness by as much as 30% (Gremmen *et al.* 2003).

9.3.5 Impact of invasions by alien plants

The greatest modification of Marion Island's vegetation by invasive plants has been caused by two species, *A. stolonifera* and *Sagina procumbens*, which are widespread on the island (Gremmen 1997) and can be found in almost all of the 23 habitats. *Agrostis stolonifera* has become dominant in seven, and *S. procumbens* in 11, of the habitats (Table 9.5). *Poa annua* has been found in 16 habitats, but it is dominant in only two. *Agrostis gigantea*, observed for the first time in 1993 at the weather station, has invaded seven habitats and was dominant in three. It reduced species richness in the invaded plant community to less than half that of uninvaded communities (N.J.M. Gremmen, unpublished data). The species has been eradicated.

There is no clear relationship between the 'invasiveness" of an alien plant species (the number of habitats it can invade and the total area in which it occurs) and the impact that it has on the communities it invades. Some species have a very restricted distribution, but have a major impact on the vegetation of the localities where they occur. For instance, *Festuca rubra* (two localities) and *Agropyron repens* (one locality) have invaded more than one habitat at the localities where they occur (Table 9.5) and both grasses form dense stands that smother the native plants. For instance, 4 m^2 sample plots in the *Festuca* stands contain only 3-5 species of vascular plants and bryophytes, whereas uninvaded vegetation in the same habitat has 7-15 species per 4 m^2 plot.

Table 9.5 Status of alien vascular species in the Marion Island habitats. See Table 9.1 for full names of the species. * = present; d = attains dominance.

Habitat	Species												Total aliens	Total dominant aliens
	Agro rep	*Agro cas*	*Agro gig*	*Agro sto*	*Alop gen*	*Cera fon*	*Fest rub*	*Poa annu*	*Poa prat*	*Rumex ac*	*Sagi pro*	*Stel med*		
Coastal Herbfield				d				*			d		3	2
Coastal Fellfield				*							d	*	3	1
Xeric Fellfield				*		*					*		3	0
Mesic Fellfield				*		*		*			d		4	1
Open Fernbrake			*	d		*		*		d	*		6	2
Closed Fernbrake			*	*		*	*	*		*	*		7	0
Mesic Fernbrake			*	*		*	*	*		*	*		7	0
Dwarf Shrub Fernbrake			*	d		*	*	*		d	*		7	1
Slope Drainage Line and Streambank	d	*	d	d		*	d	*	d		*	*	10	5
Spring and Flush				d				*					2	1
Coastal Tussock Grassland				d		*		*			*	*	5	1
Inland Tussock Grassland				d		*		*			*	*	5	1
Pedestalled Tussock Grassland				*		*		*			*		4	0
Cotula Herbfield	*	*	d	*	d		*	d			*		8	3
Biotic Mud				d				*			*		3	1
Biotic Lawn				d				d			*		3	2
Dry Mire				*									1	0
Mesic Mire			d	*						*	d		4	2

Table 9.5 Continued.

Habitat	**Species**												**Total aliens**	**Total dominant aliens**
	Agro rep	*Agro cas*	*Agro gig*	*Agro sto*	*Alop gen*	*Cera fon*	*Fest rub*	*Poa annu*	*Poa prat*	*Rumex ac*	*Sagi pro*	*Stel med*		
Wet Mire				d					*		d		3	2
Mire Drainage Line								*			*		2	0
Mesic Mire Drainage Line				d		*			*		*		4	1
Biotic Mire				*				*			d		3	1
Saline Mire				*							d		2	1
Polar Desert													0	0
Number of habitats invaded:	2	2	7	22	1	11	5	16	3	5	21	4		
Number of habitats in which dominant:	1	0	3	11	1	0	1	2	1	2	7	0		

Where *A. stolonifera* invades drainage lines and streambanks the number of native plant species is reduced by 50% compared to undisturbed sites (Fig. 9.2). The composition of the soil fauna is also significantly affected (Gremmen *et al.* 1998). *Poa pratensis* has had a similar impact on parts of north-eastern lowlands of Marion Island (Gremmen 1997). On the other hand, some widespread alien plants, e.g. *Stellaria media* and *C. fontanum* most commonly occur only as scattered individuals in the communities they invade, and they do not displace the native species. Coastal habitats are particularly susceptible to invasion by alien plants, but the invasions generally have little effect on the native species diversity. For instance *S. procumbens* readily invades, and frequently becomes dominant in, coastal herbfield and *Cotula* herbfield without significantly reducing the number of native plant species (Gremmen 1997). Similarly, where *S. procumbens*, *C. fontanum* or *A. stolonifera* have invaded fellfields, usually none of the native species are eliminated since the alien colonists occupy the open spaces in these communities.

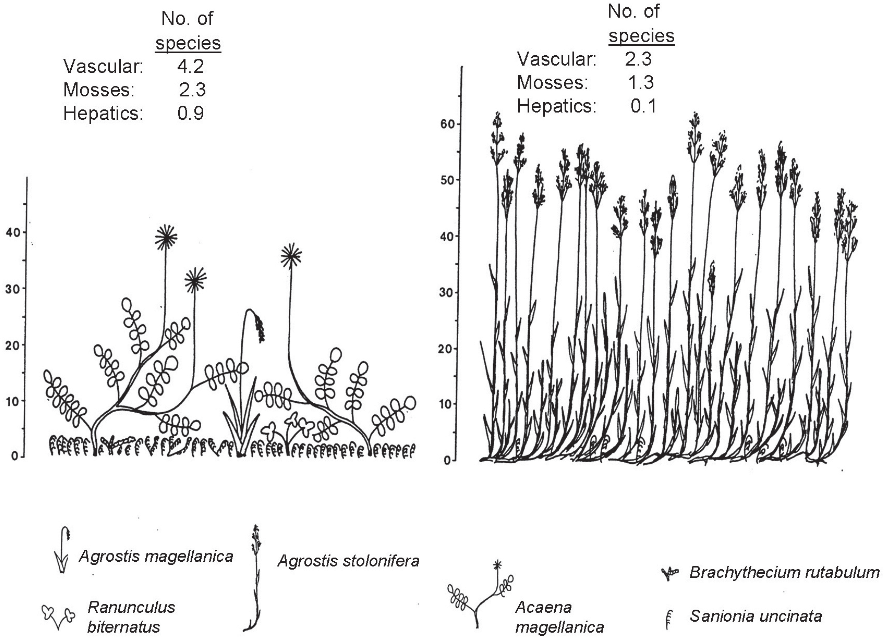


Figure 9.2 Vegetation structure of a Drainage Line and Streambank Habitat a) before and b) after invasion by *Agrostis stolonifera* (from Gremmen *et al.* 1998).

Although the impacts of alien plants may be considerable in the areas at which they occur, the total area affected by alien plants is still relatively small, at present less than 5% of the total island area. Polar Desert is at present the only habitat not colonised by invasive species.

We conclude with some subjective considerations based on our experience of the Prince Edward Islands' vegetation, which we consider to be as trustworthy as the conclusions from our research results. Like most botanists acquainted with the islands' vegetation (starting with Sir Joseph Hooker in the 19th century; Hooker 1847), when we started working on the islands we thought that the vegetation was extremely slow-growing and that succession was too slow to be easily discerned in as short a period as the lifetimes of our expected research careers. Dogma at the time was that it took thousands of years for a new lava flow to become vegetated, that the island vegetation was unproductive and largely unchanging, and that the forcing variables driving ecosystem structure and function (especially the climate) were also static, or at least would not change noticeably in our lifetime.

Thirty four years later, we have a completely different view. We know that the lowland vegetation is productive and that succession is extremely dynamic. We have seen large sections of barren lava becoming substantially vegetated (Santa Rosa Valley), and partially vegetated areas become almost completely covered with fernbrake (Hoppie's Hell). We had the privilege of standing on a still-fuming lava eruption, and subsequently being able to witness how rapidly it became colonised and covered by plants. Over 30 years we witnessed most of the mesic fellfields on the eastern lowlands become mires and open fernbrakes, and open fernbrakes become mesic fernbrakes, closed fernbrakes or mires. Pipelines have disappeared under dense carpets of vegetation and become covered by up to 20 cm of peat. We have seen the terrestrialization of large ponds and, in some instances, the subsequent reappearance of the ponds. We have seen the almost total disappearance of tussock grasslands on inland slopes, and the total disappearance of a plant community that was common in the 1970s (*Azorella-Poa* montane grassland, a cushion plant-tussock grass community on the crests of slopes; Huntley 1971). Alarmingly, on Marion Island we have seen the spread of alien plant species from the meteorological station so that two of them are now found all over the island's lowlands and have come to dominate the vegetation of large areas.

What has perhaps surprised us most has been the extent to which, and rapidity with which, the climate has changed at the islands. Over 20 years we saw the Marion Island summit change from white to red as the ice cap was lost and the scoria peaks exposed; the temperature record since 1970 tells why this was so. Rainfall declined by about 25% in the same period and we saw large, waterlogged expanses of mire become traversable. The results of our studies have allowed us to predict how ecological structure and functioning might respond to these climatic changes and we have even seen particular predictions proved true. Islands have always been particularly satisfying and rewarding subjects for studying biological and ecological processes. We have been exceedingly fortunate in the opportunity and support that enabled us to work on the Prince Edward Islands over all these years.

9.4 References

Aleksandrova, V.D. 1970. The vegetation of the tundra zones in the USSR and data about its productivity. In: Fuller, W.H. & Kevan, P.G. (Eds.). *Productivity and Conservation in Northern Circumpolar Lands*. International Union for Conservation of Nature, Morges, pp. 93-114.

Benninghof, W.S. 1974. Macrobiology and ecology in polar deserts. In: Smiley, T.L. & Zumberge, J.H. (Eds.). *Polar Deserts and Modern Man*. University of Arizona Press, Tucson. pp. 91-97.

Bergstrom, D. 1998. Plant ecology on Heard Island: a new vegetation scheme and predictions for climate change. *A.N.A.R.E. Research Notes* **101**, 3-4.

Bergstrom, D.M. & Smith, V.R. 1990. Alien vascular flora of Marion and Prince Edward Islands: new species, present distribution and status. *Antarctic Science* **2**, 301-308.

Bester, M.N., Bloomer, J.P., Bartlett, P.A., Muller, D.D., Van Rooyen, M. & Buchner, H. 2000. Final eradication of feral cats from sub-Antarctic Marion Island, southern Indian Ocean. *South African Journal of Wildlife Research* **30**, 53-57.

Bester, M.N. & Skinner, J.D. 1991. The Marion Island cat programme. *South African Journal of Antarctic Research* **21**, 117.

Blake, B.J. 1996. *Microclimate and prediction of photosynthesis at Marion Island*. M.Sc. Thesis, University of the Free State, South Africa.

Bliss, L.C. 1981. North American and Scandinavian tundras and polar deserts. In: Bliss, L.C., Heal, O.W. & Moore, J.J. (Eds.). *Tundra Ecosystems: A Comparative Analysis*. Cambridge University Press, Cambridge. pp. 8-24.

Bonner, W.N. 1985. Impact of Fur Seals on the terrestrial environment at South Georgia. In: Siegfried, W.R., Condy, P.R. & Laws, R.M. (Eds.). *Antarctic Nutrient Cycles and Food Webs*. Springer, Berlin. pp. 641-646.

Chown, S.L. & Crafford, J.E. 1992. Microhabitat temperatures at Marion Island (46°54'S, 37°45'E). *South African Journal of Antarctic Research* **22**, 51-58.

Chown, S.L., Marshall, D.J. & Pakhomov, E. 2008. Regional membership: biogeography. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 277-300.

Condy, P.R. 1978. The distribution, abundance and annual cycle of fur seals *Arctocephalus* spp. on the Prince Edward Islands. *South African Journal of Wildlife Research* **8**, 159-168.

Cooper, J., Marais, A.V.N., Bloomer, J.P. & Bester, M.N. 1995. A success story: breeding of burrowing petrels (*Procellariidae*) before and after the extinction of feral cats *Felis catus* at sub-Antarctic Marion Island. *Marine Ornithology* **23**, 33-37.

De Villiers, A.F. 1976. Littoral ecology of Marion and Prince Edward Islands (Southern Ocean). *South African Journal of Antarctic Research Supplement* **1**, 1-40.

De Villiers, M.S. & Cooper, J. 2008. Conservation and management. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 301-330.

Frenot, Y., Gloaguen, J.C., Cannavacciuolo, M. & Bellido, A. 1998. Primary succession on glacier forelands in the subantarctic Kerguelen Islands. *Journal of Vegetation Science* **9**, 75-84.

Gremmen, N.J.M. 1975. The distribution of alien vascular plants on Marion and Prince Edward Islands. *South African Journal of Antarctic Research* **5**, 25-30.

Gremmen, N.J.M. 1981. *The Vegetation of the Subantarctic Islands Marion and Prince Edward*. Geobotany 3. Junk, The Hague. 145 pp.

Gremmen, N.J.M. 1982. Alien vascular plants on Marion Island (subantarctic). *Comité National Français des Recherches Antarctiques* **51**, 315-323.

Gremmen, N.J.M. 1997. Changes in the vegetation of sub-Antarctic Marion Island resulting from introduced vascular plants. In: Battaglia, B., Valencia, J. & Walton, D.W.H. (Eds.). *Antarctic Communities: Species, Structure and Survival*. Cambridge University Press, Cambridge. pp. 417-423.

Gremmen, N.J.M., Chown, S.L. & Marshall, D.J. 1998. Impact of the introduced grass *Agrostis stolonifera* L. on vegetation and soil fauna of drainage line communities at Marion Island, sub-Antarctic. *Biological Conservation* **85**, 223-231.

Gremmen, N.J.M. & Smith, V.R. 1999. New records of alien vascular plants from Marion and Prince Edward Islands. *Polar Biology* **21**, 401-409.

Gremmen, N.J.M., Smith, V.R. & Van Tongeren, O.F.R. 2003. Impact of trampling on the vegetation of sub-Antarctic Marion Island. *Arctic, Antarctic, and Alpine Research* **35**, 442-446.

Hofmeyr, G.J.G. & Bester, M.N. 1997. Changes in population sizes and distribution of Fur Seals at Marion Island. *Polar Biology* **17**, 150-158.

Hooker, J.D. 1847. *Flora Antarctica. The Botany of the Antarctic Voyages of H.M. Ships Erebus and Terror in the Years 1839-1943*. Reeves Brothers, London.

Hughes, J.M.R. 1987. The distribution and composition of vascular plant communities on Heard Island. *Polar Biology* **7**, 153-162.

Huntley, B.J. 1970. Altitudinal distribution and phenology of Marion Island vascular plants. *Tydskrif vir Natuurwetenskappe* **10**, 255-262.

Huntley, B.J. 1971. Vegetation. In: Van Zinderen Bakker E.M., Winterbottom J.M. & Dyer R.A. (Eds.). *Marion and Prince Edward Islands: Report on the South African Biological and Geological Expedition 1965-1966*. A.A. Balkema, Cape Town. pp 98-160.

Jacka, T.H. & Budd, W.F. 1998. Detection of temperature and sea ice extent changes in the Antarctic and the Southern Ocean. *Annals of Glaciology* **27**, 553-559.

le Roux, P.C. 2008. Climate and climate change. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 39-64.

Lewis Smith, R.I. 1993. Dry coastal ecosystems on sub-Antarctic islands. In: Van der Maarel, E. (Ed.). *Ecosystems of the World 2A. Dry Coastal Ecosystems, Polar Regions and Europe*. Elsevier, Amsterdam. pp. 73-93.

Longton, R.E. 1998. *Biology of Polar Bryophytes and Lichens*. Cambridge University Press, Cambridge.

Ochyra, R., Smith, V.R., & Gremmen, N.J.M. 2003. *Thuidium delicatulum* (Hedw.) Schimp. (Thuidiaceae) – another bipolar moss disjunct from Subantarctic Marion Island. *Cryptogamie, Bryologie* **24**, 253-263.

Rand, R.W. 1956. Notes on the Marion Island fur seal. *Proceedings of the Zoological Society of London* **126**, 65-82.

Ryan, P.G. & Bester, M.N. 2008. Pelagic predators. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 121-164.

Ryan, P.G., Smith, V.R. & Gremmen, N.J.M. 2003. The distribution and spread of alien vascular plants on Prince Edward Island. *South African Journal of Marine Science* **25**, 555-562.

Schramm, M. 1986. Burrow densities and nest site preferences of petrels (*Procellariidae*) at the Prince Edward Islands. *Polar Biology* **6**, 63-70.

Skinner, J.D., Condy, P.R., Van Aarde, R.J., Bester, M.N. & Robinson, T.J. 1978. The mammals of Marion Island: a review. *South African Journal of Antarctic Research* **8**, 35-38.

Smith, V.R. 1976a. The effect of burrowing species of Procellariidae on the nutrient status of inland tussock grasslands on Marion Island. *South African Journal of Botany* **42**, 265-272.

Smith, V.R. 1976b. Standing crop and nutrient status of Marion Island (sub-Antarctic) vegetation. *South African Journal of Botany* **42**, 231-263.

Smith, V.R. 1977. Vegetation standing crop of the grey lava flows and of the eastern coastal plain on Marion Island. *South African Journal of Botany* **43**, 105-114.

Smith, V.R. 1987a. Production and nutrient dynamics of plant communities on a sub-Antarctic Island. 2. Standing crop and primary production of fjaeldmark and fernbrakes. *Polar Biology* **7**, 125-144.

Smith, V.R. 1987b. The environment and biota of Marion Island. *South African Journal of Science* **83**, 211-220.

Smith, V.R. 1987c. Production and nutrient dynamics of plant communities on a sub-Antarctic Island. 1. Standing crop and primary production of mire-grasslands. *Polar Biology* **7**, 57-75.

Smith, V.R. 1988a. Production and nutrient dynamics of plant communities on a sub-Antarctic Island. 4. Standing stocks, uptake and loss of nutrients in fjaeldmark and fernbrakes. *Polar Biology* **8**, 191-211.

Smith, V.R. 1988b. Production and nutrient dynamics of plant communities on a sub-Antarctic Island. 5. Nutrient budgets and turnover times for mire-grasslands, fjaeldmark and fernbrakes. *Polar Biology* **8**, 255-269.

Smith, V.R. 2002. Climate change in the sub-Antarctic: an illustration from Marion Island. *Climatic Change* **52**, 345-357.

Smith, V.R. 2003. Soil respiration and its determinants on a sub-Antarctic island. *Soil Biology and Biochemistry* **35**, 77-91.

Smith, V.R. 2008. Terrestrial and freshwater primary production and nutrient cycling. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 181-214.

Smith, V.R. & Froneman, P.W. 2008. Nutrient dynamics in the vicinity of the Prince Edward Islands. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 165-179.

Smith, V.R. & Mucina, L. 2006. Vegetation of Subantarctic Marion and Prince Edward Islands. In: Mucina, L. & Rutherford, M.C. (Eds.). *The Vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute, Pretoria. *Strelitzia* **19**, pp. 698-723.

Smith, V.R. & Steenkamp, M. 1990. Climatic change and its ecological implications at a sub-Antarctic Island. *Oecologia* **85**, 14-24.

Smith, V.R. & Steenkamp, M. 2001. Classification of the terrestrial habitats on sub-Antarctic Marion Island based on vegetation and soil chemistry. *Journal of Vegetation Science* **12**, 181-198.

Smith, V.R., Steenkamp, M. & French, D.D. 1993. Soil decomposition potential in relation to environmental factors on Marion Island (sub-Antarctic). *Soil Biology and Biochemistry* **25**, 1619-1633.

Smith, V.R., Steenkamp, M. & Gremmen, N.J.M. 2001. Terrestrial habitats on sub-Antarctic Marion Island: their vegetation, edaphic attributes, distribution and response to climate change. *South African Journal of Botany* **67**, 641-654.

Sumner, P.D., Meiklejohn, K.I., Boelhouwers, J.C. & Hedding, D.W. 2004. Climate change melts Marion Island's snow and ice. *South African Journal of Science* **100**, 395-398.

Taylor, B.W. 1955. The flora, vegetation and soils of Macquarie Island. *A.N.A.R.E. Reports Series B* **2**, 1-192.

Verwoerd, W.J., Russell, S. & Berruti, A. 1981. 1980 volcanic eruption reported for Marion Island. *Earth and Planetary Science Letters* **54**, 153-156.

CHAPTER 10

SPATIAL VARIATION IN THE TERRESTRIAL BIOTIC SYSTEM

MELODIE A. MCGEOCH, PETER C. LE ROUX,
ELIZABETH A. HUGO AND MAWETHU J. NYAKATYA

‘Space’ has been referred to as ‘the final frontier for ecological theory’ (Kareiva 1994). Indeed, a spatial approach to documenting and modeling variation in populations, communities and species diversity has dominated ecology for the last few decades, and resulted in significant advances in understanding (e.g. island biogeography (MacArthur & Wilson 1967), metapopulation dynamics (Hanski 1991; Tilman *et al.* 1997), and macroecology (Gaston & Blackburn 2000)). We now appreciate not only that ecological pattern and process is scale dependent, but that multiscale approaches are necessary to understand the hierarchical nature of mechanisms underlying the patterns we observe (Usher & Booth 1986; Wiens 2000; Schneider 2001; McGeoch & Price 2004). Integrating the findings from a range of hierarchical spatial scales is therefore an effective tool for generating hypotheses and identifying the scale dependent nature of pattern and mechanism in any biotic system (Bellehumeur & Legendre 1998; Noda 2004).

The islands of the Southern Ocean provide particularly convenient platforms for such an approach because terrestrial habitat boundaries are well defined, the islands are comparatively small and species poor, have only a few key alien species, and low levels of natural migration and human-mediated introductions (Bergstrom & Chown 1999). Furthermore, both plant and invertebrate taxa are particularly well-known for Marion Island (Gremmen 1981; Crafford *et al.*

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 245-276

1986; Chown *et al.* 2002). Spatial pattern in the terrestrial biota on Marion is likely to be a synthetic consequence of strong gradients along with patchiness in patterns of climate, geomorphology and nutrient availability (Gremmen 1981; Blake 1996; Smith & Steenkamp 2001). For example, colonization of the island by winged insects (such as the fairly recent arrival of *Plutella xylostella* (Lepidoptera: Plutellidae) and other air-borne propagules, is predicted to occur on the leeward side of the island, deposited there as a consequence of dominant wind and airflow patterns (Chown & Avenant 1992). The effect of nutrient availability, soil properties and altitude in structuring the terrestrial habitat is particularly clear in the plant community (Gremmen 1981; Smith & Steenkamp 2001; Gremmen & Smith 2008). Indeed, vegetation community type, together with abiotic variables, play an important role in structuring the most speciose faunal component on the Prince Edward Islands, i.e. the invertebrates.

Although *c*. 23 habitats grouped into seven habitat complexes exist on Marion Island (Smith *et al.* 2001), a clear distinction can be made between the vegetated (supporting vascular plants) and epilithic (areas between vascular cushion plants in fellfield, rocky shores, and lava outcrops) biotopes (Chown 1989). For example, the largely cryptogam-feeding, ectemnorhine weevils on the island are more speciose and abundant in the epilithic than vegetated biotope (Chown 1989, 1997). By contrast, mite and springtail abundance and richness are greater in vegetated than in epilithic habitats (Mercer *et al.* 2000; Barendse & Chown 2001). The invertebrate fauna certainly responds fairly strongly to qualitative differences between habitat types (Crafford & Scholtz 1987; Chown 1990), with several habitat-specific species and distinct differences in community composition (Hänel 1999; Barendse & Chown 2000; Mercer *et al.* 2000; Gabriel *et al.* 2001; Barendse *et al.* 2002). For example, although there is some species overlap, lower shore, upper shore and inland mite communities differ significantly (Mercer *et al.* 2000). The microarthropod communities associated with several of the dominant vascular plant species on the island are also distinct, not only in terms of some habitat specificity, but also in the relative abundances of species (Hugo *et al.* 2006). In general, arthropod densities are much higher in habitats typically characterized by vascular vegetation than in those that are not (Hänel 1999; Gabriel *et al.* 2001; Barendse *et al.* 2002). Although competitive interactions are considered unimportant in the invertebrate communities on the island, both mite and springtail communities cluster distinctly into a dozen or more plant community associations (Gabriel *et al.* 2001; Barendse *et al.* 2002; Hugo *et al.* 2006). In general, biotic interactions, at least in the plant community, are considered more prevalent and important at speciose lower altitudes, replaced by abiotic variables with an increase in elevation and concomitant decline in diversity (although altitudinal gradients are not always linear, see later discussion) (le Roux 2004; see also Körner 2003). Finally, as discussed elsewhere in this book (Chown *et al.* 2008; De Villiers & Cooper 2008), introduced and invasive species (plants, invertebrates and *Mus musculus*) are beginning to alter terrestrial biodiversity patterns, by changing local species richness, abundance and taxonomic diversity (Chown & Language 1994; Gremmen *et al.* 1998; Chown *et al.* 2002).

In this chapter we focus on one component of the terrestrial biota on Marion Island, and adopt a multiscale approach to understanding the processes driving spatial variation in this terrestrial system. We use *Azorella selago* Hook. (Apiaceae), a characteristic and keystone plant species on the island, as a model. This species is well suited for an examination of spatial variation because it is abundant and widely distributed on the island, plants have a discrete physical boundary, and are host to several other plant and invertebrate species. Furthermore, *A. selago* has been the focus of a research programme aimed at understanding not only spatial variation in the terrestrial system, but also the likely impact of climate change on the biota of Marion Island (Hugo *et al.* 2004; le Roux 2004; le Roux & McGeoch 2004; le Roux *et al.* 2005; McGeoch *et al.* 2006; le Roux & McGeoch 2008). Here we explore variation in this species, and the epiphytes and arthropods associated with it, within and across three spatial scales: (i), fine scale patterns within individual plants (plant scale), (ii) mesoscale variation across stands or patches of plants (landscape scale) and (iii) island-wide variation associated with the altitude gradient on the island and island aspect (the island scale).

10.1 The model

> Its remarkable growth form immediately attracts the attention of visitors to the islands, not only as an outstanding example of adaptation to the harsh environment, but also as a welcome cushion for the weary explorer of these rugged, tractless islands. Huntley (1972)

Azorella selago (or the 'cushion plant') is widely distributed in the sub-Antarctic (from southern South America to Heard Island) and is the member of a genus dominant in the region (Gremmen 1981). It is long-lived with a hemispherical, cushion growth form (Huntley 1972; Frenot *et al.* 1993) (cushion growth forms are considered to reduce wind stress and heat and moisture loss: Ashton & Gill 1965; Huntley 1971; Körner 2003) (Plate 10.1a). Individual plants, or cushions, have a central taproot, from which stems arise radially and branch dichotomously (Frenot *et al.* 1993). The plant's root system is well developed with extensive shallow, horizontal roots and shorter sub-vertical roots. The latter root type only produces rootlets in fine-textured soil caps and enables the plant to extract efficiently, patchily-distributed soil nutrients (Frenot *et al.* 1998). Leaves of the plant are small, tough and lobed, with petioles that form a sheath around the stem, and the plant surface is hard and compact, with the leaves tightly packed and stems generally growing close together (Orchard 1989) (Plate 10.1a, d).

On Marion Island, *A. selago* is found in a wide range of plant communities, and may take the form of small plants interspersed amongst dominant grasses, to fairly regularly dispersed, isolated cushions in fellfield habitat (Gremmen 1981) (Plate 10.1 b, c). Although *A. selago* occupies as little as 10% of the surface area of the habitat even where it is dominant (Barendse & Chown 2001), it is a conspicuous component of the vegetation (Gremmen 1981), and one of only six species that contribute significantly to the islands' standing crop (Smith 1978a). Indeed, *A. selago* is considered a keystone species on Marion Island for several reasons. It is ubiquitous (Huntley 1972; Smith *et al.* 2001) and has the greatest altitudinal range of any vascular plant on the island (from sea-level to 840 m a.s.l.). In fellfield habitat it is the dominant vascular species, where it occurs in virtual monocultures interspersed with the cryptogam-dominated epilithic biotope (Huntley 1972; Frenot *et al.* 1993). It is a pioneer and plays an important role in succession (Scott 1985; Frenot *et al.* 1998), as it colonizes loose scoriaceous slopes, recent lava flows and the forelands of retreating glaciers (Huntley 1972; Frenot *et al.* 1998). Indeed, it is strongly associated with geomorphological processes, such as terrace formation and soil accumulation in fellfield landscapes (see e.g. Selkirk 1998; Boelhouwers *et al.* 2000). Cushions add significantly to the microhabitat heterogeneity of fellfield. For example, the species retains senescent leaves that decompose to form a rich, moist, humus-like collection of organic material inside the plant (Huntley 1971). This trait, in common with cushion plants elsewhere, enables individuals to recycle their own nutrients, leading to a local accumulation of nutrients in otherwise poor soils (Nuñez *et al.* 1999; Körner 2003; le Roux & McGeoch 2004). Cushion plants (including South American *Azorella* species) have also been shown to alter local soil moisture and temperature (Cavieres *et al.* 1998; Cavieres *et al.* 2002; Arroyo *et al.* 2003).

In addition to its interaction with the abiotic environment, *A. selago* increases heterogeneity and patchiness in fellfield habitats by hosting diverse epiphyte (Huntley 1972; Brancaleoni *et al.* 2003) and invertebrate communities (Barendse & Chown 2001; Hugo *et al.* 2004). As many as 20 vascular, and at least 17 non-vascular species have been recorded growing epiphytically on *A. selago* (Table 10.1) (le Roux 2004). *Azorella selago* also facilitates the growth of other vascular plants at higher altitudes, where some species are limited to growing epiphytically on cushions (Huntley 1972; see also Alliende & Hoffmann 1985; Nuñez *et al.* 1999; Cavieres *et al.* 2002 for other cushion plant species). In addition, nine of Marion Island's 16 springtails, and 26 of its known 69 mite species are found in association with *A. selago* (Table 10.2, Chown *et al.* 2002), and the plant is thought to have acted as a refugium for arthropods during Neogene glaciations (Barendse *et al.* 2002). Microarthropod (springtail and mite) density in cushions greatly exceeds that of surrounding soils (Barendse & Chown 2001).

Table 10.1 Epiphytic plant species recorded on *Azorella selago* on Marion Island (from Huntley 1971, 1972; le Roux 2004; M.J. Nyakatya & Z. Buwa, personal observation). The list of epiphytic bryophytes and lichens remains incomplete. * Introduced species.

	Species	Family
Vascular plants	*Acaena magellanica*	Rosaceae
	Agrostis magellanica	Poaceae
	Blechnum penna-marina	Polypodiaceae
	Callitriche antarctica	Callitrichaceae
	*Cerastium fontanum**	Caryophyllaceae
	Colobanthus kerguelensis	Caryophyllaceae
	Cotula plumosa	Asteraceae
	Crassula moschata	Crassulaceae
	Hymenophyllum peltatum	Hymenophyllaceae
	Juncus scheuchzerioides	Juncaceae
	Lycopodium magellanicum	Lycopodiaceae
	Lycopodium saururus	Lycopodiaceae
	Montia fontana	Portulaceae
	*Poa annua**	Poaceae
	Poa cookii	Poaceae
	*Poa pratensis**	Poaceae
	Pringlea antiscorbutica	Brassicaceae
	Ranunculus biternatus	Ranunculaceae
	*Sagina procumbens**	Caryophyllaceae
	Uncinia compacta	Cyperaceae
Bryophytes: Mosses	*Andreaea sp.*	Andreaeaceae
	Blindia magellanica (as B. coutecta)	Seligeriaceae
	Brachythecium rutabulum	Brachytheciaceae
	Breutelia integrifolia	Bartramiaceae
	Campylopus subnitens	Dicranaceae
	Ditrichum sp. (D. conicum?)	Ditrichaceae
	Ptychomnion densifolium (as P. ringianum)	Ptychomniaceae
	Racomitrium sp. (R. lanuginosum ?)	Grimmiaceae
	Sanionia uncinata	Amblystegiaceae
Bryophytes: Liverworts	*Blepharidophyllum densifolium*	Scapaniaceae
	Clasmatocolea humilis	Geocalycaceae
	Jamesoniella sp. (J. colorata ?)	Lophoziaceae
	Jensenia pisicolor	Pallaviciniaceae
	Lophocolea randii	Geocalycaceae
	Marchantia berteroana	Marchantiaceae
Lichen	*Cladonia* sp.	Cladoniaceae

Table 10.2 Invertebrate species collected from *Azorella selago* cushions (Barendse & Chown 2001; Hugo *et al.* 2004). Abbreviations (Abrev.) used elsewhere in the chapter.

Acari	Abrev.	Collembola	Abrev.
Acari sp1	Aca1	**Arthropleona**	
Acari sp3	Aca3	*Tullbergia bisetosa*	Tbis
Acari sp4	Aca4	*Isomotoma marionensis*	Imar
Mesostigmata		*Cryptopygus dubius*	Cdub
Rhodacaridae sp.	Rhod	*Cryptopygus antarcticus travei*	Cant
Dendrolaelaps sp.	Dend	*Cryptopygus caecus*	Ccea
Cilibidae sp.	Cili	*Isotomurus cf. palustris*	Ipal
Prostigmata		**Symphypleona**	
Prostigmata sp1		*Megalothorax* sp.	Mega
Nanorchestes sp.	Nano	*Sminthurinus granulosus*	Sgra
Eupodes minutus	Emin	*Sminthurinus tuberculatus*	Stub
Rhagidia sp.	Rhag		
Ereynetes macquariensis	Emac	**Psocoptera**	
Tydeus sp.	Tyde	*Antarctopsocus jeanneli*	
Bdellodes sp.	Bdel	**Thysanoptera**	
Eryngiopus sp.	Eryn	*Apterothrips apteris*	
Balaustium sp.		**Hemiptera**	
Pygmephoridae sp.		Aphididae	
Cryptostigmata		**Coleoptera**	
Oribatidae sp1	Orib	*Ectemnorhinus* spp.	
Liochthonius australis	Laus	*Bothrometopus parvulus*	
Maquarioppia striata	Mstri	*Bothrometopus elongatus*	
Austroppia crozetensis	Acro	*Halmaeusa atriceps*	
Halozetes fulvus	Hful	**Diptera**	
Podocarus auberti		*Limnophyes minimus*	
Dometorina marionensis	Dmar	**Lepidoptera**	
Magellozetes antarcticus		*Pringleophaga marioni*	
Astigmata		*Embryonopsis halticella*	
Schwiebea talpa	Stal	**Araneae**	
Algophagus spp.	Alg1,2	*Prinerigone vagans*	
		Earthworms	
		Enchytraeid worms	

Spatial variation in *A. selago* thus has a considerable effect on the structure, composition and functioning of fellfield ecosystems, that constitute approximately half of Marion Island's surface area (Smith *et al.* 2001; Gremmen & Smith 2008). Therefore, documenting and understanding this variation is important, and increasingly so given the rapid rates of environmental change on the Prince Edward Islands (Bergstrom & Chown 1999; Chown *et al.* 2001; Smith 2002; le Roux *et al.* 2005; McGeoch *et al.* 2006; le Roux & McGeoch 2008).

10.2 The plant

At first glance, the surfaces of *A. selago* cushions appear fairly homogenous. However, closer inspection reveals these surfaces to be complex, with stems interspersed with epiphytes and patches of dead and decaying plant tissue (Plate 10.1 a, d). Along with vertical changes in cushion structure, this within-plant variation in morphology and tissue quality has several implications, including an effect on the plant's ability to survive strong winds and freezing (Ashton & Gill 1965; Cavieres *et al.* 2002; le Roux 2004). For example, the hemispherical shape so characteristic of *A. selago*, not uncommonly degrades to form crescents in older cushions, with the crescent generally advancing towards the dominant wind (Huntley 1972). Indeed, plant microclimate varies with aspect (i.e. side of the cushion), and temperatures tend to be warmest on the northern side (Fig. 10.1a), exposed to the highest solar radiation and warm, north-westerly winds (Schulze 1971). Cushion aspects are also exposed to different levels of frost-heave activity, as evidenced by differential erosion and sorting on the windward and leeward sides (J.C. Boelhouwers, personal communication). Microclimatic conditions vary not only with aspect, but also with depth inside the cushion. Temperatures inside the plant are significantly buffered, with higher minima and lower maxima than ground surface temperatures (Fig. 10.2, Nyakatya 2006, see also Chown & Crafford 1992). The difference in temperature between the plant surface and 10 cm below the surface can be as high as 2.0°C on average, with the surface warmest at 15h00 in summer and the plant interior warmest at 19h00 (Fig. 10.1). By contrast, in winter, temperature inside the plant is comparatively static, whereas the plant surface warms by 2.0°C during the day (Fig. 10.1). Therefore, cushions encompass not only structural, but also microclimatic variability that is a product of wind direction, strength and moisture content, as well as exposure (Chown & Crafford 1992). Along with within-plant heterogeneity in morphology and tissue quality, cushions thus form a microcosm of potential habitats for other species.

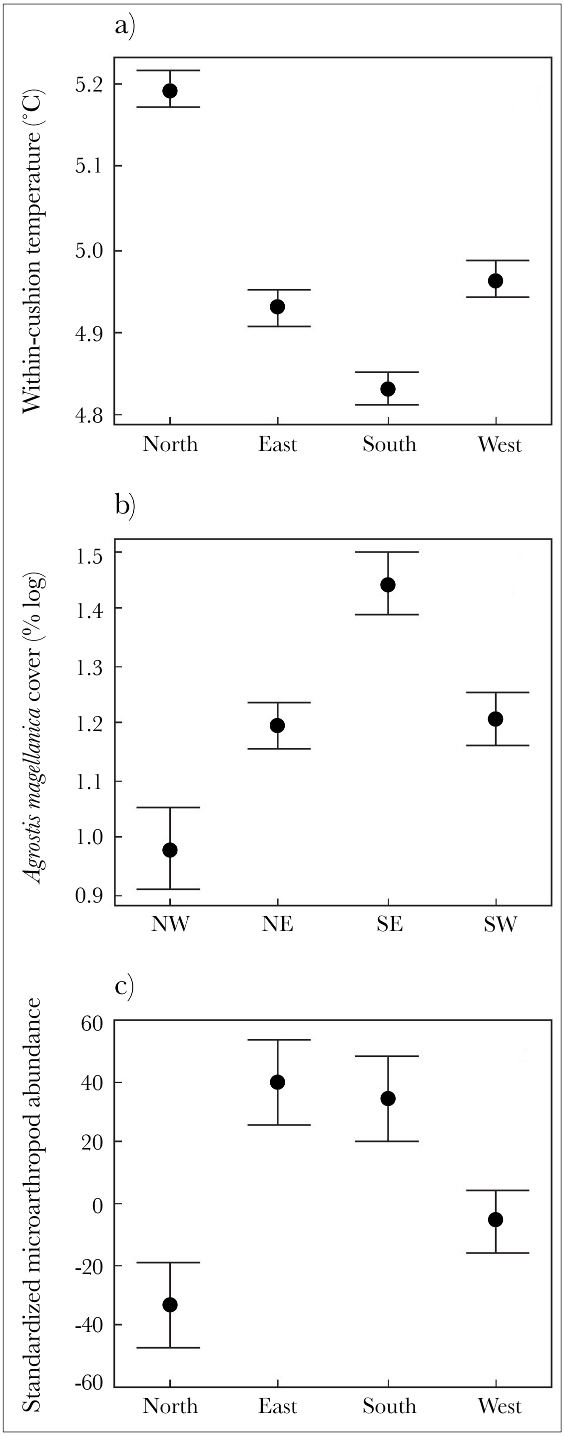


Figure 10.1 Thermal and biotic differences associated with different *Azorella selago* cushion aspects on Skua Ridge. a) Temperatures 10 mm below cushion surface, b) cover of epiphytic *Agrostis magellanica*, c) abundance of microarthropods (data from Hugo *et al.* 2004).

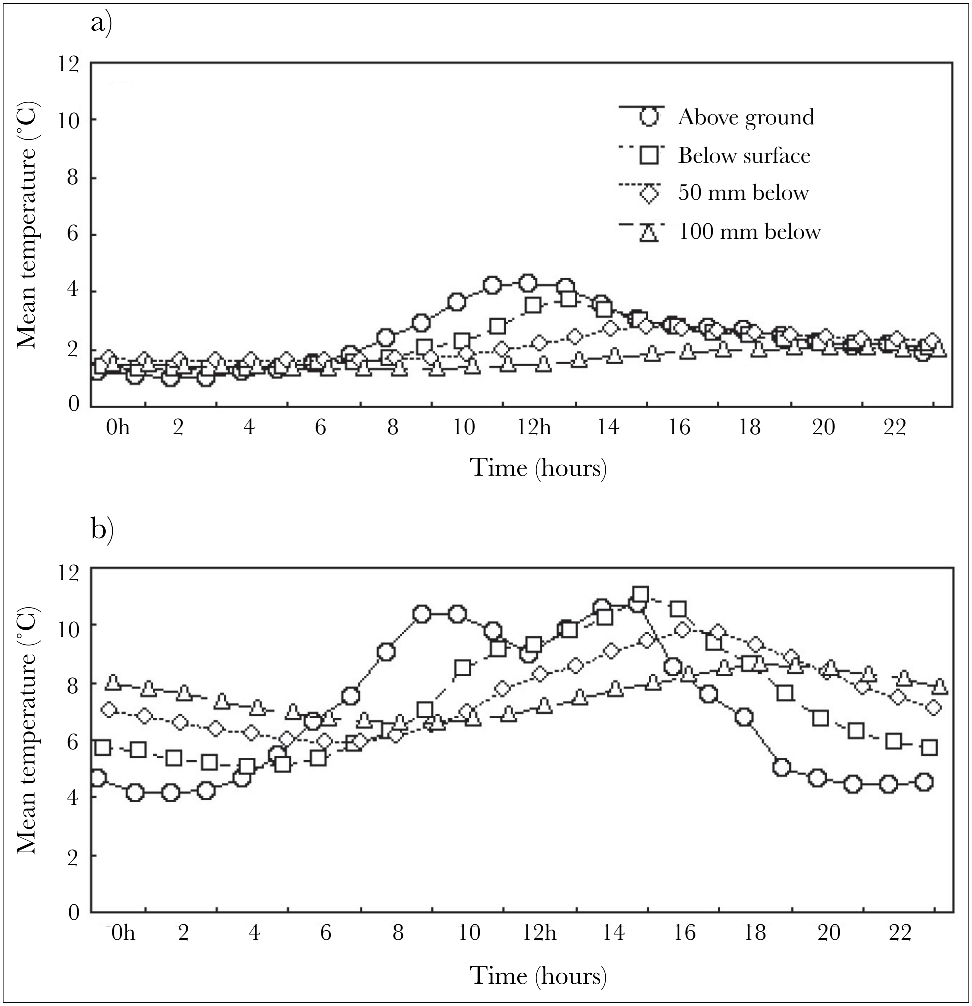


Figure 10.2 Mean hourly temperatures (n = 10 days and 4 cushions) recorded inside and adjacent to *Azorella selago* plants in a) winter and b) summer (error bars removed for clarity). Positions: ground surface, just beneath plant surface, and 50 mm and 100 mm beneath plant surface.

Within-plant temperature profiles are associated with significant differences in the distribution of both epiphytes and microarthropods. For example, on Skua Ridge (Table 10.3), the highest abundance of the dominant epiphyte, *Agrostis magellanica*, occurs on the sheltered south-east quarter of the plant (Fig. 10.1b). At the same site, mites and springtails are most abundant on the cooler, south-easterly side (Fig. 10.1c). The magnitude of this abundance difference in this case is pronounced, and amounts to a difference of 13 000 to 21 000 individuals m^{-2} (Hugo *et al.* 2004). This is a remarkable difference over such a small spatial scale, and suggests a distinct preference by the microarthropods for the southern sections of the cushion. However, the precise area of preference is dependent to some extent on the position of the site on the island, as a likely consequence of slope, exposure and topography (Hugo *et al.* 2004). The positive association of individuals as a consequence of a common preference for microhabitat quality is not unusual in arthropods (McGeoch & Chown 1997), and indeed species abundance distributions frequently reveal hot and cold density spots at multiple spatial scales (Gaston 2003; McGeoch & Price 2004). Within-plant microarthropod abundance may, however, also be driven by epiphyte abundance rather than temperature. Microarthropod community structure was found to differ (driven by higher abundances rather than differences in species richness) between areas of the plant with high epiphyte cover in comparison with those with no epiphytes (Hugo *et al.* 2004). However, there appears to be little difference in temperature in parts of the plant with and without epiphyte cover (Hugo *et al.* 2004). Leinaas *et al.* (unpublished data) also found evidence of vertical stratification of microarthropods in *A. selago*. Total and species-specific abundances in the springtails declined over a 8 cm descent into the plant, and the lower strata were dominated by eudaphic species (Leinaas *et al.*, unpublished data), similar to that detected in moss turfs in Antarctica (Usher & Booth 1984). Therefore, significant within-plant variation in microarthropod abundance occurs, that is both a consequence of epiphyte load and apparently of spatial variation in abiotic factors within cushions. Such local scale variation has been documented previously for communities in the Arctic (Coulson *et al.* 2003), and moss turves in the Antarctic (Usher & Booth 1984; Usher & Booth 1986).

At this fine scale, patterns are thus dominated by species responses to microclimate and resource quality, and the interspecific interactions that occur as a result. *Azorella selago* provides a favourable, yet in itself heterogeneous microhabitat for epiphytes, springtails and mites, with *A. magellanica* adding a level of heterogeneity for the microarthropods.

10.3 The landscape

One cannot fail to be struck by the uniform expanses of grey and black lava fellfield encountered when rising to 150 m a.s.l. and above on the island (Plate 10.1b, c). *Azorella selago* cushions dot the landscape like a chequerboard, each plant an island in a sea of cryptogam-covered lava. The physical structure of such a landscape cries out for island-biogeographic and metapopulation interpretation (see also Tepedino & Stanton 1976; Hertzberg 1997). The questions that arise, therefore, are what is the extent of variation in cushion morphology and spatial structure across stands of plants, and to what extent does this explain patterns of epiphyte and microarthropod community structure?

As outlined in the previous section, variation in microtopography and aspect alter the abiotic conditions to which cushions are exposed, which in turn to some extent determines between-plant variation in growth form and compactness (see also Jumpponen *et al.* 1999; Sage & Sage 2002; Kleier & Rundel 2004). Cushion size, however, appears to have only a weak effect on cushion temperature, supporting the proposition that the prostrate growth form reduces temperature variability (Hugo *et al.* 2004; Nyakatya & McGeoch

2008). Shading results in etiolation, loss of compactness and larger leaves, typical of plant responses to shading (Plate 10.1e; see also Bergstrom *et al.* 1997; le Roux *et al.* 2005). However, for *Azorella*, where cushion compactness is considered to be an adaptation to harsh environmental conditions (Huntley 1972), this effect may alter cushion longevity (although this has to date not been determined). While hemispherical cushions are common, and perhaps most conspicuous, several other cushion shape categories may be distinguished across the landscape, i.e. crescent (e.g. Huntley 1972), elongated (see vegetation-banked terraces: Selkirk 1998; Holness 2003), semicircular and irregular. In addition, on some parts of the island, often in association with seepages and drainages, cushions coalesce to form extensive mats (Gremmen 1981) (e.g. at the eastern base of First Red Hill, and Watertunnel Valley (Meiklejohn, personal communication).

Table 10.3 Stands of *Azorella selago* in xeric fellfield on Marion Island that are being used for long-term monitoring of population changes in this species, and the arthropods and epiphytes associated with it. Results presented in this chapter were obtained largely from data collected from these stands. Each stand is demarcated with four marker poles and numbered metal tags in some *A. selago* cushions.

Plot	Position 46°South	Position 37°East	Altitude (m a.s.l.)	Aspect	Lava type	Cushion density (m^{-2})	Closest landmark
Tafelberg							
Low	52.749’	49.651’	176	Flat	Black	1.100	Junior’s Kop
Middle	53.276’	48.125’	375	Flat	Grey	0.137	Tafelberg
High	53.670’	47.293’	588	South	Black	0.260	First Red Hill
Stony Ridge							
Low	54.917’	51.435’	176	Flat	Grey	0.901	Stony Ridge
Middle	54.608’	49.062’	380	Flat	Grey	0.299	Tate’s Hill
High	54.059’	47.978’	620	South	Black	0.146	Halfway Kop
Swartkop							
Low	55.789’	36.481’	216	N/East	Black	1.081	Skuinskop
Middle	55.818’	37.225’	415	Flat	Black	1.188	Stevje
High	56.195’	37.520’	575	Flat	Black	0.493	Bakkerkop
Mixed Pickle							
Low	52.574’	38.539’	222	N/East	Black	1.551	Neville
Middle	53.224’	38.858’	375	Flat	Black	1.124	Halfmaankop
High	53.839’	39.268’	600	Flat	Black	0.368	Saalrug
Skua Ridge							
Low	52.033’	50.283’	100	Flat	Grey	-	Skua Ridge

Cushion densities on the island generally range from 0.13-1.55 m^2 (Table 10.3). In some stands, cushion size has been found to be spatially structured with, for example, cushions up to approximately 8.0 m apart significantly similar in size (Fig. 10.3). The only significant explanatory variables found to date for cushion size across stands are the size and distance of nearest neighbouring cushions. In the stands examined, cushions were neighboured by individuals of a similar size (i.e. forming patches of similar size cushions), but larger cushions were always further apart than smaller ones (le Roux & McGeoch 2004). This suggests regular competitive exclusion of individuals in stands; a process thought to be important in this species due to its extensive root system (Frenot *et al.* 1998). Therefore, it appears that while cushion height is constrained by wind and exposure (le Roux 2004), cushion diameter may be constrained by intraspecific competition.

The distribution of *A. selago* plant size and growth rate on the island is right-skewed, with the majority of plants ranging from 0.40 to 1.15 m in diameter (Fig. 10.4). The growth rate of plants ranges between 0.7 to 21.0 mm per year (le Roux & McGeoch 2004). Growth rate is not related to plant height, and there is no clear relationship between variability in growth rate and plant size (le Roux & McGeoch 2004). Plant size and growth rate also differ significantly between sites on the island (le Roux 2004; le Roux & McGeoch 2004; Nyakatya 2006) (see following section). Using the phytometric model developed by Frenot *et al.* (1993), age estimates for *A. selago* were also found to be right-skewed (le Roux & McGeoch 2004) (Fig. 10.4). Mean plant ages range from 26 to 41 years, and the oldest plants sampled ranged between 55 and 96 years (le Roux & McGeoch 2004) (Fig. 10.4).

Cushion size and age on the island are only loosely related, and appear to be more a function of local stand characteristics than environmental gradients (le Roux & McGeoch 2004). Indeed, *Azorella* is thought to have infrequent, periodic establishment pulses, associated with periods or patches of mild and infrequent soil freezing, combined with suitable substrate conditions (Wickens 1995; Kleier & Rundel 2004; le Roux 2004). While a large proportion of the variability in cushion characteristics could not be explained (le Roux 2004), variation in soil moisture and nutrients, wind exposure and snow cover due to topographical and microclimatic variation are known to be important determinants of plant performance in high altitude and latitude communities (Frenot *et al.* 1993; Callaghan & Carlsson 1997; Jumpponen *et al.* 1999; Körner 2003). The frequency of cushions < 0.29 m in diameter on the island is significantly lower than cushions in intermediate size classes (Fig. 10.3), suggesting not only infrequent establishment, or high juvenile mortality, but possibly spatially-patchy recruitment sites. Episodic establishment is characteristic of many polar and sub-polar species (including *Azorella* species), and it is likely that *A. selago* has pulsed recruitment in response to irregular and/or unpredictable conditions, probably including mild and infrequent soil freezing, combined with suitable substrate conditions (Wickens 1995; Kleier &

Rundell 2004; le Roux 2004). Thus, in terms of cushion morphology, sufficient variability apparently exists at the landscape scale to potentially generate spatial patterns in diversity and community structure amongst the cushion inhabitants.

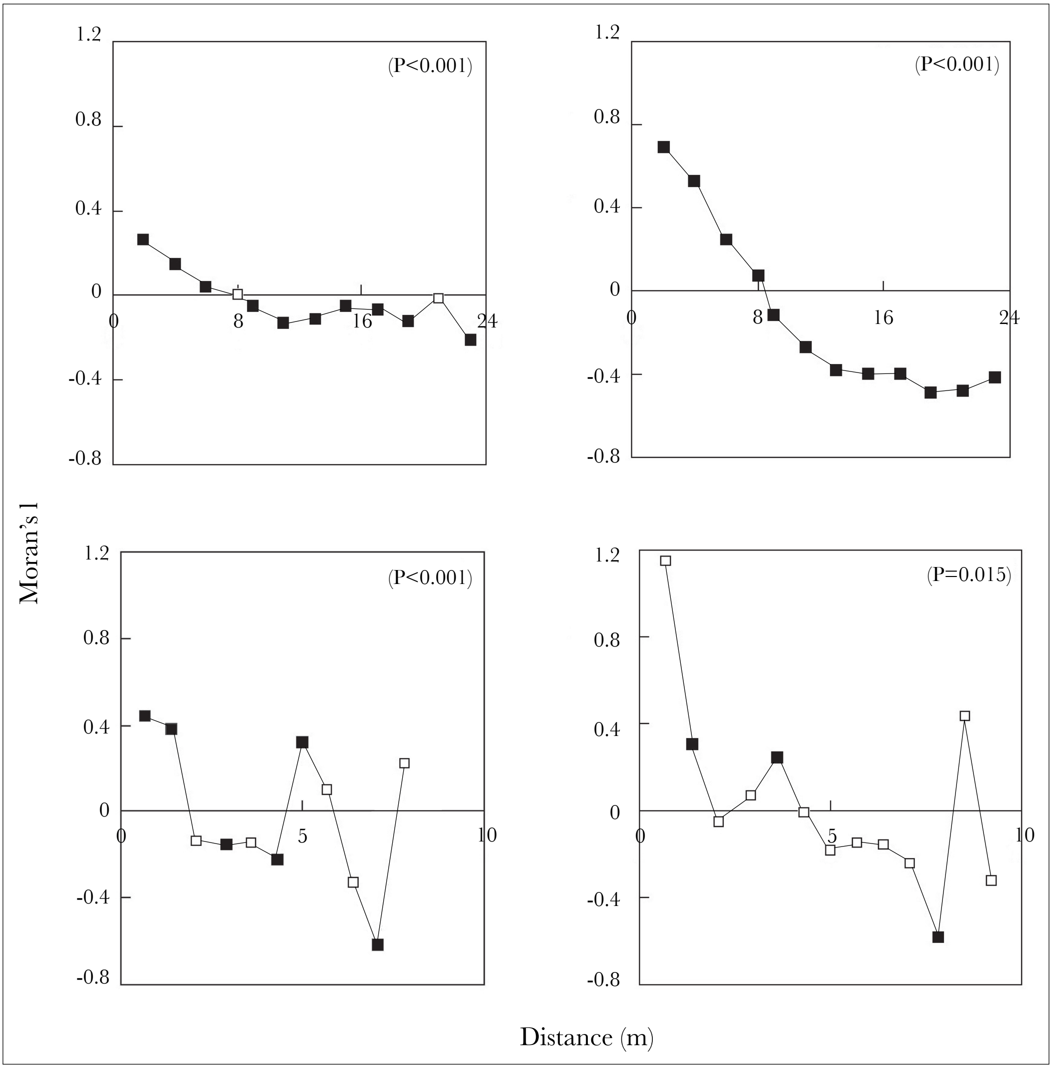


Figure 10.3 Correlograms of Moran's I-values, depicting spatial structure in the a) maximum diameter of *Azorella selago* cushions, b) the abundance of epiphytic *Agrostis magellanica* on cushions, c) abundances of the cushion-dwelling mite, *Dendrolaelaps* sp., and d) springtail, *Cryptopygus dubius*, at sites near Mixed Pickle Cove. Bonferoni-corrected overall significance of correlograms provided in frames. Significant, positive I-values denote positive spatial autocorrelation in that distance class (i.e. values of the variable in question are significantly more similar to each other than expected by chance over that distance). Filled symbols indicate significant spatial autocorrelation in that distance class. Note differences in distance scales between a, b and c, d.

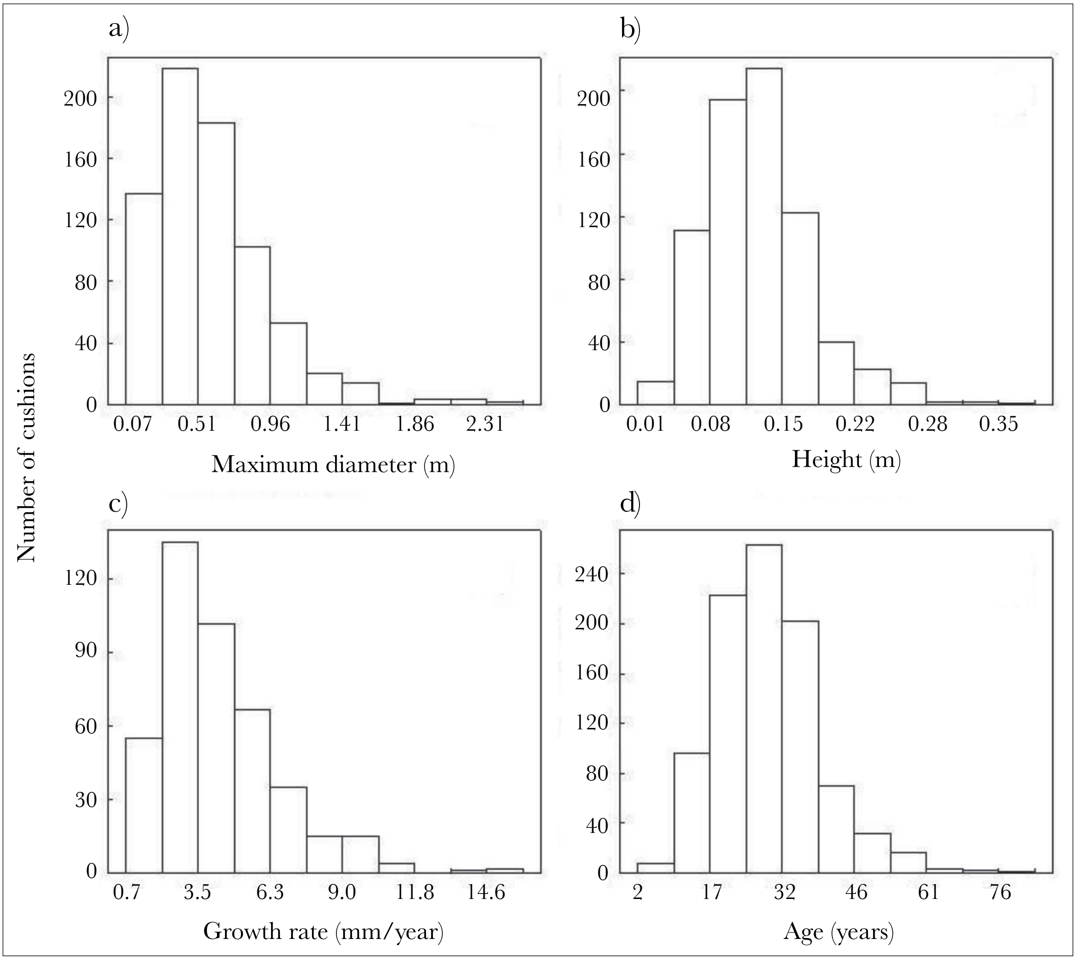


Figure 10.4 Frequency distributions of *Azorella selago* cushion a) maximum diameter (n = 738), b) height (n = 738), c) growth rate (n = 527) and d) estimated cushion age (n = 738) (with permission from le Roux & McGeoch 2004).

Several plant species are found growing epiphytically (including vascular and non-vascular species) on *A. selago* across the island (Table 10.1). By far the most dominant of these (in terms of biomass on cushions) is the grass *A. magellanica*. Nonetheless, most cushions on the island are host to a range of epiphyte species, particularly mosses (Fig 10.5, Table 10.1). Vascular plants, such as *A. magellanica* and *Ranunculus biternatus*, and other non-vascular species such as liverworts and lichens are commonly found on cushions. Indeed, the strongest spatial structure found across plants within a stand was in the dominant epiphyte (Fig. 10.3b), suggesting seed dispersal away from established grass clumps onto adjacent cushions generates patchiness in the distribution of this species across stands of *A. selago* (at least at medium to high altitudes where *A.*

magellanica is less common off cushions). Larger cushions also tend to support both more individual grasses, as well as total coverage by this grass (le Roux & McGeoch 2004).

Virtually all cushions are occupied by at least four springtail and one mite species, whereas the prevalence of other members of the microarthropod assemblage associated with *A. selago* is lower (Fig. 10.5). However, surprisingly little spatial or deterministic structure in the microarthropod community is apparent at the landscape scale (Hugo *et al.* 2004), and the abundances of only one mite and one springtail species are spatially autocorrelated, inconsistently so, across stands (Fig. 10.3c, d). No spatial structure is apparent in either total abundance or richness across any of 13 stands (Table 10.3) examined on the island. There is some evidence that cushions with large proportions of dead and decaying stem and leaf material are associated with greater microarthropod abundances (Hugo 2006). Nonetheless, cushion size and isolation have little effect on microarthropod species richness, abundance and, consequently, community structure (Hugo *et al.* 2004; Hugo 2006). These findings are comparable to studies on springtails in tussock patches in the Arctic, where total vegetation cover (as a percentage of the total area) and patch quality are more important predictors than patch size and isolation (Hertzberg 1997; Ims *et al.* 2004). However, previous studies (Barendse & Chown 2001; Barendse *et al.* 2002) have shown that the same species of microarthropods occur both in the cushions and in the epilithic matrix (albeit at far lower densities) within which they are embedded. Elsewhere (short-grass prairie), larger cushions (species from the Fabaceae and Polemoniaceae) have been found to support more species and individuals in total (Tepedino & Stanton 1976), but here there is no difference per unit area of cushions of different sizes. These results are therefore consistent with the view that microarthropods move freely between cushions and the surrounding matrix in fellfield habitat. The generally similar temperatures and moisture contents of different-sized cushions are also consistent with this view.

At the scale of the landscape, therefore, patterns in *A. selago* variability appear to be driven largely by historical events (i.e. plant recruitment), intraspecific competition that structures cushion size and dispersion, and microtopography that alters cushion exposure to wind and light. While most plants are host to epiphytes, the size and distribution of cushions is a significant determinant of the distribution of *A. magellanica* in mid-altitude fellfield habitat. By contrast, cushion characteristics appear to play comparatively little role in structuring the microarthropod assemblage at this scale.

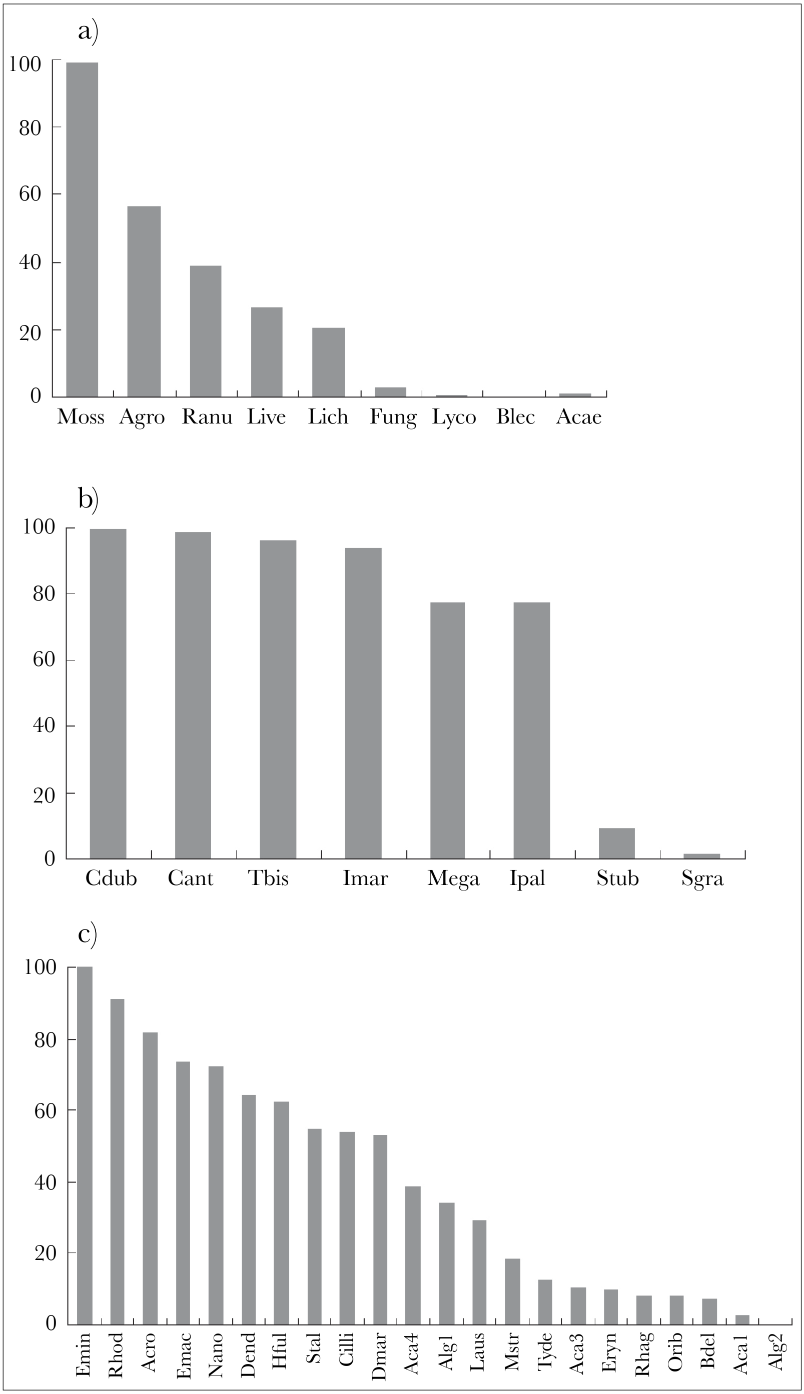


Figure 10.5 Percentage of sampled cushions occupied by a) epiphyte species ($n = 600$), b) springtail and c) mite species ($n = 431$) (Hugo 2006; Nyakatya 2006). Moss = mosses; Agro = *Agrostis*; Ranu = *Ranunculus*; Live = liverworts; Lich = lichens; Fung = fungi; Lyco = *Lycopodium*; Blec = *Blechnum*; Acae = *Acaena*. See Table 10.2 for arthropod species abbreviations.

10.4 The island

Across Marion Island, spatial variation in *A. selago*, and its inhabitants, is likely to be driven by island-wide patterns of climatic and geomorphological variation, as well as interspecific competition at lower, more plant-species rich altitudes. Island-scale abiotic patterns include strong altitude-linked declines in temperature and solar radiation with increases in wind speed, precipitation and freeze-thaw frequency (Fig. 10.6). However, soils at higher altitudes are poorly developed, and mineral-poor, with low water retention capacity (Smith 1978b). Furthermore, these abiotic gradients are not necessarily equally pronounced on the eastern and western sides of the island. The western side of the island is directly exposed to the dominant north-westerly winds, and is more frequently cloudy than the eastern side (Schulze 1971). We have shown, for example, that *A. selago* is exposed to greater temperature variation, and that summers are significantly warmer and winters cooler on the eastern than the western side of the island (Fig. 10.7a, Nyakatya & McGeoch 2008). The western side of the island thus appears to be more temperate, whereas the east is more extreme.

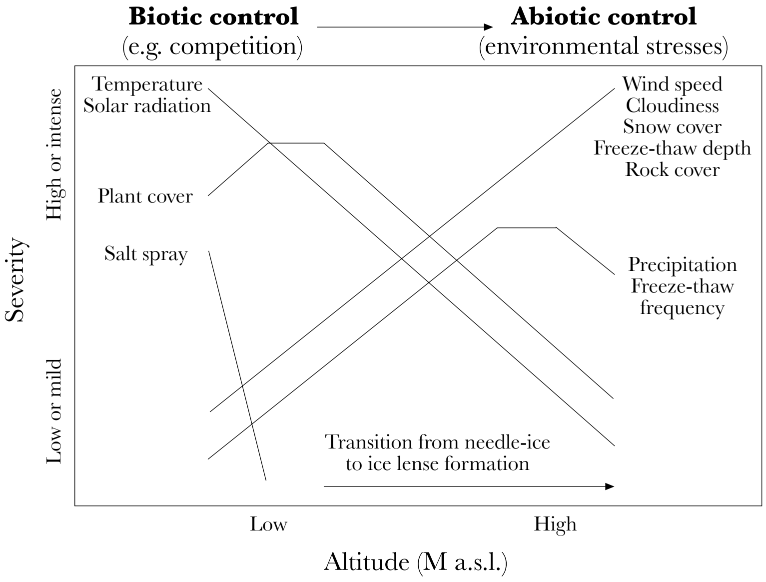


Figure 10.6 Idealized representation of altitudinal gradients in abiotic variables and plant cover on Marion Island (based on Huntley 1971; Schulze 1971; Blake 1996; Smith *et al.* 2001; Boelhouwers 2003; Holness 2003; J.A. Deere, unpublished data; Nyakatya 2006) (from le Roux 2004).

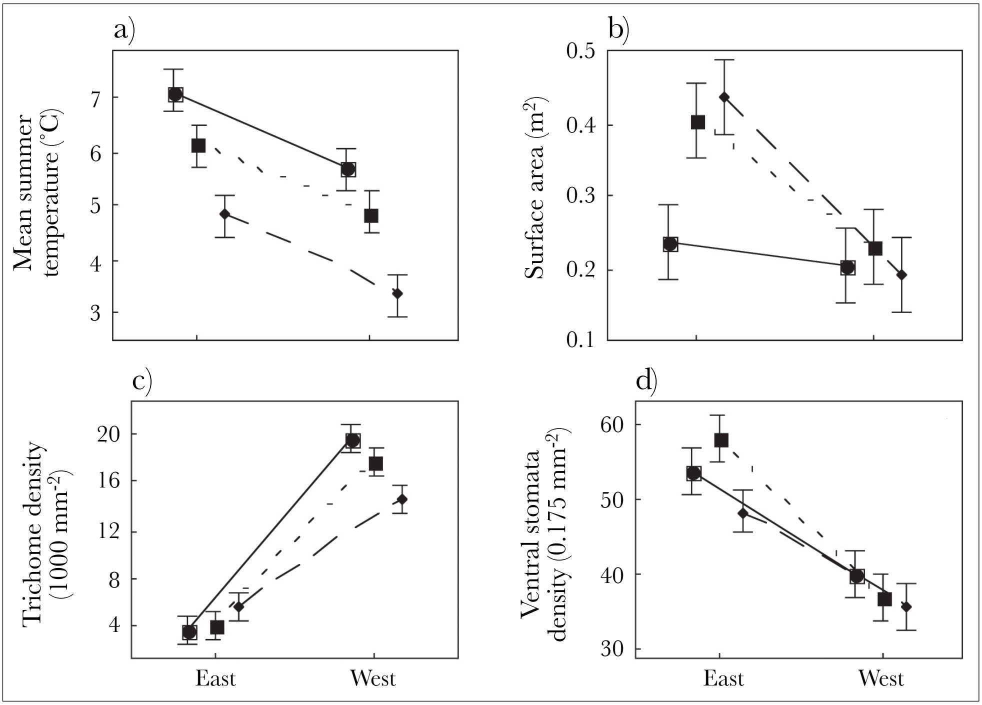


Figure 10.7 General linear model interaction plots showing mean (± s.e.) summer temperature a), cushion surface area b), trichome density c) and stomatal density d) recorded across altitudes and on different sides of Marion Island (see Table 10.3 for stand details). Diamonds (600 m a.s.l.), squares (380 m a.s.l.), circles (200 m a.s.l.).

Fellfield habitat occurs on both black and grey lava substrate on the island, and although the older grey lava stands have better developed soils, they are more nutrient poor than the geologically younger, black lava substrates (Smith 1977, 1978b). Indeed, substrate type does appear to have an effect on cushion size and density, with cushions significantly smaller and present in higher densities on black than on grey lava (Nyakatya 2006). In addition, *A. magellanica* densities tend to be higher on *A. selago* in grey than in black lava fellfield (Nyakatya 2006). This suggests that *A. selago* size and establishment patterns are to some extent related to soil structure and nutrient availability.

Azorella selago is found from sea level to approximately 750 m a.s.l. (although isolated individuals have been observed at higher elevations), and several altitudinal and aspect-related morphological and phenological trends are apparent in the species. For example, cushions at low altitudes undergo autumnal senescence earlier than high altitude plants, as do cushions on the eastern side of the island (Nyakatya 2006). This suggests a possible degree-day (time taken to accumulate a number of heat energy units) threshold for autumnal senescence, with a more rapid accumulation of heat energy units over summer at low altitudes and in the east than the converse. While *A. selago* cushions on the eastern side of the island tend to be larger than those on the west, cushion size is inconsistently related to altitude (Fig. 10.7b). Growth rate does not appear to be related to altitude, and surprisingly also not to island side (Nyakatya 2006). By contrast, leaf characteristics show clear altitudinal and aspect differences. Leaves are larger on the east and towards mid- and high altitudes, whereas trichome density is highest on the western side of the island and at higher altitudes (Fig. 10.7c) (le Roux 2004; Nyakatya 2006). Stomatal density is also highest in the east, decreasing towards higher altitudes (Fig. 10.7d). Therefore, while phenology and leaf characteristics appear to be comparatively plastic, cushion size and growth rate respond less strongly to island-scale environmental variation, with local site characteristics apparently more important.

Patterns of epiphyte abundance and cover are also strongly related to altitude (Fig. 10.8). The abundance and proportional cover of *Agrostis magellanica* peaks at mid-altitudes, although maximum abundance and cover (as well as the altitude at which this was attained) differs between gradients on different parts of the island (le Roux 2004). A mid-elevation abundance peak in this species has also been recorded from Macquarie Island (Bergstrom *et al.* 1997). The proportion of cushion surface covered by other vascular epiphyte species (i.e. excluding *A. magellanica*) is also related to altitude, and declines strongly with increasing elevation (Fig. 10.8). Other vascular epiphytes include mainly *Blechnum penna-marina*, *Acaena magellanica* and *Cotula plumosa*, that together cover on average 2.6% of cushion surfaces (with a maximum cover of nearly 50% on some cushions). Non-vascular epiphyte species richness peaks at higher altitudes (on average > 350 m a.s.l.) and declines rapidly towards sea level (Fig. 10.8). By contrast, vascular epiphyte species richness is highest at sea-level, declining gradually with increasing altitude. On Marion Island, epiphyte species richness thus peaks at mid-altitudes. Epiphytes also appear to be more frequent on cushions on the eastern than western side of the island (Nyakatya 2006). This form of taxon and locality-specific richness and abundance difference has been documented across other high latitude, altitudinal gradients (Andrew *et al.* 2003).

Of all vascular plant species on the Prince Edward Islands, *A. selago* supports amongst the highest diversity of microarthropods (Hugo *et al.* 2006). A total of 22 mite species and nine springtail species have been recorded in *A. selago* cushions from across the island, with the majority of these species having island-wide distributions (Hugo *et al.* 2006) (Table 10.2). However, in some cases contrary to findings at the plant-scale, neither cushion surface area, plant height, percentage dead tissue or percentage grass cover appear to explain observed patterns in species richness or abundance at the island scale. Nonetheless, the microarthropods do respond to both altitude and position on the island. The difference between the eastern and western sides of the island are generally more marked than those across altitude (Fig. 10.9, Hugo 2006). Mean abundance and richness of microarthropods is significantly higher in cushions on the west, with a weak, yet significant decline towards higher altitudes (Fig. 10.9, Hugo 2006). While these general patterns are clear, the responses of springtails and mites are somewhat different. The abundance of virtually all springtail species are uniformly highest at low to mid altitudes on the western side of the island, whereas the responses of individual mite species are far more heterogeneous (Hugo 2006). The abundances of some mite species peak in the east and some even towards high, rather than low altitudes (Hugo 2006). The abundances of the introduced springtail, *Isotomurus cf. palustris*, and mite, Cillibidae sp., are also higher on the west than the east. Nonetheless, the richness and abundance of introduced species in the *Azorella* microarthropod community is consistently low, and these are the only two recorded in any significant abundance in this community (see Chown *et al.* 2002

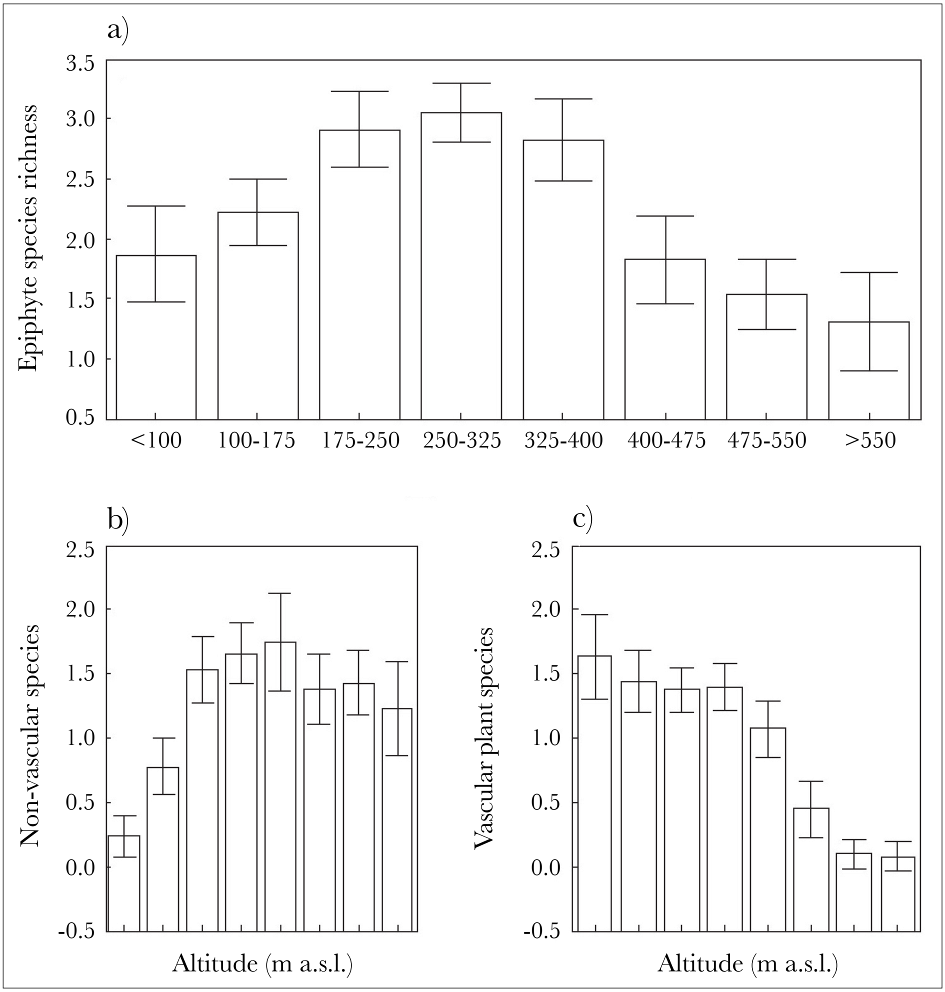


Figure 10.8 Altitudinal variation in the species richness (mean ± s.e.) of a) all epiphytes, b) non-vascular epiphytes, and c) vascular epiphytes on *Azorella selago* cushions (le Roux 2004).

for list of indigenous and invasive species). The relative abundances of the dominant species in the community do not change significantly across altitude, although there are some rank abundance changes amongst the less abundant mite and springtail species. *Eupodes minutus* dominates the mite community by at least 75% in all cases (Hugo 2006). Generally, the springtail *Cryptopygus dubius* prefers higher altitudes, whereas *Isomotoma marionensis* is dominant at mid-altitudes. In the mite community *Austroppia crozetensis* appears to prefer lower altitudes, whereas *Schwiebea talpa* prefers higher altitudes. By contrast, the rank abundance of springtail species is clearly different between the eastern and western sides of the island, with *I. marionensis* replacing *C. dubius* as the dominant species on the western side (Hugo 2006).

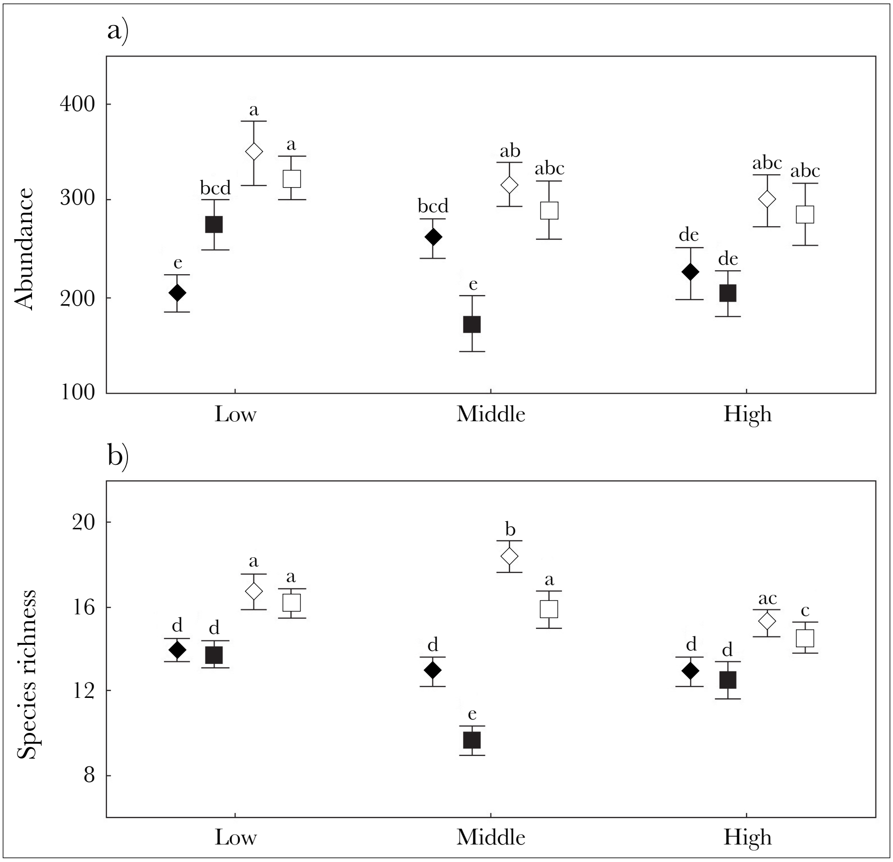


Figure 10.9 Microarthropod abundance (a) and species richness (b) per core sample across 12 stands (see Table 10.3) at low, medium and high altitudes on Marion Island. Closed symbols = east and open = west of island.

Spatial variability in *A. selago* and its epiphyte and arthropod inhabitants across Marion Island is therefore driven at least partly by island-side and altitude-related climatic differences, as well as by differences in grey and black lava fellfield substrates. Interestingly, many of the plant variables responded similarly, with contrasts between high altitude-west and low altitude-east sites. This raises the question of what abiotic environmental conditions high altitudes and the western side of the island share? Cloudy conditions are more frequent, temperature ranges lower (Nyakatya & McGeoch 2008; see also Slabber & Chown 2004) and precipitation probably higher at high altitudes and on the western side of the island, whereas the reverse is true for low altitude and eastern areas. The findings thus support the significance of abiotic drivers of terrestrial diversity patterns at intermediate and high altitudes on Marion Island.

10.5 Apparent mechanisms

The multiscale patterns in *A. selago* and its associated fauna and flora described here suggest several mechanisms important to the structure and maintenance of this system on Marion Island. In addition, some of these hypotheses are supported by work done on sub-Antarctic systems and *Azorella* species elsewhere. Nonetheless, as the hypotheses that we outline here are largely derived from mensurate rather than manipulative approaches, most remain to be tested.

First, characteristics of cushion morphology and survival correlate with microclimatic and microtopographic features. Local site conditions (such as substrate and soil properties) appear to be important for episodic seedling establishment, as well as eventual cushion size and density. The structure and dispersion patterns in *A. selago* populations across the landscape also imply intra-specific competition. Leaf morphology varies strongly with climatic differences associated with both aspect and altitude, such as radiation, precipitation and temperature fluctuations. Indeed, east-west differences emerge as a particularly important correlate with pattern in this system, often stronger than elevation. More detailed, quantitative information on meteorological differences between these two sides of the island are thus needed to explore potential mechanisms underlying these aspect-related differences.

Azorella selago contributes significantly to plant species diversity at intermediate altitudes, by hosting, particularly vascular, species that are unable to otherwise establish at these altitudes. Nonetheless, the altitudinal range of these species remains narrower than that of *A. selago*, as a likely consequence of wind and temperature (e.g. Pammenter *et al.* 1986). Indeed, wind appears to be responsible for both within- and across-cushion distribution patterns of the dominant epiphyte, *A. magellanica*. Epiphytes increase within-cushion heterogeneity and resource diversity for the microarthropod community. In some cases they also appear to alter patterns of cushion decay and longevity.

Microarthropod community patterns change along both vertical and horizontal gradients in cushion microclimate, as well as in relation to the within-cushion distribution of *A. magellanica*. Microhabitat preferences and selection by mites and springtails appears to be an important determinant of fine-scale patterns in the distribution and abundance of these taxa. The absence of landscape-level structure in the abundance or distribution of microarthropods suggests that rates of immigration and emigration exceed birth and death rates at the scale of individual cushions. Indeed, given the size and dispersal abilities of the species involved (Marshall & Chown 1995), habitat selection across a stand is unlikely. At the same time, however, cushion quality is often fairly homogeneous across stands and this is possibly also an explanation for the lack of spatial or deterministic structure in the microarthropod community at this scale. Neither island biogeography nor metapopulation dynamics offer satisfactory explanations for this system, because dispersal likely exceeds local population growth rates. However, abiotic patterns associated with both altitude and aspect do explain the island-wide richness and abundance patterns in the microarthropods. The temperate, moist, western side of the island apparently provides more suitable conditions for these species than the comparatively extreme, dry conditions on the east.

10.6 Implications of environmental change

Given the current rapid rate of environmental change on the Prince Edward Islands (as a consequence of both climate change and species invasion) (Smith & Gremmen 2001; Smith 2002; Frenot *et al.* 2005; Sumner *et al.* 2004), and observed changes elsewhere in the Antarctic (see Kennedy 1995; McGeoch 2006; le Roux & McGeoch 2007), some impact on the structure and functioning of this model system may be expected. Contrary to evidence from lower altitude communities (Chown & Gaston 2000; Gabriel *et al.* 2001; Chown *et al.* 2002; Gaston *et al.* 2003; Frenot *et al.* 2005), the system appears largely unaffected by introduced species, with only one introduced plant species (*Sagina procumbens*) commonly recorded to date on *A. selago*. Also, only two introduced microarthropods occur in *A. selago* cushions and in comparatively low numbers (see also Barendse & Chown 2001). Gabriel *et al.* (2001) showed that the introduced, warm and moist sites with high levels of organic material are preferred by the introduced springtails, whereas their presence was negligible in cold, fellfield areas. Nonetheless, given the warming trend on the Prince Edward Islands, it would be wise to monitor the presence and abundance of introduced species associated with *A. selago* and fellfield habitats.

Climate change is predicted to significantly alter patterns of primary productivity, nutrient cycling, vegetation succession and habitat structure on Marion Island (Smith & Steenkamp 1990; Smith *et al.* 2001; le Roux & McGeoch 2008). While Smith *et al.* (2001) do not predict a successional change in fellfield under continued warming and drying, mesic fellfield may become more xeric. Nonetheless, should climate change bring about an increase in the shading of cushions at low altitudes by rapidly growing vascular species (introduced or otherwise), slow-growing *A. selago* is likely to be negatively affected (le Roux 2004). The results of experimental manipulation of precipitation (Plate 1f) suggest that ongoing drying of the island will increase stem senescence and interact with wind patterns to result in a directional die back and degradation of cushions (le Roux 2004; le Roux *et al.* 2005) (Fig. 10.10a). Under current climate change trends on Marion Island, the strongest community-level predictions for the microarthropod community include a dramatic decline in abundance and biomass under reduced precipitation (McGeoch *et al.* 2006; see also Convey *et al.* 2002, 2003), although increased temperatures are predicted to affect springtail abundances positively (Coulson *et al.* 1996; Hodkinson *et al.* 1996; Convey *et al.* 2002, 2003). In the same experiment mentioned above, springtail abundance and biomass were significantly negatively affected by drying of the cushion environment (Fig. 10.10b). However, species responses are likely to be idiosyncratic, both within and across mite and springtail taxa (McGeoch *et al.* 2006). Indeed, an ongoing decline in precipitation is likely to have dramatic effects, particularly on the desiccation-sensitive springtail component of this community (McGeoch *et al.* 2006; le Roux & McGeoch 2008).

Species interactions are of course predicted to be highly sensitive to climate change, and at the same time far more complex to understand than direct effects on particular species (Sudgen 1992; McGeoch 2006). Therefore, interactions between *A. selago* as host, its epiphytes and microarthropods are likely to be altered by any direct change to one of these components. For example, while temperature amelioration may increase cushion coverage by *A. magellanica*, the decline in precipitation may curb this response (le Roux 2004). Also, the loss of microarthropods from decomposer communities has been shown to alter the composition of decomposer microflora, and to change soil quality and respiration processes (Moore *et al.* 1988; Teuben & Verhoef 1992; Taylor *et al.* 2004). This is likely to be equally true on Marion Island, because nitrogen availability is low, nutrient turnover and decomposition rates are slow, and microarthropods constitute a disproportionately large component of the decomposer community (Smith & French 1988; Smith & Steenkamp 1990; Hopkin 1997; Robinson *et al.* 2004). The complexities of such interactions, as well as the testing of mechanism underlying the multiscale patterns observed, therefore form important future research priorities for this system.

10.7 Acknowledgements

We thank C. Hänel and W. Wilkinson for their expert field assistance and dedication to the project, and D.M. Bergstrom, S.L. Chown, N.J.M. Gremmen, H.-P. Leinaas, and V.R. Smith for advice and discussion. J.C. Boelhouwers, K.I. Meiklejohn, N.J.M. Gremmen and V.R. Smith kindly read and provided helpful comments on this chapter.

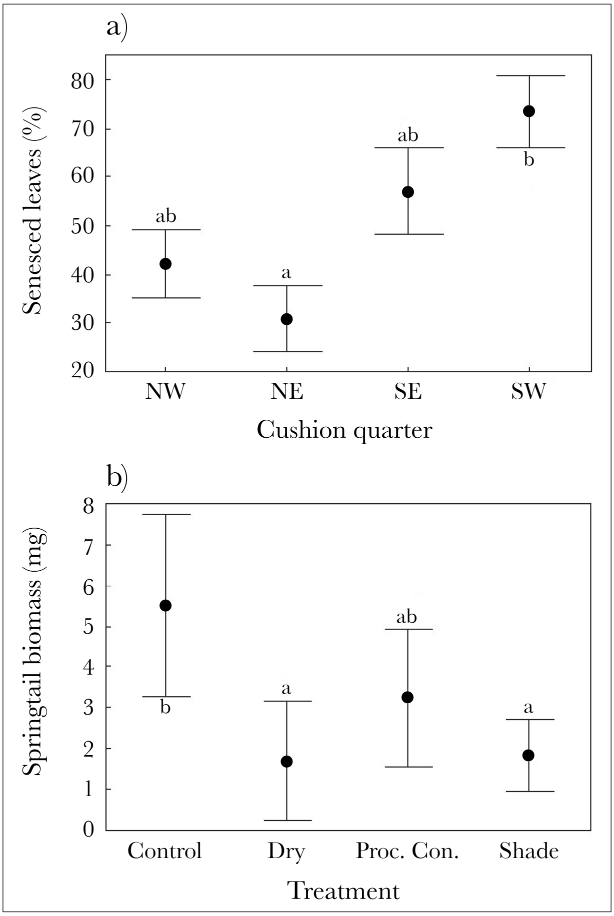


Figure 10.10 Effects of simulated climate change on *Azorella selago* and the springtails that occupy it. a) Unequal distribution of autumnal senescence across *A. selago* cushions exposed to reduced rainfall conditions (modified from le Roux *et al.* 2005). Quarters not sharing a common letter are significantly different ($P = 0.001$). NW = north-western quarter; NE = north-eastern; SE = south-eastern; SW = south-western. b) Springtail biomass (mean ± s.e.) in control cushions and under reduced rainfall conditions (Dry) and its associated procedural control (Proc. Con.), and increased shading (Shade) (modified from McGeoch *et al.* 2006). Treatments not sharing a common letter are significantly different ($P < 0.05$).

10.8 References

Alliende, M.C. & Hoffmann, A.J. 1985. Plants intruding *Laretia acaulis* (Umbelliferae), a high Andean cushion plant. *Vegetatio* **60**, 151-156.

Andrew, N.R., Rodgerson, L. & Dunlop, M. 2003. Variation in invertebrate – bryophyte community structure at different spatial scales along altitudinal gradients. *Journal of Biogeography* **30**, 731-746.

Arroyo, M.T.K., Cavieres, L.A., Peñaloza, A. & Arroyo-Kalin, M.A. 2003. Positive associations between the cushion plant *Azorella monantha* (Apiaceae) and alpine plant species in the Chilean Patagonian Andes. *Plant Ecology* **169**, 121-129.

Ashton, D.H. & Gill, A.M. 1965. Pattern and process in a Macquarie Island feldmark. *Proceedings of the Royal Society of Victoria* **79**, 235-245.

Barendse, J. & Chown, S.L. 2000. The biology of *Bothrometopus elongatus* (Coleoptera, Curculionidae) in a mid-altitude fellfield on sub-Antarctic Marion Island. *Polar Biology* **23**, 346-351.

Barendse, J. & Chown, S.L. 2001. Abundance and seasonality of mid-altitude fellfield arthropods from Marion Island. *Polar Biology* **24**, 73-82.

Barendse, J., Mercer, R.D., Marshall, D.J. & Chown, S.L. 2002. Habitat specificity of mites on sub-Antartic Marion Island. *Environmental Entomology* **31**, 612-625.

Bellehumeur, C. & Legendre, P. 1998. Multiscale sources of variation in ecological variables: modeling spatial dispersion, elaborating sampling designs. *Landscape Ecology* **13**, 15-25.

Bergstrom, D.M. & Chown, S.L. 1999. Life at the front: history, ecology and change on Southern Ocean islands. *Trends in Ecology and Evolution* **14**, 472-477.

Bergstrom, D.M., Selkirk, P.M., Keenan, H.M. & Wilson, M.E. 1997. Reproductive behaviour of ten flowering plant species on sub-Antarctic Macquarie Island. *Opera Botanica* **132**, 109-120.

Blake, B.J. 1996. *Microclimate and prediction of photosynthesis at Marion Island*. M.Sc. Thesis, University of the Orange Free State, South Africa.

Boelhouwers, J., Holness, S. & Sumner, P. 2000. Geomorphological characteristics of small debris flows on Junior's Kop, Marion Island, maritime sub-Antarctic. *Earth Surface Processes and Landforms* **25**, 341-352.

Boelhouwers, J.C., Holness, S. & Sumner, P. 2003. The maritime Subantarctic: a distinct periglacial environment. *Geomorphology* **52**, 39-55.

Brancaleoni, L., Strelin, J. & Gerdol, R. 2003. Relationships between geomorphology and vegetation patterns in subantarctic Andean tundra of Tierra del Fuego. *Polar Biology* **26**, 404-410.

Callaghan, T.V. & Carlsson, B.Å. 1997. Impacts of climate change on demographic processes and population dynamics in Arctic plants. In: Oechel, W.C., Callaghan, T.V., Gilmanov, T., Holten, J.I., Maxwell, B., Molau, U., *et al.* (Eds.). *Global Change and Arctic Terrestrial Ecosystems*. Springer, New York, pp. 129-152.

Cavieres, L., Arroyo, M.T.K., Peñaloza, A., Molina-Montenegro, M. & Torres, C. 2002. Nurse effects of *Bolax gummifera* cushion plants in the alpine vegetation of the Chilean Patagonian Andes. *Journal of Vegetation Science* **13**, 547-554.

Cavieres, L.A., Penaloza, A., Papic, C. & Tambutti, M. 1998. Nurse effect of *Laretia acaulis* (Umbelliferae) in the high Andes of central Chile. *Revista Chilena De Historia Natural* **71**, 337-347.

Chown, S.L. 1989. Habitat use and diet as biogeographic indicators for subantarctic Ectemnorhinini (Coleoptera: Curculionidae). *Antarctic Science* **1**, 23-30.

Chown, S.L. 1990. Possible effects of Quarternary climatic change on the composition of insect communities of the South Indian Ocean Province Islands. *South African Journal of Science* **86**, 386-391.

Chown, S.L. 1997. Sub-antarctic weevil assemblages: Species, structure and survival. In: Battaglia, B., Valencia, J. & Walton, D.W.H. (Eds.). *Antarctic Communities: Species, Structure and Survival*. Cambridge University Press, Cambridge, pp. 152-161.

Chown, S.L. & Avenant, N.L. 1992. Status of *Plutella xylostella* at Marion Island six years after its colonization. *South African Journal of Antarctic Research* **22**, 37-40.

Chown, S.L. & Crafford, J.E. 1992. Microhabitat temperatures at Marion Island (46°54'S 37°45'E). *South African Journal of Antarctic Research* **22**, 51-58.

Chown, S.L. & Gaston, K.J. 2000. Island-hopping invaders hitch a ride with tourists in the Southern Ocean. *Nature* **408**, 637.

Chown, S.L. & Language, K. 1994. Recently established Diptera and Lepidoptera on sub-Antarctic Marion Island. *African Entomology* **2**, 57-60.

Chown, S.L., Marshall, D.J. & Pakhomov, E. 2008. Regional membership: biogeography. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 277-300.

Chown, S.L., McGeoch, M.A. & Marshall, D.J. 2002. Diversity and conservation of invertebrates on the sub-Antarctic Prince Edward Islands. *African Entomology* **10**, 67-82.

Chown, S.L., Rodrigues, A.S.L., Gremmen, N.J.M. & Gaston, K.J. 2001. World Heritage status and the conservation of Southern Ocean islands. *Conservation Biology* **15**, 550-557.

Convey, P., Block, W. & Peat, H.J. 2003. Soil arthropods as indicators of water stress in Antarctic terrestrial habitats? *Global Change Biology* **9**, 1718-1730.

Convey, P., Pugh, P.J.A., Jackson, C., Murray, A.W., Ruhland, C.T., Xiong, F.S., *et al.* 2002. Response of Antarctic terrestrial microarthropods to long-term climate manipulations. *Ecology* **83**, 3130-3140.

Coulson, S.J., Hodkinson, I.D. & Webb, N.R. 2003. Microscale distribution patterns of high Arctic soil microarthropod communities: the influence of plant species within the vegetation mosaic. *Ecography* **26**, 801-809.

Coulson, S.J., Hodkinson, I.D., Webb, N.R., Block, W., Bale, J.S., Strathdee, A.T., *et al.* 1996. Effects of experimental temperature elevation on high-arctic soil microarthropod populations. *Polar Biology* **16**, 147-153.

Crafford, J.E. & Scholtz, C.H. 1987. Quantitative differences between the insect faunas of sub-antarctic Marion and Prince Edward Islands: a result of human intervention? *Biological Conservation* **40**, 255-262.

Crafford, J.E., Scholtz, C.H. & Chown, S.L. 1986. The insects of sub-Antarctic Marion and Prince Edward Islands; with a bibliography of Entomology of the Kerguelen Biogeographical Province. *South African Journal of Antarctic Research* **16**, 42-84.

De Villiers, M.S. & Cooper, J. 2008. Conservation and management. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 301-330.

Frenot, Y., Chown, S.L., Whinam, J., Selkirk, P.M., Convey, P., Skotnici, M., *et al.* 2005. Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews* **80**, 45-72.

Frenot, Y., Gloaguen, J.-C., Cannavacciuolo, M. & Bellido, A. 1998. Primary succession on glacier forelands in the sub-Antarctic Kerguelen Islands. *Journal of Vegetation Science* **9**, 75-84.

Frenot, Y., Gloaguen, J.-C., Picot, G., Bougère, J. & Benjamin, D. 1993. *Azorella selago* Hook used to estimate glacier fluctuations and climatic history in the Kerguelen Islands over the last two centuries. *Oecologia* **95**, 140-144.

Gabriel, A.G.A., Chown, S.L., Barendse, J., Marshall, D.J., Mercer, R.D., Pugh, P.J.A., *et al.* 2001. Biological invasions of Southern Ocean Islands: the Collembola of Marion Island as a test of generalities. *Ecography* **24**, 421-430.

Gaston, K.J. 2003. *The Structure and Dynamics of Geographic Ranges*. Oxford University Press, Oxford.

Gaston, K.J. & Blackburn, T.M. 2000. *Pattern and Process in Macroecology*. Blackwell Science, Oxford.

Gaston, K.J., Jones, A.G., Hanel, C. & Chown, S.L. 2003. Rates of species introduction to a remote oceanic island. *Proceedings of the Royal Society of London B* **270**, 1091-1098.

Gremmen, N.J.M. 1981. *The Vegetation of the sub-Antarctic Islands, Marion and Prince Edward*. Dr. W. Junk, The Hague.

Gremmen, N.J.M., Chown, S.L. & Marshall, D.J. 1998. Impact of the introduced grass *Agrostis stolonifera* on vegetation and soil fauna communities at Marion Island, sub-Antarctic. *Biological Conservation* **85**, 223-231.

Gremmen, N.J.M. & Smith, V.R. 2008. Terrestrial vegetation and dynamics. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 215-244.

Hänel, C. 1999. *The distribution and abundance of macro-invertebrates in the major vegetation communities of Marion Island and the impact of alien species*. M.Sc. Thesis, University of Pretoria, South Africa.

Hanski, I. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* **42**, 3-16.

Hertzberg, K. 1997. Migration of Collembola in a patchy environment. *Pedobiologia* **41**, 494-505.

Hodkinson, I.D., Coulson, S.J., Webb, N.R. & Block, W. 1996. Can high Arctic soil microarthropods survive elevated summer temperatures? *Functional Ecology* **10**, 314-321.

Holness, S. 2003. The periglacial record of Holocene environmental change, sub-Antarctic Marion Island. *Permafrost and Periglacial Processes* **14**, 69-74.

Hopkin, S.P. 1997. *Biology of the Springtails (Insecta: Collembola)*. Oxford University Press, Oxford.

Hugo, A.E. 2006. *Spatial patterns in the microarthropod community associated with* Azorella *selago Hook on the Prince Edward Islands*. Ph.D. Thesis, University of Stellenbosch, South Africa.

Hugo, A.E., Chown, S.L. & McGeoch, M.A. 2006. The microarthropods of sub-Antarctic Prince Edward Island: A quantitative assessment. *Polar Biology* **30**, 109-119.

Hugo, E.A., McGeoch, M.A., Marshall, D.J. & Chown, S.L. 2004. Fine scale variation in microarthropod communities inhabiting the keystone species *Azorella selago* on Marion Island. *Polar Biology* **27**, 466-473.

Huntley, B.J. 1971. Vegetation. In: Van Zinderen Bakker, E.M., Winterbottom, J.M. & Dyer, R.A. (Eds.). *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965-1966*. A.A. Balkema, Cape Town, pp. 98-160.

Huntley, B.J. 1972. Notes on the ecology of *Azorella selago* Hook. f. *Journal of South African Botany* **38**, 103-113.

Ims, R.A., Leinaas, H.P. & Coulson, S. 2004. Spatial and temporal variation in patch occupancy and population density in a model system of an arctic Collembola species assemblage. *Oikos* **105**, 89-100.

Jumpponen, A., Väre, H., Mattson, K.G., Ohtonen, R. & Trappe, J.M. 1999. Characterization of 'safe sites' for pioneers in primary succession on recently deglaciated terrain. *Journal of Ecology* **87**, 98-105.

Kareiva, P. 1994. Space: the final frontier for ecological theory. *Ecology* **75**, 1.

Kennedy, A.D. 1995. Antarctic terrestrial ecosystem response to global environmental change. *Annual Review of Ecology and Systematics* **26**, 683-704.

Kleier, C. & Rundel, P.W. 2004. Microsite requirements, population structure and growth of the cushion plant *Azorella compacta* in the tropical Chilean Andes. *Austral Ecology* **29**, 461-470.

Körner, C. 2003. *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems, 2nd ed*. Springer, Berlin.

le Roux, P.C. 2004. Azorella *selago (Apiaceae) as a model for examining climate change effects in the sub-Antarctic*. M.Sc. Thesis, University of Stellenbosch, South Africa.

le Roux, P.C. & McGeoch, M.A. 2004. The use of size as an estimator of age in the sub-Antarctic cushion plant, *Azorella selago* (Apiaceae). *Arctic, Antarctic, and Alpine Research* **36**, 608-616.

le Roux, P.C. & McGeoch, M.A. 2008. Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. *Climatic Change* **86**, 309-329.

le Roux, P.C., McGeoch, M.A., Nyakatya, M.J. & Chown, S.L. 2005. Effects of a short-term climate change experiment on a keystone plant species in the sub-Antarctic. *Global Change Biology* **11**, 1628-1639.

MacArthur, R.H. & Wilson, E.O. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton.

Marshall, D.J. & Chown, S.L. 1995. Temperature effects on locomotor activity rates of sub-Antarctic oribatid mites. *Polar Biology* **15**, 47-49.

McGeoch, M.A. 2006. Climate Change Biology. In: Riffenburgh, B. (Ed.). *Encyclopedia of the Antarctic*. Routledge, Taylor and Francis, New York, pp. 255-257.

McGeoch, M.A. & Chown, S.L. 1997. Impact of urbanisation on a gall-inhabiting Lepidoptera assemblage: the importance of reserves in urban areas. *Biodiversity and Conservation* **6**, 979-993.

McGeoch, M.A., le Roux, P.C., Hugo, A.E. & Chown, S.L. 2006. Species and community responses to short-term climate manipulation: microarthropods in the sub-Antarctic. *Austral Ecology* **31**, 719-731.

McGeoch, M.A. & Price, P.W. 2004. Spatial abundance structures in an assemblage of gall-forming sawflies. *Journal of Animal Ecology* **73**, 506-516.

Mercer, R.D., Chown, S.L. & Marshall, D.J. 2000. Mite and insect zonation on a Marion Island rocky shore: a quantitative approach. *Polar Biology* **23**, 775-784.

Moore, J.C., Walter, D.E. & Hunt, H.W. 1988. Arthropod regulation of micro- and mesobiota in below-ground detrital food webs. *Annual Review of Entomology* **33**, 419-439.

Noda, T. 2004. Spatial hierarchical approach in community ecology: a way beyond high context-dependency and low predictability in local phenomena. *Population Ecology* **46**, 105-117.

Nuñez, C.I., Aizen, M.A. & Ezcurra, C. 1999. Species associations and nurse plant effects in patches of high-Andean vegetation. *Journal of Vegetation Science* **10**, 357-364.

Nyakatya, M.J. 2006. *Patterns of variability in* Azorella *selago* Hook. (Apiaceae) *on sub-Antarctic Marion Island: climate change implications*. M.Sc. Thesis, University of Stellenbosch, South Africa.

Nyakatya, M.J. & McGeoch, M.A. 2008. Temperature variation across Marion Island associated with a keystone plant species [*Azorella selago* Hook. (Apiaceae)]. *Polar Biology* **31**, 139-151.

Orchard, A.E. 1989. *Azorella* Lamarck (Apiaceae) on Heard and Macquarie Islands, with description of a new species, *A. macquariensis*. *Muelleria* **7**, 15-20.

Pammenter, N.W., Drennan, P.M. & Smith, V.R. 1986. Physiological and anatomical aspects of photosynthesis of two *Agrostis* species at a sub-Antarctic Island. *New Phytologist* **102**, 143-160.

Robinson, C.H., Saunders, P.W., Madan, N.J., Pryce-Miller, E.J. & Pentecost, A. 2004. Does nitrogen deposition affect soil microfungal diversity and soil N and P dynamics in a high Arctic ecosystem? *Global Change Biology* **10**, 1065-1079.

Sage, R.F. & Sage, T.L. 2002. Microsite characteristics of *Muhlenbergia richardsonis* (Trin.) Rydb., an alpine C4 grass from the While Mountains, California. *Oecologia* **132**, 501-508.

Schneider, D.C. 2001. The rise of the concept of scale in ecology. *BioScience* **51**, 545-553.

Schulze, B.R. 1971. The climate of Marion Island. In: Van Zinderen Bakker, E.M., Winterbottom, J.M. & Dyer, R.A. (Eds.). *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965-1966*. A.A. Balkema, Cape Town, pp. 16-31.

Scott, L. 1985. Palynological indications of the Quaternary vegetation history of Marion Island (sub-Antarctic). *Journal of Biogeography* **12**, 413-431.

Selkirk, J.M. 1998. Active vegetation-banked terraces on Macquarie Island. *Zeitschrift fur Geomorphologie Neue Folge* **42**, 483-496.

Slabber, S. & Chown, S.L. 2004. Thermal tolerance and cold hardiness strategy of the sub-Antarctic psocid *Antarctopsocus jeanneli* Badonnel. *Polar Biology* **28**, 56-61.

Smith, V.R. 1977. The chemical composition of Marion Island soils, plants and vegetation. *South African Journal of Antarctic Research* **7**, 28-39.

Smith, V.R. 1978a. Plant ecology of Marion Island: a review. *South African Journal of Antarctic Research* **8**, 21-30.

Smith, V.R. 1978b. Soil chemistry of Marion Island (sub-Antarctic). *South African Journal of Science* **74**, 174-175.

Smith, V.R. 2002. Climate change in the sub-Antarctic: an illustration from Marion Island. *Climatic Change* **52**, 345-357.

Smith, V.R. & French, D.D. 1988. Patterns of variation in the climates, soils and vegetation of some sub-Antarctic and Antarctic islands. *South African Journal of Botany* **54**, 35-46.

Smith, V.R. & Gremmen, N.J.M. 2001. *Turgidosculum complicatulum* on sub-Antarctic Marion Island: carbon acquisition response to climate change. *Polar Biology* **24**, 455-459.

Smith, V.R. & Steenkamp, M. 1990. Climatic change and its ecological implications at a subantarctic island. *Oecologia* **85**, 14-24.

Smith, V.R. & Steenkamp, M. 2001. Classification of the terrestrial habitats on Marion Island based on vegetation and soil chemistry. *Journal of Vegetation Science* **12**, 181-198.

Smith, V.R., Steenkamp, M. & Gremmen, N.J.M. 2001. Terrestrial habitats on sub-Antarctic Marion Island: their vegetation, edaphic attributes, distribution and response to climate change. *South African Journal of Botany* **67**, 641-654.

Sudgen, A.M. 1992. Using biotic interactions to forecast the consequences of global climate change. *Trends in Ecology and Evolution* **7**, 35-36.

Sumner, P.D., Meiklejohn, K.I., Boelhouwers, J.C. & Hedding, D.W. 2004. Climate change melts Marion Island's snow and ice. *South African Journal of Science* **100**, 395-398.

Taylor, A.R., Schroter, D., Pflug, A. & Wolters, V. 2004. Response of different decomposer communities to the manipulation of moisture availability: potential effects of changing precipitation patterns. *Global Change Biology* **10**, 1313-1324.

Tepedino, V.J. & Stanton, N.L. 1976. Cushion plants as islands. *Oecologia* **25**, 243-256.

Teuben, A. & Verhoef, H.A. 1992. Direct contribution by soil arthropods to nutrient availability through body and faecal nutrient content. *Biology and Fertility of Soils* **14**, 71-75.

Tilman, D., Lehman, C.L. & Kareiva, P. 1997. Population dynamics in spatial habitats. In: Tilman, D. & Kareiva, P. (Eds.). *Spatial Ecology*. Princeton University Press, New Jersey, pp. 3-20.

Usher, M.B. & Booth, R.G. 1984. Arthropod communities in a maritime Antarctic moss-turf habitat: three dimensional distribution of mites and collembola. *Journal of Animal Ecology* **53**, 427-441.

Usher, M.B. & Booth, R.G. 1986. Arthropod communities in a maritime Antarctic moss-turf habitat: multiple scales of pattern in the mites and collembola. *Journal of Animal Ecology* **55**, 155-170.

Wickens, G.E. 1995. Llareta (*Azorella compacta*, Umbelliferae): a review. *Economic Botany* **49**, 207-212.

Wiens, J.A. 2000. Ecological heterogeneity: ontogeny of concepts and approaches. In: Hutchings, M.J., John, E.A. & Stewart, A.J.A. (Eds.). *The Ecological Consequences of Environmental Heterogeneity*. Blackwell Science, Oxford, pp. 9-31.

CHAPTER 11

REGIONAL MEMBERSHIP: BIOGEOGRAPHY

STEVEN L. CHOWN, DAVID J. MARSHALL AND EVGENY A. PAKHOMOV

The geological and climatological histories of the Prince Edward Islands are, to a first approximation, well known. Marion Island is at least half a million years old, and Prince Edward Island is probably younger (McDougall *et al.* 2001; Boelhouwers *et al.* 2008). Both islands are volcanic and are considered to represent the summits of a coalescing, basalt shield volcano, located 900 km to the west of the closest land, the geologically more heterogeneous, and in some cases much older, Crozet Islands. At no time have the islands been part of or connected to other large land masses in the Southern Ocean. From a biogeographic perspective they are therefore truly oceanic islands (Darlington 1957; Brown & Lomolino 1998; Whittaker 1998). Nonetheless, their histories have not been quiet, but have been characterized by isostasy, changing sea levels, considerable glaciation, and vulcanism following glacial retreat. The climatic change responsible for the growth and retreat of the glaciers characterized the entire planet (Jouzel *et al.* 1993), and had major effects across the majority of the Southern Ocean islands, including Marion Island, but perhaps not Prince Edward Island to the same extent (Hall 1979, 1990).

This history has, to a large degree, influenced the identities, and therefore biogeographic relationships of both the marine and terrestrial plants and animals that occur at the islands, and that have occurred there in the past. The biogeography of the biota is, in this sense, well known and simple to interpret.

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 277-300

The overwhelming majority of the groups share their closest relationships with islands that are located close by: specifically the Crozet archipelago, Kerguelen Islands, and Heard and McDonald Islands. For example, with the exception of the fern *Elaphoglossum randii*, all of the indigenous vascular plant species that occur on the Prince Edward Islands are also found on Iles Crozet (Gremmen 1981), and *E. randii* also occurs on the Kerguelen Islands. Endemism to the Prince Edward Islands is higher amongst the bryophytes, but the patterns, as much as they can be discerned, are little different to those found in vascular plants (Gremmen & Smith 2008). Amongst the insects, the *Ectemnorhinus* group of weevils, the moth genera *Pringleophaga* and *Embryonopis*, the fly genera *Apetaenus*, *Telmatogeton*, and *Paractora*, and the psocid genus *Antarctopsocus* all share species or sister species with the Crozet archipelago and often with Kerguelen, Heard and McDonald islands (Jeannel 1964; Gressitt 1970; Morrone 1998; Delettre *et al.* 2003). The springtails, mites, molluscs, freshwater crustaceans, tardigrades, and spiders show comparable biogeographic relationships (Deharveng 1981; Pugh 1993; McInnes & Pugh 1998; Marshall *et al.* 1999; Pugh *et al.* 2002; Pugh & Scott 2002; Pugh 2004). Although the pelagic birds and mammals range more widely, similar biogeographic relationships characterize these groups (Barrat & Mougin 1974). The biogeography of marine benthic taxa, especially those of the shelf, near shore and littoral zones, differs little to that of the terrestrial species. The closest ties are with the Falklands, Crozet archipelago and with Kerguelen and Heard islands (Branch *et al.* 1991a, b, 1993; Branch 1994). For pelagic taxa the situation is quite different. Water circulation keeps pelagic organisms and larval stages of benthic species within appropriate water masses allowing completion of their entire life cycle or wide dispersion of larvae, and forms the basis for a species distributional range (Beklemishev 1969; Van der Spoel & Heyman 1983). Since the opening of the Drake Passage and subsequent establishment of the Antarctic Circumpolar Current (ACC) 30-34 million years ago (Livemore *et al.* 2005), the ACC system has been a primary factor regulating pelagic species distribution patterns (Beklemishev 1969). As a consequence, no holoplanktonic endemism has been recorded around the Prince Edward Islands (Allanson *et al.* 1985; Boden & Reid 1989). Overall, the close relationships between the biotas of the Prince Edward Islands, Crozet archipelago, Kerguelen Islands, and Heard and McDonald Islands have long been recognized, such that these archipelagos are considered a biogeographic unit known either as the Kerguelen Biogeographic Province (Crafford *et al.* 1986), or the South Indian Ocean Province Islands (Lewis Smith 1984).

Nonetheless, the biota of the Prince Edward Islands also shows links to other areas. Several taxa are shared to the west with South Georgia and with the Scotia Arc islands, including several ameronothrid mite genera (e.g. *Halozetes*, *Alaskozetes*), a number of springtails (e.g. *Cryptopygus antarcticus*, but see Stevens *et al.* 2006), flies such as those in the genus *Paractora*, and several plant taxa (e.g. *Colobanthus*, Caryophyllaceae). Biogeographic similarities to the east, with Macquarie Island and the New Zealand sub-Antarctic islands (Campbell, Auckland, Snares, Antipodes, Bounty) are also apparent, and in several cases, genera of both plants and insects are circum-Antarctic in their distributions (Gressitt 1970; Greene & Walton 1975; Edgar & Connor 2000). Relationships with islands to the North (St. Paul, Amsterdam, Gough Islands) are typically less pronounced, although these tend to be stronger for highly mobile taxa such as marine pelagic species and spore-dispersed bryophytes (Muñoz *et al.* 2004), than for benthic and less mobile terrestrial groups. As is the case with the terrestrial biota, benthic crustaceans, polychaetes, mollusca and echinodermata as well as bottom-dwelling fish on the Prince Edward Islands plateau are closely linked to the Kerguelen and Crozet islands and moderately to Falklands, South Georgia and even Antarctic Peninsula regions (Branch *et al.* 1991a, b, 1993; Eastman 1993; Branch 1994; Andrássy 1998). The distributions of the marine assemblages are highly dynamic and also depend to a large degree on prevailing marine frontal conditions (Pakhomov & Chown 2003).

What precisely the relationships of past biotas were is difficult to determine because so little is known about them. In terrestrial habitats, the flora, and what is known of the fauna, were similar, at least over the past 16 000 years, and probably also during previous interglacials, to what they are today (Scott & Hall 1983). Palynological records suggest that previous interglacials may have included currently absent species such as *Cardamine*, and that during glacial periods much of the vascular flora was either absent, or restricted to refugia (probably only the cushion-plant *Azorella selago*) (Scott & Hall 1983). For marine species, paleontological evidence of their past distributions is absent. It is unlikely that the current marine fauna would be different from that during previous several intergracials. Over the short term, marine species distribution to a large extent depends on frontal positions because their circum-Antarctic distributional range may undergo marked changes as a result of climatic events, or may be related to the propagation of frontal spinouts or vagrant eddies (Gorodkov 1990; Pakhomov & Chown 2003). This is evident from the number of sub-tropical species of holoplankton (e.g. the pteropod *Cymbulia* sp. or amphipod *Phronima sedentaria*) found between the islands and fish (e.g. *Brama brama*) caught during the long-line fishing in the proximity of the islands (Pakhomov & Froneman 2000; Watkins, personal communication).

Therefore, at least on initial inspection, the biogeography of the Prince Edward Islands would appear almost entirely uncomplicated and fully resolved. However, this resolution is, to a large extent, illusory. The relationships of the faunas of the South Indian Ocean Province Islands to other islands and continents are controversial (Morrone 1998; Cox 2001). Indeed, the biogeography of the Southern Ocean islands as a whole (Fig. 11.1) is contentious, from both the historical and ecological perspectives (Holdgate 1960; Skottsberg 1960; Abbott 1974; Chown 1990a; Van de Vijver & Beyens 1999; Selmi & Boulinier 2001). It is also confounded by the fact that humans have been moving back and forth between the islands, and between the islands and surrounding southern continents, for centuries (Headland 1989), introducing and moving species around as part of their activities (Frenot *et al.* 2005). In some cases these dispersal events are easily detected and have been correctly attributed to human activity (Slabber & Chown 2002; Gaston *et al.* 2003), but in others the situation is more complex (Barnes 2002; Smith 2002; Lewis *et al.* 2003). Furthermore, even on the supposedly well explored Marion Island (Hänel & Chown 1999), new genetic techniques are revealing a colonization history and spatial structure to populations that has not previously been recognized, but which is clearly coupled to the island's geological and climatological histories (Mortimer & Jansen Van Vuuren 2006; Myburgh *et al.* 2007).

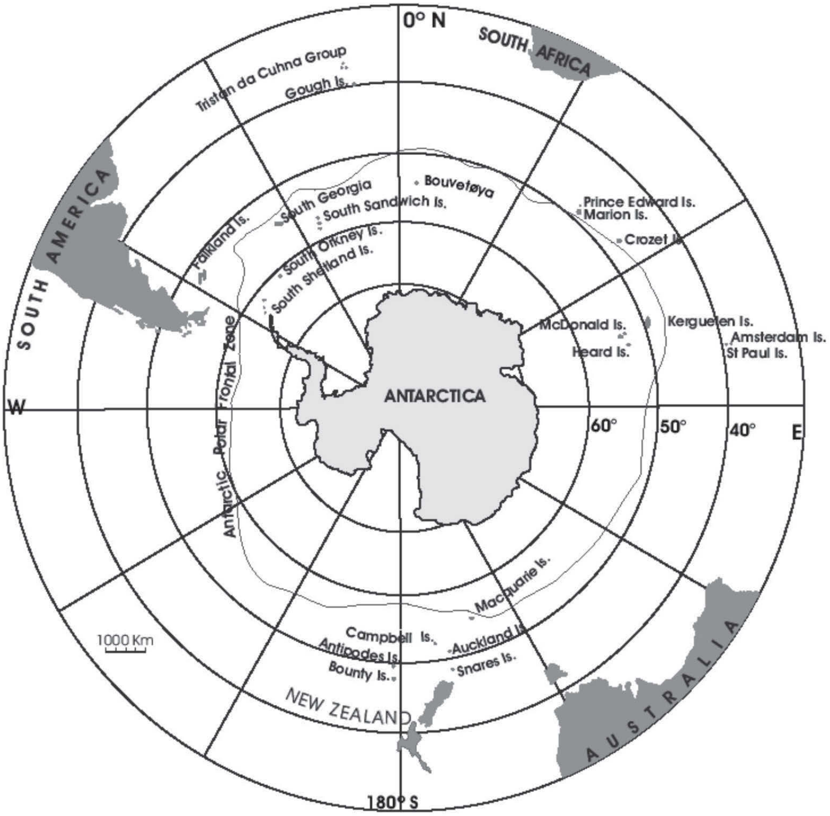


Figure 11.1 The islands of the Southern Ocean in the context of Antarctica and the southern continents.

11.1 Historical biogeography: an ongoing conundrum

The biogeography of the Southern Ocean islands has been the subject of controversy for nearly 50 years (Brundin 1966; Darlington 1970). On the one hand, it has been suggested that all of the islands share enough history and a sufficient proportion of their biotas to be considered a single biogeographic province (Holdgate 1960; Skottsberg 1960; Barrat & Mougin 1974; Chown *et al.* 1998; Van de Vijver & Beyens 1999), often known as Insulantarctica (Udvardy 1987). The other, and perhaps more widely accepted, multi-regional, view is that these similarities are not large enough to warrant inclusion of the biotas within a single biogeographic province. Proponents of the multi-regional hypothesis argue that across the Southern Ocean, island biotas differ substantially in their origins, histories, source areas, and endemicity (Gressitt 1970; Kuschel 1971; Lewis Smith 1984; Chown 1994; Morrone 1998; Cox 2001; Broughton & McAdam 2002), and as a consequence there are considerable regional differences in the structure and composition of the biotas.

Despite several recent analyses, the question of the origin and relationships of the Southern Ocean Island biotas appears to have done little but shift back and forth between these competing hypotheses, providing no convincing argument why either of the ideas should enjoy primacy. Whilst the obvious solution to these problems might seem to be a concerted, multitaxon phylogeographic study of the region, too few marine and terrestrial taxa have been examined in sufficient detail for this to be done at present (though see Bargelloni *et al.* 2000; Stevens *et al.* 2006). Moreover, the results of such an analysis might also be subject to domination by the most speciose taxa. Recently, however, nestedness analyses of a subset of terrestrial taxa have provided considerable insight into both this conundrum and the ways in which it might be solved (Greve *et al.* 2005).

A perfectly nested distribution, based on species incidences, is one in which species occurring at the site of interest are always present in a more species-rich site, whereas species absent from the site of interest never occur in a more depauperate one (Patterson & Atmar 1986). In the Insulantarctica scenario, significant nestedness might be expected, at least at a generic level, owing to similarities in the source pool of colonists across the region, or to vicariance of a once larger landmass. The latter idea has been proposed on several occasions (Jeannel 1964; see also Brundin 1966), but it is clearly incompatible with the geological history of the region as a whole (Beggs *et al.* 1990; LeMasurier & Thompson 1990; Marshall 1994; Wallace *et al.* 2002). Thus, a vicariant origin of the biotas is unlikely. Colonization and subsequent extinction or speciation would thus seem more plausible as causal mechanisms for nestedness if it were found. Given sufficient time, species' ranges can change markedly as a consequence of dispersal, speciation and extinction (Gaston & Chown 1999). In the case of the Southern Ocean islands, long-distance colonization events appear to be more plausible than once thought (e.g. Valdebenito *et al.* 1990; Wagstaff & Garnock-Jones 1998; Bargelloni *et al.* 2000; Kennedy & Spencer 2000; Anderson *et al.* 2001; Burg & Croxall 2001; Lockhart *et al.* 2001; McDowall 2002; Richardson *et al.* 2003; Muñoz *et al.* 2004; Grobler *et al.* 2006; Stevens *et al.* 2006), thus forming a potential mechanism for nestedness if it were found. Following colonization, speciation will reduce nestedness at the species level, whilst extinction might be expected to increase it (Lomolino 1996). However, the ranges of higher taxonomic levels, such as genera, are likely to remain more stable than those of species (Wright *et al.* 1998; Gaston & Chown 1999). Therefore, across the region, nestedness should be much stronger at the generic than at the species level in the Insulantarctica scenario.

Alternatively, in the multi-regional scenario, differences in endemicity, source pools and biogeographic history are likely to mean little in the way of significant nestedness across the Southern Ocean islands (as here defined), at either the generic or species levels. However, within a particular archipelago, significant nestedness should not only occur, but should also be very much greater than that found across the region.

Of course, because one of the mechanisms underlying nestedness is differential colonization ability, the extent of nestedness should vary considerably with the dispersal ability of the taxon concerned: organisms with poor dispersal abilities are apt to show much less nestedness than taxa with well-developed dispersal abilities (Greve *et al.* 2005). In the case of the Southern Ocean island taxa for which comprehensive information on distributions is available (Chown *et al.* 1998), nestedness might be expected to increase in likelihood as follows: insects < vascular plants < land birds < seabirds, inter-island benthos and fish < holoplankton, whilst acknowledging that within each of these groups dispersal ability will vary considerably. Moreover, because most non-indigenous species are likely to have been introduced directly by humans, or are likely to have colonised other parts within an archipelago following their introduction by humans to one or more islands (or to a source area), a different set of expectations might apply to alien species by comparison with the those indigenous to the islands. Given the mostly European origins of the majority of the non-indigenous species on Southern Ocean islands (Frenot *et al.* 2005), it might be expected that nestedness would be considerably higher across the Southern Ocean islands for these species than for the indigenous ones, that there would be little difference between the nestedness of alien species and genera, and that vagility might not significantly influence nestedness across the Southern Ocean islands, but would do so for individual archipelagos.

In the indigenous species, considerable nestedness has been found at the species and generic levels across the region, and substantial differences also exist between nestedness at this scale and within archipelagos (specifically the New Zealand sub-Antarctic islands) (Greve *et al.* 2005). Thus, both the Insulantarctic and multi-regional scenarios appear to enjoy support, which is perhaps not surprising given the complexity of the region (Gressitt 1970). However, much of this complexity might be a consequence of differences of vagility of the groups (insects, vascular plants, land birds, seabirds). Highly mobile taxa, such as seabirds, that, at least in some instances, have demonstrably panmictic populations in the region (Burg & Croxall 2001), show considerable nestedness. By contrast, less mobile taxa, such as the insects, are hardly nested at all when compared to both the seabirds and to assemblages from elsewhere (see Wright *et al.* 1998). In consequence, distribution patterns shown by groups with poor dispersal ability, such as weevils (Morrone 1998), are dominated by the influence of regional source pools (i.e. continental areas and large islands located close to particular archipelagos), thus providing support for a multi-regional hypothesis, whilst the distribution patterns of more mobile taxa are less subject to this constraint (Barrat & Mougin 1974) (Fig. 11.2).

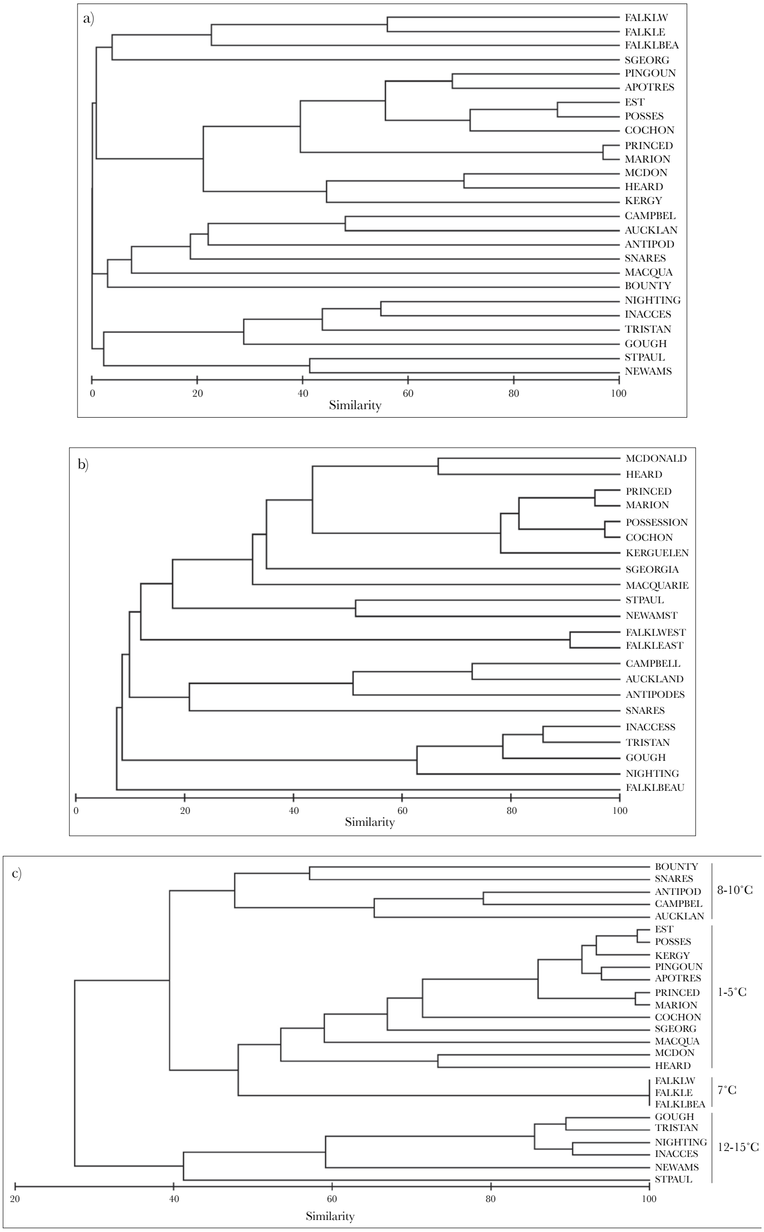


Figure 11.2 Dendrograms, based on cluster analyses using a Bray-Curtis Similarity matrix and Group Averaging, showing relationships among the Southern Ocean island biotas. a) Insects. b) Vascular plants. c) Seabirds. In c, islands of different mean annual temperature are indicated, illustrating the structuring of the faunas according to temperature. Redrawn from Greve *et al.* 2005. NEWAMS – New Amsterdam Isl.; ANTIPOD – Antipodes Isl.; AUCKLAN – Auckland Isl.; APOTRES- Apotres Isl.; BOUNTY – Bounty Isl.; CAMPBEL – Campbell Isl.; COCHON – Cochon Isl.; EST – Est Isl.; FALKBEA – Beauchene Island; FALKLE – East Falkland; FALKLW – West Falkland; GOUGH – Gough Isl.; HEARD – Heard Isl.; INACCESS – Inaccessible Isl.; KERGY – Kerguelen Isl.; MACQUA – Macquarie Isl. MARION – Marion Isl.; MCDON – McDonald Isl.; NIGHTING – Nightingale Isl.; PINGOUIN – Pingouin Isl.; POSSES – Possession Isl.; PRINCED – Prince Edward Isl.; SGEORG – South Georgia; SNARES – Snares Isl.; STPAUL – St. Paul Isl.; TRISTAN – Tristan da Cunha Isl.

Further support for this idea comes from two other sources. First, although marine organisms vary considerably in their dispersal ability (Jablonski & Lutz 1983), they are generally thought to be capable of dispersal over larger areas than is the case for many terrestrial groups (Stanley 1979; Jablonski & Lutz 1983; Chown 1997). If this is also true of Southern Ocean marine groups (although planktotrophic development is rare – Knox 1994), it might be expected that their biogeographic relationships would be less clearly multi-regional than those of terrestrial taxa, and that nestedness would consequently be much higher in marine than in terrestrial assemblages. Much of the literature on the biogeography of marine groups suggests that the fauna is more clearly separated according to their thermal preferences than regional origin (Branch 1994; Knox 1994; Razouls *et al.* 2000; Sicinski & Gillet 2002). This is true also of the highly pelagic seabirds (Fig. 11.2c). Whilst more thorough surveys of marine benthic and pelagic fish and invertebrate taxa might alter this situation (de Broyer *et al.* 2003), recent intensive explorations have revealed biogeographic patterns dominated by a temperature rather than by a regional signal (Gorny 1999; Brandt *et al.* 1999; Barnes & De Grave 2001; Selje *et al.* 2004). Likewise, nestedness of marine groups appears to be high. For example, in the case of the polychaete data provided by Branch (1994), nestedness is very high by comparison with other pelagic taxa such as the seabirds, and certainly much higher than many of the terrestrial taxa examined by Greve *et al.* (2005).

The second line of evidence supporting the importance of dispersal in determining the historical biogeography of the region comes from small, terrestrial taxa. It has been suggested that small organisms are much more likely to be panmictic than larger ones (Fenchel 1993; Finlay *et al.* 1996; but see also Wilkinson 2001; Green *et al.* 2004), and in consequence that speciation is likely to be less common and taxa more widely distributed. McInnes & Pugh's (1998) analysis of the biogeography of the Antarctic and Southern Ocean island tardigrades showed little in the way of support for a multi-regional hypothesis, but rather indicated subdivision of areas according to climate. Moreover, another small-sized, freshwater/terrestrial group, the testate amoebae, are highly nested and marginally more so than the pelagic seabirds (Greve *et al.* 2005). Curiously, the bryophyte presence-absence matrix used by Muñoz *et al.* (2004), which they claimed supports an hypothesis of dispersal by wind across the southern continents and islands, is only slightly less nested than that of the vascular plant matrix examined by Greve *et al.* (2005) (d1 for vascular plants = 0.577, and for Muñoz *et al.*'s (2004) bryophyte data = 0.475). Clearly, bryophyte dispersal across the region might not be as efficient as might at first be expected for species that can spread by means of spores and gemmae.

As expected, nestedness is significantly greater in the non-indigenous, or alien, species than in those indigenous to the islands, and the difference between generic and species levels in the former species is half as large as those in the latter. Thus, the same alien species tend to be transported to the islands and there is little regional pattern to this transport, such that genera and species have more similar nestedness than is the case for indigenous taxa. However, vagility has as much influence on the patterns found for the alien species as it has on those found in the indigenous species. The influence of dispersal ability on nestedness in the alien species seems to be a consequence of the tendency for similar plant species to be introduced across the region, whereas introduced insects typically are more regional in their origins (Greve *et al.* 2005).

Whilst the nestedness approach has not resolved the conundrum regarding the origins of the biotas, it has demonstrated that dispersal plays a major role in determining biogeographic patterns in the region, and the way that they are interpreted (see also McDowall 2002; Craig *et al.* 2003; Muñoz *et al.* 2004). Therefore, whilst early vicariance may have set the board in the Southern Ocean (Cheshire *et al.* 1995; McDowall 2002), the later game has clearly been one of dispersal. Indeed, recent studies have not only shown that dispersal must have occurred soon after the islands in the region became subaerial, but also that multiple dispersal events took place (Grobler *et al.* 2006; Stevens *et al.* 2006). Today, the rules of this dispersal game are changing as human activity increases across the region and climates warm.

11.2 Ecological biogeography: determinants of richness

Although the importance of dispersal across the Southern Ocean region is now broadly acknowledged (see previous section and Greve *et al.* 2005), the likelihood that classic species-area relationships hold for the Southern Ocean has long been considered low. Indeed, for many years the view was held that the effects of glaciation, persistent low temperatures, and considerable isolation are predominantly responsible for patterns of species richness variation across the Southern Ocean islands, and that island area is of much less significance (Gressitt 1970; Kuschel 1971; Abbott 1974; Burger 1985; Chown 1990a). Recent analyses (Chown *et al.* 1998; Selmi & Boulinier 2001; Chown *et al.* 2005) have shown that elements of both classic island biogeography theory (isolation and available area), and the influence of varying energy availability (measured as sea surface temperature) explain variation in richness of terrestrial vascular plants, terrestrial birds and mammals, and pelagic seabirds. In the case of introduced species, human occupation of the islands plays a large role too.

The richness of indigenous vascular plants across the Southern Ocean islands is related to both available area and available energy, irrespective of whether or not the analyses take spatial autocorrelation (see Lennon 2000) into account. This finding is largely in keeping with species energy theory (Wylie & Currie 1993; Evans *et al.* 2004). Area is likely to influence species richness both as a consequence of habitat heterogeneity and for reasons of changes in extinction and colonization probability (see MacArthur & Wilson 1967; Rosenzweig 1995; Ricklefs & Lovette 1999 for discussion). How precisely variation in energy availability determines variation in species richness is controversial, and might involve both the physiological tolerances of species as well as the ways in which energy is apportioned between individuals and subsequently between species

(Evans *et al.* 2004). Nonetheless, the finding that available energy (because water is typically not limiting on these islands, sea surface temperature (SST) can be used as a surrogate of richness – Hawkins *et al.* 2003) influences richness is typical of most large scale studies (reviews in Hawkins *et al.* 2003; Willig *et al.* 2003; Evans *et al.* 2004; Kalmar & Currie 2006).

The situation is more complex for the indigenous insects. Depending on the analysis (i.e. including/excluding spatial autocorrelation), distance to the closest continent, indigenous plant richness, area, and SST are all correlates of richness (Chown *et al.* 1998; Selmi & Boulinier 2001; Chown *et al.* 2005). Clearly, dispersal capabilities of the insects and isolation of the islands have been significant in influencing the richness patterns. The influence of energy can also be interpreted in much the same way that it might influence indigenous vascular plant species richness. However, the role of indigenous plant species richness in influencing insect species richness is more controversial. It has long been maintained generally that plant richness might have a substantial influence on herbivore richness (e.g. Gaston 1992; Siemann *et al.* 1998). However, this idea is contentious and recent analyses have suggested that evidence in favour of a relationship between plant and herbivore richness is perhaps weaker than was once thought, at least at large spatial scales (Hawkins & Porter 2003; Hawkins & Pausas 2004). In the present case, it is difficult to determine what the nature is of the relationship between vascular plant and insect richness. Whilst indigenous plant richness is a strong correlate of insect richness (irrespective of analytical approach), one spatially explicit approach suggests that this is a consequence of similar responses of both groups to island area (Selmi & Boulinier 2001), whilst another does not support this assertion (Chown *et al.* 2005).

In the case of the birds, pronounced differences exist between the marine, pelagic and the terrestrial species. Island age, vascular plant and insect richness are the most significant correlates of land bird richness (irrespective of the analytical approach). Thus, time for faunal accumulation, *in situ* evolution, and resource availability have all influenced land bird richness. Although energy availability (as SST) is significant in the univariate models (Chown *et al.* 1998), it is replaced by perhaps a more direct measure of resource availability (plant and insect richness). Seabird richness, by contrast, is most strongly related to chlorophyll concentration and SST, measures of energy availability, and to area. Seabirds tend to be limited by nest site availability on Southern Ocean islands (Jouventin 1990; Warham 1996), and area provides an effective surrogate measure thereof. At large scales, strong relationships between primary productivity (and sea surface temperature), measures of energy availability, and seabird species richness and abundance have previously been found (Pakhomov & McQuaid 1996; Chown & Gaston 1999). Intriguingly, a recent study at global scales has demonstrated that wind energy is also a major correlate of procellariiform species richness (Davies *et al.*, submitted ms.).

Because many of the introduced land bird species dispersed to the islands (especially the New Zealand sub-Antarctic islands and Macquarie Island) subsequent to introduction elsewhere (Turbott 1990; Young 1995), distance to the closest land mass is a strong correlate of their richness. However, introduced land bird richness is also strongly related to resource availability (in the form of insect and plant richness) as it is for the indigenous terrestrial birds, once again supporting an energy availability argument. In the analyses undertaken by Selmi & Boulinier (2001) annual numbers of human occupants was also a strong correlate of the richness of introduced land birds at the islands, and number of occupants also typically emerges as the strongest relationship for introduced mammals (Fig. 11.3). In neither case is such an outcome surprising, given that intentional and accidental releases of mammals and birds onto the islands have been widely documented (Frenot *et al.* 2005). Indeed, it would be astonishing if numbers of human occupants (scientific and logistic personnel as well as numbers of permanent residents for some islands) did not enter models of variation in richness of these groups.

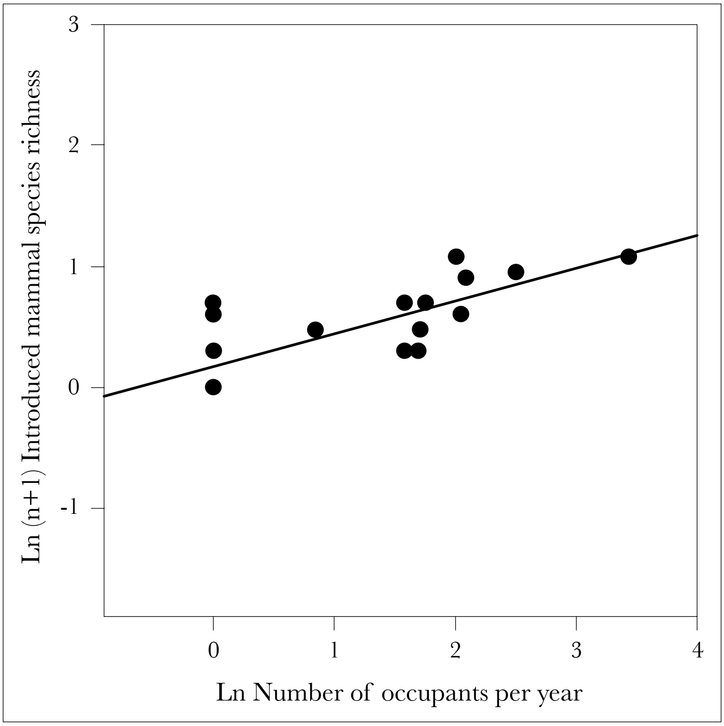


Figure 11.3 Bivariate plot of ln (n+1) introduced mammal species richness on ln number of occupants per year for the Southern Ocean islands. Redrawn from Chown *et al.* 1998.

Across the Southern Ocean Islands, visitor frequency and energy availability are significant correlates of alien vascular plant and insect species richness (Chown *et al.* 1998; Selmi & Boulinier 2001; Chown *et al.* 2005). These correlates suggest that exotic species richness is high in high energy areas for two reasons: the ecological processes that enable large numbers of species to coexist (see Evans *et al.* 2004 for review), and the historical processes that have meant enhanced propagule pressure as a consequence of high visitor frequency (e.g. Williamson 1996; Lonsdale 1999). However, visitor frequency also covaries positively with both area and energy availability (Chown *et al.* 2005). Thus, the effects of energy availability and human visitor frequency on the richness of exotic species on these islands are confounded. This situation is not likely to be unique to the Southern Ocean islands because propagule pressure and disturbance, as a consequence of human activities, are major factors influencing invasion success everywhere (Williamson 1996; Lonsdale 1999), and because energy availability and human population density typically covary positively (Rivard *et al.* 2000; Chown *et al.* 2003). In consequence, propagule pressure and disturbance, and the ecological processes that enable large numbers of species to coexist (Evans *et al.* 2004), are likely to be causally interrelated. In consequence, distinguishing the relative importance of the ecological (energy) and historical (human occupancy) effects requires that the latter be held relatively constant. Comparing patterns of invasion on Heard and Gough Islands, which have had virtually identical numbers of visits, but which differ substantially in climate and indigenous species richness, allows this to be done.

Gough Island is comparatively warm, with a mean annual temperature of 11.5°C that has remained little changed since the 1950s (Jones *et al.* 2003). It has a well-developed indigenous terrestrial vascular flora (70 species) and is home to 28 indigenous insect species. Heard Island is cold, with a mean annual temperature of 1.7°C, and extensive, though rapidly receding glaciation. It is species poor, with just 12 indigenous vascular plant and nine indigenous insect species (Chown *et al.* 2006; Turner *et al.* 2006). Humans first landed on Gough Island in 1675. However, until 1802 only one other recorded landing took place. Thereafter, the numbers of visits increased – first for sealing purposes, and later (after 1955) for science (Fig. 11.4), resulting in a total of 239 landings. Heard Island was discovered in 1855, experienced a rapid increase in visits owing to sealing until this resource was exhausted, and is once again experiencing an increase in visits for science and tourism (Fig. 11.4). In total, there have been 232 landings on the island. There are two non-indigenous plant and insect species known from Heard Island, of which the grass *Poa annua* is thought to have arrived prior to 1955, and the thrip *Apterothrips apteris* in the early 1990s. Alien species have thus established on average once every 72 years or every 116 visits. Gough Island is highly invaded, with 74 non-indigenous insects and plants generally widespread across the island. These species have established at a rate of on average one every four to five years, or with every third visit (Chown *et al.* 2005).

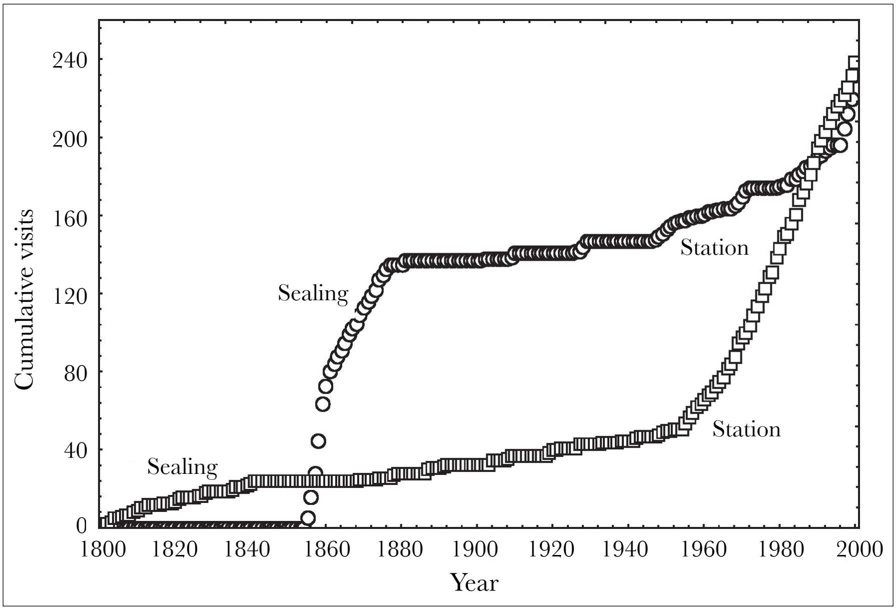


Figure 11.4 Cumulative number of landings at Heard Island (circles) and Gough Island (squares) since 1800. Prior to this time only two landings were made at Gough Island and none at Heard Island. The sealing boom years for each island are indicated, as are the dates at which permanent scientific stations were established (1947-1954 for Heard Island; 1956 onwards for Gough Island. Redrawn from Chown *et al.* 2005.

These results provide support for the hypothesis that on these islands energy availability is a major correlate of exotic species richness, and presumably a determinant thereof via the ecological processes that result in an association between energy availability, high numbers of individuals and elevated diversity in all species (Chown *et al.* 2005). Other differences between the islands, such as distance from source areas, or date of human occupation, might account for these patterns, though recent analyses have shown that this is unlikely to be the case (Chown *et al.* 1998; Selmi & Boulinier 2001). A more plausible alternative is that climate matching (see Duncan *et al.* 2003 for recent review) is responsible for these patterns, such that species from more temperate source areas have a higher likelihood of establishing on the warmer Gough Island than on the cooler Heard Island. However, many of the terrestrial exotic species recorded across the Southern Ocean region have established at both cold and warm islands, and are largely weedy European species that have broad tolerances and have established in cold to cool temperate ports in South Africa (Cape Town) and Australia (Hobart), the origin of much shipping to the region (Frenot *et al.* 2005). Therefore, it does not seem likely that strict physiological intolerance is an entirely adequate explanation of the differential richness of exotic species on Heard and Gough islands. Rather, when visitor frequency is held constant, energy availability is the major correlate of exotic species richness, though the exact mechanistic cause of this relationship requires clarification (Chown *et al.* 2005).

11.3 New developments in phylogeography

Perhaps the largest gap in our knowledge of the biogeography of the Prince Edward islands, and indeed for the Southern Ocean Islands as a whole, is the absence of area cladograms or related analyses based on molecular systematic (or phylogeographic) information. Although such analyses are starting to become more common in the region (Bargelloni *et al.* 2000; Burg & Croxall 2001; Richardson *et al.* 2003; Allegrucci *et al.* 2006; Stevens *et al.* 2006), they are largely lacking for the marine and terrestrial plants and invertebrates.

Those studies that have been undertaken indicate a close coincidence between colonization patterns and the geological and climatological histories of the islands. For example, DNA sequence data suggest that weevils in the genus *Ectemnorhinus* colonized the Prince Edward Islands 0.43 Ma (Grobler *et al.* 2006), only 70 ka after the islands' emergence (McDougall *et al.* 2001). However, even within groups, such as the *Ectemnorhinus* weevils, there are substantial differences between taxa, such that primers which work well on one group of genera fail to adequately amplify DNA for another. Likewise, searches on GenBank often reveal little but broad similarity between the taxa on the islands and those elsewhere (G.C. Grobler, unpublished data). Thus, the origins of many of the groups, and the relationships between the islands remain enigmatic. Somewhat greater success in determining colonization patterns and relationships has been had among springtails in the genus *Cryptopygus* and its close relatives (Stevens *et al.* 2006). This study demonstrated relatively recent (< 2 Ma) colonization among sub-Antarctic islands, and older diversification (11-21 Ma) on the Antarctic continent.

Smaller scale, phylogeographic (Avise *et al.* 1987) and molecular systematic studies have also been undertaken on several islands. In some instances they have revealed cryptic species, and in others complicated phylogeographic patterns. For example, in the former case, two, morphologically almost identical *Bothrometopus parvulus*-like species coexist on Marion Island rather than the single species recorded to date. Moreover, whilst two *Ectemnorhinus* species occur on Prince Edward Island, only a single species appears to exist on Marion Island, with a complex genetic structure unrelated to body size (*contra* Chown 1990b) (Grobler *et al.* 2006). In the latter case, recent work has shown complex phylogeographic structure of in mites and springtails, related to the climatic and volcanic history of Marion Island (Mortimer & Jansen Van Vuuren 2006; Myburgh *et al.* 2007). However, phylogeographic structure in invasive springtails is remarkably simple (often only a single haplotype is present), indicating that the invasion was initiated by few individuals.

These genetic patterns are overlain on a background of complex spatial relationships in assemblage structure that are a function of present ecological conditions (McGeoch *et al.* 2008), as well as substantial spatial variation in morphology and physiology (e.g. Chown & Klok 2003; Klok & Chown 2003). It is these intra-island patterns that represent one of the most interesting challenges to biologists at the islands.

11.4 Conclusions

Although the origins of several groups found on the South Indian Ocean Province Islands and the biogeographic relationships of some of the islands remain controversial, the biogeography of the region is perhaps much less of a mystery than it was in the past. New evidence, such as of the time of emergence of the Kerguelen archipelago (Wallace *et al.* 2002), the likely previous extent of the landmass in this region, and the relationships between taxa based on molecular systematic evidence (e.g. Stevens *et al.* 2006), is bound to alter some of the present interpretations. However, it seems likely that the close relationships between the Prince Edward Islands and the other South Indian Ocean Province Islands will continue to enjoy support.

What is perhaps more concerning is the evidence for such high rates of successful establishment of alien species on these islands. For example, the per ship probability of terrestrial invasion for Gough Island is 750 times higher, and for Heard Island 20 times higher, than that found for shipping-associated marine invasions in a recent global survey (Drake & Lodge 2003; Chown *et al.* 2005). Moreover, Gaston *et al.* (2003) have shown that, even taking the likely natural extinction patterns of indigenous species into account, and the fact that probably only 1 out of 10 colonizations results in the successful establishment of an alien insect species (Williamson & Fitter 1996; but see Jeschke & Strayer 2005), the rate of successful, human-mediated establishment of alien insects on Gough Island is two to three orders of magnitude greater than the natural background rate. In the context of human-mediated extinctions that are also taking place at a rate two to three orders of magnitude higher than background rates (May *et al.* 1995), these data suggest that humans are homogenizing the island biotas in two ways. Extinctions reduce the components of diversity that contribute to place distinctiveness, whereas introductions enhance those that contribute to similarity. Because invasive species are often responsible for island extinctions (Blackburn *et al.* 2004), these two routes to homogenization are closely coupled. Moreover, increasing connectivity across the region owing to science and tourism (Chown & Gaston 2000), and climatic warming (Frenot *et al.* 2005), suggest that these problems might be exacerbated in the future in the absence of appropriate conservation action. If this problem includes the transport of species indigenous to particular islands to others (e.g. Tréhen & Voisin 1984; Ernsting 1993), or the integration of geographically and genetically distinct populations, then the biogeographic signal to noise ratio is likely to become even lower, making interpretation of this complex region more difficult than it has already proven to be.

11.5 Acknowledgements

Thanks to Kevin Gaston, Niek Gremmen, Bruce Hull, Melodie McGeoch, and Philip Pugh for discussion, Jesús Muñoz for data on bryophyte distributions, Michelle Greve for running additional nestedness analyses, and Gert Grobler for providing unpublished information.

11.6 References

Abbott, I. 1974. Number of plant, insect and land bird species on nineteen remote islands in the Southern Hemisphere. *Biological Journal of the Linnean Society* **6**, 143-152.

Andrássy, I. 1998. Nematodes in the Sixth Continent. *Journal of Nematode Morphology and Systematics* **1**, 107-186.

Allanson, B.R., Boden, B., Parker, L. & Duncombe Rae, C. 1985. A contribution to the oceanology of the Prince Edward Islands. In: Siegfried, W.R., Condy, P.R. & Laws, R.M. (Eds.). *Antarctic Nutrient Cycles and Food Webs*. Springer-Verlag, Berlin Heidelberg, pp. 38-45.

Allegrucci, G., Carchini, G., Todisco, V., Convey, P. & Sbordoni, V. 2006. A molecular phylogeny of Antarctic Chironomidae and its implications for biogeographical history. *Polar Biology* **29**, 320-326.

Anderson, C.L., Rova, J.H.E. & Andersson, L. 2001. Molecular phylogeny of the tribe Anthospermeae (Rubiaceae): Systematic and biogeographic implications. *Australian Systematic Botany* **14**, 231-244.

Avise, J.C., Arnold, J., Ball, R.M., Bermingham, E., Lamb, T., Neigel, J.E., *et al.* 1987. Intraspecific phylogeography: The mitochondrial DNA bridge between population genetics and systematics. *Annual Review of Ecology and Systematics* **18**, 489-522.

Bargelloni, L., Marcato, S., Zane, L. & Partarnello, T. 2000. Mitochondrial phylogeny of notothenoids : a molecular approach to Antarctic fish evolution and biogeography. *Systematic Biology* **49**, 114-129.

Barnes, D.K.A. 2002. Invasions by marine life on plastic debris. *Nature* **416**, 808-809.

Barnes, D.K.A. & De Grave, S. 2001. Ecological biogeography of southern polar encrusting faunas. *Journal of Biogeography* **28**, 359-365.

Barrat, A. & Mougin, J.L. 1974. Donneés numériques sur la zoogéographie de l'avifane Antarctique et Subantarctique. *Comité Nationale Français des Recherches Antarctiques* **33**, 1-18.

Beklemishev, K.V. 1969. *Ecology and Biogeography of the Pelagial.* Moscow, Nauka Press, pp. 1-291.

Beggs, J.M., Challis, G.A. & Cook, R.A. 1990. Basement geology of the Campbell Plateau: implications for correlation of the Campbell Magnetic Anomaly System. *New Zealand Journal of Geology and Geophysics* **33**, 401-404.

Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L. & Gaston, K.J. 2004. Avian extinction and mammalian introductions on oceanic islands. *Science* **305**, 1955-1958.

Boden, B.P. & Reid, F.M.H. 1989. Marine plankton diatoms between Cape Town and the Prince Edward Islands (SW Indian Ocean). *South African Journal of Antarctic Research* **19**, 1-49.

Boelhouwers, J., Meiklejohn, I., Holness, S. & Hedding, D. 2008. Geology, geomorphology and climate change. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem.* African Sun Media, Stellenbosch, pp. 65-96.

Branch, M.L. 1994. The Polychaeta of subantarctic Marion and Prince Edward Islands: Illustrated keys to the species and results of the 1982-1989 University of Cape Town surveys. *South African Journal of Antarctic Research* **24**, 3-52.

Branch, M.L., Arnaud, P.M., Cantera, J. & Gianakouras, D. 1991a. The benthic Mollusca and Brachiopoda of subantarctic Marion and Prince Edward Islands. *South African Journal of Antarctic Research* **21**, 45-64.

Branch, M.L., Griffiths, C.L., Kensley, B. & Sieg, J. 1991b. The benthic Crustacea of subantarctic Marion and Prince Edward Islands: Illustrated keys to the species and results of the 1982-1989 University of Cape Town surveys. *South African Journal of Antarctic Research* **21**, 3-44.

Branch, M.L., Jangoux, M., Alva, V., Massin, C.I. & Stampanato, S. 1993. The Echinodermata of subantarctic Marion and Prince Edward Islands. *South African Journal of Antarctic Research* **23**, 37-70.

Brandt, A., Linse, K. & Muhlenhardt-Siegel, U. 1999. Biogeography of Crustacea and Mollusca of the Subantarctic and Antarctic regions. S*cientia Marina Supplement* **63**, 383-389.

Broughton, D.A. & McAdam, J.H. 2002. *The Vascular Flora of the Falkland Islands: An Annotated Checklist and Atlas*. Falklands Conservation, Stanley.

Brown, J.H. & Lomolino, M.V. 1998. *Biogeography*. Sinauer Associates, Sunderland.

Brundin, L. 1966. Transantarctic relationships and their significance as evidenced by chironomid midges. *Svenska Vteneskapsakademie Handlunge* **11**, 1-472.

Burg, T.M. & Croxall, J.P. 2001. Global relationships amongst black-browed and grey-headed albatrosses: analysis of population structure using mitochondrial DNA and microsatellites. *Molecular Ecology* **10**, 2647-2660.

Burger, A.E. 1985. Terrestrial food webs in the sub-Antarctic: Island effects. In: Siegfried, W.R., Condy, P.R. & Laws, R.M. (Eds.). *Antarctic Nutrient Cycles and Food Webs*. Springer, Berlin, pp. 582-591.

Cheshire, A.C., Conran, J.G. & Hallam, N.D. 1995. A cladistic analysis of the evolution and biogeography of *Durvillaea* (Phaeophyta). *Journal of Phycology* **31**, 644-655.

Chown, S.L. 1990a. Possible effects of Quaternary climatic change on the composition of insect communities of the South Indian Ocean Province Islands. *South African Journal of Science* **86**, 386-391.

Chown, S.L. 1990b. Speciation in the sub-Antarctic weevil genus *Dusmoecetes* Jeannel (Coleoptera: Curculionidae). *Systematic Entomology* **15**, 283-296.

Chown, S.L. 1994. Historical ecology of sub-Antarctic weevils (Coleoptera: Curculionidae): patterns and processes on isolated islands. *Journal of Natural History* **28**, 411-433.

Chown, S.L. 1997. Speciation and rarity: separating cause from consequence. In: Kunin, W.E. & Gaston, K.J. (Eds.). *The Biology of Rarity*. Chapman and Hall, London, pp. 91-109.

Chown, S.L. & Gaston, K.J. 1999. Patterns in procellariiform diversity as a test of species-energy theory in marine systems. *Evolutionary Ecology Research* **1**, 365-373.

Chown, S.L. & Gaston, K.J. 2000. Island-hopping invaders hitch a ride with tourists in the Southern Ocean. *Nature* **408**, 637.

Chown, S.L., Greenslade, P. & Marshall, D.J. 2006. Terrestrial invertebrates of Heard Island. In: Green, K. & Woehler, E.J. (Eds.). *Heard Island: Southern Ocean Sentinel*. Surrey and Beatty, Chipping Norton, pp. 91-104.

Chown, S.L., Gremmen, N.J.M. & Gaston, K.J. 1998. Ecological biogeography of southern ocean islands: Species-area relationships, human impacts, and conservation. *American Naturalist* **152**, 562-575.

Chown, S.L., Hull, B. & Gaston, K.J. 2005. Human impacts, energy availability, and invasion across Southern ocean islands. *Global Ecology and Biogeography* **14**, 521-528.

Chown, S.L. & Klok, C.J. 2003. Altitudinal body size clines: latitudinal effects associated with seasonality. *Ecography* **26**, 445-455.

Chown, S.L., Van Rensburg, B.J., Gaston, K.J., Rodrigues, A.S.L. & Van Jaarsveld, A.S. 2003. Energy, species richness, and human population size: conservation implications at a national scale. *Ecological Applications* **13**, 1233-1241.

Cox, C.B. 2001. The biogeographic regions reconsidered. *Journal of Biogeography* **28**, 511-523.

Crafford, J.E., Scholtz, C.H. & Chown, S.L. 1986. The insects of sub-Antarctic Marion and Prince Edward Islands; with a bibliography of Entomology of the Kerguelen Biogeographical Province. *South African Journal of Antarctic Research* **16**, 42-84.

Craig, D.A., Currie, D.C. & Vernon, P. 2003. *Crozetia* Davies (Diptera: Simuliidae): redescription of *Cr. crozetensis*, *Cr. seguyi*, number of larval instars, phylogenetic relationships and historical biogeography. *Zootaxa* **259**, 1-39.

Darlington, P.J. 1957. *Zoogeography. The Geographical Distribution of Animals*. John Wiley, New York.

Darlington, P.J. 1970. A practical criticism of Hennig-Brundin "phylogenetic systematics" and Antarctic biogeography. *Systematic Zoology* **19**, 1-18.

De Broyer, C., Jazdzewski, K. & Dauby, P. 2003. Biodiversity patterns in the Southern Ocean: lessons from Crustacea. In: Huiskes, A.H.L., Gieskes, W.W.C., Rozema, J., Schorno, R.M.L., Van der Vies, S.M. & Wolff, W.J. (Eds.). *Antarctic Biology in a Global Context*. Backhuys Publishers, Leiden, pp. 201-214.

Déharveng, L. 1981. Collemboles des iles subantarctiques de l'Océan Indien Mission J. Travé 1972-1973. *Comité National Française des Recherches Antarctiques* **48**, 33-108.

Delettre, Y.R., Frenot, Y., Vernon, P. & Chown, S.L. 2003. First record of *Telmatogeton* sp. (Diptera: Chironomidae) at Heard Island. *Polar Biology* **26**, 423-426.

Drake, J.M. & Lodge, D.M. 2003. Global hot spots of biological invasions: evaluating options for ballast-water management. *Proceedings of the Royal Society of London B* **271**, 575-580.

Duncan, R.P., Blackburn, T.M. & Sol, D. 2003. The ecology of bird introductions. *Annual Review of Ecology, Evolution, and Systematics* **34**, 71-98.

Eastman, J.T. 1993. *Antarctic Fish Biology. Evolution in a Unique Environment*. Academic Press, London, pp 1-322.

Edgar, E. & Connor, H.E. 2000. *Flora of New Zealand. Volume V Gramineae*. Manaaki Whenua Press, Lincoln, N.Z.

Ernsting, G. 1993. Observations on life cycle and feeding ecology of two recently introduced predatory beetle species at South Georgia, sub-Antarctic. *Polar Biology* **13**, 423-428.

Evans, K.L., Warren, P.H. & Gaston, K.J. 2004. Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews* **79**, 1-25.

Fenchel, T. 1993. There are more small than large species? *Oikos* **68**, 375-378.

Finlay, B.J., Esteban, G.F. & Fenchel, T. 1996. Global diversity and body size. *Nature* **383**, 132-133.

Frenot, Y., Chown, S.L., Whinam, J., Selkirk, P.M., Convey, P., Skotnici, M., *et al.* 2005. Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews* **80**, 45-72.

Gaston, K.J. 1992. Regional numbers of insect and plant species. *Functional Ecology* **6**, 243-247.

Gaston, K.J. & Chown, S.L. 1999. Geographic range size and speciation. In: Magurran, A.E. & May, R.M. (Eds.). *Evolution of Biological Diversity*. Oxford University Press, Oxford, pp. 236-259.

Gaston, K.J., Jones, A.G., Hänel, C. & Chown, S.L. 2003. Rates of species introduction to a remote oceanic island. *Proceedings of the Royal Society of London B* **270**, 1091-1098.

Gorodkov, K.B. 1990. Dynamics of a distributional range: a general approach. I. *Entomological Review* **69**, 287-306.

Gorny, M. 1999. On the biogeography and ecology of the Southern Ocean decapod fauna. *Scientia Marina Supplement* **63**, 367-382.

Green, J., Holmes, A.J., Westoby, M., Oliver, I., Briscoe, D., Dangerfield, M., *et al.* 2004. Spatial scaling of microbial eukaryote diversity. *Nature* **432**, 747-750.

Greene, S.W. & Walton, D.W.H. 1975. An annotated check list of the sub-Antarctic and Antarctic vascular flora. *Polar Record* **17**, 473-484.

Gremmen, N.J.M. 1981. *The Vegetation of the Subantarctic Islands Marion and Prince Edward*. Dr. W. Junk, The Hague.

Gremmen, N.J.M. & Smith, V.R. 2008. Terrestrial vegetation and dynamics. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 215-244.

Gressitt, J.L. 1970. Subantarctic Entomology and Biogeography. *Pacific Insects Monograph* **23**, 295-374.

Greve, M., Gremmen, N.J.M., Gaston, K.J. & Chown, S.L. 2005. Nestedness of Southern Ocean island biotas: Ecological perspectives on a biogeographic conundrum. *Journal of Biogeography* **32**, 155-168.

Grobler, G.C., Janse Van Rensburg, L., Bastos, A.D.S., Chimimba, C.T. & Chown, S.L. 2006. Molecular and morphometric assessment of the taxonomic status of *Ectemnorhinus* weevil species (Coleoptera, Curculionidae, Brachycerinae) from the sub-Antarctic Prince Edward Islands. *Journal of Zoological Systematics and Evolutionary Research* **44**, 200-211.

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

Hall, K.J. 1990. Quaternary glaciations in the southern ocean: sector 0° long.-180° long. *Quaternary Science Reviews* **9**, 217-228.

Hänel, C. & Chown, S.L. 1999. Fifty years at Marion and Prince Edward Islands: A bibliography of scientific and popular literature. *South African Journal of Science* **95**, 87-112.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J.F., Kaufman, D.M., *et al.* 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* **84**, 3105-3117.

Hawkins, B.A. & Pausas, J.G. 2004. Does plant richness influence animal richness?: the mammals of Catalonia (NE Spain). *Diversity and Distributions* **10**, 247-252.

Hawkins, B.A. & Porter, E.E. 2003. Does herbivore diversity depend on plant diversity? The case of California butterflies. *American Naturalist* **161**, 40-49.

Headland, R.K. 1989. *Chronological List of Antarctic Expeditions and Related Historical Events*. Cambridge University Press, Cambridge.

Holdgate, M.W. 1960. The fauna of the mid-Atlantic islands. *Proceedings of the Royal Society of London B* **152**, 550-567.

Jablonski, D. & Lutz, R.A. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. *Biological Reviews* **58**, 21-89.

Jeannel, R. 1964. Biogéographie des terres Australes de l'Océan Indien. *Revue Francaise d'Entomologie* **31**, 319-417.

Jeschke, J.M. & Strayer, D.L. 2005. Invasion success of vertebrates in Europe and North America. *Proceedings of the National Academy of Sciences of the USA* **102**, 7198-7202.

Jones, A.G., Chown, S.L., Ryan, P.G., Gremmen, N.J.M. & Gaston, K.J. 2003. Conservation threats on Gough Island: a case study for terrestrial conservation in the Southern Oceans. *Biological Conservation* **113**, 75-87.

Jouventin, P. 1990. Shy albatrosses, *Diomedea cauta salvini* breeding on Penguin Island, Crozet Archipelago, Indian Ocean. *Ibis* **132**, 126.

Jouzel, J., Barkov, N.I., Barnola, J.M., Bender, M., Chappellaz, J., Genthon, C., *et al.* 1993. Extending the Vostok ice-core record of palaeoclimate to the penultimate glacial period. *Nature* **364**, 407-412.

Kalmar, A. & Currie, D.J. 2006. A global model of island biogeography. *Global Ecology and Biogeography* **15**, 72-81.

Kennedy, M. & Spencer, H.G. 2000. Phylogeny, biogeography, and taxonomy of Australasian teals. *Auk* **117**, 154-163.

Klok, C.J. & Chown, S.L. 2003. Resistance to temperature extremes in sub-Antarctic weevils: interspecific variation, population differentiation and acclimation. *Biological Journal of the Linnean Society* **78**, 401-414.

Knox, G.A. 1994. *The Biology of the Southern Ocean*. Cambridge University Press, Cambridge.

Kuschel, G. 1971. Entomology of the Aucklands and other islands south of New Zealand: Coleoptera: Curculionidae. *Pacific Insects Monograph* **27**, 225-259.

LeMasurier, W.E. & Thomson, J.W. 1990. *Volcanoes of the Antarctic Plate and Southern Oceans*. American Geophysical Union, Washington.

Lennon, J.J. 2000. Red-shifts and red herrings in geographical ecology. *Ecography* **23**, 101-113.

Lewis, P.N., Hewitt, C.L., Riddle, M. & McMinn, A. 2003. Marine introductions in the Southern Ocean: an unrecognised hazard to biodiversity. *Marine Pollution Bulletin* **46**, 213-223.

Lewis Smith, R.I. 1984. Terrestrial plant biology of the sub-Antarctic and Antarctic. In: Laws, R.M. (Ed.). *Antarctic Ecology Vol. 1*. Academic Press, London, pp. 61-162.

Livemore, R., Nankivell, A., Eagles, G. & Morris, P. 2005. Paleogene opening of the Drake Passage. *Earth and Planetary Science Letters* **236**, 459-470.

Lockhart, P.J., McLenachan, P.A., Harell, D., Glenny, D., Hudson, D. & Jenson, U. 2001. Phylogeny, radiation, and transoceanic dispersal of New Zealand alpine buttercups: Molecular evidence under split decomposition. *Annals of the Missouri Botanic Garden* **88**, 458-477.

Lomolino, M.V. 1996. Investigating causality of nestedness of insular communities: selective immigrations or extinctions? *Journal of Biogeography* **23**, 699-703.

Lonsdale, W.M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**, 1522-1536.

MacArthur, R.H. & Wilson, E.O. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton.

Marshall, D.J., Gremmen, N.J.M., Coetzee, L., OConnor, B.M., Pugh, P.J.A., Theron, P.D., *et al.* 1999. New records of Acari from the sub-Antarctic Prince Edward Islands. *Polar Biology* **21**, 84-89.

Marshall, J.E.A. 1994. The Falkland Islands: a key element in Gondwana paleogeography. *Tectonics* **13**, 499-514.

May, R.M., Lawton, J.H. & Stork, N.E. 1995. Assessing extinction rates. In: Lawton, J.H. & May, R.M. (Eds.). *Extinction Rates*. Oxford University Press, Oxford, pp. 1-24.

McDougall, I., Verwoerd, W. & Chevallier, L. 2001. K-Ar geochronology of Marion Island, Southern Ocean. *Geological Magazine* **138**, 1-17.

McDowall, R.M. 2002. Accumulating evidence for a dispersal biogeography of southern cool temperate freshwater fishes. *Journal of Biogeography* **29**, 207-219.

McGeoch, M.A., le Roux, P.C., Hugo, E.A. & Nyakatya, M. 2008. Spatial variation in the terrestrial biotic system. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 245-276.

McInnes, S.J. & Pugh, P.J.A. 1998. Biogeography of limno-terrestrial Tardigrada, with particular reference to the Antarctic fauna. *Journal of Biogeography* **25**, 31-36.

Morrone, J.J. 1998. On Udvardy's Insulantarctica province: a test from the weevils (Coleoptera: Curculionoidea). *Journal of Biogeography* **25**, 947-955.

Mortimer, E. & Jansen Van Vuuren, B. 2006. Phylogeography of *Eupodes minutus* (Acari: Prostigmata) on sub-Antarctic Marion Island reflects the impact of historical events. *Polar Biology* **30**, 471-76.

Muñoz, J., Felicísimo, A.M., Cabezas, F., Burgaz, A.R., Martínez, I. 2004. Wind as a long-distance dispersal vehicle in the Southern Hemisphere. *Science* **304**, 1144-1147.

Myburgh, M., Chown, S.L., Daniels, S.R. & Jansen Van Vuuren, B. 2007. Population structure, propagule pressure, and conservation biogeography in the sub-Antarctic: lessons from indigenous and invasive springtails. *Diversity and Distributions* **13**, 143-154.

Pakhomov, E.A. & Chown, S.L. 2003. The Prince Edward Islands: Southern Ocean Oasis. *Ocean Yearbook* **17**, 348-379.

Pakhomov, E.A. & Froneman, P.W. 2000. Composition and spatial variability of macroplankton and micronekton within the Antarctic Polar Frontal Zone of the Indian Ocean during austral autumn 1997. *Polar Biology* **23**, 410-419.

Pakhomov, E.A. & McQuaid, C.D. 1996. Distribution of surface zooplankton and seabirds across the southern ocean. *Polar Biology* **16**, 271-286.

Patterson, B.D. & Atmar, W. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society* **28**, 65-82.

Pugh, P.J.A. 1993. A synonymic catalogue of the Acari from Antarctica, the sub-Antarctic Islands and the Southern Ocean. *Journal of Natural History* **27**, 323-421.

Pugh, P.J.A. 2004. Biogeography of spiders (Araneae: Arachnida) on the islands of the Southern Ocean. *Journal of Natural History* **38**, 1461-1487.

Pugh, P.J.A., Dartnall, H.J.G. & McInnes, S.J. 2002. The non-marine Crustacea of Antarctica and the islands of the Southern Ocean: biodiversity and biogeography. *Journal of Natural History* **36**, 1047-1103.

Pugh, P.J.A. & Scott, B. 2002. Biodiversity and biogeography of non-marine Mollusca on the islands of the Southern Ocean. *Journal of Natural History* **36**, 927-952.

Razouls, S., Razouls, C. & De Bovee, F. 2000. Biodiversity and biogeography of Antarctic copepods. *Antarctic Science* **12**, 343-363.

Richardson, J.E., Fay, M.F., Cronk, Q.C.B. & Chase, M.W. 2003. Species delimitation and the origin of populations in island representatives of *Phylica* (Rhamnaceae). *Evolution* **57**, 816-827.

Ricklefs, R.E. & Lovette, I.J. 1999. The roles of island area *per se* and habitat diversity in the species-area relationship of four Lesser Antillean faunal groups. *Journal of Animal Ecology* **68**, 1142-1160.

Rivard, D.H., Poitevin, J., Plasse, D., Carleton, M. & Currie, D.J. 2000. Changing species richness and composition in Canadian national parks. *Conservation Biology* **14**, 1099-1109.

Rosenzweig, M.L. 1995. *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.

Scott, L. & Hall, K.J. 1983. Palynological evidence for interglacial vegetation cover on Marion Island, subantarctic. *Paleogeography, Paleoclimatology and Paleoecology* **41**, 35-43.

Selje, N., Simon, M. & Brinkhoff, T. 2004. A newly discovered *Roseobacter* cluster in temperate and polar oceans. *Nature* **427**, 445-448.

Selmi, S. & Boulinier, T. 2001. Ecological biogeography of Southern Ocean Islands: The importance of considering spatial issues. *American Naturalist* **158**, 426-437.

Sicinski, J. & Gillet, P. 2002. Biogeographical affinities of polychaets from Iles Crozet. *Antarctic Science* **14**, 353-363.

Siemann, E., Tilman, D., Haarstad, J. & Richie, M. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. *American Naturalist* **152**, 738-750.

Skottsberg, C. 1960. Remarks on the plant geography of the southern cold temperate zone. *Proceedings of the Royal Society of London B* **152**, 447-457.

Slabber, S. & Chown, S.L. 2002. The first record of a terrestrial crustacean, *Porcellio scaber* (Isopoda, Porcellionidae), from sub-Antarctic Marion Island. *Polar Biology* **25**, 855-858.

Smith, S.D.A. 2002. Kelp rafts in the Southern Ocean. *Global Ecology and Biogeography* **11**, 67-69.

Stanley, S.M. 1979. *Macroevolution. Pattern and Process*. Johns Hopkins University Press, Baltimore.

Stevens, M.I., Greenslade, P., Hogg, I.D. & Sunnucks, P. 2006. Southern Hemisphere springtails: could any have survived glaciation of Antarctica? *Molecular Biology and Evolution* **23**, 874-882.

Tréhen, P. & Voisin, J.-F. 1984. Sur la présence de *Merizodus soledadinus* Guérin à Kerguelen (Coléoptères *Trechidae*). *L'Entomologiste* **40**, 53-54.

Turbott, E.G. 1990. *The Checklist of the Birds of New Zealand and the Ross Dependency, Antarctica*. 3rd ed. New Zealand Ordnance Survey, Wellington.

Turner, P.A.M., Scott, J.J. & Rozefelds, A.C. 2006. Probable long distance dispersal of *Leptinella plumosa* Hook. f. to Heard Island: habitat, status and discussion of its arrival. *Polar Biology* **29**, 160-168.

Udvardy, M.D.F. 1987. The biogeographical realm Antarctica: a proposal. *Journal of the Royal Society of New Zealand* **17**, 187-194.

Valdebenito, H.A., Stuessy, T.F. & Crawford, D.J. 1990. A new biogeographic connection between islands in the Atlantic and Pacific Oceans. *Nature* **347**, 549-550.

Van de Vijver, B. & Beyens, L. 1999. Biogeography and ecology of freshwater diatoms in Subantarctica: a review. *Journal of Biogeography* **26**, 993-1000.

Van der Spoel, S. & Heyman, R.P. 1983. *A Comparative Atlas of Zooplankton. Biological Patterns in the Oceans*. Springer Verlag, Berlin.

Wagstaff, S.J. & Garnock-Jones, P.J. 1998. Evolution and biogeography of the Hebe complex (Scrophulariaceae) inferred from ITS sequences. *New Zealand Journal of Botany* **36**, 425-437.

Wallace, P.J., Frey, F.A., Weis, D. & Coffin, M.F. 2002. Origin and evolution of the Kerguelen Plateau, Broken Ridge, and Kerguelen Archipelago: Editorial. *Journal of Petrology* **43**, 1105-1108.

Warham, J. 1996. *The Behaviour, Population Biology and Physiology of the Petrels*. Academic Press, London.

Whittaker, R.J. 1998. *Island Biogeography. Ecology, Evolution, and Conservation*. Oxford University Press, Oxford.

Wilkinson, D.M. 2001. What is the upper size limit for cosmopolitan distribution in free-living micro-organisms? *Journal of Biogeography* **28**, 285-291.

Williamson, M. 1996. *Biological Invasions*. Chapman and Hall, London.

Williamson, M. & Fitter, A. 1996. The varying success of invaders. *Ecology* **77**, 1661-1666.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. 2003. Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. *Annual Review of Ecology and Systematics* **34**, 273-309.

Wright, D.H., Patterson, B.D., Mikkelson, G.M., Cutler, A. & Atmar, W. 1998. A comparative analysis of nested subset patterns of species composition. *Oecologia* **113**, 1-20.

Wylie, J.L. & Currie, D.J. 1993. Species-energy theory and patterns of species richness: I. Patterns of bird, angiosperm, and mammal richness on islands. *Biological Conservation* **63**, 137-144.

Young, E.C. 1995. Conservation values, research and New Zealand's responsibilities for the Southern Ocean Islands and Antarctica. *Pacific Conservation Biology* **2**, 99-112.

CHAPTER 12

CONSERVATION AND MANAGEMENT

MARIENNE S. DE VILLIERS AND JOHN COOPER

Human interest in the Prince Edward Islands was initially commercial, centred on the economic worth of resources such as the large populations of breeding seals. Later, the interest was strategic due to the islands' location in the Southern Ocean between South Africa and the Antarctic Continent (Cooper & Headland 1991; Cooper 2008). This location also made the islands valuable to South Africa as a centre from which to predict weather. Although this is still an important consideration, the islands are increasingly valued for their worth in terms of research and conservation. Islands in the Southern Ocean are prized in this regard because they are few and isolated, have had relatively low levels of human impact, and have unique species assemblages. The sub-Antarctic region has experienced a relatively rapid increase in temperature compared with the rest of the world. The Prince Edward Islands, with their relatively simple terrestrial ecosystems, represent ideal sites for the study of ecosystem processes and their responses to climate change (Pakhomov & Chown 2003). The islands also act as a "frontier zone" in terms of monitoring and/or regulating environmental impacts in Antarctica (PEIMPWG 1996). Furthermore, the Prince Edward Islands and their surrounding waters serve as breeding and moulting grounds for up to five million top predators seasonally, providing feeding grounds for seabirds, seals and migrating whales, and support a commercially exploited demersal fish population (Pakhomov & Chown 2003).

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 301-330

Despite the value of the islands from a conservation and research perspective, they are subject to a number of threats. These include the introduction of alien species, the depletion of and effect of climate change on marine resources, pollution of the marine inshore and terrestrial environments, and disturbance of wildlife and significant sites. These are threats common to all Southern Ocean islands (De Villiers *et al.* 2006a) and active management is necessary to control or limit them. This chapter first summarises the evolution of the management of the Prince Edward Islands over the period of nearly sixty years since annexation. It then elaborates on the major conservation concerns at the Prince Edward Island group, and considers actions that have been or should be taken to address these concerns, thus ensuring the continued protection of the group.

12.1 The evolving management of the islands

A growing appreciation of the intrinsic ecological value of the Prince Edward Islands has been reflected by the increasing levels of protection afforded to them over the years (Cooper & Condy 1988; Visagie 1988; Cooper 1995a; PEIMPWG 1996). This protection has come in the form of national legislation, and through international instruments to which South Africa is a party (Table 12.1). After annexation in 1948, the islands (extending to the low-water mark) were first administered by the Department of Transport. They are currently managed by the South African Department of Environmental Affairs and Tourism (henceforth referred to as the Department). In 1985 this department, then the Department of Environment Affairs, took over as the management authority of the island group. The islands were administered in an essentially *ad hoc* manner for the first four decades following their annexation, with no formal document setting out management procedures. In 1982, a "Code of Conduct for the Environmental Protection of the Prince Edward Islands" was developed (Visagie 1988). This was formally adopted in 1988 (Cooper & Condy 1988) and the islands were managed according to this code of conduct until the adoption of the first management plan in 1995 (see below). Although the islands' seals and seabirds were (and still are) protected by the Sea Birds and Seals Protection Act (Act No. 46 of 1973), the islands were only accorded formal nature reserve status in November 1995, when they were declared a Special Nature Reserve (equivalent to the World Conservation Union's Protected Area Management Category Ia: area managed mainly for science or wilderness protection), in terms of the Environmental Conservation Act (Act No. 73 of 1989) (Cooper 1995a; PEIMPWG 1996; Hänel & Chown 1998).

Table 12.1 Protection offered to the Prince Edward Islands and surrounding waters by national legislation and international agreements (adapted from Chown *et al.* 2006).

	International agreement	National legislation
Terrestrial and Marine Environment	Convention on Biological Diversity (CBD)	Environment Conservation Act (No. 73 of 1989)
	Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR)	National Environmental Management Act (NEMA) (No. 107 of 1998) and subsequent amendments
	Kyoto Protocol to the United Nations Framework Convention on Climate Change	National Environmental Management: Protected Areas Act (NEMPAA) (No. 57 of 2003)
	United Nations Framework Convention on Climate Change (UNFCCC)	National Environmental Management: Biodiversity Act (NEMBA) (No. 10 of 2004)
	Montreal Protocol – Protocol for the Protection of the Ozone Layer	National Environmental Management: Air Quality Act (No. 39 of 2004)
	African Convention on the Conservation of Nature and Natural Resources (Algiers Convention)	
	Convention on Wetlands of International Importance especially as Waterfowl Habitat (Ramsar Convention)	
	World Heritage Convention – Convention Concerning the Protection of the World Cultural and Natural Heritage	
Marine environment only	Convention on Prevention of Dumping of Waste from Ships and Aircraft	Carriage of Goods by Sea Act (No. 1 of 1986)
	International Convention for the Prevention of Pollution from Ships (MARPOL)	Dumping at Sea Control Act (No. 73 of 1980)
	Paris Convention on Prevention of Marine Pollution from Land-based Sources	Hazardous Substances Act (No. 15 of 1973)
	United Nations Convention on the Law of the Sea	Marine Living Resources Act (No. 18 of 1998)
	Agreement for the Implementation of the Provisions of the United Nations Convention on the Law of the Sea	Marine Pollution (Prevention of Pollution from Ships) Act (No. 2 of 1986)
		Maritime Zones Act (No. 15 of 1994)
		National Environmental Management: Coastal Zone Management Bill

Table 12.1 Continued.

	International agreement	National legislation
Species	Agreement on the Conservation of Albatrosses and Petrels (2004)	Sea Birds and Seals Protection Act (No. 46 of 1973)
	Bonn Convention – Convention on the Conservation of Migratory Species of Wild Animals (CMS)	Marine Living Resources Act (No. 18 of 1998)
	Convention on Biological Diversity (CBD)	National Environmental Management: Biodiversity Act (NEMBA) (No. 10 of 2004)
	Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR)	Seabirds, Shorebirds and Seals Conservation Act (in draft form)
	Convention for the Conservation of Antarctic Seals	
	Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)	
	International Convention for the Regulation of Whaling (IWC)	
	International Plan of Action for Reducing Incidental Catch of Seabirds in Longline Fisheries of the Food and Agricultural Organization of the United Nations (FAO IPOA-Seabirds)	National Plan of Action for Reducing Incidental Catch of Seabirds in Longline Fisheries (in draft form)
Cultural Heritage	World Heritage Convention – Convention Concerning the Protection of the World Cultural and Natural Heritage	National Heritage Resources Act (No. 25 of 1999)
		Maritime Zones Act (No. 15 of 1994)

Since 1996, the islands have been environmentally managed by the Department's Directorate: Antarctica & Islands, acting on the advice of the Prince Edward Islands Management Committee and according to the Prince Edward Islands Management Plan (PEIMPWG 1996). The objectives of this first management plan reflected the current emphasis on conservation and research and included the maintenance of biological diversity, the minimisation of interference with natural processes and of the destruction or degradation of natural and historical features, the encouragement of activities aimed at restoring and rehabilitating damage due to local human activities, the encouragement of research supporting these aims, and the creation of an awareness of the value and fragility of the islands' ecosystems (PEIMPWG 1996).

From the end of 2007 (when the term of the current management committee expires) the management of the islands will follow the provisions of a new environmental management plan produced under contract (Chown *et al.* 2006), which currently (June 2007) has been accepted by the Department but not yet formally adopted by the Minister of Environmental Affairs and Tourism (C.A. Jacobs, personal communication). The new plan aims to ensure the ongoing protection and conservation of the islands by providing a comprehensive set of management provisions. It is much more detailed than its predecessor, following principles set out in the ISO 14000 Environmental Management Systems Standards that require harmful effects on the environment to be minimized. Significantly, it also aims to achieve continual improvement in environmental performance. The new management plan will thus be an evolving document that can be updated piecemeal as new understandings and findings are made by a process of "adaptive management." This process will be supported by regular reviews and auditing procedures, taking into account best practice as developed elsewhere in the world but especially at other Southern Ocean islands (see De Villiers *et al.* 2006a). The new plan sets out in detail provisions for management in terms of administration, biodiversity conservation, historical conservation and waste management (Chown *et al.* 2006). It defines five management zones and the activities that may take place in these, with access defined according to a permitting system. On Marion Island there is a Service Zone around the base (high level of human traffic) and a Natural Zone near the base and at the field huts (limited free walking). The rest of the island is defined as a Wilderness Zone (no general access), except for certain areas sensitive to human interference which are defined as Limited Access Zones (access to scientists and support personnel of approved projects only). All of Prince Edward Island is defined as a Protected Zone, with strict limits on the frequency and duration of visits, and the number of visitors (Chown *et al.* 2006).

In June 2006, a process began whereby responsibility for environmental management at the Prince Edward Islands was handed over by the Department's Directorate: Antarctica & Islands to its Directorate: Environmental Impact Management, to which new staff have been appointed (C.A. Jacobs, personal communication). The exact new management structure is still to be elucidated, but it is expected that the existing management committee will be replaced by a Prince Edward Islands Management Authority, appointed by the Minister in terms of the National Environmental Management: Protected Areas Act (Act No. 57 of 2003). Unlike the current management committee, the role of which was purely advisory, the management authority will have the functions of management (including the issuing of permits) and the evaluation of research proposals (PEIMPWG 1996; Chown *et al.* 2006). However, following the provisions of the act's regulations, the new management plan allows for the management authority to appoint one or more committees of experts to advise it, by way of inviting nominations from interested and affected parties (Chown *et al.* 2006).

Although the National Environmental Management: Protected Areas Act upholds the Special Nature Reserve status of the Prince Edward Islands, the National Environmental Management: Biodiversity Act (Act No. 10 of 2004) is also of particular relevance to the management of the islands. This act allows for the management authority of the islands to produce biodiversity management plans for threatened species and bioregional plans, to manage threatening processes at the islands (in particular, it requires the listing of invasive species) and to ensure the monitoring of biodiversity.

Increased concern for the islands is also evidenced by the requirement (formal since 1995) for Environmental Impact Assessments (EIAs) to be performed prior to any major construction or human activity (PEIMPWG 1996; Chown *et al.* 2006). No EIA was undertaken for the construction of the existing meteorological base on Marion Island, or for the many subsequent enlargements and reconstructions of this facility. Similarly, no EIAs were performed for the placement (and replacement) of field huts from 1974 onwards, or for the failed hydro-electric scheme constructed in the 1980s. The first EIA conducted was for the abortive proposal in the 1980s to establish an emergency landing facility for fixed-wing aircraft on Marion Island (Heymann *et al.* 1987). The construction of a new and modern research facility to replace the old base on Marion Island commenced in 2003. A scoping document, broadly equivalent to an EIA, was produced for the replacement research base which is still under construction (Environomics 2002). An EIA will be required for the decommissioning of the current base and its associated structures, and for the positioning of new field huts planned to take place in 2007 (C.A. Jacobs, personal communication).

Public awareness and co-operation is of utmost importance in the conservation of the Prince Edward Islands. Copies of the 1996 management plan and a visitors' guide (Hänel & Chown 1998) are made available to all visitors on board vessels bound for the islands, and at the base on Marion Island. A Conservation Officer, appointed on the recommendation of the management committee, accompanies relief voyages to the island and presents an on-board talk to all expedition members, highlighting the major conservation issues and ways in which these are addressed. The Conservation Officer is on hand to answer conservation-related questions during the time spent on Marion Island, and to ensure that visitors to the island adhere to their permit conditions. Codes of conduct are also described in the visitor's guide (Hänel & Chown 1998). The revised management plan addresses the raising of awareness among visitors to the islands, the training and education of personnel involved at the islands, and stresses the importance of ongoing capacity building (Chown *et al.* 2006). A member of each over-wintering team is also appointed a Conservation Officer, responsible for conservation issues outside the periods of annual relief voyages.

12.2 Major conservation concerns at the islands

12.2.1 Introductions of alien species

One of the greatest threats to biodiversity is that of biological invasion. There is a clear link between the number of alien species present on Southern Ocean islands and the number of human visitors over the last 200 years (Chown *et al.* 1998). Alien microbes, fungi, plants or animals occur on all sub-Antarctic islands and their introductions have been associated with the movement of people and cargo in connection with research and commercial and tourist activities (Frenot *et al.* 2005). In the five decades since the first terrestrial biological research expedition to the Prince Edward Islands in 1965, 63 teams have stayed for varying periods on Marion Island and various other expeditions have been made to the island group. The construction of the new research base on Marion Island, beginning in 2003, was associated with an increase in the number of annual voyages, personnel and supplies to that island. There has also been interest expressed in the islands by tour companies, with three applications for visits made in the 1990s (Heydenrych & Jackson 2000) and one offshore cruise made into the islands' territorial waters in 2002 (P.G. Ryan, personal communication). Land-based tourism is, however, prohibited in terms of the islands' current Special Nature Reserve status and the National Environmental Management: Protected Areas Act.

The Prince Edward Islands have experienced a number of introductions of alien species (e.g. Gremmen 1975; Watkins & Cooper 1986; Gremmen & Smith 1999; Chown *et al.* 2002; Frenot *et al.* 2005). These have been most numerous on Marion Island, which has received the majority of the human visitors to the island group (no base or field huts are present on Prince Edward Island). Most introductions occurred shortly after annexation in 1948, when maintaining a political presence rather than conservation was the focus of human activity at the islands. Several introductions were deliberate, such as that of German Merino Sheep *Ovis aries* in 1959 and Brown Trout *Salmo trutta* in 1964 (Watkins & Cooper 1986). Some were made through ignorance or lack of forethought, or by accident. For example, the House Mouse (*Mus musculus domesticus*, Jansen Van Vuuren & Chown 2007) was introduced to Marion Island in the early 1800s and the aggressive invading grass, the Creeping Bent *Agrostis stolonifera*, was most probably introduced with sheep fodder and first noticed on the island in 1965 (Watkins & Cooper 1986; Cooper 1995b; Cooper 2008) (Table 12.2). One of the most devastating deliberate introductions was that of the Domestic Cats *Felis catus* in 1949, in an attempt to control the House Mouse population at the meteorological base on Marion Island (Cooper 2008). The cats became feral and this resulted in the deaths of many thousands of burrowing petrels (Cooper & Fourie 1991; Cooper *et al.* 1995) (Table 12.2).

Table 12.2 Selected examples of alien species introductions and their management at Marion Island.

Alien species (status)	Details of introduction	Possible or actual effects	Management action taken or proposed	Success of management action
Mammals				
House Mouse *Mus musculus* (naturalised, widespread)	Introduced to Marion Island in the early 1800s via sealing vessels; abundant by 1818 and now widespread over the entire island.[1]	Destruction by burrowing of cushion plants *Azorella selago*,[2] consumption of seeds of plants such as the sedge, *Uncinia compacta*;[3] predation of indigenous invertebrates including the endemic flightless moth *Pringleophaga marioni* and ectemnorhine weevils[3,4] responsible for litter turnover rates and nutrient release.[1] Competition with the declining population of Lesser Sheathbills *Chionis minor* for invertebrate prey.[5] Possible predation on seabird chicks, as recorded on Gough Island.[6]	Investigation of feasibility of eradication by poison bait distributed aerially. If no action taken, global warming likely to improve mouse survival and thus increase their impacts on ecosystem functioning.[7]	*Ad hoc* trapping in research base and field huts. No official eradication or control programme yet, although draft brief has been written for a consultancy to assess feasibility of eradication.
Domestic Cat *Felis catus* (extinct)	Five individuals deliberately introduced in 1949 in an attempt to control House Mice. Feral by 1951 and population estimated at over 2000 individuals by 1975[8].	Predation on burrowing petrels. Decrease in breeding success of some species, e.g. Great-winged Petrels *Pterodroma macroptera*[9] and Blue Petrels *Halobaena caerulea*.[10] Common Diving Petrel *Pelecanoides urinatrix* presumed locally extinct due to cat predation.[11]	An eradication programme ran from 1977-1990. First utilised an introduced viral disease *Feline panleucopaenia* ("cat flu") to reduce cat numbers, followed by night-shooting, trapping and poisoning.[12]	100% successful – no cats seen on the island since 1991.[12]
Invertebrates				
Diamondbacked Moth *Plutella xylostella* (naturalised)	Thought to have reached Marion Island in 1985, on its own or with fresh cabbages supplied to the research station.[13]	Feeds on leaves and growing points of the indigenous and quite scarce Kerguelen Cabbage *Pringlea antiscorbutica*.[14] Causes occasional, severe damage but does not appear to pose a severe threat to this species.[15]	None. However, the major limiting factor for this species on Marion Island is frost,[15] and the effects of global warming may necessitate the consideration of management action.	Not applicable.

Table 12.2 Continued.

German Cockroach *Blatella germanica* (transient?)	Thought to have first been introduced to Marion with vegetable supplies.[1] During the 2003 relief voyage to Marion Island, live cockroaches were discovered in an offloaded container of canned drinks.[16]	Can act as vectors for pathogens, many of which are harmful to humans.[17] Control would involve the use of insecticides which may be detrimental to indigenous invertebrates.	Container was transported back to the supply vessel and sprayed with insecticide. All packages of drinks were visually inspected and live cockroaches were killed (about 40). [16]	Since this incident, isolated live cockroaches have occasionally been found at the base, and fumigation of the whole base is under consideration.
Plants				
Creeping Bent *Agrostis stolonifera* (naturalised, widespread)	First recorded on Marion Island in 1965, and likely to have been introduced via sheep fodder.[1]	Expanding its range and now dominates numerous habitats. Replaces the native Dwarf Shrub *Acaena magellanica* and substantially reduces plant diversity in areas where it predominates. For example, it is estimated that once all *Acaena* dominated habitats have been invaded, the total number of plant species occurring in these habitats will be reduced by 30%.[18]	Not considered feasible.[19]	Not applicable.
Quackgrass *Elymus repens* (naturalised, restricted)	Currently restricted to one large patch of about 250 m^2 on Marion Island.[19]	Considered one of the world's worst weeds. For example, it can strongly impact ecosystem nitrogen leaching.[20] On Marion Island, *E. repens* can spread rapidly and dominate other species in a stand of vegetation.[21]	Eradication process commenced in 2006, cutting of above-ground herbage followed by repeated spraying with herbicide.[22]	Not yet evaluated.
Microbes				
Fungal pathogen *Botryotina fuckeliana*	Probably transferred to Marion Island on fresh vegetables.[23]	Causes grey mould rot in vegetables. Now infects entire stands of the Kerguelen Cabbage *Pringlea antiscorbutica.*[23]	None, but no further transport of fresh produce to the islands allowed.	Not applicable.

[1]Watkins & Cooper 1986, [2]Chown & Cooper 1995, [3]Chown & Smith 1993, [4]Crafford & Scholtz 1987, [5]Huyser *et al.* 2000, [6]Angel & Cooper 2006, [7]Smith & Steenkamp 1990, [8]Van Aarde 1979, [9]Cooper & Fourie 1991, [10]Cooper *et al.* 1995, [11]Brooke 1984, [12]Bester *et al.* 2002, [13]PEIMPWG 1996, [14]Crafford & Chown 1987, [15]Crafford & Chown 1990, [16]Cooper *et al.* 2003, [17]Roth & Willis 1960, [18]Gremmen *et al.* 1998, [19]Gremmen 2004, [20]Knops *et al.* 2002, [21]Gremmen 1975, [22]S.L. Chown, personal communication, [23]Kloppers & Smith 1998.

Since the 1970s, with an increased awareness of the potential impacts of introduced non-native biota, attempts have been made to eradicate established alien species from Marion Island (Cooper *et al.* 2003). In 1984, Brown Trout were removed from the Van den Boogaard River (Cooper *et al.* 1992). Feral cats were eradicated in 1991, after a lengthy and sustained effort that began in 1977 (Bester *et al.* 2002, Table 12.2). Currently, there is a focus on the eradication or control of small, localized populations of the alien grass Red Top *Agrostis gigantea* (Gremmen & Van der Meijden 1995; Gremmen & Smith 1999; Slabber & Chown 2002). In 2006, a concerted effort was initiated to eradicate an isolated stand of Quackgrass *Elymus repens* at the site of a camp established near a shipwreck at Ship's Cove on the eastern side of the island (S. Kritzinger-Klopper & S.L. Chown, unpublished data, Plate 12.1). A plan for the management of alien vascular plants on the Prince Edward Islands has been drawn up (Gremmen 2004) and the Department's Directorate: Environmental Impact Management intends to appoint an Aliens Officer on the over-wintering team on Marion Island to continue the process of alien plant control. A feasibility study has been commissioned to investigate the eradication of the House Mouse from Marion Island and a pilot study on the likely effects of poison bait on selected non-target species was undertaken in August 2006 (J. Cooper, unpublished data). However, eradication efforts of alien species are likely to be hampered by the effects of climate change. Warmer climates will not only facilitate the establishment of alien species, but will also enable already-established species to expand their ranges and to aggravate their effects on local species and ecosystems (Pakhomov & Chown 2003).

The eradication of established alien organisms is costly, time-consuming and labour-intensive. For some species on the Prince Edward Islands, eradication is being considered, e.g. for the House Mouse on Marion Island. For others, it is simply not considered feasible, e.g. for the well-established Creeping Bent and the slug *Deroceras panormitanum* on Marion Island, and Procumbent Pearlwort *Sagina procumbens* on both Marion and Prince Edward Islands (Cooper *et al.* 2003; Ryan *et al.* 2003; Gremmen 2004). The prevention of new alien species introductions is therefore of paramount importance for the continued conservation of the islands. Prince Edward Island is one of the most pristine of the Southern Ocean Islands, having never supported any alien vertebrate species and currently only supporting three species of alien vascular plants and very few known alien invertebrates (Chown *et al.* 1998; Ryan *et al.* 2003; Hugo *et al.* 2006). Because of the link between the number of alien species introductions and the number of human visitors (Chown *et al.* 1998), the first management plan restricted visits to Prince Edward Island to only one a year, by up to six people, for a maximum of four days per visit. The new management plan calls for a limit on visits to one every two years, by a maximum of 10 people for a maximum duration of eight days (Chown *et al.* 2006). Overnight access to Marion Island will be restricted by the number of beds available at the base, i.e. 80, when the construction of the new base is completed.

In recent years, there has been a dramatic increase in the stringency of the quarantine procedures followed during visits to the islands, on the advice of the management committee (Cooper *et al.* 2003). Quarantine measures are especially strict for Prince Edward Island (Cooper *et al.* 2003; Chown *et al.* 2006), due to its relatively pristine state. These and other procedures have now been formally incorporated into the revised management plan (Chown *et al.* 2006). In an attempt to raise awareness regarding the dangers of alien introductions and to eliminate personal gear as a source of introductions, all visitors to the islands participate in a compulsory "Boot-washing Ceremony" aboard the vessel on southbound journeys, whereby all protective clothing and field gear is inspected and cleaned (Plate 12.2). Particular attention is paid to cargo items which have the potential to act as vectors for alien species (de Villiers *et al.* 2006b) – cargo containers bound for the sub-Antarctic have been found to harbour spider webs, seeds and other plant material (Whinam *et al.* 2005). Fresh produce on the islands is prohibited – leafy vegetables, especially, can harbour substantial numbers of invertebrates such as aphids, spiders, moths, beetles, nematodes and even snails. Fresh vegetables were probably the source of the fungal pathogen *Botryotina fuckeliana*, which has infected the Kerguelen Cabbage *Pringlea antiscorbutica* on Marion Island (Kloppers & Smith 1998). Due to concern over potential human-assisted introductions of avian diseases to the bird populations at the Prince Edward Islands, various restrictions are in effect regarding poultry products. These include a ban on all poultry products on Prince Edward Island. On Marion Island, only canned poultry products may be used at field huts and only canned, de-boned or irradiated (eggs) poultry products at the base (de Villiers *et al.* 2006a). The revised management plan calls for a complete ban on eggs at both islands (Chown *et al.* 2006). The risk of transmitting bovine tuberculosis and other contagious diseases through dairy products will be minimised by only allowing pasteurised and sterilised dairy products on the supply vessel and on the islands (Chown *et al.* 2006).

One major potential source of contamination during sub-Antarctic voyages is the transport used for ship-to-shore transfers (Whinam *et al.* 2005). Vessels and helicopters bound for the Prince Edward Islands are thoroughly checked. However, little is as yet known about the actual or potential transfer of littoral organisms from the supply vessel's hull or ballast water tanks to the waters surrounding the Prince Edward islands, although the potential for this does exist (e.g. Lewis *et al.* 2003). Although ballast water is typically not discharged at the islands, this might be a concern during the decommissioning of the old base, when an unloaded vessel will take on several tonnes of cargo at the island. More significantly, recent work has identified substantial hull-fouling communities on the Antarctic research/supply vessel *S.A. Agulhas*, which ordinarily undertakes the annual relief voyages to Marion Island, and large populations of the invasive mussel, *Mytilus galloprovincialis*, in its sea chests (Lee & Chown 2007).

The construction of the new research base on Marion Island, which commenced in 2003, has resulted in an additional three voyages per year to Marion Island by the *S.A. Agulhas* until construction is completed. Associated with these extra voyages are an increase in the number of visitors and in the type and quantity of provisions and supplies taken to the island. This has created new opportunities for the introduction of alien species to the island, a fact which was recognized in the scoping study for the new facility (Environomics 2002). Project Environmental Officers are appointed for each voyage during the construction phase and strict quarantine procedures are in place for construction voyages. As part of the intended decommissioning of the old base, there is to be an emphasis on site rehabilitation (including the re-establishment of natural vegetation on the site and the prevention of further spreading of alien species from it), following a comprehensive Environmental Impact Assessment (Environomics 2002).

Despite the quarantine measures now associated with voyages to the islands, previously unrecorded alien invertebrates and plants are still intermittently discovered at Marion Island. Recent introductions have mostly been found in the vicinity of the base (Hänel *et al.* 1998; Gremmen & Smith 1999). During the 2003 relief voyage to Marion Island, for example, live German Cockroaches *Blatella germanica* were discovered in offloaded containers of canned drinks (Cooper *et al.* 2003). The cockroaches were transported to the island in the cardboard packaging holding the cans, and are believed to have originated from the premises of the supplier in Cape Town. Despite a seemingly successful effort to deal with this invasion at the time, cockroaches have been occasionally found in the base buildings during or shortly after relief visits. Although incidents such as this usually involve only one or a few organisms, occasionally larger numbers of organisms are involved. For example, large numbers of House Crickets *Gryllus bimaculatus* were present on board the *S.A. Agulhas* during its southbound voyage to Marion Island in 2002. Emergency efforts to locate and kill individuals included a thorough wash-down of the vessel's decks and outer spaces (now recommended as a routine procedure for southward voyages), and none of the insects apparently survived to find their way onto the island (J. Cooper, unpublished data). By contrast, an isopod, *Porcellio scaber*, and a parasitic wasp, *Aphidius matricariae*, have established recently (Slabber & Chown 2002; Lee *et al.* 2007). In 2004, several seeds of the Australian invasive tree, Rooikrans (or Red Eye) *Acacia cyclops* were discovered in the ship's hold during a construction voyage. Although the holds were subsequently fumigated with Methyl Bromide, a trial revealed that this treatment did not prevent germination of the seeds (M.S. de Villiers, unpublished data). In October 2006 an alien plant, tentatively identified as Cats-ear *Hypochoeris radicata*, was discovered at one of the field huts on Marion Island (S.L. Chown, personal communication). *Hypochoeris radicata* was first collected on the island in 1953 and had last been seen in 2002 (Gremmen 2004). The death of approximately two thousand Macaroni Penguins *Eudyptes chrysolophus* in 2004 (Plate 12.3) was probably due to disease, as the necropsy of two affected birds indicated the presence of Avian Cholera *Pasteurella multocida* (Crawford *et al.* 2005).

Human passage through dense seabird breeding colonies has the potential to spread parasites and pathogens from one colony to another, and this incident led to the drafting of procedures to be followed in the event of future disease outbreaks (R.J.M. Crawford, personal communication). These prioritise the prevention of the spread of pathogens to other colonies by restricting access to affected colonies to scientists performing essential research, and by requiring such scientists to disinfect their outer protective clothing and footwear before moving on to other locations. The new management plan lists actions to be taken in the case of unusual wildlife mortalities, and calls for the drafting of a disease contingency plan by the islands' management authority (Chown *et al.* 2006).

Each incident of an alien species introduction identifies shortcomings in existing quarantine procedures and suggests improvements. Currently, these are discussed at management committee meetings, resulting in the ongoing development of effective quarantine procedures. This process is assisted by increased awareness on the part of the islands' management committee, researchers, support personnel and construction teams. However, it is recognized that such *ad hoc* responses to imminent or actual introductions are not ideal, and a comprehensive risk assessment was commissioned along with the updating of the management plan. The new plan includes a risk assessment framework (including species, vector and pathway risk assessments), as required under the National Environmental Management: Protected Areas Act.

12.2.2 Factors affecting marine resources

The most serious threat for many species of albatross and petrel is that of mortality associated with commercial longline fishing operations (Gales 1998). The Prince Edward Island group is an important breeding locality for nine affected species (five species of albatrosses and four species of large petrels of the genera *Macronectes* and *Procellaria*), all of which are listed as threatened or near-threatened by the World Conservation Union, and are also listed within the Agreement on the Conservation of Albatrosses and Petrels, of which South Africa is a founding Party (Cooper & Ryan 2001; BirdLife International 2004). The legal Patagonian Toothfish *Dissostichus eleginoides* fishery began in the islands' territorial waters and Exclusive Economic Zone in 1996, but illegal vessels had already been operating in the region for some time and this resulted in the near-collapse of the fishery (Pakhomov & Chown 2003). Large numbers of seabirds were estimated to have been killed on longline hooks during the first fishing season, largely due to high numbers of illegal vessels which were unlikely to be employing effective mitigation measures to prevent this (Nel *et al.* 2002a). The pelagic tuna *Thunnus* spp. fishery is the largest longline fishery in the Southern Ocean and trends in the breeding population sizes of four large procellariiform seabirds at Marion Island are matched by changes in effort by this fishery in the southern Indian Ocean (Nel *et al.* 2002a). Apart from being a primary cause of adult mortality, fisheries may have subtle impacts on seabird populations which may only become apparent over the long-term. For example, gender differences in the foraging ranges of Grey-headed Albatrosses *Thalassarche chrysostoma* and Wandering Albatrosses *Diomedea exulans* may result in differential mortality by longline fishing vessels of males and females, and this may ultimately alter the demographic structure of populations (Nel *et al.* 2000; Nel *et al.* 2002b).

In terms of the Marine Living Resources Act of 1998, no fishing is permitted inside an exclusion zone around the islands (Table 12.1). The recent extension of this zone from eight to 12 nautical miles, to include all of the territorial waters (T. Akkers, personal communication), offers full protection to the shallow waters linking the islands, to their biota, and to those seabird species affected by longlining. Protection is also enhanced for several declining populations of inshore-foraging seabirds, such as the Crozet Shag *Phalacrocorax [atriceps] melanogenis* and the Gentoo Penguin *Pygoscelis papua* (South Africa 2005). South Africa has drafted a National Plan of Action for Reducing Incidental Catch of Seabirds in Longline Fisheries (NPOA-Seabirds (Cooper & Ryan 2003; refer Table 12.1) in terms of guidelines set out by the Committee on Fisheries of the Food and Agriculture Organization of the United Nations (FAO). One of the aims of the draft plan is the reduction of seabird mortality from longlining around the Prince Edward Islands. Interim measures to reduce longline mortalities currently in place follow those adopted by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), of which South Africa is a member. These include only setting lines at night, weighing lines to maximize sinking rates, not dumping offal during setting, keeping deck lighting to a minimum, and using bird-scaring lines during setting. These measures have proved successful and, in combination with the progressive movement of fishing activities away from the islands over the years and the presence of observers on board legal vessels, contributed to a decrease in rates of seabird bycatch between 1996 and 2000 from 0.19 to 0.034 birds per 1 000 hooks (Nel *et al.* 2002c). Mortality has remained low in subsequent years (B.P. Watkins, personal communication).

The declaration of a large Marine Protected Area (MPA) around the islands is now under active consideration following a Ministerial announcement, and this will vastly expand the marine area that is legally protected (South Africa 2005; Lombard *et al.* 2007). This area is expected to include all territorial waters out to 12 nautical miles and at least some parts of the Exclusive Economic Zone out to 200 nautical miles, and will lead to the creation of one of the world's largest MPAs (South Africa 2005). The MPA will not only contribute to a national system of MPAs and to a developing network of MPAs within the Southern Ocean (including the existing marine reserves around the Australian islands of Macquarie and Heard and McDonald and New Zealand's Auckland Islands), but will also contribute to the recovery of the Patagonian Toothfish and will reduce bird bycatch by the toothfish fishery, particularly of albatrosses and petrels (Lombard *et al.* 2007). Furthermore, the MPA will allow for improved control of both legal and Illegal, Unreported and Unregulated (IUU) fishing. Currently, patrols of the waters around the islands to deter IUU fishing are carried out by naval and fisheries vessels. Three management zones are proposed within the MPA: four IUCN Category Ia reserves (13% of EEZ), two Conservation Zones (21% of EEZ) and three Category IV reserves in which regulated fishing will be allowed (remainder of the EEZ). The island group's ecosystems are hugely influenced by the relative positions of the sub-Antarctic Front and the Antarctic Polar Front. The proposed boundaries of the MPA will traverse latitudinal and longitudinal gradients, thus maximizing opportunities for incorporating the shifting position of these two oceanic fronts, which are critical to the offshore component of the Prince Edward Islands' ecosystem (Lombard *et al.* 2007). The declaration of the Marine Protected Area will also extend legal protection to cover the foraging ranges of a larger suite of seals and seabirds that breed on the Prince Edward Islands, and will offer protection to benthic and pelagic marine species of both deep waters and of sea mounts (South Africa 2005). However, even this extended protection will not cover the non-breeding ranges of many of the islands' pelagic predators, and will also not cover the foraging ranges during breeding of the more mobile species, such as the Wandering and Grey-headed Albatrosses and the Southern Elephant Seal *Mirounga leonina*.

Climate change has affected oceanic regimes, which have in turn changed the availability of seal and seabird prey close to the islands. Between 1969 and 1999, sea-surface temperature at Marion Island increased by 1.4°C (Mélice *et al.* 2003) and air temperature increased by 1.2°C (Smith 2002). The increase in sea-surface temperature may be related to a southerly shift in the mean position of the Sub-Antarctic Front, with the resultant advection of zooplankton and micronekton to the islands benefiting pelagic predators, but creating unfavourable feeding conditions for inshore feeders (Pakhomov & Chown 2003). Decreased food availability as a result of climate change has been implicated in the decline of three inshore-foraging species at the Prince Edward Islands: the Gentoo Penguin, Rockhopper Penguin *E. chrysocome* and Crozet Shag (Crawford *et al.* 2003a, 2003b, 2004). Climatic perturbations on a global scale may also influence breeding by seabirds, as evidenced by a marked difference in the breeding success of inshore and offshore foragers in 1997/1998, a season coinciding with a major *El Niño* Southern Oscillation event (Crawford *et al.* 2003c, 2004).

12.2.3 Litter, pollution and waste management

Conservation practices to deal with or prevent pollution were first outlined in 1988 (Cooper & Condy 1988) and were later described in the islands' first management plan (PEIMPWG 1996). These are summarised in de Villiers *et al.* (2006a) and have been elaborated in the revised management plan.

The principles of the waste-management practices outlined in the latter are to ensure that activities on the islands do not result in pollution, damage to the environment or the build up of waste, to reduce amounts of waste, and to consider waste storage, disposal and removal, including recycling and the reduction of waste at source (Chown *et al.* 2006). Waste-management practices for Prince Edward Island are especially stringent. Current waste-management practices at the islands have been the subject of a recent study (R. Kutranov, unpublished data).

Permanent onshore infrastructure is minimal on the Prince Edward Islands. No artificial structures currently exist on Prince Edward Island, whereas on Marion Island human activities are concentrated at the base and at eight field huts located around the island. There are, however, several obsolete structures on Marion Island, such as the derelict buildings and other structures associated with a disused hydro-electric scheme and the remains of several old field huts. The clearing of these sites is well-advanced and is expected to be completed as part of the decommissioning of the old base. It is a long-standing practice during the annual relief voyage for all onshore personnel to assist in a "chicken run," whereby the area around the base is cleared of all visible litter. Furthermore the Conservation Officer, with the aid of volunteers, undertakes "country cleanups," removing litter, rubble and defunct items such as aerial and marker poles at various field sites that have been earmarked for this purpose during annual relief visits (Plate 12.4). It is roughly estimated that about 20 tonnes of assorted materials have been removed in this way since 2002 (J. Cooper, unpublished data). This practice first began in 1992, when various construction materials were removed from the site of the small water-supply dam on the island (Cooper 1995a). All collected materials are removed from the island to continental South Africa for disposal. The new management plan calls for the continuation of such site cleanups, as well as for site rehabilitation according to an approved restoration plan (Chown *et al.* 2006). Researchers are also required to provide updated lists with GPS co-ordinates of all field markers, and unrecorded field markers are usually removed as they are encountered by Conservation Officers.

Currently, sewage at the base is not treated and is discharged directly into the sea. This will also be the practice at the new base, but it is intended that sewage will be held in a holding tank and only discharged into the sea after dark. The sewage will then be rapidly diluted by wave action and currents, and any concentration of solid content will be disseminated before daylight (Environomics 2002). Food waste (excluding poultry products, meat bones and cooking oil) is discharged directly into the ocean after dark to deter birds from scavenging from the offal, although giant petrels *Macronectes* spp. still scavenge at the waste disposal point (L. Clokie, personal communication). At the new base, it is intended that solid kitchen waste will first be macerated and flushed into a holding tank, to be discharged in the same way as sewage (Environomics 2002).

Packaging of supplies to the island is minimized as far as possible. Plastics, glass and metals are separated, separately containerized and shipped to South Africa for recycling (PEIMPWG 1996; Chown *et al.* 2006). Relatively low levels of chlorinated hydrocarbons have been found in birds' eggs collected at Marion Island in the past. However, a recorded increase in the levels of certain chemicals in the eggs of scavenging species was postulated to have as its source plastics incinerated at the base (Gardner *et al.* 1985). The incineration of plastics is no longer practiced. Non-toxic paper and cardboard waste is burnt in an outside incinerator on wind-free days, and the ash is collected and stored for shipment. It is intended that the new base will be supplied with a high-temperature incinerator to minimize atmospheric pollution. Investigations are underway to provide only biodegradable cleaning products for the new base. No other chemicals or hazardous wastes are disposed of through the waste-water system – these are stored separately in clearly marked containers for removal from the island. At field huts, human and food waste accumulates in shallow excavated pits (Plate 12.5) but the installation of alternative methods of sewage disposal is planned to coincide with the placement of the new field huts, probably in 2007 (A. Dreyer, personal communication). All other hut wastes are stored in sealable containers and transported directly back to the supply vessel by helicopter during annual relief voyages, for disposal in South Africa. On the construction site for the new research base, dedicated waste-disposal technicians keep the site free of litter, and the site is inspected daily when a Project Environmental Officer is present on the island. The burning of construction waste was initially prohibited (Environomics 2002) although large quantities of wooden packing material are permitted to be burnt on the island as a cost-saving exercise during construction of the new base. It is intended that the decommissioning of the old base will involve the complete removal of all structures as far as is feasible and as prescribed by an EIA (A. Dreyer, personal communication).

In 1980, several hundred Rockhopper Penguins died at Marion Island following the deliberate dumping of water-contaminated diesel fuel into the sea from the base (Williams 1984). Current procedures and attitudes make a recurrence of such an incident highly unlikely. Ship-to-shore transfer of diesel fuel is carefully monitored from an inflatable dinghy and the hose is pressure-tested before use. The fuel line on the island is regularly inspected for leaks and has internal valves at 30-m intervals to prevent the possibility of major spills. The supply vessel and base carry biodegradable fuel dispersant in case of spills. On shore, generator oil, diesel and other fuel waste are stored in drums which are shipped back to South Africa. The disposal of oil and other harmful substances by vessels visiting the islands is controlled by several regulations (Table 12.1). As yet, the islands have been unaffected by major oil spills such as those which have affected marine life off the South African coast. For example, the sinking of the bulk-ore carrier, the *Treasure*, near Cape Town in 2000, resulted in the oiling of almost 20 000 African Penguins *Spheniscus demersus* (Nel & Whittington 2003). Disaster was averted by a successful rehabilitation programme for oiled birds and by the temporary relocation of non-oiled birds from the area of the spill, but a similar event near the remote Prince Edward Islands would be catastrophic since there are no necessary materials and facilities on the islands to deal with the effects of a full-scale onshore oil spill. The new management plan calls for the drafting of an oil-spill contingency and rehabilitation plan (Chown *et al.* 2006).

Marine litter can have severe impacts on marine ecosystems. Plastic litter poses the greatest problem, as it is almost immune to degradation once at sea and can drift for years over vast distances (Ryan & Moloney 1993). Plastic items showing little sign of degradation are the most abundant type of beach litter (other than wood) found on the Prince Edward Islands (Ryan 1987; J. Cooper, personal observation). Such debris can become colonised by marine biota and assist in the transport of potentially invasive species to new locations through rafting. Although this issue has not been well-studied at the Prince Edward Islands, it has been demonstrated to be a real danger in other parts of the Southern Ocean (Barnes 2002; Barnes & Fraser 2003). Marine creatures can become entangled in objects such as discarded fishing line, resulting in injuries or the restriction of movement. Entangled individuals of several species of birds (Cooper & Condy 1988; Nel & Nel 1999) and all three species of seals (Hofmeyr *et al.* 2002) that breed on the Prince Edward Islands have been reported. Most of the marine debris found on Marion Island originates from the fishing industry (Ryan 1987; Nel & Nel 1999). Over the two seasons following the start of the Patagonian Toothfish industry in the Exclusive Economic Zone around the islands, there was a ten-fold increase in the incidence of fishing gear in marine debris at seabird colonies on Marion Island (Nel & Nel 1999). The incidence of entanglement of fur seals *Arctocephalus* spp. during a five-year period of long-line fishing in the waters around Marion Island was twice as high as it was during a similar period of time prior to long-line fishing in the region (Hofmeyr *et al.* 2002). Much larger proportions of wildlife populations ingest marine litter than are entangled by it (Ryan 1996). Ingested debris can cause death or debilitation by obstructing the digestive tract, or by reducing meal size or the urge to eat, and ingested plastic may be a source of toxic chemicals (summarized in Ryan 1990). Specimens of 23 of the 29 species of birds that breed at the Prince Edward Islands were examined and 17 of these were found to have ingested plastic to some degree (from Ryan 1987). Plastic particles were most frequent in Procellariiformes and the Blue Petrel *Halobaena caerulea* was the worst-affected species, with 92% of individuals found to have ingested plastic (Ryan 1987).

Several species of birds, notably burrowing petrels, are affected by light pollution associated with human activities at sea and on land. These birds are most active at night and are easily disorientated by bright lights. Especially on misty nights, they are at risk of flying into buildings or other tall structures and being injured (when they become vulnerable to predatory birds such as sub-Antarctic Skuas *Catharacta antarctica*) or killed. In the Southern Ocean, bird strikes on vessels may involve hundreds of birds; for example nearly 900 birds collided with a vessel's superstructure in South Georgia's maritime zone, and 215 of these subsequently died (Black 2005). There are no functioning outside lights at the existing base or huts on Marion Island, and all windows are fitted with black-out blinds which are closed at night. Blinds are also drawn at night on board the supply vessel when it is operating near the islands. Although night-lighting during evening work shifts has been kept to a minimum on the construction site, bird strikes do occasionally occur, e.g. on a misty evening in October 2004, 76 birds (mostly Salvin's Prions *Pachyptila salvini*) were stunned after flying into buildings (M. Wheeler, unpublished data). Bird strikes also occur at field huts (M.S. de Villiers, personal observation) but the replacement huts will be fitted with window blinds and this should reduce the number of strikes.

12.2.4 Disturbance

Human disturbance can reduce the breeding success of impacted species. Disturbance can have obvious, overt effects such as the abandonment of nests by birds and the creation of increased predation opportunities (Anderson & Keith 1980), or can cause potentially detrimental physiological changes indicated by, for example, increased stress hormone concentrations (e.g. Vleck *et al.* 2000) or increases in heart rates (e.g. Giese 1998). A reduction in the breeding success of Adélie Penguins *Pygoscelis adeliae* in Antarctica has been associated with tourist visits (Giese 1996; Woehler *et al.*1994). Perhaps the most extreme example of the potentially disastrous effects of disturbance is the death of 7 000 King Penguins *Aptenodytes patagonicus* on Macquarie Island, resulting from mass panic following the passage of an aircraft near the colony (Rounsevell & Binns 1991). On Marion Island, King Penguins at a breeding colony, and non-breeding Gentoo Penguins, also reacted with panic to overflights by a fixed-wing aircraft (Cooper *et al.* 1994a). Seals may also be sensitive to disturbance associated with aircraft activity (e.g. Born *et al.* 1999; M.S de Villiers & J. Cooper, personal observations).

During 1996 and 1997, the Department received three proposals for tourism to sub-Antarctic Marion Island, but none of these proposed visits transpired. An Environmental Impact Assessment (Heydenrych & Jackson 2000) outlined the potential positive and negative effects of land-based tourism on the island, and provided a list of recommendations should tourism be allowed. However, under the Special Nature Reserve status of the Prince Edward Islands, commercial onshore tourism is prohibited in terms of the National Environmental Management: Protected Areas Act of 2003 (see Table 12.1). In November 2002 the first vessel carrying tourists visited the island's inshore waters, although tourists were not permitted to disembark. Tourism aside, disturbance of wildlife can be caused by researchers, support personnel and logistic flight operations.

Several species of fauna on Marion Island are known to be especially vulnerable to disturbance and some broad guidelines are in place for their approach. The disappearances of colonies of both Gentoo Penguins (Crawford 1952; Crawford *et al.* 2003a) and Southern Giant Petrels *M. giganteus* (Nel *et al.* 2002a) close to the island's base are thought to have been the result of human disturbance. Breeding colonies of these species are classified as limited access zones (entrance by special permit only), with a minimum approach distance of 100 m, and the management committee has recently recommended that this also apply to colonies of Crozet Shags following the proposal of Crawford *et al.* (2003b). The numbers of Wandering Albatrosses breeding within 200 m of the base more than halved within the first two decades of human occupation (deduced from maps published by La Grange 1962; Van Zinderen Bakker Jr. 1971; Grindley 1981), suggesting that this reduction may have been due to human disturbance (Watkins 1987). A recent study has investigated minimum approach distances for key seabird and seal species on Marion Island, and the impacts of various human activities on these species. Research indicates that brooding Wandering Albatrosses approached on foot to less than 10 m show signs of alarm or aggression (Plate 12.6), reactions that are likely to be preceded by physiological stress responses, and that on Marion Island this species does not appear to have habituated to either researcher disturbance or incidental disturbance by island personnel (De Villiers *et al.* 2005). Preliminary measurements of heart rates in response to human disturbance indicate that Northern Giant Petrels *M. halli* may be as responsive to human disturbance as Southern Giant Petrels have been found to be at other sites (de Villiers *et al.* 2006b). Although the latter are colonial breeders and are thus effectively protected by the status of their colonies as limited-access zones on Marion Island, the imposition of large exclusion zones around solitarily breeding Northern Giant Petrels is not practical. Protection against disturbance could be improved by the restriction of human passage through breeding areas to designated paths.

Proposals for research on seabirds and seals on the islands require ethics approval by the relevant institutions undertaking the research. In response to a growing body of evidence that flipper-banding of penguins in the Antarctic and sub-Antarctic may compromise survival (Jackson & Wilson 2002; Petersen *et al.* 2005), all flipper-banding of penguins on the Prince Edward Islands halted in 2004 (R.J.M. Crawford, personal communication). Declines in some populations of Gentoo Penguins (Crawford *et al.* 2003a) and Southern Giant Petrels (Cooper *et al.* 2001) on Marion Island have been associated with previous intrusive research programmes which were consequently discontinued. Removal of cats from Marion Island resulted in the accidental mortality of some seabirds but had no negative effects on population levels (Bloomer & Bester 1992; Bester *et al.* 2002). Small-mammal trapping, as part of studies on the effects of mice on Marion Island, also had insignificant effects on bird populations – only four birds were caught in traps over a total of 46 500 trap-nights (Cooper *et al.* 1994b). The removal of animals from the Prince Edward

Islands for zoological gardens has taken place on several occasions in the past (Cooper 1995a) and the collection of King Penguins for this purpose is likely to take place again (C.A. Jacobs, personal communication).

Although trampling by humans in Antarctic and sub-Antarctic environments is often highly visible, little is known about its ecological effects. An assessment of the impacts of human trampling in three habitats on Marion Island revealed that responses differed, depending on soil characteristics and the structure of the original vegetation (Gremmen *et al.* 2003). In general, trampling negatively affected species richness and plant cover and tracks were associated with an increase in the number and cover of introduced species (Gremmen *et al.* 2003). Walkways connect buildings at the existing base and on the construction site for the new base, movement of personnel and the placement of construction material are restricted to temporary walkways laid down for this purpose where possible.

Concerns regarding the impacts of humans at the Prince Edward Islands largely centre on the natural environment. However, there are also concerns over the conservation of the islands' cultural heritage. At least 18 archaeological sites are known on Marion Island, and six on Prince Edward Island (Cooper & Avery 1986). These mainly date back to the sealing era in the 19th and 20th centuries, and consist of remnants of camps and field huts with associated sealing equipment, notably iron trypots used to render elephant seal blubber (Cooper & Avery 1986). There are also several known or presumed grave sites and the remains of several shipwrecks. Although the surface exposures of most known sites and artefacts have been described (Cooper & Avery 1986; Graham 1989; Boshoff *et al.* 1997; Boshoff & Van Schalkwyk 1999) and recommendations have been made for their protection and conservation (Graham 1989), no thorough archaeological studies have been undertaken on either island (Cooper 2008). Sites on Prince Edward Island tend to be less disturbed than those at Marion Island, where the extensive removal of souvenirs has taken place in the past. Sites older than 60 years are protected by the National Heritage Resources Act Number 25 of 1999 (Table 12.1) and all have the status of limited access zones in the first management plan (PEIMPWG 1996). All historical sites fall within limited-access zones and no artefacts may be handled. The new management plan calls for an updated inventory of sites and artefacts, followed by the drafting of conservation management plans for heritage resources that are identified as of high value or as being at risk (Chown *et al.* 2006).

12.3 Conclusions

Since the annexation of the Prince Edward Islands in 1948, considerable progress has been made in the conservation of the islands' biota, and management practices at the islands have been substantially improved. New initiatives which promise to advance further the conservation of the islands and their resources include a recent successful nomination to the Ramsar Convention on Wetlands of International Importance, a pending nomination to the World Heritage Convention, the latter including territorial waters out to 12 nautical miles (Table 12.1), the declaration of a Marine Protected Area around the islands (Lombard *et al.* 2007), and the revision of the islands' management plan (Chown *et al.* 2006). The National Environmental Management: Protected Areas Act, passed in 2004, also improves legal protection for the islands and this, together with the development of a Risk Assessment Plan and the intended appointment of an Aliens Officer on the Marion Island over-wintering team, will address the main conservation threat to the islands, namely the introduction of alien species. Dealing with the conservation issues affecting the island group is a full-time task rather than something which can be addressed on an *ad hoc* basis, and the recent appointment of a full-time Environmental Officer within the Department of Environmental Affairs and Tourism should address this issue. In many aspects, conservation practices at the Prince Edward Islands are as good as or better than those at other sub-Antarctic island groups (De Villiers *et al.* 2006a). Notably, and unlike at all the other groups, no fresh produce of any description may be taken to the islands and no tourism (with its attendant problems of increased risks of alien species introductions, trampling, waste management and disturbance of wildlife) is allowed.

However, there is still room for improvement. The islands and their biota are changing rapidly with global climate change. Any decrease in the resilience of species that breed on the islands or forage in the surrounding waters may result in their local extinction. Alien species introductions are a real threat, and many alien species appear to benefit from warmer climatic conditions (Chown *et al.* 2007). Quarantine procedures around voyages to the island are relatively strict, although they can still be improved. Potential access-routes include insecure storage facilities in Cape Town, inadequately treated materials transported to the islands, and ship-to-shore transport such as helicopters and inflatable dinghies. Despite rigorous quarantine procedures, several alien species have been introduced to Marion Island in recent years. Although the intention to appoint an Aliens Officer on Marion Island is commendable, the effective control or eradication of alien species on the island requires a long-term and properly-funded commitment. The introduced House Mouse on Marion Island is thought to have far-reaching environmental effects, but there has been no intensive monitoring of its population trends for several years. Despite the fact that the eradication of this species will be very expensive, this should be prioritised.

Enforcement of protective legislation onshore is excellent, but is less satisfactory offshore due to the remoteness of the islands from the mainland. Illegal, Unreported and Unregulated fishing remains a problem and has severe consequences in terms of incidental seabird mortalities. Although South Africa now has a fishery patrol vessel which can venture to the islands, the frequency of its trips is currently limited by budgetary constraints. Ongoing bilateral negotiations aimed at enhancing international monitoring, control and surveillance co-operation within the Southern Ocean may mitigate this problem. The potential exists for oil and gas exploration, especially offshore, but potentially also onshore. The islands are not protected by legislation in this regard, but the proposed Marine Protected Area will set aside representative marine areas which will not be affected by such activities.

The building of a new research base at the island will render most of the old base buildings defunct. An EIA for the removal of this infrastructure and the rehabilitation of the site has not yet been commissioned. Vast quantities of waste wood will result from the demolition of the old base, and burning of this (rather than its removal for disposal in South Africa) could pose an environmental threat. Thought could be given to alternative, cleaner energy sources than the diesel and petrol generators currently in use at the base and field huts.

A real threat to the seabird colonies on the islands is that of human-mediated disease transmission, e.g. Avian Cholera, Avian Influenza or Newcastle's Disease. Although strict quarantine procedures minimize this risk, these may not be infallible and as yet, no disease contingency plan is in place at the islands.

At the Prince Edward Islands, the effects of climate change on the establishment and spread of alien species, and on the availability of marine resources to the islands' populations of seals and seabirds, cannot be ignored. Long term databases aid in the understanding of environmental change and its effects on ecosystems in general, and populations in particular. For example, the meteorological database at Marion Island goes back to 1949, when the weather station on the island was first established, and data on Wandering Albatrosses have been collected since the establishment of the first study colonies in the 1970s. The delineation of the proposed Marine Protected Area will depend on ongoing monitoring of physical variables such as sea surface temperatures and shifts in the position of frontal systems around the islands, and biological variables such as pelagic phyto- and zooplankton and fish communities and the foraging patterns of the islands' top predators (Lombard *et al.* 2007). Long-term databases will thus be of inestimable value in the future management and conservation of the islands.

Conservation management attitudes and practices at the Prince Edward Islands have undergone considerable changes in the six decades since annexation. Time will bring new insights, and practices which are currently considered acceptable or even advanced may be subject to criticism in the future. The ideal management strategy will be sensitive to such changes and flexible enough to incorporate the best of these.

12.4 Acknowledgements

Henry Valentine (Director: Antarctica and Islands) and past and present members of the Prince Edward Islands Management Committee (PEIMC) have invested considerable time and energy in improving the conservation status of the islands. The South African National Antarctic Programme office has also made available minutes of past meetings of the Prince Edward Islands Management Committee as reference material for this chapter. Sarah Davies and Melodie McGeoch are thanked for their helpful comments on an earlier version. Over the years, many scientists have voluntarily taken on the duties of Conservation Officer during annual relief voyages to Marion Island, while various expedition members have, with enthusiasm and dedication, served as Team Conservation Officers during the time that they have made the island their home. To all those people whose passion for the islands has been channelled into their conservation and management, we offer heartfelt thanks.

12.5 References

Anderson, D.W. & Keith, J.O. 1980. The human influence on seabird nesting success: conservation implications. *Biological Conservation* **18**, 65-80.

Angel, A. & Cooper, J. 2006. A review of the impacts of the introduced rodents of Tristan da Cunha and Gough Island, South Atlantic. *Royal Society for the Protection of Birds Research Report* **No. 17**.

Barnes, D.K.A. 2002. Invasions by marine life on plastic debris. *Nature* **416**, 808-809.

Barnes, D.K.A. & Fraser, K.P.P. 2003. Rafting by five phyla on man-made flotsam in the Southern Ocean. *Marine Ecology Progress Series* **262**, 289-291.

Bester, M.N., Bloomer, J.P., Van Aarde, R.J., Erasmus, B.H., Van Rensburg, P.J.J., Skinner, J.D., *et al.* 2002. A review of the successful eradication of feral cats from sub-Antarctic Marion Island, southern Indian Ocean. *South African Journal of Wildlife Research* **32**, 65-73.

BirdLife International 2004. *Threatened Birds of the World 2004*. CD-ROM. BirdLife International, Cambridge.

Black, A. 2005. Light induced seabird mortality on vessels operating in the Southern Ocean: incidents and mitigation measures. *Antarctic Science* **17**, 67-68.

Bloomer, J.P. & Bester, M.N. 1992. Control of feral cats on sub-Antarctic Marion Island, Indian Ocean. *Biological Conservation* **60**, 211-219.

Born, E.W., Riget, F.F., Dietz, R. & Andriashek, D. 1999. Escape responses of hauled out Ringed Seals (*Phoca hispida*) to aircraft disturbance. *Polar Biology* **21**, 171-178.

Boshoff, J.J., Hart, D. & Loock, J. 1997. *Survey of Historical Sites on Marion Island*. Unpublished Report for the Prince Edward Islands Management Committee, pp. 1-44.

Boshoff, J.J. & Van Schalkwyk, J.A. 1999. *The Archaeology of Sealing Sites on Marion Island, April/May 1999*. Unpublished Report to the South African Heritage Resources Agency.

Brooke, R.K. 1984. South African Red Data Book – Birds. *South African National Scientific Programmes Report* No. **97**.

Chown, S.L. & Cooper, J. 1995. *The Impact of Feral House Mice at Marion Island and the Desirability of Eradication: Report on a Workshop held at the University of Pretoria, 16-17 February 1995*. Directorate: Antarctica & Islands, Department of Environmental Affairs and Tourism, Pretoria, pp. 1-18.

Chown, S.L., Davies, S.J. & Joubert, L. 2006. Draft Prince Edward Islands Environmental Management Plan Version 0.1. DST-NRF Centre of Excellence for Invasion Biology, University of Stellenbosch, Stellenbosch, South Africa.

Chown, S.L., Gremmen, N.J.M. & Gaston, K.J. 1998. Ecological biogeography of Southern Ocean islands: species-area relationships, human impacts, and conservation. *American Naturalist* **152**, 562-575.

Chown, S.L., McGeoch, M.A. & Marshall, D.J. 2002. Diversity and conservation of invertebrates on the sub-Antarctic Prince Edward Islands. *African Entomology* **10**, 67-82.

Chown, S.L., Slabber, S., McGeoch, M.A., Janion, C. & Leinaas, H.P. 2007. Phenotypic plasticity mediates climate change responses among invasive and indigenous arthropods. *Proceedings of the Royal Society of London B* **274**, 2531-2537.

Chown, S.L. & Smith, V.R. 1993. Climate change and the short-term impact of feral house mice at the sub-Antarctic Prince Edward Islands. *Oecologia* **96**, 508-516.

Cooper, J. 1995a. Conservation status of the Prince Edward Islands. In: Dingwall, P.R. (Ed.). *Progress in the Conservation of Subantarctic Islands. Proceedings of the SCAR/IUCN Workshop on Protection, Research and Management of Subantarctic Islands, Paimpont, France, 27-29 April, 1992*. World Conservation Union, Gland, pp. 21-30.

Cooper, J. 1995b. After the cats and trout: the mice? Removing alien vertebrates from subantarctic Marion Island. *Aliens* **1**, 17.

Cooper, J. 2008. Human history. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 331-350.

Cooper, J., Avenant, N.L. & Lafite, P.W. 1994a. Airdrops and King Penguins: a potential conservation problem at sub-Antarctic Marion Island. *Polar Record* **30**, 277-282.

Cooper, J. & Avery, G. (Eds.). 1986. *Historical Sites at the Prince Edward Islands*. South African National Scientific Programmes Report **128**, CSIR, Pretoria.

Cooper, J., Brooke, M.de L., Burger, A.E., Crawford, R.J.M., Hunter, S. & Williams, A.J. 2001. Aspects of the breeding biology of the Northern Giant Petrel (*Macronectes halli*) and the Southern Giant Petrel (*M. giganteus*) at sub-Antarctic Marion Island. *International Journal of Ornithology* **4**, 53-68.

Cooper, J. & Condy, P.R. 1988. Environmental conservation at the sub-Antarctic Prince Edward Islands: a review and recommendations. *Environmental Conservation* **15**, 317-326.

Cooper, J., Crafford, J.E. & Hecht, T. 1992. Introduction and extinction of Brown Trout (*Salmo trutta* L.) in an impoverished sub-Antarctic stream. *Antarctic Science* **4**, 9-14.

Cooper, J., de Villiers, M.S. & McGeoch, M.A. 2003. Quarantine measures to halt alien invasions of Southern Ocean Islands: the South African experience (Prince Edward Islands Special Nature Reserve). *Aliens* **17**, 37-39.

Cooper, J. & Fourie, A. 1991. Improved breeding success of Great-winged Petrels *Pterodroma macroptera* following control of feral cats *Felis catus* at subantarctic Marion Island. *Bird Conservation International* **1**, 171-175.

Cooper, J. & Headland, R.K. 1991. A history of South African involvement in Antarctica and at the Prince Edward Islands. *South African Journal of Antarctic Research* **21**, 77-91.

Cooper, J., Marais, A.v.N., Bloomer, J.P. & Bester, M.N. 1995. A success story: breeding of burrowing petrels (Procellariidae) before and after eradication of feral cats *Felis catus* at subantarctic Marion Island. *Marine Ornithology* **23**, 33-37.

Cooper, J. & Ryan, P.G. 2001. The Agreement on the Conservation of Albatrosses and Petrels: implications for research and monitoring at the Prince Edward Islands. *South African Journal of Science* **97**, 78-79.

Cooper, J. & Ryan. P.G. 2003. *South African National Plan of Action for Reducing the Incidental Catch of Seabirds in Longline Fisheries*. Unpublished Report to the Branch: Marine and Coastal Management, Department of Environmental Affairs & Tourism, pp. 1-103.

Cooper, J., Van Wyk, J.C.P. & Matthewson, D.C. 1994b. Effects of small-mammal trapping on birds at sub-Antarctic Marion Island. *South African Journal of Antarctic Research* **24**, 125.

Crafford, J.E. & Chown, S.L. 1987. *Plutella xylostella* (Lepidoptera: Plutellidae) on Marion Island. *Journal of the Entomological Society of Southern Africa* **50**, 259-260.

Crafford, J.E. & Chown, S.L. 1990. The introduction and establishment of the Diamondbacked Moth (*Plutella xylostella* L., Plutellidae) on Marion Island. In: Kerry, K.R. & Hempel, G. (Eds.). *Antarctic Ecosystems. Ecological Change and Conservation*. Springer, Berlin, pp. 354-358.

Crafford, J.E. & Scholtz, C.H. 1987. Quantitative differences between the insect faunas of sub-Antarctic Marion and Prince Edward Islands: a result of human intervention? *Biological Conservation* **40**, 255-262.

Crawford, A.B. 1952. The birds of Marion Island, Southern Indian Ocean. *Emu* **52**, 73-85.

Crawford, R.J.M., Cooper, J., du Toit, M., Greyling, M.D., Hanise, B., Holness, C.L., *et al.* 2003a. Population and breeding of the Gentoo Penguin *Pygoscelis papua* at Marion Island, 1994/95-2002/03. *African Journal of Marine Science* **25**, 463-474.

Crawford, R.J.M., Cooper, J., Dyer, B.M., Wolfaardt, A.C., Tshingana, D., Spencer, K., *et al.* 2003b. Population, breeding, diet and conservation of the Crozet Shag *Phalacrocorax [atriceps] melanogenis* at Marion Island, 1994/95-2002/03. *African Journal of Marine Science* **25**, 537-547.

Crawford, R.J.M., Duncombe Rae, C.M., Nel, D.C. & Cooper, J. 2003c. Unusual breeding by seabirds at Marion Island during 1997/98. *African Journal of Marine Science* **25**, 453-462.

Crawford, R.J.M., Duncombe Rae, C.M., Nel, D.C. & Cooper, J. 2004. Influence of climate on seabirds at sub-Antarctic Marion Island, Southern Ocean. *27th Antarctic Treaty Consultative Meeting Information Paper* IP 076.

Crawford, R.J.M., Dyer, B.M., de Villiers, M.S., Hofmeyr, G.J.G. & Tshingana, D. 2005. Mortality of Macaroni Penguins *Eudyptes chrysolophus* at Marion Island caused by Avian Cholera *Pasteurella multocida* in 2004/05. CCAMLR WG-EMM-05/.

De Villiers, M.S., Bause, M., Giese, M. & Fourie, A. 2006b. Hardly hard-hearted: heart rate responses of incubating Northern Giant Petrels (*Macronectes halli*) to human disturbance on sub-Antarctic Marion Island. *Polar Biology* **29**, 717-720.

De Villiers, M.S., Cooper, J., Carmichael, N., Glass, J.P., Liddle, G.M., McIvor, E., *et al.* 2006a. Conservation management at Southern Ocean Islands: towards the development of best-practice guidelines. *Polarforschung* **75**, 113-131.

De Villiers, M.S., Cooper, J. & Ryan, P.G. 2005. Individual variability of behavioural responses by Wandering Albatrosses (*Diomedea exulans*) to human disturbance. *Polar Biology* **28**, 255-260.

Environomics 2002. *Report on the Scoping Study for the Proposed New Base Facility at Marion Island*. Environomics, Pretoria.

Frenot, Y., Chown, S.L., Whinam, J., Selkirk, P.M., Convey, P., Skotnicki, M., *et al.* 2005. Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews* **80**, 45-72.

Gales, R. 1998. Albatross populations: status and threats. In: Robertson, G. & Gales, R. (Eds.). *Albatross Biology and Conservation*. Surrey Beatty, Chipping Norton, pp. 20-45.

Gardner, B.D., Siegfried, W.R. & Connell, A.D. 1985. Chlorinated hydrocarbons in seabird eggs from the southern Atlantic and Indian Oceans. In: Siegfried, W.R. Condy, P.R. & Laws, R.M. (Eds.). *Antarctic Nutrient Cycles and Food Webs*. Springer-Verlag, Berlin, pp. 647-651.

Giese, M. 1996. Effects of human activity on Adélie Penguin *Pygoscelis adeliae* breeding success. *Biological Conservation* **75**, 157-164.

Giese, M. 1998. Guidelines for people approaching breeding groups of Adélie Penguins (*Psygoscelis adeliae*). *Polar Record* **34**, 287-292.

Graham, T. 1989. *Cultural Resource Management of the Prince Edward Islands*. B.A. (Hons) Dissertation, University of Cape Town, South Africa.

Gremmen, N.J.M. 1975. The distribution of alien vascular plants on Marion and Prince Edward Islands. *South African Journal of Antarctic Research* **5**, 25-30.

Gremmen, N.J.M. 2004. *Management of Alien Vascular Plants on Marion and Prince Edward Islands: an Integrated Approach*. Data Analyse Ecologie, The Netherlands.

Gremmen, N.J.M., Chown, S.L. & Marshall, D.J. 1998. Impact of the introduced grass *Agrostis stolonifera* on vegetation and soil fauna communities at Marion Island, sub-Antarctic. *Biological Conservation* **85**, 223-231.

Gremmen, N.J.M. & Smith, V.R. 1999. New records of alien vascular plants from Marion and Prince Edward Islands, sub-Antarctic. *Polar Biology* **21**, 401-409.

Gremmen, N.J.M., Smith, V.R. & Van Tongeren, O.F.R. 2003. Impact of trampling on the vegetation of Subantarctic Marion Island. *Arctic, Antarctic, and Alpine Research* **35**, 442-446.

Gremmen, N.J.M. & Van der Meijden, R. 1995. Introduced *Agrostis* species at sub-Antarctic Marion Island. *South African Journal of Antarctic Research* **25**, 85-86.

Grindley, J.R. 1981. Observations of seabirds at Marion and Prince Edward Islands in April and May 1973. In: Cooper, J. (Ed.). *Proceedings of the Symposium on Birds of the Sea and Shore, 1979*. African Seabird Group, Cape Town, pp 169-188.

Hänel, C. & Chown, S.L. 1998. *An Introductory Guide to the Marion and Prince Edward Island Special Nature Reserves 50 Years after Annexation*. Department of Environmental Affairs and Tourism, Pretoria, pp. 1-80.

Hänel, C., Chown, S.L. & Davies, L. 1998. Records of alien insect species from sub-Antarctic Marion and South Georgia Islands. *African Entomology* **6**, 366-369.

Heydenrych, R. & Jackson, S. 2000. *Environmental Impact Assessment of Tourism on Marion Island*. Department of Environmental Affairs and Tourism, Pretoria, pp. 1-115.

Heymann, G., Erasmus, T., Huntley, B.J., Liebenberg, A.C., Retief, G. de F., Condy, P.R., *et al.* 1987. An environmental impact assessment of a proposed emergency landing facility on Marion Island – 1987. *South African National Scientific Programmes Report* No.**140**.

Hofmeyr, G., De Maine, M., Bester, M., Kirkman, S., Pistorius, P. & Makhado, A. 2002. Entanglement of pinnipeds at Marion Island, Southern Ocean: 1991-2001. *Australian Mammalogy* **24**, 141-146.

Hugo, E.A., Chown, S.L. & McGeoch, M.A. 2006. The microarthropods of Prince Edward Island: A quantitative assessment. *Polar Biology* **30**, 109-119.

Huyser, O., Ryan, P.G. & Cooper, J. 2000. Changes in population size, habitat use and breeding biology of Lesser Sheathbills *Chionis minor* at Marion Island: impacts of cats, mice and climate change? *Biological Conservation* **92**, 299-310.

Jackson, S. and Wilson, R.P. 2002. The potential costs of flipper-bands to penguins. *Functional Ecology* **16**, 141-148.

Jansen Van Vuuren, B. & Chown, S.L. 2007. Genetic evidence confirms the origin of the House Mouse on sub-Antarctic Marion Island. *Polar Biology* **30**, 327-332.

Kloppers, F.J. & Smith, V.R. 1998. First report of *Botryotinia fuckeliana* on Kerguelen Cabbage on the sub-Antarctic Marion Island. *Plant Disease* **82**, 710.

Knops, J.M.H., Bradley, K.L. & Wedin, D.A. 2002. Mechanisms of species impacts on ecosystem nitrogen cycling. *Ecology Letters* **5**, 454-466.

La Grange, J.J. 1962. Notes on the birds and mammals on Marion Island and Antarctica (S.A.N.A.E.). *Journal of the South African Biological Society* **3**, 27-84.

Lee, J.E. & Chown, S.L. 2007. *Mytilus* on the move: transport of an invasive bivalve to the Antarctic. *Marine Ecology Progress Series* **339**, 307-310.

Lee, J.E. Slabber, S., Jansen Van Vuuren, B., Van Noort, S. & Chown, S.L. 2007. Colonisation of sub-Antarctic Marion Island by a non-indigenous aphid parasitoid *Aphidius matricariae* (Hymenoptera, Braconidae). *Polar Biology* **30**, 1195-1201.

Lewis, P.N., Hewitt, C.L., Riddle, M. & McMinn, A. 2003. Marine introductions in the Southern Ocean: an unrecognized hazard to biodiversity. *Marine Pollution Bulletin* **46**, 213-223.

Lombard, A.T., Reyers, B., Schonegevel, L., Cooper, J., Smith-Adao, L., Nel, D.C., *et al.* 2007. Conserving pattern and process in the Southern Ocean: designing a Marine Protected Area for the Prince Edward Islands. *Antarctic Science* **19**, 39-54.

Mélice, J-L., Lutjeharms, J.R.E., Rouault, M. & Ansorge, I.J. 2003. Sea-surface temperatures at the sub-Antarctic islands Marion and Gough during the past 50 years. *South African Journal of Science* **99**, 363-366.

Nel, D.C. & Nel, J.L. 1999. Marine debris and fishing gear associated with seabirds at sub-Antarctic Marion Island, 1996/97 and 1997/98: in relation to longline fishing activity. *CCAMLR Science* **6**, 85-96.

Nel, D.C., Nel, J.C., Ryan, P.G., Klages, N.T.W., Wilson, R.P. & Robertson, G. 2000. Foraging ecology of Grey-headed Mollymawks at Marion Island, southern Indian Ocean, in relation to longline fishing activity. *Biological Conservation* **96**, 219-231.

Nel, D.G., Ryan, P.G., Crawford, R.J.M., Cooper, J. & Huyser, O.A.W. 2002a. Population trends of albatrosses and petrels at sub-Antarctic Marion Island. *Polar Biology* **25**, 81-89.

Nel, D.C., Ryan, P.G., Nel, J.L., Klages, N.T.W., Wilson, R.P., Robertson, G., *et al.* 2002b. Foraging interactions of Wandering Albatrosses *Diomedea exulans* breeding on Marion Island with long-line fisheries in the southern Indian Ocean. *Ibis* **144**, 141-154.

Nel, D.C., Ryan, P.G. & Watkins, B.P. 2002c. Seabird mortality in the Patagonian Toothfish fishery around the Prince Edward islands, 1996-2000. *Antarctic Science* **14**, 151-161.

Nel, D.C. & Whittington, P.A. 2003. *Rehabilitation of Oiled African Penguins: a Conservation Success Story*. BirdLife South Africa and the Avian Demography Unit, Cape Town.

Pakhomov, E.A. & Chown, S.L. 2003. The Prince Edward Islands: Southern Ocean oasis. *Ocean Yearbook* **17**, 348-379.

PEIMPWG (Prince Edward Islands Management Plan Working Group) 1996. *Prince Edward Islands Management Plan*. Department of Environmental Affairs & Tourism, Pretoria, pp. 1-64.

Petersen, S.L., Branch, G.M., Ainley, D.G., Boersma, P.D., Cooper, J. & Woehler, E.J. 2005. Is flipper banding of penguins a problem? *Marine Ornithology* **33**, 75-79.

Roth, L.M. & Willis, E.R. 1960. The biotic associations of cockroaches. *Smithsonian Institute Miscellaneous Collection* **141**, 1-470.

Rounsevell, D. & Binns, D. 1991. Mass deaths of King Penguins (*Aptenodytes patagonica*) at Lusitania Bay, Macquarie Island. *Aurora* **10**, 8-10.

Ryan, P.G. 1987. The origin and fate of artefacts stranded on islands in the African sector of the Southern Ocean. *Environmental Conservation*, **14**, 341-346.

Ryan, P.G. 1990. The marine plastic debris problem off southern Africa: Types of debris, their environmental effects, and control measures. In: Shomura, R.S. & Godfrey, M.L. (Eds.). *Proceedings of the Second International Conference on Marine Debris, 2-7 April 1898*. Honolulu, Hawaii.

Ryan, P.G. 1996. Plastic litter in marine systems: Impacts, sources and solutions. *Plastics Southern Africa*. **November 1996**, 20-28.

Ryan, P.G. & Moloney, C.L. 1993. Marine litter keeps increasing. *Nature* **361**, 23.

Ryan, P.G., Smith, V.R. & Gremmen, N.J.M. 2003. The distribution and spread of alien vascular plants on Prince Edward Island. *African Journal of Marine Science* **25**, 555-561.

Slabber, S. & Chown, S.L. 2002. The first record of a terrestrial crustacean, *Porcellio scaber* (Isopoda, Porcellionidae) from sub-Antarctic Marion Island. *Polar Biology* **25**, 855-858.

Smith, V.R. 2002. Climate change in the sub-Antarctic: an illustration from Marion Island. *Climate Change* **52**, 345-357.

Smith, V.R. & Steenkamp, M. 1990. Climatic change and its ecological implications at a subantarctic island. *Oecologia* **85**, 14-24.

South Africa. 2005. Towards the creation of a Marine Protected Area around South Africa's sub-Antarctic Prince Edward Islands. *28th Antarctic Treaty Consultative Meeting*, **IP 019**.

Van Aarde, R.J. 1979. Distribution and density of the feral house cat *Felis catus* on Marion Island. *South African Journal of Antarctic Research* **9**, 14-19.

Van Zinderen Bakker, E.M. Jr. 1971. The genus *Diomedea*. In: Van Zinderen Bakker, E.M., Winterbottom, J.M. & Dyer, R.A. (Eds.). *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965-1966*. Balkema, Cape Town. pp. 273-282.

Visagie, W.F. 1988. *Code of Conduct for the Prince Edward Islands*. Department of Environment Affairs, Pretoria.

Vleck, C.M., Vertalino, N., Vleck, D. & Bucher, T.L. 2000. Stress, corticosterone, and heterophil to lymphocyte ratios in free-living Adélie penguins. *The Condor* **102**, 392-400.

Watkins, B.P. 1987. Population sizes of King, Rockhopper and Macaroni Penguins and Wandering Albatrosses at the Prince Edward Islands and Gough Island, 1951-1986. *South African Journal of Antarctic Research* **17**,150-157.

Watkins, B.P. & Cooper, J. 1986. Introduction, present status and control of alien species at the Prince Edward islands, sub-Antarctic. *South African Journal of Antarctic Research* **16**, 86-94.

Whinam, J., Chilcott, N. & Bergstrom, D.M. 2005. Subantarctic hitchhikers: expeditioners as vectors for the introduction of alien organisms. *Biological Conservation* **121**, 207-219.

Williams, A.J. 1984. The status and conservation of seabirds on some islands in the African sector of the Southern Ocean. *International Council for Bird Preservation Technical Publication* **2**, 627-635.

Woehler, E.J., Penney, R.L., Creet, S.M. & Burton, H.R. 1994. Impacts of human visitors on breeding success and long-term population trends in Adélie Penguins at Casey, Antarctica. *Polar Biology* **14**, 269-274.

CHAPTER 13

HUMAN HISTORY

JOHN COOPER

Far south as they are in mid-ocean, situated well away from continental land masses and the usual sea routes, it might be thought that the sub-Antarctic islands of Marion and Prince Edward, which have never been permanently inhabited, have but a short history of little general interest. Nevertheless, interest there is, and excitement as well at times, and also some mysteries. Who first discovered the islands, who gave the individual islands their present names, who was the first person to land, and when (and how) did the House Mouse *Mus musculus* arrive on Marion Island? Unlike the other sub-Antarctic islands to be found in the southern Indian Ocean, we do not as yet have clear answers to any of these questions, and it may well be that we will never know.

The history of the Prince Edward Islands is written here from a human perspective, so the author has not been shy of including his own views and comments, idiosyncratic or otherwise. A chronological approach has been adopted in the main, with the period from discovery until the present day divided into "eras". Rather than present detailed accounts for each era (such as by including lists of ship's visits, with their dates of arrival, or of the names of team leaders of the meteorological station since annexation), an attempt has been made to bring the islands' human history to life by concentrating on selected events that have taken place over the years, so that the reader may try to gain an understanding of what it was like to visit and live on the Prince

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 331-350

Edward Islands during different times. Two neglected subjects, the early histories of the introductions of alien mammals, and the influence of South Africa's gender and racial policies from 1948 to 1994 on island life are treated separately. Of course, not all the good stories can be told in this chapter, but it is hoped that the ones selected will give the reader an understanding of the rich history of a very special place.

13.1 Who first saw the islands? The discovery era, 1663-1776

From the fifteenth to the seventeenth centuries the European world knew very little about southern Africa. The inhospitable seas south of Africa were not known at all, with the first Portuguese explorers hugging the African coastline as they ventured from the Atlantic to the Indian Oceans. At its southern tip, the Cape of Good Hope (modern Cape Town) was founded by the seventeenth century, but its early settlers first looked eastward to the Dutch East Indies, rather than to the hinterland – or southwards. In 1663 the Dutch East Indiaman *Maerseveen*, bound for Batavia from Cape Town, sailed off course and discovered (it is thought) Marion and Prince Edward Islands on the fourth of March (Graham 1989; Cooper & Headland 1991). In a time prior to chronometers, the co-ordinates given by Captain Barent Barentzoon Ham of the *Maerseveen* do not, unsurprisingly, match the islands' current positions, so there will always be some uncertainty over the islands' first discoverer (Van Zinderen Bakker *et al.* 1971). No landings were made at the time, although the *Maerseveen* approached the southerly island (which he named after his ship) close enough to note its cliffs (Leupe 1868). The more northerly island was called Dena (also known as Denia or Dina). Towards the end of the century, the Dutch Governor in Cape Town dispatched a vessel, *Wesel*, to the reported positions of *Maerseveen* and Dina to exploit the timber on the islands which he thought "were entirely covered by many trees from top to bottom" (translated from Leupe 1868). Orders were also given to report on the herbs, flowers, fish, birds and other animals that might be present, as well as on the presence of fresh water. The voyage was unsuccessful, as the islands were not located, presumably due to incorrect co-ordinates. It was just as well, as no trees of any sort would have been found, although the first attempt to report on the environment and biota of the islands was lost to history.

The Prince Edward Islands, after surviving their very first attempt at exploitation, then lapsed back into obscurity for more than a hundred years. The second, and more definite, claimant for discovering the islands is the French explorer, Marc-Macé (or Marc-Joseph) Marion du Fresne, who with the frigates *Le Mascarin* and *Marquis de Castries*, sailed from Cape Town and came across the two islands on 13 January 1772, which he named Ile de l'Espérance (modern-day Marion Island) and Ile de la Caverne (Prince Edward Island). Again, no landing was made. A collision between his two vessels while searching for an anchorage the next day seems to have been the cause (Roth 1891). This accident caused some hen coops (and the latrines) to be lost overboard, but there is no evidence of domestic chickens being the first alien species introduced by man to the islands! It also caused the first human death at the Prince Edward Islands, that of the look-out, Mathurin Le Tourneur, who was killed when the *Marquis de Castries'* foremast fell (Duyker 1994). The French observed a multitude of large white spots looking like flocks of sheep on modern-day Prince Edward Island (Roth 1891). These were most likely Wandering Albatrosses *Diomedea exulans* in "Albatross Valley", known for its high numbers of breeding birds (Underhill *et al.* 2003). This seems to be the first biological observation recorded for the islands.

The next visit was by Captain James Cook on his third and final voyage of discovery. Cook had previously searched for *Maerseveen* and Dena without success during his second voyage (Beaglehole 1961). This time, and armed with knowledge of Marion du Fresne's discovery shown to him on a chart "in a very obliging [sic] manner" by Julien Crozet (second in command of *Le Mascarin* under du Fresne) when they fortuitously met in Cape Town during his second voyage in 1775, he reached the islands on 12 December 1776 (Beaglehole 1961; Van Zinderen Bakker *et al.* 1971; Cooper & Headland 1991). Like his two predecessors, Cook did not make a landing, sailing between them in his vessels, the *Resolution* and the *Discovery*. This reflects that the Prince Edward Islands with no sheltered bays worthy of an anchorage must have appeared hugely inhospitable to the early explorers in their sailing ships. Accounts written by Cook and his officers at the time note the rugged and barren nature of the islands and the presence of much snow (Cook 1785; Beaglehole 1967).

Cook named the island group (which he specifically stated, were unnamed on his French chart) the "Prince Edward Islands" (Cook 1785; Beaglehole 1967; Cooper & Headland 1991), and did not name the islands individually, *contra* to many 20th century accounts (e.g. Marsh 1948; Van Zinderen Bakker *et al.* 1971; Linklater 1972). Why he chose to name the islands after the fourth son of King George III of Great Britain, has not been recorded anywhere. His Royal Highness the Prince Edward Augustus, later to be titled the Duke of Kent and Strathearn, was only nine years old at the time and might have appeared an unlikely choice over his older brothers. But it seems possible that Cook had met the Prince, as he had been presented to George III (who was an admirer and enthusiastic supporter) after his first voyage in 1771. Interestingly, the Canadian Province of Prince Edward Island was also named after the Prince, although only later in his life. He was known as "the forgotten son" who never became King, but he preserved the British Royal family line by fathering Queen Victoria (www.bluepete.com/Hist/BiosNS/1800-67/Kent.htm).

Exactly how Marion Island got its name remains an unsolved mystery. Cook, after leaving the Prince Edward Islands, sailed to the modern-day Crozet Islands, which he named "Morion (sic) and Crozet Islands" (Cook 1785; Beaglehole 1967). Some time during the first half of the 19th century the name Marion was transferred from the Crozets to the Prince Edwards, most probably by sealers, who formed the next group of seafarers to visit the islands (Cooper & Headland 1991).

13.2 Seal tongues for breakfast and seal skins for shoes: the period of exploitation, 1800-1930

The next recorded visitor to the islands was the sealer *Sally* (Captain Pierre Péron), which arrived on 10 February 1800, but once again made no landing (Péron 1824). The first recorded landing was from the *Catherine* in either December 1803 or January 1804, whose Captain, Henry Fanning, placed a sealing party ashore (Fanning 1834). However, Fanning laid no claim to have been the first ashore, so the name of the first person to land at the Prince Edward Islands remains unknown, although it is a near certainty to have been made from a sealing vessel (Busch 1985). A number of other sealers, mostly American, visited the island in the first decade of the century (Cooper & Avery 1986; Graham 1989; Headland 1989; Richards 1992). Initially sealers were after the valuable skins of fur seals *Arctocephalus* sp., but by the second decade Southern Elephant Seals *Mirounga leonina* were being killed and tried out for their oil as well (Richards 1992). The *Pickering*, under Samuel Edes, for example, took 7 000 fur seal skins and 50 000 gallons of elephant seal oil over the period 1818-1820.

The life of a shore sealer at the Prince Edward Islands at this time was rough and tough. They were routinely left ashore for a year, or even two, while their ship wintered in Cape Town or sailed elsewhere in more hospitable conditions than to be found in the Southern Ocean. Few sealers left written records of their sojourns, an exception being William Phelps, who under the pseudonym "Webfoot" and many years later in his life, published an account in 1871 of his two years ashore on Marion Island. In August 1818 Phelps was put ashore as a self-styled "growing boy" (born in 1802, he was only 16 years old at the time; Busch 1983) from the sealer *Pickering*, acting as he says as "cook, steward and Governor's secretary". Within the first month, three of his party of six had drowned, and more men had to be put ashore. When the water was too rough to use their boat, they carried the elephant seal blubber draped over their shoulders across the land from distant beaches to their trypots. Phelps says this was "not very hard" for a "mile or two" but it must have been for all but the strongest and fittest. They filled their casks with oil in a year and still with no sign of their promised relief, they then had little to do. Having run out of ship's stores, they lived off seals (especially elephant seal tongues), birds, eggs and fish.

Phelps describes a number of incidents in a racy style, befitting a penny novel of the times. On first going ashore he was left on his own with instructions to kill an elephant seal and cook breakfast. He had no firearm, so armed with a lance on a pole he sent it "socket-deep" into the unfortunate seal, (he chose the smallest he could find as a sensible precaution). The seal "grabbed the lance by the shank with his teeth, and drawing it from the wound, gave it a rapid whisking round; the end of the pole hit me a rap on the head and sent me sprawling". Nevertheless, Phelps persevered, eventually killed the animal, used its blubber to start a fire and fried liver and tongue for his hungry shipmates. He describes how to make a pipe bowl out of an elephant seal tooth, collect fresh Macaroni Penguin eggs by the expedient of crushing all present and returning the next day for those freshly laid over "perhaps two or three acres of ground", cure the skins of Wandering Albatrosses which he "presumed brought a good price", make moccasins out of raw seal hide stuffed with grass to cross the unforgiving black lava, and make a crude spring net out of strips of seal hide to catch giant petrels for their feathers to make mattresses. These poor birds were deliberately plucked alive to keep the feathers clean and were then released. Phelps does comment critically on the cruelty of this, but such activities may be taken as usual for the times. No doubt, the wildlife of sub-Antarctic islands suffered dreadfully at the hands of sealers, and we can only guess what population changes took place for many species, and how long it has taken them to recover.

There are several accounts on the sealing era at the Prince Edward Islands, listing vessels in chronological order (Cooper & Avery 1986; Graham 1989; Headland 1989; Richards 1992) and three short-term archaeological investigations have taken place at Marion Island to date (Graham 1989; Boshoff *et al.* 1997; Boshoff & Van Schalkwyk 1999). However, very little is known on the numbers of seals killed, and the definitive history of the sealing era waits to be properly researched and written. Such research will require visits to naval and maritime archives and museums in a number of countries to search for ship's logs and diaries of officers and crew. There are many more human stories to be told: of shipwrecks, privations and rescues (e.g. Marsh 1948). An exciting opportunity exists to combine historical and archaeological research. In this respect, the sealing sites on little-visited Prince Edward Island have not been "souvenired" as much as those on Marion unfortunately have been in the last 50 years (Cooper & Avery 1986), and a thorough investigation of that island is likely to lead to new discoveries and insights into a hard and now vanished way of life and survival.

By 1850 the sealing era was largely over, although sporadic attempts were made at the Prince Edward Islands as late as 1930, when a South African expedition killed 1 490 elephant seals. The expedition's vessel, the *Kildalkey*, was built in 1918 as a World War I mystery or Q-ship (an armed gunboat disguised as an unarmed merchant ship to hoax the enemy; Rice 1991). The ship lives on in name at Kildalkey Bay on the south-east coast of Marion Island, home to huge Macaroni *Eudyptes chrysolophus* and King Penguin *Aptenodytes patagonicus* breeding colonies and a large beach group of elephant seals, now thankfully able to rest ashore in peace (Cooper & Avery 1986; Cooper & Headland 1991).

13.3 Gentleman scientists in suits: the exploration era, 1840-1940

Other than sealers there were very few human visitors to the Prince Edward Islands in the 19th century and the first half of the next. Most vessels passed by and few made landings. The first was the British Expedition of James Clark Ross in the *Erebus* and *Terror*, bomb-vessels that fired massive mortars and therefore very strongly built to handle the inevitable recoil, thus ideally suited for exploring ice-strewn seas (Ross 1847; Ross 1982). Ross was on his way to discover the Ross Sea and Ice Shelf of Antarctica, and he did not linger at the Prince Edward Islands, unable to land due to bad weather on 21 and 22 April 1840. He did record vast numbers of penguins and fur seals "playing in the surf" – so the sealers had not yet managed to exterminate them. Dredgings and soundings were made and marine animals recovered, the first marine collections from the islands. These were however not the first collections ever taken. In 1830/31 Richard Harris of the sealer *Betsey and Sophia* had collected seabirds for scientific purposes (Cooper & Headland 1991). Several geographical features commemorate Ross's visit: Capes Crozier and Hooker (Captain of the *Terror* and expedition botanist, respectively) on Marion Island, and the Ross Rocks off the north coast of Prince Edward Island. One can only imagine that Joseph Hooker (later to attain eminence and be knighted) would have rather landed to botanize!

More than 30 years passed before the next scientific visit. The HMS *Challenger* had set of from Portsmouth, England in December 1872 on a voyage that would last until May 1876. Its primary goal was to make deep-sea observations, but when the ship arrived at the Prince Edward Islands on 26 December 1873, the weather was kind and a landing on Marion Island was affected in "uncommonly fine, sunny weather" (Linklater 1972). The next day the weather had changed and so a planned landing on Prince Edward Island was cancelled, leaving that island untouched by scientists for quite a while longer. While the scientists were ashore the Ship's Captain, George Nares of the Royal Navy, undertook a survey that resulted in the island's group's first marine chart (illustrated in Marsh 1948) that remained in use until replaced by a new one in 1950 (Goosen 1973). From accounts written (e.g. Linklater 1972) it is clear that the civilian scientists, known as "the philosophers" and teased as such by the younger naval officers, much enjoyed their short outing away from navy rule, even though their landing through thick kelp and onto slippery rocks proved difficult (Spry 1876). They had all equipped themselves with heavy sticks in case they encountered fur seals, but saw none (Moseley 1879). The incubating Wandering Albatrosses were admired but still had to succumb to a "great deal of bullying with the stick before they stand up and let one see whether they have an egg or no". Dive-bombing sub-Antarctic Skuas *Catharacta antarctica* caused trepidation (as they seem often to do to novices to sub-Antarctic islands) and as a consequence were beaten off with sticks and gun barrels. Detailed observation were made on three of the four species of penguins that occur, with the downy King Penguins eliciting much interest as "absurd objects".

Henry Moseley, aboard as Naturalist, reported that he ascended a valley to about 1 500 feet (*c.* 460 metres) over soft boggy ground at first, presumably, in his heavy Victorian dress becoming quite hot and bothered in the process, and he remarked that he found the walking "extremely tiring". No doubt the large Christmas dinner consumed the day before (Linklater 1972) also had an effect on his progress. Moseley may have been the first scientist ashore on Marion Island to note the difficulties of the terrain, but certainly not the last, as it takes some weeks or months ashore to become what is now known as "island fit". During the *Challenger*'s visit, Boot Rock, a vertical stack off the northern coast of Marion Island, was named. Cook's voyage had previously remarked on this striking feature, without naming it (Cook 1785).

After the *Challenger*, few exploring vessels arrived in the next fifty years, and none stayed for any time (Headland 1989). The German *Gauss* sailed past in 1901, as did the *Fram* in the general vicinity in 1911, with Roald Amundsen aboard on his way to the South Pole. In 1935, the British *Discovery II* engaged in oceanographic research on its third commission and visited without landing; a few years later in January 1939 the French *Bougainville* made a brief landing at Ship's Cove on Marion Island, resulting in some biological collecting (summarized in Cooper & Avery 1986 and Headland 1989).

Somewhat different to the above visits, during World War II, in 1939 and 1940, British warships called at the Prince Edward Islands, including the submarine *Olympus*, to search for signs of visits by German warships. Such visits have never been definitely proven, but may well have occurred, as the *Schleswig-Holstein* was reported to have called in 1939 (Anonynous 1982; Cooper 1986a; Halpern 1986; Headland 1989).

13.4 South Africans arrive to stay: the annexation of 1947-1948

The story of the annexation of the Prince Edward Islands is so well known it is not gone into any detail here, and readers are referred to Marsh (1948) for a detailed, first-person account, along with much on the pre-annexation history of the island group. A summary is given by Cooper & Headland (1991). John Marsh was a journalist from the Johannesburg *Star* who accompanied the S.S. *Gamtoos*, the then supply ship of the Government Guano Islands Department, to the islands in 1948, soon after they had been claimed for South Africa by personnel of the H.M.S.A.S. *Transvaal* (Plates 13.1-13.3). In the early 1970s the author sailed several times on the last voyages of the slow-moving and rolling *Gamtoos*, then the oldest vessel under South African registry, and he did not envy Marsh and his shipmates their journey one bit. Tragically, the maiden sub-Antarctic voyage of the *Gamtoos* resulted in a death. A crew member, Joseph Daniels, was hit on the head when his small boat overturned in heavy seas while off-loading cargo. He could not be revived and was buried on Marion Island some hundreds of metres south of the meteorological station overlooking the sea (Plate 13.4). A simple wooden cross, not the original (see photograph in Cooper & Avery 1986), marks the burial site to this day, being repainted annually by team members as a mark of respect.

A not so well known fact is that a member of the first occupation party who landed from the *Transvaal* to camp ashore on Gunner's Point at the site of the current station, also drowned off the island on a subsequent visit by the same vessel. In January 1948, along with 13 companions, Able Seaman J.G. Bold spent 16 days ashore under difficult conditions (Marsh 1948). Eight years later, in April 1956, the same J.G. Bold, then promoted to Petty Officer, died in similar circumstances to that of Joseph Daniels, when a small boat capsized in heavy seas (*Cape Argus* Newspaper, 18 April 1956). Intriguingly, the third person to die at the Prince Edward Islands since annexation was also a crew member who drowned offshore following a small-boat capsize, this time from the R.S. *Africana II*, which visited Marion Island during an oceanographic research cruise in April 1963 (Roets 1963). His name is not recorded in the literature, and a white cross with no inscription next to Gentoo Lake on the island may well mark his (or Bold's) passing, although it does not seem to be a grave site. Fortunately, no member of a South African team stationed ashore has died on the island, although there have been a number of medical evacuations over the years. Prior to annexation, there had been sealer deaths ashore, from exposure and from drowning as early as 1818 ("Webfoot" 1871; Marsh 1948). One definite (Boshoff & Van Schalkwyk 1999) and one likely (personal observation) pre-annexation burial site have been discovered on Marion Island. The latter awaits archaeological investigation.

Another member of the very first shore party was Captain W.D. Anderson, a military engineer. His main tasks were to search for a local water supply, consider the possibility of constructing a landing facility for aeroplanes, see if the available vegetation could be used for fuel, and to look for local materials for the mixing of concrete (Marsh 1948). It is interesting to deduce what he achieved. Clearly, there were no plants worth burning, but the author's inspections of still-existing concrete survey beacons erected at the time of annexation shows that local volcanic materials did indeed form part of the mix. Then, and much later (Heymann *et al.* 1987), the island was deemed unsuitable for a landing facility and early plans to send down a Sunderland flying boat never materialized, thwarted by the constant rough seas (Marsh 1948). However, Anderson was successful in finding clean water at a waterfall in the later-named Van den Boogaard River, north of Gunner's Point. The author has in his possession a published photograph captioned as showing "Anderson Falls" on Marion Island. It is hoped the waterfall can one day be matched with the fading cutting and the use of this historic name reinstated.

13.5 South Africans living in the sub-Antarctic, 1948 to present

A full history of the years of South African occupation since annexation will require a longer account. Indeed the subject, covering as it does, many years of scientific endeavour (summarized in other chapters in this book), as well as compelling human interest (Plates 13.5 and 13.6), needs a whole book to give it justice. In April 2006, the 63rd Team travelled to the island for their year's sojourn. Its members have taken over a rich history that includes dramatic events such as the loss of the station to fire in June 1966 and its subsequent rebuilding, rough seas which have on more than one occasion carried away whole buildings built too close to the shore, the dropping off of emergency medicines and supplies by low-flying aeroplanes, the coming ashore of Russian personnel from two Soviet stern trawlers in 1974 (when the USSR's hammer and sickle flew beside the old South African flag for a brief photo opportunity, surely for the first and last time on *Apartheid*-era South African Territory), stories of researchers benighted within a few metres of field huts invisible in the dark, field rescues of injured and exhausted team members and visitors, round-island and peak-bagging trips, and many more. Some stories are still shrouded in mystery, and may never be fully explained or refuted: a nearby nuclear "flash" in the Southern Ocean, researchers reporting their unexpected encountering of military personnel in the field, and a "structure" erected on Prince Edward Island that later mysteriously disappeared, are examples. More significantly, perhaps, each team member has taken home a wealth of personal memories to enthral a new generation, and there has been no shortage of volunteers over the years to take their place for a 13-month stay on Marion Island.

In a year or two a new base, currently been constructed adjacent to the old one at Transvaal Cove, will be occupied, and the old base torn down and its site rehabilitated. It is planned to display many of the records and memories of the previous teams at the new base, in the form of framed photographs and the many curious objects and souvenirs that have accumulated over the years. In this way the human history of the Prince Edward Islands will be preserved.

13.6 Early aliens: how some introduced mammals became established, and others not

A number of mammals have deliberately been introduced to Marion Island (Watkins & Cooper 1986). Only two species have established long-lasting populations, the House Mouse and the Domestic Cat *Felis catus* (Prince Edward Island has always been free of introduced mammals). The latter has now been eradicated from the island following a long campaign (Bester *et al.* 2002) worthy of medals, but the mice still remain. A little-known introduction about the same time as the mice was the Domestic Pig *Sus scrofa*. The early histories of these three introductions are considered here in some detail, throwing light as they do on the activities and attitudes of those visiting the island over the years.

Nothing is known of when and how the House Mouse arrived on Marion Island. Williams Phelps states there were many mice on the island when he landed in August 1818, encountered on the beaches, in caves and bird burrows and "among the snows of the mountains" having "multiplied until their name was legion" ("Webfoot" 1871). Given that the turn of the century was about the earliest they could have been introduced, they had certainly spread far in the two decades or less since the first human landing. Phelps thought that the mice had "been introduced from some sailing vessel, probably with the stores of the gang". However, it is also possible that they arrived from a shipwreck, although none were recorded by name quite this early from the Prince Edward Islands (Marsh 1948; Cooper & Avery 1986; Graham 1989; Headland 1989). However, Phelps writes of obtaining lamps "from the French wreck", so there had been at least one shipwreck prior to his arrival. Was this perhaps the source of the mice?

The mice on Marion Island show signs of originating from European populations (Berry *et al.* 1978; Jansen Van Vuuren & Chown 2007), but this tells us little of their immediate provenance. The sealing vessels known to have visited the island in the first decades of the 19th century were all originally from the United States of America (Cooper & Avery 1986; Headland 1989), but they could have picked up their unwanted rodent cargos at any of the many ports around the world – and there remains Phelps' French wreck for a future historian to investigate.

Almost two hundred years later mice are still present on Marion Island and have been the subject of much research into their effects on the island's biota (e.g. Van Aarde *et al.* 2004). Although consideration is now being given to the feasibility of their removal, this will be both difficult and expensive with current knowledge (Chown & Cooper 1995; Jackson & Van Aarde 2003). Their inadvertent introduction has proved a success story of note (from the point of view of the mice, and not of the island's conservation).

Turning to a deliberate introduction, the American sealer, *Meyars* (Captain Samuel Edes) took seal skins from the Prince Edward Islands in January/February 1804, when a "couple" (presumably a breeding pair) of domestic pigs *S. scrofa* were released on Marion Island (Graham 1989; Headland 1989; Richards 1992). At least eight feral pigs (three were large boars described as "wild and terribly ferocious creatures") were still present on the island in the period 1818-1820, so we can assume that the species commenced breeding ashore. The pigs were actively hunted to extinction by sealers left on the island by the *Pickering* as "we no doubt killed the whole stock" ("Webfoot" 1871). William Phelps has left us with a thrilling account of how the very last boar ("the worst of the lot … an ugly customer") was killed. The animal, on being cornered "made towards me with his ivory bow-chasers glistening through the froth". Phelps then remarks he "had some business in the opposite direction, and of course I hurried back to attend to it" and rather wisely left the actual capture of the pig to another in his party! They did not eat this pig, perhaps because of its rank taste, as commented on by men of the *Challenger* for Crozet pigs (see below) which were "scarcely palatable in any case, since they fed on penguins and bitter Kerguelen cabbage, *Pringlea antiscorbutica*" (Busch 1985).

It is interesting to speculate as to what would have happened if Phelps and his companions had left the pigs to multiply and spread over Marion Island. Pigs have been introduced to other islands in the Southern Ocean. Ile aux Cochons (Hog Island) in the Iles Crozet no longer has its pigs that were also introduced by sealers in the early 1800s, causing considerable damage to tussock vegetation and penguin colonies. They had disappeared by the end of the century (Bonner & Lewis Smith 1985; Clark & Dingwall 1985). Pigs were introduced to Auckland Island south of New Zealand in 1807 from a whaling vessel and had become "very numerous" by 1840 (Ross 1847; Turbott 2002). They are still present, and boosted by further introductions, considerably affect the island's megaherb fauna by uprooting, as well as by consuming albatross and cormorant eggs and chicks and disturbing burrowing petrels (Sanson & Dingwall 1995; Turbott 2002). Marion Island pigs, if they were able to survive the harsher climate, would have likely caused similar harm. We can indeed be thankful that Phelp's companions got the lot. A few pigs were kept on the island in the early 1950s in a pig sty (known as "La Grange Villa", still standing today although much dilapidated after half a century) on Boulder Beach immediately below the station. They were all eaten before they had any chance of becoming feral (la Grange 1952; Watkins & Cooper 1986).

When Phelps' shore party was visited by the sealer *General Gates* in late 1818 or early 1819 they were given a cat by its Captain, Abimelick (or Abimelech) Riggs. The animal (a female) proved useful in ridding the cave in which they lived of mice ("Webfoot" 1871). After a few months, however, "she took a notion to ramble away" and became wild. She was thereafter occasionally spotted far inland but would "bound away" on approach. Fortunately, this individual did not lead to a feral population, so it may be assumed it was not pregnant when put ashore. But the real calamity was still to come.

More than a hundred years passed before feral cats became established on Marion Island, following the deliberate introduction of five individuals in two batches in 1949 to help curb the mouse plague in the meteorological station (Van Aarde 1979; Van Aarde & Skinner 1981; Watkins & Cooper 1986). Unfortunately, animals of both sexes were taken to the island, and they, as cats will do, commenced breeding. In about September 1949 "two seven-month-old kittens born to Tootles 'Officer Commanding Cats' were brought back to South Africa" (newspaper cutting in the author's possession, entitled "Back from Marion Island. Six had the vilest winter"). This contradicts Van Aarde & Robinson (1980) who state that the first kittens were not born on the island until November 1949. Whatever the exact early history, the cat population soon burgeoned in the meteorological station, some inevitably went wild and the first feral cats were sighted 12 kilometres away from the station at Wild Cat Creek during 1951 (Van Aarde 1979). More information on exactly how the station's pet cats became feral comes from an unpublished report in the author's possession. The report, marked confidential and dated 30 July 1952, was written by the late R.W. (Bob) Rand, a biologist (the island's first) who was a member of the 8th South African Expedition from October 1951 to April 1952 (Cooper & Avery 1986). Rand states at the outset of his report that the "policy of allowing cats on the island should be halted immediately". He was of the opinion that the cats in the station were too-well fed on "choice canned fish" to make efficient mousers. He also commented on their unsanitary habits, as animals "defecating on beds and other furniture". Nevertheless, one team member allowed "nearly two dozen" to live in his bedroom. Whereas some of his fellow team members also doted on the cats, others despised them and "kick[ed] them out of the houses when they make a mess". With such treatment (and such numbers), it is not at all surprising that some "took to the hills" and became feral.

Bob Rand observed four feral cats on his trips away from the station, writing that they were living off mice and burrowing petrels. With considerable perspicacity, he called their presence the result of a "misguided policy" and considered them a menace to the island's wildlife. He recommended that the station cats be "rigidly controlled or else destroyed altogether". However, pet cats (including "Bixs", and the kittens "Rusty" and "Tommy") were still present in the station two years later in 1954 (photographs in the author's possession, taken by Sgt. W.J. Deysel, Medical Orderly of the 11th Island Team). Indeed, a single pet cat was present as late as 1974 (A.J. Williams, personal communication). Rand's report was to no avail: cats killed hundreds of thousands of burrowing petrels before their final eradication at great expense in 1991, nearly 40 years after his call for their removal (Van Aarde 1980; Bester *et al.* 2002).

13.7 Gender and race in the sub-Antarctic and the policy of Apartheid

13.7.1 Early female pioneers: thwarting the "no doors on the toilets" syndrome

As far as it is known, the first women to visit the Prince Edward Islands did not manage to get ashore. On 19 June 1849 the emigrant brig *Richard Dart* bound for New Zealand was wrecked on Prince Edward Island in thick fog. All five women aboard drowned (as did 10 children) out of a complement of 63. Only 11 men reached the shore alive (Marsh 1948). Graham (1989) gives the names of some of the passengers who drowned, including a Mrs Fitten, who was lost with her husband and child. More happily, the wives of captains and officers of sealing vessels sometimes joined their husband's expeditions in the 19th century, to avoid the loneliness of a temporarily widowed life at home, and for the adventure. They must have been courageous to go against convention in this way and put up with the inevitable privations on long uncomfortable voyages that might last well over a year. It seems likely that they did not venture ashore, and stayed away from the crew and sealing activities by restricting themselves to their cabins and to the aft decks of their vessels (Cooper 1987). On 2 December 1852 the clipper bark *Nathaniel S. Perkins* arrived at the Prince Edward Islands. Captain Gurdon L. Allyn had brought his wife along for "company", as had his mate, named Pinkham. They "tarried some days and succeeded in obtaining a small quantity of sea-elephant oil. But the prospect was slim, the animals were scarce and poor, and we bore away for other grounds" (Allyn 1879).

We now jump more than a century ahead to consider who the first woman was to come ashore at the Prince Edward Islands. In December 1974 the French Antarctic vessel *Marion du Fresne* briefly visited Marion Island. "Two boat loads of French came ashore, mainly scientists ... they brought a woman ashore, Marion's second ever" (Anonymous 1974; Cooper 1986c; A.J. Williams, personal communication). So who was the first? More is known about later pioneer visits by women. Pamela Laycock of the University of Cape Town may well be the first woman to have gone ashore on Prince Edward Island: at least there are no other claimants known. She spent the period 13-16 September 1979 camping on the island as part of an ornithological research team during a relief voyage at a time when woman were not allowed by the government's Antarctic Department to stay on Marion Island for a longer sojourn (Cooper 1986b). Pam Laycock also appears to have been the first woman to publish a scientific paper from her visit to the island group (Williams & Laycock 1981), although Sue Lane co-authored a paper two years previously on zooplankton collected from around the islands in 1976 (Grindley & Lane 1979). In 1981 Tamar Salinger of the then Transvaal Museum visited Marion Island on another relief voyage, then becoming the first woman to walk right around the island, a "right of passage" for many island inhabitants since the early sealing days ("Webfoot" 1871). With rules still in place not allowing women to be members of annual teams, it fell to Christine Hänel to be the first of her sex to spend an extended stay at the island. She arrived on 16 January 1986 as a member of the crew of the dismasted New Zealand yacht *Totorore* and was left behind by the skipper as a safety measure when the repaired yacht continued its voyage the next month (Clark 1988). Christine stayed on Marion Island, with South African Government approval as a "shipwrecked mariner", until the annual relief vessel arrived in April. During this time she also walked around the island (Cooper 1986b).

For four decades from annexation, all team members at Marion Island were male, who, perforce, had to undertake all the "household chores which are usually considered to be the responsibility of womanfolk" (King 1952). No wonder the early teams felt the need for servants (see below)! The first women to spend a full year on Marion Island as team members were the biologists Marita Cawood and Marianna Steenkamp from the then University of the Orange Free State in 1986/87. At that time women were only allowed to be team members if there was a minimum of two (for company and support, said those (males) in charge in a seemingly sexist manner). This proved difficult to organize within the small scientific community, so a full decade passed before women were again members of annual teams (Christine Hänel again and Jeanne Hurford in 1996/97, as members of the 53rd Team), but from then on their presence has been regular. To date no woman has spent a full year on the island as the sole representative of her gender. In the mid 1980s the author tried to persuade the authorities to allow Susan Jackson, then of the University of Cape Town, to spend a year on the island (as the only woman team member) to conduct physiological research on seabirds. This request was refused and she had to complete her Ph.D. (Jackson 1990) by dint of relief visits only to Marion Island in the period 1986-1988. Her thesis is the first by a woman to be awarded a higher degree for research conducted at the Prince Edward Islands. Her success in this regard was quickly followed by that of Marianna Steenkamp who completed her Ph.D. in 1991 (Steenkamp 1991).

Antwanette Lombard, a medical orderly, was the first female Team Leader (55th Team in 1998/99), and Bettine Jansen van Vuuren the first female Chief Scientist based at the island during a relief voyage (2006). Nowadays, married couples are often team members, playing their role in increasing the diversity (and it is hoped, stability) of their isolated communities. Quite a few team members of opposite sexes have formed stable relationships on the island which continued throughout the years that followed back in South Africa. To date, there has been no wedding conducted on Marion Island (as have happened at French and United Kingdom sub-Antarctic islands). However, at least one honeymoon has been spent in Marion field huts (and there have been two recent, but unofficial, accounts of conceptions). The author is proud to have played his small part in helping women realize their ambitions of "heading south" on South African expeditions, both to the islands and to the Antarctic Continent (Cooper 1979). Right on sister!

13.7.2 Racial issues: from servants to leaders

Shortly after the islands were annexed, the first meteorological team was left on the island for a six-month period from March to September 1948. We are fortunate that the Team Leader was Allan Crawford, who has published two books that include accounts of his island sojourn (Crawford 1982, 1999). He had previously spent several years on Tristan da Cunha and suggested that Tristan Islanders accompany the team as "handymen", because of their boat-handling skills and experience of life on an oceanic island (Marsh 1948; King 1952). Six islanders thus joined the team of four South Africans (Cooper & Avery 1986). On the island, the islanders occupied one building (Island or Tristan House) and the South Africans another (Union or Governor's House) (Marsh 1948; Goosen 1973). Governor's House had the better of it in terms of comfort, Tristan House initially being without any ablution facilities (Mackay 1949; R.W. Rand, unpublished report). In an unpublished report (in the author's possession) addressed to "The Director Met Services" by Alan Crawford dated 21 September 1948 on his period as "late Officer in charge Marion Island", Tristan House is described as "where non-Europeans are housed". At the time this segregation may have seemed perfectly natural (the Tristan Islanders were from a very tight-knit community after all, one they had never left before). But by the 1960s when Tristan had to be evacuated because of a volcanic eruption, the Tristan Islanders were still regarded as non-white under the (then) South African racist policies of *Apartheid* (separateness), presumably because of the St Helenan women of mixed race that had married into their community in the early 19th century (Crawford 1982).

The second team, led by D.O. Triegaardt, a Senior Meteorological Officer, arrived on the island to relieve Allan Crawford in August 1948. This team included two "South African coloured servants" (also described as "Cape Coloureds", i.e. of mixed race) whose names appear to have gone unrecorded in the published literature (La Grange 1952, 1954; Cooper & Avery 1986). This cavalier treatment, at its most charitable, may be taken as a "sign of the times", given that the Nationalist Party campaigning on a policy of rigid *Apartheid* had come to power in South Africa the very same year. In May 1952 a team member who had recently returned from the island wrote to the Director of the then Weather Bureau and under the heading "Coloured Servants" had the following request: "The need for servants for the cleaning of the base, washing of dishes, cooking and undertaking of outside work, has long been felt. I strongly recommend it, as long as the Responsible Official has a good knowledge of Coloureds and their habits and knows how to administer and control them. Servants will be useful with the proposed experiments for the breeding of sheep on the island." (translated from the original Afrikaans letter in the author's possession).

Whatever the reasons, no more servants of any race were included in island teams after the first two; members "mucking in" and taking on their share of domestic duties in the station, as teams still do today. But there remains a responsibility among the South African sub-Antarctic community to attempt to "recover" the names of the two lost persons from dusty government files, and to commemorate their services in an appropriate way. Two members of their team, Daan Triegaardt and H.M.E. Van den Boogaard, had geographical features on Marion Island named after them (a bay and a river, respectively), and this would be fitting for the unnamed two.

From the arrival of the third island team in March 1949 up until 1989 every single team member staying for an extended period at Marion Island has been classified as white under the then South African race laws. The author of this chapter well remembers being referred an application for a field assistant post in the 1980s from a South African of Indian descent on whose personnel form a government official had carefully placed a ring around his racial classification, presumably as a warning sign! Needless to say, his ambition to travel south was not realized.

Since the change of South African Government in 1994, however, this odious type of discrimination has thankfully fallen away, and nowadays a Marion Island team, including its scientists, broadly reflects the racial (and cultural) make-up of the country, as it should have all along. The first non-white person to spend a full year on Marion Island was Gerald Meyer, a meteorologist, who accompanied the 46th Team to Marion Island in 1989, over 40 years since annexation. Samantha Linnerts was the first non-white female team member, serving as a meteorologist (60th Team, in 2003/04). The first non-white Team Leader was Nole Green, the diesel mechanic of the same 60th Team.

Alvan Gabriel (entomologist and conservation officer) studied Collembola at Marion Island as a team member during the period 1999-2000 (Gabriel 1999; Gabriel *et al.* 2001). Bantu Hanise and Shadrack Podile (University of Pretoria) co-authored a publication on Killer Whales *Orca orca* based on observations made in 2000 (Pistorius *et al.* 2002). Lukhanyiso Vumazonke (Rhodes University) studied marine shrimp during an oceanographic cruise adjacent to the islands in April 2002 (Vumazonke *et al.* 2003). The first non-white persons to be awarded higher degrees for research they conducted ashore at Marion Island are Alvan Gabriel and Azwianewi Makhado, who completed their M.Sc. degrees at the Universities of Durban-Westville and of Pretoria, respectively (Gabriel 1999; Makhado 2002). The numbers continue to grow.

13.8 Postscript: looking to the future

What will befall the Prince Edward Islands in the years ahead? It seems climate change and new alien introductions will inevitably lead to slow changes in a number of aspects of their ecology, as set out elsewhere in this book – and there is always the risk of a major volcanic eruption. The islands seem set to continue to be well protected by South Africa, with a new and comprehensive management plan from 2007, a surrounding Marine Protected Area in an advanced stage of planning, and World Heritage and Wetland of International Importance nominations made to the respective conventions (De Villiers & Cooper 2008). Parliament will have to decide if commercial tourism will be allowed, but currently this seems most unlikely. The new base currently constructed should lead to more researchers working on Marion Island, which will be no bad thing, but it is hoped that visits to near-pristine Prince Edward Island will remain few and very strictly managed, as at present. The author thus expects (and hopes) that in a hundred years from now, the island group will still be regarded as a special place that continues to instil a long-lasting passion in many, if not most, who are privileged to have visited it, and that new human stories about sub-Antarctic Marion and Prince Edward Islands will continue to be told.

13.9 Acknowledgements

This chapter is dedicated to R.K. (Bob) Headland, retired Archivist of the Scott Polar Research Institute, University of Cambridge, United Kingdom, who introduced me to many fascinating early publications containing forgotten stories about the Prince Edward Islands. I thank all my many sub-Antarctic colleagues over the years for their help and their interest in the human history of the Prince Edward Islands.

13.10 References

Allyn, G.L. 1879. *The Old Sailor's Story, or a Short Account of the Life, Adventures and Voyages of Capt. Gurdon L. Allyn Including Three Trips Around the World. Written by Himself, in the Seventy-ninth and Eightieth Years of his Age*. Gordon Wilcox, Norwich.

Anonymous. 1974. News from the islands. *South African Weather Bureau News Letter* **309**, 247-248.

Anonymous. 1982. The Prince Edward Islands and World War II. *SASCAR Newsletter* **7**, 6.

Beaglehole, J.C. 1961. *The Journals of Captain James Cook on his Voyages of Discovery. II. The Voyage of the Resolution and Adventure 1772-1775*. Hakluyt Society, Cambridge.

Beaglehole, J.C. 1967. *The Journals of Captain James Cook on his Voyages of Discovery. The Voyage of the Resolution and Discovery 1776-1780. Part One*. Hakluyt Society, Cambridge.

Berry, R.J., Peters, J. & Van Aarde, R.J. 1978. Sub-Antarctic House Mice: colonization, survival and selection. *Journal of Zoology, London* **184**, 127-141.

Bester, M.N., Bloomer, J.P., Van Aarde, R.J., Erasmus, B.H., Van Rensburg, P.J.J., Skinner, J.D., *et al.* 2002. A review of the successful eradication of feral cats from sub-Antarctic Marion Island, southern Indian Ocean. *South African Journal of Wildlife Research* **32**, 65-73.

Bonner, W.N. & Lewis Smith, R.I. (Eds.). 1985. *Conservation Areas in the Antarctic. A Review Prepared by the Sub-Committee of Conservation Working Group on Biology*. Scientific Committee on Antarctic Research, Cambridge.

Boshoff, J.J., Hart, D. & Loock, J. 1997. *Survey of Historical Sites on Marion Island*. Privately Printed, Cape Town.

Boshoff, J.J. & Van Schalkwyk, J.A. 1999. *The Archaeology of Sealing Sites on Marion Island*. Unpublished Report to the South African Heritage Resources Agency.

Busch, B.C. 1983. Alta California 1840-1842. *The Journal and Observations of William Dane Phelps Master of the Ship "Alert"*. Arthur H. Clark Company, Glendale, California.

Busch, B.C. 1985. *The War Against the Seals. A History of the North American Seal Fishery*. McGill-Queen's University Press, Kingston & Montreal.

Chown, S.L. & Cooper, J. 1995. *The Impact of Feral House Mice at Marion Island and the Desirability of Eradication. Report of a Workshop held at the University of Pretoria, 16-17 February 1995*. Directorate: Antarctica & Islands, Department of Environmental Affairs and Tourism, Pretoria.

Clark, G. 1988. *The Totorore Voyage*. Century Hutchinson, Auckland.

Clark, M.R. & Dingwall, P.R. 1985. *Conservation of Islands in the Southern Ocean. A Review of the Protected Areas of Insulantarctica*. International Union or Conservation of Nature and Natural Resources, Gland & Cambridge.

Cook, J. 1785. *A Voyage to the South Pacific. Undertaken by the Command of His Majesty*. Hughes, Nicol & Cadell, London.

Cooper, J. 1979. Editorial. Studying seabirds and sexual discrimination. *Cormorant* **7**, 3.

Cooper, J. 1986a. History of the Prince Edward Islands: I. Did German warships visit during World War II? *SASCAR Newsletter* **23**, 1-2.

Cooper, J. 1986b. History of the Prince Edward Islands: II. The first female visitors. *SASCAR Newsletter* **23**, 5-6.

Cooper, J. 1986c. History of the Prince Edward Islands: III. More on early female visitors. *SASCAR Newsletter* **24**, 7.

Cooper, J. 1987. History of the Prince Edward Islands: IV. Early female visitors. *SASCAR Newsletter* **27**, 5-6.

Cooper, J. & Avery, G. (Eds.). 1986. Historical sites at the Prince Edward Islands. *South African National Scientific Programmes Report* No. **128**, 1-82.

Cooper, J. & Headland, R.K. 1991. A history of South African involvement in Antarctica and at the Prince Edward Islands. *South African Journal of Antarctic Research* **21**, 77-91.

Crawford, A.B. 1982. *Tristan da Cunha and the Roaring Forties*. Charles Skilton, Edinburgh & David Philip, Cape Town.

Crawford, A.B. 1999. *Penguins, Potatoes & Postage Stamps*. Anthony Nelson, Oswestry.

De Villiers, M.S. & Cooper, J. 2008. Conservation and management. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 301-330.

Duyker, E. 1994. *An Officer of the Blue. Marc-Joseph Marion Dufresne, South Sea Explorer, 1724-1772*. Melbourne University Press, Melbourne.

Fanning, E. 1834. *Voyages Round the World; with Selected Sketches of Voyages to the South Seas, North and South Pacific Oceans, China, etc*. O. Rich, London.

Gabriel, A.G.A. 1999. *The systematics and ecology of the Collembola of Marion Island, sub-Antarctic*. M.Sc. Thesis, University of Durban-Westville, South Africa.

Gabriel, A.G.A., Chown, S.L., Barendse, J., Marshall, D.J., Mercer, R.F.D., Pugh, P.J.A., *et al.* 2001. Biological invasions of Southern Ocean islands: the Collembola of Marion Island as a test of generalities. *Ecography* **24**, 421-430.

Goosen, J.C. 1973. *South Africa's Navy: the First Fifty Years*. W.J. Flesch & Partners, Cape Town.

Graham. T. 1989. *Cultural resource management of the Prince Edward Islands*. B.A. (Hons.) Dissertation, University of Cape Town, South Africa.

Grindley, J.R. & Lane, S. 1979. Zooplankton around Marion and Prince Edward Islands. *Comité National Française des Recherche Antarctiques* **44**, 111-125.

Halpern, A. 1986. War in the South Atlantic and Southern Ocean 1939-42. *Polar Post* **18(4)**, 80.

Headland, R.K. 1989. *Antarctic Chronology*. Cambridge University Press, Cambridge.

Heymann, G., Erasmus, T., Huntley, B.J., Liebenberg, A.C., Retief, G de F., Condy, P.R., *et al.* 1987. Report to the Minister of Environment Affairs on an environmental impact assessment of a proposed emergency landing facility on Marion Island – 1987. *South African National Scientific Programmes Report* No. **140**, 1-209.

Jackson, S. 1990. *Seabird digestive physiology in relation to foraging ecology*. Ph.D. Thesis, University of Cape Town, South Africa.

Jackson, T.R. & Van Aarde, R.J. 2003. Advances in vertebrate pest control: implications for the control of feral House Mice on Marion Island. *South African Journal of Science* **99**, 130-136.

Jansen Van Vuuren, B. & Chown, S.L. 2007. Genetic evidence confirms the origin of the House Mouse on sub-Antarctic Marion Island. *Polar Biology* **30**, 327-332.

King, J.A. 1952. South Africa in the Subantarctic. In: Simpson, F.A. (Ed.). *The Antarctic Today. A Mid-century Survey by the New Zealand Antarctic Society*. A.H. & A.W. Reed, Wellington, pp. 304-312.

La Grange, J.J. 1952. Sojourn on Marion Island. *Newsletter Weather Bureau* **39**, 4-7.

La Grange, J.J. 1954. The South African Station on Marion Island 1948-53. *Polar Record* **7**, 155-158.

Leupe, P.A. 1868. De Eialanden Dina en *Maerseveen* in den zuider Atlantischen Oceean. *Verhandelingen Berigten Betrekkeliik het Zeewezen* **2**, 242-253.

Linklater, E. 1972. *The Voyage of the Challenger*. John Murray, London.

Mackay, A.D. 1949. Marion Island Meteorological Station. *Public Works of South Africa* **10(69)**, 23-28.

Makhado, A.B. 2002. *The diet of two fur seal species* (Arctocephalus gazella *and* A. tropicalis) *at Marion Island*. M.Sc. Thesis, University of Pretoria, South Africa.

Marsh, J.H. 1948. *No Pathway Here*. Howard B. Timmins, Cape Town.

Moseley, H.N. 1879. *Notes by a Naturalist. An Account of Observations made during the Voyage of the H.M.S. "Challenger" Round the World in the Years 1872-1876, under the Command of Capt. Sir G.S. Nares, R.N., K.C.B., F.R.S., and Capt. F.T. Thomson, R.N.* T. Werner Laurie, London.

Péron, P.F. 1824. *Mémoires du Capitaine Péron sur les Voyages aux Cotes d'Afrique, en Arabie, l'Ile d'Amsterdam, aux Iles d'Anjouan et de Mayotte, aux Cotes Nord-oeust de l'Amérique, aux Iles Sandwich, a la Chine, etc*. Brissot-Thivars, Paris.

Pistorius, P.A., Taylor, F.E., Louw, C., Hanise, B., Bester, M.N., de Wet, C., *et al.* 2002. Distribution, movement, and estimated population size of Killer Whales at Marion Island, December 2000. *South African Journal of Wildlife Research* **32**, 86-92.

Rice, W.H. 1991. South African owned "Kil" Class ships. *Militaria* **21(3)**, 7-12.

Richards, R. 1992. The commercial exploitation of sea mammals at Iles Crozet and Prince Edward Islands before 1850. *Polar Monographs* **1**, 1-19.

Roets, B.A. 1963. Cruise to Marion Island in April, 1963. *South African Association for Marine Biological Research Bulletin* No. **4**, 33-35.

Ross, J.C. 1847. *A Voyage of Discovery and Research in the Southern and Antarctic Regions, During the Years 1839-43*. John Murray, London.

Ross, M.J. 1982. Ross in the Antarctic. *The Voyages of James Clark Ross in Her Majesty's Ships, Erebus & Terror 1839-1843*. Caedmon of Whitby, Whitby.

Roth, H.L. 1891. *Crozet's Voyage to Tasmania, New Zealand the Ladrone Islands, and the Philippines in the years 1771-1772*. Truslove & Shirley, London.

Sanson, L.V. & Dingwall, P.R. 1995. Conservation status of New Zealand's Subantarctic islands. In: Dingwall, P.R. (Ed.). *Progress in Conservation of Subantarctic Islands. Proceedings of the SCAR/IUCN Workshop on Protection, Research and Management of Subantarctic Islands, Paimpont, France, 27-29 April, 1992*. Gland & Cambridge, International Union of Nature and Natural Resources.

Spry, W.J.J. 1876. *The Cruise of Her Majesty's Ship "Challenger." Voyages Over Many Seas, Scenes in Many Lands*. Sampson Low, Marston, Searle & Rivington, London.

Steenkamp, M. 1991. *Decomposition and nutrient studies on sub-Antarctic Marion Island*. Ph.D. Thesis, University of the Orange Free State, South Africa.

Turbott, G. 2002. *Year Away. Wartime Coastwatching on the Auckland Islands, 1944*. Department of Conservation, Wellington.

Underhill, L.G., Petersen, S.L. & Cooper, J. 2003. Nest densities of the Wandering Albatross *Diomedea exulans* at the Prince Edward Islands, estimated using GPS. *African Journal of Marine Science* **25**, 529-535.

Van Aarde, R.J. 1979. Distribution and density of the feral House Cat *Felis catus* on Marion Island. *South African Journal of Antarctic Research* **9**, 14-19.

Van Aarde, R.J. 1980. The diet and feeding behaviour of feral cats, *Felis catus* at Marion Island. *South African Journal of Wildlife Research* **10**, 123-128.

Van Aarde, R.J. & Robinson, T.J. 1980. Gene frequencies in feral cats on Marion Island. *The Journal of Heredity* **71**, 366-368.

Van Aarde, R.J. & Skinner, J.D. 1981. The feral cat population at Marion Island: characertisics [sic], colonization and control. *Comité Nationale Française Recherches Antarctiques* **51**, 281-288.

Van Aarde, R.J., Ferreira, S.M. & Wassenaar, T.D. 2004. Do feral House Mice have an impact on invertebrate communities on sub-Antarctic Marion Island? *Austral Ecology* **29**, 215-224.

Van Zinderen Bakker, Sr., E.M., Winterbottom, J.M. & Dyer, R.A. 1971. *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965-1966*. A.A. Balkema, Cape Town.

Vumazonke, L.U., Pakhomov. E.A., Froneman, P.W. & McQuaid, C.D. 2003. Diet and daily ration of male and female caridean shrimp *Nauticaris marionis* at the Prince Edward Archipelago. *Polar Biology* **26**, 420-422.

Watkins, B.P. & Cooper, J. 1986. Introduction, present status and control of alien species at the Prince Edward Islands. *South African Journal of Antarctic Research* **16**, 86-101.

"Webfoot" [=Phelps, W.D.] 1871. *Fore and Aft; or, Leaves From the Life of an Old Sailor*. Nichols & Hall, Boston.

Williams, A.J. & Laycock, P.A. 1981. Euphausiids in the diet of some sub-Antarctic eudyptid penguins. *South African Journal of Antarctic Research* **10/11**, 27-28.

CHAPTER 14

CONCLUSION: CHANGE IN TERRESTRIAL AND MARINE SYSTEMS

STEVEN L. CHOWN AND P. WILLIAM FRONEMAN

The modern climate of the Prince Edward Islands has been described as one of the most oceanic and stable on earth (Schulze 1971; Van Zinderen Bakker 1978; le Roux 2008). Indeed, on the basis of the typically low daily amplitude of temperatures and their small variation between summer and winter, this characterization is correct. However, over both longer and shorter timescales, stability is something of a caricature. The islands have changed dramatically over the course of their history. Although much remains to be learned about the sequence of glaciation and volcanism on both islands (Boelhouwers *et al.* 2008), it is clear that they underwent considerable modification as a result of changing global climates and isostatic adjustment that was a consequence thereof.

Modern measurements of climate, which commenced in the late 1940s, have signalled ongoing change in climate too. Not only have mean annual temperatures increased and precipitation declined (Smith 2002; le Roux 2008), but a host of other changes have been effected to local climate. In turn these are thought to be having a variety of biological and geomorphological consequences. The former includes a significant increase in the effect of invasive species on local communities and species (Bergstrom & Chown 1999; Chown & Smith 1993; Chown *et al.* 2002), whilst the latter includes disappearance of Marion Island's ice plateau (Sumner *et al.* 2004), and thermal erosion and subsidence of areas previously underlain by buried glacial ice. Alterations in

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 351-372

the number of clear sky evenings are also thought to be having significant biological effects (Smith & Steenkamp 1990; Sinclair & Chown 2005).

Recent work on microclimates has also drawn an important distinction between variability in thermal regimes and their predictability. Whilst a system with no variability is clearly predictable over a wide range of timescales, a highly variable system might be either predictable or unpredictable. For example, over a seven-day period, soil temperatures on the coast at Lambert's Bay, South Africa vary between 5°C and 24°C in a predictable fashion (Deere & Chown 2006). From one day to the next it is clear that the hottest time is just after noon, and the coldest about 11-12 hours later. By contrast, at sea level on Marion Island temperature is much less variable, but importantly also much less predictable. Whilst the overall range is 7°C at most, it is never quite clear at what times the highs and lows can be expected. Autocorrelation plots or spectral analyses reveal these substantial differences in predictability, with significant autocorrelation persisting for seven days in the Lambert's Bay data, but disappearing within 11 hours for Marion Island (Deere & Chown 2006). Whilst the importance of understanding both variability and predictability has been appreciated for some time (Kingsolver & Huey 1998), especially when distinguishing marine and terrestrial environments (Vasseur & Yodzis 2004), it is only more recently that the significance of this distinction for understanding climate change responses has come to be appreciated (Ghalambor *et al.* 2006; Chown & Terblanche 2007). Indeed, the unpredictability of thermal regimes in the temperate southern hemisphere (despite a lower overall range than in the north (Bonan 2002)) is thought to be an important driver of north-south differences in biodiversity, from the physiological to the species richness levels (Chown *et al.* 2004). Not only is unpredictability reflected in the responses of the biota on the Prince Edward to local environmental circumstances, but these responses also differ markedly between marine and terrestrial species, as might be expected from differences in the thermal regimes of the two environments (Deere & Chown 2006).

14.1 Historic change and evolutionary responses

How past glaciations and volcanism affected organisms and communities at the Prince Edward Islands is poorly understood. The responses of particular plant species and past vegetation dynamics are at least partly known. Paleoecological studies have demonstrated the absence during glacial maxima of many species typical of the islands' current assemblages, and a clear vegetation succession at other times (Boelhouwers *et al.* 2008). This succession has taken place many times and is typically one from barren fellfield to *Azorella selago*-dominated fellfield to *Agrostis magellanica* and *Acaena magellanica* peatland. What remains much less clear is how glaciation and repeated volcanic events affected evolutionary processes on the island. No studies have examined intra-island evolutionary dynamics of the indigenous plants, and even such basic questions as their current mode of pollination remain largely unanswered.

Nothing is known about how past geological and climate events might have affected vertebrate populations. No sub-fossils (see Steadman 1995) are known from the islands and basalt is not fossil-bearing for obvious reasons. The 1980 volcanic event at Marion Island closed off a large haul-out area for Elephant Seals in the Kaalkoppie/Swartkop area of the island, but it seems that the seals simply moved to other beaches (M.N. Bester, personal communication). Given the mobility of the pelagic seabirds and seals, and genetic cohesion across the region amongst at least some of them (Burg & Croxall 2001), it seems likely that, despite their philopatry, local geological events would have had little, long-lasting effects on these predators. Nonetheless, even such questions as the likelihood of local population bottlenecks and the extent of migration between Marion and Prince Edward Island have not been addressed, with the exception of occasional reporting from elsewhere of animals tagged on Marion Island (Ryan & Bester 2008).

Evolutionary dynamics in the marine system are also poorly known. Whilst the biogeography of the fauna has been investigated (Chown *et al.* 2008), and regional events such as speciation in the notothenioid fish have been thoroughly examined (Bargelloni *et al.* 2000a, b; Verde *et al.* 2007), little detailed work on the phylogeography and population genetics of any marine taxa has been undertaken.

The situation with the terrestrial arthropods is different. Early work (e.g. Chown 1989, 1990a) suggested that a major evolutionary signal in the insects, both on the Prince Edward Islands and on the other South Indian Ocean Province Islands, is a clear division between the eplithic (coastal, fellfield, rockface) and the vegetated (lowland vegetation communities) biotopes. The former biotope is home to speciose assemblages, which are thought to have survived and in some cases speciated during Quaternary glacial events, and whose species are reasonably habitat specific. The latter is characterized by only a few, more modern species with low habitat specificity (Chown 1994). This signal has subsequently been verified for mites on the islands (Barendse *et al.* 2002) and for arthropods more generally across the Antarctic region (Marshall & Convey 2004).

More recent phylogeographic work has demonstrated that evolutionary dynamics on the islands are substantially more complicated than the above, rather simple scenario suggests. For example, it has long been presumed that amongst the weevils on the Prince Edward Islands, two vegetated biotope species exist which have recently speciated as a consequence of size-based assortative mating (Chown 1990b; Kuschel & Chown 1995). A combined morphological and phylogeographic study has revealed a more complex pattern, that is yet to be fully explained (Grobler *et al.* 2006). On Marion Island only a single, size-variable species apparently exists. By contrast, on Prince Edward Island, two species, which differ both in terms of their mitochondrial cytochrome oxidase I (mtCOI) sequences, and size, co-exist. The larger species has been designated a new one, *Ectemnorhinus kuscheli*, because both of the previously known species, *E. similis* and *E. marioni*, were described from Marion Island. How this situation has arisen is not clear. However, introgression of the previous species found on Marion Island may have been driven by a combination of a warming climate and substantial predation by house mice on larger weevils (Chown & Smith 1993; Grobler *et al.* 2006).

Amongst the terrestrial springtails and mites, substantial evidence of complex evolutionary events is also reflected in their phylogeography. In the indigenous springtails, haplotype diversity is extraordinarily high, especially in species such as *Cryptopygus antarcticus travei* (Myburgh *et al.* 2007), which, given its distinctiveness from other taxa with the same specific name, may represent a new species (Stevens *et al.* 2006). Moreover, this haplotype diversity is highly structured geographically, though not in a simple 'isolation-by-distance" fashion. Rather, disjunctions between localities and haplotypes seem to reflect particular geological events on the island including major glaciations and volcanic sequences. Moreover, some localities, such as Katedraalkrans, host a diverse array of haplotypes, indicating biological evidence for the status of the area as a glacial refugium, which is in keeping with geological evidence. The close match between the timing and spatial pattern of geological events and arthropod phylogeography is intriguing. It also includes other patterns, such as the remarkable dissimilarity of Kildalkey Bay to other localities, both amongst mites (Mortimer & Jansen Van Vuuren 2006) and springtails (Myburgh *et al.* 2007). Why this should be the case is not clear, although Kildalkey Bay has been identified as the likely site of first arrival for natural colonists of Marion Island (Chown & Avenant 1992).

Clearly, the study of past evolutionary dynamics on the island is in its infancy. However, modern techniques and an increasingly sophisticated understanding of the geological and climatological past of the islands suggest that such studies would provide considerable insight into the evolution of the islands' landscapes and biota. Some urgency for so doing also exists. Human activity is widely appreciated to lead to species introductions. More significantly, it has also led directly to changes in species distributions on the island (Chown *et al.* 2002). The longer the ongoing human activity, and the less attention given to quarantine procedures in transiting between one area and another, the more likely the historical signal is to be obscured by an anthropogenic one (Myburgh *et al.* 2007).

14.2 Modern change across the biological hierarchy

As is the case elsewhere in the world, three elements dominate modern change at the Prince Edward Islands: biological invasions, climate change, and exploitation. The two other significant threats to modern ecosystems, pollution (especially eutrophication) and habitat destruction (Millenium Ecosystem Assessment 2005), are of negligible importance on the islands. Contemporary human activity to date has been restricted to logistic operations and their scientific *raison d'etre* (De Villiers & Cooper 2008), and to long-line fishing (as opposed to trawling which is more destructive of the benthos, Watling & Norse 1998). The significance of the three change elements well represented on the islands differs among the terrestrial and the marine ecosystems, although the effects of these impacts cannot be entirely separated because of the close ties between the marine and terrestrial systems (Pakhomov & Chown 2003; McQuaid & Froneman 2008; Smith & Froneman 2008).

14.2.1 Biological invasions

In the terrestrial systems, commercial exploitation is non-existent. Small numbers of terrestrial species are harvested each year for scientific investigations, and typically the impact is considered negligible. By contrast, a wide range of species has been introduced, many of which are invasive and are having substantial effects on terrestrial species and ecosystems. The invasive species that wrought the most damage to terrestrial systems and species at Marion Island was the feral Domestic Cat. Although the introduced population was exterminated by 1991 (Bester *et al.* 2000), it caused substantial damage. Not only were hundreds of thousands of seabirds consumed as prey, but the cats are thought to have altered significantly nutrient dynamics at the island (Gremmen & Smith 2008). The large inland tussock grasslands previously associated with small burrowing seabird species and the manured slope crest communities typical of black lava areas have now both largely disappeared from Marion Island (see Smith 1978, 1987; Crafford & Scholtz 1986, 1987; Gremmen & Smith 2008), with a few notable exceptions in the former case. This may explain the difference in appearance of Marion Island now to what it was at annexation in 1947 when John Marsh (1948: 71) wrote: "Marion was a lovely picture. She rose, a jade jewel, out of the sea. Her lush green coat was fringed with the black lace of the cliffs and her heights draped in scintillating snow." On Prince Edward Island, large inland tussock grasslands and slope crest communities are still common. These differences between the islands, along with the presence of the feral House Mouse (*Mus musculus domesticus* – see Jansen Van Vuuren & Chown 2007 and below) on Marion Island, but not on Prince Edward Island, explain substantial differences in invertebrate assemblages and in ecosystem function, between them (Crafford & Scholtz 1987; Smith & Steenkamp 1990; Chown & Smith 1993). The eradication of cats has seen an increase in breeding success of several seabird species on Marion Island (Ryan & Bester 2008). Were all else equal, this might have spelled the return of the 'jade jewel'. Unfortunately, in modern systems, all else is rarely equal.

The direct impact of the feral House Mouse has been no less dramatic than that of the feral cats, but more controversial. Early studies noted substantial differences in invertebrate population densities between Marion Island and Prince Edward Island (Crafford & Scholtz 1987) and ascribed these partly to the presence of mice on the former. The predilection of mice for invertebrate prey, and especially caterpillars of the keystone, flightless moth, *Pringleophaga* *marioni* (see Smith & Steenkamp 1990, 1992) had been noted previously (Gleeson & Van Rensburg 1982). Subsequent empirical work, employing both temporal and spatial (among island) data, confirmed the direct impact of mice on prey such as weevils and flightless moth caterpillars, and their indirect effect on the distribution and abundance of the sedge *Uncinia compacta* (Chown & Smith 1993; Chown *et al.* 2002). Moreover, temporal studies also indicated that the importance of caterpillars in the diet of mice had declined from the late 1970s to the early 1990s (Smith *et al.* 2002), presumably reflecting a decline in prey abundance.

By contrast, later experimental exclusions of mice from fixed size plots provided no indication of changes in abundance, diversity, biomass or assemblage composition (Van Aarde *et al.* 2004). However, the authors of the work concluded that the statistical power of the experiments might have been too low to detect differences. The short duration of the experiment (four years) relative to the presumed lifespan of some of the key prey species (five years or more for *P. marioni* – Crafford 1990; at least one year for the weevil *E. similis* Chown & Scholtz 1989) may also have precluded detection of an exclusion effect. Further work, designed to test ideas that mice are food limited or are hampered by climate, which form the basis of the hypothesis that climate change is affecting mouse densities, in turn causing elevated impacts on invertebrate prey and substantial ecosystem effects (Smith & Steenkamp 1990), has continued to unveil the complexity of the situation (Van Aarde & Jackson 2007). Food supplementation did not alter overwinter survival or reproduction, although it did enhance survival during summer, suggesting a more important role for low temperatures *per se*. Increasing temperatures at the island are leading to enhanced population densities, but in turn density-dependent regulation suggests that these changes might not be as significant as previously suspected (Ferreira *et al.* 2007). Nonetheless, these studies and others suggest that low winter temperatures are limiting for the mice and that population densities now are higher than they were in the 1970s, probably as a consequence of changing climates, but not as a consequence of reduced cat predation (Ferreira *et al.* 2007).

These increases in population density are likely responsible for the substantial decline in biomass of *P. marioni* caterpillars and of weevil larvae in *Poa cookii* tussock grasslands on Marion Island (*P. marioni*: 802 to 47 mg. m^{-2}; *E. similis*: 375 to 45 mg. m^{-2}), and a similar decline in *Crassula moschata*-dominated plant communities (*P. marioni*: 683 to 20 mg. m^{-2}; *E. similis*: 305 to 56 mg. m^{-2}) (Chown *et al.* 2002). Moreover, a more detailed comparison of weevil body sizes among both islands, and including samples taken at various intervals over 20 years, and 4 000 year old samples retrieved from peat cores, supported previous conclusions (Janse Van Rensburg 2006). Thus, whilst adult weevil body sizes have been declining overall in step with increasing temperatures (see Chown & Klok 2003; Kozłowski *et al.* 2004 for a discussion of the likely mechanistic basis of this decline), a strong signal of the indirect impact of mice on weevils is nonetheless present. That is, adult weevils of a given species on Prince Edward Island are typically larger than those on Marion Island, presumably owing to the preference of mice for larger-bodied prey (Chown & Smith 1993). This size-selective predation is also thought to be responsible for genetic introgression of two weevil species that once co-existed on Marion Island (Grobler *et al.* 2006).

More recently, mice have been documented feeding directly on seabird chicks, including those of large species such as albatrosses. Early reports were confined to Gough Island (Jones *et al.* 2003; Cuthbert & Hilton 2004). However, it now appears that mice may be having similar effects on seabirds at Marion Island. Thus they constitute a direct and very real threat to seabird populations, possibly throughout the region (Wanless *et al.* 2007).

The impacts of other invasive species have been no less extensive. Plants such as the Procumbent Pearlwort (*Sagina procumbens*) and the grass *Agrostis stolonifera* have substantially altered terrestrial systems (Gremmen *et al.* 1998; Gremmen & Smith 1999). In the latter case, the grass displaces *Acaena magellanica* herbfield from river banks and can lead to a 50% reduction in plant species richness, and a substantial change in invertebrate assemblages in these areas (Gremmen *et al.* 1998). Other vascular plant invaders are having similar impacts (Gremmen & Smith 2008). In addition, some species, such as *Cerastium fontanum*, previously thought to be of little importance, are steadily increasing their abundance and distributional range on Marion Island (N.J.M. Gremmen, personal communication) with little known about the likely effects thereof. On Prince Edward Island, both *S. procumbens* and *C. fontanum* are increasing their ranges, and it seems likely that at least the former species will substantially alter ecosystem functioning at the island, in much the same way it has done on Marion Island (Ryan *et al.* 2003). The recent colonization of Marion Island by a cosmopolitan rush, *Luzula cf. multiflora*, near Sealers Cave, by an unknown thorny shrub (close to Johnny's Hill), and by *Agrostis gigantea* at the scientific station, are all testimony to ongoing colonization processes, either with or without human assistance.

What the impacts are of the introduced invertebrates is more difficult to gauge. Earthworms contribute substantially to nutrient cycling (Smith & Steenkamp 1992, 1993) and it is thought that at least one species is introduced. The very high densities of small introduced species, such as larvae of the midge *Limnophyes minimus*, are also thought to have substantially altered nutrient cycling (Hänel & Chown 1998), and this must be true also of invasive springtails, which often reach densities of tens of thousands of individuals per square metre in mire and other communities (Gabriel *et al.* 2001). In this regard, the recent introduction of the woodlouse *Porcellio scaber* (Slabber & Chown 2002) is concerning, given the total absence of large terrestrial crustaceans from the terrestrial ecosystem throughout its history. Likewise, although the recently introduced wasp *Aphidius matricariae* is a parasitoid of an introduced aphid species (*Rhopalosiphum padi*), its presence has substantially increased ecosystem complexity on the island (Lee *et al.* 2007). Previously, insect parasitism was unknown in the vegetated biotope, although in the eplithic biotope parasitism of the fly *Apetaenus littoralis* by the wasp *Kleidotoma icarus* has long been known (Crafford *et al.* 1986). Phylogeographic investigations both of this wasp and of several introduced springtail species (Myburgh *et al.* 2007) have revealed that each species is characterized by a single haplotype. Such low haplotype diversity suggests that successful colonization requires only a few individuals, as has been suggested for arthropod biological invasions on other Southern Ocean islands and elsewhere (Gaston *et al.* 2003). Therefore, propagule pressure, which is thought to be a significant factor explaining introduction success (Lockwood *et al.* 2005), is perhaps not as important in small arthropods as it is in other groups such as plants and birds.

The nature and extent of marine invasions at the Prince Edward Islands is not clear, largely owing to a lack of work on this topic. Recent studies have demonstrated that potentially invasive species such as the Mediterranean Mussel, *Mytilus galloprovincialis*, are regularly transported to the Prince Edward Islands by the research and supply vessel *S.A. Agulhas* (Lee & Chown 2007). It seems likely that other vessels have similarly transported organisms to the islands in their sea chests, as hull fouling, and in ballast water. Indeed, such transport is typical of Antarctic shipping in general, especially for vessels that might have long port layovers before proceeding south (Lewis *et al.* 2003, 2006). Offshore ecological surveys have not identified invasive species to date (Beckley & Branch 1992), although species previously thought to be cosmopolitan may in fact have a local history dating back to the arrival of the earliest sealing vessels (Lewis 2006). Ballast water exchange is also typically not in the right direction, given that cargo is mostly discharged at the islands. Nonetheless, ongoing increases in sea temperature (Mélice *et al.* 2003; le Roux 2008) and a change in zooplankton assemblages to more temperate than Antarctic (Pakhomov & Chown 2003), suggest that the potential for colonization by accidentally introduced marine species is increasing. The need for further work to clarify the pathways for and extent of marine introductions (if any) at the islands, and to identify the ways in which the pathways may be narrowed or closed, is therefore urgent.

14.2.2 Climate change and terrestrial systems

Substantial and ongoing change in the climate of the Prince Edward islands, associated with global climate change, has now been recorded in a variety of studies (summarized in le Roux 2008). From a biological perspective, it is not only the general trend of warming, and in terrestrial systems of drying, that is of significance, but also an increase in the incidence of additional solar radiation and clear-sky days, and increase in wind strength and a change in its direction.

Changing temperature regimes are unlikely to have a major direct effect on terrestrial invertebrates, at least as far as absolute temperature tolerances are concerned. These traits have been studied in a wide variety of species found on the island from several perspectives (e.g. Van der Merwe *et al.* 1997; Klok & Chown 1997, 1998, 2000, 2001, 2003; Sinclair & Chown 2003; Sinclair *et al.* 2004; Slabber & Chown 2004, 2005; Deere *et al.* 2006; Deere & Chown 2006; Slabber *et al.* 2007; Terblanche *et al.* 2007). Consideration of absolute thermal tolerances in the context of microclimate temperatures has shown that few species are likely to be unable to survive several degrees increase in temperature (Slabber 2005), although where this is the case it is clear that invasive species are more tolerant of high temperatures than their indigenous counterparts. The converse is also true, with indigenous species tending to be more tolerant of low temperatures than the invasives (Slabber *et al.* 2007). For example, the invasive slug *Deroceras panormitanum* is unable to survive more than a few degrees below 0°C, following which individuals freeze and die. The slug is typically restricted to altitudes below about 300 m, above which winter temperatures regularly decline below its lower lethal temperature of the slug. Only on the western coast, where winter temperatures tend to be higher (McGeoch *et al.* 2008), does this species occur above 300 m. Although this close fit between tolerance and altitudinal distribution would seem to militate against rapid spread of the slug around the island, given several high altitude barriers such as Long Ridge, this has not happened. Rather, humans have spread the slug by helicopter operations to hut sites around the island and the species has spread from these foci (Smith 1992; Chown *et al.* 2002).

Phenotypic plasticity is also thought to be a way in which organisms respond rapidly to environmental change (reviewed in Chown & Terblanche 2007), and indeed it has been suggested that invasive species should be more plastic than indigenous ones (Daehler 2003; Duncan *et al.* 2003). At least in the isotomid springtails this does seem to be the case for certain thermal tolerance traits (Slabber *et al.* 2007). However, in the case of temperature effects on desiccation resistance (Chown *et al.* 2007), a major factor influencing responses to global change type drought (Easterling *et al.* 2000) of the kind happening on and forecast for Marion Island, responses are more complex. Rather than differences in plasticity *per se*, it is the direction of this plasticity that differs. Thus, invasive species show an improvement in desiccation resistance when exposed to high temperatures, whereas the converse is true of the indigenous species. This may account for the substantial declines in abundance of most of the indigenous species, but little change in the abundance of the invasives, in response to simulated warming and drying (McGeoch *et al.* 2006).

An increase in the number of clear sky nights may also have a profound effect on invertebrates because of an increase in the frequency of freeze-thaw events (Smith & Steenkamp 1990). For example, caterpillars of the flightless moth *P. marioni* can tolerate freezing as long as temperatures do not decline below about -6°C (Klok & Chown 1997). In addition, they can also survive (to pupation) several successive bouts of freezing and thawing (Sinclair & Chown 2005). However, the effects of repeated exposure to low temperature (not necessarily accompanied by freezing) is deleterious, with caterpillars showing substantial declines in gut mass and a reduction in growth rates. An increase in the frequency of freeze-thaw cycles is therefore likely to have a marked influence on the population dynamics of this significant keystone species.

Likewise, if the cold hardiness strategy of freeze tolerance is typical of species found in unpredictable environments where temperatures remain close to zero (Sinclair *et al.* 2003; Chown *et al.* 2004), then species which do not utilize this strategy might well find themselves at a disadvantage compared with those that do, as freeze-thaw cycles increase in frequency. On Marion Island freeze tolerance is common among the insect species, but both mites and springtails are constrained to a strategy of freeze intolerance (Sinclair *et al.* 2003). Whether such relative differences in advantage will be detected by selection, above the direct effects of climate change on biological rates and its indirect effects on interactions between invasive and indigenous species, is difficult to tell.

Although physiological tolerances set the limits to performance, within these limits temperature nonetheless has a strong effect on performance in ectotherms because of its effect on physiological processes. Whilst individuals are not at the mercy of the temperature effect (the tyranny of Boltzmann, *sensu* Clarke & Fraser 2004), and can indeed respond over the short term to changes in thermal regimes (Hochachka & Somero 2002; Chown & Terblanche 2007), population responses may be constrained in various ways. Several studies have suggested that indigenous insect species may have shallower rate-temperature curves than their introduced counterparts (summarized in Chown *et al.* 2002), and this also appears to be the case in several species of springtails (C. Janion, H.P. Leinaas & S.L. Chown, unpublished data). What the long-term consequences of these changes in relative advantage of the indigenous and invasive species are likely to be, is not known. However, indigenous springtails are typically rare in lowland areas, whilst invasive species are absent from the highlands (Gabriel *et al.* 2001). Moreover, it has been suggested that at the sub-Antarctic island of South Georgia, invasive springtails have displaced their indigenous counterparts in low elevation communities (Convey *et al.* 1999). If the manipulative experiments undertaken in an *A. selago*-dominated fellfield (McGeoch *et al.* 2006) prove to be an accurate reflection of responses to change, then such displacement can also be expected at the Prince Edward Islands. Nonetheless, the effects on Prince Edward Island may be less pronounced given the absence of many invasive species there (Crafford *et al.* 1986; Hugo *et al.* 2006).

Curiously, despite substantial understanding of plant community structure and productivity (summarized in Gremmen & Smith 2008; Smith 2008; Smith & Froneman 2008), little is known about the likely direct responses of individual species to climate change. Some early work demonstrated that the sedge *U. compacta* is increasing its range on Prince Edward Island as a consequence of warming and drying, but is being prevented from doing so on Marion Island because of seed harvesting by mice (Chown & Smith 1993).

It has also been suggested that climate change may be enhancing the rate of spread of some alien vascular plant species at the island (Chown *et al.* 2000). However, increasing human traffic (owing to the cat eradication programme – see Bester *et al.* 2000) over the same period that the plants showed range expansion confounds interpretation to some extent. Only more recently have investigations commenced to understand changes in the altitudinal distributions of species, based on comparisons of modern data with that from careful studies made in the 1960s (Huntley 1970). This work is being accompanied by detailed investigations of the keystone cushion plant *A. selago* (le Roux *et al.* 2005; McGeoch *et al.* 2008), and interactions between the plant and the local landscape on the Marion Island. Not only is ongoing warming and drying likely to see increases in the upper elevational range of this species, but overtopping and dieback at low altitudes will probably lead to a decline in abundance at low altitudes (le Roux *et al.* 2005).

Understanding of the assemblage level effects of climate change on plants is equally poorly developed. However, this owes nothing to a lack of appreciation for the importance of doing so, and everything to the difficulty of disentangling short-term variability from long-term climate change-related effects. Many studies have made clear the substantial small-scale variability in plant assemblages at the Prince Edward Islands, associated with minor changes in topography, water availability, manuring and salt spray (Gremmen 1981; Smith *et al.* 2001; Gremmen & Smith 2008). Year to year variation in these factors has to be distinguished from long-term trends if change at the plot scale is to be correctly interpreted. Doing so requires observations over decades or, especially in the case of interactions between indigenous and invasive species, the kind of experimental work that is often frowned upon in an IUCN category I reserve. Given that few studies have been set up to do the former (and even these may fail given inappropriate time scales – see above), and the difficulty of overcoming the latter, understanding of climate change effects at this level are some way away. Nonetheless, judicious mesocosm-type studies and ethical manipulative field experiments (le Roux *et al.* 2005; McGeoch *et al.* 2006) may provide the required insights.

14.2.3 Climate change and marine systems

The impact of global climate change on the marine ecosystem of the Prince Edward Islands is only now receiving attention (Pakhomov & Chown 2003; McQuaid & Froneman 2008). Global climate change in the Southern Ocean is causing shifts in the position and intensity of the major frontal systems and changes in oceanic circulation patterns within the region of the islands. The change in ocean circulation patterns will influence the generation of far field eddies upstream of the islands resulting from the interaction of the Antarctic Circumpolar Current with the southwest Indian ridge (Lutjeharms & Ansorge 2008). Preliminary data suggest that these eddies represent important foraging grounds for several top predators found on the islands, due to the elevated macrozooplankton stocks within these features (McQuaid & Froneman 2008). Global climate change will therefore be associated with a change in the offshore food delivery to the island top predators.

The most direct effect of a meridional shift in position of the SAF has been on the species composition of the zooplankton. Over the past two decades the contribution of Antarctic species has decreased by some 20%, while at the same time, the contribution of subtropical species has increased from 6% to 26% (McQuaid & Froneman 2008). The more frequent intrusion of sub-Antarctic surface waters into the polar frontal zone will likely also result in a decrease in the total zooplankton biomass in the vicinity of the Prince Edward Islands because sub-Antarctic surface waters typically show low productivity.

Less direct than the effects of long-term changes on species composition, but perhaps more significant, are changes in hydrodynamics around the islands. These are resulting in less frequent retention of water over the island, and more common through-flow conditions (McQuaid & Froneman 2008). These changes in turn have resulted in less frequent diatom blooms over the plateau, and changes in foraging distances for land-based predators on the islands. Thus, $\delta^{13}C$ values of the swimming prawn *Nauticaris marionis* have undergone a significant decrease over the period 1984 to 2000 suggesting a shift in the primary carbon sources utilised by the shrimp. In addition, the period over which the SAF has shifted south has seen medium- to long-term increases in populations of offshore feeding birds such as Grey-headed Albatrosses and Northern Giant Petrels, that are likely to feed at the front, and a simultaneous decline in inshore feeders such as Rockhopper Penguins (Pakhomov & Chown 2003). Interestingly, species with mixed diets, like the Macaroni Penguin, have shown relatively more stable populations over the corresponding period. Patterns for smaller petrel species are difficult to gauge because they are not so readily monitored (Ryan & Bester 2008). Interactions between climate-induced changes in population size, the short-term impacts of incidental mortality (Ryan & Bester 2008), and the measures taken to reduce this mortality make forecasts of future trends complex.

14.2.4 Exploitation

With the exception of the use of lowland areas on the island for grazing by a small flock of sheep, a practise abandoned in the 1970s, no exploitation of the terrestrial environment has taken place at the islands (Cooper & Condy 1988). Habitat destruction has been limited to the small area of the scientific station (though recently the area has more than doubled owing to the construction of a new facility), to the immediate areas occupied by field huts, and to a small, dysfunctional hydroelectric plant and dam on the Van den Boogaard River, which has now been decommissioned (the Hydro Shack and Dam remain). Each year, relatively small numbers of samples are taken for scientific purposes, but the impact of this sampling is considered minor or transitory, and is regulated by South African law (see De Villiers & Cooper 2008). Past removal of geological and archaeological souvenirs has substantially depleted the numbers of 'volcanic bombs' found on the island, and has affected several sites of historical significance. Such practices are now prohibited.

Records of direct marine exploitation prior to the 1990s are scant, although anecdotal evidence exists that fishing vessels, especially from the Soviet fleet, visited the area (Cooper 2008). Very much earlier, during the 18th and early 19th centuries, commercial sealing severely reduced fur seal populations in the Southern Ocean, resulting in local extinctions at some sites. Populations at the Prince Edward Islands did not escape the effects of sealing (Cooper & Headland 1991), although the islands supported one of only three remnant populations of sub-Antarctic Fur Seals (Ryan & Bester 2008).

A legal fishery for Patagonian Toothfish *Dissostichus eleginoides* began in the islands' Exclusive Economic Zone in 1996, but illegal vessels had already been operating in the area for several years, ultimately leading to near-collapse of the fishery (Pakhomov & Chown 2003). The intense exploitation of this top predator is likely to have far reaching effects on the marine ecosystem community structure and functioning in the immediate vicinity of the islands. The extent of this impact, however, remains unclear. The illegal fishery was also responsible for substantial incidental seabird mortality (Ryan & Bester 2008). For example, it is estimated that over the four peak years of the fishery 6 000-14 000 White-Chinned Petrels and 1 000-2 500 Grey-Headed Albatrosses were killed. Several seabird species continue to suffer the effects of incidental mortality associated with various fisheries, given that their large foraging ranges overlap with these fisheries (De Villiers & Cooper 2008; Ryan & Bester 2008). Substantial efforts are underway by international organizations and via the Agreement on the Conservation of Albatrosses and Petrels to reduce the incidental impacts of fishing on pelagic seabirds, though Illegal, Unreported and Unregulated fishing continues to pose considerable problems (De Villiers & Cooper 2008). Recently, steps have been taken to declare a large Marine Protected Area (MPA) around the Prince Edward Islands, including nearby seamounts (Lombard *et al.* 2007). This MPA should substantially reduce threats to commercially significant species, and improve the conservation prospects for several of the pelagic predators nesting on the islands.

14.3 Land-sea interactions in a changing ecosystem

Marsh's (1948) 'jade jewel' and 'scintillating snow' description of Marion Island has become iconic. This is not because the island's modern appearance can be accurately captured by Marsh's phrase, but rather because the opposite is true. The permanent snow and ice have largely melted and the island is more brown now than green. These differences reflect the impacts humans are having on the Prince Edward Islands, as a consequence of their global, industrial activities, their local habit of accidentally or intentionally introducing species to places from which they were previously absent, and their need for resources to fuel a growing population, segments of which have an increasingly sophisticated desire for rare resources. This triumvirate of impacts has altered the Prince Edward Islands in a wide variety of ways, and in so doing has demonstrated that conservation of one component of the system cannot hope to succeed without attention being given to all others. A final example clearly illustrates this point.

Caterpillars of the flightless moth, *P. marioni*, are keystone species, representing a major conduit for nutrient cycling in terrestrial systems (Smith & Steenkamp 1990, 1992). They are also the preferred prey species of introduced House Mice (Smith *et al.* 2002), and are susceptible to frequent low temperature events (Sinclair & Chown 2005). Recent work has shown that the caterpillars have much higher and considerably less variable populations in recently abandoned Wandering Albatross nests (and presumably also in occupied nests) than in old nests and in other plant communities (Sinclair & Chown 2006). The reasons for this pattern are simple. Wandering Albatross nests are occupied for close to a year and have temperatures elevated by at least 5°C above ambient. Caterpillars are likely to show higher survival and growth rates in nests than elsewhere because of the elevated temperatures. Indeed, these nests may serve as a source for the population. Thus, a pelagic predator not only contributes nutrients to the system, with direct effects on the dynamics of vegetation and some of the invertebrates dependent on it (Smith 1978; Crafford & Scholtz 1986), but acts as a thermal ecosystem engineer for a species crucial to nutrient recycling in all communities. A closer and more complex interaction between the land and sea environments is difficult to envisage.

Future work will have to explore these interactions more closely. In this regard, the declaration of a large marine protected area around the islands (Lombard *et al.* 2007) is timely. This book has also made it clear that comparisons of the relative merits of Marion and Prince Edward Island from a conservation perspective, as is often done (Chown *et al.* 2001), are helpful more from a theoretical than a practical perspective. The islands and the marine environment within which they are embedded simply cannot be managed separately. Therefore, if, to use Marsh's words, there is anything in the region of 'little charm of appearance', it is lack of appreciation for the integrated nature of the Prince Edward Islands ecosystems.

14.4 References

Barendse, J., Mercer, R.D., Marshall, D.J. & Chown, S.L. 2002. Habitat specificity of mites on sub-Antarctic Marion Island. *Environmental Entomology* **31**, 612-625.

Bargelloni, L., Marcato, S., Zane, L. & Patarnello, T. 2000a. Mitochondrial phylogeny of notothenioids: a molecular approach to Antarctic fish evolution and biogeography. *Systematic Biology* **49**, 114-129.

Bargelloni, L., Zane, L., Derome, N., Lecointre, G. & Patarnello, T. 2000b. Molecular zoogeography of Antarctic euphausiids and notothenioids: from species phylogenies to intraspecific patterns of genetic variation. *Antarctic Science* **12**, 259-268.

Beckley, L.E. & Branch, G.M. 1992. A quantitative scuba-diving survey of the sublittoral macrobenthos at sub-Antarctic Marion Island. *Polar Biology* **11**, 553-563.

Bergstrom, D. & Chown, S.L. 1999. Life at the front: history, ecology and change on southern ocean islands. *Trends in Ecology and Evolution* **14**, 472-477.

Bester, M.N., Bloomer, J.P., Bartlett, P.A., Muller, D.D., Van Rooyen, M. & Büchner, H. 2000. Final eradication of feral cats from sub-Antarctic Marion Island, southern Indian Ocean. *South African Journal of Wildlife Research* **30**, 53-57.

Boelhouwers, I., Meiklejohn, I., Holness, S. & Hedding, D. 2008. Geology, geomorphology and climate change. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 65-96.

Bonan, G.B. 2002. *Ecological Climatology. Concepts and Applications*. Cambridge University Press, Cambridge.

Burg, T.M. & Croxall, J.P. 2001. Global relationships amongst black-browed and grey-headed albatrosses: analysis of population structure using mitochondrial DNA and microsatellites. *Molecular Ecology* **10**, 2647-2660.

Chown, S.L. 1989. Habitat use and diet as biogeographic indicators for sub-Antarctic Ectemnorhinini (Coleoptera: Curculionidae). *Antarctic Science* **1**, 23-30.

Chown, S.L. 1990a. Possible effects of Quaternary climatic change on the composition of insect communities of the South Indian Ocean Province Islands. *South African Journal of Science* **86**, 386-391.

Chown, S.L. 1990b. Speciation in the sub-Antarctic weevil genus *Dusmoecetes* Jeannel (Coleoptera: Curculionidae). *Systematic Entomology* **15**, 283-296.

Chown, S.L. 1994. Historical ecology of sub-Antarctic weevils (Coleoptera: Curculionidae): patterns and processes on isolated islands. *Journal of Natural History* **28**, 411-433.

Chown, S.L. & Avenant, N. 1992. Status of *Plutella xylostella* at Marion Island six years after its colonization. *South African Journal of Antarctic Research* **22**, 37-40.

Chown, S.L., Gaston, K.J. & Gremmen, N.J.M. 2000. Including the Antarctic: Insights for ecologists everywhere. In: Davison, W., Howard-Williams, C. & Broady, P. (Eds.). *Antarctic Ecosystems: Models for Wider Ecological Understanding*. New Zealand Natural Sciences, Christchurch N.Z, pp. 1-15.

Chown, S.L. & Klok, C.J. 2003. Altitudinal body size clines: latitudinal effects associated with changing seasonality. *Ecography* **26**, 445-455.

Chown, S.L., Marshall, D.J. & Pakhomov, E.A. 2008. Regional membership: biogeography. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 277-300.

Chown, S.L., McGeoch, M.A. & Marshall, D.J. 2002. Diversity and conservation of invertebrates on the sub-Antarctic Prince Edward Islands. *African Entomology* **10**, 67-82.

Chown, S.L., Rodrigues, A.S.L., Gremmen, N.J.M. & Gaston, K. 2001. World Heritage status and conservation of southern ocean islands. *Conservation Biology* **15**, 550-557.

Chown, S.L. & Scholtz, C.H. 1989. Biology and ecology of the *Dusmoecetes* Jeannel (Col. Curculionidae) species complex on Marion Island. *Oecologia* **80**, 93-99.

Chown, S.L., Sinclair, B.J., Leinaas, H.P. & Gaston, K.J. 2004. Hemispheric asymmetries in biodiversity – a serious matter for ecology. *Plos Biology* **2**, 1701-1707.

Chown, S.L., Slabber, S., McGeoch, M.A., Janion, C. & Leinaas, H.P. 2007. Phenotypic plasticity mediates climate change responses among invasive and indigenous arthropods. *Proceedings of the Royal Society of London B* **274**, 2531-2537.

Chown, S.L. & Smith, V.R. 1993. Climate change and the short-term impact of feral house mice at the sub-Antarctic Prince Edward Islands. *Oecologia* **96**, 508-516.

Chown, S.L. & Terblanche, J.S. 2007. Physiological diversity in insects: ecological and evolutionary contexts. *Advances in Insect Physiology* **33**, 50-152.

Clarke, A. & Fraser, K.P.P. 2004. Why does metabolism scale with temperature? *Functional Ecology* **18**, 243-251.

Convey, P., Greenslade, P., Arnold, R.J. & Block, W. 1999. Collembola of sub-Antarctic South Georgia. *Polar Biology* **22**, 1-6.

Cooper, J. 2008. Human history. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 331-350.

Cooper, J. & Condy, P.R. 1988. Environmental conservation at the sub-Antarctic Prince Edward Islands: a review and recommendations. *Environmental Conservation* **15**, 317-326.

Cooper, J. & Headland, R.K. 1991. A history of South African involvement in Antarctica and at the Prince Edward Islands. *South African Journal of Antarctic Research* **21**, 77-91.

Crafford, J.E. 1990. The role of feral house mice in ecosystem functioning on Marion Island. In: Kerry, K.R. & Hempel, G. (Eds.). *Antarctic Ecosystems. Ecological Change and Conservation*. Springer, Berlin, pp. 359-364.

Crafford, J.E. & Scholtz, C.H. 1986. Impact of *Embryonopsis halticella* Eaton larvae (Lepidoptera: Yponomeutidae) feeding in Marion Island tussock grassland. *Polar Biology* **6**, 191-196.

Crafford, J.E. & Scholtz, C.H. 1987. Quantitative differences between the insect faunas of sub-Antarctic Marion and Prince Edward Islands: a result of human intervention? *Biological Conservation* **40**, 255-262.

Crafford, J.E., Scholtz, C.H. & Chown, S.L. 1986. The insects of sub-Antarctic Marion and Prince Edward Islands; with a bibliography of Entomology of the Kerguelen Biogeographical Province. *South African Journal of Antarctic Research* **16**, 41-84.

Cuthbert, R. & Hilton, G. 2004. Introduced house mice *Mus musculus*: a significant predator of threatened and endemic birds on Gough Island, South Atlantic Ocean? *Biological Conservation* **117**, 483-489.

Daehler, C.C. 2003. Performance comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. *Annual Review of Ecology Evolution and Systematics* **34**, 183-211.

De Villiers, M. & Cooper, J. 2008. Conservation and management. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 301-330.

Deere, J.A. & Chown, S.L. 2006. Testing the beneficial acclimation hypothesis and its alternatives for locomotor performance. *American Naturalist* **168**, 630-644.

Deere, J.A., Sinclair, B.J., Marshall, D.J. & Chown, S.L. 2006. Phenotypic plasticity of thermal tolerances in five oribatid mite species from sub-Antarctic Marion Island. *Journal of Insect Physiology* **52**, 693-700.

Duncan, R.P., Blackburn, T.M. & Sol, D. 2003. The ecology of bird introductions. *Annual Review of Ecology, Evolution and Systematics* **34**, 71-98.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. & Mearns, L.O. 2000. Climate extremes: observations, modeling, and impacts. *Science* **289**, 2068-2074.

Ferreira, S.M., Van Aarde, R.J. & Wassenaar, T.J. 2007. Demographic responses of house mice to density and temperature on sub-Antarctic Marion Island. *Polar Biology* **30**, 83-94.

Gabriel, A.G.A., Chown, S.L., Barendse, J., Marshall, D.J., Mercer, R.D., Pugh, P.J.A., *et al.* 2001. Biological invasions on Southern Ocean islands: the Collembola of Marion Island as a test of generalities. *Ecography* **24**, 421-430.

Gaston, K.J., Jones, A.G., Hänel, C. & Chown, S.L. 2003. Rates of species introduction to a remote oceanic island. *Proceedings of the Royal Society of London B* **270**, 1091-1098.

Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.J. & Wang, G. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and Comparative Biology* **46**, 5-17.

Gleeson, J.P. & Van Rensburg, P.J.J. 1982. Feeding ecology of the house mouse *Mus musculus* on Marion Island. *South African Journal of Antarctic Research* **12**, 34-39.

Gremmen, N.J.M. 1981. *The Vegetation of the Subantarctic Islands Marion and Prince Edward* Dr. W. Junk, The Hague.

Gremmen, N.J.M., Chown, S.L. & Marshall, D.J. 1998. Impact of the introduced grass *Agrostis stolonifera* on vegetation and soil fauna communities at Marion Island, sub-Antarctic. *Biological Conservation* **85**, 223-231.

Gremmen, N.J.M. & Smith, V.R. 1999. New records of alien vascular plants from Marion and Prince Edward Islands, sub-Antarctic. *Polar Biology* **21**, 401-409.

Gremmen, N.J.M. & Smith, V.R. 2008. Terrestrial vegetation and dynamics. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 215-244.

Grobler, G.C., Janse Van Rensburg, L., Bastos, A.D.S., Chimimba, C.T. & Chown, S.L. 2006. Molecular and morphometric assessment of *Ectemnorhinus* weevil species (Coleoptera, Curculionidae, Brachycerinae) from the sub-Antarctic Prince Edward Islands. *Journal of Zoological Systematics and Evolutionary Research* **44**, 200-211.

Hänel, C. & Chown, S.L. 1998. The impact of a small, alien macro-invertebrate on a sub-Antarctic terrestrial ecosystem: *Limnophyes minimus* Meigen (Diptera, Chironomidae) at Marion Island. *Polar Biology* **20**, 99-106.

Hochachka, P.W. & Somero, G.N. 2002. *Biochemical Adaptation. Mechanisms and Processes in Physiological Evolution*. Oxford University Press, New York..

Hugo, E.A., Chown, S.L. & McGeoch, M.A. 2006. The microarthropods of Prince Edward Island: A quantitative assessment. *Polar Biology* **30**, 109-119.

Huntley B.J. 1970. Altitudinal distribution and phenology of Marion Island vascular plants. *Tydskrif vir Natuurwetenskappe* **10**, 255-262.

Janse Van Rensburg, L. 2006. *A morphological analysis of weevils from the sub-Antarctic Prince Edward Islands: an assessment of ecological influences*. Ph.D. Thesis, University of Pretoria, South Africa.

Jansen Van Vuuren, B.J. & Chown, S.L. 2007. Genetic evidence confirms the origin of the house mouse on sub-Antarctic Marion Island. *Polar Biology* **30**, 327-332.

Jones, A.G., Chown, S.L., Ryan, P.G., Gremmen, N.J.M. & Gaston, K.J. 2003. A review of conservation threats on Gough Island: a case study for terrestrial conservation in the Southern Oceans. *Biological Conservation* **113**, 75-87.

Kingsolver, J.G. & Huey, R.B. 1998. Evolutionary analyses of morphological and physiological plasticity in thermally variable environments. *American Zoologist* **38**, 545-560.

Klok, C.J. & Chown, S.L. 1997. Critical thermal limits, temperature tolerance and water balance of a sub-Antarctic caterpillar, *Pringleophaga marioni* (Lepidoptera: Tineidae). *Journal of Insect Physiology* **43**, 685-694.

Klok, C.J. & Chown, S.L. 1998. Interactions between desiccation resistance, host-plant contact and the thermal biology of a leaf-dwelling sub-Antarctic caterpillar, *Embryonopsis halticella* (Lepidoptera: Yponomeutidae). *Journal of Insect Physiology* **44**, 615-628.

Klok, C.J. & Chown, S.L. 2000. Lack of cold tolerance in a small, brachypterous sub-Antarctic fly, *Apetaenus litoralis* Eaton (Diptera: Tethinidae), from Marion Island. *African Entomology* **8**, 305-308.

Klok, C.J. & Chown, S.L. 2001. Critical thermal limits, temperature tolerance and water balance of a sub-Antarctic kelp fly, *Paractora dreuxi* (Diptera: Helcomyzidae). *Journal of Insect Physiology* **47**, 95-109.

Klok, C.J. & Chown, S.L. 2003. Resistance to temperature extremes in sub-Antarctic weevils: interspecific variation, population differentiation and acclimation. *Biological Journal of the Linnean Society* **78**, 401-414.

Kozłowski, J., Czarnoleski, M. & Dańko, M. 2004. Can optimal resource allocation models explain why ectotherms grow larger in cold? *Integrative and Comparative Biology* **44**, 480-493.

Kuschel, G. & Chown, S.L. 1995. Phylogeny and systematics of the *Ectemnorhinus*-group of genera (Insecta: Coleoptera). *Invertebrate Taxonomy* **9**, 841-863.

Lee, J.E. & Chown, S.L. 2007. *Mytilus* on the move: transport of an invasive bivalve to the Antarctic. *Marine Ecology Progress Series* **339**, 307-310.

Lee, J.E., Slabber, S., Jansen Van Vuuren, B., Van Noort, S. & Chown, S.L. 2007. Colonisation of sub-Antarctic Marion island by a non-indigenous aphid parasitoid *Aphidius matricariae* (Hymenoptera, Braconidae). *Polar Biology* **30**, 1195-1201.

Le Roux, P.C. 2008. Climate and climate change. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 39-64.

Le Roux, P.C., McGeoch, M.A., Nyakatya, M.J. & Chown, S.L. 2005. Effects of a short-term climate change experiment on a keystone plant species in the sub-Antarctic. *Global Change Biology* **11**, 1628-1639.

Lewis, P.N. 2006. *Keeping the coastlines of the Southern Ocean pest-free*. Ph.D. Thesis, University of Tasmania, Hobart.

Lewis, P.N., Bergstrom, D. & Whinam, J. 2006. Barging in: a temperate marine community travels to the sub-Antarctic. *Biological Invasions* **8**, 787-795.

Lewis, P.N., Hewitt, C.L., Riddle, M. & McMinn, A. 2003. Marine introductions in the Southern Ocean: an unrecognised hazard to biodiversity. *Marine Pollution Bulletin* **46**, 213-223.

Lockwood, J.L., Cassey, P. & Blackburn, T.M. 2005. The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution* **20**, 223-228.

Lombard, A.T., Reyers, B., Schonegevel, L.Y., Cooper, J., Smith-Adao, L.B., Nel, D.C., *et al.* 2007. Conserving pattern and process in the Southern Ocean: designing a marine protected area for the Prince Edward Islands. *Antarctic Science* **19**, 39-54.

Lutjeharms, J.R.E. & Ansorge, I.J. 2008. Oceanographic setting of the Prince Edward Islands. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 17-38.

Marsh, J.H. 1948. *No Pathway Here*. Howard B. Timmins, Cape Town.

Marshall, D.J. & Convey, P. 2004. Latitudinal variation in habitat specificity of ameronothrid mites (Oribatida). *Experimental and Applied Acarology* **34**, 21-35.

McGeoch, M.A., le Roux, P.C., Hugo, E.A. & Chown, S.L. 2006. Species and community responses to short-term climate manipulation: microarthropods in the sub-Antarctic. *Austral Ecology* **31**, 719-731.

McGeoch, M.A., le Roux, P.C., Hugo, E.A. & Nyakatya, M.J. 2008. Spatial variation in the terrestrial biotic system. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 245-276.

McQuaid, C.D. & Fronemann, P.W. 2008. Biology in the oceanographic environment. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 97-120.

Mélice, J.-L., Lutjeharms, J.R.E., Rouault, M. & Ansorge, I.J. 2003. Sea-surface temperatures at the sub-Antarctic islands Marion and Gough during the past 50 years. *South African Journal of Science* **99**, 363-366.

Millennium Ecosystem Assessment. 2005. *Ecosystems and Human Well-Being: Biodiversity Synthesis*. World Resources Institute, Washington, D.C.

Mortimer, E. & Jansen Van Vuuren, B. 2006. Phylogeography of *Eupodes minutus* (Acari: Prostigmata) on sub-Antarctic Marion Island reflects the impact of historical events. *Polar Biology* **30**, 471-476.

Myburgh, M., Chown, S.L., Daniels, S.R. & Jansen Van Vuuren, B. 2007. Population structure, propagule pressure and conservation biogeography: lessons from indigenous and invasive springtails. *Diversity and Distributions* **13**, 143-154.

Pakhomov, E.A. & Chown, S.L. 2003. The Prince Edward Islands: Southern Ocean Oasis. *Ocean Yearbook* **17**, 348-379.

Ryan, P.G. & Bester, M.N. 2008. Pelagic predators. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 121-164.

Ryan, P.G., Smith, V.R. & Gremmen, N.J.M. 2003. The distribution and spread of alien vascular plants on Prince Edward Island. *African Journal of Marine Science* **25**, 555-562.

Schulze, B.R. 1971. The climate of Marion Island. In: Van Zinderen Bakker, E.M., Winterbottom, J.M. & Dyer, R.A. (Eds.). *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965-1966*. A.A. Balkema, Cape Town, pp. 16-31.

Sinclair, B.J., Addo-Bediako, A. & Chown, S.L. 2003. Climatic variability and the evolution of insect freeze tolerance. *Biological Reviews* **78**, 181-195.

Sinclair, B.J. & Chown, S.L. 2003. Rapid responses to high temperature and desiccation but not to low temperature in the freeze tolerant sub-Antarctic caterpillar *Pringleophaga marioni* (Lepidoptera, Tineidae). *Journal of Insect Physiology* **49**, 45-52.

Sinclair, B.J. & Chown, S.L. 2005. Deleterious effects of repeated cold exposure in a freeze-tolerant sub-Antarctic caterpillar. *Journal of Experimental Biology* **208**, 869-879.

Sinclair, B.J. & Chown, S.L. 2006. Caterpillars benefit from thermal ecosystem engineering by Wandering Albatrosses on sub-Antarctic Marion Island. *Biology Letters* **2**, 51-54.

Sinclair, B.J., Klok, C.J. & Chown, S.L. 2004. Metabolism of the sub-Antarctic caterpillar *Pringleophaga marioni* during cooling, freezing and thawing. *Journal of Experimental Biology* **207**, 1287-1294.

Slabber, S. 2005. *Physiological plasticity in arthropods from Marion Island: indigenous and alien Species*. Ph.D. Thesis, University of Stellenbosch, South Africa.

Slabber, S. & Chown, S.L. 2002. The first record of a terrestrial crustacean, *Porcellio scaber* (Isopoda, Porcellionidae), from sub-Antarctic Marion Island. *Polar Biology* **25**, 855-858.

Slabber, S. & Chown, S.L. 2004. Thermal tolerance and cold hardiness strategy of the sub-Antarctic psocid *Antarctopsocus jeanneli* Badonnel. *Polar Biology* **28**, 56-61.

Slabber, S. & Chown, S.L. 2005. Differential responses of thermal tolerance to acclimation in the sub-Antarctic rove beetle *Halmaeusa atriceps*. *Physiological Entomology* **30**, 195-204.

Slabber, S., Worland, M.R., Leinaas, H.P. & Chown, S.L. 2007. Acclimation effects on thermal tolerances of springtails from sub-Antarctic Marion Island: Indigenous and invasive species. *Journal of Insect Physiology* **53**, 113-125.

Smith, V.R. 1978. Animal-plant-soil nutrient relationships on Marion Island (sub-Antarctic). *Oecologia* **32**, 239-253.

Smith, V.R. 1987. The environment and biota of Marion Island. *South African Journal of Science* **83**, 211-220.

Smith, V.R. 1992. Terrestrial slug recorded from sub-Antarctic Marion Island. *Journal of Molluscan Studies* **58**, 80-81.

Smith, V.R. 2002. Climate change in the sub-Antarctic: An illustration from Marion Island. *Climatic Change* **52**, 345-357.

Smith, V.R. 2008. Terrestrial and freshwater primary production and nutrient cycling. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 181-214.

Smith, V.R., Avenant, N.L. & Chown, S.L. 2002. The diet of house mice on a sub-Antarctic island. *Polar Biology* **25**, 703-715.

Smith, V.R & Froneman, P.W. 2008. Nutrient dynamics in the vicinity of the Prince Edward Islands. In: Chown, S.L. & Froneman, P.W. (Eds.). *The Prince Edward Islands. Land-Sea Interactions in a Changing Ecosystem*. African Sun Media, Stellenbosch, pp. 165-179.

Smith, V.R. & Steenkamp, M. 1990. Climatic change and its ecological implications at a sub-Antarctic island. *Oecologia* **85**, 14-24.

Smith, V.R. & Steenkamp, M. 1992. Soil macrofauna and nitrogen on a sub-Antarctic island. *Oecologia* **92**, 201-206.

Smith, V.R. & Steenkamp, M. 1993. Macroinvertebrates and peat nutrient mineralisation on a sub-Antarctic island. *South African Journal of Botany* **59**, 106-108.

Smith, V.R., Steenkamp, M. & Gremmen, N.J.M. 2001. Terrestrial habitats on sub-Antarctic Marion Island: their vegetation, edaphic attributes, distribution and response to climate change. *South African Journal of Botany* **67**, 641-654.

Steadman, D.W. 1995. Prehistoric extinctions of Pacific Island birds: biodiversity meets zooarchaeology. *Science* **267**, 1123-1131.

Stevens, M.I., Greenslade, P., Hogg, I.D. & Sunnucks, P. 2006. Southern Hemisphere springtails: could any have survived glaciation of Antarctica? *Molecular Biology and Evolution* **23**, 874-882.

Sumner, P.D., Meiklejohn, K.I., Boelhouwers, J.C. & Hedding, D.W. 2004. Climate change melts Marion Island's snow and ice. *South African Journal of Science* **100**, 395-398.

Terblanche, J.S., Marais, E. & Chown, S.L. 2007. Stage-related variation in rapid cold hardening as a test of the environmental predictability hypothesis. *Journal of Insect Physiology* **53**, 455-462.

Van Aarde, R.J., Ferreira, S.M. & Wassenaar, T.D. 2004. Do feral house mice have an impact on invertebrate communities on sub-Antarctic Marion Island? *Austral Ecology* **29**, 215-224.

Van Aarde, R.J. & Jackson, T.P. 2007. Food, reproduction and survival in mice on sub-Antarctic Marion Island. *Polar Biology* **30**, 503-511.

Van der Merwe, M., Chown, S.L. & Smith, V.R. 1997. Thermal tolerance limits in six weevil species from sub-Antarctic Marion Island. *Polar Biology* **18**, 331-336.

Van Zinderen Bakker, E.M. 1978. Origin and general ecology of the Marion Island ecosystem. *South African Journal of Antarctic Research* **8**, 13-21.

Vasseur, D.A. & Yodzis, P. 2004. The color of environmental noise. *Ecology* **85**, 1146-1152.

Verde, C., Lecointre, G. & di Prisco, G. 2007. The phylogeny of polar fishes and the structure, function and molecular evolution of hemoglobin. *Polar Biology* **30**, 523-539.

Wanless, R.M., Angel, A., Cuthbert, R.J., Hilton, G.M. & Ryan, P.G. 2007. Can predation by invasive mice drive seabird extinctions? *Biology Letters* **3**, 241-244.

Watling, L. & Norse, E.A. 1998. Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. *Conservation Biology* **12**, 1180-1197.

APPENDIX I

TERRESTRIAL AND FRESHWATER DIATOMS OF THE PRINCE EDWARD ISLANDS

BART VAN DE VIJVER AND NIEK J.M. GREMMEN

The only previously published information for the islands' terrestrial diatom flora is based on a collection of five species made by Moseley in 1873 (O'Meara 1877). The following list is based on extensive collections made in a wide range of habitats on both Marion and Prince Edward Islands, by N.J.M. Gremmen in 2003. Taxonomic work on not yet fully identified species is in progress. In terrestrial samples, several marine species were found, generally in small numbers. These have been listed separately at the end of this checklist. These were probably blown onto land from the surrounding ocean, or washed ashore by waves.

Reference

O'Meara E. 1877. Diatomaceae of Kerguelen's Land. *Journal of the Linnean Society, Botany* **15**, 55-59.

	Marion	Prince Edward
Achnanthes muelleri Carlson		+
Achnanthidium minutissimum (Kützing) Czarnecki	+	+
Achnanthidium modestiforme (Lange-Bertalot) Van de Vijver	+	+
Adlafia bryophila (Petersen) Lange-Bertalot	+	+

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 373-378

Adlafia bryophiloides (Manguin) Van de Vijver	+	
Adlafia minuscula (Grunow) Lange-Bertalot		+
Adlafia spec.1	+	
Amphora copulata (Kützing) Schoeman & Archibald	+	
Aulacoseira distans (Ehrenberg) Simonsen	+	+
Caloneis bacillum sensu auct. nonnull.	+	+
Caloneis marnieri Manguin	+	+
Cavinula heterostauron var. *rostrata* (Germain) Van de Vijver	+	+
Chamaepinnularia alienae (Krasske) Van de Vijver & Le Cohu	+	+
Chamaepinnularia australomediocris (Lange-Bertalot & Schmidt) Van de Vijver	+	+
Chamaepinnularia evanida (Hustedt) Lange-Bertalot	+	+
Chamaepinnularia gracilistriata Van de Vijver & Beyens	+	+
Chamaepinnularia soehrensis var. *muscicola* (Petersen) Lange-Bertalot & Krammer	+	+
Chamaepinnularia spec. 1	+	+
Craticula salsuginosa Van de Vijver & Beyens	+	+
Craticula submolesta (Hustedt) Lange-Bertalot	+	+
Cyclotella meneghiniana Kützing		+
Cymbella spec. 1	+	
Denticula sundayensis Archibald		+
Diadesmis arcuata (Heiden) Lange-Bertalot	+	+
Diadesmis comperei Le Cohu & Van de Vijver	+	+
Diadesmis contenta (Grunow) Mann	+	
Diadesmis costei Le Cohu & Van de Vijver	+	+
Diadesmis crozetikerguelensis Le Cohu & Van de Vijver	+	+
Diadesmis ingeae Van de Vijver	+	+
Diadesmis langebertalotii Le Cohu & Van de Vijver	+	+
Diadesmis latestriata Van de Vijver, Ledeganck & Beyens	+	+
Diadesmis subantarctica Le Cohu & Van de Vijver	+	+
Diadesmis vidalii Van de Vijver & Ledeganck	+	+
Diadesmis spec.1	+	
Diatomella balfouriana Greville	+	+
Diploneis subovalis Cleve	+	+
Encyonema silesiacum (Bleisch) Mann	+	+
Encyonema vulgare Krammer	+	+
Eolimnia minima (Grunow) Lange-Bertalot	+	+
Eucocconeis aretasii (Manguin) Lange-Bertalot	+	+
Eunotia exigua (Brébisson) Rabenhorst	+	
Eunotia fallax Cleve-Euler	+	+
Eunotia paludosa Grunow var. paludosa	+	+
Eunotia praerupta Ehrenberg	+	+
Eunotia spec.	+	
Fallacia lenzii (Hustedt) Mann	+	
Fragilaria capucina morph. 1 Desmazières	+	

Fragilaria capucina morph. 2 Desmazières	+	+
Fragilaria capucina morph. 3 Desmazières	+	+
Fragilaria germainii Reichardt & Lange-Bertalot	+	+
Frankophila maillardii (Le Cohu) Lange-Bertalot	+	+
Frustulia lebouvieri Van de Vijver & Gremmen	+	+
Frustulia subantarctica Van de Vijver & Beyens	+	
Frustulia vulgaris (Thwaites) De Toni	+	+
Geissleria paludosa (Hustedt) Lange-Bertalot	+	+
Gomphonema affine Kützing	+	+
Gomphonema exilissimum (Grunow) Lange-Bertalot & Reichardt	+	
Gomphonema kerguelense Manguin	+	+
Gomphonema marionense Van de Vijver & Gremmen	+	
Gomphonema subantarcticum Van de Vijver & Beyens	+	+
Gomphonema sp. 1		+
Hantzschia abundans Lange-Bertalot	+	
Hantzschia amphioxys (Ehrenberg) Grunow	+	+
Hippodonta hungarica (Grunow) Lange Bertalot, Metzeltin & Witkowski	+	
Kobayashiella subtillissima Van de Vijver & Vanhoutte	+	+
Lecohuia geniculata (Germain) Lange-Bertalot	+	+
Luticola mutica var. *mutica* (Kützing) Mann	+	+
Luticola muticopsis (Van Heurck) Mann	+	+
Luticola nivalis (Ehrenberg) Mann		+
Mayamaea atomus (Kützing) Lange-Bertalot var. *atomus*	+	+
Mayamaea atomus var. *permitis* (Kützing) Lange-Bertalot	+	+
Melosira guillauminii Manguin	+	+
Melosira varians Agardh	+	+
Melosira spec. 1	+	+
Microcostatus naumanii (Hustedt) Lange-Bertalot	+	+
Muelleria luculenta Spaulding & Kociolek	+	
Muelleria varipunctata Spaulding & Kociolek	+	+
Muelleria spec. 1	+	
Navicula arvensis Hustedt	+	+
Navicula bicephala Hustedt	+	+
Navicula ectoris Van de Vijver	+	
Navicula gregaria Donkin	+	+
Navicula perminuta Grunow	+	+
Navicula rhynchocephala Kützing	+	
Navicula veneta Kützing	+	+
Navicula venetiformis Van de Vijver & Beyens	+	
Navicula spec.		+
Naviculadicta elorantana Lange-Bertalot	+	+
Naviculadicta seminulum (Grunow) Lange Bertalot	+	+

Naviculadicta spec. 1	+	+
Naviculadicta spec. 2	+	+
Neidium aubertii Manguin	+	+
Nitzschia acidoclinata Lange-Bertalot	+	+
Nitzschia archibaldii Lange-Bertalot	+	
Nitzschia chardezii Van de Vijver & Beyens	+	
Nitzschia clausii Hantzsch	+	
Nitzschia communis Rabenhorst	+	+
Nitzschia dissipata (Hantzsch) Grunow	+	+
Nitzschia elegantula Grunow	+	
Nitzschia frustulum (Kützing) Grunow var. frustulum	+	+
Nitzschia gracilis Hantzsch	+	+
Nitzschia palea (Kützing) W. Smith	+	+
Nitzschia perminuta (Grunow) Peragallo	+	+
Nitzschia tubicola Grunow	+	+
Nitzschia valdecostata Lange-Bertalot & Simonsen	+	+
Nitzschia spec. 1		+
Opephora naveana Le Cohu		+
Orthoseira biportulata Van de Vijver & Beyens		+
Orthoseira roeseana (Rabenhorst) O'Meara	+	+
Pinnularia acidicola Van de Vijver & Le Cohu	+	+
Pinnularia acidicola var. *elongata* Van de Vijver & Le Cohu	+	+
Pinnularia acoricola Hustedt	+	
Pinnularia amae Van de Vijver; Ledeganck & Beyens	+	+
Pinnularia angliciformis Van de Vijver & Beyens	+	+
Pinnularia borealis var. *scalaris* (Ehrenberg) Rabenhorst	+	+
Pinnularia bottnica Krammer	+	+
Pinnularia carteri Krammer	+	+
Pinnularia crozetii Van de Vijver & Le Cohu	+	+
Pinnularia cuneola Reichardt		+
Pinnularia cuneorostrata (Manguin) Van de Vijver & Le Cohu	+	+
Pinnularia decrescens var. *kerguelensis* (Manguin) Van de Vijver & Le Cohu		+
Pinnularia divergentissima Grunow	+	+
Pinnularia divergentissima var. *minor* Krammer	+	+
Pinnularia dulcicola (Manguin) Van de Vijver & Le Cohu	+	
Pinnularia intermedia (Lagerstedt) Cleve	+	+
Pinnularia kerguelensis Heiden & Kolbe	+	+
Pinnularia kolbei Manguin	+	+
Pinnularia laperousii Van de Vijver & Beyens	+	
Pinnularia microstauron (Ehrenberg) Cleve	+	+
Pinnularia microstauron var. *nonfasciata* Krammer	+	+
Pinnularia microstauron var. *rostrata* Krammer		+

Pinnularia obscura Krasske	+	+
Pinnularia perirorrata Krammer	+	+
Pinnularia pisciculus Ehrenberg	+	+
Pinnularia rabenhorstii (Grunow) Krammer	+	+
Pinnularia rabenhorstii var. *raphecurvata* Van de Vijver & Beyens		+
Pinnularia rabenhorstii var. *subantarctica* Van de Vijver & Le Cohu	+	+
Pinnularia sagittiformis Van de Vijver & Beyens		+
Pinnularia schoenfelderi Krammer	+	+
Pinnularia silvatica Petersen	+	+
Pinnularia similiformis Krammer	+	+
Pinnularia "sinistriformis" (manuscriptname)	+	
Pinnularia subantarctica var. *elongata* (Manguin) Van de Vijver & Le Cohu	+	+
Pinnularia subantarctica var. *subantarctica* (Manguin) Van de Vijver & Le Cohu	+	+
Pinnularia thoenii Van de Vijver & Gremmen	+	
Pinnularia vatii Van de Vijver & Beyens	+	+
Pinnularia spec. 1	+	+
Pinnularia spec. 2		+
Pinnularia spec. 3		+
Pinnularia spec. 4		+
Pinnularia spec-crozet		+
Pinnunavis elegans (W. Smith) Okuno	+	+
Pinnunavis gebhartii (Krasske) Van de Vijver	+	+
Pinnunavis genustriata (Hustedt) Lange-Bertalot & Krammer	+	+
Pinnunavis spec. 1	+	+
Planothidium aueri (Krasske) Lange-Bertalot	+	+
Planothidium cyclophorum (Heiden) Van de Vijver	+	+
Planothidium delicatulum (Kützing) Round & Bukthiyarova	+	+
Planothidium densistriatum Van de Vijver & Beyens	+	
Planothidium engelbrechtii (Cholnoky) Lange-Bertalot	+	
Planothidium lanceolatum (Brébisson) Lange-Bertalot	+	+
Planothidium quadripunctatum (Oppenheim) Sabbe		+
Planothidium renei (Lange-Bertalot & Schmidt) Van de Vijver	+	+
Psammothidium abundans (Manguin) Bukhtiyarova & Round	+	+
Psammothidium confusiforme Van de Vijver & Beyens	+	+
Psammothidium confusum (Manguin) Van de Vijver	+	+
Psammothidium confusum var. *atomoides* (Manguin) Van de Vijver	+	
Psammothidium daonense (Lange-Bertalot) Bukhtiyarova	+	
Psammothidium germainii (Manguin) Sabbe	+	+
Psammothidium investians (Carter) Bukhtiyarova	+	+
Psammothidium manguinii (Hustedt) Van de Vijver	+	+
Psammothidium oblongellum (Oestrup) Van de Vijver	+	+
Psammothidium stauroneioides (Manguin) Bukhtiyarova	+	+

Psammothidium subatomoides (Hustedt) Bukhtiyarova & Round	+	+
Psammothidium spec. 1 (cf. germainii)	+	+
Psammothidium spec. 2	+	
Rhopalodia rupestris (W. Smith) Krammer	+	+
Sellaphora subantarctica Van de Vijver & Beyens	+	
Sellaphora tumida Van de Vijver & Beyens	+	+
Stauroforma exiguiformis (Lange-Bertalot) Flower, Jones & Round	+	+
Stauroneis fluminopsis Van de Vijver & Lange-Bertalot	+	+
Stauroneis gracilis Ehrenberg	+	
Stauroneis kriegeri Patrick	+	+
Stauroneis lardonii Van de Vijver	+	
Stauroneis lecohui Van de Vijver & Lange-Bertalot	+	
Stauroneis pseudomuriella Van de Vijver & Lange-Bertalot	+	+
Stauroneis pseudosmithii Van de Vijver & Lange-Bertalot	+	
Stauroneis sofia Van de Vijver & Lange-Bertalot	+	+
Stauroneis subaustralis Van de Vijver & Lange-Bertalot	+	
Stauroneis spec. 2	+	+
Staurosira alpestris (Krasske) Van de Vijver	+	
Staurosira circula Van de Vijver & Beyens	+	+
Staurosira pinnata Ehrenberg	+	+
Staurosira venter (Ehrenberg) Cleve & Moller	+	
Staurosira spec. 1	+	+
Surirella angusta var. *constricta* Hustedt	+	+
Marine species found in moss samples		
Amphora spec. 1	+	
Auliscus sculptus (W. Smith) Ralfs	+	
Cocconeis californica var. *kerguelensis* Heiden	+	+
Cocconeis costata Gregory	+	+
Cocconeis imperatrix Peragallo	+	
Cocconeis spec. 1	+	+
Ehrenbergia spec. 1	+	
Fragilariopsis angulata Hasle	+	+
Fragilariopsis kerguelensis (O'Meara) Hustedt	+	+
Gomphoneis spec. 1	+	
Grammatophora arcuata Ehrenberg	+	+
Lycmophora spec.	+	
Navicula marine-spec.	+	
Nitzschia marine-spec.	+	
Opephora marina (Gregory) Petit	+	
Stauroptera anuschkae Witkowski	+	+
Thalassionema nitzschioides Grunow	+	+
Thalassiosira gracilis var. *expecta* (Van Landingham) Fryxell & Hasle	+	+

APPENDIX 11

HEPATICS OF THE PRINCE EDWARD ISLANDS

NIEK J.M. GREMMEN

The first collections of hepatics of the Prince Edward Islands were made by Moseley (Mitten 1876, 1885). In the early 1950s, Rand collected on Marion Island. This collection was studied by Arnell (1953). Extensive collections were made by Huntley and Van Zinderen Bakker and other members of the 1965/66 biological and geological expedition (Grolle 1971). Schuster collected on the islands in the 1980s (Schuster 1989, 1995). In 2002, Grolle published an account of the Hepaticae of the sub-Antarctic and temperate islands of the eastern Southern Hemisphere, incorporating all the above accounts as well as unpublished collections by Gremmen. This checklist is based on the account by Grolle (2002), with one addition from unpublished data by Gremmen (*Marchantia berteroana* on Prince Edward Island).

Over the years, the number of hepatic species recorded at the Prince Edward Islands has increased steadily. This increase suggests that further collecting may well yield more species than have been listed in this checklist. The increase between the 1971 and 2002 accounts by Grolle is partly due to the detailed study of the genus *Riccardia* by Schuster (1989). Several of these species may have been present in earlier collections, but were not recognised or not treated as separate species. Synonyms commonly used in Prince Edward Islands literature have been included.

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 379-382

References

Arnell, S. 1953. List of Hepaticae collected in Marion Island by Mr R. W. Rand. *Svensk Botanisk Tidskrift* **47**, 411-423.

Grolle, R. 1971. Hepaticopsida. In: Van Zinderen Bakker, E.M., Winterbottom, J.M. & Dyer, R.A. (Eds.). *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965-1966*. A.A. Balkema, Cape Town, pp. 228-236.

Grolle, R. 2002. The Hepaticae and Anthocerotae of the subantarctic and temperate islands in the eastern Southern Hemisphere (90ºE to 0º): an annotated catalogue. *Journal of Bryology* **24**, 57-80.

Mitten, W. 1876. A list of the Musci and Hepaticae collected in Kerguelen's Island by the Rev. A.E. Eaton. *Journal of the Linnean Society of Botany* **15**, 193-197.

Mitten, W. 1885. Hepaticae. In: Hemsley W.B. (Ed.), *Report on the Scientific Results of the Voyage of H.M.S. Challenger*. Stationery Office, London. Botany **2**, 202-203.

Schuster, R.M. 1989. Studies on the hepatic flora of the Prince Edward Islands. I. Aneuraceae. *Journal of the Hattori Botanical Laboratory* **67**, 59-108.

Schuster, R.M. 1995. The Hepaticae of the Prince Edward Islands. II. On *Gymnocoleopsis* (Schust.) Schust., *Lophozia cylindriformis* (Mitt.) Steph. and the subgeneric classification of the genus *Lophozia* Dumort. *Journal of the Hattori Botanical Laboratory* **78**, 119-135.

Note: The list presented below is based on the work of Riclef Grolle, who not only published major accounts of the Prince Edward Islands hepatics, but has also identified many of my own collections from the islands. Riclef Grolle passed away recently. He will be sorely missed.

		Marion	Prince Edward
	Jungermanniales		
Acrobolbaceae	*Lethocolea radicosa* (Lehm. & Lindenb.) Grolle	+	+
	Tylimanthus tenellus (Taylor ex Lehm.) Mitt.		+
	= *Tylimanthus viridis* Mitt.		
	Acrobolbus ochrophyllus (Hook.f. & Taylor) R.M. Schust.	+	+
Cephaloziellaceae	*Cephaloziella transvaaliensis* S.W. Arnell	+	
	Cephaloziopsis randii (S.W.Arnell) Grolle	+	
	= *Cephaloziella randii* S.W.Arnell		
Geocalycaceae	*Clasmatocolea humilis*	+	+
	Clasmatocolea humilis var. *suspecta* (C.Massal.) J.J. Engel	+	
	Clasmatocolea vermicularis (Lehm.) Grolle	+	
	Leptoscyphus expansus (Lehm.) Grolle	+	+

	Lophocolea randii S.W. Arnell	+	+
	= *Chiloscyphus randii* (S.W.Arnell) J.J. Engel		
	Pachyglossa fissa (Mitt.) Herzog & Grolle	+	+
Gymnomitriaceae	*Herzogobryum atrocapillum* (Hook.f. & Tayl.) Grolle	+	+
	Herzogobryum teres (Carring. & Pearson) Grolle	+	
	Herzogobryum vermiculare (Schiffn.) Grolle	+	+
	Marsupella sparsifolia (Lindb.) Dumort.	+	
	Marsupella sparsifolia (Lindb.) Dumort.	+	
Jungermanniaceae	*Jungermannia coniflora* (Schiffn.)	+	+
Lejeuniaceae	*Colura calyptrifolia* (Hook.) Dumort.	+	
Lepidoziaceae	*Hygrolembidium ventrosum* (Mitt.) Grolle	+	
	Lepidozia laevifolia	+	+
Lophoziaceae	*Anastrophyllum auritum* (Lehm.) Steph.	+	
	Andrewsianthus carinatus Grolle	+	
	Andrewsianthus marionensis (S.W. Arnell) Grolle	+	
	= *Cephaloziella marionensis* S.W. Arnell		
	= *Lophozia marionensis* S.W. Arnell		
	Cryptochila grandiflora (Lindenb. & Gottsche) Grolle	+	+
	Gymnocoleopsis cylindriformis (Mitt.) R.M. Schust.	+	+
	= *Lophozia cylindriformis* (Mitt.) Steph.		
	Jamesoniella colorata	+	+
	Lophozia lancistipa (Grolle) R.M. Schust.	+	+
	= *Andrewsianthus lancistipus* Grolle		
	Plagiochila heterodonta (Hook.f. & Taylor) Gottsche *et al.*	+	+
	= *Plagiochila marionensis* Mitt.		
	Plagiochila minutula (Hook.f. & Taylor) Gottsche	+	+
	= *Plagiochila crozetensis* Kaal.		
Pseudolepicoleaceae	*Temnoma quadripartitum* (Hook.) Mitt.	+	+
	= *Lepidozia randii* S.W. Arnell		
Scapaniaceae	*Blepharidophyllum densifolium* (Hook.) C. Massal.	+	+
	Diplophyllum marionense S.W. Arnell	+	
Schistochilaceae	*Pachyschistochila carnosa* (Mitt.) R.M. Schust & J.J. Engel	+	+
	= *Schistochila carnosa* (Mitt.) Steph.		
Metzgeriales			
Aneuraceae	*Aneura subcanaliculata* R.M. Schust.	+	+
	Riccardia crenuliformis R.M. Schust	+	
	Riccardia diversiflora A.Evans. ssp. *paucigyna* R.M. Schust.	+	
	Riccardia georgiensis (Steph.) Hässel	+	
	Riccardia georgiensis (Steph.) Hässel ssp. *sympodea* R.M. Schust.	+	
	Riccardia leptothallus R.M. Schust.	+	
	Riccardia marionensis R.M. Schust.	+	+

	Riccardia pauciramea R.M. Schust.		+
	Riccardia russellii R.M. Schust.		+
Fossombroniaceae	*Austrofossombronia marionensis* R.M. Schust.	+	+
Metzgeriaceae	*Metzgeria furcata* (L.) Dumort.	+	+
	= *Metzgeria grollei* Kuwahara		
	= *Metzgeria marionensis* S.W. Arnell		
	= *M. decipiens* (C.Massal.) Schiffn.		
Pallaviciniaceae	*Jensenia pisicolor* (Hook.f. & Taylor) Grolle	+	+
	Symphiogyna podophylla (Thunb.) Mont. & Nees	+	+
	= *Symphyogyna marionensis* S.W. Arnell		
Marchantiales			
Marchantiaceae	*Marchantia berteroana* Lehm. & Lindenb.	+	+

APPENDIX III

Mosses of the Prince Edward Islands

Ryszard Ochyra

Mosses were first collected at the Prince Edward Islands archipelago in 1873 by H.N. Moseley, the naturalist on the Challenger Expedition that visited Marion Island. From Moseley's collection, Mitten (1876, 1885) reported 24 species, four of which were new to science. According to modern Musci taxonomic criteria, Moseley's collection contained 23 species. R.W. Rand collected some mosses on Marion Island in the early 1950s, but the first concerted effort at a complete moss collection of both islands was by B.J. Huntley and E.M. Van Zinderen Bakker (Sr.) during the South African biological and geological expedition of 1965-1966 (Van Zinderen Bakker *et al.* 1971). From the Rand, Huntley and Van Zinderen Bakker collections, Van Zanten (1971) compiled the first modern account of the moss flora of the Prince Edward Islands, reporting a total of 80 species from the two islands. Six of these were assigned only to genus. I examined all the voucher specimes in the same collections and found that they represented only 64 species. Subsequent phytosociological and taxonomical studies increased the number of mosses known to occur at the islands; Ochi (1972), Frahm (1985), Lightowlers (1986), Seppelt & Russell (1986), Ochyra & Lewis Smith (1998) and Żarnowiec (2001) each added a single species to the moss flora, and Ochyra & Hertel (1990) added four more species.

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 383-389

Between 1999 and 2003, V.R. Smith (University of Stellenbosch, South Africa) and I executed a detailed bryological survey of both Marion Island and Prince Edward Island. This resulted in the addition of 20 new records, some of which of have been published (Ochyra & Smith 2003a, b, c, 2004; Ochyra *et al.* 2003; Ochyra & Gremmen 2004). Two of these records were described as new to science, namely *Bucklandiella valdon-smithii* (Ochyra & Bednarek-Ochyra 1999, as *Racomitrium valdon-smithii*) and *Dicranella gremmenii* (Ochyra 1999). One of the collected mosses has not yet been assigned to species. Hence, currently, the moss flora of the Prince Edward Islands consists of 94 species, which makes it the third richest muscoflora in the sub-Antarctic, after South Georgia and Îles Kerguelen. Ninety-three species are known from Marion Island and 66 from Prince Edward Island. All species on Prince Edward Island, excepting one (*Warnstorfia fontinaliopsis*) also occur on Marion Island.

References

Frahm, J.-P. 1985. Afrikanische *Campylopus*-Arten (Dicranaceae, Musci). *Bryophytorum Bibliotheca* **31**, 1-216.

Lightowlers, P.J. 1986. Taxonomy and distribution of the subantarctic species of *Tortula*. *Journal of Bryology* **14**, 281-295.

Mitten, W. 1876. The Musci and Hepaticae collected by N. H. Moseley, Naturalist to H. M. S. Challenger. *Journal of the Linnean Society Botany* **15**, 59-73.

Mitten, W. 1885. Prince Edward group. Marion Island. Musci. In: Hemsley, W.B. (Ed.). *Report on the Scientific Results of the Voyage of H. M. S. Challenger during the Years 1873–1877 Under the Command of Captain George S. Nares, R. N., F. R. S. and the late Captain Frank Tourle Thomson, R. N. Botany.* **1**. Her Majesty's Stationery Office, London, pp. 219-229.

Ochi, H. 1972. A revision of African Bryoideae, Musci (First part). *The Journal of the Faculty of Education Tottori University, Natural Science* **23**, 1-126.

Ochyra, R. 1999. *Dicranella gremmenii* (Musci, Dicranaceae) sp. nov. from Subantarctic Marion Island. *Fragmenta Floristica et Geobotanica* **44**, 219-225.

Ochyra, R. & Bednarek-Ochyra, H. 1999. *Racomitrium valdon-smithii* (Musci, Grimmiaceae) sp. nov. from Subantarctic Marion Island. *Fragmenta Floristica et Geobotanica* **44**, 209-217.

Ochyra, R. & Gremmen, N.J.M. 2004. *Trematodon flexipes* Mitt. Prince Edward Island. In: T. L. Blockeel (Ed.). New national and regional bryophyte records, 10. *Journal of Bryology* **26**, 307-308.

Ochyra, R. & Hertel, H. 1990. Contribution to the moss flora of the subantarctic island Marion. *Polish Botanical Studies* **1**, 19-34.

Ochyra, R. & Lewis Smith, R.I. 1998. Antarctic species in the genus *Ditrichum* (Ditrichaceae, Bryopsida), with a description of *D. gemmiferum* sp. nov. *Annales Botanici Fennici* **35**, 33-53.

Ochyra, R. & Smith, V.R. 2003a. *Entosthodon productus* Mitt. (Funariaceae) on Marion Island – the first record in the Subantarctic. *Cryptogamie, Bryologie* **24**. 173-180.

Ochyra, R. & Smith, V.R. 2003b. *Anisothecium cardotii* (R. Br. bis) Ochyra. Marion Island. In: Blockeel, T.L. (Ed.). New national and regional bryophyte records, 8. *Journal of Bryology* **25**, 217.

Ochyra, R. & Smith, V. R. 2003c. *Syntrichia anderssonii* (Ångstr.) R. H. Zander. Marion Island. In: Blockeel, T.L. (Ed.). New national and regional bryophyte records, 8. *Journal of Bryology* **25**, 219.

Ochyra, R. & Smith, V.R. 2004. On the occurrence of *Ceratodon purpureus* (Hedw.) Brid. (Ditrichaceae) on Subantarctic Marion Island. *Cryptogamie, Bryologie* **25**, 131-135.

Ochyra, R., Smith, V.R. & Gremmen, N.J.M. 2003. *Thuidium delicatulum* (Hedw.) Schimp. (Thuidiaceae) – another bipolar moss disjunct from Subantarctic Marion Island. *Cryptogamie, Bryologie* **24**, 253-263.

Seppelt, R.D. & Russell, S. 1986. *Fissidens bryoides* Hedw., new to the moss flora of subantarctic Prince Edward Island. *Lindbergia* **12**, 57-59.

Van Zanten, B.O. 1971. Musci. In: Van Zinderen Bakker, E.M., Winterbottom, J.M. & Dyer, R.A (Eds.). *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965–1966.* A.A. Balkema, Cape Town, pp. 173-227.

Van Zinderen Bakker, E.M., Winterbottom, J.M. & Dyer, R.A. (Eds.) 1971. *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965-1966.* A.A. Balkema, Cape Town.

Żarnowiec, J. 2001. *A taxonomic monograph of the Drepanocladus aduncus group (Bryopsida: Amblystegiaceae).* Łódź Technical University, Bielsko-Biała Branch, Bielsko-Biała, 248 pp.

List of mosses known from the Prince Edward Islands and their phytogeographical affinities. Taxa newly recorded for the archipelago are marked with an asterisk. Geographical elements are: T = temperate: T–SA = South American, T–AF = African, T–AP = amphi-Pacific, T–AA = amphi-Atlantic, T–AU = Australasian, T–PA = pan-temperate, S = sub-Antarctic: S–AT = amphiatlantic, S–PA = circum sub-Antarctic, S–SIO = South Indian Ocean Province, BIP = bipolar, CPA = pan-continental.

Species	Marion	Prince Edward	Geographic element
Andreaeaceae			
Andreaea acuminata Mitt.	+	+	T–PA
A. acutifolia Hook.f. & Wilson	+	+	T–PA
**A. flabellata* Müll.Hal.	+	+	T-PA
A. regularis Müll.Hal.	+	+	T-AA
**A. mutabilis* Hook.f. & Wilson	+	+	BIP
A. alpina Hedw. (= *A. gainii* sensu Zanten)	+	+	BIP
Polytrichaceae			
Polytrichum juniperinum Hedw.	+		BIP
P. piliferum Hedw.	+		BIP
Notoligotrichum australe (Hook.f. & Wilson) G.L.Sm. (= *Psilopilum tristaniense* sensu Zanten)	+	+	T–AU

Fissidentaceae			
Fissidens bryoides Hedw.	+	+	BIP
Ditrichaceae			
**Ceratodon purpureus* (Hedw.) Brid.	+		CPA
Chrysoblastella chilensis (Mont.) Reimers (= *Cheilothela chilensis* (Mont.) Broth.)	+	+	T–PA
Ditrichum conicum (Mont.) Mitt.	+	+	T–AA
D. subaustrale Broth. (= *D. immersum* Zanten)	+	+	S–SIO
D. strictum (Hook.f. & Wilson) Hampe	+	+	T–PA
D. ditrichoideum (Cardot) Ochyra (= *D. gemmiferum* Ochyra & Lewis Smith; *Distichium capillaceum* sensu Zanten)	+	+	T–AA
**D. difficile* (Duby) M.Fleisch.	+		T–PA
Bruchiaceae			
Trematodon flexipes Mitt.	+	+	T–AU
Dicranaceae			
Kiaeria pumila (Mitt.) Ochyra (= *Holodontium pumilum* (Mitt.) Broth.)	+	+	T–PA
Dicranoloma billardierei (Brid. ex anon.) Paris	+		T–PA
Campylopus austrostramineus Thér. (= *C. cavifolius* sensu Zanten)	+		S–SIO
C. pyriformis (Schulz) Brid.	+		BIP
C. introflexus (Hedw.) Brid. (= *C. polytrichoides* sensu Zanten)	+	+	BIP
C. clavatus (R.Br.) Wilson	+	+	T–AP
C. purpureocaulis Dusén (= *C. arboricola* Cardot & Dixon)	+	+	T–AP
C. subnitens Kaal.	+	+	S–AT
C. vesticaulis Mitt.	+		T–AP
**Dicranella campylophylla* (Taylor) Broth.	+		T–PA
D. hookeri (Müll.Hal.) Cardot (=*Anisothecium hookeri* (Müll.Hal.) Broth.)	+	+	T–AA
**D. gremmenii* Ochyra (= *Ceratodon* cf. *purpureus* sensu Zanten)	+	+	S–SIO
**Dicranella* sp.	+		
Seligeriaceae			
Hymenoloma antarcticum (Müll.Hal.) Ochyra (= *Dicranoweisia brevipes* (Müll.Hal.) Cardot; *D. breviseta* Cardot)	+	+	T–PA
**H. immersum* (Mitt.) Ochyra	+	+	S–SIO
Valdonia microcarpa (Mitt.) Ochyra (= *Verrucidens microcarpus* (Mitt.) Zanten)	+	+	S–SIO
Blindia magellanica Müll.Hal.	+	+	T–PA

Pottiaceae			
Leptodontium gemmascens (Mitt.) Braithw. (= *L. proliferum* sensu Zanten)	+	+	BIP
**L. microuncinatum* Dusén (= *Tortula* cf. *geheebiopsis* sensu Zanten)	+		T–AA
Willia calobolax (Müll.Hal.) Lightowlers (= *W. austroleucophaea* sensu Zanten)	+	+	S–SIO
**Syntrichia andersonii* (Ångstr.) R.H. Zander	+		T–AP
Hennediella arenae (Besch.) R.H.Zander (= *Tortula* cf. *rubra* sensu Zanten)	+		S–PA
**H. heimii* (Hedw.) R.H.Zander	+	+	BIP
**Bryoerythrophyllum campylocarpum* (Müll.Hal.) H.A.Crum	+		BIP
Grimmiaceae			
Bucklandiella didyma (Hook.f. & Wilson) Bednarek-Ochyra & Ochyra (= *Racomitrium crispulum* sensu Zanten – group B)	+	+	T–PA
B. membranacea (Mitt.) Bednarek-Ochyra & Ochyra (= *Racomitrium membranaceum* (Mitt.) Paris; *R. crispulum* sensu Zanten – group A)	+	+	T–PA
B. orthotrichacea (Müll.Hal.) Bednarek-Ochyra & Ochyra (= *Racomitrium orthotrichaceum* (Müll.Hal.) Paris	+	+	T–AA
**B. valdon-smithii* (Ochyra & Bednarek-Ochyra) Bednarek-Ochyra & Ochyra (= *Racomitrium valdon-smithii* Ochyra & Bednarek-Ochyra)	+		S–SIO
**B. pachydictyon* (Cardot) Bednarek-Ochyra & Ochyra	+		T-AA
Racomitrium lanuginosum (Hedw.) Brid.	+	+	BIP
Guembelia kidderi (James) Ochyra & Żarnowiec (= *Grimmia kerguelensis* Cardot; *G. kidderi* James)	+	+	S–AT
Schistidium amblyophyllum (Müll.Hal.) Ochyra & Hertel (= *Schistidium stylostegium* (Müll.Hal.) Zanten)	+	+	S–AT
S. falcatum (Hook.f. & Wilson) B.Bremer	+	+	S–AT
**S. rivulare* (Brid.) Podp.	+		BIP
Funariaceae			
Entosthodon laxus (Hook.f. & Wilson) Mitt. (= *Funaria laxa* (Hook.f. & Wilson) Broth.)	+	+	T–PA
**E. productus* Mitt.	+		T–AU
Orthodontiaceae			
Orthodontium lineare Schwägr.	+		BIP

Bryaceae			
Schizymenium campylocarpum (Hook. & Arn.) A.J.Shaw (= *Mielichhoferia campylocarpa* (Hook. & Arn.) Mitt.)	+	+	T–PA
Pohlia nutans (Hedw.) Lindb.	+	+	BIP
P. wahlenbergii (F.Weber & D.Mohr) A.L.Andrews (= *P. albicans* (Wahlenb.) Lindb.)	+		BIP
**P. drummondii* (Müll.Hal.) A.L.Andrews	+		BIP
Bryum argenteum Hedw. var. *muticum* Brid. (= *B. argenteum* sensu Zanten; *B. ellipsifolium* Müll. Hal.; *B subrotundifolium* A.Jaeger)	+	+	CPA
B. nivale Müll.Hal. (= *B. clavatum* sensu Ochyra & Hertel)	+	+	T–AA
B. kerguelense Mitt.	+	+	S–SIO
B. eatonii Mitt.	+	+	S–SIO
B. laevigatum Hook.f. & Wilson	+	+	T–PA
B. dichotomum Hedw.	+	+	BIP
Anomobryum julaceum (Dicks.) P.Gaertn., B.Mey. & Scherb.	+	+	BIP
**A. werthii* Broth.	+		S–SIO
Eustichiaceae			
Eustichia longirostris (Brid.) Brid.	+		T–AA
Bartramiaceae			
Breutelia integrifolia (Taylor) A.Jaeger	+	+	T–AA
B. dumosa Mitt. (= *B. pendula* sensu Zanten)	+		T–PA
Philonotis polymorpha (Müll. Hal.) Broth. (= *Ph. cf. angustifolia* sensu Zanten)	+	+	S–AT
Ph. scabrifolia (Hook.f. & Wilson) Braithw.	+	+	T–PA
Ph. tenuis (Taylor) A.Jaeger	+	+	T–AU
Bartramia patens Brid.	+	+	T–AA
Orthotrichaceae			
Muelleriella crassifolia (Hook.f. & Wilson) Dusén	+	+	S–PA
Ptychomniaceae			
Ptychomnion densifolium (Brid.) A.Jaeger (= *P. ringianum* Broth.)	+		T–PA
Lembophyllaceae			
Acrocladium auriculatum (Mont.) Mitt.	+		T–AA
Hookeriaceae			
Distichopjyllum fasciculatum Mitt.	+	+	T–AF
D. imbricatum Mitt.	+	+	T–AF
Calyptrochaeta apiculata Hook.f. & Wilson (= *Eriopus apiculatus* (Hook.f. & Wilson) Mitt.)	+	+	T–PA

Thuidiaceae			
**Thuidium delicatulum* (Hedw.) Schimp.	+		BIP
Amblystegiaceae			
Cratoneuropsis chilensis (Lorentz) Ochyra, *comb. nov.* (Basionym: *Amblystegium chilense* Lorentz, Bot. Zeit. (Berlin) 24:188. 1866; = *Hygroamblystegium filum* (Müll.Hal) Reimers; *Cratoneuron filicinum* sensu Zanten)	+	+	BIP
Drepanocladus aduncus (Hedw.) Warnst.	+	+	BIP
D. polycarpos (Voit) Warnst.	+		BIP
**Warnstorfia fontinaliopsis* (Müll.Hal.) Ochyra		+	S–PA
Sanionia uncinata (Hedw.) Loeske (= *Drepanocladus uncinatus* (Hedw.) Warnst.)	+	+	BIP
Catagoniaceae			
Catagonium nitens (Brid.) Cardot (= *C. politum* (Hook.f. & Wilson) Broth.)	+	+	T–PA
Brachytheciaceae			
Brachytheciastrum paradoxum (Hook.f. & Wilson) Ignatov & Huttunen (= *Brachythecium paradoxum* (Hook.f. & Wilson) A.Jaeger)	+	+	T–PA
Brachythecium subplicatum (Hampe) A.Jaeger	+	+	T–AA
B. rutabulum (Hedw.) Schimp.	+	+	BIP
B. austrosalebrosum (Müll. Hal.) Kindb.	+	+	T–PA
Plagiotheciaceae			
Plagiothecium ovalifolium Cardot (= *P. platyphyllum* sensu Zanten)	+	+	S–AT
Hypnaceae			
Isopterygiopsis pulchella (Hedw.) Z. Iwats. (= *Isopterygium pulchellum* (Hedw.) A.Jaeger var. *antarcticum* (Mitt.) Zanten)	+	+	BIP
Hypnum cupressiforme Hedw.	+	+	BIP
TOTAL	93	66	

APPENDIX IV

VASCULAR PLANTS OF THE PRINCE EDWARD ISLANDS

NIEK J.M. GREMMEN AND VALDON R. SMITH

This checklist is based on Huntley (1971), with additional data from Gremmen (1975, 1982), Gremmen & Smith (1981, 1999, 2004), and Gremmen & Van der Meijden (1995). All native vascular plant species have been found on both islands, with the exception of *Elaphoglossum randii*, which is only known from Marion Island. None of the species with doubtful status have been found on Prince Edward Island. The only alien species observed on the latter island are *Cerastium fontanum*, *Poa annua* and *Sagina procumbens*.

Introduced species are marked with an asterisk. Species of which the status is not clear are indicated by (*). Only synonyms frequently used in the Prince Edward Islands literature are given.

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 390-392

References and further reading

Bergstrom, D.M. & Smith, V.R. 1990. Alien vascular flora of Marion and Prince Edward Islands: new species, present distribution and status. *Antarctic Science* **2**, 301-308.

Gremmen, N.J.M. 1975. The distribution of alien vascular plants on Marion and Prince Edward Islands. *South African Journal of Antarctic Research* **5**, 25-30.

Gremmen, N.J.M. 1982. Alien vascular plants on Marion Island (subantarctic). *Comité National Français des Recherches Antarctiques* **51**, 315-323.

Gremmen, N.J.M. & Van der Meijden, R. 1995. Introduced *Agrostis* species at sub-Antarctic Marion Island. *South African Journal of Antarctic Research* **25**, 85-86.

Gremmen, N.J.M. & Smith, V.R. 1981. *Agrostis stolonifera* L. on Marion Island (sub-Antarctic). *South African Journal of Antarctic Research* **10/11**, 33-34.

Gremmen, N.J.M. & Smith, V.R. 1999. New records of alien vascular plants from Marion and Prince Edward Islands. *Polar Biology* **21**, 401-409.

Gremmen, N.J.M. & Smith, V.R. 2004. *The Vascular Flora of Marion and Prince Edward Islands*. CD-ROM. Data Analyse Ecologie, Diever.

Huntley B.J. 1971. Vegetation. In: Van Zinderen Bakker, E.M., Winterbottom, J.M. & Dyer, R.A. (Eds.). *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965-1966*. A.A. Balkema, Cape Town, pp. 98-160.

Kaplan, Z. & Symoens, J.-J. 2005. Taxonomy, distribution and nomenclature of three confused broad-leaved *Potamogeton* species occurring in Africa and on surrounding islands. *Botanical Journal of the Linnean Society* **148**, 329-357.

Pteridophyta	
Lycopodiaceae	*Lycopodium magellanicum* Sw.
	Lycopodium saururus Lam.
Aspidiaceae	*Polystichum marionense* Alston & Schelpe
Blechnaceae	*Blechnum penna marina* Kuhn.
Grammitaceae	*Grammitis poeppigeana* (Mett.) Pichi Serm. (= *Grammitis kerguelensis* Tard.)
Hymenophyllaceae	*Hymenophyllum peltatum* (Poiret) Desv.
Polypodiaceae	*Elaphoglossum randii* Alston & Schelpe
Angiosperma: Monocotyledonae	
Potamogetonaceae	(*) *Potamogeton nodosus* Poir.
Cyperaceae	*Uncinia compacta* R.Br. = *Uncinia dikei* Nelmes

Angiosperma: Monocotyledonae (continued)	
Gramineae	* *Agropyron repens* (L.) Beaiv.
	* *Agrostis castellana* Boiss. Et Reut.
	* *Agrostis gigantea* Roth
	Agrostis magellanica Lam.
	* *Agrostis stolonifera* L.
	* *Alopecurus geniculatus* L. (listed as *Alopecurus australis* Nees by Huntley (1971))
	* *Avena sativa* L.
	* *Festuca rubra* L.
	* *Holcus lanatus* L.
	* *Poa annua*
	Poa cookii Hook.f.
	* *Poa pratensis* L.
Juncaceae	(*) *Juncus effusus* L.
	Juncus scheuchzerioides Gaud.
	(*) *Luzula* cf. *multiflora* (Retz.) Lej.
Angiosperma: Dicotyledonae	
Callitrichaceae	*Callitriche antarctica* Engelm.
Caryophyllaceae	* *Cerastium fontanum*
	Colobanthus kerguelensis Hook.f.
	* *Sagina procumbens* L. (listed as *Sagina apetala* Ard. in some accounts)
	* *Stellaria media* (L.)Vill.
Asteraceae	*Cotula plumosa* Hook.f.
	* *Hypochaeris radicata* L.
	* *Senecio* sp.
	* *Sonchus* spec.
Crassulaceae	*Crassula moschata* Forst.f. = *Tillaea moschata* DC.
Brassicaceae	*Pringlea antiscorbutica* R.Br.
Plantaginaceae	* *Plantago lanceolata* L.
Polygonaceae	* *Rumex acetosella* L.
Portulacaceae	*Montia fontana* L.
Ranunculaceae	*Ranunculus biternatus* Sm.
	Ranunculus moseleyi Hook.f.
Rosaceae	*Acaena magellanica* (Lam.) Vahl = *Acaena adscendens* Vahl.
Scrophulariaceae	*Limosella australis* R.Br.
Apiaceae	*Azorella selago* Hook.f.
Unidentified family	(*) not yet identified shrub (one single plant, first recorded in 2004)

APPENDIX V

LICHENS OF THE PRINCE EDWARD ISLANDS

DAG O. ØVSTEDAL AND NIEK J.M. GREMMEN

The first extensive lichen collections, made during the 1965/66 expedition, yielded some 45 species (Lindsay 1977). In 1982, Henssen and Hertel collected extensively on the islands (Hertel 1982, 1984; Henssen 1985, 1986; Henssen & Lumbsch 1985). Further collecting by Gremmen in the 1990s (Øvstedal & Gremmen 2001) increased the total species number to 101. More collecting in 2003 included 15 additional species (Øvstedal & Gremmen unpublished data), indicating that the inventory of the Prince Edward Islands lichen flora is incomplete. New observations based on collections from 2003 included two undescribed species, which have not yet been published. Nevertheless these species are included in this list, to make it as up-to-date as possible.

The present list contains 116 species, of which the presence on the island has been confirmed by recent studies. Several species listed by Lindsay (1977) have been placed separately at the end of this list. Because the collections on which Lindsay based his work could not be located, it was impossible for us to check some doubtful identifications in this list.

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 393-397

References

Henssen, A. 1985. A new *Zahlbrucknerella* from the subantarctic. *The Lichenologist* **17**, 301-303.

Henssen, A. 1986. *Edwardiella mirabilis*, a holocarpous lichen from Marion Island. *The Lichenologist* **18**(1), 51-56.

Henssen, A. & Lumbsch, T. 1985. A new *Gyalideopsis* from the subantarctic (lichenes). *International Journal of Mycology and Lichenology* **2**(1), 1-12.

Hertel, H. 1982. *Lecideaceae Exsiccatae*, Fasc. 4 (no 61-80). München.

Hertel, H. 1984. Über saxicole, lecideoide Flechten der Subantarktis. *Nova Hedwigia* **79**, 399-499.

Lindsay, D.C. 1977. The lichens of Marion and Prince Edward islands, southern Indian Ocean. *Nova Hedwigia* **28**, 667-689.

Øvstedal, D.O. & Gremmen N.J.M. 2001. The lichen flora of Marion and Prince Edward Islands. *South African Journal of Botany* **67**, 552-572.

	Marion	**Prince Edward**
Acarospora cf. *otagensis* H. Magn.	+	
Amandinea subplicata (Nyl.) Øvst.	+	+
Arctomia subantarctica Øvst.		+
Arthothelium evanescens Øvst.	+	
Arthroraphis citrinella (Ach.) Poelt	+	
Biatora sp.	+	
Buellia fuscoatratula A. Zahlbr.	+	
Caloplaca castellana (Räs.) Poelt	+	
Caloplaca cirrochrooides (Vain.) Zahlbr.	+	
Caloplaca cribrosa (Hue) Zahlbr.	+	
Caloplaca isidioclada Zahlbr.	+	
Caloplaca lucens (Nyl.) Zahlbr.	+	
Caloplaca sublobulata (Nyl.) Zahlbr.	+	+
Caloplaca tiroliensis Zahlbr.	+	
Carbonea assentiens (Nyl.) Hertel	+	
Carbonea phaestoma (Nyl.) Hertel		+
Carbonea superjecta (Nyl.) Hertel	+	
Carbonea vorticosa (Flk.) Hertel	+	
Catillaria impolita D.C. Lindsay	+	+
Catillaria lenticularis (Ach.) Th. Fr.	+	
Chrysothrix chlorina (Ach.) Laundon		+
Cladonia albata Stenroos		+

Cladonia cervicornis (Ach.) Flotow ssp. *mawsonii* (Dodge) Stenroos & Ahti		+
Cladonia chlorophaea (Flørke ex Sommerf.) Sprengel	+	
Cladonia marionii Stenroos	+	
Cladonia ochrochlora Flörke	+	
Cladonia cf. *poeciloclada* des Abb.		+
Cladonia pocillum (Ach.) O.-J.Rich.	+	+
Cladonia sarmentosa (Hook. & Tayl.) Dodge	+	
Cladonia cf. *tapperi* Ahti & Krog	+	+
Cladonia ustulata (Hook. & Tayl.) Leighton		+
Cladonia sp.		+
Dimerella sp.		+
Edwardiella mirabilis Henssen	+	
Fuscidea asbolodes (Nyl.) Hertel & V. Wirth	+	
Gyalecta azorellae Øvst. ined		+
Gyalideopsis subantarctica Henssen & Lumbsch	+	+
Haematomma erythromma (Nyl.) Zahlbr.	+	
Hertella subantarctica Henssen	+	
Lecanographa sp.	+	
Lecanora disjungenda (Crombie) Hertel & Rambold	+	
Lecanora flotowiana Spreng.	+	
Lecanora polytropa (Ehrh. ex Hoffm.) Rabenh.		+
Lecidea lapicida (Ach.) Ach.	+	
Lecidea lygomma Nyl.	+	+
Lecidea medusula (Dodge) Hertel.	+	+
Lepraria lobificans Nyl.		+
Lepraria neglecta (Nyl.) Lettau	+	
Leptogium crispatellum Nyl.		+
Lithographa marionensis Hertel & Rambold	+	
Lithographa subantarctica Hertel & Rambold	+	
Massalongia carnosa (Dicks.) Körber	+	
Mycoblastus caesius (Coppins & James) Tonsberg (cf.)		+
Notolecidea subcontinua (Nyl.) Hertel	+	
Opegrapha diaphoriza Nyl.		+
Orceolina kerguelensis (Tuck.) Hertel	+	+
Pannaria dichroa Nyl.	+	+
Pannaria pulvinula P.M.Jorgensen	+	+
Parmelia kerguelensis Wilson	+	+

Parmelia sulcata Taylor	+	+
Parmotrema crinitum (Ach.) Choisy	+	+
Peltigera kerguelensis Dodge	+	
Peltigera truculenta De Not.	+	+
Pertusaria cineraria Nyl.		+
Pertusaria cf *perrimosa* Nyl.	+	
Pertusaria werthii A.Zahlbr.	+	
Phyllisciella marionensis Henssen	+	
Placopsis bicolor (Tuck.) Bouly de Lesdain	+	
Placopsis macrophthalma (Hook. & Tayl.) Nyl.	+	+
Placopsis stellata (Øvst.) Henssen	+	
Poeltiaria urbanskyana (Zahlbr.) Hertel		+
Poeltidea perusta (Nyl.) Hertel & Hafellner		+
Poeltinula cerebrinella (Nyl.) Øvst.	+	
Porina leptalea (Durien & Mont.) A.L. Sm.	+	+
Pseudocyphelaria intricata (Delise) Vain.		+
Pseudocyphellaria crocata (L.) Vain.		+
Psoroma asperellum Nyl.	+	
Ramalina subfarinacea (Nyl. ex Cromb.) Nyl.		+
Ramonia subantarctica Øvst.	+	
Rhizocarpon kerguelense Dodge	+	
Rhizocarpon nidificum (Hue) Darb.	+	
Rhizocarpon postumum (Nyl.) Arnold	+	
Rinodina griseosoralifera Coppins	+	+
Rinodina peloleuca (Nyl.) Müll. Arg.		+
Schimatomma sp.		+
Scolisiosporum umbrinum (Ach.) Arnold	+	
Siphulastrum mamillatum (Hook & Taylor) D. Galloway	+	+
Sporastatia testudinea (Ach.) Massal.	+	+
Steinera sorediata P. James & Henssen	+	+
Stephanocyclos henssenianus Hertel	+	+
Stereocaulon cymosum Crombie	+	+
Stereocaulon heardii Øvst.	+	
Stereocaulon sp.	+	
Sticta fuliginosa (Hoffm.) Ach		+
Tephromela atra (Huds.) Hafellner	+	+
Tephromela eatonii (Crombie) Hertel	+	
Thelenella kerguelena (Nyl.) Mayrh.	+	

Thelocarpon subantarcticum Øvst.		+
Tremolecia atrata (Ach.) Hertel	+	
Mastodia tessellata (Hook.f. & Harv.) Hook.f. & Harv.	+	+
Usnea antarctica Du Rietz		+
Usnea maculata Stirton	+	+
Verrucaria ceutocarpa Vahlenb.	+	
Verrucaria cf. *ditmarsica* Erichsen	+	
Verrucaria durietzii Lamb	+	
Verrucaria efflorescens Øvst. ined	+	
Verrucaria halizoa Leighton	+	
Verrucaria maura Wahlenb.	+	+
Verrucaria mawsonii Dodge	+	
Verrucaria mucosa Wahlenb.	+	+
Verrucaria psycrophila Lamb	+	
Verrucaria tesselatula Nyl.	+	
Verrucaria umbilicata Øvst.	+	
Xanthoparmelia mougeotii (Schaerer ex D.Diet.) Hale	+	
Xanthoria candelaria (L.) Th. Fr.	+	
Zahlbrucknerella marionensis Henssen	+	
The following taxa were listed by Lindsay (1977), but they could not be confirmed (*i.e.* collections appear to have been lost, and species were not present in any other collection).		
Buellia coniops (Wahlenb. ex Ach.) Th.Fr.	+	
Caloplaca vitellinella (Nyl. ex Cromb.) Zahlbr.	+	
Lecidea aubertii B. de Lesd.	+	
Lecidea homalotera Nyl. ex Cromb.	+	
Lecidea cf. *interrupta* Darb.	+	
Pannaria hookeri (Borr. ex Sm.) Nyl.	+	
Parmelia saxatilis (L.) Ach.	+	
Peltigera canina (L.) Willd.		+
Peltigera polydactyla (Neck.) Hoffm.	+	
Physcia cf. *phaea* (Tuck.) Thoms.	+	+
Placopsis cf. *cribellans* (Nyl.) Räs.	+	
Usnea insularis (M.Lamb) Dodge		+
Xanthoria elegans (Link.) Th.Fr.	+	

APPENDIX VI

FRESHWATER INVERTEBRATES OF THE PRINCE EDWARD ISLANDS

EVGENY A. PAKHOMOV AND STEVEN L. CHOWN

The list of freshwater invertebrates presented here comprises the non-marine Crustacea (*Tigriopus angulatus* being recorded from brackish pools). Several of the mite species listed in Appendix VII Terrestrial Invertebrates, are either marine or freshwater species, but for ease of taxonomic reference are listed there and not here. The present list is, no doubt, relatively incomplete: few studies of the freshwater fauna have been undertaken. However, some work has been published, including that by Kok (1977) and Smith & Sayers (1971), and the recent comprehensive taxonomic and biogeographic review by Pugh *et al.* (2002). It is also worth recording here that the only other significant freshwater species found on Marion Island was the Brown Trout (*Salmo trutta* L.), which was introduced for human consumption to the Van den Boogaard River, and subsequently eradicated by the mid-1980s (Cooper *et al.* 1992).

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 398-399

References

Cooper, J., Crafford, J.E. & Hecht, T. 1992. Introduction and extinction of brown trout (Salmo trutta L.) in an impoverished subantarctic stream. *Antarctic Science* **4**, 9-14.

Kok, O.B., 1977. Lentic water types of Marion Island and Prince Edward Islands with comments on their zooplankton. *South African Journal of Antarctic Research* **7**, 2-7.

Pugh, P.J.A., Dartnall, H.J.G. & McInnes, S.J. 2002. The non-marine Crustacea of Antarctica and the islands of the Southern Ocean: biodiversity and biogeography. *Journal of Natural History* **36**, 1047-1103.

Smith, W.A. & Sayers, R.L., 1971. Entomostraca. In: Van Zinderen Bakker, E.M., Winterbottom, J.M. & Dyer, R.A. (Eds.). *Marion and Prince Edward Islands: Report on the South African Biological and Geological Expedition 1965-1966*. A.A. Balkema, Cape Town, pp. 361-372.

Phylum Arthropoda		
Class Crustacea		
Subclass Branchipoda		
Order Anomopoda	Chydoridae	*Alona weinecki* Studer, 1878
		Pleuroxus wittsteini Studer, 1878
	Daphniidae	*Daphniopsis studeri* Rühe, 1914
	Macrothricidae	*Macrothrix birsuticornis* Norman & Brady, 1867
Subclass Copepoda		
Order Calanoida	Centropagidae	*Boeckella vallentini* (Scott, 1914)
Order Harpacticoidea	Canthocamptidae	*Epactophanes richardi* Mrázek, 1893
	Harpacticidae	*Tigriopus angulatus* Lang, 1933
	Phyllognathopodidae	*Phyllognathopus insularis* Chappuis, 1940
	Thalestridae	*Marionobiotus jeanneli* Chappuis, 1940
Subclass Ostracoda		
Order Podocopida	Cyprididae	*Ilyodromus kerguelensis* G.W. Müller, 1906

APPENDIX VII

TERRESTRIAL INVERTEBRATES OF THE PRINCE EDWARD ISLANDS

STEVEN L. CHOWN AND DAVID J. MARSHALL

The list of invertebrates presented here includes free-living and parasitic species. It draws heavily on a range of works, most notably Crafford *et al.* (1986), Pugh (1993, 1994, 2004), Foissner (1996), Marshall *et al.* (1999, 2003), Chown *et al.* (2002), Pugh & Scott (2002), Pugh *et al.* (2002), Grobler *et al.* (2006), Lee *et al.* (2007), and an unpublished survey of the tardigrades undertaken by Sandra J. McInnes of the British Antarctic Survey. Considerable gaps exist in current knowledge, especially of the Annelida and Nematoda, but also of smaller groups such as the tardigrades and rotifers. The spider fauna of the islands is not well understood. At least one species (*Porrhomma antarctica* Hickman, Linyphiidae) has not been discovered since its original listing by Lawrence (1971). In their review, Khoza *et al.* (2005) make note thereof, but also list two additional species – a salticid and a miturgid, neither of which have since been recorded from the localities listed for Marion Island. The records might therefore represent contamination of samples in continental South Africa.

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 400-409

References

Chown, S.L., McGeoch, M.A. & Marshall, D.J. 2002. Diversity and conservation of invertebrates on the sub-Antarctic Prince Edward Islands. *African Entomology* **10**, 67-82.

Crafford, J.E., Scholtz, C.H. & Chown, S.L. 1986. The insects of sub-Antarctic Marion and Prince Edward Islands; with a bibliography of entomology of the Kerguelen Biogeographical Province. *South African Journal of Antarctic Research* **16**, 41-84.

Foissner, W. 1996. Terrestrial ciliates (Protozoa, Ciliophora) from two islands (Gough, Marion) in the southern oceans, with description of two new species, *Arcuospathidium cooperi* and *Oxytrichia ottowi*. *Biology and Fertility of Soils* **23**, 282-291.

Grobler, G.C., Janse Van Rensburg, L., Bastos, A.D.S., Chimimba, C.T. & Chown, S.L. 2006. Molecular and morphometric assessment of the taxonomic status of *Ectemnorhinus* weevil species (Coleoptera: Curculionidae, Entiminae) from the sub-Antarctic Prince Edward Islands. *Journal of Zoological Systematics and Evolutionary Research* **44**, 200-211.

Khoza, T.T., Dippenaar, S.M. & Dippenaar-Schoeman, A.S. 2005. The biodiversity and species composition of the spider community of Marion Island, a recent survey (Arachnida: Araneae). *Koedoe* **48**, 103-107.

Lawrence, R.F. Araneida. In: Van Zinderen Bakker, E.M., Winterbottom, J.M. & Dyer, R.A. (Eds.). *Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965-1966.* A.A. Balkema, Cape Town, pp. 301-313.

Lee, J.E. Slabber, S., Jansen Van Vuuren, B., Van Noort, S. & Chown, S.L. 2007. Colonisation of sub-Antarctic Marion Island by a non-indigenous aphid parasitoid *Aphidius matricariae* (Hymenoptera, Braconidae). *Polar Biology* **30**, 1195-1201.

Marshall, D.J., Gremmen, N.J.M., Coetzee, L., OConnor, B.M., Pugh, P.J.A., Theron, P.D. & Uekermann, E.A. 1999. New records of Acari from the sub-Antarctic Prince Edward Islands. *Polar Biology* **21**, 84-89.

Marshall, D.J., O'Connor, B.M. & Pugh, P.J.A. 2003. *Algophagus* mites (Astigmata: Algophagidae) from the sub-Antarctic Prince Edward Islands: habitat-related morphology and taxonomic descriptions. *Journal of Zoology, London* **259**, 31-47.

Pugh, P.J.A. 1993. A synonymic catalogue of the Acari from Antarctica, the sub-Antarctic Islands and the Southern Ocean. *Journal of Natural History* **27**, 323-421.

Pugh, P.J.A. 1994. Non-indigenous acari of Antarctica and the sub-Antarctic islands. *Zoological journal of the Linnean Society* **110**, 207-217.

Pugh, P.J.A. 2004. Biogeography of spiders (Araneae: Arachnida) on the islands of the Southern Ocean. *Journal of Natural History* **38**, 1461-1487.

Pugh, P.J.A., Dartnall, H.J.G. & McInnes, S.J. 2002. The non-marine Crustacea of Antarctica and the islands of the Southern Ocean: biodiversity and biogeography. *Journal of Natural History* **36**, 1047-1103.

Pugh, P.J.A. & Scott, B. 2002. Biodiversity and biogeography of non-marine Mollusca on the islands of the Southern Ocean. *Journal of Natural History* **36**, 927-952.

A. Free-living species

Species marked with a cross have been recorded previously (though possibly in error, especially in the case of the mites), but not recently (last five years). Species marked I are established species that have been introduced by humans (with dates in parentheses indicating year of discovery where known), those marked IT are introduced species that have not established. The Oligochaeta and Tardigrada records are almost certainly incomplete, and the nematodes and rotifers have been excluded because they are so poorly known. The *Ectemnorhinus*-group weevils are presently the subject of systematic revision and the status of *Pringleophaga marioni* and *P. kerguelensis* has yet to be resolved. Molecular studies suggest that in both groups the relationships among species are more complex than previously supposed.

	Protozoa, Ciliophora	
	Acineria uncinata Tucolesco, 1962	
	Arcuospathidium cooperi Foissner, 1996	
	Blepharisma bimicronucleatum Villeneuve-Brachon, 1940	
	Blepharisma steini Kahl, 1932	
	Colpoda aspersa Kahl, 1926	
	Colpoda cucullus (Müller, 1773)	
	Colpoda ecaudata (Liebmann, 1936)	
	Colpoda henneguyi Fabre-Domergue, 1889	
	Colpoda inflata (Stokes, 1884)	
	Colpoda steinii Maupas, 1883	
	Cyclidium muscicola Kahl, 1931	
	Cyrtolophosis mucicola Stokes, 1885	
	Drepanomonas exigua (?) Penard, 1922	
	Epispathidum ascendens (Wenzel, 1955)	
	Fuscheria terricola Berger *et al.*, 1983	
	Gonostomum affine (Stein, 1859)	
	Grossglockneria acuta Foissner, 1980	
	Haplocaulus terrenus Foissner, 1981	
	Holostichia tetracirrata Buitkamp & Wilbert, 1974	
	Lamtostyla hyalina Berger *et al.*, 1984	
	Lamptostyla islandica Berger & Foissner, 1988	
	Leptopharynx costatus Mermod, 1914	
	Microthorax simulans (Kahl, 1926)	
	Nivaliella plana Foissner, 1980	

	Onychodromopsis flexilis Stokes, 1887	
	Opercularia arboricola (Biegel, 1954)	
	Oxytrichia granulifera Foissner & Adam, 1983	
	Oxytrichia lanceolata Shibuya, 1930	
	Oxytrichia longigranulosa Berger & Foissner, 1989	
	Platyophyra macrostoma Foissner, 1980	
	Platyophyra vorax (Kahl, 1926)	
	Platyophyrides dragescoi Foissner, 1987	
	Protospathidum serpens (Kahl, 1930)	
	Pseudocyrtolophosis alpestris Foissner, 1980	
	Pseudoplatyophyra nana (Kahl, 1926)	
	Sathrophilus muscorum (Kahl, 1931)	
	Sterkiella histriomuscorum (Foissner *et al.*, 1991)	
	Vorticella astyliformis Foissner, 1981	
Tardigrada		
Echiniscidae	*Echiniscus* sp. 1	
	Echiniscus sp. 2	
	Echiniscus sp. 3	
	Echiniscus sp. 4	
	Echiniscus sp. 5	
	Pseudechiniscus suillus (Ehrenberg)	
Echiniscoididae	*Echiniscoides sigismundi* Richters	
Macrobiotidae	*Macrobiotus* sp. 1	
	Macrobiotus sp. 2	
	Macrobiotus sp. 3	
	Minibiotus sp.	
	Calohypsibius ornatus (Richters)	
	Dactylobiotus ambiguus (J. Murray)	
Hypsibiidae	*Diphascon* sp.	
	Ramajendas renaudii (Ramazzotii)	
	Milnesium tardigradum Doyére	
Oligochaeta		
Megascolecidae	*Microscolex kerguelarum* (Grube)	
Enchytraeidae	At least two spp.	
Crustacea		
Porcellionidae	*Porcellio scaber* Latreille	I (2001)

Acari		
Mesostigmata	Rhodacarid sp. 1	
	Rhodacarid sp. 2	
	Rhodacarid sp. 3	
	Parasitiphis brunneus (Kramer)	
	Dendrolaelaps sp.nov.	I
	Cilibid sp. 1	
	Davacarus gresitti Hunter	
Prostigmata	*Nanorchestes* sp.nov.1	
	Nanorchestes sp.nov.2	
	Nanorchestes sp.nov.3	
	Nanorchestes sp.nov.4	
	Eupodes minutus (Strandtmann)	
	Rhagidia sp.	
	Peregrinacarus reticulatus Bartsch	I
	Werthella tera Bartsch	X
	Halacarellus parilis Bartsch	
	H. novus (Lohmann)	
	H. robustus Lohmann	
	Lohmannella gaussi Lohmann	X
	Isobactrus magnus (Lohmann)	
	Rhombognathus auster Bartsch	
	Rhombognathus apsteini Lohmann	
	Rhombognathus gresitti Newell	
	Ereynetes macquariensis Fain	
	Tydeus (Pertydeus) sp. nov.	
	Bdellodes sp.nov.	
	Disparipes antarcticus Richters	I
	Neopygmephorus sp.	I
	Eryngiopus sp.nov.	
	Balaustium sp.nov.	
Cryptostigmata	*Liochthonius australis* Covarrubias	
	L. fimbriatissimus (Hammer)	X
	Hermanniella sp.	X
	Allodamaeus sp.	X
	Macquarioppia striata (Wallwork)	
	Austroppia crozetensis (Richters)	
	Alaskozetes antarcticus (Michael)	

Cryptostigmata (continued)	*A. bouvetøyaensis* Van Pletzen & Kok	X
	Halozetes belgicae (Michael)	
	H. crozetensis (Richters)	X
	H. edwardensis Van Pletzen & Kok	X
	H. fulvus Engelbrecht	
	H. marinus devilliersi Engelbrecht	
	H. marionensis Engelbrecht	
	Podacarus auberti Grandjean	
	Dometorina marionensis Van Pletzen & Kok	
	Zygoribatula subantarctica Van Pletzen & Kok	X
	Totobates marionensis Van Pletzen & Kok	
	Antarctozetes crozetensis (Richters)	X
	Ceratozetes gausii (Richters)	X
	Magellozetes antarcticus (Michael)	
	Porokalumma rotunda (Wallwork)	
Astigmata	*Schwiebea talpa subantarctica* Fain	
	Algophagus antarcticus Hughes	
	Algophagus laticollaris Fain	
	Algophagus semicollaris Fain	
	Algophagus brachytarsus Marshall *et al.*	
	Algophagus macrolithus Marshall *et al.*	
	Hyadesia halophila Fain	
	H. kerguelenensis Lohmann	
	H. subantarctica Fain	
	Neocalvolia travei Fain	
	Neocalvolia sp. nov.	
	Austranoetus kerguelenensis Fain	
	Glycyphagus domesticus (de Geer)	I
Metastigmata	*Ceratixodes uriae* White	
	Ixodes pterodromae Arthur	
	Ornithodoros capensis Neumann	
Araneida		
Desidae	*Myro kerguelenensis* Cambridge	
	M. paucispinosus Berland	
Linyphiidae	*Prinerigone vagans* (Audouin)	I

Collembola		
Neanuridae	*Friesea tilbrooki* Wise	
Hypogastruridae	*Ceratophysella denticulata* (Bagnall)	I
	Hypogastrura viatica (Tullberg)	I
Onychiuridae	*Tullbergia bisetosa* Börner	
Isotomidae	*Isotoma marionensis* Déharveng	
	I. notabilis Schäffer	I
	Cryptopygus dubius Déharveng	
	C. antarcticus travei Déharveng	
	C. caecus Wahlgren	
	C. tricuspis Enderlein	
	Isotomurus cf. palustris Müller	I
Tomoceridae	*Pogonognathellus flavescens* (Tullberg)	I (1983)
Neelidae	*Megalothorax* sp.	
Sminthuridae	*Sminthurinus tuberculatus* Delamare *et al.*	
	Sminthurinus granulosus Enderlein	
	Katianna n. sp.	
Insecta		
Psocoptera	*Antarctopsocus jeanneli* Badonnel	
Hemiptera		
Aphididae	*Macrosiphum euphorbiae* (Thomas)	I
	Myzus ascalonicus Doncaster	I
	Rhopalosiphum padi (Linnaeus)	I
Thysanoptera		
Thripidae	*Apterothrips apteris* (Daniel)	I
Coleoptera		
Curculionidae	*Bothrometopus elongatus* (Jeannel)	
	B. parvulus (C.O. Waterhouse)	
	Bothrometopus sp. nr. *parvulus*	
	B. randi Jeannel	
	Ectemorhinus kuscheli Grobler *et al.*, 2006	
	E. similis C.O. Waterhouse	
	E. marioni Jeannel now a synonym of *E. similis*	
	Palirhoeus eatoni (C.O. Waterhouse)	
Hydraenidae	*Meropathus chuni* Enderlein, 1901	
Staphylinidae	*Halmaeusa atriceps* (C.O. Waterhouse, 1875)	
	Anobiidae sp.	IT
	Dermestidae sp.	IT
	Chrysomelidae sp.	IT

Lepidoptera		
Noctuidae	*Agrotis ipsilon* (Walker)	I (1996)
	A. segetum (Denis & Schiffermuller)	XIT
	Chrysodeixis acuta (Walker)	XIT
	Cosmophila sabulifera (Guenee)	IT
	Helicoverpa armigera (Hubner)	IT
	Spodoptera exigua (Hubner)	XIT
	Thysanoplusia orichalcea (Fabricius)	XIT
Nymphalidae	*Vanessa cardui* (Linnaeus)	I
Plutellidae	*Plutella xylostella* (Linnaeus)	I (1986)
Pyralidae	*Nomophila* sp.	IT
Tineidae	*Pringelophaga kerguelensis* Enderlein	
	P. marioni Viette	
Yponomeutidae	*Embryonopsis halticella* Eaton	
Diptera		
Calliphoridae	*Calliphora vicina* Robineau-Desvoidy	I
Chironomidae	*Limnophyes minimus* Meigen	I
	Telmatogeton amphibius (Eaton)	
Drosophilidae	*Scaptomyza oxyphallus* Tsacas	I
Faniidae	*Fannia canicularis* (Linnaeus)	I
Helcomyzidae	*Paractora dreuxi* Séguy	
Lonchaeidae	*Lamprolonchaea smaragdi* (Walker)	IT
Psychodidae	*Psychoda parthenogenetica* Tonnoir	I
Sciaridae	*Lycoriella auberti* Séguy	
Tethinidae	*Apetaenus litoralis* Eaton	
	Listriomastax litorea Enderlein	
	Anthomyiidae sp.	IT
Hymenoptera		
Braconidae	*Aphidius matricariae* Haliday	I (2002)
Eucoilidae	*Kleidotoma icarus* (Quinlan)	
Formicidae	*Lepisiota capensis* (Mayr)	IT
Mollusca		
Charopidae	*Notodiscus hookeri* (Reeve)	
Limacidae	*Deroceras panormitanum* (Lessona & Pollonera)	I

B. Parasitic species

The parasitic species that have been studied are mostly fleas and parasitic lice. Little work has been done on the parasitic mites found on the island. This list of lice was obtained from <www.phthiraptera.org> on 27th July 2007 for the bird and mammal species known to be breeding on the Prince Edward Islands. In the case of the birds, this does not imply that these species have definitely been found on birds at Marion Island. The only species known from mammals at the islands is the sucking louse *Lepidophthirus macrorhini* Enderlein.

Phthiraptera	
Amblycera	
Menoponidae	*Ancistrona vagelli* (J.C. Fabricius)
	Actornithophilus pauliani Séguy
	Austromenopon affine (Piaget)
	Austromenopon atrofulvum (Piaget)
	Austromenopon elliotti Timmermann
	Austromenopon fuscofasciatum (Piaget)
	Austromenopon navigans (Kellogg)
	Austromenopon ossifragae (Eichler)
	Austromenopon pinguis (Kellogg)
	Austromenopon popellus (Piaget)
	Austromenopon stammeri Timmermann
Anoplura	
Echinophthiriidae	*Lepidophthirus macrorhini* Enderlein
Ischnocera	
Philopteridae	*Austrogoniodes bicornutus* (Kéler)
	Austrogoniodes brevipes (Giebel)
	Austrogoniodes concii (Kéler)
	Austrogoniodes cristati Kéler
	Austrogoniodes gressetti Clay
	Austrogoniodes hamiltoni Harrison
	Austrogoniodes keleri Clay
	Austrogoniodes macquariensis Harrison
	Docophoroides brevis (Dufour)
	Docophoroides murphi (Kellogg)
	Docophoroides simplex (Waterston)
	Episbates pederiformis (Dufour)
	Haffneria grandis (Piaget)
	Halipeurus pacificus Edwards

Philopteridae (continued)	*Halipeurus pelagicus* (Denny)
	Halipeurus procellariae (J.C. Fabricius)
	Harrisoniella hopkinsi Eichler
	Naubataes fuliginosus (Taschenberg)
	Naubates clypeatus (Giebel)
	Naubates heteroproctus Harrison
	Naubates prioni (Enderlein)
	Naubates pterodromi Bedford
	Nesiotinus demersus Kellogg
	Paraclisis diomedeae (J.C. Fabricius)
	Paraclisis hyalina (Neumann)
	Paraclisis miriceps (Kellogg and Kuwana)
	Paraclisis obscura (Rudow)
	Pelmatocerandra enderleini Eichler
	Pelmatocerandra setosa (Giebel)
	Perineus circumfasciatus Kéler
	Perineus concinnoides Kéler
	Perineus macronecti Palma and Pilgrim
	Philoceanus fasciatus (Carriker)
	Philoceanus garrodiae (Clay)
	Quadraceps alpha (Kellogg)
	Quadraceps houri Hopkins
	Quadraceps sellatus (Burmeister)
	Quadraceps vaginalis Timmermann
	Saemundssonia australis Timmermann
	Saemundssonia desolata Timmermann
	Saemundssonia enderleini (Eichler)
	Saemundssonia euryrhyncha (Giebel)
	Saemundssonia gaini (Neumann)
	Saemundssonia lockleyi Clay
	Saemundssonia nereis Timmermann
	Saemundssonia pterodromae Timmermann
	Saemundssonia sternae (Linnaeus)
	Trabeculus hexakon (Waterston)
	Trabeculus schillingi Rudow
Siphonaptera	
Pygiopsyllidae	*Notiopsylla kerguelensis* (Taschenberg)

APPENDIX VIII

MARINE PLANKTON OF THE PRINCE EDWARD ISLANDS REGION

EVGENY A. PAKHOMOV

Considerable oceanographic research has been undertaken in the vicinity of the Prince Edward Islands. The list provided here represents an outcome of that work, with the reference list below providing access to the appropriate literature.

References

Boden, B.P. & Parker, L.D. 1986. The plankton of the Prince Edward Islands. *Polar Biology* **5**, 81-93.

Deevey, G.B., 1976. Planktonic ostracods (Myodocopa Halocyprididae) collected on the oceanographic expedition MD03 of the "*Marion-Dufresne*". *Comité National Francais des Recherches Antarctiques* **39**, 43-46.

Grindley, J.R. & Lane, S.B. 1979. Zooplankton around Marion and Prince Edward Islands. *Comité National Francais des Recherches Antarctiques* **44**, 111-125.

Hunt, B.P.V. 2000. *Mesozooplankton community structure in the vicinity of the Prince Edward Islands (Southern Ocean) 37°50'E, 46°45'S*. MSc Thesis, Rhodes University, South Africa.

Pakhomov, E.A. & Froneman, P.W., 1999. Macroplankton/micronekton dynamics in the vicinity of the Prince Edward Islands (Southern Ocean). *Marine Biology* **134**, 501-515.

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 410-415

Pakhomov, E.A. & Froneman, P.W., 2000. Composition and spatial variability of macroplankton and micronekton within the Antarctic Polar Frontal Zone of the Indian Ocean during austral autumn 1997. *Polar Biology* **23**, 410-419.

Pakhomov, E.A., Ansorge, I.J. & Froneman, P.W., 2000. Variability in the inter-island environment of the Prince Edward Islands (Southern Ocean). *Polar Biology* **23**, 593-603.

Pakhomov, E.A., Kaehler, S. & McQuaid, C.D., 2002. Zooplankton community structure in the kelp beds of the sub-Antarctic Prince Edward Archipelago: are they a refuge for larval stages? *Polar Biology* **25**, 778-788.

KINGDOM PROTISTA	
Phylum Protozoa	
	Globigerina sp.
	Globigerinoides sp.
KINGDOM METAZOA	
Phylum Arthropoda	
Class Crustacea	
Subclass Copepoda	
Order Calanoida	*Aetideus armatus* (Boeck, 1982)
	Arietellus simplex Sars, 1905
	Calanoides acutus (Geisbrecht, 1902)
	Calanus propinquus Brady, 1883
	Calanus simillimus Giesbrecht, 1902
	Calocalanus sp.
	Candacia falcifera Farran, 1929
	Candacia maxima Vervoot, 1957
	Candacia sp.
	Centrophages sp.
	Clausocalanus brevipes Frost & Fleminger, 1968
	Clausocalanus laticeps Farran, 1929
	Ctenocalanus citer Heron & Bowman, 1971
	Ctenocalanus vanus Geisbrecht, 1988
	Eucalanus hyalinus Claus, 1866
	Eucalanus longiceps Matthews, 1925
	Eucalanus sewelli Fleminger, 1973
	Euchaeta marina (Prestandrea, 1837)
	Euchaeta sp.
	Euchirella rostromagna Wolfenden, 1911
	Gaetanus antarcticus Wolfenden, 1905

Order Calanoida (continued)	*Gaetanus minor* Farran, 1905
	Gaidius tenuispinus (Sars, 1900)
	Haloptilus oxycephalus (Geisbrecht, 1889)
	Heterorabdus austrinus Geisbrecht, 1902
	Metridia gerlachei Geisbrecht, 1902
	Metridia lucens Broeck, 1864
	Microcalanus pygmaeus (Sars, 1900)
	Microcalanus sp.
	Microsetella rosea (Dana, 1847)
	Onchocalanus cristatus (Wolfenden, 1904)
	Paraeuchaeta biloba Farran, 1929
	Paraeuchaeta exigua (Wolfenden, 1911)
	Paraeuchaeta sp.
	Pleuromamma abdominalis (Lubbock, 1856)
	Pleuromamma gracilis (Claus, 1863)
	Pleuromamma robusta (F. Dahl, 1893)
	Pleuromamma sp.
	Pseudochirella mawsoni Vervoot, 1957
	Racovitzanus antarcticus Giesbrecht, 1902
	Rhincalanus gigas Brady, 1883
	Rhincalanus nasutus Geisbrecht, 1888
	Scaphocalanus antarcticus Park, 1982
	Scaphocalanus farrani Park, 1982
	Scaphocalanus vervoorti Park, 1982
	Scolecithricella glacialis (Geisbrecht, 1902)
	Scolecithricella minor (Brady, 1883)
	Spinocalanus sp.
Order Cyclopoida	*Oithona frigida* Geisbrecht, 1902
	Oithona similis Claus, 1866
	Oncaea antarctica Heron, 1977
	Oncaea obtusa (Dana, 1852)
Order Harpacticoida	Euterpinidae gen spp.
	Glytemnestra spp.
Subclass Ostracoda	
Order Ostracoda	*Conchoecia antipoda* Müller, 1906
	Conchoecia chuni Müller, 1906
	Conchoecia elegans Sars, 1865
	Conchoecia hettacra Müller, 1906
	Conchoecia obtusata var. *antarctica* Müller, 1906
	Conchoecia serrulata Claus, 1874

Subclass Malacostraca	
Order Euphausiacea	*Bentheuphausia amblyops* G.O. Sars, 1883
	Euphausia longirostris Hansen, 1908
	Euphausia similies Sars, 1885
	Euphausia similis var. *armata* Hansen, 1911
	Euphausia spinifera Sars, 1885
	Euphausia triacantha Holt & Tattersall, 1906
	Euphausia vallentini Stebbing, 1900
	Nematoscelis megalops G.O. Sars, 1883
	Stylocheiron elongatum G.O. Sars, 1883
	Stylocheiron longicorne G.O. Sars, 1883
	Stylocheiron maximum Hansen, 1908
	Thysanoessa gregaria G.O. Sars, 1885
	Thysanoessa macrura G.O. Sars, 1885
	Thysanoessa vicina Hansen, 1911
Order Amphipoda	*Archaeoscina* sp.
	Chuneola paradoxa Woltereck, 1909
	Cyllopus magellanicus Dana, 1852
	Gondogenia spinicoxa
	Hyperiella dilatata Stebbing, 1888
	Mimonectes sphaericus Bovallius, 1885
	Hyperoche medusarum (Kröyer, 1838)
	Paraphronima gracilis Claus, 1879
	Phronima atlantica Guérin-Méneville, 1836
	Phronima sedentaria (Forskål, 1775)
	Phronimella elongata (Claus, 1862)
	Primno macropa Guérin-Méneville, 1836
	Scina latifrons Wagler, 1926
	Scina rattrayi kielhacki Wagler, 1926
	Scina sp.
	Themisto gaudichaudi (Guérin, 1825)
	Vibilia antarctica Stebbing, 1888
	Vibilia armata Bovallius, 1887
Order Decapoda	*Acanthephyra pelagica* (Risso, 1816)
	Nauticaris marionis Bate, 1888
	Nematocarcinus longirostris Bate, 1888
	Nematocarcinus sp.
	Pasiphaea longispina Lenz & Strunk, 1914
	Petalidium foliaceum Bate, 1888
	Sergestes (arcticus) Krøyer, 1855

Phylum Mollusca	
Class Gastropoda	
Order Thecosomata	*Clio pyramidata* (Linneus, 1767)
	Cymbulia peroni De Blainville, 1818
	Cymbulia sp.
	Limacina helicina (Phipps, 1774)
	Limacina inflata (d'Orbigny, 1836)
	Limacina retroversa (Flemming, 1823)
Order Gymnosomata	*Clione antarctica* Smith, 1902
	Spongiobranchia australis d'Orbigny, 1834
Class Cephalopoda	
	Alluroteuthis antarcticus Odhner, 1923
	Brachioteuthis sp.
	Chiroteuthis sp.
	Galiteuthis glacialis (Chun, 1906)
	Gonatus sp.
	Histioteuthis sp.
	Moroteuthis sp.
	Octopus sp.
Phylum Annelida	
Class Polychaeta	
	Pelagobia longicirrata Greeff, 1879
	Rhynconerella bongraini (Gravier, 1911)
	Tomopterus sp
	Travisiopsis levinseni (Southern, 1910)
	Travisiopsis lobifera (Levinsen, 1885)
	Travisiopsis sp.
	Typhloscolex mulleri Busch, 1851
	Vanadis longissima (Levinsen, 1885)
	Vanadis sp.
Phylum Ctenophora	
Order Beroida	*Beroe cucumis* Fabricius, 1780
	Beroe sp.

Phylum Cnidaria	
Class Hydrozoa	
Order Siphonophora	*Dimophyes arctica* Chun, 1897
	Diphyes sp.
	Lensia sp.
	Melophysa melo Quoy & Gaimard, 1827
	Vogtia kuruae Alvarifio, 1967
	Vogtia spinosa Keferstein & Ehlers, 1861
Order Trachymedusae	*Pantachogon* sp.
Order Narcomedusae	*Pegantha triloba* Haeckel, 1879
	Pegantha sp.
Order Anthomedusae	*Zanclea costata* Gegenbaur, 1857
Class Scyphozoa	
Order Coronatae	*Periphylla periphylla* (Peron & Lesueur, 1809)
Phylum Chaetognatha	
	Eukrohnia hamata (Mobius, 1875)
	Sagitta gazellae Ritter-Zahony, 1909
	Sagitta lyra Krohn, 1853
	Sagitta marry David, 1956
	Sagitta maxima (Conant, 1896)
	Sagitta tasmanica Thompson, 1947
Phylum Chordata	
Class Thaliacea	
Order Salpida	*Salpa thompsoni* Foxton, 1961
	Iasis zonaria (Van Beneden, 1913)
	Ihlea magalhanica (Apstein, 1894)
Class Appendicularia	
	Oikopleura spp.
	Frittilaria spp.

APPENDIX IX

MARINE BENTHIC SPECIES OF THE PRINCE EDWARD ISLANDS

EVGENY A. PAKHOMOV

Thanks to the considerable oceanographic survey work undertaken at the Prince Edward Islands, and a substantial interest in the benthos by several taxonomists (especially M.L. Branch), the benthos has been reasonably well documented at the islands, at least in terms of the species that are present. Spatial surveys have typically not been undertaken. The reference list below provides an introduction to the literature.

References

Arnaud, F. & Branch, M.L., 1991. The Pycnogonida of subantarctic Marion and Prince Edward Islands: Illustrated keys to the species. *South African Journal of Antarctic Research* **21**, 65-71.

Branch, M.L. 1994. The Polychaeta of subantarctic Marion and Prince Edward Islands: Illustrated keys to the species and results of the 1982-1989 University of Cape Town surveys. *South African Journal of Antarctic Research* **24**, 3-52.

Branch, M.L., Arnaud, P.M., Cantera, J. & Gianakouras, D., 1991. The benthic Mollusca and Brachiopoda of subantarctic Marion and Prince Edward Islands. *South African Journal of Antarctic Research* **21**, 45-64.

Branch, M.L., Griffiths, C.L., Kensley, B. & Sieg, J., 1991. The benthic Crustacea of subantarctic Marion and Prince Edward Islands: Illustrated keys to the species and results of the 1982-1989 University of Cape Town surveys. *South African Journal of Antarctic Research* **21**, 3-44.

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 416-430

Branch, M.L. & Hayward, P.J. 2005. New species of cheilostomatous Bryozoa from subantarctic Marion and Prince Edward Islands. *Journal of Natural History* **39**, 2671-2704.

Branch, M.L., Jangoux, M., Alva, V., Massin, C.I. & Stampanato, S., 1993. The Echinodermata of subantarctic Marion and Prince Edward Islands. *South African Journal of Antarctic Research* **23**, 37-70.

Rowe F.W.E. & Clark A.M., 1975. Notes on some echinoderms from Marion Island. *Bulletin Britain Museum Natural History (Zoology)* **28**, 187-190.

PHYLUM ARTHROPODA	
Class Crustacea	
Subclass Cirripedia	
Order Thoracica	
Suborder Lepadomorpha	
	Scalpellum flavum Hoek, 1883
Subclass Malacostraca	
Superorder Peracarida	
Order Amphipoda	
Suborder Gammaridea	
Acanthonotozomatidae	*Gnathiphimedia urodentata* Bellan-Santini and Ledoyer, 1986
Amphilochidae	*Gitanopsis marionis* (Stebbing, 1888)
	Gitanopsis squamosa (Thomson, 1880)
Corophiidae	*Gammaropsis longitarsus* (Schellenberg, 1931)
	Gammaropsis sp.
	Haplocheira barbimana (Thomson, 1879)
	Lembos sp.
Didymocheliidae	*Didymochelia edwardi* Bellan-Santini and Ledoyer, 1986
Eophliantidae	*Cylindryllioides mawsoni* Nicholls, 1938
Eusiridae	*Atyloella magellanica* (Stebbing, 1888)
	Atylopsis emarginatus Stebbing, 1888
	Djerboa furcipes Chevreux, 1906
	Eusiroides aberrantis Bellan-Santini and Ledoyer, 1986
	Eusiroides georgianus K.H. Barnard, 1932
	Gondogeneia spinicoxa Bellan-Santini and Ledoyer, 1974
	Harpinioides drepanocheir Stebbing, 1888
	Oradarea edentata Thurston, 1974
	Oradarea ocellata Thurston, 1974

Gammaridae	*Ceradocopsis dufresni* Bellan-Santini and Ledoyer, 1986
	Ceradocopsis kergueleni Schellenberg, 1926
	Paramoera fissicauda (Dana, 1852)
	Pontogeneiella brevicornis (Chevreux, 1906)
	Schraderia gracilis Pfeffer, 1888
Haustoriidae	*Carangolia cornuta* Bellan-Santini and Ledoyer, 1986
	Cardenio paurodactylus Stebbing, 1888
	Urothoe marionis Bellan-Santini and Ledoyer, 1986
	Urothoides lachneessa Stebbing, 1888
Ischyroceridae	*Cerapus oppositus* KH Barnard, 1932
	Ischyrocerus sp. A
	Ischyrocerus sp. B
	Jassa alonsoae Conlan, 1990
	Pseuderichthonius gaussi Schellenberg, 1926
	Pseudischyrocerus crenatipes Bellan-Santini and Ledoyer, 1986
	Pseudischyrocerus distichon (KH Barnard, 1930)
	Ventojassa georgiana (Schellenberg, 1931)
Leucothoidae	*Leucothoe spinicarpa* (Abildgraad, 1879)
	Leucothoe sp.
Liljeborgiidae	*Liljeborgia longicornis* (Schellenberg, 1931)
	Liljeborgia pseudomacronyx Bellan-Santini and Ledoyer, 1986
Lysianassidae	*Acontiostoma marionis* Stebbing, 1888
	Cheirimedon femoratus (Pfeffer, 1888)
	Hippomedon kergueleni (Miers, 1875)
	Kerguelenia antiborealis Bellan-Santini and Ledoyer, 1986
	Lepidepecreella tridactyla Bellan-Santini, 1972
	Parawaldeckia kidderi (Smith, 1876)
	Pseudorchomene coatsi (Chilton, 1912)
	Stomacontion acutibasalis (Bellan-Santini and Ledoyer, 1974)
	Stomacontion pepinii (Stebbing, 1888)
Oedicerotidae	? *Monoculodes antarcticus* KH Barnard, 1932
	Monoculodes scrabriculosus KH Barnard, 1932
	? *Oediceroides cinderella* Stebbing, 1888
Pardaliscidae	*Pardalisca marionis* Stebbing, 1888
Phoxocephalidae	*Harpinia obtusifrons* Stebbing, 1888
Pleustidae	? *Pleusymtes* sp.
Podoceridae	*Podocerus danae* Stebbing, 1888
	Podocerus danae armatus Bellan-Santini and Ledoyer, 1986
	Podocerus capillimanus Nicholls, 1938
Sebidae	*Seba saundersii* Stebbing, 1875

Stegocephalidae	*Andaniella integripes* Bellan-Santini and Ledoyer, 1986
Stenothoidae	*Probolisca ovata* (Stebbing, 1888)
	Proboloides elliptica (Schellenberg, 1931)
	Proboloides sp. A
	Proboloides sp. B
	Pseudothaumatelson cyproides Nicholls, 1938
	Stenothoe sp.
	Thaumatelson herdmani Walker, 1906
Stilipedidae	*Alexandrella inermis* Bellan-Santini and Ledoyer, 1986
Talitridae	*Hyale grandicornis* (Kroyer, 1945)
	Hyale hirtipalma (Dana, 1852)
Suborder Caprellidea	
Aeginellidae	? *Eupariambus* sp.
Order Isopoda	
Suborder Epicaridea	
Bopyridae	Bopyridae gen sp.
Suborder Valvifera	
Arcturidae	*Antarcturus aculeatus* Kussakin, 1967
	Microarcturus hirticornis (Monod, 1926)
	Neastacilla marionensis (Beddard, 1886)
Pseudidotheidae	*Arcturides cornutus* Studer, 1882
Suborder Anthuridea	
Paranthuridae	*Califanthura pingouin* Kensley, 1980
	Paranthura possessia Kensley, 1980
Suborder Flabellifera	
Serolidae	*Serolis septemcarinata* Miers, 1847
Aegidae	*Aega* cf. *crozetensis* Kussakin and Vassina, 1982
	Aega falklandica Kussakin, 1967
	Aega semicarinata Miers, 1875
Sphaeromatidae	*Gymodocella* sp.
	Dynamenella eatoni (Miers, 1875b)
	Euvallentina darwini (Cunningham, 1871)
	Exosphaeroma gigas (Leach, 1818)
Suborder Gnathiidea	
Gnathiidae	*Gnathia antarctica* (Studer, 1884)

Suborder Asellota	
Dendrotionidae	*Acanthomunna spinipes* (Vanhöffen, 1914)
Joeropsidae	*Joeropsis curvicornis* (Nicolet, 1849)
	Joeropsis marionis Beddard, 1886
Janiridae	*Austrofilius furcatus* Hodgson, 1910
	Austroniscus ectiformis Vanhöffen, 1914
	Iais pubescens (Dana, 1852)
	Ianisera trepidus Kensley, 1976
	Notasellus sarsi Pfeffer, 1887
Munnidae	*Munna instructa* Cleret, 1973
	Munna neglecta Monod, 1931
	Munna neozelanica Chilton, 1892
Santiidae	*Santia bicornis* (Cleret, 1973)
	Santia cf. *hofsteni* (Nordenstam, 1933)
	Santia cf. *marmoratus* (Vanhöffen, 1914)
Pleurogonidae	*Munnogonium* sp.
	Paramunna sp.
Order Tanaidacea	
Suborder Monokonophora	
Superfamily Apseudoidea	
Apseudidae	*Apseudes spectabilis* (Studer, 1884)
Suborder Dikonophora	
Superfamily Paratanaoidea	
Paratanaidae	*Paratanais oculatus* (Vanhöffen, 1914)
Leptocheliidae	*Pseudonototanais werthi* (Vanhöffen, 1914)
Nototanaidae	*Nototanais antarcticus* (Hodgson, 1902)
	Nototanais dimorphus (Beddard, 1886)
Superfamily Tanaoidea	
Tanaidae	*Allotanais hirsustus* (Beddard, 1886a)
	Tanais hirsustus, Stebbing, 1919
	Pancoloides litoralis (Vanhöffen, 1914)
	Sinelobus stanfordi (Richardson, 1901)
	Zeuxo phytalensis Sieg, 1980
	Zeuxoides helleri (Gerstaecker, 1888)
	Zeuxoides pseudolitoralis, Sieg, 1980

Superorder Eucarida	
Order Decapoda	
Suborder Natantia	
Campylonotidae	*Campylonotus capensis* Bate, 1888
Hippolytidae	*Chorismus antarcticus* (Pfeffer, 1887)
	Nauticaris marionis Bate, 1888
Nematocarcinidae	*Nematocarcinus lanceopes* Bate, 1888
Suborder Reptantia	
Section Branchyura	
Hymenosomatidae	*Halicarcinus planatus* Fabricius, 1793
Section Anomura	
Lithodidae	*Lithodes murrayi* Henderson, 1888
	Paralomis aculeatus (Henderson, 1888)
Paguridae	*Pagurodes inarmatus* Henderson, 1888
Parapaguridae	*Sympagurus dimorphus* (Studer, 1883)
	= *Parapagurus dimorphus* (Studer, 1883)
Galatheidae	*Munida spinosa* Henderson, 1888
Chirostylidae	*Uroptychus insignis* Henderson, 1888
PHYLUM BRACHIOPODA	
	Liothyrella sp.
	Magellania kerguelensis (Davidson, 1880)
	Platydia anomioides Scacchi, 1844
PHYLUM MOLLUSCA	
Class Solenogastres	
	Solenogastres gen. sp.
Class Bivalvia	
	Acesta sp.
	Adacnarca marionensis (Smith, 1885)
	Astarte longirostris d'Orbigny, 1846
	Condylocardia sp.
	Cuspidaria kerguelenensis Smith, 1885
	Cuspidaria cf. *tenella*, Smith, 1907
	Cyclopecten aviculoides Smith, 1885
	Escalima goughensis (Melvill & Standen, 1907)
	Gaimardia adamsiorum Osorio & Arnaud, 1984
	Gaimardia trapesina (Lamarck, 1819)
	Hiatella solida (Sowerby, 1834)
	Kellia nuculina Martens, 1881
	Kidderia minuta Dall, 1876

	Kidderia oblonga (Smith, 1898)
	Lasaea consanguinea Smith, 1877
	Laternula elliptica King & Broderip, 1831
	Limatula pygmaea (Philippi, 1845)
	Limatula simillima Thiele, 1912
	Limopsis marionensis Smith, 1885
	Lissarca miliaris (Philippi, 1845)
	Myonera fragilissima Smith, 1885
	Mysella charcoti (Lamy, 1906)
	Neolepton umbonatum Smith, 1885
	Nucula kerguelenensis Thiele, 1912
	Palliolum clathratum Martens, 1881
	Philobrya barbata Thiele, 1912
	Philobrya kerguelenensis (Smith, 1885)
	Philobrya quadrata Thiele, 1912
	Pteria sp.
	Thracia meridionalis Smith, 1885
	Thyasira marionensis Smith, 1885
	Yoldiella profundorum Melvill & Standen, 1912
	Dosinia cf. *pubescens*
	Limopsis lilliei Smith, 1915
	Lyonsiella cf. *radiata* Dall, 1889
	Class Gastropoda
	Admete specularis (Watson, 1882)
	Amauropsis anderssoni Strebel, 1906
	Amauropsis prasina (Watson, 1881)
	Anatoma euglypta (Pelseneer, 1903)
	Balcis amblia (Watson, 1883)
	Banzarecolpus austrina (Watson, 1881)
	Brookula cf. *crassicostata* (Strebel, 1908)
	Calliostoma delli McLean & Andrade, 1982
	Cerithiella cf. *werthi* Thiele, 1912
	Cerithiopsilla sp.
	Chlanidotella modesta (Martens, 1885)
	Diaphana kerguelenensis Thiele, 1912
	Eatoniella kerguelenensis regularis (Smith, 1915)
	Eatoniella subrufescens (Smith, 1875)
	Eumetula macquariensis Tomlin, 1948
	Eumetula sp.
	Falsilunatia soluta (Gould, 1847)

	Eumetula macquariensis Tomlin, 1948
	Eumetula sp.
	Fusitriton magellanicus (Roeding, 1798)
	"Jeffreysia" edwardiensis (Watson, 1886)
	Kerguelenella lateralis (Gould, 1849)
	Laevilitorina caliginosa (Gould, 1848)
	Margarella expansa (Sowerby, 1838)
	Margarella porcellana Powell, 1951
	Marseniopsis pacifica Bergh, 1886
	Microdiscula subcanaliculata (Smith, 1875)
	Nacella delesserti (Philippi, 1849)
	Omalogyra cf. *amotus* (Philippi, 1841)
	Onoba transenna (Watson, 1886)
	Onoba paucicarinata (Ponder, 1983)
	Pareuthria regulus Watson, 1883
	Powellisetia principis (Watson, 1886)
	Probuccinum edwardiensis (Watson, 1882)
	Puncturella conica (d'Orbigny, 1841)
	Retusa sp.
	Sinezona sp.
	Skenella edwardiensis (Watson, 1886)
	Solariella infundibulum (Watson, 1879)
	Spirotropis studeriana (Martens, 1878)
	Tectonatica impervia (Philippi, 1845)
	Toledonia limnaeaeformis (Smith, 1877)
	Torellia angulifera Waren, Arnaud & Cantera, 1986
	Trophon declinans Watson, 1882
	Trophon sepus Watson, 1882
	Turbonilla lamyi Hedley, 1916
	Typhlodaphne platamodes (Watson, 1881)
	Typhlodaphne translucida (Watson, 1881)
	Balcis sp.
	Bathydomus sp.
	Prosipho sp.
	Solariella sp.
	Toledonia elata Thiele, 1912

Class Polyplacophora	
	Hemiarthrum setulosum Dall, 1876
	Lepidopleurus dorsuosus Haddon, 1886
	Lepidopleurus kerguelenensis (Haddon, 1886)
	? aff *Placiphorella* sp.
Class Scaphopoda	
	Fissidentalium sp.
Class Cephalopoda	
	Octopus magnificus Villaneuva *et al.*, 1991
PHYLUM PYCNOGONIDA	
Ammotheidae	*Cilunculus kravcovi* Pushkin, 1973
	Tanystylum cavidorsum Stock, 1957
	Tanystylum neorthetum Marcus, 1940
	Tanystylum oedinotum Loman, 1923
	Tanystylum ornatum Flynn, 1928
Austrodecidae	*Pantopipetta australis* (Hodgson, 1914)
	Austrodecus elegans Stock, 1957
	Austrodecus goughense Stock, 1957
	Austrodecus tristanense Stock, 1957
Callipallenidae	*Pseudopallene glutus* Pushkin, 1975
Pycnogonidae	*Pycnogonum platylophum* Loman, 1923
Colossendeidae	*Colossendeis megalonyx megalonyx* Hoek, 1881
Endeidae	*Endeis viridis* Pushkin, 1976
Rhynochothoracidae	*Rhynchothorax australis* Hodgson, 1907
Nymphonidae	*Nymphon gracilipes* Miers, 1875
	Nymphon longicoxa Hoek, 1881
	Nymphon sp.
PHYLUM ECHINODERMATA	
Class Asteroidea	
Order Paxillosida	
Astropectinidae	*Bathybiaster loripes* Sladen, 1889
	Leptychaster kerguelenensis Smith, 1876
Order Valvatidae	
Asterinidae	*Tremaster mirabilis* Verrill, 1879
Odontasteridae	*Acodontaster elongatus* (Sladen, 1889)
	Odontaster meridionalis (Smith, 1876)
	Odontaster penicillatus (Philippi, 1870)
	Odontaster validus Koehler, 1906

Goniasteridae	*Ceramaster patagonicus* (Sladen, 1889)
	Hippasteria hyadesi Perrier, 1891
	Hippasteria falklandica Fisher, 1940
	Pseudarchaster discus Sladen, 1889
Order Spinulosida	
Solasteridae	*Crossaster penicillatus* Sladen, 1889
	Lophaster stellans Sladen, 1889
	Solaster dianae Stampanato & Jangoux
	Solaster regularis Sladen, 1889
Pterasteridae	*Diplopteraster semireticulatus* (Sladen, 1882)
	Pteraster affinis Smith, 1876
Korethrasteridae	*Peribolaster folliculatus* Sladen, 1889
Poraniidae	*Porania antarctica* Smith, 1876
Ganeriidae	*Perknaster densus* Sladen, 1889
Echinasteridae	*Henricia fisheri* AM Clark, 1962
	Henricia sp. aff. *H. obesa* (Sladen, 1889)
	Henricia praetans (Sladen, 1889)
	Henricia sp. aff. *H. simplex* (Sladen, 1889)
	Henricia sp. aff. *H. studeri* (Perrier, 1891)
Order Forcipatulida	
Labidiasteridae	*Labidiaster annulatus* Sladen, 1889
Asteriidae	*Anasterias rupicola* (Verrill, 1876)
	Anteliaster australis Fisher, 1940
	Anteliaster scaber Smith, 1876
	Diplasterias meridionalis (Perrier, 1875)
	Pedicellaster hypernotius Sladen, 1889
	Smilasterias scalprifera (Sladen, 1889)
	Smilasterias triremis (Sladen, 1889)
Class Ophiuroidea	
Suborder Euryalina	
Asteronichidae	*Asteronyx loveni* Müller & Troschel, 1842
Gorgonocephalidae	*Astrotoma agassizi* Lyman, 1875
	Gorgonocephalus chilensis (Philippi, 1858)
Suborder Ophiomyxina	
Ophiomyxidae	*Ophioscolex (Ophiolycus) nutrix* Mortensen, 1936

Suborder Gnatophiurina	
Amphiuridae	
Amphiurinae	*Amphiura algida* Koehler, 1911
	Amphiura angularis angularis Lyman, 1879
	Amphiura antarctica Studer, 1876
	Amphiura tomentosa Lyman, 1879
Amphilepidinae	*Amphilepis* sp. aff. *A. gymnopora* Hertz, 1927
Suborder Laemophiurina	
Ophiacanthidae	*Ophiacantha imago* Lyman, 1878
	Ophiacantha rosea Lyman, 1878
	Ophiacantha vivipara Ljungman, 1870
	Ophiocymbium cavernosum Lyman, 1880
	Ophiolebes scorteus Lyman, 1878
Suborder Chilophiurina	
Ophiodermatidae	*Toporkovia antarctica* (Lyman, 1882)
Ophiuridae	
Ophiurinae	*Amphiophiura* sp.
	Ophiocten amitinum Lyman, 1878
	Ophiocten banzarei Madsen, 1964
	Ophionotus hexactis (Smith, 1876)
	Ophiophycis mirabilis Koehler, 1901
	Ophiurolepis intorta (Lyman, 1878)
	Stegophiura elevata (Lyman, 1878)
Class Echinoidea	
Suborder Echinina	
Echinidae	*Sterechinus agassizi* Mortensen, 1936
Suborder Temnopleurina	
Temnopleuridae	*Pseudechinus marionis* Mortensen, 1936
Class Holothuroidea	
Order Aspidochirotida	
Synallactidae	*Mesothuria edwardensis* Massin, 1992
	Synallactes challengeri (Théel, 1886)
Gephyrothuridae	*Pseudostichopus mollis* (Théel, 1886)
Order Dendrochirotida	
Cucumariidae	*Cucumaria kerguelensis* (Théel, 1886)
	Pseudocnus laevigatus (Verrill, 1876)
	Cladodactyla crocea croceoides (Vaney, 1908)
Psolidae	*Psolidium incertum* (Théel, 1886)
	Psolus paradubiosus Carriol & Feral, 1985

Order Apodida	
Chiridotidae	*Taeniogyrus contortus* (Ludwig, 1874)
	Paradota marionensis Massin, 1992
Class Crinoidea	
Order Comatulae	
Suborder Macrophyeata	
Antedonidae	*Phrixometra exigua* (Carpenter, 1888)
	Eumorphometra hirsuta (Carpenter, 1888)
PHYLUM ANNELIDA	
Class Polychaeta	
Order Orbiniida	
Orbiniidae	*Orbiniella dayi* (Branch)
	Leitoscoloplos kerguelensis (McIntosh, 1885)
	Scoloplos (Leodamas) marginatus (Ehlers, 1897)
	Naineris sp.
Paraonidae	*Cirrophorus lyra* (Southern, 1914)
	Paraonella sp.
Order Spionida	
Spionidae	*Boccardia polybranchia* (Haswell, 1885)
	Polydora armata Langerhans, 1881
	Rhynchospio glutaea (Ehlers, 1897)
	Scolelepis marionis Branch
	? *Spiophanes bombyx* Claparéde, 1870
	Spiophanes tcherniai Fauvel, 1951
Chaetopteridae	*Chaetopterus variopedatus* Reiner, 1804
Cirratulidae	*Tharyx* sp.
	Cirratulus sp.
	Timarete antarcticus Monro, 1930
	Cirriformia sp. recorded by Day, 1971
Order Capitellida	
Capitellidae	*Capitella 'capitata'* (Fabricius, 1780)
	Notomastus latericeus Sars, 1851
	Notomastus sp.
Arenicolidae	*Abarenicola ?assimilis* Wells, 1963
Maldanidae	*Axiothella quadrimaculata* Augener, 1914
	Lumbriclymenella robusta Arwidsson, 1911
	Maldanella antarctica McIntosch, 1885
	Nichomache lumbricalis Fabricius, 1780

Order Opheliida	
Opheliidae	*Ammotrypane breviata* Ehlers, 1913
	Travisia kerguelensis McIntosch, 1885
Scalibregmidae	*Scalibregma inflatum* Rathke, 1843
Order Flabelligerida	
Flabelligeridae	? *Brada mammillata* Grube, 1877
	Flabelligera induta Ehlers, 1897
Order Terebellida	
Pectinariidae	*Petta assimilis* McIntosch, 1885
Ampharetidae	*Ampharete kerguelensis* McIntosch, 1885
	Anobothrus patagonicus (Kinberg, 1867)
Terebellidae	
Polycirrinae	*Polycirrus hamiltoni* Benham, 1921
	Polycirrus kerguelensis (McIntosch, 1885)
Thelepinae	*Thelepus extensus* Hutchings & Glasby, 1987
Amphitritinae	*Lanice marionensis* Branch
	Nicolea venustula (Montagu, 1818)
	Neoleprea streptochaeta (Ehlers, 1897)
	Axionice godfroyi (Gravier, 1911)
Trichobranchidae	*Terebellides stroemii kerguelensis* McIntosch, 1885
Sabellidae	
Fabriciinae	*Oriopsis limbata* (Ehlers, 1897)
Sabellinae	*Perkinsiana antarctica* (Kinberg, 1867)
Serpulidae	
Filograninae	*Protula tubularia tubularia* (Montagu, 1803)
Serpulinae	*Serpula vermicularis vermicularis* Linnaeus, 1767
Spirorbidae	*Helicosiphon platyspira* Knight-Jones, 1978
	Leodora perrieri (Caullery & Mesnil, 1897)
	Romanchella inventis (Harris, 1969)
	Paralaeospira levinseni (Caullery & Mesnil, 1897)
	Spirorbis patagonicus Day, 1971
Order Phyllodocida	
Suborder Phyllodociformia	
Phyllodocidae	*Genetyllis polyphylla* (Ehlers, 1897)
	Steggoa magalaensis (Kinberg, 1866)
	? *Steggoa hunteri* (Benham, 1921)
	? *Eteone aurantiaca* Smarda, 1861

Suborder Aphroditiformia	
Aphroditidae	*Laetmonice producta* Grube, 1877
Polynoidae	
Lepidonotinae	*Admetella longipedata* McIntosch, 1885
	Eulagisca corrientis McIntosch, 1885
Harmothoinae	*Eucrantis mollis* (McIntosch, 1876)
	Harmothoe crosetensis (McIntosch, 1885)
	Harmothoe magellanica (McIntosch, 1885)
	Harmothoe spinosa Kinberg, 1855
	Harmothoe ?kerguelensis
	Lagisca exanthema (Grube, 1856)
	Malmgreniella fimbria Branch
	Polyeunoa laevis McIntosch, 1885
Suborder Nereidiformia	
Hesionidae	? *Hesione* sp.
	Kefersteinia fauveli Averincev 1972
Syllidae	*Autolytus* sp. cf. *A. simplex* (Ehlers, 1900)
Exogoninae	*Exogone heterosetosa* McIntosch, 1885
	Brania rhopalophora (Ehlers, 1897)
Syllinae	*Pionosyllis nutrix* Munro, 1936
	Pionosyllis cf. *ehlersiaeformis* Augener, 1913
	Typosyllis 'variegata' (Grube, 1860)
Eusyllinae	*Amblyosyllis granosa* Ehlers, 1897
	Typosyllis sp.
	? *Pharyngeovalvata natalensis* Day, 1951
	Eusyllis blomstrandi Malmgren, 1867
	Eusyllis kerguelensis McIntosch, 1885
Nereididae	? *Neanthes kerguelensis* (McIntosch, 1885)
	Platynereis australis Smarda 1861
	Pseudoneries anomalia Gravier, 1901
Suborder Glyceriformia	
Glyceridae	*Glycerella magellanica* (McIntosch, 1885)
	Glycera kerguelensis McIntosch, 1885
	Protodorvillea kefersteini (McIntosch, 1869)
Goniadidae	*Goniada brunnea* (Treadwell, 1906 revised Moore, 1911)
Nephtyidae	*Aglaophamus ornatus* Hartman, 1967
Order Amphinomida	
Eophrosinidae	*Euphrosine cirrata* Sars, 1862

Order Eunicida	
Eunicidae	*Eunice pennata* (Muller, 1776)
	? *E. edwardsi* (McIntosch, 1885)
Onuphidae	*Nothria anoculata* Orensanz, 1974
Lumbrineridae	*Lumbrinereis* sp. aff. *L. fragilis*
	? *Lumbrinereis heteropoda* Marenzeller, 1879
PHYLUM COELENTERATA	
Class Hydrozoa	
Tubulariidae	*Tubularia* sp.
Myriothelidae	*Myriothela meridiana* Briggs, 1939
Corynidae	? *Coryne conferta* Allman, 1877
Bongainvilliidae	*Rhizorbagium antarcticum* (Hickson & Gravely)
Hydractiniidae	*Hydractinia parvispina* Hartlaub, 1905
Campanulariidae	*Campanularia subantarctica* n. sp. Millard
	Obelia geniculata (Linnaeus, 1758)
	Silicularia rosea Meyen, 1834
Sertulariidae	*Sertularella picta* (Meyen, 1834)
	Symplectoscyphus marionensis n. sp.
	Symplectoscyphus sp.
PHYLUM BRYOZOA	
Bitectiporidae	*Parkermavella corrugata* Branch & Hayward, 2005
Buffonellodidae	*Ipsibuffonella hyalina* Branch & Hayward, 2005
Bugullidae	*Cornucopina antlera* Branch & Hayward, 2005
	Cornucopina bryonyae Branch & Hayward, 2005
	Cornucopina elongata Branch & Hayward, 2005
Calloporidae	*Pyriporoides judyae* Branch & Haward, 2005
	Valdemunitella dianae Branch & Hayward, 2005
Catenicellidae	*Catenicella glabrosa* Branch & Hayward, 2005
	Talivittaticella frigida (Waters, 1904)
Cellariidae	*Paracellariae elizabethae* Branch & Hayward, 2005
Cribrilinidae	*Filaguria lithocrustata* Branch & Hayward, 2005
Hippothoidae	*Celleporella marionensis* Branch & Hayward, 2005
Lacernidae	*Phonicosia jousseaumei* Jullen, 1888
Microporellidae	*Calloporina spinosa* Branch & Hayward, 2005
	Fenestrulina pumicosa Branch & Hayward, 2005
	Microporella mandibulata Branch & Hayward, 2005
Phidoloporidae	*Reteporella gigantea* (Busk, 1884)
	Reteporellina berylae Branch & Hayward, 2005
Sclerodomidae	*Sclerodomus myriozoides* (Busk, 1884)

APPENDIX X

MARINE FISH OF THE PRINCE EDWARD ISLANDS REGION

EVGENY A. PAKHOMOV

The table below provides a list of the species caught in the vicinity of the Prince Edward Islands. Symbols are as follows: *: new records added to Gon & Klages (1988) by Pakhomov *et al.* (2001), **: fish collected during April/May 2003 survey near Marion Island (E.A. Pakhomov unpublished). Typical habitat of the group is shown in brackets next to the family: M: mesopelagic, E: epipelagic, B: benthic, BP: benthopelagic, EB: epibenthic (according to Gon & Heemstra 1990; Eastman 1993).

References

Eastman, J.T. 1993. *Antarctic Fish Biology. Evolution in a Unique Environment*. Academic Press, London, pp. 1-322.

Gon, O. & Klages, N.T.W. 1988. The marine fish fauna of the sub-Antarctic PEI. *South African Journal of Antarctic Research* **18**, 32-54.

Gon, O. & Heemstra, P.C. (Eds.) 1990. *Fishes of the Southern Ocean*. JLB Smith Institute of Ichthyology, Grahamstown, pp. 1-462.

Pakhomov, E.A., Froneman, P.W. & McQuaid, C.D. 2001. The Prince Edward Island's Life-Support System and the Variability of Living Resources in the Southern Ocean. *South African National Antarctic Research Program (SANARP)*, Final Project Report, Pretoria, South Africa, pp. 1-53.

Pakhomov, E.A., Bushula, T., Kaehler, S., Watkins, B.P. & Leslie, R.W. 2006. Structure and distribution of the slope fish community in the vicinity of the sub-Antarctic Prince Edward Archipelago. *Journal of Fish Biology* **68**, 1834-1866.

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 431-434

Taxa	Gon & Klages (1988) Pakhomov *et al.* (2001)	*IBIS* survey Pakhomov *et al.* (2005)
Myctophidae (M)		
Protomyctophum bolini	+	
Protomyctophum normani	+	
Protomyctophum choriodon	+*	
Protomyctophum tenisoni	+	
Protomyctophum sp.		+
Gymnoscopelus nicholsi	+	
Gymnoscopelus braueri	+*	+
Gymnoscopelus bolini	+	+
Gymnoscopelus hintinoides	+*	
Gymnoscopelus opistopterus	+*	
Gymnoscopelus piabilis		+
Gymnoscopelus fraseri		+
Gymnoscopelus sp.		+
Krefftichthys anderssoni	+	
Electrona subaspera	+	
Electrona carsbergi	+	
Electrona sp.		+
Diaphus sp.	+	
Lampanyctus intricarius		+
Lampanyctus achirus		+
Gonostomatidae (M)		
Vincigueria attenuata	+*	
Dyplophos rebainsi	+*	
Photichthys argenteus		+
Cyclothone sp.		+
Alepisauridae (M)		
Alepisaurus brevirostris	+	+
Stomiidae (M)		
Stomias boa boa	+*	+
Borostomias antarcticus		+
Idiacanthus atlanticus		+
Trigonolampa miriceps		+
Chauliodus sloani		+
Malacosteus niger		+

Scopelarchidae (M)		
Benthalbella macropinna		+
Scopelosaurus hamiltoni		+
Paralepididae (M)		
Magnisudis prionosa	+	+
Stemonosudis sp.	+*	
Notolepis sp.		+
Macroparalepis sp.		+
Centrolophidae (E)		
Icichthys australis		+
Centrolophidae gen sp.		+
Ceratiidae (M)		
Ceratias tentaculatus		+
Carapidae (B?)		
Echiodon cryomargarites	+*	+
Congiopodidae (B)		
Zanclorhynchus spinifer	+	+
Rajidae (B)		
Bathyraja tuff		+
Raja barnardi	+*	
Raja sp.	+*	
Archiropsettidae (B)		
Mancopsetta maculata	+	+
Mancopsetta milfordi	+	+
Pseudomancopsetta andriashevi	+	+
Exocoetidae (E?)		
Cheilopogon pinnatibarbatus altipennis	+	
Nototheniidae (B)		
Lepidonotothen larseni	+	+
Notothenia rossi	+	
Notothenia coriiceps	+	
Notothenia acuta	+	
Paranotothenia magellanica	+	+**
Gobionotothen marionensis	+	+**
Lepidonotothen squamifrons	+	+
Disssostichus eleginoides	+	+
Channichthyidae (B)		
Channichthys rhinoceratus	+	
Harpagiferidae (B)		
Harpagifer georgianus	+	

Macrouridae (BP)		
Macrourus holotrachys	+	
Macrourus carinatus		+
Coryphaenoides sp.		+
Macrouridae gen sp.		+
Moridae (B)		
Antimora rostrata	+	+
Laemonema kongi	+	+
Halargyreus johnsonii		+
Lepidion sp.	+	
Muraenolepididae (B)		
Muraenolepis marmoratus	+	+**
Muraenolepis orangiensis	+	
Alepocephalidae (EB)		
Alepocephalus sp.		+
Anotopteridae (E)		
Anotopterus pharao		+
Astronesthidae (M)		
Astronesthes boulengeri		+
Bathylagidae (M)		
Bathylagus tenuis		+
Chiasmodontidae (BP?)		
Dysalotus cf. alcock	+	
Chiasmodon niger		+
Halosauridae (BP)		
Halosauropsis macrochir		+
Liparididae (B)		
Liparididae gen. sp.		+
Melamphaidae (M)		
Poromitra crassiceps		+
Melamphaidae gen sp.		+
Gempylidae (BP)		
Paradiplospinus glacilis		+
Gadidae (B)		
Physiculus sp.		+
Platytroctidae (M)		
Platytroctidae gen. sp.		+
Notacanthidae (BP)		
Polyacanthonotus challengeri		+

APPENDIX XI

BIRDS RECORDED AT THE PRINCE EDWARD ISLANDS

PETER G. RYAN

The species reported at the Prince Edward Islands (*indicates species that have been seen ashore), is given as well as the total annual breeding population (in numbers of birds) where this is known.

Family	Species	Status/ population
Anatidae	Kerguelen Pintail *Anas eatoni*	Vagrant*
Cuculidae	Common Cuckoo *Cuculus canorus*	Vagrant*
Apodidae	Common Swift *Apus apus*	Vagrant*
Columbidae	Cape Turtle Dove *Streptopelia capicola*	Vagrant*
	European Turtle Dove *Streptopelia turtur*	Vagrant*
	Laughing Dove *S. senegalensis*	Vagrant*
Rallidae	Corncrake *Crex crex*	Vagrant*
Scolopacidae	Whimbrel *Numenius phaeopus*	Vagrant*
	Common Greenshank *Tringa nebularia*	Vagrant*
	Wood Sandpiper *T. glareola*	Vagrant*
	Terek Sandpiper *Xenus cinereus*	Vagrant*
	Common Sandpiper *Actitis hypoleucos*	Vagrant*

S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 435-437

Scolopacidae (continued)	Ruddy Turnstone *Arenaria interpres*	Vagrant*
	Pectoral Sandpiper *Calidris melanotis*	Vagrant*
	Curlew Sandpiper *C. ferruginea*	Vagrant*
	Little Stint *C. minuta*	Vagrant*
	Red Phalarope *Phalaropus fulicaria*	Rare
Chionidae	Lesser Sheathbill *Chionis minor marionensis*	4 000
Charadridae	Common Ringed Plover *Charadrius hiaticula*	Vagrant*
	Three-banded Plover *C. tricollaris*	Vagrant*
	Blacksmith Lapwing *Vanellus armatus*	Vagrant*
Laridae	Sub-Antarctic Skua *Catharacta antarctica lonnbergi*	1 700
	Parasitic Jaeger *Stercorarius parasiticus*	Rare
	Kelp Gull *Larus dominicanus*	260
	Lesser Black-backed Gull *L. fuscus*	Vagrant*
	Franklin's Gull *L. pipixcan*	Vagrant*
	Sabine's Gull *L. sabini*	Rare
	Arctic Tern *Sterna paradisaea*	Rare*
	Antarctic Tern *Sterna vittata*	60
	Kerguelen Tern *Sterna virgata*	110
Falconidae	Unidentified falcon *Falco* sp.	Vagrant*
Sulidae	Australasian Gannet *Morus serrator*	Vagrant*
Phalacrocoracidae	Crozet Shag *Phalacrocorax melanogenis*	640
Ciconiidae	White Stork *Ciconia ciconia*	Vagrant*
Ardeidae	Cattle Egret *Bubulcus ibis*	Vagrant*
	Yellow-billed Egret *Egretta intermedia*	Vagrant*
Spheniscidae	King Penguin *Aptenodytes patagonicus*	446 000
	Gentoo Penguin *Pygoscelis papua*	3 000
	Chinstrap Penguin *P. antarctica*	Vagrant*
	Macaroni Penguin *Eudyptes chrysolophus*	750 000
	Southern Rockhopper Penguin *E. chrysocome filholi*	224 000
Hydrobatidae	Wilson's Storm Petrel *Oceanites oceanicus*	Common
	Grey-backed Storm Petrel *Garrodia nereis*	2 000
	Black-bellied Storm Petrel *Fregetta tropica*	10 000
Diomedeidae	Wandering Albatross *Diomedea exulans*	7 300
	Southern Royal Albatross *D. epomophora*	Regular
	Northern Royal Albatross *D. sanfordi*	Rare
	Shy Albatross *Thalassarche cauta*	Fairly common
	Salvin's Albatross *T. salvini*	Rare
	Black-browed Albatross *T. melanophrys*	Common*
	Grey-headed Albatross *T. chrysostoma*	21 800
	Yellow-nosed Albatross *T. carteri*	15 000

Diomedeidae (continued)	Light-mantled Sooty Albatross *Phoebetria palpebrata*	700
	Dark-mantled Sooty Albatross *P. fusca*	4 400
Procellariidae	Southern Giant Petrel *Macronectes giganteus*	5 500
	Northern Giant Petrel *Macronectes halli*	1 300
	Southern Fulmar *Fulmarus glacialoides*	Fairly common
	Antarctic Petrel *Thalassoica antarctica*	Vagrant
	Pintado Petrel *Daption capense*	Common
	Great-winged Petrel *Pterodroma macroptera*	40 000
	White-headed Petrel *P. lessonii*	Fairly common*
	Soft-plumaged Petrel *P. mollis*	30 000
	Kerguelen Petrel *Lugensa brevirostris*	40 000
	Blue Petrel *Halobaena caerulea*	300 000
	Fairy Prion *Pachyptila turtur*	4 000
	Slender-billed Prion *P. belcheri*	Fairly common
	Antarctic Prion *P. desolata*	Fairly common
	Salvin's Prion *P. salvini*	700 000
	Grey Petrel *Procellaria cinerea*	12 000
	White-chinned Petrel *P. aequinoctialis*	30 000
	Cory's Shearwater *Calonectris diomedea*	Rare
	Great Shearwater *Puffinus gravis*	Rare
	Sooty Shearwater *P. griseus*	Fairly common
	Little Shearwater *P. asimilis*	Fairly common
	South Georgian Diving Petrel *Pelecanoides georgicus*	11 000
	Common Diving Petrel *P. urinatrix*	20 000
Laniidae	Red-backed Shrike *Lanius collurio*	Vagrant*
Hirundinidae	Brown-throated Martin *Riparia paludicola*	Vagrant*
	Barn Swallow *Hirundo rustica*	Vagrant*
	Common House Martin *Delichon urbica*	Vagrant*
Sylviidae	Willow Warbler *Phylloscopus trochilus*	Vagrant*
	Common Whitethroat *Sylvia communis*	Vagrant*
Muscicapidae	Unidentified flycather *Muscicapa* (*striata*?)	Vagrant*
	Mountain Wheatear *Oenanthe monticola*	Vagrant*
Passeridae	House Sparrow *Passer domesticus*	Ship-assisted*
Motacillidae	Yellow Wagtail *Motacilla flava*	Vagrant*

APPENDIX XII

MAMMALS RECORDED AT THE PRINCE EDWARD ISLANDS

MARTHÁN N. BESTER

The terrestrial and pelagic species reported at the Prince Edward Islands are listed here. Several other species are known from historical records, including the domestic dog, sheep, and feral cats. The latter were eradicated following an intensive programme that ran for several years and included hunting, trapping, poisoning, and the use of disease (Bester *et al.* 2000, 2002). A long-standing debate concerning the subspecies of the house mouse found on Marion Island was recently resolved (Jansen Van Vuuren & Chown 2007).

References

Bester, M.N., Bloomer, J.P., Bartlett, P.A., Muller, D.D., Van Rooyen, M. & Büchner, H. 2000. Final eradication of feral cats from sub-Antarctic Marion Island, southern Indian Ocean. *South African Journal of Wildlife Research* **30**, 53-57.

Bester, M.N., Bloomer, J.P., Van Aarde, R.J., Erasmus, B.H., Van Rensburg, P.J.J., Skinner, J.D., Howell, P.G. & Naudé, T.W. 2002. A review of the successful eradication of feral cats from sub-Antarctic Marion Island, Southern Indian Ocean. *South African Journal of Wildlife Research* **32**, 65-73.

Jansen van Vuuren, B. & Chown, S.L. 2007. Genetic evidence confirms the origin of the house mouse on sub-Antarctic Marion Island. *Polar Biology* **30**, 327-332.

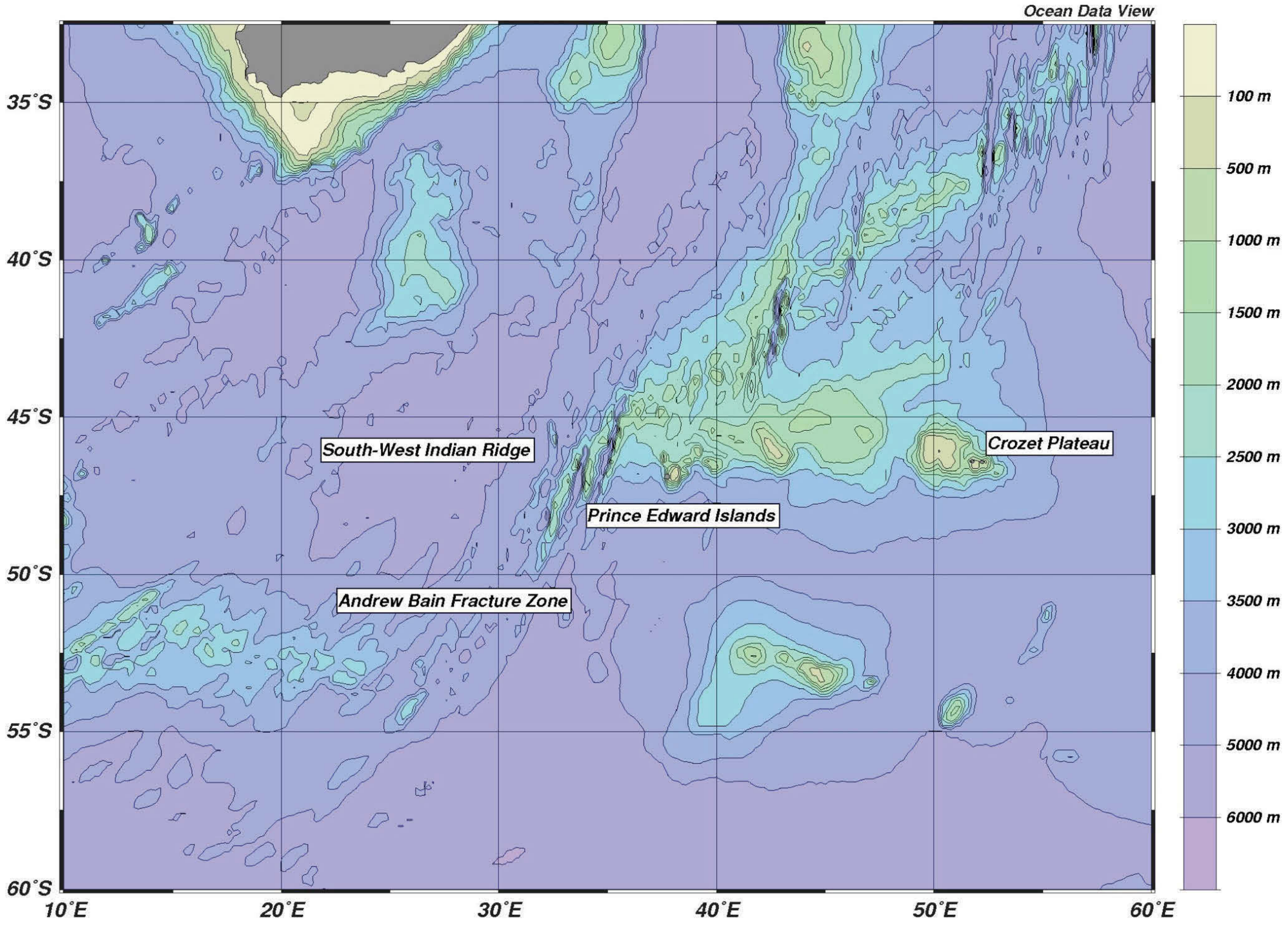
S.L. Chown & P.W. Froneman (eds.) The Prince Edward Islands • Land-Sea Interactions in a Changing Ecosystem, 438-439

Pelagic species		
Order Cetacea	*Balaena australis*	
	Balaenoptera musculus	
	Globicephala melas	
	Lagenorhynchus cruciger	
	Lagenorhynchus obscurus	
	Lissodelphis peronii	
	Mesoplodon layardii	
	Orcinus orca	
	Physeter macrocephalus	
Order Carnivora	*Arctocephalus gazella*	
	Arctocephaulus pusillus pusillus	Vagrant
	Arctocephalus tropicalis	
	Hydrurga leptonyx	Vagrant
	Leptonychotes weddellii	Vagrant
	Mirounga leonina	
Terrestrial species		
	Mus musculus domesticus	(only on Marion Island)

INDEX

PLATES

PLATE 2.1: A portrayal of the bottom topography of the ocean environment of the Prince Edward Islands. The islands lie on a peak in the lee of the South-West Indian Ridge that runs from the south-west to the north-east through this figure. The ridge forms by far the most marked bathymetric feature of the region. Note the distinct gap in this ridge at about 50° S at the Andrew Bain Fracture Zone.



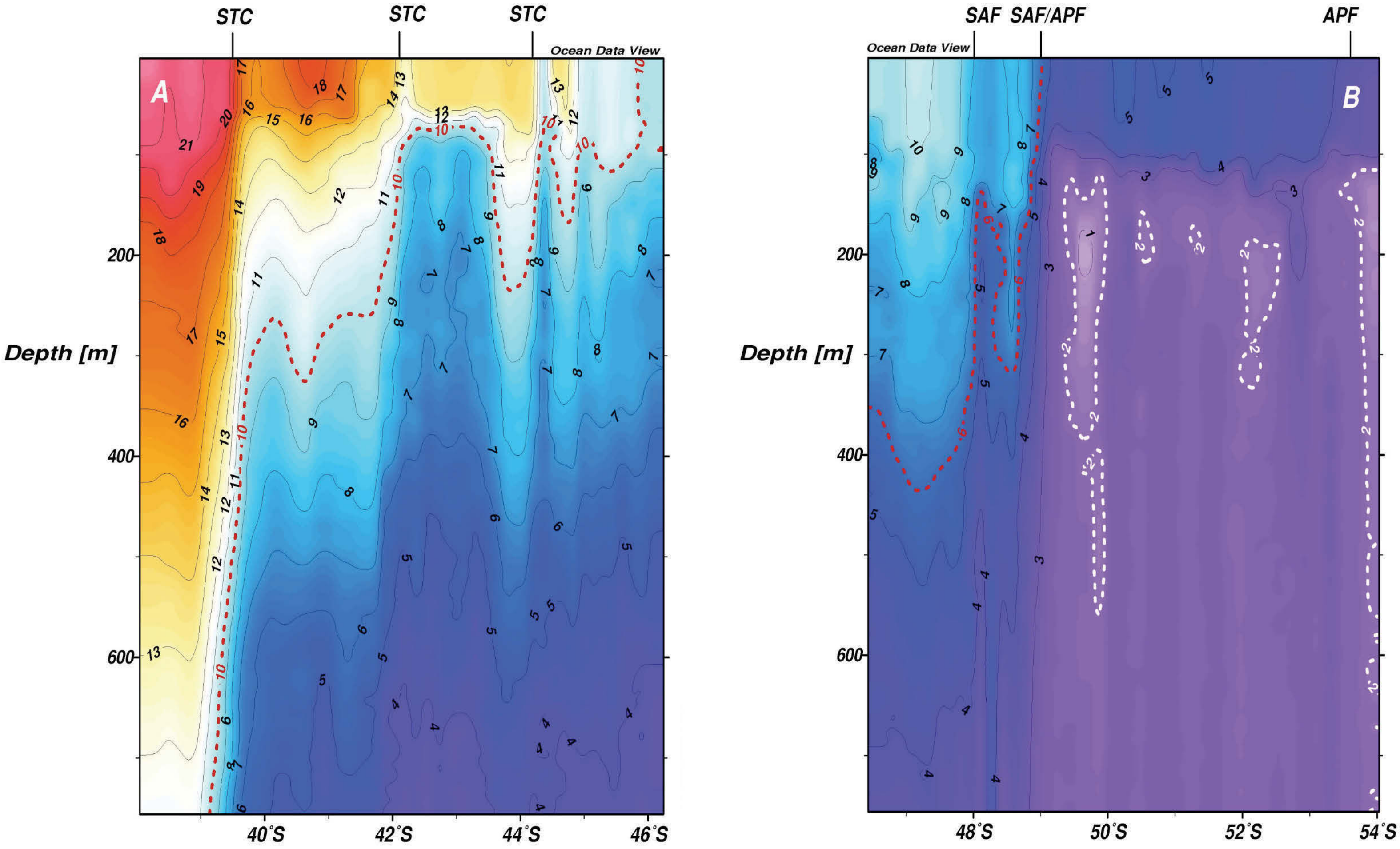
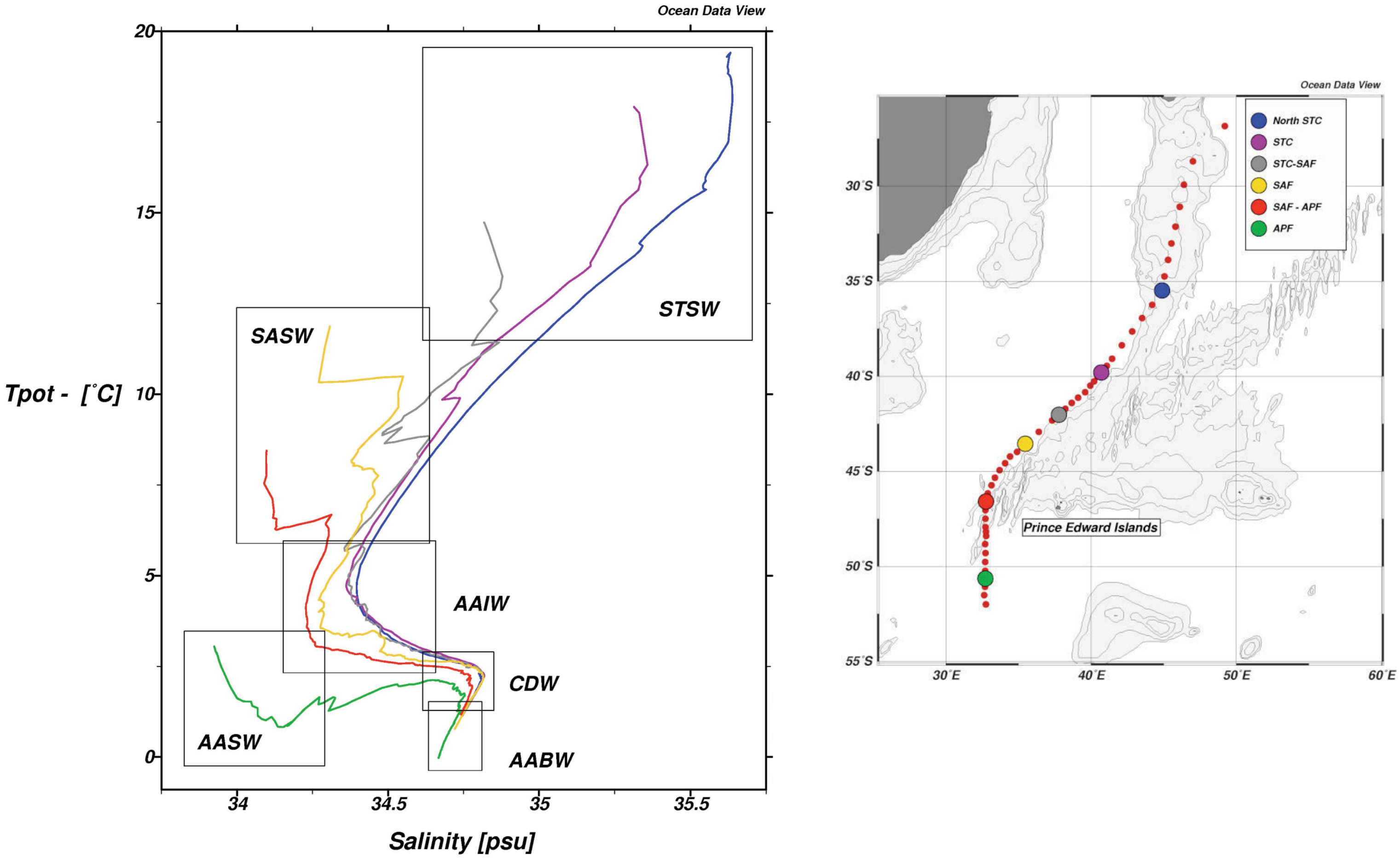


PLATE 2.2: Characteristic thermal structures of the three main fronts in the oceans surrounding the Prince Edward Islands. A) The right-hand panel represents a meridional section across the Subtropical Convergence north of the islands. B) The left-hand panel is a similar vertical temperature section intersecting also the sub-Antarctic Front just equatorward of the islands as well as the Antarctic Polar Front directly south of the islands. The structure of these fronts is not unchanging; detail of the range of variability at the sea surface is given in Table 2.2.

PLATE 2.3: Temperature-salinity (*TS*) characteristics of the water masses in the general vicinity of the Prince Edward Islands. Curves are given with increasing latitude south. The blue trace represents water north of the Subtropical Convergence, i.e. in the Subtropics (see Figs 2.1, 2.3 for location of fronts); purple, represents a *TS* profile typical of the Subtropical Convergence; grey, water between the Subtropical Convergence and the sub-Antarctic Front, i.e. in the sub-Antarctic; yellow, represents a *TS* profile typical of the sub-Antarctic Front; red, water between the sub-Antarctic Front and the Antarctic Polar Front, i.e. still in the sub-Antarctic and green, water south of the Antarctic Polar Front, i.e. in the Antarctic zone.



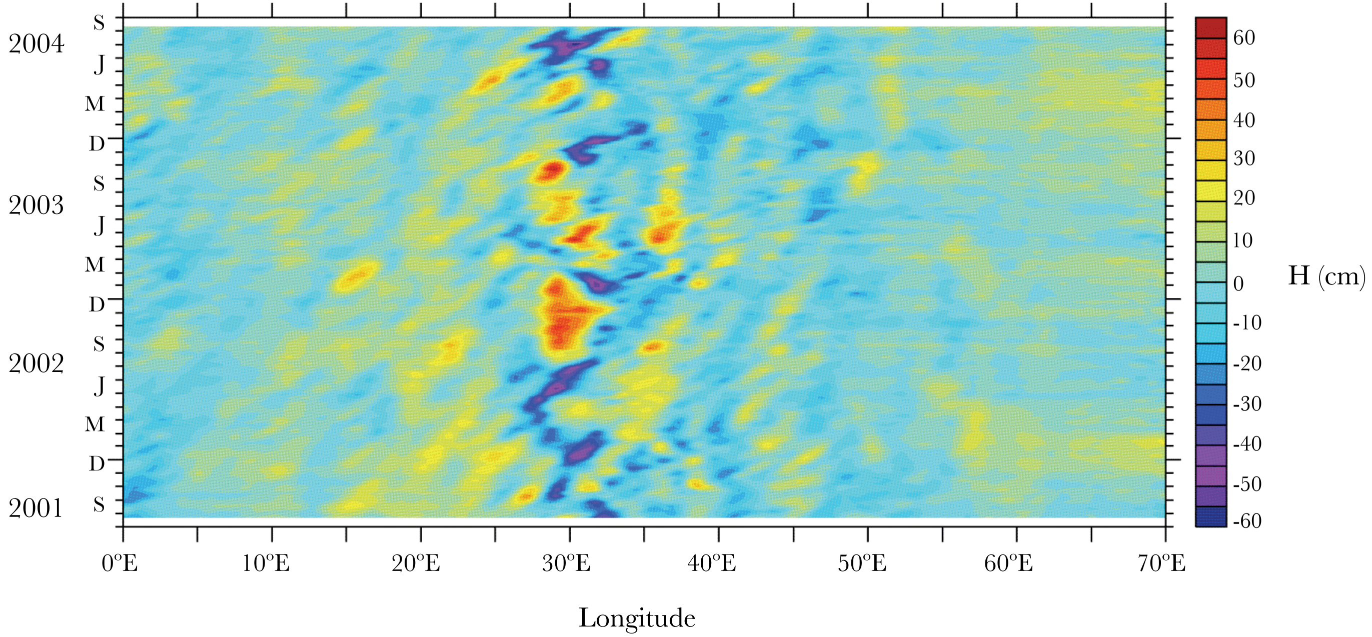
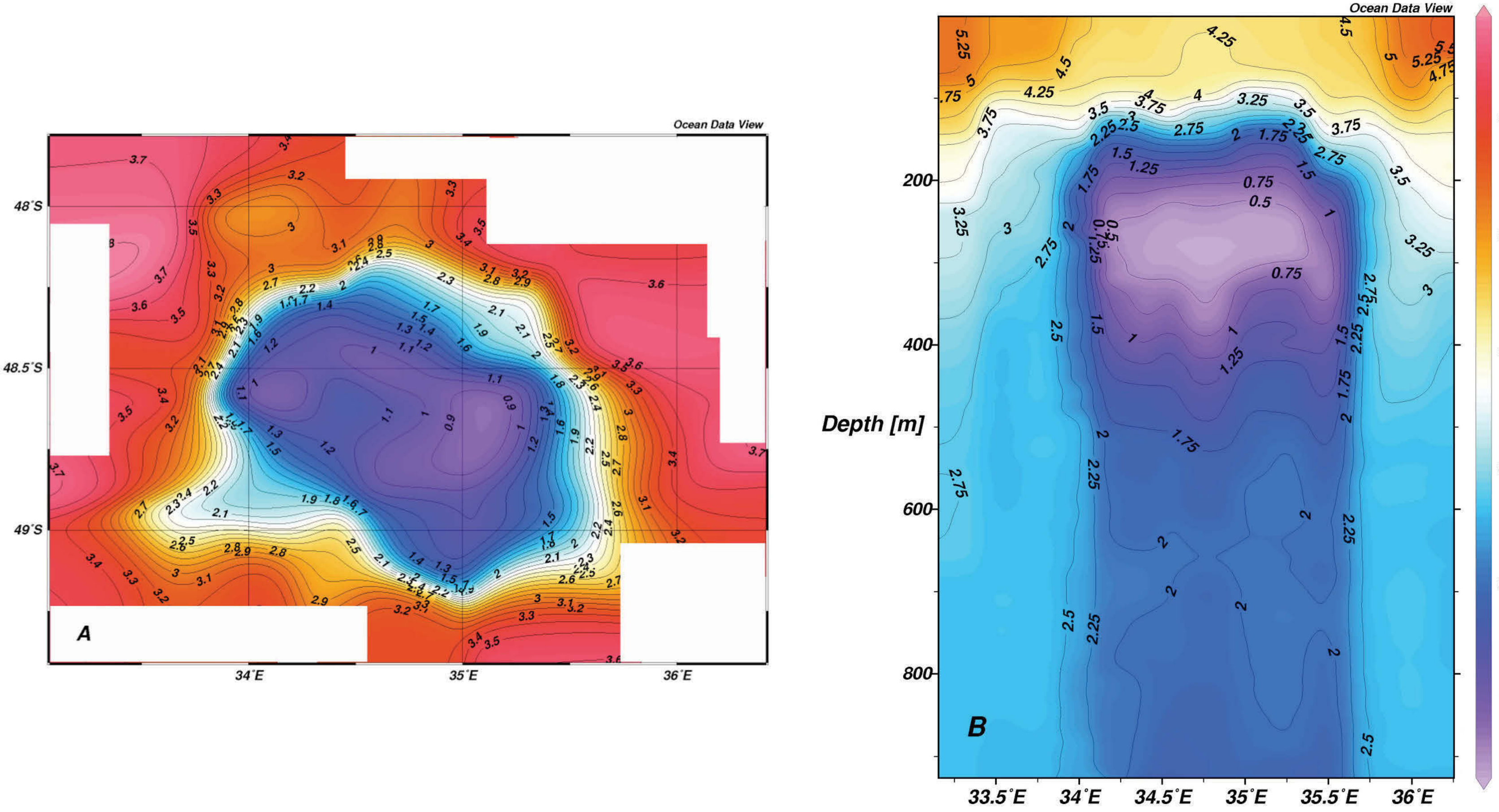


PLATE 2.4: The degree of variation in sea surface height for the ocean regions around the Prince Edward Islands. Regions of high variability (red) indicate where there are the greatest changes in the mean flow patterns. These may be due to meanders in currents, shedding of mesoscale eddies or changes in velocity of currents. Values are given in cm on the scale on the right. Note the unusual area of high mesoscale turbulence south-west of the Prince Edward Islands, centred on the Andrew Bain Fracture Zone in the South-West Indian Ridge (see also Plate 2.1).

PLATE 2.5: Hydrographic characteristics of a characteristic eddy that had an impact on the Prince Edward Islands (after Ansorge & Lutjeharms 2006). The upper panel shows a lateral view of the eddy A); the lower panel a vertical temperature section through the eddy B).



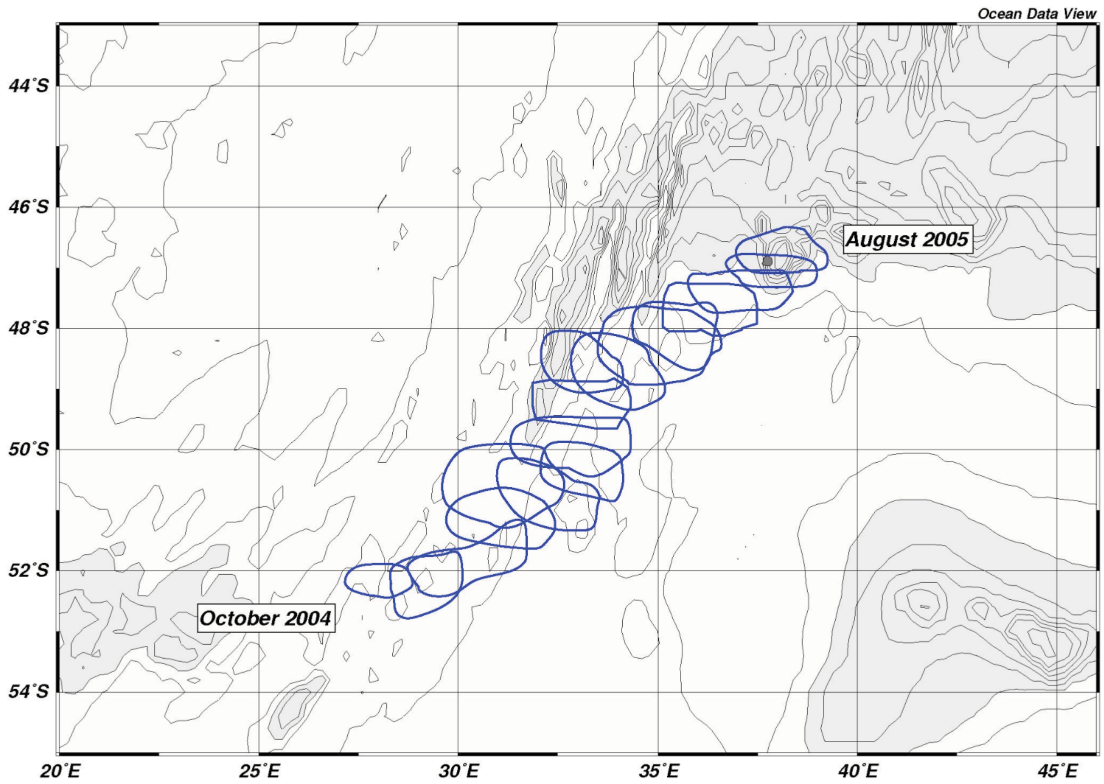


PLATE 2.6: The track of an eddy that travelled, quite characteristically, from the South-West Indian Ridge past the Prince Edward Islands (after Ansorge & Lutjeharms 2006). The eddy could be followed using its characteristic sea surface height anomaly. The dimension of the eddy is given by the blue lines for the period October 2004 to August 2005 after which it rapidly dissipated and was no longer in evidence as an anomaly in the sea height. The bottom topography is given in steps of 1 000 m and may be compared to that portrayed in Plate 2.1.

PLATE 9.1: Northern coastal plain of Marion Island. A mosaic of Mire Complex and Slope Complex habitats. The dull straw-coloured patches are Wet and Dry mires, the brighter coloured areas in the foreground are Drainage Line Mires. The dark slopes are Closed Fernbrake.

PLATE 9.2: Drainage Line Mire dominated by the grass *Agrostis magellanica* and the moss *Breutelia integrifolia*.

PLATE 9.3: Closed Fernbrake on a slope, and Dry Mire on the level area below the slope. The fernbrake comprises a dense carpet of the fern *Blechnum penna-marina* and the Dry Mire is dominated by the same fern and also the grass *Agrostis magellanica*. The fern fronds are clearly distinguishable at lower right.

PLATE 9.4: In the foreground is Mesic Fellfield dominated by green-brown cushions of *Azorella selago*. Behind the fellfield are mire communities (yellow-brown) and Closed Fernbrake slopes.

PLATE 9.5: Mesic Fellfield dominated by *Azorella selago* cushions in which the grass *Agrostis magellanica* is rooted. Smaller, shiny-green cushions (e.g. front left) are the moss *Ditrichum strictum* and the very small red cushions are *Andraea acuminata*.

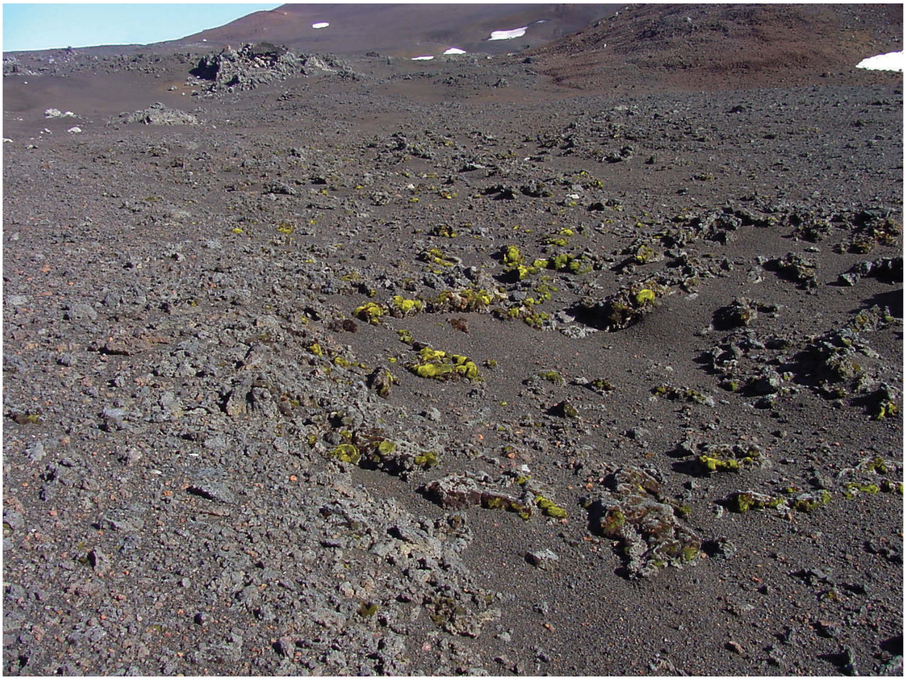


PLATE 9.6: Polar Desert at about 800 m a.s.l. on Marion Island. The yellow-green or olive-green moss cushions are *Ditrichum strictum* and *Valdonia microcarpa* and the small, dark red/black cushions are *Andraea* species.

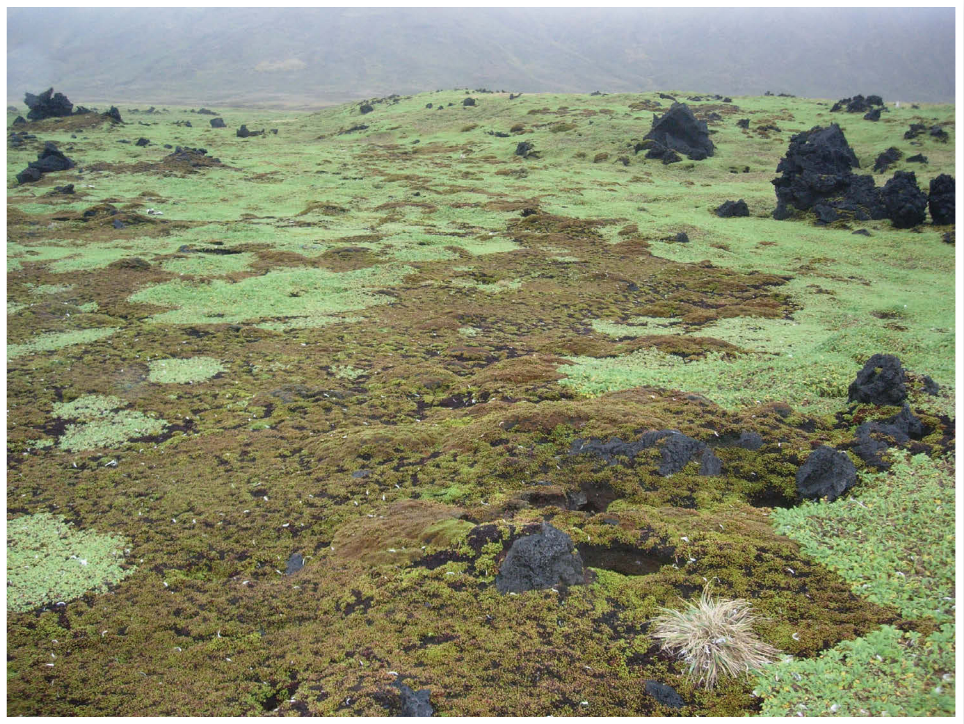


PLATE 9.7: Saltspray influenced Coastal Herbfield dominated by reddish *Crassula moschata* and light green *Cotula plumosa*.

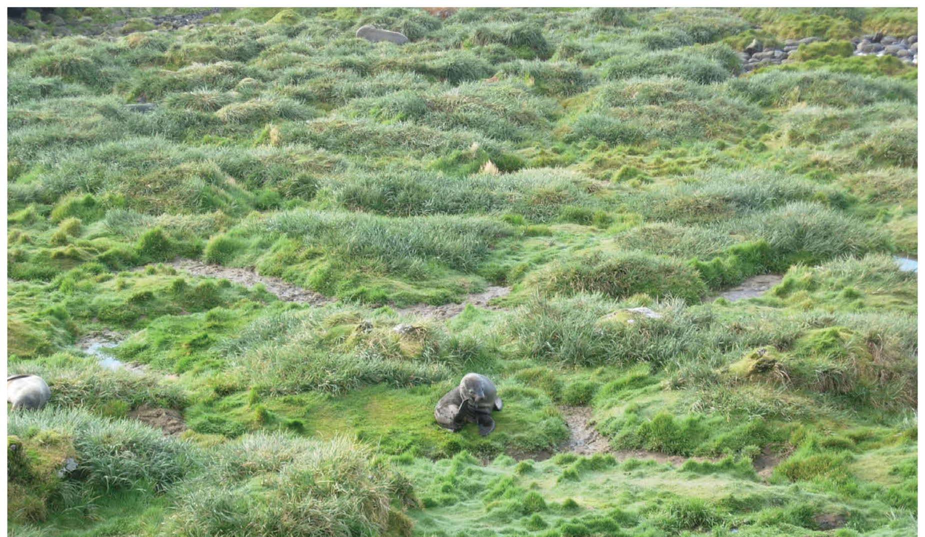


PLATE 9.8: Mosaic of Biotic Mud (right and left front), Biotic Lawn (most of foreground, e.g. where the Fur seal is sitting) and Coastal Tussock Grassland (mostly towards the back of the photograph) habitats.

a)

b)

c)

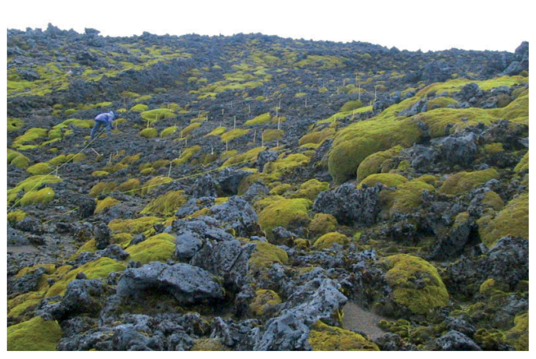


PLATE 10.1: *Azorella selago* cushion plant with epiphytic grass, *Agrostis magellanica* a). The matchbox measures 52 x 37 x 19 mm. Grey b) and c) black lava xeric fellfield habitats. Exposed d) and shaded e) leaves forming cushion surface (le Roux 2004; le Roux & McGeoch 2004). f) Polycarbonate rainout-shelter used to investigate the consequences of further reductions in rainfall on *Azorella selago* and its invertebrate community (le Roux *et al.* 2005; McGeoch *et al.* 2006).

PLATE 12.1: The eradication of an isolated stand of Quackgrass *Elymus repens* began in 2006. Here, Suzanne Kritzinger-Klopper sprays the stand with herbicide.

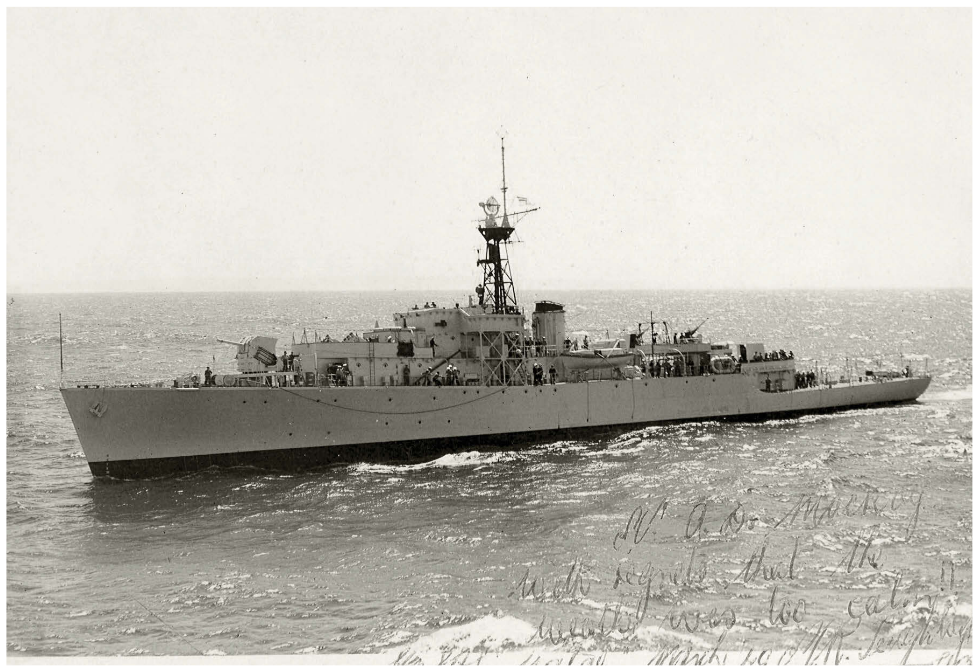
PLATE 12.2: The "Boot-washing Ceremony" held aboard the *S.A. Agulhas* is one of the quarantine measures in place to prevent alien species introductions to the Prince Edward Islands.

PLATE 12.3: In 2004, the deaths of approximately 2 000 Macaroni Penguins *Eudyptes chrysolophus* at the Kildalkey Bay colony on Marion Island was probably due to infection with Avian Cholera *Pasteurella multocida*. The strips of bare ground are the parts of the colony which were most affected. Two carcasses are visible in the foreground of the photograph.

PLATE 12.4: A team of volunteers poses with a pile of stone chips collected at the water supply dam on Marion Island, as part of a "country cleanup."

PLATE 12.5: Watertunnel field hut toilet.

PLATE 12.6: A Wandering Albatross *Diomedea exulans* protects its chick as its identification band is checked.



Mr A. D. Mackay
with regrets that the
weather was too calm!!

PLATE 13.1: *HMSAS Natal*, photographed here in March 1949, with a note presumably from the photographer '*With regrets that the weather was too calm!!*'. The *HMSAS Natal* was one of the frigates used during the annexation of the Prince Edward Islands.

PLATE 13.2: An as yet unidentified group of men during the early years of occupation of Marion Island.

PLATE 13.3: An early store built on Boulders Beach. The first two lines of writing on the wooden planks are '*Met Officer, Snoektown*'. 'Snoektown' was the code name for the annexation operation.

PLATE 13.4: An early photograph of Joseph Daniels's grave.

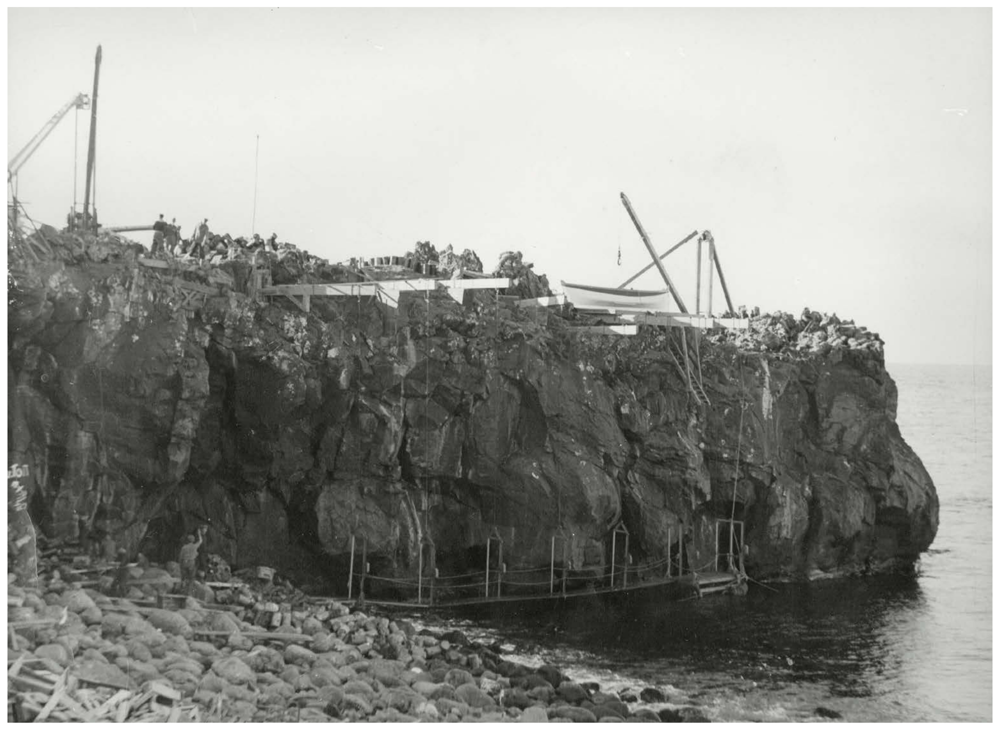


PLATE 13.5: The system used initially for getting men ashore at Marion Island. The platform could be lifted when seas were rough.

PLATE 13.6: The first store at Marion Island. The reverse of the photograph has the handwritten words '*Stores Depot Marion Island Early 1948*'.