

**The distribution and abundance of macro-invertebrates
in the major vegetation communities of Marion Island
and the impact of alien species**

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“A scientist is someone with the time and inclination to wonder”

James Lovelock

.... I wander....

Christine Hänel

Dedicated to: Marion and all the sub-Antarctic Islands

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ABSTRACT

In this study macro-invertebrates were sampled quantitatively in 10 lowland vegetation communities on Marion Island over a one-year period commencing in May 1996 as part of a larger investigation into the distribution, abundance and species energy use of invertebrates across an altitudinal transect on Marion Island. The data collected for this particular study were used to investigate the habitat specificity and seasonality of the macro-invertebrates, as well as the impact of alien species on the local community. As part of the latter study a watching brief for alien species was kept throughout the field year and the alien species list was updated accordingly. The quantitative data were also used to compare changes in the density and biomass of selected macro-invertebrate species between 1976/77 and 1996/97 by reworking the data on macro-invertebrates collected by Alan Burger in 1976/77 during the course of his work on the Lesser Sheathbill. In the current study it was found that the majority of the macro-invertebrate species are not particularly habitat specific. Rather, they generally prefer either moist mire habitats, or the more well-drained non-mire vegetation complexes. In addition, many of the species had pronounced peaks in abundance in a given season (winter, summer, autumn and spring peaks were recorded), although this seasonality varied between species and between habitats for a given species. Although this finding does not support previous generalizations concerning an absence of seasonality in sub-Antarctic invertebrates, it does show that sub-Antarctic invertebrates, like their Antarctic counterparts, may have extremely flexible life history strategies. *Limnophyes minimus* was found to be one of the most abundant alien species on the island, and reached high densities in most of the plant communities sampled, with the highest density being recorded in the *Cotula plumosa* biotically influenced community (annual mean of 4365 individuals.m⁻²) and the lowest in the *Crassula moschata* salt spray community (annual mean of 41 individuals.m⁻²). Estimates of litter ingestion indicated that *L. minimus* larvae are capable of consuming between 0.07 and 8.54 g_(dry mass).m⁻² per year, depending on the community. In some communities this litter consumption amounted to an order of magnitude more than that consumed by *Pringleophaga marioni* (Lepidoptera, Tineidae). Although the larvae of this moth species are thought to represent the bottleneck to nutrient recycling on the island, this study showed that midge larvae may also contribute substantially to this process. As a consequence, the considerable changes that have been predicted to occur in Marion Island's terrestrial ecosystem as a consequence of enhanced predation by mice on *P. marioni* larvae, may be retarded or obscured by the contribution of the midge larvae to nutrient cycling. Hence, it is suggested that greater attention be given to the small and inconspicuous elements of the alien sub-Antarctic faunas because such species may have profound consequences for ecosystem functioning on these islands. The likely impact of alien species

on the terrestrial macro-invertebrates, and the communities they belong to, was further highlighted by the dramatic decline in the biomasses of the macro-invertebrates between 1976/77 and 1996/97. Significant declines in biomass of between 83-97% were found for Lepidoptera larvae (mostly *Pringleophaga marioni*) and for weevils, the major prey species of the introduced house mouse between 1976/77 and 1996/97, although non-prey species appear to have shown either no changes (the indigenous snail *Notodiscus hookeri*) or increases in abundance (the introduced slug *Deroceras caruanae*). However, differences in sampling strategies adopted by these two studies and others investigating macro-invertebrate abundances mean that the current results may well be underestimates of change, while other studies must be interpreted with considerable caution. Nonetheless, the current findings and those of authors suggest that mice may be having pronounced impacts on the terrestrial ecosystem at Marion Island. In sum, the findings of this thesis indicate that considerably more attention must be given to well-planned collaborative work to address critically important management questions, identified by the Prince Edward Island Management Committee, and that considerable care must be taken to prevent the further introduction of alien species to sub-Antarctic islands.

CHAPTER 1. INTRODUCTION

1.1 Background, rationale and objectives

Marion Island is part of an extremely isolated archipelago, the two islands of which are 950 km distant from the nearest landmass (Îles Crozet). Because of their remoteness, relatively young geological history (Van Zinderen Bakker Sr. 1971, Walton 1985), and the rigours of the terrestrial environment, the biota of the islands is strikingly impoverished (Smith 1987). With the exception of the Lesser Sheathbill (*Chionis minor marionensis*) and the introduced house mouse (*Mus musculus*), land vertebrates are absent, as are most orders of invertebrates (Crafford *et al.* 1986). Despite the relative paucity of insect species, densities of those present are generally high (Huntley 1971, Burger 1978, 1982), and these species contribute substantially to ecosystem structure and functioning (Smith 1987).

Due to the paucity of vertebrate consumers, macro-invertebrates fulfil a vital role in nutrient recycling (Crafford 1990a, Smith & Steenkamp 1992, 1993), because they are the major primary consumers on the island (Crafford 1990b). In consequence, they are of considerable importance in the terrestrial food web (Burger 1985, Smith & Steenkamp 1990). Indeed, the indigenous, flightless moth, *Pringleophaga marioni*, is often regarded a keystone species (Klok & Chown 1997). In addition, because they are available throughout the year, invertebrates provide an important food source for overwintering terrestrial birds (Dominican Gull, *Larus dominicanus*, and the Lesser Sheathbill), once penguins and seals have left the island and the abundant summer carrion supply has been depleted (Huntley 1971, Smith 1977, Burger 1981, 1982). The introduced House Mouse also feeds predominantly on macro-invertebrates (*e.g.*, Gleeson & Van Rensburg 1982, Van Aarde *et al.* 1996). The house mouse is believed to have been present on Marion Island for more than 180 years, and it is thought to be having a significant (and increasing) impact on many macro-invertebrate species, but particularly the indigenous, flightless moth, *P. marioni*, and a number of weevil species (Crafford & Scholtz 1987, Rowe-Rowe *et al.* 1989, Crafford 1990b, Smith & Steenkamp 1990, Chown & Smith 1993, Chown & Cooper 1995).

Although considerable quantitative information exists on the population dynamics of selected insect species (*e.g.*, *Embryonopsis halticella* (Lepidoptera, Yponomeutidae) (Crafford & Scholtz 1986), *Pringleophaga marioni* (Lepidoptera, Tineidae) (Crafford 1990a), *Ectemnorhinus similis* and *E. marioni* (Coleoptera, Curculionidae) (Chown & Scholtz 1989), and habitat use has been investigated qualitatively for many of these (*e.g.*, Crafford *et al.* 1986, Chown 1989), quantitative investigations of the habitat specificity and densities of the majority of the invertebrates have not been undertaken. Such studies are necessary if a comprehensive understanding of ecosystem structure and functioning on Marion Island is to be realized. In order to address this shortfall, the

Marion Island Terrestrial Invertebrate Ecology (M.I.T.I.E.) program was initiated. Its major objectives are to obtain baseline data on all the invertebrate populations at Marion Island on a habitat specific basis across a climatic gradient, and then to examine the relationship between energy availability, body size, population density, and species energy use, in a spatially explicit manner. Whole ecosystem tests of the relationship between density, body size and energy usage, that are not based on compilations of data collected in disparate ways, are generally lacking at this scale (*e.g.*, Blackburn & Gaston 1999). Hence, providing a test of the energy equivalence rule (Blackburn & Gaston 1999) and its associated assumptions forms the major overall objective of this program.

As a first step in gathering the data to investigate species energy usage, the densities of both the meso- and macro-invertebrates in a representative range of habitat types across a variety of altitudes, had to be investigated. The work reported here forms one component of this investigation and is concerned with the macro-invertebrates occurring in the major lowland vegetation complexes (vegetated biotope of Chown 1989) identified at Marion Island. Both introduced and indigenous species have been included in the study, not only because both groups use incoming energy, but also because the introduction of alien species poses one of the greatest threats to the biota on the islands (*e.g.*, Holdgate & Wace 1961, Holdgate 1967, Wace 1986, Watkins & Cooper 1986, Cooper & Condry 1988, Chown *et al.* 1998, Gremmen *et al.* 1998, Gremmen & Smith in press). In the case of the Prince Edward Islands, the potentially severe impacts of alien species have been formally recognised and the minimization of alien introductions is a key policy of the Prince Edward Islands Management Plan (Prince Edward Island Management Plan Working Group, 1996) (PEIMP). In addition, elucidating the ecological impacts of introduced species, especially the house mouse, and selected macro-invertebrates, form two of the five specific sub-objectives of the PEIMP regarding alien species already introduced to the islands (see Part 3, Section 14, PEIMP 1996). Because the indigenous macro-invertebrates play a fundamental role in the functioning of the Marion Island terrestrial ecosystem, and because mice are thought to be having an impact on them (Crafford & Scholtz 1987, Crafford 1990b, Smith & Steenkamp 1990, Chown & Smith 1993), a second, important goal of this thesis is to present the current data on macro-invertebrate densities and compare it to the only other compatible study on macro-invertebrates. More than 20 years ago, Alan Burger investigated invertebrates as a food resource for Sheathbills. Although the results of his macro-invertebrate work have been published (principally in Burger 1978, but also in Burger 1981, 1982), the data were generally not accompanied by measures of variance that allowed meaningful comparisons with subsequent work (*e.g.*, Crafford 1987, 1990a, Crafford & Scholtz 1987, Chown & Scholtz 1989). That is, most of the means provided by Burger (1978) for each taxon in each habitat type were not accompanied by estimates of variance. Rather, estimates of variance were provided for pooled data, by taxon or by habitat, only. To address this important problem, Burger's original data

were obtained and reworked to provide means and variances of each taxon (species where possible) and by habitat. If changes in populations of the island's macro-invertebrates are to be understood, the provision of data in a useable format that can be re-examined when necessary in future is a first, and critically necessary step in this procedure (see also Sparks & Crick 1999).

The third goal of this thesis is to examine the likely influence of a small, yet highly abundant, alien macro-invertebrate species (*Limnophyes minimus*) on terrestrial nutrient recycling. Of the aliens introduced to sub-Antarctic islands, focus has mainly been on the effects of the more conspicuous elements such as feral mammals, and plants (Hunter 1990, Chapuis *et al.* 1994, Gremmen 1997). Small species, such as midges (Chironomidae, Psychodidae), that are well represented in the sub-Antarctic and occur at Marion Island (Crafford 1986), can however, achieve very high densities in terrestrial systems (*e.g.*, Delettre & Trehen 1977, Delettre 1978, Delettre & Cancela da Fonseca. 1979). Nonetheless, no quantitative assessments of the habitat use, abundance, and biomass of these species have been made, or their likely influence on terrestrial ecosystem functioning.

Finally, an updated assessment of all the alien insect species recorded at Marion Island is presented. It has been suggested that climatic amelioration (warming and drying) at the sub-Antarctic islands, associated with global warming, is likely to enhance the chances of successful establishment of alien propagules (Chown & Language 1994, Kennedy 1995, Chown *et al.* 1998). Hence regular assessments of the alien biota at the islands are necessary.

In sum, the objectives of this project can be outlined as follows:

- 1. To determine the densities (numbers and biomass) and quantify the habitat specificity of the terrestrial macro-invertebrates of the vegetated biotope at Marion Island.**
- 2. To determine whether these density estimates differ from previous estimates by comparing the present results with those obtained from a re-analysis of the data collected by Burger in 1976/77.**
- 3. To determine the extent to which introduced species contribute to macro-invertebrate assemblages in the vegetated habitats at Marion Island, and the contribution that one of these (*L. minimus*) makes to ecosystem functioning.**
- 4. To provide a re-assessment of the alien invertebrates recorded at Marion Island.**

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1.2. LOCALITY AND ENVIRONMENT OF MARION ISLAND

1.2.1. Location and topography

Marion Island and Prince Edward Island form the Prince Edward Islands (PEI) group or PEI archipelago. Together with Crozet, Kerguelen, Heard and MacDonald Islands, these islands form the South Indian Ocean Province, (also referred to as the Kerguelen Biogeographical Province) (see Lewis Smith 1984), which is one of three provinces that constitute the sub-Antarctic region. Situated in the “roaring forties” of the southern Indian Ocean, the Prince Edward Islands lie approximately 1770 km south east of Port Elizabeth, South Africa (the closest point on any continent), and 2300 km north of Antarctica’s closest point (Lützw-Holm Bay) (see Fig.1). The nearest landfall is Île aux Cochons, some 950 km to the east. The PEI lie close to each other, with the more southerly and larger island, Marion (46°54’S; 37°45’E), separated from the smaller Prince Edward Island (46°38’S; 37°57’E) by 19 km.

Marion Island is about 290 km² in area with some 72 km of mostly cliff-face coastline. The profile of the island is typically that of a shield volcano, with some modification to the western side. On the eastern half of the island there is a regular rise from the coastal plain to the peaks. On the western half of the island the coastal plain is narrow, and is bounded by a sharp rise in the form of inland or coastal cliffs, and subsequently a more gentle rise to the peaks. The island is dotted with scoria cones, the highest peak rising to 1230 m a.s.l. The lowland terrain is generally marshy with many small ponds and lakes dotted across the landscape. Further inland the terrain includes numerous fern-covered slopes, eventually giving way to volcanic lava-covered hillsides and mountains, with an ice-plateau of about 10 km² above 1000 m.

1.2.2. Geological and human history

Geologically, the Prince Edward Islands (PEI) represent the twin peaks of a coalescing shield volcano. Although apparently dormant most of the time, the volcano is still active. A minor eruption occurred in 1980, and seismic activity was recorded as recently as 1998. Marion Island is thought to have emerged between 0.5 to 1 million years ago, with the oldest lava (grey basalt) bearing marks of extensive glaciations that took place on the island as recently as 12 000 - 16 000 years ago (Verwoerd 1971, Hall 1979).

Evidence of human activity on the PEI dates back to the beginning of the 18th century, when sealers first began exploiting the animal resources on the islands. The sealing activities centred around slaughtering seals and penguins for the trade of skins and oil, and lasted until 1860, after which the impact on the animal populations had reduced their numbers so drastically that the trade had become uneconomical. However, visits to the PEI continued, although at a lower intensity, and

most notably by explorers from various corners of the globe. These early explorers only set foot on the island for very short periods, except for the various shipwrecked parties that were left as castaways for months or years until they were rescued or died. These early explorers were responsible for many of the historical items now found on and around the islands, as well as for the first charts and scientific recordings (Cooper & Avery 1986, Graham 1989, Cooper & Headland 1991).

After South Africa annexed the islands at the end of December 1947, a meteorological station was set up on Marion Island, that has been occupied and run continuously ever since. Following the first scheduled biological and geological expedition in 1965, scientific research (mainly biological) has been the other major ongoing activity on Marion Island. Prince Edward Island has however been kept unoccupied, and visits restricted for research purposes only, under controlled conditions for only a few days every other year.

Research at Marion and Prince Edward Islands has resulted in a considerable and extensive body of work, dating back at least to the Challenger expedition in 1873. To be able to access and extract information from this work is important. Not only does the published literature form a necessary part of ongoing research and monitoring at the PEI, but it can also provide critical information for decision-makers, who can profoundly alter the course of management of the islands. In the process of searching for information relevant to this work, a full literature review for the Prince Edward Islands was undertaken, and for the above reasons is included as an appendix to this thesis (Appendix 1).

1.2.3. Climate

The Prince Edward Islands have a cool hyperoceanic climate (Schulze 1971, Smith & Steenkamp 1990). Located in the middle of three water masses; the Antarctic Polar Frontal Zone (lying just to the south), the Subtropical Convergence (lying to the north) and the sub-Antarctic front (which lies very close to the islands), the small and isolated islands are subjected to the conditions of these ocean systems. At Marion Island, the primary agents affecting the weather are the strong westerly winds that blow in those latitudes, and the cyclones that frequently produce rain, snow or clear cold conditions. The most typical features characterising the weather are based on data collected from the meteorological station situated on the more sheltered east coast at Marion Island about 10 m a.s.l., and can be summarised according to Schulze (1971) as follows:

- ◆ Predominantly strong westerly winds (regularly gale force at $> 55 \text{ km hr}^{-1}$)
- ◆ High precipitation (annual average: $> 2500 \text{ mm}$)
(mainly rain, but also snow, and graupel or shotgun pellet-like ice-rain)
- ◆ Relatively low average air temperatures (annual average: 5.7°C)
(showing little diurnal and seasonal variation)
- ◆ High relative humidity (annual average: 83%)
- ◆ High degree of cloudiness
- ◆ Low incidence of sunshine (radiation) ($25 - 30 \%$ of that possible)
(an average of 3.6 hours per day)

Generally the weather conditions are relatively constant. Average temperatures hardly fluctuate more than about 4.5°C throughout the year, and 2.3°C over 24 hours. The warmest months are January to March, with an average of 7.3°C , although maximum temperatures of up to 22.3°C have been recorded. The coldest months are between June and September, during which mean temperatures are in the vicinity of 3.2°C , and minima can be as low as -6.8°C (although the wind chill factor can reduce these temperatures up to -20°C). However, conditions at higher altitudes and on the western side of the island can be substantially different. Temperatures for instance decline by 4°C to 4.5°C for every 1000 m gain in altitude, while recordings of precipitation at an altitude of 550 m a.s.l. showed almost twice the annual amount, and at 750 m dropped to almost half the amount (Blake 1996).

Microhabitat temperatures are considerably warmer than those recorded in the Stevenson Screen, particularly on calm, sunny days. Temperatures in excess of 30°C have been recorded in tussock grass (Chown & Crafford 1992), and relatively high temperatures have also been recorded on rock surfaces at 750 m a.s.l. (Blake 1996). Although the lowland “soils” are often waterlogged, rock surfaces and other material such as the tillas of tussock grasses can be remarkably dry, and species inhabiting the waterlogged, vegetated biotope tend to have lower resistance to desiccation than species inhabiting the drier epilithic biotope, and other exposed habitats (see Klok & Chown 1998 for review).

1.2.4. Vegetation

Based on climatic factors, the PEI have a tundra type biome. According to Wielgolaski (1972) tundra is an area devoid of natural forest vegetation because of unsuitable weather conditions (temperatures being too low or wind and precipitation too high for development). The vegetation of the PEI is made up of 24 indigenous vascular plant species, from 20 families (see Table 1), and over 165 cryptogams (see Table 2). On Marion Island, a further 12 species of alien vascular plants (see Table 3) have become naturalised (Gremmen 1981, personal communication).

On Marion Island the occurrence of closed plant communities is restricted to the lowland areas (below 500 m), the mountainous interior consisting largely of bare, rocky areas, vegetated only by cryptogams or covered with snow and permanent ice. Accordingly, the islands' vegetation can be divided into two major biotopes: the mainly lowland vegetated biotope (being vascular vegetation and closed plant communities), and the epilithic biotope (being areas not supporting closed plant communities and dominated by cryptogams, rock outcrops and rock walls) (Chown 1989). The vegetated biotope occupies less than half of Marion Island's total surface area, forming a patchy mosaic of some 41 plant communities (Gremmen 1981). These can be grouped into five distinct communities representing the major components of the vegetated biotope. With the exception of the epilithic, the marine and fresh water communities, the vegetated biotope therefore comprises the following five communities: swamp communities (oligotrophic mires), salt spray-influenced communities, biotically influenced communities, drainage lines and lowland slopes. Each of these communities is in turn characterised by a dominant vegetation complex, and it is these characteristic vegetation complexes that were sampled in this study (Table 4) (see also Figure 2).

Table 1. Indigenous Vascular plants of the Prince Edward Islands

Family	Species	Community							
		Vegetated biotope:				Epilithic biotope:			
		1. Salt-spray				6. Fjaeldmark			
		2. Biotically influenced				Other:			
		3. Drainage lines				7. Fresh water			
		4. Lowland slopes				8. Caves /			
		5. Mire / swamps				crevices			
SPERMOPHYTA	- ANGIOSPERMAE	1	2	3	4	5	6	7	8
	[Flowering plants]								
Apiaceae	<i>Azorella selago</i> Hook. f.						+		
Asteraceae	<i>Cotula plumosa</i> Hook. f.	+	+						
Callitrichaceae	<i>Callitriche antarctica</i> Engelm.		+						
Caryophyllaceae	<i>Colobanthus kerguelensis</i> Hook. f.						+		
Crassulaceae	<i>Crassula moschata</i> Forst. f.	+							
Brassicaceae	<i>Pringlea antiscorbutica</i> R. Br.			+					
Potamogetonaceae	<i>Potamogeton</i> sp.							+	
Portulacaceae	<i>Montia fontana</i> L.		+						
Ranunculaceae	<i>Ranunculus moseleyi</i> Hook. f.							+	
Ranunculaceae	<i>R. bitermatus</i> Sm.					+			
Rosaceae	<i>Acaena magellanica</i> (Lam.) Vahl.			+					
Scrophulariaceae	<i>Limosella australis</i> R. Br.							+	
	[Grasses and sedges]								
Cyperaceae	<i>Uncinia compacta</i> R. Br.					+			
Juncaceae	<i>Juncus scheuchzerioides</i> Gaud.					+			
Juncaceae	<i>J. cf. effusus</i> L.					+			
Poaceae	<i>Agrostis magellanica</i> Lam.					+			
Poaceae	<i>Poa cookii</i> Hook. f.		+						
14	17								
PTERIDOPHYTA	[spore bearing plants]								
Aspleniaceae	<i>Elaphoglossum randii</i> Alston & Schelpe				+				
Blechnaceae	<i>Blechnum penna-marina</i> (Poir.) Kuhn				+	+			
Grammitidaceae	<i>Grammitis kerguelensis</i> Tard.								+
Polypodiaceae	<i>Polystichum marionense</i> Alston & Schelpe				+				+
Hymenophyllaceae	<i>Hymenophyllum peltatum</i> (Poir) Desv.								+
Lycopodiaceae	<i>Lycopodium magellanicum</i> Sw.					+	+		
Lycopodiaceae	<i>L. saururus</i> Lam.						+		
6	7								
20	24								

Table 2. Cryptogram groups with examples of the most common species in the various biotopes at the Prince Edward Islands (taken from Gremmen 1981).

Group	Species	C o m m u n i t y						Total
		<u>Vegetated biotope:</u>			<u>Other:</u>			No. spp.
		1. Biotically influenced	2. Mires	3. Wood (at Juniors Kop)	5. Rocky shore	6. Coastal rocks		
		<u>Epilithic biotope:</u>						
		4. Fjaeldmark (* on new lava flows)						
		1	2	3	4	5	6	Group
MUSCI	<i>Andreaea</i> sp.				+			
	<i>Ditrichum strictum</i> (Hook. f. & Wils.) Mitt.				+			
	<i>Sanionia uncinatus</i> (Hedw.) Warnst.		+					
	<i>Racomitrium lanuginosum</i> (Hedw.) Bird.				*			79
HEPATICS	<i>Blepharidophyllum densifolium</i> (Hook.) Angstr		+					
	<i>Jamesoniella colorata</i> (Lehm.) Schiffn.		+					
	<i>Marchantia berteroana</i> L. & L.	+						
	<i>Clasmatocolea humilis</i> (H. f. & T.) Grolle			+				36
LICHENS	<i>Mastodia</i> sp.					+		
	<i>Caloplaca</i> sp.						+	
	<i>Usnea insularis</i> (M. Lamb) Dodge			+				50
Total								165

Table 3. Naturalized *alien* vascular plants on Marion Island

F a m i l y	S p e c i e s	Locality on Marion Island
SPERMOPHYTES		
Caryophyllaceae	<i>Sagina procumbens</i> Ard.	Along coastal track to Trypot Beach.
Caryophyllaceae	<i>Stellaria media</i> (L.) Vill.	In <i>Acaena</i> - <i>Poa cookii</i> slopes; Ship's Cove.
Caryophyllaceae	<i>Cerastium fontanum</i> Baumg.	Open ground along streams.
Polygonaceae	* <i>Rumex acetosella</i> L.	Gentoo Lake, rocky outcrops.
GRASSES AND SEDGES		
Poaceae	* <i>Agropyron repens</i> (L.) P. Beauv.	Ship's Cove, near cave.
Poaceae	<i>Agrostis castellana</i>	Very difficult to discern from <i>A. stolonifera</i>
Poaceae	* <i>Agrostis gigantea</i> Roth.	Met. Station, slope toward Gentoo Lake.
Poaceae	<i>Agrostis stolonifera</i> L.	On damp slopes and riverbanks.
Poaceae	* <i>Alopecurus australis</i> Nees.	One tuft at Mixed Pickle Cove.
Poaceae	* <i>Festuca rubra</i> L.	Near shipwreck cave at Ship's Cove.
Poaceae	<i>Poa annua</i> L.	All trampled biotic areas.
Poaceae	<i>Poa pratensis</i> L.	Lowland slopes (<i>e.g.</i> , Marion base to Trypot Beach)
12 [* = Restricted (5)] [Rest = Widespread (7)]		

Table 4. Plant communities representative of Marion Islands' vegetated biotope (adapted from Gremmen 1981, Gremmen unpublished).

PLANT COMMUNITIES	(1-5)	Area where found
<i>Vegetation complex</i>		
<i>Characteristic plant species</i>		
1. SALT-SPRAY COMMUNITIES		
<i>Crassula moschata</i> halophytic herbfield (Dense mats of small succulent herb) <i>Crassula moschata</i>		Shore zone areas, within a few hundred metres of the sea's influence. All along the West coast of the island, and areas such as East Cape, Duiker's Point and Storm Petrel Bay.
2. BIOTICALLY INFLUENCED COMMUNITIES (Nitrophilous plants)		
<i>Callitriche antarctica-Poa cookii</i> <i>Poa cookii</i> (and <i>Poa annua</i>)		On wet peaty and more or less heavily manured soils. Hence it forms mostly around seal haul-out areas and penguin rookeries (e.g., Macaroni Bay and Bullard Beach), but also where burrowing petrels nest in well-drained slopes
<i>Cotula plumosa</i> herbfield (Feathery leafed herb, forming luxuriant stands) <i>Cotula plumosa</i>		Generally in shallow manured soils, consisting of fibrous peat and clay.
3. DRAINAGE LINES		
<i>Acaena magellanica Brachythecium</i> complex <i>Acaena magellanica</i>		Wherever there is considerable movement of water, either below the soil surface or along streams etc.
<i>Blechnum penna-marina</i> complex <i>Blechnum penna-marina</i>		Along river banks, in springs, flushes, water tracks and drainage lines. In some areas the entire mat of flowering plants and bryophytes is afloat on moving water below.
4. LOWLAND SLOPE COMMUNITIES		
<i>Blechnum penna-marina</i> complex <i>Blechnum penna-marina</i>		On well-drained lowland slopes.
<i>Blechnum penna-marina</i> complex <i>Blechnum penna-marina</i>		Generally on slopes inland of salt-spray zone.
5. OLIGOTROPHIC MIRE (SWAMP) COMMUNITIES (Mainly mosses and graminoid-species)		
<i>Juncus scheuchzerioides-Blepharidophyllum densifolium</i> (Wet, unstable, stagnant peat's with little lateral drainage) <i>Blepharidophyllum densifolium</i> <i>Sanionia uncinatus</i> <i>Jamesoniella colorata</i>		Possibly the most common vegetation complex at low altitudes. It forms on wet peat.
		In small basins within hummocky black lava flows.



Figure 2: A view of the vegetated biotope typical of Marion Island. Examples of the different plant communities and 10 vegetation complexes sampled in 1996/97 are indicated.

Legend

<u>PLANT COMMUNITIES</u>		<u>VEGETATION COMPLEXES</u>
I.	Salt spray influenced areas :	1 = <i>Crassula moschata</i> (on cliffs along the coast).
II.	Biotically influenced areas :	2 = <i>Cotula plumosa</i> (typical in coastal areas near penguin rookeries and elephant seal haul out places).
		3 = <i>Poa cookii</i> tussock grassland (typical around albatross nests).
III.	Drainage line area :	4 = <i>Acaena magellanica</i> (typical on inland slopes or banks).
IV.	Lowland slopes :	5 = <i>Blechnum penna-marina</i> (typical on inland slopes & hillsides).
V.	Oligotrophic mires :	6 = <i>Blepharidophyllum densifolium</i> .
		7 = <i>Sanionia uncinatus</i> .
		8 = <i>Jamesoniella colorata</i> .
		9 = Mid-altitude.
		10 = High-altitude.

1.2.5 Fauna

1.2.5.1 Vertebrates

Vertebrates occurring on the Prince Edward Islands are mostly pelagic land-breeding species, including 29 species of mainly seabirds (four penguin spp., five albatross spp., 14 petrel spp. and six other spp.) and three seal species. (Hänel & Chown 1999). These vertebrates play a cardinal role in the islands' terrestrial ecosystem. They are responsible for substantial manuring on the islands (Siegfried *et al.* 1978, Williams 1978, Williams & Berruti 1978, Williams *et al.* 1978, Smith 1979), considerably influencing growth of vegetation particularly in their breeding areas (Smith 1976, 1978, Panagis 1985).

The house-mouse, *Mus musculus*, has been introduced to Marion Island, but it is absent from Prince Edward Island. Because it is a terrestrial omnivore, feeding mostly on insects (Gleeson & Van Rensburg 1982), it has a pronounced effect on both the invertebrates and the vegetation on the island (Crafford & Scholtz 1987, Rowe-Rowe *et al.* 1989, Crafford 1990b), and competes with the only true land-bird, the scavenging Sheathbill *C. minor marionensis*, for macro-invertebrate food resources (Burger 1978, 1981, 1982, Huyser 1997).

1.2.5.2 Terrestrial invertebrates

Because of the virtual absence of terrestrial, non-pelagic vertebrates on the Prince Edward Islands, invertebrates constitute the most significant primary consumers, detritivores, and, to some extent, predators (Burger 1985). The invertebrates can be broadly classed as macro- and meso-invertebrates, with the macro-fauna including all the larger and more conspicuous taxa that generally contribute most to the functioning of the terrestrial ecosystem (Burger 1985, Smith & Steenkamp 1992, 1993). In this study, macro-invertebrates include all invertebrates with the exception of the Collembola, Acarina and Tardigrada. Thus, the macro-invertebrates at Marion Island are represented by 10 Orders, of which seven fall within the Insecta, and one each within the classes Arachnida, Oligochaeta and Gastropoda. The meso-invertebrates remain poorly known, but comprise mainly two groups, the Collembola (16 species, Gabriel 1999) and Acari (more than 60 species, Marshall *et al.* 1999) (Table 5). Together, the macro- and meso- invertebrates are represented by some 116 species (including the alien component). The macro-invertebrates being made up of 30 species from the class insecta (18 indigenous and 12 naturalised aliens, see Table 6), and 10 species from the remaining classes (eight indigenous and two naturalised aliens) (Table 5). In addition to these insects, vagrant species occasionally turn up at the PEI. At Marion Island a total of 15 such transient aliens

have been sighted to date (see Table 7 and Chapter 4 of this thesis), but are not considered part of the islands' fauna, as they have not yet been recorded as breeding there.

Table 5. Species richness of the free-living terrestrial invertebrates of Marion Island.

Phylum	Class	Order	Indigenous	Alien	Total
MACRO - INVERTEBRATES					
Arthropoda	Insecta	Coleoptera	8	-	8
		Diptera	5	5	10
		Lepidoptera	3	3	6
		Hymenoptera	1	-	1
		Psocoptera	1	-	1
		Hemiptera	-	3	3
		Thysanoptera	-	1	1
			18	12	30
	Arachnida	Araneae	4	-	4
Annelida	Oligochaeta	Haplotaxida	3	1	4
Mollusca	Gastropoda	Stylommatophora	1	1	2
			8	2	10
3	4	10	26	14	40
MESO - INVERTEBRATES					
Arthropoda	Collembola	?	12	4	16
	Arachnida	Acarina	60 + ?	?	60 + ?
Tardigrada	?	?	+ ?	?	+ ?
2	3	?	72 +	4	76 +
Total					116 +

Table 6. The macro-insecta of Marion Island and their distributions.

INDIGENOUS SPECIES			Habitats of the invertebrates						T
			1. Intertidal	2. Supralittoral	3. Rock faces	4. Fellfield	5. Vegetated area	6. Marion base	O T A L
Order	Family	Species	1	2	3	4	5	6	
Coleoptera	Curculionidae	<i>Bothrometopus elongatus</i> (Jeannel)				✓			
	"	<i>B. parvulus</i> (C.O. Waterhouse)			✓	✓			
	"	<i>B. randi</i> Jeannel			✓	✓			
	"	<i>Ectemnorrhinus marioni</i> Jeannel					✓		
	"	<i>E. similis</i> Waterhouse					✓		
	"	<i>Palirhoeus eatoni</i> (C.O. Waterhouse)		✓					
	Staphylinidae	<i>Halmaeusa atriceps</i> (C.O. Waterhouse)		✓	✓	✓	✓		
	Hydraenidae	<i>Meropathus chuni</i> Enderlein	✓	✓	✓		✓		8
Diptera	Helcomyzidae	<i>Paractora dreuxi mirabilis</i> Séguy	✓						
	Tethinidae	<i>Apetaenus litoralis</i> Eaton	✓						
	"	<i>Listriomastax litorea</i> Enderlein	✓						
	Sciaridae	<i>Lycoriella aubertii</i> Séguy					✓		
	Chironomidae	<i>Telmatogeton amphibius</i> (Eaton)		✓					5
Lepidoptera	Tineidae	<i>Pringleophaga marioni</i> Viette					✓		
	"	<i>P. kerguelensis</i> Enderlein					✓		
	Yponomeutidae	<i>Embryonopsis halticella</i> Eaton					✓		3
Hymenoptera	Eucoilidae	<i>Kleidotoma icarus</i> (Quinlan)		✓					1
Psocoptera	Elipsocidae	<i>Antarctopsocus jeanneli</i> Badonnel			✓	✓			1
5	11	18							18

Table 6..... *Continued*

N A T U R A L I Z E D		A L I E N S			
Thysanoptera	Thripidae	<i>Apterothrips apteris</i> Daniel		✓	1
Diptera	Calliphoridae	<i>Calliphora vicina</i> Robineau-Desvoidy	✓	✓	
	Fanniidae	<i>Fannia canicularis</i> (Linnaeus)		✓	
	Drosophilidae	<i>Scaptomyza</i> sp. Hardy		✓	
	Psychodidae	<i>Psychoda parthenogenetica</i> Tonnoir		✓	
	Chironomidae	<i>Limnophyes minimus</i> Meigen		✓	5
Lepidoptera	Yponomeutidae	<i>Plutella xylostella</i> (Linnaeus)		✓	
	Noctuidae	<i>Agrotis ipsilon</i> (Hufnagel)			✓
	Nymphalidae	<i>Vanessa cardui</i> (Linnaeus)		✓	✓ 3
Hemiptera	Aphididae	<i>Macrosiphum euphorbiae</i> (Thomas)		✓	
	"	<i>Myzus ascalonicus</i> (Doncaster)		✓	
	"	<i>Rhopalosiphum padi</i> (L.)		✓	3
4	10	12			12
TOTAL	21	30			30

Table 7. Transient alien (vagrant) insects recorded at Marion Island.

			Habitats of the invertebrates						T
			1. Intertidal	2. Supralittoral	3. Rock faces	4. Fellfield	5. Vegetated area	6. Marion base	O
									A
									L
Order	Family	Species	1	2	3	4	5	6	
Coleoptera	Anobiidae	Anobiidae sp.						✓	
	Dermestidae	Dermestidae sp.						✓	
	Chrysomelidae *							✓	
Hemiptera	Scutelleridae	<i>Cryptacrus comes</i> Fabricius #						✓	
Diptera	Lonchaeidae	<i>Lamprolonchaea smaragdi</i> (Walker) #						✓	
	Anthomyiidae	<i>Anthomyiidae</i> sp. #						✓	
Lepidoptera	Noctuidae	<i>Chrysodeixis acuta</i> Walker						✓	
	"	<i>Cosmophila sabulifera</i> Gueneé						✓	
	"	<i>Spodoptera exigua</i> Hübner						✓	
	"	<i>Agrotis segetum</i> (Denis & Schiffermüller)						✓	
	Pyrilidae	<i>Nomophila</i> sp. #						✓	
	Noctuidae	<i>Trichoplusia orichalcea</i> (Fabricius)						✓	
	"	<i>Helicoverpa armigera</i> Hübner						✓	
Hymenoptera	Formicidae	<i>Lepisiota capensis</i> (Mayr)*						✓	
Orthoptera	Blatellidae	<i>Blatella germanica</i> L.						✓	
Total	10	15							15
*	=	Only a single dead specimen found.							
#	=	Only a single live specimen found (possibly has occurred before, but has not been recorded).							

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CHAPTER 2. TERRESTRIAL MACRO INVERTEBRATE DENSITY AND BIOMASS IN LOWLAND VEGETATION COMMUNITIES

2.1 Introduction

Because of the isolation and species poor nature of the Prince Edward Islands (Chapter 1), Marion Island can be seen as a semi-closed system, whose functioning depends principally on energy input from the surrounding ocean and atmosphere. The island receives most of its nutrients in the form of guano deposits from breeding birds and seals (Williams 1978, Williams & Berruti 1978, Williams *et al.* 1978, Siegfried *et al.* 1978, Siegfried 1981, Panagis 1985). This promotes the growth of vegetation, which in the absence of any large herbivores, results in high net primary production (Smith 1987a, b) and subsequently, substantial reserves of nutrients in the form of organic litter and peat. How these nutrients are released and re-distributed has been shown to be largely due to invertebrate consumers on the island (Crafford 1990a, Smith & Steenkamp 1992). For example, in the supralittoral zone, kelp flies enhance nutrient cycling substantially (Crafford & Scholtz 1987a, Chown 1996a), while in the vegetated zones, larvae of Coleoptera and Lepidoptera are the dominant herbivores and detritivores (Crafford & Chown 1991), with *Pringleophaga marioni* being the key contributor in the lowland vegetated biotope (Crafford 1990a, Smith & Steenkamp 1993, Klok & Chown 1997). Thus invertebrates have been recognised as crucial agents in nutrient cycling.

The local effects of global climate change are also thought to be influencing these biotic interactions. Over a period of three and a half decades (1951-1988), mean annual temperature has increased by 1°C and precipitation declined by 10 % at Marion Island (Smith & Steenkamp 1990). Mire habitats in the lowland vegetated areas have also shown a noticeable drying trend (Chown & Smith 1993). Such changes in climate are likely to have a marked effect on the island's biota. Indeed, Smith & Steenkamp (1993) predicted that climate change will affect species composition and the distribution of communities, in particular vascular plant-dominated ones, because of an increase in primary production accompanied by a greater demand by the plants for nutrients. They also suggested that a decrease in cold (said to be a regulating factor on the population of the house mouse) will lead to an increase in predation on soil macro-invertebrates, and consequently a change in ecosystem functioning because of the insectivorous diet of the mice and their size-selective predation on the most "ecologically-active" part of the invertebrate populations (large larvae), (see also Chown & Smith 1993). They argued that a decrease in invertebrate densities would in turn result in a decreased rate of nutrient cycling, and thereby effect an imbalance in primary production and decomposition. The implications of such a decline in invertebrate populations are not only highlighted in terms of the effects on decreased nutrient mineralisation (see also Klok & Chown 1997), but also on the survival of Marion Island's endemic Lesser Sheathbill subspecies *Chionis*

minor marionensis, whose over winter survival is dependent largely on the abundance of the invertebrate food-source (e.g., Burger 1978, Smith & Steenkamp 1990).

That ameliorating temperatures have already effected an increase in the mouse population on Marion Island, and that this increase together with the eradication of the cats from the Island is having a significant impact on the most important detritivorous (viz. *P. marioni* and the various weevil species) has been outlined in various studies (Crafford & Scholtz 1987b, Rowe-Rowe *et al.* 1989, Crafford 1990b, Smith & Steenkamp 1990, Chown & Smith 1993, Chown & Cooper 1995). In turn, the decline in sheathbill numbers on Marion Island has been ascribed to the decline in invertebrate numbers (Crafford & Scholtz 1987b, Huyser 1997).

Clearly the important role that invertebrates play in ecosystem functioning on Marion Island has been recognised. Nonetheless, although various studies have investigated the dynamics (e.g., Crafford & Scholtz 1986, Crafford 1990a) and habitat use (e.g., Burger 1978, Crafford *et al.* 1986) of selected species, no quantitative investigation of the habitat specificity and densities of the majority of the invertebrates has yet been undertaken. To accurately assess the role of the invertebrates in the vegetated biotope of Marion Island, an assessment of invertebrate distributions (habitat specificity) and abundances is a necessary first step. In addition, if the effect of mice on the terrestrial system is to be accurately quantified, and subsequently understood in the context of changes in the islands' climates, baseline information on their main prey species is a prerequisite.

To these ends, the densities and biomasses of all the macro-invertebrate species occurring in the lowland vegetation were obtained and examined in the context of their habitat specificity and seasonality. This chapter presents these findings together with a re-assessment of the data provided by Alan Burger (Burger 1978, data collected in 1976/77) on a subset of these species. In addition, it provides a comparison of the two data sets, to establish conclusively the present status of selected macro-invertebrate populations on Marion Island.

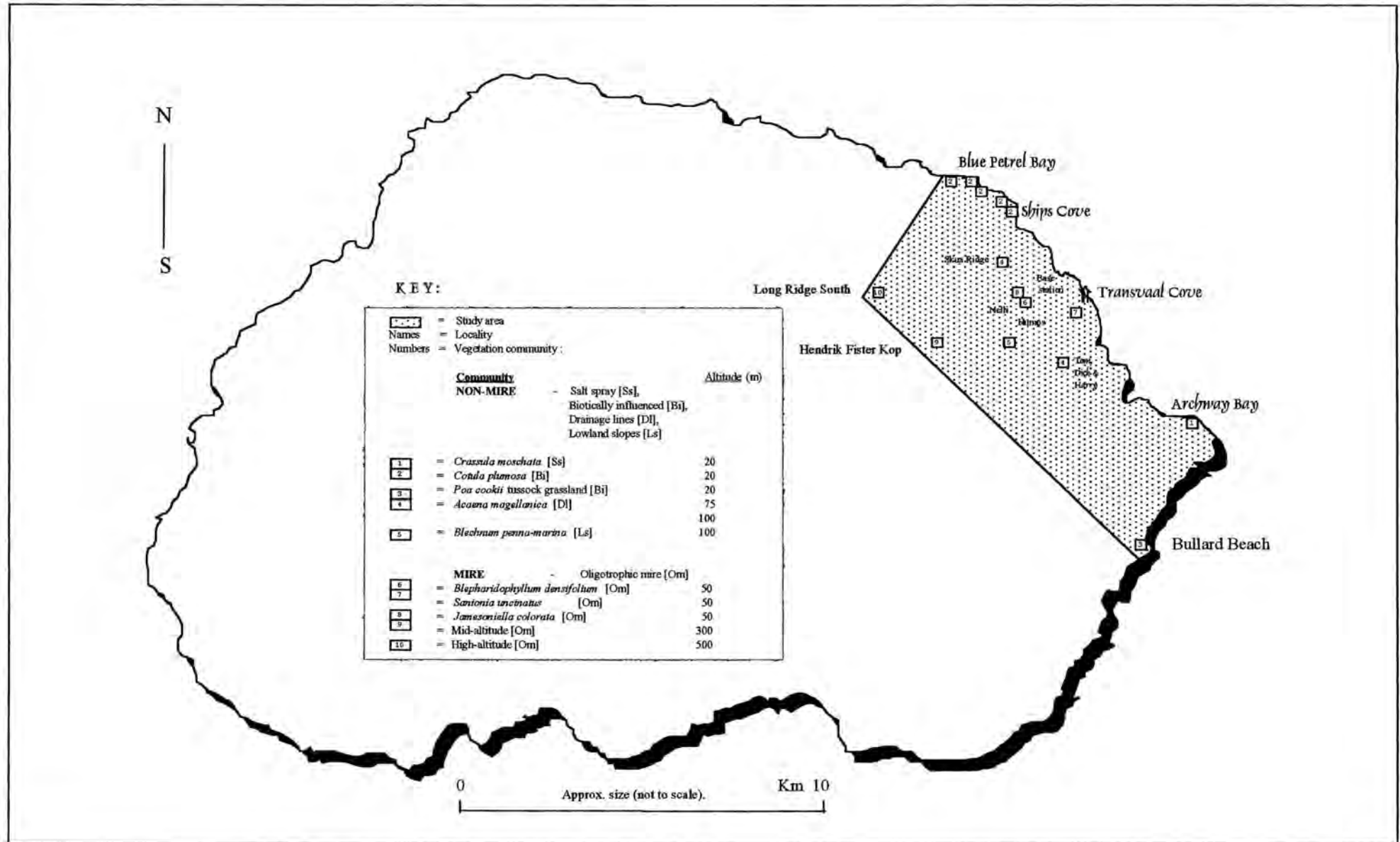


Figure 3. Study area indicating the sites where the macro-invertebrates were sampled in 1996/97 at Marion Island.

2.2 Methods

2.2.1 1996 / 97

2.2.1.1 Study sites

The study sites were all situated within a rectangular area of approximately 35 km² on the eastern side of Marion Island, that stretched east and west of the Base station at Transvaal Cove (46°52'40" S; 37°51'35" E). They were located along the coast between Bullard Beach to Blue Petrel Bay (approximately 5.5 and 4.5 direct line kms east and west of the Base station, respectively) and inland as far as Hendrik Fister Kop and Long Ridge South (each approximately 3.7 kms from the coast, or 3.7 and 5.2 direct line kms SW and W of the Base respectively) (see Fig. 3). The study sites were chosen to represent the 10 vegetation complexes, or in the case of mires, the different communities within them, of the vegetated biotope. Thus one site representing the salt spray community was situated at c. 20 m a.s.l. on the coastal cliffs just beyond Archway Bay, and comprised *Crassula moschata* as the dominant vegetation type. Five sites of *Cotula plumosa* (biotically influenced plant community) were spread along the coast between Blue Petrel Bay and Ships Cove at c. 20 m altitude, and one site of *Poa cookii* (the other plant complex representing the biotically influenced community) was situated near the coast of Bullard Beach North (at c.20 m a.s.l.) next to the Macaroni Penguin colony. Two inland sites represented *Acaena magellanica* (the drainage line community), with one at Tom, Dick and Harry (c. 75 m a.s.l.) and one at Skua Ridge (c.100 m a.s.l.), and one site representing *Blechnum penna-marina* (lowland slope community) was situated inland in the vicinity of the Nellie Humps area on a slope c.100 m a.s.l.). Of the oligotrophic mire community, a site each for *Blepharidophyllum densifolium*, *Sanionia uncinatus* and *Jamesoniella colorata* was situated between the Base station and Nellie Humps at c. 50 m a.s.l. One mid-altitude mire was situated at Hendrik Fister Kop (c. 250 m a.s.l.), and one high-altitude mire was situated on Long Ridge South at c. 400 m a.s.l. (see Fig. 3 for details).

2.2.1.2 Sampling materials and methods

In each of the 10 vegetation complexes selected, with the exception of the high-altitude mire, five 2 m x 2 m quadrates were staked out at random, and from each of these, two circular (7 cm diameter) soil cores were extracted randomly by using an O'Connor split corer (see Southwood 1978). For the high-altitude mire, only four 1 m x 1 m quadrates were laid out because of the small surface area of this site, and because no other mires can be found at this altitude on Marion Island (S. Chown personal communication with N.J.M. Gremmen). Sampling took place at bi-monthly intervals over a period of one year, from June 1996 to May 1997. Thus 10 core-samples were extracted once every

two months from each of the ten vegetation complexes selected, except for the high-altitude site, from which eight samples were taken bi-monthly, and two non-mire sites (*Crassula moschata* and *Cotula plumosa*), from which only five samples were taken in the first month using a larger (10 cm x 10 cm) box corer. All core samples were hand-sorted in the laboratory. The sample was first sorted dry, and was subsequently washed to remove any remaining macro-invertebrates. This hand-sorted and washed material was then placed in a Tullgren funnel for four days, after which remaining invertebrates were collected (mainly small chironomid larvae and spiders).

All extracted macro-arthropods were immediately placed into a solution of Formaldehyde/Acetic acid/Ethanol (FAA) and within a half to one hour thereafter, identified to species or morphospecies where the former was not possible (using Crafford *et al.* 1986, Chown 1996b unpublished key, and an invertebrate wet collection). The species were separated into their various developmental stages (adults, larvae, pupae, eggs or cocoons) and then counted, weighed wet, and with the exception of earthworms, dried to constant mass at 60°C after which they were then weighed dry (which in the case of snails was with their shells). Earthworms were not dried as confirmation of their identity was still required. Their dry mass was however estimated from a linear regression of dry mass on wet mass obtained from a separate sample of 20 earthworms that were subjected to the same treatment as the remaining macro-invertebrates.

2.2.1.3 Analysis

Abundances (numbers and biomass) were converted to densities and biomasses (m^2), and annual means (and standard errors) were calculated for each of the invertebrate species found. Seasonality for each of the species in each of the habitats was assessed by calculating bi-monthly means and standard errors for each species in a given habitat, and plotting these against months for the entire sampling period. Species were subsequently categorized as aseasonal, or seasonal with a peak in abundance and/or biomass in a given season (month).

Cluster analysis, using group averaging, double square-root transformation (to weight rare and common species equally, Clarke & Warwick 1994), and based on Bray-Curtis similarity measures was undertaken to determine the relationship between the macro-invertebrate assemblages in each plant community (PRIMER v. 4.0 was used). To test for significant differences in invertebrate assemblages between the *a priori* defined plant communities, an analysis of similarity was used (ANOSIM, see Clarke 1993). This is a non-parametric permutation procedure applied to rank similarity matrices underlying sample ordinations (Clarke 1993), in which a significant global *R*-statistic of close to one indicates distinct differences between the assemblages/habitats compared. In addition, the extent of the habitat specificity of each of the macro-invertebrate species was determined using the Indicator Value Method (Dufrêne & Legendre 1997). This assesses the degree

(expressed as a percentage) to which each species fulfils the criteria of specificity (uniqueness to a particular site or sites) and fidelity (frequency within that habitat type or types) for each habitat cluster compared with all other habitats. The higher the percentage IndVal (indicator value) obtained, the higher the specificity and fidelity values for that species, and the more representative the species is of that particular habitat (see also McGeoch & Chown 1998). The species abundance matrix from each site was used to identify indicator species, and Dufrêne and Legendre's (1997) random reallocation procedure of sites among site groups was used to test the significance of the IndVal measures for each species. Those species with significant IndVals > 50% (subjective benchmark) were then regarded as specific to the habitat or habitat level in question. The results of the IndVal analysis provide a sound indication of the number of habitats in which a given species is consistently present in reasonably high numbers. This was used as one measure of habitat specificity because it tends not to place emphasis on sporadic occurrences which may be the consequence of species occasionally wandering into other habitats as tourists (*e.g.* Gaston *et al.* 1993, Chown & Steenkamp 1996).

To determine the extent to which alien species contribute to invertebrate abundance, the percentage contribution of each species within the whole assemblage was calculated and the species were ranked.

Comparisons were also made between the current results and those obtained from the 1976/77 study (see below), to establish if invertebrate densities have changed over time. By using corresponding habitats and species groupings, the densities and biomasses of selected species determined during 1976/77 and 1996/97 were compared using Kruskal Wallis one way analysis by ranks.

2.2.2 1976 / 77

Data on the macro-invertebrate abundances (density and biomass) from 19 vegetation complexes sampled during 1976/77 at Marion Island were obtained from the original author (see acknowledgements A. Burger) in the format of hand written FORTRAN coded forms. These forms contained the numbers and biomass of the invertebrates identified from each of the habitats sampled, according to the methods described by Burger (1978). The invertebrates studied were, according to Burger (1978): earthworms (*Microscolex kerguelarum* Grube), flightless lepidoterans (*Pringleophaga marioni* Viette and *Embryonopsis halticella* Eaton), coleopteran weevils (Curculionidae, mostly *Ectemnorhinus similis* Waterhouse), spiders (*Myro* spp. Cambridge), snails (*Notodiscus hookeri* Reeve) and slugs. Species <1 mm in size and the smaller fauna, including rove-beetles (Coleoptera, Staphylinidae), small flies (Diptera), aphids (Hemiptera), Collembola and acarid

mites, were not considered, although these sometimes occurred in large numbers (Burger 1978, 1979), because Burger was interested in those species that formed the major prey items of Sheathbills. The 19 vegetation complexes sampled were also classified according to Gremmen (1981), and the numbering sequence allocated by Burger was retained in the current re-analysis.

2.2.2.1 Study site

According to Burger (1978), “Terrestrial invertebrates and the foraging activities of sheathbills and kelp gulls were studied between April 1976 and May 1977 in a 100 ha study area, 200 m wide, along 5.0 km of coastline between Prion Valley and East Cape”. Within this study site, “relative areas of 19 vegetation complexes were determined along 68 transects, each 200 paces long and perpendicular to the shoreline, spaced regularly throughout the study area”.

2.2.2.2 Sampling material and methods

“After 10 paces along a transect, the vegetation within a 10 x 10 m area was assigned to one of 19 vegetation complexes. The percentage area of each vegetation type was calculated from the aggregates. Sampling for terrestrial invertebrates occurred at randomly selected sites in each vegetation type. Generally, the samples were taken from the same patch of each vegetation type in each month. Five samples were collected from each vegetation type in the second half of each month. Each sample consisted of a core (diameter 8 cm), covering 50,5 cm³ of substrate and about 10 cm deep. Virtually all the animals were found in the upper 4 cm of substrate. A relatively small core was deliberately chosen to investigate the spatial variability of invertebrate abundance and biomass within sampling areas. Cores included live plants, litter, peat and soil. In the laboratory the cores were sorted through by hand and all the visible macro-invertebrates removed, counted, dried in a convection oven for 48 hours at 60-70°C and weighed”.

2.2.2.3 Analysis

The raw data was reworked using the same methods and format as that of the current 1996/97 study, which are outlined in section 2.2.1.3. above.

2.3 Results

2.3.1 1996 / 97

2.3.1.1 Densities and Biomass

Mean annual densities and biomasses ($\pm$ standard error (S.E.)) of the macro-invertebrates found in each of the 10 vegetation complexes are provided in Tables 8 and 9 respectively. Data regarding eggs and cocoons are not included with the species stages, but are listed at the end of the table together with data on snail shells. This is done because it was not possible to locate these stages (where appropriate) for all of the invertebrates listed, and of those found the values are in many cases not a true reflection of live or current material turnover. For example, in the case of the spider cocoons, it was not feasible to examine each cocoon in order to determine if it contained fertile material or if it was the remains of an old cocoon, which like snail shells, may take years to break down. Tables 10 and 11 provide relative abundances of each invertebrate species within a vegetation complex and across the vegetated biotope. The relative abundances of the indigenous and alien species are also indicated.

In total, 19 species are listed, of which 12 are indigenous, and seven are naturalised aliens. Of these, the most abundant species, both in terms of density and biomass, are represented by the Oligochaeta. Earthworms contribute by far the greatest amount to total dry biomass, both within the class Oligochaeta as well as to all the Orders found, comprising 69.4 % of the annual grand total (see Table 10). In terms of densities, the Enchytraeidae are by far the most numerous, contributing 57.6 % to the total numbers found (see Table 11). Thus indigenous species still contribute most, both in terms of biomass (94.1 %) and numbers (74.3 %). However, if the oligochaetes are ignored, the alien component ranks next highest in density with the midge *L. minimus* contributing 14.1 % and the aphids 10.3 %. In terms of biomass, the alien component contributes only about half of that of the indigenous species to total biomass. Nonetheless, certain species have quite similar contributions. For example, the alien slug, *Deroceras caruanae* (4.0 %) and the indigenous land snail *Notodiscus hookeri* (4.3 %) have similar relative abundances (see Table 10). Thus the Class Gastropoda ranks second in overall biomass contribution, followed by the Class Insecta represented by the lepidopteran *Pringleophaga marioni* (2.5 %) and the coleopteran *Ectemnorhinus marioni* (2.1 %).

Table 8. Annual densities (numbers m⁻²) (± S.E.) of macro-invertebrates found in 10 major vegetation complexes at Marion Island, June 1996 - May 1997. Vegetation complexes : Bleph. = *Blepharidophyllum densifolium*, San. = *Sanionia uncinatus*, HI = High altitude mire, Jamesoniella = *Jamesoniella colorata*, Mid = Mid altitude mire, Acaena = *Acaena magellanica*, Blechnum = *Blechnum penna-marina*, Cotula = *Cotula plumosa*, Crassula = *Crassula moschata*, Poa = *Poa cookii*.

Species	Mires					Non Mires				
	Bleph. n = 60	San. n = 60	HI n = 48	Jamesoniella n = 60	Mid n = 60	Acaena n = 60	Blechnum n = 60	Cotula n = 55	Crassula n = 55	Poa n = 60
INDIGENOUS										
Enchytraeidae worms	4 ± 4	0 ± 0	11 ± 8	0 ± 0	243 ± 168	33961 ± 4134	4 ± 4	25833 ± 4545	3554 ± 757	1054 ± 288
Earthworms	0 ± 0	4 ± 4	125 ± 29	17 ± 8	35 ± 14	684 ± 83	157 ± 24	3953 ± 286	634 ± 78	1252 ± 215
<i>Erigone</i> sp.	909 ± 139	1624 ± 203	65 ± 27	650 ± 95	173 ± 37	228 ± 53	11 ± 7	140 ± 25	14 ± 8	527 ± 90
<i>Myro</i> sp.	39 ± 24	9 ± 6	5 ± 5	13 ± 10	17 ± 8	42 ± 15	17 ± 8	0 ± 0	0 ± 0	0 ± 0
<i>Notodiscus hookeri</i>	4 ± 4	0 ± 0	11 ± 8	82 ± 32	147 ± 62	9 ± 9	329 ± 47	0 ± 0	0 ± 0	0 ± 0
Weevil pupae	9 ± 6	13 ± 7	0 ± 0	17 ± 8	9 ± 6	18 ± 8	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Ectemnorhinus similis</i> - Adults	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	17 ± 8	0 ± 0	0 ± 0	5 ± 5	4 ± 4
<i>Ectemnorhinus similis</i> - Larvae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	118 ± 28	0 ± 0	18 ± 11	60 ± 15	16 ± 10
<i>Ectemnorhinus marioni</i> - Adults	13 ± 7	26 ± 12	0 ± 0	61 ± 44	4 ± 4	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Ectemnorhinus marioni</i> - Larvae	95 ± 25	199 ± 65	114 ± 26	243 ± 40	247 ± 46	0 ± 0	0 ± 0	0 ± 0	0 ± 0	4 ± 4
<i>Bothrometopus elongatus</i> - Adults	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	4 ± 4	0 ± 0	5 ± 5	5 ± 5	0 ± 0
<i>Meropathus chuni</i> - Adults	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	71 ± 50	19 ± 19	0 ± 0
<i>Meropathus chuni</i> - Larvae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	9 ± 9	38 ± 30	0 ± 0
<i>Halmaeus atriceps</i> - Adults	43 ± 17	9 ± 9	0 ± 0	26 ± 13	9 ± 6	162 ± 33	0 ± 0	635 ± 160	11 ± 7	383 ± 88
<i>Halmaeus atriceps</i> - Pupae	4 ± 4	0 ± 0	0 ± 0	4 ± 4	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Halmaeus atriceps</i> - Larvae	39 ± 16	9 ± 9	0 ± 0	74 ± 21	17 ± 14	362 ± 71	17 ± 17	978 ± 126	34 ± 13	699 ± 81
<i>Pringleophaga marioni</i> - Pupae	0 ± 0	13 ± 7	0 ± 0	4 ± 4	0 ± 0	9 ± 6	0 ± 0	2 ± 2	0 ± 0	0 ± 0
<i>Pringleophaga marioni</i> - Larvae	65 ± 39	78 ± 23	0 ± 0	0 ± 0	9 ± 6	35 ± 15	0 ± 0	70 ± 19	9 ± 7	12 ± 7
<i>Embryonopsis haiticella</i> - Pupae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Embryonopsis haiticella</i> - Larvae	0 ± 0	0 ± 0	16 ± 12	0 ± 0	30 ± 22	4 ± 4	0 ± 0	13 ± 7	0 ± 0	121 ± 28
NATURALISED ALIENS										
<i>Deroceras caruanae</i>	4 ± 4	78 ± 26	0 ± 0	9 ± 6	0 ± 0	218 ± 37	0 ± 0	5 ± 5	0 ± 0	0 ± 0
<i>Apterothrips apteris</i>	0 ± 0	43 ± 26	70 ± 30	52 ± 34	61 ± 28	0 ± 0	0 ± 0	283 ± 246	52 ± 35	0 ± 0
Aphididae	576 ± 198	697 ± 189	22 ± 17	299 ± 77	26 ± 12	1406 ± 681	9 ± 9	3849 ± 1260	524 ± 279	4167 ± 2571
<i>Psychoda parthenogenetica</i> - Adults	4 ± 4	9 ± 6	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	32 ± 15	0 ± 0	4 ± 4
<i>Psychoda parthenogenetica</i> - Pupae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	22 ± 15	0 ± 0	103 ± 66	0 ± 0	0 ± 0
<i>Psychoda parthenogenetica</i> - Larvae	0 ± 0	4 ± 4	152 ± 76	4 ± 4	82 ± 29	30 ± 12	0 ± 0	144 ± 79	0 ± 0	0 ± 0
<i>Limnophyes minimus</i> - Adults	69 ± 30	48 ± 14	22 ± 13	52 ± 16	65 ± 23	17 ± 10	9 ± 9	63 ± 20	5 ± 5	13 ± 7
<i>Limnophyes minimus</i> - Pupae	13 ± 7	13 ± 7	16 ± 12	39 ± 12	95 ± 55	26 ± 15	0 ± 0	25 ± 10	0 ± 0	0 ± 0
<i>Limnophyes minimus</i> - Larvae	524 ± 124	1433 ± 499	704 ± 187	2936 ± 644	2126 ± 390	1800 ± 437	100 ± 28	5008 ± 1127	47 ± 34	543 ± 122
<i>Scaptomyza</i> sp. - Adults	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	24 ± 12	0 ± 0	0 ± 0
<i>Scaptomyza</i> sp. - Pupae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	5 ± 5	0 ± 0	0 ± 0
<i>Drosophilidae</i> sp. - Adults	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	5 ± 5	0 ± 0	0 ± 0
EGGS, COCOONS, SHELLS										
<i>Notodiscus hookeri</i> - egg?	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	4 ± 4	0 ± 0	0 ± 0	0 ± 0
<i>Notodiscus hookeri</i> - shell	9 ± 6	0 ± 0	11 ± 8	156 ± 36	95 ± 26	63 ± 18	972 ± 143	0 ± 0	0 ± 0	0 ± 0
<i>Deroceras caruanae</i> - egg	4 ± 4	22 ± 18	0 ± 0	9 ± 6	4 ± 4	381 ± 158	4 ± 4	5 ± 5	0 ± 0	0 ± 0
Earthworm egg - dark brown	0 ± 0	0 ± 0	11 ± 8	17 ± 14	17 ± 10	217 ± 75	37 ± 13	4854 ± 861	76 ± 23	215 ± 58
Earthworm egg - light	0 ± 0	0 ± 0	0 ± 0	9 ± 6	0 ± 0	134 ± 36	26 ± 10	228 ± 42	0 ± 0	34 ± 17
Enchytraeidae worm egg	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	11 ± 7	0 ± 0	27 ± 24	2 ± 2	24 ± 12
Spider cocoon - small (prob. <i>Erigone</i> sp.)	1529 ± 175	3283 ± 285	135 ± 41	680 ± 99	476 ± 67	930 ± 204	22 ± 18	130 ± 45	22 ± 11	5023 ± 725
Spider cocoon - big (prob. <i>Myro</i> sp.)	0 ± 0	0 ± 0	0 ± 0	0 ± 0	9 ± 6	48 ± 32	4 ± 4	0 ± 0	0 ± 0	0 ± 0

Table 9. Annual biomass (dried mg m⁻²) (± S.E.) of macro-invertebrates found in 10 major vegetation complexes at Marion Island, June 1996 - May 1997. Vegetation complexes : Bleph. = *Blepharidophyllum densifolium*, San. = *Sanionia uncinatus*, HI = High altitude mire, James. = *Jamesoniella colorata*, Mid = Mid altitude mire, Acaena = *Acaena magellanica*, Blechnum = *Blechnum penna-marina*, Cotula = *Cotula plumosa*, Crassula = *Crassula moschata*, Poa = *Poa cookii*.

Species	Mires					Non Mires				
	Bleph. n = 60	San. n = 60	HI n = 48	Jamesoniella n = 60	Mid n = 60	Acaena n = 60	Blechnum n = 60	Cotula n = 55	Crassula n = 55	Poa n = 60
INDIGENOUS										
Enchytraeidae worms	0 ± 0	0 ± 0	0 ± 0	0 ± 0	33 ± 24	7486 ± 902	0 ± 0	1759 ± 259	119 ± 20	55 ± 12
Earthworms	0 ± 0	25 ± 25	1689 ± 467	72 ± 43	220 ± 129	7894 ± 1745	1201 ± 268	30873 ± 3045	1640 ± 297	8957 ± 1810
<i>Erigone</i> sp.	102 ± 18	156 ± 17	8 ± 4	87 ± 14	26 ± 9	31 ± 9	2 ± 2	23 ± 7	2 ± 1	90 ± 18
<i>Myro</i> sp.	0 ± 0	10 ± 10	6 ± 6	6 ± 6	55 ± 37	150 ± 80	11 ± 7	0 ± 0	0 ± 0	0 ± 0
<i>Notodiscus hookeri</i>	51 ± 51	0 ± 0	32 ± 27	446 ± 224	530 ± 199	64 ± 64	2164 ± 409	0 ± 0	0 ± 0	0 ± 0
Weevil pupae	40 ± 31	45 ± 26	0 ± 0	74 ± 42	22 ± 18	51 ± 25	0 ± 0	0 ± 0	1 ± 1	0 ± 0
<i>Ectemnorhinus similis</i> - Adults	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	59 ± 31	0 ± 0	0 ± 0	14 ± 10	37 ± 26
<i>Ectemnorhinus similis</i> - Larvae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	200 ± 57	0 ± 0	66 ± 42	55 ± 23	41 ± 33
<i>Ectemnorhinus marioni</i> - Adults	70 ± 40	101 ± 47	0 ± 0	67 ± 36	28 ± 28	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Ectemnorhinus marioni</i> - Larvae	237 ± 77	344 ± 138	121 ± 40	325 ± 88	301 ± 86	0 ± 0	0 ± 0	0 ± 0	0 ± 0	4 ± 4
<i>Bothrometopus elongatus</i> - Adults	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	17 ± 17	0 ± 0	22 ± 22	17 ± 17	0 ± 0
<i>Meropathus chuni</i> - Adults	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	26 ± 20	6 ± 6	0 ± 0
<i>Meropathus chuni</i> - Larvae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	4 ± 3	0 ± 0
<i>Halmaeus atriceps</i> - Adults	13 ± 5	2 ± 2	0 ± 0	9 ± 5	3 ± 3	57 ± 13	0 ± 0	213 ± 56	4 ± 2	99 ± 26
<i>Halmaeus atriceps</i> - Pupae	1 ± 1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	7 ± 7	0 ± 0	1 ± 1
<i>Halmaeus atriceps</i> - Larvae	4 ± 2	1 ± 1	0 ± 0	11 ± 4	1 ± 1	47 ± 10	0 ± 0	172 ± 25	3 ± 1	82 ± 15
<i>Pringleophaga marioni</i> - Pupae	0 ± 0	207 ± 120	0 ± 0	126 ± 126	0 ± 0	85 ± 59	0 ± 0	17 ± 17	0 ± 0	0 ± 0
<i>Pringleophaga marioni</i> - Larvae	204 ± 119	443 ± 189	0 ± 0	0 ± 0	14 ± 14	230 ± 156	0 ± 0	564 ± 246	20 ± 14	8 ± 5
<i>Embryonopsis haiticella</i> - Pupae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Embryonopsis haiticella</i> - Larvae	0 ± 0	0 ± 0	8 ± 8	0 ± 0	34 ± 30	10 ± 10	0 ± 0	3 ± 2	0 ± 0	40 ± 15
NATURALISED ALIENS										
<i>Deroceras caruanae</i>	32 ± 32	1026 ± 361	0 ± 0	39 ± 36	0 ± 0	1904 ± 399	45 ± 45	3 ± 3	0 ± 0	0 ± 0
<i>Apterothrips apteris</i>	0 ± 0	1 ± 0	1 ± 0	1 ± 1	1 ± 0	0 ± 0	0 ± 0	2 ± 2	1 ± 1	0 ± 0
Aphididae	27 ± 9	36 ± 7	1 ± 1	15 ± 5	2 ± 1	69 ± 30	0 ± 0	474 ± 175	26 ± 15	176 ± 103
<i>Psychoda parthenogenetica</i> - Adults	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	3 ± 1	0 ± 0	0 ± 0
<i>Psychoda parthenogenetica</i> - Pupae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	3 ± 2	0 ± 0	17 ± 11	0 ± 0	0 ± 0
<i>Psychoda parthenogenetica</i> - Larvae	0 ± 0	0 ± 0	3 ± 2	0 ± 0	3 ± 1	2 ± 1	0 ± 0	16 ± 9	0 ± 0	0 ± 0
<i>Limnophyes minimus</i> - Adults	3 ± 1	2 ± 1	1 ± 0	2 ± 1	3 ± 1	1 ± 0	0 ± 0	4 ± 1	0 ± 0	1 ± 0
<i>Limnophyes minimus</i> - Pupae	1 ± 0	0 ± 0	1 ± 0	2 ± 1	4 ± 2	2 ± 1	0 ± 0	1 ± 1	0 ± 0	0 ± 0
<i>Limnophyes minimus</i> - Larvae	23 ± 6	55 ± 15	19 ± 4	102 ± 21	61 ± 11	55 ± 12	3 ± 1	193 ± 42	3 ± 3	25 ± 5
<i>Scaptomyza</i> sp. - Adults	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	6 ± 3	0 ± 0	0 ± 0
<i>Scaptomyza</i> sp. - Pupae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1 ± 1	0 ± 0	0 ± 0
<i>Drosophilidae</i> sp. - Adults	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	3 ± 3	0 ± 0	0 ± 0
EGGS, COCOONS, SHELLS										
<i>Notodiscus hookeri</i> - egg?	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Notodiscus hookeri</i> - shell	32 ± 25	0 ± 0	49 ± 35	464 ± 129	203 ± 58	213 ± 72	3174 ± 443	0 ± 0	0 ± 0	0 ± 0
<i>Deroceras caruanae</i> - egg	2 ± 2	11 ± 8	0 ± 0	4 ± 3	1 ± 1	175 ± 74	1 ± 1	1 ± 1	0 ± 0	0 ± 0
Earthworm egg - dark brown	0 ± 0	0 ± 0	12 ± 8	66 ± 49	7 ± 4	261 ± 111	33 ± 17	2300 ± 360	51 ± 20	160 ± 48
Earthworm egg - light	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	151 ± 44	39 ± 14	217 ± 42	10 ± 7	40 ± 20
Enchytraeidae worm egg	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1 ± 1	0 ± 0	64 ± 64	0 ± 0	1 ± 1
Spider cocoon - small (prob. <i>Erigone</i> sp.)	117 ± 13	243 ± 24	10 ± 4	0 ± 0	30 ± 5	79 ± 18	1 ± 1	38 ± 20	1 ± 1	525 ± 75
Spider cocoon - big (prob. <i>Myro</i> sp.)	0 ± 0	0 ± 0	0 ± 0	61 ± 10	24 ± 17	55 ± 40	16 ± 16	0 ± 0	0 ± 0	23 ± 23

Table 10. Percentage biomass of every invertebrate species as well as the indigenous and alien components within and across each of the 10 vegetation complexes sampled at Marion Island during 1996/97.

<i>Species</i>	Mires					Non-mires					TOT
	Bleph.	Sanionia	HI	James.	Mid	Acaena	Blechnu m	Cotula	Crassula	Poa	
Indigenous											
Enchytraeidae worms	0.0	0.0	0.0	0.0	2.4	40.6	0.0	5.1	6.2	0.6	12.5
Earthworms	0.0	1.0	89.4	5.2	16.4	42.9	35.0	89.6	85.7	93.2	69.4
<i>Erigone</i> sp.	12.6	6.3	0.4	6.3	2.0	0.2	0.1	0.1	0.1	0.9	0.7
<i>Myro</i> sp.	0.0	0.4	0.3	0.4	4.1	0.8	0.3	0.0	0.0	0.0	0.3
<i>Notodiscus hookeri</i>	6.4	0.0	1.7	32.3	39.5	0.3	63.1	0.0	0.0	0.0	4.3
Weevil pupae	5.0	1.9	0.0	5.3	1.6	0.3	0.0	0.0	0.0	0.0	0.3
<i>Ectemnorhinus similis</i>	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.2	3.6	0.8	0.6
<i>Ectemnorhinus marioni</i>	38.1	18.1	6.4	28.3	24.5	0.0	0.0	0.0	0.0	0.0	2.1
<i>Bothrometopus elongatus</i>	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.9	0.0	0.1
<i>Meropathus chuni</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.5	0.0	0.1
<i>Halmaeus atriceps</i>	2.1	0.1	0.0	1.5	0.3	0.6	0.0	1.1	0.4	1.9	1.0
<i>Pringleophaga marioni</i>	25.4	26.5	0.0	9.1	1.1	1.7	0.0	1.7	1.1	0.1	2.5
<i>Embryonopsis halticella</i>	0.0	0.0	0.4	0.0	2.6	0.1	0.0	0.0	0.0	0.4	0.1
TOTAL INDIGENOUS	89.5	54.3	98.7	88.4	94.6	88.9	98.6	97.9	98.4	97.9	94.1
Naturalised aliens											
<i>Deroceras caruanae</i>	3.9	41.8	0.0	2.8	0.0	10.3	1.3	0.0	0.0	0.0	4.0
<i>Apterothrips apteris</i>	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aphididae	3.3	1.5	0.0	1.1	0.1	0.4	0.0	1.4	1.3	1.8	1.1
<i>Psychoda parthenogenetica</i>	0.0	0.0	0.2	0.0	0.2	0.0	0.0	0.1	0.0	0.0	0.1
<i>Limnophyes minimus</i>	3.2	2.3	1.1	7.6	5.0	0.3	0.1	0.6	0.2	0.3	0.7
<i>Scaptomyza</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Drosophilidae</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TOTAL ALIEN	10.5	45.7	1.3	11.6	5.4	11.1	1.4	2.1	1.6	2.1	5.9

Table 11. Percentage abundance of every invertebrate species as well as the indigenous and alien components within and across each of the 10 vegetation complexes sampled at Marion Island during 1996/97.

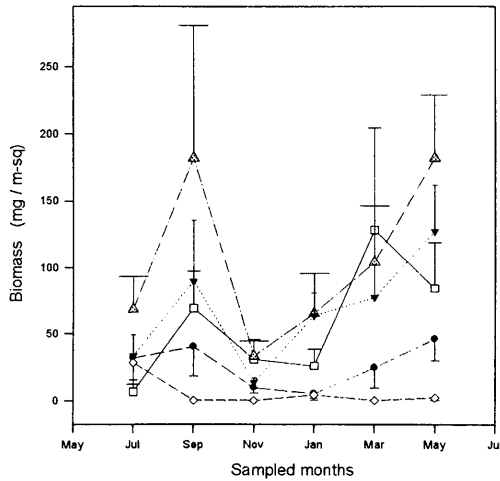
	Mires					Non-mires					
<i>Species</i>	Bleph.	Sanionia	HI	James.	Mid	Acaena	Blechnu m	Cotula	Crassula	Poa	TOT
Indigenous											
Enchytraeidae worms	0.2	0.0	0.8	0.0	7.1	86.7	0.7	62.6	70.9	12.0	57.6
Earthworms	0.0	0.1	9.3	0.4	1.0	1.7	24.1	9.6	12.6	14.2	6.1
<i>Erigone</i> sp.	37.6	37.7	4.9	14.2	5.1	0.6	1.7	0.3	0.3	6.0	3.9
<i>Myro</i> sp.	1.6	0.2	0.4	0.3	0.5	0.1	2.7	0.0	0.0	0.0	0.1
<i>Notodiscus hookeri</i>	0.2	0.0	0.8	1.8	4.3	0.0	50.4	0.0	0.0	0.0	0.5
Weevil pupae	0.4	0.3	0.0	0.4	0.3	0.0	0.0	0.0	0.0	0.0	0.1
<i>Ectemnorhinus similis</i>	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	1.3	0.2	0.2
<i>Ectemnorhinus marioni</i>	4.5	5.2	8.5	6.6	7.4	0.0	0.0	0.0	0.0	0.0	0.9
<i>Bothrometopus elongatus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
<i>Meropathus chuni</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	1.1	0.0	0.1
<i>Halmaeus atriceps</i>	3.6	0.4	0.0	2.3	0.8	1.3	2.7	3.9	0.9	12.3	3.1
<i>Pringleophaga marioni</i>	2.7	2.1	0.0	0.1	0.3	0.1	0.0	0.2	0.2	0.1	0.3
<i>Embryonopsis halticella</i>	0.0	0.0	1.2	0.0	0.9	0.0	0.0	0.0	0.0	1.4	0.2
TOTAL INDIGENOUS	50.7	46.0	26.0	26.0	27.7	91.0	82.1	76.9	87.5	46.3	74.3
Naturalised aliens											
<i>Deroceras caruanae</i>	0.2	1.8	0.0	0.2	0.0	0.6	0.0	0.0	0.0	0.0	0.3
<i>Apterothrips apteris</i>	0.0	1.0	5.3	1.1	1.8	0.0	0.0	0.7	1.0	0.0	0.5
Aphididae	23.8	16.2	1.6	6.5	0.8	3.6	1.3	9.3	10.5	47.4	10.3
<i>Psychoda parthenogenetica</i>	0.2	0.3	11.4	0.1	2.4	0.1	0.0	0.7	0.0	0.0	0.5
<i>Limnophyes minimus</i>	25.1	34.7	55.7	66.1	67.3	4.7	16.6	12.3	1.0	6.3	14.1
<i>Scaptomyza</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
<i>Drosophilidae</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TOTAL ALIEN	49.3	54.0	74.0	74.0	72.3	9.0	17.9	23.1	12.5	53.7	25.7

2.3.1.2 Seasonality

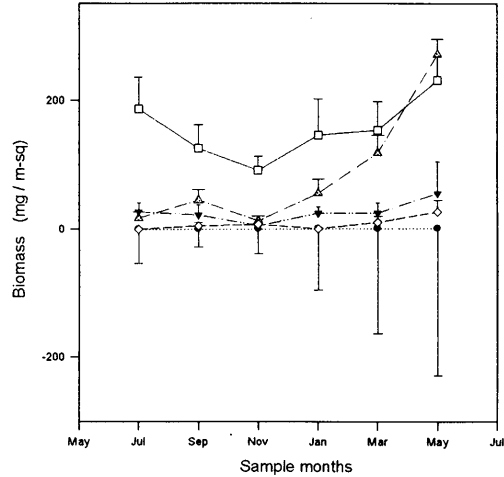
In general, the invertebrates exhibited a broad variety of seasonal patterns that were inconsistent between species and between habitats within a given species. Densities and biomasses tended to show peaks in the austral spring (August/September) and autumn (March/April), and minima occurred during winter (June/July), and in some cases during summer (between October to February). Where such patterns were evident, they were most pronounced in the mire habitats. In this regard, the midge *L. minimus* showed the most noticeable and consistent pattern throughout all the mire habitats, followed by the small spider *Erigone* sp. (Figs 4A & B). Both indigenous lepidopterans, *P. marioni* and *E. halticella*, showed similar patterns in *Poa cookii* grassland, although the density, and consequently biomass, of *E. halticella* was far higher than that of *P. marioni* (Figs 4C & D). In other vegetation complexes *P. marioni* did not exhibit this pattern, peaking at different times of the year, with summer and early winter peaks in *Cotula plumosa* (the vegetation complex in which it reached highest densities) (Fig. 4E) and most of the mires. The larvae of *E. marioni* showed a similar summer and early winter peak in *Blepharidophyllum* mires (Fig. 4F), but with earlier summer and spring peaks in the lowland mires *Jamesoniella colorata* and *Sanionia uncinatus*. However, the larvae of the other weevil species, *E. similis*, showed a tendency to peak in winter and summer when it occurred in the *Crassula moschata* and *Poa cookii* community complexes, and a clear spring and autumn peak when it occurred in *Acaena* drainage lines (the habitat in which it reached the highest density).

Earthworm seasonality differed between vegetation complexes. In *Acaena*, earthworm biomass peaked in spring (August) and then declined until it reached its lowest level in February, while in *Poa cookii* tussock grassland the opposite trend was evident, with lowest biomass in spring and a peak in summer. In the high- and mid-altitude mire habitats the trend shifted to a peaks in mid summer (November) and zeniths in early autumn (March), while the opposite was evident in the low altitude *Jamesoniella* mire.

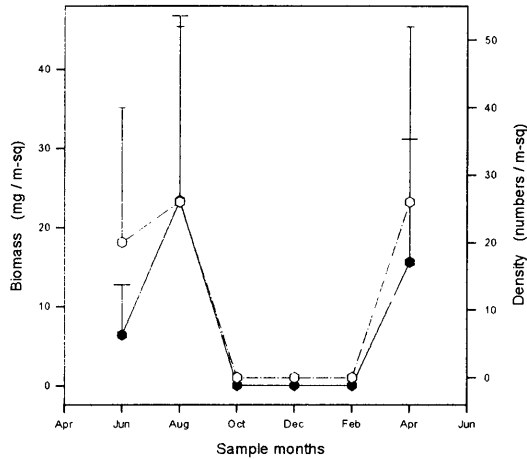
A. Seasonality of *Limnophyes minimus* in five mires habitats



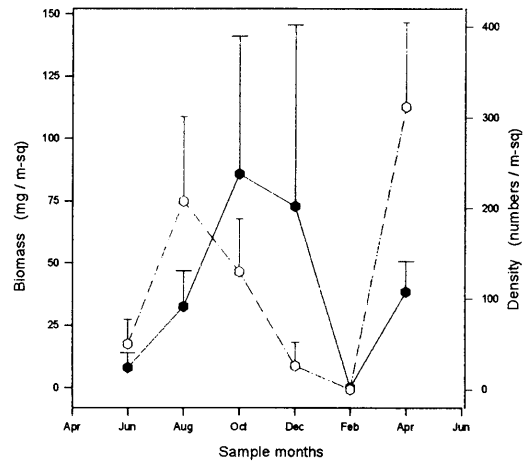
B. Seasonality of a small spider (*Erigone* sp.) in five mire habitats



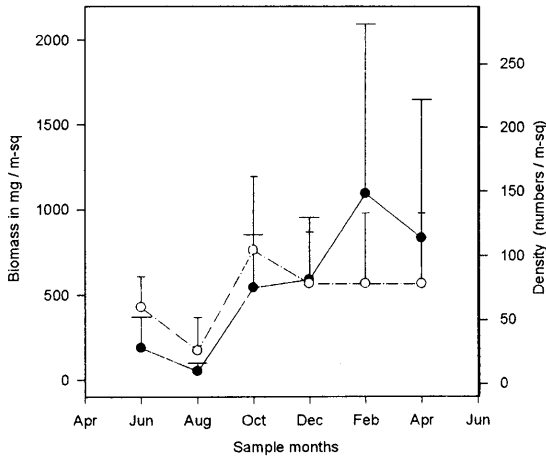
C. *Pringleophaga marioni* in *Poa cookii*



D. *Embrionopsis halticella* larvae in *Poa cookii*



E. *Pringleophaga marioni* in *Cotula plumosa*



F. *Ectemnorhinus marioni* larvae in *Blepharidophyllum* mire

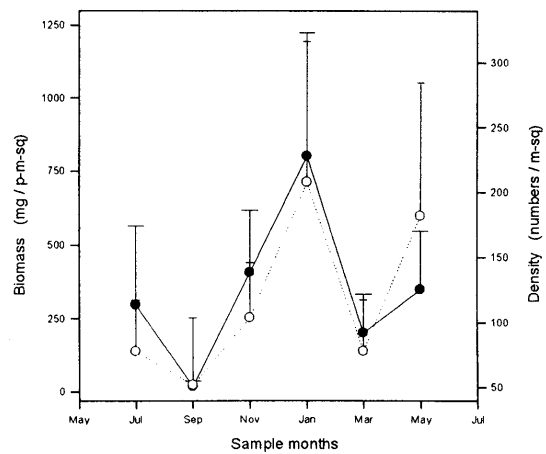


Fig. 4. Seasonality patterns of selected invertebrates. ● = *Blepharidophyllum* mire; □ = *Sanionia* mire; Δ = *Jamesoniella* mire; ▼ = Mid altitude mire; ◇ = Hi altitude mire; Graphs C., D., E. & F., solid symbols = biomass, clear symbols = density.

2.3.1.3 Habitat specificity

The cluster analysis, based on the densities of the indigenous invertebrates (Fig. 5) clearly illustrates habitat specificity in some species to either the mire habitats or the non-mire habitats, because a clear separation of these major habitat types was produced (see also Fig. 6). Within these major habitat groupings the distinction between the habitats appeared to be less well defined, suggesting reduced habitat specificity in the macro-invertebrates, although the *Blechnum* complex and high altitude mire appeared quite distinct (Figs. 5 & 6). Nonetheless, the one way analyses of similarity (ANOSIM) (Table 12) indicated that there were significant differences between the macro-invertebrate communities in most habitats, with the exception of the *Blepharidophyllum* and *Sanionia* mires, and the high and mid altitude mires, respectively. It is noteworthy that the density and biomass data revealed remarkably similar patterns (Fig. 6 and Table 12).

The indicator value analyses showed that six of the indigenous invertebrates species reached high and significant indicator values, indicating specificity to a particular group of habitats (Fig. 5). Indeed, it is clear that with the exception of *Notodiscus hookeri*, which appeared to favour *Blechnum penna-marina* fernbrake, none of the other species were specific to a single habitat. Rather, they appeared to prefer either mire habitats (with the exception of the high altitude mire) or non-mire habitats.

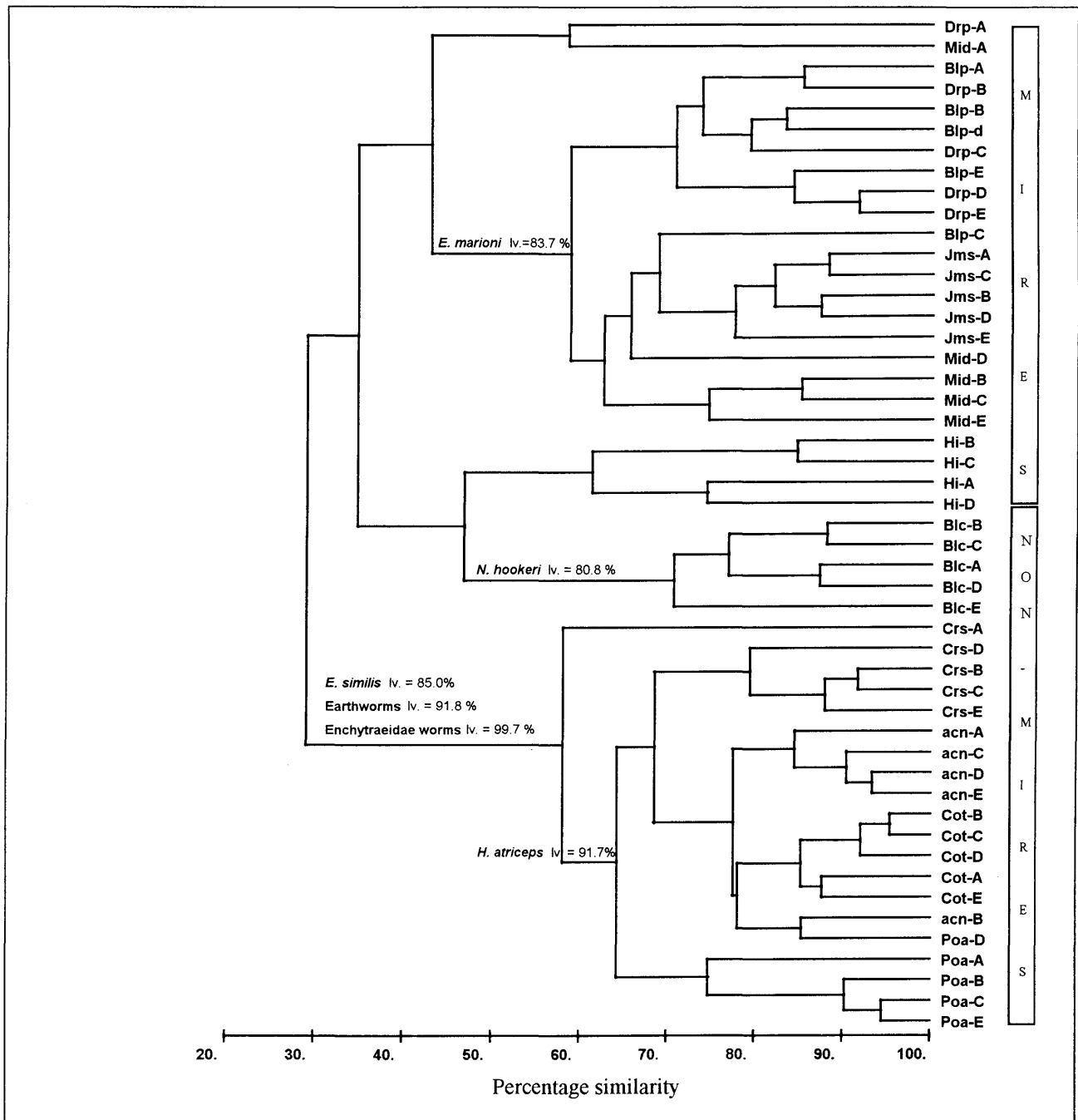
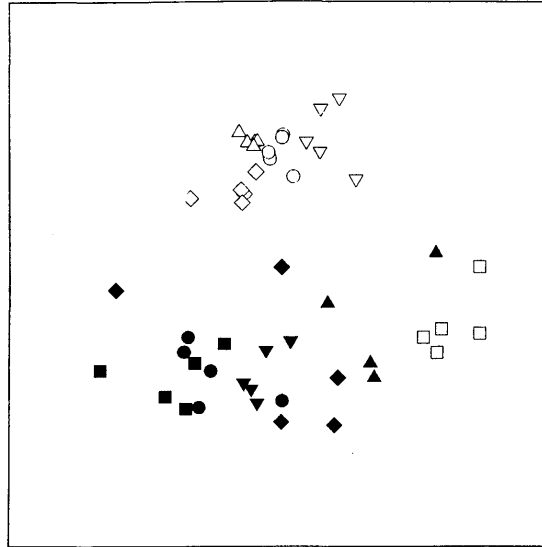


Fig. 5. Dendrogram of Bray-Curtis percentage similarities between the 49 quadrats in the 10 sampling localities, based on the densities of indigenous invertebrates. Based on the Indicator Value Analyses (Dufrêne & Legendre 1997), invertebrates that showed a significant ($p < 0.05$) habitat preference are indicated on the relevant branches of the dendrogram with their respective Indvals (Iv.). A,B,C,D,E represent the quadrats in each vegetation complex : acn = *Acaena magellanica*; Blc = *Blechnum penna-marina*; Cot = *Cotula plumosa*; Crs = *Crassula moschata*; Poa = *Poa cookii*; Blp = *Blepharidophyllum densifolium*; Drp = *Sanionia uncinatus*; Jms = *Jamesoniella colorata*; Mid = Mid-altitude mire; Hi = High-altitude mire.

a)



b)

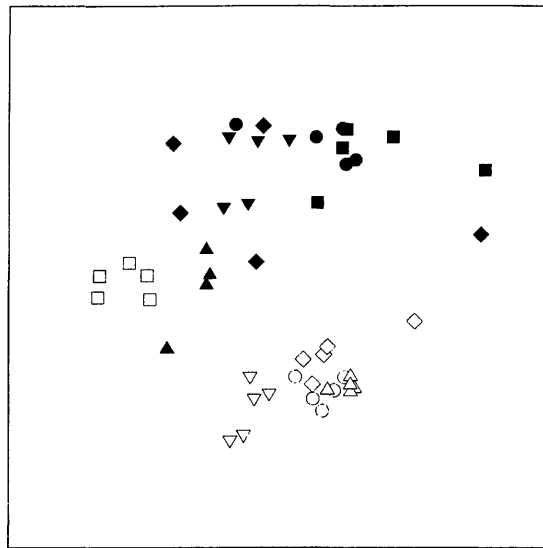


Fig. 6. MDS ordination of the ten vegetation complexes based on abundance measures of the indigenous invertebrates. **a)** = Densities (numbers m^{-2}), STRESS = 0.09; **b)** = Biomass (mg m^{-2}), STRESS = 0.13. Black symbols = mire habitats (● = *Blepharidophyllum densifolium*; ■ = *Sanionia uncinatus*; ▲ = *Jamesoniella colorata*; ▼ = Mid altitude mire; ◆ = High altitude mire). Clear symbols = non-mire habitats (O = *Acaena magellanica*, □ = *Blechnum penna-marina*, Δ = *Cotula plumosa*, ∇ = *Crassula moschata*, ◇ = *Poa cookii*).

Table 12. ONE-WAY ANOSIM (pairwise test) showing significant ($p < 0.05$) differences between vegetation complexes based on the densities (bold figures) and biomass (non-bold figures) of the macro-invertebrates in the 10 vegetation complexes of the lowland vegetated biotope. BLEP. = *Blepharidophyllum densifolium*; SAN.. = *Sanionia uncinatus*; JAMES = *Jamesoniella colorata*; MID = Mid altitude mire; HI = High altitude mire; ACN = *Acaena magellanica*, BLEC = *Blechnum penna-marina*, COT = *Cotula plumosa*, CRAS = *Crassula moschata*, POA = *Poa cookii*).

	BLEP	SAN	HI	JAMES	MID	ACN	BLEC	COT	CRAS	POA
BLEP		N.S.	0.008	N.S.	0.040	0.008	0.008	0.008	0.008	0.008
SAN	N.S.		0.016	0.016	0.024	0.008	0.008	0.008	0.008	0.008
HI	0.016	0.008		0.008	0.024	0.008	0.008	0.008	0.008	0.008
JAMS	0.024	0.008	0.008		N.S.	0.008	0.008	0.008	0.008	0.008
MID	0.048	0.016	N.S.	0.024		0.008	0.008	0.008	0.008	0.008
ACN	0.008	0.008	0.008	0.008	0.008		0.008	0.008	0.008	0.008
BLEC	0.008	0.008	0.008	0.008	0.008	0.008		0.008	0.008	0.008
COT	0.008	0.008	0.008	0.008	0.008	0.008	0.008		0.008	0.008
CRAS	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008		0.008
POA	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	

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Densities and Biomasses

Macro-invertebrate densities and biomasses are provided in Tables 13 and 14 respectively. In both tables, the annual means and standard errors ($\pm$ S.E.) are given for each species group within the 19 vegetation complexes sampled. Relative abundances obtained from these data are presented in Tables 15 & 16. Within the six groups listed (as identified by Burger 1978), a total of 10 species are represented, of which only one is a naturalised alien species; the slug *Deroceras caruanae*. Due to a number of discrepancies between the data analysis of 1976 (where a few addition errors led to some over and under estimates of total numbers and biomasses in certain vegetation communities) and the re-analysis undertaken here, the results of the re-worked data differ slightly from those presented by Burger (1978) (see Tables 15 & 16). The differences (not more than 1.9 % for a group within the total invertebrate assemblage) are fortunately small and can be considered negligible. Thus the most abundant species were by far the Earthworms (as stated by Burger 1978), which contributed 84.9 % to invertebrate biomass and 66.8 % to invertebrate density. The Lepidoptera ranked second in their contribution to biomass, although their numbers were lower than those of weevils, that ranked second in terms of density. Slugs ranked third in terms of biomass (2.3 %), but contributed less to density than did the spiders.

Table 13. Annual mean densities (numbers m⁻²) ($\pm$ S.E.) of macro-invertebrates found in 19 vegetation complexes sampled by A.

Burger 1976/77. Data from 60 cores per vegetation complex. * = vegetation complex compatible with those sampled in 1996/97. Numbers 1-19 given to the vegetation complexes correspond to those allocated by A. Burger 1978. A = Adults, P = Pupae, L = Larvae.

Vegetation complex	Earthworm		Earthworm		Lepidoptera		Lepidoptera		Weevil		Weevil		Spider		Snail		Slug	
			cocoon		Larvae		A&P		L&P		A							
1. <i>Juncus scheucherioides</i>	975 $\pm$	106	209 $\pm$	55	20 $\pm$	8	0 $\pm$	0	20 $\pm$	9	7 $\pm$	5	0 $\pm$	0	0 $\pm$	0	0 $\pm$	0
* 2. <i>Sanionia uncinatus</i>	1310 $\pm$	187	275 $\pm$	69	136 $\pm$	25	0 $\pm$	0	53 $\pm$	12	3 $\pm$	3	43 $\pm$	15	0 $\pm$	0	30 $\pm$	12
* 3. <i>Blepharidophyllum densifolium</i>	10 $\pm$	6	0 $\pm$	0	20 $\pm$	8	0 $\pm$	0	109 $\pm$	22	33 $\pm$	10	20 $\pm$	8	0 $\pm$	0	0 $\pm$	0
4. <i>Clasmatocolea humilis</i>	836 $\pm$	124	199 $\pm$	46	33 $\pm$	11	0 $\pm$	0	315 $\pm$	39	70 $\pm$	23	10 $\pm$	6	0 $\pm$	0	0 $\pm$	0
* 5. <i>Jamesoniella colorata</i>	83 $\pm$	21	27 $\pm$	14	10 $\pm$	6	0 $\pm$	0	80 $\pm$	20	20 $\pm$	8	43 $\pm$	12	0 $\pm$	0	0 $\pm$	0
6. Mixed species mire	1389 $\pm$	137	328 $\pm$	58	56 $\pm$	14	3 $\pm$	3	76 $\pm$	17	17 $\pm$	9	23 $\pm$	10	33 $\pm$	14	0 $\pm$	0
7. Degenerated bog	186 $\pm$	39	46 $\pm$	29	13 $\pm$	6	0 $\pm$	0	56 $\pm$	18	10 $\pm$	6	3 $\pm$	3	0 $\pm$	0	0 $\pm$	0
8. <i>Uncinia compacta</i> (ex <i>U. dikei</i>)	1250 $\pm$	107	249 $\pm$	46	43 $\pm$	13	0 $\pm$	0	106 $\pm$	28	23 $\pm$	8	60 $\pm$	17	146 $\pm$	41	0 $\pm$	0
* 9. <i>Blechnum penna-marina</i>	189 $\pm$	25	70 $\pm$	33	3 $\pm$	3	0 $\pm$	0	17 $\pm$	10	10 $\pm$	7	33 $\pm$	12	13 $\pm$	9	13 $\pm$	8
* 10. <i>Acaena magellanica</i>	660 $\pm$	76	149 $\pm$	44	7 $\pm$	7	0 $\pm$	0	109 $\pm$	19	30 $\pm$	10	30 $\pm$	9	3 $\pm$	3	149 $\pm$	25
11. <i>Agrostis bergiana</i>	766 $\pm$	113	116 $\pm$	48	23 $\pm$	11	0 $\pm$	0	13 $\pm$	6	0 $\pm$	0	23 $\pm$	14	23 $\pm$	10	272 $\pm$	41
* 12. <i>Crassula moschata</i> (ex <i>Tillaea moschata</i>)	428 $\pm$	41	10 $\pm$	7	80 $\pm$	17	0 $\pm$	0	109 $\pm$	18	27 $\pm$	15	3 $\pm$	3	0 $\pm$	0	3 $\pm$	3
13. <i>Cotula plumosa</i> - <i>Crassula moschata</i>	1104 $\pm$	85	235 $\pm$	49	40 $\pm$	10	7 $\pm$	5	53 $\pm$	15	13 $\pm$	6	80 $\pm$	25	0 $\pm$	0	0 $\pm$	0
14. <i>Azorella selago</i>	892 $\pm$	127	288 $\pm$	62	90 $\pm$	18	3 $\pm$	3	116 $\pm$	25	27 $\pm$	9	23 $\pm$	10	0 $\pm$	0	0 $\pm$	0
15. <i>Callitriche antarctica</i>	2924 $\pm$	427	1840 $\pm$	368	60 $\pm$	18	3 $\pm$	3	126 $\pm$	57	30 $\pm$	13	17 $\pm$	10	0 $\pm$	0	0 $\pm$	0
* 16. <i>Poa cookii</i>	2036 $\pm$	147	239 $\pm$	46	46 $\pm$	14	0 $\pm$	0	96 $\pm$	21	17 $\pm$	7	119 $\pm$	26	99 $\pm$	49	3 $\pm$	3
17. <i>Clasmatocolea vermicularis</i>	1950 $\pm$	230	365 $\pm$	59	129 $\pm$	23	0 $\pm$	0	196 $\pm$	36	30 $\pm$	12	13 $\pm$	8	0 $\pm$	0	0 $\pm$	0
* 18. <i>Cotula plumosa</i>	3896 $\pm$	523	1273 $\pm$	270	46 $\pm$	13	0 $\pm$	0	166 $\pm$	27	63 $\pm$	17	73 $\pm$	18	0 $\pm$	0	7 $\pm$	5
19. <i>Azorella selago</i> - <i>Andreaea</i> spp.	564 $\pm$	75	60 $\pm$	25	33 $\pm$	10	0 $\pm$	0	86 $\pm$	20	30 $\pm$	13	7 $\pm$	5	17 $\pm$	7	0 $\pm$	0

Table 14. Annual mean biomass (mg m⁻²) (± S.E.) of macro-invertebrates found in 19 vegetation complexes sampled by A. Burger 1976/77. Data from 60 cores per vegetation complex. * = vegetation complex compatible with those sampled in 1996/97. Numbers 1-19 given to the vegetation complexes correspond to those allocated by A. Burger 1978. A = Adults, P = Pupae, L = Larvae.

Vegetation complex	Earthworm		Lepidoptera		Weevil		Spider		Snail		Slug	
		cocoon	Larvae	A&P	L&P	A						
1. <i>Juncus scheucherioides</i>	9128 ± 1141	209 ± 55	302 ± 146	0 ± 0	60 ± 28	50 ± 36	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
* 2. <i>Sanionia uncinatus</i>	15053 ± 2237	282 ± 71	2616 ± 640	0 ± 0	245 ± 62	13 ± 13	166 ± 59	0 ± 0	0 ± 0	391 ± 166	0 ± 0	0 ± 0
* 3. <i>Blepharidophyllum densifolium</i>	103 ± 68	0 ± 0	143 ± 64	0 ± 0	302 ± 69	143 ± 44	50 ± 26	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
4. <i>Clasmatocolea humilis</i>	9778 ± 1532	199 ± 46	272 ± 107	0 ± 0	1296 ± 162	385 ± 130	33 ± 20	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
* 5. <i>Jamesoniella colorata</i>	855 ± 250	27 ± 14	99 ± 62	0 ± 0	262 ± 71	83 ± 34	149 ± 60	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
6. Mixed species mire	15726 ± 1743	328 ± 58	527 ± 152	83 ± 83	282 ± 70	83 ± 44	76 ± 34	292 ± 120	0 ± 0	0 ± 0	0 ± 0	0 ± 0
7. Degenerated bog	2404 ± 591	46 ± 29	126 ± 72	0 ± 0	182 ± 58	43 ± 25	7 ± 7	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
8. <i>Uncinia compacta</i> (ex <i>U. dikei</i>)	13850 ± 1289	249 ± 46	487 ± 162	0 ± 0	395 ± 116	103 ± 38	229 ± 73	1273 ± 371	428 ± 282	0 ± 0	0 ± 0	0 ± 0
* 9. <i>Blechnum penna-marina</i>	2132 ± 318	70 ± 33	43 ± 43	0 ± 0	80 ± 52	53 ± 38	60 ± 25	153 ± 110	259 ± 169	0 ± 0	0 ± 0	0 ± 0
* 10. <i>Acaena magellanica</i>	7477 ± 1013	149 ± 44	133 ± 133	0 ± 0	481 ± 92	159 ± 56	123 ± 44	66 ± 66	1966 ± 366	0 ± 0	0 ± 0	0 ± 0
11. <i>Agrostis bergiana</i>	7033 ± 1023	116 ± 48	504 ± 253	0 ± 0	80 ± 45	0 ± 0	99 ± 51	322 ± 134	2971 ± 419	0 ± 0	0 ± 0	0 ± 0
* 12. <i>Crassula moschata</i> (ex <i>Tillaea moschata</i>)	3040 ± 336	10 ± 7	683 ± 189	0 ± 0	305 ± 55	99 ± 55	3 ± 3	0 ± 0	40 ± 40	0 ± 0	0 ± 0	0 ± 0
13. <i>Cotula plumosa</i> - <i>Crassula moschata</i>	8495 ± 762	235 ± 49	438 ± 144	192 ± 140	172 ± 52	66 ± 34	222 ± 81	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
14. <i>Azorella selago</i>	7964 ± 1041	288 ± 62	879 ± 208	66 ± 66	342 ± 79	126 ± 44	86 ± 39	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
15. <i>Callitriche antarctica</i>	34374 ± 4438	1857 ± 240	1011 ± 131	10 ± 1	580 ± 75	179 ± 23	56 ± 7	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
* 16. <i>Poa cookii</i>	21234 ± 1726	239 ± 46	802 ± 305	0 ± 0	375 ± 83	86 ± 37	405 ± 86	1154 ± 558	43 ± 43	0 ± 0	0 ± 0	0 ± 0
17. <i>Clasmatocolea vermicularis</i>	17295 ± 2271	365 ± 59	1950 ± 453	0 ± 0	779 ± 166	146 ± 59	43 ± 25	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
* 18. <i>Cotula plumosa</i>	42911 ± 7201	1330 ± 299	965 ± 350	0 ± 0	749 ± 115	345 ± 95	288 ± 81	0 ± 0	90 ± 63	0 ± 0	0 ± 0	0 ± 0
19. <i>Azorella selago</i> - <i>Andreaea</i> spp.	6081 ± 844	60 ± 25	176 ± 54	0 ± 0	414 ± 113	219 ± 105	13 ± 10	239 ± 103	0 ± 0	0 ± 0	0 ± 0	0 ± 0

Table 15. Percentage of total invertebrate biomass in each of the 19 vegetation complexes sampled by A. Burger 1976/77, and re-analysed in this thesis.
A = Adults, P = Pupae, L = Larvae, * = vegetation complex compatible with those sampled in 1996/97, # = Values from A. Burger 1978.

Vegetation complexes	INDIGENOUS SPECIES								ALIEN SPECIES
	Earthworm	EW cocoon	Lepidoptera L	Lepi-A&P	Weevil-L&P	Weevil-A	Spider	Snail	Slug
1. <i>Juncus scheucherioides</i>	93.6	2.1	3.1	0.0	0.6	0.5	0.0	0.0	0.0
* 2. <i>Sanionia uncinatus</i>	80.2	1.5	13.9	0.0	1.3	0.1	0.9	0.0	2.1
* 3. <i>Blepharidophyllum densifolium</i>	13.9	0.0	19.3	0.0	40.8	19.3	6.7	0.0	0.0
4. <i>Clasmatocolea humilis</i>	81.7	1.7	2.3	0.0	10.8	3.2	0.3	0.0	0.0
* 5. <i>Jamesoniella colorata</i>	58.0	1.8	6.7	0.0	17.8	5.6	10.1	0.0	0.0
6. Mixed species mire	90.4	1.9	3.0	0.5	1.6	0.5	0.4	1.7	0.0
7. Degenerated bog	85.6	1.7	4.5	0.0	6.5	1.5	0.2	0.0	0.0
8. <i>Uncinia compacta</i> (ex <i>U. dikei</i>)	81.4	1.5	2.9	0.0	2.3	0.6	1.3	7.5	2.5
* 9. <i>Blechnum penna-marina</i>	74.9	2.4	1.5	0.0	2.8	1.9	2.1	5.4	9.1
* 10. <i>Acaena magellanica</i>	70.8	1.4	1.3	0.0	4.6	1.5	1.2	0.6	18.6
11. <i>Agrostis bergiana</i>	63.2	1.0	4.5	0.0	0.7	0.0	0.9	2.9	26.7
* 12. <i>Crassula moschata</i> (ex <i>Tillaea moschata</i>)	72.7	0.2	16.3	0.0	7.3	2.4	0.1	0.0	1.0
13. <i>Cotula plumosa</i> - <i>Crassula moschata</i>	86.5	2.4	4.5	2.0	1.8	0.7	2.3	0.0	0.0
14. <i>Azorella selago</i>	81.7	3.0	9.0	0.7	3.5	1.3	0.9	0.0	0.0
15. <i>Callitriche antarctica</i>	90.3	4.9	2.7	0.0	1.5	0.5	0.1	0.0	0.0
* 16. <i>Poa cookii</i>	87.2	1.0	3.3	0.0	1.5	0.4	1.7	4.7	0.2
17. <i>Clasmatocolea vermicularis</i>	84.0	1.8	9.5	0.0	3.8	0.7	0.2	0.0	0.0
* 18. <i>Cotula plumosa</i>	91.9	2.8	2.1	0.0	1.6	0.7	0.6	0.0	0.2
19. <i>Azorella selago</i> - <i>Andreaea</i> spp.	84.4	0.8	2.4	0.0	5.8	3.0	0.2	3.3	0.0
% of total biomass	84.9	2.3	4.6	0.1	2.8	0.9	0.8	1.3	2.3
# % of total biomass	86.8	2.2	3.7	0.1	2.5	0.7	0.8	1.9	1.3

Table 16. Percentage of total invertebrate numbers in each of the 19 vegetation complexes as sampled by A. Burger 1976/77, and re-analysed in this thesis. A = Adults, P = Pupae, L = Larvae, * = vegetation complex compatible with those sampled in 1996/97, # = Values from A. Burger 1978.

Vegetation complexes	INDIGENOUS SPECIES								ALIEN SPECIES
	Earthworm	EW cocoon	Lepidoptera L	Lepi-A&P	Weevil-L&P	Weevil-A	Spiders	Snail	Slug
1. <i>Juncus scheucherioides</i>	79.2	17.0	1.6	0.0	1.6	0.5	0.0	0.0	0.0
* 2. <i>Sanionia uncinatus</i>	70.8	14.9	7.3	0.0	2.9	0.2	2.3	0.0	1.6
* 3. <i>Blepharidophyllum densifolium</i>	5.2	0.0	10.3	0.0	56.9	17.2	10.3	0.0	0.0
4. <i>Clasmatocolea humilis</i>	57.1	13.6	2.3	0.0	21.5	4.8	0.7	0.0	0.0
* 5. <i>Jamesoniella colorata</i>	31.6	10.1	3.8	0.0	30.4	7.6	16.5	0.0	0.0
6. Mixed species mire	72.1	17.0	2.9	0.2	4.0	0.9	1.2	1.7	0.0
7. Degenerated bog	58.9	14.7	4.2	0.0	17.9	3.2	1.1	0.0	0.0
8. <i>Uncinia Compacta</i> (ex <i>U. dikei</i>)	66.6	13.3	2.3	0.0	5.7	1.2	3.2	7.8	0.0
* 9. <i>Blechnum penna-marina</i>	54.3	20.0	1.0	0.0	4.8	2.9	9.5	3.8	3.8
* 10. <i>Acaena magellanica</i>	58.0	13.1	0.6	0.0	9.6	2.6	2.6	0.3	13.1
11. <i>Agrostis bergiana</i>	61.9	9.4	1.9	0.0	1.1	0.0	1.9	1.9	22.0
* 12. <i>Crassula moschata</i> (ex <i>Tillaea moschata</i>)	64.8	1.5	12.1	0.0	16.6	4.0	0.5	0.0	0.5
13. <i>Cotula plumosa</i> - <i>Crassula moschata</i>	72.1	15.4	2.6	0.4	3.5	0.9	5.2	0.0	0.0
14. <i>Azorella selago</i>	62.0	20.0	6.2	0.2	8.1	1.8	1.6	0.0	0.0
15. <i>Callitriche antarctica</i>	58.5	36.8	1.2	0.1	2.5	0.6	0.3	0.0	0.0
* 16. <i>Poa cookii</i>	76.7	9.0	1.7	0.0	3.6	0.6	4.5	3.7	0.1
17. <i>Clasmatocolea vermicularis</i>	72.7	13.6	4.8	0.0	7.3	1.1	0.5	0.0	0.0
* 18. <i>Cotula plumosa</i>	70.5	23.0	0.8	0.0	3.0	1.1	1.3	0.0	0.1
19. <i>Azorella selago</i> - <i>Andreaea</i> spp.	70.8	7.5	4.2	0.0	10.8	3.8	0.8	2.1	0.0
% of total numbers	66.8	18.6	2.8	0.1	5.9	1.4	1.9	1.0	1.5
# % of total numbers	68.4	18.0	2.3	0.1	5.4	1.3	2.1	1.7	0.9

2.3.3 Comparisons

1976 / 77 versus 1996 / 97

The 1976/77 and 1996/97 studies each sampled at least eight vegetation types that were mutually comparable (Table 17), and consequently differences in the densities and biomasses of the species occurring in these habitats could be statistically assessed. Significant differences between the two periods were found in the densities and biomasses of all the invertebrates, with the exception of the slugs (Table 18, see also Figs. 7A & B). Macro-invertebrate densities showed both a significant increase and a significant decline in 1996/97 compared to the 1976/77 study, depending on the species and habitat examined. However, in terms of biomass, all the species, with the exception of snails and, in one habitat weevil larvae and pupae, showed significant declines. Because of the difference in sampling thoroughness between the two studies (see discussion 2.4.3), only the biomass data are analysed further here. Thus, Lepidoptera larvae (*P. marioni* and *E. halticella*) showed significant declines in both *Crassula moschata* saltspray vegetation (97%) and *Sanionia uncinatus* mire (83 %), while Lepidoptera adults and pupae showed no significant change. The biomass of weevil larvae and pupae declined significantly in *Cotula* herbfield (91%), *Poa cookii* tussock grassland (88%) and *Crassula moschata* saltspray vegetation (82%), although it showed a highly significant ($p < 0.01$) increase in the *Jamesoniella* mire. Weevil adult biomass declined significantly in *Cotula* herbfield (94%). Earthworms showed significant declines in biomass from 1976/77 to 1996/7 in *Sanionia* and *Jamesoniella* mires (99.8% and 92%, respectively), *Poa cookii* tussock grassland (58%), *Crassula moschata* saltspray vegetation (46%) and *Blechnum* fernbrake (44%). Spiders (*Myro* sp. only) also showed a significant decline in *Cotula* herbfield (100%) and *Poa cookii* tussock grassland (100%), and *Jamesoniella* (96%), *Sanionia* and *Blepharidophyllum* (100%) mires. No significant differences were measurable for the slugs, although examination of the abundances obtained in the current study, compared to that of 1976 (Table 16), suggests that the slugs may have increased in abundance (and spread) in the mire habitats (almost threefold in biomass), but decreased (and disappeared in the case of *Poa* and *Crassula*) in all the non-mire habitats. Although snails showed a significant decline in *Poa cookii* tussock grassland (viz. 100%), they otherwise increased significantly in biomass, especially in *Blechnum* fernbrake (i.e. 14 fold by 93%) and in *Jamesoniella* mires. Because of the considerable between-sample variation and large number of zeros in the data (many cores contained no individuals of the species concerned), the remaining differences, although seemingly great in many instances, were not statistically significant. Nevertheless, it is interesting to note that where increases were evident, these were usually of biomass, and principally in the *Jamesoniella* mire and *Blechnum* slope communities. The communities that showed the least changes were *Acaena* and *Blepharidophyllum*.

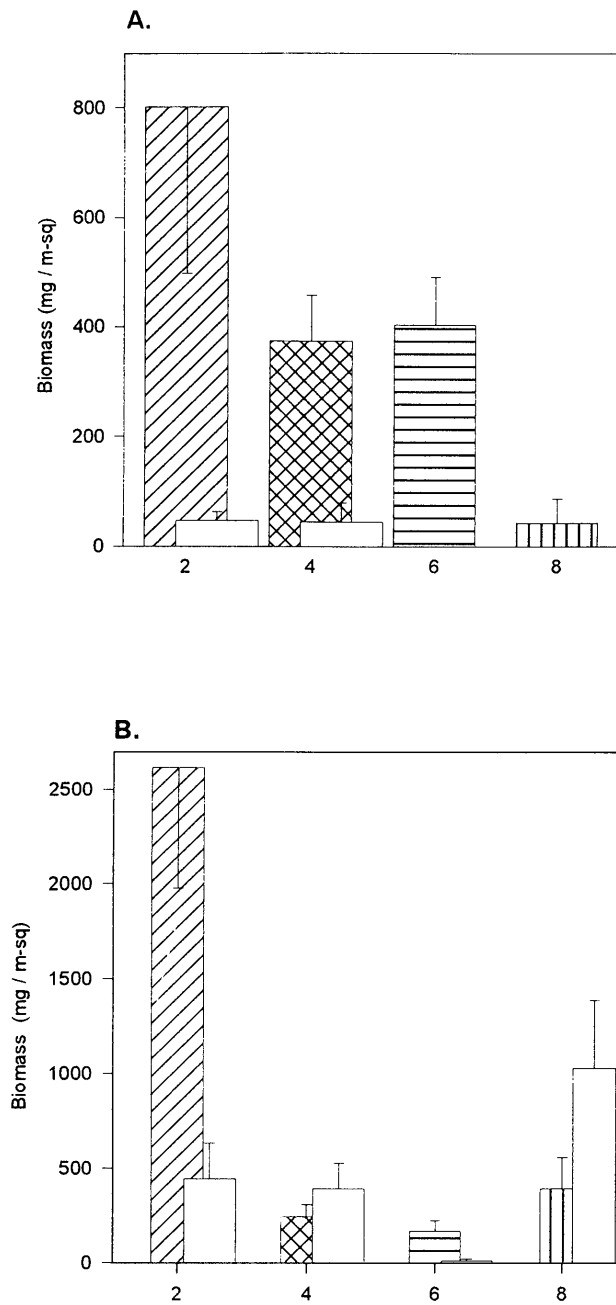


Fig. 7. Differences in invertebrate biomass found 1976/77 versus that found in 1996/97. **A.** represents *Poa cookii*, grassland. **B.** = *Sanionia uncinatus* mire. 2 = Lepidoptera larvae (*P. marioni* & *E. halticella*); 4 = Weevil larvae; 6 = Big spiders (*Myro* sp.); 8 = Slugs. Shaded bars = 1976/77; clear bars = 1996/97.

Table 17. Annual mean densities (numbers m⁻²) & biomass (mg m⁻²) ($\pm$ S.E.) of the macro-invertebrates from eight compatible vegetation complexes sampled in 1976/77 and 1996/97. Blep. = Blepharidophyllum, James. = Jamesoniella. EW = Earthworms, Lepi = Lepidoptera, Wvl = Weevils, L= larvae, A = adults, A & P = adults & pupae.

DENSITY

Species	MIRES			NON-MIRES				
	Blep	Sanionia	James.	Acaena	Blechnum	Cotula	Crassula	Poa
1976/77								
EW	10 $\pm$ 6	1310 $\pm$ 187	83 $\pm$ 21	660 $\pm$ 76	189 $\pm$ 25	3896 $\pm$ 523	428 $\pm$ 41	2036 $\pm$ 147
Lepi-L	20 $\pm$ 8	136 $\pm$ 25	10 $\pm$ 6	7 $\pm$ 7	3 $\pm$ 3	46 $\pm$ 13	80 $\pm$ 17	46 $\pm$ 14
Lepi-A&P	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
Wvl-L&P	109 $\pm$ 22	53 $\pm$ 12	80 $\pm$ 20	109 $\pm$ 19	17 $\pm$ 10	166 $\pm$ 27	109 $\pm$ 18	96 $\pm$ 21
Wvl-A	33 $\pm$ 10	3 $\pm$ 3	20 $\pm$ 8	30 $\pm$ 10	10 $\pm$ 7	63 $\pm$ 17	27 $\pm$ 15	17 $\pm$ 7
Spiders	20 $\pm$ 8	43 $\pm$ 15	43 $\pm$ 12	30 $\pm$ 9	33 $\pm$ 12	73 $\pm$ 18	3 $\pm$ 3	119 $\pm$ 26
Snail	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	3 $\pm$ 3	13 $\pm$ 9	0 $\pm$ 0	0 $\pm$ 0	99 $\pm$ 49
Slug	0 $\pm$ 0	30 $\pm$ 12	0 $\pm$ 0	149 $\pm$ 25	13 $\pm$ 8	7 $\pm$ 5	3 $\pm$ 3	3 $\pm$ 3
1996/97								
EW	0 $\pm$ 0	4 $\pm$ 4	17 $\pm$ 8	684 $\pm$ 83	157 $\pm$ 24	3953 $\pm$ 286	634 $\pm$ 78	1252 $\pm$ 215
Lepi-L	65 $\pm$ 39	78 $\pm$ 23	0 $\pm$ 0	40 $\pm$ 15	0 $\pm$ 0	83 $\pm$ 20	9 $\pm$ 7	133 $\pm$ 31
Lepi-A&P	0 $\pm$ 0	13 $\pm$ 7	4 $\pm$ 4	9 $\pm$ 6	0 $\pm$ 0	2 $\pm$ 2	0 $\pm$ 0	0 $\pm$ 0
Wvl-L&P	104 $\pm$ 26	212 $\pm$ 65	260 $\pm$ 39	136 $\pm$ 30	0 $\pm$ 0	18 $\pm$ 11	60 $\pm$ 15	21 $\pm$ 11
Wvl-A	13 $\pm$ 7	26 $\pm$ 12	61 $\pm$ 44	22 $\pm$ 9	0 $\pm$ 0	5 $\pm$ 5	9 $\pm$ 7	4 $\pm$ 4
Spiders	39 $\pm$ 24	9 $\pm$ 6	13 $\pm$ 10	42 $\pm$ 15	17 $\pm$ 8	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
Snail	4 $\pm$ 4	0 $\pm$ 0	82 $\pm$ 32	9 $\pm$ 9	329 $\pm$ 47	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
Slug	4 $\pm$ 4	78 $\pm$ 26	9 $\pm$ 6	218 $\pm$ 37	0 $\pm$ 0	5 $\pm$ 5	0 $\pm$ 0	0 $\pm$ 0

BIOMASS

1976/77								
EW	103 $\pm$ 68	15053 $\pm$ 2237	855 $\pm$ 250	7477 $\pm$ 1013	2132 $\pm$ 318	42911 $\pm$ 7201	3040 $\pm$ 336	21234 $\pm$ 1726
Lepi-L	143 $\pm$ 64	2616 $\pm$ 640	99 $\pm$ 62	133 $\pm$ 133	43 $\pm$ 43	965 $\pm$ 350	683 $\pm$ 189	802 $\pm$ 305
Lepi-A&P	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
Wvl-L&P	302 $\pm$ 69	245 $\pm$ 62	262 $\pm$ 71	481 $\pm$ 92	80 $\pm$ 52	749 $\pm$ 115	305 $\pm$ 55	375 $\pm$ 83
Wvl-A	143 $\pm$ 44	13 $\pm$ 13	83 $\pm$ 34	159 $\pm$ 56	53 $\pm$ 38	345 $\pm$ 95	99 $\pm$ 55	86 $\pm$ 37
Spiders	50 $\pm$ 26	166 $\pm$ 59	149 $\pm$ 60	123 $\pm$ 44	60 $\pm$ 25	288 $\pm$ 81	3 $\pm$ 3	405 $\pm$ 86
Snail	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	66 $\pm$ 66	153 $\pm$ 110	0 $\pm$ 0	0 $\pm$ 0	1154 $\pm$ 558
Slug	0 $\pm$ 0	391 $\pm$ 166	0 $\pm$ 0	1966 $\pm$ 366	259 $\pm$ 169	90 $\pm$ 63	40 $\pm$ 40	43 $\pm$ 43
1996/97								
EW	0 $\pm$ 0	25 $\pm$ 25	72 $\pm$ 43	7894 $\pm$ 1745	1201 $\pm$ 268	30873 $\pm$ 3045	1640 $\pm$ 297	8957 $\pm$ 1810
Lepi-L	204 $\pm$ 119	443 $\pm$ 189	0 $\pm$ 0	240 $\pm$ 156	0 $\pm$ 0	567 $\pm$ 245	20 $\pm$ 14	47 $\pm$ 16
Lepi-A&P	0 $\pm$ 0	207 $\pm$ 120	126 $\pm$ 126	85 $\pm$ 59	0 $\pm$ 0	17 $\pm$ 17	0 $\pm$ 0	0 $\pm$ 0
Wvl-L&P	276 $\pm$ 82	389 $\pm$ 138	398 $\pm$ 94	251 $\pm$ 62	0 $\pm$ 0	66 $\pm$ 42	56 $\pm$ 23	45 $\pm$ 34
Wvl-A	70 $\pm$ 40	101 $\pm$ 47	67 $\pm$ 36	77 $\pm$ 35	0 $\pm$ 0	22 $\pm$ 22	31 $\pm$ 20	37 $\pm$ 26
Spiders	0 $\pm$ 0	10 $\pm$ 10	6 $\pm$ 6	150 $\pm$ 80	11 $\pm$ 7	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
Snail	51 $\pm$ 51	0 $\pm$ 0	446 $\pm$ 224	64 $\pm$ 64	2164 $\pm$ 409	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
Slug	32 $\pm$ 32	1026 $\pm$ 361	39 $\pm$ 36	1904 $\pm$ 399	45 $\pm$ 45	3 $\pm$ 3	0 $\pm$ 0	0 $\pm$ 0

Table 18. Results of the Kruskal Wallis test for differences between the macro-invertebrates found in the 1976/77 and 1996/97 studies.
N is (120) for all except Cotula and Crassula for which it is (115). * = 0.05, ** = 0.01, *** = 0.001. # = CH data higher.

A. Numbers

	Blepharidophyllum	Sanionia	Jamesoniella	Acaena	Blechnum	Cotula	Crassula	Poa
Earthworms	3.051	71.29***	8.114**	0.051	0.119	1.436	2.048	17.08***
Lepidoptera larvae	0.025	5.476*	3.051	4.695*#	1.000	2.216	14.15***	5.450*#
Lepidoptera adults & pupae	-	3.051	1.000	2.017	-	1.091	-	-
Weevil larvae & pupae	0.190	2.811	17.46***#	0.170	3.051	31.12***	2.645	11.36**
Weevil adults	3.606	2.899	0.276	0.533	2.017	11.36**	1.013	2.668
Spiders	0.276	3.973*	7.422**	0.036	1.276	16.81***	0.917	24.99***
Snails	1.000	-	10.80**#	-	51.14***#	-	-	10.80**
Slugs	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000

B. Biomass

	Blepharidophyllum	Sanionia	Jamesoniella	Acaena	Blechnum	Cotula	Crassula	Poa
Earthworms	3.051	71.45***	9.29**	1.609	4.027*	1.717	10.24**	33.55***
Lepidoptera larvae	0.080	11.43**	3.051	2.712	1.000	0.294	15.68**	1.191
Lepidoptera adults & pupae	-	3.051	1.000	3.051	-	1.091	-	-
Weevil larvae & pupae	1.362	0.485	7.167***#	1.592	3.051	30.09***	9.675**	14.23***
Weevil adults	3.636	2.804	0.376	0.460	2.017	11.54**	0.419	1.353
Spiders	6.259*	6.050*	8.357**	0.603	1.798	16.77***	0.917	24.95***
Snails	1.000	-	10.79**#	-	45.88***#	-	-	10.80**
Slugs	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

2.4. Discussion

2.4.1 Seasonality of invertebrates

Seasonal patterns of the invertebrates appear to vary according to the habitat in which they occur, with the greatest difference being between the mire and non-mire habitats. For example, *P. marioni* & *E. marioni* both show summer and autumn peaks in mire communities, but vary in the non-mires by exhibiting both spring and/or early winter peaks in some vegetation complexes while at the same time having rather low abundances in others. Similarly the midge *L. minimus* and the small spider *Erigone* sp., show distinct shifts in seasonality, moving from spring and autumn peaks in the mire habitats to predominantly summer (and in the case of the *Erigone* sp. also autumn) peaks in the non-mires, although their seasonal patterns within the mire or non-mire communities tend to be the same (Figs. 4A & B). These examples also suggest that seasonality appears to be more pronounced in the habitat specific species such as *P. marioni* & *E. marioni*, as opposed to the ubiquitous species such as *L. minimus* and the *Erigone* sp. Seasonality may also be the consequence of interactions between herbivorous species and their hosts. Thus winter peaks in the abundances of invertebrates inhabiting mire communities may be a consequence of winter growth of in many bryophyte species in these communities (Smith 1987c). Similarly, the seasonal pattern shown by aphids (viz. peaking during summer in the *Poa* and *Cotula* complexes), may be a result both of seasonal growth (mostly spring and summer) of the host plant and high summer temperatures (see also Strathdee & Bale 1995).

Thus there are strong indications of seasonality in a number of the macro-invertebrates in specific vegetation complexes, despite the apparently aseasonal macroclimate (Schulze 1971). Thus Convey's (1996a) suggestion that seasonality may not be particularly pronounced in sub-Antarctic environments is not strongly upheld. Rather, the overall pattern appears to be one of considerable variability amongst different species and amongst habitats for a given species. This variability has been noted by previous workers (Burger 1978; Crafford & Scholtz 1986, Crafford 1987, Chown & Scholtz 1989), but there also appears to be some inter-annual consistency for a given species within a specific vegetation type. For example the seasonal variation in biomass of *P. marioni* in biotically influenced habitats documented by Crafford (1987) and in the current study are comparable, as are the patterns exhibited by the weevil larvae in the habitats investigated by Chown & Scholtz (1989) and in those examined in the current study. Similarly, the biomass of *Embryonopsis halticella* larvae in *Poa cookii* tussock grassland was found to be at its highest level in summer and its lowest level in winter both here and in the study undertaken by Crafford & Scholtz (1986). This suggests that the macro-invertebrate species on Marion Island may show significant life history flexibility, in keeping with many other Antarctic terrestrial species (Convey 1996b).

2.4.2 Habitat specificity

The results of the ordinations and cluster analyses based on the macro-invertebrate data, in conjunction with the indicator value analyses indicate that although most of the assemblages clearly differ with regard to relative abundance (and in some cases species presence), there is limited habitat specificity in the macro-invertebrate assemblages. The majority of the insect species do not show pronounced site specificity and fidelity (see Dufrêne & Legendre 1997, McGeoch & Chown 1998). In those instances where species were identified as habitat specific, this specificity was of a rather generalized nature, with the species either preferring mire or non-mire habitats. Although more pronounced habitat specificity has recently been found amongst the meso-invertebrates (Collembola and mites), both in the vegetated biotope (Gabriel 1999), as well as in fellfield (J. Barendse, personal communication) and on the shoreline (R. Mercer, personal communication), this finding is in keeping with that of most previous workers who studied macro-invertebrates on the island (e.g. Crafford 1987, 1990a, Chown and Scholtz 1989). Consequently, there are a number of key patterns identified both in this study, and in previous investigations, that deserve specific attention.

Amongst the indigenous species, the high biomass of *Pringleophaga marioni* larvae in *Sanionia* and *Blepharidophyllum* mires confirms the findings of Huntley (1971) and Burger (1978). Indeed, Burger recorded the highest biomass of this species in the former vegetation complex, with lower abundances in the biotically influenced vegetation complexes. In contrast, both Crafford (1990a) and, to some extent Gleeson (1981), found that the larvae of *P. marioni* were least abundant in the mire complex (which appears to have included *Blepharidophyllum*, but not *Sanionia*), and most abundant in *Poa cookii* tussock grassland followed by the *Crassula moschata* saltspray complex. These differences may well be due to the difference in the sampling goals and strategies of the different sets of investigators. Neither of the latter workers adopted a stratified, community based, sampling approach, whereas both this study and that of Burger (1978) did so. These differences in sampling protocol are likely to influence considerably assessments of the habitat specificity of a given species, and the latter, stratified approach is clearly preferable. Nonetheless, comparisons of larval abundances among years for specific habitats may still be undertaken bearing these caveats in mind.

Within the oligochaets, earthworms occurred in most habitats, but showed distinct preferences for the drier non-mire and more well drained high altitude mire habitats (see also Burger 1978, and Table 14). The Enchytraeidae showed a similar pattern, preferring the drier, non-mire habitats. This higher taxon has previously been ignored in most studies on Marion Island, probably because of their small size, making extraction difficult (they tend to be cryptic amongst the root hairs of plants and extremely thorough searching is required to quantify their abundances), and their relative taxonomic difficulty. Thus it is not yet clear how many species are represented on Marion

Island, nor whether they are indigenous or alien to the island. From this study it was clear that numerous, very small specimens are typically found amongst the root material of *Crassula*, while much larger specimens are usually only found in the *Acaena* drainage line vegetation.

Interestingly there appears to have been a shift in the major habitat preference of the snail *N. hookeri*, who's occurrence in the Kerguelen Province was first linked by Solem (1968) to the Kerguelen Cabbage, *Pringlea antiscorbutica* and tussock grass *P. cookii*. Although the snail has never been recorded in association with the Kerguelen Cabbage, it's association with *P. cookii* was partially substantiated by Burger (1978) who found the snail's biomass highest in *P. cookii* tussock grasslands, and mires dominated by the sedge *Uncinia compacta* and moss *Ptychomnion ringianum*. In this study, *N. hookeri* was most abundant in the *Blechnum* slope complex, followed by the mid-altitude (that also contained *Uncinia compacta*) and *Jamesoniella* mires. The reasons for this change in habitat specificity are not clear, but may well have to do with the influence of house mice on the terrestrial ecosystem in general (see section 2.4.3 below).

The alien invertebrate component appeared to show a similar variety in habitat specificity, with species such as *Limnophyes minimus* and the aphid species occurring in virtually all habitats, and others such as *Psychoda parthenogenetica* appearing to be restricted to the coastal zones (mostly enriched areas such as *Cotula* herbfield and in rotting kelp. These findings are in keeping with those of previous workers (mostly Crafford *et al.* 1986), and there does not appear to have been a considerable change in these species, with the exception perhaps of *Limnophyes minimus* (see following chapter and Crafford 1986). One species that does appear to be expanding its distribution is the slug *Deroceras caruanae*. This species is now commonly found in mire habitats (compare Tables 9 and 14) and it is thought to be spreading on the island subsequent to its relatively recent (post 1966) introduction (see Smith 1992 for additional discussion).

Although the factors that may account for the habitat specificity exhibited by the various invertebrates have not been investigated specifically, knowledge about the species history and biological requirements may well account for some of the host preferences. This is clearly the case in the diamond-backed moth *Plutella xylostella*, that is host specific to crucifers, and in some of the aphid species that are known to prefer grasses (see Crafford *et al.* 1986). Nonetheless, investigations of the factors responsible for habitat specificity (or lack of it) would certainly repay further study, especially in the case of the alien species, such as the aphids, that are likely to be important potential vectors of plant diseases. This is particularly true in the context of current climate change at the islands (Chown & Smith 1993) and the increased likelihood of alien introductions associated with such change (see Chown *et al.* 1998).

2.4.3 Comparisons between species abundances in 1976/77 and 1996/97

Although a comparison was made between Burger's data and those collected in the current study, it should be noted that conclusions cannot be based solely on the figures presented in the results, because the two studies differed principally in their aims and therefore in the thoroughness of invertebrate sampling. Burger's work concerned the behavioural ecology of the Lesser Sheathbill (Burger 1980), and consequently his invertebrate sampling concentrated only on the larger (>1 mm) and more visible macro-invertebrates that formed the major components of the Lesser Sheathbill's diet (Burger 1978, 1982). On the other hand, the current study's primary aim was to determine the abundances of all macro-invertebrates in the vegetated biotope, and therefore every macro-invertebrate in each core sample was counted. Thus, the current study included small enchytraeids and the smallest larval instars in the case of the insects. Thus the number (density) of invertebrates found in Burger's (1978) study must be considered lower than what would actually have been representative of the vegetation complex sampled at the time, while those of the current study are considered representative.

In contrast, the masses in Burger's study would not have been as severely affected, since omitting the weights of the tiny invertebrates (*e.g.*, first larval instars of weevils and lepidopterans) may not have had a marked influence on the overall biomass assessment for these species and stages because of the low individual masses of these early instars. These differences in sampling effect on numbers and biomasses clearly explain why the results indicate increases in invertebrate numbers between 1976/77 and 1996/97, but decreases in biomass, and why the increases in numbers were principally amongst the larval stages of the invertebrates, while the numbers of the other stages, and larger macro-invertebrates either showed a decrease or no significant change. Furthermore, the lumping of both *P. marioni* and *E. halticella* into one category (Lepidoptera), is misleading, as many *E. halticella* larvae were found in the current study (see especially *Poa* in Tables 8 & 9), while the lepidopterans in Burger's study were almost exclusively *P. marioni* (Burger 1978).

These kinds of differences between the two studies are not only relevant to the current comparison, but should be borne in mind when any comparisons between macro-invertebrate studies done on Marion and Prince Edward Islands are undertaken. Thus not only is the spatial nature of the study likely to be critical to the outcome (*i.e.*, stratified, plant-complex based sampling, vs. transects or other less specific sampling approaches, compare Crafford 1990a, Gleeson 1981 and Burger 1978), but the thoroughness of the sampling approach is also likely to have an effect. Samples that are sorted solely for large macro-invertebrates, over a short period, may in fact considerably under-represent the true number of individuals (and probably species) in a given sample, compared to those that seek to quantify the abundance of all the macro-invertebrates. This has profound implications for

investigations of long term changes in species abundances, and for investigations that seek to address the impacts of species on each other either via competition or predation.

In light of the above discussion, it is clear that the invertebrate abundances reported by Burger (1978) are underestimates of the true densities at the time (a factor that could not be corrected for in the direct comparison). Thus the declines in macro-invertebrate abundances (mostly biomasses) noted in the comparisons between the 1976/77 and 1996/97 sampling periods are likely to be conservative. Indeed, it seems probable that many of the non-significant declines in abundance noted for some species in at least some of the vegetation complexes would have been significant, had sampling intensity been standardized across the two studies. In addition, because of the overwhelming number of small (<1 mm) larval instars found in the current study, the increase in numbers across the two sampling periods is understandable, but misleading, in that no comparable figures for small instar larvae are available. These points are readily illustrated using weevils as an example. The fact that this group appears to have increased in number in some habitats (because of the small instars that were omitted in Burgers study), while also showing a decline in others (despite the inclusion of the small instars in the current study), suggests that the decline in numbers must be considerably greater than indicated. Likewise, if the increase in numbers is merely a reflection of the many small instars present in the current study, the corresponding decline in biomass must be the result of a decline in the number of larger-sized instars. That this decline could be due to a shift in habitat selection is doubtful, because there was an overwhelming decrease in weevil biomass for virtually all the habitats, and weevils were found to have retained the habitat specificity reported by previous workers (see section 2.3.1.3 above). The fact that small weevil larvae are probably responsible for indicating an increase in numbers across years, and therefore healthy recruitment to the population, is also misleading, because the decline in both the number and biomass of adult weevils suggests that recruitment must previously have been even higher. Furthermore, if the overall decline in weevil larvae biomass is due to the decline in the larger larval stages, it implies an added curtailing factor to recruitment.

The same scenario appears to be applicable in the case of the decline in the immature stages of the Lepidoptera (mostly *Pringleophaga marioni*), and the species *per se*. Although a difference in adult abundances could not be measured because no adults were found in the core samples, the pronounced decline in larval biomass suggests that this is the case. There is additional circumstantial evidence supporting the quantitative data on the decline of *Pringleophaga marioni*. The abundance with which *P. marioni* larvae could be found in (abandoned) Wandering Albatross nests (biotically enriched areas that are often vegetated by *P. cookii* plants) has been noted by subsequent workers (Crafford & Chown 1993, Klok & Chown 1997, personal communications). However, various researchers (specifically S.L. Chown, personal communication) have noted a decline in the number of

large (final instar) larvae found in abandoned albatross nests in 1996 compared to previous findings. Recent observations (S.L. Chown & C.J. Klok personal observations) have also revealed not only a decline in size of the moth larvae, but also in their numbers, to such an extent that where previously virtually every abandoned nest site that did not show tunnelling by mice, contained in the region of 50-100 *P. marioni* larvae, searches in April 1999 revealed at most 20 small larvae or none at all. Although albatross nests were not sampled in the current study, and cannot be compared to the situation found in the *P. cookii* grassland, these observations support the overall dramatic decline in abundance of *P. marioni* found in this study, and reported by Crafford and Scholtz (1987b).

The increase in numbers and biomass of the indigenous snail *N. hookeri* is of interest, as it rates amongst the larger of the invertebrates. This species is the only macro-invertebrates that showed an increase in biomass over the period in question, and is not amongst the prey items listed for mice (Gleeson & van Rensburg 1982, Rowe-Rowe *et al.* 1989, van Aarde *et al.* 1996), although they are amongst the food-items taken by the Lesser Sheathbills (Burger 1978, 1981, 1982). The slugs too are of interest, because they are an introduced species, but have not shown a significant change in either densities or biomass. They appear not to feature as major prey items for Sheathbills, because they did not occur in habitats frequented by Sheathbills in 1976/77 (Burger 1978), and were only recorded as trace items in the stomach contents of mice examined by Rowe-Rowe *et al.* (1989), although interestingly, some eight years later, D.G. Erasmus (personal communication) found that slugs were the sole stomach contents of a mouse stomach trapped in 1996/97.

In sum, the changes reported above suggest strongly that mice are having a pronounced and dramatic effect on the abundances of selected indigenous macro-invertebrate species on Marion Island, and provide strong support for previous statements regarding the impacts of mice (*e.g.*, Crafford & Scholtz 1987b, Smith & Steenkamp 1990, Chown & Smith 1993). The data also provide the primary mechanism underlying the decline in Lesser Sheathbill numbers on Marion Island over the past 20 years, but their relative stability on Prince Edward Island which is mouse-free (see Huyser 1997, Huyser *et al.* in press). These findings clearly constitute one the strongest of arguments for the prevention of alien introductions to the sub-Antarctic islands.

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CHAPTER 3. THE IMPACT OF A SMALL, ALIEN INVERTEBRATE *LIMNOPHYES MINIMUS* MEIGEN (DIPTERA, CHIRONOMIDAE) ON THE TERRESTRIAL ECOSYSTEM

3.1 Introduction

Like many other terrestrial island ecosystems, those on the sub-Antarctic islands are threatened most by the introduction of alien species. Introduced mammals have had and continue to have significant impacts on many of these islands, either as a consequence of their immediate activities (Bonner 1984, Leader-Williams 1988, Bloomer & Bester 1992, Chapuis *et al.* 1994, Dingwall 1995), or as a consequence of an increase in their impact as a result of increases in mean annual temperature on the islands (Smith & Steenkamp 1990, Chown & Smith 1993). However, it is not only larger, vertebrate species that have been shown to alter the structure and functioning of sub-Antarctic terrestrial ecosystems. Gremmen (1997) and Gremmen *et al.* (1998) demonstrated that *Agrostis stolonifera*, a grass first recorded on Marion Island in 1965 has spread dramatically since its discovery and reduces plant diversity in the drainage line habitats it dominates by as much as 50%. Ernsting (1993) and Ernsting *et al.* (1995) have shown that a carabid beetle introduced to the Stromness Bay region of South Georgia is having a pronounced impact on its major prey species, the perimylopod beetle *Hydromedion sparsutum*. On Kerguelen Island, the introduced *Ooptyx soledadinus* (Coleoptera, Carabidae) and *Calliphora vicina* (Diptera, Calliphoridae) are having an impact on the indigenous *Anatalanta aptera* (Diptera, Sphaeroceridae), respectively through predation and interspecific competition (Chevrier 1996, Chevrier *et al.* 1997), and on Marion Island, the herbivorous diamond-back moth (*Plutella xylostella*) is thought to be having a significant impact on its indigenous host, the Kerguelen Cabbage (Crafford & Chown 1990, Chown & Avenant 1992).

These documented cases of the impacts of introduced species on sub-Antarctic islands have tended to focus mostly on conspicuous elements of the introduced fauna: rodents, invertebrate predators and herbivores, and fairly conspicuous vascular plants. Nonetheless, there are many relatively inconspicuous alien species which occur on these islands, particularly amongst the arthropods. For example, Pugh (1994) has documented at least 55 mite species which have been introduced to the sub-Antarctic, and earlier workers noted that a variety of small insect species are not indigenous to the islands (*e.g.*, Gressitt 1970, Séguy 1971). Although a few of these relatively inconspicuous elements of the alien biota have subsequently been mentioned in the context of sub-Antarctic island conservation (*e.g.*, Watkins & Cooper 1986, Cooper & Condry 1988), there have been few attempts either to quantify their contribution to total invertebrate density on these islands, or to determine their importance to terrestrial ecosystem functioning.

This is true also of *Limnophyes minimus* Meigen (= *Limnophyes pusillus*, see Evenhuis 1989), a small, chironomid midge that is thought to have invaded many of the South Indian Ocean Province Islands (*sensu* Lewis Smith 1984) from the Palearctic (Séguy 1971, Crafford *et al.* 1986, Evenhuis 1989). Although the biology and population dynamics of this species have been investigated on Kerguelen Island (Delettre & Trehen 1977, Delettre 1978, Delettre & Cancela da Fonseca 1979), and it is known to occur on the Prince Edward (Crafford 1986) and Crozet (Chevrier 1996) archipelagos, little is known of the abundance of this species across the major lowland habitats for any of these islands. In addition, no estimates have been made of the contribution of this species to energy flow in the island ecosystems where it occurs. Hence its impact on these systems remains unknown.

This paper reports on a survey in which the abundance (numbers and biomass) of *L. minimus* was quantified and compared to the abundance of indigenous macro-invertebrates in ten vegetation complexes on Marion Island. Also provided are the estimates of the contribution this species makes to energy turnover in the island's lowland terrestrial ecosystem.

3.2 Material and methods

3.2.1 Species biology

Limnophyes minimus is parthenogenetic, and the adult females (*c.* 3 mm wing span) are short-lived and do not feed. Eggs are laid in a single string of 80 - 100 eggs, and eclosion, egg-laying and hatching occur mostly in summer (notably on Kerguelen, Delettre & Trehen 1977, Delettre & Cancela da Fonseca 1979, Crafford 1986), although these activities are extended to include early spring on Marion Island (personal observations). There are four larval instars, respectively lasting one, three, six and 41 weeks on Kerguelen Island (Delettre 1978).

3.2.2 Sampling procedure and data analysis

Although Crafford (1986) and Crafford *et al.* (1986) suggested that *L. minimus* is restricted to freshwater bodies on Marion Island, an initial survey indicated that this species may in fact be more widespread (see also Eaton 1875, Delettre & Trehen 1977). Hence in this study I sampled 10 different plant communities (Table 19), representing the major lowland community types described by Gremmen (1981), at bimonthly intervals from June 1996 to May 1997. In each community, with the exception of the high-altitude mire, five 2 m x 2 m quadrats were laid out at random, and from each of these, two circular cores were taken at random with an O'Connor split corer (7 cm diameter) (see Southwood 1978). For the high-altitude mire, only four, 1 m x 1 m quadrats were laid out because of the small surface area of this site. No other mires can be found at this altitude on Marion

Island (N.J.M. Gremmen, personal communication). The cores were subsequently sorted by hand (most macro-invertebrate larvae being removed this way), and the sorted material was placed in Tullgren funnels for four days. In both the *Cotula plumosa* and *Crassula moschata* communities, five samples were damaged during extraction and data from these cores were discarded.

All extracted macro-arthropods were identified to species level (using descriptions and figures in Crafford *et al.* 1986), counted, dried to constant mass at 60°C and weighed dry. Earthworms were identified as *Microscolex kerguelarum* (Grube) (Acanthodrilidae) but because confirmation of this identification is required, the earthworms were not dried. Their dry mass was estimated from a wet mass : dry mass relationship derived from a separate sample of 20 earthworms that were weighed wet, dried to constant mass at 60°C, and weighed dry (dry mass = 0.157 wet mass + 0.00013, $r^2 = 0.99$, $F = 1333$, $p = 0.00001$, $df = 19$). Numbers and dry mass were then expressed as units per m². For each community, yearly means (and standard errors, to accommodate sample size variation between the high mire and other communities) were calculated for *L. minimus*, and for each of the other major indigenous macro-invertebrate species, *i.e.* *Microscolex kerguelarum*, (Oligochaeta: Acanthodrilidae), *Ectemnorhinus similis* complex weevils (see Chown & Scholtz 1989), *Halmaeus atriceps* (Coleoptera, Staphylinidae), and *Pringleophaga marioni* (Lepidoptera, Tineidae). Within-community differences in the abundance (numbers and biomass) of *L. minimus* and the other major detritivorous macro-invertebrate species were tested for significance using a Kruskal-Wallis one way analysis by ranks. Pairwise comparisons of *L. minimus* and the other invertebrate species were made subsequent to the Kruskal-Wallis test using Tukey-type multiple comparisons (Zar 1996). These tests were employed because initial analyses showed that the data had unequal sample variances (see Zar 1996).

The contribution of *L. minimus* to energy flow in the terrestrial system at Marion Island was estimated based on the observation that only the larvae of this species feed (Delettre 1978, Crafford 1986). The estimate was obtained separately for each community in the following way. Mean dry mass of individual larvae was obtained from the sampling data for each community, and also (for a second estimate of ingestion rates) by assuming that larvae had a mass of 0.027 mg, equal to the mean mass of instar IV larvae on Kerguelen Island (Delettre & Trehen 1977, Delettre 1978, Y. Delettre, personal communication). These values were used to estimate dry mass ingestion of individual larvae per day, based on a relationship between dry mass and dry matter ingestion derived from data on invertebrate ingestion rates provided by Reichle (1968) ($y = 0.0627 x^{0.681}$, $r^2 = 0.755$, $F = 27.71$, $p = 0.00052$, $df = 10$). Dry mass ingestion per individual was then converted to dry mass ingestion per m² per year using the data on larval density. In an attempt to validate the use of this extrapolation it was also applied to data on the dry mass and abundance of *Pringleophaga marioni* provided by Crafford & Scholtz (1983), and Crafford (1990a). The resulting estimate was then

compared to an estimate of litter turnover, also provided by Crafford (1990a), that was based on direct measurements of ingestion rates of this species and its biomass in lowland vegetation on Marion Island. *P. marioni* was chosen for this comparison because it is one of the most important detritivore species on Marion Island, and is thought to form a “bottleneck” to nutrient recycling on the island (Crafford 1990a, b, Smith & Steenkamp 1990).

3.3 Results

Pronounced seasonality in the density and biomass of *L. minimus* was evident in most of the mire communities sampled (Fig. 8). Although there was considerable between-sample variation, densities tended to peak in the austral spring (September/October) and autumn (March/April) while they were lower during winter and summer. Biomass followed a trend similar to that of density (Fig. 8). However, seasonality in both density and biomass was less pronounced in the non-mire communities (Fig. 9).

Larval densities of *Limnophyes minimus* were highest in *Cotula plumosa* biotically-influenced communities, although high numbers were also found in *Acaena magellanica* drainage lines, and in mires dominated by *Jamesoniella colorata* and by *Sanionia uncinatus* (Table 19). These bryophyte species were dominant in the mid-altitude mire, resulting in high densities of midge larvae in this habitat too. Densities were somewhat lower in the other communities, and were lowest in the *Crassula moschata* salt spray community and the *Blechnum penna-marina* slope community. As a consequence of the small size of this species (large fourth instar larvae have a dry mass of approximately 0.12 mg), biomass in all of the communities was relatively low (Table 19).

The density and biomass of the major invertebrate groups on Marion Island also varied between habitats (Table 19). Because of the patchiness in the spatial distribution of all of the species sampled, and hence large variance estimates, substantial differences in mean density and biomass between *L. minimus* and the indigenous invertebrate species were often not significant (Tables 19 & 20). Nonetheless, a number of clear trends was apparent. Density and biomass of *Microscolex kerguelarum* were higher than those of *L. minimus* in most non-mire communities, whereas the opposite was true for the mire communities, with the exception of the higher elevation mires. Although midge larvae tended to have higher densities than those of *Pringleophaga marioni*, especially in the mire communities, the latter species had a higher biomass in most communities, and this difference was significant at least for two of the lowland mire communities (Tables 19 & 20). Few significant differences were found between *Ectemnorhinus similis* complex weevils and *L. minimus* larvae, although the former tended to occur in lower densities and to have a higher biomass than the latter in most communities (Tables 19 & 20).

The estimate for litter turnover by *Pringleophaga marioni*, based on dry biomass ($10.7 \text{ g}_{(\text{dry mass})} \cdot \text{m}^{-2}$, Table 21) was close to that obtained by Crafford (1990a) using measured ingestion rates ($10 \text{ g}_{(\text{dry mass})} \cdot \text{m}^{-2}$). Consequently, Reichle's (1968) equation was considered to be sufficiently reliable, given the errors associated with extrapolation, to obtain a reasonable estimate of litter turnover by *L. minimus* (Table 21). For comparison, litter turnover was also estimated for *P. marioni* in each community, based on the current sampling data. Unfortunately, the method did not allow for an estimation of confidence intervals for either of the species in any community. Estimates of litter turnover by *L. minimus* ranged from 0.07 to $8.54 \text{ g}_{(\text{dry mass})} \cdot \text{m}^{-2}$ per year in the vegetated biotope and exceeded estimates for *P. marioni* in four of the communities where these species co-occurred (Table 21). Where estimated litter turnover by *L. minimus* was less than that estimated for *P. marioni*, this ranged from 33% of *P. marioni*'s litter turnover in the salt spray community to 55% in the *Acaena magellanica* drainage line. Although the two estimates of ingestion provided for *L. minimus* differed in some cases, notably for drainage lines, overall the trends remained similar.

Table 19. Density (numbers m⁻²) and biomass (mg m⁻²) (mean ± S.E.) of the major macro-invertebrates in the ten communities sampled at bimonthly intervals on Marion Island from June 1996 to May 1997. All the species listed are indigenous to the islands with the exception of *L. minimus*.

	n	<i>Limnophyes minimus</i> (Diptera)	<i>Microscolex kerguelarum</i> (Oligochaeta)	<i>Ectemnorhinus similis complex</i> (Coleoptera)	<i>Pringleophaga marioni</i> (Lepidoptera)	<i>Halmaeusa atriceps</i> (Coleoptera)
Non-mire communities						
<i>Acaena magellanica</i> drainage line						
Density	60	1843 ± 442	684 ± 83	158 ± 31	44 ± 18	524 ± 80
Biomass	60	58 ± 13	7894 ± 1745	328 ± 69	316 ± 170	104 ± 17
<i>Blechnum penna-marina</i> fernbrake						
Density	60	109 ± 32	157 ± 24	0	0	0
Biomass	60	3 ± 1	1201 ± 268	0	0	0
<i>Cotula plumosa</i> biotically-influenced community						
Density	55	5096 ± 1127	3953 ± 286	23 ± 12	72 ± 19	1614 ± 229
Biomass	55	193 ± 40	28300 ± 3002	81 ± 43	532 ± 226	359 ± 62
<i>Crassula moschata</i> salt spray community						
Density	55	52 ± 39	634 ± 78	69 ± 15	9 ± 7	45 ± 16
Biomass	55	3 ± 3	1504 ± 278	80 ± 27	19 ± 13	6 ± 3
<i>Poa cookii</i> tussock grassland						
Density	60	556 ± 123	1252 ± 215	25 ± 11	12 ± 7	1082 ± 140
Biomass	60	25 ± 5	8957 ± 1810	82 ± 42	8 ± 5	182 ± 32
Mire communities						
<i>Blepharidophyllum densifolium</i> oligotrophic mire						
Density	60	606 ± 131	0	117 ± 29	65 ± 39	87 ± 31
Biomass	60	27 ± 6	0	346 ± 100	204 ± 119	17 ± 6
<i>Sanionia uncinatus</i> oligotrophic mire						
Density	60	1494 ± 499	4 ± 4	238 ± 67	91 ± 24	17 ± 12
Biomass	60	57 ± 15	25 ± 25	490 ± 151	650 ± 217	3 ± 2
<i>Jamesoniella colorata</i> oligotrophic mire						
Density	60	3027 ± 642	17 ± 8	320 ± 56	4 ± 4	104 ± 25
Biomass	60	106 ± 21	72 ± 43	465 ± 96	126 ± 126	20 ± 6
Mid altitude oligotrophic mire						
Density	60	2286 ± 408	35 ± 14	260 ± 47	9 ± 6	26 ± 15
Biomass	60	68 ± 12	220 ± 129	350 ± 101	14 ± 14	5 ± 3
High altitude oligotrophic mire						
High Alt.	48	742 ± 206	125 ± 29	114 ± 26	0	0
Biomass	48	21 ± 4	1323 ± 380	123 ± 39	0	0

Table 20. Results of the Kruskal-Wallis one way analyses by ranks of densities (numbers m⁻²) and biomasses (mg m⁻²) of the major detritivorous macro-invertebrates in the ten communities sampled. The significance levels given for each of the indigenous invertebrate species are for a Tukey-type multiple comparison of each species with *Limnophyes minimus* based on the results of the Kruskal-Wallis test (see Zar 1996). Symbols indicate where values for indigenous species were less than (-) or greater than (+) those for *Limnophyes minimus* (see Table 20).

	n	H	P	<i>Microscolex</i> <i>kerghuelarum</i>	<i>Ectemnorhinus</i> <i>similis</i> complex	<i>Pringleophaga</i> <i>marioni</i>
Non-mire communities						
<i>Acaena magellanica</i> drainage line						
Density	60	90.35	0.00001	NS	0.001 (-)	0.001 (-)
Biomass	60	105.22	0.00001	0.001 (+)	NS	0.05 (+)
<i>Blechnum penna-marina</i> fernbrake						
Density	60	90.37	0.00001	NS	NS	NS
Biomass	60	105.41	0.00001	0.01 (+)	NS	NS
<i>Cotula plumosa</i> biotically-influenced community						
Density	55	178.91	0.00001	NS	0.001 (-)	0.001 (-)
Biomass	55	179.68	0.00001	NS	0.01 (+)	NS
<i>Crassula moschata</i> salt spray community						
Density	55	115.32	0.00001	0.001 (+)	NS	NS
Biomass	55	109.42	0.00001	0.001 (+)	NS	NS
<i>Poa cookii</i> tussock grassland						
Density	60	127.87	0.00001	0.05 (+)	0.01 (-)	0.01 (-)
Biomass	60	133.05	0.00001	0.001 (+)	NS	0.05 (-)
Mire communities						
<i>Blepharidophyllum densifolium</i> oligotrophic mire						
Density	60	52.58	0.00001	0.01 (-)	NS	0.01 (-)
Biomass	60	57.65	0.00001	0.001 (-)	NS	0.01 (+)
<i>Sanionia uncinatus</i> oligotrophic mire						
Density	60	68.90	0.00001	0.001 (-)	NS	0.01 (-)
Biomass	60	58.62	0.00001	0.001 (-)	NS	NS
<i>Jamesoniella colorata</i> oligotrophic mire						
Density	60	136.94	0.00001	0.001 (-)	0.01 (-)	0.001 (-)
Biomass	60	134.64	0.00001		NS	0.001 (+)
Mid altitude oligotrophic mire						
Density	60	110.32	0.00001	0.001 (-)	NS	0.001 (-)
Biomass	60	96.79	0.00001	0.001 (+)	NS	0.001 (-)
High altitude oligotrophic mire						
Density	48	69.41	0.00001	NS	NS	0.001 (-)
Biomass	48	55.08	0.00001	NS	NS	0.001 (-)

Table 21. Estimates of the annual amount of litter ingested by *Pringleophaga marioni* (A) and *Limnophyes minimus* (B, C) calculated from mean larval dry mass, density and the regression provided by Reichle (1968). The initial estimate for *P. marioni* was based on data provided by Crafford & Scholtz (1983), and Crafford (1990a), and is close to the 10 g_(dry mass).m⁻² estimated by Crafford (1990a) using direct measurements of ingestion. The first estimate (B) for *L. minimus* was made using field data from each site, while the second (C) was based on mean larval mass across all sites for the full year (see text for detail).

Site	Ingestion g _(dry mass) .m ⁻²	Ingestion g _(dry mass) .m ⁻²	Ingestion g _(dry mass) .m ⁻²
	A. <i>Pringleophaga marioni</i>	B. <i>Limnophyes minimus</i>	C. <i>Limnophyes minimus</i>
Initial estimate	10.7	-	-
<i>Acaena</i> drainage line	3.4	1.99	3.11
<i>Blechnum</i> fernbrake	0	0.09	0.17
<i>Cotula</i> herbfield	5.97	6.48	8.54
<i>Crassula</i> salt spray	0.3	0.07	0.08
<i>Poa</i> tussock grassland	0.2	0.73	0.93
<i>Blepharidophyllum</i> mire	2.83	1.35	0.89
<i>Sanionia</i> mire	6.86	3.19	2.44
<i>Jamesoniella</i> mire	0.9	6.09	5.02
Mid altitude mire	0.3	4.06	3.62
High altitude mire	0	1.19	1.19

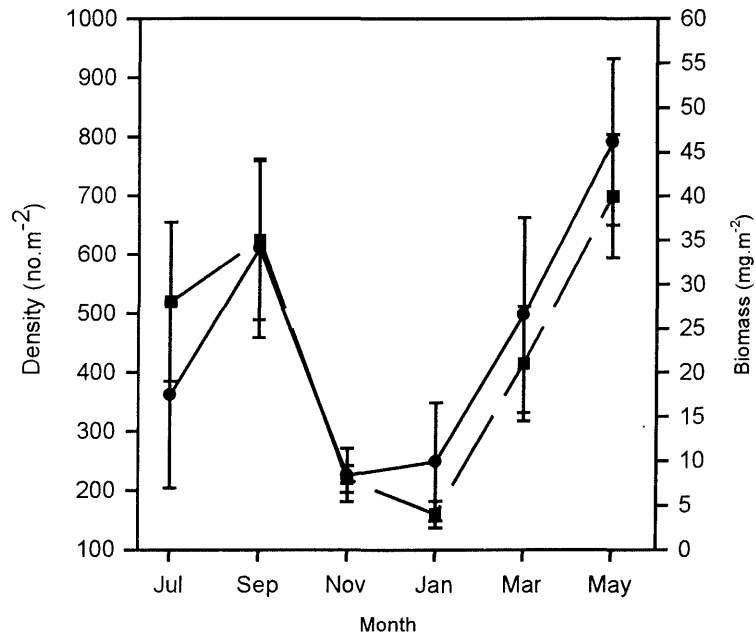


Fig. 8 Biomass (●) and density (■) (mean $\pm$ S.E.) of *Limnophyes minimus* Meigen larvae in the *Blepharidophyllum densifolium* oligotrophic mire community on Marion Island.

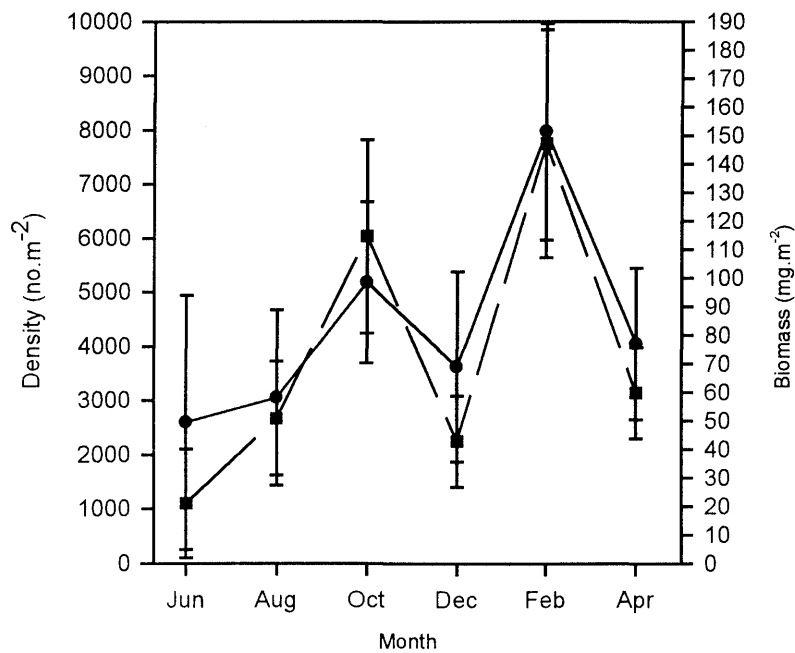


Fig. 9 Biomass (●) and density (■) (mean $\pm$ S.E.) of *Limnophyes minimus* Meigen larvae in the *Cotula plumosa* biotically influenced mire community on Marion Island.

3.4 Discussion

The Palearctic *Limnophyes minimus* has been known from sub-Antarctic islands for at least 120 years, having been described from Îles Kerguelen by Eaton (1875). Although it has been recorded from most of the South Indian Ocean Province archipelagos (the exception is Heard Island), and has been studied on Kerguelen, until now its functional importance in terrestrial ecosystems has not been fully established (but see Delettre & Trehen 1977, Delettre 1978, Delettre & Cancela da Fonseca 1979). Although there are obvious seasonal trends in the abundance of *L. minimus* on Marion Island, this species can nonetheless reach high densities, often exceeding densities of most of the indigenous, detritivorous macro-invertebrates thought to be important in nutrient recycling in the terrestrial system (i.e. *Pringleophaga marioni* larvae, *Microscolex kerguelarum*, and to a lesser extent *Ectemnorhinus similis* complex weevils, see Smith & Steenkamp 1992a, b). Indeed in the majority of the plant communities sampled, densities of the larvae of *L. minimus* were significantly higher than those of *P. marioni*, the insect species which is the most important contributor to litter turnover on Marion Island (Crafford 1990a, b, Smith & Steenkamp 1992a, b). *L. minimus* appeared to prefer habitats where soil moisture was high (see also Delettre & Trehen 1977), but salinity low, thus accounting for its low abundance in the *Blechnum penna-marina* fernbrake and salt-spray communities. In addition, there appeared to be abundance covariation between *L. minimus* and *M. kerguelarum* and this may be the consequence of the preference of earthworms for drier soils (Lee 1985) and *L. minimus* for moister ones (Crafford 1986).

Although numerical dominance did not equate to dominance in biomass in most communities (the other macro-invertebrate species generally have body masses larger than that of *L. minimus*, see Crafford 1986, Chown & Scholtz 1989, Crafford 1990a, b), high densities of *L. minimus* suggest that this species makes an important contribution to ecosystem functioning at Marion Island. Like *P. marioni* (see Crafford 1990a, b), *L. minimus* is a litter feeder (Delettre 1978), and is likely to contribute most to ecosystem functioning via the processing of litter as does *P. marioni* (Crafford 1990b), even though the two species are likely to ingest litter particles of rather different sizes because of large differences in their body mass. Thus, based on Reichle's (1968) relationship between body mass and ingestion rate, and the densities of midge larvae recorded here, it appears that *L. minimus* is an important contributor to litter decomposition at Marion Island, ingesting, at least in some communities, six to ten times more litter per year than *P. marioni* (Table 21). However, it should be noted that because the estimates of litter ingestion by *L. minimus* were based on a mean body mass of larvae and on a body mass equal to that of instar IV larvae of *L. minimus*, and because larvae may not be active for part of the year and during the pre-pupal phase (Delettre & Trehen 1977, Delettre 1978), these estimates probably lie towards the upper bound of those that are

likely to be provided by a more detailed, combined study of individual consumption rates and population structure.

Nonetheless, the large contribution made by *L. minimus* to nutrient cycling has important implications for ecosystem functioning at Marion Island. Crafford (1990a, b) argued that *P. marioni* (larvae) forms the bottleneck in nutrient recycling at Marion Island. It has therefore been described as a keystone species in the terrestrial system (Klok & Chown 1997), having major effects on litter decomposition rates, nutrient mineralization, energy turnover and peat accumulation rates (Smith & Steenkamp 1990). However, the larvae of this moth form the major prey of introduced house mice, which are thought to be having an increasingly severe impact on the caterpillars as a consequence of increasing abundance (or predation rates). These, in turn, are thought to be associated with increased mean temperatures, lower precipitation, and perhaps also the recent eradication of feral cats (which preyed on mice to some extent) (Smith & Steenkamp 1990, Chown & Smith 1993, Van Aarde *et al.* 1996). Smith & Steenkamp (1990) proposed that ecosystem functioning would be substantially altered on Marion Island due to the impact of mice on *P. marioni*. That such an impact is taking place may readily be illustrated by the considerably lower densities of *P. marioni* documented here (0.51 g.m^{-2} in *Cotula plumosa* biotically-influenced communities here, compared to 0.93 g.m^{-2} recorded by Crafford (1990a)), and the lower estimate of litter turnover by *P. marioni* found in this study (maximum of $6.86 \text{ g}_{(\text{dry mass})}.\text{m}^{-2}$ here, compared to $10 \text{ g}_{(\text{dry mass})}.\text{m}^{-2}$ suggested by Crafford (1990)), although annual variation in caterpillar densities may also contribute to this difference.

The estimates of litter turnover by *L. minimus* suggest that the change in nutrient recycling rate (associated with elevated mouse predation), proposed by Smith & Steenkamp (1990) may either not be as marked as they have suggested or may take place at a slower rate than they predicted. In particular, if *L. minimus* densities increase as those of the other macro-invertebrates, but especially *P. marioni* decline, then the system response predicted by Smith & Steenkamp (1990) may be difficult to detect.

The large effect of *L. minimus* in terrestrial systems may also extend to the other sub-Antarctic islands where this species is present. On Kerguelen Island, Delettre (1978) recorded mean densities of 2334, 927 and 1134 individuals. m^{-2} in three different vegetation complexes abutting Rivière du Château. Densities of *L. minimus* in the *Acaena* herbfield habitat on Kerguelen Island were similar to densities found in *Acaena* drainage lines in this study ($1843 \text{ individuals.m}^{-2}$), suggesting that *L. minimus* also contributes substantially to litter turnover on Kerguelen Island. Although the densities of *L. minimus* on islands of the Crozet archipelago are not known (see Chevrier 1996 for the species record), it seems reasonable to assume that this species will occur at densities similar to those found on both Marion and Kerguelen islands, given that the biotas, vegetation and climates of these three island groups are similar.

Chown & Language (1994) and Kennedy (1995) have predicted that the probability of alien species establishing on sub-Antarctic islands will increase as climates at the islands ameliorate in step with global warming (see Adamson *et al.* 1988, Smith & Steenkamp 1990, Frenot *et al.* 1997 for data). In addition, the demands for tourism to most of the sub-Antarctic islands, and hence the risk of transfer of propagules, has also increased in recent years (Dingwall 1995). In light of the above, and these findings which suggest that even small, inconspicuous elements of an introduced fauna may have substantial impacts on the ecosystems into which they have been introduced, it is clear that greater caution should be exercised with regard to the transfer of cargo and personnel to the sub-Antarctic islands (see also Cooper & Condry 1988). These findings also suggest that access to at least some of these islands should be restricted to an absolute minimum. Furthermore, this study highlights a considerable need for investigations of the impacts of these less conspicuous, alien elements of sub-Antarctic faunas on terrestrial ecosystem functioning. To date, most reviews of the conservation of sub-Antarctic islands (*e.g.*, Clark & Dingwall 1985, Dingwall 1995) have ignored alien invertebrates, despite their obvious impact on sub-Antarctic islands.

3.5 References

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CHAPTER 4. RECORDS OF ALIEN INSECT SPECIES

4.1 *Vanessa cardui* and newly established alien species

Of the conservation issues currently facing sub-Antarctic terrestrial ecosystems, the introduction, establishment and spread of alien species, and changes in interactions between indigenous and introduced species, precipitated by changing climates, are thought to be most critical (Cooper & Condry 1988, Kennedy 1995, Ernsting *et al.* 1995, Chown 1997, Chown & Block 1997, Chevrier *et al.* 1997, Gremmen 1997). Indeed, both Smith & Steenkamp (1990) and Kennedy (1995) have argued that globally driven, high rates of warming at these islands (see Allison & Keage 1986, Adamson *et al.* 1988, Smith & Steenkamp 1990, Frenot *et al.* 1997 for data from the sub-Antarctic islands) are likely to enhance the probability of establishment of alien propagules that reach them. Recent data from Marion Island suggests that this may well be the case (Chown & Language 1994).

There are consequently sound reasons for more strict monitoring of the arrival of propagules, and their establishment and subsequent spread on the sub-Antarctic islands. The positive and significant relationship between the numbers of visitors to these islands and the numbers of alien species established on them (Chown *et al.* 1998), and the trend towards increasing tourism to the islands (Dingwall 1995) provide additional motivation for reporting species that reach the islands, and recording the status of those that appear to have become established. This chapter reports on the incidence of propagule transfer to Marion Island over a full year and confirms the establishment of another alien Lepidoptera species at this island.

Monitoring of alien species was undertaken on an *ad hoc* basis at Marion Island (46°54'S 37°45'E) from May 1996 to May 1997 as part of the Marion Island Terrestrial Invertebrate Ecology programme. All alien insect species found alive (and in a few cases, dead) either at the scientific station or elsewhere on the island were recorded and notes were made of the condition of the animals (extent of wing wear, damage to tarsal segments, *etc.*), at the time of collection or sighting.

Of the alien species collected at Marion Island during this study (Table 22), most have been recorded previously and many are considered to be naturalised aliens (see Crafford *et al.* 1986). Nonetheless, over this period, painted lady butterflies, *Vanessa cardui* (Linnaeus) (Lepidoptera: Nymphalidae) (verified by collection of specimens), were reported in larger numbers than previously (Table 23). This species has been known from Marion Island since the 1970s (Chown & Language 1994, for records from the Crozet Islands see Voisin 1975). Most of the sightings of this butterfly were on the east coast from Sealers Beach to Trypot Beach. However, two specimens were seen at high altitude (at Katedraalkrans) and adults were also seen sporadically along the entire coast except for the most southerly regions (Kildalkey Bay to La Grange Kop). The large numbers of individuals

that were sighted suggests that *V. cardui* breeds on Marion Island, but no larvae have yet been collected.

Most of the other sightings of volant insects were of a blowfly *Calliphora vicina* Robineau-Desvoidy (verified by collection of specimens) that has become established at Kildalkey Bay. This species was incorrectly listed as *Calliphora croceipalpis* Jaennicke by Chown & Language (1994). Of the other species that were collected, the majority were associated with food products at the scientific station (Table 22). However, one of the *Agrotis* (Lepidoptera: Noctuidae) species collected during this period, or possibly one of those collected previously (see Crafford *et al.* 1986, Chown & Language 1994) has become established outside the buildings of the scientific station. Three mature larvae of an unidentified *Agrotis* species were collected from the *Poa annua* “lawn” in front of the scientific station on 5 February 1997. Collection during this period rules out direct transfer of the larvae from the research and supply vessel SA Agulhas because this vessel visits the island during April/May each year. In addition, transfer to the island of cargo and personnel from fishing vessels operating in the newly established patagonian toothfishery around the Prince Edward Islands took place only in October and November 1996. This suggests that the larvae were not transferred directly from a research or fishing vessel to the grassy area surrounding the scientific station, but rather hatched from eggs laid by adult moths which are seen in low numbers at lights in the base each year. Unfortunately, these larvae could not be reared through to the adult stage and a species identification is therefore unavailable.

New alien species of which only single individuals were collected include one lepidopteran, two beetle species, one hemipteran, two fly species, and an ant. To date, most of these species have not been identified (see Table 22). The Lepidoptera and Coleoptera have been deposited in the collection of the Transvaal Museum, Pretoria, the Diptera and Hemiptera in the South African National Insect Collection, Pretoria, and the Hymenoptera in the collection of the South African Museum, Cape Town.

Over the past ten years certainly two (*Plutella xylostella* (Linnaeus) (Lepidoptera, Plutellidae), *Agrotis* species), but probably three (including *V. cardui*) lepidopteran, and one fly species (*C. vicina*) have become established at Marion Island. This does not provide conclusive evidence that the rate of propagule transfer to these islands has increased, or that the chances of establishment of these propagules has improved. However, it does suggest that this might be the case and, more important, that greater care should be taken to prevent propagule transfer to these islands and that stricter vigilance is required (see also Cooper & Condry 1988, Chown *et al.* 1998). Once established on these islands, alien species can have profound and deleterious effects on the indigenous faunas, floras, and terrestrial ecosystems (e.g., Crafford & Scholtz 1987, Smith &

Steenkamp 1990, Bloomer & Bester 1992, Ernsting *et al.* 1995, Chown & Block 1997, Chevrier *et al.* 1997, Gremmen 1997).

Table 22. Alien insect species recorded at Marion Island from May 1996 to May 1997. Symbols: ▼ = new record for Marion Island; # = specimens found dead; * = specimens found in vegetation and soil samples. A = Adult, L = Larva, P = Pupa.

Species	Stage	No.	Locality	Date
Hemiptera, Aphididae				
<i>Rhopalosiphum padi</i>	A, P	>1000 *	Circuminsular	v.1996 – v.1997
<i>Macrosiphum euphorbiae</i>	A, P		Circuminsular	i-ii.1997
<i>Myzus ascalonicus</i>	A, P		Circuminsular	i-ii.1997
Hemiptera, Scutelleridae				
<i>Cryptacrus comes</i> ▼	A		Base Kitchen (amongst fresh bananas)	6.v.1996
Thysanoptera, Thripidae				
<i>Apterothrips apteris</i>	A	> 120 *	Circuminsular	vii-xi.1996, ii.1997
Coleoptera				
Anobiidae sp.	A	>1000	Laboratory, Base kitchen (in bran cereal)	v-vii.1996
Dermestidae sp.	A	1	Laboratory	25.iii.1997
Chrysomelidae sp. ▼#	A	1	Base kitchen (in muesli cereal)	04.ix.1996
Diptera, Calliphoridae				
<i>Calliphora vicina</i>	A	> 70	Kildalkey Bay	xi. 1996, i.1997
Diptera, Fanniidae				
<i>Fannia canicularis</i>	A	1	Base building	03.vii. 1996
Diptera, Drosophilidae				
<i>Scaptomyza</i> sp.	A, P	5 *	Blue Petrel Bay	x.19 1996, ii-iv.1997
Diptera, Psychodidae				
<i>Psychoda parthenogenetica</i>	A, L, P	> 100 *	Circuminsular	v.1996 – v.1997
Diptera, Chironomidae				
<i>Limnophyes minimus</i>	A, L, P	>1000 *	Circuminsular	v.1996 – v.1997
Diptera, Lonchaeidae				
<i>Lamprolonchaea smaragdi</i> (Walker) ▼	A	1	Base	
Diptera, Anthomyiidae				
<i>Anthomyiidae</i> sp. ▼	A	1	Base	
Lepidoptera, Noctuidae				
<i>Helicoverpa armigera</i>	A	2	Kildalkey Bay, outside Base	20.i.1997, 5.ii.1997
<i>Agrotis ipsilon</i>	A	2	Base kitchen, power shack	12.ii.96 & 13 ii.1997
<i>Agrotis</i> sp. (presumed <i>ipsilon</i>) ▼	L	3	Base “lawn” in front of kitchen	05.ii.1997
<i>Trichoplusia orichalcea</i>	A	1	Base kitchen	04.v.1996
Lepidoptera, Pyralidae				
<i>Nomophila</i> sp. ▼	A	1	Cape Davis	28.xi.1996
Lepidoptera, Plutellidae				
<i>Plutella xylostella</i>	A, L, P	> 100	Circuminsular (on Kerguelen cabbages)	i.1997
Lepidoptera, Nymphalidae				
<i>Vanessa cardui</i>	A	70	See Table 24	26.xi.1996 –22.iii.1997
Hymenoptera, Formicidae				
<i>Lepisiota capensis</i> ▼ #	A	1	Base Wet-laboratory	19.ii.96

Table 23. Sightings of *Vanessa cardui* on Marion Island from May 1996 to May 1997.

Date	Locality	Numbers	Total
Nov. 96	Towards Junior's Kop	1	1
Dec. 96	Duiker's Point; Katedraalkrans; Sealer's Beach	2;2;1	5
Jan. 97	Archway Bay; Base; Cape Davis; King Penguin Bay; La Grange Kop; Long Ridge; Mixed Pickle Cove; Sealer's Beach; Sealers Cave; Skua Ridge; Ship's Cove; Stony Ridge, Swartkop Point; Tom Dick & Harry; Trypot Beach; Tweeling	1;4;1;1;1; 1;1;13;1;1; 5;1;1;3;5; 1	41
Feb. 97	Base; Bullard Beach; The Fault; Sea Elephant Bay; Bullard North (inland); Long Ridge; Macaroni Bay; Repetto's; Ship's Cove; Van den Boogaard	4;2;1;1;1; 1;2;2;1;2	17
Mar. 97	Albatros Lakes; Hansen Point; Kaalkoppie; King Penguin Bay; Long Ridge; Skua Ridge	1;1;1;1;1; 1	6
Total			70

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The gathering of baseline information provides a foundation on which further work can grow and which can be used to test a variety of hypotheses. Substantiation is a tool that can convince, and is needed for the pursuit of knowledge and to curb the flames of development that run on fuel that has no reservoir. The Prince Edward Islands are such fragile reservoirs, vulnerable to man-induced changes. This has been recognised through the endeavours of research (see bibliography appended) as well as failed and aborted attempts to harness or utilise their limited resources (*e.g.*, Heymann *et al.* 1987, Condry 1988), and is the basis on which the Island group was awarded the status of Special Nature Reserves (Prince Edward Island Management Plan Working Group 1996).

In accordance with the policies set out to protect, manage and conserve the islands, this project has concentrated on gathering baseline information, presenting and interpreting the findings in view of the need for ongoing research, the imminent changes threatening the existence of indigenous species and the consequences of alien introductions on the functioning of the ecosystem. Thus this thesis presents a comprehensive quantification of the macro-invertebrate fauna (both indigenous and alien) in the vegetated biotope with respect to their overall densities, spatial distribution and seasonal patterns. These findings form part of the information gathering for the M.I.T.I.E. program, needed to investigate species energy usage in order to gain a better understanding of the functioning of the ecosystem.

This project also puts into perspective the meaning of these findings through a comparison made with data collected 20 years earlier, by showing the dramatic decline that has taken place amongst the indigenous invertebrates, whereby the principal species affected are the three litter-feeders *Microscolex kergueluarum* (earthworms), the larvae of *P. marioni* and those of *E. similis*. The decline found amongst the invertebrates not only substantiates earlier claims, but underlines the urgency with which the cause of the decline should be addressed and remedial action taken if the demise of these species is to be prevented. Given the importance of thorough sampling, highlighted in this study with respect to the invertebrates at Marion Island (*viz.* the need for an all inclusive, rather than size or prey selective sampling method, and need for habitat cognisance due to the specificity shown by the invertebrates), this study makes available all the basic information needed for any current or future studies, extrapolations and comparisons that may involve invertebrates in such aspects as predator / prey, environmental or edaphic impact assessments.

To what extent alien invertebrates influence the ecology of Marion Island is also demonstrated in this project by means of one of the smaller invertebrate species *L. minimus*, and the influence it has on the Islands' nutrient cycling in comparison to the largest and key-stone species *P. marioni*. From the noticeable number of new alien invertebrate sightings and establishments, the rate

of increase predicted by previous workers is also substantiated. The need for added precautions and where possible, eradication of alien species is thereby supported and underlined.

The high standard (integrity, quality and success) (*e.g.*, Heymann *et al.* 1987, Bester 1993, Bester *et al.* 1994, Cooper *et al.* 1995, and see appended bibliography) and therefore value of research on Marion Island has been recognised and proven. The compounding speed with which changes (some irreversible) effecting the biota are taking place (*e.g.*, this study, Gremmen *et al.* 1998), together with the increasing cuts in Government spending and funding for research in the sub- and Antarctic areas, are however factors likely to effect the selection priorities for research and management programs at the Prince Edward Islands in the future. In addition, increasing demands for the use of the Islands and their surrounding territories as a resource (*e.g.*, by the fishing and tourism industry), are adding pressures to the fragile systems (Cooper & Huyser 1995, Gosling 1997, *The Cape Argus* 1997 May 6, 7). This suggests that if the management policies of 1996 (see Prince Edward Island Management Plan Working Group 1996) are to maintain the value of the Islands' unique and limited biota as sustainable 'resources' under these pressures, an increase in collaboration between research and management programs should be taking place.

Under the current conditions and the selection criteria that determine ongoing research in the sub-Antarctic, it would appear that a greater cross-disciplinary approach would help maximise the effectiveness of research at the islands while minimising on the use of resources (financial, human resources, and the islands ecosystem). This does not imply merging, but recognising areas where overlapping data collecting could be shared, so that greater return could be achieved for less effort, and answers to problems could be solved more readily on unified results, rather than conflicting opinions based on different methods and results. The benefits of such collaborative work have already been demonstrated (*e.g.*, the botanical approach to the impact of alien plant species in relation to the entomological approach on the distribution and abundance of invertebrates (Gremmen *et al.* 1998) whereby the results of the same data set were pooled), and should be the way to address the overlapping problem of the declining invertebrate numbers and increase in mouse predation on them, said to be the cause for the invertebrate decline.

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Appendix I.

Fifty years at Marion and Prince Edward Islands:
a bibliography of scientific and popular literature

Fifty years at Marion and Prince Edward Islands: a bibliography of scientific and popular literature

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The Prince Edward Islands have now been in South Africa's possession for 50 years. Following World War II, Field Marshall J.C. Smuts, in consultation with the British government, set the annexation of the islands in motion. In December 1947, John Fairbairn read the deed of annexation on Marion Island, and Prince Edward Island was annexed a few days later in January 1948. Since then, South Africa has maintained a permanent presence at Transvaal Cove on Marion Island. At first concerned with meteorological observations, set up by Alan Crawford, activities at the station were soon expanded. Initially, the science was relatively informal, with pioneers such as Robert Rand making observations and collections of the biota. However, South African scientific work at the Prince Edward Islands was formalized when the first Biological and Geological Expedition took place over the 1965/66 summer season under the leadership of Prof. E.M. Van Zinderen Bakker Sr. Since then a scientific programme has been running at the islands, at first funded by the Department of Transport, and later by the Department of Environmental Affairs and Tourism, but always under the auspices of a research committee that has seen various guises (and now known as the South African Committee on Antarctic Research). This bibliography is concerned largely with the products of this programme.

Nonetheless, it will be clear from the references listed below that science at the Prince Edward Islands has had a much longer history than the South African involvement would suggest. Cape Hooker on Marion Island bears the name of Joseph Hooker, the eminent Victorian botanist and friend of Darwin. Collec-

tions made by H.N. Moseley from the *Challenger* expedition were the subject of much early taxonomic work, and subsequent ones by Bob Rand gave a taste of what the islands held in store for biologists. Nonetheless, it was certainly the 1965/66 expedition that set modern science at the islands in motion.

Geological, geomorphological and palaeoecological work has established a history of the islands and provided insight into their genesis and geological setting. Virtually all biological disciplines and a significant proportion of the species at Marion Island have also enjoyed attention. Seabird biology, for example, has included basic aspects of breeding, population trends, energetic physiology, feeding and prey selection, behaviour, vocalization, life history strategies, satellite tracking of local and regional foraging ranges, and more recently, the significant impacts of the long-line Patagonian toothfishery. Perhaps the most important outcome of the science at Marion Island, however, is an integrated view of ecosystem functioning. Much of the work in the 1970–1990s focused on linking systems and taxa into a synthetic view of the ecology of the island. The result of this baseline ecological work is a foundation that is proving invaluable for long-term ecological research. In particular, this fundamental ecological work has allowed the integrated investigation of two globally important research fields at the islands, that is, the nature and influence of biological invasions, and the effect of climate change on both indigenous species and their interactions with invasives. Homogenization of the global fauna is a growing concern, yet few broadly synthetic generalizations concerning invasive species have emerged. The effect of climate change on such invasions is an even less well-understood field. As a consequence of effective monitoring of alien species, and a rapid increase in mean annual temperature at

the islands (1°C) since annexation, the islands provide an invaluable natural laboratory for investigating these topics, particularly because of the absence of most invasive species on Prince Edward Island.

It is not only the research opportunities that make the islands valuable from a scientific perspective, it is also their potential for human resources development. Scanning the authors' names under the list of theses provided in this bibliography is thought-provoking. A host of respected South African biologists received their training based on work done at the islands, including those who are now on the staff of the universities of Cape Town, Natal, Port Elizabeth, Pretoria, Rhodes, Stellenbosch and Venda, the National Museum in Bloemfontein, the National Botanical Institute, Cape Nature Conservation, BirdLife South Africa, and a variety of other organizations. To date, 36 research-based higher degrees have been awarded based on work on or around the Prince Edward Islands.

This research tradition is being continued, with current work including geomorphology (University of the Western Cape and University of Pretoria), ornithology (University of Cape Town, Sea Fisheries Research Institute), mammalogy (University of Pretoria), the biology of invasions (University of Pretoria, University of Stellenbosch), species energy usage and climate change (University of Pretoria), and the biology of the land–sea interface (Rhodes University, University of Cape Town). Like all South African science, however, escalating costs and dwindling budgets are posing a significant threat to this work. Perhaps one short-term view of this trend would be to suggest that the Marion Island programme has had its day and should now give way to more pressing needs. The longer term view suggests otherwise, however. The Prince Edward Islands are ideally placed for research that has both a global and a local relevance. Climate change and invasions are here to stay. In addition, these very climate changes, and an increase in demand for tourism to the southern islands means that threats to these unique, and rather rare, ecosystems (there is little land at 47 °S), are rapidly on the increase. It is only through a research presence on the islands that these threats can be dealt with effectively, and mitigating measures implemented rapidly. It would surely be a travesty if South Africa sacrificed the Special Nature Reserves that constitute its

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eighth biome, and their potential for informing local and international science, to an ill-founded notion that much research effort, over a significant period, constitutes loose intellectual capital that should be squandered, rather than an investment that can pay significant dividends. This bibliography indicates the extent of the down-payment already made, and we hope that it will spur further investment. We dedicate this article to J.C. Smuts, E.M. van Zinderen Bakker Sr., and the hundreds of men and women who have made, and will continue to make, research at the islands possible.

Technical notes

This bibliography contains five major sections: scientific publications, theses, grey literature, popular works, and other material. Like most bibliographies, the decision whether or not to include material was often arbitrary. Whether a publication that simply mentions one of the islands in passing should be included is often difficult to decide, and cross-referencing of research papers emerging from the Marion Island programme essentially amounts to many thousands of citations. For this reason the bibliography is not complete. We believe it is sufficient for the reader to access everything that has been published on the islands, with two significant exceptions. First, the South African departments of Transport, and of Environmental Affairs and Tourism have funded work at the islands since the mid-1960s. In all cases the research committees have required interim and final reports from project leaders. We have not cited these, but they can be obtained from the Directorate Antarctica and Islands, Department of Environmental Affairs and Tourism, Private Bag X447, 0001 Pretoria. Second, from time to time, various Government Acts pertaining to the islands have been published in the *Government Gazette*. Most of these are listed in the Prince Edward Islands Management Plan, and can be obtained from the South African Government Printer or the State Library in Pretoria.

In the section dealing with theses we have included one honours report because it was the first study of its kind for the Prince Edward Islands and is an invaluable reference work. Nonetheless, we realize that many honours-level projects have been undertaken on the islands, but these are usually impossible to track down, even with a title in hand. Among the popular works, grey literature and other material, we have also excluded

some material for which we could not obtain verification of the title or source. Consequently, some material from earlier bibliographies has been excluded. In addition, where the title of cited works provides no indication of their content, we have indicated the content in brackets or immediately below the item of interest.

References under each section of the bibliography are presented alphabetically. However, to facilitate searching we have provided guide to the subject of each reference in Table 1. In addition, and following publication in this journal, the entire bibliography will be released as a downloadable file obtainable through: <http://www.up.ac.za/zoology/top.htm>

Table 1. Reference by subject category.

Subject/keyword	Reference
History	38, 215, 345, 402, 448, 664, 772, 830, 836, 845, 846, 848.
Historical	165, 357, 504, 617, 690, 772, 775.
Archaeology	768, 830.
Impact	105, 170, 176, 208, 236, 312, 318, 353, 356, 377, 378, 487, 519, 773, 782, 787, 806.
Influence	113, 177, 372, 374, 482, 483, 577, 762, 842.
Human	170, 237, 696, 776.
Alien	44, 208, 230, 313, 315, 320, 353, 354, 604, 633, 684, 689, 849.
Introduced	104, 230, 317, 318, 321, 372, 377, 604, 633.
Management	203, 208, 254, 354, 360, 494, 768, 772, 787.
Conservation	96, 119, 170, 180, 197, 203, 204, 206, 211, 213, 217, 231, 233, 237, 254, 255, 318, 372, 377, 525, 602, 717, 726, 794, 842.
Ecology	28, 86, 87, 89, 90, 91, 92, 165, 172, 208, 234, 251, 294, 302, 308, 376, 385, 423, 441, 491, 492, 572, 612, 628, 642, 651, 658, 661, 663, 665, 734, 735, 736, 741, 745, 755, 757, 762.
Ecosystem	149, 231, 286, 288, 326, 353, 372, 373, 375, 377, 442, 483, 523, 552, 558, 569, 598, 665, 703, 718, 721.
Geology	342, 672, 702, 740, 926.
Glaciation	345, 349, 351, 660, 661; 341, 350, 955.
Volcano	156, 157, 405, 674, 675; 949.
Volcanic	56, 323, 349, 576, 677.
Lava	335, 401, 570, 615, 952.
Soil; peat	245, 287, 318, 323, 324, 336, 567, 571, 575, 576, 577, 580, 587, 588, 600, 608, 609, 611, 612, 620, 765; 579, 610.
Earth	346, 349, 350.
Climate	160, 176, 283, 323, 324, 342, 543, 593, 598, 600, 606, 658, 751, 924, 925.
Weather	617, 927, 928.
Temperature	126, 132, 152, 169, 341, 421, 453, 595, 783, 857, 901.
Wind	346, 548, 895, 897, 898.
Front	268, 446, 450, 451.
Botany	21, 47, 253, 303, 364, 385, 463, 465, 477, 507, 565, 566, 570, 607, 610, 683.
Plant	2, 44, 208, 313, 315, 317, 320, 382, 384, 422, 441, 477, 478, 567, 571, 572, 573, 574, 576, 582, 583, 584, 587, 588, 589, 590, 604, 765.
Vegetation	314, 316, 317, 318, 381, 383, 535, 536, 545, 547, 566, 567, 570, 600, 738, 745, 746, 758, 923.
Flora	44, 45, 46, 310, 311, 374, 465, 476, 536, 544, 550, 827, 923, 946.
Pollen	546, 548, 657, 666.
Lichen	362, 363, 367, 591.
Hepatic	33, 337, 544.
Bryophyte	234, 520, 521, 522, 523, 599, 605, 745, 781.
Moss; musci	476, 550, 578; 649.
Fern	583, 588, 589, 590.
Microbiology	400, 578, 743.
Fungi; Mycorrhizas	47; 603.
Bacteria	287, 336, 578, 599, 601, 605, 790.
Physiology	7, 9, 13, 120, 121, 177, 412, 421, 422, 478, 479, 591, 725, 741, 769.
Mammals	73, 76, 104, 186, 225, 252, 414, 416, 417, 435, 485, 509, 511, 512, 563, 791, 825, 826, 840, 934.
Whale; dolphin; cetacean	190, 192, 843, 942; 647; 290.
Seal; <i>Arctocephalus</i>	20, 67, 68, 69, 70, 71, 72, 73, 74, 76, 77, 79, 80, 81, 84, 85, 86, 103, 179, 182, 183, 184, 185, 186, 187, 189, 191, 252, 279, 280, 370, 371, 398, 399, 406, 407, 408, 409, 410, 411, 412, 413, 414, 417, 420, 481, 482,

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	483, 485, 502, 506, 508, 512, 514, 564, 590, 696, 697, 698, 736, 748, 759, 760, 762, 771, 791, 803, 823, 841, 875, 889, 908, 914, 916, 918, 941; 69, 70, 74, 76, 84, 154, 183, 191, 252, 406, 407, 408, 409, 410, 411, 412, 414, 416, 420, 485, 697, 760.
Pinnipeds	78.
Mice	66, 176, 231, 302, 455, 519, 635, 693, 757, 761, 773, 828, 837, 838, 849, 907.
Cat	24, 55, 75, 82, 83, 94, 95, 96, 188, 213, 220, 296, 377, 628, 629, 630, 631, 632, 633, 634, 635, 636, 637, 642, 643, 644, 645, 646, 669, 670, 703, 753, 756, 766, 767, 811, 812, 837, 849, 932, 933.
Bird	2, 3, 15, 36, 55, 58, 60, 65, 87, 135, 139, 149, 151, 153, 193, 198, 199, 200, 202, 213, 219, 222, 223, 225, 241, 288, 297, 298, 299, 327, 376, 377, 378, 380, 387, 389, 392, 393, 435, 456, 469, 472, 473, 474, 475, 498, 499, 503, 517, 526, 527, 528, 530, 539, 552, 556, 558, 561, 577, 640, 651, 652, 682, 691, 692, 700, 715, 717, 719, 721, 726, 727, 741, 769, 776, 777, 803, 810, 817, 844, 866, 913, 918, 919, 921, 922, 943, 962.
Penguin	5, 6, 7, 8, 10, 11, 12, 14, 15, 16, 17, 18, 55, 56, 113, 114, 120, 121, 122, 123, 124, 126, 128, 129, 133, 134, 152, 204, 210, 224, 227, 228, 270, 271, 360, 370, 378, 419, 432, 443, 500, 639, 640, 648, 653, 682, 688, 701, 702, 704, 705, 707, 710, 711, 712, 713, 714, 715, 716, 718, 724, 725, 728, 731, 732, 733, 749, 795, 808, 820, 888.
Albatross	13, 51, 52, 53, 54, 61, 116, 117, 118, 130, 131, 216, 217, 218, 226, 301, 379, 468, 471, 688, 729, 750, 776, 788, 805, 821, 915.
Petrel	4, 57, 59, 64, 115, 125, 127, 136, 207, 213, 214, 220, 292, 293, 375, 380, 386, 388, 470, 537, 538, 540, 541, 542, 562, 618, 619, 703, 764, 776.
Sheathbill	88, 140, 141, 143, 144, 145, 146, 147, 150, 734.
Skua; gull	4, 113, 540, 560, 706, 708, 709; 88, 105, 718, 723.
Cormorant	88, 194, 195, 281, 501, 529, 718, 720.
Tern	62, 119, 138, 524.
Prion	55, 63, 127, 300, 456.
Invertebrate	139, 142, 146, 230, 353, 431, 519, 607, 610, 754.
Araneida	437.
Worm (earthworm)	38, 39, 40, 41.
Mollusc; snail	108, 295, 596; 616.
Acari; mite	245, 277, 278, 454, 495, 496, 497; 452, 453.
Ixodoidea; tick	624; 114.
Collembola	250.
Insect	2, 160, 171, 235, 237, 239, 257, 322, 354, 421, 422, 431, 618, 737, 920.
Coleoptera	158, 159, 161, 163, 164, 174, 178, 234, 260, 262, 264, 265, 266, 267, 431, 625, 638, 735.
Curculionidae	158, 159, 161, 163, 164, 172, 173, 174, 175, 178, 234, 261, 262, 263, 264, 265, 266, 267, 429, 568, 625, 638, 686, 735.
Weevil	159, 162, 164, 165, 167, 177, 178, 234, 625, 638.
Diptera	166, 229, 230, 282, 353, 549.
Fly	238.
Lepidoptera	232, 236, 421, 422, 668, 742, 755.
Plutella	168, 232, 233.
Pringleophaga	285, 421.
Nutrients	93, 148, 288, 326, 353, 390, 442, 461, 522, 554, 565, 566, 569, 571, 582, 583, 584, 589, 590, 597, 607, 610, 747, 765.
Food	16, 88, 93, 128, 139, 144, 148, 186, 376, 442, 492, 554, 556, 752, 918.
Limnology	333, 739, 873.
Water	46, 99, 101, 129, 178, 274, 330, 331, 334, 421, 426, 427, 442, 450, 459, 496, 601, 963.
Marine	88, 90, 91, 92, 102, 201, 269, 288, 307, 312, 326, 402, 404, 448, 450, 461, 487, 488, 491, 492, 513, 528, 532, 533, 826, 827, 859.
Ocean	3, 19, 31, 99, 101, 102, 170, 180, 206, 269, 272, 275, 351, 402, 424, 447, 448, 450, 451, 460, 462, 487, 488, 490, 491, 744, 763, 786, 858, 861.
Hydrology; wave	42, 462; 339.
Sea	340, 446, 490, 783, 785, 857, 901, 929, 930, 963.
Benthic; benthos	106, 108, 109, 492, 754; 32.
Off-shore	779, 793.
Intertidal	93, 752.
Littoral	251, 294, 423.
Kelp; Durvillaea	35, 229, 238; 355.
Alga	242, 253, 332.
Plankton	98, 100, 102, 329, 426, 427, 461, 486, 487, 489, 490, 491, 786.
Crustacea; isopod	109, 403, 404, 438; 181, 403, 404.
Copepod	34, 155, 404.
Fish	89, 90, 201, 205, 217, 306, 307, 308, 358, 420, 532, 780, 866.
Pisces	25, 305, 359.
Squid	5, 116, 389.

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Films

1947: Prince Edward and Marion Islands

SABC production. 16 mm black-and-white positive film documentary. 450 ft (no sound), plus shots of the shoreline from the navy's ships; row-boats approaching the islands; letters and Christmas cards being handed to the teams on the island; Naval parade; annexation of the islands and hoisting of the South African flag; HMS *Transvaal*, 1947.

1948: African Mirror remembers

SABC production. 35 mm black-and-white positive film documentary (with sound), plus annexation of Marion Island and Prince Edward by South Africa for weather station. Annexation ceremony by Comm. Diamond of South African Navy, 1948.

1948: African Mirror No. 453

SABC production. 35 mm black-and-white documentary negative film (with sound), plus occupation of Prince Edward and Marion Islands: the annexation of South Africa's new colonial possessions in the Antarctic.

1969: National Film Board

Marion Team Training 47 South.

VIDEOS

1986: Marion Cat Programme. SABC (50/50).

1990: South Trap: Marion.

(Skenia telematics) Film by Derrick Louw. 27 July. For *Trilion*, The Movie Studio, SABC.

1994: SA Island Series:

'Gondwanaland - Discovering the South'. Produced for TSS, by Prentjieswinkel Film Makers. Filmed and produced by F. van der Merwe, D. Hunter, and H. van der Merwe. Post-production supervisor L. van der Merwe. Editor M. Redelinghuys. Archival material: Prentjieswinkel Lynx films, SABC. Directed by: J. Lampen, Pro Vision.

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1997: Marion: 'Musculus and Marioni'

Filmed and produced by Mike Vincent for SABC.

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The Cape Argus 1858, Jan. 16. Wreck of the Bark Maria at Prince Edward Island. [CONSERVATIVE and MARIA on PE while engaged in loading sealers to go to Crozet].

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Seabird] appears in the Saturday 26th issue. [Seabird wrecked on PE busy with sealing activities].

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Daily Graphic 1948, Jan. 3. Island base annexed by South Africa.

Daily Mail 1948, Jan. 3. Island Claimed. - South Africa plants flag.

Daily Mirror 1948, Jan. 3. South Africa takes over island where nobody lives.

Daily Telegraph 1948, Jan. 3. South African flag in Antarctic - Island annexed.

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News Chronicle 1948, Jan. 3. S. Africa seizes an island.

The Times 1948, Jan. 3. Empire air links - South Africa occupies an island.

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Daily Telegraph 1948, Jan. 5. S. Africa may occupy island. - Establishment of weather station.

South Africa 1948, Jan. 10. South Africa overseas. [news about the Prince Edward islands annexation].

News Review 1948, Jan. 15. Polar Air-Bases?

Cape Times Week-End Magazine 1948, Feb. 7. South Africa's two new islands.

? Pretoria News paper (R.D.K.?) 1948?, Feb. 24 ? Marion Island post mark: details given.

The Illustrated London News 1948, Feb. 21. Annexed as a top-secret operation - how the occupying parties live on Prince Edward and Marion Islands: South Africa's new weather station. pp. 198, 200, 201.

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The Cape Argus 1959, Nov. 14. [Reports on the import of live chickens the death of trout while on route to Marion Island on the *Natal*]

South African Digest 1972, Aug. 11. The Inhospitable isles. *Rand Daily Mail*.

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Postel 1982, Oct. Kokop Marion vir twee jaar!

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Weekend Argus 1982, Dec. 18. Copter lifts man off island. Argus reporter.

The Argus 1982, Dec. 21. Frigate returns with hurt scientist. Staff reporter.

The Argus 1982, Dec. 21. Frigate brings scientist home. Staff reporter.

Die Burger 1982, Dec. 22. Vlugge vloot red oog van navorser.

The Argus 1984, July 10. Army doctors on way to ill scientist. Defense reporter.

The Argus 1984, July 11. Second plane leaves for Marion. Staff reporter.

The Argus 1984, July 11. Plane for Marion forced to return. Defense reporter.

The Argus 1984, July 12. Doctors radio advice on treating Marion leader. Defense reporter.

The Argus 1984, July 17. Critically ill island scientist in hospital. Shipping reporter, Trisha Bam.

The Argus 1984, July 18. Marion scientist still on critical list. Staff reporter.

The Argus 1984, July 19. Clarke still in 'critical' state. Staff reporter.

The Argus 1984, July 19. Marion Island: Medical training compulsory? Shipping reporter.

The Argus 1984, July 21. Emergency on Marion.

Eastern Province Herald 1985, June 11. Award to ship for Marion Island rescue. Herald correspondent.

Weekend Argus 1985, August 17. A king-sized family problem.

The Argus 1986, Jan. 18. City sailor stuck near Marion Island. Yachting reporter. p. 2.

Die Burger 1986, March 22. Vroue na Marion-eiland. p. 13.

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Beeld 1986 April 25. Visier is ingestel op Marion se katte.

Die Burger 1986, April 30. Marion hou dalk katte-jag.

Die Burger 1986, May 28. Swamme in sy petrol bring puma huis toe. p. 21.

Die Burger 1986, May 28. Vrou nog vol vuur vir Marion. p. 21.

Die Burger 1986, May 28. Twee lank op eiland gestrand. p. 21.

The Cape Argus 1986, May 30. Happy end to yacht drama. Yachting reporter.

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MAPS

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ARTIFACTS

Housed / displayed at: South African Museum, Cape Town; Maritime Museum, Cape Town; Transport Technology Museum (formerly *A.B.E. Eksteen Museum*), Pretoria.

PHOTOGRAPHIC MATERIAL

Photographs

Department of Environmental Affairs and Tourism: old black-and-white slides and prints, and some colour slides.

Transport Technology Museum (formerly *A.B.E. Eksteen Museum*), Pretoria: display of some old photographs.

Maritime Museum, Cape Town: collection of photographs and books by John H. Marsh.

Weather Bureau Library Pretoria: black-and-white prints, and some colour slides.

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