

Alien species and propagules in the Antarctic: movements through space and time

by

Jennifer Elizabeth Lee

*Submitted in partial fulfilment for the degree
Doctor of Philosophy in Zoology*

at

Stellenbosch University



Department of Botany and Zoology
Faculty of Science

Supervisor: Prof. Steven L. Chown

Date: October 2008

Declaration

By submitting this thesis electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the owner of the copyright thereof (unless to the extent explicitly otherwise stated) and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Jennifer E. Lee

Date: 4 February 2009

Acknowledgments

I thank Steven Chown whose boundless enthusiasm for science and passion for the Antarctic were an inspiration to me throughout this PhD. This body of work has benefited immeasurably because of his input and guidance.

Thanks to my family who have encouraged me at every step of the way. I have spent a long time away in distant places but I felt they were with me always. Being apart, but knowing we will always be together has given me strength and I am humbled by the selfless support they have given me. I specifically want to acknowledge my grandmother, Dora Smith, for instilling in me a positive and pragmatic outlook on life. She planted a seed and I hope she would be proud of what it has grown in to.

Andrew Collier has shared my highs and always been there to lift me out of my lows. He has provided great distraction and invaluable focus. A special mention goes to Brian Newham. The many cups of tea and crazy nights out under the stars, have kept life in perspective and his passion and tenderness for the great white wilderness we both love has, and continues to be, an inspiration.

Heartfelt thanks to those people who have helped me in the field, whether it was early mornings at the dockside, long wet days on Marion, or cold nights in a tent in Antarctica, I could not have done this work without you and I will be forever grateful. I am particularly indebted to Erika Nortjé, Elrike Marais, Charlene Janion and Saskia Goldberg for assistance in collection of much of the physiological data used in Chapter 7 and to Bettine Jansen van Vuuren for the genetic analyses in Chapters 6 and 7. Members of the Aliens in Antarctica project have provided insightful debate and discussion. Thanks also to the many people who have patiently given up their time to read this thesis and give valuable comment. This is particularly directed at my office mates, Justine Shaw and Peter Le Roux, whose input has improved the quality of this work significantly.

The Centre for Invasion Biology and Department of Botany and Zoology, Stellenbosch University, are thanked for financial support. The South African National Antarctic Programme provided excellent logistic support throughout this project. I would also like to acknowledge Smit Marine, and particularly Jon Klopper for the invaluable technical information he provided on the *SA Agulhas*. Marine Solutions Ltd. gave outstanding technical support for the ROV. Finally, thanks to my many friends and colleagues at the C.I.B, you guys have enriched my time in South Africa and I have many happy memories which will be with me forever.

Abstract

Although the impacts of biological invasions are widely appreciated, a bias exists in research effort to post-dispersal processes because of the difficulties of measuring propagule pressure and the detecting of newly established species. Here the Antarctic is used as a model system in which to quantify the initial dispersal of alien species and investigate the factors that contribute to the establishment and range dynamics of alien species once they have arrived in the region.

Human movements are known to transport alien species into the Antarctic, some of which have successfully established and had wide ranging consequences in recipient ecosystems. Considering terrestrial flora, this research found that over 700 seeds from 99 taxa, including some species known to be invasive, are transported into the Antarctic each year in association with South African National Antarctic Programme (SANAP) passenger luggage and cargo. The first ever assessment of propagule drop-off indicated that 30-50% of these propagules will enter the recipient environment. Further results suggested that the construction of the British Antarctic Survey Halley VI station will facilitate the transport of over 5000 seeds from 34 taxa into the region, making this a significant pathway for introductions.

Propagule pressure due to SANAP logistics is also considerable for marine species. Fouling assemblages on the external hull surfaces of the SANAP resupply vessel, the *SA Agulhas*, form only once the vessel's anti-fouling paint has been damaged by travel through sea ice and are characterised by low diversity. Ice scour prevents fouling assemblages from being transported to the Antarctic continent, but assemblages remain largely intact when travelling to sub-Antarctic Islands. In the sea-chests of the vessel populations of a known invasive, *Mytilus galloprovincialis*, were found with some individuals having survived transportation to the Antarctic region on multiple occasions.

Once species have overcome initial dispersal barriers, they face further ecological and physiological challenges in order to establish in the recipient region. The parasitoid wasp *Aphidius matricariae* was first recorded on Marion Island in 2001. Surveys around the island

show that adult abundance and the frequency of aphid parasitism are highest adjacent to a common anchor point of the *SA Agulhas* and decline away from this region. Genetic diversity was low, suggesting that the population was established from a single introduction. This highlights that high propagule pressure is not necessary for successful establishment of introduced invertebrates.

Another species that has overcome the dispersal barrier is the terrestrial slug *Deroceras panormitanum*, which was introduced to Marion Island in the 1970's and has since spread throughout much of the coastal habitat of the island. For this species range limits are set by intolerance of low temperature and salinity, and abundance structure is characterized by patches and gaps which are associated with this species inability to tolerate dry conditions.

To prevent further alien introductions in the region, targeted management of high risk pathways is required. In addition, increased vigilance is needed to detect and manage newly established aliens before their ranges expand.

Opsomming

Alhoewel die impak van biologiese indringings in die breë waardeer word, bestaan daar vooroordeel in navorsingspogings ten opsigte van na-verspreidingsprosesse, weens die moeilikhede om verspreidingseenheid druk te meet en in die opsporing van nuut gevestigde spesies. Hier word die Antarktiese streek as 'n model sisteem gebruik waarin die aanvanklike verspreiding van uitheemse spesies gekwantifiseer kan word en om die faktore wat bydrae tot die vestiging en grens dinamika van uitheemse spesies te ondersoek, wanneer hulle in 'n streek aangekom het.

Menslike bewegings is bekend daarvoor om uitheemse spesies na die Antarktik te vervoer, sommige waarvan suksesvol gevestig het en omvattende gevolge in die ontvanger ekosisteme gehad het. Aangaande terrestriële flora het hierdie navorsing gevind dat oor die 700 sade van 99 taxa, insluitende sommige spesies wat bekend is om indringend te wees, jaarliks na die Antarktik vervoer word in assosiasie met die Suid Afrikaanse Nasionale Antarktiese Program (SANAP) se bagasie en vrag. Die eerste waardebeoordeling van verspreidingseenheid afgooi het aangedui dat 30-50% van hierdie verspreidingseenhede die ontvanger omgewing sal binnedring. Verdere resultate het voorgestel dat die konstruksie van die Britse Antarktiese Opname Halley VI stasie die vervoer van 5000 sade van 34 taxa sal fasiliteer die streek in, wat dit 'n betekenisvolle weg maak vir indringings.

Verspreidingseenheid druk is ook, as gevolg van die SANAP logistiek, aanmerklik vir mariene spesies. Vuilgoed versamelings op die eksterne omhullende oppervlakte van die SANAP her-voorsieningsvaartuig, die *SA Agulhas*, vorm wanneer die vaartuig se anti-vuilgoed verf beskadig is met reis deur see-ys en word gekenmerk deur lae diversiteit. Ys skuring voorkom dat vuilgoed versamelings vervoer word na die Antarktiese kontinent, maar versamelings bly grootliks vasgeheg wanneer na sub-Antarktiese eilande gereis word. Populasies van 'n welbekende indringer, *Mytilus galloprovincialis*, is gevind in die see-storingsarea van die vaartuig, met sommige individue wat die vervoering na die Antarktiese streek oorleef het op verskeie geleenthede.

Wanneer spesies die aanvanklike verspreidingshindernisse oorkom het, staan hulle verdere ekologies en fisiologiese uitdagings in die gesig ten einde in die ontvanger streek te vestig. Die parasitiese wespe *Aphidius matricariae* is vir die eerste keer op Marion aangeteken in 2001. Opnames om die eiland toon dat volwasse oorvloed en die frekwensie van plantluis parasitisme die hoogste is aangrensend die algemene ankerpunt van die SA Agulhas en afneem weg van die omgewing af. Genetiese diversiteit was laag, wat voorstel dat die populasie gevestig het van 'n enkele bekendstelling. Dit lig uit dat hoë verspreidingseenheid druk nie nodig is vir die suksesvolle vestiging van bekendgestelde invertebrata nie.

'n Ander spesie wat die verspreidingshindernisse oorkom het is die landslak *Deroceras panormitanum* wat in die 1970's op Marion Eiland bekendgestel is en wat sedertdien versprei het oor meeste van die kushabitat van die eiland. Vir hierdie spesie word grens limiete vasgestel deur onverdraagsaamheid vir lae temperature en saliniteit en die oorvloedstruktuur word gekenmerk deur laslappe en gapings wat geassosieer word met die spesie se onvermoë om droë kondisies te hanteer.

Om verdere uitheemse bekendstellings in die streek te voorkom, word geteikende bestuur van hoë risiko weë vereis. Toenemende waaksamheid is bykomend nodig vir die opsporing en bestuur van nuutgevestigde uitheemse spesies voordat hulle grense verbreed.

Table of Contents

Declaration	i
Acknowledgments	ii
Abstract	iv
Opsomming	vi
Chapter 1 – General Introduction	
Non-indigenous species	1
The Antarctic as a model system	3
Non-indigenous species in the Antarctic	
Terrestrial introductions	6
Marine introductions	8
Climate change in the Antarctic	9
Conservation and management of non-indigenous species	
South of 60° S – the Antarctic Treaty area	10
The sub-Antarctic	12
Thesis outline	13
References	15
Chapter 2 – Breaching the dispersal barrier to invasion: quantification and management for the Antarctic	
Introduction	26
Material and methods	28
Results	35
Discussion	47
References	53
Appendices	62
Chapter 3 – Quantifying the propagule load associated with the construction of an Antarctic research station	
Introduction	71
Material and methods	72
Results	74
Discussion	77
References	79
Appendix	81
Chapter 4 – Hulls, holes and hideaways: hull fouling assemblages associated with an Antarctic supply vessel	
Introduction	83
Material and methods	86
Results	90
Discussion	93
References	96
Appendices	103

Chapter 5 – *Mytilus* on the move: transport of an invasive bivalve to the Antarctic

Introduction	106
Dry dock inspection of sea-chests	107
Implications	111
References	112

Chapter 6 – Colonisation of sub-Antarctic Marion Island by a non-indigenous parasitoid *Aphidius matricariae* (Hymenoptera, Braconidae)

Introduction	114
Material and methods	116
Results	119
Discussion	120
References	124
Appendix	129

Chapter 7 – Physiological tolerances account for range limits and abundance structure in an invasive slug

Introduction	130
Material and methods	132
Results	140
Discussion	148
References	152

Chapter 8 – Conclusion

Propagule transfer	159
Propagule survival	162
Establishment of alien species	162
Environmental controls of distribution	163
Insights from molecular ecology	164
Management implications	165
References	167

Chapter 1 – General introduction

We are living in an era characterised by globalization. Global economies depend on the movement of goods, people and services on increasingly large spatial scales (Drake and Lodge 2004, Vezina 2005, Jacks and Pendakur 2008, Procheş *et al.* 2008). The desire to have commodities at the lowest possible cost means that often goods are transported for many thousands of kilometres, crossing both political and geographic boundaries. Transportation on this unprecedented scale means that physical barriers such as rivers, oceans and mountains, which once isolated communities, are now being eroded (McNeely *et al.* 2001, Tatem and Hay 2007). The movement of goods is often associated with both the intentional and unintentional movement of species (McKinney and Lockwood 1999, Mack *et al.* 2000). Global trade drives biological invasions because of the development of interactions between source and recipient regions and creation of transport networks, with high degrees of connectivity (Drake and Lodge 2004, Tatem and Hay 2007). Major transport hubs such as international airports or container ports act as gateways to these networks, and are often characterised by high numbers of non-indigenous species and thus act as a reservoir for secondary colonisations (Drake and Lodge 2004, Meyerson and Mooney 2007).

Non-indigenous species

Any species which is moved, either intentionally or unintentionally, into a region outside its native geographic distribution is considered to be an alien (Richardson *et al.* 2000). Invasive alien species have an interaction with the recipient environment that threatens biological diversity (Colautti and MacIsaac 2004) or ecosystem functioning (O'Dowd *et al.* 2003) and have been widely recognised as one of the main threats to global biodiversity (Sala *et al.* 2000, Millennium Ecosystem Assessment 2005). Invasive alien species are found in every taxonomic group including viruses (La Deau *et al.* 2007), fungi (Schwartz *et al.* 2006), algae (Walters *et al.* 2006), vascular plants (D'Antonio and Vitousek 1992, Rejmánek 2000, Pyšek and Richardson 2007), invertebrates (Hänel *et al.* 1998, Le Pape *et al.* 2004, Ward *et al.* 2006), mammals (Jones *et al.* 2003, Jeschke and Strayer 2005), fish (Huckins *et al.* 2000, Ruesink 2005) and birds (Cassey 2001) (see <http://www.issg.org/database> for a list of the world's most problematic invaders). Such species have had substantial ecological, economic

and social impacts in almost every ecosystem type in virtually every region on the planet (Davis 2003, Matthews and Brand 2004, Matthews 2005).

Given the pervasive nature of invasive alien species and damaging effects on recipient ecosystems, it is imperative to comprehend fully what governs the spatial and temporal progression of invasions. The process of invasion consists of a number of phases with a distinct barrier being overcome at each level (Richardson *et al.* 2000, Kolar and Lodge 2001). The first barrier which must be surmounted is the initial dispersal barrier, where species are transported across a major geographical boundary to a new location outside its previous range. Once transported into a new location a species must overcome an establishment barrier by first surviving the biotic and abiotic conditions of the new location and then successfully reproducing. Once these initial barriers have been crossed, a founder population is established. However, to be considered an invasive species this founder population must expand its range within the new location and sustain populations at sites distant to that of the initial introduction (Richardson *et al.* 2000).

Invasive species are often difficult or impossible to eradicate (Gremmen *et al.* 2001, Bester *et al.* 2002, Courchamp *et al.* 2003, Regan *et al.* 2006) and therefore it is of critical conservation importance that the first stages of an invasion are understood. Propagule pressure is a measure of the number and identity of individuals crossing the initial dispersal barrier to invasion (Lockwood *et al.* 2005). Propagule pressure is a key factor in determining the success of invasions (Williamson 1996, Chown *et al.* 1998, Rouget and Richardson 2003, Chown *et al.* 2005, Colautti *et al.* 2006) and although there are numerous other factors that may also influence establishment success, propagule pressure is important in almost all cases (Colautti *et al.* 2006, Křivánek *et al.* 2006). However, despite its significance, few studies have successfully quantified the number and identity of propagules entering any region (Puth and Post 2005).

Once a species has been transported into a new region, it must face a suite of ecological and physiological challenges if it is to become established (Worner 1988, Grevstad 1999, Blackburn and Duncan 2001). Abiotic factors such as climatic suitability (McDonald *et al.* 2000, Hart *et al.* 2002, Forsyth *et al.* 2004, Lester 2005) and biotic factors such as host

availability (Grevstad 1999, van Klinken and Edwards 2002) and presence of symbionts (Schwartz *et al.* 2006) may all play an important role in determining establishment success. In many cases the patterns and processes which influence the early stages of establishment remain poorly documented as often the arrival of a species in an area goes unnoticed until it has successfully established and started to spread (Williamson 1996).

Therefore, to comprehend the threat of invasions it is necessary to understand the processes that influence each stage, from the composition and number of propagules which surmount the initial dispersal barrier, to ecological and physiological barriers which influence the establishment and spread of an alien species in a novel habitat. The Antarctic provides an ideal model system in which to address some of these questions.

The Antarctic as a model system

The Antarctic is a biogeographical region which encapsulates the sub-Antarctic islands, the maritime Antarctic and continental Antarctica (Convey 2006, Chown and Convey 2007) (Fig. 1). Essentially the region is a series of islands isolated by ocean in the case of Southern Ocean Islands and ice in the case of the ice-free areas of continental Antarctica (Fig. 2). These islands are characterised by strong geographical and historical isolation (Bergstrom and Chown 1999). Different geological histories of the regions of Antarctica have contributed to the identity of the biotas living on them, with the influence of isolation and history depending to some extent on the dispersal abilities of the taxa involved: mobile species such as seabirds are less influenced by large ocean barriers than sedentary species such as insects (Chown 1994, Muñoz *et al.* 2004, Greve *et al.* 2005, Chown and Convey 2007, Convey *et al.* 2008). The island-like situation of the Antarctic means that lessons learned from the region can be applied to island conservation more generally, which is useful given the considerable threat to island biotas (Gillespie and Roderick 2002, Ricketts *et al.* 2005).

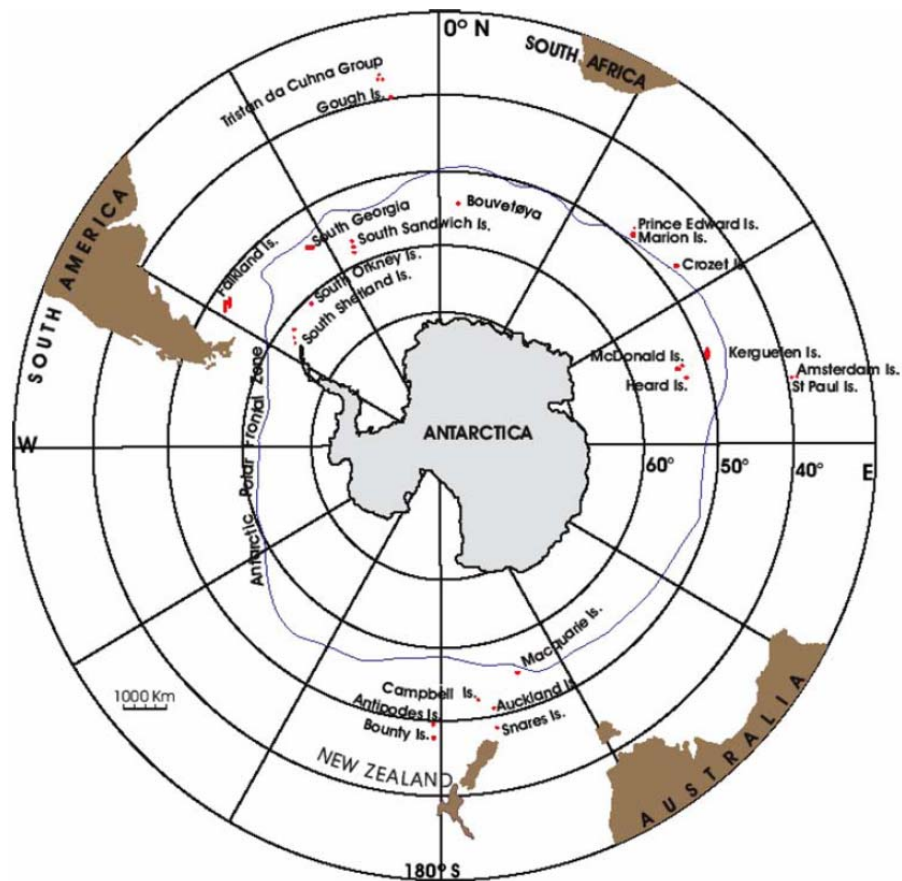


Figure 1. Schematic map of the position of the Southern Ocean Islands and Antarctic continent relative to Australia, South Africa and South America.

Despite its isolation, people have been travelling to the Antarctic for over 200 years (Hull and Bergstrom 2006). Initially most activity was focused on the sub-Antarctic islands at the periphery of the Antarctic region, a result of the land-based elements of the whaling and sealing industry (Pearson and Stehberg 2006, Cooper 2008). In the mid-20th century, some of the focus shifted away from the sub-Antarctic islands and towards the Antarctic continent. This interest in science and exploration culminated in the International Geophysical Year (1957/58) and the signing of the Antarctic Treaty in 1959 (Hull and Bergstrom 2006). These events are the foundation for modern utilization of the Antarctic, where scientists and tourists operate side-by-side. The rapid globalization and increasing human movements of the 21st century are particularly apparent in the Antarctic where the numbers of visitors and level of human influence have increased dramatically (Naveen *et al.* 2001, Lamers *et al.* 2008).



Figure 2. Marion Island, Gough Island and nunataks in Western Dronning Maud Land (location of SANAE IV station). All are isolated by areas of unsuitable habitat type, ocean in the case of Marion Island and Gough Island, ice in the case of the nunataks.

Although the level of human influence in the Antarctic is growing, the number of pathways by which alien species can enter the region is still extremely restricted. For terrestrial species, the main introduction routes are associated with expeditioners' clothing, cargo (including vehicles) and food (Whinam *et al.* 2005). For marine species, the most significant pathway is hull fouling (Lewis *et al.* 2003, 2006, ATCM-IP 37 2007), and to lesser extent with small craft (Lewis *et al.* 2006), ballast water, transport with floating plastic debris (Barnes 2002, Barnes and Fraser 2003) or with scientific equipment.

Whilst some ships and their cargos originate from northern ports and are involved in bi-polar operations, these ships commonly layover in a gateway port (i.e. the southern temperate locations from which planes and ships leave) before voyaging South. Gateways to the Antarctic are limited to just a few key access ports, namely, Hobart (Australia), Christchurch and Bluff (New Zealand), Cape Town (South Africa), Ushuaia (Argentina), Punta Arenas (Chile) and Stanley (Falkland Islands). Because of the limited number of pathways and gateway ports, the Antarctic is ideally situated to act as model system for studying the process of invasion as it is possible to adequately survey an entire pathway or route.

Non-indigenous species in the Antarctic

Terrestrial introductions

Although it is currently not known how many alien species arrive in the Antarctic as propagules, some of these species are able to survive and establish in the region. The extent of introductions is greatest in the sub-Antarctic terrestrial realm where 108 alien plants, 72 alien terrestrial invertebrates and 16 alien vertebrates have been recorded (Frenot *et al.* 2005). These introduced species have had a variety of impacts ranging in both severity and extent.

Substantial impacts by introduced invertebrate predators have been documented on several Southern Ocean Islands. On Macquarie Island, two introduced species of flatworm, *Arthurdendyus vegrandis* (Geoplanidae) and *Kontikia andersoni* (Geoplanidae) were discovered in 1997 (Greenslade *et al.* 2007). The more narrowly distributed *A. vegrandis* apparently feeds solely on earthworms. Of the six terrestrial species of earthworm on Macquarie Island, four species are regarded as alien, one endemic and one of unknown

status (Greenslade 2006), and all are at least potential prey for the flatworm. The wider ranging *K. andersoni* (Geoplanidae) likely feeds on a range of arthropods, annelids and molluscs. Given that relatively few macro invertebrate predators occur on Macquarie Island (two flatworm, three spider and six staphylinid beetle species), the continuing range expansion of two predatory flatworms has the potential to exert a profound influence on invertebrate populations at the island by altering the food web dynamics.

Interactions between introduced plants and invertebrates are also having a profound influence on community structure. For example, on Marion Island, mite abundances are higher in sites occupied by the introduced grass, *Agrostis stolonifera* relative to the control areas (Gremmen *et al.* 1998). A more complex interaction between invasive grasses, introduced reindeer (*Rangifer tarandus*) and an introduced predatory beetle and indigenous prey beetle species has been documented for South Georgia (Chown and Block 1997). The introduced predatory carabid, *Trechisibus antarcticus*, appears to be selecting for larger body sizes in the indigenous prey perimylopod *Hydromedion sparsutum* owing to considerable predation pressure (Ernsting *et al.* 1995, 1999). However, in those areas where reindeer graze most frequently, *H. sparsutum* adults are smaller than where reindeer are absent. In the former areas, reindeer promote the spread of the grazing-tolerant invasive grass *Poa annua* (and in some circumstances the somewhat less tolerant indigenous *Festuca contracta*). Despite substantial ingestion of these grasses, *H. sparsutum* larvae grow poorly on them by comparison with other, less grazing-tolerant indigenous species. In consequence, by promoting the spread of the invasive *Poa annua*, reindeer appear to be selecting indirectly for reduced body size in *H. sparsutum*, whilst selection in the opposite direction is being imposed by the introduced carabid (Chown and Block 1997).

The effects of introduced mammals are often more direct. Introduced rodents, especially house mice, are having pronounced direct effects on invertebrate populations on several islands, including Gough (Jones *et al.* 2003), Kerguelen (Le Roux *et al.* 2002), Macquarie (Copson 1986) and Marion (Crafford and Scholtz 1987, Smith 2002). On Marion Island, mice have not only led to substantial declines in populations of their preferred prey, the flightless moth *Pringleophaga marioni* (Crafford and Scholtz 1987, Chown *et al.* 2002), but have also altered ecosystem functioning. By reducing populations of the *P. marioni*, whose caterpillars

are keystone species for nutrient recycling (Smith and Steenkamp 1992), mice have had profound effects on nutrient cycling, plant growth and possibly peat formation (Smith and Steenkamp 1990). Moreover, because caterpillars constitute an important component of the diet of overwintering black-faced sheathbills (an indigenous, plover-like bird), populations of this species are also declining (Huyser *et al.* 2000). In addition, by virtue of their size-selective feeding, mice are not only changing the size distributions of the weevils on Marion Island (but not on nearby, mouse-free Prince Edward Island, Chown and Smith 1993), but may also have caused introgression of two weevil species that probably speciated sympatrically via size-based, positive-assortative mating (Chown 1990, Grobler *et al.* 2006).

Although the Antarctic continent has far fewer alien species than the surrounding islands, there are several instances of alien species surviving inside station buildings. *Lycoriella* spp. (Diptera) have been recorded in the alcohol bond at Rothera research station (UK) and in the sewerage treatment facilities at Casey research station (Australia) (Hughes *et al.* 2005) and non-native vascular plants growing in an indoor garden at Davis station (Australia) (Smith 1996). However, perhaps more relevant are the instances where species have survived for periods of several years outside the station environment (see Smith 1996 for a chronology of experimental and accidental introductions into the field and their success rate). More recently, *Poa trivialis* has survived for several years near Syowa station (Japan) and produced flowers (although the pollen was not viable) and *Poa annua* increased in abundance around Arctowski station (Poland) (Clout and de Poorter 2008).

Marine introductions

Much less information is available on the extent or impacts of invasions in the marine realm. To date there have only been seven studies which have considered the threat of non-indigenous marine species (Barnes 2002, Barnes and Fraser 2003, Lewis *et al.* 2003, 2004, 2005, 2006, Lee and Chown 2007) and physiology of typical marine invaders, especially fouling organisms, is a neglected research area. Nonetheless, there are some indications that species commonly found in temperate waters are able to survive in Antarctic waters (Clayton *et al.* 1997, Thatje and Fuentes 2003, Tavares and de Melo 2004, Lee and Chown 2007). At present it is unlikely that these species could establish long term, self-sustaining populations. However, a small rise in sea temperature could reduce the mismatch between

the development times of invasive species and the length of the growing season, decreasing the metabolic advantage of endemic, cold adapted species (Aronson *et al.* 2007).

Climate change in the Antarctic

Global climate change is having a marked effect on the abiotic environment of all Antarctic biota, both native and introduced (Chown and Smith 1993, Smith and Gremmen 2001, Bergstrom *et al.* 2006). However, the strength and direction of this change are not uniform across the region. In some parts of continental Antarctica, change in temperature and precipitation has been considerable. Thus, over the Antarctic Peninsula, the temperature has increased by approximately 0.5°C per decade, with much of the warming taking place in the winter months (Jones 1995, King and Comiso 2003, Vaughan *et al.* 2003, Turner *et al.* 2005, 2007). Liquid precipitation is also increasing (Turner *et al.* 2007) having important implications for nutrient cycling and plant growth (Callaghan *et al.* 1992). By contrast, temperatures in some Eastern Antarctic locations are declining with the Amundsen–Scott station (South Pole) experiencing a decline at a rate of -0.17°C per decade (Turner *et al.* 2005).

In the sub-Antarctic, climate change is characterised by an increase in mean temperature and a heterogeneous change in rainfall with islands such as Marion experiencing a decrease in precipitation (Le Roux *et al.* 2008), islands such as Macquarie experiencing an increase in precipitation (Kirkpatrick and Scott 2002) and islands such as Kerguelen showing no clear trend (Frenot *et al.* 1997). Glacial retreat and the reduction in the extent of permanently frozen ground is a common trend throughout the region (Frenot *et al.* 1993, Budd 2000, Boelhouwers 2003). This process exposes new ground which is often colonised by invasive alien species. For example, on Kerguelen Island pioneer species on glacier forelands include *Poa annua* and *Cerastium fontanum*, species which are invasive throughout the region (Frenot *et al.* 1998).

Increases in temperature and changing water availability are having considerable impacts on arthropod assemblages and on several plant species. Physiological data on thermal tolerances and on the relationships between development rate and temperature suggest that not only are the alien species often more thermally tolerant than their indigenous

counterparts (e.g. Slabber *et al.* 2007), but also that in response to increasing temperatures, steeper rate-development relationships will mean faster development for alien than for indigenous species (Barendse and Chown 2000). For these reasons, and because many of the indigenous species have longer life-cycles (one year or more) than those of the alien species (Chown *et al.* 2002), it is expected that alien species (many of which are invasive - see e.g. Gabriel *et al.* 2001) will be at an advantage relative to their indigenous counterparts under the predicted climate change scenarios (Chown and Convey 2007). Other work has suggested that as a consequence of greater low temperature tolerance, indigenous species are able to occupy higher elevations than alien species (e.g. Gabriel *et al.* 2001, Slabber *et al.* 2007), and might possibly have been displaced from lower elevations by large populations of thermally responsive, fast growing invasive species (Convey *et al.* 1999, Chown *et al.* 2002, Jones *et al.* 2003). Increasing temperature may therefore enable invasive alien species to occupy ever higher elevations, with likely have detrimental consequences for indigenous species and possibly also for ecosystem functioning.

The interaction between climate change and increasing frequency of human visits to the Antarctic means that the potential for the successful establishment of non-indigenous organisms in the region is growing. Although the risk of introductions to the Antarctic is lower than many parts of the planet, the potential effects of those introductions is disproportionate in the context of their impact on the regional biodiversity (Frenot *et al.* 2005). Understanding the factors which influence the movement of species in the Antarctic region is not only of critical importance for the conservation of Antarctic biota but can help to answer questions about invasions elsewhere.

Conservation status and management of non-indigenous species

South of 60° S – the Antarctic Treaty area

The first step towards regulation of non-indigenous imports to the Antarctic continent (including all land and water South of 60° S), was made in 1960 by the Scientific Committee on Antarctic Research (SCAR). SCAR drew up general rules of conduct for the preservation and conservation of living resources in Antarctica which were the first attempt at regulating the importation of non-indigenous species, parasites and diseases into Antarctica. At the first Antarctic Treaty Consultative Meeting (ATCM) in 1961, these recommendations were

incorporated into Recommendation I-VIII (Conservation of Antarctic Fauna and Flora). Regulations were developed further at ATCM-II (1962) and were subsequently incorporated into the Agreed measures for the Conservation of Antarctic Fauna and Flora (Recommendation II-II) which were then adopted at ATCM-III (1964). These measures formed the basis for controlling biological introductions until 1991, when they were further revised and re-named as the Protocol on Environmental Protection to the Antarctic Treaty, which serves to regulate introductions to the present (Smith 1996).

In line with of global concerns about the impacts of non-native species introductions, the issue of non-native introductions to the Antarctic has been raised numerous times at meetings of the Committee for Environmental Protection (CEP) in the form of information papers (IP) and working papers (WP). Initially these primarily focused on the issue of introduction of diseases that could threaten Antarctic wildlife (ATCM-IP 4 1998, ATCM-WP 32 1999, ATCM-WP 6 2000, ATCM-WP 10 2001, ATCM-WP11 2001, ATCM-IP 62 2002), but more recently have concerned the introduction of microbes, and macro flora and fauna (ATCM-WP 28 2005, ATCM-IP 63 2005, ATCM-IP 97 2005). At CEP meeting IX (2006), New Zealand submitted WP 13 and IP 46 which outlined a number of key issues including transfer of species into and within the Antarctic and the need for the development of practical preventative measures. The CEP agreed with the recommendations arising from the workshop reported in WP 13, including that *'the issue of non-native species should be given the highest priority...'*

In the Antarctic Treaty area, specific legislation has recognised the threat of non-indigenous introductions in the marine realm but this primarily focuses on ballast water. At CEP IX (2006) the United Kingdom presented WP 5 (rev. 1) "Practical Guidelines for Ballast Water Exchange in the Antarctic Treaty Area", with the aim to support early implementation of the IMO Ballast Water Convention (<http://www.imo.org>). This led to Resolution 3 (2006) which recommended that the "Practical Guidelines for Ballast Water Exchange in the Antarctic Treaty Area" be used by all ships in the Antarctic Treaty area except those referred to in Article 3, paragraph 2 of the IMO Ballast Water Management Convention. The threat of hull fouling has been recognised (ATCM-IP 37 2007), but very little information is available on the sources of, and species contributing to, hull fouling or how this may be reduced. Due to this

lack of data, no guidelines exist to reduce the risk of introducing non-native species via this pathway.

The sub-Antarctic

The sub-Antarctic Islands do not fall under the jurisdiction of the Antarctic Treaty but several general international agreements, such as the Convention on Biodiversity, and the Agreement for the Conservation of Albatrosses and Petrels, apply to the islands (Chown *et al.* 2006, Hull and Bergstrom 2006). At a National level, the New Zealand sub-Antarctic islands (Snares, Bounty, Antipodes, Auckland, and Campbell islands) are all National Nature Reserves. Macquarie Island and Heard and McDonald Islands (Australia) have the highest reservation status, Nature Reserve and Commonwealth Reserve, respectively, under their governing legislations (State and Federal). Marion and Prince Edward Island (South Africa) are classified as a Special Nature Reserve under South African legislation (National Environmental Management: Protected Areas Act) (Davies *et al.* 2007). South Georgia has National status (United Kingdom) as a Protected Area, and the Kerguelen and Crozet Islands (France) and Gough Island (United Kingdom) are all National Nature Reserves (de Villiers *et al.* 2006).

As a result of a variety of international and national legislation, most of the islands enjoy a high conservation status (de Villiers *et al.* 2006). The five New Zealand sub- Antarctic island groups, Heard and McDonald Islands, Gough Island and Macquarie Island are all World Heritage Areas (at the highest IUCN Reserve Status of Category Ia). Several other island groups in the region are also clearly eligible for World heritage status (Chown *et al.* 2001), and a nomination for the Prince Edward Islands has been submitted. Macquarie Island is listed as a UNESCO Biosphere Reserve.

Many nations have taken steps to reduce the number of non-indigenous species introductions by limiting the number of visits per season, number of visitors permitted ashore at any occasion, vessel capacity, number of landing sites, nights ashore, and/or time ashore, and often specify procedures for decontamination prior to shore transfers (such as bootwashing).

Legislation relating to island's terrestrial habitats extends to the inter-tidal zone, but separate provision has been made to protect off-shore areas. For Kerguelen, Crozet, Amsterdam and St Paul, vessels are not allowed to discharge ballast within 200 nautical miles of the islands, for Macquarie Island, 12 nautical miles and for the Prince Edward Islands 3 nautical miles. The management plans for the above mentioned islands also specify that the hulls of supply vessels must be cleaned and treated with anti fouling paint but no minimum standards are specified and no active policing is in place (de Villiers *et al.* 2006). In addition, marine areas surrounding Crozet and Kerguelen are part of the Antarctic Ocean Sanctuary for cetaceans, and those surrounding Heard and McDonald islands are part of the Indian Ocean Sanctuary for Whales and Marine Reserves exist around the New Zealand islands and Macquarie (de Villiers *et al.* 2006). However, legislation relating to the protection of these areas is primarily directed at fishing activities and pollution rather than the introduction of non-indigenous species.

Thesis outline

The general theme of this thesis is the movement of alien species across the Antarctic region and the biogeographic outcomes thereof. Key questions relating to how propagule load is affected by vector characteristics and what factors affect the initial survival and spread of alien species in novel habitats are addressed. Each research chapter has its own aims, results and discussion and is formatted as a separate manuscript: Chapters 2-4 address the issue of propagule pressure, quantifying the propagule load entering the Antarctic region from the South African gateway, through a number of pathways. Chapter 5 considers both propagule pressure and likelihood of survival through the initial dispersal stage. Chapters 6 and 7 are concerned with the latter stages of an invasion, examining establishment and spread of two alien species on Marion Island. Chapter 8 synthesises the results from each of the previous chapters, shedding light on the broader question of what mediates invasions in the Antarctic.

- In Chapter 2, the first comprehensive assessment of the propagule pressure associated with the logistics operation of a National Antarctic programme is made and the importance of propagule entrainment and drop-off is disentangled. All

pathways are considered, including cargo operations and expeditioner clothing and luggage.

- In Chapter 3, a second example of propagule pressure is considered, but here the focus shifts to examining the propagule load associated with the construction of the new British research station, Halley IV. The effect of how different transport pathways and cargo packaging affect propagule load is elucidated.
- In Chapter 4, the poorly investigated threat of invasion in the marine realm is investigated. Propagule pressure is measured by examining the development of hull fouling assemblages on the South African National Antarctic Programme re-supply vessel the *SA Agulhas* over a two-year period.
- Chapter 5 documents the transport of an invasive bivalve, *Mytilus galloprovincialis*, to the Antarctic in association with the sea-chests of the *SA Agulhas*. By considering the age structure of the population and considering the thermal environment within the sea-chests, the effects of propagule transport and propagule survival are disentangled.
- Chapter 6 documents the arrival and initial spread of a parasitoid wasp, *Aphidius matricariae*, on Marion Island, describing on the genetic structure of the introduced species and the implications of adding a new layer of trophic complexity to the island.
- In Chapter 7 the factors which influence the distributional limits and abundance structure of an alien slug, *Deroceras panormitanum*, are investigated. A combination of ecological and physiological approaches are adopted, and the importance of an integrated approach to explain the factors which delimit species range edges is highlighted.
- Finally, Chapter 8 synthesizes these results to assess the relative importance of the main pathways of introduction into the Antarctic from the South African gateway and the implications of this for the biogeography of the region. Suggestions are made as to how this work may guide the management of the threat of invasions both in the Antarctic and globally.

REFERENCES

- Aronson R.B., Thatje S., Clarke A., Peck L.S., Blake D.B., Wilga C.D. & Seibel B.A. (2007) Climate change and invasibility of the antarctic benthos. *Annual Review of Ecology Evolution and Systematics*, 38, 129-154
- ATCM-IP 37 (2007) Information Paper 37, Hull fouling as a source of marine invasion in the Antarctic, submitted by SCAR
- ATCM-IP 4 (1998) Information Paper 4, Introduction of Diseases to Antarctic Wildlife: Proposed workshop, submitted by Australia
- ATCM-IP 46 (2006) Information Paper 46, "Non-native Species in the Antarctic" A Workshop, submitted by New Zealand
- ATCM-IP 62 (2002) Information Paper 62, Draft Response Plan in the Event that Unusual Animal Deaths are Discovered, submitted by Australia
- ATCM-IP 63 (2005) Information Paper 63, Introduction of Non-native Species, Parasites and Diseases, submitted by Australia
- ATCM-IP 97 (2005) Information Paper 97, Update on Boot and Clothing Decontamination Guidelines and the Introduction and Detection of Diseases in Antarctic Wildlife; IAATO's perspective, submitted by IAATO
- ATCM-WP 10 (2001) Working Paper 10, Report on the open-ended intersessional contact group on Diseases of Antarctic Wildlife: Report 1 – Review and Risk Assessment, submitted by Australia
- ATCM-WP 11 (2001) Working Paper 11, Report on the open-ended intersessional contact group on Diseases of Antarctic Wildlife: Report 2 – Practical Measures to Diminish Risk (Draft), submitted by Australia
- ATCM-WP 13 (2006) Working paper 13, Non-native Species in the Antarctic. Report of a Workshop, submitted by New Zealand
- ATCM-WP 28 (2005) Working Paper 28, Measures to address the unintentional introduction and spread of Non-native Biota and Disease into the Antarctic Treaty Area, submitted by Australia
- ATCM-WP 32 (1999) Working Paper 32, Report to ATCM XXIII on outcomes from the Workshop on Diseases of Antarctic Wildlife, submitted by Australia
- ATCM-WP 5 (2006) Working Paper 5, Practical Guidelines for Ballast Water Exchange in the Antarctic Treaty Area, submitted by United Kingdom

- ATCM-WP 6 (2000) Working Paper 6, Diseases of Antarctic Wildlife, submitted by Australia
- 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
- 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
- Barnes D.K.A. (2002) Invasions by marine life on plastic debris. *Nature*, 416, 808-809
- 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., Convey P. & Huiskies A.H.L. (eds.) (2006) *Trends in Antarctic Terrestrial and Limnetic Ecosystems*. Springer, Dordrecht, The Netherlands
- Bester M.N., Bloomer J.P., van Aarde R.J., Erasmus B.H., van Rensburg P.J.J., Skinner J.D., Howell P.G. & Naude 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
- Blackburn T.M. & Duncan R.P. (2001) Determinants of establishment success in introduced birds. *Nature*, 414, 195-197
- Boelhouwers J. (2003) Sensitivity and responses to climate change in the sub-Antarctic periglacial environment. In: *Eighth international conference on permafrost* (eds. Phillips M., Springman S.M. & Arenson L.U.) International Permafrost Association, Zurich, Switzerland
- 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
- Callaghan T.V., Sonesson M. & Sømme L. (1992) Responses of terrestrial plants and invertebrates to environmental change at high latitudes. *Philosophical Transactions of the Royal Society of London B*, 338, 279-288
- Cassey P. (2001) Are there body size implications for the success of globally introduced land birds? *Ecography*, 24, 413-420
- Chown S.L. & Block W. (1997) Comparative nutritional ecology of grass-feeding in a sub-Antarctic beetle: the impact of introduced species on *Hydromedion sparsutum* from South Georgia. *Oecologia*, 111, 216-224

- 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. & 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. (1990) Speciation in the sub-Antarctic weevil genus *Dusmoecetes* Jeannel (Coleoptera: Curculionidae). *Systematics and 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., Davies S. & Joubert L. (2006) *Prince Edward Islands environmental management plan version 0.1*. Centre for Invasion Biology, Stellenbosch
- 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., 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
- Clayton M.N., Wiencke C. & Klöser H. (1997) New records of temperate and sub-Antarctic marine benthic macroalgae from Antarctica. *Polar Biology*, 17, 141-149
- Clout M. & De Poorter M. (2008) Invasive Alien Species: Global Lessons and Antarctic Implications. In: *Non-native Species in the Antarctic* (ed. Rogan-Finnemore M.) Gateway Antarctica Special Publication, Christchurch, New Zealand
- Colautti R.I. & MacIsaac H.J. (2004) A neutral terminology to define 'invasive' species. *Diversity and Distributions*, 10, 135-141
- Colautti R.I., Grigorovich I.A. & MacIsaac J. (2006) Propagule pressure: a null model for biological invasions. *Biological Invasions*, 8, 1023-1037

- Convey P. (2006) Antarctic climate change and its influences on terrestrial ecosystems. In: *Trends in Antarctic Terrestrial and Limnetic Ecosystems* (eds. Bergstrom D.M., Convey P. & Huiskes A.H.L.) Springer, Dordrecht, The Netherlands
- Convey P., Gibson J.A.E., Hillenbrand C.D., Hodgson D.A., Pugh P.J.A., Smellie J.L. & Stevens M.I. (2008) Antarctic terrestrial life - challenging the history of the frozen continent? *Biological Reviews*, 83, 103-117
- 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 *The Prince Edward Islands. Land-sea interactions in a changing ecosystem* (eds. S.L. Chown & Froneman P.W.) Africa Sun Media, Stellenbosch, South Africa
- Copson G.R. (1986) The diet of the introduced rodents *Mus musculus* L. and *Rattus rattus* L. on Subantarctic Macquarie Island. *Australian Journal of Wildlife Research*, 133, 441-445
- Courchamp F., Chapuis J.L. & Pascal M. (2003) Mammal invaders on islands: impact, control and control impact. *Biological Reviews*, 78, 347-383
- 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
- D'Antonio C.M. & Vitousek P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, 23, 63-87
- Davies S.J., Chown S.L., Joubert L.J. (2007) Renewed management system and provisions for South Africa's sub-Antarctic islands. *Papers and Proceedings of the Royal Society of Tasmania*, 141, 115-120
- Davis M.A. (2003) Biotic globalization: Does competition from introduced species threaten biodiversity? *Bioscience*, 53, 481-489
- de Villiers M.S., Cooper J., Carmichael N., Glass J.P., Liddle G.M., McIvor E., Micol T., Roberts A. (2006) Conservation management at Southern Ocean Islands: towards the development of best practice guidelines. *Polarforschung*, 75, 113-131
- 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 Series B*, 271, 575-580

- Ernsting G., Block W., MacAlister H. & Todd C. (1995) The invasion of the carnivorous carabid beetle *Trechisibus antarcticus* on South Georgia (sub-Antarctic) and its effect on the endemic herbivorous beetle *Hydromedion spassutum*. *Oecologia*, 103, 34-42
- Ernsting G., Brandjes G.J., Block W. & Isaaks J.A. (1999) Life-history consequences of predation for a subantarctic beetle: evaluating the contribution of direct and indirect effects. *Journal of Animal Ecology*, 68, 741-752
- Forsyth D.M., Duncan R.P., Bomford M. & Moore G. (2004) Climatic suitability, life-history traits, introduction effort, and the establishment and spread of introduced mammals in Australia. *Conservation Biology*, 18, 557-569
- Frenot Y., Chown S.L., Whinam J., Selkirk P.M., Convey P., Skotnicki M. & Bergstrom D.M. (2005) Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews*, 80, 45-72
- Frenot Y., Gloaguen J.-C. & Tréhen P. (1997) Climate change in Kerguelen Islands and colonisation of recently deglaciated areas by *Poa kerguelensis* and *P. annua*. In: *Antarctic communities: species, structure and survival* (eds. Battaglia B., Valencia J. & Walton D.) Cambridge University Press, Cambridge
- 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. & Smith V.R. (2001) Biological invasions on Southern Ocean Islands: the Collembola of Marion Island as a test of generalities. *Ecography*, 24, 421-430
- Gillespie R.G. & Roderick G.K. (2002) Arthropods on islands: Colonisation, speciation, and conservation. *Annual Review of Entomology*, 47, 595-632
- Greenslade P. (2006) *The invertebrates of Macquarie Island*. Department of Environment and Heritage, Australian Antarctic Division, Kingston
- Greenslade P., Stevens M.I. & Edwards R. (2007) Invasion of two exotic flatworms to subantarctic Macquarie Island. *Polar Biology*, 30, 961-967

- Gremmen N.J.M., Barendse J. & Orr I. (2001) Invasion and eradication of *Sagina Procumbens* L. (Procumbent pearlwort) on Gough Island. *Aliens*, 14, 19-20
- 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
- Greve M., Gremmen N.J.M., Gaston K.J. & Chown S.L. (2005) Nestedness of Southern Ocean Island biotas: ecological perspectives on a biogeographical conundrum. *Journal of Biogeography*, 32, 155-168
- Grevstad F.S. (1999) Factors influencing the chance of population establishment: implications for release strategies in biocontrol. *Ecological Applications*, 9, 1439-1447
- 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
- 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
- Hart A.J., Tullett A.G., Bale J.S. & Walters K.F.A. (2002) Effects of temperature on the establishment potential in the U.K. of the non-native glasshouse biocontrol agent *Macrolophus caliginosus*. *Physiological Entomology*, 27, 112-123
- Huckins C.J.F., Osenberg C.W. & Mittelbach G.G. (2000) Species introduction and their ecological consequences: an example with congeneric sunfish. *Ecological Applications*, 10, 612-625
- Hughes K.A., Walsh S., Convey P., Richards S. & Bergstrom D.M. (2005) Alien fly populations established at two Antarctic research stations. *Polar Biology*, 28, 568-570
- Hull B.J. & Bergstrom D.M. (2006) Antarctic terrestrial and limnetic ecosystems conservation and management. In: *Trends in Antarctic Terrestrial and Limnetic Ecosystems* (eds. Bergstrom D.M., Convey P. & Huiskes A.H.L) Springer, Dordrecht, The Netherlands
- 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

- Jacks D.S. & Pendakur K. (2008) Global trade and the maritime transport revolution. *Journal of Economic History*, 68, 614-614
- 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 United States of America*, 102, 7198-7202
- Jones A.G., Chown S.L. & Gaston K.J. (2003) Introduced house mice as a conservation concern on Gough Island. *Biodiversity and Conservation*, 12, 2107-2119
- Jones P.D. (1995) Recent variations in mean temperature and the diurnal temperature range in the Antarctic. *Geophysics Research Letters*, 22, 1345-1348
- King J.C. & Comiso J.C. (2003) The spatial coherence of interannual temperature variations in the Antarctic Peninsula. *Geophysics Research Letters*, 30, 1040
- 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
- Kolar C.S. & Lodge D.M. (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution*, 16, 199-204
- Křivánek M., Pyšek P. & Jarošík V. (2006) Planting history and propagule pressure as predictors of invasion by woody species in a temperate region. *Conservation Biology*, 20, 1487-1498
- La Deau S.L., Kilpatrick A.M. & Marra P.P. (2007) West Nile virus emergence and large-scale declines of North American bird populations. *Nature*, 447, 710-713
- Lamers M., Haase D. & Amelung B. (2008) Facing the elements: analysing trends in Antarctic tourism. *Tourism Review*, 63, 15-27
- Le Pape O., Guerault D. & Desaunay Y. (2004) Effect of an invasive mollusc, American slipper limpet *Crepidula fornicata*, on habitat suitability for juvenile common sole *Solea solea* in the Bay of Biscay. *Marine Ecology-Progress Series*, 277, 107-115
- Le Roux P.C. (2008) Climate and climate change. In: *The Prince Edward Islands - Land-Sea Interactions in a Changing Ecosystem* (eds. Chown S.L. & Froneman P.W.) African SunMedia, Stellenbosch, South Africa
- Le Roux V., Chapuis J-L., Frenot Y. & Vernon P. (2002) Diet of the house mouse (*Mus musculus*) on Guillou Island, Kerguelen archipelago, Subantarctic. *Polar Biology*, 25, 49-57

- 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
- Lester P.J. (2005) Determinants for the successful establishment of exotic ants in New Zealand. *Diversity and Distributions*, 11, 279-288
- Lewis P.N., Bergstrom D.M. & 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
- Lewis P.N., Riddle M.J. & Hewitt C.L. (2004) Management of exogenous threats to Antarctica and the sub-Antarctic islands: balancing risks from TBT and non-indigenous marine organisms. *Marine Pollution Bulletin*, 49, 999-1005
- Lewis P.N., Riddle M.J. & Smith S.D.A. (2005) Assisted passage or passive drift: a comparison of alternative transport mechanisms for non-indigenous coastal species into the Southern Ocean. *Antarctic Science*, 17, 183-191
- 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
- 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
- Matthews S. & Brand K. (2004) *Africa Invaded – the growing danger of alien invasive species*. Global Invasive Species Programme, South African National Biodiversity Institute, Cape Town, South Africa
- Matthews S. (2005) *South America Invaded – the growing danger of alien invasive species*. Global Invasive Species Programme, South African National Biodiversity Institute, Cape Town, South Africa
- McDonald J.R., Head J., Bale J.S. & Walters K.F.A. (2000) Cold tolerance, overwintering and establishment potential of *Thrips palmi*. *Physiological Entomology*, 25, 159-166
- McKinney M.L. & Lockwood J.L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution*, 14, 450-453
- McNeely J.A., Mooney, H.A., Neville L.E., Sche P.J. & Waage J.K (eds.) (2001) *Global strategy on Invasive Alien Species* Published by IUCN, Gland, Switzerland, on behalf of the Global Invasive Species Programme

- Meyerson L.A. & Mooney H.A. (2007) Invasive alien species in an era of globalization. *Frontiers in Ecology and the Environment*, 5, 199-208
- Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-being: Biodiversity Synthesis*. World Resources Institute, Washington DC.
- Munõz 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
- O'Dowd D.J., Green P.T. & Lake P.S. (2003) Invasional 'meltdown' on an oceanic island. *Ecology Letters*, 6, 812-817
- Pearson M. & Stehberg R. (2006) Nineteenth century sealing sites on Rugged Island, South Shetland Islands. *Polar Record*, 42, 335-347
- Procheş S., Wilson J.R.U., Vamosi J.C. & Richardson D.M. (2008) Plant diversity in the human diet: Weak phylogenetic signal indicates breadth. *Bioscience*, 58, 151-159
- Puth L.M. & Post D.M. (2005) Studying invasion: have we missed the boat? *Ecology Letters*, 8, 715-721
- Pyšek P. & Richardson D.M. (2007) Traits associated with invasiveness in alien plants. In: *Ecological Studies, Vol. 139* (ed. Nentwig W) Springer-Verlag, Berlin
- Regan T.J., McCarthy M.A., Baxter P.W.J., Panetta F.D. & Possingham H.P. (2006) Optimal eradication: when to stop looking for an invasive plant. *Ecology Letters*, 9, 759-766
- Rejmánek M. (2000) Invasive plants: approaches and predictions. *Austral Ecology*, 25, 497-506
- Richardson D.M., Pyšek P., Rejmánek M., Barbour M.G., Panetta F.D. & West C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, 6, 93-107
- Ricketts T.H., Dinerstein E., Boucher T., Brooks T.M., Butchart S.H.M., Hoffmann M., Lamoreux J.F., Morrison J., Parr M., Pilgrim J.D., Rodrigues A.S.L., Sechrest W., Wallace G.E., Berlin K., Bielby J., Burgess N.D., Church D.R., Cox N., Knox D., Loucks C., Luck G.W., Master L.L., Moore R., Naidoo R., Ridgely R., Schatz G.E., Shire G., Strand H., Wettengel W. & Wikramanayake E. (2005) Pinpointing and preventing imminent

- extinctions. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 18497-18501
- Rouget M. & Richardson D.M. (2003) Inferring process from pattern in plant invasions: A semimechanistic model incorporating propagule pressure and environmental factors. *American Naturalist*, 162, 713-724
- Ruesink J.L. (2005) Global analysis of factors affecting the outcome of freshwater fish introductions. *Conservation Biology*, 19, 1883-1893
- Sala O.E., Chapin F.S., Armesto J.J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., Huenneke L.F., Jackson R.B., Kinzig A., Leemans R., Lodge D.M., Mooney H.A., Oesterheld M., Poff N.L., Sykes M.T., Walker B.H., Walker M. & Wall D.H. (2000) Global biodiversity scenarios for the year 2100. *Science*, 287, 1770-1774
- Schwartz M.W., Hoeksema J.D., Gehring C.A., Johnson N.C., Klironomos J.N., Abbott L.K. & Pringle A. (2006) The promise and the potential consequences of the global transport of mycorrhizal fungal inoculum. *Ecology Letters*, 9, 501-515
- 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 R.I.L. (1996) Introduced plants in Antarctica: Potential impacts and conservation issues. *Biological Conservation*, 76, 135-146
- 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. (1992) Macroinvertebrates and litter nutrient release on a sub-Antarctic island. *South African Journal of Botany*, 58, 105-116
- Smith V.R. (2002) Climate change in the sub-Antarctic: An illustration from Marion Island. *Climatic Change*, 52, 345-357
- Tatem A.J. & Hay S.I. (2007) Climatic similarity and biological exchange in the worldwide airline transportation network. *Proceedings of the Royal Society of London B*, 274, 1489-1496

- Tavares M. & De Melo G.A.S. (2004) Discovery of the first known benthic invasive species in the Southern Ocean: the North Atlantic spider crab *Hyas araneus* found in the Antarctic Peninsula. *Antarctic Science*, 16, 129-131
- Thatje S. & Fuentes V. (2003) First record of anomuran and brachyuran larvae (Crustacea: Decapoda) from Antarctic waters. *Polar Biology*, 26, 279-282
- Turner J., Lachlan-Cope T., Colwell S. & Marshall G.J. (2005) A positive trend in western Antarctic Peninsula precipitation over the last 50 years reflecting regional and Antarctic-wide atmospheric circulation changes. *Annals of Glaciology*, 41, 85-91
- Turner J., Overland J.E. & Walsh J.E. (2007) An Arctic and Antarctic perspective on recent climate change. *International Journal of Climatology*, 27, 277-293
- van Klinken R.D. & Edwards O.R. (2002) Is host-specificity of weed biological control agents likely to evolve rapidly following establishment? *Ecology Letters*, 5, 590-596
- Vaughan D.G., Marshall G.J., Connolley W.M., Parkinson C., Mulvaney R., Hodgson D.A., King J.C., Pudsey C.J. & Turner J. (2003) Recent rapid regional climate warming on the Antarctic Peninsula. *Climatic Change*, 60, 243-274
- Vezina S. (2005) Environmental management in a global economy. *CIM Bulletin*, 98
- Walters L.J., Brown K.R., Stam W.T. & Olsen J.L. (2006) E-commerce and *Caulerpa*: unregulated dispersal of invasive species. *Frontiers in Ecology and the Environment*, 4, 75-79
- Ward D.F., Beggs J.R., Clout M.N., Harris R.J. & O'Connor S. (2006) The diversity and origin of exotic ants arriving in New Zealand via human-mediated dispersal. *Diversity and Distributions*, 12, 601-609
- Whinam J., Chilcott N. & Bergstrom D.M. (2005) Subantarctic hitchhikers: expeditioners as vectors for the introduction of alien organisms. *Biological Conservation*, 121, 207-219
- Williamson M. (1996) *Biological invasions*. Chapman and Hall, London
- Worner S.P. (1988) Ecoclimatic assessment of potential establishment of exotic pests. *Journal of Economic Entomology*, 81, 973-983

Chapter 2 - Breaching the dispersal barrier to invasion: quantification and management for the Antarctic

INTRODUCTION

Increasing globalization and human movement have amplified the rates and extent of species introductions. Most habitats on the planet now harbour introduced species and, for many groups, no asymptote to introductions is in sight (McKinney and Lockwood 1999, Sala *et al.* 2000, Davis 2003, Sax and Gaines 2003, Meyerson and Mooney 2007, Sax and Gaines 2008). Moreover, once established, some alien species are able to colonise a variety of environments, substantially reducing populations of selected indigenous species (sometimes to extinction – e.g. Blackburn *et al.* 2004) and/or fundamentally altering ecosystem functioning (Mack *et al.* 2000, Richardson and van Wilgen 2004, Asner and Vitousek 2005). These impacts can be substantial, both in ecological and economic terms (Pimentel *et al.* 2000, Marais *et al.* 2004). In consequence, translocation of species by humans is recognised as one of the most significant threats to global biodiversity (Ricciardi 2007), and has been accorded a high status in policy interventions and research agendas (Millennium Ecosystem Assessment 2005, Buckley 2008, Hulme *et al.* 2008).

Nonetheless, the importance of understanding the causes and consequences of biological invasions is not novel. Indeed, the ecological and economic significance of invasions have been recognized formally at least since Elton's (1958) early work, but in a more comprehensive, directed fashion since the inception of the Scientific Committee on Problems of the Environment (SCOPE) program on biological invasions (Macdonald *et al.* 1986, Mooney and Drake 1989). Much research effort has now been focused on both understanding and predicting invasions, and specifically which species might invade, given their characteristics, and which communities or areas might be most invasible (Daehler 2003, Duncan *et al.* 2003, Richardson and Pyšek 2006). Although several general patterns have emerged (e.g. Lawton and Brown 1986, Pyšek 1998, Lockwood 1999, Vazquez and Simberloff 2001, Prinzig *et al.* 2002, Thuiller *et al.* 2005, Richardson and Pyšek 2006, van Kleunen *et al.* 2008), perhaps one of the strongest is the significant role of propagule pressure both for introduction and for invasion success (Williamson 1996, D'Antonio *et al.*

2001, Rouget and Richardson 2003, Lockwood *et al.* 2005, Memmott *et al.* 2005). Moreover, from a management perspective, the substantially lower costs of prevention relative to later control have been widely recognized (Mack *et al.* 2000, Courchamp *et al.* 2003, Gren 2008). In consequence, the importance of understanding propagule pressure and the pathways of introduction has recently been repeatedly emphasized (Wonham *et al.* 2005, Minton *et al.* 2005, Hulme *et al.* 2008, Reaser *et al.* 2008, Sax and Gaines 2008).

For intentionally introduced species, initial propagule translocation constitutes a single process. However for unintentionally transported species, which often have small and cryptic propagules, initial propagule translocation should in fact be split into two distinct phases: entrainment, when propagules become associated with a vector and transported from source points to new locations, and drop-off, when those propagules become disassociated with their vector and enter the recipient environment. These are the first steps in a multi-step process (translocation, establishment, spread) that might result in eventual invasion of a given area and transformation of local systems (see Elton 1958, Carlquist 1965, Richardson *et al.* 2000, Williamson 2006, Theoharides and Dukes 2007, Milbau and Stout 2008). The transitions from introduction to establishment, and from establishment to invasion are becoming increasingly well investigated (Duncan 1997, Grevstad 1999, Blackburn and Duncan 2001a, b, Miller *et al.* 2002, Roy *et al.* 2002, Wolfe 2002, Cassey *et al.* 2004, Forsyth *et al.* 2004, Suarez *et al.* 2005). By contrast, and despite its importance, of understanding initial dispersal and the pathways by which it occurs is much more poorly studied (Puth and Post 2005). Although some early investigations were concerned with pathways and propagule pressure along them (Wace 1977, Macdonald *et al.* 1986), and the numbers thereof are now increasing (e.g. Whinam *et al.* 2005, Caton *et al.* 2006, Lewis *et al.* 2006, Liebhold *et al.* 2006, Ward *et al.* 2006, Blackburn and Cassey 2007, Lee and Chown 2007, Davidson *et al.* 2008) the extent of work remains small. From the perspectives of scientific understanding and the development of management interventions, such a situation is unhelpful (Puth and Post 2005, Hulme *et al.* 2008).

Here, I therefore address the extent of seed propagule pressure along the major pathways of introduction to the Antarctic region, including the continent and its surrounding islands. This region is appropriate for such a study for several reasons. First, a variety of alien species

have successfully colonised the region, several of which have become invasive (reviewed in Frenot *et al.* 2005). Second, the countries managing the surrounding islands, and the Antarctic Treaty System, responsible for the governance of the area south of 60° S, have identified biological invasions as one of the most significant conservation threats in the region (de Villiers *et al.* 2006, Mansfield and Gilbert 2008). Third, the pathways of invasion to the region can be readily investigated owing to the fact that both the islands and the continent are relatively isolated from other landmasses (Clarke *et al.* 2005), the pathways (shipping, or air traffic to the continent only) are well-understood, and are predominantly vector and stowaway based (see Hulme *et al.* 2008 for classification), the frequency of transit is low (Frenot *et al.* 2005, Whinam *et al.* 2005), and concern for conservation often overrides any other concerns (such as economic efficiency) making the kinds of surveys required for such an assessment relatively straightforward.

Specifically, the propagule translocation associated with the South African National Antarctic Programme (SANAP) logistics operation is quantified. I determine what propagules become entrained with cargo and expeditioner clothing and how this relates to the local source propagule pool, then investigate what proportion of propagules that become entrained drop-off and enter the environment. I then examine how this relates to the alien species which are established and consider what insight this might provide into past and present movements of alien species in the region. Finally, I examine how this unintentional transfer can be managed by considering what vector characteristics relate to high propagule load and high propagule drop-off and also the efficacy of commonly employed mitigation measures.

MATERIAL AND METHODS

Background to the SANAP logistics operation

Assessments of propagule load were made over a two year period and concerned all of the stations re-supplied by the SANAP re-supply vessel, the *SA Agulhas*. For cargo surveys, propagule surveys were conducted on two voyages to Gough Island (40°20'S, 09°54'W), four voyages to Marion Island (46°54'S, 37°45'E), and two voyages to the South African National Antarctic Expedition IV base (SANAE, Dronning Maud Land, Antarctica) (71°40'S, 02°51'W). For passenger luggage, surveys were conducted on one voyage to Gough Island, three to Marion Island and two to SANAE. Typically these voyages occur in the austral summer, with

Gough Island being re-supplied in September, Marion Island in March and SANAE in December. However because of the ongoing construction of a new research station on Marion Island, two additional voyages were undertaken in August 2006 and August 2007.

Local propagule pool

Between March 2006 and May 2007 all SANAP cargo was packed at a warehouse in Paarden Eiland, an industrial area close to the main cargo dock in Cape Town. Paarden Eiland has large areas of waste ground supporting substantial stands of weedy species. The stores were then re-located to a site on the Victoria and Alfred Waterfront, a commercial development with no substantial propagule sources close by (Appendix A).

To establish the taxonomic composition of propagule sources near to each of the cargo warehouses, vegetation surveys were undertaken. A series (4 in each case) of 500 m transects were walked in four opposing directions away from each of the warehouses and the presence of all vascular plant species encountered along the transect was recorded. Taxonomic composition of the vegetation surrounding the cargo stores was then compared with the taxonomic composition of propagules found in cargo by calculating proportion of shared taxa (see below for cargo survey methods).

To determine potential propagule sources for passenger luggage, information on recent travel history was gathered from expeditioners. Passengers were asked to complete an anonymous questionnaire detailing what countries they had visited for more than 24 hours in the previous 12 months. Because of the large area in which propagules could have become entrained in passenger luggage, it was not possible to make a quantitative comparison of propagule pool and entrained propagules. However, data on whether passengers had visited regions that are climatically similar to the areas serviced by SANAP is valuable in elucidating the establishment likelihood of entrained propagules.

Entrainment in cargo

The SANAP uses a range of containers to transfer cargo from the central stores in Cape Town to research stations on Marion, Gough and SANAE. The primary type of container used to re-supply Gough and Marion Island is a 4.6 m³ shipping container, while SANAE is resupplied

using mainly 36 m³ shipping containers (Appendix B). A container, irrespective of size, was considered a single cargo unit.

For each voyage c. 20 cargo units were surveyed. To ensure samples were not biased by the way in which cargo units were stored or cleaned prior to use, units were randomly selected from the voyage packing list. Entrained propagules were collected from both the inner and outer surfaces of containers using a vacuum cleaner (Electrolux Ultima 1700 watt or Black and Decker V2405) fitted with a nylon mesh filter between the crevice nozzle and the succession pipe, and a pair of tweezers. Samples were categorised according to the location of the warehouse, voyage destination, and the volume of the cargo unit.

Entrainment in passenger luggage

For each voyage c. 20 passengers were randomly selected from a passenger list and asked to submit their field work clothing for inspection. Typically this included: a pair of waterproof over-trousers, waterproof jacket, polar fleece, woolly hat, gloves, socks, bags and footwear. Entrained propagules were collected using a similar method to the cargo surveys. For each item of clothing a nylon mesh filter was fitted between the crevice nozzle and the succession pipe of a vacuum cleaner (Philips, Performer Animal Care or Electrolux Ultima 1700 watt). Each item then was methodically searched using the crevice nozzle of the vacuum cleaner to collect loose material and a pair of tweezers to pick out deeply entrained material. Whinam *et al.* (2005) indicated that jacket pockets, the inside of shoes and seam-lines were likely places to find entrained propagules, so particular attention was paid to these areas. Collections were sorted by item and expeditioner. In addition, note was made of whether the item was issued by SANAP or was the participant's personal property, whether or not Velcro[®] was present on the item, and the destination where the clothing was to be used.

Identification and statistical analyses of propagules in passenger luggage and cargo samples

Where possible, seeds were identified to genus level using seed identification guides (Botha 1999, Cappers *et al.* 2006) and online resources (<http://data.kew.org/sid>, <http://www.oardc.ohio-state.edu/seedid>). In 33 cases for passenger luggage samples and 24

cases for cargo surveys, it was not possible to identify an individual seed to family or genus level. In these instances the seed was assigned to an 'unknown morphotype' category.

To determine whether sampling had adequately detected all taxa entrained within both clothing and cargo, rarefaction curves for samples collected on each voyage were constructed at the genus and family level using the non-parametric Chao 2 estimator (EstimateS v8.0, Gotelli and Colwell 2001, Magurran 2004).

Taxonomic composition of propagules from cargo and clothing from each of the different categories (see above for category descriptions), as well as overall taxonomic similarity between propagules from cargo and clothing, was compared using one-way Analyses of similarity (ANOSIM) based on Bray-Curtis similarities, and were conducted in Primer (v. 5.1.2 Plymouth Marine Laboratory, Clarke and Warwick 2001). Because of the high number of items which contained very few propagules (Fig. 1 and Fig. 3), data were square root transformed prior to analyses.

The ANOSIM test statistic, R , has a theoretical range between -1 and +1 and is a measure of the difference between average ranked values of Bray-Curtis similarities among replicates within (r_w) and between (r_b) treatments.

$$R = (r_b - r_w) / ((n - (n - 1) / 2) / 2)$$

Positive R values represent larger between-treatment compared to within treatment similarities. An R value of zero represents the null hypothesis of no difference. Negative R values are unlikely as they would correspond to similarities across sites being higher than those within sites. The significance level of the R statistic is calculated by comparing the observed R value to that which is computed from 1000 random permutations (Clarke and Warwick 2001).

The taxonomic composition of propagules found in clothing and cargo was compared with the taxonomic composition of species which are known to be established aliens in the Antarctic region as a whole (including all sub-Antarctic islands) by calculating the proportion of shared taxa. In addition, proportion of shared taxa were calculated individually for Marion

and Gough Island (J.D. Shaw and S.L Chown unpublished data). Comparisons were not made for SANAE as no aliens are known to be established in the Dronning Maud Land region.

Finally, Generalized Linear Models (SAS 3.0, SAS Institute Inc, USA) were implemented to compare the numbers of propagules found the different categories (see above for description of categories) of passenger luggage and cargo. Number of seeds per item was the response variable and for cargo, packing location and destination were used as categorical predictors. For clothing, item, presence of Velcro®, whether or not it was issued by SANAP, and destination were used as categorical predictors. Because of the high numbers of samples with low numbers of propagules (Fig. 1 and Fig. 3) a Poisson distribution and a log-link function was assumed. The model was corrected for overdispersion.

Propagule drop-off

The proportion of seeds entrained in cargo and passenger luggage that actually enter the environment was estimated by measuring the degree of propagule drop-off on the re-supply voyage to SANAE in December 2007. The annual voyage involves the transport of c. 100 expeditioners and 800 m³ of cargo from Cape Town c. 5600 km by ship to the Dronning Maud Land coast. Here cargo is transferred to sledges and towed by tracked vehicle c. 150 km inland to the research station. Passengers are flown directly from the vessel to the station by helicopter (Appendix C).

Three size classes of seed were used in the experiment (Liu *et al.* 2008): *Avena sativa* (mean mass 31.5 mg), *Lolium perene* (mean mass 2 mg) and *Agrostis stolonifera* (mean mass 0.06 mg). To ensure homogeneity, seeds were purchased from a bulk seed supply agent (Advance Seed, Krugersdorp, South Africa). Because of strict environmental legislation (see <http://v3.ats.aq/e/cep.htm>), it was necessary to sterilize all seeds which were to be used in the experiment. To achieve this, seeds were heated to 180 °C for 48 h as pilot trials indicated that this was sufficient to prevent germination. Seeds were then sprayed with a water-insoluble blue spray paint (Spectra Spray, South Africa) to ensure ease of re-identification upon recovery. Before deployment, a random sample of the marked, heat-treated seeds was subject to germination trials at 21 °C 12:12 (light:dark) to ensure that the sterilization was successful (see below for detailed methodology).

Because partial recovery, if uncorrected for in analyses, would result in an inflated estimate of drop-off, prior to the experiment an estimate of the accuracy of the sampling protocol was made. Thirty seeds (ten from each size class) were placed into ten sets of field clothing, and 300 seeds (100 from each size class) were placed into 20 cargo units which ranged in volume between 4.6 and 36 m³. The same sampling protocols used for the passenger luggage and cargo surveys (see above) were used to recover seeds immediately. Because there was no opportunity for drop-off, if the sampling protocol was 100% efficient, all seeds should be recovered. Therefore, any values lower than 100% can be attributed to sampling inaccuracy. This was averaged for each seed class and cargo/luggage type, and subtracted from the experimental values to give a corrected drop-off value (Table 1 provides percentage of seeds that were missed for each category of item. These values were subsequently used to calculate in the the correction factor).

Table 1. Mean $\pm$ S.D. percentage of seeds that were missed due to sampling inaccuracy. These values were subsequently used to calculate the correction factor.

	N	<i>Avena</i>	<i>Lolium</i>	<i>Agrostis</i>
Cargo				
Container	8	14 $\pm$ 8.62	19 $\pm$ 10.74	39 $\pm$ 8.40
Reefer	3	43 $\pm$ 5.01	52 $\pm$ 9.42	33 $\pm$ 4.14
Skidoo	9	39 $\pm$ 7.15	56 $\pm$ 6.51	53 $\pm$ 12.60
Clothing				
Bag	10	18 $\pm$ 13.98	27 $\pm$ 10.59	58 $\pm$ 12.29
Boots	10	15 $\pm$ 9.72	22 $\pm$ 9.19	51 $\pm$ 11.01
Fleece	10	17 $\pm$ 8.23	26 $\pm$ 5.16	46 $\pm$ 6.99
Gloves	10	12 $\pm$ 7.89	19 $\pm$ 9.94	53 $\pm$ 9.49
Hat	10	17 $\pm$ 12.52	24 $\pm$ 10.75	47 $\pm$ 6.75
Jacket	10	11 $\pm$ 11.97	23 $\pm$ 10.59	49 $\pm$ 9.94
Socks	10	18 $\pm$ 14.76	24 $\pm$ 11.74	49 $\pm$ 7.38
Trousers	10	19 $\pm$ 11.97	27 $\pm$ 13.37	53 $\pm$ 10.59

During cargo packing in Cape Town, 26 cargo units ranging in volume from 3.96 to 40.56 m³ were seeded with 30 seeds per m³ from each size class. These cargo units were then loaded into the ship's hold and transferred by sleds towed by tracked vehicles to SANAE station. Immediately upon arrival at SANAE station, containers were surveyed using a hand held

vacuum cleaner (Black and Decker V2405) fitted with a nylon mesh filter to recover any remaining seeds. To obtain a measure of drop-off when cargo was being moved around within Antarctica, 12 cargo units, which had not previously been used in the experiment were seeded using the same specifications as when seeding cargo for the initial stage of the journey. These seeds were recovered at the end of the season, approximately one month later.

As part of the SANAP policy to reduce non-indigenous introductions to the Antarctic region, prior to arriving at any SANAP station all passengers are subject to a 'boot washing' procedure where clothing and equipment are checked for propagules. Immediately after this procedure, marked, sterilised seeds (30 seeds per item, 10 of each size class) were placed in the field clothing of 12 passengers (8 station-based personnel and 4 field-based personnel). Items included in the experiment were: outer jacket, outer trousers, hat, gloves, socks, boots, and rucksacks. Approximately one month later, at the end of the field season, any remaining seeds were recovered using the standard passenger luggage survey methodology (see above).

Sampling inaccuracy was corrected for by subtracting the mean number of seeds not detected through experimental error (Table 1) from the drop-off values observed for cargo and passenger luggage (see above). A Generalized Linear Model assuming a binomial distribution and a logit-link function was implemented in R.3.2.1 to compare the drop-off values in cargo using size class of seed voyage stage as categorical predictors. A second model was constructed to compare the drop-off values in passenger luggage using clothing item, size class of seed and station based or field based designation as categorical predictors.

Effect of washing on germinability

To test the effect of washing treatments on germinability, four species from genera commonly found entrained in passenger luggage were selected: *Avena sativa*, *Lolium perenne*, *Poa trivialis* and *Agrostis stolonifera*. Seeds were treated under conditions representative of those which would be available to expeditioners using a home washing machine. These were: no detergent (distilled water), biological washing powder (Skip Intelligent, Unilever, South Africa), and a non-detergent based soap designed for washing

outdoor clothing (Tech Wash, Nikwax, UK). Batches of 100 randomly selected seeds from a commercial seed mix of the relevant species (Advanced Seed, South Africa) were each added to 50 ml of each of the treatment solutions and held at test temperatures of 20, 30, 40, 50 and 60 °C for one hour using a Grant LTD6 waterbath (Grant Instruments, Cambridge, UK). Thereafter, excess water was removed and seeds were placed in batches of 25 on nutrient agar (Merck Biolab Bacteriological agar, Wadeville, Gauteng, South Africa) and placed in an incubator at 21 °C on a 12:12 (light:dark) cycle. Seeds were checked daily for the emergence of the radicle for up to 8 days, after which time fungal contamination halted the experiment.

Performance curves of temperature against number of days until germination were constructed for each species and each treatment. Logit regressions using a quasi-Newton function (Statistica v8, StatSoft. Inc., Tulsa, USA) were used to determine the temperature at which 50% mortality is reached (LT50). The influence of temperature and washing treatment on germination was analysed using a Generalized Linear Model in R.2.3.1 assuming a binomial error distribution and using a logit-link function.

RESULTS

Initial examination revealed samples often contained fragments of invertebrates, organic material and plant parts and seeds. Although the organic material likely contained microorganisms, and some plant fragments may have been capable of vegetative growth, these could not be identified and were excluded. The most abundant propagule type was seeds (Appendix D). Whilst it is accepted that not all of the seeds collected would be viable, analyses have focused on these as an easily quantifiable and identifiable propagule which is a reasonable first step, given the significance of vascular plants as invasives in the region (Frenot *et al.* 2005).

Local propagule pool and entrainment in cargo

In total, 193 items of cargo were surveyed and 800 seeds collected (Table 2) with representatives from 22 families and 57 genera (Appendix E). The majority of samples contained very few seeds although some items contained as many as 47 (Fig. 1). The volume of cargo items significantly affected the total seed load ($\chi^2 = 38.93$, $df = 1$, $p < 0.001$) and so volume was included as a covariate in all subsequent analyses.

Table 2. Mean number of seeds ($\pm$ S.E.) found in cargo sampled on voyages to Gough and Marion Island and, SANAE.

Destination	Gough	Marion	SANAE
Cargo units sampled	42	108	43
Mean $\pm$ S.E. seeds per unit	2.24 $\pm$ 0.43	3.69 $\pm$ 0.77	7.14 $\pm$ 1.76

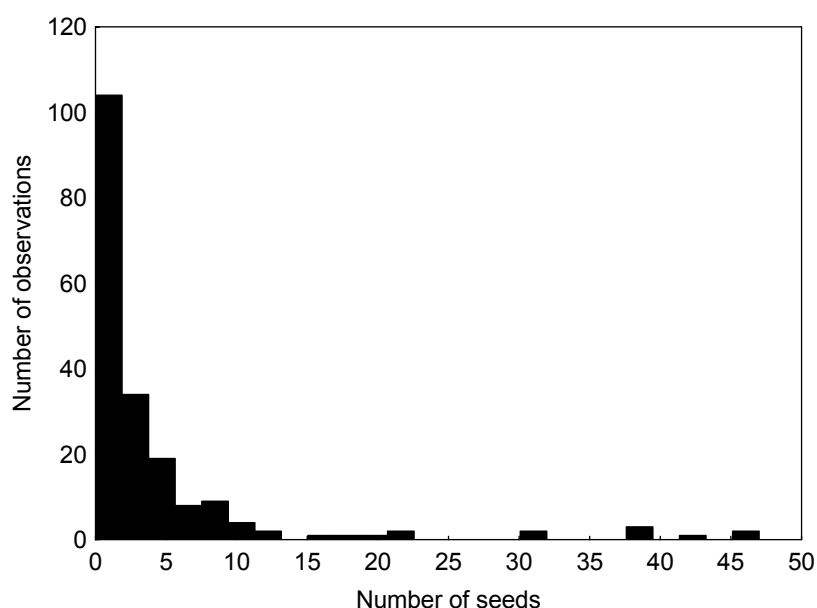


Figure 1. Frequency distribution of number of seeds found in cargo

Using the Chao2 estimator, rarefaction curves for both family and genus level richness were constructed for each voyage and all reached their asymptote, indicating that sampling was sufficient to detect the majority of taxonomic groups (Fig. 2) and therefore allowed analyses of taxonomic similarity to be conducted. Small differences in taxonomic composition at family and genus level were found in samples destined for each of the research stations, and differences were also found between samples collected from cargo packed at the Waterfront and Paarden Eiland at the genus level (Table 3). However, the effect size is small and in all cases the *R* value was close to zero and so although differences are statistically significant, they are not biologically relevant.

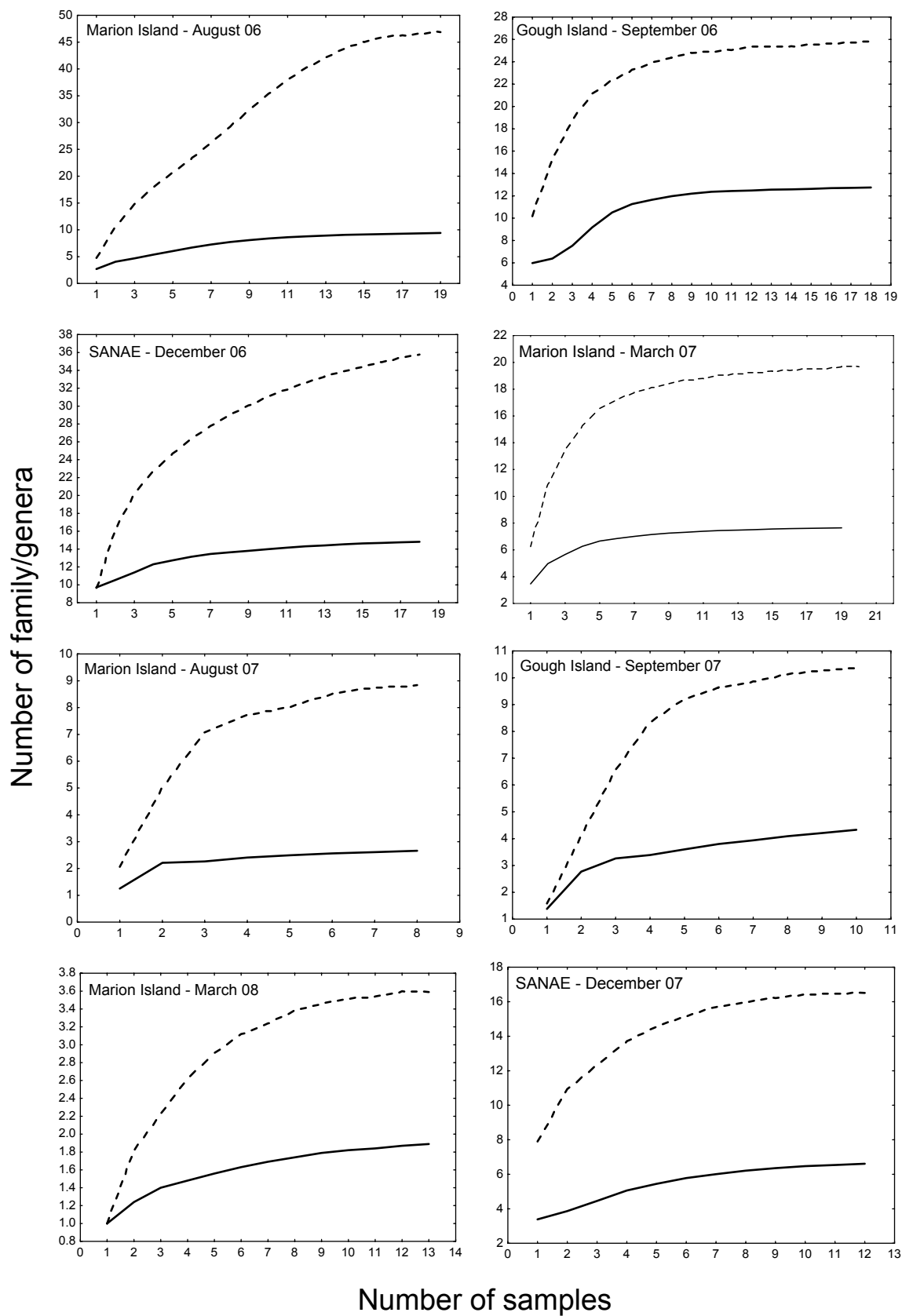


Figure 2. Sample based rarefaction curves showing the increase in numbers of family (solid line) and genera (solid line) with increasing number of cargo units sampled for each voyage

Table 3. ANOSIM global test *R* values for taxonomic similarity in different classes of cargo. * Indicates significance at 0.05, ** indicates significance at <0.001.

Class	Family	Genus
Packing location	0.017	0.05*
Voyage destination	0.072**	0.037*

The vegetation surveys revealed that 56 species of vascular plant were present within a 500 m radius of the Paarden Eiland Stores and 13 species within 500 m of the Waterfront stores (Appendix F). Twenty four of these species are known to be established aliens in the Antarctic and a further 12 have congeners that are known to be established aliens (Frenot *et al.* 2005, J.D. Shaw & S.L. Chown, unpublished data). For cargo packed at Paarden Eiland, 76.6% of families and 77.5% of genera found in the local vegetation were found in the cargo. For cargo packed at the Waterfront 75.0% of families and 84.6 % of genera found in the local vegetation were found in the cargo.

Of the propagules that were entrained within cargo, 70.0% of the families and 63.79% of the genera were from taxa that are known to be established aliens in the Antarctic. When only Marion Island cargo and aliens are included, 20.0% of families and 15.7% of genera found in the cargo are established aliens on the island. For cargo travelling to Gough Island, 35.7% of families and 16.6 % of genera found in cargo are established aliens on the island.

When considering what proportion of established alien species in the Antarctic region are found in samples, when all known aliens are included 21.8% of alien families and 18.4 % of alien genera are represented. However when Marion Island is considered separately, 66% of families and 52.9% of genera which are known aliens on the island were found amongst cargo samples, and for Gough Island 55% of alien families and 29.4% of alien genera were found amongst samples.

Entrainment in passenger luggage

Over the two year sampling period, 606 seeds were collected from 933 items of clothing originating from 127 passengers (Table 4). Data were strongly right skewed with the majority

of items surveyed containing no seeds although four samples harboured more than 20 seeds (Fig. 3). Twenty families and 70 genera were represented (Appendix D).

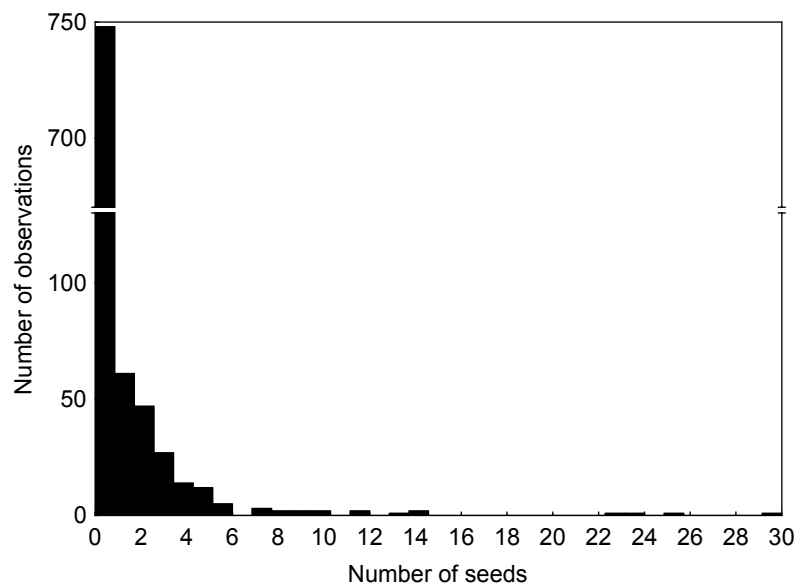


Figure 3. Distribution of propagule loads found in expeditioner clothing. Note the scale break between 150 and 600 observations indicating that the majority of samples contained no propagules.

Table 4. Mean number of seeds ($\pm$ S.E.) found in passenger luggage sampled on voyages to Gough and Marion Island and SANAE.

Destination	Gough	Marion	SANAE
Items sampled	64	451	418
Mean seeds per item $\pm$ S.E.	0.69 ± 0.24	0.95 ± 0.14	0.36 ± 0.05
Expeditioners sampled	12	58	57
Mean number of seeds per expeditioner $\pm$ S.E.	4.4 ± 1.80	7.13 ± 1.25	2.67 ± 0.43

Rarefaction curves for both family and genus level richness were constructed for each voyage using the Chao2 estimator and all reached their asymptote indicating that sampling was sufficient to detect the majority of taxonomic groups (Fig. 4). For all categories of passenger luggage, *R* values are close to zero indicating that taxonomic composition of propagules found in samples was similar (Table 5). Significant differences in taxonomic composition of propagules were found between items but the effect size is extremely small and therefore not considered biologically relevant. This is likely a statistical artefact of the large sample size (Clarke and Warwick 2001).

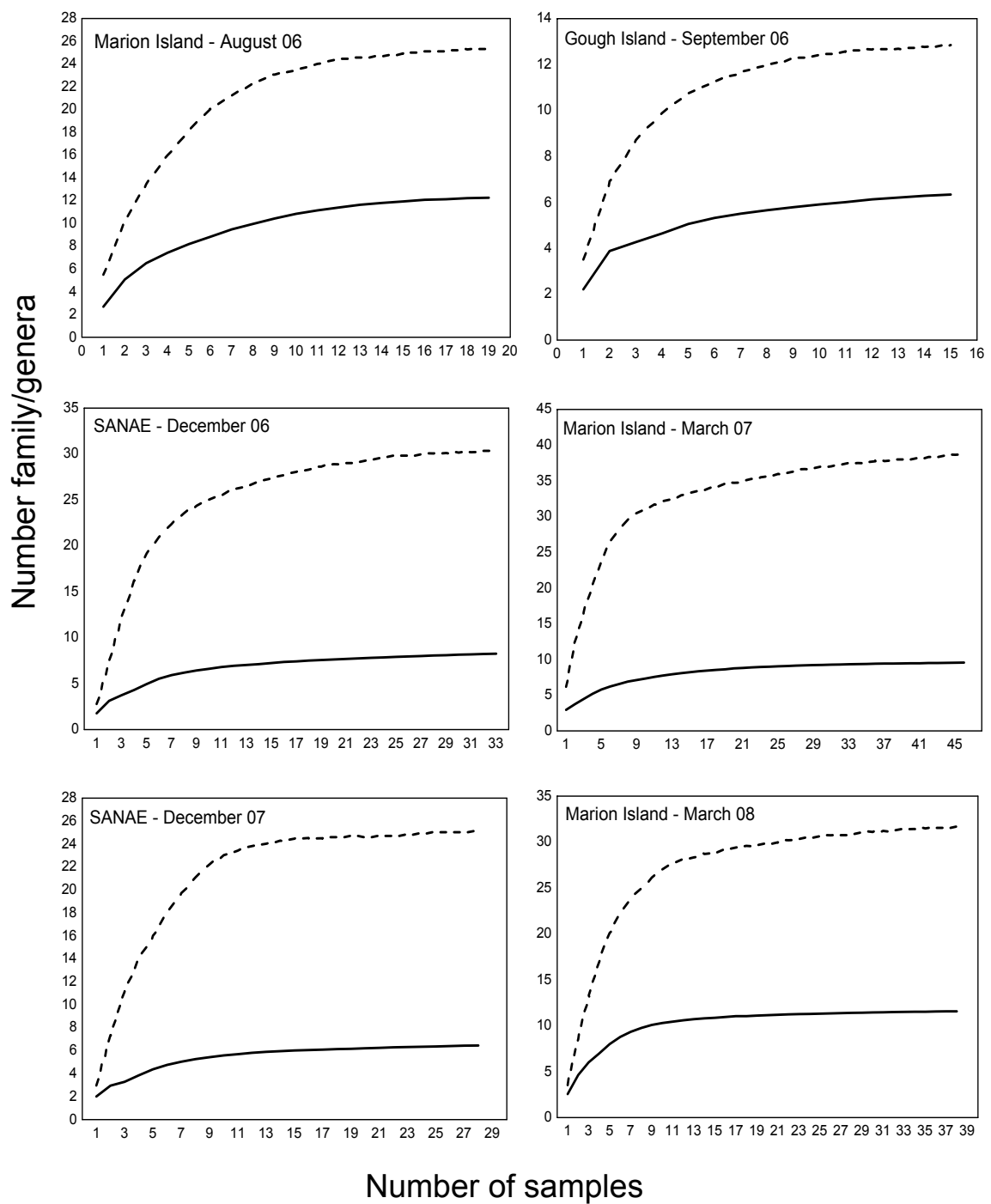


Figure 4. Sample based rarefaction curves showing the increase in numbers of family (solid line) and genera (dashed line) with increasing number of passenger luggage items sampled for each voyage.

Table 5. ANOSIM global test *R* values for taxonomic similarity in different classes of passenger luggage. * Indicates significance at 0.05, ** indicates significance at <0.001.

Class	Family	Genus
Voyage destination	0.015	0.003
Item	0.041*	0.043**
Presence of Velcro	0.02	0.04
Issue	0.009	0.009

Of the propagules that were entrained within passenger luggage, 80.0% of the families and 64.28% of the genera were from taxa that are known to be established aliens in the Antarctic. When only propagules collected from passengers travelling to Marion Island were considered, 30.0% of families and 17.3% of genera found in luggage are established aliens on the island. For Gough Island, 50% of families and 25 % of genera found in luggage are established aliens on the island.

When considering what proportion of alien species already established in the Antarctic region are found in samples, 25% of alien families and 22.3 % of alien genera are represented. For Marion Island, 100% of families and 70.5% of genera which are known aliens on the island were found amongst passenger luggage samples. For Gough Island, which has a much more diverse alien flora, the representation is much less with 33.3% of alien families and 17.6% of alien genera found amongst samples.

Questionnaire data revealed that between all expeditioners, 28 countries had been visited in the 12 months prior to participating in the survey (Fig. 6). Most of the countries visited by expeditioners are at mid to-high latitudes with a temperate or cold-temperate climate, and so at the very coarsest scale are climatically similar to the island stations visited by SANAP. What is more, many of established Antarctic aliens originate in these areas (Frenot *et al.* 2005). A high proportion of expeditioners surveyed had recently travelled in the Antarctic (47.2%).

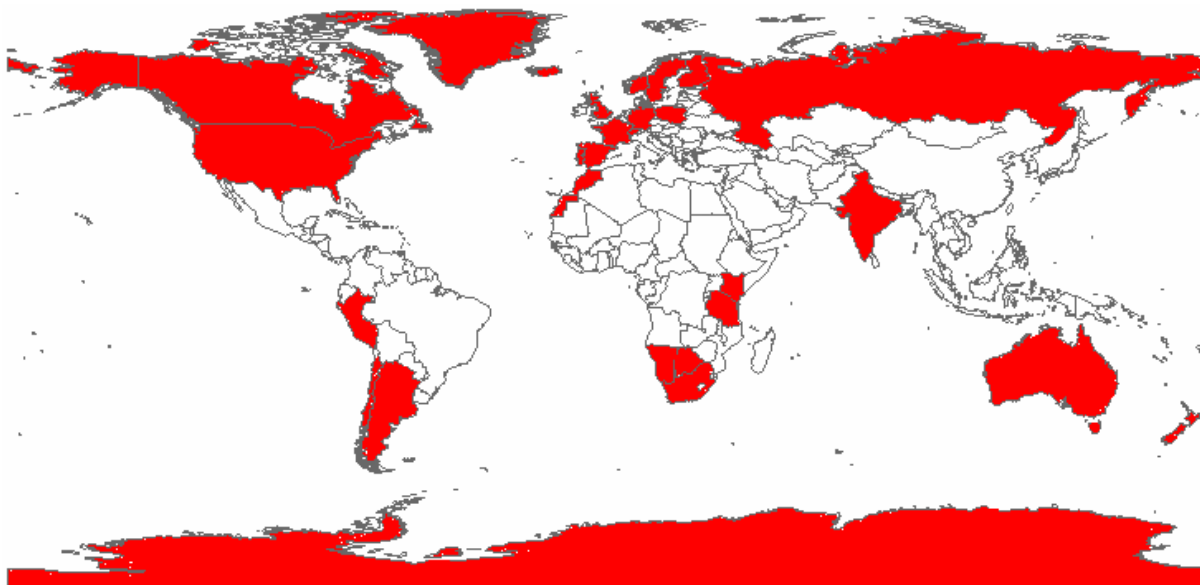


Figure 6. Countries and regions visited by expeditioners in the 12 months prior to participating in the passenger luggage survey.

Comparison of composition of propagules in passenger luggage and in cargo

Many taxa were found in both cargo and passenger luggage samples (Appendix E) although a greater number of families and genera were found in passenger luggage. Small statistical differences in taxonomic composition of seeds found in cargo and passenger luggage were found at the family (ANOSIM global test $R = 0.22$, $p < 0.001$) and the genus (ANOSIM global test $R = 0.117$, $p < 0.001$) level. However, although statistically significant, because R is close to zero they are not considered biologically relevant.

Drop-off

Seed size had no effect on drop-off rate from cargo ($\chi^2 = 2.41$, $df = 2$, $p = 0.503$) or clothing ($\chi^2 = 1.64$, $df = 2$, $p = 0.64$). For cargo, mean drop-off was 20.3% (S.D. = 0.18). Voyage stage had no significant effect on the drop-off rate ($\chi^2 = 0.87$, $df = 1$, $p = 0.675$). For clothing, mean drop-off rate was 53.6% (S.D. = 28.8). Drop-off did not differ significantly between clothing items ($\chi^2 = 7.49$, $df = 7$, $p = 0.588$), or between personnel who were field based, versus personnel who were station based ($\chi^2 = 7.49$, $df = 2$, $p = 0.882$). When only items which contained Velcro® were considered (i.e. jackets, trousers, bags), items which contained

Velcro® had a lower drop-off rate than items which did not contain Velcro® ($\chi^2 = 5.085$, df = 1, $p = 0.0241$) (Fig.7).

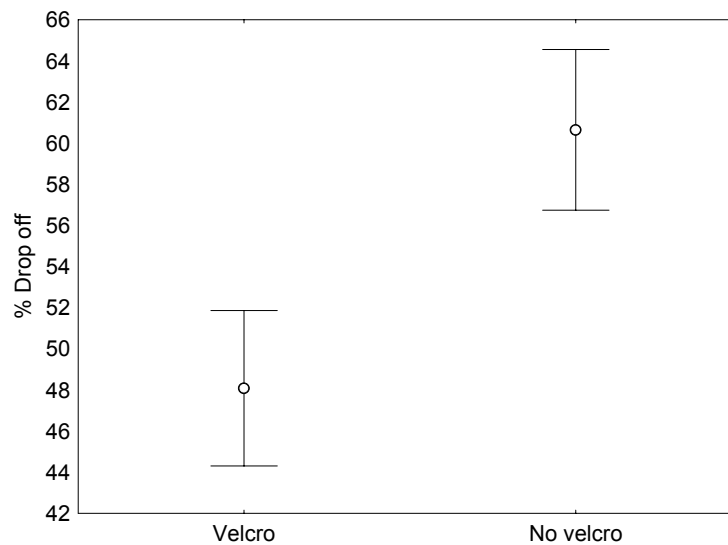


Figure 7. Mean ($\pm$ S.E.) percentage of seeds which dropped off clothing items with Velcro and without Velcro after correction factor had been applied.

Mitigation

Propagule entrainment was not equal across the items surveyed. By identifying vectors and pathways which carry high propagule loads, management action can be targeted, and the threat of invasion reduced.

For cargo, packing location had a significant effect on propagule load with cargo from the Paarden Eiland stores having a greater seed load than that from the Waterfront stores ($\chi^2 = 35.53$, df = 1, $p < 0.001$) (Fig. 8a). This is perhaps unsurprising given the greater abundance and diversity of propagules in the local source pool at Paarden Eiland (Appendix F) and gives a clear indication that an effective way to reduce entrainment is to reduce the abundance of local propagule sources. Voyage destination had no effect on propagule load ($\chi^2 = 5.36$, df = 2, $p = 0.068$) (Fig. 8b).

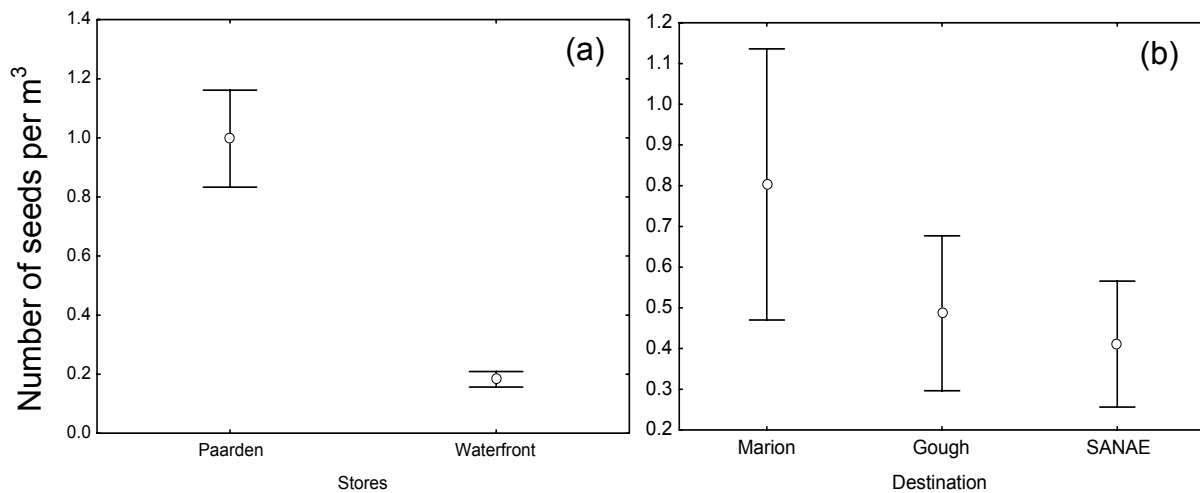


Figure 8. Mean ($\pm$ S.E.) number of seeds per m³ found in (a) cargo items packed at Paarden Eiland and the Waterfront stores (b) cargo items destined for Marion, Gough and SANAE.

For clothing, Generalized Linear Models indicated that some categories of clothing harboured substantially more seeds than others, and therefore it is these items which cleaning processes or management action should be targeted. Number of seeds per item varied significantly with destination ($\chi^2 = 44.50$, $df = 2$, $p < 0.001$) (Fig. 9a), with items surveyed on the way to Marion and Gough Islands having substantially higher seed loads than those surveyed on the way to SANAE. Number of entrained seeds also varied significantly with item ($\chi^2 = 102.74$, $df = 7$, $p < 0.001$) (Fig. 9b), with socks and bags having the greatest seed loads. Passengers own clothing harboured greater numbers of seeds than clothing which was issued by SANAP ($\chi^2 = 67.33$, $df = 1$, $p < 0.001$) (Fig. 9c). Presence of Velcro® was not significant when included in the main model ($\chi^2 = 0.73$, $df = 1$, $p = 0.39$) but when only items which commonly had Velcro® (waterproof trousers and waterproof jackets) were included in analyses, those with Velcro® harboured a greater number of seeds than those without it ($\chi^2 = 5.75$, $df = 1$, $p = 0.016$) (Fig. 9d).

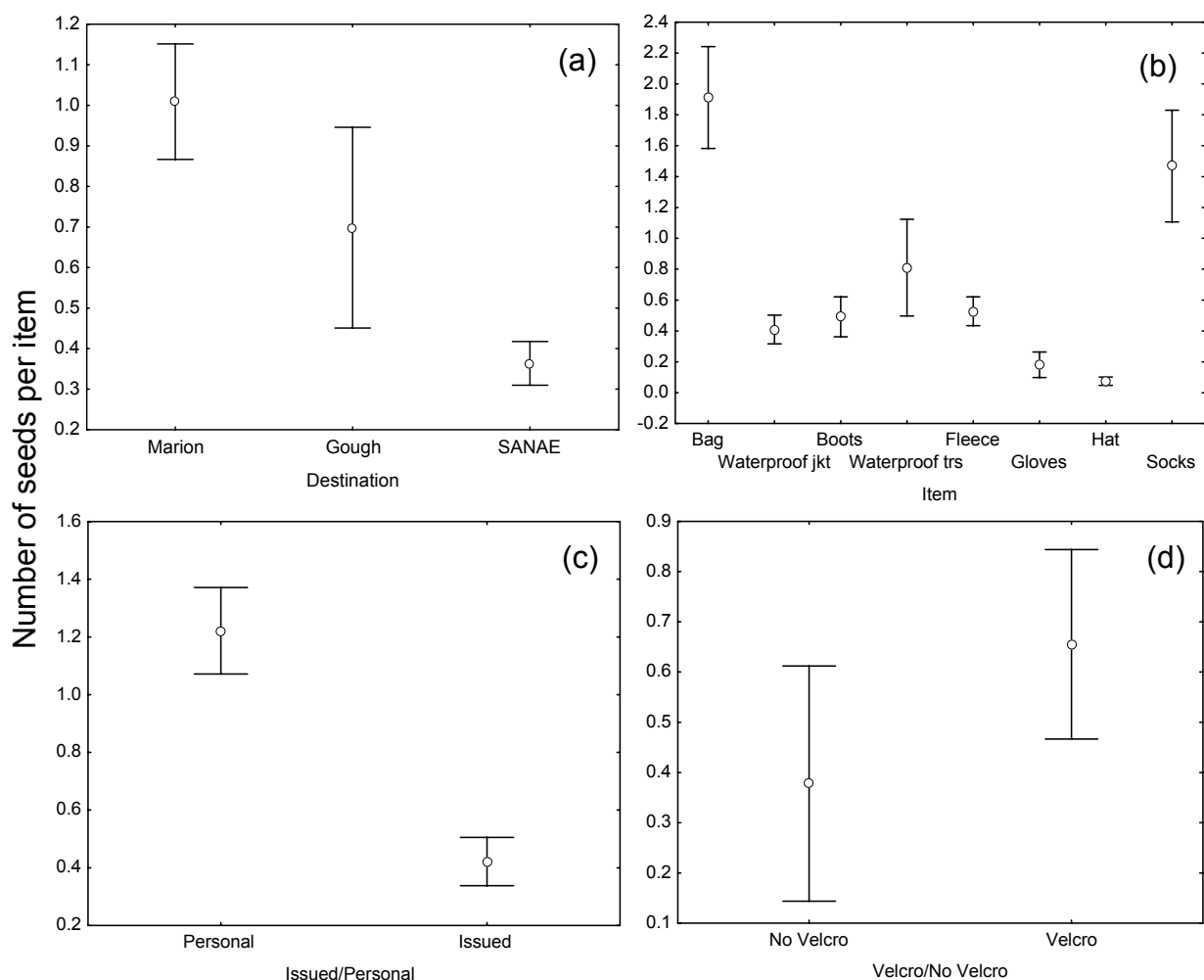


Figure 9. Mean ($\pm$ S.E.) number of seeds found per item in each category of passenger luggage.

The most commonly employed cleaning technique, and the one which is most readily available to expeditioners, is washing in a commercial washing machine. For all species, washing temperature had a significant effect on germinability, but no significant effect of washing treatment was found, except for *Avena sativa* which had low germinability when exposed to biological washing powder (Table 6). High levels of germinability were retained when seeds were exposed to washing temperatures commonly used to clean outdoor clothing (i.e. 40°C). Germinability did not start to decline until seeds were exposed to temperatures in excess of 50 °C and seeds were not sterilized until they had been exposed to temperatures of 70 °C (Fig. 10). Although standard washing machines are capable of operating in excess of this temperature, and so are at least in theory capable of sterilising seeds, washing garments made of specialist fabrics at high temperatures can affect their durability and performance (Grimshaw 2005). Temperature at which 50% of the population fail to germinate ranged between 39 and 53 °C (Table 6). Many specialist fabrics can be

safely washed at these temperatures indicating that although washing does not sterilize seeds, it may have some effect on the germination ability.

Table 6. GLZ results for effect of temperature and treatment on germination in four Poaceae species and mean $\pm$ S.D. LT50 in °C under each washing treatment. *A. sativa* never achieved 50% germination success under a biological washing powder treatment and therefore it was not possible to calculate LT50. * Indicates significance at < 0.05, ** indicates significance at <0.001.

	<i>Avena sativa</i>	<i>Lolium Perene</i>	<i>Poa trivialis</i>	<i>Agrostis stolonifera</i>
GLZ				
χ^2 Temperature (df=6)	53.33**	57.20**	65.24**	61.50**
χ^2 Treatment (df=2)	71.71*	62.46	64.91	62.23
LT50				
Distilled water	47.6 $\pm$ 0.63	53.0 $\pm$ 0.70	50.7 $\pm$ 0.86	50.4 $\pm$ 0.62
Tech Wash	39.5 $\pm$ 1.05	52.0 $\pm$ 0.70	50.3 $\pm$ 0.28	49.2 $\pm$ 1.1
Biological washing powder	-	49.3 $\pm$ 0.70	48.1 $\pm$ 1.93	47.5 $\pm$ 1.47

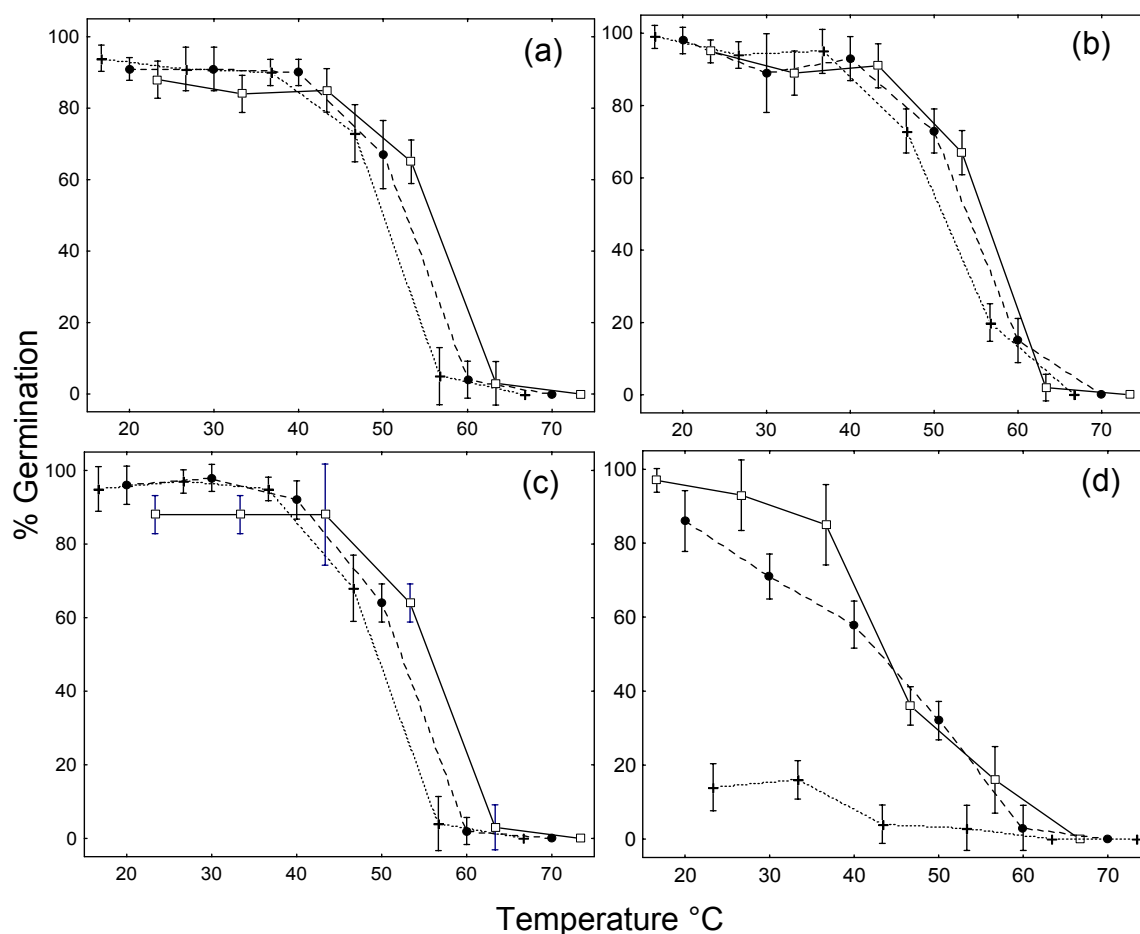


Figure 10. Effect of temperature on germination on (a) *Agrostis stolonifera*, (b) *Lolium perene*, (c) *Poa trivialis* and (d) *Avena sativa* after washing with distilled water ($\square$), Tech Wash ($\bullet$) and a biological washing powder ($+$).

DISCUSSION

Patterns and their implications

Owing to the ban on the introduction of plants and animals to Antarctic and many of its surrounding islands (de Villiers *et al.* 2006, Mansfield and Gilbert 2008), the major introduction pathway to the region is a vector-based, stowaway one (see Hulme *et al.* 2008). Only for islands with permanent human settlements (such as Tristan da Cunha and the Falkland Islands), are other pathways likely to be involved. Nonetheless, even within the single pathway that is significant for most of the region, much variation exists in the numbers (and to some extent the identities) of propagules associated with different source areas and items. This variation suggests that several options are open to reduce the extent of propagule transfer, as is required by national and international legislation across the region, by relatively straightforward, and in many cases cost-effective, interventions.

In terms of taxon identity, the cargo and passenger luggage surveys revealed that seeds from similar genera and families were being entrained by both pathways and that variation among items within each category was low. Given the diverse travel histories of expeditioners and therefore large potential pool of species which had the potential to become entrained, and the different exposure histories of cargo and luggage, this suggests that a relatively small pool of weedy species is being entrained by both methods, and that specific adaptations for zoochory (Liu *et al.* 2008) are unimportant. Thus, encounter frequency, such as with commonly entrained groups with high reproductive outputs (e.g. Asteraceae and Poaceae) (see also Pyšek and Richardson 2007) is the major method of entrainment. Indeed, the distribution of propagule number amongst the various taxonomic groups suggests that this is the case, with the proportions of propagules in the various taxonomic groups (Appendix E) reflecting not only those families known to contain the highest numbers of invasives worldwide (Pyšek 1998), but also reflecting to a large extent, the distribution among genera and families of the species known to have been introduced to the Antarctic region (Frenot *et al.* 2005). For example, all of the families and 70% of genera that are known aliens on Marion Island were found in passenger luggage samples. By contrast, for Gough Island, the current propagule input represents much less of the established alien flora on the island which indicates that some aliens were introduced via

pathways that are now obsolete. For example, two alien genera (*Solanum* and *Verbena*) were not found in any of the samples collected. In the case of *Solanum tuberosum* this is because the species was introduced intentionally and has now escaped human control (Jones *et al.* 2003), so representing a different invasion pathway (escape – Hulme *et al.* 2008). However, it is thought that *Verbena bobariensis*, was introduced unintentionally (Ryan 2007), probably during station construction, and so should probably be considered a different pathway to ordinary relief voyages because construction materials are known to harbour and often different propagule loads (Bergstrom and Smith 1990).

The relatively high similarity of the propagule load across the cargo and luggage suggests either that entrainment is highly local, or is simply occurring in highly disturbed areas that often have similar suites of weedy species (Prinzing *et al.* 2002). The fact that the propagule identity of the less invaded Waterfront cargo site is entirely nested within that of the Paarden Eiland site which harboured many more species is certainly indicative that entrainment from highly disturbed areas is most significant. In consequence, the present data support the idea that transport hubs provide ideal stepping stones for invasive species as these facilities are commonly in semi-industrial locations, close to areas of disturbed ground and are likely to receive high numbers of alien species from across the globe (Pauchard and Alaback 2004, Blumenthal 2006, Hierro *et al.* 2006). Indeed, it seems likely that the SANAP logistics operation forms a small component of a much larger, globally self-perpetuating cycle, whereby weedy species proliferate in disturbed areas, in consequence have an elevated chance of becoming entrained in cargo and transported to other, similarly disturbed habitats, and in turn act as a source population to facilitate invasion to other locations (Greenberg *et al.* 1997, Alston and Richardson 2006). This has important implications for biosecurity policy for the Antarctic because nearly all Antarctic shipping operations use commercial ports, and because substantial volumes of cargo are moved through interconnected transport networks (Drake and Lodge 2004).

As well as transporting a substantial diversity of propagules, logistics operations also transfer substantial numbers of propagules. Expeditioners on the SANAP programme carry on average between 2.67 (SANAE) and 7.13 (Marion Island) seeds per person (Table 4). At present, the only other nation which has attempted to quantify the propagule pressure

associated with a national Antarctic programme is Australia (Whinam *et al.* 2005). Here it was found that on average passengers were each carrying *ca.* 15 seeds, substantially more than the values calculated for South African expeditioners. The difference in propagule load could be attributed to the operational procedure of the respective Antarctic programmes with South African expeditioners often using their clothing for the first time only once they arrive in the Antarctic, whereas at the time the Whinam *et al.* (2005) study was conducted, Australian expeditioners routinely used their equipment for field training in the Tasmanian alpine regions to departure (Chown 2003) where substantial propagule entrainment could have occurred. Nonetheless, it is clear that expeditioners' luggage and cargo act as vectors for a variety of alien, and often invasive species that either have established in the region or could do so.

Most logistics operations centre round a research station, where all cargo and expeditioners are initially offloaded, and where the majority of alien species first become established (Bergstrom and Smith 1990). However, modern logistics operations are facilitating rapid discharge to the field (via fixed wing aircraft in Antarctica and helicopters in Antarctica and on the islands). In consequence, logistics operations could facilitate the rapid range expansion and jump dispersal of newly established aliens (Bergstrom and Smith 1990, Gremmen and Smith 1999). Moreover, the presence of endemics such as *Acaena magellanica* in samples indicates that expeditioners also transport native species. Some native invertebrate species are known to have complex genetic structure (Fрати *et al.* 2001, Mortimer and Jansen van Vuuren 2007, Myburgh *et al.* 2007) and there are indications that vascular plant populations may display a similar pattern (Mortimer *et al.* 2008). Transportation of species between populations could homogenize population genetic structure (Olden *et al.* 2004), with significant impacts not only on modern understanding of evolutionary dynamics in the region (Myburgh *et al.* 2007), but also on the evolution of the species (Fрати *et al.* 2001, Stevens and Hogg 2003) and their ability to withstand the rapid environmental change common to many islands and the Antarctic Peninsula (Convey 2006). Moreover, at least in Antarctica, where long-distance flights between field sites are becoming more common, the risks for the movement of species to sites where they have not occurred previously might also be higher than is perhaps currently acknowledged (although see Bergstrom *et al.* 2006, Chown and Convey 2007). Although vascular plants are not of

concern here, the principles apply as much, or perhaps more so, to species such as invertebrates, mosses and algae.

Mitigation

Although many nations have procedures in place to reduce propagule load, and prevent the spread of alien species, it is clear, from this survey of SANAP, that has stringent procedures in place (Davies *et al.* 2007), that substantial numbers of propagules are still likely being transported into the Antarctic region (Cooper *et al.* 2003, Whinam *et al.* 2005, Hughes *et al.* 2006, Lewis *et al.* 2006). Therefore, if the flow of alien species into the region is to be halted, an urgent need exists to develop improved mitigation measures. By examining the characteristics of those items which not only contain high numbers of propagules but also those which have a high drop-off rate, where such management action should be targeted can be readily identified.

For cargo, entrainment and drop-off is greatest when the cargo is being intensively handled such as at warehouses and during loading and off-loading areas. To minimise the numbers of propagules which are entrained in cargo, ideally it should be loaded in an area free from weedy plants and areas of waste ground. Equally, because drop-off is also highest in these areas, careful monitoring and immediate removal of any newly established species will help prevent the spread of aliens into other areas. This has shown to be successful on Macquarie Island where two introduced plants (*Anthoxanthum odoratum* and *Rumex crispus*) with highly localized distributions were removed and have not since re-colonised (Copson and Whinam 2001). Cargo containers can also be designed to have a minimum of surfaces that promote seed entrainment (Whinam *et al.* 2005), can be inspected and cleaned inside prior to loading, and can easily be sprayed down and inspected prior to transfer to a cargo hold (either aircraft or ship). Such measures typically do not require large infrastructure and personnel investments, and, where expensive containers are to be replaced, they can be phased in as older items age or are damaged. In the case of warehouses situated close to vacant, weed-infested land, a change to a new warehousing area, or the development of an appropriate spraying programme (if possible given that the land may be under different ownership) is likely to mean much greater costs. However, these costs are likely to be low relative to the costs of eradication efforts (Gremmen *et al.* 2001, Bester *et al.* 2002).

In the case of expeditioner luggage, it is clear that items such as bags and socks have high propagule loads and that personal gear poses a higher risk than items that are issued by the logistics operator (which has all items thoroughly cleaned between field trips). Simple, but effective measures, such as the use of new socks for all expeditions and the thorough cleaning of bags will clearly substantially reduce propagule load. Moreover, careful inspection and cleaning of personal gear along with that issued should also reduce the propagule load. Especially for transits by ship, typically plenty of time is available for such gear inspections and cleaning (Whinam *et al.* 2005, de Villiers and Cooper 2008). For transport by air, inspections should be undertaken in advance of departure from the final, pre-Antarctic destination, because logistics often dictate rapid (or at least unpredictable) deployment in the field. After Whinam *et al.* (2005) highlighted the risk of Velcro® as a biosecurity risk, the Scientific Committee on Antarctic Research countries discouraged the use of clothing with Velcro® (Hull and Bergstrom 2006). Here I confirm Whinam's (2005) finding, showing that items with Velcro® do indeed harbour greater numbers of propagules than those without. However when the effects of entrainment and drop-off are disentangled, although Velcro® may harbour substantial propagule loads, these propagules are less likely to be expelled into the environment than propagules on Velcro® free items. Therefore, simply eliminating Velcro® from field clothing is an ineffective way to reduce the risk of invasion.

The washing of clothing is one of the most commonly applied procedures to remove propagules (Chown *et al.* 2006, de Villiers *et al.* 2006, de Villiers and Cooper 2008). However, a clear conflict of interest exists between performance of clothing and the chance of alien introduction. Washing procedures had varying success from being relatively effective (e.g. high temperature treatments or biological washing powder on species such as *Avena sativa*) to having almost no effect (e.g. low temperature treatments and Tech wash). Although standard washing procedures are likely to reduce the number of viable propagules, some will survive, and because small founder populations have sometimes led to invasions (Gaston *et al.* 2003, Scott and Kirkpatrick 2005, Lee *et al.* 2007) simply reducing propagule pressure is ineffective. If invasions are to be halted entirely, propagule pressure needs to be reduced to as close to zero as feasible. However, washing protocols which would sterilise

seeds, such as high temperature treatments, would also damage many commonly used fabrics (<http://www.gore-tex.com/remote/Satellite/content/care-center/washing-instructions>, Grimshaw 2005), leading to a dramatic reduction in their performance. Possible alternatives include irradiation (Luckman 2000) or exposure to extreme low temperatures (Sharp and Hallman 1994). However implementation of such protocols would need a substantial policy revision and investment in infrastructure.

An alternative to inspection and washing is to ship new clothing to the research station of interest and to leave it there once it has been used initially (either for the return of long-term visitors or for re-issue to new expeditioners). This practise is currently being implemented by the Australian Antarctic Division for high risk items such as gaiters (D. Bergstrom Pers. Com.). Although this would not prevent intra-island (sub-Antarctic) or intra-area (Antarctic continent) movement of propagules, it would prevent the introduction of exogenous species. Research stations would need to be equipped with the means to clean and maintain equipment, but no substantial new infrastructure would be required. This therefore may be the most economically and ecologically sensible way to reduce the flow of alien species into the region with expeditioner clothing.

Synthesis and applications

The current work has demonstrated that substantial propagule pressure is associated with current scientific operations to the Antarctic, but that relatively straightforward measures are available to reduce this pressure. Most significantly, a change in the inspection and issuing procedures for expeditioner luggage, and relatively inexpensive changes in cargo operations are likely to result in substantially reduced propagule loads. These procedures, at least in terms of expeditioners, apply as much to the tourist industry (<http://www.iaato.org>) as they do to science logistics. However, they may be much more difficult to apply to large station construction operations, as are currently taking place across the region (<http://cep.ats.aq/cep/index>), and a different approach may be required. Moreover, the problem of propagule exchange within islands or between areas in Antarctica is yet to be adequately resolved.

REFERENCES

- Alston K.P. & Richardson D.M. (2006) The roles of habitat features, disturbance, and distance from putative source populations in structuring alien plant invasions at the urban/wildland interface on the Cape Peninsula, South Africa. *Biological Conservation*, 132, 183-198
- Asner G.P. & Vitousek P.M. (2005) Remote analysis of biological invasion and biogeochemical change. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 4383-4386
- Bergstrom D.M. & Smith V.R. (1990) Alien vascular flora of Marion and Prince Edwards Islands: new species, present distribution and status. *Antarctic Science*, 2, 301-308
- Bergstrom D.M., Convey P. & Huiskies A.H.L. (eds.) (2006) *Trends in Antarctic Terrestrial and Limnetic Ecosystems*. Springer, Dordrecht, The Netherlands
- Bester M.N., Bloomer J.P., Van Aarde R.J., Erasmus B.H., Van Rensburg P.J.J., Skinner J.D., Howell P.G. & Naude 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
- Blackburn T.M. & Cassey P. (2007) Patterns of non-randomness in the exotic avifauna of Florida. *Diversity and Distributions*, 13, 519-526
- Blackburn T.M. & Duncan R.P. (2001a) Determinants of establishment success in introduced birds. *Nature*, 414, 195-197
- Blackburn T.M. & Duncan R.P. (2001b) Establishment patterns of exotic birds are constrained by non-random patterns in introduction. *Journal of Biogeography*, 28, 927-940
- 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
- Blumenthal D.M. (2006) Interactions between resource availability and enemy release in plant invasion. *Ecology Letters*, 9, 887-895
- Botha C. (1999) *Common weeds of crops and gardens in southern Africa*. ARC-Grain Crops Institute, South Africa
- Buckley Y.M. (2008) The role of research for integrated management of invasive species, invaded landscapes and communities. *Journal of Applied Ecology*, 45, 397-402
- Cappers R.T.J., Bekker R.M. & Jans J.E.A. (2006) *Digital Seed Atlas of the Netherlands*. Barkhuis Publishing, Groningen, The Netherlands

- Carlquist S. (1965) *Island life - A natural history of islands of the world*. The Natural History Press, New York
- Cassey P., Blackburn T.M., Jones K.E. & Lockwood J.L. (2004) Mistakes in the analysis of exotic species establishment: source pool designation and correlates of introduction success among parrots (Aves: Psittaciformes) of the world. *Journal of Biogeography*, 31, 277-284
- Caton B.P., Dobbs T.T. & Brodel C.F. (2006) Arrivals of hitchhiking insect pests on international cargo aircraft at Miami International Airport. *Biological Invasions*, 8, 765-785
- 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. (2003) *The probability of Introduction of Non-indigenous Species to Heard and McDonald Islands: Taxa, Risks, and Mitigation*. Report prepared for Australian Antarctic Division, Kingston, Tasmania
- Chown S.L., Davies S. & Joubert L. (2006) *Prince Edward Islands environmental management plan version 0.1*. Centre for Invasion Biology, Stellenbosch
- Clarke A., Barnes D.K.A. & Hodgson D.A. (2005) How isolated is Antarctica? *Trends in Ecology and Evolution*, 20, 1-3
- Clarke K.R. & Warwick R.M. (2001) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Plymouth Marine Laboratory, Plymouth, UK
- Convey P. (2006) Antarctic climate change and its influences on terrestrial ecosystems. In: *Trends in Antarctic Terrestrial and Limnetic Ecosystems* (eds. Bergstrom D.M., Convey P. & Huiskes A.H.L.) Springer, Dordrecht, The Netherlands
- Cooper J., de Villiers M.S. & McGeogh M.A. (2003) Quarantine measures to halt alien invasion of Southern Ocean Islands: the South African experience. *Aliens*, 17, 37- 39
- Copson G. & Whinam J. (2001) Review of ecological restoration programme on subantarctic Macquarie Island: pest management progress and future directions. *Ecological Management and Restoration*, 2, 129-138
- Courchamp F., Chapuis J.L. & Pascal M. (2003) Mammal invaders on islands: impact, control and control impact. *Biological Reviews*, 78, 347-383

- 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
- D'Antonio C., Levine J. & Thomsen M. (2001) Ecosystem resistance to invasion and the role of propagule supply: a California perspective. *Journal of Mediterranean Ecology*, 2, 233-245
- Davidson I.C., McCann L.D., Fofonoff P.W., Sytsma M.D. & Ruiz G.M. (2008) The potential for hull-mediated species transfers by obsolete ships on their final voyages. *Diversity and Distributions*, 14, 518-529
- Davies S.J., Chown S.L. & Joubert L.J. (2007) Renewed management system and provisions for South Africa's sub-Antarctic islands. *Papers and Proceedings of the Royal Society of Tasmania*, 141, 115-120
- Davis M.A. (2003) Biotic globalization: Does competition from introduced species threaten biodiversity? *Bioscience*, 53, 481-489
- de Villiers M.S & Cooper J. (2008) Conservation and management. In: *The Prince Edward Islands: Land-Sea Interactions in a Changing Ecosystem* (eds. Chown S.L. & Froneman P.W.) African SunMedia, Stellenbosch, South Africa
- de Villiers M.S., Cooper J., Carmichael N., Glass J.P., Liddle G.M., Mclvor E., Micol T., Roberts A. (2006) Conservation management at Southern Ocean Islands: towards the development of best practice guidelines. *Polarforschung*, 75, 113-131
- 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
- Duncan R.P. (1997) The role of competition and introduction effort in the success of passeriform birds introduced to New Zealand. *American Naturalist*, 149, 903-915
- Duncan R.P., Blackburn T.M. & Sol D. (2003) The ecology of bird introductions. *Annual Review of Ecology Evolution and Systematics*, 34, 71-98
- Elton C.S. (1958) *The ecology of invasions by animals and plants*. University of Chicago Press, Chicago
- Forsyth D.M., Duncan R.P., Bomford M. & Moore G. (2004) Climatic suitability, life-history traits, introduction effort, and the establishment and spread of introduced mammals in Australia. *Conservation Biology*, 18, 557-569

- Fрати F., Spinsanti G. & Dallai R. (2001) Genetic variation of mtCOII gene sequences in the collembolan *Isotoma klovstadi* from Victoria Land, Antarctica: evidence for population differentiation. *Polar Biology*, 24, 934-940
- Frenot Y., Chown S.L., Whinam J., Selkirk P.M., Convey P., Skotnicki M. & Bergstrom D.M. (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
- Gotelli J.N. & Colwell R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4, 379-391
- Greenberg C.H., Crownover S.H. & Gordon D.R. (1997) Roadside soils: A corridor for invasion of xeric scrub by nonindigenous plants. *Natural Areas Journal*, 17, 99-109
- 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., Barendse J. & Orr I. (2001) Invasion and eradication of *Sagina procumbens* L. (Procumbent pearlwort) on Gough Island. *Aliens*, 14, 19-20
- Gren I.M. (2008) Economics of alien invasive species management - choices of targets and policies. *Boreal Environment Research*, 13, 17-32
- Grevstad F.S. (1999) Factors influencing the chance of population establishment: implications for release strategies in biocontrol. *Ecological Applications*, 9, 1439-1447
- Grimshaw J. (2005). *Atmospheric degradation of fabrics used in ski clothing*. MSc Thesis, University of Leeds, UK
- Hierro J.L., Villarreal D., Eren Ö., Graham J.M. & Callaway R.M. (2006) Disturbance facilitates invasion: the effects are stronger abroad than at home. *American Naturalist*, 168, 144-156
- Hughes K.A., Ott S., Bolter M. & Convey P. (2006). Colonisation processes. In: *Trends in Antarctic Terrestrial and Limnetic Ecosystems* (eds. Bergstrom D.M., Convey P. & Huiskes A.H.L.) Springer, Dordrecht, The Netherlands
- Hull B.J. & Bergstrom D.M. (2006) Antarctic terrestrial and limnetic ecosystems conservation and management In: *Trends in Antarctic terrestrial and Limnetic Ecosystems*: (eds. Bergstrom D.M., Convey P., Huiskes A.H.L.) Springer, Dordrecht, The Netherlands

- Hulme P.E., Bacher S., Kenis M., Klotz S., Kuhn I., Minchin D., Nentwig W., Olenin S., Panov V., Pergl J., Pyšek P., Roques A., Sol D., Solarz W. & Vila M. (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. *Journal of Applied Ecology*, 45, 403-414
- 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
- Lawton J.H. & Brown K.C. (1986) The population and community ecology of invading insects. *Philosophical Transactions of the Royal Society of London B*, 314, 607-617
- 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., Bergstrom D.M. & Whinam J. (2006) Barging in: a temperate marine community travels to the sub-Antarctic. *Biological Invasions*, 8, 787-795
- Liebholt A.M., Work T.T., McCullough D.G. & Cavey J.F. (2006) Airline baggage as a pathway for alien insect species invading the United States. *American Entomologist*, 2, 28-54
- Liu K., Eastwood R.J., Flynn S., Turner R.M. & Stuppy W.H. (2008) Seed Information Database (release 7.1, May 2008) <http://www.kew.org/data/sid>
- Lockwood J.L. (1999) Using taxonomy to predict success among introduced avifauna: relative importance of transport and establishment. *Conservation Biology*, 13, 560-567
- 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
- Luckman G.J. (2000) Food irradiation: Australian quarantine regulatory attitude toward food exports. *Radiation Physics and Chemistry*, 57, 235-237
- Macdonald I.A.W., Kruger F.J. & Ferrar A.A. (1986) *The Ecology and management of Invasions in Southern Africa*. Oxford University Press, Cape Town
- Mack R.N., Simberloff D., Lonsdale W.N., Evans H., Clout M. & Bazzaz F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, 10, 689-710
- Magurran A.E. (2004) *Measuring biological diversity*. Blackwell Science Ltd, Malden

- Mansfield B. & Gilbert N. (2008) Availability and applicability of legal tools for managing non-native species. In: *Non-native Species in the Antarctic* (ed. Rogan-Finnemore M.) Gateway Antarctica Special Publication, Christchurch, New Zealand
- Marais C., van Wilgen B.W. & Stevens D. (2004) The clearing of invasive alien plants in South Africa: a preliminary assessment of costs and progress. *South African Journal of Science*, 100, 97-103
- 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
- Memmott J., Craze P.G., Harman H.M., Syrett P. & Fowler S.V. (2005) The effect of propagule size on the invasion of an alien insect. *Journal of Animal Ecology*, 74, 50-62
- Meyerson L.A. & Mooney H.A. (2007) Invasive alien species in an era of globalization. *Frontiers in Ecology and the Environment*, 5, 199-208
- Milbau A. & Stout J.C. (2008) Factors associated with alien plants transitioning from casual, to naturalized, to invasive. *Conservation Biology*, 22, 308-317
- Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-being: Biodiversity Synthesis*. World Resources Institute, Washington, DC.
- Miller A.W., Hewitt C.L. & Ruiz G.M. (2002) Invasion success: does size really matter? *Ecology Letters*, 5, 159-162
- Minton M.S., Verling E., Miller A.W. & Ruiz G.M. (2005) Reducing propagule supply and coastal invasions via ships: effects of emerging strategies. *Frontiers in Ecology and the Environment*, 3, 304-308
- Mooney H.A. & Drake J.A. (1989) Biological invasions: A SCOPE program overview. In: *Biological Invasions - A Global Perspective*, SCOPE 37. (eds. Drake J.A., Mooney H.A., di Castri F., Groves R.H., Kruger F.J., Rejmanek M. & Williamson M.) John Wiley & Sons Ltd, Chichester, UK
- Mortimer E. & Jansen van Vuuren B. (2007) Phylogeography of *Eupodes minutus* (Acari: Prostigmata) on sub-Antarctic Marion Island reflects the impact of historical events. *Polar Biology*, 30, 471-476
- Mortimer E., McGeoch M.A., Daniels S.R. & Jansen van Vuuren B. (2008) Growth form and population genetic structure of *Azorella selago* on sub-Antarctic Marion Island. *Antarctic Science*, 20, 381-390

- 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
- 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
- Pauchard A. & Alaback P.B. (2004) Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of south-central Chile. *Conservation Biology*, 18, 238-248
- Pimentel D., Lach L., Zuniga R. & Morrison D. (2000) Environmental and economic costs of nonindigenous species in the United States. *Bioscience*, 50, 53-64
- Prinzing A., Durka W., Klotz S. & Brandl R. (2002) Which species become aliens? *Evolutionary Ecology Research*, 4, 385-405
- Puth L.M. & Post D.M. (2005) Studying invasion: have we missed the boat? *Ecology Letters*, 8, 715-721
- Pyšek P. & Richardson D.M. (2007) Traits associated with invasiveness in alien plants. In: *Ecological Studies, Vol. 139* (ed. Nentwig W.) Springer-Verlag, Berlin
- Pyšek P. (1998) Is there a taxonomic pattern to plant invasions? *Oikos*, 82, 282-294
- Reaser J.K., Meyerson L.A. & Von Holle B. (2008) Saving camels from straws: how propagule pressure-based prevention policies can reduce the risk of biological invasion. *Biological Invasions*, 10, 1085-1098
- Ricciardi A. (2007) Are modern biological invasions an unprecedented form of global change? *Conservation Biology*, 21, 329-336
- Richardson D.M. & Pyšek P. (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography*, 30, 409-431
- 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
- Richardson D.M., Pyšek P., Rejmánek M., Barbour M.G., Panetta F.D. & West C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, 6, 93-107

- Rouget M. & Richardson D.M. (2003) Inferring process from pattern in plant invasions: A semimechanistic model incorporating propagule pressure and environmental factors. *American Naturalist*, 162, 713-724
- Roy K., Jablonski D. & Valentine J.W. (2002) Body size and invasion success in marine bivalves. *Ecology Letters*, 5, 163-167
- Ryan P. (2007) *Field guide to the animals and plants of Tistan da Cunha and Gough Island*. Pisces publications, Newbury, UK
- Sala O.E., Chapin F.S., Armesto J.J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., Huenneke L.F., Jackson R.B., Kinzig A., Leemans R., Lodge D.M., Mooney H.A., Oesterheld M., Poff N.L., Sykes M.T., Walker B.H., Walker M. & Wall D.H. (2000) Global biodiversity scenarios for the year 2100. *Science*, 287, 1770-1774
- Sax D.F. & Gaines S.D. (2003) Species diversity: from global decreases to local increases. *Trends in Ecology and Evolution*, 18, 561-566
- Sax D.F. & Gaines S.D. (2008) Species invasions and extinction: The future of native biodiversity on islands. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 11490-11497
- Scott J.J. & Kirkpatrick J.B. (2005) Changes in sub-Antarctic Heard Island vegetation at sites occupied by *Poa annua*, 1987-200. *Arctic, Antarctic and Alpine Research*, 37, 366-371
- Sharp J.L. & Hallman G.J. (1994) *Quarantine Treatments for Pests of Food Plants*. Westview Press, Boulder, Colorado.
- Stevens M.I. & Hogg I.D. (2003) Long-term isolation and recent range expansion from glacial refugia revealed for the endemic springtail *Gomphiocephalus hodgsoni* from Victoria Land, Antarctica. *Molecular Ecology*, 12, 2357-2369
- Suarez A.V., Holway D.A. & Ward P.S. (2005) The role of opportunity in the unintentional introduction of nonnative ants. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 17032-17035
- Theoharides K.A. & Dukes J.S. (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist*, 176, 256-273
- Thuiller W., Richardson D.M., Pyšek P., Midgley G.F., Hughes G.O. & Rouget M. (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology*, 11, 2234-2250

- van Kleunen M., Manning J.C., Pasqualetto V. & Johnson S.D. (2008) Phylogenetically independent associations between autonomous self-fertilization and plant invasiveness. *American Naturalist*, 171, 195-201
- Vazquez D.P. & Simberloff D. (2001) Taxonomic selectivity in surviving Introduced insects in the United States. In: *Biotic homogenization* (eds. Lockwood J.L., McKinney M.L.) Kluwer Academic/Plenum Publishers, New York
- Wace N. (1977) Assessment of dispersal of plant species – the car borne flora of Canberra. *Proceedings of the Ecological Society of Australia*, 10, 167-186
- Ward D.F., Beggs J.R., Clout M.N., Harris R.J. & O'Connor S. (2006) The diversity and origin of exotic ants arriving in New Zealand via human-mediated dispersal. *Diversity and Distributions*, 12, 601-609
- Whinam J., Chilcott N. & Bergstrom D.M. (2005) Subantarctic hitchhikers: expeditioners as vectors for the introduction of alien organisms. *Biological Conservation*, 121, 207-219
- Williamson M. (1996) *Biological Invasions*. Chapman and Hall, London
- Williamson M. (2006) Explaining and predicting the success of invading species at different stages of invasion. *Biological Invasions*, 8, 1561-1568
- Wolfe L.M. (2002) Why alien invaders succeed: support for the escape-from-enemy hypothesis. *American Naturalist*, 160, 705-711
- Wonham M.J., Lewis M.A. & MacIsaac H.J. (2005) Minimizing invasion risk by reducing propagule pressure: a model for ballast-water exchange. *Frontiers in Ecology and the Environment*, 3, 473-478

APPENDIX A

Locations of the two warehouse locations used by the SANAP logistics operation (a) Paarden Eiland, an industrial area close to the main cargo docks in Cape Town. Note the abundant weedy species growing in close proximity to the stores entrance. (b) Victoria and Alfred Waterfront, a new commercial development in the CBD of Cape Town (<http://www.places.co.za>).



APPENDIX B

The two types of containers used by SANAP (a) a smaller 4.3 m³ container used for resupplying Marion and Gough bases. This type of small container is used as all cargo to these stations is transferred using helicopter which have a maximum lift of 4 tonne (b). Larger 36 m³ shipping containers used to resupply SANAE station where cargo is transferred overland and so mass is not an issue (<http://www.antarctica.ac.uk>).



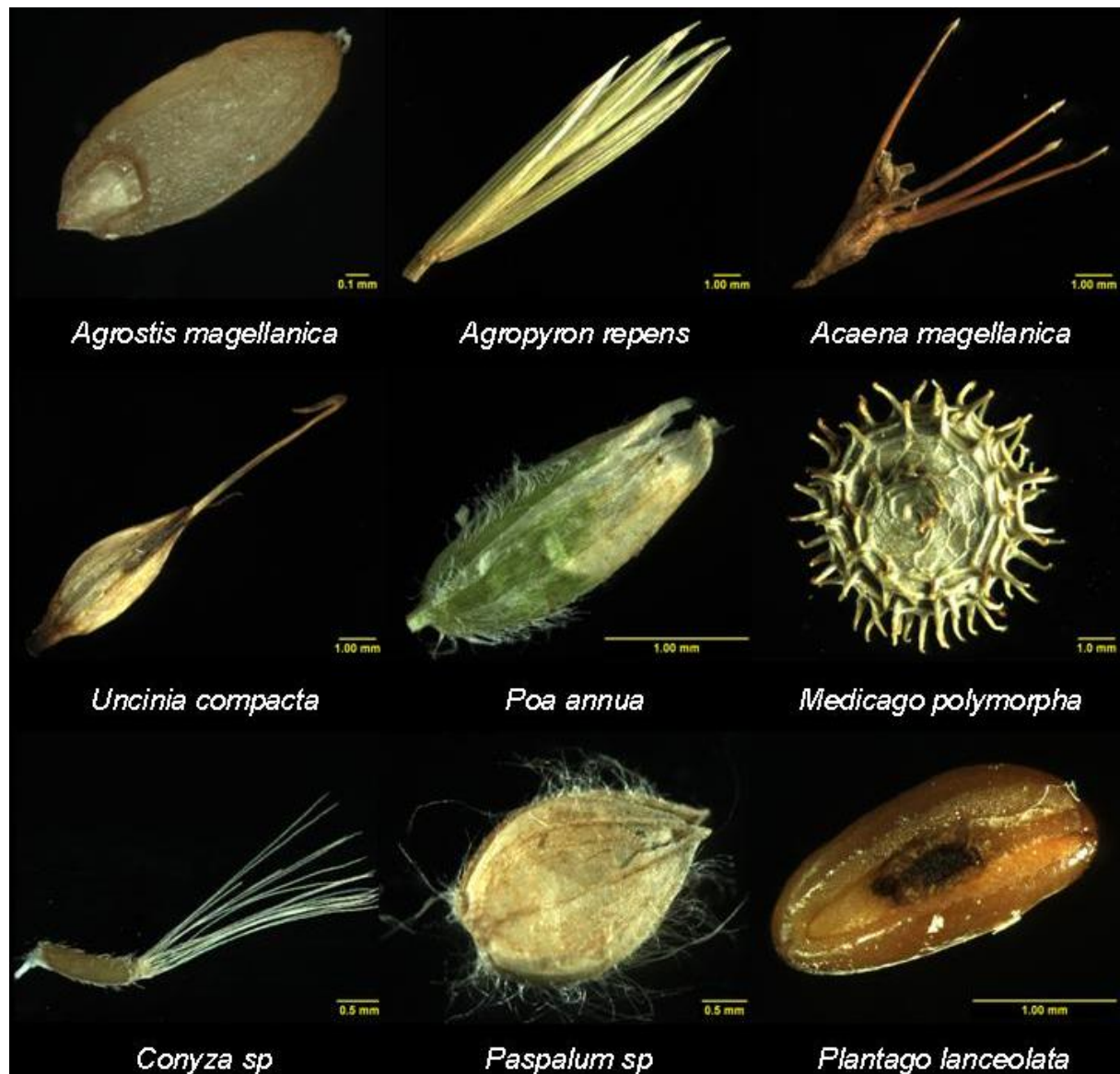
APPENDIX C

(a) SANA E station is located on a remote nunatak 150 km from the Dronning Maud Land coast (b) Tracked vehicles are used to transport cargo the 150 km inland from the edge of the ice sheet where the *SA Agulhas* off loads cargo to SANA E station, where as expeditioners are transferred by helicopter.



APPENDIX D

Examples of some of the seeds found in expeditioner clothing and cargo.



APPENDIX E

Percentage of families and genera found in cargo and passenger luggage samples.

Family	Cargo	Passenger luggage	Genus	Cargo	Passenger luggage
<i>Amaranthaceae</i>	1.71	0.83	<i>Alternanthera</i>	1.71	
			<i>Chenopodium</i>		0.83
<i>Asteraceae</i>	45.52	5.94	<i>Arctotheca</i>	1.28	
			<i>Conyza</i>	23.04	2.15
			<i>Cotula</i>	0.71	
			<i>Echinops</i>		1.16
			<i>Galinsoga</i>	0.14	0.50
			<i>Gnaphalium</i>		0.17
			<i>Hypochaeris</i>	0.71	0.17
			<i>Inula</i>	2.13	0.50
			<i>Lactuca</i>	0.85	
			<i>Matricaria</i>		0.17
			<i>Picris</i>	1.28	
			<i>Senecio</i>	3.27	
			<i>Solidago</i>	0	0.17
			<i>Sonchus</i>	1.99	0.66
			<i>Tagetes</i>	0.43	0.17
			<i>Taraxacum</i>	9.67	
			<i>Xanthium</i>		0.17
<i>Brassicaceae</i>	1.71	0.50	<i>Brassica</i>	0.57	
			<i>Capsella</i>		0.17
			<i>Lepidium</i>	1	0.17
			<i>Sisymbrium</i>	0.14	0.17
<i>Caryophyllaceae</i>	5.69	4.13	<i>Amaranthus</i>	2.56	
			<i>Cerastium</i>		0.17
			<i>Rumex</i>		0.66
			<i>Sagina</i>		3.30
			<i>Silene</i>	0.71	
			<i>Stellaria</i>	2.42	
<i>Chenopodiaceae</i>	1		<i>Chenopodium</i>	0.71	
			<i>Salsola</i>	0.28	
<i>Convolvulaceae</i>	0.43		<i>Ipomoea</i>	0.43	
<i>Cucurbitaceae</i>	1.28		<i>Cucurbita</i>	1.28	
<i>Cyperaceae</i>	1.71	6.77	<i>Cyperus</i>	1.71	2.48
			<i>Carex</i>		0.83
			<i>Uncinia</i>		3.47
<i>Ericaceae</i>		0.17	<i>Erica</i>		0.17
<i>Fabaceae</i>	1	2.31	<i>Medicago</i>		0.66

Continued

Family	Cargo	Passenger luggage	Genus	Cargo	Passenger luggage
			<i>Trifolium</i>	0.57	1.65
			<i>Vicia</i>	0.43	
<i>Geraniaceae</i>	0.43	0.33	<i>Geranium</i>		0.33
			<i>Foeniculum</i>	0.28	
<i>Juncaceae</i>		0.17	<i>Luzula</i>		0.17
<i>Lamiaceae</i>	0.28	0.66	<i>Glechoma</i>		0.17
			<i>Salvia</i>	0.28	
			<i>Scutellaria</i>		0.50
<i>Malvaceae</i>		0.33	<i>Malva</i>		0.33
<i>Orobanchaceae</i>		0.50	<i>Striga</i>		0.50
<i>Oxalidaceae</i>	0.85	0.17	<i>Oxalis</i>	0.85	0.17
<i>Papaveraceae</i>		0.17	<i>Papaver</i>		0.17
<i>Plantaginaceae</i>	0.85	1.82	<i>Plantago</i>	0.85	0.66
<i>Plumbaginaceae</i>		0.33	<i>Armeria</i>		0.33
<i>Poaceae</i>	27.6	63.20	<i>Agrostis</i>	12.23	30.53
			<i>Anthoxanthum</i>		0.17
			<i>Arrhenatherum</i>		2.31
			<i>Avena</i>	0.57	4.29
			<i>Brachypodium</i>		1.65
			<i>Briza</i>	0.57	0.33
			<i>Bromus</i>		1.65
			<i>Calmagrostis</i>		1.49
			<i>Chloris</i>	0.57	
			<i>Cynodon</i>	0.57	0.66
			<i>Dactylis</i>		0.83
			<i>Dactyloctenium</i>	1.28	0.83
			<i>Deschampsia</i>		0.17
			<i>Digitaria</i>	1	0.33
			<i>Eleusine</i>	0.43	0.17
			<i>Elymus</i>		2.48
			<i>Eragrostis</i>	0.43	
			<i>Festuca</i>		1.98
			<i>Holcus</i>		0.33
			<i>Hordeum</i>		0.66
			<i>Imperata</i>	0.57	
			<i>Lamarckia</i>		0.17
			<i>Leymus</i>		0.17
			<i>Lolium</i>	1.99	3.96
			<i>Panicum</i>		0.17
			<i>Paspalum</i>		1.65
			<i>Phalaris</i>		0.83

Continued

Family	Cargo	Passenger luggage	Genus	Cargo	Passenger luggage
			<i>Phragmites</i>		0.17
			<i>Poa</i>	5.97	4.46
			<i>Sorghum</i>	0.71	0.33
			<i>Spartina</i>		0.33
			<i>Tragus</i>	0.71	
			<i>Vulpia</i>		0.17
<i>Polygonaceae</i>	1	0.33	<i>Polygonum</i>		0.33
			<i>Rumex</i>	1	
<i>Rosaceae</i>	2.42	5.12	<i>Acaena</i>		5.12
			<i>Fragaria</i>	0.71	
			<i>Malus</i>	0.71	
			<i>Pyrus</i>	0.14	
			<i>Rubus</i>	0.57	
			<i>Sorbus</i>	0.28	
<i>Rubiaceae</i>	1		<i>Galium</i>	1	
<i>Sapindaceae</i>	0.28		<i>Acer</i>	0.28	
<i>Solanaceae</i>		0.17	<i>Nicotiana</i>		0.17
<i>Ulmaceae</i>		0.33	<i>Ulmus</i>		0.33
<i>Urticaceae</i>	1.56		<i>Urtica</i>	1.56	
<i>Zygophyllaceae</i>	0.14	0.17	<i>Tribulus</i>	0.14	0.17
Unknown	3.41	7.0	Unknown	3.41	7

APPENDIX F

Species of vascular plant growing within 500 m of the cargo packing locations at Paarden Eiland and the Waterfront.

Family	Genus	Species	Paarden Eiland	Waterfront
Amaranthaceae	<i>Alteranthera</i>	<i>pungens</i>	x	
	<i>Amaranthus</i>	<i>hybridus</i>	x	
Apiaceae	<i>Foeniculum</i>	<i>vulgare</i>	x	
Asteraceae	<i>Arcotheca</i>	<i>calendula</i>	x	
	<i>Cirsium</i>	<i>vulgare</i>	x	
	<i>Conyza</i>	<i>albida</i>	x	x
		<i>canadensis</i>	x	
	<i>Cotula</i>	<i>australis</i>	x	x
	<i>Galinsoga</i>	<i>parviflora</i>	x	
	<i>Hypochoeris</i>	<i>radicata</i>	x	
	<i>Inula</i>	<i>graveolens</i>	x	x
	<i>Lactuca</i>	sp.	x	
	<i>Picris</i>	<i>echiodes</i>	x	x
	<i>Senecio</i>	<i>consanguineus</i>	x	x
	<i>Solidago</i>	sp.	x	
	<i>Sonchus</i>	<i>asper</i>	x	x
	<i>Tagetes</i>	<i>minuta</i>	x	
	<i>Taraxacum</i>	<i>officinale</i>	x	x
	<i>Xanthium</i>	<i>spinosum</i>	x	
Brassicaceae	<i>Lepidium</i>	<i>bonariense</i>	x	
	<i>Sisymbrium</i>	<i>capense</i>	x	
Caryophyllaceae	<i>Silene</i>	<i>gallica</i>	x	
	<i>Stellaria</i>	<i>media</i>	x	x
Chenopodiaceae	<i>Chenopodium</i>	<i>carinatum</i>	x	
Convolvulaceae	<i>Ipomoea</i>	sp.	x	
Cyperaceae	<i>Cyperus</i>	<i>rotundus</i>	x	
Euphorbiaceae	<i>Chamaesyce</i>	<i>prostrate</i>	x	
Fabaceae	<i>Medicago</i>	<i>polymorpha</i>	x	
	<i>Melilotus</i>	sp.	x	
	<i>Trifolium</i>	<i>repens</i>	x	
	<i>Vicia</i>	<i>sativia</i>	x	
Malvaceae	<i>Malva</i>	<i>parviflora</i>	x	
Oxalidaceae	<i>Oxalis</i>	sp.	x	
Poaceae	<i>Agrostis</i>	sp.	x	x
	<i>Avena</i>	<i>fatua</i>	x	
	<i>Briza</i>	sp.	x	
	<i>Bromus</i>	<i>catharticus</i>	x	
	<i>Chloris</i>	sp.	x	
	<i>Cynodon</i>	<i>dactylon</i>	x	
	<i>Dactyloctenium</i>	<i>aegyptium</i>	x	
	<i>Digitaria</i>	<i>sanquinalis</i>	x	
	<i>Eragrostis</i>	sp.	x	

Continued

Family	Genus	Species	Paarden Eiland	Waterfront
	<i>Eleusine</i>	sp.	x	x
	<i>Imperata</i>	sp.		
	<i>Lolium</i>	<i>multiflorum</i>	x	x
		<i>perenne</i>	x	
	<i>Poa</i>	<i>annua</i>	x	x
	<i>Sorghum</i>	<i>halepense</i>	x	
	<i>Tragus</i>	sp.	x	
Plantaginaceae	<i>Plantago</i>	<i>lanceolata</i>	x	
		<i>major</i>	x	
Polygonaceae	<i>Emex</i>	<i>australis</i>	x	
	<i>Polygonum</i>	<i>aviculare</i>	x	
	<i>Rumex</i>	<i>Crispus</i>	x	x
Rubiaceae	<i>Galium</i>	sp.	x	
Urticaceae	<i>Urtica</i>	<i>Urens</i>	x	

Chapter 3 - Quantifying the propagule load associated with the construction of an Antarctic research station

INTRODUCTION

Biological invasions are one of the primary concerns for the conservation of Antarctica and its surrounding islands (Bergstrom and Chown 1999, Frenot *et al.* 2005). Although non-indigenous species are not as extensively established on the Antarctic continent as they are on the surrounding islands, they have become one of the foremost concerns of the Committee for Environmental Protection (CEP), the body charged with the conservation of Antarctica (Clout and De Poorter 2008). The CEP has recognized that the prevention of the introduction of non-indigenous species is the most effective step in preventing biological invasions (Mansfield and Gilbert 2008). In consequence, quantifying the potential risks posed by different introduction routes is of considerable importance.

However, research concerning the invasion process in the Antarctic is as much biased to post-dispersal processes and impacts as it is elsewhere (compare Convey *et al.* 2008 and Puth and Post 2005). Only a few studies have documented the relationship between likelihood of introduction and vector numbers (Chown *et al.* 1998), the nature of microbial entry pathways (e.g. Hughes 2003), the role of ballast water and hull fouling (e.g. Lewis *et al.* 2003, Lee and Chown 2007), and the relative significance of transport methods for terrestrial propagules (Whinam *et al.* 2005). In addition, although several of these studies highlight introduction pathways, they do not quantify propagule pressure in a manner that might enable further explicit assessment of risk. Because initial dispersal is the stage in the invasion process on which all others depend (Richardson *et al.* 2000), and because propagule pressure is such a significant correlate of introduction and subsequent invasion success (Lockwood *et al.* 2005, Richardson and Pyšek 2006), the quantification of propagule pressure is essential for understanding the human-assisted colonisation process, and how it might be managed to reduce the risk of introductions. Such quantification can provide insights readily applicable to a variety of situations (see Puth and Post 2005), and because of the island-like nature of the Antarctic (Chown and Convey 2007) and considerable threat by invasions to

island biotas elsewhere (Vitousek 2002, Causton *et al.* 2006) is of substantial value in this context.

Non-indigenous terrestrial species can enter the Antarctic via cargo operations, personal clothing and equipment, and construction materials. For tourist operators the most significant pathway is likely to be via personal clothing as these vessels offload little or no cargo in the region. In contrast, national operators transport large volumes of cargo and it is these operations are thought to be amongst the most effective at transporting propagules (Whinam *et al.* 2005). Specifically several invasions in the region have been attributed to propagule transport with building materials (Bergstrom and Smith 1990, Slabber and Chown 2002, Jones *et al.* 2003). Moreover, large quantities of cargo and packing materials are shipped into the Antarctic each year to build and maintain research facilities. Indeed, at present, many nations are replacing or erecting new stations in the Antarctic or have just done so, *viz.* Marion Island (South Africa), Atka Bay (Germany), Utsteinen Nunatak (Belgium), Halley Bay (U.K.), Schirmacher Oasis (India); South Pole (U.S.A.), and Dome A (European consortium). At present 37 year-round and 16 summer-only stations operate in the region (<http://www.comnap.aq>), all of which require upkeep. According to the Protocol on Environmental Protection, if a station cannot be maintained it has to be removed.

Here the construction of the Halley VI station on the Brunt Ice shelf, Droning Maud Land, Antarctica is used to provide a first estimate of the propagule pressure likely associated with the construction of a typical Antarctic research station. The Halley VI construction (<http://www.antarctica.ac.uk>) is ideal for this question because a variety of construction materials are sourced and stored in different locations, enabling comparisons to be made among cargo types and localities.

MATERIAL AND METHODS

It is expected that 16 000 m³ of materials will be required to construct Halley VI. In December 2007, *c.* 6400 m³ of that cargo was shipped from South Africa to Antarctica. Prior to shipment, cargo was assembled in Cape Town, and stored either in the open at the dock side, or in a warehouse close (*c.* 10 km) to the docks. The warehouse was located in a small industrial estate and no substantial propagule sources were located close by. By contrast, at

the dockside, close to and in the cargo storage area, large areas of waste ground with dense stands of weedy vegetation were present.

All of the steel space frames and fibre glass panels used in the construction of the station were manufactured in South Africa, whereas internal fixtures and fittings were shipped from the U.K. and Europe. In total, 865 m³ of cargo comprising 92 individual units ranging in volume from 0.2 to 27.5 m³ was sampled. Although the range of cargo sampled at each location was similar, because of space constraints at the warehouse the majority of large volume items were stored at the dockside. Cargo was divided into materials packed in wooden shipping cases (n=56), materials packed onto pallets (n=26), and loose material stored inside shipping containers (n=10).

Cargo was carefully examined and small seeds and larger clumps of vegetative material were collected using tweezers. A hand held vacuum cleaner (Black and Decker V2405) fitted with a mesh filter was used to gather fine material. Samples were stored in the dark at room temperature (c. 23°C). During processing, organic material, plant material and invertebrate fragments were found in the samples. Although the organic material likely contained high numbers of microorganisms and some plant fragments may have been capable of vegetative growth, it was not possible to identify and accurately quantify these groups and they were excluded from further analyses. Thus, only seeds were considered here, a reasonable first step given the significance of vascular plants as invasive alien species in the region (Frenot *et al.* 2005). All seeds were identified to genus level. To determine whether sampling had gone to completion, non-parametric Chao 2 estimators were calculated using EstimateS (v8.0) and rarefaction curves were constructed for genus- and family-level data (Gotelli and Colwell 2001).

A Generalized Linear Model assuming a Poisson distribution and using a log-link function (SAS 3.0, SAS Institute Inc, USA) was implemented to compare the number of propagules in different types of cargo and cargo which had been stored in the different locations, while correcting for cargo volume. To compare the taxonomic composition of propagules from different shipping routes and cargo types, data were square root transformed, Bray-Curtis similarities calculated, and a one-way Analysis of Similarity (ANOSIM) conducted in Primer

(5.1.2 Plymouth Marine Laboratory) to determine significance of the differences among cargo types and storage locations. Thereafter, mean number of seeds per cubic meter were calculated for each cargo type and sampling location and scaled up to give approximate number of propagules transported for the construction of the entire station.

RESULTS

In total, 176 seeds representing 15 families and 34 genera were collected (Appendix), and sampling had gone to completion (Fig. 1). Mean propagule load across all items was 0.31 seeds.m⁻³ (S.D. = 0.67), and the Asteraceae (32.1%) and Poaceae (30.4%) were most commonly represented. Cargo sampled at the dock side had significantly higher propagule loads than cargo stored in the nearby warehouse ($\chi^2 = 36.30$, df = 1, $p < 0.001$). Cargo packed on pallets had significantly higher propagule loads than loose items or those stored in wooden cases ($\chi^2 = 16.04$, df = 2, $p < 0.001$) (Fig. 2). Slight differences in taxonomic composition were found between cargo sampled at the dockside and cargo sampled at the warehouse but the effect size is small and not considered to be biologically relevant. Samples from different cargo types were taxonomically similar at the genus and the family level (Table 1).

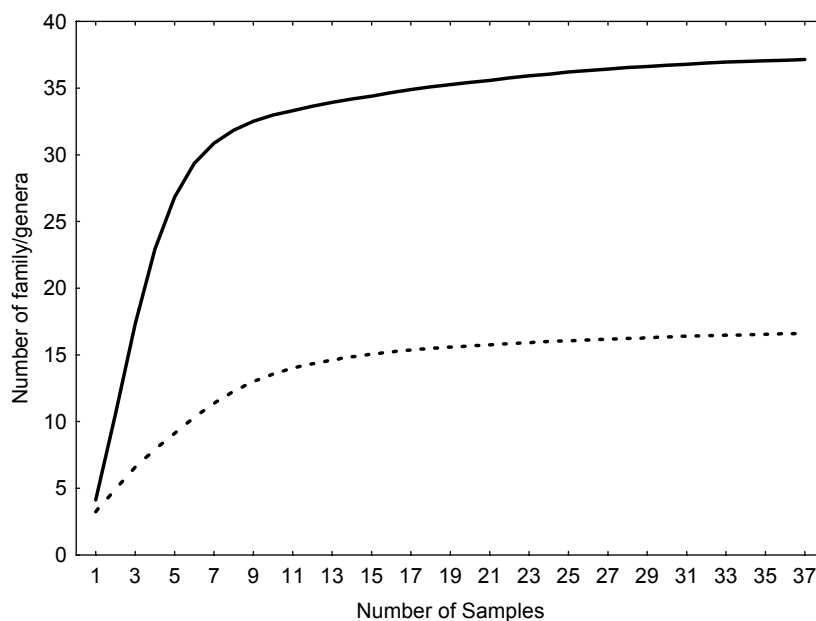


Figure 1. Sample based rarefaction curves showing the increase in numbers of families (dashed line) and genera (solid line) with increasing number of samples.

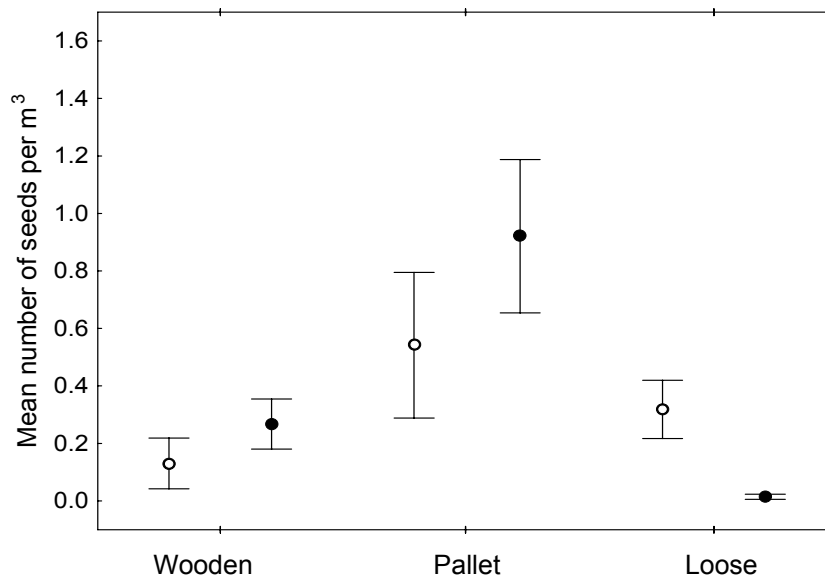


Figure 2. Mean numbers ($\pm$ S.E.) of seeds per m^3 for cargo types stored at the dockside (●) and warehouse (○).

Table 1. ANOSIM global test R values for taxonomic similarity in different classes of cargo. * Indicates significance at 0.05, ** indicates significance at <0.001 .

Class	Family	Genus
Packing location	0.31 **	0.087**
Cargo type	0.043	0.006

Based on the proportion of each cargo type at each sampling location and using the mean number of seeds per m^3 for each category, the total propagule load of the cargo was estimated as 2203 seeds for the 2007/2008 season (Table 2). It is expected that a further c. 9400 m^3 of cargo will be required to complete construction, and assuming cargo composition similar to that found here, a further 3217 seeds will be transported, bringing the estimated total to 5423 for the construction of Halley VI.

Table 2. Volumes and predicted numbers of seeds for each cargo type stored at dockside and warehouse locations (Photos – B. Newham).

Location	Cargo Type (units sampled)	Seeds counted	Vol. 2007 (m ³)	Predicted no. seeds 2007	Predicted vol. 2008 (m ³)	Predicted no. seeds 2008
 Dockside	Loose Items (5)	2	2080.62	30.16	3034.12	43.99
	Wooden Case (18)	65	1667.43	446.37	2431.57	650.93
	Pallet (9)	78	1430.90	1317.57	2086.64	1921.38
 Warehouse	Loose Items (5)	8	189.84	60.46	276.83	88.17
	Wooden Case (38)	7	654.06	118.25	953.80	172.44
	Pallet (17)	16	430.67	233.24	628.03	340.14
Total		176	6453.52	2206.06	9410.99	3217.05

DISCUSSION

Although no plant or animal could establish on the ice shelf at Halley VI, it is clear that the construction of an Antarctic research station, many of which are located on ice-free ground (<http://www.comnap.aq/>), is likely to introduce substantial numbers of propagules, a high proportion of which are from taxa that include invasive species (Appendix). The Asteraceae and Poaceae both contain substantial numbers of species known to be invasive in the region (Frenot *et al.* 2005, Chwedorzewska 2008) and globally (Daehler 1998). The prevalence of common taxa in the propagule load lends further support to the idea of a self-sustaining cycle, and illustrates how invaders can undergo rapid increases in range size, with species that are common in disturbed areas, such as docksides, becoming entrained in cargo and then transported to other similar locations where they are likely to again become entrained (Shimono and Konuma 2008). On a global scale, such entrainment has important implications for biosecurity policy, but is also important in a regional context because of the central place cargo model used in many Antarctic areas. On sub-Antarctic islands, the central storage areas at bases often have a high prevalence of alien species (Bergstrom and Smith 1990) and if these become entrained within cargo, resupply may facilitate jump dispersal to inaccessible areas. The potential for such a situation on the Antarctic Peninsula is developing rapidly given the spread of the otherwise uncommon invasive alien, *Poa annua*, at Arctowski Station on King George Island (Chwedorzewska 2008).

While tourist and scientific cruises represent a high proportion of the total traffic in the Antarctic region compared with voyages dedicated to construction (Lamers *et al.* 2008), the latter are potentially problematic because of the volume of cargo involved and the difficulty of reducing its propagule load (Whinam *et al.* 2005). In consequence, and as I have shown, cargo for construction represents a major vector for non-indigenous species. This is especially concerning given much station-building activity in the region (see above and <http://cep.ats.aq/cep/index>) and ongoing climatic change at some sites (Chown and Convey 2007). Moreover, the propagule loads documented here also suggest that cargo shipping globally may be a major vector of weedy species. All of the species found entrained in dockside cargo were found growing in the waste ground area of the docks and it thus appears that the propagules were locally sourced. If propagule loads on cargo bound for other ports is anywhere close to what I have found here, the global propagule load is likely

to be substantial. Here I found 176 seeds on 865 m³ of cargo for one voyage, while at the Port of Cape Town alone 3400 vessels and c. 48 770 000 gross tonnes of cargo were handled in 2006 (<http://www.ports.co.za/cape-town.php>).

Nonetheless, management action to reduce propagule transfer can be taken, by selecting carefully the type of packing approach adopted, and more importantly, by making sure that wherever possible closed warehousing is used and docksides remain free of weedy species. Such approaches will be especially significant for shipping *en route* to and among sites on the Antarctic Peninsula, which, from a temperate invasive species perspective, is showing rapid climatic amelioration.

REFERENCES

- 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. & Smith V.R. (1990) Alien vascular flora of Marion and Prince Edwards Islands: new species, present distribution and status. *Antarctic Science*, 2, 301-308
- Causton C.E., Peck S.B., Sinclair B.J., Roque-Albelo L., Hodgson C.J. & Landry B. (2006) Alien insects: Threats and implications for conservation of Galapagos Islands. *Annals of the Entomological Society of America*, 99, 121-143
- 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., 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
- Chwedorzewska K.J. (2008) *Poa annua* L. in Antarctic: searching for the source of introduction. *Polar Biology*, 31, 263-268
- Clout M. & De Poorter M. (2008) Invasive Alien Species: Global Lessons and Antarctic Implications. In: *Non-native Species in the Antarctic* (ed. Rogan-Finnemore M.) Gateway Antarctica Special Publication, Christchurch, New Zealand
- Convey P., Gibson J.A.E., Hillenbrand C.D., Hodgson D.A., Pugh P.J.A., Smellie J.L. & Stevens M.I. (2008) Antarctic terrestrial life - challenging the history of the frozen continent? *Biological Reviews*, 83, 103-117
- Daehler C.C. (1998) The taxonomic distribution of invasive angiosperm plants: Ecological insights and comparison to agricultural weeds. *Biological Conservation*, 84, 167-180
- Frenot Y., Chown S.L., Whinam J., Selkirk P.M., Convey P., Skotnicki M. & Bergstrom D.M. (2005) Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews*, 80, 45-72
- Gotelli N.J. & Colwell R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4, 379-391
- Hughes K.A. (2003) Aerial dispersal and survival of sewage-derived faecal coliforms in Antarctica. *Atmospheric Environment*, 37, 3147-3155
- Jones A.G., Chown S.L. & Gaston K.J. (2003) Introduced house mice as a conservation concern

- on Gough Island. *Biodiversity and Conservation* 12, 2107-2119
- Lamers M., Haase D. & Amelung B. (2008) Facing the elements: analysing trends in Antarctic tourism. *Tourism Review*, 63, 15-27
- 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
- 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
- Mansfield B. & Gilbert N. (2008) Availability and applicability of legal tools for managing non-native species. In: *Non-native Species in the Antarctic* (ed. Rogan-Finnemore M.) Gateway Antarctica Special Publication, Christchurch, New Zealand
- Puth L.M. & Post D.M. (2005) Studying invasion: have we missed the boat? *Ecology Letters*, 8, 715-721
- Richardson D.M. & Pyšek P. (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography*, 30, 409-431
- Richardson D.M., Pyšek P., Rejmánek M., Barbour M.G., Panetta F.D. & West C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, 6, 93-107
- Shimono Y. & Konuma A. (2008) Effects of human-mediated processes on weed species composition in internationally traded grain commodities. *Weed Research*, 48, 10-18
- 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
- Vitousek P.M. (2002) Oceanic islands as model systems for ecological studies. *Journal of Biogeography*, 29, 573-582
- Whinam J., Chilcott N. & Bergstrom D.M. (2005) Subantarctic hitchhikers: expeditioners as vectors for the introduction of alien organisms. *Biological Conservation*, 121, 207-219

APPENDIX A

Summary of families and genera found in cargo and the percentage of the total propagule load that was found in samples collected from cargo at the dockside and samples collected from cargo at the warehouse.

Family	Genera	Dock side	Warehouse
Amaranthaceae	<i>Amaranthus</i>	1.14	
Asteraceae	<i>Arctotheca</i>	1.14	
	<i>Conyza</i>	5.12	2.84
	<i>Galinsoga</i>	4.55	
	<i>Hypochoeris</i>	1.70	
	<i>Inula</i>	1.70	
	<i>Pseudognaphalium</i>	2.84	5.11
	<i>Senecio</i>	2.84	
	<i>Taraxacum</i>	3.98	
	<i>Xanthium</i>	1.14	
Brassicaceae	<i>Capsella</i>		1.77
	<i>Lepidium</i>	3.97	0.57
Caryophyllaceae	<i>Stellaria</i>		1.14
	<i>Spergula</i>		0.57
Chenopodiaceae	<i>Chenopodium</i>	1.14	0.57
Cyperaceae	<i>Cyperus</i>	2.84	
Fabaceae	<i>Melilotus</i>		1.14
	<i>Vicia</i>	2.84	
Malvaceae	<i>Malvastrum</i>	2.27	
Oxalidaceae	<i>Oxalis</i>	0.57	
Papaveraceae	<i>Papaver</i>		1.70
Plantaginaceae	<i>Plantago</i>	3.98	
Poaceae	<i>Agrostis</i>	5.68	
	<i>Briza</i>		0.57
	<i>Bromus</i>	1.70	
	<i>Chloris</i>	0.57	
	<i>Dactylon</i>	3.98	

Continued

Family	Genera	Dock side	Warehouse
	<i>Digitara</i>	2.27	
	<i>Hordeum</i>	7.39	
	<i>Lolium</i>	2.27	
	<i>Poa</i>	3.98	1.70
	<i>Sorghum</i>	1.14	
Polygonaceae	<i>Rumex</i>	4.55	
Scrophulaceae	<i>Striga</i>	3.41	

Chapter 4 - Hulls, holes and hideaways: hull fouling assemblages associated with an Antarctic supply vessel

INTRODUCTION

The introduction of species to environments in which they have not evolved is one of the major threats to marine ecosystem function and biodiversity (e.g. Lubchenco 1991). These introductions occur through a range of mechanisms, including shipping activities, aquaculture, the connection of waterways through canals, and the activities of research facilities (Ruiz *et al.* 1997, Godwin 2003). However, introductions associated with shipping take primacy as the cause for marine non-indigenous species (NIS) introductions worldwide (Mills *et al.* 1993, Bax *et al.* 2001, Streftaris *et al.* 2005, Flagella *et al.* 2006, Mineur *et al.* 2007). Propagules are transported in ballast water (Carlton 1996, Ruiz *et al.* 1997, Grigorovich *et al.* 2003, Holeck *et al.* 2004) and on the hulls of ocean going vessels (Gollasch 2002, Lewis *et al.* 2003, Mineur *et al.* 2007), and are moved around the world by a growing global network of shipping traffic (Drake and Lodge 2004).

The ecological and economic impacts of species introduced with ballast water are so extensive that substantial legislation exists to reduce the flow of introductions via this pathway (Ruiz *et al.* 2000, Hewitt and Campbell 2007, Barry *et al.* 2008). Principally this involves the International Convention on the Control and Management of Ship's Ballast Water and Sediments (B.W.M. 2005). The recommendations of the Convention are focused on mid-ocean ballast water exchange (IMO Resolution A.868(20)) as a means to prevent the transfer of water (and organisms) between coastal habitats. In contrast, biofouling remains largely unmanaged, and recent bans on the use of tri-butyl tin in anti fouling paints are likely to result in increases in fouling until suitable alternatives are developed (Hewitt and Campbell 2007).

Marine introductions are of particular concern in Antarctica, because one of the main routes of transport of goods and people (scientists, logistics staff and tourists) to the continent is via ships. It is highly likely that these vessels also transport non-indigenous species to the region (Lewis *et al.* 2003, Tavares and De Melo 2004, Lee and Chown 2007). Unlike the rest

of the world, ballast water introductions are typically of little concern in Antarctica as few vessels discharge ballast in the region, and it is prevented by the Antarctic Treaty (ATCM-Resolution 3 2006). Therefore biofouling is the greatest potential pathway for marine introductions and investigations have shown this potential could be realised (Hewitt and Campbell 2001, Lewis *et al.* 2003, Minchin and Gollasch 2003).

For economic reasons, commercial shipping typically has short port layover times (Lewis *et al.* 2003) and this prevents the accumulation of large fouling assemblages (Godwin 2004). However for Southern Ocean shipping, port layover times can be substantial during the austral winter, allowing large fouling assemblages to accumulate. Furthermore, because of the generally low travel speeds of these vessels, fouling communities can develop unhindered by physical disruption (e.g. shear stress) (Davidson *et al.* 2008).

The risks of biological invasions in the Antarctic are only now being fully appreciated (Frenot *et al.* 2005). Whilst the threats and consequences of terrestrial invasions have been quantified and assessed for some areas, demonstrating that invasive species can cause extinctions and the alteration of ecosystem functioning (Frenot *et al.* 2005, Bergstrom *et al.* 2006, Chown *et al.* 2008), the picture for marine systems in the Antarctic is less clear (Aronson *et al.* 2007). To date there have been few published studies which explicitly consider the threat of marine introductions into the Southern Ocean as a result of shipping traffic (Lewis *et al.* 2003, Tavares and De Melo 2004, Clarke *et al.* 2005, Lewis *et al.* 2005, Barnes *et al.* 2006, Lewis *et al.* 2006, Lee and Chown 2007). Whilst it might seem plausible that the decline in temperature associated with the Antarctic Polar Frontal Zone would pose a barrier to introductions, this is not necessarily the case. Natural variation in temperature, and increases associated with global warming (Meredith and King 2005, Turner *et al.* 2005, 2006, 2007, Chapman and Walsh 2007), might enable species to survive in a region generally considered too extreme for them. Indeed there have been several documented cases of species which are usually found in temperate regions surviving in Antarctic waters (Clayton *et al.* 1997, Thatje and Fuentes 2003, Tavares and De Melo 2004, Lee and Chown 2007).

Each year more than 60 tourist (<http://www.iaato.org>) and 69 scientific support vessels (<http://www.comnap.aq>) leave temperate ports and travel to the Antarctic. All at least have

the potential to transport non-indigenous species into the region. However, the level of risk posed by these vessels has not been fully assessed. It is known that for some gateway ports such as Cape Town harbour several highly invasive such as the European shore-crab, *Carcinus maenas*, and that surrounding areas are home to species that are also highly invasive, such as the Mediterranean mussel, *Mytilus galloprovincialis* (Robinson *et al.* 2005). Given the provisions of the Antarctic Treaty and its associated protocols (Mansfield and Gilbert 2008), as well as the management plans for many of the Southern Ocean Islands visited by scientific support vessels (de Villiers *et al.* 2006), which all call for prevention of biological invasions, there is a substantial need for understanding the likely risks posed by hull fouling in the region.

Understanding of hull fouling in the Antarctic is currently limited to only a few ‘snapshot’ studies which have examined assemblages only once or twice (Lewis *et al.* 2003, 2004), and although globally this field has received more attention, it is overall still poorly studied relative to the biosecurity posed (Carlton and Hodder 1995, Gollasch 2002, Floerl 2003, Godwin 2003, Floerl and Inglis 2005, Mineur *et al.* 2007, Davidson *et al.* 2008). Whilst such studies provide basic information on the types of organisms which typically associate with ships hulls, they are likely to underestimate the total diversity of biota being transported, since fouling assemblages develop and change over time (Berntsson and Jonsson 2003, Bram *et al.* 2005). Furthermore, sampling events often take place when the hull is occupied by a climax community (Mineur *et al.* 2007) which, whilst showing maximum abundances of fouling biota, may represent a low diversity state (Berntsson and Jonsson 2003). To appreciate fully the range of biota transported in association with ship’s hulls, it is necessary to examine all developmental stages of assemblages and to assess the temporal scale over which they develop.

As a first step to achieving this, I undertook systematic surveys of the hull of the South African National Antarctic Programme (SANAP) supply vessel the *SA Agulhas* over a period of two years. I tracked the development and change of fouling communities from immediately after the vessel left dry dock, through two complete re-supply seasons. Biota which become entrained with the hull will be highly related to the propagule source pool (Palmer 1988 although see da Fonseca-Genevois *et al.* 2006), and so species level identifications will not

be comparable between locations. Therefore rather than focusing at the species level, here, biota have been broadly classified into four functional groups: biofilms and slimes, fine and filamentous algae, macro algae and macro fauna.

MATERIAL AND METHODS

The *SA Agulhas* is a flat-bottomed, ice-strengthened cargo vessel, 115 m in length. To prevent accumulation of fouling biota, the vessel is fitted with a cathodic protection system and the hull and sea-chests of are painted with Interspeed 340 (International Paints), a controlled depletion, selfpolishing anti-fouling paint containing a gum resin polymer system and copper oxide and zinc oxide biocides. The vessel is based in Cape Town and its primary purpose is to re-supply the SANAP research stations on Marion Island (46°54'S, 37°45'E), Gough Island (40°20'S, 09°54'W), and in Dronning Maud Land (71°40'S, 02°51'W) (continental Antarctica). Typically these voyages occur in the austral summer, with Gough Island being re-supplied in September, Marion Island in March and South African National Antarctic Expedition station (Dronning Maud Land) in December.

Measurement of sampling error

Other studies investigating hull fouling assemblages, such as Lewis *et al.* (2003), have used scrapers to collect samples for later identification. This method is advantageous as it allows closer examination of organisms post-sampling and thus potentially more accurate identification. Collecting physical samples of organisms may also allow researchers to test the organisms viability. However, in addition to the logistical difficulties associated with using SCUBA, scraping hulls to collect samples is likely to dislodge organisms that may settle onto sub-strata and subsequently establish (Minchin and Gollasch 2003). Whilst this is unimportant when the vessel is docked in Cape Town, it would clearly be a concern for the Antarctic region, where several of the present surveys were undertaken to understand the extent of transportation of hull fouling assemblages to the ship's destinations.

Using a remote photographic capture device allows easy and safe access to hull surfaces but may be limited by the difficulties of classifying organisms correctly. However, previous studies (e.g. Carleton and Done 1995, Hughes and Atkinson 1997, Mayfield *et al.* 2000, Floerl and Inglis 2005), have successfully used similar equipment and methods to determine the

composition of benthic communities. Because inaccurate classification of biota was likely to be the primary source of error in this methodology, the confidence limits of this photographic surveying method in comparison to a physical scraping method were determined.

The vessel *SA Agulhas* was put into dry dock in June 2006 for 14 days. Immediately prior to dry docking, underwater photography techniques were used to take images of twenty 0.01 m² areas of fouled hull. Once the vessel was in dry dock, the previously photographed areas were scraped clean. Samples were stored in 70% ethanol and later identified at the laboratory. Identification of these samples was the prime source of data used to construct the list of species found in each fouling class, although some macro fauna (*Ciona intestinalis* and *Obelia dichotoma*) which were not present at the time of this test were added later (Table 1). Following Coutts and Taylor (2003), biota from the scrapings and the photographic images were classified as being fine algae or slime, filamentous algae, macro algae or macro fauna. To compare the composition of assemblages identified the two methods, Bray-Curtis similarities were calculated and a one-way Analysis of Similarity (ANOSIM) was conducted in Primer (5.1.2 Plymouth Marine Laboratory).

Table 1. Description of fouling classes. Adapted from Coutts and Taylor (2003)

Class	Taxa
Class A	Biofilms Slime Fine algae
Class B – Filamentous algae	<i>Cladophora</i> sp. (Chlorophyta) <i>Ceramium</i> sp. (Rhodophyta) <i>Ectocarpus siliculosus</i> (Phaeophyta)
Class C – Macro algae	<i>Ulva</i> sp. (Chlorophyta) <i>Enteromorpha intestinalis</i> (Chlorophyta) <i>Grateloupia filicina</i> (Rhodophyta)
Class D – Macro fauna	<i>Ciona intestinalis</i> (Ascidiacea) <i>Obelia dichotoma</i> (Hydrozoa) <i>Lepas</i> sp. (Cirripedia)

Hull surveys

Between August 2006 and May 2008, 12 surveys of the hull were carried out. For the first part of the sampling period, until April 2007, when not at sea, the vessel was docked at quay

500 in Cape Town harbour. After this time, the vessel moved its permanent berth to the Victoria and Alfred Waterfront, approximately 1 km away (Appendix A). Both sites are commercial docks which are protected by a harbour wall and are likely to have a similar propagule source pool.

Surveys of the hull were carried out in Cape Town harbour immediately before departure for Marion Island, Gough Island and the Dronning Maud Land coast and then again as soon as possible after arrival at the islands or in Antarctica. Operational constraints, such as the presence of thrusters, the main screw and discharge ports meant that it was not possible to survey the rear 40 m of the ship's hull (indicated in Fig. 1). In addition, the first 5 m of the hull was not included in surveys as this region slopes steeply; thus, a 2 m transect would cover a smaller area than a 2 m transect conducted on the vertical hull surface towards the centre of the vessel. Whilst the underside of the ship was classified as a single zone due to homogeneous abiotic conditions and the difficulty in identifying transect boundaries, the port and starboard hull surfaces were divided into ten, 2 m wide transects separated by 4 m (Fig. 1).

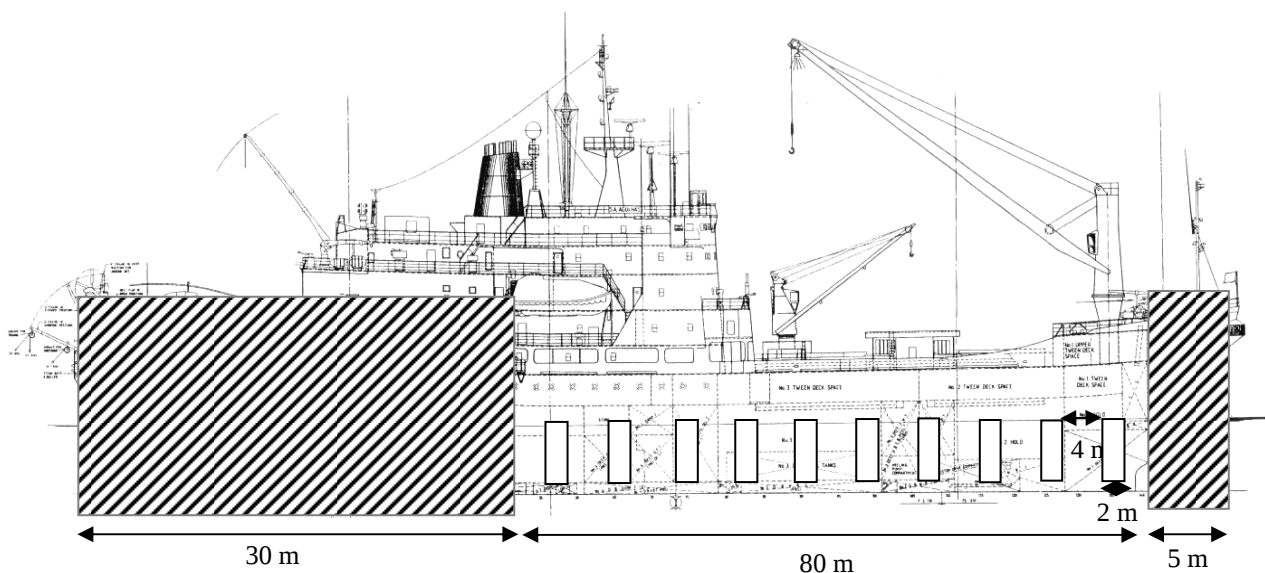


Figure 1. No sampling zones for the *SA Agulhas* indicated by hatched box to fore and aft of vessel. From the foremost edge of the aft no sampling zone, ten 2m sampling zones were be demarked every 4 m along the length of the ship spanning a total of 80 m, in each of these 2 m sampling zones 10 still images of the 0.01 m² quadrat were randomly extracted from the video footage from each sampling event.

A Videoray Explorer Remotely Operated Vehicle (ROV) unit (Videoray, USA) was used to capture continuous video footage at a rate of 15 mb/sec of each transect. A quadrat was fitted to the unit so that when it was perpendicular to the side of the vessel a 0.01 m² section was demarcated. Digital footage was stored in the form of an MPEG2 file. Images were randomly extracted from the MPEG2 files using VirtualDub 1.6.15 (Avery Lee) software. Only frames which were in focus and contained the requisite 0.01 m² area were used. Because of the difficulty in obtaining frames which met these criteria for surveys that were conducted in Antarctic locations, it was possible only to use ten frames from each port and starboard transect and twenty from the underside of the vessel. This represented one percent of the total submerged area of the hull. A grid was superimposed on each frame so that each sector of the grid represented 5% of the total quadrat and the coverage by abiotic and biotic variables (see below) were estimated. Abiotic variables were the proportion of intact paint and proportion of paint which had been damaged in some way, either by abrasion from ice or floating debris or by the addition of rubber from the fenders. Biotic variables comprised four classes: micro algae and slime, filamentous algae, macro algae and macro fauna (Coutts and Taylor 2003).

The influence of time on the abundance of different classes of fouling was analysed using a Generalized Linear Model in R.2.3.1 assuming a binomial error distribution and using a logit-link function. Time since last dry dock was used as a continuous predictor, and fouling cover as a categorical predictor. A second GLM model was used to compare fouling cover before and after voyages. Total fouling cover (from all classes) and voyage stage were included as parameters in the model.

To visualise the change in abundance of the different fouling classes over time, and so better assess successional changes in community composition, a cubic polynomial spline was fitted to the mean fouling per transect for each fouling category (Statistica V8, Statsoft, USA).

RESULTS

Measurement of sampling error

The taxonomic composition of samples collected by taking physical samples and samples collected using underwater photography were highly similar (ANOSIM global test $R = 0.021$, $p = 0.99$, when R is 1, samples within sites are more similar to each other than samples from other sites, when R is 0, similarities within and between sites are the same). Thus, the photographic survey method was judged an acceptable means by which to assess the taxonomic composition of fouling assemblages.

Hull surveys

Assemblages found on the *SA Agulhas* were characterised by a low diversity. In total only nine species were identified (in comparison with 56 identified by Lewis *et al.* 2003) (Table 1). These are all species known to occur within the Table Bay area (Robinson *et al.* 2005), and have a cosmopolitan distribution (Ocean Biogeographic Information System 2008) (see Appendix B for distribution maps). However, the distribution of these organisms over the surface of the hull was not even. Across all voyages, the starboard and underside of the vessel had significantly less fouling than the port side ($\chi^2 = 703.28$, $df = 2$, $p < 0.001$). The starboard side lies against the harbour wall when the vessel is in port and is in constant contact with fenders, indicating that light, and low disturbance are important for the development of fouling assemblages.

Between August 2006 and December 2006 the anti-fouling paint on the hull remained intact, and provided comprehensive protection against the settlement of fouling biota. During this period, no macro algae or macro fauna were found, with only biofilms and fine algae attached to the hull surface (Fig. 2). In December 2006 and again in December 2007, the vessel travelled to the Dronning Maud Land coast and *en route* passed through substantial amounts of sea ice (Appendix C). In December 2006 c. 30% of the antifouling coating was removed from the hull due to ice scour. It is likely that an equivalent amount of antifouling coating was removed when the vessel passed through the ice in December 2007, but because of the extensive fouling assemblages which were present on the pre-voyage survey, it was not possible to evaluate the state of the underlying substrate to make a before and after comparison. Upon returning to Cape Town, paint free areas were rapidly recolonised

by macro algae and macro fauna, groups that were previously not present (Fig. 2) indicating that ice scour plays a pivotal role in determining the formation and extent of fouling assemblages.

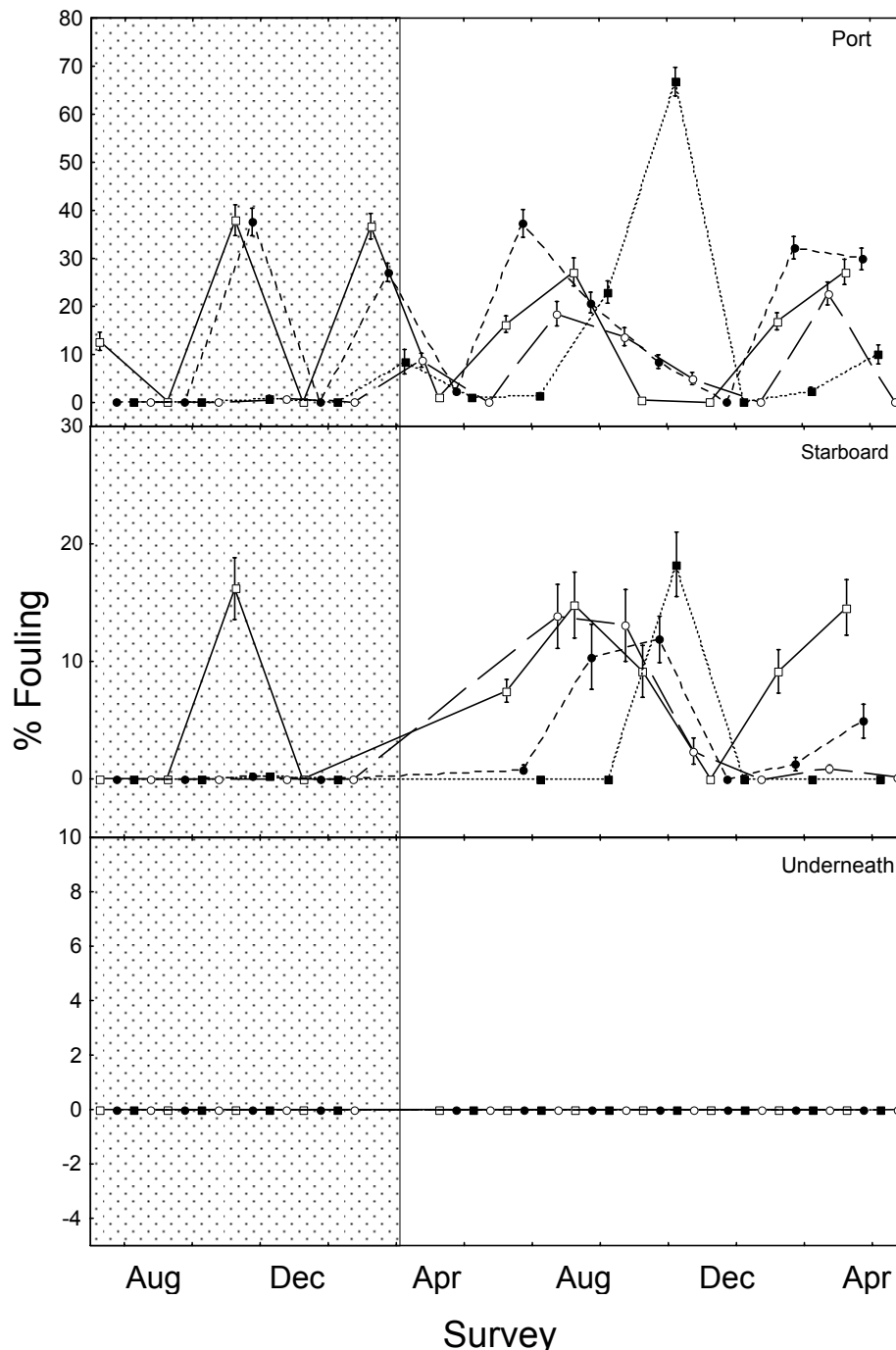


Figure 2. Mean ($\pm$ S.E.) percentage surface of the ships hull that was covered by biota from each of the fouling four classes: class A ($\square$), class B ($\bullet$), class C ($\blacksquare$), class D ($\circ$), in the three sampling zones: port (top panel), starboard (middle panel) and underneath (bottom panel). The first shaded portion, indicates the period when the vessel was docked at quay 500, whilst the latter un-shaded portion represents the period the vessel was docked at the V&A waterfront.

Ice scour removes all biota attached to the external surfaces of the hull, thus leading to a significant reduction in the extent of fouling recorded on surveys before and after sea ice travel ($\chi^2 = 742.1$, $df = 3440$, $p < 0.001$) (Fig. 4). When travelling to Marion and Gough Island the vessel does not encounter sea ice, and although there is a significant reduction in the extent of fouling assemblages ($\chi^2 = 54.3$, $df = 5348$, $p < 0.001$), a substantial proportion of assemblages remain intact, thus presenting a potential biosecurity threat (Fig. 3.).

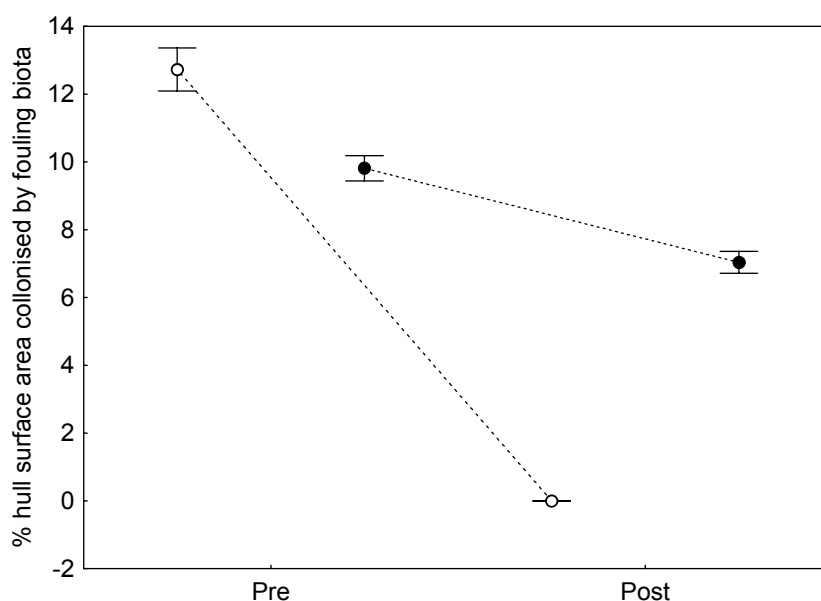


Figure 3. Mean ($\pm$ S.E.) fouling cover before and after travel through sea ice (○) and travel not involving sea ice (●)

Successional processes were complex, but essentially follow a cyclical pattern (Fig 4.). Initially the most abundant class of biota were fine and filamentous algae which are typical of early succession phases. In December 2006, the vessel first passed through sea ice, when the vessel returned to port and the hull surface was recolonised, these groups declined in abundance and macro algae and macro fauna became dominant. When the ship passed through ice in December 2007, this late successional community was removed and once again biota from early successional stages dominated assemblages. However, probably because a greater amount of the hull surface was free from anti-fouling paint, after a second passage through the ice, this process appeared to occur more rapidly.

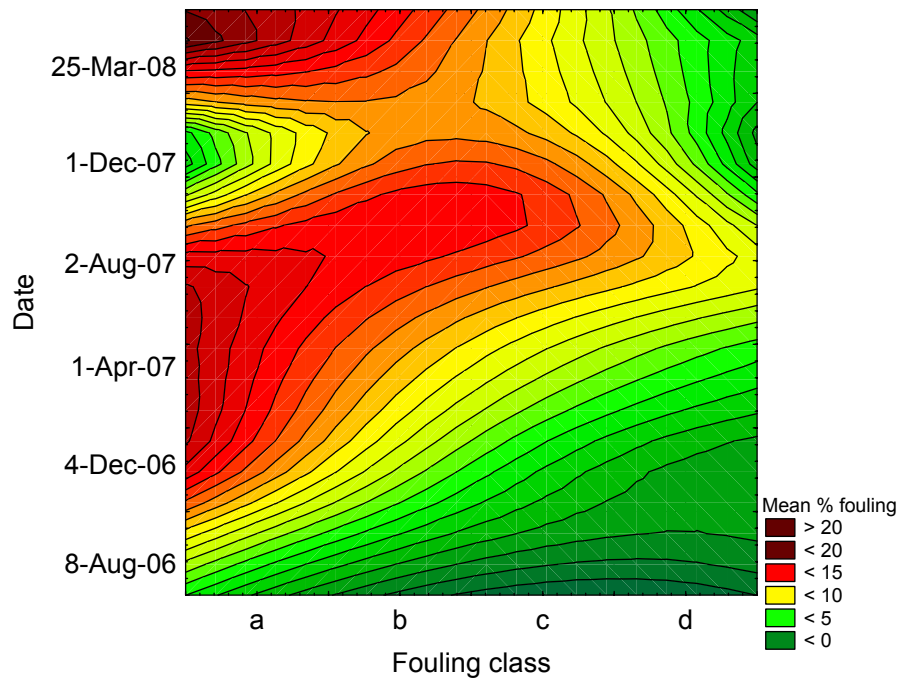


Figure 4. Mean % fouling per transect fitted with a cubic spline (stiffness 0.15), showing the changes in relative abundance of each of the fouling classes over time.

DISCUSSION

The *SA Agulhas* has the potential to transport substantial numbers, if not a substantial diversity of sessile marine biota into the Antarctic region as a hull fouling assemblage. However, the magnitude of this fouling is dependent on the extent to which the antifouling coating of the hull has been damaged by previous exposure to ice, with large assemblages only accumulating during the first layover period once the vessel had travelled through ice for the first time after repainting in dry-dock. If this pattern applies more broadly, and there is every indication that it does (see Lewis *et al.* 2003), it has two important implications for management of biological invasions in Antarctic marine systems. First, any locations visited after a ship has travelled through ice and accumulated fouling assemblages, are at a heightened risk of invasion. In the case of the *SA Agulhas*, this means that such complete assemblages are transported to Marion and Gough Islands. Second, any location visited after a vessel has travelled through ice but before it has returned to a temperate port is at low risk from invasions via this pathway. At present, even in the summer months, large stretches of the Antarctic are surrounded by pack ice (Simmonds and Jacka 1995, Yuan and Martinson 2000) and whilst this is the case, the continent remains relatively protected.

However, due to recent reductions in the extent of sea ice (de la Mare 1997, Eicken and Lemke 2001), in some years it is possible to access parts of the Antarctic, especially the Antarctic Peninsula, Bellingshausen and Amundsen Seas, without passing through any sea ice, potentially exposing marine communities in these areas to an increased risk of invasion.

Although the diversity of biota associated with the hull of the *SA Agulhas* was low, known invasive species are present. For example, *Ciona intestinalis* is a common invader of mussel beds and can form dense colonies which depress local species richness through competitive exclusion (Blum *et al.* 2007, Lambert 2007). This species is found throughout the world but as yet is unknown in the Antarctic region. However, it is known from the Arctic, in the Russian port of Murmansk (68°58'N, 33°5'E), where its critical thermal minima was recorded as 0°C (Dybern 1965). Therefore, temperature would not be a barrier to survival and it seems highly probable that if suitable habitat were available, *C. intestinalis* would be able to establish in the Antarctic.

It is not known if other species found associated with the *SA Agulhas* would be able to establish in the regions visited by the ship. However, given that the mean annual temperature difference between Cape Town and Marion Island is between c.10 and 7°C, and 5 and 0°C between Cape Town and Gough Island (Mélise *et al.* 2003) it seems likely that at least some of the fouling biota would be able to survive. If the full biosecurity threat of this pathway is to be comprehended, a pressing need exists to establish the environmental tolerances of fouling biota and their likely competitive interactions with indigenous biota, given that competition is a significant process structuring marine benthic and intertidal systems (Dayton 1971, Barnes and Kuklinski 2004, Guichard 2004).

At least for SANAP, and for vessels from other Antarctic operations using the port as a gateway to Antarctica, in part this task is simplified by the low diversity of biota found on the *SA Agulhas*. Ironically, the explanation for this low diversity, and the reduced biosecurity risk by comparison with the port of Hobart (see Lewis *et al.* 2003) , may be because of the presence of an invasive species, *Carcinus maenas* in Cape Town harbour (Robinson *et al.* 2005). This crab is a voracious predator (Floyd and Williams 2004, Miron *et al.* 2005, although also see Breen and Metaxas 2008) and the high densities found in the harbour may

have eliminated many other species (Le Roux *et al.* 1990, Robinson *et al.* 2005) and prevented extensive assemblages from developing. Although no comfort for the conservation of species indigenous to the shores of South Africa (but see Hampton and Griffiths 2007), *C. maenas* may be inadvertently be reducing the risk of invasion of the Antarctic region by species that might otherwise have been common in the harbour. However, whether this benefit might be outweighed by the fact that the hull fouling assemblages are dominated by widespread, tolerant species, capable of establishing in many regions, is not yet clear.

One important limitation to this study is the poor knowledge of the diversity of the near-shore environment in many Antarctic locations relative to the size of the region (although see Grindley 1978, Barnes 2006, Lutjeharms and Ansorge 2008). Because of this poor state of knowledge, it is not possible to know whether any potential invasive species have been introduced (but see Thatje and Fuentes 2003, Tavares and De Melo 2003, Aronson 2007), and whether the species transported on ships hulls are being moved outside their previous distributional ranges and therefore can be considered alien (Richardson *et al.* 2000) or are simply being moved around within their distributional ranges. Even if the latter is the case, host and recipient regions may contain populations with different genetic characteristics, so resulting in genetic homogenization (Olden 2006). If this question is to be answered, there is urgent need to identify and characterise native and introduced biota at the molecular level (Booth *et al.* 2007).

Until such time as a full biosecurity assessment can be made, the risk of introducing non-native species could be minimised by having more frequent dry dockings and changing the time of dry docking to immediately after a vessel returns from Antarctica. By doing this, the period when hull surface with damaged anti-fouling paint is available for settlement is minimised and as a result the habitats most at risk from marine introduction (in the SA *Agulhas'* case Marion and Gough Islands) would not be exposed to such great propagule pressure. Alternatively, port lay-over times could be reduced so that large fouling assemblages cannot accumulate. Although this would mean finding additional charters for the vessel during the austral winter, it is consistent with the modern need for economic efficiency which dictates that ships should spend most of their lifetime at sea.

REFERENCES

- Aronson R.B., Thatje S., Clarke A., Peck L.S., Blake D.B., Wilga C.D. & Seibel B.A. (2007) Climate change and invasibility of the Antarctic benthos. *Annual Review of Ecology Evolution and Systematics*, 38, 129-154
- ATCM-Resolution 3 (2006) Practical Guidelines for Ballast Water Exchange in the Antarctic Treaty Area
- B.W.M (2005) International Convention on the Control and Management of Ship's Ballast Water and Sediments, International Maritime Organization, London, United Kingdom. <http://www.imo.org>
- Barnes D.K.A. (2006) A most isolated benthos: coastal bryozoans of Bouvet Island. *Polar Biology*, 29, 114-119
- 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
- Barnes D.K.A. & Kuklinski P. (2004) Variability of competition at scales of 10^1 , 10^3 , 10^5 , and 10^6 m: encrusting arctic community patterns. *Marine Biology*, 145, 361-372
- Barry S.C., Hayes K.R., Hewitt C.L., Behrens H.L., Dragsund E. & Bakke S.M. (2008) Ballast water risk assessment: principles, processes, and methods. *Ices Journal of Marine Science*, 65, 121-131
- Bax N., Carlton J.T., Mathews-Amos A., Haedrich R.L., Howarth F.G., Purcell J.E., Rieser A. & Gray A. (2001) The control of biological invasions in the world's oceans. *Conservation Biology* 15, 1234-1246
- Bergstrom D.M., Convey P. & Huiskies A.H.L. (eds.) (2006) *Trends in Antarctic Terrestrial and Limnetic Ecosystems*. Springer, Dordrecht, The Netherlands
- Berntsson K.M. & Jonsson P.R. (2003) Temporal and spatial patterns in recruitment and succession of a temperate marine fouling assemblage: A comparison of static panels and boat hulls during the boating season. *Biofouling*, 19, 187-195
- Blum J.C., Chang A.L., Liljestrom M., Schenk M.E., Steinberg M.K. & Ruiz G.M. (2007) The non-native solitary ascidian *Ciona intestinalis* (L.) depresses species richness. *Journal of Experimental Marine Biology and Ecology*, 342, 5-14
- Booth D., Provan J. & Maggs C.A. (2007) Molecular approaches to the study of invasive seaweeds. *Botanica Marina*, 50, 385-396

- Bram J.B., Page H.M. & Dugan J.E. (2005) Spatial and temporal variability in early successional patterns of an invertebrate assemblage at an offshore oil platform. *Journal of Experimental Marine Biology and Ecology*, 317, 223-237
- Breen E. & Metaxas A. (2008) A comparison of predation rates by non-indigenous and indigenous crabs (Juvenile *Carcinus maenas*, juvenile *Cancer irroratus*, and adult *Dyspanopeus sayi*) in laboratory and field experiments. *Estuaries and Coasts*, 31, 728-737
- Carleton J.H. & Done T.J. (1995) Quantitative video sampling of coral reef benthos: large scale application. *Coral Reefs*, 14, 35-46
- Carlton J.T. (1996) Pattern, process, and prediction in marine invasion ecology. *Biological Conservation*, 78, 97-106
- Carlton J.T. & Hodder J. (1995) Biogeography and dispersal of coastal marine organisms - Experimental studies on a replica of a 16th-century sailing vessel. *Marine Biology*, 121, 721-730
- Chapman W.L. & Walsh J.E. (2007) A synthesis of Antarctic temperatures. *Journal of Climate*, 20, 4096-4117
- Chown S.L., Lee J.E. & Shaw J.D. (2008) Conservation of Southern Ocean Islands: Invertebrates as exemplars. *Journal of Insect Conservation*, 12, 277-291
- Clarke A., Barnes D.K.A. & Hodgson D.A. (2005) How isolated is Antarctica? *Trends in Ecology and Evolution*, 20, 1-3
- Clayton M.N., Wiencke C. & Kloser H. (1997) New records of temperate and sub Antarctic marine benthic macroalgae from Antarctica. *Polar Biology*, 17, 141-149
- Coutts A.D.M. & Taylor M.D. (2003) Biofouling on merchant vessels in New Zealand. In: *Hull fouling as a mechanism for marine invasive species introductions; proceedings of a workshop on current issues and potential management strategies* (ed. Godwin L.S.) Honolulu, Hawaii
- da Fonseca-Genevois V., Somerfield P.J., Neves M.H.B., Coutinho R. & Moens T. (2006) Colonisation and early succession on artificial hard substrata by meiofauna. *Marine Biology*, 148, 1039-1050
- Davidson I.C., McCann L.D, Fofonoff W.P., Sytsma M.D. & Ruiz G.M. (2008) The potential for hull-mediated species transfers by obsolete ships on their final voyages. *Diversity and Distributions*, 14, 518-529

- Dayton P.K. (1971) Competition, disturbance, and community organization - provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs*, 41, 351-&
- de la Mare W.K. (1997) Abrupt mid-twentieth-century decline in Antarctic sea-ice extent from whaling records. *Nature*, 389, 57–60
- de Villiers M.S., Cooper J., Carmichael N., Glass J.P., Liddle G.M., Mclvor E., Micol T., Roberts A. (2006) Conservation management at Southern Ocean Islands: towards the development of best practice guidelines. *Polarforschung*, 75, 113-131
- 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
- Dybern B.I. (1965) The life cycle of *Ciona intestinalis* (L.) f. typical in relation to the environmental temperature. *Oikos*, 16, 109-131
- Eicken H. & Lemke P. (2001) *The response of polar sea ice to climate variability and change.* In: *Climate of the 21st century: changes and risks* (eds. Lozán J.L., Graßl H. & Hupfer P.) GEO, Hamburg
- Flagella M.M., Soria A. & Buia M.C. (2006) Shipping traffic and introduction of non-indigenous organisms: Study case in two Italian harbours. *Ocean & Coastal Management*, 49, 947-960
- Floerl O. (2003) Factors that influence hull fouling on ocean-going vessels. In: *Hull fouling as a mechanism for marine invasive species introductions: proceedings of a workshop on current issues and potential management strategies* (ed. Godwin L.S.) Honolulu, Hawaii
- Floerl O. & Inglis G.J. (2005) Starting the invasion pathway: the interaction between source populations and human transport vectors. *Biological Invasions*, 7, 589-606
- Floyd T. & Williams J. (2004) Impact of green crab (*Carcinus maenas* L.) predation on a population of soft-shell clams (*Mya arenaria* L.) in the Southern Gulf of St. Lawrence. *Journal of Shellfish Research*, 23, 457-462
- Frenot Y., Chown S.L., Whinam J., Selkirk P.M., Convey P., Skotnicki M. & Bergstrom D.M. (2005) Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews*, 80, 45-72

- Godwin L.S. (2003) Hull fouling of maritime vessels as a pathway for marine species invasions to the Hawaiian Islands. *Biofouling*, 19, 123-131
- Godwin L.S. (2004) Maritime activities as a mechanism for introducing marine alien species: issues and management. In: *Hull fouling as a mechanism for invasive species introductions: proceedings of a workshop on current issues and potential management strategies* (ed. Godwin L.S.) Honolulu, Hawaii
- Gollasch S. (2002) The importance of ship hull fouling as a vector of species introductions into the North Sea. *Biofouling*, 18, 105-121
- Grigorovich I.A., Colautti R.I., Mills E.L., Holeck K., Ballert A.G. & MacIsaac H.J. (2003) Ballast-mediated animal introductions in the Laurentian Great Lakes: retrospective and prospective analyses. *Canadian Journal of Fisheries and Aquatic Sciences*, 60, 740-756
- Grindley J.R. (1978) Marine ecosystems of Marion Island. *South African Journal of Antarctic Research*, 8, 38-42
- Guichard F. (2004) Competition landscapes: scaling up local biotic and abiotic processes in heterogeneous environments. *Theoretical Population Biology*, 66, 101-111
- Hampton S.L. & Griffiths C.L. (2007) Why *Carcinus maenas* cannot get a grip on South Africa's wave-exposed coastline. *African Journal of Marine Science*, 29, 123-126
- Hewitt C.L. & Campbell M.L. (2001) The Australian distribution of the introduced sphaeromatid isopod *Paracerceis sculpta* (Homes 1904). *Crustaceana*, 78, 925-936
- Hewitt C.L. & Campbell M.L. (2007) Mechanisms for the prevention of marine bioinvasions for better biosecurity. *Marine Pollution Bulletin*, 55, 395-401
- Holeck K.T., Mills E.L. & MacIsaac H.J. (2004) Bridging troubled waters: Biological invasions, transoceanic shipping, and the Laurentian Great Lakes. *Bioscience*, 54, 919-929
- Hughes D.J. & Atkinson R.J.A. (1997) A towed video survey of megafaunal bioturbation in the north-eastern Irish Sea. *Journal of the Marine Biology Association*, 77, 635-653
- Lambert G. (2007) Invasive sea squirts: A growing global problem. *Journal of Experimental Marine Biology and Ecology*, 342, 3-4
- Le Roux P.J., Branch G.M. & Joska M.A.P. (1990) On the distribution, diet and possible impact of the invasive European shore crab *Carcinus Maenas* (L) along the South-African coast. *South African Journal of Marine*, 9, 85-93
- 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

- Lewis P., Bergstrom D. & 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
- Lewis P.N., Riddle M.J. & Smith S.D.A. (2005) Assisted passage or passive drift: a comparison of alternative transport mechanisms for non-indigenous coastal species into the Southern Ocean. *Antarctic Science*, 17, 183-191
- Lubchenco J. (1991) The Sustainable Biosphere Initiative - an Ecological Research Agenda - a report from the Ecological Society of America. *Ecology*, 72, 371-412
- Lutjeharms J.R.E. & Ansorge I.J. (2008) Oceanographic setting of the Prince Edward Islands. In: *The Prince Edward Islands: Land-Sea Interactions in a Changing Ecosystem* (eds. Chown S.L. & Froneman P.W.) African SunMedia, Stellenbosch, South Africa
- Mansfield B. & Gilbert N. (2008) Availability and applicability of legal tools for managing non-native species. In: *Non-native Species in the Antarctic* (ed. Rogan-Finnemore M.) Gateway Antarctica Special Publication, Christchurch, New Zealand
- Mayfield S., Branch G.M. & Cockcroft A.C. (2000) Relationships among diet, growth rate, and food availability for the South African rock lobster, *Jasus lalandii* (Decapoda, Palinuridea). *Crustaceana*, 73, 815-834
- 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
- Meredith M.P. & King J.C. (2005) Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophysical Research Letters*, 32, 5
- Mills E.L., Leach J.H., Carlton J.T. & Secor C.L. (1993) Exotic species in the Great-Lakes - A history of biotic crises and anthropogenic introductions. *Journal of Great Lakes Research*, 19, 1-54
- Minchin D. & Gollasch S. (2003) Fouling and ships' hulls: how changing circumstances and spawning events may result in the spread of exotic species. *Biofouling*, 19, 111-122
- Mineur F., Johnson M.P., Maggs C.A. & Stegenga H. (2007) Hull fouling on commercial ships as a vector of macroalgal introduction. *Marine Biology*, 151, 1299-1307

- Miron G., Audet D., Landry T. & Moriyasu M. (2005) Predation potential of the invasive green crab (*Carcinus maenas*) and other common predators on commercial bivalve species found on Prince Edward Island. *Journal of Shellfish Research*, 24, 579-586
- Ocean Biogeographic Information System. (2008) <http://www.iobis.org>
- Olden J.D. (2006) Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography*, 33, 2027-2039
- Palmer M.A. (1988) Dispersal of marine meiofauna - a review and conceptual-model explaining passive transport and active emergence with implications for recruitment. *Marine Ecology-Progress Series*, 48, 81-91
- Richardson D.M., Pyšek P., Rejmánek M., Barbour M.G., Panetta F.D. & West C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, 6, 93-107
- Robinson T.B., Griffiths C.L., McQuaid C. & Rius M. (2005) Marine alien species of South Africa - status and impacts. *African Journal of Marine Science*, 27, 297-306
- Ruiz G.M., Carlton J.T., Grosholz E. & Hines A.H. (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms extent and consequences. *American Zoologist*, 37, 621-632
- Ruiz G.M., Rawlings T.K., Dobbs F.C., Drake L.A., Mullady T., Huq A. & Colwell R.R. (2000) Global spread of microorganisms by ships. *Nature*, 408, 49-50
- Simmonds I. & Jacka T.H. (1995) Relationships between the interannual variability of sea ice and the Southern Oscillation. *Journal of Climate*, 8, 637-647
- Streftaris N., Zenetos A. & Papathanassiou E. (2005) Globalisation in marine ecosystems: The story of non-indigenous marine species across European seas. *Oceanography and Marine Biology - an Annual Review*, 43, 419-453
- Tavares M. & De Melo G.A.S. (2004) Discovery of the first known benthic invasive species in the Southern Ocean: the North Atlantic spider crab *Hyas araneus* found in the Antarctic Peninsula. *Antarctic Science*, 16, 129-131
- Thatje S. & Fuentes V. (2003) First record of anomuran and brachyuran larvae (Crustacea: Decapoda) from Antarctic waters. *Polar Biology*, 26, 279-282
- Turner J., Lachlan-Cope T., Colwell S. & Marshall G.J. (2005) A positive trend in western Antarctic Peninsula precipitation over the last 50 years reflecting regional and Antarctic-wide atmospheric circulation changes. *Annals of Glaciology*, 41, 85-91

- Turner J., Lachlan-Cope T.A., Colwell S., Marshall G.J. & Connolley W.M. (2006) Significant warming of the Antarctic winter troposphere. *Science*, 311, 1914-1917
- Turner J., Overland J.E. & Walsh J.E. (2007) An Arctic and Antarctic perspective on recent climate change. *International Journal of Climatology*, 27, 277-293
- Yuan X. & Martinson D.G. (2000) Antarctic sea ice extent and its global connectivity. *Journal of Climate*, 13, 1697–1718

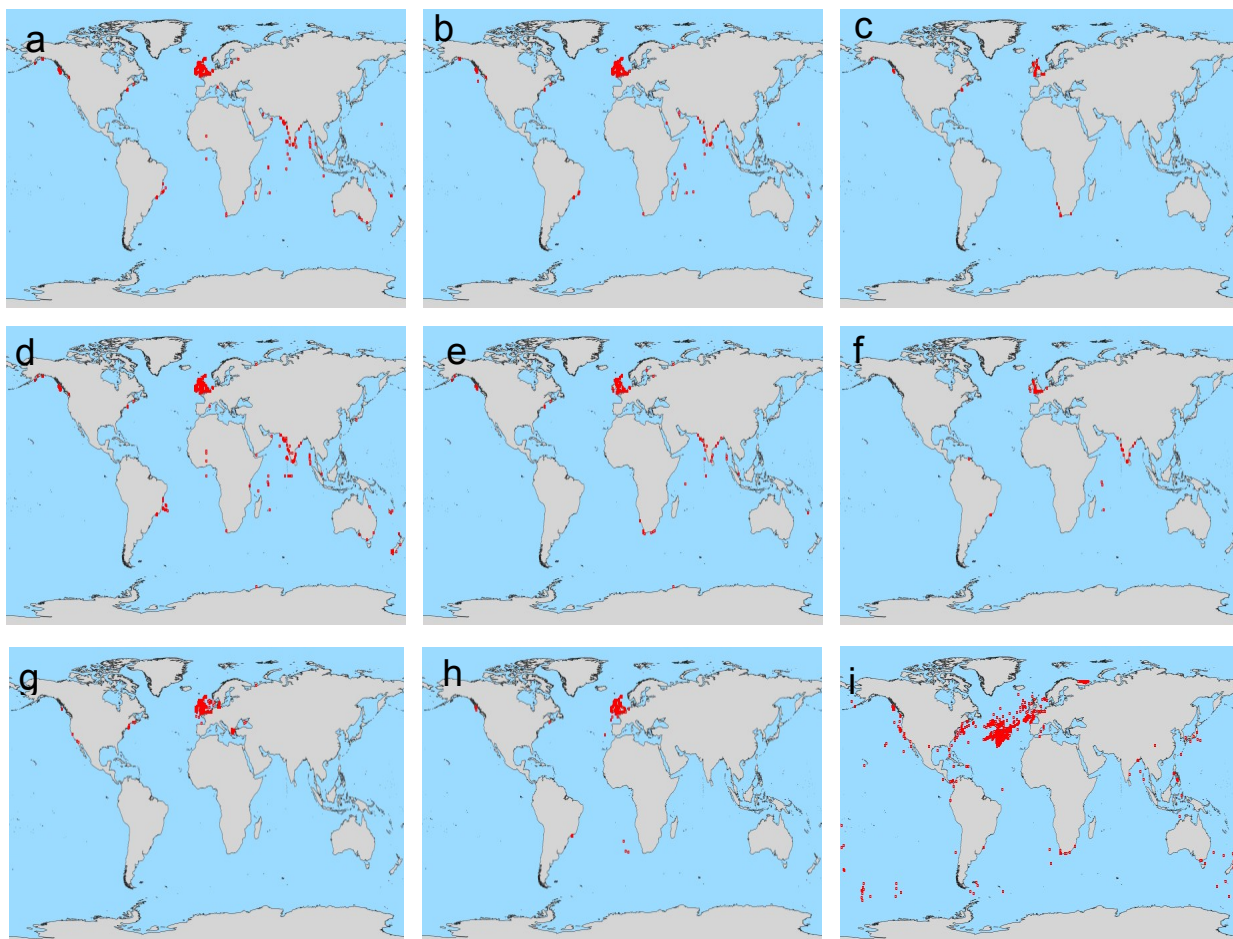
APPENDIX A

Google Earth satellite image showing the locations where the *SA Agulhas* was docked during the sampling period.



APPENDIX B

Distribution of the nine species of fouling biota found on the SA *Agulhas* (source: Ocean Biogeographic Information System 2008). (a) *Cladophora* sp. (b) *Ceramium* sp. (c) *Ectocarpus silicosus* (d) *Ulva* sp. (e) *Enteromorpha intestinalis* (f) *Grateloupia filicina* (g) *Ciona interstitialis* (h) *Oblia dichotoma* (i) *Lepas* sp.



APPENDIX C

(a) The *SA Agulhas* passing through dense sea ice on its way to the Dronning Maud Land coast (b) substantial amounts of the antifouling coating on the ships hull (red) were removed during this passage.



Chapter 5 - *Mytilus* on the move: transport of an invasive bivalve to the Antarctic

Published as: 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 doi: 10.3354/meps339307

INTRODUCTION

Biological invasions threaten nearly every major habitat type on earth (Millennium Ecosystem Assessment 2005), and the impacts of non-indigenous species (NIS) are significant even in remote regions such as the Antarctic (Frenot *et al.* 2005). Whilst the study of NIS in the terrestrial realm is well developed, understanding of marine NIS and the extent to which they might become invasive in the Antarctic is less extensive (Barnes 2002, Lewis *et al.* 2003).

Countless vessels, including tourist ships, fishing vessels and scientific support vessels enter the Antarctic region each year. The age, voyage schedule, antifouling regime and home ports of these vessels are diverse, presumably resulting in substantial variation in the diversity and abundance of NIS which are transported (Lewis *et al.* 2003). One notable feature of vessels entering the Antarctic is that few of them discharge ballast water at high latitudes. Instead, ballast water is more usually taken aboard in Antarctic waters, after cargo offloading, and subsequently discharged in temperate waters. Therefore introductions via ballast water discharge are relatively unimportant in this region.

By contrast, good evidence exists that Antarctic supply vessels have the potential to introduce NIS to the region as hull fouling assemblages (Lewis *et al.* 2003, 2004, 2006). Large fouling assemblages accumulate when vessels are subject to long port layovers such as those experienced by Antarctic support vessels during the austral winter. In this regard, sea-chests, which are covered recesses into the hull from which water for the engines' cooling systems is drawn, are likely to be an important transport route for NIS to high latitudes. Fouling assemblages in sea-chests are protected from the shearing forces found elsewhere on the

hull, but they still experience a constant flow of nutrients. Moreover, in high latitude areas characterized by extensive sea ice, these assemblages are sheltered from the ice scour which typically removes the majority of fouling assemblages elsewhere on the hull (Lewis *et al.* 2004).

Here the first assessment of the dominant organism dwelling in the sea-chests of the supply vessel used by the South African National Antarctic Programme (SANAP), the *SA Agulhas* is provided. The vessel is based in Cape Town harbour which is home to several highly invasive species, including the Mediterranean mussel, *Mytilus galloprovincialis* and the European green crab *Carcinus maenas* (Robinson *et al.* 2005). *M. galloprovincialis* probably entered the harbour by ship(s) (Branch and Steffani 2004), and it seems equally likely that this species can leave by the same means. I show that *M. galloprovincialis* predominates in the sea-chests of the *SA Agulhas*, and based on an estimate of the age-structure of the population demonstrate that at least some individuals in this population have survived multiple voyages to the Antarctic region.

DRY DOCK INSPECTION OF SEA-CHESTS

The *SA Agulhas* undertakes several voyages into the Antarctic region each year (Fig. 1). The hull and sea-chests of the vessel are painted with Interspeed 340 (International Paints), a controlled depletion, self-polishing anti-fouling paint containing a gum rosin polymer system and copper oxide and zinc oxide biocides. The vessel is also fitted with a cathodic protection system. The anti-fouling paint and the cathodic protection system were last replenished in June 2003. Whilst the sea-chests have a volume of only 6 m³, they contain several baffles and have a complex internal structure, and so have a surface area of c. 42 m², thus providing a substantial potential habitat area.

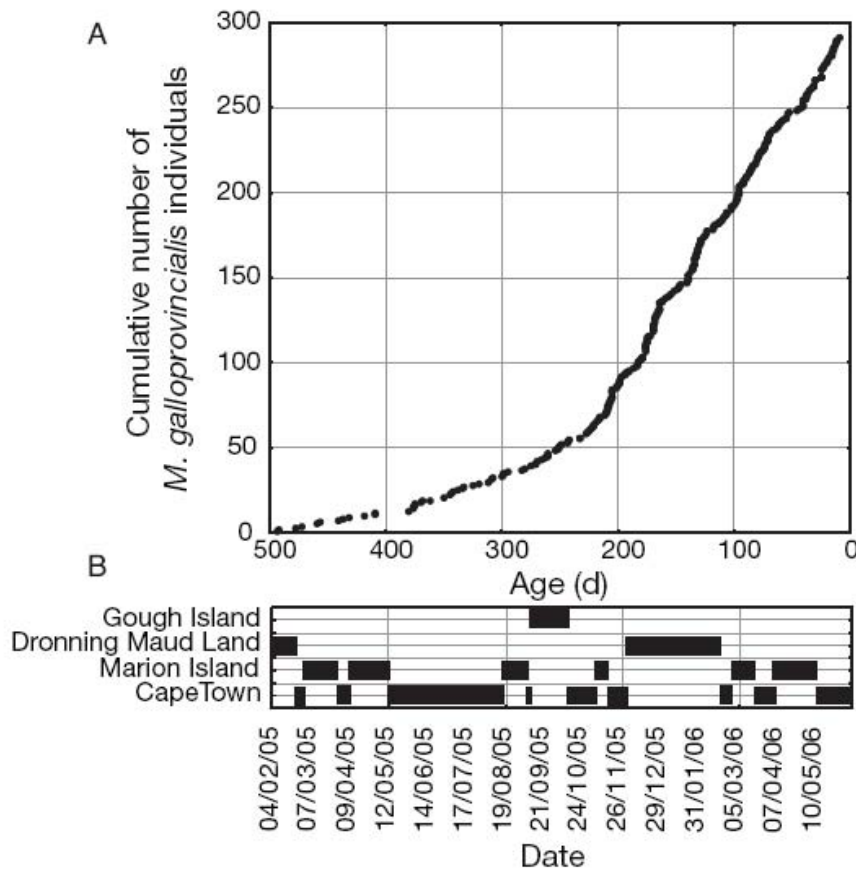


Figure 1. Cumulative frequency distribution of *Mytilus galloprovincialis* individuals collected from the sea-chests of the SA *Agulhas* (upper panel) and the voyage schedule of the vessel (lower panel). For the upper panel, samples were taken from the sea-chests on 10/06/2006 and ages were estimated from mussel size (see text). The frequency distribution indicates, for example, that only 50 of the sampled individuals were older than 250 days, whereas more than 90 individuals were younger than 100 days. The position of an individual in the upper panel also indicates, based on its age, the locations to which it has travelled as shown in the lower panel, viz. an individual will have travelled to all locations to its right in the lower panel.

In June 2006, within 24 hours of the vessel entering the dry dock, the sea-chests were inspected. During the inspections, ten 0.1 m² quadrats were randomly placed within each of the vessel's two main sea-chests. Fouling cover was recorded and representative samples of all organisms were collected for later identification in the laboratory. Fouling cover ranged from 100% cover on exposed surfaces subject to high water flow to 10% in more sheltered areas of the sea-chests, giving a mean cover of 59.5% (S.D. = 43.03) for the port sea-chest and a mean of 64.5% (S.D. = 33.37) for the starboard sea-chest. Assemblages were dominated by *Mytilus galloprovincialis* (Fig. 2), although individuals of *Aulacomya ater*

(Mollusca, Bivalvia), *Notomegabalanus algicola* (Crustacea, Cirripedia), and *Ciona intestinalis* (Chordata, Ascidiacea) were also found. *M. galloprovincialis* specimens were stimulated with a sharp tap to elicit valve closure and individuals that did not respond (20 of a total of 311) were considered dead and excluded from subsequent analyses. Mitutoyo digital callipers were used to measure the maximum shell length of all live specimens to the nearest μm . Individuals <1 mm were not included because accurate identification of these individuals was not possible. The mean shell length was 23.12 (S.D. = 13.17) mm and the maximum was 55.9 mm.

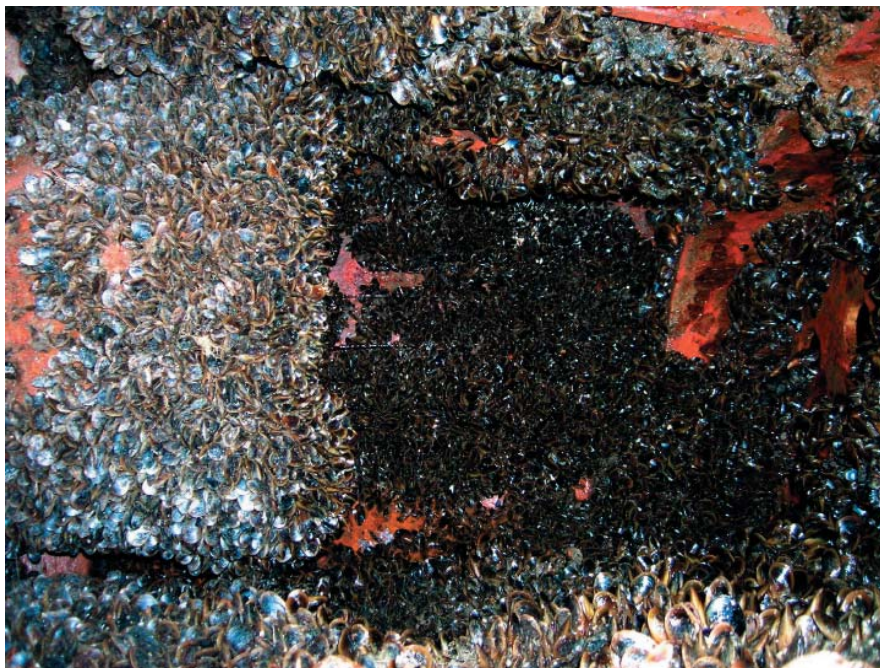


Figure 2. Fouling assemblages in the sea-chests of the *SA Agulhas* were dominated by *Mytilus galloprovincialis*

Mytilus galloprovincialis has variable growth rates that are strongly influenced by temperature, air exposure and water flow (van Erkom Schurink and Griffiths 1993). Although sea-chests are permanently flooded, both temperature and water flow within the sea-chests of the *SA Agulhas* are highly variable. When the ship is in port, there is almost no water flow through the sea-chests, whilst it can rise to $1000 \text{ m}^3 \cdot \text{h}^{-1}$ when the ship is at sea (J. Klopper personal communication). Similarly, water temperatures range from a mean of -1.6°C when the ship is stationed off Dronning Maud Land to a mean of 15.5°C when it is berthed in Cape

Town harbour (33°55'S, 18°26'E) (temperatures obtained from Advanced Very High Resolution Radiometer remotely sensed data, see <http://satori.gso.uri.edu>). No growth rate estimations for these conditions are available. However, a conservative estimate of *M. galloprovincialis* growth rate was obtained from data provided for a colony of *M. galloprovincialis* grown at approximately 15°C with high water circulation and zero aerial exposure at Saldanha Bay, 110 km north of Cape Town (van Erkom Schurink and Griffiths 1993). The age of specimens found in the sea-chests of the *SA Agulhas* at a given length was estimated using the equations provided by van Erkom Schurink and Griffiths (1993):

$$l(t) = a + bt - ct^2 \quad (1)$$

$$t(l) = \frac{b - \sqrt{b^2 - 4cl}}{2c} \quad (2)$$

where l is length in mm, t is age in months, and a , b and c are constants. According to van Erkom Schurink and Griffiths (1993), b was 5.197 and c was 0.108. Whilst van Erkom Schurink and Griffiths (1993) set a to 20.25 and measured the growth of individuals above this size, here a was set to 0 because many individuals in the present study were less than 20.25 mm in length. Using these values, individuals collected from the *SA Agulhas* were estimated to range from 0.31 to 16.23 months in age. These age estimates are conservative because growth rates are slower at lower temperatures (Seed 1976, van Erkom Schurink and Griffiths 1993).

Therefore, *M. galloprovincialis* has been transported to the Antarctic region in the sea-chests of the *SA Agulhas* on multiple occasions (Fig 1). *M. galloprovincialis* reaches maturity at approximately 25 mm in length (C. Griffiths, personal communication). In consequence, larvae could have been released at any of the locations visited by the vessel. The minimum survival temperature of *M. galloprovincialis* is 0°C (Braby and Somero 2006), and some individuals of the *SA Agulhas* population have clearly survived at least -1.6°C. Growth in this species has been recorded at a minimum temperature of 3°C (Seed 1976). Given that sea surface temperature varies annually between 5 and 8°C at Marion Island and between 10 and 16°C at Gough Island (Mélise *et al.* 2003), establishment of larvae or of displaced adults or immatures could have taken place at these islands. Long-term survival and growth under

Antarctic conditions seems less likely, but it is clear that other marine NIS can survive in the region (Clayton *et al.* 1997, Tavares and De Melo 2004) and warming temperatures could increase this number dramatically (Aronson *et al.* 2007).

IMPLICATIONS

The transport of *M. galloprovincialis* from Cape Town harbour to various locations throughout the broader Antarctic region and its survival of these conditions demonstrate that temperate species are capable of short-term survival under polar conditions. They also show that Antarctic supply vessels are important vectors for NIS and that the antifouling technology employed by such vessels has limited effectiveness. Given the provisions of the Antarctic Treaty and its associated protocols, as well as the management plans of many Southern Ocean islands, the confirmed transport and survival of a known invasive species (Branch and Steffani 2004) to the Antarctic is cause for concern. Further research is now needed to determine if *M. galloprovincialis* is capable of reproduction in Antarctic waters, to assess the extent to which research vessels based in other locations carry similar fouling loads, and to determine best practises for addressing these problems given the unique operating conditions of these vessels. Moreover, inspection of the intertidal areas of both Gough and Marion Islands for populations of this invasive species should be undertaken.

REFERENCES

- Aronson R.B., Thatje S., Clarke A., Peck L.S., Blake D.B., Wilga C.D. & Seibel B.A. (2007) Climate change and invasibility of the Antarctic benthos. *Annual Review of Ecology Evolution and Systematics*, 38, 129-154
- Barnes D.K.A. (2002) Invasions by marine life on plastic debris. *Nature*, 416, 808-809
- Braby C.E. & Somero G.N. (2006) Following the heart: temperature and salinity effects on heart rate in native and invasive species of blue mussels (genus *Mytilus*). *Journal of Experimental Biology*, 209, 2554-2566
- Branch G.M. & Steffani C.N. (2004) Can we predict the effects of alien species? A case-history of the invasion of South Africa by *Mytilus galloprovincialis* (Lamarck). *Journal of Experimental Marine Biology and Ecology*, 300, 189-215
- Clayton M.N., Wiencke C. & Klöser H. (1997) New records of temperate and sub-Antarctic marine benthic macroalgae from Antarctica. *Polar Biology*, 17, 141-149
- Frenot Y., Chown S.L., Whinam J., Selkirk P.M., Convey P., Skotnicki M. & Bergstrom D.M. (2005) Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews*, 80, 45-72
- 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
- Lewis P.N., Riddle M.J. & Hewitt C.L. (2004) Management of exogenous threats to Antarctica and the sub-Antarctic islands: balancing risks from TBT and non-indigenous marine organisms. *Marine Pollution Bulletin*, 49, 999-1005
- 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, DC.
- Robinson T.B., Griffiths C.L., McQuaid C. & Rius M. (2005) Marine alien species of South Africa - status and impacts. *African Journal of Marine Science*, 27, 297-306
- Seed R. (1976) Ecology. In: *Marine mussels: their ecology* (ed. Bayne B.L.). Cambridge University Press, Cambridge

- Tavares M. & De Melo G.A.S. (2004) Discovery of the first known benthic invasive species in the Southern Ocean: the North Atlantic spider crab *Hyas araneus* found in the Antarctic Peninsula. *Antarctic Science*, 16, 129-131
- van Erkom Schurink E. & Griffiths C.L. (1993) Factors affecting the relative growth rates in four South African mussel species. *Aquaculture*, 109, 257-273

Chapter 6 - Colonisation of sub-Antarctic Marion Island by a non-indigenous aphid parasitoid *Aphidius matricariae* (Hymenoptera, Braconidae)

Published as: Lee J., 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. doi: 10.1007/s00300-007-0277-z

INTRODUCTION

Biological invasions and climate change are having considerable impacts on the Southern Ocean Islands. The former have added substantially to species richness. In the process they have had profound effects on the populations of several indigenous species and have substantially altered the structure and functioning of local ecosystems (Chapuis *et al.* 1994, Chown and Block 1997, Gremmen *et al.* 1998, Bester *et al.* 2002, Le Roux *et al.* 2002, Gaston *et al.* 2003, Frenot *et al.* 2005). Whilst climate change has had marked effects on indigenous species (e.g. Chown and Smith 1993, Smith *et al.* 2001), one of its most pronounced realized and predicted impacts is an interaction with biological invasions. The impacts of invasive alien species already present on the islands are mounting (reviewed in Bergstrom and Chown 1999, Frenot *et al.* 2005), and it has been suggested that rising temperatures are likely to facilitate colonisation and the subsequent spread of newly introduced species (Kennedy 1995, Walther *et al.* 2002, Frenot *et al.* 2005).

Whether colonisation success has increased in recent years is difficult to determine because unsuccessful colonisations typically go unrecorded (see also Williamson 1996). For most of the Southern Ocean Islands the time series of observations is also too short to determine whether successful colonisations have increased over time. Moreover, on many of the islands the extent of human activity has increased in step with ameliorating temperatures, making it difficult to disentangle the effects of propagule pressure and climate change (but see Chown *et al.* 2005). Nonetheless, over several decades, repeated surveys on many islands have been undertaken to ascertain the rates of recent colonisation by new species

and rates of range extension of alien species (e.g. Chown and Language 1994, Gremmen and Smith 1999, Frenot *et al.* 2001, Gaston *et al.* 2003, Turner *et al.* 2006).

On the Prince Edward Islands, surveys of the larger Marion Island (46°54'S, 37°55'E) are typically undertaken on an annual basis, though these are often restricted to commonly used areas such as the field station and field huts, and to the main paths connecting these areas (Gremmen and Smith 1999, Slabber and Chown 2002). Access to the smaller island, Prince Edward, is strictly regulated by the Prince Edward Islands Management Plan (Anonymous 1996), and in consequence surveys are less frequent, but typically more spatially comprehensive (e.g. Ryan *et al.* 2003). Over the last two decades, surveys on Marion Island have detected the colonisation and establishment of several new plant and invertebrate species (Table 1). Here the 8th successful colonisation and establishment of an invertebrate or plant species on Marion Island during this period is reported, and present range extent of this aphid parasitoid is documented.

Table 1. Plant and invertebrate species known to have colonised, or to have colonised and established reproducing populations on Marion Island since the mid 1980s.

Species	Reference
Colonised	
<i>Senecio</i> sp. (Asteraceae)	Gremmen and Smith 1999
<i>Sonchus</i> sp. (Asteraceae)	Gremmen and Smith 1999
Unidentified woody shrub	Chown and Convey 2007
Established	
Plants	
<i>Agrostis gigantea</i> (Poaceae)	Gremmen and Smith 1999
<i>Luzula cf. multiflora</i> (Juncaceae)	Gremmen and Smith 2004
Invertebrates	
<i>Pogonognathellus flavescens</i> (Collembola, Tomoceridae)	Chown <i>et al.</i> 2002
<i>Calliphora vicina</i> (Diptera, Calliphoridae)	Hänel <i>et al.</i> 1998
<i>Thysanoplusia orichalcea</i> (Lepidoptera, Noctuidae)	Hänel <i>et al.</i> 1998
<i>Plutella xylostella</i> (Lepidoptera, Plutellidae)	Crafford and Chown 1987
<i>Porcellio scaber</i> (Crustacea, Porcellionidae)	Slabber and Chown 2002

MATERIAL AND METHODS

Although the scientific station at Marion Island has been permanently occupied since 1947, regular, virtually annual surveys for new invertebrate species have only been undertaken since the early 1980s (Crafford *et al.* 1986, Chown and Avenant 1992, Slabber and Chown 2002). Since 2003 the intensity of surveys increased after the detection of the isopod *Porcellio scaber* (Slabber and Chown 2002). In the period 2003 - May 2006, twice yearly surveys were undertaken around the island at field huts, which are regularly spaced along the island's c. 70 km long coastline and in areas *en route* to them. During one of these surveys (April 2003), several flight-capable individuals of a parasitoid wasp were collected from *Poa cookii* tussocks and *Poa annua* sward growing on an overhang at Boulders Beach just below the scientific station. Subsequent searches revealed additional individuals at Trypot Beach and a single individual at Goodhope Bay some 16 km to the south-west of the station (Fig. 1). Additional sampling was undertaken and individuals sent off for identification in June 2004. At the same time, mummified individuals of the aphid *Rhopalosiphum padi* (Linnaeus) were observed in routinely collected samples. They were dissected and the presence of wasp larvae, pupae and newly eclosed (though not emerged) adults in mummified aphids was confirmed (Appendix).

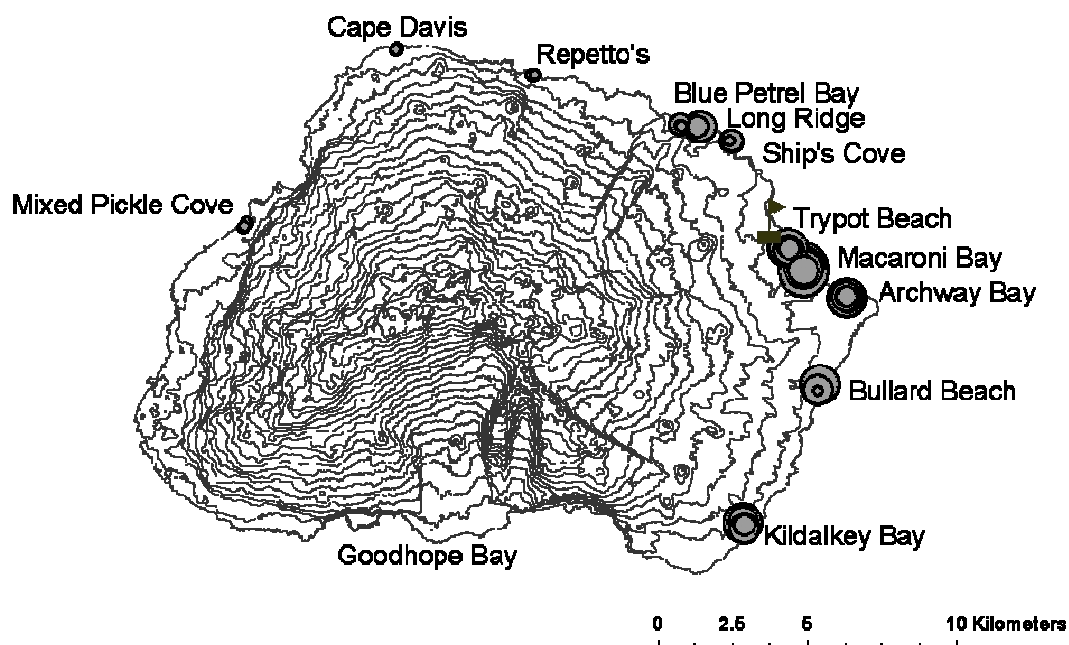


Figure 1. Sampling locations around the coastal habitat of Marion Island. Graduated symbols represent the frequency of aphids parasitized at each at of the sites. The meteorological station (triangular flag) and Good Hope Bay are marked for reference only.

In April 2006, quantitative surveys were undertaken at sites dominated by *Poa cookii*, one of the major hosts of *R. padi* at Marion Island (Crafford *et al.* 1986). *Poa cookii* tussock grasslands or large areas of *P. cookii* tend to be restricted to the eastern side of the island in coastal areas with considerable manuring (Smith *et al.* 2001), although substantial patches of the grass can be found elsewhere. At each site, three to five, 10 x 10 m quadrats in an area dominated by *P. cookii* were selected at random and demarcated. The quadrats were separated by at least 10 m and no more than 100 m. The number of quadrats varied with patch size, and only those patches in which three or more quadrats could be placed at least 10 m apart were sampled. All accessible *P. cookii* clumps within the site were sampled by beating and all invertebrates collected into a sorting tray. In the field, all aphid individuals (three species, all introduced, viz. *R. padi*, *Myzus ascalonicus* and *Macrosiphum euphorbiae*, occur on Marion Island, Crafford *et al.* 1986) were collected using an aspirator and stored in labelled specimen jars. Preliminary investigations of several hundred aphid individuals (including all three aphid species) showed that only *R. padi* individuals are parasitized, and it was reasonably straightforward to recognize *R. padi* in the field (based on Crafford *et al.* 1986 and on Blackman and Eastop 1974). Where quadrats delivered fewer than 100 *R. padi* individuals, additional quadrats were surveyed and samples from the low abundance quadrats were discarded. In the laboratory, all aphids were identified and all *R. padi* individuals were preserved in 100% ethanol. Thereafter, the individuals were dissected and the numbers of individuals that were parasitized or had indications of parasitoid emergence were counted. The frequency of parasitism was recorded as the proportion of individuals that contained live parasitoids and as the proportion of individuals that showed any sign (including emergence) of parasitism. Adult abundance was also estimated as the number of adult wasps per quadrat. Frequency of parasitism and variation in adult abundance was compared among sites using a Generalized Linear Model assuming a binomial distribution and using a logit-link function, and assuming a Poisson distribution and using a log-link function, respectively. The model was corrected for overdispersion.

Molecular data were used to verify the conventional taxonomic identification of the *Aphidius* species found on Marion Island and to determine the number of haplotypes of the species

present on the island. In the case of springtails introduced to the island, Myburgh *et al.* (2007) only found single haplotypes for these species, by contrast with the much more diverse indigenous species. They suggested that colonisation by single haplotypes was likely the norm for introduced species, owing to small founder populations. Therefore, here the molecular data were also used to investigate this hypothesis. The 18S rDNA was amplified and sequenced using the primer pair NS12+ and 18S V4.lo1 as described in Sanchis *et al.* (2000). This region was chosen since it represents one of the more variable portions of the 18S rDNA. Sequences were aligned and compared to those generated by Sanchis *et al.* (2000). Both parsimony and maximum likelihood topologies were constructed (the optimal evolutionary model was determined with Modeltest version 3.7, Posada and Crandall 1998) and confidence in clusterings was generated through 1000 bootstrap replications. To document the spatial distribution of genetic variation across Marion Island, the mitochondrial cytochrome oxidase subunit I (COI) gene was targeted for thirty-three wasps collected from nine localities across the species' distribution range (Mixed Pickle Field Hut n = 2, Blue Petrel Bay n = 4, Long Ridge n = 4, Ship's Cove n = 4, Trypot Beach n = 4, Macaroni Bay n = 4, Archway n = 3, Bullard Beach n = 4, Kildalkey Bay n = 4) (see Fig. 1 for sampling locations). For the COI amplification, I used the primer combination LCO1490 and HCO2198 as described by Folmer *et al.* (1994).

Total genomic DNA was extracted using the DNeasy Tissue Kit (Qiagen). Standard polymerase chain reactions (PCR) were set up for both the 28S rDNA and the COI gene. The temperature regime for all PCR reactions was 96°C for 2 min followed by 30 cycles of 96°C for 40 s, 42°C for 30 s and 72°C for 45 s. A final extension cycle at 72°C for 5 min completed the reactions. Amplicons were directly cycle sequenced using BigDye chemistry (version 3, Applied Biosystems). Unincorporated dye label was removed by sephadex columns before the samples were run on an ABI 3100 automated sequencer (Applied Biosystems). Electropherograms were checked using Sequence Navigator (Applied Biosystems, version 1.01) and aligned by eye. The gene sequences were aligned with Clustal X 1.81 (Thompson *et al.* 1997) using the multiple alignment mode. All alignments were checked by eye. Sequences were submitted to GENBANK under accession numbers EF077525 – EF077526.

RESULTS

Both conventional taxonomic assessments, based on adult morphology, and molecular investigations based on 668 base pairs of the 18S rDNA, identified the parasitoid as *Aphidius matricariae* Haliday (Hymenoptera, Braconidae). For the molecular identification both parsimony and maximum likelihood (optimal model of evolution: HKY + I (0.9394) + G (0.5454); Ti:Tv = 2.3:1) analysis retrieved similar topologies which clustered the Marion Island *Aphidius* haplotype with *A. matricariae* (uncorrected sequence distance between these taxa is 0.15% *cf.* $\pm$ 1% between other recognized species). As was the case for the Sanchis *et al.* (2000) study, the topologies received low overall bootstrap support for nodes.

To investigate the spatial distribution of genetic variation, 651 base pairs of the COI gene were sequenced for thirty three specimens collected across their range on Marion Island (see Fig. 1). These COI characters were translated into 217 functional amino acids. No stop codons or other irregularities were found confirming the authenticity of the sequences. The average AT-content for our data was 74.5%. The base frequency homogeneity test, as performed in PAUP (Swofford 2001), indicated no significant deviation across taxa ($p=1$). A single haplotype characterized all specimens, suggesting that the initial colonisation was made by very few individuals, or perhaps a single female.

The quantitative surveys showed that some sites, especially to the north of Long Ridge, either had no individuals present or the species was rare (Mixed Pickle Cove). By contrast, south of Long Ridge, as far as Kildalkey Bay, parasitism frequency varied between 5 and 20%, and was especially high between Archway Bay and Trypot Beach, with the highest frequencies at Macaroni Bay (Fig. 2, Generalized Linear Model, $\chi^2 = 78.90$, $df = 10$, $p < 0.0001$). The same pattern was evident in adult abundance, although significant differences were found between fewer of the sites (Fig.2, Generalized Linear Model, $\chi^2 = 112.46$, $df = 10$, $p < 0.0001$).

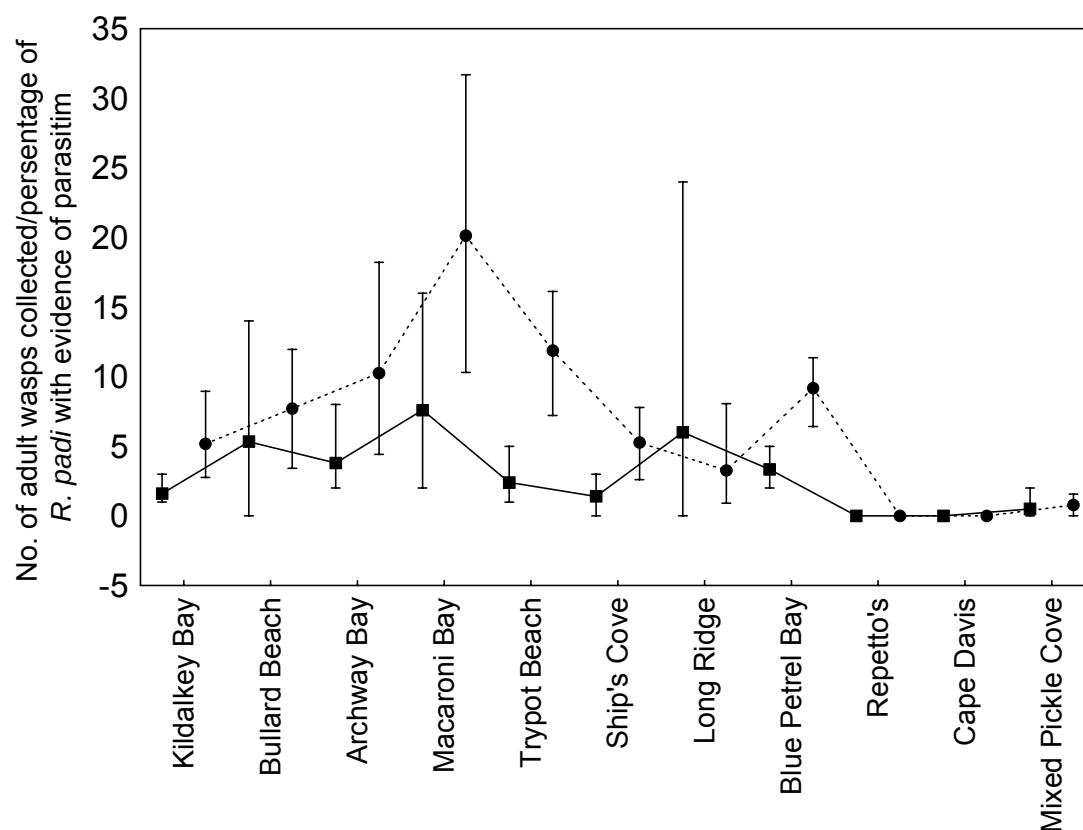


Figure 2. Mean, minimum and maximum frequency of aphids parasitized (●) and mean, minimum and maximum number of adult wasps collected (■) in a 10 m x 10 m quadrat at each of the *P. cookii* sites sampled at Marion Island in April/May 2006 (n = 9 sites and 33 samples). The connecting lines are for clarification and do not imply interpolation.

DISCUSSION

Prior to the 1980s, surveys at Marion Island for the arrival of introduced plant and animal species were not conducted routinely, although several species (at least 10 vascular plant and 8 insect species) were known to have been introduced and have established by that time (Gremmen 1981, Crafford *et al.* 1986). Since the mid 1980s at least ten new species have been observed to have colonised Marion Island, of which seven have established populations that are reproducing either sexually or asexually (Hänel *et al.* 1998, Gremmen and Smith 1999, Chown *et al.* 2002, Slabber and Chown 2002). This parasitoid wasp represents the eleventh known colonist and eighth presently known species to have established a reproducing population. Conventional, morphological taxonomic assessment, confirmed by molecular sequence data for 18S rDNA, has recognized this species as *Aphidius matricariae*.

Aphidius matricariae is now a cosmopolitan species having been introduced into several regions, such as the Nearctic, and has been recorded from 81 countries (Yu *et al.* 2005), including South Africa (Starý 1967). Approximately 115 species of aphid are used as hosts by *A. matricariae*, and this parasitoid wasp has been used in several biological control programmes to control pest aphid species (Yu *et al.* 2005). The apparent restriction of *A. matricariae* to a single host species on Marion Island, despite the presence of two other aphid species that are known hosts elsewhere (Gillespie *et al.* 2002, Yu *et al.* 2005), suggests that specific genotypes might be associated with specific host species, and that only a few individuals probably colonised Marion Island. In other parasitoids, evidence for genotype-based host-specificity is mixed (e.g. Baer *et al.* 2004, Kankare *et al.* 2005).

Whilst *A. matricariae* may have been present on Marion Island for some time prior to its detection, regular invertebrate monitoring surveys make it unlikely that the delay between its initial colonisation and first detection was large. Therefore, it seems likely that this species arrived on the island somewhere between April 2001 and April 2003. Since its first detection in April 2003, *A. matricariae* has been found throughout much of the coastal habitat of Marion Island.

When a species is detected in a new and remote location, establishing whether that species arrived as a consequence of anthropogenic activities or natural dispersal is problematic. In the case of highly mobile taxa, such as many small flying insects or various plant taxa, it is possible that introduction may have occurred naturally, via long distance wind dispersal (Gressitt 1956, Chown and Avenant 1992, Muñoz *et al.* 2004). However, in the case of *A. matricariae*, it seems likely that the species was introduced through human endeavour for two major reasons. First, parasitism frequency and adult densities of *A. matricariae* were highest at Macaroni Bay (Fig. 1), and declined away from this site in either direction along the coast where appropriate habitats are found. Although several models for the expansion of the range of a colonising species exist (Gaston 2003), the most typical is one where occupancy increases first, followed by a later increase in abundance at occupied sites (Hengeveld 1989, Gaston 2003, see also Wilson *et al.* 2004). Presuming ideal environmental conditions throughout the area and some dispersal limitation, this would result in declines in

abundance away from the site of first colonisation, at least during the initial stages of colonisation.

Under such a model, Macaroni Bay would qualify as the most likely point of entry for this species given high densities there. Additional circumstantial evidence bears out this idea. The South African National Antarctic Programme re-supply vessel, the *SA Agulhas*, typically lies at anchor between 500 and 1000 m south east of Macaroni Bay (J. Klopper personal communication, J.E. Lee personal observation). Whilst fresh fruit and vegetables are not allowed onto the island under the Prince Edward Islands Management Plan (Anonymous 1996), they are used on the vessel and stored in large quantities in a galley hold that opens via a hatch onto the poop deck. Moreover, *Aphidius* sp. individuals have been collected from flying insect traps deployed on the ship (J.E. Lee unpublished data). Second, models of natural colonisation of the island suggest that the Kildalkey Bay area is the most likely entry point for natural colonists (Chown and Avenant 1992). However densities of the parasitoid were typically much lower at this site than at Macaroni Bay, despite extensive *P. cookii* stands (Gremmen 1981) and high densities of *R. padi* at the former site. Finally, in the 33 specimens sequenced only one haplotype was found. Low haplotype diversity is typical of introduced species elsewhere (Tsutsui *et al.* 2000, Colautti *et al.* 2005, Lindholm *et al.* 2005) and in the sub-Antarctic (Myburgh *et al.* 2007), though it does not necessarily mean that natural colonisation could not have taken place.

Assuming that Macaroni Bay was the first and only site of entry of *A. matricariae*, that its most distant locality is Mixed Pickle Cove, 22.5 km from Macaroni Bay along the coast, that dispersal has not been assisted by humans or other animals, and that dispersal has taken place at a uniform rate, *A. matricariae* has dispersed at a rate of 20 m per day since its first reported sighting. This rate of dispersal is equivalent to that seen in other small parasitoid species (e.g. Langhof *et al.* 2005).

Irrespective of the precise route of introduction, *A. matricariae* has successfully established an extensive population from what is likely to have been a small founder event, possibly consisting of a single gravid female. Small founder populations are known to have

established successfully on other oceanic islands (see Gaston *et al.* 2003 for discussion), suggesting that propagule pressure (reviewed in Lockwood *et al.* 2005) is unlikely to be a major correlate of invasion in taxa such as small invertebrates. In consequence, if prevention of ongoing invasions, as is required by the Prince Edward Islands Management Plan (Anonymous 1996), and as is accepted as good practise for the region (Frenot *et al.* 2005), is to be effective, a reduction of propagule pressure will be insufficient. Rather, propagule pressure from small invertebrates has to be reduced to zero.

REFERENCES

- Anonymous (1996) *Prince Edward Islands Management Plan*. Department of Environmental Affairs and Tourism, Pretoria
- Baer C.F., Tripp D.W., Bjorksten T.A. & Antolin M.F. (2004) Phylogeography of a parasitoid wasp (*Diaeretiella rapae*): no evidence of host-associated lineages. *Molecular Ecology*, 13, 1859-1869
- 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
- Bester M.N., Bloomer J.P., van Aarde R.J., Erasmus B.H., Van Rensburg P.J.J., Skinner J.D., Howell P.G. & Naude 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
- Blackman R.L. & Eastop V.P. (1974) *Aphids on the world's crops*. John Wiley & Sons, New York
- Chapuis J.L., Boussès P. & Barnaud G. (1994) Alien mammals, impact and management in the French Subantarctic islands. *Biological Conservation*, 67, 97-104
- Chown S.L. & Avenant N. (1992) Status of *Plutella xylostella* at Marion Island six years after its colonisation. *South African Journal of Antarctic Research*, 22, 37-40
- Chown S.L. & Block W. (1997) Comparative nutritional ecology of grass-feeding in a sub-Antarctic beetle: the impact of introduced species on *Hydromedion sparsutum* from South Georgia. *Oecologia*, 111, 216-224
- Chown S.L. & Convey P. (2007) Spatial and temporal variability across life's hierarchies in the Antarctic. *Philosophical Transactions of the Royal Society of London B*, 362, 2307-2301
- 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. & Language K. (1994) Recently established Diptera and Lepidoptera on sub-Antarctic Marion Island. *African Entomology*, 2, 57-76
- 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. & 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
- 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
- Colautti R.I., Manca M., Viljanen M., Ketelaars H.A.M., Bürgi H., Macisaac H.J. & Heath D.D. (2005) Invasion genetics of the Eurasian spiny waterflea: evidence for bottlenecks and gene flow using microsatellites. *Molecular Ecology*, 14, 1869-1879
- Folmer O., Black M., Hoeh W., Lutz R. & Vrijenhoek R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294-299
- Frenot Y., Chown S.L., Whinam J., Selkirk P.M., Convey P., Skotnicki M. & Bergstrom D.M. (2005) Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews*, 80, 45-72
- 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
- Gaston K.J. (2003) *The structure and dynamics of geographic ranges*. Oxford University Press, Oxford
- 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
- Gillespie D.R., Shipp J.L., Raworth D.A. & Footitt R.G. (2002) *Aphis gossypii* Glover, melon/cotton aphid, *Aulacorthum solani* (Kaltenbach), foxglove aphid, *Macrosiphum euphorbiae* (Thomas), potato aphid, and *Myzus persicae* (Sulzer), green peach aphid (Homoptera: Aphididae). In: *Biological control programmes in Canada, 1981-2000* (eds. Mason P.G. & Huber J.T.) CAB Publishing, Oxon, U.K. and New York, U.S.A.
- 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. (2004) The *flora of Marion and Prince Edward Islands* CD-ROM. Data Analyse Ecologie, The Netherlands
- 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. (1956) Some distribution patterns of Pacific Island faunae. *Systematic Zoology*, 5, 32-47
- 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
- Hengeveld R. (1989) *Dynamics of biological invasions*. Chapman and Hall, London
- Kankare M., Van Nouhuys S. & Hanski I. (2005) Genetic divergence among host-specific cryptic species in *Cotesia melitaeorum* aggregate (Hymenoptera: Braconidae), parasitoids of checkerspot butterflies. *Annals of the Entomological Society of America*, 98, 382-394
- Kennedy A.D. (1995) Antarctic terrestrial ecosystem response to global environmental change. *Annual Review of Ecology and Systematics*, 26, 683-704
- Langhof M.R., Meyhofer H.M., Poehling & Gathmann A. (2005) Measuring the field dispersal of *Aphidius colemani* (Hymenoptera: Braconidae). *Agriculture, Ecosystems and Environment*, 107, 137-143
- Le Roux V., Chapuis J-L., Frenot Y. & Vernon P. (2002) Diet of the house mouse (*Mus musculus*) on Guillou Island, Kerguelen archipelago, Subantarctic. *Polar Biology*, 25, 49-57
- Lindholm A.K., Breden F., Alexander H.J., Chan W-K., Thakurta S.G. & Brooks R. (2005) Invasion success and genetic diversity of introduced populations of guppies *Poecilia reticulata* in Australia. *Molecular Ecology*, 14, 3671-3682
- 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
- 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
- Posada D. & Crandall K. (1998) Modeltest: testing the model of DNA substitution. *Bioinformatics*, 14, 817-818
- 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.
- Sanchis A., Latorre A., González-Candelas F. & Michelena J.M. (2000) An 18S rDNA-based molecular phylogeny of Aphidiinae (Hymenoptera: Braconidae). *Molecular Phylogenetics and Evolution*, 14, 180-194
- Schulze B.R. (1971) The climate of Marion Island. In: *Marion and Prince Edward Islands. Report on the South African biological and geological expedition 1965-1966* (eds. van Zinderen Bakker E.M., Winterbottom J.M., Dyer R.A.) A. A. Balkema, Cape Town, 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
- 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
- Starý P. (1967) A review of hymenopterous parasites of citrus pest aphids of the world and biological control projects (Hym., Aphidiidae; Hom., Aphidoidea). *Acta Entomologica Bohemoslovaca*, 64, 37-61
- Swofford D.L. (2001) PAUP*: phylogenetic analysis using parsimony (*and other methods), Beta Version 4.0b2. Sunderland, MA: Sinauer Associates
- Thompson J.D., Gibson T.J., Plewniak F., Jeanmougin F. & Higgins D.G. (1997) The Clustal X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research*, 24, 4876-4882
- Tsutsui N.D., Suarez A.V., Holway D.A., Case T.J. (2000) Reduced genetic variation and success of an invasive species. *Proceedings of the National Academy of Sciences of the United States of America*, 97, 5948-5953

- 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
- Walther G-R., Post E., Convey P., Menzel A., Parmesan C., Beebee T.J.C., Fromentin J-M., Hoegh-Guldberg O. & Bairlein F. (2002) Ecological responses to recent climate change. *Nature*, 416, 389-395
- Williamson M. (1996) *Biological invasions*. Chapman and Hall, London
- Wilson R.J., Thomas C.D., Fox R., Roy D.B. & Kunin W.E. (2004) Spatial patterns in species distributions reveal biodiversity change. *Nature*, 432, 393-396
- Yu D.S., van Achterberg K. & Horstmann K. (2005) World Ichneumonoidea 2004. Taxonomy, Biology, Morphology and Distribution. CD/DVD. Taxapad, Vancouver, Canada.
<http://www.taxapad.com>

APPENDIX

(a) Mumified *Rhopalosiphum padi* (b) Larva emerging from a mummified *R. padi*



Chapter 7 - Physiological tolerances account for range limits and abundance structure in an invasive slug

Accepted for publication as: Lee J.E., Janion C., Marais E., Jansen van Vuuren B & Chown S.L. Physiological tolerances account for range limits and abundance structure in an invasive slug. *Proceedings of the Royal Society of London B. In press* doi: 10.1098/rspb.2008.1240

INTRODUCTION

The structure, limits and dynamics of species ranges and the mechanisms underlying them are among the most significant topics in ecology. Indeed, recent work demonstrating that many macroecological patterns can be derived from spatial variation in aggregation (Storch *et al.* 2008), and that human activities are fundamentally altering species ranges (Channell and Lomolino 2000, Parmesan 2006), has re-emphasized their importance. Much theory now exists concerning how range margins might be set by the interaction of ecological and evolutionary processes. Most simply, a population of any given species will persist in an area that is within the reach of individuals given their dispersal ability (or human assistance for introduced species), and where abiotic and biotic conditions are such that birth rates exceed death rates (Brown 1984, Hoffmann and Blows 1994, Holt and Keitt 2000, 2005, Soberón 2007). Even where conditions are not favourable, individuals may still persist owing to a rescue effect, or temporal variation in conditions, frequently making range margins dynamic and diffuse, rather than sharp (Gaston 2003, Crozier 2004). Why populations often do not evolve to overcome local environmental constraints adds further complexity to the questions of how range margins are set and change (see Hoffmann *et al.* 2003, Alleaume-Benharira *et al.* 2006, Chown and Terblanche 2007, de Mazancourt *et al.* 2008, Hoffmann and Willi 2008 for discussion).

A large and growing empirical literature exists concerning range limits (see reviews in Brown *et al.* 1996, Gaston 2003, Parmesan *et al.* 2005). Nonetheless, several important questions remain unresolved. For example, in the case of the physiological basis of range limits, Gaston (2003) argued that even if it is demonstrated that individuals cannot survive conditions beyond the range edge, this situation might have not have arisen primarily because of the species' physiological tolerances, but because other factors might have limited the species range, with subsequent loss of physiological tolerance. Thus, a fit between physiological

tolerance, climatic conditions and the range margin can have more than one interpretation. Recent work has also highlighted several problems with assumptions that are typically made about the role of environmental range limitation (e.g. Davis *et al.* 1998, Austin 2007, Brooker *et al.* 2007, Sax *et al.* 2007, Chown and Gaston 2008). Indeed, only a few studies simultaneously investigate the form of abundance change across a range margin, propose how this change might be linked to a causal environmental factor (or dispersal limitation), demonstrate how the purported mechanism operates at the physiological level, discount the primacy of other, non-physiological factors, and provide some indication of what mechanisms might be constraining evolutionary change to overcome the ecological constraint. Even where much of the evidence has been provided (e.g. Hill and Hodkinson 1992, Crozier 2004, Bird and Hodkinson 2005, Battisti *et al.* 2006, Crozier and Dwyer 2006, Musolin 2007), often the focus remains on one part of the species range margin despite the importance of understanding patterns and processes across the species range (Gaston 2003, Franco *et al.* 2006, Thomas *et al.* 2006, Merrill *et al.* 2008).

Early generalizations concerning the form of abundance structure (see Brown 1984, Hengeveld 1990 for review) are also now being questioned. Recent empirical work has shown that a unimodal abundance structure is not especially widely supported, owing to much greater complexity of patterns across full ranges or partial components thereof (Brewer and Gaston 2002, Sagarin and Gaines 2002a, McGeoch and Price 2004). However, additional empirical work is required before the generality of these complex abundance structures can be confirmed (Sagarin *et al.* 2006). What the causal basis is of abundance structure also remains largely unanswered empirically (Gaston 2003). Two significant constraints face any study attempting to further work in this area. First, the form of abundance structure must be established before any other work can proceed. Then, appropriate spatial variation in likely causal factors must be investigated and the significance of the factors verified either experimentally, or by some independent means. Doing so is by no means trivial (Brewer and Gaston 2003, Klok *et al.* 2003), and more so where an explicit metacommunity framework (Leibold *et al.* 2004) is required.

This study address' both major questions, specifically examining the factors responsible for range limits and for variation in abundance structure in a slug species that has invaded an

isolated, oceanic island. This system was chosen for two major reasons. First, the slug is thought to be having profound impacts on functioning of the island's terrestrial ecosystem (Smith 2007). Second, because of the relative simplicity of the island's food web (Burger 1985) and small number of terrestrial species (Gaston *et al.* 2001), teasing out the factors responsible for setting range limits and variation in abundance structure should be relatively straightforward. Therefore, the system should be useful for testing several assumptions that have been made about the form that variation in abundance and in environmental factors should take if a causal relationship exists between them (e.g. Caughley *et al.* 1988, Sagarin *et al.* 2006).

MATERIAL AND METHODS

(a) Site and species

This work was undertaken on sub-Antarctic Marion Island (46°54'S, 37°45'E), which has a cool, wet, windy climate that has shown substantial change over the last 50 years (Le Roux and McGeoch 2008). *Deroceras panormitanum* (Pollonera) (Gastropoda: Limacidae) is an air-breathing land slug of Mediterranean origin which is now virtually cosmopolitan (Holland *et al.* 2007). Although it is known as an invasive in the sub-Antarctic only from Marion Island, it is also invasive on Tristan da Cunha, the Chatham Islands, and in New Zealand (Pugh and Scott 2002), and is also an introduced species in South Africa, with the first records from 1963 (Smith 1992). *Deroceras panormitanum* was first introduced to Marion Island in the 1970s, probably with fresh produce shipped from South Africa to the island's research station (Smith 1992). It was initially restricted to the vicinity of the research station (Smith 1992), but was later moved to many other areas likely via the wooden containers initially used for the restocking of field huts (Chown *et al.* 2002). It is a generalized detritivore, and is not known to have particular feeding preferences elsewhere in its range (Holland *et al.* 2007) or on Marion Island (J.E. Lee unpublished data). Southern Ocean Island systems have few predators, parasitoids and parasites (Vernon *et al.* 1998), and although the introduced house mouse, *Mus musculus*, is a predator of several invertebrate species on Marion Island (Crafford and Scholtz 1987, Smith *et al.* 2002), no records exist of this species feeding on slugs under any circumstances (Gleeson and van Rensburg 1982, Smith *et al.* 2002). Furthermore, no reports have been made of parasitism or disease in *D. panormitanum* from

Marion Island, despite such records being available for other invertebrates on the island (e.g. Chown and Scholtz 1989, Theodorides and Chown 1992, Lee *et al.* 2007).

(b) Assumptions of the current approach

In using this invasive species and island system I explicitly make three key assumptions. First, that abundance structure and range limits in a relatively isolated part of a species range can be used to understand such processes more generally (see Brown 1984, Hengeveld 1990, Gaston 2003 for support for this assumption). Second, that island situations can be used to investigate mechanisms underlying species range and abundance structure (as is frequently done for species on the islands that constitute the United Kingdom, and elsewhere – see e.g. Hodkinson *et al.* 1999, Thomas *et al.* 2001, Gaston and Blackburn 2003, Gaston *et al.* 2006). Third, that in this specific instance dispersal from other populations of the species to the island no longer takes place, and has not taken place at least for the past several decades. Given the very stringent management plan that is presently in place, and the management conditions that have been in operation since the 1990s (details in Chown and Froneman 2008), this latter assumption is defensible.

(c) Abundance structure and range limits

During April 2007 and April 2008 surveys to determine the distribution and abundance of *D. panormitanum* were made of much of the coastal and inland habitat of Marion Island using a stratified random sampling approach. The stratification was by habitat type (see Chown and Froneman 2008 for a description thereof) and included biotic, drainage line, mire, saltspray, fernbrake and fellfield habitats. Each time a habitat type was entered, while traversing the coastal plain, and along several altitudinal gradients, a sample was taken at least 10 m from the habitat type boundary. Each sample consisted of a 0.09 m² quadrat that was searched thoroughly to the soil surface for slugs. If a habitat type was continuous in one direction for more than 500 m (at the classification resolution I used, several habitats are continuous in this way, e.g. mire, fellfield), additional plots were surveyed until the point that a new habitat type was reached. To confirm the altitudinal limits of the species, areas of suitable habitat were surveyed for an additional 100 m altitude above the highest quadrat at which a slug was found in that area. For each quadrat, slug abundance, latitude, longitude and habitat type were recorded.

Two approaches were adopted for investigating the form of the spatial density variation. First, density data (as slugs.m⁻²) for each quadrat were plotted spatially using ArcGIS (v9.1 ESRI, California, USA), and a natural neighbour algorithm (Sambridge *et al.* 1995) was used to interpolate abundance structure (in the form of density). Then, based on the clear coastal and elevational limits revealed by the former approach, all density data were plotted against altitude to determine the form of their relationship. In particular, the data were inspected for thresholds or gradients of the form predicted by Caughley *et al.* (1988), and the latter confirmed using quantile regression as implemented in Blossom Statistical Software W2008.04.02 (USGS, Fort Collins, Colorado, USA) (Cade and Richards 2005). To investigate the upper altitude decline in density, the quantile function (0.95) was used with density as the dependent variable. To investigate the lower altitude end of the distribution it was necessary to consider altitude the dependent variable and to examine the 0.1 quantile.

(d) Environmental correlates

To investigate the proximate correlates of density variation across the island a Generalized Linear Model was built in Statistica v.8 (Statsoft, Tulsa, Oklahoma, USA) (assuming a Poisson error distribution and using a log-link function, corrected for overdispersion). The model included a third order polynomial for trend surface analysis based on mean-centred latitude and longitude (see Legendre and Legendre 1998) and altitude as continuous predictors, and habitat type as a categorical predictor. The best fit model was sought using the Akaike information criterion (AIC) and Akaike weights (Johnson and Omland 2004). Because it seemed likely that aspect might also affect slug density, the analysis was repeated including aspect as a categorical factor. Aspect was determined from the Marion Island digital elevation model (Meiklejohn and Smith 2008) at a 20 m resolution and these values were subsequently binned to north, south, east, west and flat categories. Owing to low slug densities in most vegetation types, only the drainage line and biotic vegetation types were included in this analysis.

Altitude is an indirect environmental variable (Austin 2007), and is a proxy for variation in a variety of other, direct environmental variables. The most notable environmental change with altitude on Marion Island is a decline in temperature, and perhaps an increase in

rainfall, although changes in both variables may be non-linear (Blake 1996, Deere *et al.* 2006, Nyakatya and McGeoch 2008). Owing to the remote nature of most of the island, temperature data over the full altitudinal transect are available only for the eastern part of the island (Deere *et al.* 2006) and for a small western area (Nyakatya and McGeoch 2008). Here, I examined the eastern data set over the period 2002-2007, spanning the altitudinal range 0-400 m a.s.l. at 100 m intervals.

The temperature data used in this study represent soil surface temperatures recorded using iButton ThermoChron loggers (Model DS 1922L and DS 1921G; accurate to $\pm 0.5^{\circ}\text{C}$, Dallas Semiconductors, Dallas, TX, USA). Frequency distributions of the hourly temperature data were plotted to determine the frequency of various temperature conditions at each elevation, although summary statistics were also calculated for each elevation. The long-term record was used because range margins may well be set by occasional extreme events (Gaines and Denny 1993, Gaston 2003). Rainfall data were available for three sites only (25 m, 550 m, 750 m) from Blake (1996).

A sharp edge at the seaward side of the species range (see Results), but high densities at this edge, suggested that a change in substrate quality might be responsible for the range margin. I hypothesized that the most likely driver of this margin, given what is known of slug biology in general (South 1992), would be salinity, especially since during initial surveys it became clear that coastal sites protected from salt spray had relatively high slug densities. To determine the effect of environmental salinity on slug densities, 56 sites on areas both sheltered from and exposed to salt spray, and at varying distances from the sea, were surveyed using the methods described above, and soil samples were taken at each site. Samples were air dried and exchangeable sodium was quantified (BemLab, Somerset West, South Africa). A Generalized Linear Model (assuming a Poisson distribution, using a log-link function and corrected for overdispersion) was used to investigate the significance of distance and exchangeable Na as continuous predictors of slug density.

I further hypothesized that variation in the density of *D. panormitanum*, associated with habitat types, might be related to temperature and humidity conditions characterising the various habitats for several reasons. 1) Poor desiccation resistance of slugs and their strategy

of behavioural avoidance of desiccation (South 1992); 2) the dry conditions typical of exposed sites at the island (despite high rainfall, see Klok and Chown 1998 for discussion); 3) poor tolerance of low temperatures in molluscs (Ansart and Vernon 2003); 4) generalized detritivory in the species.

For examining the effect of vegetation on temperature and humidity a Vaisala HUMICAP® HM 34 humidity and temperature meter (Vaisala inc., Woburn, MA, USA) was used to measure relative humidity and temperature at 1 m above ground level and, to represent the space inhabited by *D. panormitanum*, underneath the vegetation canopy, in five habitat types (drainage line, fernbrake, biotic, fellfield and mire). Fellfield vegetation is dominated by compact cushions of *Azorella selago* where it was not possible to take readings from inside the cushion without causing extensive damage. Here, values from the cushion surface were used, because this is the only habitable part of the plant for *D. panormitanum*. Relative humidity (RH) and temperature were measured across a range of 30 to 100% RH and 2 to 16°C at the 1 m height. Across these conditions, differences between the temperature at 1 m and within the vegetation, and humidity at 1 m and vegetation were used to estimate the buffering capacity of the vegetation. The extent to which these differences varied with habitat types was compared among habitat types using a one-way ANOVA.

(e) Physiological traits

Supercooling point determinations

The slugs were collected from Trypot Beach with forceps into 250 ml plastic jars and returned to the laboratory within two hours of collection. During transit, containers were stored inside backpacks. Owing to high cloudiness and low ambient temperatures that characterize the island, temperatures in the backpacks were close to ambient. On return to the laboratory, slugs were sorted into new 250 ml containers at low densities (15-20 individuals per container), and placed into a Labcon incubator set at 5°C (12L:12D). The containers were divided into two experimental groups, “starved” and “fed”. The starved group received no food for the eight day acclimation period, while the “fed” group received fresh and dying *Cotula plumosa* leaves (a vascular plant species typical of the biotic habitat) *ad libitum*. High humidity was ensured for both groups by placing the containers into a large plastic container that contained distilled water. Containers were rotated on a daily basis to avoid possible shelf

effects.

After the eight day acclimation period, the “fed” group was further divided into two groups, namely “wet” and “dry” groups. All individuals used in the experiments were weighed using a Mettler AE163 (Mettler-Toledo, Columbus, U.S.A) electronic balance with a resolution of 0.01 mg and placed inside 1.5 ml eppendorf vials with a T-type copper-constantan thermocouple (40 SWG) inserted between the individual and the eppendorf vial wall. The slugs were kept in place with cotton wool: with dry cotton wool for individuals in the “dry” group and cotton wool that was moistened with distilled water for the “wet” group. The eppendorf vials were then placed into a custom-built Peltier controlled cooling device (see Sinclair *et al.* 2003 for details) and held at $\pm 3^{\circ}\text{C}$ for 20 minutes to equilibrate. After the equilibration period, the animals were cooled at a rate of 0.1°C per minute. Sixteen individuals were examined at a time and the thermocouple from each individual was attached to one of two eight-channel PC-08 (Picotech, UK) data loggers connected via RS-232 serial ports to a standard desktop computer, which recorded temperature every second. The supercooling point (SCP) was taken as the lowest temperature reached prior to the freezing exotherm (latent heat of crystallization, see Lee 1987). A General Linear Model was used to examine the effects of treatment (wet, dry, starved) and mass on SCP. Supercooling point values were also obtained for field fresh individuals in the same manner as above and a second model was used to investigate SCP variation among the four treatments (excluding mass). Given the small effect size of the treatments, all data were grouped for plotting SCP distributions against altitude. A further experiment, data from which were not included in the above, grouped data set, maintaining individuals as above, but at 0, 5, 10 or 15°C , revealed that acclimation has little effect on the supercooling point (as found for many other molluscs – Ansart and Vernon 2003).

Lethal Limits

Measurement of lower lethal temperatures (LLT) provides insight into whether pre-freeze mortality is biologically significant (Bale 1993). For LLT determination, groups of eight field fresh slugs (two replicates per treatment) were placed into 1.5 ml eppendorf vials. As above, a thermocouple was inserted between each slug and the wall of the vial. Animals were placed into the Peltier cooling device and cooled at a rate of $0.1^{\circ}\text{C}.\text{min}^{-1}$ (within the range

measured in the field) until the test temperature was reached (between 0 and -12°C at 1°C intervals), where the temperature was maintained for two hours. Animals were subsequently removed and placed on a petri dish containing moistened filter paper and allowed to recover at 5°C. After 24 hours, survival was scored as alive if an animal was able to move around the petri dish. Logistic regression, implemented in Statistica v.8, was used to determine the temperature at which 50% and 99% (taken as 100%) mortality was reached. Upper lethal limits were not measured because pilot data indicated upper lethal temperatures ($32.4 \pm 1.0^\circ\text{C}$) much higher than those likely to be encountered in the field.

Desiccation

Time to death was determined at three relative humidities (see below). Animals ($n = 20$) were placed singly into 20 ml polypropylene vials within a sealed plastic container. The plastic container contained distilled water, saturated NaCl solution or silica gel to obtain relative humidities of 100%, 76% or c. 7%, respectively. These humidities represent the variety of conditions found on Marion Island, including the effects of high wind speeds and the absence of a boundary layer (Chown and Froneman 2008). Survival was scored every two hours for 20 hours in the 7% and 76% treatments and for 82 hours for the 100% relative humidity treatment. Desiccation rate was calculated as total water lost per unit time ($\text{g}\cdot\text{h}^{-1}$) and a General Linear Model was used to examine the effect of relative humidity and body mass on desiccation rate.

Salinity tolerance

Large areas of the slug's potential range on the island are affected by salt spray. Therefore salinity tolerance is likely to be an important determinant of the position of the seaward boundary and the abundance structure of populations in coastal habitats. Here, salinity tolerance (time to death) was measured for slugs exposed to sea water at 0% dilution (pure sea water), 50% dilution, 75 % dilution and 100 % dilution (distilled water), reflecting conditions from the supralittoral to the upland environment of the island (Chown and Froneman 2008). For each treatment, 20 animals were placed singly into 50 ml plastic containers lined with an absorbent, inorganic pad. The pad was moistened with seawater diluted to the various test concentrations and positioned so the animals were in constant contact with it. Survival was scored hourly for the 100% and 50% dilutions and daily for the

70% and 0% dilutions. Salinity was converted to Na (mg/kg) equivalents assuming that undiluted seawater has a value of 10572 mg/kg, and the effect of salinity on survival was investigated using a Generalized Linear Model assuming a Poisson distribution, using a log-link function and corrected for overdispersion.

Metabolic rates

The effects of test temperature (5, 10, 15, 20, 25 and 30°C), acclimation temperature (0, 5, 10 and 15°C) and mass on standard metabolic rate were estimated by measuring VCO₂ at rest. New, acclimated individuals were used for each temperature x acclimation assessment. Initially, slugs were weighed using a Mettler AE163 electronic balance (with a resolution of 0.01 mg) and placed into a 5 ml plastic cuvette. Air, scrubbed of CO₂ (using soda lime) and water (using silica gel and Drierite®, Xenia, OH, USA) was bubbled through a copper coil placed inside a water bath (Grant LTD6, Grant Instruments, Cambridge, UK) to re-humidify the air to 70% RH (temperature required to produce set humidity calculated using Unwin and Corbet 1991). The flow rate was set at 100 ml/min and regulated using a Sidetrak Mass Flow Controller, (Monterey, USA). The humidified air was then passed into a Sable Systems (Sable Systems International, Las Vegas, U.S.A.) multiplexer, which switched the airstream through eight different cuvettes, seven of which each contained a slug and the eighth which was used for baselining (see Terblanche *et al.* 2005 for a full description). The multiplexer system switched the airstream between cuvettes every 15 minutes before passing it to a calibrated infrared gas analyzer (Li-Cor Li7000, Lincoln, NE, USA) which measured CO₂ production. The empty cuvette was used for baselining ten minutes before and after each trial. When the VCO₂ of a given slug was not being measured, a supplementary humidified airstream was used to flush the cuvette at a flow rate of approximately 100ml/min to prevent CO₂ and water build-up. Data were recorded using Li7000 software and were exported as a text file and the subsequently imported to ExpeData (v 10.019, Sable Systems International) for initial analysis of respirometry data. For each set of seven recordings, CO₂ traces were baseline corrected in ExpeData. Based on visual observation of slug activity it was clear that they did not move frequently in the cuvettes. Nonetheless, the lowest VCO₂ sections of each recording were selected (only continuous gas exchange was shown) and mean VCO₂ calculated. Following Lighton (1991), CO₂ in ppm was converted to ml.hr⁻¹ which was used in all subsequent analyses. A general linear model was used to explore the effect of acclimation,

test temperature and $\log_{10}$ mass (continuous variable) on $\log_{10}\text{VCO}_2$ using a homogeneity of slopes approach in Statistica v.8. Acclimation was not significant ($F(4, 362) = 1.01, p = 0.40$), nor were any of the interactions ($0.20 < p < 0.64$). An additional model including only test temperature and $\log_{10}$ mass was then used to investigate their effects on metabolic rate variation.

(f) Genetic diversity

Although the relationship between evolutionary capacity and variation in genetic markers is not straightforward (Hoffmann *et al.* 2003, Dlugosch and Parker 2008), diminished variation may still indicate an inability for a given population further to evolve. In consequence I used a neutral marker (mitochondrial COI) to investigate the extent of genetic variation, at least for this locus, in the slug population.

Slugs were collected from around the island, and specifically Swartkop Point ($n=4$), Mixed Pickle Cove ($n = 4$), Cape Davis ($n = 4$), Rooks Bay ($n = 4$), Repettos Hill ($n=4$), Skua Ridge ($n = 1$), Greyheaded Albatross Ridge ($n = 3$), and the Research Station ($n = 1$). Slugs were stored in absolute ethanol. Laboratory protocols followed those described in Lee *et al.* (2007) and Chown *et al.* (2008). In short, DNA was extracted using the Qiagen (Valencia, California) DNeasy Blood and Tissue Kit. The mitochondrial COI gene was targeted using the primers LCO1490 and HCO2198 described by Folmer *et al.* (1994). The sequences generated were deposited in GenBank (accession number - FJ358222), aligned with Clustal X (Thompson *et al.* 1997) using the multiple alignment mode, and haplotypes identified using Collapse 1.2 (Posada 2004) and verified in Arlequin 3.1 (Excoffier *et al.* 2005).

RESULTS

A total of 1109 quadrats was surveyed around the island and between 2 and 494 m altitude. The abundance frequency distribution was right-skewed – most quadrats contained no slugs and the highest density was 344 slugs.m^{-2} (Fig. 1). The natural neighbour interpolation revealed a complex abundance structure with patches and gaps (Fig. 2). Unsurprisingly, the best fit model for the density data ($\text{AIC} = 203364, w_i = 0.99$) included all terms in the trend surface third order polynomial, and also included altitude and habitat type, with the latter variables being highly significant (Table 1). Abundances were highest in the biotic and

drainage line habitats and low elsewhere (Fig. 3a). In these latter habitats, aspect was also a significant predictor of density (the best fit model included all spatial terms, vegetation, altitude and aspect, $AIC = 203517$, $w_i = 0.94$, see Table 2), with densities being highest in north and east-facing slopes and flat areas (Fig. 3b).

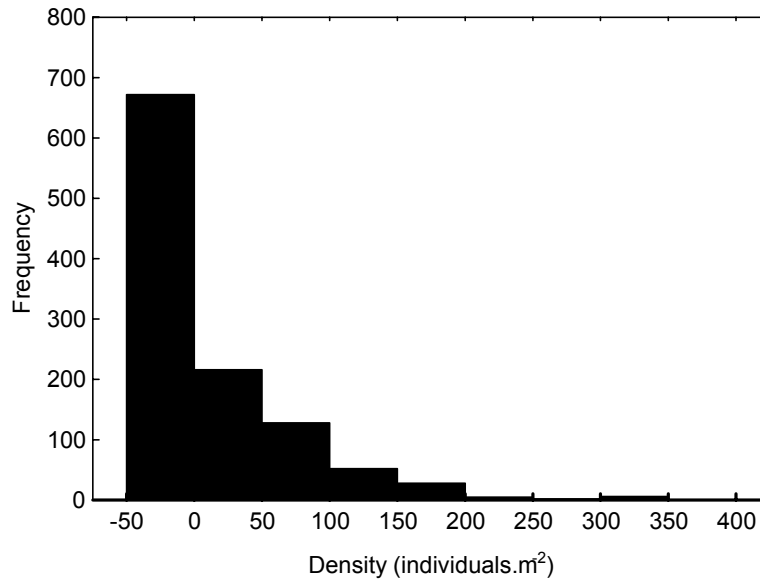


Figure 1. Frequency distribution of density across the 1109 quadrats sampled on Marion Island.

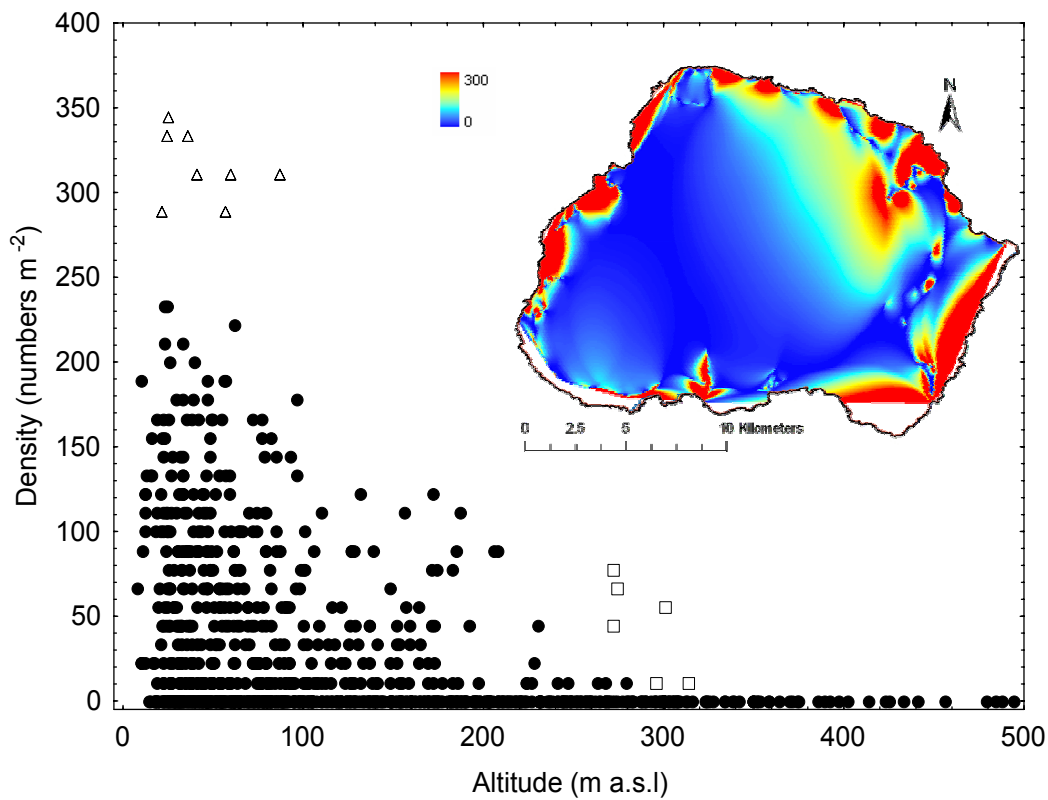


Figure 2. *Deroceras panormitanum* density plotted against altitude for all 1109 quadrats sampled on Marion Island. The open triangles indicate Trypot Beach on the east coast and

the open squares the high altitude site above Micked Pickle Cove. The inset shows the natural neighbour interpolation of slug density (numbers.m⁻²) across the island.

Table 1. Outcome of a Generalized Linear Model (assuming a Poisson distribution, using a log-link function and corrected for overdispersion) investigating the effects of the terms from a 3rd order trend surface polynomial for latitude and longitude, altitude and habitat type on the density of *D. panormitanum*.

Variable	df	χ^2	P
Latitude	1	28.5	0.0001
Longitude	1	6.2	0.013
Latitude * Longitude	1	5.4	0.021
Latitude ²	1	4.7	0.029
Longitude ²	1	3.9	0.048
Latitude ² * Longitude	1	5.2	0.022
Longitude ² * Latitude	1	5.2	0.023
Latitude ³	1	18.8	0.0001
Longitude ³	1	8.1	0.004
Altitude	1	165.2	0.0001
Habitat type	5	1677.7	0.0001
Deviance/df	1093/1093 = 1		

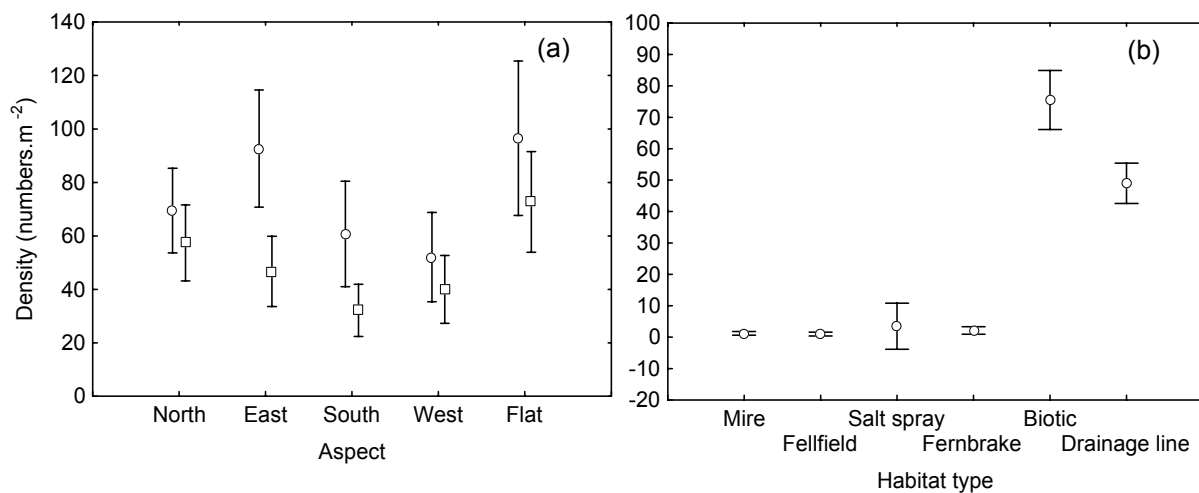


Figure 3. (a) Weighted marginal means ($\pm$ 95% C.I.) of slug density in each of the seven habitat types investigated, obtained from a Generalized Linear Model including spatial terms, altitude and habitat. (b) Weighted marginal means ($\pm$ 95% C.I.) of slug density in the biotic (○) and drainage line (□) habitats, obtained from a Generalized Linear Model including spatial terms, altitude, aspect and the two habitats.

Table 2. Outcome of a Generalized Linear Model (assuming a Poisson distribution, using a log-link function and corrected for overdispersion) investigating the effects of the terms from a 3rd order trend surface polynomial for latitude and longitude, altitude and habitat type and aspect on the density of *D. panormitanum* in the drainage line and biotic habitats only.

Variable	df	χ^2	P
Latitude	1	6.4	0.0114
Longitude	1	6.3	0.012
Latitude * Longitude	1	2.2	0.136
Latitude ²	1	42.3	0.0001
Longitude ²	1	29.3	0.0001
Latitude ² * Longitude	1	4.3	0.038
Longitude ² * Latitude	1	66.6	0.0001
Latitude ³	1	11.0	0.0009
Longitude ³	1	2.5	0.116
Altitude	1	86.1	0.0001
Habitat type	1	3.4	0.065
Aspect	4	13.4	0.009
Aspect * Habitat type	4	3.4	0.488
Deviance/df	447/447 = 1		

At the landscape scale, the coastal gaps often coincided with high elevation ridges reaching the coast, and the patches with biotically influenced vegetation associated with seal and seabird colonies, and also with drainage lines along high elevation ridges. Across the full elevational range sampled, a clear threshold in density occurs on the coast (supported by the 0.1 quantile slope of -0.081), whilst a gradual decline in density is associated with an increase in elevation (supported by the significantly negative 0.95 quantile slope of -0.364, $p < 0.0001$). The relatively high density of slugs above 200 m was found mostly at a site above Mixed Pickle Cove on the west coast (Fig. 2).

Mean annual soil surface temperature declines in a linear fashion with altitude ($r_s = -0.99$, $p < 0.01$), and the number of hours below 0°C likewise increases rapidly with elevation ($r_s = 0.95$, $p < 0.05$). However, absolute minima and maxima, and number of hours below -3°C (a critical threshold for the slug, see below) show more complex variation, with 200 m having an exceptionally low absolute minimum and 31 days with temperatures below -3°C over the full period (Table 3). Whilst temperatures did not decline below -3°C at 300 m, the number of days below this temperature increased again from 400 m (Table 3) (and indeed above that

altitude to 1000 m, data not shown). Previous recordings by Blake (1996) indicated that precipitation does not decline with altitude, but rather shows an increase to 550 m (from 2873 mm at sea level to 4653 at 550 m).

Table 3. Mean, standard deviation, minimum and maximum temperatures across an eastern altitudinal transect on Marion Island between 2002 and 2007, and number of hours and days within that period that were less than or equal to 0°C and less than or equal to -3°C, the mean supercooling point of *D. panormitanum*. Rare, light snow cover likely explains the extreme temperatures at 200 m compared with the higher sites that receive more snow.

Altitude (m a.s.l.)	N	Mean (S.D.)	Min	Max	Hours (days) ≤ 0 °C	Hours (days) ≤ - 3 °C
0	38465	6.31 (2.80)	-1.0	22.5	165 (13)	0
100	38430	5.53 (3.00)	-0.5	20.0	295 (35)	0
200	38609	4.96 (3.31)	-10.0	19.0	1397 (141)	396 (31)
300	38675	4.54 (3.13)	-1.5	19.0	2258 (198)	0
400	37258	3.84 (3.37)	-8.0	20	4540 (398)	234 (17)

At the coastal margin, analysis of the additional surveys including estimates of exchangeable sodium revealed that distance to the coast was not a significant explanatory variable ($\chi^2 = 0.75$, $p = 0.39$), although exchangeable sodium was ($\chi^2 = 33.0$, $p < 0.0001$), with density dropping to zero above 3000 mg Na/kg (Fig. 4).

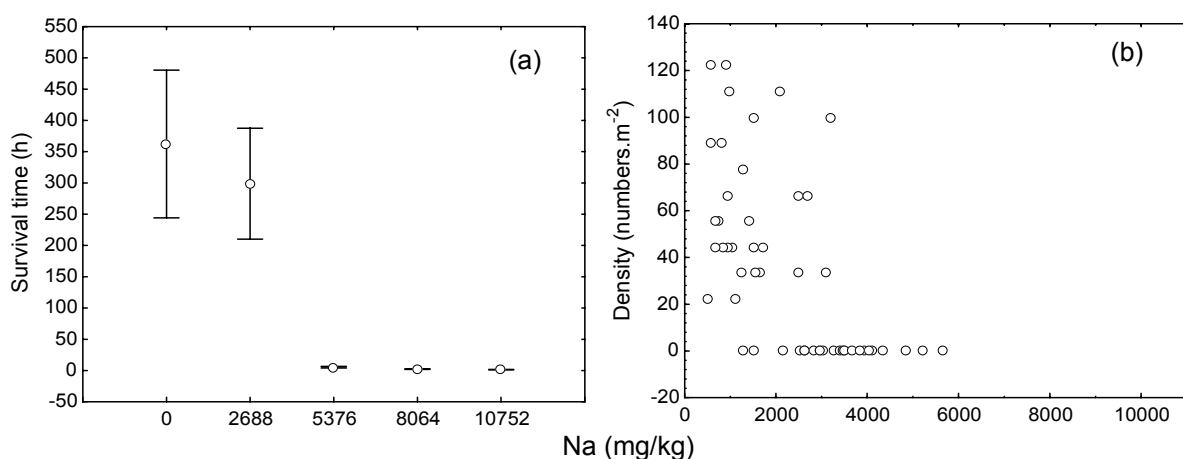


Figure 4. (a) Mean ($\pm$ 95% C.I.) survival of *D. panormitanum* exposed to different seawater concentrations (converted to Na equivalents in mg/kg). (b) *D. panormitanum* density in 56 coastal quadrats plotted against soil exchangeable Na concentration.

Within the range margins, the biotic and drainage line sites, which had the highest slug densities (Fig. 3a), did not differ in temperature differential between the 1 m measurement and the vegetation surface or subsurface from the other sites ($F_{(4,384)} = 0.79$, $p = 0.53$). By contrast, the high density habitat types had significantly higher humidities within the vegetation than outside it than did the other sites ($F_{(4,384)} = 26.8$, $p < 0.001$, Fig. 5).

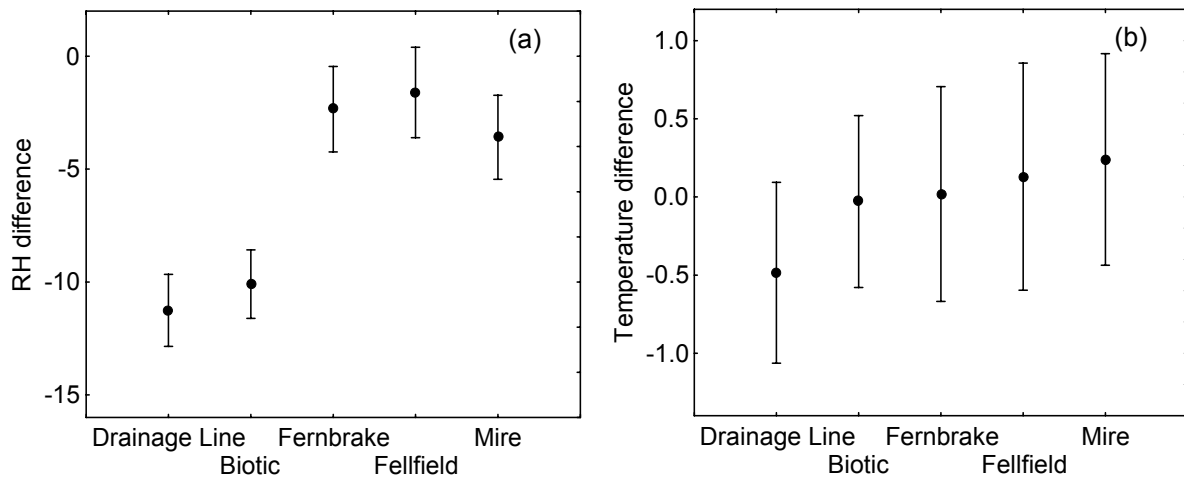


Figure 5. Least-squares means ($\pm$ 95% C.I.) of temperature (a) and relative humidity (b) differences between measurements at 1 m above, and at or below the vegetation surface, for each of the habitats sampled on Marion Island.

The thermal tolerance data indicated that the slugs are unable to survive temperatures lower than -6.4°C , and lower than -2.6 to -3.3°C on average (Table 4). Although the treatments had a significant effect on SCP ($F_{(2, 111)} = 10.3$, $p < 0.001$), as did the positive relationship with mass ($F_{(1, 111)} = 28.6$, $p < 0.001$), the overall effect size was less than 0.5°C . This was true also of acclimation. Although its effect was significant ($F_{(3, 116)} = 7.2$, $p < 0.001$), the largest difference among treatments was 0.53°C . Indeed, it seems clear that *Deroceras panormitanum*'s upper elevational range margin coincides closely with the elevation where the lower thermal limits are occasionally exceeded by soil surface temperature minima (Fig. 6), at least on the eastern half of the island. The metabolic rate data further revealed a linear decline in functioning with temperature ($\log_{10}\text{VCO}_2 = 0.0186 * \text{temperature} - 1.251$, $t = 23.9$, $p < 0.0001$, partial correlation = 0.77, Fig. 7). By contrast, salinity tolerance declined in a step-like manner with increasing Na concentration, with zero survival above 3000 mg/kg Na

($\chi^2 = 407.4$, $p < 0.0001$, Fig. 4). High humidity conditions (76% RH) resulted in a mass-corrected desiccation rate of $c. 2.4 \pm 0.32 \text{ mg.h}^{-1}$ (LS mean $\pm$ S.E.), whereas at 7% this increased five fold to $12.5 \pm 0.31 \text{ mg.h}^{-1}$ (Fig. 8).

Table 4. Mean, minimum and maximum values in °C for supercooling points following three laboratory treatments and from field fresh individuals. The lower lethal temperature value is the temperature at which 50% mortality occurred, estimated from a logistic regression, as well as the temperature at which survival declined to zero.

Parameter	N	Mean (SE)	Min	Max
SCP (dry)	47	-3.4 (0.12)	-6.4	-2.2
SCP (wet)	36	-3.0 (0.04)	-3.3	-2.4
SCP (starved)	32	-3.4 (0.04)	-3.8	-3.0
SCP (field)	29	-3.1 (0.05)	-3.8	-2.6
LLT	112	LT50 = -2.6	LT100 = -4.3	

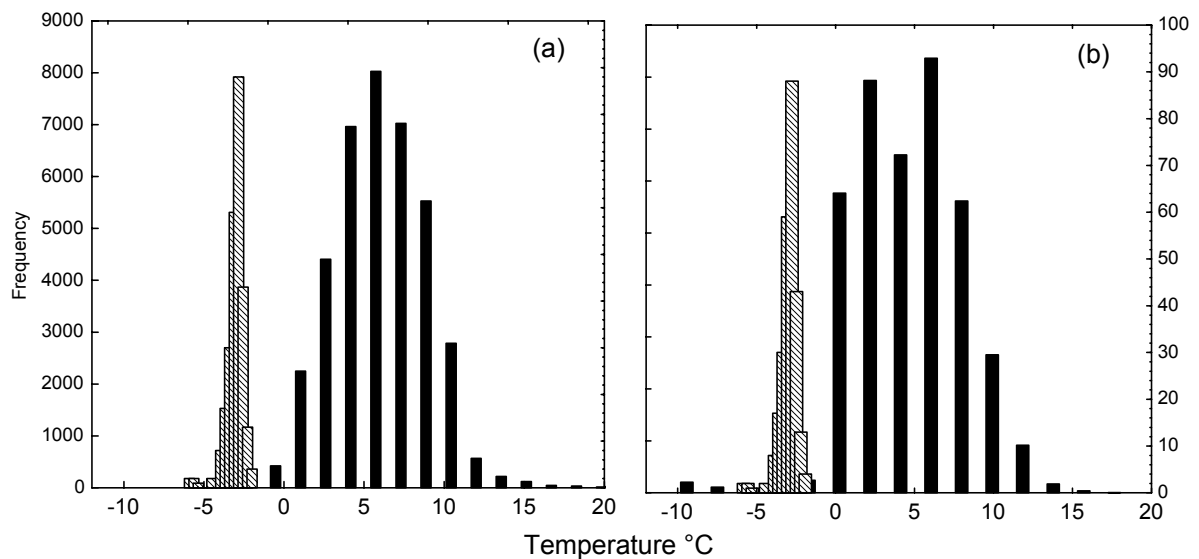


Figure 6. Frequency distributions of soil surface temperature (closed bars) and the supercooling points (SCP) of *D. panormitanum* (hatched bars) at (a) sea level ($\approx 10 \text{ m a.s.l.}$) and at (b) 200 m a.s.l. Note that the lowest soil temperatures at 200 m lie beyond the frequency distribution of the SCPs.

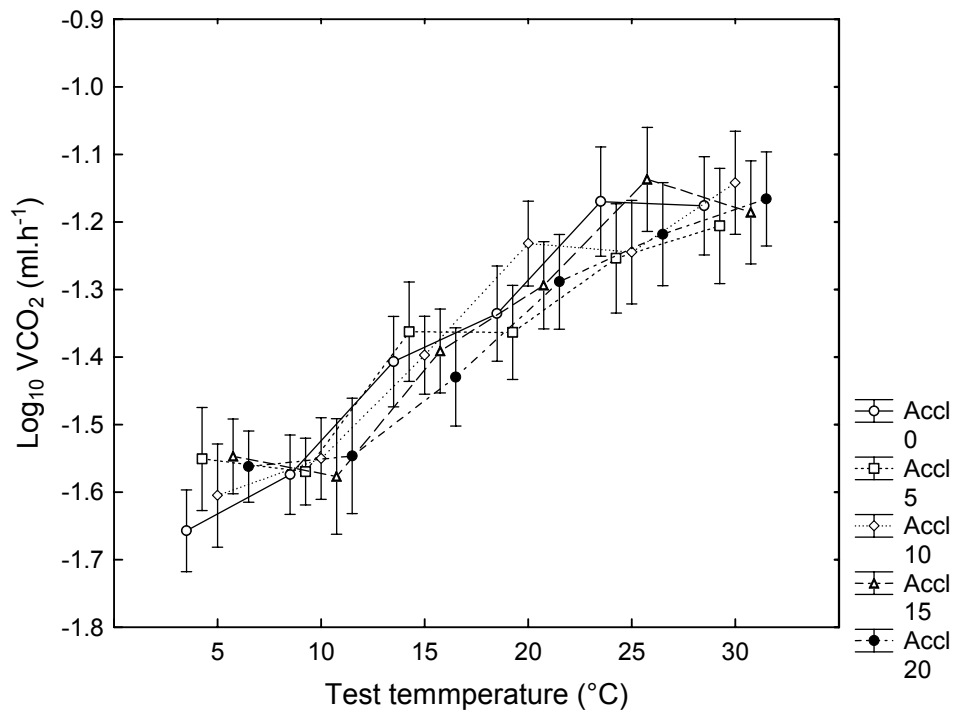


Figure 7. Weighted marginal means ($\pm$ 95% C.I.) metabolic rate (estimated as VCO_2) of *D. panormitanum* across six test temperatures following eight days of acclimation to five different temperatures (Accl). The acclimation effects were not significant. Lines are for guidance only.

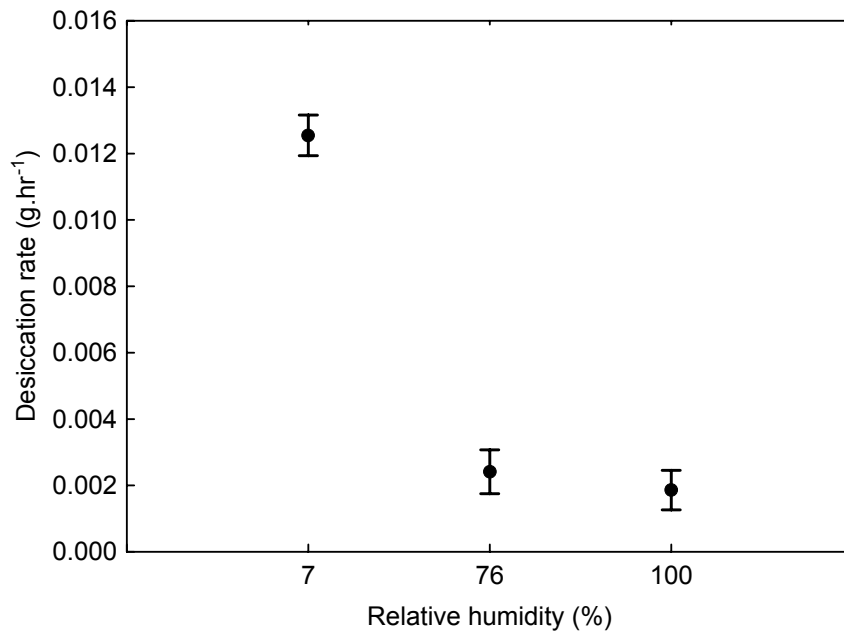


Figure 8. Least squares means $\pm$ 95% C.I. (corrected for initial mass) of desiccation rate in *D. panorminatum* measured at three different relative humidities. The low humidity rate differed significantly from the other values ($F_{(2, 51)} = 379.3$, $p < 0.0001$).

The mt COI sequence data indicated that a single haplotype characterizes all 25 individuals examined.

4. DISCUSSION

Despite its restriction to the lower elevations of Marion Island, the abundance structure of *D. panormitanum* does not take the form of a simple unimodal distribution as was once widely thought to be the case (Brown 1984, Hengeveld 1990). Rather, it is characterized by patches of high and gaps of low density. Even over the elevational range taken as a whole (i.e. ignoring other spatial variation), density does not peak in the centre, but rather is highest close to the coastal margin, declining inland up to c. 200 m a.s.l. For an island of this overall, elliptical shape and with a considerable change in elevation, a central peak in abundance might be expected to take a torus-like form, but this was clearly not the case for *D. panormitanum*. Complex abundance structures are now considered the norm rather than the exception, with little evidence for an ‘abundant centre distribution’ either across entire ranges or partial components thereof (Brewer and Gaston 2002, Sagarin and Gaines 2002b, Gaston 2003, McGeoch and Price 2004, Sagarin *et al.* 2006).

In most continental situations, the mechanisms underlying spatial variation in abundance structure are likely to be complex, including not only physiological tolerances and resource preferences, but also spatial variation in parasitism and predation, dispersal ability and interactions across the metacommunity (see e.g. Brewer and Gaston 2002, 2003, Klok *et al.* 2003, and also Leibold *et al.* 2004, de Mazancourt *et al.* 2008). On Marion Island, the scope of interactions between slugs and other species is likely to be small. No predation or parasitism has been recorded, and detritus is an abundant resource in the system owing to the absence of major herbivores (Chown and Froneman 2008). Indeed, the current investigation indicates substantial habitat preference in *D. panormitanum*, for biotic and drainage line habitats, which seem to be associated with high humidities in these habitats by comparison with fellfield, mire and fernbrake. The former habitats share few other characteristics, differing substantially in their total nutrient pools, and dominant vascular plants (Poaceae and Asteraceae vs. Rosaceae) (Chown and Froneman 2008). Moreover, the physiological data indicated that *D. panormitanum* is highly susceptible to desiccation. Indeed, for its size and metabolic rate it has exceptionally high water loss rates by

comparison with other terrestrial invertebrates such as velvet worms and insects (see Klok and Chown 1998, Clusella-Trullas and Chown 2008 for data and rationale for such a comparison). In consequence, it seems likely that habitat selection, to reduce desiccation, which can substantially compromise survival (South 1992), is the major contributor to spatial variation in abundance structure within the limits of this species' range on Marion Island.

Unlike the expectation for most organisms (MacArthur 1972, Brown 1984, Brown *et al.* 1996), in *D. panormitanum* both the coastal and higher elevation range margins appeared to be set by abiotic conditions. On the coastal side, a clear stepped or threshold decline in density was found overall (supported by the quantile slope close to zero) and substrate salinity appeared to be responsible for this change in density. Individuals of *D. panormitanum* cannot survive direct exposure to more than c. 3000 mg/kg Na, and as soon as this value is exceeded in the soil substrate density declines to zero, irrespective of the distance from the sea, as indicated by the additional survey data. In other words, where coastal sites are highly protected and include the biotic habitat they form favourable sites, such as Trypot Beach (Fig. 1). This threshold-like change in density associated with a change in substrate quality (in this case Na content) provides support for Caughley *et al.*'s (1988) contention that changes in substrate should lead to a stepped range margin.

Although the partial nature of this study (i.e. not over the full distribution of the species), and the relatively simple nature of the food web on the island (Burger 1985, Gaston *et al.* 2001) might account for the unimportance of biotic factors in setting the lower elevation range limit, other studies have reached similar conclusions concerning the significance of abiotic range limitation (see Merrill *et al.* (2008) for an example for a lower elevational limit, and Mercader and Scriber (2008) for the southern range limit of a northern butterfly species). Like many other biological generalizations, those concerning the significance of abiotic vs. biotic range limitation of species' range margins may have several exceptions.

Having said that, it seems clear that the upper elevational limit to the *D. panormitanum* population on Marion Island is set by temperature. The physiological investigations indicated that *D. panormitanum* is incapable of surviving below a mean of -3°C and a minimum of -6.4°C. These temperatures are exceeded at 200 m a.s.l., albeit on an infrequent basis.

Nonetheless, as indicated by the SCP and soil surface temperature frequency distributions, these infrequent low temperature events would be sufficient to eliminate the entire population. At a few sites above 200 m a.s.l., slug densities as high as 50-80 slugs.m⁻² were found. If occasional extreme temperatures are responsible for setting the range margin, then temporal variation in its edge might be expected (see e.g. Crozier 2003, 2004), a plausible expectation given mean slug locomotion rates of 5.0 to 7.9 m.h⁻¹ (on a flat surface) at temperatures between 0 and 5°C (unpublished data). Moreover, six of these sites were restricted to the west coast of Marion Island, just above Mixed Pickle Cove. Recent work has shown that this area has both milder winter soil surface temperatures and cooler summer ones than the eastern part of the island (Nyakatya and McGeoch 2008) which may account for the persistence of slugs in reasonable densities at 300 m a.s.l. Indeed, the existence of a thermal refuge beyond the usual limits of the species supports the idea that low temperature is a limiting factor (see Gaston 2003 for additional examples). Of course, it might be argued that the unavailability of habitats might also have contributed to range limitation given the change in habitat type with elevation on the island (Chown and Froneman 2008). However, several drainage line and biotic sites (associated with burrowing seabirds) above 200 m were examined and found to be free of slugs.

Whilst the edge of the range at the higher elevations does seem to be set by an absolute temperature limit, the decline in density with elevation is more difficult to explain. Caughley *et al.* (1988) suggested that if density shows a ramp-like decline, and 'well-being' a similar change, climate is likely the factor affecting a species boundary. Here, density certainly showed a clear linear decline as demonstrated by the quantile regression. Similarly, mean annual temperature declines and the number of days below 0°C increases rapidly with elevation. Based on the decline in standard metabolic rate with temperature, and assuming that metabolic rate can be used as a proxy for performance or well-being (see discussion in Chown and Gaston 1999), it seems likely that the decline in density may be a consequence of a decline in performance, or, perhaps as a consequence, time available for activity, as elevation increases. Few other reasons to explain the decline in abundance with elevation seem plausible, especially since precipitation does not decline with elevation (as far as is known), habitats remain available, and predation is non-existent. The only other potential explanation for the decline in density might be an indirect interaction with the major

indigenous detritivore on the island, caterpillars of the flightless moth *Pringleophaga marioni* (Smith 2007), owing to altitudinal variation in predation pressure by mice on this species (Phiri *et al.* 2008). However, detritus does not seem to be a limiting factor on Marion Island given that so much of it ends up being transformed to peat (Smith 2007). In consequence, the decline in temperature with elevation likely accounts for the decline in slug density.

In conclusion, it appears that the lower and upper elevational range margins of *D. panormitanum* are set by its physiological tolerances, of salinity and low temperature, respectively. Whilst it might be argued that some other factor has set the species' range margins, and tolerances have subsequently evolved to reflect the situation (Gaston 2003) the absence of other limiting factors make such a supposition implausible. Moreover, although the mt COI neutral marker is unlikely to reflect fully the evolutionary potential of this island population (Dlugosch and Parker 2008), the single haplotype found does suggest that it has passed through a considerable bottleneck. Only further work will reveal the extent to which this may have been limiting and may be limiting in the future. The latter is especially significant, since although current and forecast climate change at the island includes increases in mean annual temperature, these are being accompanied by increases in the frequency of freeze-thaw events owing to more common clear sky conditions (Chown and Froneman 2008). Thus, the future may well see higher slug densities over a narrower elevational range than is presently the case.

REFERENCES

- Alleaume-Benharira M., Pen I.R. & Ronce O. (2006) Geographical patterns of adaptation within a species' range: interactions between drift and gene flow. *Journal of Evolutionary Biology*, 19, 203-215
- Ansart A. & Vernon P. (2003) Cold hardiness in molluscs. *Acta Oecologia*, 24, 95-102
- Austin M. (2007) Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling*, 200, 1 - 19
- Bale J.S. (1993) Classes of insect cold hardiness. *Functional Ecology*, 7, 751-753
- Battisti A., Stastny M., Buffo E. & Larsson S. (2006) A rapid altitudinal range expansion in the pine processionary moth produced by the 2003 climatic anomaly. *Global Change Biology*, 12, 662-671
- Bird J. M. & Hodkinson I.D. (2005) What limits the altitudinal distribution of *Craspedolepta* species (Sternorrhyncha: Psylloidea) on fireweed? *Ecological Entomology*, 30, 510-520
- Blake B. (1996) *Microclimate and prediction of photosynthesis at Marion Island*. M.Sc. Thesis. Bloemfontein, R.S.A.: University of the Free State
- Brewer A. M. & Gaston K.J. (2002) The geographical range structure of the holly leaf-miner. I. Population density. *Journal of Animal Ecology*, 71, 99-111
- Brewer A.M. & Gaston K.J. (2003) The geographical range structure of the holly leaf-miner. II. Demographic rates. *Journal of Animal Ecology*, 72, 82-93
- Brooker R.W., Travis J.M.J., Clark E.J. & Dytham C. (2007) Modelling species' range shifts in a changing climate: the impacts of biotic interactions, dispersal distance and the rate of climate change. *Journal of Theoretical Biology*, 245, 59-65
- Brown J.H. (1984) On the relationship between abundance and distribution of species. *American Naturalist*, 124, 255-279
- Brown J.H., Stevens G.C. & Kaufman D.M. (1996) The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology Systematics*, 27, 597-623
- Burger A.E. (1985) Terrestrial food webs in the sub-Antarctic: island effects. In: *Antarctic nutrient cycles and food webs* (eds. W. R. Siegfried, P. R. Condy & R. M. Laws) Springer, Berlin

- Cade, B. S. & Richards, J. D. (2005) *User manual for Blossom statistical software*. Fort Collins, Co.: USGS.
- Caughley G., Grice D., Barker R. & Brown B. (1988) The edge of the range. *Journal of Animal Ecology*, 57, 771-785
- Channell R. & Lomolino M.V. (2000) Dynamic biogeography and conservation of endangered species. *Nature*, 403, 84-86
- Chown S.L. & Froneman P.W. (eds.) (2008) *The Prince Edward Islands - Land-sea interactions in a changing ecosystem*. African SunMedia, Stellenbosch, South Africa
- Chown S.L. & Gaston K.J. (1999) Exploring links between physiology and ecology at macro-scales: the role of respiratory metabolism in insects. *Biological Reviews*, 74, 87-120
- Chown S.L. & Gaston K.J. (2008) Macrophysiology for a changing world. *Proceedings of the Royal Society of London B*, 275, 1469-1478
- 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. & Terblanche J.S. (2007) Physiological diversity in insects: ecological and evolutionary contexts. *Advances in Insect Physiology* 33, 50-152
- 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. & Jansen van Vuuren B. (2008) DNA barcoding and the documentation of alien species establishment on sub-Antarctic Marion Island. *Polar Biology*, 31, 651-655
- Clusella-Trullas S. & Chown S.L. (2008) Investigating onychophoran gas exchange and water balance as a means to inform current controversies in arthropod physiology. *Journal of Experimental Biology*, 211, 3139-3146
- 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
- Crozier L. (2003) Winter warming facilitates range expansion: cold tolerance of the butterfly *Atalopedes campestris*. *Oecologia*, 135, 648-656
- Crozier L. (2004) Warmer winters drive butterfly range expansion by increasing survivorship. *Ecology*, 85, 231-241

- Crozier L. & Dwyer G. (2006) Combining population-dynamic and ecophysiological models to predict climate-induced insect range shifts. *American Naturalist*, 167, 853-866
- Davis A.J., Jenkinson L.S., Lawton J.H., Shorrocks B. & Wood S. (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature* 391, 783-786
- de Mazancourt C., Johnson E. & Barraclough T.G. (2008) Biodiversity inhibits species' evolutionary responses to changing environments. *Ecology Letters*, 11, 380-388.
- 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
- Dlugosch K.M. & Parker I.M. (2008) Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. *Molecular Ecology*, 17, 431-449
- Excoffier L., Laval G. & Schneider S. (2005) Arlequin ver. 3.0: An integrated software package for population genetics data analysis. *Evolution and Bioinformatics. Online* 1, 47-50.
- Folmer O., Black M., Hoeh W., Lutz R. & Vrijenhoek R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294-299
- Franco A.M.A., Hill J.K., Kitschke C., Collingham Y.C., Roy D.B., Fox R., Huntley B. & Thomas C. D. (2006) Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biology*, 12, 1545-1553
- Gaines, S.D. & Denny, M.W. (1993) The largest, smallest, highest, lowest, longest, and shortest: extremes in ecology. *Ecology*, 74, 1677-1692.
- Gaston K.J. (2003) *The structure and dynamics of geographic ranges*. Oxford University Press, Oxford
- Gaston K.J. & Blackburn T.M. (2003) Dispersal and the interspecific abundance-occupancy relationship in British birds. *Global Ecology and Biogeography*, 12, 373-379
- Gaston K.J., Borges P.A.V., He F.L. & Gaspar C. (2006) Abundance, spatial variance and occupancy: arthropod species distribution in the Azores. *Journal of Animal Ecology*, 75, 646-656
- Gaston K.J., Chown S.L. & Mercer R.D. (2001) The animal species-body size distribution of Marion Island. *Proceedings of the Natural Academy of Science of the United States of America*, 98, 14493-14496

- 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
- Hengeveld R. (1990) *Dynamic biogeography*. Cambridge University Press, Cambridge
- Hill J.K. & Hodkinson I.D. (1992) Effects of temperature on phenological synchrony and altitudinal distribution of jumping plant lice (Hemiptera: Psylloidea) on dwarf willow (*Salix lapponum*) in Norway. *Ecological Entomology*, 20, 237-244
- Hodkinson I.D., Bird J., Miles J.E., Bale J.S. & Lennon J.J. (1999) Climatic signals in the life histories of insects: the distribution and abundance of heather psyllids (*Strophingia* spp.) in the UK. *Functional Ecology*, 13, 83-95
- Hoffmann A.A. & Blows M.W. (1994) Species borders: ecological and evolutionary perspectives. *Trends Ecology and Evolution*, 9, 223-227
- Hoffmann A.A., Hallas R.J., Dean J.A. & Schiffer M. (2003) Low potential for climatic stress adaptation in a rainforest *Drosophila* species. *Science*, 301, 100-102
- Hoffmann A.A. & Willi Y. (2008) Detecting genetic responses to environmental change. *Nature Reviews Genetics*, 9, 421-432
- Holland K.D., McDonnell M.J. & Williams N.S.G. (2007) Abundance, species richness and feeding preferences of introduced molluscs in native grasslands of Victoria, Australia. *Austral Ecology*, 32, 626-634
- Holt R.D. & Keitt T.H. (2000) Alternative causes for range limits: a metapopulation perspective. *Ecology Letters*, 3, 41-47
- Holt R.D. & Keitt T.H. (2005) Species' borders: a unifying theme in ecology. *Oikos*, 108, 3-6
- Johnson J.B. & Omland K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology and Evolution*, 19, 101-108
- 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 Insect Physiology*, 44, 615-628
- Klok C.J., Chown S.L. & Gaston K.J. (2003) The geographical range structure of the Holly Leaf-miner. III. Cold hardiness physiology. *Functional Ecology*, 17, 858-868
- 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

- Lee J.E., Slabber S., Jansen van Vuuren B., Van Noort S. & Chown S.L. (2007) Colonisation of sub-Antarctic Marion Island by non-indigenous aphid parasitoid *Aphidius matricariae* (Hymenoptera Braconidae). *Polar Biology*, 30, 1195-1201
- Legendre P. & Legendre L. (1998) *Numerical ecology*. Elsevier, Amsterdam
- Leibold M.A., Holyoak M., Mouquet N., Amarasekare P., Chase J.M., Hoopes M.F., Holt R.D., Shurin J.B., Law R., Tilman D., Loreau M. & Gonzalez A. (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, 7, 601-613
- Lighton J.R.B. (1991) Insects: measurements. In: *Concise Encyclopedia on Biological and Biomedical Measurement Systems* (ed. Payne P.A.) Pergamon Press, Oxford
- MacArthur R.H. (1972) *Geographical ecology*. New York: Harper and Row.
- McGeoch M.A. & Price P.W. (2004) Spatial abundance structures in an assemblage of gall-forming sawflies. *Journal of Animal Ecology*, 73, 506-516
- Meiklejohn K.I. & Smith V.R. (2008) Surface areas of altitudinal zones on sub-Antarctic Marion Island. *Polar Biology*, 31, 259-261
- Mercader R.J. & Scriber J.D. (2008) Asymmetrical thermal constraints on the parapatric species boundaries of two widespread generalist butterflies. *Ecological Entomology*, 33, 537-545
- Merill R.M., Gutiérrez D., Lewis O.T., Gutiérrez J., Díez S.B. & Wilson R.J. (2008) Combined effects of climate change and biotic interactions on the elevational range of a phytophagous insect. *Journal of Animal Ecology*, 77, 145-155
- Musolin D.L. (2007) Insects in a warmer world: ecological, physiological and life-history responses of true bugs (Heteroptera) to climate change. *Global Change Biology*, 13, 1565-1585
- 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
- Parmesan C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, 37, 637-669
- Parmesan C., Gaines S., Gonzalez L., Kaufman D.M. Kingsolver J., Townsend Peterson A. & Sagarin R. (2005) Empirical perspectives on species borders: from traditional biogeography to global change. *Oikos*, 108, 58-75

- Phiri E.E., McGeoch M.A. & Chown S.L. (2008). Spatial variation in structural damage to a keystone plant species in the sub-Antarctic: interactions between *Azorella selago* and invasive house mice. *Antarctic Science*, in press.
- Posada D. (2004) *COLLAPSE*. Boston: Free Software Foundation Inc.
- 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
- Sagarin R.D. & Gaines S.D. (2002a) The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecology Letters*, 5, 137-147
- Sagarin R.D. & Gaines S.D. (2002b) Geographical abundance distributions of coastal invertebrates: using one-dimensional ranges to test biogeographic hypotheses. *Journal of Biogeography*, 29, 985-997
- Sagarin R.D., Gaines S.D. & Gaylord B. (2006) Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology and Evolution*, 21, 524-530
- Sambridge M., Braun J. & McQueen H. (1995) Geophysical parameterization and interpolation of irregular data using natural neighbours. *Geophysical Journal International* 122, 837-857
- Sax D.F., Stachowicz J.J., Brown J.H., Bruno J.F., Dawson M.N., Gaines S.D., Grosberg R.K., Hastings A., Holt R.D., Mayfield M.M., O'Connor M.I. & Rice W.R. (2007) Ecological and evolutionary insights from species invasions. *Trends in Ecology and Evolution*, 22, 465-471
- Sinclair B.J., Klok C.J., Scott M.B., Terblanche J.S. & Chown S.L. (2003) Diurnal variation in supercooling points of three species of Collembola from Cape Hallett, Antarctica. *Journal of Insect Physiology*, 49, 1049-1061
- Smith V.R. (1992) Terrestrial slug recorded from sub-Antarctic Marion Island. *Journal of Molluscan Studies*, 58, 80-81
- Smith V.R. (2007) Introduced slugs and indigenous caterpillars as facilitators of carbon and nutrient mineralization on a sub-Antarctic island. *Soil Biology and Biochemistry*, 39, 709-713
- 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

- Soberón J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, 10, 1115-1123
- South A. (1992) *Terrestrial slugs: biology, ecology and control*. Chapman and Hall, London
- Storch D., Šizling A.L., Reif J., Polechová J., Šizlingova E. & Gaston K.J. (2008) The quest for a null model for macroecological patterns: geometry of species distributions at multiple spatial scales. *Ecology Letters*, 11, 771-784
- Terblanche J.S., Klok C.J. & Chown S.L. (2005) Temperature-dependence of metabolic rate in *Glossina morsitans morsitans* (Diptera, Glossinidae) does not vary with gender, age, feeding, pregnancy or acclimation. *Journal of Insect Physiology*, 51, 861-870
- Theodorides J. & Chown S.L. (1992) On the occurrence of *Gregarina munieri* (A. Schneider) (Apicomplexa, Eugregarina, Gregarinidae) in weevils (Coleoptera, Curculionidae) from Marion Island. *Bulletin de la Société Française de Parasitologie*, 10, 27-29
- Thomas C.D., Bodsworth E.J., Wilson R.J., Simmons A.D., Davies Z.G., Musche M. & Conradt L. (2001) Ecological and evolutionary processes at expanding range margins. *Nature*, 411, 577-581
- Thomas C.D., Franco A.M.A. & Hill J.K. (2006) Range retractions and extinction in the face of climate warming. *Trends in Ecology and Evolution*, 21, 415-416
- Thompson J.D., Gibson T.J., Plewniak F., Jeanmougin F. & Higgins D.G. (1997) The Clustal X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research*, 24, 4876-4882
- Unwin D.M. & Corbet S.A. (1991) *Insects, plants and microclimate*. Slough: The Richmond Publishing Co.
- Vernon P., Vannier G. & Tréhen P. (1998) A comparative approach to the entomological diversity of polar regions. *Acta Oecologia*, 19, 303-308

Chapter 8 – Conclusion

The extent of human travel in the Antarctic is increasing rapidly, breaking down dispersal barriers to remote islands (Powell *et al.* 2008), and rapid climate is starting to reduce some of the physiological barriers faced by non-indigenous species (Convey 2001, Gerighausen *et al.* 2003, Robinson *et al.* 2003, Aronson *et al.* 2007). These two factors place the Antarctic at high risk from alien species introductions. In this study I examined the extent to which these barriers have been eroded by the logistics operations of national Antarctic programmes and, by using the Antarctic as a model system, discussed how these findings can be of global application.

Propagule transfer

In Chapter 1, it was demonstrated that the South African National Antarctic Programme (SANAP) is responsible for the introduction of a considerable number and diversity of propagules into Antarctic terrestrial systems. Many of the propagules which are transferred with passenger luggage and cargo are established aliens in the region, indicating that sustained propagule pressure could play an important role in the population dynamics of these groups.

Propagule entrainment was not equal across all categories of vector and some items of clothing such as trousers, socks and bags harboured considerably more propagules than other items such as hats and gloves. For cargo the degree of propagule entrainment was determined by the volume of the cargo item and whether it was packed in a warehouse which was close to an abundant propagule source. An assessment of the extent to which entrained propagules dropped off was made and showed that between c. 30-50% of propagules which become entrained in clothing and cargo will enter the recipient environment. Velcro had previously been recognised as a material which posed a high risk of introducing non-native species (Whinam *et al.* 2005), and whilst high numbers of seeds did become entrained, drop-off rate was low indicating that this material does not pose as great a biosecurity threat as previously thought.

Comparison of propagule loads from South African expeditioners and Australian expeditioners showed that substantial differences existed between the two operators (Whinam *et al.* 2005) and suggests that equally great differences may exist between other national operators. These differences need to be quantified if regional mitigation measures are to be implemented.

Another related issue not addressed in Chapter 1 is whether tourists and scientists pose different risks of introducing non-indigenous species. Tourists are certainly the most numerous visitors (Naveen *et al.* 2001, Lamers *et al.* 2008), but are typically ship-based with individuals only spending a short time ashore at any one location. In contrast, scientists are much less numerous, but often spend many more person-days ashore and travel to more remote and environmentally sensitive areas (Hull and Bergstrom 2006). The International Polar Year programme, Aliens in Antarctica, is an international collaboration that brings together propagule pressure data from 24 national operators, and 17 tourist operators (<http://www.aliensinantarctica.aq>). The data from this project will be added to the Aliens in Antarctica global data set and, once analyses are complete, will contribute to the first ever biome wide assessment of propagule pressure.

In Chapter 2 it was demonstrated that the construction of a research station can introduce substantial numbers of propagules. Based on quantitative assessment of different classes of cargo, it is predicted that over 5000 seeds will be entrained in the cargo needed to construct the British Antarctic Survey (BAS) Halley VI station. Many nations are currently undertaking major construction projects in the Antarctic, and if propagule loads are comparable, this pathway should be considered as a major biosecurity threat.

In Chapter 3, I examined propagule transfer in the marine realm and showed that although the diversity of species transported on the *SA Agulhas* is low (probably because of high predation rates from *Carcinus maenas* in Cape Town harbour), large hull fouling assemblages are transported to areas which are not surrounded by sea ice. As with propagule loads in expeditioner clothing, there appears to be substantial variation between nations. Lewis *et al.* (2003) showed that Australian vessels carry very different fouling biota to the South African

vessel. This is not surprising given the different propagule source pools of the vessels (compare Thresher 1999 to Robinson *et al.* 2005) and the different anti-fouling regimes.

Most of vessels leaving for the Antarctic depart from South American ports, either Ushuaia or Punta Arenas (<http://www.IAATO.com>), and many of these vessels are bound for the Antarctic Peninsula where in some years they may not encounter sea ice to scour the hull. However, little information is available on the propagule source pool in these areas (although see Kim *et al.* 2004, Castilla *et al.* 2005, Rico and Gappa 2006, Neves *et al.* 2007) and no information about the extent or diversity of fouling communities on vessels leaving from them. Of particular concern are fishing vessels (raised by Argentina at the Committee for Environmental Protection Meeting CEP-IX 2006) as these vessels are often dry docked infrequently and so may have limited anti-fouling protection.

The difficulty of understanding the dynamics of marine introductions is further exacerbated by our relatively poor knowledge of Antarctic marine diversity (given the size of the Antarctic region – for review see Clarke and Johnson 2003), making the detection of novel organisms problematic. These are clear gaps in our understanding and need to be urgently addressed if we are to fully comprehend the threat of marine invasions in the Antarctic. The Census of Antarctic Marine Life (CAML) (ATCM-IP 32 2007) is beginning to address this issue but given the scale of the task it is likely that it will be some time before comprehensive baseline data is available. In the mean time surveys should be focused on areas which receive the highest volume of shipping traffic, and hence are at the greatest risk of invasion.

One clear trend in both marine and terrestrial propagule transfer (Chapters 2-4) is that species which are common in the local source pool are the ones which are most likely to become entrained and transported, and also the ones which are most likely to establish, thus forming a self sustaining cycle. For example, the majority of seeds found in cargo and clothing belonged to Poaceae and Asteraceae, and both of these families contain substantial numbers of species known to be invasive in the region (Frenot *et al.* 2005, Chwedorzewska 2008) and globally (Daehler 1998). Because both global and regional transport networks show a high degree of connectivity (Drake and Lodge 2004, Tatem and Hay 2007), the potential for rapid and extensive range expansion of alien species is great. If this cycle is to

be broken then a change in management strategy is needed to firstly reduce propagule pressure, and then heightened vigilance and long term monitoring to detect and manage newly established aliens.

Propagule survival

In Chapter 5 it was demonstrated that some species can survive transport to regions which were previously considered to be too extreme for them. Such misconceptions may be because of our inadequate understanding of the physiology of common propagules or because of our inadequate understanding of the abiotic stresses which biota experience during transport. Although for some species complete data on environmental tolerances are available (Sinclair *et al.* 2006, Overgaard *et al.* 2008), for many species these data are poor, only considering a single life stage or physiological parameter, and for others the data simply do not exist. Data are also scarce on the abiotic characteristics of major vectors (e.g. conditions in a ship's internal spaces) although there is some suggestion that the spatial and temporal variation in abiotic variables such as temperature and humidity are substantial (J.E. Lee unpublished data).

To complete our understanding of initial propagule dispersal and to be able to relate this to later stages of invasion, we need to understand not only what propagules are transported but also the physiological characteristics of those propagules and the abiotic parameters of the environment in which they are transported.

Establishment of alien species

After propagules have survived dispersal, the next question is whether those propagules would be able to cross further barriers to invasion and survive in the physical environment of the recipient region (Richardson *et al.* 2000). In some places this is undoubtedly a considerable challenge, but the prevalence of invasive species in some areas of the Antarctic indicates that this challenge has been surmounted (Frenot *et al.* 2005). Furthermore, under predicted climate change scenarios, at least some parts of the Antarctic are forecast to undergo warming (Turner *et al.* 2007). This may allow the establishment of species in habitats that were previously unsuitable (Aronson *et al.* 2007).

Once a species has established and spread beyond the site of initial introduction it may be impossible to eradicate. This is particularly the case for mobile invertebrate species such as the parasitoid wasp *Aphidius matricariae*, described in Chapter 6. The impacts of introduced species on recipient ecosystems can be severe (e.g. in the Antarctic region: Rowe-Rowe *et al.* 1989, Chapuis *et al.* 1994, Chown & Block 1997, Gremmen *et al.* 1998, Hänel and Chown 1998), but are often poorly understood. For example, *A. matricariae* adds a layer of complexity to the food web on Marion Island, but we do not yet understand how this will affect food web stability in this system. To fully understand the impacts of invasive species in the Antarctic we need to look at both direct and indirect impacts. This task is partly simplified by the relatively low numbers of species and simple trophic interactions (Chown and Smith 1993, Gremmen and Smith 2008), found in Antarctic systems, ideally placing them to act as a model system to understand these issues which have global implications.

Environmental controls of distribution

Information on the physiological tolerances of biota is especially useful in the Antarctic, because although in many temperate climates, species distributions are controlled by biotic variables such as niche availability (Pulliam 2000, Duyck *et al.* 2006, Moore and Elmendorf 2006), competition (Bullock *et al.* 2000) or predation (Bohan *et al.* 2000), in the Antarctic this is not necessarily the case. Establishment and range dynamics are more often limited by abiotic factors. In Chapter 7 it was demonstrated that for *Deroceras panomitanum*, range limits on Marion Island were set by the species inability to survive low temperature events at high altitude and salt intolerance at the coast. Across Marion Island slug density did not conform to an abundant centre distribution. Rather, abundance structure is characterized by patches and gaps which are associated with this desiccation-sensitive species' preference for biotic and drainage line habitats that share few characteristics except for their high humidity below the vegetation surface.

In addition to the need to assess physiological parameters, is the necessity of obtaining a better understanding of fine scale environmental variables. Much of the climatic data which is available is at the macro scale: concerning environmental variables on a scale of hours and at locations which are chosen primarily because of their ease of access rather than their biological relevance. However, macro scale data cannot always adequately represent the

situation at the micro scale (Chown and Crafford 1992). At present we do not understand precisely how data from the two spatial scales are related. In Chapter 7 the importance of the influence of micro climate on determining the abundance structure of *D. panormitanum* was demonstrated, and it is probable that micro climate has an equally important effect on the distribution of other species. Therefore, there is a need to understand better fine scale climatic variation, how it relates to current macroclimatic trends and how this will be influenced by different climate change scenarios.

Insights from molecular ecology

I examined taxonomic trends in propagule dispersal at the genus and family level and investigated establishment and secondary dispersal at the species level. Whilst these have been the currency of invasion biology for several decades (Elton 1958), in recent times the application of molecular techniques has highlighted the need to examine finer taxonomic resolutions (Tsutsui *et al.* 2000, Lee 2002, Bais *et al.* 2003) as this may help to understand better the spatial and temporal dynamics of invasion. In Chapters 6 and 7 it was shown that at least two introduced invertebrate species on Marion Island are characterised by a single haplotype. This low genetic diversity, could limit populations' ability to evolve and overcome local environmental constraints (Hoffmann *et al.* 2003, Alleaume-Benharira *et al.* 2006, Chown and Terblanche 2007). Better understanding the relationship between adaptation, range dynamics and genetic diversity, is needed if we are to fully comprehend what limits species ranges and how these may change in relation to climate change.

Equally as important as the low genetic diversity of recently introduced species is the complex genetic structure seen in many indigenous populations (Fanciulli *et al.* 2001, Skotnicki *et al.* 2004, Myburgh *et al.* 2007). On sub-Antarctic Marion Island, complex genetic structuring of populations of native invertebrates exists, probably because of isolation in refugia during the last glacial maxima (Hall 2002, Boelhouwers *et al.* 2007) promoting population divergence as a consequence of vicariance (Myburgh *et al.* 2007). In continental Antarctica, many such isolated populations exist on remote nunataks and preliminary data indicates that there can be substantial genetic variation between these populations (Fanciulli *et al.* 2001, Stevens and Hogg 2003). Whilst these populations remain isolated, genetic diversity will be maintained. However, with the aid of mechanised transport, field parties are

able to travel between once isolated nunataks. If propagules are transported between sites this could lead to genetic homogenization. To comprehend fully the risk of homogenization, it is necessary to better understand fine-scale variation in genetic diversity and the causes and consequences thereof.

Management implications

Annex II of the CEP and many of the management plans for sub-Antarctic islands clearly state that introductions of non-indigenous species must be prevented and accordingly national operators have made provision to adhere to this. However, this work clearly demonstrates that substantial numbers of propagules are still entering the Antarctic in association with logistics operations and therefore there is urgent need to modify current management practices. This section comprises of a list of recommendations that will reduce the extent of propagule transfer and likelihood of establishment of alien species.

Terrestrial introductions

- Expeditioner clothing should be inspected before arrival in an Antarctic location and all removed.
- For items which present a particularly high biosecurity risk, such as socks, national operators should issue new items for each voyage.
- To prevent the inter-regional transfer of propagules, operators should consider leaving used clothing for re-issue at the research station where it has been used.
- In areas that are classed as environmentally sensitive, restrictions should be placed on the number of personnel going ashore.
- Efforts should be made to reduce propagule sources in close proximity to cargo loading areas. This could be achieved through the use of herbicides to eradicate locally occurring weedy species and traps to catch crawling and flying invertebrates inside cargo storage areas.
- Cargo containers should be cleaned prior to loading and the construction of the containers should facilitate this.
- Fresh produce presents a high risk of introducing non-indigenous species and should not be allowed on research stations or on re-supply vessels that come in close proximity to colonisable habitat.

- Landing gear of fixed and rotary winged aircraft should be carefully checked for entrained propagules before being used to deploy personnel to field sites.
- Where possible, aircraft should land in designated areas which should be checked regularly for the presence of alien species.
- Regular surveys of cargo storage areas at research stations and at field huts should be made so that newly established aliens are detected before they have undergone significant range expansion.
- In the event of a non-indigenous species being detected, national operators should have an established protocol of how to deal with the situation. This should involve establishing the identity of the species, accurate mapping of its current distribution and the involvement of suitable experts to determine what remedial measures should be taken.

Marine introductions

- Re-supply vessels should spend the minimum time in port to prevent the accumulation of fouling assemblages. This may necessitate finding additional charters in the austral winters.
- Intervals between dry-docking and replenishment of anti-fouling protection should be decreased and ideally should occur as soon as possible after extensive sea-ice travel.
- Accumulation of fouling biota in sea-chests is more problematic, but fouling may be reduced by periodic flushing with a backflow of high temperature water from the engines. Research would be needed to determine the appropriate temperature and duration of this procedure.

REFERENCES

- Alleaume-Benharira M., Pen I.R. & Ronce O. (2006) Geographical patterns of adaptation within a species' range: interactions between drift and gene flow. *Journal of Evolutionary Biology*, 19, 203-215
- Aronson R.B., Thatje S., Clarke A., Peck L.S., Blake D.B., Wilga C.D. & Seibel B.A. (2007) Climate change and invasibility of the Antarctic benthos. *Annual Review of Ecology Evolution and Systematics*, 38, 129-154
- ATCM-IP 32 (2007) Information Paper 32, Census of Antarctic Marine Life (CAML), submitted by Australia & SCAR
- Bais H.P., Vepachedu R., Gilroy S., Callaway R.M. & Vivanco J.M. (2003) Allelopathy and exotic plant invasion: From molecules and genes to species interactions. *Science*, 301, 1377-1380
- Boelhouwers J., Meiklejohn I., Holness S. & Hedding D. (2007) Geology, geomorphology and change. In: *The Prince Edward Islands - Land-Sea interactions in a changing ecosystem* (eds. Chown S.L. & Froneman W.P.) African SunMedia, Stellenbosch, South Africa
- Bohan D.A., Bohan A.C., Glen D.M., Symondson W.O.C., Wiltshire C.W. & Hughes L. (2000) Spatial dynamics of predation by carabid beetles on slugs. *Journal of Animal Ecology*, 69, 367-379
- Bullock J.M., Edwards R.J., Carey P.D. & Rose R.J. (2000) Geographical separation of two *Ulex* species at three spatial scales: does competition limit species' ranges? *Ecography*, 23, 257-271
- Castilla J.C., Uribe M., Bahamonde N., Clarke M., Desqueyroux-Faundez R., Kong I., Moyano H., Rozbaczylo N., Santelices B., Valdovinos C. & Zavala P. (2005) Down under the southeastern Pacific: marine non-indigenous species in Chile. *Biological Invasions*, 7, 213-232
- Chapuis J.L., Boussès P. & Barnaud G. (1994) Alien mammals, impact and management in the French Subantarctic islands. *Biological Conservation*, 67, 97-104
- Chown S.L. & Block W. (1997) Comparative nutritional ecology of grass-feeding in a sub-Antarctic beetle: the impact of introduced species on *Hydromedion sparsutum* from South Georgia. *Oecologia*, 111, 216-224

- 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. & 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
- Chwedorzewska K.J. (2008) *Poa annua* L. in Antarctic: searching for the source of introduction. *Polar Biology*, 31, 263-268
- Clarke A. & Johnston N.M. (2003) Antarctic marine benthic diversity. *Oceanography and Marine Biology: an Annual Review*, 41, 47-114
- Convey P. (2001) Terrestrial ecosystem responses to climate changes in the Antarctic. In: *"Fingerprints" of climate change* (eds. Walther G.-R., Burga C.A. & Edwards P.J.) Kluwer Academic, New York
- Daehler C.C. (1998) The taxonomic distribution of invasive angiosperm plants: Ecological insights and comparison to agricultural weeds. *Biological Conservation*, 84, 167-180
- 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
- Duyck P.F., David P. & Quilici S. (2006) Climatic niche partitioning following successive invasions by fruit flies in La Réunion. *Journal of Animal Ecology*, 75, 518-526
- Elton C.S. (1958) *The ecology of invasions by animals and plants*. University of Chicago Press, Chicago
- Fanciulli P.P., Summa D., Dallai R. & Frati F. (2001) High levels of genetic variability and population differentiation in *Gressittacantha terranova* (Collembola, Hexapoda) from Victoria Land, Antarctica. *Antarctic Science*, 13, 246-254
- Frenot Y., Chown S.L., Whinam J., Selkirk P.M., Convey P., Skotnicki M. & Bergstrom D.M. (2005) Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews*, 80, 45-72
- Gerighausen U., Bräutigam K., Mustafa O. & Peter H.-U. (2003) Expansion of vascular plants on an Antarctic island - a consequence of climate change? In: *Antarctic Biology in a Global Context* (eds. Huiskes A.H.L., Gieskes W.W.C., Rozema J., Schornno R.M.L, van der Vies S.M. & Wolff W.J.) Backhys Publishers, Leiden

- 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: *The Prince Edward Islands- Land-sea interactions in a changing ecosystem* (eds. Chown S.L. & Froneman P.W.) African SunMedia, Stellenbosch, South Africa
- 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. (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
- Hoffmann A.A., Hallas R.J., Dean J.A. & Schiffer M. (2003) Low potential for climatic stress adaptation in a rainforest *Drosophila* species. *Science*, 301, 100-102
- Hull B.J. & Bergstrom D.M. (2006) Antarctic terrestrial and limnetic ecosystems conservation and management. In: *Trends in Antarctic Terrestrial and Limnetic Ecosystems* (eds. Bergstrom D.M., Convey P. & Huiskes A.H.L.) Springer, Dordrecht, The Netherlands
- Kim M.S., Yang E.C., Mansilla A. & Sung M.B. (2004) Recent introduction of *Polysiphonia morrowii* (Cerarniales, Rhodophyta) to Punta Arenas, Chile. *Botanica Marina*, 47, 389-394
- Lamers M., Haase D. & Amelung B. (2008) Facing the elements: analysing trends in Antarctic tourism. *Tourism Review*, 63, 15-27
- Lee C.E. (2002) Evolutionary genetics of invasive species. *Trends in Ecology and Evolution*, 17, 386-391
- 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
- Moore K.A. & Elmendorf S.C. (2006) Propagule vs. niche limitation: untangling the mechanisms behind plant species' distributions. *Ecology Letters*, 9, 797-804
- 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

- 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
- Neves C.S., Rocha R.M., Pitombo F.B. & Roper J.J. (2007) Use of artificial substrata by introduced and cryptogenic marine species in Paranagua Bay, southern Brazil. *Biofouling*, 23, 319-330
- Overgaard J., Tomcala A., Sorensen J.G., Holmstrup M., Krogh P.H., Simek P. & Kostal V. (2008) Effects of acclimation temperature on thermal tolerance and membrane phospholipid composition in the fruit fly *Drosophila melanogaster*. *Journal of Insect Physiology*, 54, 619-629
- Powell R.B., Kellert S.R. & Ham S.H. (2008) Antarctic tourists: ambassadors or consumers? *Polar Record*, 44, 233-241
- Pulliam H.R. (2000) On the relationship between niche and distribution. *Ecology Letters*, 3, 349-361
- Richardson D.M., Pyšek P., Rejmánek M., Barbour M.G., Panetta F.D. & West C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, 6, 93-107
- Rico A. & Gappa J.L. (2006) Intertidal and subtidal fouling assemblages in a Patagonian harbour (Argentina, southwest Atlantic). *Hydrobiologia*, 563, 9-18
- Robinson S.A., Wasley J. & Tobin A.K. (2003) Living on the edge - plants and global change in continental and maritime Antarctica. *Global Change Biology*, 12, 1681-1718
- Robinson T.B., Griffiths C.L., McQuaid C. & Rius M. (2005) Marine alien species of South Africa - status and impacts. *African Journal of Marine Science*, 27, 297-306
- 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
- Sinclair B.J., Roberts S.P. & Gibbs A.G. (2006) Gene transcription during exposure to, and recovery from, cold and desiccation stress in *Drosophila melanogaster*. *Integrative and Comparative Biology*, 46, 131-131
- Skotnicki M.L., Mackenzie A.M., Ninham J.A. & Selkirk P.M. (2004) High levels of genetic variability in the moss *Ceratodon purpureus* from continental Antarctica, subantarctic Heard and Macquarie Islands, and Australasia. *Polar Biology*, 27, 687-698

- Stevens M.I. & Hogg I.D. (2003) Long-term isolation and recent range expansion from glacial refugia revealed for the endemic springtail *Gomphiocephalus hodgsoni* from Victoria Land, Antarctica. *Molecular Ecology*, 12, 2357-2369
- Tatem A.J. & Hay S.I. (2007) Climatic similarity and biological exchange in the worldwide airline transportation network. *Proceedings of the Royal Society of London B*, 274, 1489-1496
- Thresher R.E. (1999) Diversity, impacts and options for managing invasive marine species in Australian waters. *Australian Journal of Environmental Management*, 6, 137-148
- Tsutsui N.D., Suarez A.V., Holway D.A. & Case T.J. (2000) Reduced genetic variation and the success of an invasive species. *Proceedings of the National Academy of Sciences of the United States of America*, 97, 5948-5953
- Turner J., Overland J.E. & Walsh J.E. (2007) An Arctic and Antarctic perspective on recent climate change. *International Journal of Climatology*, 27, 277-293
- Whinam J., Chilcott N. & Bergstrom D.M. (2005) Subantarctic hitchhikers: expeditioners as vectors for the introduction of alien organisms. *Biological Conservation*, 121, 207-219